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BIFURCATIONS OF A TWO-DIMENSIONAL DISCRETE-TIME PREDATOR-PREY MODEL

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Dedicated to the 65th birthday of the dear Professor Mehmed Nurkanović

ABSTRACT. In this paper, we study the dynamics and bifurcation of a two-dimensional discrete-time predator-prey model. The existence and local stability of the equilibrium points of the model are analyzed algebraically. It is shown that the model can undergo a transcritical bifurcation at the equilibrium point on the x-axis and a Neimark-Sacker bifurcation in a small neighborhood of the unique positive equilibrium point. Some numerical simulations are presented to illustrate our theoretical results.

1. INTRODUCTION AND PRELIMINARIES

The ecological theory aims to provide reasonable explanations for interactions among biological populations in nature using dynamic models to predict the distribution and structure of populations. Since Lotka and Volterra constructed the well-known Lotka-Volterra ecosystem model, the use of mathematical models to explain complex ecological properties has become common in biology. Among them, predator-prey systems, which can explain predation relationships, have been intensively studied and made significant progress in the 1980s (see [1,9]).

The classical and well known Lotka–Volterra model is given by

$$\begin{aligned} x' &= rx - \alpha xy, \\ y' &= -dy + \gamma xy, \end{aligned} \tag{1.1}$$

where $r > 0$ is the growth rate (in the absence of the predator) and $d > 0$ represents the decay rate of the predator in the absence of the prey. The positive parameters α and γ determine the consumption rate and consumption-energy rate, respectively. A criticism of the model is the structural instability, since a small change in the equations can eliminate the existence of periodic orbits (see [15]). Another criticism of (1.1) is the assumption of exponential growth for the prey population.

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Verhulst in [25] introduced the so-called logistic growth model, assuming limited resources and resulting in convergence to a positive carrying capacity, known as a modified predator-prey model

$$\begin{aligned} x' &= rx\left(1-\tfrac{x}{K}\right)-\alpha xy, \\ y' &= -dy+\gamma xy, \end{aligned} \tag{1.2}$$

where the parameters r, α, d, and γ have the same biological interpretation as in (1.1) and the additional parameter $K > 0$ that represents the carrying capacity of the prey population was introduced. The dynamics of (1.2) differs from the behavior of the solutions of the classical Lotka–Volterra model (1.1).

In contrast to (1.1), where solutions cycle periodically about the coexistence equilibrium with x-amplitude and y-amplitude dependent on initial conditions, no periodic orbits exist for (1.2). If the prey consumption-energy rate of the predator γ satisfies $\gamma > \frac{d}{K}$, then the coexistence equilibrium is globally asymptotically stable. If, however, $\gamma < \frac{d}{K}$, then the prey-only equilibrium is globally asymptotically stable (see [3]). In the ecological community, many populations do not vary in numbers continuously. Therefore, it is particularly important to study discrete models. A discrete model has multiple periodic bifurcations, chaotic properties and generates periodic orbits, while a continuous one produces only simple S-shaped curves (see [5,11,13,14,21]). In [24] the authors observed a discrete predator–prey model based on the same assumptions as (1.2) because discrete mathematical models are often more appropriate for modelling non overlapping generations, such as monocarpic plants and semelparous fish species. A discretization of a predator–prey model that is related to our model was introduced in [20] as

$$\begin{aligned} X_{n+1} &= \frac{(1+r_1\varphi_1(h))X_n}{1+\varphi_1(h)(a_{11}X_n+a_{12}Y_n)}, \\ Y_{n+1} &= \frac{(1+r_2\varphi_2(h)-\varphi_2(h)a_{21}X_n)Y_n}{1+\varphi_2(h)a_{22}Y_n}. \end{aligned} \tag{1.3}$$

In our paper, we consider a predator-prey model after conducting the following analysis. The population at time $n+1$ can be described as a factor $f(n)$ of the population at time n, that is, $X_{n+1} = f(n)X_n$. The factor $f(n)$ is determined by growth and decline processes. Thus, we may express the population at time $n+1$ as

$$X_{n+1} = f(n)X_n = \frac{1+p(n)}{1+q(n)}X(n),$$

where $p(n)$ captures the processes contributing to the increase of the population and $q(n)$ captures the processes contributing to the decrease in the population between time steps n and $n+1$. We can consider the interaction of several species X_i, for $i = 1,2,\ldots,k$. In this case, species X_i at time $n+1$ is expressed by

$$X_i(n+1) = \frac{1+p_i(t,X_1,X_2,\ldots,X_k)}{1+q_i(t,X_1,X_2,\ldots,X_k)}X_i(n). \tag{1.4}$$

In our case, X_i, for $i = 1,2$, represents the prey and the predator. We assume that the prey population increases with a constant growth rate $r > 0$. Thus, the growth contribution is $p(n) = r$. We also assume that competition and predation are the factors responsible for any decline in the prey population. More precisely, for the prey population, we consider

$$q(n) = \frac{r}{K}X_n + \alpha Y_n,$$

where the carrying capacity is given by $K > 0$ and the intra-specific competition for the prey population is given by $\frac{r}{K}$ and predation rate $\alpha > 0$. We therefore obtain the recurrence for the prey as

$$X_{n+1} = \frac{1+r}{1+\frac{r}{K}X_n + \alpha Y_n}X_n. \tag{1.5}$$

For the predator population, we assume that the predator population declines with a constant rate $d > 0$, and captures the decline due to predation resulting in $q(n) = d + Y_n$, and the growth rate depends on the consumption of the prey, and hence is proportional to the size of the prey population. We therefore consider $p(n) = \gamma X_n$, where $\gamma > 0$ is the prey consumption-energy rate of the predator. This results in the recurrence for the predator

$$Y_{n+1} = \frac{(1+\gamma X_n)}{1+d+Y_n}Y_n. \tag{1.6}$$

Hence, we analyse the following model

$$\begin{aligned} X_{n+1} &= \frac{1+r}{1+\frac{r}{K}X_n + \alpha Y_n}X_n, \\ Y_{n+1} &= \frac{1+\gamma X_n}{1+d+Y_n}Y_n, \end{aligned} \tag{1.7}$$

where the initial conditions X_0, Y_0 are assumed to be nonnegative and the parameters r, K, α, γ and d are assumed to be positive.

The rest of this paper is organized as follows. The second section presents the local stability of the equilibrium solutions. In the third section, we prove that the system exhibits transcritical and Neimark-Sacker bifurcation. Neimark–Sacker bifurcation, as an interesting phenomenon, has been examined in many papers using normal form theory, which simplifies dynamical systems by reducing the number of terms in the equations and introducing symmetry into the system (see [7, 10, 12, 17, 18]).

2. Local stability of equilibrium points

First we will determine the equilibrium points of system (1.7). From

$$\overline{X} = \frac{1+r}{1+\frac{r}{K}\overline{X}+\alpha\overline{Y}}\overline{X}, \quad \overline{Y} = \frac{1+\gamma\overline{X}}{1+d+\overline{Y}}\overline{Y}$$

we obtain the following equilibrium points $E_0 = (0,0)$, $E_1 = (K,0)$, $E_2 = (0,-d)$ and unique positive equilibrium $E_+ = \left(\frac{K(r+\alpha d)}{r+K\alpha\gamma}, \frac{r(K\gamma-d)}{r+K\alpha\gamma}\right)$ for $\gamma > \frac{d}{K}$. The equilibrium point E_2 is inadequate because of its biological interpretation. Denote with T the map associated with the system (1.7), i.e.,

$$T\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} f(x,y) \\ g(x,y) \end{pmatrix},$$

for

$$f(x,y) = \frac{(1+r)x}{1+\frac{r}{K}x+\alpha y}, \quad g(x,y) = \frac{(1+\gamma x)y}{1+d+y}. \tag{2.1}$$

The Jacobian matrix of the map T at the equilibrium point $E = (x,y)$ is given by

$$J_T(x,y) = \begin{bmatrix} \dfrac{(r+1)K^2(y\alpha+1)}{(K+rx+Ky\alpha)^2} & -\dfrac{(r+1)K^2 x\alpha}{(K+rx+Ky\alpha)^2} \\ \dfrac{\gamma y}{d+y+1} & \dfrac{(d+1)(x\gamma+1)}{(d+y+1)^2} \end{bmatrix}. \tag{2.2}$$

Hence, the partial derivatives of the functions f and g in (1.7) satisfy

$$\frac{\partial f(x,y)}{\partial x} = \frac{(r+1)K^2(y\alpha+1)}{(K+rx+Ky\alpha)^2} > 0, \quad \frac{\partial f(x,y)}{\partial y} = -\frac{(r+1)K^2 x\alpha}{(K+rx+Ky\alpha)^2} < 0,$$

$$\frac{\partial g(x,y)}{\partial x} = \frac{\gamma y}{d+y+1} > 0, \quad \frac{\partial g(x,y)}{\partial y} = \frac{(d+1)(x\gamma+1)}{(d+y+1)^2} > 0.$$

The following Lemma states that the solutions of System 1.7 are bounded.

Lemma 2.1. *The solutions of System (1.7) with nonnegative initial conditions are bounded for $n \geq 0$. Precisely, $X_n \in [0, \max\{X_0, K\}]$ and $Y_n \in [0, 1+\gamma \cdot \max\{X_0, K\}]$ for all $n \geq 0$.*

Proof. Notice that $X_n, Y_n \geq 0$ holds for nonnegative initial conditions. Additionally, if $X_0 = 0$, then $X_n = 0$ for all $n \geq 0$. If $Y_0 = 0$, then $Y_n = 0$ for all $n \geq 0$. If $X_0 > 0$ and $Y_0 \geq 0$, then $X_n > 0$ for all $n \geq 0$. If $X_0 \geq 0$ and $Y_0 > 0$, then $Y_n > 0$ for all $n \geq 0$.

