Competitive species.

last lecture!

$x, y \geq 0$ populat. of species

Model without explicit formulas (qualitative!)

$$\begin{cases} \dfrac{dx}{dt} = M(x,y)\,x \\ \dfrac{dy}{dt} = N(x,y)\,y \end{cases}$$

model

M, N growth rates

population dynamics: zero remains zero:

at $x=0$ $\dot{x}=0$
$y=0$ $\dot{y}=0$ } nullclines

other nullclines:
$\dot{x}=0$ if $M(x,y)=0$
$\dot{y}=0$ if $N(x,y)=0$

Assumptions:

(1) compete for same resources: if x increases then N decreases
y " M "

$$\frac{\partial M}{\partial y} < 0 \quad , \quad \frac{\partial N}{\partial x} < 0$$

(2) no red. large populations (overcrowding bad for all)

$\exists K > 0$, s.t. $M(x,y) < 0$ and $N(x,y) < 0$ if $x \geq K$ or $y \geq K$.

(3) in absence of 2nd species the 1st species ~~then~~ growth below critical level and decreases above.

$\exists a, b > 0$ s.t. $M(x,0) > 0$ if $x < a$ and $M(x,0) < 0$ if $x > a$

(in abs of y, $x \to a$)

$N(0,y) > 0$ if $y < b$ and $N(0,y) < 0$ if $y > b$.

(in abs of x, $y \to b$)

This is the model! What can we conclude?

Result: populations tend to an asymptotically stable equilibrium as $t \to \infty$. (might be unique, but need not be (bi-stability)).

From the assumption (1), it follows that the nullcline determined by $M(x,y)=0$ is a graph over x, i.e. has the form $y=g(x)$ $\quad x \in [0,a]$

suppose $M(a,b)=0$ then $\frac{\partial M}{\partial y}(a,b) < 0$ (in particular $\neq 0$!)

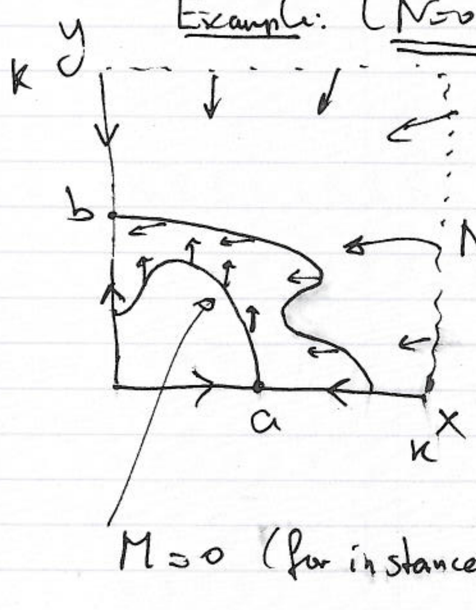
$\overset{\text{IFT}}{\Rightarrow}$ $\exists!$ $b(x)$ such that for all x near a

$$M(x, b(x)) = 0 \qquad (\text{with } b(a)=b)$$

this holds (locally) everywhere on the nullcline $\Rightarrow$ is a graph.

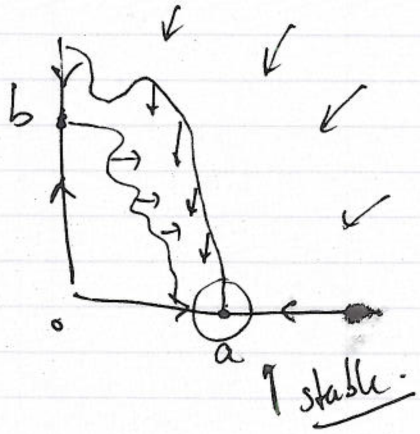
Similarly, since $\frac{\partial N}{\partial x} < 0$ we have that $N=0$ is a graph over y.

Example: ($N=0$ lies above $M=0$)



$(0,b)$ is an asympt stable eq. pt with basin of attraction is $\{(x,y) \mid y>0\}$.

Different situation: $M=0$ lies above $N=0$ $\Rightarrow$ $(a,0)$ asympt stable



simple situations!

What happens if the nullclines $M=0$ and $N=0$ intersect?

$\Rightarrow$ equilibria! (this will change the flow substantially).

But there are some simplifying features:

the Jacobian at equilibria cannot have complex eigenvalues!

