

Cyclical behavior of genotype frequencies in a two-locus population under fluctuating haploid selection

(temporal fluctuations/cycles/T-cycles/chaotic behavior)

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ABSTRACT Numerical iterations have shown that periodic haploid two-locus selection with nonoverlapping generations can produce large-scale cyclical behavior with a period differing significantly from the environmental period. Among other types, we observed slowly damping oscillations with very long periods, stable T-cycles with a length containing several environmental periods, and chaotic-like dynamics. Possible biological implications are discussed.

Earlier work has shown (1–3) that, in population genetic models with both continuous and discrete times, stationary diploid selection can produce stable oscillations of allele frequencies. Periodic changes in selection coefficients caused by variation of external conditions are considered among other factors maintaining polymorphism in natural populations (4–6). In these systems, one can consider polymorphic fixed points across periods for any of the environmental states under consideration. Rather unexpectedly, we found that these points can show long-term periodic changes along a trajectory with a period much longer than that of the environmental fluctuations generating them.

DESCRIPTION OF THE MODEL

We consider a standard model of a diploid diallelic two-locus infinite population with panmixia and nonoverlapping generations subject to haploid selection. The selection coefficients are functions of environmental states that change periodically. The evolutionary operator for two consecutive generations can be written as

$$\begin{aligned}x_1' &= w_{11}(x_1 - rD)/W, \\x_2' &= w_{12}(x_2 + rD)/W, \\x_3' &= w_{13}(x_3 + rD)/W, \\x_4' &= w_{14}(x_4 - rD)/W.\end{aligned}\quad [1]$$

In each equation, x_j ($j = 1, \dots, 4$) values are the frequencies of the haplotypes AB , Ab , aB , and ab , respectively; w_{ij} is the fitness of the haplotype j in the environmental state i ; r is the rate of recombination between the two loci; $D = x_1x_4 - x_2x_3$ is the linkage disequilibrium coefficient; $W = w_{11}x_1 + w_{12}x_2 + w_{13}x_3 + w_{14}x_4 - (w_{11} - w_{12} - w_{13} + w_{14})rD$.

We will consider a class of periodic environments that can be represented mathematically as $(S_1e_1, Ne_2, S_2e_3, Ne_4)$. S_1e_1 is a sequence of length e_1 of states with the same selection regime S_1 , and S_2e_3 is an analogous sequence of length e_3 with selection regime S_2 . In general, regimes S_1 and S_2 could be different. Ne_2 and Ne_4 designate sequences of selectively

neutral states of lengths e_2 and e_4 . Let $E = e_1 + e_2 + e_3 + e_4$ be the environmental period length.

As a limiting case for environments of this type, one can consider situations with $e_1 = e_3 = 1$ and $e_2 = e_4 = \infty$. Such a model approximates the evolutionary situation discussed by Gillespie (7). He argues that molecular evolution is episodic, with short bursts of rapid evolution interspersed between long periods of very slow change.

For this limiting case, the evolutionary operator for the whole "period" can be represented in the following form:

$$\begin{aligned}P_A' &= P_A(w_{11}P_B + w_{12}(1 - P_B))/W_1, \\P_B' &= P_B(w_{11}P_A + w_{13}(1 - P_A))/W_1, \\W_1 &= w_{11}P_AP_B + w_{12}P_A(1 - P_B) + w_{13}(1 - P_A)P_B \\&\quad + w_{14}(1 - P_A)(1 - P_B), \\P_A' &= P_A(w_{21}P_B + w_{22}(1 - P_B))/W_2, \\P_B' &= P_B(w_{21}P_A + w_{23}(1 - P_A))/W_2, \\W_2 &= w_{21}P_AP_B + w_{22}P_A(1 - P_B) + w_{23}(1 - P_A)P_B \\&\quad + w_{24}(1 - P_A)(1 - P_B).\end{aligned}\quad [2]$$

Here P_A and P_B are the frequencies of alleles A and B . The limiting equations were obtained from Eq. 1, taking into account the fact that for the portion of the period without selection, the allele frequencies do not change, leading in the limit to linkage equilibrium (8–10).

