Dynamical Systems of a Gonosomal Evolution Operator

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Preliminaries from Biology

A population is a summation of all the organisms of the same group or species, which live in a particular geographical area, and have the capability of interbreeding.

A gene is the molecular unit of heredity of a living organism.

An allele is one of a number of alternative forms of the same gene.

A free population means random mating in the population: where all individuals are potential partners. This assumes that there are no mating restrictions, neither genetic or behavioural, therefore all recombination is possible.

Bisexual population (BP) means all the organisms of one type must belong to the same sex. Thus, it is possible to speak of male and female types.

In the life sciences the population dynamics branch studies the size and age composition of populations as dynamical systems. These investigations are motivated by their application to population growth, ageing populations, or population decline.

The population dynamics is a well developed branch of mathematical biology, which has a history of more than two hundred years [1], although more recently the branch of mathematical biology has greatly increased. Many concrete models of mathematical biology described by corresponding non-linear evolution operator.

[1] Bacaër N. A short history of mathematical population dynamics. Springer-Verlag, London. (2011)

We study dynamical system generated by a concrete non-linear multidimensional operator describing a gonosomal evolution. Our model is related to a bisexual population. We note that investigation of dynamical systems generated by evolution operators of free and bisexual population can be reduced to the study of nonlinear dynamical systems [2], [3], [4].

[2] Ganikhodzhaev R.N., Mukhamedov F.M. and Rozikov U.A. Inf. Dim. Anal. Quant. Prob. Rel. Fields. 14(2), (2011), 279–335.

[3] Kesten H. Adv. Appl. Probab. 2(2) (1970), 1–82; 179–228.

[4] Rozikov U.A. Asia Pacific Math. Newsletter. 3(1) (2013), 6–11.

Heredity of hemophilia.

Hemophilia is a genetic disorder linked to the X chromosome, it is due to mutations in two genes located at the end of the long arm of gonosome X. This is a lethal recessive genetic disease that is lethal in the homozygous state, it follows that if X^h denotes the X chromosome carrying hemophilia, there are only two female genotypes: XX and XX^h (genotype X^hX^h is lethal) and two male genotypes: XY and X^hY. The results of the four kinds of crosses are:

$$
\begin{aligned}
XX \times XY &\to \frac{1}{2}XX,\ \frac{1}{2}XY,\\
XX \times X^hY &\to \frac{1}{2}XX^h,\ \frac{1}{2}XY,\\
XX^h \times XY &\to \frac{1}{4}XX,\ \frac{1}{4}XX^h,\ \frac{1}{4}XY, \frac{1}{4}X^hY,\\
XX^h \times X^hY &\to \frac{1}{3}XX^h,\ \frac{1}{3}XY,\ \frac{1}{3}X^hY.
\end{aligned}
$$

To define an evolution operator of Hemophilia, let us introduce the following

$$\mathrm{S}^3 = \left\{ \mathrm{s} = (\mathrm{x}, \mathrm{y}, \mathrm{u}, \mathrm{v}) \in \mathbb{R}^4 : \ \mathrm{x} \geq 0,\ \mathrm{y} \geq 0,\ \mathrm{u} \geq 0,\ \mathrm{v} \geq 0,\ \mathrm{x} + \mathrm{y} + \mathrm{u} + \mathrm{v} = 1 \right\}$$

the three-dimensional simplex;

$$\mathcal{O} = \{\mathrm{s} = (\mathrm{x}, \mathrm{y}, \mathrm{u}, \mathrm{v}) \in \mathrm{S}^3 : (\mathrm{x}, \mathrm{y}) = (0,0) \text{ or } (\mathrm{u}, \mathrm{v}) = (0,0)\};$$

