Chaos in a Predator-Prey Model with an Omnivore$^*$†

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Abstract

The dynamics of the planar two-species Lotka-Volterra predator-prey model are well-understood. Onto such a predator-prey model, we introduce a third species, a scavenger of the prey. Our model allows for two scenarios, one where the scavenger is also a predator of the original prey, and one where the presence of the scavenger simply inhibits the prey. We show all trajectories are bounded in forward time, and numerically demonstrate persistent cascades of period-doubling orbits over a wide range of parameter values.

1 Introduction

Pioneering work by Lotka [13, 14] and Volterra [25] successfully captured the oscillations in populations of a predator and its prey. The classical set of data is the Canadian lynx and snowshoe hare pelt-trading records of the Hudson Bay Company that span almost a century [16]. Since the introduction of this equation, the field of mathematical ecology has flourished and a significant literature devoted to studying variants of this equation has been established.

Our goal is to introduce a third species to the classical predator-prey equations in a biologically reasonable way. We characterize the third species first as an omnivore who is also a predator of the prey, and consumes the carcasses of the predator, but has no inhibitory effects on the population of the predator. A possible triple of such species are hyena/lion/antelope, where the hyena scavenges lion carcasses and preys upon antelope. Second, we consider the effects of a scavenger of the predator that inhibits the prey, but has no benefit from that interaction. A possible triple of such species are water scavenger beetle/trout/mayfly, where the scavenger beetle consumes trout carcasses and inhibits mayfly larvae. For both of these models we completely characterize the dynamics in each of the coordinate planes (the dynamics of any two species in the absence of the third), show that in the three-dimensional model all orbits are bounded, and finally characterize the dynamics of all orbits in the case that there is

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no interior fixed point. When the interior fixed point exists, we analytically show that a fixed point undergoes a Hopf bifurcation, and numerically demonstrate a bounded paired period doubling cascade.

There is significant literature on tritrophic, or three species, food chain models. General Volterra models were considered by Smale [23], under the assumption that the coefficient of the quadratic term is negative, and showed the possible existence of strange attractors. Arneodo, et al [3] show that for \( n \geq 4 \), the simplest Volterra models may exhibit chaotic behavior. In [4], they specialize to Volterra equations with \( n = 3 \) and numerically demonstrate the existence of Hopf bifurcations in their system, and conclude that when all the coefficients are positive, they cannot use the method of Shilnikov [22] to show the existence of strange attractors because there is no focus on the coordinate planes. In contrast, under the assumption that each of the three species has diverse frequencies in oscillations of pairwise interations, it has been shown [8, 15, 15] that there exists a strange attractor. Kuznetsov [11] studied global bifurcations in tritrophic food chains for the Rosenzweig-MacAuther model and constructed organizing centers of overall bifurcations. Perhaps the work closest in nature to the one presented here can be found in [24]. Tanabe and Namba [24] numerically demonstrate that the addition of an omnivore (defined as feeding on more than one trophic level [17, 18]) leads to a Hopf bifurcation and period doubling cascade. We consider a slightly different model than Tanabe [24], for which all orbits are bounded, yet a Hopf bifurcation gives rise to period doubling cascades. In contrast to the unbounded cascades seen in [24], our model gives rise to bounded paired cascades, as defined in [20, 21].

The paper is organized as follows. We begin with a review of the dynamics of the classic two-species Lotka-Volterra predator-prey model in section 2 as a foundation for adding the third species. We then add an omnivore to the model in section 3, and discuss global stability of trajectories in each of the coordinate planes in section 3.1. A local analysis of the three-dimensional equilibria can be found in section 3.2 and in section 3.3, we show that all orbits remain bounded. In section 3.4, we classify the omega-limit set of all positive trajectories when there is no interior fixed point. Section 3.5 contains a description of the numerically computed Hopf bifurcation that leads to a bounded paired cascade. We conclude with a discussion in section 5.

2 Review of Analysis of the Predator Prey Model

2.1 The Planar Lotka-Volterra System

In this section, we review well-known results of the planar Lotka-Volterra model. The differential equations that model the population dynamics of a predator and a prey are:

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y - bx), \\
\frac{dy}{dt} &= y(-c + x).
\end{align*}
\]

Here, \( y(t) \) and \( x(t) \) represent, respectively, a predator population and its prey population as functions of time. The dynamics between \( x \) and \( y \) are given by Lotka-Volterra equation with a carrying capacity on the prey, \( x \). The coefficients on the birth term
in the prey (coefficient of \( x \) in the first equation) and the efficacy that the predator benefits from the prey (coefficient on the \( xy \) term) have been set to one through three changes of variables. The remaining parameters are:

- \( b \) is associated with the carrying capacity of \( x \)
- \( c \) represents the natural death rate of the predator in the absence of prey.

