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Research Article

Bifurcation Analysis in Population Genetics Model with Partial Selfing

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A new model which allows both the effect of partial selfing selection and an exponential function of the expected payoff is considered. This combines ideas from genetics and evolutionary game theory. The aim of this work is to study the effects of partial selfing selection on the discrete dynamics of population evolution. It is shown that the system undergoes period doubling bifurcation, saddle-node bifurcation, and Neimark-Sacker bifurcation by using center manifold theorem and bifurcation theory. Numerical simulations are presented not only to illustrate our results with the theoretical analysis, but also to exhibit the complex dynamical behaviors, such as the period-3, 6 orbits, cascade of period-doubling bifurcation in period-2, 4, 8, and the chaotic sets. These results reveal richer dynamics of the discrete model compared with the model in Tao et al., 1999. The analysis and results in this paper are interesting in mathematics and biology.

1. Introduction

Evolutionary game theory was extended to the genetic model. The notion of an evolutionary stable strategy (ESS) which was proposed by Smith [1] (1982) is important. And the basic static solution concept of an ESS has been quite successful in predicting the equilibrium behavior of individuals in a population. A series of papers were devoted to the genetic matrix game models. But previous studies on the matrix game models all assumed that genetic mating was random. For example, Lessard [2] (1984) analyzed a frequency-dependent two-phenotype selection model of single-locus with multiallele. Cressman [3] (1996) studied a two-species evolutionary dynamics. Cressman et al. [4] (2003) discussed evolutionarily stable sets in the genetic model of natural selection. Tao et al. [5] (1999) investigated the discrete frequency dynamics of two phenotype diploid models. In fact, in genetic mating, there exists partial selfing selection (Rocheleau and Lessard [6]). From [6], each individual can reproduce by selfing or random outcrossing with constant probabilities, respectively, in a population. After considering partial selfing selection, we establish a nonlinear frequency dynamics, which becomes more realistic but more complicated.

We consider a one-locus two-allele model where genotypic fitness is an exponential function of the expected payoff and the frequency. Suppose that each individual of the population can reproduce by selfing with constant probability β. If $\beta = 0$, then there is no partial selfing selection, which was discussed in [5]. If $\beta \neq 0$, then one-dimensional discrete-time dynamical systems are extended to two-dimensional systems, which lead to great effect on the genetic model. It was shown in [7] that a stable polymorphic equilibrium is not an ESS under some condition. In this paper, we focus on the bifurcation analysis of the genetic model. We find that the model admits the unstable period doubling bifurcation, the saddle-node bifurcation, and the Neimark-Sacker bifurcation, which are new interesting phenomena when considering partial selfing selection.

2. Model

Consider a diploid population with nonoverlapping generations and establish a genetic model with one locus and two alleles A_1 and A_2. The fitness of population individual is frequency-dependent (i.e., it depends on the genetic makeup of the population concerned). To show the results, the following assumptions will be made:

(i) Mendelian segregation;
(ii) sex ratio is independent of genotype;
(iii) no gametic selection;
(iv) the fecundity of offspring is equal;
(v) no mutation or migration.

According to [6], each individual can reproduce by selfing or random outcrossing with probability β or $1-\beta$ $(0<\beta<1)$, respectively, in the population. P_{ij} and P'_{ij} are the frequencies of genotypes A_iA_j in the current generation and in the next generation, respectively. The genotypic frequency of genotype A_iA_j among adults in the current generation is $\widetilde{P}_{ij}$. The corresponding selection values of genotypes A_iA_j are $F_{A_iA_j}$. p and p' are the frequencies of allele A_1 in the current generation and in the next generation, respectively. q and q' are the frequencies of allele A_2 in the current generation and in the next generation, respectively. $\widetilde{p}$ and $\widetilde{q}$ are genotypic frequencies of allele A_1 and allele A_2 among adults in the current generation, respectively. u_{ij} (or $1-u_{ij}$) is the fraction of individuals of genotype A_iA_j which play pure strategy R_1 (or R_2). After selection but before mating, we have

$$\begin{aligned}\widetilde{P}_{11}&=\frac{F_{A_1A_1}P_{11}}{\left[F_{A_1A_1}P_{11}+F_{A_1A_2}P_{12}+F_{A_2A_2}P_{22}\right]},\\ \widetilde{P}_{12}&=\frac{F_{A_1A_2}P_{12}}{\left[F_{A_1A_1}P_{11}+F_{A_1A_2}P_{12}+F_{A_2A_2}P_{22}\right]},\\ \widetilde{P}_{22}&=\frac{F_{A_2A_2}P_{22}}{\left[F_{A_1A_1}P_{11}+F_{A_1A_2}P_{12}+F_{A_2A_2}P_{22}\right]}.\end{aligned}\tag{1}$$

After mating and reproduction, there are

$$\begin{aligned}P'_{11}&=\beta\left[\widetilde{P}_{11}+\frac{1}{4}\widetilde{P}_{12}\right]+(1-\beta)\left[\widetilde{P}_{11}+\frac{1}{2}\widetilde{P}_{12}\right]^2,\\ P'_{12}&=\beta\left[\frac{1}{2}\widetilde{P}_{12}\right]+2(1-\beta)\left[\widetilde{P}_{11}+\frac{1}{2}\widetilde{P}_{12}\right]\left[\widetilde{P}_{22}+\frac{1}{2}\widetilde{P}_{12}\right],\\ P'_{22}&=\beta\left[\widetilde{P}_{22}+\frac{1}{4}\widetilde{P}_{12}\right]+(1-\beta)\left[\widetilde{P}_{22}+\frac{1}{2}\widetilde{P}_{12}\right]^2.\end{aligned}\tag{2}$$

In our paper, the fitness $F_{A_iA_j}$ is taken to be an exponential function of the expected payoff as [6]. Assume that an individual in the population can use one of two strategies R_1 and R_2; each individual plays the same pure strategy throughout its lifetime. And the payoff matrix is

$$\begin{bmatrix}a_{11}&a_{12}\\a_{21}&a_{22}\end{bmatrix}.\tag{3}$$

Let x be the proportion of individuals using strategy R_1; then, we can get that the expected payoffs to R_1 and R_2 are

$$\begin{aligned}\varphi_1&=xa_{11}+(1-x)a_{12},\\ \varphi_2&=xa_{21}+(1-x)a_{22}.\end{aligned}\tag{4}$$

