Intermittent Chaos in Population Dynamics

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In modelling single species with discrete, non-overlapping generations, one usually assumes that the density at time $t + 1$ is a function of the density at time t: $N_{t+1} = f(N_t)$. The dynamical behaviour of this system depends on the parameters in the function f. It commonly changes, as a parameter increases, from a stable equilibrium through a series of bifurcations into stable cycles, to chaotic motion. It is implicit in the assumptions of the model that the population consists of identical individuals. In this paper it is shown that variation within the population can lead to a different route to chaos. Invasion of a mutant phenotype into a resident population can elicit intermittency. This kind of chaotic behaviour consists of regular motion most of the time with short intermittent periods in which the system fluctuates wildly.†

1. Introduction

It is an open question whether complex dynamical behaviour is common in natural populations. It occurs in many of the theoretical models that have been studied. Depending on the choice of parameters in these models, population densities move on periodic or quasiperiodic orbits, or their motion is chaotic. Consider for example a single species with discrete, non-overlapping generations. It can be modelled by assuming that the density N_{t+1} at time $t + 1$ is a function of the density at time t:

$$N_{t+1} = f(N_t),$$

where $f: \mathbb{R}_+ \to \mathbb{R}_+$ maps the set of positive real numbers to itself. Usually f is chosen in a "humped" form, and such that ($f(N) > N$ for small, positive N. These conditions imply that the population can grow if small, and that there is negative feedback at high densities corresponding to density-dependent mortalities. The non-trivial equilibrium densities are given by the solutions of the equation $f(N) = N$, $N > 0$, and usually f is chosen in a way that there is only one such

solution N^*. The most interesting feature of the model is the dynamical behaviour of the system if the population is perturbed away from the equilibrium density N^*. This behaviour is determined by the derivative of f at N^*, i.e. by $(df/dN)(N^*)$. If $|(df/dN)(N^*)| < 1$, the equilibrium point is stable, with perturbed densities going back to N^* exponentially or via damped oscillations. If $|(df/dN)(N^*)| > 1$, the dynamics get more complicated, ranging from periodic motion to chaos. One such model, studied extensively by Hassell (1975) and Hassell *et al.* (1976), is the following:

$$N_{t+1} = \lambda \cdot N_t \cdot (1 + aN_t)^{-b}. \tag{1}$$

Here $\lambda > 1$ is the fecundity of the species, and a, $b \in \mathbb{R}_+$ are parameters which influence the equilibrium density and describe the type of competition that leads to density-dependent mortality (for details see Hassell, 1975). N^* is given by

$$N^* = \frac{\lambda^{1/b} - 1}{a},$$

and it is easily seen that

$$\frac{df}{dN}(N^*) = 1 - \tilde{b},$$

where $\tilde{b} = b(1 - \lambda^{-1/b}) > 0$. The equilibrium N^* is stable if $\tilde{b} < 2$. If $\tilde{b}$ increases above 2, the equilibrium becomes unstable: a bifurcation occurs and a stable two-cycle evolves, which itself becomes unstable as $\tilde{b}$ increases further, bifurcating into a stable four-cycle. After going through a series of stable 2^n-cycles as $\tilde{b}$ grows, the system finally reaches chaos, a state in which it no longer exhibits regular behaviour. The route to chaos via bifurcations is common for single species models (May & Oster, 1976).

If model (1) is written in the form

$$N_{t+1} = w(N_t) \cdot N_t, \qquad (2)$$

then $w(n) = \lambda(1 + aN)^{-b}$ is the fitness function of the population, i.e. the reproductive output per individual. It is implicitly assumed that there is no variation in the population, because the fitness function is the same for all individuals. In this article I want to show that variation can lead to a different type of chaos than that described by May & Oster (1976). To do this I regard the fitness function, respectively, the parameters λ, a and b, as properties of a particular