The presence of these terms, combined with the death term on the prey, guarantee that all positive orbits are bounded.

### 2.2 Analysis of Equilibria

There are generically \((bc \neq 1)\) three equilibria for the planar system:

A \((0,0)\): For all \( bc \), the origin \((0,0)\) is a saddle with the \( y \)-axes as the stable manifold and the \( x \)-axes as the unstable manifold.

B \((1/b,0)\): This equilibrium point represents the limiting population of the prey as \( 1/b \) in absence of the predator. This equilibrium is a stable node for \( bc > 1 \), a saddle for \( bc < 1 \), and a singular stable node for \( bc = 1 \).

C \((c,1-bc)\): A nontrivial equilibrium \((c,1-bc)\) corresponds to a stable node for \( bc < 1 \), and coincides with equilibrium B when \( bc = 1 \) (and is not nonnegative for \( bc > 1 \)).

### 2.3 Global Analysis

The Liapunov function

\[
\ell(x,y) = y - (1-bc)\ln y + x - c\ln x - (bc-1-(1-bc)\ln(1-bc)+c-c\ln c)
\]

can be used to prove that \((c,1-bc)\) is asymptotically stable for all initial conditions with \( x(0) > 0 \), \( y(0) > 0 \), provided \( 1-bc > 0 \). Otherwise, for \( 1-bc \leq 0 \), the fixed point \((\frac{1}{b},0)\) is asymptotically stable for all initial conditions with \( x(0) > 0 \), \( y(0) > 0 \) (and \( z(0) = 0 \)). This can be shown by composing any positive solution \((x(t),y(t))\) with the function

\[
F(x,y) = x^\frac{1}{b}y.
\]

Then \( \frac{d\ell}{dt} = \frac{1}{b}F(x,y)(1-y-bc) < 0 \), which implies that all positive solutions limit to the axes, which implies that no positive periodic solutions exist. So, by the Poincaré-Bendixson Theorem, all positive orbits must limit to the only stable node on the axes, namely \((1/b,0)\).

Biologically, if \( bc \geq 1 \) then the system cannot sustain the predator. The predator population goes extinct, while the prey limits to its carrying capacity. In the case \( bc < 1 \), both species persist and limit to \((c,1-bc)\).

In summary, if \( bc > 1 \), then all trajectories with \( x(0) > 0 \) and \( y(0) > 0 \) go to \((1/b,0)\), and if \( bc \leq 1 \), they approach \((c,bc-1)\). The system undergoes a transcritical bifurcation when \( bc = 1 \).

### 3 A Three Species Population Model

Onto the planar predator-prey system above, we consider a model that includes the effects of a third species \( z \) who is a predator of the prey \( x \), and consumes the carcasses of
the predator $y$, but has no inhibitory effects on the population of the predator. Many studies have shown that omnivory is commonly found in food chains [5, 6, 2]. The model proposed here is similar to [24], however their model do not have the biologically desirable feature of bounded orbits for all nonnegative initial conditions, which we prove analytically for our model. Moreover, when the fixed point is not in positive space, we completely characterize the dynamics of all nonnegative trajectories.

The dynamics of the system are quite intricate when the interior fixed point exists in positive space. In this case, we compute parameter regimes where the fixed point undergoes a Hopf bifurcation. Additionally, we present numerical data which shows parameter regimes where hysteresis occurs. Lastly, the system contains a region in parameter space that exhibits bounded paired cascades with a period three orbit.

