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ON AGE-SPACE STRUCTURE OF AN AUTOSOMAL DIPLOID POPULATION DYNAMICS MODEL

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ABSTRACT

We discuss an age-structured autosomal polylocal multiallelic diploid population dynamics deterministic model taking into account random mating of sexes, females' pregnancy and its dispersal in whole space. Dispersal mechanism is described by the diffusion one with constant dispersal moduli while the birth moduli depend on the spatial density of the total population with a time delay. It is assumed that the population consists of male, single (nonfertilized) female, and fertilized female subclasses. Using the method of the fundamental solution for the uniformly parabolic second-order differential operator with bounded Hölder continuous coefficients we prove the existence and uniqueness theorem for the classic solution of the Cauchy problem for this model. We analyze population's growth and decay, too. Mutation is not considered in this paper.

1. INTRODUCTION

In a recent paper [4] we have proposed a general deterministic model for an age-structured autosomal polylocal multiallelic diploid population dynamics taking into account random mating of sexes without formation of the permanent male-female pair, females' pregnancy, possible destruction of the fetus (abortion), and female sterility periods after abortion and delivery. The class of the population of the given genotype is divided into five components: one male and four female, the latter four being the single (nonfertilized) female, fertilized female, female from the sterility period after abortion, and female from the 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 females' sterility periods are independent of individuals or time. Observe that this model neglects mutation of genes. In the case of the simplified model where abortion and sterility period after delivery are neglected the unique global classic solvability of that model for an unlimited population has been proved.

In the paper [6] we considered the same simplified model as in [4] letting, in addition, the population to disperse in whole space with the dispersal mechanism described by the general linear elliptic differential operator of second order. In that model we did not let birth moduli to depend on either the density of the total population or, more generally, on the population itself.

In the present paper we are interested in the model in [6] with simplified both the dispersal mechanism and mating law, and generalized birth moduli. The simplification consists in replacing the dispersal mechanism of the model in [6] by the diffusion one with constant dispersal moduli, and not letting the fertilization rate to depend on the characteristic of the mated male. Generalizing the model in [6] we let birth moduli to depend on the spatial density of the total population with a time delay. The aim of this article is to prove the existence and uniqueness of a classic solution of the Cauchy problem for this model.

The plan for this paper is as follows. In Sect.3 we formulate the problem. Sect.4 represents hypotheses and results. In Sect.5 we recall some results concerning the solvability and uniquenees of the Cauchy problem for the linear differential parabolic operator of second order with a parameter. Sect.6 is devoted to proving the solvability theorem.

2. NOTATION

We examine the population whose autosomal character is controlled by l loci of a pair of homologous chromosomes and a gene of the jth locus can be in any of m_j alleles. Let us recall notations in [4]:

$s = \begin{pmatrix} s_{11} & \dots & s_{1l} \\ s_{21} & \dots & s_{2l} \end{pmatrix}$ and $k = \begin{pmatrix} k_{11} & \dots & k_{1l} \\ k_{21} & \dots & k_{2l} \end{pmatrix}$, where s_{ij}, $k_{ij} = \overline{1, m_j}$, $j = \overline{1, l}$, $i = 1, 2$: the genotypes (the homologous pairs of chromosomes, where $s_{11} \cdots s_{1l}$, $k_{11} \cdots k_{1l}$ are paternal and $s_{21} \cdots s_{2l}$, $k_{21} \cdots k_{2l}$ maternal chromosomes) for a male and a female, respectively;

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

t: time;

E^m: Euclidean space (habitat of population) of dimension m;

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

$u_{1s}(x, t, \tau_1)$: the age-space density of males of the s genotype at age τ_1, location x and time t;

$u_{2k}(x, t, \tau_2)$: the age-space density of single (nonfertilized) females of the k genotype at age τ_2, location x and time t;

$u_{3sk}(x, t, \tau_1, \tau_2, \tau_3)$: the age-space density of fertilized females of the k genotype at age τ_2, position x and time t whose embryo is at age τ_3 and that were fertilized by males at age τ_1 and of the s genotype;

$p_{sk}(x, t, \tau_1, \tau_2)$: the density of probability to become fertilized for a female from the pair formed of male of the s genotype at age τ_1 and female of the k genotype at age τ_2, location x and time t;

$\nu_{1s}(x,t,\tau_1)$, $\nu_{2k}(x,t,\tau_2)$ and $\nu_{3sk}(x,t,\tau_1,\tau_2,\tau_3)$: the death rates of males, single and fertilized females of characteristics (s,τ_1), (k,τ_2) and $(s,\tau_1;k,\tau_2)$, respectively, at position x and time t;

$X_k(x,t,\tau_2)$: the gain density of single females of characteristic (k,τ_2) by the females which have had a delivery at position x and time t;

$Y_k(x,t,\tau_2)$: the loss rate of single females of characteristic (k,τ_2) due to conception at location x and time t;

$\omega^i_{sk}(x,t,\tau_1,\tau_2)$: the probability a zygote to be of genotype i provided that the pair of parents had characteristic $(s,\tau_1;k,\tau_2)$;

$\sigma_1 = (\tau_{11},\tau_{12}]$, $0 < \tau_{11} < \tau_{12} < \infty$: the female sexual activity interval, $\overline{\sigma}_1 = [\tau_{11},\tau_{12}]$;

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

$\sigma_2(\tau_3) = (\tau_{21}+\tau_3,\tau_{22}+\tau_3]$, $0 < \tau_{21} < \tau_{22} < \infty$, $\overline{\sigma}_2(\tau_3) = [\tau_{21}+\tau_3,\tau_{22}+\tau_3]$;

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

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

$n_1(x,t)$: the spatial density of males with ages from σ_1 at location x and time t;

$b_{1sk}(x,t,\tau_1,\tau_2,n(x,t-T))$ and $b_{2sk}(x,t,\tau_1,\tau_2,n(x,t-T))$: the average numbers of male and female offspring, respectively, produced at position x and time t by a fertilized female of characteristics $(s,\tau_1;k,\tau_2)$, $\tau_3 = T$;

$u^0_{1s}(x,\tau_1)$, $u^0_{2k}(x,\tau_2)$, $u^0_{3sk}(x,\tau_1,\tau_2,\tau_3)$: the initial distributions;

