

UPDATING GILLESPIE WITH CONTROLLED CHAOS

In a seminal paper Gillespie (1977) showed that the distribution of offspring numbers in a variable environment is crucial for the outcome of evolution. More precisely, "Natural selection . . . works in such a way that increasing the variance in offspring number of a genotype will decrease its fitness" (Gillespie 1977, p. 1013). It follows that if two genotypes have the same average number of offspring, then the one with the lower variance of offspring numbers will increase in frequency. In the present note I combine this line of thinking with chaos theory and show that the course of evolution can also be determined by higher moments of the distribution of offspring numbers. Natural selection acting on higher moments can cause a population to evolve from chaos to a stable equilibrium.

Recently, Shinbrot et al. (1993) showed how small perturbations in chaotic systems can be used to elicit many types of regular dynamics. I have shown (Doebeli 1993) how controlling chaos can work in simple ecological models by slightly adjusting the intrinsic growth rate of a population. Under some circumstances a controlled phenotype has a selective advantage over an uncontrolled phenotype with the same nominal parameter values, and invasion of a controlled mutant into an uncontrolled resident transforms a chaotic population into one with a stable equilibrium. This is possible if the mutant has a higher average growth rate than the resident and hence a higher average number of offspring.

Below I recall the ideas of controlled chaos using a different model and adjusting a different demographic parameter. It turns out that in the system considered, a controlled mutant can always invade an uncontrolled resident. But now the controlled phenotype typically has a slightly lower average number of offspring. Thus Gillespie's evolutionary principle must be at work, although in this setting the variance of offspring numbers is not due to stochasticity in the environment but to fluctuations caused by density dependence. Indeed, in many cases the mutant has a lower variance of offspring numbers, which confirms Gillespie's assertions. However, in other cases the variance of the mutant is larger, so that on the basis of Gillespie's argument invasibility is counterintuitive. In these cases, invasion is possible because of natural selection acting on the higher moments of the distribution of offspring numbers. Even though the average offspring number is lower and the variance is higher, the mutant's distribution is more skewed to the right than that of the resident, so that the geometric mean fitness of the mutant is higher. The difference in skewness is caused by the control mechanism of the mutant.

The present note thus combines two observations. First, higher moments of the distribution of offspring numbers can determine evolutionary processes. Second, this effect enables phenotypes that control their chaotic dynamics to invade uncontrolled residents and to transform chaos into a stable equilibrium.

CONTROLLING CHAOS

Consider a population with discrete generations that is modeled by the difference equation

$$x_{t+1} = f(x_t) = \frac{\lambda x_t}{1 + (ax_t)^b}. \quad (1)$$

This equation was introduced by Maynard Smith and Slatkin (1973) and considered by Bellows (1981) to be the most generally applicable because of its mathematical flexibility. In equation (1), x_t denotes the population density in generation t , and λ , a , and b are demographic parameters: $\lambda > 1$ is the intrinsic growth rate, $a > 0$ measures how well the individuals can cope with the environment, and $b \geq 1$ describes the type of competition that leads to density dependence ($b \sim 1$ corresponds to contest, $b \gg 1$ to scramble competition). What determines the dynamics of the population is the slope of f at the equilibrium x^* . From $f(x^*) = x^*$, $x^* > 0$, one sees that

$$x^* = \frac{(\lambda - 1)^{1/b}}{a} \quad (2)$$

and hence that

$$\frac{df}{dx}(x^*) = 1 - b \frac{\lambda - 1}{\lambda}. \quad (3)$$

If the modulus of this derivative is less than one, the equilibrium x^* is stable. As it increases above one, the system displays the familiar period-doubling route to chaos (May and Oster 1976). The parameter a does not influence the dynamics. It affects only the equilibrium density, which corresponds to the carrying capacity of the population.

