STABILITY PROBLEM FOR THE AGE-DEPENDENT PREDATOR - PREY MODEL

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Abstract. The paper deals with the age-dependent model which is a generalization of the classical Lotka-Volterra model. Age structure of both species, predators and preys is concerned. The model is based on the system of partial differential and integro-differential equations. We study the existence and uniqueness of the solution for the considered population problem. The stability problem for trivial stationary solution of the model is also proved.

1. Introduction. In the paper we are concerned with multipopulation model based on the Lotka-Volterra one. This classical model describes the competition of two populations, predators and preys. It is based on a system of ordinary differential equations and leads to periodic solutions. The Lotka-Volterra model [24] assumes that effectiveness of hunting is constant, independent of physical predispositions of the predator as well the prey. A justified modification of the model takes age structure into consideration. In ecology the effectiveness of a hunting or an escape depends on the features of both sides, particularly, age of predator and prey. There are many other papers concerning the generalization of the Lotka-Volterra model but analyzing the problem of dependence on the age only fragmentarily. For example, a prey-predator system in a specific habitat with two zones, free and reserved [12]; with habitat complexity [3] (with references therein); multi-dimensional Lotka-Volterra system [14] or Lotka-Volterra multi-species systems [1, 2]; age-dependent prey-predator system [7] with delays [6, 19, 26] or diffusion [11]. Introducing age structure in population models remarkably increase their complexity. Hence in many papers age-dependence of one species, either predator or prey, is ignored. Such models are based on the systems combining partial differential equations with

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ordinary or delay differential equations, for example [7, 10, 15, 16, 17, 20, 21, 22] (with references therein). In the present paper we consider more general description of populations dynamics. We concern age structure of both species, predators and preys. Therefore our model is based on the system of partial differential and integro-differential equations. We assume that mortality of preys is the effect of predators hunting or depends on natural causes. Additionally, we consider the reproduction of predators, not only as the result their physical predispositions connected with their age, but also as the consumption of the energy from biomass acquired during every single successful hunting. Some papers also present models with age structure approach for predators and preys, but under assumptions influencing in different manner on dynamics of both populations: in [13] the mortality of preys depends only on the size of predator population and vice versa; the model under the assumption of variations of maturation periods of both populations, but without the influence of one species on the reproduction process of the second one [5]; the model based on coupled McKendrick-von Foerster equations each augmented by the term describing the interactions of two species and under the assumption that the mortality and reproduction depend on the size of considered population [23].

In Section 2 we give a general description of the model, its variables, parameters and basic assumptions. The problem of natural mortality for preys is not considered separately in the Lotka-Volterra model. In [9] we described age-dependent model based on this classical one and in analogy to it we did not introduce natural mortality for preys. We only assumed that preys are eaten by predators. However it is justified, considering age structure in a model, to take a connection between age of preys and their mortality into consideration. In this paper we complement the assumptions of the model presented in [9] and introduce natural mortality of preys. We assume that preys either are eaten by predators or die of natural death. Next Sections 3 and 4 contains formulation of the population problem and the proof of the existence and uniqueness of the solutions. The presented proof, with small modifications, is analogical to the main result of the paper [9] where we considered the model but without natural mortality for preys. In Section 5 we give the condition for the existence of stationary solution of the model. The discussion about the stability problem for trivial stationary solution is presented in Section 6.

2. Model. There are two basic variables in our model

- \( u_1(t, x) \) denotes density of a population of predators of age \( x \) at time \( t \),
- \( u_2(t, x) \) denotes density of a population of preys of age \( x \) at time \( t \).

We assume that predators generally die of natural death. We can express their mortality by the classical McKendrick-von Foerster equation (see [18] and [25])

\[
\frac{\partial u_1}{\partial t} + \frac{\partial u_1}{\partial x} = -\lambda(x)u_1(t, x) \tag{1}
\]

where \( \lambda \) is called death-modulus. Preys either are eaten by predators or die of natural causes. We assume that the parameter \( \alpha(x, y) \) denotes the effectiveness of a hunt during a contact of a prey of age \( x \) with a predator of age \( y \). Then the equation describing the mortality of preys has the form

\[
\frac{\partial u_2}{\partial t} + \frac{\partial u_2}{\partial x} = -\int_0^\infty \alpha(x, y)u_1(t, y)dy \cdot u_2(t, x) - \mu(x)u_2(t, x). \tag{2}
\]

In [9] we presented analogical equation but without natural mortality for preys. According to the classical Lotka-Volterra model we assume that food resources
for preys are unlimited. The birth process for preys is described by the following “renewal” equation

\[ u_2(t, 0) = \int_0^\infty \beta(x)u_2(t, x)dx \] (3)

where \( \beta \) is called birth-modulus. We assume that a predator gains energy needed for a reproduction as the result of successful hunting. The coefficient \( k \) is biomass conversion of hunted preys. It denotes energy derived from a hunting used up in the process of reproduction

\[ u_1(t, 0) = k \int_0^\infty \int_0^\infty \alpha(x,y)u_2(t, x)u_1(t,y)dxdy. \] (4)

3. Solutions. We consider system (1)–(4) with the initial conditions

\[ u_1(0, x) = v_1(x), \quad u_2(0, x) = v_2(x) \] (5)

where \( v_1, v_2 \) are continuous non-negative and integrable functions \([0, \infty) \to \mathbb{R}\) satisfying the conditions

\[ v_1(0) = k \int_0^\infty \int_0^\infty \alpha(x,y)v_2(x)v_1(y)dxdy, \]

\[ v_2(0) = \int_0^\infty \beta(x)v_2(x)dx. \]

