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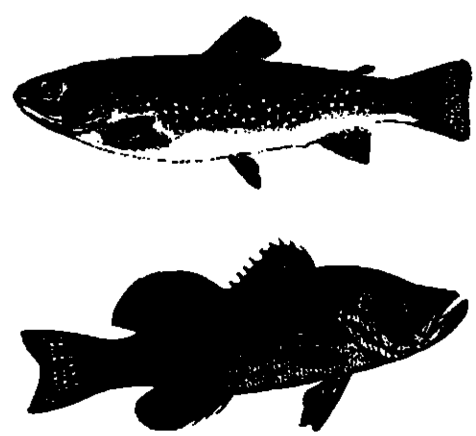
COMAP

Module 628

Competitive Hunter Models

Frank R. Giordano
Stanley C. Leja



Applications of Differential Equations to Biological and Social Sciences

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Modules and Monographs in Undergraduate Mathematics and Its Applications (UMAP) Project

The goal of UMAP was to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications to be used to supplement existing courses and from which complete courses may eventually be built.

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COMPETITIVE HUNTER MODELS

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Title: COMPETITIVE HUNTER MODELS

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Math Field: Mathematical modeling and differential equations.

Applications Field: Biological and social sciences.

Abstract: Various assumptions about the growth in isolation of a single species are modeled and analyzed both graphically and analytically. Scenarios involving two species competing for the same resources are modeled resulting in a system of differential equations. The equilibrium points of the resulting system are analyzed graphically to determine the stability. The module concludes by emphasizing the limitations of a graphical analysis. Students learn: 1) to combine various assumptions about single species growth to model the growth of competing species; and 2) to analyze the stability of the resulting system graphically and appreciate the limitations of such an analysis.

Prerequisites: An understanding of the derivative.

1. INTRODUCTION

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. We refer to such relationships as "predator-prey" behavior. Two species may depend upon one another for mutual support such as when a bee uses a plant's pollen as a food source while providing an essential service for that plant. Such relationships are referred to as "mutualisms." Another possibility is that two or more species compete against one another for a common food source or even compete for survival as is the case in a military confrontation between two armies. In this module we will develop some elementary models to explain such competitive situations. These models are generally called "competitive hunter" models.

Our interest in modeling competitive situations is to answer some questions about the species being studied. Will one species eventually dominate the other and drive it to extinction? Will the species coexist? If so, will the populations reach equilibrium levels or will they vary in some predictable fashion? Additionally, we are interested in how sensitive the answers to the above questions are to the initial population levels and the sensitivity of the answers to external perturbations such as natural disasters, development of new weapons, etc.

Since we are modeling the rates of change of populations with respect to time, our models will inevitably involve differential equations, or in a discrete analysis, difference equations. Even with the simplest assumptions these equations are often nonlinear and generally cannot be solved analytically. Nevertheless qualitative information about the behavior of the populations sufficient to answer the above questions can often be obtained by simple graphical analysis, requiring only a basic understanding of the derivative. We will demonstrate how graphical analysis can be used to answer qualitatively questions such as:

1. Is coexistence of the two species possible?
2. How sensitive are the solutions to initial population levels and external perturbations?

We will also point out limitations of such an analysis, and the conditions which require a mathematically more sophisticated analysis.

Exercises:

1.1. Describe two situations in which one or more species serve as the food source for another species.

1.2. Describe two situations in which two or more species compete for the same food source.

2. SINGLE SPECIES GROWTH

Before addressing the more difficult situation of two species competing in some fashion, let us first examine several ways in which the population of a single species might grow. We will analyze our single species model in a graphical manner analogous to that to be used for a two species model. Let us assume that we are modeling animals which depend upon their environment for their food source and that:

1. All animals are identical, i.e., no need to consider females and males separately. In addition, age is not relevant.
2. Responses to the environment are instantaneous, i.e., no time lags.
3. No immigration or emigration, i.e., changes are due to birth and death only.
4. The environment can support unlimited quantities of the animal in question.

Let us define the following quantities:

$N(t)$: population level at time t.

Δt: unit of time.

b: fraction of animals which reproduce per unit time Δt.

d: fraction of animals which die per unit time Δt.

