Chap 6. Applications to Biological Models

6.1 Predator - Prey Model

Consider a pair of species as predator & prey. Let x be the population of the preys and y be that of the predators. For instance, we may think of them as rabbits & foxes. We want to build an ODE system, hence a dynamical system, to model the change of x & y over time.

Here we will mainly focus on the interaction between x & y. Thus we may ignore other affects. Concretely, we assume:

① Prey population x is the total food supply for the predators.

② There are unlimited food supply for the preys

Building the model: First we consider x

(i) · if $y=0$, then the change of x over time t follows the Malthus Law, i.e. the rate of the change is proportional to its population:

$$x' = ax, \quad a>0 \text{ intrinsic annual growth rate}$$

(in particular $t=1$ means 1 year)

· if $y \neq 0$, then it has a negative effect on the growth of x, where the interaction may be interpreted as bxy for some $b>0$.

hence, we obtain

$$x' = ax - bxy \quad , a, b > 0. \tag{1}$$

(ii) Then we consider y. If $x=0$, then y dies out because the lacking of food. Hence it's reasonable to put

$$y' = -cy \quad , \quad c > 0.$$

The more predators we have, the more they are dying.

If $x \neq 0$, then it certainly has a positive effect on the growth of y. Again, the effect of the interaction may be interpreted as dxy &

$$y' = -cy + dxy \quad , \quad c, d > 0 \tag{2}$$

Put (1) & (2) together, we obtain the predator-prey model

$$\begin{cases} x' = ax - bxy \\ y' = -cy + dxy \end{cases} \quad a, b, c, d > 0. \tag{*}$$

~~It~~ It defines a planar nonlinear system. In reality, $x \geq 0$ & $y \geq 0$. Thus we may focus on the first qudrant.

How to study this model? Let's try to apply all the techniques we've learned so far, starting from the simpler ones

Step 1: Linearization around equilibria.

So we find all equilibria via $\begin{cases} ax - bxy = 0 \\ -cy + dxy = 0 \end{cases}$

$$\begin{cases} x(a-by) = 0 \\ y(dx-c) = 0 \end{cases} \Rightarrow \begin{cases} x=0, \text{ or } y = \frac{a}{b} \\ y=0, \text{ or } x = \frac{c}{d} \end{cases}.$$ Hence

we obtain equilibria $(0,0)$, $(\frac{c}{d}, \frac{a}{b})$.

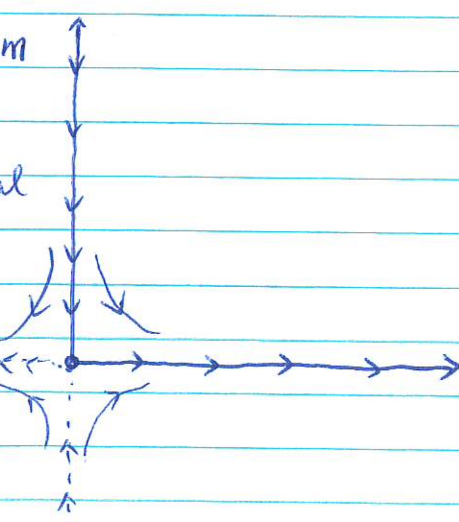
Let $F(x,y) = \begin{bmatrix} ax-bxy \\ -cy+dxy \end{bmatrix}$, then $DF(x,y) = \begin{bmatrix} a-by, & -bx \\ dy, & -c+dx \end{bmatrix}$

In particular, $DF(0,0) = \begin{bmatrix} a, & 0 \\ 0, & -c \end{bmatrix} \Rightarrow a$ & $-c$ are two eigen-values $\Rightarrow \vec{0}$ is a saddle of $\vec{u}' = DF(0,0)\vec{u}$ $\Rightarrow (0,0)$ is a saddle as well. In fact, this is not difficult to see. Based on the equation (*),

$$\begin{cases} x' = ax-bxy \\ y' = -cy+dxy \end{cases}$$ ~~若 If $y(0)=0$ then y $y(t_0)=0$, then~~ $y(t) \equiv 0$ for all $t \in \mathbb{R}$, is a solution of the second equation, regardless of what is $x(t)$. On the other hand, if $y(t) \equiv 0$, then $x' = ax$. Thus

