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SOLVABILITY AND ASYMPTOTIC BEHAVIOR OF A POPULATION PROBLEM TAKING INTO ACCOUNT RANDOM MATING AND FEMALES' PREGNANCY

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Two deterministic age-sex-structured population dynamics models are discussed taking into account random mating of sexes (without formation of permanent male-female couples), possible destruction of the fetus (abortion), and female's pregnancy. One of them deals with both random and directed diffusion in the whole space while in the other the population is assumed to be nondispersing. The population consists of three components: one male and two female, the latter two being the single (nonfertilized) female and the fertilized one. The case of a separable solution of the limited nondispersing population (in which death moduli can be decomposed into the sum of two terms where one of them depends on time and age and the other is a function of time and the population size) is analyzed. The existence of a unique solution of the Cauchy problem for the nondispersing population model is proved and its longtime behavior is demonstrated. An analogous situation for the dispersing population is analyzed, too.

Keywords: population dynamics, random mating, gestation of females, migration

1. Introduction

In recent years there has been considerable interest in the dynamics of bisexual populations with or without both age structure and spatial diffusion. Such models are of paramount importance for genetics (see e.g. (Svirezhev and Passekov, 1990) and references therein) and epidemiology, in particular for modeling sexually transmitted diseases (see e.g. references in (Hadeler, 1993)). Both random mating, without formation of permanent male-female couples, and monogamous marriage models (see e.g. (Frederickson, 1971; Hoppensteadt, 1975; Staroverov, 1977; Hadeler, 1993) and references therein) are usually used. A common feature of these works is that their

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analyses are based on a division of the population into a small number of subpopulations, usually into male and female or single male, single female and pair subclasses.

In a recent paper (Skakauskas, 1994) we developed a general deterministic model for an age-sex-structured population dynamics taking into account random mating of sexes without formation of permanent male-female couples, female's pregnancy, possible miscarriage (abortion) of the fertilized female, and female's sterility periods following abortion and delivery. The population is divided into five components: one male and four female, the latter four being the single (nonfertilized) female, fertilized female, female in a sterility period after abortion, and female in a sterility one following delivery. Each sex has three age-grades: pre-reproductive, reproductive, and post-reproductive. It is assumed that for each sex the commencement of each grade as well as the duration of the gestation and female sterility periods are independent of individuals or time. Latter, in (Skakauskas, 1996), we generalized this model for the spatially dispersing population in the whole space. The mechanism of spatial dispersal in the last model is described by an integral operator.

In the present paper, we simplify the model of (Skakauskas, 1996) by neglecting the female sterility periods above, replace its dispersal mechanism by that of random and directed diffusion, and, in the case of a limited population with death rates depending on the spatial density of population, we examine separable solutions to this new model. We emphasize that a possible miscarriage of the fertilized female is taken into account. We also consider this model for the nonlimited nondispersing population, prove the existence of its unique solution, and, in the special case in which all the vital rates of the fertilized female do not depend on the age of the mated male, establish its longtime behavior. Furthermore, we construct a separable solution to this model for a limited population, and demonstrate its asymptotic behavior as time tends to infinity. In the case of a separable solution for the nondispersing population the death rates are decomposed into the sum of two terms where one of them depends on time and age while the other one is a function of time and the total population.

In (Skakauskas, 1998) we analyzed a model analogous to the present one, but without possible female's abortion, i.e. $X_a = 0$ in system (1). All the results of the present paper are direct generalizations of those in (Skakauskas, 1998) to the population whose fertilized females may miscarry.

The paper is organized as follows. Section 3 deals with the analysis of the nondispersing population model and consists of four subsections. In Section 3.1, we prove the existence and uniqueness theorem for the nonlimited population model. In Section 3.2 (resp. 3.3) in the case of specialized initial distributions (resp., general initial distributions) and stationary vital rates of the nonlimited population, we obtain a separable solution (resp., the asymptotic behavior of the general solution). In Section 3.4, we obtain a separable solution for the limited population model as well as for stationary vital rates, demonstrate its asymptotics as time goes to infinity. Finally, in Section 4 we present a separable solution to the dispersing limited population model. The discussion in Section 5, including some comments about the models, concludes this paper.

2. Notation

We follow the notation of (Skakauskas, 1994; 1996; 1998):

τ_1, τ_2 and τ_3: the ages of male, female, and embryo, respectively;

t: time;

E^m: Euclidean space of dimension m;

$x = (x_1, x_2, \dots, x_m)$: the spatial position in E^m;

$n(x,t)$: the spatial density of the total population at location x and time t;

$u_1(x,t,\tau_1)$: the age-space density of males at age τ_1, location x and time t;

$u_2(x,t,\tau_2)$: the age-space density of single (nonfertilized) females at age τ_2, location x and time t;

$u_3(x,t,\tau_1,\tau_2,\tau_3)$: the age-space density of fertilized females at age τ_2, position x and time t whose embryo is at age τ_3 and that were fertilized by a male at age τ_1;

$p(x,t,\tau_1,\tau_2,n(x,t))$: the density of probability to become fertilized for a female from the male-female pair formed of a male at age τ_1 and a female at age τ_2, at location x and time t;

$\nu_1(x,t,\tau_1,n(x,t))$ (resp. $\nu_2(x,t,\tau_2,n(x,t))$): the death rate of males at age τ_1 (resp. single females at age τ_2), position x and time t;

$\nu_3(x,t,\tau_1,\tau_2,\tau_3,n(x,t))$: the death rate of fertilized females at age τ_2, position x and time t whose embryo is at age τ_3 and that were fertilized by a male at age τ_1;

$\chi(x,t,\tau_1,\tau_2,\tau_3,n(x,t))$: the abortion rate of fertilized females at age τ_2, position x and time t whose embryo is at age τ_3 and that were fertilized by a male at age τ_1;

$X_c(x,t,\tau_2)$: the single female loss due to conception at age τ_2, location x and time t;

$X_a(x,t,\tau_2)$: the single female gain by the females which have had an abortion at age τ_2, location x and time t;

$X_b(x,t,\tau_2)$: the single female gain by the females which have had a delivery at age τ_2, position x and time t;

$\sigma_1 = (\tau_{11}, \tau_{12}]$, $0 < \tau_{11} < \tau_{12} < \infty$: the male sexual activity interval, $\bar\sigma_1 = [\tau_{11}, \tau_{12}]$;

$\sigma_3 = (0, T]$, $0 < T < \infty$: the female gestation interval, $\bar\sigma_3 = [0, T]$;

$\sigma_2(\tau_3) = (\tau_{21} + \tau_3, \tau_{22} + \tau_3]$, $0 < \tau_{21} < \tau_{22} < \infty$, $\bar\sigma_2(\tau_3) = [\tau_{21} + \tau_3, \tau_{22} + \tau_3]$;

$\sigma_2(0)$, $\sigma_2(T)$: the female fertilization and reproduction (delivery) intervals, respectively;

$\sigma_a = (\tau_{21}, \tau_{22} + T]$: the female abortion interval;

$b_1(x,t,\tau_1,\tau_2,n(x,t-T))$ and $b_2(x,t,\tau_1,\tau_2,n(x,t-T))$: the average numbers of the male and female offspring, respectively, produced at time t at position x by a fertilized female of characteristic (τ_1, τ_2, T);

$\kappa_{1r}(x,t,\tau_1,n(x,t))$, $\kappa_{2r}(x,t,\tau_2,n(x,t))$, $\kappa_{3r}(x,t,\tau_1,\tau_2,\tau_3,n(x,t))$: the diffusion moduli for random dispersal;

$\kappa_{1d}(x,t,\tau_1,n(x,t))$, $\kappa_{2d}(x,t,\tau_2,n(x,t))$, $\kappa_{3d}(x,t,\tau_1,\tau_2,\tau_3,n(x,t))$: the diffusion moduli for directed dispersal;

$u_1^0(x,\tau_1)$, $u_2^0(x,\tau_2)$, $u_3^0(x,\tau_1,\tau_2,\tau_3)$: the initial distributions;

$\tau_2^0 = 0$, $\tau_2^1 = \tau_{21}$, $\tau_2^2 = \min(\tau_{21}+T,\tau_{22})$, $\tau_2^3 = \max(\tau_{21}+T,\tau_{22})$, $\tau_2^4 = \tau_{22}+T$, $\tau_2^5 = \infty$;

$I = (0,\infty)$, $\bar I = [0,\infty)$, $I_4 = (\tau_2^4,\infty)$, $\bar I_4 = [\tau_2^4,\infty)$, $I_s = (\tau_2^s,\tau_2^{s+1}]$, $\bar I_s = [\tau_2^s,\tau_2^{s+1}]$, $s = 0,1,2,3$;

$I^* = (0,t^*]$, $\bar I^* = [0,t^*]$, $t^* < \infty$;

$Q_1 = \{(t,\tau_1) \in I \times I\}$, $Q_2 = \{(t,\tau_2) \in I \times (I \setminus \bigcup_{s=1}^{4} \{\tau_2^s\})\}$;

$Q_3 = \{(t,\tau_1,\tau_2,\tau_3) \in I \times \sigma_1 \times \sigma_2(\tau_3) \times \sigma_3\}$, where $\sigma_2(\tau_3) \times \sigma_3 := \{(\tau_2,\tau_3) : \tau_2 \in \sigma_2(\tau_3),\ \tau_3 \in \sigma_3\}$;

$\widehat D_1 = \partial/\partial t + \partial/\partial\tau_1$, $\widehat D_2 = \partial/\partial t + \partial/\partial\tau_2$, $\widehat D_3 = \widehat D_2 + \partial/\partial\tau_3$;

$\tilde D_i$, $i = 1,2,3$: the directional derivative in the positive direction of characteristics of the operator $\widehat D_i$;

$D_1 = \sqrt{2}\tilde D_1$, $D_2 = \sqrt{2}\tilde D_2$, $D_3 = \sqrt{3}\tilde D_3$;

div, ∇: the divergence and gradient operators, respectively;

$[u_2|_{\tau_2=\tau_2^i}]$: the jump of u_2 at the plane $\tau_2 = \tau_2^i$;

$$\Omega(\tau_2) = \begin{cases} [0,\tau_2-\tau_{21}], & \tau_2 \in (\tau_{21},\tau_{21}+T],\\ [0,T], & \tau_2 \in (\tau_{21}+T,\tau_{22}],\\ [\tau_2-\tau_{22},T], & \tau_2 \in (\tau_{22},\tau_{22}+T] \end{cases}$$

if $\tau_{22}-\tau_{21} > T$, and

$$\Omega(\tau_2) = \begin{cases} [0,\tau_2-\tau_{21}], & \tau_2 \in (\tau_{21},\tau_{22}],\\ [\tau_2-\tau_{22},\tau_2-\tau_{21}], & \tau_2 \in (\tau_{22},\tau_{21}+T],\\ [\tau_2-\tau_{22},T], & \tau_2 \in (\tau_{21}+T,\tau_{22}+T] \end{cases}$$

if $\tau_{22}-\tau_{21} \le T$;

$L^1(D)$: the Banach space of integrable functions on D, where D is an open set (non necessarily bounded);

$C(D)$: a class of bounded continuous functions in D;

$C^1(D)$: a class of continuously differentiable functions in D with bounded partial derivatives.

