Interactive Dynamic Systems

Interactive situations occur in the study of economics, ecology, electrical circuits, mechanical systems, celestial mechanics, control systems, and so forth.

For example, the study of the dynamics of population growth of various plants and animals is an important ecological application of mathematics. Different species interact in a variety of ways. One animal may serve as the primary food source for another, commonly referred to as a "predator–prey" relationship. Two species may depend upon one another for mutual support, such as a bee's using a plant's nectar as food while simultaneously pollinating that plant; such a relationship is referred to as "mutualism". Another possibility occurs when two or more species compete against one another for a common food source or even compete for survival (like a military confrontation between two armies).

In modeling interactive situations involving the dynamics of population growth, we are interested in the answers to certain questions concerning the species under investigation. For instance, will one species eventually dominate the other and drive it to extinction? Can the species coexist? If so, will their populations reach equilibrium levels, or will they vary in some predictable fashion? Moreover, how sensitive are the answers to the preceding questions relative to the initial population levels or to external perturbations (such as natural disasters, development of chemical or biological agents used to control the population, and so forth?

A Competitive Hunter Model

Let's turn our attention to how different species might compete for common resources.

Problem identification

Imagine a small pond that is mature enough to support wildlife. We desire to stock the pond with game fish, say trout and bass.

Let $x(t)$ denote the population of the trout at any time t, and let $y(t)$ denote the bass population.

- Is coexistence of the two species in the pond possible? If so, how sensitive is the final solution of population levels to the initial stockage levels and external perturbations?

Assumptions

The level of the trout population $x(t)$ depends on many variables: the initial level x_0; the capability of the environment to support trout, the amount of competition for limited resources, the existence of predators, and so forth. Initially, we assume that the environment can support an unlimited number of trout, so that in isolation:

$$\frac{dx}{dt} = ax \quad \text{for } a>0.$$

(Later we may find it desirable to refine the model and use a limited growth assumption.) Next, we modify the preceding differential equation to take into account the competition of the trout with the bass population for living space and a common food supply. The effect of the bass population is to decrease the growth rate of the trout population. This decrease is roughly proportional to the number of possible interactions between the two species, so one submodel is to assume that the decrease is proportional to the product of x and y. These considerations are modeled by the equation:

$$\frac{dx}{dt} = ax - bxy = (a-by)x. \qquad (1)$$

The intrinsic growth rate $k = a - by$ decreases as the level of the bass population increases. The constants a and b indicate the degrees of "self-regulation" of the trout population and its "competition" with the bass population, respectively. These coefficients must be determined experimentally or by analyzing historical data.

The situation for the bass population is analyzed in the same manner. Thus we obtain the following autonomous system of two first-order differential equations for our model:

$$\begin{cases} \dfrac{dx}{dt} = (a - by)x \\[2ex] \dfrac{dy}{dt} = (m - nx)y \end{cases} \qquad (2)$$

where $x(0) = x_0$, $y(0) = y_0$, and $a, b, m,$ and n are all positive constants. This model is useful in studying the growth patterns of species exhibiting competitive behavior like the trout and bass.

Analysis of the Model

One of our concerns is whether the trout and bass populations reach equilibrium levels. If so, then we will know whether coexistence of the two species in the pond is possible. The only way such a state can be achieved is that both populations stop growing; that is

$$\frac{dx}{dt} = 0, \quad \frac{dy}{dt} = 0.$$

Thus, we seek the equilibrium points of the system (2).

$$\begin{cases} (a - by)x = 0 \\ (m - nx)y = 0 \end{cases} \Rightarrow \begin{pmatrix} x = 0 \\ y = 0 \end{pmatrix} \quad \begin{pmatrix} y = a/b \\ x = m/n \end{pmatrix}$$

There are two equilibrium points $\begin{pmatrix} x = 0 \\ y = 0 \end{pmatrix}$ and $\begin{pmatrix} x = m/n \\ y = a/b \end{pmatrix}$

Are these points stable or unstable?

i) $\begin{pmatrix} x=0 \\ y=0 \end{pmatrix}$ $\quad \dfrac{dx}{dt} = ax - bxy$

$$\dfrac{dy}{dt} = my - nxy \quad \Leftrightarrow \quad \vec{x}' = \underbrace{\begin{pmatrix} a & 0 \\ 0 & m \end{pmatrix}}_{A} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} -bxy \\ -nxy \end{pmatrix}$$

The matrix $\begin{pmatrix} a & 0 \\ 0 & m \end{pmatrix}$ has two positive eigenvalues $\lambda_1 = a > 0$, $\lambda_2 = m > 0$

Then $\begin{pmatrix} x=0 \\ y=0 \end{pmatrix}$ is an unstable node.