Suppose now that the parameters λ and b have values coding for chaos, that is, such that the modulus of equation (3) is large enough. Suppose further that, given a nominal value a_0 , we can adjust the parameter a by small amounts in each generation, so that the ability to cope with the environment, and hence the carrying capacity, changes slightly. We then write $x_{t+1} = f(x_t, a)$ to stress the dependence of the system on the parameter a . If $|x_t - x^*|$ is small, that is, if the system is close to the equilibrium in some generation t , then, for values a_t close to the nominal value a_0 , one can approximate the dynamics of the system linearly:

$$x_{t+1} - x^* = \frac{\partial f}{\partial x}(x^*, a_0) \cdot (x_t - x^*) + \frac{\partial f}{\partial a}(x^*, a_0) \cdot (a_t - a_0). \quad (4)$$

Now we assume that we can control the change in the parameter a by adjusting it linearly according to the density

$$a_t - a_0 = c \cdot (x_t - x^*), \quad (5)$$

where c is a constant to be determined. Substituting equation (5) into equation (4) we get

$$x_{t+1} - x^* = \left[\frac{\partial f}{\partial x}(x^*, a_0) + c \cdot \frac{\partial f}{\partial a}(x^*, a_0) \right] \cdot (x_t - x^*) . \tag{6}$$

If we choose c such that the modulus of the expression in brackets is less than one, the system will now asymptotically approach the equilibrium x^* . Evaluating the partial derivatives, we get the condition

$$\left| 1 - b \frac{\lambda - 1}{\lambda} - c \cdot \frac{b(\lambda - 1)^{b+1/b}}{a_0^2 \lambda} \right| < 1 . \tag{7}$$

The optimal value for the control constant c occurs when the modulus is zero, and we obtain the equation

$$c_{\text{opt}} = \left(1 - b \frac{\lambda - 1}{\lambda} \right) \cdot \frac{a_0^2 \lambda}{b(\lambda - 1)^{b+1/b}} . \tag{8}$$

In practice, we have to specify when to apply the control, that is, what it means that $|x_t - x^*|$ is small. Because the system is chaotic, given any $\epsilon > 0$, there will be a generation t for which $|x_t - x^*| < \epsilon$. Thus, in view of equation (5), in principle, very small adjustments are enough to stabilize the system at x^* . The smaller we allow the adjustments to be, the longer it might take until the system finally gets close enough to x^* , but because of chaos it will eventually happen.

With a small alteration, the mechanism also makes sense as an adaptive strategy applied by the individuals of a population to control the dynamics. For this we have to imagine individuals that change their ability to cope with the environment according to their density. It follows from equation (8) that c_{opt} is negative (because the modulus of $1 - b[\lambda - 1/\lambda]$ codes for chaos) and hence from equation (5) that the adjustment of a consists of a decrease if $x_t > x^*$ and of an increase if $x_t < x^*$. Consequently (recall eq. [2]), the adaptation consists of a higher ability to cope with the environment, and hence a higher carrying capacity, if the density of the population in a given generation is above x^* and of a lower carrying capacity if the density is below x^* . If this adaptation is to be displayed by a population, the adjustments should occur according to equation (5), but they should not depend on the fact that x_t is very close to x^* . Rather, the adjustments should be made in all generations, but in order to be biologically reasonable they should never be larger than a certain percentage, say 5%, of the nominal value a_0 . It is easy to see that a population adapted in this way controls its own dynamics and exhibits a stable equilibrium after an initial phase of fluctuating densities.

INVASION OF CONTROLLING MUTANTS

Suppose there is a resident population described by the difference equation (1) and exhibiting chaos, and suppose a mutant phenotype tries to invade the resident. When is invasion possible? Since the mutant is initially rare, the number of offspring of the mutant in each generation depends on the density of the resident. Let $w_m(x)$ be the fitness function of the mutant, which calculates the number

of offspring per individual when the density is x . Let $\{x_t\}$ be the (chaotic) density time series of the resident. Then the mutant can invade if the geometric mean of the numbers $w_m(x_t)$ is larger than one. Mathematically, this is expressed as the condition (Metz et al. 1992)

$$\lim_{T \rightarrow \infty} \left(\prod_{t=0}^{T-1} w_m(x_t) \right)^{1/T} > 1. \quad (9)$$

Now consider a mutant that has the same nominal parameter values as the chaotic resident but that controls its dynamics with the adaptive strategy described above. Numerical simulations show that such a mutant can always invade the resident. Invasion results in a high density of the mutant, which is then able to control the dynamics of the whole system: invasion leads from chaos to stable equilibrium. But why is the mutant able to invade?

