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On certain modification of age-dependent predator-prey model.

Abstract This work proposes a new model of coexistence of a predator population with a population of prey. In works [5] and [7] it is assumed that the number of prey aged x eaten by predators aged y is directly proportional to the number of prey aged x and the number of predators aged y. This paper presents a more general model. First of all, the dependency is functional, i.e. the chances of being eaten are affected by the structure of the whole population. In addition, this dependence is not bilinear because the predator, after satisfying its hunger, will give up the hunt for prey.

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1. Introduction The classical Lotka-Volterra model [15] is described by the system of differential equations

$$\begin{cases} \frac{dx}{dt} &= \alpha x - \beta xy \\ \frac{dy}{dt} &= k\beta xy - my \end{cases} \tag{1}$$

where x denotes the biomass of preys and y that of predators. This model assumes that each contact of a predator with its prey ends up with the predator eating the prey. In papers [1], [2], [4], [12], [14] the more general model is also assumed

$$\begin{cases} \frac{dx}{dt} &= f(x)\alpha x - g(x,y)x \\ \frac{dy}{dt} &= kg(x,y)x - mxy \end{cases} \tag{2}$$

where g is called the trophic function and denotes the number of prey eaten by one predator within a particular unit of time and f denotes the capacity of the area, i.e. the number of prey capable of fitting in the whole area in question. The model, which is called the Arditi–Ginzburg model, declines the assumptions that the only problem for prey is the predator and that each

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contact of the predator with its prey ends up with the predator eating the prey. In paper [2] there is an overview of various forms of the trophic function. In papers [5] and [7] an analogical model of (1) is presented in the case when the chance of eating the prey by the predator depends on the age of the predator and the age of the prey. This assumption, however, is somewhat simplifying. The predator will not necessarily choose to hunt the prey which happens to be encountered. Knowing that it can hunt down better prey to provide more food, or weaker one which can be hunted with less effort, the predator will not necessarily hunt any prey it encounters. Therefore, the dependence of the number of prey eaten on the structure of both populations in this model is not function-wise, but functional. Moreover, in order to develop the predator needs to eat a certain amount of prey. At some point, after having eaten enough prey, it will not hunt as actively as before. Hence, the assumed bilinearity of the functional describing the consumption of prey is also too limiting.

2. Age-dependent model

At first, let us recall the model from paper [5]. The two basic variables in the model are as follows:

- $u_1(t,x)$ 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 a natural death. We can express their mortality by classical McKendrick-von Foerster equation (see [10] and [13])

$$\frac{\partial u_1}{\partial t} + \frac{\partial u_1}{\partial x} = -\lambda(x)u_1(t,x). \tag{3}$$

Prey is either eaten by predators or dies a natural death. We assume that the parameter $\alpha(x,y)$ denotes the effectiveness of hunting during the contact of the prey aged x with the predator aged y. Then, the equation describing the mortality of the prey takes the following form

$$\frac{\partial u_2}{\partial t} + \frac{\partial u_2}{\partial x} = -\int_0^\infty \alpha(x,y)u_1(t,y)dy \cdot u_2(t,x) - \mu(x)u_2(t,x). \tag{4}$$

In paper [6] we present an analogical equation but without the natural mortality for prey. According to the classical Lotka-Volterra model we assume that food resources for prey are unlimited. The birth process of prey is described by means of the following renewal equation

$$u_2(t,0) = \int_0^\infty \beta(x)u_2(t,x)dx. \tag{5}$$

We assume that a predator gains energy needed for reproduction as a result of successful hunting. The coefficient k is the biomass conversion of the hunted prey. It denotes the energy derived from hunting used in the process of reproduction

$$u_1(t,0) = k\int_0^\infty\int_0^\infty \alpha(x,y)u_2(t,x)u_1(t,y)dxdy. \tag{6}$$

We are considering the system with the following initial conditions

$$u_1(0,x) = v_1(x), \quad u_2(0,x) = v_2(x). \tag{7}$$

In this paper we will consider the age-dependent analogue of the Rosenzweig-MacArthur model, i.e. the particular case of the Arditi-Ginzburg model, where the trophic function depends only on the population of prey.

3. Age-dependent Rosenzweig-MacArthur model In the classical Arditi-Ginzburg model function f characterizes the suppression of prey reproduction connected with the limited capacity of the environment. Therefore, it is a decreasing function which zeroes above value M characterizing the maximum number of prey that can fit in the environment. A classical example is the following function

$$f(x) = \max\{M - ax, 0\}.$$

In the age-dependent model $\gamma(x)$ will denote the biotope resources used by the prey aged x. Then, the resources used by the entire population of prey will be as follows

$$\int_0^\infty \gamma(x)u_2(t,x)dx.$$

Therefore, the biotope resources consumed within the unit of time cannot be exceeded. In accordance with the age-independent models, these resources will be marked as M. So, the renewal equation for prey (5) will take the following form

$$u_2(t,0) = f\left(\int_0^\infty \gamma(x)u_2(t,x)dx\right)\int_0^\infty \beta(x)u_2(t,x)dx \tag{8}$$