Furthermore, we take the fitness function

$$F_{A_iA_j}=u_{ij}e^{\varphi_1}+\left(1-u_{ij}\right)e^{\varphi_2}.\tag{5}$$

Since system (2) is on the simplex $S_3=\{(P_{11},P_{12},P_{22})\mid P_{11}+P_{12}+P_{22}=1;P_{11},P_{12},P_{22}\geq 0\}$, we can get the following system:

$$\begin{aligned}P'_{11}&=\beta\frac{F_{A_1A_1}P_{11}+(1/4)F_{A_1A_2}P_{12}}{\overline{F}}\\ &\quad+(1-\beta)\frac{\left(F_{A_1A_1}P_{11}+(1/2)F_{A_1A_2}P_{12}\right)^2}{\overline{F}^2},\\ P'_{12}&=\beta\frac{(1/2)F_{A_1A_2}P_{12}}{\overline{F}}+2(1-\beta)\\ &\quad\times\left(\left(F_{A_1A_1}P_{11}+\frac{1}{2}F_{A_1A_2}P_{12}\right)\right.\\ &\qquad\left.\times\left(F_{A_2A_2}(1-P_{11}-P_{12})+\frac{1}{2}F_{A_1A_2}P_{12}\right)\right)\\ &\quad\times\left(\overline{F}^2\right)^{-1},\end{aligned}\tag{6}$$

where

$$\begin{aligned}x&=P_{11}u_{11}+P_{12}u_{12}+P_{22}u_{22},\\ \varphi_i&=xa_{i1}+(1-x)a_{i2},\\ F_{A_iA_j}&=u_{ij}e^{\varphi_1}+\left(1-u_{ij}\right)e^{\varphi_2},\\ \overline{F}&=F_{A_1A_1}P_{11}+F_{A_1A_2}P_{12}+F_{A_2A_2}P_{22}.\end{aligned}\tag{7}$$

From (1) and (2), we obtain

$$\widetilde{p}=\widetilde{P}_{11}+\frac{1}{2}\widetilde{P}_{12}=P'_{11}+\frac{1}{2}P'_{12}=p'.\tag{8}$$

Obviously, it is difficult to use p and q to denote the genotypic frequency P_{ij} directly. If the population is polymorphic (i.e., $0<p<1$), we can use the fixation index F (wright 1949 [8]) according to [6]. The genotypic frequencies can be written in the form

$$\begin{aligned}P_{11}&=p^2+pqF,\\ P_{12}&=2pq(1-F),\qquad P_{22}=q^2+pqF,\end{aligned}\tag{9}$$

where $-1\leq F\leq 1$. The value of F varies from one generation to the next.

Equations (1) to (9) can deduce that

$$\begin{aligned}p'&=p\frac{(p+qF)\left(u_{11}e^{\varphi_1}+(1-u_{11})e^{\varphi_2}\right)+(1-F)q\left(u_{12}e^{\varphi_1}+(1-u_{12})e^{\varphi_2}\right)}{\overline{F}},\\ F'&=\beta\left[1-\frac{1-F}{2}\left(\frac{p}{1-\left(1-\left(F_{A_2A_2}/F_{A_1A_2}\right)\right)(q+pF)}\right.\right.\\ &\qquad\left.\left.+\frac{q}{1-\left(1-\left(F_{A_1A_1}/F_{A_1A_2}\right)\right)(p+qF)}\right)\right],\end{aligned}\tag{10}$$

where

$$\begin{aligned} x_{A_1} &= (p+qF)\,u_{11} + q\,(1-F)\,u_{12}, \\ x_{A_2} &= (q+pF)\,u_{22} + p\,(1-F)\,u_{12}, \\ x\,(p,F) &= \left(p^2 + pqF\right)u_{11} + 2pq\,(1-F)\,u_{12} \\ &\quad + \left(q^2 + pqF\right)u_{22} \\ &= p x_{A_1} + q x_{A_2}, \\ \varphi_i &= x a_{i1} + (1-x)\,a_{i2}, \\ F_{A_iA_j} &= u_{ij} e^{\varphi_1} + \left(1-u_{ij}\right)e^{\varphi_2}, \\ \overline{F} &= x e^{\varphi_1} + (1-x)\,e^{\varphi_2}. \end{aligned} \tag{11}$$

Throughout the paper, we discard the degenerate situations where all u_{ij} are identical or where $\gamma = 0$ and suppose that A_iA_j is not the genotype in the parental generation.

3. Model Analysis and Basic Definitions

Recall Definition 1 in [7], which is a similar definition of phenotypic and genotypic equilibria under partial selfing selection according to [2]. The two types of the equilibria include all situations in which the population is in equilibrium.

Definition 1. A phenotypic equilibrium is an equilibrium where all pure strategies in current use have equal expected payoff. A genotypic equilibrium is a nonphenotypic equilibrium where the effective fitnesses of all alleles present in the current population are equal. The effective fitness of allele A_i is defined to be $[P_{ii}F_{A_iA_i} + (1/2)P_{12}F_{A_1A_2}]/[P_{ii} + (1/2)P_{12}]$. (In addition, in the case $p = 0$, the effective fitness of allele A_1 is $F_{A_1A_2}$. In the case $p = 1$, the effective fitness of allele A_2 is $F_{A_1A_2}$.)

According to Definition 1, a phenotypic equilibrium is an equilibrium where all pure strategies in current use have equal expected payoff. So, a polymorphic phenotypic equilibrium exists if and only if $\varphi_1 = \varphi_2$. Then, we have

$$\varphi_2 - \varphi_1 = x\,(a_{21} - a_{11}) + (1-x)\,(a_{22} - a_{12}) = \gamma\,(x - \xi), \tag{12}$$

where $\gamma = a_{12} - a_{22} + a_{21} - a_{11}$, and $\xi = (a_{12} - a_{22})/(a_{12} - a_{22} + a_{21} - a_{11})$.

Let (p^*, F^*) denote polymorphic phenotypic equilibrium; then, we have the Jacobian matrix at (p^*, F^*) of system (10)

$$A^* = \begin{bmatrix} 1 - k_{11}\gamma & k_{12}\gamma \\ k_{21}\gamma & \dfrac{\beta}{2} - k_{22}\gamma \end{bmatrix}, \tag{13}$$

where

$$\begin{gathered} u = u_{11} + u_{22} - 2u_{12}, \qquad a = u_{11} - u_{12}, \\ b = u_{22} - u_{12}, \qquad F^* = \frac{\beta}{2-\beta}, \\ k_2 = p^{*2}\,(u_{22} - u_{12}) + q^{*2}\,(u_{11} - u_{12}), \\ k = u_{12} - u_{11} + p^* u, \qquad z = u_{22} - u_{12} - p^* u, \\ k_{11} = p^*\,(1-p^*)\,(z + F^*k)\left[(2-F^*)\,z + F^*k\right], \\ k_{12} = p^{*2} q^{*2} u\,(z + F^*k), \\ k_{21} = \frac{\beta}{2}\,(1-F^*)\,(p^*q^*u + F^*k_2)\left[(2-F^*)\,z + F^*k\right], \\ k_{22} = \frac{\beta}{2}\,(1-F^*)\,p^*q^*u\,(p^*q^*u + F^*k_2). \end{gathered} \tag{14}$$

We studied the system (10) and obtained Theorem 3.1 (i) and (ii) in [7]. In [7], the authors showed that a stable polymorphic equilibrium is not an ESS under some condition. In this paper, we focus on the bifurcation of system (10). For convenience, we present some lemmas and theorems of the stability of polymorphic phenotypic equilibrium in [7] at first.