$n_0(x,t)$: the initial spatial density of the total population at location x and time $t \in [-T,0]$;

$\sigma = \sigma_1 \times \sigma_2(T)$, $\overline{\sigma} = \overline{\sigma}_1 \times \overline{\sigma}_2(T)$, $d\sigma = d\tau_1 d\tau_2$;

$\tau^0_2 = 0$, $\tau^1_2 = \tau_{21}$, $\tau^2_2 = \min(\tau_{21}+T,\tau_{22})$, $\tau^3_2 = \max(\tau_{21}+T,\tau_{22})$, $\tau^4_2 = \tau_{22}+T$, $\tau^5_2 = \infty$;

$I = (0,\infty)$, $\overline{I} = [0,\infty)$, $I_4 = (\tau^4_2,\infty)$, $I_j = (\tau^j_2,\tau^{j+1}_2]$, $j = \overline{0,3}$;

$I^* = (0,t^*]$, $\overline{I}^* = [0,t^*]$, $t^* < \infty$;

$Q^1 = \{(x,t,\tau_1) \in E^m \times I \times I\}$, $\overline{Q}^1 = E^m \times \overline{I} \times \overline{I}$;

$Q^2 = \{(x,t,\tau_2) \in E^m \times I \times (I \setminus \bigcup_{j=1}^{4} \tau^j_2)\}$, $\overline{Q}^2 = \overline{Q}^1 = E^m \times \overline{I} \times \overline{I}$;

$Q^3 = \{(x,t,\tau_1,\tau_2,\tau_3) \in E^m \times I \times \sigma_1 \times \sigma_2(\tau_3) \times \sigma_3\}$, $\overline{Q}^3 = E^m \times \overline{I} \times \overline{\sigma}_1 \times \overline{\sigma}_2(\tau_3) \times \overline{\sigma}_3$;

$[u_{2k}|_{\tau_2=\tau^j_2}]$: the jump of the function u_{2k} at the plane $\tau_2 = \tau^j_2$;

$\widehat{D}_1 = \partial/\partial t + \partial/\partial\tau_1$, $\widehat{D}_2 = \partial/\partial t + \partial/\partial\tau_2$, $\widehat{D}_3 = \widehat{D}_2 + \partial/\partial\tau_3$; $D_1 = \sqrt{2}\tilde{D}_1$, $D_2 = \sqrt{2}\tilde{D}_2$, $D_3 = \sqrt{3}\tilde{D}_3$;

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

a_{1s}, a_{2k}, a_{3sk} : the spatial dispersal moduli of males, single females, and fertilized females, respectively;

Δ : the Laplace operator;

$L_{1s}(x,t,\tau_1) = a_{1s}\Delta - \nu_{1s}(x,t,\tau_1)$;
$L_{2k}(x,t,\tau_2) = a_{2k}\Delta - \nu_{2k}(x,t,\tau_2)$;
$L_{3sk}(x,t,\tau_1,\tau_2,\tau_3) = a_{3sk}\Delta - \nu_{3sk}(x,t,\tau_1,\tau_2,\tau_3)$;
$L^1(\eta;\Omega)$: the Banach space of functions $f(\eta,\cdot)$ integrable on Ω;
$C^0(E^m \times J_1 \times \ldots \times J_r)$, $J_j = (J_{j1}, J_{j2}), J_{j1} < J_{j2} < \infty$, $j = \overline{1,r}$: the Banach space of uniformly bounded continuous in $E^m \times J_1 \times \ldots \times J_r$ functions $f(x,\xi_1,\xi_2,\ldots,\xi_r)$;
$C^{\alpha,0,\ldots,0}(E^m \times J_1 \times \ldots \times J_r)$: the Banach space of functions $f(x,\xi_1,\xi_2,\ldots,\xi_r)$ belonging to $C^0(E^m \times J_1 \times \ldots \times J_r)$, which are Hölder continuous in $(E^m \times J_1 \times \ldots \times J_r)$ with exponent $\alpha \in (0,1)$ in x uniformly with respect to $(\xi_1,\xi_2,\ldots,\xi_r)$, i.e. having the finite Holder seminorm with respect to x (see [2]);
The letters s and k will be used in this paper only for the notation of genotypes of male and female, respectively.

3. STATEMENT OF THE PROBLEM

In this paper we discuss a model consisting of the following nonlinear system of integrodifferential equations, for u_{1s}, u_{2k}, u_{3sk},

$$(D_1 - L_{1s})u_{1s} = 0 \text{ in } Q^1, \tag{1}$$

$$(D_2 - \tilde{L}_{2k})u_{2k} = X_k, \quad \tilde{L}_{2k} = L_{2k} - Y_k \text{ in } Q^2, \tag{2}$$

$$Y_k = \begin{cases} 0, \ \tau_2 \notin \sigma_2(0), \\ n_1^{-1}\sum\limits_s \int\limits_{\sigma_1} p_{sk}u_{1s}\,d\tau_1, \ n_1 = \sum\limits_s \int\limits_{\sigma_1} u_{1s}\,d\tau_1, \ \tau_2 \in \sigma_2(0), \end{cases} \tag{3}$$

$$X_k = \begin{cases} 0, \ \tau_2 \notin \sigma_2(T), \\ \sum\limits_s \int\limits_{\sigma_1} u_{3sk}|_{\tau_3=T}\,d\tau_1, \ \tau_2 \in \sigma_2(T), \end{cases} \tag{4}$$

$$(D_3 - L_{3sk})u_{3sk} = 0 \text{ in } Q^3 \tag{5}$$

supplemented with the conditions

$$u_{1s}|_{t=0} = u_{1s}^0, \ u_{2k}|_{t=0} = u_{2k}^0 \text{ in } E^m \times I, \tag{6}$$

$$u_{3sk}|_{t=0} = u_{3sk}^0 \text{ in } E^m \times \sigma_1 \times \sigma_2(\tau_3) \times \sigma_3, \tag{7}$$