Let \( \varphi = (\varphi_1, \varphi_2) : [0, T] \to \mathbb{R}^2 \), where \( T > 0 \), be a continuous function satisfying the conditions

\[ \varphi_1(0) = v_1(0), \quad \varphi_2(0) = v_2(0). \] (6)

We first consider an auxiliary problem, that is equations (1), (2) with conditions (5), (6) and

\[ u_1(t, 0) = \varphi_1(t), \quad u_2(t, 0) = \varphi_2(t). \] (7)

A solution of this problem is (see [8] or [9])

\[ u_1(t, x) = \begin{cases} \varphi_1(t - x)e^{-\int_0^t \lambda(s)ds} & \text{for } x \leq t \\ v_1(x - t)e^{-\int_0^t \lambda(s)ds} & \text{for } x > t \end{cases} \] (8)

and

\[ u_2(t, x) = \begin{cases} \varphi_2(t - x)e^{-\int_0^t \mu(s)ds}e^{-\int_0^t R(s,x-s)ds} & \text{for } x \leq t \\ v_2(x - t)e^{-\int_0^t \mu(s)ds}e^{-\int_0^t R(t-s,x-s)ds} & \text{for } x > t \end{cases} \] (9)

where

\[ R(t, x) = \int_0^\infty \alpha(x, y)u_1(t, y)dy. \] (10)

Define the operator \( \Theta : C([0, T], \mathbb{R}^2) \to C([0, T], \mathbb{R}^2) \),

\[ \Theta \varphi = ((\Theta \varphi)_1, (\Theta \varphi)_2) : [0, T] \to \mathbb{R}^2 \]

on a Banach space \( C([0, T], \mathbb{R}^2) \) with the norm

\[ ||\varphi|| = \sup_{t \in [0, T]} (|\varphi_1(t)| + |\varphi_2(t)|) \] (11)

by the formula

\[ (\Theta \varphi)_1(t) = k \int_0^\infty R(t, x)u_2(t, x)dx, \quad (\Theta \varphi)_2(t) = \int_0^\infty \beta(x)u_2(t, x)dx. \]

Now we shall define the solution of system (1)–(5) for \( t \in [0, T] \), where \( T > 0 \). In the following we will assume that \( T \) is arbitrary.
Definition 3.1. By the solution of (1)-(4) with initial conditions (5) we mean the function \( u = (u_1, u_2) \in L^1([0, T] \times \mathbb{R}^2) \cap C([0, T] \times \mathbb{R}^2) \) defined by (8), (9), when the function \( \varphi \) is a fixed-point of the operator \( \Theta \) i.e. \( \Theta \varphi = \varphi \).

4. Existence and uniqueness of the solutions.

Theorem 4.1. Let \( \alpha, \beta, \lambda, \mu \geq 0 \). We assume also that \( \beta \in L^\infty((0, \infty)) \) and \( \alpha \in L^\infty((0, \infty)^2) \). Then, system of differential equations (1)-(4) with initial conditions (5) has exactly one non-negative solution on the set \( [0, T] \times [0, \infty) \).

Proof. Let \( X_T \) denotes the space of all continuous, non-negative functions \( \varphi : [0, T] \to \mathbb{R}^2 \) satisfying conditions (6) and the estimation

\[
\varphi_2(t) \leq \tilde{\beta} e^{\tilde{\beta} t} \| v_2 \|_{L^1},
\]

where \( \tilde{\beta} = \| \beta \|_{L^\infty} \). We shall prove that \( \Theta : X_T \to X_T \). First let us show that \( \Theta \varphi : [0, T] \to \mathbb{R}^2 \) is continuous. We claim that the families \( \{ u_i(t, \cdot) \}_{t \in [0, T]}, i = 1, 2 \) are uniformly integrable. Select some \( \varepsilon > 0 \). From the integrability of \( v_i \) there exists \( c > 0 \) such that

\[
\int_{\{ v_i(x) \geq c \}} |v_i(x)| dx < \varepsilon.
\]

Let \( c' = \max\{ c, \max_{t \in [0, T]} \varphi_i(t) \} \). From (8), (9) it follows that \( \{ x : u_i(t, x) > c' \} \subset \{ x : v_i(t, x) > c \} \) which completes the claim. Since \( \alpha \) does not depend on \( t \) so the boundedness of \( \alpha \) yields the uniform boundedness of \( R \) with respect to \( t \). In consequence the families \( \{ R(t, \cdot)u_2(t, \cdot) : t \in [0, T] \} \) and \( \{ \beta(\cdot)u_2(t, \cdot) : t \in [0, T] \} \) are uniformly integrable. From this it follows the continuity of the integrals \( \int_0^\infty R(t, x)u_2(t, x) dx \) and \( \int_0^\infty \beta(x)u_2(t, x) dx \) with respect to \( t \). The functions \( \Theta \varphi_1 \) and \( \Theta \varphi_2 \) are continuous since

\[
(\Theta \varphi)_1(t) = k \int_0^\infty R(t, x)u_2(t, x) dx
\]

and

\[
(\Theta \varphi)_2(t) = \int_0^\infty \beta(x)u_2(t, x) dx.
\]

