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UNIQUE SOLVABILITY OF AN AGE–STRUCTURED POPULATION MODEL WITH CANNIBALISM

DAVID W. ZACHMANN

ABSTRACT. A modification of the McKendrick–Von Foerster population balance equation is used to model populations in which: (i) no individual lives past age $a = L$ and (ii) young individuals, $0 < a < L^* < L$, are cannibalized by the older, $L^* < a < L$ individuals. The balance equation is formulated as an equivalent integral equation and the contraction mapping principle is used to establish the unique solvability. The existence and stability of equilibrium solutions are considered.

1. Introduction. Let $\rho = \rho(t, a)$ denote the population density of individuals of age a at time t and let

$$D\rho = \lim_{h \to 0} \frac{\rho(t+h, a+h) - \rho(t, a)}{h}.$$

if ρ is continuously differentiable, then $D\rho = \frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a}$. The McKendrick-Von Foerster population balance equation, McKendrick 1926, Von Foerster 1959, states

$$D\rho = -\gamma\rho$$

where γ is a nonnegative quantity, often called the death modulus, which determines the rate of removal of individuals from the population due to death. As noted by Gurtin and MacCamy, 1974, the death modulus, γ, may depend on ρ, total population density, age, and time, etc.

The equations considered in this paper are based on the above population balance equation and were motivated by a desire to model populations in which

(i) individuals live to a maximum age of $a = L$;

(ii) young individuals, $0 < a < L^* < L$ are preyed upon (cannibalized) by the older individuals, $L^* < a < L$.

The conditions (i) and (ii) are idealizations of those exhibited by

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many insect and fish populations. Let

$$P(t) = \int_{L^*}^{L} \rho(t,a)da \tag{1.1}$$

denote the density of older, predatory individuals in the population at time t. Conditions (i) and (ii) are incorporated into the population balance law as follows.

$$D\rho = -\delta(t,a,P(t))\rho, \;\; \delta(t,a,P(t)) \in \mathbf{R}^+ \;\; \begin{array}{c} t>0 \\ 0<a<L^* \\ P(t)>0 \end{array} \tag{1.2}$$

$$D\rho = -\frac{\lambda}{L-a}\rho, \;\; \lambda \in \mathbf{R}^+, L^* \leq a < L, t > 0 \tag{1.3}$$

$$\rho(t,0) = B(t,P(t)) = \int_{L^*}^{L} \beta(t,a,P(t))\rho(t,a)da, \;\; t > 0 \tag{1.4}$$

$$\rho(0,a) = \theta(a), \;\; 0 \leq a < L \tag{1.5}$$

where $\mathbf{R}^+ = \{x : x \geq 0\}$. In equation (1.2) the death modulus $\delta(t,a,P)$ is motivated by (ii). If $\delta_P > 0$, equation (1.2) reflects a situation in which the death rate of the young increases with the number of predatory individuals in the population. If young individuals are removed at a rate proportional to the number of encounters between young and old, then the death modulus in equation (1.2) could be taken to be a constant multiple of $P(t)$.

With a death modulus as in equation (1.3), it follows from equation (2.6) that

$$\pi(a) = \left(\frac{L-a}{L-L^*}\right)^{\lambda}, \;\; L^* < a < L, \lambda > 0$$

represents the probability that an individual of age L^* survives to age a, given a maximum life span of $a = L$. Large values of λ correspond to a high initial mortality rate, while small values of λ indicate most individuals survive nearly to age L. This behavior of $\pi(a)$ allows representation of many observed mortality curves. See, for example, Slobodkin, 1961, Figure 4.1. The death modulus of Eq. (1.3) has been used by Stafford et al., 1983, to describe grasshopper survival curves.

Equation (1.4) asserts that the number of "newborns" is dependent on the size of the population of older individuals. B is assumed to be a continuous function from $\mathbf{R}^+$ to $\mathbf{R}^+$. The initial age distribution in the population is given by $\theta(a)$, where θ is assumed to be a nonnegative–valued continuous function. For the initial population distribution to be consistent with the birth dynamics, it is assumed that

$$\theta(0) = B(P(0)).$$

The above consistency condition ensures that $\rho(t,a)$ is continuous across the line $t = a$.

