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THE EVOLUTION OF NON-MIGRATING LIMITED PANMICTION POPULATION

Vladas SKAKAUSKAS

Vilnius University, Department of Differential Equations and Numerical Analysis
Naugarduko St. 24, 2600 Vilnius, Lithuania

Abstract. In this paper, taking into account the size, age structure and pregnancy of females, the model, which describes the evolution of non-migrating limited panmiction population, composed of two-sexes, is considered. In case, where reproductive period is equal or less than gestation period, death rates and fecundation function depend on population size, the unique solvability of the model is established.

Key words: limited panmiction population, evolution, unique solvability, reproductive period, gestation period.

1. Problem formulation. The unique solvability for the model, which describes the evolution of non-migrating unlimited (demographic functions are independent of population size) panmiction population, was studied by Skakauskas (1994) taking into account age of individuals and pregnancy of the females. In this paper by neglecting destruction of the foetus and organism restoration period after delivery the unique solvability for the model describing the evolution of non-migrating limited population is proved. We consider the case, where reproductive period is equal or less than gestation period, death rates and fecundation function depend on population size.

Suppose that:

$N(t)$ is population size (total density) and $y(t,\tau_y)$, $x(t,\tau_x)$, $z(t,\tau_y,\tau_x,\tau_z)$ are numbers density for males, single and fecundated females respectively, where t is time, τ_y, τ_x, τ_z are ages for males, females and embriou's, respectively;

$p(t,\tau_y,\tau_x,N)$ is fecundation function and $\nu^y(t,\tau_y,N)$, $\nu^x(t,\tau_x,N)$, $\nu^z(t,\tau_y,\tau_x,\tau_z,N)$ are death rates for males, single and fecundated females, respectively;

$\sigma_x(\tau_z) = (\tau_{1x}+\tau_z,\tau_{2x}+\tau_z]$. $\sigma_y = (\tau_{1y},\tau_{2y}]$, $\sigma_x(0)$ are reproductive intervals for males and females, respectively, and $\sigma_z = (0,T]$ is gestation interval;

$\sigma = \sigma_y \times \sigma_x(T)$, $E = \{(\tau_y, \tau_x, \tau_z) \in \sigma_y \times \sigma_x(\tau_z) \times \sigma_z\}$;

$E^y = \{(t, \tau_y) \in R_2^+ = (0,\infty) \times (0,\infty)\}$, $E^x = \{(t,\tau_x) \in (0,\infty) \times ((0,\infty) \setminus \bigcup_{i=1}^{4} \tau_i)\}$, $E^z = \{(t,\tau_y,\tau_x,\tau_z) : (t,\tau_y,\tau_z) \in (0,\infty) \times \sigma_y \times \sigma_z, \tau_x \in \sigma_x(\tau_z)\}$, where $\tau_1 = \tau_{1x}$, $\tau_2 = \tau_{2x}$, $\tau_3 = \widetilde{\tau}_{1x} = \tau_{1x} + T$, $\tau_4 = \widetilde{\tau}_{2x} = \tau_{2x} + T$;

$[x(t,\tau_i)]$ is a jump of the function x at the line $\tau_x = \tau_i$;

$2^{-1/2} D^y y$, $2^{-1/2} D^x x$, $3^{-1/2} D^z z$ represents directional derivative along the positive direction of characteristics of operators

$$L^y = \frac{\partial}{\partial t} + \frac{\partial}{\partial \tau_y}, \quad L^x = \frac{\partial}{\partial t} + \frac{\partial}{\partial \tau_x}, \quad L^z = L^x + \frac{\partial}{\partial \tau_z},$$

respectively. The system

$$D^y y = -y\nu^y \quad \text{in } E^y, \tag{1}$$

$$D^x x = -x d^x + X \quad \text{in } E^x, \tag{2}$$

$$D^z z = -z\nu^z \quad \text{in } E^z, \tag{3}$$

$$d^x = \nu^x + \begin{cases} 0, & \tau_x \notin \sigma_x(0), \\ n^{-1} \int_{\sigma_y} yp \, d\tau_y, & \tau_x \in \sigma_x(0), \end{cases} \tag{4a}$$

$$n = \int_{\sigma_y} y \, d\tau_y, \tag{4b}$$

$$X = \begin{cases} 0, & \tau_x \notin \sigma_x(T), \\ \displaystyle\int_{\sigma_y} z(\cdot, T) \, d\tau_y, & \tau_x \in \sigma_x(T), \end{cases} \tag{5}$$

$$N = \int_0^\infty x \, d\tau_x + \int_0^\infty y \, d\tau_y + \int_E z \, d\tau_y d\tau_x d\tau_z, \tag{6}$$

subject to conditions

$$y(\cdot, 0) = \int_\sigma b^y z(\cdot, T) \, d\tau_y d\tau_x, \tag{7}$$

$$x(\cdot, 0) = \int_\sigma b^x z(\cdot, T) \, d\tau_y d\tau_x, \tag{8}$$

$$z(\cdot\,,0) = n^{-1}xyp, \tag{9}$$

$$[x(\cdot\,,\tau_i)] = 0, \quad i = \overline{1,4}, \tag{10}$$

$$y(0,\cdot) = y^0, \quad x(0,\cdot) = x^0, \quad z(0,\cdot) = z^0 \tag{11}$$

governs the population evolution. Here point argument represents obvious arguments of the functions. In general case of limited populations the birth rate of females b^x and males b^y descendants depend on $t,\ \tau_y,\ \tau_x,\ N(t-T)$. Hence for $t \in [-T, 0]$ the function N must be given. Under respective restrictions, as will be seen later, the dependence $b^x,\ b^y$ on N will not influence on unique solvability of the problem $(1)-(11)$. Thus it is assumed, that both vital rates b^x and b^y are given functions of arguments $t,\ \tau_y,\ \tau_x$. Moreover, it is assumed, that functions $x^0(\tau_x),\ y^0(\tau_y),\ z^0(\tau_y,\tau_x,\tau_z)$ satisfy reconcilable conditions, i. e., $(7)-(10)$ conditions for $t=0$. Demographic $\nu^y,\ \nu^x,\ \nu^z,\ p,\ b^x,\ b^y$ and initial $y^0,\ x^0,\ z^0$ functions are non-negative. As it follows from the biological meaning $y,\ x,\ z$ must be also non-negative functions.

