Small-gain theorems for predator-prey systems

Patrick De Leenheer[1], David Angeli[2], and Eduardo D. Sontag[3]

[1] Department of Mathematics and Statistics, Arizona State University, Tempe, AZ 85287, USA leenheer@math.la.asu.edu
[2] Dip. di Sistemi e Informatica Universitá di Firenze, Via di S. Marta 3, 50139 Firenze, Italy, angeli@dsi.unifi.it
[3] Department of Mathematics, Rutgers University, New Brunswick, NJ 08903, USA http://www.math.rutgers.edu/~ sontag, sontag@control.rutgers.edu

Abstract. We present a global stability result for Lotka-Volterra systems of the predator-prey type. It turns out that these systems can be interpreted as feedback interconnections of two monotone control systems possessing particular input-output properties. The proof is based on a small-gain theorem, adapted to a setting of systems with multiple equilibrium points. Our main result provides a sufficient condition to rule out oscillatory behavior which often occurs in predator-prey systems.

1 Introduction

Predator-prey systems have been -and still are- attracting a lot of attention [6, 11, 8] since the early work of Lotka and Volterra. It is well-known that these systems may exhibit oscillatory behavior, the best known example being the classical Lotka-Volterra predator-prey system, see e.g. [6, 7], defined by

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

where x and z denote the predator, respectively the prey concentrations 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. It is also well-known that this system is not structurally stable and perturbations in the coefficients destroy this qualitative picture.

However, structurally stable predator-prey systems with isolated periodic solutions can be found as well. One example (which is still low-dimensional but not of the Lotka-Volterra type) is Gause's model [7] which admits isolated periodic solutions under suitable conditions [8]. Oscillatory behavior is possible for systems in the class of Lotka-Volterra predator-prey systems, but then the number of predator and prey species is necessarily greater than two. To illustrate this we provide an example with 2 predator species and 1 prey species. We also assume that the predator species are *mutualistic* [7], which is the case for instance if the predator population is stage-structured. (e.g. consisting of young and adults)

Example

Consider the parameterized (parameter $k > 0$) Lotka-Volterra predator-prey system with 2 predator species x_1 and x_2 and 1 prey species z :

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

One could interpret x_1 as the immature and x_2 as the mature predators.

For every $k > 0$ there is a nontrivial equilibrium point at $(1,1,1)$ and the Routh-Hurwitz criterion reveals that it 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 1 stable (and hence real) eigenvalue and 2 unstable eigenvalues. It can be shown that for $k - k_c > 0$ but small, the unstable eigenvalues must be complex conjugate with nontrivial imaginary part. In [4] we have shown that a supercritical Hopf bifurcation occurs a at the critical value k_c.

The example suggests that oscillatory behavior is to be expected in the following Lotka-Volterra predator-prey system:

$$\begin{pmatrix} \dot{x} \\ \cdots \\ \dot{z} \end{pmatrix} = \mathrm{diag}(x, z)(\begin{pmatrix} A & \vdots & B \\ \cdots & \cdots & \cdots \\ -C & \vdots & D \end{pmatrix} \begin{pmatrix} x \\ \cdots \\ z \end{pmatrix} + \begin{pmatrix} r_1 \\ \cdots \\ r_2 \end{pmatrix}) \tag{2}$$

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

H: For system (2), A and D are Metzler and stable and $B, C \geq 0$

where the inequalities on the matrices B and C should be interpreted entry-wise. (A matrix is a Metzler matrix if its off-diagonal entries are non-negative and stable if it only has eigenvalues with negative real part.) The given example satisfies this assumption.

Here we consider whether oscillations or more complicated behavior of system (2) can be ruled out.

To system (2) one can associate two Input/Output (I/O) systems:

$$\dot{z} = \mathrm{diag}(z)(Dz + r_2 + Cu(t)), \quad w = z \tag{3}$$

and

$$\dot{x} = \mathrm{diag}(x)(Ax + r_1 + Bv(t)), \quad y = x \tag{4}$$

where $u(t)$ is a (component-wise) non-positive and $v(t)$ a (component-wise) non-negative input signal and w and y are output signals. These I/O-systems are *monotone* in the sense of [1] (a precise definition of such systems is given later). To each I/O system we associate an *I/O quasi-characteristics* k_w, respectively k_y (see Definition 2). This is a mapping between the input and output space capturing the ability of an I/O system to convert a constant input in a converging output with a limit which is (almost) independent of initial conditions. The I/O quasi-characteristic assigns to every input its corresponding output limit.

Notice that system (2) is a *negative feedback interconnection* of system (3) and system (4) by setting:

$$v = w, \ u = -y. \tag{5}$$

This allows the use of results from theories on interconnected control systems -in particular small-gain theorems- to prove global stability. Our main result can informally be stated as follows:

Theorem 1. *The feedback system* (3), (4) *and* (5) *possesses an (almost) globally attractive equilibrium point provided the discrete-time system*

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

possesses a globally attractive fixed point.

