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ON PREDATOR-PREY SYSTEMS AND SMALL-GAIN THEOREMS

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Abstract. This paper deals with an almost global convergence result for Lotka-Volterra systems with predator-prey interactions. These systems can be written as (negative) feedback systems. The subsystems of the feedback loop are monotone control systems, possessing particular input-output properties. We use a small-gain theorem, adapted to a context of systems with multiple equilibrium points to obtain the desired almost global convergence result, which provides sufficient conditions to rule out oscillatory or more complicated behavior that is often observed in predator-prey systems.

1. Introduction.

Since the early work Lotka and Volterra, predator-prey systems have continued to attract significant attention [7, 17, 10]. It is well known that these systems may exhibit oscillatory behavior; the best-known is the classic Lotka-Volterra predator-prey system (see [7, 9]). This system is defined by

$$\begin{pmatrix}\dot{x}\\ \dot{z}\end{pmatrix} = \mathrm{diag}(x,\, z)\left(\begin{pmatrix}0 & +a_{12}\\ -a_{21} & 0\end{pmatrix}\begin{pmatrix}x\\ z\end{pmatrix} + \begin{pmatrix}-r_1\\ r_2\end{pmatrix}\right),$$

where x and z denote the predator and prey concentrations respectively, and a_{12}, a_{21}, r_1 and r_2 are positive constants. The phase portrait consists of an infinite number of periodic solutions centered around an equilibrium point and this system is not structurally stable. In fact, Hofbauer and Sigmund have demonstrated that the more general (but not necessarily predator-prey type) Lotka-Volterra system:

$$\begin{pmatrix}\dot{x}\\ \dot{z}\end{pmatrix} = \mathrm{diag}(x,\, z)\left(\begin{pmatrix}a_{11} & a_{12}\\ a_{21} & a_{22}\end{pmatrix}\begin{pmatrix}x\\ z\end{pmatrix} + \begin{pmatrix}r_1\\ r_2\end{pmatrix}\right),$$

where there is no restriction on the signs of the parameters a_{ij}, r_k, does not exhibit nontrivial *isolated* periodic solutions. Hence, compelling evidence of oscillatory

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behavior in predator-prey systems is not provided by the classic Lotka-Volterra predator-prey system or by any two-dimensional Lotka-Volterra system. But as we will demonstrate, oscillations can be found in different predator-prey models.

One predator-prey system that is still low-dimensional but not of the Lotka-Volterra type is Gause's model [9], which allows isolated periodic solutions under suitable conditions [10]:

$$\begin{aligned} \dot{x} &= x(q(z) - d) \\ \dot{z} &= zg(z) - xp(z), \end{aligned} \tag{1}$$

where $g(z)$ is the growth rate of the prey in absence of the predator (often $zg(z)$ is logistic) and $p(z)$ is the so-called predator functional response, a non-negative, increasing function that is zero at zero (often of Michaelis-Menten type). If the function $q(z)$ is proportional to $p(z)$ then the proportionality factor is called the conversion rate. Finally, $d > 0$ is the death rate of predators.

Oscillatory behavior can also be found *within* the class of Lotka-Volterra predator-prey systems, but the number of predator and prey species must be larger than two. As an illustration, we will provide two examples with two predator species and one prey species. A common property for these examples is that the predator species are *mutualistic*; that is, the effect of one predator on another is not negative. This might occur if the predator population is stage-structured, for example, if it consists of immature and mature predator species.

Example 1

Consider the parameterized (parameter $k > 0$) Lotka-Volterra predator-prey system with two predator species x_1 and x_2 and one prey species z:

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{z} \end{pmatrix} = \operatorname{diag}(x_1, x_2, z) \left(\begin{pmatrix} -1 & 1 & 1 \\ 1 & -2 & 0 \\ 0 & -k & -3 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ z \end{pmatrix} + \begin{pmatrix} -1 \\ 1 \\ k+3 \end{pmatrix} \right). \tag{2}$$

Suppose that x_1 and x_2 are interpreted as the immature and the mature predators. Notice that only the mature predator kills its prey but does not consume it. The immature predators on the other hand, do not kill but do consume the prey. This means that the predator population consists of adults who hunt for food for their young but do not eat the prey themselves. Obviously the mature predator must find food elsewhere, and this is reflected in the $x_2.(+1)$ term in the $\dot{x}_2$ equation in System (2). For every $k > 0$, there is a nontrivial equilibrium point at $(1, 1, 1)$, and a simple application of the Routh-Hurwitz criterion reveals that this equilibrium point is locally asymptotically stable if $k \in (0, k_c)$, where $k_c := 57$. For $k > k_c$, however, the linearization at $(1, 1, 1)$ possesses one stable (and hence real) eigenvalue and two unstable eigenvalues. For $k - k_c > 0$ small enough, the unstable eigenvalues must be complex conjugate with nontrivial imaginary part. This suggests the occurrence of a Hopf bifurcation at the critical value k_c. In fact, we determined the occurrence of a supercritical Hopf bifurcation and hence the existence of stable oscillatory behavior for System (2) (see Fig. 1).

To establish this, we used the method outlined in [5], p. 153 and the software Maple to perform some of the calculations,which involve a series of steps. A simple translation to the equilibrium point $(1, 1, 1)^T$ is performed by setting $z = x - (1, 1, 1)^T$. In the new z-coordinates, the equations are $\dot{z} = A(k)z + \operatorname{diag}(z)A(k)z$, where $A(k)$ is the interaction matrix corresponding to the Lotka-Volterra system

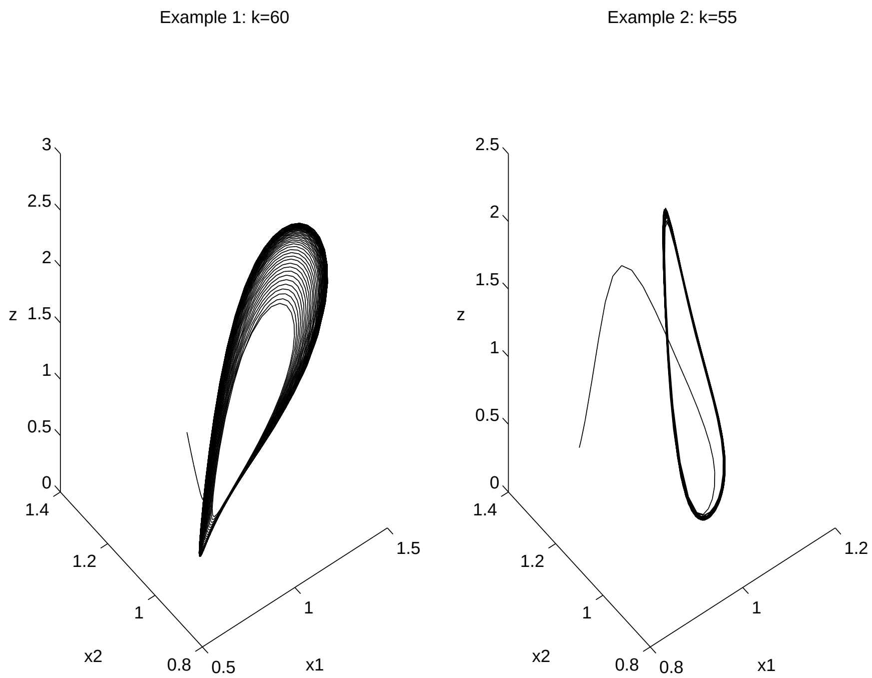

Figure 1. Oscillations in Examples 1 and 2 (initial condition $(0.8, 1.1, 0.9)$, integration over $[0, 200]$).

