Lotka-Volterra Dynamics - An introduction.

Steve Baigent, UCL.

Last updated:

March 2, 2010

Abstract

This short course is intended to give a 10 hour introduction to the mathematical analysis of Lotka-Volterra population models. We will begin by studying in detail some examples of two species models, before moving on to general population models for the interactions of n species. We will study systems of differential equations on $\mathbb{R}^n$ of the form

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

where $f : \mathbb{R}^n \to \mathbb{R}^n$ is smooth. Mostly we will be studying the standard Lotka-Volterra models, by which I mean $f_i(x) = r_i + \sum_{j=1}^{n} a_{ij} x_j$ for some constant $r_i \in \mathbb{R}$ and constant real matrix $A = ((a_{ij}))$.

Chapter 1

Two-species Lotka-Volterra systems

1.1 Some Motivating Examples

Before moving on to general $n-$species Lotka-Volterra systems, we will examine in detail some Lotka-Volterra systems that model the dynamics of two interacting populations. These models serve as examples of the various classes of models that we are able to analyse in the $n-$species generalisation.

1.1.1 Predator-Prey

In 1926 Volterra came up with a model to describe the evolution of predator and prey fish populations in the Adriatic Sea. Let $N(t)$ denote the prey population and $P(t)$ the predator population at time $t \geq 0$. He assumed that

1. In the absence of predators ($P = 0$) the per capita prey growth rate ($\frac{1}{N}\frac{dN}{dt}$) of the prey population N was constant, but fell linearly as a function of predator population P when predation was present ($P > 0$);

2. In the absence of prey ($N = 0$) the per capita growth rate of the predator ($\frac{1}{P}\frac{dP}{dt}$) was constant (and negative), and increased linearly with the prey population N when prey was present ($N > 0$).

Thus the model introduced by Volterra reads

$$\begin{aligned}\frac{1}{N}\frac{dN}{dt} &= a - bP \\ \frac{1}{P}\frac{dP}{dt} &= cN - d\end{aligned} \tag{1.1}$$

where $a, b, c, d > 0$ are constants. It turns out that this model can be treated by separation of variables. We find that

$$-\frac{(cN-d)}{N}\frac{dN}{dt}+\frac{(a-bP)}{P}\frac{dP}{dt}=0,$$

or

$$\frac{d}{dt}\left\{d\log N - cN + a\log P - bP\right\} = 0.$$

We introduce the following notation: $\mathbb{R}_{\geq 0} = \{x \in \mathbb{R} : x \geq 0\}$ and $\mathbb{R}_{>0} = \{x \in \mathbb{R} : x > 0\}$. Define $H : \mathbb{R}^2_{\geq 0} \to \mathbb{R}$ by

$$H(N, P) = d\log N - cN + a\log P - bP,$$

Then H is constant along a solution $(N(t), P(t))$ (for t where the solution exists, which in this case is all $t \geq 0$). We consider the solutions for various initial populations $(N_0, P_0) = (N(0), P(0)) \in \mathbb{R}^2_{\geq 0}$.

First suppose that $(N_0, P_0) \in \mathbb{R}^2_{>0}$. Then $H(N_0, P_0)$ is finite and all trajectories $(N(t), P(t))$ evolve so that $H(N(t), P(t)) = H(N(0), P(0)) = H(N_0, P_0) =$ constant. Moreover, they must satisfy $(N(t), P(t)) \in \mathbb{R}^2_{>0}$ for each $t \geq 0$, by finiteness of $H(N_0, P_0)$. It is easy to see that H is a strictly concave function. Moreover, $H(N, P) \to -\infty$ as $|(N, P)| \to \infty$ or where $NP \to 0$ in $\mathbb{R}^2_{\geq 0}$. It therefore has a unique maximum where $\nabla H = 0$, i.e. where

$$\frac{c}{N} - d = 0, \frac{a}{P} - b = 0 \Rightarrow (N, P) = \left(\frac{c}{d}, \frac{a}{b}\right).$$

Notice that this corresponds to the unique non-zero steady state of the system (1.1). Since H is strictly concave with a unique maximum in the positive quadrant, every trajectory with $N_0 > 0, P_0 > 0$ must be a closed curve (since it coincides with the projection onto $\mathbb{R}^2_{\geq 0}$ of the curve formed from the intersection the graph the concave function H and a horizontal plane). Thus the interior orbits are a set of closed curves each passing through the initial condition $(N(0), P(0))$.

On the other hand if $N_0 = 0$ but $P_0 > 0$, we see that an explicit solution of (1.1) is $N(t) = 0, P(t) = P_0 e^{-dt}$. Actually, as we shall see (Chapter 2, Theorem 4), any such solution must be unique, so this is *the* solution through $(0, P_0)$. Clearly the solution approaches the origin along the line $N = 0$ exponentially as $t \to \infty$. Similarly if $N_0 > 0$ but $P_0 = 0$ the solution $N(t) = N_0 e^{at}$ goes to infinity along the line $P = 0$ exponentially as $t \to \infty$.

We thus have a complete qualitative understanding of Volterra's model. It is worth noting for future reference that we were able to establish that any orbit $(N(t), P(t))$ could be defined for all $t \geq 0$ (actually for all $t \in \mathbb{R}$) and that if $N(0) \geq 0, P(0) \geq 0$ then $N(t) \geq 0, P(t) \geq 0$ for all $t \geq 0$. In other words our model makes basic sense for all $t \geq 0$. This should not be taken for granted; it is not difficult to construct "models" for which the solutions fail to exist beyond a certain

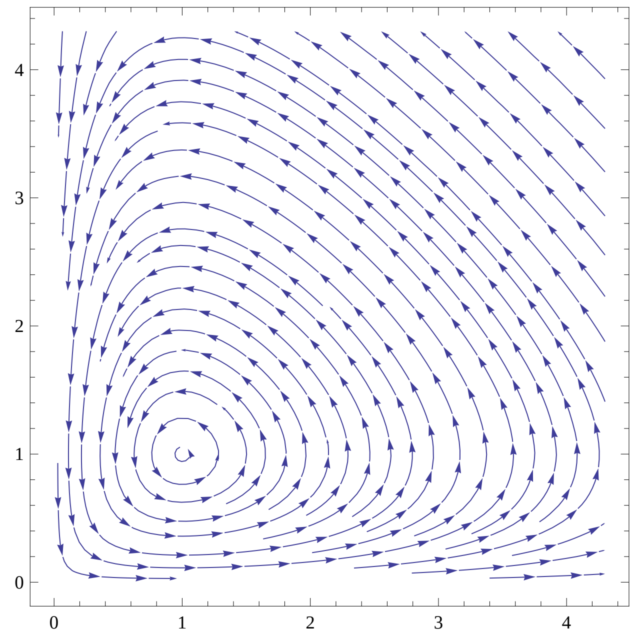

Figure 1.1: Solutions to the two-species predator prey model (1.1)

time, or where the orbits pass out of the first quadrant, and thus fail to make sense (populations must be non-negative!).

In fact the system (1.1) is *Hamiltonian*, with H taken to be the Hamiltonian function. The system can be written in canonical Hamiltonian form by introducing canonical coordinates $p = \log N$, $q = \log P$ whereupon $H(N,P)$ transforms to $h(p,q) = dp - ce^p + aq - be^q$. The Lotka-Volterra equations then become the canonical equations of Hamilton:

$$\begin{aligned} \frac{dp}{dt} &= \frac{1}{N}\frac{dN}{dt} = a - bP = a - be^q = \frac{\partial h}{\partial q} \\ \frac{dq}{dt} &= \frac{1}{P}\frac{dP}{dt} = cN - d = ce^p - d = -\frac{\partial h}{\partial p}. \end{aligned}$$

Volterra's Principle

Suppose that $N_0 > 0, P_0 > 0$. If T is the period of the closed orbit through (N_0, P_0) then

$$\begin{aligned} \frac{\dot{N}}{N} &= a - bP \\ \log N(T) - \log N(0) &= \int_0^T a - bP(\tau)\, d\tau \end{aligned}$$

$$0 \;=\; aT - b\int_0^T P(\tau)\,d\tau \quad \text{(using periodicity)}$$

Thus the average over a period T is

$$\frac{1}{T}\int_0^T P(t)\;dt = \frac{a}{b}.$$

and with a similar expression for the average of N. We obtain a similar result for more general systems in Chapter 2 Theorem 8.

Ecological considerations

There are several points of criticism worth noting for the Volterra-Lokta model. Changing the birth and death rates does nothing but change the period of the oscillation - i.e. no population can dominate, and there is no possibility of either population being driven to extinction. For certain ecological conditions (fitness of species, etc.) one would expect one species to win regardless of initial conditions. In addition the system is structurally unstable. Any model is an approximation of a real system. For a model to be successful, one would expect that typically a small modification to the model would produce similar results, i.e. would give a topologically unchanged phase space picture.

1.1.2 Competition

Recall that for a single population of density N, the simplest density dependent per capita growth rate is linear and gives rise to the *Logistic equation*:

$$\frac{dN}{dt} = \rho N\left(1 - \frac{N}{K}\right). \tag{1.2}$$

This has the explicit solution

$$N(t) = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-\rho t}}.$$

With this explicit expression for the density, it is easy to see that $N(t) \to K$ as $t \to \infty$ for all $N_0 > 0$. Solutions are plotted in Figure 1.2. Note that as $t \to \infty$ we have $N(t) \to K$. The density K is the maximum population density that the environment can carry and is called the *environmental carrying capacity.* The quadratic term in (1.2) represents competition between members of the same population for resources, i.e. *intraspecific* competition. For a model of competition within an environment supporting two-species, there are two types of competition: intraspecific and *interspecific*, the latter being competition between the two different species. To build a simple model for such competition we start with two independent logistic

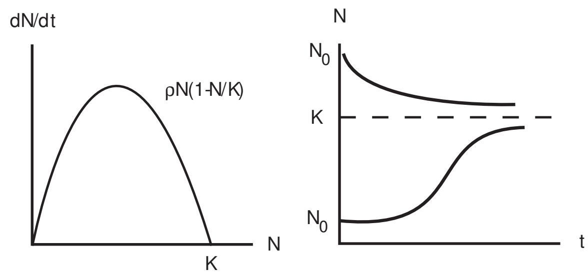

Figure 1.2: Solutions to the logistic equation (1.2)

models for the population densities N_1, N_2 and add an extra term in each to model the interspecific competition:

$$\begin{aligned} \frac{dN_1}{dt} &= \rho_1 N_1 \left(1 - \frac{N_1}{K_1} - c_1 N_2\right) \\ \frac{dN_2}{dt} &= \rho_2 N_2 \left(1 - \frac{N_2}{K_2} - c_2 N_1\right). \end{aligned} \tag{1.3}$$

Note that in the absence of interspecific competition, each species grows to its respective carrying capacity. The relative sizes of $c_1, c_2 > 0$ determine the competitiveness of each species.

First let's determine what happens at the boundaries of $\mathbb{R}^2_{\geq 0}$. Clearly the origin is a steady state, so solutions starting there stay there. We note that, employing the solution to the single-species logistic equation,

$$N_1(t) = 0, N_2(t) = \frac{N_{20}}{\frac{N_{20}}{K_2} + (1 - \frac{N_{20}}{K_2})e^{-\rho_2 t}}$$

is a solution of (1.3), with initial condition $N_1(0) = N_{10} = 0, N_2(0) = N_{20} > 0$. Thus all initial states $(0, N_{20})$ with $N_{20} > 0$ go exponentially to $(0, K_2)$. Similarly all states $(N_{10}, 0)$ with $N_{10} > 0$ end up at $(K_1, 0)$.

All other solutions with initial conditions $(N_{10}, N_{20}) \in \mathbb{R}^2_{>0}$ satisfy $(N_1(t), N_2(t)) \in \mathbb{R}^2_{>0}$ for all $t \geq 0$. But, of course, solutions could end up, in the limit, on the boundary, i.e. on the axes. (It is not difficult to show that they can not go to infinity.)

To ease calculations, we first set $u_i = N_i/K_i$ for $i = 1, 2$ and $a_{12} = c_1 K_2$, $a_{21} = c_2 K_1$. We also introduce a dimensionless time $\tau = \rho_1 t$ and set $\rho = \rho_2/\rho_1$. This gives a set of equations with fewer parameters (but which have the same behaviour)

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1 (1 - u_1 - a_{12} u_2) \\ \frac{du_2}{d\tau} &= \rho u_2 (1 - u_2 - a_{21} u_1) \end{aligned} \tag{1.4}$$

Our first step is to locate the nullclines (i.e. the lines on which $\dot{u}_1 = 0$ or $\dot{u}_2 = 0$):

$$u_1 = 0 \quad \text{and} \quad 1 - u_1 - a_{12}u_2 = 0 \tag{1.5}$$
$$u_2 = 0 \quad \text{and} \quad 1 - u_2 - a_{21}u_1 = 0 \tag{1.6}$$

Hence steady states occur at points

$$(u_1^*, u_2^*) = (0,0),\ (1,0),\ (0,1), P = \left(\frac{1 - a_{12}}{1 - a_{12}a_{21}}, \frac{1 - a_{21}}{1 - a_{12}a_{21}} \right).$$

This last steady state is only feasible (non-negative populations!) when either

1. $a_{12} > 1$ and $a_{21} > 1$, since then also $1 - a_{12}a_{21} < 0$;
2. $a_{12} < 1$ and $a_{21} < 1$, since then also $1 - a_{12}a_{21} > 0$;

Hence we have either 3 or 4 steady states. There are 4 cases to consider and we can construct sketches for the phase planes in each:

Case I $a_{12} < 1$ and $a_{21} < 1$;
The steady state P attracts all of the interior of $\mathbb{R}^2_{>0}$. The remaining 3 steady states are unstable. The steady state $(0,0)$ is an unstable node, and both $(1,0)$ and $(0,1)$ are saddles.

Case II $a_{12} > 1$ and $a_{21} > 1$;
The steady state P is unstable. The steady state $(0,0)$ is an unstable node, and both $(1,0)$ and $(0,1)$ are stable nodes. A separatrix (not shown) splits the phase plane into two regions; above the seperatrix trajectories go to the steady state $(1,0)$ and below they go to the steady state $(0,1)$. Orbits starting on the separatrix and not at the origin converge to the interior steady state;

Case III $a_{12} < 1$ and $a_{21} > 1$. There is no interior steady state P. The steady states $(0,0)$ and $(0,1)$ are unstable, but $(1,0)$ is stable and interior trajectories go to this steady state.

Case IV $a_{12} > 1$ and $a_{21} < 1$
There is no interior steady state P. The steady states $(0,0)$ and $(1,0)$ are unstable, but $(0,1)$ is stable and interior trajectories go to this steady state.

Considering all these possibilities, we see that whatever the parameter values, the population always starts or tends to a finite steady state. In particular there can be no population explosion or total extinction, nor oscillations.