* follows from geometric assumptions (but I do not understand the argument in HSD chap 11)

* other way: $Df(x,y)$ $\quad$ f is vectorfield.

$$A = \begin{pmatrix} xM_x & xM_y \\ yN_x & yN_y \end{pmatrix} = Df(x,y) \qquad M_x = \frac{\partial M}{\partial x}(x,y) \qquad M_y = \frac{\partial M}{\partial y}(x,y)$$

recall $M_y < 0$, $N_x < 0$

$\Rightarrow$ calculate $(\mathrm{Tr}\, A)^2 - 4 \det(A) = \underbrace{(xM_x - yN_y)^2}_{\geq 0} + \underbrace{4xy N_x M_y}_{> 0}$!

$\Rightarrow$ look how evals dep. on Tr and Det $\Rightarrow$ evals cannot be complex

(chap 4 HSD)

$\Rightarrow$ equilibria are
* saddles (1D stable and 1D unstable manifold)
* attractors (neg real eval)
* repellers (pos " ")

it also follows that regions between nullclines have either:

* incoming flow on boundary
* outgoing flow on the boundary

if we get to a region where flow is "incoming" $\Rightarrow$ boundary of region contains ω-limit set.

$\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \| $

$\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ eq. soln. !!

We cannot have ω-limit sets that are periodic solns, because of the PB theorem (should encircle eq., not possible because of stable and unstable manifolds of equilibria).

Some more detailed analysis $\Rightarrow$ at most two asymp. stable equilibria.

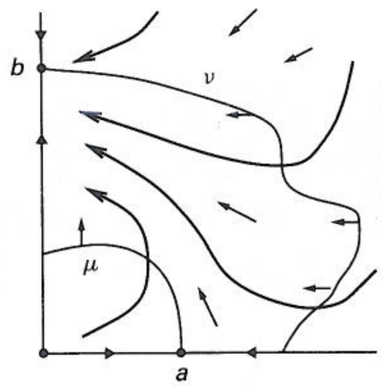


Figure 11.8 The phase portrait when μ and ν do not meet.

The nullclines μ and ν and the coordinate axes bound a finite number of connected open sets in the upper-right quadrant: These are the basic regions where $x' \neq 0$ and $y' \neq 0$. They are of four types:

$$\text{A:}\quad x' > 0,\ y' > 0, \qquad \text{B:}\quad x' < 0,\ y' > 0;$$
$$\text{C:}\quad x' < 0,\ y' < 0, \qquad \text{D:}\quad x' > 0,\ y' < 0.$$

Equivalently, these are the regions where the vector field points northeast, northwest, southwest, or southeast, respectively. Some of these regions are indicated in Figure 11.9. The boundary $\partial\mathcal{R}$ of a basic region $\mathcal{R}$ is made up of points of the following types: points of $\mu \cap \nu$, called *vertices*; points on μ or ν but not on both nor on the coordinate axes, called *ordinary* boundary points; and points on the axes.

A vertex is an equilibrium; the other equilibria lie on the axes at $(0,0)$, $(a,0)$, and $(0,b)$. At an ordinary boundary point $Z \in \partial\mathcal{R}$, the vector field is either vertical (if $Z \in \mu$) or horizontal (if $Z \in \nu$). This vector points either into or out of $\mathcal{R}$ since μ has no vertical tangents and ν has no horizontal tangents. We call Z an *inward* or *outward* point of $\partial\mathcal{R}$, accordingly. Note that, in Figure 11.9, the vector field either points inward at all ordinary points on the boundary of a basic region, or else it points outward at all such points. This is no accident, for we have:

Proposition. *Let $\mathcal{R}$ be a basic region for the competitive species model. Then the ordinary boundary points of $\mathcal{R}$ are either all inward or all outward.*

Proof: There are only two ways in which the curves μ and ν can intersect at a vertex P. As y increases along ν, the curve ν may either pass from below μ to above μ, or from above to below μ. These two scenarios are illustrated in Figures 11.10a and b. There are no other possibilities since we have assumed that these curves cross transversely.

Since $x' > 0$ below μ and $x' < 0$ above μ, and since $y' > 0$ to the left of ν and $y' < 0$ to the right, we therefore have the following configurations for the vector field in these two cases. See Figure 11.11.

In each case we see that the vector field points inward in two opposite basic regions abutting P, and outward in the other two basic regions.