For more details concerning population densities and vital rates we refer the reader to (Skakauskas, 1994; 1996).

3. Spatially Homogeneous Model

The model we consider in this section can be derived from the general one in (Skakauskas, 1994) by neglecting the sterility periods after abortion and delivery. It consists of the following system of nonlinear integrodifferential equations for $u_1,\ u_2,\ u_3$:

$$D_1 u_1 = -\nu_1 u_1 \quad \text{in} \quad Q_1, \tag{1a}$$

$$D_2 u_2 = -\nu_2 u_2 - X_c + X_b + X_a \quad \text{in} \quad Q_2, \tag{1b}$$

$$D_3 u_3 = -(\nu_3 + \chi) u_3 \quad \text{in} \quad Q_3, \tag{1c}$$

$$X_c = \begin{cases} 0, & \tau_2 \notin \sigma_2(0), \\ \int\limits_{\sigma_1} u_3\big|_{\tau_3=0}\, \mathrm{d}\tau_1, & \tau_2 \in \sigma_2(0), \end{cases} \tag{1d}$$

$$X_b = \begin{cases} 0, & \tau_2 \notin \sigma_2(T), \\ \int\limits_{\sigma_1} u_3\big|_{\tau_3=T}\, \mathrm{d}\tau_1, & \tau_2 \in \sigma_2(T), \end{cases} \tag{1e}$$

$$X_a = \begin{cases} 0, & \tau_2 \notin \sigma_a, \\ \int\limits_{\Omega(\tau_2)} \mathrm{d}\tau_3 \int\limits_{\sigma_1} \chi u_3\, \mathrm{d}\tau_1, & \tau_2 \in \sigma_a, \end{cases} \tag{1f}$$

$$n = \int\limits_I u_1\, \mathrm{d}\tau_1 + \int\limits_I u_2\, \mathrm{d}\tau_2 + \int\limits_{\sigma_3} \mathrm{d}\tau_3 \int\limits_{\sigma_2(\tau_3)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} u_3\, \mathrm{d}\tau_1, \tag{1g}$$

supplemented with the conditions

$$u_k\big|_{t=0} = u_k^0, \quad k = 1,2 \quad \text{in} \quad I, \tag{2a}$$

$$u_3\big|_{t=0} = u_3^0 \quad \text{in} \quad \sigma_1 \times \sigma_2(\tau_3) \times \sigma_3, \tag{2b}$$

$$u_k\big|_{\tau_k=0} = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_k u_3\big|_{\tau_3=T}\, \mathrm{d}\tau_1, \quad k = 1,2 \quad \text{in} \quad I, \tag{2c}$$

$$u_3\big|_{\tau_3=0} = p u_1 u_2 / \int\limits_{\sigma_1} u_1(t,\xi)\, \mathrm{d}\xi \quad \text{in} \quad I \times \sigma_1 \times \sigma_2(0), \tag{2d}$$

$$\left[u_2\big|_{\tau_2=\tau_2^s}\right] = 0, \quad s = 1,2,3,4 \quad \text{in} \quad I, \tag{2e}$$

$$n(t) = \omega(t), \quad t \in [-T, 0], \tag{2f}$$

and describes evolution of the population without spatial dispersal. In addition to (2) we assume that the initial distributions u_1^0, u_2^0, u_3^0 satisfy the following compatibility conditions:

$$u_k^0\big|_{\tau_k=0} = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_k\big|_{t=0} u_3^0\big|_{\tau_3=T}\,\mathrm{d}\tau_1, \quad k=1,2; \tag{3a}$$

$$\left[u_2^0\big|_{\tau_2=\tau_2^i}\right] = 0, \quad i=1,2,3,4; \tag{3b}$$

$$u_3^0\big|_{\tau_3=0} = p\big|_{t=0} u_1^0 u_2^0 \Big/ \int\limits_{\sigma_1} u_1^0\,\mathrm{d}\tau_1 \quad \text{in} \quad \sigma_1 \times \sigma_2(0). \tag{3c}$$

As follows from the foregoing, given functions ν_1, ν_2, ν_3, p, χ, b_1, b_2, u_1^0, u_2^0, u_3^0, ω and the unknown ones u_1, u_2, u_3 must be positive-valued, otherwise they have no biological significance.

As in (Skakauskas, 1998; Svirezhev and Passekov, 1990), for the mating law, on the right-hand side of (2d) we use a simplified harmonic mean type function. According to Svirezhev and Passekov (1990) this simplified mating law means some degree of poligamy. The use of the harmonic mean type function

$$\frac{p u_1 u_2}{\int\limits_{\sigma_1} u_1\,\mathrm{d}\tau_1 + \int\limits_{\sigma_2(0)} u_2\,\mathrm{d}\tau_2}$$

leads to a much more stronger nonlinearity in model (1)–(3), and we do not consider it in this paper.

We limit ourselves to the case

$$\nu_i\big(t,\tau_i,n(t)\big) = \tilde{\nu}_i(t,\tau_i) + \nu\big(t,n(t)\big), \quad i=1,2, \tag{4a}$$

$$\nu_3\big(t,\tau_1,\tau_2,\tau_3,n(t)\big) = \tilde{\nu}_3(t,\tau_1,\tau_2,\tau_3) + \nu\big(t,n(t)\big), \tag{4b}$$

$$p\big(t,\tau_1,\tau_2,n(t)\big) = p(t,\tau_1,\tau_2), \tag{4c}$$

$$\chi\big(t,\tau_1,\tau_2,\tau_3,n(t)\big) = \chi(t,\tau_1,\tau_2,\tau_3), \tag{4d}$$

$$b_i\big(t,\tau_1,\tau_2,n(t-T)\big) = b_i(t,\tau_1,\tau_2), \quad i=1,2. \tag{4e}$$

Observe that, because of the constraint (4e), there is no need to formulate the condition $n(t)=\omega(t)$ for $t\in[-T,0]$ in this case. We also assume the multiple deliveries including overlapping between successive generations, i.e. $\tau_{22}-\tau_{21}>T$, $\tau_2^2=\tau_{21}+T$, $\tau_2^3=\tau_{22}$. All the results obtained in this paper can be easily modified and applied for the opposite case, too.

3.1. Solvability of Model (1)–(4) in Case $\nu(t,n)\equiv 0$

In this subsection, we establish the existence and uniqueness of a solution to (1)–(4) in the case where $\nu(t,n) = 0$ and obtain its upper estimate.

We first examine solvability of model (1)–(4). To do this, we rewrite it in the integral form as follows:

$$u_1 = \begin{cases} u_{1*}(\tau_1 - t;\tau_1) \stackrel{\text{def}}{\equiv} u_1^0(\tau_1 - t)\exp\left\{-\int\limits_{\tau_1-t}^{\tau_1} \tilde{\nu}_1(\xi + t - \tau_1, \xi)\,\mathrm{d}\xi\right\}, & t \le \tau_1, \quad (5a) \\ u_1^*(t-\tau_1;\tau_1) \stackrel{\text{def}}{\equiv} u_1(t-\tau_1, 0)\exp\left\{-\int\limits_0^{\tau_1} \tilde{\nu}_1(\xi + t - \tau_1, \xi)\,\mathrm{d}\xi\right\}, & t \ge \tau_1, \quad (5b) \end{cases}$$

$$u_3 = \begin{cases} u_{3*}(\tau_3 - t, \tau_1, \tau_2 - \tau_3; \tau_3) \stackrel{\text{def}}{\equiv} u_3^0(\tau_1, \tau_2 - t, \tau_3 - t) \\ \quad \times \exp\left\{-\int\limits_{\tau_3 - t}^{\tau_3} (\tilde{\nu}_3 + \chi)\Big|_{(\xi+t-\tau_3, \tau_1, \xi+\tau_2-\tau_3, \xi)} \mathrm{d}\xi\right\}, & t \le \tau_3, \quad (6a) \\ u_3^*(t-\tau_3, \tau_1, \tau_2 - \tau_3; \tau_3) \stackrel{\text{def}}{\equiv} \left(p\, u_1\, u_2 \Big/ \int\limits_{\sigma_1} u_1\,\mathrm{d}\xi\right)\Bigg|_{(t-\tau_3, \tau_1, \tau_2-\tau_3)} \\ \quad \times \exp\left\{\int\limits_0^{\tau_3} (\tilde{\nu}_3 + \chi)\Big|_{(\xi+t-\tau_3, \tau_1, \xi+\tau_2-\tau_3, \xi)} \mathrm{d}\xi\right\}, & t \ge \tau_3, \quad (6b) \end{cases}$$