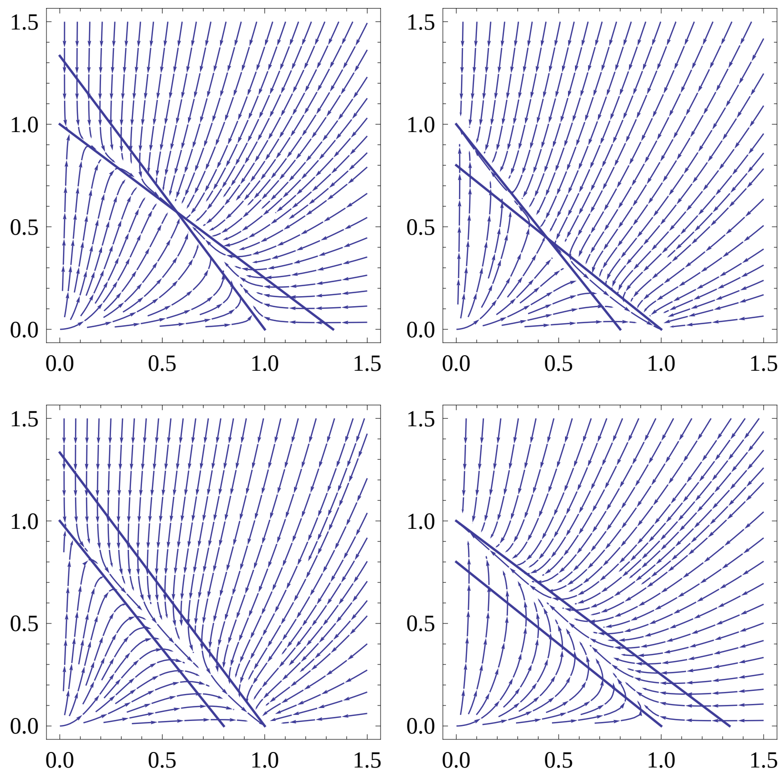

Figure 1.3: The possible phase plane plots for the Lokta-Volterra model (1.3). The thick straight lines are nullclines. From left to right, top to bottom we have: (i) $\alpha_{12} = 0.75, \alpha_{21} = 0.75$, (ii) $\alpha_{12} = 1.25, \alpha_{21} = 1.25$, (iii) $\alpha_{12} = 0.75, \alpha_{21} = 1.25$, (iv) $\alpha_{12} = 1.25, \alpha_{21} = 0.75$. In all case we have $\rho = 2$.

Ecological considerations

In terms of the ecology, we understand the 4 cases as follows:

Case I $a_{12} < 1$ and $a_{21} < 1$;
If the interspecific competition is not too strong the two populations can cooexist stably, but at lower populations than their respective carrying capacities;

Case II $a_{12} > 1$ and $a_{21} > 1$;
Interspecific competition is aggressive and ultimately one population wins, while the other is driven to extinction. The winner depends upon which has the starting advantage;

Case III, IV $a_{12} < 1$ and $a_{21} > 1$ or $a_{12} > 1$ and $a_{21} < 1$;
Interspecific competition of one species dominates the other and, since the

stable node in each case globally attracts $\mathbb{R}^2_{>0}$, the species with the strongest competition always drives the other to extinction.

Non-existence of (isolated) periodic orbits

In fact, we can easily show that no isolated oscillations are possible by using the Bendixson-Dulac theorem:

Theorem 1 (Bendixson-Dulac) *Let $U \subseteq \mathbb{R}^2$ be an open, simply connected set and $f : U \to \mathbb{R}^2$ a continuously differentiable function, and $w : U \to \mathbb{R}_{>0}$ such that div(w(x)f(x)) has non-zero constant sign in U. Then the system $\dot{x} = f(x)$ cannot have a periodic orbit within U.*

We thus have [8]

Theorem 2 *The two species Lotka-Volterra system*

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

has no isolated periodic orbits in $\mathbb{R}^2_{>0}$.

Proof: Suppose that there is a periodic orbit $\gamma \subset \mathbb{R}^2_{>0}$, and let Γ be the interior of γ. Then $\bar{\Gamma}$ is a compact simply-connected and invariant set and hence must contain a steady state (see Theorem 5 in Chapter 2) and this steady state must lie in Γ, since it cannot belong to the periodic orbit $\gamma = \partial\bar{\Gamma}$. Either this steady state is isolated, or there is a line of steady states. In the latter case we cannot have periodic solutions, since they would contain a steady state. Otherwise we have $bf - ce \neq 0$. Now search for a Dulac function $w(x, y) = x^{\alpha-1}y^{\beta-1}$. Then $w > 0$ in the interior Γ and

$$\mathrm{div}(w(F, G)) = w_x F + w_y G + w F_x + w G_y = w(\alpha(a+bx+cy)+bx+\beta(d+ex+fy)+fy)$$

(after some calculation). Now choose α, β to satisfy

$$\begin{aligned} \alpha b + \beta e &= -b \\ \alpha c + \beta f &= -f \end{aligned}$$

which is possible since $bf - ce \neq 0$ to obtain $\mathrm{div}(w(F, G)) = \delta w$ where $\delta = a\alpha + d\beta$. But then by the Bendixson-Dulac theorem we must have $\delta = 0$, since otherwise $\mathrm{div}(w(F, G))$ would be non-zero constant sign in Γ. If $\delta = 0$ then $w(F, G) = (-\psi_y, \psi_x)$ for some ψ. We then have that all orbits satisfy $\psi(x(t), y(t)) =$ const. If one orbit γ is periodic, then it cannot be isolated.

1.1.3 Mutualism

In this case each of the two species benefit from the presence of the other, so that the interaction terms change sign in the previous model to give

$$\begin{aligned} \frac{dN_1}{dt} &= \rho_1 N_1 \left(1 - \frac{N_1}{K_1} + c_1 N_2\right) \\ \frac{dN_2}{dt} &= \rho_2 N_2 \left(1 - \frac{N_2}{K_2} + c_2 N_1\right). \end{aligned} \tag{1.7}$$

(We continue to assume that there is intraspecific competition.) Using the same simplifications as before we obtain

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1 \left(1 - u_1 + a_{12} u_2\right) \\ \frac{du_2}{d\tau} &= \rho u_2 \left(1 - u_2 + a_{21} u_1\right) \end{aligned} \tag{1.8}$$

where $a_{12} > 0$ and $a_{21} > 0$. The effect of changing the sign of the interaction terms on the nullclines is to change the sign of their gradients. Now the two nullclines that are not the axes have positive gradient, and either cross once at a non-zero steady state $\bar{u}$ (when $a_{12}a_{21} < 1$) or diverge and never cross. Thus we always have the three steady states $(0,0), (1,0), (0,1)$, and also, when $a_{12}a_{21} < 1$,

$$\bar{u} = \left(\frac{1 + a_{21}}{1 - a_{12}a_{21}}, \frac{1 + a_{12}}{1 - a_{12}a_{21}}\right).$$

In each case it is not difficult to determine the phase plane portrait (see figure 1.4). When there is a non-zero steady state $\bar{u}$, all interior orbits converge to it. On the other hand, when all the steady states lie on the coordinate axes, all interior orbits diverge to infinity. Notice that the steady state $\bar{u} = (\bar{u}_1, \bar{u}_2)$ has $\bar{u}_1 > 1$ and $\bar{u}_2 > 1$ so that the species converge to populations exceeding their carrying capacities.

If we look at the case where there are 4 steady states, the orbits are bounded and we get convergence of interior orbits to $\bar{u}$. Notice that far enough along an orbit, say $t \geq t_0$, u_1 and u_2 are thereafter changing monotonically in time. Thus if we know that the orbit is bounded, $u_1(t)$, $u_2(t)$ are bounded and monotonic in t for $t \geq t_0$ and hence $u_1(t)$ and $u_2(t)$ must converge to limits U_1 and U_2 and (U_1, U_2) must be a steady state.

We note that the Jacobian matrix J for (1.8) has the sign structure

$$J = \begin{pmatrix} * & \geq 0 \\ \geq 0 & * \end{pmatrix},$$

i.e. off-diagonal elements are non-negative. Such systems are said to be **cooperative**. In 2 dimensions a bounded cooperative flow must converge to a steady state [8]:

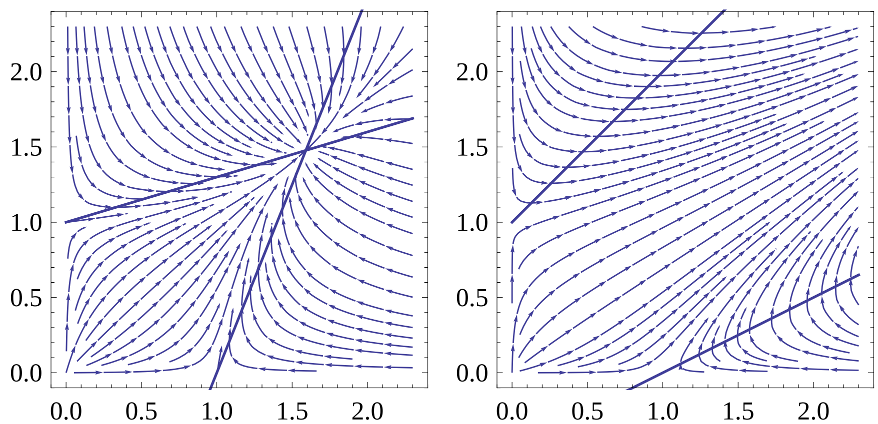

Figure 1.4: Phase planes for 2 species Lotka-Volterra with mutualistic interactions. (Here $a_{12} = 0.4, a_{21} = 0.3$ on the left, and $a_{12} = 2.0, a_{21} = 1.0$ on the right.)

Theorem 3 (Convergence of bounded planar cooperative systems) *If $f : \mathbb{R}^2 \to \mathbb{R}^2$ is C^1 and such that $\partial f_i/\partial x_j \geq 0$ when $i \neq j$, and $\dot{x} = f(x)$ has a bounded forward orbit $x(t)$ through x_0, then $x(t)$ converges to a steady state.*

Proof: By boundedness, the solution $x(t)$ exists for all time $t \geq 0$ (see next chapter). If $\dot{x} = f(x)$ with $x = (x_1, x_2)$ and $f = (f_1, f_2)$ then $v = \dot{x}$ satisfies $\dot{v} = Df(x)v$. We split $\mathbb{R}^2$ into the 4 quadrants: $C_1 = \mathbb{R}^2_{\geq 0}$, $C_3 = -C_1$, $C_2 = (-\mathbb{R}_{\geq 0}) \times (\mathbb{R}_{\geq 0})$ and $C_4 = -C_2$. First we show that if $v(t_0) \in C_1$ for some $t_0 \geq 0$ then $v(t) \in C_1$ for all $t \geq t_0$. Indeed, if at some $t = t_1 \geq t_0$ we have $v_1(t_1) = 0$ and $v_2(t_1) \geq 0$ then $\dot{v_1}(t_1) = \frac{\partial f_1}{\partial x_2}(x(t_1))v_2(t_1) \geq 0$, so that v_1 increases from 0 or stays there. On the otherhand, if at some $t = t_2 \geq t_0$ we have $v_2(t_2) = 0$ and $v_1(t_2) \geq 0$ then $\dot{v_2}(t_2) = \partial f_2/\partial x_1(x(t_2))v_1(t_2) \geq 0$ so v_2 increases from zero or stays there. Thus $v(t_0) \in C_1 \Rightarrow v(t) \in C_1$ for all $t \geq t_0$. A similar argument works for C_3. Now if, for some $t_3 \geq 0$, $v(t_3) \in C_2$, then either $v(t)$ advances into one of C_1 or C_3 and then stays there, or $v(t)$ must remain in C_2 for all $t \geq t_3$, and similarly for C_4. Whatever happens, $v(t)$ will be confined to one quadrant after some time, after which the signs of $v_1 = \dot{x_1}, v_2 = \dot{x_2}$ remain constant, and hence the $x_i(t)$ change monotonically. By boundedness, the monotone orbit must thus converge. $\Box$.

It's not difficult to see we can apply the result to the Lokta-Volterra cooperation model on $\mathbb{R}^2_{\geq 0}$, since this set is forward invariant.

Moreover, the same proof works when the sign structure is

$$J = \begin{pmatrix} * & \leq 0 \\ \leq 0 & * \end{pmatrix}.$$

Such systems are called *competitive.* The only modification in the proof is that one shows that all orbit velocities in C_2 or C_4 stay there, and that velocities in C_1 or C_3 stay there or enter one of C_2 or C_4.

Thus recall the two-species competition equation:

$$\begin{aligned}
\frac{dN_1}{dt} &= \rho_1 N_1 \left(1 - \frac{N_1}{K_1} - c_1 N_2\right) \\
\frac{dN_2}{dt} &= \rho_2 N_2 \left(1 - \frac{N_2}{K_2} - c_2 N_1\right)
\end{aligned}$$

has such structure. One can show that all orbits starting in $\mathbb{R}^2_{\geq 0}$ are bounded (they are eventually confined to $[0, K_1] \times [0, K_2]$) and so will converge to a steady state. In Chapter 6 we will examine in greater detail the implication of the structure of the Jacobian matrix on the dynamics.

Chapter 2

Lyapunov methods for Lotka-Volterra Systems

2.1 Some basic dynamical systems results

In what follows $U \subseteq \mathbb{R}^n$ is an open set, $\mathbb{R}_{\geq 0} = \{x \in \mathbb{R} : x \geq 0\}$ and $\mathbb{R}_{>0} = \{x \in \mathbb{R} : x > 0\}$. We will consider autonomous differential equations of the form

$$\dot{x} = f(x), \ \ x(t_0) = x_0 \in U. \tag{2.1}$$

Definition 1 *We say that the vector field $f : U \to \mathbb{R}^n$ generates the flow $\varphi_t : U \to U$ where $\varphi_t(x) = \phi(x,t)$ for $x \in U$ and t in some interval $I = (a,b) \subseteq \mathbb{R}$ for some $a, b \in \mathbb{R}$ if*

$$\left.\frac{d\phi(x,t)}{dt}\right|_{t=\tau} = f(\phi(x,\tau)), \ \forall x \in U, \ \tau \in I.$$

Note that $\varphi_0(x) = x$ and $\varphi_t(\varphi_s(x)) = \varphi_{t+s}(x)$ when defined. Often we are given an initial condition $x(0) = x_0$, in which case $\varphi_t(x_0) = x(t) = \phi(x_0, t)$ represents the solution or orbit to (2.1) with initial condition $x(0) = x_0$.

Theorem 4 (Picard's existence theorem) *Given an open set $U \subseteq \mathbb{R}^n$, a function $f : U \to \mathbb{R}^n$ that is locally Lipschitz in $x \in U$ and a point $x_0 \in U$, the differential equation $\dot{x} = f(x)$ with $x(t_0) = x_0$ has a unique solution $x : I \to U$ on some open interval I containing t_0.*

In fact, solutions exist for as long as $x(t) \in U$. Solutions may leave U after some finite time. For example, $\dot{x} = kx$ has solution $x(t) = e^{kt}x_0$, or in terms of the flow $\varphi_t(x) = e^{kt}x$. Such a solution exists forward in time and backwards in time, i.e. the time interval I on which the solution exists is $I = \mathbb{R}$. On the other hand, $\dot{x} = 1 + x^2$ has solution $x(t) = \tan(t + \tan^{-1}(x_0))$ or in flow notation $\varphi_t(x) = \tan(t + \tan^{-1}(x))$ and this solution leaves any interval of $\mathbb{R}$ in finite time. Consider also $\dot{x} = -\frac{1}{2x}$ which has the solution $x(t) = x_0\sqrt{1 - t/x_0^2}$ and leaves $U = \mathbb{R}$ when $t = x_0^2$.

In all the examples that we work with, the vector fields are polynomial vector fields, i.e. each component of the field is a polynomial. Thus these functions are smooth and locally Lipschitz. What is not clear is whether these differential equations have solutions that make sense in that the populations remain non-negative for all time if they start non-negative. Nor is it clear whether solutions blow-up in finite time, or whether they converge to equilibria, or whether there is other dynamics.

