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Change of dynamic regimes in the population of species with short life cycles: Results of an analytical and numerical study

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ABSTRACT

There is a phenomenon of multiregimism found in the elementary mathematical model of population dynamics, meaning the possibility for different dynamic regimes to exist under the same conditions, with transition to these regimes dependent on the initial numerical values. The effect in question comes into existence in the model which has several different limiting regimes (attractors): equilibrium, regular fluctuations, and chaotic attractor. The revealed phenomenon of multiregimism lets us explain the initiation of fluctuations as well as disappearance of fluctuations. Adequacy of the model's dynamic regimes is depicted by their correlation with the actual dynamics of population size of bank vole (*Myodes glareolus*). It is shown that the impact of climatic factors on a reproductive process of a population noticeably extends the range of possible dynamic regimes and, in fact, leads to random migration over attraction basins of these regimes.

1. Introduction

The fluctuations in the population of species with short life cycles, particularly small mammals (rodents), remain one of the most exciting and mysterious ecological phenomena. To date, numerous empirical data have been amassed to demonstrate regular fluctuations of population size, as well as evident transitions between different dynamic regimes.

The most well-known and prominent examples of the transition of dynamic regimes are the disappearance of cycles in the populations of lemming (*Lemmus lemmus*) (Kausrud et al., 2008; Coulson and Malo, 2008; White, 2011) and some species of vole (Henttonen and Wallgren, 2001; Cornulier et al., 2013; Rai, 2004; Elmhagen et al., 2011).

Some situations have been found in which slight fluctuations around the equilibrium give way to oscillatory or chaotic regimes. For example, a tendency for practically monotonous growth was observed in the population of snow goose (*Chen caerulescens*) in New York, USA. For a long time, the population presented irregular fluctuations, which were presumably caused by intraspecific competition for vital resources (Special Snow Goose Harvest Opportunity). Another kind of dynamic regime violation is connected with the explicit change of cycle length. In particular, a transition from a two-year fluctuation to a three-year one was noted in the population of evening grosbeak (*Coccothraustes vespertinus*) in Canada and northern USA (Kelling, Population Trends). Similar effects are revealed in the populations of lemming and some kinds of voles, as their noted cycles are within periods 2, 3, and 4 (Hansen et al., 1999; Schaffer et al., 2001; Chernyavskii and Lazutkin, 2004; Zhigalskii, 2011; Krebs, 2013).

Moreover, situations have occurred in which non-interacting, virtually identical populations of similar species reveal different dynamics. In particular, laboratory experiments demonstrated that under the same initial population size and similar conditions, two periodic regimes of opposite phases can be noted in the populations of *Tribolium castaneum* (Henson et al., 1998).

Therefore, situations occur in which local populations display different (sometimes fundamentally different) regimes of population dynamics under the same demographic parameters. This phenomenon, that is, the dependence of observed regimes on initial conditions, is referred to as "multistability" (Kuznetsov et al., 2012) in the theory of dynamical systems. The appearance of different dynamic regimes depends on whether the system has several attractors; each of them can be a stable point, as well as a limit set (e.g., invariant curve). Specifically, the term "multistability" in this context is not representative of the essence of the phenomenon occurring in actual objects (different regimes of population dynamics depending on the initial conditions). We find

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that using a new notion called “multiregimism” is appropriate. The transition of dynamic regimes observed in nature is sufficiently explained by multiregimism because the effects of external factors can be regarded as modifications to the initial conditions.

Nowadays, research into the mechanisms leading to the transitions of observed dynamic regimes in populations arouse considerable interest: a number of concepts and hypotheses provide an explanation for the appearance and disappearance of number fluctuations (Kostova and Carlsen, 2005; Hendriks and Mulderb, 2012; Chernyavskii and Lazutkin, 2004; Zhigalskii, 2011; Krebs, 2013; Ginzburg and Colyvan, 2004; Inchausti and Ginzburg, 1998; Elmhagen et al., 2011; Hanski et al., 1993; Frisman et al., 2011).

In the current study, the phenomenon of multiregimism is presented and investigated through a quite uncomplicated mathematical model of a population of a species with a short life cycle (fast maturing of juveniles). The adequacy of the obtained model for dynamic regimes is illustrated by correlating the regimes with the actual population dynamics of mouse-like rodents, namely, the bank vole (*Myodes glareolus*) (Zhigalskii, 2011, 2012).

2. Description and formalization of the short life cycle of a population: Model of population dynamics

The life cycle of practically any population of a species with several offspring in the course of a reproduction season can be described with the scheme shown in Fig. 1. This graph shows the major stages of the population’s annual development. We describe the peculiarities of the life cycle of populations with short life cycles, taking populations of mouse-like rodents as example (Fig. 1).

