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A predator-prey diffusion model in age-dependent population dynamics

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1. Introduction

In this paper we study an age-dependent predator-prey model with spatial movement in which the predator species has a tendency to eat the prey species in the specific age-interval. Age-dependent diffusion models for a single biological species were first proposed by Gurtin [4], where the population density of the species $u = u(a, t, x)$ is governed by the following:

$$Du + \lambda u = k\Delta u \tag{1.1}$$

with the boundary condition at $a = 0$

$$u(0, t, x) = \int_0^\infty \beta u(a, t, x)\, da\,. \tag{1.2}$$

Here a stands for age, t for time and x for spatial position. The operator $\boldsymbol{D}$ is defined by

$$(\boldsymbol{D}u)(a, t, x) = \lim_{h\to 0} \frac{1}{h}(u(a + h, t + h, x) - u(a, t, x))\,. \tag{1.3}$$

The functions λ and β denote the death modulus and the birth modulus of the population, respectively, both of which in general depend on a, t, x, u itself and the total population density

$$P(t, x) = \int_0^\infty u(a, t, x)\, da\,. \tag{1.4}$$

The equation (1.1) is the so-called balance equation and (1.2) describes the birth process of the species.

Nonlinear age-dependent population models (including several interacting populations) without spatial diffusion have been studied by many authors (see, for instance, Gurtin and MacCamy [5], Webb [11] and the references therein). The existence and uniqueness of solutions in age-dependent diffusion models for a single species has been also investigated (see, for instance, Busenberg and Iannelli [1], Di Blasio [2], Kunisch, Schappacher and Webb [7] and MacCamy

[8]). Among them, in [1] and [8] several types of nonlinear diffusion terms are treated and the asymptotic behavior of solutions is also investigated.

We extend such models so as to describe the predator-prey interaction in age-dependent diffusion problems. Suppose that the spatial domain is a one-dimensional bounded open interval $(0, l)$. Let $u(a, t, x)$ and $v(t, x)$ denote the population density of the prey and the predator, respectively. Here we neglect the age-dependence of the predator. Then, our model consists of

$$Du + \left(\lambda_1 + \lambda_2 P + \frac{\mu(a)v}{1+Q}\right)u = k_1 u_{xx} \quad (a > 0, 0 < x < l) \tag{1.5}$$

and

$$v_t + \left(\varepsilon_1 + \varepsilon_2 v - \frac{1}{1+Q}\int_0^\infty c(a)\mu(a)u\,da\right)v = k_2 v_{xx} \quad (0 < x < l) \tag{1.6}$$

with $P(t, x)$ defined by (1.4) and

$$Q(t, x) = \int_0^\infty \mu(a)h(a)u(a, t, x)\,da\,. \tag{1.7}$$

Here $\mu(a)$ denotes the intrinsic predation rate, $c(a)$ shows the effect of the predation on the growth rate of the predator and $Q(t, x)$ means the average "quantity" (the total number counted with the weighted function $h(a)$) of the prey which could be eaten by a predator in absence of the limitations of its digestive capacity. The total predation "quantity" per predator is assumed to be bounded and $Q(t, x)$ is so normalized that its supremum should be one. The functional form of the predation term $\mu(a)uv/(1 + Q)$ in our model is based on the cannibalism model of Diekmann, Nisbet, Gurney and van den Bosch [3]. From a biological point of view, we require that $u(a, t, x) \geq 0$ and $v(t, x) \geq 0$. We study the equations (1.4)–(1.7) supplemented with the boundary conditions

$$u(0, t, x) = \int_0^\infty \beta(a, P(t, x))u(a, t, x)\,da\,, \tag{1.8}$$

$$u_x(a, t, x) = v_x(t, x) = 0 \qquad (x = 0, l) \tag{1.9}$$

and the initial conditions

$$u(a, 0, x) = u_0(a, x) \geq 0\,, \qquad v(0, x) = v_0(x) \geq 0\,. \tag{1.10}$$

This paper proceeds as follows: In Section 2, we consider the initial-boundary value problem (1.4)–(1.10). By the integration of the equation for u along the characteristics $a - t = \text{constant}$, we transform the problem into a system of integral equations for P, Q, v and $B(t, x) = u(0, t, x)$ and prove the global existence and uniqueness of regular solutions. In Section 3, we find spatially homogeneous stationary solutions of the form $(\bar{u}(a), 0)$ which correspond to the extinction of the predator, and investigate their local stability. Let us give a brief explanation of our results under the assumption $\beta(a, P) \equiv \beta(a)$. Define by

$$N = \int_0^\infty \beta(a)e^{-\lambda_1 a}\, da \tag{1.11}$$

the net reproductive rate of the prey population at the trivial solution $(0, 0)$. If $N < 1$, then

$$\lim_{t\to\infty} P(t, x) = \lim_{t\to\infty} v(t, x) = 0\,,$$

that is, both of the species become extinct. If $N > 1$, then $(0, 0)$ is unstable and there exists a unique stationary solution of the form $(\bar{u}(a), 0)$ with $\bar{u}(a) > 0$. Let

$$\bar{S} = \frac{1}{1 + \bar{Q}} \int_0^\infty c(a)\mu(a)\bar{u}(a)\, da - \varepsilon_1 \tag{1.12}$$

with

$$\bar{Q} = \int_0^\infty \mu(a)h(a)\bar{u}(a)\, da\,. \tag{1.13}$$

$\bar{S}$ is the growth rate of the predator population at $(\bar{u}(a), 0)$. If $\bar{S} < 0$, then $(\bar{u}(a), 0)$ is stable, while, if $\bar{S} > 0$, then it is unstable.