where f is the function analogous to that used in the Arditi-Ginzburg model. Let us now consider what the trophic function may look like. Since it depends not only on the number of prey but also on their age structure, it will not be a function, but a functional. Function α must be replaced by a certain functional. Let

$$A(v_1, v_2)(x)$$

denote the number of prey aged x eaten by all the predators within the given age structure of predators and prey. Clearly, in the model considered in [5], [7], [8] the functional takes the following form

$$A(v_1, v_2)(x) = \int_0^\infty \alpha(x,y)v_1(y)dy \cdot v_2(x).$$

Of course, it is natural to assume that

$$A(v_1, v_2)(x) \le \int_0^\infty \alpha(x,y)v_1(y)dy \cdot v_2(x) \tag{9}$$

for a certain function α, and that functional A is increasing with respect to both variables. Let ρ denote the nutritional values of meat of the prey aged x. In this situation equation (4) takes the following form

$$\frac{\partial u_2}{\partial t} + \frac{\partial u_2}{\partial x} = -A(u_1(t,\cdot), u_2(t,\cdot))(x) - \mu(x)u_2(t,x). \tag{10}$$

Similarly, equation (6) obtains the following form

$$u_1(t,0) = \int_0^\infty \rho(x)A(u_1(t,\cdot), u_2(t,\cdot))(x)dx. \tag{11}$$

Thus, our system of equations takes the following form

$$\begin{cases} \frac{\partial u_1}{\partial t} + \frac{\partial u_1}{\partial x} & = & -\lambda(x)u_1(t,x) \\ \frac{\partial u_2}{\partial t} + \frac{\partial u_2}{\partial x} & = & -A(u_1(t,\cdot), u_2(t,\cdot))(x) - \mu(x)u_2(t,x) \\ u_1(t,0) & = & \int_0^\infty \rho(x)A(u_1(t,\cdot), u_2(t,\cdot))(x)dx \\ u_2(t,0) & = & f\left(\int_0^\infty \gamma(x)u_2(t,x)dx\right)\int_0^\infty \beta(x)u_2(t,x)dx. \end{cases} \tag{12}$$

4. Solutions The structure of the solution to system (12) is a natural modification of the structure described in [5], [8], where v_1, v_2 are the continuous non-negative and integrable functions $[0,\infty) \to \mathbb{R}$ satisfying the conditions

$$v_1(0) = \int_0^\infty \rho(x)A(v_1, v_2)(x)dx,$$

$$v_2(0) = f\left(\int_0^\infty \gamma(x)v_2(x)dx\right)\int_0^\infty \beta(x)v_2(x)dx.$$

For $T > 0$ let $\varphi = (\varphi_1, \varphi_2) : [0,T] \to \mathbb{R}^2$ is a continuous function satisfying the conditions

$$\varphi_1(0) = v_1(0), \quad \varphi_2(0) = v_2(0). \tag{13}$$

At first we consider an auxiliary problem, that is equations $(12)_1$, $(12)_2$ with conditions (7), (13) and

$$u_1(t,0) = \varphi_1(t), \;\; u_2(t,0) = \varphi_2(t). \tag{14}$$

The solution to the problem can be expressed in the form (see [6] or [8])

$$u_1(t,x) = \begin{cases} \varphi_1(t-x)e^{-\int_0^x \lambda(s)ds} & \text{for} \quad x \le t \\ v_1(x-t)e^{-\int_0^t \lambda(x-s)ds} & \text{for} \quad x > t. \end{cases} \tag{15}$$

Until then, the model does not differ from the one in [5], [7], [8]. However, a different procedure has to be applied in order to determine the formula for u_2. Let us consider the function

$$\psi : [0,T] \times [0,\infty) \to \mathbb{R}$$

and define

$$u_2(t,x) = \begin{cases} \varphi_2(t-x)e^{-\int_0^x \mu(s)ds} + \int_0^t e^{-\int_s^x \mu(x-\tau)d\tau}\psi(s, s+t-x)ds \\ \qquad\qquad\qquad\qquad\qquad\qquad \text{for } x \le t \\ v_2(x-t)e^{-\int_0^t \mu(x-s)ds} + \int_0^t e^{-\int_0^{t-s} \mu(x-\tau)d\tau}\psi(s, s+x-t)ds \\ \qquad\qquad\qquad\qquad\qquad\qquad \text{for } x > t. \end{cases} \tag{16}$$

Formulas (15) and (16) result naturally from the fact that equations (12) along the characteristics are ordinary differential equations, and the characteristics are straight lines parallel to the straight line $x = t$ (see [9], [11]). Let us now define space $\mathcal{X}$ by the following formula

$$\mathcal{X} = \left\{ \psi \in C([0,T],[0,\infty)) : \psi(t,\cdot) \in L^1([0,\infty)), \lim_{x\to\infty} \psi(t,x) = 0 \right\}.$$

Having defined u_1 and u_2, we can determine the operator

$$\mathfrak{A} : \mathcal{X} \to \mathcal{X}$$

by means of the following formula

$$(\mathfrak{A}\psi)(t,x) = A(u_1(t,\cdot), u_2(t,\cdot))(x)$$

where u_1 and u_2 are defined by formulas (15) and (16). We now need to define the functional space in which operator $\mathfrak{A}$ will have the fixed-point property and let ψ_0 be the fixed point. Now let u_1 be defined by formula (15) and $\hat{u}_2$ - by formula (16) after substituting ψ with ψ_0. Further procedure is a copy of the procedure described in [5], [7], [8].

