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Research Article

Global Asymptotic Stability for Discrete Single Species Population Models

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We present some basic discrete models in populations dynamics of single species with several age classes. Starting with the basic Beverton-Holt model that describes the change of single species we discuss its basic properties such as a convergence of all solutions to the equilibrium, oscillation of solutions about the equilibrium solutions, Allee's effect, and Jillson's effect. We consider the effect of the constant and periodic immigration and emigration on the global properties of Beverton-Holt model. We also consider the effect of the periodic environment on the global properties of Beverton-Holt model.

1. Introduction

The following difference equation is known as *Beverton-Holt model*:

$$x_{n+1} = \frac{ax_n}{1 + x_n}, \quad x_0 \geq 0 \ n = 0, 1, \ldots, \tag{1}$$

where $a > 0$ is a rate of change (growth or decay) and x_n is the size of population at nth generation. It was introduced by Beverton and Holt in 1957 and depicts density dependent recruitment of a population with limited resources in which resources are not shared equally. It assumes that the per capita number of offspring is inversely proportional to a linearly increasing function of the number of adults.

Let $P(n)$ be the size of a population in generation n.

Suppose that μ is the net reproductive rate, that is, the number of offspring that each individual leaves before dying if there is no limitation in resources. Then the Beverton-Holt model is given by

$$\frac{P(n+1)}{P(n)} = \frac{\mu}{1 + ((\mu - 1)/K) P(n)}, \quad x_0 \geq 0, \tag{2}$$

where $K > 0$ is carrying capacity. This leads to the equation

$$P(n+1) = \frac{\mu P(n)}{1 + ((\mu - 1)/K) P(n)}, \quad n = 0, 1, \ldots \tag{3}$$

which by the substitution $x_n = ((\mu-1)/K)P(n)$ reduces to (1), where $a = \mu$.

The model is well studied and understood and exhibits the following properties.

Theorem 1. *Equation (1) has the following properties:*

(1) *Equation (1) has two equilibrium points* 0 *and* $a - 1$ *when* $a > 1$.

(2) *All solutions of (1) are monotonic (increasing or decreasing sequences).*

(3) *If* $a \leq 1$, *then the equilibrium point* 0 *is the* global attractor *(i.e.,* $\lim_{n\to\infty} x_n = 0$*).*

(4) *If* $a > 1$, *then the equilibrium point* $a - 1$ *is the global attractor (i.e.,* $\lim_{n\to\infty} x_n = a - 1$, *when* $x_0 > 0$*).*

(5) *Both equilibrium points are* globally asymptotically stable*; that is, they are global attractors with the property that small changes of initial condition* x_0 *result in small changes of the corresponding solution* $\{x_n\}$.

(6) *Equation (1) can be solved explicitly and has the following solution:*

$$x_n = \frac{1}{1/(a-1) + \left(1/x_0 - 1/(a-1)\right) 1/a^n} \quad if\ a \neq 1$$
$$x_n = \frac{1}{n + 1/x_0}, \quad if\ a = 1, \tag{4}$$

which implies all the above-mentioned properties of (1).

See, for example, [1–6].

The following difference equation is known as *Beverton-Holt model with constant immigration or stocking*

$$x_{n+1} = \frac{ax_n}{1 + x_n} + h, \quad x_0 \geq 0\ n = 0, 1, \ldots, \tag{5}$$

where $a > 0$ is a rate of change (growth or decay), $h > 0$ is a constant immigration, and x_n is the size of population at nth generation. The simple substitution $y_n = x_n - h$ reduces (5) to the so-called *Riccati's equation*

$$y_{n+1} = \frac{ay_n + ah}{y_n + 1 + h}, \quad n = 0, 1, \ldots \tag{6}$$

which is well studied and understood (see [7, 8]) and exhibits the following properties.

Theorem 2. *(1) Equation (5) has one positive equilibrium point $\overline{y}$.*

(2) All solutions of (5) are monotonic (increasing or decreasing sequences) and bounded.

(3) The equilibrium point $\overline{y}$ is a global attractor and is globally asymptotically stable.

(4) Furthermore, (5) can be solved explicitly and has the following solution:

$$y_n = (a + 1 + h) \frac{(w_0 - w_-) w_+^{n+1} - (w_+ - w_0) w_-^{n+1}}{(w_0 - w_-) w_+^n - (w_+ - w_0) w_-^n} - 1 - h, \tag{7}$$

where $w_\pm = (1/2)(1 \pm \sqrt{1 - 4\mathscr{R}})$ and $\mathscr{R} = a/(a + 1 + h)^2$ and

$$w_0 = \frac{y_0 + 1 + h}{a + 1 + h}. \tag{8}$$

The biological implications of this model are that the constant immigration eliminates the possibility of zero equilibrium and so all solutions get attracted to the unique positive equilibrium solution.

The *Beverton-Holt model with emigration or harvesting* leads to the equation

$$x_{n+1} = \frac{ax_n}{1 + x_n} - h, \quad x_0 \geq 0\ n = 0, 1, \ldots, \tag{9}$$

where $a > 0$ is a rate of change (growth or decay) and $h > 0$ is a constant emigration. The solution of (9) is given by (7), where h should be replaced by $-h$.

Equation (9) has quite different dynamics than (5), since it can have 0, 1, or 2 equilibrium solutions, depending on the values of the expression

$$D = (1 + h - a)^2 - 4h. \tag{10}$$

The following results hold for (9).

Theorem 3. *Equation (9) exhibits one of the following three dynamic scenarios:*

(1) *If $D < 0$ then every solution of (9) satisfies $\lim_{n\to\infty} x_n = \infty$. In addition, every solution is increasing.*

(2) *If $D = 0$ then (9) has a single equilibrium $\overline{x}$ which is nonhyperbolic and every solution of (9) satisfies $\lim_{n\to\infty} x_n = -\infty$ if $x_0 < \overline{x}$ and $\lim_{n\to\infty} x_n = \overline{x}$ if $x_0 > \overline{x}$. In addition, every solution is decreasing.*

(3) *If $D > 0$ then (9) has two positive equilibrium solutions $\overline{x}_- < \overline{x}_+$, where $\overline{x}_-$ is a repeller and $\overline{x}_+$ is locally asymptotically stable. Every solution of (9) satisfies $\lim_{n\to\infty} x_n = -\infty$ if $x_0 < \overline{x}_-$ and $\lim_{n\to\infty} x_n = \overline{x}_+$ if $x_0 > \overline{x}_-$. In addition, every solution which starts in $(\overline{x}_-, \overline{x}_+)$ is increasing, while the other nonconstant solutions are decreasing.*

The biological implications of this model are that the constant emigration or harvesting introduces the possibility of the threshold such that if the initial population is below that threshold the population goes to extinction.

See Elaydi [2], Kulenović and Ladas [7], Kulenović and Merino [8], and Thieme [6].

The following difference equation is known as *Beverton-Holt model with periodic immigration or stocking*:

$$x_{n+1} = \frac{ax_n}{1 + x_n} + h_n, \quad x_0 \geq 0\ n = 0, 1, \ldots, \tag{11}$$

where $a > 0$ is a rate of change (growth or decay), $h_n > 0$ is a periodic immigration or stocking, and x_n is the size of population at nth generation. The substitution $y_n = x_n - h_n$ reduces (11) to the so-called *Riccati's equation* with periodic coefficients

$$y_{n+1} = \frac{ay_n + ah_n}{y_n + 1 + h_n}, \quad n = 0, 1, \ldots \tag{12}$$

which is, very recently, studied and understood and exhibits the following properties; see [9, 10].

Theorem 4. *Equation (11) has the following properties:*

(1) *Equation (11) has the unique nonnegative periodic solution $\overline{x}_n$, whose period equals the period of $h_n > 0$.*

(2) *The periodic solution $\{\overline{x}_n\}$ is the global attractor of all solutions of (11).*

(3) *There is a procedure for finding the explicit solution of (11). In particular, there are explicit formulas for the cases when h_n is periodic sequence with periods 2, 3, 4.*

The biological implications of model (11) are that the periodic immigration imposes its periodicity on the solutions of the model and so all solutions get attracted to the unique periodic solution whose period equals the period of immigration.

Case of periodic emigration is quite different as this emigration may introduce the periodic threshold which would imply the extinction scenario if the initial population is below that threshold.

See Grove et al. [9, 10].

The following difference equation is known as the *Beverton-Holt model with periodic environment*:

$$x_{n+1} = \frac{\mu K_n x_n}{K_n + (\mu - 1) x_n}, \quad x_0 \geq 0 \ n = 0, 1, \ldots, \tag{13}$$

where $\mu > 1$ is a rate of change (growth or decay), $K_n > 0$ is a periodic sequence of period p modeling periodicity of environment (periodic supply of food, energy, etc.), and x_n is the size of population at nth generation.