2. Unique solvability. We shall study the existence and the uniqueness of non-negative solution of the equations $(1)-(11)$. Denoting

$$\begin{aligned} &\overline{x}(t) = x(t,0),\\ &\overline{y}(t) = y(t,0),\\ &\overline{z}(t,\tau_y,\tau_x) = z(t,\tau_y,\tau_x,0),\\ &d^y = \nu^y, \quad d^z = \nu^z, \end{aligned} \tag{12a-e}$$

$$F_1(\gamma) = \gamma(r_0^\gamma)\exp\left\{-\int_0^t d^\gamma(r_\eta^\gamma,\, N)\,d\eta\right\} + \int_0^t X(r_\alpha^\gamma)\,\exp\left\{-\int_\alpha^t d^\gamma(r_\eta^\gamma,\, N)\,d\eta\right\}\,d\alpha, \tag{13}$$

$$X(r_\alpha^\gamma) = 0, \quad \gamma = y,\ z,$$

$$F_2(\gamma,\,\mu) = \gamma(h_\mu^\gamma)\exp\left\{-\int_\mu^{\tau_\gamma} d^\gamma(h_\eta^\gamma,\, N)\,d\eta\right\} + \int_\mu^{\tau_\gamma} X(h_\alpha^\gamma)\,\exp\left\{-\int_\alpha^{\tau_\gamma} d^\gamma(h_\eta^\gamma,\, N)\,d\eta\right\}\,d\alpha, \tag{14}$$

$$X(h_\alpha^\gamma) = 0, \quad \gamma = y,\, z;$$

from (1) – (3), (11) we have integral representations of functions $y,\ z,\ x$, i. e.:

$$y = \begin{cases} F_1(y), & y(r_0^y) = y^0(\tau_y - t), \quad 0 \leqslant t \leqslant \tau_y, \\ F_2(y,\, 0), & y(h_0^y) = \overline{y}(t - \tau_y), \quad 0 \leqslant \tau_y < t, \end{cases} \tag{15}$$

$$z = \begin{cases} z_1 = F_1(z), & z(r_0^z) = z^0(\tau_y,\, \tau_x - t,\, \tau_z - t), \\ & 0 \leqslant t \leqslant \tau_z, \\ z_2 = F_2(z,\, 0), & z(h_0^z) = \overline{z}(t - \tau_z,\, \tau_y,\, \tau_x - \tau_z), \\ & 0 \leqslant \tau_z < t, \end{cases} \tag{16}$$

$$x = \begin{cases} F_1(x), & x(r_0^x) = x^0(\tau_x - t), \\ & 0 \leqslant t \leqslant \tau_x - \tau_i, \quad \tau_x \in (\tau_i,\, \tau_{i+1}], \\ F_2(x,\, \tau_i), & t > \tau_x - \tau_i, \quad \tau_x \in (\tau_i,\, \tau_{i+1}]; \\ & x(h_0^x) = \overline{x}(t - \tau_x), \quad t > \tau_x \in [0,\, \tau_1]; \end{cases} \tag{17}$$

here $i = \overline{0,4}$, $\tau_0 = 0$, $\tau_5 = \infty$ and $r_\eta^s = (\eta,\, \eta + \tau_s - t)$, $h_\eta^s = (\eta + t - \tau_s, \eta)$, $s = x,\, y$, $r_\eta^z = (\eta, \tau_y, \eta + \tau_x - t, \eta + \tau_z - t)$, $h_\eta^z = (\eta + t - \tau_z, \tau_y, \eta + \tau_x - \tau_z, \eta)$ are sets of arguments written in brackets. In (13), (14) argument of N coincides with the first argument of r_η^γ, h_η^γ, respectively.

Using (15) – (17), (12) – (14), (7) – (9) we obtain

$$N = n_y + n_x + n_z, \tag{18}$$

where

$$n_y = \int_0^t F_2(y,\, 0)\, d\tau_y + \int_t^\infty F_1(y)\, d\tau_y, \tag{19}$$

$$n_x = \sum_{i=0}^{4} \left\{ \int_{\tau_i}^{\alpha_i(t)} F_2(x,\, \tau_i)\, d\tau_x + \int_{\alpha_i(t)}^{\tau_{i+1}} F_1(x)\, d\tau_x \right\}, \tag{20}$$

$$n_z = \int_0^{\beta(t)} d\tau_z \int_{\sigma_x(\tau_z) \times \sigma_y} F_2(z,\, 0)\, d\tau_x\, d\tau_y + \int_{\beta(t)}^{T} d\tau_z \int_{\sigma_x(\tau_z) \times \sigma_y} F_1(z)\, d\tau_x\, d\tau_y, \tag{21}$$

where $\alpha_i(t) = \min(t+\tau_i,\ \tau_{i+1})$, $\beta(t) = \min(t,\ T)$. Using step by step method we shall prove, that (18) is integral equation for N.

Let $t \in (0, T]$. From (16a) we obtain function $z = z_1 = z(N)$, which together with (5), (7), (8), (12a,b) determines $X(N)$, $\overline{x}(N)$, $\overline{y}(N)$. Taking into account these functions from (15), (4), (17) we get $y(N)$, $n(N)$, $d^x(N)$, $x(N)$. Substituting $y(N)$, $x(N)$ into (9), (12c) and using (16b) we obtain $z = z_2 = z(N)$ for $t \leqslant \tau_z + T$. Finally, knowing $x(N)$, $y(N)$, $z(N)$, from (19)–(21) we obtain $n_y(N)$, $n_x(N)$, $n_z(N)$, substituting which into (18) we get an integral equation $N = V_1(N)$. Here $z(N)$, $\overline{x}(N)$, $\overline{y}(N)$, $d^x(N)$, $X(N)$, $x(N)$, $y(N)$, $n(N)$, $n_y(N)$, $n_x(N)$, $n_z(N)$, $V_1(N)$ are right-hand sides of equations (16), (8), (7), (4a), (5), (17), (15), (4b), (19), (20), (21), (18), respectively.

