006.337

Two Species Population Dynamics

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Introduction

In my project I will attempt to represent the three main types of population dynamics which can occur in a system when two species interact with each other in the same environment.

One such interaction is when one of the species serves as food for the other. This is known as predation which can be represented by (+, -). Lotka (1925) and Volterra (1926) developed the first models of the predator-prey system. These early models were purely deductive: there was no attempt to verify assumptions from field or laboratory data. This trend has now been reversed. There are now considerable experimental data available which can be used to determine the validity of earlier models and most importantly, to help develop more realistic general models.

Another situation involving interacting populations is one in which two species have a common prey or food source. This is known as the competitive hunters interaction which is represented by (-, -).

A third situation is when two species enhance each other. This is known as cooperation or symbiosis and is represented by (+, +).

1. Predation

Predation is when one species known as the predator, has an inhibiting effect on the growth of the other species, known as the prey. The prey in return, has an accelerating effect on the predator.

Many different forms of the Predator-Prey system have been suggested. I will attempt to explain as best as possible a few of the different modifications.

Case A:

The simplest system is based on the following assumptions:

- In the absence of the prey, the predator species experiences Malthusian decay
- In the absence of the predator, the prey species experiences Malthusian growth
- The food source for the prey species is essentially unlimited
- The only food available to the predator is the prey
- The species are living in a homogeneous environment

If we let $x = x\,(t)$ denote the number of prey at time t

$y = y\,(t)$ denote the number of predators at time t

Then the system becomes:

$$\left.\begin{aligned} \frac{dx}{dt} &= lx \\ \frac{dy}{dt} &= -ky \end{aligned}\right\} \quad \begin{aligned} &, l > 0 \\ &, k>0 \end{aligned}$$

Case B:

If we incorporate interaction into this system and assume the change in each is directly proportional to the product xy of the numbers x and y of prey/ predator then the system becomes:

$$\left.\begin{aligned} \frac{dx}{dt} &= x\,(\,l-ny\,) \\ \frac{dy}{dt} &= y\,(\,mx-k\,) \end{aligned}\right\} \quad \begin{aligned} &, l, n > 0 \\ &, m, k > 0 \end{aligned}$$

l, n, m, k are all assumed to be positive constants for simplicity

where l: is the intrinsic rate of increase of the prey

k: is the death rate of the predators in the absence of the prey

n: is the coefficient of attack

m: is the conversion factor of prey into more predator individuals

Further assumptions which can be made in addition to the one previously stated are:

- The number of kills of prey by predator is proportional to the frequency of encounters between the two species.
- In isolation, the rate of change of population of one species is proportional to the population of that species.
- Reproduction of both populations is assumed ~~continuous and~~ implies a complete overlapping of generations and continual, non-seasonal breeding.

I will not discuss this system further except to say the solution of the system is:

y^l*e^-ny = k*e^mx*x^-k

and its trajectories near the equilibrium point (k/m , l/n) in the xy-plane are approximately ellipses. This system was studied extensively in the class lectures.

Case C:

One alternative to the first system is the Predator-Prey system without age structure suggested by Volterra. Volterra used the following equations to describe the interaction between a prey and its predator:

$$\left.\begin{aligned} \frac{dx}{dt} &= ax - bx^2 - cxy = x\,(a - bx - cy) \\ \frac{dy}{dt} &= -fy + gxy = y\,(-f + gx) \end{aligned}\right\} \quad \text{a, b, c, f, c} > 0 \text{ constants}$$

The assumptions used in the above system are:

- In the absence of Predation, the prey experiences logistic growth with a rate of increase 'a' and a carrying capacity 'a/b'
- The rate at which prey is eaten is proportional to the product of the densities of predator and prey.
- The effects of interactions within and between species are instantaneous

In order to get some idea as to what possible solutions of this system are we find the equilibrium points and draw phase plane diagrams.

Phase plane:

If $\frac{dx}{dt} = 0$ then this implies $\begin{cases} x = 0 \\ a - bx - cy = 0 \end{cases} \rightarrow \begin{array}{l} x = 0 \\ y = a/c - bf/cg \end{array}$

If $\frac{dy}{dt} = 0$ then this implies $\begin{cases} y = 0 \\ -f + gx = 0 \end{cases} \rightarrow \begin{array}{l} y = 0 \\ x = f/g \end{array}$

Mathematical analysis:

$x > f/g \rightarrow -f + gx > 0 \rightarrow dy/dt > 0$: move vertically upward

$x < f/g \rightarrow -f + gx < 0 \rightarrow dy/dt < 0$: move vertically downward

Points in the xy-plane above $a - bx - cy = 0$ imply $dx/dt < 0$: move left

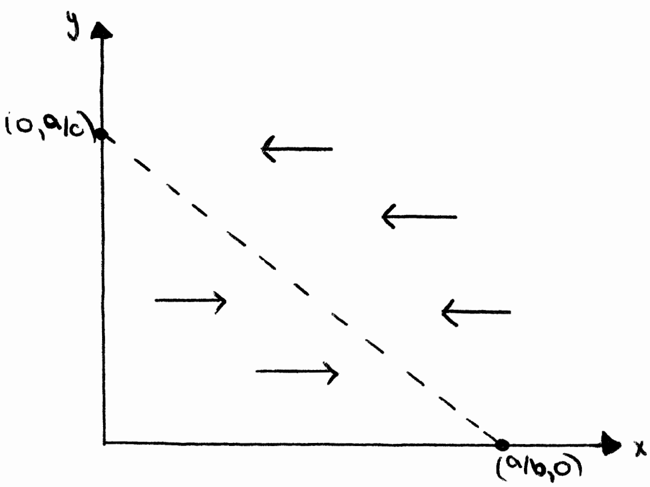
Points in the xy-plane below $a - bx - cy = 0$ imply $dx/dy > 0$: move right