$$\mathrm{S}^{2,2} = \mathrm{S}^3 \setminus \mathcal{O}.$$

Note that

$$\operatorname{Int} \mathrm{S}^{2,2} = \operatorname{Int} \mathrm{S}^3,$$

and that

$$\partial \mathrm{S}^{2,2} \subsetneq \partial \mathrm{S}^3.$$

Bisexual population: Evolution operator

Let $F = \{XX, XX^h\}$ and $M = \{XY, X^hY\}$ be sets of genotypes. Assume that state of the set F is given by a real vector (x, y) and state of M by a real vector (u, v). Then a state of the set $F \cup M$ is given by the vector $t = (x, y, u, v)$. If $t' = (x', y', u', v')$ is a state of the system $F \cup M$ in the next generation, then by the above rule we get the evolution operator $W : S^{2,2} \to S^{2,2}$ defined by

$$W : \begin{cases} x' = \dfrac{2xu + yu}{4(x+y)(u+v)}, \\ y' = \dfrac{6xv + 3yu + 4yv}{12(x+y)(u+v)}, \\ u' = \dfrac{6xu + 6xv + 3yu + 4yv}{12(x+y)(u+v)}, \\ v' = \dfrac{3yu + 4yv}{12(x+y)(u+v)}. \end{cases} \tag{1.1}$$

The main problem

The main problem for a given operator W and arbitrarily initial point $\mathrm{s}^{(0)} \in \mathrm{S}^{2,2}$, is to describe the limit points of the trajectory

$$\{\mathrm{s}^{(\mathrm{m})}\}_{\mathrm{m}=0}^{\infty}, \text{ where } \mathrm{s}^{(\mathrm{m})} = \mathrm{W}^{\mathrm{m}}(\mathrm{s}^{(0)}) = \underbrace{\mathrm{W}(\mathrm{W}(...\mathrm{W}}_{\mathrm{m}}(\mathrm{s}^{(0)}))...).$$

Remark

In their work [5] U.A. Rozikov and R. Varro considered normalized gonosomal evolution operator (1.1) of a sex linked inheritance. They proved that the operator W has a unique nonhyperbolic fixed point $s_0 = (\frac{1}{2}, 0, \frac{1}{2}, 0)$ and there is an open neighborhood $U(s_0) \subset S^{2,2}$ of s_0 such that for any initial point $s \in U(s_0)$, the limit point of trajectories $\{W^m(s)\}$ tends to s_0. Moreover they made a conjecture for an initial point $s \in S^{2,2}$.

[5] Rozikov U.A., Varro R. Discont. Nonlinear. and Complexity., V.5, N.2, p.173-185.(2016)

In our work [6] we proved that conjecture.

Theorem 1

The operator $W : S^{2,2} \to S^{2,2}$ given by (1.1) has unique nonhyperbolic fixed point $s_0 = (\frac{1}{2}, 0, \frac{1}{2}, 0)$ and for any initial point $s \in S^{2,2}$ we have

$$\lim_{m\to\infty} W^m(s) = s_0 = (\frac{1}{2}, 0, \frac{1}{2}, 0). \quad (1.2)$$

The proof of this theorem also available at the recent book[7].

[6] Absalamov A.T. Discont. Nonlinear. and Complexity. V.10, N.1, p.143-149. (2021)

[7] Rozikov U.A., Population dynamics: algebraic and probabilistic approach. World Sci. Publ. Singapore. (2020), 460 pages.

Biological interpretations of the Theorem 1

This Theorem 1 has the following biological interpretations: Let $s^{(0)} = (x^{(0)}, y^{(0)}, u^{(0)}, v^{(0)}) \in S^{2,2}$ be an initial state (the probability distribution on the set $\{XX, XX^h; XY, X^hY\}$ of genotypes), when time goes to infinity, the population tends to the equilibrium state $s_0 = (\frac{1}{2}, 0, \frac{1}{2}, 0)$, meaning that the future of the population is stable: genotypes XX and XY are survived always, but the genotypes XX^h and X^hY will asymptotically disappear. Consequently, only healthy chromosomes will survive.

From biological interpretations of the result (1.2) we can see that problem of investigating the behavior of trajectories of the operator (1.1) is great importance in understanding of the hemophilia at a sex linked inheritance.

We have tried to find how faster or slower trajectories of the operator (1.1) tends to its unique fixed point [8].