A flow $\varphi_t : U \to U$ where $t \in \mathbb{R}$ is actually a more of a general mathematical object, i.e. it need not necessarily be generated by a differential equation. See, for example, [15]. Many authors reserve the term flow to one which is defined on all of $\mathbb{R}$ and semiflow for one defined on $t \geq 0$. For a flow (defined for all time) the properties that we use are: For each $x \in U$, $t \in \mathbb{R}$,

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

If φ_t is defined for all $t \in \mathbb{R}$ and is generated by an autonomous differential equation with $C^1(U)$ vector field then $\phi(\cdot, t) = \varphi_t(\cdot)$ is such that $\phi \in C^1(\mathbb{R} \times U)$. In practice the restriction that φ_t be defined for all $t \in \mathbb{R}$ is not prohibitive, since one may replace $\dot{x} = f(x)$ by $\dot{x} = f(x)/(1 + |f(x)|)$ (which amounts to a rescaling of time) and this second system is defined for all $t \in \mathbb{R}$.

Let $U \subseteq \mathbb{R}^n$ be open. For convenience, suppose below that the flow $\varphi_t : U \to U$ is defined <u>for all $t \in \mathbb{R}$</u>.

Definition 2 (Orbit) *The (forward) orbit of $x \in U$ is the set $O^+(x) = \{\varphi_t(x) : t \geq 0\}$.*

Definition 3 (Steady state) *A steady state of $\dot{x} = f(x)$ is a point $x \in U$ for which $f(x) = 0$.*

By Theorem 4, if at some finite $t = t_0$ we have $f(x(t_0)) = 0$ then the unique solution is $x(t) = x(t_0) =$ constant for all $t \in \mathbb{R}$. Note that not all differential equations have steady states, e.g. $\dot{x} = 1 + x^2$ on $\mathbb{R}$.

Definition 4 (Invariant set) *A 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 $t \in \mathbb{R}$.*

Definition 5 (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 $t \geq 0$.*

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

Theorem 5 *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).

We recall that a topological space X is *sequentially compact* if every bounded infinite set has a limit point. For a metric space, compactness and sequential compactness coincide. 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 of 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 6 (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 7 (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 limits backwards in time:

Definition 8 (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 9 (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.

Proof: First we show that $\omega(x)$ is invariant. This is obvious if it is empty, so suppose $p \in \omega(x)$. Then there exists $t_k \to \infty$ such that $\varphi_{t_k}(x) \to p$ as $k \to \infty$. For any $t \in \mathbb{R}$ fixed we have $\varphi_{t_k+t}(x) = \varphi_{t_k}(\varphi_t(x)) = \varphi_t(\varphi_{t_k}(x)) \in O^+(x)$ for k large enough, and taking the limit as $k \to \infty$ we obtain, with $s_k = t_k + t \to \infty$, $\varphi_{s_k}(x) \to \varphi_t(p)$ as $k \to \infty$, which shows that $\varphi_t(p) \in \omega(x)$ and since $t \in \mathbb{R}$ is arbitrary, $\omega(x)$ is invariant.

Next we prove $\omega(x) = \bigcap_{t \geq 0} \overline{O^+(\varphi(x,t))}$. Suppose that $y \in \omega(x)$. We have $\varphi_{t_k}(x) \to y$ for some $t_k \to \infty$. Fix $t \geq 0$. Then $t_k \geq t$ for all k sufficiently large and so $\varphi_{t_k}(x) \in O^+(\varphi_t(x))$ for all k sufficiently large. This shows $y \in \overline{O^+(\varphi_t(x))}$ for all $t \geq 0$. Thus $y \in \bigcap_{t\geq 0} \overline{O^+(\varphi_t(x))}$, giving $\omega(x) \subseteq \bigcap_{t\geq 0} \overline{O^+(\varphi(x,t))}$. Conversely, if $y \in \bigcap_{t \geq 0} \overline{O^+(\varphi_t(x))}$ then $y \in \overline{O^+(\varphi_s(x))}$ for each $s = 1, 2, \ldots$. Hence for each $s = 1, 2, \ldots$, there is a sequence $y_s^k \in O^+(\varphi_s(x))$ such that $y_s^k \to y$ as $k \to \infty$. Given $\epsilon > 0$, for each $k = 1, 2, \ldots$ there exists an N_k such that $|y^k_{N_k} - y| < 1/k$ for each $k = 1, 2, \ldots$. Moreover, $y^k_{N_k} = \varphi_{t_k}(x)$ for some $t_k \geq N_k$. Clearly, by construction, $t_k \to \infty$ as $k \to \infty$. Hence $\varphi_{t_k}(x) = y^k_{N_k} \to y$ as $t_k \to \infty$ which shows that $y \in \omega(x)$.

This also shows that $\omega(x)$ is closed, as it is the intersection of closed sets. To show property 2, note that $\omega(x)$ is compact and non-empty since it is the intersection of non-empty, nested, compact (closed and bounded) sets $\overline{O^+(\varphi_t(x))}$ for each $t \geq 0$ (use the Cantor intersection theorem). □

It can also be shown that if $O^+(x)$ has compact closure then $\omega(x)$ is also a connected set.

For example, $\dot{x} = 1$ 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

$$\begin{aligned} \dot{x} &= x - y - x(x^2+y^2) \\ \dot{y} &= x + y - y(x^2+y^2). \end{aligned} \tag{2.2}$$

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. $S^1 = \{(x, y) : x^2 + y^2 = 1\}$ 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 $(x, y) \neq (0, 0)$, $\omega((x, y)) = S^1$, and otherwise $\omega((0, 0)) = \{(0, 0)\}$.

The use 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 $x(t) = \sqrt{2t + x(0)^2} \to \infty$ 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. Hence there exists a sequence $t_k \to \infty$ as $k \to \infty$ and a $p \in \omega(x_0)$ 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, $\omega(x_0) = \{p\}$. $\square$.

2.1.1 Stability

We continue to suppose that the flow φ_t exists <u>for all $t \in \mathbb{R}$</u>.

Definition 10 (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 11 (Asymptotic stability) *A steady state x^* is said to be locally 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 the simple harmonic oscillator (pendulum) the pendulum resting vertically downwards is Lyapunov stable but not asymptotically stable unless there is damping such as air resistance.

Definition 12 (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 13 (Global stability) *If $B(x^*) = U$ then x^* is said to be globally asymptotically stable on U.*

2.2 Applications to Lotka-Volterra Systems

Consider the model

$$\dot{x}_i = x_i f_i(x), \quad i = 1, \ldots, n. \tag{2.3}$$

where each $f_i : \mathbb{R}^n \to \mathbb{R}^n$ is C^1. Then we apply the Picard Existence Theorem (Theorem 4) to conclude local existence and uniqueness of solutions for any initial condition. 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 uniqueness tells us that these species are absent for all time for which the solutions exist. Hence

Theorem 6 *For the model (2.3) the coordinate axes and the subspaces spanned by them, and $\mathbb{R}^n_{>0}$, are all forward invariant.*

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

Now we specialise to $f(x) = r + Ax$ for $A = ((a_{ij}))$ a real $n \times n$ matrix:

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j), \quad i = 1, \ldots, n. \tag{2.4}$$

Theorem 7 (Interior steady states [8]) *There exists an interior steady state $p \in \mathbb{R}^n_{>0}$ if and only if (2.4) has (ω or α) limit points in $\mathbb{R}^n_{>0}$.*

Proof: Suppose that there exists no steady state in $\mathbb{R}^n_{>0}$ so that $L : \mathbb{R}^n \to \mathbb{R}^n$ defined by $L(x) = r + Ax$ is such that $L(x) \neq 0$ for $x \in \mathbb{R}^n_{>0}$. Let $K = L(\mathbb{R}^n_{>0})$. This is an open convex set. Then there exists a hyperplane H separating the origin from K of the form $H = \{x \in \mathbb{R}^n : x \cdot c = \epsilon\}$ for some unit vector $c \in \mathbb{R}^n$ and $\epsilon > 0$ and $x \cdot c > \epsilon > 0$ for all $x \in K$. Now consider the function $V(x) = \sum_{i=1}^{n} c_i \log(x_i)$. Then on $\mathbb{R}^n_{>0}$ we have $\frac{dV}{dt} = \sum_{i=1}^{n} c_i \frac{\dot{x}_i}{x_i} = c \cdot L(x) > \epsilon > 0$ since $L(x) \in K$. Now if $p \in \mathbb{R}^n_{>0}$ is a limit point, with $x(t_k) \to p$ we have $\dot{V}(x(t_k)) \to \dot{V}(p) \geq \epsilon > 0$. So there cannot be an interior limit point (see Theorem 9 below). $\square$

Thus the theorem says that if $r + Ax = 0$ has no solutions in $\mathbb{R}^n_{>0}$ then every orbit must converge to the boundary or go to infinity. In particular, if $\mathbb{R}^n_{>0}$ has a periodic orbit, it must also have an interior steady state. Another way to see this is to average around the periodic orbit; if $x_i^* > 0$ is the average over the periodic orbit then one finds $Ax^* + r = 0$:

Theorem 8 (Time Averages [8]) *Suppose that $x(t)$ is a periodic orbit of (2.4) of period T. Then if (2.4) has a unique interior steady state $x^* \in \mathbb{R}^n_{>0}$,*

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

Proof: We have

$$\begin{aligned} \frac{1}{T}\int_0^T \frac{\dot{x}_i(t)}{x_i(t)}\,dt &= \frac{1}{T}\int_0^T r_i + (Ax(t))_i\,dt \\ 0 = \frac{1}{T}[\log x(T) - \log x(0)] &= r + \left(A\left\{\frac{1}{T}\int_0^T x(t)\,dt\right\}\right) \end{aligned}$$

Now use that A has inverse A^{-1}:

$$0 = A^{-1}r + \frac{1}{T}\int_0^T x(t)\,dt,$$

so that

$$\frac{1}{T}\int_0^T x(t)\,dt = -A^{-1}r = x^*,$$

as required. □.

2.3 LaSalle's Invariance Principle

We start with a basic result for Lyapunov functions:

Theorem 9 (Lyapunov functions [8]) *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. If for some solution $x(t)$ with initial condition $x(0) = x_0 \in U$ the time derivative $\dot{V} = DVf$ satisfies $\dot{V}(x(t)) \leq 0$, then $\omega(x) \cap U \subseteq \dot{V}^{-1}(0)$.*

Proof: If $p \in \omega(x) \cap U$ then $\exists\ t_k \to \infty$ such that $x(t_k) \to p$. Since $\dot{V}(x(t_k)) \leq 0$ we have by continuity $\dot{V}(p) \leq 0$. Now suppose that $\dot{V}(p) \neq 0$. Then $\dot{V}(p) < 0$. If $p(t)$ is the solution with $p(0) = p$ then, since V cannot increase along an orbit, and $\dot{V}(p) < 0$,

$$V(p(t)) < V(p) \quad \forall t > 0. \tag{2.5}$$

Similarly $V(x(t_k)) \leq V(x(t))$ for all $t_k \geq t \geq 0$. Taking the limit as $k \to \infty$ we have

$$V(p) \leq V(x(t)) \quad \forall t \geq 0. \tag{2.6}$$

But for all $t \geq 0$ we have $x(t_k + t) \to p(t)$ as $k \to \infty$ (using continuity to initial conditions), so that by (2.5) taking k large enough we have $V(x(t_k + t)) < V(p)$, which contradicts (2.6) and shows that $\dot{V}(p) = 0$ as required. □

Of course $\omega(x)$ might be empty. For example, $\dot{x} = -1$ has empty omega limit sets, but $V(x) = 0, x \leq 0$ and $V(x) = x^2$ for $x > 0$ is continuously differentiable and $\dot{V}(x) \leq 0$. In some cases, such as when V is convex and coercive[1] an orbit $x(t)$ will be bounded and hence $\omega(x)$ will be non-empty.

We also have the tighter result (e.g. page 127 in [15]):

Theorem 10 *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) $\dot{V}(x) \leq 0$ 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; (c) if $\dot{V}(x) > 0$ for all $x \in U \setminus \{x_0\}$, x_0 is unstable.*

[1] A coercive function $V : U \to \mathbb{R}$ satisfies $|V(x)| \to \infty$ as $|x| \to \partial U$.

Example

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

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, $\dot{r} = r - r^3$. Thus taking $V(x,y) = \sqrt{x^2+y^2}$ 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 $\dot{V}^{-1}(0) = \{(0,0)\} \cup S^1$ (S^1 is the unit circle). Applying LaSalle's invariance principle we get $\omega((x,y)) = S^1$ whenever $(x,y) \neq (0,0)$.

Example

$$\dot{x} = x(-\alpha + \gamma y) \tag{2.7}$$

$$\dot{y} = \alpha x - (\gamma x + \delta) y \quad (\alpha, \beta, \delta > 0) \tag{2.8}$$

This system has a unique steady state $(0,0)$, and one can show that $\mathbb{R}^2_{\geq 0}$ is forward invariant. Adding (2.7) and (2.8) 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 $\dot{V}^{-1}(0) = \{(s,0) : s \in \mathbb{R}\}$. Take $U = \mathbb{R}^2_{\geq 0}$. Then 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 subset of $\{(s,0) : s \in \mathbb{R}_{\geq 0}\}$ for the flow of (2.7) and (2.8) is the origin. Thus $\omega((x,y)) = \{(0,0)\}$ $\forall (x,y) \in \mathbb{R}^2_{\geq 0}$.

Example: Two species Lotka-Volterra

Consider the two species Lotka-Volterra system

$$\begin{aligned}\dot{x} &= x(a + bx + cy)\\ \dot{y} &= y(d + ex + fy).\end{aligned} \tag{2.9}$$

Suppose that (2.9) has a unique interior steady state, say $(x^*, y^*) \in \mathbb{R}^2_{>0}$. Thus $bf - ce \neq 0$. We consider the function $V : \mathbb{R}^2_{\geq 0} \to \mathbb{R}$ defined by

$$V(x,y) = \alpha\left(x - x^* - x^* \log\left(\frac{x}{x^*}\right)\right) + \beta\left(y - y^* - y^* \log\left(\frac{y}{y^*}\right)\right),$$

where $\alpha, \beta > 0$. Then $V(x^*, y^*) = 0$ and $V(x,y) > 0$ for all $(x,y) \neq (x^*, y^*)$. Moreover, on $\mathbb{R}^2_{>0}$

$$\begin{aligned}
\frac{d}{dt}V &= V_x(x,y)\dot{x} + V_y(x,y)\dot{y} \\
&= \alpha\left(1 - \frac{x^*}{x}\right)x(a + bx + cy) + \beta\left(1 - \frac{y^*}{y}\right)y(d + ex + fy) \\
&= \alpha\,(x - x^*)\,(a + bx + cy) + \beta\,(y - y^*)\,(d + ex + fy) \\
&= \alpha\,(x - x^*)\,(b(x - x^*) + c(y - y^*)) + \beta\,(y - y^*)\,(e(x - x^*) + f(y - y^*))
\end{aligned}$$

(using that $a + bx^* + cy^* = 0$ and $d + ex^* + fy^* = 0$). Now set $X = x - x^*$ and $Y = y - y^*$ to obtain

$$\frac{d}{dt}V = \alpha X(bX + cY) + \beta Y(eX + fY) = \alpha b X^2 + \beta f Y^2 + (\alpha c + \beta e)XY.$$

We may write this as

$$\frac{d}{dt}V = (X \;\; Y)\begin{pmatrix} b & e \\ c & f \end{pmatrix}\begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix}\begin{pmatrix} X \\ Y \end{pmatrix}.$$

Now let $A = \begin{pmatrix} b & c \\ e & f \end{pmatrix}$ and $D = \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix}$, so that

$$\frac{d}{dt}V = (X \;\; Y)A^T D\begin{pmatrix} X \\ Y \end{pmatrix} = \frac{1}{2}(X \;\; Y)\left\{A^T D + DA\right\}\begin{pmatrix} X \\ Y \end{pmatrix}.$$

Hence if we can choose α, β such that the symmetric matrix $A^T D + DA$ is negative definite, we will have $\dot{V} \leq 0$ with equality if and only if $(X, Y) = (0, 0)$, i.e. $x = x^*, y = y^*$. Therefore we require that $M = A^T D + DA = \begin{pmatrix} 2b\alpha & c\beta + e\alpha \\ c\beta + e\alpha & 2f\beta \end{pmatrix}$ has negative eigenvalues. This is the case if

$$\operatorname{trace}(M) < 0 \text{ and } \det M > 0.$$

That is

$$b\alpha + f\beta < 0 \text{ and } \Delta = 4fb\alpha\beta - (c\beta + e\alpha)^2 > 0.$$

From the second relation, $fb > 0$ (since we are assuming $\alpha, \beta > 0$) so that f and b are non-zero and of the same sign, and thus from the first condition we must have $\alpha b < 0$ and $\beta f < 0$, i.e. $b < 0, f < 0$.

