

Predator-Prey Modelling

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Abstract

Nonlinear analysis is applied to three different predator-prey models to determine the behavior of solutions. For each system of differential equations, equilibrium points are found and examined. Linearizations are constructed for interesting equilibrium points and classified based on the parameters of the system. Changes to some parameters in some systems do not change the fundamental behavior of solution curves in the phase plane, while others can change stable equilibrium points into unstable points and vice versa.

1. Introduction

As long as there is interest in studying living things, there will be a need to model populations mathematically, specifically sets of populations with predator-prey interactions. They can be used to make testable predictions about the behavior of a number of populations, and provide clues as to why they behave the way they do. Sometimes it is necessary to go a step further and manipulate populations, but doing so requires knowing what can be manipulated, how, when, and what the results will be. Which set of mathematical tools are the right ones for the application? The answer comes from the data.

2. Examining The Data

Suppose the following tables contain the population data for two populations in isolation.

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Year	Population 1	Population 2
2000	10000	5000
2001	20000	10000
2002	40000	20000
2003	80000	40000
2004	160000	80000

A number of observations could be made about this data. One is that both populations are clearly exponential. Population 1 seems to obey the equation $P = 10000 \cdot 2^{t-2000}$ where P is the population and t is the year. Population 2, similarly, seems to fit the equation $P = 5000 \cdot 2^{t-2000}$.

Another more interesting observation is that both population growth rates seem to be proportional to the size of the population. Mathematically, $P' = rP$, where the P' is dP/dt (the growth rate of the population) and r is some constant. This is known as the Malthusian model, and it is a differential equation. A different way of expressing this relationship is $P'/P = r$. In other words, the growth rate of the population per individual is constant.

The second representation of the model makes it clear that the equation is separable. Solving it proceeds as follows.

$$\begin{aligned}\frac{P'}{P} &= r \\ \int \frac{1}{P} dP &= \int r dt \\ \ln |P| &= rt + C\end{aligned}$$

Negative population values do not make sense, so

$$\begin{aligned}\ln P &= rt + C \\ P &= e^{rt+C} \\ P &= e^C e^{rt} \\ P &= Ae^{rt}.\end{aligned}$$

To find a particular equation representing either Population 1 or Population 2 from above, it would be necessary to find particular values for the constants A and r , which is relatively easy.

This example provides two important pieces of information. The first is that populations can be modelled quite well by differential equations. More than one population, then, would require more than

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one differential equation — a system of differential equations. Two noninteracting species might be modelled by a system like

$$\begin{aligned}A' &= f(A) \\ B' &= g(B)\end{aligned}\tag{1}$$

The second important piece of information is that finding an equation describing a particular population means finding a solution to the differential equation (or system of differential equations). As the DEs used to model populations become more and more complicated, this will not always be possible. Also, it will be impossible to consider each equation independently as systems will generally be of the form:

$$\begin{aligned}A' &= f(A, B) \\ B' &= g(A, B)\end{aligned}\tag{2}$$

instead of the form of system (1).

3. Building A Model

One simple system that is both nonlinear and models interaction (like system (2)) is

$$\begin{aligned}H' &= rH - dHP \\ P' &= -sP + fHP.\end{aligned}\tag{3}$$

This system models two populations: H (herbivores, the prey species) and P (predators). The parameters r , d , s , and f are positive. When there are no predators, the herbivore equation simplifies to $H' = rH$, the malthusian model for a single population from earlier. The natural growth rate r is greater than 0 so the population grows when it is the only population inhabiting an area. In the absence of prey, the predator equation simplifies to $P' = -sP$. The natural growth rate $-s$ is less than 0 so the predator population shrinks in absence of food. HP is the number of herbivore-predator interactions (more of each population means more interactions population). Some positive portion of those interactions, dHP decreases the growth rate of the prey species, and some other positive portion of those interactions, fHP increases the predator species growth rate.

Another way of looking at these systems is to divide the prey equation through by the number of prey and the predator equation by the number of predators. This requires, of course, that neither population

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be 0.

$$\begin{aligned}\frac{H'}{H} &= r - dP \\ \frac{P'}{P} &= -s + fH\end{aligned}\tag{4}$$

The reproduction rate of the average prey is some constant r , but as more predators are added to the environment the reproduction rate decreases until it is 0 and then becomes more and more negative with the continued increase in predator density. Similarly, when there are no prey, the “reproduction” rate of the average predator is negative – it will starve. When there are sufficient prey to sustain that predator but no additional offspring, it will not produce any. When there are more than enough prey, the predators will produce increasing offspring with increasing food resources.

4. Analyzing Model 1

One tool from nonlinear analysis that can be applied to system (3) is examining the linearization around an equilibrium point using the Jacobian. In order to do this, we need to find the Jacobian for the system and plug in the values for the equilibrium point in question.

The equilibrium points are found by finding the intersections of the H and P nullclines. The H nullclines are found as follows.

$$\begin{aligned}H' &= rH - dHP \\ 0 &= rH - dHP \\ 0 &= H(r - dP)\end{aligned}$$

If $H(r - dP) = 0$ then $H = 0$ (the equation of one nullcline) or $r - dP = 0$.

$$\begin{aligned}r - dP &= 0 \\ r &= dP \\ P &= \frac{r}{d}\end{aligned}$$

So the H nullclines are $H = 0$ and $P = r/d$. The P nullclines are found similarly.

$$\begin{aligned}P' &= -sP + fHP \\ 0 &= -sP + fHP \\ 0 &= P(-s + fH)\end{aligned}$$

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The P nullclines are $P = 0$ and $H = s/f$.

There are two points where the H and P nullclines intersect. The first is rather obvious: $(0, 0)$. If there are no predators and no prey, it is unsurprising that both populations are not changing. The second one, however, $(s/f, r/d)$ is an equilibrium point with positive populations (remember that all parameters are positive).

The next step is to find the Jacobian so that a linearization can be found for the area surrounding the equilibrium point.

$$\begin{aligned}\frac{\partial H'}{\partial H} &= r - dP & \frac{\partial H'}{\partial P} &= -dH \\ \frac{\partial P'}{\partial H} &= fP & \frac{\partial P'}{\partial P} &= -s + fH\end{aligned}$$

$$J(H, P) = \begin{bmatrix} r - dP & -dH \\ fP & -s + fH \end{bmatrix}$$

Finally, the linearization at the interesting equilibrium point is:

$$J(s/f, r/d) = \begin{bmatrix} 0 & -ds/f \\ fr/d & 0 \end{bmatrix}.$$

The trace of the matrix is 0 and the determinant is sr , which is positive. This tells us that the linearization is a center. This seems to suggest that solutions very close to the equilibrium point are limit cycles, but this is not necessarily the case. The Jacobian is an approximation of the behavior of the system that gets better and better as one approaches the equilibrium point. It is not perfect. If the equilibrium point were very clearly a spiral source or spiral sink, for example, tiny imperfections would not cause significant differences between the linearization and the original system. In the degenerate case of a center, however, these imperfections matter very much. Slight deviations could make the system behave like a tightly spinning spiral source or spiral sink, or the system could yield limit cycles. The actual behavior of system (3) is illustrated in Figure 1.