We consider the following three-species model:

\[
\begin{align*}
\frac{dx}{dt} &= x(1 - y - z - bx), \\
\frac{dy}{dt} &= y(-c + x), \\
\frac{dz}{dt} &= z(-e + fx + gy - \beta z),
\end{align*}
\]

where $y(t)$ and $x(t)$ represent, respectively, a predator population and its prey population as functions of time. The dynamics between $x$ and $y$ in the absence of $z$ are as described in section 2. The dynamics of the third species include a carry capacity and a natural death term. As before, there is no loss in generality in having the coefficients of several of the monomials in the first two differential equation equal to one, as four successive coordinate changes transform the most general model into this model. All parameters are assumed to be nonnegative with $b, c$ are as described in section 2.1. The remaining parameters are interpreted as follows:

- $e$ represents the natural death rate of the omnivore in the absence of resources,
- $f$ is associated with the efficiency that $z$ preys upon $x$
- $g$ is associated with the efficiency that $z$ benefits from carcasses of $y$
- $\beta$ is associated with the carrying capacity of $z$

It should be noted that this system is quadratic and is a generalized Lotka-Volterra system with simple Type I functional responses.

### 3.1 Analysis of Coordinate Planes

The coordinate planes $x = 0, y = 0$ and $z = 0$ are invariant, since if $x = 0$, then so is $\dot{x}$, and similarly for $y$ and $z$. The analysis of the dynamics on the $z = 0$ plane can be found in section 2.2.

Consider the $x = 0$ plane, or the dynamics of the predator and the scavenger, in the absence of the prey. The dynamics are are given by the two-dimensional system

\[
\begin{align*}
\frac{dy}{dt} &= -cy, \\
\frac{dz}{dt} &= z(-e + gy - \beta z),
\end{align*}
\]
The origin, a stable node, is the only fixed point in the first quadrant, the biologically relevant region where $y$ and $z$ are non-negative. Since $c > 0$, $y$ limits to zero, and hence, so does $z$, because $e, \beta$ are both positive. Therefore, any initial condition $y(0) \geq 0$ and $z(0) \geq 0$ will approach the origin.

In the $y = 0$ plane, where the omnivore $z$ preys upon $x$ and both $x$ and $z$ are limited by carrying capacity, the dynamics are given by a two-dimensional equation:

\[
\begin{aligned}
\frac{dx}{dt} &= x(1 - z - bx), \\
\frac{dz}{dt} &= z(-e + fx - \beta z),
\end{aligned}
\]

(4)

This is a predator-prey system with a carrying capacity on both the predator $z$ and the prey $x$ whose analysis is similar to that of 2.1. There are two nonnegative equilibria on the coordinate axes: $(0, 0)$ (a saddle), $(\frac{1}{b}, 0)$ (a node for $f - be < 0$ and a saddle for $f - be > 0$). Also, there is an interior fixed point: $(x_*, z_*) = (\frac{e + \beta}{f + \beta b}, \frac{f - be}{f + \beta b})$. The origin is a saddle with the stable and unstable manifold corresponding to the $x$ and $z$ axes, respectively. If the interior fixed point exists in positive space, then the Liapunov function $G(x, z) = fx - fx_*lnx + z - z_*lnz - (fx - fx_*lnx + z_* - z_*lnz)$ can be used to show global stability of the interior fixed point. If the interior fixed point does not exist in positive space, then one can use a function of type $x^e z$ to show that all solutions approach the coordinate axes, and use Poincaré-Bendixson to conclude that all orbits must approach $(\frac{1}{b}, 0)$.

We conclude by summarizing that the coordinate planes are invariant, that there are no periodic solutions on the positive coordinate planes, and that all positive trajectories on those planes approach equilibria.

### 3.2 Analysis of Equilibria for the Three-Species Model

The three equilibria from the planar system (1) persist in the three dimensional system with the third coordinate set to zero: $(0, 0, 0), (1/b, 0, 0), (c, 1 - bc, 0)$ and the equilibria from (4) persists with the second coordinate set to zero. Additionally, there is a third interior equilibrium:

\[
\left( c, \frac{\beta + e - fc - bc\beta}{g + \beta}, \frac{-e + fc + g - gbc}{g + \beta} \right).
\]

The stability of each equilibrium was analyzed using the eigenvalues of the Jacobian. The results are as follows:

**A** $(0, 0, 0)$: The origin $(0, 0, 0)$ has corresponding eigenvalues of the Jacobian $-c, -e$ and corresponds to a saddle.

**B** $(1/b, 0, 0)$: The equilibrium point $(1/b, 0, 0)$ has corresponding eigenvalues of the Jacobian $-1, -c + \frac{1}{b}, -e + \frac{1}{b}$ and is a stable node for $bc > f$ and $bc > 1$, otherwise it is a saddle.

