Research article

Discrete time model of sexual systems

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ABSTRACT

Small factors are the biggest contributors to the biggest changes in an ecosystem which may lead to its demise. Simple things such as tweaking the humidity or tampering with the temperature can be the downfall of the habitants and the ecosystem itself. These changes can be observed right now with the consistent temperature increase on Earth along with the slew of issues that come with global warming. A small change in a few degrees in temperature can perish an entire food supply and the habitat of many already endangered beings forcing them to either adapt or die. Within such an ecosystem the main reason it withstands the test of time boils down to one simple thing; reproduction. This creates the natural question of asking oneself: How does an ecosystem replenish itself and is able to resist collapsing? To even begin considering this thought, one must realise that the size of the population is the key to gaining a deeper understanding as two constituents that are important from evolutionary theory are survival and reproduction. The case of asexual reproducers, it is not difficult to see any alterations that can be introduced to increase reproductivity. Meanwhile, for sexual reproducers, the evolution to increase reproductivity can be observed by looking into the generational data of the species. A certain group of time-based dynamic systems that are connected to a sexual system are the point of contention. The suggested model is a dynamic representation of a hermaphrodite population which is described through quadratic stochastic operators. The key findings offer fresh insights into the future of hermaphrodite populations, that is perhaps a probable solution to prevent the decline of endangered or at-risk species. This demonstrates a fresh perspective on reproduction, which is explored through a purely mathematical approach.

1. Introduction

An ecosystem is a delicate balance between living and non-living things that work together to maintain life. Factors like temperature and reproduction are interconnected and can cause the entire system to collapse if disrupted. Even small changes can harm the

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food supply and endanger many species unless they adapt [1]. Therefore an ecosystem's longevity boils down to reproduction [2]. This raises the question of how an ecosystem replenishes itself and avoids collapse [3].

Evolutionary theory states that survival and reproduction are the main factors that control the size of any population. Sexual reproducers have evolved over many generations to increase reproduction whilst asexually reproducing species can easily increase their reproductive rate which creates ease in introducing alterations [4,5].

Plenty of research has been conducted to optimize the reproductive rate of sexual reproducers [6–8]. Game theory as well as the energy costs and benefits of mating displays are two examples of such research [9]. Another important aspect is sex allocation, where resources are allocated differently to male and female reproduction. This theory shows that sexual reproducers decide how to allocate resources to each sex [10]. The allocation is different for dioecious species, where the sex of the offspring determines the allocation, and sequential hermaphrodites, where the initial sex and time of sex switch determines the allocation [11].

Sex allocation is another crucial aspect to consider. To comprehend the fundamental concept, one must realize that resources are distributed differently between male and female reproduction [10]. Therefore, this theory shows that sexual reproducers decide how to allocate resources to male versus female reproduction. The allocation is changed in dioecious population where the sex is fixed. Consequently the decision to allocate resources lies with the sex of the offspring. In the case of sequential hermaphrodites the allocation depends on two factors: the initial sex and the time of the sex switch [11]. Evidently, the underlying question that fuels these research topics is the optimisation of reproductivity.

There are many nonlinear (stochastic) models which describe some real life situations (see e.g. [12–16]). Quadratic models are one of the simplest ones in the class of these kind of models. Bernstein [17] introduced quadratic stochastic operators that frequently appear in many genetic models, especially those related to heredity. Thus, one can conclude that the evolution of populations can be determined by quadratic stochastic operators (QSOs) (see [18–25]). A study has been undertaken by Lyubich [2] who has shown that a few generations later, the dynamics of a population changes due to selection and reproduction.

If a community of organisms is closed with respect to reproduction, then it is called a *free population*. In this community, each individual reside to one of the types from the set $E := \{1, \ldots, m\}$, and each organism is sexually reproducing and considered the direct offspring of its parents (father and mother). Therefore, this research considers these types, following [2]. Let the types of the parents be given by i and j. Such a parent pair determines the probability $q_{ij,k}$ of type k for the first generation of direct descendants. Furthermore, it is referred as the heredity coefficient. It is evident that $q_{ij,k} \geq 0$ and

$$q_{ij,k} = q_{ji,k}, \quad \sum_{k=1}^{m} q_{ij,k} = 1, \quad i,j,k \in E. \tag{1}$$