Lemma 2. *$x^* = x(p^*, F^*) = \xi(0 < \xi < 1)$ is an interior ESS if and only if $\gamma > 0$.*

Lemma 3. *If $k_{11} > 0$, then $(\beta/2)k_{11} + k_{22} > 0$. If $k_{11} < 0$, then $((2+\beta)/4)k_{11} + k_{22} > 0$.*

Theorem 4. *Suppose that (p^*, F^*) is a polymorphic phenotypic equilibrium.*

(i) *Suppose that $k_{11} > 0$. If x^* is not an ESS, then (p^*, F^*) is unstable. If x^* is an ESS, then (p^*, F^*) is stable for $0 < \gamma < \gamma_{c\gamma_2}$.*

(ii) *Suppose that $k_{11} < 0$. If x^* is an ESS, then (p^*, F^*) is unstable. If x^* is not an ESS, then (p^*, F^*) is stable for $\gamma_{c\gamma_1} < \gamma < 0$.*

(iii) *Suppose that $k_{11} = 0$. If $a \neq b$, then (p^*, F^*) is unstable for $\gamma \neq (\beta \pm 2)/2k_{22}$. If $a = b$, then (p^*, F^*) is stable for $\gamma \in (0, 4(\beta+2)/\beta a^2(1 - F^{*2}))$, unstable for $\gamma \in (-\infty, -4/a^2(1 - F^{*2})F^*) \cup (-4/a^2(1 - F^{*2})F^*, 0) \cup (4(\beta+2)/\beta a^2(1 - F^{*2}), +\infty)$.*

Proof. Consider only the case $k_{11} > 0$ since the proof of the case $k_{11} < 0$ is analogous. From the Jacobian matrix A^* at (p^*, F^*), we have

$$\begin{aligned} \det A^* &= -\left(\frac{\beta}{2}k_{11} + k_{22}\right)\gamma + \frac{\beta}{2}, \\ \operatorname{tr} A^* &= \frac{2+\beta}{2} - \gamma\,(k_{11} + k_{22}). \end{aligned} \tag{15}$$

If x^* is not an ESS, then $\gamma < 0$ from Lemma 2. The inequality $k_{11}\gamma < 0$ implies that $\operatorname{tr} A^* > \det A^* + 1$. So, (p^*, F^*) is unstable. If x^* is an ESS, then $\gamma > 0$. By the discussion on the monotone function, we can obtain the following inequalities:

$$\det A^* < 1, \qquad \left|\operatorname{tr} A^*\right| < \det A^* + 1. \tag{16}$$

So, (p^*, F^*) is stable.

Now, we discuss the stability of (p^*, F^*) when $k_{11} = 0$. If $u = 0$, then $k_{11} = 0$. If $k_{11} = 0$, we have the following.

Case 1. $(p^*, F^*) = (p_2, \beta/(2-\beta))$, where $p_2 = (2b - uF^*)/2u(1-F^*)$ and $F^* = \beta/(2-\beta)$.

Case 2. $(p^*, F^*) = (p_1, \beta/(2-\beta))$, where $p_1 = (b - aF^*)/u(1 - F^*)$ and $F^* = \beta/(2-\beta)$.

We only prove Case 1 since Case 2 is analogous.

Write

$$\begin{gathered} a_1 = k_{12}\gamma, \qquad b_1 = \frac{\beta}{2} - k_{22}\gamma, \\ a_{11} = -2u(1-F^*)^2 p^* q^* z\gamma, \\ a_{12} = p^{*2} q^{*2} u \left[2k + \left(z + F^* k\right) p^* q^* u\gamma\right] \gamma, \\ a_{22} = p^* q^* u \left[2\left(1 - 2p^*\right)\left(z + F^* k\right) - p^* q^* u \left(1 - F^*\right)\right] \gamma, \\ b_{11} = -\beta, u(1-F^*)^2 \left[p^* q^* u + \left(bp^{*2} + aq^{*2}\right) F^*\right] \gamma, \end{gathered} \tag{17}$$

and let $P = \left(\begin{smallmatrix} 1 & -a_1/(1-b_1) \\ 0 & 1 \end{smallmatrix}\right)$. Using the translation

$$\begin{pmatrix} p \\ F \end{pmatrix} = P \begin{pmatrix} \mu \\ \nu \end{pmatrix} + \begin{pmatrix} p_2 \\ F^* \end{pmatrix}, \tag{18}$$

system (10) becomes

$$\begin{aligned} \mu' = \mu &+ \frac{1}{2} \\ &\times \left[a_{11}\left(\mu - \frac{a_1}{1-b_1}\nu\right)^2 + a_{12}\nu\left(\mu - \frac{a_1}{1-b_1}\nu\right) + a_{22}\nu^2\right] \\ &+ \frac{a_1}{2\left(1-b_1\right)} \cdot \left[b_{11}\left(\mu - \frac{a_1}{1-b_1}\nu\right)^2\right. \\ &\qquad\qquad \left. + b_{12}\nu\left(\mu - \frac{a_1}{1-b_1}\nu\right) + b_{22}\nu^2\right] + \text{h.o.t}, \\ \nu' = b_1\nu & \\ &+ \frac{1}{2}\left[b_{11}\left(\mu - \frac{a_1}{1-b_1}\nu\right)^2 + b_{12}\nu\left(\mu - \frac{a_1}{1-b_1}\nu\right) + b_{22}\nu^2\right] \\ &+ \text{h.o.t.} \end{aligned} \tag{19}$$

By center manifold theory, we can obtain the following reduced system which is locally homeomorphic with system (10):

$$\mu' = \mu + \frac{1}{2}\left(a_{11} + \frac{a_1}{1-b_1} b_{11}\right)\mu^2 + O\left(\mu^3\right), \tag{20}$$

where $(1/2)(a_{11} + (a_1/(1-b_1))b_{11}) = p^* q^* uz(1-F^*)^2\gamma\{(1/(1/p^* q^* u[p^* q^* u + F^*(aq^{*2} + bp^{*2})\gamma]F^*(1-F^*)) + 1) - 1\}$. If $a \neq b$, then $z \neq 0$. So, we have $(1/2)(a_{11} + (a_1/(1-b_1))b_{11}) \neq 0$. If $a = b$, we can calculate the reduced system by similar analysis,

$$x' = x + k_3 x^3 + O\left(x^4\right), \tag{21}$$

where $k_3 = -(1-F^*)^2 a^2\gamma/(1 + (1/4)a^2(1-F^{*2})F^*\gamma)$. It is easy to obtain the results. This completes the proof. □

4. Bifurcation Analysis

Based on the analysis in Section 3, we discuss the period doubling bifurcations, the saddle-node bifurcation, and the Neimark-Sacker bifurcation of the positive fixed point (P^*, F^*) in this section. We choose parameter γ as a bifurcation parameter to study the period doubling bifurcations and the Neimark-Sacker bifurcation and parameter δ as a bifurcation parameter to study the saddle-node bifurcation by using center manifold theorem and bifurcation theory in [9, 10]. Suppose that k_{ij} is the same as that in (14).

