Leslie matrix models as "stroboscopic snapshots" of McKendrick PDE models

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Abstract. High dimensional Leslie matrix models have long been viewed as discretizations of McKendrick PDE models. However, these two fundamental classes of models can be linked in a completely different way. For populations with periodic birth pulses, Leslie models of any dimension can be viewed as "stroboscopic snapshots" (in time) of an associated impulsive McKendrick model; that is, the solution of the discrete model matches the solution of the corresponding continuous model at every discrete time step. In application, McKendrick models of populations with birth pulses can be used to identify the state of the population between the discrete census times of the associated Leslie model. Furthermore, McKendrick models describing populations with near-synchronous birth pulses can be viewed as realistic perturbations of the associated Leslie model.

Key words: Leslie model – McKendrick model – Poincaré map – Birth pulses – Seasonal births

1 Introduction

Population models fall into two fundamental categories: discrete and continuous. In the discrete category, Leslie matrix models constitute the basic class of age-structured models. McKendrick partial differential equation (PDE) models play the same role in the category of continuous models.

What are the mathematical connections between these two famous classes of models? One well-known answer is that Leslie models are discretizations of their PDE analogs. By simultaneously shrinking the

discrete time step size to zero and increasing the number of age classes accordingly in the Leslie model, one obtains in the limit the McKendrick model. Uribe made this connection mathematically rigorous in [10]. Of course, the Leslie model of choice in a given application is often low dimensional, and is hence too coarse a discretization to bear much relation to the associated PDE.

This paper presents a completely different kind of mathematical connection between Leslie models and McKendrick models. In brief, Leslie models (of arbitrary dimension) describing populations with periodic birth pulses are shown to be "stroboscopic snapshots" in time of certain associated impulsive McKendrick models. That is, the solution of the Leslie model matches the solution of the PDE model at every discrete time step of the Leslie model; the Leslie model therefore becomes a Poincaré map near periodic solutions of the PDE. *However, the straightforward modelling approach does not yield the expected mathematical results, and requires a careful reformulation before the appropriate theorems can be proved.* In particular, the straightforward "naive" McKendrick model which one might write down for a population with pulsed births does *not* approximate the typical discrete model; an example of this is presented in Sect. 1.1. In order for the two types of models to give similar predictions, great care must be given to the assumptions in the McKendrick model.

The nonlinear rates in Leslie matrices must rely on the value of the state variable at the beginning of the discrete time interval in order to generate an "average" rate throughout that interval. This can be a poor approximation when nonlinear rates do not occur more or less "instantaneously", and when populations change during the interval. For populations with seasonal birth pulses, Leslie models can be viewed as idealizations in which births and all other nonlinear interactions occur in periodic instantaneous pulses [1]. As Gyllenberg et al. [5] and White et al. [11] have pointed out in recent papers, a more realistic model is usually a "hybrid" containing discrete seasonal birth pulses but continuous within-season nonlinear interactions. The mathematical connection between Leslie and McKendrick models presented in this paper will allow the array of more realistic McKendrick models to be viewed as perturbations of idealized Leslie models. The approach can also be used to complete the continuous dynamics which occur within the discrete time intervals of Leslie models.

First, we motivate the mathematical approach by formally examining a McKendrick PDE corresponding to a simple Ricker-type map for an imaginary population with seasonal reproduction. The major mathematical difficulty is illustrated and formally resolved. Section 2 contains two general mathematical results: the proofs appear in the

appendices. In Sect. 3, we apply the approach to an experimental population with near-synchronous birth pulses using the "LPA" *Tribolium* model of Costantino et al. [3, 4]. Section 4 contains a summary of the mathematical connection between McKendrick and Leslie models for populations with seasonal births, and paves the way for a discussion of the biological connections between these two modelling approaches.

1.1 Simple motivating example

Consider a population having overlapping generations and a seasonal birth pulse occurring once a year. Assume the population is censused at the end of one-year discrete time intervals, immediately before the reproductive pulse. Suppose the fraction of animals surviving one year is $e^{-\mu}$, and reproduction is density-regulated in the manner of the Ricker equation:

$$x_{m+1} = bx_m e^{-cx_m - \mu} + e^{-\mu} x_m$$

$$x_0 = P_0 > 0 \tag{1}$$

$$m \in \{0, 1, 2, \dots\}$$

with $\mu, b, c > 0$. An associated McKendrick PDE is

$$\begin{cases} \rho_t + \rho_a = -\mu\rho(t, a) \\ \rho(t, 0) = \beta(t)y(t)e^{-cy(t)} \\ \rho(0, a) = \varphi(a) \end{cases} \tag{2}$$

where

$$y(t) \doteq \int_0^\infty \rho(t, a)\,da \tag{3}$$

$$\beta(t) \doteq \begin{cases} \frac{b}{\varepsilon} & \text{if } 0 \le t \bmod 1 \le \varepsilon \\ 0 & \text{otherwise} \end{cases} \tag{4}$$

$$P_0 = \int_0^\infty \varphi(a)\,da$$

$$t, a \ge 0$$

for small $\varepsilon > 0$. (The symbol $\doteq$ stands for "is defined to be".) The McKendrick model (2) is nonautonomous because of the periodic forcing (seasonality) in the birth rate $\beta(t)$. (The same effect of pulsed births can be obtained with an autonomous PDE if the birth rate is impulsive in age; see Sect. 4.) The Ricker-type map (1), however, is

autonomous because it samples the population size only once every period.

The age distribution solutions of (2) will be traveling waves

$$\rho(t, a) = \begin{cases} \varphi(a - t)e^{-\mu t} & \text{if } t < a \\ \beta(t - a)y(t - a)e^{-cy(t-a)}e^{-\mu a} & \text{if } t \geqq a \end{cases} \qquad (5)$$

consisting of a "train" of spikes having compact support and width ε (see Fig. 1). If we integrate both sides of (5) in age and simplify, we obtain

$$y(t) = \int_0^t \beta(s)y(s)e^{-cy(s)}e^{-\mu(t-s)}ds + e^{-\mu t}y(0) \qquad (6)$$

and so by (4), for all $m \in \{0, 1, 2, \ldots\}$,

$$y(m + 1) = \frac{b}{\varepsilon}\int_m^{m+\varepsilon} y(s)e^{-cy(s)}e^{-\mu(m+1-s)}ds + e^{-\mu}y(m) \qquad (7)$$

The temptation is strong to "formally" take $\varepsilon \to 0$ and obtain the recursion map (1) for the limiting solution y^0. However, the state variable y not only depends on ε, but is actually developing jump discontinuities over each time interval $[m, m + \varepsilon]$ as $\varepsilon \to 0$ due to the occurrence of the birth pulses on these intervals. The average value $\langle y^0(m)e^{-cy^0(m)}e^{-\mu}\rangle \doteq \lim_{\varepsilon \to 0}\frac{1}{\varepsilon}\int_m^{m+\varepsilon} y(s)e^{-cy(s)}e^{-\mu(m+1-s)}ds$ of the integrand across the developing jump is not, in fact, $y^0(m)e^{-cy^0(m)}e^{-\mu}$ (see Fig. 2A). Appendix A gives a simple analytic illustration of the failure of this approach.