Under our simplifying assumptions the population at some time $t + \Delta t$ depends upon the population at time t plus births minus deaths. That is

$$N(t + \Delta t) = N(t) + bN(t)\Delta t - dN(t)\Delta t.$$

which is a difference equation. Rearrangement yields:

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = (b - d)N(t) = rN(t)$$

where $r = b - d$ is called the <u>intrinsic growth rate</u>. We will approximate the solution to the difference equation with the differential equation:

(1) $$\lim_{\Delta t \to 0} \frac{N(t + \Delta t) - N(t)}{\Delta t} = \frac{dN}{dt} = rN$$

with

$$N(t = 0) = N_0.$$

Noting that dN/dt is a linear function of N, we can readily graph dN/dt versus N for positive N as a straight line with positive slope r.

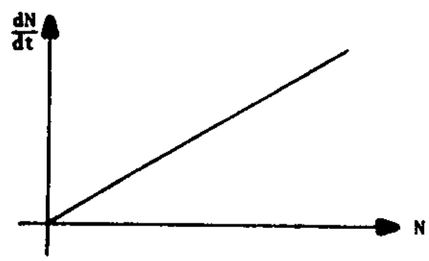

Figure 1. Graph of dN/dt versus N.

We now ask ourselves what happens to N as t increases when the initial population size, N_0, is given. It is important to note that our independent variable is now t. For any starting value $N > 0$ we see that the initial slope is positive. Under assumption 2 this will cause N to increase immediately yielding a larger slope. The graph is shown by the solid curve in Figure 2, which indicates N grows without bound.

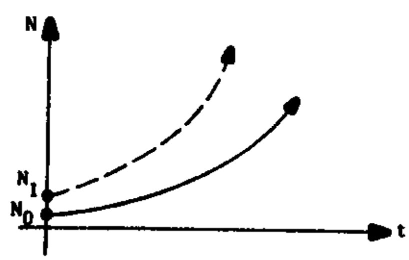

Figure 2. Graph of N(t).

We are also interested to see what effect a different initial population level has on our graph. If $N_1 > N_0$ is the initial value, then for $r > 0$ we have $rN_1 > rN_0$, so the graph of N in this case increases more rapidly at the outset (see the dashed curve in Figure 2).

While assumption 4 is realistic for a number of situations such as bacteria growth, it must be refined to more realistically model animal growth. Let us assume that as N increases there is competition within the species for resources. At some point in time, this will cause the intrinsic growth rate to decrease as N increases. In this case r is now a function of N. For example, we may decide that there is some population limit, $N = K$ above which the environment can no longer support growth in the population. Thus the growth rate will become negative. One expression for r that will cause it to become negative when N exceeds K is:

$$r = r_0(1 - N/K) \quad \text{for } K > 0 \text{ and } r_0 > 0.$$

Growth under this formulation is generally called <u>logistic growth</u>. For this case our model becomes

$$(2) \qquad dN/dt = r_0(1 - N/K)N \quad \text{with } N(t = 0) = N_0$$

which is known as the <u>logistic equation</u>. Differentiating both sides of this equation with respect to N will help us graph its solution.

To graph the family of solutions of the logistic equation, i.e., N versus t, we must analyze what happens for various initial values of N. For $0 < N_0 < K/2$, dN/dt is positive and increasing (positive portion of graph in Figure 3). After $N = K/2$ growth continues but at a decreasing rate (negative portion of graph in Figure 3).

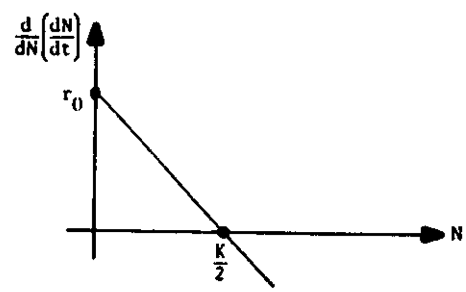

Figure 3. Graph of $\frac{d}{dN}\left(\frac{dN}{dt}\right) = r_0(1 - 2N/K)$.

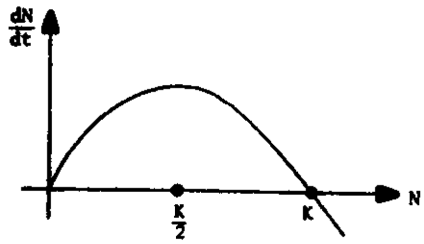

Figure 4. Graph of $\frac{dN}{dt}$.

