

Period-doubling reversals and chaos in simple ecological models

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The period-doubling route to chaos is a well known feature of a range of simple, nonlinear difference equations routinely used in modelling biological populations. It is not generally understood, however, that the process may easily break down and suddenly reverse, giving rise to distinctive period-halving bifurcations. These reversals may act to control, and possibly prevent, the onset of chaos.

THEORETICAL notions of balance, stability and change have all been instrumental in shaping our perceptions of ecological and biological processes^{1,2}. Even the earliest human societies developed some rudimentary formulation of the background assumption of ecology: the 'balance of nature' concept¹. The belief in a stable, ordered equilibrium world, in which nature is normally considered to exist in balance, generally remained unchallenged for millennia. Yet the concepts of imbalance, variability and indeterminate chance events proved to be of crucial importance, so much so that by 1930 the celebrated British ecologist Charles Elton could safely state that: "'The balance of nature' does not exist, and perhaps never existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude"³. It took decades for the ecological community to digest Elton's message, and even as late as 1980, Simberloff found it necessary to stress the significance of probabilism, arguing that what might be noise to the physicist "is music to the ecologist"⁴.

It was not until 1974, however, that Robert May demonstrated that this seemingly stochastic behaviour could in fact be explained by the highly complex and chaotic behaviour that arises from nonlinearities in the simplest deterministic population models, an insight which has had a radical impact both in ecology and elsewhere.

Here I review some of the basic concepts pertaining to chaos in population models and reexamine the conditions under which it occurs. The period-doubling route to chaos (described below), thought to be generic to the family of 'single-humped' one-dimensional maps, may in important cases be absent. For many models, a seemingly minor structural perturbation with real ecological justification is all that is required to break down and reverse the expected period-doubling route to chaos. If these models are taken to illustrate population dynamics in the real world, then chaos may be a fragile process, the well known 'universal' behaviour being easily inhibited. More importantly, these period-doubling reversals may be used to control chaos, as they have the potential to suppress dangerous chaotic fluctuations.

First-order equations

Simple nonlinear difference equations provide a unifying framework for a diverse array of mathematical models encompassing a wide range of disciplines⁵⁻¹⁰. Without loss of generality, the following study is set in an ecological context where the variable N_t represents the population size or biomass of a species in generation t , and satisfies a general first-order equation of the form:

$$N_{t+1} = F(N_t). \quad (1)$$

Here F is a one-dimensional map reflecting nonlinear density-dependent growth⁵. Unless otherwise stated, it is assumed that F is 'single-humped' (possessing a unique maximum) with a shape

controlled only by one parameter, such as r . The time-evolution of the population model is found by iterating the equation from an initial population $N_1 > 0$, to yield the sequence:

$$N_1 \rightarrow N_2 = F(N_1) \rightarrow N_3 = F(N_2) \rightarrow N_4 = F(N_3) \rightarrow \dots$$

Under these bare specifications, equation (1) displays an intricate structure of cyclical solutions governed only by the parameter r (Fig. 1).

When F belongs to a general class of 'single-humped' functions, termed here U -functions, equation (1) displays a bifurcation structure that is 'universal' in that: first, the bifurcation structure conforms with Feigenbaum's period-doubling route to chaos whereby the number of stable periodic points successively double as the parameter r increases, in a manner that is ultimately independent of the specific form of the U -function⁹; second, as r approaches a critical value r_c , an infinite number of fixed points emerge and the population dynamics become chaotic; and third, when r is increased beyond r_c , a chaotic regime is entered that contains an ordered U (universal) sequence of periodic windows¹¹.

Reversals in a model of immigration

Surprisingly, the precise conditions that determine whether F actually belongs to the special class of U -functions, and so inherits these properties, are unknown^{11,13}. But it has been suggested that to exclude all cases of anomalous non-universal behaviour would necessarily "restrict the underlying class of transformations [U -functions] rather drastically"¹¹. There is thus a need to assess whether U -functions are general enough to represent ecological processes usefully, and to question how robust their dynamics might be to small but realistic structural changes.

To gain some understanding of the problem, consider the well known model of logistic population growth:

$$N_{t+1} = F(N_t) = N_t \exp[r(K - N_t)] \quad (2)$$

which displays all the features characteristic of a U -function. Equation (2) has become a model for illustrating the transition to chaos in one-dimensional maps⁵⁻⁷. In biological terms, the parameter r reflects the population's natural growth rate, and K reflects the carrying capacity of the environment and may be scaled to unity ($K=1$) without loss of generality.