Initially the population's distribution is described by the vector $\mathbf{x} = (x_1, x_2, \ldots, x_m)$. Here, each x_k is represents the fraction of the type k in the total population. It is notices that the vector $\mathbf{x}$ belongs to

$$S^{m-1} = \left\{ \mathbf{x} = (x_k) \in \mathbb{R}^m : \sum_{i \in E} x_i = 1, \ x_i \geq 0, \ i \in E \right\},$$

which is the set of all probability distributions on E. In the case of random interbreeding (i.e. panmixia), the pairs i and j appear with the probability $x_i x_j$. Consequently, the type k in the next generation is calculated as

$$\mathcal{Q}(\mathbf{x})_k = \sum_{i,j=1}^{m} q_{ij,k} x_i x_j, \quad k \in E. \tag{2}$$

So, one defines the mapping $\mathbf{x} \mapsto \mathcal{Q}(\mathbf{x})$ which is the evolutionary operator called *quadratic stochastic operator (QSO)*. Selection and reproduction are two significant factors that contribute to the change of state in the following generations during the evolution of a population. A zygotic organism that is bisexual with a sexual differentiation of gametes is not excluded in the model that involves a quadratic stochastic operator, even in the case of hermaphroditism [2]. Organisms that can be both sexes and self-fertilize in some cases are referred to as simultaneous hermaphrodites [26].

A given $\mathbf{x}^{(0)} \in S^{m-1}$, one defines its trajectory $\{\mathbf{x}^{(n)}\}$ under $\mathcal{Q}$ by

$$\mathbf{x}^{(n+1)} = \mathcal{Q}(\mathbf{x}^{(n)}), \quad n \geq 0.$$

One can see that $\mathbf{x}^{(n)} = \mathcal{Q}^n(\mathbf{x}^{(0)})$. The main aim of the current article is to explore the asymptotic behaviour of trajectories associated with a class of random QSO. The fact that this problem remains unsolved even in low-dimensional contexts highlights the need for further study into the dynamics of quadratic stochastic operators.

According to Ulam's conjecture [27], which is based on numerical calculations, the sequence of averages

$$\frac{1}{n}\left(\mathbf{x} + \mathcal{Q}(\mathbf{x}) + \cdots + \mathcal{Q}^{n-1}(\mathbf{x})\right) \tag{3}$$

converges for every QSO $\mathcal{Q}$ and any $\mathbf{x} \in S^{m-1}$. However, Zakharevich's findings, as published in [28] demonstrates that the limit of (3) does not exist for the mapping of S^2 described by

$$\mathcal{V}(x_1, x_2, x_3) = \left(x_1^2 + 2x_1 x_2, x_2^2 + 2x_2 x_3, x_3^2 + 2x_1 x_3\right), \ (x_1, x_2, x_3) \in S^2. \tag{4}$$

The findings, suggest that Ulam's conjecture is generally false. Moreover, [29–31] present various extensions of the mapping (4).

Recently, in [22], almost surely converge of random dynamics of QSOs to one of the vertices of the simplex has been established which contrasts to the deterministic set-up of the trajectories. The reader is referred to [32], for a recent development on the theory of quadratic stochastic operators. Therefore, the purpose is to explore a particular class of discrete-time dynamical systems produced by non-Volterra QSOs. The goal is to create deterministic and random dynamical models for a hermaphrodite population with the help of non-Volterra QSOs, utilising techniques from discrete-time dynamical systems. The primary outcome of this study is going to shed light into the future of populations of this type.

2. Gonochoristic system

In this section, we start discussing the concept of F-QSO. As we mentioned earlier, the set E is expanded by adding an "empty-body" element "0", so one denotes $E_0 = E \cup \{0\}$. Now, the sets of "females" and "males" are interpreted as $F = \{1, 2, \ldots, m_1\}$ ($m_1 < m$) and $M = E \setminus F = \{m_1 + 1, \ldots, m\}$, respectively. One defines the heredity coefficients by

$$q_{ij,k} = \begin{cases} \delta_{k0}, & \text{if } (i,j) \in \big((F \cup \{0\}) \times (F \cup \{0\})\big) \cup \big((M \cup \{0\}) \times (M \cup \{0\})\big); \\ \geq 0, & \text{if } (i \in F) \wedge (j \in M), \text{ for all } k, \end{cases} \tag{5}$$

where δ_{ij} is the Kronecker symbol. The coefficients in (5) have a clear biological interpretation: a "child" k is produced when its parents belong to the different sets F and M. It's important to note that, in some cases, the coefficient $q_{ij,0}$ can be positive if one or both of the parents are ill and unable to produce a child. The first and second equalities in (5) indicate that if the parents have the same gender or one is an empty-body, then their offspring will always be an empty-body. The third equality of (5) means that if the parents have different genders and neither is an empty-body, then their offspring can be any one of a type $0, \ldots, m$. The QSO in this scenario is expressed as follows:

$$Q : \begin{cases} x'_0 = 1 - 2 \sum_{i=1}^{m_1} \sum_{j=m_1+1}^{m} \big(1 - q_{ij,0}\big) x_i x_j; \\ x'_k = 2 \sum_{i=1}^{m_1} \sum_{j=m_1+1}^{m} q_{ij,k} x_i x_j, \quad k \in E. \end{cases} \tag{6}$$

As per [33], the QSO defined by (6) is referred to as the *F-quadratic stochastic operator*.

