Article

About a modification of Beddington-Free-Lawton model of parasite-host system dynamics

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Abstract
Current publication is devoted to the construction of modification of well-known Beddington – Free – Lawton model of parasite – host system dynamics and its analysis. In basic model and in modified model there is one and the same assumption that under the determined values of sizes of interacting populations number of attacked hosts is determined by Poisson' law. In modified model it was took into account that hosts, which were attacked two or more times by parasites, die, and it doesn't lead to the increase of parasite population size. For modified model population dynamic regimes and structure of the space of model parameters are analyzed.

Keywords parasite–host system; discrete time model.

1 Introduction

Big number of publications are devoted to construction of models and analysis of population dynamics of predator – prey (or parasite – host) system (see, for example, Brauer and Castillo-Chavez, 2001; Kolmogoroff, 1936; Kostitzin, 1937; Turchin, 2003; Lotka, 1920, 1925; Volterra, 1931, and many others). All publications can be conditionally divided onto several groups. Part of articles are devoted to methodological problems, to analysis of possible variants of population size fluctuations at various types of interaction between populations and self-regulation etc. (see, for example, Berezovskaya et al., 2005; Csetenyi and Logofet, 1989; Logofet, 1993; May, 1974, 1975; May and Oster, 1976, and others). Other part of publications is devoted to the problem of comparison of theoretical (model) results with real datasets (Berryman, 1981, 1991, 1992, 1995; Tonnang et al., 2009, 2010; Varley et al., 1978; Golubev et al., 1980 and others). One more part of publications is devoted to the use of discrete time mathematical models as a base for various ecological theories (see, for example, Isaev and Girs, 1975; Isaev and Khlebopros, 1973, 1977; Isaev et al., 2009; Nedorezov and Utyupin, 2011).

It is important to note, that before the comparison of theoretical and empirical datasets (as before the use of one or other models as the base of various population theories) we have to be sure, that selected mathematical model corresponds to observed process. If model doesn't correspond to observed phenomenon a'priori, it can lead to unrealistic results (see, for example, Gilpin, 1973). Thus, solutions of methodological problems of modeling of population processes are of extreme interest and important stage in analysis of every concrete biological species.

In current publication we analyze one of possible modifications of well-known discrete time mathematical model of parasite – host system dynamics, which was first presented in article by Beddington et al. (1975). In this publication authors used the following approach for modifying of Nicholson – Bailey model (Nicholson and Bailey, 1935). Authors assumed that for the fixed values of hosts and parasitoids the quota of non-attacked hosts (which produce the next generation) is equal to the probability P of the event, that stochastic variable with Poisson distribution is equal to zero. Respectively, the quota of attacked hosts in population is equal to $1-P$. Note that similar ideas were used in some other models of parasite – host interaction (Rogers, 1972; Thompson, 1929). Authors assumed also that number of parasites of new generation is equal to the number of infected hosts multiplied by constant, which is less than one. It is obvious, because not every attacked host transforms into viable parasite of new generation.

One more assumption of authors of model (Beddington et al., 1975) is following: the quota of attacked hosts depends on number of parasites only. Obviously, in general case this quota must depend on the relation of numbers of interacting populations. In current publication we followed the first author’s assumption. But we have to note, that this assumption correlates with additional limits for the domain of applicability of the model to the description of interaction of species: model doesn’t work in the domain of phase space where number of hosts is much bigger than number of parasites (multiplied on the number of hosts which can be attacked by one parasite).

2 Description of Model

Let x_k be the number of hosts, y_k be the number of parasites at time moment k. Let’s assume that host population dynamics is described by the Moran – Ricker model (Moran, 1950; Ricker, 1954) when number of parasites is equal to zero:

$$x_{k+1} = Ax_k e^{-\alpha x_k}. \qquad (1)$$

Coefficient A is maximum birth rate of population, α is a coefficient of self-regulation. It is possible to point out a huge number of publications which are devoted to analysis of model (1) and its application to various species (see, for example, May, 1974, 1975; May and Oster, 1974; Tonnang et al., 2009, 2010; Nedorezov et al., 2008; Nedorezov and Sadykova, 2008, 2010). In particular, it was proved that cyclic regimes and chaos can be observed in model (1) under various values of model parameters.