4.1. Period Doubling Bifurcation.

In the analysis of period doubling bifurcations, we take γ as the bifurcation parameter and prove that there is period doubling bifurcation at the fixed point (p^*, F^*) for $\gamma = \gamma_{c\gamma_2}$. When $\gamma = \gamma_{c\gamma_2}$, the characteristic polynomial of Jacobian matrix at (p^*, F^*) is

$$\lambda^2 + \frac{\left(4-\beta^2\right)k_{11}}{2\left[(2+\beta)k_{11} + 4k_{22}\right]}\lambda - \frac{\beta(\beta+2)k_{11} + 8k_{22}}{2\left[(2+\beta)k_{11} + 4k_{22}\right]} = 0. \tag{22}$$

We have the following characteristic values of (22):

$$\lambda_1 = -1, \qquad \lambda_2 = s = \frac{\beta(\beta+2)k_{11} + 8k_{22}}{2\left[(2+\beta)k_{11} + 4k_{22}\right]}. \tag{23}$$

Let

$$C = \begin{bmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{bmatrix} = \begin{bmatrix} (\beta+2)k_{11} & 4k_{12} \\ -4k_{21} & (\beta+2)k_{11} \end{bmatrix}, \tag{24}$$

And let D denote C^{-1}. Then,

$$\begin{aligned} D &= \begin{bmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{bmatrix} \\ &= \frac{1}{(\beta+2)^2 k_{11}^2 + 16k_{12}k_{12}} \begin{bmatrix} (\beta+2)k_{11} & -4k_{12} \\ 4k_{21} & (\beta+2)k_{11} \end{bmatrix}. \end{aligned} \tag{25}$$

Denote the right-hand side of (10) by $\left(\begin{smallmatrix} \bar{p} \\ \bar{F} \end{smallmatrix}\right)$, and use the translation

$$\begin{pmatrix} p \\ F \end{pmatrix} = C\begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} p^* \\ F^* \end{pmatrix}, \qquad \gamma = \gamma_{c\gamma_2} + \lambda; \tag{26}$$

system (10) becomes

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} -1 & 0 \\ 0 & s \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} H(x, y, \lambda) \\ G(x, y, \lambda) \end{pmatrix}, \tag{27}$$

where

$$\begin{aligned} H(x, y, \lambda) = {} & x + d_{11}\left(f(x, y, \lambda) - p^*\right) \\ & + d_{12}\left(g(x, y, \lambda) - F^*\right), \\ G(x, y, \lambda) = {} & -sy + d_{21}\left(f(x, y, \lambda) - p^*\right) \\ & + d_{22}\left(g(x, y, \lambda) - F^*\right). \end{aligned} \tag{28}$$

It is easy to obtain that

$$\begin{gathered} \begin{pmatrix} H(0, 0, \lambda) \\ G(0, 0, \lambda) \end{pmatrix} = 0, \\ \left.\begin{pmatrix} \dfrac{\partial H(x, y, \lambda)}{\partial x} & \dfrac{\partial H(x, y, \lambda)}{\partial y} \\ \dfrac{\partial G(x, y, \lambda)}{\partial x} & \dfrac{\partial G(x, y, \lambda)}{\partial y} \end{pmatrix}\right|_{(x,y,\lambda)=(0,0,0)} = 0, \\ \begin{aligned} \left.\frac{\partial^2 H(x, y, \lambda)}{\partial x \partial \lambda}\right|_{(x,y,\lambda)=(0,0,0)} &= d_{11}\left(-c_{11}k_{11} + c_{21}k_{21}\right) \\ &\quad + d_{12}\left(c_{11}k_{21} - c_{21}k_{22}\right) \\ &= -\frac{\left[(\beta + 2)k_{11} + 4k_{22}\right]^2}{(\beta + 2)^2 k_{11} + 16k_{22}}. \end{aligned} \end{gathered} \tag{29}$$

According to Lemma 3, there are

$$(\beta + 2)k_{11} + 4k_{22} \neq 0, \qquad (\beta + 2)^2 k_{11} + 16k_{22} > 0. \tag{30}$$

So, we have

$$c = -2\frac{\partial^2 H(x, y, \lambda)}{\partial x \partial \lambda} > 0. \tag{31}$$

In order for system (27) to undergo period doubling bifurcation, we require that the following L is not zero [10]:

$$L = -2H_{xxx} - 3H_{xx}^2 - \frac{6}{1 - s}G_{xx}H_{xy}. \tag{32}$$

If $k_{11} \neq 0$, then $|s| < 1$ for $k_{11} > 0$, $|s| > 1$ for $k_{11} < 0$.

From the previous analysis and the theorem in [10], we have the following result.

Proposition 5. *Suppose that* (p^*, F^*) *is a polymorphic phenotypic equilibrium. If* $k_{11} \neq 0$ *and* $L \neq 0$, *then system* (10) *undergoes a period doubling bifurcation at* (p^*, F^*) *for* $\gamma = \gamma_{c\gamma_2}$.

Moreover, we have the following.

(i) If $k_{11} > 0$ and $L > 0$ ($L < 0$), then period doubling bifurcation happens for $\gamma < \gamma_{c\gamma_2}$ ($\gamma > \gamma_{c\gamma_2}$). And 2-periodic points are saddle points (asymptotically stable nodes).

(ii) If $k_{11} < 0$ and $L > 0$ ($L < 0$), then period doubling bifurcation happens for $\gamma < \gamma_{c\gamma_2}$ ($\gamma > \gamma_{c\gamma_2}$). And 2-periodic points are unstable nodes (saddle points).