This section discusses the sexual system of gonochorism, where the organism is either male or female and does not undergo any sex change, as per [34]. Conversely, in a hermaphroditic population, individuals can act as either male or female and maintain only one active gonadal tissue, as observed in species like Lythrypnus dalli [35]. More precisely, fish and mammals are usually gonochoric, as per [36,37], while nematodes are mostly hermaphroditic.

Theorem 2.1 ([33]). *If the heredity coefficients* $\{q_{ij,k}\}$ *adhere to* (5), *then, for any* $\mathbf{x}^{(0)} \in S^m$, *the trajectory* $\{\mathbf{x}^{(n)}\}_{n=0}^{\infty}$ *of the operator defined by* (6) *approaches to the single fixed point* $\mathbf{e}_0 := (1, \underbrace{0, 0, \ldots, 0}_{m})$ *at an exponential rate.*

3. Hermaphrodite system

This section is concerned with hermaphrodites, where the way of expressing the reproductive role can vary. For instance, males can change to females (protandry) or females can change to males (protogyny), as stated in [38–40]. The clownfish (genus Amphiprion) is an example of a colourful reef fish that lives in a symbiotic relationship with sea anemones, while wrasses (Family Labridae) are a type of reef fish where protogyny is prevalent.

Let us consider the setting $E_0 = E \cup \{0\}$, and

$$F_1 = \{1, 2, 3, \ldots, m_1\}, \quad M_1 = \{m_1 + 1, \ldots, m\}.$$

In this case, F_1-QSO can be expressed as shown in (6).

Assume that σ be a permutation of E. Then, we consider the permutations of F_1 and M_1 as follows:

$$F_2 = \{\sigma(1), \sigma(2), \sigma(3), \ldots, \sigma(m_1)\}, \quad M_2 = \{\sigma(m_1 + 1), \ldots, \sigma(m)\}.$$

Then, the corresponding F_2-QSO is governed by

$$Q_\sigma : \begin{cases} x'_0 = 1 - 2 \sum_{i \in F_2} \sum_{j \in M_2} \big(1 - q^\sigma_{ij,0}\big) x_i x_j; \\ x'_{\pi(k)} = 2 \sum_{i \in F_2} \sum_{j \in M_2} q^\sigma_{ij,\pi(k)} x_i x_j, \quad k = 1, 2, \ldots, m, \end{cases} \tag{7}$$

where

$$q^{\sigma}_{ij,\sigma(k)} = q^{\sigma}_{ji,\sigma(k)} \geq 0, \quad k \in E_0; \quad \sum_{k=0}^{m} q^{\sigma}_{ij,\sigma(k)} = 1, \quad \text{for all } i \in F_2, j \in M_2. \tag{8}$$

The evolution operator for the examined case is defined by a fixed natural number t as follows: if $0 < n \leq t$, where n is natural, $\mathcal{Q}_1$ is applied, and if $n > t$, $\mathcal{Q}_{\sigma}$ is applied. Consequently, its trajectory of the evolution operator is represented by

$$Q^n(\mathbf{x}) := \begin{cases} \mathcal{Q}_1^n(\mathbf{x}), & \text{if } n \leq t \\ \mathcal{Q}_1^t \circ \mathcal{Q}_{\sigma}^{n-t}(\mathbf{x}), & \text{if } n > t. \end{cases} \tag{9}$$

Theorem 3.1. *When the heredity coefficients $\{q_{ij,k}\}$ and $\{q^{\sigma}_{ij,\pi(k)}\}$ satisfy conditions (6) and (8), respectively, the operator given by (9) has a single fixed point $\mathbf{e}_0$. Additionally, its trajectory $\{\mathbf{x}^{(n)}\}_{n=0}^{\infty}$ exponentially converges to $\mathbf{e}_0$, for every $\mathbf{x}^{(0)} \in S^m$.*

Proof. This theorem's proof relies on the next theorem's proof (refer to the following section). □

4. Hermaphrodites system: multiple sex

Sequential hermaphroditism is when organisms experience multiple sex changes throughout their lifetime [39,40]. For instance, the California sheephead wrasse is a coral reef fish that can change from male to female if they are unsuccessful in reproduction and from female to male to maintain flexibility when they exhibit submissive behaviour. However, other wrasse species such as the moon wrasse, the yellowhead wrasse, and the bluehead wrasse can only change from female to male, while the humphead wrasse can only change from male to female. In other words, each organism in these species will undergo a gender change at some point in their life.

