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TIME LAGS AND DENSITY DEPENDENCE IN AGE DEPENDENT TWO SPECIES COMPETITION

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Sufficient conditions are obtained for the existence and linear stability of time independent age distributions in two species competition with age and time lagged density dependent mortality and fertility functions.

1. Introduction

Let $P_1(t)$ and $P_2(t)$ denote the total population sizes (or biomasses) at time $t \geq 0$ of two interacting species living in a common habitat and competing for a common pool of resources. The competition for resources will be implicit in our model similar to that in the two species Lotka-Volterra competition system. Assuming constant sex ratios in the two species we can consider $P_1(t)$ and $P_2(t)$ to be the population of females only; immigration, emigration and internal dispersion in the habitat are assumed to play no significant role in the dynamics of the community.

We suppose that the two species contain respectively $\rho_1(a, t)da$ and $\rho_2(a, t)da$ individuals with ages between a and $a + da$ $(a \geq 0)$ at time t so that we have

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$$(1.1)\qquad P_1(t) = \int_0^\infty \rho_1(a,\, t)da \ , \quad P_2(t) = \int_0^\infty \rho_2(a,\, t)da \ , \quad t \geq 0 \ .$$

The rates of change of the two species densities are by definition $D\rho_1(a,\, t)$ and $D\rho_2(a,\, t)$ where

$$(1.2)\qquad D\rho_i(a,\, t) = \lim_{h\to 0} \frac{\rho_i(a+h, t+h)-\rho_i(a, t)}{h} \ , \quad i = 1, 2 \ .$$

Assuming the existence of the limits in (1.2) we consider the following time lagged model system

$$(1.3)\qquad \begin{cases} D\rho_1(a,\, t) + f_1\big(a,\, P_1(t),\, P_2(t-\tau)\big)\rho_1(a,\, t) = 0 \ , \\ D\rho_2(a,\, t) + f_2\big(a,\, P_1(t-\tau),\, P_2(t)\big)\rho_2(a,\, t) = 0 \ , \end{cases} \quad a > 0 \ , \quad t > 0 \ ,$$

$$(1.4)\qquad \begin{cases} \rho_1(0,\, t) = \int_0^\infty b_1\big(a,\, P_1(t),\, P_2(t-\tau)\big)\rho_1(a,\, t)da \ , \\ \rho_2(0,\, t) = \int_0^\infty b_2\big(a,\, P_1(t-\tau),\, P_2(t)\big)\rho_2(a,\, t)da \ , \end{cases} \quad t > 0 \ ,$$

$$(1.5)\qquad \rho_i(a,\, s) = \varphi_i(a,\, s) \ , \quad a > 0 \ , \quad s \in [-\tau,\, 0] \ , \quad i = 1, 2 \ ,$$

$$(1.6)\qquad P_i(s) = \int_0^\infty \varphi_i(a,\, s)da \ , \quad s \in [-\tau,\, 0] \ ,$$

where τ is some fixed nonnegative constant; f_1 and f_2 denote the age and density dependent mortality rates with time lags in interspecific interactions, b_1 and b_2 denote the age and density dependent fertility functions again having time lags in the interspecific interactions; φ_1 and φ_2 denote the initial age distributions needed for the formulation of the model.

The model system (1.1)-(1.6) will be meaningful only if φ_1, φ_2, f_1, f_2, b_1, b_2 are nonnegative functions of the respective arguments. Also since the total initial populations have to be finite, $\varphi_i(\cdot,\, s)$ should belong to $L_1(\mathbb{R}^+)$ for each $s \in [-\tau,\, 0]$. We have specifically assumed that f_i and b_i $(i = 1, 2)$ are independent of t explicitly and this assumption can be interpreted to represent the temporal uniformity of the environment.

One of the fundamental questions for (1.1)-(1.6) is the following; under what conditions on f_i, b_i and τ does the system (1.1)-(1.4) have time independent nontrivial solutions, and when such solutions exist, are they stable with respect to some suitable stability criterion? When such stable time invariant solutions exist for (1.1)-(1.4) we say that the two species community has a stable age distribution. Existence of a stable age distribution is the analogue of the existence of a stable steady state for the corresponding age independent system.

In this article we investigate the above question for the case of a competitive interaction with some additional constraints on the vital rates f_i and b_i $(i = 1, 2)$. Age dependent population systems without time delays have been considered by several authors (Gurtin and MacCamy [3, 4, 5], Gurtin and Levine [6], Haimovici [7] and Rotenberg [8]). The question of the relation between an age independent system and a corresponding age dependent system has been considered by Gurtin and MacCamy [4] and Gurtin and Levine [6] who have established an asymptotic (as $t \to \infty$) relation between such models by constructing a higher dimensional lumped parameter system (in terms of ordinary differential equations) to represent the age dependent distributed parameter system. Assuming the existence of stationary age distributions Haimovici [7] considers their stability in a system of two interacting populations explicitly taking into consideration the dynamical nature of the habitat's resources and pollution.

In this article we add another realistic feature namely time lags in the age dependent models and obtain sufficient conditions for the existence of stationary age distributions in (1.1)-(1.4) and show that the time lags in interspecific interactions have no effect on the linear stability of the age distributions although the decay rates of perturbations will depend on the magnitudes of the time delays. Such "harmless" nature of time lags in interspecific interactions have been noted by the author for the age independent models in [1, 2].

2. Existence and uniqueness of solutions

We first narrate our assumptions on the vital rates of f_i and b_i $(i = 1, 2)$ so that the system (1.1)-(1.6) will denote a competition system. Let $BC[0, \infty)$ denote the linear space of bounded continuous real functions on $[0, \infty)$ with the norm defined by

$$\|f\| = \{\max|f(t)|, \ t \in [0, \infty)\} .$$

Let K_1 be the cone of nonnegative functions of $BC[0, \infty)$. Let $C[-\tau, 0]$ denote the space of real continuous functions with a norm defined by $\|g\| = \{\max|g(s)|, \ s \in [-\tau, 0]\}$; let K_2 be the nonnegative cone of functions in $C[-\tau, 0]$. We present our first set of assumptions on f_i, b_i and φ_i for $i = 1, 2$.

