6.337 Project Mathematical Modelling Interacting Populations: Predator Prey Model Prof: Dr. T.G. Berry

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Interacting Populations Predator Prey Model - Modified Lotka Volterra model

I. Introduction

of a biological system. In particular a two species system with interaction between the species. The type of model studied in the species of the speci a direct relationship between two species. This type of phenomenon occurs frequently in nature in a wide scope of areas.

One example, of a predator prey model is the relation between the snowshoe rabbit and the lynx species. From previous historical records of the pelts of the lynx and the snowshoe rabbit a periodic pattern of the populations of each species suggests that there is a dependency between them. By comparison of the populations of each species in the same time frame, suggest that the lynx (as the predator) and the snowshoe rabbit (as the prey) have a cyclic population pattern. Other occurrences of wildlife predator prey relationships occur for small rodents, rabbits, grouse as prey species and foxes, lynx as predator species.

Certain sets of aquatic species appear to have cyclic population pattern. In particular the interaction between small plankton-eating fish and sharks that feed on these small fish. If the effect of fishing by fishermen is removed and the only predator of the small fish are the sharks then a predator prey relation can exist. With the unlimited environment of the sea the prey species would thrive causing a direct increase in the shark population and further on exhibiting a cyclic pattern in populations. This type of model can be further expanded to include two types of fish with one being the prey and the other being the predator.

The models of any particular predator prey relation between species can be useful in the conservation of either species. Certain decisions on introducing species into different environments at a specific time in the cycle of the system can be either of the extremes of being disastrous or beneficial. Also the model presented in this project will give a clearer understanding of a relationship between species.

II. Abstraction

In nature, there are certain species which have a dependency between each other. One relationship that has interesting interpretation is the predator prey phenomenon. Through experimental and general observations certain predator and prey species exhibit cyclic patterns in terms of population. The predator species for this model refers to the species which feeds solely upon the prey species. The prey species for this model refers to the species which has an abundant food supply not directly related to the predator species.

Particular observed population data reflects certain trends such as:

When the prey population is high the predator's thrive and thus a sharp increase in the predator's population occurs.

When both the predator and prey populations are high then the predator population tends to increase thus causing a decrease in the prey population.

When the predator population is high the prey population decreases.

When both the predator and prey populations are low the prey population tends to increase due to the abundant food supply.

And then a repetition of these trends occurs in sequence.

It would be helpful to predict the populations of either the predator or prey species or predict the change in the populations of either species based on population trends. Also, based on the present and past knowledge of the two species will a species become extinct or become over populated? Another question would be to determine if either species population would reach a lower limit and be in danger of becoming extinct. Through the following mathematical analysis, some of these question or statements can be answered and help explain the behavior of either species.

It is plausible to suggest that the tendencies of both species populations can be modelled based upon the following relations and key assumptions.

Define the following variables:

Let x represent the population of the prey species.

Let y represent the population of the predator species.

Let t represent time.

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NOTE: The variables x and y are discrete non-continuous variables and the variable t is a continuous variable. However, in order to analyze this problem mathematically we will assume that x and y are continuous and later interpret the results as discrete values.

Therefore dx/dt is the rate of change in the prey species population over time t.

Therefore dy/dt is the rate of change in the predator species population over time t.

Assumption #1: The prey species is the only food source for the predator species. This assumption will allow for the determination of the predator species population to be solely dependent on the prey as a source of food. This interprets as the predators population is solely determined by the prey population. Any change in population of the prey species will cause a change in the predator population.

Assumption #2: The population of the prey species has a maximal carrying capacity based on a limited environment. This assumption will allow for the model to place a limit on the number of species of the prey population in relation to a limited environment.

First consider the relative growth or decline in population of each species in the absence of other. That is consider the prey species with no predators and the predator species with no prey.

Assumption #3: If the population consists only of the predator species type then the predator species will exhibit a Malthusian decline in population. This assumption sets the generalized behavior of the population of the predator. This translates into the equation: dy/dt = -l y

where l is a positive constant of proportionality.

This relation says that the change in population of the predator is proportional to the present population of the predator y. Or in other words the predator population exhibits a Malthusian decay. Assumption #4: If the population consists only of the prey species type then the prey species will exhibit a Logistic growth with a certain set carrying capacity. This assumption sets the generalized behavior of the population of the prey. This translates into the equation: dx/dt = kx(1-x/C)

where k is positive constant.

where C is a constant carrying capacity of the environment for the prey species which is also positive.

This relation says that the change in population of the prey is (the potential growth rate) times (the proportion of the population yet to be realized). Or in other words the prey population exhibits logistic growth.