$$u_{1s}|_{\tau_1=0} = \sum_{ik}\int\limits_{\sigma} b_{1ik}(x,t,\cdot,n(x,t-T))u_{3ik}|_{\tau_3=T}\,\omega_{ik}^s\,d\sigma \text{ in } E^m \times I, \tag{8}$$

$$u_{2k}|_{\tau_1=0} = \sum_{si}\int\limits_{\sigma} b_{2si}(x,t,\cdot,n(x,t-T))u_{3si}|_{\tau_3=T}\,\omega_{si}^k\,d\sigma \text{ in } E^m \times I, \tag{9}$$

$$n(x,t) = \begin{cases} \sum\limits_s \int\limits_I u_{1s}d\tau_1 + \sum\limits_k \int\limits_I u_{2k}d\tau_2 + \\ \sum\limits_{sk} \int\limits_{\sigma_3} d\tau_3 \int\limits_{\sigma_2(\tau_3)} d\tau_2 \int\limits_{\sigma_1} u_{3sk}d\tau_1 \text{ in } E^m \times I, \\ n_0(x,t) \text{ in } E^m \times [-T,0], \end{cases} \tag{10}$$

$$u_{3sk}|_{\tau_3=0} = p_{sk}u_{1s}u_{2k}/n_1 \text{ in } E^m \times I \times \sigma_1 \times \sigma_2(0), \tag{11}$$

$$[u_{2k}|_{\tau_2=\tau_2^j}] = 0,\ j = \overline{1,4} \text{ in } E^m \times I, \tag{12}$$

and governs evolution of the population with dispersal in whole space. In addition, we assume that initial distributions u_{1s}^0, u_{2k}^0, u_{3sk}^0, n_0 satisfy the following compatibility conditions

$$u_{1s}^0|_{\tau_{1s}=0} = \sum_{ik} \int_\sigma b_{1ik}|_{t=0} u_{3ik}^0|_{\tau_3=T} \omega_{ik}^s|_{t=0}\, d\sigma \text{ in } E^m,$$

$$u_{2k}^0|_{\tau_{2k}=0} = \sum_{si} \int_\sigma b_{2si}|_{t=0} u_{3si}^0|_{\tau_3=T} \omega_{si}^k|_{t=0}\, d\sigma,\ [u_{2k}^0|_{\tau_2=\tau_2^j}] = 0,$$

$$l = \overline{1,4} \text{ in } E^m,$$

$$u_{3sk}^0|_{\tau_3=0} = p_{sk}|_{t=0} u_{1s}^0 u_{2k}^0 / \int_{\sigma_1} u_{1s}^0\, d\tau_1 \text{ in } E^m \times \sigma_1 \times \sigma_2(0). \tag{13}$$

$$n_0|_{t=0} = \sum_s \int_I u_{1s}^0 d\tau_1 + \sum_k \int_I u_{2k}^0 d\tau_2 +$$

$$\sum_{sk} \int_{\sigma_3} d\tau_3 \int_{\sigma_2(\tau_3)} d\tau_2 \int_{\sigma_1} u_{3sk}^0 d\tau_1 \text{ in } E^m.$$

As it follows from the foregoing given functions ν_{1s}, ν_{2k}, ν_{3sk}, p_{sk}, b_{1sk}, b_{2sk}, u_{1s}^0, u_{2k}^0, u_{3sk}^0, n_0, $\omega_{ik}^s, \omega_{si}^k$ and the unknown ones u_{1s}, u_{2k}, u_{3sk} must be positive-valued, otherwise they have no biological significance. Our purpose is to find u_{1s}, u_{2k}, u_{3sk} verifying (1)-(13).

Observe that, for one-locus Mendel's population, $\omega_{sk}^i = \frac{1}{4}(\delta_{s_{11}}^{i_{11}} + \delta_{s_{21}}^{i_{11}})(\delta_{k_{11}}^{i_{21}} + \delta_{k_{21}}^{i_{21}})$, where δ_β^γ designates the Kronecker symbol (see [7]).

4. HYPOTHESES AND RESULTS

Unless otherwise stated, assumptions listed in this section hold throughout the paper:

(H_1) $p_{sk} = p_k(x,t,\tau_2) \in C^{\alpha,0,0}(E^m \times \overline{I} \times \overline{\sigma}_2(0))$ *does not depend on the characteristic of the mated male and has the compact support in* x *(* $supp\ p_k(\cdot,t,\tau_2)$*) for any set* (t,τ_2)*;*

(H_2) $\omega_{sk}^i \in C^0(E^m \times \overline{I} \times \overline{\sigma}_1 \times \overline{\sigma}_2(T))$, b_{1sk}, $b_{2sk} \in C^0(E^m \times \overline{I} \times \overline{\sigma}_1 \times \overline{\sigma}_2(T) \times \overline{I})$ *are nonnegative functions;*

(H_3) $\nu_{1s} \in C^{\alpha,0,0}(\overline{Q}^1)$, $\nu_{2k} \in C^{\alpha,0,0}(\overline{Q}^2)$, $\nu_{3sk} \in C^{\alpha,0,0,0,0}(\overline{Q}^3)$ *are nonnegative functions;*

(H_4) a_{1s}, a_{2k}, a_{3sk} *are positive constants;*

(H_5) $u_{2k}^0(x,\tau_2) \in C^0(E^m \times \overline{I})$ *is nonnegative integrable w.r.t.* $\tau_2 \in I$, $u_{3sk}^0(x,\tau_1,\tau_2,\tau_3) \in C^0(E^m \times \overline{\sigma}_1 \times \overline{\sigma}_2(\tau_3) \times \overline{\sigma}_3)$ *and* $n_0(x,t) \in C^0(E^m \times [-T,0])$ *are nonnegative,* $u_{1s}^0(x,\tau_1) \in C^0(E^m \times \overline{I})$ *is strictly positive integrable w.r.t.* $\tau_1 \in I$*, and all the densities* u_{1s}^0, u_{2k}^0, u_{3sk}^0, $n_0(x,0)$ *verify (13).*

Now we list theorems for solvability of model (1)-(13), population growth and its decay. The first of them will be proved in Sect. 6 while proof of the other two theorems is the same as that in [6].

