On the Population Evolution Problem with the Harmonic Mean Type Mating Law and Females' Pregnancy

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Abstract. A model for an age-sex-structured nonlimited population dynamics with the harmonic mean type mating law and females' pregnancy is presented. The existence and uniqueness theorem for the general case of vital rates is proved, the extinction and growth of the population are considered, and a class of the product (separable) solutions is obtained.

Key words: population dynamics, random mating, age-sex-structured population.

1. Introduction

In the recent paper (Skakauskas, 1996), we proved the existence and uniqueness theorem for an age-sex-structured limited population dynamics model, which takes into account mating of sexes and females' pregnancy. In that model, the population is divided into three components: one male and three female, the latter three being single (nonfertilized) female, fertilized female, and female from sterility period 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 gestation and sterility periods are independent of individuals or time. That model includes the directional derivatives $D_1u_1/\sqrt{2}$, $D_2u_2/\sqrt{2}$, $D_3u_3/\sqrt{3}$, $D_4u_4/\sqrt{3}$, and the mating function $f = pu_1u_2/\int_{\sigma_1} u_1 d\tau_1$ (see notation in Section 2).

In the present paper, for a nonlimited population, we modify the model mentioned above replacing the function f by $\tilde{f} = pu_1u_2/(\int_{\sigma_1} u_1 d\tau_1 + \int_{\sigma_{23(0)}} u_2 d\tau_2)$ and derivatives D_1, D_2, D_3, D_4 by operators $\hat{D}_1, \hat{D}_2, \hat{D}_3, \hat{D}_4$ (see notation in Section 2), prove the existence and uniqueness theorem for this new model, and obtain a class of product (separable) solutions.

The paper is organized as follows. In Section 3, we present the model. Section 4 lists main hypotheses and results. The proof of existence and uniqueness theorem, a majorant for density of single females, and a class of product solutions are given in Section 5.

2. Notation

We use the following notation:

 $\tau_1, \tau_2, \tau_3, -$ ages of male, female, and embryo, respectively;

 τ_4 – time passed after delivery;

 $u_1(t, \tau_1)$ – the age-density of males at the age τ_1 and time t;

 $u_2(t, \tau_2)$ – the age-density of single females at the age τ_2 and time t;

 $u_3(t, \tau_1, \tau_2, \tau_3)$ – the age density of fertilized females at the age τ_2 and time t whose embryo is at the age τ_3 and that were fertilized by males at the age τ_1 ;

 $u_4(t, \tau_1, \tau_2, \tau_4)$ – the age-density of females from the sterility period at the age τ_2 and time t for whom time τ_4 has passed after delivery and that were fertilized by males at the age τ_1 ;

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

 $\nu_3(t, \tau_1, \tau_2, \tau_3)$ – the death rate of fertilized females at the age τ_2 and time t whose embryo is at the age τ_3 and that were fertilized by males at the age τ_1 ;

 $\nu_4(t, \tau_1, \tau_2, \tau_4)$ – the death rate of females from the sterility period at the age τ_2 and time t for whom time τ_4 has passed after delivery and that were fertilized by females at the age τ_1 ;

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

 $X(u_4) = X(t, \tau_2)$ – the single female gain density by females at the age τ_2 and time t for whom time T_{24} has passed after delivery;

 $Y(u_1, u_2)$ – the single female loss rate due to conception at the age τ_2 and time t; $\sigma_1 = [\tau_{11}, \tau_{12}], 0 < \tau_{11} < \tau_{12} < \infty$ – the male sexual activity interval;

 $\sigma_3 = (0, T_{23}], 0 < T_{23} < \infty$ – the female gestation interval, $\overline{\sigma}_3 = [0, T_{23}];$

 $\sigma_{23}(\tau_3) = [\tau_{21} + \tau_3, \tau_{22} + \tau_3], 0 < \tau_{21} < \tau_{22} < \infty;$

 $\sigma_{23}(0)$ and $\sigma_{23}(T_{23})$ – the female fertilization and delivery intervals;

 $\sigma_4 = (0, T_{24}], 0 < T_{24} < \infty$ – the female sterility interval after delivery, $\overline{\sigma}_4 = [0, T_{24}];$

 $\sigma_{24}(\tau_4) = [\tau_{21} + T_{23} + \tau_4, \tau_{22} + T_{23} + \tau_4];$

 $b_1(t, \tau_1, \tau_2)$ and $b_2(t, \tau_1, \tau_2)$ – the average numbers of male and female offspring produced by a female at the age τ_2 and time t who was fertilized by a male at the age τ_1 ; $u_{10}(\tau_1), u_{20}(\tau_2), u_{30}(\tau_1, \tau_2, \tau_3), u_{40}(\tau_1, \tau_2, \tau_4)$ – the initial distributions;

 $\tau_2^0 = 0, \tau_2^1 = \tau_{21}, \tau_2^2 = \tau_{21} + T_{23} + T_{24}, \tau_2^3 = \tau_{22}, \tau_2^4 = \tau_{22} + T_{23} + T_{24}$ (for the case of multiple deliveries);

$$\begin{aligned} Q_1 &= (0, \infty), \, \overline{Q}_1 = [0, \infty), Q_2 = (0, \infty) \bigcup_{s=1}^4 \{\tau_2^s\}, \, \overline{Q}_2 = [0, \infty); \\ Q_3 &= \sigma_1 \times \sigma_{23}(\tau_3) \times \sigma_3, \quad \overline{Q}_3 = \sigma_1 \times \sigma_{23}(\tau_3) \times \overline{\sigma}_3, \, \text{where } \sigma_{23}(\tau_3) \times \sigma_3 := \{(\tau_2, \tau_3) : \tau_2 \in \sigma_{23}(\tau_3), \, \tau_3 \in \sigma_3\}; \end{aligned}$$

 $Q_4 = \sigma_1 \times \sigma_{24}(\tau_4) \times \sigma_4, \quad \overline{Q}_4 = \sigma_1 \times \sigma_{24}(\tau_4) \times \overline{\sigma}_4, \text{ where } \sigma_{24}(\tau_4) \times \sigma_4 := \{(\tau_2, \tau_4) : \tau_2 \in \sigma_{24}(\tau_4), \tau_4 \in \sigma_4\};$

 $[u_2(\tau_2^j)]$ – a jump discontinuity of u_2 at the plane $\tau_2 = \tau_2^j$;

D – a domain not necessarily bounded, \overline{D} – closure of D; $C^0(\overline{D})$ (resp. $C^0(D)$) – a class of bounded continuous functions in \overline{D} (resp. D); $C^1(D)$ – a class of functions $f(x_1, \ldots, x_m)$ such that $\partial f/\partial x_i \in C^0(D)$, $i = \overline{1, m}$; $C^{1,0}(D)$ – a class of functions $f(x_1, \ldots, x_m)$ such that $\partial f/\partial x_1 \in C^0(D)$; $\widehat{D}_1 = \partial/\partial t + \partial/\partial \tau_1$, $\widehat{D}_2 = \partial/\partial t + \partial/\partial \tau_2$, $\widehat{D}_3 = \widehat{D}_2 + \partial/\partial \tau_3$, $\widehat{D}_4 = \widehat{D}_2 + \partial/\partial \tau_4$; $D_1 = \sqrt{2}\widetilde{D}_1$, $D_2 = \sqrt{2}\widetilde{D}_2$, $D_3 = \sqrt{3}\widetilde{D}_3$, $D_4 = \sqrt{3}\widetilde{D}_4$; \widetilde{D}_i , i = 1, 2, 3, 4 – the directional derivative in the positive direction of characteristics

 D_i , i = 1, 2, 3, 4 – the directional derivative in the positive direction of characteristics of the operator \hat{D}_i .