$dy/dt = 0$: when $x = 0$, $y = a/c$

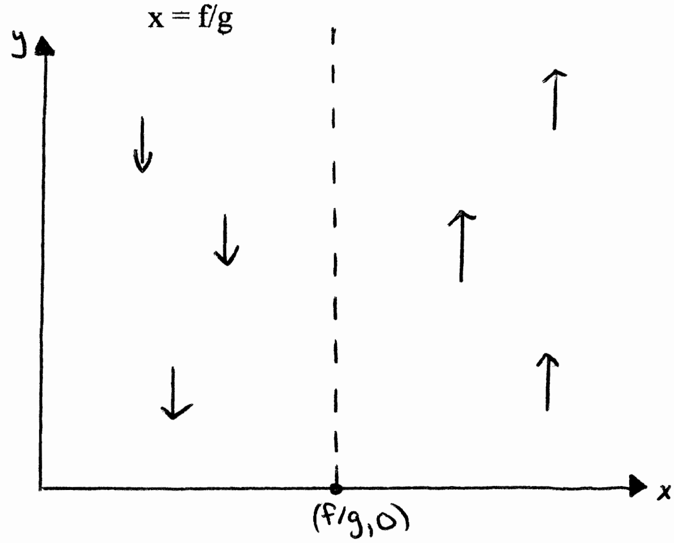
when $y = 0$, $x = a/b$

$dx/dt = 0$: when $y = 0$, $x = f/g$

$y = a/c - bx/c$

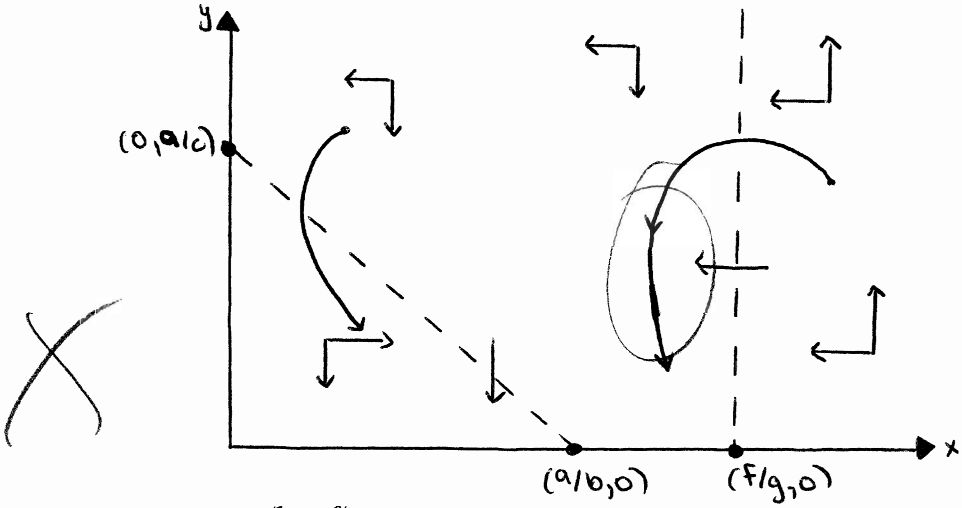


$x = f/g$

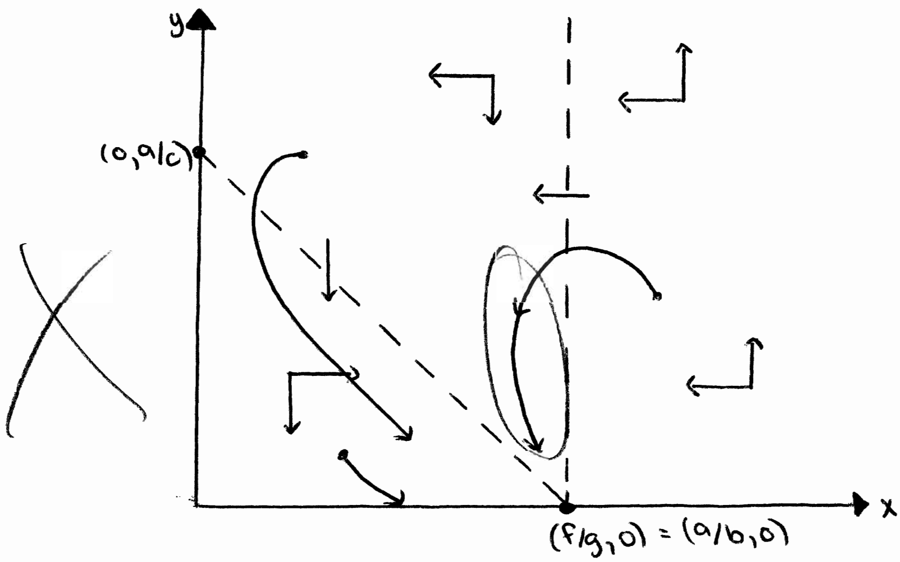


The possible outcomes of this model depend on the relative positions of the isoclines. Therefore, there are three phase plane cases to consider.

i. $a/b < f/g$



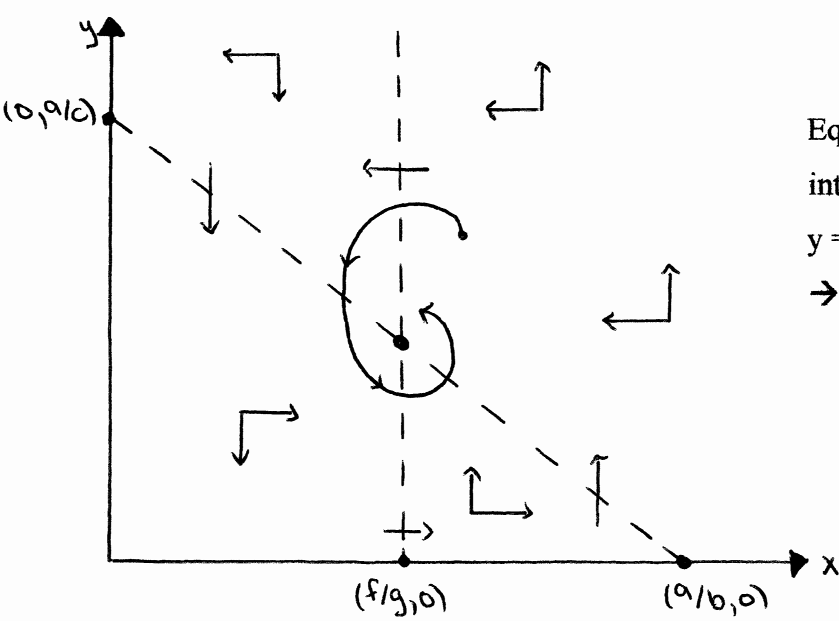
ii. $a/b = f/g$



Equilibrium point:

(f/g , 0) = (a/b , 0)

iii. $a/b > f/g$



Equilibrium point at the intersection of x = f/g and y = a/c – bx/c

→ [f/g , (ag-bf)/cg]

The first case indicates extinction of the predator species while the second case indicates spiraling towards the equilibrium point $x = f/g$ and $y = 0$. The third case indicates that possible trajectories asymptotically approach the equilibrium point (f/g, $(ag-bf)/cg$).

<u>Stability Analysis:</u> *For case iii.*

$$\frac{dx}{dt} = x\,(a-bx-cy)$$
$$\frac{dy}{dt} = y\,(gx-f)$$

Let $u = x - f/g$ $\rightarrow$ $x = u + f/g$

$v = y - \{(ag-bf)/cg\}$ $\rightarrow$ $y = v + \{(ag-bf)/cg\}$

$$\frac{dx}{dt} = \frac{du}{dt} = \left(u + \frac{f}{g}\right)\left[a - b\left(u + \frac{f}{g}\right) - c\left(v + \frac{ag-bf}{cg}\right)\right]$$
$$= \left(u + \frac{f}{g}\right)\left[a - bu - \frac{bf}{g} - c\left(\frac{vcg + ag - bf}{cg}\right)\right]$$
$$= \left(u + \frac{f}{g}\right)\left[a - bu - \frac{bf}{g} - cv - a + \frac{bf}{g}\right]$$
$$= (u + f/g)[-bu - cv]$$
$$\frac{dy}{dt} = \frac{dv}{dt} = \left(v + \frac{ag-bf}{cg}\right)\left[g\left(u + \frac{f}{g}\right) - f\right]$$
$$= \left(v + \frac{ag-bf}{cg}\right)\left[gu + f - f\right]$$
$$= \left(v + \frac{ag-bf}{cg}\right)(gu)$$

Assuming that u,v are both "small" we have:

$$\left.\begin{aligned}\frac{du}{dt} &\sim \frac{f}{g}(-bu - cv)\\ \frac{dv}{dt} &\sim \left(\frac{ag-bf}{c}\right)^{*} u\end{aligned}\right\}$$

assuming we may ignore terms involving uv. We have linearized the equations.

$$\frac{du}{dv} = \frac{f(-bu-cv)}{gu(ag-bf)/c} = \frac{f(-bu-cv)c}{g(ag-bf)u}$$

$$= \frac{fc(-bu-cv)}{gu(ag-bf)} = \frac{l(hu+jv)}{mu} = \frac{lhu+ljv}{mu}$$

where: $l = fc$

$h = -b$

$j = -c$

$m = (ag-bf)g$

This is a homogeneous first order differential equation thus:

Set $u = wv$

$$\frac{du}{dt} = w + v\frac{dw}{dv}$$

Therefore the above equation becomes:

$$w + v\frac{dw}{dv} = \frac{lhwv + ljv}{mwv} = \frac{v(lhw + lj)}{v(mw)} = \frac{lhw + lj}{mw}$$

$$v\frac{dw}{dv} = \frac{lhw + lj}{mw} - w = \frac{lhw + lj - w\hat{}2m}{mw}$$

$$\frac{mw}{lhw + lj - mw\hat{}2}\,dw = \frac{dv}{v}$$

$$\int \frac{mw}{lhw + lj - mw\hat{}2}\,dw = \int \frac{dv}{v}$$

$$= \ln |v| + C$$

Looking at the bottom of the left hand side:

