Chapter 3

Two species models

In this chapter we will study two species N_1 and N_2 occupying the same habitat and interacting, e.g. competing for resources, predation, symbiosis, etc. The general form of the models we will consider is

$$\begin{aligned} \frac{dN_1}{dt} &= F_1(t, N_1, N_2) \\ \frac{dN_2}{dt} &= F_2(t, N_1, N_2). \end{aligned} \tag{3.1}$$

The model (3.1) is a coupled pair of ordinary differential equations, which given initial data $N_1(0) - N_{10}, N_2(0) = N_{20}$ and reasonable assumptions on the regularity of F_1 and F_2 have a unique solution for all $t \geq 0$.

In many cases, F_1, F_2 will not depend explicitly on time, i.e. $F_1 = F_1(N_1, N_2)$ and $F_2 = F_2(N_1, N_2)$. Such systems are called **autonomous**. Thus the vector field (F_1, F_2) giving the velocity of a point (N_1, N_2) is fixed in time. To study such systems we can construct the **phase plane**, i.e. a picture of the solution trajectories mapped out by points $(N_1(t), N_2(t))$ as t varies over $(-\infty, +\infty)$. In particular we identify the steady state populations:

Definition 3 *The steady states of the system (3.1) are the solutions of* $dN_1/dt = 0 = dN_2/dt$*:*

$$\begin{aligned} F_1(N_1, N_2) &= 0 \\ F_2(N_1, N_2) &= 0. \end{aligned} \tag{3.2}$$

The lines upon which trajectories are horizontal or vertical have special names:

Definition 4 *We call* $F_1(N_1, N_2) = 0$ *and* $F_2(N_1, N_2) = 0$ *the* **nullclines** *of (3.1), i.e. they are the curves upon which either* $dN_1/dt = 0$ *or* $dN_2/dt = 0$*.*

The points where the nullclines (but not different branches of the same nullcline) cross are precisely the steady states. Each phase plane sketch includes the nullcllines, the steady states, and a collection of trajectories that start in varies parts of the plane. The individual trajectories are solutions of

$$\frac{dN_1}{dN_2} = \frac{F_1(N_1,N_2)}{F_2(N_1,N_2)},\ N_1(0) = N_{10}, N_2(0) = N_{20}. \tag{3.3}$$

In some cases the complete picture of the solutions of (3.1) can be established just by considering the nullclines, steady states and how the sign of dN_1/dN_2 changes as we go between regions demarked by nullclines. In some cases, however, this level of detail is insufficient, and we must study more carefully how (3.1) behaves near a steady state by considering its linearised form about that steady state.

1 Rules aiding construction of the phase plane

We list the following set of rules that help with the construction of the phase plane of the system (3.1):

1. trajectories cross vertically the nullcline

   $$F_1(N_1,N_2) = 0$$

   since here $dN_1/dt = 0$;

2. trajectories cross horizontally the nullcline

   $$F_2(N_1,N_2) = 0$$

   since here $dN_2/dt = 0$;

3. in regions enclosed by nullclines dN_1/dN_2 has constant sign, i.e. trajectories are either rising or falling;

4. trajectories can only go flat or vertical across nullclines;

5. steady states are where any branches of nullclines $F_1(N_1,N_2) = 0$ and $F_2(N_1,N_2) = 0$ cross.

In some cases further analysis (linear stability analysis of (3.1)) is required to further characterise the detailed behaviour near a steady state, such as, for example, to distinguish between simple non-oscillatory behaviour (e.g. tending directly to a steady state) or oscillatory behaviour (spiralling in to the steady state).

Example: Construction of the phase plane I

Suppose we are given

$$\begin{aligned} dN_1/dt &= F_1(N_1,N_2) = N_2 \\ dN_2/dt &= F_2(N_1,N_2) = -N_1. \end{aligned}$$

This is not a particularly realistic 2 species population model (it is, in fact, a model for a simple harmonic oscillator), but it serves as a simple example of how the phase plane can be reconstructed. The nullclines are

$$N_2 = 0,\ N_1 = 0,$$

i.e. the two axes of the plane. The nullclines cross at the unique steady state $(0,0)$. One may put a series of arrows at various points in the plane that point in the direction of (F_1, F_2) at those points. On $N_1 = 0$ where $\dot{N}_2 = 0$ these arrows point horizontally to the left when $N_2 > 0$ and horizontally to the right when $N_2 < 0$. Similarly on $N_2 = 0$ where $\dot{N}_1 = 0$ the arrows point vertically upwards when $N_1 > 0$ and vertically downwards when $N_1 < 0$. In the interior of the first quadrant $\dot{N}_1 < 0, \dot{N}_2 > 0$ so that the trajectory is moving upwards to the left, and so on. Notice that there is not enough information to know whether the actual trajectories spiral inwards, outwards or otherwise. However, for this simple example, the trajectories satisfy

$$\frac{dN_1}{dN_2} = -\frac{N_2}{N_1},$$

which is a separable ode and can be integrated immediately to yield

$$N_1(t)^2 + N_2(t)^2 = \text{ constant } = N_{10}^2 + N_{20}^2.$$

The solution trajectories are therefore all circles centred on the origin. The origin is neutrally stable, also known as a **centre**.

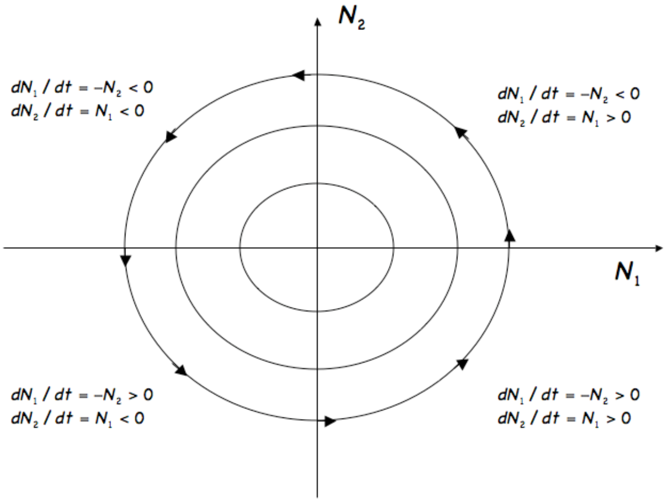

Figure 3.1: The phase plane for $dN_1/dt = -N_2$, $dN_2/dt = N_1$. The inequalities in each quadrant are for the interior of each quadrant, and indicate how N_1 and N_2 are changing along an orbit. Note that without knowing that $N_1^2 + N_2^2$ is conserved, we would not know that the orbits are circles - there is nothing in the sign of the velocities that guarantees that the orbits are not spirals.

