Anticipatory Systems in Population Dynamics

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Abstract

This paper deals with anticipatory systems and their use when describing the population dynamics of single species discrete systems. In doing so, it starts from Rosen's original definition of anticipatory system and its extending in the papers of Dubois. Then the concepts of incursion and hyperincursion are briefly explained and their applications to modeling discrete dynamic systems are outlined. A detailed analysis is given of the population model described by the first order difference equation, where the relative population size at future time is a cubic polynomial function of the population size at the present. Consequently, the corresponding incursive and hyperincursive models are formulated and the stability of their equilibrium solutions (trajectories) is studied.

Keywords: Anticipatory systems, Incursion, Hyperincursion, Population dynamics, Difference equations.

1 Introduction

Anticipatory systems are considered as systems that contain a representation of the system itself. The concept of anticipatory system was introduced by Robert Rosen (1985) using the following definition. An **Anticipatory System** is a system containing a predictive model of itself and/or its environment, which allows it to change state at an instant in accord with the model's prediction to a latter instant. According to Rosen, **anticipation** constitutes the principal difference between systems involving living organisms (biological systems) and systems without the presence of living organisms (e.g. manufacturing and transport systems).

In this paper we shall confine ourselves to anticipatory systems of discrete type. Rosen's concept appears from the fact that the state of anticipatory system at time $t = n$ is determined by the state of its model at time $t = n+1$, while the state of the predictive model is not affected by the system. Let $\mathbf{x}_n$ be a vector of state variables of the system and ξ_n a vector of state variables of its predictive model. According to Dubois (1998b) we can describe an anticipatory system using a system of two difference equations

$$\mathbf{x}_{n+1} = F\left(\mathbf{x}_n, \xi_{n+1}\right), \tag{1.1a}$$

$$\xi_{n+1} = G\left(\xi_n\right). \tag{1.1b}$$

If we accept that the state of the predictive model is independent on the system, we come to a contradiction because such model cannot be true predictive model of the system itself.

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This contradiction was removed by Dubois (1998b), whose interpretation of anticipatory systems starts from the following system of difference equations

$$\mathbf{x}_{n+1} = F\left(\mathbf{x}_n, \xi_{n+1}\right), \tag{1.2a}$$

$$\xi_{n+1} = F\left(\mathbf{x}_n, \xi_{n+1}\right). \tag{1.2b}$$

Equation (1.2a) is evidently identical to equation (1.1a). However, equation (1.2b) tells that the future state of the system and its predictive model at time $t = n+1$ is a function of the state of the system at time $t = n$ and the state of the model at time $t = n+1$. In case the system and its model are identical, the equations (2ab) can be reduced to only one difference equation

$$\mathbf{x}_{n+1} = F\left(\mathbf{x}_n, \mathbf{x}_{n+1}\right),$$

which means that the future state of the system depends not only on its present state but also on its future state.

In the following Section we shall briefly discuss the concepts of incursion and hyperincursion introduced to the theory of dynamical systems by Dubois (1998a). The remaining Sections will be devoted to a detailed analysis of a simple population model $x_{n+1} = rx_n^2\left(1 - x_n\right)$.

2 Concepts of Incursion and Hyperincursion

For the sake of simplicity, let us consider a one-dimensional discrete dynamical system, the evolution of which is described by a recursive difference equation

$$x_{n+1} = f\left(\ldots, x_{n-1}, x_n, \mathbf{p}\right), \tag{2.1}$$

where x is the state variable of the system, $\mathbf{p}$ the vector of control parameters and time variable takes the values $n = 0, 1, \ldots$. It means that the future state of the system at time $t = n+1$ (x_{n+1}) is uniquely determined (through function *f*) by the values of the state variable at past and present times.

The concept of **incursion (implicit** or **inclusive recursion)** was introduced by Dubois (1998a, 1998b) for the description of the evolution of a discrete dynamical system using a difference equation

$$x_{n+1} = f\left(\ldots, x_{n-1}, x_n, x_{n+1}, \ldots, \mathbf{p}\right),$$

From this equation it follows that the future state of the system at time $t = n+1$ (x_{n+1}) depends not only on its past and present states ($\ldots, x_{n-1}, x_n$) but also on its future states $\left(x_{n+1}, \ldots\right)$. Therefore, the concept of incursion represents evidently an extension of the concept of current recursion.