$lj + lhw - mw\hat{}2 = c + bw + aw\hat{}2$ where $c = lj$, $b = lh$, $a = m$

$c + bw - aw\hat{}2 = c - a(w\hat{}2 - b/a\,w)$

$= c - (w\hat{}2 - b/a\,w + b\hat{}2/4a\hat{}2 - b\hat{}2/4a\hat{}2)$

$= c - a(w\hat{}2 - b/a\,w + b\hat{}2/4a\hat{}2) + b\hat{}2/4a$

$= c + b\hat{}2/4a - a(w - b/2a)\hat{}2$

$= (4ac + b\hat{}2)/4a - a(w - b/2a)\hat{}2$

1. If $\frac{a^2}{b^2 + 4ac} > 0$: $\frac{4ac + b^2}{4a}\left[1 - \left(\frac{4a^2}{b^2 + 4ac}\right)\left(w - \frac{b}{2a}\right)^2\right]$

Let $\frac{2a}{\sqrt{b^2 + 4ac}}\left(w - \frac{b}{2a}\right) = \sin\theta$

$\rightarrow \frac{4ac + b^2}{4a}\left(1 - \sin^2\theta\right) = \frac{4ac + b^2}{4a}\cos^2\theta$

$w - \frac{b}{2a} = \frac{\sqrt{b^2 + 4ac}}{2a}\sin\theta \qquad \rightarrow \quad w = \frac{b}{2a} + \frac{\sqrt{b^2 + 4ac}}{2a}\sin\theta$

$\theta = \sin^{-1}\left[\frac{2a}{\sqrt{b^2 + 4ac}}\left(w - \frac{b}{2a}\right)\right]$

$dw = \frac{\sqrt{b^2 + 4ac}}{2a}\cos\theta\, d\theta$

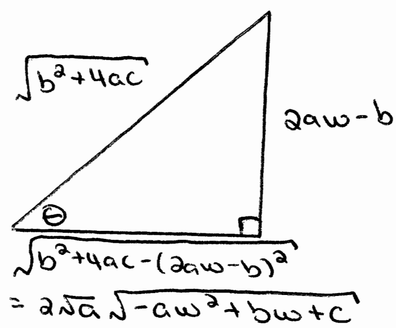
Therefore,

$$\int \frac{-a\left[\frac{b}{2a} + \frac{\sqrt{b^2+4ac}}{2a}\right]\sin\theta}{\frac{4ac+b^2}{4a}\cdot\cos^2\theta}\;\frac{\sqrt{b^2+4ac}}{2a}\cos\theta\, d\theta$$

$$= -\int \frac{(b+\sqrt{b^2+4ac})\sin\theta\;\sqrt{b^2+4ac}}{(4ac+b^2)\cos\theta}\, d\theta = -\int\left[\frac{b}{\sqrt{b^2+4ac}}\tan\theta\, d\theta + \int \tan\theta\, d\theta\right]$$

$$= \int \frac{-b}{\sqrt{b^2+4ac}}\tan\theta\, d\theta + \int -\tan\theta\, d\theta$$

$$= \frac{-b}{\sqrt{b^2+4ac}}\left[\ln|\sec\theta|\right] - \left[\ln|\sec\theta|\right] + \text{Constant}$$



$$= \left[\frac{-b}{\sqrt{b^2+4ac}} - 1\right]\ln\left|\frac{\sqrt{b^2+4ac}}{2\sqrt{a}\sqrt{-aw^2+bw+c}}\right| + \text{Constant}$$

$$= -\frac{1}{2}\left(\frac{b}{\sqrt{b^2+4ac}} + 1\right)\ln(-aw^2+bw+c) + D$$

$$= -\frac{1}{2}\left[\frac{-h}{\sqrt{h^2+4mlj}} + 1\right]\ln\left[-mw^2+lhw+lj\right] + D$$

$$\Rightarrow -\frac{1}{2}\left[\frac{-h}{\sqrt{h^2+4mlj}} + 1\right]\ln\left[-mw^2+lhw+lj\right] = \ln|v| + C$$

2. If $\dfrac{a^2}{b^2+4ac} < 0$: $\dfrac{4ac+b^2}{4a}\left[1+\left(\dfrac{-4a^2}{b^2+4ac}\right)\left(w-\dfrac{b}{2a}\right)^2\right]$

Let $\dfrac{2a}{\sqrt{-b^2-4ac}}\left(w-\dfrac{b}{2a}\right)=\tan\theta$

$\rightarrow \dfrac{4ac+b^2}{4a}\left(1+\tan^2\theta\right)=\dfrac{4ac+b^2}{4a}\sec^2\theta$

$w-\dfrac{b}{2a}=\dfrac{\sqrt{-b^2-4ac}}{2a}\tan\theta \rightarrow w=\dfrac{b}{2a}+\dfrac{\sqrt{-b^2-4ac}}{2a}\tan\theta$

$\theta=\tan^{-1}\left[\dfrac{2a}{\sqrt{-b^2-4ac}}\left(w-\dfrac{b}{2a}\right)\right]$

$dw=\dfrac{\sqrt{-b^2-4ac}}{2a}\sec^2\theta\, d\theta$

Therefore,

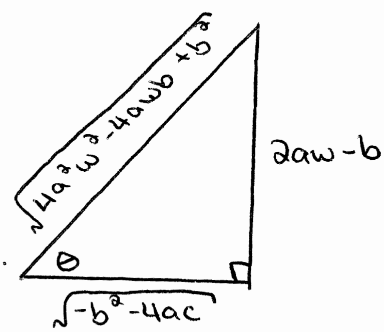
$$\int \frac{-a\left[b/2a+\frac{\sqrt{-b^2-4ac}}{2a}\cdot\tan\theta\right]}{\frac{4ac+b^2}{4a}\cdot\sec^2\theta}\cdot\frac{\sqrt{-b^2-4ac}}{2a}\sec^2\theta\, d\theta$$

$$=\int -\frac{\left[b+\sqrt{-b^2-4ac}\right]\tan\theta\sqrt{-b^2-4ac}\, d\theta}{4ac+b^2}=\int\frac{-b\sqrt{-b^2-4ac}}{4ac+b^2}\tan\theta\, d\theta+\int\tan\theta\, d\theta$$

$$=\frac{-b\sqrt{-b^2-4ac}}{4ac+b^2}\left[\ln|\sec\theta|\right]+\left[\ln|\sec\theta|\right]+\text{Constant}$$

$$=\left[\frac{-b\sqrt{-b^2-4ac}}{4ac+b^2}+1\right]\ln|\sec\theta|+\text{Constant}$$

$$=\left[\frac{-b\sqrt{-b^2-4ac}}{4ac+b^2}+1\right]\ln\left|\frac{\sqrt{4a^2w^2-4awb+b^2}}{\sqrt{-b^2-4ac}}\right|+\text{Constant}$$



$$=\left[\frac{-lh\sqrt{-l^2h^2-4mlj}}{4mlj+l^2h^2}+1\right]\ln\left[\frac{\sqrt{4m^2w^2-4mlhw+h^2l^2}}{-l^2h^2-4mlj}\right]+\text{Const.}$$

$$\Rightarrow\left[\frac{-lh\sqrt{-l^2h^2-4mlj}}{4mlj+l^2h^2}+1\right]\ln\left[\frac{\sqrt{4m^2w^2-4mlhw+h^2l^2}}{-l^2h^2-4mlj}\right]=\ln|v|+c.$$

In both cases we can't determine whether the possible trajectories are elliptic and/or closed, as suggested by the phase plane diagram.