ii) $\begin{pmatrix} x = m/n \\ y = a/b \end{pmatrix}$ Set $u = x - \frac{m}{n}$, $v = y - \frac{a}{b}$. Then

$$\frac{du}{dt} = \frac{dx}{dt} = a\left(u + \frac{m}{n}\right) - b\left(u + \frac{m}{n}\right)\left(v + \frac{a}{b}\right) = au + \frac{am}{n} - b\left(uv + \frac{a}{b}u + \frac{m}{n}v + \frac{ma}{nb}\right)$$

$$= \cancel{au} + \cancel{\frac{am}{n}} - buv - \cancel{au} - \frac{mb}{n}v - \cancel{\frac{ma}{n}} = -\frac{mb}{n}v - buv$$

$$\frac{dv}{dt} = \frac{dy}{dt} = m\left(v + \frac{a}{b}\right) - n\left(u + \frac{m}{n}\right)\left(v + \frac{a}{b}\right) = mv + \frac{ma}{b} - n\left(uv + \frac{a}{b}u + \frac{m}{n}v + \frac{ma}{nb}\right)$$

$$= \cancel{mv} + \cancel{\frac{ma}{b}} - nuv - \frac{na}{b}u - \cancel{mv} - \cancel{\frac{ma}{b}} = -\frac{na}{b}u - nuv$$

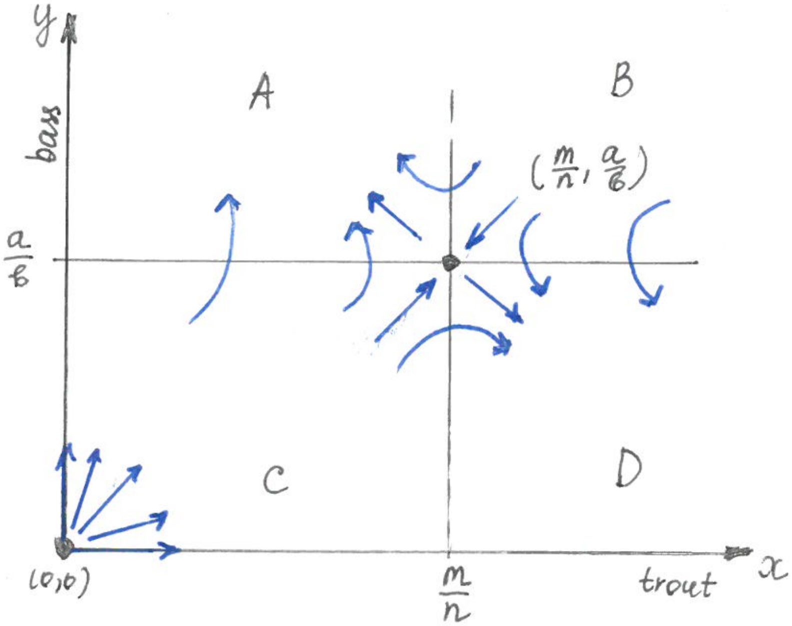
We rewrite the system in the form

$$\frac{d}{dt}\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} 0 & -\frac{mb}{n} \\ -\frac{na}{b} & 0 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} -buv \\ -nuv \end{pmatrix}$$

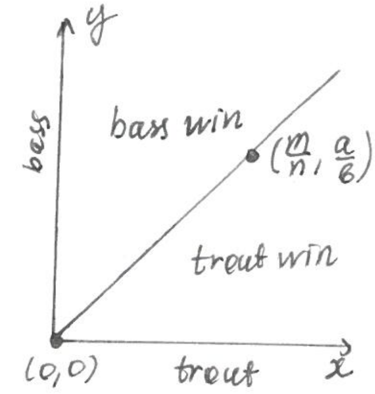
The eigenvalues of the matrix

$$\begin{pmatrix} 0 & -\frac{mb}{n} \\ -\frac{na}{b} & 0 \end{pmatrix} \text{ are } \lambda^2 - \frac{m\cancel{b}}{\cancel{n}} \cdot \frac{\cancel{n}a}{\cancel{b}} = \lambda^2 - ma = 0 \Rightarrow \lambda = \pm\sqrt{ma}$$

Therefore the equilibrium point $\begin{pmatrix} m/n \\ a/b \end{pmatrix}$ is a saddle (unstable).



Phase portrait near the equilibrium point



Qualitative results of analyzing the competitive hunter model.

