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# The evolutionary advantage of controlled chaos

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## SUMMARY

In a chaotic system, many different patterns of motion are simultaneously present. Very small changes in the initial conditions can greatly alter the system's trajectory. Here a one-dimensional difference equation is used to explain how these properties can be exploited to control the chaotic dynamics of a population. Applying small perturbations according to a simple rule drives the density of the population to a stable state. Moreover, the population can inflict these perturbations on itself: it can exert self control. Under some circumstances, such a mechanism confers an evolutionary advantage. A mutant exerting self control can invade an uncontrolled but otherwise equal resident population. Invasion of the mutant stabilizes the previously fluctuating population density. The system considered here is a subject to a form of  $K$  selection. Even if the mutant's  $K$  value is less than that of the resident, self control can still make invasion possible, but in that case invasion does not stabilize the system. It may instead lead to intermittent chaos.

## 1. INTRODUCTION

Simple ecological models can exhibit very complex dynamical behaviour. This was discovered by May (1974, 1976), and initiated a debate about the possibility of chaos in real ecosystems. Probably the most influential study in this respect was done by Hassell *et al.* 1976. They estimated the parameters of a one-dimensional difference equation for 24 insect populations and found that all but two of these populations had a stable equilibrium. This led to the more or less widespread belief that chaos is scarce in natural populations.

One of the prominent features of chaos is a very sensitive dependence of the dynamical behaviour on initial conditions, leading in practice to unpredictability. But even if natural systems do behave unpredictably, it was argued by Berryman & Millstein (1989) that this is due to stochasticity in the environment rather than to determine chaos. There have been attempts to explain the apparent scarcity of chaos by group selection arguments (Thomas *et al.* 1980; Berryman & Millstein 1989). These authors suggest that chaotic fluctuations cause population crashes after which the population is threatened by extinction in a stochastic environment. Some authors have studied what sort of dynamic behaviour is favoured by individual selection on demographic parameters (cf. Muller & Ayala 1981; Hansen 1992; Ferrière & Clobert 1992; Gatto 1993; Ferrière & Gatto 1993; Doebeli 1994*a*). However, the results from these studies are not clear cut, some suggesting that chaotic dynamics are favoured by evolution (see Ferrière & Clobert 1992; Ferrière & Gatto 1993). Schaffer & Kot (1986*a*) and Sugihara & May (1990) have given examples of real systems exhibiting chaos. The time-series analysis of measles outbreaks (Sugihara & May

1990; Schaffer & Kot 1986*b*) seems particularly convincing. Nevertheless, chaos continues to have a negative image among ecologists because of its apparent untestability and randomness.

In this article I focus on a particularly interesting property of chaotic systems, and show how it can be put to use in an ecological and evolutionary context. In an excellent review article, Shinbrot *et al.* (1993) showed how chaotic systems can be controlled by slight perturbations to elicit almost any kind of regular behaviour one might wish. Two basic features of chaos make this procedure possible. One is the sensitive dependence on initial conditions, already mentioned, the other is the fact that many different dynamical behaviours are simultaneously present in a chaotic system, although most or all of them are unstable. For example, in a one-dimensional discrete system (such as the logistic equation) that exhibits chaotic motion, an infinite number of initial conditions lead to (unstable) periodic motion (see Schuster 1984, chapter 3). Moreover, cycles of any desired length usually occur. One can now exploit sensitivity to initial conditions to steer the system's trajectory close to one of these periodic orbits (whichever seems desirable). By slight perturbations, the system is then kept close to this cycle and in effect behaves as if the cycle were stable. The same procedure can subsequently be used to jump to another kind of behaviour, e.g. to another cycle. This is in striking contrast to the situation where a system really does have a stable cycle. In such an instance, to jump to another cycle of, say, different period usually means to change the system altogether.

Here I show how this process can work in a population modelled by one-dimensional difference equation exhibiting chaos. As a model I use the well-known Ricker equation (Ricker 1954). In this model the dynamical behaviour is determined by the intrinsic

growth rate of the species. I will show how a population whose 'normal' growth rate codes for chaos can nevertheless remain at its equilibrium density by slightly adjusting its growth rate to the circumstances each year. This adjustment consists of increasing the growth rate in years of high density effects and decreasing it in years of lower density. Then I argue that a population exhibiting such a control mechanism has an evolutionary advantage: Invasion of a mutant phenotype that uses the control can force a population with complex dynamics to an equilibrium state (figure 1).