To prove that the function \( \Theta \varphi_2 \) satisfies inequality (12) we estimate

\[
(\Theta \varphi)_2(t) = \int_0^\infty \beta(x)u_2(t, x) dx
\]

\[
= \int_0^t \beta(x)\varphi_2(t - x)e^{-\int_0^t \mu(s) ds - \int_{t - x}^t R(s - x - t) ds} dx + \int_t^\infty \beta(x)u_2(x - t) e^{-\int_0^x \mu(s) ds - \int_{x - t}^x R(s - x - t) ds} dx
\]

\[
\leq \int_0^t \beta(x)\varphi_2(t - x) dx + \int_t^\infty \beta(x)v_2(x - t) dx
\]

\[
= \int_0^t \beta(t - x)\varphi_2(x) dx + \int_0^\infty \beta(x + t) v_2(x) dx
\]

\[
\leq \tilde{\beta} \int_0^t \beta e^{\tilde{\beta} x} dx \| v_2 \|_{L^1} + \beta \| v_2 \|_{L^1} = \tilde{\beta} e^{\tilde{\beta} t} \| v_2 \|_{L^1}.
\]
This means that \( \Theta : \mathcal{T} \to \mathcal{T} \). Let now \( \varphi, \overline{\varphi} \in \mathcal{T} \). Let \( \overline{\varphi}_1, \overline{\varphi}_2 \) be given by formulas (8), (9) with \( \varphi \) replaced by \( \overline{\varphi} \) and let 

\[
\overline{R}(t, x) = \int_0^\infty \alpha(x, y)\overline{\varphi}_1(t, y)dy.
\]

We shall estimate the differences \(|u_i(t, x) - \overline{\varphi}_i(t, x)|\) for \( i = 1, 2 \). For \( x \leq t \) we have 

\[
|u_1(t, x) - \overline{\varphi}_1(t, x)| = \left| \varphi_1(t - x)e^{-\int_0^x \lambda(s)ds} - \varphi_1(t - x)e^{-\int_0^x \lambda(s)ds} \right| \\
\leq |\varphi_1(t - x) - \overline{\varphi}_1(t - x)|.
\]

For \( x > t \) clearly \( u_1(t, x) = \overline{\varphi}_1(t, x) \). Hence 

\[
|R(t, x) - \overline{R}(t, x)| \leq \int_0^t \alpha(x, y)|\varphi_1(t - y) - \overline{\varphi}_1(t - y)|dy \\
\leq \sup_{y \in [0, t]} \alpha(x, y) \int_0^t |\varphi_1(s) - \overline{\varphi}_1(s)|ds \leq \alpha_0(x) \int_0^t |\varphi_1(y) - \overline{\varphi}_1(y)|dy
\]

where \( \alpha_0(x) = \sup_{y \in [0, t]} \alpha(x, y) \). By the above it follows that 

\[
\left| e^{-\int_{t-x}^t R(s, x+s+t)ds} - e^{-\int_{t-x}^t \overline{R}(s, x+s+t)ds} \right| \\
\leq \left| \int_{t-x}^t R(s, x+s-t)ds - \int_{t-x}^t \overline{R}(s, x+s-t)ds \right| \\
\leq \int_{t-x}^t \alpha_0(x+s-t) \int_0^s |\varphi_1(y) - \overline{\varphi}_1(y)|dyds \\
\leq \int_0^t \alpha_0(x-s) \int_0^{t-s} |\varphi_1(y) - \overline{\varphi}_1(y)|dyds \\
\leq \int_0^t |\varphi_1(y) - \overline{\varphi}_1(y)| \int_0^{t-y} \alpha_0(x-s)dsdy \\
\leq t \cdot \sup_{z \in [0, t]} \alpha_0(z) \int_0^t |\varphi_1(y) - \overline{\varphi}_1(y)|dy.
\]

We now estimate the difference \(|u_2(t, x) - \overline{\varphi}_2(t, x)|\). For \( x > t \) 

\[
|u_2(t, x) - \overline{\varphi}_2(t, x)| = v_2(x - t)e^{-\int_0^x \mu(s)ds} |e^{-\int_0^t R(s, t-s)ds} - e^{-\int_0^t \overline{R}(s, t-s)ds} | \\
\leq v_2(x - t) \int_0^t |R(t - s, t - s) - \overline{R}(t - s, t - s)|ds \\
= v_2(x - t) \int_0^t |R(s, t - s + s) - \overline{R}(s, t - s + s)|ds \\
\leq v_2(x - t) \int_0^t \alpha_0(x - s + s) \int_0^{t-s} |\varphi_1(y) - \overline{\varphi}_1(y)|dyds \\
\leq v_2(x - t) \int_0^t \alpha_0(x - s) \int_0^{t-s} |\varphi_1(y) - \overline{\varphi}_1(y)|dyds \\
= v_2(x - t) \int_0^t |\varphi_1(y) - \overline{\varphi}_1(y)| \int_0^{t-y} \alpha_0(x-s)dsdy
\]
Thus the metric \( \rho \) is equivalent to the usual metric defined by (11) in \( C([0,T], \mathbb{R}^2) \) and in consequence the metric space \((X_T, \rho)\) is complete. We have
\[ e^{-\gamma t} \left( |(\Theta \varphi)_1(t) - (\Theta \varphi)_1(t)| + |(\Theta \varphi)_2(t) - (\Theta \varphi)_2(t)| \right) \leq Ke^{-\gamma t} \int_0^t e^{\gamma s} ds \cdot \rho(\varphi, \varphi) = \frac{K}{\gamma} \rho(\varphi, \varphi). \]

Since the right-hand side does not depend on \( t \), we observe that
\[
\rho(\Theta \varphi, \Theta \varphi) = \sup_{\varphi \in [0, T]} e^{-\gamma t} \left( |(\Theta \varphi)_1(t) - (\Theta \varphi)_1(t)| + |(\Theta \varphi)_2(t) - (\Theta \varphi)_2(t)| \right) \leq \frac{K}{\gamma} \rho(\varphi, \varphi).
\]

Let choose \( \gamma \) such that \( \frac{K}{\gamma} < 1 \). The assertion of the theorem follows from the Banach fixed point theorem.

