Order and chaos in a model of population biology

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1 Introduction

The ancient Greeks meant under *chaos* ($\chi\alpha o\sigma$) the infinite empty space which existed before all things. The later Roman conception interpreted chaos as the original crude shapeless mass into which the Architect of the world introduced order and harmony. In the present day, scientists understand the chaos as a state of disorder and irregularity in a dynamical system. The goal of this theme is to reveal some of the mysteries of this concept using a very simple model of population biology.

Mathematical modeling is aimed to predict how a system will evolve as time progresses. Given certain observable or experimentally determined parameters, the population biologist is interested in what happens to an initial population of x_0 members. Does the population tend to zero as time goes on, leading to extinction of the species? Does the population become arbitrarily large, indicating eventual overcrowding? Or does the population fluctuate periodically or even irregularly? The most general question is: given x_0, what can we say about the long-term behavior of the population?

This paper is addressed to readers who like the challenge of applying mathematics to real-life problems. A good prerequisite for understanding it would be to know how to find solutions of quadratic equations involving parameters as well as derivatives of polynomials. Some skills in exploring software packages like computer algebra systems would support better understanding.

2 Modeling population growth: the discrete logistic model

What is a population-dynamic model? It is simply a law which, given some biological species, allows us to predict the development of that species in time. Time is measured in increments $n = 0\bullet 1\bullet 2\bullet\bullet\bullet\bullet$ (years, months, days, hours, or other specific time-units). The size of the population is measured at time n by the number of species y_n.

The count of a population depends on many environmental conditions such as food supply, space, climate, as well as on the interaction with other species such as the predator/prey relation ship, etc. One of the first models of population growth goes back to the Belgian mathematician *Pierre François Verhulst* and his work around 1845. He assumes that there is some maximal possible population size Y, which is supported by the environment. If the actual population y_n at time n is smaller than Y the population will grow; if y_n is larger than Y, the population must decrease. First we normalize the population count by setting $z_n = y_n \bullet Y$, thus for all $n = 0\bullet 1\bullet 2\bullet\bullet\bullet\bullet$, z_n ranges between 0 and 1. Let the rate at which the population increases or decreases from time n to the next time $n+1$ is given by the quantity $\dfrac{z_{n+1}-z_n}{z_n}$. Verhulst supposes that the growth rate is proportional to $1-z_n$; the latter expression can be interpreted as the part of environment, which has not been used up by the population till the time moment n. After introducing a proportional constant q, which does not depend on n, we obtain

$$\frac{z_{n+1}-z_n}{z_n} = q(1-z_n);$$

solving the last equation with respect to z_{n+1} leads to the *Verhulst's discrete model*

$$z_{n+1} = z_n + qz_n(1-z_n)\bullet \quad n = 0\bullet 1\bullet 2\bullet\bullet\bullet\bullet \tag{1}$$

We shall reformulate the Verhulst's model (1) in another form, which is simpler and more convenient for investigation. Using the substitutions $x_n = \dfrac{q}{1+q}z_n$ and $r = 1+q$ we obtain

$$x_{n+1} = \frac{q}{1+q}z_{n+1} = \frac{q}{1+q}\left(z_n + qz_n(1-z_n)\right) = (1+q)\cdot\frac{q}{1+q}z_n\cdot\left(1-\frac{q}{1+q}z_n\right) = r\,x_n\,(1-x_n)\bullet$$

The equation

$$x_{n+1} = r\,x_n\,(1 - x_n)\bullet \quad n = 0\bullet 1\bullet 2\bullet\bullet\bullet\bullet \qquad (2)$$

is known as the *discrete logistic model*. The condition $0 \leq x_n \leq 1$ for all n imposes the relation $0 \bullet\ \ r \leq 4$. Consider r as a parameter and define the function

$$f_r(x) = r\,x\,(1 - x)\bullet \quad x \in [0\bullet 1]\bullet \quad r \in (0\bullet 4]\bullet \qquad (3)$$

Then (2) can be rewritten in the form $x_{n+1} = f_r(x_n)\bullet \ \ n = 0\bullet 1\bullet 2\bullet\bullet\bullet\bullet$ The function f_r from (3) is called the *logistic function*. Figure 1 presents the graphs of $y = f_r(x)$ for different values of the parameter r. The plots visualize also the bisector of the first quadrant, the line $y = x$, called further *bisector* for short.