$$u_2 = \begin{cases} u_{2*}(\tau_2 - t;\tau_2) \stackrel{\text{def}}{\equiv} u_2^0(\tau_2 - t)\exp\left\{-\int\limits_{\tau_2-t}^{\tau_2} (\tilde{\nu}_2 + \nu_{2c})\Big|_{(\xi+t-\tau_2,\xi)} \mathrm{d}\xi\right\} \\ \quad + \int\limits_{\tau_2-t}^{\tau_2} \exp\left\{-\int\limits_x^{\tau_2} (\tilde{\nu}_2 + \nu_{2c})\Big|_{(\xi+t-\tau_2,\xi)} \mathrm{d}\xi\right\} \\ \quad \times (X_b + X_a)\big|_{(x+t-\tau_2,x)}\,\mathrm{d}x, \qquad t \le \tau_2 - \tau_2^i, \quad \tau_2 \in I_i, \quad i = \overline{0,4}, & (7a) \\ u_2^*(t-\tau_2;\tau_2) \stackrel{\text{def}}{\equiv} u_2(\tau_2^i + t - \tau_2, \tau_2^i)\exp\left\{-\int\limits_{\tau_2^i}^{\tau_2} (\tilde{\nu}_2 + \nu_{2c})\Big|_{(\xi+t-\tau_2,\xi)} \mathrm{d}\xi\right\} \\ \quad + \int\limits_{\tau_2^i}^{\tau_2} \exp\left\{-\int\limits_x^{\tau_2} (\tilde{\nu}_2 + \nu_{2c})\Big|_{(\xi+t-\tau_2,\xi)} \mathrm{d}\xi\right\} \\ \quad \times (X_b + X_a)\big|_{(x+t-\tau_2,x)}\,\mathrm{d}x, \qquad t > \tau_2 - \tau_2^i, \quad \tau_2 \in I_i, \quad i = \overline{0,4} & (7b) \end{cases}$$

with $[u_2(t,\tau_2^i)]=0,\ i=1,2,3,4,$

$$u_i(t,0)=\int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_i u_3|_{\tau_3=T}\,\mathrm{d}\tau_1,\quad i=1,2, \tag{8}$$

$$\nu_{2c}(t,\tau_2)=\begin{cases} 0, & \tau_2\notin\sigma_2(0),\\ \int\limits_{\sigma_1} pu_1\,\mathrm{d}\xi\Big/\int\limits_{\sigma_1} u_1\,\mathrm{d}\tau_1, & \tau_2\in\sigma_2(0). \end{cases} \tag{9}$$

Then we insert (6) into (2c) and (1e), (1f) to obtain

$$u_k(t,0)=\begin{cases} \int\limits_{\sigma_1}\mathrm{d}\tau_1\int\limits_{\sigma_2(T)} b_k u_{3*}|_{\tau_3=T}\,\mathrm{d}\tau_2, & 0\le t\le T, \quad (10a)\\ \int\limits_{\sigma_2(T)} u_2(t-T,\tau_2-T)F(b_k)\big|_{\tau_3=T}\,\mathrm{d}\tau_2, & t>T, \quad (10b)\end{cases}$$

$$X_b=\begin{cases} \int\limits_{\sigma_1} u_{3*}|_{\tau_3=T}\,\mathrm{d}\tau_1, & 0<t\le T,\quad \tau_2\in\sigma_2(T), \quad (11a)\\ u_2(t-T,\tau_2-T)F(1)\big|_{\tau_3=T}, & t>T,\quad \tau_2\in\sigma_2(T), \quad (11b)\end{cases}$$

$$X_a=\begin{cases} \int\limits_0^t u_2(t-\tau_3,\tau_2-\tau_3)F(\chi)\,\mathrm{d}\tau_3 \\ \quad +\int\limits_t^{\tau_2-\tau_{21}}\mathrm{d}\tau_3\int\limits_{\sigma_1}\chi u_{3*}\,\mathrm{d}\tau_1, & 0<t\le\tau_2-\tau_{21},\quad \tau_2\in I_1,\\ \int\limits_0^{\tau_2-\tau_{21}} u_2(t-\tau_3,\tau_2-\tau_3)F(\chi)\,\mathrm{d}\tau_3, & t>\tau_2-\tau_{21},\quad \tau_2\in I_1,\end{cases} \tag{12}$$

$$X_a=\begin{cases} \int\limits_0^t u_2(t-\tau_3,\tau_2-\tau_3)F(\chi)\,\mathrm{d}\tau_3 \\ \quad +\int\limits_t^{T}\mathrm{d}\tau_3\int\limits_{\sigma_1}\chi u_{3*}\,\mathrm{d}\tau_1, & 0<t\le T,\quad \tau_2\in I_2,\\ \int\limits_0^{T} u_2(t-\tau_3,\tau_2-\tau_3)F(\chi)\,\mathrm{d}\tau_3, & t>T,\quad \tau_2\in I_2,\end{cases} \tag{13}$$

$$X_a = \begin{cases} \int\limits_{\tau_2-\tau_{22}}^{T} d\tau_3 \int\limits_{\sigma_1} \chi u_{3*} \, d\tau_1, & 0 < t \le \tau_2 - \tau_{22}, \quad \tau_2 \in I_3, \quad \text{(14a)} \\ \int\limits_{\tau_2-\tau_{22}}^{t} u_2(t-\tau_3, \tau_2-\tau_3) F(\chi) \, d\tau_3 & \\ \quad + \int\limits_{t}^{T} d\tau_3 \int\limits_{\sigma_1} \chi u_{3*} \, d\tau_1, & \tau_2 - \tau_{22} < t \le T, \quad \tau_2 \in I_3, \quad \text{(14b)} \\ \int\limits_{\tau_2-\tau_{22}}^{T} u_2(t-\tau_3, \tau_2-\tau_3) F(\chi) \, d\tau_3, & t > T, \quad \tau_2 \in I_3, \quad \text{(14c)} \end{cases}$$

where

$$F(f)(t,\tau_2,\tau_3) = \int\limits_{\sigma_1} f(t,\tau_1,\tau_2,\tau_3) u_1(t-\tau_3,\tau_1) p(t-\tau_3,\tau_1,\tau_2-\tau_3)$$

$$\times \exp\left\{ -\int\limits_0^{\tau_3} (\tilde{\nu}_3 + \chi)\big|_{(\xi+t-\tau_3,\tau_1,\xi+\tau_2-\tau_3,\xi)} \, d\xi \right\} d\tau_1 \bigg/ \int\limits_{\sigma_1} u_1(t-\tau_3,\tau_1) \, d\tau_1,$$

$$f = 1, \chi, b_i \qquad (15)$$

and $k = 1, 2$. We also add to this system equation (1g). Equations (10) and (11) include the delayed argument $t - T$. This allows us to examine problem (5)–(15) going along the axis t by the step of size T.

Let $t \in (0, T]$. Equations (10a) and (11a) show that $u_1(t,0)$, $u_2(t,0)$, and $X_b(t,\tau_2)$ are determined by u_{3*} (see (6a)) and are consequently known. Then, by (5), we find u_1, and after that, by (9), we construct ν_{2c}. The right-hand side of (7) for $\tau_2 \in \bar{I}_0$ is now known while, for $\tau_2 \in \bar{I}_4$, it includes $u_2(t, \tau_2^4)$, which should be found by solving (7) for $\tau_2 \in \bar{I}_3$. Equations (12)–(14) show that $X_a(u_3)$ involves $u_2(t-\tau_3, \tau_2-\tau_3)$ with $t-\tau_3 \le t$, $\tau_2-\tau_3 \le \tau_2$ for $\tau_2 \in \bar{I}_1 \cup \bar{I}_2$ and $t-\tau_3 \le t-\tau_2+\tau_2^3$, $\tau_2 - \tau_3 \le \tau_2^3$ for $\tau_2 \in \bar{I}_3$. Hence $X_a(u_3)$ includes $u_2(t,\tau_2)$, and (7), with $\tau_2 \in I_1 \cup \bar{I}_2$ and $u_2(t, \tau_2^1)$ being determined, is a linear integral equation of Volterra type for u_2. The right-hand side of (7) (and therefore u_2) for $\tau_2 \in \bar{I}_3$ is known whenever u_2 for $\tau_2 \in \bar{I}_2$ is known. Under appropriate restrictions on ν_1, ν_2, ν_3, b_1, b_2, p, χ, u_1^0, u_2^0, u_3^0 (e.g., ν_1, ν_2, ν_3, u_1^0, u_2^0, u_3^0 are nonnegative and continuous, and b_1, b_2, p, χ are nonnegative, continuous, and bounded) this integral equation has a unique continuous solution. At last, using (6) with known u_1 and u_2, we can construct u_3.

Notice that compatibility conditions (3) ensure the continuity of functions u_1 and u_2 across the lines $t = \tau_1$ and $t = \tau_2 - \tau_2^i$, $i = 0, 1, 2, 3, 4$, respectively, and the continuity of u_3 across the planes $t = \tau_1 + \tau_3$, $t = \tau_2 - \tau_2^i$, $i = 0, 1, 2, 3$, $t = \tau_3$.

Let $t \in (T, 2T]$. Having obtained u_1 and u_2 for $t \in [0, T]$, by (10b) and (**11**b) we construct $u_1(t,0)$, $u_2(t,0)$ and $X_b(t,\tau_2)$, then by (5) and (9) we obtain u_1 and ν_{2c} and, finally, solving (7) as above, we get u_2 for $\tau_2 \in \bar{I}$.

Going along the t axis with the step of size T and using the previous arguments we can construct a unique continuous solution to (5)–(16) for $t \in \bar{I}^*$. Finally, by (1g), we determine the total population n.