A1. $f_1 \in C(\mathbb{R}^+ \times K_1 \times K_2, \mathbb{R}^+)$, $f_1 \geq d_1^*$ on $\mathbb{R}^+ \times K_1 \times K_2$,
$f_2 \in C(\mathbb{R}^+ \times K_2 \times K_1, \mathbb{R}^+)$, $f_2 \geq d_2^*$ on $\mathbb{R}^+ \times K_2 \times K_1$,
$(d_1^*, d_2^*$ are positive constants$)$;

f_1 and f_2 are Lipschitzian with respect to their last two arguments uniformly in $a \in \mathbb{R}^+$; that is, for $i = 1, 2$,

$$|f_i(a, P_1', P_2') - f_i(a, P_1'', P_2'')| \leq d_i[\|P_1' - P_1''\| + \|P_2' - P_2''\|]$$

$(d_1, d_2$ are positive constants$)$,

$$\partial f_1/\partial P_1, \ \partial f_1/\partial P_2 \in C(\mathbb{R}^+ \times K_1 \times K_2, \mathbb{R}^+) ,$$

$$\partial f_2/\partial P_1, \ \partial f_2/\partial P_2 \in C(\mathbb{R}^+ \times K_2 \times K_1, \mathbb{R}^+) .$$

A2. $b_1 \in C(\mathbb{R}^+ \times K_1 \times K_2, \mathbb{R}^+)$, $b_1 \leq \beta_1^*$ on $\mathbb{R}^+ \times K_1 \times K_2$,
$b_2 \in C(\mathbb{R}^+ \times K_2 \times K_1, \mathbb{R}^+)$, $b_2 \leq \beta_2^*$ on $\mathbb{R}^+ \times K_2 \times K_1$,
$(\beta_1^*, \beta_2^*$ are positive constants$)$;

b_1, b_2 are Lipschitzian with respect to their last two arguments uniformly in $a \in \mathbb{R}^+$; that is, for $i = 1, 2$,

$$|b_i(a, P_1', P_2') - b_i(a, P_1'', P_2'')| \leq \beta_i[\|P_1' - P_1''\| + \|P_2' - P_2''\|]$$

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$(\beta_1, \beta_2$ are positive constants$)$,

$b_i(\cdot, P_1, P_2) \in L^\infty(\mathbf{R}^+, \mathbf{R}^+)$ for fixed P_1, P_2 , $i = 1, 2$,

$$\frac{\partial b_1}{\partial P_2}, \frac{\partial b_1}{\partial P_2} \in C\left(\mathbf{R}^+ \times K_1 \times K_2, \mathbf{R}^-\right) ,$$

$$\frac{\partial b_2}{\partial P_1}, \frac{\partial b_2}{\partial P_2} \in C\left(\mathbf{R}^+ \times K_2 \times K_1, \mathbf{R}^-\right) .$$

A3. $\varphi_i(\cdot, s) \in L^1(\mathbf{R}^+, \mathbf{R}^+) \cap C(\mathbf{R}^+, \mathbf{R}^+)$ for each $s \in [-\tau, 0]$, $i = 1, 2$.

By a solution of (1.1)-(1.6) on $[0, T]$ we mean $\rho_i : \mathbf{R}^+ \times [-\tau, T] \to \mathbf{R}^+$ $(i = 1, 2)$ with the following properties:

S1. $\rho_i(\cdot, t) \in L^1(\mathbf{R}^+, \mathbf{R}^+)$ for each $t \in [-\tau, T]$;

S2. $\rho_i(a, \cdot) \in C([-\tau, T], \mathbf{R}^+)$ for each $a \in \mathbf{R}^+$;

S3. $D\rho_i$ exists along the characteristics $t - a =$ constant on $\mathbf{R}^+ \times \{\mathbf{R}^+ \cap [0, T]\}$ and is continuous $(i = 1, 2)$;

S4. ρ_i satisfies the system (1.1)-(1.6) for $(a, t) \in \mathbf{R}^+ \times [-\tau, T]$.

Let us first convert the system (1.1)-(1.6) into an equivalent system of integral equations. For brevity we denote by P the pair (P_1, P_2) . If we let

$$\rho_i(a+x, t+x) = \tilde{\rho}_i(x) , \quad i = 1, 2 ,$$

then (1.3) considered at $(a+x, t+x)$ becomes

$$\frac{d\tilde{\rho}_i(x)}{dx} + f_i\left(a+x, P(t+x)\right)\tilde{\rho}_i(x) = 0$$

which has a solution of the form

$$\tilde{\rho}_i(x) = \tilde{\rho}_i(0)\exp\left[-\int_0^x f_i\left(a+s, P(t+s)\right)ds\right]$$

and hence

$$(2.1)\qquad \rho_i(a+x,\ t+x) = \rho_i(a,\ t)\exp\left[-\int_0^x f_i\big(a+s,\ P(t+s)\big)ds\right] .$$

For $a \geq t$ we choose $(a,\ t) = (a-t,\ 0)$ in (1.3) and $x = t$ in (2.1) so that

$$(2.2)\qquad \rho_i(a,\ t) = \varphi_i(a-t,\ 0)\exp\left[-\int_0^t f_i\big(a-t+s,\ \mathbf{P}_i(s)\big)ds\right] ,$$
$$0 \leq t \leq a\ ,\quad i = 1,\ 2\ ,$$

with

$$\mathbf{P}_1(s) = \big(P_1(s),\ P_2(s-\tau)\big)\ ,$$
$$\mathbf{P}_2(s) = \big(P_1(s-\tau),\ P_2(s)\big)\ .$$

For $0 \leq a < t$ we choose $(a,\ t) = (0,\ t-a)$ in (1.3) and $x = a$ in (2.1) so that

$$(2.3)\qquad \rho_i(a,\ t) = B_i(t-a)\exp\left[-\int_0^a f_i\big(s,\ \mathbf{P}_i(t-a+s)\big)ds\right] ,$$
$$t > a \geq 0\ ,\quad i = 1,\ 2\ ,$$

where

$$(2.4)\qquad B_i(t) = \rho_i(0,\ t)\ ,\quad i = 1,\ 2\ ,\quad t \geq 0\ .$$

Define M_i and L_i $(i = 1,\ 2)$ as follows:

$$(2.5)\qquad \begin{aligned} M_i\big(a,\ t,\ \mathbf{P}_i(t)\big) &= \exp\left[-\int_0^{t-a} f_i\big(s,\ \mathbf{P}_i(a+s)\big)ds\right] ,\\ L_i\big(a,\ t,\ \mathbf{P}_i(t)\big) &= \exp\left[-\int_0^t f_i\big(a+s,\ \mathbf{P}_i(s)\big)ds\right] . \end{aligned}$$

