A continuous, age-structured insect population model

Shandelle M. Henson

Department of Mathematics, University of Arizona, Tucson, AZ 85721, USA.
e-mail: henson@math.arizona.edu

Abstract. A continuous age-structured model of cannibalistic insect populations is constructed and analyzed. The model is a continuous analog of the model used in the recent work of Costantino et al. in which discrete modeling, mathematical analysis, statistical techniques, and laboratory experiments were used to demonstrate the presence of nonlinear dynamics, including chaos, in laboratory *Tribolium* cultures. A special case of the continuous model (no larva-on-egg cannibalism) is analyzed and the results are compared to the analogous special case of the discrete model.

1. Introduction

One of the most important issues in population biology concerns the observed complex fluctuations of population numbers in time. The premise that the fluctuations might be largely due to deterministic nonlinearities rather than stochastic noise has stimulated much interest and discussion. The hypothesis that natural populations might in fact exhibit chaotic dynamics is contrary to classical notions and has been particularly controversial. Experimental verification or falsification of the existence of nonlinear dynamics in populations is difficult due to the problems associated with connecting models with data, and those encountered in manipulating ecological systems [1, 2, 8, 16, 22].

Costantino, Cushing, Dennis, and Desharnais [2–9, 17, 21] have recently tested nonlinear population theory by analyzing a discrete

mathematical model of the flour beetle *Tribolium*, statistically connecting it to data, and conducting laboratory experiments designed both to validate the model and document its predictions. They used the age-structured nonlinear Leslie model

$$L(t + 1) = bA(t)e^{-c_{el}L(t) - c_{ea}A(t)}$$

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

$$A(t + 1) = P(t)e^{-c_{pa}A(t)} + (1 - \mu_a)A(t)$$

(termed the "LPA model"). $L(t)$ denotes the number of feeding larvae, $P(t)$ denotes the number of nonfeeding larvae, pupae, and callow adults, and $A(t)$ denotes the number of adults. Since each of the L and P life stages requires approximately 14 days, the discrete time unit in the model is taken to be two weeks. $b > 0$ denotes the average number of larvae recruited per adult per unit time in the absence of cannibalism, $\mu_l, \mu_a > 0$ are the larval and adult probabilities per unit time of dying from causes other than cannibalism, and the exponentials represent the probabilities per unit time that individuals survive cannibalism. The egg stage, which has four to five day duration, was omitted in the LPA model.

By manipulating adult mortality rate in the laboratory, they were able to demonstrate transitions in beetle populations between periodic 2-cycles, equilibria, and aperiodic oscillations as predicted by the model. They also documented transitions between equilibria, invariant loops, chaos, and 3-cycles, as well as the presence of "saddle phenomena" in the data. In this way, they have shown the presence of nonlinear dynamics in populations.

In order to realize their goals, the Costantino et al. team had to link a model to data with unprecedented thoroughness. In the process, they produced a population model thoroughly validated in its quantitative as well as qualitative predictive successes. The continuous analogs of discrete Leslie models are McKendrick–von Foerster type partial differential equation (PDE) models. (Some of the mathematical connections between these two famous classes of models are made rigorous in [18, 19, 24].) McKendrick models have been studied extensively, both analytically and numerically, in the literature; however, there is little connection to data, and certainly none to the extent of the Costantino et al. work. One would naturally wish to know if the popular McKendrick-type models can describe flour beetle population dynamics as successfully as the discrete Leslie-type LPA model, and whether they predict the same nonlinear transitions for *Tribolium*.

The first step in this program is to study the direct analogs of the discrete modeling and compare results. This includes mathematical

analysis and numerical studies of the continuous analog, as well as statistically connecting it to the data. The next step is to enhance the McKendrick model (for example, by including an egg stage, by making the birth rate age-dependent, by including a size-structuring variable and individual growth rate submodel, etc.) and producing new hypotheses to be tested in the laboratory.

This paper starts the project by deriving and analyzing a continuous analog of the discrete LPA model. In Sect. 2 we begin with a continuous age-structured model which includes an egg stage, and then formally shrink the egg stage duration to zero in order to obtain a continuous model analogous to the discrete one.

The first mathematical analyses of the discrete LPA model, appearing in [8], studied the special case $c_{el} = 0$ (no larva-on-egg cannibalism). Sect. 3 contains the mathematical analysis of the continuous version of this special case. Equilibria and Hopf bifurcations to periodic solutions are studied both analytically and numerically. Section 4 summarizes these mathematical results, compares them to the analogous results in the discrete setting, and rephrases them in more biological terms.

In later work, we will make statistical connections between the continuous analog of the LPA model and the laboratory data, study the general continuous model with and without an egg stage and various other modifications, compare the results with the predictions of the discrete LPA model, and generate new testable laboratory hypotheses.

2. Continuous model

Hastings and Costantino presented a continuous *Tribolium* model in [13, 14, 15]. They explained oscillatory behavior in data sets by mathematically modeling and analyzing egg-larval cannibalistic interactions. They showed that changes in the duration of the larval stage relative to that of the egg stage can give rise to Hopf bifurcations of periodic solutions, and suggested that the resulting bifurcation diagrams be "confirmed" by placing experiments in various regimes of parameter space. This experimental methodology of "confirming" bifurcation diagrams was eventually realized in the work of Costantino et al. as described in the Introduction; however, the LPA model was discrete, with fixed lifestage durations and no egg stage.

The continuous model finally constructed in this section will be an analog of the LPA model, and will thus differ from the Hastings and Costantino model in [13–15] by having fixed lifestage durations and

no egg stage. We first, however, present the continuous model including an egg stage, and then formally derive the model without an egg stage by shrinking the egg stage duration to zero.

2.1. Continuous model with egg stage

The continuous age-structured *Tribolium* model proposed by Costantino and Desharnais [1] and Hastings and Costantino [13–15] is a nonlinear McKendrick-type PDE:

$$\frac{\partial \rho_\varepsilon}{\partial t} + \frac{\partial \rho_\varepsilon}{\partial a} = - \delta_\varepsilon(a, \rho_\varepsilon(t, \cdot)) \rho_\varepsilon$$

$$\rho_\varepsilon(t, 0) = \beta A_\varepsilon(t) \tag{1}$$

$$\rho_\varepsilon(0, a) = \varphi(a)$$

where

$$\delta_\varepsilon(a, \rho_\varepsilon(t, \cdot)) = \begin{cases} C_{ea} A_\varepsilon(t) + C_{el} L_\varepsilon(t) & a \leq \varepsilon \\ v_l & \varepsilon < a \leq a_P \\ c_{pa} A_\varepsilon(t) & a_P < a \leq a_A \\ v_a & a_A < a \end{cases}$$

and

$$E_\varepsilon(t) = \int_0^\varepsilon \rho_\varepsilon(t, a)\, da$$

$$L_\varepsilon(t) = \int_\varepsilon^{a_P} \rho_\varepsilon(t, a)\, da$$

$$P_\varepsilon(t) = \int_{a_P}^{a_A} \rho_\varepsilon(t, a)\, da$$

$$A_\varepsilon(t) = \int_{a_A}^\infty \rho_\varepsilon(t, a)\, da.$$

Here $\rho_\varepsilon(t, a)$ is the per unit age density of beetles at time $t \geq 0$ and age $a \geq 0$, $\varepsilon > 0$ is the duration of the egg stage, $a_P > \varepsilon$ is the age of pupation, and $a_A > a_P$ is the age of maturation. $E_\varepsilon(t)$, $L_\varepsilon(t)$, $P_\varepsilon(t)$, and $A_\varepsilon(t)$ are the numbers of eggs, larvae, pupae, and adults at time t. $\beta > 0$ is the per capita birth rate, and δ_ε is a per capita death rate due to cannibalism in the case of eggs and pupae, and due to non-cannibalistic "natural" mortality rates $v_l, v_a > 0$ in the case of larvae and adults. (Under laboratory culture conditions, the natural mortality rates of

eggs and pupae are low [1]. In this model, as in the LPA model, they are assumed to be zero.) The parameters $C_{ea}, C_{el}, c_{pa} \geqq 0$ represent coefficients of adult-on-egg, larva-on-egg, and adult-on-pupa cannibalism respectively. Finally, $\varphi(a) \geqq 0$ gives the initial age distribution of the population.

When $\varepsilon = a_L$, where a_L denotes the length of the flour beetle egg stage (about four or five days), we refer to (1) as the "cELPA model". The cELPA model is a first order nonlinear hyperbolic PDE with a nonstandard boundary condition (for the basic theory of these kinds of equations, see Webb [25]).

We will discuss the connections between the LPA parameters and the continuous model parameters at the end of Sect. 2.2.

2.2. *Continuous model without egg stage*

In order to obtain a continuous model analogous to the discrete LPA model, we now formally shrink the egg stage to zero (i.e., let $\varepsilon \to 0$) in model (1). In so doing, we follow the same procedure as Diekmann *et al.* in [10] (see also [12]).