$\begin{cases} x' = ax \\ y(t) \equiv 0 \end{cases}$ is like a one dimensional system sits inside the planar system. Clearly, it lives on the x-axis

For $x'=ax$, $x=0$ is the only equilibrium pt & is a source.



Similarly, $\begin{cases} x(t) \equiv 0 \\ y' = -cy \end{cases}$ is a 1-dimesonal system sits inside the planar system & it lives on the y-axis.

0 is a sink of $y' = -cy$

From the local phase portraits, it's clearly that $(0,0)$ is a saddle & $W^s(\vec{0}) = y\text{-axis} \setminus \{\vec{0}\}$ & $W^u(\vec{0}) = x\text{-axis} \setminus \{\vec{0}\}$.

Now consider the second equilibrium pt $(\frac{c}{d}, \frac{a}{b})$.

$$DF(\tfrac{c}{d}, \tfrac{a}{b}) = \begin{bmatrix} a - b\frac{a}{b}, & -b\cdot\frac{c}{d} \\ d\cdot\frac{a}{b}, & -c+d\cdot\frac{c}{d} \end{bmatrix} = \begin{bmatrix} 0, & -\frac{bc}{d} \\ \frac{ad}{b}, & 0 \end{bmatrix}$$

$\Rightarrow p(\lambda) = \lambda^2 + ac = 0 \Rightarrow \lambda_{1,2} = \pm\sqrt{ac}\cdot i \Rightarrow \vec{0}$ is a center of the linearized system $\vec{u}' = DF(\frac{c}{d}, \frac{a}{b})\vec{u}$.

Thus Linearization does not work here.

Next, we want to try if it's Hamiltoniam system.

Recall $\begin{cases} x' = f(x,y) \\ y' = g(x,y) \end{cases}$ is Hamiltonian if & only if

$-\dfrac{\partial f}{\partial x} = \dfrac{\partial g}{\partial y}$. Back to $\begin{cases} x' = ax - bxy \\ y' = -cy + dxy \end{cases}$ $(*)$

$f = ax - bxy \Rightarrow -\dfrac{\partial f}{\partial x} = -a + by$

$g = -cy + dxy \Rightarrow \dfrac{\partial g}{\partial y} = -c + dx$

Clearly, they are different functions $\Rightarrow (*)$ is not Hamiltonian.

Then what can we do?

Even though $(*)$ is not Hamiltonian, it may still have first integrals, i.e a function $L: \mathbb{R}^2 \to \mathbb{R}$ that stay constant along trajectories.

How to find a first integral L?

Note if $L(x,y)$ is a first integral, then

$$\frac{d}{dt} L(x(t), y(t)) = 0 \Rightarrow \frac{\partial L}{\partial x} \cdot x' + \frac{\partial L}{\partial y} y' = 0$$

$$\Rightarrow \frac{\partial L}{\partial x} x(a-by) + \frac{\partial L}{\partial y} y(dx-c) = 0$$

$$\Rightarrow \frac{\partial L}{\partial x} \cdot x \Big/ dx-c = \frac{\partial L}{\partial y} \cdot y \Big/ by-a .$$

If $\frac{\partial L}{\partial x}$ depends only on x & $\frac{\partial L}{\partial y}$ depends only on y, then both sides become single variable functions. Moreover, one is in x & the other is in y. Then this can only happen if both sides are constant functions, i.e. there is a $e \in \mathbb{R}$ s.t.

$$\frac{\partial L}{\partial x} \frac{x}{dx-c} = \frac{\partial L}{\partial y} \frac{y}{by-a} = e.$$