Example 6. Let $u_{11} = 0.6$, $u_{12} = 0.9$, $u_{22} = 0.3$, $\beta = 0.4$, and $\xi = 0.6515625$. There are two polymorphic phenotypic equilibria $(p_1^*, F^*) = (0.6944444, 0.25)$ and $(p_2^*, F^*) = (0.75, 0.25)$. For (p_1^*, F^*), we have $k_{11}(p_1^*, F^*) = 0.4475911459 \times 10^{-3} > 0$ and $L(p_1^*, F^*) = -4.839394634 < 0$. Then, period doubling bifurcation happens for $\gamma > \gamma_{c\gamma_2} = 149.7775520$, and 2-periodic points are asymptotically stable nodes. For (p_2^*, F^*), we have $k_{11}(p_2^*, F^*) = -0.1318359375 \times 10^{-3} < 0$ and $L(p_2^*, F^*) = 9.126558784 > 0$. Then, period doubling bifurcation happens for $\gamma < \gamma_{c\gamma_2} = 186.1395138$, and 2-periodic points are unstable nodes.

The effects of partial selfing selection on the dynamics of population evolution are shown further in Figures 1, 2, and 3. More complex dynamical behaviors of the genetic system are exhibited by numerical simulations. In Figure 1, the partial selfing selection leads period doubling bifurcation to emerge earlier, and leads chaos to emerge earlier. In Figure 3, the model exhibits the complex dynamical behaviors, such as the period-3, 6 orbits, cascade of period-doubling bifurcation in period-2, 4, 8, and the chaotic sets. By choosing β as a bifurcation parameter, we show that the complex dynamical behaviors such as the period-3, 4, 6 orbits, cascade of period-doubling bifurcation in period-2, 4, 8, and the chaotic sets can occur as β crosses some critical values in Figure 2.

4.2. Saddle-Node Bifurcation.

We take ξ as the bifurcation parameter for studying the saddle-node bifurcation by using center manifold theorem.

If $\xi^* = u_{22} - ((uF^* - 2b)^2/4u(1 - F^*))$, then there is unique polymorphic phenotypic equilibrium, and $(p^*, F^*) = ((2b - uF^*)/2u(1 - F^*), F^*)$. The Jacobian matrix of (p^*, F^*) is

$$A^* = \begin{pmatrix} 1 & k_{12}^*\gamma \\ 0 & \dfrac{\beta}{2} - k_{22}^*\gamma \end{pmatrix}, \tag{33}$$

where $k_{12}^* = (2b - uF^*)^2(2a - uF^*)^2(b - a)F^*/32u(1 - F^*)^2$ and $k_{22}^* = (\beta/32)(((2b - uF^*)(2a - uF^*))/u^2(1 - F^*)^2)[4ab + 2(a - b)^2F^* - u^2F^{*2}]$.

The characteristic values of A^* are

$$\lambda_1 = 1, \qquad \lambda_2 = \frac{\beta}{2} - k_{22}{}^*\gamma, \tag{34}$$

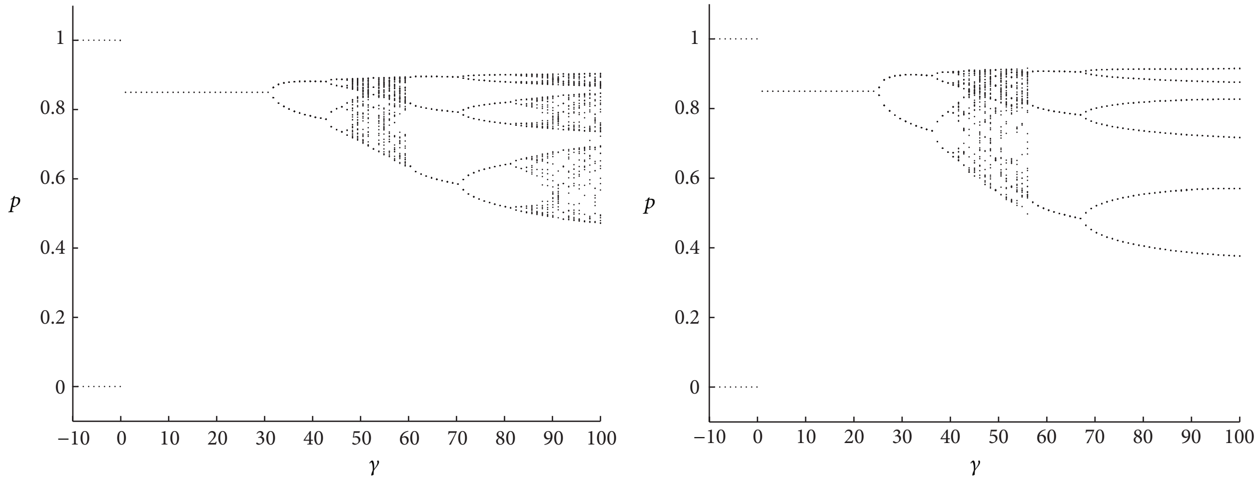
where $\gamma \neq (\beta \pm 2)/2k_{22}^*$ can make sure that $|\lambda_2| \neq 1$.

Using the translation

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 & -\dfrac{k_{12}^*\gamma}{(1 - \beta/2) + k_{22}^*\gamma} \\ 0 & 1 \end{pmatrix} \begin{pmatrix} p - p^* \\ F - F^* \end{pmatrix}, \tag{35}$$

we have

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & \lambda^* \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} f_1\left(x, y, \tilde{\xi}\right) \\ g_1\left(x, y, \tilde{\xi}\right) \end{pmatrix}, \tag{36}$$



(a)

(b)

FIGURE 1: $u_{11} = 1$, $u_{12} = 0.5$, $u_{22} = 0$, and $\xi = 0.85$. If $\gamma < 0$, then all interior trajectories evolve to the stable monomorphic equilibria ($p^* = 0$ and $p^* = 1$). (a) For $\beta = 0$, there is unique polymorphic phenotypic equilibrium $(p^*, F^*) = (0.85, 0.25)$, which is stable for $0 < \gamma < \gamma_{c\gamma_2} = 31.37254902$. (b) For $\beta = 0.4$, there is unique polymorphic phenotypic equilibrium $(p^*, F^*) = (0.85, 0.25)$, which is stable for $0 < \gamma < \gamma'_{c\gamma_2} = 25.09803922$.