Models incorporating cannibalism in age–structured population have been considered by Gurtin and Levine. In their approach the effects of cannibalism are accounted for in the birth dynamics in contrast to incorporating the cannibalism in the death modulus as is done here. Swick has considered populations in which individuals have a finite maximum life span. To ensure no individual lives past age $a = L$, Swick's model allows the death modulus to become unbounded as a approaches L, but away from $a = L$ requires the death modulus to be bounded by one. This boundedness requirement away from $a = L$ is not imposed here. Also, of the hypotheses H_0 through H_5 assumed in Swick, 1977, hypotheses H_1, H_4 and H_5 fail to hold for the model equations (1.1)-(1.5). Wollkind and Logan, 1978, and Wollkind, Hastings and Logan, 1980, have also considered populations with finite life span. In their analysis the death modulus was independent of P and a.

For $\delta > 0$ the system (1.1)-(1.5) represents a cannibalistic population. However, for the special case $\delta = 0$ the situation is quite different. When $\delta = 0$ equation (1.2) states that the death rate of young individuals is zero so the system represents a population in which the young are perfectly protected.

2. Existence. The goal in this section is to establish the existence of a solution to the model equations (1.1)-(1.5). Let $C^+[0,T]$ denote the class of nonnegative–valued functions which are continuous for $0 \le t \le T$. Assume the functions $\theta(a), \delta(a,t,P)$ and $\beta(a,t,P)$ are continuous and that δ satisfies a Lipschitz condition in P.

DEFINITION. $\rho(t,a)$ is a solution to the system (1.1)-(1.5) for $0 \leq t \leq T$ if

(i) $\rho(t,a) \geq 0, 0 < a < L$ and $\rho(t,a) = 0, a \geq L$.

(ii) $P(t)$ defined by (1.1) is in $C^+[0,T]$.

(iii) $D\rho$ exists and ρP satisfy equations (1.1)-(1.5).

The existence of a solution is established as follows. First it is shown that the system (1.1)-(1.5) has a solution if and only if $P(t)$ satisfies a Volterra integral equation. A local existence result, existence of a solution for T sufficiently small, is then established. Finally, a global solvability result is established with the aid of an a priori estimate of the solution.

THEOREM 2.1. *Let* $T = \min\{L^*, L - L^*\}$. $\rho(t,a)$ *is a solution of equations* (1.1)-(1.5) *for* $0 \leq t \leq T$ *if and only if* $P \in C^+[0,T]$ *satisfies*

(2.1)

$$P(t) = \int_{L^*+t}^{L} \theta(a-t)\Big(\frac{L-a}{L-a+t}\Big)^{\lambda} da$$

$$+ \int_{L^*}^{L^*+t} \theta(a-t)\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} \exp\Big(-\int_0^{L^*+t-a} \delta(s, a-t+s, P(s))ds\Big)da.$$

PROOF. If $\rho(t,a)$ is a solution of equations (1.1)-(1.5), $0 \leq t_0 \leq T$, $0 < a < L^*$ and $\overline{\rho}(h) = \rho(t_0 + h, a_0 + h)$, then equation (1.2) implies

$$\frac{d\overline{\rho}}{dh} = -\delta(t_0 + h, a_0 + h, P(t_0 + h))\overline{\rho}(h)$$

which can be integrated to obtain

$$\overline{\rho}(h) = \overline{\rho}(0) \exp\Big(-\int_0^h \delta(t_0 + s, a_0 + s, P(t_0 + s))ds\Big)$$

or

(2.2)

$$\rho(t_0 + h, a_0 + h) = \rho(t_0, a_0) \exp\Big(-\int_0^h \delta(t_0 + s, a_0 + s, P(t_0 + s))ds\Big).$$

If $0 < a < t < T$, in equation (2.2) set $a_0 = 0, h = a$ and $t_0 = t - a$ to obtain

(2.3)

$$\rho(t,a) = B(t-a, P(t-a)) \exp\Big(-\int_0^a \delta(t-a+s, s, P(t-a+s))ds\Big),$$

$$0 < a < t < T.$$

If $0 < t < a < L^*$, in equation (2.2) set $t_0 = 0, h = t$ and $a_0 = a - t$ to obtain

$$(2.4)\quad \rho(t,a) = \theta(a-t)\exp(-\int_0^t \delta(s, a-t+s, P(s))ds),\ 0 < t < a < L^*.$$