Then we have $\begin{cases} \frac{\partial L}{\partial x} = e \frac{dx-c}{x} \\ \frac{\partial L}{\partial y} = e \frac{by-a}{y} \end{cases}$ In fact, there is no reason that we cannot set $e=1$. Hence $\begin{cases} \frac{\partial L}{\partial x} = d - \frac{c}{x} \\ \frac{\partial L}{\partial y} = b - \frac{a}{y} \end{cases}$

In particular, L may be chosen as

$$L(x) = \int (d - \tfrac{c}{x}) dx + \int (b - \tfrac{a}{y}) dy = dx - c \log(x) + by - a \log(y)$$

Thus, we've found ~~an~~ first integral

$$L(x,y) = dx - c\log x + by - a\log y \qquad x>0,\ y>0$$

of the system (+). It's clearly nonconstant on any open balls like $B_r(\vec{x}) = \{\vec{y} : |\vec{x}-\vec{y}|<r\}$.

In particular, like Hamiltonian systems, level sets $L^{-1}(e) = \{(x,y) : L(x,y)=e\}$ are trajectories. However, given the terms $\log(x)$ & $\log(y)$, it's not easy to plot the level curves $L^{-1}(e)$.

We are actually going to use Poincaré-Bendixon together with a rough picture of the vector field to determine the dynamical systems.

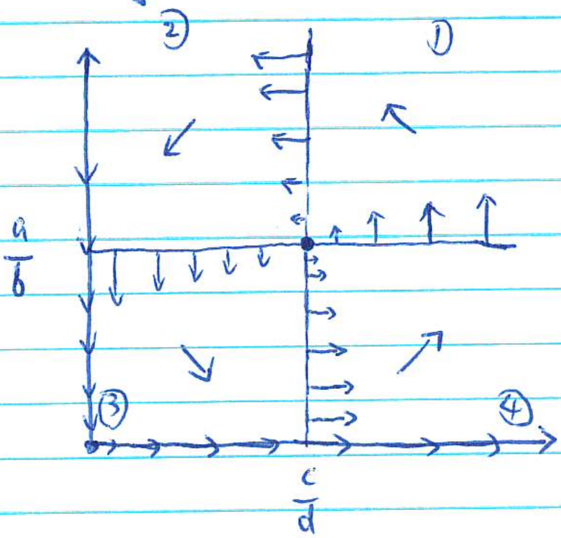
$$\begin{cases} x' = ax - bxy \\ y' = -cy + dxy \end{cases}$$

① $\begin{cases} x'<0 \\ y'>0 \end{cases}$ $(-,+)$

② $\begin{cases} x'<0 \\ y'<0 \end{cases}$ $(-,-)$

③ $\begin{cases} x'>0 \\ y'<0 \end{cases}$ $(+,-)$

④ $\begin{cases} x'>0 \\ y'>0 \end{cases}$ $(+,+)$



$y' = -cy + dxy = 0$ corresponds to curves on which vectors are horizontal, called h-nullcline.

$-cy + dxy = y(dx-c) = 0$

$\Rightarrow y = 0$ or $x = \frac{c}{d}$

$y=0$ ↓ x-axis; $x=\frac{c}{d}$ ↓ vertical line

On h-nullclines, $y'=0$ & $x' = bx(\frac{a}{b} - y)\begin{cases} >0 & \text{if } y<\frac{a}{b} \\ <0 & \text{if } y>\frac{a}{b} \end{cases}$

Similarly, $x' = ax - bxy = x(a-by) = 0$ are v-nullclines on which vectors are vertical. It gives

$x=0$ ↳ y-axis $y = \frac{a}{b}$ ↳ horizontal lines

$$y' = dy\left(x - \frac{c}{d}\right)\begin{cases} >0 & x>\frac{c}{d} \\ <0 & x<\frac{c}{d} \end{cases}$$

One can imagine that trajectories going around the equilibrium $(\frac{c}{d}, \frac{a}{b})$. Actually, we have that

Theorem: All trajectories in the first quadrant are cycles, if we count $(\frac{c}{d}, \frac{a}{b})$ as a trivial cycle.

