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Supercycles, strange attractors and chaos in a standard model of population genetics

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Abstract

We carried out a detailed investigation of the standard multilocus genetic system. We evaluated the characteristics of the dynamics of several types of such a system allowing to classify the complex trajectories: the Lyapunov exponent, the information entropy, the information dimension and the capacity. It is shown that such dynamic systems manifest auto-oscillations, strange attractors, and chaos. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The biological applications of complex system dynamics concern ecology, morphogenesis and evolutionary theory [1]. Evolution may be viewed as the formation of new macroscopic patterns [1]. The study of the pattern and amount of genetic variability under different combinations of evolutionary forces is a major theme of theoretical population genetics [2]. Complex dynamical behavior of purely ecological models and ecological–genetical models are well known (see, e.g., Ref. [3] and references therein). Complex dynamics has been found in purely genetic two-locus models with constant parameters for a continuous time case [4]. To our knowledge, only one example of a discrete time model with constant coefficients has been studied so far [5]. Recently, we have shown that complex dynamics is a typical phenomenon for multi-locus genetic systems with a cyclical variation of parameters [6–8]. It is interesting to interpret these results using the methods developed for the analysis of complex physical systems [9–12]. In this paper a four-locus diallelic system subjected to a cyclically varying environment is investigated. It is shown that for a certain range of parameters the

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system manifests autooscillations, period-doubling, chaotic behaviour, strange attractors and frequency locking. The entropy, the dimension [11] and the Lyapunov exponent [13] of the system are evaluated.

2. The model and basic equations

We investigate the behaviour of a dynamic system which represents an infinite population with panmixia and non-overlapping generations. Assume that four linked diallelic loci $A_i/a_i (i=1,\dots,4)$ affect the selected trait u in such a way that $u=u(g)=\sum_{i=1}^{4} u_i(g)$. The effect of the ith locus of the genotype g is specified as $u_i(g)=d_i$ for A_iA_i, $d_i(1+h_i)$ for A_ia_i, and 0 for a_ia_i, where $d_i > 0$ is the additive effect of the ith locus, and h_i is its dominance effect. For cyclical selection, the fitness $w_t(u)$ of a genotype with trait value u at the environmental state t is defined by the fitness function $w_t(u(g))=F(u(g)-z_t)$ where z_t is the trait optimum selected for at the environmental state t. For example, one can use the fitness function $F(u(g)-z_t)=\exp\{-[u(g)-z_t]^2 s^{-2}\}$. The evolution of the genetic system is described by the multi-dimensional map [2]

$$x_m^{n+1} = \sum_{i,j} \frac{w_n(u(g_{ij}))P_{ij,m}x_i^n x_j^n}{W}\,, \tag{1}$$

where the gamete frequencies x_i^n and x_i^{n+1} in adjacent generations are the phase variables which obey the following condition: $\sum_{i=1}^{16} x_i = 1$, $x_i \geqslant 0$ where $P_{ij,m} \geqslant 0$ is the probability of producing gamete m by a genotype g_{ij} that resulted from union of gametes i and j in the previous generation. $P_{ij,m}$ depends on the distribution of the selected loci among chromosomes and on the rate of recombination r between the adjacent loci within the chromosome. Clearly, $\sum P_{ij,m} = 1$. The mean fitness W has the form [2]: $W = \sum_m \sum_{i,j} w_t(u(g_{ij}))P_{ij,m}x_ix_j$. Different types of cyclical selection regimes can be defined by a finite ordered set $\{z_1|n_1, z_2|n_2, \dots, z_q|n_q\}$ where z_t is the selected optimum at the tth environmental state, and n_t is the longitude of the tth state, so that the period length p has the form $p = n_1+n_2+\cdots+n_q$. Two extreme types of the map, Eq. (1), resulting in complex limiting behaviour (CLB) have been considered in theoretical population genetics. The first type is characterized by constant fitness coefficients $w(g_{ij})$. The second type includes models with fitness coefficients $w(g_{ij})$ which depend on phase variables. The model considered in this paper comprises a third, intermediate, type with fitness coefficients that do not depend on the phase variables. In physical systems such kind of dependence can result in a dynamic phenomenon referred to as parametric oscillations [14]. We characterize the limiting behaviour of the trajectories for a complex attractor using the maximal Lyapunov exponents $\lambda_{\max}$, the information entropy I, the capacity d_C and information dimension d_I [11,13,15]:

$$\lambda_{\max}(b) = \frac{1}{N_p} \sum_{i=1}^{m-b} \sum_{\langle \mathbf{k},\mathbf{h} \rangle} \ln \left[\frac{\|\mathbf{X}_{i+1}^j(\mathbf{k}) - \mathbf{X}_{i-1}^j(\mathbf{h})\|}{\|\mathbf{X}_i^j(\mathbf{k}) - \mathbf{X}_i^j(\mathbf{h})\|} \right], \tag{2}$$

$$I(\varepsilon) = -\sum_{i=1}^{N(\varepsilon)} P_i \ln P_i, \qquad d_C = \lim_{\varepsilon\to 0}\frac{\ln N(\varepsilon)}{\ln(1/\varepsilon)}, \qquad d_I = \lim_{\varepsilon\to 0}\frac{I(\varepsilon)}{\ln(1/\varepsilon)}. \tag{3}$$

Here the distance between the lattice points **k** and **h** has the form [13]:

$$\|\mathbf{X}_i^j(\mathbf{k}) - \mathbf{X}_i^j(\mathbf{h})\| = \left[\sum_{u=i}^{i+b-1} (x_u^j(\mathbf{k}) - x_u^j(\mathbf{h}))^2\right]^{1/2}. \tag{4}$$

The vectors $\mathbf{X}_i^j(\mathbf{k})$ correspond to a given b; the points **k** and **h** are chosen in such a way that the distance defined by Eq. (4) is less than the maximum initial separation which belongs to the interval (0, 1), and the total number of pairs $\langle \mathbf{k},\mathbf{h}\rangle$ is N_p[13]. P_i is the probability contained within the ith cube of side ε, $N(\varepsilon)$ is the minimal number of p-dimensional cubes of side ε needed to cover an attractor.

3. Results and discussion

The numerical analysis of the map, Eq. (1), proves the existence of essentially complex phenomena in population genetics due to cyclical selection. The selection model considered demonstrates supercycles, strange attractors and chaotic-like behaviour. The system simultaneously participates in two types of motion. The first type of motion is caused directly by the cyclical selection, and it is characterized by a short period which is equal to that of the environmental period p. The motion of the second type can be either periodic or more complex. The periodic motion has the period length which is usually much larger than p. The second type of motion is to some extent analogous to the anharmonism [14] in physical systems. We are interested in the driven motion of the second type. The trajectory is observed only at this state taken at intervals of the length p. Such a choice means that we actually study the dynamic system governed by the map, Eq. (1), which is iterated p times during the selection cycle. We call a cycle belonging to such a trajectory as a supercycle, since each point of it corresponds to a full selection cycle. The main types of the system complex behaviour are presented in the following pictures.

Fig. 1a demonstrates a projection of a supercycle on a plane. Its comparatively complex structure is due to the high dimensionality of the phase space. Its spectrum presented in Fig. 1b corresponds to a cyclical motion and consists of two broadened lines. The estimation of the Lyapunov exponent according to Eq. (2) yields the value of $\lambda_{\max} \to 0$. The capacity and the information dimension, Eq. (3), are calculated for the two-dimensional projection (see Fig. 1a) since the calculating of these quantities in general case of 15 dimensions is hardly possible [16]. Choosing $\varepsilon = 1/200$ we find that $d_C = 1.22$ and $d_I = 1.08$. The value of $\lambda_{\max}$ shows that the motion in our case is cyclical, indeed; the value of d_I is close to the expected unit, while the value of d_C is larger than the expected one. However, the capacity and the information dimension decrease with a decrease of ε. For $\varepsilon = 1/1000$ they reach the following values: $d_C = 1.18$ and $d_I = 1.03$. Consider the examples of more complex behaviour presented in Figs. 2 and 3.