Assuming $x_n > 0$ and rewriting (13) as

$$\frac{1}{x_{n+1}} = \frac{K_n + (\lambda - 1) x_n}{\lambda K_n x_n}, \tag{14}$$

the substitution $y_n = 1/x_n$ reduces (13) to the linear nonautonomous equation

$$y_{n+1} = \frac{1}{\mu} y_n + p_n, \quad x_0 \geq 0 \ n = 0, 1, \ldots, \tag{15}$$

where $p_n = (\mu - 1)/\mu K_n$. The solution of (15) is given as

$$y_n = \frac{1}{\mu^n} y_0 + \sum_{k=0}^{n-1} \frac{1}{\mu^{n-k-1}} p_k \tag{16}$$

and it is well studied and understood and exhibits the following properties.

Theorem 5. *Equation (15) has the following properties:*

(1) *Equation (15) has the unique nonnegative periodic solution $\overline{y}_n$, with period equal to p.*

(2) *The periodic solution $\{\overline{y}_n\}$ is the global attractor of all solutions of (15).*

(3) *The* periodic environment is deleterious *in the sense that the size of population in periodic environment is smaller than the average of sizes in p constant environments. We say that in this case the periodic solution is an* attenuant cycle. *Mathematically, this means that*

$$\frac{1}{p}\left(\overline{y}_1 + \cdots + \overline{y}_p\right) < \frac{1}{p}\left(\left(K_1 - 1\right) + \cdots + \left(K_p - 1\right)\right), \tag{17}$$

where $K_i - 1$ is the equilibrium of (1) when $a = K_i$.

Theorem 5 gives an example of so-called *Jillson's effect* that refers to any change in global behavior caused by a periodic fluctuation of the environment; see [11, 12].

See [9, 11, 13–17] for some mathematical models with periodic coefficients.

The following difference equation, known as *sigmoid Beverton-Holt model*, is mathematically the simplest Beverton-Holt type model that exhibits Allee's effect:

$$x_{n+1} = \frac{a x_n^2}{1 + x_n^2}, \quad x_0 \geq 0 \ n = 0, 1, \ldots, \tag{18}$$

where $a > 0$ is a rate of change (growth or decay) and x_n is the size of population at nth generation. The model is well studied and understood and exhibits the following properties.

Theorem 6. *(1) Equation (1) has either one equilibrium point* 0 *when $a < 2$ or two equilibrium points* 0 *and* 1*, when $a = 2$, or three equilibrium points* 0 *and $\overline{x}_- = (a - \sqrt{a^2 - 4})/2 < \overline{x}_+ = (a + \sqrt{a^2 - 4})/2$ when $a > 2$.*

(2) All solutions of (1) are monotonic (increasing or decreasing sequences) and bounded.

(3) If $a < 2$, then the equilibrium point 0 *is the global attractor.*

(4) If $a = 2$, then the equilibrium point 0 *is the attractor with* the basin of attraction $\mathscr{B}(0) = [0, 1)$ *and* 1 *is nonhyperbolic with the basin of attraction $\mathscr{B}(1) = (1, \infty)$.*

(5) If $a > 2$, then there are two attractors: 0 *with the basin of attraction $\mathscr{B}(0) = [0, \overline{x}_-)$ and $\overline{x}_+$ with the basin of attraction $\mathscr{B}(\overline{x}_+) = (\overline{x}_-, \infty)$.*

The biological implications of this model are that it exhibits so-called *Allee's effect* (the social dysfunction and failure to mate successfully when population density falls below a certain threshold) in the sense that if the initial size x_0 is smaller than $\overline{x}_-$ the population goes to extinction. See [18].

In this paper we extend Theorems 1–6 to the case of several generation model with special emphasis on three-generation model. We prove general results about asymptotic stability, both local and global, which cover all kinds of transition or response functions such as linear (also known as Holling type I functions) [19], Beverton-Holt (also known as Holling type II functions or Holling hyperbolic functions), sigmoid Beverton-Holt (also known as Holling type III functions or sigmoid functions), and exponential functions. In order to do so, we introduce some tools in Section 2 which contains some global attractivity results for monotone systems and some difference inequalities results which lead to precise global attractivity results for nonautonomous asymptotically autonomous difference equations. In Sections 3 and 4 we obtain fairly general results for local and global asymptotic stability of kth generations model that extends all results in this section. In the special case of three-generation model we find the precise basins of attraction of all locally stable equilibrium solutions and locally stable period-two solutions.

2. Preliminaries

In this part we present basic tools which we use to extend the results in Section 1 to more general models that includes several age groups or generations.

2.1. Global Attractivity Results for Monotone Systems. Let $\preceq$ be a partial order on $\mathbb{R}^n$ with nonnegative cone P. For $x, y \in \mathbb{R}^n$ the *order interval* $[\![x, y]\!]$ is the set of all z such that $x \preceq z \preceq y$. We say $x \prec y$ if $x \preceq y$ and $x \neq y$ and $x \ll y$ if $y - x \in \operatorname{int}(P)$. A map T on a subset of $\mathbb{R}^n$ is *order preserving* if $T(x) \preceq T(y)$ whenever $x \prec y$, *strictly order preserving* if $T(x) \prec T(y)$ whenever $x \prec y$, and *strongly order preserving* if $T(x) \ll T(y)$ whenever $x \prec y$.

Let $T : R \to R$ be a map with a fixed point $\overline{x}$ and let R' be an invariant subset of R that contains $\overline{x}$. We say that $\overline{x}$ is stable (asymptotically stable) relative to R' if $\overline{x}$ is a stable (asymptotically stable) fixed point of the restriction of T to R'.

The next result in [20] is stated for order preserving maps on $\mathbb{R}^n$. See [21] for a more general version valid in ordered Banach spaces. See [22–24] for related results.

Theorem 7. *For a nonempty set $R \subset \mathbb{R}^n$ and $\preceq$, a partial order on $\mathbb{R}^n$, let $T : R \to R$ be an order preserving map, and let $a, b \in R$ be such that $a \prec b$ and $[\![a, b]\!] \subset R$. If $a \preceq T(a)$ and $T(b) \preceq b$, then $[\![a, b]\!]$ is an invariant set and*

(i) *there exists a fixed point of T in $[\![a, b]\!]$,*

(ii) *if T is strongly order preserving, then there exists a fixed point in $[\![a, b]\!]$ which is stable relative to $[\![a, b]\!]$,*

(iii) *if there is only one fixed point in $[\![a, b]\!]$, then it is a global attractor in $[\![a, b]\!]$ and therefore asymptotically stable relative to $[\![a, b]\!]$.*

The following result in [20] is a direct consequence of the trichotomy result of Dancer and Hess in [21].

Corollary 8. *If the nonnegative cone of $\preceq$ is a generalized quadrant in $\mathbb{R}^n$, and if T has no fixed points in $[\![u_1, u_2]\!]$ other than u_1 and u_2, then the interior of $[\![u_1, u_2]\!]$ is either a subset of the basin of attraction of u_1 or a subset of the basin of attraction of u_2.*

Consider the general kth order difference equation

$$x_{n+1} = f\left(x_n, x_{n-1}, \ldots, x_{n-k+1}\right), \quad n = 0, 1, \ldots, \tag{19}$$

where $f : \mathbb{R}^k \to \mathbb{R}$ is continuous function and suppose that 0 and $x_- > 0$ are two equilibrium solutions of (19). By introducing new variables

$$\begin{aligned} u_n^1 &= x_{n-k+1}, \\ u_n^2 &= x_{n-k+2}, \\ &\vdots \\ u_n^k &= x_n \end{aligned} \tag{20}$$

we rewrite (19) as the system

$$\begin{aligned} u_{n+1}^1 &= u_n^2, \\ u_{n+1}^2 &= u_n^3, \\ &\vdots \\ u_{n+1}^{k-1} &= u_n^k, \\ u_{n+1}^k &= f\left(u_n^k, u_n^{k-1}, \ldots, u_n^1\right) \end{aligned} \tag{21}$$

whose corresponding map has the form

$$T\left(\begin{pmatrix} u^1 \\ u^2 \\ \vdots \\ u^{k-1} \\ u^k \end{pmatrix}\right) = \begin{pmatrix} u^2 \\ u^3 \\ \vdots \\ u^k \\ f\left(u^k, \ldots, u^1\right) \end{pmatrix}. \tag{22}$$

The map T is nondecreasing map with respect to the ordering $\preceq$ in $\mathbb{R}^k$ defined as

$$\begin{aligned} &\mathbf{u} \preceq \mathbf{v} \Longleftrightarrow \\ &u_i \leq v_i, \quad i = 1, \ldots, k, \end{aligned} \tag{23}$$

where $\mathbf{u} = (u_1, \ldots, u_k)$, $\mathbf{v} = (v_1, \ldots, v_k)$, in the sense that

$$\begin{aligned} &\mathbf{u} \preceq \mathbf{v} \Longrightarrow \\ &T(\mathbf{u}) \preceq T(\mathbf{v}), \end{aligned} \tag{24}$$

for every $\mathbf{u}, \mathbf{v} \in \mathbb{R}^k$. Set $\mathbf{0} = (0, 0, \ldots, 0)$, $\mathbf{x}_- = (x_-, x_-, \ldots, x_-)$. The interval $[\![\mathbf{0}, \mathbf{x}_-]\!] = \{\mathbf{x} : \mathbf{0} \preceq \mathbf{x} \preceq \mathbf{x}_-\}$ is an invariant set for the map T, that is, $T([\![\mathbf{0}, \mathbf{x}_-]\!]) \subset [\![\mathbf{0}, \mathbf{x}_-]\!]$. Consequently, by Corollary 8, the interior of the interval $[\![\mathbf{0}, \mathbf{x}_-]\!]$ is a part of the basin of attraction of one of two fixed points $\mathbf{0}, \mathbf{x}_-$.

