

A Lotka-Volterra Three-species Food Chain

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In the 1920s, the Italian mathematician Vito Volterra [8] proposed a differential equation model to describe the population dynamics of two interacting species, a predator and its prey. He hoped to explain the observed increase in predator fish (and corresponding decrease in prey fish) in the Adriatic Sea during World War I. Such mathematical models have long proven useful in describing how populations vary over time. Data about the various rates of growth, death, and interaction of species naturally lead to models involving differential equations.

Independently, in the United States, the very equations studied by Volterra were derived by Alfred Lotka [6] to describe a hypothetical chemical reaction in which the chemical concentrations oscillate.

The Lotka-Volterra model [2] consists of the following system of differential equations:

$$\begin{cases} \frac{dx}{dt} = ax - bxy, \\ \frac{dy}{dt} = -cy + dxy, \end{cases} \quad (1)$$

where $y(t)$ and $x(t)$ represent, respectively, the predator population and the prey population as functions of time. The parameters $a, b, c, d > 0$ are interpreted as follows:

- a represents the natural growth rate of the prey in the absence of predators,
- b represents the effect of predation on the prey,
- c represents the natural death rate of the predator in the absence of prey,
- d represents the efficiency and propagation rate of the predator in the presence of prey. (Using the letter d is traditional; the reader is trusted to observe from context when we wish to indicate differentiation using this same letter.)

To analyze this system in a straightforward manner, divide the second equation of (1) by the first,

$$\frac{dy}{dx} = \frac{dy}{dt} \bigg/ \frac{dx}{dt} = \frac{y(-c + dx)}{x(a - by)},$$

and solve the resulting separable ODE. This gives the family of equations

$$a \ln y - by + c \ln x - dx = C,$$

where C is the constant of integration. It can be shown that the maximum value C_* of the left-hand side of the above equation occurs at $(c/d, a/b)$. FIGURE 1 depicts

the family of trajectories of (1) in the xy -plane with parameters $a = b = c = d = 1$; readers may test their biological savvy by determining why the trajectories circulate counterclockwise. FIGURE 2 plots the behavior of a particular solution over time.

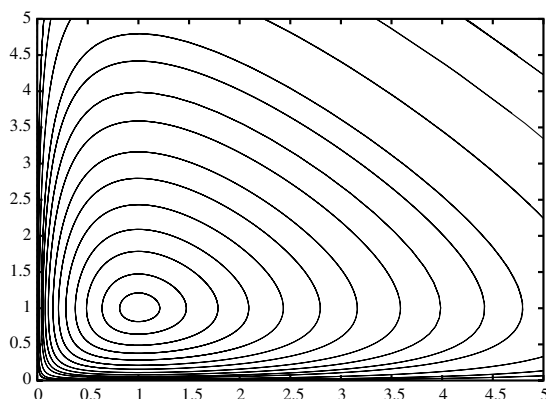


Figure 1 A family of closed orbits in the xy -plane circulating about $(1, 1)$ with $a = b = c = d = 1$

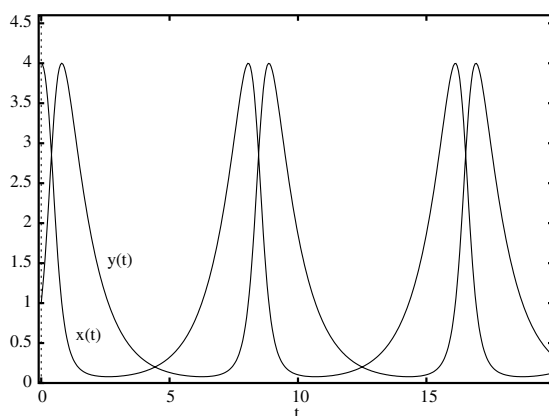


Figure 2 A solution with initial conditions $(x, y) = (4, 1)$ with parameters $a = b = c = d = 1$

The predator-prey model predicts a phase-shifted periodic behavior in the populations of both species with a common period. This behavior is seen in the historical records of the Hudson's Bay Company, which recorded the annual number of pelts of hare (prey) and lynx (predator) collected from 1845–1935 [3].

In this paper, we completely characterize the qualitative behavior of a linear three-species food chain where the dynamics are given by classic (nonlogistic) Lotka-Volterra type equations. The Lotka-Volterra equations are typically modified by making the prey equation a logistic (Holling-type [5]) equation to eliminate the possibility of unbounded growth of the prey in the absence of the predator. We study a more basic nonlogistic system that is the direct generalization of the classic Lotka-Volterra equations. Although the model is more simplified, the dynamics of the associated system are quite complicated, as the model exhibits degeneracies that make it an excellent instructional tool whose analysis involves advanced topics such as: trapping regions, nonlinear analysis, invariant sets, Lyapunov-type functions (F and G in what follows), the stable/center manifold theorem, and the Poincaré-Bendixson theorem.

