

Article

About a modification of Rogers model of parasite-host system dynamics

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Received 17 August 2011; Accepted 20 September 2011; Published online 5 March 2012

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Abstract

In current publication there is the consideration of mathematical model of parasite-host system dynamics for the populations with non-overlapping generations. Within the framework of considering model it is assumed that appearance of individuals of new generation correlates with the death of individuals of the previous one. It is also assumed that between time moments of appearance of individuals of new generations there are the monotonous and independent decreasing of population sizes of interacting species in a result of influence of self-regulative mechanisms and natural death. All survived individuals of the host produce the eggs synchronically, and part of these eggs is attacked by parasites. In model it is assumed that the time for the appearance of hosts and parasites from the eggs is much less than the length of time interval between closed generations. It allows describing of the process of appearance of new generations as “jumps” in changing of population’s sizes. For considering model the dynamic regimes of interacting populations are analyzed for various values of model parameters and various assumptions about mechanism of interaction of species. In particular, there is the determination of conditions for parameters when the regimes of population outbreaks are observed in model.

Key words parasite-host system dynamics; mathematical model; outbreak regimes.

1 Introduction

Big number of publications are devoted to analyses of parasite – host system dynamics (see, for example, Kolmogoroff, 1936; Bailey, 1970; Bazykin, 1985; Odum, 1975; Maynard Smith, 1974; Kostitzin, 1937; Lotka, 1920, 1925; Volterra, 1931; Nedorezov, 1986, and others). In most cases when description of interaction process of both species is presented in rather universal form (for example, as it is realized in Lotka – Volterra model of predator – prey system dynamics; Lotka, 1920, 1925; Volterra, 1931), there are no possibilities to separate predator – prey system and parasite – host system. Moreover, in various situations it is impossible to separate predator – prey system and resource – consumer system: In both cases we observe the process of interaction of species which belong to various trophic levels. And one of interacting species has negative results of this interaction, and another one has positive results.

At the same time, it is easy to point out some population effects which underline qualitative differences for these ecological systems. For example, in natural conditions we can observe increasing or decreasing of food flow into the system in the process of interaction of insects with food plants (Isaev et al., 1984, 2001, 2009).

This effect is realized within the framework of resource – consumer system (with positive feedback it is observed for *Xylotrehus altaicus* Gebl. and *Monogamus urussovi* Fisch.; Isaev et al., 2009), but its realization within the framework of predator – prey system looks rather strange and doubtful.

If interaction of species in predator – prey system has a continuous nature, at the same time the process of interaction of species in parasite – host system may have a discrete nature. For example, we can observe discrete process in interaction of parasites and hosts in the situations, when parasites attack host's eggs and host's pupae, and appearance of new generations of hosts has a synchronic nature. In such situations the process of interaction of both species is determined by the sojourn time of hosts in the respective individual's phase (egg or pupa). For many species the length of time interval of staying in one or other phase is much less than life time of individuals. This allows modeling of process of interaction between species as jumps of trajectories of population sizes changing in time.

In current publication we analyze the situation when independent development of interacting populations is described by the Verhulst' equation (Verhulst, 1838), and the probability of host to be attacked by parasite corresponds to Roger's expression (Sharov, 1986).

2 Model

Let $x(t)$ be the population size of hosts at time t , and $y(t)$ be the population size of parasites at the same time. Like in other continuous – discrete models of population dynamics (Kostitzin, 1937; Poulsen, 1979; Aagard-Hansen, Yeo, 1984; Nedorezov, 1986; Nedorezov, Nedorezova, 1995; Nedorezov, Utyupin, 2011; and others) we shall assume that there exists the set of fixed time moments $\{t_k\}$, $t_{k+1} - t_k = h = const > 0$, $k = 0, 1, 2, \dots$, of appearance of individuals of new generations of both populations. We shall also assume that between these time moments population sizes decrease monotonously. Decreasing of population size is determined by the process of natural death of individuals, and by the process of influence of self-regulative mechanisms (Verhulst, 1838):

$$\begin{aligned} \frac{dx}{dt} &= -\alpha_1 x - \beta_1 x^2, \\ \frac{dy}{dt} &= -\alpha_2 y - \beta_2 y^2. \end{aligned} \quad (1)$$

In (1) coefficients α_j , $j = 1, 2$, are the intensities of natural death rates in populations, and β_j , $j = 1, 2$, are the coefficients of self-regulation, $\alpha_j, \beta_j > 0$.