(2). To obtain the desired result, we need to show that for the z-system two conditions from the Hopf bifurcation theorem are satisfied when k passes through the critical value $k_c = 57$. The first transversality condition of the Hopf bifurcation theorem (which expresses that the complex pair of eigenvalues of $A(k)$ crosses the imaginary axis at k_c) is easily verified using the information from the Routh-Hurwitz criterion and the relationship between eigenvalues of $A(k)$ and the numbers from a Routh-Hurwitz table. The second condition requires the calculation of a number a associated to the z system at the critical value k_c (see [5, equation (3.4.11)]). From now on fix k at k_c and denote $A(k_c)$ by A. A linear transformation $z = TX$ is performed to put A in block-diagonal form $\tilde{A}$, where the upper 2×2-block corresponds to the imaginary eigenvalue pair $\{\pm\sqrt{10}i\}$ and the lower 1×1-block corresponds to the stable eigenvalue -6. This leads to $\dot{X} = \tilde{A}X + T^{-1}\,\mathrm{diag}(TX)AX$. The problem now is that an approximation of the center manifold for this system to *at least quadratic terms* should be computed to verify the mentioned second condition. To compute this approximation we used Maple. This approximation is in turn used to calculate the number a, (see [5, equation (3.4.11)]). For this particular example, a is negative, which allows us to conclude that a supercritical Hopf bifurcation occurs.

Example 2

Consider the parameterized (parameter $k > 0$) Lotka-Volterra predator-prey systems with two predators and one prey species:

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{z} \end{pmatrix} = \mathrm{diag}(x_1, x_2, z) \left(\begin{pmatrix} -1 & \frac{7}{2} & \frac{1}{2} \\ 0 & -2 & 1 \\ -k & -\frac{k}{2} & -\frac{3}{2} \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ z \end{pmatrix} + \begin{pmatrix} -3 \\ 1 \\ \frac{3}{2}(k+1) \end{pmatrix} \right). \tag{3}$$

As in Example 1, $(1, 1, 1)$ is always an equilibrium point, and a supercritical Hopf bifurcation occurs at $k = k_c$ where $k_c = 105/2 = 52.5$ - again illustrating (stable) oscillatory behavior (see Fig. 1).

Equipped with convincing evidence for possible oscillations in three-dimensional Lotka-Volterra predator-prey systems, it might be expected that this or even more complicated behavior is possible in the typically higher-dimensional Lotka-Volterra predator-prey system presented below, which will be the primary focus of attention in this paper:

$$\begin{pmatrix} \dot{x} \\ \dot{z} \end{pmatrix} = \mathrm{diag}(x, z) \left(\begin{pmatrix} A & B \\ -C & D \end{pmatrix} \begin{pmatrix} x \\ z \end{pmatrix} + \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} \right), \tag{4}$$

where x is k-dimensional and z is $(n-k)$-dimensional. Throughout this paper, we make the following assumption:

H: For System (4), A and D are Metzler and stable and $B, C \geq 0$,

where the inequalities on the matrices B and C should be interpreted entrywise. Recall that a matrix is a Metzler matrix if its off-diagonal entries are non-negative. A matrix is stable if it only has eigenvalues with negative real part. Examples 1 and 2 satisfy these properties.

Some remarks concerning system (4) are necessary.

Remark 1. *System* (4) *is a Lotka-Volterra predator-prey system consisting of k predator species x and $(n-k)$ prey species z. The interaction within both subcommunities is mutualistic. For the predator subcommunity, this differs from the usual assumption that the interaction between them is competitive.*

Remark 2. *There are no restrictions (nor will any restrictions be introduced later in this paper) on the signs of the components of r_1 and r_2. These components are the death or growth rates of the species that do not originate from the interaction with the other species.*

In this paper, we consider whether oscillations or more complicated behavior of System (4) can be ruled out. In fact, we are mainly interested in the more restrictive problem of finding conditions for the existence of an (almost) globally asymptotically stable equilibrium point. In view of Examples 1 and 2, this is a nontrivial problem.

In general, Lotka-Volterra systems may display complicated behavior, ranging from oscillatory behavior, over heteroclinic cycles to chaos. See [9], especially for its extensive source material. For results on competitive systems, we refer to [11, 3] and for predator-prey systems to [17]. In the latter reference, however (and also in other work on predator-prey systems), the usual assumption is that when in isolation, the predator populations and the prey populations interact competitively. This is different from our assumption that they interact in a mutualistic way.

We also point out that extensive literature [16, 12, 18, 19, 20] exists on the subject of the related class of systems consisting of two competing subcommunities

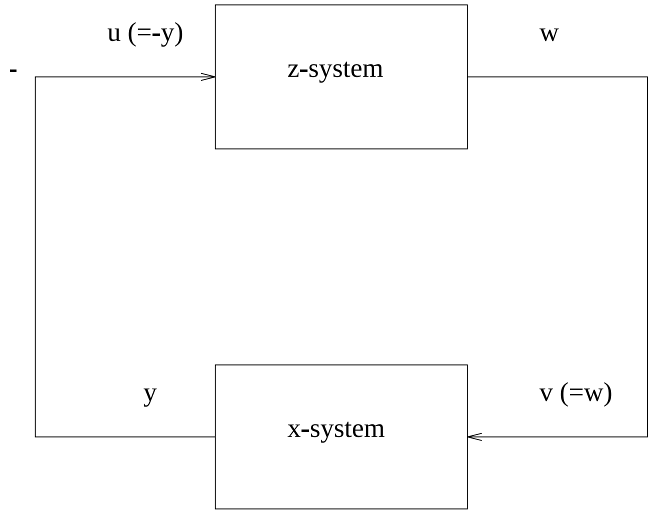

FIGURE 2. Feedback interconnection

of mutualists. If Lotka-Volterra interactions are assumed, these systems are given by the following equations:

$$\begin{pmatrix} \dot{x} \\ \dot{z} \end{pmatrix} = \operatorname{diag}(x,z)\left(\begin{pmatrix} A & -P \\ -Q & D \end{pmatrix}\begin{pmatrix} x \\ z \end{pmatrix} + \begin{pmatrix} r_1 \\ r_2 \end{pmatrix}\right), \tag{5}$$

where A, D are Metzler and stable and $P, Q \geq 0$. The mentioned references are devoted to global stability properties of equilibria and to persistence. Remarkable results have been obtained for this class. However, we emphasize that there is a fundamental difference between System (5) and our System (4). Indeed, the flow of System (5) is monotone [6, 13], while the flow of our model (4) does not possess this property. Monotonicity is often useful in establishing convergence to and stability of equilibria. The lack of a monotonicity for System (4) forces one to use different tools to prove (almost) global stability of equilibria. We believe that the perspective of control systems might be useful in achieving this. We elaborate briefly on this claim in the next paragraph.

To System (4) one can associate two input/output (I/O) systems:

$$\begin{aligned} \dot{z} &= \operatorname{diag}(z)(Dz + r_2 + Cu(t)) \\ w &= z, \end{aligned} \tag{6}$$

and

$$\begin{aligned} \dot{x} &= \operatorname{diag}(x)(Ax + r_1 + Bv(t)) \\ y &= x, \end{aligned} \tag{7}$$

where $u(t)$ is a (componentwise) nonpositive input signal and $v(t)$ a (componentwise) nonnegative input signal; w and y are output signals. These I/O systems *are* monotone in accordance with [1] (we shall provide a precise definition of monotone I/O systems in a later section).