If $\rho(t,a)$ is a solution of equations (1.1)-(1.5), $0 < t_o < T, L^* \leq a < L$ and $\overline{\rho}(h)$ as above, then equation (1.3) implies

$$\frac{d\overline{\rho}}{dh} = \frac{-\lambda\overline{\rho}}{L - a_0 - h}$$

which, when integrated, yields

$$\overline{\rho}(h) = \overline{\rho}(0)\Big(\frac{L - a_0 - h}{L - a_0}\Big)^\lambda$$

or

$$(2.5)\qquad \rho(t_0 + h, a_0 + h) = \rho(t_0, a_0)\Big(\frac{L - a_0 - h}{L - a_0}\Big)^\lambda.$$

If $L^* < a < L^* + t, t < T$, in equation (2.5) set $a_0 = L^*, h = a - L^*, t_0 = t - a + L^*$ to obtain

$$(2.6)\qquad \rho(t,a) = \rho(t - a + L^*, L^*)\Big(\frac{L - a}{L - L^*}\Big)^\lambda.$$

From equation (2.4) it follows that

$$\rho(t-a+L^*, L^*) = \theta(L^*-t+a-L^*)\exp\Big(-\int_0^{t-a+L^*} \delta(s, a-t+s, P(s))ds\Big)$$

so equation (2.6) can be written as

(2.7)

$$\rho(t,a) = \theta(a - t)\exp\Big(-\int_0^{L^*+t-a} \delta(s, a - t + s, P(s))ds\Big)\Big(\frac{L - a}{L - L^*}\Big)^\lambda,$$
$$L^* < a < L^* + t,\ t < T.$$

If $L^* + t < a < L, t < T$, in equation (2.5) set $t_0 = 0, h = t$ and $a_0 = a - t$ to obtain

$$(2.8)\qquad \rho(t,a) = \theta(a - t)\Big(\frac{L - a}{L - a + t}\Big)^\lambda,\ L^* + t < a < L, t < T.$$

Now, from equation (1.1), (2.7) and (2.8), it follows that if $\rho(t,a)$ is a solution of equations (1.1)-(1.5), then P satisfies the integral equation (2.1)

To establish the converse assume $P \in C^+[0,T]$ satisfies equation (2.1). Since θ is nonnegative, $\rho(t,a)$, defined by equations (2.3), (2.4), (2.7) and (2.8), is clearly nonnegative. From equations (2.2) and (2.5) $D\rho$ is seen to exist. Finally a straightforward calculation shows ρ, P satisfies (1.1)-(1.5) which completes the proof of Theorem 2.1.

In the proof of Theorem 2.1 it may not be apparent why T was chosen to be the minimum of L^* and $L - L^*$. Requiring $T \leq L^*$ limits the effect of the birth dynamics to the victim population so that the integral equation (2.1) for P does not depend on the birth function. Since B is, in general, nonlinear, the restriction $T \leq L^*$ precludes one source of nonlinearity from the integral equation for P. If T is not required to satisfy $T \leq L - L^*$, then the density of the predatory segment of the population could not be expressed as simply as in equations (2.7)-(2.8), but would instead be a composition of such expressions.

It is convenient to express the integral equation (2.1) in abbreviated form as

$$P(t) = G(t) + F(P(t)).$$

where

$$G(t) = \int_{L^*+t}^{L} \theta(a-t)\Big(\frac{L-a}{L-a+t}\Big)^{\lambda} da \tag{2.9}$$

and

(2.10)

$$F(P(T)) = \int_{L^*}^{L^*+t} \theta(a-t)\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} \exp\Big(-\int_0^{L^*+t-a} \delta(s, a-t+s, P(s))ds\Big).$$

It is clear that F maps $C^+[0,T]$ into $C^+[0,T]$. It is also clear that for t bounded away from zero that $G(t)$ is a continuous, nonnegative function. However, since $(\frac{(L-a)}{(L-a+t)})^{\lambda}$ is discontinuous at $t = 0, a = L$, it is not immediate that G is continuous at $t = 0$.

LEMMA. *If $G(0)$ is defined to be $\int_{L^*}^{L} \theta(a)da, G(t)$ is continuous at* $t = 0$.

