

## About a non-parametric model of bisexual population dynamics

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### Abstract

In current publication non-parametric model (model of Kolmogorov's type) is analyzed. It is assumed that birth rates in population depend on relation between males and females, and death rates depend on total size of population. For conditions of pure qualitative type for birth and death rates possible dynamic regimes are determined.

**Key words:** model of population dynamics, sexual structure, dynamic regimes

### Introduction

Sex structure plays extremely important role in population dynamics (see, for example, Geodakjan, 1965, 1981, 1991). We have to take into account existence of this structure analyzing epidemiological situations with sexually-transmit diseases, some methods of population size management are based on input of sterile individuals into the system etc. (Iannelli, Martcheva, Milner, 2005; Nedorezov, 1978, 1979, 1983, 1986). Thus, constructing and testing of mathematical models of bi-sexual population dynamics are among very actual problems of modern modeling.

In 1949 Kendall gave a description of model of population dynamics which contains individuals of two types:  $F(t)$  and  $M(t)$  are the numbers of females and males in population at moment  $t$ ,

$$\begin{aligned}\frac{dF}{dt} &= -\mu F + \frac{1}{2} B(F, M) = P(F, M), \\ \frac{dM}{dt} &= -\mu M + \frac{1}{2} B(F, M) = Q(F, M).\end{aligned}\tag{1}$$

In model (1) coefficient  $\mu$  is an intensity of death rate (Malthusian parameter),  $\mu = \text{const} > 0$ , and function  $B(F, M)$  describes a reproduction process:

$$\begin{aligned}\forall (F, M) \in R_+^2 \quad B(F, M) \geq 0, \quad B(0, M) = B(F, 0) = 0, \\ \frac{\partial B}{\partial F} > 0, \quad \frac{\partial B}{\partial M} > 0 \quad \text{for } F, M > 0.\end{aligned}\tag{2}$$

In (2)  $R_+^2 = \{(F, M) : F \geq 0, M \geq 0\}$ . Conditions (2) are obvious: if number of males or females is equal to zero we have no reasons to talk about production process; increase of number of males or females leads to increase of the respective rates.

Model (1)-(2) has the following properties. If  $F(0) = 0$  or  $M(0) = 0$  then for all  $t > 0$  we have  $F(t) \equiv 0$  or  $G(t) \equiv 0$  respectively. At the same time other variable decreases monotonously. It means that origin is locally stable knot. Taking into account that

$$\frac{\partial P}{\partial M} = \frac{1}{2} \frac{\partial B}{\partial M} > 0, \quad \frac{\partial Q}{\partial F} = \frac{1}{2} \frac{\partial B}{\partial F} > 0,$$

we get that isocline of vertical inclines  $P = 0$  is univocal with respect to  $F$ ; isocline of horizontal inclines  $Q = 0$  is univocal with respect to  $M$ .

Difference of equations (2) gives the following relation:

$$\frac{d(F - M)}{dt} = -\mu(F - M).$$

Thus, for initial values  $F(0) = F_0, M(0) = M_0$  we have

$$F(t) - M(t) = (F_0 - M_0)e^{-\mu t}.$$

It means that within the framework of model (1)-(2) initial difference between females and males converges to zero asymptotically. If  $F_0 = M_0$  then for all  $t > 0$  we have  $F(t) \equiv M(t)$ .

For the situation when  $F_0 = M_0$  and interaction between males and females has a pure stochastic nature,  $B(F, M) = FM$ , we have the following equation:

$$\frac{dF}{dt} = -\mu F + \frac{1}{2} F^2.$$

This equation has two stationary states: stable point  $F_1 = 0$  and unstable point  $F_2 = 2\mu$ . If  $F_0 < F_2$  then population degenerates asymptotically,  $F(t) \rightarrow 0$  when  $t \rightarrow \infty$ . If we have the inverse inequality,  $F_0 > F_2$ , then population size becomes equal to infinity during the finite time  $t^*$ :

$$F(t) = \frac{2\mu}{1 - Ce^{\mu t}}, \quad C = \frac{F_0 - 2\mu}{F_0}, \quad t^* = \frac{1}{\mu} \ln \left( \frac{F_0}{F_0 - 2\mu} \right).$$