As we have shown, f is increasing in the first variable, but it does not imply that the sequence of iterates, X_n, is increasing. In fact, X_n is increasing if the forward operator, $\triangle X_n = X_{n+1} - X_n$ is positive. We will distinguish two scenarios, when $X_n \leq K$ and $X_n > K$. If $X_n \leq K$, then

$$X_{n+1} = f(X_n, Y_n) \leq f(K, Y_n) = \frac{(1+r)K}{1+r+\alpha Y_n} \leq K.$$

For $X_n > K$, since

$$\triangle X_n = X_{n+1} - X_n = \frac{1+r}{1+\frac{r}{K}X_n + \alpha Y_n} X_n - X_n = \frac{X_{n+1}}{1+r}\left[r\left(1-\frac{X_n}{K}\right) - \alpha Y_n\right] < 0,$$

we have that X_n decreases in that case. Then X_n is convergent. Suppose X_n does not converge to K. Then $\lim_{n\to\infty} X_n = \widehat{X} > K$. However,

$$\begin{aligned}\widehat{X} &= \lim_{n\to\infty} X_{n+1} = \lim_{n\to\infty} \frac{(1+r)X_n}{1+\frac{r}{K}X_n + \alpha Y_n} \\ &\leq \lim_{n\to\infty} \frac{(1+r)X_n}{1+\frac{r}{K}X_n} < \frac{(1+r)\widehat{X}}{1+r} = \widehat{X},\end{aligned}$$

which is a contradiction. This implies that $X_n \leq \max\{X_0, K\}$ for all $n \geq 0$. We now show that Y_n is bounded. Since,

$$Y_{n+1} = \frac{(1+\gamma X_n)Y_n}{1+d+Y_n} < 1 + \gamma X_n \leq 1 + \gamma \cdot \max\{X_0, K\},$$

the conclusion follows. □

The Jacobian matrix at equilibrium E_0 is $J_T(E_0) = \begin{bmatrix} 1+r & 0 \\ 0 & \frac{1}{1+d} \end{bmatrix}$. It is obvious that $\lambda_1 = 1 + r > 1$ and $\lambda_2 = \frac{1}{1+d} < 1$, so the equilibrium point E_0 is unstable, more precisely a saddle point for all values of parameters.

Furthermore,

$$\begin{aligned}T(0,y) &= \left(0, \frac{y}{1+d+y}\right) = \left(0, \frac{yd}{(1+d)(d+y) - y}\right), \\ T^2(0,y) &= \left(0, \frac{yd}{(1+d)^2(d+y) - y}\right), \\ &\vdots \\ T^n(0,y) &= \left(0, \frac{yd}{(1+d)^n(d+y) - y}\right).\end{aligned}$$

So, $\lim_{n\to\infty} T^n(0,y) = (0,0)$ which implies that the y-axis is a stable manifold for equilibrium E_0. Similarly,

$$T(x,0) = \left(\frac{K(1+r)x}{K+rx}, 0\right),$$

$$T^2(x,0) = \left(\frac{K(1+r)^2 x}{K+\left((1+r)^2-1\right)x}, 0\right),$$

$$\vdots$$

$$T^n(x,0) = \left(\frac{K(1+r)^{2^{n-1}} x}{K+\left((1+r)^{2^{n-1}}-1\right)x}, 0\right).$$

Hence, $\lim_{n\to\infty} T^n(x,0) = (K,0)$ which implies that the x-axis is an unstable manifold for the equilibrium point E_0.
This completes the proof of the following Lemma.

Lemma 2.2. *Consider System* (1.7) *with positive initial conditions. The equilibrium point E_0 is a saddle point, with the x-axis and y-axis representing the unstable and stable manifolds, respectively.*

For visual ilustration see Figure 1.

The Jacobian matrix at equilibrium E_1 is $J_T(E_1) = \begin{bmatrix} \frac{1}{1+r} & -\frac{K\alpha}{1+r} \\ 0 & \frac{1+K\gamma}{1+d} \end{bmatrix}$. The corresponding eigenvalues are $\lambda_1 = \frac{1}{1+r} < 1$ and

$$\lambda_2 = \frac{K\gamma+1}{d+1} \begin{cases} < 1 \text{ for } K\gamma < d, \\ = 1 \text{ for } K\gamma = d, \\ > 1 \text{ for } K\gamma > d. \end{cases}$$

For $K\gamma = d$, we will determine conditions for local semi-stability of the nonhyperbolic equilibrium point E_1 using center manifold theory. First, we shift the equilibrium point E_1 of system (1.7) to the origin by letting $u_n = x_n - K$, $v_n = y_n$. So, we have the following system

$$\begin{aligned} u_{n+1} &= \frac{u_n - \alpha K v_n}{1+\frac{r}{K}u_n + r + \alpha v_n}, \\ v_{n+1} &= \frac{(1+\frac{d}{K}u_n + d)v_n}{1+d+v_n}, \end{aligned} \tag{2.3}$$

which has $(0,0)$ as an equilibrium point. The Jacobian matrix J_0 at the zero equilibrium is $J_0 = \begin{bmatrix} \frac{1}{1+r} & -\frac{\alpha K}{1+r} \\ 0 & 1 \end{bmatrix}$. The corresponding eigenvalues are $\lambda_1 = \frac{1}{1+r}$, $\lambda_2 = 1$, and corresponding eigenvectors $v_1 = \begin{bmatrix} 1 & 0 \end{bmatrix}^T$, $v_2 = \begin{bmatrix} -\frac{\alpha K}{r} & 0 \end{bmatrix}^T$. System (2.3) can be written as

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} = J_0 \begin{bmatrix} u_n \\ v_n \end{bmatrix} + \begin{bmatrix} \xi(u_n, v_n) \\ \eta(u_n, v_n) \end{bmatrix} \tag{2.4}$$

where

$$\begin{aligned} \xi(u_n, v_n) = & -\frac{r}{K(1+r)^2}u_n^2 + \frac{(r-1)\alpha}{(1+r)^2}u_n v_n + \frac{K\alpha^2}{(1+r)^2}v_n^2, \\ \eta(u_n, v_n) = & \frac{d}{(1+d)K}u_n v_n - \frac{1}{1+d}v_n^2. \end{aligned} \tag{2.5}$$

Let

$$\begin{bmatrix} u_n \\ v_n \end{bmatrix} = P \begin{bmatrix} t_n \\ s_n \end{bmatrix}, \tag{2.6}$$

where P is the matrix that diagonolizes J_0 defined by $P = \begin{bmatrix} 1 & -\frac{K\alpha}{r} \\ 0 & 1 \end{bmatrix}$. The inverse matrix of P is $P^{-1} = \begin{bmatrix} 1 & \frac{K\alpha}{r} \\ 0 & 1 \end{bmatrix}$ and $P^{-1}J_0P = \begin{bmatrix} \frac{1}{r+1} & 0 \\ 0 & 1 \end{bmatrix}$. By (2.6) we have

$$\begin{aligned} u_n = & t_n - \tfrac{K}{r}\alpha s_n, \\ v_n = & s_n, \end{aligned} \tag{2.7}$$

and substituting (2.7) into (2.5) we have

$$\begin{aligned} \xi(u_n, v_n) = & \xi_1(t_n, s_n) = \frac{\alpha}{r+1}s_n t_n - \frac{r}{K(r+1)^2}t_n^2, \\ \eta(u_n, v_n) = & \eta_1(t_n, s_n) = \frac{d}{(1+d)K}s_n t_n - \frac{r+d\alpha}{r(d+1)}s_n^2. \end{aligned} \tag{2.8}$$

Thus (2.4) can be written as

$$P\begin{bmatrix} t_{n+1} \\ s_{n+1} \end{bmatrix} = J_0 P \begin{bmatrix} t_n \\ s_n \end{bmatrix} + \begin{bmatrix} \xi_1(t_n, s_n) \\ \eta_1(t_n, s_n) \end{bmatrix},$$

or

$$\begin{bmatrix} t_{n+1} \\ s_{n+1} \end{bmatrix} = P^{-1}J_0P \begin{bmatrix} t_n \\ s_n \end{bmatrix} + P^{-1}\begin{bmatrix} \xi_1(t_n, s_n) \\ \eta_1(t_n, s_n) \end{bmatrix},$$

i.e.,

$$\begin{bmatrix} t_{n+1} \\ s_{n+1} \end{bmatrix} = \begin{bmatrix} \dfrac{1}{r+1} & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} t_n \\ s_n \end{bmatrix} + \begin{bmatrix} \xi_2(t_n, s_n) \\ \eta_2(t_n, s_n) \end{bmatrix},$$

where

$$\begin{aligned}\xi_2(t_n,s_n) &= -\frac{K\alpha(r+d\alpha)}{r^2(d+1)}s_n^2+\frac{(d+r+2dr)\alpha}{r(r+1)(d+1)}s_nt_n-\frac{r}{K(r+1)^2}t_n^2,\\ \eta_2(t_n,s_n) &= -\frac{r+d\alpha}{r(d+1)}s_n^2+\frac{d}{K(d+1)}s_nt_n.\end{aligned}$$

