SIAM J. APPL. MATH.
Vol. 65, No. 2, pp. 684–701

BOOMING AND CRASHING POPULATIONS AND EASTER ISLAND*

BILL BASENER† AND DAVID S. ROSS‡

Abstract. The population of Easter Island grew steadily for some time and then suddenly decreased dramatically. This is not the sort of behavior predicted by the usual logistic differential equation model of an isolated population or by the predator-prey model for a population using resources. We present a mathematical model that predicts this type of behavior when the growth rate of the resources, such as food and trees, is less than the rate at which resources are harvested. Our model is expressed mathematically as a system of two first-order differential equations, both of which are generalized logistic equations. Numerical solution of the equations, using realistic parameters, predicts values very close to archaeological observations of Easter Island. We analyze the model by using a coordinate transformation to blow up a singularity at the origin. Our analysis reveals surprisingly rich dynamics including a degenerate Hopf bifurcation.

Key words. Easter Island, population dynamics

AMS subject classifications. 92D02, 91D02, 37N02

DOI. 10.1137/S0036139903426952

1. The model.

At one time inhabitants of Easter Island prospered. They were sufficiently sophisticated, artistically and technologically, to build and transport the enormous mysterious statues for which the island is famous. Yet when westerners first came in contact with the island in the late eighteenth century, the inhabitants lived meagerly in flimsy huts and there were no trees left on the island. The island is extremely isolated, surrounded by over 1000 miles of ocean. Archaeological records indicate that a small group, about 50 to 150 people, sailed to Easter Island between 400 and 700 AD. The population grew to about 10,000 between 1200 and 1500 AD. It is thought that at this time the inhabitants built the biggest statues, had large boats, sailed on the ocean for fishing, and used the abundant large trees for building. The inhabitants overused the resources to the point of starvation and the island's human population decreased drastically. As a consequence of the population's actions, the large trees and other resources completely disappeared from the island. For a more detailed discussion of the history of Easter Island, see [4] and [8].

Neither of the standard elementary types of population models, logistic models and predator-prey models, predicts this sort of growth and decline. We present a system of differential equations for an isolated population that uses self-replenishing resources (such as trees, plants, and animals) which exhibits this booming and crashing behavior. We prove that if the population uses resources too quickly relative to the rate at which the resources replenish themselves, then the population will increase and then disappear in finite time. If the population uses the resources more slowly, then the population and resources do not disappear. A thorough characterization of solutions for various parameter values is given in Figure 5.

*Received by the editors April 30, 2003; accepted for publication (in revised form) April 19, 2004; published electronically January 27, 2005.

http://www.siam.org/journals/siap/65-2/42695.html

†Department of Mathematics and Statistics, Rochester Institute of Technology, College of Science, 85 Lomb Memorial Drive, Rochester, NY 14623 (wfbsma@vmsmail.rit.edu).

‡Department of Mathematics and Statistics, Rochester Institute of Technology, College of Science, 85 Lomb Memorial Drive, Rochester, NY 14623, and the Archimedes Project, Kaiser Permanente (dsrsma@rit.edu).

For our model, let P be a population and let R be the amount of resources. Our model is given by (1). To derive these equations, we assume that the resources would equilibrate in the absence of people. So when the population is zero the equation for the resources should be the standard logistic equation with $c, K > 0$. As in the standard logistic model we call c the growth rate of the resources and K the carrying capacity. The constant c has units of inverse time; it is the fraction by which the resource supply would increase per unit time were the resource supply far from the island's carrying capacity. The carrying capacity K has the same units as R; it is the maximum resource supply that the island can support.

The term $-hP$ accounts for the harvesting of the resources. The constant h, the harvesting constant, has units of reciprocal time; it is on the order of the reciprocal of the average lifetime of members of the population. The population P has units of persons, as does R; one unit of the resources is the amount of resources required to support a member of the population through his or her lifetime. We assume that the resources are accessible so that the amount of harvesting is proportional only to the population. This is a reasonable assumption for people on a small island.

At any given time the size of the population that our island can support depends on the amount of resources on the island. Given our choice of units, the island has the capacity to support R people. The evolution of the population is described by a logistic equation with the carrying capacity equal to R.

$$\begin{aligned} \frac{\mathrm{d}R}{\mathrm{d}t} &= cR\left(1 - \frac{R}{K}\right) - hP, \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= aP\left(1 - \frac{P}{R}\right). \end{aligned} \tag{1}$$

The positive constant a has units of inverse time. The quantity aP is the net growth rate of the population in circumstances in which resources are abundant. Observe that when there are no resources ($R = 0$) the carrying capacity for the population is zero. This makes sense, but it causes mathematical trouble in the form of a singularity on the P-axis. The P/R term in (1) places our model in the class of ratio-dependent models, a class that has recently received much attention in the population biology literature. (See [9].) In fact, a discrete predator-prey model analogous to ours has been used by Eberhardt in [5].

The main virtues of this model are that it incorporates a variable carrying capacity for the population and that it is based on a simple but sensible account of the interaction between a population and its resources. Moreover, the predictions of this model match archeological data for the population of Easter Island; the predictions of standard models, such as the logistic model and the Lotka–Volterra model, do not. Of course a model's prediction matching data is not sufficient, though it is necessary, to establish the model's validity.

Our model is notable for the singularity in (1) when $R = 0$. Other models of populations similar to that of Easter Island do not involve such singularities; recent contributions to the literature have favored modified Lotka–Volterra models. Anderies [1] presents a general form for such models:

$$\begin{aligned} \frac{\mathrm{d}R}{\mathrm{d}t} &= \rho(R) - H(R, P), \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= G(H, R)P. \end{aligned} \tag{2}$$

Here, $\rho(R)$ is the growth rate of the resources, $H = H(R,P)$ is the rate at which resources are harvested, and $G(H,R)P$ is the growth rate of the population; that is, G is the difference between the per person birth and death rates.

Brander and Taylor [3] choose the logistic form $\rho(R) = cR(1 - R/K)$ that we use in (1). Their harvesting rate is proportional to PR, while ours is simply proportional to P. For G, they use the linear function $G(H,R) = (b - d + \phi R)$, where b is the birth rate, d is the death rate, and ϕ is a constant. (The function $P(t)$, in Anderies's work and in the work of some other researchers in this field, is the labor pool, whereas we have considered, instead, the entire population.)

The harvesting model of Brander and Taylor accounts for the fact that as resources become scarce, less of the resources will be harvested per person. In our model, by contrast, the same amount of resources is harvested per person in all conditions. Consequently, our model does not capture details of low-resource conditions. The harvesting model, in which the harvesting rate is proportional to the amount of resources, seems to err in the other direction; it probably produces an underestimate of the harvesting rate in conditions of scarce resources. The truth is probably somewhere between the two models. While scarcity should diminish the harvesting rate, there will be a tendency for members of the population to maintain their standard of living at the cost of depleting resources. For conditions of plenty, our model seems sensible, and the assumption that the harvesting rate is proportional to the resources probably overestimates the harvesting rate.

Brander and Taylor use a population growth rate model in which the difference between the per person birth and death rates, $(b - d + \phi R)$, which is negative in the absence of resources, increases linearly with resources. In our population growth model, the difference between the per person birth and death rates is $a(1 - P/R)$, which is proportional to the unused fraction of the island's carrying capacity.

The per person growth rate of Brander and Taylor has the familiar mathematical form of an exponential decay model in conditions of scarcity. In the absence of resources, the population in the Brander and Taylor model dies out exponentially. Our model has the population, along with the resources, die out exponentially in some cases and in finite time in other cases. The appealing feature, in our model, of allowing the population to die out in finite time comes at the cost of an unbounded per person death rate. As resources increase, the model of Brander and Taylor has the difference between the per person birth and death rates become arbitrarily large. In our model, when resources are more than sufficient for the population, the difference between the per person birth and death rates approaches a finite positive constant.

Brander and Taylor derive their model in the framework of neoclassical economics; they justify the form of their harvesting rate by maximizing a Cobb–Douglas utility function. Anderies [2] takes a similar approach. He improves on their model by introducing a more general type of utility function, a Stone–Geary utility function. In this way, Anderies allows for a structural change in the culture when resources are scarce. He derives a continuous per person harvesting rate that is constant in conditions of scarcity and approaches a smaller constant asymptotically like $1/R$ in conditions of great abundance. This extra level of detail allows Anderies to fit the population data of Easter Island better than Brander and Taylor. (See graphs in [1] and [2].)