It will now follow from (1.1), (1.3), (2.2)-(2.5) that

$$(2.6)\qquad P_i(t) = \int_0^t B_i(a)M_i\big(a,\ t,\ \mathbf{P}_i(t)\big)da + \int_0^\infty \varphi_i(a,\ 0)L_i\big(a,\ t,\ \mathbf{P}_i(t)\big)da\ ,$$
$$t > 0\ ,\quad i = 1,\ 2\ ,$$

$$(2.7)\qquad P_i(s) = \Phi_i(s) = \int_0^\infty \varphi_i(a,\ s)da\ ,\quad s \in [-\tau,\ 0]\ ,\quad i = 1,\ 2\ ,$$

$$(2.8)\quad B_i(t) = \int_0^t B_i(a)b_i\big(t-a,\ \mathbf{P}_i(t)\big)M_i\big(a,\ t,\ \mathbf{P}_i(t)\big)da + \int_0^\infty b_i\big(a+t,\ \mathbf{P}_i(t)\big)\varphi_i(a,\ 0)L_i\big(a,\ t,\ \mathbf{P}_i(t)\big)da\ ,$$

$$i = 1,\ 2\ ,\quad t > 0\ .$$

The equivalence of (2.6)-(2.8) with (1.1)-(1.6) is established by the following whose proof is identical to a similar result of Gurtin and MacCamy [*4*]; hence we omit the details of the proof of the following.

THEOREM 1. *Suppose the system* (1.1)-(1.6) *satisfies the conditions* A_1, A_2, A_3. *If* $(\rho_1,\ \rho_2)$ *is a solution of* (1.1)-(1.6) *then the total populations* P_1, P_2 *and the birth rates* B_1, B_2 *satisfy the integral equations* (2.6)-(2.8). *Conversely if* P_1, P_2, B_1, B_2 *are nonnegative continuous solutions of* (2.6)-(2.8) *on* $[0,\ T]$ *and if* ρ_1, ρ_2 *are defined by* (2.2)-(2.4) *on* $\mathbf{R}^+ \times [0,\ T]$ *then such* ρ_1, ρ_2 *provide a solution of* (1.1)-(1.6) *on* $\mathbf{R}^+ \times [0,\ T]$.

The following *a priori* estimates are useful to prove our existence theorem below. It will immediately follow from the bounds for f_i and b_i that

$$(2.9)\qquad \begin{aligned} &M_i(a,\ t,\ \mathbf{P}) \le \exp\big[-d_i^*(t-a)\big] \le 1\ ,\ \text{if}\ \ t \ge a\ ,\\ &L_i(a,\ t,\ \mathbf{P}) \le \exp\big[-d_i^*t\big]\ . \end{aligned}$$

From (2.7)-(2.8) we derive that

$$B_i(t) \le \int_0^t \beta_i^*B_i(a)\exp\big[-d_i^*(t-a)\big]da + \beta_i^*\Phi_i(0)\exp\big[-d_i^*t\big]\ ,\quad i = 1,\ 2\ ,$$

and hence by Gronwall's inequality,

$$(2.10)\qquad B_i(t) \le \beta_i^*\Phi_i(0)\exp\big[\delta_it\big]\ ,\quad \delta_i = \beta_i^* - d_i^*\ .$$

(2.5), (2.6) and (2.10) lead to

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$$(2.11)\quad |P_i(t)-\Phi_i(0)| \le \int_0^t \beta_i^*\Phi_i(0)\exp[\delta_i a-d_i^*(t-a)]da + \int_0^\infty \varphi_i(a,\ 0)|1-\exp(-d_i^*t)|da$$

$$\le \beta_i^*\Phi_i(0)\exp(\beta_i^*t)\left\{\frac{1-\exp[-(d_i^*+\beta_i^*)t]}{d_i^*+\beta_i^*}\right\} + \Phi_i(0)d_i^*t$$

$$\le [\beta_i^*\Phi_i(0)\exp(\beta_i^*t)+\Phi_i(0)d_i^*]t \quad \text{for} \quad t > 0 .$$

We can now prove the following result on the existence and uniqueness of solutions of the integral equations (2.6)-(2.8).

THEOREM 2. *Assume that the system* (1.1)-(1.6) *satisfies the hypotheses* A_1, A_2, A_3. *Then there exists a unique set of continuous functions* $(P_1,\ P_2,\ B_1,\ B_2)$ *such that*

$$P_i : \mathbf{R}^+ \to \mathbf{R}^+ ,\quad B_i : \mathbf{R}^+ \to \mathbf{R}^+ \quad (i = 1,\ 2) ,$$

which satisfy the integral equations (2.6)-(2.8).

Proof. We will first show the existence of local solutions on some (possibly small) interval $[0,\ T] \subset \mathbf{R}^+$ such that

$$P_i \in C([0,\ T],\ \mathbf{R}^+) ,\quad B_i \in C([0,\ T],\ \mathbf{R}^+) ,\quad i = 1,\ 2 ,$$

satisfying (2.6)-(2.8) and then show the P_i and B_i can be continued as solutions for any finite interval in $\mathbf{R}^+$.

For some fixed positive number T we let

$$C^+[-\tau,\ T] = \{f \in C([-\tau,\ T],\ \mathbf{R}) \mid f \ge 0\} .$$

Let $\|\cdot\|_T$ denote the supremum norm in $C^+[-\tau,\ T]$. Then for any $(x,\ y) \in C^+[-\tau,\ T] \times C^+[-\tau,\ T]$ we define

$$\|(x,\ y)\| = \|x\|_T + \|y\|_T ,$$

$$C_T = C^+[-\tau,\ T] ,\quad C_T^2 = C^+[-\tau,\ T] \times C^+[-\tau,\ T] .$$

Members of C_T will be denoted by z_t with the meaning that $z(t+s) = z_t(s)$ for $s \in [-\tau,\ 0]$ and $t \in [0,\ T]$. Now for any fixed

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$P_t = (P_{1t}, P_{2t}) \in C_T^2$, (2.8) is a linear system of uncoupled Volterra integral equations in $B = (B_1, B_2)$ and hence (2.8) will have a unique continuous solution under the assumptions A₁-A₃. Let us denote such a solution by

$$B(t) = B^T(P_t) \ , \quad t \in [0, T] \ ,$$

or

$$B_1(t) = B_1^T(P_{1t}, P_{2t}) \ , \quad B_2(t) = B_2^T(P_{1t}, P_{2t}) \ , \quad t \in [0, T] \ .$$