2 Behaviour on the boundary of the first quadrant

The kind of ode population models considered in this course are part of a larger class of systems called *Kolmogorov systems*. Such systems take the form $\dot{x}_i = x_i f_i(x_1,\dots,x_n)$ for $i = 1,\dots,n$ where n is the number of species and the smooth functions f_i describe the per capita growth rate for the ith species. One of the key properties of such systems is that if at some time t^* we have $x_i(t^*) = 0$ for $i \in J$ (where $J \subset \{1,2,\dots,n\}$ is some nonempty set) then $x_i(t) = 0$ for all t and $i \in J$. In our planar models this means that trajectories starting on the axes stay on the axes, and interior trajectories cannot reach the axes in finite time. Hence to find what happens to a trajectory starting at $x_1 = 0$ we simply solve

$$\dot{x}_2 = x_2 f_2(0,x_2), \;\; x_2(0) \;\; \text{given},$$

which is a ode in one variable, as for the single species models of the first 2 chapters. Hence drawing the trajectories on each axes in the phase plane is a relatively simple task for planar Kolmogorov systems.

Example: The Lotka-Volterra competition equations

Recall the Logistic equation for a single speces:

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

Here ρ is the linear birth rate, and K the carrying capacity. For two species N_1, N_2 living in the same habitat, but not interacting, we simply have

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

The competition in these equations intraspecific (i.e. between the same species). When the species compete with each other (for nesting sites, food, etc.), the interspecific competition is detrimental to both specie's per capita growth rates. The simplest model is to say that the per capital growth rates decrease linearly with the density of the other species. The competition equations then become

$$\begin{aligned} \frac{dN_1}{dt} &= \rho_1 N_1\left(1 - \frac{N_1}{K_1} - \frac{c_1}{\rho_1}N_2\right) \\ \frac{dN_2}{dt} &= \rho_2 N_2\left(1 - \frac{N_2}{K_2} - \frac{c_2}{\rho_2}N_1\right), \end{aligned} \tag{3.4}$$

where $c_1, c_2 > 0$ measure the strength of the interspecific competition. To ease calculations, we first set $u_i = N_i/K_i$ for $i = 1,2$ and $a_{12} = c_1 K_2/\rho_1$, $a_{21} = c_2 K_1/\rho_2$. We also introduce a dimensionless time $\tau = \rho_1 t$ and set $\rho = \rho_2/\rho_1$. This gives the simpler set of equations (fewer parameters)

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1\left(1-u_1-a_{12}u_2\right) \\ \frac{du_2}{d\tau} &= \rho u_2\left(1-u_2-a_{21}u_1\right). \end{aligned} \tag{3.5}$$

Our first step is to locate the nullclines: These are

$$u_1 = 0 \quad \text{and} \quad 1-u_1-a_{12}u_2 = 0 \tag{3.6}$$

$$u_2 = 0 \quad \text{and} \quad 1-u_2-a_{21}u_1 = 0. \tag{3.7}$$

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]

1. $a_{12} > 1$ and $a_{21} > 1$, since then also $1-a_{12}a_{21} < 0$; OR
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. As we indicate in Figure 3.2 there are 4 cases to consider:

Case I $a_{12} < 1$ and $a_{21} < 1$;
Case II $a_{12} > 1$ and $a_{21} > 1$;
Case III $a_{12} < 1$ and $a_{21} > 1$;
Case IV $a_{12} > 1$ and $a_{21} < 1$.

Now let us determine what happens on the axes. Suppose first that initially $u_2 = 0$, so that the evolution is on the u_1 axis. We find $u_1(t)$ by solving the first equaton in (3.5) with $u_2 = 0$:

$$\dot{u}_1 = u_1(1-u_1).$$

This is just the Logistic equation with $\rho = 1, K = 1$. Provided $u_1(0) > 0$ we have $u_1(t) \to 1$ as $t \to \infty$. Similarly we find when $u_1(0) = 0$ then $\dot{u}_2 = \rho u_2(1-u_2)$ and hence $u_2(t) \to 1$ as $t \to \infty$ if $u_2(0) > 0$ (see Figure 3.3).

Let us consider the case I in detail (see figure 3.4). We have already dealt with the boundary behaviour. Consider an interior trajectory $A1$. It starts (as drawn, at least) in region $R1$ that lies below both nullclines $1-u_1-a_{12}u_2 = 0$ and $1-u_2-a_{21}u_1 = 0$ so that here $\dot{u}_1 > 0, \dot{u}_2 > 0$ and the trajectory therefore advances in the direction shown. This trajectory has positive gradient provided that it does not cross a nullcline. In fact, all trajectories in $R1$ have positive gradient. Following $A1$ we see that it cannot turn back on itself, and so must cross the nullcline where $\dot{u}_1 = 0$, whereby its gradient becomes negative since then, in $R3$ we

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[1] For simplicity here we do not consider the cases where $a_{12} = 1$ and/or $a_{21} = 1$.

