

The LPA Model

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1 Introduction

Since the seminal papers of Lewis and Leslie in the 1940's [28, 29, 30], difference equations have played an important role in population dynamics and ecology. The utilization of models based on difference equations ranges from investigations of a very theoretical nature (a notable example being their seminal role in the development of chaos theory [31, 32, 33]) to studies of a very applied nature (see [2] for many examples). A difference equation model that has been particularly successful in applications to population dynamics and ecology is the so-called "LPA model". The success of this model is due to the fact that it has been rigorously connected to real data by statistical parameterization and validation methods and shown capable of quantitatively accurate descriptions and predictions by means of controlled experiments. The model has played a key role in many projects designed to document and study the predictions of nonlinear theory (including chaos) [2, 11]. While this kind of success is common, even expected, in many other scientific disciplines (the so-called "hard" sciences), it is rather unprecedented in ecology where mathematical models are all too commonly used only for theoretical speculations and expected to provide no more than qualitative accuracy, "guesstimates", or verbal metaphors. Because of the role it has played – and is continuing to play – in population dynamics and ecology, the LPA model is a worthy object of study for mathematicians interested in difference equations. In this paper I summarize the mathematical results known about the LPA model. I will also discuss many open questions. In addition to the LPA model itself, there are also a number of variants of the model that have also played important roles in applications. One example is a periodically forced LPA model which I discuss in Section 4. In Section 5 I mention several other variations of the LPA model that have received less mathematical attention.

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2 Basic properties of the LPA model

The LPA model is the nonlinear (Leslie) matrix model

$$\begin{pmatrix} L(t+1) \\ P(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & b \exp\left(-\frac{c_{el}}{V}L(t) - \frac{c_{ea}}{V}A(t)\right) \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp\left(-\frac{c_{pa}}{V}A(t)\right) & 1 - \mu_a \end{pmatrix} \begin{pmatrix} L(t) \\ P(t) \\ A(t) \end{pmatrix}.$$

This matrix equation is equivalent to the system

$$L(t+1) = bA(t) \exp\left(-\frac{c_{el}}{V}L(t) - \frac{c_{ea}}{V}A(t)\right) \quad (2.1)$$

$$P(t+1) = (1 - \mu_l)L(t) \quad (2.2)$$

$$A(t+1) = P(t) \exp\left(-\frac{c_{pa}}{V}A(t)\right) + (1 - \mu_a)A(t). \quad (2.3)$$

of three difference equations.

It is useful as a guide to mathematical investigations of the system (2.1)-(2.3) to understand some of the biological interpretations for the equations. The name of the model derives from the biological interpretation of three state variables used in the applications from which the model arose. The laboratory experiments utilized species of insects from the genus *Tribolium* (flour beetles) which have three life cycle stages. The state variables $L(t)$, $P(t)$, $A(t)$ denote the number of individuals, at time t , present in the larval, pupal, and adult stages respectively. The exponential terms appearing in the equations arise from contacts among individuals that decrease survival probabilities. The exponential form of the nonlinearities derive from a Poisson process involving random encounters among individual organisms [6]. These encounters are assumed inversely proportional to habitat size V , which accounts for the parameter ratios appearing in the exponential terms. (This law has been validated for *Tribolium* by laboratory experiments.) The parameter $b > 0$ is the *inherent* per adult recruitment of larvae (“inherent” means when the negative effects of encounters among individuals are negligible). The two parameters μ_l and μ_a satisfy $0 < \mu_l < 1$, $0 < \mu_a \leq 1$ and represent death rates (the fractions of the larvae and adult stages that die each unit of time). For notational simplicity one can assume, without loss of generality, that $V = 1$. There are, however, applications in which it is advantageous to keep V in the model equations. In applications involving *Tribolium* the intra-stage contacts are cannibalistic encounters, and in that context the parameters c_{el} , c_{ea} , and c_{pa} are called “cannibalism coefficients”.

Although developed with a particular organism in mind, system (2.1)-(2.3) can be an appropriate model for other organisms possessing three life cycle stages. In this regard, it should be noted that the model assumes that the unit of time is equal to that spent by individuals in the larvae stage. This assumption accounts for the lack of an additive term (such as, for example, $(1 - \mu)L(t)$) on the right hand side of (2.1) that would account for larvae at time t which are still larvae at time $t + 1$. Another assumption of the model is that the time spent in the pupal stage is identical to that spent in the larvae stage. Hence, there appears no additive term (such as $(1 - \mu)P(t)$) on the right hand side of (2.2) that accounts for pupae at time t which are still pupae at time $t + 1$. Finally, in equation (2.3) the model assumes that all pupae successfully emerge as adults (in the absence of

encounters with adults). This accounts for the absence of a multiplicative factor $1 - \mu_p$ in the first term on the right hand side of (2.3). A more general three life cycle stage model would contain some or all of these additional terms. However, these biological assumptions present in the LPA model (2.1)-(2.3) are appropriate for *Tribolium* populations. In this paper we restrict our attention to this model.

In applications to population dynamics, one is interested only in nonnegative values of the three state variables. It is clear from the difference equations (2.1)-(2.3) that

$$\begin{pmatrix} L(0) \\ P(0) \\ A(0) \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \implies \begin{pmatrix} L(t) \\ P(t) \\ A(t) \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

and

$$\begin{pmatrix} L(0) \\ P(0) \\ A(0) \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \implies \begin{pmatrix} L(t) \\ P(t) \\ A(t) \end{pmatrix} \neq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \quad (2.4)$$

for all $t = 1, 2, 3, \dots$. That is to say, the nonnegative cone is forward invariant.

Moreover, all orbits in the nonnegative cone are (forward) bounded. To see this note from (2.1) and (2.2) that

$$0 \leq L(t+1) \leq bA(t) \exp\left(-\frac{c_{pa}}{V}A(t)\right) \leq b\frac{V}{c_{pa}e}$$

for $t = 0, 1, 2, \dots$ and consequently

$$0 \leq P(t+1) \leq (1 - \mu_l) b\frac{V}{c_{pa}e}$$

for $t = 1, 2, 3, \dots$. In other words

$$\begin{aligned} 0 \leq L(t) &\leq b\frac{V}{c_{pa}e}, & t = 1, 2, 3, \dots \\ 0 \leq P(t) &\leq (1 - \mu_l) b\frac{V}{c_{pa}e} & t = 2, 3, 4, \dots \end{aligned}$$

For $t \geq 2$ we find from (2.3) that

$$0 \leq A(t+1) \leq (1 - \mu_l) b\frac{V}{c_{pa}e} + (1 - \mu_a) A(t)$$

from which the inequality

$$0 \leq A(t) \leq \frac{1}{\mu_a} (1 - \mu_l) b\frac{V}{c_{pa}e} + (1 - \mu_a)^{t-2} A(2) \quad t = 3, 4, 5, \dots$$

follows by an induction. After a finite number of iterations

$$0 \leq A(t) \leq 2\frac{1 - \mu_l}{\mu_a} b\frac{V}{c_{pa}e}.$$

Thus, there is a compact set in the nonnegative cone inside of which all nonnegative orbits lie after a finite number of steps.

From (2.1)-(2.3) we have, for orbits in the nonnegative cone, the inequalities

$$\begin{aligned} 0 \leq L(t+1) &\leq bA(t) \\ 0 \leq P(t+1) &\leq (1 - \mu_l) L(t) \\ 0 \leq A(t+1) &\leq P(t) + (1 - \mu_a) A(t) \end{aligned} \quad (2.5)$$

for all $t = 0, 1, 2, \dots$. An induction shows

$$\begin{aligned} 0 &\leq L(t) \leq x(t) \\ 0 &\leq P(t) \leq y(t) \\ 0 &\leq A(t) \leq z(t) \end{aligned} \tag{2.6}$$

where $x(t), y(t), z(t)$ are defined by the linear system

$$\begin{aligned} x(t+1) &= bz(t) \\ y(t+1) &= (1 - \mu_l) y(t) \\ z(t+1) &= y(t) + (1 - \mu_a) z(t) \end{aligned} \tag{2.7}$$

with initial conditions $x(0) = L(0) \geq 0$, $y(0) = P(0) \geq 0$, and $z(0) = A(0) \geq 0$. If $\mu_a < 1$ the coefficient matrix

$$\begin{pmatrix} 0 & 0 & b \\ 1 - \mu_l & 0 & 0 \\ 0 & 1 & 1 - \mu_a \end{pmatrix} \tag{2.8}$$

associated with the linear system (2.7) is irreducible and primitive. (Its fourth power is positive.) Therefore, (2.8) has a real, positive, simple, and strictly dominant r eigenvalue [1]. The dominant eigenvalue is less than 1 if

$$n \doteq \frac{1 - \mu_l}{\mu_a} b < 1$$

and greater than 1 if $n > 1$ [6, 9].

Consequently, if $n < 1$ it follows that all solutions of (2.7) tend to the origin as $t \rightarrow +\infty$. From (2.6) we see $n < 1$ also implies that all orbits of the LPA model (lying in the nonnegative cone) tend to the origin as $t \rightarrow +\infty$. Furthermore, the matrix (2.8) is the Jacobian of the LPA model at the origin and, as a result, $n < 1$ also implies the origin is locally asymptotically stable (LAS) [6, 16].