If we don't want to have such dynamical effect within the framework of considering model when model can be applied to the description of population dynamics during finite time interval, we can assume, for example, that birth rate  $B(F, M)$  is a linear function of population size (Kendall, 1949). But it looks more productive the following way: it is obvious that birth rate cannot increase up to plus infinity if number of males increases unboundedly at fixed value of females; it means that the following relation is truthful:

$$\lim_{M \rightarrow \infty} B(F, M) = aF, \quad a = \text{const} > 0.$$

It means that limit value of birth rate depends on number of females and coefficient  $a$  which characterizes maximum properties of females. The following relation must be truthful too: for fixed value of number of males unlimited increasing of females gives the following result:

$$\lim_{F \rightarrow \infty} B(F, M) = cM, \quad c = \text{const} > 0.$$

In this relation parameter  $c$  characterizes maximum possibilities of males. In most primitive case function  $B(F, M)$  can be presented in the form:

$$B(F, M) = \frac{acFM}{1 + cM + aF}. \quad (3)$$

For particular case  $F_0 = M_0$  model (1)-(2) with function (3) has the form:

$$\frac{dF}{dt} = -\mu F + \frac{g_1 F^2}{1 + g_2 F}. \quad (4)$$

In (4)  $g_1 = ac/2 = \text{const} > 0$ ,  $g_2 = a + c = \text{const} > 0$ . Equation (4) is particular case of well-known Bazykin' model (Bazykin, 1969, 1985) when self-regulation in population doesn't exist ( $\mu = \text{const} > 0$ ). Model (4) has following properties: origin is stable equilibrium for all values of parameters. If the following inequality is truthful

$$g_1 > \mu g_2 \quad (5)$$

model (4) has non-trivial stationary state:

$$\bar{F} = \frac{\mu}{g_1 - \mu g_2}.$$

Thus, if inequality (5) isn't truthful origin is global stable equilibrium, and population eliminates for all initial values of variable. If inequality (5) is truthful population eliminates if  $F_0 < \bar{F}$ ; if  $F_0 > \bar{F}$  population size goes to plus infinity. Within the framework of Bazykin' model (Bazykin, 1969, 1985) when  $\mu$  is a positive linear monotonous increasing function on  $F$ , population size cannot increase unboundedly and stabilizes at non-zero level.

In publications by L. Ginzburg and G. Yuzefovich (1968) and Gimelfarb A. et al. (1974) problems of the dynamics of sexes in bisexual population were analyzed:

$$\frac{dM}{dt} = \alpha F - \beta M, \quad \frac{dF}{dt} = (\gamma - \delta)F. \quad (6)$$

Within the framework of model (6) it is assumed that all coefficients are constant,  $\alpha, \beta, \gamma, \delta = \text{const} > 0$ . It is obvious if inequality  $\gamma < \delta$  is truthful number of females in population

converges to zero for all non-negative initial values. Thus, population asymptotically eliminates. If  $\gamma > \delta$  number of females increases exponentially (to plus infinity).

Modification of model (6) for the situation when intra-population self-regulative mechanisms are taken into account gives the following system of differential equations:

$$\frac{dM}{dt} = \alpha F - \beta M - \varepsilon(F + M)M, \quad \frac{dF}{dt} = (\gamma - \delta)F - \omega(F + M)F. \quad (7)$$

In (7) coefficients of self-regulation are constants,  $\varepsilon, \omega = const > 0$ . Model (7) has the following properties. There exists stable invariant compact  $\Delta$  in non-negative part of phase plane:

$$\Delta = \left[0, \frac{\alpha}{\varepsilon}\right] \times \left[0, \frac{\gamma - \delta}{\omega}\right].$$