A simple example of incursion is the description of system dynamics in the form

$$x_{n+1} = f\left(x_n, x_{n+1}, \mathbf{p}\right), \tag{2.2}$$

where the value of the state variable at each instant $t = n+1$ is a function of the values of this variable at times $t = n$ and $t = n+1$. Such system represents an anticipatory system of itself because the function f (describing the system dynamics) is a carrier of the system model. When replacing the argument x_{n+1} in (2.2) with the equation (2.2) itself, we have

$$x_{n+1} = f\left(x_n, f\left(x_n, x_{n+1}, \mathbf{p}\right), \mathbf{p}\right),$$

which means that the system explicitly contains a predictive model of itself. If an anticipatory system includes a model of itself, then this model must carry also a model of itself and so on until infinity. Therefore, there is denumerable number of such models nested (embedded) in each other. It is very important to remember that the evolution of an anticipatory system is not explicitly controlled from outside the system but is determined by the system itself.

In some cases, the incursive difference equation (2.2) can have more solutions, i.e. provide at each instant $t = n$ more possible future states x_{n+1}. For the indication of such cases, Dubois (1998a) proposed the term **hyperincursion**. Therefore, hyperincursion is an incursion with multiple solutions. The problems of hyperincursion will be analyzed in the Section 3.3.

3 Analysis of Population Model

We shall consider populations with a fixed time interval between individual generations or a fixed interval between individual their size measurements. In this case we can simply describe population size by a sequence $\{x_n\}$, with x_0 denoting the initial population size (at time t_0), x_1 the population size at the first generation (at time t_1), x_2 the population size at the second generation , and so on. It is evident that the population size at each stage $t = 1, 2, \ldots$ is determined by the population sizes in the past. If we suppose the population size changes only through births and deaths and, moreover, the births and deaths rates are constant, we can describe the population evolution by a simple linear difference equation

$$x_{n+1} = rx_n,$$

where the parameter r is called the **intrinsic growth rate**. Its value represents the per capita growth rate corresponding to the case, when the population size is small enough to be negligibly affected by resource limitations. The linear model given above with a constant growth rate independent of population size (**Malthus' model**) is not available for real populations except possibly very small populations that are not limited by both their territory size and quantity of accessible resources.

Much more realistic are nonlinear population models, the review of which is given in the monograph of Brauer and Castillo-Chávez (2000). For example, the difference equations

$$x_{n+1} = \frac{rx_n}{x_n + A} \quad \text{and} \quad x_{n+1} = \frac{rx_n^2}{x_n^2 + A}$$

were proposed as descriptions of populations that die out completely in each generation and have birth rates saturating for large population sizes. One of the most frequently applied nonlinear models is the **logistic model** represented by the following difference equation

$$x_{n+1} = rx_n\left(1 - \frac{x_n}{K}\right),$$

where the parameter K is called the **carrying capacity of environment** for a given population. Its value denotes a limit population size, at which available resources make still possible the population development. This model describes the population evolution with a growth rate that decreases to zero as the population becomes large.

In this paper we will consider a slightly modified model described by the first order nonlinear difference equation

$$x_{n+1} = rx_n^2\left(1 - \frac{x_n}{K}\right). \tag{3.1}$$

According to Smítal (1988), this model is closer to reality but its dynamics are very complicated. Therefore, the remaining part of this Section will be devoted to a detailed analysis of the population model (3.1) by using the theory of discrete dynamic systems presented e.g. in (Brauer and Castillo-Chávez, 2000; Smítal, 1988).

Anticipatory modeling of population dynamics was recently studied in the papers of Dubois (2003) and Akhmet et al. (2006).

3.1 Classical (recursive) model

Suppose we have the population model (3.1) in the form

$$x_{n+1} = rx_n^2\left(1 - x_n\right). \tag{3.2}$$

This recursive model is an example of a threshold model described in the paper of Marotto (1982). In our model the state variable x represents relative size of some population living in an environment with limited resources ($K = 1$). We will study the population dynamics as a function of the value of parameter $r \in [0, 27/4]$. It is evident that the function $f_r(x) = rx^2(1-x)$ represents a continuous mapping of interval $[0,1]$ into itself. Graphs of the function for selected values of r are given in the Fig. 1. Basic information on the model (3.2) can be obtained by determining its equilibrium points that are solutions of the algebraic equation

$$rx^2(1-x) = x.$$

After rearrangement of the equation we have

$$x\left(rx^2 - rx + 1\right) = 0. \tag{3.3}$$

Trivial solution of the equation (3.3) is $x = 0$ and, therefore, the model (3.2) has equilibrium point $\alpha = 0$ for all values of *r*. This equilibrium is evidently asymptotically stable because $f_r'(\alpha) = 0$.