2. Existence and uniqueness

In this section we consider the initial-boundary value problem

$$\begin{cases} \boldsymbol{D}u + \left(\lambda_1 + \lambda_2 P(t, x) + \dfrac{\mu(a)v}{1 + Q(t, x)}\right)u = k_1 u_{xx} & (a > 0, 0 < x < l) \\ v_t + \left(\varepsilon_1 + \varepsilon_2 v - \dfrac{1}{1 + Q(t, x)} \displaystyle\int_0^\infty c(a)\mu(a)u\, da\right)v = k_2 v_{xx} & (0 < x < l) \end{cases} \tag{2.1}$$

$$\begin{cases} u(0, t, x) = \displaystyle\int_0^\infty \beta(a, P(t, x))u(a, t, x)\, da & (0 < x < l) \\ u_x(a, t, 0) = u_x(a, t, l) = 0 & (a > 0) \\ v_x(t, 0) = v_x(t, l) = 0 & \end{cases} \tag{2.2}$$

$$\begin{cases} u(a, 0, x) = u_0(a, x) & (a \ge 0, 0 \le x \le l) \\ v(0, x) = v_0(x) & (0 \le x \le l)\,, \end{cases} \tag{2.3}$$

where

$$(\boldsymbol{D}u)(a, t, x) = \lim_{h\to 0}\frac{1}{h}(u(a + h, t + h, x) - u(a, t, x))\,, \tag{2.4}$$

(2.5) $$P(t, x) = \int_0^\infty u(a, t, x)\, da$$

and

(2.6) $$Q(t, x) = \int_0^\infty \mu(a)h(a)u(a, t, x)\, da\,.$$

Throughout this paper we assume the following:

(A.1) $\beta \in C(\boldsymbol{R}_+ \times \boldsymbol{R}_+)$ is non-negative and bounded. Furthermore, $\beta(\cdot, P)$ is locally Lipschitz continuous from $\boldsymbol{R}_+$ to $L^\infty(\boldsymbol{R}_+)$;

(A.2) $\mu(a)$, $h(a)$ and $c(a)$ are all non-negative, bounded, continuous functions on $\boldsymbol{R}_+$;

(A.3) $\lambda_1, \lambda_2, k_1, k_2, \varepsilon_1$ and ε_2 are all positive constants.

Here we set $\boldsymbol{R}_+ = [0, \infty)$.

By *a global solution* of (2.1)–(2.3) we mean a pair of non-negative functions $(u, v) = (u(a, t, x), v(t, x))$ such that $u \in C(\boldsymbol{R}_+ \times \boldsymbol{R}_+ \times [0, l])$, $u(\cdot, t, x) \in L^1(\boldsymbol{R}_+)$, $u_x \in C((0, \infty) \times (0, \infty) \times [0, l])$, u_{xx}, $\boldsymbol{D}u \in C((0, \infty) \times (0, \infty) \times (0, l))$, $v \in C(\boldsymbol{R}_+ \times [0, l])$, $v_x \in C((0, \infty) \times [0, l])$, v_{xx}, $v_t \in C((0, \infty) \times (0, l))$ and (u, v) satisfies the equations (2.1)–(2.3) for all $t > 0$.

Here we state the main result of this section.

THEOREM 2.1. *Suppose, in addition to* (A.1)–(A.3), *that the following conditions are imposed on the initial functions u_0 and v_0*:

(A.4) $u_0 \in C(\boldsymbol{R}_+ \times [0, l]) \cap L^1(\boldsymbol{R}_+, C[0, l])$, $\quad u_0(a, x) \geq 0$ *and*

$$u_0(0, x) = \int_0^\infty \beta(a, P_0(x))u_0(a, x)\, da$$

with

$$P_0(x) = \int_0^\infty u_0(a, x)\, da\,;$$

(A.5) $v_0 \in C[0, l]$ *and* $v_0(x) \geq 0$.

Then, there exists a unique global solution of (2.1)–(2.3).

We first state some results from the theory of parabolic equations which will be used in the proof of our theorem.

LEMMA 2.2. *Consider the initial-boundary value problem*:

(2.7) $$\begin{cases} w_t = kw_{xx} + \xi(t, x)w & (t > 0, 0 < x < l) \\ w_x(t, 0) = w_x(t, l) = 0 & (t > 0) \\ w(0, x) = w_0(x) & (0 \leq x \leq l) \end{cases}$$

and the integral equation associated with (2.7):

$$w(t, x) = \int_0^l N(kt, x, y) w_0(y)\, dy$$

$$+ \int_0^t ds \int_0^l N(k(t-s), x, y)\xi(s, y) w(s, y)\, dy \tag{2.8}$$

$$(t \geq 0,\ 0 \leq x \leq l),$$

where $w_0 \in C[0, l]$, $\xi \in C(\boldsymbol{R}_+ \times [0, l])$, $N(t, x, y)$ *denotes the fundamental solution of*

$$\begin{cases} w_t = w_{xx} & (0 \leq x \leq l) \\ w_x(t, 0) = w_x(t, l) = 0 \end{cases}$$

and k *is a positive constant. Then, the following assertions hold*:

(i) *There exists a unique solution* $w \in C(\boldsymbol{R}_+ \times [0, l])$ *of* (2.8).

(ii) *Let* $w = w(t, x|\xi)$ *denote the solution of* (2.8) *together with its dependence on* ξ. *Then, for any* $T > 0$ *and any* $r > 0$, *there are some constants* M_1, $M_2 > 0$ *such that if* $\|\xi\|_T$, $\|\tilde{\xi}\|_T \leq r$, *then*

$$|w(t, x|\xi)| \leq M_1 \tag{2.9}$$

$$|w(t, x|\xi) - w(t, x|\tilde{\xi})| \leq M_2 \int_0^t |\xi(s, \cdot) - \tilde{\xi}(s, \cdot)|_\infty\, ds \tag{2.10}$$

for $(t, x) \in [0, T] \times [0, l]$. *Here,* $\|\cdot\|_T$ *and* $|\cdot|_\infty$ *denote the usual sup-norm in* $C([0, T] \times [0, l])$ *and in* $C[0, l]$, *respectively.*

(iii) *If* $w(t, x)$ *is a solution of* (2.7), *then* $w = w(t, x|\xi)$. *Assume, in addition, that* $\xi(t, x)$ *is locally Hölder continuous on* $(0, \infty) \times [0, l]$ *with respect to* x. *Then* $w(t, x|\xi)$ *also satisfies* (2.7).