The mathematical difficulty is due to our assumption that newborns in the cohort spike arriving during the time interval $[m, m + \varepsilon]$ are reproductively mature, and hence give birth, as soon as they themselves are born. When ε is small, this is not a good assumption from a biological standpoint. If instead we define the number of reproductive individuals $y(t)$ in equations (2) and (3) to be

$$y(t) \doteq \int_\varepsilon^\infty \rho(t, a)da,$$

then no animals enter the reproductive age interval $[\varepsilon, \infty)$ during the reproductive time interval $[m, m + \varepsilon]$. In this case, the jump discontinuities in y develop on the time intervals $[m + \varepsilon, m + 2\varepsilon]$ when the new cohort spikes enter the age interval $[\varepsilon, \infty)$, and will no longer be a problem in the integral equation for y, which is now

$$y(t) = \begin{cases} e^{-\mu t}\int_{\varepsilon-t}^\infty \varphi(s)ds & \text{if } t < \varepsilon \\ \int_0^{t-\varepsilon} \beta(s)y(s)e^{-cy(s)}e^{-\mu(t-s)}ds + e^{-\mu t}P_0 & \text{if } t \geqq \varepsilon \end{cases} \qquad (8)$$
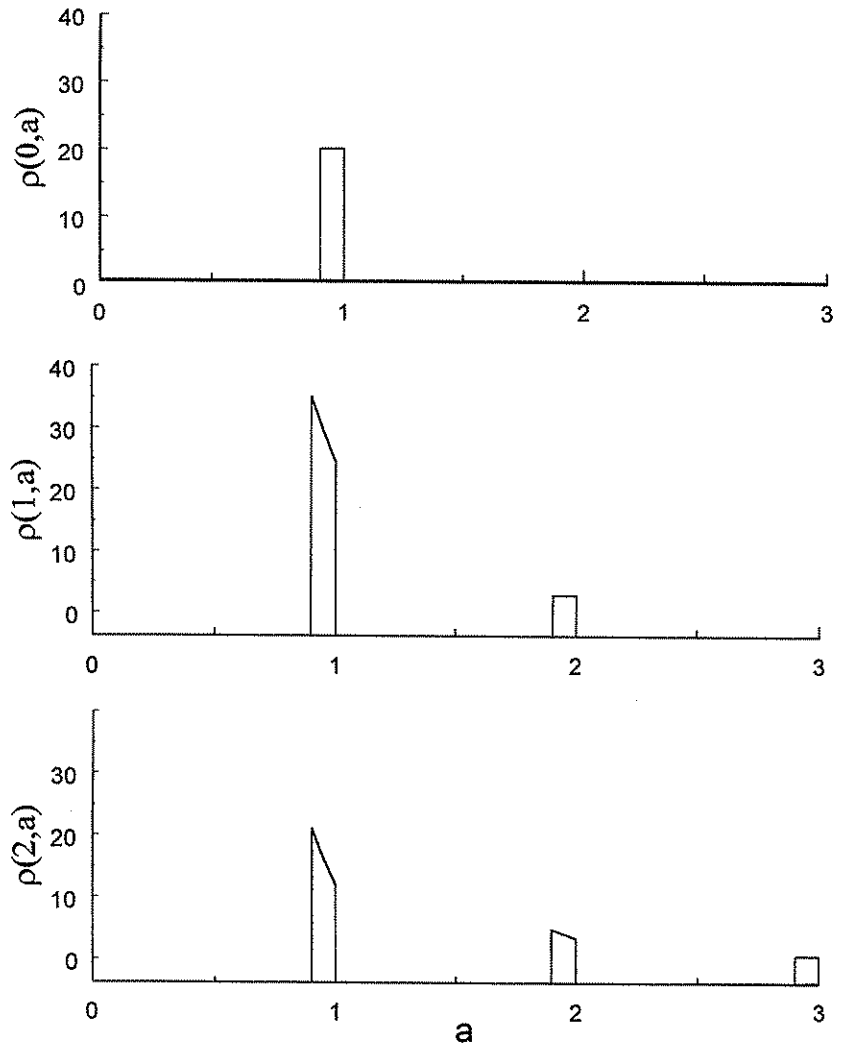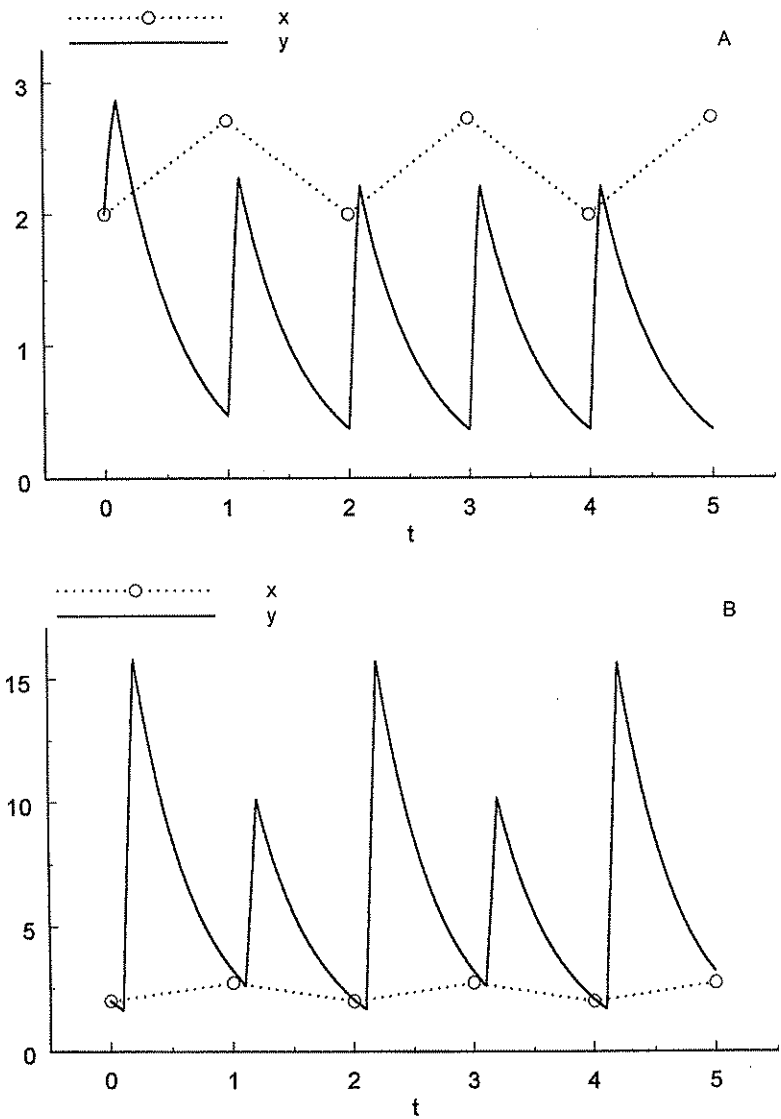
Fig. 1. Age distribution of model (2) at times $t = 0, 1, 2$. Here $b = 9e^2$, $c = 1$, $\mu = 2$, $\varepsilon = 0.1$, $P_0 = 2$, $\varphi(a) = 20$ for $0.9 \leqq a \leqq 1$, and $\varphi(a) = 0$ otherwise