5. A Second Model

Linearization produced useful information about system (3), but that model has a serious deficiency — the prey population grows according to the Malthusian model in absence of predators. This might be realistic for some populations in the laboratory for short periods of time, but in the wild most

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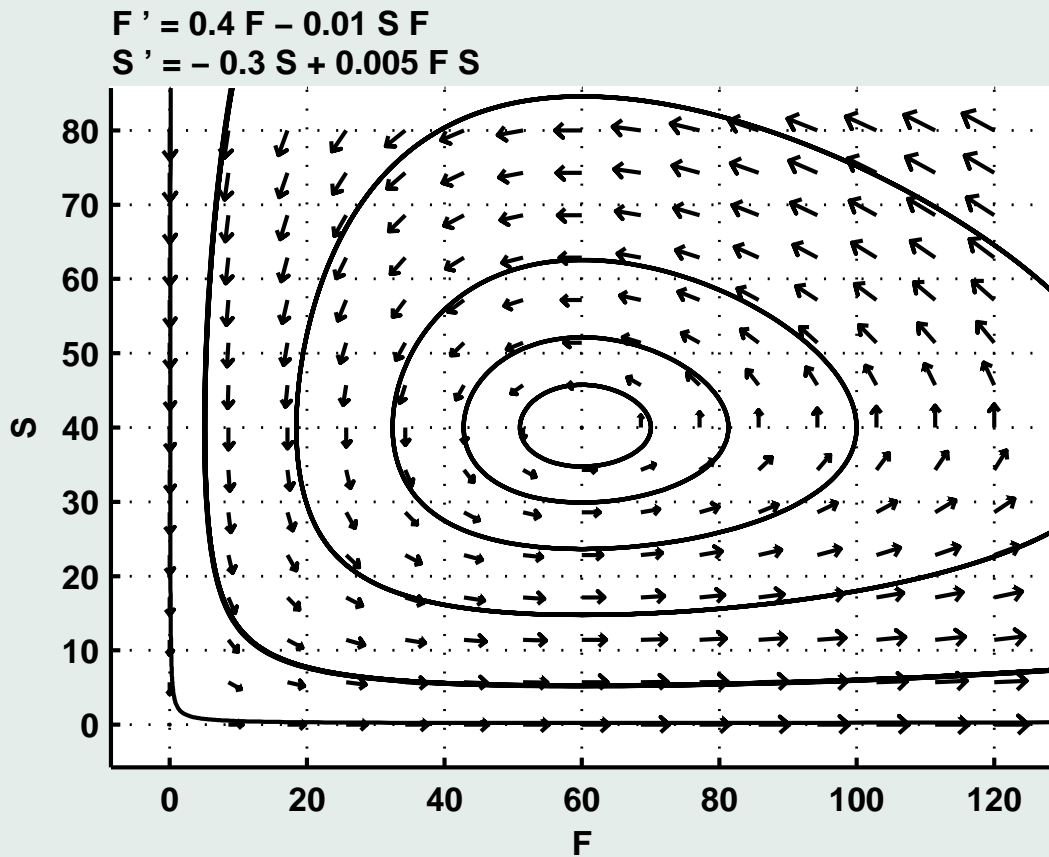


Figure 1: A Simple System

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populations are limited in some way. The logistic equation, $H' = r(1 - H/K)H$ models this nicely for a single population. When H is small there is very little intraspecific competition for resources, $1 - H/K$ is close to 1, and the reproductive rate per individual $H'/H = r(1 - H/K)$ is very close to r . As H increases, intraspecific competition increases, $1 - H/K$ approaches 0, and the reproductive rate per individual approaches 0. Replacing the expression accounting for the prey populations's reproductive rate in system (3) with the comparable expression from the logistic equation gives the second model:

$$\begin{aligned} H' &= r \left(1 - \frac{H}{K}\right) H - dHP \\ P' &= -sP + fHP \end{aligned} \quad (5)$$

The system's equilibrium points are found much the same way as they were for system (3). First, the H nullclines are found.

$$\begin{aligned} H' &= r \left(1 - \frac{H}{K}\right) H - dHP \\ 0 &= r \left(1 - \frac{H}{K}\right) H - dHP \\ 0 &= H \left(r \left(1 - \frac{H}{K}\right) - dP \right) \end{aligned}$$

This implies that either $H = 0$, the first nullcline, or that $r(1 - H/K) - dP = 0$.

$$\begin{aligned} 0 &= r \left(1 - \frac{H}{K}\right) - dP \\ dP &= r \left(1 - \frac{H}{K}\right) \\ P &= \frac{r}{d} \left(1 - \frac{H}{K}\right) \end{aligned}$$

The H nullclines are $H = 0$ and $P = (r/d)(1 - H/K)$. The P nullclines are the same as they were in system (3): $P = 0$ and $H = s/f$.

Now there are three intersections: $(0, 0)$, $(K, 0)$, $(s/f, r/d - sr/(Kf))$. The first exists for the same reason as the equilibrium point at the origin in system (3). The second is new but easily explained. When there are no predators and the initial prey population is exactly the carrying capacity of the

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environment K neither population would be expected to change. The third, however, provides an interesting opportunity for analysis.

This time, deriving the Jacobian takes slightly more work.

$$\begin{aligned}\frac{\partial H'}{\partial H} &= r \left(1 - \frac{H}{K}\right) + rH \left(-\frac{1}{K}\right) - dP \\ &= r - \frac{r}{K}H - \frac{r}{K}H - dP \\ &= r - \frac{2r}{K}H - dP \\ \frac{\partial H'}{\partial P} &= -dH\end{aligned}$$

The partial derivatives of P' remain unchanged since the predator model has not changed. The Jacobian, then, is:

$$J(H, P) = \begin{bmatrix} r - 2rH/K - dP & -dH \\ fP & -s + fH \end{bmatrix}.$$

Finally, the linearization at the interesting equilibrium point is:

$$J\left(\frac{s}{f}, \frac{r}{d} - \frac{sr}{Kfd}\right) = \begin{bmatrix} -rs/(Kf) & -ds/f \\ (rKf - rs)/(dK) & 0 \end{bmatrix}$$

The trace of the matrix is $-rs/(Kf)$, which must be negative since all parameters are positive. The determinant, then, decides whether the equilibrium point behaves like a saddle, sink, spiral sink, or one of three degenerate cases. It will be some sort of sink or spiral sink as long as

$$\det\left(J\left(\frac{s}{f}, \frac{r}{d} - \frac{sr}{Kfd}\right)\right) = \frac{sr(Kf - s)}{Kf} > 0.$$

All parameters are positive, so the determinant is positive and the equilibrium point is a sink as long as $Kf - s > 0$.

