Weakly coupled hyperbolic systems modeling the circulation of FeLV in structured feline populations

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Abstract

Global existence and regularity results are provided for weakly coupled first order hyperbolic systems modeling the propagation of the Feline Leukemia Virus (FeLV), a retrovirus of domestic cats (Felis catus). In a simple example we find a threshold parameter yielding endemic stationary states. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

We shall be concerned with the development of a mathematical model describing the propagation of Feline Leukemia Virus (FeLV), a feline retro-virus, see [1–3], within a population of domestic cats (Felis catus). The clinical course of FeLV infection begins with an exposed stage lasting on an average from three to four weeks. At the conclusion of the exposed stage approximately two-thirds of the infected cats develop immunity and may be considered as clinically recovered; they have normal life expectancy and fertility rate and their offspring are free of the disease. The remainder of the cats becomes infective and infectious for the rest of their life. The
accompanying viremia causes various disorders which accelerate the mortality process. Typically
the life expectancy of fully infected cats does not exceed 20 months. The presence of the virus
causes most pregnancies to abort and infected kittens die almost immediately. Therefore we may
assume no vertical transmission of the disease [1–3]. The disease is transmitted horizontally
through social contact (amicable, hostile, and mating) between infective and susceptible cats.

The mechanism producing the splitting to the right of block E in Fig. 1 will be detailed in the
next section. We feel that three time variables can play an important role in the disease dynamics.
The first will be the elapsed time, the second will be the chronological age of the individual
animals and the third will be the age of the disease in a given animal. This will lead to time dependent
bi-variate distributions which give population time dependent densities with respect to chrono-
logical age and age of the disease in a given individual. Typically epidemic models only involve
elapsed time and age of the disease. However, the use of two structural age variables for epidemic
was introduced over 20 years ago in [4]. If the chronological age is to be considered, one com-
partmentalizes the population into two distinct age categories [5]. In the work at hand we wish to
take advantage of the methodology of age-dependent population dynamics [6,7], to model
chronological age-dependence. As we shall see in the subsequent development, this will produce
first order hyperbolic equations with two structural variables rather the customary one. Section 4
will be devoted to the analysis of endemic states of a simple example.

2. Basic model

To put matters in perspective, we begin with the introduction of a model which describes the
dynamics of a disease-free feline population. If \( \rho(a,t) \) denotes the time-dependent population
density with respect to chronological age \( a \) and elapsed time \( t \), we have

\[
\begin{align*}
\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} &= -\lambda(a,t)\rho, \quad t \geq 0, \quad a \geq 0, \\
\rho(a,0) &= \rho_0(a), \quad a \geq 0, \\
\rho(0,t) &= \int_0^\infty \beta(a,t)\rho(a,t)\,da \quad t \geq 0.
\end{align*}
\]  

(2.1)
We assume that the birth rate $\beta(a, t)$ is non-negative and smooth and that the initial distribution $\rho_0(\cdot)$ is non-negative and continuously differentiable and belongs to $L_1(0, \infty)$. System (2.1) is the basic Kermack and McKendrick equation. Thorough discussions of Kermack and McKendrick equations are given in [6,7]. We point out that the original Kermack and McKendrick paper contains models including the time since infection [8,9].

In Fig. 1, we labeled susceptible, fully infected (infective) and removed (recovered) classes of the feline population by $S$, $I$ and $R$. We introduce the state variables $u(a, t)$, $z(a, t)$ and $w(a, t)$ to denote their time dependent densities with respect to age. The mathematical description of the exposed or latent class will be a bit more involved. Here we shall need to keep track of the age of the infection (the elapsed time since contracting the disease) as well as the chronological age of the individual and the elapsed time. This will necessitate a state variable $\phi(a, b, t)$ depending on chronological age, $a$, and age of the disease, $b$, as well as time, $t$. We should point out that we only track the age of the infection for the exposed class. A more complete model might also track the age of infection for the fully infective class because the mortality of infected cats clearly depends more heavily upon the age of infection that it does upon chronological age. However, our present purpose is to discuss the general methodology of using doubly age structured models rather than produce detailed models.

We make the assumption that the period of latency or incubation is the same for all cases, having length $\tau > 0$. This means that, $b$, the age since infection satisfies

$$0 \leq b \leq \tau.$$  \hspace{1cm} (2.2)

We introduce the function, $\tau(a) = \min\{\tau, a\}$. The time dependent variable $\phi(a, b, t)$ represents the bivariate density with respect to chronological age and time elapsed since contacting the disease: we observe that $\mathcal{R}$, the domain of interest for us is given by

$$\mathcal{R} = \{(a, b, t), \ t \geq 0, \ 0 \leq b \leq \tau(a), \ 0 \leq a < \infty\}. \hspace{1cm} (2.3)$$

We may assume that

$$\phi(a, b, t) \equiv 0 \quad \text{for} \quad a \leq b, \ 0 \leq t. \hspace{1cm} (2.4)$$

This is a mathematical condition consistent with the biological assumption of no vertical transmission of the disease. We have introduced the variable $\phi(a, b, t)$ to track the progression of the disease from inception to the end of the period of latency (or incubation). The time-dependent density of the exposed class is computed by

$$v(a, t) = \int_0^{\tau(a)} \phi(a, b, t) \, db. \hspace{1cm} (2.5)$$

We postulate that the susceptible class is subject to a linear mortality process with removal rate

$$\lambda(a, t) \geq 0. \hspace{1cm} (2.6)$$

Consequently, the differential equation for $u(a, t)$ will have a loss term of the form $\lambda(a, t)u(a, t)$ on the right-hand side. Similarly we introduce a linear removal term, $\lambda_1(a, b, t)\phi(a, b, t)$ for the exposed class. We feel there may be some deleterious effect due to the presence of the virus and hence it will be reasonable to assume that

$$\lambda_1(a, b, t) \geq \lambda(a, t) \geq \lambda^\ast > 0. \hspace{1cm} (2.7)$$
The birth process will be specified in the traditional manner with the definition of a birth function, \[6,7\], at the age boundary \(a = 0\). Transfer from the susceptible class to the exposed class will be brought about by an incidence function, \(f(u, v, w, z)(a, t)\) which will be more fully described later. For the time being, we only remark that \(f(u, v, w, z)(a, t) \geq 0\).