Associated to both these I/O systems are what we termed *I/O quasi characteristics* k_w and k_y (see Definition 2.2). Such a characteristic is a mapping between the input and output space of an I/O system, that captures the ability to convert a constant input into a converging output, where the limit is (almost) independent of initial conditions. The I/O quasi characteristic assigns to every input its corresponding output limit.

Notice that System (4) can easily be identified as the *negative feedback interconnection* of Systems (6) and (7) (see Fig. 2), by setting:

$$\begin{aligned} v &= w \\ u &= -y. \end{aligned} \tag{8}$$

The fact that System (4) is a feedback interconnection of two systems opens up the toolbox from the theory of interconnected control systems to prove global stability. One particular tool we will use is a so-called small-gain theorem. An informal statement of our main result follows.

THEOREM 1.1. *If the discrete-time system*

$$u_{k+1} = -(k_y \circ k_w)(u_k)$$

possesses a globally attracting fixed point, then the feedback System (6)-(8)*, or equivalently* System (4) *possesses an (almost) globally attracting equilibrium point.*

As an illustration of this result, we will provide sufficient conditions for the gain k in Examples 1 and 2, guaranteeing that the condition of Theorem 1.1 is satisfied.

The development of a theory for monotone control systems has been initiated in [1]. A particular small-gain theorem has been proved there, but it is not applicable in our context. An appropriate extension is given in [2], however, and this allows us to formulate sufficient conditions for the existence of an almost globally attracting equilibrium point of System (4). Note that this is the strongest achievable convergence property for a Lotka-Volterra system since these systems typically possess multiple equilibrium points. (For instance, zero is *always* an equilibrium point; of course it is usually an uninteresting one from a biological point of view.)

2. Preliminaries.

2.1. Monotone I/O systems and a small-gain theorem.

The material in this section occurs in a far more general setting in [1, 2]; however, for our purposes, we restrict our analysis to a narrower framework, namely, I/O systems described by differential equations. Consider the following I/O system:

$$\begin{aligned} \dot{x} &= f(x,u) \\ y &= h(x), \end{aligned} \tag{9}$$

where $x \in \mathbb{R}^n$ is the state, $u \in U \subset \mathbb{R}^m$ the input and $y \in Y \subset \mathbb{R}^p$ the output. It is assumed that f and h are smooth (that is, continuously differentiable) and that the input signals $u(t) : \mathbb{R} \to U$ are Lebesgue measurable functions and locally essentially bounded (i.e. for every compact time interval $[T_m, T_M]$, there is some compact set C such that $u(t) \in C$ for almost all $t \in [T_m, T_M]$). This implies that solutions with initial states $x_0 \in \mathbb{R}^n$ are defined for all inputs $u(.)$ and will be denoted by $x(t, x_0, u(.))$, $t \in I$, where I is the maximal interval of existence for this solution. (See [14] for a general theoretical framework for the analysis of I/O systems.) From now on we will assume that a fixed set $X \subset \mathbb{R}^n$ is given, which is the closure of its interior. The set X is assumed to be *forward invariant*, that is, for all inputs $u(.)$ and for every $x_0 \in X$, it holds that $x(t, x_0, u(.)) \in X$, for all

$t \in I \cap \mathbb{R}_+$. Henceforth, initial conditions are restricted to this set X. We will be particularly interested in cases where $X = \mathbb{R}^n_+$, $U = \mathbb{R}^m_+$ or $U = -\mathbb{R}^m_+$.

We denote the usual partial order on $\mathbb{R}^n$ by $\preceq$; that is, for $x, y \in \mathbb{R}^n$, $x \preceq y$ means that $x_i \leq y_i$ for $i = 1, \dots, n$. The state space X (input space U, output space Y) inherits the partial order from $\mathbb{R}^n$ ($\mathbb{R}^m$, $\mathbb{R}^p$) as the former sets are subsets of the latter ones. We say that X (or U or Y) is a *lattice* if for all $x_1, x_2 \in X$ (U, Y), both $\inf(x_1, x_2)$ and $\sup(x_1, x_2)$ exist in X (U, Y). The partial order on $\mathbb{R}^m$ carries over to the set of input signals in a natural way (hence we use the same notation for the partial order on this latter set): $u(.) \preceq v(.)$ if $u(t) \preceq v(t)$ for almost all $t \geq 0$. The next definition introduces the concept of a monotone I/O system, which means that ordered initial conditions and input signals lead to subsequent ordered solutions.

Definition 2.1. *The I/O system* (9) *is monotone (with respect to the usual partial orders) if the following conditions hold:*

$$x_1 \preceq x_2 \text{ and } u(.) \preceq v(.) \Rightarrow x(t, x_1, u(.)) \preceq x(t, x_2, v(.)) \text{ for all } t \in (I_1 \cap I_2) \cap \mathbb{R}_+. \tag{10}$$

and

$$h \text{ is a monotone map, i.e. } x_1 \preceq x_2 \Rightarrow h(x_1) \preceq h(x_2). \tag{11}$$

Remark 3. *We refer to* [1] *for tests to check whether a given I/O system is monotone.*

Remark 4. *Since no confusion about the partial orders on input, state, and output spaces is possible here (we always mean the usual partial order $\preceq$), we will hereafter refer to monotone I/O systems and not explicitly mention the involved partial orders. However, we emphasize that in general the concept of a monotone I/O system requires the enumeration of these partial orders (see* [1]*).*

Of particular interest is how an I/O system behaves when it is supplied with a *constant* input. Next we introduce a notion wthat implies this behavior is fairly simple [2].

Definition 2.2. *The I/O system* (9) *possesses an input/state (I/S)* quasi characteristic *$k_x : U \to X$ if for every constant input $u \in U$ (and using the same notation for the corresponding $u(.)$) and for each initial state $x_0 \in X$, the solution $x(t, x_0, u)$ is well defined for all $t \in \mathbb{R}_+$, and there exists a set of measure zero B_u such that*

$$\forall x_0 \in X \setminus B_u : \lim_{t \to +\infty} x(t, x_0, u) = k_x(u). \tag{12}$$

If System (9) *possesses an I/S quasi characteristic k_x then it also possesses an input/output (I/O) quasi characteristic $k_y : U \to Y$ defined as $k_y := h \circ k_x$.*

Remark 5. *An important property of a static I/S or I/O quasi characteristic of a monotone I/O system is that it is a monotone map. Indeed, for any pair of constant inputs $u \preceq v$, one may find an initial condition $x_0 \in X \setminus (B_u \cup B_v)$ such that* (10) *is satisfied when choosing $x_1 = x_2 = x_0$. Upon taking limits for $t \to +\infty$ of both sides of the last inequality in* (10) *and using* (12)*, we see that k_x is monotone. The same is true for an I/O quasi characteristic k_y since the output map is monotone by* (11)*, and the composition of monotone maps is monotone.*

We are ready to state the main tool in proving stability for Lotka-Volterra predator-prey systems. This is a special case of a more general result proved in

[2]. Below we use the concept of an *almost globally attracting equilibrium point* of an autonomous system, which means that there exists an equilibrium point of this system that attracts all solutions which are not initiated in a certain set of measure zero. Similarly, an *almost globally asymptotically stable equilibrium point* is an equilibrium point that is stable (in the Lyapunov sense) and almost globally attracting.