This model can be extended to allow for other ecological factors. Numerous sub-populations relying either on refuges for protection, or on an influx of individuals by immigration, must for example have a floor ($\lambda > 0$) below which the population level never falls. To model this, McCallum⁸ modified equation (2) as follows:

$$N_{t+1} = N_t \exp[r(1 - N_t)] + \lambda, \quad \lambda > 0 \quad (3)$$

with $N_t > \lambda$. The constant term λ is intended to represent either the number of immigrants per generation or, if a refuge exists, that small sub-population which becomes isolated and therefore largely released from density-dependent effects.

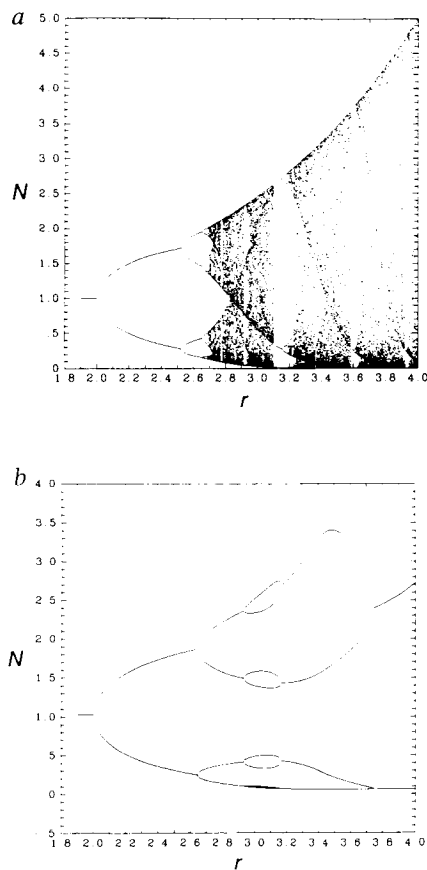


FIG. 1 Bifurcation diagram for a, equation (2); b, equation (3), $\lambda = 0.06$. For each of 1,100 values of r , the respective equation was iterated 700 times and the last 200 points were plotted. The bifurcation diagram in a summarizes the periodic and aperiodic dynamics of the logistic population model:

$$N_{t+1} = F(N_t) = N_t \exp [r(K - N_t)]. \quad (B1)$$

To review briefly some of the principal ideas involved, first note that the iterates of the model form a p -cycle of period p , if for some t , $N_t = N_{t+p}$ but $N_t \neq N_{t+j}$ for any integer j where $1 \leq j < p$. The model then repeatedly cycles through p distinct points and the stability of the cycle can be deduced from standard analytic or numerical techniques^{6,7}. For values of $r < 2$, one sees from the bifurcation diagram that the equation possesses an attracting equilibrium point. By increasing r to a value slightly greater than $r = 2$, the equilibrium bifurcates and a two-cycle is born; the model then alternates between two population levels $N_1 \rightarrow N_2 \rightarrow N_1 \rightarrow N_2 \rightarrow N_1 \rightarrow \dots$. By raising r yet further, the two-cycle bifurcates and forms a four-cycle $N_1 \rightarrow N_2 \rightarrow N_3 \rightarrow N_4 \rightarrow N_1 \rightarrow N_2 \rightarrow \dots$. Increasing r in this same manner, yields an infinite succession of bifurcations so creating a hierarchy of stable cycles of periods 2, 4, 8, 16, \dots , 2^n ($n \rightarrow \infty$). This succession of bifurcations develops at a geometric rate and accumulates asymptotically as $n \rightarrow \infty$ at $r = r_c$. For the above logistic map $r_c = 2.6924$ where aperiodic dynamics begin. Beyond this point of accumulation the bifurcation diagram displays a highly complicated chaotic regime interspersed with periodic windows. Each window is characterized by its own specific periodicity (that accords with the U -sequence¹¹) and period-doubling cascade. For example, a period-3 window is clearly visible in the bifurcation diagram, beginning at $r = 3.1024$. An enlargement of the window would reveal a period-doubling cascade with a hierarchy of cycles of period $3, 3 \cdot 2^1, 3 \cdot 2^2, 3 \cdot 2^3, \dots, 3 \cdot 2^n$ ($n \rightarrow \infty$).