We have not embedded our model in neoclassical economic theory; we have simply made some plausible assumptions. We shall show, in section 2, that with reasonable values of the parameters, our model fits the archaeological data for Easter Island closely. In the rest of the paper, we elaborate upon what we consider our model's other virtue: its exceptionally rich dynamics. We expect that this feature of the model makes it valuable as an example of the sorts of behavior that even a simple two-dimensional population model can exhibit.

Discussions of mathematical models like ours—models of the interaction of a human population and its resources—often include speculation about implications of the analysis for the population of the earth as a whole. We shall do this too, but with misgivings; models like ours do not capture the causes of the growth and advancement of modern technological societies. For example, one of the premises of our model is that resources grow and flourish independent of humans, that the only effect that the humans have on the resources is that the humans harvest them. This is a simplification even for the case of the Easter Islanders, who probably engaged in some of the cultivation of resources that is a hallmark of technological civilizations. For modern civilization, even the idea of resources as something given, apart from humans, is wrong; human ingenuity turns natural materials and phenomena into resources. Finally, at the most abstract level, models like ours do not even address the essential issues of the survival of a species that does things like construct mathematical models of its interaction with its environment.

That said, our model suggests a scenario not often considered for the overpopulation of the Earth. If a population overuses its resources (for our model, if $h > c$), the population will become large while the resources decrease. This situation results in a gradual exponential population growth for an extended period of time and then a sudden catastrophic elimination of the population. (See Figure 2.)

In section 2 we compare numerical approximations of solutions to archaeological data of Easter Island. In section 3 we prove our main theorem and describe general behavior of solutions.

2. Archaeological data of Easter Island and the world population. In this section we compare the population of Easter Island and the population predicted by a numerical solution of (1). We also provide a projection of the world population under the assumption the humans are overusing their resources. It is well accepted that numerical models do not provide accurate numbers for projecting human populations, in part because the constants (growth rate, etc.) for human populations depend on ever-changing social and technological factors. However, mathematical models do provide the approximate "shape" of the graph of a human population. We provide the Easter Island model in part as confirmation that the shape of solutions to (1) is reasonable for the human population and apply a solution with this shape to the world's human population.

A good summary of Easter Island history is given in Cohen's excellent text [4] on global population:

> The best current estimate is that the population began with a boatload of settlers in the first half millennium after Christ, perhaps around 400 A.D. The population remained low until about A.D. 1100. Growth then accelerated and the population then doubled every century until about 1400. Slower growth continued until at most 6000 to 8000 people occupied the island around 1600. The maximum population may have reached 10,000 people in A. D. 1680. A Decline then set in. Jean François de Galaup Comte de La Pérouse, who visited the island in 1786, estimated a population of 2000, and this estimate is now accepted as roughly correct.

The graph of population as a function of time for a numerical approximation to system 1 is shown in Figure 1. Note that the solution matches Cohen's historical estimate until around 1780. However, the population of Easter Island did not actually disappear as it does in the model. We expect that once the population became small enough, factors other than those considered in the model became important for the population. For example, records suggest that the people on Easter Island changed their diet to smaller animals and grasses after their larger ecosystem was destroyed.

In the numerical solution graphed in Figure 1 we used $a = .0044$, which is consistent with historical observations of developing countries prior to the second world war. We took the island's carrying capacity, K, to be $70,000$. It has been estimated (see [4]) that the amount of fertile land needed to supply food for one person is approximately 350 square meters, varying to a great degree depending on the type of land and climate. The area of Easter Island is approximately 166,000,000 square meters. If all of it were fertile and if it were farmed efficiently, there would be enough food for 475,000 people. Since only some of the land is farmable, this makes our approximation of $K = 70,000$ reasonable. The values $c = 0.001$ and $h = 0.025$ are more difficult to justify; we chose these values to fit the data. Note, however, that h is on the order of the reciprocal of a lifespan as suggested in section 1.

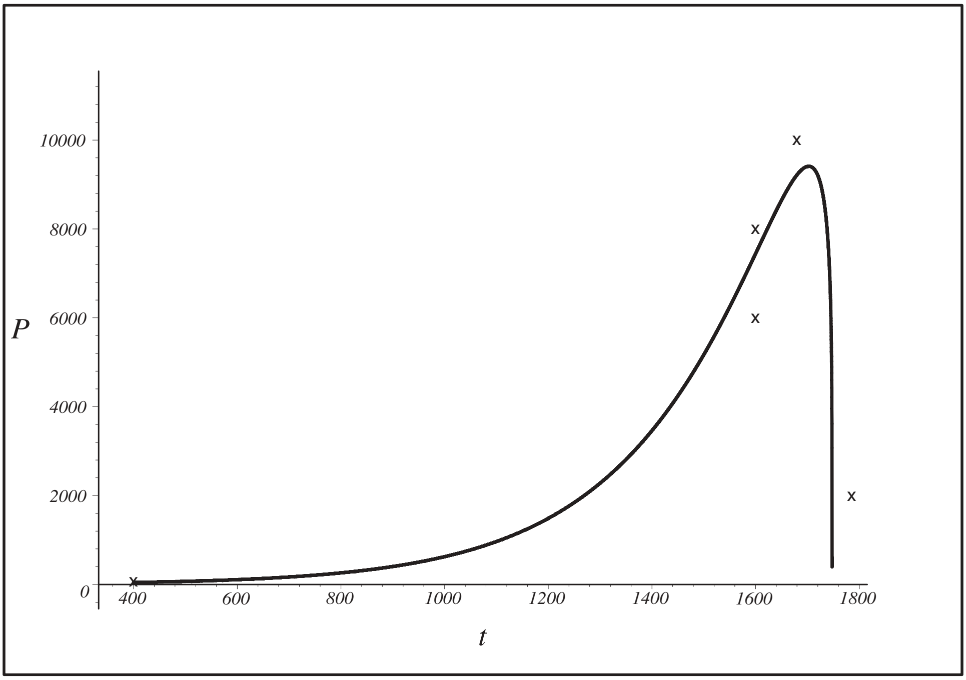

FIG. 1. *The graph of population versus time for a solution to* (1) *modeling the population of Easter Island. Each "x" is a data point approximated using archaeology.*

We do not claim that Figure 1 proves that the population of Easter Island evolved according to the dynamics of (1). But we think it suggests that these equations do provide a reasonable model for an isolated population with limited self-replenishing resources.

A numerical approximation of the world's population using (1) is shown in Figure 2. All of the units are in billions. We assume that the Earth's population in the year 2000 is 6 (billion). For this approximation we use the carrying capacity of the Earth as $K = 1000$. Approximations to the carrying capacity of the Earth vary widely, as do definitions of what the carrying capacity means. Estimations vary from 1 billion to 1,000 billion, (see [4]), and we choose the upper limit. The growth rate of the Earth's human population has been in the range from 1.73 to over 2 (again, see [4]). We use a conservative estimate of $a = 1.5$. We choose c and h to model a situation where humans are barely overusing resources, $h = 0.6$, $c = 0.5$. The model suggests that the Earth's human population will grow steadily until it reaches a maximum of 350 billion in the year 2350, and then over the next 20 years the population will decrease until either extinction or another model, such as small local farmers, becomes appropriate. As stated earlier, we make no claim to the accuracy of these numbers other than that the prospect of a collapse of a population, instead of a gradual leveling off, is an important scenario to consider. Recall that by Figure 5, the long term behavior of the solution, extinction or equilibrium, depends only on the harvesting rate and the growth rate of the resources.