Now consider three cases: (i) $ce = 0$, (ii) $ce > 0$, (iii) $ce < 0$.

First if $ce = 0$ then either $c = 0$ or $e = 0$ or both. If $c = 0$ but $e \neq 0$ then $\Delta = \alpha(4fb\beta - e^2\alpha)$ and so choose $\alpha = 1$ and $\beta = \frac{e^2}{2fb}$ to ensure $\Delta > 0$. Similarly if $e = 0$ but $c \neq 0$ choose $\beta = 1$ and $\alpha = \frac{c^2}{2fb}$. If $e = 0$ and $c = 0$ choose $\alpha = 1 = \beta$. Notice that in each instance $\det A > 0$.

Now if $ce > 0$, then either $c, e > 0$ or $c, e < 0$. We have

$$\Delta = 4fb\alpha\beta - (c\beta + e\alpha)^2 = 4\alpha\beta(fb - ce) - (c\beta - e\alpha)^2 = 4\alpha\beta \det A - (c\beta - e\alpha)^2$$

Now choose $\alpha = 1$ and $\beta = e/c$ so that, since c, e have the same sign, $\Delta = 4e \det A/c > 0$ if $\det A > 0$. Since we already know that $f, b < 0$, so that $\mathrm{trace} A = b + f < 0$, we conclude that A should satisfy $f, b < 0, \det A > 0$. Finally if $ce < 0$ then choose $\alpha = 1$ and $\beta = -e/c$ to obtain $\Delta = -4 \det Ae/c > 0$ since e, c have opposite signs.

Using Theorem 10 with $U = \mathbb{R}^2_{>0}$ we see that if A satisfies $f, b < 0, \det A > 0$ then the non-zero steady state attracts all interior points.

To conclude, we have shown

Theorem 11 (Goh [9]) *Suppose the system*

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

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 $\det A > 0$.

More generally we have

Theorem 12 (Goh [10]) *Suppose that the Lotka-Volterra system $\dot{x}_i = x_i f_i(x) = x_i(r_i + \sum_{j=1}^n a_{ij}x_j)$, $i = 1, \dots, n$ 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 $\alpha_i \in \mathbb{R}$ are to be found. Then we compute on $\mathbb{R}^n_{>0}$

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

This can be rewritten as

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

where $D = \mathrm{diag}(\alpha_1, \dots, \alpha_n)$. Now generalise the argument of Theorem 11. $\square$.

2.3.1 Example: Food chains [11], [8]

Suppose we have n species in a food chain. Species 1 is prey for species 2, species 2 predates on species 1 but is prey for species 3, etc. The nth species predates on species $n-1$, but is not hunted itself.

$$\begin{aligned}
\dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2) \\
\dot{x}_j &= x_j(-r_j + a_{j,j-1}x_{j-1} - a_{jj}x_j - a_{j,j+1}x_{j+1}, \quad (j = 2, \dots, n-1), \\
\dot{x}_n &= x_n(-r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n).
\end{aligned}$$

All constants $r_i > 0$, $a_{ij} \geq 0$. Let $w_i(x) := \dot{x}_i / x_i$.

Let us suppose that there is a unique interior steady state p and consider

$$V(x) = \sum_{i=1}^{n} c_i(x_i - p_i \log x_i).$$

Then

$$\dot{V} = \sum_{i=1}^{n} c_i \left(\dot{x}_i - p_i \frac{\dot{x}_i}{x_i} \right) = \sum_{i=1}^{n} c_i \left(x_i - p_i \right) w_i.$$

Since p is an interior steady state, $w(p) = 0$, so with $a_{1,0} = 0$ and $a_{n,n+1} = 0$,

$$\begin{aligned}
\dot{V} &= \sum_{i=1}^{n} c_i \left(x_i - p_i \right) \left(w_i(x) - w_i(p) \right) \\
&= \sum_{i=1}^{n} c_i(x_i - p_i) \left((a_{i,i-1}(x_{i-1} - p_{i-1}) - a_{ii}(x_i - p_i) - a_{i,i+1}(x_{i+1} - p_{i+1}) \right) \\
&= -\sum_{i=1}^{n} c_i a_{ii}(x_i - p_i)^2 + \sum_{i=1}^{n-1} (x_i - p_i)(x_{i+1} - p_{i+1})(-c_i a_{i,i+1} + c_{i+1} a_{i+1,i}).
\end{aligned}$$

Now chose $c_i > 0$ with $c_1 = 1$ and

$$c_{i+1} = \frac{a_{i,i+1}}{a_{i+1,i}} c_i, \quad (i = 2, \dots, n) \tag{2.10}$$

so that $\dot{V} = -\sum_{i=1}^{n} c_i a_{ii}(x_i - p_i)^2 \leq 0$, with equality if and only if $x = p$. Now apply Theorem 10. $\square$.

If $a_{ii} = 0$ for all $i \geq 2$ (so that the predators are not subject to intraspecific competition), we have

$$\dot{V} = -a_{11}(x_1 - p_1)^2.$$

Thus for any $x \in \mathbb{R}^n_{>0}$,

$$\omega(x) \cap \mathbb{R}^n_{>0} \subseteq \{(p_1, s_2, \dots, s_n) : s_i > 0, i = 2, \dots, n\}.$$

But $\omega(x)$ must be invariant. Then $0 = \dot{x}_1 = p_1(r_1 - a_{11}p_1 - a_{12}s_2)$ so that $s_2 = p_2$ (by uniqueness of the interior steady state), and so on, giving $\omega(x) = \{p\}$ and again we get global convergence on $\mathbb{R}^n_{>0}$ to the interior steady state p.

If $a_{11} = 0$ also, then

$$V(x) = \sum_{i=1}^{n} c_i(x_i - p_i \log x_i),$$

with c_i defined by (2.10) is a conserved quantity and the flow occurs on the set $V^{-1}(x(0))$. We will consider systems with conserved quantities in the next chapter.

Chapter 3

Conservative Lotka-Volterra Systems

Recall that in Chapter 1 we found that Volterra's two-species predator-prey model was (in suitable coordinates) canonically Hamiltonian. In this chapter we will examine the generalisation of this to n species.

Definition 14 (Conservative Lotka-Volterra) *We will say that (2.4) 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.

Example

Recall the two-species Lotka-Volterra system

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

which becomes $\dot{x}_i = x_i(r_i + \sum_j a_{ij}x_j)$ where $r = (a, -d)^T$, $A = \begin{pmatrix} 0 & -b \\ c & 0 \end{pmatrix}$. Now choose $D = \mathrm{diag}(1/c, 1/b)$ so that $AD = J = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$ which is skew-symmetric. This effectively makes a change of coordinates $u_1 = cN$, $u_2 = bP$ to give

$$\begin{aligned} \frac{1}{u_1}\frac{du_1}{dt} &= a - u_2 \\ \frac{1}{u_2}\frac{du_2}{dt} &= u_1 - d, \end{aligned}$$

which, as we have seen, are canonically Hamiltonian.

More generally, a change of coordinates $y_i = x_i/d_i$ transforms (2.4) 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 a $n \times n$ skew-symmetric matrix then* $\det A = (-1)^n \det A$. *Hence when n is odd, A is singular.*

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

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, [14]). Let C^∞ denote the space of smooth functions $\mathbb{R}^n \to \mathbb{R}$.

Definition 15 (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. $\{f, gh\} = \{f, g\}h + g\{f, h\}$ *[Liebnitz 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 (2.4) we note that there's a graphical way of testing whether a Lotka-Volterra system is conservative:

Proposition 1 (Volterra [19]) *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 ($AD + DA^T = 0$). 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.

The food chain example of the previous chapter serves as an example, but caution: The matrix $A = ((a_{ij}))$ in that example is the interaction matrix only up to signs.

3.1 Volterra's construction [19, 3]

We start with the skew-symmetric system

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij} x_j), \quad a_{ij} = -a_{ji}. \tag{3.1}$$

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 (3.1) becomes the second order system

$$\ddot{Q}_i = \dot{Q}_i(r_i + \sum_{j=1}^{n} a_{ij} \dot{Q}_j). \tag{3.2}$$

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

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

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 (3.1) is canonically Hamiltonian in the new coordinates P, Q with Hamiltonian function

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

and the standard Poisson bracket

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

3.2 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

$$\dot{y}_i = \sum_{j=1}^{n} a_{ij}(e^{y_j} - x_j^*) = \sum_{j=1}^{n} a_{ij} \frac{\partial H}{\partial y_j}, \tag{3.3}$$

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

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

$$\{f, g\} = \sum_{i=1}^{n} \nabla f \cdot A \nabla g$$

provides a suitable Poisson bracket. This is left as an exercise.

When $\det A \neq 0$, so that $n = 2m$ for some m we can actually put (3.3) in canonical form. To this end we make the change of coordinates $z = By$ where B is an invertible matrix to be chosen. We get

$$\dot{z} = B\dot{y} = BA\nabla_y H(y) = BAB^{-1} \nabla_z h(z),$$

where $h(z) = H(B^{-1}z)$. To obtain the standard canonical form we need to choose B to satisfy

$$BAB^{-1} = \begin{pmatrix} 0_m & -I_m \\ I_m & 0_m \end{pmatrix} = J_{2m},$$

where $0_m, I_m$ are the $m \times m$ zero and identity matrices respectively. That such an (orthogonal matrix) B exists when $\det A \neq 0$ is a standard result from alternating forms (e.g. page 237 in [2]).

In our Lotka-Volterra problem, we may choose

$$\{f, g\} = \sum_{i=1}^{m} \nabla f J_{2m} \nabla g.$$

We can check that for a given $H(z)$ that

$$\dot{z}_k = \{z_k, H\} = \begin{cases} \dfrac{\partial H}{\partial z_{k+m}} & k = 1, \ldots, m \\ -\dfrac{\partial H}{\partial z_{k-m}} & k = m+1, \ldots, 2m. \end{cases}$$

In the original coordinates x, we have that (3.1) is Hamiltonian with Hamiltonian function $h(x) = \sum_{i=1}^{n}(x_i - x_i^* \log x_i)$ and Poisson bracket

$$\{f, g\} = \sum_{j<k} a_{jk} x_j x_k \left(\frac{\partial f}{\partial x_j} \frac{\partial g}{\partial x_k} - \frac{\partial g}{\partial x_j} \frac{\partial f}{\partial x_k} \right), \tag{3.4}$$

which yield the Lotka-Volterra equations as

$$\dot{x}_i = \sum_{j=1}^{n} a_{ij} x_i x_j \frac{\partial h}{\partial x_j}.$$

Remarks:

1. The x^* need not lie in the first quadrant.
2. 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: 3 species food chain

Consider the Lotka-Volterra system for 3 interacting species:

$$\begin{aligned} \dot{x}_1 &= x_1(r_1 + \omega_1 x_2 - \omega_2 x_3) \\ \dot{x}_2 &= x_2(r_2 - \omega_1 x_1 + \omega_3 x_3) \\ \dot{x}_3 &= x_3(r_3 + \omega_2 x_1 - \omega_3 x_2) \end{aligned} \tag{3.5}$$

where $\omega_1, \omega_2, \omega_3 > 0$. 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

$$v^T r = \omega_3 r_1 + \omega_1 r_3 + \omega_2 r_2 = 0 \tag{3.6}$$

($v = (\omega_3,\omega_2,\omega_1)$) 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 (3.6) 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 (3.6). The Poisson bracket

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

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 (3.6). The dynamics lies on the intersection of the surfaces $h(x) = h(x(0))$ and $C(x) = C(x(0))$ in the first quadrant.

Existence of periodic orbits

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

$$Z = \log\left(A - e^X - e^Y + \frac{r_2}{\omega_1}X - \frac{r_1}{\omega_1}Y\right) \tag{3.7}$$

$$Z = \frac{B - \omega_3 X - \omega_2 Y}{\omega_1}. \tag{3.8}$$

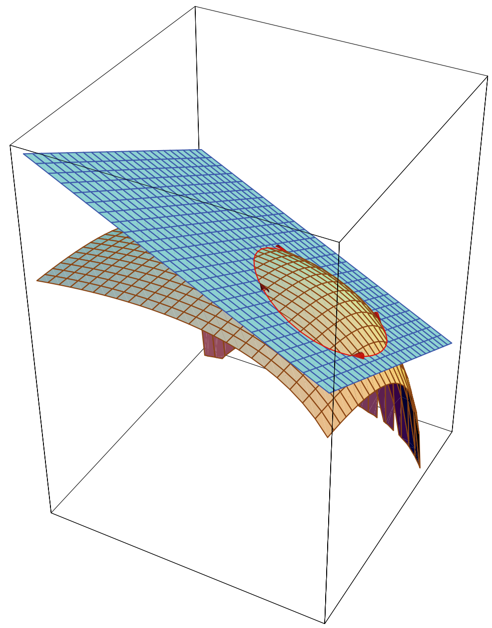

Figure 3.1: A periodic solution to the three species model (3.5)

The first surface is concave where the logarithm is defined. Searching for periodic orbits then becomes the study of how the surface (3.7) intersects the plane (3.8). An example a periodic orbit is shown in figure 3.1.

Other interesting interactions can be studied by changing the signs of the ω_i.

3.2.1 Example 2 [3]

$$\begin{aligned} \dot{x}_1 &= x_1(-1 + x_2) \\ \dot{x}_2 &= x_2(1 - x_1 + a x_3) \\ \dot{x}_3 &= x_3(-1 - a x_2 + x_4) \\ \dot{x}_4 &= x_4(1 - x_3) \end{aligned} \tag{3.9}$$

This has the skew-symmetric interaction matrix

$$A = \begin{pmatrix} 0 & 1 & 0 & 0 \\ -1 & 0 & a & 0 \\ 0 & -a & 0 & 1 \\ 0 & 0 & -1 & 0 \end{pmatrix}$$

When $a = 0$ we obtain two uncoupled predator prey models, with x_1, x_3 the predators and x_2, x_4 the prey. So we are interested in the coupled case $a > 0$, for which now species 3 becomes prey for species 2, so we get the chain $x_1 \to x_2 \to x_3 \to x_4$

(where the arrow means “predates on”). The matrix A has $\det A = 1$, and (skew-symmetric) inverse

$$A^{-1} = \begin{pmatrix} 0 & -1 & 0 & -a \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 \\ a & 0 & 1 & 0 \end{pmatrix}.$$

Thus there is a unique solution $q = (1+a, 1, 1, 1+a)^T$ to $Aq + r = 0$ where $r = (-1, 1, -1, 1)^T$. The Hamiltonian can be taken to be

$$h(x) = x_1 + x_2 + x_3 + x_4 - (1+a)\log(x_1 x_4) - \log(x_2 x_3).$$

and the Poisson bracket as given by (3.4). The Poisson bracket is now non-degenerate (since $\det A \neq 0$) and so there are no Casimirs.