## 2. CONTROLLING CHAOS IN THE RICKER MODEL

In this article I use the Ricker equation to describe a population with non-overlapping generations, in which density regulation operates before reproduction. In this case the equation has the form

$$N_{t+1} = F(N_t) = \lambda_0 N_t \exp(-qN_t). \quad (1)$$

The density of the population in generation  $t$  is  $N_t$ , and  $\lambda_0$  is the intrinsic growth rate of the species. The parameter  $q > 0$  and determines, together with  $\lambda_0$ , the equilibrium density  $N^*$ , for which  $F(N^*) = N^*$ , hence  $N^* = \ln(\lambda_0)/q$ . The dynamics of equation (1) around the equilibrium are determined by the derivative of  $F$  at this point:  $(dF/dN)/(N^*) = 1 - \ln(\lambda_0)$ . As  $\lambda_0$  increases, the system displays the familiar period-doubling bifurcation pattern leading to chaos (for a thorough discussion of this phenomenon see May & Oster (1976)). Chaos first occurs at a value of  $\lambda_0$  of approximately  $e^{2.7}$ . In the sequel I assume that  $\lambda_0$  has a value coding for chaos. I explain how one can control the system so that it stays at its equilibrium density even though this point is unstable.

Let us assume that the parameter  $\lambda_0$  is adjustable in each generation. Accordingly, we write  $F(N, \lambda)$  instead of  $F(N)$  as in equation (1) to stress the dependence of the system on the intrinsic growth rate. Suppose further that the system is close to the equilibrium density  $N^*$  at some time  $t$ , i.e. that  $|N_t - N^*|$  is small. Then, for parameter values close to  $\lambda_0$ , one can approximate the dynamics of system (1) by the linearized problem around the point  $(N^*, \lambda_0)$ :

$$N_{t+1} - N_t = (\partial F/\partial N)(N^*, \lambda_0) \cdot (N_t - N^*) + (\partial F/\partial \lambda)(N^*, \lambda_0) \cdot (\lambda_t - \lambda_0), \quad (2)$$

where  $\lambda_t$  is the adjusted value in generation  $t$ . To determine this value, one applies the linear control law

$$(\lambda_t - \lambda_0) = -c(N_t - N^*), \quad (3)$$

where  $c$  is a constant. Substituting (3) into (2) yields

$$N_{t+1} - N^* = [(\partial F/\partial N)(N^*, \lambda_0) - c \cdot (\partial F/\partial \lambda)(N^*, \lambda_0)] \cdot (N_t - N^*). \quad (4)$$

Thus  $N_{t+1}$  will stay close to  $N^*$ , and will asymptotically approach it if the modulus of  $[(\partial F/\partial N)(N^*, \lambda_0) - c \cdot (\partial F/\partial \lambda)(N^*, \lambda_0)]$  is smaller than 1. Evaluating the partial derivatives in equation (4) leads to the following condition on the control constant  $c$ :

$$|1 - \ln(\lambda_0) - c[\ln(\lambda_0)/q\lambda_0]| < 1. \quad (5)$$

The optimal control constant  $c_{\text{opt}}$ , i.e. the control for which the approach to  $N^*$  is fastest, is given by  $1 - \ln(\lambda_0) - c[\ln(\lambda_0)/q\lambda_0] = 0$ , hence  $c_{\text{opt}} = \{[1 - \ln(\lambda_0)]q\lambda_0\}/[\ln(\lambda_0)]$ . In practice, for a given control  $c$  satisfying condition (5), one has to specify when to apply the perturbation to the system, i.e. one has to specify what it means for  $N_t$  to be close to  $N^*$ . Because the system is chaotic, given any  $\epsilon > 0$  there is a time  $t$  for which  $|N_t - N^*| < \epsilon$ , no matter how small  $\epsilon$  is. Thus, whatever small value of  $\epsilon$  we choose, the system's chaotic behaviour will bring its trajectory to lie in an  $\epsilon$ -region of  $N^*$  at some point in time, after which the system gets trapped in this region by the control mechanism. It might take a long time but eventually the system behaves as if  $N^*$  were a stable equilibrium.