phenotype. One can then ask what kind of parameters imply an evolutionary advantage. More precisely, given a resident population consisting of only one phenotype, one can ask when a mutant phenotype with a different fitness function is able to invade the resident. Metz *et al.* (1992) derived a criterion for the parameters of a mutant phenotype to allow invasion. It is shown that for suitable choices of these parameters a successful invasion can result in intermittent chaos. In this form of irregular motion the total density, i.e. the sum of the densities of the resident and of the mutant, remains close to the equilibrium density of the resident for a long time, undergoes fluctuations for a short, intermittent period, and then returns to values close to the equilibrium density, from where it starts to fluctuate again after a long period, and so on. This type of chaos was first described in the literature by Pomeau & Manneville (1980). Generally it occurs as a parameter a increases through a critical value a_c. While $a < a_c$ the system returns to regular motion after small disturbances. As a increases above a_c, small disturbances result in the
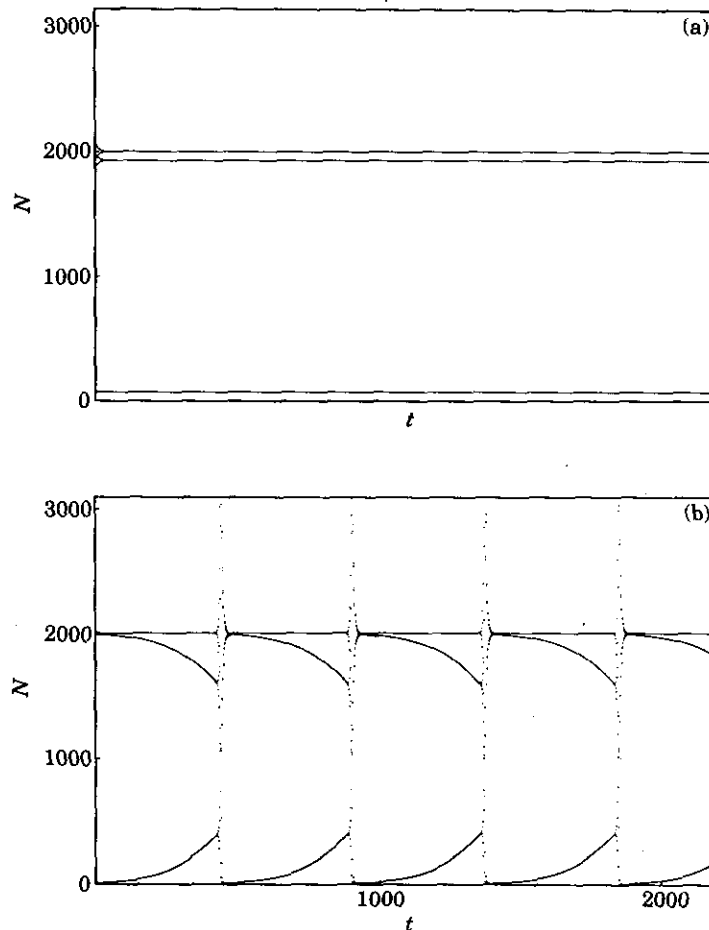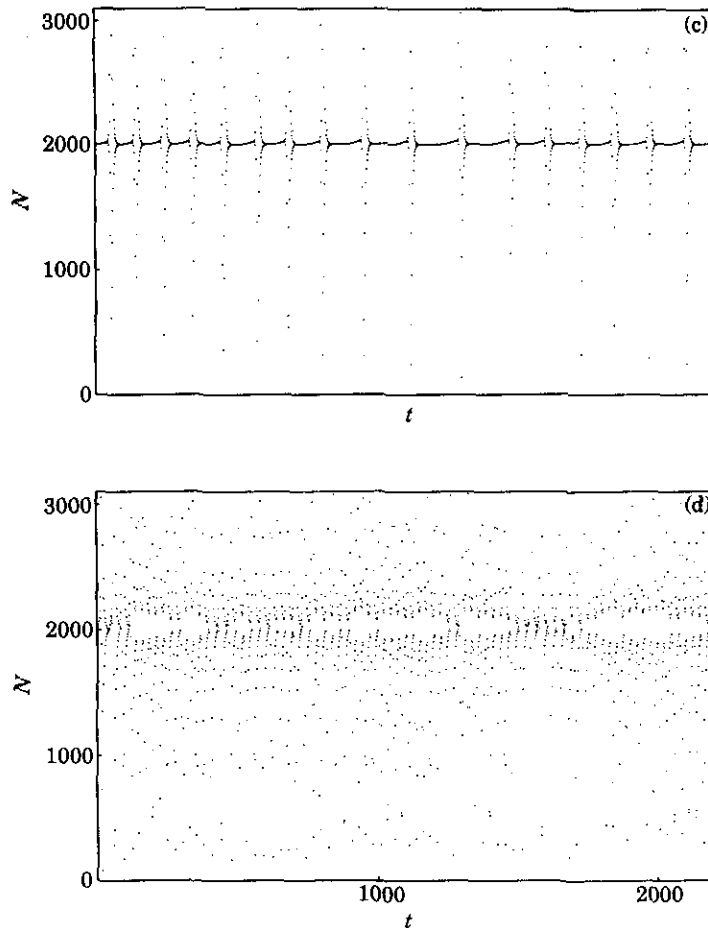