Let $t \in (T, 2T]$. Knowing relation $z = z_2 = z(N)$ for $t \leqslant \tau_z + T$ allows us to repeat analogous argumentation and to obtain an integral equation $N = V_2(N)$ and so on.

As a result of our argumentation we derive an integral equation $N = V(N)$ for $t \in (0, \infty)$.

Let

$$\max_{s=x,y} \int\limits_{\sigma_x(T)} \sup_{t,\tau_y} b^s \, d\tau_x = B^*, \qquad \sup_{\tau_x \in [0,\,\tau_4]} x^0 = a,$$

$$\int\limits_{\sigma_y} \sup_{\tau_x,\tau_z} z^0 \, d\tau_y = aq/B^*, \qquad \sup_{t,\tau_y,\tau_x,\,N} p = p^*,$$

$$\sup_{t,\tau_y,N} \nu^y = \nu^{y*}, \qquad \inf_{t,\tau_x,N} \nu^x = \nu^x_*,$$

$$\inf_{t,\tau_y,N} \nu^y = \nu^y_*, \qquad \inf_{t,\tau_y,\tau_x,\tau_z,N} \nu^z = \nu^z_*,$$

$$\int\limits_0^\infty y^0 \, d\tau_y = n^0_y, \qquad \int\limits_0^\infty x^0 \, d\tau_x = n^0_x,$$

$$\int\limits_{\sigma_y} y^0 \, d\tau_y = n^0, \qquad h_x = \tau_2 - \tau_1 \leqslant T,$$

$$\gamma = \gamma_x + \gamma_y + \gamma_z,$$

$$\gamma_x = ah_x + \max\Big(n^0_x - \int\limits_{\sigma_x(T)} x^0 \, d\tau_x,\ a(1+q)/\nu^x_*\Big),$$

$$\gamma_y = \max\left(n_y^0, aq/\nu_*^y\right), \quad \nu_z = ah_x p^* T \max\left(1, q/p^* B^*\right).$$

If region is not shown, *sup* and *inf* must be taken according to shown arguments from function definition region. Let $C_\gamma = \{N(t) : N \in C([0,\infty)),\ 0 < N \leqslant \gamma\}$.

Theorem 1. *Assume that:* 1) y^0, x^0, z^0, p, ν^x, ν^y, ν^z *are non-negative continuous functions,* b^x *and* b^y *are bounded non-negative and continuos in* t *and piecewise continuous functions in* $\tau = (\tau_y, \tau_x)$, 2) B^*, a, p^*, ν^{y*}, ν_*^y, ν_*^x, ν_*^z, n_y^0, n_x^0 *are positive constants,* 3) $B^* p^* \exp\{-T\nu_*^z\} \leqslant q \leqslant \min(1, \nu_*^x B^*)$. *Then operator* V *acts in space* C_γ *and estimates*

$$0 \leqslant y(N) \leqslant \begin{cases} y^0(\tau_y - t)\exp\{-t\nu_*^y\}, & 0 \leqslant t \leqslant \tau_y < \infty, \\ aq^{k+1}\exp\{-\tau_y \nu_*^y\}, & k\tau_4 < t - \tau_y \leqslant (k+1)\tau_4, \\ & \tau_y \in [0,\infty), \end{cases} \tag{22}$$

$$0 \leqslant x(N) \leqslant \begin{cases} x^0(\tau_x - t)\exp\{-t\nu_*^x\}, & 0 \leqslant t \leqslant \tau_x \in [0, \tau_3], \\ a, & 0 \leqslant t \leqslant \tau_x \in [\tau_3, \tau_4], \\ x^0(\tau_x - t)\exp\{-t\nu_*^x\}, & 0 \leqslant t \leqslant \tau_x - \tau_4, \\ & \tau_x \in [\tau_4, \infty), \\ aq^{k+1}\exp\{-\tau_x \nu_*^x\}, & k\tau_4 < t - \tau_x \leqslant (k+1)\tau_4, \\ & \tau_x \in [0, \tau_3], \\ aq^{k+1}, & k\tau_4 < t - \tau_x \leqslant (k+1)\tau_4, \\ & \tau_x \in [\tau_3, \tau_4], \\ aq^k \exp\{-\nu_*^x(\tau_x - \tau_4)\}, & (k-1)\tau_4 < t - \tau_x \leqslant k\tau_4, \\ & \tau_x \in [\tau_4, \infty), \end{cases} \tag{23}$$

$$k = 0,\ 1, \dots,$$

$$\begin{aligned} &0 \leqslant n_x(N) \leqslant \gamma_x, \quad 0 < n_y(N) \leqslant \gamma_y, \\ &0 \leqslant n_z(N) \leqslant \gamma_z, \quad 0 < V(N) \leqslant \gamma \end{aligned} \tag{24}$$

are true.

Proof. We shall consider the case $T \leqslant \tau_1$; arguments for the opposite case are similar. Let $N \in C_\gamma$. From (19), construction of operator V and assumptions of theorem it is clear, that $0 < n_y^0 \exp\{-t\nu^{y*}\} \leqslant n_y(N) \in C([0,\infty))$, $0 < V(N) \in C([0,\infty))$. We shall prove the validity of estimates (22)–(24) using step by step method.