If we now move along μ or ν to the next vertex along this curve, we see that adjacent basic regions must maintain their inward or outward configuration. Therefore, at all ordinary boundary points on each basic region, the vector field either points outward or points inward, as required. ■

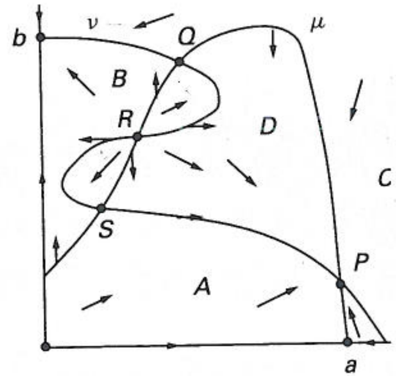


Figure 11.9 The basic regions when the nullclines μ and ν intersect.

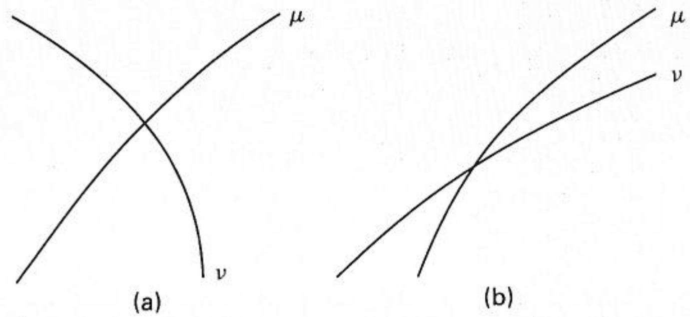
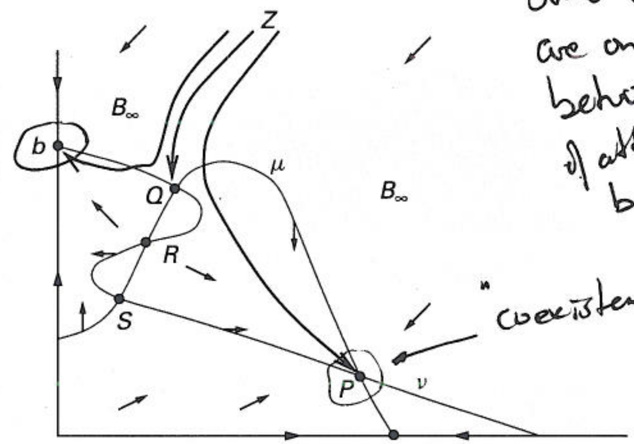


Figure 11.10 In (a), ν passes from below μ to above μ as y increases. The situation is reversed in (b).

"y wins"



other equilibria are on boundary between basins of attraction of b and P.

"coexistence"

Figure 11.14 Note that solutions on either side of the point Z in the stable curve of Q have very different fates.

For example, this analysis tells us that, in Figure 11.14, only P and $(0, b)$ are asymptotically stable; all other equilibria are unstable. In particular, assuming that the equilibrium Q in Figure 11.14 is hyperbolic, then it must be a saddle because certain nearby solutions tend toward it, while others tend away. The point Z lies on one branch of the stable curve through Q. All points in the region denoted B_∞ to the left of Z tend to the equilibrium at $(0, b)$, while points to the right go to P. Thus as we move across the branch of the stable curve containing Z, the limiting behavior of solutions changes radically. Since solutions just to the right of Z tend to the equilibrium point P, it follows that the populations in this case tend to stabilize. On the other hand, just to the left of Z, solutions tend to an equilibrium point where $x = 0$. Thus in this case, one of the species becomes extinct. A small change in initial conditions has led to a dramatic change in the fate of populations. Ecologically, this small change could have been caused by the introduction of a new pesticide, the importation of additional members of one of the species, a forest fire, or the like. Mathematically, this event is a jump from the basin of P to that of $(0, b)$.

11.4 Exploration: Competition and Harvesting

In this exploration we will investigate the competitive species model where we allow either harvesting (emigration) or immigration of one of the species. We consider the system

$$x' = x(1 - ax - y)$$
$$y' = y(b - x - y) + h.$$

Here a, b, and h are parameters. We assume that $a, b > 0$. If $h < 0$, then we are harvesting species y at a constant rate, whereas if $h > 0$, we add to the population y at a constant rate. The goal is to understand this system completely for all possible values of these parameters. As usual, we only consider the regime where $x, y \geq 0$. If $y(t) < 0$ for any $t > 0$, then we consider this species to have become extinct.