**Corollary 1.** System of differential equations (1)–(4) with initial conditions (5) has exactly one non-negative solution on the set \([0, \infty) \times [0, \infty)\).

We next show that under some additional conditions the solution of the problem is the classical one.

**Proposition 1.** Assume that \( \alpha, \beta, v_1, v_2 \) are of class \( C^1 \), the derivatives of \( \alpha \) are bounded and
\[
\int_0^\infty \beta(x)v_2'(x) dx = v_2'(0) + v_2(0)\mu(0) + v_2(0)\int_0^\infty \alpha(0, y)v_1(y) dy \tag{13}
\]
\[
v_1'(0) + \int_0^\infty \int_0^\infty \alpha(x, y)(\lambda(y)v_2(x)v_1(y) - v_2'(x)v_1(y) - v_2(x)v_1'(y)) dx dy = 0, \tag{14}
\]
then the solution of problem (1)–(5) given by (8) and (9) is the classical solution.

**Proof.** Applying (1) and (10) we have
\[
\frac{\partial R}{\partial x} = \int_0^\infty \frac{\partial \alpha(x, y)}{\partial x} u_1(t, y) dy
\]
and
\[
\frac{\partial R}{\partial t} = \int_0^\infty \alpha(x, y) \frac{\partial u_1(t, y)}{\partial t} dy = - \int_0^\infty \alpha(x, y)\lambda(y)u_1(t, y) dy - \int_0^\infty \alpha(x, y) \frac{\partial u_1(t, y)}{\partial y} dy
\]
where
\[
\int_0^\infty \alpha(x, y) \frac{\partial u_1(t, y)}{\partial y} dy = -\alpha(x, 0)u_1(t, 0) - \int_0^\infty \frac{\partial \alpha(x, y)}{\partial y} u_1(t, y) dy.
\]
The above integrals are convergent, which follows from (8) and the assumptions. Then \( R \) is of class \( C^1 \). Moreover
\[
\varphi_2(t) = \int_0^\infty \beta(x)u_2(t, x) dx
\]
\[
= \int_0^t \beta(x)\varphi_2(t - x)e^{-\int_0^t \mu(s) ds e^{-\int_{t-s}^t R(s, x + s - t) ds} dx} + \int_t^\infty \beta(x)v_2(x - t)e^{-\int_0^{x-t} \mu(x-s) ds e^{-\int_{t-s}^t R(t-s, x-s) ds} dx} dx
\]
The differentiability of $I_1$ follows that where

\[
\phi
\]

Therefore, $\phi$ is differentiable and

\[
I_2(t) = \int_0^t \beta(t-x) \varphi_2(x) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,x-s) ds} dx + \int_0^\infty \beta(x+t) v_2(x) e^{-\int_0^t \mu(s+x-t) ds} e^{-\int_0^t R(t-s,x+s-t) ds} dx = I_1(t) + I_2(t).
\]

The differentiability of $I_1$ is obvious and

\[
I_2(t) = \int_0^\infty \beta(x+t) v_2(x) e^{-\int_0^t \mu(s+x-t) ds} e^{-\int_0^t R(t-s,x+s-t) ds} dx + \int_0^\infty \beta(x+t) v_2(x) e^{-\int_0^t \mu(s+x-t) ds} e^{-\int_0^t R(t-s,x+s-t) ds} dx + \int_0^\infty \beta(x+t) v_2(x) e^{-\int_0^t \mu(s+x-t) ds} e^{-\int_0^t R(t-s,x+s-t) ds} dx \\
\times (-R(0,x) + R(t,x+t)) \frac{\partial R(t,x+t)}{\partial t} dx.
\]

Therefore, $\varphi_2$ is differentiable. Analogously we can prove the differentiability of $\varphi_1$. According to formulas (8) and (9) and from the differentiability of $v_1$ and $v_2$ it follows that $u_1$ and $u_2$ are differentiable on the sets $\{(t,x) : t < x\}$ and $\{(t,x) : t > x\}$. It is now sufficient to consider the problem on the half-line $\{(t,x) : t = x\}$. Let us notice that

\[
u_1(t,t) = \varphi_1(0) e^{-\int_0^t \lambda(s) ds} = v_1(0) e^{-\int_0^t \lambda(s) ds}
\]

and

\[
u_2(t,t) = \varphi_2(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds} = v_2(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds}.
\]