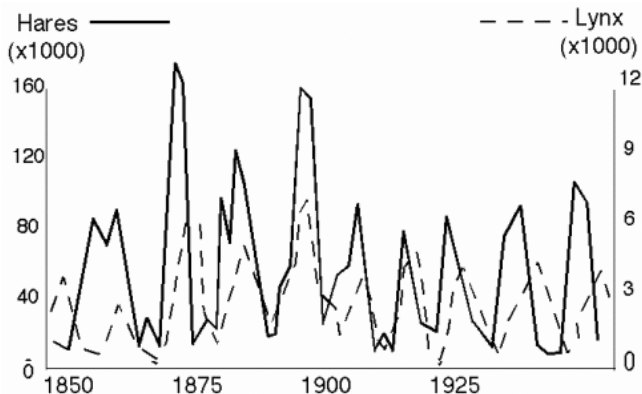


Figure 3 Historical plots of hare and lynx pelts collected by the Hudson's Bay Company

The model

The ecosystem that we wish to model is a linear three-species food chain where the lowest-level prey x is preyed upon by a mid-level species y , which, in turn, is preyed upon by a top level predator z . Examples of such three-species ecosystems include: mouse-snake-owl, vegetation-hare-lynx, and worm-robin-falcon. The model we propose to study is

$$\begin{cases} \frac{dx}{dt} = ax - bxy \\ \frac{dy}{dt} = -cy + dxy - eyz \\ \frac{dz}{dt} = -fz + gyz, \end{cases} \quad (2)$$

for $a, b, c, d, e, f, g > 0$, where a, b, c and d are as in the Lotka-Volterra equations and:

- e represents the effect of predation on species y by species z ,
- f represents the natural death rate of the predator z in the absence of prey,
- g represents the efficiency and propagation rate of the predator z in the presence of prey.

Since populations are nonnegative, we will restrict our attention to the nonnegative octant $\{(x, y, z) \mid x \geq 0, y \geq 0, z \geq 0\} \subset \mathbb{R}^3$ and the positive octant $\mathbb{R}_+^3 = \{(x, y, z) \mid x > 0, y > 0, z > 0\} \subset \mathbb{R}^3$.

Analysis of the model

The coordinate planes We first show that each coordinate plane is invariant with respect to the system (2). In general, a surface S is invariant with respect to a system of differential equations if every solution that starts on S does not escape S . The property of invariant coordinate planes matches biological considerations, since if some species is extinct, it will not reappear.

The following result appears in most advanced texts on differential equations [1]. In such texts, the invariant surface S is usually given as the level set of a function $G(x, y, z)$, which is called a first integral of the system (2).

THEOREM 1. Let S be a smooth closed surface without boundary in \mathbb{R}^3 and

$$\begin{aligned}\frac{dx}{dt} &= f(x, y, z), \\ \frac{dy}{dt} &= g(x, y, z), \\ \frac{dz}{dt} &= h(x, y, z),\end{aligned}\tag{3}$$

where f , g , and h are continuously differentiable. Suppose that \mathbf{n} is a normal vector to the surface S at (x, y, z) , and for all $(x, y, z) \in S$ we have that

$$\mathbf{n} \cdot \left\langle \frac{dx}{dt}, \frac{dy}{dt}, \frac{dz}{dt} \right\rangle = 0.$$

Then S is invariant with respect to the system (3).

Let S be the plane $z = 0$, note that the vector $\langle 0, 0, 1 \rangle$ is always normal to S , and that at the point $(x, y, 0)$ of S we have

$$\left\langle \frac{dx}{dt}, \frac{dy}{dt}, \frac{dz}{dt} \right\rangle = \langle ax - bxy, -cy + dxy, 0 \rangle.$$

Thus,

$$\langle 0, 0, 1 \rangle \cdot \langle ax - bxy, -cy + dxy, 0 \rangle = 0.$$

Similar arguments show that each coordinate plane is invariant.

Next, we solve each of the three corresponding planar (two variable) systems in the respective coordinate planes. We first notice that in absence of the top predator ($z = 0$), the model reduces to the classic Lotka-Volterra equations with closed trajectories centered at the equilibrium $(c/d, a/b, 0)$, for all values of the parameters.