Let $t=\varkappa(s)=\Omega(s)+O(s^4)$, where $\Omega(s)=As^2+Bs^3$, $A,\ B\in\mathbb{R}$ is the central manifold, and where map $\varkappa(s)$ must satisfy the center manifold equation

$$\varkappa(\lambda_2 s+\eta_2(\varkappa(s),s))-\lambda_1\varkappa(s)-\xi_2(\varkappa(s),s)=0. \tag{2.9}$$

From (2.9) we obtain the following system

$$\begin{aligned}\frac{B}{r+1}-B+\frac{2A(r+d\alpha)}{r(d+1)}+\frac{\alpha A(d+r+2dr)}{r(d+1)(r+1)} &= 0,\\ A-\frac{A}{r+1}+\frac{K\alpha(r+d\alpha)}{r^2(d+1)} &= 0,\end{aligned}$$

with the solution

$$A=-\frac{K\alpha(r+1)(r+d\alpha)}{r^3(d+1)},$$

$$B=-\frac{K\alpha(r+1)\left(2r^2+r(\alpha+4d\alpha+2)+3d\alpha\right)(r+d\alpha)}{r^5(d+1)^2}.$$

Finally, we obtain that the dynamics of the system (1.7) is reduced to the dynamics of the following one-dimensional map

$$G(s)=s+\eta_2(\Omega(s),s)=s-\frac{r+d\alpha}{r(d+1)}s^2-\frac{\alpha d(r+d\alpha)(r+1)}{r^3(d+1)^2}s^3.$$

Since $\frac{d}{ds}G(0)=1$ and $\frac{d^2}{ds^2}G(0)=-\frac{2(r+d\alpha)}{r(d+1)}<0$, from Theorem 1.6 of [16], the equilibrium E_1 of (1.7) is an unstable fixed point, that is semi-stable from above. Recall the fact that $\lim_{n\to\infty}T^n(x,0)=(K,0)$.
This completes the proof of the following Lemma.

Lemma 2.3. *Consider System* (1.7) *with positive initial conditions and* $\gamma_0=\frac{d}{K}$. *The equilibrium point* E_1 *is LAS for* $\gamma<\gamma_0$, *a non-hyperbolic point of semi-stable type (stable from above) for* $\gamma=\gamma_0$ *and a saddle point for* $\gamma>\gamma_0$ *with the x-axis as a stable manifold.*

For visual representation see Figure 1.
In order to determine the stability of the positive equilibrium $E_+=\left(\frac{K(r+\alpha d)}{r+K\alpha\gamma},\frac{r(K\gamma-d)}{r+K\alpha\gamma}\right)$ for $K\gamma>d$ we will use the following Lemma which can be easily proved by applying the relations between roots and coefficients of the quadratic equation, see [4,6].

Lemma 2.4. *Assume that $\Phi(\lambda)=\lambda^2-TrJ_T\lambda+DetJ_T$ is a polynomial associated to the characteristic equation. Suppose that $\Phi(1)>0$ and λ_1 and λ_2 are the two roots of $\Phi(\lambda)=0$. Then*

a) $|\lambda_1|<1$ and $|\lambda_2|<1$ iff $\Phi(-1)>0$ and $\Phi(0)<1$.
b) $|\lambda_1|>1$ and $|\lambda_2|>1$ iff $\Phi(-1)>0$ and $\Phi(0)>1$.
c) $|\lambda_1|<1$ and $|\lambda_2|>1$ (or $|\lambda_1|>1$ and $|\lambda_2|<1$) iff $\Phi(-1)<0$.
d) λ_1 and λ_2 are complex and $|\lambda_1|=|\lambda_2|=1$ iff $(TrJ_T)^2-4DetJ_T<0$ and $DetJ_T=1$.
e) $\lambda_1=-1$ and $\lambda_2\neq-1$ iff $\Phi(-1)=0$ and $TrJ_T\neq-2$,
f) $\lambda_1=\lambda_2=-1$ iff $\Phi(-1)=0$ and $TrJ_T=-2$.

The Jacobian matrix of equilibrium $E_+=(x,y)$, by applying the equilibrium relations

$$\begin{aligned} &rx+\alpha yK=rK,\\ &d+y=x\gamma, \end{aligned} \tag{2.10}$$

has the form

$$J_T(E_+)=\begin{bmatrix} \dfrac{\alpha y+1}{r+1} & -\dfrac{\alpha x}{r+1} \\ \dfrac{\gamma y}{\gamma x+1} & \dfrac{d+1}{\gamma x+1} \end{bmatrix}.$$

Further, the characteristic polynomial of the Jacobian matrix $J(E_+)$ is given by

$$\Phi(\lambda)=\lambda^2-\left(\frac{\alpha y+1}{r+1}+\frac{d+1}{\gamma x+1}\right)\lambda+\frac{(d+1)(y\alpha+1)+\alpha\gamma xy}{(r+1)(\gamma x+1)}. \tag{2.11}$$

First, let us check if $\Phi(1)>0$ in E_+. To facilitate easier calculation, let us introduce a change $\beta=r(K\gamma-d)>0$ from which $K=\frac{\beta+rd}{r\gamma}$, $x=\frac{(\beta+dr)(r+d\alpha)}{\gamma(\alpha\beta+r^2+dr\alpha)}$ and $y=\frac{\beta r}{\alpha\beta+r^2+dr\alpha}$. Now,

$$\Phi(1)=\frac{r\beta(r+d\alpha)}{(r+1)(r^2(d+1)+r(\alpha d^2+\alpha d+\beta)+\alpha\beta(d+1))}>0,$$

and $\lambda_1\neq1$, $\lambda_2\neq1$ in E_+.
Further, for

$$\begin{aligned} \varphi_0(\beta) \;=\; &\beta^2\alpha\left(3r^2+r(4\alpha+5d\alpha+2)+4\alpha(d+1)\right)\\ &+\beta r\left(r^2+r(6\alpha+7d\alpha+2)+8\alpha(d+1)\right)(r+d\alpha)\\ &+2r^2(r+2)(d+1)(r+d\alpha)^2, \end{aligned}$$

we have

$$\Phi(-1)=\frac{\varphi_0(\beta)}{(r+1)(r^2+dr\alpha+\alpha\beta)(r^2(d+1)+r(\alpha d^2+\alpha d+\beta)+\alpha\beta(d+1))},$$

and $\Phi(-1)>0$. So, $\lambda_1\neq-1$, $\lambda_2\neq-1$ in E_+.

Let us calculate $\Phi(0)-1=\lambda_1\lambda_2-1$ in E_+. For

$$\varphi_1(\beta)=\beta^2\alpha(d\alpha-1)-\beta r(r+\alpha+1)(r+d\alpha)-r^2(d+1)(r+d\alpha)^2,$$

we obtain

$$\lambda_1\lambda_2-1=\frac{r\varphi_1(\beta)}{(r+1)(r^2+dr\alpha+\alpha\beta)(r^2(d+1)+r(\alpha d^2+\alpha d+\beta)+\alpha\beta(d+1))}.$$

Notice that

$$\varphi_1(\beta)=0\Leftrightarrow\beta=\beta_\pm=\frac{r(r+d\alpha)(r+\alpha+1\pm\Psi)}{2\alpha(d\alpha-1)},$$

where

$$\Psi=\sqrt{r^2+2r(\alpha+1)+(\alpha+2d\alpha-1)^2}. \tag{2.12}$$

For $d\alpha-1>0$ we have $\beta_-<0$, $r(K\gamma-d)=\beta_+$ or $\gamma=\frac{d}{K}+\frac{\beta_+}{rK}=\gamma_c$. We distinguish the following two cases .

1.) If $d\alpha-1\leq 0$, then $\lambda_1\lambda_2-1<0$, i.e., $\lambda_1\lambda_2<1$ and by using Lemma 2.4 we obtain $|\lambda_{1,2}|<1$.
2.) If $d\alpha-1>0$, then
   a) $\lambda_1\lambda_2=1$ for $\gamma=\gamma_c$,
   b) $\lambda_1\lambda_2<1$ for $\gamma<\gamma_c$,
   c) $\lambda_1\lambda_2>1$ for $\gamma>\gamma_c$,

   where

$$\gamma_c=\frac{d}{K}+\frac{(r+d\alpha)(r+\alpha+1+\Psi)}{2\alpha(d\alpha-1)K}. \tag{2.13}$$

Hence, if $d\alpha\leq 1$ or ($d\alpha>1$ and $\gamma<\gamma_c$), we obtain $\Phi(0)=\lambda_1\lambda_2<1$, i.e., E_+ is LAS. Further, if $d\alpha>1$ and $\gamma>\gamma_c$, we get $\Phi(0)=\lambda_1\lambda_2>1$, i.e., E_+ is a repeller. Since,

$$\varphi_2(\beta)=\beta^2\alpha(r+1)+\beta r(r+d\alpha)(2r+\alpha+d\alpha+1)+r^2(d+1)(r+d\alpha)^2>0,$$

we have

$$\lambda_1+\lambda_2-2=\frac{-r\varphi_2(\beta)}{(r+1)(r^2+dr\alpha+\alpha\beta)(\beta(r+\alpha(d+1))+r(d+1)(r+d\alpha))}<0.$$

For $d\alpha>1$ and $\gamma=\gamma_c$, $DetJ_T=\Phi(0)=\lambda_1\lambda_2=1$ holds, which implies

$$(TrJ_T)^2-4DetJ_T=(\lambda_1+\lambda_2)^2-4\lambda_1\lambda_2<2^2-4\cdot 1=0.$$

So, by Lemma 2.4, equilibrium E_+ is a non-hyperbolic point with complex-conjugate eigenvalues $|\lambda_{1,2}|=1$.