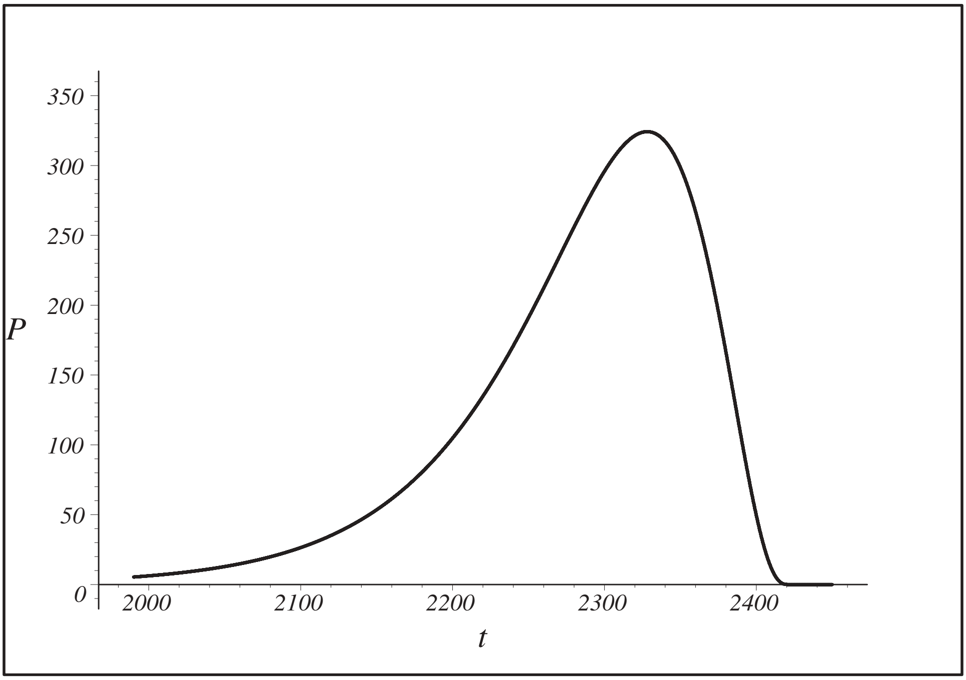

FIG. 2. *The graphs of population and resources versus time for a solution to* (1) *modeling the world's population.*

3. Analysis of the equations. Solutions of (1) fall into three qualitatively different categories: solutions that are asymptotic to an equilibrium point with $P, R > 0$, solutions that approach the singularity at $P = R = 0$, and periodic solutions. A characterization of solutions for various values of h and c is given in Figure 5.

The nullclines provide some insight into the behavior of the system. The nullcline on which $\mathrm{d}P/\mathrm{d}t = 0$ consists of the lines

$$P = 0, \quad P = R.$$

The nullcline on which $\mathrm{d}R/\mathrm{d}t = 0$ is the parabola $P = (c/h)R\left(1 - \frac{R}{K}\right)$ or

$$P = \frac{-c}{hK}R^2 + \frac{c}{h}R$$

(this can be determined by setting $\mathrm{d}R/\mathrm{d}t = 0$ and solving for P). These nullclines are shown, along with the direction field and a numerically integrated solution, in Figures 3 and 4. The parabola $P = (\frac{-c}{hK})R^2 + \frac{c}{h}R$ always intersects the line $P = 0$ at $(0,0)$ and $(K,0)$. The point $(K,0)$ is an equilibrium point, but the point $(0,0)$ is a singular point. The parabola $P = (\frac{-c}{hK})R^2 + \frac{c}{h}R$ intersects the line $P = R$ at $(0,0)$ and, if $c > h$, at $(\frac{K}{c}(c-h), \frac{K}{c}(c-h))$. A characterization of solutions is given in Figure 5.

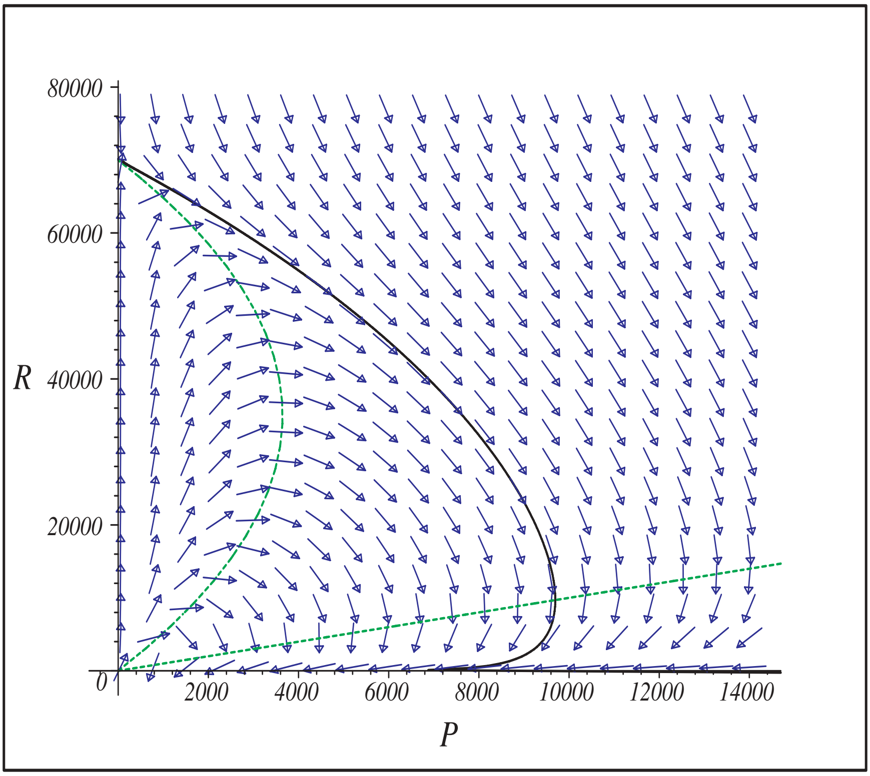

FIG. 3. *The direction field for* (1) *is shown along with the nullclines and one numerically integrated solution. The constants are* $a = .004, c = .01, K = 25000, h = .015$. *The initial condition for the solution is* $P = 75, R = K$, *which were approximately the values when settlers first landed on Easter Island.*

We simplify the equations without loss of generality by rescaling time so that $a = 1$. This puts the differential equations in the form

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left(1 - \frac{P}{R}\right), \tag{3}$$

$$\frac{\mathrm{d}R}{\mathrm{d}t} = cR\left(1 - \frac{R}{K}\right) - hP. \tag{4}$$

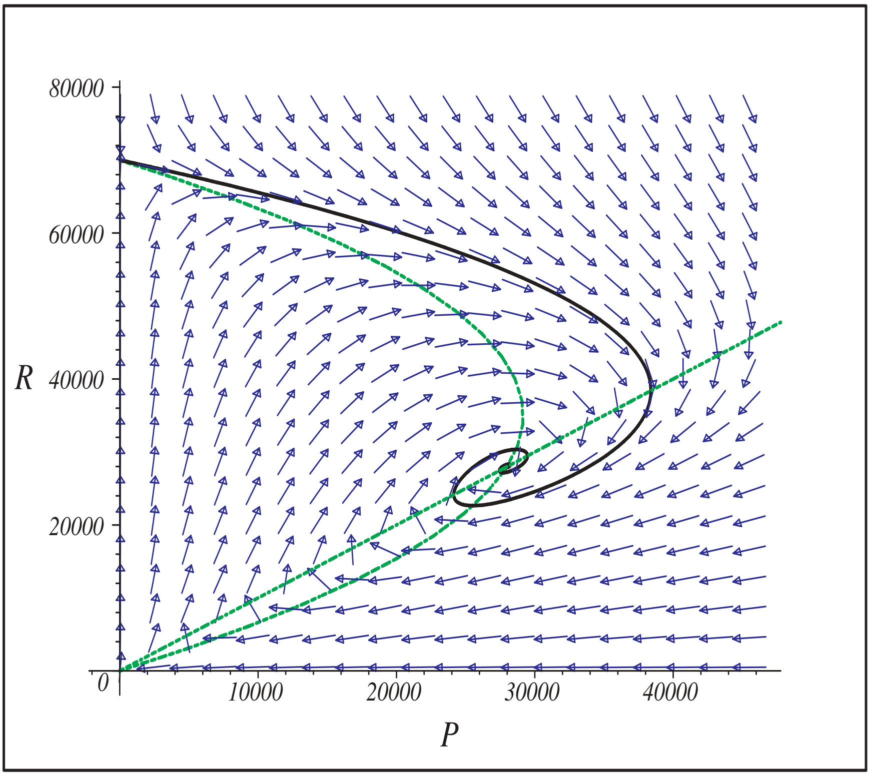

Fig. 4. *The direction field for* (1) *is shown along with the nullclines and one numerically integrated solution. The constants are* $a = .004, c = .01, K = 25000, h = .005$. *The initial condition for the solution is* $P = 75, R = K$, *which were approximately the values when settlers first landed on Easter Island. (Note that the singularity along the* P*-axis causes improperly drawn vectors along the* P*-axis.)*