When analyzing other equilibrium points that are solutions of the equation

$$rx^2 - rx + 1 = 0, \tag{3.4}$$

we can distinguish three cases depending on the value of parameter *r*.

In case $r < 4$, the discriminant of (3.4) is negative, which means that $\alpha = 0$ is only equilibrium point of the model and each trajectory generated by any point $x_0 \in [0,1]$ tends to zero. Biological interpretation of this situation is simple: each population controlled by the model (3.2) is dying out.

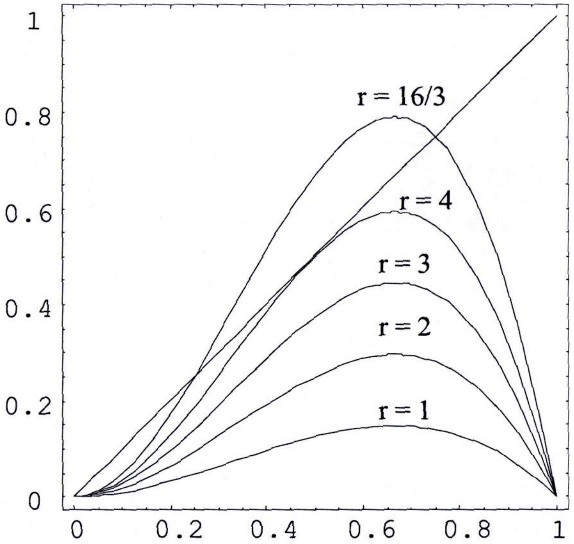

Figure 1: Graphs of $f_r(x)$ for $r = 1;\ 2;\ 3;\ 4$ and $16/3$.

For $r = 4$ the discriminant of (3.4) is zero and, therefore, the corresponding equation has double root $x = 1/2$, which means that $\beta = 1/2$ is another equilibrium point of the model. A more detailed analysis (Smítal, 1988) indicates that this equilibrium point is neither asymptotically stable nor unstable.

In case $r > 4$, the equilibrium point $\beta = 1/2$ bifurcates into two equilibrium points

$$\beta_1 = \frac{r - \sqrt{r^2 - 4r}}{2r} = \frac{1}{2} - \sqrt{\frac{1}{4} - \frac{1}{r}};\ \beta_2 = \frac{r + \sqrt{r^2 - 4r}}{2r} = \frac{1}{2} + \sqrt{\frac{1}{4} - \frac{1}{r}}.$$

Since $0 < \beta_1 < \beta_2 < 1$ and $f_r'(\beta_1) > 1$, the equilibrium point β_1 is unstable for all values of $r \in (4, 16/3)$. Similarly, we can find that β_2 represents an asymptotically stable equilibrium point of the model for $r \in (4, 16/3)$. For $r > 16/3$ we have $f_r'(\beta_2) < -1$ and, therefore, the equilibrium point β_2 becomes unstable.

As soon as the value r exceeds $16/3$, periodic trajectories (trajectories with cycles) appear: first trajectories with period 2, later in successive steps trajectories with period 2^2, 2^3, ... *etc* and, finally, starting from $r \doteq 5.89$, trajectories become chaotic.

Now, let us show how to find the trajectories with period 2. When searching for them, it is enough to solve the equation

$$f_r(f_r(x)) = r^3 x^4 (1-x)^2 \left[1 - rx^2(1-x)\right] = x.$$

After eliminating the equilibrium points alpha, beta_1 and beta_2 we obtain just two real points γ_1 and γ_2 lying within $[0,1]$ and constituting the cycle with period 2. For example, if $r = 6$, then $\gamma_1 \doteq 0.60287$, $\gamma_2 \doteq 0.86603$. The periodic trajectories with other periods can be obtained in a similar way.

A more detailed analysis of the population model (3.2) given in (Smítal, 1988) showed the existence of two threshold values of the population size.

Since $f_r(1) = 0$, there is a point $\delta \in (\beta_2, 1)$ such that $f_r(\delta) = \beta_1$. Then, for any trajectory $\{x_n\}$ the following limit conditions are satisfied

$$\lim_{n\to\infty} x_n = \begin{cases} 0, \text{ if } x_0 \in [0, \beta_1) \cup (\delta, 1] \\ \beta_1, \text{ if } x_0 = \beta_1 \text{ or } x_0 = \delta \end{cases}.$$

We can also find a critical value $r_C \doteq 6.6$ of parameter r such that

$$f_r(x) \in (\beta_1, \delta) \text{ for } x \in (\beta_1, \delta) \text{ and } r \in (4, r_C).$$

From the conditions mentioned above, it follows that β_1 and δ are the searched threshold values. From the biological point of view, the theoretical results can be interpreted as follows.