The susceptible density is described by a hyperbolic partial differential equation of the form

\[
(S_1) \quad \frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\lambda(a, t)u - f(u, v, w, z)(a, t), \quad t \geq 0, \ a \geq 0,
\]

with

\[
(S_2) \quad u(a, 0) = u_0(a), \quad a \geq 0,
\]

and

\[
(S_3) \quad u(0, t) = B_1(t)
\]

\[
= \int_0^\infty \beta_1(a, t)u(a, t) \, da + \int_0^\infty \beta_1(a, t)w(a, t) \, da
\]

\[
+ \int_0^\infty \int_0^{\epsilon(a)} \beta_2(a, b, t)\phi(a, b, t) \, db \, da, \quad t \geq 0.
\]

The birth rates \(\beta_1(a, t)\) and \(\beta_2(a, b, t)\) are assumed to be non-negative and smooth on \(\mathcal{R}\). We further assume that \(\beta_1(\cdot, t) \in L_1([0, \infty))\) and \(\beta_2(\cdot, t) \in L_1([0, \infty) \times (0, \tau))\). The birth rate from the susceptible class and the recovered class are the same. It also seems natural to assume that

\[
\beta_1(a, t) \geq \beta_2(a, b, t) \geq 0 \quad \text{for} \ (a, b, t) \in \mathcal{R}.
\] (2.9)

The birth function, \(B_1(t)\), for the susceptible class depends upon the density of the exposed class as well as upon the densities of the susceptible and the recovered classes. Since we have assumed that individuals fully infected with FeLV and infectious do not reproduce our model does not include a contribution to the birth process from the fully infected class.

We follow the reasoning of Hoppensteadt [4] and make the following assumption about the population of the exposed class.

**Assumption.** The change in the exposed population which has chronological age \(a\) and in which the age of the disease is \(b\) in a time interval of length \(h\) is proportional to the size of population and \(h\). The constant of proportionality is equal to the negative of the age (chronological and disease) specific mortality rate \(\lambda_1(a, b, t)\). Thus,

\[
\phi(a + h, b + h, t + h) - \phi(a, b, t) = -\lambda_1(a, b, t)\phi(a, b, t)h.
\] (2.10)

Dividing both sides of the above by \(h\) and passing to the limit as \(h \rightarrow 0\), we have

\[
(E_1) \quad \frac{\partial \phi}{\partial t} + \frac{\partial \phi}{\partial a} + \frac{\partial \phi}{\partial b} = -\lambda_1(a, b, t)\phi \quad \text{for} \ (a, b, t) \in \mathcal{R}.
\]

Entry into the exposed class occurs at the age boundary \(b = 0\) via transfer from the susceptible class; we have

\[
(E_2) \quad \phi(a, 0, t) = B_2(a, t) = f(u, v, w, z)(a, t)
\]
we point out that this plays the role of a birth function for the exposed class. We specify an initial population density with
\[
(E_3) \quad \phi(a, b, 0) = \phi_0(a, b) \quad \text{for } (a, b, 0) \in \mathcal{R}.
\]
Of course we have previously assumed that \( \phi(a, b, t) \equiv 0 \) for \( a \leq b \).

If we formally integrate equation \( (E_1) \) as \( b \) varies from 0 to \( \tau(a) \), we obtain the following equation for the time-dependent density of the exposed class:
\[
\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} = -\int_0^{\tau(a)} \lambda_1(a, b, t)\phi(a, b, t) db + \phi(a, 0, t) - \phi(a, \tau(a), t)
\]
\[
= -\int_0^{\tau(a)} \lambda_1(a, b, t)\phi db + f(u, v, w, z)(a, t) - \phi(a, \tau(a), t), \tag{2.11}
\]
\[
v(a, 0) = \int_0^{\tau(a)} \phi_0(a, b) db, \quad a \geq 0, \tag{2.12}
\]
\[
v(0, t) = 0, \quad t \geq 0. \tag{2.13}
\]

We recall that at the conclusion of the period of latency approximately two-thirds of the infected population is able to withstand the infection and gains permanent immunity via the process of exposure. The remaining third progresses to the terminal stage of fully developed FeLV and becomes infectious. The time-dependent age densities of the fully infected and recovered cats are denoted \( z(a, t) \) and \( w(a, t) \), respectively. In this infectious phase individuals interact with susceptibles to produce exposed. We let \( q \in (0, 1) \) denote the fraction of the exposed population which acquires immunity at the completion of the period of exposure. Consequently \( (1 - q) \) will denote the fraction which becomes fully infected. We have the following equations for \( z(a, t) \) and \( w(a, t) \):

\[
(I_1) \quad \frac{\partial z}{\partial t} + \frac{\partial z}{\partial a} = -\lambda_2(a, t)z + (1 - q)\phi(a, \tau, t), \quad t \geq 0, \quad a \geq \tau,
\]
\[
(I_2) \quad z(a, 0) = z_0(a), \quad a \geq \tau,
\]
\[
(I_3) \quad z(a, t) = 0, \quad t \geq 0, \quad 0 \leq a \leq \tau
\]

and

\[
(R_1) \quad \frac{\partial w}{\partial t} + \frac{\partial w}{\partial a} = -\lambda_3(a, t)w + q\phi(a, \tau, t), \quad t \geq 0, \quad a \geq \tau,
\]
\[
(R_2) \quad w(a, 0) = w_0(a), \quad a \geq \tau,
\]
\[
(R_3) \quad w(a, t) = 0, \quad t \geq 0, \quad 0 \leq a \leq \tau.
\]

The lack of vertical transmission is once again manifest, this time via \((I_3)\) and \((R_3)\). We assume that the mortality is greatly enhanced during the fully infected phase, i.e.
\[
\{\lambda_2(a, t)|a \geq \tau, \ t \geq 0\} \supseteq \sup\{\lambda(a, t)|a \geq \tau, \ t \geq \tau\}. \tag{2.14}
\]

Because recovered individuals show no ill effects of the disease, it would be reasonable to assume that \( \lambda_3(a, t) = \lambda(a, t) \) for \( a \geq \tau \), however, handling the more general case
\[
\lambda_3(a, t) \geq \lambda(a, t) \quad \text{for } t \geq 0, \quad a \geq \tau, \tag{2.15}
\]
introduces no further complication. Finally, for technical reasons, we assume that all the mortality (or removal) rates and the birth rates are uniformly bounded.