We may write (1) in equivalent integral equation form by integrating along the "characteristics"

$$\frac{dt}{ds} = 1$$

$$\frac{da}{ds} = 1 \tag{2}$$

$$\frac{d\rho_\varepsilon}{ds} = -\delta_\varepsilon(a, \rho_\varepsilon(t, \cdot))\rho_\varepsilon(t, a)$$

After solving the first two equations in (2) with initial conditions $t(0) = t_0, a(0) = 0$ for the case $t \geqq a$ and initial conditions $t(0) = 0$, $a(0) = a_0$ for the case $t < a$, one can integrate the third equation to find

$$\rho_\varepsilon(t, a) = \begin{cases} \beta A_\varepsilon(t-a) \exp\left[-\int_0^a \delta_\varepsilon(\sigma, \rho_\varepsilon(t-a+\sigma, \cdot))\, d\sigma\right], & 0 < a \leqq t \\ \\ \varphi(a-t) \exp\left[-\int_{a-t}^a \delta_\varepsilon(\sigma, \rho_\varepsilon(t-a+\sigma, \cdot))\, d\sigma\right], & a > t \end{cases}$$

$$\tag{3}$$

From (3) one can see that the fraction of eggs produced at time $t - a$ which survive egg cannibalism and hatch is

$$\exp\left[-\int_0^\varepsilon C_{ea} A_\varepsilon(t - a + \sigma)\, d\sigma - \int_0^\varepsilon C_{el} L_\varepsilon(t - a + \sigma)\, d\sigma\right] \quad (4)$$

The main difficulty in shrinking the egg stage to zero is that egg survivorship (4) approaches one as $\varepsilon \to 0$ unless we simultaneously increase the cannibalism rates C_{ea} and C_{el}. As $\varepsilon \to 0$, we wish to increase C_{ea} and C_{el} in such a way as to preserve the appropriate egg survivorship. Therefore, we assume C_{ea} and C_{el} are proportional to $1/\varepsilon$, in particular $C_{ea} = a_L c_{ea}/\varepsilon$ and $C_{el} = a_L c_{el}/\varepsilon$, where $c_{ea}, c_{el} \geqq 0$ are the egg cannibalism rates when $\varepsilon = a_L$.

We now take the formal limit of (3) as $\varepsilon \to 0$. Note that

$$\int_0^\varepsilon \delta_\varepsilon(\sigma, \rho_\varepsilon(t - a + \sigma, \cdot))\, d\sigma = C_{ea} \int_0^\varepsilon A_\varepsilon(t - a + \sigma)\, d\sigma$$

$$+ C_{el} \int_0^\varepsilon L_\varepsilon(t - a + \sigma)\, d\sigma$$

$$= c_{ea} a_L \int_0^1 A_\varepsilon(t - a + \varepsilon\sigma)\, d\sigma$$

$$+ c_{el} a_L \int_0^1 L_\varepsilon(t - a + \varepsilon\sigma)\, d\sigma$$

$$\overset{\varepsilon \to 0}{\to} \left[c_{ea} A_0(t - a) + c_{el} L_0(t - a)\right] a_L.$$

Therefore, the formal limiting system is

$$\rho_0(t, a) =$$

$$\begin{cases} \beta A_0(t - a)\exp\left[-(c_{el} L_0(t - a) + c_{ea} A_0(t - a))a_L \right. \\ \left. \quad - \int_0^a \delta_0(\sigma, \rho_0(t - a + \sigma, \cdot))\, d\sigma\right], \quad 0 < a \leqq t \\ \varphi(a - t)\exp\left[-\int_{a-t}^a \delta_0(\sigma, \rho_0(t - a + \sigma, \cdot))\, d\sigma\right], \quad a > t \end{cases}$$

$$(5)$$

where

$$\delta_0(a, \rho_0(t, \cdot)) \doteq \begin{cases} \nu_l & 0 < a \leqq a_P \\ c_{pa} A_0(t) & a_P < a \leqq a_A \\ \nu_a & a_A < a. \end{cases} \quad (6)$$

After dropping subscripts, we see that the limiting system (5) solves the McKendrick equation

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\delta(a, \rho)\rho$$

$$\rho(t, 0) = \beta A(t) \exp[-(c_{el}L(t) + c_{ea}A(t))a_L] \qquad (7)$$

$$\rho(0, a) = \varphi(a)$$

where δ is given by (6). We refer to (7) as the "cLPA model", and take it as the continuous version of the discrete "LPA model".

One can see from an investigation of (5) that the density-independent mortalities μ_l and μ_a in the discrete model are related to v_l and v_a by the survivorship formulas $e^{-v_l a_P} = 1 - \mu_l$ and $e^{-14v_a} = 1 - \mu_a$. Similar considerations show c_{el}, c_{ea}, and c_{pa} in the LPA model are analogous to $c_{el}a_L$, $c_{ea}a_L$, and $c_{pa}(a_A - a_P)$ in the cLPA model. The larval recruitment rate b in the discrete model corresponds to β in the continuous model. (Of course, if the cLPA and LPA models are parameterized with the same data, one does not expect their corresponding parameters to have the exact same values, because of the difference in modeling methodology. For a discussion of the correspondence between discrete and continuous model parameters in the context of an ongoing *Tribolium* experiment in which larval recruitment is periodic and beetle cohorts are synchronized, see [18]. In this special case, the LPA model essentially becomes a stroboscopic snapshot of the cLPA model at 2 week intervals, and the correspondence of parameters is mathematically exact.)

In later papers, the cELPA and cLPA models will be analyzed in general. In this paper, however, we focus on the special case $c_{el} = 0$ in the spirit of the early discrete work.

3. Analysis of Special Case $c_{el} = 0$

3.1. Equivalent system of FDEs

Since we wish to compare our results with those from the discrete model, we want to follow the numbers of animals in the age classes $L(t)$, $P(t)$, and $A(t)$ instead of the density distribution $\rho(t, a)$. Integrating the cLPA model (with $c_{el} = 0$)

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\delta(a, \rho)\rho$$

$$\rho(t, 0) = \beta A(t) \exp[-c_{ea}A(t)a_L]$$

$$\rho(0, a) = \varphi(a) \tag{8}$$

$$A(t) \doteq \int_{a_A}^{\infty} \rho(t, a) \, da$$

$$\delta(a, \rho(t, \cdot)) \doteq \begin{cases} v_l & 0 < a \leqq a_P \\ c_{pa} A(t) & a_P < a \leqq a_A \\ v_a & a_A < a \end{cases}$$

with respect to age a over the age intervals $[0, a_P]$, $[a_P, a_A]$, and $[a_A, \infty)$ gives rise to a system of functional differential equations (FDEs) in $L(t)$, $P(t)$, and $A(t)$. For example,

$$\frac{dL}{dt}(t) = \frac{d}{dt} \int_0^{a_P} \rho(t, a) \, da = -\int_0^{a_P} \left(\frac{\partial \rho}{\partial a}(t, a) + \delta(a, \rho(t, \cdot))\rho(t, a) \right) da$$

$$= \rho(t, 0) - \rho(t, a_P) - v_l L(t)$$

$$= \beta A(t) \exp[-c_{ea} A(t) a_L] - \rho(t, a_P) - v_l L(t)$$

From Equation (5) we have

$$\rho(t, a_P) = \beta A(t - a_P) \exp[-c_{ea} A(t - a_P) a_L - v_l a_P]$$

when $t \geqq a_P$ and

$$\rho(t, a_P) = \varphi(a_P - t) \exp[-v_l t]$$

when $t < a_P$.

In this manner we obtain the following system of FDEs:

$$\frac{dL}{dt}(t) = \beta A(t) \exp[-c_{ea} A(t) a_L] - v_l L(t) - \beta A(t - a_P)$$

$$\exp[-c_{ea} A(t - a_P) a_L - v_l a_P]$$

$$\frac{dP}{dt}(t) = \beta A(t - a_P) \exp[-c_{ea} A(t - a_P) a_L - v_l a_P] - c_{pa} A(t) P(t)$$

$$- \beta A(t - a_A) \exp\left[-c_{ea} A(t - a_A) a_L - v_l a_P \right. \tag{9}$$

$$\left. - c_{pa} \int_{a_P}^{a_A} A(t - a_A + \sigma) \, d\sigma \right]$$

$$\frac{dA}{dt}(t) = \beta A(t - a_A) \exp\left[-c_{ea} A(t - a_A) a_L - v_l a_P \right.$$

$$\left. - c_{pa} \int_{a_P}^{a_A} A(t - a_A + \sigma) \, d\sigma \right] - v_a A(t)$$

for $t \geqq a_A$, where the initial functions $(L(t), P(t), A(t))$ for $t \in [0, a_A]$ are restricted to the solutions of

$$\frac{dL}{dt}(t) = \beta A(t) \exp[-c_{ea}A(t)a_L] - v_l L(t)$$

$$- \begin{cases} \beta A(t - a_P) \exp[-c_{ea}A(t - a_P)a_L - v_l a_P] & t \geqq a_P \\ \varphi(a_P - t) \exp[-v_l t] & t < a_P \end{cases}$$

$$\frac{dP}{dt}(t) =$$

$$\begin{cases} \beta A(t - a_P) \exp[-c_{ea}A(t - a_P)a_L - v_l a_P] & t \geqq a_P \\ \varphi(a_P - t) \exp[-v_l t] & t < a_P \end{cases} - c_{pa}A(t)P(t)$$