Thus, we have proved the following Theorem:

Theorem 2.1. *Let α,γ,r,d,K be positive parameters such that $\gamma>\frac{d}{K}$ and γ_c is given by (2.13). The unique positive equilibrium point E_+ of the System* (1.7) *is:*

(1) locally asymptotically stable if

$$d\alpha \le 1 \quad \textit{and} \quad \gamma > \frac{d}{K},$$

or

$$d\alpha > 1 \quad \textit{and} \quad \frac{d}{K} < \gamma < \gamma_c,$$

(2) non-hyperbolic with complex conjugate eigenvalues if

$$d\alpha > 1 \quad \textit{and} \quad \gamma = \gamma_c,$$

(3) a repeller if

$$d\alpha > 1 \quad \textit{and} \quad \gamma > \gamma_c.$$

3. BIFURCATIONS IN THE SYSTEM

In this section, we prove that system exhibits two type of bifurcations: transcritical and Neimark-Sacker bifurcation.

Theorem 3.1. *If* $\gamma = \frac{d}{K}$, *then* $E_1 = E_+$ *and System* (1.7) *undergoes a transcritical bifurcation.*

Proof. According to the theorems in [2, 22, 23], one interior equilibrium point branches off from E_1 when γ passes the threshold $\gamma_0 = \frac{d}{K}$.
Recall that the Jacobian matrix of map T at equilibrium E_1 for $\gamma = \gamma_0 = \frac{d}{K}$ is

$$JT_\gamma(E_1,\gamma_0) = J_T\,(K,0)\,|_{\gamma_0=\frac{d}{K}} = \begin{bmatrix} \dfrac{1}{1+r} & -\dfrac{K\alpha}{1+r} \\ 0 & 1 \end{bmatrix}.$$

Let the eigenvectors $v = [-\frac{K\alpha}{r}, 1]^T$ and $w = [0,1]^T$ indicate the eigenvectors corresponding to $\lambda_2 = 1$ of $JT_\gamma(E_1,\gamma_0)$ and $J^T T_\gamma(E_1,\gamma_0)$, respectively. We can get

$$T'_\gamma = \begin{bmatrix} 0 \\ \dfrac{xy}{1+d+y} \end{bmatrix} \Rightarrow T'_\gamma(E_1,\gamma_0) = \begin{bmatrix} 0 \\ 0 \end{bmatrix},$$

and

$$JT'_\gamma = \begin{bmatrix} 0 & 0 \\ \dfrac{y}{1+d+y} & \dfrac{x(1+d)}{(1+d+y)^2} \end{bmatrix} \Rightarrow JT'_\gamma(E_1,\gamma_0) = \begin{bmatrix} 0 & 0 \\ 0 & \dfrac{K}{1+d} \end{bmatrix},$$

i.e.,

$$JT'_\gamma(E_1,\gamma_0)v = \begin{bmatrix} 0 & 0 \\ 0 & \dfrac{K}{1+d} \end{bmatrix} \begin{bmatrix} -\dfrac{K\alpha}{r} \\ 1 \end{bmatrix} = \begin{bmatrix} 0 \\ \dfrac{K}{1+d} \end{bmatrix}.$$

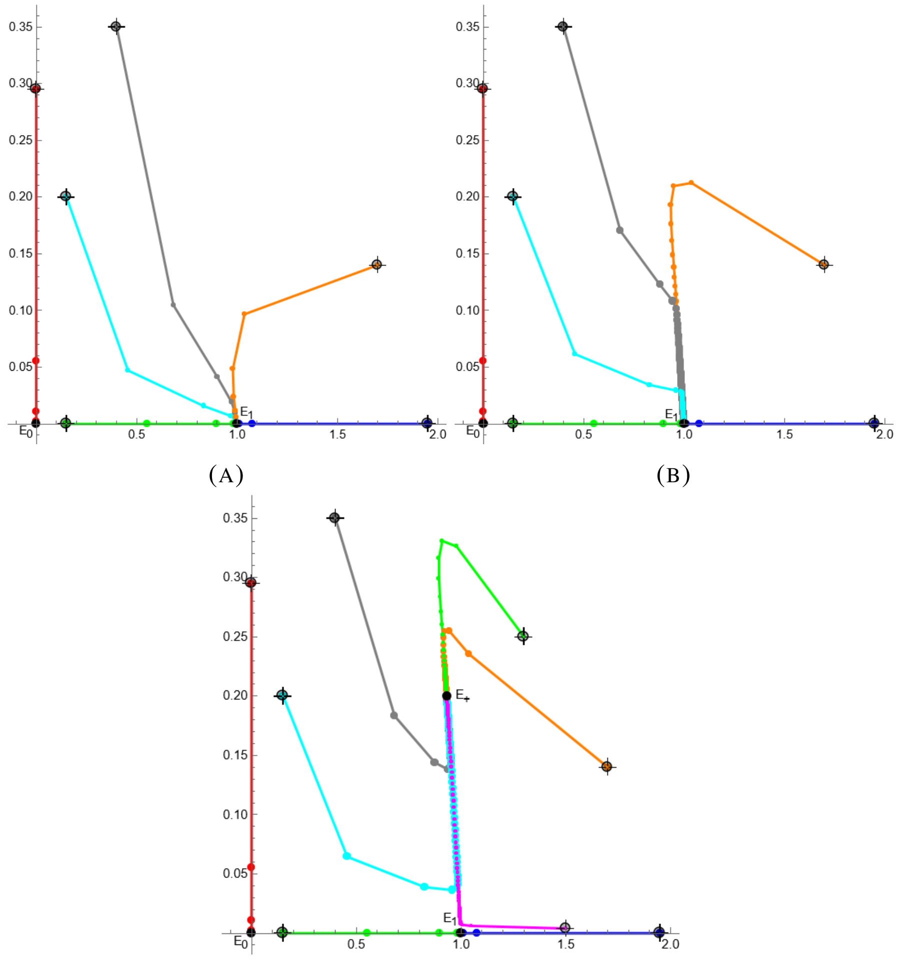


FIGURE 1. Phase portraits for $K = 1, d = 4, \alpha = 2, r = 6$ and
(A) $\gamma = 1.5 < \gamma_0$, (B) $\gamma = 4 = \gamma_0$, (C) $\gamma = 4.5 > \gamma_0$.

Further,

$$J^2T_\gamma(v,v) = \begin{bmatrix} \dfrac{\partial^2 f}{\partial x^2}v_1^2 + 2\dfrac{\partial^2 f}{\partial x \partial y}v_1v_2 + \dfrac{\partial^2 f}{\partial y^2}v_2^2 \\ \dfrac{\partial^2 g}{\partial x^2}v_1^2 + 2\dfrac{\partial^2 g}{\partial x \partial y}v_1v_2 + \dfrac{\partial^2 g}{\partial y^2}v_2^2 \end{bmatrix},$$

$$J^2T_\gamma(E_1,\gamma_0)(v,v) = \begin{bmatrix} 0 \\ -2\frac{r+d\alpha}{r(d+1)} \end{bmatrix}.$$

Therefore,

$$\Psi_1 = w^T T'_\gamma (E_1, \gamma_0) = 0,$$

$$\Psi_2 = w^T J\left(T'_\gamma\right)(E_1, \gamma_0)\, v = \frac{K}{1+d} > 0,$$

$$\Psi_3 = w^T J^2 T_\gamma (E_1, \gamma_0)(v, v) = -2\frac{r + d\alpha}{r(d+1)} < 0.$$

From Sotomayor's theorem in [23], System (1.7) undergoes a transcritical bifurcation at $E_1 = (K, 0)$ when $\gamma = \gamma_0 = \frac{d}{K}$. □

Hence, when the prey population reaches its maximum growth rate at a specific boundary of $\gamma = \frac{d}{K}$, a transcritical bifurcation occurs. This boundary also serves as the invasion boundary for prey populations. Once this boundary is reached, predator populations begin to invade, causing the exclusion equilibrium to lose stability and a locally stable interior equilibrium to emerge. In general, the physical interpretation of a local transcritical bifurcation reflects a change in the system's dynamics in terms of stability. Specifically, a critical population threshold appears, beyond which alternative system states arise. This phenomenon is also referred to as an exchange of stability, as two equilibrium points interchange their stability properties during the bifurcation process (see [19]).