Fig. 1(a,b).

FIG. 1(c,d).

FIG. 1. The total density N is plotted against time t (which is a discrete variable). N is determined iteratively by eqn (5). Invasion is simulated by introducing a small amount of mutant individuals into the stable resident population. Fixed parameter values are $\bar{b}_m = 5$, $\bar{b}_r = 1.8$, $b_m = 500$, $b_r = 2.1$, $a_r = 0.003$, hence $N_r^* = 2000$. The values for λ_i determined by b_i and $\bar{b}_i$, $i = m, r$, are $\lambda_m \sim 152$ and $\lambda_r \sim 60$. (a) $N_m^*/N_r^* = 1$. Besides N also the densities N_m (lower graph) and N_r (middle graph) are shown. The system evolves rapidly to a new equilibrium where both densities N_m and N_r are positive, and where $N = N_r^*$. (b) $N_m^*/N_r^* = 1.002$. Intermittency has set in. Again the densities N_m and N_r are shown. As N_m increases N_r decreases, while N remains constant, until N_m is big enough to drive the dynamics of the system for a short time period, after which it is back at low values. (c) $N_m^*/N_r^* = 1.02$. Only N is shown. Qualitatively the same behaviour is seen as in 1(b), but the frequency of the outbursts is higher. (d) $N_m^*/N_r^* = 1.09$. As N_m^*/N_r^* further increases intermittency starts to dissolve into a completely erratic motion.

following behaviour: for most of the time the system tracks the regular motion, except for short periods in which it fluctuates wildly. For values of a such that $a - a_c$ is small the magnitude of these fluctuations is approximately constant in time and independent of a, and the frequency of the outbursts is approximately proportionate to $(a - a_c)^{-1/2}$ (for more details on the intermittency route to chaos and the conditions under which it occurs see Schuster (1984, chapter 4).

If such behaviour exists in nature, its most obvious biological implication is that one might fail to detect chaotic dynamics if density data are collected over a period of time in which the system stays close to the equilibrium density. It might also stand as an alterna-

tive explanation for occasional population outbursts, which are usually explained by a combination of weather and interspecific interactions. The model used here could also serve to describe changes in density and gene-frequency at a locus with two alleles in a haploid population (May, R., personal communication). In this framework it generalizes some of the attempts to understand gene-for-gene host–parasite interactions, cf. May & Anderson (1983). One conclusion from their paper is that density- and frequency-dependent selection can maintain genetic polymorphism, and may do so in chaotic fashion. The results here then add yet another possibility to the range of dynamical behaviour in this context: intermittency.

2. The Invasion Scenario

Assume that one is given a resident population N_r consisting of one phenotype and described by model (2). Its fitness function $w_r(N)$ is given by parameters λ_r, a_r and b_r. Note that this is a special case of a non-constant fitness function that is determined by the environment, the relevant component of the environment being the density of the population. Suppose further that there is a mutant phenotype N_m with fitness function $w_m(N)$ given by parameters λ_m, a_m

