Mathematical model for number dynamics of populations with varying reproductive age

Galina Neverova, Efim Frisman
Institute for Complex Analysis of Regional Problems
Far Eastern Branch Russian Academy of Sciences, Biobidzhan, Russia,
Galina.nev@gmail.com

Abstract: This paper investigates a two-component model of population dynamics with seasonal reproduction. Density-dependent regulation is realized by varying the reproductive age. Analytical and numerical research of the model is made, and the model is approved using data on the natural population number. It is shown that the regulation of reproductive age is realized primarily by the number of mature animals. The growth of juvenile survival leads to the emergence of biennial oscillation.

Keywords: density-dependent regulation, dynamics of population, dynamic modes, stability loss.

1 INTRODUCTION

The analysis of character and mechanisms of oscillations in natural population number still remains one of the key problems in population biology. The cyclic and chaotic modes discovery in the simplest models of biological population dynamics [Ricker, 1954; May, 1974; Shapiro and Luppov, 1983] has given a new impact impulse to the nature of population fluctuations research. Substantiation and development of the population matrix models [Leslie, 1945; Lefkovitch, 1965; Jensen, 1995; Caswell, 2001; Logofet, 2008] makes it possible to describe and study in detail the role and significance of the age structure and stages of maturity for the population recurrence support and evolution.

In particular, it was shown that there was a possibility of fluctuations and chaos existence in populations with age structure, in the event that the average lifetime reproductive rate of the population is sufficiently high [Hastings, 1992; Lebreton, 1996; Kooi, Kooijman, 1999; Kaitala et al., 2000]. The directional change in demographic parameters of populations may cause a loss of the population stability and call forth the irregular dynamics. However, for the structured isolated population, the actually found periods are extremely narrow and many of natural species demonstrate evidently stable or quasicyclic dynamics [Bobyrev, Kriksinov, 2006; Lutton-Brock et al., 1997; Wickens, York, 1997; Kendall et al., 1998; Siriwardena et al., 1998; Bjornstad et al., 1999; Fewster et al., 2000; Freckleton, Watkinson, 2002; Ginzburg et al., 2010].

In this paper we trace the evolutionary scenarios of oscillatory and chaotic modes in the populations having a simple age structure. At the same time, the nonlinear interaction of different age groups of individuals in forming the population demographic parameters, observed in nature, are taken into account. This statement of the problem allows revealing the fundamentally new evolutionary scenarios of chaotic modes of dynamics when density-dependent regulation of
population growth is realized by varying numbers of mature animals. In nature the reproductive age of mammals may vary due to an increase in density caused by population growth. For example, in a population of voles (*Clethrionomys rutilus*) inhabiting the taiga zone of Russia, high population density leads to a change in reproductive age, which ultimately reduces the number of births. This phenomenon has also been observed in populations of African elephants and foxes. In this paper, we propose a model describing the dynamics of populations in which the regulation is realized by varying numbers of mature individuals. We have made an analytical and numerical investigation of the proposed model and tested it using data on natural population numbers.

2 MATHMATICAL MODEL

We use a discrete time two-component model for describing population dynamics regulated by changing reproductive age. This model is a modification of the system investigated by other researchers [Frisman et al., 2011]. We consider the population which, by the end of each reproductive season, consists of two age groups: juveniles (immature individuals) and adults (participants in the reproductive process). We assume that the time between two reproductive seasons is enough for the juveniles to become adults. The equations of population dynamics are as follows:

\[
\begin{align*}
    x_{n+1} & = ay_n + s \cdot (1 - d(x_n, y_n)) \cdot x_n \\
    y_{n+1} & = s d(x_n, y_n) x_n + vy_n,
\end{align*}
\]  

(1)

where \(x\) is a number of juveniles, \(y\) is a number of adults, \(n\) is a reproductive season number, \(a\) is the birth rate, \(s\) (\(0 \leq s < 1\)) and \(v\) (\(0 \leq v \leq 1\)) are the survival rates of juveniles and adults, respectively. Function \(d(x, y)\) is an exponential function selected following Ricker’s model [Ricker, 1954] and has the form:

\[d(x, y) = de^{-\alpha + \beta y},\]

where \(d\) (\(0 \leq d < 1\)) is the coefficient describing the fraction of individuals who became mature in the absence of density-dependent factors. \(\alpha\) and \(\beta\) are the intensities of the part of individuals who became mature decline because of the growth of juvenile and adult numbers, respectively. The function \(d(x, y)\) monotonously decreases as its arguments increase.