What if $Kf \leq s$? Recall that the P coordinate of equilibrium point is $r/d(1 - s/Kf)$. If Kf were smaller than s , $(1 - s/Kf)$ would be less than one and the equilibrium point would imply a negative predator population, which cannot happen. In other words, as long as that equilibrium point remains above the H axis, it will be some kind of sink. This is illustrated in Figure 2, a phase portrait of a

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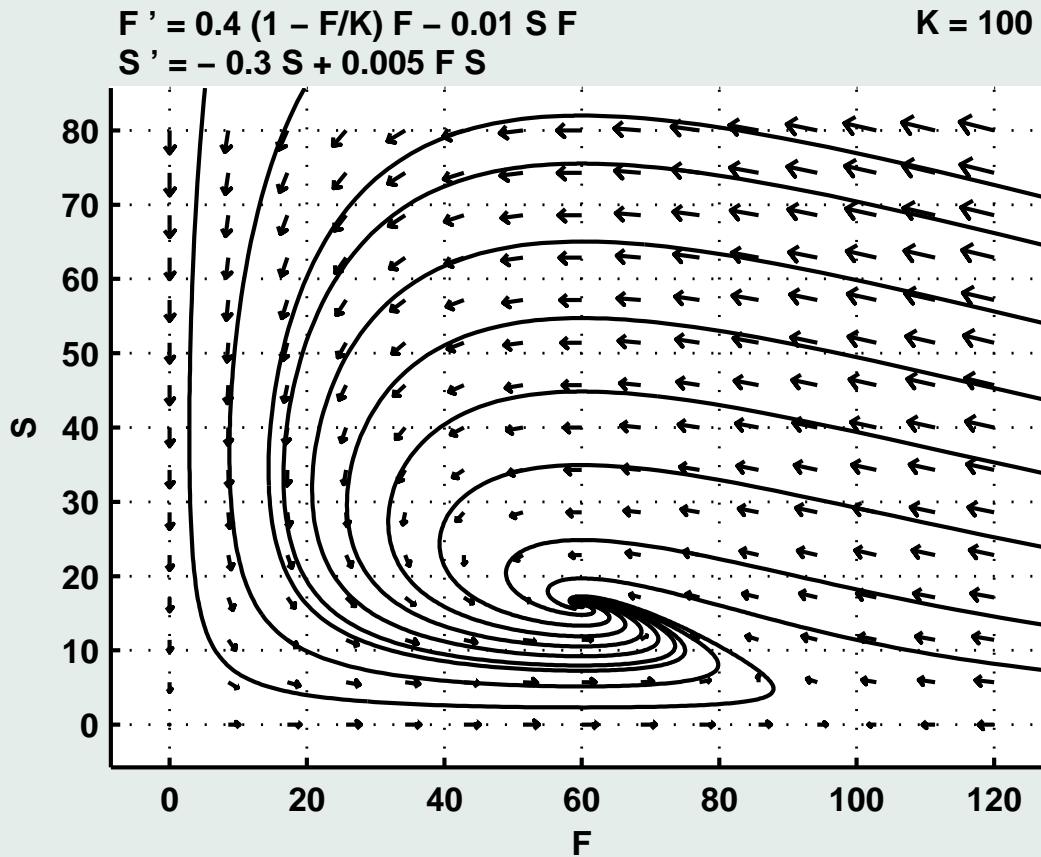


Figure 2: A System Based On The Logistic Model

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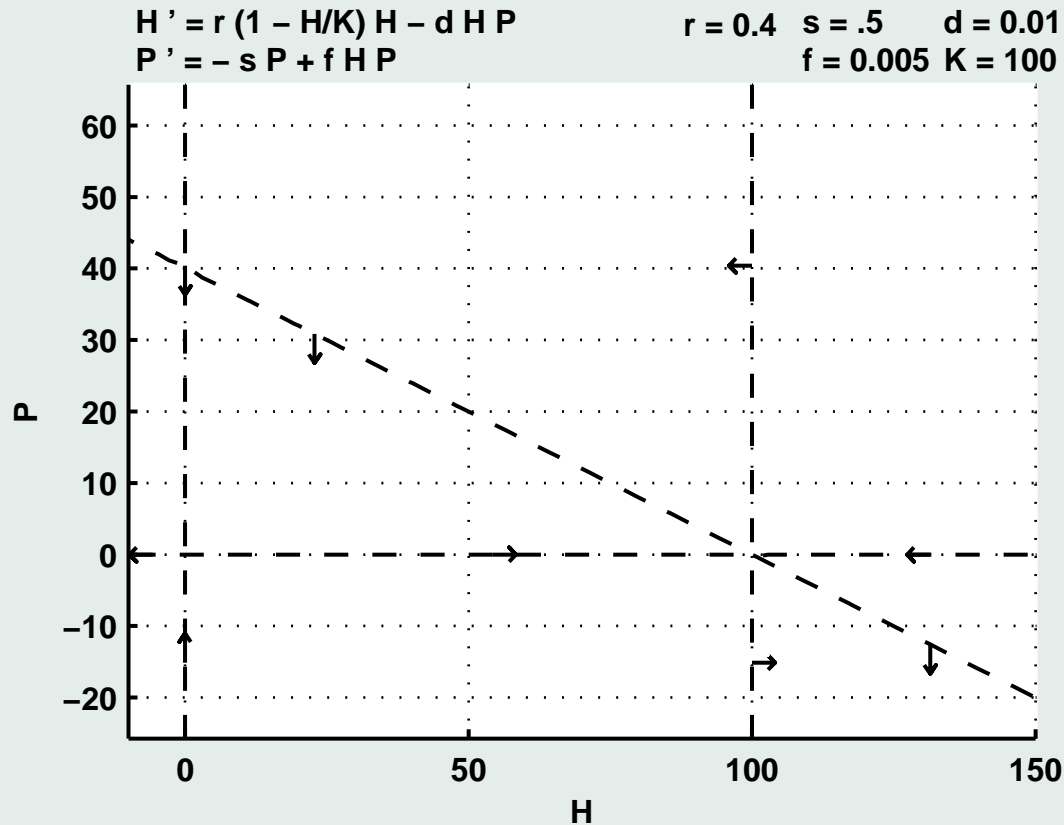