**C** $(c, 1 - bc, 0)$: The equilibrium point $(c, 1 - bc, 0)$ has corresponding eigenvalues of the Jacobian $-e + fc + g - gbc, \frac{1}{2}(-bc + \sqrt{c(b^2c - 4 + 4bc)})$. One can show that
if the second and third eigenvalues are real, then they are negative. So this fixed point is stable if and only if \(-e + fc + g - gbc < 0\). For \(bc < \frac{4}{5+\gamma}\), the quantity in the square root of the second and third eigenvalues is negative yielding a stable spiral in the \(xy\) plane, and the reverse for \(bc > \frac{4}{5+\gamma}\), yielding a stable node in the \(xy\) plane. (Note that the first eigenvalue is the numerator of the \(z\)-coordinate of the interior fixed point).

\[
D \left( \frac{\beta+e}{b+\beta}, 0, \frac{-be+f}{b+\beta} \right): \text{The equilibrium point} \left( \frac{\beta+e}{b+\beta}, 0, \frac{-be+f}{b+\beta} \right) \text{has corresponding eigenvalues of the Jacobian} -c + \frac{\beta+e}{b+\beta} \frac{1}{2} (-\beta z - bx \pm \sqrt{(\beta z - bx)^2 - 4zf\lambda}), \text{where} \ x = \frac{\beta+e}{b+\beta} \text{and} \ z = \frac{-be+f}{b+\beta}, \text{which are positive if} -be + f > 0. \text{It is easy to show that if the second and third eigenvalues are real, then they are both negative. Hence this fixed point is stable if and only if} \ \frac{\beta+e}{b+\beta} < c. \text{Note that this condition is satisfied if and only if the} y\text{-coordinate of the interior fixed point is negative.}
\]

\[
E \left( c, \frac{\beta+e-fc-bc\beta}{g+\beta}, \frac{-e+fc+g-gbc}{g+\beta} \right): \text{The eigenvalues of the Jacobian are sufficiently messy as to require us to resort to the Routh-Hurwitz method. The coefficients of the characteristic polynomial are:} 1, \beta z + bx, bxz + yz + z f \lambda, xyz(\beta + g), \text{where} \ x, y, z \text{are the coordinates of the interior fixed point (which are positive). The constants from the Routh-Hurwitz criterion are:} 1, \beta z + bx, Z, xyz(\beta + g), \text{where} \ Z = \frac{x}{\beta z + bx} \left( b\beta^2 z^2 - zgy + b^2 x \beta z + bxy + z^2 f \beta + z x^2 b \right). \tag{5}
\]

Hence, only \(Z\) is of undetermined sign. If \(Z > 0\) then the eigenvalues all have negative real part whereas if \(Z < 0\) then 2 eigenvalues have positive real part. Moreover when \(Z = 0\) (since the constant term of the characteristic polynomial is strictly non-zero) there are 2 purely complex eigenvalues. If one has a path in parameter space \(\gamma(s)\) with \(Z(\gamma(0)) = 0\) and \(\frac{d}{ds} \big|_{s=0} Z(\gamma(s)) \neq 0\) then a Hopf bifurcation occurs at \(\gamma(0)\).

### 3.3 Bounded Orbits

A biologically important characteristic of the model is that the population size of all three populations remains bounded. The carrying capacity on both \(x\), the prey, and the omnivore \(z\), ensure that the orbits remain bounded as shown in this section. In particular, we prove that any trajectory with positive initial conditions is eventually contained in a particular bounded region.

The analysis of the bounded orbits naturally breaks into two cases: the case where \(bc \geq 1\) and the case where \(bc < 1\). We begin with the case \(bc \geq 1\):

**Lemma 3.1.** In the case \(bc \geq 1\), trajectories go to \((1/b, 0, 0)\) when \(-be + f \leq 0\) and to \((\frac{\beta+e}{b+\beta}, 0, \frac{-be+f}{b+\beta})\) when \(-be + f \geq 0\).

**Proof.** As earlier, we compose solutions \((x(t), y(t), z(t))\) with the function \(F(x, y, z) = x^2y\). We obtain \(\frac{dx}{dt} = \frac{1}{b} F(x, y, z) (1 - y - z - bc)\). This implies that for any positive initial conditions, \(x^2y \to 0\). This implies that the dynamics approach the \(xz\) or the \(yz\) planes. In the \(yz\) plane all trajectories approach the origin, which is a saddle in the full
system. Thus, all solutions approach (and shadow) trajectories in the $xz$ plane. In the event that $-be + f \leq 0$ then trajectories approach $(1/b, 0, 0)$, whereas if $-be + f \geq 0$ then trajectories approach $(\frac{\beta + e}{b_0 + f}, 0, -\frac{be + f}{b_0 + f})$. In the event that $-be + f = 0$ both fixed points coalesce.