As N approaches N = K, dN/dt approaches 0 (see the dashed curve in Figure 5). For $N_0 > K$, dN/dt is initially negative causing N to decrease. As N decreases dN/dt becomes less negative, approaching zero as N approaches K. Finally, if $N_0 = 0$ or if $N_0 = K$, we have zero growth, or equilibrium. Sketching N versus t for representative initial population levels we have:

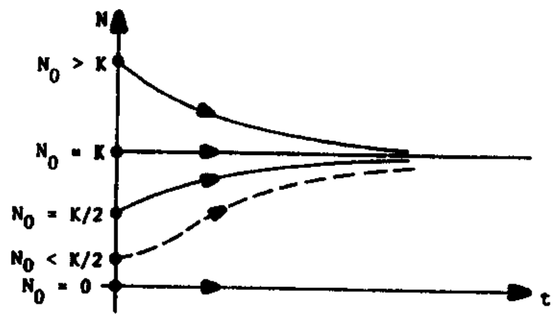

Figure 5. Family of solutions for logistic equation.

In this case we see that for $N_0 > 0$, N approaches K regardless of the initial value of N. The values N = 0 and N = K are "equilibrium" values in that our model predicts zero growth at these values. Note also that N = K is a stable equilibrium point in the sense that for any initial value near N = K our population will approach N = K as t becomes large. Conversely, N = 0 is unstable in the sense that any initial population, however small, will cause N to move away from 0 and approach K for large t.

In this treatment of single species growth, we have presented only those aspects necessary for an elementary understanding of competitive models. For a more general discussion of the assumptions in single species growth, see the UMAP Monograph Introduction to Population Modeling by James C. Frauenthal [2].

Exercises:

2.1. Analyze Equation 1 graphically for $r < 0$.

2.2. Solve Equation 1 analytically.

2.3. Show analytically that the solution to Equation 2 is:

$$N = \frac{N_0}{e^{-r_0 t} + \frac{N_0}{K}\left(1 - e^{-r_0 t}\right)} .$$

2.4. What does the solution predict about N as t becomes large?

---

3. COMPETITIVE HUNTER MODEL

Now that we have seen two ways of modeling single species growth, let us turn our attention to how two different species might compete for common resources. Suppose we have a small pond which is mature enough to support wildlife and we would like to stock the pond with game fish. We will use trout and bass and denote the population of each by $x(t)$ and $y(t)$ respectively. We would like to know if coexistence is possible and how sensitive the final solution is to the initial stockage levels and external perturbations.

The level of the trout depends on many variables, such as initial level, x_0, of the trout population, the ability of the environment to support trout, level of competition for resources, existence of predators, etc. As an initial assumption let us assume that the environment can support an unlimited number of trout, i.e., in isolation

(3) $\qquad dx/dt = ax \qquad \text{for } a > 0.$

Since the above assumption is unrealistic for many situations, we will now refine this assumption. Assume that the effect of the bass population is to decrease the growth rate of the trout population, since both populations compete for the same food and living space. The decrease in the growth rate of the trout is roughly proportional to the number of possible interactions between the two species, i.e., in proportion to the product of x and y. This is modeled by the equation

(4) $dx/dt = ax - bxy = (a - by)x.$

The intrinsic growth rate $r = a - by$ decreases as the level of the bass population increases. The constants a and b indicate the degrees of "self-regulation" and "competition" respectively. These coefficients must be determined experimentally or by analyzing historical data. In practice, they are difficult to estimate.

If we analyze the situation for the bass in a similar manner, we have the following model:

(5)
$$dx/dt = (a - by)x$$
$$dy/dt = (m - nx)y$$

where $x(0) = x_0$, $y(0) = y_0$, and a, b, m, and $n > 0$. Thus we have a <u>system</u> of two differential equations which we can use to study the growth patterns of species exhibiting competitive behavior.

<u>Exercises</u>:

3.1. List three important considerations that are ignored in the development of the competitive hunter model.

3.2. Develop a model for the growth of trout and bass assuming that in isolation trout demonstrate exponential decay, (i.e., in Equation 3, $a < 0$) and that in isolation the bass population grows logistically with a population limit, K.

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4. GRAPHICAL ANALYSIS

One of the questions we are interested in answering is whether or not the population levels of the bass and trout reach equilibrium levels. The only way such a state can be achieved is that neither population is growing, i.e., $dx/dt = dy/dt = 0$. We will call these points of zero growth <u>equilibrium points</u>. Using graphical analysis we can determine the equilibrium point(s) and analyze their stability in a manner roughly similar to our analysis of the logistics equation's equilibrium points, $N = 0$ and $N = K$.

For Equations 5, the equilibrium points are $x = y = 0$ and $x = m/n$, $y = a/b$. If one graphs the population level of bass, y, versus the population level of trout, x, we can depict the portions of the graph where $dx/dt = 0$, $dy/dt = 0$, and where both growth rates are simultaneously equal to zero (Figure 6). Thus if our initial stockage levels were precisely at these points there would be no growth.

