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THE EVOLUTION OF MIGRATING TWO-SEXES POPULATIONS

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Abstract. The equations describing the evolution of migrating populations composed of two-sexes are derived taking into account the size, age structure, panmiction mating of sexes, pregnancy of females, possible abortions as well as the females organism restoration periods after abortions and delivery. In partial case, which neglects females organism restoration period, the unique solvability of the model is proved and the condition for population to vanish is obtained.

Key words: panmiction mating, population evolution, gestation and restoration periods, migration.

1. Introduction. Using integral operator Svirezhev (1987) proposed the deterministic model of migrating in unbounded area R_2 population without sexes and age structure. He also derived and widely used diffusion approximation of this model. Diffusion approximation of migration in biology as well as its analogue in chemist kinetics are widely known (see Svirezhev, 1987; Murray, 1983; Kolmogorov *et al.*, 1937; Fisher, 1937). Gurtin (1973) proposed another diffusion approximation of migrating population taking into account age of individuals. The model developed by Skakauskas (1994) includes: age and sex of individuals; pregnancy of females; possible destruction of the foetus (abortions); organism restoration periods after abortions and delivery; panmiction mating of sexes. In this paper we propose the model which in addition to Skakauskas (1994) includes the migration of individuals. In the case, where abortions and females restoration intervals are neglected, we prove the unique solvability of our model.

2. Construction of the model. Suppose that:
$t, \tau_x, \tau_y \in I = (0,\infty)$, $\overline{I} = [0,\infty)$, $s = (s_1, s_2) \in R_2 = (-\infty,\infty) \times$

$(-\infty, \infty)$, $ds = ds_1 ds_2$, $\xi = (\xi_1, \xi_2) \in R_2$, $d\xi = d\xi_1 d\xi_2$, $d_s R_2 = [s_1, s_1 + ds_1] \times [s_2, s_2 + ds_2]$, $d_\xi R_2 = [\xi_1, \xi_1 + d\xi_1] \times [\xi_2, \xi_2 + d\xi_2]$, where t – time, τ_x and τ_y are ages of males and females, respectively, R_2 is populated area.

$y(t, \tau_y, s) d\tau_y ds$ is the expectation at the moment t of the number of females of age $\tau \in [\tau_y, \tau_y + d\tau_y]$ staying in the area $d_s R_2$;

$x(t, \tau_x, s) d\tau_x ds$ is the expectation at the moment t of the number of single females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$ staying in the area $d_s R_2$;

$z(t, \tau_y, \tau_x, \tau_z, s) d\tau_y d\tau_x d\tau_z ds$ is the expectation at the moment t of the number of fecundated females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$ staying in the area $d_s R_2$ whose embryou's age is $\tau \in [\tau_z, \tau_z + d\tau_z]$ which were fecundated by males of age $\tau \in [\tau_y, \tau_y + d\tau_y]$;

$u(t, \tau_y, \tau_x, \tau_u, s) d\tau_y d\tau_x d\tau_u ds$ is the expectation at the moment t of the number of females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$ staying in the area $d_s R_2$ for which time $\tau \in [\tau_u, \tau_u + d\tau_u]$ after abortion has passed and which were fecundated by males of age $\tau \in [\tau_y, \tau_y + d\tau_y]$;

$v(t, \tau_y, \tau_x, \tau_v, s) d\tau_y d\tau_x d\tau_v ds$ is the expectation at the moment t of the number of females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$ staying in the area $d_s R_2$ for which time $\tau \in [\tau_v, \tau_v + d\tau_v]$ after delivery has passed and which were fecundated by males of age $\tau \in [\tau_y, \tau_y + d\tau_y]$;

$Q(t, \tau_y, \tau_x, s) d\tau_y d\tau_x ds$ is the expectation at the moment t of couples staying in the area $d_s R_2$ which are formed of females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$ and males of age $\tau \in [\tau_y, \tau_y + d\tau_y]$;

$P(t, \tau_y, \tau_x, s) dt$ is the probability to become pregnant in the time interval $[t, t + dt]$ for a female from the male-female pair with characteristics (τ_y, s), (τ_x, s);

$\chi(t, \tau_y, \tau_x, \tau_z, s) dt$ is the probability that the abortion took place in the time interval $[t, t + dt]$ for a female with characteristics $(\tau_y, \tau_x, \tau_z, s)$;