Model Interpretation

The graphical analysis conducted so far **leads** us to the preliminary conclusion that, under the assumptions of our model, reaching equilibrium levels of both species is highlx unlikely. Furthermore, the initial stockage levels turns out to be important in determining which of two species might survive. Perturbations of the system may also affect the outcome of the competition. Thus, mutual coexistence of the species is highly improbable. This phenomenon is known as the Principle of Competitive Exclusion. Moreover, the initial conditions completely determine the outcome. Any perturbation causing a switch from one region (say below the line joining the two equilibrium points) to the other region (above the line) would change the outcome. Actually the curve separating the starting points in which the bass win from those in which the trout win may not be a straight line. One of the limitations of our graphical analysis is that we have not determined that separating curve precisely. If we are satisfied with our model, we may very well want to determine that separating boundary.

A Predator - Prey Model

We study a model of population growth of two species in which one species is the primary food source for the other. One example of such situation occurs in the Southern Ocean, where the baleen whales eat the Antarctic krill, Euphausia superboa, as their principle food source. Another example is wolves and rabbits in a closed forest; the wolves eat the rabbits for their principle food source and the rabbits eat vegetation in the forest. Still other examples include sea otters as predators and abalone as prey; and the ladybird beetle, Novius cardinalis, as predator and the cottony cushion insect, Icerya puchasi, as prey.

Problem Identification

Let's take a closer look at the situation of the baleen whales and Antarctic krill. The whales eat the krill live on the plankton in the sea. If the whales eat too many krill, so that the krill cease to be abundant, the food supply of the whales is greatly reduced. Then the whales will starve or leave the area in search of a new supply of krill. As the population of baleen whales dwindles, the krill population makes a comeback since not so many of them are being eaten. As the krill population increases, the food supply for the whales grows and, consequently, so does the baleen whale population. And more baleen whales are eating more and more krill again. In the pristine environment, does this cycle continue indefinitely or does one of the species eventually die out? The baleen whales in the Southern Ocean have been overexploited to the extent that their current population is around one-sixth its estimated pristine level. Thus there appears to be a surplus of Antarctic krill. (Already something like 100,000 tons of krill are being harvested annually.) What effect does exploitation of the whales have on the balance between the whale and krill populations? What are the implications that a krill fishery may hold for the depleted stocks of baleen whales and for other species like seals, seabirds, penguins, and fish that depend on krill for their main source of food?

The ability to answer such questions is important to management of multispecies fisheries.

Assumptions

Let $x(t)$ denote the Antarctic krill population at any time t, and let $y(t)$ denote the population of baleen whales in the Southern Ocean. The level of the krill population depends on a number of factors including the ability of the ocean to support them, the existence of competitors for the plankton they ingest, the presence and levels of predators, and so forth. As a rough, first model, let's start by assuming that the ocean can support an unlimited number of krill so that

$$\frac{dx}{dt} = ax \qquad \text{for } a > 0.$$

Second, assume that the krill are eaten primarily by the baleen whales (so neglect any other predators). Then the growth rate of the krill is diminished in a way that is proportional to the number of interactions between them and the baleen whales. One interaction assumption leads to the differential equation:

$$\frac{dx}{dt} = ax - bxy = (a - by)x \qquad (3)$$

Notice that the intrinsic growth rate $k = a - by$ decreases as the level of the baleen whale population increases. The constants a and b indicate the degrees of "self-regulation" of the krill population and the "predatoriness" of the baleen whales, respectively. These coefficients must be determined experimentally or from historical data. So far our first equation (3) governing the growth of the krill population looks just like either of the equations in the competitive hunter model.

Next, consider the baleen whale population $y(t)$. In the absence of krill the whales have no food, so we will assume that their population declines at a rate proportional to their numbers. This assumption produces the exponential decay equation:

$$\frac{dy}{dt} = -my \qquad \text{for } m>0$$

However, in the presence of krill the baleen whale population increases at a rate proportional to the interactions between the whales and their krill food supply. Thus, the preceding equation is modified to give

$$\frac{dy}{dt} = -my + nxy = (-m+nx)y \qquad (4)$$

Notice from (4) that the intrinsic growth rate $r=-m+nx$ of the whales increases as the level of the krill population increases. The positive coefficients m and n would be determined experimentally or from historical data. Putting the results (3) and (4) together gives the following autonomous system of differential equations for our predator-prey model:

$$\begin{cases} \dfrac{dx}{dt} = (a-by)x \\ \dfrac{dy}{dt} = (-m+nx)y \end{cases} \qquad (5)$$

where $x(0)=x_0$, $y(0)=y_0$, a, b, m, and n are all positive constants. The system (5) governs the interaction of the baleen whales and Antarctic krill populations under our unlimited growth assumptions and in the absence of their competitors and predators.

Graphical Analysis of the Model

Let's determine whether the krill and whale populations reach equilibrium levels.