If we supply this solution (B_1, B_2) in (2.6) we find that (2.6) will be satisfied if and only if (P_{1t}, P_{2t}) is a fixed point of the operator

$$\Pi(P_t) = \{\Pi_1(P_{1t}, P_{2t}), \Pi_2(P_{1t}, P_{2t})\}$$

where Π_1 and Π_2 respectively denote the right sides of (2.6) for $i = 1, 2$. It is not difficult to see from the nature of M_i, L_i and the hypotheses on f_i, b_i, φ_i that

$$B : C_T^2 \to C_T^2 \quad \text{and} \quad \Pi : C_T^2 \to C_T^2$$

(which guarantees the nonnegativity of P_i and B_i). We will first show that there exist positive constants r^*, t^* such that Π is a mapping of a sphere

$$S_{t^*}(\Phi, r^*) = \left\{P_t = (P_{1t}, P_{2t}) \in C_{t^*}^2 \mid \|P_t - \Phi_t\|_{t^*} \le r^*\right\}$$

into itself and also is a contraction where Φ_t is defined on $[-\tau, t^*]$ by the following:

(2.12)
$$\Phi_t = (\Phi_{1t}, \Phi_{2t}) \ ;$$

$$\Phi_{it} = \begin{cases} \int_0^\infty \varphi_i(a, s)da & \text{for} \quad s \in [-\tau, 0] \ , \\ \int_0^\infty \varphi_i(a, 0)da & \text{for} \quad s \in [0, t^*] \ . \end{cases}$$

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We note that similar to (2.11) one gets the estimates

$$|\Pi_i(P)(t)-\Phi_i(0)| \le \{\beta_i^*\Phi_i(0)\exp[\beta_i^* t]+\Phi_i(0)d_i^*\}t$$

which together with (2.7) and (2.12) lead to

$$\|\Pi(P_t)-\Phi_t\|_{t^*} \le \left(\sum_{j=1}^{2} \|\Phi_{jt}\|_{t^*}[\beta_j^* \exp(\beta_j^* t)+d_i^*]\right)t^* . \tag{2.13}$$

Thus if we choose

$$r^* = T\sum_{j=1}^{2} \|\Phi_{jt}\|_t[\beta_j^* \exp(\beta_j^* T)+d_j^*]$$

then Π is a mapping of $S_{t^*}(\Phi, r^*)$ into itself for all $t^* \le T$. We then will have to show that for small $t^* > 0$, Π is a contraction.

Let $P_t^{(1)}$ and $P_t^{(2)}$ be arbitrarily chosen in $S_{t^*}(\Phi, r^*)$ and consider $\left|\Pi_1\left(P_t^{(1)}\right)-\Pi_1\left(P_t^{(2)}\right)\right|$ for $t \le t^*$. Corresponding to the chosen $P_t^{(1)}$, $P_t^{(2)}$ we let $B^{(1)}(a) = B\left(P_t^{(1)}\right)$ and $B^{(2)}(a) = B\left(P_t^{(2)}\right)$. Then from (2.6),

$$\begin{aligned}\left|\Pi_1(P^{(1)}(t))-\Pi_1(P^{(2)}(t))\right| &\le \left|\int_0^t B_1^{(1)}(a)\left\{M_1\left(a, t, P_t^{(1)}\right)-M_1\left(a, t, P_t^{(2)}\right)\right\}da\right| \\ &+ \left|\int_0^t \left[B_1^{(1)}(a)-B_2^{(2)}(a)\right]M_1\left(a, t, P_t^{(2)}\right)da\right| \\ &+ \left|\int_0^t \varphi_1(a, 0)\left[L_1\left(a, t, P_t^{(1)}\right)-L_1\left(a, t, P_t^{(2)}\right)\right]da\right| \\ &= J_1 + J_2 + J_3 \quad \text{(say)}.\end{aligned}$$

Using the elementary inequality

$$|e^x-e^y| \le |x-y| \quad \text{for } x, y \le 0$$

we derive from (2.5) that

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$$\left|M_1\left(a,\ t,\ P_t^{(1)}\right)-M_1\left(a,\ t,\ P_t^{(2)}\right)\right|$$

$$\le \int_0^{t-a} \left|f_1\left(s,\ P_t^{(1)}(a+s)\right)-f_1\left(s,\ P_t^{(2)}(a+s)\right)\right|ds$$

$$\le d_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} \quad \text{(using A}_1\text{)}.$$

Now, using (2.10),

$$|J_1| \le \int_0^t \beta_i^*\Phi_1(0)e^{\delta_1 a}\left(\int_0^{t-a} d_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}ds\right)da$$

$$\le d_1\beta_1^*\Phi_1(0)t^2\left\|P_t^{(1)}-P_t^{(2)}\right\|e^{\delta_1 t}/2 .$$

In a similar way

$$|J_3| \le \int_0^\infty \varphi_1(a,\ 0)\left[\int_0^t \left|f_1\left(a+s,\ P_t^{(1)}(s)\right)-f_1\left(a+s,\ P_t^{(2)}(s)\right)\right|ds\right]da$$

$$\le d_1\Phi_1(0)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}t .$$

Now we have to estimate $\left|B_1^{(1)}(a)-B_1^{(2)}(a)\right|$ in order to estimate J_2 ; from (2.8),

$$B_1^{(1)}(a) - B_1^{(2)}(a)$$

$$= \int_0^a \left[B_1^{(1)}(\sigma)-B_1^{(2)}(\sigma)\right]b_1\left(a-\sigma,\ P_t^{(1)}(a)\right)M_1\left(\sigma,\ a,\ P_t^{(1)}(a)\right)d\sigma + \int_0^a B_1^{(2)}(\sigma)$$

$$\times \left[b_1\left(a-\sigma,\ P_t^{(1)}(a)\right)M_1\left(\sigma,\ a,\ P_t^{(1)}(a)\right)-b_1\left(a-\sigma,\ P_t^{(2)}(a)\right)M_1\left(\sigma,\ a,\ P_t^{(2)}(a)\right)\right]d\sigma$$

$$+ \int_0^\infty \varphi_1(\sigma,\ 0)\left[b_1\left(\sigma+a,\ P_t^{(1)}(a)\right)-b_1\left(\sigma+a,\ P_t^{(2)}(a)\right)\right]L_1\left(\sigma,\ a,\ P_t^{(1)}(a)\right)d\sigma$$

$$+ \int_0^\infty \varphi_1(\sigma,\ 0)b_1\left(\sigma+a,\ P_t^{(2)}(a)\right)\left[L_1\left(\sigma,\ a,\ P_t^{(1)}(a)\right)-L_1\left(\sigma,\ a,\ P_t^{(2)}(a)\right)\right]d\sigma$$

$= R_1 + R_2 + R_3 + R_4$ (say).