**Lemma 3.2.** In the case $bc < 1$, any trajectory $(x(t), y(t), z(t))$ with positive initial conditions $(x_0, y_0, z_0)$, enters a bounded trapping region $S$ (see figure 1) in finite time.

![Figure 1: Consider the $z$-independent region $S_R$ bounded by the coordinate planes, by $xy^b = R$ for $c \leq x \leq R$, by $y = b_R/c$ for $0 < x \leq c$ and and by the $x = R$ for $0 < y \leq 1$. For $bc < 1$, all trajectories with positive initial conditions will enter the region $S_R$ and never leave.](image)

**Proof.** For each $R > \frac{1}{b}$, we construct a surface $S_R$ bounded by $x = 0$ by $y = 0$, by $xy^b = R$ for $c \leq x \leq R$, by $y = \sqrt[bc]{R/c}$ for $0 < x \leq c$ and and by the $x = R$ for $0 < y \leq 1$. Each such surface is independent of $z$ and these surfaces exhaust all points in first open octant outside of the rectangle whose corners are the origin and $(x, y) = (c, 1)$. Each such (outside the rectangle) point $(x, y, z)$ is associated uniquely with one value of $R$.

We will show that for any solution $(x(t), y(t), z(t))$ with $R(x(y, z)) > \frac{1}{b}$ then $\frac{dR}{dt} < 0$. Let $(x, y, z)$ be such that $R(x,y,z) > \frac{1}{b}$. Let $(x(t), y(t), z(t))$ be the solution with $x(0) = x$, $y(0) = y$, and $z(0) = z$. If $x \geq \frac{1}{b}$ then clearly $\frac{dx}{dt} = \frac{dR}{dt} < 0$. If $c < x < \frac{1}{b}$ then $y > 1$ and $\frac{dR}{dt} = xy^b(1 - bcy - z) \leq xy^b(1 - y - z)$ which strictly negative. If $x < c$ then $\frac{dR}{dt} = \frac{dx}{dt}$ which is negative for $x < c$. If $x = c$ then $y > 1$, and $\frac{dy}{dt} = y \cdot c \cdot (1 - bcy - z) < 0$ which implies that $y$ is at a relative maximum, so locally, $x$ is decreasing and $y$ is at a relative maximum so $R$ is strictly decreasing on an open interval about $t = 0$, with the possible exception of $t = 0$, which implies that $R$ is decreasing on the entire interval. A bit more detailed analysis shows that for any
fixed $R > \frac{1}{2}$, all positive orbits will enter $S_R$ in a finite amount of time that depends only on the initial conditions and the value of $R$. Thus, after a finite amount of time we have that $x(t) < \frac{2}{5}$ and $y(t) < \sqrt{\frac{2}{bc}}$.

Thus (after amount finite time), $\frac{dG}{dt} = z(-e+fx+gy-\beta z) \leq z(-e+\frac{2f}{5}+g\sqrt{\frac{2}{bc}}-\beta z)$ which is clearly bounded away from zero for values of $z > \frac{1}{b}(\frac{2f}{5}+g\sqrt{\frac{2}{bc}})$ Therefore, all trajectories are attracted to a finite region in three space in a finite length of time.

We then have the following theorem, as a consequence of Lemma 3.1 and 3.2:

**Theorem 3.3.** All trajectories with positive initial conditions are bounded in forward time.

### 3.4 Summary of Limiting Behavior

In the previous section, we showed that all trajectories with positive initial conditions are bounded, as would be expected biologically. In this section, we further clarify the limiting behavior of the trajectories if the interior fixed point does not exist. As was mentioned previously, if the interior fixed point exists then all the other fixed points are unstable and no trajectory approaches the coordinate planes. All orbits are bounded, but the dynamics of the trajectories exhibit complicated dynamical structures, such as Hopf bifurcations, hysteresis, and period double cascades (see section 3.5) and the limiting dynamics cannot analytically be classified.