We are most concerned about solutions that approach the origin, solutions that correspond to the disappearance of both the resources and the population. Standard local analysis near $(0, 0)$ is not possible because of the singularity there. We blow up this singularity through a change of variables. Let

$$\begin{aligned} z &= P, \\ \xi &= P/R. \end{aligned} \tag{5}$$

The equations in these new coordinates are

$$\begin{aligned} z' &= z(1 - \xi), \\ \xi' &= (h - 1)\xi^2 + (1 - c)\xi + \frac{c}{K} z. \end{aligned} \tag{6}$$

Note that the new system is free of singularities. We are most interested in values of the new coordinates for which P and R are both positive. For these values the change of variables is invertible. Note that the change of variables takes the first quadrant in P, R-coordinates to the first quadrant in z, ξ-coordinates, it takes vertical lines to themselves, and it is the identity mapping ($z = P, \xi = R$) along the parabola

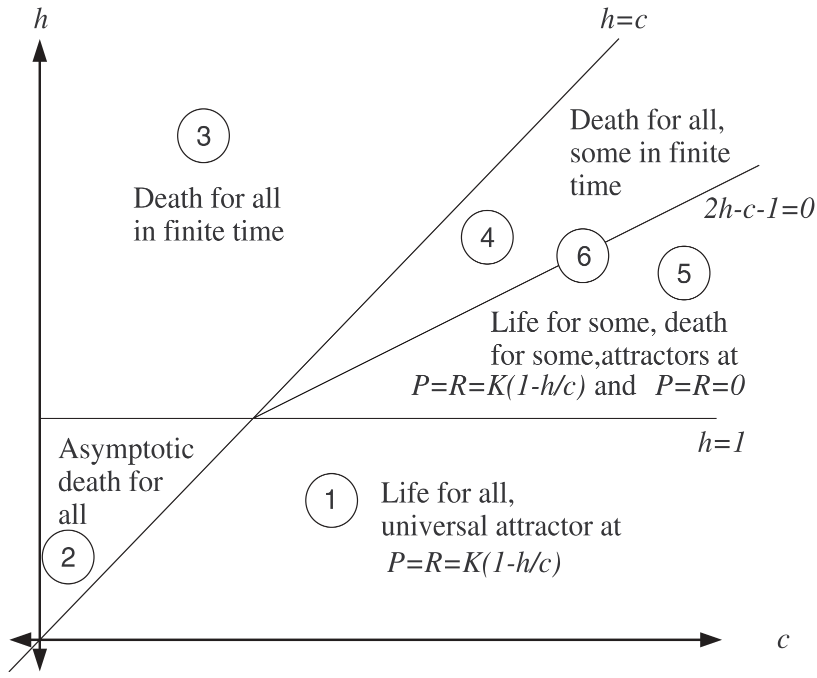

FIG. 5. *The long-term behavior of solutions depending on the growth rate of resources, c, and the harvesting rate, h. The number in each region indicates the corresponding proposition.*

$P = R^2$. Also, the region near $(0,0)$ with $P, R > 0$ has been "blown up" to the region near the positive ξ-axis. In particular, if an orbit approaches (0,0) with P and R asymptotically proportional to each other, the corresponding orbit in (z, ξ) will approach the point $(0, \Theta)$, where Θ is the asymptotic proportion. If P approaches 0 faster than R, we have $\xi \to 0$, and if P approaches 0 slower than P, we get $\xi \to \infty$. Behavior near the positive P-axis is obscured. However, behavior here is easy to understand in P, R-coordinates: the equation for the resources reduces to a logistic equation and the population grows.

We denote the first quadrant $\{(z,\xi)\,|\,z > 0, \xi > 0\}$ by Ω and denote the region $\{(z,\xi)\,|\,z \geq 0, \xi > 0\}$ by Ω^*. Although the positive ξ-axis does not correspond to distinct values of P and R—the whole axis corresponds to $P = R = 0$—we need it to analyze asymptotic behavior. Our main tool will be the Lyapunov function $\lambda : \Omega \to \mathbb{R}$,

$$\lambda(z,\xi) = z^{2h-2}\left(\frac{K}{2c}\xi^2 - \frac{K}{c}\xi + \frac{z}{2h-1} + \frac{K}{2c} - \frac{K(1-h/c)}{2h-2}\right),$$

the properties of which will be established in Lemma 2. First we establish some qualitative behavior of the system. By linearizing the system about the point $\{(z,\xi)\}$ we obtain the Jacobian

$$J = \begin{bmatrix} 1-\xi & z \\ \dfrac{c}{K} & 2(h-1)\xi + 1 - c \end{bmatrix}.$$

The equilibrium points of our system are

- $(0,0)$, at which J has eigenvalues 1 and $1-c$;
- $(0, \frac{c-1}{h-1})$, at which J has eigenvalues $\frac{h-c}{h-1}$ and $c-1$;
- $(K(1-h/c), 1)$, at which J has eigenvalues $\frac{2h-c-1\pm\sqrt{(2h-c-1)^2-4(c-h)}}{2}$.

The behavior of solutions depends in a surprisingly complex way on the constants h and c. This dependence is summarized in Figure 5. Our main tools in establishing this characterization are Lemma 2, which establishes the properties of a Lyapunov function, and Lemma 3.

We shall begin our analysis with some lemmas about basic structural features of the system. We shall then use these lemmas to characterize the qualitative behavior of the system for various values of h and c.

LEMMA 1. *The regions Ω and Ω^* are both positive invariant. That is, if a solution is in one of these regions initially, then it remains in the region as long as it exists.*

Proof. The ξ-axis is invariant and the vector field is pointing into the first quadrant along the positive z-axis. Specifically, if $z > 0$ and $\xi = 0$, then $z' = z$ and $\xi' = \frac{c}{K} > 0$. If $z = 0$ and $\xi > 0$, then $z' = 0$ and $\xi' = (h-1)\xi^2 + (1-c)\xi$. ◻

Note that the regions are not negative invariant and that it is possible that orbits become unbounded in finite time.

LEMMA 2. *Let*

$$\lambda(z,\xi) = z^{2h-2}\left(\frac{K}{2c}\xi^2 - \frac{K}{c}\xi + \frac{z}{2h-1} + \frac{K}{2c} - \frac{K(1-h/c)}{2h-2}\right).$$

(a) *If $2h-c-1=0$, λ is constant on trajectories in Ω.*
(b) *If $2h-c-1<0$, λ is strictly decreasing on trajectories in Ω that are not equilibria.*
(c) *If $2h-c-1>0$, λ is strictly increasing on trajectories in Ω that are not equilibria.*

Proof. A direct (but not short) computation yields

$$\lambda' = (2h-c-1)(K/c)(\xi-1)^2 z^{2h-2},$$

where $'$ denotes the derivative with respect to time. Statement (a) follows directly from this computation.

To prove (b), assume $2h-c-1<0$. Note that $\lambda' < 0$ except when $\xi = 1$. By differentiating twice more, we obtain

$$\begin{aligned}
\lambda'' = &\ (2h-c-1)\frac{K}{c}[2(\xi-1)(\xi')z^{2h-2} + (\xi-1)^2(2h-2)z^{2h-1}z'],\\
\lambda''' = &\ (2h-c-1)\frac{K}{c}[2(\xi')(\xi')z^{2h-2} + 2(\xi-1)(\xi'')z^{2h-2}\\
&+2(\xi-1)(\xi')(2h-2)z^{2h-1}z' + 2(\xi-1)(\xi')(2h-1)z^{2h-1}z'\\
&+(\xi-1)^2(2h-2)(2h-1)z^{2h}(z')^2 + 2(\xi-1)(\xi')(2h-1)z^{2h-1}z''].
\end{aligned}$$

When $\xi = 1$, we have $\lambda'' = 0$ and λ''' is strictly negative unless $\xi' = 0$. Since the only points with $\xi = 1$ and $\xi' = 0$ are equilibria, statement (b) follows. Statement (c) is proven similarly. ◻

If x_e is an equilibrium point, a function L defined on a neighborhood of x_e is called a Lyapunov function if it has a minimum at x_e and is strictly decreasing on all trajectories other than x_e. The existence of a Lyapunov function establishes x_e as an attractor or a stable equilibrium (see [7].) When the level sets of L are compact and

x_e is a global minimum, the point x_e is a global attractor. Since the level sets of λ are not all compact, we use topological methods to understand global behavior.

We say that an orbit $\gamma(t)$ is *positively bounded* if the positive orbit $O^+(\gamma) = \{\gamma(t) \,|\, t > 0\}$ is bounded. We say that γ is *positively unbounded* if $O^+(\gamma)$ is unbounded. Lemma 2 allows us to prove Lemma 3, which characterizes the long term behavior of positively bounded solutions.

