



# Dynamics of populations with delayed density dependent birth rate regulation



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## ABSTRACT

This study focuses on the Moran–Ricker model with time lag for the dynamics of limited homogeneous population. The reduction of required resources is caused by their consumption by the previous generation, which corresponds to delayed density dependence. The model shows multimodality. The population can demonstrate different types of dynamics (i.e., stable, periodic, or chaotic) at the same values of demographic parameters. The Moran–Ricker model with time lag can successfully describe the population dynamics of some insect species. The point estimations of population parameters are statistically significant. The obtained point estimates that correspond to real population dynamics are located in a quasi-periodic fluctuation area and adjoin other dynamic modes. A variation of the values of demographic parameters or random fluctuations of the current population size can lead to dynamic mode change. The investigation of the possible model dynamic modes near the found point estimation of parameters is necessary to identify the dynamic modes between which transition may occur.

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## 1. Introduction

The “golden age” of mathematical biology began in the first half of the 20th century and was marked by a burst of studies that determined the subsequent development of theoretical ecology (Lotka, 1925; Volterra, 1931; Kostitzin, 1937). The mathematical bases of these works were elegant models based on systems of differential equations. These models can describe many population phenomena observed in natural biological communities successfully, including population dynamics fluctuations, interspecies relations, competition displacement, and autoregulation processes.

Owing to the works of May (1974, 1975), Shapiro (1972) and Shapiro and Luppov (1983), the mathematical population biology in the early 70s acquired simple and impressive models based on recurrence equations. These models adequately describe the dynamics of the species with seasonal breeding. Incidentally, the recurrence equations are easily analyzed numerically using rapidly evolving computer technology. These “simple” models have a vari-

ety of dynamic modes, which evolve in a very complicated way with the change in values of model parameters.

Repeated attempts to directly apply simple models based on recurrence equations to describe and forecast the dynamics of natural populations were often unproductive: model curves, while capturing the trend changes, poorly described dynamics of real populations (Dennis and Taper, 1994; Myers, 1999; Nedorezov and Sadykova, 2008; Nedorezov, 2010; Frisman et al., 2015b). The description of the population dynamics significantly improves if time lag is introduced in the equations (Turchin, 1990, 2003; Berryman and Turchin, 2001; Isaev et al., 2001; Sadykova and Nedorezov, 2013; Nedorezov and Sadykova, 2015). Delayed density-dependence can arise as a result of interspecific interaction or the adverse effect of high population size on the fecundity of the next generation (Prout and McChesney, 1985; Turchin, 1990; Williams and Liebhold, 1995). The strongest results in studies describing the dynamics of real populations have been obtained for the Moran–Ricker model and its modifications with time lag (Kendall et al., 1999; Turchin, 2003; Turchin et al., 2003; Jonzén et al., 2005; Bechtol and Kruse, 2009; Sadykova and Nedorezov, 2013; Nedorezov and Sadykova, 2015).

In particular, the Moran–Ricker model with and without time lag was applied to the description and analysis of the population dynamics of red king crab off Kodiak Island (Bechtol and Kruse,

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2009). Also this model with time lag has been applied to describe and analyze the dynamics of the Larch budmoth (*Zeiraphera diniana* Gn.) (Sadykova and Nedorezov, 2013; Nedorezov and Sadykova, 2015). As a rule, the focus of applied studies was on the estimation of qualitative and quantitative indicators that characterized the quality of correspondence between the model and the empirical datasets.

Many studies (e.g. May and Oster, 1976; Skaletskaya et al., 1979) are devoted to detailed theoretical investigation of dynamical modes of the Moran–Ricker model without time lag. The central point of these studies is the conditions of stability of non-trivial equilibrium. It has been shown that stability loss occurs with increasing values of reproductive potential, and a further complication of the dynamics happens according to the Feigenbaum scenario. In particular conditions of appearance and stability of the two-year and three-year cycles for this model were obtained (Skaletskaya et al., 1979; Nedorezov, 2013). One of the most important theoretical results, namely the proof of uniqueness of the stable attractor in a Moran–Ricker model without time lag, was first obtained by M.V. Jacobson (Jacobson, 1976). The attractor type is determined by the model parameters and does not depend on the initial conditions (initial value of population size) (Skaletskaya et al., 1979).