Theorem 2

For the trajectory $(x^{(m)}, y^{(m)}, u^{(m)}, v^{(m)})$ of the operator (1.1) the following hold:

$$\frac{c_1}{m} \le \frac{1}{2} - x^{(m)} \le \frac{c_2}{m}, \quad \frac{c_3}{m} \le y^{(m)} \le \frac{c_4}{m},$$
$$\frac{c_5}{m} \le \frac{1}{2} - u^{(m)} \le \frac{c_6}{m}, \quad \frac{c_7}{m} \le v^{(m)} \le \frac{c_8}{m}.$$

where c_1, c_2, c_3, c_4, c_5, c_6, c_7, c_8 are positive constants.

[8] Absalamov A.T. Uzbek Math. Jour. No 4. p. 4-11. (2019)

Now consider a bisexual population which consists females partitioned into types indexed by $\{1, 2, \ldots, n\}$ and the males partitioned into types indexed by $\{1, 2, \ldots, \nu\}$[9], [10], [11].

Let $\gamma^{(f)}_{ik,j}$ and $\gamma^{(m)}_{ik,l}$ be inheritance coefficients defined as the probability that a female offspring is type j and, respectively, that a male offspring is of type l, when the parental pair is ik $(i, j = 1, \ldots, n;$ and $k, l = 1, \ldots, \nu)$. These quantities satisfy the following

$$\begin{aligned} &\gamma^{(f)}_{ik,j} \geq 0, \quad \gamma^{(m)}_{ik,l} \geq 0, \\ &\sum_{j=1}^{n} \gamma^{(f)}_{ik,j} + \sum_{l=1}^{\nu} \gamma^{(m)}_{ik,l} = 1, \quad \text{for all } \ i, k, j, l. \end{aligned} \tag{1.3}$$

[9] Lyubich Y.I. Mathematical structures in population genetics. Springer-Vergar, Berlin (1992)

[10] Rozikov U.A., Population dynamics: algebraic and probabilistic approach. World Sci. Publ. Singapore. 2020

[11] Rozikov U.A., Zhamilov U.U. Ukraine Math. Jour. 63(7) (2011), 985–998

Define $(\mathrm{n}+\nu-1)-$dimensional simplex:

$$\mathrm{S}^{\mathrm{n}+\nu-1}=\left\{\mathrm{s}=(\mathrm{x}_1,\ldots,\mathrm{x}_\mathrm{n},\mathrm{y}_1,\ldots,\mathrm{y}_\nu)\in[0,1]^{\mathrm{n}+\nu}:\sum_{\mathrm{i}=1}^{\mathrm{n}}\mathrm{x}_\mathrm{i}+\sum_{\mathrm{j}=1}^{\nu}\mathrm{y}_\mathrm{j}=1\right\}.$$

Denote

$$\mathcal{O}=\left\{\mathrm{s}\in\mathrm{S}^{\mathrm{n}+\nu-1}:(\mathrm{x}_1,\ldots,\mathrm{x}_\mathrm{n})=(0,\ldots,0)\,\mathrm{or}\,(\mathrm{y}_1,\ldots,\mathrm{y}_\nu)=(0,\ldots,0)\right\}.$$

$$\mathcal{S}^{\mathrm{n},\nu}=\mathrm{S}^{\mathrm{n}+\nu-1}\setminus\mathcal{O}.$$

Following [12] define an evolution operator $V : \mathcal{S}^{n,\nu} \to \mathcal{S}^{n,\nu}$ (which is called normalized gonosomal operator) as

$$V : \begin{cases} x'_j = \dfrac{\sum_{i,k=1}^{n,\nu} \gamma_{ik,j}^{(f)} x_i y_k}{\left(\sum_{i=1}^{n} x_i\right)\left(\sum_{j=1}^{\nu} y_j\right)}, & j = 1, \dots, n \\ y'_l = \dfrac{\sum_{i,k=1}^{n,\nu} \gamma_{ik,l}^{(m)} x_i y_k}{\left(\sum_{i=1}^{n} x_i\right)\left(\sum_{j=1}^{\nu} y_j\right)}, & l = 1, \dots, \nu. \end{cases} \tag{1.4}$$

[12] Rozikov U.A., Varro R. Discont. Nonlinear. and Complexity. 5 (2016), 173–185.