THEOREM 1. *Under the hypotheses* $(H_1)-(H_5)$ *problem (1)-(12) has for any*

I^* an unique nonnegative classic (see [2,3]) solution such that $u_{1s} \in C^0(E^m \times \overline{I}^* \times \overline{I}) \bigcap L^1(x,t;I)$, $u_{2k} \in C^0(E^m \times \overline{I}^* \times \overline{I}) \bigcap L^1(x,t;I)$, $u_{3sk} \in C^0(E^m \times \overline{I}^* \times \overline{\sigma}_1 \times \overline{\sigma}_2(\tau_3) \times \overline{\sigma}_3)$.

Let us introduce the following notions

$$\widehat{b} = \max_{s,k}\{\sum_j \int\limits_{\sigma_2(T)} \sup_{i,\, E^m \times \overline{I} \times \overline{\sigma}_1 \times \overline{I}} \big(b_{1ij}\omega_{ij}^s\big)\, d\tau_2,$$

$$\sum_j \int\limits_{\sigma_2(T)} \sup_{i,\, E^m \times \overline{I} \times \overline{\sigma}_1 \times \overline{I}} \big(b_{2ij}\omega_{ij}^k\big)\, d\tau_2\}, \quad \widehat{p} = \sup_{k,\, E^m \times \overline{I} \times \overline{\sigma}_2(0)} p_k,$$

$$\tilde{\nu}_2 = \inf_{k,\, E^m \times \overline{I} \times (\overline{I}_2 \cup \overline{I}_3)} \nu_{2k}, \quad \widehat{u} = \max_{s,k}\big(\sup_{E^m \times \overline{I}} u_{1s}^0,\ \sup_{E^m \times \overline{I}} u_{2k}^0\big),$$

$$\widehat{u}_3 = \max_{s,k}\big(\sum_i \sup_{E^m \times \overline{\sigma}_2(T)} \int\limits_{\sigma_1} u_{3ik}^0|_{\tau_3 = T}\omega_{ik}^s\, d\tau_1,$$

$$\sum_i \sup_{E^m \times \overline{\sigma}_2(T)} \int\limits_{\sigma_1} u_{3si}^0|_{\tau_3 = T}\omega_{si}^k\, d\tau_1\big),$$

$$Q_*^3 = \{(x,t,\tau_1,\tau_2,\tau_3) : x \in E^m,\ 0 < t \le \tau_3,\ \tau_1 \in \sigma_1,\ \tau_2 \in \sigma_2(\tau_3),\ \tau_3 \in \sigma_3\},$$

$$Q^{3*} = \{(x,t,\tau_1,\tau_2,\tau_3) : x \in E^m,\ t > \tau_3,\ \tau_1 \in \sigma_1,\ \tau_2 \in \sigma_2(\tau_3),\ \tau_3 \in \sigma_3\}.$$

THEOREM 2. *Assume $(H_1) - (H_5)$ hold, and let $\tilde{\nu}_2 > 0$. Then*

(i) $$\sum_s \int\limits_{\sigma_1} u_{3sk}\, d\tau_1 \le \begin{cases} \widehat{u}_3 \ \text{in } Q_*^3 \\ \widehat{p} \sup\limits_{y \in E^m} u_{2k}(y, t-\tau_3, \tau_2 - \tau_3) \ \text{in } Q^{3*} \text{ for } t - \tau_3 \in \overline{I}^*, \end{cases}$$

(ii) $u_{1s},\ u_{2k} \le \delta\, \gamma^j\, \widehat{u}$ *for* $t \in (jT, (j+1)T] \cap [0,t^*]$, $x \in E^m$, $\tau_1,\ \tau_2 \in \overline{I}$,
where $j = 0,1,\ldots,$ $\gamma = \max(\widehat{b}\,\widehat{p}, 1, \widehat{p}/\tilde{\nu}_2)$ *and* $\delta = \max\big(\widehat{b}\,\widehat{u}_3/\widehat{u}, 1, \widehat{u}_3/\widehat{u}\,\tilde{\nu}_2\big)$,
(or more roughly $u_{1s},\ u_{2k} \le \delta\, \widehat{u}\, \gamma^{t/T}$*).*

Define

$$q = \widehat{b}\,\widehat{u}_3/\widehat{u}, \ \tilde{\nu} = \min_{s,k}\big(\inf_{\overline{Q}_1} \nu_{1s},\ \inf_{\overline{Q}_2} \nu_{2k}\big),$$

$$\omega_0 = \{(x,t,\xi) : x \in E^m,\ 0 \le t \le \xi,\ \xi \in \overline{I}\},$$

$$\omega_j = \{(x,t,\xi) : x \in E^m,\ (j-1)\tau_2^4 < t - \xi \le j\tau_2^4,\ t \le t^*,\ \xi \in \overline{I}\},\ j = 1,2,\ldots$$

THEOREM 3. *Assume the hypotheses $(H_1) - (H_5)$ hold and let* $\widehat{b}\,\widehat{p} \le q \le \min(1, \tilde{\nu}\,\widehat{b})$, $\tilde{\nu} > 0$. *Then* $\max\limits_{s,k}\{\sup\limits_{(x,t,\tau_1) \in \omega_j} u_{1s},\ \sup\limits_{(x,t,\tau_2) \in \omega_j} u_{2k}\} \le \widehat{u}q^j$.

COROLLARY 4. *Let assumptions of Th.3 hold. If $q < 1$, then the population vanishes as t increases.*

5. SOME PROPERTIES OF THE PARABOLIC OPERATOR OF SECOND ORDER

In this section we collect some results concerning the solvability and uniqueness of the Cauchy problem for the linear differential parabolic operator of second order (see [2,3,5]) with a parameter.

