ON THE LPA MODEL WITH $\mu_a = 1$

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Dedicated to Professor Mustafa R. S. Kulenović on the occasion of his 70th birthday

ABSTRACT. In this article we establish conditions for the local stability of the positive fixed point for the structured population model of Dennis, Desharnais, Cushing, and Costantino (or LPA model) where no adults survive longer than a single time step and when there is a specific one-parameter bifurcation. Also, we study local and global behavior of orbits for which at least one component is equal to zero, and establish conditions for the existence of a curve contained in the union of the coordinate planes which is invariant for the map associated with the model.

1. INTRODUCTION

This article will focus on the behavior of the Larvae/Pupae/Adult (LPA) model, which was first introduced by Dennis, Desharnais, Cushing, and Costantino [4] in 1995. The LPA model is a three-dimensional age-structured population model which describes the interactions, in particular cannibalization, between the life stages of the flour beetle *Tribolium castaneum*. The authors of [4] analyzed and validated the LPA model through laboratory experiments, a feature that is highly desirable for a population model. Indeed, [4] has been cited hundreds of times and spurred further analysis of the model's dynamical behavior over the past two decades, see for example [3], [5], [6], and [8].

The flour beetle has four life stages- egg, larva, pupa, and adult. An individual moves from one life stage to the next over a time span of roughly two weeks. Let $x_1(t)$, $x_2(t)$, and $x_3(t)$ be the number of larvae, pupae, and adults at time step $t \in \mathbb{N}$. The LPA model is given by

$$
\begin{aligned}
x_1(t+1) &= b x_3(t) e^{-c_{el} x_1(t) - c_{ea} x_3(t)} \\
x_2(t+1) &= (1 - \mu_l) x_1(t) \\
x_3(t+1) &= x_2(t) e^{-c_{pa} x_3(t)} + (1 - \mu_a) x_3(t).
\end{aligned}
\tag{1.1}
$$

with $t \geq 0$ and $(x_1(0), x_2(0), x_3(0)) \in \mathbb{R}_+^3 := \{(x_1, x_2, x_3) \colon x_1 \geq 0, x_2 \geq 0, x_3 \geq 0\}$. In equation (1.1), the parameter b represents the average number of viable eggs laid by an adult over a two week time step. It is assumed that cannibalization occurs as a result of random encounters of eggs with larvae and adults and of pupae with adults, which is modeled by Poisson distributions with nonnegative search efficiency parameters c_{el}, c_{ea}, and c_{pa}, respectively. The nonnegative parameters μ_l and μ_a correspond to the mortality rates of the larvae and adults, respectively. The egg population is not explicitly measured since it is assumed that any surviving eggs laid by adults during a time step will have hatched into larvae by the next time step.

In population models, the *net reproduction number* (or *net reproductive rate*) R is the average number of female offspring that a single female has in her lifetime [7]. The critical value $R = 1$ is the bifurcation value at which the origin loses its stability, i.e. the threshold value between persistence or extinction of the populations. For the LPA model, the net reproduction number is given by

$$R = \frac{b\,(1 - \mu_l)}{\mu_a}. \tag{1.2}$$

Next we present a synopsis, taken from [3], of some known facts about the dynamical behavior of system (1.1) (see [2] and [3]). All orbits defined by (1.3) are nonnegative and bounded for $t > 0$. The map associated with system (1.1) is dissipative. If the net reproduction number R is less than 1, then the zero equilibrium $(0, 0, 0)$ is locally asymptotically stable (LAS) and attracts all orbits in the nonnegative octant. As R increases above 1, a bifurcation occurs which results in the instability of the zero equilibrium and the creation of a positive equilibrium. For all $R > 1$ there exists one and only one positive equilibrium which may or may not be stable. The system (1.1) is uniformly persistent with respect to the origin. Only in some special cases is it known when the positive equilibrium is stable.

The case studied in this article is $\mu_a = 1$, which was investigated in [3]. Biologically, setting $\mu_a = 1$ assumes that no adults survive longer than a single time step. In this case (1.2) gives $b = R/(1 - \mu_l)$, and the parameter b may be replaced by the parameter R with $R > 0$ [3]. The LPA model with $\mu_a = 1$ is

$$
\begin{aligned}
x_1(t+1) &= \tfrac{R}{1-\mu_l}\, x_3(t)\, e^{-c_{el} x_1(t) - c_{ea} x_3(t)} \\
x_2(t+1) &= (1 - \mu_l)\, x_1(t) \\
x_3(t+1) &= x_2(t)\, e^{-c_{pa} x_3(t)}
\end{aligned}
\tag{1.3}
$$

Following [3], define a point $(x_1(0), x_2(0), x_3(0))$ to be *fully synchronous* if exactly two of the components are equal to zero, and *partially synchronous* if exactly one of the components is equal to zero [3]. By direct inspection of (1.3) one can see that if a point $(x_1(0), x_2(0), x_3(0))$ is fully (partially) synchronous, then the entire orbit $\{(x_1(t), x_2(t), x_3(t))\}_{t \geq t_0}$ is as well. Thus fully synchronous orbits are subsets of the positive coordinate axes, and partially synchronous orbits are subsets of the positive coordinate planes. See Fig. 1.

(a)   (b)
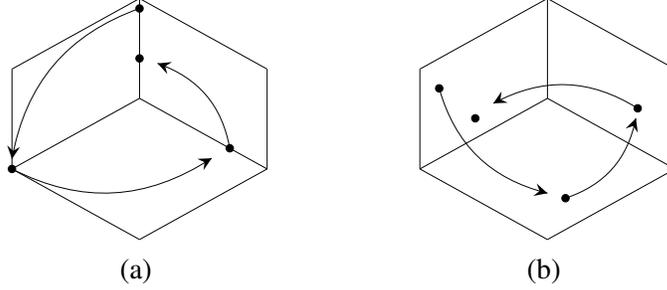
FIGURE 1. (a) *A fully synchronous orbit of T is contained in the union of the nonnegative semiaxes.* (b) *A partially synchronous orbit of T is contained in the union of the coordinate quadrants.*

It is stated in [3] that the bifurcation at $R = 1$ for the special case $\mu_a = 1$ is nongeneric and that an exchange of equilibrium stability does not occur: Theorem 1 in [3] states that the positive fixed point is unstable for all allowable parameter values and $R > 1$ with $R - 1$ sufficiently small. However, the latter statement is incorrect, as there is an elementary algebra error in the proof (for details see Section 2). In [3] it is shown that for $R > 1$ there exists a positive fully synchronous 3-cycle

$$\{(q_1,0,0),(0,q_2,0),(0,0,q_3)\} \tag{1.4}$$

with

$$q = (q_1,q_2,q_3) := \left(\frac{1}{c_{ea}(1-\mu_l)} \ln(R), \frac{1}{c_{ea}} \ln(R), \frac{1}{c_{ea}} \ln(R) \right). \tag{1.5}$$

The parameter range $1 < R < e^2$ and $(c_{pa} - c_{ea})(1 - \mu_l) + c_{el} > 0$ was discussed in detail and it was shown that (1.4) globally attracts all synchronous orbits (Theorem 5 in [3]). Theorem 2 of [3] states that the dynamics of fully synchronous orbits are governed by Ricker maps and that there is a period-doubling route to chaos for nontrivial solutions on the positive coordinate axes. Also Theorem 7 in [3] establishes for the case $1 < R < e^2$ and $(c_{pa} - c_{ea})(1 - \mu_l) + c_{el} > 0$ the existence of an "invariant loop" of the LPA model (1.3) consisting of synchronous orbits. The loop has the form of a "cycle chain" in that it is made up of the 3-cycle (1.4) and invariant sets of synchronous orbits that heteroclinically connect the three phases of the 3-cycle [3]. Furthermore, in the case $(c_{pa} - c_{ea})(1 - \mu_l) + c_{el} < 0$ and letting $\gamma = -\frac{(c_{pa}-c_{ea})(1-\mu_l)+c_{el}}{c_{ea}^2(1-\mu_l)}$, the existence of a positive partially synchronous 3-cycle is established. It is given by

$$\left\{ \left(\frac{\ln(R)}{c_{ea}(1-\mu_l)}, 0, \gamma \ln(R) \right), \left(\frac{\gamma R^{c_{pa}/c_{ea}} \ln(R)}{(1-\mu_l)}, \frac{\ln(R)}{c_{ea}}, 0 \right), \left(0, \gamma R^{c_{pa}/c_{ea}} \ln(R), \frac{\ln(R)}{c_{ea}} \right) \right\}. \tag{1.6}$$