$\nu^x(t, \tau_x, s) dt$, $\nu^y(t, \tau_y, s) dt$, $\nu^z(t, \tau_y, \tau_x, \tau_z, s) dt$, $\nu^u(t, \tau_y, \tau_x, \tau_u, s) dt$, $\nu^v(t, \tau_y, \tau_x, \tau_v, s) dt$ are the probabilities that individuals with respective characteristics (τ_x, s), (τ_y, s), $(\tau_y, \tau_x, \tau_z, s)$, $(\tau_y, \tau_x, \tau_u, s)$, $(\tau_y, \tau_x, \tau_v, s)$ will die in time interval $[t, t + dt]$;

$q^x(t, \tau_x, \xi, s) d\xi dt$, $q^y(t, \tau_y, \xi, s) d\xi dt$, $q^z(t, \tau_y, \tau_x, \tau_z, \xi, s) d\xi dt$, $q^u(t, \tau_y, \tau_x, \tau_u, \xi, s) d\xi dt$, $q^v(t, \tau_y, \tau_x, \tau_v, \xi, s) d\xi dt$ are the probabilities that individuals with respective characteristics (τ_x, s), (τ_y, s), $(\tau_y, \tau_x, \tau_z, s)$, $(\tau_y, \tau_x, \tau_u, s)$, $(\tau_y, \tau_x, \tau_v, s)$ due to migration from position $s \in R_2$ will get into area $d_\xi R_2$ in the time interval $[t, t+dt]$;

$X(t,\tau_x,s)d\tau_x ds dt$ is a change due to conceiving, abortions and birth in the time interval $[t, t+dt]$ of the expectation of the number of single females of age $\tau \in [\tau_x, \tau_x + d\tau_x]$;

$m_x^+(t,\tau_x,s)d\tau_x ds dt$, $m_y^+(t,\tau_y,s)d\tau_y ds\,dt$, $m_z^+(t,\tau_y,\tau_x,\tau_z,s)d\tau_y d\tau_x d\tau_z ds\,dt$, $m_u^+(t,\tau_y,\tau_x,\tau_u,s)d\tau_y d\tau_x d\tau_u ds\,dt$, $m_v^+(t,\tau_y,\tau_x,\tau_v,s)d\tau_y d\tau_x d\tau_v ds\,dt$ are the expectations of the individuals with the respective characteristics (τ_x, s), (τ_y, s), (τ_y,τ_x,τ_z,s), (τ_y,τ_x,τ_u,s), (τ_y,τ_x,τ_v,s) that due to migration will get into the area $d_s R_2$ in the time interval $[t, t+dt]$;

$m_x^-(t,\tau_x,s)d\tau_x ds\,dt$, $m_y^-(t,\tau_y,s)d\tau_y ds\,dt$, $m_z^-(t,\tau_y,\tau_x,\tau_z,s)d\tau_y d\tau_x d\tau_z ds\,dt$, $m_u^-(t,\tau_y,\tau_x,\tau_u,s)d\tau_y d\tau_x d\tau_u ds\,dt$, $m_v^-(t,\tau_y,\tau_x,\tau_v,s)d\tau_y d\tau_x d\tau_v ds\,dt$ are the expectations of the individuals with the respective characteristics (τ_x, s), (τ_y, s), (τ_y,τ_x,τ_z,s), (τ_y,τ_x,τ_u,s), (τ_y,τ_x,τ_v,s) that due to migration will leave the area $d_s R_2$ in the time interval $[t, t+dt]$;

$b^x(t,\tau_y,\tau_x,s)$, $b^y(t,\tau_y,\tau_x,s)$ are numbers of female and male offsprings born at the moment t from a female with the characteristics (τ_y,τ_x,s);

$2^{-1/2}D^y y$, $2^{-1/2}D^x x$, $3^{-1/2}D^z z$, $3^{-1/2}D^u u$, $3^{-1/2}D^v v$ represent the directional derivatives along the positive direction of the characteristics of the operators $L^y = \frac{\partial}{\partial t} + \frac{\partial}{\partial \tau_y}$, $L^x = \frac{\partial}{\partial t} + \frac{\partial}{\partial \tau_x}$, $L^z = L^x + \frac{\partial}{\partial \tau_z}$, $L^u = L^x + \frac{\partial}{\partial \tau_u}$, $L^v = L^x + \frac{\partial}{\partial \tau_v}$, respectively;

$\sigma_{xz}(\tau_z) = (\tau_{1x} + \tau_z, \tau_{2x} + \tau_z]$, $\sigma_{xv}(\tau_v) = (\tilde{\tau}_{1x} + \tau_v, \tilde{\tau}_{2x} + \tau_v]$, $\sigma_{xu}(\tau_u) = (\tau_{1x} + \tau_u, \tilde{\tau}_{2x} + \tau_u]$, where $\tilde{\tau}_{kx} = \tau_{kx} + \kappa_z$, $k = 1,2$; $\sigma_y = (\tau_{1y}, \tau_{2y}]$ and $\sigma_{xz}(0)$ are reproductive intervals for males and females, respectively;