Remark

The dynamics of this operator has not been completely studied yet.
In book [13] several recently obtained results related to this main problem are given.
This operator considered by Rozikov U.A., and Zhamilov U.U., in [14] as $V : \mathcal{S}^{n-1} \times \mathcal{S}^{\nu-1} \to \mathcal{S}^{n-1} \times \mathcal{S}^{\nu-1}$ which leads to study on the dynamics of Quadratic Stochastic Operators of a Two-Sex Population. Furthermore, this operator $V : \mathcal{S}^{n,\nu} \to \mathcal{S}^{n,\nu}$ also considered in [15] under the following condition

$$\begin{aligned} \textstyle\sum_{j=1}^{n} \gamma_{ik,j}^{(f)} &= a \textstyle\sum_{j=1}^{n} \theta_{ik,j}, \\ \textstyle\sum_{l=1}^{\nu} \gamma_{ik,l}^{(m)} &= (1-a) \textstyle\sum_{l=1}^{n} \theta_{ik,l}, \end{aligned} \tag{1.5}$$

where

$$\theta_{ik,j} \geq 0 \quad \text{and} \quad \sum_{j=1}^{n} \theta_{ik,j} = 1, \qquad \text{for all} \ \ i, k, j, l.$$

[13] Rozikov U.A., Population dynamics: algebraic and probabilistic approach. World Sci. Publ. Singapore. 2020.

[14] Rozikov U.A., Zhamilov U.U. Ukrain Math. Jour., Vol. 63, No. 7, p. 1136-1153. 2011.

[15] Boxonov Z.S., Rozikov U.A. Uzbek Math. Jour., No. 2, p.17-32, (2018)

We consider the special case: $\mathrm{n} = \nu = 2$ and the following coefficients:

$$
\begin{array}{llll}
\gamma^{(\mathrm{f})}_{11,1} = \mathrm{a} & \gamma^{(\mathrm{f})}_{11,2} = 0 & \gamma^{(\mathrm{m})}_{11,1} = \mathrm{b} & \gamma^{(\mathrm{m})}_{11,2} = 0 \\
\gamma^{(\mathrm{f})}_{12,1} = 0 & \gamma^{(\mathrm{f})}_{12,2} = \sigma_1 & \gamma^{(\mathrm{m})}_{12,1} = \sigma_2 & \gamma^{(\mathrm{m})}_{12,2} = 0 \\
\gamma^{(\mathrm{f})}_{21,1} = 0 & \gamma^{(\mathrm{f})}_{21,2} = \mathrm{a} & \gamma^{(\mathrm{m})}_{21,1} = \mathrm{b} & \gamma^{(\mathrm{m})}_{21,2} = 0 \\
\gamma^{(\mathrm{f})}_{22,1} = 0 & \gamma^{(\mathrm{f})}_{22,2} = \mathrm{a} & \gamma^{(\mathrm{m})}_{22,1} = 0 & \gamma^{(\mathrm{m})}_{22,2} = \mathrm{b}.
\end{array} \tag{1.6}
$$

Note that coefficients (1.6) does not satisfy condition (1.5).

Then corresponding evolution operator $V_1 : S^{2,2} \to S^{2,2}$ is

$$V_1 : \begin{cases} x' &= \dfrac{axu}{(x+y)(u+v)} \\ y' &= \dfrac{\sigma_1 xv + ayu + ayv}{(x+y)(u+v)} \\ u' &= \dfrac{\sigma_2 xv + bxu + byu}{(x+y)(u+v)} \\ v' &= \dfrac{byv}{(x+y)(u+v)}, \end{cases} \tag{1.7}$$

where coefficients satisfy

$$a + b = \sigma_1 + \sigma_2 = 1, \quad a, b, \sigma_1, \sigma_2 > 0.$$

Remark 3

From the probabilities (1.6) one can notice that type 1 of females (resp. type 2 of males) can be born only if both parents have type 1 (resp. 2). Type 2 of females (resp. type 1 of males) can not be born if both parents have type 1 (resp. 2).

