

Trait Evolution in two–sex Populations

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Abstract. We present an individual–based model of phenotypic trait evolution in two–sex populations, which includes semi–random mating of individuals of the opposite sex, natural death and intra–specific competition. By passing the number of individuals to infinity, we derive the macroscopic system of nonlinear differential equations describing the evolution of trait distributions in male and female subpopulations. We study solutions, give criteria for persistence or extinction, and state a theorem on asymptotic stability, which we apply to particular examples of trait inheritance.

Keywords and phrases: individual–based model, phenotypic evolution, two–sex populations, system of nonlinear evolution equations, asymptotic stability.

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1. Introduction

Over last few decades two–sex populations were often studied from the viewpoint of mathematical modelling (see e.g. [2, 18, 20, 28]). One of the first attempted descriptions of birth rate and mating functions in two–sex populations were given in [17, 19, 21]. In the paper [14] two assumptions on mating function were stated and its general form was provided. The above–mentioned models exhibit exponential growth due to the lack of competition. Addition of intra– and inter–sexual competition to the models leads to logistic terms and results in more realistic bounded solutions and usually causes stabilization of population size (see e.g. [27, 31]). One of the reasons for the interest in more complicated two–sex models comes from attempts to describe sexually transmitted diseases in human population (see [10, 15]). Modern models use more and more advanced mathematical tools, such as partial differential equations or stochastic processes, in order to include some of the complicated structures of populations. For example, description of age–structured two–sex populations can lead to systems of nonlinear transport or evolution equations (see e.g. [6, 35]).

In this paper we study constant lifetime phenotypic trait evolution in two–sex populations, using techniques of individual–based modeling. In spite of the vast literature concerning this type of models in evolutionary biology and population dynamics, a great deal of them describe asexual populations (see [7, 11, 13]). Only few models concerning hermaphroditic organisms have appeared so far (see [8, 34]). To the extent of our knowledge, there is a lack in the field of individual–based modeling for two–sex

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populations and mathematical analysis of equations derived as macroscopic approximations. Nonetheless, similar macroscopic limits have appeared in literature in different context, e.g., as Boltzmann-type kinetic equations for particle systems (see [23–25]). In particular, some of the macroscopic limits of individual-based models can lead to well-known models of population dynamics, e.g., logistic equation and Lotka–Volterra system (see [22]). We refer to [3] Chapter 8 and the citations within for a rich review on existing literature corresponding to individual-based modeling of different physical and biological phenomena.

In this paper a phenotypic trait is not sex-linked, i.e., all the trait-coding genes lie outside the sex chromosome (allosome). We distinguish two subpopulations of males and females of the same species, and assume that the mating is semi-random, i.e., there is a function of individual capability of mating, which depends on individual’s trait and sex. This function is a rate at which every individual mates with a random partner, which is chosen from all living individuals of the opposite sex according to some distribution also based on the capability function (see [1, 32–34]). After mating an offspring is born, and its sex is male or female with probability $\frac{1}{2}$ by virtue of Fisher’s principle on sex ratio (see [12]). The phenotypic trait is inherited from parents as a mean parental trait with some stochastic noise. Moreover, individuals can die naturally or in intra-specific competition at trait-dependent rates. All of the above events happen randomly in discrete population in continuous time. The evolution of population is described by a sequence of measure-valued stochastic processes (individual-based model).

The main goal of the paper is to study macroscopic equations, which are derived as a limit of the stochastic processes considered, when the number of individuals tends to infinity. We obtain the system of two nonlinear differential equations, which describe the evolution of trait distributions in male and female subpopulations, respectively. We study existence and uniqueness of the solutions, and examine total numbers of males and females – we give criterion for persistence of population, and also show when extinction occurs. The most important result concerns asymptotic stability of solutions: we investigate when the distributions of phenotypic traits in male and female subpopulations tend to a stationary solution, which is identical for the both sexes. This implies that the distribution of non-sex-linked phenotypic traits become the same for males and females after long time. In order to show applications of our result, we give two examples of mean parental trait inheritance with different forms of stochastic noise.

The structure of the paper is the following: in the next section we explain notation and gather all the model assumptions. Also in that part, we describe the individual-based model and introduce stochastic processes, discuss their existence and state the limit theorem, which gives the equation for macroscopic approximation of studied stochastic processes. In Section 3, we derive and study equations for trait distributions in male and female subpopulations. We consider existence and uniqueness of solutions and study total numbers of the subpopulations. Criteria for persistence and extinction are given. In Section 4, a theorem on asymptotic stability of trait distributions is stated and proven. Section 5 includes examples of trait inheritance and applications of our asymptotic results. In Section 6 we summarize our work and give future perspectives for extending the model.

2. The model

2.1. Assumptions and parameters of model

We assign every individual some element from a set $\mathbb{X} := X \times \{\varphi, \sigma\}$, where X is non-empty subset of \mathbb{R}^d for some $d \in \mathbb{N}$. The first coordinate of \mathbb{X} ’s members describes individual’s phenotypic trait, the second one its sex (φ corresponds to female and σ is male). Both phenotypic trait and sex are assumed to be constant in individual’s lifetime. We simply call elements of \mathbb{X} traits. For convenience sake we also consider following sets $\mathbb{F} := X \times \{\varphi\}$, $\mathbb{M} := X \times \{\sigma\}$. We also impose the following useful convention: if $\mathbf{x} \in \mathbb{X}$ is an individual’s trait, then we denote by the same, but non-bold letter x its phenotypic trait, i.e., x is the first coordinate of \mathbf{x} .

2.1.1. Mating

We adapt semi-random mating/coagulation models (see [8, 32–34]) to the two-sex population case: an individual of trait $\mathbf{x} \in \mathbb{X}$ has a rate $p(\mathbf{x})$ of initial capability of mating, at which it starts mating by choosing a partner of the opposite sex. A female (resp. male) chooses a partner of trait \mathbf{y} from a set of all living males (resp. females) from the distribution

$$\frac{p(\mathbf{y})}{\sum_i p(\mathbf{w}_i)},$$

where the sum in the denominator extends over all living males (resp. females), and \mathbf{w}_i are their traits. In other words, if the trait distribution in current population is described by some measure μ , then mating rate $m(\mathbf{x}, \mathbf{y}, \mu)$ of individuals of traits \mathbf{x}, \mathbf{y} is

$$m(\mathbf{x}, \mathbf{y}, \mu) = p(\mathbf{x}) \mathbb{1}_{\mathbb{F}}(\mathbf{x}) \frac{p(\mathbf{y}) \mathbb{1}_{\mathbb{M}}(\mathbf{y})}{\int_{\mathbb{M}} p(\mathbf{w}) \mu(d\mathbf{w})} + p(\mathbf{x}) \mathbb{1}_{\mathbb{M}}(\mathbf{x}) \frac{p(\mathbf{y}) \mathbb{1}_{\mathbb{F}}(\mathbf{y})}{\int_{\mathbb{F}} p(\mathbf{w}) \mu(d\mathbf{w})}, \quad (2.1)$$

where $\mathbb{1}_A$ is an indicator function of set A . We assume that the function p is positive, continuous and upper-bounded by some constant $\bar{p} > 0$.

2.1.2. Trait inheritance

We assume that after every mating a new individual is born, and according to Fisher's principle (see [12]), is male or female with probability $\frac{1}{2}$. We consider only these phenotypic traits which are not sex-linked. We assume that if $x, y \in X$ are parental phenotypic traits, then the offspring's trait z comes from distribution $k(x, y, dz)$. We assume that for every $x, y \in X$ the measure $k(x, y, \cdot)$ is a Borel probability measure and for every bounded and continuous function $f: X \rightarrow \mathbb{R}$, the mapping $(x, y) \mapsto \int_X f(z) k(x, y, dz)$ is continuous. Moreover, we suppose that $k(x, y, \cdot) = k(y, x, \cdot)$ for every $x, y \in X$. Denote by $K(x, y, \cdot)$ a measure on \mathbb{X} defined for every Borel subset $A \subset X$ by $K(x, y, A \times \{\mathcal{Q}\}) = K(x, y, A \times \{\mathcal{Q}\}) = \frac{1}{2} k(x, y, A)$.

2.1.3. Natural death and competition

We assume that if an individual has trait \mathbf{x} , then it can die naturally at rate $D(\mathbf{x})$. Moreover, we consider intra-specific competition (see [13, 34]): in current population described by a measure μ , an individual with trait \mathbf{x} dies in competition with rate $C(\mathbf{x}, \mu) := \int_{\mathbb{X}} U(\mathbf{x}, \mathbf{y}) \mu(d\mathbf{y})$. Function $U(\mathbf{x}, \mathbf{y})$ describes “how often” individual with trait \mathbf{x} loses competition with one of trait \mathbf{y} (so-called competition kernel). We assume that the functions D and U are positive, continuous and upper-bounded by \bar{D}, \bar{U} respectively.

2.1.4. Population dynamics

We consider a finite population in continuous time. At a random time individuals with traits \mathbf{x}, \mathbf{y} mate with rate $m(\mathbf{x}, \mathbf{y}, \mu)$ given by formula (2.1), where $\mu = \sum_{i=1}^n \delta_{\mathbf{w}_i}$, provided the current population consists of individuals with traits $\mathbf{w}_1, \dots, \mathbf{w}_n$. After mating an offspring is born with probability 1. Its sex is male or female with probability $\frac{1}{2}$ and its phenotypic trait comes from distribution $k(x, y, \cdot)$. Moreover, an individual of trait \mathbf{x} can die naturally at rate $D(\mathbf{x})$ or losing competition with other members of population at rate $C(\mathbf{x}, \mu)$. All the events and interactions are assumed to take place independently.