$\sigma_z = (0, \kappa_z]$, $\sigma_u = (0, \kappa_u]$, $\sigma_v = (0, \kappa_v]$ are gestation and restoration intervals after the abortion and the delivery, respectively;

$\sigma = \sigma_y \times \sigma_{xz}(\kappa_z)$, $E^y = \{(t,\tau_y,s) \in I \times I \times R_2\}$;

$E^x = \big\{(t,\tau_x,s) \in I \times \big(I \setminus \bigcup_{i=1}^{6} \tau_i\big) \times R_2,\ \tau_k = \tau_{kx},\ \tau_{k+2} = \tilde{\tau}_{kx} + \kappa_v,\ k = 1,2,\ \tau_5 = \tau_{1x} + \kappa_u,\ \tau_6 = \tilde{\tau}_{2x} + \kappa_u\big\}$;

$E^z = \big\{(t,\tau_y,\tau_x,\tau_z,s) \in I \times \sigma_y \times \sigma_{xz}(\tau_z) \times \sigma_z \times R_2\big\}$;

$E^u = \big\{(t,\tau_y,\tau_x,\tau_u,s) \in I \times \sigma_y \times \sigma_{xu}(\tau_u) \times \sigma_u \times R_2\big\}$;

$E^v = \big\{(t,\tau_y,\tau_x,\tau_v,s) \in I \times \sigma_y \times \sigma_{xv}(\tau_v) \times \sigma_v \times R_2\big\}$;

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

$$\omega(\tau_x) = \begin{cases} [0, \tau_x - \tau_{1x}], & \tau_x \in (\tau_{1x}, \widetilde{\tau}_{1x}], \\ [0, \kappa_z], & \tau_x \in (\widetilde{\tau}_{1x}, \tau_{2x}], \\ [\tau_x - \tau_{2x}, \kappa_z], & \tau_x \in (\tau_{2x}, \widetilde{\tau}_{2x}], \end{cases}$$

for $\tau_{2x} - \tau_{1x} \geqslant \kappa_z$ and

$$\omega(\tau_x) = \begin{cases} [0, \tau_x - \tau_{1x}], & \tau_x \in (\tau_{1x}, \tau_{2x}], \\ [\tau_x - \tau_{2x}, \tau_x - \tau_{1x}], & \tau_x \in (\tau_{2x}, \widetilde{\tau}_{1x}], \\ [\tau_x - \tau_{2x}, \kappa_z], & \tau_x \in (\widetilde{\tau}_{1x}, \widetilde{\tau}_{2x}], \end{cases}$$

for $\tau_{2x} - \tau_{1x} < \kappa_z$.

Upon using the balance relation, we obtain the system

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

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

$$D^z z = -z(\nu^z + \chi) + m_z^+ - m_z^- \quad \text{in } E^z, \tag{3}$$

$$D^u u = -u\nu^u + m_u^+ - m_u^- \quad \text{in } E^u, \tag{4}$$

$$D^v v = -v\nu^v + m_v^+ - m_v^- \quad \text{in } E^v, \tag{5}$$

$$X = -\begin{cases} 0, & \tau_x \notin \sigma_{xz}(0), \\ \int\limits_{\sigma_y} z(\cdot, 0, s)\, d\tau_y, & \tau_x \in \sigma_{xz}(0), \end{cases} + \begin{cases} 0, & \tau_x \notin \sigma_{xu}(\kappa_u), \\ \int\limits_{\sigma_y} u(\cdot, \kappa_u, s)\, d\tau_y, & \tau_x \in \sigma_{xu}(\kappa_u), \end{cases} + \begin{cases} 0, & \tau_x \notin \sigma_{xv}(\kappa_v), \\ \int\limits_{\sigma_y} v(\cdot, \kappa_v, s)\, d\tau_y, & \tau_x \in \sigma_{xv}(\kappa_v), \end{cases} \tag{6}$$

$$\begin{aligned} m_\alpha^- &= \alpha \int\limits_{R_2} q^\alpha(\cdot, \xi, s)\, d\xi, \\ m_\alpha^+ &= \int\limits_{R_2} q^\alpha(\cdot, s, \xi)\, \alpha(\cdot, \xi)\, d\xi, \quad \alpha = y, x, z, u, v \end{aligned} \tag{7}$$