Now when $a = 0$ the projections $(x_1(t), x_2(t))$ and $(x_3(t), x_4(t))$ of the full solution are individually periodic with periods T_1, T_2 and in general $T_1/T_2 \notin \mathbb{Q}$, so that we typically have almost periodic solutions, and periodic solutions only if $T_1/T_2 \in \mathbb{Q}$. What happens when $a > 0$?

Lemma 4 (Periodic orbits [3]) *For any $a > -1$ the invariant 2-plane*

$$\Pi = \{(x_1, x_2, x_3, x_4) \in \mathbb{R}^n_{>0} : x_1 = (1+a)x_3, x_4 = (1+a)x_2\}$$

is formed of periodic orbits of the system (3.9).

Proof: We look for solutions of the form

$$\begin{array}{rcl} x_1(t) & = & (1+a)u(t) \\ x_2(t) & = & v(t) \\ x_3(t) & = & u(t) \\ x_4(t) & = & (1+a)v(t). \end{array} \tag{3.10}$$

We have

$$\dot{v} = \dot{x}_2 = x_2(1 - x_1 - ax_3) = v(1 - (1+a)u + au) = v(1-u)$$

and

$$\dot{u} = \dot{x}_3 = x_3(-1 - ax_2 + x_4) = u(-1 - av + (1+a)v) = u(-1+v).$$

and similarly $(1+a)\dot{u} = \dot{x}_1 = -x_1 + x_1x_2 = (1+a)u(-1+v)$, $(1+a)\dot{v} = \dot{x}_4 = x_4 - x_4x_3 = (1+a)v(1-u)$. That is u, v satisfy the predator-prey equations for 2 species and thus the first quadrant of the uv-plane consists of periodic orbits around the point $(u, v) = (1, 1)$. Thus any initial condition $x(0) \in \Pi$ gives rise to a planar period orbit around the unique steady state $q = (1+a, 1, 1, 1+a)^T$ (which corresponds to $(u, v) = (1, 1)$). $\square$

Chapter 4

Cooperative Lotka-Volterra Systems

We will consider the general Lotka-Volterra system

$$\dot{x}_i = F_i(x) := x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j), \quad (i = 1, \dots, n). \tag{4.1}$$

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 non-negative. 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 the sign structure

$$\begin{pmatrix} * & \geq 0 & \geq 0 & \cdots & \geq 0 & \geq 0 \\ \geq 0 & * & \geq 0 & \cdots & \geq 0 & \geq 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \geq 0 & \geq 0 & \geq 0 & \cdots & \geq 0 & * \end{pmatrix}$$

We recall that such systems are called *cooperative*.

Definition 16 (Cooperative matrix) *We will say that any real $n \times n$ matrix with the above sign structure is* cooperative.

We met a two-dimensional cooperative system in the first chapter for two species and used that bounded orbits of two-dimensional cooperative systems converged to a steady state. This result applied to general two-dimensional systems of the form $\dot{x}_i = f_i(x)$, $i = 1, 2$ with $\frac{\partial f_i}{\partial x_i} \geq 0$ for $i \neq j$, so long as a given orbit had compact closure. Extending such ideas to higher dimensional cooperative systems (not just

Lotka-Volterra systems) is possible, with extra conditions imposed, and is dealt with briefly in Chapter 6. The special form of the Lotka-Volterra system (4.1), however, submits to fairly elementary techniques.

Some notation

In what follows we will use the following notation for 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 begin with

Lemma 5 (Unbounded orbits [8]) *If the matrix A has a left eigenvector $v > 0$ with eigenvalue $\lambda > 0$ then (4.1) has interior solutions that are unbounded as $t \to \infty$.*

Proof: We have $vA = \lambda v$ where $v > 0$ and chosen such that $\sum_i v_i = 1$. Consider

$$P(x) = \prod_{i=1}^{n} x_i^{v_i}, \text{ so that } \quad \log P(x) = \sum_{i=1}^{n} v_i \log x_i$$

Then

$$\frac{\dot{P}}{P} = \sum_{i=1}^{n} \frac{v_i \dot{x}_i}{x_i} = v \cdot (r + Ax) = v \cdot (r + \lambda x).$$

Now $v \cdot x \geq \prod_i x_i^{v_i}$ (by the generalised arithmetic-geometric mean inequality) and hence

$$\frac{\dot{P}}{P} = v \cdot (r + \lambda x) \geq v \cdot r + \lambda \prod_i x_i^{v_i} = v \cdot r + \lambda P.$$

Thus $\dot{P} \geq P(v \cdot r + \lambda P)$, so that solutions with $x(0) = x_0$ such that $P(x_0) > -v \cdot r / \lambda$ will go to infinity. □

In particular, if $r \gg 0$, and such a vector v exists, then all interior orbits go to infinity. Note that this lemma is true for any interaction matrix A that has a non-negative left eigenvector with positive eigenvalue, not just cooperative A.

To utilise such a lemma, we need to know that the interaction matrix A has a non-negative left eigenvector. The following Perron-Frobenius theorem is fundamental:

Theorem 13 (Perron-Frobenius) *If A is a $n \times n$ real matrix with non-negative entries. Then*

- *there exists a unique non-negative eigenvalue λ which is dominant in the sense that $\lambda \geq |\mu|$ for all other eigenvalues μ of A;*
- *A has left and right eigenvectors $u > 0$ and $v > 0$ associated with λ (i.e. $uA = \lambda u$ and $Av = \lambda v$).*

If A is also irreducible then we have $\lambda > |\mu|$ (and λ is simple) and $v \gg 0$ and $u \gg 0$ in the above statements.

Recall that 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 has $a_{ij} \geq 0$ for $i \neq j$ this becomes $Ad \ll 0$.

Lemma 6 *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 non-negative 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 in particular

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

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.

Conversely, suppose that A is stable and has non-negative off-diagonal elements. For $c > 0$ sufficiently large $B = A + cI$ is a non-negative 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, $\rho(B) < c$ (here $\rho(B)$ is the spectral radius of B). 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 $Ad = -(1, \ldots, 1)^T \ll 0$. $\square$.

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.*

We also have the following (see, for example, Theorem 15.1.1 in [8]):

Theorem 14 (Global convergence for cooperative Lotka-Volterra) *Suppose that the system (4.1) (with each $r_i > 0$) has a unique interior steady state x^* and that A has non-negative off-diagonal elements. Then x^* is globally asymptotically stable on $\mathbb{R}^n_{>0}$ and all (boundary) orbits are uniformly bounded as $t \to \infty$.*

Proof: By corollary 1 A is stable and hence is negatively diagonally dominant by lemma 6, 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 10, $x(t) \to x^*$ as $t \to \infty$. By the same token all boundary orbits are uniformly bounded (≤ 0 in the last inequality). $\square$.

Chapter 5

Competitive Lotka-Volterra Systems

Now we consider the Lotka-Volterra system

$$\dot{x}_i = x_i(r_i - \sum_{j=1}^{n} a_{ij} x_j) = F_i(x), \;\; i = 1, \ldots, n, \tag{5.1}$$

under the special conditions that $a_{ij} > 0$ for all $1 \le i, j \le n$ (**caution:** notice the change of sign in (5.1)). This means that each species competes with all other species including itself. If some $r_i \le 0$ then it is clear that $x_i(t) \to 0$ as $t \to \infty$ since $\mathbb{R}^n_{\ge 0}$ is invariant and

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

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 7 *Since $a_{ij} > 0$ and $r_i > 0$, all orbits of (5.1) are bounded.*

Proof: $\mathbb{R}^n_{\ge 0}$ is invariant and

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

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

We recall the two species competition model

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1\left(1-u_1-a_{12}u_2\right)\\ \frac{du_2}{d\tau} &= \rho u_2\left(1-u_2-a_{21}u_1\right)\end{aligned}$$

where each species has carrying capacity 1 under the normalisation chosen. In the two cases $a_{12}<1, a_{21}>1$ and $a_{21}<1, a_{12}>1$ there is no interior steady states, i.e. all steady states lie on the boundary (they are $(0,0)$, $(1,0)$ and $(0,1)$).

We recall Theorem 7 which states: There exists an interior steady state $x^* \in \mathbb{R}^n_{>0}$ if and only if (2.4) (which is (5.1) for general A, r) has ω or α limit points in $\mathbb{R}^n_{>0}$. Hence if (5.1) has no interior steady states, all interior orbits must approach the coordinate axes or their subspaces.

Let us introduce the following further restrictions on the r_i, a_{ij} (see [20]):

$$(A)\ \frac{r_j}{a_{jj}}<\frac{r_i}{a_{ij}},\ \ 1\le i<j\le n \text{ and } (B)\ \frac{r_j}{a_{jj}}>\frac{r_i}{a_{ij}},\ \ n\ge i>j\ge 1 \tag{5.2}$$

Then we have

Lemma 8 *Under the assumption (5.2), the competitive system (5.1) has no interior steady state.*

Proof: Any interior steady state x^* must satisfy

$$\frac{a_{i1}}{r_i}x_1^*+\frac{a_{i2}}{r_i}x_2^*+\cdots+\frac{a_{in}}{r_i}x_n^*=1,\ i=1,\ldots,n.$$

Thus we have the $n-1$ relations

$$\left(\frac{a_{11}}{r_1}-\frac{a_{i1}}{r_i}\right)x_1^*+\left(\frac{a_{12}}{r_1}-\frac{a_{i2}}{r_i}\right)x_2^*+\cdots+\left(\frac{a_{1n}}{r_1}-\frac{a_{in}}{r_i}\right)x_n^*=0,\ i=2,\ldots,n.$$

Thus with $i=n$

$$\left(\frac{a_{11}}{r_1}-\frac{a_{n1}}{r_n}\right)x_1^*+\left(\frac{a_{12}}{r_1}-\frac{a_{n2}}{r_n}\right)x_2^*+\cdots+\left(\frac{a_{1n}}{r_1}-\frac{a_{nn}}{r_n}\right)x_n^*=0.$$

Using (5.2), we see that each of the brackets are negative so that we must have $x^*=0$. Hence there is no interior steady state. $\Box$.

Take a plane Π_δ with outward normal $\underline{1}=(1,\ldots,1)$ distance δ from the origin: This has equation $\sum_{i=1}^n x_i=\delta$. Where Π_δ intersects with $\mathbb{R}^n_{\ge 0}$,

$$\langle \underline{1}, F\rangle \ge \left(\min_i r_i\right)\delta-\sum_{i,j=1}^n a_{ij}x_ix_j \ge \delta\left(\min_i r_i-\left(\max_{i,j} a_{ij}\right)\delta\right).$$

Hence for $\delta > 0$ small enough $\langle \underline{1}, F\rangle > 0$ at points where Π_δ intersects $\mathbb{R}^n_{\geq 0}$. This is true for all $0 < \delta < \epsilon$ for some $\epsilon > 0$. Thus there is an $\epsilon > 0$, such that for any initial conditions $x(0) > 0$, we have $\sum_{i=1}^n x_i(t) \geq \epsilon$ for all $t \geq T_\epsilon$ for some $T_\epsilon > 0$.

We now compute

$$\begin{aligned}
\frac{d}{dt}\left(x_n^{1/r_n}x_1^{-1/r_1}\right) &= \frac{\dot{x}_n}{r_n}\left(x_n^{-1+1/r_n}x_1^{-1/r_1}\right) - \frac{\dot{x}_1}{r_1}\left(x_n^{1/r_n}x_1^{-1-1/r_1}\right) \\
&= \left(x_n^{1/r_n}x_1^{-1/r_1}\right)\left\{\frac{\dot{x}_n}{r_n x_n} - \frac{\dot{x}_1}{r_1 x_1}\right\} \\
&= \left(x_n^{1/r_n}x_1^{-1/r_1}\right)\left\{\left(\frac{a_{11}}{r_1} - \frac{a_{n1}}{r_n}\right)x_1 + \cdots + \left(\frac{a_{1n}}{r_1} - \frac{a_{nn}}{r_n}\right)x_n\right\}
\end{aligned}$$

Hence

$$x_n(t) = x_n(0)\left(\left(\frac{x_1(t)}{x_1(0)}\right)^{1/r_1}\exp\left\{\int_0^t \sum_{i=1}^n -\Omega_{n,i}x_i(\tau)\,d\tau\right\}\right)^{r_n}$$

where $\Omega_{k,i} = \frac{a_{ki}}{r_k} - \frac{a_{1i}}{r_1}$. Note that $\Omega_{n,i} > 0$ for $i = 1, \ldots, n$. Now $\sum_{i=1}^n \Omega_{n,i}x_i(\tau) \geq \epsilon \min_i \Omega_{n,i}$ (for $\tau \geq T_\epsilon$), and so since x_1 is bounded we must have $x_n(t) \to 0$ as $t \to \infty$. Similarly we find that

$$x_{n-1}(t) = x_{n-1}(0)\left(\left(\frac{x_1(t)}{x_1(0)}\right)^{1/r_1}\exp\left\{\int_0^t \sum_{i=1}^n -\Omega_{n-1,i}x_i(\tau)\,d\tau\right\}\right)^{r_{n-1}}. \tag{5.3}$$

We know that $\Omega_{n-1,i} > 0$ for $i = 1, \ldots, n-1$, but we do not know the sign of $\Omega_{n-1,n}$. However, we do know that $x_n(t) \to 0$ as $t \to \infty$. If $\Omega_{n-1,n} > 0$ then it is clear that $x_{n-1}(t) \to 0$ as $t \to \infty$. Otherwise, we know that given any $\theta > 0$, there is some T_θ such that for $t \geq T_\theta$ we have $0 < x_n(t) \leq \theta$. But then, for $\tau > T_\epsilon$

$$\begin{aligned}
\sum_{i=1}^n \Omega_{n-1,i}x_i(\tau) &= \Omega_{n-1,n}x_n(\tau) + \sum_{i=1}^{n-1}\Omega_{n-1,i}x_i(\tau) \\
&\geq \Omega_{n-1,n}x_n(\tau) + \left(\min_{1\leq i\leq n-1}\Omega_{n-1,i}\right)\sum_{i=1}^{n-1}x_i(\tau) \\
&= \left(\Omega_{n-1,n} - \left(\min_{1\leq i\leq n-1}\Omega_{n-1,i}\right)\right)x_n(\tau) + \left(\min_{1\leq i\leq n-1}\Omega_{n-1,i}\right)\sum_{i=1}^{n}x_i(\tau) \\
&\geq \left(\Omega_{n-1,n} - \left(\min_{1\leq i\leq n-1}\Omega_{n-1,i}\right)\right)x_n(\tau) + \left(\min_{1\leq i\leq n-1}\Omega_{n-1,i}\right)\epsilon.
\end{aligned}$$

Now choose $\theta > 0$ small enough so that for $\tau \geq \max\{T_\epsilon, T_\theta\}$ we have that

$$\sum_{i=1}^n \Omega_{n-1,i}x_i(\tau) \geq \eta \text{ for some } \eta > 0.$$

This shows from (5.3) that $x_{n-1}(t) \to 0$ as $t \to \infty$. We repeat the argument to show that $x_i(t) \to 0$ as $t \to \infty$ for $i = 2, \ldots, n$. Thus far we have shown that if $q \in \omega(x)$ then $q_i = 0$ for $i = 2, \ldots, n$. As $\omega(x)$ is connected and invariant, the only possibility is that (for $x \neq 0$) $\omega(x) = \{(\frac{a_{11}}{r_1}, 0, \ldots, 0)\}$ (since the origin is an unstable node). Thus we have shown (see [20])

Theorem 15 (Extinction in Competitive Lotka-Volterra) *If the inequalities (5.2) hold then* $\left(\dfrac{r_1}{a_{11}}, 0, \ldots, 0\right)$ *is globally attracting on* $\mathbb{R}^n_{>0}$.