If  $(M_0, F_0) \in \Delta$  then for all  $t > 0$  we have  $(M(t), F(t)) \in \Delta$ . Origin is a saddle point: axe  $M$  is incoming separatrix. If  $F_0 = 0$  then population eliminates for all  $M_0 \geq 0$ . Isocline of horizontal inclines contains two branches which are determined by the following equations:

$$F = 0, \quad F + M = \frac{\gamma - \delta}{\omega}.$$

Isocline of vertical inclines is monotonic increasing function:

$$F = \frac{\beta M + \varepsilon M^2}{\alpha - \varepsilon M}.$$

This function intersects origin and has asymptote  $M = \alpha / \varepsilon$ . Dulac criterion (Andronov, Vitt, Khykin, 1959) with function  $1/F$  shows that there are no limit cycles in  $\{(M, F) : M \geq 0, F > 0\}$ . It means that within the framework of model (7) there no periodic fluctuations of population size, and for all initial values  $F_0 > 0$  sizes of both sexes asymptotically stabilize at one stationary level.

*Remark.* Some of problems of model (1)-(2) were pointed out above. But it is important to point out one additional problem of models of (1)-(2) type. For every fixed values of model variables  $F$  and  $M$  we have fixed value of function  $B$  that means that we have fixed value of pregnant females. This property of model doesn't correspond to reality, and number of pregnant females can vary from zero up to  $F(t)$ . Respectively, for every fixed values of model variables  $F$  and  $M$  we have to have a certain variety of values of function  $B$ . This problem can be solved in one way only if we have one or more additional variables which described dynamics of pregnant females, number of existing families etc. (Nedorezov, 1979, 1986).

Further development of this scientific direction was connected with analysis of changing of population size at input of sterile males into the system (see, for example, Bazykin, 1967; Alexeev, Ginzburg, 1969; Brezhnev, Ginzburg, 1974; Brezhnev et al., 1975; Nedorezov, 1979, 1983, 1986),

with constructing and analysis of models which contain three or more variables (families, pregnant females, sex-age structures etc.; Kendall, 1949; Goodman, 1953, 1967; Pollard, 1973; Yellin, Samuelson, 1974, 1977; Nedorezov, 1979, 1986; Hadelers, Waldstatter, Worz-Busekros, 1988; Hadelers, Ngoma, 1990; Hadelers, 1992, 1993; Pertsev, 2000; Iannelli, Martcheva, Milner, 2005 and others). L. Ginzburg (1969) analyzed model of predator-prey system dynamics in a situation when individuals in interacting populations were divided into two sexes. In publications by L.V. Nedorezov and Yu.V. Utyupin (2003, 2011) continuous-discrete model (system of ordinary differential equations with impulses) of bisexual population dynamics was analyzed. In several publications discrete models (models with discrete time) of bisexual population dynamics were constructed and analyzed (Hadelers, Waldstatter, Worz-Busekros, 1988; Hadelers, Ngoma, 1990; Hadelers, 1992, 1993; Castillo-Chaves et al., 2002).

In current publication we analyze non-parametric (model of Kolmogorov' type) model of bisexual population dynamics. Within the framework of model we don't assume that there are the equivalence for birth rates and death rates. In model there are two basic assumptions: self-regulation depends on total population size, and birth rates depend on relation between males and females.

### Description of model

Let  $M(t)$  be a number of males in population at moment  $t$ ,  $F(t)$  be a number of females in population at the same time moment. Let  $L_1(N)$  and  $L_2(N)$  are intensities of death rates for males and females respectively,  $N(t) = M(t) + F(t)$  is a total population size. It is obvious that these functions must be positive for all values of their arguments (it follows directly from the biological sense of these functions). Like in previous models we'll assume that following conditions are truthful for both functions:

$$L_j(0) > 0, L_j(+\infty) = +\infty, \frac{dL_j}{dN} > 0, j = 1,2. \quad (8)$$

Let  $S_1(M, F)$  and  $S_2(M, F)$  are the intensities of birth process of males and females respectively. Thus,  $S_1(M, F)F$  is a speed of increasing of number of males in population;  $S_2(M, F)F$  is a speed of increasing of number of females in population.