subject to conditions

$$\alpha(\cdot,0,s) = \int\limits_{\sigma} b^{\alpha} z(\cdot,\kappa_z,s)d\tau_y d\tau_x, \quad \alpha = y,x, \tag{8}$$

$$z(\cdot,0,s) = QP, \tag{9}$$
$$v(\cdot,0,s) = z(\cdot,\kappa_z,s), \tag{10}$$
$$u(\cdot,0,s) = \int\limits_{\omega(\tau_x)} \chi\, z\, d\tau_z, \tag{11}$$

$$x(0,\cdot) = x^0(\tau_x,s), \quad y(0,\cdot) = y^0(\tau_y,s), \quad z(0,\cdot) = z^0(\tau_y,\tau_x,\tau_z,s),$$
$$u(0,\cdot) = u^0(\tau_y,\tau_x,\tau_u,s), \quad v(0,\cdot) = v^0(\tau_y,\tau_x,\tau_v,s), \tag{12}$$

$$[x(\cdot,\tau_x,s)] = 0,$$
$$\tau_x = \tau_{1x}, \tau_{2x}, \tau_{1x} + \kappa_u, \widetilde{\tau}_{2x} + \kappa_u, \widetilde{\tau}_{1x} + \kappa_v, \widetilde{\tau}_{2x} + \kappa_v, \tag{13}$$

which governs the evolution of the population. If in (7) and (8) the letter α is not an index, then it denote the respective function. The point-argument of functions in the (6) – (13) denotes respective obvious arguments. We suppose that the non-negative demographic functions $\nu^x, \nu^y, \nu^z, \nu^u, \nu^v, Q, P, b^x$, $b^y, q^x, q^y, q^z, q^u, q^v$ and non-negative initial functions x^0, y^0, z^0, u^0, v^0 as well as bounded reproductive intervals are given. In the case of limited population demographic functions depend on densities x, y, z, u, v. It is also assumed, that initial functions x^0, y^0, z^0, u^0, v^0 satisfy reconcilable conditions, i.e., conditions (8) – (11), (13) for $t = 0$. In the case of the panmiction mating (see Svirezhev and Pasekov, 1982) the function $Q = xyn_y^{-1}$, $n_y = \int\limits_{\sigma_y} y(t,\tau_y,s)d\tau_y$. Functions x, y, z, u and v define the solution of the problem (1) – (13).

3. Solvability of the model. We consider the particular case of nonlimited population, when the abortions and the restoration periods are neglected. Then from (1) – (13) we obtain the following system

$$D^y y = -yd^y + m_y^+ \quad \text{in } E^y, \tag{14}$$

$$D^x x = -xd^x + m_x^+ + X_b \quad \text{in } E^x, \tag{15}$$

$$D^z z = -zd^z + m_z^+ \quad \text{in } E^z, \tag{16}$$

$$X_b = \begin{cases} 0, & \tau_x \notin \sigma_{xz}(\kappa_z), \\ \int\limits_{\sigma_y} z(\cdot, \kappa_z, s)\, d\tau_y, & \tau_x \in \sigma_{xz}(\kappa_z), \end{cases} \tag{17}$$

$$d^\alpha = \nu^\alpha + \int\limits_{R_2} q^\alpha(\cdot, \xi, s)\, d\xi, \quad \alpha = y, z,$$

$$d^x = \nu^x + \int\limits_{R_2} q^x(\cdot, \xi, s)\, d\xi$$

$$+ \begin{cases} 0, & \tau_x \notin \sigma_{xz}(0), \\ n_y^{-1} \int\limits_{\sigma_y} yP d\tau_y, \quad n_y = \int\limits_{\sigma_y} y d\tau_y, & \tau_x \in \sigma_{xz}(0), \end{cases} \tag{18}$$

$$m_\alpha^+ = \int\limits_{R_2} q^\alpha(\cdot, s, \xi)\alpha(\cdot, \xi) d\xi, \quad \alpha = x, y, z \tag{19}$$

subject to conditions

$$\alpha(\cdot, 0, s) = \int\limits_\sigma b^\alpha z(\cdot, \kappa_z, s) d\tau_y d\tau_x, \quad \alpha = y, x, \tag{20}$$

$$z(\cdot, 0, s) = xyPn_y^{-1}, \tag{21}$$

$$[x(\cdot, \tau_x, s)] = 0, \quad \tau_x = \tau_{1x}, \tau_{2x}, \widetilde{\tau}_{1x}, \widetilde{\tau}_{2x}, \tag{22}$$

$$x(0, \cdot) = x^0, \quad y(0, \cdot) = y^0, \quad z(0, \cdot) = z^0; \tag{23}$$

here $\widetilde{\tau}_{kx} = \tau_{kx} + \kappa_z$, $k = 1, 2$; non-negative functions $x^0, y^0, z^0, b^x, b^y, P$, ν^x, ν^y, ν^z, q^x, q^y, q^z are given as the non-negative functions x, y, z should be found. If in the (19) and (20) the letter α is not index, then it denotes the respective function. The functions x^0, y^0, z^0 should satisfy the conditions (20) – (22) for $t = 0$. Sets (t, τ_y, s), $(t, \tau_y, \tau_x, \tau_z, s)$ and (t, τ_x, s) are the arguments of the functions d^y, d^z and d^x, respectively. The following theorem is valid.