The total population \( \rho(a, t) = u(a, t) + v(a, t) + w(a, t) + z(a, t) \) satisfies

\[
\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \lambda(a, t)u = \begin{cases} 
- \int_0^a \rho_1(a, b, t) \, \mathrm{d}b, & 0 < a < \tau, \\
- \int_\tau^a \rho_1(a, b, t) \, \mathrm{d}b + \rho_2w + \rho_3z, & \tau < a,
\end{cases} 
\]  

with

\[
\rho(a, 0) = u_0(a) + \int_0^a \phi_0(a, b) \, \mathrm{d}b, \quad 0 < a < \tau,
\]

\[
\int_\tau^a \phi_0(a, b) \, \mathrm{d}b + w_0(a) + z_0(a), \quad \tau < a
\]  

and

\[
\rho(0, t) = \int_0^\infty \beta_1(a, t)u(a, t) \, \mathrm{d}a + \int_0^\infty \beta_1(a, t)w(a, t) \, \mathrm{d}a
\]

\[
+ \int_0^\tau \int_0^{r(a)} \beta_2(a, b, t) \phi(a, b, t) \, \mathrm{d}b \, \mathrm{d}a, \quad t \geq 0.
\]  

We now turn our attention to the specifics of horizontal transmission and set

\[
f(u, v, w, z)(a, t) = \begin{cases}
\int_{\tau}^{\infty} \gamma_1(a, a', t) \frac{z(a', t)}{\rho(a', t)} \, \mathrm{d}a' u(a, t) & \text{proportionate mixing,} \\
\int_{\tau}^{\infty} \gamma_2(a, a', t) z(a', t) \, \mathrm{d}a' u(a, t) & \text{mass action.}
\end{cases}
\]  

Here the contact number \( \gamma_1(a, a', t) \) and the contact rate \( \gamma_2(a, a', t) \) are smooth and non-negative functions in \( L^\infty((0, +\infty) \times (\tau, +\infty) \times (0, T)) \), \( \gamma_1 \in L^\infty((0, +\infty) \times (0, T); L^1(\tau, +\infty)) \). Our choice of incidence function requires a bit of discussion. Our subsequent analysis would also support an incidence which differentiates between inter-cohort and intra-cohort infection resulting in a term of the form

\[
f(u, v, w, z)(a, t) = \left[ \gamma_1(a, t)z(a, t) + \int_{\tau}^{\infty} \gamma_2(a, a', t) z(a', t) \, \mathrm{d}a' \right] u(a, t)
\]

more consistent with the methodology of Busenberg and Cooke [5] and Busenberg et al. [9]. However, there does not seem to be sufficient scientific motivation for a bias favoring transmission between individuals of the same age. The disease being mostly transmitted through amicable social contacts between individuals having different ages, \([1–3]\), an inter-cohort force of infection may be more realistic. The statement in Theorem 1 still holds for an intra–inter-cohort transmission mode, the proof being far more intricate. It is perhaps more significant that we have chosen to distinguish between incidence terms of so-called ‘proportionate mixing’ and ‘mass action’ type. The analysis in [3] shows that a mass action incidence coupled with an exponential growth is more appropriate for urban groups of stray cats while they are establishing, contact rates increasing with population size, a proportionate mixing incidence coupled with an exponential growth being more acceptable for cat populations growing in nonanthropized habitats, in which case the virus cannot regulate the host population. See also [10]. For later use set

\[
f(u, v, wz)(a, t) = H(u, v, w, z)(a, t)u(a, t).
\]
3. Main result

Our existence result will follow directly from the representation of solutions. One may view the equation for susceptibles as being a standard demographic equation for \( u(a,t) \) with ‘mortality rate’ \( \lambda(a,t) + H(a,t) \) and apply arguments of Webb [6] to observe that

\[
    u(a,t) = \begin{cases} 
        u_0(a-t) \exp \left\{ - \int_0^t [\lambda(a-t+s,s) + H(a-t+s,s)] \, ds \right\} & \text{for } a \geq t, \\
        B_1(t-a) \exp \left\{ - \int_0^a [\lambda(x,t-a+x) + H(x,t-a+x)] \, dx \right\} & \text{for } t > a. 
    \end{cases} 
\]  

(3.1)

As a preliminary to providing a formal representation of \( \phi(a,b,t) \), we examine the first order hyperbolic equation

\[
    \partial \theta / \partial t + \partial \theta / \partial x + \partial \theta / \partial y = -\lambda(x,y,t) \theta \quad \text{for } x, y, t \geq 0
\]

with initial conditions:

\[
    \begin{align*}
    \theta(x,0,t) &= h(x,t), \\
    \theta(0,y,t) &= 0, \\
    \theta(x,y,0) &= g(x,y).
    \end{align*}
\]

An argument using characteristics will produce the following formula for \( \theta(x,y,t) \):

\[
    \theta(x,y,t) = \begin{cases} 
        h(x-y,t-y) \exp \left\{ - \int_0^y \lambda(x-y+s,s,t-y+s) \, ds \right\} & \text{for } x \geq y, \ t \geq y, \\
        0 & \text{for } y \geq x, \ t \geq 0 \\
        g(x-t,y-t) \exp \left\{ - \int_0^y \lambda(x-t+s,y-t+s) \, ds \right\} & \text{for } x \geq y, \ y \geq t.
    \end{cases}
\]

If \( h(\ , \ ) \) and \( g(\ , \ ) \) are continuous \( \theta(x,y,t) \) can have discontinuity at the hyperplanes, \( x = t, x = y \), and \( y = t \). The foregoing should convince us that we will need three equations to define \( \phi(a,b,t) \) with \( \phi_0(\ , \ ) \) playing the role of \( g(\ , \ ) \) and

\[
    B_2(a,t) = f(u,v,w,z)(a,t) = H(a,t)u(a,t)
\]

(3.2)

playing the role of \( h(\ , \ ) \). We have

\[
    \phi(a,b,t) = \begin{cases} 
        \phi_0(a-t,b-t) & \text{for } a \geq b, \ b \geq t, \\
        0 & \text{for } b > a, \ t \geq 0, \\
        u(a-b,t-b)H(a-b,t-b) & \text{for } a \geq b, \ t > b
    \end{cases}
\]

(3.3)

and, using (3.1), the last expression in (3.3) reads
solution to the SEIR system modeling FeLV. We shall set our solutions in the linear space 
\[ \mathcal{X} = \mathcal{X}_1 \times \mathcal{X}_2 \times \mathcal{X}_3 \times \mathcal{X}_4 \]
where
\[ \mathcal{X}_i = L_1((0, \infty)) \quad \text{for } i = 1, 3, 4, \]
and
\[ \mathcal{X}_2 = L_1((0, \infty) \times (0, \tau)) \]
and
\[ \left\| u, \phi, z, w \right\|_X = \left\| u \right\|_{X_1} + \left\| \phi \right\|_{X_2} + \left\| z \right\|_{X_3} + \left\| w \right\|_{X_4}. \]

Subsequent arguments will show that our solutions will lie in the space \( \mathcal{X} \). We shall comment on this choice subsequently. The integral representations immediately imply that the non-negativity of the initial data \((u_0, \phi_0, z_0, w_0)\) insures that mild solutions remain non-negative.