It is naturally to assume that intensities  $S_j(M, F) \geq 0$ ,  $j = 1,2$ , are non-negative for all values of their arguments, and these intensities are equal to zero if number of males in population is equal to zero:

$$S_1(0, F) = S_2(0, F) = 0. \quad (9)$$

For all values of males and females intensities  $S_j(M, F)$  are bounded by any constants:

$$S_j(M, F) \leq K_j = \text{const} < \infty, \quad j = 1, 2. \quad (10)$$

Intensities  $S_j(M, F)$  increase with increase of males (it is obvious that increase of males leads to increase of number of pregnant females), and decrease with increase of females in population (increase of females in population at fixed number of males leads to decrease of average number of pregnant females). Thus, the following inequalities are truthful:

$$\frac{\partial S_j}{\partial M} > 0, \quad \frac{\partial S_j}{\partial F} < 0, \quad j = 1, 2. \quad (11)$$

In particular case it is possible to assume that  $S_j(M, F) = S_j(\gamma M - F) = S_j(\theta)$  with the following property:  $dS_j(\theta)/d\theta > 0$ . Parameter  $\gamma > 0$  characterizes potential possibilities of males.

Like in (1), dynamics of population we'll described with following system of differential equations:

$$\frac{dM}{dt} = S_1(M, F)F - L_1(N)M, \quad \frac{dF}{dt} = S_2(M, F)F - L_2(N)F. \quad (12)$$

### Some properties of model (8)-(12)

1. If  $F_0 = F(0) = 0$  then for all  $t > 0$  we have  $F(t) \equiv 0$ . In this situation dynamics of males is described by the first equation of system (12):

$$\frac{dM}{dt} = -L_1(M)M.$$

From conditions (8) we obtain that  $M(t) \rightarrow 0$  at  $t \rightarrow \infty$ . Respectively, if  $M_0 = M(0) = 0$  from conditions (9) we obtain that for all  $t > 0$  we have  $M(t) \equiv 0$ . In this situation dynamics of females is described by the second equation of system (12):

$$\frac{dF}{dt} = -L_2(F)F.$$

From conditions (8) we obtain that  $F(t) \rightarrow 0$  at  $t \rightarrow \infty$ . Thus, origin is a stable knot, and for all non-negative initial values of variables trajectories of system (12) cannot intersect boundaries of the first quadrant (coordinate lines are integral sets of the system). There are no other stationary states of considering system in finite part of phase plane.

2. From the second equation of system (12) we can obtain that for all  $t > 0$  variable  $F(t) \leq F^*$  if initial value  $F(0) \leq F^*$  where  $F^*$  is solution of algebraic equation

$$K_2 - L_2(F)F = 0.$$

From conditions (8) we obtain that this solution  $F^*$  exists and unique. Note, that for all  $F > F^*$  speed  $dF/dt$  is negative. For the first variable  $M(t)$  we have the similar property: if  $M(0) \leq M^*$  then for all  $t > 0$  variable  $M(t) \leq M^*$  where  $M^*$  is solution of algebraic equation

$$K_1 F^* - L_1(M)M = 0.$$

From conditions (8) we obtain that this solution  $M^*$  exists and unique. For all  $M > M^*$  speed  $dM/dt$  is negative. Thus, there exists stable invariant compact  $\Delta$  on the phase plane:

$$\Delta = [0, M^*] \times [0, F^*].$$

We can conclude that solutions of system (12) are bounded and exist for all  $t > 0$ .