Figure 3: A System Based On The Logistic Model

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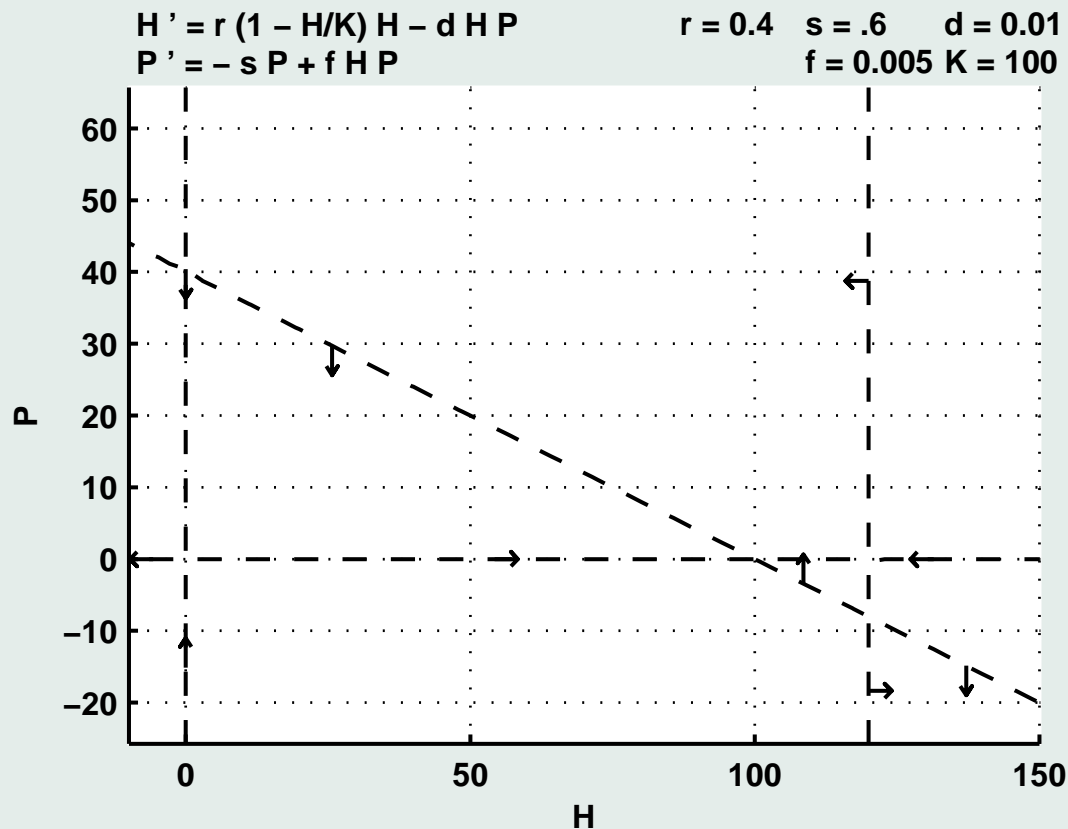


Figure 4: A System Based On The Logistic Model

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system with the same form as system (5). Figures 3 and 4 show what happens to the equilibrium point when $Kf = s$ and $Kf < s$, respectively.

The solutions to system (3) are startlingly different from the solutions to system (5). Those in the first, simpler, model cycle around the equilibrium point. Every time the solution passes close to the P axis, a small perturbation in the environment (e.g. the accidental death of a normally insignificant portion of the prey population) might be enough to push the prey population down to 0. This would not happen to the solution curve itself since there is another solution running down the P axis which it cannot cross, but this is a possibility for the population represented by the solution. A similar problem appears later in the cycle when the solution curve comes close to the H axis. A small perturbation in the predator population could cause extinction of the predator species. Again, there is another solution running along the H axis that solutions started in the first quadrant cannot cross, but this is a risk for the population modelled by system (3). Both of these possibilities would threaten both populations each cycle.

System (5) in comparison is much safer. After a maximum of one pass through both danger zones, the solution spirals away from possible extinction and toward the interesting equilibrium point.

6. A Further Refinement

That analysis of system (5) is encouraging. Assuming the equilibrium point is sufficiently far away from both axes to protect each population from random perturbations, solutions starting sufficiently close to the interesting equilibrium point would seem to guarantee stable, safe populations as time approaches infinity. However, there is a serious problem with system (5).

6.1. Linear Predation

Recall that the herbivore equation from system (5) is defined as

$$H' = r \left(1 - \frac{H}{K} \right) H - dHP.$$

In other words, the harm done to the growth rate of the prey population by the predator population is dHP . Put another way, the harm done to the prey population per predator is dH . On the surface, this assumption seems to make sense. The more predator-prey interactions there are (i.e. the larger HP becomes), the more prey fatalities there will be in a given space of time. But that would mean that

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in a given time interval, each predator would have to kill dH prey, or some fixed fraction of the prey population. This linear predation, illustrated in Figure 5, is not realistic.

If there are four predators and forty prey, predators might be expected to kill a certain fraction of the prey population in a given amount of time. Would four predators be expected to kill that same fraction of forty million prey? Of forty trillion? No. Predators have a limited capacity kill (a predator constantly killing prey still has a maximum kill rate), and an even more limited motivation to kill (full predators are less motivated to kill than hungry predators).

6.2. A Better Predation Model

A better function $y(H)$ for predation is required. At a minimum, it must satisfy two conditions:

- $y(0) = 0$, and
- $\lim_{H \rightarrow \infty} y(H)$ must be some constant

In other words, when there are no prey, the predation rate should be zero. Predators cannot do any damage to a nonexistent prey population. Also, as prey population approaches infinity (and as a result the prey density for a fixed area approaches infinity), predation should have an upper limit of w at which predators are killing as many prey as they would under completely optimal conditions. This is called saturation of the predation rate.

One function that meets both of these requirements is

$$y(H) = w \frac{H}{D + H}, \quad (6)$$

illustrated in Figure 6. The solid line is a graph of predation rate $y(H)$ v. prey population, and the dotted line is the limit of the predation function as the prey population approaches infinity.

There are any number of functions that satisfy the two conditions mentioned above. However, there are three very desirable properties of equation (6).

1. The function's limit as H approaches infinity is obvious without doing any computations.
2. The function will be easy to manipulate later when finding the linearization.
3. The function's parameters, w and D , have meaning.

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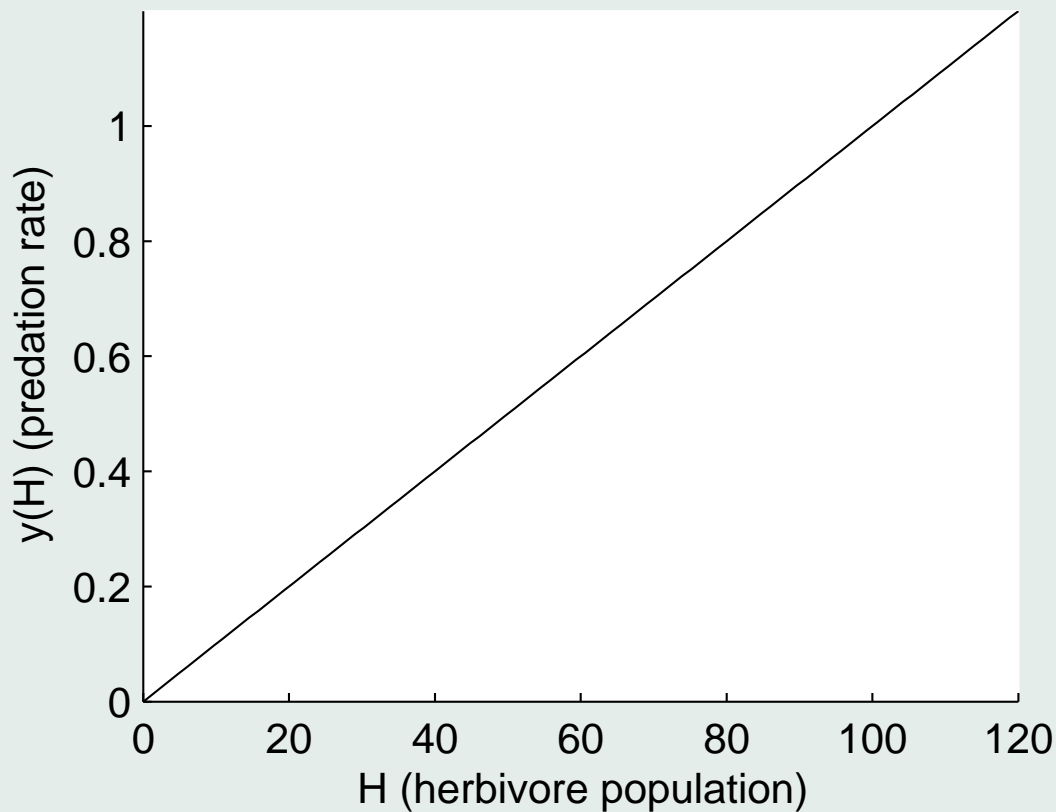