3. The model

The model to be considered in this paper consists of the following system of integrodifferential equations for u_1, u_2, u_3, u_4 ,

$$\begin{aligned} \partial u_1 / \partial t + \partial u_1 / \partial \tau_1 &= -\nu_1 u_1, \quad t > 0, \ \tau_1 \in Q_1, \\ \partial u_2 / \partial t + \partial u_2 / \partial \tau_2 &= -(\nu_2 + Y(u_1, u_2)) u_2 + X(u_4), \quad t > 0, \ \tau_2 \in Q_2, \\ \partial u_3 / \partial t + \partial u_3 / \partial \tau_2 + \partial u_3 / \partial \tau_3 &= -\nu_3 u_3, \quad t > 0, \ (\tau_1, \tau_2, \tau_3) \in Q_3, \\ \partial u_4 / \partial t + \partial u_4 / \partial \tau_2 + \partial u_4 / \partial \tau_4 &= -\nu_4 u_4, \quad t > 0, \ (\tau_1, \tau_2, \tau_4) \in Q_4, \\ Y(u_1, u_2) &= \begin{cases} 0, & \tau_2 \notin \sigma_{23}(0), \\ \int_{\sigma_1} p u_1 \, \mathrm{d} \tau_1' / \left(\int_{\sigma_1} u_1 \, \mathrm{d} \tau_1' + \int_{\sigma_{23}(0)} u_2 \, \mathrm{d} \tau_2' \right), & \tau_2 \in \sigma_{23}(0), \\ Y(u_4) &= \begin{cases} 0, & \tau_2 \notin \sigma_{24}(T_{24}), \\ \int_{\sigma_1} u_4 |_{\tau_4 = T_{24}} \, \mathrm{d} \tau_1', & \tau_2 \in \sigma_{24}(T_{24}), \end{cases} \end{aligned}$$
(3.1)

which supplemented with the conditions

$$\begin{aligned} u_k|_{\tau_k=0} &= \int_{\sigma_1} \mathrm{d}\tau_1 \int_{\sigma_{23}(T_{23})} b_k u_3|_{\tau_3=T_{23}} \,\mathrm{d}\tau_2, \quad k = 1, 2, \\ u_3|_{\tau_3=0} &= p u_1 u_2 / \left(\int_{\sigma_1} u_1 \,\mathrm{d}\tau_1' + \int_{\sigma_{23(0)}} u_2 \,\mathrm{d}\tau_2' \right), \quad t > 0, \ (\tau_1, \tau_2) \in \sigma_1 \times \sigma_{23}(0), \\ u_4|_{\tau_4=0} &= u_3|_{\tau_3=T_{23}}, \quad (\tau_1, \tau_2) \in \sigma_1 \times \sigma_{24}(0), \\ [u_2|_{\tau_2=\tau_2^s}] &= 0, \quad s = \overline{1, 4}, \\ u_k|_{t=0} &= u_{k0} \text{ in } \overline{Q}_k, \ k = \overline{1, 4} \end{aligned}$$
(3.2)

describes dynamics of the population. In addition to (3.2) we assume that the initial distributions u_{10} , u_{20} , u_{30} , u_{40} satisfy the following compatibility conditions

$$u_{k0}(0) = \int_{\sigma_1} d\tau_1 \int_{\sigma_{23}(T_{23})} b_k|_{t=0} u_{30}|_{\tau_3 = T_{23}} d\tau_2, \quad k = 1, 2,$$
(3.3)

$$\begin{aligned} u_{30}|_{\tau_{3}=0} &= p|_{t=0} u_{10} u_{20} / \left(\int_{\sigma_{1}} u_{10} \, \mathrm{d}\tau_{1}' + \int_{\sigma_{23}(0)} u_{20} \, \mathrm{d}\tau_{2}' \right), \ (\tau_{1}, \tau_{2}) \in \sigma_{1} \times \sigma_{23}(0), \\ u_{40}|_{\tau_{4}=0} &= u_{30}|_{\tau_{3}=T_{23}}, \quad (\tau_{1}, \tau_{2}) \in \sigma_{1} \times \sigma_{24}(0), \\ [u_{20}(\tau_{2}^{s})] &= 0, \quad s = \overline{1, 4}. \end{aligned}$$

As follows from the foregoing, given functions $\nu_1, \nu_2, \nu_3, \nu_4, p, b_1, b_2, u_{10}, u_{20}, u_{30}, u_{40}$ and the unknown ones u_1, u_2, u_3, u_4 must be positive valued, otherwise they have no biological significance. Because of the mating law model (3.1)–(3.3) is nonlinear.

4. Hypotheses and main results

We use the following hypotheses:

$$0 < \nu_k \in C^1([0,\infty) \times \overline{Q}_k), \quad k = \overline{1,4},$$

$$0
$$0 < b_k \in C^{1,0}([0,\infty) \times \sigma_1 \times \sigma_{23}(T_{23})),$$

$$0 < u_{k0} \in C^1(\overline{Q}_k), \quad k = \overline{1,4},$$

$$0 < \tau_{ij} = \operatorname{const} < \infty, \quad i, j = 1,2;$$

$$0 < T_{2s} = \operatorname{const} < \infty, \quad s = 3, 4.$$

(H)$$

Theorem 1. Assume that all the hypotheses (H) and conditions (3.3) hold. Then, for any finite $t^* > 0$, problem (3.1), (3.2) has a unique strictly positive solution u_1, u_2, u_3, u_4 such that:

$$\begin{split} u_{1} &\in C^{0}\big([0,t^{*}] \times \overline{Q}_{1}\big) \cap C^{1}\Big(\big([0,t^{*}] \times \overline{Q}_{1}\big) \setminus \big\{(t,\tau_{1}) : t = \tau_{1}\big\}\Big), \\ u_{2} &\in C^{0}\big([0,t^{*}] \times \overline{Q}_{2}\big) \cap C^{1}\Big(\big([0,t^{*}] \times \overline{Q}_{2}\big) \setminus \big\{(t,\tau_{2}) : \\ \tau_{2} &= t, t + \tau_{2}^{1}, t + \tau_{2}^{2}, t + \tau_{2}^{3}, t + \tau_{2}^{4}, \tau_{2}^{1}, \tau_{2}^{2}, \tau_{2}^{2}, \tau_{2}^{3}, \tau_{2}^{4}\big\}\Big), \\ u_{3} &\in C^{0}\big([0,t^{*}] \times \overline{Q}_{3}\big) \cap C^{1}\Big(\big([0,t^{*}] \times \overline{Q}_{3}\big) \setminus \big\{(t,\tau_{1},\tau_{2},\tau_{3}) : \\ \tau_{3} &= t, t - \tau_{1}; \tau_{2} &= t, t + \tau_{2}^{1}, t + \tau_{2}^{2}, t + \tau_{3}^{3}, \tau_{1}^{1}, \tau_{2}^{2}, \tau_{2}^{3}\big\}\Big), \\ u_{4} &\in C^{0}\big([0,t^{*}] \times \overline{Q}_{4}\big) \cap C^{1}\Big(\big([0,t^{*}] \times \overline{Q}_{4}\big) \setminus \big\{(t,\tau_{1},\tau_{2},\tau_{4}) : \\ \tau_{4} &= t, t - T_{23}, t - T_{23} - \tau_{1}; \\ \tau_{2} &= t, t + \tau_{2}^{1}, t + \tau_{2}^{2}, t + \tau_{3}^{3}, t + \tau_{4}^{4}, \tau_{2}^{2}, \tau_{3}^{3}, \tau_{4}^{4}\big\}\Big), \\ \int_{\sigma_{1}} u_{1} \, d\tau_{1} + \int_{\sigma_{23}(0)} u_{2} \, d\tau_{2} \in C^{1}\big([0,t^{*}]\big). \end{split}$$

5. Justification of Results

5.1. Proof of Theorem 1

We consider the case of multiply deliveries, i.e., $\tau_2^3 - \tau_2^1 > T_{23} + T_{24}$. The apposite case we can analyze in the similar way.

Define

$$n(t) = \int_{\sigma_1} u_1 \, \mathrm{d}\tau_1 + \int_{\sigma_{23}(0)} u_2 \, \mathrm{d}\tau_2, \tag{5.1}$$

$$q(t,\tau_2) = \int_{\sigma_1} p u_1 \,\mathrm{d}\tau_1,\tag{5.2}$$

$$B_k(t) = u_k(t,0), \quad k = 1,2.$$
 (5.3)

We first obtain the formal integral representations of u_1, u_2, u_3, u_4 . Integrating Eqs. (3.1) over characteristics together with conditions (3.2), we obtain:

$$u_{3} = \begin{cases} u_{30}(\tau_{1}, \tau_{2} - t, \tau_{3} - t) \\ \times \exp\left\{-\int_{0}^{t} \nu_{3}(x, \tau_{1}, x + \tau_{2} - t, x + \tau_{3} - t) \,\mathrm{d}x\right\}, & 0 \leqslant t \leqslant \tau_{3}, \\ (pu_{1}u_{2}/n)|_{(t - \tau_{3}, \tau_{1}, \tau_{2} - \tau_{3})} \\ \times \exp\left\{-\int_{0}^{\tau_{3}} \nu_{3}(x + t - \tau_{3}, \tau_{1}, x + \tau_{2} - \tau_{3}, x) \,\mathrm{d}x\right\}, & 0 \leqslant \tau_{3} \leqslant t, \end{cases}$$
(5.4)

$$u_{4} = \begin{cases} u_{40}(\tau_{1}, \tau_{2} - t, \tau_{4} - t) \\ \times \exp\left\{-\int_{0}^{t} \nu_{4}(x, \tau_{1}, x + \tau_{2} - t, x + \tau_{4} - t) \, \mathrm{d}x\right\}, & 0 \leqslant t \leqslant \tau_{4}, \\ u_{30}(\tau_{1}, \tau_{2} - t, T_{23} + \tau_{4} - t) \\ \times \exp\left\{-\int_{0}^{t - \tau_{4}} \nu_{3}(x, \tau_{1}, x + \tau_{2} - t, x + T_{23} + \tau_{4} - t) \, \mathrm{d}x \\ -\int_{0}^{\tau_{4}} \nu_{4}(x + t - \tau_{4}, \tau_{1}, x + \tau_{2} - \tau_{4}, x) \, \mathrm{d}x\right\}, & \tau_{4} \leqslant t \leqslant T_{23} + \tau_{4}, \end{cases}$$
(5.5)
$$(pu_{1}u_{2}/n)|_{(t - \tau_{4} - T_{23}, \tau_{1}, \tau_{2} - \tau_{4} - T_{23})} \\ \times \exp\left\{-\int_{0}^{T_{23}} \nu_{3}(x + t - \tau_{4} - T_{23}, \tau_{1}, x + \tau_{2} - \tau_{4} - T_{23}, x) \, \mathrm{d}x \\ -\int_{0}^{\tau_{4}} \nu_{4}(x + t - \tau_{4}, \tau_{1}, x + \tau_{2} - \tau_{4}, x) \, \mathrm{d}x\right\}, & t \geqslant \tau_{4} + T_{23}, \end{cases}$$

$$u_{1} = \begin{cases} u_{10}(\tau_{1} - t) \exp\left\{-\int_{0}^{t} \nu_{1}(x, x + \tau_{1} - t) \,\mathrm{d}x\right\}, & 0 \leq t \leq \tau_{1}, \\ B_{1}(t - \tau_{1}) \exp\left\{-\int_{t-\tau_{1}}^{t} \nu_{1}(x, x + \tau_{1} - t) \,\mathrm{d}x\right\}, & 0 \leq \tau_{1} \leq t, \end{cases}$$
(5.6)

$$u_{2} = \begin{cases} u_{20}(\tau_{2} - t) \exp\left\{-\int_{0}^{t} \nu_{2}(x, x + \tau_{2} - t) \,\mathrm{d}x\right\}, \\ 0 \leqslant t \leqslant \tau_{2}, \ \tau_{2} \in [0, \tau_{2}^{1}], \\ B_{2}(t - \tau_{2}) \exp\left\{-\int_{t - \tau_{2}}^{t} \nu_{2}(x, x + \tau_{2} - t) \,\mathrm{d}x\right\}, \\ 0 \leqslant \tau_{2} \leqslant t, \ \tau_{2} \in [0, \tau_{2}^{1}], \end{cases}$$
(5.7)

$$U(t) = u_2(t, \tau_2^1), \quad \left[u_2(t, \tau_2^1)\right] = 0, \tag{5.8}$$

$$u_{2} = \begin{cases} u_{21} = u_{20}(\tau_{2} - t) \exp\left\{-\int_{0}^{t} \left(\nu_{2} + \frac{q}{n}\right)\Big|_{(x, x + \tau_{2} - t)} \,\mathrm{d}x\right\}, \\ 0 \leqslant t \leqslant \tau_{2} - \tau_{2}^{1}, \\ u_{22} = U(\tau_{2}^{1} + t - \tau_{2}) \exp\left\{-\int_{\tau_{2}^{1} + t - \tau_{2}}^{t} \left(\nu_{2} + \frac{q}{n}\right)\Big|_{(x, x + \tau_{2} - t)} \,\mathrm{d}x\right\}, \\ t > \tau_{2} - \tau_{2}^{1} \end{cases}$$
(5.9)