Now we show that $n \in C^1(I^*)$. By (1g) and (5)–(7) it follows that

$$
\begin{aligned}
n = {} & \int_0^t u_1^*(x; t-x)\,\mathrm{d}x + \int_0^\infty u_{1*}(x; t+x)\,\mathrm{d}x + \sum_{k=0}^{4} \int_{-\tau_2^k}^{t-\tau_2^k} u_2^*(x; t-x)\,\mathrm{d}x \\
& + \sum_{k=0}^{3} \int_{\tau_2^k}^{\tau_2^{k+1}-t} u_{2*}(x; t+x)\,\mathrm{d}x + \int_{\tau_2^4}^{\infty} u_{2*}(x; t+x)\,\mathrm{d}x \\
& + \int_0^t \mathrm{d}x \int_{\sigma_2(0)} \mathrm{d}\tau_2 \int_{\sigma_1} u_1(x,\tau_1) u_2(x,\tau_2) a(x,\tau_1,\tau_2; t-x)\,\mathrm{d}\tau_1 \\
& + \int_0^{\max(T-t,0)} \mathrm{d}x \int_{\sigma_2(0)} \mathrm{d}\tau_2 \int_{\sigma_1} u_{3*}(x,\tau_1,\tau_2; x+t)\,\mathrm{d}\tau_1,
\end{aligned}
\tag{16}
$$

where

$$
a(t,\tau_1,\tau_2;\tau_3) = \frac{p(t,\tau_1,\tau_2)}{\int_{\sigma_1} u_1(t,\xi)\,\mathrm{d}\xi} \exp\left\{ - \int_0^{\tau_3} (\tilde{\nu}_3 + \chi)\big|_{(\xi+t,\tau_1,\xi+\tau_2,\xi)}\,\mathrm{d}\xi \right\}.
$$

Again using (5)–(7) we observe that u_{1*}, u_1^*, u_{2*}, u_2^*, u_{3*}, u_3^* and a are continuously differentiable with respect to the last of their arguments. Hence D_1u_1, D_2u_2, D_3u_3 by (1) are continuous in Q_1, Q_2, Q_3, respectively, and, by (16), $n \in C^1(I^*)$, provided that $\int_0^\infty u_{1*}(x; t+x)\,\mathrm{d}x$ and $\int_{\tau_2^4}^\infty u_{2*}(x; t+x)\,\mathrm{d}x$ belong to $C^1(I^*)$, too. Thus we have proved the following result:

Theorem 1. *Assume that:*

(H1) p, χ, b_1, b_2, $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$ *are nonnegative;*

(H2) $p \in C\big(\bar{I}^* \times \bar{\sigma}_1 \times \bar{\sigma}_2(0)\big)$, $\tilde{\nu}_3$ *and* $\chi \in C\big(\bar{I}^* \times \bar{\sigma}_1 \times \bar{\sigma}_2(\tau_3) \times \bar{\sigma}_3\big)$,

$\tilde{\nu}_i \in C\left(\bar{I}^* \times \bar{I}\right)$, $b_i \in C\big(\bar{I}^* \times \bar{\sigma}_1 \times \bar{\sigma}_2(T)\big)$, $i = 1, 2$,

$u_3^0 \in C\big(\bar{\sigma}_1 \times \bar{\sigma}_2(\tau_3) \times \bar{\sigma}_3\big)$, $u_i^0 \in C\left(\bar{I}\right) \cap L^1(I)$, $i = 1, 2$.

Then in the case $\nu(t,n) \equiv 0$ problem (1)–(4) has a unique nonnegative continuous solution for $t \in \bar{I}^*$. If, in addition, the integrals

$$\int_{\tau}^{\infty} u_1^0(x)\tilde{\nu}_i(t,t+x)\exp\left\{-\int_{x}^{t+x}\tilde{\nu}_i(\xi-x,\xi)\,\mathrm{d}\xi\right\}\mathrm{d}x, \quad i=1,2$$

converge for any $\tau > 0$ and all $t \in I^*$, then $\dot{n} \in C^1(I^*)$.

Now we want to obtain an upper estimate for u_1, u_2, and $\int_{\sigma_1} u_3\,\mathrm{d}\tau_1$. To do this, we substitute

$$u_2(t,\tau_2) = u_2(t-\tau_2,0)\,U_2(t,\tau_2), \quad t > \tau_2 \tag{17}$$

into (7b), (10b)–(14b) and, making the change of variable $z = x - \tau_3$, we get

$$\begin{aligned} U_2(\tau_2+\eta,\tau_2) &= U_2(\tau_2^i+\eta,\tau_2^i)\exp\left\{-\int_{\tau_2^i}^{\tau_2}(\tilde{\nu}_2+\nu_{2c})\big|_{(\xi+\eta,\xi)}\,\mathrm{d}\xi\right\} \\ &+ \int_{\tau_2^i}^{\tau_2}\exp\left\{-\int_{x}^{\tau_2}(\tilde{\nu}_2+\nu_{2c})\big|_{(\xi+\eta,\xi)}\,\mathrm{d}\xi\right\} \\ &\times\left\{F(1)(x+\eta,x,T)\,U_2(\eta+x-T,x-T)\right. \\ &+\left.\int_{\tilde{\Omega}(x)} F(\chi)(x+\eta,x,x-z)U_2(\eta+z,z)\,\mathrm{d}z\right\}\mathrm{d}x, \\ &\qquad t>\tau_2, \quad \tau_2\in I_i, \quad i=0,1,2,3,4, \end{aligned} \tag{18}$$

$$u_i(t,0) = \begin{cases} \displaystyle\int_{\sigma_2(T)}\mathrm{d}\tau_2\int_{\sigma_1} b_i u_{3*}\big|_{\tau_3=T}\,\mathrm{d}\tau_1, & 0 \le t \le T, \quad (19a) \\ \displaystyle\int_{\sigma_2(T)} u_2(t-T,\tau_2-T)\,F(b_i)\big|_{\tau_3=T}\,\mathrm{d}\tau_2, & T \le t \le \tau_2^2, \quad (19b) \\ \displaystyle\int_{\tau_2^2}^{t} u_2(t-\tau_2,0)U_2(t-T,\tau_2-T)F(b_i)\big|_{\tau_3=T}\,\mathrm{d}\tau_2 & \\ \displaystyle\quad+\int_{t}^{\tau_2^4} u_2(t-T,\tau_2-T)F(b_i)\big|_{\tau_3=T}\,\mathrm{d}\tau_2, & t\in\left(\tau_2^2,\tau_2^4\right], \quad (19c) \\ \displaystyle\int_{\sigma_2(T)} u_2(t-\tau_2,0)U(t-T,\tau_2-T)F(b_i)\big|_{\tau_3=T}\,\mathrm{d}\tau_2, & t > \tau_2^4, \quad (19d) \end{cases}$$

where $j = 1, 2,\ \eta = t - \tau_2,\ U_2(t, 0) = 1,\ [U_2(t, \tau_2^k)] = 0,\ k = 1, 2, 3, 4$, and

$$\widetilde{\Omega}(x) = \begin{cases} [\tau_2^1, x], & x \in \bar{I}_1, \\ [x - T, x], & x \in \bar{I}_2, \\ [x - T, \tau_2^3], & x \in \bar{I}_3. \end{cases} \tag{20}$$

Formula (17) reduces the problem of finding $u_2(t, \tau_2)$ for $t > \tau_2$ to that of finding $U_2(t, \tau_2)$ with simplified conditions.

Now we analyze (18). We have

$$U_2(\tau_2 + \eta) = \exp\left\{ - \int_0^{\tau_2} \tilde{\nu}_2(\xi + \eta, \xi)\, \mathrm{d}\xi \right\}, \quad \tau_2 \in \bar{I}_0,$$

$$U_2(\tau_2 + \eta) = U_2(\tau_2^4 + \eta, \tau_2^4) \exp\left\{ - \int_{\tau_2^4}^{\tau_2} \tilde{\nu}_2(\xi + \eta, \xi)\, \mathrm{d}\xi \right\}, \quad \tau_2 \in \bar{I}_4.$$

Having obtained $U_2(\tau_2^4 + \eta, \tau_2^4)$, based on the right-hand side of the last equation we can construct $U_2(t, \tau_2)$ for $\tau_2 \in \bar{I}_4$. When $U_2(t, \tau_2)$ for $\tau_2 \in \bar{I}_2$ is known, then analogously to (7), we can show that so is the right-hand side of (18) for $\tau_2 \in \bar{I}_3$. Thus it remains to solve (18) for $\tau_2 \in I_1 \cup \bar{I}_2$. Since

$$\int_{x-T}^{x} F(\chi)(x + \eta, x, x - z) U_2(\eta + z, z)\, \mathrm{d}z$$

$$= \int_{\tau_2^1 + kT}^{x} F(\chi)(x + \eta, x, x - z) U_2(\eta + z, z)\, \mathrm{d}z$$

$$+ \int_{x-T}^{\tau_2^1 + kT} F(\chi)(x + \eta, x, x - z) U_2(\eta + z, z)\, \mathrm{d}z$$

for $x \in (\tau_2^1 + kT, \min(\tau_2^3, \tau_2^1 + (k+1)T)]$, $k = 1, 2, \ldots, s$, where s is the integer part of $(\tau_2^3 - \tau_2^1)/T$, eqn. (18) for $\tau_2 \in I_1 \cup \bar{I}_2$ represents a system of successively and globally solvable Volterra-type integral equations for U_2, provided that u_1 is known and all the conditions of Theorem 1 with $\bar{I}^*$ replaced by $\bar{I}$ hold. Hence $U_2(t, \tau_2)$ is a nonnegative, bounded and continuous function on $\bar{I} \times \bar{I}$. Moreover, $U_2 \le U_2^*$, U_2^* being a unique solution to (18) with $F(f)(t, \tau_2, \tau_3)$ and ν_{2c} replaced by

$$F^*(f^*)(t, \tau_2, \tau_3) = f^*(t, \tau_2, \tau_3)\, p^*(t - \tau_3, \tau_2 - \tau_3)$$

$$\times \exp\left\{ - \int_0^{\tau_3} (\nu_{3*} + \chi_*)\big|_{(\xi + t - \tau_3, \xi + \tau_2 - \tau_3, \xi)}\, \mathrm{d}\xi \right\},$$

and

$$\nu_{2c*} = \begin{cases} 0, & \tau_2 \notin \sigma_2(0), \\ p_*(t,\tau_2), & \tau_2 \in \sigma_2(0), \end{cases}$$

respectively, where $f^* = 1$, χ^* and

$$p^*(t,\tau_2) = \sup_{\tau_1 \in \bar\sigma_1} p, \qquad p_*(t,\tau_2) = \inf_{\tau_1 \in \bar\sigma_1} p,$$

$$\nu_{3*}(t,\tau_2,\tau_3) = \inf_{\tau_1 \in \bar\sigma_1} \tilde\nu_3, \qquad \chi_*(t,\tau_2,\tau_3) = \inf_{\tau_1 \in \bar\sigma_1} \chi.$$

Letting

$$b = \sup_{j,\bar I} \int\limits_{\sigma_2(T)} U_2(t-T,\tau_2-T)F(b_j)(t,\tau_2,T)\,\mathrm{d}\tau_2, \quad u^* = \sup_{t\in[0,\tau_2^4]} u_2(t,0)$$

and using (19d) we conclude that

$$u_j(t,0) \le b^k u^* \quad \text{for} \quad t \in (k\tau_2^4,(k+1)\tau_2^4], \quad k=1,2,\ldots, \quad j=1,2, \tag{21}$$

or, more roughly, $u_j \le u^* b^{t/\tau_2^4}$, $j=1,2$. Clearly, $b \le b^*$, where

$$b^* = \sup_{j,\bar I} \int\limits_{\sigma_2(T)} \tilde U_2(t-T,\tau_2-T)F^*(b_j^*)(t,\tau_2,T)\,\mathrm{d}\tau_2$$

with $b_j^*(t,\tau_2) = \sup_{\tau_1\in\bar\sigma_1} b_j$.