$$-\begin{cases} \varphi(a_A - t) \exp\left[-v_l(a_P - a_A + t) - c_{pa}\int_{a_P}^{a_A} A(t - a_A + \sigma)\,d\sigma\right] \\ \qquad 0 < a_A - t \leqq a_P \\ \varphi(a_A - t) \exp\left[-c_{pa}\int_{a_A - t}^{a_A} A(t - a_A + \sigma)\,d\sigma\right] \\ \qquad a_P < a_A - t \end{cases} \tag{10}$$

$$\frac{dA}{dt}(t) = \begin{cases} \varphi(a_A - t) \exp\left[-v_l(a_P - a_A + t) - c_{pa}\int_{a_P}^{a_A} A(t - a_A + \sigma)\,d\sigma\right] \\ \qquad 0 < a_A - t \leqq a_P \\ \varphi(a_A - t) \exp\left[-c_{pa}\int_{a_A - t}^{a_A} A(t - a_A + \sigma)\,d\sigma\right] \\ \qquad a_P < a_A - t \end{cases}$$

$$- v_a A(t)$$

3.2. Equilibria

The equilibrium equations for (9) are

$$\beta A \exp[-c_{ea}Aa_L](1 - \exp[-v_l a_P]) - v_l L = 0 \tag{11}$$

$$\beta A \exp[-c_{ea}Aa_L - v_l a_P](1 - \exp[-c_{pa}(a_A - a_P)A]) - c_{pa}AP = 0$$
$$(12)$$

$$\beta A \exp[-c_{ea}Aa_L - v_l a_P - c_{pa}(a_A - a_P)A] - v_a A = 0. \quad (13)$$

Henceforth the "naught" subscript will refer to equilibria. There are two equilibria: the "trivial solution" $(0, 0, 0)$ corresponding to extinction of the population, and a unique nontrivial equilibrium (L_0, P_0, A_0) given by

$$A_0 = \frac{-v_l a_P - \ln(v_a/\beta)}{c_{pa}(a_A - a_P) + c_{ea}a_L}$$

$$L_0 = \frac{v_a}{v_l}[\exp(v_l a_P) - 1] A_0 \exp[c_{pa}A_0(a_A - a_P)] \quad (14)$$

$$P_0 = \frac{v_a}{c_{pa}}[\exp[c_{pa}A_0(a_A - a_P)] - 1].$$

The nontrivial equilibrium is positive if and only if the larval recruitment rate β exceeds a certain critical value β_{cr}; specifically, if and only if

$$\beta > \beta_{cr} \doteq v_a e^{v_l a_P}.$$

Furthermore, each component of (L_0, P_0, A_0) is a strictly increasing function of β—that is, the steady state value of each lifestage increases with larval recruitment rate.

The equilibrium age distribution

$$\rho_0(a) = \begin{cases} \beta A_0 \exp[-c_{ea}A_0 a_L - v_l a], & 0 \leq a < a_P \\ \beta A_0 \exp[-c_{ea}A_0 a_L - v_l a_P - c_{pa}A_0(a - a_P)], \\ \quad a_P \leq a < a_A \\ \beta A_0 \exp[-c_{ea}A_0 a_L - v_l a_P - c_{pa}A_0(a_A - a_P) - v_a(a - a_A)], \\ \quad a_A \leq a \end{cases}$$
$$(15)$$

of the cLPA model (8) can be recovered from (L_0, P_0, A_0) by means of (5) or (10). Conversely, the equilibrium (L_0, P_0, A_0) can be recovered from the equilibrium age distribution $\rho_0(a)$ by means of

$$L_0 = \int_0^{a_P} \rho_0(a)\, da$$

$$P_0 = \int_{a_P}^{a_A} \rho_0(a)\, da$$

$$A_0 = \int_{a_A}^{\infty} \rho_0(a)\, da.$$

3.3. Simplifying the linearization

Note that the adult equation in the FDE model (9) is decoupled (unfortunately this will not be the case if $c_{el} > 0$). It would be nice if we could justify focusing our analysis on just this one equation. Our stability analysis will rest on linearization theory – inspection of the eigenvalues (roots of the characteristic equations of the linearizations). The results in this section will allow us to study the linearization of the cLPA model (8) by studying the linearization of the *adult* equation in the FDE model (9).

Let $\rho_0(a)$ be an equilibrium solution of (8) and $A_0 = \int_{a_A}^{\infty} \rho_0(s)\, ds$. The linearization of the equation for the variation $\rho - \rho_0$ is

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial a} = -\chi(a) x(t, a) - \tau(a) \int_{a_A}^{\infty} x(t, s)\, ds$$

$$x(t, 0) = \beta(1 - c_{ea} a_L A_0) \exp\left[-c_{ea} a_L A_0 \right] \int_{a_A}^{\infty} x(t, s)\, ds$$

where

$$\chi(a) \doteq \begin{cases} v_l & 0 < a \leqq a_P \\ c_{pa} A_0 & a_P < a \leqq a_A \\ v_a & a_A < a \end{cases}$$

$$\tau(a) \doteq \begin{cases} 0 & 0 < a \leqq a_P \\ c_{pa} \rho_0(a) & a_P < a \leqq a_A \\ 0 & a_A < a \end{cases}$$

Note that in the definition of $\tau(a)$, $\rho_0(a)$ becomes $\beta A_0 \exp[-c_{ea} A_0 a_L - v_l a_P - c_{pa} A_0 (a - a_P)]$ by means of (15).

In the following theorem we show that linear PDEs of the form

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\mu(a)\rho(t, a) - v(a) \int_{m}^{\infty} \rho(t, s)\, ds \tag{16}$$

$$\rho(t, 0) = \gamma \int_{m}^{\infty} \rho(t, a)\, da$$

$$\mu(a) = \kappa \quad \text{for } a \geqq m$$

with maturation delay $m > 0$ have the same characteristic equations as linear FDEs of the form

$$\frac{dA}{dt}(t) = \gamma A(t - m) e^{-\int_0^m \mu(a)\, da} - e^{-\int_0^m \mu(a)\, da} \int_0^m v(a) A(t - m + a) e^{\int_0^a \mu(s)\, ds} da$$

$$\tag{17}$$

$$- \kappa A(t) - A(t) \int_m^{\infty} v(a)\, da$$

McKendrick PDEs in which all nonlinearities arise from dependencies on the total number of adults often have linearizations of the form (16). The linear FDE (17) arises from linearizing the FDE obtained by integrating such a nonlinear PDE over the adult age class. Theorem 1 says, roughly, that *if the only nonlinearities in a McKendrick age-structured PDE model with maturation delay m arise from dependencies on the total number of adults, then, locally, one only need study the dynamics of the adult subpopulation.*

In particular, we will apply Theorem 1 to the cLPA model (8) by choosing

$$
\mu(a) = \begin{cases} v_l & 0 < a \leqq a_P \\ c_{pa}A_0 & a_P < a \leqq a_A \\ v_a & a_A < a \end{cases}
$$

$$
v(a) = \begin{cases} 0 & 0 < a \leqq a_P \\ c_{pa}\beta A_0 \exp[-c_{ea}A_0 a_L - v_l a_P - c_{pa}A_0(a - a_P)] & a_P < a \leqq a_A \\ 0 & a_A < a \end{cases}
$$

$$
\gamma = \beta(1 - c_{ea}a_L A_0)\exp[-c_{ea}a_L A_0]
$$

$$
m = a_A
$$

$$
\kappa = v_a \tag{18}
$$

Theorem 1.   *The linear PDE* (16) *and the linear FDE* (17) *have the same characteristic equation on the set* $\{\lambda \in C | \mathrm{Re}(\lambda) > -\kappa\}$.