Although we shall not provide a formal existence proof we feel that a few comments are in order. If we examine (3.1)–(3.4) we may observe that computation of \( u(a, t) \), \( \phi(a, b, t) \), \( w(a, t) \) and \( z(a, t) \) is possible given \( u_0(a) \), \( \phi_0(a, b) \), \( v_0(a) \), \( z_0(a) \) and \( H(a, t) \). Knowledge of \( u(a, t) \), \( v(a, t) \), \( w(a, t) \), \( z(a, t) \), \( u_0(a) \), \( \phi_0(a, b) \), \( v_0(a) \) and \( z_0(a) \) allows the computation of \( H(a, b) \).
This observation sets the stage for a fixed point algorithm. We will assume that $u_0(a), \phi_0(a,b), v_0(a)$ and $z_0(a)$ are smooth enough and that $h(a,t)$ is a piecewise smooth function. If we skip ahead to Appendix A we can apply formulae (A.1)–(A.5) to compute $\tilde{u}(a,t)$, $\tilde{\phi}(a,t)$, $\tilde{w}(a,t)$ and $\tilde{z}(a,t)$. We can now define

$$
\tilde{h}(a,t) = \begin{cases} 
\int_t^\infty \gamma_1(a,a',t) \frac{\tilde{z}(a',t)}{\tilde{\rho}(a',t)} \, da' & \text{proportionate mixing}, \\
\int_t^\infty \gamma_2(a,a',t) \tilde{z}(a',t) \, da' & \text{mass action}.
\end{cases}
$$

(3.8)

Lemma A.1 of Appendix A will guarantee $\tilde{u}, \tilde{\phi}, \tilde{w}, \tilde{z}$ are non-negative strong solutions to (H.1)–(H.4). We may now use Lemma A.2 to guarantee that for each $T > 0$ there exists a constant $C(T)$ depending solely upon $u_0, \phi_0, w_0, z_0$ and the coefficients $\beta_1$ and $\beta_2$ so that

$$
\sup_{0 \leq t \leq T} \left\{ \|\tilde{u}(\cdot,t)\|_1, \|\tilde{\phi}(\cdot,t)\|_1, \|\tilde{w}(\cdot,t)\|_1, \|\tilde{z}(\cdot,t)\|_1 \right\} \leq C(T),
$$

(3.9)

then

$$
0 \leq \tilde{h}(a,t) \leq \begin{cases} 
\sup_{0 \leq t \leq T, \alpha < a < +\infty} \int_t^\infty \gamma_1(a,a',t) \, da' & \text{proportionate mixing}, \\
C(T) \|\gamma_2\|_{\infty,(0,T)\times(0,\infty)} & \text{mass action}.
\end{cases}
$$

(3.10)

Thus let $\mathcal{K}$ be the set of non-negative quadruples $(u,v,w,z)$ which satisfy (3.9) and let $h$ be defined as in (3.8). Then, let $(\tilde{u}, \tilde{v}, \tilde{w}, \tilde{z})$ be the strong solution obtained via our algorithm. Proceeding as in [6, Chapter 1], we can show the mapping $J : \mathcal{K} \to \mathcal{K}$ given by

$$
J(u,v,w,z) = (\tilde{u}, \tilde{v}, \tilde{w}, \tilde{z})
$$

is a strict contraction in the $L_1$ norm for $T$ small enough. Actually this follows from (3.9) and (3.10) because the only nonlinear term in the FeLV system i.e., the incidence term, is globally Lipschitz continuous on $\mathcal{K}$. Technically speaking more are required for the case of proportionate mixing because the incidence term is not Lipschitz continuous at the origin. However we can return to Eqs. (2.16) and (S1)–(S4) and utilize lower solution argument to guarantee that $\tilde{\rho}(a,t) \geq \tilde{u}(a,t) > 0$ for $a \geq \tau$ when $u_0(a) > 0$. Moreover we can extend this mapping by the unique extension property to $\mathcal{K}$ in $L_1$. The strict contraction property will allow us to obtain a solution on $\mathcal{K}$ for small $T$; uniqueness and the continuation of solutions to a maximal interval of existence, [6, Chapter 2]. The uniform bounds in (3.9) yield global existence. Even in the simple case considered in [6] these computations are rather lengthy and involved. The case at hand is much more complex and the incorporation of a detailed proof would alter the intent of the paper.

We summarize the foregoing discussion by stating the following theorem.

**Theorem 1.** Assume that the coefficients in the FeLV system are non-negative and satisfy: $\lambda, \beta_1, \beta_2, \beta_3 \in L^\infty((0,\infty) \times (0,T)), \lambda, \gamma_1, \gamma_2 \in L^\infty((0,\infty) \times (\tau,\infty) \times (0,T))$, with $\gamma_1 \in L^\infty((0,\infty) \times (0,T) \times L^1(\tau,\infty))$.

For each non-negative quadruple $(u_0, \phi_0, z_0, w_0)$ in $\mathcal{K}$ with $u_0$ positive, there exists a unique non-negative quadruple $(u(a,t), \phi(a,b,t), z(a,t), w(a,t))$ of functions providing a mild solution to the FeLV system.

If we assume that the initial data is continuously differentiable, the mild solutions are continuously differentiable except for possible jump discontinuities when $a = t$ and $a = t + \tau$. 
One can also address questions of regularity. If we assume that the initial functions, \(u_0, \phi_0, z_0, w_0\), are continuously differentiable, it is straightforward to use the integral representations to differentiate the quadruple, \((u(a,t), \phi(a,b,t), z(a,t), w(a,t))\) for \(a > t\) and observe that Eqs. \((S_1)–(S_3), (E_1)–(E_3), (I_1)–(I_3)\) and \((R_1)–(R_3)\) are satisfied.