THEOREM 2.1. *Consider the following two I/O systems:*

$$\dot{x}_1 = f_1(x_1, u_1), \quad y_1 = h_1(x_1) \tag{13}$$
$$\dot{x}_2 = f_2(x_2, u_2), \quad y_2 = h_2(x_2), \tag{14}$$

where $x_i \in X_i \subset \mathbb{R}^{n_i}$, $u_i \in U_i \subset \mathbb{R}^{m_i}$ *and* $y_i \in Y_i \subset \mathbb{R}^{p_i}$ *for* $i = 1, 2$. *Suppose that* $Y_1 \subset U_2$ *and* $-Y_2 \subset U_1$ *and that the I/O systems are interconnected through a (negative) feedback loop:*

$$u_2 = y_1 \tag{15}$$
$$u_1 = -y_2. \tag{16}$$

Assume that U_1, U_2, Y_1 *and* Y_2 *are closed lattices and that:*

1. *Both I/O systems* (13) *and* (14) *are monotone;*
2. *Both I/O systems* (13) *and* (14) *possess continuous I/S quasi characteristics* k_{x_1} *and* k_{x_2} *respectively (and thus also I/O quasi characteristics* k_{y_1} *and* k_{y_2}*);*
3. *All forward solutions of the feedback system* (13)-(16) *are bounded.*

Then the feedback system possesses an almost globally attracting equilibrium point $(\bar{x}_1, \bar{x}_2) \in X_1 \times X_2$ *if the following discrete-time system, defined on* U_1 *as*

$$u_{k+1} = -(k_{y_2} \circ k_{y_1})(u_k), \tag{17}$$

possesses a globally attracting fixed point $\bar{u} \in U_1$. *In that case,* $(\bar{x}_1, \bar{x}_2) = (k_{x_1}(\bar{u}), (k_{x_2} \circ k_{y_1})(\bar{u}))$.

This result and similar ones following later in this paper, are called *small-gain theorems*. The last condition is often referred to as a *small-gain condition*. We will use this terminology hereafter. (For another example of the application of small-gain ideas in biology, see [15].)

2.2. **Boundedness and stability of Lotka-Volterra systems.** Consider the classic Lotka-Volterra system:

$$\dot{x} = \mathrm{diag}(x)(Ax + r), \tag{18}$$

where $x \in \mathbb{R}^n$ and $r \in \mathbb{R}^n$. Note that there are no assumptions on the sign of the entries of A or the components of r. It is possible to show that $\mathbb{R}^n_+$ is a forward invariant set for (18); see, for example Theorem 3 in [1] and also the section 2.3 of this paper for a more general result on forward invariance of $\mathbb{R}^n_+$ of I/O Lotka-Volterra systems. Hereafter, we will therefore assume that initial conditions are restricted to $\mathbb{R}^n_+$. The following result characterizes *uniformly bounded* Lotka-Volterra systems [9]. Recall that a Lotka-Volterra system is uniformly bounded if there exists a compact, absorbing set $K \subset \mathbb{R}^n_+$; that is, for all $x_0 \in \mathbb{R}^n_+$, there is a $T(x_0) \geq 0$ such that $x(t, x_0) \in K$ for all $t \geq T(x_0)$. Below we use the notation $\mathrm{int}(\mathbb{R}^n_+)$ for the interior points of $\mathbb{R}^n_+$ (i.e., those vectors in $\mathbb{R}^n_+$ having only strictly positive components).

LEMMA 2.1. *System* (18) *is uniformly bounded if and only if*

$$\exists\, c \in \operatorname{int}(\mathbb{R}^n_+) :\ -Ac \in \operatorname{int}(\mathbb{R}^n_+), \tag{19}$$

and every principal sub-matrix of A has the same property ([8, p.188, Exercise 15.2.7]).

Matrices satisfying condition (19) are known as B-matrices.

We will now restrict our attention to Lotka-Volterra systems with an interaction matrix A, which is Metzler. But first we collect some well-known facts about the stability of Metzler matrices (see [9]). They are consequences of the Perron-Frobenius theorem, see, for instance [13, 9].

LEMMA 2.2. *A Metzler matrix is stable if and only if it is diagonally dominant* ([8, p.181, Exercise 15.1.1])*, that is,*

$$\exists\, d \in \operatorname{int}(\mathbb{R}^n_+) :\ -Ad \in \operatorname{int}(\mathbb{R}^n_+). \tag{20}$$

If A is a stable Metzler matrix, then (20) *obviously also holds for every principal submatrix of A, implying that every principal submatrix of A is also stable. In other words, a Metzler matrix is stable if and only if it is a* B*-matrix.*

The following result is an immediate application of results in [16, 9, 8]. The support set of $x \in \mathbb{R}^n_+$ is defined as $\operatorname{supp}(x) := \{y \in \mathbb{R}^n_+ |\ y_i > 0 \text{ if } x_i > 0\}$.

LEMMA 2.3. *If A is a stable Metzler matrix, then System* (18) *possesses a unique equilibrium point $\bar{x}$ that is globally asymptotically stable with respect to initial conditions in its support set* $\operatorname{supp}(\bar{x})$*. Suppose that x^e is an equilibrium point of* (18)*. Then x^e is globally asymptotically stable with respect to initial conditions in* $\operatorname{supp}(x^e)$ *(and hence $x^e = \bar{x}$) if and only if the following condition is satisfied*)[8, p.191, Exercise 15.3.1])*.:*

$$Ax^e + r \le 0. \tag{21}$$

REMARK 6. *For future reference, we provide an explicit characterization of an arbitrary equilibrium point $x^e \in \mathbb{R}^n_+$ (which is not necessarily $\bar{x}$ from the above lemma) of System* (18) *in the event A is a stable Metzler matrix. If $x^e \in \mathbb{R}^n_+$ is an equilibrium point of System* (18)*, then there exists a partition I, J of the index set $N := \{1, 2, \dots, n\}$ (i.e., $N = I \cup J$ and $I \cap J = \emptyset$, where one of the sets I or J could be empty) such that $x^e_i = 0$ for $i \in I$ and $x^e_j > 0$ for $j \in J$. This implies that for all $j \in J$, the j-th component of the vector $Ax^e + r$ must be zero. Equivalently, denoting the vector (x^e_j), $j \in J$ by x^e_s, there must exist a principal submatrix A_s of A (which is also stable and hence invertible by Lemma* 2.2*) such that*

$$x^e_s = -A_s^{-1} r_s,$$

where r_s is obtained from r by deleting all components r_i with $i \in I$.

We are now in a position to prove a boundedness result for the system of interest (4).