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The effective changes in population of either species is influenced by the encounters between each species. The number of encounters that can occur between pairs of each species is x time y or (xy). Effectively the xy term represents the interdependence of the predator and prey species.

Assumption #5: The interaction between the species is detrimental to the prey species and beneficial to the predator species at rates proportional to xy. The proportional rates allow for a relative measure of the influence of one species on

This produces the following model

$$dx/dt = kx(1-x/C) - nxy$$
 (1)

dy/dt = -1y + mxy

another.

where n and m are positive constants of proportionality.

Assumption #6: An important underlying assumption is that the only changes relating to either populations of the species are due to the existence of each species. No outer influence will be considered in changing the population of the species. This assumption simplifies the focus of the model towards the relationship between the species rather than the relationship of the environment surrounding the species.

Motivation?

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III. Mathematical Analysis:

The equation set (1)above is a nonlinear differential autonomous system of equations. Since there is no known way to solve the system in general, with the use of qualitative theory certain properties of the solutions can be determined. The mathematical restrictions on the system of equation are as follows:

$$dx/dt = kx(1-x/C) - nxy$$

 $dy/dt = -l y + mxy$

k, l, m, n, and C are positive constants (>0)

x, y are populations of the prey and predator species respectively thus x and y are nonnegative(>=0). This places the solutions meaningful to the model in the first quadrant (i.e. x>=0 and y>=0).

Phase Plane analysis

In order to concentrate the phase plane analysis on the relation between x and y, the time dependency is suppressed. The modified phase plane analysis will project the solution curve of the system onto the xy - plane. This is known as the orbits, trajectory or path of the system of equations. The property of the system of equations being autonomous allows for this kind of phase plane analysis.



Determination of nullclines:

$$dx/dt = kx(1-x/C) - nxy$$
$$= x(k - kx/C - ny)$$

Consider the nullclines of x in which dx/dt = 0.

$$0 = x (k - kx/C - ny)$$

Either
$$x=0$$
 or $k - kx/C - ny = 0$

The nullcline x=0 is a vertical line passing through the origin.

The nullcline k - kx/C - ny = 0 can be written in the two forms:

$$y = k/n - kx/Cn$$

 $x = C - Cny/k$

in which the form y = k/n - kx/Cn is a straight line with y-intercept k/n. Since k,C,n are non-negative the slope of the line is -k/Cn which is a negative slope. From the second form of this equation the x-intercept is determined to be C. This equation will be denoted (for later reference) by

Lx:
$$y=k/n - kx/Cn$$

The trajectories in the phase plane cross the x nullclines vertically.

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Consider the nullclines of y.
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$$dy/dt = -1 y + mxy$$
$$= y (mx - 1)$$

Nullclines of y occur where dy/dt = 0.

$$0 = v (mx - 1)$$

Either y=0 or mx-l=0

The nullcline y=0 is a horizontal line passing through the origin.

The nullcline mx-l=0 can be written in the form x=l/m. This nullcline is a vertical line passing through the point x=l/m, y=0. Since l and m are both greater than 0 thus l/m is greater than 0.

The trajectories in the phase plane cross the y nullclines horizontally.

Determining the direction elements of the phase plane on either side of each nullcline. Lets consider the following cases:

I. If
$$x < 1/m$$

mx<1

mx-l<0

but dy/dt = y (mx - l)

Since $y \ge 0$ and mx-1 < 0 this gives dy/dt < = 0.

Thus for x < 1/m the y direction element is decreasing.

II. If x>1/m

mx>1

mx-l>0

but dy/dt = y (mx - l)

Since y>=0 and mx-l>0 this gives dy/dt>=0.

Thus for x>1/m the y direction element is increasing.

III. If
$$y < -kx/Cn+k/n$$

$$ny < -kx/C + k$$

$$0 < -kx/C + k -ny$$

but
$$dx/dt = -kx^2/C + kx - nxy = x(-kx/C + k - ny)$$

Since x > = 0 and 0 < -kx/C + k -ny this gives dx/dt > = 0.

Thus for y < -kx/Cn+k/n the x direction element is increasing.

IV. If
$$y > -kx/Cn+k/n$$

$$ny > -kx/C + k$$

for considered?

$$0 > -kx/C + k -ny$$

but $dx/dt = -kx^2/C + kx - nxy = x(-kx/C + k - ny)$

Since x>=0 and 0>-kx/C+k-ny this gives dx/dt <=0.

Thus for y > -kx/Cn+k/n the x direction element is decreasing.