PROOF. Let

$$M = \max_{0 \le a \le L} \theta(a)$$

$$G(t) - G(0) = \int_{L^*+t}^{L} \theta(a-t)\left(\frac{L-a}{L-a+t}\right)^{\lambda} da - \int_{L^*}^{L} \theta(a)da$$

which, letting $\alpha = a - t$, implies

$$G(t) - G(0) = \int_{L^*}^{L-t} \theta(\alpha)\left(\left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda} - 1\right)d\alpha - \int_{L-t}^{L} \theta(\alpha)d\alpha.$$

Since

$$0 \le \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda} \le 1$$

for $L^* \le \alpha \le L - t$ it follows from the last equation that

$$|G(t) - G(0)| \le M\left(\int_{L^*}^{L-t} \left(1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda}\right)d\alpha + t\right).$$

To complete the proof of the lemma it is sufficient to show

$$\int_{L^*}^{L-t} \left(1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda}\right)d\alpha$$

approaches zero as t approaches zero. For $0 < \lambda \le 1$ it follows from (2.11) that

$$1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda} \le 1 - \left(\frac{L-\alpha-t}{L-\alpha}\right) = \frac{t}{L-\alpha}.$$

Thus, in the case $0 < \lambda \le 1$,

$$\int_{L^*}^{L-t} \left(1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda}\right)d\alpha \le \int_{L^*}^{L-t} \frac{t}{L-\alpha}d\alpha = t\ln(L-L^*) - t\ln t$$

which approaches zero as t approaches zero.

For $1 < \lambda$ it follows from (2.11) that

$$1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda} \le 1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{N} = \sum_{j=1}^{N}(-1)^{j+1}\binom{N}{j}\left(\frac{t}{L-\alpha}\right)^{j},$$

where N is any positive integer satisfying $N \geq \lambda$ and $\binom{N}{j} = \frac{N!}{((N-j)!j!)}$ is a binomial coefficient. If $\lambda > 1$, then

$$\int_{L^*}^{L-t} \left(1 - \left(\frac{L-\alpha-t}{L-\alpha}\right)^{\lambda}\right) d\alpha \leq \sum_{j=1}^{N} (-1)^j \binom{N}{j} \int_{L^*}^{L-t} \left(\frac{t}{L-\alpha}\right)^j d\alpha.$$

In the above sum of integrals the term with $j = 1$ has already been seen to have limit zero as t tends to zero. For $1 < j \leq N$,

$$\int_{L^*}^{L-t} \left(\frac{t}{L-\alpha}\right)^j d\alpha = t^j \left(\frac{(L-L^*)^{1-j} - t^{1-j}}{1-j}\right),$$

which clearly approaches zero with t. This completes the proof of the lemma.

The next result establishes the local existence of a solution to the integral equation (2.1) and, in view of Theorem 2.1, to the system (1.1)-(1.5). In the next theorem the time T for which existence of a solution can be assured may be smaller than the time T in Theorem 2.1 for which equation (2.1) is equivalent to equations (1.1)-(1.5).

THEOREM 2.2. *Assume* $\delta(t, a, P(t))$ *satisfies*

$$|\delta(t, a, P(t)) - \delta(t, a, Q(t))| < \sigma |P(t) - Q(t)|, \ \sigma \in \mathbf{R}^+.$$

If $T \leq \min\{L^*, L - L^*\}$ *and* $T < \sqrt{\frac{2}{M\sigma}}$, *then the sequence*

$$P_0(t) = G(t), \ P_n(t) = G(t) + F(P_{n-1}(t)), \ n = 1, 2, \cdots$$

converges to a function $P(t) \in C^+[0,T]$ *which satisfies equation* (2.1). *Moreover,* $P(t)$ *is the only solution of equation* (2.1) *in* $C^+[0,T]$.

PROOF. From the lemma and the fact that $F : C^+[0,T] \to C^+[0,T]$, it follows that if the sequence $P_n(t)$ converges to $P(t)$, then $P(t) \in C^+[0,T]$. To show the $P_n(t)$ converge, first note that

$$|P_1(t) - P_0(t)| = F(P_0(t)) \leq TM$$

where the last inequality follows immediately from equation (2.10) and $0 \le \theta(a-t) \le M$. For $n \ge 2$,

$$
\begin{aligned}
|P_n(t) - P_{n-1}(t)| &= |F(P_{n-1}(t)) - F(P_{n-2}(t))| \\
&= \Big| \int_{L^*}^{L^*+t} \theta(a-t)\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} \\
&\Big(\exp\Big(-\int_0^{L^*+t-a} \delta(s, a-t+s, P_{n-1}(s)ds)ds\Big) \\
&-\exp\Big(\int_0^{L^*+t-a} \delta(s, a-t+s, P_{n-2}(s))ds\Big)\Big) da \\
&\le M \int_{L^*}^{L^*+t} \Big|\exp\Big(-\int_0^{L^*+t-a} (s, a-t+s, P_{n-1}(s)ds)ds\Big) \\
&-\exp\Big(\int_0^{L^*+t-a} \delta(s, a-t+s, P_{n-2}(s))ds\Big)\Big| da.
\end{aligned}
$$