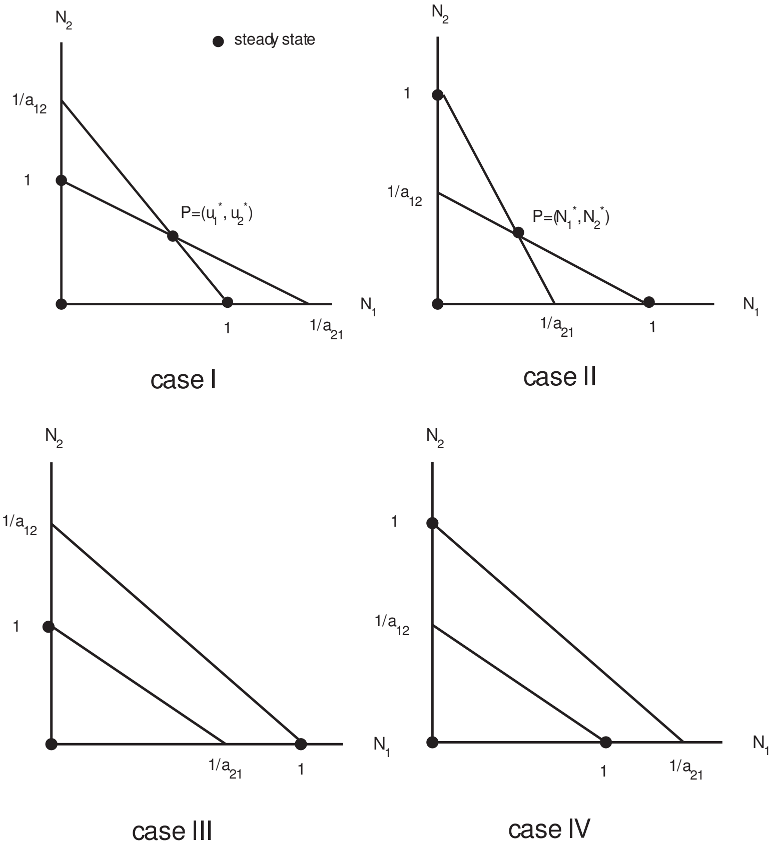


Figure 3.2: The possible nullcline crossings for the Lokta-Volterra model (3.4)

have $\dot{u}_1 < 0, \dot{u}_2 > 0$. The trajectory thus goes vertical across $\dot{u}_1 = 0$ and continues upwards to the left. It cannot leave $R3$, since to re-enter $R1$ is needs to cross it vertically and thus must go horizontal first, and it cannot enter $R2$ since trajectories cross the boundary between $R2$ and $R3$ downwards. Hence $A1$ ends at the interior steady state. A similar argument works for $A2$. In $R3$ the trajectories are above the nullclines $1 - u_1 - a_{12}u_2 = 0$ and $1 - u_2 - a_{21}u_1 = 0$ so that here $\dot{u}_1 < 0, \dot{u}_2 < 0$. $A2$ enters from $R2$ into $R3$ where it is then trapped and must end at the interior steady state. After some practice, it is possible to draw the trajectory directions by noting their directions on the nearby boundary. We can thus construct sketches for the phase planes in each of these 4 cases:

Case I $a_{12} < 1$ and $a_{21} < 1$;
The steady state P attracts all interior trajectories. The remaining 3 steady states are unstable.

Case II $a_{12} > 1$ and $a_{21} > 1$;
The steady state P is unstable. The steady state $(0,0)$ is unstable, and both $(1,0)$ and $(0,1)$ are stable. A separatrix splits the phase plane into two regions; above the seperatrix interior trajectories go to the steady state $(1,0)$ and below they go to the steady state $(0,1)$

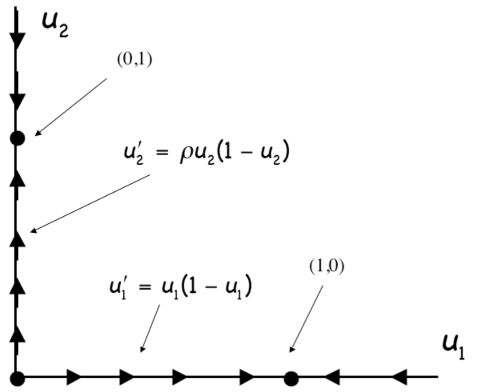


Figure 3.3: The trajectories on the boundary for the phase plane of the Lokta-Volterra model (3.4). These trajectories stay on the axes and tend to the normalised carrying capacities if the initial population is not at the origin.

Case III $a_{12} < 1$ and $a_{21} > 1$;
There is no 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 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 tends (globally, i.e. whatever the initial populations are) to a finite steady state. In particular there can be no population explosion or total extinction, nor oscillations.

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 coexist stably, but at lower populations than their respective carrying capacities. Thus although the species may coexist, the price that they pay for competing with each other is that they do not reach the population density that they would have achieved (i.e. their carrying capacity) with the other species absent;

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;

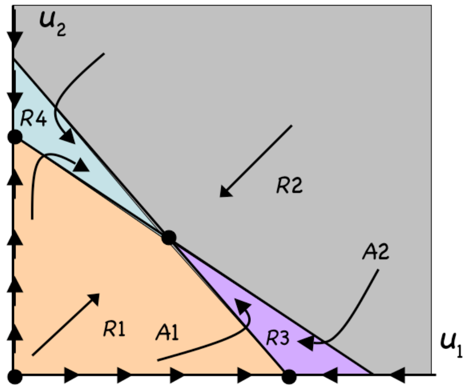


Figure 3.4: Building the phase plane for case I of the competition model (3.4). The (non-zero) nullclines divide the first quadrant into 4 regions $R1 - R4$. In each region, the trajectories are curves where the gradient has constant sign. The direction so trajectories can be determined by continuation from the boundaries.

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 is globally stable, the species with the strongest competition always drives the other to extinction.

3 Predator-Prey systems

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

1. in the absence of predators the per capita prey growth rate was constant, but fell of linearly as a function of predator population when predation was present;
2. in the absence of prey the per capita growth rate of the predator was contsant (and -ve), and increased linearly with the prey population when prey was present.