When evaluated at integer values of t, (8) becomes

$$y(0) = \int_{\varepsilon}^{\infty} \varphi(s)ds$$

$$y(1) = \frac{b}{\varepsilon} \int_0^{\varepsilon} y(s)e^{-cy(s) - \mu(1-s)}ds + e^{-\mu}P_0$$

$$y(m+1) = \frac{b}{\varepsilon} \int_m^{m+\varepsilon} y(s)e^{-cy(s) - \mu(m+1-s)}ds + e^{-\mu}y(m) \quad \text{for } m \geq 1$$

Fig. 2. Time series for state variable y in models (6) and (8). The parameters and initial data are the same as in Figure 1. A) Here $y(t) \doteq \int_0^\infty \rho(t, a)da$ in (2) and $x(t)$ is the solution of (1). B) Here $y(t) \doteq \int_\varepsilon^\infty \rho(t, a)da$ in (2) and $x(t)$ is the solution of (1)

Formally, we now obtain

$$y^0(m + 1) = by^0(m)e^{-cy^0(m) - \mu} + e^{-\mu}y^0(m)$$

$$y^0(0) = P_0$$

in the limit as $\varepsilon \to 0$, where y^0 is the limiting solution of (8). Intuitively, the solution of the discrete map (1) can be viewed as a sequence of

"snapshots", taken at integer times, of the limiting solution y^0 (see Fig. 2B). *The mathematical key is to ensure the age class y is not itself undergoing a pulse (developing an unbounded derivative) while it is giving rise to the birth pulse.*

In the next section we generalize this formal approach and make it mathematically rigorous.

2 General mathematical results

2.1 Notation

The following notation will hold throughout the remainder of the paper. Let $\mathbb{N} \doteq \{0, 1, 2, \ldots\}$, $\mathbb{N}^+ \doteq \{1, 2, 3, \ldots\}$, $\mathbb{R}^+ \doteq [0, \infty)$, $\mathbb{R}_n^+ \doteq [0, \infty)^n$, and $t, a \in [0, \infty)$. $n \geq 1$ will be the fixed integer dimension of the Leslie model with $\mathbb{D} \doteq \{1, 2, \ldots, n\}$. $\varepsilon \in (0, 1/8)$ will be a small positive real parameter. Sums with ill-defined indices, such as $\sum_{i=1}^0$, are taken to be zero. $L(\mathbb{A}, \mathbb{B})$ will denote the set of Lebesgue measurable functions from $\mathbb{A}$ to $\mathbb{B}$, and $C(\mathbb{X})$ the set of continuous functions on $\mathbb{X}$.

2.2 The two models

Let

$$x(m + 1) = M(x(m))x(m)$$

$$x(0) = P \tag{9}$$

be an autonomous Leslie model, where $x = (x_1, x_2, \ldots, x_n)^\perp$, $P = (P_1, P_2, \ldots, P_n)^\perp$, $m \in \mathbb{N}$, and the "projection" matrix M is given by

$$M(x) =$$

$$
\begin{pmatrix}
b_1 f_1(x)e^{-\mu_0} & b_2 f_2(x)e^{-\mu_0} & b_3 f_3(x)e^{-\mu_0} & \cdots & b_n f_n(x)e^{-\mu_0} \\
e^{-c_1 p_1(x) - \mu_1} & 0 & 0 & \cdots & 0 \\
0 & e^{-c_2 p_2(x) - \mu_2} & 0 & \cdots & 0 \\
0 & 0 & \ddots & \cdots & \vdots \\
\vdots & \vdots & \cdots & \cdots & \vdots \\
0 & 0 & \cdots & e^{-c_{n-1} p_{n-1}(x) - \mu_{n-1}} & e^{-c_n p_n(x) - \mu_n}
\end{pmatrix}.
$$

Here the parameters $P_i, b_i, c_i, \mu_i \in \mathbb{R}^+$ for all allowable subscripts i. The $e^{-\mu_0}$ factors in the first now appear because we will be assuming

the birth pulses occur immediately *following* the census times $m \in \mathbb{N}$. $e^{-\mu_0}$ is the fraction of newborns which survive until the next census time.

Define

$$p_j(y) \doteq p_n(y) \quad \forall j > n \, \forall y \in \mathbb{R}_n^+$$

$$c_j \doteq c_n \quad \forall j > n$$

$$\mu_j \doteq \mu_n \quad \forall j > n$$

For each ε, consider the nonautonomous McKendrick model

$$\begin{cases} \rho_t + \rho_a = -\Delta(a, y(t))\rho(t, a) \\ \rho(t, 0) = B(t, y(t)) \\ \rho(0, a) = \varphi(a) \end{cases} \tag{10}$$

where

$$y(t) \doteq (y_1(t), y_2(t), \dots, y_n(t))^{\perp}$$

$$y_i(t) \doteq \int_{i-1+3\varepsilon}^{i+3\varepsilon} \rho(t, a)\,da \quad \text{for } i \in \mathbb{D}\backslash\{n\}$$

$$y_n(t) \doteq \int_{n-1+3\varepsilon}^{\infty} \rho(t, a)\,da$$

$$\Delta(a, y) \doteq c(a)p(a, y) + \mu(a)$$

$$B(t, y) \doteq \sum_{i=1}^{n} \beta_i(t) f_i(y) y_i$$

and

$$p(a, y) \doteq \begin{cases} p_i(y) & \text{if } i \leq a < i+1 \\ 0 & \text{otherwise} \end{cases} \quad \text{for } i \in \mathbb{N}^+$$

$$c(a) \doteq \begin{cases} \frac{c_i}{\varepsilon} & i + \varepsilon \leq a \leq i + 2\varepsilon \\ 0 & \text{otherwise} \end{cases} \quad \text{for } i \in \mathbb{N}^+$$

$$\mu_i \doteq \int_i^{i+1} \mu(a)\,da \quad \text{for } i \in \mathbb{N}$$

$$\beta_i(t) \doteq \begin{cases} \frac{b_i}{\varepsilon} & 0 \leq t \bmod 1 \leq \varepsilon \\ 0 & \text{otherwise} \end{cases} \quad \text{for } i \in \mathbb{D} \text{ and all } t \geq 0$$

$$\varphi(a) \doteq \begin{cases} \frac{P_i}{\varepsilon} & i - \varepsilon \leq a \leq i \\ 0 & \text{otherwise} \end{cases} \quad \text{for } i \in \mathbb{D}$$