The dynamical behavior of partially synchronous solutions and the local stability of the partially synchronous 3-cycle (1.6) are left as open problems in [3]. The dynamics of the system in the interior of the non-negative octant were not treated.
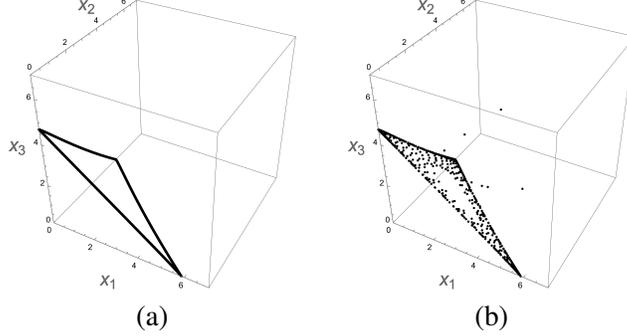
FIGURE 2. *Example from [3] (Figure 1 in page 666). (a) The synchronous cycle chain of the system* (1.3) *is shown for* $c_{el} = c_{pa} = c_{ea} = 0.1$, $\mu_l = 0.2$, $R = 1.6$. (b) *An orbit of Eq.* (1.3) *approaches the cycle chain in (a) in an outwardly spiralling manner. The initial conditions are* $x_1(0) = x_2(0) = x_3(0) = 10$.

The goals of this article are to: (i) give a complete description of the local stability character of the positive equilibrium of (1.3) as R increases above the critical value $R = 1$, with $R - 1$ sufficiently small (discussed in Section 2), (ii) give a description of global dynamics of partially synchronous solutions of (1.3) (discussed in Section 3), and (iii) determine properties of the "cycle chain" in Theorem 7 of [3] and expand the range of parameters for the existence of this set (discussed in Section 4).

2. LOCAL STABILITY OF THE POSITIVE FIXED POINT

Theorem 1 in [3] addresses the local stability character of the positive equilibrium of the LPA model (1.3) for values of R that are larger than 1 with $R - 1$ small. However, Theorem 1 in [3] states incorrectly that the positive fixed point is unstable for all $R > 1$ with $R - 1$ sufficiently small. There is an elementary algebra error in the proof of the result, specifically in the formula for the expansion of $|\sigma_2(\varepsilon)|^2$ in page 660 of [3], where $\sigma_2(\varepsilon)$ represents a characteristic value associated with the positive fixed point at $R = 1 + \varepsilon$ such that $\sigma_2(0)$ is not a real number. The correct expansion is given by $|\sigma_2|^2 = 1 + \frac{1-\mu_\ell}{3}\Delta\varepsilon + O(\varepsilon^2)$, where Δ is given by (2.2) below. With this correction, this expansion could be used to prove the cases for which $\Delta \neq 0$ of the main result of this section (Theorem 2.1). In this section an approach different than the one in [3] is used, with the benefit that both cases $\Delta \neq 0$ and $\Delta = 0$ are treated effectively.

The map associated with the LPA model (1.3) is $T : \mathbb{R}^3_+ \to \mathbb{R}^3_+$, where

$$T(x_1, x_2, x_3) := \left(\frac{R x_3 \, e^{-c_{el} x_1 - c_{ea} x_3}}{1 - \mu_l}, (1 - \mu_l) x_1, x_2 \, e^{-c_{pa} x_3} \right). \qquad (2.1)$$

Theorem 2.1. *For positive parameters c_{ea}, c_{pa}, c_{el} and μ_l with $\mu_l < 1$ of the LPA model* (1.3), *let*

$$\Delta := \tfrac{1}{2}\left(-2c_{ea} + c_{pa} + \frac{c_{el}}{1-\mu_l} \right). \tag{2.2}$$

There exists $\varepsilon > 0$ such that if $1 < R < 1+\varepsilon$, then T at the positive fixed point has one real characteristic value which belongs to $(0,1)$, and a pair of complex conjugate characteristic values with magnitude ρ, where

    (i) *$\rho > 1$ if $\Delta > 0$, or if $\Delta = 0$ and $(2-\sqrt{2})\,c_{pa} \le c_{ea} < (2+\sqrt{2})\,c_{pa}$, and*

    (ii) *$\rho < 1$ in all cases not included in* (i).

Thus the positive fixed point is unstable in case (i) *and L.A.S. in case* (ii).

Proof. The following equations are satisfied by fixed points of T:

$$\frac{R x_3\, e^{-x_3 c_{ea} - c_{el} x_1}}{1-\mu_l} = x_1 \quad , \quad x_1(1-\mu_l) = x_2 \quad , \quad x_2\, e^{-x_3 c_{pa}} = x_3. \tag{2.3}$$

From (2.3) it follows that a nontrivial fixed point x must satisfy

$$x_1 = \frac{x_3\, e^{c_{pa} x_3}}{1-\mu_l} \quad , \quad x_2 = x_3\, e^{c_{pa} x_3} \quad , \quad R = e^{c_{ea} x_3 + c_{pa} x_3 + \frac{c_{el} x_3\, e^{c_{pa} x_3}}{1-\mu_l}}. \tag{2.4}$$

The third equation in (2.4) implies that R is an increasing function of x_3 for $x_3 \ge 0$. Thus R with $R \ge 1$ and x_3 with $x_3 \ge 0$ are in one-to-one (smooth) correspondence. Motivated by this fact, define

$$R(\alpha) := e^{c_{ea}\alpha + c_{pa}\alpha + \frac{c_{el}\alpha e^{c_{pa}\alpha}}{1-\mu_l}}, \quad \alpha \ge 0, \tag{2.5}$$

and

$$T_\alpha(x_1, x_2, x_3) := \left(\frac{R(\alpha) x_3\, e^{-c_{el} x_1 - c_{ea} x_3}}{1-\mu_l}, (1-\mu_l) x_1, x_2\, e^{-c_{pa} x_3} \right), \quad \alpha \ge 0. \tag{2.6}$$

For each $\alpha > 0$, the map T_α has a unique fixed point given by

$$\left(\frac{\alpha e^{c_{pa}\alpha}}{1-\mu_l}, \alpha e^{c_{pa}\alpha}, \alpha \right). \tag{2.7}$$

A straightforward calculation (omitted) gives the characteristic polynomial of the Jacobian matrix of T_α in (2.6) at the fixed point (2.7), namely

$$\chi_\alpha(t) := t^3 + \frac{\alpha((1-\mu_l)c_{pa} + c_{el} e^{\alpha c_{pa}})}{1-\mu_l} t^2 + \frac{\alpha^2 c_{el} c_{pa} e^{\alpha c_{pa}}}{1-\mu_l} t + \alpha c_{ea} - 1. \tag{2.8}$$