Thus

$$\begin{aligned} \frac{1}{N}\frac{dN}{dt} &= a - bP \\ \frac{1}{P}\frac{dP}{dt} &= cN - d \end{aligned} \tag{3.8}$$

where $a, b, c, d > 0$ are constants. It turns out that this model has an explicit integration. We find that

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

or

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

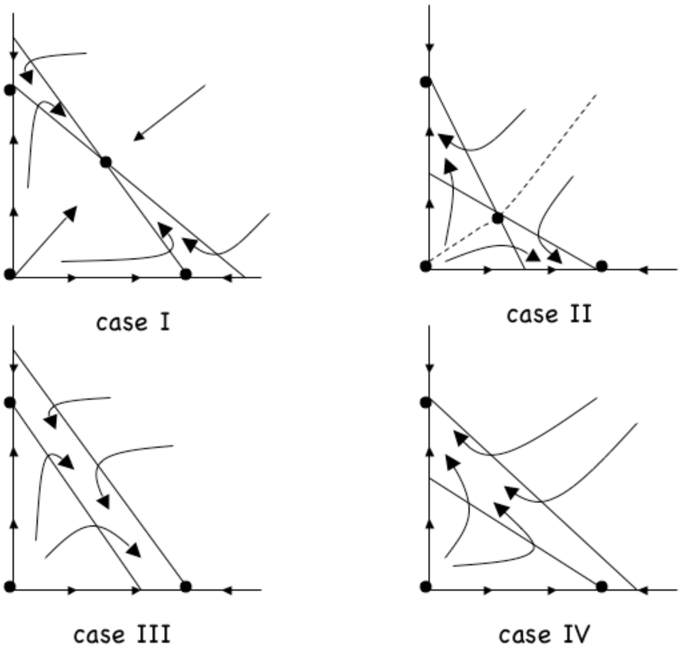


Figure 3.5: The 4 topologically distinct phase planes for the Lokta-Volterra model (3.4)

If we set

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

then all trajectories $(N(t),P(t))$ evolve so that $H(N(t),P(t)) = H(N(0),P(0)) =$ constant , i.e they are the projections of the the level curves of H. Now we claim that H is a concave function. Note that

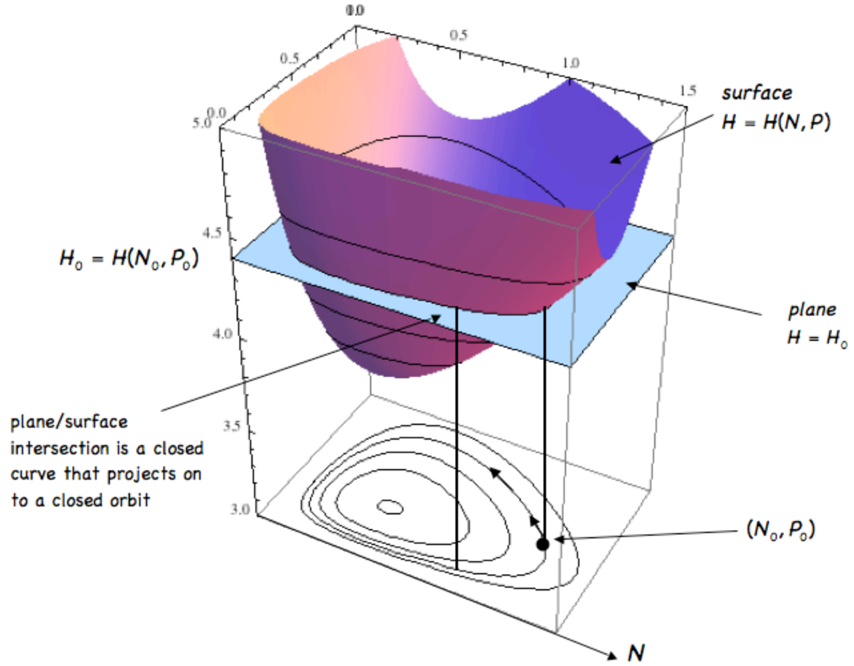
$$H_{NN} = d/N^2,\ H_{PP} = a/P^2,\ H_{NP} = H_{PN} = 0,$$

so that $H_{NN}H_{PP} - H_{NP}^2 = ad/(NP)^2 > 0$ and $H_{NN} > 0, H_{PP} > 0$, and hence H is convex. It is strictly convex for $NP > 0$. The minimum of H occurs where $\nabla H = 0$, i.e. where

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

Notice that this corresponds to the unique steady state of the system (3.8). Since H is strictly convex with a unique minimum in the positive quadrant, every trajectory must be a closed curve. Thus the orbits are a one-parameter (the value of H) set of closed curves starting at the steady state.

The Lokta-Volterra equations are actually canonically Hamiltonian (in appropriate coordinates) and so are not structurally stable. This means that a small change in the model will not typically lead to another Hamiltonian system, nor one where the phase plane is topologically equivalent. In general we will end up



plane/surface intersection is a closed curve that projects on to a closed orbit

Figure 3.6: Orbits for the classic predator-prey model. The orbits are the level sets of H, i.e. each orbit is a projection of the intersection of a plane $H = H_0$ with the surface $H = H(N,P)$. NB: This figure, and many of the figures in the notes were produced using the CurvesGraphics Mathematica package by Gianluca Gorni, Department of Mathematics and Computer Science, University of Udine, Italy.

with a dissipative system. For a biological system life is the constant struggle against increasing entropy where irreversible processes play an important role. In this light, a Hamiltonian system cannot model a 'living' system. There are several points of criticism worth noting for the Volterra-Lokta model:

1. There is no possibility of either population being driven to extinction;
2. Changing the birth and death rates does nothing but change the period of the oscillation - i.e. noone can dominate;
3. For certain ecological conditions (fitness of species, etc.) one would expect one species to win regardless of initial conditions, but this does not happen.

We will now take a digression into *Linear stability analysis* for pairs of autonomous ODEs.