for $\tau_2 \in [\tau_2^1, \tau_2^2]$,

$$u_{2} = \begin{cases} u_{23} = u_{20}(\tau_{2} - t) \exp\left\{-\int_{0}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \\ + \int_{0}^{t} \widetilde{X}(y, y + \tau_{2} - t) \exp\left\{-\int_{y}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \,\mathrm{d}y, \\ 0 \leqslant t \leqslant \tau_{2} - \tau_{2}^{2}, \\ u_{24} = u_{20}(\tau_{2} - t) \exp\left\{-\int_{0}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \\ + \int_{\tau_{2}^{2} + t - \tau_{2}}^{t} \widetilde{X}(y, y + \tau_{2} - t) \exp\left\{-\int_{y}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \,\mathrm{d}y, \quad (5.10) \\ \tau_{2} - \tau_{2}^{2} \leqslant t \leqslant \tau_{2} - \tau_{2}^{1}, \\ u_{25} = U(\tau_{2}^{1} + t - \tau_{2}) \exp\left\{-\int_{\tau_{2}^{1} + t - \tau_{2}}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \\ + \int_{\tau_{2}^{2} + t - \tau_{2}}^{t} \widetilde{X}(y, y + \tau_{2} - t) \exp\left\{-\int_{y}^{t} \left(\nu_{2} + \frac{q}{n}\right)\big|_{(x,x+\tau_{2}-t)} \,\mathrm{d}x\right\} \,\mathrm{d}y, \\ t \geqslant \tau_{2} - \tau_{2}^{1} \geqslant \widetilde{T} \end{cases}$$

for $au_2 \in [au_2^2, au_2^3], \ \widetilde{T} = T_{23} + T_{24},$

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$$u_{2} = \begin{cases} u_{20}(\tau_{2}-t)\exp\left\{-\int_{0}^{t}\nu_{2}(x,x+\tau_{2}-t)\,\mathrm{d}x\right\} \\ +\int_{0}^{t}\widetilde{X}(y,y+\tau_{2}-t)\exp\left\{-\int_{y}^{t}\nu_{2}(x,x+\tau_{2}-t)\,\mathrm{d}x\right\}\,\mathrm{d}y, \\ 0 \leqslant t \leqslant \tau_{2}-\tau_{2}^{3}, \\ u_{2}(\tau_{2}^{3}+t-\tau_{2},\tau_{2}^{3})\exp\left\{-\int_{\tau_{2}^{3}+t-\tau_{2}}^{t}\nu_{2}(x,x+\tau_{2}-t)\,\mathrm{d}x\right\} \\ +\int_{\tau_{2}^{3}+t-\tau_{2}}^{t}\widetilde{X}(y,y+\tau_{2}-t)\exp\left\{-\int_{y}^{t}\nu_{2}(x,x+\tau_{2}-t)\,\mathrm{d}x\right\}\,\mathrm{d}y, \\ t \geqslant \tau_{2}-\tau_{2}^{3}, \end{cases}$$
(5.11)

 $[u_2(t,\tau_2^3)] = 0$ for $\tau_2 \in [\tau_2^3, \tau_2^4]$,

$$u_{2} = \begin{cases} u_{20}(\tau_{2} - t) \exp\left\{-\int_{0}^{t} \nu_{2}(x, x + \tau_{2} - t) \,\mathrm{d}x\right\}, \ 0 \leq t \leq \tau_{2} - \tau_{2}^{4}, \\ u_{2}(\tau_{2}^{4} + t - \tau_{2}, \tau_{2}^{4}) \exp\left\{-\int_{\tau_{2}^{4} + t - \tau_{2}}^{t} \nu_{2}(x, x + \tau_{2} - t) \,\mathrm{d}x\right\}, \\ t \geq \tau_{2} - \tau_{2}^{4}, \end{cases}$$
(5.12)

 $[u_2(t, \tau_2^4)] = 0$ for $\tau_2 \in [\tau_2^4, \infty)$. Now, by (5.1), (5.9) and (5.10), we obtain the following integral equation:

$$n = \int_{\sigma_1} u_1 \, \mathrm{d}\tau_1 + \int_{\tau_2^1}^{\tau_2^1 + t} u_{22} \, \mathrm{d}\tau_2 + \int_{\tau_2^1 + t}^{\tau_2^2} u_{21} \, \mathrm{d}\tau_2$$

+
$$\int_{\tau_2^2}^{\tau_2^2 + t} u_{24} \, \mathrm{d}\tau_2 + \int_{\tau_2^2 + t}^{\tau_2^3} u_{23} \, \mathrm{d}\tau_2, \quad 0 \leqslant t \leqslant \widetilde{T},$$

$$n = \int_{\sigma_1} u_1 \, \mathrm{d}\tau_1 + \int_{\tau_2^1}^{\tau_2^2} u_{22} \, \mathrm{d}\tau_2 + \int_{\tau_2^2}^{t + \tau_2^1} u_{25} \, \mathrm{d}\tau_2$$

+
$$\int_{t + \tau_2^1}^{t + \tau_2^2} u_{24} \, \mathrm{d}\tau_2 + \int_{t + \tau_2^2}^{\tau_2^3} u_{23} \, \mathrm{d}\tau_2, \quad \widetilde{T} \leqslant t \leqslant \tau_2^3 - \tau_2^2,$$

$$n = \int_{\sigma_1} u_1 \, \mathrm{d}\tau_1 + \int_{\tau_2^1}^{\tau_2^2} u_{22} \, \mathrm{d}\tau_2 + \int_{\tau_2^2}^{t + \tau_2^1} u_{25} \, \mathrm{d}\tau_2$$

$$+ \int_{t+\tau_{2}^{1}}^{\tau_{2}^{3}} u_{24} d\tau_{2}, \quad \tau_{2}^{3} - \tau_{2}^{2} \leqslant t \leqslant \tau_{2}^{3} - \tau_{2}^{1},$$

$$n = \int_{\sigma_{1}}^{\tau_{1}} u_{1} d\tau_{1} + \int_{\tau_{2}^{1}}^{\tau_{2}^{2}} u_{22} d\tau_{2} + \int_{\tau_{2}^{2}}^{\tau_{2}^{3}} u_{25} d\tau_{2}, \quad t \geqslant \tau_{2}^{3} - \tau_{2}^{1}$$
(5.13)

if $\tau_{22} - \tau_{21} \ge 2\widetilde{T}$, and

$$n = \int_{\sigma_{1}}^{\tau_{1}} u_{1} \, \mathrm{d}\tau_{1} + \int_{\tau_{2}^{1}}^{t+\tau_{2}^{1}} u_{22} \, \mathrm{d}\tau_{2} + \int_{t+\tau_{2}^{1}}^{\tau_{2}^{2}} u_{21} \, \mathrm{d}\tau_{2}$$

$$+ \int_{\tau_{2}^{2}}^{t+\tau_{2}^{2}} u_{24} \, \mathrm{d}\tau_{2} + \int_{t+\tau_{2}^{2}}^{\tau_{2}^{3}} u_{23} \, \mathrm{d}\tau_{2}, \quad 0 \leq t \leq \tau_{2}^{3} - \tau_{2}^{2},$$