NUMERICAL RESULTS

Model 1. For an environment with period E , we define fitness coefficients of the model described by Eq. 1 as follows.

$$\text{For } S_1, w_{11} = 1, w_{12} = 0.5, w_{13} = 0.6, \text{ and } w_{14} = 0.22 \quad (i = 1, \dots, e_1).$$

$$\text{For } S_2, w_{11} = 0.1, w_{12} = 0.2, w_{13} = 0.165, \text{ and } w_{14} = 0.425 \quad (i = e_1 + e_2 + 1, \dots, e_1 + e_2 + e_3).$$

$$\text{For the remaining cases, } w_{ij} = 1. \quad [3]$$

Note that the fitness coefficients have been chosen so that the product of the fitnesses of a genotype in the two regimes is roughly constant for all genotypes. Therefore, the net change of haplotype frequencies in period E is very small, although the difference at the end of S_1 and S_2 may be large.

Step i. Let $e_1 = e_3 = 1$, $e_2 = e_4 = 2$, and $r = 0.5$. Starting from the initial point $x_1 = 0.5316$, $x_2 = 0.1107$, $x_3 = 0.2851$, and $x_4 = 0.0726$, we obtain the spiral trajectory shown in Fig.

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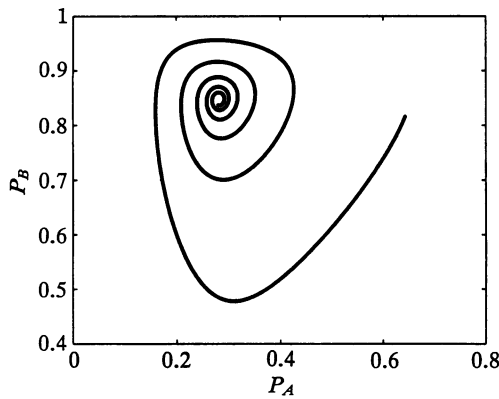


FIG. 1. Fragment of system 1 ($e_1 = e_3 = 1$ and $e_2 = e_4 = 2$) trajectory in the space (P_A, P_B) . The fitnesses are given in the text. The system starts at $P_A = x_1 + x_2 = 0.6423$ and $P_B = x_1 + x_3 = 0.8167$ and spirals inward.

1. The length of the first cycle is approximately $500E$ (i.e., 3000 generations). Therefore, environmental fluctuations with a relatively short period ($E = 6$) can produce much larger gradually damping oscillations of allele frequencies.

The same type of behavior could be observed for other values of r —e.g., $r \in (0.35, 0.5)$. To estimate the dependence of the period length (L) on r , we used the approximation $L = 2\pi/\arccos[\text{Re}(\lambda)/|\lambda|]$, where λ is the complex dominant eigenvalue of the Jacobian matrix at the corresponding polymorphic fixed point. We found that for the set of parameters 3, $L(r)$ increases from 477 to 643 when r decreases from 0.5 to 0.35. For $r < 0.35$, the system converges monotonically to a polymorphic fixed point.

One could ask how robust the long-term damping oscillations caused by short-term cyclical selection are with respect to changed selection coefficients. A simple way to investigate the robustness of the effect is to calculate the range of values of each selection coefficient w_{1j} and w_{2j} ($j = 1, \dots, 4$) compatible with the cyclic behavior, provided all other selection coefficients are as specified by set 3. The following ranges were obtained for $r = 0.5$ and the initial point $x_1 = 0.278682$, $x_2 = 0.073231$, $x_3 = 0.505663$, and $x_4 = 0.142424$.