At integer values $t = m$ of time, the population age-distribution will consist of a train of cohort spikes supported on the age intervals

$[j - \varepsilon, j], j \in \{1, 2, \ldots, n + m\}$. At these times, $y_i(m) = \int_{i-1+3\varepsilon}^{i+3\varepsilon} \rho(m, a) da$ will recover the number of individuals of ages $[i - \varepsilon, i]$. The birth and death pulses occur on the time intervals $[m, m + \varepsilon]$ and $[m + \varepsilon, m + 2\varepsilon]$, respectively, and are staggered so the age classes y_i are not undergoing death pulses while giving birth (see also hypothesis H1 in Sect. 2.4). Density-independent death rates such as μ need not be pulsed.

The discontinuities in the y_i develop on the time intervals $[m + \varepsilon, m + 2\varepsilon]$ (when the death pulses occur) and $[m + 3\varepsilon, m + 4\varepsilon]$ (when the cohort spikes enter the y_i age intervals $[i - 1 + 3\varepsilon, i + 3\varepsilon]$). These mathematical technicalities (plus H1 in Sect. 2.4) will ensure the age class y_i is not itself undergoing a pulse (developing an unbounded derivative) during the time it is giving rise to a birth or death pulse.

2.3 Alternate model formulations

In the proofs of the theorems, we will need alternate forms of models (9) and (10). It is straightforward to verify the Leslie model (9) satisfies

$$x_i(m + 1) =$$

$$\begin{cases} P_{i-m-1}e^{-\sum_{j=i-m-1}^{i-1}[c_j p_j(x(j+m-i+1))+\mu_j]} \\ \quad \text{if } m + 1 < i \\ [\sum_{j=1}^{n} b_j f_j(x(m-i+1))x_j(m-i+1)]e^{-\mu_0}e^{-\sum_{j=1}^{i-1}[c_j p_j(x(j+m-i+1))+\mu_j]} \\ \quad \text{if } m + 1 \geq i \end{cases}$$

$$x_n(m + 1) = \tag{11}$$

$$\begin{cases} \sum_{j=n-m-1}^{n} P_j e^{-\sum_{q=j}^{j+m}[c_q p_q(x(q-j))+\mu_q]} & \text{if } m + 1 < n \\ \sum_{r=0}^{m-n+1}\left\{[\sum_{j=1}^{n} b_j f_j(x(r))x_j(r)]e^{-\mu_0}e^{-\sum_{q=1}^{n-1}[c_q p_q(x(q+r))+\mu_q]}\right\} \\ \quad + \sum_{j=1}^{n} P_j e^{-\sum_{q=j}^{m+j}[c_q p_q(x(q-j))+\mu_q]} & \text{if } m + 1 \geq n \end{cases}$$

for $i \in \mathbb{D} \setminus \{n\}$.

An analogous reformulation for equation (10) arises from formally integrating along its characteristics to obtain

$$\rho(t, a) = \begin{cases} \varphi(a - t)e^{-\int_{a-t}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} & \text{if } t < a \\ B(t - a, y(t - a))e^{-\int_{0}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} & \text{if } t \geq a \end{cases} \tag{12}$$

and then integrating equation (12) over each age class $[i - 1 + 3\varepsilon, i + 3\varepsilon]$ to produce a system of integral equations in the

state variables $y_1, y_2, \ldots, y_n$:

$$y_i(t) =$$

$$
\begin{cases}
\int_{i-1+3\varepsilon}^{i+3\varepsilon} \varphi(a-t)e^{-\int_{a-t}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \text{if } t < i-1+3\varepsilon \\[2mm]
\int_{i-1+3\varepsilon}^{t} B(t-a, y(t-a))e^{-\int_{0}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \text{if } i-1+3\varepsilon \leqq t < i+3\varepsilon \\[1mm]
\quad + \int_{t}^{i+3\varepsilon} \varphi(a-t)e^{-\int_{a-t}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \\[2mm]
\int_{i-1+3\varepsilon}^{i+3\varepsilon} B(t-a, y(t-a))e^{-\int_{0}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \text{if } i+3\varepsilon \leqq t
\end{cases}
$$

$$y_n(t) = \tag{13}$$

$$
\begin{cases}
\int_{n-1+3\varepsilon}^{\infty} \varphi(a-t)e^{-\int_{a-t}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \text{if } t < n-1+3\varepsilon \\[2mm]
\int_{n-1+3\varepsilon}^{t} B(t-a, y(t-a))e^{-\int_{0}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da & \text{if } n-1+3\varepsilon \leqq t \\[1mm]
\quad + \int_{t}^{\infty} \varphi(a-t)e^{-\int_{a-t}^{a} \Delta(\alpha, y(t-a+\alpha))d\alpha} da &
\end{cases}
$$

for $i \in \mathbb{D} \setminus \{n\}$.

Our theorems will concern system (13) rather than the motivating PDE (10).

2.4 Hypotheses

The following hypotheses will be used:

H1) There exist disjoint sets $\mathbb{A}$ and $\mathbb{B}$ with $\mathbb{D} = \mathbb{A} \cup \mathbb{B}$ such that $p_i(y) \equiv 0$ for all $i \in \mathbb{A}$; and for all $j \in \mathbb{B}$, $p_j(y)$ depends only upon those y_i with $i \in \mathbb{A}$.

H1*) $p_n(y) \equiv 0$; and for all $i \in \mathbb{D} \setminus \{n\}$, $p_i(y) = p_i(y_n)$ depends only upon y_n.

H2) $\mu \in L(\mathbb{R}^+, \mathbb{R}^+)$; and $p_i, f_i \in L(\mathbb{R}_n^+, \mathbb{R}^+)$ for all $i \in \mathbb{D}$.