3 MODEL RESEARCH

In this paper, we investigate a situation where the parameter \(d\) equals 1 for the function \(d(x, y) = de^{-\alpha + \beta y}\). This equation corresponds to the natural populations in which all newborn individuals become mature in the absence of overpopulation. This model has five parameters; hence, it is possible to form a view of the emerging dynamic modes in the system on the basis of research into particular cases, when \(\alpha = 0, \beta = 0, \alpha = \beta\). Investigation of the special problems allows analyzing the dynamic modes of the system describing a situation when there is dominant class oppressing another age group.

3.1 Case 1: reproductive age depends on the number of individuals in the mature class \((\alpha = 0)\).

In this particular case, our model is as follows:

\[
\begin{align*}
    x_{n+1} & = ay_n + s(1 - \exp(-\beta \cdot y_n)) \cdot x_n \\
    y_{n+1} & = s \cdot \exp(-\beta \cdot y_n) \cdot x_n + vy_n
\end{align*}
\]  

(2)
The substitutions $\beta \cdot x \to x$ and $\beta \cdot y \to y$ transform (2) into
\[
\begin{align*}
  x_{n+1} &= ay_n + s(1 - \exp(-y_n)) \cdot x_n, \\
  y_{n+1} &= s \cdot \exp(-y_n) \cdot x_n + vy_n.
\end{align*}
\] (3)

The only non-trivial stationary solution of (3) exists if $0 \leq s < 1$ and $0 \leq v < 1$, $as + v > 1$ and has form:
\[
\begin{align*}
  \bar{x} &= \frac{a + v - 1}{1 - s} \ln \frac{s(a + v - 1)}{(1 - v)(1 - s)}, \\
  \bar{y} &= \ln \frac{s(a + v - 1)}{(1 - v)(1 - s)}.
\end{align*}
\] (4)

The standard method of finding the stability domain is based on the following theorem: Solutions of the equation $\lambda^2 + p\lambda + q = 0$ belong to the circle $|\lambda| < 1$ if and only if $|p| - 1 < q < 1$. Another study [Shapiro and Luppov, 1983] shows that the inequalities define in the plane $(p, q)$ a “triangle of stability.” Its boundaries are given by the lines:

1. $q = -1 - p$, on this line one of the eigenvalues $\lambda$ is equal to 1;
2. $q = p - 1$, on this line one of the eigenvalues $\lambda$ is equal to -1;
3. $q = 1$, on this line eigenvalues are complex numbers $\lambda_1 \lambda_2 = 1$, and on the segment $(-2 < p < 2)$, limiting the “stability triangle”, they are also conjugate:

$$
\lambda_1 = \exp(i\phi), \quad \lambda_2 = \exp(-i\phi).
$$

The stability boundaries of the nontrivial equilibrium (4) are determined based on the eigenvalue values of characteristic polynomials for linearized system (3):

$$
\begin{align*}
  \lambda &= 1 : 1 - v - as = 0, \\
  \lambda &= -1 : \frac{(1 - s)(1 - v)}{s(a + v - 1)} \left( -s(a + v - 1)(s + 1) \ln \frac{s(a + v - 1)}{(1 - s)(1 - v)} - vs - as - s \right) + vs - s + 1 + v = 0, \\
  q &= 1 : \left( \frac{s^2(a + v - 1)}{1 - s} \ln \frac{s(a + v - 1)}{(1 - s)(1 - v)} + vs + as \right) \frac{(1 - s)(v - 1)}{s(a + v - 1)} = 1.
\end{align*}
$$ (5) (6) (7)

The stability domain for the non-zero equilibrium (4) is formed by the curves (5) and (6). The curve (7) does not restrict the stability domain of the stationary point. The boundary of stability (5) coincides with the existence condition of the trivial equilibrium. The behavior of the curve (6) depending on the parameter values $s$ is shown in Figure 1. Evidently, the area stability of nontrivial equilibrium (4) is narrowed with increasing values of coefficient $s$.

\[\text{Figure 1. Maps of dynamic modes at} \quad \alpha = 0 \quad \text{on the parameter plane} \quad v, a.\]
\[\text{The numbers are marked periods of observed oscillations.}\]
In this case, the stability loss of non-zero equilibrium occurs through period doubling. The resulting dynamic modes in the irregular dynamics area are presented in Figure 1. Thus, if the reproductive age of individuals depends on the number of people in the mature group, then the increase in juvenile survival leads to occurring oscillation, and narrows the region of demographic parameters where the population develops in a stable manner.