Figure 5: Linear Predation

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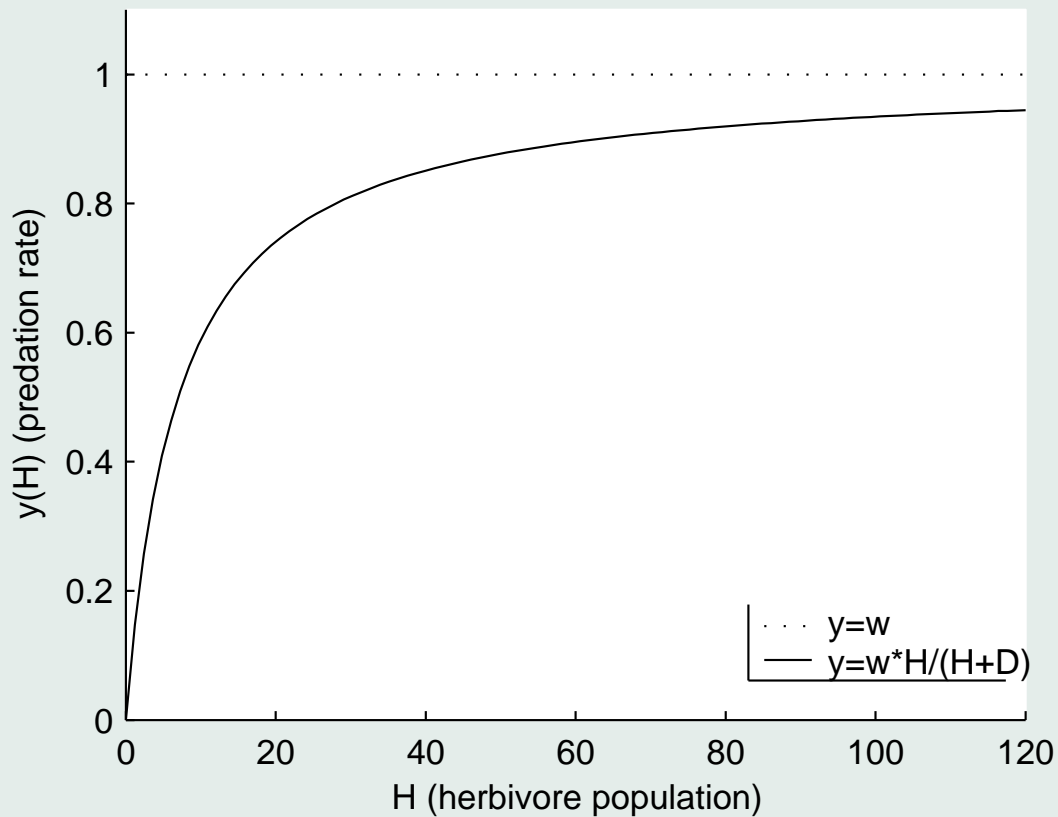


Figure 6: Revised Predation

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The predation function's limit as H approaches infinity is w , so w is the maximum predation rate. Increasing or decreasing the value of D decreases or increases the rate at which the predation function approaches its limit. D could then be interpreted as the predator search time, the amount of time the average predator would have to search to find and kill a prey, or alternately as the quality of cover afforded the prey by the environment. Increasing the quality of cover increases the predator search time. Decreasing the quality of cover decreases the predator search time.

With this new model for predation, the modified prey equation can be written

$$\begin{aligned} H' &= r \left(1 - \frac{H}{K} \right) H - Py \\ y &= w \frac{H}{H + D} \end{aligned}$$

or alternately

$$H' = r \left(1 - \frac{H}{K} \right) H - Pw \frac{H}{H + D} \quad (7)$$

7. A New Predator Model

The revised prey model more accurately reflects how the prey population growth rate responds to particular predator and prey population combinations, but the predator equation from systems (3) and (5) is still lacking.

$$P' = -sP + fHP$$

implies that as the prey population approaches infinity, the predator growth rate approaches infinity as well.

A better model would consider a natural growth rate for predators assuming that they have unlimited resources, and represent the actual growth rate as a number less than that. If the predator population is less than the maximum carrying capacity defined by the limiting resource, the predator population should grow at a rate somewhere between 0 and its maximum growth rate. If the predator population is more than the carrying capacity defined by the limiting resource, the predator population should shrink. This suggests that the predator population might be governed by an equation similar to the logistic equation. For example:

$$P' = s \left(1 - \frac{P}{Q} \right) P$$

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where s is the natural growth rate and Q is the carrying capacity of the environment.

There is one problem left, and that is that the limiting resource in predator population growth is assumed to be a function of the prey population, whereas the parameter Q is a constant. If we let J be the number of prey required to support one predator at equilibrium, then HJ^{-1} is the number of predators that a population of H prey can support at equilibrium. Replacing Q with HJ^{-1} gives the new predator equation

$$P' = s \left(1 - \frac{P}{HJ^{-1}} \right) P. \quad (8)$$

8. Analyzing Model 3

Together, equations (7) and (8) form a new system.

$$\begin{aligned} H' &= r \left(1 - \frac{H}{K} \right) H - Pw \frac{H}{H + D} \\ P' &= s \left(1 - \frac{P}{HJ^{-1}} \right) P \end{aligned} \quad (9)$$

The parameters are listed here for reference.

- r and s are the natural growth rates of the prey and predators, respectively.
- K is the carrying capacity of the environment for the prey.
- J is the number of prey required to support one predator at equilibrium.
- w is the maximum predation rate.
- D is the predator search time, or alternately the quality of the cover afforded the prey by the environment.