2.2. Stochastic processes and limit theorem

Denote by $\mathcal{M}(\mathbb{X})$ the set of all finite Borel measures on \mathbb{X} . For any $N \in \mathbb{N}$ we define the following sequence of subsets of $\mathcal{M}(\mathbb{X})$

$$\mathcal{M}^N = \left\{ \frac{1}{N} \sum_{i=1}^n \delta_{\mathbf{w}_i} : n \in \mathbb{N}, \mathbf{w}_i \in \mathbb{X} \right\}. \quad (2.2)$$

We study a sequence $(\nu^N)_{N \in \mathbb{N}}$ of \mathcal{M}^N -valued, continuous time stochastic processes given by the infinitesimal generators

$$\begin{aligned} L^N \phi(\nu) = & N \int_{\mathbb{X}} \int_{\mathbb{X}} \int_{\mathbb{X}} \left(\phi\left(\nu + \frac{1}{N} \delta_{\mathbf{z}}\right) - \phi(\nu) \right) m(\mathbf{x}, \mathbf{y}, \nu) K(x, y, d\mathbf{z}) \nu(d\mathbf{x}) \nu(d\mathbf{y}) \\ & + N \int_{\mathbb{X}} \left(\phi\left(\nu - \frac{1}{N} \delta_{\mathbf{x}}\right) - \phi(\nu) \right) \left(D(\mathbf{x}) + \frac{1}{N} C(\mathbf{x}, \nu) \right) \nu(d\mathbf{x}) \end{aligned} \quad (2.3)$$

for any measurable and bounded $\phi: \mathbb{X} \rightarrow \mathbb{R}$. Notice that the processes given by the above generators are jump processes on \mathcal{M}^N . The first term on the right-hand side of (2.3) describes mating and trait inheritance including Fisher's principle. The second term on the right-hand side of (2.3) corresponds to natural death and competition, whose rate is rescaled by the factor $\frac{1}{N}$. Given initial value $\nu_0^N \in \mathcal{M}^N$, under the model's assumptions, there exists a \mathcal{M}^N -valued Markov process $(\nu_t^N)_{t \geq 0}$ with infinitesimal generator (2.3) (see [13]). For any measure $\mu \in \mathcal{M}(\mathbb{X})$ and measurable function $\phi: \mathbb{X} \rightarrow \mathbb{R}$, we denote by $\langle \mu, \phi \rangle$ the integral $\int_{\mathbb{X}} \phi(\mathbf{x}) \mu(d\mathbf{x})$. We proceed to the macroscopic approximation theorem.

Theorem 2.1. *Suppose that the sequence of initial values $(\nu_0^N)_{N \in \mathbb{N}}$ converges to some measure $\nu \in \mathcal{M}(\mathbb{X})$ in topology of weak convergence of measures. Then for every $T > 0$ the sequence $(\nu^N)_{N \in \mathbb{N}}$ converges in distribution in the Skorokhod space $\mathcal{D}([0, T], \mathcal{M}(\mathbb{X}))$ to the deterministic and continuous flow of measures $\mu: [0, T] \rightarrow \mathcal{M}(\mathbb{X})$ satisfying for every $0 \leq t \leq T$ the following equation*

$$\begin{aligned} \langle \mu_t, \phi \rangle = & \langle \mu_0, \phi \rangle + \int_0^t \int_{\mathbb{X}} \int_{\mathbb{X}} \int_{\mathbb{X}} \phi(\mathbf{z}) m(\mathbf{x}, \mathbf{y}, \mu_s) K(x, y, d\mathbf{z}) \mu_s(d\mathbf{x}) \mu_s(d\mathbf{y}) ds \\ & - \int_0^t \int_{\mathbb{X}} \phi(x) \left(D(\mathbf{x}) + \int_{\mathbb{X}} U(\mathbf{x}, \mathbf{y}) \mu_s(d\mathbf{y}) \right) \mu_s(d\mathbf{x}) ds \end{aligned} \quad (2.4)$$

for any measurable and bounded $\phi: \mathbb{X} \rightarrow \mathbb{R}$.

The proof of Theorem 2.1 is standard and can be adapted e.g. from [32]. Similar results in the spirit of Theorem 2.1 are well-known in the literature. For example papers [7, 11, 13] introduce individual-based models of asexual populations and give probabilistic interpretations for some nonlinear macroscopic equations with linear growth terms. Nonlinear production operators also appeared in literature on individual-based modeling: in models of hermaphroditic populations (see [8, 34]) and phytoplankton dynamics (see [1, 32–34]). Equation (2.4) is also closely-related to Boltzmann-type kinetic equations (see e.g. [3] Chapter 8 and [22–25]). Note that in discussed models, every two individuals can meet each other to form a pair. In equation (2.4) one can clearly distinguish male and female subgroups. The first integral operator on the right-hand side describes an intra-sexual mating. To the extend of our knowledge there is no similar model of two-sex populations derived as a macroscopic approximation of individual-based models.

Notice that for fixed function $\phi: \mathbb{X} \rightarrow \mathbb{R}$ equation (2.4) is well-defined with the aid of a standard integral \int_0^t of real-valued functions. Nonetheless, we want to consider it to be a differential equation on the set $\mathcal{M}(\mathbb{X})$ of finite Borel measures on \mathbb{X} . To this end, we recall some basic facts from the theory of differential equations on convex sets (see e.g. [9]). We follow Chapter 4 of [26].

Consider a vector space E , its linear subspace E_0 equipped with a norm $\|\cdot\|_0$ and some nonempty, convex subset $D \subset E$ such that $u - v \in E_0$ for every $u, v \in D$. Then the norm $\|u - v\|_0$ defines a metric on D . We suppose that D is a complete metric space with this metric. Denote by $\|\cdot\|$ any extension of $\|\cdot\|_0$ to the whole space E . Now, if $f: [a, b] \rightarrow (0, \infty)$ and $u: [a, b] \rightarrow D$ are continuous functions defined on interval some $[a, b] \subset \mathbb{R}$, then the Riemann integral

$$\int_{[a, b]} f(t) u(t) dt$$

exists and is defined only by the norm $\|\cdot\|_0$ as a limit of sequence of the Riemann sums. Moreover, given $u: [a, b] \rightarrow D$, $u_0 \in E_0$ and $t_0 \in [a, b]$, the condition $u'(t_0) = u_0$, defined in standard way as a limit

of certain difference quotients, also depends only on $\|\cdot\|_0$ (see [26] Chapter 4 for details). Now, given operators $R, Q: D \rightarrow D$, we can consider the equation

$$\frac{d}{dt}u + Ru = Qu, \quad t \geq 0,$$

where d/dt is a strong derivative of unknown function u . Since, for $u: [0, \infty) \rightarrow D$ the difference $Qu - Ru$ belongs to E_0 , the notion of solution of the above differential equation does not depend on the extended norm $\|\cdot\|$ but only on $\|\cdot\|_0$.

In the above context, the notation used in (2.4) is equivalent to writing down the following equation

$$\frac{d}{dt}\mu_t(d\mathbf{z}) + \left(D(\mathbf{z}) + \int_{\mathbb{X}} U(\mathbf{z}, \mathbf{y})\mu_t(d\mathbf{y}) \right) \mu_t(d\mathbf{z}) = \int_{\mathbb{X}} \int_{\mathbb{X}} m(\mathbf{x}, \mathbf{y}, \mu_t) K(x, y, d\mathbf{z}) \mu_t(d\mathbf{x}) \mu_t(d\mathbf{y})$$

on the set $\mathcal{M}(\mathbb{X})$. Here and later on, we use the convention, that $d(x)\nu(dx)$ denotes an absolutely continuous measure with respect to the measure ν with density $d(x)$, i.e., the measure $A \mapsto \int_A d(x)\nu(dx)$. In the next section, we consider the existence and uniqueness of solutions of the above equation in the total variation norm of measures.

3. System of macroscopic equations

3.1. The system and solutions

Define $m_t(A) = \mu_t(A \cap \{\mathcal{D}\})$ and $f_t(A) = \mu_t(A \cap \{\mathcal{Q}\})$ – the measures describing evolution of traits in male and female subpopulations, respectively. Setting $\phi = \mathbb{1}_{A \times \{\mathcal{D}\}}$ and $\psi = \mathbb{1}_{A \times \{\mathcal{Q}\}}$ in (2.4) for every measurable set $A \subset X$, we obtain the following system

$$\begin{cases} \frac{d}{dt}m_t(dz) = \int_X \int_X p(x, y, m_t, f_t) k(x, y, dz) f_t(dx) m_t(dy) \\ \quad - \left(D_m(z) + \int_X U_{m,m}(z, y) m_t(dy) + \int_X U_{m,f}(z, y) f_t(dy) \right) m_t(dz), \\ \frac{d}{dt}f_t(dz) = \int_X \int_X p(x, y, m_t, f_t) k(x, y, dz) f_t(dx) m_t(dy) \\ \quad - \left(D_f(z) + \int_X U_{f,m}(z, y) m_t(dy) + \int_X U_{f,m}(z, y) f_t(dy) \right) f_t(dz), \end{cases} \quad (3.1)$$

where

1. $p(x, y, \mu, \nu) := \frac{1}{2} p_f(x) p_m(y) \left(\frac{1}{\int_X p_m(w) \mu(dw)} + \frac{1}{\int_X p_f(w) \nu(dw)} \right)$,
2. $p_f(x) := p((x, \mathcal{Q}))$, $p_m(x) := p((x, \mathcal{D}))$ – individual capabilities of mating in the female and respectively, male subpopulations,
3. $D_f(x) := D((x, \mathcal{Q}))$, $D_m(x) := D((x, \mathcal{D}))$ – natural death rates in the female and respectively, male subpopulations,
4. $U_{f,f}(x, y) := U((x, \mathcal{Q}), (y, \mathcal{Q}))$ – competition kernel between females,
5. $U_{m,m}(x, y) := U((x, \mathcal{D}), (y, \mathcal{D}))$ – competition kernel between males,
6. $U_{m,f}(x, y) := U((x, \mathcal{D}), (y, \mathcal{Q}))$ – competition kernel describing the rate of competition loss of the males due to females,
7. $U_{f,m}(x, y) := U((x, \mathcal{Q}), (y, \mathcal{D}))$ – competition kernel describing the rate of competition loss of the females due to males.

Note that system (3.1) is a trait-structured population analogue of some classic two-sex population models well-known from the literature. For example, our model contains more general, trait-dependent version of some of the mating functions studied in [14, 17, 19], and intra- and inter- sexual competition considered in [27, 31].

Recall that for any finite Borel measure μ on X we can introduce the total variation norm by the formula $\|\mu\|_{\text{TV}} := \sup_f \int_X f(x)\mu(dx)$, where the supremum is taken over the set of all measurable functions $f: X \rightarrow \mathbb{R}$ such that $|f(x)| \leq 1$ for all $x \in X$. The proof of the following result can be easily adapted from the proof of Theorem 2 in [34].