$$n = \int_{\sigma_{1}}^{\tau_{1}} u_{1} \, \mathrm{d}\tau_{1} + \int_{\tau_{2}^{1}}^{t+\tau_{2}^{1}} u_{22} \, \mathrm{d}\tau_{2} + \int_{t+\tau_{2}^{1}}^{\tau_{2}^{2}} u_{21} \, \mathrm{d}\tau_{2} + \int_{\tau_{2}^{2}}^{\tau_{2}^{3}} u_{24} \, \mathrm{d}\tau_{2},$$

$$\tau_{2}^{3} - \tau_{2}^{2} \leq t \leq T_{23},$$

$$n = \int_{\sigma_{1}}^{\tau_{1}} u_{1} \, \mathrm{d}\tau_{1} + \int_{\tau_{2}^{1}}^{\tau_{2}^{2}} u_{22} \, \mathrm{d}\tau_{2} + \int_{\tau_{2}^{2}}^{t+\tau_{2}^{1}} u_{25} \, \mathrm{d}\tau_{2} + \int_{t+\tau_{2}^{1}}^{\tau_{2}^{3}} u_{24} \, \mathrm{d}\tau_{2},$$

$$T_{23} \leq t \leq \tau_{2}^{3} - \tau_{2}^{1},$$

$$n = \int_{\sigma_{1}}^{\tau_{1}} u_{1} \, \mathrm{d}\tau_{1} + \int_{\tau_{2}^{1}}^{\tau_{2}^{2}} u_{22} \, \mathrm{d}\tau_{2} + \int_{\tau_{2}^{2}}^{\tau_{2}^{3}} u_{25} \, \mathrm{d}\tau_{2}, \quad t \geq \tau_{2}^{3} - \tau_{2}^{1},$$

$$(5.14)$$

 $\text{if } \tau_{22} - \tau_{21} < 2\widetilde{T}.$

For the sake of brevity we write this integral equation for n as follows

$$n = K(n; t, X, B_1, B_2, q, U),$$
(5.15)

where:

 $\widetilde{X}(t,\tau_2)$ is defined by $(\mathbf{3.1})_6$ provided that $u_4|\tau_4=T_{24}$ is known,

 $B_k(t)$ is defined by (5.3), (3.2)₁ provided that $u_3|_{\tau_3=T_{23}}$ is known,

q is defined by (5.2), (5.6) provided that B_1 is known,

U is defined by (5.8), (5.7) provided that B_2 is known.

We examine (5.15) going along the t axis by a step of size $h = T_{23} + \min(\tau_{11}, \tau_{21}, T_{24})$. The first step. From (5.4) we find u_3 for $t \leq \tau_3$ (and hence $u_3|_{\tau_3=T_{23}}$ for $t \leq T_{23}$). Then we construct by (5.2) and (2.2) R_1 for $t \in [0, T_1]$ and find by (5.6) and (5.7).

Then we construct, by (5.3) and $(3.2)_1$, B_k for $t \in [0, T_{23}]$ and find, by (5.6) and (5.7),

 u_k for $0 < t \le \tau_k + T_{23}$, $k = 1, 2, \tau_1 \in (0, \infty)$, $\tau_2 \in (0, \tau_{21}]$. Thus we know $u_k(t, \tau_{k1})$ for $0 \le t \le T_{23} + \tau_{k1}$, k = 1, 2. Hence q, by (5.2), $\int_{\sigma_1} u_1 d\tau_1$, and U, by (5.8), are also known for $t \in [0, \tau_{11} + T_{23}]$ and $t \in [0, \tau_{21} + T_{23}]$, respectively. From (5.5) we find u_4 for $0 \le t \le \tau_4 + T_{23}$ (and hence $u_4|_{\tau_4=T_{24}}$ for $0 \le t \le T_{23} + T_{24}$). This allows us, by (3.1)₆, to construct \widetilde{X} . Thus (5.15) is an integral equation for n(t), $t \in [0, h]$.

From (5.13) and (5.14) it is easy to see, by definition of u_{2i} , $i = \overline{1, 5}$, that $K(n'', \cdot) > K(n', \cdot)$, if n'' > n', and $0 < K(\int_{\sigma_1} u_1 d\tau_1, \cdot) < K(n, \cdot) < K(\infty, \cdot)$. This allows us to solve (5.15) by the iteration method starting with $n^0 = \int_{\sigma_1} u_1 d\tau_1$ and to obtain the monotonically increasing sequence $K(n^m, \cdot)$, which converges, since it is bounded. Moreover, from (5.13) and (5.14) it follows that

$$|n^{m+1} - n^m| \leq \kappa \int_0^t |n^m - n^{m-1}| \, \mathrm{d}x, \quad m = 1, 2, \dots,$$

where κ is a positive constant. Hence

$$\left|n^{m+1} - n^{m}\right| \leqslant \frac{\kappa^{m} t^{m}}{m!} c, \quad c = \sup_{t \in [0,h]} \left(K(\infty, \cdot) - \int_{\sigma_{1}} u_{1} \,\mathrm{d}\tau_{1} \right), \quad m = 1, 2, \dots,$$

and the sequence $\{n^m\}$ converges uniformly to a strictly positive function $n \in C^0([0, h])$ because of the hypotheses (H). Knowing n, B_1, B_2, q, U , we find, by (5.9)–(5.12), the function u_2 for $(t, \tau_2) \in [0, h] \times [\tau_2^1, \infty)$.

The second step. From (5.4) we find u_3 for $\tau_3 \leq t \leq h + \tau_3$ (and hence $u_3|_{\tau_3=T_{23}}$ for $T_{23} \leq t \leq T_{23} + h$). Then, by (5.3) and (3.2)₁, we construct B_k for $T_{23} < t \leq T_{23} + h$ and, by (5.6) and (5.7), we find u_k for $\tau_k + T_{23} < t \leq \tau_k + T_{23} + h, k = 1, 2, \tau_1 \in (0, \infty)$, $\tau_2 \in (0, \tau_{21}]$. Thus, we know $u_k(t, \tau_{k1})$ for $\tau_{k1} + T_{23} \leq t \leq \tau_{k1} + T_{23} + h$. Hence q, by (5.2), $\int_{\sigma_1} u_1 d\tau_1$, and U, by (5.8), are also known for $t \in [\tau_{11} + T_{23}, \tau_{11} + T_{23} + h]$ and $t \in [\tau_{21} + T_{23}, \tau_{21} + T_{23} + h]$, respectively. Now from (5.5) we find u_4 for $t \in (\tau_4 + T_{23}, \tau_4 + T_{23} + h]$ (and hence $u_4|_{\tau_4=T_{24}}$ for $t \in (T_{24} + T_{23}, T_{24} + T_{23} + h]$)). This allows us to construct \widetilde{X} for $t \in (T_{24} + T_{23}, T_{24} + T_{23} + h]$. Thus we again have an integral equation for $n(t), t \in (h, 2h]$. Using the same method, as above, we construct its solution $n \in C^0([h, 2h])$.

