

NONLINEAR MATING MODELS FOR POPULATIONS WITH NON-OVERLAPPING GENERATIONS

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**NONLINEAR MATING MODELS FOR
POPULATIONS WITH NON-OVERLAPPING
GENERATIONS**

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extensions will be published elsewhere.

1 Introduction

The discrete-time analogue of the Malthus model is given by

$$P(t+1) = \lambda P(t), \quad P(0) = P_0, \quad (DM)$$

where $P(t)$ is the population at generation t and λ is the multiplicative growth factor per generation [27, 29-31]. Hence, for the initial population size $P_0 > 0$ the model predicts unbounded geometric growth if $\lambda > 1$; geometric decline to extinction if $\lambda < 1$; and no growth ($P(t) = P_0$) if $\lambda = 1$.

Two-sex models with various mating strategies have been developed but mostly at the level of the gene (see Crow and Kimura [9]). Developing useful mating models at the level of the individual has proved difficult. Nevertheless, successful first-level approaches have been developed for continuous-time models by Kendall [23], Keyfitz [24], McFarland [32], Fredrickson [10], Pollard [35], Hoppensteadt [18], and more recently by Castillo-Chavez *et al.* [1-7], Caswell [8], Haderer *et al.* [12-17], Hsu [19-22], Martcheva [28]; to name a few). Analogue stochastic pair-formation models have also been developed (see Luo *et al.* [26]).

In this article we extend the continuous-time pair formation models of Kendall [23], Keyfitz [24], Fredrickson [10], Pollard [35] and Haderer *et al.* [12-17] to populations with discrete non-overlapping generations. This discrete-time pair-formation model is capable of supporting geometric solutions, and hence, it can be extended to heterogeneous mixing populations that support stable pair distributions (see Castillo-Chavez *et al.* [5,6], Luo *et al.* [26]).

The paper is organized as follows: Section 2 introduces the basic two-sex discrete-time model with non-overlapping generations; Section 3 explores the possibilities of constant solutions, sets conditions for the existence of geometric solutions, and, establishes conditions for the stability of geometric solutions; Section 4 gives an illustrative example; Section 5 discusses some of the implications of our work.

2 Homogeneous Discrete-Time Pair-Formation Model

At generation t , we let $x(t)$ denote the population size of single females; $y(t)$ denote the population size of single males; $p(t)$ denote the population size of pairs (couples); $p_x(t)$ denote the population size of coupled females; and $p_y(t)$ denote the population size of coupled males. We further assume sequential monogamy, that is, $p(t) = p_x(t) = p_y(t)$. Hence, the total population size at generation t , $T(t)$, is given by $T(t) \equiv x(t) + y(t) + 2p(t)$. The model is built assuming an implicit sequential process which is typical of many discrete-time models (see Caswell [8]) but not essential. Hence, it is assumed that survival of females (μ_x), males (μ_y) or pairs ($\mu_x\mu_y$) is required before reproduction, pair-formation, and pair-dissolution ($0 \leq \mu_x, \mu_y \leq 1$). At the end of each generation, new females [respectively, males] are born, from surviving pairs, at the per-capita production rate of β_x [respectively, β_y] per generation; the fraction $(1 - \mu_x)$ [respectively, $(1 - \mu_y)$] of females [respectively, males] are removed (death or retirement from mating activities); and, it is assumed that couples separate independently with probability $(1 - \sigma)$.

The populations of single females and single males increase by the death

of a partner (widows become single), separation of couples (“divorcees” become single) or birth (delay in recruitment is not assumed). Individuals are removed from the single classes by mating (pair-formation), pair-dissolution, or death. The functions $G : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, 1]$ and $H : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, 1]$ denote the state-dependent probability functions that model the likelihood of not having a successful interaction (that is, an interaction that results in the creation of a heterosexual pair) given that you had a contact with a potential partner, that is, a single female (if you are a male) or a single male (if you are a female). Hence, G and H are functions of the population vectors at generation t , $(x(t), y(t), p(t))$. The pair-formation (marriage) function, a function of the population vectors $(x(t), y(t), p(t))$, is denoted by $\phi : [0, \infty) \times [0, \infty) \times [0, \infty) \rightarrow [0, \infty)$. Fredrickson [10], Hadelar et al.[12-17], Kendall [23], Keyfitz [24], McFarland [32] and Pollard [35] have proposed various functional forms of ϕ that satisfy the following properties (and a few more) for all $(x(t), y(t), p(t)) \in [0, \infty) \times [0, \infty) \times [0, \infty)$; $u(t), v(t), w(t) \geq 0$; and $k \in [0, \infty)$:

(i)

$$\phi(x(t), y(t), p(t)) \geq 0,$$

(ii)

$$\phi(x(t)+u(t), y(t)+v(t), p(t)+w(t)) \geq \phi(x(t), y(t), p(t)), \text{ for } u(t), v(t), w(t) \geq 0,$$

(iii)

$$\phi(kx(t), ky(t), kp(t)) = k\phi(x(t), y(t), p(t)),$$

(iv)

$$\phi(x(t), 0, p(t)) = \phi(0, y(t), p(t)) = 0.$$

We assume that at least properties (i), (ii) and (iii) for ϕ are satisfied throughout. Our assumptions and definitions lead to the following discrete-time pair-formation nonlinear homogeneous model:

$$\left. \begin{aligned} x(t+1) &= (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p(t) + \mu_x x(t) G(x(t), y(t), p(t)), \\ y(t+1) &= (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p(t) + \mu_y y(t) H(x(t), y(t), p(t)), \\ p_x(t+1) &= \sigma \mu_x \mu_y p(t) + \mu_x x(t) (1 - G(x(t), y(t), p(t))), \\ p_y(t+1) &= \sigma \mu_x \mu_y p(t) + \mu_y y(t) (1 - H(x(t), y(t), p(t))), \end{aligned} \right\} (1)$$

where $p(t+1) = p_x(t+1) = p_y(t+1)$, in other words, the last equation is redundant. We will have sequential monogamy only if the total rates of pair-formation of males and females per-generation match. Hence, we assume throughout that

$$\mu_x x(t) (1 - G(x(t), y(t), p(t))) = \mu_y y(t) (1 - H(x(t), y(t), p(t))) \equiv \phi(x(t), y(t), p(t)). \quad (*)$$

Property (*) implies that the specification of the probability function G prescribes H and ϕ implicitly, provided that steps are taken to guarantee that $0 \leq H(x(t), y(t), p(t)) \leq 1$, otherwise the system may exhibit negative solutions (a “negative” number of pairs in at least some generations).

From System (1), with both $0 \leq G(x(t), y(t), p(t)) \leq 1$ and $0 \leq H(x(t), y(t), p(t)) \leq 1$, one sees that $T(t)$ obeys the equation

$$T(t+1) = (\beta_x \mu_x \mu_y + \beta_y \mu_y \mu_x + \mu_x + \mu_y) p(t) + \mu_x x(t) + \mu_y y(t).$$

Hence, whenever the females and males have the same survival probability [that is, if $\mu = \mu_x = \mu_y$] $T(t)$ satisfy

$$T(t+1) \equiv (\beta_x + \beta_y) \mu^2 p(t) + \mu T(t),$$

that is, individuals either die or survive and reproduce.

If the probability function $G(x(t), y(t), p(t))$ is given, then

$$H(x(t), y(t), p(t)) = 1 - \frac{\mu_x x(t)(1 - G(x(t), y(t), p(t)))}{\mu_y y(t)},$$

and

$$\phi(x(t), y(t), p(t)) = \mu_x x(t)(1 - G(x(t), y(t), p(t))).$$

Since $0 \leq H(x(t), y(t), p(t)) \leq 1$ solutions $(x(t), y(t), p(t))$ must belong to the set

$$\Omega := \{(x(t), y(t), p(t)) \mid 0 \leq \frac{x(t)}{y(t)} \leq \frac{\mu_y}{\mu_x(1 - G(x(t), y(t), p(t)))}\}.$$

The homogeneity assumption implies that Ω is positively invariant on the set of geometric solutions of System (1) with initial conditions in Ω .