As before, the analysis of this system begins with finding the equilibrium points. In this case, finding the nullclines requires more work. The prey nullclines are found as follows.

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$$\begin{aligned}
 H' &= r \left(1 - \frac{H}{K} \right) H - Pw \frac{H}{H+D} \\
 0 &= r \left(1 - \frac{H}{K} \right) H - Pw \frac{H}{H+D} \\
 0 &= H \left(r \left(1 - \frac{H}{K} \right) - \frac{Pw}{H+D} \right)
 \end{aligned}$$

Either $H = 0$ or $r(1 - H/K) - Pw/(H + D) = 0$.

$$\begin{aligned}
 0 &= r \left(1 - \frac{H}{K} \right) - \frac{Pw}{H+D} \\
 \frac{Pw}{H+D} &= r \left(1 - \frac{H}{K} \right) \\
 Pw &= r \left(1 - \frac{H}{K} \right) (H+D) \\
 P &= \frac{r}{w} \left(1 - \frac{H}{K} \right) (H+D)
 \end{aligned}$$

The two prey nullclines are then $H = 0$ and $P = (r/w)(1 - H/K)(H + D)$. The second equation is a parabola on the phase plane with zeros at K and $-D$. All parameters are positive so the point $(-D, 0)$, implying a negative prey population, has no meaning, but knowledge of both roots of the function does give the location of the vertex of the parabola which could still have a positive prey component. Further manipulation of the equation for the second nullcline gives

$$P = -\frac{r}{wk}H^2 + \frac{rK - rD}{wK}H + \frac{rD}{w}.$$

All parameters are positive, so the coefficient on H^2 is negative meaning the parabola opens down. For some values of K and D then, the vertex of the parabola could be in the first quadrant. The predator

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nullclines are found the similarly.

$$\begin{aligned} P' &= s \left(1 - \frac{P}{HJ^{-1}} \right) P \\ 0 &= s \left(1 - \frac{P}{HJ^{-1}} \right) P \end{aligned}$$

Either $P = 0$ or $s(1 - P/(HJ^{-1})) = 0$

$$\begin{aligned} 0 &= s \left(1 - \frac{P}{HJ^{-1}} \right) \\ 0 &= 1 - \frac{P}{HJ^{-1}} \\ 1 &= \frac{P}{HJ^{-1}} \\ P &= \frac{H}{J} \end{aligned}$$

The two predator nullclines are then $P = 0$ and $P = H/J$.

The equilibrium points are found from the intersections of the nullclines. As in system (5) there is an equilibrium point at $(K, 0)$. However, there is no equilibrium point at $(0, 0)$. While it still makes sense that an environment with no predators and no prey would remain in that state for all time, a prey population of zero would make P' undefined. The interesting equilibrium point, in this case, is the one where the nontrivial prey nullcline intersects the nontrivial predator nullcline in the first quadrant. This intersection is shown in Figure 7.

While the exact coordinates for the interesting equilibrium point can be found¹ by setting the equations for the nontrivial equilibrium points equal to each other and solving for H , this provides very little useful information. The expressions for the trace and determinant of the Jacobian at that point involve so many parameters that it is difficult to distill any useful information. Instead, declare the equilibrium point to have the coordinates (H^*, P^*) , and then divide H , P , D , and K by H^* . Now that $H = H/H^*$, the new H^* is 1 and the new P^* is J^{-1} . With this in mind, taking the partial derivatives

¹It is $((JrK - JrD - wK + \sqrt{(JrK - JrD - wK)^2 + 4J^2r^2DK})/(2rJ), (JrK - JrD - wK + \sqrt{(JrK - JrD - wK)^2 + 4J^2r^2DK})/(2rJ^2))$.

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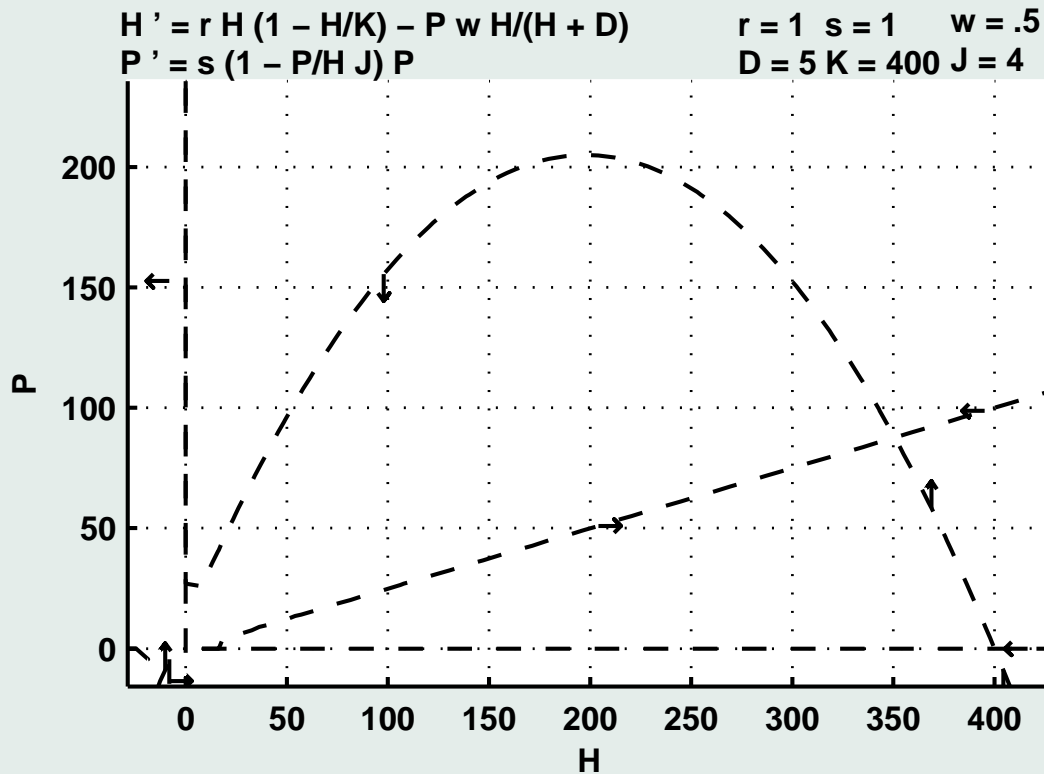


