

Stable cycling in discrete-time genetic models

(two-locus models/directional selection/epistasis/bifurcations)

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ABSTRACT Examples of stable cycling are discussed for two-locus, two-allele, deterministic, discrete-time models with constant fitnesses. The cases that cycle were found by using numerical techniques to search for stable Hopf bifurcations. One consequence of the results is that apparent cases of directional selection may be due to stable cycling.

The causes of cycling in populations, which include predator–prey oscillations, the role of time delays, and amplification of environmental disturbances have long been a topic of research in population biology (1, 2). Selection within a single population would be an alternate, and possibly quite general, explanation of cycling. These cycles could provide an explanation of curious behavior observed in one-locus genetic experiments. In this paper, one example of stable cycling in a discrete-time, constant-fitness, two-locus, two-allele model will be discussed, and general features of all the examples I have found thus far will also be included. In ref. 3 cycling that results from genotype–environment interactions is discussed. The only other reported instance of stable cycling due to genetic causes alone is the independent work of Akin (4), who recently proved the existence of stable cycles arising from a Hopf bifurcation in the continuous time, two-locus, two-allele model. This paper complements and extends the work of Akin by dealing with a discrete-time model and examining the behavior of the cycling populations, rather than proving the existence of cycles. Akin employed an asymptotic, analytic approach, whereas I have used a numerical approach.

BACKGROUND AND METHODS

The model used in this study is the usual deterministic two-allele discrete-generation model (5) with alleles *A* and *a* at the *A* locus and *B* and *b* at the *B* locus. The frequencies (and “names”) of the four chromosomal types *AB*, *Ab*, *aB*, *ab* are x_1 , x_2 , x_3 , x_4 , respectively. Let w_y (with $w_y = w_{ji}$ and $w_{14} = w_{23} = 1$) be the fitness of an individual with chromosomes x_i and x_j .

Let *D* be the disequilibrium,

$$D = x_1x_4 - x_2x_3,$$

p_A be the frequency of allele *A*, p_B that of allele *B*, so that

$$p_A = x_1 + x_2, p_B = x_1 + x_3.$$

Finally, let *r* be the recombination rate between the two loci.

The evolution of this system is described by

$$x_i' = \bar{w}^{-1} (x_i w_i + \epsilon_i r D) \quad i = 1 \text{ to } 4.$$

Here $\epsilon_1 = \epsilon_4 = -1$, $\epsilon_2 = \epsilon_3 = 1$, and the marginal mean fitness of x_i is

$$w_i = \sum_{j=1}^4 w_{ij} x_j,$$

and the mean fitness of the population is

$$\bar{w} = \sum_{i=1}^4 w_i x_i.$$

The technique used to identify cases that cycle is a numerical search for stable Hopf bifurcation (6, 7) based on the ideas in refs. 8 and 9. The first step is to pick (at random) a point p_A , p_B , *D* and a value for *r*. Then various fitness matrices corresponding to this equilibrium are generated (because this is a linear system as explained in ref. 8). Stable Hopf bifurcation (6, 7) is sought by looking for examples where the Jacobian

$$a_{ij} = \partial x_i' / \partial x_j,$$

evaluated at the equilibrium, has a real eigenvalue between -1 and 1 and a pair of complex eigenvalues with modulus close to one. Next the value of *r* is varied to yield a single-parameter family of fitness matrices and values of *r* corresponding to a single equilibrium point. The resulting models are then iterated to check for stable cycling, arising as a result of the Hopf bifurcation, for values of *r* where the equilibrium point is unstable.

RESULTS

A number of examples exhibiting stable cycling were generated in the fashion described. There are several properties common to all of these examples. First, the period of the cycle for values of *r* near the bifurcation point is always greater than 100 generations, and the cycle period increases as *r* is moved away from the point of bifurcation. The period at the bifurcation point can be simply calculated from the imaginary part of the eigenvalues at the bifurcation point (7). The eigenvalues at the bifurcation point are of the form $e^{\pm i\theta}$, and the period is $2\pi/\theta$. Because this last quantity is not in general an integer, the cycles do not in general have a period that is an integer. Second, in all the numerical examples, the fitness matrix

$$\begin{matrix} & BB & Bb & bb \\ AA & \left(\begin{matrix} w_1 & w_2 & w_3 \\ w_4 & w_5 & w_6 \\ w_7 & w_8 & w_9 \end{matrix} \right) \\ Aa & & & \\ aa & & & \end{matrix}$$

always satisfies the inequality:

$$w_5 > \max(w_2, w_4, w_6, w_8).$$

[1]

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Table 1. A fitness matrix that leads to stable cycling, for $r = 0.20632 - \lambda$, for $0 \leq \lambda \leq 0.04182$

	<i>BB</i>	<i>Bb</i>	<i>bb</i>
<i>AA</i>	$0.81804 + 0.499\lambda$	$0.61018 + 1.61288\lambda$	1.33068
<i>Aa</i>	$0.42623 + 2.64925\lambda$	1.0	0.22458
<i>aa</i>	0.80724	0.46357	1.41881

Also at least three of the following four inequalities hold:

$$\begin{aligned}
 w_4 &< \min(w_1, w_7) \\
 w_6 &< \min(w_3, w_9) \\
 w_2 &< \min(w_1, w_3) \\
 w_8 &< \min(w_7, w_9).
 \end{aligned}
 \tag{2}$$

Thus, strong epistasis is necessary for cycling.