For a trajectory starting on the plane $y = 0$, equations (2) reduce to:

$$\begin{cases} \frac{dx}{dt} = ax \\ \frac{dy}{dt} = 0 \\ \frac{dz}{dt} = -fz. \end{cases}$$

The equation $dz/dt = -fz$ implies that $z(t) \rightarrow 0$ exponentially as $t \rightarrow \infty$, while $dx/dt = ax$ implies that x grows exponentially as $t \rightarrow \infty$. Notwithstanding the unbounded growth of x , this behavior fits with what we would expect biologically in the absence of mid-level species y . That is, x is free from predation and z is without a source of food. The trajectories in the xz -plane can be directly computed from the separable equation:

$$\frac{dz}{dx} = \frac{dz}{dt} \bigg/ \frac{dx}{dt} = \frac{-fz}{ax}$$

that has solution $z = Kx^{-f/a}$ (see FIGURE 4).

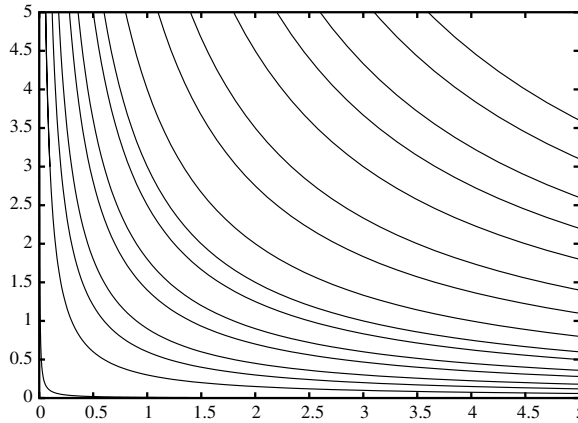


Figure 4 A family of trajectories $z = Kx^{-f/a}$ in the xz -plane with $a = b = c = d = e = f = g = 1$

For solutions starting in the plane $x = 0$, we see that (2) reduces to

$$\begin{cases} \frac{dx}{dt} = 0 \\ \frac{dy}{dt} = -cy - eyz \\ \frac{dz}{dt} = -fz + gyz. \end{cases}$$

Since $dy/dt \leq -cy$, as $t \rightarrow \infty$ we have $y(t) \rightarrow 0$. This, in turn, will cause $z(t) \rightarrow 0$, as $t \rightarrow \infty$. Note that dz/dy is also separable and has solutions of the form

$$-f \ln y + gy = -c \ln z - ez + K$$

in the yz -plane. The reader may wish to verify that, if a solution starts in this plane with $y > f/g$, then z will have a maximum value when y has dropped back to f/g . This makes sense biologically: under these circumstances, the predator z may temporarily grow in numbers while it exhausts the prey y , but then tend to extinction itself, having no replenished food source. To summarize, all species eventually become extinct in the absence of bottom-level prey x .

Equilibria and linear analysis In the analysis of systems of differential equations it is often useful to consider solutions that do not change with time, that is, for which $dx/dt = 0$, $dy/dt = 0$, and $dz/dt = 0$. Such solutions are called equilibria, steady-states, or fixed points. For system (2) there are two equilibria located at $(0, 0, 0)$ and $(c/d, a/b, 0)$. The special case $a/b = f/g$, which we will study in detail later as a borderline case, yields a ray of fixed points parameterized by: $(s, a/b, (ds - c)/e)$, where $s \geq c/d$.

An equilibrium is called asymptotically stable if solutions starting close enough to the equilibrium tend to that equilibrium. If the system of differential equations (3) can be linearized, that is, if f , g , and h have continuous partials in x , y , and z , then the stability of an equilibrium (x_0, y_0, z_0) often can be determined by the stability of

(x_0, y_0, z_0) in the associated linearized system:

$$\begin{cases} \frac{dx}{dt} = \frac{\partial f}{\partial x}x + \frac{\partial f}{\partial y}y + \frac{\partial f}{\partial z}z \\ \frac{dy}{dt} = \frac{\partial g}{\partial x}x + \frac{\partial g}{\partial y}y + \frac{\partial g}{\partial z}z \\ \frac{dz}{dt} = \frac{\partial h}{\partial x}x + \frac{\partial h}{\partial y}y + \frac{\partial h}{\partial z}z, \end{cases}$$

where all partials are evaluated at (x_0, y_0, z_0) . The behavior of the linearized system at (x_0, y_0, z_0) is determined by the eigenvalues of the Jacobian matrix:

$$J(x, y, z) = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} & \frac{\partial f}{\partial z} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} & \frac{\partial g}{\partial z} \\ \frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} & \frac{\partial h}{\partial z} \end{bmatrix}$$

evaluated at (x_0, y_0, z_0) .