The nullclines determined split the phase plane solutions into three different cases, when only solutions in the first quadrant are considered.

Case 1: The line Lx has a x-intercept less than 1/m.

Case 2: The line Lx has a x-intercept equal to 1/m.

Case 3: The line Lx has a x-intercept greater than 1/m.

In order to analysis the stability of equilibrium points, the use of the following theorem will aid in this analysis. This theorem is taken from the book ¹An Introduction to Differential Equations and Their Applications by S.L. Campbell page 504-505.

Theorem

The system of nonlinear autonomous equations

$$x'=f(x,y). (1)$$

$$y'=g(x,y).$$

Suppose that (r,s) is an equilibrium point of (1).

Define $a=f_X(r,s)$

 $b=f_V(r,s)$

 $c=g_X(r,s)$

 $d=g_V(r,s)$

Let v₁,v₂ be roots of the characteristic polynomial

$$v^2$$
 - (a+d)v + ad - bc

Then

- 1. If $v_1,v_2>0$ then equilibrium is unstable.
- 2. If v₁,v₂<0 then equilibrium is asymptotically stable.
- 3. If v₁,v₂ are nonzero and of opposite signs, the equilibrium is unstable.

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¹Stephen L. Campbell, <u>An Introduction to Differential Equations and Their Applications</u>, 2nd ed. (Belmount: Wadsworth Publishing Company, 1990), p. 504.

- 4. If v_1 and v_2 are complex conjugates and v_1 =A+Bi, v_2 =A-Bi with B not equal 0, then A>0 means the equilibrium is unstable and a spiral repeller, while A<0 means the equilibrium is asymptotically stable and a spiral attractor.
- 5. If v_1 or $v_2=0$ then no immediate information is given.

The partial derivatives required to use this theorem for our analysis are as follows:

$$a=f_X(x,y) = k - 2kx/C - ny$$

$$b=f_Y(x,y) = -nx$$

$$c=g_X(x,y) = my$$

$$d=g_Y(x,y) = mx-1$$

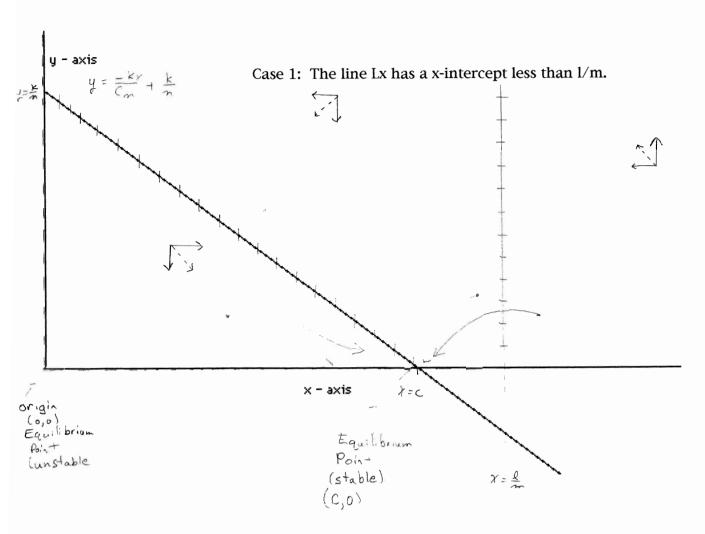
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There is one common equilibrium point x=0,y=0 which exists in each of the three cases. This point corresponds to the situation where there are zero predators and zero prey. Through the analysis of above, the values obtained are a=k, b=0,c=0,d=1. The resulting equation is $v^2 - (k+1)v + k1$ with roots 1 and k which are both positive. By the theorem this point is unstable (section 1). To expand on this equilibrium, it is unstable since any increase in the number of prey x cause a logistic growth in x by the equation dx/dt = kx(1-x/C) - nxy = kx(1-x/C) since y=0. This result is due to the assumption #4.

However, if only the number of predators y is increased the system returns to the equilibrium x=0,y=0 by a Malthusian decay equation. The equation dy/dt = -l y + mxy becomes dy/dt=-ly since x=0. This indicates any change in only the y variable causes a Malthusian decay of the y predators back to the equilibrium point x=0,y=0. This result is due to the assumption #3. From the equilibrium point x=0,y=0 an increase in both x and y (i.e. the number of predators and number of prey) causes the system to move away from the x=0,y=0 equilibrium.

Considering each case separately the equilibrium points will be determined and anticipated trajectories will be sketched on the following pages.