Suppose that π_s is a permutation of E, and $\psi_s : E \to E$ is a mapping, for any natural s. Let $E_0 = E \cup \{0\}$ be as before. Now, we consider the following sets

$$F_s = \{\pi_s(1), \pi_s(2), \pi_s(3), \dots, \pi_s(\psi_s(m_1))\}, \quad M_s = \{\pi_s(\psi_s(m_1 + 1)), \dots, \pi_s(m)\}.$$

Then the corresponding F_s-QSO with the matrix $\mathbf{q}^{\pi_s} = \left(q^{\pi_s}_{ij,k} \right)_{i,j,k \in E_0}$ has the form

$$Q_{\pi_s} : \begin{cases} x'_0 = 1 - 2 \sum_{i \in F_s} \sum_{j \in M_s} \left(1 - q^{\pi_s}_{ij,0} \right) x_i x_j; \\ x'_{\pi_{s+1}(k)} = 2 \sum_{i \in F_s} \sum_{j \in M_s} q^{\pi_s}_{ij,\pi_s(k)} x_j x_j, \quad k = 1, 2, \dots, m, \end{cases} \tag{10}$$

where the coefficients $\{q^{\pi_s}_{ij,k}\}$ satisfy the conditions

$$q^{\pi_s}_{ij,\pi_s(k)} = q^{\pi_s}_{ji,\pi_s(k)} \geq 0, \quad k \in E_0; \quad \sum_{k=0}^{m} q^{\pi_s}_{ij,\pi_s(k)} = 1, \quad \forall i \in F_s, j \in M_s, \quad s > 0. \tag{11}$$

Denote $\mathcal{K}_{\pi} = \{Q_{\pi_s}, s = 1, \dots, m!\}$. The set $\mathcal{K}_{\pi}$ can be compactly embedded into $\mathbb{R}^{(m+1)^3}$ (since QSO Q_{π_s} is determined by a cubic matrix $\mathbf{q}^{\pi_s}$). The Borel σ-algebra on the set $\mathcal{K}_{\pi}$ is denoted $\mathcal{H}$.

Let $(\Omega, \mathfrak{F}, \mathbb{P})$ be a probability space. A measurable mapping $G : \Omega \to \mathcal{K}_{\pi}$ is said to be a *random F-quadratic stochastic operator* if $G^{-1}(\mathcal{H}) \subset \mathfrak{F}$, where

Assume that for each $Q_{\pi_s} \in \mathcal{K}_{\pi}$ is assigned a positive probability p_s $(1 \leq s \leq m!)$, $p_1 + \dots + p_{m!} = 1$. Now, to start the process, one chooses an initial state $\mathbf{x}^{(0)} \in S^m$ and selects an operator from $\mathcal{K}_{\pi}$. The probability of choosing Q_{π_s} is p_s $(1 \leq s \leq m!)$. The randomly chosen operator is denoted by T_1, and the state at time $n = 1$ becomes $\mathbf{x}^{(1)} = T_1\left(\mathbf{x}^{(0)}\right)$. At time $n = 2$, a new operator T_2, is chosen independently from $\mathcal{K}_{\pi}$ according to the assigned probabilities. The state at time $n = 2$ then becomes $\mathbf{x}^{(2)} = T_2\left(\mathbf{x}^{(1)}\right) = T_2 T_1\left(\mathbf{x}^{(0)}\right)$.

This process allows us to create a random dynamical system, which can be expressed as

$$\mathbf{x}^{(n+1)} = T_{n+1}\left(\mathbf{x}^{(n)}\right) = T_{n+1} T_n \cdots T_1\left(\mathbf{x}^{(0)}\right), \quad n \geq 1.$$

The sequence $\{T_n : n \geq 1\}$ is a collection of independent QSOs from $\mathcal{K}_{\pi}$ with the common distribution $P = \{p_1, \dots, p_{m!}\}$.

Theorem 4.1. *Assuming $P = \{p_1, \dots, p_{m!}\}$ is a shared distribution on the set $\mathcal{K}_{\pi}$, we have*

$$\mathbb{P}\left(\lim_{n \to \infty} T_n(\mathbf{x}) = \mathbf{e}_0 \right) = 1,$$

which means that every trajectory converges almost surely.