4. The endemic threshold for a simple example

We shall consider a simplified version of the FeLV model. We shall assume that the birth and mortality rates do not depend on the variable \(t\). In the absence of the infection we shall expect the feline population to satisfy:

\[
\begin{align*}
&\dot{\rho} + \frac{\partial \rho}{\partial a} = -\lambda(a)\rho, \\
&\rho(a,0) = \rho_0(a), \\
&\rho(0,t) = \int_0^\infty \beta(a)\rho(a,t) da,
\end{align*}
\]

for \(a \in [0, \infty)\) and \(t > 0\).

The longtime behavior of solutions to (4.1) is well documented [6,7]; in our case it can be completely determined by the value of the characteristic integral given by the formula

\[
\sigma = \int_0^\infty \beta(a) \exp \left( - \int_0^\infty \lambda(s) ds \right) da.
\]

(4.2)

In the sequel we shall make use of the following:

\(\sigma < 1\) implies that \(\rho(a,t)\) converges to zero as \(t \to + \infty\) uniformly on each \([0,A], A < + \infty\).\n
(4.3)

We return to the systems outlined in the preceding section. If we integrate \(\phi(a,b,t)\) with respect to \(b\) and compute the sum

\[
\theta(a,t) = u(a,t) + v(a,t) + z(a,t) + w(a,t),
\]

we may observe that \(\theta(a,t)\) satisfies the following inequality:

\[
\begin{cases}
\dot{\theta} + \frac{\partial \theta}{\partial a} \leq \lambda(a)\theta, \\
\theta(a,0) \leq u_0(a) + v_0(a) + z_0(a) + w_0(a) \\
\theta(t,0) \leq \int_0^\infty \beta(a)\theta(a,t) da.
\end{cases}
\]

(4.4)

The characteristic integral in the case of age independent birth and mortality rates, \(\beta\) and \(\lambda\), may evaluated as

\[
\sigma = \int_0^\infty \beta e^{-\lambda a} da = \beta/\lambda.
\]

(4.5)

We may apply a comparison principle for population equations [11] to observe that \(\theta(a,t) \leq \rho(a,t)\). Therefore, \(\beta/\lambda < 1\) implies that \(\lim_{t \to \infty} \theta(a,t) = 0\) uniformly in the sense of (4.3) and hence that

\[
\lim_{t \to \infty} u(a,t) = \lim_{t \to \infty} v(a,t) = \lim_{t \to \infty} w(a,t) = \lim_{t \to \infty} z(a,t) = 0.
\]

(4.6)
In this case the representation formula (2.19) together with (4.6) will yield
\[
\lim_{t \to \infty} \varphi(x, t) = 0. \tag{4.7}
\]

If we restrict our attention to a model having only inter-cohort mass action transmission, we have an incidence term of the form
\[
f(u, v, w, z) = ku(a, t) \int_{\tau}^{\infty} z(a, t) \, da = ku(a, t)z^*(t) \tag{4.8}
\]
for \( k > 0 \). We further assume that the birth rates from the susceptible offspring and recovered classes are identical and given by a constant \( \beta > 0 \) and we ignore the offspring of the exposed, say \( \beta_2 = 0 \). The mortality rates are also assumed to be constant with the rates from the susceptible and recovered classes coinciding. These assumptions produce a system of the form
\[
\begin{align*}
\partial u / \partial t + \partial u / \partial a &= -\lambda u - kuz^*(t), \\
u(a, 0) &= u_0(a), \\
u(0, t) &= \int_{\tau}^{\infty} \beta u(a, t) \, da + \int_{\tau}^{\infty} \beta w(a, t) \, da, \\
\partial \phi / \partial t + \partial \phi / \partial a + \partial \phi / \partial b &= -\lambda_1 \phi, \\
\phi(a, b, 0) &= \phi_0(a, b), \\
\phi(a, 0, t) &= ku(a, t)z^*(t), \\
\phi(0, b, t) &= 0, \\
\partial w / \partial t + \partial w / \partial a &= -\lambda w + q\phi(\tau, a, t), \\
w(\tau, t) &= 0, \\
w(a, 0) &= w_0(a), \\
\partial z / \partial t + \partial z / \partial a &= -\lambda_2 z + (1 - q)\phi(\tau, a, t), \\
z(\tau, t) &= 0, \\
z(a, 0) &= z_0(a).
\end{align*} \tag{4.9} \tag{4.10} \tag{4.11} \tag{4.12}
\]
Here, \( \lambda < \lambda_1 = \lambda_\phi \ll \lambda_2 = \lambda_z \).

The steady state equations for (4.9)–(4.12) appear below.
\[
\begin{align*}
du / da &= -\lambda u - kuz^* \quad \text{for } a \geq 0, \\
u(0) &= \beta \int_{\tau}^{\infty} u(a) \, da + \beta \int_{\tau}^{\infty} w(a) \, da, \\
\partial \phi / \partial a + \partial \phi / \partial b &= -\lambda_1 \phi, \quad \text{for } a \geq 0, \ b \geq 0, \\
\phi(a, 0) &= ku(a)z^* \quad \text{for } a \geq 0, \\
\phi(0, b) &= 0, \quad \text{for } b \geq 0, \\
dw / da &= -\lambda w + q\phi(a, \tau), \quad \text{for } a \geq \tau, \\
w(\tau) &= 0.
\end{align*} \tag{4.13} \tag{4.14} \tag{4.15}
\]
\[ \frac{dz}{da} = -\lambda_2 z + (1 - q)\phi(a, \tau) \quad \text{for } a \geq \tau, \]
\[ z(\tau) = 0. \quad (4.16) \]

Here it is understood that \( z^* = \int_{\tau}^{\infty} z(a) \, da \). We now can apply elementary arguments to represent solutions to (4.13)–(4.16) and obtain
\[ u(a) = u_0 e^{-(\lambda_1 + k \tau)a} \]
\[ u_0 = u(0) = \int_{\tau}^{+\infty} \beta u(a) \, da + \int_{\tau}^{+\infty} \beta w(a) \, da, \quad (4.17) \]
\[ \phi(a, b) = \begin{cases} 
0 & \text{if } a < b \\
\exp(-\lambda_1 (a - b) z^*) & \text{if } a \geq b,
\end{cases} \quad (4.18) \]
\[ w(a) = \int_{\tau}^{a} e^{-\lambda (a - s)} q \phi(s, \tau) \, ds, \quad (4.19) \]
\[ z(a) = \int_{\tau}^{a} e^{-\lambda_1 (a - s)} (1 - q) \phi(s, \tau) \, ds. \quad (4.20) \]