If on the other hand, the interior fixed point does not exist, then all trajectories limit to the coordinate planes, and hence will limit to one of the equilibrium points (which we will demonstrate in this section). Which equilibrium point depends on whether $bc \geq 1$ or $bc < 1$. For $bc \geq 1$, trajectories go to $(1/b,0,0)$ when $-be + f \leq 0$ and to $(\frac{\beta + e}{b^2 + f},0,-\frac{be + f}{b^2 + f})$ when $-be + f \geq 0$, as was shown in lemma 3.1. If on the other hand, $bc \geq 1$, then the limiting behavior depends on whether $-e + g + fc - gbc \geq 0$ or $\beta + e - fc - b/e \geq 0$, as is shown in the next theorem:

**Theorem 3.4.** Let $bc < 1$.

1. If $-e + g + fc - gbc \leq 0$ and $\beta + e - fc - b/e \geq 0$ then all positive trajectories approach $(c,1-bc,0)$.
2. If $-e + g + fc - gbc \geq 0$ and $\beta + e - fc - b/e \leq 0$ then all trajectories approach $(\frac{\beta + e}{b^2 + f},0,-\frac{be + f}{b^2 + f})$.

**Proof.** For case (1), define $G(x,y,z) = x^a y^b g^c z$ with $\frac{dG}{dt} = G(x,y,z)(-e+g+fc-gbc-(g+\beta)z) \leq -G(x,y,z)(g+\beta)z$. This implies that for any positive initial conditions, we have that $G(x,y,z) \to 0$. Therefore, either $x \to 0$ or $y \to 0$ or $z \to 0$, that is, the omega limit set of the trajectory must be an invariant structure in the coordinate planes. Since the coordinate planes do not have any periodic orbits, the omega limit sets of trajectories with positive initial conditions must be an invariant set in one of the coordinate planes. Since both $(0,0,0)$ and $(\frac{\beta + e}{b^2 + f},0,-\frac{be + f}{b^2 + f})$ are both saddles, the only remaining stable fixed point is $(c,1-bc,0)$, so all positive trajectories approach this fixed point.
In case (2), define \( H(x, y, z) = x^\beta y^{b+1} z^{-1} \) with \( \frac{dH}{dt} = H(x, y, z)(\beta + e - fc - b\beta c - (g + \beta)y) \leq -H(x, y, z)(g + \beta)y, \) then for any positive initial conditions, we have that \( H(x, y, z) \to 0 \) (this is since \( z \) has been shown bounded above). Since the coordinate planes do not have any periodic orbits, the omega limit sets of trajectories with positive initial conditions must be an equilibrium point in one of the coordinate planes. Since \( (\frac{\beta + e}{b+1}, 0, \frac{-be+g}{b+1}) \) is the only stable fixed point, all trajectories approach this fixed point. (it is an elementary exercise to show that if \( 1 - be > 0 \) and \( \beta + e - fc - b\beta c \leq 0 \), then \( -be + f \geq 0 \)).

The below table exhaustively summarizes the limiting behavior of all positive trajectories when the interior fixed point does not exist:

<table>
<thead>
<tr>
<th>( bc \geq 1 )</th>
<th>( f - be \leq 0 )</th>
<th>( (1/b, 0, 0) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( bc \geq 1 )</td>
<td>( f - be \geq 0 )</td>
<td>( (\frac{\beta + e}{b+1}, 0, \frac{-be+g}{b+1}) )</td>
</tr>
<tr>
<td>( bc &lt; 1 )</td>
<td>( -e + g + fc - gbc \geq 0 ) and ( \beta + e - fc - b\beta c \leq 0 )</td>
<td>( (\frac{\beta + e}{b+1}, 0, \frac{-be+g}{b+1}) )</td>
</tr>
<tr>
<td>( bc &lt; 1 )</td>
<td>( -e + g + fc - gbc \leq 0 ) and ( \beta + e - fc - b\beta c \geq 0 )</td>
<td>( (c, 1 - bc, 0) )</td>
</tr>
</tbody>
</table>

Note that if both \( -e + g + fc - gbc \leq 0 \) and \( \beta + e - fc - b\beta c \leq 0 \) then their sum is negative, but the sum is \( (1 - bc)(\beta + g) \) which implies that if both are negative then \( bc > 1 \), so our list is exhaustive for all cases when the fixed point is not positive. If the interior fixed point does not exist, then at least one of the populations become extinct. For instance, in the last line of the previous table, the omnivore population becomes extinct and the populations of the predator and prey limit to the a classical constant predator-prey solutions as discussed in section 2. Considering the middle two lines of the table, the predator becomes extinct, and the prey and the omnivore co-exist, limiting to constant populations. For trajectories that approach the \((1/b, 0, 0)\), both the predator and omnivore will become extinct, and the prey population limits to 1/b.