It follows from equation (3) that, if the control is applied, the perturbed parameter  $\lambda_t$  is given by

$$\lambda_t = \lambda_0 - c(N_t - N^*). \quad (6)$$

Because we can choose the  $\epsilon$ -region from above to be as small as we want, we see that, in principle, extremely small perturbations are enough to stabilize the system, although the smaller we allow them to be the longer it might take until the system gets trapped. Note that, because  $\lambda_0$  codes for chaos, we have  $(1 - \ln \lambda_0) < -1$  (as  $1 - \ln \lambda_0$  is the derivative of  $F$  at  $N^*$ ). It follows that, if  $c > 0$ , then condition (5) can never be met. Thus the control  $c$  must be negative. We now conclude from equation (6) that the perturbed parameter  $\lambda_t$  is greater than  $\lambda_0$  if and only if  $N_t > N^*$ . Thus the growth rate should be increased in years of high density and decreased in years of low density. This is intuitively clear, because density dependence acts before reproduction: a high density causes a big subsequent drop in the population, and the few remaining individuals should increase their fecundity to decrease density fluctuations.

In principle, the control mechanism might be applied to stabilize a population by adding or removing offspring. However, there is an inherent difference between this ecological system and physical or chemical systems, for which the control perturbations are necessarily applied by some agent outside the system. Namely, the population might have evolved to apply the control mechanism itself by regulating its growth rate according to its density, that is, the population might exert self control. Of course, the control mechanism described above does not make much sense for a population controlling itself. Why should the adjustment only take place if the difference between the actual density and  $N^*$  is small? To make the self control mechanism more realistic, the following rule could be applied. First, a control constant  $c$  satisfying condition (5) should be used. Then the growth rate should be adjusted each year according to equation (6), independently of the value of  $|N_t - N^*|$ , but subject to the constraint that it cannot vary more than, say, 10% from the nominal  $\lambda_0$ , hence is subject to  $0.9\lambda_0 \leq \lambda_t \leq 1.1\lambda_0$ . It is easy to verify numerically that such a procedure works equally well: the population density gets stabilized at  $N^*$ . (Note that the speed of convergence to  $N^*$  depends again on the constraint on the adjusted parameter  $\lambda_t$ .)