Influence of parasites on host population dynamics can be taken into account by various ways. For example, for fixed values x_k and y_k the quota q of uninfected hosts (and these hosts can only produce the next generation) increases with decrease of number of parasites. If number of parasites is equal to zero the quota q is equal to one. With unlimited growth of parasites q converges to zero asymptotically. In particular case q can be presented in the following form:

$$q = e^{-\gamma y}. \qquad (2)$$

In expression (2) y is the number of parasites, coefficient γ, $\gamma = const > 0$, is efficiency of parasitism. Amount of this coefficient depends on various factors and conditions, and in particular, it depends on the type of parasite’s strategy in finding hosts. Expression (2) can be explained in other way. Namely, it is assumed a’priori that probability of every separated host to be infected by parasites is determined by Poisson law. Thus, expression (2) is the probability of event that one host will not be infected.

Taking into account expression (2) the equation (1) can be transformed into the form:

$$x_{k+1} = Ax_k e^{-\alpha x_k} e^{-\gamma y_k}. \qquad (3)$$

Respectively, we have that $1-q$ is the probability of event that every host will be attacked by parasite or parasites. If we assume that every attacked host can potentially produce one viable parasite, we have the following equation for changing of number of parasites in time:

$$y_{k+1} = Abx_k e^{-\alpha x_k}(1-e^{-\gamma y_k}) . \qquad (4)$$

Non-negative coefficient b, $b = const < 1$, allows to take into account in the model the event that not every attacked host transforms into viable parasite. Part of individuals can die in a result of impacts of various stochastic factors, part of individuals can die in a result of effect of over-infection etc. Thus, combination of equations (3) and (4) gives us Beddington – Free – Lawton model of parasite – host system dynamics (Beddington et al., 1975).

It is important to note that for various natural populations (for example, for insects; Isaev et al., 2009; Nedorezov, 1986) model (3)-(4) gives unrealistic description of interaction between two species. The point is that hosts, which were attacked two or more times, die without increase of number of parasites (over-infection effect). This effect realizes in all situations when host's body doesn't contain enough food for normal development of two or more parasite's larvae.

Let's consider the following modification of model (3)-(4) when successive development of parasite's larva is possible if and only if host was attacked one time only. Within the limits of assumptions, which were used for the construction of Beddington – Free – Lawton model, the probability that host was attacked by one parasite only is determined by the expression:

$$q_1 = \gamma y e^{-\gamma y} .$$

Taking it into account, we have the following equation for parasites dynamics:

$$y_{k+1} = Ab\gamma x_k y_k e^{-\alpha x_k} e^{-\gamma y_k} . \qquad (5)$$

Combination of equations (3) and (5) gives us modified Beddington – Free – Lawton model with over-infection effect.

3 Properties of Model

With linear transformation of variables considering model can be presented in following form (without loosing a generality of analysis we can assume that $\alpha = 1$ and $\gamma = 1$):

$$x_{k+1} = Ax_k e^{-y_k - x_k} , \; y_{k+1} = Cx_k y_k e^{-x_k - y_k} . \qquad (6)$$

It is obvious that $A, C = const > 0$ and $C < A$. Initial values of population sizes must be non-negative, $x_0, y_0 \geq 0$. Model (6) has the following properties:

1. If $x_0 = 0$ and $y_0 > 0$ then $x_k \equiv 0$, $y_k \equiv 0$ for all $k > 0$. If $x_0 > 0$ and $y_0 = 0$ then $y_k \equiv 0$ for all $k > 0$; in this case host dynamics describes by the Moran – Ricker model (Moran, 1950; Ricker, 1954).

2. Stable invariant compact Δ exists in R_+^2:

$$\Delta \subset R_+^2 = \{(x, y) : x \geq 0, y \geq 0\} .$$

If $(x_0, y_0) \in \Delta$ then for all $k > 0$ $(x_k, y_k) \in \Delta$. If $(x_0, y_0) \notin \Delta$ then trajectory of model (6) converges to Δ asymptotically:

$$\Delta = \left[Ae^{-1}, Ce^{-2}\right].$$

3. Stationary state $(0,0)$ is complex equilibrium. If $A < 1$ this point is global stable equilibrium. In this case we have a regime of non-conditional extinction of both interacting populations. Intersection of bifurcation line $A = 1$ at $A > 1$ equilibrium $(0,0)$ is a saddle type point with characteristic values $\lambda_1 = A$ and $\lambda_2 = 0$. It also leads to appearance of stationary state $(\ln A, 0)$. On Fig. 1 domain of stability of stationary state $(0,0)$ is marked by yellow color.