Repeating our argument, we can construct u_1, u_2, u_3, u_4 , and (hence B_1, B_2, q, U) for any finite $t^* > 0$. Direct calculation together with the hypotheses (H) show that $n \in C^1([0, t^*])$. This completes the proof of Theorem 1.

5.2. Majorants for u_1, u_2

In this subsection, we consider the case where

$$\nu_2(t,\tau_2) \ge \nu_*(\tau_2) > 0, \quad 0 < b_k(t,\tau_1,\tau_2) \le b^*(\tau_2), \quad 0 < p(t,\tau_1,\tau_2) \le p^*(\tau_2)$$

$$\nu_* \in C^0([0,\infty)), \quad b^* \in C^0(\sigma_{23}(T_{23})), \quad p^* \in C^0(\sigma_{23}(0)). \tag{5.16}$$

It is easy to see that u_1 and u_2 constructed in Section 5.1 have the following majorants \tilde{u}_1 and \tilde{u}_2 , respectively, where

$$\widetilde{u}_{1} = \begin{cases} u_{10}(\tau_{1}-t)\exp\left\{-\int_{0}^{t}\nu_{1}(x,x+\tau_{1}-t)\,\mathrm{d}x\right\}, & 0 \leqslant t \leqslant \tau_{1}, \\ \widetilde{u}_{2}(t-\tau_{1},0)\exp\left\{-\int_{0}^{\tau_{1}}\nu_{1}(x+t-\tau_{1},x)\,\mathrm{d}x\right\}, & 0 \leqslant \tau_{1} \leqslant t, \end{cases}$$

and \widetilde{u}_2 is the unique strictly positive solution of the system

$$\begin{split} D_{2}\widetilde{u}_{2} &= -\nu_{*}\widetilde{u}_{2} + \begin{cases} 0, \quad \tau_{2} \notin \sigma_{24}(T_{24}), \ t > 0, \\ \int & u_{4}|_{\tau_{4}=T_{24}} \ \mathrm{d}\tau_{1}, \quad \tau_{2} \in \sigma_{24}(T_{24}), \ 0 < t \leqslant \widetilde{T}, \\ p^{*}(\tau_{2} - \widetilde{T})\widetilde{u}_{2}(t - \widetilde{T}, \ \tau_{2} - \widetilde{T}), \quad \tau_{24} \in \sigma_{24}(T_{24}), \ t \geqslant \widetilde{T}, \\ [\widetilde{u}_{2}(t, \tau_{2}^{s})] &= 0, \quad s = 2, 4, \ t \geqslant 0, \\ \widetilde{u}_{2}(0, \tau_{2}) &= u_{20}(\tau_{2}), \quad \tau_{2} \in [0, \infty), \\ \widetilde{u}_{2}(t, 0) &= \begin{cases} \int & \mathrm{d}\tau_{2}b^{*}(\tau_{2}) \int & u_{3}|_{\tau_{3}=T_{23}} \ \mathrm{d}\tau_{1}, \quad t \leqslant T_{23}, \\ \int & \sigma_{23}(T_{23}) & \mathrm{d}\tau_{2}p^{*}(\tau_{2} - T_{23})b^{*}(\tau_{2})\widetilde{u}_{2}(t - T_{23}, \ \tau_{2} - T_{23}), \quad t \geqslant T_{23}, \end{cases} \end{split}$$

where $u_3|_{\tau_3=T_{23}}$ for $0 \le t \le T_{23}$ and $u_4|_{\tau_4=T_{24}}$ for $0 \le t \le \widetilde{T} = T_{23} + T_{24}$ are defined by (5.4) and (5.5), respectively. Because of the delay argument $t - \widetilde{T}$, function \widetilde{u}_2 can be constructed by using the argument similar to that used in 5.1 for construction of u_2 . Moreover, for $t > \tau_2$, we have

$$\begin{aligned} \widetilde{u}_{2} &= \widetilde{u}_{2}(t - \tau_{2}, 0)v(\tau_{2}), \end{aligned}$$

$$dv/d\tau_{2} &= -\nu_{*}v + \begin{cases} 0, & \tau_{2} \notin \sigma_{24}(T_{24}), \\ p^{*}(\tau_{2} - \widetilde{T})v(\tau_{2} - \widetilde{T}), & \sigma_{2} \in \sigma_{24}(T_{24}), \end{cases}$$

$$v(0) &= 1, \quad [v(\tau_{2}^{s})] = 0, \quad s = 2, 4. \end{aligned}$$
(5.17)

Clearly, $v(\tau_2) \in C^0([0,\infty))$. Now we find the upper estimate for $\widetilde{u}_2(t,0)$. Let $t > \tau_{22} + T_{23}$. Then

$$\begin{aligned} \widetilde{u}_{2}(t,0) &= \int_{\sigma_{23(0)}} p^{*}(x)b^{*}(x+T_{23})\widetilde{u}_{2}(t-T_{23},x) \,\mathrm{d}x \\ &= \int_{\sigma_{23(0)}} p^{*}(x)b^{*}(x+T_{23})\widetilde{u}_{2}(t-T_{23}-x,0)v(x) \,\mathrm{d}x \\ &= \int_{\sigma_{23(0)}}^{t-b} \widetilde{u}_{2}(y,0)p^{*}(t-T_{23}-y)b^{*}(t-y)v(t-y-T_{23}) \,\mathrm{d}y, \\ &b &= T_{23} + \tau_{21}, a = T_{23} + \tau_{22} \end{aligned}$$

and hence

$$\widetilde{u}_2(t,0) \leqslant \xi \int_{t-a}^{t-b} \widetilde{u}_2(y,0) \,\mathrm{d}y, \quad \xi = \sup_{\tau_2} p^* b^* v.$$

From this inequality we derive, by induction, the following estimate

$$\widetilde{u}_{2}(t,0) \leq \xi \eta (1+\xi b)^{j},$$

 $\eta = \int_{0}^{a} \widetilde{u}_{2}(x,0) \, \mathrm{d}x \quad \text{for} \quad a+jb \leq t \leq a+(j+1)b, \quad j=0,1,\ldots,$

or

$$\widetilde{u}_2(t,0) \leqslant \xi \eta (1+\xi b)^{\frac{t-a}{b}}, \quad t \ge a.$$