Animals that survive the winter emerge from under the snow during spring and start propagating themselves. As a rule, at the time when the snow completely melts, the whole population will have consisted of two age groups. The first group (with the value x_n) includes first-time participants in the reproductive process (those born under the snow). The second group (with the value y_n) includes last year’s participants in reproduction that have survived the winter. During the reproduction period (spring–summer–autumn) the population is expanded with newborns, as mature animals produce several offspring during the spring–summer period. The underyearlings also participate in the reproductive process and produce offspring; their number is represented by p_1 in the scheme. Populations with fast-maturing juveniles are characterized by a high specific growth rate, which can decrease as the density of the population grows through autoregulation caused by stress. Stress syndrome conditioned by redundant density can result in the decline of sexual activity and fertility to the point of the dissolution of already existing embryos (Chernyavskii and Lazutkin, 2004; Zhigalskii, 2011, 2012; Krebs, 2013; Odum, 1971; Frisman et al., 2010; Novikov et al., 2012 and many others). Such populations may demonstrate different levels of participation of juveniles in the reproductive process depending on density. Generally, the regulation mechanisms of a population size are characterized by high complexity and realized mostly through density-dependent birth regulations closer to the end of the reproduction season or when the population size reaches its peak. In late autumn, the population “goes under the snow” for the whole winter. As this phenomenon occurs, the population includes underyearlings of the recent litter that have not participated in the reproduction (with the value p_2). Mature adults can continue reproducing during the winter under the influence of climatic and other factors. Such undersnow reproduction is observed among many species of mouse-like rodents, particularly voles, lemmings, and other rodents. (Krebs, 2013; Chernyavskii and Lazutkin, 2004; Zhigalskii, 2011, 2012; Hansen et al., 1999). Over the winter, immature underyearlings reach sexual maturity.

Thus, at the beginning of a new reproduction season when the snow has melted, the population is represented by two age groups again. The first group comprises juveniles that have hardly reached maturity, particularly those born under the snow. The size of this group is denoted by x_{n+1}. The second group comprises “adults” that have survived the winter and participated in last year’s reproduction (y_{n+1}).

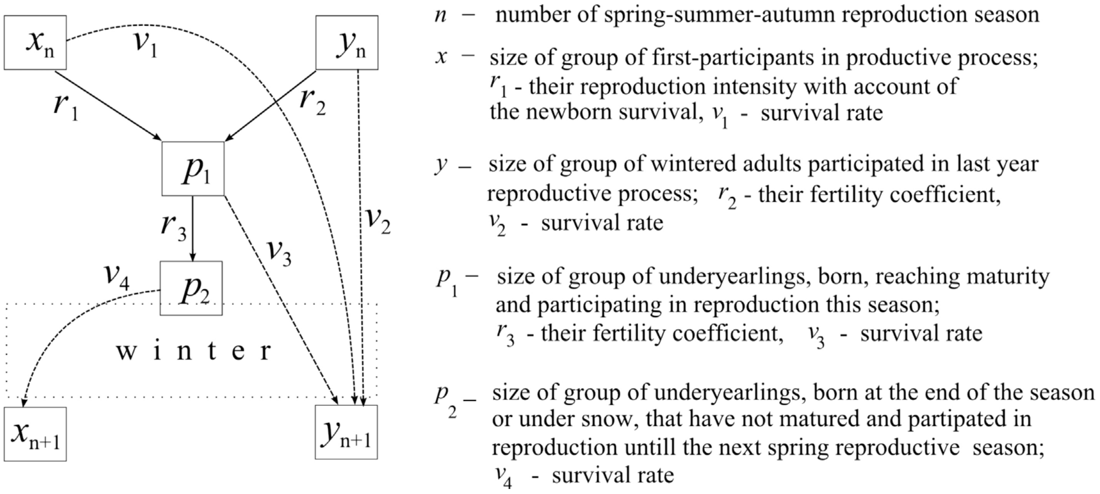
The suggested scheme (Fig. 1) leads to the following dependences:

$$p_1 = r_1 x_n + r_2 y_n, \quad p_2 = r_3 p_1, \quad x_{n+1} = v_4 p_2, \quad y_{n+1} = v_3 p_1 + v_1 x_n + v_2 y_n.$$

Therefore,

$$\begin{aligned} x_{n+1} &= v_4 r_3 (r_1 x_n + r_2 y_n), \\ y_{n+1} &= (v_3 r_1 + v_1) x_n + (v_3 r_2 + v_2) y_n. \end{aligned} \tag{1}$$

Hence, the population dynamics of mouse-like rodents can be described with a system of two equations connecting the values of the two defined groups in successive generations. We consider that density-dependent regulation is necessary in completing the mathematical simulation. This regulation is achieved by decreasing the birth rate, which is attributable to increasing population size. Notably, the most significant decrease in birth rate occurs closer to



n – number of spring-summer-autumn reproduction season

x – size of group of first-participants in productive process; r_1 - their reproduction intensity with account of the newborn survival, v_1 - survival rate

y – size of group of wintered adults participated in last year reproductive process; r_2 - their fertility coefficient, v_2 - survival rate

p_1 – size of group of underyearlings, born, reaching maturity and participating in reproduction this season; r_3 - their fertility coefficient, v_3 - survival rate

p_2 – size of group of underyearlings, born at the end of the season or under snow, that have not matured and partipated in reproduction untill the next spring reproductive season; v_4 - survival rate

Fig. 1. Life cycle of populations with short life cycles using mouse-like rodents as example.