Our results illustrate a recently developed theory for monotone control systems [1, 2].

Important note: Due to space constraints we leave out all proofs. They can be found in an extended version of this paper; see [4].

2 Preliminaries

First we will review a small-gain theorem which applies to a particular class of I/O systems.

Consider the following I/O system:

$$\dot{x} = f(x, u), \ \ y = h(x) \tag{6}$$

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 g are smooth (say continuously differentiable) and that the input signals $u(t) : \mathbb{R} \to U$ are Lebesgue measurable functions and locally essentially bounded. Solutions are then defined and unique and we denote the solution with initial state $x_0 \in \mathbb{R}^n$ and input signal $u(.)$ by $x(t, x_0, u(.))$, $t \in \mathcal{I}$ where $\mathcal{I}$ is the maximal interval of existence. We will also assume that a forward invariant set $X \subset \mathbb{R}^n$ is given, meaning that for all inputs $u(.)$ and for every $x_0 \in X$ it holds that $x(t, x_0, u(.)) \in X$, for all $t \in \mathcal{I} \cap \mathbb{R}_+$. Initial conditions shall be restricted to the X in the sequel.

The usual partial order on $\mathbb{R}^n$, denoted by $\preceq$, is to be understood component-wise, i.e. $x \preceq y$ means that $x_i \leq y_i$ for $i = 1, ..., n$. As a subset of $\mathbb{R}^n$ ($\mathbb{R}^m$, $\mathbb{R}^p$), the state space X (input space U, output space Y) inherits its partial order. Similarly, the set of input signals then also has a (obvious) partial order: $u(.) \preceq v(.)$ if $u(t) \preceq v(t)$ for almost all $t \geq 0$. Next we define the concept of a monotone I/O system.

Definition 1. *The I/O system* (6) *is monotone if the following conditions hold:*

$$x_1 \preceq x_2,\ u(.) \preceq v(.) \Rightarrow x(t, x_1, u(.)) \preceq x(t, x_2, v(.)),\ \forall\, t \in (\mathcal{I}_1 \cap \mathcal{I}_2) \cap \mathbb{R}_+. \quad (7)$$

and

$$x_1 \preceq x_2 \Rightarrow h(x_1) \preceq h(x_2). \quad (8)$$

A key role in our main result is played by the following concept.

Definition 2. *Assume that X has positive measure. System* (6) *has 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 $u(.)$), there is a zero-measure set $\mathcal{B}_u$ such that:*

$$\lim_{t \to +\infty} x(t, x_0, u) = k_x(u),\ \forall\, x_0 \in X \setminus \mathcal{B}_u. \quad (9)$$

If system (6) *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 $k_y := h \circ k_x$.*

The following result can be found in [2]. A system possesses an *almost globally attractive equilibrium point* if it has an equilibrium point that attracts all solutions not initiated in a set of measure zero. If in addition, this equilibrium point is stable, we call it *almost globally asymptotically stable.*

Theorem 2. *Consider two I/O systems:*

$$\dot{x}_1 = f_1(x_1, u_1), \quad y_1 = h_1(x_1) \quad (10)$$
$$\dot{x}_2 = f_2(x_2, u_2), \quad y_2 = h_2(x_2) \quad (11)$$

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 $i = 1, 2$. Assume that $Y_1 = U_2$ and $Y_2 = -U_1$ and that these systems are connected via a negative feedback loop:

$$u_2 = y_1,\ u_1 = -y_2. \quad (12)$$

Suppose that:

1. *Systems* (10) *and* (11) *are monotone I/O systems.*
2. *Systems* (10) *and* (11) *have continuous I/S quasi-characteristics k_{x_1} and k_{x_2} respectively (and also I/O quasi-characteristics k_{y_1} and k_{y_2}).*
3. *The forward solutions of the full system* (10) $-$ (12) *are bounded.*

If the following discrete-time system, defined on U_1*:*

$$u_{k+1} = -(k_{y_2} \circ k_{y_1})(u_k) \tag{13}$$

possesses a globally attractive fixed point $\bar{u} \in U_1$*, then the full system has an almost globally attractive equilibrium point* $(\bar{x}_1, \bar{x}_2) \in X_1 \times X_2$ *and is such that* $(\bar{x}_1, \bar{x}_2) = (k_{x_1}(\bar{u}), (k_{x_2} \circ k_{y_1})(\bar{u}))$.

This result is called a *small-gain theorem* and the last condition will be referred to as a *small-gain condition.*

Next we specialize to (autonomous) Lotka-Volterra systems and provide a boundedness and a stability result.

