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AN EVOLUTIONARY EQUATION AND LIMIT THEOREM FOR GENERAL GENETIC SYSTEMS WITHOUT SELECTION

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There are a large number of works on the limiting behavior of the dynamical systems arising in mathematical genetics (of populations). However, most of them are devoted to the investigation of rather simple (but important for applications) special cases. Certain authors have at various times proposed unifying schemes (see [1]–[3] and their subsequent development in [4]–[6] respectively). But until now, mainly because of combinatorial difficulties, a common description of the evolution of genetic systems has not been given (although some authors [6]–[8] have come quite close to such a description). In the present note, following the lead of [2], [5], [7], [8], we derive a common equation of evolution for populations with nonoverlapping generations in the absence of selection. On the basis of this result, we then establish a general theorem on the convergence of trajectories and investigate the rate of convergence to equilibrium.

1. Description of the mechanism of splitting of genes. Let $L = \{1, \cdots, l\}$ denote the set of loci(¹) and let $n_i \geq 2$ denote the number of alleles at the ith locus. We denote by a_{ik}, $i = 1, \cdots, l$; $k = 1, \cdots, n_i$, the kth gene of the ith locus. Let N be a natural number and let $\sigma = \{\sigma_1, \cdots, \sigma_l\}$ be a certain system of subsets of the set $\mathfrak{N} = \{1, \cdots, N\}$. For each $i = 1, \cdots, l$ we define on the set σ_i a function $h_i(s)$ with values in the set $\{1, \cdots, n_i\}$ of indices of the genes of the ith locus. The structure described uniquely determines a commutative monomial

$$g = \prod_{1 \leq i \leq l} \prod_{s \in \sigma_i} a_{i h_i(s)}, \tag{1}$$

which is called a *gamete with characteristic* σ. Different gametes with one and the same characteristic differ in the collections of functions $\{h_i\}$. The set of all gametes with characteristic σ is denoted by Γ_σ and called a *section of gametes*.

The above notions have the following genetic meaning: $\mathfrak{N}$ is the set of chromosome indices with the possible repetition of identical chromosomes in polyploid gametes being taken into account, σ_i is the set of indices of the chromosomes containing the ith locus and $h_i(s)$ is the index of the gene at the ith locus in the sth chromosome of a gamete g.

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(¹) For the genetic terminology used by us, see, for example, [5].

Let $\nu = \{\nu_1, \cdots, \nu_l\}$ be an arbitrary system of subsets of the set $\mathfrak{N}$ and let $\phi = \{\phi_1, \cdots, \phi_l\}$ be a system of mappings $\phi_i : \nu_i \to \mathfrak{N}$. Then the functions $k_i'(j) = k_i(\phi_i(j))$ are defined on the preimages $\sigma_i' = \phi_i^{-1}(\sigma_i)$. The monomial

$$g' = \prod_{1\le i\le l} \prod_{j\in\sigma_i'} e_{i k_i'(j)} \tag{2}$$

is called a *subgamete* of the gamete g. It will be convenient below to treat the passage from a gamete g to a subgamete g' as the action of a certain operator: $g' = \Delta_\phi g$. If Im $\phi_i \subset \sigma_i$, $i = 1, \cdots, l$, we will say that the system ϕ *belongs to the characteristic* σ. We will also say that two systems of mappings ϕ and ψ constitute a *partition for the characteristic* σ and write $\phi |_\sigma \psi$, if for each $i = 1, \cdots, l$ the domains of definition Dom ϕ_i and Dom ψ_i constitute a partition of the set σ_i.

Suppose given two "parent" characteristics ε and ω and an "offspring" characteristic σ. The partitions $\phi |_\sigma \psi$, for which ϕ belongs to the characteristic ε and ψ belongs to the characteristic ω are called *admissible* for the triple $(\varepsilon, \omega; \sigma)$. Any probability distribution on the set of admissible partitions is called a *linkage distribution* for the given triple of characteristics $(\varepsilon, \omega; \sigma)$ and the corresponding probabilities are denoted by $p_{\varepsilon,\omega}(\phi |_\sigma \psi)$. Genetically, a linkage distribution describes the probabilities of all possible recombinations for the given characteristics of the parent and offspring gametes.