If for example

$$G(x(t), y(t), p(t)) = \frac{p(t)}{\epsilon x(t) + y(t) + p(t)}$$

where the constant $\epsilon \in [0, 1]$, is a measure of interference competition between females, then

$$H(x(t), y(t), p(t)) = 1 - \frac{\mu_x x(t)(\epsilon x(t) + y(t))}{\mu_y y(t)(\epsilon x(t) + y(t) + p(t))} \text{ and}$$

$$\phi(x(t), y(t), p(t)) \equiv \frac{\mu_x x(t)(\epsilon x(t) + y(t))}{\epsilon x(t) + y(t) + p(t)},$$

provided $(x(t), y(t), p(t))$ belong to the set

$$\Omega := \{(x(t), y(t), p(t)) \mid 0 \leq \frac{x(t)}{y(t)} \leq \frac{\mu_y(\epsilon x(t) + y(t) + p(t))}{\mu_x(\epsilon x(t) + y(t))}\}.$$

3 Results

If we let $(x(t), y(t), p(t)) = (x, y, p)$ in \mathbb{R}_+^3 , then the reproduction function of System (1) is given by the map $F : \mathbb{R}_+^3 \rightarrow \mathbb{R}_+^3$ defined by $F(x, y, p) =$

$$\begin{bmatrix} (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p + \mu_x x G(x, y, p) \\ (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p + \mu_y y H(x, y, p) \\ \sigma \mu_x \mu_y p + \mu_x x (1 - G(x, y, p)) \end{bmatrix},$$

where $1 - G(x, y, p) \geq 0$. F^t is the map F composed with itself t times, and $F_i^t(x, y, p)$ is the i^{th} component of F^t evaluated at the point (x, y, p) . Therefore, F^t gives the population densities in generation t . The set of iterates of the map F is therefore equivalent to the set of all density sequences generated by System (1).

The fixed points of F satisfy the equation $F(x, y, p) = (x, y, p)$. That is,

$$(\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p - x + \mu_x x G(x, y, p) = 0 \quad (2)$$

$$(\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p - y + \mu_y y H(x, y, p) = 0 \quad (3)$$

$$-p + \sigma \mu_x \mu_y p + \mu_x x - \mu_x x G(x, y, p) = 0 \quad (4)$$

Using Equation (2), (3) and (4) and the fact that $\mu_x x(t)(1 - G(x(t), y(t), p(t))) = \mu_y y(t)(1 - H(x(t), y(t), p(t)))$ leads to

$$\left. \begin{aligned} \frac{x}{p} &= \frac{\beta_x \mu_x \mu_y + \mu_x - 1}{1 - \mu_x}, \\ \frac{y}{p} &= \frac{\beta_y \mu_y \mu_x + \mu_y - 1}{1 - \mu_y}. \end{aligned} \right\} (5)$$

Equation (4) implies that $\phi(x, y, p) = p(1 - \sigma \mu_x \mu_y)$. System (5) and the homogeneity condition on ϕ imply that

$$(1 - \sigma \mu_x \mu_y) p = p \phi \left(\frac{\beta_x \mu_x \mu_y + \mu_x - 1}{1 - \mu_x}, \frac{\beta_y \mu_y \mu_x + \mu_y - 1}{1 - \mu_y}, 1 \right). \quad (6)$$

Parameters in System (1) are not likely to satisfy Equation (6). Hence constant solutions are not generic. We therefore focus on a search for geometric

solutions, that is solutions of the form

$$\left. \begin{aligned} x(t) &= \lambda^t x_0, \\ y(t) &= \lambda^t y_0, \\ p(t) &= \lambda^t p_0. \end{aligned} \right\} (7)$$

Substituting (7) in System (1), leads to the following nonlinear eigenvalue problem:

$$\left. \begin{aligned} \lambda x_0 &= (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p_0 + \mu_x x_0 - \phi(x_0, y_0, p_0), \\ \lambda y_0 &= (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p_0 + \mu_y y_0 - \phi(x_0, y_0, p_0), \\ \lambda p_0 &= \sigma \mu_x \mu_y p_0 + \phi(x_0, y_0, p_0). \end{aligned} \right\} (8)$$

From (8) we see that,

$$\left. \begin{aligned} \phi(x_0, y_0, p_0) &= (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p_0 + (\mu_x - \lambda) x_0, \\ \phi(x_0, y_0, p_0) &= (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p_0 + (\mu_y - \lambda) y_0, \\ \phi(x_0, y_0, p_0) &= (-\sigma \mu_x \mu_y + \lambda) p_0. \end{aligned} \right\} (9)$$