where

$$\begin{aligned}
f_1 &= a^*\widetilde{\xi} + \frac{1}{2}\left[a_{11}(x - B_0 y)^2 + a_{12} y\,(x - B_0 y) + a_{22} y^2 \right.\\
&\qquad \left. + a_{01}\,(x - B_0 y)\,\widetilde{\xi} + a_{02} y\widetilde{\xi} + a_{03}\widetilde{\xi}^2\right]\\
&\quad + \frac{1}{2}B_0\left[b_{11}(x - B_0 y)^2 + b_{12}\,(x - B_0 y)\,y + b_{22} y^2\right.\\
&\qquad \left. + b_{01}\,(x - B_0 y)\,\widetilde{\xi} + b_{02} y\widetilde{\xi} + b_{03}\widetilde{\xi}^2\right] + \text{h.o.t},\\
g_1 &= b^*\widetilde{\xi} + \frac{1}{2}\left[b_{11}(x - B_0 y)^2 + b_{12} y\,(x - B_0 y) + b_{22} y^2\right.\\
&\qquad \left. + b_{01}\,(x - B_0 y)\,\widetilde{\xi} + b_{02} y\widetilde{\xi} + b_{03}\widetilde{\xi}^2\right] + \text{h.o.t},\\
\lambda^* &= \frac{\beta}{2} - k_{22}{}^*\gamma, \qquad B_0 = \frac{k_{12}^*\gamma}{(1 - \beta/2) + k_{22}^*\gamma},\\
a^* &= \frac{a - b}{2} p^* q^* F^* \gamma \frac{1 - \beta/2}{1 - (\beta/2) + k_{22}{}^*\gamma},\\
b^* &= \frac{\beta\gamma}{8u}\left[4ab - u^2 F^{*2} + 2F^*(a - b)^2\right],\\
a_{11} &= -2u(1 - F^*)^2 p^* q^* z\gamma,\\
a_{12} &= p^{*2} q^{*2} u\left[2k + (z + F^* k)\,p^* q^* u\gamma\right]\gamma,\\
a_{22} &= p^* q^* u\left[2\,(1 - 2p^*)\,(z + F^* k) - p^* q^* u\,(1 - F^*)\right]\gamma,\\
b_{11} &= -\beta u(1 - F^*)^2\left[p^* q^* u + \left(b p^{*2} + a q^{*2}\right) F^*\right]\gamma.
\end{aligned} \tag{37}$$

By the center manifold theory, we know that the stability of $(0, 0)$ near $\widetilde{\xi} = 0$ can be determined by a one-parameter family of equations on a center manifold, which can be represented as follows:

$$\begin{aligned}
W^c(0) = &\left\{\left(x, y, \widetilde{\xi}\right) \in R^3 \mid y = h\left(x, \widetilde{\xi}\right), h(0, 0),\right.\\
&\left. = 0, Dh(0, 0) = 0 \in R^3\right\}
\end{aligned} \tag{38}$$

for x and $\widetilde{\xi}$ sufficiently small. Assume that a center manifold has the form

$$h\left(x, \widetilde{\xi}\right) = l_0\widetilde{\xi} + l_1 x\widetilde{\xi} + l_2 x^2 + l_3\widetilde{\xi}^2 + O\left(\left(|x| + |\widetilde{\xi}|\right)^3\right). \tag{39}$$

The center manifold must satisfy

$$\begin{aligned}
N\left(h\left(x, \widetilde{\xi}\right)\right) = {}& h\left(A^* x + f_1, \widetilde{\xi}\right)\\
&- \lambda^* h\left(x, \widetilde{\xi}\right) - g_1\left(x, h\left(x, \widetilde{\xi}\right), \widetilde{\xi}\right) = 0.
\end{aligned} \tag{40}$$

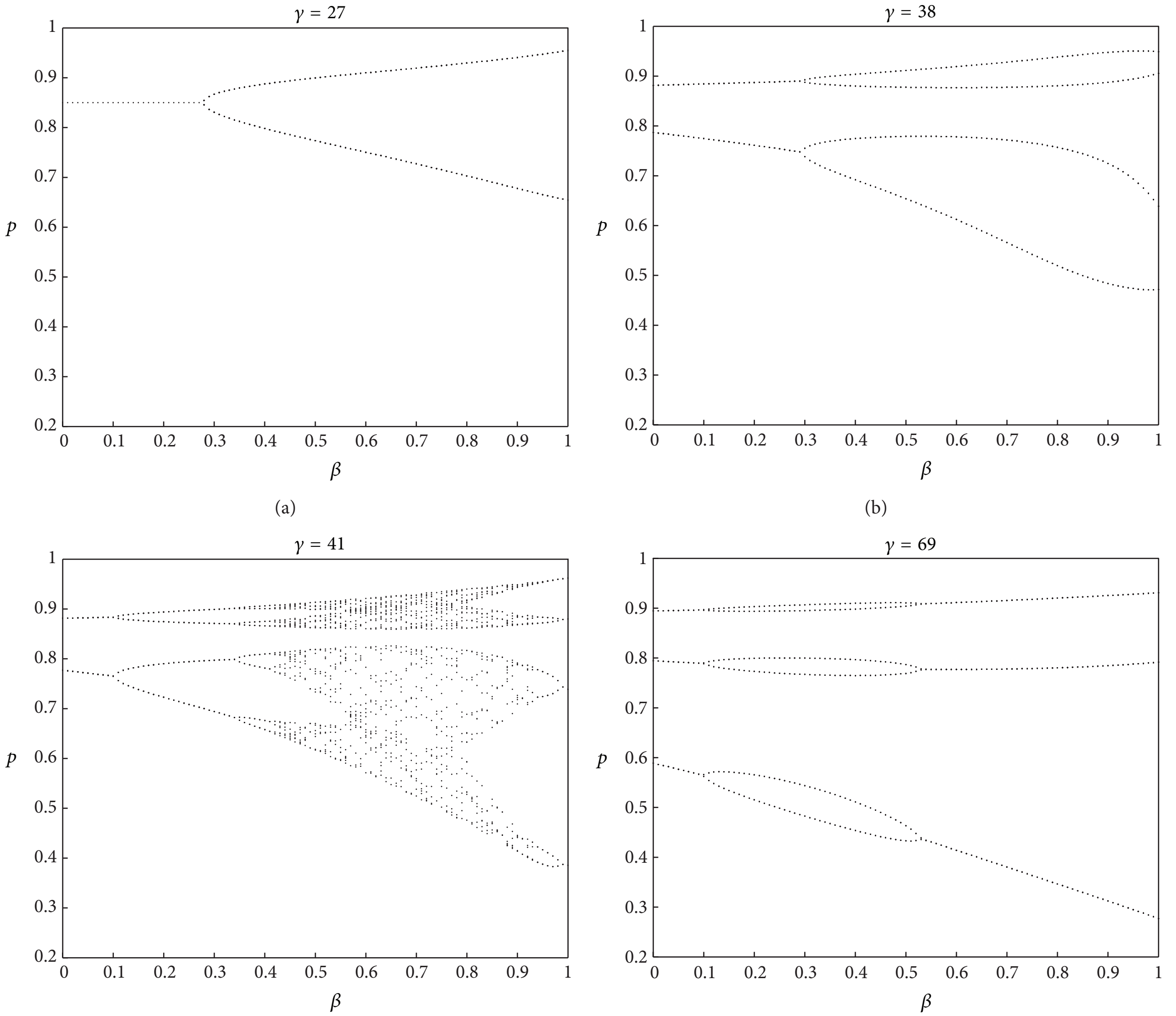
So, we obtain the map restricted to the center manifold

$$x \longrightarrow f\left(x, \widetilde{\xi}\right) = x + c_1\xi + c_2 x^2 + O\left(\left(|x| + |\widetilde{\xi}|\right)^2\right), \tag{41}$$

where $c_1 = ((a - b)/2)p^* q^* F^* \gamma((1 - \beta/2)/(1 - (\beta/2) + k_{22}{}^*\gamma))$, and $c_2 = -((a - b)/4)p^* q^*(1 - F^*)u\gamma(\beta/(1 - (\beta/2) + k_{22}{}^*\gamma))$.