Figure 7: Nullclines For Model 3

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at $(H^* = 1, P^* = J^{-1})$ gives:

$$\begin{aligned}
 \left. \frac{\partial H'}{\partial H} \right|_{(H^*, P^*)} &= r \left(1 - \frac{H^*}{K} \right) + r H^* \left(-\frac{1}{K} \right) - \left(\frac{(H^* + D) P w - P w H^*}{(H + D)^2} \right) \\
 &= r \left(1 - \frac{1}{K} - \frac{1}{K} \right) - J^{-1} w \frac{D - 1}{(H + D)^2} \\
 &= r \left(-\frac{1}{K} + \frac{w}{r J (1 + D)^2} \right) \\
 \left. \frac{\partial H'}{\partial P} \right|_{(H^*, P^*)} &= 0 - w \frac{H^*}{H^* + D} \\
 &= -\frac{w}{1 + D} \\
 \left. \frac{\partial P'}{\partial H} \right|_{(H^*, P^*)} &= s P^* \left(-P^* J \left(-\frac{1}{H^{*2}} \right) \right) \\
 &= \frac{s}{J} \\
 \left. \frac{\partial P'}{\partial P} \right|_{(H^*, P^*)} &= s \left(1 - \frac{P^*}{H^*} J \right) + s P^* \left(-\frac{J}{H^*} \right) \\
 &= -s.
 \end{aligned}$$

The Jacobian at $(H^* = 1, P^* = J^{-1})$, then, is

$$J(H^* = 1, P^* = J^{-1}) = \begin{bmatrix} r \left(-K^{-1} + w (r J)^{-1} (1 + D)^{-2} \right) & -w(1 + D)^{-1} \\ s/J & -s \end{bmatrix}$$

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In order to analyze the behavior of the system near the equilibrium point, the trace and determinant of the linearization must be found.

$$\begin{aligned}
 & \begin{vmatrix} r \left(-K^{-1} + w (rJ)^{-1} (1 + D)^{-2} \right) & -w(1 + D)^{-1} \\ s/J & -s \end{vmatrix} \\
 = & -sr \left(-K^{-1} + w (rJ)^{-1} (1 + D)^{-2} \right) + swJ^{-1}(1 + D)^{-1} \\
 = & \frac{sr}{K} - \frac{srw}{rJ(1 + D)^2} + \frac{srw(1 + D)}{rJ(1 + D)^2} \\
 = & sr \left(\frac{1}{K} + \frac{w + wD - w}{rJ(1 + D)^2} \right) \\
 = & sr \left(\frac{1}{K} + \frac{wD}{rJ(1 + D)^2} \right)
 \end{aligned}$$

All parameters are positive, so the determinant must be positive.

If the trace is less than zero, the system behaves like some kind of spiral sink or sink around the equilibrium point. Setting up this inequality and manipulating it gives another inequality that makes it clear when this condition is and is not met.

$$\begin{aligned}
 r(-K^{-1} + w(rJ)^{-1}(1 + D)^{-2}) - s &< 0 \\
 -\frac{1}{K} + \frac{w}{rJ}(1 + D)^{-2} &< s/r \\
 -\frac{1}{K} + (1 - 1/K)(1 + D)(1 + D)^{-2} &< s/r \\
 -\frac{1}{K} + \frac{1 - 1/K}{1 + D} &< s/r \\
 \frac{1 - 1/K - 1/K(1 + D)}{1 + D} &< s/r \\
 \frac{K - 1 - 1(1 + D)}{K(1 + D)} &< s/r \\
 \frac{K - D - 2}{K(1 + D)} &< s/r \\
 \frac{2((K - D)/2 - 1)}{K(1 + D)} &< s/r
 \end{aligned}$$

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Notice that the expression $(K - D)/2$ is a term in the numerator of the fraction on the left side of the inequality, and recall that it is the H -coordinate of the vertex of the prey nullcline. Since H , K , and D have been divided through by the original H^* , the inequality $(K - D)/2 < 1$ is equivalent to stating that the vertex is to the left of the equilibrium point. If this is so, $(K - D)/2 - 1$ will be negative, and the inequality will be true for all values of the (always positive) parameters. If the equilibrium point is to the right of the vertex, then all solutions started sufficiently close to the equilibrium point will approach it as time approaches infinity. This is illustrated in Figure 8.

If the equilibrium point is to the left of the vertex then both fractions will be positive. If s/r is still larger than $(K - D - 2)/(K + KD)$, the equilibrium point will still be stable (see Figure 9). Otherwise, solutions started near the equilibrium point will travel away from the equilibrium point and out toward a limit cycle (see Figure 10).

In other words, the equilibrium point is stable if a sufficiently large number of prey are required to support a single predator (i.e. J is large enough), or failing that, if the predator population in ideal predator conditions responds sufficiently more quickly than the prey population in ideal prey conditions (i.e. s/r is large enough).

9. Final Thoughts

System (9) offers a true variety of different behaviors depending on the values of the parameters, so it is natural to wonder how one might manipulate a real-world predator-prey system to achieve desired stability. Algebraically, it is easy to manipulate the parameters to turn an unstable equilibrium point into a stable equilibrium point. One might raise J , raise D , lower K , raise s , lower r , or lower w .

However, it manipulating a single parameter in the real world can be more difficult. Raising s or lowering r would mean interfering with the natural reproductive rate of one species while leaving its other behavior unchanged. One might raise J by lowering the nutritional value of the prey to the predator (e.g. by reducing the nutritional value of the prey's own food), but how would this affect the prey's health and longevity?

Also, it is important to keep in mind that these systems are definitely not linear. While solutions that start near equilibrium points will behave similarly to their counterparts in the linearization, there is no guarantee of this further away. Do solutions that start near unstable equilibrium points spiral off into increasingly unstable loops, or approach a limit cycle? Further analysis is necessary to fully determine the behavior of the systems.

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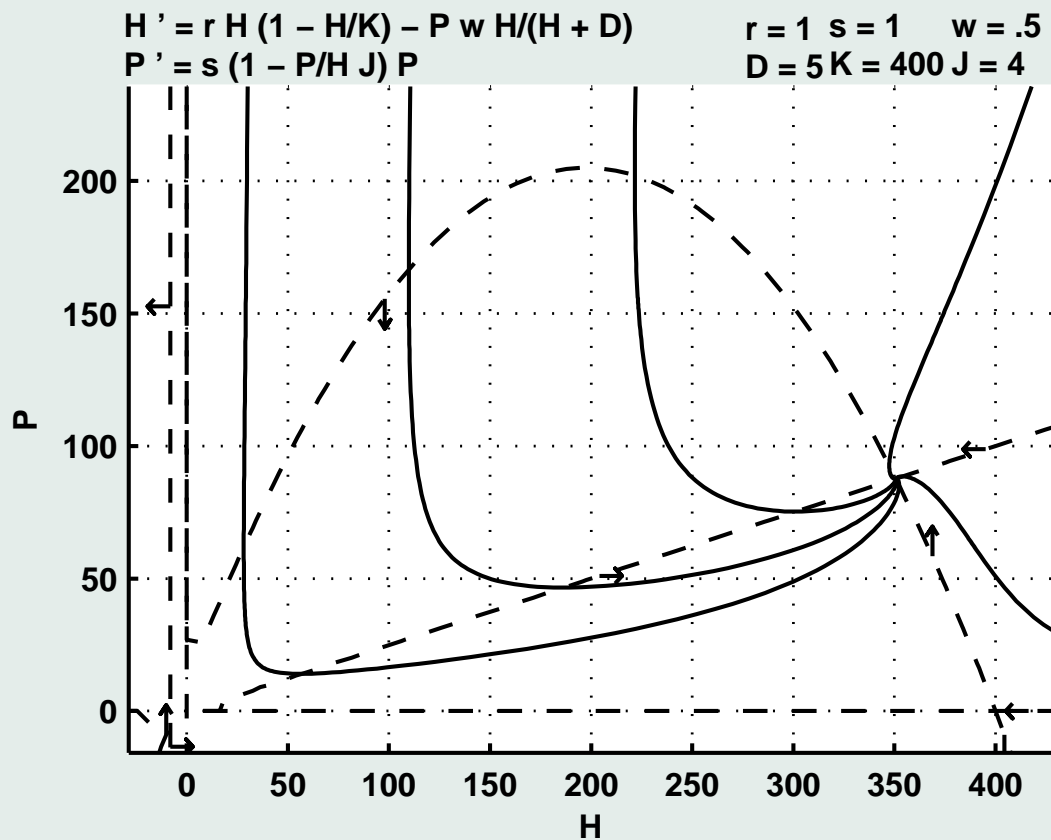