The last inequality and $|e^{-x} - e^{-y}| \le |x-y|$ for $x, y > 0$ shows (2.12)

$$
\begin{aligned}
|P_n(t) - P_{n-1}(t)| &\le M \int_{L^*}^{L^*+t} \Big| \int_0^{L^*+t-a} \delta(s, a-t+s, P_{n-1}(s)) \\
&- \delta(s, a-t+s, P_{n-2}(s))ds \Big| da \\
&\le M\sigma \int_{L^*}^{L^*+t} (L^* + t - a) \max_{0 \le s \le T} |P_{n-1}(s) - P_{n-2}(s)| \\
&= M\sigma(t^2/2) \max_{0 \le s \le T} |P_{n-1}(s) - P_{n-2}(s)|
\end{aligned}
$$

so that

$$\max_{0 \le t \le T} |P_n(t) - P_{n-1}(t)| \le \frac{M\sigma T^2}{2} \max_{0 \le s \le T} |P_{n-1}(s) - P_{n-2}(s)|.$$

Using the above and $|P_1(t) - P_0(t)| \le TM$ in an induction argument yields

$$\max_{0 \le t \le T} |P_n(t) - P_{n-1}(t)| < \frac{\sigma^{n-1} M^n T^{2n-1}}{2^{n-1}}.$$

Now the ratio test shows that $\sum_{n=1}^{\infty} |P_n(t) - P_{n-1}(t)|$ converges uniformly for $0 \le t \le T$ and therefore that $P_n(t)$ converges uniformly for

$0 \le t \le T$ provided

$$\frac{M\sigma T^2}{2} < 1 \text{ or } T < \sqrt{\frac{2}{M\sigma}}.$$

To complete the proof of Theorem 2.2 assume $P, Q \in C^+[0,T]$ satisfy

$$P(t) = G(t) + F(P(t)) \text{ and } Q = G(t) + F(Q(t)).$$

Then, by (2.12),

$$\max_{0\le t\le T} |P(t) - Q(t)| \le \frac{M\sigma T^2}{2} \max_{0\le s\le T} |P(s) - Q(s)|$$

which, since $M\sigma T^2 \backslash 2 < 1$, is a contradiction unless $Q(t)$ is identically equal to $P(t)$.

Theorem 2.2 shows that the integral equation (2.1) can be uniquely solved for $P(t)$ on $0 \le t \le T_0 = T$. Then, from Theorem 2.1, it follows that $\rho(t,a)$ satisfying equations (1.1)-(1.5) can be found for $0 \le a \le L$, $0 \le t \le T_0$. Now, using $\rho(T_0, a)$ in place of $\theta(a)$ in the above local existence argument, $P(t)$, and thus $\rho(t,a)$, can be advanced over the time interval $T_0 \le t \le T_1$. The time step T_1 is restricted by $T_1 - T_0 \le \min\{L^*, L - L^*\}$ and

$$T_1 - T_0 < \sqrt{\frac{2}{m_1\sigma}}, \quad m_1 = \max_{0\le a\le L} \rho(T_0, a).$$

Repeating the local existence argument allows the solution $\rho(t,a)$ to be advanced successively over the intervals $T_{i-1} \le t \le T_i, i = 1, 2, \cdots$, where $T_i - T_{i-1} < \min\{L^*, L - L^*\}$ and

$$T_i - T_{i-1} < \sqrt{\frac{2}{m_i\sigma}}, \quad m_i \max_{0\le a\le L} \rho(T_{i-1}, a).$$

A global existence result cannot be obtained unless the situation $\sum_{i=1}^{\infty}(T_i - T_{i-1}) < \infty$, which occurs when m_i increases too rapidly, can be ruled out. To establish the global existence of the solution to equations (1.1)-(1.5) it is sufficient to show that the solution can be advanced to an arbitrary, fixed time $t = T_*$ with a sequence of local arguments with time steps $T_i - T_{i-1}$ bounded away from zero.