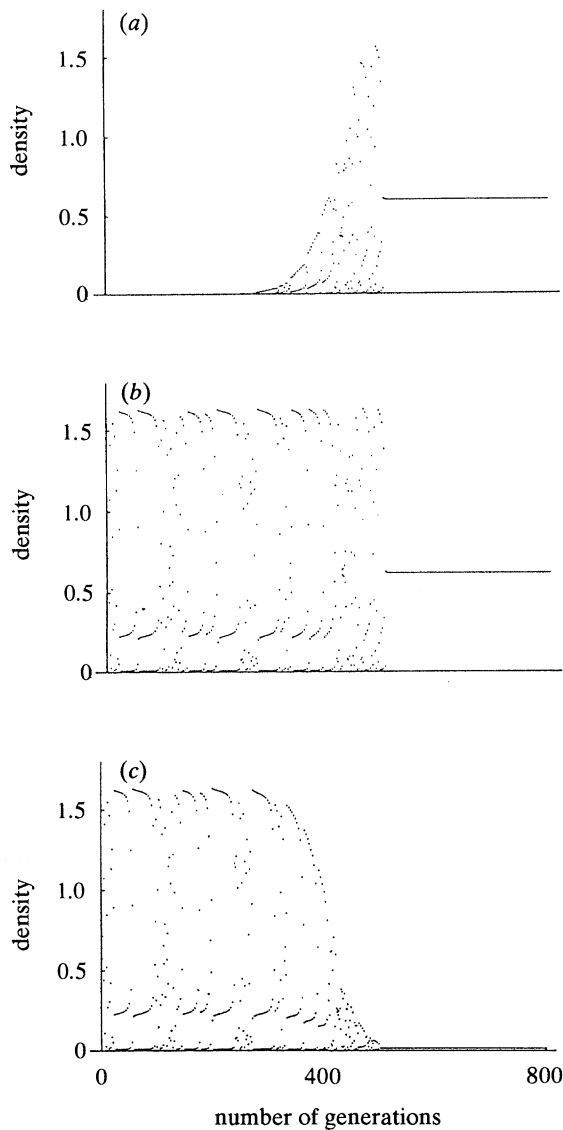


Figure 1. Invasion leading to stability. For the first 100 generations the resident follows the Ricker model (see equation (1)) with  $\lambda_0 = e^{3.1}$  and  $q = 5$ . The motion is chaotic. After 100 generations a few mutants are introduced that have the same parameters in the basic Ricker model, but that exert self control. The dynamics of the whole system are described by the following rules. Let  $N_t = N_{1,t} + N_{2,t}$  be the total density of the population at time  $t$ , where  $N_{1,t}$  is the resident's and  $N_{2,t}$  is the mutant's density. Then  $N_{1,t+1} = \lambda_0 N_{1,t} \exp(-qN_t)$ ,  $N_{2,t+1} = \lambda_t N_{2,t} \exp(-qN_t)$ , where  $\lambda_t = \lambda_0$  if  $N_t \leq N^*$ , and  $\lambda_t = \lambda_0 - c(N_t - N^*)$  if  $N_t > N^*$ . ( $N^*$  is the equilibrium density, and the control constant  $c$  is set such that the modulus of the multiplying factor in equation (4) equals 0.5.) We also impose the constraint that if  $\lambda_t > 1.1 \cdot \lambda_0$  then  $\lambda_t = 1.1 \cdot \lambda_0$ , i.e. that the growth rate cannot be increased by more than 10% of the nominal value  $\lambda_0$ . (a) After an initial phase of gradual average increase, the self-controlled mutant dominates the system and its density becomes stable. At the same time, (b) the total density is stabilized at  $N^*$ , while (c) the density of the resident is stabilized at a very low value. The densities ( $y$ -axis) are shown in successive generations ( $x$ -axis). The behaviour shown is typical. In all simulations, a similar process was observed as long as the fecundity  $\lambda_0$  coded for chaos, and as long as the control  $c$  was chosen such that it satisfied equation (5).