Theorem. *Let b^x, b^y be non-negative continuous functions in t as well as bounded and piecewise continuous functions in $\tau = (\tau_y, \tau_x)$ and let*

$x^0, y^0, z^0, P, \nu^x, \nu^y, \nu^z, q^x, q^y, q^z$ be non-negative continuous functions, such that:

1)
$$n_0 = \int_{\sigma_y} y^0 \, d\tau_y, \quad \sup P = P^*, \quad \max_{\alpha=x,y} \sup \alpha^0 = a,$$
$$\inf \left(\nu^\alpha + \int_{R_2} q^\alpha(\cdot, \xi, s) \, d\xi \right) = d_*^\alpha,$$
$$\int_{R_2} q^\alpha(\cdot, s, \xi) \, d\xi \leqslant \beta^\alpha < d_*^\alpha, \quad \alpha = x, y, z,$$
$$\max_{\alpha=x,y} \int_{\sigma_z(\kappa_z)} \sup_{t,\tau_y,s} b^\alpha \, d\tau_x = B^*,$$
$$\int_{\sigma_y} \sup_{\tau_x,\tau_z,s} z^0 \, d\tau_y = aq\,(B^*)^{-1},$$
$$P^* B^* \exp\{-\kappa_z\,(d_*^z - \beta^z)\} \leqslant q \leqslant \min(1, B^*\,(d_*^x - \beta^x))\,;$$

here $n^0, P^*, a, d_*^y, d_*^z, d_*^x, B^*, \beta^x, \beta^y, \beta^z$ and $\sup d^y$ are positive bounded constants; operators $\sup$ and $\inf$, if they are not specified, are taken on the entire domain of definition;

2) *$\kappa_z < \tau_{1x}$, $\tau_{2x} - \tau_{1x} > \kappa_z$, and integrals*

$$\int_{R_2} q^\alpha(\cdot, \xi, s) \, d\xi, \quad \int_{R_2} q^\alpha(\cdot, s, \xi) \, d\xi, \quad \alpha = x, y, z$$

converge uniformly.

Then problem (14) – (23) has unique positive continuous solution, such that $D^y y$, $D^z z$, $D^x x$ are continuous functions and following estimates are valid:

$$y \leqslant \begin{cases} a \exp\{-t\,(d_*^y - \beta^y)\}, & 0 \leqslant t \leqslant \tau_y < \infty, \\ aq^{k+1} \exp\{-\tau_y\,(d_*^y - \beta^y)\}, & k\tau_4 < t - \tau_y \leqslant (k+1)\tau_y, \\ & \tau_y \in (0, \infty), \end{cases} \tag{24}$$

$$
x \leqslant \begin{cases}
a \exp\left\{-t\left(d_*^x - \beta^*\right)\right\}, & 0 \leqslant t \leqslant \tau_x, \\ & \tau_x \in (0, \tau_1], \\
a q^{k+1} \exp\left\{-\tau_x\left(d_*^x - \beta^x\right)\right\}, & k\tau_4 < t - \tau_x \leqslant (k+1)\tau_4, \\ & \tau_x \in (0, \tau_1], \\
a \exp\left\{-t\left(d_*^x - \beta^x\right)\right\}, & 0 \leqslant t \leqslant \tau_x - \tau_1, \\ & \tau_x \in (\tau_1, \tau_2], \\
a \exp\left\{-(\tau_x - \tau_1)\left(d_*^x - \beta^x\right)\right\}, & \tau_x - \tau_1 < t \leqslant \tau_x, \\ & \tau_x \in (\tau_1, \tau_2], \\
a, & 0 \leqslant t \leqslant \tau_x, \\ & \tau_x \in (\tau_2, \tau_4], \\
a \exp\left\{-t\left(d_*^x - \beta^x\right)\right\}, & 0 \leqslant t \leqslant \tau_x - \tau_4, \\ & \tau_x \in (\tau_4, \infty), \\
a q^{k+1} \exp\left\{-(\tau_x - \tau_1)\left(d_*^x - \beta^x\right)\right\}, & k\tau_4 < t - \tau_x \leqslant (k+1)\tau_4, \\ & \tau_x \in (\tau_1, \tau_2], \\
a q^{k+1}, & k\tau_4 < t - \tau_x \leqslant (k+1)\tau_4, \\ & \tau_x \in (\tau_2, \tau_4], \\
a q^{k+1} \exp\left\{-(\tau_x - \tau_4)\left(d_*^x - \beta^x\right)\right\}, & (k-1)\tau_y < t - \tau_x \leqslant k\tau_y, \\ & \tau_x \in [\tau_4, \infty);
\end{cases} \tag{25}
$$