Before proving this fact, we explore a bit more the first integral

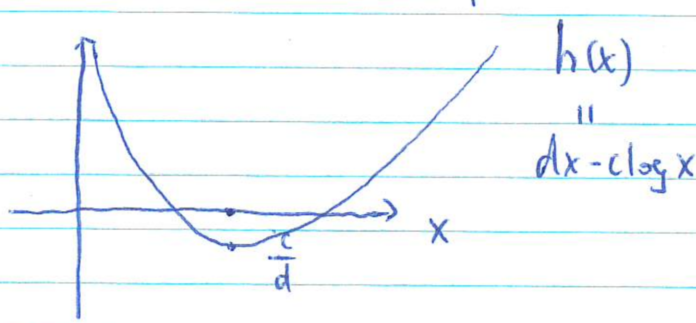
$$L(x,y) = dx - c\log x + by - a\log y \quad , a, b, c, d > 0.$$

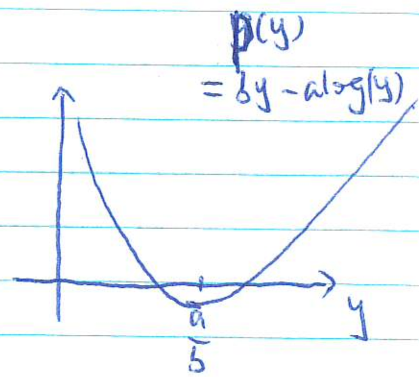
Consider the single variable function

$h(x) = dx - c\log(x), \quad x > 0.$

Clearly, $\lim_{x\to\infty} h(x) = \infty$ & $\lim_{x\to 0} h(x) = \infty$. (1)

And $h'(x) = d - \frac{c}{x} \Rightarrow x = \frac{c}{d}$ is the only critical pt. Moreover $h''(x) = \frac{c}{x^2} > 0 \Rightarrow \frac{c}{d}$ is a local minimal pt. Together with property (1), $\frac{c}{d}$ is actually a global minimal pt.





Similarly, for $p(y) = by - a\log(y)$, $y = \frac{a}{b}$ is a global minimal pt.

Thus the equilibrium pt $(\frac{c}{d}, \frac{a}{b})$ is actually a global minimum of $L(x,y) = h(x) + p(y)$, i.e.

$L(x,y) > L(\frac{c}{d}, \frac{a}{b})$, $\forall (x,y)$ in the first quadrant & $(x,y) \neq (\frac{c}{d}, \frac{a}{b})$.

Moreover, the level sets of L, $L^{-1}(e)$, is both bounded & bounded away from x-axis & y-axis since $L(x,y) \to \infty$ as (x,y) goes to infinity or to x-axis $(y=0)$ or y-axis $(x=0)$.

Hence, for any constant e s.t. $L(\frac{c}{d}, \frac{a}{b}) < e < \infty$, $L^{-1}(e)$ is a bounded, closed set that contains no equilibria.

Proof of the Thm: Now, pick any (x,y) in the first quadrant s.t.

$$(x,y) \neq (\tfrac{c}{d}, \tfrac{a}{b})$$

there is a e between $L(\frac{c}{d}, \frac{a}{b})$ & ∞ s.t.