Equilibrium points:

$$\left.\begin{aligned} \frac{dx}{dt} &= 0 = (a-by)x \\ \frac{dy}{dt} &= 0 = (-m+nx)y. \end{aligned}\right\} \Rightarrow \begin{pmatrix} x=0 \\ y=0 \end{pmatrix} \ \& \ \begin{pmatrix} x = m/n \\ y = a/b \end{pmatrix}$$

Are these points stable or unstable?

(i) $\begin{pmatrix} x=0 \\ y=0 \end{pmatrix}$

$$\begin{aligned} \frac{dx}{dt} &= ax - bxy \\ \frac{dy}{dt} &= -my + nxy \end{aligned} \Rightarrow \begin{pmatrix} x \\ y \end{pmatrix}' = \underbrace{\begin{pmatrix} a & 0 \\ 0 & -m \end{pmatrix}}_{A} \begin{pmatrix} x \\ y \end{pmatrix} + \underbrace{\begin{pmatrix} -bxy \\ nxy \end{pmatrix}}_{\vec{g}(x,y)}$$

The matrix $\begin{pmatrix} a & 0 \\ 0 & -m \end{pmatrix}$ has two eigenvalues $\lambda_1 = a > 0$, $\lambda_2 = -m < 0$.

Then $\begin{pmatrix} x=0 \\ y=0 \end{pmatrix}$ is an unstable saddle.

ii) $\begin{pmatrix} x = m/n \\ y = a/b \end{pmatrix}$ Set $u = x - \frac{m}{n}$, $v = y - \frac{a}{b}$. Then

$$\frac{du}{dt} = \frac{dx}{dt} = a\left(u + \frac{m}{n}\right) - b\left(u + \frac{m}{n}\right)\left(v + \frac{a}{b}\right) = -\frac{mb}{n}v - buv$$

$$\frac{dv}{dt} = \frac{dy}{dt} = -m\left(v + \frac{a}{b}\right) + n\left(u + \frac{m}{n}\right)\left(v + \frac{a}{b}\right) = -mv - \frac{ma}{b} + n\left(uv + \frac{a}{b}u + \frac{m}{n}v + \frac{ma}{nb}\right)$$

$$= \cancel{-mv} - \cancel{\frac{ma}{b}} + nuv + \frac{na}{b}u + \cancel{mv} + \cancel{\frac{ma}{b}} = \frac{na}{b}u + nuv$$

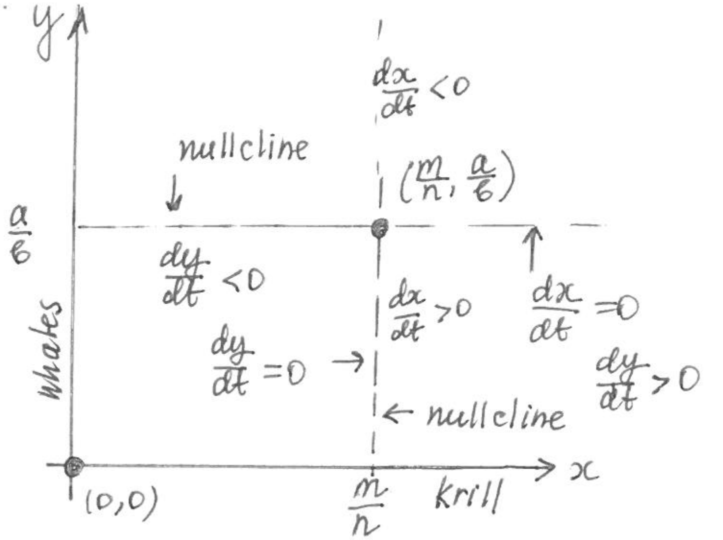
We rewrite the system in the form

$$\frac{d}{dt}\begin{pmatrix} u \\ v \end{pmatrix} = \underbrace{\begin{pmatrix} 0 & -\frac{mb}{n} \\ \frac{na}{b} & 0 \end{pmatrix}}_{A} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} -buv \\ nuv \end{pmatrix}$$

The eigenvalues of the matrix A $\quad \lambda^2 + \frac{m\cancel{b}}{\cancel{n}} \cdot \frac{\cancel{n}a}{\cancel{b}} = 0 \Rightarrow \lambda = \pm i\sqrt{ma}$

are pure imaginary. The equilibrium point $\left(\frac{m}{n}, \frac{a}{b}\right)$ is more complicated to analyze.