Now from (5b) and (17), by (21), the estimates

$$u_1 \le b^k u^* \exp\left\{ -\int\limits_0^{\tau_1} \tilde\nu_1(\xi+t-\tau_1,\xi)\,\mathrm{d}\tau_1 \right\}, \quad t-\tau_1 \in \big(k\tau_2^4,(k+1)\tau_2^4\big],$$

$$u_2 \le b^k u^* U_1(t,\tau_2), \qquad t-\tau_2 \in (k\tau_2^4,(k+1)\tau_2^4], \qquad k=1,2,\ldots \tag{22}$$

immediately follow, while (6b) shows that

$$\int\limits_{\sigma_1} u_3\,\mathrm{d}\tau_1 \le u_2(t-\tau_3,\tau_2-\tau_3)p^*(t-\tau_3,\tau_2-\tau_3)$$
$$\times \exp\left\{ -\int\limits_0^{\tau_3} (\nu_{3*}+\chi_*)\big|_{(\xi+t-\tau_3,\xi+t-\tau_3,\xi)}\,\mathrm{d}\xi \right\}$$

for $t > \tau_3$.

Thus we have the following assertion.

Theorem 2. *Under (H1) and (H2) of Theorem 1 the estimates (21) and (22) hold.*

Corollary 1. *If $b<1$, then the population dies.*

Remark 1. Theorems 1 and 2 remain true if we let b_i, $i=1,2$ in (4) depend on $n(t-T)$ and be uniformly bounded.

3.2. Product Solutions to Model (1)–(4) with $\nu(t,n)\equiv 0$

In this subsection, we deal with the situation of stationary vital functions $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$, χ, p, b_1, b_2 and special initial distributions u_1^0, u_2^0, u_3^0, and construct the corresponding solution.

Substituting

$$n = n^0 \exp\{\lambda t\}, \qquad u_i = u_i^0 \exp\{\lambda t\}, \qquad i = 1,2,3 \tag{23}$$

into (1)–(4) with given n^0 and λ being a constant gives the following system:

$$\begin{cases} \mathrm{d}u_1^0/\mathrm{d}\tau_1 = -(\lambda + \tilde{\nu}_1)u_1^0, \\ \mathrm{d}u_2^0/\mathrm{d}\tau_2 = -(\lambda + \tilde{\nu}_2)u_2^0 - X_c\left(u_3^0\big|_{\tau_3=0}\right) + X_b\left(u_3^0\big|_{\tau_3=T}\right) + X_a(u_3^0), \\ D_3^* u_3^0 = -(\lambda + \tilde{\nu}_3 + \chi)u_3^0, \end{cases} \tag{24}$$

subject to

$$u_k^0(0) = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_k u_3^0\big|_{\tau_3=T}\,\mathrm{d}\tau_1, \qquad [u_2^0(\tau_2^i)] = 0,$$

$$i = 1,2,3,4, \qquad k = 1,2,$$

$$u_3^0\big|_{\tau_3=0} = p u_1^0 u_2^0 \Big/ \int\limits_{\sigma_1} u_1^0(\xi)\,\mathrm{d}\xi,$$

$$n^0 = \int\limits_I u_1^0\,\mathrm{d}\tau_1 + \int\limits_I u_2^0\,\mathrm{d}\tau_2 + \int\limits_{\sigma_3} \mathrm{d}\tau_3 \int\limits_{\sigma_2(\tau_3)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} u_3^0\,\mathrm{d}\tau_1,$$

where $2^{-1/2}D_3^*$ is the directional derivative in the positive direction of characteristics of the operator $\partial/\partial\tau_2 + \partial/\partial\tau_3$.

Letting

$$\begin{aligned} &\tilde{\nu}_1,\ \tilde{\nu}_2 \in C(\bar{I}), \quad \chi \text{ and } \tilde{\nu}_3 \in C\big(\bar{\sigma}_1 \times \bar{\sigma}_2(\tau_3) \times \bar{\sigma}_3\big), \quad p \in C\big(\bar{\sigma}_1(0)\big), \\ &b_1 \text{ and } b_2 \in C\big(\bar{\sigma}_1 \times \bar{\sigma}_2(T)\big), \end{aligned} \tag{25}$$

it is easy to verify that (24) has the following solution:

$$u_1^0 = c_{1\lambda}c_{2\lambda}f_{1\lambda}(\tau_1), \qquad u_2^0 = c_{2\lambda}f_{2\lambda}(\tau_2),$$

$$u_3^0 = c_{2\lambda}\tilde{f}_{2\lambda}(\tau_2 - \tau_3)f_{3\lambda}(\tau_1, \tau_2 - \tau_3, \tau_3)\exp\{-\lambda\tau_2\},$$

where

$$f_{1\lambda} = \exp\left\{ -\lambda\tau_1 - \int\limits_0^{\tau_1} \tilde{\nu}_1(\xi)\,\mathrm{d}\xi \right\}, \qquad f_{2\lambda}(\tau_2) = \tilde{f}_{2\lambda}(\tau_2)\exp\{-\lambda\tau_2\},$$

$$f_{3\lambda}(\tau_1, \tau_2 - \tau_3, \tau_3) = \left(f_{1\lambda}(\tau_1) \Big/ \int\limits_{\sigma_1} f_{1\lambda}(\xi)\, \mathrm{d}\xi \right) p(\tau_1, \tau_2 - \tau_3)$$
$$\times \exp\left\{ -\int\limits_0^{\tau_3} (\tilde{\nu}_3 + \chi)\big|_{(\tau_1, \xi + \tau_2 - \tau_3, \xi)}\, \mathrm{d}\xi \right\},$$

$$c_{1\lambda} = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_1 \tilde{f}_{2\lambda}(\tau_2 - T) f_{3\lambda}(\tau_1, \tau_2 - T, T) \exp\{-\lambda\tau_2\}\, \mathrm{d}\tau_1,$$

$$c_{2\lambda} = n^0 \left\{ c_{1\lambda} \int\limits_I f_{1\lambda}\, \mathrm{d}\tau_1 + \int\limits_I f_{2\lambda}\, \mathrm{d}\tau_2 + \int\limits_{\sigma_3} \mathrm{d}\tau_3 \right.$$
$$\left. \times \int\limits_{\sigma_2(\tau_3)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} \tilde{f}_{2\lambda}(\tau_2 - \tau_3) f_{3\lambda}(\tau_1, \tau_2 - \tau_3, \tau_3) \exp\{-\lambda\tau_2\}\, \mathrm{d}\tau_1 \right\}^{-1},$$

λ is a real root of the characteristic equation

$$\widetilde{Q}(\lambda) \stackrel{\text{def}}{\equiv} \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_2 \tilde{f}_{2\lambda}(\tau_2 - T) f_{3\lambda}(\tau_1, \tau_2 - T, T)$$
$$\times \exp\{-\lambda\tau_2\}\, \mathrm{d}\tau_1, \qquad \widetilde{Q}(\lambda) = 1, \tag{26}$$

such that $\int_I u_i^0(\xi)\, \mathrm{d}\xi < \infty$, $i = 1, 2$, $\tilde{f}_{2\lambda}$ is a solution of the integro-differential equation

$$\mathrm{d}\tilde{f}_{2\lambda}/\mathrm{d}\tau_2 + (\tilde{\nu}_2 + \nu_{2\lambda})\tilde{f}_{2\lambda} = \begin{cases} 0, & \tau_2 \notin \sigma_2(T), \\ A_\lambda(\tau_2 - t, T)\tilde{f}_{2\lambda}(\tau_2 - T), & \tau_2 \in \sigma_2(T) \end{cases}$$
$$+ \begin{cases} 0, & \tau_2 \notin \sigma_a, \\ \int\limits_{\Omega(\tau_2)} B_\lambda(\tau_2, \tau_3)\tilde{f}_{2\lambda}(\tau_2 - \tau_3)\, \mathrm{d}\tau_3, & \tau_2 \in \sigma_a \end{cases} \tag{27}$$

with

$$\tilde{f}_{2\lambda}(0) = 1, \qquad \left[\tilde{f}_{2\lambda}(\tau_2^i)\right] = 0, \qquad i = 1, 2, 3, 4,$$

$$A_\lambda(\tau_2 - \tau_3, \tau_3) = \int\limits_{\sigma_1} f_{3\lambda}(\tau_1, \tau_2 - \tau_3, \tau_3)\, \mathrm{d}\tau_1,$$

$$B_\lambda(\tau_2, \tau_3) = \int\limits_{\sigma_1} \chi(\tau_1, \tau_2, \tau_3) f_{3\lambda}(\tau_1, \tau_2 - \tau_3, \tau_3)\, \mathrm{d}\tau_1,$$

$$\nu_{2\lambda}(\tau_2) = \begin{cases} 0, & \tau_2 \notin \sigma_2(0), \\ \int\limits_{\sigma_1} p f_{1\lambda}(\tau_1)\,\mathrm{d}\tau_1 \Big/ \int\limits_{\sigma_1} f_{1\lambda}(\tau_1)\,\mathrm{d}\tau_1, & \tau_2 \in \sigma_2(0). \end{cases}$$

From (27), for $\tau_2 \in \bar{I}_0 \cup \bar{I}_4$, we have

$$\tilde{f}_{2\lambda} = \exp\left\{ -\int\limits_0^{\tau_2} \tilde{\nu}_2(\xi)\,\mathrm{d}\xi \right\}, \quad \tilde{f}_{2\lambda} = \tilde{f}_{2\lambda}(\tau_2^4)\exp\left\{ -\int\limits_{\tau_2^4}^{\tau_2} \tilde{\nu}_2(\xi)\,\mathrm{d}\xi \right\},$$

whereas, for $\tau_2 \in \bar{I}_1 \cup \bar{I}_2 \cup \bar{I}_3$, unique solvability of this equation can be established analogously to that of (18).