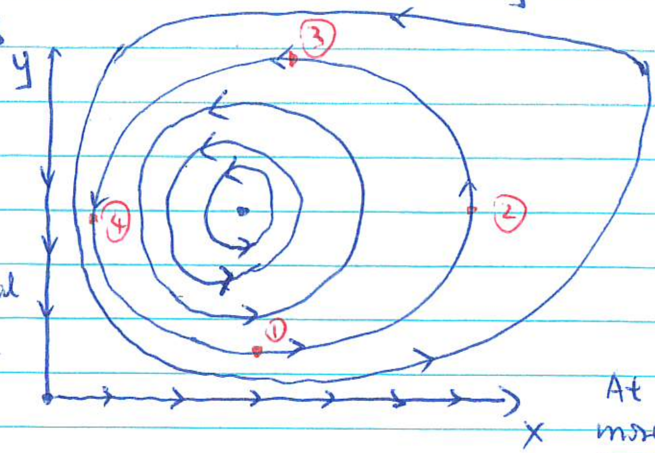
$$L(x,y) = e.$$

$\Rightarrow (x,y) \in L^{-1}(e) \Rightarrow$ the trajectory of (x,y) & $\omega(x,y)$ are all contained in $L^{-1}(e)$. In particular, $\omega(x,y)$ is nonempty, bounded & contains no equilibria

$\Rightarrow \omega(x,y)$ is a cycle. If $(x,y) \notin \omega(x,y)$, then $\omega(x,y)$ is a limit cycle, which cannot happen since the system has a non-trivial first integral $L(x,y)$

$\Rightarrow (x,y) \in \omega(x,y)$ & $\omega(x,y)$ is the trajectory of (x,y) $\square$

Combining the vector field, we may sketch the phase portraits as



The L-value is kind of like energy, the smaller the L is, the biological system is more stable

The longer the L-value is, the big the fluctuation of the system is. At some pt, it becomes more dangerous.

Pick four pts on a trajectory to understand the real life model:

At point ①, ~~both~~ predator ~~& prey~~ population reach the minimal value, thus prey has less ~~one~~ the least number of enemies. Thus x grows fastest. But as x grows, predators get more & more food supplies. Thus y starts to increase as well. But the more y we have, the slower the x grows. Before the pt ②, they both grow. At pt ②, ~~x~~ prey get so many enemies, that it starts to decrease. Though x decreases, y still have sufficient food supplies to grow. Before ③, x keeps decreasing & y keeps growing, but with a slower & ~~so~~ slower speed. At ③, y reaches its maximum & x become ~~real~~ relatively small so that y do not have ~~eng~~ enough food to grow, it starts to decrease.

Now, both x & y decrease. As y decreases, x decreases slower & slower as it gets less & less enemies. ~~Once passes pt~~ At pt ④, ~~y~~ x reaches its minimum & y become small enough for x starting to grow. Thus after ④, x grows & y keep decreasing as the food supply is still very limited. But as x growing, the decreasing speed of y become smaller & smaller. At pt ①, y reaches its minimum & x grows to a point that y has enough food supplies to grow again. Now we start to repeat the previous process.

In mathematices, the trajectory is a cycle. Back to biological model, it's some subtle balance. One can imagine, if we add hunter for x & x ~~d~~ prey species extinct, then soon y will extinct. On the hand, if hunters are for y & y extinct, then x grows. However, in this case, we have to at least use the logistic model for x, ~~But~~ instead of the Malthus Model. But in fact, in reality, too many x can easily cause extra problems such as deseaes among x which may lead to the extinction of x, too. Thus, it's not good idea to break the natural balance.

6.2 Competitive Species Model

We again consider a model of two species, say x & y which also represent their population. But instead of predator & prey type of relation, we assume they compete for a common food supply. e.g. rabbits & sheep, both feed on grass.

Basic assumption: Limit food supply.
In particular, in the absence of either species, the other follows logistic law. The co-existence of both species has a negative effect on both populations. Thus it's reasonable to set up the equations as

$$\begin{cases} x' = a_1 x\left(1 - \frac{x}{L_1}\right) - b_1 xy \\ y' = a_2 x\left(1 - \frac{x}{L_2}\right) - b_2 xy \end{cases}$$

where $x \geq 0$, $y \geq 0$ are variables & $a_i, b_i, L_i > 0$ are constants. In particular, a_1 is the intrinsic annual growth rate of x & a_2 of y. L_1 is the carrying capacity of x & L_2 of y.