LEMMA 3. *Suppose that* $2h-c-1 \neq 0$. *Any positively bounded solution beginning in* Ω *is asymptotic to an equilibrium point (in* Ω^**).*

Proof. The ω-limit set of a solution curve is defined to be

$$\omega(\gamma) = \cap_{s>0}\overline{\cup_{t>s}\gamma(t)},$$

where the overbar denotes closure. It is a standard result [7] that a point p is in $\omega(\gamma)$ if and only if there is a sequence $\{t_n\}$ with $t_n \to \infty$ as $n \to \infty$ such that $\gamma(t_n) \to p$. This follows directly from the definition of $\omega(\gamma)$. Another standard result [7] is that any positively bounded solution has a nonempty ω-limit set. This result follows from the Bolzano–Weierstrass theorem applied to the set $\{\gamma(n) \,|\, n \in \mathbb{N}\}$. Define the ω_Ω-limit set of γ by $\omega_\Omega(\gamma) = \omega(\gamma) \cap \Omega$.

For this proof let $\gamma(t) = (z(t), \xi(t))$ denote a positively bounded solution of the differential equation beginning from an initial condition in Ω. Since λ is strictly monotonic on trajectories and continuous on Ω, it must be constant on the ω_Ω-limit set of any solution. Hence the ω_Ω-limit set of any solution is the (possibly empty) union of equilibrium points.

We claim that if $\omega_\Omega(\gamma)$ contains an equilibrium point $p \in \Omega$, then $\omega(\gamma) = p$. For any $\delta > 0$ there is a time $s \in \mathbb{R}$ such that $\gamma(t) \in B_\delta(p)$ for all $t > s$. Were this not so, then for every $\delta > 0$ the set $\partial(B_\delta(p)) \cap \gamma$ (where $\partial(B_\delta(p)) = \{(z,\xi) \,|\, z^2 + \xi^2 = \delta\}$) would be infinite and hence have a limit point in $\partial(B_\delta(p))$, which we call p_δ. Then $p_\delta \in \omega(\gamma)$ for each δ, and the limit of p_δ as $\delta \to 0$ is p. Since our equilibrium points are isolated, infinitely many of these points are nonequilibrium points, which is impossible.

We have shown that $\omega(\gamma)$ either is a single equilibrium point in Ω or is contained in $\Omega^* - \Omega$. We claim that if $\omega(\gamma) \subseteq \Omega^* - \Omega$, then it consists of a single equilibrium point. Let $p \in \Omega^* - \Omega$ such that p is not an equilibrium point. Since $\Omega^* - \Omega$ is the positive ξ-axis, p is either in the stable manifold or in the unstable manifold of an equilibrium point in $\Omega^* - \Omega$. If p is in the stable or unstable manifold of a sink or source, then it cannot be an ω-limit point of an orbit in Ω. Suppose that p is in the unstable manifold of an equilibrium point $p_e \in \Omega^* - \Omega$ and $p \in \omega(\gamma)$ for some $\gamma(t)$. The unstable manifold of p_e in Ω consists of an orbit extending into Ω. By the Lambda lemma (see [6]), this orbit is in $\omega(\lambda)$, contradicting our earlier assertion that the only points of $\omega(\gamma)$ in Ω are equilibrium points. Similarly, p cannot be in the stable manifold of a saddle. Hence, an ω-limit set of a positively bounded orbit in Ω is a single equilibrium point. □

In the next two lemmas we characterize unbounded solutions.

LEMMA 4. *If* $h < 1$, *then all orbits are positively bounded.*

Proof. Suppose that $\gamma(t)$ is positively unbounded. We claim that either $\xi \to \infty$ or $z \to \infty$. Otherwise, there exist an $M > 0$ and a sequence $t_1, t_2, \ldots$ with $t_n \to \infty$ as $n \to \infty$ such that $||\gamma(t_n)|| < M$ for all n. Then by the Bolzano–Weierstrass theorem the set $\{\gamma(t_n) \,|\, n \in \mathbb{N}\}$ would have a limit point $x_0 \in B_M((0,0))$. This limit point would be in the ω-limit set of γ. By the argument in the proof of Lemma 3, $\gamma(t)$ would have to be asymptotic to x_0 and γ would be bounded.

The Poincaré sphere is a standard tool for analyzing the behavior of a two-dimensional differential equation near infinity. (See [7, p. 169].) A simple calculation using the Poincaré sphere shows that for $h < 1$ there are no orbits asymptotic to infinity. In the notation of [7], $P_2(X, Y) = -XY$, $Q_2(X, Y) = (h-1)Y^2$, and hence the only equilibrium points on the circle at infinity are $\pm(1, 0, 0)$ and $\pm(0, 1, 0)$, and none of these have a stable manifold which intersects Ω. ◻

LEMMA 5. *If $h > 1$, then any positively unbounded orbit has the property that $z(t) \to 0$ and $\xi(t) \to \infty$ as $t \to t_*$ for some finite t_*. Moreover, if $\xi > \max\{1, \frac{c-1}{h-1}\}$ at any time along an orbit, then the orbit is positively unbounded.*

Proof. Assume $h > 1$. Consider an orbit with initial condition (z_0, ξ_0) with $z > 0$ and $\xi > \max\{1, \frac{c-1}{h-1}\}$. We will show that any such orbit has the property that $z(t) \to 0$ and $\xi(t) \to \infty$ as $t \to t_* < \infty$. For such an orbit,

$$\begin{aligned} \xi' &= (h-1)\xi\left(\xi + \frac{1-c}{h-1}\right) + \frac{c}{K}z \\ &> (h-1)\xi\left(\xi + \frac{1-c}{h-1}\right) > 0. \end{aligned}$$

Hence, $\xi(t) > \max\{1, \frac{c-1}{h-1}\}$ and $\xi'(t) > (h-1)\xi(\xi + \frac{1-c}{h-1}) > 0$ for all $t > 0$.

The differential inequality $\xi' \geq (h-1)\xi(\xi + \frac{1-c}{h-1})$ implies that ξ behaves like a solution of $x' = x^2$; it approaches infinity in finite time. More precisely, this differential inequality can be integrated to yield

$$\left(\frac{\xi(\xi_0 + \frac{1-c}{h-1})}{\xi_0(\xi + \frac{1-c}{h-1})}\right)^{\frac{1}{1-c}} > e^t,$$

which implies that $\xi \to \infty$ before $t = (\ln(\xi_0 + \frac{1-c}{h-1}) - \ln(\xi_0))/(1-c) < \ln(\frac{h-c}{h-1})/(1-c) < \infty$.

We now show that $z(t) \to 0$ for this orbit. Since $z' = z(1-\xi)$ and $\xi \to \infty$, it follows that $z(t)$ is eventually monotonic decreasing. Since $z(t)$ is bounded below by 0, $z(t)$ converges to some value $z_* \geq 0$. Since $\xi' = (h-1)\xi^2 + (1-c)\xi + \frac{c}{K}z$ and z is bounded, $\xi(t)$ is eventually monotonic increasing. Without loss of generality, assume that the initial condition for this orbit is (z_0, ξ_0) and that z is monotonic decreasing and ξ is monotonic increasing for all $t \geq 0$. The positive orbit $(z(t), \xi(t))$, $t \geq 0$, then corresponds to the graph of a function $z = f(\xi)$, $f : (\xi_0, \infty) \to (z_*, z_0)$. Then

$$\frac{\mathrm{d}f}{\mathrm{d}\xi} = \frac{\mathrm{d}z/\mathrm{d}t}{\mathrm{d}\xi/\mathrm{d}t} < 0,$$

and by the fundamental theorem of calculus

$$\begin{aligned} z_0 - z_* &= \int_{\xi_0}^{\infty} f'(\xi)\mathrm{d}\xi \\ &= \int_{\xi_0}^{\infty} \frac{f(\xi)(1-\xi)}{(h-1)\xi^2 + (1-c)\xi + \frac{c}{K}f(\xi)}\mathrm{d}\xi. \end{aligned} \tag{7}$$

Note that $f'(\xi) < 0$ because $\xi' > 0$ and $z' < 0$. Since $z_* \leq f(\xi) \leq z_0$ for all ξ,

$$\frac{f(\xi)(1-\xi)}{(h-1)\xi^2 + (1-c)\xi + \frac{c}{K}f(\xi)} < \frac{z_*(1-\xi)}{(h-1)\xi^2 + (1-c)\xi + \frac{c}{K}z_0}.$$

Observe that

$$\lim_{\xi\to\infty} \frac{\frac{z_*(1-\xi)}{(h-1)\xi^2+(1-c)\xi+\frac{c}{K}z_*}}{\frac{-1}{\xi}} \geq \frac{z_*}{(h-c)} \geq 0,$$

with equality if and only if $z_* = 0$. If $z_* \neq 0$, the limit comparison test for indefinite integrals implies that the integral in (7) diverges because the integral

$$\int_{\xi_0}^{\infty} \frac{-1}{\xi} \mathrm{d}\xi$$

diverges. This is a contradiction since $z_0 - z_*$ is finite. Hence $z(t) \to z_* = 0$.