The point $[1, 0, 0]$ is a solution of System (9) whenever $\lambda = \mu_x$ and the point $[0, 1, 0]$ is also a solution of System (9) whenever $\lambda = \mu_y$. Consequently, $[(\mu_x)^t, 0, 0]$ and $[0, (\mu_y)^t, 0]$ are the trivial geometric solutions of System (1) and the population eventually becomes extinct whenever $0 \leq \mu_x, \mu_y < 1$. We now look for nontrivial solutions, that is, solutions where $x_0 > 0, y_0 > 0$ and $p_0 > 0$. From System (9) we find that

$$\left. \begin{aligned} (-\sigma \mu_x \mu_y + \lambda) p_0 &= (\beta_x \mu_x \mu_y + (1 - \mu_y) \mu_x + (1 - \sigma) \mu_x \mu_y) p_0 + (\mu_x - \lambda) x_0, \\ (-\sigma \mu_x \mu_y + \lambda) p_0 &= (\beta_y \mu_y \mu_x + (1 - \mu_x) \mu_y + (1 - \sigma) \mu_x \mu_y) p_0 + (\mu_y - \lambda) y_0. \end{aligned} \right\} (10)$$

From (10) we have that

$$\left\{ \begin{aligned} \frac{x_0}{p_0} &= \frac{\beta_x \mu_x \mu_y + \mu_x - \lambda}{\lambda - \mu_x}, \\ \frac{y_0}{p_0} &= \frac{\beta_y \mu_y \mu_x + \mu_y - \lambda}{\lambda - \mu_y}, \end{aligned} \right.$$

using the homogeneity condition on ϕ leads to $\phi(\frac{x_0}{p_0}, \frac{y_0}{p_0}, 1) = (-\sigma \mu_x \mu_y + \lambda)$. Substituting the above expressions for $\frac{x_0}{p_0}, \frac{y_0}{p_0}$ leads to the characteristic

equation of System (1):

$$-\sigma\mu_x\mu_y + \lambda = \phi\left(\frac{\beta_x\mu_x\mu_y}{\lambda - \mu_x} - 1, \frac{\beta_y\mu_y\mu_x}{\lambda - \mu_y} - 1, 1\right). \quad (11)$$

Hence, the existence of geometric solutions depends on proving the existence of positive λ -solutions to (11) with initial condition (x_0, y_0, p_0) in the set Ω . This is established in Lemma 3.1.

Lemma 1 *Equation (11), the characteristic equation, has a unique real solution λ^* if and only if*

$$\mu_x < \frac{([\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)])}{2(1 - \sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)]^2 - 4\mu_y(1 - \sigma\mu_y)(\phi_p(1, 0, 0) - \phi_y(1, 0, 0))}}{2(1 - \sigma\mu_y)}$$

and

$$\mu_y < \frac{([\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)])}{2(1 - \sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)]^2 - 4\mu_x(1 - \sigma\mu_x)(\phi_p(0, 1, 0) - \phi_x(0, 1, 0))}}{2(1 - \sigma\mu_x)},$$

where the discriminants $\Delta_x, \Delta_y \geq 0$.

The proof of Lemma 3.1 can be found in [8]. We proceed to establish conditions for the stability of exponential solutions.

The matrix equation for System (1) is

$$u(t+1) = Au(t) + f(u(t)), \quad (12)$$

where

$$A = \begin{bmatrix} \mu_x & 0 & \mu_x + \beta_x \mu_x \mu_y - \sigma \mu_x \mu_y \\ 0 & \mu_y & \mu_y + \beta_y \mu_x \mu_y - \sigma \mu_x \mu_y \\ 0 & 0 & \sigma \mu_x \mu_y \end{bmatrix}, \quad u = [x, y, p]' \in \mathbb{R}_+^3 \text{ and}$$

$f(u) = [-\phi(x, y, p), -\phi(x, y, p), \phi(x, y, p)]'$ is homogeneous ($' = \text{transpose}$).