Proof. Substitution of the exponential Ansatz $A(t) = ce^{\lambda t}$ into Equation (17) gives rise to the characteristic equation

$$
\lambda = \gamma e^{-\int_0^m \mu(a)\,da} e^{-\lambda m} - e^{-\int_0^m \mu(a)\,da} e^{-\lambda m} \int_0^m v(a) e^{\lambda a} e^{\int_0^a \mu(s)\,ds}\,da
$$

$$
- \kappa - \int_m^\infty v(a)\,da. \tag{19}
$$

To find the characteristic equation of the PDE (16), we first convert it into equivalent integral equation form by integrating along its characteristics:

$$
\rho(t, a) = \rho(t - a, 0)e^{-\int_0^a \mu(\alpha)\,d\alpha}
$$

$$
- e^{-\int_0^a \mu(\alpha)\,d\alpha} \int_0^a \int_m^\infty v(\alpha) e^{\int_0^a \mu(z)\,dz} \rho(t - a + \alpha, y)\,dy\,d\alpha \tag{20}
$$

where

$$\rho(t, 0) = \gamma \int_m^\infty \rho(t, a) \, da \tag{21}$$

If we substitute (20) into (21), set $\rho(t, a) = Q(a)e^{\lambda t}$, and utilize $Q(0) = \gamma \int_m^\infty Q(a) \, da$ from Equation (21), we obtain the characteristic equation

$$1 = e^{-\int_0^m \mu(\alpha) \, d\alpha} \left[\gamma \frac{e^{-\lambda m}}{\lambda + \kappa} - \int_m^\infty \int_0^m e^{-\kappa(a-m)} e^{-\lambda a} \nu(\alpha) e^{\lambda \alpha} e^{\int_0^\alpha \mu(z) \, dz} \, d\alpha \, da \right.$$

$$\left. - \int_m^\infty \int_m^a e^{-\kappa(a-m)} e^{-\lambda a} \nu(\alpha) e^{\lambda \alpha} e^{\int_0^\alpha \mu(z) \, dz} \, d\alpha \, da \right]$$

$$= e^{-\int_0^m \mu(\alpha) \, d\alpha} \left[\gamma \frac{e^{-\lambda m}}{\lambda + \kappa} - \frac{e^{-\lambda m}}{\lambda + \kappa} \int_0^m \nu(\alpha) e^{\lambda \alpha} e^{\int_0^\alpha \mu(z) \, dz} \, d\alpha \right.$$

$$\left. - \int_m^\infty \int_\alpha^\infty e^{-\kappa(a-m)} e^{-\lambda a} \nu(\alpha) e^{\lambda \alpha} e^{\int_0^\alpha \mu(z) \, dz} \, da \, d\alpha \right]$$

for $\mathrm{Re}(\lambda) > -\kappa$. Upon further simplification, we obtain

$$\lambda + \kappa = e^{-\int_0^m \mu(\alpha) \, d\alpha} \left[\gamma e^{-\lambda m} - e^{-\lambda m} \int_0^m \nu(\alpha) e^{\lambda \alpha} e^{\int_0^\alpha \mu(z) \, dz} \, d\alpha \right]$$

$$- \int_m^\infty \nu(\alpha) \, d\alpha. \qquad \square$$

We now use Theorem 1 to study the stability of the trivial and positive equilibria.

3.4. Stability of trivial equilibrium

At the extinction equilibrium $(L_0, P_0, A_0) = (0, 0, 0)$, the linearization

$$x'(t) = \beta x(t - a_A) e^{-\nu_l a_P} - \nu_a x(t)$$

of the adult FDE (9c) obtains from linearizing (9c) or from substituting (18) into (17). The characteristic equation is

$$\lambda = \beta e^{-\nu_l a_P} e^{-\lambda a_A} - \nu_a.$$

This equation has a unique real root λ_0 which is negative when $\beta < \beta_{cr} \doteq \nu_a e^{\nu_l a_P}$, and positive when $\beta > \beta_{cr}$.

The real and imaginary parts of any complex root $\alpha + i\varphi$ with $\varphi \neq 0$ must satisfy the equations

$$\alpha = \beta e^{-\nu_l a_P} e^{-\alpha a_A} \cos(\varphi a_A) - \nu_a$$

$$\varphi = -\beta e^{-\nu_l a_P} e^{-\alpha a_A} \sin(\varphi a_A)$$

and from these equations it is easy to deduce that $\alpha < \lambda_0$. By [11] (Chapter VII, Theorem 6.8),

Theorem 2. *The trivial solution* $(0, 0, 0)$ *is locally asymptotically stable when* $\beta < \beta_{cr}$ *and unstable when* $\beta > \beta_{cr}$.

Recall that the nontrivial equilibrium (L_0, P_0, A_0) is positive if and only if $\beta > \beta_{cr}$. Typically, we expect an exchange of stability between the trivial and nontrivial equilibria at β_{cr}. In the next section we verify this; i.e., we show the positive equilibria are stable for β greater than (but close to) β_{cr}.

3.5. Stability of positive equilibrium

The linearization

$$x'(t) = x(t - a_A) v_a (1 - c_{ea} a_L A_0) - v_a c_{pa} A_0 \int_{a_P}^{a_A} x(t - a_A + \sigma)\, d\sigma - v_a x(t)$$

of the adult FDE (9c) at the positive equilibrium A_0 obtains from linearizing (9c) or from substituting (18) into (17). The characteristic equation is

$$\lambda = v_a (1 - c_{ea} a_L A_0) e^{-\lambda a_A} - v_a c_{pa} A_0 \int_{a_P}^{a_A} e^{\lambda(\sigma - a_A)}\, d\sigma - v_a. \qquad (22)$$

Equation (22) is linear in v_a and $v_a A_0$, and hence may be written in terms of real and imaginary parts as

$$M(\alpha, \varphi) \begin{pmatrix} v_a \\ v_a A_0 \end{pmatrix} = \begin{pmatrix} \alpha \\ \varphi \end{pmatrix} \qquad (23)$$

for a 2×2 matrix $M(\alpha, \varphi)$ where $\lambda = \alpha + \varphi i$.

Recall from Equation (14) that the adult equilibria A_0 are in one-one correspondence with the parameter β; in fact β can be eliminated in the model equations by means of

$$\beta = \beta_{cr} \exp(A_0 [c_{ea} a_L + c_{pa}(a_A - a_P)]). \qquad (24)$$

A_0 is thereby introduced as a model parameter, and we can study the roots of the characteristic equation as functions of the adult equilibrium level A_0.

In order to prove the stability of small positive equilibria, we must show all the eigenvalues λ are in the left half complex plane for small values of $A_0 > 0$. We first prove a series of lemmas.

Lemma 3. *There exists a zero eigenvalue if and only if $A_0 = 0$. In fact, for sufficiently small $A_0 \geqq 0$, there is a largest real eigenvalue λ_0 which is negative if $A_0 > 0$ and zero if $A_0 = 0$.*

Proof. The first statement follows from Equation (22). Also, Equation (22) can be written as $F(\lambda) = G(\lambda)$ where

$$F(\lambda) = \begin{cases} \lambda + v_a + v_a c_{pa} A_0 \frac{1}{\lambda}(1 - e^{-\lambda(a_A - a_P)}) & \lambda \neq 0 \\ v_a + v_a c_{pa} A_0 (a_A - a_P) & \lambda = 0 \end{cases}$$

$$G(\lambda) = v_a e^{-\lambda a_A}(1 - c_{ea} a_L A_0)$$

are continuous functions of λ. For sufficiently small $A_0 \geqq 0$, G is a strictly decreasing function of λ which crosses the vertical axis at $G(0) = v_a(1 - c_{ea} a_L A_0) > 0$. Also, there exists an $\varepsilon > 0$ such that for sufficiently small $A_0 \geqq 0$, F is a strictly increasing function of λ on $[-\varepsilon, \infty]$ which crosses the vertical axis at $F(0) = v_a[1 + c_{pa} A_0 (a_A - a_P)] \geqq G(0)$. Thus, for sufficiently small $A_0 \geqq 0$, the graphs of F and G must intersect at some $\lambda = \lambda_0$ which is negative if $A_0 > 0$ and zero if $A_0 = 0$. $\square$

Equation (23) may be written

$$\alpha = v_a(1 - c_{ea} a_L A_0) e^{-\alpha a_A} \cos(\varphi a_A) - v_a$$

$$+ \frac{v_a c_{pa} A_0}{\alpha^2 + \varphi^2} (\alpha e^{-\alpha(a_A - a_P)} \cos[\varphi(a_A - a_P)]$$

$$- \alpha - \varphi e^{-\alpha(a_A - a_P)} \sin[\varphi(a_A - a_P)]) \tag{25}$$

$$\varphi = -v_a(1 - c_{ea} a_L A_0) e^{-\alpha a_A} \sin(\varphi a_A)$$

$$- \frac{v_a c_{pa} A_0}{\alpha^2 + \varphi^2} (\varphi e^{-\alpha(a_A - a_P)} \cos[\varphi(a_A - a_P)]$$

$$- \varphi + \alpha e^{-\alpha(a_A - a_P)} \sin[\varphi(a_A - a_P)]) \tag{26}$$

in order to prove:

Lemma 4. *Let $A_0 = 0$. Then the only eigenvalue with zero real part is the zero eigenvalue. All nonzero eigenvalues are in the left half complex plane, and are uniformly bounded away from the imaginary axis.*

Proof. Let $A_0 = 0$. Then Equations (25) and (26) become

$$\alpha = v_a e^{-\alpha a_A} \cos(\varphi a_A) - v_a \tag{27}$$

$$\varphi = -v_a e^{-\alpha a_A} \sin(\varphi a_A). \tag{28}$$

If $\alpha = 0$, then $\cos(\varphi a_A) = 1$ and so $\sin(\varphi a_A) = 0$; hence $\varphi = 0$. If $\alpha > 0$, then by (27) $\alpha < v_a \cos(\varphi a_A) - v_a \leqq 0$ which is a contradiction, and so nonzero eigenvalues must have negative real part. If there were a sequence of nonzero eigenvalues $\{\alpha_n + i\varphi_n\}_{n=1}^{\infty}$ in the left half complex plane with $\alpha_n \to 0$, then by (27) $\cos(\varphi_n a_A) \to 1$ and so $\sin(\varphi_n a_A) \to 0$. By (28), $\varphi_n \to 0$. However, small nonzero values of φ_n cannot satisfy equation (28) because the two sides of the equation would have opposite signs. Thus, from some point on in the sequence, $\varphi_n = 0$ which introduces a sign contradiction into equation (27). $\square$