here $k = 0, 1, 2, \ldots$.

Proof. Let's define:

$$
\begin{aligned}
\overline{x}(t, s) &= x(t, 0, s), \\
\overline{y}(t, s) &= y(t, 0, s), \\
\overline{z}(t, \tau_y, \tau_x, s) &= z(\cdot, 0, s),
\end{aligned} \tag{26a − c}
$$

$$
\begin{aligned}
F_1(\gamma) =& \gamma(r_0^\gamma) \exp\left\{ - \int_0^t d^\gamma(r_\eta^\gamma)\, d\eta \right\} \\
&+ \int_0^t \exp\left\{ - \int_\alpha^t d^\gamma(r_\eta^\gamma)\, d\eta \right\} \left\{ m_\gamma^+(r_\alpha^\gamma) + X_b(r_\alpha^\gamma) \right\} d\alpha,
\end{aligned} \tag{26d}
$$

$$F_2(\gamma,\mu) = \gamma(h^{\gamma}_{\mu}) \exp\left\{ -\int\limits_{\mu}^{\tau_\gamma} d^{\gamma}(h^{\gamma}_{\eta})\,d\eta \right\}$$
$$+\int\limits_{\mu}^{\tau_\gamma} \exp\left\{ -\int\limits_{\alpha}^{\tau_\gamma} d^{\gamma}(h^{\gamma}_{\eta})\,d\eta \right\} \left(m^{+}_{\gamma}(h^{\gamma}_{\alpha}) + X_b(h^{\gamma}_{\alpha})\right)\,d\alpha, \quad (26e)$$

where $X_b(r^{\gamma}_{\alpha}) = 0$, $X_b(h^{\gamma}_{\alpha}) = 0$ for $\gamma = y, z$. If in (26a-e) the letter γ is not index, then it denote the respective function. From (14) – (16), (22), (23) and (26a-e) we obtain the formal integral representation of the functions z, y, x:

$$z = F_1(z), \quad z(r^{z}_{0}) = z^{0}(\tau_y, \tau_x - t, \tau_z - t, s), \quad 0 \leqslant t \leqslant \tau_z, \quad (27)$$

$$z = F_2(z, 0), \quad z(h^{z}_{0}) = \overline{z}(t - \tau_z, \tau_y, \tau_x - \tau_z, s), \quad 0 \leqslant \tau_z < t, \quad (28)$$

$$y = F_1(y), \quad y(r^{y}_{0}) = y^{0}(\tau_y - t, s), \quad 0 \leqslant t \leqslant \tau_y, \quad (29)$$

$$y = F_2(y, 0), \quad y(h^{y}_{0}) = \overline{y}(t - \tau_y, s), \quad 0 \leqslant \tau_y < t, \quad (30)$$

$$x = F_1(x), \quad x(r_0) = x^{0}(\tau_x - t, s), \quad 0 \leqslant t \leqslant \tau_x - \tau_i, \quad \tau_x \in (\tau_i, \tau_{i+1}], \quad (31)$$

$$x = F_2(x, \tau_i), \quad t > \tau_x - \tau_i, \quad \tau_x \in (\tau_i, \tau_{i+1}]; \quad (32)$$

here: $i = \overline{0,4}$, $\tau_0 = 0$, $\tau_1 = \tau_{1x}$, $\tau_2 = \widetilde{\tau}_{1x}$, $\tau_3 = \tau_{2x}$, $\tau_4 = \widetilde{\tau}_{2x}$, $\tau_5 = \infty$; $r^{z}_{\eta} = (\eta, \tau_y, \eta + \tau_x - t, \eta + \tau_z - t, s)$, $h^{z}_{\eta} = (\eta + t - \tau_z, \tau_y, \eta + \tau_x - \tau_z, \eta, s)$, $r^{y}_{\eta} = (\eta, \eta + \tau_y - t, s)$, $h^{y}_{\eta} = (\eta + t - \tau_y, \eta, s)$, $r^{x}_{\eta} = (\eta, \eta + \tau_x - t, s)$ and $h^{x}_{\eta} = (\eta + t - \tau_x, \eta, s)$ are sets of arguments written in brackets. By adding to (26) – (32) the formulas (17) – (21), we obtain a system of integral equations. We shall prove the unique solvability of this system in the space of non-negative continuous functions.