Let $t \in (0,T]$. By (7), (8), (12a,b), (5) and assumptions of theorem we get estimates

$$(\nu_*^x)^{-1}X(N) \leqslant a, \quad \max\left(\sup_t \overline{x}(N),\, \sup_t \overline{y}(N)\right) \leqslant a. \tag{25}$$

From (15), (17), (25) we derive following inequalities

$$y(N) \leqslant \begin{cases} y^0(\tau_y - t)\exp\{-t\nu_*^y\}, & 0 \leqslant t \leqslant \tau_y < \infty, \\ aq\exp\{-\tau_y\nu_*^y\}, & 0 \leqslant \tau_y < t, \end{cases} \tag{26}$$

$$x(N) \leqslant \begin{cases} x^0(\tau_x - t)\exp\{-t\nu_*^x\}, & 0 \leqslant t \leqslant \tau_x \leqslant \tau_3, \\ aq\exp\{-\tau_x\nu_*^x\}, & 0 \leqslant \tau_x < t, \quad \tau_x \leqslant \tau_3. \end{cases} \tag{27}$$

Taking into account the condition 3) of theorem, estimates (25) – (27) and Gronwal's lemma we get following estimates

$$x(N) \leqslant a, \quad \tau_x \in [\tau_3, \tau_4], \tag{28}$$

$$x(N) \leqslant \begin{cases} x^0(\tau_x - t)\exp\{-t\nu_*^x\}, & 0 \leqslant t \leqslant \tau_x - \tau_4, \\ & \tau_x \in [\tau_4, \infty), \\ a\exp\{-\nu_*^x(\tau_x - \tau_4)\}, & t > \tau_x - \tau_4, \\ & \tau_x \in [\tau_4, \infty). \end{cases} \tag{29}$$

Let $t \in (T, 2T]$. By (27) and condition 3) of theorem from (7), (8), (12a,b), (5) we find

$$\begin{aligned} (\nu_*^x)^{-1}X(N) &\leqslant p^*(\nu_*^x)^{-1}\exp\{-\tau_x\nu_*^z\}\,x(t-T, \tau_x - T) \\ &\leqslant \begin{cases} q, & \tau_x < t, \\ 1, & \tau_x \geqslant t, \end{cases} \end{aligned} \tag{30}$$

$$\max\left(\sup_t \overline{x}(N), \sup_t \overline{y}(N)\right) \leqslant p^* a B^* \exp\{-T\nu_*^z\} \leqslant aq. \tag{31}$$

Thus we obtain the estimates (25), but for $t \in (T, 2T]$. Therefore the estimates (26) – (29) are valid for $t \in (t, 2T]$.

Repeating these arguments yields (30), (31) and (26) – (29) for $2T < t \leqslant \tau_3$. The estimates (26), (27), (29) hold for $\tau_3 < t \leqslant \tau_4$, while (28) must be changed by estimate

$$X(N) \leqslant a\begin{cases} q, & \tau_3 \leqslant \tau_x \leqslant t, \\ 1, & \tau_x > t. \end{cases} \tag{32}$$

For $t \in (\tau_4, \tau_4 + T]$ we get estimates

$$\max\Big(\sup_t \overline{x}(N), \sup_t \overline{y}(N)\Big) \leqslant aq^2, \\ x(N) \leqslant aq, \quad \tau_x \in [\tau_3, \tau_4]. \tag{33}$$

Using (33) and repeating our argumentation, we obtain (22), (23). From here and by (18) – (21) one can easily deduce estimate (24), which proves the theorem. Note that $V(N) \leqslant \gamma$ if though $N \in (0, \infty)$. Let $||N|| = \sup_t |N|$, $\nu_* = \min(\nu_*^y, \nu_*^x, \nu_*^z)$.

Theorem 2. *Assume that:* 1) *assumptions of Theorem* 1 *hold,* 2) *functions* ν^x, ν^y, ν^z, p *are Lipshitz continues in* N *with constants* $\varkappa_x$, $\varkappa_y$, $\varkappa_z$, $\varkappa_p$, *respectively,* 3) $f(t) = n(N)^{-1} \int\limits_{\tau_1}^{\tau_2} x(N)\, d\tau \leqslant f_0 = \text{const}$ *for* $N \in C_\gamma$. *Then* $||V_i(N_2) - V_i(N_1)|| \leqslant \varepsilon ||N_2 - N_1||$, *where* $\varepsilon(\nu_*) \to 0$ *monotonically when* $\nu_* \to \infty$.

Proof. Let $N_s \in C_\gamma$, $s = 1, 2$. Assume, that: 1) $\varepsilon(\xi)$ is bounded positive monotonically converging to zero function when $\xi \to \infty$; 2) C is a positive constant, independent of ν_*^x, ν_*^y, ν_*^z; 3) $F(N_s) = F_s$, $s = 1, 2$, $F_2 - F_1 = \Delta F$; 4) $P_{\xi s}^{u\gamma} = \exp\{-\int\limits_\xi^u \nu_s^\gamma \, d\eta\}$, $\nu_s^\gamma = \nu^\gamma(l_\eta^\gamma, N_s)$, $l_\eta^\gamma = r_\eta^\gamma$, h_η^γ, where argument of function N_s is the same as the first that of the collection l_η^γ.

Note that function $\overline{z}(t - T, \tau_y, \tau_x - T) = \overline{z}^T$ for $t \in ((i-1)T, iT]$, $i = 2, 3, \ldots$ is expressed by values of functions x, y, N for $t \in ((i-2)T, (i-1)T]$, which must be found by solving equation $N = V_{i-1}(N)$. Therefore for consideration of solvability of the equation $N = V_i N$ function $\overline{z}^T$ holds to be known.

We shall get estimate of norm $||V_i(N_2) - V_i(N_1)||$ for $t \in ((i-1)T, iT]$. Throughout the rest of this paper we shall use the estimate

$$\begin{aligned} |\Delta P_\xi^{u\gamma}| = |P_{\xi 2}^{u\gamma} - P_{\xi 1}^{u\gamma}| \leqslant & \exp\{-(u - \xi)\nu_*^\gamma\}(u - \xi)\kappa_\gamma ||\Delta N|| \\ \leqslant & \varepsilon(\nu_*^\gamma) ||\Delta N||, \\ \varepsilon(\nu_*^\gamma) = & \kappa_\gamma / e\nu_*^\gamma, \quad \xi \leqslant u, \end{aligned}$$

without refering to it.