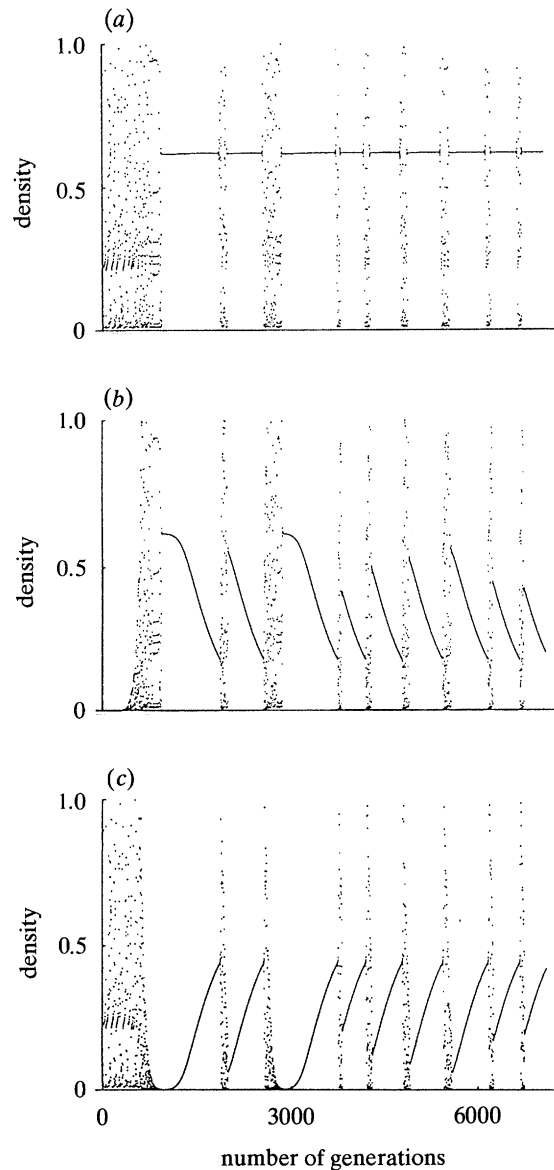


Figure 2. The same parameter values and the same rules for the dynamics of the system as for figure 1 are applied, except that the  $q$  value for the invading self-controlled mutant is set at 5.025. This implies that the invader has a smaller equilibrium density than the resident. Invasion results in intermittent chaos as described in the text. During the periods of almost constant total population density (a), the density of the self-controlled phenotype gradually decreases (b), while (c) the density of the uncontrolled phenotype increases. The figures show the densities ( $y$ -axis) in successive generations ( $x$ -axis). Again the observed behaviour is typical as long as the  $q$  value of the invader is close enough to (but higher than) the  $q$  value of the resident. The fluctuations during the intermittent outbursts all have comparable size, and the length of the laminar phases of nearly constant total density have a probability distribution whose mean can be approximately calculated from the parameters of the system. For a thorough treatment of intermittency, we refer the reader to Schuster (1984), chapter 4.

In the uncontrolled Ricker model, the density of the population is smaller than the equilibrium density  $N^*$  in most generations because, once it gets above  $N^*$ , it is usually brought back to quite low values by the density effect, and it only gradually builds up again. Thus, in the self-controlled Ricker system just de-

scribed, the nominal value  $\lambda_0$  would have little biological meaning because the actual fecundity of the species at any one time very rarely lies near  $\lambda_0$ . To give more meaning to  $\lambda_0$  as the ‘usual’ fecundity the self-control mechanism can be changed to react only to densities that are higher than  $N^*$ . The fecundity  $\lambda_t$  is then adjusted according to equation (6) only if  $N_t - N^* > 0$ , the adjustment being subject to the same constraint as before. Again it is easy to verify numerically that this mechanism is also able to stabilize the density at  $N^*$ . Now the fecundity is equal to  $\lambda_0$  most of the time, and occasionally it is higher. In conclusion, a population whose ‘normal’ fecundity codes for chaos can nevertheless stabilize itself at its equilibrium density. It can do so if its members are able to detect years in which there is a large density effect. In such years the survivors of competition should increase their reproductive output. This might seem biologically unrealistic because competition depletes resources. Nevertheless, it is conceivable that the few individuals surviving strong competition can increase their fecundity if the fecundity depends on factors that are not influenced by competition for resources. More complicated models have to be analysed to see the details of such a situation.

### 3. THE ADVANTAGE OF SELF CONTROL

I now compare in an evolutionary context a population using the self-control mechanism described at the end of the last section with an uncontrolled population. I first want to make a few remarks concerning selection on the parameters in the uncontrolled Ricker model. Let us write the model in the form  $N_{t+1} = w(N_t) \cdot N_t$ , where  $w(N) = \lambda_0 \exp(-qN)$  is the fitness function. This function depends on the environment, which is given by the density of the population. Suppose there is a mutant phenotype  $N_i$  with fitness function  $w_i(N) = \lambda_i \exp(-q_i N)$  trying to invade the resident population. The invasion will be successful if the fitness of the mutant is, on average, greater than 1 when  $N_i$  is rare. If  $N_i$  is rare, the environment of the invader consists almost entirely of the resident population. In this situation, the appropriate criterion for invasion is (Metz *et al.* 1992):

$$\lim_{T \rightarrow \infty} (1/T) \sum_{t=0}^{T-1} \ln w_i(N_t) > 0, \quad (7)$$

where  $N_t$  is the time series of the resident population. (This is really just saying that  $w_i(N_t)$  should be greater than 1 on average.) To calculate the left-hand side of (7), first observe that the corresponding quantity for the resident population has to be 0, because the resident persists through time, i.e. it neither grows nor declines on average. Consequently  $\lim_{T \rightarrow \infty} (1/T) \sum_{t=0}^{T-1} \ln w(N_t) = 0$ , which, upon substituting the expression for  $w(N)$ , yields

$$\lim_{T \rightarrow \infty} (1/T) \sum_{t=0}^{T-1} N_t = (\ln \lambda_0)/q. \quad (8)$$