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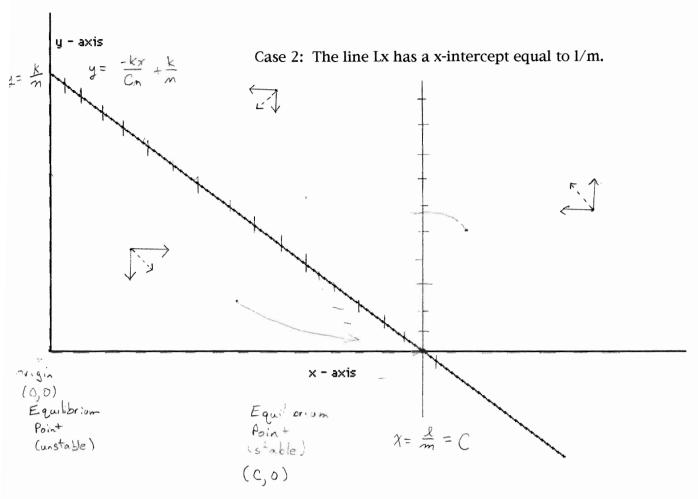
Case 1: The line Lx has a x-intercept less than 1/m. (i.e. C < 1/m) By the phase plane analysis there are two equilibrium points which are x=0,y=0 and y=0,x=C.

Consider the equilibrium point y=0,x=C. Through the analysis of the previous theorem the values a=k-2k, b=-nC, c=0, d=mC-l are obtained. The resulting equation is v^2 - (-k + mC-l)v + -k(mC-l) with roots v_1 = -k and v_2 =mC-l. Consider the sign of mC-l, by the case I condition

C<1/m

mC-l<0 which indicates v2<0

Also, since k>0, we have -k<0. Therefore both roots v_1 and v_2 are less than zero and by theorem this point is a stable equilibrium (section 2).

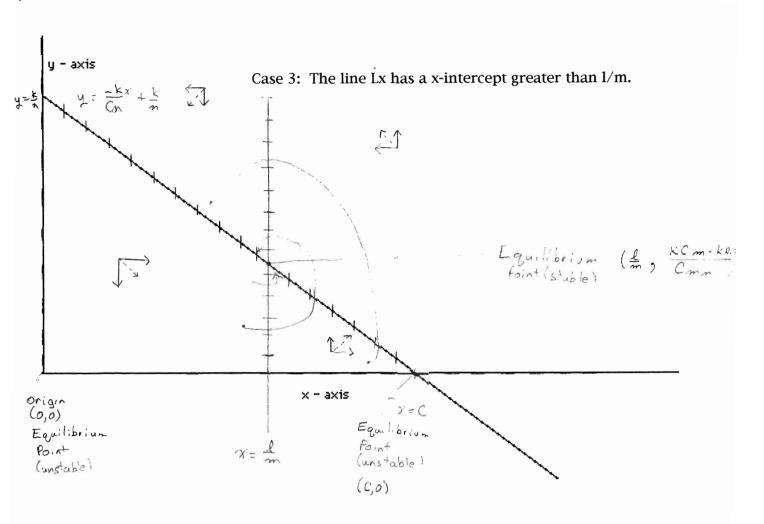


Case 2: The line Lx has a x-intercept equal to 1/m.

By the phase plane analysis there are two equilibrium points which are x=0,y=0 and y=0,x=C=1/m.

Consider the equilibrium point y=0,x=C=l/m. Through the analysis of the previous theorem the values a=k-2k, b=-nC, c=0, d=mC-l are obtained. The resulting equation is v^2 - (-k + mC-l)v + -k(mC-l) with roots v_1 = -k and v_2 =mC-l. Consider the sign of mC-l/by the case II condition

This gives v2=0, thus the resulting relations applied to the theorem gives no information about the stability of the equilibrium point. However, the sketched trajectories in the phase plain suggest that the equilibrium point y=0, x=C=1/m is stable.



Case 3: The line Lx has a x-intercept greater than 1/m.

By the phase plane analysis there are three equilibrium points which are x=0,y=0 and y=0,x=C and x=1/m, y=(kCm-kl)/Cmn.

Consider the equilibrium point y=0,x=C. Through the analysis of the previous theorem the values a=k-2k, b=-nC, c=0, d=mC-l are obtained. The resulting equation is v^2 - (-k + mC-l)v + -k(mC-l) with roots v_1 = -k and v_2 =mC-l. Consider the sign of mC-l, by the case III condition

C>l/m mC-l>0 which indicates v₂>0

Also since k>0, we have -k<0. Therefore the root $v_1<0$ and the root $v_2>0$ and by theorem this point is a unstable equilibrium (section 3). However, if y=0, always, and a change in x occurs the system returns to equilibrium y=0,x=C. This is due to the equation $dx/dt = x(-kx/C + k - ny) = -kx^2/C + kx$ since y=0. This new equation is a logistic law for the x population. This result interprets that if no predators are in the population then the prey population exhibits a logistic growth. This is assumption #4.