### 3.2 Case 2: reproductive age depends on the number of individuals in the juvenile group ($\beta = 0$).

The dynamic equations in this case are as follows:

$$\begin{align*}
    x_{n+1} & = ay_n + s (1 - \exp(-\alpha \cdot x_n)) \cdot x_n, \\
    y_{n+1} & = s \cdot \exp(-\alpha \cdot x_n) \cdot x_n + vy_n.
\end{align*}$$

(8)

The substitutions $\alpha \cdot x \to x$ and $\alpha \cdot y \to y$ transform (8) into the system

$$\begin{align*}
    x_{n+1} & = ay_n + s (1 - \exp(-x_n)) \cdot x_n, \\
    y_{n+1} & = s \cdot \exp(-x_n) \cdot x_n + vy_n.
\end{align*}$$

(9)

The system (9) has unique non-zero stationary solution:

$$\begin{align*}
    \bar{x} & = \ln \left( \frac{s(a + v - 1)}{1 - v} \right), \\
    \bar{y} & = s \cdot \frac{(1 - v)(1 - s)}{(1 - v)(s(a + v - 1))} \ln \left( \frac{s(a + v - 1)}{1 - v} \right).
\end{align*}$$

(10)

Inequalities $0 \leq s < 1, 0 \leq v < 1$ and $as + v > 1$ are necessary for its existence.

Boundaries of the stability domain for the non-zero stationary solution (10) are defined by the following conditions:

$$\begin{align*}
    \lambda = 1 & : 1 - v - as = 0, \\
    \lambda = -1 & : (v + 1)(s + 1) - \frac{(1 - s)(1 - v)(a + v + 1)}{a + v - 1} \left( \ln \left( \frac{(1 - s)(1 - v)}{s(a + v - 1)} \right) + 1 \right) = 0, \\
    q & = 1 : vs - \frac{(1 - s)(1 - v)(a + v)}{a + v - 1} \left( \ln \left( \frac{(1 - s)(1 - v)}{s(a + v - 1)} \right) + 1 \right) = 1.
\end{align*}$$

(11)

(12)

(13)

The stability boundary (11) coincides with the existence condition of the zero equilibrium. On the parameters plane $(a, v)$ at $0 \leq v < 1$ the curve (12) is in the area $a < (1 - v)/s$ and below the curve (11).
Curve 13 restricts the stability domain of the non-zero equilibrium (10), and its behavior depending on the parameter values $s$ is shown in Figure 2. There is an added map of dynamic modes at fixed value of the juvenile survival parameter (Figure 3).

The growth parameter value $s$ leads to a narrowing of the area stability of the nontrivial equilibrium. When the coefficient $s$ reaches a critical value $s = 0.513$, the increase of the parameter leads to an expansion of the stability domain. The parametric portrait of the parameter plane $(v, s)$ illustrates why there is an extension of the area stability.

![Figure 4. The curve (13) for fixed values of the parameter $a$](image)

![Figure 5. Map of dynamic modes at $a = 100$ on the parameters plane $v, s$. The numbers are marked periods of observed oscillations.](image)

In this type of density-dependent regulation, the irregular oscillations occur at periods representing the high reproductive abilities of individuals. This condition is typical for species having several offspring during a breeding season. Loss of stability may happen only if the solutions for the characteristic equation of system (9) are conjugate at $|\lambda|$ transition through 1.

### 3.3 Case 3: reproductive age depends on the number of all population ($\alpha = \beta$).

Population dynamics equations for this population type are as follows:

\[
\begin{align*}
    x_{n+1} &= ay_n + s(1 - \exp(-\alpha \cdot x_n - \alpha \cdot y_n)) \cdot x_n, \\
    y_{n+1} &= s \cdot \exp(-\alpha \cdot x_n - \alpha \cdot y_n) \cdot x_n + vy_n.
\end{align*}
\]  
(14)

Substitutions $\alpha \cdot x \rightarrow x$ and $\alpha \cdot y \rightarrow y$ transform (14) to

\[
\begin{align*}
    x_{n+1} &= ay_n + s(1 - \exp(-x_n - y_n)) \cdot x_n, \\
    y_{n+1} &= s \cdot \exp(-x_n - y_n) \cdot x_n + vy_n.
\end{align*}
\]  
(15)