Thus $\chi_0(t) = t^3 - 1$, and the roots of $\chi_0(t)$ are the cubic roots of unity: 1, $\tfrac{1}{2}(-1 + \sqrt{3})$, and $\tfrac{1}{2}(-1 - \sqrt{3})$. Let λ_0 be one of these values. Since λ_0 has multiplicity one, $\left.\frac{\partial \chi_\alpha(t)}{\partial t}\right|_{t=\lambda_0} \ne 0$, and the Implicit Function Theorem applied to $\chi_\alpha(\lambda) = 0$ gives the existence of a neighborhood $\mathcal{J}$ of 0 on which λ is a smooth function of α satisfying

$$\lambda(0) = \lambda_0 \quad \text{and} \quad \chi_\alpha(\lambda(\alpha)) = 0 \quad \text{for } \alpha \in \mathcal{J}. \tag{2.9}$$

Derivative values $\lambda^{(\ell)}(0)$, $\ell \geq 1$ can be obtained with implicit differentiation, in particular,

$$\lambda'(0) = -\left.\frac{\frac{\partial \chi_\alpha(t)}{\partial \alpha}}{\frac{\partial \chi_\alpha(t)}{\partial t}}\right|_{t=\lambda(0), \alpha=0} = -\frac{c_{el} + c_{pa}(1 - \mu_l)}{3(1 - \mu_l)} - \frac{c_{ea}}{3\lambda_0^2}. \qquad (2.10)$$

Set $\rho(\alpha) := |\lambda(\alpha)|^2 = \lambda(\alpha)\overline{\lambda(\alpha)}$ for $\alpha \in \mathcal{J}$. The product rule gives

$$\rho^{(m)}(0) = \sum_{k=0}^{m} \binom{m}{k} \lambda^{(k)}(0)\overline{\lambda^{(m-k)}(0)}, \quad m = 0, 1, 2, \ldots. \qquad (2.11)$$

By using relation (2.11), the order m Taylor expansion of $\rho(\cdot)$ about 0,

$$\rho(\alpha) = \rho(0) + \rho'(0)\alpha + \cdots + \frac{\rho^{(m)}(0)}{m!}\alpha^m + O(|\alpha|^{m+1}) \qquad (2.12)$$

may be written in terms of $\lambda^{(\ell)}(0)$, $\ell = 0, \ldots, m$. This is done next for the cases (A) $\lambda(0) = 1$ and (B) $\lambda(0) = \frac{1}{2}(1 \pm \sqrt{3}i)$.

(A) If $\lambda_0 = 1$, from (2.10) we get

$$\lambda'(0) = -\left.\frac{\frac{\partial \chi_\alpha(t)}{\partial \alpha}}{\frac{\partial \chi_\alpha(t)}{\partial t}}\right|_{t=1} = -\frac{c_{el} + (1 - \mu_l)(c_{ea} + c_{pa})}{3(1 - \mu_l)}. \qquad (2.13)$$

From $\lambda(0) = 1$, (2.11) and (2.13) we have

$$\rho'(0) = \lambda'(0)\overline{\lambda(0)} + \overline{\lambda'(0)}\lambda(0) = -\frac{2(c_{el} + (1 - \mu_l)(c_{ea} + c_{pa}))}{3(1 - \mu_l)}. \qquad (2.14)$$

With $\rho(0) = |\lambda(0)|^2 = 1$ and (2.14), expansion (2.12) with $m = 1$ takes the form

$$\rho(\alpha) = 1 - \left(\frac{2(c_{el} + (1 - \mu_l)(c_{ea} + c_{pa}))}{3(1 - \mu_l)}\right)\alpha + O(\alpha^2). \qquad (2.15)$$

Thus $\rho(\alpha) < 1$ for α positive and close enough to 0. Since $\rho(\alpha)$ is the square of the modulus of an eigenvalue of the Jacobian matrix of T_α at the positive fixed point, one can see that the corresponding root $\lambda(\alpha)$ is inside the unit disk of the complex plane for all positive α that are sufficiently small. Further, for α sufficiently small, $\lambda(\alpha)$ is a real number, and $\lambda(\alpha) \in (0, 1)$.

(B) If $\lambda_0 = \frac{1}{2}(1 \pm \sqrt{3})$, calculations similar to those in case (i) give the following expansion:

$$\rho(\alpha) = 1 + \frac{1}{3}\left(\frac{c_{el}}{1 - \mu_l} + c_{pa} - 2c_{ea}\right)\alpha + O(\alpha^2). \qquad (2.16)$$

If $\frac{c_{el}}{1 - \mu_l} + c_{pa} - 2c_{ea} = 0$, then the Taylor expansion of $\rho(\alpha)$ is

$$\rho(\alpha) = 1 - \frac{1}{3}\left((c_{ea} - (2 - \sqrt{2})c_{pa})(c_{ea} - (2 + \sqrt{2})c_{pa})\right)\alpha^2 + O(\alpha^3). \qquad (2.17)$$

If both $\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea} = 0$ and $\left(c_{ea} - (2-\sqrt{2})\,c_{pa}\right)\left(c_{ea} - (2+\sqrt{2})\,c_{pa}\right) = 0$, then

$$\rho(\alpha) = 1 - \frac{1}{6}\,\beta\,c_{pa}^{\,3}\,\alpha^3 + O(\alpha^4), \text{ where } \beta = \begin{cases} -11+8\sqrt{2} & \text{if } c_{ea} = (2+\sqrt{2})\,c_{pa} \\ -11-8\sqrt{2} & \text{if } c_{ea} = (2-\sqrt{2})\,c_{pa} \end{cases}. \quad (2.18)$$

Table 1 summarizes the formulas for this case.

Case	Condition	Taylor expansion of $\rho(\alpha) = \|\lambda(\alpha)\|^2$ about $\alpha = 0$ with $\lambda(0) = \frac{1}{2}\left(1+\sqrt{3}\,i\right)$ or $\lambda(0) = \frac{1}{2}\left(1-\sqrt{3}\,i\right)$
(a)	$\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea} \neq 0$	$1 + \frac{1}{3}\left(\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea}\right)\alpha + O(\alpha^2)$
(b)	$\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea} = 0,$ $c_{ea} \neq (2+\sqrt{2})\,c_{pa},$ and $c_{ea} \neq (2-\sqrt{2})\,c_{pa}$	$1 + \frac{1}{3}\left(-c_{ea}^2 + 4c_{ea}c_{pa} - 2c_{pa}^2\right)\alpha^2 + O(\alpha^3)$
(c)	$\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea} = 0$ and $c_{ea} = (2+\sqrt{2})\,c_{pa}$	$1 - \frac{1}{6}\left(-11+8\sqrt{2}\right)c_{pa}^{\,3}\,\alpha^3 + O(\alpha^4)$
	$\frac{c_{el}}{1-\mu_l} + c_{pa} - 2c_{ea} = 0$ and $c_{ea} = (2-\sqrt{2})\,c_{pa}$	$1 - \frac{1}{6}\left(-11-8\sqrt{2}\right)c_{pa}^{\,3}\,\alpha^3 + O(\alpha^4)$

TABLE 1. *Taylor expansions of $\rho(\alpha)$ for case ii.*

One can see that the linear term of equation (2.16) and the quadratic term of (2.17) are positive if and only if $\Delta > 0$ or $\Delta = 0$ and $(2-\sqrt{2})c_{pa} < c_{ea} < (2+\sqrt{2})c_{pa}$, and negative otherwise, whereas the cubic term of equation (2.18) is always negative. Thus (i) and (ii) hold for all α sufficiently close to zero. Formula (2.5) gives R as an increasing function of α for $\alpha > 0$ and $R = 1$ for $\alpha = 0$, so the conclusion follows for some value of $\varepsilon > 0$. $\quad\square$

The proof of Theorem 2.1 has the following corollary, which gives a geometric interpretation to the relation $\Delta = 0$.