For system (2),

$$J(x, y, z) = \begin{bmatrix} a - by & -xb & 0 \\ yd & -c + dx - ez & -ye \\ 0 & zg & -f + gy \end{bmatrix}.$$

Simply examining the eigenvalues of $J(x_0, y_0, z_0)$ gives us information about the dynamics near the equilibrium of the original system. If all eigenvalues of $J(x_0, y_0, z_0)$ have negative real part then (x_0, y_0, z_0) is asymptotically stable. If any eigenvalue has positive real part then (x_0, y_0, z_0) is not asymptotically stable.

A powerful tool used to analyze the dynamics of a nonlinear system near an equilibrium is the Center Manifold Theorem (for a technical treatment, see Chapter 3 of Guckenheimer and Holmes [4]). The reader unfamiliar with manifolds will find that, informally, this is a generic term to encompass sets such as nonsingular curves and surfaces.

The Center Manifold Theorem states that associated with each equilibrium (x_0, y_0, z_0) there exist invariant sets containing (x_0, y_0, z_0) , called the stable manifold, the unstable manifold, and a center manifold. The stable and unstable manifolds are unique, but there may be more than one center manifold.

The dimensions of these sets are given by the number of eigenvalues of $J(x_0, y_0, z_0)$ having negative, positive, and zero real part, respectively. Moreover, each such manifold is tangent to the real space that is spanned by the eigenvectors associated with that manifold. On the stable manifold all trajectories tend toward the equilibrium as $t \rightarrow \infty$, and on the unstable manifold all trajectories tend away from the equilibrium as $t \rightarrow \infty$. However, the theorem gives no conclusion concerning the direction of the flow of trajectories on a center manifold.

For example, suppose $J(x_0, y_0, z_0)$ has a single eigenvalue λ_1 having positive real part, and two eigenvalues λ_2, λ_3 having negative real part. Then there exists an unstable manifold associated with λ_1 , which is a one-dimensional curve passing through (x_0, y_0, z_0) that is tangent to the eigenvector corresponding to λ_1 . There also exists an invariant stable manifold, which is a two-dimensional surface containing (x_0, y_0, z_0) whose tangent plane at (x_0, y_0, z_0) is given by the span of the eigenvectors associated with λ_2 and λ_3 . In this case, there is no center manifold.

Let us apply this theorem to the equilibrium $(0, 0, 0)$ of system (2). The Jacobian matrix $J(0, 0, 0)$ has eigenvalues a , $-c$, and $-f$ with eigenvectors $\langle 1, 0, 0 \rangle$, $\langle 0, 1, 0 \rangle$, and $\langle 0, 0, 1 \rangle$, respectively. First note that this equilibrium is not asymptotically stable since we have an eigenvalue with positive real part, namely a . By the Center Manifold Theorem, this positive eigenvalue has a corresponding one-dimensional unstable manifold (a curve), which is tangent to $\langle 1, 0, 0 \rangle$ at the equilibrium $(0, 0, 0)$. As we saw previously, this unstable curve turns out to be the x -axis. Corresponding to the two negative eigenvalues is an invariant two-dimensional stable manifold, that is, an invariant surface through $(0, 0, 0)$ on which solutions move toward $(0, 0, 0)$. This stable surface intersects $(0, 0, 0)$ tangent to the plane spanned by the two eigenvectors $\langle 0, 1, 0 \rangle$ and $\langle 0, 0, 1 \rangle$. Again, using our previous analysis, we see that the stable manifold turns out to be the yz -plane itself. Note that as there are no eigenvalues with zero real part, so there is no center manifold in this case.

At the equilibrium $(c/d, a/b, 0)$, the eigenvalues of $J(c/d, a/b, 0)$ are $(ga - fb)/b$ along with the purely imaginary numbers $\pm\sqrt{ac}i$. For $ga \neq fb$ we use the Center Manifold Theorem to conclude that associated with the eigenvalue $(ga - fb)/b$ there is a one-dimensional invariant curve, which is tangent at $(c/d, a/b, 0)$ to the eigenvector $\langle 1, (fb - ag)d/b^2c, (ab^2cd + b^2df^2 - 2abdfg + a^2dg^2)/ab^2ce \rangle$. This curve is stable if $ga - fb < 0$ and unstable if $ga - fb > 0$. Corresponding to the two eigenvalues with zero real part, there exists a two-dimensional invariant center manifold passing through $(c/d, a/b, 0)$ tangent to the two-dimensional real subspace of the complex space spanned by the complex eigenvectors $\langle 1, \pm(\sqrt{acd})/bci, 0 \rangle$, namely the xy -plane itself. Using our prior analysis, we can conclude that the xy -plane is indeed invariant, and hence is a center manifold, but we cannot conclude that it is unique.