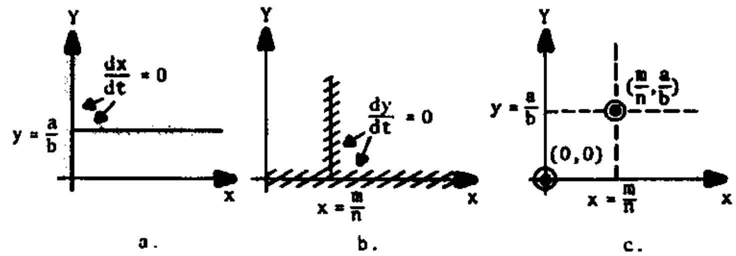

Figure 6. Determining equilibrium points graphically.

Considering the approximations necessary in any model, it is inconceivable that we would estimate the values of the parameters a, b, m, and n precisely. Also, the population count (x_0, y_0) would be subject to large measurement errors. Thus a far more interesting question is what happens in the vicinity of these points. Do we approach the points or not?

To investigate this question graphically, we must analyze the motion of any pair of population levels, (x,y). Recall that we graphically determined the equilibrium points by suggesting a graph of y versus x. The slope of any particular curve is dy/dx. This slope can be determined by using the following equation.

$$dy/dx = \frac{dy/dt}{dx/dt} .$$

This equation is an application of the chain rule.

Since we only need to estimate dy/dx, it will generally suffice to know the direction of dx/dt and dy/dt in the first quadrant of the plane. In our example, the line x = m/n divides the xy plane into two regions. In the left region dy/dt is positive, and in the right it is negative as illustrated in Figure 7.

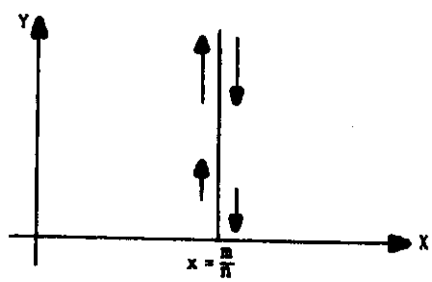

Figure 7. Direction of $\frac{dy}{dt}$.

Similarly, the line $y = a/b$ determines the region where dx/dt is positive or negative.

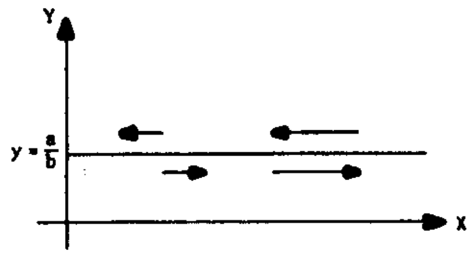

Figure 8. Direction of $\frac{dx}{dt}$.

Another useful bit of information is that along the line $y = a/b$, $dx/dt = 0$. Therefore this line must be crossed vertically. Similarly, along the line $x = m/n$, $dy/dt = 0$ which implies that this line must be crossed horizontally. Finally, along the y axis motion must be vertical and along the x axis motion must be horizontal. Illustrating, we have

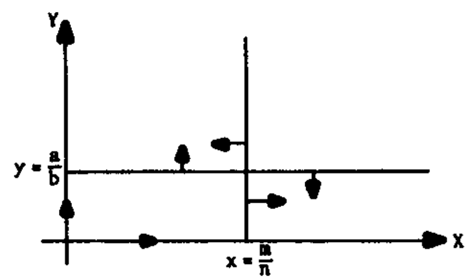

Figure 9. Motion when one derivative equals zero.

Putting our information together on a single graph, we see that we have four distinct regions (A,B,C,D) for the possible directions of dy/dt (Figure 10).

Analyzing the motion in the vicinity of (0,0), we see that all motion is away from that point. In the vicinity of $(m/n, a/b)$ we see that only two paths exist (one from Region B and the other from Region C) which lead to the equilibrium point, but that on all other paths motion will be away from the point (Figure 11).