The origin is a “trivial” equilibrium of the LPA model (2.1)-(2.3). Its global asymptotic stability when $n < 1$ means, in the biological context, that the population goes extinct for all initial conditions. The quantity n has an important biological interpretation, namely, it is the expected number of offspring per individual per life time [2, 6]. The inequality $n < 1$ means, then, that on average individuals do not replace themselves by reproduction. Given this biological interpretation of n , we expect $n > 1$ to imply that the population will not go extinct. Since the dominant eigenvalue of the Jacobian matrix (2.8) is greater than 1, the origin is in fact unstable [6, 16]. However, the origin might have a stable manifold and some nonnegative orbits might approach it. If $\mu_a < 1$ we will show that the origin cannot have a stable manifold that intersects the nonnegative cone (except at the origin).

In addition to the (positive) dominant eigenvalue, the Jacobian matrix (2.8) has the complex conjugate pair of eigenvalues

$$\begin{aligned} \lambda_{\pm} &= \alpha \pm \beta i \\ \alpha &= \frac{1}{3}s_a - \frac{1}{2}\gamma - \frac{1}{18}\frac{s_a^2}{\gamma} \\ \beta &= \frac{\sqrt{3}}{2}\frac{1}{\gamma}\left(\gamma^2 - \frac{1}{9}s_a^2\right) > 0 \end{aligned}$$

where

$$\gamma \doteq \left(\frac{1}{2} b s_l + \frac{1}{27} s_a^3 + \left(\frac{1}{27} b s_a^3 s_l + \frac{1}{4} b^2 s_l^2 \right)^{1/2} \right)^{1/3} > 0$$

$$s_l \doteq 1 - \mu_l > 0, \quad s_a \doteq 1 - \mu_a > 0.$$

These complex conjugate eigenvalues (calculated with the aid of an algebraic computer program) satisfy

$$|\lambda^\pm| < 1 \quad \text{when} \quad \mu_a < 1 \tag{2.9}$$

$$|\lambda^\pm| = (b s_l)^{2/3} = n^{2/3} \quad \text{when} \quad \mu_a = 1.$$

The stable manifold at the origin is tangent to the plane spanned by the real and imaginary parts of a complex eigenvector associated with λ^- (or its conjugate λ^+) [6, 16]. An eigenvector associated with eigenvalue λ^- is the vector

$$\begin{pmatrix} \lambda^- (\lambda^- - s_a) \\ (\lambda^- - s_a) s_l \\ s_l \end{pmatrix}$$

whose real and imaginary parts are

$$\begin{pmatrix} -\frac{1}{2} (\alpha^2 + \beta^2) \\ \frac{1}{2\alpha} (\beta^2 - \alpha^2) s_l \\ s_l \end{pmatrix}, \quad \begin{pmatrix} -\frac{\beta}{2\alpha} (\alpha^2 + \beta^2) \\ -\beta s_l \\ s_l \end{pmatrix}.$$

Since both of these real vectors have components of opposite signs, the plane they span intersects the nonnegative cone only at the origin. It follows that in a neighborhood of the origin the stable manifold intersects the nonnegative cone only at the origin. From this fact, and from (2.4), we see that an orbit in the nonnegative cone cannot approach the origin. In the terminology of [25], the origin is an isolated invariant set in the nonnegative cone that is its own stable set. By Theorem 4.1 of [25], the origin is uniformly persistent. This means that there exists a positive constant $\mu > 0$ such that

$$\liminf_{t \rightarrow +\infty} (L(t) + P(t) + A(t)) \geq \mu > 0$$

for all orbits in the nonnegative cone (except the origin).

We have seen that when $n > 1$ and $\mu_a < 1$ all nonnegative orbits are (forward) bounded and cannot approach the origin. A fundamental problem is to describe the omega limit set of such orbits. First we point out that when $n > 1$ there exists a positive equilibrium (i.e., an equilibrium all of whose components are positive) and this equilibrium is the only nontrivial, nonnegative equilibrium. To see this consider the equilibrium equations

$$L = bA \exp\left(-\frac{c_{el}}{V}L - \frac{c_{ea}}{V}A\right) \tag{2.10}$$

$$P = (1 - \mu_l)L \tag{2.11}$$

$$A = P \exp\left(-\frac{c_{pa}}{V}A\right) + (1 - \mu_a)A \tag{2.12}$$

of (2.1)-(2.3). Equations (2.12) and (2.11) respectively imply

$$P = \mu_a A \exp\left(\frac{c_{pa}}{V}A\right), \quad L = \frac{\mu_a}{1 - \mu_l} A \exp\left(\frac{c_{pa}}{V}A\right). \tag{2.13}$$

If $A = 0$ then $L = P = 0$. Suppose $A > 0$. A substitution of (2.13) into equation (2.10) yields (after some simplification) the equation

$$\frac{c_{el}}{V} \frac{\mu_a}{1 - \mu_l} A \exp\left(\frac{c_{pa}}{V} A\right) + \left(\frac{c_{ea}}{V} + \frac{c_{pa}}{V}\right) A = \ln n \quad (2.14)$$

for A . The left hand side of this equation, as a function of A , vanishes for $A = 0$ and is strictly increasing and unbounded for $A > 0$. We conclude that for $\ln n > 0$ there is a unique, positive solution $A = A_n > 0$ of equation (2.14) which, when used in equations (2.13), yields a positive equilibrium of the LPA model. Note that

$$A_1 = 0, \quad \frac{dA_n}{dn} > 0 \quad \text{for } n > 1 \quad \text{and} \quad \lim_{n \rightarrow +\infty} A_n = +\infty. \quad (2.15)$$

(For $\ln n < 0$ there is a unique, negative solution of (2.14) which yields a negative equilibrium of the LPA model. Thus, a transcritical bifurcation of two equilibrium branches occurs at the origin when $n = 1$.)

When $n > 1$ the positive equilibrium becomes a candidate for an attractor in the nonnegative cone. However, little is known about the stability properties of this equilibrium. When $\mu_a < 1$ it is known that when $n > 1$ is sufficiently close to 1 the positive equilibrium is LAS. This is the familiar ‘‘exchange of stability’’ phenomenon that generically occurs at a transcritical bifurcation. A proof using Liapunov-Schmidt methods appears in [6]. Another way to prove this fact is by considering the characteristic polynomial p of the Jacobian

$$J = \begin{pmatrix} -\frac{c_{el}}{V} b A \exp\left(-\frac{c_{ea}}{V} A - \frac{c_{el}}{V} L\right) & 0 & \left(1 - \frac{c_{ea}}{V} A\right) b \exp\left(-\frac{c_{ea}}{V} A - \frac{c_{el}}{V} L\right) \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp\left(-\frac{c_{pa}}{V} A\right) & -\frac{c_{pa}}{V} P \exp\left(-\frac{c_{pa}}{V} A\right) + 1 - \mu_a \end{pmatrix}$$

of the LPA model. An evaluation of J at the positive equilibrium (using the equilibrium equations (2.10)-(2.12)) yields

$$J(n) = \begin{pmatrix} -\frac{c_{el}}{V} \frac{\mu_a}{1 - \mu_l} A \exp\left(\frac{c_{pa}}{V} A\right) & 0 & \frac{\mu_a}{1 - \mu_l} \left(1 - \frac{c_{ea}}{V} A\right) \exp\left(\frac{c_{pa}}{V} A\right) \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp\left(-\frac{c_{pa}}{V} A\right) & -\frac{c_{pa}}{V} \mu_a A + 1 - \mu_a \end{pmatrix}$$

and

$$\begin{aligned} p(\lambda, A) &= \lambda^3 + \left(\frac{c_{el}}{V} \frac{\mu_a}{1 - \mu_l} A \exp\left(\frac{c_{pa}}{V} A\right) + \frac{c_{pa}}{V} \mu_a A - 1 + \mu_a\right) \lambda^2 \\ &+ \frac{c_{el}}{V} \frac{\mu_a}{1 - \mu_l} \left(\frac{c_{pa}}{V} \mu_a A - 1 + \mu_a\right) A \exp\left(\frac{c_{pa}}{V} A\right) \lambda \\ &+ \left(\frac{c_{ea}}{V} A - 1\right) \mu_a. \end{aligned} \quad (2.16)$$

The positive equilibrium is a function of n and therefore so are the eigenvalues $\lambda = \lambda_n$.

When $n = 1$, the positive equilibrium collapses to the origin and the Jacobian reduces to the Leslie matrix (2.8). Therefore, the eigenvalues of J at $n = 1$ are $\lambda = 1$ and λ^\pm . Let $\lambda = \lambda_n$ denote the eigenvalue of J that satisfies $\lambda_1 = 1$. An implicit differentiation of $p(\lambda_n, A_n) = 0$ with respect to n yields

$$\frac{\partial}{\partial \lambda} p(\lambda_n, A_n) \frac{d\lambda_n}{dn} + \frac{\partial}{\partial A} p(\lambda_n, A_n) \frac{dA_n}{dn} = 0$$

and

$$\frac{d\lambda_n}{dn} = -\frac{\frac{\partial}{\partial A} p(\lambda_n, A_n) \frac{dA_n}{dn}}{\frac{\partial}{\partial \lambda} p(\lambda_n, A_n)}.$$

A calculation shows of the partial derivatives of p are

$$\begin{aligned} \left. \frac{\partial p(\lambda, A)}{\partial A} \right|_{(\lambda, A)=(1,0)} &= \frac{\mu_a}{1 - \mu_l} \left(\frac{c_{pa}}{V} (1 - \mu_l) + \frac{c_{el}}{V} \mu_a + \frac{c_{ea}}{V} (1 - \mu_l) \right) > 0 \\ \left. \frac{\partial p(\lambda, A)}{d\lambda} \right|_{(\lambda, A)=(1,0)} &= 1 + 2\mu_a > 0. \end{aligned}$$

It follows (from (2.15)) that

$$\left. \frac{d\lambda_n}{dn} \right|_{n=1} < 0$$

and hence $\lambda_1(n) < 1$ for $n > 1$ sufficiently close to 1.