From (7), (8), (5), (16) we deduce folowing estimates

$$|\Delta\overline{y}| \leqslant \left\{ \begin{array}{ll} \int\limits_{\sigma} b^y z^0 |\Delta P_0^{tz}|\, d\tau_y d\tau_x, & 0 \leqslant t \leqslant T \\ \int\limits_{\sigma} b^y \overline{z}^T |\Delta P_0^{Tz}| d\tau_y d\tau_x, & t > T \end{array} \right\} \leqslant aq\varkappa_z T||\Delta N||, \quad (34)$$

$$|\Delta\overline{x}| \leqslant aq\varkappa_z T||\Delta N||, \quad (35)$$

$$|\Delta X| \leqslant C||\Delta N||, \quad (36)$$

as from (15), (22), (34) we get

$$|\Delta n_y| \leqslant \int\limits_0^\infty y^0\, |\Delta P_0^{ty}|\, d\tau_y + \int\limits_0^t \{\overline{y}_1\, |\Delta P_0^{\tau_y y}| + P_{02}^{\tau_y y}\, |\Delta\overline{y}|\}\, d\tau_y$$
$$\leqslant \varepsilon(\nu_*)||\Delta N||. \quad (37)$$

We shall evaluate the sum $|\Delta n_x| = \left| \sum\limits_{i=0}^{4} \int\limits_{\tau_i}^{\tau_{i+1}} \Delta x d\tau_x \right|$. For $\tau_x \in (0, \tau_1]$ from (17), (23), (35) we deduce inequality

$$|\Delta x| \leqslant \left\{ \begin{array}{ll} x^0(\tau_x - t)|\Delta P_0^{tx}|, & 0 \leqslant t \leqslant \tau_x, \\ \overline{x}_2 |\Delta P_0^{\tau_x x}| + P_{01}^{\tau_x x} |\Delta\overline{x}|, & t > \tau_x, \end{array} \right\}$$
$$\leqslant Q(t, \tau_x)||\Delta N||, \quad (38)$$

$$Q(t, \tau_x) = \left\{ \begin{array}{ll} x^0(\tau_x - t)\varkappa_x / e\nu_*^x, & 0 \leqslant t \leqslant \tau_x, \\ aq\exp\{-\tau_x \nu_*^x\}(\varkappa_x \tau_x + \varkappa_z T), & t > \tau_x, \end{array} \right\} \leqslant \varepsilon(\nu_*).$$

Thus

$$\int\limits_0^{\tau_1} |\Delta x| d\tau_x \leqslant \varepsilon(\nu_*)||\Delta N||. \quad (39)$$

Consider $\int\limits_{\tau_1}^{\tau_2} |\Delta x| d\tau_x$. Using (2), (10) for Δx we obtain the estimate

$$|\Delta x| \leqslant \left\{ \begin{array}{ll} \int\limits_0^t S^x(t, \xi)\, [(x_1 |\Delta d^x|) | r_\xi^x]\, d\xi, & 0 \leqslant t \leqslant \tau_x - \tau_1, \\ S^x(\tau_x, \tau_1)\, [|\Delta x| | h_{\tau_1}^x] & \\ \quad + \int\limits_{\tau_1}^{\tau_x} S^x(\tau_x, \xi)\, [(x_1 |\Delta d^x|) | h_\xi^x]\, d\xi, & t > \tau_x - \tau_1. \end{array} \right. \quad (40)$$

Here and in the rest $S^x(t,\xi) = \exp\{-\nu_*^x(t-\xi)\}$, $[g|r_\xi^x] = g(r_\xi^x)$, $[g|h_\xi^x] = g(h_\xi^x)$. By (4), (37) and assumption 2) of theorem we get

$$|\Delta d^x| \leqslant \left(C + n_1^{-1}\varepsilon(\nu_*)\right) ||\Delta N||, \tag{41}$$

which together with (40), (23) gives the estimate

$$|\Delta x| \leqslant ||\Delta N||\varepsilon(\nu_*) \begin{cases} 1 + \varphi(t,\tau_x), & 0 \leqslant t \leqslant \tau_x - \tau_1, \\ 1 + \psi(t,\tau_x) + F(t,\tau_x), & t > \tau_x - \tau_1, \end{cases} \tag{42}$$

where

$$\varphi(t,\tau_x) = \int_0^t S^x(t,\xi)\left[(x_1(n_1)^{-1})\,|r_\xi^x\right] d\xi,$$

$$\psi(t,\tau_x) = \int_{\tau_1}^{\tau_x} S^x(\tau_x,\xi)\left[(x_1(n_1)^{-1})\,|h_\xi^x\right] d\xi,$$

$$\varepsilon F(t,\tau_x) = S^x(\tau_x,\tau_1)Q(h_{\tau_1}^x) \leqslant S^x(\tau_x,\tau_1)\varepsilon(\nu_*).$$

Using Assumption 3) of Theorem 2 and estimate (42) enables us to deduce, that

$$\begin{aligned} &\int_{\tau_1}^{\tau_2} |\Delta x| d\tau_x \\ &\leqslant ||\Delta N||\varepsilon(\nu_*)\left\{1 + \int_{\tau_1}^{u} (F(t,\tau_x) + \psi(t,\tau_x))\, d\tau_x + \int_u^{\tau_2} \varphi(t,\tau_x)\, d\tau_x\right\} \\ &\leqslant ||\Delta N||\varepsilon\left\{1 + 2\int_0^t S^x(t,\xi)f(\xi)\, d\xi + \int_{\tau_1}^u F\, d\tau_x\right\} \\ &\leqslant \varepsilon(\nu_*)||\Delta N||, \end{aligned} \tag{43}$$

where $u = \min(t+\tau_1,\tau_2)$.

Consider $\int_{\tau_2}^{\tau_3} |\Delta x|\, d\tau_x$. Using (17) and (23) one can write the inequality

$$|\Delta x| \leqslant \begin{cases} x^0(\tau_x - t)|\Delta P_0^{tx}| \\ \leqslant \varepsilon(\nu_*)x^0(\tau_x - t)||\Delta N||, & 0 \leqslant t \leqslant \tau_x - \tau_2, \\ S^x(\tau_x,\tau_2)\left[|\Delta x||h_{\tau_2}^x\right] + a|\Delta P_{\tau_2}^{\tau_x x}|, & t > \tau_x - \tau_2, \end{cases} \tag{44}$$

which shows that

$$\int_{\tau_2}^{\tau_3} |\Delta x|\, d\tau_x \leqslant \varepsilon(\nu_*)\|\Delta N\| + \int_m^t S^x(t,\varrho)|\Delta x|\big|_{(\varrho,\tau_2)}\, d\varrho,$$
$$m = \tau_2 + t - \min(t+\tau_2, \tau_3).$$