Corollary 2.1. *Let λ be as in (2.9), with $\lambda(0) \in \left\{\frac{1}{2}(1-\sqrt{3}\,i), \frac{1}{2}(1+\sqrt{3}\,i)\right\}$. Then $\Delta = 0$ if and only if the curve $\lambda(\cdot)$ is tangential to the unit circle at the contact point $\lambda(0)$.*

Proof. Since $\mathrm{re}(\lambda(0)) = -\frac{1}{2}$ and $1/\lambda(0)^2 = -\overline{\lambda(0)}$, relation (2.10) gives

$$
\begin{aligned}
\mathrm{re}\left(\lambda(0)\,\overline{\lambda'(0)}\right) &= \mathrm{re}\left(\lambda(0)\left(-\frac{c_{el}+c_{pa}\,(1-\mu_l)}{3\,(1-\mu_l)} + \frac{c_{ea}}{3}\overline{\lambda(0)}\right)\right) \\
&= -\frac{1}{2}\left(-\frac{c_{el}+c_{pa}\,(1-\mu_l)}{3\,(1-\mu_l)}\right) + \frac{c_{ea}}{3} \\
&= \frac{-2\,c_{ea}\,(1-\mu_l)+c_{el}+c_{pa}\,(1-\mu_l)}{6\,(1-\mu_l)} \\
&= \tfrac{1}{3}\Delta.
\end{aligned}
\tag{2.19}
$$

Thus $\Delta = 0$ is equivalent to the relation $|\lambda(0)+\lambda'(0)|^2 = |\lambda(0)|^2 + |\lambda'(0)|^2$. The statement follows from this, (2.10), and the relations $|\lambda(0)| = 1$ and $\lambda'(0) \neq 0$. $\square$

3. Synchronous orbits

In this section we establish local and global dynamics of synchronous orbits of (1.3). It is shown in [3] that for $R \in (1, e^2)$, there exists a unique fully synchronous 3-cycle for all allowable parameters, there exists a partially synchronous 3-cycle for some parameter choices, and if the partially synchronous 3-cycle exists, it is unique. We begin by reviewing some calculations from [3]. The identities satisfied by period three points of the map T in (2.1) are

$$
\begin{aligned}
x_1 &= Rx_1 \exp\Big(-c_{ea}(1-\mu_l)x_1 e^{-c_{pa}x_2}e^{-c_{pa}x_3} \\
&\qquad -x_2\,e^{-c_{pa}x_3}\left(c_{pa}+b\,c_{el}\,e^{-bc_{el}e^{-c_{el}x_1-c_{ea}x_3}-c_{ea}x_2\,e^{-c_{pa}x_3}}\right)\Big), \\
x_2 &= Rx_2 \exp\left(-c_{pa}x_3 - c_{ea}x_2 e^{-c_{pa}x_3} - b\,c_{el}\,x_3\,e^{-c_{el}x_1-c_{ea}x_3}\right), \\
x_3 &= Rx_3 \exp\left(-c_{el}x_1 - c_{ea}x_3 - c_{pa}(1-\mu_l)x_1\,e^{-c_{pa}x_2\,e^{-c_{pa}x_3}}\right).
\end{aligned}
\tag{3.1}
$$

To find synchronous 3-cycles, substitute $x_2 = 0$ in system (3.1) to obtain

$$
\begin{aligned}
x_1 &= Rx_1\,e^{-c_{ea}\,(1-\mu_l)\,x_1}, \\
x_3 &= Rx_3\,e^{-c_{el}x_1-c_{ea}x_3-c_{pa}\,(1-\mu_l)\,x_1}.
\end{aligned}
\tag{3.2}
$$

Solving (3.2) for x_1 and x_3 yields the following three non-trivial period 3 points:

$$
\left(0,0,\tfrac{\ln(R)}{c_{ea}}\right),\quad \left(\tfrac{\ln(R)}{c_{ea}(1-\mu_l)},0,0\right),\quad \text{and}\quad \left(\tfrac{\ln(R)}{c_{ea}(1-\mu_l)},0,-\tfrac{(c_{pa}-c_{ea})(1-\mu_l)+c_{el}}{c_{ea}^2(1-\mu_l)}\ln(R)\right).
\tag{3.3}
$$

Neither of the first two points in (3.3) belong to a partially synchronous 3-cycle, since each has more than one zero entry. With Δ as in (2.2) and γ defined by

$$
\gamma := \frac{-\Delta - c_{ea}}{c_{ea}^2} = -\frac{(c_{pa}-c_{ea})(1-\mu_l)+c_{el}}{c_{ea}^2(1-\mu_l)},
\tag{3.4}
$$

the partially synchronous cycle of the third point in (3.3) is

$$\left\{ \left(\frac{\ln(R)}{c_{ea}(1-\mu_l)}, 0, \gamma \ln(R) \right), \left(\frac{\gamma R^{c_{pa}/c_{ea}} \ln(R)}{(1-\mu_l)}, \frac{\ln(R)}{c_{ea}}, 0 \right), \left(0, \gamma R^{c_{pa}/c_{ea}} \ln(R), \frac{\ln(R)}{c_{ea}} \right) \right\}. \quad (3.5)$$

We will need the following lemma, which is probably a known result. For $A \subset \mathbb{R}^k$, we denote with A° the interior of the set A.

Lemma 3.1. *Let* $s = (s_1, s_2) \in (\mathbb{R}_+^2)^\circ$, $o = (0,0)$ *and* $U : [o, s] \to [o, s]$ *be a map of the form* $U(\xi_1, \xi_2) = (U_1(\xi_1), U_2(\xi_1, \xi_2))$. *Assume*

(i) $U([o, s]^\circ) \subset [o, s]^\circ$.
(ii) U *has an interior fixed point* (ξ_1^+, ξ_2^+) *which is locally asymptotically stable (L.A.S.).*
(iii) $U_1^n(\xi_1) \to \xi_1^+$ *whenever* $\xi_1 \in (0, s_1]$.
(iv) *For every* $\xi_2 \in (0, s_2]$, $U^n(\xi_1^+, \xi_2) \to (\xi_1^+, \xi_2^+)$.
(v) U *is smooth on a neighborhood of* $(\xi_1^+, 0)$, *and* $(\xi_1^+, 0)$ *is a saddle point of* U *with a local stable manifold that is a subset of the line through* $(0,0)$ *and* $(\xi_1^+, 0)$.

Then (ξ_1^+, ξ_2^+) *attracts every orbit with initial point in* $[o, s]^\circ$.

Proof. Let $(\xi_1, \xi_2) \in [o, s]^\circ$ (so in particular $\xi_1 > 0$), and set $(\xi_1(n), \xi_2(n)) := U^n(\xi_1, \xi_2)$, $n = 1, 2, \dots$. Note $(\xi_1(n), \xi_2(n)) \in [o, s]^\circ$ for $n \geq 0$. By (iii), $\xi_1(n) \to \xi_1^+$ as $n \to \infty$. Hence the orbit of (ξ_1, ξ_2) under U has at least one accumulation point (ξ_1^+, ξ_2^*) on the line segment joining $(\xi_1^+, 0)$ to (ξ_1^+, s_2). We claim ξ_2^* can be chosen to be different from 0. Otherwise there do not exist accumulation points (ξ_1^+, ξ_2^*) that are not $(\xi_1^+, 0)$, in which case $U^n(\xi_1, \xi_2) \to (\xi_1^+, 0)$, which is impossible by (i) and (v). Assume (ξ_1^+, ξ_2^*) is an accumulation point of the orbit of (ξ_1, ξ_2) with $\xi_2^* \neq 0$. By (ii), there exists a neighborhood O of (ξ_1^+, ξ_2^+) such that O is a subset of the basin of (ξ_1^+, ξ_2^+). By (iv), there exists $m > 0$ such that $U^m(\xi_1^+, \xi_2^*) \in O$. By continuity of U^m, there exists a neighborhood $\mathcal{V}$ of (ξ_1^+, ξ_2^*) such that $U^m(\mathcal{V}) \subset O$. Choose n_0 so that $U^n(\xi_1, \xi_2) \in \mathcal{V}$. It follows that $U^{n_0+m}(\xi_1, \xi_2) \in O$. Thus $U^n(\xi_1, \xi_2) \to (\xi_1^+, \xi_2^+)$ as $n \to \infty$. $\square$

The following result establishes parameter values for which a unique partially synchronous 3-cycle exists as well as the local stability character and basin of attraction for the fully- and the partially synchronous 3-cycles.