For this operator W and arbitrarily initial point $s^{(0)} \in S^{2,2}$, we have studied [16] the trajectory $\{s^{(m)}\}_{m=0}^{\infty}$, where

$$s^{(m)} = V_1^m(s^{(0)}) = \underbrace{V_1(V_1(...V_1}_{m}(s^{(0)}))...).$$

[16] Absalamov A.T., Rozikov U.A. Lobachevskii Journal of Mathematics. (Submitted)

Fixed point

A point s is called a fixed point of the operator V_1 if $s = V_1(s)$. The set of all fixed points denoted by $\mathrm{Fix}(V_1)$.
The set of all fixed points of operator (1.7) is $\mathrm{Fix}(V_1) = F_{11} \cup F_{12}$, where

$$F_{11} = \Big\{(0, a, u, v): \quad u + v = b, \quad u,\ v \in [0, b]\Big\}$$

and

$$F_{12} = \Big\{(x, y, b, 0): \quad x + y = a, \quad x,\ y \in [0, a]\Big\}.$$

Definition 4

A fixed point s of the operator V_1 is called hyperbolic if its Jacobian J at s has no eigenvalues on the unit circle.

Definition 5

A hyperbolic fixed point s is called:
i) attracting if all the eigenvalues of the Jacobi matrix J(s) are less than 1 in absolute value;
ii) repelling if all the eigenvalues of the Jacobi matrix J(s) are greater than 1 in absolute value;
iii) a saddle otherwise.

It is not hard to see that $\lambda_1 = 0$, $\lambda_2 = 1$, $\lambda_3 = 1 - \frac{y}{b}$ and $\lambda_1 = 0$, $\lambda_2 = 1$, $\lambda_3 = 1 - \frac{x}{a}$ are eigenvalues of the fixed points of the forms F_{11} and F_{12} respectively. By these definitions we see that all fixed points of the operator (1.7) are nonhyperbolic fixed points.

Theorem 6

For any initial point $(x, y, u, v) \in S^{2,2}$ the sequence

$$V_1^m(x, y, u, v) = (x^{(m)}, y^{(m)}, u^{(m)}, v^{(m)})$$

is convergent and

$$\lim_{m\to\infty} x^{(m)} \cdot v^{(m)} = 0.$$

Define the following sets:

$$T_0 = \Big\{(x, y, u, v) \in S^{2,2} : \lim_{m\to\infty} x^{(m)} = \lim_{m\to\infty} v^{(m)} = 0 \Big\},$$
$$T_1 = \Big\{(x, y, u, v) \in S^{2,2} : \lim_{m\to\infty} v^{(m)} = 0, \quad \lim_{m\to\infty} x^{(m)} \in (0, a]\Big\},$$
$$T_2 = \Big\{(x, y, u, v) \in S^{2,2} : \lim_{m\to\infty} x^{(m)} = 0, \quad \lim_{m\to\infty} v^{(m)} \in (0, b]\Big\}.$$

Corollary 7

For any initial point $t = (x, y, u, v) \in S^{2,2}$ the ω-limit set $\omega(t)$ of the operator (1.7) consists a single point and

$$\omega(t) \in \begin{cases} \{(0, a, b, 0)\} & \text{if } t = (x, y, u, v) \in T_0, \\ F_{12} & \text{if } t = (x, y, u, v) \in T_1, \\ F_{11} & \text{if } t = (x, y, u, v) \in T_2. \end{cases} \qquad (1.8)$$

Definition 8

An operator V_1 is called regular if for any initial point $s^{(0)} \in S^{2,2}$, the limit

$$\lim_{m \to \infty} V_1^m(s^{(0)})$$

exists.

The following is a corollary of Theorem 6.

Corollary 9

The operator (1.7) is regular.