Now consider an orbit with initial condition (z_0, ξ_0) with $z_0 > 0$ and $\xi_0 \leq \max\{1, \frac{c-1}{h-1}\}$. We will show that if $\xi(t)$ is bounded, then so is $z(t)$. This will complete the proof of the $h > 1$ portion of the lemma. Suppose, to obtain a contradiction, that $z(t)$ is unbounded for some orbit $(z(t), \xi(t))$. Since the set $\xi' = 1$ is a parabola opening to the left, there is some M such that if $z > M$, then $\xi' > 1$. Since $z(t)$ is unbounded and $z'(t) = z(\xi - 1) < z$, there are times $t_a < t_b$ with $z(t) > M$ for all $t \in [t_a, t_b]$ and $t_b - t_a > \max\{1, \frac{c-1}{h-1}\}$. Since Ω is positive invariant, $\xi(t_a) > 0$. Hence,

$$\xi(t_b) > \xi(t_b) - \xi(t_a) = \int_{t_a}^{t_b} \xi' \mathrm{d}t > \int_{t_a}^{t_b} 1 \mathrm{d}t > t_b - t_a > \max\left\{1, \frac{c-1}{h-1}\right\}.$$

Therefore, by the previous assertion, $\xi(t) \to \infty$ and $z(t) \to 0$. This proves that $z(t)$ is bounded for positive time for all orbits. ∎

In the course of this proof, we have established an upper bound on the time a population takes to disappear if the orbit begins in Ω with $\xi > \max\{1, \frac{c-1}{h-1}\}$. Specifically, $\xi \to \infty$ before $t = (\ln(\xi_0 + \frac{1-c}{h-1}) - \ln(\xi_0))/(1-c) < \ln(\frac{h-c}{h-1})/(1-c)$. This implies that $P(t), R(t) \to 0$ while $t < \ln(\frac{h-c}{h-1})/(1-c) < \infty$.

Proposition 1. *Suppose that $h < c$ and $h < 1$. Then all solutions beginning in Ω are asymptotic to the stable equilibrium at $(z, \xi) = (\Gamma, 1)$, where $\Gamma = K(1 - h/c)$. Hence, in P, R-coordinates, all solutions beginning in the first quadrant are asymptotic to the equilibrium at $(P, R) = (\Gamma, \Gamma)$.*

Proof. Since $h < 1$, by Lemma 4 every solution is bounded and approaches an equilibrium solution. For these parameter values the equilibrium solutions in Ω^* are $(0, 0)$, $(K(1 - h/c), 1)$, and possibly $(0, \frac{c-1}{h-1})$. The only equilibrium with a nonempty stable manifold in Ω is $(K(1 - h/c), 1)$. Hence, all solutions are asymptotic to this equilibrium. ∎

Proposition 2. *If $h > c$ and $h < 1$, then $(z, \xi) \to (0, \frac{c-1}{h-1})$ as $t \to \infty$ for all solutions. Hence, $(P, R) \to (0, 0)$ as $t \to \infty$ with*

$$\frac{P}{R} \sim \frac{c-1}{h-1}.$$

Proof. Since $h < 1$, by Lemma 4 all solutions are bounded. The only equilibrium point in Ω^* with a nonempty stable manifold in Ω is $(0, \frac{c-1}{h-1})$. By Lemma 3, all solutions are asymptotic to $(0, \frac{c-1}{h-1})$. ∎

An alternative proof of Proposition 2 is based on the Lyapunov function

$$L = \frac{1}{2}\left(\xi + \frac{1-c}{h-1}\right)^2 + \frac{c}{K}z$$

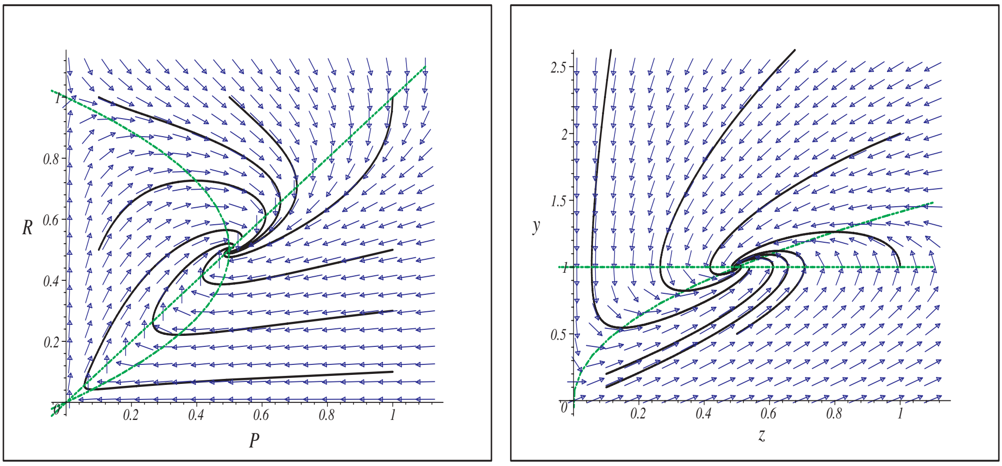

FIG. 6. *The phase planes with $c = 1$, $h = 0.5$, and $K = 1$ satisfying the hypothesis of Proposition* 1. *The nullclines are indicated by dashed lines.*

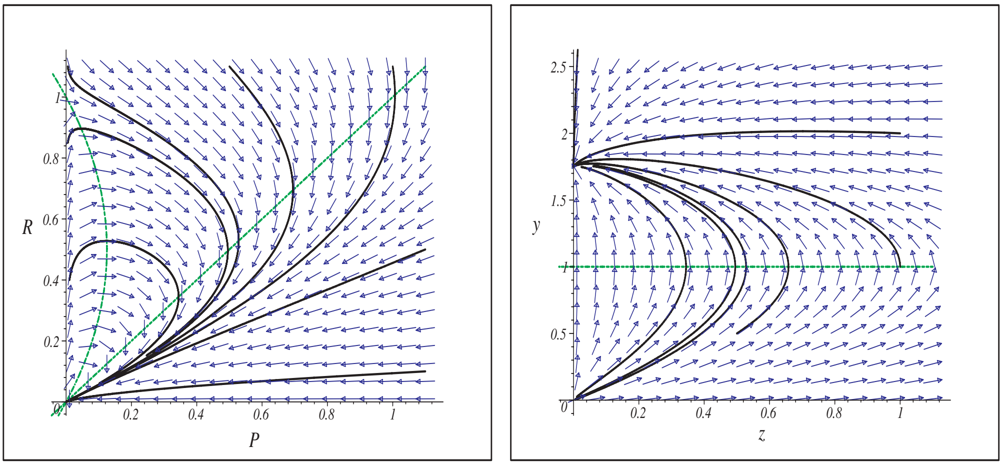

FIG. 7. *The phase planes with $c = 0.3$, $h = 0.6$, and $K = 1$ satisfying the hypothesis of Proposition* 2. *The same set of initial conditions is used for the solutions shown in each coordinate system. The nullclines are indicated by dashed lines.*

with

$$\frac{\mathrm{d}L}{dt} = (h-1)\xi\left(\xi + \frac{1-c}{h-1}\right)^2 + \frac{c}{K}\left(\frac{h-c}{h-1}\right)z,$$

which is negative when $c < h < 1$. Moreover, the level sets of L are compact. This constitutes an alternate proof that $(0, \frac{c-1}{h-1})$ is a global attractor.