Theorem 3.1. *The LPA model with* $\mu_a = 1$ *and* $R > 1$ *satisfies the following conditions:*

(a) *A partially synchronous 3-cycle exists if and only if* $\Delta < -c_{ea}$, *and if it exists it is unique.*
(b) *If* $\Delta < -c_{ea}$ *and* $R \in (1, e^2)$, *the characteristic values associated with the partially synchronous 3-cycle are real, with two of them stable and the remaining one unstable.*
(c) *If* $\Delta < -c_{ea}$ *and* $R \in (1, e^2)$, *then the partially synchronous 3-cycle attracts all nontrivial partially synchronous orbits.*

(d) *If $\Delta \geq -c_{ea}$ and $R \in (1, e^2)$, then the fully synchronous 3-cycle attracts all nontrivial synchronous orbits.*

Proof. (a) Note that the condition $\Delta < -c_{ea}$ is equivalent to $\gamma > 0$. Thus the statement follows from this and (3.5).

(b) If $y = \left(\frac{\gamma R^{c_{pa}/c_{ea}} \ln(R)}{(1 - \mu_l)}, \frac{\ln(R)}{c_{ea}}, 0 \right)$ from (3.5), a calculation gives that the matrix product $DT(T^2(y)) \cdot DT(T(y)) \cdot DT(y)$ is triangular. Thus the eigenvalues associated with this product appear on the diagonal, and they are readily found to be

$$\lambda_1 = 1 - c_{ea} \gamma \ln(R), \quad \lambda_2 = 1 - \ln(R), \text{ and } \lambda_3 = R^{1 - \frac{\gamma \left(c_{pa}(1 - \mu_l) + c_{el} R^{c_{pa}/c_{ea}} \right)}{1 - \mu_l}}. \tag{3.6}$$

Now

$$c_{ea} \gamma = -\frac{(c_{pa} - c_{ea})(1 - \mu_l) + c_{el}}{c_{ea}(1 - \mu_l)} = 1 - \frac{c_{pa}}{c_{ea}} - \frac{c_{el}}{c_{ea}(1 - \mu_l)} < 1. \tag{3.7}$$

From the formulas of λ_1 and λ_2, the inequality $\gamma > 0$, and from (3.7) we have

$$|\lambda_1| < 1 \text{ and } |\lambda_2| < 1 \text{ for all } R \in \left(1, \min \left\{ e^2, e^{\frac{2}{\gamma c_{ea}}} \right\} \right) = (1, e^2). \tag{3.8}$$

To verify $\lambda_3 > 1$ for $R \in (1, e^2)$, (3.6) can be used to write $\lambda_3 = R^{\Lambda(R)}$ where

$$\Lambda(\rho) := 1 - \frac{\gamma}{1 - \mu_l} \left(c_{pa}(1 - \mu_l) + c_{el} \rho^{c_{pa}/c_{ea}} \right) \quad \text{for } \rho > 0. \tag{3.9}$$

Thus it suffices to prove $\Lambda(R) > 0$ for $1 \leq R \leq e^2$. Now the derivative $\Lambda'(\rho) = -\frac{c_{el} c_{pa} \gamma \rho^{(c_{pa} - c_{ea})/c_{ea}}}{c_{ea}(1 - \mu_\ell)}$ is negative for $\rho > 0$, so $\Lambda(\cdot)$ is a decreasing function. Therefore the proof of (b) will be complete once we verify that $\Lambda(e^2)$ is positive. For this purpose we introduce the auxiliary function $\phi(\tau) := 2e^\tau + e^{2\tau}(\tau - 1) - \tau$, $\tau \geq 0$. Note the function $\phi(\cdot)$ is positive for $\tau \geq 0$, which can be deduced from the relations $\phi(0) = 1$, $\phi'(0) = 0$, and the positive character of $\phi''(\tau) = 2e^\tau(1 + 2\tau e^\tau)$ for $\tau \geq 0$. From the definition of ϕ and relation $-\frac{\gamma c_{el}}{1 - \mu_l} = \gamma^2 c_{ea}^2 + \gamma(c_{pa} - c_{ea})$ from (3.4), the following identity can be shown to be valid:

$$\Lambda(e^2) = \left(1 - \gamma c_{ea} e^{\frac{c_{pa}}{c_{ea}}} \right)^2 + \gamma c_{ea} \phi \left(\frac{c_{pa}}{c_{ea}} \right). \tag{3.10}$$

From (3.10) and the positive character of $\phi(\cdot)$, we conclude $\Lambda(e^2) > 0$. This completes the proof of (b).

(c) Each of the points in the 3-cycle (3.5) is a fixed point of T^3. Set $K^\circ_{\{i,j\}} := K_{\{i,j\}} \setminus \left(K_{\{i\}} \cup K_{\{j\}} \right)$. Since $T^3(K_{\{i,j\}}) \subset K_{\{i,j\}}$ and $T^3(K_{\{i\}}) \subset K_{\{i\}}$, we have $T^3(K^\circ_{\{i,j\}}) \subset K^\circ_{\{i,j\}}$. Also, under the hypothesis, T^3 has a unique fixed point $x_{\{i,j\}}$ in $K^\circ_{\{i,j\}}$, which is one of the points in (3.5). Therefore the statement to be proved is that every point in $K^\circ_{\{i,j\}}$ is attracted to $x_{\{i,j\}}$. Consider the case $\{i, j\} = \{1, 3\}$. We have,

$$T^3(x_1, 0, x_3) = \left(R x_1 e^{-c_{ea}(1 - \mu_l) x_1}, 0, R x_3 e^{-c_{el} x_1 - c_{ea} x_3 - c_{pa}(1 - \mu_l) x_1} \right), \tag{3.11}$$

and define $U : \mathbb{R}^2_+ \to \mathbb{R}^2_+$ by

$$U(\xi_1,\xi_2) = \left(R\xi_1\, e^{-c_{ea}(1-\mu_l)\xi_1}, R\xi_2\, e^{-c_{el}\xi_1 - c_{ea}\xi_2 - c_{pa}(1-\mu_l)\xi_1} \right). \tag{3.12}$$

From (3.5), the interior fixed point of U is $(\bar{\xi}_1,\bar{\xi}_2) := \left(\frac{\ln(R)}{c_{ea}(1-\mu_l)}, \gamma\ln(R) \right)$. The components of $U = (U_1,U_2)$ are bounded:

$$U_1(\xi_1,\xi_2) \leq \frac{R}{c_{ea}(1-\mu_l)e} \quad \text{and} \quad U_2(\xi_1,\xi_2) \leq \frac{R}{c_{ea}\,e} \quad \text{for} \quad (\xi_1,\xi_2) \in \mathbb{R}_+^2. \tag{3.13}$$