Consider the classical Lotka-Volterra system:

$$\dot{x} = \mathrm{diag}(x)(Ax + r) \tag{14}$$

where $x \in \mathbb{R}^n$ and $r \in \mathbb{R}^n$. It is well-known that $\mathbb{R}^n_+$ is a forward invariant set for (14) and thus we always assume that initial conditions are restricted to $\mathbb{R}^n_+$. Recall that a Lotka-Volterra system is uniformly bounded [7] if there exists a compact, absorbing set $K \subset \mathbb{R}^n_+$, i.e. 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 $\mathbb{R}^n_+$.

Lemma 1. *(Exercise* 15.2.7*, p.*188 *in [7]) System* (14) *is uniformly bounded if and only if*

$$\exists c \in \mathrm{int}(\mathbb{R}^n_+) : \ -Ac \in \mathrm{int}(\mathbb{R}^n_+). \tag{15}$$

and every principal sub-matrix of A *has the same property.*

We will soon specialize to Lotka-Volterra systems with a Metzler interaction matrix A. First we recall some facts about the stability of these matrices [7] which are based on the Perron-Frobenius Theorem [9, 7].

Lemma 2. *(Theorem* 15.1.1*, p.*181 *in [7]) A Metzler matrix is stable if and only if it is diagonally dominant, i.e.*

$$\exists d \in \mathrm{int}(\mathbb{R}^n_+) : \ -Ad \in \mathrm{int}(\mathbb{R}^n_+). \tag{16}$$

If A *is a stable Metzler matrix then* (16) *holds for every principal sub-matrix of* A *as well, implying that every principal sub-matrix of* A *is stable and thus that system* (14) *is uniformly bounded.*

The following result is an immediate application of results in [10, 7]. The support set of $x \in \mathbb{R}^n_+$ is defined as $\mathrm{supp}(x) := \{y \in \mathbb{R}^n_+ \,|\, y_i > 0 \text{ if } x_i > 0\}$.

Lemma 3. *(Theorem* 15.3.1*, p.*191 *in [7]) If* A *is a stable Metzler matrix, then system* (14) *possesses a unique equilibrium point* $\bar{x}$ *which is globally asymptotically stable with respect to initial conditions in its support set* $\mathrm{supp}(\bar{x})$*. Suppose that* x^e *is an equilibrium point of* (14)*. Then* x^e *is globally asymptotically stable with respect to initial conditions in* $\mathrm{supp}(x^e)$ *(and hence* $x^e = \bar{x}$*) if and only if the following condition is satisfied:*

$$Ax^e + r \leq 0 \tag{17}$$

The previous results allow us to state a boundedness result for system (2).

Lemma 4. *The solutions of system* (2) *are uniformly bounded provided* **H** *holds.*

Now we consider Lotka-Volterra systems with inputs:

$$\dot{x} = \text{diag}(x)(Ax + r + Bu) \tag{18}$$

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. It can be shown that $\mathbb{R}^n_+$ is forward invariant, see [4] and therefore we restrict initial conditions to $\mathbb{R}^n_+$.

Lemma 5. *If A is a stable Metzler matrix, then system* (18) *possesses a continuous I/S quasi-characteristic $k_x : U \to \mathbb{R}^n_+$.*

Finally, we consider a scalar discrete-time system:

$$x_{k+1} = g(x_k) \tag{19}$$

where $g : \mathbb{R}_+ \to \mathbb{R}_+$ is some given, possibly non-smooth map.

Lemma 6. *Suppose that $\bar{x}$ is a fixed point of system* (19) *in $\mathbb{R}_+$. If there exists an $\alpha \in [0,\, 1)$ such that for all $x \in \mathbb{R}_+$ with $x \neq \bar{x}$:*

$$|g(x) - \bar{x}| \;\leq\; \alpha\, |x - \bar{x}| \tag{20}$$

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

3 Main results

We return to the study of system (2) or equivalently, (3) – (5) and summarize some of its properties assuming **H** holds.

1. Following [1], the I/O systems (3) and (4) are *monotone*.
2. The systems (3), (4) have *continuous I/S quasi-characteristics* k_z, respectively k_x (and I/O quasi-characteristics $k_w \equiv k_z$, respectively $k_y \equiv k_x$) by lemma 5.
3. By lemma 4 the solutions of system (2) are uniformly bounded.

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

Theorem 3. *If* **H** *holds, then system* (2) *possesses an almost globally attractive equilibrium point $(\bar{z}, \bar{x}) \in \mathbb{R}^n_+$, provided that the discrete-time system*

$$u_{k+1} = -(k_y \circ k_w)(u_k) \tag{21}$$

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

In general it is hard to determine whether the discrete-time system (21) has a globally attractive fixed point, but easier under the following condition:

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

The biological interpretation is that to a prey species it is irrelevant by which predator its individuals are eaten and, there is no prey-selection by the predator species.