We may rewrite the equation as

$$\begin{cases} x' = a_1/L_1 \cdot x \cdot \left(L_1 - x - \frac{b_1 L_1}{a_1} y\right) \\ y' = a_2/L_2 \cdot y \left(L_2 - y - \frac{b_2 L_2}{a_2} y\right) \end{cases}$$

For simplicity, we further rewrite it as

$$\begin{cases} x' = x(a - x - by) \\ y' = y(c - y - dx) \end{cases} \quad a, b, c, d > 0, \quad \begin{matrix} x \geq 0 \\ y \geq 0 \end{matrix} \qquad (*)$$

Here it's ok to set $\frac{a_i}{L_i} = 1$. But one need to keep the carrying capacity & the constants before y in x' & before x in y'. From now on. we will focus on the system (*).

Some observations:

① If $y=0$, i.e. on the x-axis, there is a 1-dimensional logistic type of system. Precisely,

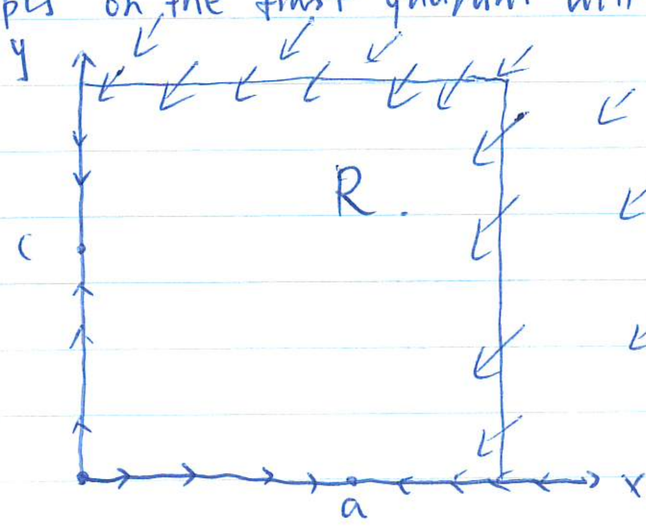
$\begin{cases} x' = x(a-x) \\ y=0 \end{cases}$ is a 1-dimensional system embedded into this 2 dimensional system. Similarly, $\begin{cases} x=0 \\ y' = y(c-y) \end{cases}$ is a 1 dimensional system embedded into this planar system

② If x or y is very large, then $x' = x(a-x-by) < 0$, $y' = y(c-y-dx) < 0$

$\Rightarrow (x', y')$ pointing to southwest. In particular, we may draw a large rectangle in the form

$$R = \{(x,y) : 0 \le x \le k, 0 \le y \le k\}$$

that is positively invariant. Moreover, the trajectory of all pts on the first quadrant will enter this rectangle



So to understand the future of the trajectories, we only need to focus on such a large rectangle.

Let consider the system further. Recall

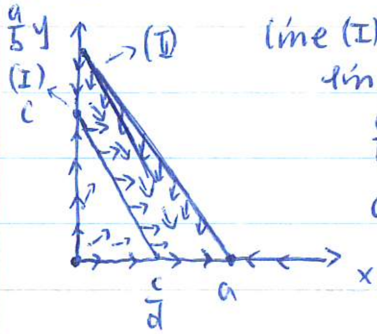
$$\begin{cases} x' = x(a-x-by) \\ y' = y(c-y-dx) \end{cases} \Rightarrow \text{h-nullclines } y(c-y-dx)=0$$

$\Rightarrow y=0$ & $c-y-dx=0$ or $y=-dx+c$ $\begin{cases} (0,c) \\ (\frac{c}{d},0) \end{cases}$ (I)

v-nullcline $x(a-x-by)=0 \Rightarrow x=0$ & $a-x-by=0$

or $x=-by+a$. $\begin{cases} (a,0) \\ (0,\frac{a}{b}) \end{cases}$ (II)