Lemma 5. *There exists a positive real number M such that for all sufficiently small $A_0 > 0$, all eigenvalues λ with positive real part satisfy $|\lambda| < M$.*

Proof. If not, then there is a sequence of positive equilibria $\{A_{0n}\}$ with $A_{0n} \to 0$ and a corresponding sequence of eigenvalues $\{\alpha_n + i\varphi_n\}$ in the right half complex plane such that $\alpha_n \to \infty$ or $|\varphi_n| \to \infty$. The reader can check that the right hand sides of both Equations (25) and (26) are therefore bounded as $n \to \infty$, while at least one of the left hand sides is unbounded. $\square$

Lemma 6. *There is no sequence of eigenvalues in the right half complex plane approaching zero as $A_0 \to 0^+$.*

Proof. Suppose there exists a sequence of positive equilibria $\{A_{0n}\}$ with $A_{0n} \to 0$ and a corresponding sequence of eigenvalues $\{\alpha_n + i\varphi_n\}$ in the right half complex plane such that $\alpha_n \to 0$ and $\varphi_n \to 0$. Small positive A_{0n}, small nonnegative α_n and small $|\varphi_n|$ make the right hand side of (25) negative, which is a contradiction. $\square$

The following stability theorem utilizes the above lemmas and continuity in verifying all eigenvalues are in the left half complex plane for sufficiently small $A_0 > 0$.

Theorem 7. *For all sufficiently small $A_0 > 0$ (that is, for all sufficiently small $\beta - \beta_{cr} > 0$), the positive equilibrium (L_0, P_0, A_0) of (9) is locally asymptotically stable.*

Proof. If not, then there exist a sequence of positive equilibria $\{A_{0n}\}$ with $A_{0n} \to 0$ and a corresponding sequence of eigenvalues $\{\lambda_n\}$ in the right half complex plane. By Lemma 5, there exists $M > 0$ such that $|\lambda_n| < M$ for all n, and so $\{\lambda_n\}$ has a convergent subsequence. Without loss of generality we may assume $\{\lambda_n\}$ converges. By Lemmas 3, 4 and continuity, $\lambda_n \to 0$, which contradicts Lemma 6. $\square$

Thus, when larval recruitment exceeds β_{cr} but is not too large, the positive life-stage steady state predicted by the cLPA model (8) is stable.

3.6. Loss of stability of positive equilibria via Hopf bifurcations

As parameters vary, roots of (22) may cross the imaginary axis in the complex plane. The first such crossing of an eigenvalue into the right half complex plane as A_0 increases from small positive numbers is associated with loss of stability of the equilibrium A_0. This corresponds to a Hopf bifurcation of periodic solutions if the eigenvalue crosses the imaginary axis with nonzero speed (see [11], Chapter X, Theorem 2.7). That is, population steady states of larger value may be unstable, and the population may develop periodic cycling. The imaginary part φ of the first eigenvalue which crosses the imaginary axis corresponds to the frequency of the periodic cycle near the bifurcation point, and the period of the cycle is given by $2\pi/\varphi$.

In this section we locate the boundaries in parameter space along which the real part α of some eigenvalue vanishes – in other words, the boundaries along which Hopf bifurcations *may* occur. In the Appendix it is shown that, generically speaking, the first eigenvalue to cross these stability boundaries does so with nonzero speed and hence gives rise to a Hopf bifurcation.

Fix $\alpha = 0$. Then Equation (23) becomes

$$M(0, \varphi)\begin{pmatrix} v_a \\ v_a A_0 \end{pmatrix} = \begin{pmatrix} 0 \\ \varphi \end{pmatrix}. \tag{29}$$

Except at isolated values of φ for which $|M(0, \varphi)| = 0$, we obtain v_a and $v_a A_0$ (and hence A_0) as functions of φ by

$$\begin{pmatrix} v_a \\ v_a A_0 \end{pmatrix} = M(0, \varphi)^{-1}\begin{pmatrix} 0 \\ \varphi \end{pmatrix}. \tag{30}$$

This yields the curves in (v_a, A_0) space, parameterized by φ, along which Hopf bifurcations may occur (see [11], Chapter XI). After algebraic simplification we obtain

$$A_0(\varphi) = \frac{\cos(\varphi a_A) - 1}{c_{ea} a_L \cos(\varphi a_A) + \dfrac{c_{pa}}{\varphi} \sin[\varphi(a_A - a_P)]}$$

and

$$v_a(\varphi) = \frac{-\varphi}{\sin(\varphi a_A)(1 - c_{ea} a_L A_0(\varphi)) + \dfrac{c_{pa}}{\varphi} A_0(\varphi)(\cos[\varphi(a_A - a_P)] - 1)} \tag{31}$$

Both $A_0(\varphi)$ and $v_a(\varphi)$ are even functions of φ and so we need only consider positive φ for which $A_0(\varphi), v_a(\varphi) > 0$.
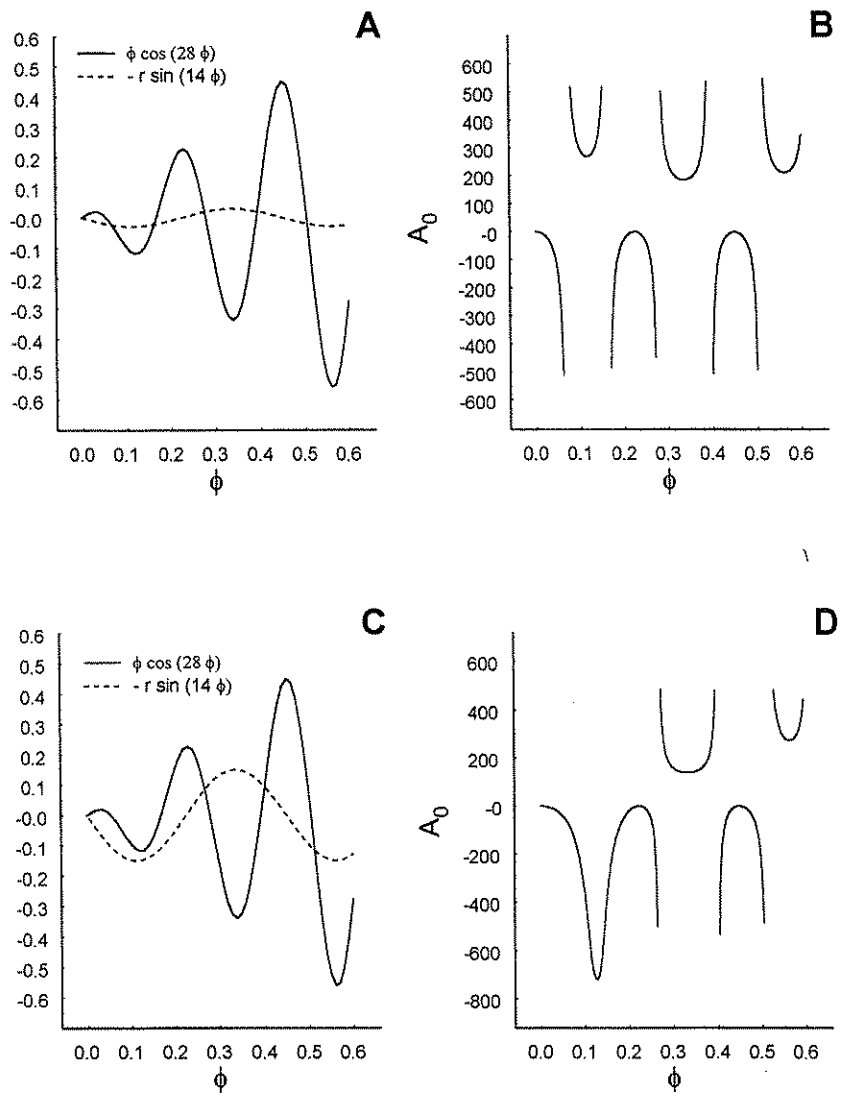
Fig. 1. cLPA model with $c_{el} = 0$: Positive values of $A_0(\varphi)$ are generated when $\varphi \cos(28\varphi) < -r \sin(14\varphi)$. Parameter values are $a_L = 4$, $a_P = 14$, $a_A = 28$, $\beta = 7.5$, $c_{ea} = 0.0025$, $c_{el} = 0$, $v_a = 0.00029$, and $v_l = 0.022$. Here $r \doteq c_{pa}/(a_L c_{ea})$. **A and B** $c_{pa} = 0.00029$ so $r = 0.029$; **C and D** $c_{pa} = 0.0015$ so $r = 0.15$.