PROOF OF THEOREM 2.1. Let (u, v) be a solution of (2.1)–(2.3). For any fixed $c \geq 0$, define $u^1(t, x) = u(t + c, t, x)$. Then u^1 satisfies the following:

$$\begin{cases} u_t^1 + \lambda(t + c, t, x|P, Q, v)u^1 = k_1 u_{xx}^1 & (t > 0, 0 < x < l) \\ u_x^1(t, 0) = u_x^1(t, l) = 0 & (t > 0) \\ u^1(0, x) = u_0(c, x) & (0 \leq x \leq l), \end{cases} \tag{2.11}$$

where

$$\lambda(a, t, x|P, Q, v) = \lambda_1 + \lambda_2 P(t, x) + \frac{\mu(a)v(t, x)}{1 + Q(t, x)}. \tag{2.12}$$

The first equation of (2.11) implies $u_t^1 \leq k_1 u_{xx}^1$, so it follows from the comparison theorem that

$$u^1(t, x) \le \int_0^l N(k_1 t, x, y) u_0(c, y)\, dy \le |u_0(c, \cdot)|_\infty .$$

By setting $c = a - t$, we have $u(a, t, x) \le |u_0(a - t, \cdot)|_\infty$ for $a \ge t$. Thus, the assumption $u_0 \in L^1(\boldsymbol{R}_+, C[0, l])$ implies that the integral $\int_0^\infty u(a, t, x)\, da$ is uniformly convergent on any compact set of $\boldsymbol{R}_+ \times [0, l]$, so the functions $P(t, x)$ and $Q(t, x)$, defined by (2.5) and by (2.6), respectively, become continuous on $\boldsymbol{R}_+ \times [0, l]$. As $\lambda(a, t, x | P, Q, v)$, defined by (2.12), is also continuous, it follows from Lemma 2.2 that u^1 satisfies

$$(2.13) \qquad \begin{aligned} u^1(t, x) = &\int_0^l N(k_1 t, x, y) u_0(c, y)\, dy \\ &- \int_0^t ds \int_0^l N(k_1(t - s), x, y) \lambda(s + c, s, y | P, Q, v) u^1(s, y)\, dy . \end{aligned}$$

Next, for any fixed $c \ge 0$, we define $u^2(a, x) = u(a, a + c, x)$. Then, u^2 satisfies the following:

$$(2.14) \qquad \begin{cases} u_a^2 + \lambda(a, a + c, x | P, Q, v) u^2 = k_1 u_{xx}^2 & (a > 0, 0 < x < l) \\ u_x^2(a, 0) = u_x^2(a, l) = 0 & (a > 0) \\ u^2(0, x) = B(c, x) & (0 \le x \le l) \end{cases}$$

with $B(t, x) = u(0, t, x)$, from which we have

$$(2.15) \qquad \begin{aligned} u^2(a, x) = &\int_0^l N(k_1 a, x, y) B(c, y)\, dy \\ &- \int_0^a ds \int_0^l N(k_1(a - s), x, y) \lambda(s, s + c, y | P, Q, v) u^2(s, y)\, dy . \end{aligned}$$

Concerning the integral equations (2.13) and (2.15) we now state

LEMMA 2.3. *Let* $X = \{f \in C(\boldsymbol{R}_+ \times [0, l]) | f(t, x) \ge 0\}$. *The following assertions hold*:

(i) *For any* $c \in \boldsymbol{R}_+$ *and* $(P, Q, v) \in X^3$, *there exists a unique solution* $u^1 \in X$ *of* (2.13). *We denote such a solution by* $u^1 = \Phi(t, c, x | P, Q, v)$ *in order to indicate its dependence on* c, P, Q *and* v. *Then, for any fixed* $(P, Q, v) \in X^3$, $\Phi \in C(\boldsymbol{R}_+ \times \boldsymbol{R}_+ \times [0, l])$ *and* $\Phi_x \in C((0, \infty) \times \boldsymbol{R}_+ \times [0, l])$. *Furthermore,*

$$(2.16) \qquad 0 \le \Phi(t, c, x | P, Q, v) \le |u_0(c, \cdot)|_\infty ,$$

and for any $T > 0$ *and* $r > 0$, *there is some constant* $M_3 > 0$ *such that, if* $\|P\|_T$, $\|v\|_T \le r$, *then*

$$
\begin{aligned}
&|\Phi(t, c, x|P, Q, v) - \Phi(t, c, x|\tilde{P}, \tilde{Q}, \tilde{v})| \\
(2.17) \qquad &\le M_3 |u_0(c, \cdot)|_\infty \int_0^t \{|P(s, \cdot) - \tilde{P}(s, \cdot)|_\infty \\
&+ |Q(s, \cdot) - \tilde{Q}(s, \cdot)|_\infty + |v(s, \cdot) - \tilde{v}(s, \cdot)|_\infty\}\, ds
\end{aligned}
$$

holds for $(t, c, x) \in [0, T] \times \boldsymbol{R}_+ \times [0, l]$.

(ii) *For any* $c \in \boldsymbol{R}_+$ *and* $(B, P, Q, v) \in X^4$ *there exists a unique solution* $u^2 \in X$ *of* (2.15). *We denote such a solution by* $u^2 = \Psi(a, c, x|B, P, Q, v)$ *in order to indicate its dependence on* c, B, P, Q *and* v. *Then, for any fixed* $(B, P, Q, v) \in X^4$, $\Psi \in C(\boldsymbol{R}_+ \times \boldsymbol{R}_+ \times [0, l])$ *and* $\Psi_x \in C((0, \infty) \times \boldsymbol{R}_+ \times [0, l])$. *Furthermore,*

$$
(2.18) \qquad 0 \le \Psi(a, c, x|B, P, Q, v) \le |B(c, \cdot)|_\infty
$$

and for any $T > 0$ *and* $r > 0$, *there is some constant* $M_4 > 0$ *such that, if* $\|B\|_T$, $\|\tilde{P}\|_T$, $\|\tilde{v}\|_T \le r$, *then*

$$
\begin{aligned}
&|\Psi(a, c, x|B, P, Q, v) - \Psi(a, c, x|\tilde{B}, \tilde{P}, \tilde{Q}, \tilde{v})| \\
(2.19) \qquad &\le M_4\Big(|B(c, \cdot) - \tilde{B}(c, \cdot)|_\infty + \int_c^{a+c} \{|P(s, \cdot) - \tilde{P}(s, \cdot)|_\infty \\
&+ |Q(s, \cdot) - \tilde{Q}(s, \cdot)|_\infty + |v(s, \cdot) - \tilde{v}(s, \cdot)|_\infty\}\, ds\Big)
\end{aligned}
$$

holds for $a, c \ge 0$, $a + c \le T$, $x \in [0, l]$.