This relation together with (42) enables us to deduce the estimate

$$\int_{\tau_2}^{\tau_3} |\Delta x|\, d\tau_x \leqslant \varepsilon(\nu_*)(1+\widetilde{R}_1)\|\Delta N\|,$$

where

$$\widetilde{R}_1 = \int_m^t S^x(t,\varrho) \left\{ \begin{matrix} \varphi(\varrho,\tau_2), & 0 \leqslant \varrho \leqslant h_x, \\ \psi(\varrho,\tau_2) + F(\varrho,\tau_2), & \varrho > h_x, \end{matrix} \right\} d\varrho \leqslant \varepsilon(\nu_*) + R_1,$$
$$R_1 = \int_m^t S^x(t,\varrho) \left\{ \begin{matrix} \varphi(\varrho,\tau_2), & 0 \leqslant \varrho \leqslant h_x, \\ \psi(\varrho,\tau_2), & \varrho > h_x, \end{matrix} \right\} d\varrho.$$

For an estimate R_1 we consider two cases $h_1 = T - h_x \leqslant h_x$ and $h_1 > h_x$.

If $h_1 \leqslant h_x$ then $R_1 = R_{11},\ R_{12},\ R_{13},\ R_{14}$ for $t \in [0,h_1],\ (h_1,h_x],\ (h_x,T],\ (T,\infty)$, respectively, where

$$R_{11} = \int_0^t \widetilde{\varphi}\, d\varrho, \qquad R_{12} = \int_{t-h_1}^t \widetilde{\varphi} d\varrho,$$
$$R_{13} = \int_{t-h_1}^{h_x} \widetilde{\varphi} d\varrho + \int_{h_x}^t \widetilde{\psi}\, d\varrho, \quad R_{14} = \int_{t-h_1}^t \widetilde{\psi}\, d\varrho,$$

here and throughout the rest of this paper $\widetilde{\varphi} = \varphi(\varrho,\tau_2)S^x(t,\varrho)$, $\widetilde{\psi} = \psi(\varrho,\tau_2)$ $S^x(t,\varrho)$. As $f \leqslant f_0$, then $\max\{R_{11}, R_{12}, 1/2R_{13}, R_{14}\} \leqslant \int_0^t S^x(t,\varrho)f(\varrho)d\varrho \leqslant$ $(\nu_*)^{-1}$, and $R_1 \leqslant \varepsilon(\nu_*)$.

If $h_1 > h_x$, then $R_1 = R_{11},\ R_{12},\ R_{13},\ R_{14}$ for $t \in [0, h_x],\ (h_x, h_1],\ (h_1, T],\ (T, \infty)$, respectively, where

$$R_{11} = \int_0^t \widetilde{\varphi}\, d\varrho, \qquad R_{12} = \int_0^{h_x} \widetilde{\varphi}\, d\varrho + \int_{h_x}^t \widetilde{\psi}\, d\varrho,$$

$$R_{13} = \int_{t-h_1}^{h_x} \widetilde{\varphi}\, d\varrho + \int_{h_x}^t \widetilde{\psi}\, d\varrho, \quad R_{14} = \int_{t-h_1}^t \widetilde{\psi}\, d\varrho.$$

As $f \leqslant f_0$, then $\max(R_{11},\ R_{14},\ 1/2R_{12},\ 1/2R_{13}) \leqslant \int_0^t S^x(t, \varrho) f(\varrho) d\varrho \leqslant (\nu_*)^{-1}$, and $R_1 \leqslant \varepsilon(\nu_*)$.

Thus

$$\int_{\tau_2}^{\tau_3} |\Delta x| d\tau_x \leqslant \varepsilon(\nu_*) ||\Delta N||. \tag{45}$$

Consider $\int_{\tau_3}^{\tau_4} |\Delta x| d\tau_x$. By (17), (23), (36) for Δx one can deduce the estimate

$$|\Delta x| \leqslant a \left|\Delta P_0^{tx}\right| + \int_0^t \left\{X_1 \left|\Delta P_\xi^{tx}\right| + P_{\xi 2}^{tx} |\Delta X|\right\} d\xi \leqslant \varepsilon(\nu_*) ||\Delta N||$$

for $0 \leqslant t \leqslant \tau_x - \tau_3$ and

$$\begin{aligned} |\Delta x| \leqslant & a \left|\Delta P_{\tau_3}^{\tau_x x}\right| + S^x(\tau_x, \tau_3) \left[|\Delta x| |h_{\tau_3}^x\right] \\ & + \int_{\tau_3}^{\tau_x} \left\{S^x(t, \xi) |\Delta X| + X_1 \left|\Delta P_\xi^{\tau_x x}\right|\right\} d\xi \\ \leqslant & S^x(\tau_x, \tau_3) \left[|\Delta x| |h_{\tau_3}^x\right] + \varepsilon(\nu_*) ||\Delta N|| \end{aligned}$$

for $t > \tau_x - \tau_3$.

Thus

$$|\Delta x| \leqslant \varepsilon(\nu_*) ||\Delta N|| + \begin{cases} 0, & 0 \leqslant t \leqslant \tau_x - \tau_3, \\ S^x(\tau_x, \tau_3) \left[|\Delta x| |h_{\tau_3}^x\right], & t > \tau_x - \tau_3, \end{cases} \tag{46}$$

$$\int_{\tau_3}^{\tau_4} |\Delta x|\, d\tau_x \leqslant \varepsilon(\nu_*)\|\Delta N\| + \int_{\tau_3}^{u} S^x(\tau_x, \tau_3)\left[|\Delta x|\big|h^x_{\tau_3}\right] d\tau_x$$
$$\leqslant \varepsilon(\nu_*)\|\Delta N\| + \widetilde{R}_2,$$
$$\widetilde{R}_2 = \int_m^t S^x(t,\varrho)|\Delta x|\,\big|_{(\varrho,\tau_3)}\, d\varrho,$$
$$m = \tau_3 + t - u, \quad u = \min(t+\tau_3, \tau_4).$$