Functions

$$\tilde{f}_{2\lambda}(\tau_2 - T), \quad \exp\left\{ -\int\limits_0^{\tau_1} \tilde{\nu}_1(\xi)\,\mathrm{d}\xi \right\} \quad \text{and} \quad \exp\left\{ -\int\limits_0^{T} (\tilde{\nu}_3 + \chi)\big|_{(\tau_1, \xi+\tau_2-T, \xi)}\,\mathrm{d}\xi \right\}$$

mean the probability for the female to survive till the age $\tau_2 - T$, probability for the male to survive till the age τ_1, and probability for the embryo to survive till the age T, provided that his mother has been fertilized at age $\tau_2 - T$ by his father at age τ_1, respectively.

In the general case, the distribution of roots of (26) is an *open problem*, but we look for a real root and, in the case where p, b_2, $\tilde{\nu}_3$, χ are τ_1-independent, we have

$$\nu_{2\lambda} = \nu_{2c} = \begin{cases} 0, & \tau_2 \notin \sigma_2(0), \\ p(\tau_2), & \tau_2 \in \sigma_2(0), \end{cases}$$

$$A(\tau_2 - \tau_3, \tau_3) = p(\tau_2 - \tau_3)\exp\left\{ -\int\limits_0^{\tau_3} (\tilde{\nu}_3 + \chi)\big|_{(\xi+\tau_2-\tau_3, \xi)}\,\mathrm{d}\xi \right\}, \tag{28}$$

$$A_\lambda(\tau_2 - T, T) = A(\tau_2 - T, T), \quad B_\lambda(\tau_2, \tau_3) = \chi(\tau_2, \tau_3)A(\tau_2 - \tau_3, \tau_3).$$

Hence $f(\tau_2) \overset{\mathrm{def}}{\equiv} \tilde{f}_{2\lambda}(\tau_2)$ does not depend on λ and represents a unique solution to the following equation:

$$\mathrm{d}f/\mathrm{d}\tau_2 + (\tilde{\nu}_2 + \nu_{2c})f = \begin{cases} 0, & \tau_2 \notin \sigma_2(T), \\ A(\tau_2 - T, T)f(\tau_2 - T), & \tau_2 \in \sigma_2(T) \end{cases}$$

$$+ \begin{cases} 0, & \tau_2 \notin \sigma_a, \\ \int\limits_{\tilde{\Omega}(\tau_2)} \chi(\tau_2, \tau_2 - x)A(x, \tau_2 - x)f(x)\,\mathrm{d}x, & \tau_2 \in \sigma_a \end{cases} \tag{29}$$

with $f(0)=1,\ [f(\tau_2^k)]=0,\ k=1,2,3,4$ and $\tilde\Omega(\tau_2)$ defined by (20). Thus (26) may be written in the form

$$\begin{aligned} Q(b_2,f,A)(\lambda) &\overset{\text{def}}{\equiv} \int\limits_{\sigma_2(T)} b_2 f(\tau_2-T)A(\tau_2-T,T)\exp\{-\lambda\tau_2\}\,\mathrm{d}\tau_2, \\ Q(b_2,f,A)(\lambda) &= 1. \end{aligned} \tag{30}$$

As is well known, the roots $\lambda_k=\alpha_k+i\beta_k,\ i=\sqrt{-1}$ of (30) are such that $\beta_0=0,\ \operatorname{sign}\alpha_0=\operatorname{sign}(Q(b_2,f,A)-1),\ \alpha_k<\alpha_0$ for $k=1,2,\dots,$ provided that $b_2 f(\tau_2-T)A(\tau_2-T)\in L^1(\sigma_2(T))$. Clearly, λ_0 is a simple root.

Now we turn to the problem of the existence of real roots of (26) in the general case. Assume that

$$p_*(\tau_2)=\inf_{\tau_1\in\sigma_1} p,\quad b_{2*}(\tau_2)=\inf_{\tau_1\in\sigma_1} b_2,\quad \nu_{3*}(\tau_2,\tau_3)=\inf_{\tau_1\in\sigma_1}\tilde\nu_3,\quad \chi_*(\tau_2,\tau_3)=\inf_{\tau_1\in\sigma_1}\chi,$$

$$p^*(\tau_2)=\sup_{\tau_1\in\sigma_1} p,\quad b_2^*(\tau_2)=\sup_{\tau_1\in\sigma_1} b_2,\quad \nu_3^*(\tau_2,\tau_3)=\sup_{\tau_1\in\sigma_1}\tilde\nu_3,\quad \chi^*(\tau_2,\tau_3)=\sup_{\tau_1\in\sigma_1}\chi,$$

$$A_*(\tau_2-\tau_3,\tau_3)=p_*(\tau_2-\tau_3)\exp\left\{-\int\limits_0^{\tau_3}(\nu_3^*+\chi^*)\big|_{(\xi+\tau_2-\tau_3)}\,\mathrm{d}\xi\right\},$$

$$A^*(\tau_2-\tau_3,\tau_3)=p^*(\tau_2-\tau_3)\exp\left\{-\int\limits_0^{\tau_3}(\nu_{3*}+\chi_*)\big|_{(\xi+\tau_2-\tau_3)}\,\mathrm{d}\xi\right\},$$

$$\nu_{2c*}(\tau_2)=\begin{cases}0, & \tau_2\notin\sigma_2(0),\\ p_*(\tau_2), & \tau_2\in\sigma_2(0),\end{cases}\qquad \nu_{2c}^*(\tau_2)=\begin{cases}0, & \tau_2\notin\sigma_2(0),\\ p^*(\tau_2), & \tau_2\in\sigma_2(0),\end{cases}$$

and let f_* and f^* obey the following equations:

$$\begin{aligned} \mathrm{d}f_*/\mathrm{d}\tau_2+(\tilde\nu_2+\nu_{2c}^*)\,f_* &= \begin{cases}0, & \tau_2\notin\sigma_2(T),\\ A_*(\tau_2-T,T)f_*(\tau_2-T), & \tau_2\in\sigma_2(T)\end{cases} \\ &+\begin{cases}0, & \tau_2\notin\sigma_a,\\ \displaystyle\int\limits_{\tilde\Omega(\tau_2)}\chi_*(\tau_2,\tau_2-x)A_*(x,\tau_2-x)f_*(x)\,\mathrm{d}x, & \tau_2\in\sigma_a\end{cases} \end{aligned} \tag{31}$$

with $f_*(0)=1,\ [f_*(\tau_2^i)]=0,\ i=1,2,3,4,$ and

$$\begin{aligned} \mathrm{d}f^*/\mathrm{d}\tau_2+(\tilde\nu_2+\nu_{2c*})f^* &= \begin{cases}0, & \tau_2\notin\sigma_2(T),\\ A^*(\tau_2-T,T)f^*(\tau_2-T), & \tau_2\in\sigma_2(T)\end{cases} \\ &+\begin{cases}0, & \tau_2\notin\sigma_a,\\ \displaystyle\int\limits_{\tilde\Omega(\tau_2)}\chi^*(\tau_2,\tau_2-x)A^*(x,\tau_2-x)f^*(x)\,\mathrm{d}x, & \tau_2\in\sigma_a\end{cases} \end{aligned} \tag{32}$$

with $f^*(0)=1$, $[f^*(\tau_2^i)]=0$, $i=1,2,3,4$. Then, by using (27), (31) and (32), it is easy to prove that $f_* \le f \le f^*$ for all τ_2. Hence

$$Q(b_{2*}, f_*, A_*) - 1 < \widetilde{Q}(\lambda) - 1 < Q(b_2^*, f^*, A^*) - 1. \tag{33}$$

As b_{2*}, b_2^*, A_*, A^* and f_*, f^* are continuous and bounded, both the sides of (33) have unique real roots λ_* and λ^*, respectively. Thus (26) has a real root $\lambda' \in (\lambda_*, \lambda^*)$. Let $\lambda'' = \max_i \lambda_i'$ for the case of some real roots of (26) and let us denote by λ_0 the values of λ_0 (the real root of (30)) and λ'' though they may be different. Now we are in a position to state the following assertion.

Theorem 3. *Given $n^0 > 0$ and nonnegative nontrivial functions p, χ, b_1, b_2, $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$ satisfying all the conditions (25), if $\int_\tau^\infty \exp\{-x\lambda_0 - \int_\tau^x \nu_i(\xi)\,\mathrm{d}\xi\}\,\mathrm{d}x$, $i=1,2$ with λ_0 a root of (26) converges for any $\tau > 0$, then problem (1)–(4) admits a separable solution (23), unique at least when p, χ, b_2 and $\tilde{\nu}_3$ are τ_1-independent.*

3.3. Asymptotic Behavior of the General Solution to Model (1)–(4) with $\nu(t,n)\equiv 0$

In this subsection, we shall establish the longtime behavior of the general solution to system (1)–(4) with stationary vital rates $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$, p, χ, b_1, b_2 for the case where $\nu(t,n)\equiv 0$ and p, χ, $\tilde{\nu}_3$, b_1, b_2 do not depend on the age τ_1 of a mated male. Under these restrictions function (15) at $\tau_3 = T$ becomes $F(b_i)(\tau_2,T) = A(\tau_2,T)b_i(\tau_2)$, $A(\tau_2,T)$ being defined by (28). In the case under consideration, all the coefficients in (18) and the condition for U_2 at $\tau_2=0$ do not depend on t. Hence $U_2(t,\tau_2) = f(\tau_2)$ with f defined by (29).