Thus there exists the Laplace transform $f(\lambda)$ of $\tilde{u}_2(t,0)$. Letting $\rho(\tau_2) = p^*(\tau_2 - T_{23})b^*(\tau_2)$, we obtain

$$\begin{split} f(\lambda) &= \int_{0}^{\infty} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) \, \mathrm{d}t = \int_{0}^{b} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) \, \mathrm{d}t \\ &+ \int_{b}^{\infty} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) \, \mathrm{d}t = \int_{0}^{b} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) \, \mathrm{d}t \\ &+ \int_{b}^{\infty} \exp\{-\lambda t\} \left(\int_{b}^{\min(t,a)} \rho(\tau_{2}) \widetilde{u}_{2}(t-\tau_{2},0) v(\tau_{2}-T_{23}) \, \mathrm{d}\tau_{2} \right. \\ &+ \int_{\min(t,a)}^{a} \rho(\tau_{2}) \widetilde{u}_{2}(t-T_{23},\tau_{2}-T_{23}) \, \mathrm{d}\tau_{2} \right) \, \mathrm{d}t = \int_{0}^{b} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) \, \mathrm{d}t \\ &+ \int_{b}^{a} \exp\{-\lambda t\} \, \mathrm{d}t \int_{t}^{a} \rho(\tau_{2}) \widetilde{u}_{2}(t-T_{23},\tau_{2}-T_{23}) \, \mathrm{d}\tau_{2} \\ &+ \int_{b}^{a} \mathrm{d}\tau_{2} \rho(\tau_{2}) v(\tau_{2}-T_{23}) \int_{\tau_{2}}^{\infty} \exp\{-\lambda t\} \widetilde{u}_{2}(t-\tau_{2},0) \, \mathrm{d}t \\ &= I(\lambda) + R(\lambda) f(\lambda), \end{split}$$

where

$$R(\lambda) = \int_{b}^{a} \rho(\tau_2) v(\tau_2 - T_{23}) \exp\{-\lambda \tau_2\} d\tau_2,$$

$$I(\lambda) = \int_{0}^{b} \exp\{-\lambda t\} \widetilde{u}_{2}(t,0) dt + \int_{b}^{a} \exp\{-\lambda t\} dt \int_{t}^{a} \rho(\tau_{2}) \widetilde{u}_{2}(t - T_{23}, \tau_{2} - T_{23}) d\tau_{2}.$$

Hence

$$f(\lambda) = I(\lambda) / \{1 - R(\lambda)\}.$$

It is well known that equation $R(\lambda) = 1$ has a unique real rooth λ_0 and conjugate pairs of single complex roots $\lambda_i = 1, 2, ...$ such that $Re\lambda_i < \lambda_0$. $I(\lambda)$ is an analytic function, thus, using the method of rectangle contour integral (Bellman, 1963), we can evaluate the inverse Laplace transform obtaining

$$\widetilde{u}_2(t,0) \sim \widetilde{u}_2^{as}(t,0) = \kappa \exp\{\lambda_0 t\}, \quad \kappa = I(\lambda_0)/\{-dR/d\lambda\}|_{\lambda=\lambda_0},$$

and, by (5.17),

$$\widetilde{u}_2(t,\tau_2) \sim \kappa v(\tau_2) \exp\left\{\lambda_0(t-\tau_2)\right\}$$

for large $t > \tau_2$. If $\lambda_0 < 0$, then solution of problem (3.1)–(3.3) extincts provided that (5.16) and hypotheses (H) hold.

5.3. A Class of Product Solutions

In this subsection, we consider the case of stationary vital functions b_1 , b_2 , p, ν_1 , ν_2 , ν_3 , ν_4 and examine the product solutions of system (3.1), (3.2)_{1,2,3,4} of the form:

$$u_{1} = \exp\left\{\lambda(t-\tau_{1})\right\} f_{1}(\tau_{1})u_{10}, \quad f_{1}(0) = 1,$$

$$u_{2} = \exp\left\{\lambda(t-\tau_{2})\right\} f_{2}(\tau_{2})u_{20}, \quad f_{2}(0) = 1,$$

$$u_{3} = \exp\{\lambda t\} f_{3}(\tau_{1},\tau_{2},\tau_{3})u_{20}, \quad f_{3}|_{\tau_{3}=0} = pn^{-1}f_{1}f_{2}\exp\left\{-\lambda(\tau_{1}+\tau_{2})\right\},$$

$$n = \int_{\sigma_{1}} f_{1}(\tau_{1})\exp\{-\lambda\tau_{1}\} d\tau_{1} + \int_{\sigma_{23}(0)} f_{2}(\tau_{2})\exp\{-\lambda\tau_{2}\} d\tau_{2}u_{20}/u_{10}, \quad (5.18)$$

$$u_{4} = \exp\{\lambda t\} f_{4}(\tau_{1},\tau_{2},\tau_{4})u_{20}, \quad f_{4}|_{\tau_{4}=0} = f_{3}|_{\tau_{3}=T_{23}},$$

where λ , $u_{10} > 0$, $u_{20} > 0$ are constants.

Substituting of (5.18) into (3.1), $(3.2)_{1,2,3,4}$ leads to the following equations:

$$f_{1}' = -\nu_{1}f_{1}, \quad f_{1}(0) = 1,$$

$$f_{2}' = -\nu_{2}f_{2} - f_{2} \begin{cases} 0, & \tau_{2} \notin \sigma_{23}(0) \\ \int \\ \sigma_{1} & pn^{-1}f_{1}(\tau_{1}) \exp\{-\lambda\tau_{1}\} d\tau_{1}, \quad \tau_{2} \in \sigma_{23}(0) \end{cases}$$
(5.19)

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$$+ \begin{cases} 0, & \tau_2 \notin \sigma_{24}(T_{24}), \\ \int_{\sigma_1} f_4 \big|_{\tau_4 = T_{24}} \exp\{\lambda \tau_2\} \, \mathrm{d}\tau_1, \quad \tau_2 \in \sigma_{24}(T_{24}), \end{cases}$$
(5.20)

$$f_{2}(0) = 1, \ \left[f_{2}(\tau_{2}^{s})\right] = 0, \ s = \overline{1, 4}, \\ \partial f_{3}/\partial \tau_{2} + \partial f_{3}/\partial \tau_{3} = -(\nu_{3} + \lambda)f_{3},$$

$$f_3|_{\tau_3=0} = pn^{-1} f_1 f_2 \exp\left\{-\lambda(\tau_1 + \tau_2)\right\},\tag{5.21}$$

$$\partial f_4 / \partial \tau_2 + \partial f_4 / \partial \tau_4 = -(\nu_4 + \lambda) f_4, \quad f_4 \big|_{\tau_4 = 0} = f_3 \big|_{\tau_3 = T_{23}},$$
(5.22)

$$1 = \int_{\sigma_1} d\tau_1 \int_{\sigma_{23}(T_{23})} b_1 f_3 \big|_{\tau_3 = T_{23}} d\tau_2 u_{20} / u_{10},$$
(5.23)

$$1 = \int_{\sigma_1} d\tau_1 \int_{\sigma_{23}(T_{23})} b_2 f_3 \big|_{\tau_3 = T_{23}} d\tau_2,$$
(5.24)

where \boldsymbol{n} is defined by $(5.18)_4$ and the prime denotes differentiation.