Consider the equilibrium point x=l/m and y=(kCm-kl)/Cmn. Through the analysis of the previous theorem the values

a=-kl/Cm b=-nl/m c=(kCm-kl)/Cn d=0

The resulting equation is v^2 - $(-kl/Cm)v + (kCml-kl^2)/mC$. Instead of considering the roots, if $(kCml-kl^2)$ is positive then the roots must be negative since kl/Cm is positive. (i.e. $x^2 + ax + c$ has negative real roots (x+e)(x+f) if both a and c are positive provided $a^2-4c>0$.)

Consider kCml-kl²

$$=$$
 lk (Cm-l)

By the case III condition, C>l/m. Therefore, Cm-l>0, k,l>0 which gives (kCml- kl^2)/m to be positive. The result is then that v_1 and v_2 are both negative roots and by theorem this point is a stable equilibrium (section 2).

Solving the simultaneous system of equations.

$$dx/dt = kx(1-x/C) - nxy$$
$$dy/dt = -l y + mxy$$

k, l, m, n, and C are positive constants (>0)

Try to solve the simultaneous equation by eliminating t.

$$dx/dy = (kx(1-x/C)-nxy)/(mxy-ly)$$
$$= x(k - kx/C - ny)/y(mx-l)$$

By applying direct techniques to solve this differential equation no solutions can be found with the constants m,n,l,k,C>0.

A special case that has a solution would be to let the constant l=0 and k=0.

$$dx/dy = -nxy/mxy$$

$$dx/dy = -n/m$$

$$m dx = -n dy$$

(integrate both sides of the equation)

$$mx = -ny$$

$$y = -mx/n + C$$

depends on initial point

This solutions implies that there is a linear relationship between the predator and prey model. The equation has a negative slope with a y intercept of 0. Thus the only point that is in the region applicable to this model is x=0, and y=0. The

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analysis of this point has previously been determined. This solution gives no further information of the simultaneous system of equations.

IV. Interpretation

The physical interpretation of the mathematical analysis of each separate case gives interesting results. Before considering each case, lets give more meaning to the constants involved in this mathematical model.

dx/dt = kx(1-x/C) - nxy

dy/dt = -1y + mxy

k, l, m, n, and C are positive constants (>0)

Considering first the equation dx/dt which gives the change in the prey population. As in the system of equation C represents the carrying capacity of the environment for the prey species. Based on the logistic law the constant k represents a rate of change of the prey species. In the equation dx/dt the constant n can be interpreted as the detrimental rate constant for the prey due to the effect of the relationship of the predators and prey.

Considering the second equation dy/dt which gives the change in the predator population. The constant I represent the rate of change of the predator species by the Malthusian law. The other constant appearing in the equation is m which can be interpreted as a beneficial rate constant for the predator species due to the effect of the relationship of the predators and prey. In total there are five constants to be determined in this model. Since four of the constants represent proportionality relations, the estimation of these parameters is very difficult.

Considering each case separate, the physical interpretation is as follows.

Case 1: The line Lx has a x-intercept less than 1/m.

From the previous phase plane analysis, at any starting point in the first quadrant the trajectory of the curve approaches the equilibrium point y=0, x=C. This implies that the predator population becomes extinct and the prey population approaches the carrying capacity of the environment. The sketched trajectory curves approach the equilibrium point from all directions in the phase plane. Once this equilibrium point is reached the state of the populations of both species remain at this point because the point is a stable equilibrium. This is

true since an absence of the predator population does not affect the prey population. This case occurs when C<1/m. A more meaningful interpretation of this inequality is as follows: The carrying capacity of the prey (x) population is less than the ratio of the constant of proportionality (l) of the Malthusian decay of the predator species divided by the beneficial proportional rate (m) of the predators due to the interaction between species. In other words, the prey carrying capacity is less than the ratio of the relative change in the predator population based on the detrimental constant (l) divided by the beneficial constant (m) of the predators.

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Case 2: The line Lx has a x-intercept equal to 1/m.