Our graphical analysis thus far leads us to the preliminary conclusion that, under the assumptions of our

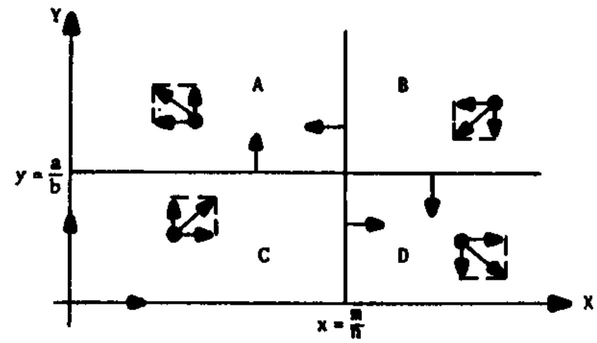

Figure 10. Composite graphical analysis.

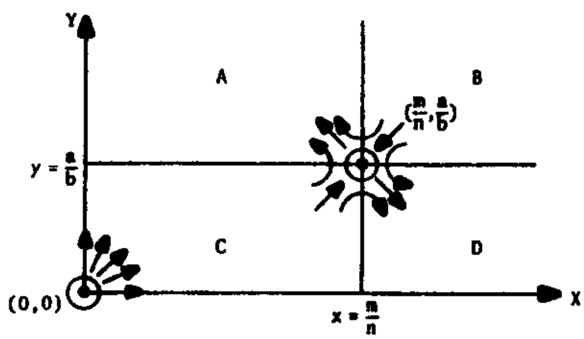

Figure 11. Motion near equilibrium points.

model, reaching equilibrium levels of both species is highly unlikely. Furthermore, the initial conditions are important and perturbations may change the outcome of the competition.

Exercise

4.1. Recall the model you developed in Exercise 3.2. Analyze graphically the motion in the vicinity of the equilibrium points of your model. Is coexistence possible?

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5. THE XY PLANE

Up to this point the purpose of the graphical analysis has been to determine the direction of motion in the vicinity of equilibrium points. It is tempting to analyze the behavior of our system for any starting point in the first quadrant of the xy plane. Given some starting point (x_0, y_0), the locus of points traced by the motion as t increases is called the path or trajectory. While we will not in general be able to completely determine all paths, there are some properties of the type of systems of differential equations that we are studying that will enable us to increase our understanding of the behavior our model predicts.

Given the system:

$$dx/dt = ax - b\ xy$$

$$dy/dt = my - n\ xy$$

we note that the derivative

$$\frac{dy}{dx} = \frac{(my - n\ xy)}{(ax - b\ xy)}$$

at any point (x,y) is a function of the position (x,y) only and is independent of the time t of arrival at the position. Further, when given values for a, b, m, and n, we see that dy/dx has a unique value for each (x,y). Systems of differential equations in which the independent variable, in this case t, does not appear explicitly are called autonomous systems and possess certain properties which we offer without proof:

1. Through any point (x_0, y_0) in the xy plane there is at most one path of the system.
2. A path which passes through at least one point that is not an equilibrium point cannot cross itself unless it is a closed curve.
3. An equilibrium point cannot be reached in finite time from a starting point that is not an equilibrium point.

Properties 1 and 2 follow intuitively from an examination of dy/dx. In our example we see that as we approach the equilibrium point (m/n,a/b) the derivative dx/dt and dy/dt approaches zero demonstrating property 3.

The implications of these three properties are that from a starting point that is not an equilibrium point, the resulting motion:

1. Will move along the same path regardless of the starting time.
2. Cannot return to the starting point unless the motion is periodic.

3. Can never cross another path.
4. Can only approach an equilibrium point.

Thus the resulting motion will either:

1. Approach an equilibrium point.
2. Move on or approach a closed path.
3. Go to infinity.

Applying the above properties to the previously developed information about our system, we can sketch paths for some typical starting points in Figure 12. The dashed line represents the unique trajectory for a particular starting point, (x_0, y_0).

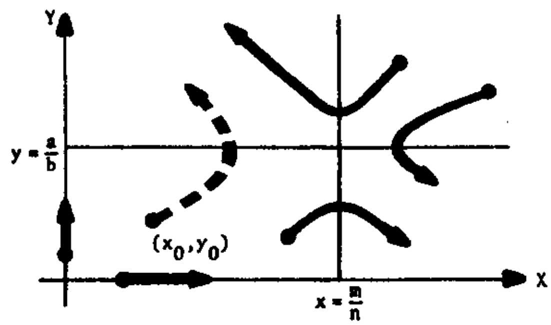

Figure 12. Family of trajectories for Competitive Hunter Model.