H3) There exists $M \in \mathbb{R}^+$ such that for all $a \in \mathbb{R}^+$ and $y, x \in \mathbb{R}_n^+$,

$$|p(a, y) - p(a, x)| \leqq M|y - x|$$

H4) There exists $M \in \mathbb{R}^+$ such that for all $t \in \mathbb{R}^+$ and $y, x \in \mathbb{R}_n^+$,

$$0 \leqq B(t, y) \leqq M$$

and

$$|B(t, y) - B(t, x)| \leqq M|y - x|$$

The two major theorems hold under hypotheses H1–H4. For notational simplicity in the proofs, we will utilize the stronger assumption H1* instead of H1. Hypothesis H1 ensures the age class y_i is not itself suffering a death pulse while it is impulsively affecting another

class. The Lipschitz conditions H3–H4 provide the contraction mapping used in the proof of Theorem 1. Hypothesis H4 is a typical population birth rate "crowding" assumption. The Lipschitz condition H3 on the death rate is not so typical but will hold for most applications. While H3 (along with H4) is sufficient to provide the contraction mapping in the proof of Theorem 1, it is not necessary and can be weakened at the expense of unilluminating technicalities.

2.5 Main theorems

Algebraic simplification of (13) and evaluation at $t = m + 1$ will lead us (in Appendix B) to a system of integral equations essentially having the form

$$y^\varepsilon(m + 1) = \frac{1}{\varepsilon} \int_m^{m+\varepsilon} G(s, y^\varepsilon)\,ds.$$

It will be clear that a formal evaluation $y^0(m + 1) = G(m, y^0)$ in the limit as $\varepsilon \to 0$ will lead to the expected recursion formula (11). Roughly speaking, we will establish this formal calculation by first showing $G(m, y^0) \doteq \lim_{\varepsilon \to 0} G(m, y^\varepsilon)$ exists, and then showing $G(s, y^\varepsilon)$ does not become arbitrarily steep near integer values of s as $\varepsilon \to 0$. The two main theorems are now stated; their supporting lemmas and proofs appear in Appendices C–E.

Theorem 1. *Assume hypotheses H1–H4. For each ε, equation (13) has a unique solution $y^\varepsilon \in C(\mathbb{R}^+)$.*

Theorem 2. *Assume hypotheses H1–H4. For all $m \in \mathbb{N}$, $y^0(m) \doteq \lim_{\varepsilon \to 0} y^\varepsilon(m)$ exists, and*

$$y^0(m) = x(m),$$

where x is the solution of (9).

3 Application to a *Tribolium* model

The Leslie-type discrete *Tribolium* "LPA" model

$$\begin{cases} L(m + 1) = bA(m)e^{-c_{el}L(m) - c_{ea}A(m)} \\ P(m + 1) = (1 - \mu_l)L(m) \\ A(m + 1) = P(m)e^{-c_{pa}A(m)} + (1 - \mu_a)A(m) \end{cases} \qquad \text{(LPA)}$$

$$m \in \mathbb{N}$$

has been thoroughly validated by Costantino et al. using laboratory data (see [3, 4], and the references therein). It has been used to design laboratory experiments that have successfully produced a variety of nonlinear dynamical phenomena, including chaos, in flour beetle populations. The discrete time interval is 14 days. $L(t)$ denotes the number of feeding larvae at census t, $P(t)$ denotes the number of nonfeeding larvae, pupae, and callow adults, and $A(t)$ denotes the number of adults. μ_l and μ_a are the per unit time larval and adult probabilities of dying from causes other than cannibalism, and exponential $e^{-c_{pa}A}$ represents the probability per unit time that a pupa survives cannibalism by adults. Since the egg stage is short relative to the 14 day time step, Costantino et al. made the simplifying assumption that the egg stage has duration zero. b therefore denotes the average number of larvae recruited per adult per unit time in the absence of cannibalism, while $e^{-c_{el}L-c_{ea}A}$ represents the fractional reduction of larval recruitment due to cannibalism of eggs by larvae and adults.

In order to study the dynamics of a *Tribolium* population whose birth rate is periodically pulsed, Costantino et al. and the author have designed and initiated a laboratory experiment in which a pulse of new larvae enters the larval class immediately *following* each 2-week census. In this experiment, the life stages are therefore censused when the animals are at the end of their current lifestage, and the beetles enter the next stage immediately after census. The LPA model is easily modified to describe post-census pulsing:

$$\begin{cases} L(m+1) = bA(m)e^{-c_{el}L(m)-c_{ea}A(m)}(1-\mu_l) \\ P(m+1) = L(m)e^{-c_{pa}A(m)} \\ A(m+1) = (1-\mu_a)(P(m)+A(m)) \end{cases} \tag{14}$$

Let $(L(0), P(0), A(0))^{\perp} = (L_0, P_0, A_0)^{\perp}$. Then the PDE analog of (14) is

$$\rho_t + \rho_a = -[c(a)y_3(t) + \mu(a)]\rho(t,a)$$

$$\rho(t,0) = \beta(t)y_3(t)\exp[-c_{el}y_1(t) - c_{ea}y_3(t)] \tag{15}$$

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

where the units of time are 14 days,

$$y_1(t) \doteq \int_{3\varepsilon}^{1+3\varepsilon} \rho(t,a)da$$

$$y_2(t) \doteq \int_{1+3\varepsilon}^{2+3\varepsilon} \rho(t,a)da$$

$$y_3(t) \doteq \int_{2+3\varepsilon}^{\infty} \rho(t, a)da$$

and

$$\mu(a) \doteq \begin{cases} -\ln(1 - \mu_l) & 0 \leq a < 1 \\ 0 & 1 \leq a < 2 \\ -\ln(1 - \mu_a) & 2 \leq a \end{cases}$$

$$c(a) \doteq \begin{cases} \frac{c_{pa}}{\varepsilon} & 1 + \varepsilon \leq a \leq 1 + 2\varepsilon \\ 0 & \text{otherwise} \end{cases}$$

$$\beta(t) \doteq \begin{cases} \frac{b}{\varepsilon} & 0 \leq t \bmod 1 \leq \varepsilon \\ 0 & \text{otherwise} \end{cases} \quad \text{for } t \geq 0$$

$$\varphi(a) \doteq \begin{cases} \frac{L_0}{\varepsilon} & 1 - \varepsilon \leq a \leq 1 \\ \frac{P_0}{\varepsilon} & 2 - \varepsilon \leq a \leq 2 \\ \frac{A_0}{\varepsilon} & 3 - \varepsilon \leq a \leq 3 \\ 0 & \text{otherwise} \end{cases}$$

To compare this impulsive McKendrick *Tribolium* model with nonimpulsive counterparts in the literature, see [2, 6–8], and [9].