We cannot tell whether the motion is periodic, asymptotically stable, or unstable. Thus we must perform a further analysis. What we have:

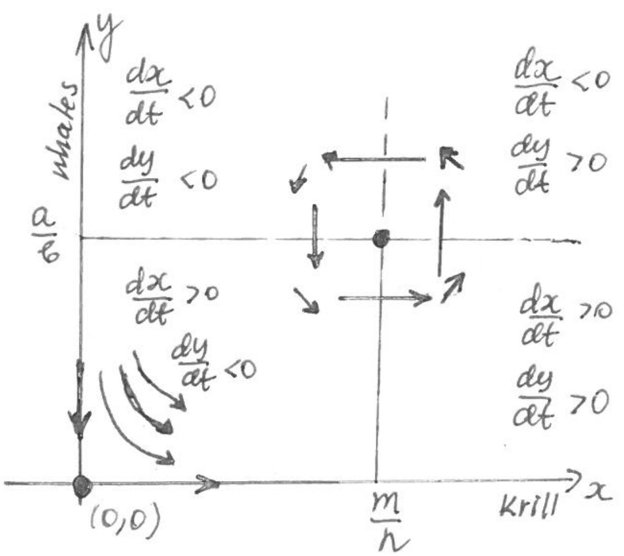


Along the vertical line $x = \frac{m}{n}$ and the x-axis in the phase plane, the growth dy/dt in the baleen whale population is zero; along the horizontal line $y = a/b$ and the y-axis, the growth dx/dt in the krill population is zero.

We analyze the directions of dx/dt and dy/dt in the phase plane.

The vertical line $x = m/n$ divides the phase plane into two half-planes. In the left half-plane, dy/dt is negative, and in the right half-plane it is positive. In the similar way, the horizontal line $y = a/b$ determines two half-planes. In the upper half-plane, dx/dt is negative, and in the lower half-plane it is positive.

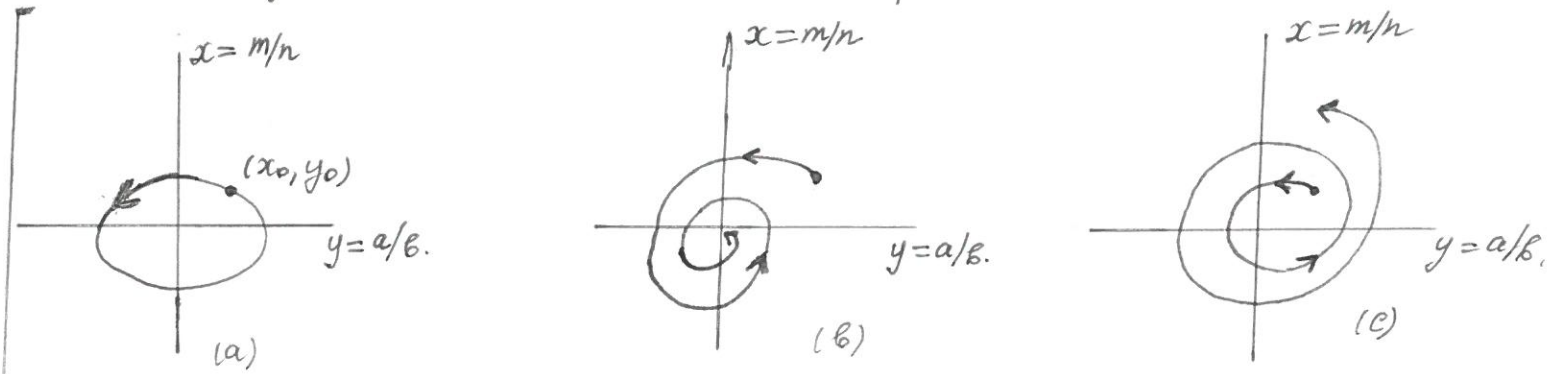
The directions of the associated trajectories are indicated below



Along the y-axis, motion must be vertical and toward the equilibrium point $(0,0)$, and along the x-axis, motion must be horitontal and away from the equilibrium point $(0,0)$.

We can see that the equilibrium point $(0,0)$ is unstable. Entrance to the point is along the line $x = 0$, where there is no krill population. Thus the whale whale population declines to zero in the absence of its primary food supply. All other trajectories recede from the equilibrium point

The equilibrium point $(m/n, a/b)$ is more complicated to analyze. The information given by the figure is insufficient to distinguish between the three possible motions:



These possible trajectory motions (a) periodic motion, (b) motion toward an asymptotically stable equilibrium point; and (c) motion near an unstable equilibrium point.

An analytic solution of the model

The system has the family of solutions

$$\begin{pmatrix} x(t) = x_0 e^{at} \\ y(t) = 0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} x(t) = 0 \\ y(t) = y_0 e^{-mt} \end{pmatrix}$$

Thus, both the x and y axes are trajectories of the system. This implies that every solution $x(t), y(t)$ of (5) which starts in the first quadrant $x > 0, y > 0$ at time $t = t_0$ will remain there for all future time $t \geq t_0$.