4. Jacoby matrix determined in point $(\ln A, 0)$ is following:

$$J(\ln A, 0) = \begin{pmatrix} 1 - \ln A & -\ln A \\ 0 & \dfrac{C \ln A}{A} \end{pmatrix}.$$

Thus, characteristic numbers are following:

$$\lambda_1 = 1 - \ln A, \; \lambda_2 = \frac{C \ln A}{A}.$$

Consequently, if the following inequalities are truthful the stationary state $(\ln A, 0)$ is global stable equilibrium:

$$1 < A < e^2, \; C < \frac{A}{\ln A}, \tag{7}$$

On Fig. 1 domain of stability of this stationary state is marked by red color. Bifurcation curve 1 on Fig. 1 is determined by the equation:

$$C = \frac{A}{\ln A}. \tag{8}$$

If first inequality in (7) isn’t truthful, $A > e^2$, and the second inequality in (7) is truthful, then stationary state $(\ln A, 0)$ becomes unstable, and there appears global stable (in R_+^2) attractor on x axis. Note that curve (8) is monotonic increasing unlimited function, and it leads to very interesting dynamic effect. For every fixed value of parameter C increase of the amount of parameter A leads to extinction of parasites. It looks natural that increase of parameter A (for example, in a result of increase of productivity of hosts) leads to the respective increase of the base of existence of population of parasites, and to increase of number of parasites. On the other hand, increase of parameter A leads to increase of variation of host fluctuations, and, moreover, cyclic fluctuations of hosts can be observed in the domain where number of hosts is extremely low. In the end it leads to parasite extinction.

On Fig. 2 bifurcation diagrams are presented. The pointed out dynamical effect can be easily observed on Fig. 2b: if $A \approx 18$ we have coordinates of stable attractors in positive part of phase space, but after $A \geq 19$ there are stable attractors on axis x only (Fig. 2a). As we can see on Fig. 2 various cyclic regimes can be realized in model (6). Note, that before the value $A = 10$ (Fig. 2) bifurcation diagrams have no relation to model (6) because parameter A must be bigger or equal to C.

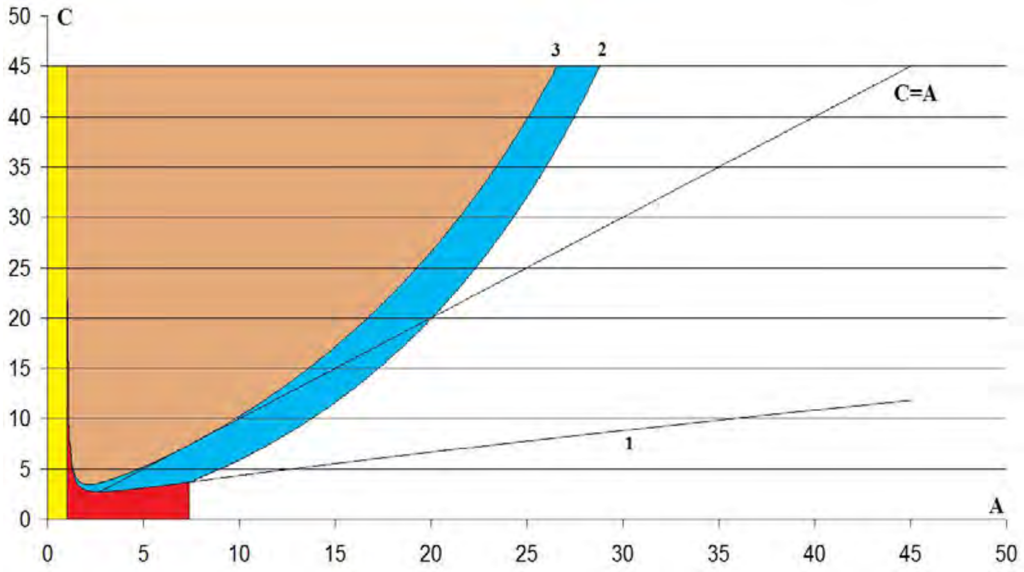


Fig. 1 Domains of stability of equilibriums of model (6).