The proof of Lemma 2.3 is easy, so we omit it.

From the definitions of u^1 and u^2, we obtain the following expression for the solution u:

$$
(2.20) \qquad u(a, t, x) = \begin{cases} \Phi(t, a - t, x|P, Q, v) & (a \ge t) \\ \Psi(a, t - a, x|B, P, Q, v) & (a \le t)\,. \end{cases}
$$

Here we have chosen c as $c = a - t$ and $c = t - a$ when $a \ge t$ and when $a \le t$, respectively. By the substitution of (2.20) into the first equation of (2.2), (2.5) and (2.6), we have

$$
\begin{aligned}
(2.21) \qquad B(t, x) &= \int_0^t \beta(a, P(t, x))\Psi(a, t - a, x|B, P, Q, v)\, da \\
&+ \int_0^\infty \beta(a + t, P(t, x))\Phi(t, a, x|P, Q, v)\, da\,,
\end{aligned}
$$

$$
(2.22) \qquad P(t, x) = \int_0^t \Psi(a, t - a, x|B, P, Q, v)\, da + \int_0^\infty \Phi(t, a, x|P, Q, v)\, da
$$

$$Q(t, x) = \int_0^t \mu(a)h(a)\Psi(a, t-a, x|B, P, Q, v)\,da \tag{2.23}$$
$$+ \int_0^\infty \mu(a+t)h(a+t)\Phi(t, a, x|P, Q, v)\,da\,.$$

Our next step is to regard

$$\eta(t, x) = \frac{1}{1 + Q(t, x)} \int_0^\infty c(a)\mu(a)u(a, t, x)\,da \tag{2.24}$$

as a known function and to solve the problem:

$$\begin{cases} v_t + (\varepsilon_1 + \varepsilon_2 v - \eta(t, x))v = k_2 v_{xx} & (t > 0, 0 < x < l) \\ v_x(t, 0) = v_x(t, l) = 0 & (t > 0) \\ v(0, x) = v_0(x) & (0 \le x \le l)\,. \end{cases} \tag{2.25}$$

Let $\eta \in C(\boldsymbol{R}_+ \times [0, l])$. If v is a solution of (2.25), then $v(t, x) = w(t, x|\xi)$, where

$$\xi = \xi(t, x|v) \equiv \eta(t, x) - \varepsilon_1 - \varepsilon_2 v(t, x) \tag{2.26}$$

and $w(\cdot, \cdot|\xi)$ is defined in Lemma 2.2 with k and $w_0(x)$ replaced by k_2 and by $v_0(x)$, respectively. We define the mapping $L: C(\boldsymbol{R}_+ \times [0, l]) \to C(\boldsymbol{R}_+ \times [0, l])$ by $(Lv)(t, x) = w(t, x|\xi(\cdot, \cdot|v))$. Then, any solution of (2.25) must be a fixed point of the mapping L. Conversely, we assume, in addition, that $\eta(t, x)$ is locally Hölder continuous on $(0, \infty) \times [0, l]$ with respect to x. Then, by Lemma 2.2 (iii), we see that any fixed point of L is really a solution of (2.25). Concerning fixed points of L we have

LEMMA 2.4. *L has a unique fixed point in $C(\boldsymbol{R}_+ \times [0, l])$, which we denote by $v = v(t, x|\eta)$. Then, the following estimates hold: For any $T > 0$ and $r > 0$ there are some constants M_5, $M_6 > 0$ such that if $\|\eta\|_T$, $\|\tilde{\eta}\|_T \le r$, then*

$$0 \le v(t, x|\eta) \le M_5 \tag{2.27}$$

$$|v(t, x|\eta) - v(t, x|\tilde{\eta})| \le M_6 \int_0^t |\eta(s, \cdot) - \tilde{\eta}(s, \cdot)|_\infty\,ds \tag{2.28}$$

hold for $(t, x) \in [0, T] \times [0, l]$.

PROOF. We have

$$(Lv)(t, x) \ge 0\,, \tag{2.29}$$

which, together with (2.8) and (2.26), implies that for any $T > 0$, there is some constant $K_1 > 0$ with

$$(Lv)(t, x) \le K_1 \tag{2.30}$$

for $(t, x) \in [0, T] \times [0, l]$ and for any non-negative function $v(t, x)$. Also, for any $T > 0$ and $r > 0$, there is some constant $K_2 > 0$ such that if $\|v\|_T$, $\|\tilde{v}\|_T \leq r$, then

$$|(Lv)(t, x) - (L\tilde{v})(t, x)| \leq K_2 \int_0^t |v(s, \cdot) - \tilde{v}(s, \cdot)|_\infty \, ds \tag{2.31}$$

for $(t, x) \in [0, T] \times [0, l]$. Define the sequence of functions $\{v_n(t, x)\}_{n \geq 0}$ by

$$v_0(t, x) \equiv v_0(x)$$

$$v_n(t, x) = (Lv_{n-1})(t, x) \qquad n = 1, 2, \ldots .$$

Then, by the use of standard arguments we prove that the limit $v^*(t, x) = \lim_{n \to \infty} v_n(t, x)$ exists and that v^* is a fixed point of L in $C(\boldsymbol{R}_+ \times [0, l])$. (2.31) also implies the uniqueness of fixed points of L. The remainder of the lemma is easily proved by (2.9) and (2.10), so we omit the details.