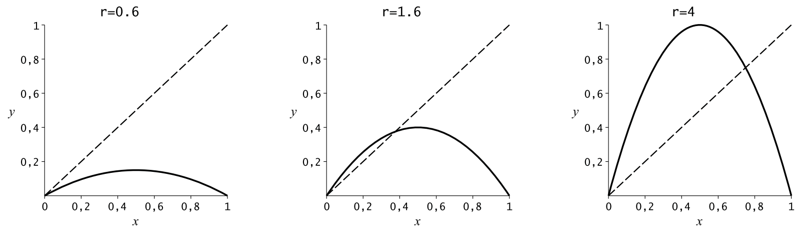

Figure 1: Graphs of the logistic function $y = f_r(x)$ for different values of r

Let $x \in [0\bullet 1]$ be a point. Define

$$f_r^1(x) = f_r(x)\bullet \ \ f_r^2(x) = f_r(f_r(x))\bullet \ \ f_r^3(x) = f_r(f_r^2(x))\bullet\bullet\bullet\bullet\bullet \ f_r^n(x) = f_r(f_r^{n-1}(x))\bullet\bullet\bullet\bullet$$

Thus, f_r^n denotes the n-fold composition of f_r with itself. We call f_r^n the n-th iterate of f_r.

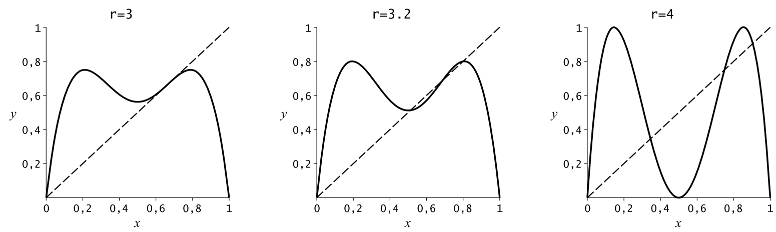

Figure 2: Graphs of the second iterate $y = f_r^2(x)$ for different values of r

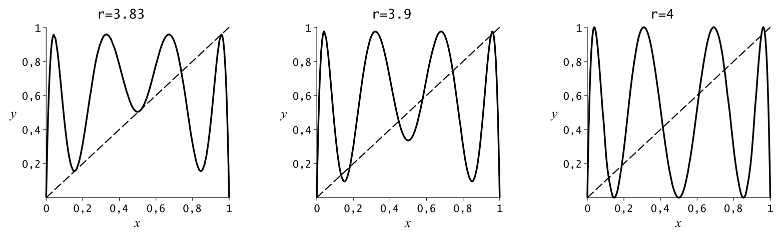

Figure 3: Graphs of the third iterate $y = f_r^3(x)$ for different values of r

Figures 2 and 3 show the graphs of the second iterate $y = f_r^2(x)$ and of the third iterate $y = f_r^3(x)$ respectively for different values of $r \geq 3$, as well as the line $y = x$.

For $x_0 \in [0\bullet 1]$ we can write $x_1 = f_r^1(x_0)$, $x_2 = f_r^2(x_0)$, $x_3 = f_r^3(x_0)\bullet\bullet\bullet\bullet\bullet\, x_n = f_r^n(x_0)\bullet\bullet\bullet\bullet$ Therefore, using the function f_r we may predict the population size x_0 by simply iterating it. It sounds very easy, right? Surprisingly, this logistic model was completely understood in the late 1990s, thanks to the work of hundreds of mathematicians.