If a population doesn't reach at least the size β_1, it is dying out. The same conclusion holds for the case the population size exceeds the second threshold value δ. If a population reaches the size from (β_1, δ), then

- it tends to asymptotically stable equilibrium state β_2 (for $r \le 16/3$) or
- it behaves in different ways but cannot die out (for $16/3 < r < r_C$) or
- it can actually die out (for $r > r_C$).

It is clear that the dynamics of the model (3.2) is much more complicated, when compared with the dynamics of the well-known logistic model.

3.2 Incursive model

An associated incursive model can be built from (3.2) in writing

$$x_{n+1} = rx_n^2\left(1 - x_{n+1}\right), \tag{3.5}$$

where the saturation factor is now a prediction function of the population size at time $t = n+1$. This model was analyzed in the more general context by Dubois (2000). It is evident that the model (3.5) represents the model of an anticipatory system.

When replacing x_{n+1} in the saturation factor by equation (3.5) itself, we get an incursive model

$$x_{n+1} = rx_n^2\left(1 - rx_n^2\left(1 - x_{n+1}\right)\right).$$

In continuing to replace x_{n+1} by itself, we can obtain an infinite sequence of models nested in each other

$$x_{n+1} = rx_n^2\left(1 - rx_n^2\left(1 - rx_n^2\left(1 - rx_n^2\left(1 - rx_n^2\left(1 - rx_n^2\left(1 - \ldots\right)\right)\right)\right)\right)\right).$$

This difference equation can be simplified to

$$x_{n+1} = rx_n^2\sum_{n=0}^{\infty}\left(-rx_n^2\right)^n = \frac{rx_n^2}{1 + rx_n^2}. \tag{3.6}$$

As we can see, the value of state variable x at future time $t = n+1$ is expressed as an infinite series that converges to a simple function of the value of the same variable at present time $t = n$. The replacement procedure described above made possible to transform the incursive model (3.5) to the recursive one (3.6).

Comment. The same result can be obtained much more simply by solving equation (3.5) with respect to x_{n+1}.

Let us investigate a population, the evolution of which is controlled by equation (3.6). The function $g_r(x) = rx^2/\left(1 + rx^2\right)$ represents evidently a continuous mapping of $[0,1]$ into itself. Graphs of the function for some values of r are given in Fig. 2.

As we can see from Fig. 2, the model (3.6) has asymptotically stable equilibrium point $\alpha = 0$ for all values of r. It means that the trajectories generated by any point x_0 lying in a certain neighborhood of this point tend to zero. Therefore, in this case a population is dying out.

In the case $r = 4$ another equilibrium point $\beta = 1/2$ with an interesting property appears. The trajectories generated by any point $x_0 \in [0, \beta)$ tend to α, while the trajectories starting from any point $x_0 \in [\beta, 1]$ converge to β.

For $r > 4$ the equilibrium point β splits into two other equilibrium points

$$\beta_1 = \frac{-\sqrt{r}\sqrt{r-4} + r}{2r}, \quad \beta_2 = \frac{\sqrt{r}\sqrt{r-4} + r}{2r},$$

the first of them being evidently unstable ($f'(\beta_1) > 1$) and the second asymptotically stable $\left(0 < f'(\beta_2) < 1\right)$. It is easy to show that the trajectories generated by any point $x_0 \in [\beta_1, 1)$ tend to β_2, while those starting from $x_0 \in [0, \beta_1)$ go to α.

The attempts to find periodic trajectories with period 2 were not successful. Therefore, according to the Šarkovskij theorem (1964), the incursive model (3.5) shows neither periodic nor chaotic trajectories.

It is clear that the dynamics of the incursive model (3.5) is rather simple. Any population controlled by the models either dies out or tends to the equilibrium state β_2. There are neither periodic (asymptotically periodic) nor chaotic trajectories.