LEMMA 2.4. *The solutions of* System (4) *are uniformly bounded provided* **H** *holds.*

Proof. By Lemma 2.1, it suffices to show that the matrix

$$\tilde{A} = \begin{pmatrix} A & B \\ -C & D \end{pmatrix}$$

is a B matrix or equivalently that $\tilde{A}$ and all its principal submatrices satisfy condition (19). Since A and D are stable Metzler matrices by **H**, it follows from Lemma

2.2 that there exists $d_1 \in \mathrm{int}(\mathbb{R}^k_+)$ and $d_2 \in \mathrm{int}(\mathbb{R}^{(n-k)}_+)$ such that $-Ad_1 \in \mathrm{int}(\mathbb{R}^k_+)$ and $-Dd_2 \in \mathrm{int}(\mathbb{R}^{(n-k)}_+)$. Since $B, C \geq 0$ by **H**, there exists a sufficiently large real number $\alpha > 0$ such that

$$\tilde{A}\begin{pmatrix}\alpha d_1\\ d_2\end{pmatrix} = \begin{pmatrix}A & B\\ -C & D\end{pmatrix}\begin{pmatrix}\alpha d_1\\ d_2\end{pmatrix} \in -\,\mathrm{int}(\mathbb{R}^n_+).$$

Since by Lemma 2.2, the principal submatrices of A and D are also Metzler and stable and therefore also satisfy the diagonally dominance condition (20), the same argument we used to prove that $\tilde{A}$ satisfies (19) can be used to prove that all principal submatrices of $\tilde{A}$ also satisfy (19). This concludes the proof. □

2.3. **Lotka-Volterra systems with inputs.** Consider a classic Lotka-Volterra system subject to an input:

$$\dot{x} = \mathrm{diag}(x)(Ax + r + Bu), \tag{22}$$

where $x \in \mathbb{R}^n$, $u \in U$ is the input. We assume that $U = \mathbb{R}^m_+$ or $U = -\mathbb{R}^m_+$. The input signals $u(.) : \mathbb{R} \to U$ are Lebesgue measurable and locally essentially bounded functions. Note that there is no assumption on the sign of the entries of B or on the components of r. It can be shown that $\mathbb{R}^n_+$ is forward invariant. This follows from an application of Theorem 3 in [1]. To apply this result, we first denote the right-hand side of (22) as $f(x, u)$ and observe that f is locally Lipschitz in x, locally uniformly in u. Secondly, denoting $f_D(x) := \{f(x, u)|\ u \in D\}$, where D is an arbitrary compact subset of U, we need to verify whether

$$\forall x \in \mathbb{R}^n_+ :\ f_D(x) \subset T_x\mathbb{R}^n_+$$

holds, where $T_x\mathbb{R}^n_+$ is the tangent cone to $\mathbb{R}^n_+$ at $x \in \mathbb{R}^n_+$. This cone is defined as follows:

$$T_x\mathbb{R}^n_+ := \{\lim_{h_i \searrow 0} \frac{1}{h_i}(y_i - x)|\ y_i \to x \text{ while } y_i \in \mathbb{R}^n_+ \text{ and } h_i > 0 \text{ as } i \to +\infty\}.$$

This second condition is also easily verified, yielding that $\mathbb{R}^n_+$ is forward invariant for System (22). Hence, hereafter we will always restrict initial conditions to $\mathbb{R}^n_+$.

Lemma 2.5. *If A is a stable Metzler matrix, then* System (22) *possesses a continuous I/S* quasi characteristic $k_x : U \to \mathbb{R}^n_+$.

Proof. Step 1*: Existence of k_x*

This follows immediately from the first part of Lemma 2.3. Denote the stable equilibrium point corresponding to an arbitrary $u \in U$ as $k_x(u)$. Then the set B_u of nonconverging initial conditions is $\mathbb{R}^n_+ \setminus \mathrm{supp}(k_x(u))$, which is a subset of the boundary of $\mathbb{R}^n_+$. Clearly, B_u is of measure zero.

Step 2*: Continuity of k_x*

To prove continuity of k_x it is sufficient to show that k_x is a locally bounded function (i.e., for every compact set $C \subset U$, $k_x(C)$ is a bounded set) and that the graph of k_x is a closed set. By Lemma 2.3 and Remark 6 we know that for every $u \in U$, there is a unique equilibrium point $k_x(u)$ for which the vector $[k_x(u)]_s$ of nonzero components can be explicitly characterized as

$$[k_x(u)]_s = -A_s^{-1}(u)(r_s(u) + [Bu]_s),$$

where $r_s(u)$ and $[Bu]_s$ are obtained from r and Bu, respectively, by deleting those components corresponding to zero components of $k_x(u)$. Note the explicit dependence of A_s, r_s, and $[Bu]_s$ on u. Local boundedness of $k_x(u)$ will follow from the following chain of (in)equalities, where $|.|$ denotes any norm on $\mathbb{R}^n$ (or on a lower dimensional space $\mathbb{R}^l$ with $l < n$) and $||.||$ stands for its associated matrix norm:

$$\begin{aligned}
|k_x(u)| &= |[k_x(u)]_s| \\
&= \left|-A_s^{-1}(u) \,.\, (r_s(u) + [Bu]_s)\right| \\
&\leq \left|\left|-A_s^{-1}(u)\right|\right| \,.\, (|r_s(u)| + |[Bu]_s|) \\
&\leq \left|\left|\int_0^\infty \mathrm{e}^{A_s(u)t} \; dt \right|\right| \,.\, (|r| + |Bu|) \\
&\leq \int_0^\infty \left|\left|\mathrm{e}^{A_s(u)t}\right|\right| \; dt \,.\, (|r| + ||B|| \,.\, |u|) \\
&\leq \int_0^\infty M_s \, \mathrm{e}^{\lambda_F(A_s(u))t} \, dt \,.\, (|r| + ||B|| \,.\, |u|) \\
&\leq \frac{M_s}{-\lambda_F(A_s(u))} \,.\, (|r| + ||B|| \,.\, |u|) \\
&\leq \frac{M}{-\lambda_F(A)} \,.\, (|r| + ||B|| \,.\, |u|)\,,
\end{aligned}$$

where we denoted the dominating Perron-Frobenius eigenvalue of a Metzler matrix P (see [4]), by $\lambda_F(P)$, $M := \max(M_s)$ (see item 2 below for the definition of M_s; note that $\max(M_s)$ exists since there are only a finite number of principal submatrices and hence only a finite number of M_s's) and we used the following facts:

1. In the fourth step, we used the identity $-P^{-1} = \int_0^\infty \mathrm{e}^{Pt}\, dt$ for any stable matrix P and the fact that all principal submatrices of a stable Metzler matrix are stable; see Lemma 2.3. (This last fact is also used in the seventh step when performing the integration.)
2. For any Metzler matrix P_s, $||\,\mathrm{e}^{P_s t}\,|| \leq M_s \, \mathrm{e}^{\lambda_F(P_s)t}$ for some constant $M_s > 0$ in the sixth step.
3. $\lambda_F(P_s) \leq \lambda_F(P)$ for any principal submatrix P_s of a Metzler matrix P (this follows from an immediate application of Corollary 1.6 in [4]) in the last step.

Next, we will prove that:

$$\mathrm{graph}(k_x) := \{(u, x) \in U \times \mathbb{R}^n_+ | x = k_x(u)\}$$

is a closed set in the topology $U \times \mathbb{R}^n_+$ (recall that $U = \mathbb{R}^m_+$ or $U = -\mathbb{R}^m_+$).

Define:

$$V := \{(u, y) \in U \times \mathbb{R}^n_+ | Ay + r + Bu \leq 0 \text{ and } y^T(Ay + r + Bu) = 0\},$$

Clearly V is a closed set with respect to the subspace topology. Now it follows from Lemma 2.3 and the particular form of (22) that $\mathrm{graph}(k_x) = V$, so $\mathrm{graph}(k_x)$ is also closed, thus concluding the proof. □

2.4. **Global asymptotic stability of fixed points of scalar non-increasing maps.** In this section, we collect some results for checking global asymptotic stability of fixed points of discrete-time systems satisfying a particular condition.