Theorem 3.1. *Suppose that $p_f, p_m, D_f, D_m, U_{f,f}, U_{f,m}, U_{m,f}, U_{m,m}$ are measurable, upper-bounded and bounded from below by some positive constants. For every $\mu_0, \nu_0 \in \mathcal{M}(X)$ there exists a unique pair of functions $\mu, \nu: [0, \infty) \rightarrow \mathcal{M}(X)$, which is the solution of system (3.1) with initial condition μ_0, ν_0 . The functions μ_t, ν_t are continuous and bounded in the norm $\|\cdot\|_{\text{TV}}$.*

If we additionally suppose that for every $x, y \in X$ there exists a density $\kappa(x, y, \cdot) \in L^1$ of measure $k(x, y, dz)$ with respect to the Lebesgue measure, then using the Radon–Nikodym theorem, we can also prove the following theorem.

Theorem 3.2. *Under the assumptions of Theorem 3.1, if μ_0, ν_0 have densities $u_0, v_0 \in L^1$ with respect to the Lebesgue measure, then for every $t \geq 0$ the corresponding solutions μ_t, ν_t of (3.1) have densities $u(t, \cdot), v(t, \cdot) \in L^1$ with respect to the Lebesgue measure. The functions $u(t, z), v(t, z)$ are unique solutions of the following system*

$$\begin{cases} \frac{\partial}{\partial t} u(t, z) = \int_X \int_X p(x, y, u(t, w), v(t, w)) \kappa(x, y, z) u(t, x) v(t, y) dx dy \\ \quad - \left(D_m(z) + \int_X U_{m,m}(z, y) u(t, y) dy + \int_X U_{m,f}(z, y) v(t, y) dy \right) u(t, z), \\ \frac{\partial}{\partial t} v(t, z) = \int_X \int_X p(x, y, u(t, w), v(t, w)) \kappa(x, y, z) u(t, x) v(t, y) dx dy \\ \quad - \left(D_f(z) + \int_X U_{f,m}(z, y) u(t, y) dy + \int_X U_{f,m}(z, y) v(t, y) dy \right) v(t, z). \end{cases} \tag{3.2}$$

Similar systems of equations, describing age-structured populations, can be found in literature on population dynamics. For example in [6] an age-structured model includes gestation period. The existence of permanent (stationary) solutions is proven. In [37] another model, including logistic term, is proposed. The authors show the existence of an equilibrium and investigate its properties. Equation (3.2) can be seen as a pair of coupled kinetic equations (see [23–25]). Similar type of coupled nonlinear equations was derived as a macroscopic limit and partially studied from the standpoint of densities in [22]. Notice that, in our case individual’s trait is assumed to be constant lifetime, what distinguishes our model from the age-structured models. Constant lifetime traits result in the lack of terms with $\partial/\partial z$ in equations (3.2). Therefore, we can study more general measure-valued solutions of (3.1) in total variation norm. To the extend of our knowledge, there is no other paper concerning systems of equations of precisely the same structure as (3.1).

3.2. Total numbers of males and females

In this chapter we consider a case when all of the rates $D_m, D_f, U_{m,m}, U_{m,f}, U_{f,m}, U_{f,f}$ are constant and positive. We assume that p_m, p_f are constant, non-negative and $p_m + p_f > 0$. If $p_m = 0$ (resp. $p_f = 0$), then we suppose that function $p(x, y, \mu, \nu)$ in (3.1) has the form $\frac{p_f}{2\mu(X)}$ (resp. $\frac{p_m}{2\nu(X)}$). Under the above

assumptions, system (3.1) reads as follows

$$\left\{ \begin{array}{l} \frac{d}{dt}m_t(dz) = \frac{p_f F(t) + p_m M(t)}{2M(t)F(t)} \int_X \int_X k(x, y, dz) f_t(dx) m_t(dy) \\ \quad - \left(D_m + U_{m,m}M(t) + U_{m,f}F(t) \right) m_t(dz), \\ \frac{d}{dt}f_t(dz) = \frac{p_f F(t) + p_m M(t)}{2M(t)F(t)} \int_X \int_X k(x, y, dz) m_t(dx) f_t(dy) \\ \quad - \left(D_f + U_{f,m}M(t) + U_{f,f}F(t) \right) f_t(dz), \end{array} \right. \quad (3.3)$$

where $M(t) := m_t(X)$ and $F(t) := f_t(X)$. In order to investigate asymptotic properties of total numbers of individuals in male and female subpopulations, let us denote $\lambda(t) := (p_f F(t) + p_m M(t))/2$. Integrating both sides of equations of system (3.3), we obtain

$$\left\{ \begin{array}{l} M'(t) = \lambda(t) - (D_m + U_{m,m}M(t) + U_{m,f}F(t))M(t), \\ F'(t) = \lambda(t) - (D_f + U_{f,m}M(t) + U_{f,f}F(t))F(t). \end{array} \right. \quad (3.4)$$

The value $\lambda(t)\Delta t$ is a number of newborns in each subpopulation in a small time interval $[t, t + \Delta t]$. This number is identical in males and females due to the Fisher's principle. The form of $\lambda(t)$ in our model generalizes some of the birth rates studied before in literature. For instance some of the rates investigated in [14, 17, 19] can be obtained simply by taking $p_m = p_f = 1$ and $p_m = 0, p_f = 1$. However, since our equations contain additional terms, which are responsible for competition, the solutions exhibit asymptotic properties different than exponential growth of the above models. Similar intersexual competition terms were studied in [31] Section 4. A particular case of system (3.4) appeared also in [27] and the existence of globally asymptotically stable stationary solution was obtained. We provide a result concerning the same type of asymptotic behavior, but in more general setting. In particular, we prove that the convergence to globally asymptotically stationary solution is exponential, i.e. the distance between any solution at time t and the stationary point can be bounded by ae^{-bt} , where $a, b > 0$.

Theorem 3.3. *Consider solution $(M(t), F(t))$ of system (3.4) with initial condition (M_0, F_0) , where $M_0, F_0 > 0$. Suppose that the inequality*

$$\frac{p_m}{D_m} + \frac{p_f}{D_f} > 2 \quad (3.5)$$

holds. Then the population persists, i.e., there exist unique $\bar{M}, \bar{F} > 0$ such that $(M(t), F(t)) \rightarrow (\bar{M}, \bar{F})$ exponentially, as $t \rightarrow \infty$. On the contrary, if the inequality

$$\frac{p_m}{D_m} + \frac{p_f}{D_f} \leq 2, \quad (3.6)$$

holds, then the population extincts, i.e., $(M(t), F(t)) \rightarrow (0, 0)$ exponentially, as $t \rightarrow \infty$.

Proof. Suppose that condition (3.5) holds. Firstly, we show that the following system of polynomial equations

$$\left\{ \begin{array}{l} p_m M + p_f F - 2D_m M - 2U_{m,m}M^2 - 2U_{m,f}FM = 0, \\ p_m M + p_f F - 2D_f F - 2U_{f,m}MF - 2U_{f,f}F^2 = 0. \end{array} \right. \quad (3.7)$$

has a unique non-trivial solution (\bar{M}, \bar{F}) . Denote by h_1 and h_2 curves given by first and second equation, respectively. Notice, that if $p_m - 2D_m = \frac{U_{m,m}p_f}{U_{m,f}}$, or $p_f - 2D_f = \frac{U_{f,f}p_m}{U_{f,m}}$, then one can easily show that the system has only one positive solution. Denote the implicit formulas for both curves $F_1(M) = \frac{p_m M - 2D_m M - 2U_{m,m}M^2}{2U_{m,f}M - p_f}$ and $M_2(F) = \frac{p_f F - 2D_f F - 2U_{f,f}F^2}{2U_{f,m}F - p_m}$ and let $A = \frac{p_f}{2U_{m,f}}$, $B = \frac{p_m}{2U_{f,m}}$. Then

1. if $p_m - 2D_m > \frac{U_{m,m}p_f}{U_{m,f}}$, and $p_f - 2D_f > \frac{U_{f,f}p_m}{U_{f,m}}$, then

$$\lim_{M \nearrow A} F_1(M) = -\infty, \lim_{M \searrow A} F_1(M) = +\infty, \lim_{F \nearrow B} M_2(F) = -\infty, \lim_{F \searrow B} M_2(F) = +\infty,$$

2. if $p_m - 2D_m > \frac{U_{m,m}p_f}{U_{m,f}}$, and $p_f - 2D_f < \frac{U_{f,f}p_m}{U_{f,m}}$, then

$$\lim_{M \nearrow A} F_1(M) = -\infty, \lim_{M \searrow A} F_1(M) = +\infty, \lim_{F \nearrow B} M_2(F) = +\infty, \lim_{F \searrow B} M_2(F) = -\infty,$$

3. if $p_m - 2D_m < \frac{U_{m,m}p_f}{U_{m,f}}$, and $p_f - 2D_f > \frac{U_{f,f}p_m}{U_{f,m}}$, then

$$\lim_{M \nearrow A} F_1(M) = +\infty, \lim_{M \searrow A} F_1(M) = -\infty, \lim_{F \nearrow B} M_2(F) = -\infty, \lim_{F \searrow B} M_2(F) = +\infty,$$

4. if $p_m - 2D_m < \frac{U_{m,m}p_f}{U_{m,f}}$, and $p_f - 2D_f < \frac{U_{f,f}p_m}{U_{f,m}}$, then

$$\lim_{M \nearrow A} F_1(M) = +\infty, \lim_{M \searrow A} F_1(M) = -\infty, \lim_{F \nearrow B} M_2(F) = +\infty, \lim_{F \searrow B} M_2(F) = -\infty.$$

Moreover one can check that the vector $[U_{m,m}, U_{m,f}]$ (resp. $[U_{f,m}, U_{f,f}]$) is parallel to the other asymptote of h_1 (resp. h_2). Since in all of the above cases each of h_1 and h_2 has two different asymptotes, there must be that h_1 and h_2 are hyperbolas or two straight lines. Since the lines $p_f F + (p_m - 2D_m)M = 0$, $(p_f - 2D_f)F + p_m M = 0$ are tangent lines at $(0, 0)$ to h_1 and h_2 , respectively, from (3.5) one can prove the following inequality

$$p_m p_f > (p_m - 2D_m)(p_f - 2D_f),$$

which implies that h_2 lies above h_1 in some right neighborhood of 0 in the following sense: $F_1(M) < F_2(M)$ for small $M > 0$ (here $F_2(M)$ is an explicit formula for F derived from the second equation of (3.7)). Now it is easy to check that in every case such two curves must cross at exactly one positive point (by virtue of the Darboux property of continuous functions). From now on, we denote by (\bar{M}, \bar{F}) the unique solution to system (3.7).