Moreover we have

\[
\frac{\partial}{\partial t} \left[ v_2(t-x) e^{-\int_0^t \mu(s-x) ds} e^{-\int_0^t R(t-s,x-s) ds} \right]_{t=x}
\]

\[
= -v_2'(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds} - v_2(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds} \mu(0)
\]

\[
- v_2(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds} \frac{\partial}{\partial t} \left[ \int_0^t R(t-s,x-s) ds \right]_{t=x}
\]

and

\[
\frac{\partial}{\partial t} \left[ \varphi_2(t-x) e^{-\int_0^t \mu(s-x) ds} e^{-\int_0^t R(s,x+s-t) ds} \right]_{t=x}
\]

\[
= \varphi_2'(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds}
\]

\[
- \varphi_2(0) e^{-\int_0^t \mu(s) ds} e^{-\int_0^t R(s,s) ds} \frac{\partial}{\partial t} \left[ \int_0^x R(t-s,x-s) ds \right]_{t=x}
\]

where

\[
\varphi_2'(0) = \beta(0) \varphi_2(0) + \int_0^\infty \beta'(x) v_2(x) dx = -\int_0^\infty \beta(x) v_2'(x) dx.
\]

By assumption (13) we have the equality of one-sided derivatives with respect to $t$ for the function $u_2$. Let us notice that for $x > 0$

\[
\frac{\partial u_1}{\partial t} \bigg|_{t=0} = -v_1'(x) - v_1(x) \lambda(x)
\]
and in consequence
\[
\frac{\partial R(t,x)}{\partial t}|_{t=0} = \int_0^\infty \alpha(x,y)(-v_1'(y) - v_1(y)\lambda(y))dy
\]
and
\[
\frac{\partial}{\partial t} R(t,x+t)|_{t=0} = -\int_0^\infty \alpha(x,y)(v_1(y)\lambda(y) + v_1'(y))dy + \int_0^\infty \frac{\partial \alpha(x+t,y)}{\partial t}|_{t=0} v_1(y)dy
\]
where \( \frac{\partial \alpha(x,y)}{\partial t}|_{t=0} = \frac{\partial \alpha(x,y)}{\partial x} \). Therefore
\[
\varphi_1(t) = k \int_0^t R(t,x)\varphi_2(t-x)e^{-\int_0^t \mu(s)ds}e^{-\int_{t-s}^t R(s,x+s-t)ds}dx
\]
\[
+ k \int_t^\infty R(t,x)v_2(x-t)e^{-\int_0^t \mu(s)ds}e^{-\int_{t-s}^t R(s,x+s-t)ds}dx
\]
\[
= k \int_0^t R(t,x)\varphi_2(t-x)e^{-\int_0^t \mu(s)ds}e^{-\int_{t-s}^t R(s,x+s-t)ds}dx
\]
\[
+ k \int_0^\infty R(t,x+v_2(x-t)e^{-\int_0^t \mu(s)ds}e^{-\int_{t-s}^t R(s,x+s-t)ds}dx
\]
and
\[
\varphi_1'(0) = kR(0,0)\varphi_2(0) + k \int_0^\infty \frac{\partial}{\partial t} R(t,x+t)|_{t=0} v_2(x)dx
\]
\[
= k \int_0^\infty \alpha(0,y)v_1(y)dyv_2(0) - k \int_0^\infty \int_0^\infty \alpha(x,y)v_2(x)v_1'(y)dxdy
\]
\[
- k \int_0^\infty \int_0^\infty \alpha(x,y)v_2(x)v_1(y)\lambda(y)dxdy + k \int_0^\infty \int_0^\infty \frac{\partial \alpha(x,y)}{\partial x}v_2(x)v_1(y)dxdy
\]
\[
= \int_0^\infty \int_0^\infty \alpha(x,y)(\lambda(y)v_2(x)v_1(y) - v_2'(x)v_1(y) - v_2(x)v_1'(y))dxdy.
\]
Since
\[
\frac{\partial}{\partial t} \left[ \varphi_1(t-x)e^{-\int_0^t \lambda(s)ds} \right]_{t=x} = \varphi_1'(0)e^{-\int_0^t \lambda(s)ds},
\]
\[
\frac{\partial}{\partial t} \left[ v_1(x-t)e^{-\int_0^t \lambda(s-x)ds} \right]_{t=x} = -v_1'(0)e^{-\int_0^t \lambda(s)ds} - v_1(0)e^{-\int_0^t \lambda(s)ds} \lambda(0),
\]
then by (14) we have the equality of one-sided derivatives with respect to \( t \) for the function \( u_1 \). Both functions \( u_1 \) and \( u_2 \) fulfill equations (1) and (2), therefore the equality of their one-sided derivatives with respect to \( t \) implies the equality of their one-sided derivatives with respect to \( x \).

**Remark 1.** The classical solution of (1)–(5) is the solution in the sense of Definition 3.1. Moreover, the function \( u \) differentiable in \([0,T] \times \mathbb{R}_+\) which is the solution of (1)–(5) in the sense of Definition 3.1 is also the classical solution under the assumptions of Proposition 1.