Consider the following scalar discrete-time system:

$$x_{k+1} = g(x_k), \tag{23}$$

for some given map $g : \mathbb{R}_+ \to \mathbb{R}_+$. At this point, we make no continuity or smoothness assumptions for g. Our main assumption regarding System (23) will be the following:

M: g is nonincreasing that is, $x_1 \leq x_2 \Rightarrow g(x_1) \geq g(x_2)$.

A *nontrivial two-periodic point* of System (23) is a number $a \in \mathbb{R}_+$ such that $g(a) = b$, for some $b \in \mathbb{R}_+$ with $b \neq a$, and $g(b) = a$. For every integer $i > 1$, we denote $g \circ g \circ ... \circ g$ (g appears i times in this composition) as g^i. Although the following facts are known, it is hard to give a reference for their proofs. Therefore, we include them in the appendix.

Lemma 2.6. 1. *Suppose that* **M** *holds. Then for each* $x_0 \in \mathbb{R}_+$, *there exist* $y^1, y^2 \in \mathbb{R}_+$ *such that*

$$g^{2n}(x_0) \to y^1 \quad \text{and} \quad g^{2n+1}(x_0) \to y^2$$

as $n \to +\infty$, *and both convergences are monotonic.*

2. *Suppose that* **M** *holds and that* g *is continuous. Then* $g(y^1) = y^2$ *and* $g(y^2) = y^1$, *so both* y^1 *and* y^2 *are fixed points of* g^2. *If* g^2 *has a unique fixed point* y, *then* y *is a globally asymptotically stable fixed point for System* (23).
3. *Suppose that* **M** *holds and that* g *is continuous. Then System* (23) *possesses a unique fixed point* $\bar{x} \in \mathbb{R}_+$. *Moreover,* $\bar{x}$ *is globally asymptotically stable if and only if the map* g *does not possess nontrivial two-periodic points.*

Proof. See appendix. □

The next result provides an obvious condition to prove global asymptotic stability of a fixed point of System (23). Note that once more we do not impose any continuity or smoothness assumption on g.

Lemma 2.7. *Suppose that* $\bar{x}$ *is a fixed point of System* (23) *in* $\mathbb{R}_+$. *If there exists an* $\alpha \in (0,\, 1)$ *such that for all* $x \in \mathbb{R}_+$ *with* $x \neq \bar{x}$

$$|\, g(x) - \bar{x} \,| \;\leq\; \alpha \,|\, x - \bar{x} \,|, \tag{24}$$

then $\bar{x}$ *is globally asymptotically stable.*

Proof. The proof follows from a standard contraction mapping argument: condition (24) is equivalent to $|g^k(x) - \bar{x}| \leq \alpha^k |x - \bar{x}|$ for all $x \in \mathbb{R}_+$ and all integers $k > 1$. Now $\alpha < 1$ implies that $\lim_{k\to\infty} g^k(x) = \bar{x}$. (Local) stability is also obvious. □

3. Main results.

Recall the system of interest:

$$\begin{pmatrix} \dot{x} \\ \dot{z} \end{pmatrix} = \text{diag}(x, z) \left(\begin{pmatrix} A & B \\ -C & D \end{pmatrix} \begin{pmatrix} x \\ z \end{pmatrix} + \begin{pmatrix} r_1 \\ r_2 \end{pmatrix} \right), \tag{25}$$

where $x \in \mathbb{R}^k_+$ and $z \in \mathbb{R}^{(n-k)}_+$ and for which **H** is assumed to hold. Also recall that System (25) can be written as the feedback interconnection of two systems:

$$\dot{z} \;=\; \text{diag}(z)(Dz + r_2 + Cu),\; w = z \tag{26}$$

$$\dot{x} \;=\; \text{diag}(x)(Ax + r_1 + Bv),\; y = x \tag{27}$$

$$v \;=\; w \tag{28}$$

$$u \;=\; -y, \tag{29}$$

where $u \in -\mathbb{R}^k_+$ and $v \in \mathbb{R}^{(n-k)}_+$. It is clear that the input spaces, $-\mathbb{R}^k_+$ and $\mathbb{R}^{(n-k)}_+$, and the output spaces, $\mathbb{R}^{(n-k)}_+$ and $\mathbb{R}^k_+$, are closed lattices. We summarize some of the properties of this feedback system:

1. Following [1], the I/O system (26) is monotone in the state $z \in \mathbb{R}_+^{(n-k)}$, with the input and the output $u \in -\mathbb{R}_+^n$ and $w \in \mathbb{R}_+^{(n-k)}$, respectively (recall that the orders are the usual partial orders $\preceq$ on the respective spaces); note that the output function is merely the identity on $\mathbb{R}_+^{(n-k)}$. Similarly, the I/O system (27) is monotone in the state $x \in \mathbb{R}_+^k$, with the input and the output $v \in \mathbb{R}_+^{(n-k)}$ and $y \in \mathbb{R}_+^k$, respectively; here, the output function is also the identity on $\mathbb{R}_+^k$.
2. By Lemma 2.5, the I/O systems (26) and (27) possess *continuous I/S quasi characteristics* k_z and k_x resepctively (and I/O quasi characteristics $k_w \equiv k_z$ and $k_y \equiv k_x$, respectively).
3. By Lemma 2.4, the solutions of System (25) are bounded (in fact, they are uniformly bounded).

Next, we state and prove the main result of this paper.

THEOREM 3.1. *If* **H** *holds, then System* (25) *possesses an almost globally attracting equilibrium point* $(\bar{x}, \bar{z}) \in \mathbb{R}_+^n$, *provided that the discrete-time system*

$$u_{k+1} = -(k_y \circ k_w)(u_k), \tag{30}$$

which is defined on $-\mathbb{R}_+^k$, *possesses a globally attracting fixed point* $\bar{u}$. *In that case* $(\bar{x}, \bar{z}) = ((k_x \circ k_w)(\bar{u}), k_z(\bar{u}))$.

Proof. The theorem is proved if the conditions of Theorem 2.1 are verified. We have already shown that the first three conditions (monotonicity, existence of continuous I/S and I/O quasi characteristics, and boundedness of solutions) and the small-gain condition are satisfied. The latter holds because of the assumption that (30) possesses a globally attracting fixed point $\bar{u} \in -\mathbb{R}_+^k$. □

REMARK 7. *Although this is not apparent from the above proof, it can be shown that under the conditions of Theorem* 3.1 *the zero-measure set of nonconvergent initial conditions of System* (25) *is (a subset of) the boundary of* $\mathbb{R}_+^n$. *This also implies that all solutions initiated in the interior of* $\mathbb{R}_+^n$ *converge to the equilibrium point* $(\bar{x}, \bar{z})$. *We refer to* [2] *for more on this.*

REMARK 8. *Note that no (local) stability information is provided by Theorem* 3.1, *as only a convergence result is given. However, we shall illustrate below that the small-gain condition in Theorem* 3.1 *may imply local stability of the equilibrium point, by simply checking the stability properties of the linearization at the equilibrium point.*

Of course it is in general very hard to determine whether the discrete-time system (30) possesses a globally attracting fixed point. Under an extra, fairly natural condition for System (25), this task may be simplified, as we will see below. This condition is the following rank condition:

$$\mathbf{R}\text{: Rank } (B) = \text{Rank } (C) = 1.$$

The biological interpretation of condition **R** is that there is neither prey-selection by predators nor does it matter to a prey species by which predator its individuals are eaten.