The sequence of points $x_0\bullet x_1\bullet x_2\bullet\bullet\bullet\bullet\bullet x_n\bullet\bullet\bullet\bullet$ is called the *orbit* of x_0 under f_r; the starting point x_0 for the orbit is called the *initial value* or *initial point* of the orbit.

Our goal is to understand the orbit structure for sufficiently large n, without computing every time consecutively all the terms $x_1\bullet x_2\bullet\bullet\bullet\bullet\bullet x_n$. This is what scientists call *long-term prediction of the model*.

3 Cobweb plotting: graphical presentation of orbits

A point x, such that $f_r(x) = x$ holds true, is called a *fixed point* of the logistic function. Graphically, the fixed points are the intersecting points of the graphs of $y = x$ and $y = f_r(x)$.

A point x, such that $f_r^2(x) = x$, but $f_r(x) \neq x$, is called a *period-2 point* of $f_r(x)$. Graphically, the period-2 points are intersecting points of the graphs of $y = x$ and $y = f_r^2(x)$.

A point x, such that $f_r^n(x) = x$ and n is the smallest such positive integer, is called a *period-n point* of $f_r(x)$. Graphically, the period-n points are intersecting points of the graphs of $y = x$ and $y = f_r^n(x)$.

Assume that the initial value x_0 is a fixed point of f_r, i. e. $f_r(x_0) = x_0$. Then we have

$$x_1 = f_r(x_0) = x_0\bullet\ x_2 = f_r(x_1) = f_r(x_0) = x_0\bullet\bullet\bullet\bullet\bullet x_n = f_r(x_{n-1}) = x_0\bullet\bullet\bullet\bullet;$$

the orbit of x_0 is the constant sequence $x_0\bullet x_0\bullet\bullet\bullet\bullet\bullet x_0\bullet\bullet\bullet\bullet$ for all over the time. The population is predictable in long run.

Assume now that the initial value x_0 is a period-2 point of f_r, i. e. $f_r^2(x_0) = x_0$. We have

$$x_1 = f_r(x_0)\bullet\ \ x_2 = f_r(x_1) = f_r^2(x_0) = x_0\bullet\ \ x_3 = f_r(x_2) = f_r(x_0) = x_1\bullet$$
$$x_4 = f_r(x_3) = f_r(x_1) = x_0\bullet\ \ x_5 = f_r(x_4) = f_r(x_0) = x_1\bullet\bullet\bullet\bullet$$

and the orbit of x_0 is $x_0\bullet x_1\bullet x_0\bullet x_1\bullet\bullet\bullet\bullet\bullet x_0\bullet x_1\bullet\bullet\bullet\bullet$; it repeats itself building a *cycle with period 2*, which we shall also call a *period-2 cycle* or *period-2 orbit* for short. The population is predictable although it oscillates between two values for all over the time.

Task 1. Write down the orbit corresponding to a period-3 point x_0. How does the orbit look like when x_0 is a period-n point ($n \bullet\ 3$)?

Consider the case, when the initial value x_0 is not a fixed point of f_r. A useful way to visualize the orbit of x_0 is via *graphical iteration* or *cobweb plotting*. As before, we display the curve $y = f_r(x)$ and the bisector $y = x$ on one picture (Figure 4). Starting at the point $X = (x_0\bullet x_0)$ on the bisector (Figure 4, $r = 0\bullet 8$), we draw a vertical line to the graph of f_r reaching the graph at $(x_0\bullet f_r(x_0)) = (x_0\bullet x_1)$. Then we draw a horizontal line back to the bisector, ending at $(x_1\bullet x_1)$. We repeat the procedure from $(x_1\bullet x_1)$. This technique works because the points on the bisector $y = x$ have the same distance from both axes x and y.

Figure 4 visualizes orbits of different initial points x_0 under iteration of f_r for different values of r. In the first plot ($r = 0\bullet 8$), 0 is the unique fixed point of f_r. Starting with $x_0 = 0\bullet 4$, its orbit goes closer and closer to 0 as n increases.