Thus, if (u, v) is a solution of (2.1)–(2.3), then $(B, P, Q, v) \in X^4$ satisfies (2.21)–(2.23) and

$$v(t, x) = v(t, x \mid \eta) \tag{2.32}$$

with

$$\begin{aligned} \eta(t, x) = \frac{1}{1 + Q(t, x)} \bigg(& \int_0^t c(a)\mu(a)\Psi(a, t - a, x \mid B, P, Q, v) \, da \\ & + \int_0^\infty c(a + t)\mu(a + t)\Phi(t, a, x \mid P, Q, v) \, da \bigg) . \end{aligned} \tag{2.33}$$

Conversely, let $(B, P, Q, v) \in X^4$ satisfy (2.21), (2.22), (2.23), (2.32) and (2.33), then, by Lemma 2.3, P_x, Q_x and η_x belong to $C((0, \infty) \times [0, l])$. If we define $u(a, t, x)$ as in (2.20), then, by Lemma 2.2 (iii), (u, v) is a solution of (2.1)–(2.3). Thus, to establish Theorem 2.1, it is sufficient to show

LEMMA 2.5. *There exists a unique solution* $(B, P, Q, v) \in X^4$ *of* (2.21), (2.22), (2.23), (2.32) *and* (2.33).

PROOF. First let $(P, Q, v) \in X^3$ be fixed and define $\mathscr{F} : X \to X$ by

$$\begin{aligned} (\mathscr{F}B)(t, x) = & \int_0^t \beta(a, P(t, x))\Psi(a, t - a, x \mid B, P, Q, v) \, da \\ & + \int_0^\infty \beta(a + t, P(t, x))\Phi(t, a, x \mid P, Q, v) \, da . \end{aligned}$$

Then, it follows that for any $T > 0$ there is some constant $K_3 > 0$ with

$$|(\mathscr{F}B)(t,x)-(\mathscr{F}\tilde{B})(t,x)|\leq K_3\int_0^t|B(s,\cdot)-\tilde{B}(s,\cdot)|_\infty\,ds$$

for $(t, x) \in [0, T] \times [0, l]$, from which we obtain that for each $(P, Q, v) \in X^3$ there is a unique solution $B \in X$ of (2.21). We denote such a solution by $B(t, x|P, Q, v)$ in order to indicate its dependence on P, Q and v. Then, by the use of Gronwall's inequality the following estimates hold:

(i) For any $T > 0$, there is some constant $K_4 > 0$ with

$$0 \leq B(t, x|P, Q, v) \leq K_4 \tag{2.34}$$

for $(t, x) \in [0, T] \times [0, l]$

(ii) For any $T > 0$ and $r > 0$, there is some constant $K_5 > 0$ such that if $\|P\|_T$, $\|\tilde{P}\|_T$, $\|\tilde{v}\|_T \leq r$, then

$$\begin{aligned}|B(t,x|P,Q,v)&-B(t,x|\tilde{P},\tilde{Q},\tilde{v})|\\&\leq K_5\Big(|P(t,\cdot)-\tilde{P}(t,\cdot)|_\infty+\int_0^t\{|P(s,\cdot)-\tilde{P}(s,\cdot)|_\infty\\&\quad+|Q(s,\cdot)-\tilde{Q}(s,\cdot)|_\infty+|v(s,\cdot)-\tilde{v}(s,\cdot)|_\infty\}\,ds\Big)\end{aligned}\tag{2.35}$$

for $(t, x) \in [0, T] \times [0, l]$.

Denote by $F_1(t, x|P, Q, v)$, $F_2(t, x|P, Q, v)$ and $F_3(t, x|P, Q, v)$ the right-hand side of (2.22), of (2.23) and of (2.32), respectively, with B replaced by $B(\cdot,\cdot|P,Q,v)$. Then, $F_i \in X$ $(i = 1, 2, 3)$ and, by (2.16)–(2.19), (2.27), (2.28), (2.34) and (2.35), the following estimates hold:

(i) For any $T > 0$, there is some constant $K_6 > 0$ with

$$\textstyle\sum_{i=1}^3 F_i(t, x|P, Q, v) \leq K_6 \tag{2.36}$$

for $(t, x) \in [0, T] \times [0, l]$.

(ii) For any $T > 0$ and $r > 0$, there is some constant $K_7 > 0$ such that if $\|P\|_T$, $\|\tilde{P}\|_T$, $\|\tilde{v}\|_T \leq r$, then

$$\begin{aligned}\textstyle\sum_{i=1}^3 &|F_i(t,x|P,Q,v)-F_i(t,x|\tilde{P},\tilde{Q},\tilde{v})|\\&\leq K_7\int_0^t\{|P(s,\cdot)-\tilde{P}(s,\cdot)|_\infty+|Q(s,\cdot)-\tilde{Q}(s,\cdot)|_\infty\\&\quad+|v(s,\cdot)-\tilde{v}(s,\cdot)|_\infty\}\,ds\end{aligned}\tag{2.37}$$

for $(t, x) \in [0, T] \times [0, l]$.

Using these estimates we see that there exists a unique solution $(P, Q, v) \in X^3$ of $P(t, x) = F_1(t, x|P, Q, v)$, $Q(t, x) = F_2(t, x|P, Q, v)$ and $v(t, x) = F_3(t, x|P, Q, v)$. This completes the proof of Lemma 2.5.

3. Stability analysis of stationary solutions

In this section we consider the case when the birth function $\beta(a, P)$ is independent of P and study spatially homogeneous stationary solutions of (2.1)–(2.3) which correspond to the extinction of the predator. We write $\beta(a, P) \equiv \beta(a)$. Note that such a solution is of the form $(\bar{u}(a), 0)$ with $\bar{u} \in C(\boldsymbol{R}_+) \cap C^1(0, \infty)$, $\bar{u}(a) \geq 0$ and

$$(3.1) \qquad \begin{cases} \dfrac{d\bar{u}}{da} + (\lambda_1 + \lambda_2 \bar{P})\bar{u} = 0 & (a > 0) \\ \bar{u}(0) = \displaystyle\int_0^\infty \beta(a)\bar{u}(a)\, da\,, \end{cases}$$

where

$$(3.2) \qquad \bar{P} = \int_0^\infty \bar{u}(a)\, da\,.$$

It is obvious that $(0, 0)$ is always a stationary solution. The following proposition, which is a special case of [5] Theorem 6, gives a necessary and sufficient condition for the existence of stationary solutions of the form $(\bar{u}(a), 0)$ with $\bar{u}(a) \not\equiv 0$.