Case D:

Another alternative to the Predator – Prey system is the one suggested by Leslie. The equation for the prey is identical to Volterra's prey equation (including the $-bx^2$ term which is effectively a damping term). The equation for the predator is similar to the logistic equation but has been modified to allow for the density of the prey. The equations are:

$$\left.\begin{aligned} \frac{dx}{dt} &= ax - bx^2 - cxy = x(a - bx - cy) \\ \frac{dy}{dt} &= ey - \frac{fy^2}{x} = y\left(e - \frac{fy}{x}\right) \end{aligned}\right\} \quad \begin{array}{l} a, b, c, e, f > 0 \\ \text{constants} \end{array}$$

where the term y/x arises from the fact that this ratio ought to affect the growth of the predator.

For the predator equation we can see that:

- If x/y is large (many prey per predator) the predator population increases exponentially
- If x/y = f/e , the predator is at equilibrium
- If x/y < f/e , the predator decreases in numbers due to inability to obtain food.

The essential difference between Volterra's and Leslie's equations of the problem is:

- For the Volterra model, whether the predator increases or decreases in number depends only on the density of the prey
- For the Leslie model, it depends on the number of prey per predator.

good

Volterra's equations are usually preferred because they relate the rate of increase of the predators to the rate (cxy) at which prey are being eaten whereas in Leslie's equations there is no relationship between the rate at which a predator eats and the rate at which it reproduces.

In order to try and get a feeling about possible solutions we will again consider the phase plane diagrams.

Phase plane:

If $dx/dt = 0$ then $\begin{cases} x = 0 \\ a - bx - cy = 0 \end{cases}$ $\rightarrow$ $\begin{matrix} x = 0 \\ y = a/c - bx/c \end{matrix}$

If $dy/dt = 0$ then $\begin{cases} y = 0 \\ e - fy/x = 0 \end{cases}$ $\rightarrow$ $\begin{matrix} y = 0 \\ y = ex/f \end{matrix}$

Analysis:

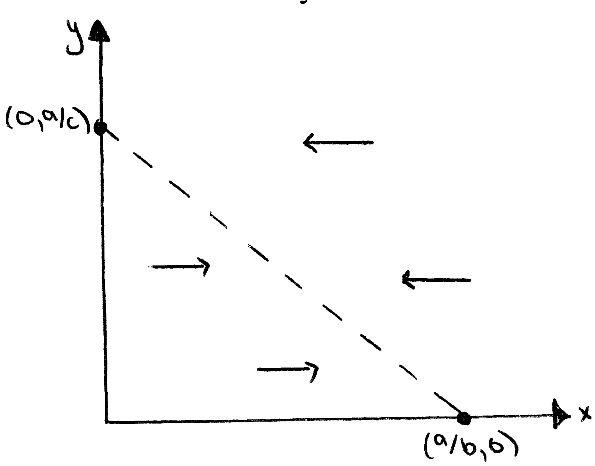
- Points above $a - bx - cy = 0$ $\rightarrow$ $dx/dt < 0$: move left
- Points below $a - bx - cy = 0$ $\rightarrow$ $dx/dy > 0$: move right
- Points above $y = ex/f$ $\rightarrow$ $dy/dt < 0$: move downward
- Points below $y = ex/f$ $\rightarrow$ $dy/dt > 0$: move upward

$dx/dt = 0$: when $x = 0$, $y = a/c$

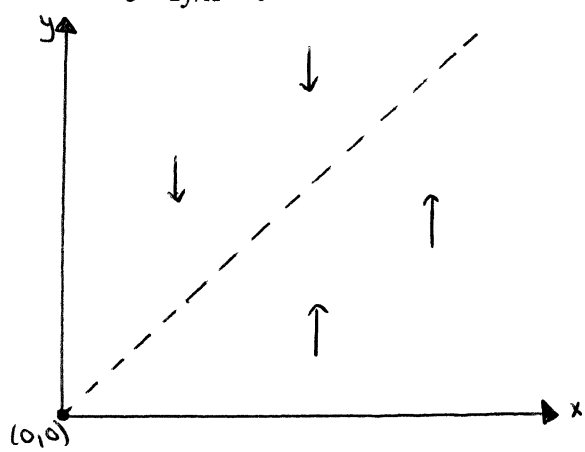
when $y = 0$, $x = a/b$

$dy/dt = 0$: when $x = 0$, $y = 0$

$a - bx - cy = 0$



$e - fy/x = 0$



There will be an equilibrium point at the intersection of $dy/dt = 0$ and $dx/dt = 0$, i.e. $a - bx - cy = 0$ and $e - fy/x = 0$.

$a - bx - cy = 0$ $\qquad$ $e - fy/x = 0$

$a - bx - cex/f = 0$ $\qquad$ $y = ex/f$

$a = bx + cex/f$

$a = xfb/f + xce/f$

$\rightarrow x = \dfrac{af}{fb+ce}$

$e - \dfrac{fy}{a/b - cyb} = 0$ $\qquad$ $x = a/b - cyb$

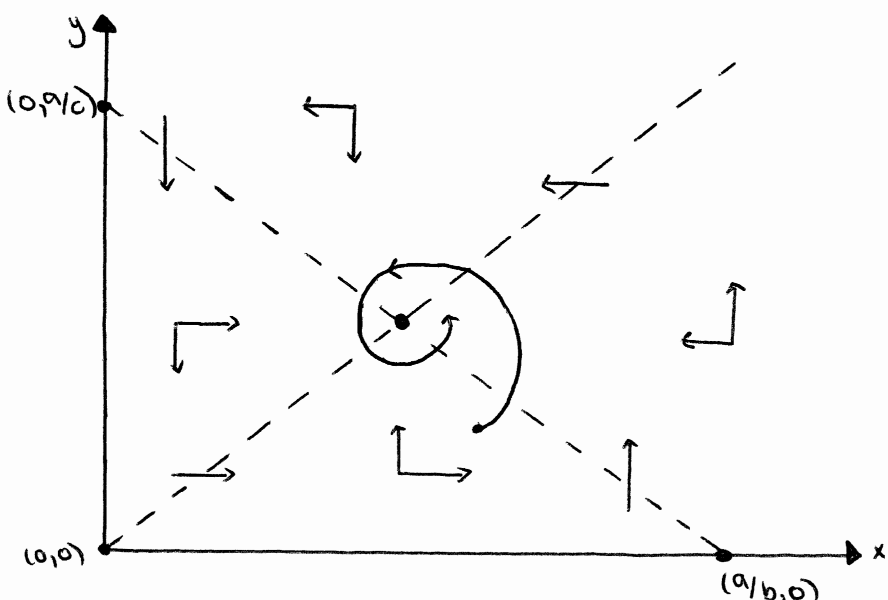
$e = \dfrac{fy}{(a-cy)/b}$

$e = \dfrac{fyb}{a-cy}$

$fyb = e\,(a - cy)$

$fyb + ecy = ea$

$\rightarrow y = \dfrac{ea}{fb + ec}$



Possible trajectories appear to spiral toward the equilibrium point:

$$\left(\frac{af}{bf+ce}, \frac{ea}{bf+ce}\right)$$

Other Cases:

There are many other possible cases and modifications of the predator- prey model which can be made. One such modification is where some number, say xr, of the prey find some cover which makes them inaccessible to the predator. This implies that if there was an amount of cover capable of protecting a limited number of prey, and if those prey unable to occupy this cover were killed, then all prey above some fixed number would be killed. The equations associated with this case are:

$$\frac{dx}{dt} = ax - cy\,(x - xr)$$

$$\frac{dy}{dt} = -ey + c'y\,(x - xr)$$

Another possible modification is when the predator has a constant food intake. The equations then become:

$$\frac{dx}{dt} = (a - bx)x - cy$$

$$\frac{dy}{dt} = -ey + c'y = (c' - e)y$$

Other interesting cases which could be considered are:

- One in which the abundance of the predator is limited by the abundance of the prey. This requires that the number of prey taken by each predator must decrease as the abundance of the prey decreases; if this weren't the case, changes in prey abundance could have no regulating influence on the predator.
- An alternative is that each predator takes a fixed quantity of prey, but that as the prey becomes less abundant, the predators must spend an increasing proportion of their time searching, and so have less time for successful reproduction.