3. Isocline of horizontal inclines of trajectories contains two branches:  $F = 0$  and

$$Q = S_2(M, F) - L_2(N) = 0.$$

From conditions (8) and (11) we obtain that

$$\frac{\partial Q}{\partial F} = \frac{\partial S_2}{\partial F} - \frac{dL_2}{dN} < 0.$$

Thus,  $Q = 0$  is a single-valued function with respect to  $M$ . If  $K_2 < L_2(0)$  (sufficient condition) then population eliminates for all initial values, and origin becomes a global stable state.

4. Isocline of vertical inclines consists of two branches too:  $M = 0$  and

$$P = \frac{F}{M} S_1(M, F) - L_1(N) = 0. \tag{13}$$

Conditions (8)-(11) don't allow presenting important conclusion about behavior of function (13). Thus, we have to use additional limits. For example, it is naturally to assume that intensity of birth rate increases slower than  $M$ :

$$\frac{\partial}{\partial M} \left( \frac{S_1}{M} \right) < 0. \tag{14}$$

With inequality (14) function (13) has the following property:

$$\frac{\partial P}{\partial M} = F \frac{\partial}{\partial M} \left( \frac{S_1}{M} \right) - \frac{dL_1}{dN} < 0.$$

Thus,  $P = 0$  is a single-valued function with respect to  $F$ .

5. Use of Dulac criterion (Andronov, Vitt, Khykin, 1959) with function  $1/(MF)$  shows that there are no limit cycles in positive part of phase plane. Note, that inequality (14) is sufficient condition for absence of cyclic fluctuations in system. Respectively, the inverse inequality in (14) is necessary condition for existence of population size changing in time.