For values of $\lambda \ll 1$, equation (3) might be viewed as a structural perturbation of equation (2). But the two models possess very different and qualitatively distinct dynamics. Figure 1b displays the bifurcation diagram of equation (3) when $\lambda = 0.06$. It explicitly illustrates a form of 'bubbling'¹³ in which the expected period-doubling bifurcation process curtails and reverses, giving

rise to period-halving bifurcations. Successive orbits of periods 1, 2, 4, 8, 4, 2 occur as r increases from zero. Increasing small period nonlinearity (r), and thus the severity of density-dependence, ultimately tends to stabilize the oscillations rather than producing chaotic population dynamics. Numerical calculations find no indication of stable cycles with a period greater than eight. On comparing the diagrams in Fig. 1, it is clear that this phenomenon of period-halving is not observed in equation (2). Furthermore, the anomaly of period-doubling reversals or bubbling derives from structurally perturbing what has been understood to be a U -function, in this case by an amount that is only 6% of the total carrying capacity.

A more complete investigation reveals the extent to which λ suppresses the period-doubling route to chaos. Figure 2 outlines the behaviour of equation (3) over a range of values in r - λ parameter space and demarcates regions in which the model exhibits stable orbits of periods $p = 1, 2, 4$ or > 4 . The model population is generally found either at equilibrium ($p = 1$) or characterized by a stable 2-cycle. Only a relatively small region of parameter space represents chaotic behaviour.

General occurrence of period-doubling reversals

Analysis of a number of common difference equation models reveals that perturbations of the type used above often lead to the suppression of chaos and the initiation of a reversal with period-doubling, eventually followed by period-halving as the parameter r is increased. The phenomenon occurs in models of the crown-of-thorns starfish⁸, insect populations^{14,15}, perennial grass inhibited by plant litter¹⁶, annual plant populations¹⁷, host-parasitoid interactions¹⁸, and systems of competing species⁷. The effect itself has already been observed in several models of genetic selection¹⁹, microbial predator-prey chemostats²⁰, phytoplankton-herbivore interactions (J. Steele and M. Pascual, personal communication), cardiac cell stimulation²¹, and coevolutionary host-parasite models²², but has generally not been properly interpreted and has almost never been framed in terms of the single-hump one-dimensional map (but see ref. 23). The presence of reversals has also been documented in other areas of research, ranging from models of magnetoconvection²⁴ and rotating galaxies²⁵, to a neuronal model of psychotic human behaviour²⁶. Also notable is Swinney's classic study^{27,28} of a chemical reaction in a stirred flow reactor yielding important empirical confirmation.

The explanation for this reversal of period-doubling in a broad class of function F is simple. As demonstrated in Box 1, the phenomenon may arise whenever a single-humped map has a point about which the function flattens out into a 'plateau'. Bifurcations are governed first by the 'hump', which is largely responsible for period-doubling; and second, by the concavity of the 'plateau' and its height (above the x -axis), factors which are conducive to period-halving. In some cases, the same argument can be extended to the analysis of one-dimensional maps

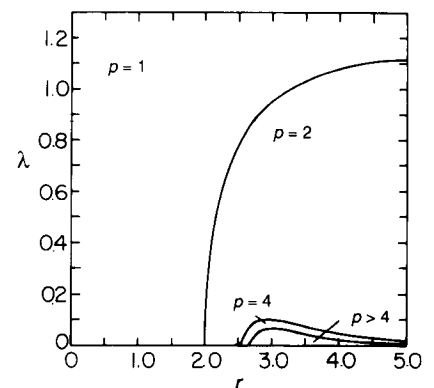


FIG. 2 Regions in r - λ parameter space for equation (3) characterized by low-order stable cycles of periods $p = 1, 2, 4, > 4$ as determined numerically.

BOX 1 The reversal of a period-doubling cascade

To explain how a period-doubling cascade reverses, it is useful to examine the graph of the single humped function F which has been scaled by various values of the parameter r for analysis of the equation $N_{t+1} = rF(N_t)$. F has a plateau region that flattens out for large N_t . The plateau can occur whenever there is a point of inflection or if the second derivative $F''(N)$ suddenly changes sign to the right of the critical point. The fixed points N^* may be found graphically at the intersections of the 45° line $N_{t+1} = N_t$ and the curve $rF(N_t)$. The stability of N^* is ensured if the slope $S(N) = rF'(N)$ of the curve at the intersection point satisfies $|S(N^*)| < 1$ (refs 5, 6).

Suppose the parameter r is continuously increased from zero. When the nontrivial stable fixed point $N = N^* > 0$ appears (at which point $S(N^*) > 0$), increasing r further serves to reduce $S(N^*)$, until $S(N^*) = -1$, when a period-doubling bifurcation occurs⁴⁰; the fixed point N^* becomes unstable and a stable two-cycle is born. A succession of period-doublings may follow in the usual manner as r is gradually increased. Consider now the case when r is large. Graphically the equilibrium point $N = N^*$ is stable because it lies in the plateau region where $S(N^*) \approx 0$. (The existence of this single stable equilibrium depends chiefly on the concavity and height of the plateau in a manner which can be expressed rigorously. For example, equation (3) has a plateau that is too steep to permit a stable equilibrium, even as $r \rightarrow \infty$, where it instead exhibits a stable two-cycle.) As r is gradually reduced, $S(N^*)$ continuously decreases, until $S(N^*) = -1$, when a period-doubling bifurcation occurs; again the fixed point N^* becomes unstable and a stable two-cycle emerges. As r is reduced further a succession of period-doubling can similarly result.