5.1 Smale's Construction

One might be led to believe 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 [16]. Consider a more general model of **total competition**:

$$\dot{x}_i = x_i M_i(x) = F_i(x), \ (i = 1, \ldots, n), \tag{5.4}$$

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

$$\frac{\partial \dot{x}_i}{\partial x_j} = x_i \frac{\partial M_i}{\partial x_j} < 0 \ \text{ all } i, j \text{ if } x_i > 0. \tag{5.5}$$

Thus the Jacobian has negative off-diagonal elements. In other words competition for resources. The second condition says that there are finite resources and that the populations can not grow indefinitely. Notice that the strict inequality in (5.5) means that the Jacobian DF is irreducible (see page 50 in Chapter 6 for a definition of irreducibility).

Smale showed that examples of systems satisfying (5.4) 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.

5.1.1 The construction

We follow the presentation in [7]. Let $\Delta_1 = \{x \in \mathbb{R}^n_{\geq 0} : \|x\|_1 = 1\}$ be the standard 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 $h_i(x) = x_i g_i(x)$ 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 lower dimensional set and this severely restricts the possibilities. However, much more is possible when $n \geq 4$.)

5.2 Carrying Simplices

A bounded totally competitive system with the origin unstable has a unique invariant manifold that attracts the first quadrant minus the origin. We will give an example[1] of such a system where the invariant manifold can be explicitly found - it is a 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

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

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 $|x| > K$.

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

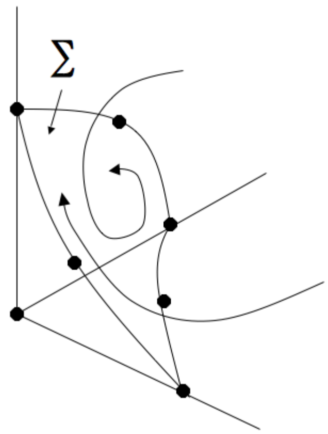

Figure 5.1: The Carrying Simplex attracts all orbits except the origin and contains any ω limit set and in particular all steady states except the origin.

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 [6]

Theorem 16 (The Carrying Simplex) *Given (5.4) 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 unit 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 5.2 we display 3 examples of the carrying simplex for totally competitive Lotka-Volterra systems. What is curious is that each of the surfaces seems to have Gaussian curvature of constant sign (see, for example, [21]).

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.

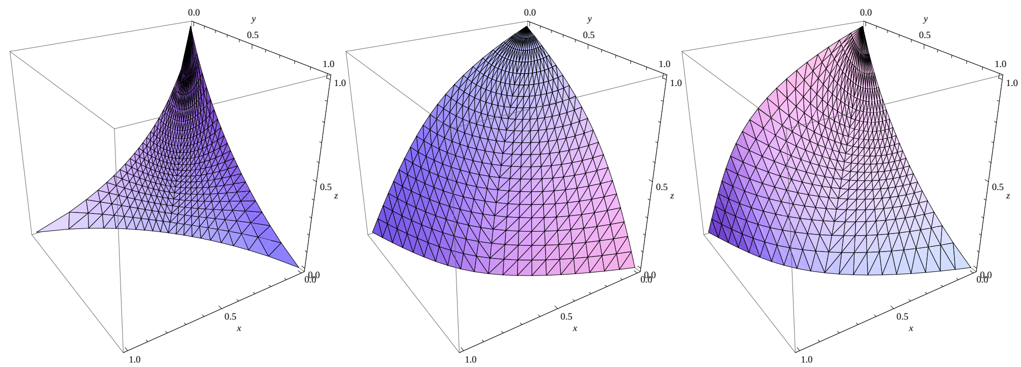

Figure 5.2: Examples of the carrying simplex for competitive the 3 dimensional Lotka-Volterra equations. From left to right the carrying simplex is (i) convex, (ii) concave and (iii) saddle-like.

5.2.1 Example: Periodic orbits in 3 Species Competition

We consider the nice example of an eventually periodic competitive system [13]

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

where $\alpha + \beta = 2$. Let

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

Then

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

Moreover

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

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?

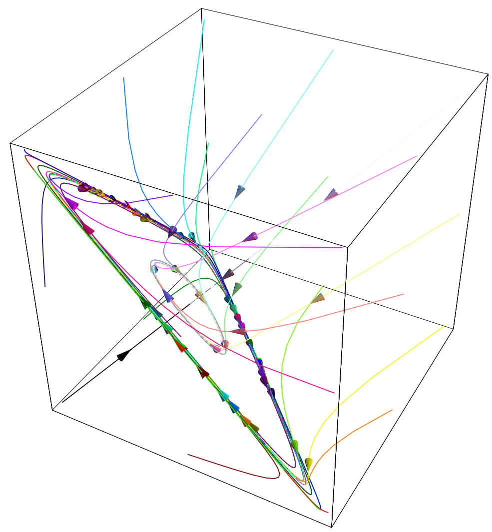

Figure 5.3: Periodic orbits in a model of May and Leonard [13]. Note the carrying simplex is the usual simplex in $\mathbb{R}^3_{\geq 0}$ and it clearly attracts all orbits apart from the origin.

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 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 get closed contours, i.e. the solutions are periodic. (This is the projection of the dynamics on Σ onto the $xy-$plane.)

Chapter 6

Monotone Lotka-Volterra systems

In this chapter I give a very brief introduction to monotone dynamical systems. This is a very rich topic and I have tried to make it more accessible by mostly specialising to cooperative dynamical systems on the strongly ordered space $\mathbb{R}^n$. The interested reader should consult the referenced papers, and in particular the very comprehensive [7], for details on more general orderings on Banach spaces, etc.

The main idea is that of a monotone flow which preserves a partial order. For the two species cooperative model the partial order on $\mathbb{R}^2_{\geq 0}$ that we used (implicitly) was

$$(x_1, x_2) \geq (y_1, y_2) \quad \text{if and only if } x_1 \geq y_1 \text{ and } x_2 \geq y_2.$$

Or, equivalently,

$$(x_1, x_2) \geq (y_1, y_2) \quad \text{if and only if } (x_1 - y_1, x_2 - y_2) \in \mathbb{R}^2_{\geq 0}.$$

Clearly not all points in $\mathbb{R}^2$ can be ordered with this order: $(0, 1)$ and $(1, 0)$ are unordered points in this ordering since $(1, 0) - (0, 1) = (1, -1) \notin \mathbb{R}^2_{\geq 0}$. When we work with cooperative vector fields F, that is DF has non-negative off-diagonal elements, we use the *standard ordering* $\geq$ defined by $v \geq u \Leftrightarrow v - u \in \mathbb{R}^n_{\geq 0}$. Let $\Omega \subseteq \mathbb{R}^n$ be an open set and $F : \Omega \to \mathbb{R}^n$ a C^1 vector field generating a semiflow $\varphi_t : \Omega \to \Omega$ via

$$\dot{x} = F(x).$$

Suppose also that the Jacobian matrix $DF(x)$ is *cooperative* (non-negative off-diagonal elements) for each $x \in \Omega$. Then if $u, v \in \Omega$ are points in $\mathbb{R}^n$ that are ordered via the standard ordering, one can show that

$$u \geq v \text{ and } t \geq 0 \Rightarrow \varphi(u, t) \geq \varphi(v, t).$$

More generally an order $\geq_K$ can be defined via $x \geq_K y \Leftrightarrow x - y \in K$ where $K \subset \mathbb{R}^n$ is a positive cone, i.e. $\mathbb{R}_{\geq 0} K \subseteq K$, $K + K \subseteq K$, $K \cap (-K) = \{0\}$. If a vector field F is not cooperative, it may be possible to find a cone K such that the flow φ generated by F satisfies

$$u \geq_K v \text{ and } t \geq 0 \Rightarrow \varphi(u,t) \geq_K \varphi(v,t).$$

There does not appear to be any prescription for finding a cone, if one exists, for a given system of odes.

6.0.2 Some Notation

Where possible we will work in some generality [7], working with a general metric space X that is also endowed with an order relation $R \subset X \times X$ that satisfies, for all $x, y, z \in X$,

1. Reflexive: $(x,x) \in R$;
2. Transitive: $(x,y) \in R$ and $(y,z) \in R \Rightarrow (x,z) \in R$;
3. Antisymmetric: $(x,y) \in R$ and $(y,x) \in R \Rightarrow x = y$.

The ordering R makes X into an *ordered space*. We also assume that the ordering on X is compatible with the metric of X: If $x_n \to x$ and $y_n \to y$ and $(x_n, y_n) \in R$ for all n then $(x,y) \in R$. That is to say that R is closed in the metric topology of X. For the standard ordering $\leq$ on $\mathbb{R}^n$ this is clearly true.

We will also use the following notation:

- $x < y \Leftrightarrow (x,y) \in R$ and $x \neq y$.
- $x \ll y \Leftrightarrow (x,y) \in \mathrm{int}R$,

where $\mathrm{int}R$ is the interior of R. The example that we will be using is R on $\mathbb{R}^n$ given by $(x,y) \in R \Leftrightarrow x_i \leq y_i$ for all $i = 1, \ldots, n$. We have:

- $x \leq y \Leftrightarrow x_i \leq y_i$ 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 $i = 1, \ldots, n$.

If X is an ordered set, will write $[x,y]$ for the set $\{z \in X : x \leq z \leq y\}$, which may be empty, and $[[x,y]]$ for the set $\{z \in X : x \ll z \ll y\}$.

Here we will assume that <u>X is *strongly ordered*</u>:

1. If $U \subset X$ is open and $x \in U$ then there exists $a, b \in U$ such that $x \in [[a,b]]$,
2. if $U \subset X$ is open and $a, b \in U$, $a \neq b$, then there exists $x \in U$ such that $x \in [[a,b]]$.

6.0.3 Suprema, infima, maxima and minima in ordered sets

Definition 17 (Supremum) *Let $S \subseteq X$. The supremum of S, if it exists, is the unique point $x \in X$ that satisfies: $x \geq S$, and whenever $y \in X$ is such that $y \geq S$ then $y \geq x$.*

Definition 18 (Infimum) *Let $S \subseteq X$. The infimum of S, if it exists, is the unique point $x' \in X$ that satisfies: $x' \leq S$, and whenever $y' \in X$ is such that $y' \leq S$ then $x' \geq y'$.*

It will also be useful to define maxima and minima in ordered sets:

Definition 19 (Maximum) *Let $S \subseteq X$ be any set. A maximal element of S is any point $s \in S$ such that if $x \in S$ and $x \geq s$ then $x = s$.*

Definition 20 (Minimum) *Let $S \subseteq X$ be any set. A minimal element of S is any point $s \in S$ such that if $x \in S$ and $x \leq s$ then $x = s$.*

For our chosen ordered space $(X, \leq) = (\mathbb{R}^n, \leq)$ we have the following result:

Lemma 9 *If $C \subset (\mathbb{R}^n, \leq)$ is non-empty and compact then it contains a maximum and minimum in C w.r.t. the ordering $\leq$. Moreover, C has a unique infimum and supremum in $\mathbb{R}^n$ w.r.t. the ordering $\leq$.*

(See for example figure 6.1.)

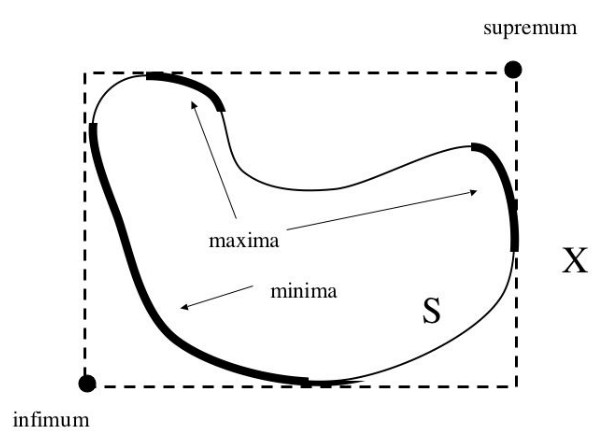

Figure 6.1: The supremum, infimum and maxima and minima w.r.t. $\leq$ for a compact subset S of $\mathbb{R}^2$.

6.0.4 Monotone semiflows

Let $\varphi : X \times \mathbb{R}_{\geq 0} \to X$ be a semiflow say as defined by a system of differential equations. We say that φ is

- Monotone if whenever $x \leq y$ then $\varphi(x, t) \leq \varphi(y, t)$ for all $t \geq 0$;
- Strongly monotone if whenever $x < y$ then $\varphi(x, t) \ll \varphi(y, t)$ for all $t > 0$.

6.0.5 Convergence of monotone flows

As might be expected, compactness will play a role here. We will need a result analogous to the convergence of bounded monotone sequences in $\mathbb{R}$:

Lemma 10 *Let K be a compact subset of X. Then every monotone sequence in K converges (to a point in K).*

This is clearly true for our ordered space $(\mathbb{R}^n, \leq)$, since we just look at the monotone convergence of each component.

For convenience we continue to take X to be strongly ordered. Then we have (e.g. [7]):

Lemma 11 (Convergence criterion) *Suppose that $\varphi : X \times \mathbb{R}_{\geq 0} \to X$ is a monotone semiflow. Suppose that the orbit of $x \in X$ has compact closure and that for some $T > 0$ we have $x \leq \varphi(x, T)$. Then the orbit of x is periodic. If the stronger condition $x \ll \varphi(x, T)$ holds, then the orbit of x converges: $\varphi(x, t) \to p$ as $t \to \infty$ for some steady state $p \in X$.*

Proof: First suppose that $x \leq \varphi(x, T)$. By monotonicity of φ, we have $\varphi(x, t) \leq \varphi(x, T + t)$ for all $t \geq 0$. In particular we have $\varphi(x, kT) \leq \varphi(x, (k+1)T)$ for all $k = 1, 2, \ldots$. Since the orbit is bounded, we have a bounded increasing sequence $\varphi(x, kT)$ which must converge to some $p \in \omega(x)$ by lemma 10. Now

$$\begin{aligned}\varphi(p, T + t) &= \varphi(\lim_{k\to\infty} \varphi(x, kT), T + t) \\ &= \lim_{k\to\infty} \varphi(\varphi(x, kT), T + t) = \lim_{k\to\infty} \varphi(\varphi(x, (k+1)T), t) = \varphi(p, t),\end{aligned}$$

which shows that $\varphi(p, \tau)$ is periodic in τ, period T. Now we must show that $\omega(x)$ is equal to this periodic orbit, $O^+(p)$. First we show $\omega(x) \subseteq O^+(p)$. If $q \in \omega(x)$ then $\exists\ t_i \to \infty$ with $\varphi(x, t_i) \to q$. Write $t_i = k_i T + r_i$ where $r_i \in [0, T)$ for each i. Then, choosing a subsequence such that $r_{i_s} \to r \in [0, T)$ we have

$$\varphi(x, t_{i_s}) = \varphi(\varphi(x, k_{i_s} T), r_{i_s}) \to \varphi(p, r) = q,$$

showing that $q \in O^+(p)$. On the other hand, $\varphi(x, kT) \to p$ as $k \to \infty$, so that $\varphi(x, kT + t) \to \varphi(p, t)$ and hence $\varphi(p, t) \in \omega(x)$. This shows that $w(x)$ consists of the periodic orbit through p.