Now, by virtue of the estimate (21) we may apply the Laplace transform to (19) to obtain

$$\begin{aligned}
\widehat{u}_2(\lambda,0) = &\int_0^{\tau_2^2} \exp\{-\lambda t\}\,\mathrm{d}t \int_{\sigma_2(T)} b_2(\tau_2)\,\mathrm{d}\tau_2 \int_{\sigma_1} u_3(t,\tau_1,\tau_2,T)\,\mathrm{d}\tau_1 \\
&+ \int_{\tau_2^2}^{\tau_2^4} \exp\{-\lambda t\}\,\mathrm{d}t \left\{ \int_{\tau_2^2}^{t} u_2(t-\tau_2,0) f(\tau_2-T) F(b_2)(\tau_2,T)\,\mathrm{d}\tau_2 \right. \\
&\left. + \int_t^{\tau_2^4} u_2(t-T,\tau_2-T) F(b_2)(\tau_2,T)\,\mathrm{d}\tau_2 \right\} \\
&+ \int_{\tau_2^4}^{\infty} \exp\{-\lambda t\}\,\mathrm{d}t \int_{\sigma_2(T)} u_2(t-\tau_2,0) f(\tau_2-T) F(b_2)(\tau_2,T)\,\mathrm{d}\tau_2
\end{aligned}$$

or $\widehat{u}_2(\lambda,0) = \psi(\lambda) + \widehat{u}_2(\lambda,0)Q(b_2,f,A)(\lambda)$ with Q defined by (30) and

$$\psi(\lambda) = \int_0^{\tau_2^2} \exp\{-\lambda t\}\,\mathrm{d}t \int_{\sigma_2(T)} b_2(\tau_2)\,\mathrm{d}\tau_2 \int_{\sigma_1} u_3(t,\tau_1,\tau_2,T)\,\mathrm{d}\tau_1$$

$$+ \int_{\tau_2^2}^{\tau_2^4} \exp\{-\lambda t\}\,\mathrm{d}t \int_t^{\tau_2^4} u_2(t-T,\tau_2-T)F(b_2)(\tau_2,T)\,\mathrm{d}\tau_2.$$

Hence

$$\widehat{u}_2(\lambda,0) = \psi(\lambda)/\big(1-Q(b_2,f,A)\big).$$

We can now find the inverse Laplace transform of this equation. Noting that $\psi(\lambda)$ is an analytic function of λ and applying the method of the rectangular contour integral (Bellman and Cooke, 1963) we have

$$u_1(t,0) \sim c_{1\lambda_0}c_{2\lambda_0}\exp\{t\lambda_0\},$$

$$u_2(t,0) \sim c_{2\lambda_0}\exp\{t\lambda_0\}, \qquad c_{2\lambda_0} = -\psi(\lambda_0)/(\mathrm{d}Q/\mathrm{d}\lambda)|_{\lambda=\lambda_0},$$

where λ_0 is a real root of (30). This together with (17), (5b), (6b), and (1g) lead to the following longtime ($t > \max(\tau_1,\tau_2)$) asymptotic formulas:

$$u_1(t,\tau_1) \sim u_1^{\mathrm{as}} \stackrel{\mathrm{def}}{\equiv} c_{1\lambda_0}c_{2\lambda_0}\exp\left\{\lambda_0(t-\tau_1) - \int_0^{\tau_1}\tilde{\nu}_1(\xi)\,\mathrm{d}\xi\right\},$$

$$u_2(t,\tau_2) \sim u_2^{\mathrm{as}} \stackrel{\mathrm{def}}{\equiv} c_{2\lambda_0}f(\tau_2)\exp\{\lambda_0(t-\tau_2)\},$$

$$u_3(t,\tau_1,\tau_2,\tau_3) \sim u_3^{\mathrm{as}} \stackrel{\mathrm{def}}{\equiv} c_{2\lambda_0}f(\tau_2-\tau_3)f_{3\lambda_0}(\tau_1,\tau_2-\tau_3,\tau_3)\exp\{\lambda_0(t-\tau_2)\},$$

$$n \sim n^{\mathrm{as}} \stackrel{\mathrm{def}}{\equiv} \int_I u_1^{\mathrm{as}}\,\mathrm{d}\tau_1 + \int_I u_2^{\mathrm{as}}\,\mathrm{d}\tau_2 + \int_{\sigma_3}\mathrm{d}\tau_3\int_{\sigma_2(\tau_3)}\mathrm{d}\tau_2\int_{\sigma_1}u_3^{\mathrm{as}}\,\mathrm{d}\tau_1 \tag{34}$$

with

$$c_{1\lambda_0} = \int_{\sigma_2(T)} b_1(\tau_2)f(\tau_2-T)A(\tau_2-T,T)\exp\{-\lambda_0\tau_2\}\,\mathrm{d}\tau_2,$$

$f_{3\lambda_0}$ and A being defined in Subsection 3.2. Clearly, n^{as} exists if $\tilde{\nu}_1$ and $\tilde{\nu}_2$ satisfy additional restrictions. It is also evident that population dies if $\lambda_0 < 0$, and grows if $\lambda_0 > 0$, as $t \to \infty$.

We have proved the following result:

Theorem 4. *Let* $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$, p, χ, b_1, b_2 *be nonnegative and the latter five do not depend on* τ_1. *If*

$$p \in C(\bar{\sigma}_2(0)), \quad \nu_3 \quad \text{and} \quad \chi \in C(\bar{\sigma}_2(\tau_3) \times \bar{\sigma}_3),$$

$$\nu_i \in C(\bar{I}), \quad b_i \in C(\bar{\sigma}_2(T)), \quad i = 1, 2,$$

$$u_3^0 \in C(\bar{\sigma}_1 \times \bar{\sigma}_2(\tau_3) \times \bar{\sigma}_3), \quad u_i^0 \in C(\bar{I}) \cap L^1(I), \quad i = 1, 2,$$

and λ_0 *is a real root of (30) such that the integrals*

$$\int_{\tau}^{\infty} \exp\left\{ -\lambda_0 x - \int_{\tau}^{x} \tilde{\nu}_i(\xi)\, \mathrm{d}\xi \right\} \mathrm{d}x, \quad i = 1, 2$$

converge for any $\tau > 0$, *then (24) exhibit the longtime* ($t > \max(\tau_1, \tau_2)$) *behavior of the general solution to problem (1)–(4) with* $\nu(t, n) \equiv 0$.

3.4. Model (1)–(4) with $\nu(t,n) \neq 0$

In this subsection, we consider model (1)–(4) with $\nu(t, n) \geq 0$, show how it can be reduced to that with $\nu(t, n) = 0$ and an additional equation for n, and in the special case of vital rates establish its asymptotic behavior.

Substitution of

$$\begin{cases} u_1 = f(t) U_1(t, \tau_1), & \text{(35a)} \\ u_2 = f(t) U_2(t, \tau_2), & \text{(35b)} \\ u_3 = f(t) U_3(t, \tau_1, \tau_2, \tau_3), & \text{(35c)} \\ n = f(t) N(t), & \text{(35d)} \\ f(0) = 1, & \text{(35e)} \end{cases}$$

into (1)–(4) gives problem (1)–(4) with $\nu(t, n) = 0$ and u_1, u_2, u_3, n replaced by U_1, U_2, U_3, N, respectively, and the equation

$$f' = -\nu(t, f N)) f, \quad f(0) = 1, \tag{36}$$

where the prime denotes differentiation. The problem for U_1, U_2, U_3 and N has been analyzed in Section 3. Hence U_1, U_2, U_3 and N are known. If $N \in C(\bar{I}^*)$, $\nu(t, n) \in C(\bar{I} \times \bar{I})$ and is positive and Lipschitz continuous w.r.t. n, then (36) has a unique solution in $C^1(I^*) \cap C(\bar{I}^*)$. Furthermore, $n \leq N$ because $f \leq 1$.

We see that the age distribution is governed by U_1, U_2, U_3 and does not depend on the effects of changes in the environmental factors described by function $\nu(t, n(t))$. The age evolution, however, influences the behavior of the total population n via the function N in (35d) and (36).

We conclude this subsection with the following result, for the model under consideration, analogous to that of Langlais and Milner (1990) for Kostova and Milner's model (Kostova and Milner, 1995). To do this, let $u = (u_1, u_2, u_3)$, $U = (U_1, U_2, U_3)$, $U^{\mathrm{as}} = (U_1^{\mathrm{as}}, U_2^{\mathrm{as}}, U_3^{\mathrm{as}})$ and consider the stationary case of $\tilde{\nu}_1$, $\tilde{\nu}_2$, $\tilde{\nu}_3$, p, χ, b_1, b_2, $\nu(n)$. Then the following theorem can be proved.

Theorem 5. *Let all the conditions of Theorem 4 hold and assume* $\nu \geq 0$. *Then:*

(a) $\lim_{t\to\infty} u = 0$ *if* $\lambda_0 < \nu(n)$ *for all* $n \in (0, n^0]$;

(b) $\lim_{t\to\infty} u = \infty$ *if* $\lambda_0 > 0$ *and* $\lambda_0 > \nu(n)$ *for all* $n \in [n^0, \infty)$;

(c) $\lim_{t\to\infty} u = \lim_{t\to\infty} U^{\mathrm{as}} n_* / N^{\mathrm{as}}$, $0 < n_* < \infty$ *if either* $\lambda_0 > 0$ *and* $\lambda_0 = \nu(n_*)$, $\nu'(n_*) > 0$, *or* $\lambda_0 = 0$ *and* $\nu(n_*) = 0$, $\nu'(n_*) > 0$, *where the prime denotes differentiation, and* U^{as}, N^{as} *are represented by (34) with* u^{as}, n^{as} *replaced by* U^{as}, N^{as}, *respectively.*

The proof is based on the analysis of the longtime behavior of the solution to (36). The condition $\nu'(n_*) > 0$ ensures the stability of equilibria n_*.