The reasoning given in the above discussion leads to the following result for general difference equation (19).

Theorem 9. *Consider (19), where $f : \mathbb{R}^k \to \mathbb{R}$ is continuous, nondecreasing in all variables and bounded function with the lower and upper bound L and U, respectively. If (19) has two equilibrium points $x_L < x_U$, such that x_L is unstable and x_U is asymptotically stable, then the equilibrium x_L is globally asymptotically stable within its basin of attraction which contains $[L, x_L)^{k+1}$ and the equilibrium x_U is globally asymptotically stable within its basin of attraction which contains $(x_L, x_U]^{k+1} \cup [x_U, U]^{k+1}$.*

2.2. Difference Inequalities. In this section we give some basic results on difference inequalities which we will use later to extend some of our results for autonomous equation to the case of asymptotically autonomous difference equations. See [25, 26].

Theorem 10. *Let $n \in N_{n_0}^+ = \{n_0, n_0 + 1, \ldots\}$ and $g(n, u, v)$ be a nondecreasing function in u and v for any fixed n. Suppose that, for $n \geq n_0$, the inequalities*

$$\begin{aligned} y_{n+1} &\leq g\left(n, y_n, y_{n-1}\right), \\ u_{n+1} &\geq g\left(n, u_n, u_{n-1}\right) \end{aligned} \tag{25}$$

hold. Then

$$y_{n_0-1} \le u_{n_0-1}, \qquad y_{n_0} \le u_{n_0} \tag{26}$$

implies that

$$y_n \le u_n, \qquad n \ge n_0. \tag{27}$$

Proof. Suppose that (27) is not true. Then, there exists a smallest $k \in N_{n_0}^+$ such that

$$y_{k+1} > u_{k+1}. \tag{28}$$

By using (25) and (26) and the monotone character of g, it follows from

$$y_k \le u_k, \qquad y_{k-1} \le u_{k-1} \tag{29}$$

that

$$y_{k+1} \le g(k, y_k, y_{k-1}) \le g(k, u_k, u_{k-1}) \le u_{k+1}, \tag{30}$$

which is a contradiction. □

Applying Theorem 10 twice, we obtain the following result.

Corollary 11. *Suppose that $g_1(n,u,v)$ and $g_2(n,u,v)$ are two functions defined on $N_{n_0}^+ \times \mathbb{R}^2$ and nondecreasing with respect to u and v. Let*

$$g_2(n, u_n, u_{n-1}) \le u_{n+1} \le g_1(n, u_n, u_{n-1}). \tag{31}$$

Then

$$L_n \le u_n \le U_n, \tag{32}$$

where L_n and U_n are the solutions of the difference equations

$$\begin{aligned} U_{n+1} &= g_1(n, U_n, U_{n-1}), \quad U_{n_0} \ge u_{n_0},\ U_{n_0-1} \ge u_{n_0-1}, \\ L_{n+1} &= g_2(n, L_n, L_{n-1}), \quad L_{n_0} \le u_{n_0},\ L_{n_0-1} \le u_{n_0-1}. \end{aligned} \tag{33}$$

An immediate extension of Theorem 10 is the following result.

Theorem 12. *Let y_i, $n = 0, 1, 2, \ldots$, be sequences satisfying*

$$\begin{aligned} y_{n+1} &\le g_1(n, y_n, \ldots, y_{n-p}), \\ u_{n+1} &\ge g_2(n, u_n, \ldots, u_{n-p}), \end{aligned} \tag{34}$$

where g_i is nondecreasing with respect to its argument. Then,

$$\begin{aligned} y_{n_0-p} &\le u_{n_0-p}, \\ &\vdots \\ y_{n_0-1} &\le u_{n_0-1}, \\ y_{n_0} &\le u_{n_0} \end{aligned} \tag{35}$$

implies

$$y_n \le u_n, \quad n \ge n_0. \tag{36}$$

Theorem 13. *Consider the difference equation*

$$x_{n+1} = a_n f(x_n), \quad n = 0, 1, \ldots, \tag{37}$$

where f is nondecreasing function. Assume that

$$\lim_{n\to\infty} a_n = a, \tag{38}$$

and let

$$y_{n+1} = a f(y_n), \quad n = 0, 1, \ldots \tag{39}$$

be the limiting difference equation. Assume that there exists $\epsilon_0 > 0$ such that every solution of difference equation

$$y_{n+1} = A f(y_n), \quad n = 0, 1, \ldots \tag{40}$$

converges to a constant solution $\overline{y}_A$ for every $A \in (a-\epsilon_0, a+\epsilon_0)$. If

$$\lim_{A\to a} \overline{y}_A = \overline{y}, \tag{41}$$

then every solution of the difference equation (37) satisfies

$$\lim_{n\to\infty} x_n = \overline{y}. \tag{42}$$

Proof. In view of (39) for every $\epsilon > 0$ there exists $N = N(\epsilon) > 0$ such that

$$\begin{aligned} &n \ge N(\epsilon) \Longrightarrow \\ &|a_n - a| < \epsilon \Longleftrightarrow \\ &a - \epsilon < a_n < a + \epsilon, \end{aligned} \tag{43}$$

which implies

$$\begin{aligned} &n \ge N(\epsilon) \Longrightarrow \\ &(a-\epsilon) f(x_n) \le x_{n+1} = a_n f(x_n) < (a+\epsilon) f(x_n). \end{aligned} \tag{44}$$

Now, assume that $\epsilon \le \epsilon_0$ and consider two equations of the form (40), where $A = a - \epsilon$ and $A = a + \epsilon$. By Corollary 11 we have that

$$\ell_n \le x_n \le u_n, \quad n \ge N(\epsilon), \tag{45}$$

where $\{\ell_n\}$ satisfies

$$\ell_{n+1} = (a-\epsilon) f(\ell_n) \quad n \ge N(\epsilon) \tag{46}$$

and $\{u_n\}$ satisfies

$$u_{n+1} = (a+\epsilon) f(u_n) \quad n \ge N(\epsilon). \tag{47}$$

In view of the assumptions

$$\lim_{n\to\infty} \ell_n = \lim_{n\to\infty} u_n = \overline{y}, \tag{48}$$

which completes the proof. □

Example 14. The difference equation

$$y_{n+1} = (1 + a_n) y_n, \quad n = 0, 1, \ldots, \tag{49}$$

where $a_n \geq 0$, $n = 0, 1, \ldots$, and $y_0 \geq 0$, has a solution

$$y_n = \prod_{k=0}^{n-1} (1 + a_k) y_0, \tag{50}$$

which is convergent if and only if $\sum_{k=0}^{\infty} a_k$ is convergent. In this case $\lim_{k\to\infty} a_k = 0$ and the limiting equation is

$$x_{n+1} = x_n, \quad n = 0, 1, \ldots. \tag{51}$$

Similarly, $\sum_{k=0}^{\infty} a_k$ can be divergent and yet $\lim_{k\to\infty} a_k = 0$ with the limiting equation (51). This shows that if the limiting equation is nonhyperbolic the dynamics of original equation can be very diverse.

Example 15. The difference equation

$$y_{n+1} = b_n \frac{y_n}{1 + y_n}, \quad n = 0, 1, \ldots, \tag{52}$$

where $y_0 > 0$, $b_n > 0$, $n = 0, 1, \ldots$, and $\lim_{n\to\infty} b_n = 1$, can be transformed into

$$u_{n+1} = B_n (1 + u_n), \quad n = 0, 1, \ldots, \tag{53}$$

where $B_n = 1/b_n$, $u_n = 1/y_n$. Solving (53) and going back to y_n we obtain

$$y_n = \left(\prod_{k=0}^{n-1} (1 + a_k) \frac{1}{y_0} + \sum_{k=0}^{\infty} \prod_{i=k}^{n-1} (1 + a_i) \right)^{-1} \tag{54}$$

that is convergent if and only if $\sum_{k=0}^{\infty} a_k$ and $\sum_{k=0}^{\infty} \prod_{i=k}^{n-1} (1 + a_i)$ are convergent, where $1/b_i = 1 + a_i$, $1 = 1, 2, \ldots$.