Task 2. For $r = 0\bullet 8$ compute several points of the orbit using a calculator or an appropriate software, starting each time with different $x_0 \in (0\bullet 1)$.

As you have found, the result will be the same: all orbits tend to 0. The fixed point 0 is called *attracting fixed point* or *stable fixed point*. In the second plot ($r = 2$), there exist two fixed points, $\zeta_0 = 0$ and $\zeta_1 = 0\bullet 5$. In this case each of the fixed points acts differently on the orbits starting near (but not precisely on) ζ_0 or ζ_1. You may convince yourself that all initial values, even near $\zeta_0 = 0$, are moved away from 0, but attracted by $\zeta_1 = 0\bullet 5$ as n increases. In this case ζ_1 is the attracting point, whereas ζ_0 is called

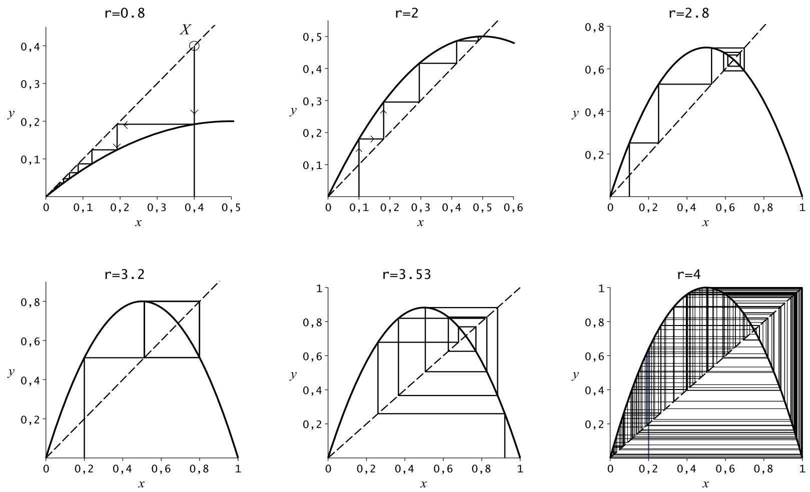

Figure 4: Orbits under iteration of f_r for different values of r

repelling fixed point or *unstable fixed point*. The case $r = 2{\bullet}8$ is similar to the previous one: the orbit of $x_0 = 0{\bullet}1$ tends to the stable fixed point $\zeta_1 \approx 0{\bullet}6$, building a spiral around it.

The case $r = 3{\bullet}2$ is different. The fixed points of f_r are $\zeta_0 = 0$ and $\zeta_1 \approx 0{\bullet}7$. The graphical iteration technique shows that ζ_0 and ζ_1 are repelling for any initial value $x_0 \in (0{\bullet}1)$. Where do orbits go now?

Task 3. Use a calculator or an appropriate software to convince yourself that for $r = 3{\bullet}2$ and for every choice of the initial value x_0 the orbits oscillate between two values, $\zeta_2 \approx 0{\bullet}5$ and $\zeta_3 \approx 0{\bullet}8$.

The orbit is attracted to ζ_2 every two iterates, and to ζ_3, on alternate iterates. Such orbit is called *stable period-2 cycle*. For $r = 3{\bullet}53$ the orbit on Figure 4 presents a *stable period-4 cycle*; $x_0 = 0{\bullet}2$ is attracted by the period-4 points $\{\zeta_4{\bullet}\zeta_5{\bullet}\zeta_6{\bullet}\zeta_7\}$, where $\zeta_4 \approx 0{\bullet}4$, $\zeta_5 \approx 0{\bullet}5$, $\zeta_6 \approx 0{\bullet}8$ and $\zeta_7 \approx 0{\bullet}9$.

The examples and the graphic visualizations on Figure 4 show that changing r leads to quite different behavior of the logistic model: new stable fixed points are 'born' and stable periodic orbits of period 2 and 4 appear. It is the existence of stable fixed points or stable periodic orbits that means predictability of the population size in long-run. Some intuition tells us that as r continues to increase, higher period orbits (e. g. period-8, period-16 etc.) can appear. Does this period-doubling effect ever stop? What happens if it eventually stops?