Note that intraspecific and interspecific competition is typically modelled by the Moran–Ricker model function without time lag (Maunder, 1997; Todd et al., 2004; Golinski et al., 2008; Frisman et al., 2011, 2015a). The models of local populations with a simple age structure, in which density dependent regulation is described by an exponential function, like the Moran–Ricker equation without time lag, have recently been actively investigated (Frisman et al., 2011, 2015a, 2016; Zhdanova and Frisman, 2016). These models reveal the phenomenon of multimodality, or the possibility for different stable dynamic modes (stable, periodic, chaotic) to exist under the same conditions, their transition determined by initial population size. This implies that the random variation of the current population size may lead to a change of the observed dynamic mode. These results allow to suggest that the Moran–Ricker model with a time lag should have a complex dynamic behavior. However, no theoretical study of this model with time lag has been ever published. To the best of our knowledge, no study has addressed problems of multistability and multimodality regarding this model. We set out to fill these apparent gaps.

Investigation of dynamic modes of the model aims to identify and analyze the effects that may occur in natural populations due to the influence of delayed density dependent regulation. Thus, the goal of this article is detailed study of the dynamic modes of the Moran–Ricker model with time lag. We apply our results to description of insect population dynamics. The results of our analytical and numerical analysis of the model are studied in detail and compared with real population census.

The general form of the Moran–Ricker model with the time lag is represented by the following equation:

$$x_{n+1} = ax_n \exp\left(-\sum_{i=0}^{i=m} b_i x_{n-i}\right) \quad (1)$$

where  $x_n$  is the population size at time moment  $n$ ,  $n$  is reproductive season number, and  $a$  is reproductive potential. The factor of

$$\exp\left(-\sum_{i=0}^{i=m} b_i x_{n-i}\right)$$

characterizes the environmental limitation of population growth, and  $m$  is the time lag value corresponding to the number of years during which the necessary available resources constrain population development.

With  $m = 0$  Eq. (1) is reduced to the basic well-studied Moran–Ricker model (Moran, 1950; Ricker, 1954; Skaletskaya et al., 1979):

$$x_{n+1} = ax_n \exp(-b_0 x_n).$$

Parameter  $b_0$  is the scaling coefficient, which determines the intensity of the density-dependent limitation and indirectly characterizes the carrying capacity because if  $x_n = 1/b_0$ , then the number of the next generation reaches the maximum population size of the species. Thus, each generation “receives” the same volume of necessary available resources regardless of the previous population size. This may be true for species whose carrying capacity fully recovers between breeding seasons. Otherwise, the decrease in resources owing to their consumption by previous generations should be considered. Eq. (1) considers the previous generations’ impact on population dynamics. This study examines the features of dynamic behavior of model (1) for the time lag values of 1 and 2.

## 2. Dynamic modes of the model with one year time lag ( $m = 1$ )

The Moran–Ricker model with time lag 1 can be expressed as follows:

$$x_{n+1} = ax_n \exp(-b_0 x_n - b_1 x_{n-1}). \quad (2)$$

Coefficient  $b_1$  characterizes the reduction of required resources owing to their consumption by the previous generation. The decrease in required resources can be interpreted as a reduction of the reproductive potential of the current population generation. This process corresponds to delayed density dependence. Parameter  $b_0$  characterizes the intensity of the density-dependent limitation under the constraint of resources per individual. The one-year time lag allows resources to be fully recovered during two reproductive seasons.

Introduction of a new variable  $y_n = x_{n-1}$  reduces Model (2) to a system of two recurrence equations without time lag with three parameters:

$$\begin{cases} x_{n+1} = ax_n \exp(-b_0 x_n - b_1 y_n) \\ y_{n+1} = x_n \end{cases} \quad (3)$$

or, after substitutions  $b_0 x_n \rightarrow x_n$  and  $b_1 y_n \rightarrow y_n$ , to system

$$\begin{cases} x_{n+1} = ax_n \exp(-x_n - \rho \cdot y_n), \\ y_{n+1} = x_n \end{cases} \quad (4)$$

where  $\rho = b_1/b_0$ . Parameter  $\rho$  characterizes the previous generation “participation” in the density-dependent regulation of the population birth rate. No “participation” means  $\rho = 0$ , and system (2) is reduced to the classical Moran–Ricker model. If  $\rho = b_1/b_0 < 1$  ( $b_1 < b_0$ ), then the previous generation “participation” in the density-dependent regulation of the population birth rate does not exceed the “participation” of the current generation. Thus, the resources used by a population are significantly recovered between two successive periods of reproduction. The situation is inverse if  $\rho = b_1/b_0 > 1$  ( $b_1 > b_0$ ). The previous generation “participation” in the density-dependent regulation of the population birth rate is more than the “participation” of the current generation. The higher the value of parameter  $\rho$  ( $\rho > 1$ ), the fewer resources are available for the next generation.

System (4) has only one non-trivial invariant point

$$\bar{x} = \bar{y} = \frac{1}{1+\rho} \ln a, \quad a > 0. \quad (5)$$

The solution increases monotonically with the increasing values of parameter  $a$  (for any constant value of  $\rho$ ) but decreases monotonically

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