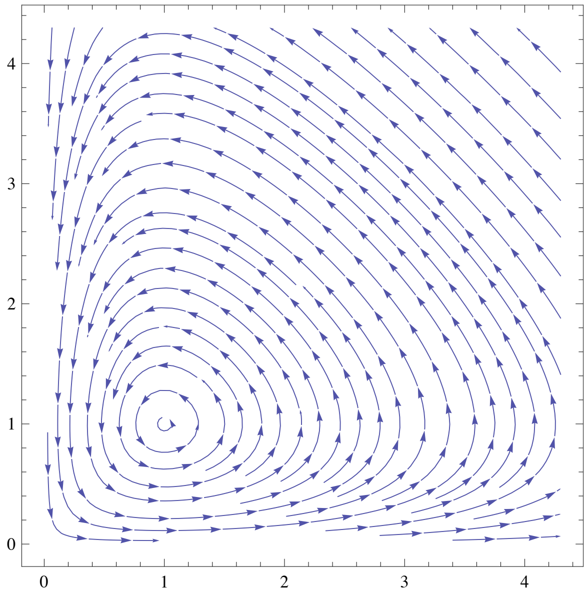


Figure 3.7: Nested periodic orbits for the classic predator-prey model. Boundary trajectories are not shown. All interior trajectories a periodic and enclose the unique interior steady state at $(1,1)$.

3.1 Digression: Linear stability analysis of planar odes

In many of the models we meet in the course, we will need to study the behaviour of trajectories close to steady states for the system

$$\begin{aligned} \frac{dx}{dt} &= f(x,y) \\ \frac{dy}{dt} &= g(x,y). \end{aligned} \tag{3.9}$$

We assume that $P=(a,b)$ is a steady state of (3.9). Thus

$$f(a,b)=0=g(a,b). \tag{3.10}$$

Consider the evolution of a trajectory close to P, and write $x(t)=a+X(t)$ and $y(t)=b+Y(t)$. We may expand in (3.9) using the Taylor expansion:

$$\begin{aligned} \frac{dX}{dt} &= f(a,b)+f_x(a,b)X+f_y(a,b)Y+\cdots \\ \frac{dY}{dt} &= g(a,b)+g_x(a,b)X+g_y(a,b)Y+\cdots. \end{aligned}$$

Using (3.10), this becomes

$$\begin{aligned}\frac{dX}{dt} &= f_x(a,b)X + f_y(a,b)Y + \cdots \\ \frac{dY}{dt} &= g_x(a,b)X + g_y(a,b)Y + \cdots .\end{aligned}$$

Close to P, $|X(t)|, |Y(t)| \ll 1$ this system is well-approximated by the linearised version obtained by neglecting second order terms in X, Y:

$$\begin{aligned}\frac{dX}{dt} &= f_x(a,b)X + f_y(a,b)Y \\ \frac{dY}{dt} &= g_x(a,b)X + g_y(a,b)Y.\end{aligned} \tag{3.11}$$

Notice that since we are neglecting higher order than linear terms, the linear approximation will only potentially give a good indication of the full nonlinear system while $X(t), Y(t)$ remain small.

Now let $\mathbf{X}(t) = (X(t), Y(t))^T$ and

$$M = \begin{pmatrix} f_x(a,b) & f_y(a,b) \\ g_x(a,b) & g_y(a,b) \end{pmatrix}.$$

Then (6.12) can be rewritten in matrix form:

$$\frac{d\mathbf{X}(t)}{dt} = M\mathbf{X}(t). \tag{3.12}$$

This has steady state $(0,0)$ (which corresponds to $(x,y) = (a,b)$). For a trajectory of the linearised system (3.12) starting at $\mathbf{X}(0) = \mathbf{X}_0$,

$$\mathbf{X}(t) = \exp(Mt)\mathbf{X}_0.$$

If M has two distinct eigenvalues λ_1, λ_2 with corresponding eigenvectors $\mathbf{v}_1, \mathbf{v}_2$ then

$$\mathbf{X}(t) = \alpha e^{\lambda_1 t}\mathbf{v}_1 + \beta e^{\lambda_2 t}\mathbf{v}_2, \tag{3.13}$$

where α, β are defined by the decomposition $\mathbf{X}_0 = \alpha\mathbf{v}_1 + \beta\mathbf{v}_2$ (using linear independence of $\mathbf{v}_1, \mathbf{v}_2$). When the two eigenvalues are equal (and therefore real) we have

$$\mathbf{X}(t) = e^{\lambda t}(\mathbf{X}_0 + ct\mathbf{v}) \tag{3.14}$$

for some real c (which may be zero).

To find the (local) stability of the steady state (a,b) we examine the dynamics of (3.12) which has solution (3.13). If (a,b) is stable then for small $\mathbf{X}_0$, the solution $\mathbf{X}(t)$ will eventually decay to the origin $(0,0)$ and this happens, according to (3.13), when both eigenvalues have negative real parts.

Let us list the various possibilities for behaviour near a steady state

1. $\lambda_1 \neq \lambda_2 \in \mathbb{R}$
    (a) $\lambda_1 < \lambda_2 < 0$ - stable node.

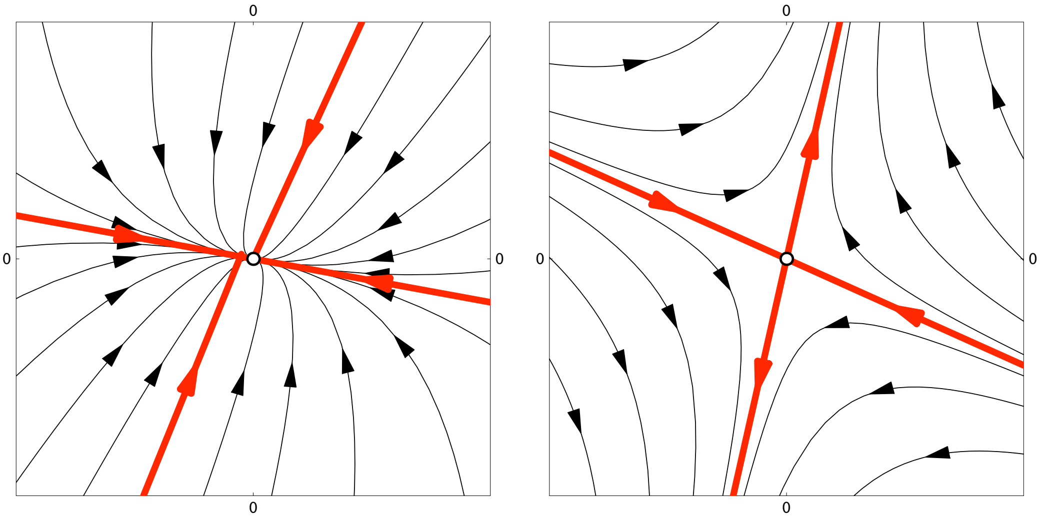


Figure 3.8: Linear stability for real eigenvalues: (i) $\lambda_1, \lambda_2 < 0$ (stable node) and (ii) $\lambda_1\lambda_2 < 0$ (saddle). The thick (red) lines are in the direction of the eigenvectors.