THEOREM 2.3. *Assume B satisfies the growth condition $B(t, P(t)) \leq bP(t), b \geq 0$. If $T_i - T_{i-1} = \Delta t$, where $\Delta t > 0$ satisfies*

$$\Delta t \leq \min\{L^*, L - L^*\}$$

$$\Delta t \leq \sqrt{\frac{2}{M\sigma}}, \quad M = \max_{0\leq a\leq L} \theta(a)$$
$$\Delta t \leq \sqrt{\frac{2}{M_1\sigma}}, \quad M_1 = bM(L - L^*)$$

and, for $T_* > L^*$,

$$\Delta t \leq \sqrt{\frac{2}{M_2\sigma}}, \quad M_2 = M_1 e^{b(T_* - L^*)}.$$

Then Theorems 2.1 *and* 2.2 *can be used to advance the solution $P(t), \rho(t,a)$ of equations* (1.2)-(1.5) *to the time $t = T_*$.*

PROOF. To establish Theorem 2.3 it is sufficient to show ρ satisfies the a prioiri estimates

$$\rho(t,a) \leq \theta(a), \quad t \leq a \leq L$$
$$\rho(t,a) \leq bM(L - L^*), \quad a \leq t \leq L^*$$

and

$$\rho(t,a) \leq bM(L - L^*)e^{b(T_* - L^*)} \ , L^* \leq t \leq T_*, \ \ 0 \leq a \leq L.$$

The first of these estimates follows immediately from equation (2.4), (2.7) and (2.8). To establish the second estimate note that equations (1.2) and (1.3) imply $D\rho \leq 0$, so

$$\rho(t,a) \leq B(t - a, P(t - a)) \leq bP(t - a).$$

Since $\rho(t,a) \leq M$ for $t \leq a \leq L^*, P(t - a)$ is bounded by $M(L - L^*)$ for $a \leq t \leq L^*$ and the second estimate follows.

Finally, consider the case $L^* \leq t \leq T_*, 0 \leq a \leq L$. From $\rho(t,a) \leq bP(t - a)$ it is seen that the extreme case which must be considered in obtaining an a priori estimate on $\rho(t,a)$ is that in which P increases at the maximum rate allowed by the growth condition on B. In this case $\rho(t,a) \le bP(T_*)$, for $L^* \le t \le T_*, o \le a \le L$, so it remains only to estimate $P(T_*)$. Integrating

$$D\rho = \frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} \le 0$$

from $a = L^*$ to $a = L$ yields

$$\frac{dP}{dt} - \rho(t, L^*) \le 0,$$

so

$$\frac{dP}{dt} \le \rho(t, L^*) \le bP(t - L^*).$$

If P is increasing, then $P(t) \ge P(t - L^*)$ and $dP/dt \le bP(t)$ from which it follows that $P(t) \le P(L^*)e^{b(t-L^*)}$. Thus $P(T_*) \le M(L - L^*)e^{b(T_*-L^*)}$ or

$$\rho(t,a) \le bM(L - L^*)e^{b(T_*-L^*)}, L^* \le t \le T_*\ 0 \le a \le L$$

which completes the proof.

COROLLARY. *If B is uniformly bounded, $B(t, P(t)) \le B^*$ then Δt need only satisfy*

$$\Delta t \le \min(L^*, L - L^*, \sqrt{\frac{2}{M\sigma}}, \sqrt{\frac{2}{B^*\sigma}}\}.$$

3. Existence and stability of equilibrium solutions. Suppose the birth and death dynamics in the model do not depend explicitly on time. Then the system (1.1)-(1.4) has the form

$$P(t) = \int_{L^*}^{L} \rho(t,a)da \tag{3.1}$$

$$D\rho = -\gamma(a, P)\rho,\ 0 < a < L^* \tag{3.2}$$

$$D\rho = -\frac{\lambda}{L-a}\rho,\ L^* < a < L \tag{3.3}$$

$$(3.4) \qquad \rho(0,t) = \int_{L^*}^{L} \beta(a,P)\rho(t,a)da.$$

Let $\overline{P}$ be a fixed positive number and let $\overline{\rho} = \overline{\rho}(a)$ be continuous for $0 < a < L$ and continuously differentiable for $0 < a < L^*$ and $L^* < a < L$. An equilibrium solution is defined to be a pair $\overline{P}, \overline{\rho}$ satisfying (3.1)-(3.4). Cushing and Salem, 1982, and Cushing, 1983, 1984, 1985 have studied the existence and stability of equilibrium solutions of a system of the form (3.1)-(3.4). In place of the specific death modulus given in (3.2)-(3.3), Cushing assumes a general, continuous death modulus. It appears that many of his results could be modified to apply to the problem considered here.