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2. Competition

Competition is a situation in which two species have a common prey or food source. In this case the predators are in competition with each other. Each removes from the environment a resource that would stimulate the growth of the population of the other. That is, each species is inhibited not only by members of its own species, but also by those of the other.

Case A:

The simplest competition model is based on:

- Food exists in unlimited supply
- In the absence of either species, assume the remaining species experiences Malthusian growth

The system is :
$$\left.\begin{aligned} \frac{dx}{dt} &= lx \\ \frac{dy}{dt} &= ky \end{aligned}\right\} \quad \begin{aligned} &l, k > 0 \\ &\text{constants} \end{aligned}$$

Case B:

Since we know that competition is detrimental for both species, we will include a competition term to each which reduces the growth rates by an amount, which is proportional to the product of existing population sizes. This is known as the encounter principle.

The assumptions are similar to the ones made for the predator prey model of case B:

- In the absence of one of the predators, the other predator's population increases at a rate proportional to its size.
- There is a sufficient number of prey to sustain any level of predator population.

The system then becomes:

$$\left.\begin{aligned} \frac{dx}{dt} &= lx - nxy \\ \frac{dy}{dt} &= ky - mxy \end{aligned}\right\} \quad \begin{array}{l} k, l, m, n > 0 \\ \text{constants} \end{array}$$

This system is essentially the predator-prey model with k replaced by –k, and m replaced by –m. I will not discuss this model any further since it was discussed in class.

Case C:

One possible modification is to remove the unlimited environment assumption and assume that in the absence of either species that the other experiences logistic growth. This implies that each population increases exponentially when rare, and approaches an equilibrium without oscillations. Therefore, an analysis of the following equations cannot tell us whether competitive interactions are likely to give rise to oscillatory behavior, since they have been chosen to exclude that possibility.

The equations are:

$$\left.\begin{aligned} \frac{dx}{dt} &= lx - px^2 - nxy = x\,(\,l - px - ny\,) \\ \frac{dy}{dt} &= ky - qy^2 - mxy = y\,(\,k - qy - mx\,) \end{aligned}\right\} \quad \begin{array}{l} l, p, n, q, m, k > 0 \\ \text{constants} \end{array}$$

where

l, p : logistic parameters for species x if it is living alone

k,q : logistic parameters for species y if it is living alone

n : measures the degree to which the presence of species y affects the growth of species x

m: measures the degree to which the presence of species x affects the growth of species y

-ny : measures the inhibiting effect of species y on the reproduction of species x

-mx: measures the inhibiting effect of species x on the reproduction of species y

It is reasonable to say that the species compete if n and m are positive.

An equilibrium exists when dx/dt = 0 and dt/dt = 0, i.e. when no change takes place in time.

<u>Phase plane:</u>

If $\frac{dx}{dt} = 0$ then $x(1 - px - ny) = 0$ → $x = 0$
$1 - px - ny = 0$

$\frac{dy}{dt} = 0$ then $y(k - qy - mx) = 0$ → $y = 0$
$k - qy - mx = 0$

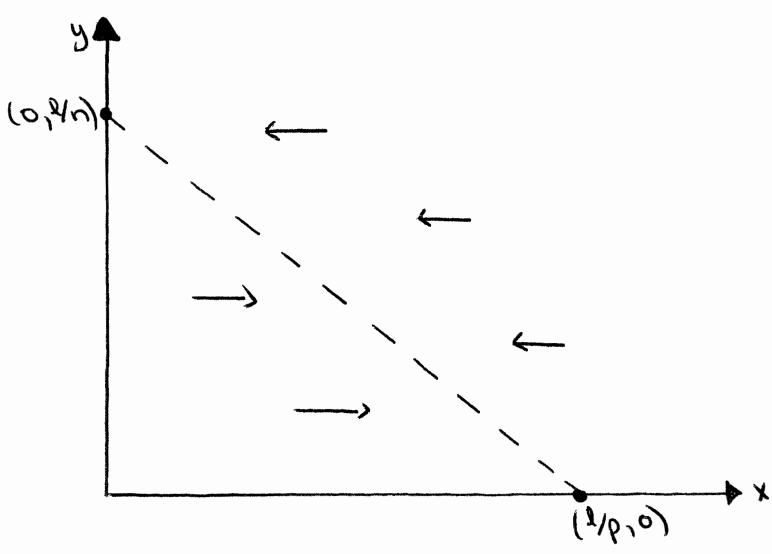
Two equilibrium points are given by: $dx/dt = 0$: when $x = 0$, $y = k/m$
$dy/dt = 0$: when $y = 0$, $x = l/p$

These correspond to the equilibrium densities of each species in the absence of the other.

l- px – ny = 0 :

Any values of the densities x and y of the two populations can be represented as a point on the xy- plane. (Since the densities cannot be negative, the point must lie in the first quadrant.) For any point above and to the right of the isocline, the value of $1 - px - ny$ will be negative. Hence $dx/dt < 0$, and x will decrease. For points below and to the left of the isocline, $dx/dt > 0$, and x will increase. i.e.

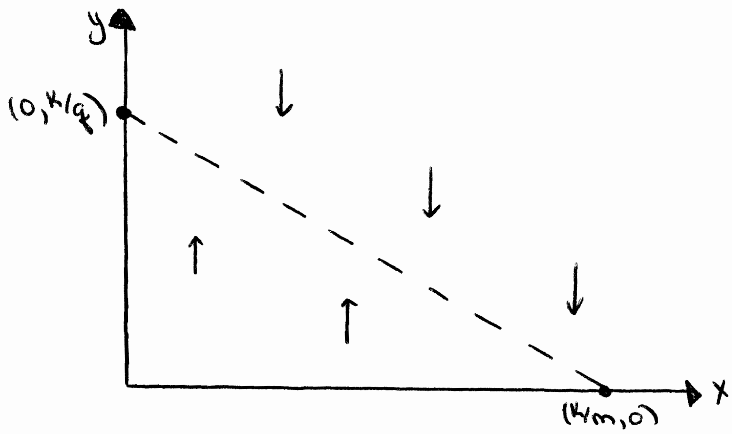
- For points above $1 - px - ny = 0$, $dx/dt < 0$: move left
- For points below $1 - px - ny = 0$, $dx/dt > 0$: move right



k-qy – mx = 0 :

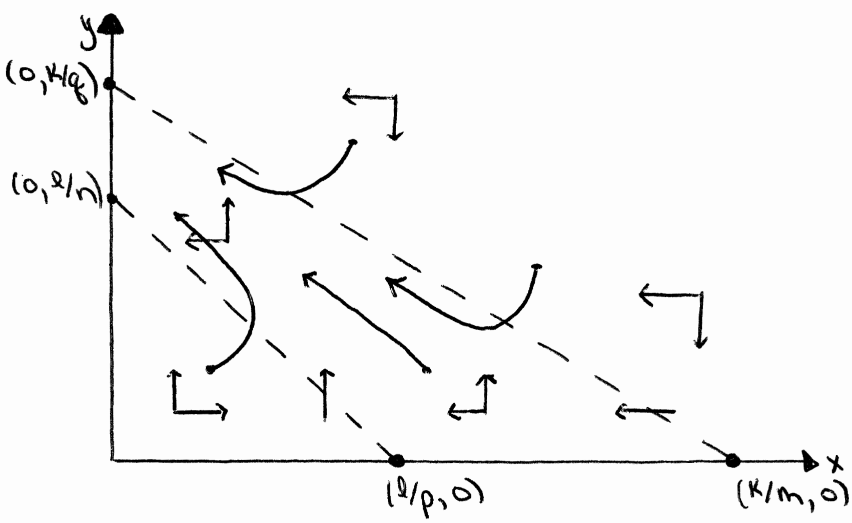
Mathematical analysis:

- For points above $k - qy - mx = 0$, $dy/dt < 0$: move downward
- For points below $k - qy - mx = 0$, $dy/dt > 0$: move upward



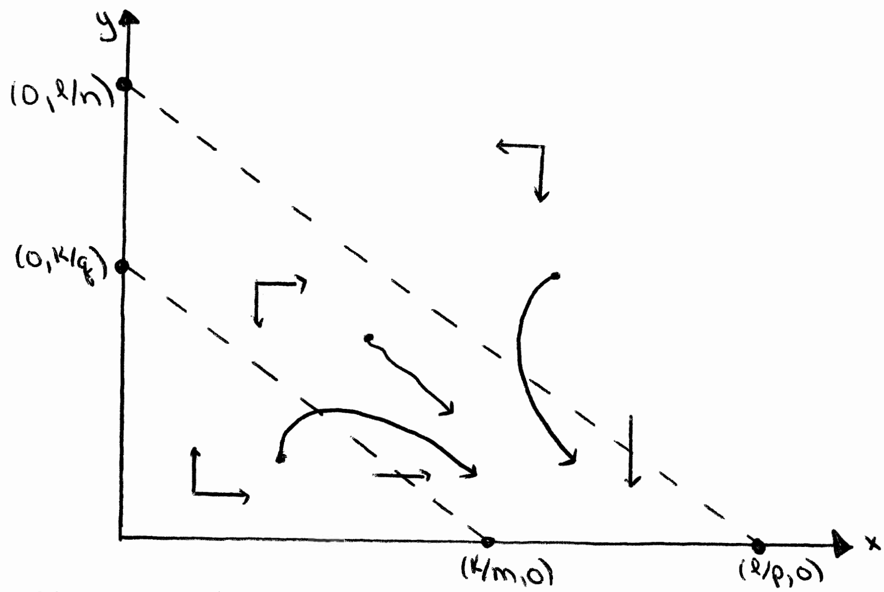
The possible outcomes of this model depend on the relative positions of the isoclines and whether or not they intersect. Therefore, there are four cases to consider:

i. *$k/q > l/n$ and $k/m > l/p$*



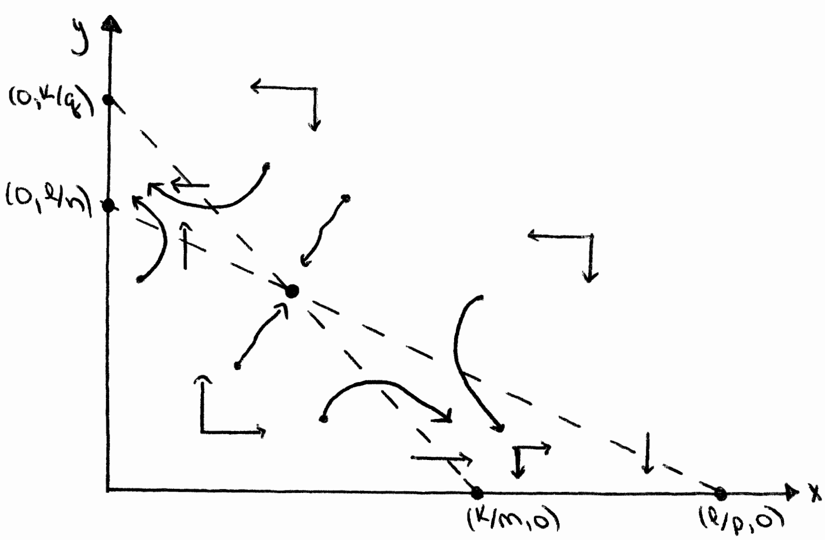
This corresponds to extinction of the x species. Because the isoclines do not intersect, no equilibrium exists with both species present.

ii. *l/n > k/q and l/p > k/m*



This corresponds to extinction of the y species. Again, no equilibrium with both species present exists.

iii. *l/p > k/m and k/q > l/n*

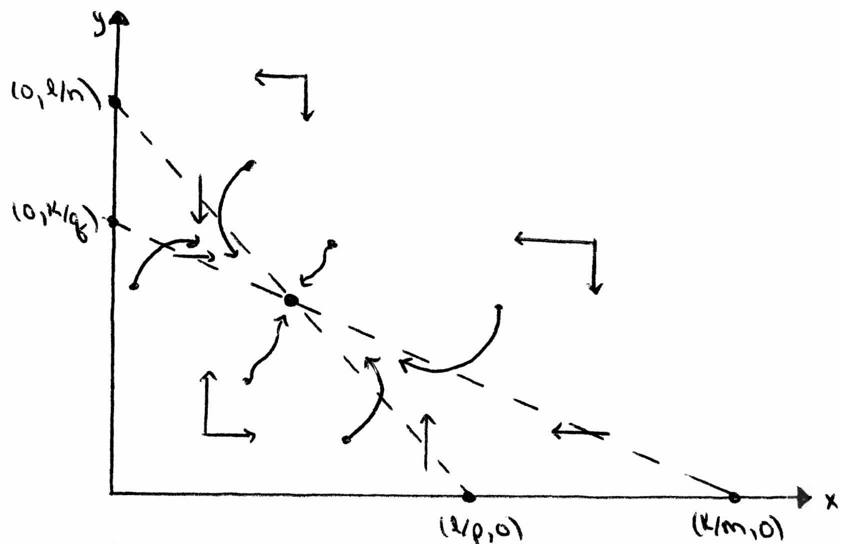


A third equilibrium exists in this case at the intersection of l-px-ny = 0 and k-qy -mx = 0.

The equilibrium point is : $x = \dfrac{kn - lq}{mn - pq}$ $\qquad y = \dfrac{lm - pk}{mn - pq}$

This phase plane suggests that the equilibrium is unstable where the ' winner ' depends on the initial densities of the two species.

iv. $l/p < k/m$ and $l/n > k/q$



From the phase plane we can see that this equilibrium point is stable.

From all four phase plane diagrams we can see that a slight change in the initial population sizes can have a catastrophic effect on the ultimate behavior of competition models which have strict requirements for the coexistence of two competing species. Which of the two species survives depends on the initial conditions.

For cases i. and ii. , the species that survives is the one having the greater effect on the other species- the dominant competitor. In case iii. , the slightest disturbance leads to the elimination of one of the species depending on the direction of the disturbance. Each species inhibits the population growth of the other species more than itself. In case iv. , each species inhibits its own growth more that that of the other species.

If the rates of increase of each species are equal, i.e. l and k , then the conditions for stability become $p > m$ and $q > n$. These imply that an increase in numbers of either species inhibits its own growth more than it inhibits its competitor. If both species have identical requirements, one species is likely to be more efficient and will eliminate its competitor. This is known as the principle of competitive exclusion. As De Bach (1966) explained:

> " Different species which coexist indefinitely in the same habitat must have different ecological niches, that is, they must not be ecological homologues."

In other words, if the species are limited by different resources then the inequalities above will hold and then coexistence is logically possible. Otherwise, extinction of one of the species is inevitable. However, it was found in numerous laboratory experiments that one of the two species was eliminated sooner or later.

Taking a closer look at case iv. we consider the significance of the conditions for stable co-existence of the two species, $l/n > k/q$ and $l/p < k/m$.

We know that l and k represent the intrinsic rates of increase of the two species when rare. So, suppose for simplicity that $l = k$. Then $l/n > k/q$ and $l/p < k/m$ reduce to,

$1/n > 1/q$ and $1/p < 1/m$

or $n < q$ and $p > m$ since all constants are positive

These conditions can be stated verbally as :

1. The inhibiting effect of y on x is less that that of y on itself
2. The inhibiting effect of x on y is less that that of x on itself

Thus, if for example the species were limited by food and if their food was in part common and in part species-specific, these conditions would probably be satisfied. But, if the two species were microorganisms each of which released into the surrounding medium a toxic substance which had a greater inhibiting effect on the other species that itself, then the situation would correspond to the case where $l/n < k/q$ and $l/p > k/m$. This is simply case iii above , an unstable equilibrium.