Figure 8: Equilibrium Point Right of Vertex, Stable

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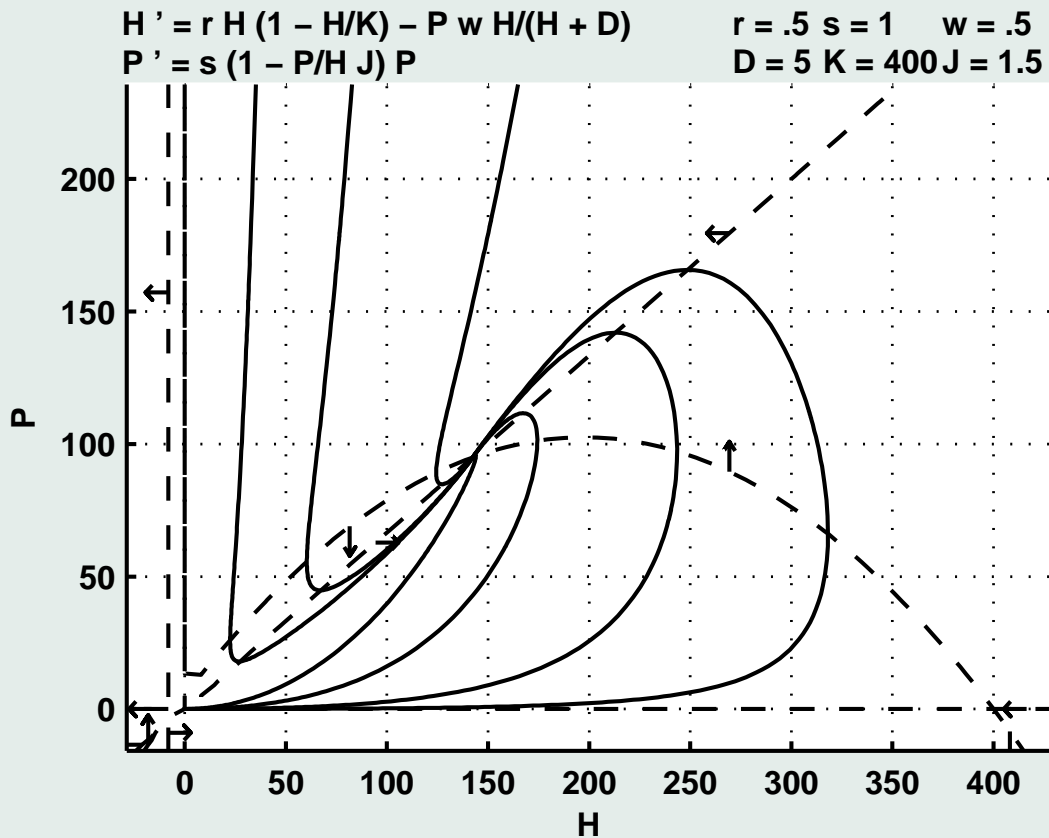


Figure 9: Equilibrium Point Left of Vertex, Stable

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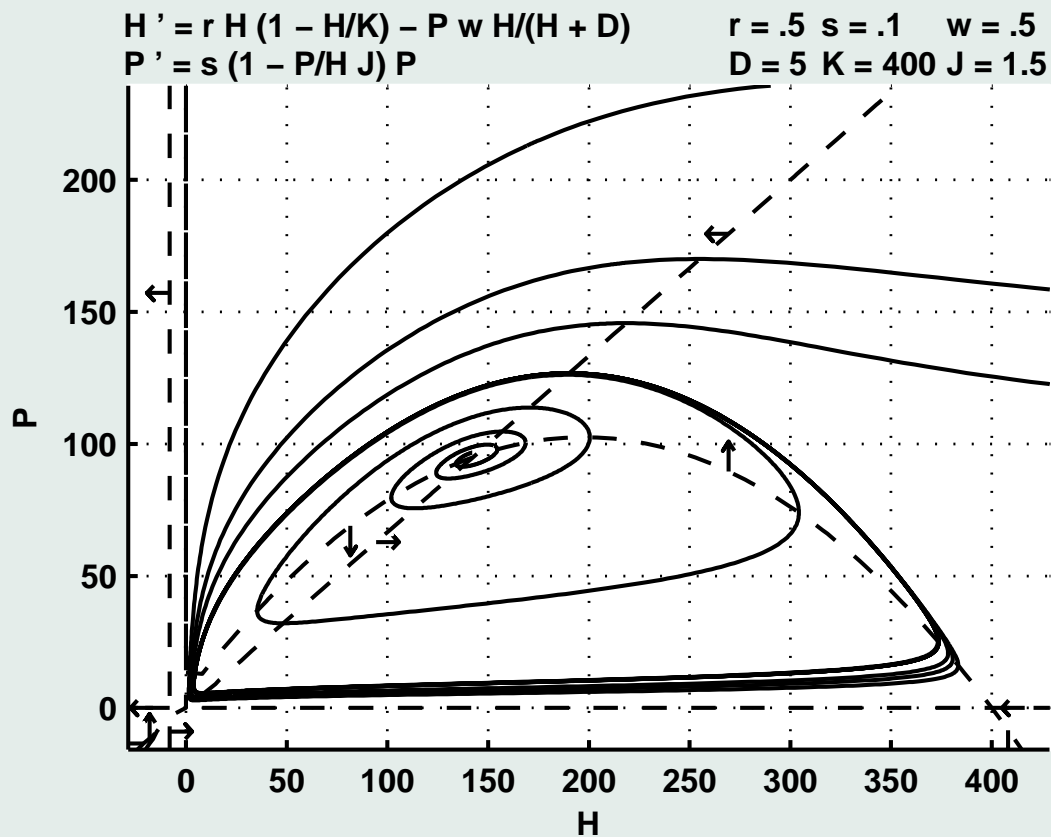


Figure 10: Equilibrium Point Left of Vertex, Unstable

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