$A_0(\varphi) > 0$ requires

$$\varphi \cos(\varphi a_A) < -r \sin[\varphi(a_A - a_P)] \tag{32}$$

where $r \doteq c_{pa}/(c_{ea} a_L)$. This ratio r of parameters will be used in Section 4 to compare our results with those in the discrete case.
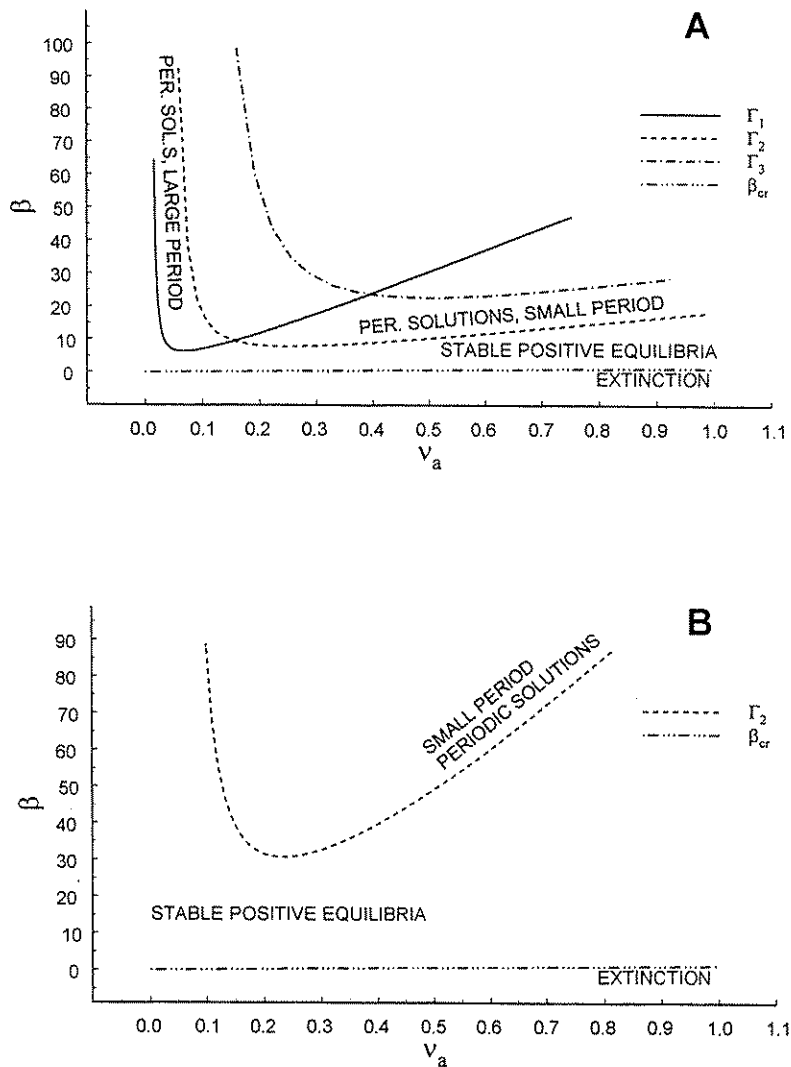
Fig. 2. cLPA model with $c_{el} = 0$: Possible configurations in (v_a, β) parameter plane of boundaries along which some eigenvalue has zero real part. Γ_1 disappears for larger values or r. Parameter values are $a_L = 4$, $a_P = 14$, $a_A = 28$, $c_{ea} = 0.0025$, $c_{el} = 0$, and $v_l = 0.022$. Here $r \doteq c_{pa}/(a_L c_{ea})$. **A** $c_{pa} = 0.00029$ so $r = 0.029$; **B** $c_{pa} = 0.0015$ so $r = 0.15$.

Henceforth, we take the parameters a_P and a_A to be the discrete LPA beetle model estimations $a_P = 14$ days and $a_A = 28$ days, and we take $a_L = 4$ days. When r is small (approximately $r < \pi/28$), Inequality (32) is satisfied on infinitely many φ intervals $L_1, L_2, \ldots, L_n, \ldots$ which alternately lie inside of and include the interval $((4n - 3)\pi/56$, $(4n - 1)\pi/56)$, and ultimately "approach" said interval as $n \to \infty$. For
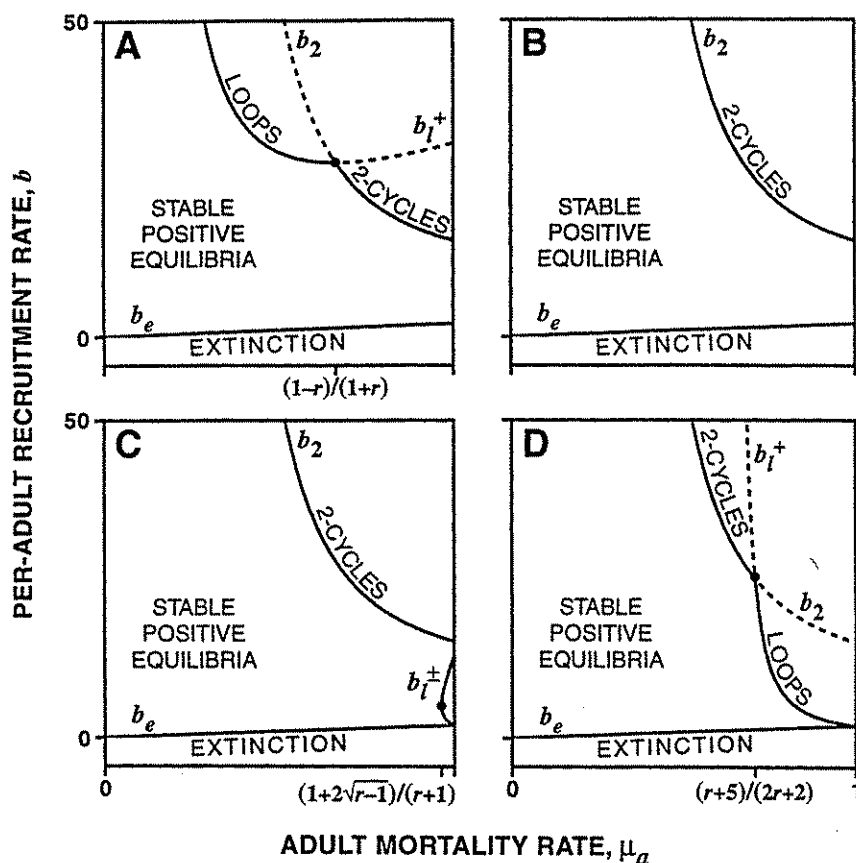
Fig. 3. Discrete LPA model with $c_{el} = 0$: Possible configurations in (μ_a, b) parameter plane of boundaries along which some eigenvalue has zero real part. Here $r = c_{pa}/c_{ea}$ and $\mu_l = 0.5128$. **A** $0 < r < 1$; **B** $1 < r < 2$; **C** $2 < r < 3$; **D** $r > 3$. In **A**, $r = 0.2$; in **B**, $r = 1.6$; in **C**, $r = 2.9$; in **D**, $r = 9.0$. (This figure is reprinted from [8] with the permission of the publisher.)

larger r, the first interval L_1 disappears, and for successively larger r's successively more odd-subscripted intervals disappear (Fig. 1).

In order for $v_a(\varphi)$ to be positive for $\varphi \in L_n$, the denominator of (31) must be negative. As φ approaches (from the right) the left endpoint of an interval L_n, $A_0(\varphi)$ approaches positive infinity, and $\sin(28\varphi)$ is positive and close to one. Thus, the denominator of (31) approaches negative infinity, and so $v_a(\varphi)$ approaches zero from above.

Thus, for each interval L_n, there exists an interval $I_n \subseteq L_n$ having the same left endpoint as L_n such that the parameters $A_0(\varphi)$ and $v_a(\varphi)$ are positive on I_n. For $\varphi \in I_n$, a curve Γ_n is generated parametrically in the (v_a, A_0) plane. These Γ_n are the stability boundaries.

The stability boundaries in (v_a, A_0) space may be transformed into boundaries in (v_a, β) space by means of Equations (24) and (31). This is done in Fig. 2 to admit comparison with the discrete analog in Fig. 3.

4. Summary

We have derived a continuous model (7) analogous to the discrete LPA model, and have mathematically analyzed the special case $c_{el} = 0$. The results of our analysis parallel the analysis in [8] of the corresponding special case of the discrete model (Table 1).

Both models admit the zero equilibrium $(0, 0, 0)$ and a unique nontrivial equilibrium (L_0, P_0, A_0) . The trivial solution gives up its stability to a branch of positive equilibria bifurcating from zero at the given critical value of the larval recruitment rate. In both models, the trivial equilibrium $(0, 0, 0)$ is unstable if and only if a positive equilibrium exists; and in both models the positive equilibrium is an increasing function of larval recruitment and is stable for small A_0. That is, both models always predict extinction of the population when larval recruitment is below some critical value (so there are no Allee effects). Whenever larval recruitment exceeds this critical value, there is a unique positive steady state. The value of this steady state tends to zero as the larval recruitment approaches the critical value from the right, and increases with increasing larval recruitment rate. The steady state is stable for small population sizes when the recruitment rate is near the critical value.