Let us note, that in (1) it is assumed that there is no interaction between species on the time intervals $[t_k, t_{k+1})$. Interaction of considering populations is concentrated in time moments t_k . It is also mean that within the framework of model it is assumed that the process of eggs production is realized synchronically by all hosts, during short time period these eggs can be attacked by parasites, and appearance of individuals of new generations is realized synchronically too. And the length of time interval when we can observe all these marked processes, is much less than life time of individuals h . This assumption allows us to describe the process of changing of population sizes as “jump” of model trajectory at fixed time moments t_k .

Let $x(t_{k+1} - 0)$ and $y(t_{k+1} - 0)$ be the sizes of populations before “jumps” of trajectories (numbers of survived individuals to moment t_{k+1}). Thus solution of system (1) can be presented in the following form:

$$x(t_{k+1} - 0) = \frac{x_k}{a_1 + b_1 x_k}, \quad y(t_{k+1} - 0) = \frac{y_k}{a_2 + b_2 y_k}. \quad (2)$$

In (2) $x_k = x(t_k)$ and $y_k = y(t_k)$ are the initial values of population sizes at moment t_k , and positive parameters have the forms:

$$a_i = \exp(\alpha_i h), \quad b_i = \frac{\beta_i}{\alpha_i} (\exp(\alpha_i h) - 1), \quad i = 1, 2.$$

Let x_{k+1} and y_{k+1} be the population sizes after the birth process, Q be the function which is equal to quota of hosts which were not attacked by parasites (respectively, $1 - Q$ is a quota of attacked hosts), and R be a coefficient of productivity of hosts. Below we shall assume that $R = const > 0$. But in general case this function may depend on average host population size (Nedorezov, Nedorezova, 1995; Nedorezov, Utyupin, 2011; Tonnang et al., 2009). Thus we have the following relation for changing of host population size at fixed time moments:

$$x_{k+1} = Rx(t_{k+1} - 0)Q. \quad (3)$$

In (3) product $Rx(t_{k+1} - 0)$ is equal to number of eggs which were produced by survived hosts. Denote as c , $0 < c < 1$, $c = const$, the quota of new parasites which appear from all parasitized host's eggs. Thus we have the following equation for parasite population size changing at fixed time moments:

$$y_{k+1} = Rx(t_{k+1} - 0)(1 - Q). \quad (4)$$

Taking into account expressions (2) equations (3) and (4) can be presented as follows:

$$x_{k+1} = \frac{Rx_k}{a_1 + b_1 x_k} Q = F(x_k, y_k), \quad y_{k+1} = \frac{cRx_k}{a_1 + b_1 x_k} (1 - Q) = G(x_k, y_k). \quad (5)$$

Function Q must depend on two arguments. First of all, it depends on number of produced eggs, i.e. it depends on product $Rx(t_{k+1} - 0)$. The second, function Q depends on the number of parasites survived to moment t_{k+1} : $y(t_{k+1} - 0)$. It is obvious if number of survived parasites is equal to zero function Q is equal to one. For every fixed value of number of parasites increase of number of hosts leads to increase of value of function Q . For every fixed value of number of hosts increase of number of parasites leads to decrease of value of function Q . Thus, we have the following conditions for function Q :

$$0 \leq Q(x, y) \leq 1, \quad Q(x, 0) = 1, \quad Q(x, y) \xrightarrow{x \rightarrow \infty} 1, \quad Q(x, y) \xrightarrow{y \rightarrow \infty} 0,$$

$$\frac{\partial Q}{\partial x} > 0, \quad \frac{\partial Q}{\partial y} < 0. \quad (6)$$

In particular case function Q can be presented in the form:

$$Q(x, y) = \exp\left(-\frac{\gamma T}{1 + \gamma x T_h}\right).$$

It is obvious that all conditions (6) are satisfied. This function is used in Roger's model of parasite – host system dynamics (Sharov, 1986). Parameter γ is normally interpreted as characteristics of effectiveness of search process of victims by parasites. Parameter T is equal to the length of life time of parasite. Parameter T_h is equal to the length of time interval of interaction of parasite with one host. Below we use this function for numerical calculations.

3 Some Properties of Model (5)

(1) If coefficient of self-regulation β_1 in population of hosts is greater than zero, $\beta_1 > 0$, then sizes of both populations are limited for all finite initial values. There exists a stable invariant compact Δ which contains the origin, and trajectories of system (5) cannot intersect boundaries of this compact if initial values belong to $\text{int } \Delta$, $(x_0, y_0) \in \text{int } \Delta$.