Equations (5.19), (5.21), (5.22) have the following solution

$$f_{1} = \exp\left\{-\int_{0}^{\tau_{1}}\nu_{1}(x) dx\right\},$$

$$f_{3} = n^{-1}p(\tau_{1}, \tau_{2} - \tau_{3})f_{1}(\tau_{1})f_{2}(\tau_{2} - \tau_{3})\exp\left\{-\lambda(\tau_{1} + \tau_{2}) - \int_{0}^{\tau_{3}}\nu_{3}(\tau_{1}, x + \tau_{2} - \tau_{3}, x) dx\right\},$$

$$f_{4} = n^{-1}p(\tau_{1}, \tau_{2} - \tau_{4} - T_{23})f_{1}(\tau_{1})f_{2}(\tau_{2} - \tau_{4} - T_{23})\exp\left\{-\lambda(\tau_{1} + \tau_{2}) - \int_{0}^{\tau_{4}}\nu_{4}(\tau_{1}, x + \tau_{2} - \tau_{4}, x) dx - \int_{0}^{T_{23}}\nu_{3}(\tau_{1}, x + \tau_{2} - \tau_{4} - T_{23}, x) dx\right\}.$$
(5.25)

Thus (5.20) can be written as follows:

$$f_{2}' = -\nu_{2}f_{2} - f_{2} \begin{cases} 0, & \tau_{2} \notin \sigma_{23}(0), \\ \int_{\sigma_{1}} pn^{-1}f_{1}(\tau_{1})\exp\{-\lambda\tau_{1}\} d\tau_{1}, & \tau_{2} \in \sigma_{23}(0) \end{cases}$$
(5.26)
+
$$f_{2}(\tau_{2} - T_{24} - T_{23}) \begin{cases} 0, & \tau_{2} \notin \sigma_{24}(T_{24}), \\ n^{-1}\int_{\sigma_{1}} f_{1}(\tau_{1})\exp\{-\lambda\tau_{1}\}Q(\tau_{1},\tau_{2}) d\tau_{1}, & \tau_{2} \in \sigma_{24}(T_{24}), \end{cases}$$
(5.26)
$$f_{2}(0) = 1, \quad [f_{2}(\tau_{2}^{s})] = 0, \quad s = \overline{1, 4}, \end{cases}$$

where

$$Q(\tau_1, \tau_2) = p(\tau_1, \tau_2 - T_{23} - T_{24}) \exp \left\{ -\int_0^{T_{24}} \nu_4(\tau_1, x + \tau_2 - T_{24}, x) \, \mathrm{d}x - \int_0^{T_{23}} \nu_3(\tau_1, x + \tau_2 - T_{23} - T_{24}) \, \mathrm{d}x \right\}.$$

Equation (5.26) is linear and can be easily solved. Let $f_2(\tau_2) = F(\tau_2, \lambda, n)$ denote its solution. Then (5.23), (5.24) and (5.18)₄ can be written as follows:

$$1 = \int_{\sigma_1} d\tau_1 \int_{\sigma_2(T_{23})} b_1 n^{-1} p(\tau_1, \tau_2 - T_{23}) f_1(\tau_1) F(\tau_2 - T_{23}, \lambda, n)$$

$$\times \exp\left\{-\lambda(\tau_1 + \tau_2) - \int_{0}^{T_{23}} \nu_3(\tau_1, x + \tau_2 - T_{23}, x) dx\right\} d\tau_2 u_{20}/u_{10},$$

$$1 = \int_{\sigma_1} d\tau_1 \int_{\sigma_2(T_{23})} b_2 n^{-1} p(\tau_1, \tau_2 - T_{23}) f_1(\tau_1) F(\tau_2 - T_{23}, \lambda, n)$$

$$\times \exp\left\{-\lambda(\tau_1 + \tau_2) - \int_{0}^{T_{23}} \nu_3(\tau_1, x + \tau_2 - T_{23}, x) dx\right\} d\tau_2, \quad (5.27)$$

$$n = \int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda\tau_1\} d\tau_1 + \int_{\sigma_2(0)} F(\tau_2, \lambda, n) \exp\{-\lambda\tau_2\} d\tau_2 u_{20}/u_{10}.$$

The existence and distribution of roots of system (5.27) in general case is an *open prob-lem*, but in special cases their real solution exists. Indeed, in the case where:

(H₇) b_1, b_2, p are positive constants,

(H₈) $\nu_1, \nu_2 > 0$ are continuos,

 (H_9) $\nu_3 > 0$ does not depend on τ_1, τ_2 and is continuous,

 (H_{10}) $\nu_4 > 0$ does not depend on τ_1 and is continuously differentiable, from $(5.27)_{1,3}$ we obtain

$$n = N(\lambda) := \left(\int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} \, \mathrm{d}\tau_1 \right)^2 / \left(\int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} \, \mathrm{d}\tau_1 - q_1^{-1} \exp\{\lambda T_{23}\} \right), \quad \lambda \in (-\infty, \lambda^*),$$
(5.28)

where λ^* is a unique real root of the equation

$$\int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} d\tau_1 - q_1^{-1} \exp\{\lambda T_{23}\} = 0,$$
$$q_1 = b_1 p \exp\left\{-\int_0^{T_{23}} \nu_3(x) dx\right\}.$$

Hence

$$n^{-1} \int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} d\tau_1$$

= 1 - q_1^{-1} \exp\{\lambda T_{23}\} / \int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} d\tau_1 \to \begin{cases} 0, & \lambda \to \lambda^*, \\ 1, & \lambda \to -\infty. \end{cases}

From $(5.27)_2$ and (5.28) we have

$$n^{-1} \int_{\sigma_1} f_1(\tau_1) \exp\{-\lambda \tau_1\} d\tau_1$$

= $q_2^{-1} \exp\{\lambda T_{23}\} / \int_{\sigma_{23}(0)} F(\tau_2, \lambda, N(\lambda)) \exp\{-\lambda \tau_2\} d\tau_2,$
 $q_2 = b_2 p \exp\left\{-\int_{0}^{T_{23}} \nu_3(x) dx\right\}.$

The last two equations lead to the following equation for λ

$$0 = K(\lambda) := 1 - \left(q_2 \int_{\sigma_{23}(0)} F(\tau_2, \lambda, N(\lambda))\right) \exp\left\{-\lambda(T_{23} + \tau_2)\right\} d\tau_2)^{-1} - \left(q_1 \int_{\sigma_1} f_1(\tau_1) \exp\left\{-\lambda(T_{23} + \tau_1)\right\} d\tau_1\right)^{-1}.$$

Function $K(\lambda)$, $\lambda \in (-\infty, \lambda^*)$ changes its sign and, hence, has a real solution $\lambda_0 \in (-\infty, \lambda^*)$, $\operatorname{sign} \lambda_0 = \operatorname{sign} K(0)$. Then $n = N(\lambda_0)$, and from $(5.27)_{1,2}$ it follows that $u_{20}/u_{10} = b_2/b_1$. It is evident that hypotheses $(H_7) - (H_{10})$ ensure the positivity and differentiability of f_i , $i = \overline{1, 4}$.

Theorem 2. Under the hypotheses $(H_7) - (H_{10})$ problem (3.1), $(3.2)_{1,2,3,4}$ has the product solution of type (5.18).

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Populiacijos su harmoninio tipo kryžminimosi dėsniu ir patelių nėštumu evoliucijos problema

Vladas SKAKAUSKAS

Pasiūlytas nelimituotos populiacijos su harmoninio tipo kryžminimosi dėsniu ir patelių nėštumu amžiaus ir lyčių struktūros dinamikos modelis. Bendruoju gyvybinių greičių atveju įrodyta sprendinio egzistencijos ir vienaties teorema, išnagrinėtas populiacijos augimas ir jos išnykimas ir rasti separabeliniai sprendiniai.