Theorems 1 and 2 apply, so there exists a unique solution $y^\varepsilon(t) = (y_1^\varepsilon(t), y_2^\varepsilon(t), y_3^\varepsilon(t))^\perp$ in $C(\mathbb{R}^+)$ of the integral formulation of (15) for which

$$\lim_{\varepsilon \to 0} y_1^\varepsilon(m) = L(m); \qquad \lim_{\varepsilon \to 0} y_2^\varepsilon(m) = P(m); \qquad \lim_{\varepsilon \to 0} y_3^\varepsilon(m) = A(m)$$

for all $m \in \mathbb{N}$.

System (14) is an idealization which assumes instantaneously pulsed births *as well as* other nonlinear interactions. Equation (15) advances in two directions: first, for very small ε, it predicts the continuous dynamics in between the 14 day predictions of (14); and second, it allows more realistic pulses (of duration ε). However, (15) still requires the adult-on-pupal cannibalism to be pulsed; and in both models, cannibalism of eggs is instantaneous because of the simplifying modeling assumption that the egg stage is of zero duration.

Although the cannibalism rates in (15) must be pulsed in order to recover (14) as $\varepsilon \to 0$, in reality they are not pulsed, but continuous, in this experiment. The most realistic model is probably a PDE model in which the birth rate is pulsed but the cannibalism rates are not. Such a model can be viewed as a realistic perturbation of (15), which in turn can be considered a perturbation of (14). After sufficient data is collected from the ongoing experiment, we will parameterize these various

kinds of models in order to compare the success of the modelling strategies.

4 Discussion

In summary, for populations with seasonal births, discrete Leslie models of any dimension can be viewed as stroboscopic snapshots in time of an analogous continuous McKendrick model. Near periodic orbits of the McKendrick model (13), the Leslie model (9) therefore becomes a Poincaré map or "first return map" of (13). Thus, the most basic class of discrete population models can be derived from the most basic class of continuous population models under the assumptions of instantaneously pulsed births and nonlinear interactions.

The derivation given in this paper is not the only way to set up such a connection between Leslie models and McKendrick models. For example, an identical theory can be derived by pulsing the birth rate in age instead of time, as long as the initial population is in discrete cohorts. That is, if each individual can give birth only at integer ages, and if the initial population age distribution consists of spikes situated at integer ages, then the dynamics will be the same as if births were allowed only at integer times. In this case, model (13) would be autonomous. Also, one could model the birth pulse in (10) to occur just *prior to* the discrete census time in (9) rather than just after the census time, so that the animals are in the *beginning* of their current life stage whenever they are censused in (9). Furthermore, hypothesis H1 could be dropped so that every class could affect every other class; but the nonlinear interactions would have to be staggered so as not to interfere with each other.

In most applications with seasonal births, the other nonlinear interactions will probably not be pulsed, and it may or may not be necessary to use a "hybrid" model with discrete births and continuous within-season death rates rather than a Leslie model. The mathematical connection between Leslie and McKendrick models presented in this paper allows the array of more realistic McKendrick models to be viewed as perturbations of the idealized situation described by the Leslie model.

As was demonstrated in the Introduction, the straightforward "naive" approach for deriving a Leslie model from the impulsive McKendrick model does not work. If the birth and death pulses and age class boundaries are not appropriately staggered the impulsive PDE does not yield the Leslie recursion formula. Suppose, however, the straightforward approach *is* taken with the PDE. What kind of

model emerges as $\varepsilon \to 0$? Will it satisfy some discrete recursion formula, and if so, which one? How will it relate to a Leslie model? Would such a model be useful? The answers to these questions will be considered in a future paper.

Finally, the pulsed-birth *Tribolium* experiment described in Sect. 3 is a first attempt to address the biological connections between the McKendrick and Leslie modelling approaches. In particular, the mathematical connection discussed in this paper forces us to examine in detail various biological assumptions made by modellers, and to consider carefully the interpretations of parameters in both classes of models. The discrete and continuous models used to guide this experiment provide testable hypotheses regarding the effect of periodically pulsing *Tribolium* larval recruitment. As we saw in the Introduction, the predictions of the straightforward "naive" impulsive McKendrick model will be quite different from the predictions of the discrete model (14) and its correctly constructed McKendrick model analog (15). The experiment is designed to test the predictions of these various approaches.

5 Appendices

A. Failure of straightforward approach

Consider the Volterra integral equation

$$x(t) = \int_0^t d(s)x(s)ds + x_0$$

where

$$d(s) = \begin{cases} \frac{c}{\varepsilon} & \text{if } 0 < s < \varepsilon \\ 0 & \text{otherwise} \end{cases}$$

The solution is

$$x^\varepsilon(t) = \begin{cases} x_0 e^{ct/\varepsilon} & \text{if } 0 \leqq t < \varepsilon \\ x_0 e^c & \text{if } t \geqq \varepsilon \end{cases}$$

and so the limiting solution x^0 is

$$x^0(t) = \begin{cases} x_0 & \text{if } t = 0 \\ x_0 e^c & \text{if } t > 0 \end{cases}$$

rather than the naive formal calculation $x^0(t) = cx_0 + x_0$.

B. *Simplification of model (13)*

Algebraic simplification of (13) evaluated at $t = m + 1$ yields

$$y_i(m+1) = \begin{cases} \frac{1}{\varepsilon}\int_{i-m-1-\varepsilon}^{i-m-1} G_1^{i,m}(s,y)ds & \text{if } m+1 < i \\ \frac{1}{\varepsilon}\int_{m-i+1}^{m-i+1+\varepsilon} G_2^{i,m}(s,y)ds & \text{if } m+1 \geq i \end{cases} \quad \text{for } i \in \mathbb{D}\backslash\{n\}$$

$$y_n(m+1) = \begin{cases} \sum_{j=n-m-1}^{n} \frac{1}{\varepsilon}\int_{j-\varepsilon}^{j} G_3^{n,m,j}(s,y)ds & \text{if } m+1 < n \\ \sum_{r=0}^{m-n+1} \frac{1}{\varepsilon}\int_{r}^{r+\varepsilon} G_4^{n,m,r}(s,y)ds & \text{if } m+1 \geq n \\ + \sum_{j=1}^{n} \frac{1}{\varepsilon}\int_{j-\varepsilon}^{j} G_5^{n,m,j}(s,y)ds \end{cases} \quad (16)$$

where

$$G_1^{i,m}(s,y) = P_{i-m-1}e^{-\sum_{j=i-m-1}^{i-1}\frac{1}{\varepsilon}\int_{j+\varepsilon}^{j+2\varepsilon}c_jp_j(y(\alpha-s))d\alpha}S_1(s)$$