Now we show, that the stationary solution (\bar{M}, \bar{F}) is globally asymptotically stable, provided the initial conditions M_0, F_0 are positive. Let $\rho(M, F) = -1/(MF)$. Then for any $F, M > 0$

$$\frac{\partial}{\partial M}(\rho H_1)(M, F) + \frac{\partial}{\partial F}(\rho H_2)(M, F) \geq \frac{U_{m,m}}{F} + \frac{U_{f,f}}{M} > 0,$$

where H_1 and H_2 are functions from right-hand sides of the first and second equation of system (3.4), respectively. Since solutions of the system are upper-bounded, from the Dulac-Bendixon theorem $(M(t), F(t))$ tends to one of the stationary points, as $t \rightarrow \infty$. Next we show that $(0, 0)$ is retracting. Denote $\beta(t) := p_m M(t)/D_m + p_f F(t)/D_f$. From (3.4) we obtain

$$\beta'(t) = \left(\frac{p_m}{D_m} + \frac{p_f}{D_f} - 2 \right) \lambda(t) - C_1 p_m^2 M^2(t) - 2C_2 p_m p_f M(t)F(t) - C_3 p_f^2 F^2(t), \quad (3.8)$$

where $C_1, C_2, C_3 > 0$ are some constants. Let $C = \max\{C_1, C_2, C_3\}$. Then

$$\beta'(t) \geq \lambda(t) \left(\frac{p_m}{D_m} + \frac{p_f}{D_f} - 2 - 4C\lambda(t) \right).$$

If $M(t), F(t)$ are small enough that $0 < \lambda(t) < \frac{p_m}{4CD_m} + \frac{p_f}{4CD_f} - \frac{1}{2C}$, then $\beta'(t) > 0$, and at least one of the functions $M(t), F(t)$ grows strictly. It shows that $(0, 0)$ is indeed a retracting point.

Now we prove that the convergence to (\bar{M}, \bar{F}) is exponential. It is sufficient to show, that all the eigenvalues of the linearized system at (\bar{M}, \bar{F}) have negative real parts. Using standard calculations and

equalities (3.7), one can show that every such eigenvalue λ satisfies the following quadratic equation $\lambda^2 + \omega_1\lambda + \omega_2 = 0$, where $\omega_1 := U_{m,m}\bar{M} + \frac{p_f}{2}\frac{\bar{F}}{\bar{M}} + U_{f,f}\bar{F} + \frac{p_m}{2}\frac{\bar{M}}{\bar{F}}$ and

$$\omega_2 := \frac{p_m}{2}\frac{\bar{M}^2}{\bar{F}}U_{m,m} + \frac{p_f}{2}\frac{\bar{F}^2}{\bar{M}}U_{f,f} + \frac{p_f}{2}U_{f,m}\bar{F} + \frac{p_m}{2}U_{m,f}\bar{M} + \left(U_{m,m}U_{f,f} - U_{m,f}U_{f,m}\right)\bar{M}\bar{F}.$$

Clearly $\omega_1 > 0$. By Vieta's formulas it is sufficient to show that also $\omega_2 > 0$. Suppose that $U_{f,m} \leq U_{m,f}$ (resp. $U_{m,f} \leq U_{f,m}$). Then from the first (resp. the second) equation of system (3.7) we obtain $U_{m,f}U_{f,m}\bar{M}\bar{F} < \frac{p_f}{2}U_{f,m}\bar{F} + \frac{p_m}{2}U_{f,m}\bar{M}$ (resp. $U_{m,f}U_{f,m}\bar{M}\bar{F} < \frac{p_f}{2}U_{m,f}\bar{F} + \frac{p_m}{2}U_{m,f}\bar{M}$). In the both cases the following inequality

$$U_{m,f}U_{f,m}\bar{M}\bar{F} < \frac{p_f}{2}U_{f,m}\bar{F} + \frac{p_m}{2}U_{m,f}\bar{M}$$

holds. Finally, $\omega_2 > \frac{p_m}{2}\frac{\bar{M}^2}{\bar{F}}U_{m,m} + \frac{p_f}{2}\frac{\bar{F}^2}{\bar{M}}U_{f,f} + U_{m,m}U_{f,f}\bar{M}\bar{F} > 0$, which proves that the convergence to (\bar{M}, \bar{F}) is exponential.

Now we proceed to the proof of the extinction part of Theorem 3.3. Let us suppose that inequality (3.6) is satisfied. Notice that from (3.7) it follows that

$$\left(\frac{p_m}{D_m} + \frac{p_f}{D_f} - 2\right)\lambda = AM^2 + BMF + CF^2,$$

where $\lambda = p_m M/2 + p_f F/2$ and $A, B, C > 0$ are some constants. Since the left-hand side of the above equality is non-positive and the right-hand side is non-negative, there is no positive solution, and consequently $M = F = 0$ is the only solution to the system. Moreover, from (3.8) it follows that $\beta'(t) \leq -C\beta(t)$, where $C > 0$ is some constant. Then $\beta(t) \rightarrow 0$ exponentially, and thus $(M(t), F(t)) \rightarrow (0, 0)$, as $t \rightarrow \infty$. \square

Suppose that (3.5) holds. Substitutions $m_t(dz) = M(t)\mu_t(dz)$ and $f_t(dz) = F(t)\nu_t(dz)$ in (3.3) and following time change $t \mapsto \int_0^t \frac{\lambda(s)}{M(s)} ds$ lead to the system

$$\begin{cases} \frac{d}{dt}\mu_t(dz) + \mu_t(dz) = \int_X \int_X k(x, y, dz)\mu_t(dx)\nu_t(dy), \\ \frac{d}{dt}\nu_t(dz) + A(t)\nu_t(dz) = A(t) \int_X \int_X k(x, y, dz)\mu_t(dx)\nu_t(dy), \end{cases} \quad (3.9)$$

where $A(t) := M(t)/F(t)$ converges exponentially to $A := \bar{M}/\bar{F} > 0$ when $t \rightarrow \infty$. Notice, that if μ_0, ν_0 are probability measures, then for every $t > 0$, solutions μ_t, ν_t are probability measures as well. We denote by $\mathcal{M}_{\text{Prob}}$ the set of all Borel probability measures on X .

System (3.9) is a trait-structured generalization of some of the models appearing in the literature on population dynamics. For example in [38] a bisexual, non-marriage model is proposed in a form of two nonlinear ODE's describing evolution of numbers of males and females. It is proven that any solution of the ODE system tends asymptotically to a finite sex-ratio, what resembles the results of Theorem 3.3 of the present paper.

4. Asymptotic stability of trait distribution

4.1. Statement of the main result

In this section we assume that X is closed interval of real numbers. From Theorem 3.3, under condition (3.5), male and female subpopulations sizes stabilize at positive levels. It implies that $A(t) \rightarrow A$ exponentially, as $t \rightarrow \infty$, where $A = \bar{M}/\bar{F} > 0$. Denote $\mathcal{P}(\mu, \nu)(dz) = \int_X \int_X k(x, y, dz)\mu(dx)\nu(dy)$. In this section,

we study long time behavior of the following system

$$\begin{cases} \mu'_t + \mu_t = \mathcal{P}(\mu_t, \nu_t), \\ \nu'_t + A\nu_t = A\mathcal{P}(\mu_t, \nu_t). \end{cases} \tag{4.1}$$

Later on, we compare solutions of initial system with certain solutions of (4.1) in order to obtain asymptotic behavior also for solutions of (3.9). We assume that

$$\int_X |z|k(x, y, dz) \leq a_1 + a_2|x| + a_3|y|, \tag{4.2}$$

for some constants $a_1, a_2, a_3 > 0$, and

$$\int_X zk(x, y, dz) = \frac{x + y}{2}. \tag{4.3}$$

The above condition is a reasonable biological assumption and means that the expected offspring's trait is a mean parental trait.

For any $\gamma \geq 1$ and $\alpha \leq \beta$ we introduce $\mathcal{M}_\gamma := \{\mu \in \mathcal{M}_{\text{Prob}} : \int_X |x|^\gamma \mu(dx) < \infty\}$ and $\mathcal{M}_{[\alpha, \beta]} := \{\mu \in \mathcal{M}_1 : \alpha \leq \int_X x\mu(dx) \leq \beta\}$. For any two measures $\mu, \nu \in \mathcal{M}_1$, we define the Wasserstein distance by the formula

$$d(\mu, \nu) = \sup_{f \in \text{Lip}_1} \int_X f(z)(\mu - \nu)(dz), \tag{4.4}$$

where Lip_1 is a set of all functions $f: X \rightarrow \mathbb{R}$ such that $|f(x) - f(y)| \leq |x - y|$, for any $x, y \in X$. Denote by $\mathcal{K}(x, y, \cdot)$ the cumulative distribution function of the measure $k(x, y, \cdot)$, i.e., $\mathcal{K}(x, y, z) = k(x, y, X \cap (-\infty, z])$. The main theorem of the paper is

Theorem 4.1. *Fix $\alpha, \beta \in X$, $\alpha \leq \beta$. Suppose that*

(i) *for all $y, z \in X$ the function $\mathcal{K}(x, y, z)$ is absolutely continuous with respect to x and for every $a, b, y \in X$*

$$\int_X \left| \frac{\partial}{\partial x} \mathcal{K}(a, y, z) - \frac{\partial}{\partial x} \mathcal{K}(b, y, z) \right| dz < 1,$$

(ii) *there exist constants $\gamma > 1$, $C > 0$ and $L < 1$ such that*

$$\int_X |x|^\gamma \mathcal{P}(\mu, \nu)(dx) \leq C + L \max \left\{ \int_X |x|^\gamma \mu(dx), \int_X |x|^\gamma \nu(dx) \right\}.$$

for every $\mu, \nu \in \mathcal{M}_\gamma \cap \mathcal{M}_{[\alpha, \beta]}$.