**Remark 2.** Conditions (13) and (14), which guarantee that the solution is classical one are not restrictive from ecological point of view. If equalities (13) and (14) are not fulfilled, then the lack of differentiability of the solution of (1)–(5) can appear only on the line \( t = x \). However, in biological description the variable \( t \) denotes starting time of the observation, which can be selected arbitrarily. Thus there is not any “privileged” line \( t = x \). Therefore in biological realities the assumption that the solution of the problem is classical one is natural.
5. Stationary solutions. In this section we study solutions of (1)–(4) independent of time \( t \).

\[
\begin{align*}
\pi'_1(x) &= -\lambda(x)\pi_1(x) \\
\pi'_2(x) &= -\int_0^\infty \alpha(x,y)\pi_1(y)dy \cdot \pi_2(x) - \mu(x)\pi_2(x) \\
\pi_2(0) &= \int_0^\infty \beta(x)\pi_2(x)dx \\
\pi_1(0) &= k \int_0^\infty \int_0^\infty \alpha(x,y)\pi_2(x)\pi_1(y)dxdy.
\end{align*}
\] (15)

Hence we get the following stationary solutions

\[
\begin{align*}
\pi_1(x) &= \pi_1(0)e^{-\int_0^x \lambda(\tau)d\tau}, \\
\pi_2(x) &= \pi_2(0)e^{-\int_0^x \mu(\tau)d\tau}e^{-\pi_1(0) \int_0^x \rho(\tau)d\tau}
\end{align*}
\] (16)

fulfilling conditions

\[
\begin{align*}
\pi_1(0) &= \pi_1(0)\pi_2(0)k \int_0^\infty \rho(x)e^{-\int_0^x \mu(\tau)d\tau}e^{-\pi_1(0) \int_0^x \rho(\tau)d\tau}dx \\
\pi_2(0) &= \pi_2(0) \int_0^\infty \beta(x)e^{-\int_0^x \mu(\tau)d\tau}e^{-\pi_1(0) \int_0^x \rho(\tau)d\tau}dx,
\end{align*}
\]

where

\[
\rho(x) = \int_0^\infty \alpha(x,y)e^{-\int_0^y \lambda(\tau)d\tau}dy.
\]

We get the following corollary.

**Corollary 2.** System (1)–(4) has positive stationary solution if and only if

\[
\int_0^\infty \beta(x)e^{-\int_0^x \mu(\tau)d\tau}dx \geq 1.
\] (17)

**Proof.** It is obvious that (17) is the necessary condition for the existence of positive stationary solution of (1)–(4). We prove that (17) is also sufficient. Define

\[
H(z) = \int_0^\infty \beta(x)e^{-\int_0^x \mu(\tau)d\tau}e^{-z \int_0^x \rho(\tau)d\tau}dx.
\]

By assumption we have \( H(0) > 1 \). Moreover, it is easily seen that \( \lim_{z \to \infty} H(z) = 0 \). Since \( H \) is continuous there exists such \( z > 0 \) that \( H(z) = 1 \). Let \( \pi_1(0) = z \), then for

\[
\pi_2(0) = \frac{1}{k \int_0^\infty \rho(x)e^{-\int_0^x \mu(\tau)d\tau}e^{-\pi_1(0) \int_0^x \rho(\tau)d\tau}dx} \]

we get the desired conclusion.

The equality in (17) would imply a balancing of the reproduction of preys parallel to the absence of predators. In this situation there would exist infinitely many stationary solutions with \( \pi_1(x) = 0 \). Inequality (17) is equivalent to the lack of independent balancing of the reproduction of preys but only with predators’ interference.

6. Stability problem. In this section we prove stability for trivial stationary solution of system (1)–(5) in the situation when its non-trivial solutions do not exist. More precisely, we show that under some assumptions trivial stationary solution is the unique and is asymptotically stable.
Lemma 6.1. Let \( M(t) = \sup_{s \geq 0} e^{-\int_s^{t+} \mu(\tau) d\tau} \). Assume that

\[
\int_0^\infty M(t) dt = M < \infty
\]

and system (1)–(5) satisfies

\[
\int_0^\infty \beta(x) e^{-\int_s^t \mu(s) ds} dx < 1
\]

and

\[
\lim_{x \to \infty} \beta(x) = 0.
\]

Then

\[
\lim_{t \to \infty} u_2(t, x) = 0.
\]

Proof. Recall that the function \( \varphi_2 \) is a fixed-point of the operator \( \Theta \). It is obvious that

\[
\varphi_2(t) \leq \int_0^t \beta(x) e^{-\int_s^x \mu(s) ds} \varphi_2(t-x) dx + \sup_{s \geq t} \beta(s) \|v_2\|_{L^1}.
\]

Hence

\[
\varphi_2(t+h) \leq \int_0^{t+h} \beta(x) e^{-\int_s^x \mu(s) ds} \varphi_2(t-h-x) dx + \sup_{s \geq t+h} \beta(s) \|v_2\|_{L^1}
\]

\[
= \int_0^h \beta(x) e^{-\int_s^x \mu(s) ds} \varphi_2(t+h-x) dx + \int_h^{t+h} \beta(x) e^{-\int_s^x \mu(s) ds} \varphi_2(t-h-x) dx + \sup_{s \geq t+h} \beta(s) \|v_2\|_{L^1} = I_1 + I_2 + I_3.
\]

Clearly,

\[
I_1 \leq \beta \int_t^{t+h} \varphi_2(x) dx
\]

and

\[
I_2 \leq \gamma \sup_{s \leq t} \varphi_2(s)
\]

where

\[
\gamma = \int_0^\infty \beta(x) e^{-\int_s^x \mu(s) ds} dx.
\]

Let \( \varepsilon = \frac{1}{3}(1 - \gamma) \). There exist \( t_0 \) and \( h > 0 \) such that \( I_3 < \varepsilon \) for any \( t > t_0 \). Furthermore for any \( t \) there exists \( h_1 \) such that \( I_1 < \varepsilon \) for \( h \in (0, h_1) \). In consequence

\[
\varphi_2(t+h) \leq \gamma \sup_{s \leq t} \varphi_2(s) + 2\varepsilon.
\]