The reason is found in the distribution of offspring numbers. For the resident, this distribution is given by the set $\{w_r(x_t)\}$, where, according to equation (1),

$$w_r(x) = \frac{\lambda}{1 + (a_0 x)^b} \quad (10)$$

is the reproductive output per resident individual at density x . Note that the geometric mean of $\{w_r(x_t)\}$ is equal to one, since the resident neither grows nor declines on average (i.e., it persists through time). The mutant's distribution $\{w_m(x_t)\}$ is determined by its fitness function

$$w_m(x) = \frac{\lambda}{1 + (ax)^b}, \quad (11)$$

where

$$a = a_0 + c \cdot (x - x^*) \quad (12)$$

according to equation (5). The constant c is given by equation (6), and the adjustment of a is subject to $0.95 \cdot a_0 \leq a \leq 1.05 \cdot a_0$; that is, if a as calculated from equation (12) is smaller (greater) than $0.95a_0$ ($1.05a_0$), we set $a = 0.95a_0$ ($1.05a_0$). The moments of this distribution determine the geometric mean fitness of the invading mutant. Intuitively, the odd moments measure the skewness of the distribution, while the even moments measure its width. Extrapolating from Gillespie's principle, larger even moments tend to decrease the geometric mean, while larger odd moments, that is, skewness to the right, tend to increase the geometric mean. This argument can be made more formal by considering the Taylor series expansion of the logarithm

$$\log(1 + x) = \sum_{k=0}^{\infty} \frac{(-1)^k x^{k+1}}{k+1} = x - \frac{x^2}{2} + \frac{x^3}{3} - \dots$$

Since the mutant is always able to invade, one would expect the distribution $\{w_m(x_t)\}$ to have larger odd moments and smaller even moments than the distribution $\{w_r(x_t)\}$. However, in most cases the first moment of the mutant, that is, the

arithmetic mean number of offspring, is lower than that of the resident. Therefore, higher moments must be responsible for the fact that invasion is possible. In some cases invasion can be attributed to Gillespie's principle: the second moment, that is, the variance, of $\{w_m(x_t)\}$ is lower than that of $\{w_r(x_t)\}$. That the variance of the mutant is lower makes sense intuitively, for consider again the control mechanism of the mutant. It works by increasing the carrying capacity in generations with high density, which dampens the subsequent crash, and by decreasing the carrying capacity in generations of low density, which dampens the subsequent outbreak. This dampening of fluctuations should lead to a lower variance of offspring numbers and hence to a selective advantage. However, two factors tend to prove this intuition wrong: increasing the complexity of the resident dynamics, that is, the modulus of equation (3), and increasing the growth rate λ . Both factors shift the selection pressure from the variance to higher moments of the distribution of offspring numbers. In general, numerical simulations indicate that there is a number n such that the following holds: (i) the odd moments of $\{w_m(x_t)\}$ of order $< n$ are smaller, while the even moments of $\{w_m(x_t)\}$ of order $< n$ are larger than those of $\{w_r(x_t)\}$, so that all moments of order $< n$ favor the resident and hence contradict invasion; (ii) for moments of order $\geq n$ the opposite holds, so that moments of order $\geq n$ favor the mutant. Thus invasion is due to moments of order $\geq n$. In figure 1 the number n is shown for different combinations of the intrinsic growth rate λ and the modulus of equation (3). In many cases $n \geq 3$, which means that the variance of the mutant is higher than that of the resident (and the average number of offspring is still lower), yet the mutant is able to invade. Under these conditions the third and higher moments determine the course of evolution. Despite a higher variance, the skewness of the distribution $\{w_m(x_t)\}$ implies a higher geometric mean fitness for the mutant. This leads to an extension of Gillespie's evolutionary principle: natural selection also acts on higher moments of the distribution of offspring numbers. In fact, selection on higher moments can overcome selection on the first, second, and even the third moments, as the examples reported here show. The results also indicate that selection acting on higher moments becomes more important with increasing variability in offspring number.