Then for every $\mu_0, \nu_0 \in \mathcal{M}_{[\alpha, \beta]}$ there exists unique solution $\mu, \nu: [0, \infty) \rightarrow \mathcal{M}_{[\alpha, \beta]}$ of system (4.1) with initial values μ_0, ν_0 . Moreover, there exists unique measure $\mu^ \in \mathcal{M}_{[\alpha, \beta]}$ such that $\mathcal{P}(\mu^*, \mu^*) = \mu^*$, and for every initial measures $\mu_0, \nu_0 \in \mathcal{M}_{[\alpha, \beta]}$ corresponding solutions μ_t, ν_t converge to μ^* in space $(\mathcal{M}_{[\alpha, \beta]}, d)$, as $t \rightarrow \infty$.*

The concept of the above theorem comes from [34], where criteria for asymptotic stability of a single equation of the form $u' + u = \mathcal{P}(u, u)$ were studied. Nonetheless, since the problem of the present paper is two-dimensional, we cannot use these techniques directly. In particular, it is not clear if the criteria for asymptotic stability of the single equation imply conditions (i) and (ii) from the above theorem without any additional assumptions. Moreover, we have to pay more attention to mean values of the distributions, since they vary in time, what was not a case in [34]. Thus, we have to introduce different space setting, i.e., space of measures with mean values belonging to some interval of positive length. Additionally, since various constants A may appear in system (4.1), while comparing coordinates of two different solutions of this system, we do not know which one attains the maximum, what makes the problem of approaching of solutions more complex than in [34].

4.2. Convergence of measures

In order to investigate asymptotic properties of the solutions, we recall some basic theory concerning convergence of measures. We start with method of computing Wasserstein distance, which can be found in [34] as Lemma 1.

Lemma 4.2. *The Wasserstein distance between measures $\mu, \nu \in \mathcal{M}_1$ can be computed by the formula*

$$d(\mu, \nu) = \int_X |\Phi(x)| dx, \tag{4.5}$$

where $\Phi(z) = (\mu - \nu)(X \cap (-\infty, z])$ is a cumulative distribution function of the signed measure $\mu - \nu$.

Consider probability measures μ and $\mu_n, n \in \mathbb{N}$, on the set X . We recall that the sequence $(\mu_n)_{n \in \mathbb{N}}$ converges weakly to μ , if for any continuous and bounded function $f: X \rightarrow \mathbb{R}$

$$\int_X f(x) \mu_n(dx) \rightarrow \int_X f(x) \mu(dx),$$

as $n \rightarrow \infty$. It is well-known that the convergence in Wasserstein distance implies weak convergence of measures. Moreover, the space of probability Borel measures on any complete metric space is also a complete metric space with the Wasserstein distance (see e.g. [4, 30]). The convergence of a sequence $(\mu_n)_{n \in \mathbb{N}}$ to μ in the space $\mathcal{M}_{1,q} := \{\mu \in \mathcal{M}_1 : \int_X x \mu(dx) = q\}$ is equivalent to the following condition (see [36], Definition 6.7 and Theorem 6.8)

$$\mu_n \rightarrow \mu \text{ weakly, as } n \rightarrow \infty \quad \text{and} \quad \lim_{R \rightarrow \infty} \limsup_{n \rightarrow \infty} \int_{X_R} |x| \mu_n(dx) = 0, \tag{C}$$

where $X_R := \{x \in X : |x| \geq R\}$. For any measure $\mu \in \mathcal{M}_1$ we denote by $\mathbb{E}\mu$ its mean value, i.e., $\mathbb{E}\mu = \int_X x \mu(dx)$.

Lemma 4.3. *Assume that $\alpha, \beta \in X, \alpha \leq \beta, m > 0$ and $\gamma > 1$. Consider the family*

$$\mathcal{M}_{[\alpha, \beta], \gamma, m} := \left\{ \mu \in \mathcal{M}_1 : \alpha \leq \int_X x \mu(dx) \leq \beta, \int_X |x|^\gamma \mu(dx) \leq m \right\}.$$

Then $\mathcal{M}_{[\alpha, \beta], \gamma, m}$ is relatively compact subset of $(\mathcal{M}_{[\alpha, \beta]}, d)$.

Proof. Fix any sequence $(\mu^n)_{n \in \mathbb{N}}$ of measures from $\mathcal{M}_{[\alpha, \beta], \gamma, m}$. Since $\alpha \leq \mathbb{E}\mu \leq \beta$ there exists a subsequence $(p_n)_{n \in \mathbb{N}}$ such that $\lim_n \mathbb{E}\mu^{p_n} = E$ for some $\alpha \leq E \leq \beta$. Consider sequence of measures $(\bar{\mu}^{p_n})_{n \in \mathbb{N}}$ given by

$$\bar{\mu}^{p_n} = \begin{cases} a_n \mu^{p_n} + (1 - a_n) \delta_\beta, & \text{if } \mathbb{E}\mu^{p_n} \leq E, \\ a_n \mu^{p_n} + (1 - a_n) \delta_\alpha, & \text{if } \mathbb{E}\mu^{p_n} > E, \end{cases}$$

where $a_n \in [0, 1]$ satisfies $\mathbb{E}\bar{\mu}^{p_n} = a_n \mathbb{E}\mu^{p_n} + (1 - a_n) \beta = E$ (resp. $\mathbb{E}\bar{\mu}^{p_n} = a_n \mathbb{E}\mu^{p_n} + (1 - a_n) \alpha = E$). From $\lim_n \mathbb{E}\mu^{p_n} = E$, it follows that $a_n \rightarrow 1$ and $\lim_n d(\mu^{p_n}, \bar{\mu}^{p_n}) = 0$, and moreover

$$\int_X |x|^\gamma \bar{\mu}^{p_n}(dx) \leq a_n \int_X |x|^\gamma \mu^{p_n}(dx) + (1 - a_n) (|\alpha|^\gamma + |\beta|^\gamma) \leq m + |\alpha|^\gamma + |\beta|^\gamma < \infty.$$

The above inequality, together with Markov inequality, implies that condition (C) holds (see remarks after Lemma 1 in [34]). Consequently, there exist $\mu^* \in \mathcal{M}_{1,E}$ and some subsequence $(q_n)_{n \in \mathbb{N}}$ of the sequence $(p_n)_{n \in \mathbb{N}}$ such that $\lim_n d(\bar{\mu}^{q_n}, \mu^*) = 0$. Finally,

$$d(\mu^{q_n}, \mu^*) \leq d(\mu^{q_n}, \bar{\mu}^{q_n}) + d(\bar{\mu}^{q_n}, \mu^*) \rightarrow 0,$$

as $n \rightarrow \infty$. □

4.3. Proof of the main result

We split the proof of Theorem 4.1 into a sequence of lemmas.

Lemma 4.4. *Assume that condition (i) of Theorem 4.1 is satisfied. Then*

$$d(\mathcal{P}(\mu^1, \nu^1), \mathcal{P}(\mu^2, \nu^2)) < \max \{d(\nu^1, \nu^2), d(\mu^1, \mu^2)\} \quad (4.6)$$

for any $\mu^1, \mu^2, \nu^1, \nu^2 \in \mathcal{M}_1$ such that $\int_X x\mu^1(dx) = \int_X x\mu^2(dx)$ and $\int_X x\nu^1(dx) = \int_X x\nu^2(dx)$.

Proof. Denote by Φ the cumulative distribution function of signed measure $\mu_1 - \mu_2$, and consider $\Phi^+(x) := \max\{0, \Phi(x)\}$ and $\Phi^-(x) := \max\{0, -\Phi(x)\}$. The assumption $\int_X x\mu^1(dx) = \int_X x\mu^2(dx)$ implies

$$\int_X \Phi^+(x)dx = \int_X \Phi^-(x)dx = \frac{1}{2} \int_X |\Phi(x)|dx.$$

Since Φ^+ and Φ^- are non-negative and have the same integral condition (i) implies

$$\int_X \left| \int_X \frac{\partial}{\partial x} \mathcal{K}(x, y, z) \Phi^+(x) dx - \int_X \frac{\partial}{\partial x} \mathcal{K}(x, y, z) \Phi^-(x) dx \right| dz < \int_X \Phi^+(x) dx.$$

Integrating by parts we obtain

$$\int_X \mathcal{K}(x, y, z) \Phi(dx) = - \int_X \frac{\partial}{\partial x} \mathcal{K}(x, y, z) \Phi(x) dx$$

and consequently by Lemma 4.2

$$\int_X \left| \int_X \mathcal{K}(x, y, z) \Phi(dx) \right| dz < \frac{1}{2} \int_X |\Phi(x)| dx = \frac{1}{2} d(\mu^1, \mu^2).$$

In the same way we prove that if Ψ is the cumulative distribution function of signed measure $\nu^1 - \nu^2$, then

$$\int_X \left| \int_X \mathcal{K}(x, y, z) \Psi(dy) \right| dz < \frac{1}{2} \int_X |\Psi(y)| dy = \frac{1}{2} d(\nu^1, \nu^2).$$

Now, since

$$\mathcal{P}(\mu^1, \nu^1) - \mathcal{P}(\mu^2, \nu^2) = \int_X \int_X k(x, y, dz) \left(\mu^1(dx)(\nu^1 - \nu^2)(dy) + \nu^2(dy)(\mu^1 - \mu^2)(dx) \right),$$

we finally obtain

$$\begin{aligned} d(\mathcal{P}(\mu^1, \nu^1), \mathcal{P}(\mu^2, \nu^2)) &\leq \int_X \int_X \left| \int_X \mathcal{K}(x, y, dz) \Psi(dy) \right| dz \mu^1(dx) \\ &\quad + \int_X \int_X \left| \int_X \mathcal{K}(x, y, dz) \Phi(dx) \right| dz \nu^2(dx) < \frac{d(\nu^1, \nu^2) + d(\mu^1, \mu^2)}{2}, \end{aligned}$$

which implies (4.6). \square

Lemma 4.5. *Assume that (4.6) is satisfied for all $\mu^1, \mu^2, \nu^1, \nu^2 \in \mathcal{M}_1$ such that $\int_X x\mu^1(dx) = \int_X x\mu^2(dx)$ and $\int_X x\nu^1(dx) = \int_X x\nu^2(dx)$. Fix $\mu_0^1, \mu_0^2, \nu_0^1, \nu_0^2 \in \mathcal{M}_1$ satisfying $\int_X x\mu_0^1(dx) = \int_X x\mu_0^2(dx)$ and $\int_X x\nu_0^1(dx) = \int_X x\nu_0^2(dx)$. Denote by (μ_t^1, ν_t^1) and (μ_t^2, ν_t^2) solutions of system (4.1) with initial conditions (μ_0^1, ν_0^1) and (μ_0^2, ν_0^2) , respectively. Then $\mu_t^1, \nu_t^1, \mu_t^2, \nu_t^2 \in \mathcal{M}_{[\alpha, \beta]}$ for some $\alpha, \beta \in X$ and any $t > 0$, and*

$$\max \{d(\nu_s^1, \nu_s^2), d(\mu_s^1, \mu_s^2)\} > \max \{d(\nu_t^1, \nu_t^2), d(\mu_t^1, \mu_t^2)\} \quad (4.7)$$

for $0 \leq s < t \leq T$ provided $\mu_T^1 \neq \mu_T^2$ and $\nu_T^1 \neq \nu_T^2$.