Proposition 3.1. *If* (3.1)–(3.2) *has a non-trivial solution, then*

$$(3.3) \qquad \int_0^\infty \beta(a) e^{-\lambda_1 a}\, da > 1$$

holds. Conversely, if (3.3) *holds, then there exists a unique solution* $\bar{u}(a)$ $(\not\equiv 0)$ *of* (3.1)–(3.2) *and it is given by*

$$(3.4) \qquad \bar{u}(a) = \bar{B} e^{-(\lambda_1 + p^*)a}$$

with

$$(3.5) \qquad \bar{B} = \lambda_2^{-1} p^*(\lambda_1 + p^*)\,,$$

where p^* *is a unique positive root of*

$$(3.6) \qquad \int_0^\infty \beta(a) e^{-(\lambda_1 + p^*)a}\, da = 1\,.$$

We first consider the case when

$$(3.7) \qquad \int_0^\infty \beta(a) e^{-\lambda_1 a}\, da < 1\,.$$

The following proposition claims that in the case of (3.7) both of the species will become extinct for large time.

PROPOSITION 3.2. *Let* (3.7) *hold and let* (u, v) *be the solution of* (2.1)–(2.3), *then*

$$\lim_{t\to\infty} P(t, x) = \lim_{t\to\infty} v(t, x) = 0 . \tag{3.8}$$

PROOF. Define $\tilde{u}(a, t, x) = e^{\lambda_1 t}u(a, t, x)$. Then, $\tilde{u}$ satisfies

$$\begin{cases} D\tilde{u} \le k_1 \tilde{u}_{xx} & (a, t > 0, 0 < x < l) \\ \tilde{u}_x(a, t, 0) = \tilde{u}_x(a, t, l) = 0 & (a, t > 0) \\ \tilde{u}(a, 0, x) = u_0(a, x) & (a \ge 0, 0 \le x \le l) . \end{cases}$$

Using the comparison theorem, we have

$$u(a, t, x) \le \begin{cases} |u_0(a - t, \cdot)|_\infty e^{-\lambda_1 t} & (a \ge t) \\ |B(t - a, \cdot)|_\infty e^{-\lambda_1 a} & (a \le t) , \end{cases} \tag{3.9}$$

where $B(t, x) = u(0, t, x)$. By the first equation of (2.2) and (3.9) we have

$$B(t, x) \le \int_0^t \beta(a)e^{-\lambda_1 a}|B(t - a, \cdot)|_\infty \, da + \bar{\beta}\|u_0\|_{L^1}e^{-\lambda_1 t} ,$$

with $\bar{\beta} = \sup\{\beta(a) | a \in \boldsymbol{R}_+\}$ and $\|u_0\|_{L^1} = \int_0^\infty |u_0(a, \cdot)|_\infty \, da$, and the assumption (3.7) implies

$$B(t, x) \le Ce^{-pt} \tag{3.10}$$

with some constants $C > 0$ and $p \in (0, \lambda_1)$. (3.10) implies

$$P(t, x) \le \int_0^t e^{-\lambda_1 a}|B(t - a, \cdot)|_\infty \, da + \|u_0\|_{L^1}e^{-\lambda_1 t} \le C'e^{-pt}$$

with some constant $C' > 0$. This means $\lim_{t\to\infty} P(t, x) = 0$, and so, for sufficiently large t,

$$v_t + (\varepsilon_1/2)v \le k_2 v_{xx} .$$

Then, the comparison theorem implies that $\lim_{t\to\infty} v(t, x) = 0$. This completes the proof.

We next consider the case of (3.3). Moreover, the following condition is imposed on the birth function $\beta(a)$:

$$\beta \in C^1(0, \infty) \quad \text{and} \quad \beta' \in L^1(0, \infty) . \tag{A.6}$$

If we take $u_0(a, x) \equiv u_0(a)$ and $v_0(x) \equiv 0$, then $v(t, x) \equiv 0$, $u(a, t, x)$ is independent of x and is governed by

$$
(3.11) \qquad \begin{cases} Du + (\lambda_1 + \lambda_2 P)u = 0 & (a, t > 0) \\ u(0, t) = \displaystyle\int_0^\infty \beta(a)u(a, t)\, da & (t > 0) \\ P(t) = \displaystyle\int_0^\infty u(a, t)\, da & (t > 0) \\ u(a, 0) = u_0(a)\,. & (a \geq 0)\,. \end{cases}
$$

(3.3) implies that $u \equiv 0$ is an unstable equilibrium of (3.11), that is, the trivial solution (0, 0) is unstable in our full system. (It is proved in Marcati [9] that under the assumption that the age-interval is finite and $u_0(a) \not\equiv 0$, the solution of (3.11) tends to the unique non-trivial stationary solution $\bar{u}(a)$ as $t \to \infty$.)

In what follows we investigate the local stability of the stationary solution $(\bar{u}(a), 0)$ with $\bar{u}(a)$ defined in (3.4), (3.5). Set $w(a, t, x) = u(a, t, x) - \bar{u}(a)$ and consider the linearized version of (2.1)–(2.3):

$$
(3.12) \qquad \begin{cases} Dw + (\lambda_1 + \lambda_2 \bar{P})w + \lambda_2 \bar{u}(a)p + \dfrac{\mu(a)\bar{u}(a)}{1 + \bar{Q}} v = k_1 w_{xx} \\ w(0, t, x) = \displaystyle\int_0^\infty \beta(a) w(a, t, x)\, da \\ w_x(a, t, 0) = w_x(a, t, l) = 0 \\ v_t + \left(\varepsilon_1 - \dfrac{1}{1 + \bar{Q}} \displaystyle\int_0^\infty c(a)\mu(a)\bar{u}(a)\, da\right) v = k_2 v_{xx} \\ v_x(t, 0) = v_x(t, l) = 0\,, \end{cases}
$$

where

$$
p(t, x) = \int_0^\infty w(a, t, x)\, da\,,
$$

$$
\bar{P} = \int_0^\infty \bar{u}(a)\, da
$$

and

$$
\bar{Q} = \int_0^\infty \mu(a) h(a) \bar{u}(a)\, da\,.
$$

If (3.12) has no eigenvalues in the right half-plane $Re\, \gamma \geq 0$, then $(\bar{u}(a), 0)$ is stable in our full nonlinear system, while if (3.12) has at least one eigenvalue with a positive real part, then $(\bar{u}(a), 0)$ is unstable. This is proved in Gurtin and MacCamy [5] for the case of the absence of spatial movement, and it is easily seen that their methods can be applied to our diffusion model. So, in order to find eigenvalues of the linearized problem (3.12), we set $w(a, t, x) = \tilde{w}(a, x)e^{\gamma t}$ and $v(t, x) = \tilde{v}(x)e^{\gamma t}$ with $\gamma \in \boldsymbol{C}$. Then, $(\tilde{w}, \tilde{v})$ satisfies