In this case $\lim_{k\to\infty} a_k = 0$ and the limiting equation is

$$x_{n+1} = \frac{x_n}{1 + x_n}, \quad n = 0, 1, \ldots. \tag{55}$$

This shows that if the limiting equation is nonhyperbolic the dynamics of original equation can be very diverse and not well described by dynamics of limiting equation.

Example 16. The difference equation (52), where $b_n > 0$, $n = 0, 1, \ldots$, $\lim_{n\to\infty} b_n = a$, and $y_0 > 0$, has simple behavior in the hyperbolic case, that is, when $a \neq 1$. Indeed Theorem 13 implies that in this case the global dynamics of (52) are the same as the global dynamics of the limiting equation (1), described in Theorem 1. Thus the following result holds:

$$\begin{gathered} \lim_{n\to\infty} b_n = a \begin{cases} < 1 \\ > 1 \end{cases} \Longrightarrow \\ \lim_{n\to\infty} x_n = \begin{cases} 0, & \text{if } x_0 \geq 0 \\ a - 1, & \text{if } x_0 > 0. \end{cases} \end{gathered} \tag{56}$$

Similarly an application of Theorem 13 gives the following result.

Example 17. Consider the difference equation

$$x_{n+1} = a_n \frac{x_n^2}{1 + x_n^2}, \quad x_0 \in \mathbb{R} \ a_n \geq 0, \ n = 0, 1, \ldots, \tag{57}$$

where (38) holds. Then the following result holds:

$$\begin{gathered} \lim_{n\to\infty} a_n = a \begin{cases} < 2 \\ > 2 \end{cases} \Longrightarrow \\ \lim_{n\to\infty} x_n = \begin{cases} 0, & \text{if } 0 \leq x_0 < \overline{x}_- \\ \overline{x}_+, & \text{if } x_0 > \overline{x}_-, \end{cases} \end{gathered} \tag{58}$$

where $\overline{x}_- < \overline{x}_+$ are the positive equilibrium solutions of the corresponding limiting equation

$$x_{n+1} = a \frac{x_n^2}{1 + x_n^2}, \quad n = 0, 1, \ldots. \tag{59}$$

In this case difference equation exhibits Allee's effect.

Theorem 18. *Consider the difference equation*

$$x_{n+1} = a_n f_1(x_n) + b_n f_2(x_{n-1}), \quad n = 0, 1, \ldots, \tag{60}$$

where f_1, f_2 are nondecreasing functions and

$$\begin{gathered} \lim_{n\to\infty} a_n = a, \\ \lim_{n\to\infty} b_n = b, \end{gathered} \tag{61}$$

and the limiting difference equation

$$y_{n+1} = a f_1(y_n) + b f_2(y_{n-1}), \quad n = 0, 1, \ldots. \tag{62}$$

Assume that there exists $\epsilon_0 > 0$ such that every solution of difference equation

$$y_{n+1} = A f_1(y_n) + B f_2(y_{n-1}), \quad n = 0, 1, \ldots \tag{63}$$

converges to a constant solution $\overline{y}_{A,B}$ for every $A \in (a - \epsilon_0, a + \epsilon_0)$ and $B \in (b - \epsilon_0, b + \epsilon_0)$. If

$$\lim_{A\to a, B\to b} \overline{y}_{A,B} = \overline{y}, \tag{64}$$

where $\overline{y}$ is an equilibrium solution of the limiting difference equation (62), then every solution of the difference equation (60) satisfies

$$\lim_{n\to\infty} x_n = \overline{y}. \tag{65}$$

Proof. In view of (61) for all $\epsilon > 0$ there exist $N_1(\epsilon) > 0$ and $N_2(\epsilon) > 0$such that

$$\begin{aligned} n \geq N_1(\epsilon) &\Longrightarrow \\ |a_n - a| < \epsilon &\Longleftrightarrow \\ a - \epsilon < a_n < a + \epsilon, \\ n \geq N_2(\epsilon) &\Longrightarrow \\ |b_n - b| < \epsilon &\Longleftrightarrow \\ b - \epsilon < b_n < b + \epsilon. \end{aligned} \tag{66}$$

Let $N = \max(N_1, N_2)$. Then $n \geq N(\epsilon)$ implies

$$\begin{aligned} (a-\epsilon) f_1(x_n) + (b-\epsilon) f_2(x_{n-1}) &\leq x_{n+1} \\ &= a_n f_1(x_n) + b_n f_2(x_{n-1}) \\ &< (a+\epsilon) f_1(x_n) + (b+\epsilon) f_2(x_{n-1}). \end{aligned} \tag{67}$$

Now, assume that $\epsilon \leq \epsilon_0$ and consider two equations of the form (62). In view of Corollary 11 we have that

$$\ell_n \leq x_n \leq u_n, \quad n \geq N(\epsilon), \tag{68}$$

where $\{\ell_n\}$, $\{u_n\}$ satisfy

$$\begin{aligned} \ell_{n+1} &= (a-\epsilon) f_1(\ell_n) + (b-\epsilon) f_2(\ell_{n-1}), \\ &\qquad n \geq N(\epsilon), \\ u_{n+1} &= (a+\epsilon) f_1(u_n) + (b+\epsilon) f_2(u_{n-1}), \\ &\qquad n \geq N(\epsilon). \end{aligned} \tag{69}$$

In view of the assumption (64) we have that

$$\lim_{n\to\infty} \ell_n = \lim_{n\to\infty} u_n = \overline{y}, \tag{70}$$

which by (68) implies (65). □

Theorem 18 has an immediate extension to the kth order difference equation of the form

$$x_{n+1} = \sum_{i=0}^{k-1} a_i(n) f_i(x_{n-i}), \quad n = 0, 1, \ldots. \tag{71}$$

Theorem 19. *Consider the difference equation (71), where f_i, $i = 0, 1, \ldots, k-1$, are nondecreasing functions and*

$$\lim_{n\to\infty} a_i(n) = \alpha_i, \quad i = 0, \ldots, k-1 \tag{72}$$

and the limiting difference equation

$$y_{n+1} = \sum_{i=0}^{k-1} \alpha_i f_i(x_{n-i}), \quad n = 0, 1, \ldots. \tag{73}$$

Assume that there exists $\epsilon_0 > 0$ such that every solution of difference equation

$$y_{n+1} = \sum_{i=0}^{k-1} A_i f_i(x_{n-i}), \quad n = 0, 1, \ldots \tag{74}$$

converges to a constant solution $\overline{y}_{\alpha_i}$ for every $A_i \in (\alpha_i - \epsilon_0, \alpha_i + \epsilon_0)$. If

$$\lim_{A_i \to \alpha_i, i=0,\ldots,k} \overline{y}_{A_i} = \overline{y}, \tag{75}$$

where $\overline{y}$ is an equilibrium solution of the limiting difference equation (73), then every solution of the difference equation (71) satisfies (65).

3. Single Species Two-Generation Models

We start with an example of cooperative system which is feasible mathematical model in population dynamics that illustrates Theorems 7, 9, and 10 and Corollary 8. This system can be considered as cooperative Leslie two-generation population model, where each generation helps growth of the other.

Example 20. Consider the cooperative system

$$\begin{bmatrix} x_{n+1} \\ y_{n+1} \end{bmatrix} = \begin{bmatrix} a & \dfrac{b}{1+y_n} \\ \dfrac{c}{1+x_n} & d \end{bmatrix} \begin{bmatrix} x_n \\ y_n \end{bmatrix}, \quad n = 0, 1, \ldots, \tag{76}$$

where $a, b, c, d > 0$, $x_0, y_0 \geq 0$. The equilibrium solutions (x, y) satisfy equation

$$\begin{bmatrix} (1-a)x \\ (1-d)y \end{bmatrix} = \begin{bmatrix} \dfrac{b}{1+y} \\ \dfrac{c}{1+x} \end{bmatrix}, \tag{77}$$

which implies that system (76) has always the zero equilibrium $E_0(0,0)$ and if it has positive equilibrium solutions $E_+(\overline{x}, \overline{y})$ then it is necessarily $a < 1$, $d < 1$, in which case there is the unique equilibrium solution given as

$$\begin{aligned} \overline{x} &= \frac{b}{1-a} \frac{\overline{y}}{1+\overline{y}}, \\ \overline{y} &= \frac{bc - (1-d)(1-a)}{(1-d)(b+1-a)}, \end{aligned} \tag{78}$$

when

$$(1-a)(1-d) < bc. \tag{79}$$

The Jacobian matrix of the map T associated with system (76) is

$$J_T = \begin{bmatrix} a & \dfrac{b}{(1+y)^2} \\ \dfrac{c}{(1+x)^2} & d \end{bmatrix}. \tag{80}$$

Thus the Jacobian matrix of the map T at the zero equilibrium $E_0(0,0)$ is

$$J_T(E_0) = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \tag{81}$$

and at the positive equilibrium $E_+(\overline{x},\overline{y})$ is

$$J_T(E_+) = \begin{bmatrix} a & \dfrac{b}{(1+\overline{y})^2} \\ \dfrac{c}{(1+\overline{x})^2} & d \end{bmatrix} = \begin{bmatrix} a & \dfrac{(1-a)^2}{b}\dfrac{\overline{x}^2}{\overline{y}^2} \\ \dfrac{(1-d)^2}{c}\dfrac{\overline{y}^2}{\overline{x}^2} & d \end{bmatrix}. \tag{82}$$

The local stability of system (76) is described by the following result.