If **H** and **R** hold, one can find nonzero vectors $b, \gamma \in \mathbb{R}_+^k$ and $c, \beta \in \mathbb{R}_+^{(n-k)}$ with $B = b\beta^T$ and $C = c\gamma^T$ and such that system (2) simplifies to:

$$\dot{z} = \text{diag}(z)(Dz + r_2 + cu), \quad w = \beta^T z \tag{22}$$

$$\dot{x} = \text{diag}(x)(Ax + r_1 + bv), \quad y = \gamma^T x \tag{23}$$

$$v = w, \; u = -y \tag{24}$$

where $u \in -\mathbb{R}_+$ and $v \in \mathbb{R}_+$. Then another application of theorem 2 yields:

Corollary 1. *If* **H** *and* **R** *hold, then system* $(22)-(24)$*, possesses an almost globally attractive equilibrium point* $(\bar{z}, \bar{x}) \in \mathbb{R}_+^n$*, if the* **scalar** *discrete-time system*

$$u_{k+1} = -(k_y \circ k_w)(u_k) \tag{25}$$

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

Example (continued)

Defining $b = (1\ 0)^T$, $\beta = 1$, $c = k$ and $\gamma = (0\ 1)^T$, system (1) can be re-written in the form (22)-(24). The characterization (17) in lemma 3 allows to compute the I/O quasi-characteristics k_w and k_y. Then the transformation $\tilde{u}_k = -u_k$, transforms system (25) to:

$$\tilde{u}_{k+1} = \begin{cases} (-\frac{k}{3})\tilde{u}_k + (1 + \frac{k}{3}) \text{ for } \tilde{u}_k \in [0,\, 1 + \frac{3}{2k}] \\ \frac{1}{2} \text{ for } \tilde{u}_k > \frac{3}{2k} \end{cases} \tag{26}$$

It is easy to verify that system (26) has a fixed point $\bar{\tilde{u}}$ in the interval $(0, 1 + \frac{3}{2k})$. If we choose $\alpha > 0$ as follows::

$$\alpha = \frac{k}{3} < 1 \tag{27}$$

the conditions of lemma 6 are satisfied. Note that condition (27) is close to a necessary condition for global asymptotic stability of $\bar{\tilde{u}}$. (indeed, if $\frac{k}{3} > 1$ then $\bar{\tilde{u}}$ is unstable) By corollary 1, we get that system (1) possesses an almost globally attractive equilibrium point at $(1,1,1)^T$ under condition (27). The small-gain condition (27) also yields that the equilibrium point is locally stable by recalling that $(1,1,1)^T$ is locally asymptotically stable if $0 < k < k_c = 57$. It can be shown that the domain of attraction of $(1,1,1)^T$ is the interior of $\mathbb{R}_+^3$, see [4]. Simulations performed in [4], suggest that the equilibrium point remains almost globally asymptotically stable for intermediate k-values (i.e. $k \in (3,\, 57)$).

References

1. D. Angeli and E.D. Sontag, Monotone control systems, arXiv.org math.OC/0206133 and submitted (prelim. version in cdrom proc. 41st CDC, 2002).
2. D. Angeli, P. De Leenheer and E.D. Sontag, A small-gain theorem for almost global convergence of monotone systems, in preparation.
3. A. Berman and R.J. Plemmons, Nonnegative Matrices in the Mathematical Sciences, Academic Press, New York, 1979.
4. P. De Leenheer, D. Angeli and E.D. Sontag, On predator-prey systems and small-gain theorems, submitted.
5. M.W. Hirsch, Systems of differential equations which are competitive or cooperative II: convergence almost everywhere. SIAM J. Math. Anal. 16, 423-439 (1985).
6. M.W. Hirsch and S. Smale, Differential Equations, Dynamical Systems and Linear Algebra, Academic Press, New York, 1974.
7. J. Hofbauer and K. Sigmund, Evolutionary Games and Population Dynamics, Cambridge University Press, Cambridge, 1998.
8. S.B. Hsu, T.B. Hwang and Y. Kuang, Global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system, J. Math. Biol. 42, 489-506 (2001).
9. H.L. Smith, Monotone Dynamical Systems, AMS, Providence, 1995.
10. Y. Takeuchi and N. Adachi, The existence of globally stable equilibria of ecosystems of the generalized Volterra type, J. Math. Biol. 10, 401-415 (1980).
11. Y. Takeuchi and N. Adachi, Oscillations in prey-predator Volterra models. In: H.I. Freedman and C. Strobeck (eds), Population Biology. Lect. Notes in Biomath. 52, Springer-Verlag, Heidelberg, 320-326 (1983).