PROPOSITION 3. *If $h > c$ and $h > 1$, then $z \to 0$ and $\xi \to \infty$ in finite time for all solutions. Hence, (P, R) goes to the singularity at $(0, 0)$ in finite time with*

$$\frac{P}{R} \to \infty.$$

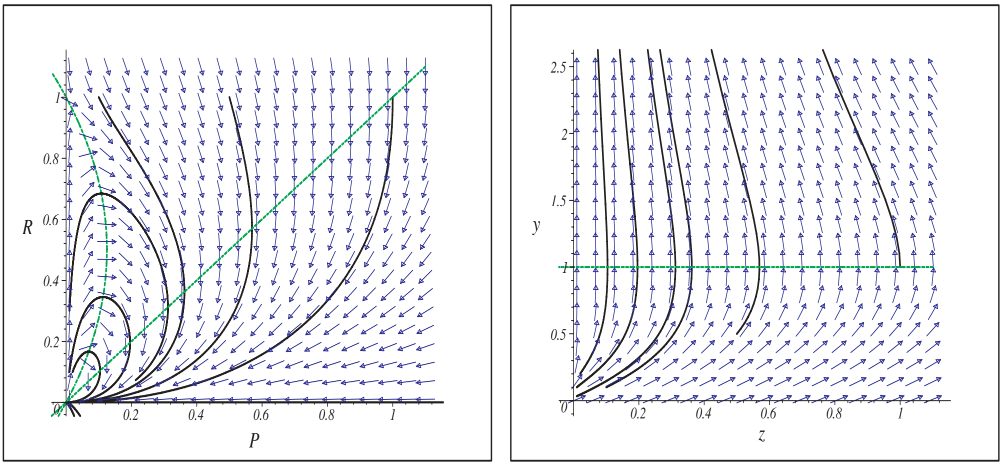

FIG. 8. *The phase planes with $c = 1$, $h = 2$, and $K = 1$ satisfying the hypothesis of Proposition* 3. *The nullclines are indicated by dashed lines.*

Proof. For our parameter values the only equilibrium solutions in Ω^* are $(0, 0)$ and possibly $(0, \frac{c-1}{h-1})$. The equilibrium $(0, 0)$ is unstable and $(0, \frac{c-1}{h-1})$ is unstable if $(0, \frac{c-1}{h-1}) \in \Omega^*$. Therefore, there are no solutions in Ω that are asymptotic to an equilibrium solution. By Lemma 3, all solutions are unbounded. By Lemma 5, $z(t) \to 0$ and $\xi(t) \to \infty$ in finite time for all solutions. ∎

PROPOSITION 4. *Suppose that $h < c$, $h > 1$, and $2h - c - 1 > 0$. For almost every solution, $z(t) \to 0$ and $\xi(t) \to \infty$ in finite time. There is one solution with $\xi(t) \to \frac{c-1}{h-1}$ and one unstable equilibrium solution at $(K(1 - h/c), 1)$.*

In P, R-coordinates, almost every solution goes to the singularity at $(0, 0)$ in finite time with

$$\frac{P}{R} \to \infty.$$

There is one solution that is asymptotic to $(0, 0)$ with $P/R \sim \frac{c-1}{h-1}$ and one unstable equilibrium solution at $(K(1 - h/c), K(1 - h/c))$.

Proof. For our parameter values the equilibrium solutions in Ω^* are $(0, 0)$, $(0, \frac{c-1}{h-1})$, and $(K(1 - h/c), 1)$. The equilibrium at $(0, 0)$ is a saddle with its stable manifold contained in $\Omega^* - \Omega$. The equilibrium at $(0, \frac{c-1}{h-1})$ is a saddle, and its stable manifold is a solution extending into Ω. The equilibrium at $(K(1 - h/c), 1)$ is unstable. Therefore, all solutions except $(K(1 - h/c), 1)$ and the stable manifold $(0, \frac{c-1}{h-1})$ are unbounded by Lemma 3. By Lemma 5, $z(t) \to 0$ and $\xi(t) \to \infty$ in finite time for these solutions. ∎

PROPOSITION 5. *Suppose that $h < c$, $h > 1$, and $2h - c - 1 < 0$. Let A denote the region*

$$0 < z < \frac{-K(2h - 1)}{2c} \left(\xi^2 - 2\xi + \frac{2h - c - 1}{h - 1} \right).$$

All orbits that intersect A approach the equilibrium point $(\Gamma, 1)$ asymptotically; in fact, these solutions constitute the basin of attraction of this sink. The single solution stable manifold of $(0, \frac{c-1}{h-1})$ is a separatrix. All other solutions have the property that $z \to 0$, $\xi \to \infty$ in finite time.

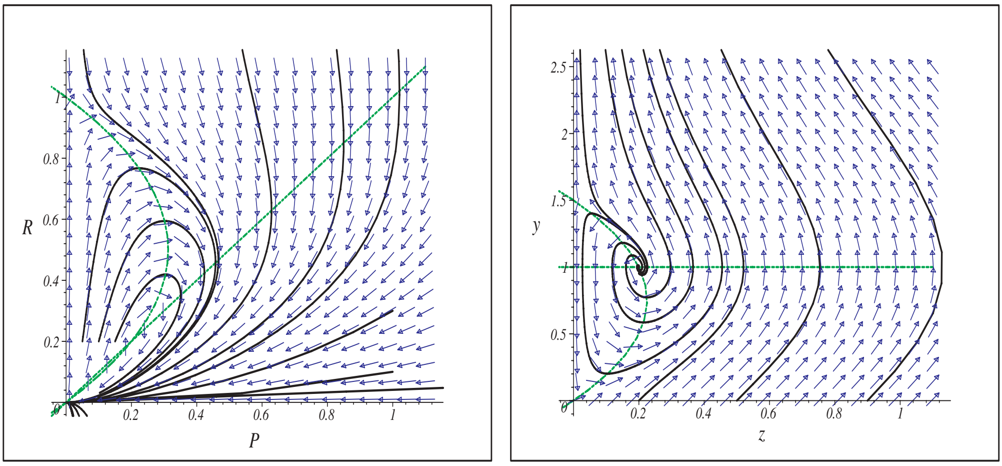

FIG. 9. *The phase planes with $c = 2.5$, $h = 2$, and $K = 1$ satisfying the hypothesis of Proposition* 4. *The nullclines are indicated by dashed lines.*

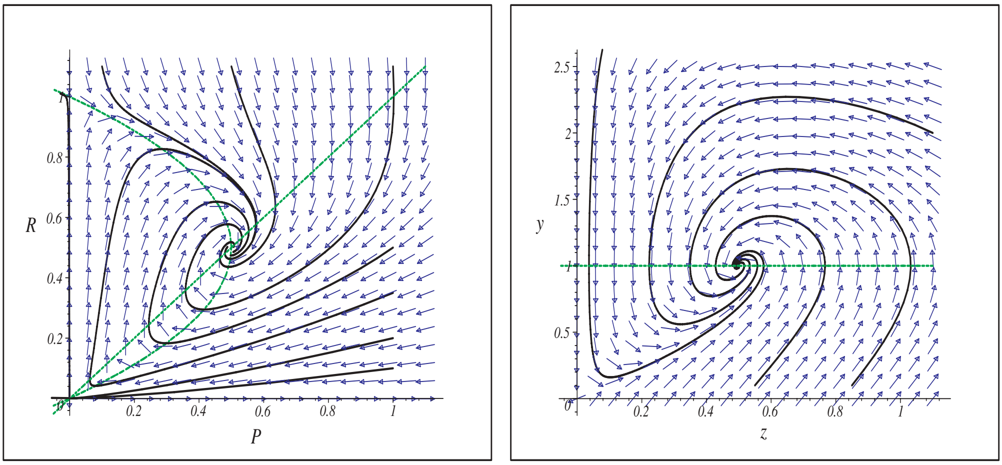

FIG. 10. *The phase planes with $c = 3$, $h = 1.5$, and $K = 1$ satisfying the hypothesis of Proposition* 5. *The nullclines are indicated by dashed lines.*

In P, R-coordinates, there is an open set of orbits which are asymptotic to the equilibrium at $(P, R) = (\Gamma, \Gamma)$. There is an open set of orbits which approach $(0, 0)$ in finite time. There is a single solution that is asymptotic to $(0, 0)$ with $P/R \sim \frac{c-1}{h-1}$ as $t \to \infty$, and this solution is the separatrix between the two open sets.