The consequence of the invasion of the mutant is stable equilibrium dynamics for the whole population. Quite different dynamics can result if an evolutionary trade-off is assumed for the control mechanism. In general, given a resident with chaotic dynamics described by equation (1), the problem of when a mutant can invade whose dynamics are also of the form described by equation (1) but given by a different set of parameters is difficult and currently under investigation (Doebeli 1995). However, if it is assumed that two of the three parameters of the mutant are the same as for the resident, selection on the third parameter can easily be described: the mutant can invade if the third parameter is such that the mutant's equilibrium density (eq. [2]) is higher than that of the resident. Thus a higher λ , a lower a , and a lower b all imply invasion if the other two parameters are fixed. An evolutionary trade-off for the control mechanism can therefore be incorporated by assuming that the controlled mutant has a lower λ , a higher (nominal) a_0 , or a higher b . If the trade-off is too large, the mutant

λ J	2	3	4	5	6	7	8	9
2,5	1	1	2	2	2	2	2	2
5	2	2	2	2	3	3	3	3
10	2	2	2	3	3	3	3	3
20	2	2	3	3	3	3	3	3
40	2	2	3	3	3	3	3	4
80	2	2	3	3	3	3	3	5

FIG. 1.—Lowest-order moment favoring the mutant. For different parameter values the number n is listed such that moments of the distributions of offspring numbers that are of order $<n$ favor the uncontrolled resident and moments of order $\geq n$ favor the controlled mutant (see text). In all cases invasion is possible and is thus due to selection on moments of order $\geq n$. To obtain the distributions $\{w_m(x_t)\}$ and $\{w_r(x_t)\}$, the resident time series $\{x_t\}$ was obtained by first iterating eq. (1) long enough to eliminate transients, i.e., to let the trajectory approach the chaotic attractor, and then by iterating 250,000 times. The distributions were then obtained by applying the functions w_r and w_m described in the text to this time series. In all cases the parameter a was set to a (nominal) value of 0.1, while the intrinsic growth rate λ and the modulus J of eq. (3), determining the dynamics of the resident, were varied. For fixed λ , J is given by a choice of the parameter b . For low λ and J , all moments favor the mutant ($n = 1$). Increasing λ and J tends to increase n and thus to shift selection pressure onto higher moments. In the most extreme case (*lower right corner*), the first four moments all place the mutant at a disadvantage, yet invasion is possible.

cannot invade, but if invasion is possible it often results in intermittent chaos (fig. 2): the mutant is able to invade and temporarily stabilize the dynamics; in this state the density of the mutant starts to decline again, because at the equilibrium the mutant is an inferior competitor to the resident because of the trade-off. For the same reason the density of the resident is increasing, until its chaotic dynamics dominate the system. After a short period of erratic fluctuations the resident's density is back at low values, and the mutant controls the dynamics again for a relatively long time. The result is a form of "almost stable" chaos. I have described other evolutionary invasion scenarios that lead to intermittent chaos in earlier articles (Doebeli 1993, 1994).

DISCUSSION

This note is about combining two evolutionary problems. The first concerns the evolution of simple population dynamics. Since it was realized by May (1976) that chaos occurs as a rule in even the simplest ecological models, there has been considerable debate about how often complex dynamics occur in natural systems.