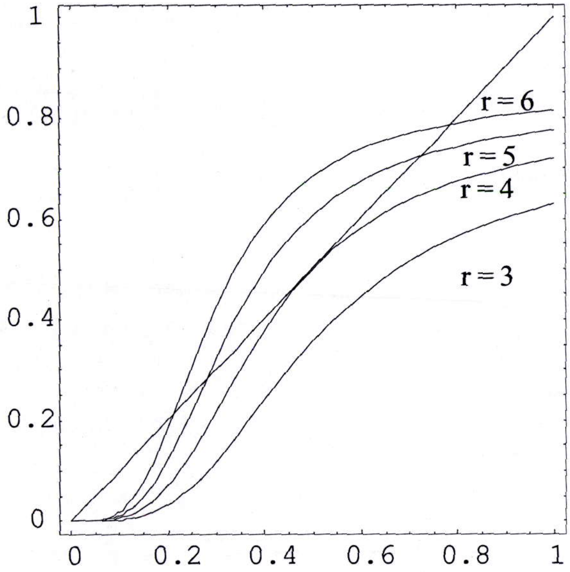

Figure 2: Graphs of $g_r(x)$ for $r = 3$; 4; 5 and 6.

3.3 Hyperincursive model

A simple example of hyperincursive model is given by the following difference equation

$$x_{n+1} = rx_n x_{n+1}(1 - x_{n+1}). \tag{3.7}$$

When solving (3.7) with respect to x_{n+1}, we get two solutions

$$x_{n+1} = \begin{cases} 0 & (3.8a) \\ \dfrac{rx_n - 1}{rx_n} & (3.8b) \end{cases}$$

It means that each iterate x_n generates at each time step two different values x_{n+1}, the first of them (zero solution) being uninteresting from biological point of view. Therefore, we will continue in analyzing the second solution.

The function $h_r(x) = (rx-1)/rx$ represents a continuous mapping of $(0,1]$ into $(-\infty,1]$. The graphs of the function for $r = 3;\ 4;\ 5$ and 6 are given in Fig. 3.

For $r < 4$ the models controlled by equation (3.8b) have no equilibrium points at all. In case $r = 4$ there is only one equilibrium point $\beta = 1/2$ that is asymptotically stable for trajectories generated by any point $x_0 \in [\beta,1]$.

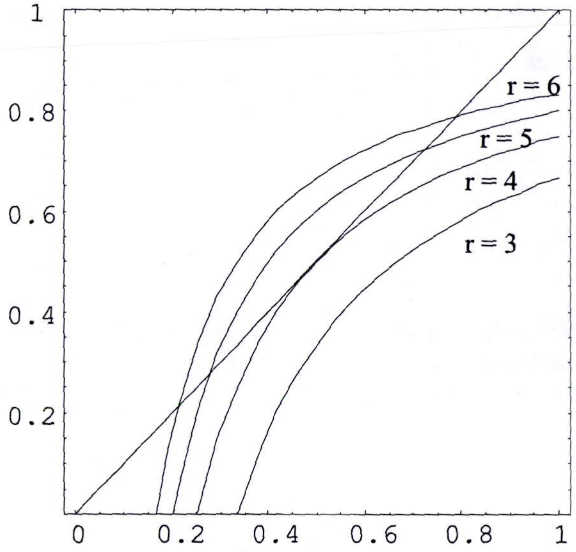

Figure 3: Graphs of $h_r(x)$ for $r = 3;\ 4;\ 5$ and 6.

As it is evident from Fig. 3, for $r > 4$ the model possesses two equilibrium points:

$$\beta_1 = \frac{-\sqrt{r}\sqrt{r-4}+r}{2r}, \quad \beta_2 = \frac{\sqrt{r}\sqrt{r-4}+r}{2r},$$

the former being unstable and the latter asymptotically stable for trajectories generated by any point $x_0 \in (\beta_1,1]$.

With respect to the course of $h_r(x)$, the behavior of the model (3.8b) is rather strange. For any $r > 0$ the trajectories generated by the point $x_0 = 1/r$ terminate (after two time steps) at $x_2 = -\infty$. In case $r > 4$ the trajectories generated by any $x_0 \in (0,\beta_1)$ also tend to β_2 but pass through points that have no biological interpretation. Therefore, the hyperincursive model seems to be unrealistic.

4 Conclusions

The analysis of our population model proved that the use of the concepts of incursion and hyperincursion results in a substantial change in the model dynamics. While the classical (recursive) model (3.2) shows a complicated behavior (equilibrium points, periodic and even chaotic trajectories), the dynamics of the incursive model (3.5) (model of an anticipatory system) is very simple (only equilibrium points). These conclusions are similar to those made recently when studying the dynamics of the logistic population model (Křivý, 2006). The hyperincursive model (3.7) seems to be unrealistic.

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