If $\mu_a < 1$ then, for n close to 1, the remaining two eigenvalues are close to the complex eigenvalues λ^\pm which have magnitude less than 1 (see (2.9)). It follows in this case that all three eigenvalues of J are inside the unit circle when $n > 1$ is close to 1, and the positive equilibrium is LAS.

However, if $\mu_a = 1$ then the stability of the positive equilibrium is determined by the complex eigenvalues $\lambda^\pm(n)$ for $n > 1$. These eigenvalues have magnitude 1 when $n = 1$ (see (2.9)) and the problem is to determine their magnitude for $n > 1$. It is shown in [8] that $|\lambda^\pm(n)| > 1$ for $n > 1$ close to 1 and therefore that the positive equilibrium is unstable in this case.

In the following theorem we summarize the facts we have obtained so far about the LPA model.

Theorem 2.1 *The following hold for the LPA model (2.1)-(2.3).*

(a) *Orbits associated with nonnegative initial conditions remain (forward) bounded and in the nonnegative cone for all $t = 0, 1, 2, \dots$*

(b) *If $n < 1$ then the origin is locally asymptotically stable and globally attracting in the nonnegative cone.*

(c) *If $n > 1$ there exists a unique nonnegative, nontrivial equilibrium and this equilibrium is positive.*

(d) *If $\mu_a < 1$ and $n > 1$ then the LPA model is uniformly persistent on the nonnegative cone with respect to the origin.*

(e) *If $\mu_a < 1$ then the positive equilibrium is locally asymptotically stable for $n > 1$ sufficiently close to 1.*

(f) *If $\mu_a = 1$ then the positive equilibrium is unstable for $n > 1$ sufficiently close to 1.*

For $n < 1$ the the origin is globally asymptotically stable. Little is known about the global asymptotic stability of the positive equilibrium when $n > 1$. I conjecture that the positive equilibrium is globally asymptotically stability for $n > 1$ sufficiently close to 1, but I have no proof of this assertion. One known global stability result concerns the special case when

$$c_{el} = 0. \tag{2.17}$$

In this case, it is shown in [42] that the positive equilibrium is globally asymptotically stable if

$$1 < n < \min \left\{ e, \frac{1 - \mu_a}{\mu_a} \frac{c_{ea}}{c_{pa}} e \right\}.$$

This condition requires $\mu_a < 1$ and the inequality

$$r \doteq \frac{c_{pa}}{c_{ea}} < \frac{1 - \mu_a}{\mu_a} e$$

for the ratio r of cannibalism coefficients. The case (2.17), about which more is said in the next section, is an interesting mathematical case, but it is not relevant to the applications that have been made to *Tribolium* populations. (Larval on egg cannibalism is very significant in *Tribolium* populations.) Global stability results when $c_{el} > 0$ would be of interest.

The local stability results in Theorem 2.1 are valid for $n > 1$ close to 1. In the next section we show that the positive equilibrium is not LAS for all $n > 1$.

3 Non-equilibrium dynamics

We begin by examining the positive equilibrium of the LPA model (2.1)-(2.3) when $\mu_a < 1$. In the proof of Theorem 2.1 we saw that all three eigenvalues λ of the Jacobian J evaluated at the positive equilibrium lie inside the unit circle for n sufficiently close to 1. In order for the positive equilibrium to lose stability as n increases, at least one eigenvalue must migrate outside the unit circle. Eigenvalues λ are the roots of the characteristic polynomial (2.16) where $A = A_n$ is the third component of the positive equilibrium. From the constant term of this polynomial we see that the product of the three eigenvalues of J is larger than 1 if $A_n > (1 + \mu_a)V/c_{ea}\mu_a$. From (2.15) we have the following result.

Theorem 3.1 *There exists a number $n^* > 1$ such that positive equilibrium of the LPA model (2.1)-(2.3) is unstable for $n > n^*$.*

Let $n_1 \leq n^*$ be the smallest value of $n > 1$ for which a root of the characteristic polynomial $p(\lambda, A_n)$ lies on the unit circle. Then $1 < n < n_1$ implies the positive equilibrium is LAS. The number n_1 is the smallest candidate for a local bifurcation point at which the positive equilibrium destabilizes and a bifurcation to another attractor occurs. Local bifurcations are classified according to the location where a root leaves the unit circle [17]. Note that $\lambda = 1$ cannot be a root of $p(\lambda, A(n))$ for any $n > 1$, as the calculation

$$p(1, A_n) = \frac{c_{pa}}{V} \mu_a A_n + \frac{c_{el}}{V} \frac{\mu_a}{1 - \mu_l} \left(\frac{c_{pa}}{V} \mu_a A_n + \mu_a \right) A_n \exp \left(\frac{c_{pa}}{V} A_n \right) + \frac{c_{ea}}{V} \mu_a A_n > 0$$

shows. This implies that certain types of local bifurcations of positive equilibria, such as transcritical, saddle-node, and pitchfork bifurcations, never occur in the LPA model for $n > 1$ [17]. (This is, of course, consistent with the fact that there is a unique positive equilibrium for $n > 1$.) There are only two ways the positive equilibrium can lose stability at n_1 (or any other value of $n > 1$): a root of $p(\lambda, A_n)$ at $n = n_1$ equals either -1 or $e^{i\theta}$ for some θ satisfying $0 < \theta < \pi$. In the first case a period doubling bifurcation “generically” occurs in which a 2-cycle comes into existence. In the second case an invariant loop bifurcation “generically” occurs (sometimes called a Neimark-Sacker or discrete Hopf bifurcation) in which an aperiodic attractor comes into existence. (Certain technical sufficiency conditions are needed to guarantee that these bifurcations actually occur [17].) It turns out that both of these types of local bifurcations are possible, depending on the values of the model parameters. See Figure 1.

There are few rigorous bifurcation results for the model (2.1)-(2.3). One special case for which period doubling and invariant loop bifurcation points n_1 have been

calculated is when $c_{el} = 0$. In [13] it is shown in this case that $p(\lambda, A_n)$ has root $\lambda = -1$ when

$$n = n_1 = \exp\left(\frac{2}{\mu_a}\right)$$

and a pair of complex conjugate roots of magnitude equal to 1 when

$$n = n_1 = \exp\left(\frac{K^\pm(\mu_a, r)}{\mu_a}\right)$$

where

$$K^\pm(\mu_a, r) \doteq -\frac{1}{2} \frac{1+r}{1-r} [(r-3)\mu_a + 1] \\ \pm \frac{1}{2} \frac{1+r}{1-r} \left([(r-3)\mu_a + 1]^2 + 4(1-r)(1-\mu_a)(2\mu_a + 1) \right)^{1/2}.$$

While these formulae allow us to draw “parameter maps” that show the boundaries in parameter space where equilibrium destabilization occurs, rigorous proofs that local bifurcations occur at these points are currently lacking, as is the determination of the bifurcation characteristics (e.g., whether the bifurcation is supercritical or subcritical and whether the non-equilibrium attractors that result are stable or unstable).

Bifurcations have played a central role in the applications of the LPA model (2.1)-(2.3). Although the quantity n is a mathematically and biologically useful bifurcation parameter, other model parameters can be used as a bifurcation parameter. For example, the parameters μ_a and c_{pa} were used in the bifurcation experiments involving *Tribolium* described in [11]. An interesting special case arises from the “route-to-chaos” experiment in those studies. In that experiment μ_a was experimentally manipulated to equal 0.96 and a complicated sequence of bifurcations, that included chaotic dynamics, was observed as c_{pa} increases. These bifurcations have only been studied numerically. No rigorous mathematical analysis has been made of the bifurcation sequence and the chaotic attractors it contains. The fact that $\mu_a = 0.96$ in that well-known experiment motivates a study of the LPA model for $\mu_a = 1$. Although this case is not covered by some of the basic results presented in Sec. 2, it turns out to be a mathematically tractable case. A first study of this case appears in [8].

With $\mu_a = 1$ in (2.1)-(2.3) the coordinate axes are invariant. In fact, orbits on the axes move sequentially from one to the next, re-visiting each axis every third step. We call these orbits *fully synchronized* (a name that derives from the biological application in which the three life cycle stages are never mutually present). An orbit is fully synchronized if and only if its initial condition is fully synchronized (i.e., contains two zeroes). If we denote every third L component by x

$$x(t) = L(3t), \quad t = 0, 1, 2, \dots$$

we find that $x(t)$ satisfies the so-called Ricker map

$$x(t+1) = nx(t) \exp(-cx(t))$$

with

$$n = b(1 - \mu_l), \quad c \doteq c_{ea}(1 - \mu_l) > 0.$$

In so far as fully synchronous orbits are concerned, it follows that the LPA model with $\mu_a = 1$ exhibits the famous period doubling route-to-chaos with respect to the dynamics at every third step. (A similar result follows if either of the other two

coordinate axes is considered.) For example, if $1 < n$ the Ricker equation has a unique positive equilibrium $x = c^{-1} \ln n$. This equilibrium corresponds to a fully synchronous 3-cycle of the LPA model. The Ricker equilibrium is (asymptotically) stable and globally attracting (on the positive axis) if $1 < n < e^2$ and consequently the 3-cycle is (asymptotically) stable and globally attracting with respect to fully synchronous, positive orbits of the LPA model. For $n > e^2$ the Ricker equation has a 2-cycle and this 2-cycle corresponds to a fully synchronous 6-cycle of the LPA model. A cycle of period p of the Ricker equation produces a fully synchronous $3p$ -cycle of the LPA model. A quasi-periodic or chaotic orbit of the Ricker map produces a similar type of fully synchronous orbit of the LPA model. The stability properties of Ricker orbits is inherited by the LPA orbits when one restricts attention to fully synchronous orbits (motion on the coordinate axes).