Case I:



line (I) is below line (II)

$\frac{a}{b} > c$

$a > \frac{c}{d}$

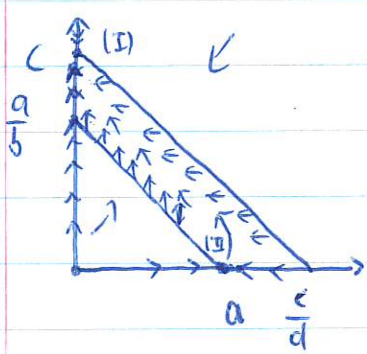
- On line (I) vectors (x', y') are horizontal as $y'=0$
- above (I) $c-y-dx<0$, i.e. $y'<0$
- below (I) $c-y-dx>0$, i.e. $y'>0$

similarly,

- on line (II), vectors (x', y') are vertical as $x'=0$
- above (II), $a-x-by<0$, i.e. $x'<0$
- below (II), $a-x-by>0$, i.e. $x'>0$

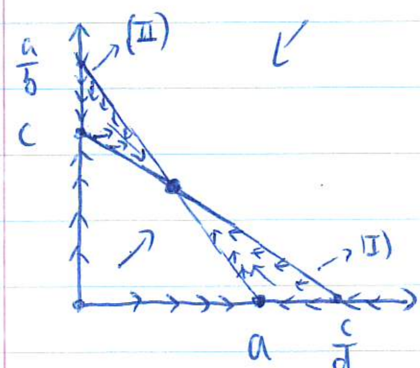
From the vector field, one can see the region enclosed by (I), (II), x-axis & y-axis are positively invariant. Basically, other than the y-axis, all other trajectories will this region & eventually go to the equilibrium pt $(a,0)$, which is a sink. In some sense in this case, the species x wins the competition & as a consequence, the species y extincts with the existence & x. It's clearly that $(0,c)$ is a saddle & $(0,0)$ is a source.

Case II:



(I) is above (II). Similary to case (I), $c > \frac{a}{b}$, $a < \frac{c}{d}$ in this case $(0,c)$ becomes a ~~globall~~ global sink that attracts all solutions other than those on x-axis. $(0,0)$ is a source & $(a,0)$ is a saddle. Y wins the competition & X extincts.

Case III:



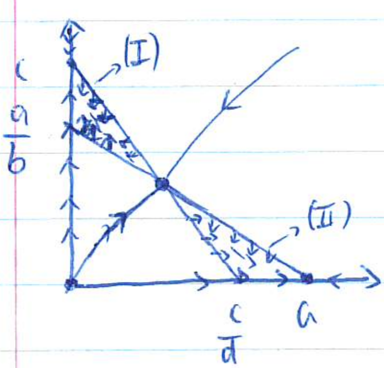
$\frac{a}{b} > c$ & $a < \frac{c}{d}$. We has a new equilibrium pt given by

$$\begin{cases} a-x-by=0 \\ c-y-dx=0 \end{cases} \Rightarrow \text{It's } \left(\frac{cb-a}{bd-1}, \frac{\cancel{ab}\,ad-c}{bd-1}\right)$$

This new equilibria becomes a global sink. $(0,c)$ & $(a,0)$ are saddle & $(0,0)$ is a source.

x & y win-win, coexistence.

Case IV:



$c > \frac{a}{b}$ & $a > \frac{c}{d}$. In this case There is a new equilibrium pt given by $\begin{cases} a-x-by=0 \\ c-y-dx=0 \end{cases}$ But it's a saddle, the stable manifold of it ~~sper~~ separate the first quadrant into 2 region. In one region, the trajectories go to $(0,c)$, in the other, they go to $(a,0)$. So each species has their own safe & dangerous regions.