Exercise:

5.1. Sketch typical paths for motion in the xy plane for your solutions to Exercise 4.1.

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6. MODEL INTERPRETATION

Although our graphical analysis was straight-forward, we have gained some useful qualitative information. First, under our assumptions, mutual coexistence of competing species is highly improbable. This phenomenon is known as the Principle of Competitive Exclusion or Gause's Principle. Secondly, the initial conditions completely determine the outcome. In our example, we can portray this result as follows:

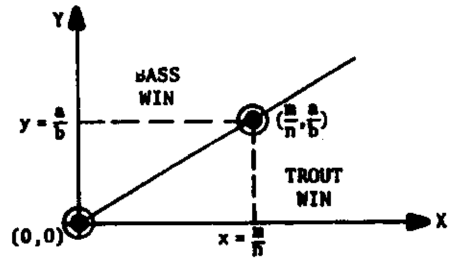

Figure 13. Qualitative results of analysis.

Thus the initial conditions would determine the outcome. Further any perturbation which would cause a switch from one region of the above graph to the other would change the outcome.

Exercises:

6.1. How might the model developed in the module be validated? Include a discussion of how the various parameters (a, b, m, and n) would be estimated.

6.2. How could state conservation authorities use this model to insure the survival of both species?

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7. LIMITATIONS OF GRAPHICAL ANALYSIS

The purpose of this module was to introduce the phenomenon of competitive hunter models without solving analytically the differential equations involved. Graphical analysis is a powerful tool for accomplishing this and it should be attempted to obtain a qualitative understanding of the behavior the model predicts. At this point one may wish to refine the model or obtain more precise information about the predictions of the given model using more sophisticated mathematical techniques.

We should be aware of the limitations of a graphical analysis. The information provided by the analysis is restricted. For example, we did not precisely determine the curve that divides those starting points in which the bass win from those in which the trout win. We may very well wish to do this if we are happy with our model.

We will not always be able to determine the nature of the motion even close to an equilibrium point using only a graphical analysis. In the discussion that follows, we will analyze an equilibrium point at (0,0). The point (0,0) may be the result of a simple translation from a point in the first quadrant. Consider as an example an equilibrium point at (0,0) and the following graph:

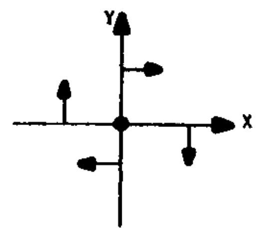

Figure 14. Translated equilibrium point.

The above information would not be sufficient to distinguish among the following three cases:

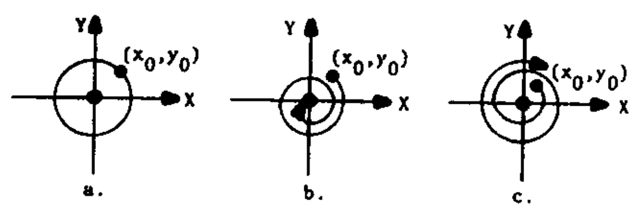

Figure 15. Limitation of graphical stability analysis.

Note that each of the above possible graphs yields radically different conclusions about the nature of the given equilibrium point. At this point we must attempt other methods to determine the nature of the equilibrium point. These include solving the system of differential equations if possible, performing a linearized stability analysis if the system satisfies certain conditions, and using Liapounov's Direct Method which requires some skill in determining an appropriate Liapounov function. For an excellent general discussion of the stability of systems of differential equations, see Boyce and DiPrima [1].

Another limitation of the graphical method concerns predicting the behavior away from the equilibrium point. In the above example we might use additional information to conclude that the motion near the equilibrium point was away from the equilibrium point as in Figure 15c, and be tempted to draw the following graph:

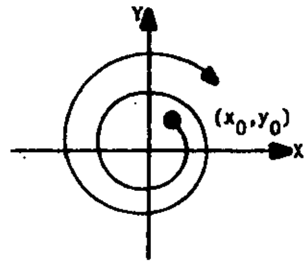

Figure 16. Limitation of graphical trajectory analysis.

This might lead us to conclude that the populations would grow without bound. However, in the following example

$$dx/dt = y + x - x(x^2 + y^2) \tag{6}$$
$$dy/dt = -x + y - y(x^2 + y^2)$$

even though (0,0) is the only possible equilibrium point, at $x^2 + y^2 = 1$ the motion becomes $dy/dx = -x/y$ which describes a circle. The correct graph for the system described by Equations 6 is:

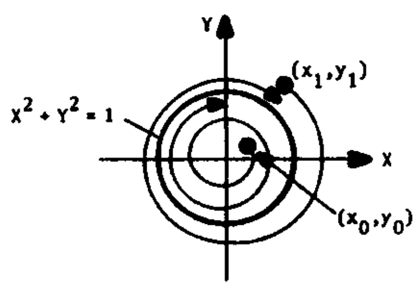

Figure 17. Limit cycle behavior.

where $x^2 + y^2 = 1$ is called a limit cycle. If you start "inside" or "outside" $x^2 + y^2 = 1$ (except for the origin) you approach $x^2 + y^2 = 1$. If you start on $x^2 + y^2 = 1$ you never leave this trajectory and your resulting population behavior is periodic.