Set $s := \left(\frac{e}{c_{ea}(1-\mu_l)}, \frac{e}{c_{ea}} \right)$. With $o = (0,0)$ we have $U\left(\mathbb{R}_+^2\right) \subset [o,s]$ and $U\left((\mathbb{R}_+^2)^\circ\right) \subset [o,s]^\circ$. Therefore to obtain the desired conclusion, it is sufficient to verify that the restriction of U to $[o,s]$ satisfies the hypotheses of Lemma 3.1. Note that $U([o,s])]^\circ) \subset U[o,s]^\circ$ since $R \in (1,e^2)$ by hypothesis. The Jacobian matrix of U at the positive fixed point $(\bar{\xi}_1,\bar{\xi}_2)$ is a lower triangular matrix, where the diagonal entries are exactly the first λ_1 and λ_2 in (3.6), and thus by (3.8) $(\bar{\xi}_1,\bar{\xi}_2)$ is L.A.S. if $1 < R < e^2$. This gives condition (ii) of Lemma 3.1. Verification of condition (v) is similar and we skip the details. Note that U_1 as a function of ξ_1 alone is a Ricker map with a globally asymptotically stable positive fixed point, and thus satisfies the hypothesis (iii) of Lemma 3.1 with $\bar{\xi}_1 = \frac{\ln(R)}{c_{ea}(1-\mu_l)}$. Similarly, $U_2(\bar{\xi}_1,\cdot)$ is a Ricker map with a globally asymptotically stable fixed point, so hypothesis (iv) is satisfied. Thus Lemma 3.1 and the relation $U\left((\mathbb{R}_+^2)^\circ\right) \subset [o,s]^\circ$ imply that every point in $K_{\{1,3\}}^\circ$ is attracted to $x_{\{1,3\}}$. The proofs of the corresponding statements for $K_{\{1,2\}}$ and $K_{\{2,3\}}$ are similar.

(d) From Theorem 2 in [3], a unique fully synchronous 3-cycle exists and attracts all fully synchronous orbits for $R \in (1,e^2)$. Further, it is shown in Theorem 5 of [3] that the synchronous 3-cycle attracts all partially synchronous orbits if $(c_{pa} - c_{ea})(1-\mu_l) + c_{el} > 0$, which is equivalent to $\Delta > -c_{ea}$. It remains to show that all partially synchronous orbits are attracted to the unique fully synchronous 3-cycle when $\Delta = -c_{ea}$, but a proof of this statement proceeds in the same way as the proof of (c), so we do not show it here. $\qquad\square$

4. EXISTENCE OF AN INVARIANT CURVE

In this section we prove that if $R > 1$ is such that $R - 1$ is sufficiently small, there exists an invariant curve contained in the union of the coordinate planes. For fixed but otherwise arbitrary positive constants $c_{ea}, c_{el}, c_{pa}, \mu_l$ with $\mu_l < 1$, let

$$\begin{aligned} r &:= \left(\frac{R}{(1-\mu_l)c_{ea}e}, \frac{R}{c_{ea}e}, \frac{R}{c_{ea}e} \right) \quad \text{and} \\ C &:= [o,r] = \{(x_1,x_2,x_3) \in \mathbb{R}_+^3 : 0 \leq x_i \leq r_i\}. \end{aligned} \tag{4.1}$$

Proposition 4.1. *The set C is invariant under T, and $T^3(\mathbb{R}_+^3) \subset C$.*

Proof. If $x \in C$, then using the fact that $x_3 e^{-c_{ea}x_3} \leq 1/(c_{ea}e)$ for $x_3 \geq 0$, we have

$$
\begin{array}{rclcl}
T_1(x) & = & \frac{R}{(1-\mu_l)}\,x_3\,e^{-c_{ea}x_3}\,e^{-c_{el}x_1} & \leq & \frac{R}{(1-\mu_l)\,c_{ea}\,e}\,, \\[4pt]
T_2(x) & = & (1-\mu_l)\,x_1 & \leq & \frac{R}{c_{ea}\,e}\,, \\[4pt]
T_3(x) & = & x_2\,e^{-c_{pa}x_3} & \leq & \frac{R}{c_{ea}\,e}\,,
\end{array}
\tag{4.2}
$$

therefore $T(x) \in C$ and C is invariant. Consider the orbit of a point $(x_1(0), x_2(0),$ $x_3(0)) \in \mathbb{R}_+^3$ under T. Since $x_3 e^{-c_{ea}x_3} \leq \frac{1}{c_{ea}e}$ for $x_3 \geq 0$, we have $x_1(t) \leq \frac{R}{(1-\mu_l)c_{ea}e}$ for all $t \geq 1$. Since $x_2(t+1) = (1-\mu_l)x_1(t)$, we conclude that $x_2(t) \leq \frac{R}{c_{ea}e}$ for all $t \geq 2$ which in turn implies, since $x_3(t+1) = x_2(t)e^{-c_{pa}x_3(t)} \leq x_2(t)$, that $x_3(t) \leq \frac{R}{c_{ea}e}$ for all $t \geq 3$. Thus every orbit enters $[o, r]$ in at most three steps. $\qquad\square$

For $i \in \{1, 2, 3\}$, we use the short-hand notation $\{x_i = 0\}$ to denote the set $\{(x_1, x_2, x_3) \in \mathbb{R}^3 : x_i = 0\}$. The following proposition concerns the dynamics of the restriction of T^3 to $C \cap \{x_i = 0\}$.

Proposition 4.2. *Assume $R > 1$. For all $R > 1$ such that $R - 1$ is sufficiently small, and for each $i \in \{1, 2, 3\}$, there exists a smooth curve $C_i \subset C \cap \{x_i = 0\}$ that joins all the nontrivial fixed points of T^3 in $C \cap \{x_i = 0\}$ and is is invariant under T^3. Furthermore, there is a smooth parametrization of C_i such that at any point of C_i, the velocity vector $\mathbf{v}$ has a zero entry, a positive entry, and a negative entry in a suitable order.*

Proof. First note the restriction of T^3 to $C \cap \{x_i = 0\}$ is a diffeomorphism of $C \cap \{x_i = 0\}$ onto its image. Indeed, a calculation gives for all $(x, y, z) \in C$, and with H a suitable function of (x, y, z) and the parameters,

$$
\det DT^3(x, y, z) = R^3 \left(z\,c_{ea} - 1\right)\left(y\,c_{ea} - e^{zc_{pa}}\right)\left(x\,c_{ea}\,(u_l - 1) + e^{yc_{pa}e^{-zc_{pa}}}\right)e^H > 0.
$$

Thus T^3 is locally one-to-one on $C \cap \{x_i = 0\}$. Since $T^3(x, y, z) = (0, 0, 0)$ implies $(x, y, z) = (0, 0, 0)$, by Lemma 2.3.4 in [1] T^3 is also one-to-one on $C \cap \{x_i = 0\}$.

We now set $i = 1$ for the rest of this proof (a proof for the cases $i = 2$ and $i = 3$ is almost identical, and we do not supply it here). A calculation (omitted) shows $(0, q_2, 0)$ is a saddle point of T^3, with $DT^3(0, q_2, 0)$ having eigenvalue $R > 1$ and associated eigenvector

$$
v = \left(0, -\ln(R)(c_{pa}(1-\mu_l)(1-\ln(R)) + c_{el}R), +c_{ea}(1-\mu_l)(R + \ln(R) - 1)\right).
$$

For $R > 1$ and $R - 1$ sufficiently small $\operatorname{sign}(v) = (0, -, +)$. In this case there exists a local (smooth) unstable manifold $W_{loc}^u \subset C \cap \{x_1 = 0\}$ that is tangential to v at $(0, q_2, 0)$. The arc-length parametrization of W_{loc}^u with initial point $(0, q_2, 0)$ may be assumed (without loss of generality) to be such that the tangent vector at any point of W_{loc}^u has the sign configuration $(0, -, +)$. We claim a parametrization of the global unstable manifold $W^u = \cup_{\ell=1}^\infty (T^3)^\ell(W_{loc}^u)$ has the same sign property. First note $(T^3)^\ell(W_{loc}^u) \subset (T^3)^{\ell+1}(W_{loc}^u)$. Arguing by induction, suppose $\ell > 0$ is such that $E := (T^3)^\ell(W_{loc}^u)$ has a smooth parametrization $(0, y(\sigma), z(\sigma))$, $\alpha \leq \sigma \leq \beta$ with $\operatorname{sign}(v') = \operatorname{sign}(0, y'(\sigma), z'(\sigma)) = (0, -, +)$. The set $T^3(E)$ is parametrized by $T^3(0, y(\sigma), z(\sigma))$, and it satisfies $E \subset T^3(E)$. Note

$$\tfrac{d}{d\sigma}(T^3(0,y(\sigma),z(\sigma))) = DT_x^3(0,y(\sigma),z(\sigma)) \cdot (0,y'(\sigma),z'(\sigma)). \qquad (4.3)$$