5. If the second inequality in (7) isn't truthful the stationary state $(A/C, \ln A - A/C)$ appears in positive part of phase space. The Jacoby matrix determined in this point has the form:

$$J(A/C, \ln A - A/C) = \begin{pmatrix} (C-A)/A & -A/C \\ (C/A-1)(\ln A - A/C & 1 - \ln A + A/C \end{pmatrix}.$$

Thus, we have the following equation for characteristic values:

$$\lambda^2 + \lambda(\ln A - 2) + 1 - \frac{A}{C} = 0. \tag{9}$$

Consequently, if values of model parameters belong to the domain which is bounded by the curves

$$C = \frac{4A}{4\ln A - \ln^2 A},\ C = \frac{A}{4l - \ln A},$$

(Fig. 1, curves 3 and 2 resp.) roots of equation (9) are real and its absolute values are less than one. Under these conditions the stationary state is stable. In the domain which is over the curve 3 (Fig. 1, this domain is marked by brown color) stationary state has complex roots with radius which is less than one. In this situation we have fading fluctuations near stationary state. But curve 3 is in the domain where $C \geq A$. Thus, regime of fading fluctuations cannot be realized in considering model.

As we can see on Fig. 1, increase of parameter C for some fixed values of parameter A can lead to asymptotic stabilization of both populations on one non-zero level. On Fig. 3 there are bifurcation diagrams which were obtained for $A = 10$. For these diagrams parameter C changes from 0 to 10. If amount of parameter C is small enough cycle of the length 2 on the x axis is global stable attractor (for determination of coordinates of asymptotically stable attractors model run free 10000 steps for 400 various initial values of population sizes and for every fixed values of model parameters). After intersection of critical value (Fig. 3) we can see stable limit cycle of the length 2 in positive part of phase space. Intersection of the next bifurcation value leads to appearance of global stable equilibrium in positive part of phase space.

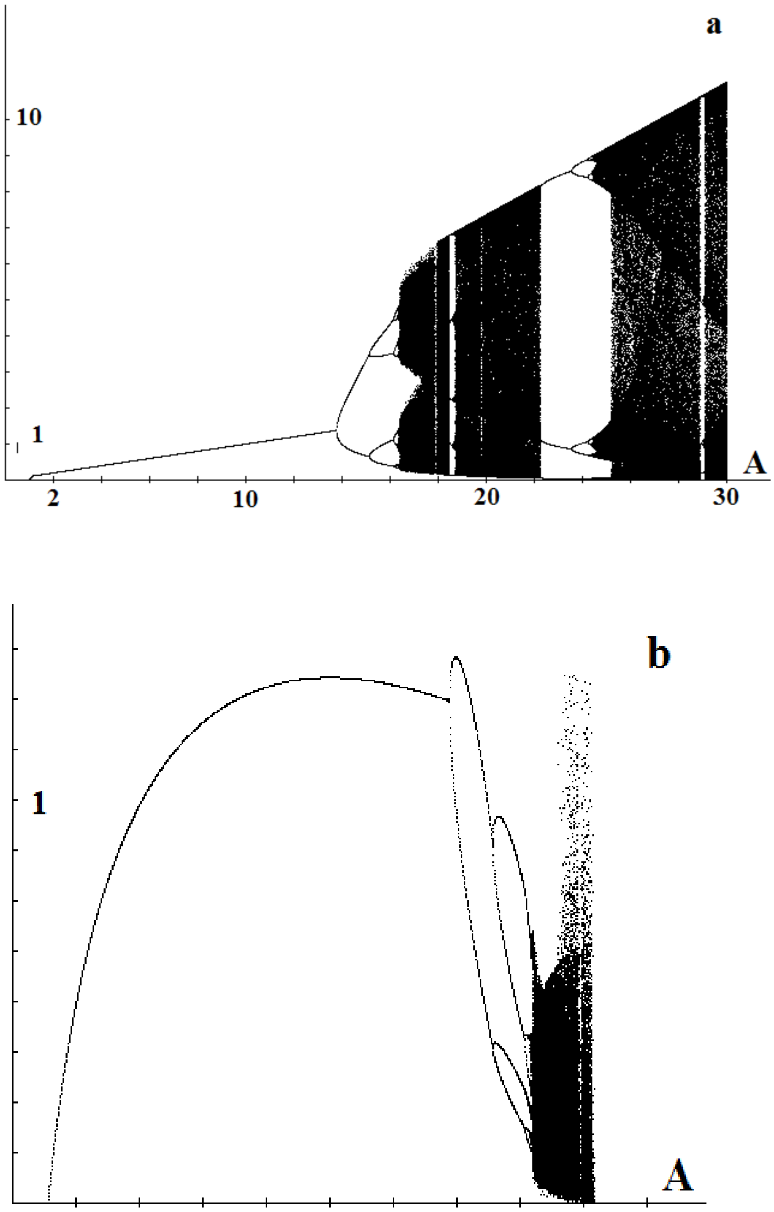
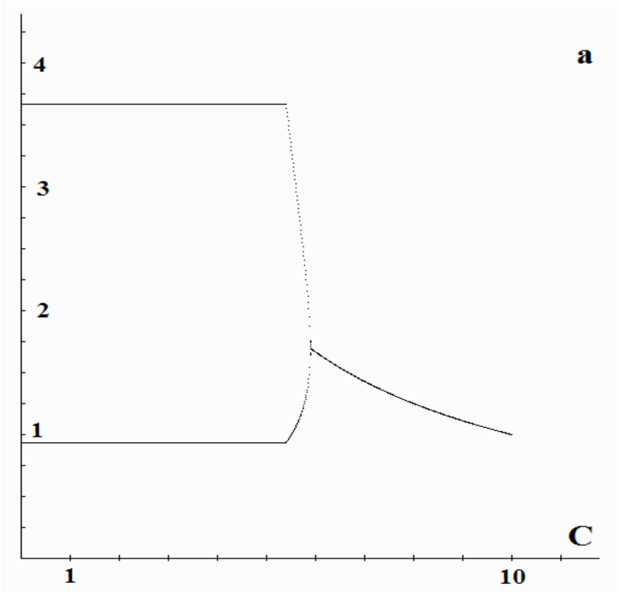