4. Case of a Separable Solution to a Spatially Inhomogeneous Model

In this section, we deal with a model analogous to that in Section 3, but for the population with spatial dispersal (random as well as directed (Gurtin and MacCamy, 1977)) in the whole space and examine its separable solution. This model is a direct generalization of that in (Skakauskas, 1998) to the case where abortions may occur for the fertilized female and consists of the system of nonlinear integro-differential equations for u_1, u_2, u_3,

$$
\begin{aligned}
D_1 u_1 &= -\nu_1 u_1 + \operatorname{div}\left(\kappa_{1r} \nabla u_1 + \kappa_{1d} u_1 \nabla n\right) \quad \text{in } E^m \times Q_1, \\
D_2 u_2 &= -\nu_2 u_2 - X_c + X_b + X_a + \operatorname{div}\left(\kappa_{2r} \nabla u_2 + \kappa_{2d} u_2 \nabla n\right) \quad \text{in } E^m \times Q_2, \\
D_3 u_3 &= -(\nu_3 + \chi) u_3 + \operatorname{div}\left(\kappa_{3r} \nabla u_3 + \kappa_{3d} u_3 \nabla n\right) \quad \text{in } E^m \times Q_3, \qquad (37)
\end{aligned}
$$

$$
X_c = \begin{cases} 0, & \tau_2 \notin \sigma_2(0), \\ \displaystyle\int_{\sigma_1} u_3|_{\tau_3=0} \, \mathrm{d}\tau_1, & \tau_2 \in \sigma_2(0), \end{cases}
$$

$$
X_b = \begin{cases} 0, & \tau_2 \notin \sigma_2(T), \\ \displaystyle\int_{\sigma_1} u_3|_{\tau_3=T} \, \mathrm{d}\tau_1, & \tau_2 \in \sigma_2(T), \end{cases}
$$

$$X_a = \begin{cases} 0, & \tau_2 \notin \sigma_a, \\ \int\limits_{\Omega(\tau_2)} \mathrm{d}\tau_3 \int\limits_{\sigma_1} \chi u_3 \,\mathrm{d}\tau_1, & \tau_2 \in \sigma_a, \end{cases}$$

$$n = \int\limits_I u_1 \,\mathrm{d}\tau_1 + \int\limits_I u_2 \,\mathrm{d}\tau_2 + \int\limits_{\sigma_3} \mathrm{d}\tau_3 \int\limits_{\sigma_2(\tau_3)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} u_3 \,\mathrm{d}\tau_1,$$

supplemented with the conditions

$$\begin{aligned}
&u_k|_{t=0} = u_k^0, \quad k = 1,2 \ \text{ in } \ E^m \times I,\\
&u_3|_{t=0} = u_3^0 \ \text{ in } \ E^m \times \sigma_1 \times \sigma_2(\tau_3) \times \sigma_3,\\
&u_k|_{\tau_k=0} = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_k u_3|_{\tau_3=T} \,\mathrm{d}\tau_1, \quad k = 1,2 \ \text{ in } \ E^m \times I,\\
&u_3|_{\tau_3=0} = p u_1 u_2 \Big/ \int\limits_{\sigma_1} u_1(t,\xi)\,\mathrm{d}\xi \ \text{ in } \ E^m \times I \times \sigma_1 \times \sigma_2(0),\\
&\Big[u_2\big|_{\tau_2=\tau_2^s}\Big] = 0, \quad s = 1,2,3,4 \ \text{ in } \ E^m \times I,\\
&n(x,t) = \omega(x,t) \ \text{ in } \ E^m \times [-T,0].
\end{aligned} \tag{38}$$

In addition to (38), we assume that the initial distributions satisfy the following compatibility conditions:

$$\begin{aligned}
&u_k^0\big|_{\tau_k=0} = \int\limits_{\sigma_2(T)} \mathrm{d}\tau_2 \int\limits_{\sigma_1} b_k\big|_{t=0} u_3^0\big|_{\tau_3=T} \,\mathrm{d}\tau_1, \quad k = 1,2;\\
&\Big[u_2^0\big|_{\tau_2=\tau_2^i}\Big] = 0, \quad i = 1,2,3,4 \ \text{ in } \ E^m;\\
&u_3^0\big|_{\tau_3=0} = p\big|_{t=0} u_1^0 u_2^0 \Big/ \int\limits_{\sigma_1} u_1^0 \,\mathrm{d}\tau_1 \ \text{ in } \ E^m \times \sigma_1 \times \sigma_2(0).
\end{aligned} \tag{39}$$

Further, we restrict our attention to the situation where vital functions p, χ, b_1, b_2, ν_1, ν_2, ν_3 and initial distributions u_1^0, u_2^0, u_3^0 can be written as follows:

$$\nu_i\big(x,t,\tau_i,n(x,t)\big) = \tilde{\nu}_i(t,\tau_i) + \nu\big(x,t,n(x,t)\big), \quad i = 1,2, \tag{40a}$$

$$\nu_3\big(x,t,\tau_1,\tau_2,\tau_3,n(x,t)\big) = \tilde{\nu}_3(t,\tau_1,\tau_2,\tau_3) + \nu\big(x,t,n(x,t)\big), \tag{40b}$$

$$p\big(x,t,\tau_1,\tau_2,n(x,t)\big) = p(t,\tau_1,\tau_2), \tag{40c}$$

$$\chi\big(x,t,\tau_1,\tau_2,\tau_3,n(x,t)\big) = \chi(t,\tau_1,\tau_2,\tau_3), \tag{40d}$$

$$b_i\big(x,t,\tau_1,\tau_2,n(t-T)\big) = b_i(t,\tau_1,\tau_2), \quad i = 1,2, \tag{40e}$$

$$\kappa_{ir} = \kappa_r\big(x,t,n(x,t)\big), \quad \kappa_{id} = \kappa_d\big(x,t,n(x,t)\big), \quad i=1,2,3, \tag{40f}$$

$$u_3^0(x,\tau_1,\tau_2,\tau_3) = U_3^0(\tau_1,\tau_2,\tau_3)f^0(x), \quad u_i^0(x,\tau_i) = U_i^0(\tau_i)f^0(x), \quad i=1,2. \tag{40g}$$

The sixth of these conditions allows all the subclasses of the population to evolve with the same random and directed diffusion moduli while the other ones are analogous to that in model (1)–(4), but depend on an individual's location.

As in Section 3, because of the restrictions (40e), the condition on n for $t \in [-T,0]$ must be dropped. Conditions (40) allow us to find the solution to (37)–(40) of the form

$$n(x,t) = N(t)f(x,t), \quad u_3(x,t,\tau_1,\tau_2,\tau_3) = U_3(t,\tau_1,\tau_2,\tau_3)f(x,t), \tag{41a}$$

$$u_i(x,t,\tau_i) = U_i(t,\tau_i)f(x,t), \quad i=1,2. \tag{41b}$$

Inserting (41) into (37)–(40) we find that U_1, U_2, U_3 and N satisfy (1)–(4) which we have analyzed in Section 3 and f satisfy the following differential equation:

$$\partial f/\partial t = -\nu(x,t,f\,N)\,f + \operatorname{div}\big(\kappa_r(x,t,f\,N) + \kappa_d(x,t,f\,N)\,f\big)\nabla f,$$

$$f(x,0) = f^0(x) \tag{42}$$

with N known. Obviously, (42) is a direct generalization of (39) for the population with diffusion.

Observe that if we let problem (42) have a unique bounded classical solution $f(x,t)$ such that coefficients $\nu(x,t,N(t)f(x,t))$, $\kappa_r(x,t,N(t)\,f(x,t))$, $\kappa_d(x,t,N(t)f(x,t))$ are sufficiently smooth, then, by the comparison principle, $f \le \sup_x f^0(x)$ as long as f exists. Hence $n \le N(t)\sup_x f^0(x)$.

Equation (42) has extensive literature (Gurtn and MacCamy, 1982), and all the results appropriate to (42) (e.g., the existence of traveling waves or the existence and localization of a weak solution in special cases), apply to the system (37)–(40), too.

5. Discussion

In this paper, we consider the population whose subclasses death rates can be decomposed by (4) (or (40) for the dispersing population) into the sum of two terms. The first represents death rates by natural causes and by thoses which do not depend on the population size (e.g., environmental pollution by a human activity) while the other one, being the same for all the subclasses, describes the environment influence depending on the population size (e.g., the effect of limited trophic resources). An analogous decomposition of the death rate with the first term depending only on the age was used by Busenberg and Iannelli (1985) and Langlais and Milner (1994) for the Gurtin-MacCamy and Kostova-Milner models, respectively.

Biologically, it is evident that the number of newborns produced by a female at moment t should depend on the population state at the fertilization moment, but there is no dependence on that at the moment of delivery. Thus in the case of a limited population in (1)–(4) (or (37)–(40)) the numbers of offspring b_1 and b_2 involve the total population $n(t-T)$ (or $n(x,t-T)$ for the dispersing population).

Model (1)–(4) of the nondispersing population is nonlinear, but in the case of a nonlimited population ($\nu \equiv 0$), due to the delay of size T, it can be reduced to a system of linear equations for $t \in (kT,(k+1)T]$, $k = 1,2,\ldots$. They are of Volterra's type, while the right-hand side of (18) is a known function if abortions cannot occur. The same assertion holds true for the equations describing the age distributions U_1, U_2, U_3 in the separable solution of the miscarrying population both with and without spatial dispersal.

The age distribution in the separable solution of the limited population models with as well as without spatial dispersal is governed by U_1, U_2, U_3 and does not depend on the effects of changes in the environmental factors described by the function $\nu(t,n(t))$. Moreover, for the dispersing population, it does not depend on spatial dispersal. The age evolution, however, influences the behavior of the total population n via the function N in (35d) and (36) (or (41a) and (42)).

In the general case of stationary functions b_1, b_2, p, ν_3 and χ, the characteristic equation $\widetilde{Q}(\lambda) = 1$, $\widetilde{Q}(\lambda)$ being defined by (26), has a unique real root at least when conditions of Theorem 3 hold and $\widetilde{Q}(\lambda)$ is monotonous, and may admit some real roots if $\widetilde{Q}(\lambda)$ oscillates. Thus there may exist some separable solutions to models (1)–(4) and (37)–(40). The distribution of roots in a general case is an *open problem*.

Only in the case where b_1, b_2, p, ν_3 and χ are stationary and τ_1-independent we were able to get the asymptotic behavior of u_1, u_2, u_3. In this case one can see that λ_0 is increased if in some age class $b_2(\tau_2)$ is increased.

The dispersing population model (37)–(40) admits a separable solution (41) only if diffusion moduli are the same for all the subpopulations above.

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