The phase plane in this case, has the trajectories of the solution curve approaching the equilibrium point y=0,x=C. This implies that the predator population becomes extinct and the prey population approaches the carrying capacity of the environment. Once this equilibrium point is reached the state of the populations of both species remain at this point because the point is a stable equilibrium. This is true since an absence of the predator population does not affect the prey population. As in case 1, the same result occurs with the predators becoming extinct. However, the sketched trajectory curves each approach the equilibrium point from below the line y=-kx/Cn+k/n. This means that the predator population approaches zero when the prey population was at its minimum and is increasing.

Case 3: The line Lx has a x-intercept greater than 1/m.

The phase plane diagram of this case implies that at any points in the first quadran with y>0 causes the trajectory curves to approach the equilibrium point x=1/m, y=(kCm-kl)/Cmn. This implies that the predator population approaches the population (kCm-kl)/Cmn and the prey population approaches l/m. This case indicates that both the predator and prey species will not become extinct. There is a balance of the species in which a population of either species approaches a stable equilibrium point. The trajectories of the solution curve approach the equilibrium point spiralling in a counterclockwise direction. At this equilibrium point the species both remain at this population. Also in the phase plane there is another equilibrium x=C, y=0 point which is unstable. This point corresponds to the predator population being zero and the prey population having reached its carrying capacity. This point corresponds to the assumption #4. If at this

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equilibrium point an increase in the predator population occurs the trajectory of the solution curve moves away from the equilibrium x=C, y=0.

Common interpretation of all three cases.

The equilibrium point y=0,x=0 corresponds to the situation where there are no predator or prey and this analysis is trivial and uninteresting. One interpretation not reflected by the previous analysis is the behavior of the predator population in the absence of the prey. The solution curve of the predator population will reflect a Malthusian decay based on the assumption #3. Also the other interpretation of the behavior of the prey population with the predator population of zero reflects the logistic law based on the assumption #4.

NOTE: Based on the above analysis there is no indication of the time it takes to reach an equilibrium point. The variable t was removed from the analysis involved in constructing the phase plane. To determine the time t of reaching the equilibrium points the variable t must be reintroduced and the solution would then become more difficult.

V. Conclusions

The mathematical model presented in this project assumed a logistic law for the prey and a Malthusian law for the predator population. The resulting equations including the terms involved in the interaction between the species had no general solution. However, the behavior of the solution for the three possible cases is analyzed through the modified phase plain analysis. Through this analysis several finite equilibrium points where determined. Neither species had or approached an infinite population corresponding to an equilibrium point. This restriction parallels to the finite natural phenomena of the predator prey relation found in nature.

One observation of this model is that the prey species never becomes extinct. One possible improvement would be to incorporate a model that contained a case where the prey species may become extinct. Another plausible modification would be to allow the predator to survive on an alternative food source, thus removing the strict assumption that the only food source of the predator is the

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prey. An inherent flaw with this model occurs due to the strict inequality involving the constants defined. If C<=l/m the predator species becomes extinct but if C>l/m the predator species thrives. Since the estimation of the constants in the system is difficult a slightest error in l,m or C would wrongly predict the predator species existence.

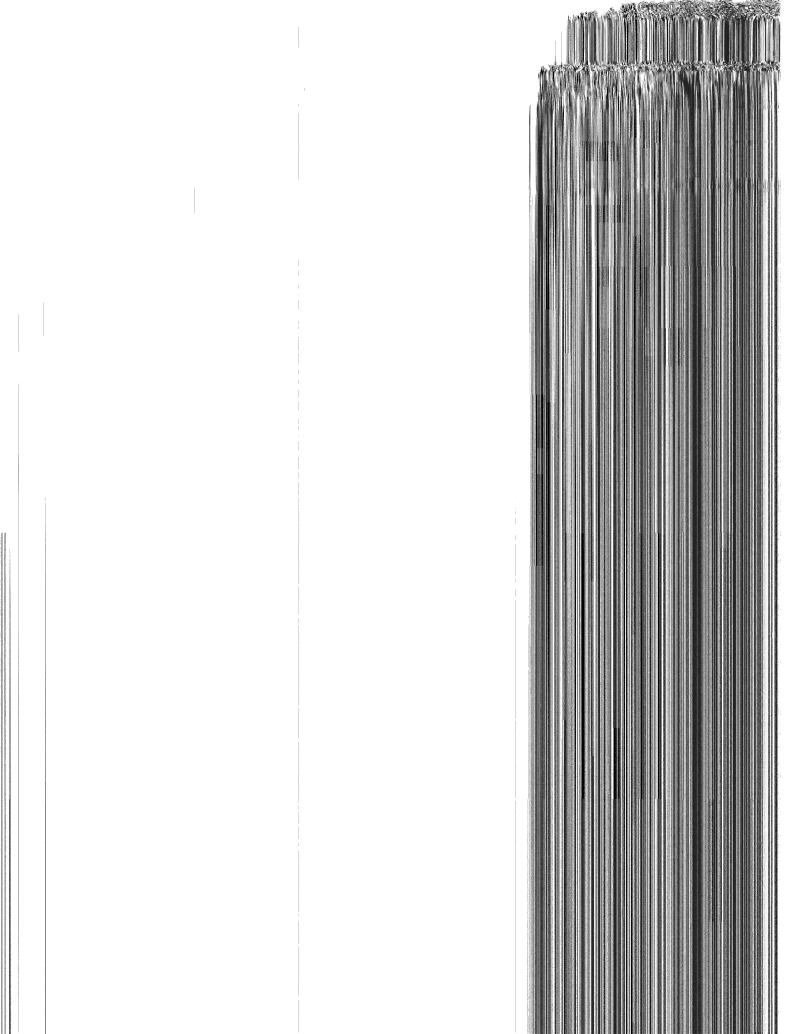
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Although this model doesn't take in consideration all the possible outcomes of the relation between a predator and a prey species, the main outcomes are predicted. The phase plain provides a sufficient approximate solution to the model even though no general mathematical solution can be found. By a few basic assumptions, the behavior of either species is predicted and the conclusion drawn appear to agree with the natural occurrence of this phenomenon.