The trajectories of (5), for $x, y \neq 0$ are the solution curves of the first-order equation

$$\frac{dy}{dx} = \frac{(-m + nx)y}{(a - by)x}$$

This equation is separable, since we can write it in the form

$$\frac{(a - by)}{y} dy = \frac{(-m + nx)}{x} dx \iff \left(\frac{a}{y} - b\right) dy = \left(-\frac{m}{x} + n\right) dx$$

Integration of each side yields

$$a \ln y - by = nx - m \ln x + k_1$$

or

$$a \ln y + m \ln x - by - nx = k_1$$

where k_1 is a constant.

Using properties of the natural logarithm and exponential functions, this last equation can be rewritten as

$$\frac{y^a x^m}{e^{by+nx}} = K \quad \text{or} \quad \frac{y^a}{e^{by}} \cdot \frac{x^m}{e^{nx}} = K \qquad (6)$$

where K is a constant. This equation defines the solution trajectories in the phase plane. We now show that these trajectories are closed and represent periodic motion.

The predator-prey trajectories are periodic

Lemma 1 Equation (6) defines a family of closed curves for $x, y > 0$.

Proof Our first step is to determine the behavior of the functions

$$f(y) = \frac{y^a}{e^{by}} \quad \text{and} \quad g(x) = \frac{x^m}{e^{nx}} \quad \text{for } x \text{ and } y \text{ positive.}$$

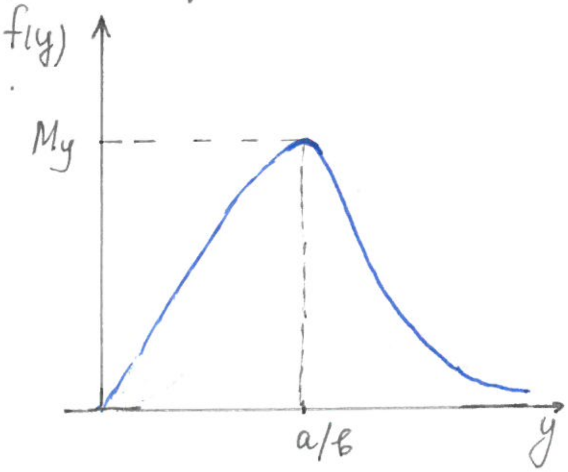
Observe that $f(0) = 0$, $f(\infty) = 0$, and $f(y) > 0$ for $y > 0$. Computing

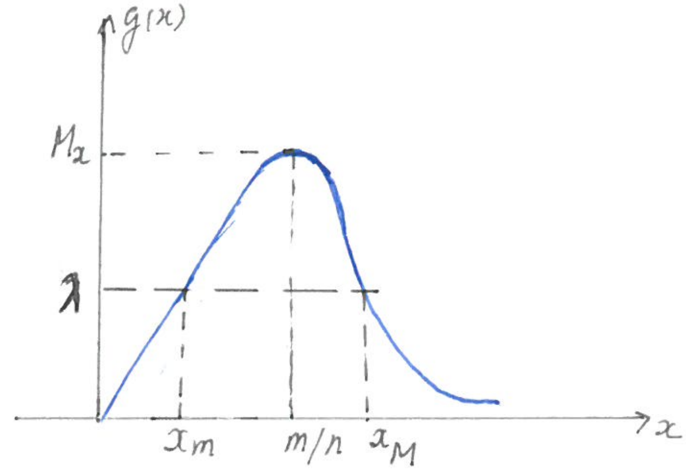
$$f'(y) = a y^{a-1} e^{-by} + y^a e^{-by} \cdot (-b) = \frac{a y^{a-1} - b y^a}{e^{by}} = \frac{y^{a-1}(a - by)}{e^{by}},$$

we see that $f(y)$ has a single critical point at $y = a/b$. Consequentely, $f(y)$ achieves its maximum value

$$M_y = \frac{(a/b)^a}{e^a} \quad \text{at } y = a/b \text{, and}$$

the graph of $f(y)$ has the form:





Similarly, $g(x)$ achieves its maximum value

$$M_x = \frac{(m/n)^m}{e^{mx}} \quad \text{at} \quad x = m/n.$$

From this analysis we conclude that equation (6) has no solution $x, y > 0$ for $K > M_x M_y$, and the single solution

$$x = m/n \quad \text{and} \quad y = a/b \quad \text{for} \quad K = M_x M_y.$$

Thus, we need only consider the case $K = \lambda M_y$, where λ is a positive number less than M_x.

Observe first that the equation $\frac{x^m}{e^{nx}} = \lambda$ has one solution $x = x_m < \frac{m}{n}$, and one solution $x = x_M > m/n$.