With $\mu_a = 1$ it is also true that the coordinate planes are invariant and that an orbit lying in the coordinate planes moves sequentially from one to the other. Let

$$\begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix}$$

denote every third point on an orbit of the LPA model (2.1)-(2.3). An orbit lying in a coordinate plane (but not on a coordinate axis) always has one zero and is called *partially synchronized*. After three steps a partially synchronized orbit returns to the same coordinate plane. Consider, for example, the (L, A) coordinate plane. From (2.1)-(2.3) we find that an initial condition in this plane results, at every third step, in an orbit satisfying the two dimensional system

$$x(t+1) = nx(t) \exp(-cx(t)) \quad (3.1)$$

$$z(t+1) = [n \exp(-\alpha x(t))] z(t) \exp(-\beta z(t)) \quad (3.2)$$

where

$$\begin{aligned} \alpha &\doteq c_{el} + c_{pa} (1 - \mu_l) \\ \beta &\doteq c_{ea}. \end{aligned}$$

This system has nonnegative equilibria

$$\begin{pmatrix} x \\ z \end{pmatrix} = \begin{cases} (0, 0) \\ \left(\frac{1}{c} \ln n, 0\right) & \text{if } n > 1 \\ \left(\frac{1}{c} \ln n, \frac{\gamma}{\beta} \ln n\right) & \text{if } n > 1 \text{ and } \gamma > 0 \end{cases}$$

where

$$\gamma \doteq 1 - \frac{\alpha}{c} = \frac{(c_{ea} - c_{pa})(1 - \mu_l) - c_{el}}{c_{ea}(1 - \mu_l)}.$$

A linearization analysis shows the following results:

$$\begin{aligned} \begin{pmatrix} 0 \\ 0 \end{pmatrix} & \text{ is a repeller if } n > 1 \\ \begin{pmatrix} \frac{1}{c} \ln n \\ 0 \end{pmatrix} & \begin{cases} \text{ is LAS stable if } 1 < n < e^2 \text{ and } \gamma < 0 \\ \text{ is a saddle if } 1 < n < e^2, \gamma > 0 \\ \text{ is a saddle if } n > e^2, \gamma < 0 \\ \text{ is a repeller if } n > e^2, \gamma > 0 \end{cases} \\ \begin{pmatrix} \frac{1}{c} \ln n \\ \frac{\gamma}{\beta} \ln n \end{pmatrix} & \begin{cases} \text{ is LAS stable if } 1 < n < \min \{e^2, e^{2/\gamma}\} \text{ and } \gamma > 0 \\ \text{ is a saddle if } \gamma > 1 \text{ and } e^{2/\gamma} < n < e^2 \\ \text{ is a saddle if } 0 < \gamma < 1 \text{ and } e^2 < n < e^{2/\gamma} \\ \text{ is a repeller if } n > \max \{e^2, e^{2/\gamma}\}. \end{cases} \end{aligned}$$

Of these many cases, only the case

$$1 < n < e^2 \text{ and } \gamma < 0 \quad (3.3)$$

has been analyzed in detail.

In the system (3.1)-(3.2) the first equation shows that the x -component satisfies a Ricker equation which is uncoupled from the second equation. Thus, an initial condition $x(0) > 0$ equation (3.1) determines a sequence $x(t)$, which when substituted into equation (3.2) produces a non-autonomous Ricker equation for the dynamics of the z -component. Under the assumption (3.3) it follows that $\lim_{t \rightarrow +\infty} x(t) = c^{-1} \ln n$ and equation (3.2) becomes ‘‘asymptotically autonomous’’ with a ‘‘limiting equation’’ obtained by replacing $x(t)$ with its limit $c^{-1} \ln n$. Let $w(t)$ denote the solutions of the limiting equation

$$w(t+1) = n^\gamma w(t) \exp(-\beta w(t)).$$

This is a Ricker equation and from (3.3) it follows that $\lim_{t \rightarrow +\infty} w(t) = 0$. Known theorems concerning asymptotically autonomous difference equations [5] relate the dynamics of this limiting equation to those of (3.2). In [8] these theorems are used to show that the equilibrium $(x, z) = (c^{-1} \ln n, 0)$ is globally attracting in the positive (x, z) quadrant.

A completely analogous analysis can also be carried out in the other two coordinate planes with regard to the equilibrium points $(x, y) = (0, \beta^{-1} \ln n)$ and $(y, z) = (0, \beta^{-1} \ln n)$. It follows, under assumption (3.3), that all orbits $(x(t), y(t), z(t))$ starting in a coordinate plane asymptotically equilibrate. What this result means for the LPA model is that all orbits $(L(t), P(t), A(t))$ lying in the coordinate planes asymptotically approach a 3-cycle located on the coordinate axes, namely the cycle defined by the three axis points

$$\begin{pmatrix} L \\ P \\ A \end{pmatrix} = \begin{pmatrix} \frac{1}{c} \ln n \\ 0 \\ 0 \end{pmatrix} \longrightarrow \begin{pmatrix} 0 \\ \frac{1}{\beta} \ln n \\ 0 \end{pmatrix} \longrightarrow \begin{pmatrix} 0 \\ 0 \\ \frac{1}{\beta} \ln n \end{pmatrix}. \quad (3.4)$$

These three points are also fixed points of the three step (second composite) LPA map, which we denote by

$$\begin{pmatrix} x_1 \\ y_1 \\ z_1 \end{pmatrix} \doteq \begin{pmatrix} \frac{1}{c} \ln n \\ 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} x_2 \\ y_2 \\ z_2 \end{pmatrix} \doteq \begin{pmatrix} 0 \\ \frac{1}{\beta} \ln n \\ 0 \end{pmatrix}, \quad \begin{pmatrix} x_3 \\ y_3 \\ z_3 \end{pmatrix} \doteq \begin{pmatrix} 0 \\ 0 \\ \frac{1}{\beta} \ln n \end{pmatrix} \quad (3.5)$$

The cases other than (3.3) provide open problems concerning the asymptotic dynamics of synchronous orbits of the LPA model when $\mu_a = 1$. It is worth noting, however, that in terms of the original model parameters, the condition $\gamma < 0$ (i.e., $(c_{ea} - c_{pa})(1 - \mu_l) - c_{el} < 0$) holds for the experimentally estimated values of the parameters in the *Tribolium* experiments.

Theorem 3.2 [8] *Under assumptions*

$$\mu_a = 1, \quad 1 < n < e^2, \quad (c_{ea} - c_{pa})(1 - \mu_l) - c_{el} < 0 \quad (3.6)$$

all synchronous orbits of the LPA model (2.1)-(2.3) tend asymptotically to the fully synchronous 3-cycle (3.4).

More can be said about the case (3.3). In the full, three dimensional phase space of the LPA model, the fully synchronous 3-cycle (3.4) is unstable. A calculation of the products of the Jacobian evaluated at the three points of the 3-cycle shows, in fact, that the 3-cycle is a saddle, with a two dimensional stable manifold (the coordinate planes) and a one dimensional unstable manifold [8]. What is the attractor of nonsynchronous orbits in this case?

We return, for a moment, to the general case of the LPA model when $\mu_a = 1$. It was shown in Sec. 2 that there exists a (unique) positive equilibrium when $n > 1$. It was also shown that when, in addition, $\mu_a < 1$ the positive equilibrium is stable at least for n near 1. It turns out, however, that when $\mu_a = 1$ this is no longer true. A tedious perturbation analysis carried out in [8] shows that for all $n > 1$ near 1 the positive equilibrium is a saddle (with a one dimensional stable manifold and a two dimension stable manifold on which the equilibrium is a stable spiral). Therefore, in case (3.3) when $n > 1$ is close to 1, neither the origin, the positive equilibrium, nor the fully synchronous 3-cycle are stable attractors.

The reason for the failure of the exchange of stability principle for the transcritical bifurcation at the origin when $n = 1$ is seen from the Jacobian (2.8) of the LPA model evaluated at the origin and with $\mu_a = 1$. The eigenvalues of that matrix are the cube roots of $n = b(1 - \mu_l)$ and hence are the cube roots of unity when $n = 1$. Thus, when $\mu_a = 1$ the origin loses stability as n increases through 1 because *all three* eigenvalues leave the unit circle simultaneously and, as a result, the bifurcation is “nongeneric”. The eigenvalue that crosses at +1 is associated with the transcritical bifurcation of two equilibrium branches at $n = 1$ and the existence of the positive equilibrium for $n > 1$. The two complex eigenvalues that also occur at $n = 1$ would be associated, in a generic situation (when they were the only eigenvalues crossing the unit circle at $n = 1$), with the bifurcation of an invariant loop. This suggests the bifurcation of an invariant loop from the origin at $n = 1$.