If the quadruple \((u, \phi, w, z)\) is a steady state solution, then
\[ w(a) = \int_{\tau}^{a} e^{-\lambda (a - s)} q e^{-\lambda_1 s} k u(s - \tau) z^* \, ds \\
= \int_{\tau}^{a} e^{-\lambda (a - s)} q e^{-\lambda_1 s} k u_0 e^{-\lambda_1 (a - s) z^*} \, ds \\
= e^{-\lambda_1 a} q k u_0 z^* e^{-\lambda_1 (a - \tau)} \int_{\tau}^{a} e^{-k (s - \tau) z^*} \, ds. \quad (4.21) \]

If we introduce the last expression of (4.21) into the equation yielding the initial condition of (4.17) we obtain
\[ u_0 = \beta u_0 \int_{0}^{+\infty} e^{-(\lambda_1 + k \tau)a} \, da + e^{-\lambda_1 \tau q} \beta k u_0 z^* \int_{\tau}^{+\infty} e^{-\lambda (a - \tau)} \int_{\tau}^{a} e^{-k z^*(s - \tau)} \, ds \, da. \quad (4.22) \]

From (4.17) we may observe that the first component of a steady state solution \( u(\cdot) \neq 0 \) only in case \( u(0) = u_0 \neq 0 \). If \( u_0 \neq 0 \), then we may observe that (4.22) reduces to
\[ 1 = \beta \int_{0}^{+\infty} e^{-(\lambda_1 + k \tau)a} \, da + e^{-\lambda_1 \tau q} \beta k z^* \int_{\tau}^{+\infty} e^{-\lambda (a - \tau)} \int_{\tau}^{a} e^{-k z^*(s - \tau)} \, ds \, da. \quad (4.23) \]

We now introduce a real valued function \( h(z^*) \) defined by the equation
\[ h(z^*) = \beta \int_{0}^{+\infty} e^{-(\lambda_1 + k \tau)a} \, da + e^{-\lambda_1 \tau q} \beta k z^* \int_{\tau}^{+\infty} e^{-\lambda (a - \tau)} \int_{\tau}^{a} e^{-k z^*(s - \tau)} \, ds \, da. \quad (4.24) \]

It is clear that
\[ h(0) = \beta \int_{0}^{+\infty} e^{-\alpha z^*} \, da = \beta / \lambda. \quad (4.25) \]

If \( h(0) < 1 \), then previous arguments guarantee that all solutions converge uniformly to zero and consequently there will exist no non-trivial steady state solutions to (4.9)–(4.12). It also is straightforward that \( h(z^*) > 0 \). Further analysis will convince one that
\[ h(z^*) = \frac{\beta}{\lambda + kz^*} + e^{-\lambda t_1} \beta \left[ \frac{1}{\lambda} - \frac{1}{\lambda + kz^*} \right]. \] (4.26)

Hence \( h \) is decreasing on \([0, +\infty)\) because \( 0 \leq q \leq 1, \lambda_1 > 0 \) and \( \tau \geq 0 \); also
\begin{equation}
\lim_{z^* \to +\infty} h(z^*) = e^{-\lambda t_1} q \beta / \lambda.
\end{equation} (4.27)

Thus there will exist an unique \( z^* > 0 \) which satisfies (4.23) if and only if
\begin{equation}
e^{-\lambda t_1} q \beta < \lambda < \beta.
\end{equation} (4.28)

Having found \( z^* \), we wish to describe the steady state solution \((u(a), \phi(a, b))\) and the associated quadruple \((u(a), v(a), w(a), z(a))\). We commence with the observation that
\[
z(a) = \int_\tau^a e^{-\lambda_2(a-s)} (1 - q) \phi(s, \tau) ds
\]
\[
= (1 - q) \int_\tau^a e^{-\lambda_2(a-s)} e^{-\lambda t_1} k u_0 e^{-(\lambda + k z^*)(s-\tau)} z^* ds
\]
\[
= (1 - q) e^{-\lambda t_1} k u_0 z^* \int_\tau^a e^{-\lambda_2(a-s)} e^{-(\lambda + k z^*)(s-\tau)} ds.
\] (4.29)

Recalling that \( z^* = \int_\tau^\infty z(a) da \), we integrate (4.29) on \([\tau, \infty)\) to obtain the equation
\begin{equation}
z^* = \int_\tau^\infty z(a) da = (1 - q) e^{-\lambda t_1} k u_0 z^* \int_\tau^{+\infty} \int_\tau^a e^{-\lambda_2(a-s)} e^{-(\lambda + k z^*)(s-\tau)} ds da.
\end{equation} (4.30)

We can solve this equation uniquely for \( u_0 \) and immediately find \( u(a) \) by applying (4.17). The recovered and the infectious densities, \( w(a) \) and \( z(a) \) can be computed via the formulae
\begin{equation}w(a) = e^{-\lambda t_1} k u_0 z^* e^{-\lambda_2(a-\tau)} \int_\tau^a e^{-k z^*(s-\tau)} ds
\end{equation} (4.31)
and
\begin{equation}z(a) = (1 - q) e^{-\lambda t_1} k u_0 z^* \int_\tau^a e^{-\lambda_2(a-s)} e^{-(\lambda + k z^*)(s-\tau)} ds.
\end{equation} (4.32)

It is now possible to utilize (4.18) to find \( \phi(a, b) \). Finally \( v(a) \) may be computed by integration with respect to the variable \( b \). We point out that once a value for \( z^* \) is determined \( u, v, w, z \) and \( \phi \) can be found in closed form.

The parameter \( \sigma = \beta / \lambda \) establishes a threshold for the exponentially growth or decay of the feline population in absence of FeLV. Next \( e^{-\lambda t_1} q \beta / \lambda \) is a threshold for the existence of non-trivial steady state solutions. In the parlance of mathematical epidemiology such steady states are called endemic steady states. In recent years more attention has been paid to the modeling of endemic diseases which do not die out and are always present albeit at varying levels of intensity [5]. Typically one expects the admissibility of endemic states to be determined by the relationship between the birth and mortality rates. The case at hand has not been an exception to this general rule of thumb.

We summarize the foregoing analysis as the following theorem.
Theorem 2. If the birth and the mortality rates, $\beta$ and $\lambda$, are age-independent, then in systems (4.9)–(4.12) $q e^{-2\lambda t} \sigma = q e^{-2\lambda t} \beta/\lambda$ serves as a threshold parameter for steady state solutions. If $\sigma = \beta/\lambda < 1$, then systems (4.9)–(4.12) admits no trivial steady state solution and given any non-negative initial data the total population $\theta(a,t) = u(a,t) + v(a,t) + z(a,t) + w(a,t)$ converges uniformly to zero. If $\sigma > 1$, then the system has an unique steady state solution if and only if $q e^{-2\lambda t} \beta < \lambda < \beta$.