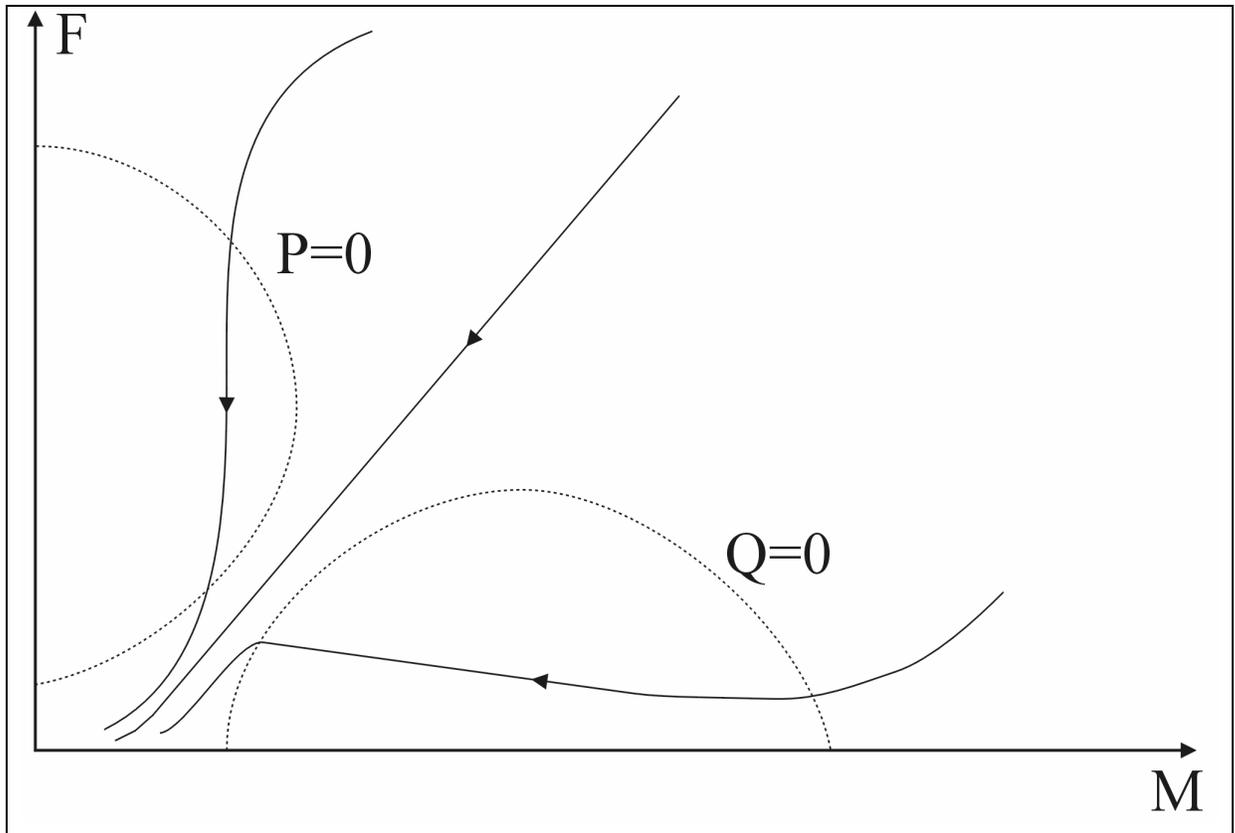
**Dynamical regimes**

If we have a parametric model (model of Volterra type) we have the following main goal: we have to present a structure of a space of model parameters and to point out dynamical regimes which correspond to each part of space of parameters. When we have a non-parametric model (model of Kolmogorov type) we have other main goal: in a result of analysis we have to present dynamical regimes which can be realized in model in principle, and their realization not in a contradiction with considering restrictions on the types of functions in right-hand sides of equations. Below we'll consider some simplest dynamic regimes of model (12) – restrictions (8)-(11) and (14) don't allow presenting all dynamic regimes.

1. If algebraic system

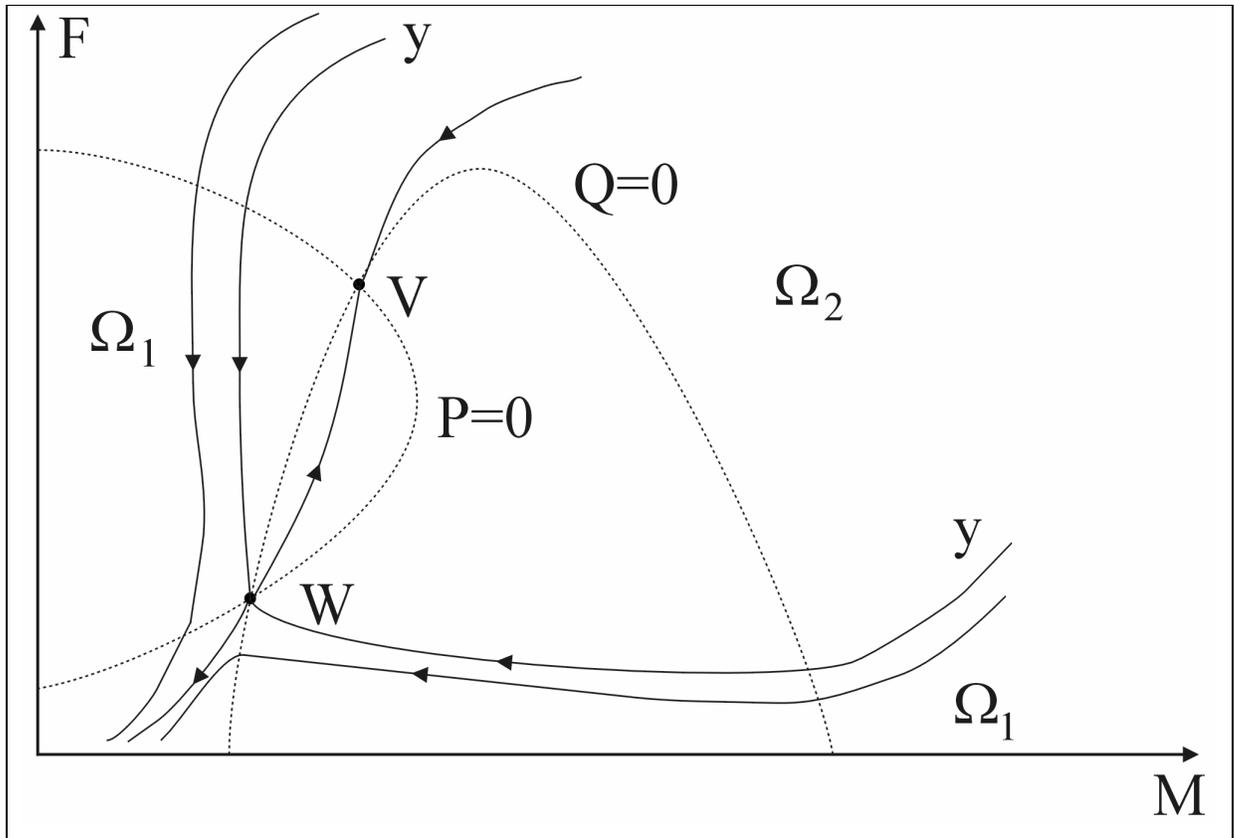
$$S_1(M, F)F - L_1(N)M = 0, S_2(M, F) - L_2(N) = 0 \tag{15}$$