In the special case $ga = fb$, the Jacobian matrix evaluated at any of the fixed points $(s, a/b, (ds - c)/e)$, with $s \geq c/d$, has three eigenvalues with zero real part. Thus, each such fixed point has a three-dimensional center manifold, which does not help us determine the dynamics near these fixed points.

The case $ga = fb$ Plots of trajectories using a numerical solver suggest that the system contains invariant surfaces. In particular, the projection of any trajectory in \mathbb{R}_+^3 onto the xz -plane lies entirely within one of the curves depicted in FIGURE 4. This suggests that the surfaces $z = Kx^{-f/a}$ are invariant in \mathbb{R}_+^3 . These surfaces are filled with periodic orbits enclosing the ray of fixed points $(s, a/b, (ds - c)/e)$, with $s \geq c/d$ (see FIGURE 5). We will demonstrate this analytically later.

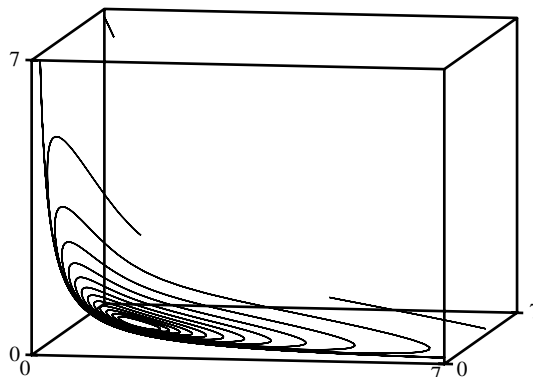


Figure 5 A family of closed orbits on the surface $z = Kx^{-f/a}$ in xyz -space with parameters $a = b = c = d = e = f = g = K = 1$

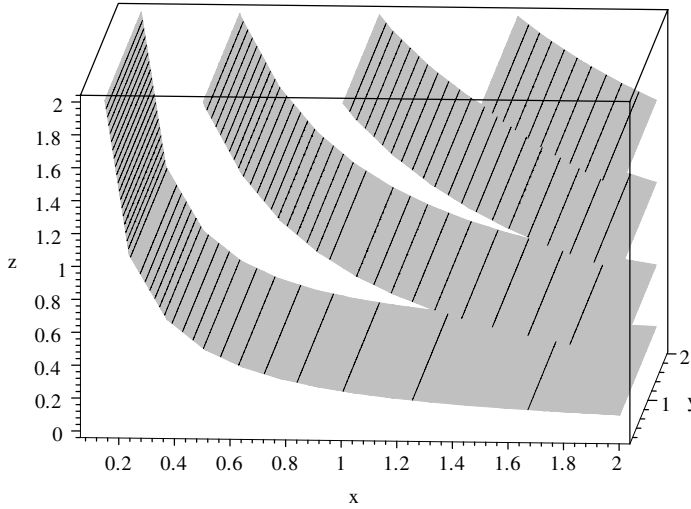


Figure 6 The surfaces $z = Kx^{-f/a}$ with $a = f = 1$

PROPOSITION 2. Let $ga = fb$. The surfaces defined by $z = Kx^{-f/a}$ are invariant with respect to (2).

Proof. The vector $\mathbf{n} = \langle (Kf/a)x^{-(1+f/a)}, 0, 1 \rangle$ is always normal to $-Kx^{-f/a} + z = 0$. Consider

$$\begin{aligned} \mathbf{n} \cdot \left\langle \frac{dx}{dt}, \frac{dy}{dt}, \frac{dz}{dt} \right\rangle &= \left\langle K \frac{f}{a} x^{-\frac{f}{a}-1}, 0, 1 \right\rangle \cdot \langle ax - bxy, -cy + dxy - eyz, -fz + gyz \rangle \\ &= (ax - bxy) \left(K \frac{f}{a} x^{-\frac{f}{a}-1} \right) - fz + gyz \\ &= fKx^{-\frac{f}{a}} - \frac{bfyK}{a} x^{-\frac{f}{a}} - fKx^{-\frac{f}{a}} + gyKx^{-\frac{f}{a}} = 0. \end{aligned}$$