The mechanism described includes all of the usually considered methods of formation of gametes in meiosis for parents and offspring of arbitrary polyploid type and for arbitrary sexual differentiation of gametes, in particular, for partial sex-linkage and in the presence of more than two sexes.(2)

2. Description of the mechanism of intermixing of genes. The intermixing of genes in a population is effected by means of *crossings*, *mutations* and *migrations*. Our description of intermixing is based on the spatially genealogical structure of a population. Suppose two natural numbers s and r are given for each characteristic σ (biologically, s is the number of areas exchanged by migrants and r is the number of different zygote genotypes). By a *spatially genealogical localization* (s.g.l.) of a section of gametes Γ_σ is meant a triple $X = (\sigma; \alpha, \beta)$, where $\alpha = 1, \cdots, s$ and $\beta = 1, \cdots, r$. The number α is called the *area* of the s.g.l., while the number β is called the *origin* of the s.g.l. The pair $(\sigma; \alpha)$ is called the *spatial localization* (s.l.) of the section Γ_σ, while the pair $(\sigma; \beta)$ is called the *genealogical localization* (g.l.) of the section Γ_σ.

Suppose given two "parent" s.g.l.'s $X = (\varepsilon; \cdot)$ and $Y = (\omega; \cdot)$ and an "offspring" s.g.l. $Z = (\sigma; \cdot)$. To each triple $(X, Y; Z)$ there must correspond a certain linkage distribution $p_{X,Y}(\phi |_Z \psi) = p_{\varepsilon,\omega}(\phi |_\sigma \psi)$. This determines the contribution of meiosis in the intermixing of genes under crossings.

Mutations are described by assigning to each locus i and each s.g.l. $(\sigma; \alpha, \beta)$ a column stochastic matrix

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(2) Crossing sexes, though not in the sense of S. Lee [9] but in the usual way, i.e. pairwise.

$$U^{(i)}(\sigma;\alpha,\beta)=(u^{(i)}_{\nu,\nu'}(\sigma;\alpha,\beta))_{\nu,\nu'=1}^{m_i}.$$

An element $u^{(i)}_{\nu,\nu'}(\sigma;\alpha,\beta)$ is interpreted as the probability of the gene $a_{i\nu}$ going over into the gene $a_{i\nu'}$ under the given s.g.l. We define the *full mutation matrix* $U(\sigma;\beta)$ by setting[3]

$$U(\sigma;\alpha,\beta)=\bigotimes_{1\le i\le l}[U^{(i)}(\sigma;\alpha,\beta)]^{\otimes n}$$

and then forming the direct sum

$$U(\sigma;\beta)=\sum_{1\le\alpha\le s}U(\sigma;\alpha,\beta).$$

Migrations are described by assigning to each g.l. $(\sigma;\beta)$ a row-stochastic matrix

$$V(\sigma;\beta)=(v_{\alpha,\alpha'}(\sigma;\beta))_{\alpha,\alpha'=1}^{s}.$$

An element $v_{\alpha,\alpha'}(\sigma;\beta)$ is interpreted as the probability of a migration from the area α' into the area α under the given g.l.

The act of intermixing consists of successive acts of mutation and migration, it being assumed below without loss of generality that the act of mutation follows the act of migration.[4] The *matrix of the act of intermixing* is defined as $W(\sigma;\beta)=(V(\sigma;\beta)\otimes 1_m)U(\sigma;\eta)$, where 1_m is the identity matrix of order $m=|\Gamma_\sigma|=\prod_1^l m_i$.

Suppose given a natural number T (the "generation time") and, for each "moment of time" $t=1,\cdots,T$, the matrix $W_t(\sigma;\beta)$ of the act of intermixing during the moment t. The *matrix of intermixing per generation* is defined as the product $W(\sigma;\beta)=W_T(\sigma;\beta)\cdots W_1(\sigma;\beta)$.

5. Evolutionary equation. We will say that the *state of a population* is given if with each s.g.l. $(\sigma;\alpha,\beta)$ there is associated a certain probability distribution $x_g(\sigma;\alpha,\beta)$ for the gametes g of the section Γ_σ. This distribution is conveniently written as a formal linear combination