By the uniform Lipschitz continuity of b_1 in A₂ we get

$$\left|b_1\left(a+\sigma,\ P_t^{(1)}(a)\right)-b_1\left(\sigma+a,\ P_t^{(2)}(a)\right)\right| \le \beta_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} \quad \text{for} \quad a \in [0,\ t^*]$$

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and hence we have

$$|R_3(a)+R_4(a)| \le \beta_1\Phi_1(0)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} + \Phi_1(0)\beta_1 d_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} a ,$$

$$|R_2(a)| = \left[\int_0^a \left[B_1^{(2)}(\sigma)\left\{b_1\left(a-\sigma, P_t^{(1)}(a)\right)-b_1\left(a-\sigma, P_t^{(2)}(a)\right)\right\}M_1\left(\sigma, a, P_t^{(1)}(a)\right)\right.\right.$$
$$\left.\left. +b_1\left(a-\sigma, P_t^{(2)}(a)\right)\left\{M_1\left(\sigma, a, P_t^{(1)}(a)\right)-M_1\left(\sigma, a, P_t^{(2)}(a)\right)\right\}\right]d\sigma\right]$$
$$\le \int_0^a \left[\beta_1^*\Phi_1(0)e^{\delta_1 a}\beta_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}+\beta_1 d_1\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}(a-\sigma)\right]d\sigma$$
$$\le \beta_1^*\Phi_1(0)e^{\delta_1 a}\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}\left\{\beta_1 a+d_1 a^2/2\right\} .$$

Thus

$$\left|B_1^{(1)}(a)-B_1^{(2)}(a)\right|$$
$$\le \int_0^a \left|B_1^{(1)}(\sigma)-B_1^{(2)}(\sigma)\right|\beta_1^* d\sigma$$
$$+ \Phi_1(0)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}\left\{\beta_1+\beta_2 d_1 a+\beta_1^*\left(\beta_2 a+d_1 a^2/2\right)e^{\delta_1 a}\right\}$$
$$\le \beta_1^* \int_0^a \left|B_1^{(1)}(\sigma)-B_1^{(2)}(\sigma)\right|d\sigma + \left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} g_1(a)$$

where $g_1(a) \to \beta_1$ as $a \to 0$. By Gronwall's inequality it will follow that

$$\left|B_1^{(1)}(a)-B_1^{(2)}(a)\right| \le \left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*}\{g_1(a)+O(a)\} .$$

Using this estimate for $R_1(a)$ we get

$$|R_1(a)| \le \left|\int_0^a \left[B_1^{(1)}(\sigma)-B_1^{(2)}(\sigma)\right]b_1\left(a-\sigma, P_t^{(1)}(a)\right)M_1\left(\sigma, a, P_t^{(1)}(a)\right)d\sigma\right|$$
$$\le \beta_1^*\left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} O(a) \quad \text{as} \quad a \to 0 .$$

Thus

$$\left|B_1^{(1)}(a)-B_1^{(2)}(a)\right| \le \left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} O(1) \quad \text{as} \quad a \to 0$$

and hence

$$\left|\Pi_1\left(P_t^{(1)}\right)-\Pi_1\left(P_t^{(2)}\right)\right| \le \left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} O(t) \quad \text{as} \quad t \to 0$$

which together with a similar bound for $\left|\Pi_2\left(P_t^{(1)}\right)-\Pi_2\left(P_t^{(2)}\right)\right|$ leads to

$$\left\|\Pi\left(P_t^{(1)}\right)-\Pi\left(P_t^{(2)}\right)\right\| \le \left(r^*+\|\Phi_t\|_{t^*}\right)\left\|P_t^{(1)}-P_t^{(2)}\right\|_{t^*} O(t^*)$$

as $t^* \to 0$ showing that if t^* is small enough, the mapping Π on $S_{t^*}(\Phi, r^*)$ is a contraction. Hence the system (2.6)-(2.8) has a unique solution for $0 \le t \le t^*$ for t^* sufficiently small and positive.

Now if $[0, T]$ is any finite interval on $\mathbb{R}^+$, we can consider $[0, T]$ as a finite union of intervals of length less than or equal to t^*. Since the estimate (2.11) is valid for any finite interval we can extend the solution of (2.6)-(2.8) from $[0, t^*]$ to $[0, T]$ and this completes the proof.

3. Stationary age distributions and their linear stability

We will now establish the existence of time independent solutions ρ_1^*, ρ_2^* of (1.1)-(1.6); such solutions satisfy

$$\text{(3.1)} \qquad \frac{d\rho_i^*(a)}{da} + f_i\left(a, P_1^*, P_2^*\right)\rho_i^*(a) = 0 \;, \quad i = 1, 2 \;, \quad a > 0 \;,$$

$$\text{(3.2)} \qquad P_i^* = \int_0^\infty \rho_i^*(a)da \;, \quad i = 1, 2 \;,$$

$$\text{(3.3)} \qquad \rho_i^*(0) = \int_0^\infty b_i\left(a, P_1^*, P_2^*\right)\rho_i^*(a)da \;, \quad i = 1, 2 \;.$$

All solutions of (3.1) are of the form

$$\text{(3.4)} \quad \rho_i^*(a) = \rho_i^*(0)\exp\left[-\int_0^a f_i\left(s, P_1^*, P_2^*\right)ds\right] \;, \quad i = 1, 2 \;, \quad a \ge 0 \;,$$

which together with (3.3) lead to

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$$
(3.5)\qquad
\begin{aligned}
1 &= \int_0^\infty b_1(a,\ P_1^*,\ P_2^*)\exp\left[-\int_0^a f_1(s,\ P_1^*,\ P_2^*)ds\right]da\ ,\\
1 &= \int_0^\infty b_2(a,\ P_1^*,\ P_2^*)\exp\left[-\int_0^a f_2(s,\ P_1^*,\ P_2^*)ds\right]da\ .
\end{aligned}
$$

Thus the existence of stationary solutions of (1.1)-(1.6) reduces to the existence of a pair of positive constants P_1^*, P_2^* satisfying (3.5). We can now prove the following.