(b) $\lambda_1 > \lambda_2 > 0$ - unstable node.

(c) $\lambda_1\lambda_2 < 0$ - saddle (unstable)

(The reader may wish to ask themselves what happens when $\lambda_1\lambda_2 = 0$)

2. Complex eigenvalues
Then $\lambda_1 = \mu + iw, \lambda_2 = \mu - iw$ and

$$\mathbf{X}(t) = \Re\{e^{\mu t}(\alpha \mathbf{v}_1 e^{iwt} + \beta \mathbf{v}_2 e^{-iwt})\}$$

Hence we have spirals. If $\mu < 0$ the trajectories go to the steady state (stable spiral), for $\mu > 0$ they leave (unstable spiral). When $\mu = 0$ the linearised system gives concentric ellipses (but caution: we need to consider the nonlinear terms to get true picture as this linear system is not structurally stable).

3. $\lambda_1 = \lambda_2$ Now the Jordan form of M is

$$\begin{pmatrix} a & 0 \\ b & a \end{pmatrix}.$$

There are two cases:

(a) $b = 0$
Then we have what is known as a ‘star’ - all trajectories approach the origin along straight lines (all lines through origin are eigenvectors) when $a < 0$, and leave origin when $a > 0$.

(b) $b \neq 0$

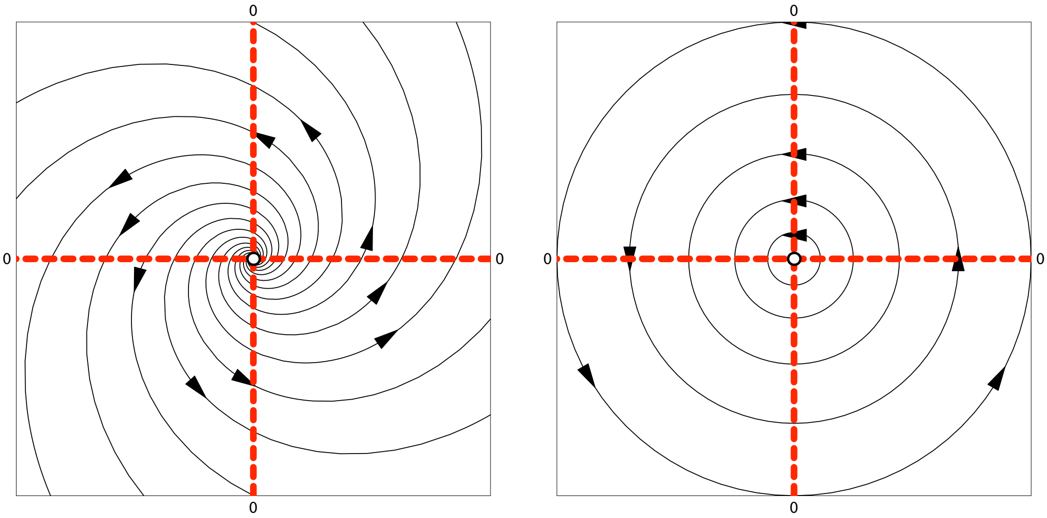


Figure 3.9: Linear stability for complex eigenvalues: (i) $\lambda = \mu \pm iw, \mu > 0$ (unstable spiral) and (ii) $\lambda = \pm iw$ (centre).

Then there is only one linearly independent eignevector and we have behaviour as shown in Figure 4.12).

The following lemma is very useful when determining the nature of eigenvalues. Recall that the trace of a matrix is the sum of its diagonal elements.

Lemma 1 *Let M be a 2×2 matrix with eigenvalues λ_1, λ_2. Then*

$$\lambda_1 + \lambda_2 = \textit{Trace}\, M, \tag{3.15}$$

$$\lambda_1 \lambda_2 = \det M. \tag{3.16}$$

Proof: Let $M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$. Then the characteristic equation for the eigenvalues λ reads $\det(M - \lambda I) = 0$ which becomes

$$\lambda^2 - (a+d)\lambda + (ad - bc) = 0,$$

or equivalently

$$\lambda^2 - \text{Trace}\, M\lambda + \det M = 0.$$

On the other hand, if $\lambda^2 - \text{Trace}\, M\lambda + \det M$ has roots λ_1, λ_2 then $\lambda^2 - \text{Trace}\, M\lambda + \det M = (\lambda - \lambda_1)(\lambda - \lambda_2)$. Multiplying out the last product and comparing coefficients in λ gives the desired formulae.

Corollary 1 *Let $S = (a,b)$ be a steady state of some planar ode and M the 2×2 real stability matrix at (a,b).*