Proof. Taking the mean value of both sides of equations in (4.1), from condition (4.3) we obtain

$$\begin{cases} m'(t) = \frac{1}{2}(n(t) - m(t)), \\ n'(t) = \frac{A}{2}(m(t) - n(t)). \end{cases} \quad (4.8)$$

where $m(t) = \int_X x\mu_t(dx)$ and $n(t) = \int_X xv_t(dx)$. From above system we obtain $m(t) - n(t) = (m_0 - n_0)e^{-(1+A)t/2}$. Thus, if $m_0 \geq n_0$ (resp. $m_0 < n_0$), then from (4.8) function $m(t)$ decreases (resp. increases) and $n(t)$ increases (resp. decreases), so $m(0) \geq m(t) \geq n(t) \geq n(0)$ (resp. $m(0) \leq m(t) \leq n(t) \leq n(0)$). Consequently, $\mu_t, \nu_t \in \mathcal{M}_{[\alpha, \beta]}$ for any $t > 0$, where $\alpha := \min\{m(0), n(0)\}$ and $\beta := \max\{m(0), n(0)\}$.

Fix s, t such that $0 \leq s < t \leq T$. Every solution of system (4.1) is of the following form

$$\begin{cases} \mu_t = e^{s-t}\mu_s + \int_s^t e^{r-t}\mathcal{P}(\mu_r, \nu_r)dr, \\ \nu_t = e^{A(s-t)}\nu_s + A \int_s^t e^{A(r-t)}\mathcal{P}(\nu_r, \mu_r)dr. \end{cases} \quad (4.9)$$

From Lemma (4.4) we obtain

$$\begin{cases} e^t d(\mu_t^1, \mu_t^2) < e^s d(\mu_s^1, \mu_s^2) + \int_s^t e^r \max\{d(\nu_r^1, \nu_r^2), d(\mu_r^1, \mu_r^2)\}dr, \\ e^{At} d(\nu_t^1, \nu_t^2) < e^{As} d(\nu_s^1, \nu_s^2) + A \int_s^t e^{Ar} \max\{d(\nu_r^1, \nu_r^2), d(\mu_r^1, \mu_r^2)\}dr. \end{cases} \quad (4.10)$$

We divide the interval $[0, T]$ into subintervals $I_n := [t_n, t_{n+1}]$ such that the sign of the difference $d(\mu_t^1, \mu_t^2) - d(\nu_t^1, \nu_t^2)$ is fixed for every $t \in I_n$. Consider any such interval I_n and suppose for example that $d(\mu_t^1, \mu_t^2) \leq d(\nu_t^1, \nu_t^2)$ for every $t \in I_n$. From the second inequality of (4.10) we obtain for $s, t \in I_n$

$$e^{At} \max\{d(\nu_t^1, \nu_t^2), d(\mu_t^1, \mu_t^2)\} < e^{As} \max\{d(\nu_s^1, \nu_s^2), d(\mu_s^1, \mu_s^2)\} + A \int_s^t e^{Ar} \max\{d(\nu_r^1, \nu_r^2), d(\mu_r^1, \mu_r^2)\}dr,$$

and from Gronwall inequality we obtain (4.7) for $t, s \in I_n$. If in any interval the inequality is reversed, i.e. $d(\mu_t^1, \mu_t^2) \geq d(\nu_t^1, \nu_t^2)$ for $t \in I_n$, then we use the first inequality of (4.10) and again from Gronwall inequality we obtain (4.7). Since intersection of intervals I_n and I_{n+1} is nonempty, (4.7) holds for any $0 \leq s < t \leq T$. \square

Lemma 4.6. *Assume that condition (ii) from Theorem 4.1 is satisfied. Then for every pair of measures $\mu_0, \nu_0 \in \mathcal{M}_\gamma$ the orbits $\mathcal{O}(\mu_0), \mathcal{O}(\nu_0)$ are relatively compact subsets of $\mathcal{M}_{[\alpha, \beta]}$. Moreover, $\text{cl } \mathcal{O}(\mu_0), \text{cl } \mathcal{O}(\nu_0) \subset \mathcal{M}_{[\alpha, \beta]} \cap \mathcal{M}_\gamma$, where cl is closure in $(\mathcal{M}_{[\alpha, \beta]}, d)$.*

Proof. Fix $\mu_0, \nu_0 \in \mathcal{M}_\gamma$ such that $\int_X |x|^\gamma \mu_0(dx), \int_X |x|^\gamma \nu_0(dx) \leq m_0$ for some $m_0 > 0$. Since from Lemma 4.5 we obtain $\alpha \leq \int_X x\mu_t(dx), \int_X xv_t(dx) \leq \beta$ for some $\alpha, \beta \in X$ and every $t > 0$, then the relative compactness of orbits follows from Lemma 4.3 provided we prove the following upper-bounds

$$\int_X |x|^\gamma \mu_t(dx) \leq M \quad \text{and} \quad \int_X |x|^\gamma \nu_t(dx) \leq M, \quad (4.11)$$

for some $M \geq m_0$ and any $t > 0$. Notice that the set $Y := C([0, T], \mathcal{M}_{[\alpha, \beta], \gamma, M} \times \mathcal{M}_{[\alpha, \beta], \gamma, M})$ is a closed subset of $C([0, T], \mathcal{M}_{[\alpha, \beta]} \times \mathcal{M}_{[\alpha, \beta]})$, and map $\Lambda(\mu, \nu)_t = (\Lambda^1(\mu, \nu)_t, \Lambda^2(\mu, \nu)_t)$, where $\Lambda^1(\mu, \nu)_t = e^{-t}\mu_0 + \int_0^t e^{r-t}\mathcal{P}(\mu_r, \nu_r)dr$ and $\Lambda^2(\mu, \nu)_t = e^{-At}\nu_0 + A \int_0^t e^{A(r-t)}\mathcal{P}(\mu_r, \nu_r)dr$ is contraction for sufficiently small $T > 0$, whose unique fixed point is $t \mapsto (\mu_t, \nu_t)$. We will show that the set Y is invariant with respect to Λ , i.e., $\Lambda(Y) \subset Y$ for some constant $M > 0$. We calculate

$$\begin{aligned} \int_X |x|^\gamma \Lambda^1(\mu, \nu)_t(dx) &= e^{-t} \int_X |x|^\gamma \mu_0(dx) + \int_0^t e^{r-t} \int_X |x|^\gamma \mathcal{P}(\mu_r, \nu_r)dr \\ &\leq e^{-t} \int_X |x|^\gamma \mu_0(dx) + \int_0^t e^{r-t} \left(C + L \max \left\{ \int_X |x|^\gamma \mu_r(dx), \int_X |x|^\gamma \nu_r(dx) \right\} \right) dr \\ &\leq e^{-t} \int_X |x|^\gamma \mu_0(dx) + \int_0^t e^{r-t} (C + LM) dr \leq M, \end{aligned}$$

for M such big that $C + LM \leq M$. In the same way, we show that $\int_X |x|^\gamma \Lambda^2(\mu, \nu)_t(dx) \leq M$ for some constant $M > 0$. Consequently, orbits are relatively compact. \square

Consider a family $(S(t))_{t \geq 0}$ of transformations on set $\mathcal{M}_{[\alpha, \beta]} \times \mathcal{M}_{[\alpha, \beta]}$ given by the formula $S(t)(\mu_0, \nu_0) = (S_1(t)\mu_0, S_2(t)\nu_0) = (\mu_t, \nu_t)$, where (μ_t, ν_t) is the solution of system (4.1) with initial condition (μ_0, ν_0) . Consider ω -limit set for $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]}$, i.e.,

$$\omega(\mu, \nu) = \left\{ (\bar{\mu}, \bar{\nu}) : (\bar{\mu}, \bar{\nu}) = \lim_{n \rightarrow \infty} (\mu_{t_n}, \nu_{t_n}) \text{ for some sequence } (t_n)_{n \in \mathbb{N}} \text{ s.t. } t_n \rightarrow \infty \right\}.$$

Proof of Theorem 4.1. Take measures $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]} \cap \mathcal{M}_\gamma$. From Lemma 4.6 the orbits $\mathcal{O}(\mu), \mathcal{O}(\nu)$ are relatively compact in $\mathcal{M}_{[\alpha, \beta]}$. Consequently $\omega(\mu, \nu)$ is nonempty and compact set. Moreover, for $t > 0$ $S(t)(\omega(\mu, \nu)) = \omega(\mu, \nu)$. Suppose that $\omega(\mu, \nu)$ has more than one element. Then we can find (μ_1, ν_1) and (μ_2, ν_2) which maximize the function $\max \{d(\mu_1, \mu_2), d(\nu_1, \nu_2)\}$. For any $t > 0$ there exist $(\bar{\mu}_1, \bar{\nu}_1)$ and $(\bar{\mu}_2, \bar{\nu}_2)$ such that $S(t)(\bar{\mu}_1, \bar{\nu}_1) = (\mu_1, \nu_1)$ and $S(t)(\bar{\mu}_2, \bar{\nu}_2) = (\mu_2, \nu_2)$. From condition (i), Lemma 4.4 and Lemma 4.5 we obtain

$$\max \{d(\mu_1, \mu_2), d(\nu_1, \nu_2)\} = \max \{d(S_1(t)(\bar{\mu}_1, \bar{\nu}_1), S_1(t)(\bar{\mu}_2, \bar{\nu}_2)), \\ d(S_2(t)(\bar{\mu}_1, \bar{\nu}_1), S_2(t)(\bar{\mu}_2, \bar{\nu}_2))\} < \max \{d(\bar{\mu}_1, \bar{\mu}_2), d(\bar{\nu}_1, \bar{\nu}_2)\}. \quad (4.12)$$