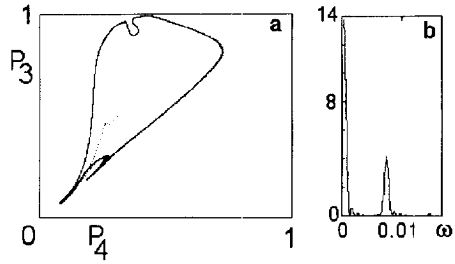

Fig. 1. The supercycle caused by a cyclical selection for a trait controlled by four additive loci. (a) Projection of the trajectory on the phase plane (P_3, P_4). (b) The spectral density (in arbitrary units) of the time series corresponding to the changes of P_3.

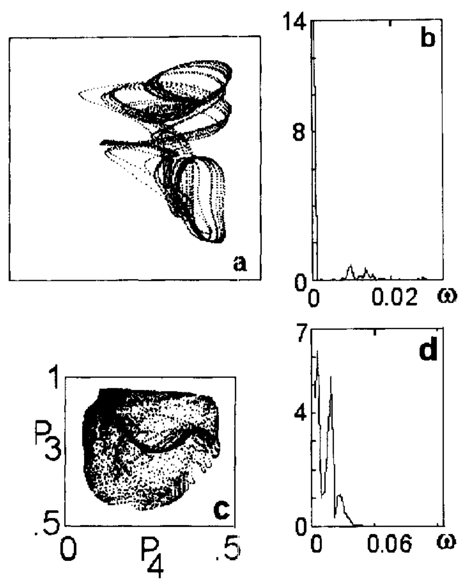

Fig. 2. Complex trajectories caused by cyclical selection for a trait controlled by four additive loci. (a) Projection of the non-cyclical complex trajectory on a phase plane demonstrating the resemblance between the attractor and the Lorenz attractor. (b) The spectral density (in arbitrary units) of the time series corresponding to the changes of P_3. (c) A fragment of the complex attractor trajectory for 20 000 environmental periods (from 30 001 to 50 000). (d) The spectral density (in arbitrary units) of the time series corresponding to the changes of P_3.

The special projection of the attractor shown in Fig. 2a allows to specify its Lorentz attractor-like structure. The Lyapunov exponent is positive, $\lambda_{\max} \approx 0.002$, and shows some variation along the trajectory in fourth decimal position. Consequently, the attractor is chaotic [11]. For $\varepsilon = 1/200$ and $1/1000$ we find, respectively, that $d_C = 1.65, 1.51$ and $d_I = 1.60, 1.50$. The attractor's spectrum presented in Fig. 2b shows the frequency-locking effect which is similar to that in laser systems [12,17].

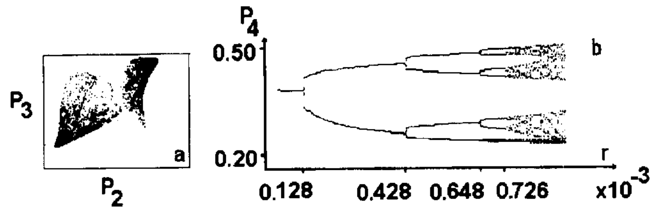

Fig. 3. Complex attractor caused by cyclical selection for a trait controlled by four dominant loci. (a) A fragment of the trajectory for 20 000 environmental periods (from 30 001 to 50 000). (b) Bifurcation diagram with r taken as a bifurcation parameter.

The attractors shown in Fig. 2c and Fig. 3a demonstrate no explicit Lorentz features. They are chaotic since their Lyapunov exponents $\lambda_{max} \approx 0.04$ and 0.03, respectively. The capacity and information dimension of these attractors have for $\varepsilon = 1/200$ and $1/1000$ the following values, respectively: for that in Fig. 2c $d_C = 1.57, 1.88$ and $d_I = 1.28, 1.28$; for that in Fig. 3a $d_C = 1.40, 1.38$ and $d_I = 1.21, 1.26$.

Consider the bifurcation diagram (Fig. 3b) preceding the attractor shown in Fig. 3a. This bifurcation cannot be identified as a Feigenbaum one since the ratio of two consequent bifurcation intervals considerably differs from the Feigenbaum constant [14]. It is rather similar to the Hopf one since three consequent steps of a period-doubling are identified [14].

4. Conclusions

We investigated numerically the dynamic system generated by the multi-dimensional map, Eq. (1). It demonstrates CLB like supercycles and more complex attractors including chaotic ones. The studied genetic system manifests the general features of complex nonlinear systems known in fluid dynamics, optics and theoretical ecology [1,2,12,17,18].

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