THEOREM 3.1. *There exists an equilibrium solution if and only if* $\overline{P}$ *satisfies*

$$(3.5) \qquad \int_{L^*}^{L} \beta(a,P)\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} da \cdot \exp\Big(-\int_0^{L^*} \gamma(a,P)da\Big) = 1.$$

Moreover, if $\overline{P}$ *satisfies* (3.5), *the corresponding equilibrium density function is given by*

$$(3.6) \qquad \overline{\rho}(a) = \frac{\overline{P}(\lambda+1)}{L-L^*}\Big(\frac{L-a}{L-L^*}\Big)^{\lambda}, \; L^* < a < L$$

$$(3.7) \quad \overline{\rho}(a) = \int_{L^*}^{L} \beta(a,\overline{P})\overline{\rho}(a)da \cdot \exp(-\int_0^a \gamma(h,\overline{P})dh), \; 0 < a < L^*.$$

PROOF. In equilibrium (3.2) reads

$$\overline{\rho}'(a) = -\gamma(a,\overline{P})\overline{\rho}, \; 0 < a < L^*,$$

which is easily integrated to obtain

$$\overline{\rho}(a) = \rho_0 \exp\Big(-\int_0^a \gamma(h,\overline{P})dh\Big), \; 0 < a < L^*,$$

where the constant ρ_0 is given by

$$(3.8) \qquad \rho_0 = \int_{L^*}^{L} \beta(a,\overline{P})\overline{\rho}(a)da.$$

Similarly, integrating (3.3) yields

$$(3.9)\qquad \overline{\rho}(a) = \rho_0\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} \exp\Big(-\int_0^{L^*} \gamma(a,P)da\Big),\ L^* < a < L.$$

By putting $\overline{\rho}$ from equation (3.9) into (3.8) and dividing out ρ_0, it follows that condition (3.5) is necessary for the existence of an equilibrium solution. If condition (3.5) holds, then it is easy to verify that $\overline{\rho}$, given by equations (3.6)-(3.7), satisfies the system (3.1)-(3.4). Thus, equation (3.5) is necessary and sufficient for the existence of an equilibrium solution and the proof is complete.

In the case $\gamma(a,P) \equiv 0$, the content of equation (3.5) is that each individual must be replaced for equilibrium to persist. For $\gamma(a,P) > 0$ equation (3.5) asserts that, in addition to replacing itself, each individual must produce an excess equal to the number it will consume during its predatory stage.

For the remainder of the section assume the birth modulus in equation (3.5) is age–independent and let

$$(3.10)\qquad \beta = \beta(P),$$

denote the per capita reproduction rate. Also assume the death modulus γ, in equation (3.2) has the form

$$(3.11)\qquad \gamma = \sigma P,\ \sigma = \text{const.} > 0$$

Equation (3.11) can be used to model a situation in which the removal rate of young is proportional to the number of encounters between young, prey, and older, cannibalistic individuals.

COROLLARY 3.2. *If β and γ are as in equations (3.10)-(3.11), then an equilibrium solution exists if and only if $\overline{P}$ satisfies*

$$(3.12)\qquad \frac{L-L^*}{\lambda+1}\beta(\overline{P})\exp(-\sigma\overline{P}L^*) = 1.$$

Moreover, if $\overline{P}$ satisfies (3.12), the corresponding equilibrium density function is given by equation (3.6) for $L^* < a < L$ and

$$(3.13)\qquad \overline{\rho}(a) = \overline{P}\beta(\overline{P})\exp(-\sigma\overline{P}a),\ 0 < a < L^*.$$

PROOF. Equation (3.12) follows immediately by putting expressions (3.10)-(3.11) into condition (3.5). All that must be verified is the continuity of the density function $\overline{\rho}$ defined piecewise by equations (3.6) and (3.13). Comparing (3.6) and (3.13) evaluated at $a = L^*$ we find

$$\frac{\overline{P}(\lambda+1)}{L-L^*} = \overline{P}\beta(\overline{P})\exp(-\sigma\overline{P}L^*)$$

which is seen to be equivalent to condition (3.12) so $\overline{\rho}$ is continuous.