1. *If $\det M < 0$ then M has eigenvalues of opposite sign and S is a saddle;*

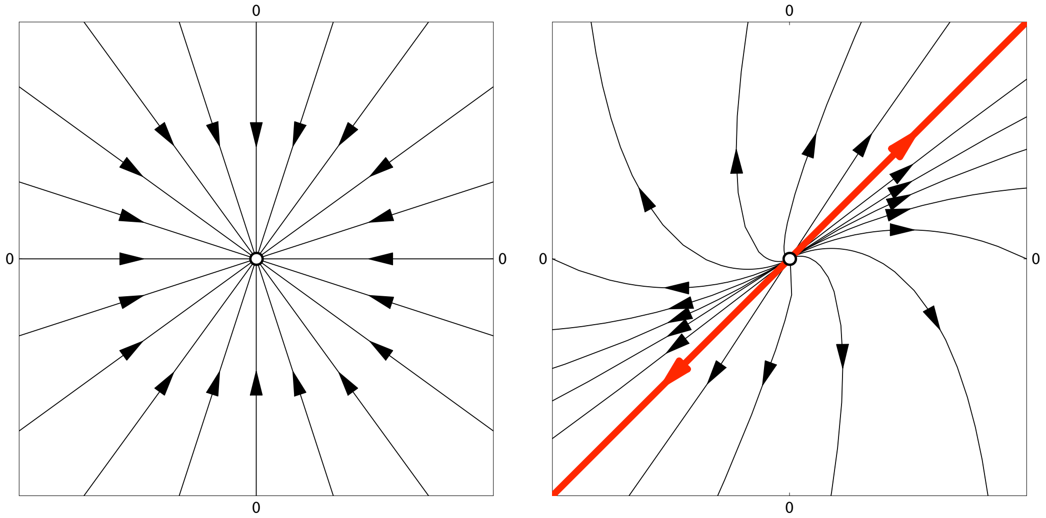


Figure 3.10: Linear stability for equal eigenvalues: (i) Jordan form $\begin{pmatrix} a & 0 \\ 0 & a \end{pmatrix}$ and (ii) Jordan form $\begin{pmatrix} a & 0 \\ b & a \end{pmatrix}$ $(b \neq 0)$.

2. *If* $\det M > 0$ *and Trace* $M < 0$ *then the real parts of the eigenvalues of* M *are negative and* S *is locally stable.*
3. *If* $\det M > 0$ *and Trace* $M > 0$ *then the real parts of the eigenvalues of* M *are positive and* S *is unstable.*
4. *If* $\det M > 0$ *and* $(\text{Trace } M)^2 \geq 4\det M$ *then* S *is a node and if* $(\text{Trace } M)^2 < 4\det M$ *then* S *is a spiral.*

1 Linear stability analysis of the LV competition model

We will now demonstrate how the above linear stability analysis works with the competition model:

$$
\begin{aligned}
\frac{du_1}{d\tau} &= f(u_1,u_2) = u_1\,(1-u_1-a_{12}u_2) \\
\frac{du_2}{d\tau} &= g(u_1,u_2) = \rho u_2\,(1-u_2-a_{21}u_1)
\end{aligned}
\tag{3.17}
$$

The first thing we have to do is compute the matrix

$$
M = \begin{pmatrix} f_{u_1} & f_{u_2} \\ g_{u_1} & g_{u_2} \end{pmatrix}.
$$

We find that at the point (u_1,u_2) that

$$
M_{(u_1,u_2)} = \begin{pmatrix} 1-u_1-a_{12}u_2-u_1 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-u_2-a_{21}u_1)-\rho u_2 \end{pmatrix}.
\tag{3.18}
$$

There are always the 3 steady states $(0,0)$, $(1,0)$ and $(0,1)$. There may be a fourth and interior steady state.

1. $(u_1,u_2)=(0,0)$. Here
$$M_{(0,0)}=\begin{pmatrix}1 & 0\\ 0 & \rho\end{pmatrix}.$$
Since the eigenvalues of a triangular matrix are its diagonal elements, we see that the eigenvalues of the linear stability matrix at the origin are $1,\rho$. Since these are both positive we conclude that $(0,0)$ is an unstable node.

2. $(u_1,u_2)=(1,0)$. Here
$$M_{(1,0)}=\begin{pmatrix}-1 & -a_{12}\\ 0 & \rho(1-a_{21})\end{pmatrix}.$$
Thus the eigenvalues are $-1,\rho(1-a_{21})$ and hence $(1,0)$ is a stable node if $a_{21}>1$ and a saddle if $a_{21}<1$.

3. $(u_1,u_2)=(0,1)$. Here
$$M_{(0,1)}=\begin{pmatrix}1-a_{12} & 0\\ -\rho a_{21} & -\rho\end{pmatrix}.$$
Thus the eigenvalues are $1-a_{21},-\rho$ and hence $(0,1)$ is a stable node if $a_{12}>1$ and a saddle if $a_{12}<1$.

Finally, when the interior steady state (u_1^*,u_2^*) exists, so that $a_{12},a_{21}>1$ or $a_{12},a_{21}<1$, we obtain
$$M_{(u_1^*,u_2^*)}=\begin{pmatrix}(1-u_1^*-a_{12}u_2^*)-u_1^* & -a_{12}u_1^*\\ -\rho a_{21}u_2^* & \rho(1-u_2^*-a_{21}u_1^*)-\rho u_2^*\end{pmatrix}.$$
Now since (u_1^*,u_2^*) is an interior steady state $1-u_1^*-a_{12}u_2^*=0=1-u_2^*-a_{21}u_1^*$ and hence the bracketed expressions in the last matrix vanish and we have
$$M_{(u_1^*,u_2^*)}=\begin{pmatrix}-u_1^* & -a_{12}u_1^*\\ -\rho a_{21}u_2^* & -\rho u_2^*\end{pmatrix}. \tag{3.19}$$
Notice that we left M in the form (3.18) in order to obtain the simple form of the stability matrix at the the interior steady state in (3.19). In order to determine the nature of the eigenvalues of $M_{(u_1^*,u_2^*)}$ we use Corollary 1. We see that Trace $M=-u_1^*-\rho u_2^*<0$ and $\det M=\rho u_1^*u_2^*(1-a_{12}a_{21})$. Hence if $a_{12}<1,a_{21}<1$ then S is locally stable (we do not bother to distinguish between a focus and a spiral), and if $a_{12}>1,a_{21}>1$ then S is a saddle.

These calculations can be checked by referring back to the phase plane plots in Figure 3.5.