$$G_2^{i,m}(s,y) = \left[\sum_{j=1}^{n} b_jf_j(y(s))y_j(s)\right]e^{-\sum_{j=1}^{i-1}\frac{1}{\varepsilon}\int_{j+\varepsilon}^{j+2\varepsilon}c_jp_j(y(\alpha+s))d\alpha}S_2(s)$$

$$G_3^{n,m,j}(s,y) = P_je^{-\sum_{q=j}^{j+m}\frac{1}{\varepsilon}\int_{q+\varepsilon}^{q+2\varepsilon}c_qp_q(y(\alpha-s))d\alpha}S_1(s)$$

$$G_4^{n,m,r}(s,y) = \left[\sum_{j=1}^{n} b_jf_j(y(s))y_j(s)\right]e^{-\sum_{q=1}^{m-r}\frac{1}{\varepsilon}\int_{q+\varepsilon}^{q+2\varepsilon}c_qp_q(y(\alpha+s))d\alpha}S_2(s)$$

$$G_5^{n,m,j}(s,y) = P_je^{-\sum_{q=j}^{m+j}\frac{1}{\varepsilon}\int_{q+\varepsilon}^{q+2\varepsilon}c_qp_q(y(\alpha-s))d\alpha}S_1(s)$$

$$S_1(s) = e^{-\int_s^{s+m+1}\mu(\alpha)d\alpha}$$

$$S_2(s) = e^{-\int_0^{m+1-s}\mu(\alpha)d\alpha}$$

A formal evaluation of (10) as $\varepsilon \to 0$ produces the recursion formula (11). We rigorously establish this formal calculation in Appendices C–E.

C. *Proof of Theorem 1*

Theorem 1. *Assume hypotheses H1–H4. For each ε, equation (13) has a unique solution $y^\varepsilon \in C(\mathbb{R}^+)$.*

Proof. The system of integral equations (13) defines an operator equation

$$y = T_1 y$$

with $T_1: C[0,k] \to C[0,k]$ for all $k \in \mathbb{R}^+$.

Using the Lipschitz conditions H3–H4 and the contraction mapping principle, one can show there exists $\delta_1 > 0$ such that T_1 has

a unique fixed point $y^\varepsilon \in C[0, \delta_1]$. It is then possible to rewrite the operator equation as

$$y = T_2 y$$

where T_2 is contraction on $\{z \in C[0, \delta_2] : z|_{[0, \delta_1]} = y^\varepsilon\}$ for some $\delta_2 > 0$, and so extend the solution y^ε to $[0, \delta_2]$. It is straightforward to show that for repeated applications of the contraction mapping principle, the δ_i are bounded away from zero; hence the solution can be extended to arbitrarily large intervals. $\qquad\square$

D. Definitions and lemmas

We invent the following definition:

Definition 1. Let $\mathscr{F} = \{f^\varepsilon(s)\}_{\varepsilon > 0}$ be a family of functions defined on $\mathbb{X} \subseteq \mathbb{R}$, and $\alpha > 0$. $\mathscr{F}$ is α-equiregular at $k \in \mathbb{X}$ is and only if

$$\forall \gamma > 0 \exists \delta > 0 \forall \varepsilon < \delta \forall s \in [k, k + \alpha\varepsilon)(|f^\varepsilon(s) - f^\varepsilon(k)| < \gamma).$$

Clearly α-equiregularity at k implies α'-equiregularity at k for $\alpha' < \alpha$. Also, if g is globally Lipschitz and $\{f^\varepsilon(s)\}_{\varepsilon > 0}$ is α-equiregular at k, then $\{g(f^\varepsilon(s))\}_{\varepsilon > 0}$ is also α-equiregular at k.

Lemma 3. Let $\mathscr{F} = \{f^\varepsilon(s)\}_{\varepsilon > 0}$ and $\alpha \geq 1$. If $\mathscr{F}$ is α-equiregular at k and $f^0(k) \doteq \lim_{\varepsilon \to 0} f^k(k)$ exist, then

$$\lim_{\varepsilon \to 0} \frac{1}{\varepsilon} \int_{k + (\alpha - 1)\varepsilon}^{k + \alpha\varepsilon} f^\varepsilon(s) ds = f^0(k).$$

Proof. Let $\gamma > 0$. Then there is $\delta_1 > 0$ such that whenever $\varepsilon < \delta_1$, $|f^\varepsilon(s) - f^\varepsilon(k)| < \frac{\gamma}{2}$ for all $s \in [k, k + \alpha\varepsilon)$. Also, there exists $\delta_2 > 0$ such that for all $\varepsilon < \delta_2$, $|f^\varepsilon(k) - f^0(k)| < \frac{\gamma}{2}$. Select $\delta = \min\{\delta_1, \delta_2\}$. Then for $\varepsilon < \delta$, we have $|f^\varepsilon(s) - f^0(k)| = |f^\varepsilon(s) - f^\varepsilon(k) + f^\varepsilon(k) - f^0(k)| \leq |f^\varepsilon(s) - f^\varepsilon(k)| + |f^\varepsilon(k) - f^0(k)| < \gamma$ for all $s \in [k, k + \alpha\varepsilon)$. Therefore, for all $\varepsilon < \delta$ and $s \in [k, k + \alpha\varepsilon)$,

$$f^0(k) - \gamma < f^\varepsilon(s) < f^0(k) + \gamma$$

and hence

$$f^0(k) - \gamma < \frac{1}{\varepsilon} \int_{k + (\alpha - 1)\varepsilon}^{k + \alpha\varepsilon} f^\varepsilon(s) ds < f^0(k) + \gamma$$

for all $\varepsilon < \delta$. $\qquad\square$

Lemma 4. Assume hypotheses H1*–H4. Let $y^\varepsilon(t)$ be the solution of (13) and let $m \in \mathbb{N}$. Then $\{y_i^\varepsilon(t)\}_{\varepsilon > 0}$ is 1-equiregular at m for all $i \in \mathbb{D}$, and $\{y_n^\varepsilon(t)\}_{\varepsilon > 0}$ is 3-equiregular at m.

Proof. First note from equation (10) that for each $i \in \mathbb{D}$ and $m \in \mathbb{N}$, $y_i^\varepsilon(m)$ is bounded as function of ε.