Inequality (4.12) contradicts the definition of (μ_1, ν_1) and (μ_2, ν_2) . Hence $\omega(\mu, \nu) = \{(\mu^*, \nu^*)\}$, and $S(t)(\mu^*, \nu^*) = (\mu^*, \nu^*)$ for every $t > 0$. Consequently, $\mu^* = \mathcal{P}(\mu^*, \nu^*) = \nu^*$. According to Lemma 4.4 operator \mathcal{P} has only one fixed point (μ^*, μ^*) , so the limit $\lim_{t \rightarrow \infty} S(t)(\mu, \nu)$ does not depend on $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]} \cap \mathcal{M}_\gamma$. Consider now any measures $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]}$. Since the set $\mathcal{M}_{[\alpha, \beta]} \cap \mathcal{M}_\gamma$ is dense in $\mathcal{M}_{[\alpha, \beta]}$, for every $\varepsilon > 0$ there exists $\bar{\mu}, \bar{\nu} \in \mathcal{M}_{[\alpha, \beta]} \cap \mathcal{M}_\gamma$ such that $d(\mu, \bar{\mu}), d(\nu, \bar{\nu}) < \varepsilon$. Since $\lim_{t \rightarrow \infty} S(t)(\bar{\mu}, \bar{\nu}) = (\mu^*, \mu^*)$ there exists t_ε such that $d(S_1(t)(\bar{\mu}, \bar{\nu}), \mu^*) < \varepsilon$ and $d(S_2(t)(\bar{\mu}, \bar{\nu}), \mu^*) < \varepsilon$ for every $t > t_\varepsilon$. Since from Lemma 4.5 $S_1(t)$ are contractions we obtain

$$d(S_1(t)(\mu, \nu), \mu^*) \leq d(S_1(t)(\mu, \nu), S_1(t)(\bar{\mu}, \bar{\nu})) + d(S_1(t)(\bar{\mu}, \bar{\nu}), \mu^*) < 2\varepsilon,$$

and similarly $d(S_2(t)(\mu, \nu), \mu^*) < 2\varepsilon$ for $t > t_\varepsilon$, which completes the proof. \square

4.4. Corollaries and further theorems on stability

We start with investigation on the mean value of the limiting distribution μ^* .

Corollary 4.7. *Under assumptions of Theorem 4.1,*

$$\int_X x \mu^*(dx) = \frac{A \int_X x \mu_0(dx) + \int_X x \nu_0(dy)}{A + 1}. \quad (4.13)$$

Proof. Denote $\bar{x} := \int_X x \mu^*(dx)$, $m(t) := \int_X x \mu_t(dx)$ and $n(t) := \int_X x \nu_t(dx)$. Since $\mu_t, \nu_t \rightarrow \mu^*$ and $\mu_t, \nu_t \in \mathcal{M}_{[\alpha, \beta]}$, we have also $m(t), n(t) \rightarrow \bar{x}$ as $t \rightarrow \infty$. From (4.8) it follows that $\frac{d}{dt}(Am(t) + n(t)) = 0$. Consequently,

$$Am(0) + n(0) = \lim_{t \rightarrow \infty} (Am(t) + n(t)) = (A + 1)\bar{x},$$

which gives formula (4.13). \square

Now we proceed to a result on asymptotic stability of solutions in stronger convergence. The proof of the following result can be adapted from the proof of Theorem 4 in [34].

Corollary 4.8. *Assume that the measure $k(x, y, dz)$ has bounded and continuous density with respect to the Lebesgue measure, and suppose that assumptions of Theorem 4.1 are satisfied. Then the stationary measure μ^* has continuous and bounded density u^* with respect to the Lebesgue measure. Moreover, for every $\mu_0, \nu_0 \in \mathcal{M}_{[\alpha, \beta]}$, corresponding solutions μ_t, ν_t of (4.1) can be written in the form $\mu_t = e^{-t}\mu_0 + \bar{\mu}_t$, $\nu_t = e^{-At}\nu_0 + \bar{\nu}_t$, where $\bar{\mu}_t, \bar{\nu}_t$ are absolute continuous measures with respect to the Lebesgue measure, whose densities are continuous and bounded and converge to u^* uniformly, as $t \rightarrow \infty$.*

Until now, we have studied asymptotic properties of autonomous system (4.1). Now we investigate asymptotic properties of solutions to the initial system (3.9) by comparing them with proper solutions of (4.1). This idea comes from [29], but it differs significantly since our system is nonlinear. Since the dynamical system is no longer autonomous, the following theorem constitutes a new result, which do not belong to the framework of [34].

Theorem 4.9. *Suppose that (3.5) is satisfied and conditions (i), (ii) of Theorem 4.1 hold with $\alpha = \beta$. Then there exists $\mu^* \in \mathcal{M}_{1,\alpha}$ such that for any $\mu_0, \nu_0 \in \mathcal{M}_{1,\alpha}$ coordinates of solution (μ_t, ν_t) of system (3.9) with initial value (μ_0, ν_0) converge to μ^* in $\mathcal{M}_{1,\alpha}$ as $t \rightarrow \infty$.*

Proof. Fix $s \geq 0$ and let (μ_t^1, ν_t^1) and (μ_t^2, ν_t^2) be solutions of (4.1) and (3.9) such that $\mu_s^1 = \mu_s^2 := \mu_s$ and $\nu_s^1 = \nu_s^2 := \nu_s$. Then $\int_X x \mu_t^1(dx) = \int_X x \mu_t^2(dx)$ and $\int_X x \nu_t^1(dx) = \int_X x \nu_t^2(dx)$ for any $t \geq s$, and consequently from (3.9), (4.1) and (4.6) it follows that

$$\begin{cases} e^t d(\mu_t^1, \mu_t^2) < e^s d(\mu_s^1, \mu_s^2) + \int_s^t e^r \max \{d(\nu_r^1, \nu_r^2), d(\mu_r^1, \mu_r^2)\} dr, \\ e^{At} d(\nu_t^1, \nu_t^2) < e^{As} d(\nu_s^1, \nu_s^2) + A \int_s^t e^{Ar} \max \{d(\nu_r^1, \nu_r^2), d(\mu_r^1, \mu_r^2)\} dr + e^{At} G(s, t), \end{cases} \quad (4.14)$$

where

$$G(s, t) := c \left| e^{-\int_s^t A(w)dw} - e^{A(s-t)} \right| + c \int_s^t |A(r) e^{-\int_r^t A(w)dw} - A e^{A(r-t)}| dr$$

and $c > 0$ is a constant such that $d(\nu_r^2, 0), d(\mathcal{P}(\mu_r^2, \nu_r^2), 0) < c$ for every $r > 0$ (such constant c exists, because $\nu_r^2, \mathcal{P}(\mu_r^2, \nu_r^2) \in \mathcal{M}_1$ for every $r > 0$ due to assumption (4.2)).

We divide the interval $[s, \infty)$ into a sequence of subintervals $(I_n)_{n \in \mathbb{N}}$ of lengths $|I_n| \leq 1$ such that the sign of the difference $d(\mu_r^1, \mu_r^2) - d(\nu_r^1, \nu_r^2)$ is fixed for every $r \in I_n$. Fix $n \in \mathbb{N}$. From appropriate inequality from (4.14), by Gronwall lemma we obtain for $s_n, t_n \in I_n$

$$\max \{d(\nu_{t_n}^1, \nu_{t_n}^2), d(\mu_{t_n}^1, \mu_{t_n}^2)\} < \max \{d(\nu_{s_n}^1, \nu_{s_n}^2), d(\mu_{s_n}^1, \mu_{s_n}^2)\} + H(s_n, t_n), \quad (4.15)$$

where $H(s, t) = e^{A(t-s)} G(s, t)$. Notice that for any $s_n, t_n \in I_n$, $s_n \leq t_n$

$$\begin{aligned} H(s_n, t_n) &\leq c \left| e^{-\int_{s_n}^{t_n} (A(w)-A)dw} - 1 \right| + c \int_{s_n}^{t_n} |A(r) - A| dr + cA \int_{s_n}^{t_n} \left| e^{-\int_r^{t_n} (A(w)-A)dw} - 1 \right| dr \\ &\leq 2c \int_{s_n}^{t_n} |A(w) - A| dw + cA \int_{s_n}^{t_n} \int_r^{t_n} |A(w) - A| dw dr \leq C \int_{s_n}^{t_n} |A(w) - A| dw \end{aligned}$$

where $C = c(2 + A)$. Since $\mu_s^1 = \mu_s^2 = \mu_s$ and $\nu_s^1 = \nu_s^2 = \nu_s$, from above inequality and (4.15) we obtain

$$\max \{d(\nu_t^1, \nu_t^2), d(\mu_t^1, \mu_t^2)\} < C \int_s^t |A(w) - A| dw. \quad (4.16)$$

Notice that since $(M(t), F(t))$ converges to (\bar{M}, \bar{F}) exponentially, as $t \rightarrow \infty$, the function $A(t) = M(t)/F(t)$ tends to $A = \bar{M}/\bar{F}$ exponentially as well, i.e., there exists constants $a, b > 0$ such that $|A(t) - A| \leq ae^{-bt}$ for all $t \geq 0$. Fix $\varepsilon > 0$ and take $s > 0$ such that $Ce^{-bs}/b < \varepsilon/4$. Let (μ_t, ν_t) be solution of (3.9) with initial value (μ_0, ν_0) and $(\bar{\mu}_t, \bar{\nu}_t)$ be solution of (4.1) such that $(\bar{\mu}_s, \bar{\nu}_s) = (\mu_s, \nu_s)$. Then for a large enough $t > s$ that $\max \{d(\mu^*, \bar{\mu}_t), d(\mu^*, \bar{\nu}_t)\} \leq \varepsilon/2$, inequality (4.16) implies

$$\begin{aligned} \max \{d(\nu_t, \mu^*), d(\mu_t, \mu^*)\} &< \max \{d(\nu_t, \bar{\nu}_t), d(\mu_t, \bar{\mu}_t)\} + \max \{d(\mu^*, \bar{\mu}_t), d(\mu^*, \bar{\nu}_t)\} \\ &\leq \frac{C}{b} (e^{-bs} - e^{-bt}) + \max \{d(\mu^*, \bar{\mu}_t), d(\mu^*, \bar{\nu}_t)\} \leq \varepsilon, \end{aligned}$$

which completes the proof. \square

Combining Corollary 4.8 and Theorem 4.9, one can deduce the following

Corollary 4.10. *Assume that the measure $k(x, y, dz)$ has bounded and continuous density with respect to the Lebesgue measure and suppose that assumptions of Theorem 4.9 are satisfied. If u_0, v_0 are bounded and continuous densities of initial measures μ_0, ν_0 of solutions μ_t, ν_t to (3.9), then the densities of the measures μ_t, ν_t converge uniformly to continuous and bounded density u^* of stationary measure μ^* , as $t \rightarrow \infty$.*

5. Examples

Following examples come from considerations on hermaphroditic populations (see [34]), however they are also biologically reasonable for the two-sex populations case.