If $L(u) = x + y + 2p$ (L is a metric), then $L(\lambda^t u_0) = \lambda^t(x_0 + y_0 + 2p_0) = \lambda^t L(u_0)$. Hence, the introduction of the new variable $w(t) = \frac{u(t)}{L(u(t))}$ implies that a geometric solution $u(t) = \lambda^t u_0$ corresponds to $w(t) = \frac{\lambda^t u_0}{\lambda^t L(u_0)} = \frac{u_0}{L(u_0)}$, that is, to a constant solution in \mathbb{R}_+^3 . A simple computation transforms System (12) into the following nonlinear (non-homogeneous) system of equations for $w(t)$:

$$w(t+1) = \frac{Aw(t) + f(w(t))}{L(Aw(t) + f(w(t)))}. \quad (13)$$

Its fixed point, w_∞ , satisfy the equation

$$w_\infty = \frac{Aw_\infty + f(w_\infty)}{L(Aw_\infty + f(w_\infty))}$$

where $L(Aw_\infty + f(w_\infty))$ is a number (due to the homogeneity of L). Consequently, the fixed points or constant solutions of Equation (13) satisfy the nonlinear eigenvalue problem

$$\lambda^* w_\infty = Aw_\infty + f(w_\infty), \quad (14)$$

where λ^* is a constant. In fact, Equation (14) is equivalent to Equation (8).

Dividing the total population size in System (13) lead to the following nonlinear nonhomogeneous system:

$$\left. \begin{aligned} w(t+1) &= \frac{Aw(t) + f(w(t))}{L(Aw(t) + f(w(t)))} \\ L(w(t)) &= 1, \end{aligned} \right\} (15)$$

where $L(Aw(t) + f(w(t)))$, is a function of t which will be denote by $\lambda(t)$. Time-independent solutions of System (15) must satisfy the following non-linear eigenvalue problem

$$\left. \begin{aligned} Aw_0 + f(w_0) &= \lambda^* w_0 \\ L(w_0) &= 1 \end{aligned} \right\} (16)$$

where $\lambda^* = L(Aw_0 + f(w_0))$ or equivalently, the following approximate linear system (whenever w_0 is very small):

$$\left. \begin{aligned} Aw_0 + f'(w_0)w_0 &= \lambda^* w_0 \\ L(w_0) &= 1. \end{aligned} \right\} (17)$$

Here, $f'(w_0)$ a 3×3 matrix, is the Jacobian matrix at w_0 . Since $f'(w_0)$ is a homogeneous function of degree zero, in System (12), then $B \equiv A + f'(w_0)$ is its Jacobian matrix at w_0 . Furthermore, the first equation in System (17) implies that λ^* is an eigenvalue of B with corresponding eigenvector w_0 .

We take the perturbation $\chi(t) = w(t) - w_0$ in System (15) and linearize $f(w)$ around w_0 . Consequently, we obtain

$$\chi(t+1) = w(t+1) - w_0 = \frac{B\chi(t) - w_0L(B\chi(t))}{\lambda^* + L(B\chi(t))}.$$

Hence, the linearization of the right-hand-side of System (15) is

$$\chi(t+1) = \frac{B\chi(t) - w_0L(B\chi(t))}{\lambda^* + L(B\chi(t))}. \quad (18)$$

The Jacobian matrix of System (15), $J(w_0)\chi(t)$ is therefore given by

$$J(w_0)\chi(t) = \frac{B\chi(t) - w_0L(B\chi(t))}{\lambda^* + L(B\chi(t))}. \quad (19)$$

Therefore, $\chi(t) \rightarrow 0$ as $t \rightarrow \infty$ whenever all the eigenvalues of $J(w_0)$ are less than one in absolute value. Now, we relate the condition that all the

eigenvalues of $J(w_0)$ are less than one in absolute value to an equivalent condition for the matrix B . These results are stated in the next theorem and its corollary.

Theorem 2 *If $\lambda \neq \lambda^*$ is an eigenvalue of B corresponding to an eigenvector v , then $\frac{\lambda}{2\lambda^* - \lambda}$ is an eigenvalue of $J(w_0)$ corresponding to an eigenvector $V = w_0 - v$ [that is, $J(w_0)V = \frac{\lambda}{\lambda^* + L(BV)}V$, where $V = w_0 - v$]. Conversely, if $\lambda \neq \frac{\lambda^*}{\lambda^* + L(BV)}$ is an eigenvalue of $J(w_0)$ with corresponding eigenvector V , then $\lambda(\lambda^* + L(BV))$ is an eigenvalue of B corresponding to an eigenvector $v = V + \frac{1}{\lambda(\lambda^* + L(BV)) - \lambda^*}w_0L(BV)$.*

The proof of Theorem 4.1 and Corollary 4.2 are in [8].