From the first equation of the system (5) we have the following relation:

$$x_{k+1} \leq \frac{Rx_k}{a_1 + b_1x_k} < \frac{R}{b_1}.$$

The second equation gives us the following inequality:

$$y_{k+1} \leq \frac{cRx_k}{a_1 + b_1x_k} < \frac{cR^2}{a_1b_1 + b_1R}.$$

Thus, compact Δ has the following form:

$$\Delta = \left[0, \frac{R}{b_1} \right] \times \left[0, \frac{cR^2}{a_1b_1 + b_1R} \right].$$

Note, that limits of compact Δ don't depend on the value of parameter b_2 . It means that population sizes will be bounded even in a case when parasites have no intra-population self-regulative mechanisms. Additionally, it is possible to point out stable invariant compact δ : $\delta \subset \Delta$.

(2) For all values of model parameters the origin is stationary state of the system (5). If initial host population size is equal to zero, $x_0 = 0$, then trajectory of system comes into origin after one time step. Thus, axis y is incoming into origin integral trajectory.

If initial value of parasites is equal to zero, $y_0 = 0$, then host dynamics describes by the well-known Kostitzin' model (Kostitzin, 1937):

$$x_{k+1} = \frac{Rx_k}{a_1 + b_1x_k}.$$

If in Kostitzin' model the following inequality $R < a_1$ is truthful, hosts eliminate for all initial value of population size. Respectively, if this condition is realized for parameters of model (5), the origin is global stable state of the system: Both populations extinct for all possible values of population sizes.

If the inverse inequality is truthful, $R > a_1$, then stationary state $((R - a_1)/b_1, 0)$ on the axis x is observed. If initial value of parasites is equal to zero, $y_0 = 0$, then number of hosts will stabilize

asymptotically at this non-zero level $(R - a_1)/b_1$. In this case the origin is unstable stationary state, and at positive initial value of population hosts don't eliminate.

For the particular case when function Q can be presented in the following form:

$$Q(x, y) = Q\left(\frac{Ay}{1 + Bx}\right),$$

where $A, B = const > 0$ are any positive parameters (for example, such functions are observed in Hassell' model and Rogers' model of parasite – host system dynamics; Sharov, 1986; Hassell, 1984), conditions of stability of the stationary state on the axis x can be presented in the following manner. Taking into account that Jacobian matrix calculated in stationary point has the form

$$J\left(\frac{R - a_1}{b_1}, 0\right) = \begin{pmatrix} \frac{a_1}{R} & \frac{R - a_1}{b_1} \frac{\partial Q}{\partial y}(0) \\ 0 & -\frac{c(R - a_1)}{b_1} \frac{\partial Q}{\partial y}(0) \end{pmatrix}.$$

Thus, we have the following conditions for local stability of the stationary state $((R - a_1)/b_1, 0)$:

$$R > a_1, \left| \frac{\partial Q}{\partial y}(0) \right| < \frac{b_1}{c(R - a_1)}.$$

3. Let's consider the particular case when

$$Q(x, y) = \exp\left(-\frac{Ay}{1 + Bx}\right). \tag{7}$$

In (7) x is the number of survived hosts to the respective fixed time moment, y is the number of survived parasites to the same time moment. These amounts are determined by the expressions (2). So, we have

$$Q(x_k, y_k) = \exp\left(-\frac{Ay_k(a_1 + b_1x_k)}{(a_2 + b_2y_k)(a_1 + b_1x_k + Bx_k)}\right).$$