Now suppose we have the stronger inequality $x \ll \varphi(x,T)$. Then since X is strongly ordered we may find a $z \in X$ such that $z \in [[x, \varphi(x,T)]]$, and there exists δ such that $\varphi(z,\tau) \in [[x, \varphi(x,T)]]$ for all $\tau \in [0,\delta)$. But now we have, by monotonicity,

$$\varphi(x, iT) \leq \varphi(\varphi(z,\tau), iT) \leq \varphi(\varphi(x,T), iT) = \varphi(\varphi(x,iT),T)$$

for $i = 1, 2, \ldots$, and the bounded increasing sequence $\varphi(x,iT) \to p$, and $\varphi(\varphi(x,iT),T) \to \varphi(p,T) = p$ as $i \to \infty$. Hence $\varphi(\varphi(z,\tau),iT) \to p$ as $i \to \infty$ for all $\tau \in [0,\delta)$. In particular, taking $\tau = 0$ gives $\varphi(z,iT) \to p$ as $i \to \infty$. Hence $\varphi(\varphi(z,\tau),iT) \to \varphi(p,\tau) = p$ as $i \to \infty$ for all $\tau \in [0,\delta)$. This shows that p is a steady state and thus $\omega(x) = O^+(p) = p$, as required. $\square$.

There are some interesting implications of this (see Corollary 2.4 in [4]):

Corollary 2 *A monotone semiflow does not have an attracting periodic orbit.*

Proof: Let $C \subset X$ be a periodic orbit which attracts a neighbourhood N of C. Pick any $p \in C$ and any $x \in N$ such that $x \gg p$. Since x is attracted to C, $\omega(x) = C$ and $p \in \omega(x)$. Therefore there exists $T > 0$ such that $\varphi(x,T)$ belongs to the neighbourhood $W = \{z \in X : z \ll x\}$. Since then $\varphi(x,T) \ll x$, lemma 11 implies that the periodic orbit $\omega(x)$ is a singleton: $C = \{p\}$ and C cannot be a non-trivial periodic orbit. $\square$.

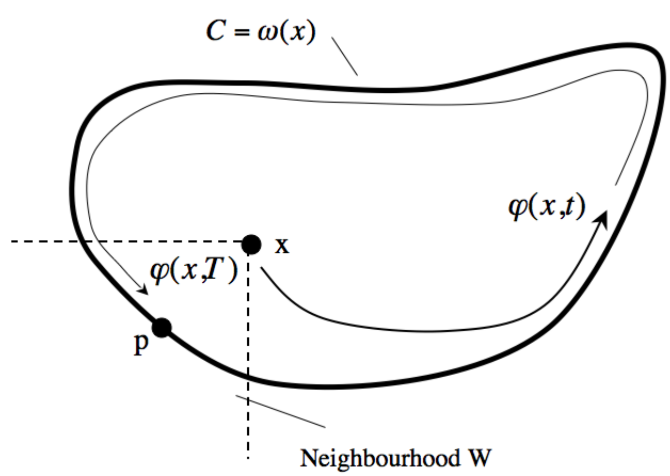

Figure 6.2: Periodic orbits of monotone flows cannot be attracting

We also have (Proposition 1.5 in [7]):

Lemma 12 (Non-ordering of periodic orbits) *A periodic orbit of a monotone semiflow is unordered.*

Proof: Let $O(x)$ be the periodic orbit under the flow φ and suppose that T is its minimal period. Suppose that z is another point on the orbit such that $x \leq z$ (i.e. is ordered w.r.t. x). Since $O(x)$ is compact, by lemma 9 there is a maximal element $M \in O(x)$, i.e. an M such that $M \geq z \geq x$. By monotonocity, $\varphi(M,t) \geq \varphi(z,t) \geq \varphi(x,t)$ and so for some t_0 we have, by periodicity, $\varphi(x,t_0) = M$ and hence $\varphi(M,t_0) \geq \varphi(x,t_0) = M$. By maximality, $M = \varphi(M,t_0)$ and hence t_0 is an integer multiple of T and we get $x = \varphi(x,t_0) = M$ and hence $x = z = M$. $\square$.

Thus a periodic orbit for a cooperative or competitive system is unordered. For example, the periodic orbits of the three-dimensional competitive system of Leonard and May [13], lie on the simplex in $\mathbb{R}^3_{\geq 0}$. Thus if (x,y,z) and (x',y',z') are any two points on a periodic orbit they satisfy $x+y+z = 1 = x'+y'+z'$. Since we are in $\mathbb{R}^3_{\geq 0}$ this can only happen if the two points are the same point.

6.0.6 Cooperative systems and monotonicity on $X \subseteq \mathbb{R}^n$

Now let us examine which differential equations give rise to monotone flows on $X \subseteq \mathbb{R}^n$. We recall

Definition 21 (Irreducibility) *An $n \times n$ matrix $A = ((a_{ij}))$ is irreducible if whenever $\{1,\ldots,n\}$ is expressed as the disjoint union of two non-empty subsets S, T then for every $i \in S$ there exists $k, j \in T$ such that $a_{ij} \neq 0$ and $a_{ki} \neq 0$.*

From a graph perspective, the directed graph with vertices $1,\ldots,n$ and with directed edges connecting i to j if $a_{ij} > 0$ is such that there is a path between any two vertices (i.e. is connected). The following Kamke theorem (see, e.g., [1], [5], [17]) gives conditions on the Jacobian matrix Df for the flow to be ordered.

Definition 22 (p-convexity) *A set $V \subseteq \mathbb{R}^n$ is $p-$convex if whenever $x \leq y$ for $x, y \in V$ then $\lambda x + (1-\lambda)y \in V$ for all $\lambda \in [0,1]$.*

So any convex set in $(\mathbb{R}^n, \leq)$ is also $p-$convex, but the reverse is not necessarily true as seen from figure 6.3. In what follows we will assume that the flow is defined for all $t \geq 0$. We will use the very useful trick: If $f : U \subset \mathbb{R}^n \to \mathbb{R}^1$ is C^1 on the open convex set U, then for $x, y \in U$,

$$f(x) - f(y) = \int_0^1 \frac{d}{ds} f(sx + (1-s)y)\, ds = \left(\int_0^1 Df(sx + (1-s)y)\, ds \right)(x - y).$$

Theorem 17 *Let $X \subseteq \mathbb{R}^n$ be $p-$convex and open and suppose that $f : X \to \mathbb{R}^n$ is a C^1 cooperative vector field, i.e. $Df(x)$ is a cooperative matrix for each $x \in X$. If φ is a semiflow generated by f then it is monotone. Moreover, when $Df(x)$ is also irreducible for each $x \in X$, φ is strongly monotone.*

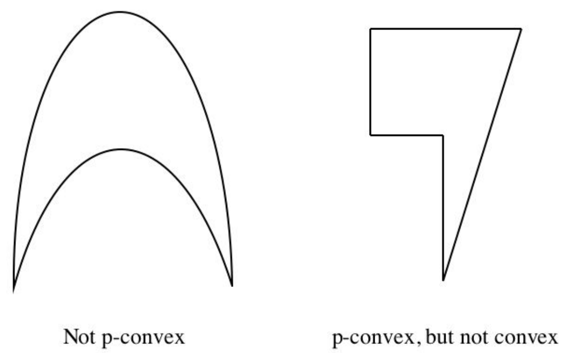

Figure 6.3: $p-$convexity of ordered sets (here using the standard order on $\mathbb{R}^2_{\geq 0}$)

Proof: Let $x, y \in X$. Fix $\tau > 0$. Then, supposing that $x \geq y$,

$$\begin{aligned} \frac{d\varphi}{dt}(x,t) - \frac{d\varphi}{dt}(y,t) &= f(\varphi(x,t)) - f(\varphi(y,t)) \\ \frac{d}{dt}(\varphi(x,t) - \varphi(y,t)) &= \int_0^1 Df(\theta\varphi(x,t) + (1-\theta)\varphi(y,t))\, d\theta\, (\varphi(x,t) - \varphi(y,t)). \end{aligned}$$

(Here we have used $p-$convexity for the integral.) Set $z(t) = \varphi(x,t) - \varphi(y,t)$. Then we have $\dot{z} = M(t)z$ where

$$M(t) = \int_0^1 Df(\theta\varphi(x,t) + (1-\theta)\varphi(y,t))\, d\theta$$

has non-negative off-diagonal entries. Now there exists $c > 0$ such that $cI + M(t)$ has non-negative entries everywhere and positive entries down the diagonal for all $t \in [0, \tau]$. Thus $\dot{z} + cz = (cI + M(t))z$ and so with $w = e^{ct}z$ we have $\dot{w} = (cI + M(t))w$, where $cI + M(t)$ has non-negative entries everywhere.

Now suppose that $x > y$, so that $x_i \geq y_i$ for all i, but some $x_k \neq y_k$ and that $Df(x)$ is irreducible for all $x \in X$. For each i we have,

$$\dot{w}_i(t) = cw_i(t) + \int_0^1 \left(\sum_{j=1}^{n} \frac{\partial f_i}{\partial x_j}(\theta\varphi(x,t) + (1-\theta)\varphi(y,t))w_j(t) \right) d\theta.$$

The integrand above is a continuous function of θ for each t and hence, for each i, there exists $\theta = \theta_i(t) \in [0,1]$ such that $\int_0^1 \sum_{j=1}^{n} \frac{\partial f_i}{\partial x_j}(\theta\varphi(x,t) + (1-\theta)\varphi(y,t))w_j(t)\, d\theta =$

$\sum_{j=1}^{n} \frac{\partial f_i}{\partial x_j}(\theta_i(t)\varphi(x,t)+(1-\theta_i(t))\varphi(y,t))w_j(t)$. With $m_{ij}(t) = \frac{\partial f_i}{\partial x_j}(\theta_i(t)\varphi(x,t)+(1-\theta_i(t))\varphi(y,t))$ we have

$$\dot{w}_i(t) = \sum_{j=1}^{n}(c\delta_{ij} + m_{ij}(t))w_j(t).$$

Suppose that at $t = t_0$ we have $w_i(t_0) = x_i(t_0) - y_i(t_0) = 0$ for $i \in S$ and $w_i(t_0) = x_i(t_0) - y_i(t_0) > 0$ for $i \in T$, where $S \cup T = \{1, \ldots, n\}$. Then we have

$$\dot{w}_i(t_0) = \sum_{j \in T} m_{ij}(t_0)w_j(t_0) \text{ for each } i \in S.$$

But $(m_{i1}(t_0), \ldots, m_{in}(t_0))$ is a row of Df and hence by irreducibility, there is a $j \in T$ such that $m_{ij}(t_0) > 0$ and since $w_j(t_0) > 0$ when $j \in T$ we have $\dot{w}_i(t_0) > 0$ for all $i \in S$. Thus for all $k = 1, \ldots, n$ we have $w_k(t) \gg 0$ for $t \in (t_0, \delta)$ for some $\delta > t_0$. Moreover, $\dot{w}(t) \gg 0$ for all $t \in (t_0, \delta)$ so $\delta = \infty$.

For the reducible case, consider $\dot{w} = (cI + \epsilon E + M(t))w$ where $\epsilon > 0$ is small and E is the $n \times n$ matrix of ones. Then if $x > y$, the solution w_ϵ to $\dot{w} = (cI+\epsilon E+M(t))w$ satisfying $w_\epsilon(0) = x - y > 0$ satisfies $w_\epsilon(t) \gg 0$ for all $t > 0$. Let $\epsilon \to 0$ to obtain $w(t) = \varphi(x,t) - \varphi(y,t) \geq 0$ for all $t \geq 0$, where $w(t)$ solves $\dot{w} = (cI + M(t))w$. $\square$

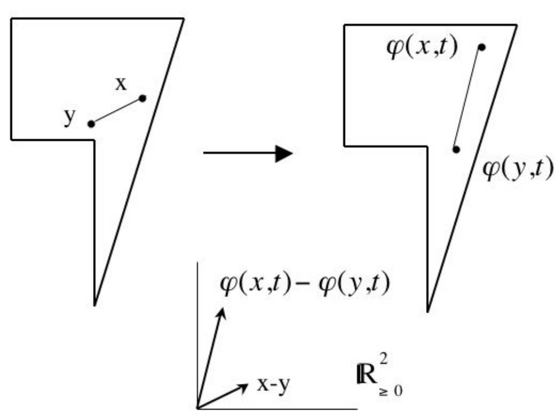

Figure 6.4: Cooperative flow preserves ordering of points

6.0.7 Example: Compartmental models

Consider a simple continuous time compartmental model: Let $p = (p_1, \ldots, p_n)$ be the system state and $r_{ij} \geq 0$ the flow rate from compartment i to compartment j.

Let Q be the matrix defined by

$$Q_{ij} = \begin{cases} -\sum_{k\neq i} r_{ik} & i = j \\ r_{ji} & i \neq j \end{cases}$$

Then Q has zero column sums and the states p (column vectors) evolve on a hyperplane according to $\dot{p} = Qp$. Notice that Q is a cooperative matrix and so the theorem says the flow on $\mathbb{R}^n$ is monotone. We can check this explicitly: the exact solution is $p(t) = e^{Qt}p_0$ (where $p_0 = p(0)$) and it is easy to see that if $p_0 \geq q_0$ then $\varphi(p_0, t) - \varphi(q_0, t) = P(t)(p_0 - q_0)$ where $P(t) = e^{Qt} \geq 0$ is a stochastic matrix. Thus the flow is monotone. When Q is irreducible, $P(t) \gg 0$ for $t > 0$ and the flow is strongly monotone.

The following result is known for global convergence when the steady state is unique (Theorem 3.3 in [4], Theorem 5 in [12]).

Theorem 18 *Let $X = \mathbb{R}^n$ or $\mathbb{R}^n_{\geq 0}$, and suppose that $\varphi : X \times \mathbb{R}_{\geq 0} \to X$ is a monotone semiflow with respect to the standard ordering $\leq$. Suppose further that X contains a unique steady state x^* and that every orbit in X has compact closure. Then every orbit converges to x^*.*

(This theorem applies under more general conditions, but its simple form here will suffice.)

Proof: Choose $x \in X$ and consider $\omega(x)$, which is non-empty and compact due to compact orbit closure. Since $\omega(x)$ is compact, lemma 9 gives the existence of a unique infimum $m = \inf \omega(x)$ and supremum $M = \sup \omega(x)$.

Let $q \in \omega(x)$ be arbitrary. Then $m \leq q$ and hence $\varphi(m, t) \leq \varphi(q, t)$ for each t by monotonicity. By invariance of $\omega(x)$, for each $t \geq 0$ we may find a $q_t \in \omega(x)$ such that $\varphi(q_t, t) = q$. Now $m \leq q_t$ and hence $\varphi(m, t) \leq \varphi(q_t, t) = q$ which, since m is the greatest lower bound of $\omega(x)$, gives $\varphi(m, t) \leq m$ for all $t \in \mathbb{R}_{\geq 0}$.