Claim 1. Consider system (76).

(1) The positive equilibrium $E_+(\overline{x},\overline{y})$ of system (76) is locally asymptotically stable when (79) holds.

(2) The zero equilibrium $E_0(0,0)$ of system (76) is locally asymptotically stable if $bc < (1-a)(1-d)$; it is a saddle point if $bc > (1-a)(1-d)$; it is a nonhyperbolic equilibrium if $bc = (1-a)(1-d)$.

Proof. (1) After simplification the characteristic equation of $J_T(E_+)$ becomes

$$\lambda^2 - (a+d)\lambda + ad - \frac{(1-a)^2(1-d)^2}{bc} = 0. \tag{83}$$

In view of Theorem 1.1.1 in [7] or Theorem 2.13 in [8] E_+ is locally asymptotically stable if

$$a + d < 1 + ad - \frac{(1-a)^2(1-d)^2}{bc} < 2 \tag{84}$$

holds. The inequality $a + d < 1 + ad - (1-a)^2(1-d)^2/bc$ is equivalent to (79) and the inequality $1 + ad - (1-a)^2(1-d)^2/bc < 2$ is equivalent to $ad - 1 < (1-a)^2(1-d)^2/bc$, which, in view of $a < 1$, $d < 1$, is always satisfied.

(2) The characteristic equation of $J_T(E_0)$ becomes

$$\lambda^2 - (a+d)\lambda + ad - bc = 0. \tag{85}$$

In view of Theorem 2.13 in [8] E_0 is locally asymptotically stable if $bc < (1-a)(1-d)$ and it is a saddle point if $bc > (1-a)(1-d)$. Finally, if $bc = (1-a)(1-d)$ then E_0 is a nonhyperbolic equilibrium point ($\lambda_1 = 1$) of stable type ($\lambda_2 \in (-1,1)$) if $a + d < 2$, of unstable type $\lambda_2 > 1$ if $a + d > 2$, and of resonance type $(1,-1)$ if $a + d = 2$. □

By using Theorems 7, 9, 10, and 18 and Corollary 8 we can formulate the following result which describes the global dynamics of system (76).

Theorem 21. *Consider system (76).*

(1) *If $a \geq 1$ then $\lim_{n\to\infty} x_n = \infty$ and $\lim_{n\to\infty} y_n = \infty$ if $d \geq 1$ and $\lim_{n\to\infty} y_n = c/(1-d)$, if $d < 1$.*

(2) *If $d \geq 1$ then $\lim_{n\to\infty} y_n = \infty$ and $\lim_{n\to\infty} x_n = \infty$ if $a \geq 1$ and $\lim_{n\to\infty} x_n = b/(1-a)$, if $a < 1$.*

(3) *The positive equilibrium $E_+(\overline{x},\overline{y})$ of system (76) is globally asymptotically stable when (79) holds.*

(4) *The zero equilibrium $E_0(0,0)$ of system (76) is globally asymptotically stable when $a < 1$, $d < 1$, and*

$$bc \leq (1-a)(1-d) \tag{86}$$

hold.

Proof. (1) If $a \geq 1$ then the first equation of system (76) implies $x_{n+1} > ax_n \geq x_n$, which shows that $\{x_n\}_{n=1}^{\infty}$ is an increasing sequence, and because there is no positive equilibrium in this case we have that $\lim_{n\to\infty} x_n = \infty$. In view of Theorem 18 $\{y_n\}_{n=1}^{\infty}$ is converging to the asymptotic solution of the limiting equation

$$y_{n+1} = c + dy_n, \quad n = 1, 2, \ldots \tag{87}$$

which completes the proof in this case.

(2) The proof in this case is similar to the proof of case (1) and is omitted.

(3) Assume that (79) holds. In view of Claim 1 E_0 is a saddle point and E_+ is locally asymptotically stable. By using Corollary 8 we conclude that the interior of ordered interval $[\![E_0, E_+]\!]$ is attracted to E_+. Furthermore, any solution of system (76) different from E_0 which starts on coordinate axis in one step enters the interior of ordered interval $[\![E_0, E_+]\!]$ and so converges to E_+. Every solution of system (76) satisfies

$$\begin{aligned} x_{n+1} &\leq ax_n + b, \\ y_{n+1} &\leq c + dy_n, \\ &\qquad n = 0, 1, \ldots, \end{aligned} \tag{88}$$

which, in view of Theorem 10, means that

$$\begin{aligned} x_n &\leq u_n, \\ y_n &\leq v_n, \\ &\qquad n = 0, 1, \ldots, \end{aligned} \tag{89}$$

where $\{u_n\}$, $\{v_n\}$ satisfy

$$\begin{aligned} u_{n+1} &= au_n + b, \\ v_{n+1} &= c + dv_n, \\ &\qquad n = 0, 1, \ldots. \end{aligned} \tag{90}$$

Since, $a < 1$, $d < 1$, we obtain that

$$\begin{aligned} x_n &\leq \frac{b}{1-a} + \varepsilon_0 = U_x, \\ y_n &\leq \frac{c}{1-d} + \varepsilon_0 = U_y, \end{aligned} \tag{91}$$

for some $\varepsilon_0 > 0$ and $n \geq N(\varepsilon_0)$. In view of (iii) of Theorem 7 every solution which starts in the interior of ordered interval $[\![E_+, (U_x, U_y)]\!]$ is attracted to E_+. Since system (76) is strictly cooperative we conclude that the whole ordered interval

$[\![E_+, (U_x, U_y)]\!]$ is attracted to E_+. If a solution starts at (x_0, y_0) in the complement of $[\![E_0, E_+]\!] \cup [\![E_+, (U_x, U_y)]\!]$ one can find the points $(x_l, y_l) \in [\![E_0, E_+]\!]$ and $(x_u, y_u) \in [\![E_+, (U_x, U_y)]\!]$ such that $(x_l, y_l) \preceq_{ne} (x_0, y_0) \preceq_{ne} (x_u, y_u)$. Since T is monotone map we have that $T^n(x_l, y_l) \preceq_{ne} T^n(x_0, y_0) \preceq_{ne} T^n(x_u, y_u)$ for $n \geq 1$, which implies that $\lim_{n\to\infty} T^n(x_0, y_0) = E_+$ because $\lim_{n\to\infty} T^n(x_l, y_l) = \lim_{n\to\infty} T^n(x_u, y_u) = E_+$.

(4) In view of condition (86), system (76) has only the zero equilibrium. By using (91) we have that the map T associated with system (76) has an invariant rectangle $[\![E_0, (U_x, U_y)]\!]$, with the unique equilibrium point E_0, and by Theorem 7 every solution which starts in this rectangle must converge to E_0. The fact that the rectangle $[\![E_0, (U_x, U_y)]\!]$ is also attractive completes the proof. □

The following difference equation is known as density dependent Leslie matrix model with two age classes, juveniles and adults:

$$x_{n+1} = \frac{a_1 x_n}{1 + b_1 x_n} + \frac{a_2 x_{n-1}}{1 + b_2 x_{n-1}}, \quad n = 0, 1, \ldots, \tag{92}$$

where the parameters a_1, a_2, b_1, and b_2 are positive real numbers and the initial conditions x_{-1} and x_0 are nonnegative real numbers. Here x_n is the size of population at nth generation. This model was considered first by Kulenović and Yakubu [27] in 2004 and later by Franke and Yakubu [15–17], where the extensions of this model to the periodic environment were considered.

Theorem 22. *The density dependent Leslie matrix model (92) exhibits the following properties:*

(1) *Equation (92) has always the zero equilibrium and when $a_1 + a_2 > 1$ has the unique positive equilibrium $\overline{x}$.*

(2) *Assume $a_1 + a_2 < 1$. Then the zero equilibrium of (92) is globally asymptotically stable.*

(3) *Assume $a_1 + a_2 > 1$. Then the unique positive equilibrium $\overline{x}$ of (92) is globally asymptotically stable.*

(4) *Assume that $a_1 + a_2 > 1$ holds. All solutions of (92) satisfy*

$$\lim_{n\to\infty} \frac{x_{n+1} - \overline{x}}{x_n - \overline{x}} = \lambda_\pm(\overline{x}), \tag{93}$$

where $\lambda_\pm(\overline{x})$ are the real roots of characteristic equation at the equilibrium $\overline{x}$.

(5) *Equation (92) has both, the oscillatory and nonoscillatory solutions. The oscillatory solutions have the semicycles of length one, with the possible exception of the first semicycle.*

An application of Theorems 18 and 22 yields the following.