If \( \varphi_2 \) was not bounded then for any \( t_1 \) there would exist \( t \) and \( h \) such that \( t > t_1 \) and

\[
\varphi_2(t+h) \geq \sup_{s \leq t} \varphi_2(s).
\]

However, it contradicts inequality (22). Therefore \( \varphi_2 \) is bounded and inequality (22) implies that there exists \( t_1 \) such that

\[
\varphi_2(t) \leq \gamma_1 \sup_{s \leq t_1} \varphi_2(s)
\]

for all \( t \geq t_1 \) and some \( \gamma_1 \in (\gamma, 1) \). Denote \( \Phi_2 = \sup_{s \leq t_1} \varphi_2(s) \). (22) implies also that there exists \( t_2 \geq t_1 \) such that \( \varphi_2(t) \leq \gamma_1 \sup_{s \leq t_2} \varphi_2(s) \) for all \( t \geq t_2 \). But we
Proof. Applying (9) we can estimate
\[ \varphi_2(t) \leq \int_0^{t-t_n} \beta(x)e^{-\int_0^x \mu(s)ds} \varphi_2(t-x)dx + \int_{t-t_n}^{t} \beta(x)e^{-\int_0^x \mu(s)ds} \varphi_2(t-x)dx + \sup_{s \geq t} \beta(s)\|v_2\|_{L^1}. \]

Hence
\[ \varphi_2(t) \leq \gamma_1^n \Phi_2 \int_0^{t-t_n} \beta(x)e^{-\int_0^x \mu(s)ds} dx + \Phi_2 \int_{t-t_n}^{t} \beta(x)e^{-\int_0^x \mu(s)ds} dx + \sup_{s \geq t} \beta(s)\|v_2\|_{L^1}. \]

The desired conclusion follows from the three obvious facts
\[ \int_0^{t-t_n} \beta(x)e^{-\int_0^x \mu(s)ds} dx \leq \int_0^\infty \beta(x)e^{-\int_0^x \mu(s)ds} dx = \gamma < \gamma_1, \]
\[ \lim_{t \to \infty} \int_{t-t_n}^{t} \beta(x)e^{-\int_0^x \mu(s)ds} dx = 0, \]
\[ \lim_{t \to \infty} \sup_{s \geq t} \beta(s)\|v_2\|_{L^1} = 0. \]

Fix \( \varepsilon > 0 \). Since \( \gamma_1 < 1 \) there exists \( n \), not dependent on \( t \), such that
\[ \gamma_1^{n+1} \Phi_2 < \frac{\varepsilon}{3}. \]

It follows that for \( n \) we have
\[ \gamma_1^n \Phi_2 \int_0^{t-t_n} \beta(x)e^{-\int_0^x \mu(s)ds} dx < \frac{\varepsilon}{3} \]
and there exists such \( t_0 > 0 \) that for any \( t > t_0 \)
\[ \int_{t-t_n}^{t} \beta(x)e^{-\int_0^x \mu(s)ds} dx < \frac{\varepsilon}{3} \]
and
\[ \sup_{s \geq t} \beta(s)\|v_2\|_{L^1} < \frac{\varepsilon}{3}. \]

In consequence
\[ \varphi_2(t) < \varepsilon, \]
from which the convergence \( \varphi_2(t) \to 0 \) follows. To complete the proof it is easy to notice that for \( t > x \)
\[ u_2(t, x) \leq \varphi_2(t). \]

\[ \square \]

**Corollary 3.** The condition \( \lim_{t \to \infty} \|u_2(t, \cdot)\|_{L^1} = 0 \) holds under assumptions (18)–(20).

**Proof.** Applying (9) we can estimate
\[ \|u_2(t, \cdot)\|_{L^1} \leq \int_0^t e^{-\int_0^x \mu(s)ds} \varphi_2(t-x)dx + \int_t^\infty e^{-\int_0^x \mu(s)ds} \varphi_2(x-t)dx = J_1 + J_2. \]
For some $t_0$ we get
\[ J_1 = \int_0^t e^{-\int_0^t \mu(s)ds} \varphi_2(t-x)dx = \int_0^{t_0} e^{-\int_0^t \mu(s)ds} \varphi_2(t-x)dx + \int_{t_0}^t e^{-\int_0^t \mu(s)ds} \varphi_2(t-x)dx = J_{11} + J_{12}. \]

Clearly,
\[ J_{11} \leq M \varphi_2(t-t_0), \quad J_{12} \leq \Phi_2 \int_0^\infty e^{-\int_0^t \mu(s)ds} dx, \quad J_2 \leq M(t)\|v_2\|_{L^1}. \]

To complete the proof it is sufficient to notice that for arbitrary $\varepsilon > 0$ we can fix $t_0$ such that $J_{12} < \frac{\varepsilon}{3}$. Thus, for sufficiently large $t$ also $J_{11} < \frac{\varepsilon}{3}$ and $J_2 < \frac{\varepsilon}{3}$.

**Theorem 6.2.** Let $\Lambda(x) = \sup_{x \geq 0} e^{-\int_s^x \lambda(s)ds}$. Assume that $\int_0^\infty \Lambda(x)dx = \Lambda < \infty$ and system (1)-(5) fulfills conditions (18)-(20). Then trivial stationary solution of system (1)-(5) is asymptotically stable in $L^1(0, \infty)$.