If **H** and **R**, hold then there exist nonzero vectors $b, \gamma \in \mathbb{R}_+^k$ and $c, \beta \in \mathbb{R}_+^{(n-k)}$ such that $B = b\beta^T$ and $C = c\gamma^T$. (Note that these vectors are not unique since scalar multiples can be found satisfying the same conditions.) It follows that System

(25) can be written as the following feedback interconnection:

$$\begin{aligned} \dot{z} &= \mathrm{diag}(z)(Dz + r_2 + cu),\, w = \beta^T z & (31)\\ \dot{x} &= \mathrm{diag}(x)(Ax + r_1 + bv),\, y = \gamma^T x & (32)\\ v &= w & (33)\\ u &= -y, & (34)\end{aligned}$$

where $u \in -\mathbb{R}_+$ and $v \in \mathbb{R}_+$. As before, the I/O systems (31) and (32) are monotone and possess continuous I/S and I/O quasi characteristics k_z, k_x and $k_w \equiv \beta^T k_z$, $k_y \equiv \gamma^T k_x$ and boundedness of solutions is immediate from lemma 2.4. Another straightforward application of theorem 2.1 yields the following corollary.

Corollary 3.1. *If* **H** *and* **R** *hold, then System* (25)*, or equivalently the feedback System* (31)-(34)*, possesses an almost globally attracting equilibrium point* $(\bar{x}, \bar{z}) \in \mathbb{R}^n_+$*, provided that the scalar discrete-time system*

$$u_{k+1} = -(k_y \circ k_w)(u_k), \tag{35}$$

which is defined on $-\mathbb{R}_+$*, possesses a globally attracting fixed point* $\bar{u}$*. In that case,* $(\bar{x}, \bar{z}) = ((k_x \circ \beta^T k_z)(\bar{u}), k_z(\bar{u}))$.

Remark 9. *Notice that the small-gain condition in Corollary* 3.1 *is equivalent to the following small-gain condition:*

The scalar discrete-time system

$$\tilde{u}_{k+1} = (k_y \circ k_w)(-\tilde{u}_k) := g(\tilde{u}_k), \tag{36}$$

which is defined on $\mathbb{R}_+$*, possesses a globally attracting fixed point* $\bar{\tilde{u}}$.

This equivalence follows immediately from the coordinate transformation $\tilde{u}_k = -u_k$*. Observe that* $g : \mathbb{R}_+ \to \mathbb{R}_+$ *is a scalar and continuous map since* k_y *and* k_w *are continuous by Lemma* 2.5*. Also, Remark* 5 *implies that* k_w *and* k_y *are monotone and that* g *is thus non-increasing (or, equivalently, satisfies* **M***). But then Lemma* 2.6*, part* 3*, and Lemma* 2.7 *can be used to verify whether the small-gain condition for System* (36)*, or equivalently for System* (35)*, is satisfied. This may lead to the simplification presented in Corollary* 3.1 *as we will illustrate below on both examples from the introduction.*

Remark 10. *Both remarks following Theorem* 3.1 *apply to Corollary* 3.1 *as well.*

Example 1 *(continued)*

Define $b = (1\ 0)^T$, $\beta = 1$, $c = k$, and $\gamma = (0\ 1)^T$, and rewrite System (2) from Example 1 in the form (31)-(34). Using the characterization (21) in Lemma 2.3, the I/O quasi characteristics k_w and k_y are computable, yielding the following explicit form for System (36):

$$\tilde{u}_{k+1} = \begin{cases} (-\frac{k}{3})\tilde{u}_k + (1 + \frac{k}{3}) \text{ for } \tilde{u}_k \in [0,\, 1 + \frac{3}{2k}] \\ \frac{1}{2} \text{ for } \tilde{u}_k > \frac{3}{2k}. \end{cases} \tag{37}$$

Since $k > 0$, it is easily verified that the conditions of part 3 of Lemma 2.6 are satisfied, and thus System (37) possesses a fixed point $\bar{\tilde{u}}$. It is easily checked that $\bar{\tilde{u}} \in (0,\, 1 + \frac{3}{2k})$. Choosing $\alpha > 0$ as

$$\alpha = \frac{k}{3} < 1, \tag{38}$$

we see that the conditions of Lemma 2.7 are satisfied. Notice that condition (38) is very close to a necessary condition for global asymptotic stability of $\bar{\tilde{u}}$. Indeed, if

$\frac{k}{3} > 1$, then $\bar{\tilde{u}}$ is (locally) unstable. Corollary 3.1 implies that System (2) possesses an almost globally attracting equilibrium point at $(1,1,1)^T$, if condition (38) holds. Of course, the small-gain condition (38) also yields that the equilibrium point is locally stable, by recalling from Example 1 that $(1,1,1)^T$ is locally asymptotically stable if $0 < k < k_c = 57$. Remark 7 implies that the domain of attraction of $(1,1,1)^T$ contains the interior of $\mathbb{R}^3_+$. In fact, the interior of $\mathbb{R}^3_+$ *is* the domain of attraction, since it is not difficult to see that the boundary of $\mathbb{R}^3_+$ is an invariant set for System (3). Finally, note that the small-gain condition (38) is very strong compared to the local stability condition $k < 57$. However, as we have shown, it guarantees the much stronger property of *almost global asymptotic stability.*

Example 2 *(continued)*

Define $b = (1/2\ 1)^T$, $\beta = 1$, $c = k$, and $\gamma = (1\ 1/2)^T$, and rewrite System (3) from Example 2 in the form (31)-(34). The I/O quasi characteristics k_w and k_y are computable using the characterization (21) in Lemma 2.3 and yield the following explicit form for System (36):

$$\tilde{u}_{k+1} = \begin{cases} (-\frac{5}{3}k)\tilde{u}_k + \frac{5k+3}{2} \text{ for } \tilde{u}_k \in I_1 := [0, \frac{3}{2} + \frac{2}{3k}] \\ (-\frac{1}{6}k)\tilde{u}_k + \frac{k+2}{4} \text{ for } \tilde{u}_k \in I_2 := (\frac{3}{2} + \frac{2}{3k}, \frac{3}{2}(1+\frac{1}{k})] \\ \frac{1}{4} \text{ for } \tilde{u}_k \in I_3 := (\frac{3}{2}(1+\frac{1}{k}), +\infty). \end{cases} \tag{39}$$

Since $k > 0$, it is easily verified that the conditions of part 3 of Lemma 2.6 are satisfied and thus System (37) possesses a fixed point $\bar{\tilde{u}}$. It is easily checked that $\bar{\tilde{u}} \in (0, \frac{3}{2} + \frac{2}{3k})$. Choosing $\alpha > 0$ as:

$$\alpha = \frac{5}{3}k < 1, \tag{40}$$

we see that the conditions of Lemma 2.7 are satisfied since the slope of g on the interval I_1 equals $-5k/3$, which is smaller than the slopes of g on the intervals I_2 and I_3 that equal $-k/6$ and 0, respectively. Notice that condition (40) is very close to a necessary condition for global asymptotic stability of $\bar{\tilde{u}}$. Indeed, if $\frac{5}{3}k > 1$, then $\bar{\tilde{u}}$ is (locally) unstable. Now it follows from Corollary 3.1 that System (3) possesses an almost globally attracting equilibrium point at $(1,1,1)^T$, provided condition (40) holds. Obviously, this small-gain condition (40) also yields that this equilibrium point is locally stable. Recall from Example 2 that an application of the Routh-Hurwitz criterion showed that $(1,1,1)^T$ is locally asymptotically stable if $0 < k < k_c = 105/2$. Remark 7 implies that the domain of attraction of $(1,1,1)^T$ contains the interior of $\mathbb{R}^3_+$. In fact, the interior of $\mathbb{R}^3_+$ *is* the domain of attraction, since the boundary of $\mathbb{R}^3_+$ is easily seen to be an invariant set for System (3). Note that the small-gain condition (40) is very strong compared to the local stability condition $k < 105/2$. However, as we have shown, it guarantees the much stronger property of *almost global asymptotic stability.*

Finally, we performed a few simulations to see what happens for k-values in the interval $(3/5, 105/2)$. Using Mathematica, the solutions corresponding to initial condition $x(0) = (0.1, 0.1, 0.1)^T$ are plotted for two different k-values in Figures 3 and 4. It appears that the solutions converge in an oscillatory manner to the equilibrium point $(1,1,1)^T$. This might indicate that for intermediate k-values, the equilibrium point $(1,1,1)^T$ is also almost globally asymptotically stable.