By condition (41) and the saddle-node bifurcation theorem in [9], we can state the following result.

Proposition 7. *Suppose that (p^*, F^*) is a polymorphic phenotypic equilibrium. If $\beta \in (0, \min\{4b/(a + 3b), 4a/(3a + b)\})$, $(a - b)u\gamma \neq 0$, $ab > 0$, and $\gamma \neq (\beta \pm 2)/2k_{22}^*$, then system* (10) *undergoes a saddle-node bifurcation at (p^*, F^*) for $\xi = \xi^*$ where $p^* = (2b - uF^*)/2u(1 - F^*)$, $\xi^* = u_{22} - ((uF^* - 2b)^2/4u(1 - F^*)$, and $k_{22}^* = (\beta/32)((2b - uF^*)(2a - uF^*)/u^2(1 - F^*)^2)[4ab + 2(a - b)^2 F^* - u^2 F^{*2}]$.*



(a) (b)

(c) (d)

Figure 2: $u_{11} = 1$, $u_{12} = 0.5$, $u_{22} = 0$, and $\xi = 0.85$. When $\gamma = 27$, (p^*, F^*) is stable for $\beta \in (0, \beta^*)(\beta^* = 0.27875)$. Stable 2-periodic points emerge at $\beta = \beta^*$. When $\gamma = 38$, stable 2-periodic points become stable 4-periodic points with the increase of β. When $\gamma = 41$, there is chaos for $0.47 < \beta < 0.49$. When $\gamma = 69$, stable 3-periodic points become stable 6-periodic points and then become stable 3-periodic points again.

Moreover, if $u > 0$, then two new polymorphic phenotypic equilibria are created for $\xi > \xi^*$ and disappear for $\xi < \xi^*$. If $u < 0$, then two new polymorphic phenotypic equilibria are created for $\xi < \xi^*$ and disappear for $\xi > \xi^*$. (see Figure 4).

In Proposition 7, the conditions $\beta \in (0, \min\{4b/(a + 3b), 4a/(3a + b)\})$ and $ab > 0$ guarantee that $p^* = (2b - uF^*)/2u(1-F^*) \in (0, 1)$. If there is no partial selfing selection (i.e., $\beta = 0$), then the saddle-node bifurcation does not occur. This means that the parameter β of partial selfing selection leads to more complex dynamical behavior of the genetic system.

4.3. Neimark-Sacker Bifurcation. We take γ as the bifurcation parameter and prove the existence of Neimark-Sacker bifurcation. The characteristic polynomial of Jacobian matrix at (p^*, F^*) is

$$\lambda^2 + M(\gamma)\lambda + N(\gamma) = 0, \tag{42}$$

where

$$\begin{aligned} M(\gamma) &= (k_{11} + k_{22})\gamma - \frac{\beta + 2}{2}, \\ N(\gamma) &= -\left(\frac{\beta}{2}k_{11} + k_{22}\right)\gamma + \frac{\beta}{2}. \end{aligned} \tag{43}$$

If the following condition is satisfied

$$M(\gamma)^2 - 4N(\gamma) < 0, \tag{44}$$

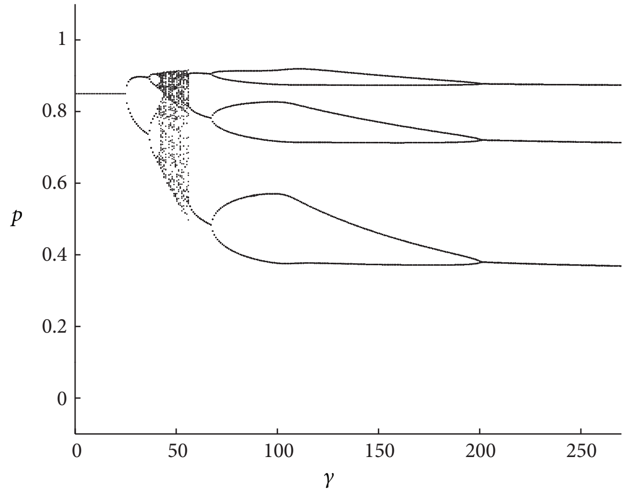


Figure 3: $u_{11} = 1$, $u_{12} = 0.5$, $u_{22} = 0$, $\xi = 0.85$, and $\beta = 0.4$. As γ is sufficiently large, there are stable 3-periodic points (at $\gamma \simeq 56.5$), and then stable 6-periodic points occur at $\gamma \simeq 67.5$. And stable 3-periodic points occur at $\gamma \simeq 201$ again.

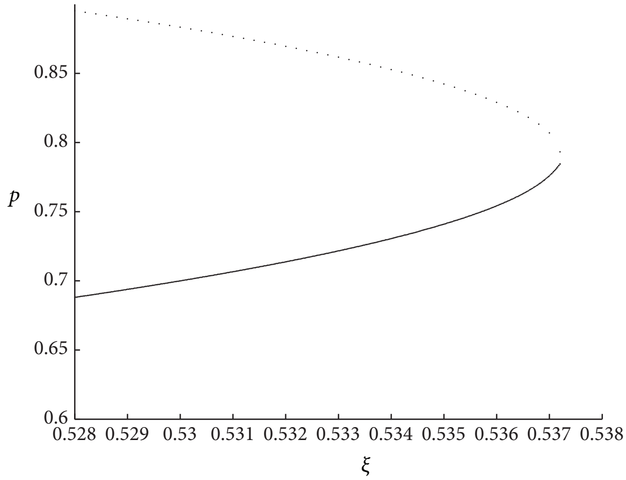


Figure 4: $u_{11} = 0.5$, $u_{12} = 1$, $u_{22} = 0$, $\beta = 0.6$, and $\gamma = 10$. A saddle-node bifurcation happens for (p^*, F^*, ξ^*), where $p^* = 0.7916666665, F^* = 0.4285714286$, and $\xi^* = 0.5372023808$. Two new polymorphic phenotypic equilibria are created for $\xi < \xi^*$ and disappear for $\xi > \xi^*$.

then the eigenvalues of the characteristic equation are complex conjugate. When $\gamma = \gamma_0 = (\beta - 2)/(k_{11}\beta + 2k_{22})$, (44) is equivalent to

$$k_{11} < 0. \tag{45}$$

If condition (45) is satisfied, we can calculate that

$$\begin{gathered} d = \frac{d\left|\lambda(\gamma)\right|}{d\gamma}\bigg|_{\gamma = \gamma_0} = -\frac{1}{2}\left(\frac{\beta}{2}k_{11} + k_{22}\right) \neq 0, \\ \lambda^j(\gamma_0) \neq 1, \quad j = 1, 2, 3, 4, \quad \left|\lambda(\gamma_0)\right| = N(\gamma_0)^{1/2}. \end{gathered} \tag{46}$$

Next, we study the normal form of (10) when $\gamma = \gamma_0$.