Finally, in all the cases examined, the stable cycle disappeared as a result of a "blue sky" bifurcation (ref. 10, page 567; ref. 11, chapter 12). In this bifurcation, as r is varied one portion of the cycle approaches a saddle point and then suddenly disappears. Consequently, as r is varied in this manner, the period of the cycle approaches infinity, and each cycle consists of a long time period spent near the equilibrium, and a relatively short time away from the equilibrium, with corresponding relatively rapid changes in gene frequencies. A specific example with these features is outlined in Table 1 and illustrated in Figs. 1 and 2. The equilibrium point is approximately, $p_A = 0.88568$, $p_B = 0.82474$, $D = 0.05414$. The Hopf bifurcation occurs at $\lambda = 0$ (see Table 1), and the blue sky bifurcation occurs at approximately $\lambda = 0.04182$.

DISCUSSION

The appearance of cycling in two-locus, two-allele models shown here for discrete time and shown independently by Akin (4) for continuous time has a number of implications for population biology and genetics. First, another potential cause of cycling in populations has been shown. Even though the fitness

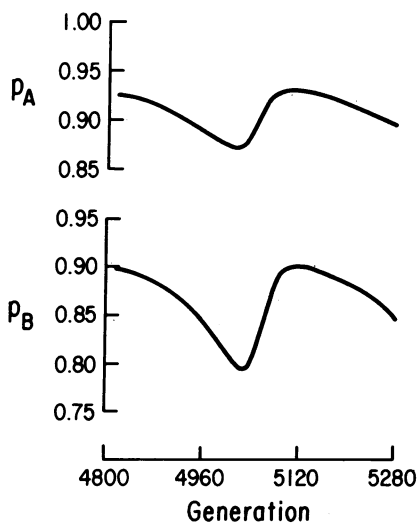


FIG. 1. The stable cycle for the fitness matrix of Table 1, for $r = 0.175$ ($\lambda = 0.03132$). D cycles in a similar fashion.

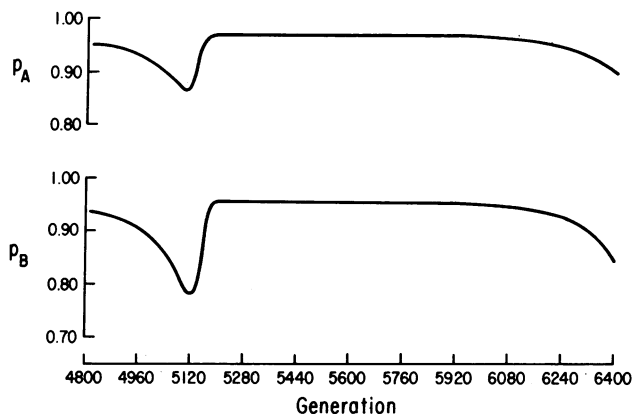


FIG. 2. The stable cycle for the fitness matrix of Table 1, for $r = 0.1648$ ($\lambda = 0.04152$), near the blue sky bifurcation. D cycles in a similar fashion. Note the long period of little gene frequency change.

values required seem rather special—satisfying Eqs. 1 and 2 with large epistasis—the marginal fitnesses (5) at each single locus are quite reasonable. Also, in the context of more loci and more alleles, it is possible that cycling might arise with more reasonable fitness values. The form of the fitness matrices that lead to stable cycling is similar to that of the fitness matrices that give rise to marginal underdominance at a stable equilibrium (8). Most cases of stable cycling, in fact, exhibit induced underdominance for those values of r when the equilibrium point is stable.

The form of the stable cycles is of interest. The cycles can have a very long time with little gene frequency change, followed by a relatively short time of rapid change (Fig. 2). Hence, cases of apparent directional selection may result from cyclic behavior, with a period far too long to observe in real populations.

What is needed now is a study of cycling in more complex models with more loci and more alleles to help assess the likelihood and importance of cycling in genetic models. In the two-locus case studied here, the phenomenon is rare in the sense that large epistasis is required (Eqs. 1 and 2). However, all fitness matrices sufficiently close to a matrix that leads to cycling will also lead to cycling.

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