Although the general invariant loop bifurcation theorem (Neimark/Sacker or discrete Hopf Theorem) cannot be used for the nongeneric case bifurcation at $n = 1$, the existence of an invariant loop can be proved in case (3.3) by a straightforward analysis as follows. With regard to the dynamics of every third step (the second composite of the LPA model), the first equilibrium point in (3.5) lies in both the (x, z) and the (x, y) coordinate planes. We saw above that in the (x, z) plane all positive orbits tend to this equilibrium while in the (x, y) all orbits tend to the second equilibrium point in (3.5). Therefore, the (one dimensional) unstable manifold of the first equilibrium point [6] tends to the second equilibrium point. That is to say, there a heteroclinic orbit lying in the (x, y) coordinate plane that

connects the first two equilibrium points in (3.5). Similarly, there are heteroclinic orbits lying in the (y, z) and (x, z) coordinate planes that connect the second to the third and the third to the first equilibrium points respectively. This set of three equilibria and their connecting heteroclinic orbits form an invariant loop. In terms of the original (one step) LPA model, each of the three equilibria (3.5) correspond, as initial points, to the three different phases of the 3-cycle (3.4). The heteroclinic orbits are partially synchronized orbits connecting the three phases of the 3-cycle.

Theorem 3.3 [8] *Under assumptions (3.6) there exists an invariant loop for the LPA model (2.1)-(2.3) having the form of a cycle chain of synchronous orbits. The cycle chain consists of the fully synchronous 3-cycle (3.4) and partially synchronous orbits that heteroclinically connect the three temporal phases of the 3-cycle.*

The 3-cycle is unstable in the three dimensional phase space of the LPA model. When (3.6) holds, numerical simulations suggest, however, that the synchronous cycle chain on which the 3-cycle lies is an attractor (for nonnegative orbits) at least for $n > 1$ close to 1 [8]. A rigorous proof of this is currently unavailable. If this is true, then we see in this case that the nongeneric bifurcation at $n = 1$ results in both a positive equilibrium and an invariant loop, but it is the invariant loop that inherits the stability from the origin.

Many open questions remain concerning the case $\mu_a = 1$. When $\gamma > 0$ replaces $\gamma < 0$ in (3.6), the equilibrium $(x, z) = (c^{-1} \ln n, \gamma \beta^{-1} \ln n)$ gives rise to a partially synchronous 3-cycle. Does this produce a cycle chain invariant loop for the LPA model? If so, when is it stable? When $n > e^2$ the Ricker equation (3.1) has non-equilibrium attractors, including chaos. What kind of attractors do these produce for the planar system (3.1)-(3.2)? What kind of synchronous orbits of the LPA model do they yield?

Recall that $\mu_a = 0.96$ has been an important case in applications. Another open mathematical question is how the dynamics in the case $\mu_a = 1$ relate to those when μ_a is near 1.

4 The periodically forced LPA model

The LPA model (2.1)-(2.3) is an autonomous model; all parameters are assumed constant in time. The majority of models used in the mathematical ecology literature are autonomous, even though real world ecological systems are likely to be significantly influenced by external forces. If random external forces are taken into account (i.e., perturbations in the model system that are described probabilistically rather than deterministically), then a model determines a stochastic process. At the other extreme, if the external forces have strong pattern of regularity, which can be reasonably modeled deterministically, then the dynamic model becomes non-autonomous. An example of external fluctuations that can show such regularity are those related to natural cycles such as daily, monthly, or seasonal oscillations in physical and/or biological parameters. In laboratory experiments, such as those carried out using *Tribolium* and the LPA model, environmental fluctuations can be held to a minimum (temperature, humidity, nutrient availability, habitat size, etc.). On the other hand, in controlled laboratory experiments one can also deliberately fluctuate an environmental parameter, in order to study the resulting effects on the population dynamics. In the case of laboratory cultures of *Tribolium* such an experiment was reported by Jillson [26]. In this experiment the

habitat of the beetle cultures (the volume of flour medium) was changed according to a periodic schedule. Jillson noted in one of his experiments (he performed experiments using several different periodic patterns of volume changes) that the total biomass of *Tribolium* was significantly higher in the oscillating habitat than it was in a habitat held constant at the average volume. This observation was noteworthy for at least two reasons. First, it suggested that a population manager might increase yield by periodically oscillating resource availability, rather than holding it constant. Second, Jillson's experimental result contradicts what at the time was a commonly held tenet that fluctuating environments were deleterious to biological populations [35, 34, 36]. Jillson made no mathematical study of his experiment, but a mathematical explanation of his result has been obtained by using the LPA model, suitably modified to account for periodically oscillating volumes V [4, 7, 18, 19, 22].

If a sequence $V(t) > 0$ of period p is substituted for V in (2.1)-(2.3), the result is the periodically forced LPA model

$$L(t+1) = bA(t) \exp\left(-\frac{c_{el}}{V(t)}L(t) - \frac{c_{ea}}{V(t)}A(t)\right) \quad (4.1)$$

$$P(t+1) = (1 - \mu_l) L(t) \quad (4.2)$$

$$A(t+1) = P(t) \exp\left(-\frac{c_{pa}}{V(t)}A(t)\right) + (1 - \mu_a) A(t). \quad (4.3)$$

An important mathematical problem is to determine the long term dynamics of solutions with nonnegative initial conditions. It is clear from the equations that nonnegative (positive) initial conditions produce nonnegative (positive) solutions.

The origin is an equilibrium point of the periodic LPA model (4.1)-(4.3). As for the autonomous LPA model, *the origin is LAS and it globally attracts all non-negative solutions if $n < 1$* . The proof of this statement follows closely that of the autonomous case since the inequalities (2.5) remain valid for the periodic model (4.1)-(4.3).

Suppose $n > 1$. The linearization of (4.1)-(4.3) at the origin has coefficient matrix (2.8) which, as we noted in Sec. 2, has a real eigenvalue greater than 1 (if also $\mu_a < 1$). Thus, as in the autonomous case, *the origin is unstable when $n > 1$ and $\mu_a < 1$* .

Furthermore, *when $n > 1$ solutions of (4.1)-(4.3) are (forward) bounded*. The proof of this fact follows from the same comparison argument given for the autonomous case in Section 2 once the inequalities

$$\begin{aligned} 0 \leq L(t+1) &\leq bA(t) \exp\left(-\frac{c_{pa}}{V_m}A(t)\right) \leq b\frac{V_m}{c_{pa}e}, \quad \text{for } t = 0, 1, 2, \dots \\ 0 \leq P(t+1) &\leq (1 - \mu_l) b\frac{V_m}{c_{pa}e}, \quad \text{for } t = 1, 2, 3, \dots \\ 0 \leq A(t+1) &= (1 - \mu_l) b\frac{V_m}{c_{pa}e} + (1 - \mu_a) A(t), \quad \text{for } t = 2, 3, 4, \dots \end{aligned}$$

are noted. Here $V_m = \max V(t) > 0$.

The challenge is to determine the asymptotic properties of solutions when $n > 1$. A first approach is to obtain basic results for the periodic LPA model that parallel those of the autonomous LPA model in Theorem 2.1. For example, is the

periodic LPA model (4.1)-(4.3) uniformly persistent with respect to the origin (and nonnegative orbits) when $n > 1$? This result has been established for period $p = 2$ in [22], but has not been proved for periods $p > 2$. (Perhaps the proof in [22] can be generalized to the case $p > 2$.) It is shown in [7] (using degree theory) that when $\mu_a < 1$ the periodic LPA model has an unbounded continuum of positive p -cycles for values of $n > 1$ that bifurcates from the origin at $n = 1$. This continuum is the counterpart to the continuum of (unique) positive equilibria that exists for all $n > 1$ in the autonomous case. Aside from its unboundedness, little is known about the continuum and the properties of the p -cycles lying on it. One case that has been studied in some detail is period $p = 2$ case.

When $p = 2$, we can write $V(t) = \langle V \rangle (1 + \alpha(-1)^t)$ where $\langle V \rangle > 0$ is the average of the cycle and $|\alpha|$ is the relative amplitude. Absorbing $\langle V \rangle$ into the coefficients c_{el} , c_{ea} , c_{pa} we write

$$V(t) = 1 + \alpha(-1)^t \quad (4.4)$$

in the periodic LPA model equations (4.1)-(4.3). In [18] it is shown, for a general class of periodic maps, that the bifurcating continuum of positive p -cycles has a parameterization (Liapunov-Schmidt expansion) near the origin for n near 1, and formulas for calculating the lowest order terms are given. When applied to the $p = 2$ periodic LPA model, these formulas yield the expansions

$$\begin{aligned} L_\alpha(t) &= \frac{\mu_a}{1 - \mu_l} \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)(t) \\ P_\alpha(t) &= \mu_a \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)(t) \\ A_\alpha(t) &= \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)(t) \\ n &= 1 + \left(c_{ea} + \frac{\mu_a}{1 - \mu_l} c_{el} + c_{pa} \right) \frac{1}{1 - \alpha^2} \varepsilon_\alpha + O(|\varepsilon_\alpha^2|) \end{aligned} \quad (4.5)$$

for the positive 2-cycles near the bifurcation point (i.e., for small $\varepsilon_\alpha > 0$) [22]. In each equation $O(|\varepsilon_\alpha^2|)(t)$ represents terms that are 2-periodic in t and of order two or higher in ε_α for small $|\varepsilon_\alpha|$. The subscript α denotes dependence on the (amplitude/phase) parameter α .

The expansions (4.5) can be used to approximate the dominant eigenvalue associated with the linearization of the model taken at the 2-cycle in order to determine the cycle's stability. It turns out that the dominant eigenvalue has the expansion

$$1 - 2 \frac{\mu_a}{1 + 2\mu_l} \left(c_{ea} + \frac{\mu_a}{1 - \mu_l} c_{el} + c_{pa} \right) \frac{1}{1 - \alpha^2} \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)$$

and hence is less than 1 for $\varepsilon_\alpha > 0$ small. This shows that the bifurcating 2-cycles are LAS for $n > 1$ close to 1.