LEMMA 5. (see [5]). *Let*

$$\Lambda(x,t,\beta) = \partial/\partial t - \sum_{i,j=1}^{m} b_{ij}\partial^2/\partial x_i \partial x_j - \sum_{i=1}^{m} \tilde{b}_i \partial/\partial x_i + \tilde{b}_0$$

be a uniformly parabolic operator depending on a parameter $\beta \in J = [\beta_1, \beta_2]$, $\beta_1 < \beta_2 < \infty$ *with coefficients verifying the following conditions*

$b_{ij}(x,t,\beta) \in C^{\alpha,\alpha/2,0}(E^m \times \overline{I}^* \times J)$, $i,j = \overline{1,m}$,

$\tilde{b}_i(x,t,\beta) \in C^{\alpha,0,0}(E^m \times \overline{I}^* \times J)$, $i = \overline{0,m}$

and assume that

$0 < u^0(x,\beta) \in C^0(E^m \times J)$,

$0 < f(x,t,\beta) \in C^0(E^m \times \overline{I}^* \times J)$, $|f(x,t,\beta) - f(y,t,\beta)| \leq \kappa t^{-\gamma}|x-y|^\alpha$

with κ *a constant and* $\gamma \in (0,1)$. *Then the problem*

$$\Lambda u = f \text{ in } E^m \times \overline{I}^* \times J, \; u(x,0,\beta) = u^0 \text{ in } E^m \times J \tag{14}$$

has a unique stictly positive in $E^m \times \overline{I}^* \times J$ *classic (see [2]) solution*

$$u(x,t,\beta) = \int_{E^m} \Gamma(x,t;y,0;\beta) u^0(y,\beta)\, dy$$

$$+ \int_0^t d\tau \int_{E^m} \Gamma(x,t;y,\tau;\beta) f(y,\tau,\beta) dy, \; u \in C^0(E^m \times \overline{I}^* \times I), \tag{15}$$

where $\Gamma(x,t;y,\tau;\beta)$ *is the fundamental solution of the operator* $\Lambda(x,t,\beta)$.

Lemma 5 generalizes the classic result with $\gamma = 0$ to the case with $\gamma \in (0,1)$. It shows also the continuity of u in $E^m \times \overline{I}^* \times I$. Observe that

$$|\int_{E^m} \{\Gamma(x,t;y,\tau;\beta) - \Gamma(x',t;y,\tau;\beta)\} f(y,\xi,\beta)\, dy| \leq \kappa_1 |x-x'|(t-\tau)^{-1/2} \tag{16}$$

for $f \in C^0(E^m \times \overline{I}^* \times J)$, where κ_1 is a constant.

6. PROOF OF THEOREM 1.

Now we are in position to prove Th.1. We limit ourselves to the case of multiple deliveries, i.e. $T < \tau_{22} - \tau_{21}$, $\tau_2^2 = \tau_{21} + T, \tau_3^2 = \tau_{22}$. The opposite case can be considered in the similar way.

Set

$Q^1 = Q^1_* \cup Q^{1*}$, $E^m \times I \times I = \bigcup_{j=0}^{4} Q^2_j$, $Q^2_j = E^m \times I \times I_j = Q^2_{j*} \cup Q^{2*}_j$, $j = \overline{0,4}$,
$Q^3 = Q^3_* \cup Q^{3*}$, where
$Q^1_* = \{(x,t,\tau_1) : x \in E^m,\, 0 < t \le \tau_1,\, \tau_1 \in I\}$,
$Q^{1*} = \{(x,t,\tau_1) : x \in E^m,\, t > \tau_1,\, \tau_1 \in I\}$,
$Q^2_{j*} = \{(x,t,\tau_2) : x \in E^m,\, 0 < t \le \tau_2 - \tau_2^j,\, \tau_2 \in I_j\}$,
$Q^{2*}_j = \{(x,t,\tau_2) : x \in E^m,\, t > \tau_2 - \tau_2^j,\, \tau_2 \in I_j\}$,
$Q^3_* = \{(x,t,\tau_1,\tau_2,\tau_3) : x \in E^m,\, 0 < t \le \tau_3,\, \tau_1 \in \sigma_1,\, \tau_2 \in \sigma_2(\tau_3),\, \tau_3 \in \sigma_3\}$,
$Q^{3*} = \{(x,t,\tau_1,\tau_2,\tau_3) : x \in E^m,\, t > \tau_3,\, \tau_1 \in \sigma_1,\, \tau_2 \in \sigma_2(\tau_3),\, \tau_3 \in \sigma_3\}$.

Let $\tau_1 = t + \eta_1$ and $\tau_2 = t + \eta_2$ be characteristics of the operators $\widehat{D}_1$ and $\widehat{D}_2$, respectively, and assume that $\tau_2 = t+\eta_3$, $\tau_3 = t+\eta_4$ mean characteristics of $\widehat{D}_3$. Here η_1, η_2, η_3, η_4 denote parameters of characteristics. Letting
$L_{1s}(x,t,t+\eta_1) = L_{1s*}(x,t,\eta_1)$, $u_{1s}(x,t,t+\eta_1) = u_{1s*}(x,t,\eta_1)$ in Q^1_*,
$L_{1s}(x,\tau_1-\eta_1,\tau_1) = L^*_{1s}(x,\tau_1,-\eta_1)$,
$u_{1s}(x,\tau_1-\eta_1,\tau_1) = u^*_{1s}(x,\tau_1,-\eta_1)$ in Q^{1*},
$L_{2k}(x,t,t+\eta_2) = L_{2k*}(x,t,\eta_2)$, $u_{2k}(x,t,t+\eta_2) = u_{2k*}(x,t,\eta_2)$,
$Y_k(x,t,t+\eta_2) = Y_{k*}(x,t,\eta_2)$, $X_k(x,t,t+\eta_2) = X_{k*}(x,t,\eta_2)$ in $\bigcup_{j=0}^{4} Q^2_{j*}$,