has no solutions in positive part of phase plane, origin is global stable equilibrium. Population eliminates for all non-negative finite initial values (fig. 1).



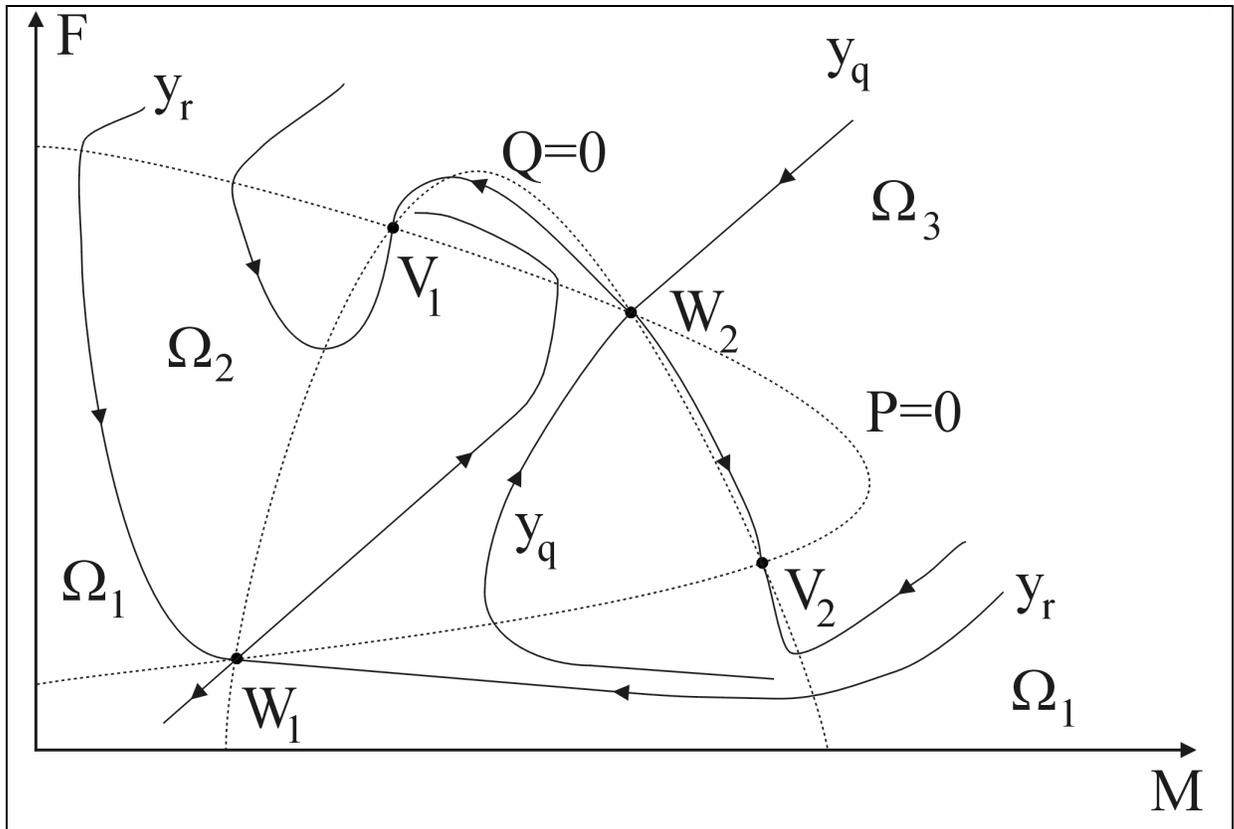
**Fig. 1.** Regime of population elimination for all initial values of variables.  $P = 0$  and  $Q = 0$  are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