These facts about the periodic LPA model are summarized in the theorem below. More details can be found in [7, 18, 22].

Theorem 4.1 *Assume $V(t) > 0$ is a p -periodic sequence. The following hold for the periodically forced LPA model (4.1)-(4.3).*

(a) *Orbits associated with nonnegative initial conditions are (forward) bounded and remain in the nonnegative cone for all $t = 0, 1, 2, \dots$.*

(b) *If $n < 1$ then the origin is locally asymptotically stable and global attracts all nonnegative solutions.*

(c) If $\mu_a < 1$ there exists an unbounded continuum of positive p -cycles for positive values of $n > 1$ that bifurcates from the origin at $n = 1$.

(d) If $\mu_a < 1$ and $p = 2$ then the LPA model is uniformly persistent on the nonnegative cone with respect to the origin for $n > 1$.

(e) If $\mu_a < 1$ and $p = 2$ then the positive equilibrium is locally asymptotically stable for $n > 1$ sufficiently close to 1.

There are several interesting, unsolved problems left open by this theorem. Is the range of n values associated with the continuum in (c) the entire half line $n > 1$ (i.e., is there a positive p -cycle for every $n > 1$)? For a given value of n is the p -cycle from the continuum the only positive cycle? Under what conditions are the positive p -cycles from the continuum LAS? Unstable? Globally attracting (for positive orbits)? What kinds of bifurcations do they undergo? Do (d) and (e) hold for periods $p > 2$? For $n > 1$ the case $\mu_a = 1$ has not been studied.

The existence and stability results in Theorem 4.1 do not address the issue of interest in Jillson's experiment, namely the unexpected increase in population numbers observed in the periodically fluctuating volumes. Although Jillson conducted experiments using several different periods, he observed an increase in population numbers only when the period of the flour volume oscillation was $p = 2$. For this reason studies of this problem using (4.1)-(4.3) have concentrated on the period $p = 2$ case.

To address Jillson's observation by using the periodic LPA model, we need to relate the attractor of the periodic model ($\alpha \neq 0$) to that of the autonomous model ($\alpha = 0$). One way to do this, under the assumption that the attractors in both cases are cycles (an equilibrium is a 1-cycle), is to compare averages. This can be done component-wise (comparing the cycle average of the L -stage components and so on) or, more in keeping with Jillson's result, using the cycle averages of total population numbers $L + P + A$. If the cycle average is greater in the periodic case (all other model parameters equal), then we say that the periodic forcing has caused a *resonance*; if it is less, we say an *attenuation* occurs as a result of the periodic forcing.

In general, whether resonance or attenuation occurs in periodically forced difference equations depends on the type of nonlinearities and on the values of parameters that appear in the equations. Resonance never occurs in certain types of one dimensional monotone maps [10]. On the other hand, for a general class of period $p = 2$ forced difference equations that exhibit a bifurcation of positive equilibria from the origin, Henson [19] gives conditions under which attenuation or resonance occurs near the bifurcation point [19].

Both attenuation and resonance is possible in the LPA model, depending on the parameter values. For example, it is shown in [22] that attenuation always occurs for $n > 1$ near 1, but that for n is sufficiently large resonance occurs for some values of the model parameters.

For $n > 1$ near 1 we can see why attenuation occurs by making use of the expansions (4.5), from which follow the expansions

$$\begin{aligned}\langle L_\alpha(t) \rangle &= \frac{\mu_a}{1 - \mu_l} \varepsilon_\alpha + O(|\varepsilon_\alpha^2|) \\ \langle P_\alpha(t) \rangle &= \mu_a \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)\end{aligned}$$

$$\begin{aligned}\langle A_\alpha(t) \rangle &= \varepsilon_\alpha + O(|\varepsilon_\alpha^2|) \\ n &= 1 + \left(c_{ea} + \frac{\mu_a}{1 - \mu_l} c_{el} + c_{pa} \right) \frac{1}{1 - \alpha^2} \varepsilon_\alpha + O(|\varepsilon_\alpha^2|)\end{aligned}$$

for the cycle averages of each 2-cycle component. For autonomous case $\alpha = 0$ we have the expansions

$$\begin{aligned}L_0 &= \frac{\mu_a}{1 - \mu_l} \varepsilon_0 + O(|\varepsilon_0^2|) \\ P_0 &= \mu_a \varepsilon_0 + O(|\varepsilon_0^2|) \\ A_0 &= \varepsilon_0 + O(|\varepsilon_0^2|) \\ n &= 1 + \left(c_{ea} + \frac{\mu_a}{1 - \mu_l} c_{el} + c_{pa} \right) \varepsilon_0 + O(|\varepsilon_0^2|)\end{aligned}$$

for the positive equilibria for $n > 1$ near 1. In order to make a comparison between the equilibria and the cycle averages for the same value of n , we need to choose the parameter ε_α so that

$$\frac{1}{1 - \alpha^2} \varepsilon_\alpha = \varepsilon_0.$$

Thus,

$$\begin{aligned}L_0 - \langle L_\alpha(t) \rangle &= \alpha^2 \frac{\mu_a}{1 - \mu_l} \varepsilon_0 + O(|\varepsilon_0^2|) \\ P_0 - \langle P_\alpha(t) \rangle &= \alpha^2 \mu_a \varepsilon_0 + O(|\varepsilon_0^2|) \\ A_0 - \langle A_\alpha(t) \rangle &= \alpha^2 \varepsilon_0 + O(|\varepsilon_0^2|).\end{aligned}$$

and for $\varepsilon_0 > 0$ sufficiently small it follows for all $\alpha \neq 0$ that

$$L_0 - \langle L_\alpha(t) \rangle > 0, \quad P_0 - \langle P_\alpha(t) \rangle > 0, \quad A_0 - \langle A_\alpha(t) \rangle > 0.$$

We see that there is a component-wise attenuation for $\varepsilon_0 > 0$ small (i.e., $n > 1$ close to 1). It follows, of course, that there is also an attenuation in total population size

$$L_0 + P_0 + A_0 > \langle L_\alpha(t) \rangle + \langle P_\alpha(t) \rangle + \langle A_\alpha(t) \rangle.$$

as well.

Theorem 4.2 *Consider the 2-periodically forced LPA model (4.1)-(4.3) with $V(t)$ given by (4.4) and $\mu_a < 1$. For $n > 1$ sufficiently close to 1 the locally asymptotically stable, positive 2-cycles that bifurcate from the origin at $n = 1$ (see Theorem 4.1) are (component-wise) attenuant.*

This Theorem does not provide an explanation of Jillson's experimental observation. However, resonance can occur in the periodic LPA model when $n > 1$ is sufficiently large. A numerical example appears in Figure 3, in which the positive 2-cycles change from attenuant to resonant as n increases. In [22] sufficient conditions for resonance when $n > 1$ is large were obtained using regular perturbation techniques.

Implicit function based proofs show, if $n > 1$ and $\mu_a < 1$, that there exist positive 2-cycles for $|\alpha|$ sufficiently small, that these cycles are infinitely differentiable functions of α , and that they approach the equilibrium as $\alpha \rightarrow 0$. These 2-cycles

have Taylor expansions

$$\begin{aligned} L_\alpha(t) &= L_0 + L_1(t)\alpha + L_2(t)\alpha^2 + O(\alpha^3)(t) \\ P_\alpha(t) &= P_0 + P_1(t)\alpha + P_2(t)\alpha^2 + O(\alpha^3)(t) \\ A_\alpha(t) &= A_0 + A_1(t)\alpha + A_2(t)\alpha^2 + O(\alpha^3)(t) \end{aligned} \quad (4.6)$$

where $O(\alpha^3)(t)$ represents terms that are 2-periodic in t and of order three or higher in α for small $|\alpha|$ and (L_0, P_0, A_0) is the positive equilibrium of the autonomous LPA model (which is assumed hyperbolic). It turns out that $\langle L_1(t) \rangle = \langle P_1(t) \rangle = \langle A_1(t) \rangle = 0$ and some tedious calculations using (4.6) show

$$\lim_{n \rightarrow +\infty} \langle L_\alpha(t) \rangle - L_0 = 2 \frac{c_{pa}\mu_a^2 + 2c_{ea}\mu_a - 2c_{ea}}{\mu_a^2 c_{pa} c_{el}} \alpha^2 + O(\alpha^3) \quad (4.7)$$

$$\lim_{n \rightarrow +\infty} \langle P_\alpha(t) \rangle - P_0 = 2 \frac{c_{pa}\mu_a^2 + 2c_{ea}\mu_a - 2c_{ea}}{\mu_a^2 c_{pa} c_{el}} (1 - \mu_l) \alpha^2 + O(\alpha^3) \quad (4.8)$$

$$\lim_{n \rightarrow +\infty} \langle A_\alpha(t) \rangle - A_0 = 4 \frac{1 - \mu_a}{\mu_a^2 c_{pa}} \alpha^2 + O(\alpha^3). \quad (4.9)$$

From the coefficients of α^2 in these expressions, one can determine conditions on the model parameters under which these limits are positive or negative for small $|\alpha|$ and hence when the components of the 2-cycle are resonant or attenuant for large n .