$$\begin{aligned}
 w_{11} = 1.0 &\Rightarrow (w_{11} - 0.008, w_{11} + 0.015). \\
 w_{12} = 0.5 &\Rightarrow (w_{12} - 0.010, w_{12} + 0.010). \\
 w_{13} = 0.6 &\Rightarrow (w_{13} - 0.005, w_{13} + 0.005). \\
 w_{14} = 0.22 &\Rightarrow (w_{14} - 0.010, w_{14} + 0.010). \\
 w_{21} = 0.1 &\Rightarrow (w_{21} - 0.000, w_{21} + 0.001). \\
 w_{22} = 0.2 &\Rightarrow (w_{22} - 0.005, w_{22} + 0.003). \\
 w_{23} = 0.165 &\Rightarrow (w_{23} - 0.001, w_{23} + 0.001). \\
 w_{24} = 0.425 &\Rightarrow (w_{24} - 0.012, w_{24} + 0.020). \quad [4]
 \end{aligned}$$

It should be emphasized that polymorphism does not necessarily disappear outside these ranges; it could be maintained, although without damping oscillations. It is also worth mentioning that the range of selection coefficients producing oscillatory behavior may be increased further if the coefficients are changed in a concordant manner. Specifically, let us change the coefficients w_{1i} and w_{2i} such that their product remains constant. Then, for $r = 0.5$ and the initial point of the paragraph above, the following pairs of conjugated ranges are compatible with an oscillatory regime, provided the other coefficients remain unchanged.

$$\begin{aligned}
 w_{11} &\in (1.0 - 0.40, 1.0 + 0.05); & w_{21} &= 0.1/w_{11}. \\
 w_{12} &\in (0.5 - 0.04, 0.5 + 0.20); & w_{22} &= 0.1/w_{12}. \\
 w_{13} &\in (0.6 - 0.03, +\infty); & w_{23} &= 0.099/w_{13}. \\
 w_{14} &\in (0.22 - 0.15, 0.22 + 0.01); & w_{24} &= 0.0935/w_{14}.
 \end{aligned}$$

Therefore, we can imagine that in the eight-dimensional space of fitness coefficients, the set of points representing systems with cyclical behavior includes a four-dimensional surface surrounded by an eight-dimensional domain. It would be of interest to check whether or not these oscillatory dynamics will indeed be maintained if selection coefficients are changed randomly within the calculated eight-dimensional cube 4. Fig. 2 illustrates the stability of the oscillatory-like behavior of the system.

Step ii. A next step is to check whether these long-term damping oscillations occur with other lengths and structures of the environmental period. We found the same general pattern when all the components of the environmental period were increased. For instance, let $e_1 = e_3 = 2$ and $e_2 = e_4 = 8$. Starting with the point $(x_1 = 0.0162, x_2 = 0.0294, x_3 = 0.8096, x_4 = 0.1448)$, we obtained the pattern shown in Fig. 3. To estimate the dependence of the period length on the recombination rate, $L(r)$ was calculated as described above. For the same selection regime and starting point, $L(r)$ increases from 173 to 182 when r decreases from 0.5 to 0.3 and then decreases to 172 when r decreases to 0.08. For $r < 0.08$, the system is not polymorphic.

Similarly, dozens of long-term periods were found for $e_1 = e_3 = 7$ and $e_2 = e_4 = 10$ starting from the same point. We stress that this effect is characteristic not only of isolated fitness vectors but also of some eight-dimensional domain.

Step iii. So far we have considered alternating selected and neutral states. The only role of the latter is to allow recombination. To determine the impact of this factor on long-term oscillatory behavior, we considered the limiting system 2, which amounts to complete randomization during the neutral regime.

The damping of oscillations in such a system is extremely slow and the oscillatory period approaches one to two thousand generations. For example, with fitness coefficients for S_1 of $w_{11} = 1, w_{12} = 0.5, w_{13} = 0.6,$ and $w_{14} = 0.22$ ($i = 1, \dots, e_1$) and for S_2 of $w_{21} = 0.1, w_{22} = 0.155, w_{23} = 0.16371,$ and $w_{24} = 0.44636$ ($i = e_1 + e_2 + 1, \dots, e_1 + e_2 + e_3$) and starting from $P_A = 0.0025$ and $P_B = 0.94$, we obtain the trajectory of Fig. 4A. The allele frequencies at the fixed point are approximately $P_A = 0.001686$ and $P_B = 0.940330$ (or 0.002831 and 0.977239 for the other component of the cycle). The eigenvalue of the Jacobian at this point can be characterized by module 0.999993 and $L \approx 3986$. This explains the behavior of the trajectory.