We remark that the assumption of age-independent birth and mortality rates was made only for reasons of ease of computation. If the birth rate and the mortality rate are dependent upon the age variable $a$ analogous results could have been obtained. In the future the authors plan to examine more detailed models described by coupled systems involving bivariate density functions of the form $\varphi(a,b,t)$.

As a concluding biological remark, one should note that in absence of infection, the feline population experiences a Malthusian decay ($\sigma < 1$) or growth ($\sigma > 1$): see (4.1)–(4.3); when $\beta < \lambda$ it goes to 0 as time gets large and the infectious disease just accelerates this process, while when $\beta > \lambda$ the feline population is exponentially increasing is time. Our result may be interpreted this way: if

$$e^{-2\lambda t} \beta < \lambda < \beta$$

then the feline population growth is regulated by the infectious disease while if

$$\lambda < e^{-2\lambda t} \beta \left( \leq \beta \right)$$

this is not the case anymore.

Last, when the latency period is ignored, a simple SIR model with constant coefficients describing the propagation of FeLV reads

$$S' = \beta(S + R) - \lambda S - kSI,$$
$$I' = - (\lambda + \gamma) I + (1 - q) kSI,$$
$$R' = - \lambda R + qkSI.$$

It is shown in [3] that when $\beta < \lambda$ the population goes extinct while when $\lambda < \beta$ there is a unique asymptotically locally stable stationary endemic state if and only if $q \beta < \lambda < \beta$ which is obviously consistent with (4.33) above upon letting $\tau \to 0$.

Appendix A

In this section, we compute a priori bounds for solutions to a SEIR model with mass action kinetics. We begin by considering a linear system of hyperbolic equations

$$\partial u/\partial t + \partial u/\partial a = -\lambda(a,t)u + h(a,t)u, \quad 0 < a < +\infty, t > 0,$$
$$u(a,0) = u_0(a), \quad 0 < a < +\infty,$$
$$u(0,t) = \int_0^\infty \beta_1(a,t)u(a,t) da + \int_0^\infty \beta_1(a,t)w(a,t) da + \int_0^\infty \int_0^\infty \beta_2(a,b,t)\phi(a,b,t) db da, \quad t > 0,$$

(H.1)
Lemma A.1. Let the initial data
\[ \frac{\partial \phi}{\partial t} + \frac{\partial \phi}{\partial a} a + \frac{\partial \phi}{\partial b} b = -\lambda_1(a, b, t) \phi, \quad 0 < a < +\infty, 0 < b < r, \quad t > 0, \]
\[ \phi(a, 0, t) = h(a, t) u, \quad 0 < a < +\infty, \quad t > 0, \]
\[ \phi(0, b, t) = 0, \quad 0 < b < r, \quad t > 0, \]
\[ \phi(a, b, 0) = \phi_0(a, b), \quad 0 < a < +\infty, \quad 0 < b < r, \]

\[ \frac{\partial w}{\partial t} + \frac{\partial w}{\partial a} a = -\lambda_3(a, t) w + q \phi(a, \tau, t), \quad 0 < a < +\infty, \quad t > 0, \]
\[ w(a, 0) = w_0(a), \quad 0 < a < +\infty, \]
\[ w(\tau, t) = 0, \quad t > 0. \] 

We may also compute the solutions
\[ \frac{\partial z}{\partial t} + \frac{\partial z}{\partial a} a = -\lambda_2(a, t) z + (1 - q) \phi(a, \tau, t), \quad 0 < a < +\infty, \quad t > 0, \]
\[ z(a, 0) = z_0(a), \quad 0 < a < +\infty, \]
\[ z(\tau, t) = 0, \quad t > 0, \] 

using \( \phi(a, b, t), u(a, t), z(a, t) \). An application of standard linear theory [6,7] yields the following result which we state without proof.

Lemma A.1. Let the initial data \((u_0(\ ), \phi_0(\ ), w_0(\ ), z_0(\ ))\) be continuously differentiable and belong to \(L_1(\mathbb{R}_+ \times L_1(\mathbb{R}_+ \times (0, \tau)) \times L_1(\mathbb{R}_+ \times L_1(\mathbb{R}_+))\) and let \(h(\ ,\ )\) be a smooth function with \(h \in C(\mathbb{R}_+; L_1(\mathbb{R}))\). If the birth rate functions \(\beta_1, \beta_2\) and the death rate functions \(\lambda, \lambda_1, \lambda_2, \lambda_3\) satisfy the previous conditions there exists a unique strong solution to (H.1)–(H.4). Moreover we can show that these solutions satisfy the integral equations

\[ u(a, t) = \begin{cases} 
  u_0(a - t) \exp \left\{ - \int_0^t [\lambda(a - t + s, s) + h(a - t + s, s)] ds \right\} & \text{for } a \geq t, \\
  B_1(a - t) \exp \left\{ - \int_0^t [\lambda(a, t - a + x) h(x, t - a + x)] dx \right\} & \text{for } a \leq t,
\end{cases} \]

\[ \phi(a, b, t) = \begin{cases} 
  \phi_0(a - t, b - t) \exp \left\{ - \int_0^t \lambda_1(a - t + s, b - t + s, s) ds \right\} & \text{for } a > b, \quad b \geq t, \\
  u(a - b, t - b) \exp \left\{ - \int_0^{b \lambda_1(a - b + x, x, t - b + x, x) dx \right\} & \text{for } a > b, \quad b > 0 \quad \text{for } a \leq b.
\end{cases} \]