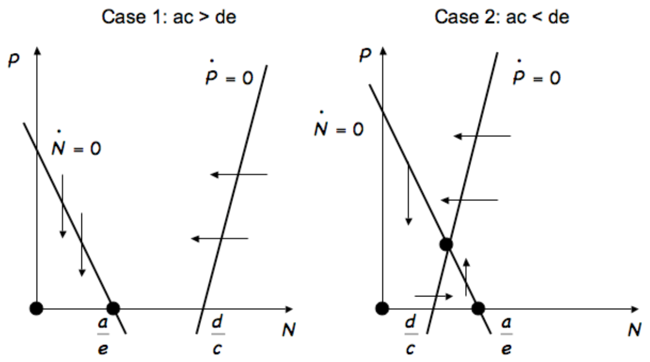


Figure 3.11: The possible nullcline crossings for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)).

Example: Predator-Prey with intraspecific competition

Now we consider the classic Predator-Prey model with additional interactions, namely intraspecific competition.

$$\begin{aligned} \dot{N} &= N(a - eN - bP) &= F(N,P) \qquad (3.20)\\ \dot{P} &= P(-d - fP + cN) &= G(N,P). \qquad (3.21) \end{aligned}$$

Thus we have the original predator-prey model with the intraspecific competition terms $-eN^2$ and $-fP^2$ added. Recall that in the original model $e = 0, f = 0$ and we obtain a continuum of periodic orbits around the interior steady state. What happens when $e > 0, f > 0$?

Let us consider the nullclines. These are solutions to:

$$\dot{N} = 0: \quad N = 0 \text{ or } a - eN - bP = 0,$$

$$\dot{P} = 0: \quad P = 0 \text{ or } -d + cN - fP = 0.$$

The two possible cases are plotted in Figure 3.11. In case 1, there are only two steady states $(0,0)$ and $(a/e,0)$, but when $ac > de$ there is a third non-zero steady state, say (N^*,P^*).

On the boundary $P = 0$ we have $\dot{N} = N(a - eN)$ so the trajectories tend to $N = a/e$ if $N(0) \neq 0$. On $N = 0$, we have $\dot{P} = -P(d + fP) \leq 0$ with equality if and only if $P = 0$, so that trajectories tend to $P = 0$.

In case 1, it is possible to fill in the trajectories to complete the phase space plot. However, in case 2, while it is clear that the trajectories near the non-zero steady state cycle around the steady state, it is not obvious whether these trajectories are closed paths or spirals (or something else?). To complete the phase plots we need to determine the correct behaviour of the trajectories near to steady states, i.e. perform the linear stability analysis.

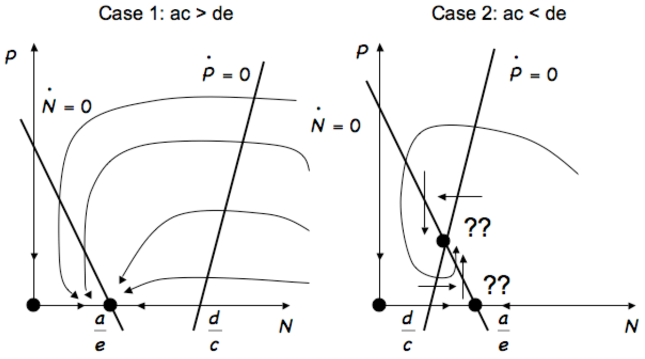


Figure 3.12: The possible phase space plots for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)).

For the stability matrix we obtain

$$M = \begin{pmatrix} F_N & F_P \\ G_N & G_P \end{pmatrix} = \begin{pmatrix} (a - eN - bP) - eN & -bN \\ cP & (-d - fP + cN) - fP \end{pmatrix}.$$

Hence at $(0,0)$ we have

$$M_{(0,0)} = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix},$$

so that the eigenvalues $a, -d$ are of opposite sign showing that the origin is a saddle. At $(a/e, 0)$ we have

$$M_{(a/e,0)} = \begin{pmatrix} -a & -ba/e \\ 0 & -d + ca/e \end{pmatrix},$$

The eigenvalues of $M_{(a/e,0)}$ are thus $-a < 0$ and $-d + ca/e$. In the case $ca < de$, so that there is no interior steady state, $(a/e, 0)$ is a stable node, whereas when $ca > de$, so that the interior steady state exists, $(a/e, 0)$ is a saddle.

Finally when $ca > de$ we consider the linear stability of (N^*, P^*). We have

$$M_{(N^*,P^*)} = \begin{pmatrix} -eN^* & -bN^* \\ cP^* & -fP^* \end{pmatrix},$$

Trace $M_{(N^*,P^*)} = -eN^* - fP^* < 0$ and $\det M_{(N^*,P^*)} = N^*P^*(ef + bc) > 0$, so that the eigenvalues of $M_{(N^*,P^*)}$ have negative real parts. Hence when it exists (N^*, P^*) is locally stable.

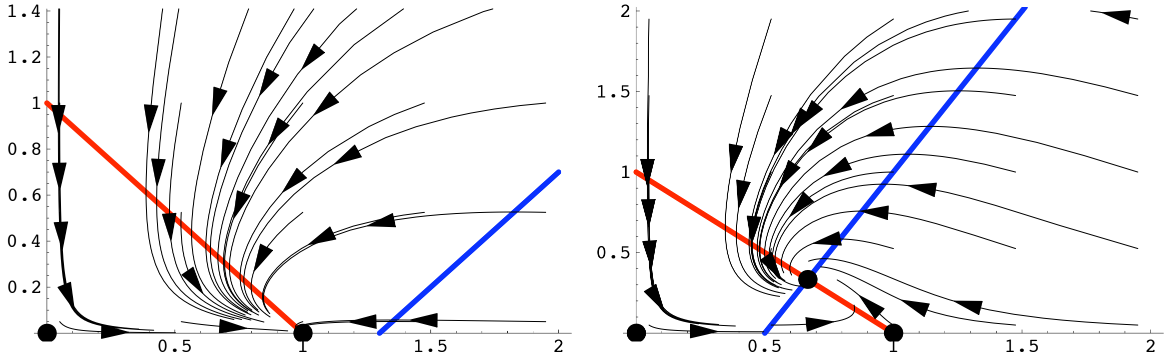


Figure 3.13: Phase space plots for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)). Left $ca < de$ where there are just two steady states, right $ca > de$ where the interior steady state now exists and is locally stable with a spiral.