FIG. 2. The total density N is plotted against time t. N is determined by eqn (5). Invasion is simulated as for Fig. 1. Fixed parameter values are $N_m^*/N_r^* = 1.02$, $b_m = 500$, $\bar{b}_r = 1.8$, $b_r = 2.1$, $a_r = 0.003$, hence $N_r^* = 2000$. As in Fig. 1 b_r and $\bar{b}_r$ determine $\lambda_r \sim 60$. (a) $\bar{b}_m = 2.75$, hence $\lambda_m \sim 16$. The system approaches a limit cycle of period 2. Note that this $\bar{b}_m$ value codes for a stable cycle of much higher period if only the mutant population is present. (b) $\bar{b}_m = 5$, hence $\lambda_m \sim 152$. The same as 1(c), now for 10 000 time steps. (c) $\bar{b}_m = 12$, hence $\lambda_m \sim 1.9 \times 10^5$. Obvious intermittency, but compared to (b) the frequency of the outbursts is much lower. On the other hand, these outbursts are less evenly distributed over time.

and b_m. When both phenotypes are present, the relevant component of the environment is the total density $N_t = N_{r,t} + N_{m,t}$. Thus the time development of the mutant phenotype is given by

$$N_{m,t+1} = w_m(N_t) \cdot N_{m,t}. \tag{3}$$

In the invasion scenario the mutant is rare, hence $N_t \cong N_{r,t}$ in (3). The mutant can invade if its fitness function is on average > 1, i.e. if

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \log w_m(N_{r,t}) > 0. \tag{4}$$

This is precisely the invasion criterion of Metz et al. (1992) (see Box 2 therein).

In the sequel it is assumed that the resident population is at a stable equilibrium N_r^*, i.e. it is assumed that the corresponding value $\bar{b}_r = b_r(1 - \lambda_r^{-1/b_r}) < 2$. Then $N_{r,t} \equiv N_r^* = (\lambda_r^{1/b_r} - 1)/a_r$, and inequality (4) becomes

$$\lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \log \lambda_m \left[1 + \frac{a_m(\lambda_r^{1/b_r} - 1)}{a_r} \right]^{-b_m} > 0.$$

Since there is no time dependence, this inequality becomes upon rearranging:

$$\frac{\lambda_m^{1/b_m} - 1}{a_m} > \frac{\lambda_r^{1/b_r} - 1}{a_r}.$$

In other words, the mutant is able to invade if its equilibrium density is bigger than that of the resident. Of course, this is not a condition on the dynamics of the mutant. In the remainder of the article some of the phenomena that occur when the parameters of the mutant's fitness function code for chaos are described, i.e. when $\bar{b}_m = b_m(1 - \lambda_m^{-1/b_m})$ is much larger than 2. I thus analysed numerically what happens to a population when a mutant phenotype with complex dynamics invades a resident population that has a stable equilibrium.

3. Results

Results were obtained by numerically simulating the following equations, describing the situation outlined in the previous section:

$$N_{r,t+1} = \lambda_r N_{r,t}(1 + a_r(N_{r,t} + N_{m,t}))^{-b_r}$$

$$N_{m,t+1} = \lambda_m N_{m,t}(1 + a_m(N_{r,t} + N_{m,t}))^{-b_m}. \tag{5}$$

Here N_r and N_m are the densities of the resident and of the mutant as before. To initialize the simulations it is assumed that the resident is at its equilibrium N_r^* and then a small amount of individuals of the mutant phenotype was introduced. Of course, the outcome of the simulations depended on the particular choice of parameters. To keep things simple two main routes of parameter change were followed. The first followed
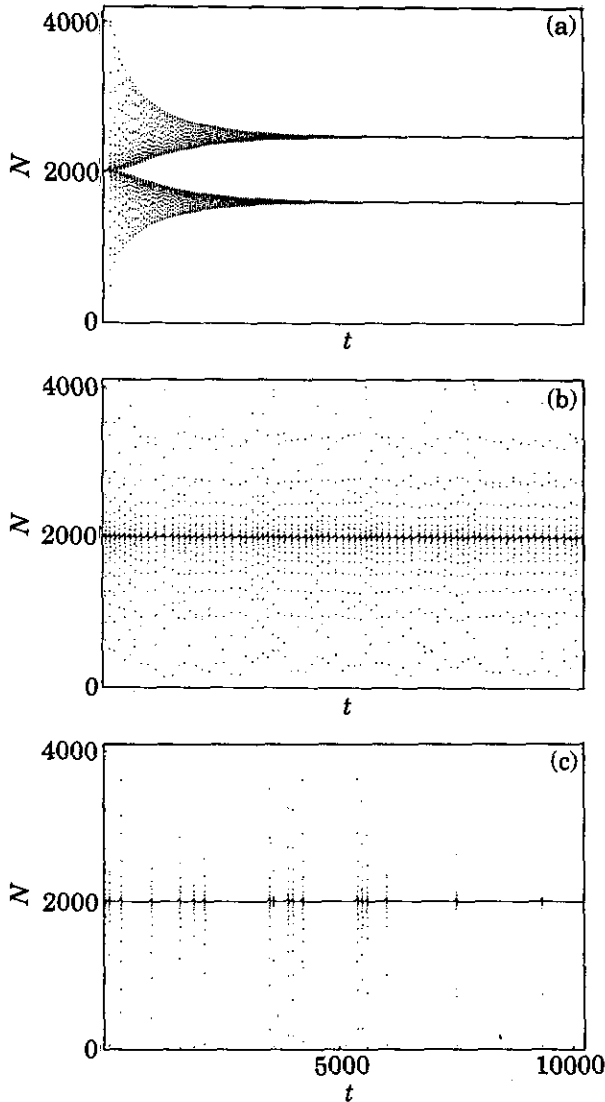
the system's behaviour as the equilibrium density N_m^* of the mutant increased across a given fixed value of N_r^*, while the dynamics of the mutant was determined by a fixed value of $\tilde{b}_m$ which was >2. The second tracked the behaviour as the dynamics of the mutant got more complicated, i.e. as the parameter $\tilde{b}_m$ increased, while N_m^*/N_r^* was set at a given value which was slightly bigger than 1, i.e. such that invasion was possible.

Along the first route the parameter values were $\tilde{b}_m = 5$ and $\tilde{b}_r = 1 \cdot 8$. For $N_m^* < N_r^*$ the system returned to the equilibrium state $N_m = 0$ and $N_r = N_r^*$, i.e. invasion was not possible, as predicted. If $N_m^* = N_r^*$, the system evolved to a state in which the total density was again N_r^*, but the densities of both types were now positive. This can be thought of as a neutral state. As N_m^* increased above N_r^*, the system exhibited intermittent chaotic dynamics: for long time periods the total density $N = N_r + N_m$ was close to the equilibrium density N_r^*, while it fluctuated wildly for short intermittent periods. In the period where N was constant, the density N_m of the mutant gradually built up from low values, while N_r decreased, until N_m was big enough so that its complex dynamics could cause fluctuations, after which N_m was back at low values and started to grow again. Thus the irregular motion was caused by N_m taking on high enough values for its dynamic to drive the system for a short period, during which it was eventually brought back to low values by fluctuations. Corresponding time series are shown in Fig. 1 for different values of N_m^*/N_r^*. Figure 1(a) shows the approach to the equilibrium value $N_r^* = 2000$ as $N_m^*/N_r^* = 1$. Here, as in Fig. 1(b), the graph at the top is the total density N, while the other ones represent the densities N_r (upper) and N_m (lower) respectively. In Fig. 1(b) $N_m^*/N_r^* = 1 \cdot 002$, and intermittency has set in. In Fig. 1(c) $N_m^*/N_r^* = 1 \cdot 02$. Only the total density is shown. Intermittency is still present, but the frequency of the outbursts is higher than in Fig. 1(b). In Fig. 1(d) $N_m^*/N_r^* = 1 \cdot 09$, and intermittency starts to dissolve into a completely erratic motion.

Of course, the system's behaviour depended on other parameters as well, in particular on the values for λ_m and λ_r for which $\tilde{b}_m = 5$ and $\tilde{b}_r = 1 \cdot 8$. There was a threshold value for λ_r below which the intermittency ceased to exist. As λ_r decreased through this threshold, the system exhibited a stable limit cycle of period 2 for a relatively large range of λ_r-values. If λ_r decreased further, there was a small range of higher order periodic or quasi-periodic orbits, after which λ_r and hence N_r^* was small enough for the dynamics of the mutant to dominate, with the system behaving according to the value of $\tilde{b}_m$. Similarly, there was a

threshold value for λ_m above which intermittency disappeared, and a similar route to chaos as for decreasing λ_r was observed for increasing λ_m. The particular parameter values used to obtain Fig. 1 are listed in the legend.