1. First assume that $h = 0$. Give a complete synopsis of the behavior of this system by plotting the different behaviors you find in the a, b parameter plane.
2. Identify the points or curves in the ab–plane where bifurcations occur when $h = 0$ and describe them.
3. Now let $h < 0$. Describe the ab–parameter plane for various (fixed) h-values.
4. Repeat the previous exploration for $h > 0$.
5. Describe the full three-dimensional parameter space using pictures, flip books, 3D models, movies, or whatever you find most appropriate.

EXERCISES

1. For the SIRS model, prove that all solutions in the triangular region Δ tend to the equilibrium point $(\tau, 0)$ when the total population does not exceed the threshold level for the disease.

2. Sketch the phase plane for the following variant of the predator/prey system:

$$x' = x(1 - x) - xy$$
$$y' = y\left(1 - \frac{y}{x}\right).$$

3. A modification of the predator/prey equations is given by

$$x' = x(1 - x) - \frac{axy}{x + 1}$$
$$y' = y(1 - y)$$

where $a > 0$ is a parameter.

We obtain $\dot{L} \equiv 0$ provided

$$\frac{x\,dF/dx}{dx - c} \equiv \frac{y\,dG/dy}{by - a}.$$

Since x and y are independent variables, this is possible if and only if

$$\frac{x\,dF/dx}{dx - c} = \frac{y\,dG/dy}{by - a} = \text{constant}.$$

Setting the constant equal to 1, we obtain

$$\frac{dF}{dx} = d - \frac{c}{x},$$
$$\frac{dG}{dy} = b - \frac{a}{y}.$$

Integrating, we find

$$F(x) = dx - c\log x,$$
$$G(y) = by - a\log y.$$

Thus the function

$$L(x, y) = dx - c\log x + by - a\log y$$ freak!

is constant on solution curves of the system when $x, y > 0$.

By considering the signs of $\partial L/\partial x$ and $\partial L/\partial y$ it is easy to see that the equilibrium point $Z = (c/d, a/b)$ is an absolute minimum for L. It follows that L [or, more precisely, $L - L(Z)$] is a Liapunov function for the system. Therefore Z is a stable equilibrium.

We note next that there are no limit cycles; this follows from Corollary 6 in Section 10.6 because L is not constant on any open set. We now prove the following theorem.

Theorem. *Every solution of the predator/prey system is a closed orbit (except the equilibrium point Z and the coordinate axes).*

Proof: Consider the solution through $W \neq Z$, where W does not lie on the x- or y-axis. This solution spirals around Z, crossing each nullcline infinitely often. Thus there is a doubly infinite sequence $\cdots < t_{-1} < t_0 < t_1 < \cdots$ such that $\phi_{t_n}(W)$ is on the line $x = c/d$, and $t_n \to \pm\infty$ as $n \to \pm\infty$. If W is not on a closed orbit, the points $\phi_{t_n}(W)$ are monotone along the line

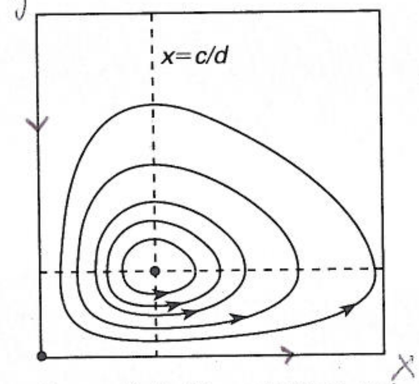


Figure 11.5 The nullclines and phase portrait for the predator/prey system.

$x = c/d$, as discussed in the previous chapter. Since there are no limit cycles, either $\phi_{t_n}(W) \to Z$ as $n \to \infty$ or $\phi_{t_n}(W) \to Z$ as $n \to -\infty$. Since L is constant along the solution through W, this implies that $L(W) = L(Z)$. But this contradicts minimality of $L(Z)$. This completes the proof. ■

The phase portrait for this predator/prey system is displayed in Figure 11.5. We conclude that, for any given initial populations $(x(0), y(0))$ with $x(0) \neq 0$ and $y(0) \neq 0$, other than Z, the populations of predator and prey oscillate cyclically. No matter what the populations of prey and predator are, neither species will die out, nor will its population grow indefinitely.