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$$\frac{dx}{dt} = kx \left(1 - \frac{x}{c}\right) - nxy$$

$$= x \left(k - \frac{kx}{c} - ny\right)$$

$$\frac{dy}{dt} = -lx + mxy$$

$$= y \left(mx - l\right)$$

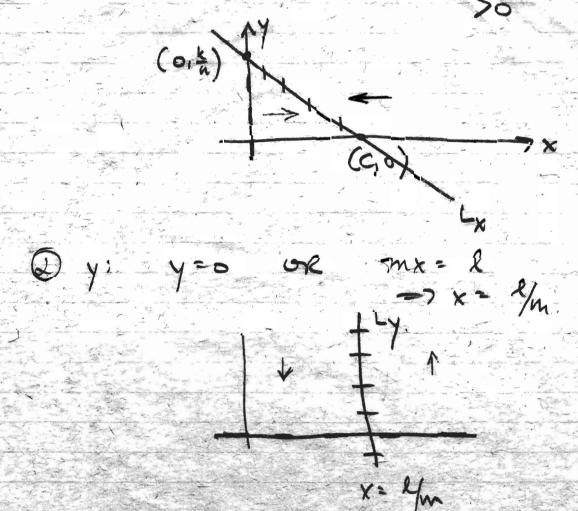
$$Null clines$$

$$0 : x = 0 \text{ of } h - \frac{kx}{c} - ny = 0$$

$$y = \frac{k}{c} - \frac{kx}{nc}$$

$$y = \frac{k}{c} - \frac{kx}{nc}$$

$$y = \frac{k}{c} - \frac{kx}{nc}$$



DIRECTION FIELD ELEMENTS.

x < 2/m => mx-1 <0

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x ? 2/m -> mx-l>0 dy 70.1

@ y> & - kx ny > k - kx O > k - Ax -ny

> $0 > \frac{dx}{dt}$ y Z & - MX -> ny L k- KY

Och - kx - ny O < ox

$$f(r,s)=0$$

$$g(r,s)=0$$

$$x' = f(x,y) = f(r,s) + \frac{\partial f}{\partial x}(r,s)(x-r) + \frac{\partial f}{\partial y}(r,s)(y-s)$$

$$y' = g(x,y) = g(r,s) + \frac{\partial g}{\partial x}(r,s)(x-r) + \frac{\partial g}{\partial y}(r,s)(y-s)$$

$$u = x-r$$

$$y = v-s$$

$$u' = \frac{\partial f}{\partial x}(r,s) = u + \frac{\partial f}{\partial y}(r,s) = v$$

$$v' = \frac{\partial g}{\partial x}(r,s) = \frac{\partial g}{\partial y}(r,s) = v$$

$$\left(u' = \left(\frac{\partial f}{\partial x}(r,s)\right) = \frac{\partial g}{\partial y}(r,s) = v$$

$$\left(u' = \left(\frac{\partial g}{\partial x}(r,s)\right) = \frac{\partial g}{\partial y}(r,s) = v$$