Conditions of our theorem allow us to solve (19), (26d) and (27) by method of iterations and to get the estimate

$$z \leqslant \exp\{-t(d^{z}_{*} - \beta^{z})\} \sup_{\tau_x, \tau_z, s} z^{0}, \quad 0 \leqslant t \leqslant \tau_z \leqslant \kappa_z. \quad (33)$$

Therefore

$$\int\limits_{\sigma_y} z\,d\tau_y \leqslant \int\limits_{\sigma_y} \sup_{\tau_y, \tau_x, s} z^{0}\,d\tau_y = aq(B^{*})^{-1}, \quad 0 \leqslant t \leqslant \tau_z \leqslant \kappa_z. \quad (34)$$

By using condition (20) and inequalities (33), (34) we obtain the estimate

$$\max(\sup \overline{x}, \sup \overline{y}) \leqslant aq, \quad 0 \leqslant t \leqslant \kappa_z. \tag{35}$$

Acting in the same way we prove the existence of unique non-negative continuous solution of (29) and obtain the estimate

$$y \leqslant a \exp\left\{-t(d_*^y - \beta^y)\right\}, \quad 0 \leqslant t \leqslant \tau_y. \tag{36}$$

Now we consider (28), (30) – (32) using step by step method with respect to the argument t.

Let $t \in (0, \kappa_z]$. Taking into account the estimate (35), as in the case of (27), we prove unique solvability of (30) and (31), (32) for $\tau_x \in (0, \tau_1] \cup (\tau_1, \tau_2]$ and obtain the inequalities

$$y \leqslant aq \exp\left\{-\tau_y(d_*^y - \beta^y)\right\}, \quad 0 \leqslant \tau_y \leqslant t, \tag{37}$$

$$x \leqslant a \begin{cases} \exp\left\{-t(d_*^x - \beta^x)\right\}, & 0 \leqslant t \leqslant \tau_x, \\ \exp\left\{-\tau_x(d_*^x - \beta^x)\right\}, & 0 \leqslant \tau_x < t, \end{cases} \quad \text{for } \tau_x \in (0, \tau_1], \tag{38}$$

$$x \leqslant a \begin{cases} \exp\left\{-t(d_*^x - \beta^x)\right\}, & 0 \leqslant t \leqslant \tau_x - \tau_1, \\ \exp\left\{-(\tau_x - \tau_1)(d_*^x - \beta^x)\right\}, & t > \tau_x - \tau_1, \end{cases} \quad \text{for } \tau_x \in (\tau_1, \tau_2]. \tag{39}$$

Let $\tau_x \in (\tau_2, \tau_3] \cup (\tau_3, \tau_4]$. Assume that Kx is the right-hand side of (31) and (32). Suppose that A is the class of non-negative continuous and bounded by constant a functions $g(t, \tau_x, s)$ with the norm $\| g \| = \sup | g |$. By using the conditions of our theorem we prove that the operator K acts in the class A and is contractive. Hence (31) and (32) have unique solutions in the class A and

$$x \leqslant a, \quad \tau_x \in (\tau_2, \tau_3] \cup (\tau_3, \tau_4]. \tag{40}$$

Let $\tau_x \in (\tau_4, \infty)$. Using inequalities $x(\tau_4 + \tau_x - t, \tau_4, s) \leqslant a$, $x^0 \leqslant a$ and acting as in the case $\tau_x \in (0, \tau_1]$ we prove the unique solvability of (31) and (32) in the space of non- negative continuous functions and obtain the estimate

$$x \leqslant a \begin{cases} \exp\left\{-t(d_*^x - \beta^x)\right\}, & 0 \leqslant t \leqslant \tau_x - \tau_4, \\ \exp\left\{-(\tau_x - \tau_4)(d_*^x - \beta^x)\right\}, & t > \tau_x - \tau_4. \end{cases} \tag{41}$$

Knowing the functions y and x for $t \in (0, \kappa_z]$, we consider (28) for $t \in (\tau_z, \tau_z + \kappa_z]$. Acting in the same way as in the case of (27) we prove the unique solvability of (28) and obtain the estimate

$$z \leqslant P^* \exp\{-\tau_z(d_*^z - \beta^z)\} \sup_{t,s} y n_y^{-1} \sup_{t,\tau_x,s} x. \tag{42}$$