Let $i < n$. When $t \in [m, m + \varepsilon)$, (13) become

$$y_i^\varepsilon(t) = \frac{1}{\varepsilon} \int_{i-\varepsilon}^{i} P_i e^{-\int_s^{s+t} \mu(\alpha)d\alpha} ds$$

if $m = 0$, and

$$y_i^\varepsilon(t) = \begin{cases} \frac{1}{\varepsilon} \int_{i-m-\varepsilon}^{i-m} G_1^{i,m-1}(s, y^\varepsilon) e^{-\int_{s+m}^{s+t} \mu(\alpha)d\alpha} ds & \text{if } m < i \\ \frac{1}{\varepsilon} \int_{m-i}^{m-i+\varepsilon} G_2^{i,m-1}(s, y^\varepsilon) e^{-\int_{m-s}^{t-s} \mu(\alpha)d\alpha} ds & \text{if } m \geqq i \end{cases}$$

if $m > 0$. Thus, in any case,

$$|y_i^\varepsilon(t) - y_i^\varepsilon(m)| \leqq y_i^\varepsilon(m) \max_{s \in [i-\varepsilon, i]} |e^{-\int_s^{s+t} \mu(\alpha)d\alpha} - 1|$$

which can be made arbitrarily small for all sufficiently small ε. Therefore, $\{y_i^\varepsilon(t)\}_{\varepsilon > 0}$ is 1-equiregular at m.

Let $i = n$. When $t \in [m, m + 3\varepsilon)$, (13) becomes (under hypothesis H1*)

$$y_n(t) = \frac{1}{\varepsilon} \int_{n-\varepsilon}^{n} P_n e^{-\int_s^{s+t} \mu(\alpha)d\alpha} ds$$

if $m = 0$ and

$$y_n(t) = \begin{cases} \sum_{j=n-m}^{n} \frac{1}{\varepsilon} \int_{j-\varepsilon}^{j} G_3^{n,m-1,j}(s, y) e^{-\int_{s+m}^{s+t} \mu(\alpha)d\alpha} ds & \text{if } m < n \\ \sum_{r=0}^{m-n} \frac{1}{\varepsilon} \int_{r}^{r+\varepsilon} G_4^{n,m-1,r}(s, y) e^{-\int_{m-s}^{t-s} \mu(\alpha)d\alpha} ds & \text{if } m \geqq n \\ \quad + \sum_{j=1}^{n} \frac{1}{\varepsilon} \int_{j-\varepsilon}^{j} G_5^{n,m-1,j}(s, y) e^{-\int_{s+m}^{s+t} \mu(\alpha)d\alpha} ds \end{cases}$$

if $m > 0$. Thus,

$$|y_n^\varepsilon(t) - y_n^\varepsilon(m)| \leqq y_n^\varepsilon(m) \sum_{j=n}^{n+m} \max_{s \in [j-\varepsilon, j]} |e^{-\int_s^{s+3\varepsilon} \mu(\alpha)d\alpha} - 1|$$

which can be made arbitrarily small for sufficiently small ε. Therefore, $\{y_n^\varepsilon(t)\}_{\varepsilon > 0}$ is 3-equiregular at m. $\qquad\square$

E. Proof of Theorem 2

Theorem 2. *Assume hypotheses H1*–H4. For all $m \in \mathbb{N}$, $y^0(m) \doteq \lim_{\varepsilon \to 0} y^\varepsilon(m)$ exists, and $y^0(m) = x(m)$, where x is the solution of (9).*

Proof. The theorem holds for $m = 0$ since $y^\varepsilon(0) = P$ for all ε.

Suppose the theorem holds for all $m' \leq m$. From Appendix B,

$$y_i^\varepsilon(m+1) = \begin{cases} \frac{1}{\varepsilon}\int_{i-m-1}^{i-m-1+\varepsilon} G_1^{i,m}(s-\varepsilon, y^\varepsilon)ds & \text{if } m+1 < i \\ \frac{1}{\varepsilon}\int_{m-i+1}^{m-i+1+\varepsilon} G_2^{i,m}(s, y^\varepsilon)ds & \text{if } m+1 \geq i \end{cases} \quad \text{for } i \in \mathbb{D}\backslash\{n\}$$

$$y_n^\varepsilon(m+1) = \begin{cases} \sum_{j=n-m-1}^n \frac{1}{\varepsilon}\int_j^{j+\varepsilon} G_3^{n,m,j}(s-\varepsilon, y^\varepsilon)ds & \text{if } m+1 < n \\ \sum_{r=0}^{m-n+1} \frac{1}{\varepsilon}\int_r^{r+\varepsilon} G_4^{n,m,r}(s, y^\varepsilon)ds & \text{if } m+1 \geq n \\ + \sum_{j=1}^n \frac{1}{\varepsilon}\int_j^{j+\varepsilon} G_5^{n,m,j}(s-\varepsilon, y^\varepsilon)ds \end{cases}$$

Essentially, we wish to show the integrands have ε-limits and are 1-equiregular so we can apply Lemma 3.

Consider the case $m+1 \geq i$ for $i < n$. Under hypothesis H1*, G_2 is

$$G_2^{i,m}(s, y^\varepsilon) = B(s, y^\varepsilon(s))e^{-\sum_{j=1}^{i-1}\frac{1}{\varepsilon}\int_{j+\varepsilon}^{j+2\varepsilon} c_j p_j(y_n^\varepsilon(\alpha+s))d\alpha} e^{-\int_0^{m+1-s}\mu(\alpha)d\alpha}$$

By Lemma 4, $\{y_n^\varepsilon(t)\}_{\varepsilon>0}$ is 3-equiregular, and hence 2-equiregular, at each integer. By induction, Lemma 3, and hypothesis H3,

$$\lim_{\varepsilon\to 0} e^{-\sum_{j=1}^{i-1}\frac{1}{\varepsilon}\int_{j+\varepsilon}^{j+2\varepsilon} c_j p_j(y_n^\varepsilon(\alpha+m-i+1))d\alpha} = e^{-\sum_{j=1}^{i-1} c_j p_j(y_n^0(j+m-i+1))}$$

exists. Thus, by induction, H2, and H4,

$$\lim_{\varepsilon\to 0} G_2^{i,m}(m-i+1, y^\varepsilon) = x_i(m+1).$$

Also, it is straightforward to show $\{G_2^{i,m}(s, y^\varepsilon)\}_{\varepsilon>0}$ is 1-equiregular at $s = m-i+1$ using the induction hypothesis, Lemma 4, and assumptions H1*–H4. (The 3-equiregularity of $\{y_n^\varepsilon(t)\}_{\varepsilon>0}$ is used at this stage.)

Thus, by Lemma 3,

$$\lim_{\varepsilon\to 0} y_i^\varepsilon(m+1) = \lim_{\varepsilon\to 0} \frac{1}{\varepsilon}\int_{m-i+1}^{m-i+1+\varepsilon} G_2^{i,m}(s, y^\varepsilon)ds$$

$$= \lim_{\varepsilon\to 0} G_2^{i,m}(m-i+1, y^\varepsilon)$$

$$= x_i(m+1).$$

The other cases are similar. □

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