The system (15) may have only one non-trivial stationary solution (16), it exists if $0 \leq s < 1$ and $0 \leq v < 1$, $as + v > 1$.

\[
\begin{align*}
    x &= \frac{1 - v - a}{a + 1 + v - s - 1} \ln \left( \frac{(1 - s)(1 - v)}{s(a + v - 1)} \right), \\
    y &= \frac{s - 1}{a + 1 + v - s - 1} \ln \left( \frac{(1 - s)(1 - v)}{s(a + v - 1)} \right).
\end{align*}
\]  
(16)

Stability loss of solution (16) may happen only if the solutions for the characteristic equation of system (15) are conjugate at $|\lambda|$ transition through 1. Emerging dynamic modes are presented in Figure 6.
In this case, the system behavior is similar to the case when the density-dependent regulation realizes only the juvenile group. The stability loss is accompanied by an invariant curve formation. At the same time, the number of the juvenile class is the dominant factor because the addition of mature group influence does not have any new effects (comparison cases $\beta = 0$ and $\alpha = \beta$).

We compare parametric portraits for cases $\beta = 0$ (density-dependent regulation of population realizes only juvenile class) and $\alpha = \beta$ (density-dependent regulation of population realizes total population number) (Figure 7). At the same birth rate, case 3 has a narrower area of demographic parameters where there is irregular dynamics, than case 2. In Figure 7, the area of chaotic dynamic is domain bounded by the red or blue curve and the axis of ordinates. It should be noted that at high birth rates, the difference between these types of regulation is practically absent. Hence, at the density-dependent regulation of type 3, the influence of adult group size on the immature individuals number shows that becoming mature is unimportant (Figure 7).

3 SIMULATIONS

The next step is the application of equations describing the varying reproductive age, to the description and analysis of population dynamics on the basis of data on natural population number.

For the forest vole kind of Microtus, the characteristic fluctuation of reproductive age is a result of an increase in population size. From the available data, we use the estimates of field vole (Microtus oeconomus) population size in the Altai Mountains [Efimov, Kovaleva, 2001]. The data refer to the number of harvested individuals. We assume that the number of harvested individuals is proportional to total population size; therefore, harvest size is taken for the population relative
number. By the Levenberg–Marquardt algorithm, it was estimated through the model parameters: $a = 16.7$, $s = 0.49$, $v = 0.15$, $\alpha = 0.00094$, $\beta = 25.4$.

The obtained coefficients are biologically meaningful. A low survival rate of mature individuals corresponds to the short lifespan of this species. The value of birth rate does not contradict the biological characteristics of this species. The founded estimations of intraspecific interactions between individuals show that reproductive age is highly dependent on the number of individuals in the mature group.

This model may also be applied to describing the dynamics of the fox population. In a litter of fox, there are usually 4 to 6 or 12 to 13 pups. Some female foxes begin to participate in reproduction at the age of one, and the remaining individuals reach sexual maturity at the age of two. Such regulation of reproductive age changes the existing age structure of populations and affects fertility. There are years when up to 60% of the females of this species remain without posterity. This condition is due to the fact that the mating period of foxes and its effectiveness depend on the weather and the animals’ weight. Estimation of model coefficients for the fox population is demonstrated by the Levenberg–Marquardt algorithm: $a = 8.7$, $s = 0.62$, $v = 0.41$, $\alpha = 0.004$, $\beta = 1.78$. The simulation results are shown in Fig. 8.

4 CONCLUSION

If density-dependent regulation of reproductive age is realized by mature group size, then the growth of juvenile survival leads to the emergence of biennial oscillation. If the reproductive age depends only on the number of the immature class or the total population figure, then irregular oscillations occur at periods representing the high reproductive abilities of individuals. This aspect is characterized in the case of species having several offspring during a breeding season. An increase in the juvenile survival rate may lead to number fluctuations. However, if more than half the number of immature individuals survives, then the population size is stabilized, and the fluctuations are possible only at a high birth rate.

ACKNOWLEDGMENTS

This work is in part supported by the Russian Foundation for Fundamental Research (no. 11-01-98512-r_vostok_a) and the Far Eastern Branch of the Russian Academy of Sciences (nos. 12-I-OBN-05, 12-II-SU-06-007).

REFERENCES