Before answering these questions, let us consider the case $r = 4$ in Figure 4. The single orbit of $x_0 = 0{\bullet}2$ under f_4 shows a complicated behavior: it looks like that the orbit doesn't come to rest and appears to randomly fill out the entire interval $[0{\bullet}1]$, without being predictable. Such orbit behavior is what we call *chaos*.

4 Stability and bifurcations of fixed points

To find a fixed point of f_r, we have to solve the equation $f_r(x) = x$ within $x \in [0{\bullet}1]$, where r is a parameter, $r \in (0{\bullet}4]$. Obviously, $f_r(x) = x$ is equivalent to $rx(1-x) = x$.

Task 4. Show that f_r has two fixed points in $[0{\bullet}1]$, $\zeta_0 = 0$ and $\zeta_1 = 1 - \dfrac{1}{r}$.

The solution of Task 4 implies that the logistic function f_r has a unique fixed point $\zeta_0 = 0$ for $r \in (0{\bullet}1)$ and two fixed points for $r \geq 1$; at $r = 1$, both fixed points coalesce, $\zeta_0 = \zeta_1 = 0$.

Stability test of fixed points. A fixed point ζ of f_r is *attracting* or *stable* if the derivative of $f_r(x)$, evaluated at ζ is in magnitude less than 1, i. e. if $|f_r'(\zeta)| \bullet\ 1$ holds true. The fixed point ζ of f_r is *repelling* or *unstable* if $|f_r'(\zeta)| \bullet\ 1$ is satisfied.

Task 5. Find the derivative $f_r'(x)$ of the logistic function $f_r(x)$ and prove that $f_r'(\zeta_0) = r(1-2\zeta_0) = r$, $f_r'(\zeta_1) = r(1-2\zeta_1) = 2-r$. Prove that $|f_r'(\zeta_0)| \bullet\ 1$ iff $0 \bullet\ r \bullet\ 1$, and $|f_r'(\zeta_1)| \bullet\ 1$ iff $1 \bullet\ r \bullet\ 3$.

Now we can conclude that for $r \in (0\bullet 1)$ the fixed point ζ_0 is attracting; for $r \in (1\bullet 3)$ the fixed point ζ_1 is attracting, but ζ_0 is repelling (Figure 4, the orbits for $r = 0\bullet 8$, $r = 2$ and $r = 2\bullet 8$).

There is just one case not covered by the Stability test, namely the case $|f_r'(\zeta)| = 1$ for a fixed point ζ. For $r = 1$ we have $\zeta_0 = \zeta_1$ and $f_r'(\zeta_0) = f_r'(\zeta_1) = 1$, i. e. the second fixed point ζ_1 has been 'born' from ζ_0, followed by an exchange of stability between ζ_0 and ζ_1. We say that a *bifurcation* of ζ_0 has occurred.

Assume now that $r \bullet\ 3$ and consider the second iterate $f_r^2(x)$. The fixed points of $f_r^2(x)$ are solutions of the equation $f_r^2(x) = x$, which is equivalent to $x(1-r+rx)\left(r^2x^2 - r(r+1)x + r + 1\right) = 0$. Obviously, the fixed points $\zeta_0 = 0$ and ζ_1 of f_r are also fixed points of $f_r^2(x)$. To find the period-2 points of f_r, we have to solve (with respect to x) the quadratic equation

$$r^2x^2 - r(r+1)x + r + 1 = 0\bullet \tag{4}$$

Task 6. Show that if $r \bullet\ 3$, there are two real positive roots of (4), ζ_2 and ζ_3, such that

$$\zeta_2 = \frac{1}{2r}\left(r+1-\sqrt{(r+1)(r-3)}\right)\bullet \quad \zeta_3 = \frac{1}{2r}\left(r+1+\sqrt{(r+1)(r-3)}\right)\bullet \tag{5}$$