We would like to describe the sets T_0, T_1 and T_2 implicitly.
There are three cases for p_1, p_2.

$$\begin{aligned} &1. \quad p_1 = p_2 = 1, \\ &2. \quad p_1 > 1 > p_2 > 0, \\ &3. \quad p_2 > 1 > p_1 > 0. \end{aligned} \tag{1.9}$$

where

$$p_1 = \frac{\sigma_1}{a}, \qquad p_2 = \frac{\sigma_2}{b}.$$

when $p_1 = p_2 = 1$ i.e. when $\sigma_1 = a$, $\sigma_2 = b$

$$\Omega_\theta = \Big\{(x,y,u,v) \in S^{2,2} : \quad \frac{v}{u+v} = \frac{x}{x+y} + 1 - \theta\Big\}$$

is an invariant surface respect to the operator (1.7) and it holds that

$$\bigcup_{\theta\in[0,1)} \Omega_\theta = T_2 = \Big\{(x,y,u,v) \in S^{2,2} : yv > xu\Big\},$$

$$\bigcup_{\theta\in(1,2]} \Omega_\theta = T_1 = \Big\{(x,y,u,v) \in S^{2,2} : yv < xu\Big\},$$

$$\Omega_1 = T_0 = \Big\{(x,y,u,v) \in S^{2,2} : yv = xu\Big\}$$

and that

$$\Omega_{\theta_1} \cap \Omega_{\theta_2} = \emptyset \ \text{ for any } \ \theta_1 \neq \theta_2.$$

Thus it suffices to study the dynamical system on each invariant surfaces Ω_θ, we have the following

Theorem 10

The following assertions hold

(i) For any initial point $t = (x, y, u, v) \in T_0$, we have

$$\lim_{m\to\infty} V_1^m(t) = (0; a; b; 0).$$

(ii) If $\theta \in (1, 2]$ then for any initial point $t = (x, y, u, v) \in \Omega_\theta$ the following holds

$$\lim_{m\to\infty} V_1^m(t) = (a(\theta - 1); a(2 - \theta); b; 0).$$

(iii) If $\theta \in [0, 1)$ then for any initial point $t = (x, y, u, v) \in \Omega_\theta$ the following holds

$$\lim_{m\to\infty} V_1^m(t) = (0; a; b\theta; b(1 - \theta)).$$

Corollary 11

The operator (1.7) has infinitely many fixed points and for each such fixed point there are disjointed trajectories which converge to those fixed points, i.e. any trajectory started at a point of the invariant set converges to the corresponding fixed point. Thus there is one-to-one correspondence between such invariant sets and the set of fixed points.

Conjecture.

If $p_1 > 1 > p_2 > 0$ (or $p_2 > 1 > p_1 > 0$) then for each fixed point $p \in \mathrm{Fix}(W)$ there exists unique invariant surface $\Gamma_p \subset S^{2,2}$, such that for any initial point $s^{(0)} \in \Gamma_p$ the limit of its trajectory (under operator (1.7)) converges to the fixed point p. Moreover,

$$\bigcup_{p \in \mathrm{Fix}(V_1)} \Gamma_p = S^{2,2}.$$

Let $s^{(0)} = (x, y, u, v) \in S^{2,2}$ be an initial state, i.e. the probability distribution on the set of female and male types.
The following are interpretations of our results:

- The set of all fixed points is subset of the boundary of $S^{2,2}$ means that at least one type of female or male in future of population will surely disappear.
- The existence of invariant surfaces means that if states of the population initially satisfied a relation (described the invariant set) then the future of the population remains in the same relation.
- Regularity of the operator means that for any initial state of the population we can explicitly determine its limit (final) state.
- For any $s^{(0)} \in T_0$ as time goes to infinity the type 1 of female and type 2 of males will disappear (die).
- For any $s^{(0)} \in T_1$ as time goes to infinity the type 2 of males will disappear.
- For any $s^{(0)} \in T_2$ as time goes to infinity the type 1 of females will disappear.

Thank you for your attention.

Articles

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