From (28) we derive the inequality

$$\rho(t, \tau_x, \tau_z, s) \overset{\text{def}}{=} \int_{\sigma_y} z d\tau_y \leqslant P^* \exp\{-\tau_z d_*^z\} \sup_{t,\tau_x,s} x$$
$$+ \beta^z \int_0^{\tau_z} \exp\{-\tau_z - \alpha)d_*^z\} \sup_{t,\tau_x,s} \rho \, d\alpha,$$

which allows us to obtain the estimate

$$\int_{\sigma_y} z \, d\tau_y \leqslant \sup_{t,\tau_x,s} \rho \leqslant P^* \exp\{-\tau_z(d_x^z - \beta^z)\} \sup_{t,\tau_x,s} x \leqslant aq(B^*)^{-1}, \tag{43}$$

for $t \in (\tau_z, \tau_z + \kappa_z]$.

Let $t \in (\kappa_z, 2\kappa_z]$. Using inequality (43) for $\tau_z = \kappa_z$ from (20) we get

$$\max(\sup \overline{x}, \sup \overline{y}) \leqslant aq. \tag{44}$$

The estimate (43) for $\tau_z = \kappa_z$ and inequality (44) are the estimates (34) and (35) but for interval $(\kappa_z, 2\kappa_z]$.

Using the same method as for $t \in (0, \kappa_z]$ we can prove the unique solvabulity of (28), (30) – (32). The estimates (37), (38), (40), (41) and (42) are valid for $t \in (\kappa_z, 2\kappa_z]$, as the estimate (39) should be replaced by

$$x \leqslant a \exp\{-(\tau_x - \tau_1)(d_*^x - \beta^x)\} \begin{Bmatrix} 1, & t \leqslant \tau_x \\ q, & t > \tau_x \end{Bmatrix}, \tag{45}$$

for $\tau_x \in (\tau_1, \tau_2]$.

Continuing our argumentatios we prove the unique solvability of (28), (30) – (32) and that the estimates (37), (38), (40), (41) and (45) remain valid for $t \leqslant \tau_2$.

Let $t \in (\tau_2, \tau_4]$. Acting as above we can prove the solvability of (28), (30) – (32) and that the estimates (37), $(38)_2$, (41), $(45)_2$ remain valid. Using inequality

$$\int_{\sigma_y} z(\cdot, \kappa_z, s)\, d\tau_y \leqslant aqB^{*-1} \begin{cases} 1, & t \leqslant \tau_x, \\ q, & \tau_x < t, \end{cases} \tag{46}$$

and acting in the same way as in the case of derivation of inequality (40) we obtain the estimate

$$x \leqslant a \begin{cases} 1, & t \leqslant \tau_x, \\ q, & \tau_x < t. \end{cases} \tag{47}$$

Therefore the estimate (40) remains valid for $t \in (\tau_2, \tau_4]$.

Let $t \in (\tau_4, 2\tau_4]$. Acting as above we can prove the unique solvability of (28), (30) – (32) and obtain the estimates

$$\int_{\sigma_y} z(\cdot, \kappa_z, s)\, d\tau_y \leqslant aq^2(B^*)^{-1} \quad \text{for } \tau_x \in (\tau_2, \tau_4],$$
$$\max(\sup \overline{x}, \sup \overline{y}) \leqslant aq^2.$$

Proceeding our argumentations we prove the unique solvability of the problem (14) – (23), obtain the estimates (24), (25) and the inequalities

$$\max(\sup \overline{x}, \sup \overline{y}) \leqslant aq^{k+1},$$
$$k\tau_4 < t \leqslant (k+1)\tau_4, \quad k = 0, 1, 2, \ldots. \tag{48}$$

The estimate (48) completes the proof of our theorem. From this estimate we conclude that the population vanishes if $q < 1$.

Note. We considered the case $\kappa_z < \tau_{1x}$, $\tau_{2x} - \tau_{1x} > \kappa_z$. The other cases can be considered by the same method.

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MIGRUOJANČIŲ DVILYČIŲ POPULIACIJŲ EVOLIUCIJA

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Gautos lygtys, aprašančios dvilytės migruojančios populiacijos evoliuciją, įskaitant individų amžių, patelių nėštumą, galimą vaisiaus žuvimą ir organizmo reabilitaciją po gimdymo bei vaisiaus žuvimo. Kai nepaisoma vaisiaus žuvimo ir reabilitacijos intervalų, įrodytas vienintelis modelio išsprendžiamumas.