Fig. 4B shows a similar trajectory. In this case, for S_1 , $w_{11} = 1, w_{12} = 0.5, w_{13} = 0.6,$ and $w_{14} = 0.22$ ($i = 1, \dots, e_1$) and,

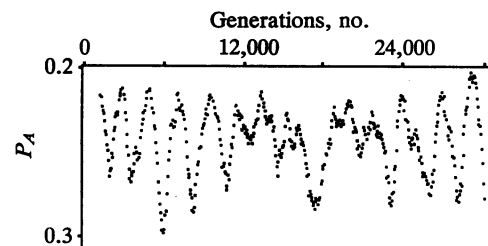


FIG. 2. Variations in P_A in system 1 resulting from stochastic fluctuations of the selection coefficients from period to period (evenly distributed within the eight-dimensional cube 4). The graph shows the dynamics of the system for generations 138,000–162,000.

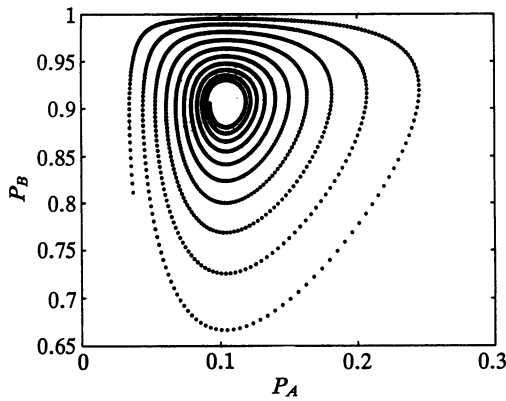


FIG. 3. Trajectory of system 1 ($e_1 = e_3 = 2$ and $e_2 = e_4 = 8$) in the space (P_A, P_B) . The fitnesses are given in the text. The system starts at $P_A = 0.0456$ and $P_B = 0.8258$.

for S_2 , $w_{11} = 0.1$, $w_{12} = 0.155$, $w_{13} = 0.16378$, and $w_{14} = 0.44629$ ($i = e_1 + e_2 + 1, \dots, e_1 + e_2 + e_3$) and starting point $P_A = 0.0025$ and $P_B = 0.94$. The allele frequencies at the fixed point are approximately $P_A = 0.00535$ and $P_B = 0.94173$ (or 0.008969 and 0.977742 for the other component of the cycle).

Several remarks should be made about the trajectories of the system in the vicinity of the polymorphic fixed point. It is easy to check that at any point (P_A, P_B) the Jacobians of transformations 2i and 2ii may be represented in the following form:

$$\begin{vmatrix} [w_{j1}P_B + w_{j2}(1 - P_B) - P'_A dW_{jA}]/W_j & [P_A(w_{j1} - w_{j2}) - P'_A dW_{jB}]/W_j^2 \\ [P_B(w_{j1} - w_{j3}) - P'_B dW_{jA}]/W_j^2 & (w_{j1}P_A + w_{j3}(1 - P_A) - P'_B dW_{jA})/W_j \end{vmatrix},$$

where $j = 1, 2$ and dW_{jA} and dW_{jB} are the derivatives of W_j with respect to P_A and P_B ,