Hence, the equation

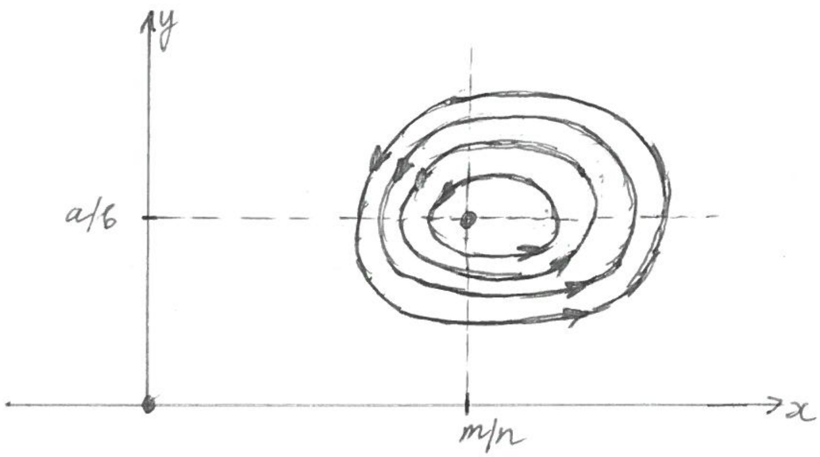
$$f(y) = y^a e^{-by} = \left(\frac{\lambda}{x^m e^{-nx}}\right) M_y$$

$$\boxed{\begin{aligned} &\text{If } x < x_m \Rightarrow x^m e^{-nx} < \lambda \Rightarrow \\ &\lambda \cdot e^{nx} x^{-m} > 1 \Rightarrow \\ &f(y) = y^a e^{-by} = K e^{nx} x^{-m} \\ &\quad = \lambda M_y e^{nx} x^{-m} > M_y \end{aligned}}$$

has no solution y when $x < x_m$ or $x > x_M$. It has the single solution $y = a/b$ when $x = x_m$ or $x = x_M$, and it has two solutions $y_1(x)$ and $y_2(x)$ for each x between x_m and x_M.

- The smaller solution $y_1(x)$ is always less than a/b, while the larger solution $y_2(x)$ is always greater than a/b.

- As x approaches either x_m or x_M, both $y_1(x)$ and $y_2(x)$ approaches a/b. Consequently, the curves defined by (6) are closed for x and y positive, and have the following form



Moreover, none of these closed curves (with the exception of $x = m/n$, $y = a/b$) contain any equilibrium points of (5). Therefore, all solutions $x(t), y(t)$ of (5), with $x(0)$ and $y(0)$ positive, are periodic functions of time.

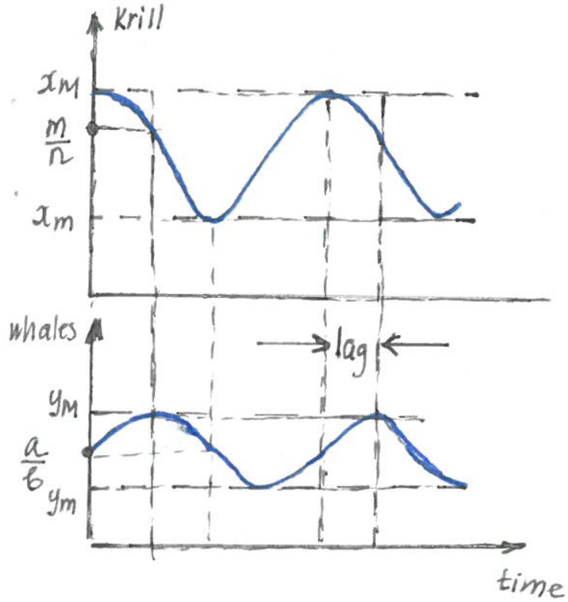
That is to say, each solution $x(t)$, $y(t)$ of (5) with $x(0)$ and $y(0)$ positive, has the property that

$$x(t+T) = x(t) \quad \text{and} \quad y(t+T) = y(t) \text{ for some positive } T.$$

Model Interpretation.

What conclusions can be drawn from the trajectories? First, because the trajectories are closed curves, they predict that, under the assumptions of our model (5), neither the baleen whales nor the Antarctic krill will become extinct.

The second observation is that along a single trajectory the two populations fluctuate between their maximum and minimum values. That is, starting with populations in the region where $x > m/n$ and $y > a/b$, the krill population will decline and the whale population increase untill the krill population reaches the level $x = m/n$, at which point the whale population also begins to decline. Both populations continue to decline until the whale population reaches the level $y = a/b$ and the krill population begins to increase. And so on, around the trajectory. <u>Recall that the trajectories never cross.</u>



The whale population lags behind the krill population as both populations fluctuate cyclically between their maximum and minimum values.