Now let us introduce overcrowding into the prey equation. As in the logistic model in Chapter 1, the equations for prey, in the absence of predators, may be written in the form

$$x' = ax - \lambda x^2.$$

We also assume that the predator population obeys a similar equation

$$y' = -cy - \mu y^2$$

when $x = 0$. Incorporating the assumptions above yields the *predator/prey equations for species with limited growth*:

$$x' = x(a - by - \lambda x)$$
$$y' = y(-c + dx - \mu y).$$

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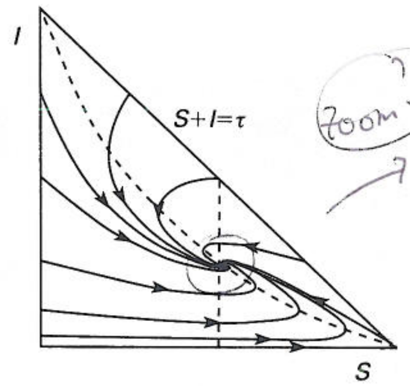

zoom

stable p.c

we don't know !!

Figure 11.3 The nullclines and phase portrait in Δ for the SIRS system. Here $\beta = \nu = \mu = 1$ and $\tau = 2$.

assume that, in the absence of predators, the prey population grows at a rate proportional to the current population. That is, as in Chapter 1, when $y = 0$ we have $x' = ax$ where $a > 0$. So in this case $x(t) = x_0 \exp(at)$. When predators are present, we assume that the prey population decreases at a rate proportional to the number of predator/prey encounters. As in the previous section, one simple model for this is bxy where $b > 0$. So the differential equation for the prey population is $x' = ax - bxy$.

For the predator population, we make more or less the opposite assumptions. In the absence of prey, the predator population declines at a rate proportional to the current population. So when $x = 0$ we have $y' = -cy$ with $c > 0$, and thus $y(t) = y_0 \exp(-ct)$. The predator species becomes extinct in this case. When there are prey in the environment, we assume that the predator population increases at a rate proportional to the predator/prey meetings, or dxy. We do not at this stage assume anything about overcrowding. Thus our simplified predator/prey system (also called the Volterra-Lotka system) is

$$\begin{aligned} x' &= ax - bxy = x(a - by) \\ y' &= -cy + dxy = y(-c + dx) \end{aligned}$$

where the parameters $a, b, c,$ and d are all assumed to be positive. Since we are dealing with populations, we only consider $x, y \geq 0$.

As usual, our first job is to locate the equilibrium points. These occur at the origin and at $(x, y) = (c/d, a/b)$. The linearized system is

$$X' = \begin{pmatrix} a - by & -bx \\ dy & -c + dx \end{pmatrix} X,$$

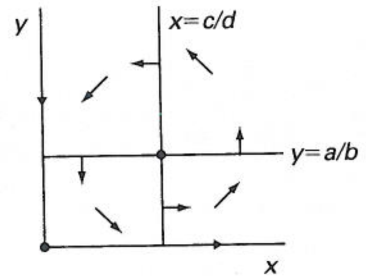

Figure 11.4 The nullclines and direction field for the predator/prey system.

so when $x = y = 0$ we have a saddle with eigenvalues a and $-c$. We know the stable and unstable curves: They are the y- and x-axes, respectively.

At the other equilibrium point $(c/d, a/b)$, the eigenvalues are pure imaginary $\pm i\sqrt{ac}$, and so we cannot conclude anything at this stage about stability of this equilibrium point.

We next sketch the nullclines for this system. The x-nullclines are given by the straight lines $x = 0$ and $y = a/b$, whereas the y-nullclines are $y = 0$ and $x = c/d$. The nonzero nullcline lines separate the region $x, y > 0$ into four basic regions in which the vector field points as indicated in Figure 11.4. Hence the solutions wind in the counterclockwise direction about the equilibrium point.

From this, we cannot determine the precise behavior of solutions: They could possibly spiral in toward the equilibrium point, spiral toward a limit cycle, spiral out toward "infinity" and the coordinate axes, or else lie on closed orbits. To make this determination, we search for a Liapunov function L. Employing the trick of *separation of variables*, we look for a function of the form

$$L(x, y) = F(x) + G(y).$$

Recall that $\dot{L}$ denotes the time derivative of L along solutions. We compute

$$\begin{aligned} \dot{L}(x, y) &= \frac{d}{dt} L(x(t), y(t)) \\ &= \frac{dF}{dx} x' + \frac{dG}{dy} y'. \end{aligned}$$

Hence

$$\dot{L}(x, y) = x \frac{dF}{dx}(a - by) + y \frac{dG}{dy}(-c + dx).$$