To examine the stability of an equilibrium solution to the system (3.1)-(3.4), set

$$\rho = \overline{\rho}(a) + u(t,a), \ \ 0 < a < L^*, t > 0$$

$$\rho = \overline{\rho}(a) + v(t,a), \ \ L^* < a < L, t > 0$$

$$P = \overline{P} + p(t), \ \ t > 0.$$

For the birth and death dynamics defined by (3.10)-(3.11), a calculation shows that to first order in the perturbations u, v and p, the following system must be satisfied.

$$u_t + u_a = -\sigma\overline{P}u - \sigma p\overline{\rho}, \ \ 0 < a < L^*, t > 0 \tag{3.14}$$

$$v_t + v_a = -\frac{\lambda}{L-a}v, \ \ L^* < a < L, \ t > 0 \tag{3.15}$$

$$p = \int_{L^*}^{L} v\,da, \ \ t > 0 \tag{3.16}$$

$$u(0,t) = (\overline{P}\beta_P(\overline{P}) + \beta(P)), \ \ t > 0 \tag{3.17}$$

$$u(t, L^*) = v(t, L^*), \ \ t > 0. \tag{3.18}$$

To continue the linearized stability analysis, set

$$u = U(a)e^{zt}, \ \ v = V(a)e^{zt}, \ \ p = p_0 e^{zt} \tag{3.19}$$

in the system (3.14)-(3.18) to obtain

$$zU + U' = -\sigma \overline{P} U - \sigma p_0 \overline{p}(a),\ 0 < a < L^* \tag{3.20}$$

$$zV + V' = -\frac{\lambda}{L-a} V,\ L^* < a < L \tag{3.21}$$

$$p_0 = \int_{L^*}^{L} V(a)da \tag{3.22}$$

$$U(0) = [\overline{P}\beta_P(\overline{P}) + \beta(\overline{P})]p_0 \tag{3.23}$$

$$U(L^*) = V(L^*). \tag{3.24}$$

Since $\overline{p}(a)$ is given by equation (3.13) for $0 < a < L^*$, (3.20) can be solved, subject to (3.23), to give

$$U(a) = p_0\Big(\overline{P}\beta_P(\overline{P}) + \beta(\overline{P}) - \frac{\sigma\overline{P}\beta(\overline{P})(e^{za} - 1)}{z}\Big)e^{-(\sigma\overline{P}+z)a}.$$

Solving (3.21) for V yields

$$V(a) = \text{const. } e^{-za}\Big(\frac{L-a}{L-L^*}\Big)^{\lambda}.$$

Using the continuity condition (3.24) to fix the constant in the last equation gives

$$V = p_0\Big(\overline{P}\beta_p(\overline{P}) + \beta(\overline{P}) - \frac{\sigma\overline{P}\beta(\overline{P})(e^{zL^*} - 1)}{z}\Big)e^{-za}\Big(\frac{L-a}{L-L^*}\Big)^{\lambda}.$$

Finally, if the last equation is integrated from $a = L^*$ to $a = L$, it follows from equation (3.22) that z must satisfy the equation

$$\Big(\overline{P}\beta_P(\overline{P}) + \beta(\overline{P}) - \frac{\sigma\overline{P}\beta(\overline{P})(e^{zL^*} - 1)}{z}\Big)\int_{L^*}^{L} e^{-za}\Big(\frac{L-a}{L-L^*}\Big)^{\lambda} da = 1. \tag{3.25}$$

Since the perturbations (3.19) decay in time if and only if the real part of z is negative, we have the following result.

THEOREM 3.3. *The equilibrium solution* $\overline{P}, \overline{p}$ *is stable if and only if all solutions* z *of* (3.25) *have negative real part.*

THEOREM 3.4. *A sufficient condition for an equilibrium solution to be unstable is*

$$\beta_P(\overline{P}) > \sigma\beta(\overline{P})L^*. \tag{3.26}$$

PROOF. Let $F(z)$ denote the expression on the left side of equation (3.25) and consider the case of real z with $z \geq 0$. Evaluating F at $z = 0$ gives

$$F(0) = (\overline{P}\beta_P(\overline{P}) + \beta(\overline{P}) - \sigma\overline{P}\beta(\overline{P})L^*)\frac{L - L^*}{\lambda + 1}$$

which, in view of (3.12), shows

$$F(0) = \overline{P}(\beta_P(\overline{P}) - \sigma\beta(\overline{P})L^* + \exp(\sigma\overline{P}L^*).$$

Thus, if (3.26) holds, then $F(0) > 1$. Since $\lim_{z\to\infty} F(z) = 0$, it follows from the intermediate value theorem that $F(z)$ has a positive solution, and the equilibrium solution is unstable.

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DEPARTMENT OF MATHEMATICS, COLORADO STATE UNIVERSITY, FORT COLLINS, CO 80523