In summary, as r increases from zero the phenomenon of period-doubling must eventually be followed (at least for large r) by period-halving. (The breakdown in period-doubling occurs when for some stable k -cycle $\{N_i\}_{i=1, \dots, k}$, the slope of the k -fold map $F^k(N_i)$ is constrained so that $S(N_i) = r^k F^k(N_i) > -1$ and a period-doubling bifurcation cannot take place.) For similar reasons, perturbations that serve to translate the plateau vertically upwards yield the same qualitative result.

The function F in this example has been chosen as 'spiked' only to aid in the visualization of the process whereby period-doubling reversals are initiated. Its spiked shape is not essential to the general argument because vertical perturbations may also considerably enhance or initiate a reversal (as seen in Box 2).

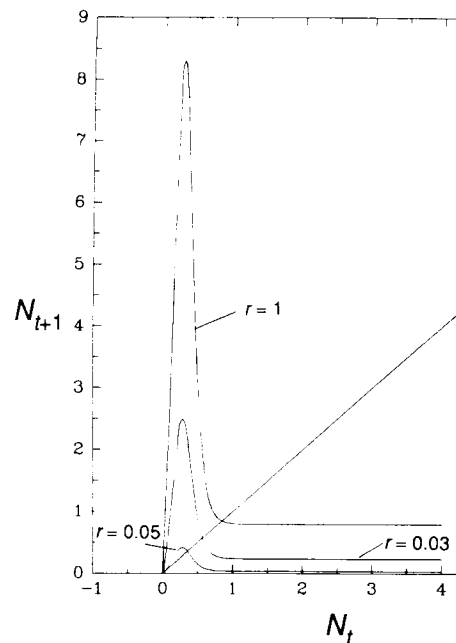
It is instructive to examine the alternative, though perhaps less biologically relevant⁶, quadratic model of logistic growth:

$$N_{t+1} = F(N_t) = rN_t(1 - N_t) \tag{C1}$$

F being a well known U -function. That F is purely concave-down explains in part why it fails to exhibit reversals after being perturbed to the form:

$$N_{t+1} = RN_t(1 - N_t) - \lambda, \quad \lambda > 0 \tag{C2}$$

To see this more directly, note that the perturbed map is, up to a linear change of coordinates, identical to equation (C1), the two maps being connected by the relation $r^2 = R^2 + 4R\lambda$. Hence equation (C2) must also be a U -function and, like equation (C1), follows the same period-doubling route to chaos as R and/or λ increase from zero, without ever exhibiting the phenomenon of period-halving. □

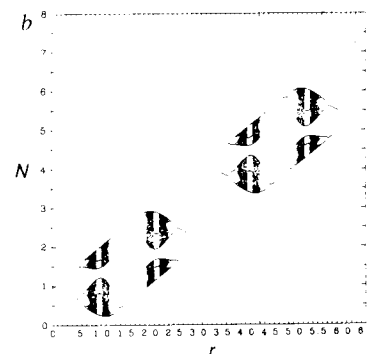
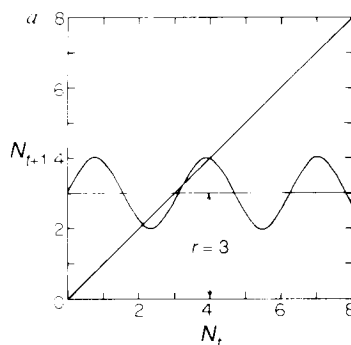