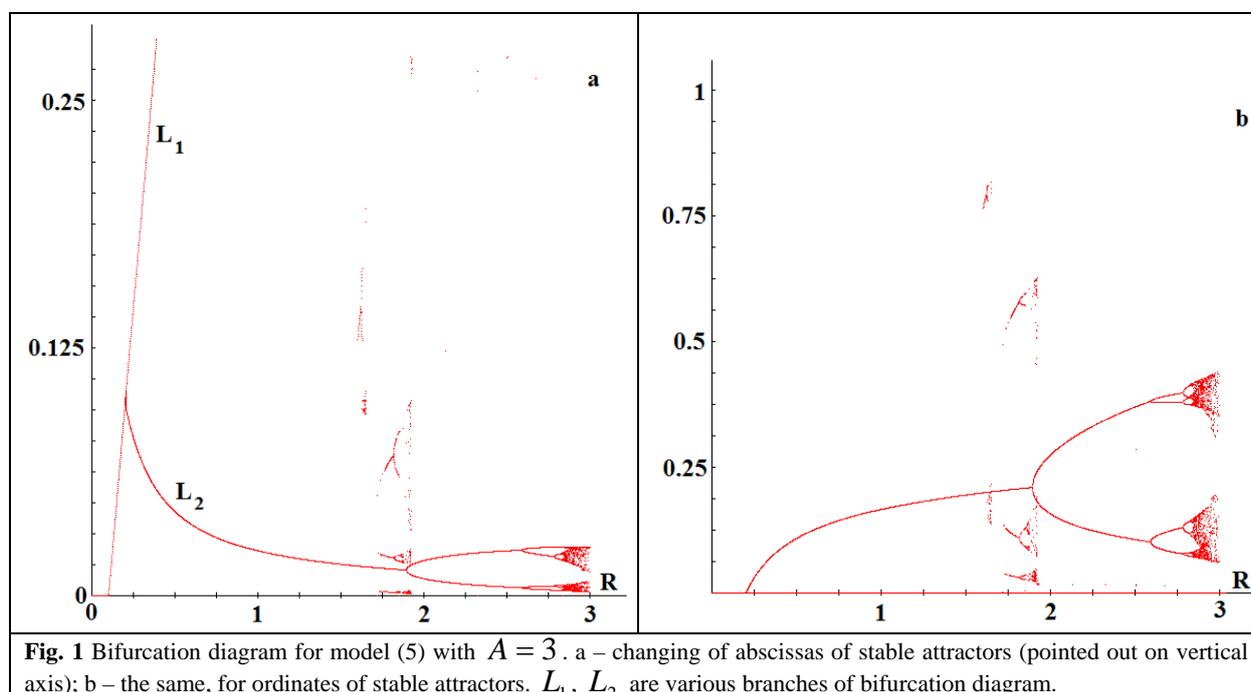
On Fig. 1 there is the bifurcation diagram for model (5) which was obtained for the following values of parameters: $a_1 = 0.1, b_1 = 1, a_2 = 0.2, b_2 = 0.001, A = 3, B = 1, c = 1$. Parameter R (host's productivity) changes from 0 to 4 (Fig. 1a) or to 3 (Fig. 1b).

Diagram (Fig. 1) was calculated under the following conditions. For every initial values of population sizes model had 10000 ("empty") steps for converging to stable dynamic regime. For every value of parameter R number of various initial values of population sizes was 400.

On Fig. 1a abscissa of stable stationary state $((R - a_1)/b_1, 0)$ is out of the picture. But for all values of considering parameters this point is a stable attractor. Respectively, on Fig. 1b part of axis R is of red color: Part of trajectories converges to this stable attractor.

As we can see on this diagram (Fig. 1), if R is small the origin is global stable state. Increase of the value of R leads to appearance of the point $((R - a_1)/b_1, 0)$ on axis x . On Fig 1a it corresponds to straight line L_1 which is determined by the equation