Now, we prove that the system undergoes a Neimark-Sacker bifurcation when $\gamma = \gamma_c$. In order to check the first and the second degeneracy conditions, we will rewrite the eignevalues in the polar form $\lambda = \sqrt{\lambda_1\lambda_2}e^{\pm i\theta(\gamma)}$. Recall that $r(K\gamma - d) = \beta > 0$ and $d\alpha - 1 = A > 0$. So,

$$|\lambda(\gamma)| = \sqrt{\lambda_1\lambda_2} = \sqrt{\frac{(d+1)(y\alpha+1) + \alpha\gamma xy}{(r+1)(\gamma x+1)}}. \tag{3.1}$$

Further, we obtain

$$\frac{d(|\lambda(\gamma_c)|)}{d\gamma} = \frac{1}{2\sqrt{\lambda_1\lambda_2}|_{\gamma=\gamma_c}} \frac{(r+d\alpha)Kr\left(a_0A^2 + a_1A + a_2\right)}{(r+K\alpha\gamma_c)^2(r+1)(r+(r+\alpha+d\alpha)K\gamma_c)^2} > 0,$$

since

$$\begin{aligned}
a_0 &= \frac{2\alpha(\beta+dr)^2}{r^2} > 0,\\
a_1 &= \alpha(4r+3(\alpha+1))d^2 + r(r+4\alpha)d + r^2\\
&\quad + \frac{\beta^2\alpha(2r+3(\alpha+1)) + 2\beta r\alpha(3d(r+\alpha+1)+2r)}{r^2} > 0,\\
a_2 &= \frac{\alpha(\beta(r+\alpha+1) + r((r+\alpha+1)d+r))^2}{r^2} > 0.
\end{aligned}$$

The condition $\lambda_1\lambda_2|_{\gamma=\gamma_c} = 1$ is equivalent to

$$d - r + \gamma x(\alpha y - r - 1) + \alpha y(d+1)|_{\gamma=\gamma_c} = 0. \tag{3.2}$$

Notice that $\tan(\theta_0) = \frac{\sqrt{4\lambda_1\lambda_2-(\lambda_1+\lambda_2)^2}}{\lambda_1+\lambda_2} > 0$, so $e^{ki\theta_0} \neq 1$, i.e., $\lambda^k(\gamma_c) \neq 1$ for $k = 1,2,3,4$. It implies that the second degeneracy condition is satisfied (see [8], Theorem 15.31). Hence, there is a Neimark–Sacker bifurcation at $\gamma = \gamma_c$. In order to determine the criticality of the bifurcation and obtain the normal form of System (3.3), when $\gamma = \gamma_c$, we first translate the equilibrium point $E_+ = (x,y)$ to the origin using the substitution:

$$u_n = x_n - x,$$
$$v_n = y_n - y,$$

so we get

$$\begin{aligned} u_{n+1} &= \frac{(1+r)(u_n+x)}{1+r+\frac{r}{K}u_n+\alpha v_n} - x \\ v_{n+1} &= \frac{(1+\gamma(u_n+x))(v_n+y)}{1+v_n+\gamma x} - y. \end{aligned} \tag{3.3}$$

Let us define the function

$$F\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \dfrac{(1+r)(u+x)}{1+r+\frac{r}{K}u+\alpha v} - x \\ \dfrac{(1+\gamma(u+x))(v+y)}{1+v+\gamma x} - y \end{pmatrix}. \tag{3.4}$$

Then $F(u,v)$ has the unique fixed point $(0,0)$. Rewrite the System (3.3) in the following form

$$\begin{bmatrix} u_{n+1} \\ v_{n+1} \end{bmatrix} = J_F(0,0)\begin{bmatrix} u_n \\ v_n \end{bmatrix} + \begin{bmatrix} H_1(u_n,v_n) \\ H_2(u_n,v_n) \end{bmatrix}, \tag{3.5}$$

where

$$J_F(0,0) = J_T(E_+) = \begin{bmatrix} \dfrac{\alpha y+1}{r+1} & -\dfrac{\alpha x}{r+1} \\ \dfrac{\gamma y}{\gamma x+1} & \dfrac{d+1}{\gamma x+1} \end{bmatrix},$$

$$H_1(u_n,v_n) = -\frac{\alpha y+1}{r+1}u_n + \frac{\alpha x}{r+1}v_n + \frac{(1+r)(u_n+x)}{1+r+\frac{r}{K}u_n+\alpha v_n} - x,$$

$$H_2(u_n,v_n) = -\frac{\gamma y}{\gamma x+1}u_n - \frac{d+1}{\gamma x+1}v_n + \frac{(1+\gamma(u+x))(v+y)}{1+v+\gamma x} - y.$$

System (3.3) has complex eigenvalues, let us denote them with $\lambda = s + it$ and $\overline{\lambda} = s - it$. From the corresponding characteristic equation for (2.11) we get

$$s = \frac{1}{2}(\lambda + \overline{\lambda}) = \frac{1}{2}\left(\frac{\alpha y + 1}{r+1} + \frac{d+1}{x\gamma + 1}\right) \text{ and } t^2|_{\gamma=\gamma_c} = 1 - s^2. \tag{3.6}$$

Further, let

$$\begin{bmatrix} u_n \\ v_n \end{bmatrix} = P \begin{bmatrix} z_n \\ w_n \end{bmatrix},$$

where z_n and w_n are new variables and

$$P = \begin{bmatrix} -\frac{\alpha x}{r+1} & 0 \\ \frac{d+r-\gamma x(\alpha y+1)-\alpha y+dr}{2(x\gamma+1)(r+1)} & -t \end{bmatrix}, \quad P^{-1} = \begin{bmatrix} -\frac{r+1}{\alpha x} & 0 \\ -\frac{d+r-\gamma x(\alpha y+1)-\alpha y+dr}{2tx\alpha(x\gamma+1)} & -\frac{1}{t} \end{bmatrix}$$

are such that $P^{-1}J_F(0,0)P = \begin{bmatrix} s & -t \\ t & s \end{bmatrix}$ with $\begin{vmatrix} s & -t \\ t & s \end{vmatrix} = 1$. Hence, from System (3.5) we obtain

$$\begin{bmatrix} z_{n+1} \\ w_{n+1} \end{bmatrix} = P^{-1}J_F(0,0)P \begin{bmatrix} z_n \\ w_n \end{bmatrix} + P^{-1} \begin{bmatrix} H_1(z_n, w_n) \\ H_2(z_n, w_n) \end{bmatrix}$$

i.e.,

$$\begin{bmatrix} z_{n+1} \\ w_{n+1} \end{bmatrix} = \begin{bmatrix} s & -t \\ t & s \end{bmatrix} \begin{bmatrix} z_n \\ w_n \end{bmatrix} + P^{-1} \begin{bmatrix} H_1(z_n, w_n) \\ H_2(z_n, w_n) \end{bmatrix}. \tag{3.7}$$

Considering the fact that p_{21} in P and P^{-1} can be equal or not equal to zero, we will distinguish two cases:

Case 1: $d + r - \gamma_c x(\alpha y + 1) - \alpha y + dr = 0$,
Case 2: $d + r - \gamma_c x(\alpha y + 1) - \alpha y + dr \neq 0$.

Consider **Case 1**. In order to prove the existance of a Neimark-Sacker bifurcation, (2.10) and (3.2) must hold, i.e.,:

$$\begin{aligned} d + r - x(\alpha y + 1)\gamma_c - \alpha y + dr &= 0, \\ d - r + x(\alpha y - r - 1)\gamma_c + \alpha y(d+1) &= 0, \\ rx + \alpha y K - rK &= 0, \\ d + y - x\gamma_c &= 0. \end{aligned} \tag{3.8}$$

The positive solution of system (3.8) is:

(a) for $r = 3\alpha$

$$(x, y, d, \gamma_c) = \left(\frac{K}{3}, 2, \frac{3\alpha + 2}{\alpha}, \frac{3(5\alpha + 2)}{\alpha K}\right),$$

(b) for $r \neq 3\alpha$

$$(x, y, d, \gamma_c) = \left(\frac{(\alpha + 3r + 3 - \Gamma)K}{2r}, \frac{-\alpha - r - 3 + \Gamma}{2\alpha}, \frac{r+2}{\alpha}, \frac{\alpha + 2r + 3 + \Gamma}{\alpha K}\right),$$

where

$$\Gamma = \sqrt{5r^2 + 2r(3\alpha+7) + (\alpha+3)^2}.$$

Case 1 (a)
The corresponding characteristic equation for (2.11) is now of the form

$$\lambda^2 - \frac{2(2\alpha+1)}{3\alpha+1}\lambda + 1 = 0, \tag{3.9}$$

with eigenvalues

$$\lambda = \frac{2\alpha+1+i\sqrt{\alpha(5\alpha+2)}}{3\alpha+1}, \quad \overline{\lambda} = \frac{2\alpha+1-i\sqrt{\alpha(5\alpha+2)}}{3\alpha+1}.$$

Further,

$$P = \begin{bmatrix} -\dfrac{\alpha K}{3(3\alpha+1)} & 0 \\ 0 & -t \end{bmatrix} \quad \text{and} \quad P^{-1} = \begin{bmatrix} -\dfrac{3(3\alpha+1)}{\alpha K} & 0 \\ 0 & -\dfrac{1}{t} \end{bmatrix},$$

where, from (3.6), $t = \frac{\sqrt{\alpha(5\alpha+2)}}{3\alpha+1}$. The Jacobian matrix of $F(u,v)$ at the equilibrium point is given by

$$J_F(0,0) = \begin{bmatrix} \dfrac{2\alpha+1}{3\alpha+1} & -\dfrac{\alpha K}{3(3\alpha+1)} \\ \dfrac{3(5\alpha+2)}{K(3\alpha+1)} & \dfrac{2\alpha+1}{3\alpha+1} \end{bmatrix},$$

and in (3.7) the functions $H_1(u_n,v_n)$ and $H_2(u_n,v_n)$ have the following form:

$$\begin{aligned} H_1(z_n,w_n) &= \tfrac{(2\alpha+1)K\alpha}{3(3\alpha+1)^2} z_n + \tfrac{\alpha K t}{3(3\alpha+1)} w_n + \tfrac{\alpha K((2\alpha+1)z_n - w_n(3\alpha+1)t)}{3(3\alpha+1)(\alpha t w_n - (3\alpha+1)) + 3\alpha^2 z_n}, \\ H_2(z_n,w_n) &= \tfrac{\alpha(5\alpha+2)}{(3\alpha+1)^2} z_n + \tfrac{(2\alpha+1)t}{3\alpha+1} w_n + \tfrac{t w_n(2(2\alpha+1)(3\alpha+1) - \alpha(5\alpha+2)z_n) + 2\alpha(5\alpha+2)z_n}{(3\alpha+1)(\alpha t w_n - 2(3\alpha+1))}. \end{aligned}$$