5.1. Inheritance of mean parental trait with additive noise

We suppose that $X = \mathbb{R}$. If $x, y \in \mathbb{R}$ are parental traits, then we suppose that $\frac{x+y}{2} + Z$ is trait of their offspring, where Z is zero-mean random variable distributed with some density h . We assume that $\mathbb{E}Z^2 < \infty$ and $h(z) > 0$ for all $z \in X$. Then the measure $k(x, y, dz)$ has following density

$$\kappa(x, y, z) = h\left(z - \frac{x+y}{2}\right).$$

It is easy to check that $\frac{\partial}{\partial x} \mathcal{K}(x, y, z) = -\frac{1}{2}h\left(z - \frac{x+y}{2}\right)$, and condition (i) from Theorem 4.1 is satisfied if

$$\int_{-\infty}^{\infty} |h(z-a) - h(z-b)| dx < 2$$

for all $a, b \in \mathbb{R}$. The above inequality is valid, since h is probability density function, positive everywhere.

Now we proceed to condition (ii). Fix two measures $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]}$. Then

$$\begin{aligned} \int_{-\infty}^{\infty} z^2 \mathcal{P}(\mu, \nu)(dz) &= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \left(\left(z - \frac{x+y}{2}\right)^2 + \left(z - \frac{x+y}{2}\right)(x+y) + \frac{(x+y)^2}{4} \right) \\ &\quad \times h\left(z - \frac{x+y}{2}\right) \mu(dx) \nu(dy) dz \leq \mathbb{E}Z^2 + \frac{1}{4} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (x+y)^2 \mu(dx) \nu(dy) \\ &= \mathbb{E}Z^2 + \frac{1}{2} \left(\int_{-\infty}^{\infty} x \mu(dx) \right) \left(\int_{-\infty}^{\infty} x \nu(dx) \right) + \frac{1}{2} \max \left\{ \int_{-\infty}^{\infty} x^2 \mu(dx), \int_{-\infty}^{\infty} x^2 \nu(dx) \right\}. \end{aligned}$$

Since μ, ν have their first moments upper-bounded by β , condition (ii) of Theorem 4.1 is satisfied with $\gamma = 2$, $C = \mathbb{E}Z^2 + \frac{1}{2} \max\{\alpha^2, \beta^2\}$ and $L = \frac{1}{2}$. From Theorem 4.1 there exists unique limiting distribution $\mu^* \in \mathcal{M}_{[\alpha, \beta]}$ with first moment (4.13) such that any solution (μ_t, ν_t) to system (4.1) satisfies $\mu_t, \nu_t \rightarrow \mu^*$ in $\mathcal{M}_{[\alpha, \beta]}$. If additionally h is bounded and continuous, limiting measure μ^* has continuous and bounded density u^* and convergence of absolute continuous parts of μ_t, ν_t is uniform by Corollary 4.8. If $\alpha = \beta$ one can also use Theorem 4.9 to conclude asymptotic properties of system (3.9).

It turns out that, in this case of trait inheritance, it is possible to find the limiting distribution μ^* explicitly. The distribution has the form of an infinite measure convolution. In the case when h has 0-mean normal distribution with standard deviation σ , then the limiting distribution is also normal, with mean $\bar{x} = \alpha = \beta$ and standard deviation $\sqrt{2}\sigma$ (see [34]).

5.2. Inheritance of mean parental trait with multiplicative noise

The following example is more reasonable for description of non-negative traits such as average body mass or height. Thus we suppose that $X = [0, \infty)$. If x, y are parental traits, then the trait of offspring is given by $(x + y)Z$, where Z is $[0, 1]$ -valued random variable with mean $\frac{1}{2}$, distributed with density h . Then the density $\kappa(x, y, \cdot)$ of measure $k(x, y, dz)$ has the form

$$\kappa(x, y, z) = \frac{1}{x + y} h\left(\frac{z}{x + y}\right),$$

for $z \in [0, x + y]$, $x + y > 0$ or $\kappa(x, y, z) = 0$ otherwise. Assume that there exists $\varepsilon > 0$ such that support of the function h contains $(0, \varepsilon)$. One can easily compute

$$\frac{\partial}{\partial x} \mathcal{K}(x, y, z) = -h\left(\frac{z}{x + y}\right) \frac{z}{(x + y)^2}.$$

The condition (i) of Theorem 4.1 is equivalent to

$$\int_0^\infty \left| h\left(\frac{z}{a}\right) \frac{z}{a^2} - h\left(\frac{z}{b}\right) \frac{z}{b^2} \right| dz < 1,$$

for all $a, b \in [0, \infty)$. The above inequality is satisfied, since the function h has mean equal to $\frac{1}{2}$, and the interval $(0, \varepsilon)$ is in its support. Now we check condition (ii). Take $\mu, \nu \in \mathcal{M}_{[\alpha, \beta]}$. Then

$$\begin{aligned} \int_0^\infty z^2 \mathcal{P}(\mu, \nu) dz &= \mathbb{E}Z^2 \int_0^\infty \int_0^\infty (x + y)^2 \mu(dx) \nu(dy) \\ &\leq 2\mathbb{E}Z^2 \left(\int_{-\infty}^\infty x \mu(dx) \right) \left(\int_{-\infty}^\infty x \nu(dx) \right) + 2\mathbb{E}Z^2 \max \left\{ \int_{-\infty}^\infty x^2 \mu(dx), \int_{-\infty}^\infty x^2 \nu(dx) \right\}. \end{aligned}$$

Since the first moments of the measures μ, ν are bounded by β and $2\mathbb{E}Z^2 < 2\mathbb{E}Z = 1$, condition (ii) is satisfied with $\gamma = 2$, $C = 2\mathbb{E}Z^2 \max\{\alpha^2, \beta^2\}$ and $L = 2\mathbb{E}Z^2$.

Finally, using Theorem 4.1 (resp. Theorem 4.9 in case $\alpha = \beta$) we conclude that system (4.1) (resp. system (3.9)) has unique globally asymptotically stable stationary distribution (μ^*, μ^*) . Since κ is not bounded even if h is so, we cannot use Corollary 4.8. Nonetheless, one can show convergence of densities in L^1 space, as $t \rightarrow \infty$ (see [34]).

6. Conclusions

In the paper we introduced some individual-based model in order to describe the evolution of non-sex-like phenotypic traits in two-sex populations. The model includes semi-random mating of individuals of the opposite sex, natural death and intra-specific competition. Having passed the number of individuals to infinity, we derived the macroscopic system of equations for evolution of trait distributions. The main results of the investigation on solutions of the system are: existence and uniqueness of solutions in space of measures, study of total numbers of males and females in order to derive criteria for persistence or extinction, formulation of the conditions implying existence of the unique stable distribution and its asymptotic stability. Moreover, under additional assumptions, we studied the existence and asymptotic properties of solutions from the standpoint of their densities.

Now we interpret some of the results in biological language. We start with inequalities (3.5) and (3.6). If we consider the numbers $\alpha_m = p_m/D_m$ and $\alpha_f = p_f/D_f$ as an environmental adaptation of males and females, then (3.5) implies that the mean environmental adaptation in population is greater than one. On average, one dying individual is replaced by more than one newborn, and consequently whole the population persists. The opposite inequality (3.6) leads to extinction of both subpopulations. A possible scenario assumes that one of the numbers α_m, α_f is strictly smaller than 1. Despite this, it is still possible

that (3.5) holds. It means, that the whole population can survive, although one of the subpopulations has smaller mating rate. In particular, if we take $p_m = 0$, then populations with minor male mating rates are also covered by our model. In that case the growth of the population depends on female mating and death rates, and inequality $p_f/D_f > 2$ means that the population persists.

The existence and asymptotic stability of the stable distribution μ^* , and the fact that this distribution is the same for both male and female populations is an intuitive consequence of Fisher's principle and inheritance of traits which are non-sex-linked. The result suggests that after a long time two-sex populations behave as they were hermaphroditic, provided we investigate only the evolution of non-sex-linked traits. This result enlarges the area of applications of the hermaphroditic model derived and studied in [34] also to two-sex populations. Notice that the paces of convergence to stationary distribution may differ between males and females, due to the dependence on the function $A(t)$ and its limit A .

The future perspectives for the model presented in the paper are multidirectional. The most interesting issue would be to study analogous model including assortative mating of individuals with aid of trait-dependent marriage functions instead of semi-random mating (see e.g. [16,37]). Marriage functions reflect preferences for possible partners in the population and influence the shape of the trait distribution. The long-time behavior of the corresponding macroscopic equations could answer how big this influence is in stable population, and what shape of limiting distribution we should expect. Since in that case trait distributions also satisfy similar transport equations (such as (4.1) with some nonlinear operator \mathcal{P} describing assortative mating), one can expect that if the distributions converge to a stationary point, then the limiting distributions should be identical for males and females. This is again due to the Fisher principle. On the other hand, if the distributions do not stabilize, they can possibly exhibit other behavior than approaching each other. Another issue is to study how trait values of individuals affect their fitness. Since in general our model allows to include trait-dependent rates, it would be interesting to study long-time behavior of corresponding solutions in case when there are two different fitness optima for males and females (see e.g. [5]).

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