This simply means that the average density is just the equilibrium density  $N^*$ . (Note that this is not obvious

*a priori*.) Using equation (8) to evaluate (7) now yields the condition

$$(\ln \lambda_i/q_i) > (\ln \lambda_0/q). \quad (9)$$

That is, the mutant can invade if its equilibrium density is greater than that of the resident. This is a form of  $K$  selection. In fact, it is easy to see that condition (9) is the condition not only for invasion but also for competitive dominance: if condition (9) is satisfied, the invading mutant will drive the resident to extinction (for the precise argument see Gatto (1993), Appendix A). Thus, the parameters of the Ricker model undergo  $K$  selection, and evolution will maximise the equilibrium density subject to biological feasibility.

Suppose now that there is a resident population exhibiting chaotic dynamics (i.e.  $\lambda_0 \gtrsim e^{2.7}$ ), and that a mutant tries to invade which has the same parameters in the basic Ricker model, but exerts the self control mechanism described at the end of the last section. That is, the mutant increases its fecundity in years in which the total density of the population (i.e. the mutant’s plus the resident’s) is higher than the equilibrium  $N^*$ . It does so subject to constraints as mentioned in section 2. The result of the invasion attempt is depicted in figure 1. Invasion is possible and transforms the previously erratically fluctuating population into a population whose density is stabilized at  $N^*$ . In this state the resident is still present, i.e. it is not driven to extinction by the invader. However, the density of the invader is much higher.

The self control mechanism of the mutant implies that its average fecundity is slightly higher than that of the resident. This selective advantage adds a new aspect to the invasion criterion given by equation (9), requiring that the mutant’s equilibrium density be higher than that of the resident. Having the same equilibrium density is enough for a self-controlled mutant. The control mechanism itself enables invasion and leads to simple dynamics for the whole population. In fact, for some choices of the parameters, invasion of a self-controlled mutant is even possible if its equilibrium density is smaller than that of the resident. However, in such a situation, invasion does not lead to stability. Instead, a very interesting behaviour occurs which is called intermittent chaos. In this type of complex motion the total density of the population stays close to the equilibrium density of the self-controlled phenotype for long periods, with intermittent outbursts of erratic density fluctuations. This is shown in figure 2. The stable periods are characterized by dominance of the controlled phenotype, its control mechanism stabilizing the total density. But at the same time the density of this phenotype is gradually decreasing, while the density of the uncontrolled phenotype increases, until its chaotic dynamics dominate the system for a short intermittent period. After this period the density of the controlled phenotype is back at high values and the process starts again. For population dynamics this kind of behaviour has been reported by Vandermeer (1993) in a continuous time model, and by Doebeli (1994*b*) in a discrete time model different to the one used here.

## 4. DISCUSSION

As the name suggests, chaotic systems are generally thought of as being unpredictable and unmanageable. Shinbrot *et al.* (1993) advocate quite a different view. They showed how very small perturbations can be used in the presence of chaos to elicit almost any kind of regular behaviour. This is in striking contrast to non-chaotic systems. Applying these ideas to ecology, it is conceivable that a system manager can stabilize fluctuating population densities with subtle interventions if he knows which parameter to alter. By means of an admittedly unrealistically simple difference model, I have shown here that such a parameter could be the growth rate of a species. Adding a few offspring in years of high competition, and removing a few in years of low competition, stabilizes even highly chaotic Ricker systems.

Apart from perturbations being applied from the outside, a population may evolve so that its behaviour controls its own dynamics. The population would then have to adjust demographic parameters according to clues from the environment. In the Ricker model the relevant component of the environment is the density of the population. To trap it at equilibrium it is sufficient for the population to increase its reproductive output by small amounts in years of high density effects. The possibility of such self control mechanisms casts some doubts on methods of estimating parameters to prove chaotic motion, for the mean fecundity of a controlled population is almost the same as that of an uncontrolled population exhibiting chaos.