$$G(\sigma;\alpha,\beta)=\sum_{g\in\Gamma_\sigma}x_g(\sigma;\alpha,\beta)g.$$

The corresponding collection $G(\sigma;\beta)=\{G(\sigma;\alpha,\beta)\}_{\alpha=1}^{s}$ is called the *state* of the g.l. $(\sigma;\beta)$. To each g.l. $\overline{X}=(\sigma;\beta)$ there corresponds in a natural way the collection of s.g.l.'s $\{X_\alpha\}_{\alpha=1}^{s}$, where $X_\alpha=(\sigma;\alpha,\beta)$. Let $P_{\overline{X},\overline{Y}}(\phi_{\Sigma}^{1}\psi)$ denote the matrix $\operatorname{diag}\{P_{X_1Y_1}(\phi_{\Sigma_1}^{1}\psi)\cdots P_{X_sY_s}(\phi_{\Sigma_s}^{1}\psi)\}$. We linearly extend the operators Δ_ϕ to the formal linear combinations of gametes $G(\sigma;\alpha,\beta)$ and put

$$\Delta_\phi G(\sigma;\beta)=\{\Delta_\phi G(\sigma;1,\beta)\ldots\Delta_\phi G(\sigma;s,\beta)\}.$$

The *evolutionary equation for a population* determines the state of the population at

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(3) This construction is motivated by the independence of the mutations at different loci in the absence of selection.

(4) Also, we note that several successive mutations (migrations) can be combined into a single mutation (migration).

the $(n+1)$th generation as a function of its state at the nth generation. In "block" notation with respect to the g.l.'s it has the form

$$G_{n+1}(\bar{Z}) = W(\bar{Z}) \sum_{\bar{X},\bar{Y}} q(\bar{X},\bar{Y};\bar{Z}) \sum_{\eta,\theta} P_{\bar{X},\bar{Y}}(\eta|_Z\theta)\,\Delta_\eta G_n(\bar{X})\,\Delta_\theta G_n(\bar{Y}); \tag{3}$$

here $\bar{X}$, $\bar{Y}$, $\bar{Z}$ are g.l.'s, $q(\bar{X},\bar{Y};\bar{Z})$ is a nonnegative diagonal matrix determining the relative contribution of the states of the g.l.'s $\bar{X}$ and $\bar{Y}$ to the state of the g.l. $\bar{Z}$, $\sum_{\bar{X},\bar{Y}} q(\bar{X},\bar{Y};\bar{Z}) = \operatorname{diag}(1,\cdots,1)$, and the multiplication of the vectors in (3) is componentwise.

4. Limit theorem. For any initial state G_1 equation (3) determines a *trajectory* $G_1, G_2, G_3, \cdots$. To investigate the asymptotic behavior of the trajectories, we employ the method of *exact linearization* (cf. [2], [5], [7], [8]). We fix a system ν of subsets of the set $\bar{X}$ and consider a set of pairs $(\bar{X},\phi)$ in which $\bar{X}$ is a g.l. and ϕ is a system of mappings such that $\operatorname{Dom}\phi = \nu$ and ϕ belongs to the characteristic of $\bar{X}$. If two pairs $(\bar{Z},\eta)$ and $(\bar{Y},\theta)$ from the indicated set are given in a definite order, then the following matrix is determined:

$$\begin{aligned} W_\chi(\bar{Z})\Big\{\Big[\sum_{\bar{X}} q(\bar{Y},\bar{X};\bar{Z}) \sum_{\chi\cdot\varphi=\theta} P_{\bar{Y},\bar{X}}(\theta|_Z\chi) \\ + \sum_{\bar{X}} q(\bar{X},\bar{Y};\bar{Z}) \sum_{\chi\cdot\varphi=\theta} P_{\bar{X},\bar{Y}}(\chi|_Z\theta)\Big] \otimes I_{W_\psi}\Big\}, \end{aligned} \tag{4}$$

where $\bar{Z} = (\sigma,\cdot)$, $W_\chi(\bar{Z})$ is found from the identity $\Delta_\chi W(\bar{Z}) = W_\chi(\bar{Z})\Delta_\chi$, and the multiplication of the systems of mappings is termwise. We denote the matrix consisting of the blocks (4) corresponding to all possible $(\bar{X},\theta)$, $(\bar{Y},\eta)$ by Q_ν.

Theorem 1. *For the convergence of all of the trajectories it is necessary and sufficient that all of the matrices Q_ν not have eigenvalues $\lambda \neq 1$ for which $|\lambda| = 1$.*

We note that when the condition of Theorem 1 is not satisfied, the trajectories converge to a finite limit cycle.

Theorem 2. *Under the fulfillment of the condition of Theorem 1 every trajectory converges at the rate of a geometric progression whose ratio is equal to the largest modulus of the eigenvalues of the matrices Q_ν in the disk $|\lambda| < 1$.*

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