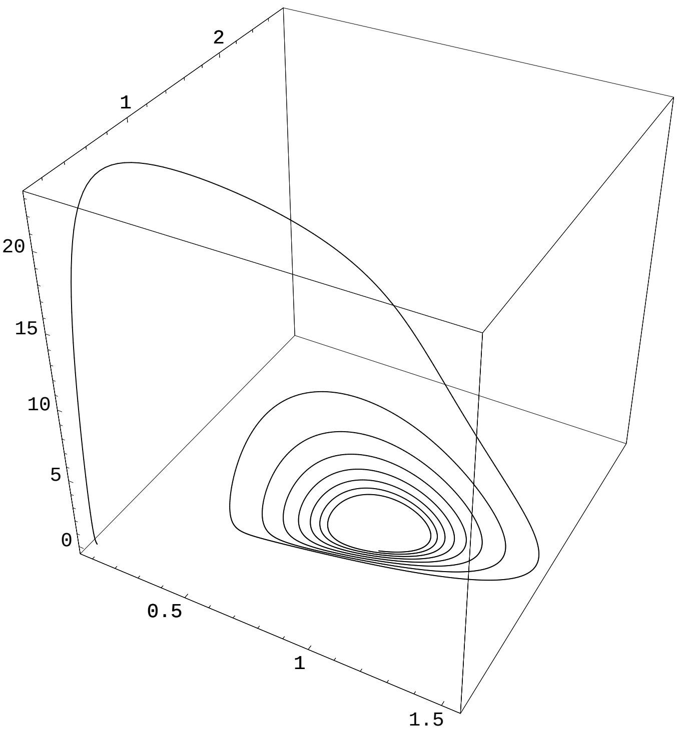

FIGURE 3. Solution for $k = 30$. (initial condition $(0.1, 0.1, 0.1)$, integration over [0,90])

4. Appendix: Proof of Lemma 2.6.

1. Let $p(x) := g^2(x)$. Note that p, and therefore every power p^n is nondecreasing. Consider the sequence $x_n := p^n(x_0) = g^{2n}(x_0)$. Since p is bounded (because $p(x) = g(g(x)) \leq g(0)$), the sequence $\{x_n\}$ is bounded. If $x_0 \leq x_1$, then $x_n = p^n(x_0) \leq p^n(x_1) = x_{n+1}$. If $x_0 \geq x_1$, then $x_n = p^n(x_0) \geq p^n(x_1) = x_{n+1}$. Therefore, the sequence $\{x_n\}$ is monotonic. Thus $x_n \to y^1$ for some y^1.

   The same argument applies to the sequence $z_n := p^n(z_0) = g^{2n+1}(x_0)$, where we defined $z_0 := g(x_0)$, resulting in $z_n \to y^2$.
2. If g is continuous, then $g^{2n}(x_0) \to y^1$ implies $g^{2n+1}(x_0) = g(g^{2n}(x_0)) \to g(y^1)$, so $y^2 = g(y^1)$, and a similar argument shows that $g(y^2) = y^1$. This implies that $g^2(y^i) = y^i$, for $i = 1, 2$.

   Thus, if y is the unique fixed point of g^2, necessarily $y^1(x_0) = y^2(x_0) = y$, for all x_0, which means that $p^n(x_0) \to y$, for all x_0. This in turn implies that y is a globally attracting fixed point of System (23).

   To prove stability of y, consider any interval of the form $[a, b]$ with $a \leq y \leq b$. If $p(a) < a$, then monotonicity of $\{p^n(a)\}$ would imply that $p^n(a)$ converges to a limit l satisfying $l < a$, which contradicts that $a \leq y$, so $p(a) \geq a$. Similarly, $p(b) \leq b$, implying that the interval $[a, b]$ is forward invariant under p since p is non-increasing. Next, consider the interval $[g(b), g(a)]$, which contains $g(y) = y$; for the same reasons, this interval is forward invariant under p. Therefore, $[A, B]$ is forward invariant under g, where $A = \min\{a, g(b)\}$ and $B = \max\{b, g(a)\}$. This proves stability of the fixed point y of System (23).

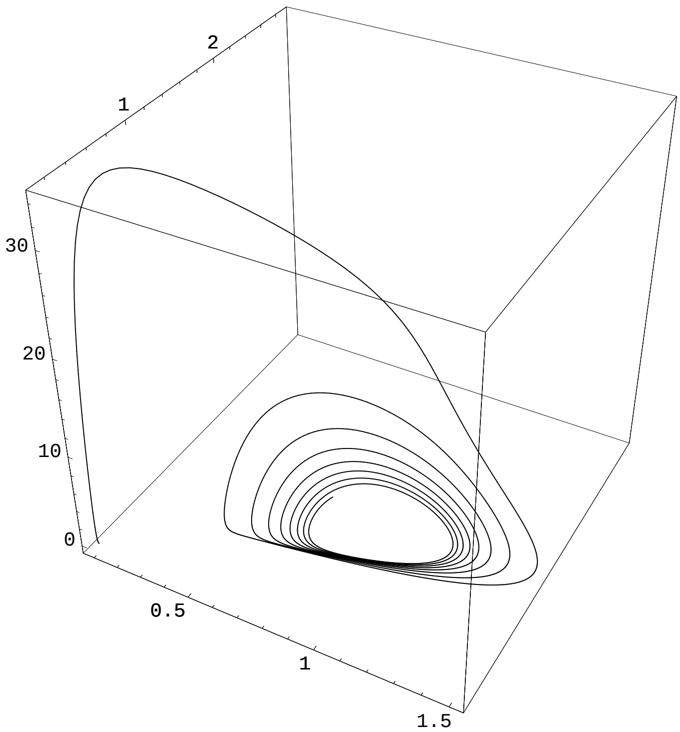

FIGURE 4. Solution for $k = 46$. (initial condition $(0.1, 0.1, 0.1)$, integration over [0,90])

3. *Existence and uniqueness of a fixed point*
   Existence of a fixed point follows from an application of the intermediate-value theorem to the (continuous) function $g(x) - x$, which is restricted to the closed interval $[0, g(0)]$ and relies on the fact that g is nonincreasing. We will denote the unique fixed point by $\bar{x}$.
   Global asymptotic stability of $\bar{x}$
   Necessity of the nonexistence of nontrivial two-periodic points is obvious. To prove sufficiency, note that if there are no nontrivial two-periodic points for g, then the map g^2 possesses only one fixed point $\bar{x}$. The result now follows from the previous item.

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