Finally our assumptions about the growth of the populations have been intentionally quite restrictive. For an excellent discussion of population modeling in a more general context, see Frauenthal [2].

8. REFERENCES

[1] Boyce, William E. and DiPrima, Richard C., Elementary Differential Equations and Boundary Value Problems, 2nd Edition. (New York: John Wiley and Sons, 1969.)

[2] Frauenthal, James C., Introduction to Population Modeling. (Newton, MA: Education Development Center, Inc., 1979.)

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9. MODEL EXAM

1. Develop a model for the growth of trout and bass assuming that in isolation each species would demonstrate logistic growth with population limits K_1 and K_2 respectively.

2. Is coexistence possible? Assume coefficients for your model such that an equilibrium point exists inside the 1st quadrant. Analyze graphically the motion in the vicinity of the equilibrium points of your model.

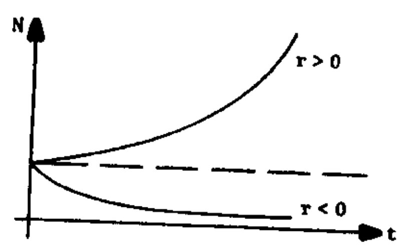
3. Sketch typical paths for motion in the xy plane for your model.

10. ANSWERS TO EXERCISES

1.1. Predator-fox, prey-rabbits; predator-lion, prey-zebra.

1.2. Trout, bass; squirrels, chipmunks.

2.1.



With r > 0 we have exponential growth, with r < 0 we have exponential decay.

2.2. $$\int \frac{dN}{N} = \int r\,dt \quad \Rightarrow \quad N = c_1 e^{rt};$$

initial conditions $\Rightarrow$ $N = N_0 e^{rt}$.

2.3. Partial fraction decomposition $\Rightarrow$

$$\int \frac{dN}{(1 - N/K)N} = \int \frac{1/K\ dN}{(1 - N/K)} + \int \frac{dN}{N} = \int r_0 dt \Rightarrow$$

$$- \text{Ln}(1 - N/K) + \text{Ln}\ N = r_0 t + C \quad \Rightarrow$$

$$\frac{N}{1 - N/K} = c_1 e^{r_0 t} \quad \Rightarrow N = \frac{c_1}{e^{-r_0 t} + \frac{c_1}{K}} .$$

Using initial condition $N(t = 0) = N_0$ $\Rightarrow$

$$N_0 = \frac{c_1}{1 + \frac{c_1}{K}} \quad \Rightarrow \quad c_1 = \frac{N_0}{1 - \frac{N_0}{K}} .$$

Finally, substitute c_1 into equation for N and algebraically manipulate the equation to get it in required form.

2.4. $$\lim_{t \to \infty} e^{r_0 t} = 0 \Rightarrow N(t) \to K.$$

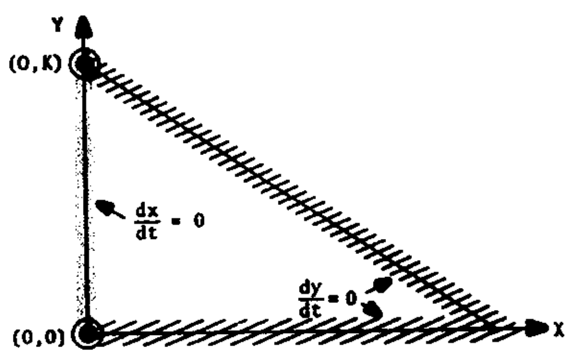
3.1. Seasonal variations, nonconformity of environment, effects of other interactions, unexpected disasters, etc.