Case D:

Since the logistic equations cannot in general, be explicitly solved, we can make a simplification. The simplification that permits a solution of the equations consists of assuming that for an individual of either species, the inhibitory effect of all other individuals (for both species) is the same. Then each individual of both species behaves as if it were competing with a population of size $N = x + py$. Here, N is the size of the "effective inhibiting population" which is the same for both species. And p allows for the fact that the members of the two species may differ from one another in their inhibitory effect.

If individuals of species y make a smaller difference on the resources that individuals of species x, then $p < 1$. Conversely, if species x is the less demanding competitor, $p > 1$. The equations are then:

$$\frac{dx}{dt} = lx - (pN)x$$

$$\frac{dy}{dt} = ky - (qN)y$$

The solution of these differential equations however, is beyond the mathematical level I have achieved at this point.

3. Cooperation (Symbiosis)

Cooperation is when each species has an accelerating effect on the growth of the other. Very little work has been done on models of cooperation. Two such models, which I will attempt to explain as fully as possible, were presented by Lotka-Volterra. They consider :

1. A model without carrying capacities
2. A model with carrying capacities

Case A:

The set of equations for the model without carrying capacities is:

$$\left.\begin{aligned} \frac{dx}{dt} &= x\,(\,l + ny\,) \\ \frac{dy}{dt} &= y\,(\,k + mx) \end{aligned}\right\} \quad \begin{array}{l} l,\, n,\, k,\, m > 0 \\ \text{constants} \end{array}$$

Phase plane:

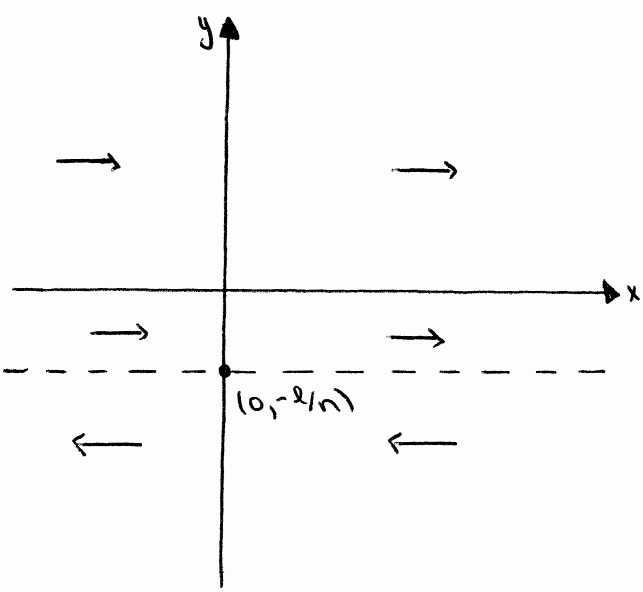
If $dx/dt = 0$ then $\begin{cases} x = 0 \\ l + ny = 0 \quad \rightarrow \quad y = -l/n \end{cases}$

If $dy/dt = 0$ then $\begin{cases} y = 0 \\ k + mx = 0 \quad \rightarrow \quad x = -k/m \end{cases}$

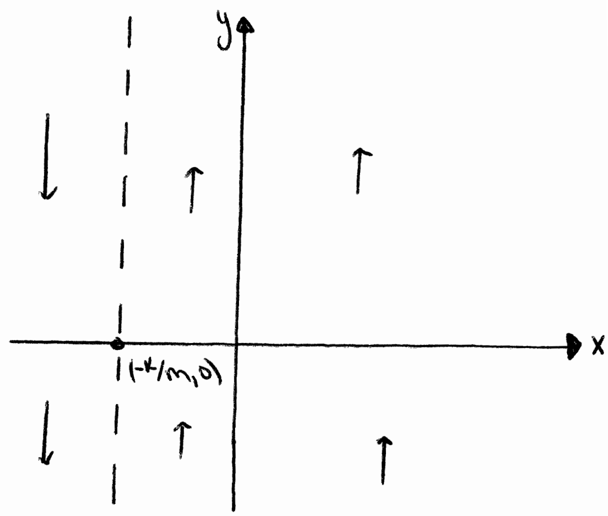
Mathematical analysis:

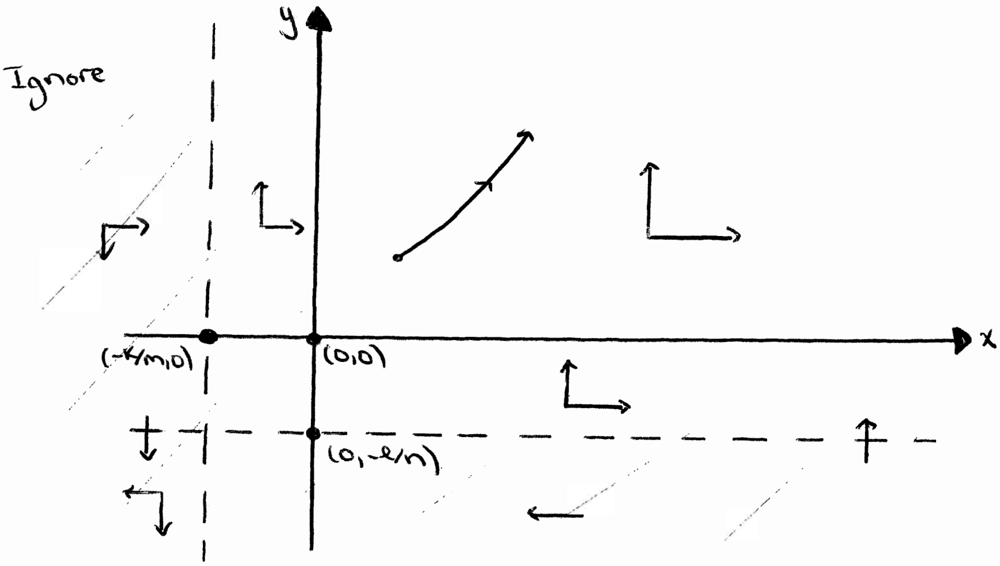
- when $y > -l/n$ this implies $l+ny>0$ → $dx/dt > 0$: move right
- when $y < -l/n$ this implies $l+ny< 0$ → $dx/dt < 0$: move left
- when $x >- k/m$ this implies $k+mx>0$ → $dy/dt > 0$: move upward
- when $x < -k/m$ this implies $k+mx<0$ → $dy/dy < 0$: move downward

$y = -l/n$



$x = -k/m$





Since we are only interested in solutions in the first quadrant, there is only one equilibrium at (0,0) which is unstable. Thus, no matter what the initial populations of each species are, both seem to grow unbounded. This conclusion is unrealistic since we know that most if not all, species eventually reach carrying capacities. This leads us to the second Lotka-Volterra model for cooperation.