$$dW_{jA} = w_{j1}P_B + w_{j2}(1 - P_B) - w_{j3}P_B - w_{j4}(1 - P_B),$$

$$dW_{jB} = w_{j1}P_A + w_{j2}P_A + w_{j3}(1 - P_A) - w_{j4}(1 - P_A),$$

and (P'_A, P'_B) is the image of the state (P_A, P_B) . If the two parts of the transformation 2 are equal, which means that only one selection regime characterizes the system, then for the fixed point one will obtain $P'_A = P_A$ and $P'_B = P_B$. In this special case, only one stable point can exist, and if so, it has the form $P_A = (w_2 - w_4)/(w_1 - w_2 - w_3 + w_4)$ and $P_B = (w_3 - w_4)/(w_1 - w_2 - w_3 + w_4)$. At this point the Jacobian is equal (for both $j = 1$ and 2) to

$$J = \begin{vmatrix} 1 & -(w_1 - w_3)(w_2 - w_4)/\sigma \\ -(w_1 - w_2)(w_3 - w_4)/\sigma & 1 \end{vmatrix},$$

where $\sigma = w_1w_4 - w_2w_3$. This will be referred to as the epistatic parameter (we assume that $\sigma \neq 0$). In this case the fixed point is unstable or neutral, because $\text{Sp}(J) = 2$. In fact the eigenvalues are $1 \pm [(w_1 - w_3)(w_2 - w_4)(w_1 - w_2)(w_3 - w_4)]^{1/2}/\sigma$, so that the fixed point is real and repelling.

Consider an environment with Eq. 2i \neq Eq. 2ii. Let the point (P_A, P_B) be transformed into (P'_A, P'_B) by operator 2i and then into (P''_A, P''_B) by operator 2ii. It is clear that at the fixed point, $P'_A = P_A$ and $P''_B = P_B$. The Jacobians of these two transformations can be written in the form

$$J_1 = \begin{vmatrix} P'_A(1 - P'_A)/[P_A(1 - P_A)] & P_A(1 - P_A)\sigma_1/W_1^2 \\ P_B(1 - P_B)\sigma_1/W_1^2 & P'_B(1 - P'_B)/[P_B(1 - P_B)] \end{vmatrix}$$

and

$$J_2 = \begin{vmatrix} P_A(1 - P_A)/[P'_A(1 - P'_A)] & P'_A(1 - P'_A)\sigma_2/W_2^2 \\ P'_B(1 - P'_B)\sigma_2/W_2^2 & P_B(1 - P_B)/[P'_B(1 - P'_B)] \end{vmatrix},$$

so that the Jacobian of the evolutionary operator along the full period is $J_{12} = J_1J_2$. Thus $\text{Sp}(J_{12}) = 2 + \sigma_1\sigma_2[\pi(P_A)\pi(P'_B) + \pi(P'_A)\pi(P_B)]/(W_1W_2)^2$, where $\pi(u) = u(1 - u)$.

Clearly the inequality $\sigma_1\sigma_2 < 0$ is the necessary condition for the stability of the polymorphic fixed point—i.e., the epistatic parameters must be of opposite signs. In all of the previous

examples of oscillatory convergence to the polymorphic fixed point this condition holds. The condition for existence of complex eigenvalues of J_{12} is the inequality $\text{Sp}(J_{12})^2 - 4 \det(J_1)\det(J_2) < 0$. After some transformation we have

$$\begin{aligned} & (\sigma_1\sigma_2)^2/(W_1W_2)^4[\pi(P_A)\pi(P'_B) - \pi(P'_A)\pi(P_B)]^2 \\ & + 4\sigma_1\sigma_2[\pi(P_A)\pi(P'_B) - \pi(P'_A)\pi(P_B)]/(W_1W_2)^2 \\ & + 4\pi^2(P_A)\pi^2(P'_B)\sigma_2^2/[\pi(P_A)\pi(P_B)W_2^4] \\ & + 4\pi^2(P_A)\pi^2(P_B)\sigma_1^2/[\pi(P'_A)\pi(P'_B)W_1^4] < 0. \end{aligned}$$

It can be seen that the inequality tends to be true when, for instance, σ_1 and σ_2 are small (because $\sigma_1\sigma_2$ is negative).