$L_{2k}(x,\tau_2-\eta_2,\tau_2) = L^*_{2k}(x,\tau_2,-\eta_2)$, $u_{2k}(x,\tau_2-\eta_2,\tau_2) = u^*_{2k}(x,\tau_2,-\eta_2)$,
$Y_k(x,\tau_2-\eta_2,\tau_2) = Y^*_k(x,\tau_2,-\eta_2)$,
$X_k(x,\tau_2-\eta_2,\tau_2) = X^*_k(x,\tau_2,-\eta_2)$ in $\bigcup_{j=0}^{4} Q^{2*}_j$,
$L_{3sk}(x,t,\tau_1,t+\eta_3,t+\eta_4) = L_{3sk*}(x,t,\tau_1,\eta_3,\eta_4)$, $u_{3sk}(x,t,\tau_1,t+\eta_3,t+\eta_4) = u_{3sk*}(x,t,\tau_1,\eta_3,\eta_4)$ in Q^3_*,
$L_{3sk}(x,\tau_3-\eta_4,\tau_1,\tau_3+\eta_3-\eta_4,\tau_3) = L^*_{3sk}(x,\tau_3,\tau_1,-\eta_4,\eta_3-\eta_4)$,
$u_{3sk}(x,\tau_3-\eta_4,\tau_1,\tau_3+\eta_3-\eta_4,\tau_3) = u^*_{3sk}(x,\tau_3,\tau_1,-\eta_4,\eta_3-\eta_4)$ in Q^{3*},
$\tilde{L}_{2k*} = L_{2k*} - Y_{k*}$, $\tilde{L}^*_{2k} = L^*_{2k} - Y^*_k$
and taking (1)-(12) on the respective characteristics we obtain:

$$(\partial/\partial t - L_{1s*})u_{1s*} = 0 \text{ in } Q^1_*,\ u_{1s*}(x,0,\eta_1) = u^0_{1s}(x,\eta_1),$$
$$(\partial/\partial \tau_1 - L^*_{1s})u^*_{1s} = 0 \text{ in } Q^{1*},\ u^*_{1s}(x,0,-\eta_1) = u_{1s}(x,-\eta_1,0),$$
$$(\partial/\partial t - \tilde{L}_{2k*})u_{2k*} = X_{k*} \text{ in } \bigcup_{j=0}^{4} Q^2_{j*},\ u_{2k*}(x,0,\eta_2) = u^0_{2k}(x,\eta_2), \tag{17}$$
$$(\partial/\partial \tau_2 - \tilde{L}^*_{2k})u^*_{2k} = X^*_k \text{ in } Q^{2*}_j,\ u^*_{2k}(x,\tau_2^j,-\eta_2) = u_{2k}(x,\tau_2^j-\eta_2,\tau_2^j),\ j = \overline{0,4},$$
$$(\partial/\partial t - L_{3sk*})u_{3sk*} = 0 \text{ in } Q^3_*,\ u_{3sk*}(x,0,\tau_1,\eta_3,\eta_4) = u^0_{3sk}(x,\tau_1,\eta_3,\eta_4),$$
$$(\partial/\partial \tau_3 - L^*_{3sk})u^*_{3sk} = 0 \text{ in } Q^{3*},\ u^*_{3sk}(x,0,\tau_1,-\eta_4,\eta_3-\eta_4) = u_{3sk}(x,-\eta_4,\tau_1,\eta_3-\eta_4,0).$$

By virtue of $(H_3)-(H_5)$ the operators L_{1s*}, L_{2k*}, L_{3sk*}, L^*_{1s}, L^*_{2k}, L^*_{3sk} and initial distributions $u_{1s*}(x,0,\eta_1)$, $u_{2k*}(x,0,\eta_2)$, $u_{3sk*}(x,0,\tau_1,\eta_3,\eta_4)$ satisfy all the conditions of Lemma 5. If Y_{k*}, Y^*_k, $u_{1s}(x,-\eta_1,0)$, $u_{2k}(x,\tau_2^j-\eta_2,\tau_2^j)$, $u_{3sk}(x,-\eta_4,\tau_1,\eta_3-\eta_4,0)$ and X_{k*}, X^*_k are known and satisfy all the conditions of Lemma 5, then system (17) degenerates into separate problems for u_{1s*}, u^*_{1s}, u_{2k*}, u^*_{2k}, u_{3sk*}, u^*_{3sk}, respectively, of type (14). Then denoting by
$\Gamma_{1s*}(x,t;y,\xi;\eta_1)$, $\Gamma^*_{1s}(x,\tau_1;y,\xi;-\eta_1)$, $\Gamma_{2kj*}(x,t;y,\xi;\eta_2)$, $\Gamma^*_{2kj}(x,\tau_2;y,$

$\xi;-\eta_2)$, $\Gamma_{3sk*}(x,t;y,\xi;\tau_1,\eta_3,\eta_4)$, $\Gamma^*_{3sk}(x,\tau_3;y,\xi;\tau_1,-\eta_4,\eta_3-\eta_4)$ the fundamental solutions of operators

$\partial/\partial t-L_{1s*}$, $\partial/\partial\tau_1-L^*_{1s}$, $\partial/\partial t-\tilde{L}_{2k*}$, $\partial/\partial\tau_2-\tilde{L}^*_{2k}$, $\partial/\partial t-L_{3sk*}$, $\partial/\partial\tau_3-L^*_{3sk}$

in Q^1_*, Q^{1*}, Q^2_{j*}, Q^{2*}_j, Q^3_*, Q^{3*}, respectively, and, applying general formula (15) to u_{1s*}, u_{2k*}, u_{3sk*}, u^*_{1s}, u^*_{2k}, u^*_{3sk}, from (17) we obtain the system

$$u_{1s*}(x,t,\eta_1)=\int_{E^m}\Gamma_{1s*}(x,t;y,0;\eta_1)u^0_{1s}(y,\eta_1)dy \text{ in } Q^1_*,$$

$$u^*_{1s}(x,\tau_1,-\eta_1)=\int_{E^m}\Gamma^*_{1s}(x,\tau_1;y,0;-\eta_1)\,u_{1s}(y,-\eta_1,0)dy \text{ in } Q^{1*},$$

$$u_{2k*}(x,t,\eta_2)=\int_{E^m}\Gamma_{2kj*}(x,t;y,0;\eta_2)\,u^0_{2k}(y,\eta_2)dy+$$
$$\int_0^t d\xi\int_{E^m}\Gamma_{2kj*}(x,t;y,\xi;\eta_2)X_{k*}(y,\xi,\eta_2)dy \text{ in } Q^2_{j*},$$

$$u^*_{2k}(x,\tau_2,-\eta_2)=\int_{E^m}\Gamma^*_{2kj}(x,\tau_2;y,\tau_2^j;-\eta_2)u_{2k}(y,\tau_2^j-\eta_2,\tau_2^j)dy+$$
$$\int_{\tau_2^j}^{\tau_2} d\xi\int_{E^m}\Gamma^*_{2kj}(x,\tau_2;y,\xi;-\eta_2)X^*_k(y,\xi,-\eta_2)dy \text{ in } Q^{2*}_j,$$