Example 23. Consider the difference equation

$$x_{n+1} = \frac{c_1(n) x_n}{1 + b_1 x_n} + \frac{c_2(n) x_{n-1}}{1 + b_2 x_{n-1}}, \quad n = 0, 1, \ldots, \tag{94}$$

where the parameters $c_1(n)$, $c_2(n)$, b_1, and b_2 are positive real sequences and numbers and the initial conditions x_{-1} and x_0 are nonnegative real numbers. Assume

$$\lim_{n\to\infty} c_i(n) = a_i > 0, \quad i = 1, 2. \tag{95}$$

If either $a_1 + a_2 < 1$ or $a_1 + a_2 > 1$, then the global dynamics of nonautonomous difference equation (94) are the same as the global dynamics of the limiting equation (92) and are described by Theorem 22.

Remark 24. Similarly, as for the Beverton-Holt equation the difficult case is when the limiting equation (92) is nonhyperbolic. In this case the dynamics of nonautonomous equation can be quite different than the dynamics of the limiting equation.

4. Local and Global Dynamics of Several Generation Models

We consider the following difference equation as a generalization of density dependent Leslie matrix model with two age classes:

$$x_{n+1} = \sum_{i=0}^{k} a_i f_i(x_{n-i}), \quad n = 0, 1, \ldots, \tag{96}$$

where the parameters $a_i \geq 0$, $i = 0, \ldots, k$, $\sum_{i=0}^{k} a_i > 0$, and $f_i(u)$ satisfy the following conditions:

$$f_i : [0, \infty) \longrightarrow [0, \infty), \quad f_i(u) \leq u, \ u \geq 0 \tag{97}$$

for all $i = 0, 1, \ldots, k$. Equation (96) is called density dependent Leslie matrix model with $k+1$ age classes. See [28] for some global asymptotic stability results for such model.

Examples of functions which satisfy condition (97) are

$$\begin{aligned} f(u) &= u, \\ f(u) &= \frac{u}{1+u}, \\ f(u) &= \frac{u^2}{1+u^2}, \\ f(u) &= 1 - e^{-u}. \end{aligned} \tag{98}$$

The first three functions in (98) are also called *Holling functions of types I, II,* and *III* (see [1, 6, 19]) and are widely used in modeling. Condition (97) implies that $f_i(0) = 0$, $i = 0, \ldots, k$, and that 0 is always an equilibrium of (96). Furthermore, if there exists a positive equilibrium $\overline{x} > 0$, then $\sum_{i=0}^{k} a_i \geq 1$.

First we state and prove the local stability result for (96) which is sharp.

Theorem 25. *Consider (96) subject to condition (97) and assume that the functions f_i, $i = 0, \ldots, k$, are differentiable at the equilibrium $\overline{x}$ of (96). Then the equilibrium $\overline{x}$ of (96) is one of the following:*

(a) *Locally asymptotically stable if* $\sum_{i=0}^{k} a_i f_i'(\overline{x}) < 1$

(b) *Nonhyperbolic and locally stable if* $\sum_{i=0}^{k} a_i f_i'(\overline{x}) = 1$

(c) *Unstable if* $\sum_{i=0}^{k} a_i f_i'(\overline{x}) > 1$.

Proof. This result is the consequence of Theorem 3 in Janowski and Kulenović [29] applied to the linearization

$$x_{n+1} = \sum_{i=0}^{k} a_i f_i'(\overline{x}) x_{n-i}, \quad n = 0, 1, \ldots \tag{99}$$

of (96) at the equilibrium $\overline{x}$. □

The global result is simple to state and apply.

Theorem 26. *Consider (96) subject to condition (97). The zero equilibrium* $\overline{x} = 0$ *of (96) is globally asymptotically stable if*

$$\sum_{i=0}^{k} a_i < 1. \tag{100}$$

Proof. The result is an immediate consequence of Corollary 1 in [29] applied to the following linearization of (96):

$$x_{n+1} = \sum_{i=0}^{k} a_i \frac{f_i(x_{n-i})}{x_{n-i}} x_{n-i} = \sum_{i=0}^{k} g_i x_{n-i}, \quad n = 0, 1, \ldots \tag{101}$$

In this case

$$\sum_{i=0}^{k} g_i = \sum_{i=0}^{k} a_i \frac{f_i(x_{n-i})}{x_{n-i}} \le \sum_{i=0}^{k} a_i < 1 \tag{102}$$

and Corollary 1 in [29] implies the global asymptotic stability of the zero equilibrium. □

Assume that (96) has a positive equilibrium $\overline{x} > 0$. Then (100) is not satisfied; that is, $\sum_{i=0}^{k} a_i \ge 1$.

The global result requires an additional condition which is well known.

Theorem 27. *Consider (96) subject to condition (97) and*

$$\left| f_i(u) - f_i(\overline{x}) \right| \le C_i \left| u - \overline{x} \right|, \quad u > 0, \tag{103}$$

where $C_i > 0$ *are constants, for all* $i = 0, \ldots, k$. *The equilibrium* $\overline{x}$ *of (96) is globally asymptotically stable if*

$$\sum_{i=0}^{k} a_i C_i < 1 \tag{104}$$

is satisfied.

Proof. If $f_i(u)$ is differentiable on $[0, \infty)$ then condition (103) follows from the condition

$$\left| f_i'(u) \right| \le C_i, \quad i = 0, 1, \ldots, k, \ u > 0. \tag{105}$$

The result is an immediate consequence of Corollary 1 in [29] applied to the following linearization of (96):

$$\begin{aligned} x_{n+1} - \overline{x} &= \sum_{i=0}^{k} a_i \frac{f_i(x_{n-i}) - f_i(\overline{x})}{x_{n-i} - \overline{x}} (x_{n-i} - \overline{x}) \\ &= \sum_{i=0}^{k} g_i (x_{n-i} - \overline{x}), \quad n = 0, 1, \ldots, \end{aligned} \tag{106}$$

which, by substitution $y_n = x_n - \overline{x}$, becomes the linearized equation

$$y_{n+1} = \sum_{i=0}^{k} g_i y_{n-i}, \quad n = 0, 1, \ldots, \tag{107}$$

where

$$g_i = a_i \frac{f_i(x_{n-i}) - f_i(\overline{x})}{x_{n-i} - \overline{x}}, \quad i = 0, \ldots, k. \tag{108}$$

Now we have

$$\sum_{i=0}^{k} \left| g_i \right| = \sum_{i=0}^{k} \left| a_i \frac{f_i(x_{n-i}) - f_i(\overline{x})}{x_{n-i} - \overline{x}} \right| \le \sum_{i=0}^{k} a_i C_i < 1, \tag{109}$$

which in view of Corollary 1 in [29] proves global asymptotic stability of $\overline{x}$. □

By using the monotone convergence results in [7, 8, 30] we obtain the following powerful global asymptotic stability result for (96).

Theorem 28. *Consider (96) subject to the condition*

$$f_i(u) \le U_i, \quad u \ge 0, \ i = 0, \ldots, k, \tag{110}$$

where $f_i(u)$ *is nondecreasing for every* u. *If there exists a constant* $L > 0$ *such that*

$$\sum_{i=0}^{k} a_i \ge \frac{L}{\min_{i=0,\ldots,k} f_i(L)}, \tag{111}$$

then if (96) has the unique positive equilibrium $\overline{x}$, *it is globally asymptotically stable.*

Proof. Set

$$F(u_0, u_1, \ldots, u_k) = \sum_{i=0}^{k} a_i f_i(u_i), \quad u_i \ge 0, \ i = 0, \ldots, k. \tag{112}$$

Then $F(u_0, u_1, \ldots, u_k) \le \sum_{i=0}^{k} a_i U_i = U$. Furthermore, if there exists a constant $L > 0$ such that $u_i \ge L$, $i = 0, \ldots, k$, then in view of (111) we would have

$$\begin{aligned} F(u_0, u_1, \ldots, u_k) &= \sum_{i=0}^{k} a_i f_i(u_i) \ge \sum_{i=0}^{k} a_i f_i(L) \\ &\ge \min_{i=0,\ldots,k} f_i(L) \sum_{i=0}^{k} a_i \ge L. \end{aligned} \tag{113}$$

This shows that the interval $[L, U]$ is an invariant interval for the function $F(u_0, u_1, \ldots, u_k)$, which is nondecreasing in all its arguments. In view of the theorem in [7, 30], the fact that (96) has the unique positive equilibrium $\overline{x}$ implies that this equilibrium is globally asymptotically stable. □

An application of Theorems 25–27 gives the following result for Leslie or Beverton-Holt model with k generations.