If \( b \leq t \) and \( b < a \) we have

\[ \phi(a, b, t) = \begin{cases} 
  u_0(a - t) h(a - b, t - b) \exp \left\{ - \int_0^{t-b} [\lambda(a - t + s, s) + h(a - t + s, s)] ds \right\} \\
  \exp \left\{ - \int_0^{b \lambda_1(a - b + x, x, t - b + x, x) dx \right\} & \text{for } t \leq a, \\
  B(t - a) h(a - b, t - b) \exp \left\{ - \int_0^{a - b \lambda_1(a, t - a + x, x, t - a + x) dx \right\} \\
  \exp \left\{ - \int_0^{a \lambda_1(a - b + x, x, t - b + x, x) dx \right\} & \text{for } t \leq a,
\end{cases} \]

\[ z(a, t) = \begin{cases} 
  z_0(a - t) \exp \left\{ - \int_0^t \lambda_2(at - s, s) ds \right\} \\
  + (1 - q) \int_0^t \exp \left\{ - \int_s^t \lambda_2(a - t + r, r) \right\} \phi(a - t + s, s, s) ds \quad \text{for } a \geq t, \\
  (1 - q) \int_t^a \exp \left\{ - \int_s^t \lambda_2(r, r + t - a) dr \right\} \phi(s, \tau, s + t - a) ds \quad \text{for } t > a,
\end{cases} \]
The following lemma guarantees an a priori bound for \( k \) to attention to strong solutions. We consider two cases the first being a for strong solutions will extend to the case of mild solutions. For this reason we confine our initial data, death and birth rates we can compute a priori estimates for mild solutions by first

\[
L_w \leq \left\{ \begin{array}{ll}
w_0(a-t) \exp \left\{ -\int_0^t \lambda_3(at+s)ds \right\} \\
+q \int_0^t \exp \left\{ -\int_s^t \lambda_3(a-r)dr \right\} \phi(a-t+s)ds \\
(1-q) \int_t^a \exp \left\{ -\int_s^t \lambda_3(r)dr \right\} \phi(s)ds
\end{array} \right.
\tag{A.4}
\]

We remark that functions which satisfy (A.1)–(A.4) are frequently called mild solutions. If we do not place smoothness assumptions on \( h(, ) \) and the initial data we obtain mild solutions, but we are not guaranteed that the mild solutions satisfy the system of partial differential equations. Nevertheless, if we can find a priori bounds for strong solutions which depend only upon the initial data, death and birth rates we can compute a priori estimates for mild solutions by first approximating the mild solutions with systems admitting strong solutions and applying continuous extension arguments.

If \( u(a,t), \phi(a,b,t), z(a,t) \) and \( w(a,t) \) are mild solutions satisfying (A.1)–(A.4) and

\[
v(a,t) = \int_0^{\tau(a)} \phi(a,b,t)db,
\]

where \( \tau(a) = \min\{a, \tau\} \), we define

\[
\rho(a,t) = u(a,t) + v(a,t) + z(a,t) + w(a,t).
\]

The following lemma guarantees an a priori bound for \( \|\rho(,t)\|_{1,(0,\infty)} \).

**Lemma A.2.** If the initial \( (u_0(, ), \phi_0(, ), w_0(, ), z_0(, )) \) is non-negative and belongs to \( L_1(\mathbb{R}_+) \times L_1(\mathbb{R}_+ \times (0, \tau)) \times L_1(\mathbb{R}_+) \times L_1(\mathbb{R}_+) \), the functions \( \beta_1, \beta_2, \lambda, \lambda_1, \lambda_2, \lambda_3 \) and uniformly bounded and non-negative, then there exists an unique non-negative quadruple functions \( (u(a,t), \phi(a,b,t), w(a,t), z(a,t)) \) which satisfy (A.1)–(A.4). Moreover there exists a constant \( C_0(T) \) for \( T > 0 \) which depends only upon the initial data, the functions \( \beta_1, \beta_2, \lambda, \lambda_1, \lambda_2, \lambda_3 \) so that

\[
\sup_{t \in [0,T]} \|\rho(,t)\|_{1,(0,\infty)} \leq C_0(T).
\]

There also exists a constant \( C_\infty(T) \) depending only upon the \( L_\infty \) norms of initial data, \( \beta_1, \beta_2, \lambda, \lambda_1, \lambda_2, \lambda_3 \) so that

\[
\sup_{t \in [0,T]} \|\rho(,t)\|_{\infty,(0,\infty)} \leq C_\infty(T).
\]

**Proof.** We refer to the preceding discussion. The existence theory will follow from arguments concerning smooth initial data and a smooth \( h(a,t) \). The integral representation immediately yields that \( u(a,t), \phi(a,b,t), w(a,t), z(a,t) \geq 0 \). This discussion also implies that bounds obtained for strong solutions will extend to the case of mild solutions. For this reason we confine our attention to strong solutions. We consider two cases the first being \( a \in [0, \tau] \) in which we have \( w(a,t) = z(a,t) \equiv 0 \) and the second \( a > \tau \). In the first case we may integrate (H.2) as \( b \) varies from 0 to \( \tau(a) \) and add the result to (H.1) to observe that

\[
\partial \rho / \partial t + \partial \rho / \partial a = -\left( \lambda(a,t)u + \int_0^{\tau(a)} \lambda_1 \phi(a,b,t)db \right) - \phi(a,\tau(a),t) \leq -\lambda(a,t)\rho
\]
because $\lambda_1(a, b, t) \geq \lambda(a, t)$ and $\phi(a, \tau(a), t) \geq 0$. If $a > \tau$ we have

$$\nabla \rho / \nabla t + \nabla \rho / \nabla a = -\left(\lambda(a, t)u + \int_0^t \lambda_1(a, b, t) \, db + \lambda_3 w + \lambda_2 z\right) \leq -\lambda(a, t)\rho$$

because $\lambda(a, t) \leq \min\{\lambda_1(a, b, t), \lambda_2(a, t), \lambda_3(a, t)\}$. We also have

$$\rho(a, 0) = u_0(a) + \begin{cases} \int_0^a \phi_0(a, b) \, db, & 0 < a < \tau, \\ \int_0^\tau \phi_0(a, b) \, db + w_0(a) + z_0(a), & \tau < a, \end{cases}$$

and

$$\rho(0, t) = \int_0^\infty \beta_1(a, t) u(a, t) \, da + \int_0^\infty \beta_1(a, t) w(a, t) \, da$$

$$+ \int_0^\infty \int_0^{r(a)} \beta_2(a, b, t) \phi(a, b, t) \, db \, da \leq \int_0^\infty \beta^*(a, t) \rho(a, t) \, da, \quad t \geq 0,$$

where $\beta^*(a, t) \geq \max\{\beta_1(a, t), \|\beta_2(a, t)\|_{\infty,[0,1]}\}$. We now obtain our $L_1$ and $L_\infty$ a priori estimates of $\rho(\cdot, t)$ by immediate application of the comparison principle for population equations [11].

We conclude this section with the observation that Lemma A.2 can also be applied immediately to obtain a priori $L_1$ and $L_\infty$ estimates for the nonlinear system of Section 3.

References