If $t_2 \geq t_1$, using that $\varphi(m, t) \leq m$ for $t \geq 0$, we have

$$\varphi(m, t_2) = \varphi(\varphi(m, t_2 - t_1), t_1) \leq \varphi(m, t_1),$$

so that the orbit $\varphi(m, t)$ is non-increasing in t and has compact closure. Now pick $p, q \in \omega(m)$. There exists $t_i, s_i \to \infty$ such that $\varphi(m, t_i) \to p$ and $\varphi(m, s_i) \to q$. Since $\varphi(m, t)$ is non-increasing choose a subsequence t'_i such that $t'_i \geq s_i$ and then $\varphi(m, t'_i) \leq \varphi(m, s_i)$. Take limits to get $p \leq q$. Similarly we get $q \leq p$ and hence $p = q$ and $\omega(m) = \{p\}$. Since $\omega(m)$ is invariant, p is a steady state.

Uniqueness of the steady state x^* implies that $\omega(m) = \{x^*\}$.

In a similar way we may show that $M \leq \varphi(M, t)$ and $\omega(M) = \{x^*\}$.

Thus we have that

$$\varphi(m, t_i) \leq m \leq \omega(x) \leq M \leq \varphi(M, s_i).$$

Taking the limit as $s_i, t_i \to \infty$ gives $\{x^*\} = \{m\} \leq \omega(x) \leq \{M\} = \{x^*\}$ and hence $\omega(x) = \{x^*\}$, as required. $\square$.

Remark R1:

If we do not know that the steady state is unique, we obtain that if $z \in \omega(x)$ then there exists steady states $x_1^*, x_2^* \in X$ such that, with $m = \inf \omega(x)$, $M = \sup \omega(x)$,

$$\omega(m) = \{x_1^*\} \leq z \leq \{x_2^*\} = \omega(M).$$

6.0.8 Identifying cooperative dynamical systems

A system can be sometimes be rendered cooperative by a change of coordinates. Consider a vector field f on an open set Ω. Suppose that $A = Df$ has the following properties:

- If $i \neq j$ then $\mathrm{sgn}(a_{ij})$ is constant in Ω;
- $a_{ij}a_{ji} \geq 0$ in Ω.

Now let Γ be the graph constructed as follows: Take vertices $1, \ldots, n$ and give an edge between vertices i, j a sign $\sigma_{ij} = \mathrm{sgn}(a_{ij})$ if there exists a $p \in \Omega$ such that $Df_{ij}(p) \neq 0$. Then

Theorem 19 *f is cooperative (competitive) w.r.t. some orthant in $\mathbb{R}^n$ if and only if every closed loop in Γ the number of negative labels σ is even (odd).*

This means that a bona-fide cooperative system (with Df having non-negative off-diagonal elements) can be constructed by change of coordinates.

6.1 Example: Global convergence in a cooperative system

This example, see [18], brings together some of the ideas developed in the lectures.

We consider a population model for n interacting species of the form

$$\dot{x}_i = x_i f_i(x) = F_i(x), \quad i = 1, \ldots, n. \tag{6.1}$$

where f is a C^1 function. We suppose that

T1 $Df(x)_{ij} \geq 0$ for $i \neq j$ and $x \in \mathbb{R}^n_{\geq 0}$;

T2 If $x \geq y \geq 0$ then $Df(y) \geq Df(x)$.

T3 $f(0) \gg 0$.

Condition T1 is pairwise cooperation between all the species. T2 means that cooperation diminishes as the populations grow, and condition T3 means that in the absence of the other $n-1$ species, the single species can survive. Then we have [18]

Theorem 20 *Consider the system defined by (6.1) together with the conditions T1-T3. Then*

H1 Equation (6.1) has at most one interior steady state;

H2 If (6.1) has no interior steady state then every interior orbit escapes to infinity;

H3 If (6.1) has an interior steady state x^* then it is asymptotically stable and $\varphi(x,t) \to x^*$ for all $x \in \mathbb{R}^n_{>0}$.

It is worth attaching a concrete example to this result: The cooperative Lotka-Volterra system (4.1) in Chapter 4 satisfies all the conditions of the theorem (T2 is satisfied as $Df = A$, the constant interaction matrix).

We will show that if an interior steady state exists then interior orbits are bounded, so that every omega limit set is compact and non-empty, and that any two distinct interior steady states cannot be ordered. Global convergence will then follow by remark $R1$ above: There must exist steady states p, q such that $p \leq \omega(x) \leq q$ (we will show that p, q must be interior) and hence by uniqueness of ordered interior steady states $p = q$ implies $\omega(x) = \{p\}$.

Just a few preliminary results before the main proof:

(1) For any $x \gg 0$ such that $f(x) \gg 0$ we have $\varphi(x,s) \gg x$ for small $s > 0$. To see this use

$$\varphi(x,s) - x = \int_0^1 \frac{d}{d\theta}\varphi(x,\theta s)\,d\theta = \int_0^1 f(\varphi(x,\theta s))\,d\theta s \gg 0$$

for small enough $s > 0$.

(2) $T2$ gives for $a \geq b$

$$Df(a) \leq \int_0^1 Df(\theta a + (1-\theta)b)\,d\theta \leq Df(b).$$

(3) $s(Df(x)) \geq s(Df(y))$ if $x \leq y$. This follows by application of the Perron-Frobenius theorem (Theorem 13, page 34) as follows (by sketch). Since $Df(x), Df(y)$ are cooperative, then $Df(x) + cI \geq 0$ and $Df(y) + dI \geq 0$ for large enough $c, d > 0$. Now let E be the n square matrix of ones and note that for all $\epsilon > 0$ the matrices $Df(x) + dI + \epsilon E$, $Df(y) + dI + \epsilon E$ are irreducible and positive. Thus by the Perron-Frobenius theorem there exists positive and simple eigenvalues $\lambda(\epsilon) + c, \mu(\epsilon) + d$ and eigenvectors $u(\epsilon) \gg 0, v(\epsilon) \gg 0$ such that $(Df(x) + \epsilon E)v(\epsilon) = \lambda(\epsilon)v(\epsilon)$ and $u(\epsilon)^T(Df(y) + \epsilon E) = \mu(\epsilon)u(\epsilon)^T$. But then

$$\begin{aligned} \lambda(\epsilon)u(\epsilon)^T v(\epsilon) &= u(\epsilon)^T(Df(x) + \epsilon E)v(\epsilon) \\ \mu(\epsilon)u(\epsilon)^T v(\epsilon) &= u(\epsilon)^T(Df(y) + \epsilon E)v(\epsilon) \end{aligned}$$

and so

$$(\lambda(\epsilon) - \mu(\epsilon))u(\epsilon)^T v(\epsilon) = u(\epsilon)^T (Df(x) - Df(y))v(\epsilon) \geq 0$$

for all $\epsilon > 0$. Since $u^T(\epsilon)v(\epsilon) > 0$, we must have $\lambda(\epsilon) \geq \mu(\epsilon)$ for all $\epsilon > 0$. Taking the limit as $\epsilon \to 0$ and using continuity of the dominant and simple eigenvalues as $\epsilon \to 0$, $\lambda(0) \geq \mu(0)$, from which the result follows.

(4) We show that if $x \gg 0$ then $\omega(x) \subset \mathbb{R}^n_{>0}$. So in particular, if an interior orbit converges to a steady state p then $p \in \mathbb{R}^n_{>0}$.

Given any $x \gg 0$, $\exists \alpha \in (0,1)$ such that $\xi = \alpha x \gg 0$ and $f(\xi) \gg 0$. Let $y \in \xi + \mathbb{R}^n_{\geq 0}$. Then whenever $y_i = \xi_i$ then

$$f_i(y) = f_i(\xi) + \int_0^1 Df_i(\theta y + (1-\theta)\xi)\, d\theta (y - \xi) > \sum_{j \neq i} \int_0^1 \frac{\partial f_i}{\partial x_j}(\xi + \theta u)(y_i - \xi_j)\, d\theta \geq 0.$$

Hence $f_i(y) > 0$. This means that $\dot{x}_i = x_i f_i(x) > 0$ at y and thus $\Omega = \xi + \mathbb{R}^n_{\geq 0}$ is forward invariant. Now $x \gg \xi$ and hence $\varphi_t(x) \gg \varphi_t(\xi) \geq \xi$ and hence if $p \in \omega(x)$ then $p \geq \xi \gg 0$.

Step 1: <u>If there is no interior steady state, interior orbits go to infinity.</u>

We show that if there is no interior steady state, all interior orbits escape to infinity [18]. Hence suppose that (6.1) has no interior steady state. If $y \in \mathbb{R}^n_{>0}$ is such that its orbit has finite interval of existence $[0, \eta(y))$ then necessarily $|\varphi(y,t)| \to \infty$ as $t \to \eta(y)-$. Otherwise, the forward flow from $y \in \mathbb{R}^n_{>0}$ exists for all time, and for sufficiently small $\tau > 0$, $f(\tau y) \gg 0$, and the forward flow from $x_\tau := \tau y$ also exists for all time (since, by monotonicity $\varphi(x_\tau, s) \leq \varphi(y, s)$ for all $s \geq 0$). We know that $\varphi(x_\tau, s) \gg x_\tau$ for small s and thus if the orbit through x_τ were bounded we could conclude by lemma 11 that it would converge to a steady state p. By item 4 above, this steady state p would have to belong to $\mathbb{R}^n_{>0}$, which contradicts that there is no interior steady state. Thus the orbit through x_τ must be unbounded. By the ordering $\varphi(x_\tau, s) \leq \varphi(y, s)$, this implies that $\varphi(y,t)$ is unbounded.

Step 2 <u>Uniqueness of ordered interior steady states.</u>

First we show that if p is an interior steady state it is stable. For we have

$$0 = f(p) = f(0) + \int_0^1 Df(\theta p)\, d\theta\, p.$$

But $Df(p) \leq \int_0^1 Df(\theta p)\, d\theta \leq Df(0)$ by $T2$. Hence $0 \gg -f(0) \geq Df(p)p$. Thus by lemma 6 on page 35 we see that $A = Df(p)$ must be stable (and thus, in particular, invertible). Now for uniqueness: Suppose that p, q are interior

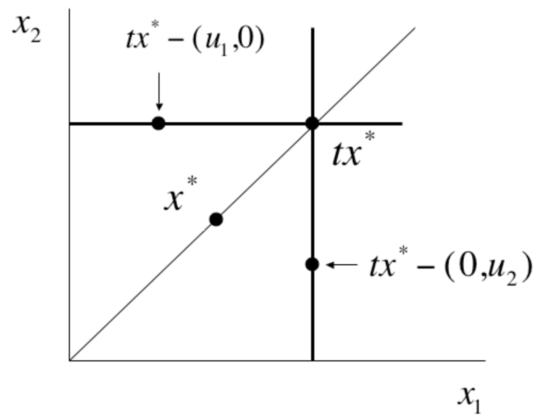

Figure 6.5: The hyperplanes passing through tx^*.

steady states such that $p \leq q$. Then $Df(q) \leq A := \int_0^1 Df(\theta p + (1-\theta)q)\,d\theta \leq Df(p)$ and so $s(A) \leq s(Df(p)) < 0$. Hence A is invertible and

$$0 = f(p) - f(q) = A(p-q) \Rightarrow p = q.$$

Step 3 <u>If there exists an interior steady state, all orbits are bounded.</u>

The function $g(s) = f(sx^*)$ has $g(0) = f(0) \gg 0$ and $g(1) = f(x^*) = 0$. Moreover, $g'(s) = Df(sx^*)x^*$. But then $g'(s_1) = Df(s_1x^*)x^* \leq Df(s_2x^*)x^* = g'(s_2)$ for $s_1 \geq s_2$. Hence g_i is concave for each i. It is now clear that for each i, $g_i(s) > 0$ for $s \in [0,1)$, and $g_i(s) < 0$ for $s > 1$.

Let $s > 1$ be given. Then

$$\begin{aligned} \varphi_t(sx^*) &= sx^* + \int_0^t \frac{d}{d\tau}\varphi_\tau(sx^*)\,d\tau \\ &= sx^* + \int_0^t f(\varphi_\tau(sx^*))\,d\tau \\ &\ll sx^* \end{aligned}$$

for t small enough. Since this is true for all $s > 1$, all orbits are bounded.

Now put it all together: If an interior steady state exists then all orbits in $\mathbb{R}^n_{>0}$ have compact closure. Let $x \gg 0$ and suppose $z \in \omega(x) \gg 0$ (which is nonempty by compact closure). Note that $m = \inf \omega(x) \gg 0$, $M = \sup \omega(x) \gg$

0, so that $\omega(m) \gg 0$ and $\omega(M) \gg 0$. By remark R1, there exists steady states p, q with $p \leq z \leq q$ and $p \gg 0, q \gg 0$. By uniqueness of the ordered interior steady states we must have $p = z = q$ and hence $\omega(x) = \{p\}$. $\Box$.

Bibliography

[1] W. A. Coppel. Stability and Asymptotic Behaviour of Ordinary Differential Equations. D. C. Heath, Boston, 1965.

[2] P. M. Cohn, Classic Algebra.Wiley 2000.

[3] P. Duarte, R. L. Fernandes, W. M. Olivia. Dynamics on the attractor of the Lotka-Volterra equations. *J. Diff Eqns* 149, 143–189 (1998).

[4] M. W. Hirsch. The dynamical systems approach to differential equations. *Bull. Am. Math. Soc.*, 11, No. 1, 1–64 (1984).

[5] M. W. Hirsch. Systems of Differential Equations that are Competitive or Cooperative II: Convergence almost everywhere. *SIAM J. Math. Anal.*, 16, No. 3, 423–439 (1985).

[6] M. W. Hirsch. Systems of differential equations which are competitive or cooperative: III. Competing species. *Nonlinearity*, 1, 51–71 (1988).

[7] M. W. Hirsch and H. L. Smith. Monotone Dynamical Systems. In Handbook of Differential Equations, Ordinary Differential Equations (second volume). Elsevier, Amsterdam, 2005.

[8] J. Hofbauer and K. Sigmund. Evolutionary Games and Population Dynamics. CUP 2002.

[9] B. S. Goh. Global Stability in Two Species Interactions. *J. Math Biol.*, 3, 313–318 (1976).

[10] B. S. Goh. Stability in Models of Mutualism. *The American Naturalist*, 113, No. 2, 261–275 (1979).

[11] G. W. Harrison. Global Stability of Food Chains. *The American Naturalist*, 113, No. 3, 455–457 (1979).

[12] P. De Leenheer, D. Angeli and E. D. Sontag. A tutorial on monotone systems-with an application to chemical reaction networks. *Proc. 16th Int. Symp. Mathematical Theory of Networks and Systems*, 2004, Leuven, Belgium.

[13] R. W. May and W. J. Leonard. Nonlinear aspects of competition between three species. *SIAM J. Applied Math*, 29, 243–253 (1975).

[14] J. E. Marsden and T. Ratiu. Introduction to Mechanics and Symmetry. Texts in Applied Mathematics Vol 17. Springer-Verlag, 1994.

[15] L. Perko. Differential Equations and Dynamical Systems (Third Edition). Texts in Applied Mathematics 7. Springer, 2001.

[16] S. Smale. On the Differential Equations of Species in Competition. *J. Math Biol.*, 3, 5–7 (1976).

[17] H. L. Smith. Monotone Dynamical Systems. AMS, Providence, R.I., 1995.

[18] H. L. Smith. On the asymptotic behavior of a class of deterministic models of competing species. *SIAM J. Appl. Math*, 46, No. 3, 368–375 (1986).

[19] V. Volterra. Leçons sur la Théoerie Mathématique de la Lutte pour la Vie. Gauthier-Villars et Cie., Paris, 1931.

[20] M. L. Zeeman. Extinction in Competitive Lotka-Volterra Systems. em Proc. Am. Math. Soc., 123, No. 1, 87–96 (1995).

[21] 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).