Proof. Given $\mathbf{x} \in S^m$, let us define

$$\varphi_n(\mathbf{x}) = \sum_{i=\pi_n(1)}^{\pi_n(\psi_n(m_1))} \sum_{j=\pi_n(\psi_n(m_1+1))}^{\pi_n(m)} x_i x_j. \tag{12}$$

By employing (10), (11) and (12), for each $k \in E$, one finds

$$x_{\pi_{n+1}(k)}^{(n+1)} = 2 \sum_{i=\pi_n(1)}^{\pi_n(\psi_n(m_1))} \sum_{j=\pi_n(\psi_n(m_1+1))}^{\pi_n(m)} q_{ij,\pi_n(k)}^{\pi_s} x_i x_j$$

$$\leq 2 \sum_{i=\pi_n(1)}^{\pi_n(\psi_n(m_1))} \sum_{j=\pi_n(\psi_n(m_1+1))}^{\pi_n(m)} x_i x_j = 2\varphi_n\left(\mathbf{x}^{(n)}\right). \tag{13}$$

Now, $\varphi_{n+1}\left(\mathbf{x}^{(n+1)}\right)$ can be estimated:

$$\varphi_{n+1}\left(\mathbf{x}^{(n+1)}\right) \leq \frac{1}{4} \left(\sum_{i=\pi_{n+1}(1)}^{\pi_{n+1}(\psi_{n+1}(m_1))} x_i + \sum_{j=\pi_{n+1}(\psi_{n+1}(m_1+1))}^{\pi_{n+1}(m)} x_j \right)^2$$

$$= \frac{1}{4}\left(1 - x_0^{(n+1)}\right)^2. \tag{14}$$

The expression for $\mathbf{x}_0^{(n+1)}$ together with (14) implies

$$\varphi_{n+1}(\mathbf{x}^{(n+1)}) \leq \left(\sum_{i=\pi_n(1)}^{\pi_n(\psi_n(m_1))} \sum_{j=\pi_n(\psi_n(m_1+1))}^{\pi_n(m)} \left(1 - q_{ij,0}^{\pi_n}\right) x_i x_j \right)^2$$

$$\leq \left(\sum_{i=\pi_n(1)}^{\pi_n(\psi_n(m_1))} \sum_{j=\pi_n(\psi_n(m_1+1))}^{\pi_n(m)} x_i x_j \right)^2$$

$$= \left(\varphi_n(x^{(n)})\right)^2, \quad n \geq 0. \tag{15}$$

Note that $\varphi_n\left(\mathbf{x}^{(n)}\right) \leq 1/4$ for any $n = 0, 1, \ldots$. Hence, by (15) one gets

$$\varphi_n(x^{(n)}) \leq \left(\frac{1}{4}\right)^{2^n} \tag{16}$$

This together with (13), (16) yields

$$\lim_{n\to\infty} x_{\pi_n(k)}^{(n)} = 0, \quad \text{for every} \ \ k \in E$$

which means

$$\lim_{n\to\infty} \mathbf{x}^{(n)} = \mathbf{e}_0,$$

for every $\mathbf{x}^{(0)} \in S^m$. The last equality yields that $\mathbf{e}_0$ is the only fixed point of the evolution operator. This completes the proof. $\square$

5. Conclusions

This paper introduces a novel dynamical model for a hermaphrodite population, where all types of individuals change their gender within each generation. This behaviour is observed in populations of bidirectional hermaphrodites, such as coral-dwelling wrasses.

The key discovery is Theorem 4.1, which aids in comprehending the future of these organisms. The model described in Equation (6) predicts the distribution of the species over time using a dynamic approach, as shown by Theorem 2.1. However, it is important to note that the model only accounts for genetic factors and not environmental ones. Theorem 4.1 states that the "empty body" will most likely dominate the future of this population type, as seen in Equation (10).

The mathematical findings confirm that a bidirectional hermaphroditic population of Labridae, like the Green Wrasse, which is classified as a threatened animal on the Red List (IUCN 2021), faces extinction. Despite the fact that individuals change gender to preserve and boost the population size, the population ultimately dwindles towards extinction.

Lastly, this model does not take into account parameters such as birth, mortality, immigration, etc. If included, these parameters may pose a challenge in creating the model and may not be mathematically feasible. Nevertheless, more sophisticated models that incorporate other factors can serve as a foundation for future expansion of this paper.

CRediT authorship contribution statement

Uygun Jamilov: Conceived and designed the experiments; Performed the experiments; analyzed and interpreted the data; Wrote the paper.

Farrukh Mukhamedov: Conceived and designed the experiments; Performed the experiments; Contributed reagents, materials, analysis tools or data.

Farzona Mukhamedova: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

No data was used for the research described in the article.

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