### 3.5 Period Doubling of the Interior Fixed Point

In the previous section, we classified the limiting behavior of all trajectories in the case that the interior fixed point does not exist. The dynamics of the trajectories when the interior fixed point does exist is much more complex. We investigate this behavior through a sequence of examples that demonstrate that first the interior fixed point goes through a sequence of Hopf bifurcations that eventually leads to a period double cascade.

To begin, we fix the parameters \( b = .9, c = .1, f = .1, g = 13 \) and show bifurcation diagrams in \( e \) for decreasing \( \beta \). Initially, for \( \beta > 18.70856 \), the initial fixed point is stable throughout the entire range of \( e \). When \( \beta \approx 18.70856 \) the interior fixed point, shown in 2(b), experiences a supercritical Hopf bifurcation at \( e \approx 11.340375 \), and the limit cycle shown in 2(c) is born. That limit cycle persists in parameter space until undergoing a second supercritical bifurcation and collapsing onto the stable fixed point, illustrated in 2(d). (Note that the values for \( \beta \) and \( e \) have been obtained from formula (5)).

As \( \beta \) decreases further, the system’s dynamics become more complex. For \( \beta \approx 15 \), the system experiences another two sequential Hopf bifurcations, only this time
Figure 2: For fixed values of $b, c, f, g$, figure 2(a) illustrates a bifurcation diagram in $e$ for $\beta \approx 18.70856$. Note that the fixed point (illustrated in 2(b)) experiences a supercritical Hopf bifurcation at $e \approx 11.340375$. The periodic orbit shown in 2(c) persists in parameter space $e$ until it experiences another supercritical Hopf bifurcation and the stable limit cycle bifurcates back to the (stable) interior fixed point as shown in 2(d).
Figure 3: For $\beta \approx 15$, figure 3(a) illustrates a bifurcation diagram in $e$. The stable fixed point (illustrated in 3(b)) experiences a subcritical Hopf bifurcation at $e \approx 10.72532712$. The limit cycle shown in 2(c) experiences another supercritical Hopf bifurcation at $e \approx 11.57454385$ and the stable limit cycle bifurcates to the stable fixed point shown in 3(d).

One is subcritical (at approximately $e \approx 10.72532712$) and one is supercritical ($e \approx 11.57454385$), forming a cardioid shape. Figure 3(a) also shows a small parameter interval in $e$, immediately preceding the subcritical Hopf, where both the stable fixed point and the stable limit cycle co-exist exhibiting two simultaneous stable structures.

Figure 4 illustrates the period doubling cascade that occurs as $\beta$ decreases from 4. For $\beta = 3.7$, figure 4(a) shows the periodic orbit bifurcating through a period doubling bifurcation which again undergoes a period halving bifurcation. In figure 4(b), there is a second period doubling producing a period 4 orbit that can be seen around $e \approx 8$. A period 8 orbit appears in 4(c) and a period 16 appears in figure 4(d), although it’s a little difficult to count all the orbits. The classic period doubling cascade appears in figure 4(f) for $\beta = 3.1$. A period 3 orbit appears after further decreasing $\beta$ to 2.8, which is shown in Figure 4(g) and blown up in Figure 4(h). The appearance of the period three orbit implies the existence of an infinite number of other periodic orbits [12]. In contrast to the period doubling cascade produced by the logistic equation, which get more complicated as the parameter increases, we obtain bounded paired cascades that contained within a compact interval.
Figure 4: For $f = 0.1, g = 18, b = .9, c = .1$, this sequence of figures illustrates two period doubling cascade as the parameter $\beta$ decreases from 3.7 to 2.8, where period three orbit is shown.
4 Analysis of the Predator Prey Model with Scavengers

In this section, we modify the previous three-species model and show that when the omnivore becomes a scavenger, the bounded paired cascade persists. A review by Devault et al [7] indicates that terrestrial scavenging has been underestimated by the ecological community. Many examples are cited in the literature: the impact of fishery discards on benthic scavengers [19], the impact of elk carrion on large carnivore populations [10], and a model of wolf-elk populations is studied, in [26]. (For a more complete list see [9].)