$$u_{3sk*}(x,t,\tau_1,\eta_3,\eta_4)=\int_{E^m}\Gamma_{3sk*}(x,t;y,0;\tau_1,\eta_3,\eta_4)u^0_{3sk}(y,\tau_1,\eta_3,\eta_4)dy$$
in Q^3_*,

$$u^*_{3sk}(x,\tau_3,\tau_1,-\eta_4,\eta_3-\eta_4)=$$
$$\int_{E^m}\Gamma^*_{3sk}(x,\tau_3;y,0;\tau_1,-\eta_4,\eta_3-\eta_4)u_{3sk}(y,-\eta_4,\tau_1,\eta_3-\eta_4,0)dy \text{ in } Q^{3*},$$

which by (4) and (6-9) can be written as follows:

$$u_{1s}(x,t,\tau_1)=\int_{E^m}\Gamma_{1s*}(x,t;y,0;\tau_1-t)u^0_{1s}(y,\tau_1-t)\,dy \text{ in } Q^1_*, \tag{18}$$

$$u_{1s}(x,t,\tau_1)=\int_{E^m}\Gamma^*_{1s}(x,\tau_1;y,0;t-\tau_1)\,u_{1s}(y,t-\tau_1,0)\,dy \text{ in } Q^{1*}, \tag{19}$$

$$u_{2k}(x,t,\tau_2)=$$
$$\int_{E^m}\Gamma_{2kj*}(x,t;y,0;\tau_2-t)u^0_{2k}(y,\tau_2-t)\,dy \text{ in } Q^2_{j*} \text{ for } j=0,1,4, \tag{20}$$

$$u_{2k}(x,t,\tau_2)=\int_{E^m}\Gamma_{2kj*}(x,t;y,0;\tau_2-t)u^0_{2k}(y,\tau_2-t)\,dy$$
$$+\sum_s\int_0^t d\xi\int_{E^m} dy\Gamma_{2kj*}(x,t;y,\xi;\tau_2-t) \tag{21}$$
$$\int_{\sigma_1} u_{3sk}(y,\xi,\tau_1,\xi+\tau_2-t,T)\,d\tau_1 \text{ in } Q^2_{j*} \text{ for } j=2,3,$$

$$u_{2k}(x,t,\tau_2)=\int_{E^m}\Gamma^*_{2kj}(x,\tau_2;y,\tau_2^j;t-\tau_2)\,u_{2k}(y,\tau_2^j+t-\tau_2,\tau_2^j)\,dy \text{ in } Q^{2*}_j \tag{22}$$
for $j=0,1,4$,

$$u_{2k}(x,t,\tau_2)=\int_{E^m}\Gamma^*_{2kj}(x,\tau_2;y,\tau_2^j;t-\tau_2)u_{2k}(y,\tau_2^j+t-\tau_2,\tau_2^j)\,dy$$
$$+\sum_s\int_{\tau_2^j}^{\tau_2} d\xi\int_{E^m} dy\Gamma^*_{2kj}(x,\tau_2;y,\xi;t-\tau_2)$$
$$\int_{\sigma_1} u_{3sk}(y,\xi+t-\tau_2,\tau_1,\xi,T)\,d\tau_1 \text{ in } Q^{2*}_j \text{ for } j=2,3, \tag{23}$$

$$u_{3sk}(x,t,\tau_1,\tau_2,\tau_3) = \int_{E^m} \Gamma_{3sk*}(x,t;y,0;\tau_1,\tau_2-t,\tau_3-t)u^0_{3sk}(y,\tau_1,\tau_2-t,\tau_3-t)\,dy \text{ in } Q^3_*, \quad (24)$$

$$u_{3sk}(x,t,\tau_1,\tau_2,\tau_3) = \int_{E^m} \Gamma^*_{3sk}(x,\tau_3;y,0;\tau_1,t-\tau_3,\tau_2-\tau_3)$$
$$u_{3sk}(y,t-\tau_3,\tau_1,\tau_2-\tau_3,0)\,dy \text{ in } Q^{3*}, \quad (25)$$

$$u_{3sk}(x,t,\tau_1,\tau_2,0) = p_{sk}(x,t,\tau_1,\tau_2)u_{1s}(x,t,\tau_1)u_{2k}(x,t,\tau_2)/n_1(x,t), \quad (26)$$

$$n_1 = \sum_i \int_{\sigma_1} u_{1i}(x,t,\tau_1)\,d\tau_1,$$

$$u_{1s}(x,t,0) = \sum_{ik} \int_{\sigma} b_{1ik}(x,t,\tau_1,\tau_2,n(x,t-T))\,u_{3ik}(x,t,\tau_1,\tau_2,T)\omega^s_{ik}\,d\sigma, \quad (27)$$

$$u_{2k}(x,t,0) = \sum_{si} \int_{\sigma} b_{2si}(x,t,\tau_1,\tau_2,n(x,t-T))\,u_{3si}(x,t,\tau_1,\tau_2,T)\omega^k_{si}\,d\sigma. \quad (28)$$

$$n(x,t) = \begin{cases} \sum_s \int_I u_{1s}d\tau_1 + \sum_k \int_I u_{2k}d\tau_2 + \\ \sum_{sk} \int_{\sigma_3} d\tau_3 \int_{\sigma_2(\tau_3)} d\tau_2 \int_{\sigma_1} u_{3sk}d\tau_1 \text{ in } E^m \times I, \\ n_0(x,t) \text{ in } E^m \times [-T,0], \end{cases} \quad (29)$$

We must add to (22) and (23) the continuity condition $[u_{2k}|_{\tau_2=\tau_2^j}] = 0$, $j = \overline{1,4}$.