Now you can see that at $r = 3$ the two roots coalesce, $\zeta_2 = \zeta_3 = \dfrac{2}{3}$; moreover, $\zeta_2 = \zeta_3 = \zeta_1$ and $f_r'(\zeta_1) = -1$ for $r = 3$. So, for $r = 3$, ζ_1 is neither stable nor unstable according to our Stability test; at this critical value for r, the two new points ζ_2 and ζ_3 are 'born' from ζ_1. It can be proved directly, that $f_r(\zeta_2) = \zeta_3$ and $f_r(\zeta_3) = \zeta_2$ are satisfied. This is again a *bifurcation* of the fixed point, called the *period-doubling bifurcation* of the fixed point. Denote by r_1 the bifurcation value $r = 3$, i. e. $r_1 = 3$.

Task 7. Find the derivative of $f_r^2(x)$ and show that $|(f_r^2)'(\zeta_2)| = |(f_r^2)'(\zeta_3)| = |f_r'(\zeta_2)| \cdot |f_r'(\zeta_3)| \bullet\ 1$ iff $3 \bullet\ r \bullet\ 1+\sqrt{6}$.

The period-2 points ζ_2 and ζ_3 are attracting for $3 \bullet\ r \bullet\ 1+\sqrt{6}$; for these values of r, the previous two points ζ_0 and ζ_1 are repelling. For $r = r_2 = 1+\sqrt{6} \approx 3\bullet 4494897$, the fixed points ζ_2 and ζ_3 are neither stable nor unstable. We can expect that at $r = r_2$, new fixed points will be 'born', the period-4 points of f_r. Using numerical techniques, it is possible to determine a next bifurcation value r_3 of the parameter, $r_3 \approx 3\bullet 5440903$, such that for $r \in (r_2\bullet r_3)$, there exist exactly four real positive solutions ζ_4, ζ_5, ζ_6 and ζ_7, which bifurcate pair-wise from ζ_2 and ζ_3 at $r = r_2$. At $r = r_3$, the period-8 points are 'born' in such a way, that each one of ζ_4, ζ_5, ζ_6 and ζ_7 bifurcates into two new points. It can be shown that the period-8 points are stable until r reaches the next bifurcation value $r_4 \approx 3\bullet 5644073$, where the period-16 points are 'born'. Figure 5(a) visualizes the stable branches of the fixed points, the period-2, period-2^2 and period-2^3 points of f_r as functions of r. It seems natural to assume, that there is an infinite sequence of bifurcation parameter values

$$r_1\bullet r_2\bullet r_3\bullet r_4\bullet\bullet\bullet\bullet\bullet r_{k-1}\bullet r_k\bullet r_{k+1}\bullet\bullet\bullet \tag{6}$$

such that at each r_k, the stable period-2^k points of f_{r_k} are replaced by period-2^{k+1} points; the previous, lower period points continue to exist, but as unstable ones. During a computer simulation, only a finite number of cycles is distinguishable due to the finite computational precision. The sequence (6) is convergent, that is there exist $r^* \in (3\bullet 4)$ such that r_k tends to r^* as k increases, $r^* \approx 3\bullet 569944\bullet\bullet\bullet\bullet\ 4$.

Consider the case $r = 4$ and denote $f_4(x) = 4x(1-x)$. We can conclude from the graphs of f_4, f_4^2 and f_4^3 on Figures 1, 2 and 3 respectively, that f_4 has 2 fixed points, 0 and $3\bullet 4$, and that they are both unstable (check it!); f_4^2 has 2^2 fixed points, f_4^3 has 2^3 fixed points, and by induction f_4^n possesses 2^n fixed points, all in the interval $[0\bullet 1]$. The four fixed points of f_4^2 include 0 and $3\bullet 4$ plus a pair of period-2 points; the