Thus, the surface $z = Kx^{-f/a}$ is invariant with respect to (2). ■

Next, we implicitly solve the differential equation on each surface. For fixed K with $z = Kx^{-f/a}$, the system (2) becomes

$$\begin{cases} \frac{dx}{dt} = ax - bxy, \\ \frac{dy}{dt} = -cy + dxy - eyKx^{-\frac{f}{a}}. \end{cases} \quad (4)$$

Again taking the quotient of the equations, we find a separable equation,

$$\frac{dy}{dx} = \frac{dy}{dt} \bigg/ \frac{dx}{dt} = \frac{y(-c + dx - eKx^{-\frac{f}{a}})}{x(a - by)},$$

which we solve to obtain the implicit solution:

$$a \ln y - by + c \ln x - dx - \frac{eaK}{f} x^{-\frac{f}{a}} = C \quad (5)$$

on the surface $z = Kx^{-f/a}$. For fixed K , the family of closed curves (5) $C \leq C_K$, fills up the surface $z = Kx^{-f/a}$, where C_K is the maximum value of the left-hand side of (5). This value is attained at the fixed point given by the intersection of the line $(s, a/b, (ds - c)/e)$ and the surface $z = Kx^{-f/a}$.

We sketch the proof that the trajectory given by (5) is closed for any fixed $C < C_K$. One first uses techniques from calculus to show that the trajectory lies in a bounded region. Since $C < C_K$ is fixed, this trajectory cannot tend to the fixed point associated with C_K . The Poincaré-Bendixson Theorem [4] tells us that the trajectory is either a closed orbit or tends to a closed orbit. To rule out the latter, one can show that for fixed x , the solutions of (5) have at most two solutions for y , and vice versa.

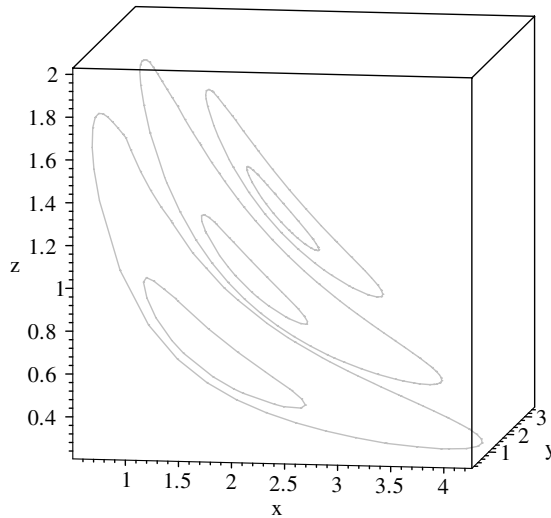


Figure 7 Several closed trajectories with $a = b = c = d = e = f = g = 1$

This completely characterizes the behavior in the special case $ga = fb$. Biologically, all three species persist and have populations that vary periodically over time with a common period. FIGURE 8 below depicts the plot of a particular periodic solution. Note the relative positions of the three maxima, with the lowest-level prey population peaking first, followed by a peak in the population in the mid-level species, with

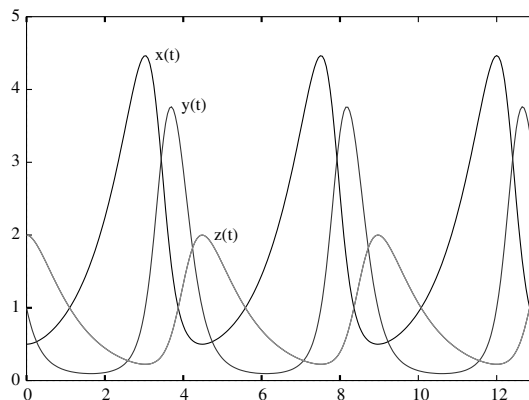


Figure 8 A solution with initial conditions $(x, y, z) = (.5, 1, 2)$ with parameters $a = b = c = d = e = f = g = 1$

the maximum in the top predator population coming last, as one would expect from biological considerations.

The cases $ga \neq fb$ We first consider the case $ga < fb$. Plots of solutions using a numerical solver suggest that all solutions spiral down to the xy -plane and tend to a periodic solution (see FIGURE 9).