Further,

$$\begin{bmatrix} f(z_n,w_n) \\ g(z_n,w_n) \end{bmatrix} = P^{-1} \begin{bmatrix} H_1(z_n,w_n) \\ H_2(z_n,w_n) \end{bmatrix},$$

i.e.,

$$\begin{aligned} f(z,w) &= \frac{-\alpha((2\alpha+1)z - w(3w\alpha+1)t)(z\alpha + (3\alpha+1)tw)}{(3\alpha+1)(3(3\alpha+1)(\alpha t w - (3\alpha+1)) + 3\alpha^2 z)}, \\ g(z,w) &= \frac{w\alpha(2\alpha+1)((5\alpha+2)z - (3\alpha+1)tw)}{(3\alpha+1)^2(tw\alpha - 2(3\alpha+1))}. \end{aligned}$$

Now, for $f(x,y)$ we get

$$\frac{\partial^2 f(0,0)}{\partial z^2} = \frac{2\alpha^2(2\alpha+1)}{(3\alpha+1)^3}, \qquad \frac{\partial^2 f(0,0)}{\partial w^2} = -2\alpha^2\frac{5\alpha+2}{(3\alpha+1)^3},$$
$$\frac{\partial^2 f(0,0)}{\partial z\partial w} = \frac{\alpha(\alpha+1)\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^3}, \qquad \frac{\partial^3 f(0,0)}{\partial z^3} = \frac{6\alpha^4(2\alpha+1)}{(3\alpha+1)^5},$$
$$\frac{\partial^3 f(0,0)}{\partial w^3} = -\frac{6\alpha^3(5\alpha+2)\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^5}, \qquad \frac{\partial^3 f(0,0)}{\partial z\partial w^2} = \frac{2\alpha^3(5\alpha+2)}{(3\alpha+1)^5},$$
$$\frac{\partial^3 f(0,0)}{\partial z^2\partial w} = \frac{2\alpha^3(3\alpha+2)\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^5},$$

and for $g(x,y)$

$$\frac{\partial^2 g(0,0)}{\partial z\partial w} = -\frac{\alpha(2\alpha+1)(5\alpha+2)}{2(3\alpha+1)^3}, \qquad \frac{\partial^2 g(0,0)}{\partial z^2} = 0,$$
$$\frac{\partial^2 g(0,0)}{\partial w^2} = \frac{(2\alpha+1)\alpha\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^3}, \qquad \frac{\partial^3 g(z,w)}{\partial z^2\partial w} = 0,$$
$$\frac{\partial^3 g(0,0)}{\partial w^3} = \frac{3\alpha^3(2\alpha+1)(5\alpha+2)}{2(3\alpha+1)^5}, \qquad \frac{\partial^3 g(0,0)}{\partial z^3} = 0,$$
$$\frac{\partial^3 g(0,0)}{\partial z\partial w^2} = -\frac{\alpha^2(2\alpha+1)(5\alpha+2)\sqrt{\alpha(5\alpha+2)}}{2(3\alpha+1)^5}.$$

Now, we have

$$\begin{aligned}
\xi_{20} &= \frac{1}{8}\{(f_{zz}-f_{ww}+2g_{zw})+i(g_{zz}-g_{ww}-2f_{zw})\} \\
&= \frac{1}{8}\left(\frac{\alpha\left(4\alpha^2-3\alpha-2\right)}{(3\alpha+1)^3}+i\left(-\frac{\alpha(4\alpha+3)\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^3}\right)\right), \\
\xi_{11} &= \frac{1}{4}\{(f_{zz}+f_{ww})+i(g_{zz}+g_{ww})\} \\
&= \frac{1}{4}\left(-\frac{2\alpha^2}{(3\alpha+1)^2}+\frac{(2\alpha+1)\alpha\sqrt{\alpha(5\alpha+2)}}{(3\alpha+1)^3}i\right), \\
|\xi_{11}|^2 &= \left(-\frac{2\alpha^2}{4(3\alpha+1)^2}\right)^2+\left(\frac{(2\alpha+1)\alpha\sqrt{\alpha(5\alpha+2)}}{4(3\alpha+1)^3}\right)^2 \\
&= \frac{\alpha^3\left(17\alpha+52\alpha^2+56\alpha^3+2\right)}{16(3\alpha+1)^6},
\end{aligned}$$

$$\begin{aligned}\xi_{02} &= \frac{1}{8}\left\{(f_{zz}-f_{ww}-2g_{zw})+i(g_{zz}-g_{ww}+2f_{zw})\right\}\\ &= \alpha\frac{24\alpha^2+15\alpha+2}{8(3\alpha+1)^3}+\alpha\frac{\sqrt{2\alpha+5\alpha^2}}{8(3\alpha+1)^3}i,\\ |\xi_{02}|^2 &= \frac{\alpha^2\left(96\alpha^3+88\alpha^2+25\alpha+2\right)}{32(3\alpha+1)^5},\end{aligned}$$

$$\begin{aligned}\xi_{21} &= \frac{1}{16}\left\{(f_{zzz}+f_{zww}+g_{zzw}+g_{www})+i(g_{zzz}+g_{zww}-f_{zzw}-f_{www})\right\}\\ &= \frac{1}{16}\left(\frac{\alpha^3\left(59\alpha+54\alpha^2+14\right)}{2(3\alpha+1)^5}+i\frac{\alpha^2\left(38\alpha^2+7\alpha-2\right)\sqrt{2\alpha+5\alpha^2}}{2(3\alpha+1)^5}\right),\\ \operatorname{Re}\left\{\bar{\lambda}\xi_{21}\right\} &= \frac{\alpha^3\left(298\alpha^3+283\alpha^2+91\alpha+10\right)}{32(3\alpha+1)^6}.\end{aligned}$$

Finally, it is necessary to calculate the following coefficient

$$a(\gamma_c) = -\operatorname{Re}\left\{\frac{(1-2\lambda)\bar{\lambda}^2}{1-\lambda}\xi_{11}\xi_{20}\right\}-\frac{1}{2}|\xi_{11}|^2-|\xi_{02}|^2+\operatorname{Re}\left\{\bar{\lambda}\xi_{21}\right\}, \tag{3.10}$$

which in our case is

$$a(\gamma_c) = -\frac{\alpha^3(5\alpha+2)(2\alpha+1)\left(37\alpha^2+25\alpha+4\right)}{32(3\alpha+1)^7} < 0.$$

So we proved the following theorem.

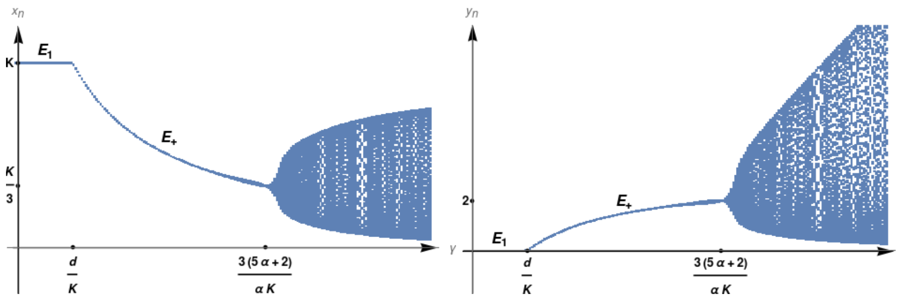
Theorem 3.2. *System (1.7) undergoes a supercritical Neimark–Sacker bifurcation at* $E_+ = \left(\frac{K}{3},2\right)$ *when* $r = 3\alpha$, $d = \frac{3\alpha+2}{\alpha}$, $\gamma = \gamma_c = \frac{3(5\alpha+2)}{\alpha K}$. *There exists* $\delta > 0$ *such that a unique stable closed invariant curve bifurcates from the coexistence equilibrium and exists for* $\gamma_c < \gamma < \gamma_c + \delta$.

The difference in the dynamics predicted between the model introduced here and the analogous continuous model is that there is a supercritical Neimark–Sacker bifurcation at the parameter $\gamma = \gamma_c$. Consequently, the coexistence equilibrium remains positive, but loses its local stability and orbits are attracted to a closed curve even for large γ_c.

In Figure 2, one-parameter bifurcation diagrams show how the stability of the equilibrium points depends on the parameter $\gamma > 0$ with respect to (A) X_n component and (B) Y_n component. A transcritical bifurcation occurs when $\gamma = \frac{d}{K}$ where $E_1 = E_+$ and a Neimark-Sacker bifurcation occurs when $\gamma = \frac{3(5\alpha+2)}{\alpha K}$.

In Figure 3 the phase portrait depicts how a smooth invariant cycle bifurcates from the fixed point E_+ by changing the value of the parameters.

The bifurcation diagrams and phase portraits were generated by Dynamica, (see [16]).



(A) (B)

FIGURE 2. Bifurcation diagrams were produced using the parameter values: $K = 1, d = 4, \alpha = 2, r = 6, \gamma_c = 18$ and $\gamma \in (0, 30)$.