A prominent question in population dynamics is what kind of dynamical behaviour should result from natural selection? In the absence of controls the Ricker model is subject to a form of  $K$  selection: evolution tends to maximize the equilibrium density of the population. Higher equilibrium densities can be achieved under both simple and complex dynamics, i.e. for both low and high intrinsic growth rates. Therefore selection does not favour a particular kind of dynamics in this model. Assuming then that there is a growth rate implying chaos and an equilibrium density maximized subject to biological constraints, the self-control mechanism described above can invade the population and stabilize its density (figure 1). Although the self-controlled mutant has the same equilibrium density, its average growth rate is slightly higher than that of the resident because of the control mechanism. Thus such a mechanism enables the system to evolve from complex to simple dynamics although evolution due to  $K$  selection has ceased. In fact, the mechanism can even reverse the direction of selection under certain conditions. It is possible that a self-controlled mutant can invade a resident with a slightly higher equilibrium density. Such an invasion results in intermittent chaos (figure 2): for most of the time the total density is near the equilibrium, except for intermittent periods during which it fluctuates irregularly. This form of 'almost stable' chaos would be indistinguishable from a stable equilibrium if density measurements were made in the long phases of nearly constant population size.

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## REFERENCES

- Berryman, A. A. & Millstein, J. A. 1989 Are ecological systems chaotic – and if not, why not? *Trends Ecol. Evol.* **4**, 26–28.
- Doebeli, M. 1994a Some effects of phenotypic variation and sexual reproduction on population dynamics. (Submitted.)
- Doebeli, M. 1994b Intermittent chaos in population dynamics. *J. theor. Biol.* (In the press.)
- Ferrière, R. H. & Clobert, J. 1992 Evolutionary stable age at first reproduction in a density-dependent model. *J. theor. Biol.* **157**, 253–267.
- Ferrière, R. H. & Gatto, M. 1993 Chaotic population dynamics can result from natural selection. *Proc. R. Soc. Lond. B* **251**, 33–38.
- Gatto, M. 1993 The evolutionary optimality of oscillatory and chaotic dynamics in simple population models. *Theor. Popul. Biol.* **43**, 310–336.
- Hansen, T. F. 1992 Evolution of stability parameters in single-species population models: stability or chaos? *Theor. Popul. Biol.* **42**, 199–217.
- Hassell, M. P., Lawton, J. H. & May, R. M. 1976 Patterns of dynamical behaviour in single-species populations. *J. Anim. Ecol.* **45**, 471–486.
- May, R. M. 1974 Biological populations with non-overlapping generations: Stable points, stable cycles and chaos. *Science, Wash.* **186**, 645–647.
- May, R. M. 1976 Simple mathematical models with very complicated dynamics. *Nature, Lond.* **261**, 459–467.
- May, R. M. & Oster, G. F. 1976 Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* **110**, 573–599.
- Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. 1992 How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* **7**, 198–202.
- Mueller, L. D. & Ayala, F. J. 1981 Dynamics of single-species population growth: stability or chaos? *Ecology* **62**, 1148–1154.
- Ricker, W. E. 1954 Stock and recruitment. *J. Fish. Res. Bd Can.* **11**, 559–623.
- Schaffer, W. M. & Kot, M. 1986a Chaos in ecological systems: the coals that Newcastle forgot. *Trends Ecol. Evol.* **1**, 58–63.
- Schaffer, W. M. & Kot, M. 1986b Differential systems in ecology and epidemiology. In *Chaos* (ed. A. V. Holden), pp. 158–178. Manchester University Press.
- Schuster, H. G. 1984 *Deterministic chaos: an introduction*. Weinheim: Physik Verlag.
- Shinbrot, T., Grebogi, C., Ott, E. & Yorke, J. A. 1993 Using small perturbations to control chaos. *Nature, Lond.* **363**, 411–417.
- Sugihara, G. & May, R. M. 1990 Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. *Nature, Lond.* **344**, 734–741.
- Thomas, W. R., Pomerantz, M. J. & Gilpin, M. E. 1980 Chaos, asymmetric growth and group selection for dynamical stability. *Ecology* **61**, 1312–1320.
- Vandermeer, J. 1993 Loose coupling of predator-cycles: entrainment, chaos, and intermittency in the classic MacArthur consumer-resource equations. *Am. Nat.* **141**, 687–716.

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