In the sketch we can see the krill population fluctuates between its maximum and minimum values over one complete cycle. Notice that when the krill are plentiful, the whale population has its maximum rate of increase, but that the whale population reaches its maximum value after the krill population is on the decline. The predator lags behind the prey in a cyclic fashion.

The effects of harvesting

For given initial population levels $x(0) = x_0$ and $y(0) = y_0$, the whale and krill populations will fluctuate with time around one of the closed trajectories.

Let T denote the time it takes to complete one full cycle and return to the starting point. Now the average levels of the krill and baleen whale populations over the time cycle are defined by the integrals

$$\bar{x} = \frac{1}{T}\int_0^T x(t)\,dt \qquad \text{and} \qquad \bar{y} = \frac{1}{T}\int_0^T y(t)\,dt$$

respectively. Now, from equation $\frac{dx}{dt} = ax - bxy = (a - by)x$,

$$\frac{1}{x}\left(\frac{dx}{dt}\right) = a - by$$

so that integration of both sides from $t=0$ to $t=T$ leads to

$$\int_0^T \left(\frac{1}{x}\right)\left(\frac{dx}{dt}\right) dt = \int_0^T (a-by)\, dt$$

or $$\ln(x(T)) - \ln(x(0)) = aT - b\int_0^T y(t)\,dt$$

Because of the periodicity of the trajectory, $x(T)=x(0)$, and this last equation gives the average value:

$$\bar{y} = \frac{a}{b}$$

In an analogous manner, it can be shown that

$$\bar{x} = \frac{m}{n}.$$

Therefore, the average levels of the predator and prey populations are in fact their equilibrium levels. Let's see what this means in terms of harvesting krill.

Let's assume that the effect of fishing for krill is to decrease its population level at a rate $rx(t)$. The constant r indicates the "intensity" of fishing and includes such factors as the number of fishing vessels at sea, the number of fishermen casting nets for krill, and so forth. Since less food is now available for the baleen whales, assume the whale population also decreases at a rate $ry(t)$. Incorporating these fishing assumptions into our model, we obtain the refined model:

$$\frac{dx}{dt} = (a-by)x - rx = [(a-r) - by]x \qquad (7)$$

$$\frac{dy}{dt} = (-m+nx)y - ry = [-(m+r) + nx]y$$

The autonomous system (7) is of the same form as (5) (provided that $a-r>0$) with a replaced by $a-r$ and m replaced by $m+r$. Thus, the new average population levels will be

$$\bar{x} = \frac{m+r}{n} \quad \text{and} \quad \bar{y} = \frac{a-r}{b}$$

Consequentley, a moderate amount of harvesting krill (so that $r<a$) actually increases the average level of krill and decreases the average baleen whale population (under our assumptions for the model.) The increase in krill population is beneficial to other species in the Southern Ocean (seals, seabirds, penguins, and fish) that depend on the krill for their main food source. The fact that some fishing increases the number of krill is known as Volterra's principle.
The autonomous system (5) was first proposed by Lotka (1925) and Volterra (1931) as a simple model of predator-prey interaction.

Conversely, a reduced level of of fishing increases the number of whales, on the average, decreases the number of krill.

The Lotka-Volterra model can be modified to reflect the situation in which both the predator and the prey are diminished by some kind of depleting force, such as when applying insecticide treatments that destroy both the insect predator and its insect prey.

In 1868 the accidental introduction into the United States of the cottony cushion insect (Icerya purchasi) from Australia threatened to destroy the American citrus industry. To counteract this situation, a natural Australian predator, a ladybird beetle (Novius cardinalis) was imported. The beetles kept the scale insects down to a relatively low level. When DDT was discovered to kill scale insects, formers applied in in the hopes of reducing even further the scale insect population. However, DDT turned out to be fatal to the beetle as well and the overall effect of using the insecticide was to increase the numbers of the scale insects.

The number of biologists and ecologists argue that the Lotka-Volterra model (5) is unrealistic because the system is not asymptotically stable, whereas most observable natural predator-prey systems tend to equilibrium levels as time evolves. Nevertheless, regular population cycles, as suggested by the trajectories do occur in nature. Some scientists have proposed models other than the Lotka-Volterra model that do exhibit oscillations that are asymptotically stable (so that the trajectories approach equilibrium solutions). One such model is given by

$$\frac{dx}{dt} = ax + bxy - rx^2$$

$$\frac{dy}{dt} = -my + nxy - sy^2$$

In this last autonomous system, the term rx^2 indicates the degree of internal competition of the prey for their limited resource (such as food and space), and the term sy^2 indicates the degree of competition among the predators for the finite amount of available prey. An analysis of this model is more difficult than that presented for the Lotka-Volterra model, but it can be shown that the trajectories of the model are not periodic and tend to equilibrium levels. The constants r and s are positive and would be determined by experimentation or historical data.