With $+$ and $-$ and 0 denoting positive, negative and zero entries, and with $+0$ and -0 denoting non-negative and non-positive entries, from (4.3) and the Appendix we have

$$\text{sign}\left(\tfrac{d}{d\sigma}(T^3(0,y(\sigma),z(\sigma)))\right) = \begin{pmatrix} + & 0 & 0 \\ +0 & + & -0 \\ +0 & 0 & + \end{pmatrix} \begin{pmatrix} 0 \\ - \\ + \end{pmatrix} = \begin{pmatrix} 0 \\ - \\ + \end{pmatrix}. \qquad (4.4)$$

This completes the proof of the claim. It follows from the claim, the definition of global unstable manifold, and compactness of $C \cap \{x_1 = 0\}$ that both endpoints of W^u are fixed points of T^3. If $\Delta \geq -c_{ea}$, then by Theorem 3.1 there are only two fixed points $(0,q_2,0)$ and $(0,0,q_3)$ in $C \cap \{x_1 = 0\}$ and we are done; if $\Delta < -c_{ea}$, then by Theorem 3.1 there is a third fixed point $(0,p_1,p_2) := \left(0, \gamma R^{c_{pa}/c_{ea}} \ln(R), \frac{\ln(R)}{c_{ea}}\right)$ in $C \cap \{x_1 = 0\}$. In this case each of $(0,q_2,0)$ and $(0,0,q_3)$ has an associated unstable manifold with the required monotonicity, which connect $(0,q_2,0)$ to $(0,p_1,p_2)$ and $(0,p_1,p_2)$ to $(0,0,q_3)$, respectively. The union of these manifolds is the curve C_1, which in this case is precisely the stable manifold of T^3 at $(0,p_2,p_3)$. $\qquad\square$

The main result of this section is the following.

Theorem 4.1. *For each $R > 1$ such that $R - 1$ is sufficiently small, there exists a simple closed curve C in the union of the coordinate planes, which is invariant for the map T and contains the points of every synchronous and fully synchronous 3-cycle. Furthermore, the section of the curve in each coordinate plane has a smooth parametrization such that at any point, the velocity vector v has a zero entry, a positive entry, and a negative entry in a suitable order.*

Proof. Set $C := C_1 \cup C_2 \cup C_3$, where C_i is the curve in $\{x_i = 0\}$ given by Proposition 4.2. We claim $T(C_1) = C_2$, $T(C_2) = C_3$ and $T(C_3) = C_1$. To prove $T(C_1) = C_2$, note first that T maps $C \cap \{x_1 = 0\}$ into $C \cap \{x_2 = 0\}$, and T maps fixed points of T^3 to fixed points of T^3. Also if $w = T(v)$ with $v \in C_1$, then

$$\begin{aligned} \lim_{n\to\infty}(T^3)^{-n}(w) &= \lim_{n\to\infty}(T^3)^{-n}(Tv) \\ &= T(\lim_{n\to\infty}(T^3)^{-n}(v)) \\ &= T(q_1,0,0) \\ &= (0,q_2,0), \end{aligned} \qquad (4.5)$$

which implies that $w \in C_2$, by uniqueness of the unstable manifold. It follows that $T(C_1) \subset C_2$. Since T maps endpoints of C_1 to endpoints of C_2, $T(C_1) = C_2$ follows. Similarly, $T(C_2) = C_3$ and $T(C_3) = C_1$. Therefore $T(C) = C$. Note that any two curves C_i, C_j with $i \neq j$ have a single common point, which is a point of the 3-cycle of T. The rest of the statement is a consequence of Proposition 4.2 and the fact that points of a 3-cycle of T are fixed points of T^3. $\qquad\square$

5. LOCAL STABILITY CHARACTER OF THE POSITIVE EQUILIBRIUM: GRAPHICAL EXAMPLES

In this section we present some tables and graphical depictions of numerical examples. Figures 3 and 4 are graphical depictions of the modulus of the eigenvalues of the Jacobian of the map at the positive equilibrium point for various parameter values, where the parameter R has been replaced by α and the map T_α is given in the proof of Theorem 2.1 by equation (2.6). Figure 5 consists of plots of orbits generated with parameter conditions outlined in Theorem 2.1.

(a)   (b)   (c)
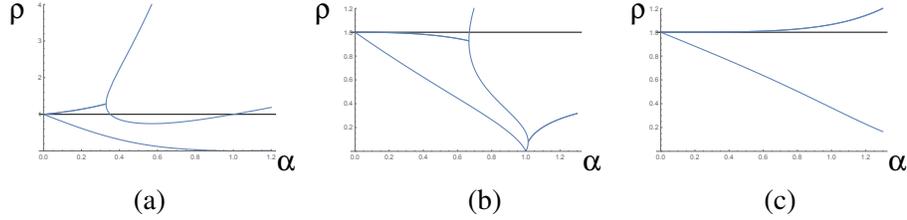
FIGURE 3. *Plot of the magnitude ρ of the characteristic values as a function of α in Case (i) of Theorem 2.1. (a) $\Delta > 0$. (b) $\Delta = 0$ and $(2 - \sqrt{2})c_{pa} < c_{ea} < (2 + \sqrt{2})c_{pa}$. (c) $\Delta = 0$ and $c_{ea} = (2 - \sqrt{2})c_{pa}$. For parameter values see Table 2.*

(a)   (b)

(c)   (d)
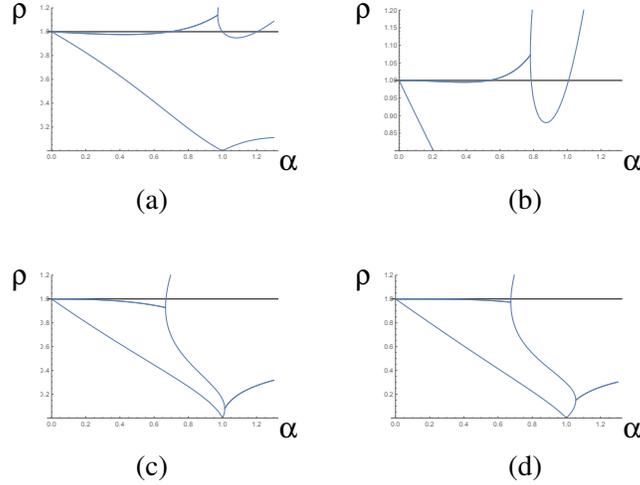
FIGURE 4. *Plot of the magnitude ρ of the characteristic values as a function of α in Case (ii) of Theorem 2.1. (a) $\Delta < 0$. (b) $\Delta = 0$ and $c_{ea} < (2 - \sqrt{2})c_{pa}$. (c) $\Delta = 0$ and $(2 + \sqrt{2})c_{pa} < c_{ea}$. (d) $\Delta = 0$ and $c_{ea} = (2 + \sqrt{2})c_{pa}$. For parameter values see Table 2.*