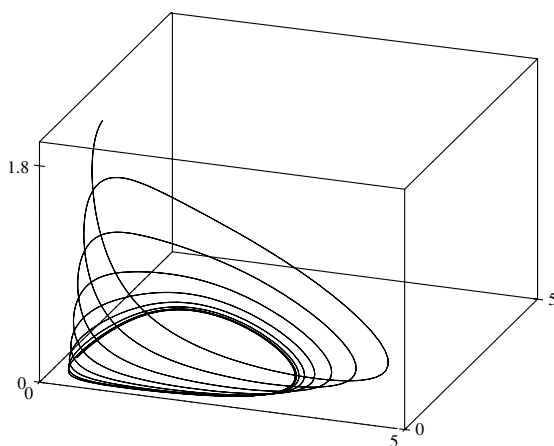


Figure 9 A trajectory in xyz -space with initial conditions $(\frac{1}{2}, 1, 2)$ with $a = b = c = d = e = f = 1$ and $g = 0.88$

We show that solutions move down across the surfaces $z = Kx^{-f/a}$ from higher values of K to lower values of K . More formally:

PROPOSITION 3. *Let $ga < fb$ and $F(x, y, z) = zx^{f/a}$. Then for any solution $(x(t), y(t), z(t))$ of (1) in \mathbb{R}_+^3 we have*

$$\frac{d}{dt}F(x(t), y(t), z(t)) < 0.$$

Proof.

$$\begin{aligned} \frac{d}{dt}F(x(t), y(t), z(t)) &= \nabla F(x(t), y(t), z(t)) \cdot \langle x'(t), y'(t), z'(t) \rangle \\ &= (ax - bxy) \frac{f}{a} zx^{\frac{f}{a}-1} + x^{\frac{f}{a}}(-fz + gy) \\ &= \left(g - \frac{bf}{a}\right) yzx^{\frac{f}{a}} < 0. \end{aligned}$$

This proposition implies that solutions travel down across the level surfaces of the function F , which are precisely $K = zx^{f/a}$. This proposition, however, is not sufficient to conclude that all solutions approach the plane $z = 0$, since the surfaces $z = Kx^{-f/a}$ tend to the union of the coordinate planes $z = 0$ and $x = 0$ as $K \rightarrow 0$.

To show that all solutions approach $z = 0$, we build a compact trapping region consisting of the xy -plane and the surface $by - a \ln y + dx - c \ln x + aez/f = C$. This surface arises naturally by extending equation (5) to three dimensions. Intuitively, this previously invariant surface (in the case $ga = fb$) will no longer be invariant in the case $ga < fb$, but will aid us in the construction of a trapping region.

Such a trapping region is bounded by the surface shown in FIGURE 10.

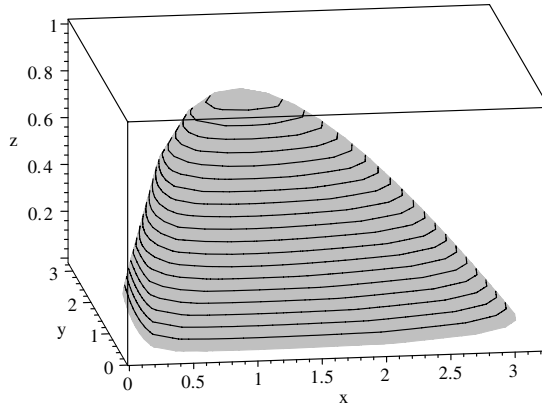


Figure 10 A particular trapping region with $a = b = c = d = e = f = 1$

PROPOSITION 4. Let $ga < fb$ and $G(x, y, z) = by - a \ln y + dx - c \ln x + aez/f$. Then for any solution $(x(t), y(t), z(t))$ of (1) in \mathbb{R}_+^3 we have

$$(d/dt)G(x(t), y(t), z(t)) < 0.$$

Proof. Let $(x(t), y(t), z(t))$ be a solution to (2) in \mathbb{R}_+^3 . Consider

$$\begin{aligned} \frac{d}{dt}[G(x(t), y(t), z(t))] &= \nabla G(x, y, z) \cdot \langle x'(t), y'(t), z'(t) \rangle \\ &= (d - c/x)(a - bxy) + (b - a/y)(-cy + dxy - eyz) \\ &\quad + (ae/f)(-fz + gyz) \\ &= eyz(ag/f - b) < 0. \end{aligned}$$

The above proposition implies that solutions travel down the level surfaces of G as time increases. In particular, a solution starting with initial condition (x_0, y_0, z_0) at time t_0 can never travel to a region in \mathbb{R}_+^3 where $G(x, y, z) \geq G(x_0, y_0, z_0)$. Further, since the xy -plane is invariant, the solution will be trapped in the region bounded below by the xy -plane and above by the surface $by - a \ln y + dx - c \ln x + aez/f = G(x_0, y_0, z_0)$ for all $t > t_0$ (see FIGURE 10).