$$\text{(3.13)} \qquad \begin{cases} \tilde{w}_a + (\lambda_1 + p^* + \gamma)\tilde{w} + \lambda_2 \bar{u}(a)\tilde{p} + \dfrac{\mu(a)\bar{u}(a)}{1 + \bar{Q}}\tilde{v} = k_1 \tilde{w}_{xx} \\ \tilde{w}(0, x) = \displaystyle\int_0^\infty \beta(a)\tilde{w}(a, x)\, da \\ \tilde{w}_x(a, 0) = \tilde{w}_x(a, l) = 0 \end{cases}$$

with

$$\text{(3.14)} \qquad \tilde{p}(x) = \int_0^\infty \tilde{w}(a, x)\, da\,,$$

and

$$\text{(3.15)} \qquad \begin{cases} (S + \gamma)\tilde{v} = k_2 \tilde{v}_{xx} \\ \tilde{v}_x(0) = \tilde{v}_x(l) = 0 \end{cases}$$

with

$$\text{(3.16)} \qquad S = \varepsilon_1 - \frac{1}{1 + \bar{Q}} \int_0^\infty c(a)\mu(a)\bar{u}(a)\, da\,.$$

We first find solutions $\tilde{w}(a, x)$ of (3.13), (3.14) for any fixed $\tilde{v}(x)$.

LEMMA 3.3. *There exists some constant* γ_0 $(0 < \gamma_0 < p^*)$ *such that* (3.13)–(3.14) *has a unique solution* $\tilde{w}(a, x)$ *for* $Re\,\gamma > -\gamma_0$ *and for any fixed* $\tilde{v} \in C^2[0, l]$ *with* $\tilde{v}_x(0) = \tilde{v}_x(l) = 0$.

The proof of this lemma will be given at the end of this section. On the other hand, we see that (3.15)–(3.16) has non-trivial solutions if and only if

$$\gamma = -S - (k_2/l^2)n^2\pi^2 \qquad (n = 0, 1, 2, \dots)\,.$$

Combining these results we obtain the following:

(i) If $S > 0$, then each eigenvalue γ of (3.13)–(3.16), if it exists, satisfies $Re\,\gamma \le -min\,(\gamma_0, S)$.

(ii) If $S < 0$, then (3.13)–(3.16) has at least one real positive eigenvalue.

Thus, we have

THEOREM 3.4. *Assume* (3.3) *and* (A.6). *Then, we have the following*:

(i) *If* $S > 0$, *then the stationary solution* $(\bar{u}(a), 0)$ *is exponentially asymptotically stable in* $L^1(\boldsymbol{R}_+, C[0, l]) \times C[0, l]$.

(ii) *If* $S < 0$, *then it is unstable.*

PROOF OF LEMMA 3.3. The proof is similar to the proof of Marcati and Serafini [10] where linear age-dependent diffusion models are treated. Let $Y = C[0, l]$ and define the linear operator A in Y by

$$Au = k_1 \frac{d^2 u}{dx^2} \tag{3.17}$$

for $u \in \mathscr{D}(A) \equiv \{u \in C^2[0, l] | u'(0) = u'(l) = 0\}$. Then, A generates an analytic semi-group $\{T(t)\}_{t \geq 0}$ which satisfies

$$\|T(t)\| \leq 1 \quad \text{for} \quad t \in \boldsymbol{R}_+ , \tag{3.18}$$

where $\|\cdot\|$ denotes the operator norm in Y. By means of these operators, the first equation and the last one of (3.13) are rewritten as an ordinary differential equation in Y:

$$\frac{d\tilde{w}}{da} + (\lambda_1 + p^* + \gamma)\tilde{w} + \lambda_2 \bar{u}(a)\tilde{p} + \frac{\mu(a)\bar{u}(a)}{1 + \bar{Q}}\tilde{v} = A\tilde{w}$$

or equivalently,

$$\begin{aligned} \tilde{w}(a) &= e^{-(\lambda_1 + p^* + \gamma)a} T(a)\tilde{b} \\ &\quad - \lambda_2 \bar{B} e^{-(\lambda_1 + p^*)a} \int_0^a e^{-\gamma s} T(s)\, ds\, \tilde{p} + f_\gamma(a)\tilde{v} , \end{aligned} \tag{3.19}$$

where

$$\tilde{b} = \tilde{w}(0) \tag{3.20}$$

$$f_\gamma(a) = -\frac{\bar{B}}{1 + \bar{Q}} e^{-(\lambda_1 + p^*)a} \int_0^a \mu(a - s) e^{-\gamma s} T(s)\, ds . \tag{3.21}$$

Substituting (3.19) into the second equation of (3.13) and (3.14), we obtain

$$\begin{aligned} \begin{bmatrix} \tilde{b} \\ \tilde{p} \end{bmatrix} &= \int_0^\infty \begin{bmatrix} \beta(a) \\ 1 \end{bmatrix} e^{-(\lambda_1 + p^* + \gamma)a} T(a)\, da\, \tilde{b} \\ &\quad - \lambda_2 \bar{B} \int_0^\infty \begin{bmatrix} \beta(a) \\ 1 \end{bmatrix} e^{-(\lambda_1 + p^*)a}\, da \int_0^a e^{-\gamma s} T(s)\, ds\, \tilde{p} \\ &\quad + \int_0^\infty \begin{bmatrix} \beta(a) \\ 1 \end{bmatrix} f_\gamma(a)\, da\, \tilde{v} . \end{aligned} \tag{3.22}$$