In contrast to the omnivore where the omnivore is a predator of the prey $x$, and consumes the carcasses of the predator $y$, and benefits from both interactions, the scavenger consumes benefits from the interaction with the predator and inhibits the prey, but has no benefit from that interaction. In terms of the previous model, we set $f = 0$:

$$\begin{align*}
\frac{dx}{dt} &= x(1 - y - z - bx), \\
\frac{dy}{dt} &= y(-c + x), \\
\frac{dz}{dt} &= z(-e + gy - \beta z),
\end{align*}$$

(6)

We briefly summarize how the results from the omnivore hold for the model with scavengers:

- **Coordinate Planes:** The analysis of the coordinate planes is exactly the same for the plane $x = 0$, and for $y = 0$ the interior fixed point only exists in negative space, so all trajectories with positive initial conditions limit to the stable node $(1/b, 0, 0)$.

- **Equilibria:** The equilibria $(0, 0, 0), (1/b, 0, 0), (c, 1 - bc, 0), (\frac{\beta + e}{b\beta + f}, 0, -\frac{e}{\beta})$ and analysis presented for the omnivore in section 3.2 persist for the scavenger by setting $f = 0$.

- **Bounded Orbits:** The scavenger model maintains the biologically important feature of bounded orbits. Lemma 3.1 becomes

**Lemma 4.1.** In the case $bc \geq 1$, trajectories go to $(1/b, 0, 0)$,

with a proof similar to the one presented for lemma 3.1. Lemma 3.2 holds, and for $bc < 1$ trajectories with positive initial conditions enter the trapping region $S$ in finite time and correspond to bounded trajectories. Therefore theorem 3.3 holds as well, and all trajectories for the scavenger are bounded in forward time.

- **Summary of Limiting Behavior:** The limiting behavior of positive trajectories are summarized in the following table for certain parameter regimes:

<table>
<thead>
<tr>
<th>$bc \geq 1$</th>
<th>$bc &lt; 1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-e + g(1 - bc) \leq 0$ and $\beta + e - fc - b\beta c \geq 0$</td>
<td>$(c, 1 - bc, 0)$</td>
</tr>
</tbody>
</table>

(1/b, 0, 0)
As with the omnivore analysis, if the interior fixed point exists, then the dynamics become complicated and we are unable to classify the limit of trajectories.

• **Cascades:** As with the omnivore, the model with the scavengers demonstrate bounded paired cascades. As with the previous example, the system undergoes two consecutive supercritical Hopf bifurcations, which as the parameter varies from $\beta = 25$ to $\beta = 20$ induces hysteresis with a cardioid-shaped bifurcation diagram. A bounded paired cascade ensues and is illustrated in figure 5.

5 Discussion

We have demonstrated that a three-species omnivore model and a three-species scavenger model exhibit bounded paired cascades with period three orbits. We have shown that these models have the biologically desirable property that all orbits remain bounded. We further hypothesize that the scavenger model is the simplest three-species model of this type to have bounded orbits and cascades. The model (6) has five positive parameters. In order for the orbits to remain bounded $b, c, \beta$ must be non-zero. If $g = 0$, then the role of the scavenger is decoupled from the predator and the prey. If $e = 0$, then local analysis of the Hopf bifurcations show that the Hopf bifurcations do not occur in positive space.

Recent work by Sander, Alligood and Yorke [1, 20, 21] have considered period doubling cascades as a route to chaos in maps. In particular, they defined bounded cascades, prove that bounded cascades always come in pairs, and classify the type of bounded paired cascade shown in figures 4 and 5 as off-on-off chaos. The Off-On-Off Chaos Theorem suggests that systems that exhibit off-on-off chaos have infinitely many bounded paired cascades and at most finitely many unbounded cascades. They further show that time-$2\pi$ maps of the forced double-well Duffing and the forced damped pendulum exhibit this type of chaos. We believe for an appropriate Poincaré section, the time-$t$ map of both the omnivore and the scavenger models presented in this paper fall into this category.

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References


Figure 5: For $f = 0, g = 18, b = .9, c = .1$, this sequence of figures illustrates two period doubling cascade as the parameter $\beta$ decreases from 6.5 to 4.8. For parameter values $\beta = 5.0$ and $\beta = 4.95$, period three orbits are shown.


References