Let us define 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

$$\|\varphi\| = \sup_{t\in[0,T]} (|\varphi_1(t)| + |\varphi_2(t)|) \tag{17}$$

by means of the following formulas

$$\begin{aligned} (\Theta\varphi)_1(t) &= \int_0^\infty \rho(x)A(u_1(t,\cdot), \hat{u}_2(t,\cdot))(x)dx, \\ (\Theta\varphi)_2(t) &= f\left(\int_0^\infty \gamma(x)\hat{u}_2(t,x)dx\right) \int_0^\infty \beta(x)\hat{u}_2(t,x)dx. \end{aligned}$$

Now we will consider the solution to system (12) with initial conditions (7) for $t \in [0,T]$.

DEFINITION 4.1 By the solution to (12) with initial conditions (7) we consider the function $u = (u_1, u_2) \in L^1([0,T] \times \mathbb{R}_+, \mathbb{R}^2) \cap C([0,T] \times \mathbb{R}_+, \mathbb{R}^2)$ defined by (15) and (16), when the function φ is a fixed-point of the operator Θ i.e. $\Theta\varphi = \varphi$.

REMARK 4.2 The classical solution to (12) with initial conditions (7) is the solution in the sense of Definition 4.1. Moreover, function u differentiable in $[0,T] \times \mathbb{R}_+$ which is the solution to (12) in the sense of Definition 4.1 is also the classical solution.

By the technique analogous to that of [8] the following theorem can be proved

THEOREM 4.3 *Let $\beta, \lambda, \rho \geq 0$. We assume also that $\beta \in L^\infty(0,\infty)$. Let $A : (L^1([0,\infty)))^2 \to L^1([0,\infty))$ satisfy condition (9) and satisfy a Lipschitz condition with respect to the second variable. Then, system (12) with initial conditions (7) has exactly one non-negative solution on set $[0,\infty) \times [0,\infty)$.*

PROOF In the first instance we can notice that if we define $\bar{u}_2$ replacing ψ by $\bar{\psi}$ in formula (16), we will get the following estimate

$$|u_2(t,x) - \bar{u}_2(t,x)| \leq \int_0^t |\psi(s, s+|t-x|) - \bar{\psi}(s, s+|t-x|)|ds.$$

For further considerations we will use a slightly modified Bielecki method [3]. On the space $\mathcal{X}$ we will define a norm with the help of the following formula

$$\|\psi\| = \sup_{t\in[0,T]} e^{-\gamma t}\|\psi(t,\cdot)\|_{L^1}$$

where a proper constant γ will be chosen. Therefore,

$$\|u_2(t,\cdot) - \bar{u}_2(t,\cdot)\| \leq \int_0^t \|\psi - \bar{\psi}\|ds = \frac{1}{\gamma}(1 - e^{-\gamma t})\|\psi - \bar{\psi}\|.$$

Thus, it follows from the definition of $\mathfrak{A}$ and Lipschitz continuity of A that

$$\|\mathfrak{A}\psi - \mathfrak{A}\bar{\psi}\| \leq \frac{C}{\gamma}\|\psi - \bar{\psi}\|$$

where C is the Lipschitz constant for the operator A. Choosing $\gamma > C$ from the Banach fixed-point theorem, we can insert the fixed point in equation (16) in the place of ψ and continuing with reasoning as mentioned above, i.e. copying the procedures used in [5], [8], [7] we will get the conclusion. ■

5. Conclusions It turns out that the age-dependent model can be considered with the non-linear trophic function. Interestingly, the proof method does not require the use of a new mathematical apparatus, it only requires a more subtle use of the existing one. What is particularly encouraging is a bit wider look at the Bielecki method, which may be useful in others applications.

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Pewna modyfikacja modelu drapieżca-ofiara zależnego od wieku

Antoni Leon Dawidowicz i Anna Poskrobko

Streszczenie Praca niniejsza proponuje nowy model koegzystencji populacji drapieżcy z populacją ofiar. W pracach [5] i [7] założono, że liczba ofiar w wieku x zjadanych przez drapieżcę w wieku y jest wprost proporcjonalna do liczby ofiar w wieku x i do liczby drapieżców w wieku y. W niniejszej pracy zaprezentowany jest ogólniejszy model. Przede wszystkim zależność jest funkcjonalna, czyli na szanse zjedzenia ma wpływ struktura całej populacji. Poza tym zależność ta nie jest dwuliniowa, gdyż drapieżca po zaspokojeniu głodu zrezygnuje z polowania na ofiary.

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[a]The database maintained by European Mathematical Society, FIZ Karlsruhe, and the Heidelberg Academy of Sciences. Former Zentralblatt für Mathematik

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