Case B:

The set of equations for the Lotka-Volterra model with carrying capacities is:

$$\left.\begin{aligned} \frac{dx}{dt} &= x\left(1 - \frac{lx}{g} + ny\right) \\ \frac{dy}{dt} &= y\left(k + mx - \frac{ky}{f}\right) \end{aligned}\right\} \quad \begin{array}{l} l, g, n, k, m, f > 0 \\ \text{constants} \end{array}$$

Phase plane:

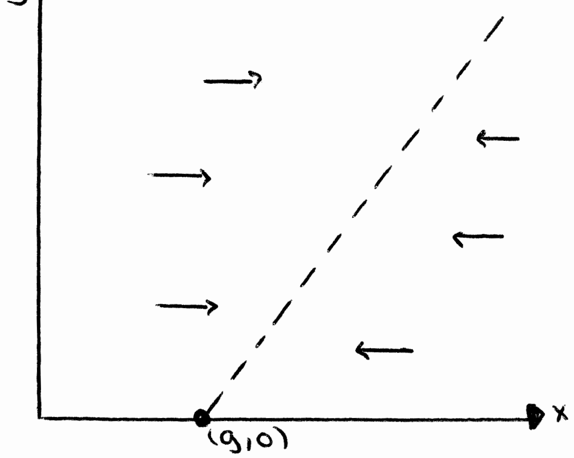
If $dx/dt = 0$: then $\begin{cases} x = 0 \\ 1 - \dfrac{lx}{g} + ny = 0 \end{cases}$

If $dy/dt = 0$: then $\begin{cases} y = 0 \\ k + mx - \dfrac{ky}{f} = 0 \end{cases}$

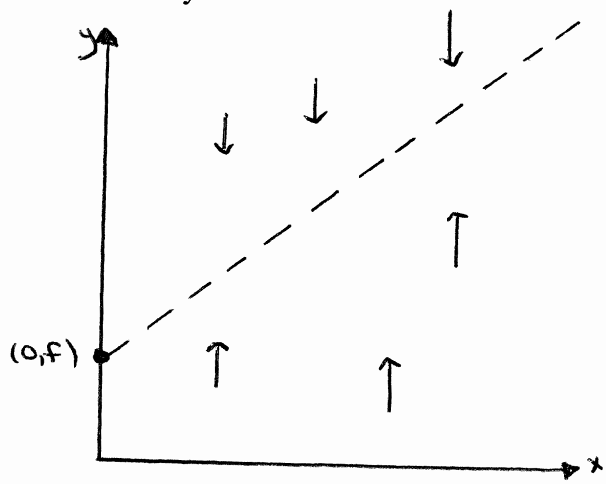
Mathematical analysis:

- Points above $l - lx/g + ny = 0$ imply $dx/dt > 0$: move right
- Points below $l - lx/g + ny = 0$ imply $dx/dt < 0$: move left
- Points above $k + mx - ky/f = 0$ imply $dy/dt < 0$: move down
- Points below $k + my - ky/f = 0$ imply $dy/dt > 0$: move up

$l\text{-}lx/g + ny = 0$



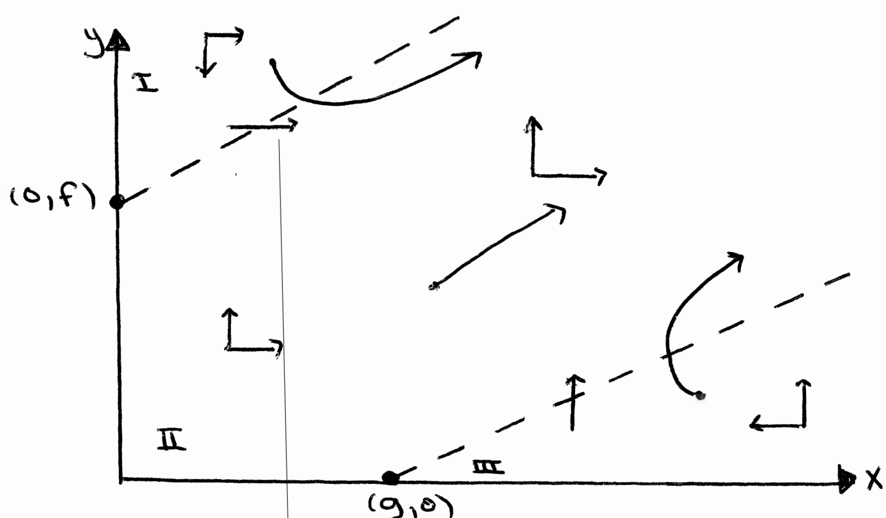
$k + mx - ky/f = 0$



There are two equilibrium points : (g, 0) ; (0,f)

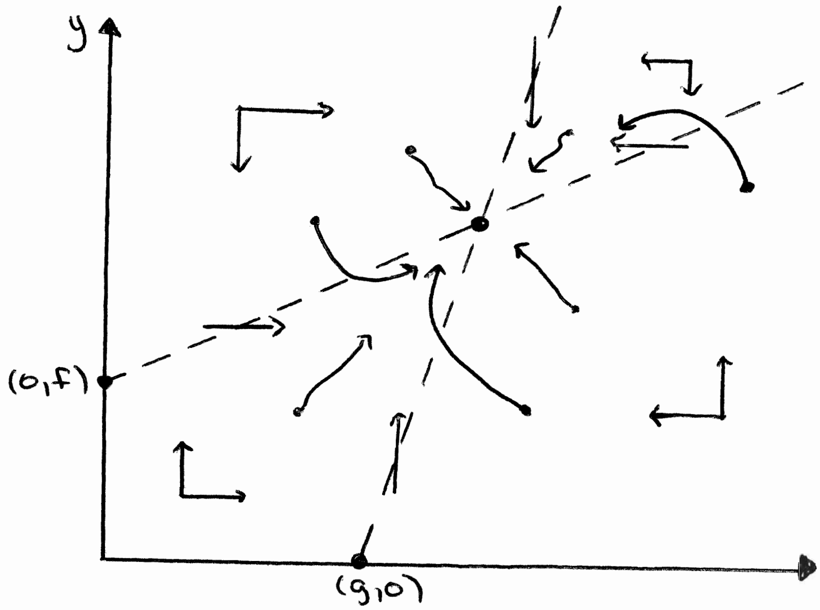
There are two cases to consider.

i.



All possible solutions starting in regions 1 & 3 cross into 2 eventually. Meanwhile, all solutions that start in 2 remain there and grow unboundedly.

ii.



Third equilibrium point exists at the intersection of the two lines:

l-lx/g+ny = 0 and k+mx-ky/f = 0

$$1 - \frac{lx}{g} + n\left(f + \frac{mxf}{k}\right) = 0 \qquad\qquad y = f + \frac{mxf}{k}$$

$$1 + nf = \frac{lx}{g} - \frac{nmxf}{k}$$

$$l + nf = x\left(\frac{l}{g} - \frac{nmf}{k}\right) = x\left(\frac{lk - nmfg}{gk}\right)$$

$$(1 + nf)\left(\frac{gk}{lk - nmfg}\right) = x \qquad\qquad \rightarrow x = \frac{gk\,(1 + nf)}{lk - nmfg}$$

$$k + m\left(\frac{gk(l+nf)}{lk - nmfg}\right) = \frac{ky}{f}$$

$$\frac{k(kl + mgl)}{(lk - nmfg)k} = \frac{y}{f} \qquad\qquad \rightarrow y = \frac{lf\,(k + mg)}{lk - nmfg}$$

Thus, an equilibrium exists at: $x = \frac{gk(l+nf)}{lk-nmfg}$ $\quad y = \frac{lk(k+mg)}{lk-nmfg}$

This equilibrium point seems to be stable since all possible trajectories approach it regardless of where they start in the xy-plane. This implies that the two species reach a point at which they can coexist together in the same environment, i.e. equilibrium is reached.

Conclusion

There are many ecological factors that have been omitted from the models I have considered including:

1. Nonuniformity of the environmental conditions. The simple models will have their best validity only over small geographical areas and short periods of time since the ecological system under investigation will not be uniform in space or in time.
2. Individual differences in organisms constituting the population.
3. The ecosystem is not isolated from the rest of the world. Animals may enter or leave at any time.
4. Random disturbances. An unexpected fire, flood, or epidemic affects population levels immediately and often with catastrophic results.
5. Effects of other species which interact with the system. For example, in the predator-prey model, the prey will have more then one enemy (predator) , while the predator does not limit its diet to just one prey.

In spite of the fact that I have not taken into account many factors, some of which are suggested above, it is sometimes found that actual populations behave in a manner very similar to that predicted by the simple models. Possible explanations for this are:

- The factors neglected may indeed be of negligible importance.
- Some of the neglected factors may be important, but may cancel each other out.
- The resemblance of a model to the real-life process it is intended to represent maybe not be as close as it seems. Closer investigation of the predictions of the model and the actual situation may reveal crucial differences.

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