Table 1

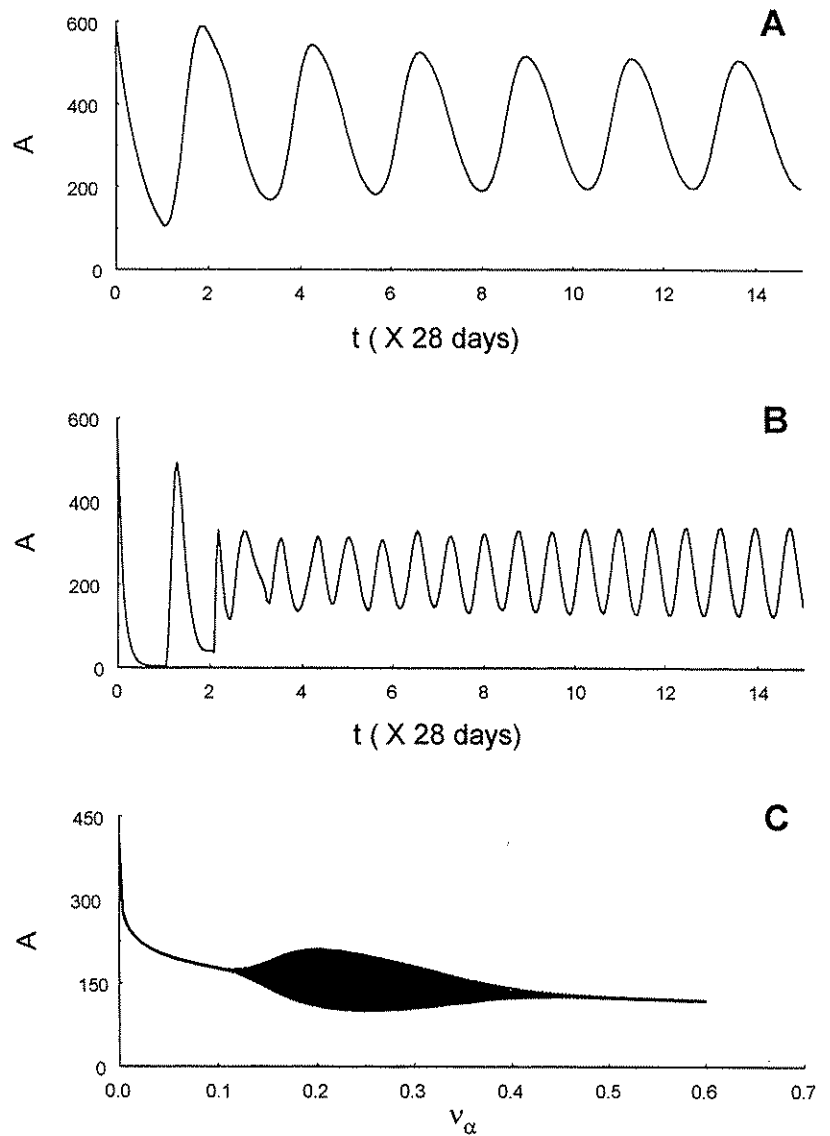| Discrete LPA model ($c_{el} = 0$)	FDE cLPA model ($c_{el} = 0$)
$A_0 = \dfrac{\ln(1 - \mu_l) - \ln(\mu_a/b)}{c_{pa} + c_{ea}}$	$A_0 = \dfrac{\ln(e^{-v_l a_P}) - \ln(v_a/\beta)}{c_{pa}(a_A - a_P) + c_{ea}a_L}$
$L_0 = \dfrac{\mu_a}{(1 - \mu_l)} A_0 \exp(c_{pa}A_0)$	$L_0 = \dfrac{v_a}{v_l}[\exp(v_l a_P) - 1]A_0 \exp[c_{pa}A_0(a_A - a_P)]$
$P_0 = \mu_a A_0 \exp(c_{pa}A_0)$	$P_0 = \dfrac{v_a}{c_{pa}}(\exp[c_{pa}A_0(a_A - a_P)] - 1)$
$b_{cr} \doteq \dfrac{\mu_a}{1 - \mu_l}$	$\beta_{cr} \doteq v_a e^{v_l a_P}$
Equilibria → invariant loops	Equilibria → periodic sol.s, high period
Equilibria → 2-cycles	Equilibria → periodic sol.s, low period

Fig. 4. cLPA model with $c_{el} = 0$: Parameter values are $a_L = 4$, $a_P = 14$, $a_A = 28$, $c_{ea} = 0.0025$, $c_{el} = 0$, and $v_l = 0.022$. Here $r \doteq c_{pa}/(a_L c_{ea})$. **A** Time series with $\beta = 10$, $v_a = 0.06$, and $c_{pa} = 0.00029$. This is in the region of large period periodic solutions in Fig. 2A. **B** Time series with $\beta = 10$, $v_a = 0.3$, and $c_{pa} = 0.00029$. This is in the region of small period periodic solutions in Fig. 2A. **C** Bifurcation diagram generated along the line $\beta = 40$ in Figure 2B. Here $c_{pa} = 0.0015$. Stable equilibria undergo a Hopf bifurcation to periodic solutions, which then undergo another bifurcation back to stable equilibria.

For small r ($r \doteq c_{pa}/c_{ea}$ in the discrete model, $r \doteq c_{pa}/(c_{ea}a_L)$ in the continuous model), loss of stability of the positive equilibrium occurs as certain boundaries are crossed in the (μ_a, b) (Fig. 3) or (v_a, β) (Fig. 2) parameter plane. Thus, when the adult-on-pupa cannibalism rate is small compared to adult-on-egg cannibalism rate, the models predict destabilization of the steady state as the adult mortality rate increases. On the other hand, adult-on-pupa cannibalism rates which are large compared to adult-on-egg cannibalism rates promote stability of the steady state.

In the discrete model, the equilibrium can bifurcate into an invariant loop or a 2-cycle. In the continuous model, the equilibrium can bifurcate into a periodic solution of higher period or a periodic solution of lower period. Note the similarities between the Γ_1 and Γ_2 boundaries in the continuous model (Fig. 2), and the b_l^+ and b_2 boundaries in the discrete model (Fig. 3). For small values of r, Γ_1 and Γ_2 both exist, and correspond to the bifurcation of periodic solutions of larger and smaller periods (i.e. smaller and larger frequencies φ), respectively. In the discrete case, the boundaries b_l^+ and b_2 correspond to invariant loops (with some period-locked cycles) and 2-cycles. For larger r, Γ_1 and b_l^+ disappear. However, the last two possibilities in the discrete case (Fig. 3C and 3D) do not appear to correspond to analogous configurations in the continuous case since Γ_1 cannot reappear for larger values of r.

The boundary Γ_1 approximately corresponds to $0.07 < \varphi < 0.16$, which gives periodic cycles of periods 39-90 days. Measured in time units of 2 weeks, cycles near this boundary have periods ranging from 1.4 to 3.2. Boundary Γ_2 approximately corresponds to $0.28 < \varphi < 0.39$, that is, periodic cycles of periods 16-22 days (periods 0.57–0.79 when measured in units of 2 weeks) (see Fig. 4). While the locations of the Γ_n boundaries in (v_a, β) parameter space depend on the values of the other parameters, the Γ_n frequency intervals only depend on the parameters a_P and a_A (which we have fixed at $a_P = 14$ days and $a_A = 28$ days). Therefore we can, for example, compare boundaries Γ_2 and b_2 in terms of period. The discrete LPA model predicts the advent of 28 day cycles ("2-cycles") on the boundary b_2, while the continuous cLPA model predicts cycles with period between 16 and 22 days on the boundary Γ_2.

We are currently using statistical techniques to connect the general cLPA model (with $c_{el} > 0$) to data. Once the cLPA model is parameterized, it will be used to generate bifurcation diagrams analogous to those generated by the discrete LPA model. These final state diagram predictions will be compared to those of the discrete model, and to the data gathered by Costantino et al. In this way we will test

the robustness of the results obtained by Costantino et al. as well as test the predictive capabilities of the cLPA model.

Appendix

Equation (29) may be written

$$0 = v_a(1 - c_{ea}a_L A_0)\cos(\varphi a_A) - v_a - \frac{v_a c_{pa} A_0}{\varphi}\sin[\varphi(a_A - a_P)] \quad (33)$$

$$\varphi = -v_a(1 - c_{ea}a_L A_0)\sin(\varphi a_A) - v_a - \frac{v_a c_{pa} A_0}{\varphi}(\cos[\varphi(a_A - a_P)] - 1) \quad (34)$$

Theorem 8. *Let Γ_n be a curve in the (v_a, A_0) parameter plane along which the real part α of some eigenvalue vanishes. Then the set of $\varphi \in I_n$ for which $\partial\alpha/\partial v_a \neq 0$ on Γ_n is open and dense in I_n.*

Proof. By continuity, the set of $\varphi \in I_n$ for which $\alpha' \doteq \partial\alpha/\partial v_a = 0$ on Γ_n is closed in I_n, and so the set of $\varphi \in I_n$ corresponding to $\alpha' \neq 0$ on Γ_n is open in I_n. To see that this set is also dense in I_n, suppose $\alpha' = 0$ on Γ_n for all φ in some open interval $J \subseteq I_n$. By differentiating Equations (25) and (26) with respect to v_a (holding A_0 constant), evaluating at $\alpha = 0$ and $\alpha' = 0$, and simplifying using Equation (33), we can show that

$$28\varphi^2\sin(28\varphi)[1 - c_{ea}a_L A_0] - c_{pa}A_0\sin[14\varphi] + 14c_{pa}A_0\varphi\cos[14\varphi] = 0 \quad (35)$$

for all $\varphi \in J$.