Corollary 3 *The geometric solution with positive geometric ratio λ^* is stable if λ^* is a simple eigenvalue of B and*

$$0 < \lambda < \lambda^* \text{ for all eigenvalues } \lambda \text{ of } B$$

and unstable if

$$\lambda > \lambda^* \text{ for some eigenvalue } \lambda \text{ of } B.$$

Putting the above results together we have that

Theorem 4 *System (1) always has two geometric trivial solutions at*

$$[(\mu_x)^t, 0, 0] \text{ and } [0, (\mu_y)^t, 0].$$

If

$$\mu_x < \frac{([\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)])}{2(1 - \sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)]^2 - 4\mu_y(1 - \sigma\mu_y)(\phi_p(1, 0, 0) - \phi_y(1, 0, 0))}}{2(1 - \sigma\mu_y)}$$

and

$$\mu_y < \frac{([\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)])}{2(1 - \sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)]^2 - 4\mu_x(1 - \sigma\mu_x)(\phi_p(0, 1, 0) - \phi_x(0, 1, 0))}}{2(1 - \sigma\mu_x)}$$

then a stable, positive nontrivial geometric solution exists. Moreover, if

$$\mu_x > \frac{([\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)])}{2(1 - \sigma\mu_y)} +$$

$$\frac{\sqrt{[\mu_y(1 - \sigma\mu_y) - (1 - \beta_y\mu_y)\phi_y(1, 0, 0) - \phi_p(1, 0, 0)]^2 - 4\mu_y(1 - \sigma\mu_y)(\phi_p(1, 0, 0) - \phi_y(1, 0, 0))}}{2(1 - \sigma\mu_y)}$$

then $[(\mu_x)^t, 0, 0]$ is stable, $[0, (\mu_y)^t, 0]$ is unstable and there is no positive nontrivial geometric solution. Also, if

$$\mu_y > \frac{([\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)])}{2(1 - \sigma\mu_x)} +$$

$$\frac{\sqrt{[\mu_x(1 - \sigma\mu_x) - (1 - \beta_x\mu_x)\phi_x(0, 1, 0) - \phi_p(0, 1, 0)]^2 - 4\mu_x(1 - \sigma\mu_x)(\phi_p(0, 1, 0) - \phi_x(0, 1, 0))}}{2(1 - \sigma\mu_x)}$$

then $[(\mu_x)^t, 0, 0]$ is unstable, $[0, (\mu_y)^t, 0]$ is stable and there is no positive nontrivial geometric solution, where $\Delta_x, \Delta_y \geq 0$.

4 Example

Consider System (1) with

$$G(x, y, p) = \frac{p}{y + p},$$

where (x, y, p) belong to the set

$$\Omega := \{(x, y, p) \mid 0 \leq \frac{x}{y} \leq \frac{y + p}{y}\}.$$

Then

$$H(x, y, p) = 1 - \frac{x}{(y + p)}$$

and

$$\phi(x, y, p) = \frac{\mu_x xy}{y + p}.$$

If we assume that $\mu_x = \mu_y = \beta_x = \beta_y = \sigma$, then the characteristic Equation (11) has a positive real solution at

$$\lambda^* = \frac{\sigma[2 + \sigma^2(1 - \sigma^2)] + \sigma^3 \sqrt{4 + (1 - \sigma^2)^2}}{2(1 - \sigma^2)},$$

while System (15) has a unique positive fixed point at

$$[x_0, y_0, p_0] = \left[\frac{(1 - \sigma^2) + \sqrt{4 + (1 - \sigma^2)^2}}{2}, \frac{(1 - \sigma^2) + \sqrt{4 + (1 - \sigma^2)^2}}{2}, 1 \right] \in \Omega.$$

5 Conclusions

In this article we extend the pair-formation models of Kendall [23], Keyfitz [24], Fredrickson [10], Pollard [35] and Hadeler *et al.*'s [12-17] to populations with discrete non-overlapping generations. Our results on the existence and stability of geometric solutions parallel those of Hadeler *et al.* even for the

case when the marriage function ϕ is a function of p , the population size of pairs. Our formalism allows for the exploration of mating systems on population with complex (chaotic) dynamics. In fact, when $\mu = \mu_x = \mu_y$, then $T(t)$ is seen to satisfy

$$T(t + 1) = F(p(t)) + \mu T(t).$$

Hence, the exploration of various forms for F on the dynamics of a two-sex population represents an interesting class of mathematical problems for systems of nonlinear difference equations.

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