Case 1 (b)

The corresponding characteristic equation for (2.11) is now of the form

$$\lambda^2 + \frac{r+\alpha+1-\Gamma}{r+1}\lambda + 1 = 0 \tag{3.11}$$

with eigenvalues

$$\lambda = \frac{-r-\alpha-1+\Gamma+i\sqrt{(3r+\alpha+3-\Gamma)(r-\alpha+1+\Gamma)}}{2(r+1)},$$

$$\bar{\lambda} = \frac{-r-\alpha-1+\Gamma-i\sqrt{(3r+\alpha+3-\Gamma)(r-\alpha+1+\Gamma)}}{2(r+1)}.$$

Now,

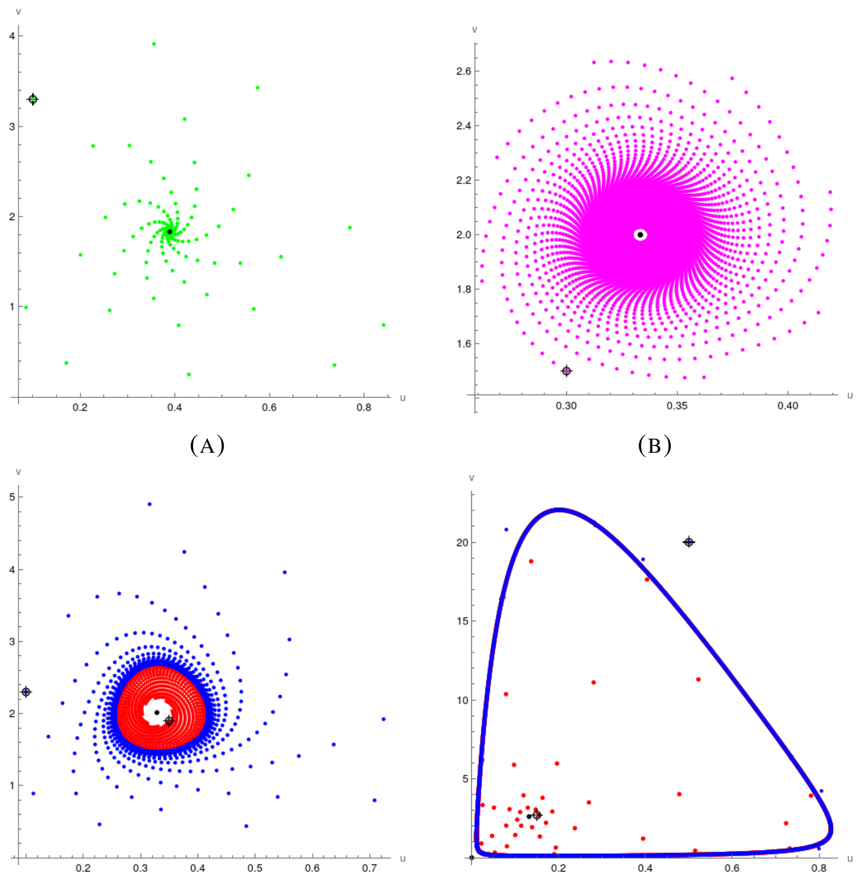
$$P = \begin{bmatrix} -\dfrac{\alpha x}{r+1} & 0 \\ 0 & -t \end{bmatrix}, \quad P^{-1} = \begin{bmatrix} -\dfrac{r+1}{\alpha x} & 0 \\ 0 & -\dfrac{1}{t} \end{bmatrix},$$

where

$$t = \frac{\sqrt{(3r+\alpha+3-\Gamma)(r-\alpha+1+\Gamma)}}{2(r+1)}.$$

Furthermore, we get

$$f(z,w) = -\frac{y\alpha+1}{r+1}z - tw - \frac{(r+1)^2(r+1-\alpha z)K}{\alpha\left(K(r+1)^2 - rx\alpha z - Kt\alpha(r+1)w\right)} + \frac{r+1}{\alpha},$$



(A) (B)

(C) (D)

FIGURE 3. Phase portraits for $K = 1, d = 4, \alpha = 2, r = 6$ and
(A) $\gamma = 15 < \gamma_c = 18$, $(x_0, y_0) = (0.1, 3.3)$,
(B) $\gamma = \gamma_c = 18$, $(x_0, y_0) = (0.3, 1.5)$,
(C) $\gamma = 18.3 > y_c$, $(x_0, y_0) = (0.35, 1.9)$, $(x_0, y_0) = (0.1, 2.3)$,
(D) $\gamma = 50 >> y_c$, $(x_0, y_0) = (0.154, 2.7)$, $(x_0, y_0) = (0.5, 20)$.

$$g(z,w) = -\frac{xy\alpha\gamma}{(x\gamma+1)(r+1)t}z - \frac{d+1}{\gamma x+1}w - \frac{(y-tw)((x\gamma+1)(r+1)-x\alpha\gamma z)}{(r+1)(x\gamma+1-tw)t} + \frac{y}{t}.$$

Applying an analogous procedure like in **Case 1 (a)** results in highly complex expressions. Therefore, we provide results for specific numerical values.

Let us choose the following parameter values $r = 5$, $\alpha = 2$ and $K = 1$. Now, we obtain $\Gamma = \sqrt{280} = 2\sqrt{2}\sqrt{35}$ and

$$M(x,y,d,\gamma) = \left(\frac{10-\sqrt{2}\sqrt{35}}{5}, \frac{\sqrt{2}\sqrt{35}-5}{2}, \frac{7}{2}, \frac{2\sqrt{2}\sqrt{35}+15}{2}\right).$$

The characteristic equations is

$$\lambda^2 + \frac{4-\sqrt{2}\sqrt{35}}{3}\lambda + 1 = 0,$$

with the eigenvalue $\lambda = \frac{\sqrt{2}\sqrt{35}-4}{6} + \frac{\sqrt{8\sqrt{2}\sqrt{35}-50}}{6}i$, where $t = \frac{\sqrt{8\sqrt{2}\sqrt{35}-50}}{6}$. So, one can calculate

$$\left.\frac{\partial^2 f(0,0)}{\partial z^2}\right|_M = \left.\frac{2rx\alpha(K+Kr-rx)}{(r+1)^3 K^2}\right|_M = \frac{7\sqrt{7}\sqrt{10}-55}{27},$$

$$\begin{aligned}
\left.\frac{\partial^2 f(0,0)}{\partial w^2}\right|_M &= -\left.\frac{2\alpha t^2}{r+1}\right|_M = \frac{25-4\sqrt{2}\sqrt{35}}{27},\\
\left.\frac{\partial^2 f(0,0)}{\partial z\partial w}\right|_M &= \left.\frac{\alpha(K+Kr-2rx)t}{(r+1)^2 K}\right|_M = \frac{\sqrt{2}\sqrt{4\sqrt{2}\sqrt{35}-25}}{108},\\
\left.\frac{\partial^3 f(0,0)}{\partial z^3}\right|_M &= \left.\frac{6r^2x^2\alpha^2(K+Kr-rx)}{(r+1)^5 K^3}\right|_M = \frac{125\sqrt{2}\sqrt{35}-1040}{162},\\
\left.\frac{\partial^3 f(0,0)}{\partial w^3}\right|_M &= -\left.\frac{6\alpha^2 t^3}{(r+1)^2}\right|_M = -\frac{\sqrt{2}\sqrt{11\,980\sqrt{7}\sqrt{10}-99\,625}}{162},\\
\left.\frac{\partial^3 f(0,0)}{\partial z\partial w^2}\right|_M &= \left.\frac{2\alpha^2(K+Kr-3rx)t^2}{(r+1)^3 K}\right|_M = \frac{160-19\sqrt{2}\sqrt{35}}{54},\\
\left.\frac{\partial^3 f(0,0)}{\partial z^2\partial w}\right|_M &= \left.\frac{2rx\alpha^2(2K+2Kr-3rx)t}{(r+1)^4 K^2}\right|_M\\
&= \frac{\sqrt{2}\sqrt{4\sqrt{2}\sqrt{35}-25}\left(8\sqrt{2}\sqrt{35}-65\right)}{162}.
\end{aligned}$$

Similarly, for $g(x,y)$

$$\left.\frac{\partial^2 g(0,0)}{\partial z^2}\right|_M = 0, \quad \left.\frac{\partial^3 g(0,0)}{\partial z^3}\right|_M = 0, \quad \left.\frac{\partial^3 g(0,0)}{\partial z^2 \partial w}\right|_M = 0,$$

$$\left.\frac{\partial^2 g(0,0)}{\partial w^2}\right|_M = \left.\frac{2(x\gamma - y + 1)t}{(x\gamma+1)^2}\right|_M = -\frac{\left(4\sqrt{2}\sqrt{35}-43\right)\sqrt{2}\sqrt{4\sqrt{2}\sqrt{35}-25}}{243},$$

$$\left.\frac{\partial^2 g(0,0)}{\partial z \partial w}\right|_M = \left.\frac{x(y - x\gamma - 1)\alpha\gamma}{(x\gamma+1)^2(r+1)}\right|_M = \frac{194-35\sqrt{2}\sqrt{35}}{486},$$

$$\left.\frac{\partial^3 g(0,0)}{\partial w^3}\right|_M = \left.\frac{6(x\gamma+1-y)t^2}{(x\gamma+1)^3}\right|_M = \frac{27\,820-3283\sqrt{7}\sqrt{10}}{6561},$$

$$\left.\frac{\partial^3 g(0,0)}{\partial z \partial w^2}\right|_M = \left.\frac{-2x(x\gamma - y + 1)\alpha\gamma t}{(x\gamma+1)^3(r+1)}\right|_M = \frac{\left(167\sqrt{70}-1613\right)\sqrt{2}\sqrt{4\sqrt{2}\sqrt{35}-25}}{19\,683}.$$