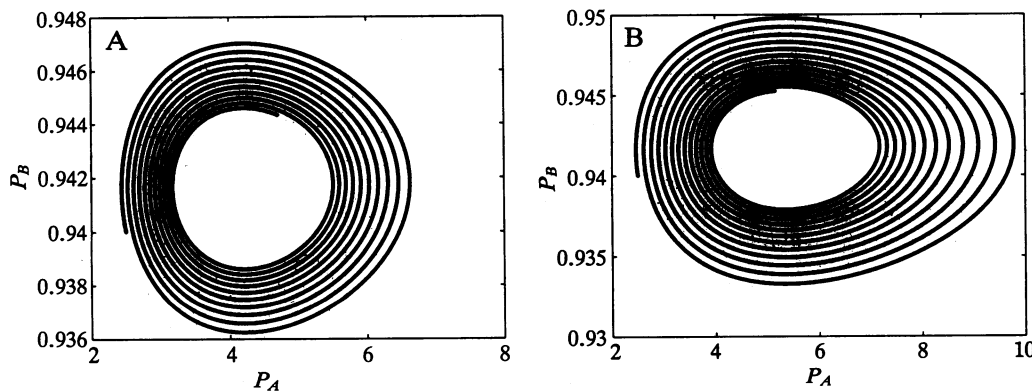


FIG. 4. Fragment of system 2 trajectories in the space (P_A, P_B) . (A and B) Different sets of fitnesses and initial points, as given in the text. The total length of the portion shown in the graph is $50,000E$ in A and $30,000E$ in B. P_A is expressed $\times 10^{-3}$.

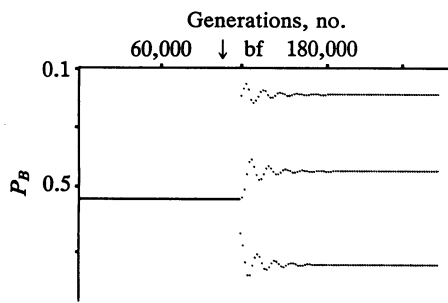


FIG. 5. Formation of a 3-cycle from a stable polymorphic point in system 1 caused by a very slight abrupt change in w_{i4} (from 0.43501 to 0.42901) for the selection regime S_2 of Eq. 5. The time of the change is indicated as bf. The graph shows the values of P_B at the end of each full environmental period, E , where $E = (S_1e_1, Ne_2, S_2e_3, Ne_2)^{n_1}(S_1e_4, Ne_5, S_2e_6, Ne_5)^{n_2}$, with $e_1 = 2, e_2 = 4, e_3 = 2, e_4 = 7, e_5 = 10$, and $e_6 = 7; n_1 = 17$ and $n_2 = 12$.

However, in this case the real part of the eigenvalues will be very close to unity. Therefore, the oscillations, if they exist, will damp very slowly. In the example considered in this section (Fig. 4A), we have $\sigma_1 = -0.80, \sigma_2 = 0.019, Sp(J_{12}) = 1.9999688, \det(J_1) = 0.6648690, \det(J_2) = 1.5040154$, and $Sp(J_{12})^2 - 4 \det(J_1)\det(J_2) = -0.0000183 < 0$.

Therefore, the analysis of the limiting system 2 has shed some light on the long-term damping oscillations caused by short-term cyclical fluctuations of selection coefficients.

Model 2. An increase in the complexity of the environmental changes can lead to new effects. Consider system 1 with this periodic environment: $E = (S_1e_1, Ne_2, S_2e_3, Ne_2)^{n_1}(S_1e_4, Ne_5, S_2e_6, Ne_5)^{n_2}$, where n_1 and n_2 are the number of successive reiterations of elementary periods, each belonging to the class considered above (model 1, steps i and ii). The fitness coefficients are as follows.