BOX 2 Cardiac chaos

SIMPLE difference equations are also valuable biological models. The complex rhythms of the human heart^{21,29} and the control of chaotic cardiac arrhythmia⁴¹ have been the subject of intense investigation with these modelling techniques. In fact, the two-parameter family of circle maps has been used extensively to simulate cardiac dynamics²⁹. Period-doubling reversals are also a fundamental phenomenon in these models. Consider the degree-zero circle map:

$$N_{t+1} = \sin(\alpha N_t) + r \tag{D1}$$

(This is a slightly simplified form of the usual circle map, but no generality is lost in this context.) Most analyses (but see ref. 42) use numerical techniques to compute the equation's 'skeleton', that is, the locus in parameter space of superstable cycles, those periodic cycles whose trajectory contains the critical point of the map. Instead, here we begin by examining more closely the relationship N_{t+1} versus N_t (Fig. a, with parameters $\alpha = 2$, $r = 3$). Notice that fixed points occur at the intersection of this graph with the 45° line $N_{t+1} = N_t$. For a fixed value of α , increasing r serves to shift the points of bifurcation, weaving them successively through a series of humps and valleys. This can result in a corresponding series of period-doubling reversals with a periodically recurring bubbling structure as seen in the bifurcation diagram of the circle map (with $\alpha = 2$) displayed in b. There is a striking correspondence between this bifurcation diagram and that determined from an empirical model of periodically stimulated embryonic chick heart cells as found in ref. 21. □



with multiple critical points such as the bimodal maps used for modelling insect populations (see below), or the degree-zero circle map used for modelling periodically stimulated biological cells²⁹.

Single-humped functions F that gently flatten out, often exponentially or simply asymptotically, occur in a number of one-dimensional maps supposed to model real systems^{9,14,17,27,28} which are unlikely generally to be U -functions. The class of functions that will not exhibit the 'universal' behaviour described above may thus be large. Furthermore, slight perturbations of a map can augment the effects of a plateau (should one exist) and cause breakdown or distortion of universal behaviour by initiating a period-doubling reversal.

Two-dimensional maps

The reversal of period-doubling cascades in two-dimensional maps surprisingly yields to mathematical analysis far more readily than the one-dimensional case treated above^{30,32}. In many of the former maps, reversals are now understood to be inevitable and known to occur infinitely often. 'Antimonotonicity', as the phenomenon has been termed^{30,32}, has definite implications for ecological models where higher dimensional maps are often appropriate^{33,34}.

Consider, for example, a simple two-dimensional ecological model (with two time lags):

$$N_{t+1} = RN_t(1 - N_t) - kN_{t-1} \quad (5)$$

where next generation's population is dependent not only on the current population, but also on the previous generation. Viewed in this way, the parameter k might be interpreted as a simple structural perturbation of the basic model.

In fact (as a simple change of coordinates immediately shows), equation (5) is equivalent to the widely studied Henon map, now known to exhibit dramatic antimonotone behaviour; for relatively large parameter regions an infinite number of period-doubling reversals occur^{30,32}. Yet, as noted in Box 1, when $k = 0$, equation (5) fails to exhibit period-doubling reversals for any parameter setting. It appears that period-doubling reversals again arise from the presence of a structural perturbation. Further, if this specific example is an indicator, the phenomenon may be more prominent in models of higher dimension.

Dawson *et al.*^{31,32} have argued that one-dimensional cubic maps with two critical points serve as models for antimonotonic-

ity in two-dimensional maps. The argument outlined in Box 1 explains how multiple critical points can initiate period-doubling reversals. The theoretical underpinnings of antimonotone behaviour are extremely complicated and not yet fully elaborated. It is currently a subject of intense research interest.

Discussion

Although physicists have observed several examples of period-doubling in the laboratory, the same cannot be said for ecologists in their studies of communities, where evidence for chaotic dynamics is hard to come by and difficult to confirm³⁵. Theoretical speculations using simple mathematical models are useful in filling this void but, as shown here, do not yield robust conclusions about the incidence of chaos and tend to suggest that it is somewhat fragile and easily inhibited. Moreover, as a recent study has shown³⁶, chaotic dynamics appear to be relatively uncommon in a wide range of simple nonlinear systems for both low-order polynomial maps and ordinary differential equations, when analysed over realistic operational parameter regimes. Taken together, these findings might suggest that the fluctuations and variability we witness in the natural world are probably of stochastic origin, but this conclusion may be premature. The parameters giving rise to complex dynamics may be of little consequence, as it is unclear how readily they can be translated into real-world systems, and the actual ecological validity of some of the better known equations has recently been under dispute^{34,37}. Furthermore, it is unrealistic to expect simple models to correspond, detail for detail, to the intricacies of the very complex natural world^{38,39}. The basic problem rather serves to highlight further the need for theoretical ecologists to better assess the prevalence of low-dimensional chaos.

Of more practical importance, the results reported here indicate that ecological factors such as immigration and predation may significantly control and impede the onset of chaos, thereby suppressing erratic, and possibly dangerous, population fluctuations. The extent to which the phenomenon may occur in real ecosystems awaits future clarification, although McCallum's pioneering study constitutes an important first step⁸. Our ability to gain further insights concerning nonlinearities and chaos in the natural world will depend on further exploration and study of these concepts. □

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