To follow the second route to chaos N_m^*/N_r^* was fixed at $1 \cdot 02$, and again $\tilde{b}_r = 1 \cdot 8$. The critical value when intermittency sets in was then $+\infty$: if $\tilde{b}_m$ was large, the (average) frequency of the intermittent outbursts was low; these outbursts were unevenly distributed over time. As $\tilde{b}_m$ decreased, the intermittent periods occurred more frequently and more evenly over time. Also, the regular motion present for most of the time developed into a cycle of period 2 with increasing amplitude. Below a certain value intermittency disappeared, and a stable limit cycle of period 2 evolved, which was present until another threshold was reached below which the mutant population was able to eliminate the other type, hence the system's dynamics were that of the mutant given by $\tilde{b}_m$. Figure 2(a)–(c) correspond to increasing values of $\tilde{b}_m$. In Fig. 2(a) the approach of the total density to a cycle of period 2 is shown. Figure 2(b) is the same as Fig. 1(c) for longer times. In Fig. 2(c) the frequency of the intermittent time periods is low, the time intervals between them are of uneven size. Again, the values of the other parameters influenced the dynamics. The values chosen for Fig. 2 are listed in the legend.

In general, for given values of $\tilde{b}_m$ and $\tilde{b}_r$, the dynamics tended to be more complex for low values of λ_m and high values of λ_r. For example, high values for λ_m caused a shift of the threshold $\tilde{b}_c$ to the right. Also, higher values of N_m^*/N_r^* made the dynamics more complex. Given a fixed value of $\tilde{b}_m$, the intermittent behaviour was seen for $b' \leqslant \tilde{b}_r < 2$, where $b' > 0$ depended on $\tilde{b}_m$. A rather curious observation was the following: in all the numerical simulations with $N_m^*/N_r^* > 1$, $\tilde{b}_r < 2$ and $\tilde{b}_m > 2$, the region in parameter space for which there was intermittency was surrounded by a relatively large region for which the system had a stable limit cycle of period 2, independent of the particular dynamical behaviour of the mutant population that was coded for by $\tilde{b}_m$.

4. Conclusions

Introducing variation into a population modelled by $N_{t+1} = \lambda N_t (1 + aN_t)^{-b}$ elicits intermittent chaos for the total density if the parameter values are appropriately chosen. Invasion of a mutant phenotype with complex dynamics into a resident population with simple dynamics can cause the total density to remain constant over long periods of time,

while it fluctuates for short intermittent time periods. This type of chaos is different from that described in May & Oster (1976). Since the condition for invasion is a higher equilibrium density of the mutant, the system undergoes a form of K-selection. However, invasion does not usually lead to the extinction of the resident population, as is often assumed when studying evolutionary population dynamics (see e.g. Ferrière & Clobert, 1992 or Marrow *et al.*, 1993). Rather, in the situation considered here successful invasion usually results in coexistence. Even if the invading mutant has very complex dynamics when alone, the dynamical behaviour of the coexisting phenotypes can be regular due to simple dynamics of the resident [see Fig. 2(a)].

In population dynamical models intermittent phenomena have been observed by Mikhailov (1992) and by Vandermeer (1993). Mikhailov (1992) studied a stochastic differential equation with spatial diffusion term. The presence of noise causes rare, spatially and temporally confined population outbursts. These "spikes" wander in space due to diffusion, and they are separated by large regions with very low population density. In this model the intermittent outbursts are due to stochastic effects and not to deterministic chaos.

Vandermeer (1993) showed the existence of deterministic intermittent chaos in a predator–prey model set in continuous time. Again the intermittent population outbursts occur on a background of very low population densities.

In Doebeli (in press) another invasion scenario is discussed that leads to the kind of intermittency reported in the present paper, where the regular motion during most of the time consists of staying near the equilibrium density. If such dynamical behaviour exists in nature, one obvious implication is the possible failure to detect complex dynamics if population densities are measured outside the intermittent periods of fluctuations. This would lead one to believe that the population density is at a stable equilibrium when in fact it could start to fluctuate unpredictedly.

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