Taking both propositions together, we have shown that for $ga < fb$, all trajectories beginning in \mathbb{R}_+^3 tend to the plane $z = 0$. Some further analysis can be done to show that the center manifold of the fixed point $(c/d, a/b, 0)$ is the plane $z = 0$ and that it is unique. Thus, except for the one trajectory that corresponds to the stable manifold of $(c/d, a/b, 0)$, all solutions approach a periodic solution in the xy -plane. Biologically, this implies that the top predator z tends to extinction, while the species x and y tend to exhibit traditional Lotka-Volterra periodic behavior in the absence of z . The plot of the solution in FIGURE 11 exhibits this behavior.

The case $ga > fb$ is analogous, except that all trajectories starting in \mathbb{R}_+^3 escape each of the previous trapping regions and all trajectories travel up the surfaces $z = Kx^{-f/a}$, that is, $z(t)$ approaches $+\infty$ as $t \rightarrow \infty$. This implies that the populations of the species x and z tend to $+\infty$, albeit non-monotonically, while the population of y over time experiences larger and larger fluctuations. FIGURE 12 depicts a particular solution that exhibits this behavior.

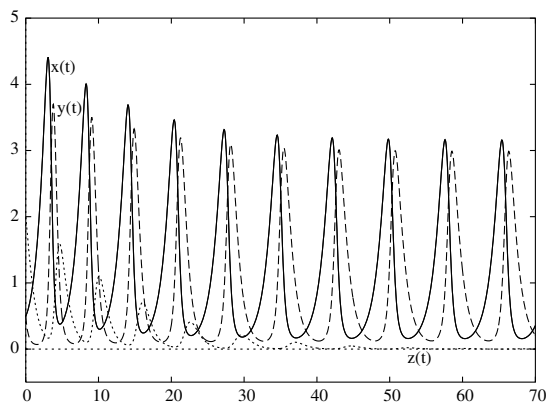


Figure 11 A solution with initial conditions $(1/2, (1/2), 2)$ with $a = b = c = d = e = f = 1$ and $g = 0.88$

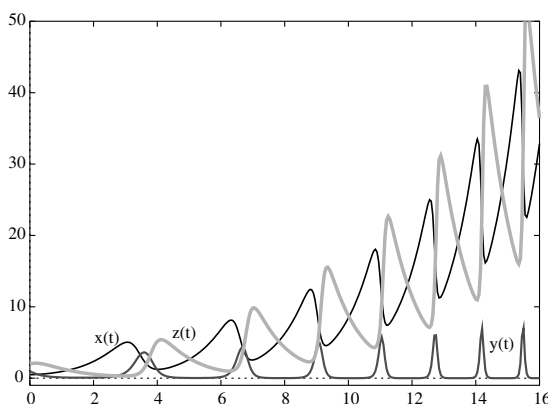


Figure 12 A solution with initial conditions $(x, y, z) = (.5, 1, 2)$ with parameters $g = 1.6$ and $a = b = c = d = e = f = 1$

Conclusion and comments

The overall long-term persistence of top species z in (2) hinges solely on the parameters a , b , f , and g . In particular, if $ag < fb$, then species z dies out, while if $ag \geq fb$, then species z survives, growing without bound in the case $ag > fb$. This coincides with our intuition as larger values of a and g are explicitly beneficial to species z , while larger values of b and f are inhibitory to species z . It is quite interesting to note that the parameters most directly related to mid-level species y (namely c , d and e) in no way affect whether species z will become extinct or not. In effect, species y is simply acting as a conduit between the top and bottom species. Furthermore, the model does not allow for the possibility of the extinction of species y while species x persists.

This basic model of a three-species food chain makes an excellent guided exploration/group project in a mathematical modeling or differential equations course and can easily be modified to model more complicated biological behavior. Lastly, the analysis of this model involves many advanced techniques typically used in the analysis of more complicated biological models that are not typically seen in standard models, e.g., non-isolated fixed points, trapping regions, and invariant sets.

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Proof by Poem: The RSA Encryption Algorithm

Take two large prime numbers, q and p .
 Find the product n , and the totient ϕ .
 If e and ϕ have GCD one
 and d is e 's inverse, then you're done!
 For sending m raised to the e
 reduced mod n gives secre- c .

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