THEOREM 3. *Assume that* f_i *and* b_i *satisfy* (A_1) *and* (A_2) *and let*

$$
(3.6)\quad F_i(P_1,\ P_2) = \int_0^\infty b_i(a,\ P_1,\ P_2)\exp\left[-\int_0^a f_i(s,\ P_1,\ P_2)ds\right]da\ ,\qquad i = 1,\ 2\ ,\quad P_1 \ge 0\ ,\quad P_2 \ge 0\ ,
$$

and suppose the following hold:

(3.7) A_4. $F_i(0,\ 0) > 1$, $i = 1,\ 2$;

A_5. *there exists a positive constant* C *for which*

$$
(3.8)\qquad
\begin{aligned}
F_1(C,\ 0) &< F_2(C,\ 0)\ ,\\
F_1(0,\ C) &> F_2(0,\ C)\ .
\end{aligned}
$$

Then there exists a unique pair $(P_1^*,\ P_2^*)$ *of real numbers* $P_1^* > 0$, $P_2^* > 0$ *such that*

$$
(3.9)\qquad F_1(P_1^*,\ P_2^*) = 1 = F_2(P_1^*,\ P_2^*)
$$

and the unique nonnegative solution of (3.1)-(3.3) *is given by*

(3.10)

$$
\rho_i^*(a) = \left(P_i^*\ \exp\left[-\int_0^a f_i(s,\ P_1^*,\ P_2^*)ds\right]\right)\Big/\left(\int_0^\infty \exp\left[-\int_0^a f_i(s,\ P_1^*,\ P_2^*)ds\right]da\right)\ ,\qquad i = 1,\ 2\ ,\quad a \ge 0\ .
$$

Proof. Consider the elements of the surfaces defined by

$$
z = F_1(P_1,\ P_2)\ ,\quad z = F_2(P_1,\ P_2)\ ,\quad P_1 \ge 0\ ,\quad P_2 \ge 0\ ,
$$

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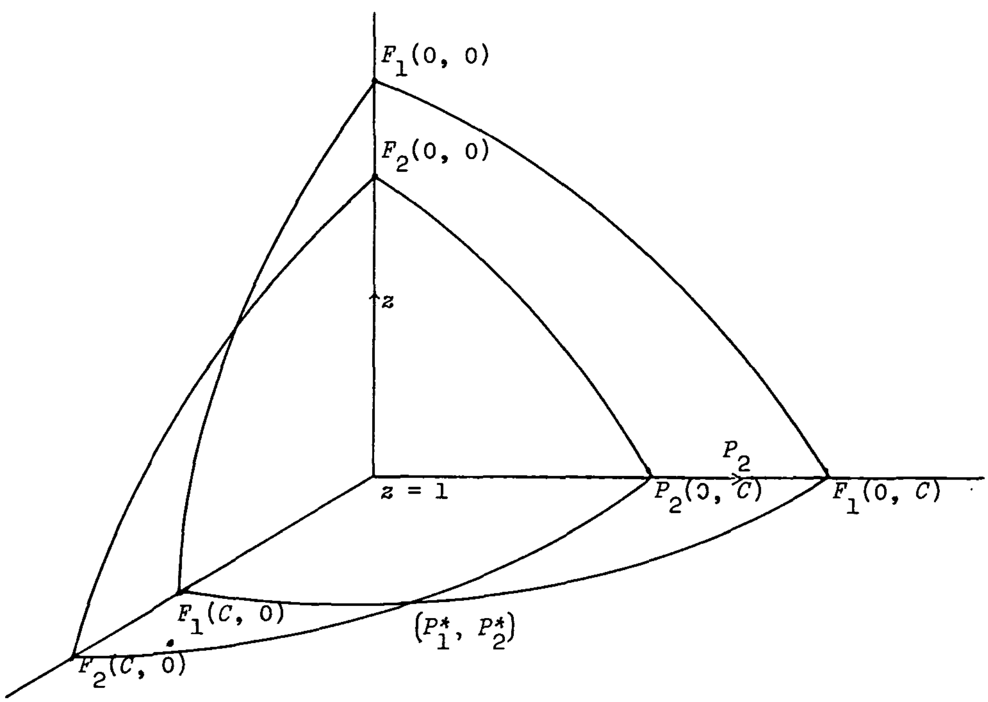
in the (P_1, P_2, z) space. By hypothesis (A₁) we have $\partial F_i/\partial P_j < 0$ and, by (A₂), $\partial b_i/\partial P_j \le 0$ for all $P_1 \ge 0$, $P_2 \ge 0$, $i = 1, 2$, $j = 1, 2$. Hence by (A₄) the intersections of these surfaces with the plane $z = 1$ define two curves on the $z = 1$ plane connecting the lines $\{z = 1, P_1 = 0, P_2 \ge 0\}$ and $\{z = 1, P_2 = 0, P_1 \ge 0\}$. These two curves are defined by

$$F_1(P_1, P_2) = 1 \text{ and } F_2(P_1, P_2) = 1 , \quad P_1, P_2 \ge 0 ,$$

which by (A₅) will intersect at a unique point say (P_1^*, P_2^*) with $P_1^* > 0$, $P_2^* > 0$ (see figure). The uniqueness of the point (P_1^*, P_2^*) is a consequence of the smoothness of the surfaces $z = F_1(P_1, P_2)$ and $z = F_2(P_1, P_2)$.



(The figure corresponds to the case $F_1(0, 0) > F_2(0, 0) > 1$. The other possibility $1 < F_1(0, 0) \le F_2(0, 0)$ is treated similarly.) It will now follow that for such a pair (P_1^*, P_2^*) the unique nonnegative solution of (3.1)-(3.3) is given by (3.10).