Fig. 2 Bifurcation diagrams for model (6) at $C = 10$. a – changing of abscissas of stable attractors in phase space at increase of parameter A (number of hosts); b – changing of ordinates of stable attractors in phase space of the same attractors (number of parasites).



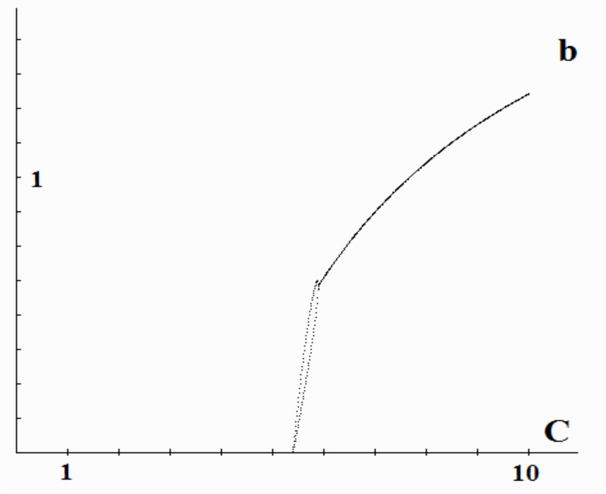


Fig. 3 Bifurcation diagrams for model (6) at $A = 10$. a – changing of abscissas of stable attractors in phase space at increase of parameter C (number of hosts); b – changing of ordinates of stable attractors in phase space of the same attractors (number of parasites).

4 Conclusion

Analysis of modified Beddington – Free – Lawton model of parasite – host system dynamics shows that in model can be realized complicated dynamical regimes, in particular, cycles of various length. Numerical analysis of model allows us to conclude that in most cases parasites play the role of stabilizer of the system. Increase of surviving of parasites can lead to the transformation of initially complicated dynamical regime to much simpler regime. Sometimes it can lead to the regime with one global stable equilibrium in positive part of phase space.

It is also important to point out very interesting dynamical regime which can be observed in model at increase of productivity of hosts. Increase of the value of the respective parameter at fixed value of other parameter of model leads to asymptotic extinction of parasites.

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