Define the matrix-valued function $\mathscr{K}(a)$ by

$$\mathscr{K}(a) = \begin{bmatrix} K_{11}(a) & K_{12}(a) \\ K_{21}(a) & K_{22}(a) \end{bmatrix}$$

with

$$\begin{bmatrix} K_{11}(a) \\ K_{21}(a) \end{bmatrix} = \begin{bmatrix} \beta(a) \\ 1 \end{bmatrix} e^{-(\lambda_1+p^*)a} T(a)$$

and

$$\begin{bmatrix} K_{12}(a) \\ K_{22}(a) \end{bmatrix} = -\lambda_2 \bar{B} T(a) \int_a^\infty \begin{bmatrix} \beta(s) \\ 1 \end{bmatrix} e^{-(\lambda_1+p^*)s}\, ds\,.$$

The boundedness of β and (3.18) yield the estimate

$$\| K_{ij}(a) \| \leq \text{constant} \cdot e^{-(\lambda_1+p^*)a}\,,$$

which implies that the Laplace transform $\mathscr{K}^*(\gamma) = [K_{ij}^*(\gamma)]$ of $\mathscr{K}(a)$ exists for $Re\, \gamma > -(\lambda_1 + p^*)$. Then, (3.22) takes the simpler form

$$[1 - \mathscr{K}^*(\gamma)]\vec{x} = \vec{F}_\gamma \tilde{v} \qquad (Re\, \gamma > -(\lambda_1 + p^*)) \tag{3.23}$$

with

$$\vec{x} = \begin{bmatrix} \tilde{b} \\ \tilde{p} \end{bmatrix}, \qquad \vec{F}_\gamma = \int_0^\infty \begin{bmatrix} \beta(a) \\ 1 \end{bmatrix} f_\gamma(a)\, da\,. \tag{3.24}$$

Conversely, if $\vec{x} \in Y^2$ satisfies (3.23), then $\tilde{w}(a)$ in (3.19) is a solution of (3.13)–(3.14). Thus, our problem has been reduced to solving the equation (3.23) in Y^2.

Our next step is to discuss about the distribution of the values of γ for which $1 - \mathscr{K}^*(\gamma)$ is invertible. For this purpose we denote by $D(\gamma)$ the "determinant" of $1 - \mathscr{K}^*(\gamma)$, that is,

$$D(\gamma) = (1 - K_{11}^*(\gamma))(1 - K_{22}^*(\gamma)) - K_{12}^*(\gamma) K_{21}^*(\gamma)\,. \tag{3.25}$$

From the fact that the components of $1 - \mathscr{K}^*(\gamma)$ are commutative with each other, it follows that if $D(\gamma)$ has a bounded inverse, so does $1 - \mathscr{K}^*(\gamma)$. In fact, the inverse of $1 - \mathscr{K}^*(\gamma)$ is given by

$$[1 - \mathscr{K}^*(\gamma)]^{-1} = D(\gamma)^{-1} \begin{bmatrix} 1 - K_{22}^*(\gamma) & -K_{12}^*(\gamma) \\ -K_{21}^*(\gamma) & 1 - K_{11}^*(\gamma) \end{bmatrix}. \tag{3.26}$$

An easy calculation shows that

$$D(\gamma) = 1 - \int_0^\infty e^{-\gamma s} \varphi(s) T(s)\, ds\,, \tag{3.27}$$

where

$$\varphi(s) = e^{-(\lambda_1+p^*)s} \beta(s) - p^* \int_s^\infty \beta(a) e^{-(\lambda_1+p^*)a}\, da\,. \tag{3.28}$$

Since $D(\gamma)$ has a bounded inverse in Y if and only if $1 \in \rho(1 - D(\gamma))$, it is sufficient to study the spectrum of

$$1 - D(\gamma) = \int_0^\infty e^{-\gamma s}\varphi(s)T(s)\,ds\,.$$

Set

$$\Phi_\gamma(z) = \int_0^\infty e^{(z-\gamma)s}\varphi(s)\,ds \quad (Re\, z < Re\, \gamma + \lambda_1 + p^*) \tag{3.29}$$

then $\Phi_\gamma(A) = 1 - D(\gamma)$. In view of the spectral mapping theorem (see, Hille [6], for instance), we obtain

$$\sigma(1 - D(\gamma)) = \sigma(\Phi_\gamma(A)) = \Phi_\gamma(\sigma(A)) \cup \{0\}\,. \tag{3.30}$$

We next study the scalar function $\Phi_\gamma(z)$. (3.28) and (3.29) imply that

$$\Phi_\gamma(z) = \begin{cases} 1 - p^* \displaystyle\int_0^\infty a\beta(a)e^{-(\lambda_1+p^*)a}\,da & (z = \gamma) \\ \left(1 + \dfrac{p^*}{\gamma - z}\right)\displaystyle\int_0^\infty \beta(a)e^{-(\lambda_1+p^*+\gamma-z)a}\,da - \dfrac{p^*}{\gamma - z} & (z \neq \gamma)\,. \end{cases} \tag{3.31}$$

Therefore, z is a root of $\Phi_\gamma(z) = 1$ if and only if either of the following conditions holds:

(i) $$z = \gamma + p^*\,.$$

(ii) $$z \neq \gamma \quad \text{and} \quad \int_0^\infty \beta(a)e^{-(\lambda_1+p^*+\gamma-z)a}\,da = 1\,.$$

From the theory of analytic functions it follows that there is some constant $\bar{p}$ $(0 < \bar{p} < p^*)$ with

$$\int_0^\infty \beta(a)e^{-(\lambda_1+p)a}\,da \neq 1 \tag{3.32}$$

for $Re\, p > \bar{p}$ and $p \neq p^*$. Consequently,

$$\Phi_\gamma(z) \neq 1 \quad \text{for} \quad Re\, z < Re\, \gamma + p^* - \bar{p}\,. \tag{3.33}$$

Now, let $Re\, \gamma > -(p^* - \bar{p})$. Since $\sigma(A)$ lies in the left half-plane $Re\, \gamma \leq 0$, it follows from (3.30) and (3.33) that $D(\gamma)$ has a bounded inverse, and therefore, (3.23) has a unique solution in Y^2 given by

$$\vec{x} = (1 - \mathscr{K}^*(\gamma))^{-1}\vec{F}_\gamma\tilde{v}\,. \tag{3.34}$$

This completes the proof.

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