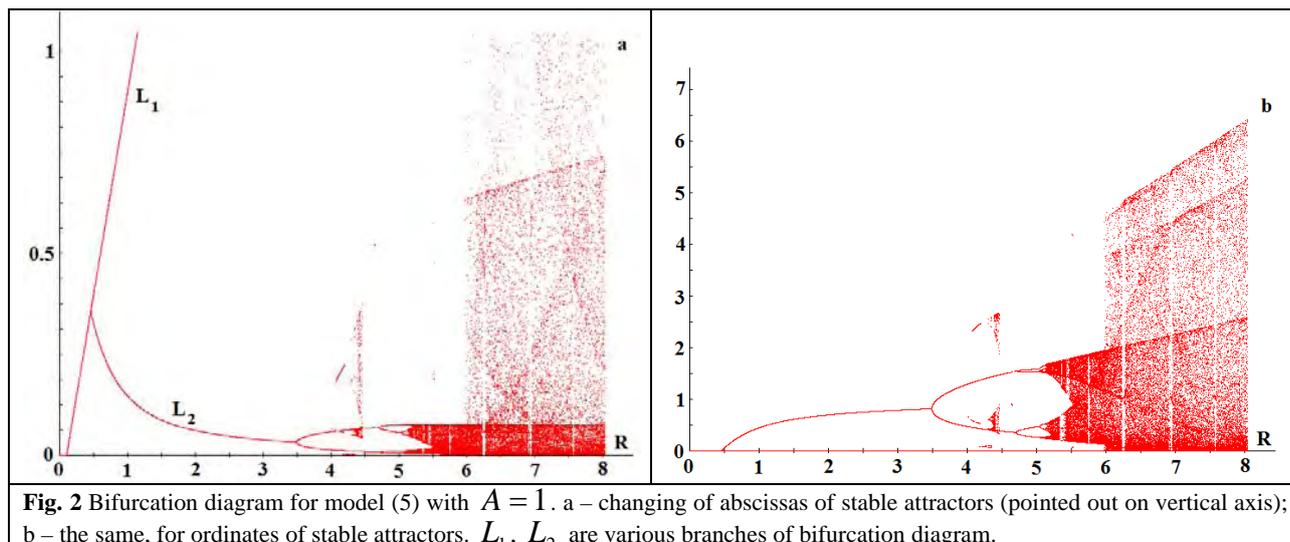
$$L_1 = \frac{R - a_1}{b_1}.$$



Initially this point is global stable attractor, and parasites eliminate for all possible initial values of populations. Next bifurcation correlates with appearance of new branch L_2 of diagram on Fig. 1a. On Fig. 1b it corresponds to monotonic increasing curve. It is obvious that in such a situation we have to have unstable attractor in phase space with separatrix curves which separate zones of attraction of two stable equilibria: non-trivial stationary state and $((R - a_1)/b_1, 0)$. Thus we have the dynamic regime (for $R \leq 1.5$) which contains two stable levels, and doesn't contain stable cycles (respectively, algebraic system $\{F(x, y) = 0, G(x, y) = 0\}$ has three roots at least). This regime was called as fixed outbreak in Isaev – Khlebopros classification (Isaev et al., 1984, 2001, 2009; Nedorezov, 1986, 1997), and it can be observed in natural conditions.

If $R \in [1.5, 2]$, we can observe complicated dynamical regimes which are out of any classifications of population dynamics. Algebraic system $\{F(x, y) = 0, G(x, y) = 0\}$ has at least five roots for non-negative values of variables.

If $R \geq 2$, we have a sequence of dynamic regimes which can be identified as analogs of the regime of fixed outbreak (with unstable non-trivial stationary state and existing stable periodic fluctuations of both populations). Further increasing of parameter R leads to realization of very interesting population effect: if $R \geq 3$ point $((R - a_1)/b_1, 0)$ becomes a global stable equilibrium again. The similar population effect is observed within the framework of modification of Beddington – Free – Lawton model of parasite – host system dynamics (Ivanchikov, Nedorezov, 2011).



The bifurcation diagram on Figure 2 was obtained for smaller value of parameter A : $A = 1$. All other parameters of the system have the same values like on Fig. 1 (and conditions for drawing these pictures are the same). This diagram shows that we have the regime of elimination of both populations; we may have the regime with global stable equilibrium on x axis ($(R - a_1)/b_1, 0$); we may have various modifications of fixed outbreak (Isaev et al., 1984, 2001, 2009; Nedorezov, 1986, 1997). But sometimes we may have the regime of fixed outbreak with additional third stable attractor (Fig. 2) which can be characterized by big enough variation of population sizes.

4 Conclusion

At the beginning analysis of mathematical model of the Kolmogorov' type of predator – prey system dynamics was in the base of Isaev – Khlebopros classification of forest insect population dynamics (Isaev et al., 1984, 2001, 2009; Nedorezov, 1986, 1997). Later analyses of some other models of the same type (for example, model of population – food plant system dynamics, model of competition of two species etc.; Nedorezov, 1989, 1995, 1999) allowed obtaining the similar results within the frameworks of these models. But all these models need in concrete modifications because ordinary differential equations don't allow taking into account some basic characteristics, which are typical for insect populations in boreal zone. First of all, we have to take into account that development of insect populations has a synchronic type. Appearance of new generations is realized during short time period which is much smaller than the life time of individuals. Note, that in models, which were constructed as systems of ordinary differential equations, appearance of new individuals has a continuous nature that doesn't correspond to reality.

Moreover, high level of aggregation in a description of interaction between species in such models doesn't allow giving a good answer on to the question about the nature of model which contains outbreak regimes: We have no chance to separate predator – prey and parasite – host systems. All these problems led to the necessity of further development of mathematical base for phenomenological theory of forest insect population dynamics (Isaev et al., 1984, 2001, 2009; Nedorezov, 1986, 1997). This publication is also devoted to the development of model base of pointed out ecological theory.

It is obvious that considered model hasn't high level of aggregation in a description of process of interaction between species like we have in models of the Kolmogorov's type. On the other hand, considered

model we cannot interpret as a model of predator – prey system dynamics. Additionally, in model we took into account the discrete nature of the process of appearance of new generations, which is more suitable for the description of insect population dynamics in boreal zone.

Analysis of properties of model showed that there is a rich set of dynamical regimes. Some of obtained regimes are well-known (fixed outbreak and various modifications of fixed outbreak). But some regimes are new and need in more detailed and deep analysis.

Acknowledgement

Publication was supported by the RFFI grant N 11-04-01295.

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