For $S_1, w_{i1} = 1, w_{i2} = 0.5, w_{i3} = 0.6$, and $w_{i4} = 0.22$

$$(i = 1, \dots, e_1).$$

For $S_2, w_{i1} = 0.1, w_{i2} = 0.2, w_{i3} = 0.1616$, and $w_{i4} = 0.43501$

$$(i = e_1 + e_2 + 1, \dots, e_1 + e_2 + e_3). \quad [5]$$

Note again that $w_{i1}w_{i2} \approx 0.1$. Let $r = 0.5, e_1 = 2, e_2 = 4, e_3 = 2, e_4 = 7, e_5 = 10$, and $e_6 = 7$. For the particular case of $n_1 = 17$ and $n_2 = 12$ and the initial point $x_1 = 0.015249, x_2 = 0.002033, x_3 = 0.677736$, and $x_4 = 0.304981$, the simple graph shown before the time bf in Fig. 5 is obtained. This part corresponds to stable forced oscillations with a period equal to the full environmental period. It can be considered as a stable polymorphic fixed point, if we study the behavior of P_A and P_B between consecutive periods. (In Figs. 5 and 6, the graph shows P_B at the last generation of each period.) What happens if the selection coefficients are suddenly changed? The part of the graph starting at time bf shows the appearance of a stable T -cycle ($T = 3$). This strikingly different pattern follows from a seemingly trivial change in $S_2, w_{i4} = 0.43501 \rightarrow w_{i4} = 0.42901$.

Now consider again system 5 with coefficients corresponding to those of Fig. 5, with the exception that $w_{i4} = 0.433120$ in S_2 . The initial point is $x_1 = 0.000216, x_2 = 0.000481, x_3 = 0.309366$, and $x_4 = 0.689937$. We now show a series of transformations of the system behavior caused by stepwise changes of w_{i4} in S_2 . Fig. 6 shows the following conversions: (i) from the initial 4-cycle to a 12-cycle, due to a change in w_{i4} from 0.433120 to 0.432220; (ii) from the 12-cycle to chaotic-like behavior, due to change in w_{i4} from 0.432220 to 0.431320; (iii) from chaotic-like behavior to a 3-cycle, due to change in w_{i4} from 0.431320 to 0.430420. Fig. 6D shows a fragment of the 12-cycle in more detail.