We can now solve (35) for A_0 in terms of φ along the curve Γ_n on interval J. This, along with the equation for A_0 along Γ_n in (30), can be used to eliminate A_0 and obtain the identity

$$c_{pa}\sin(14\varphi)\cos(28\varphi) - 14c_{pa}\varphi\cos(14\varphi)\cos(28\varphi) - 28c_{ea}a_L\varphi^2\sin(28\varphi)$$

$$-c_{pa}\sin(14\varphi) + 14c_{pa}\varphi\cos(14\varphi) - 28c_{pa}\varphi\sin(14\varphi)\sin(28\varphi) = 0$$

on J. An application of product trigonometric identities yields the identity

$$\tfrac{1}{2}c_{pa}\sin(42\varphi) - 28c_{ea}a_L\varphi^2\sin(28\varphi) - \tfrac{3}{2}c_{pa}\sin(14\varphi)$$

$$+ 7c_{pa}\varphi\cos(42\varphi) - 7c_{pa}\varphi\cos(14\varphi) = 0$$

on J. This is a contradiction since the five functions in this proposed identity are linearly independent on J.

Therefore, there is no open interval $J \subseteq I_n$ such that $\alpha' = 0$ along Γ_n for all $\varphi \in J$. Thus, the set of $\varphi \in I_n$ giving rise to $\alpha' \neq 0$ on Γ_n is dense in I_n. $\square$

The set D of fixed $A_0 > 0$ corresponding to some boundary Γ_n in the (v_a, A_0) plane as v_a varies from left to right must have the form $D = [d, \infty]$ or $D = (d, \infty)$. For $A_0 \in D$, let $v_a^{A_0}$ denote the least v_a such that the ordered pair (v_a, A_0) lies on some curve Γ_n. (The existence of a least such v_a can be deduced by contradiction from the fact that for fixed A_0, $v_a(\varphi)$ is unbounded as $\varphi \to \infty$.) We wish to show that for generic fixed $A_0 \in D$, the stable equilibrium A_0 undergoes a Hopf bifurcation at $(v_a^{A_0}, A_0)$ as v_a is varied from left to right. First, however, we need a lemma stating that the leftmost Γ_n boundries do not intersect each other in a dense fashion.

Lemma 9. *The set $T \doteq \{A_0 \in D \| \exists n \exists m \, (v_a^{A_0}, A_0) \in \Gamma_n \cap \Gamma_m\}$ is not dense in any open interval in D.*

Proof. It suffices to show that T is not dense in any bounded open interval in D. Suppose $S \subset D$ is a bounded open interval and $T \cap S$ is dense in S. The set $\{(v_a^{A_0}, A_0) \| A_0 \in S\}$ is bounded in the (v_a, A_0) plane, and so the right hand side of Equation (34) is bounded as well (recall $\varphi \geq \pi/56$). Thus, the left hand side φ is also bounded, which implies that only a finite number of curves Γ_n generate the intersections indexed by the set $T \cap S$. Without loss of generality, there exist two boundaries Γ_i and Γ_j such that the set $\{A_0 \in S \| (v_a^{A_0}, A_0) \in \Gamma_i \cap \Gamma_j\}$ is dense in S. By continuity, $\Gamma_i = \Gamma_j$ on the set $\{(v_a^{A_0}, A_0) \| A_0 \in S\}$. A rather tedius investigation of Equation (30) shows this to be a contradiction. $\square$

Theorem 10. *Let H be the set of $A_0 \in D$ for which $\partial\alpha/\partial v_a \neq 0$ at $v_a = v_a^{A_0}$, where $\alpha + i\varphi$ is some eigenvalue such that $\alpha = 0$ when $v_a = v_a^{A_0}$. Then H is open and dense in D.*

Proof. H is open in D since its complement is closed. To show that H is dense in D, we suppose there exists an open interval $U \subseteq D$ such that $H \cap U = \phi$. Now, by the previous lemma, there exists an $n \in Z^+$ and an open interval $V_n \subseteq U$ such that $(v_a^{A_0}, A_0) \in \Gamma_n$ for all $A_0 \in V_n$. This section of the curve Γ_n which is indexed by $A_0 \in V_n$ corresponds to an open φ − interval $J \subseteq I_n$. Moreover, $\partial\alpha/\partial v_a = 0$ on Γ_n for all $\varphi \in J$, which violates Theorem 8. Thus, every open interval $U \subseteq D$ contains points of H, and so H is dense in D. $\square$

References

[1] Costantino, R. F., and R. A. Desharnais 1991. Population Dynamics and the Tribolium Model: Genetics and Demography. Springer-Verlag, New York. pp. 24–36

[2] Costantino, R. F., Cushing, J. M., Dennis, B., and R. A. Desharnais 1995. Experimentally induced transitions in the dynamic behaviour of insect populations. Nature 375:227–230

[3] Costantino, R. F., Desharnais, R. A., Cushing, J. M., and B. Dennis 1997. Chaotic dynamics in an insect population. Science 275:389–391

[4] Costantino, R. F., Cushing, J. M., Dennis, B., Desharnais, R. A., and S. M. Henson 1998. Resonant population cycles in temporally fluctuating habitats. Bull. Math. Biol. 60:247–273

[5] Cushing, J. M. 1995. Systems of difference equations and structured population dynamics. Proceedings of the First International Conference on Difference Equations (Eds. S. N. Elaydi et al.) Gordon and Breach, pp. 123–132

[6] Cushing, J. M., Dennis, B., Desharnais, R. A., and R. F. Costantino 1997. An interdisciplinary approach to understanding nonlinear ecological dynamics. Ecol. Model. 92 (1996), 111–119

[7] Cushing, J. M., Dennis, B., Desharnais, R. A., and R. F. Costantino 1998. Moving toward an unstable equilibrium: saddle nodes in population systems. J. Animal Ecol. 67:298–306

[8] Dennis, B., Desharnais, R. A., Cushing, J. M., and R. F. Costantino 1995. Nonlinear demographic dynamics: Mathematical models, statistical methods, and biological experiments. Ecol. Monogr. 65(3):261–281

[9] Dennis, B., Desharnais, R. A., Cushing, J. M., and R. F. Costantino 1997. Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. J. Animal Ecol. 66:704–729

[10] Diekmann, O., Nisbet, R. M., Gurney, W. S. C., and F. van den Bosch 1986. Simple mathematical models for cannibalism: A critique and a new approach. Math. Biosci. 78:21–46

[11] Diekmann, O., van Gils, S. A., Verduyn Lunel, S. M., and H.-O. Walther 1995. Delay Equations: Functional-, Complex-, and Nonlinear Analysis. Applied Mathematical Sciences, Vol. 110, Springer-Verlag, New York

[12] Gurtin, M. E., and D. S. Levine 1979. On predator-prey interactions with predation dependent on age of prey. Math. Biosci. 47:207–219

[13] Hastings, A 1987. Cycles in cannibalistic egg-larval interactions. J. Math. Bol. 24:651–666

[14] Hastings, A., and R. F. Costantino 1987. Cannibalistic egg-larva interactions in Tribolium: an explanation for the oscillations in popoulation numbers. Am. Nat. 130:36–52

[15] Hastings, A., and R. F. Costantino 1991. Oscillations in population numbers: age-dependent cannibalism. J. Animal Ecol . 60:471–482

[16] Hastings, A., Hom, C. L., Ellner, S., Turchin, P., and H. C. J. Godfray 1993. Chaos in ecology: is mother nature a strange attractor? Ann. Rev. Ecol. and Syst. 24:1–33

[17] Henson, S. M., and J. M. Cushing 1997. The effect of periodic habitat fluctuations on a nonlinear insect population model. J. Math. Biol. 36:201–226

[18] Henson, S. M. 1998. Leslie matrix models as "stroboscopic snapshots" of McKendrick PDE models. J. Math. Biol. 37:309–328

[19] Hofbauer, J., Hutson, V., and W. Jansen 1987. Coexistence for systems governed by difference equations of Lotka-Volterra type. J. Math. Biol. 25:553–570

[20] Kuang, Y. 1993. Delay Differential Equations with Applications in Population Dynamics. Academic Press, Inc., San Diego, CA. pp. 91–93

[21] Kuang, Y., and J. M. Cushing 1995. Global stability in a nonlinear difference-delay equation model of flour beetle population growth. J. Difference Equations and Applications, 2:31–37

[22] May, R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. Science 186:645–647

[23] Smith, H. L. 1993. Reduction of structured population models to threshold-type delay equations and functional differential equations. A case study. Math. Biosci. 113:1–24

[24] Uribe, Guillermo 1993. On the relationship between continuous and discrete models for size structured population dynamics. PhD Dissertation. Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson

[25] Webb, G. F. 1985. Theory of Nonlinear Age-Dependent Population Dynamics, Marcel Dekker, Inc., New York