2. If algebraic system (15) has two solutions in positive part of phase plane the trigger regime is realized for population: there are two stable attractors on phase plane (fig. 2). Incoming separatrix  $y$  of saddle point  $W$  divides zones of attraction of origin and stable equilibrium  $V$ . If initial sizes of sexes are rather small (within the limits of zone of elimination  $\Omega_1$ ; fig. 2) population eliminates asymptotically. If initial values belong to another zone (zone of stabilization  $\Omega_2$ ) sizes of both sexes stabilize asymptotically at unique level.



**Fig. 2.** Trigger regime of population dynamics.  $V$  is stable stationary state.  $W$  is saddle point.  $y$  is incoming separatrix of saddle point  $W$ .  $\Omega_1$  is zone of population elimination;  $\Omega_2$  is zone of population stabilization.  $P = 0$  and  $Q = 0$  are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

3. In general case within the limits of model (12) dynamic regimes with several stationary states in positive part of phase plane can be realized (see, for example, fig. 3). When difference between total numbers of sizes which correspond to various stable stationary states are rather big, it can be considered as direct analog of the regime of fixed outbreak (Isaev, Nedorezov, Khlebopros, 1978, 1980; Isaev et al., 1984, 2001).



**Fig. 3.** Dynamical regime with three stable attractors: origin,  $V_1$ , and  $V_2$ .  $y_r$  is incoming separatrix of saddle point  $W_1$ , boundary of attraction zone of origin.  $y_q$  is incoming separatrix of saddle point  $W_2$ , boundary of attraction zones of  $V_1$ , and  $V_2$ .  $\Omega_1$  is zone of population elimination (attraction zone of origin);  $\Omega_2$  is zone of population stabilization at point  $V_1$ ;  $\Omega_3$  is zone of population stabilization at point  $V_2$ .  $P=0$  and  $Q=0$  are the main isoclines of vertical and horizontal inclines of model trajectories respectively.

### Conclusion

Analysis of model of bisexual population dynamics shows that in general case dynamic regimes with several non-trivial stationary states can be observed for the system. It means that changing of sizes of sexes (under the influence of various management methods) can lead as to transaction of system from one stable level to another one, as to elimination of population. Existence of several stable levels in positive part of phase plane can be a reason of unstable behavior of system in zone of stability (Isaev, Nedorezov, Khlebopros, 1978, 1980).

As it was pointed out above two-dimensional models of bisexual population dynamics have serious problems and need in modifications. It can be achieved introducing additional variables (for number of sexual pairs or families, number of pregnant females etc.; Kendall, 1949; Goodman, 1953, 1967; Pollard, 1973; Yellin, Samuelson, 1974, 1977; Nedorezov, 1979, 1986; Iannelli,

Martcheva, Milner, 2005), or taking account that death and birth processes have different nature (birth process may have a discrete nature; Nedorezov, Utyupin, 2003, 2011) and so on.

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