**Proof.** Combining (8) and (10) yields
\[ R(t, x) \leq \int_0^t \alpha(x, y) \varphi_1(t-y) e^{-\int_0^y \lambda(s)ds} dy + \bar{\alpha}\|v_1\|_{L^1} \Lambda(t), \]

where $\bar{\alpha} = \|\alpha\|_{L^\infty}$. We have
\[ \varphi_1(t) = k \int_0^\infty R(t, x) u_2(t, x) dx, \]

then
\[ \varphi_1(t) \leq k \sup_x R(t, x) \|u_2(t, \cdot)\|_{L^1} \leq k \int_0^t \bar{\alpha} \varphi_1(t-y) e^{-\int_0^y \lambda(s)ds} \|u_2(t, \cdot)\|_{L^1} dy + k\bar{\alpha}\|v_1\|_{L^1} \Lambda(t) \|u_2(t, \cdot)\|_{L^1}. \]

By Corollary 3, there exists $\eta$ such that
\[ k\bar{\alpha} \Lambda \|u_2(t, \cdot)\|_{L^1} \leq \eta < 1 \]

for $t$ large enough. Therefore
\[ \varphi_1(t+h) \leq k \int_0^h \bar{\alpha} \varphi_1(t+h-y) \Lambda(y) \|u_2(t+h, \cdot)\|_{L^1} dy \]
\[ + k \int_h^{t+h} \bar{\alpha} \varphi_1(t+h-y) \Lambda(y) \|u_2(t+h, \cdot)\|_{L^1} dy + k\bar{\alpha}\|v_1\|_{L^1} \Lambda(t+h) \|u_2(t+h, \cdot)\|_{L^1} = I_1 + I_2 + I_3. \]

Clearly,
\[ I_1 \leq k\bar{\alpha} \|u_2(t+h, \cdot)\|_{L^1} \sup_{s \leq t} \varphi_1(s) \int_t^{t+h} \Lambda(t+h-y) dy \]

and
\[ I_2 \leq \eta \sup_{s \leq t} \varphi_1(s). \]

Let $\varepsilon = \frac{1}{3}(1 - \eta)$. There exist $t_0$ and $h > 0$ such that $I_1 < \varepsilon$ and $I_3 < \varepsilon$ for any $t > t_0$. In consequence
\[ \varphi_1(t+h) \leq \gamma \sup_{s \leq t} \varphi_1(s) + 2\varepsilon. \]
Repeating the reasoning from the proof of Lemma 6.1, if $\varphi_1$ was not bounded then, for any $t_1$ there would exist $t$ and $h$ such that $t > t_1$ and

$$\varphi_1(t + h) \geq \sup_{s \leq t} \varphi_1(s).$$

This contradicts inequality (23). Therefore $\varphi_1$ is bounded. Denote $\Phi_1 = \sup_{s \geq t} \varphi_1(s)$. To complete the proof it is sufficient to notice that $\varphi_1(t) \leq k\Phi_1\bar{\alpha}\Lambda\|u_2(t, \cdot)\|_{L^1} + k\bar{\alpha}\|v_1\|_{L^1}\Lambda(t)\|u_2(t, \cdot)\|_{L^1}$

and

$$\|u_1(t, \cdot)\|_{L^1} \leq \int_0^t e^{-\int_0^s \lambda(s)ds} \varphi_1(t - x)dx + \int_t^\infty e^{-\int_0^s \lambda(x-s)ds} v_1(x-t)dx.$$

7. **Summary.** In the paper we have presented the necessary and sufficient condition for the existence of positive stationary solution of the age-dependent predator-prey model. If the non-trivial stationary solutions of the model do not exist then its trivial solution is asymptotically stable under some assumptions which have justifiable biological interpretation. For example, assumption (18) has such obvious ecological justification. On account of biological interpretation we can assume that $\mu$ is an increasing function (the mortality of preys increase with their age) and $\mu \geq \bar{\mu}$, where $\bar{\mu}$ is some constant. Then $M(t) = \sup_{s \geq 0} e^{-\int_0^s \lambda(s)ds} \varphi_1(t-x)dx \leq e^{-\bar{\mu}t}$. Hence we get the convergence of the integral $\int_0^\infty M(t)dt$. Analogously we can consider the mortality of predators $\lambda$ and the convergence of $\int_0^\infty \Lambda(t)dt$. Assumption (20) reflects a diminishing decrease of reproductiveness of preys depending on their age. Theorem 6.2 determines the conditions of stability for stationary solutions which means the factors conditioning the dying out of small populations of both predators and preys. The crucial assumption which guarantees the extinction of both populations is (19). Additionally, we can notice that inequality (19) indicates the lack of influence of predators’ presence on asymptotical behaviour of population structure of preys. We can even say more, that apart from the situation when $\int_0^\infty \beta(x)e^{-\int_0^s \mu(s)ds}dx = 1$ the presence of the population of predators does not depend on the development of a population of preys. If we consider system (2)-(3) with $\alpha \equiv 0$ then its trivial solution will be the unique one. Inequality (19) is equivalent to asymptotic stability such reduced system.

We have not yet been able to settle the question about stability problem for non-trivial stationary solutions. We suppose that under some assumptions also these solutions are stable. Significant difficulty in proving this fact is non-linearity of the system, occurring in equations (2) and (4).

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