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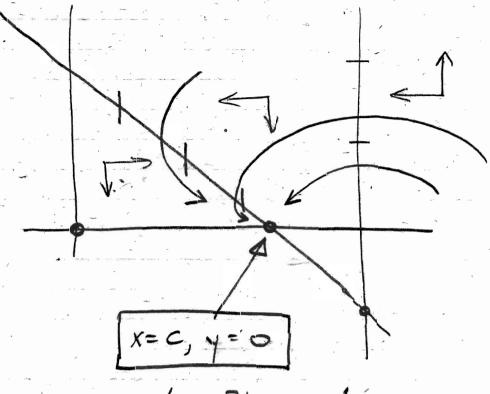
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$$\left(u' = \frac{\partial g}{\partial x}(r,s)\right) = v$$

$$\left(u' =$$

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

CASE (1)

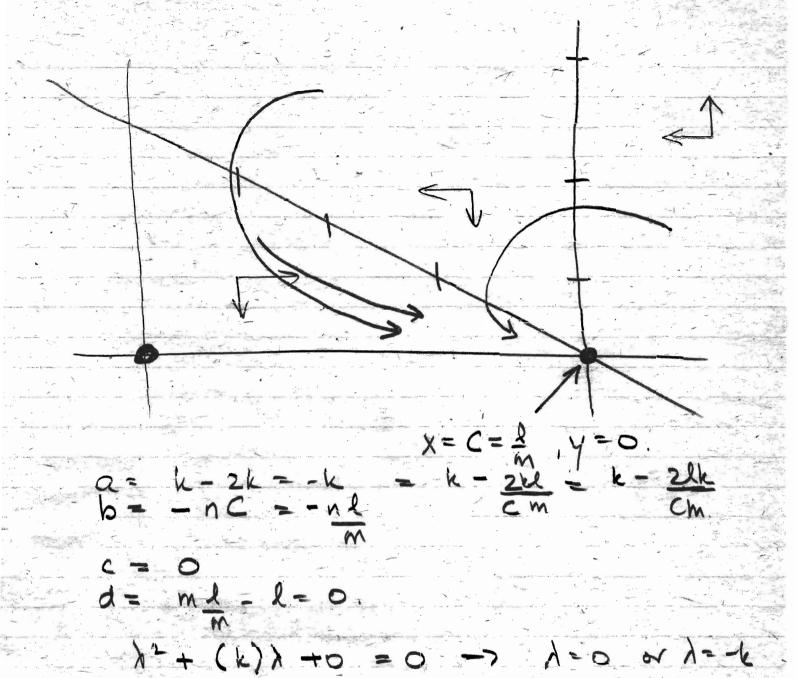


$$a = k - 2k = -k$$

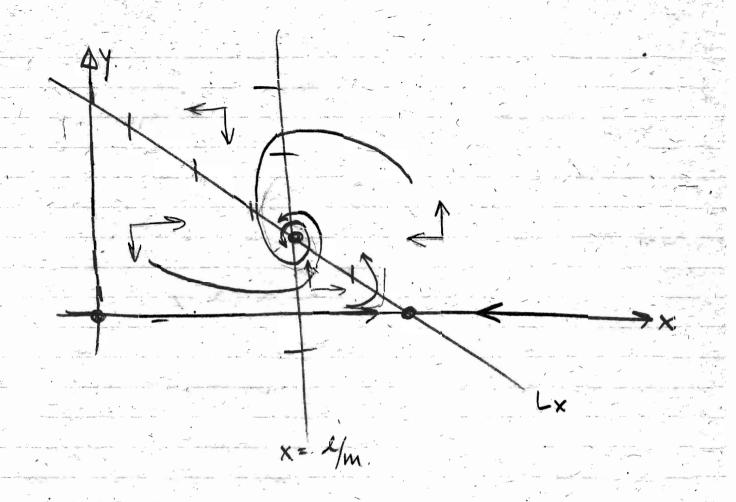
$$b = -nC$$

but
$$C < \frac{1}{m} \Rightarrow mC-l < 0$$
, $\int rover$
regarine

Stable)



Inconclusive



 $\frac{dx}{dt} = x(k - \frac{kx}{c} - ny)$ dy = y(mx-l) Not very interesting $\frac{dx}{dt} = -nxy$ $\frac{dy}{dt} = mxy$ $\frac{dx}{dt} = n$ b (xoryo) nulclines for x=0, y=0. dy = -m -> y = -m x + E) depedo on (xo. 40). equilibrem reached

fossible Modification $\frac{dx}{dt} = \ell(x-\overline{x})(1-\frac{x}{\epsilon}) - nxy$ dy = mxy. - ky northed logistic murenum vable (in the absorber)