Now we will prove that (18)-(29) represent the solution of (1)-(13). Consider system (18)-(29) moving along the axis t by the step of size T. Since L_{1s*}, L_{2k*} in $Q^2_{0*} \cup Q^2_{4*}$, and L_{3sk*} satisfy the conditions of Lemma 5, formulas (18), (20) for $j=0$, and (24) express strictly positive functions u_{1s}, u_{2k} and u_{3sk} in Q^1_*, $Q^2_{0*} \cup Q^2_{4*}$ and Q^3_*, respectively. Hence $n_1|_{\text{supp } p_{sk}(\cdot,t,\tau_1,\tau_2)} \geq \tilde{n}_1$, and by virtue of (H_1) we observe that

$$p_{sk}(x,t,\tau_1,\tau_2)u_{1s}(x,t,\tau_1)/n_1(x,t) \in C^0(E^m \times [0,\tau_{11}] \times \overline{\sigma}_1 \times \overline{\sigma}_2(0)),$$

where $\tilde{n}_1$ is a positive constant, while from (24) by (16) it follows that

$$|u_{3sk}(x,t,\tau_1,\tau_2,\tau_3) - u_{3sk}(y,t,\tau_1,\tau_2,\tau_3)| \leq \kappa_1|x-y|\,t^{-1/2} \text{ in } Q^3_* \quad (30)$$

with κ_1 a constant.

Let $t \in [0,T]$ and assume $\omega_1 = E^m \times [0,T] \times \overline{I}$. By means of (27), (28), (29), (H_2), (H_5) and due to the continuity of u_{3sk} (see Lemma 5) we obtain continuous $u_{1s}(x,t,0)$ and $u_{2k}(x,t,0)$ $\forall(x,t) \in E^m \times [0,T]$. Now from (19) and (22) for $j=0$ we get continuous u_{1s} and u_{2k} in $Q^{1*} \cap \omega_1$ and $Q^{2*}_0 \cap \omega_1$, respectively. Then by (H_1),

$$Y_k(x,t,\tau_2) = \begin{cases} 0, \ \tau_2 \notin \sigma_2(0) \\ p_k, \ \tau_2 \in \sigma_2(0), \end{cases}$$

and (H_4) shows that $\tilde{L}_{2k*}$ and $\tilde{L}^*_{2k}$ satisfy all the conditions of Lemma 5 in $\left(Q^2_{1*} \cup Q^2_{2*}\right) \cap \omega_1$ and $\left(Q^{2*}_1 \cup Q^{2*}_2\right) \cap \omega_1$, respectively. Then (20) and (22) for $j=1$ yield u_{2k} in $\left(Q^2_{1*} \cup Q^{2*}_1\right) \cap \omega_1$, while from (21) and (23) by (24) and (30) we get u_{2k} in $\left(Q^2_{2*} \cup Q^2_{3*}\right) \cap \omega_1$ and $\left(Q^{2*}_2 \cup Q^{2*}_3\right) \cap \omega_1$, respectively. Eq. (22) for $j = 4$ gives u_{2k} in $Q^{2*}_4 \cap \omega_1$. Recalling the maximum principle and using (H_5) and (29) we prove the continuity of $n(x,t)$.

Let $t \in (T, 2T]$ and assume $\omega_2 = E^m \times [T, 2T] \times \overline{I}$. Knowing u_{1s} and u_{2k} for $t \in [0,T]$, by (26), (H_1) and because of $n_1|_{\text{supp p}_k(\cdot,t,\tau_2)} \geq \tilde{n}_1$ we get continuous $u_{3sk}(x,t,\tau_1,\tau_2,0)$ for $t \in (\tau_3, T]$, then by (25) we obtain $u_{3sk}(x,t,\tau_1,\tau_2,\tau_3)$ for $t \in (\tau_3, \tau_3 + T]$. From (27) and (28), by using (H_2) and known continuous $n(x,t)$, $u_{3sk}|_{\tau_3=T}$, we get continuous $u_{1s}|_{\tau_1=0}$ and $u_{2k}|_{\tau_2=0}$, too. Then by virtue of (19) with known $u_{1s}|_{\tau_1=0}$ and by (22) with known $u_{2k}|_{\tau_2=0}$ we obtain u_{1s} and u_{2k} in $Q^{1*} \cap \omega_2$ and $Q^{2*}_0 \cap \omega_2$, respectively. Now by (22) for $j = 1$, (23) for $j = 2$, (21) for $j = 2$, (23) for $j = 3$, (22) for $j = 4$, and (20) for $j = 4$ we construct u_{2k} in $\left(\bigcup\limits_{j=1}^{4} Q^{2*}_j \cup Q^2_{2*}\right) \cap \omega_2$.

Proceeding our reasoning we obtain u_{1s}, u_{2k} and u_{3sk} for $t \in [2T, t^*]$. Restrictions (13) ensure the continuity of u_{1s}, u_{2k}, u_{3sk} across the lines $t = \tau_1$, $t = \tau_2$, $t = \tau_3$, respectively. So Th.1 is proved. □

REFERENCES

[1] A. Friedman, *Differential equations with partial derivatives of the parabolic type*, Mir, Moscow, 1968 (in Russian).

[2] M.G. Garoni, J.L. Menaldi, *Green functions for second order parabolic integro-differential problems,* Pitman Research Notes in Mathematics, Series 275 ISSN 0269-3677, New York, 1992.

[3] O.A. Ladyzhenskaya, V.A. Solonnikov, N.N. Ural'tseva, *Linear and Quasilinear equations of parabolic type*, Nauka, Moscow, 1967 (in Russian).

[4] V. Skakauskas, *An evolution model of an autosomal polylocal polyallelic diploid population taking into account crossing-over and gestation period,* Lith. math. J., **34**, No. 3 (1994), P. 288–300.

[5] V. Skakauskas, *A mathematical analysis of an age-sex-space-structured population dynamics model with random mating and females' pregnancy,* Informatica (Lith. Acad. of Sci.) ISSN 068-1952, **9**, No. 3 (1998) (to appear).

[6] V. Skakauskas, *A mathematical analysis of an age-space-structured autosomal diploid population dynamics model with random mating and females' pregnancy,* Lith. math. J. **38** No. 4 (1998) (to appear).

[7] Yu. Svirezhev, V.P. Passekov, *Fundamentals of mathematical evolutionary genetics. Kluwer academic publishers,* Dordrecht, 1990.