Now to examine the linear stability of the stationary age distributions ρ_1^*, ρ_2^* we let

$$(3.11)\quad \begin{cases} \rho_i(a, t) = \rho_i^*(a) + u_i(a, t) , \\ P_i(t) = P_i^* + p_i(t) , \quad i = 1, 2 , \quad a > 0 , \quad t > 0 , \\ p_i(t) = \int_0^\infty u_i(a, t)da , \end{cases}$$

in (1.1)-(1.5) and derive the following variational system after neglecting the nonlinear terms in the perturbations u_i and p_i $(i = 1, 2)$. (Such a procedure of linear stability analysis can be justified as has been done in Gurtin and MacCamy [4].)

$$(3.12)\quad \begin{cases} Du_i(a, t) = -f_i(a, P_1^*, P_2^*)u_i(a, t) - \rho_i^*(a)\left\{\sum_{i=1}^{2} \frac{\partial f_i}{\partial P_j^*} p_{ij}(t)\right\} , \\ u_i(0, t) = \int_0^\infty b_i(a, P_1^*, P_2^*)u_i(a, t)da + \int_0^\infty \rho_i^*(a)\left\{\sum_{j=1}^{2} \frac{\partial b_i}{\partial P_j^*} p_{ij}(t)\right\}da \end{cases}$$

where $i = 1, 2$ and

$$(3.13)\quad \begin{aligned} p_{11}(t) &= p_1(t) , & p_{12}(t) &= p_2(t-\tau) , \\ p_{21}(t) &= p_1(t-\tau) , & p_{22}(t) &= p_2(t) . \end{aligned}$$

To consider the asymptotic behaviour as $t \to \infty$ of solutions of (3.12) we let

$$(3.14)\quad \begin{cases} u_i(a, t) = \xi_i(a)\exp[\lambda t] , \quad \xi_i(a) \to 0 \text{ as } a \to \infty , \\ p_i(t) = p_i^* \exp[\lambda t] , \qquad i = 1, 2 , \quad a > 0 , \quad t > 0 , \\ p_i^* = \int_0^\infty \xi_i(a)da . \end{cases}$$

Using (3.14) in (3.12)-(3.13),

$$\frac{d\xi_i}{da} + \lambda\xi_i = -f_i\left(a,\ P_1^*,\ P_2^*\right)\xi_i(a) - \rho_i^*(a)\left\{\sum_{j=1}^{2} \frac{\partial f_i}{\partial P_j^*} p_{ij}^*\right\} ,$$

(3.15)

$$\xi_i(0) = \int_0^\infty b_i\left(a,\ P_1^*,\ P_2^*\right)\xi_i(a)da + \int_0^\infty \rho_i^*(a)\left\{\sum_{j=1}^{2} \frac{\partial b_i}{\partial P_j^*} p_{ij}^*\right\}da ,$$

where $i = 1, 2$, and

$$p_{11}^* = p_1^* ,\quad p_{12}^* = p_2^* \exp\{-\lambda\tau\} ,$$

$$p_{21}^* = p_1^* \exp\{-\lambda\tau\} ,\quad p_{22}^* = p_2^* .$$

If we integrate the first of (3.15) and use the fact that $\xi_i(a) \to 0$ as $a \to \infty$ we can derive that p_1^* and p_2^* are governed by

$$(3.16)\quad \lambda p_1^* - \int_0^\infty \rho_1^*(a)\left[\left(\frac{\partial b_1}{\partial P_1^*} - \frac{\partial f_1}{\partial P_1^*}\right)p_1^* + \left(\frac{\partial b_1}{\partial P_2^*} - \frac{\partial f_1}{\partial P_2^*}\right)p_2^* e^{-\lambda\tau}\right]da$$

$$= \int_0^\infty \left[b_1\left(a,\ P_1^*,\ P_2^*\right)-f_1\left(a,\ P_1^*,\ P_2^*\right)\right]\xi_1(a)da ,$$

$$(3.17)\quad \lambda p_2^* - \int_0^\infty \rho_2(a)\left[\left(\frac{\partial b_2}{\partial P_1^*} - \frac{\partial f_2}{\partial P_1^*}\right)p_1^* e^{-\lambda\tau} + \left(\frac{\partial b_2}{\partial P_2^*} - \frac{\partial f_2}{\partial P_2^*}\right)p_2^*\right]da$$

$$= \int_0^\infty \left[b_2\left(a,\ P_1^*,\ P_2^*\right)-f_2\left(a,\ P_1^*,\ P_2^*\right)\right]\xi_2(a)da .$$

From the first of (3.15) we get

$$(3.18)\quad \xi_i(a) = \left\{\xi_i(0)\rho_i^*(a)/\rho_i^*(0)\exp[\lambda a]\right\}$$

$$- \rho_i^*(a)\exp[-\lambda a] \int_0^a \left\{\sum_{j=1}^{2} \frac{\partial f_i}{\partial P_j^*} p_{ij}^*\right\}e^{\lambda s}ds ,\quad i = 1, 2 ,$$

which by the second of (3.15) becomes,

$$(3.19)\quad \xi_i(a) = \left[\rho_i^*(a)/\rho_i^*(0)c_i \exp(\lambda a)\right]\left[\int_0^\infty \rho_i^*(a)\left\{\sum_{j=1}^{2} \frac{\partial b_i}{\partial P_j^*} p_{ij}^*\right\}da\right.$$

$$\left. - \int_0^\infty b_i\left(a,\ P_1^*,\ P_2^*\right)\rho_i^*(a)e^{-\lambda a}\left\{\int_0^a \left(\sum_{j=1}^{2} \frac{\partial f_i}{\partial P_j^*} p_{ij}^*\right)e^{\lambda s}ds\right\}da\right]$$

$$- \rho_i^*(a)e^{-\lambda a} \int_0^a \left\{\sum_{j=1}^{2} \frac{\partial f_i}{\partial P_j^*} p_{ij}^*\right\}e^{\lambda s}ds ,\quad i = 1, 2 ,$$

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where

$$(3.20)\quad c_i = 1 - \frac{1}{\rho_i^*(0)} \int_0^\infty b_i\left(a,\ P_1^*,\ P_2^*\right)\rho_i^*(a)e^{-\lambda a}da\ ,\quad i = 1,\ 2\ .$$