3.2. This model assumes the number of interactions is proportional to the product of x and y.

$$\frac{dx}{dt} = (a - by)x, \qquad a < 0$$

$$\frac{dy}{dt} = m(1 - \frac{y}{K})y - n\ xy = y(m - \frac{m}{K}\ y - nx).$$

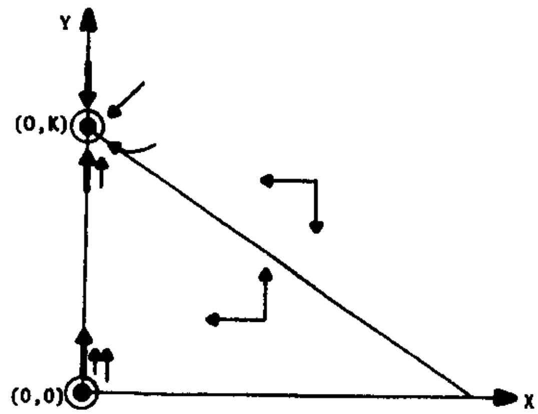
4.1.



$\frac{dx}{dt} = 0$ at $x = 0$ and $y = \frac{a}{b}$ (remember $\frac{a}{b} < 0$)

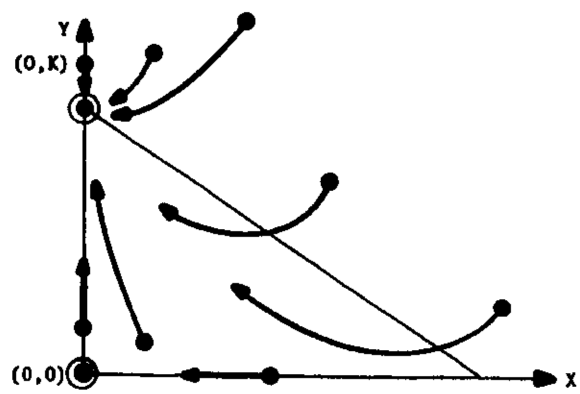
$\frac{dy}{dt} = 0$ at $y = 0$ and $y = K - \frac{Kn}{m} x$

→ equilibrium points at (0,0) and (0,K).



→ Coexistence is not possible because eventually trout die out and bass reach their population limit.

5.1.



6.1. First, the coefficients a, b, m, and n need to be determined by sampling or by analyzing historical data. Therefore, more specific graphical predictions can be made. These predictions would then have to be compared to actual population growth patterns. If the predictions match actual results, we have partially validated our model. If necessary, more tests could be run. However, it should be remembered that the primary purpose of a graphical analysis is to analyze the behavior qualitatively.

6.2. With reference to Figure 11, attempt to maintain the fish populations in Region B through stocking and regulation (open and closed seasons). For example, should Regions A or D be entered, restocking the appropriate species can cause a return to Region B.

11. ANSWERS TO MODEL EXAM

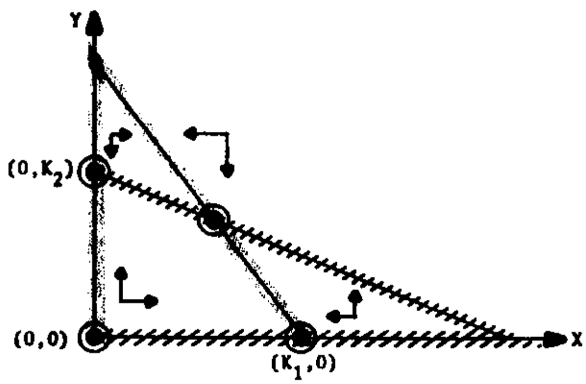
1. $\frac{dx}{dt} = a(1 - \frac{x}{K_1})x - b\,xy.$

   $\frac{dy}{dt} = m(1 - \frac{y}{K_2})y - n\,xy.$

2. $\frac{dx}{dt} = 0$ when $x = 0$ or $y = \frac{a}{b} - \frac{a}{bK_1}x.$

   $\frac{dy}{dt} = 0$ when $y = 0$ or $y = K_2 - \frac{K_2 n}{m}x.$

   Picking $a/b > K_2$ and $m/n > K_1$ we insure an equilibrium point exists inside the 1st quadrant.



Graphical analysis implies 4 equilibrium points exist. They are $(0,K_2)$ $(0,0)$, $(K_1,0)$, and the point of intersection of the two boundaries in the 1st quadrant. All these equilibrium points are unstable but the point of intersection. The possibility of co-existence is predicted by this model.

NOTE: If you assumed $K_2 > a/b$ and $K_1 > m/n$ graphical analysis implies the same 4 equilibrium points exist, but in this case

$(0,K_2)$ and $(K_1,0)$ are stable and the remaining two points are unstable. Coexistence is not predicted with this model. Similarly, coexistence is not predicted if you assumed no intersection point in the first quadrant.

4.