For example, for small amplitudes α and sufficiently large n we see from (4.9) that the A component of the 2-cycles is resonant. On the other hand, the L and P components are resonant (attenuant) if $c_{pa}\mu_a^2 + 2c_{ea}\mu_a - 2c_{ea} > 0$ (< 0). Thus, we find that it is possible for some components to be resonant while others are attenuant. By summing the three limits (4.7)-(4.9) we can determine conditions under which the total population size is resonant or attenuant from the α^2 coefficient in

$$\begin{aligned} &\lim_{n \rightarrow +\infty} \langle L_\alpha(t) + P_\alpha(t) + A_\alpha(t) \rangle \\ &= 2 \left((2 - \mu_l) \frac{c_{pa}\mu_a^2 + 2c_{ea}\mu_a - 2c_{ea}}{\mu_a^2 c_{pa} c_{el}} + 2 \frac{1 - \mu_a}{\mu_a^2 c_{pa}} \right) \alpha^2 + O(\alpha^3). \end{aligned}$$

These results show that the question of resonance posed by Jillson's experiment is a complicated one. Moreover, there is yet another issue. In order to be meaningful in applications the 2-cycles (4.6) must be stable. If the equilibrium (L_0, P_0, A_0) is LAS then, for $|\alpha|$ small, so are the 2-cycles. It turns out, however, that this is not the case for parameter values estimated from Jillson's data (see the caption of Figure 3). Instead, for those parameters the autonomous LPA model has an unstable equilibrium and the attractor is a 2-cycle.

Consequently, to address Jillson's resonance question we have to ask what happens when the LPA model with a stable 2-cycle is periodically forced? A perturbation analysis in α can also be carried out in this case. The result is that for α small there exist two stable 2-cycles. These cycles result from the two different phases of the 2-cycle of the autonomous case, but they themselves are not (in general) shifted of one another. This result is a corollary of a general theorem of Henson [20] in which a perturbation analysis is done for a general class of difference equations when the autonomous case has a stable q -cycle and the system is periodically forced with period r (also see [41]). Moreover, Henson shows that of all the cycles

of the forced system that perturb from the phase shifts of the q -cycle at least one is attenuant and at least one is resonant.

When applied to the LPA model (4.1)-(4.3) and (4.4), Henson's results show for the Jillson estimated parameters that there exist two LAS 2-cycles, one resonant and one attenuant, for small amplitude forcing. Thus, for small α there exist in this case two stable 2-cycles (perturbations of the phases of the stable 2-cycle of the autonomous model $\alpha = 0$) and one unstable 2-cycle (a perturbation of the unstable equilibrium of the autonomous model $\alpha = 0$). This multiple attractor scenario has been experimentally verified by laboratory experiments using *Tribolium* [21].

In Jillson's experiment, however, $\alpha = 0.6$ and numerical simulations show there are not multiple attractors, but instead a globally attracting 2-cycle. Numerical simulations suggest an explanation for this. As α is increased from 0, the unstable 2-cycle and the stable attenuant 2-cycle collide and annihilate one another in a saddle node bifurcation at approximately $a = 0.45$ [4], leaving a globally attracting resonance 2-cycle for $\alpha > 0.45$. There are at this time no mathematical proofs of these assertions.

As we see, many challenging mathematical questions concerning periodically forced difference equations have arisen from applications involving the LPA model. While some results have been obtained, there remain numerous open questions concerning the existence, stability, and resonance of cycles induced by periodic forcing (including a rigorous explanation of the Jillson experiment).

5 Concluding remarks

In this paper I have discussed the LPA model and one of its variations (the periodically forced LPA model). Other variations of the model have arisen in applications, most of which have been little studied from a rigorous mathematical point of view. In this final section, I briefly discuss some of these variations.

Animals come in whole numbers. Even so, most mathematical models in population dynamics utilize state space variables that are continuous. This is the case of the LPA models in the previous sections. In recent studies it has been shown how restriction of state variables in the LPA model to a finite lattice of values (such as whole integers or to a finite number of densities obtained from integers divided by volume) explains distinctive patterns observed in data that find no explanation from the continuous state space version of the model [11, 23, 27]. An example of an "integerized" LPA model results from simply rounding the right hand sides of each equation (2.1)-(2.3) to the nearest integer. This rather ad hoc mathematical way of obtaining an integer model can be replaced by a more sophisticated derivation from an integer valued probabilistic model [11]. The continuous state space LPA model (2.1)-(2.3) derives from that probabilistic model by taking the expectations (means) of the random state variables. On the other hand, a deterministic model that remains integer valued results from the modes of the random state variables. Thus, the "mean" LPA models treated in this paper can be derived from a stochastic "master" model, but so can an integer valued "mode" LPA model, which it turns out is given by the difference equations

$$\begin{aligned} L(t+1) &= \text{floor} \left[bA(t) \exp \left(-\frac{c_{el}}{V} L(t) - \frac{c_{ea}}{V} A(t) \right) \right] \\ P(t+1) &= \text{floor} [(1 - \mu_l) L(t)] \\ A(t+1) &= \text{floor} \left[P(t) \exp \left(-\frac{c_{pa}}{V} A(t) \right) \right] + \text{floor} [(1 - \mu_a) A(t)]. \end{aligned}$$

($\text{floor } [x]$ is the largest integer less than or equal to x). The mathematical properties of such integerized versions of the LPA model have not been studied in a systematic or rigorous way. It is not difficult to show that the nonnegative cone (on the lattice) is forward invariant for these integerized LPA models, that all nonnegative orbits are bounded, and, as a result, that all orbits become periodic after a finite number of steps. However, a study remains to be made of the set of final periodic states, their uniqueness or lack of uniqueness, their regions of attraction, and so on. Other interesting questions concern the relationship among the dynamics of the mean, integer, and random LPA models; see [11, 27, 24].

A genetics variation of the LPA model has recently played a role in experimental studies of how genetic adaptation can alter a population's dynamics. For the case of 2 alleles at a single locus the model takes the form [3]

$$\begin{aligned} L_i(t+1) &= \frac{2}{i!(2-i)!} p^{2-i}(t) q^i(t) b_i A(t) \exp(-c_{el}L(t) - c_{ea}A(t)) \\ P_i(t+1) &= (1 - \mu_{l,i}) L_i(t) \\ A_i(t+1) &= P_i(t) \exp(-c_{pa}A(t)) + (1 - \mu_a) A_i(t) \end{aligned} \quad (5.1)$$

where $i = 0, 1, 2$ and

$$\begin{aligned} L(t) &= \sum_{i=0}^2 L_i(t), & P(t) &= \sum_{i=0}^2 P_i(t), & A(t) &= \sum_{i=0}^2 A_i(t) \\ p(t) &= \frac{A_0(t) + \frac{1}{2}A_1(t)}{A(t)}, & q(t) &= 1 - p(t). \end{aligned}$$

(A number of simplifying biological assumptions have been made in order to attain this model, including random mating, a Hardy-Weinberg distribution of newly formed zygotes, and the restriction that all three genotypes have the same cannibalism coefficients and adult stage survival rates.) In this model L_0 and L_2 are the larval numbers of the homozygote population and L_1 is the larval numbers of the heterozygote population. The notation is similar for the pupal and adult stages P_i and A_i .

If initially only the homozygote population $i = 0$ is present, then the nine dimensional genetics LPA model (5.1) reduces to the three dimensional LPA model (2.1)-(2.3) with $L(t) = L_0(t)$, $P(t) = P_0(t)$, $A(t) = A_0(t)$.

With other genetic strains present, some algebraic manipulations show that the total numbers L , P , and A satisfy the equations

$$\begin{aligned} L(t+1) &= b(t)A(t) \exp(-c_{el}L(t) - c_{ea}A(t)) \\ P(t+1) &= (1 - \mu_l(t-1)) L(t) \\ A(t+1) &= P(t) \exp(-c_{pa}A(t)) + (1 - \mu_a) A(t) \end{aligned} \quad (5.2)$$

where

$$\begin{aligned} b(t) &\doteq p^2(t)b_0 + 2p(t)q(t)b_1 + q^2(t)b_2 \\ \mu_l(t) &\doteq \frac{p^2(t)b_0\mu_{l,0} + 2p(t)q(t)b_1\mu_{l,1} + q^2(t)b_2\mu_{l,2}}{b(t)}. \end{aligned}$$

From the similarity of the equations (5.2) and the LPA model (2.1)-(2.3) one can see how the genetics (embodied in $b(t)$ and $\mu_l(t)$) cause the parameters b and μ_l in the LPA model to change with time. From this point of view, genetic change and

adaptation in a population is expressed as parameter changes in the LPA model. As we have seen, parameter changes in the LPA model can result in dynamic bifurcations. The experiment reported in [3] (involving the adaptation of species of *Tribolium* to the pesticide malathion) documented such dynamic changes as predicted by the genetic LPA model (5.1).

A mixture of population dynamics and genetics is unusual in biomathematical modeling. This, together with its role in the genetics experiments involving flour beetles, make the genetics LPA model (5.1) an interesting model to investigate mathematically. There has been virtually no analysis made of the model.

Another interesting variation of the LPA model arises from the historical importance of *Tribolium* in the theory of ecological competition. During the formulation of competition theory in the 1940-1950's, laboratory experiments utilizing two species of *Tribolium* were influential in establishing some fundamental principles relating to the concepts of ecological niche, limiting similarity of species, and competitive exclusion or coexistence [37, 38, 39, 40]. A basic tenet was formulated that an ecological community could have no more species than the number of available (limited) resources and, in particular, that two similar species relying on one resource could not coexist indefinitely. This principle is supported by many mathematical models (including the famous two species model of Lotka/Volterra). Given this history and the recent establishment of the LPA model as an accurate model for the dynamics of *Tribolium*, it is interesting to consider a competition version of the LPA model.