Taking into account (44), (42) we get

$$\widetilde{R}_2 \leqslant \|\Delta N\|\varepsilon(\nu_*) + \int_{m-h_1}^{t-h_1} S^x(t,\eta)\left\{\begin{array}{ll} 0, & -h_1 \leqslant \eta \leqslant 0, \\ |\Delta x|\Big|_{(\eta,\tau_2)}, & \eta > 0, \end{array}\right\} d\eta$$
$$\leqslant \varepsilon(1+R_2)\|\Delta N\|,$$
$$R_2 = \int_{m-h_1}^{t-h_1} S^x(t,\eta)\left\{\begin{array}{ll} 0, & -h_1 \leqslant \eta \leqslant 0, \\ \varphi(\eta,\tau_2), & 0 \leqslant \eta \leqslant h_x, \\ \psi(\eta,\tau_2), & \eta > h_x, \end{array}\right\} d\eta.$$

But $R_2 = 0,\ R_{21},\ R_{22},\ R_{23}$ for $t \in [0,h_1],\ (h_1,T],\ (T,T+h_x],\ (T+h_x,\infty)$, respectively, where

$$R_{21} = \int_0^{t-h_1} \widetilde{\varphi} d\varrho, \quad R_{22} = \int_{t-T}^{h_x} \widetilde{\varphi} d\varrho + \int_{h_x}^{t-h_1} \widetilde{\psi} d\varrho, \quad R_{23} = \int_{t-T}^{t-h_1} \widetilde{\psi} d\varrho.$$

As

$$R_{2k} \leqslant \int_0^{t-h_1} S^x(t,\xi)\, f(\xi)\, d\xi, \quad k = 1,3,$$
$$R_{22} \leqslant \int_0^{h_x} S^x(t,\xi)\, f(\xi) d\xi + \int_0^{t-h_1} S^x(t,\xi)\, f(\xi) d\xi,$$

$f \leqslant f_0$, then $R_2 \leqslant \varepsilon(\nu_*)$. Hence

$$\int_{\tau_3}^{\tau_4} |\Delta x| d\tau_x \leqslant \varepsilon(\nu_*)\|\Delta N\|. \tag{47}$$

Consider $\int\limits_{\tau_4}^{\infty} |\Delta x| d\tau_x$. Using (17), (46), (23) we get

$$|\Delta x| \leqslant \begin{cases} x^0(\tau_x - t)|\Delta P_0^{tx}|, & 0 \leqslant t \leqslant \tau_x - \tau_4, \\ a\left|\Delta P_{\tau_4}^{\tau_x x}\right| \\ \quad + S^x(\tau_x, \tau_4)\left[|\Delta x|\left|h_{\tau_4}^x\right]\right., & t > \tau_x - \tau_4, \end{cases}$$

$$\int\limits_{\tau_4}^{\infty} |\Delta x| d\tau_x \leqslant \varepsilon(\nu_*)\|\Delta N\| + \widetilde{R}_3,$$

$$\widetilde{R}_3 = \int\limits_{-h_x}^{t-h_x} S^x(t,\eta) \left\{ \begin{matrix} 0, & -h_x \leqslant \eta \leqslant 0, \\ |\Delta x|\big|_{(\eta,\tau_3)}, & \eta > 0, \end{matrix} \right\} d\eta.$$

Taking into account (44), (42) we deduce

$$\widetilde{R}_3 \leqslant \begin{cases} 0, \quad 0 \leqslant t \leqslant h_x, \\ \varepsilon(\nu_*)\|\Delta N\| \\ \quad + \int\limits_{-h_1}^{t-T} S^x(t,\varrho) \left\{ \begin{matrix} 0, & -h_1 \leqslant \varrho \leqslant 0, \\ |\Delta x|\big|_{(\varrho,\tau_{2x})}, & \varrho > 0, \end{matrix} \right\} d\varrho, & t > h_x, \end{cases}$$

$$\widetilde{R}_3 \leqslant \varepsilon(\nu_*)\|\Delta N\| \left(1 + R_3\right),$$

$$R_3 = \begin{cases} 0, \quad 0 \leqslant t \leqslant T, \\ \int\limits_0^{t-T} S^x(t,\varrho) \left\{ \begin{matrix} \varphi(\varrho,\tau_2), & 0 \leqslant \varrho \leqslant h_x, \\ \psi(\varrho,\tau_2), & \varrho > h_x, \end{matrix} \right\} d\varrho, & t > T. \end{cases}$$

But $R_3 = 0,\ R_{31},\ R_{32}$ for $t \in [0,T],\ (T, T+h_x],\ (T+h_x, \infty)$, respectively, where

$$R_{31} = \int\limits_0^{t-T} \widetilde{\varphi}\, d\varrho, \quad R_{32} = \int\limits_0^{h_x} \widetilde{\varphi} d\varrho + \int\limits_{h_x}^{t-T} \widetilde{\psi}\, d\varrho.$$

Since

$$R_{31} \leqslant \int\limits_0^{t-T} S^x(t,\xi) f(\xi)\, d\xi,$$

$$R_{32} \leqslant \int\limits_0^{h_x} S^x(t,\xi) f(\xi) d\xi + \int\limits_0^{t-T} S^x(t,\xi) f(\xi)\, d\xi, \quad f \leqslant f_0,$$

the estimate $R_3 \leqslant \varepsilon(\nu_*)$ is obtained. Thus

$$\int_{\tau_4}^{\infty} |\Delta x| d\tau_x \leqslant \varepsilon(\nu_*)||\Delta N||. \tag{48}$$

Accounting (39), (43), (45), (47), (48) one can deduce following estimate

$$|\Delta n_x| \leqslant \varepsilon(\nu_*)||\Delta N||. \tag{49}$$

Consider $|\Delta n_z|$. By (21) we get $|\Delta n_z| \leqslant I_1 + I_2$, where

$$I_1 = \int_{\beta}^{T} d\tau_z \int_{\sigma_x(\tau_z)\times\sigma_y} |\Delta F_1|\, d\tau_x\, d\tau_y,$$

$$I_2 = \int_{0}^{\beta} d\tau_z \int_{\sigma_x(\tau_z)\times\sigma_y} |\Delta F_2|\, d\tau_x d\tau_y.$$

But $I_1 \leqslant \varepsilon(\nu_*)||\Delta N||$.