Theorem 29. *The Beverton-Holt model with k generations*

$$x_{n+1} = \sum_{i=0}^{k} a_i \frac{x_{n-i}}{1 + x_{n-i}}, \quad n = 0, 1, \ldots, \ a_i \geq 0, \ \sum_{i=0}^{k} a_i > 0, \tag{114}$$

has the following properties:

(a) *If $\sum_{i=0}^{k} a_i < 1$, then the zero equilibrium is globally asymptotically stable.*

(b) *If $\sum_{i=0}^{k} a_i = 1$, then the zero equilibrium is nonhyperbolic and locally stable.*

(c) *If $\sum_{i=0}^{k} a_i > 1$, then the positive equilibrium $\overline{x} = \sum_{i=0}^{k} a_i - 1$ is globally asymptotically stable.*

Proof. Now (a) follows from Theorems 25 and 26 and the fact that

$$\sum_{i=0}^{k} a_i \frac{x_{n-i}}{1 + x_{n-i}} < \sum_{i=0}^{k} a_i < 1, \quad n = 0, 1, \ldots. \tag{115}$$

In the case of (c), the global asymptotic stability of the positive equilibrium $\overline{x}$ follows from Theorem 28 with L and U as $U = \sum_{i=0}^{k} a_i$ and $0 < L \leq \overline{x}$. □

Theorem 30. *The sigmoid Beverton-Holt model with k generations*

$$x_{n+1} = \sum_{i=0}^{k} a_i \frac{x_{n-i}^2}{1 + x_{n-i}^2}, \quad n = 0, 1, \ldots; \ a_i \geq 0, \ \sum_{i=0}^{k} a_i > 0, \tag{116}$$

where the initial conditions are nonnegative numbers, has the following properties:

(a) *If $\sum_{i=0}^{k} a_i < 2$, then the zero equilibrium is globally asymptotically stable.*

(b) *If $\sum_{i=0}^{k} a_i = 2$, then the zero equilibrium is globally asymptotically stable within its basin of attraction which contains $[0, 1)^{k+1}$. The positive equilibrium $\overline{x} = 1$ is locally nonhyperbolic and is global attractor within its basin of attraction which contains $[1, \infty)^{k+1}$.*

(c) *If $\sum_{i=0}^{k} a_i > 2$, then the zero equilibrium is globally asymptotically stable within its basin of attraction which contains $[0, \overline{x}_-)^{k+1}$. The larger positive equilibrium $\overline{x}_+$ is globally asymptotically stable within its basin of attraction which contains $(\overline{x}_-, \infty)^{k+1}$.*

Proof. The linearized equation of (116) at an equilibrium point $\overline{x}$ is

$$x_{n+1} = \sum_{i=0}^{k} 2a_i \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} x_{n-i}, \quad n = 0, 1, \ldots \tag{117}$$

and the characteristic equation of (117) is

$$\lambda^{k+1} = \sum_{i=0}^{k} 2a_i \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} \lambda^{k-i}. \tag{118}$$

Theorem 25 implies the local stability of the zero and the positive equilibrium points. Observe that the equilibrium equation of (116) can have at most two positive solutions.

When $\sum_{i=0}^{k} a_i < 2$ (116) has only the zero equilibrium and can be linearized as

$$x_{n+1} = \sum_{i=0}^{k} a_i \frac{x_{n-i}}{1 + x_{n-i}^2} x_{n-i} = \sum_{i=0}^{k} g_i x_{n-i}, \quad n = 0, 1, \ldots. \tag{119}$$

Since $u/(1 + u^2) \leq 1/2$ for every u we have

$$\sum_{i=0}^{k} g_i \leq \sum_{i=0}^{k} \frac{a_i}{2} < 1, \quad n = 0, 1, \ldots \tag{120}$$

which by Theorem 2 in [29] or Theorem 27 implies that the zero equilibrium is globally asymptotically stable.

The positive equilibrium $\overline{x}$ satisfies

$$x^2 - \sum_{i=0}^{k} a_i x + 1 = 0, \tag{121}$$

which either has one positive solution $\overline{x} = 1$ when $\sum_{i=0}^{k} a_i = 2$ or has two positive solutions when $\sum_{i=0}^{k} a_i > 2$.

In the case when $\sum_{i=0}^{k} a_i = 2$, the characteristic equation (118) takes the form

$$\lambda^{k+1} = \sum_{i=0}^{k} \frac{a_i}{2} \lambda^{k-i}, \tag{122}$$

with $\lambda = 1$ as a solution, which shows that $\overline{x} = 1$ is stable and nonhyperbolic equilibrium.

In the case when $\sum_{i=0}^{k} a_i > 2$, we have two positive equilibrium solutions $\overline{x}_\pm$ which satisfy (121) and so $\overline{x}_- < 1 < \overline{x}_+$. In view of Theorem 3 in [29] $\overline{x}$ is locally asymptotically stable if and only if

$$\sum_{i=0}^{k} 2a_i \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} < 1 \tag{123}$$

which by (121) implies

$$2 < \overline{x}\sum_{i=0}^{k} a_i = \overline{x}^2 + 1 \Longleftrightarrow \quad \overline{x} > 1. \tag{124}$$

Similarly one can show that the equilibrium $\overline{x} > 1$ is unstable if and only if $\overline{x} < 1$. Consequently, $\overline{x}_+$ is locally asymptotically stable and $\overline{x}_-$ is unstable.

Every solution of (116) satisfies $x_n \le \sum_{i=0}^{k} a_i = U$, $n = k+1, k+2, \ldots$. Using this it follows that the interval $[\![\mathbf{x}_-, \mathbf{U}]\!]$, where $\mathbf{U} = (U, U, \ldots, U)$, is invariant set for monotone map T, which contains the unique fixed point $\mathbf{x}_-$. In view of Theorem 7 every orbit of T converges to $\mathbf{x}_-$, which means that $\lim x_n = x_-$ as $n \to \infty$.

Assume that $\sum_{i=0}^{k} a_i > 2$. Then (116) has two positive equilibrium solutions $x_- < x_+$, where x_- is unstable and x_+ is asymptotically stable. In a similar way to the above the interior of the ordered interval $[\![\mathbf{0}, \mathbf{x}_-]\!]$ is a subset of the basin of attraction $\mathscr{B}(\mathbf{0})$, and the union of the interiors of the ordered intervals $[\![\mathbf{x}_-, \mathbf{x}_+]\!]$ and $[\![\mathbf{x}_+, \mathbf{U}]\!]$ is a subset of the basin of attraction $\mathscr{B}(\mathbf{x}_+)$. □

An application of Theorem 19 and the global attractivity result proved in [27] for constant coefficient case gives the following global attractivity result for asymptotically constant k-stage Beverton-Holt model:

$$x_{n+1} = \sum_{i=0}^{k-1} a_i(n) \frac{x_{n-i}}{1 + x_{n-i}}, \quad x_{-k+1}, \ldots, x_0 \ge 0,\ a_i(n) \ge 0,\ i = 0, \ldots, k-1;\ n = 0, 1, \ldots. \tag{125}$$

Example 31. Consider the difference equation (125) where (72) holds. Then the following result holds:

$$\lim_{n\to\infty} \sum_{i=0}^{k-1} a_i(n) = a \begin{cases} < 1 \\ > 1 \end{cases} \Longrightarrow \quad \lim_{n\to\infty} x_n = \begin{cases} 0, & \text{if } x_{1-k}, \ldots, x_0 \ge 0 \\ a - 1, & \text{if } x_{1-k}, \ldots, x_0 > 0. \end{cases} \tag{126}$$

Example 32. Consider the difference equation

$$x_{n+1} = \sum_{i=0}^{k} a_i(n) \frac{x_{n-i}^2}{1 + x_{n-i}^2}, \quad n = 0, 1, \ldots;\ a_i \ge 0,\ \sum_{i=0}^{k} a_i > 0, \tag{127}$$

where (72) holds. Then the following result holds:

$$\lim_{n\to\infty} \sum_{i=0}^{k-1} a_i(n) = a \begin{cases} < 2 \\ > 2 \end{cases} \Longrightarrow \quad \lim_{n\to\infty} x_n = \begin{cases} 0, & \text{if } x_m \in [0, \overline{x}_-),\ m = 1-k, \ldots, 0 \\ \overline{x}_+, & \text{if } x_m \in (\overline{x}_-, \infty),\ m = 1-k, \ldots, 0, \end{cases} \tag{128}$$

where $\overline{x}_-$ is the smaller and $\overline{x}_+$ is the bigger positive equilibrium.

It should be noticed that Examples 31 and 32 do not cover a nonhyperbolic case, which is the case when $\lim_{n\to\infty} \sum_{i=0}^{k-1} a_i(n) = 1$ and $\lim_{n\to\infty} \sum_{i=0}^{k-1} a_i(n) = 2$, respectively.

Finally, in the case of the nonautonomous difference equation (71), where the sequences $a_i(n) \ge 0$, $i = 0, \ldots, k$, $\sum_{i=0}^{k} a_i(n) > 0$, $n = 0, 1, \ldots$, and $f_i(u)$ satisfy (97), the global attractivity and global stability results in [29] give some robust global stability results.