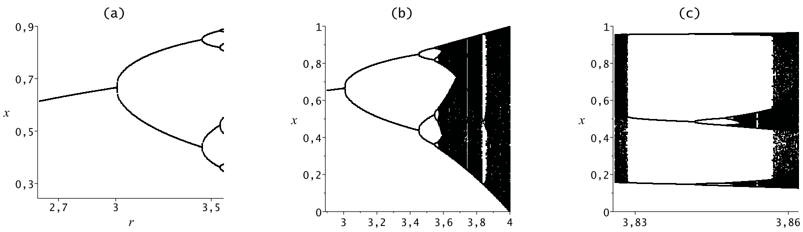

Figure 5: (a), (b) Bifurcation diagrams; (c) The period-3 window

latter can be computed using formulae (5) for $r = 4$; the period-2 points are unstable. Among the 8 fixed points of f_4^3, two are the fixed points 0 and $3\bullet 4$, and the other 6 form two *period-3* cycles; among the 16 fixed points of f_4^4 there are two fixed points, two period-2 points and 12 periodic points of period 4. In general, for each positive integer n there exists an orbit of period-n for f_4. However, if we chose a random initial point in $(0\bullet 1)$ and plot its orbit under iteration of f_4, we can hardly observe any of these cycles as in the last case of Figure 4.

5 Paths to the chaos

Careful numerical computation shows that for $r \leq r^*$, the orbit of any initial point $x_0 \in (0\bullet 1)$ is predictable in the following sense. Let us take two initial points x_0 and $\bar{x}_0$ such that $|x_0 - \bar{x}_0| \bullet \varepsilon$ with arbitrarily small $\varepsilon \bullet 0$. Then for sufficiently large time-moment n we have $f_r^n(x_0) \approx f_r^n(\bar{x}_0)$, i. e. orbits of *close* initial points remain *close*. We say that there is no sensitive dependence on initial conditions.

The function $f_4(x)$ shows in turn *sensitive dependence on initial conditions*. More precisely, for any initial point $x_0 \in (0\bullet 1)$ and any arbitrarily small $\varepsilon \bullet 0$, there exist a second point $\bar{x}_0$ such that $|x_0 - \bar{x}_0| \bullet \varepsilon$, and there exists a distance $d \bullet 0$, so that the inequality $|f_4^n(x_0) - f_4^n(\bar{x}_0)| \geq d$ holds for sufficiently large n. In other words, the two orbits of x_0 and $\bar{x}_0$ will be at least d units apart after a sufficiently large number of iterations. The orbit of x_0 is called a *chaotic orbit*. A chaotic orbit can neither manage to find a stable fixed point to be attracted to, nor is it a periodic one.

The behavior of the logistic model is predictable for $r \leq r^*$, but for $r = 4$ it is unpredictable (chaotic). Our intuition tell us that in the range $r^* \bullet r \bullet 4$ there will be a transition from order into chaos. Figure 5(b) shows an interesting aspect of the paths to the chaos. For $r \bullet r^*$, the orbits appear to fill out subintervals (sets) of $[0\bullet 1]$ or the entire interval $[0\bullet 1]$ (for $r = 4$). These sets have very special (fractal) structure and are difficult to describe. One of their characteristics is that they can abruptly appear or disappear, being interlaced by "white windows". The largest such window is shown in magnified form for r between $1 + \sqrt{8} \approx 3\bullet 83$ and $3\bullet 85$ in Figure 5(c). It is also called the *period-3 window*, because for $r = 1 + \sqrt{8}$ the period-3 points of f_r are 'born'. The period-3 cycle is followed by a period doubling bifurcation, which creates a period-6 orbit and so on. An important theorem, stating that if a solution of period-3 exists for a value $\bar{r}$, then chaotic solutions exist for $r \bullet \bar{r}$, was published by Sharkovskii (1964).

Recommended further reading

- Alligood K. T., Sauer T. D., Yorke J. A. *Chaos: An Introduction to Dynamical Systems*, Springer, New York, 1996.
- Peitgen H.-O., Jürgens H., Saupe D. *Fractals for the Classroom. Part One: Introduction to Fractals and Chaos*, Springer, New York, 1992.