Fig.	3(a)	3(b)	3(c)	4(a)	4(b)	4(c)	4(d)
c_{ea}	1	1	$2 - \sqrt{2}$	1	1	1	1
c_{pa}	1	1	1	1	$\frac{59}{32}$	$\frac{5}{32}$	$1 + \frac{\sqrt{2}}{2}$
c_{el}	2	$\frac{1}{2}$	$\frac{3}{2} - \sqrt{2}$	$\frac{1}{4}$	$\frac{5}{64}$	$\frac{7}{8}$	$\frac{7}{8}$
μ_l	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{31}{59}$	$-\frac{3}{4} + \frac{7\sqrt{2}}{8}$

TABLE 2. *Parameter values of Figs. 3 and 4.*

(a)

(b)

(c)

(d)

	c_{ea}	c_{pa}	c_{el}	μ_l	α	Δ
Fig. 5 (a)	2	1	0.3	$\frac{1}{2}$	0.1	-2.4
Fig. 5 (b)	2	1	1	$\frac{1}{2}$	0.1	-1
Fig. 5 (c)	1	2	1	$\frac{1}{2}$	0.1	2
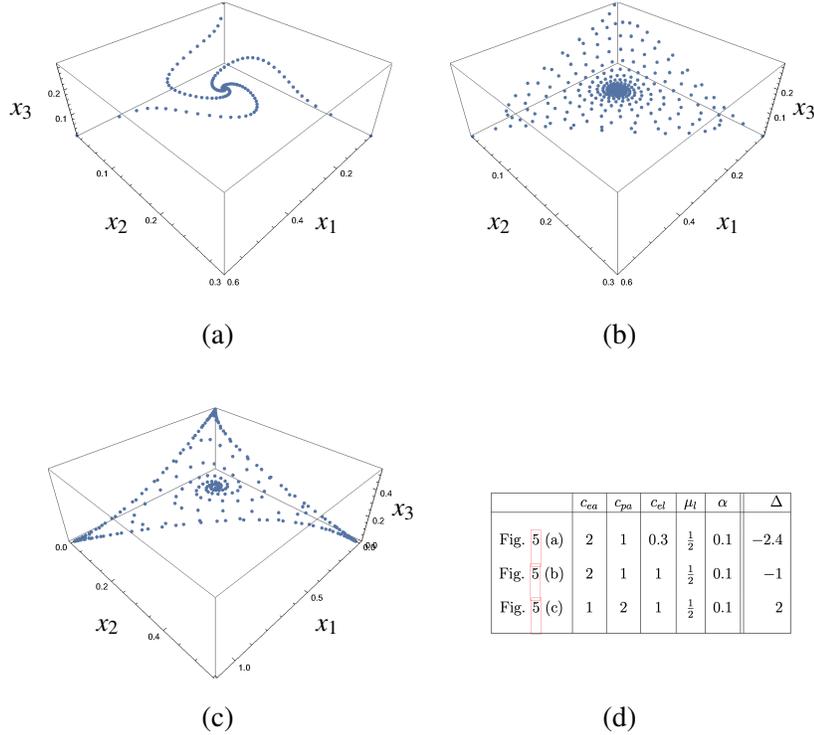
FIGURE 5. *Numerical examples of the dynamical behavior of the LPA map.* (a) $\Delta < -c_{ea}$. *The orbit with initial condition* $(x_1(0), x_2(0), x_3(0))$ $= (0.6, 0.01, 0.01)$ *is attracted to the positive equilibrium point.*
(b) $-c_{ea} < \Delta < 0$. *The orbit with initial condition* $(x_1(0), x_2(0), x_3(0)) =$ $(0.6, 0.01, 0.01)$ *is attracted to the positive equilibrium point.*
(c) $\Delta > 0$. *The orbit with initial condition* $(x_1(0), x_2(0), x_3(0)) =$ $(0.244281, 0.12214, 0.09)$ *is attracted to the heteroclinic orbit cycle which forms the boundary of the carrying simplex* Σ_α.
(d) *Parameter values used in (a), (b) and (c).*

6. CONCLUSIONS

The LPA model with $\mu_a = 1$ was studied in this work. For values of the parameter R that are larger than 1 but close enough to 1, the local stability character of the positive equilibrium was completely characterized in Theorem 2.1. Global dynamics on the boundary of the non-negative octant were also determined in Theorem 3.1 whenever $1 < R < e^2$. Finally Theorem 4.1 guarantees the existence of an invariant curve contained in the union of the coordinate planes that appears as R increases above the critical value 1. The work remaining in the analysis of the LPA model with $\mu_a = 1$ includes mainly the study of global dynamics in the interior of the nonnegative cone when a positive equilibrium exists. This will be treated in the upcoming article [9].

ACKNOWLEDGMENTS

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7. APPENDIX: SIGNS OF THE ENTRIES OF DT^3 AT $(0, y, z)$

Claim: With C as in Proposition 4.1, if $(0, y, z) \in C \cap \{x_1 = 0\}$, then $\text{sign}(J) = \begin{pmatrix} + & 0 & 0 \\ +0 & + & -0 \\ +0 & 0 & + \end{pmatrix}$.

Proof. Write $J := DT^3(0, y, z) = (J_{[1]} | J_{[2]} | J_{[3]})$, where $J_{[i]}$ is the i-th column of J. A calculation gives the following formulas:

$$J_{[1]} = \begin{pmatrix} R\exp\left(ye^{-zc_{\mathrm{pa}}}\left(\dfrac{Rc_{\mathrm{el}}\exp\left(\frac{Rzc_{\mathrm{el}}e^{-zc_{\mathrm{ea}}}}{u_l-1}-yc_{\mathrm{ea}}e^{-zc_{\mathrm{pa}}}\right)}{u_l-1}-c_{\mathrm{pa}}\right)\right) \\[20pt] \dfrac{R^2yzc_{\mathrm{el}}^2\exp\left(-z\left(\frac{Rc_{\mathrm{el}}e^{-zc_{\mathrm{ea}}}}{1-u_l}+c_{\mathrm{pa}}\right)-\left(c_{\mathrm{e\,a}}\left(ye^{-zc_{\mathrm{pa}}}+z\right)\right)\right)}{1-u_l} \\[20pt] Rze^{-zc_{\mathrm{ea}}}\left(c_{\mathrm{pa}}\left(u_l-1\right)e^{yc_{\mathrm{pa}}}\left(-e^{-zc_{\mathrm{pa}}}\right)-c_{\mathrm{el}}\right) \end{pmatrix},$$

$$J_{[2]} = \begin{pmatrix} 0 \\[12pt] R\left(e^{zc_{\mathrm{pa}}}-yc_{\mathrm{ea}}\right)\exp\left(\dfrac{Rzc_{\mathrm{el}}e^{-zc_{\mathrm{ea}}}}{u_l-1}+yc_{\mathrm{ea}}\left(-e^{-zc_{\mathrm{pa}}}\right)-2zc_{\mathrm{pa}}\right) \\[12pt] 0 \end{pmatrix},$$

$$J_{[3]} = \begin{pmatrix} 0 \\[12pt] -\dfrac{Ry\left(Rc_{\mathrm{el}}\left(zc_{\mathrm{ea}}-1\right)e^{zc_{\mathrm{pa}}}+c_{\mathrm{pa}}\left(u_l-1\right)e^{zc_{\mathrm{ea}}}\left(e^{zc_{\mathrm{pa}}}-yc_{\mathrm{ea}}\right)\right)\exp(H)}{u_l-1} \\[12pt] e^{-zc_{\mathrm{ea}}}\left(R-Rzc_{\mathrm{ea}}\right) \end{pmatrix},$$

where

$$H := \left(\dfrac{Rzc_{\mathrm{el}}e^{-zc_{\mathrm{ea}}}}{u_l-1}-\left(c_{\mathrm{ea}}\left(ye^{-zc_{\mathrm{pa}}}+z\right)\right)-2zc_{\mathrm{pa}}\right).$$

The statement follows from Proposition 4.1 and direct inspection of the columns of J given above. $\qquad\square$

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