Hence,

$$\xi_{20} = \frac{1}{8}\left(\frac{64\sqrt{2}\sqrt{35}-526}{243} + \frac{\left(16\sqrt{35}-95\sqrt{2}\right)\sqrt{4\sqrt{2}\sqrt{35}-25}}{486}i\right),$$

$$\xi_{11} = \frac{1}{4}\left(\frac{\sqrt{70}-10}{9} - \frac{\left(4\sqrt{2}\sqrt{35}-43\right)\sqrt{2}\sqrt{4\sqrt{2}\sqrt{35}-25}}{243}i\right),$$

$$|\xi_{11}|^2 = \frac{6593\sqrt{2}\sqrt{35}}{236196} - \frac{27145}{118098},$$

$$\xi_{02} = \frac{1}{8}\left(\frac{134\sqrt{2}\sqrt{35}-914}{243} + \frac{\left(16\sqrt{35}-77\sqrt{2}\right)\sqrt{4\sqrt{2}\sqrt{35}-25}}{486}i\right),$$

$$\xi_{21} = \frac{1}{16}\left(\frac{5140-529\sqrt{70}}{6561} - \frac{\left(638\sqrt{35}-3247\sqrt{2}\right)\sqrt{4\sqrt{2}\sqrt{35}-25}}{19\,683}i\right),$$

$$\operatorname{Re}\left\{\bar{\lambda}\xi_{21}\right\} = \frac{1}{16}\left(\frac{31847\sqrt{70}-256880}{59049}\right),$$

and

$$\operatorname{Re}\left\{\frac{(1-2\lambda)\bar{\lambda}^2}{1-\lambda}\xi_{11}\xi_{20}\right\} = \frac{1031917\sqrt{2}\sqrt{35}}{5668704} - \frac{4313177}{2834352}.$$

Finally, we obtain

$$a(\gamma_c) = \frac{20207875}{22674816} - \frac{303425\sqrt{2}\sqrt{35}}{2834352},$$

$$a(\gamma_c) \approx -4.4636 \times 10^{-3} < 0$$

which confirms the existence of the supercritical Neimark-Sacker bifurcation under the above stated assumptions. So the following proposition holds.

Proposition 3.1. *System (1.7) undergoes a supercritical Neimark–Sacker bifurcation at* $E_+ = \left(\frac{10-\sqrt{2}\sqrt{35}}{5}, \frac{\sqrt{2}\sqrt{35}-5}{2}\right)$ *when* $r=5$, $K=1$, $\alpha=2$, $d=\frac{7}{2}$, $\gamma=\gamma_c=\frac{2\sqrt{2}\sqrt{35}+15}{2}$. *Then, there exists* $\delta>0$ *such that a unique stable closed invariant curve bifurcates from the coexistence equilibrium and exists for* $\gamma_c<\gamma<\gamma_c+\delta$.

Remark 3.1. In **Case 2** all expresions become extremely complicated. Let us introduce some part of that tedious calculation. For instance, System (3.8) becomes

$$\begin{aligned} d-r-x\gamma_c+y\alpha+dy\alpha-rx\gamma_c+xy\alpha\gamma_c=0,\\ rx+\alpha Ky-rK=0,\\ d+y-\gamma_c x=0. \end{aligned}$$

Its solution is in the following form:
$(x,y,\gamma)=\left(\frac{(r+\alpha+2d\alpha-1-\Psi)K}{2r}, \frac{r-\alpha-2d\alpha+1+\Psi}{2\alpha}, \frac{r^2+r(\alpha+d\alpha+1)+d\alpha(\alpha+2d\alpha-1)+(r+d\alpha)\Psi}{2\alpha(d\alpha-1)K}\right)$
where Ψ is given with relation (2.12). The characteristic equation is now

$$\lambda^2+\frac{r^2+r(\alpha-d\alpha+3)+d\alpha(2d\alpha+\alpha-5)+4-(r+d\alpha)\Psi}{2(d\alpha-1)(r+1)}\lambda+1=0 \quad (3.12)$$

with the eigenvalue

$$\lambda=\frac{-r^2-r(\alpha-d\alpha+3)-d\alpha(2d\alpha+\alpha-5)-4+(r+d\alpha)\Psi+\sqrt{\Phi}}{4(d\alpha-1)(r+1)},$$

where

$$\begin{aligned}\Phi \;=\; &(r+d\alpha)(r+\alpha+2d\alpha-1-\Psi)\cdot\left[r^2+r(\alpha-5d\alpha+7)\right.\\ &\left.+2d^2\alpha^2+d\alpha^2-9d\alpha+8-(r+d\alpha)\Psi\right].\end{aligned}$$

Notice that for $r=3\alpha$ and $p_{21}=0$ equation (3.12) becomes (3.9), and for $r\neq 3\alpha$ and $p_{21}=0$ equation (3.12) becomes (3.11). Consequently, the application of analogous methodological procedures, albeit involving substantially more intricate analytical expressions, allows the formulation of the Neimark–Sacker theorem.

Theorem 3.3. *System (1.7) undergoes a supercritical Neimark–Sacker bifurcation at* $E_+=\left(\frac{(r+\alpha+2d\alpha-1-\Psi)K}{2r}, \frac{r-\alpha-2d\alpha+1+\Psi}{2\alpha}\right)$ *when* $d\alpha>1$ *and*

$$\gamma=\gamma_c=\frac{d}{K}+\frac{(r+d\alpha)(r+\alpha+1+\Psi)}{2\alpha(d\alpha-1)K},$$

$\Psi=\sqrt{r^2+2r(\alpha+1)+(\alpha+2d\alpha-1)^2}$. *Then, there exists* $\delta>0$ *such that a unique stable closed invariant curve bifurcates from the coexistence equilibrium and exists for* $\gamma_c<\gamma<\gamma_c+\delta$.

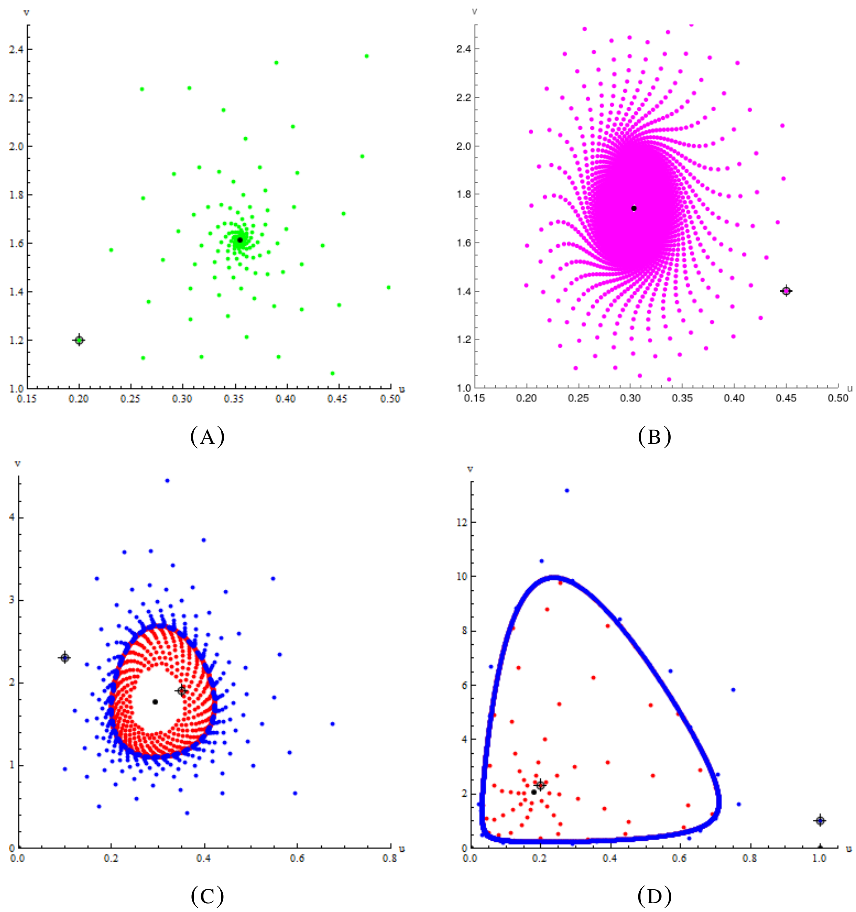


FIGURE 4. Phase portraits for $K = 1, d = 3, \alpha = 2, r = 5$ and
(A) $\gamma = 13 < \gamma_c = \frac{37+11\sqrt{14}}{5}$, $(x_0, y_0) = (0.2, 1.2)$,
(B) $\gamma = \gamma_c = \frac{37+11\sqrt{14}}{5}$, $(x_0, y_0) = (0.45, 1.4)$
(C) $\gamma = \frac{40+11\sqrt{14}}{5} > y_c$, $(x_0, y_0) = (0.35, 1.9)$, $(x_0, y_0) = (0.1, 2.3)$,
(D) $\gamma = \frac{100+11\sqrt{14}}{5} >> y_c$, $(x_0, y_0) = (0.2, 2.3)$, $(x_0, y_0) = (1, 1)$.

In Figure 3, we present phase portraits analogous to those in Figure 2, but this time for the parameter values stated in Theorem 3.3 such that $r \neq 3\alpha$ and $p_{21} \neq 0$.

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