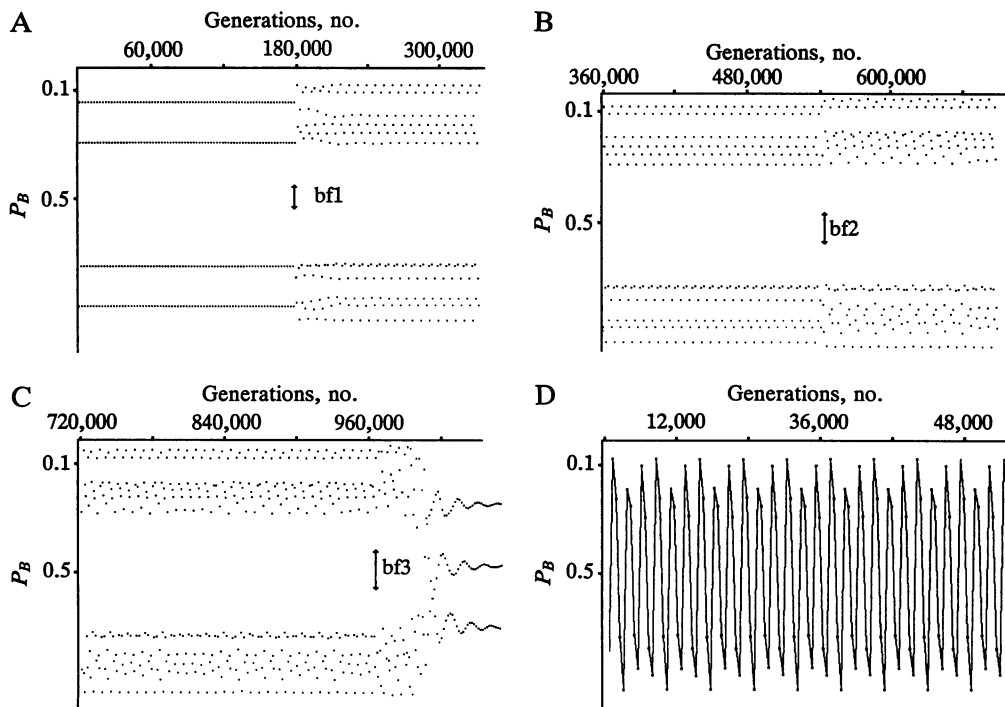


FIG. 6. Series of transformations of the behavior of system 1 caused by a chain of abrupt changes in w_{i4} for the selection regime S_2 of Eq. 5. The period structure is given in Fig. 5. The times of change are indicated by arrows at bf1, bf2, and bf3. (A) Transformation of a 4-cycle into a 12-cycle. (B) Transformation of the 12-cycle into chaotic-type behavior. (C) Transformation of chaotic-like behavior into a 3-cycle. (D) A detailed fragment of the 12-cycle, in which the consecutive points are connected by straight lines. Note that the mode of any next regime depends significantly on the phase of the previous cycle at which the change of the fitness coefficient occurred.

Especially interesting is the chaotic-like behavior. We tested whether or not small variations in the initial point of this behavior will result in close trajectories. This is not the case; a change of 10^{-6} in any of the coordinates of the initial points has produced, after 1000 full environmental periods, a divergence in all decimal places. This is characteristic of chaotic behavior (e.g., ref. 11). In all other regimes, no such instability of the trajectories was observed.

DISCUSSION

Despite the relatively simple structure of these haploid selection models, they manifest diverse cyclical modes of behavior. The large period length of these oscillations induced by short-period changes in the environment was quite unexpected. This seems analogous to effects found for systems with diploid selection in a constant environment (1–3). But in our case the period length described for model 1 approaches thousands of generations when the period of environmental change is 6–10 generations. In our second model, the transformation in the neutral portion of the period produces linkage equilibrium. This corresponds to an infinite number of generations without selection. This can be considered as a limiting case of situations with very long periods of neutral behavior alternating with short periods of strong selection (7).

Damping oscillations in the first model were found to be rather robust with respect to variation in selection coefficients. Moreover, stochastic variation of these coefficients within a certain range produces oscillatory behavior, preventing the convergence to a (polymorphic) fixed point. The last fact suggests some speculations about the possible evolutionary significance of this mode of population behavior.

The same genetic structure imposed on different patterns of environmental change can produce quite different kinds of limiting cyclical behavior. Thus, in the samples of model 2, environments with relatively long periods generate short T -cycles with lengths of 3–12 and chaotic-like behavior. Earlier, in genetic systems with constant selection regimes only very long cycles were observed (1–3), and Hastings (3) asked whether short cycles are possible in such systems. Akin (quoted in ref. 10) found an example of such a behavior, a cycle with a length of 2, but with a recombination rate exceeding 0.75, which is biologically unrealistic. It can be shown numerically that Akin's evolutionary operator, applied to a changing environment (for example, with two states and a period length of 20–30 generations), produced T -cycles with a length of 2. By an appropriate choice of selection

coefficients, this mode of behavior can be obtained with recombination rates arbitrarily close to 0.5, although exceeding this value. It is worth mentioning here that the metrical theory of recombination and some experimental evidence indicate that small excesses beyond 0.5 are possible (12).

One can ask how effective the proposed mechanism of long-period fluctuations caused by short-period changes of conditions is. At least partially, the answer to this question depends on possible candidates for the initial short-period fluctuations. In this connection, we can think about seasonal environmental changes, 11-year sun activity cycles, and such. According to the proposed mechanism, these cycles could in principle produce oscillations of any length for organisms, thus providing an environmental basis for the evolution of higher organisms, for example, plankton or coral reef organisms affecting higher forms such as vertebrates. These latter forms can produce new cycles, and so on. This mechanism differs from oscillations caused by coevolution of antagonistic species, such as host–parasite or predator–prey relationships, because it does not involve any kind of mutual effects.

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