Consider I_2. Denoting $u = t - \min(t, T)$ and using obtained above estimates, we get

$$I_2 = I_2^{12} \leqslant \int_u^t d\xi \int_{\sigma_y} d\tau_y \int_{\sigma_x(0)} \Big\{ |x_1 - x_2| y_1 p_1 n_1^{-1} P_{\xi 1}^{tz}$$
$$+ x_2 p_1 n_1^{-1} P_{\xi 1}^{tz} |y_1 - y_2| + x_2 y_2 n_1^{-1} P_{\xi 1}^{tz} |p_1 - p_2|$$
$$+ x_2 y_2 p_2 n_1^{-1} \left|P_{\xi 1}^{tz} - P_{\xi 2}^{tz}\right| + x_2 y_2 p_2 n_1^{-1} n_2^{-1} P_{\xi 2}^{tz} |n_1 - n_2| \Big\} d\tau_x$$
$$\leqslant \int_u^t \Big\{ p_* \int_{\sigma_x(0)} |x_1 - x_2| d\tau_x + p_* \int_{\sigma_y} |y_1 - y_2| d\tau_y n_1^{-1} \int_{\sigma_x(0)} x_2 d\tau_x$$
$$+ \varkappa_p ||N_1 - N_2|| a h_x n_1^{-1} \int_{\sigma_y} y_2 d\tau_y$$
$$+ \varkappa_z p_* ||N_1 - N_2|| (t - \xi) a h_x n_1^{-1} \int_{\sigma_y} y_2 d\tau_y +$$

$$+ p_* n_1^{-1} \int\limits_{\sigma_x(0)} x_2 d\tau_x \varepsilon \|N_1 - N_2\| \Big\} S^x(t,\xi) d\xi$$

$$\leqslant \int\limits_u^t \Big\{ \left(1 + n_2 n_1^{-1}\right)\varepsilon + \varkappa_p a h_x n_2 n_1^{-1}$$

$$+ \varkappa_z p_* a h_x (t-\xi) n_2 n_1^{-1} + \varepsilon n_2 n_1^{-1} \Big\} S^x(t,\xi) d\xi \|N_1 - N_2\|$$

$$\leqslant \varepsilon(\nu_*)\big(1 + \sup_t \left(n_2 n_1^{-1}\right)\big)\|N_1 - N_2\|.$$

By equation $I_2^{12} = I_2^{21}$ we get another estimate

$$I_2^{12} \leqslant \varepsilon(\nu_*)\left(1 + \sup_t \left(n_1 n_2^{-1}\right)\right)\|N_1 - N_2\|.$$

These estimates show, that $I_2 \leqslant \varepsilon(\nu_*)\|\Delta N\|$. Hence

$$|\Delta n_z| \leqslant \varepsilon(\nu_*)\|\Delta N\|. \tag{50}$$

Using (18), (37), (49), (50) one can deduce the estimate

$$|V_i(N_2) - V_i(N_1)| \leqslant \varepsilon(\nu_*)\|\Delta N\|,$$

which completes the proof of our theorem.

Let $\widetilde{\nu}_*$ be solution of equation $\varepsilon(\nu_*) = 1$.

Theorem 3. *Assume that:* 1) *assumptions of Theorem* 2 *are satisfied,* 2) $\nu_* > \widetilde{\nu}_*$. *Then equation* $N = V(N)$ *has unique solution in* C_γ.

Proof. If $\varepsilon < 1$, then operator V_i is contractive. Since ε is independent of i, successive consideration of equations $N = V_i(N)$, $i = 1, 2, \dots$ proves the Theorem 3.

COROLLARY. If assumptions of Theorem 3 are satisfied, then problem (1) – (11) has unique non-negative cotinuous solution, such that estimates (22), (23) hold and $D^y y$, $D^z z$ are continuous in E^y, E^z, respectively, while $D^x x$ is piecewise continuous in E^x.

NOTE. Assuption 3) of Theorem 2 holds, f. e., if $\nu^x(t,\tau,N) \geqslant \nu^y(t,\tau,N)$, $b^x(t,\tau_y,\tau_x) \leqslant b^y(t,\tau_y,\tau_x)$ $\forall$ (t,τ,N), (t,τ_y,τ_x) and $x^0(\tau) \leqslant y^0(\tau)$ for $\tau \in [0,\tau_2]$.

Using the same method in case $h_x > T$ it can be shown that analogue of Theorem 1 and Theorems 2, 3 are true. However it is not clear when the basic condition 3) of Theorem 2 is satisfied.

REFERENCES

Skakauskas, V. (1994). An evolution model of an autosomal polylocal polyallelic diploid population taking into account crossing-over and gestation period. *Lithuanian Mathematical Journal,* **3**, 288–300.

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V. Skakauskas has graduated from the Leningrad University (Faculty of Mathematics and Mechanics) in 1965. He received Ph.D. degree from the Leningrad University in 1971. He is a Associated Professor and head of the Department of Differential Equations and Numerical Analysis at Vilnius University. His research interests include modelling in fluids and gas mechanics, physics, ecology and genetics.

NEMIGRUOJANČIOS LIMITUOTOS PANMIKSINĖS POPULIACIJOS EVOLIUCIJA

Vladas SKAKAUSKAS

Nagrinėjama nemigruojančios limituotos populiacijos evoliucija, kai demografinės funkcijos priklauso nuo populiacijos dydžio. Populiaciją sudaro dvi lytys. Be to, priimamas dėmesin individų amžius. Patelės gali būti pastojusios arba ne. Nepaisoma patelės vaisiaus žuvimo bei patelių reabilitacijos intervalo po gimdymo. Reproduktyvieji individų laikotarpiai laikomi baigtiniais. Populiacijos evoliucijos modelį sudaro integrodiferencialinių lygčių sistema trūkiais koeficientais su integralinėmis sąlygomis. Kai demografinės (mirtingumo, gimstamumo, apsivaisinimo) funkcijos tenkina specialias sąlygas, įrodytas uždavinio vienintelio klasikinio sprendinio egzistavimas bei gauti sprendinio įverčiai.