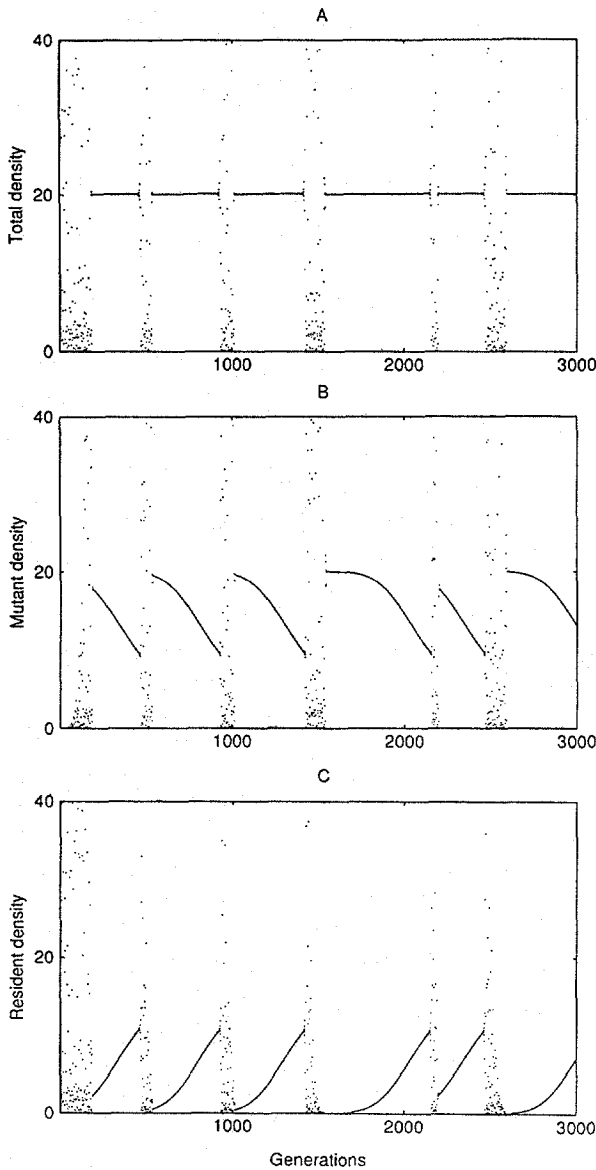


FIG. 2.—Invasion leading to intermittent chaos. After a few hundred generations a small amount of controlling mutants is introduced into a chaotic resident population. A trade-off for the control mechanism is given by assuming a lower intrinsic growth rate of the mutant. The invading mutant is able to control the dynamics of the whole system temporarily (A). In this state the mutant's density gradually declines (B), because at the carrying capacity it is competitively inferior to the resident because of the trade-off. At the end of the stable period the resident's density has increased enough for its chaotic dynamics to dominate the system (C). After a short, intermittent period the mutant is again able to control the dynamics, and the process starts anew. Note that the length of the stable periods is not always the same and instead is given by a statistical distribution (Schuster 1984, chap. 4). The parameter values for the figure were as follows: $a = 0.1$, $b = 4.21$, and $\lambda = 20$ for the resident; $a = 0.1$ (nominal), $b = 4.21$, and $\lambda = 19.7$ for the controlling mutant.

It is widely believed that chaos does not occur frequently (Berryman and Millstein 1989; but see Hastings et al. 1993). However, evolutionary arguments for this belief usually involve group selection (Thomas et al. 1980), in part because theoretical studies based on individual selection suggest that both simple and complex dynamics can evolve (e.g., Turelli and Petry 1980; Ferrière and Gatto 1993). The mechanism reported here belongs to the class in which individual selection leads to evolution from complex to simple dynamics: a phenotype that controls its dynamics by adjusting demographic parameters has a selective advantage over an uncontrolled phenotype exhibiting chaos.

The second evolutionary problem concerns the reasons for this selective advantage. Typically, the invading mutant has a lower average number of offspring. However, since it can invade, its mean geometric fitness must be larger than that of the resident. Following Gillespie (1977), this should be due to a lower variance of the offspring numbers of the mutant. Since the control mechanism tends to dampen fluctuations, this is intuitively expected and indeed correct in some cases (fig. 1). But with increasing complexity of the dynamics and hence increasing variance of offspring numbers, the intuition tends to be incorrect, and the mutant can have a higher variance as well as a lower average number of offspring. The selection pressure then shifts to higher moments. This confirms Gillespie's insight that in a variable environment, which is given here by fluctuating densities, the distribution of offspring numbers determines the course of evolution. What is new here is that selection on the third and higher moments can also be crucial and that it can overcome selection on the first and second moments. A mutant with a lower average and a higher variance of offspring numbers is able to invade if its distribution is more skewed to the right than that of the resident. If evolutionary trade-offs between the control mechanism and the parameters in the model, for example, the intrinsic growth rate, are incorporated, the average offspring number of the mutant is even lower, but selection acting on higher moments can still make invasion possible. Under these circumstances invasion can result in intermittent chaos (fig. 2). Every time the controlled mutant stabilizes the density at the equilibrium, its density gradually decreases, owing to the trade-off, and stabilization ceases for a short period. Note that intermittent chaos in natural populations would not be distinguished from stable equilibrium dynamics if measurements were made during the long phases of constant dynamics.

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