Now supplying $\xi_1(a)$ and $\xi_2(a)$ from (3.19) in (3.16)-(3.17) we derive that

$$(3.21)\quad \begin{aligned} &(\lambda-A_{11})p_1^* - A_{12}p_2^* \exp(-\lambda\tau) = g_{11}(\lambda)p_1^* + g_{12}(\lambda)p_2^* \exp(-\lambda\tau)\ , \\ &-A_{21}p_1^* \exp(-\lambda\tau) + (\lambda-A_{22})p_2^* = g_{21}(\lambda)p_1^* \exp(-\lambda\tau) + g_{22}(\lambda)p_2^*\ , \end{aligned}$$

where

$$(3.22)\quad A_{ij} = \int_0^\infty \rho_i^*(a)\left[\frac{\partial b_i}{\partial P_j^*} - \frac{\partial f_i}{\partial P_j^*}\right]da\ ,$$

$$\begin{aligned}(3.23)\quad g_{ij}(\lambda) = {}& \left[\rho_i^*(0)c_i\right]^{-1}\left\{\int_0^\infty \sigma_i(a)\rho_i^*(a)e^{-\lambda a}da\right\} \\ & \times \left\{\int_0^\infty \left[\rho_i^*(a)\ \frac{\partial b_i}{\partial P_j^*} - b_i\left(a,\ P_1^*,\ P_2^*\right)\rho_i^*(a)e^{-\lambda a}\left(\int_0^a \frac{\partial f_i}{\partial P_j^*}\ e^{\lambda s}ds\right)\right]da\right\} \\ & - \int_0^\infty \sigma_i(a)\rho_i^*(a)e^{-\lambda a}\left(\int_0^a \frac{\partial f_i}{\partial P_j^*}\ e^{\lambda s}ds\right)da\ ,\quad i,\ j = 1,\ 2\ ,\end{aligned}$$

$$(3.24)\quad \sigma_i(a) = b_i\left(a,\ P_1^*,\ P_2^*\right) - f_i\left(a,\ P_1^*,\ P_2^*\right)\ ,\quad i = 1,\ 2\ .$$

To solve the linear perturbational system (3.12) it is enough to find the constants $\lambda,\ p_1^*,\ p_2^*$ satisfying (3.21) since one can then use (3.19) to find the perturbations from (3.14). A nontrivial solution $\left(p_1^*,\ p_2^*\right)$ for (3.21) will exist if and only if λ is a root of the equation

$$\det\begin{bmatrix} \lambda-\left(A_{11}+g_{11}(\lambda)\right) & -\left(A_{12}+g_{12}\right)e^{-\lambda\tau} \\ -\left(A_{21}+g_{21}\right)e^{-\lambda\tau} & \lambda-\left(A_{22}+g_{22}(\lambda)\right) \end{bmatrix} = 0$$

or equivalently

$$(3.25)\quad \lambda^2 - \lambda\left(A_{11}+A_{22}\right) + A_{11}A_{22} - A_{12}A_{21}\exp[-2\lambda\tau] = \lambda S_1(\lambda) + S_2(\lambda,\ \tau)$$

where

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$$S_1(\lambda) = g_{11}(\lambda) + g_{22}(\lambda) ,$$

$$S_2(\lambda, \tau) = [A_{21}g_{12}(\lambda)+A_{12}g_{21}(\lambda)+g_{12}(\lambda)g_{21}(\lambda)]\exp[-2\lambda\tau] - A_{11}g_{22}(\lambda) - A_{22}g_{11}(\lambda) - g_{11}(\lambda)g_{22}(\lambda) .$$

The following result establishes the linear local asymptotic stability of the stationary age distributions $\rho_1^*(a)$ and $\rho_2^*(a)$.

THEOREM 4. *Assume the following:*

A6. $0 < \beta_i^* < d_i^*$ $(i = 1, 2)$ (*see* (A1) *and* (A2)) ;

A7. $\{A_{11}+A_{22}+\|S_1(0)\|\}^2 < 4\{(A_{11}A_{22}-A_{12}A_{21})-\|S_2(0)\|\}$,

$$\|S_1(0)\| = |g_{11}(0)| + |g_{22}(0)| ,$$

$$\|S_2(0)\| = |A_{11}g_{12}(0)| + |A_{12}g_{21}(0)| + |g_{12}(0)g_{21}(0)| + |A_{11}g_{22}(0)| + |A_{22}g_{11}(0)| + |g_{11}(0)g_{22}(0)| .$$

Then all the roots of (3.25) *have negative real parts and hence the perturbations* $u_i(a, t) = \xi_i(a)\exp[\lambda t] \to 0$ *as* $t \to \infty$ *for* $i = 1, 2$ *and* $a \geq 0$.

Proof. Define $F_1(\lambda, \tau)$ and $F_2(\lambda, \tau)$ as follows:

$$F_1(\lambda, \tau) = \lambda^2 - \lambda(A_{11}+A_{22}) + A_{11}A_{22} - A_{12}A_{21} \exp(-2\lambda\tau) ;$$

$$F_2(\lambda, \tau) = \lambda S_1(\lambda) + S_2(\lambda, \tau) .$$

Using (A6) one can show that for λ with $\text{Re}(\lambda) \geq 0$, c_1 and c_2 are positive and bounded away from zero. Now since $A_{ij} > 0$ and $\tau \geq 0$ we find from the nature of the dependence of g_{ij} on λ that for all $\lambda = \mu \pm i\omega$ with $\mu \geq 0$ and $\omega \geq 0$ we have

$$(3.26) \quad |F_1(\lambda, \tau)-F_2(\lambda, \tau)| \geq |F_1(\lambda, 0)| - |F_2(\lambda, \tau)| \geq |\lambda|^2 - |\lambda|\{A_{11}+A_{22}+\|S_1(0)\|\} + \{A_{11}A_{22}-A_{12}A_{21}-\|S_2(0, \tau)\|\} \geq [(|\lambda|-p)^2+q]^2$$

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where

$$p = \{A_{11}+A_{22}+\|S_1(0)\|\}/2 ,$$

$$q = \left\{4\left|\left(A_{11}A_{22}-A_{12}A_{21}\right)-\|S_2(0, \tau)\|\right|-\left|A_{11}+A_{22}+\|S_1(0)\|\right|^2\right\}/2 .$$

It will now follow, from (A) and (3.26), $F_1(\lambda, \tau) = F_2(\lambda, \tau)$ cannot have roots with zero or positive real parts and this completes the proof.

In conclusion we remark that the condition (3.7) means that the net reproduction rates of each species is greater than unity; a condition of this type is well known in age dependent populations. (3.8) can be interpreted to mean that the intraspecific competitive inhibition is higher than that of the interspecific interaction. The conditions of Theorem 4 are analytical and do not lend themselves for any worthwhile interpretation in terms of the model parameters.

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