Use the translation

$$\begin{pmatrix} p \\ F \end{pmatrix} = \begin{pmatrix} -\dfrac{1}{k_{21}}\sqrt{-k_{11}\left[\left(\dfrac{\beta+2}{4}\right)^2 k_{11} + k_{22}\right]} & -\dfrac{\beta+2}{4}\dfrac{k_{11}}{k_{21}} \\ 0 & 1 \end{pmatrix} \times \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} p^* \\ F^* \end{pmatrix}; \tag{47}$$

system (10) becomes

$$\begin{pmatrix} x' \\ y' \end{pmatrix} = \begin{pmatrix} -\dfrac{M(\gamma_0)}{2} & -\dfrac{\sqrt{4 - M(\gamma_0)^2}}{2} \\ \dfrac{\sqrt{4 - M(\gamma_0)^2}}{2} & -\dfrac{M(\gamma_0)}{2} \end{pmatrix} \times \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} H(x, y) \\ G(x, y) \end{pmatrix}, \tag{48}$$

where $m = -(1/k_{21})\sqrt{-k_{11}[((\beta + 2)/4)^2 k_{11} + k_{22}]}$, $n = -((\beta + 2)/4)(k_{11}/k_{21})$,

$$\begin{aligned} H(x, y) &= \frac{1}{m}\left(f(x, y) - p^*\right) - \frac{n}{m}\left(g(x, y) - F^*\right) \\ &\quad + \frac{M(\gamma_0)}{2}x + \frac{\sqrt{4 - M(\gamma_0)^2}}{2}y, \\ G(x, y) &= \left(g(x, y) - F^*\right) \\ &\quad - \frac{\sqrt{4 - M(\gamma_0)^2}}{2}x + \frac{M(\gamma_0)}{2}y. \end{aligned} \tag{49}$$

In order for system (48) to undergo Neimark-Sacker bifurcation, we require that the following discriminatory quantity C_0 is not zero [9]:

$$C_0 = -\mathrm{Re}\left[\frac{(1 - 2\lambda)\bar{\lambda}^2}{1 - \lambda}\xi_{11}\xi_{20}\right] - \frac{1}{2}\left|\xi_{11}\right|^2 - \left|\xi_{02}\right|^2 + \mathrm{Re}\left(\bar{\lambda}\xi_{21}\right), \tag{50}$$

where

$$\begin{aligned} \xi_{20} &= \frac{1}{8}\left[\left(H_{xx} - H_{yy} + 2G_{xy}\right) + i\left(G_{xx} - G_{yy} - H_{xy}\right)\right], \\ \xi_{11} &= \frac{1}{4}\left[\left(H_{xx} + H_{yy}\right) + i\left(G_{xx} + G_{yy}\right)\right], \\ \xi_{02} &= \frac{1}{8}\left[\left(H_{xx} - H_{yy} - 2G_{xy}\right) + i\left(G_{xx} - G_{yy} + 2H_{xy}\right)\right], \\ \xi_{21} &= \frac{1}{16}\left[\left(H_{xxx} + H_{xyy} + G_{xxy} + G_{yyy}\right)\right. \\ &\quad \left. + i\left(G_{xxx} + G_{xyy} - H_{xxy} - H_{yyy}\right)\right]. \end{aligned} \tag{51}$$

From previous analysis and the theorem in [9], we have the following theorem.

Proposition 8. *Suppose that* (p^*, F^*) *is a polymorphic phenotypic equilibrium of system* (10). *If* $k_{11} < 0$ *and* $C_0 \neq 0$, *then system* (10) *undergoes a Neimark-Sacker bifurcation at* (p^*, F^*) *for* $\gamma_0 = (\beta - 2)/(k_{11}\beta + 2k_{22})$.

Moreover, if $d = -(1/2)((\beta/2)k_{11} + k_{22}) < 0$ and $C_0 < 0$, then an attracting invariant closed curve bifurcates from (p^*, F^*) for $\gamma < \gamma_0$. If $d = -(1/2)((\beta/2)k_{11} + k_{22}) < 0$ and $C_0 > 0$, then a repelling invariant closed curve bifurcates from (p^*, F^*) for $\gamma > \gamma_0$.

Example 9. Let $u_{11} = 0.8$, $u_{12} = 0.4$, $u_{22} = 1$, $\beta = 0.75$, and $\xi = 0.776$. We have that $(p^*, F^*) = (0.8, 0.6)$ is a polymorphic phenotypic equilibrium which satisfies $k_{11} < 0$. According to $C_0 = -3.1284538 < 0$, and $d = -(1/2)((\beta/2)k_{11} + k_{22}) < 0$, we have that the invariant closed curve bifurcates from (p^*, F^*) for $\gamma < \gamma_0 = -65.76178451$ being attracting. Let $u_{11} = 0.5$, $u_{12} = 1$, $u_{22} = 0$, $\xi = 0.549287$, and $\beta = 38/69$. We have that $(p^*, F^*) = (0.79, 0.38)$ is a polymorphic phenotypic equilibrium which satisfies $k_{11} < 0$. According to $C_0 = 2.5988353 > 0$ and $d = -(1/2)((\beta/2)k_{11} + k_{22}) < 0$, the invariant closed curve bifurcates from (p^*, F^*) for $\gamma > \gamma_0 = -34.72413828$ being repelling.

5. Conclusion

A discrete population genetics model with partial selfing selection is investigated. We assume that each individual can reproduce by selfing or random outcrossing with probability β or $1 - \beta$ $(0 < \beta < 1)$, respectively, in the population. Some population, such as human population, does not mate at random. So, the partial selfing selection model is reasonable.

In this paper, the conditions for the stability of polymorphic phenotypic equilibria are obtained by the Jury conditions and the center manifold theorem. ESS is not the necessary condition of the stability of the polymorphic phenotypic equilibria. The theoretical analysis and numerical simulations present the existence of stable and unstable period doubling bifurcations, saddle-node bifurcation, and Neimark-Sacker bifurcation. Numerical simulations exhibit more complex dynamical behavior of the genetic system under partial selfing selection.

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