Proof. By solving $\lambda = 0$ we obtain

$$z = \frac{-K(2h-1)}{2c}\left(\xi^2 - 2\xi + \frac{2h-c-1}{h-1}\right).$$

It is easy to see that $\lambda < 0$ on A and $(\Gamma, 1) \in A$. Observe that the only equilibrium point in $\overline{A}$ whose stable manifold has a nonempty intersection with A is $(\Gamma, 1)$. Since $\lambda'(t) < 0$ for all orbits in Ω by Lemma 2, all orbits are forward asymptotic to $(\Gamma, 1)$.

The stable manifold of $(0, \frac{c-1}{h-1})$ in Ω is a single orbit. Denote this orbit by $\alpha(t)$.

Near $(0, \frac{c-1}{h-1})$, there is a well-defined notion of above and below α. Orbits just above α follow the unstable manifold of $(0, \frac{c-1}{h-1})$ up the ξ-axis. Eventually $\xi(t) > \frac{c-1}{h-1}$ for these solutions. Since $2h-c-1 < 0$, we have $c-1 > 2(h-1)$ and $\frac{c-1}{h-1} = \max\{1, \frac{c-1}{h-1}\}$. Therefore, $\xi(t) \max\{1, \frac{c-1}{h-1}\}$ for each of these solutions and $z(t) \to 0$, $\xi(t) \to \infty$ by Lemma 5.

Orbits just below α follow the unstable manifold of $(0, \frac{c-1}{h-1})$ down the ξ-axis into the region A, and these orbits are asymptotic to $(\Gamma, 1)$. Therefore, α is the separatrix between orbits asymptotic to $(\Gamma, 1)$ and ones that approach $(0, \infty)$ in finite time. By Lemmas 3 and 5, every orbit is asymptotic to $(\Gamma, 1)$, $(0, \frac{c-1}{h-1})$, or $(0, \infty)$. $\square$

PROPOSITION 6. *Suppose that $h < c$, $h > 1$, and $2h - c - 1 = 0$. Let A denote the region*

$$0 < z < \frac{-K(2h-1)}{2c}\left(\xi^2 - 2\xi\right).$$

There is a heteroclinic orbit from $(0,0)$ to $(0, \frac{c-1}{h-1})$. The boundary of A consists of this orbit, a heteroclinic orbit in $\Omega^* - \Omega$ from $(0,0)$ to $(0, \frac{c-1}{h-1})$, and these two equilibrium points. All orbits inside A are periodic. All orbits outside of A approach $(0, \infty)$ in finite time.

In P, R-coordinates, there is a heteroclinic orbit from $(K, 0)$ to $(0,0)$. This orbit together with the orbit in the R-axis from $(0,0)$ to $(K,0)$ and these two equilibrium points forms a limit cycle. Orbits within this limit cycle are all periodic. Orbits outside of this limit cycle approach $(0,0)$ in finite time.

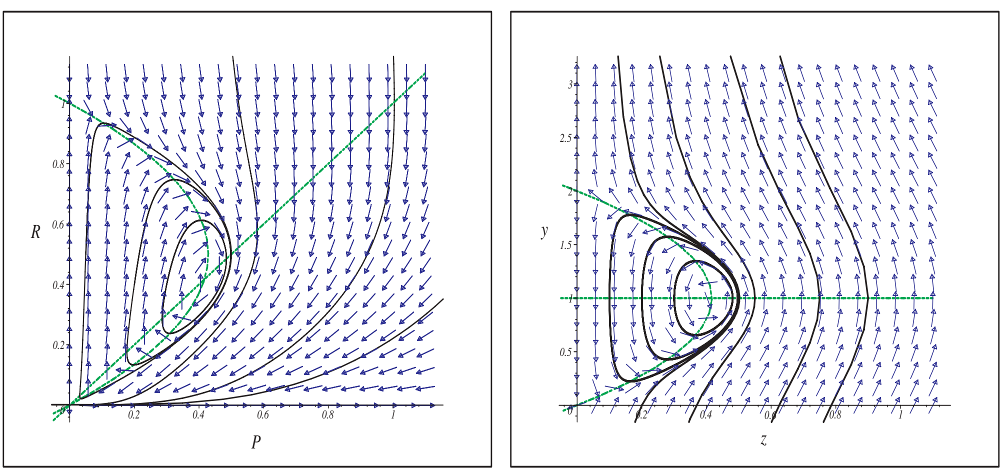

FIG. 11. *The phase planes with $c = 6$, $h = 3.5$, and $K = 1$ satisfying the hypothesis of Proposition* 6. *The nullclines are indicated by dashed lines.*

Proof. For this case, $\lambda'(t) = 0$ by Lemma 2, so λ is an integral of the system. We want to show that it is a nondegenerate integral. The gradient of λ is

$$\nabla\lambda = \Bigg((2h-2)z^{2h-3}\left(\frac{K}{2c}\xi^2 - \frac{K}{c}\xi + \frac{z}{2h-1} + \frac{K}{2c} - \frac{K(1-h/c)}{2h-2}\right) + \frac{z^{2h-2}}{2h-1}, z^{2h-2}\frac{K}{c}(\xi - 1)\Bigg).$$

Since $\partial\lambda/\partial\xi = z^{2h-2}\frac{K}{c}(\xi - 1)$, if $\nabla\lambda = 0$ in Ω, then $\xi = 1$. Substituting $\xi = 1$ into $\partial\lambda/\partial z = 0$ gives $z = \Gamma$. Hence, the only point in Ω where $\nabla\lambda = \mathbf{0}$ is the equilibrium $(\Gamma, 1)$, and λ is nondegenerate.

From (3) with $2h - c - 1 = 0$, solving $\lambda = 0$, we get

$$z = \frac{-K(2h-1)}{2c}\left(\xi^2 - 2\xi\right).$$

This is a parabola opening to the left. It intersects the ξ-axis at $\xi = 0, \frac{c-1}{h-1}$. Since λ is constant along solutions, this parabola is a heteroclinic orbit.

By direct computation, $\lambda(1,\Gamma) = \frac{-\Gamma^{2h-1}}{(2h-2)(2h-1)}$. The orbits with $\frac{-\Gamma^{2h-1}}{(2h-2)(2h-1)} < \lambda < 0$ are nested periodic orbits in A that enclose convex regions containing $(1,\Gamma)$. This follows from differentiation of λ.

There are no equilibria outside $\overline{A}$. Hence, by the Poincaré–Bendixson theorem, all orbits outside of A are unbounded. By Lemma 5, all of these orbits approach $(0,\infty)$ in finite time. ∎

In conclusion we note that our system undergoes a degenerate Hopf bifurcation when $h < c$, $h > 1$, and $2h - c - 1$ changes sign. The equilibrium at $(K(1 - h/c), 1)$ changes from a spiral source for $2h - c - 1 > 0$ to a spiral sink for $2h - c - 1 > 0$. When such a transition occurs through a classic Hopf bifurcation, a single periodic orbit emerges from (or contracts to) the equilibrium point. The Hopf bifurcation theorem (see [7]) identifies a large class of conditions under which such bifurcations occur. Our system falls through the cracks of the theorem; the theorem applies to all systems except those whose Taylor coefficients at the equilibrium satisfy a certain equation, and the Taylor coefficients of our system satisfy that equation.

REFERENCES

[1] J. M. Anderies, *On modeling human behavior and institutions in simple ecological economic systems*, Ecological Economics, 35 (2000), pp. 393–412.

[2] J. M. Anderies, *Econimic development, demographics, and renewable resources: A dynamical systems approach*, Environment and Development Economics, 8 (2003), pp. 219–246.

[3] J. A. Brander and M. S. Taylor, *The simple economics of Easter Island: A Ricardo-Malthus model of renewable resource use*, American Economic Review, 88 (1998), pp. 119–138.

[4] J. Cohen, *How Many People Can the Earth Support?*, W. W. Norton and Company, New York, 1995.

[5] L. L. Eberhardt, *Is wolf predation ratio-dependent?*, Canadian J. Zoology, 76 (1997), pp. 380–386.

[6] A. Katok and B. Hasselblatt, *Introduction to the Modern Theory of Dynamical Systems*, Cambridge University Press, Cambridge, UK, 1995.

[7] L. Perko, *Differential Equations and Dynamical Systems*, Springer-Verlag, New York, 1993.

[8] C. L. Redman, *Human Impact on Ancient Environments*, University of Arizona Press, Tucson, AZ, 1999.

[9] P. Turchin, *Complex Population Dynamics: A Theoretical/Empirical Synthesis*, Princeton University Press, Princeton, NJ, 2003.