In particular, it is interesting to compare the predictions of a LPA competition model to those of the classical Lotka/Volterra model (and similar competition models). Such a study was initiated in [14]. The competition LPA model results from two copies of the system (2.1)-(2.3) which have been coupled as follows:

$$\begin{aligned}
 L(t+1) &= BA(t) \exp\left(-\frac{c_{EL}}{V}L(t) - \frac{c_{EA}}{V}A(t)\right) \exp\left(-\frac{c_{El}}{V}l(t) - \frac{c_{Ea}}{V}a(t)\right) \\
 P(t+1) &= (1 - \mu_L) L(t) \\
 A(t+1) &= P(t) \exp\left(-\frac{c_{PA}}{V}A(t)\right) \exp\left(-\frac{c_{Pa}}{V}a(t)\right) + (1 - \mu_A) A(t) \\
 l(t+1) &= bAa(t) \exp\left(-\frac{c_{el}}{V}l(t) - \frac{c_{ea}}{V}a(t)\right) \exp\left(-\frac{c_{eL}}{V}L(t) - \frac{c_{eA}}{V}A(t)\right) \\
 p(t+1) &= (1 - \mu_l) l(t) \\
 a(t+1) &= p(t) \exp\left(-\frac{c_{pa}}{V}a(t)\right) \exp\left(-\frac{c_{pA}}{V}A(t)\right) + (1 - \mu_a) a(t).
 \end{aligned}$$

Some results concerning asymptotic dynamics appear in [14], including analyses of the extinction equilibrium (in which both species are absent) and the competitive exclusion equilibria (in which one species is absent), a persistence result when both $n_1 = B(1 - \mu_L)/\mu_A > 1$ and $n_2 = b(1 - \mu_l)/\mu_a > 1$, and some existence and bifurcation results for coexistence (positive) equilibria. However, a great deal is unknown about the asymptotic dynamics of this six dimensional system (the properties of attractors, their uniqueness or lack of uniqueness, their bifurcations as parameters change, and so on). Given the model's high dimensionality and large number of parameters, it perhaps comes as no surprise that complicated non-equilibrium dynamics are possible, including chaotic dynamics [14], unlike the famous Lotka/Volterra equations.

Interestingly, recent numerical studies have also shown that the model can possess scenarios that are not found in classical competition theory [14, 15]. For example, it is possible for the system to possess two exclusion attractors (equilibria) and a coexistence attractor (a 2-cycle in which both species are present) and, as a result, whether or not one species goes extinct or both coexist depends on the initial conditions. (There is even some evidence for this scenario in the historical experiments involving *Tribolium* carried out by T. Park [15].) Currently there is no mathematical proof of this dynamic scenario, or for any of the many other complicated scenarios of multiple attractors that have been discovered by numerical simulations.

Difference equations have a long history of application to population dynamics. The LPA model has a distinctive place in that history because of its close ties with data and of its key role in a long list of experimental studies. For a mathematician the model, and its many variations, provide many interesting problems to study and abundant opportunities to make meaningful contributions to both theoretical and applied population biology.

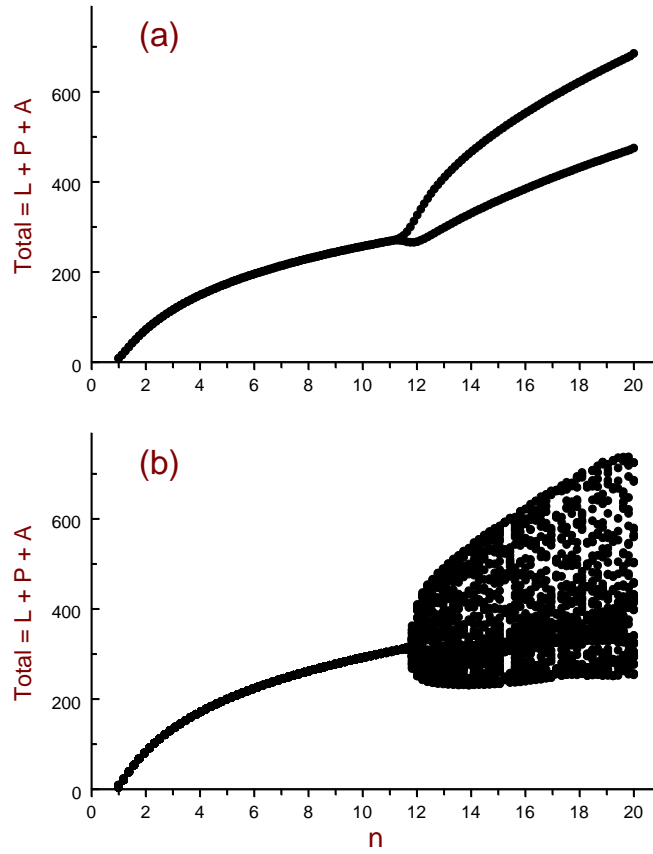


FIGURE 1. Bifurcation diagrams are shown in which the total “population size” $L + P + A$ of the attractor of the LPA model (2.1)-(2.3) is plotted against n . In both plots $\mu_l = 0.2$, $c_{el} = 0.01$, $c_{ea} = 0.01$, $c_{pa} = 0.005$, and $V = 1$. In (a) $\mu_a = 0.5$ and in (b) $\mu_a = 0.96$.

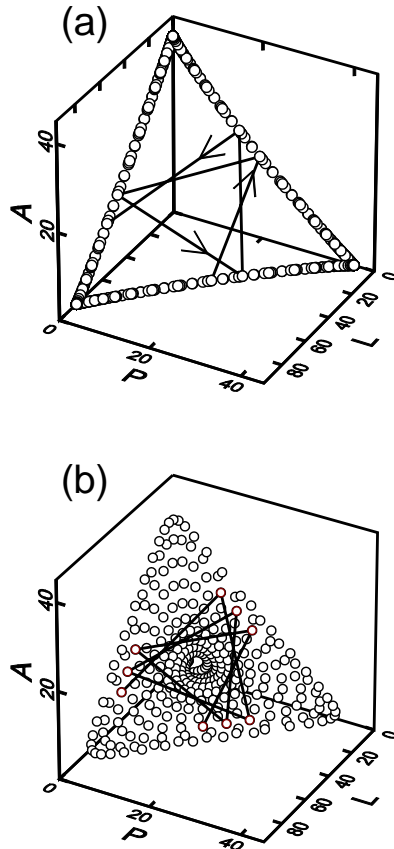


FIGURE 2. (a) The cycle chain in Theorem 3.3 is shown for parameter values $\mu_a = 1$, $\mu_l = 0.5$, $c_{el} = 0.007$, $c_{ea} = 0.01$, $c_{pa} = 0.01$, and $V = 1$. (b) A positive orbit is shown approaching the cycle chain in (a). Initial conditions are $(L(0), P(0), A(0)) = (4, 2, 2)$. Several consecutive points are connected by straight lines in order to show the temporal sequence.

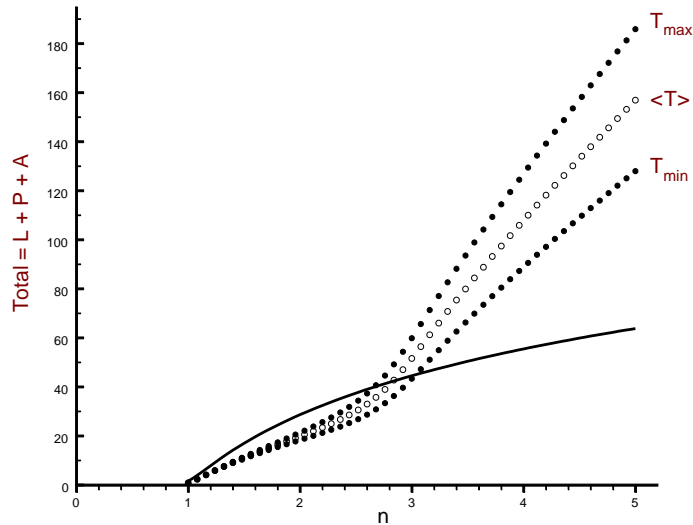


FIGURE 3. The solid line shows the equilibrium total population size $T = L + P + A$ of the autonomous LPA model as a function of $n = b(1 - \mu_l)/\mu_a$. Parameter values are those estimated from the control cultures of Jillson's experiment [12]: $\mu_a = 0.1542$, $\mu_l = 0.4794$, $c_{el} = 0.0584$, $c_{ea} = 0.0058$, $c_{pa} = 0.0105$, $b = 4.445$ with $V = 1$ (representing the volume occupied by the standard laboratory volume of 20g of flour medium). The lines of solid circles show the maxima T_{\max} and minima T_{\min} of the positive 2-cycles from the periodically forced LPA model with the same parameter values and $\alpha = 0.6$ (which is the relative amplitude of Jillson's resonance experiment). The line of open circles shows the cycle averages $\langle T \rangle = (T_{\max} + T_{\min})/2$ of the 2-cycles. For n less than 2.8 (approximately) the cycle averages are less than the equilibria; they are greater for n greater than 2.8. For n greater than 3 (approximately) even the cycle minima are greater than the equilibria. This diagram is consistent with the attenuation assertion of Theorem 4.2, but shows resonance for n sufficiently large. Note that the estimated value of $n = 15.18$ for Jillson's experiment does not appear in this graph.

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