Theorem 33. *Consider (71) subject to (97). If $a_i(n)$ are bounded sequences for $i = 0, \ldots, k$ and*

(i)

$$\sum_{i=0}^{k} \max_{n=0,1,\ldots} \{a_i(n)\} \le a < 1, \tag{129}$$

for some constant $a > 0$, then the zero equilibrium is globally asymptotically stable,

(ii)

$$\sum_{i=0}^{k} \max_{n=0,1,\ldots} \{a_i(n)\} \le 1, \tag{130}$$

then the zero equilibrium is stable.

In the special case $k = 2$, based on the results in [20], we obtain more precise description of the basins of attraction of the equilibrium points as well as the period-two solutions. See also [31–33]. The general theory of competitive and cooperative systems is given in [3, 4, 22, 23, 34–36]. The Leslie model with 2 generations which exhibits Allee's effect may possess up to three minimal period-two solutions which in certain cases may have substantial basins of attraction as it was shown in [37]. We summarize the results in [37] as follows.

Theorem 34. *Consider the difference equation*

$$x_{n+1} = a_0 \frac{x_n^2}{1 + x_n^2} + a_1 \frac{x_{n-1}^2}{1 + x_{n-1}^2}, \quad n = 0, 1, \ldots, \tag{131}$$

where $a_0, a_1 \ge 0$, $a_0 + a_1 > 0$. Then

(a) *if $a_0 + a_1 < 2$ then the zero equilibrium of (131) is globally asymptotically stable,*

(b) *if $a_0 + a_1 = 2$, then the zero equilibrium of (131) is globally asymptotically stable within its basin of attraction which is the region below the global stable manifold $\mathscr{W}^s(E)$, $E(1,1)$ in the Northeast ordering. The positive equilibrium $\overline{x} = 1$ is locally nonhyperbolic and is global attractor within its basin of attraction, which is the region above the global stable manifold $\mathscr{W}^s(E)$ in the Northeast ordering,*

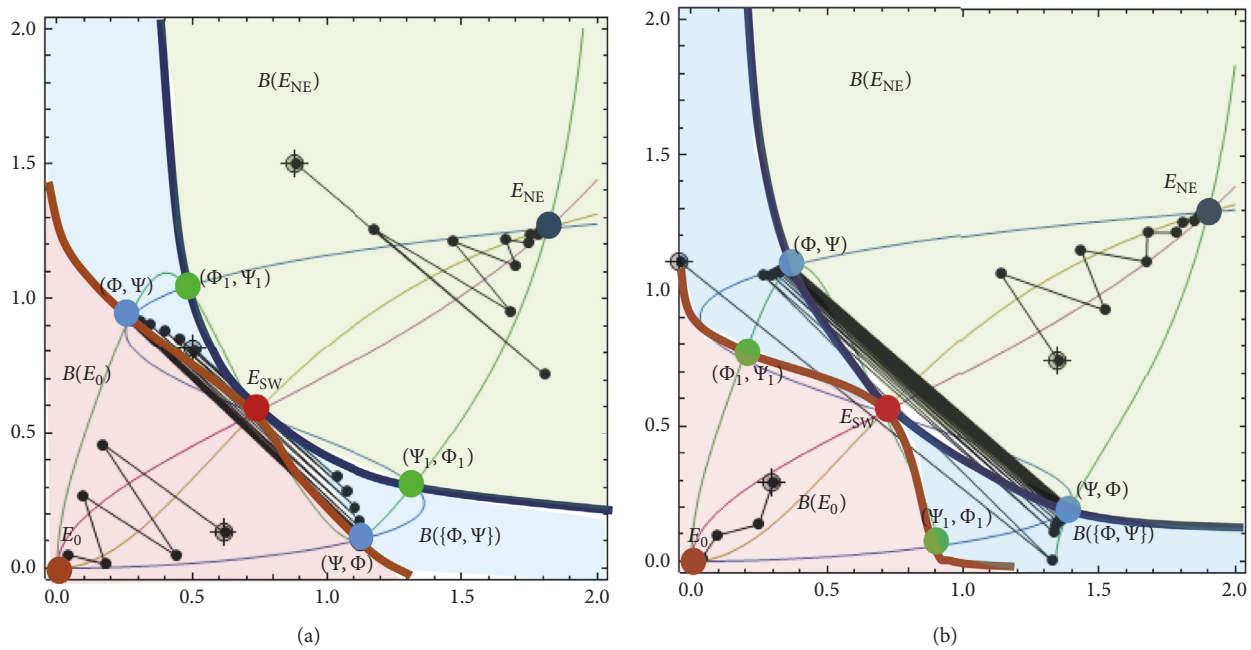

FIGURE 1: (a) Visual illustration of Theorem 34, case (d). (b) Visual illustration of Theorem 34, case (f).

(c) *if $a_0 + a_1 > 2$, then (131) has three equilibrium points $x_0 = 0 < \overline{x}_- < \overline{x}_+$ and zero, one, two, or three minimal period-two solutions. If there is no minimal period-two solutions and the equilibrium point E_- is a saddle point, then the zero equilibrium is globally asymptotically stable within its basin of attraction which is the region below the global stable manifold $\mathscr{W}^s(E_-)$, $E_- = (\overline{x}_-, \overline{x}_-)$ in the Northeast ordering. The larger positive equilibrium $\overline{x}_+$ is the global attractor within its basin of attraction, which is the region above the global stable manifold $\mathscr{W}^s(E_-)$ in the Northeast ordering,*

(d) *If $a_0 + a_1 > 2$ and (131) has one minimal period-two solution $\{\Phi, \Psi\}$ which is a saddle point then the boundary between the basins of attraction of $E_0(x_0, x_0)$ and $E_+ = (\overline{x}_+, \overline{x}_+)$ is the union of the stable manifolds of E_- and the stable manifolds of the period-two points $\mathscr{W}^s(P)$ and $\mathscr{W}^s(Q)$, $P = (\Phi, \Psi)$, $Q = (\Phi, \Psi)$,*

(e) *If $a_0 + a_1 > 2$ and (131) has two minimal period-two solutions $\{\Phi_i, \Psi_i\}$, $i = 1, 2$, where one of them is a saddle point and the other one is nonhyperbolic solution of the stable type, then the boundary between the basins of attraction of $E_0(x_0, x_0)$ and $E_+ = (\overline{x}_+, \overline{x}_+)$ is the union of the stable manifolds of E_- and the period-two points $\mathscr{W}^s(P)$ and $\mathscr{W}^s(Q)$, $P = (\Phi, \Psi)$, $Q = (\Phi, \Psi)$. Furthermore, the basin of the attraction of the nonhyperbolic period-two solution is the region between the stable manifolds of two period-two solutions $\{\Phi_i, \Psi_i\}$, $i = 1, 2$,*

(f) *If $a_0 + a_1 > 2$ and (131) has three minimal period-two solutions $\{\Phi_i, \Psi_i\}$, $i = 1, 2, 3$, such that $\{\Phi_1, \Psi_1\} \preceq_{ne} \{\Phi_2, \Psi_2\} \preceq_{ne} \{\Phi_3, \Psi_3\}$, where $\{\Phi_i, \Psi_i\}$, $i = 1, 3$, are saddle points and $\{\Phi_2, \Psi_2\}$ is locally asymptotically stable, then the boundary of the basins of attraction of $E_0(x_0, x_0)$ is the stable manifold of $\{\Phi_1, \Psi_1\}$, the boundary of the basins of attraction of E_+ is the stable manifold of $\{\Phi_3, \Psi_3\}$, and the basin of the attraction of the period-two solution $\{\Phi_2, \Psi_2\}$ is the region between the stable manifolds of two period-two solutions $\{\Phi_i, \Psi_i\}$, $i = 1, 3$.*

See Figure 1 for visual interpretation of cases (d) and (f). See Figure 2 for visual interpretation of case (e).

Proof. The linearized equation of (131) at an equilibrium point $\overline{x}$ is

$$x_{n+1} = 2a_0 \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} x_n + 2a_1 \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} x_{n-1}, \qquad n = 0, 1, \ldots \tag{132}$$

and the characteristic equation of (132) is

$$\lambda^2 = 2a_0 \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2} \lambda + 2a_1 \frac{\overline{x}}{\left(1 + \overline{x}^2\right)^2}. \tag{133}$$

The linearized equation (133) at the zero equilibrium is $\lambda^2 = 0$, which shows that the zero equilibrium is locally asymptotically stable. The linearized equation (133) at the equilibrium $\overline{x} = 1$ is $\lambda^2 = (1/2)\lambda + 1/2$, with the eigenvalues $\lambda_1 = 1$, $\lambda_2 = (a_0 - 2)/2 \in (-1, 0)$, which shows that $\overline{x} = 1$ is the nonhyperbolic equilibrium of stable type. The necessary and sufficient condition for the equilibrium $\overline{x} = 1$ to be nonhyperbolic is $a_0 + a_1 = 2$. The necessary and sufficient

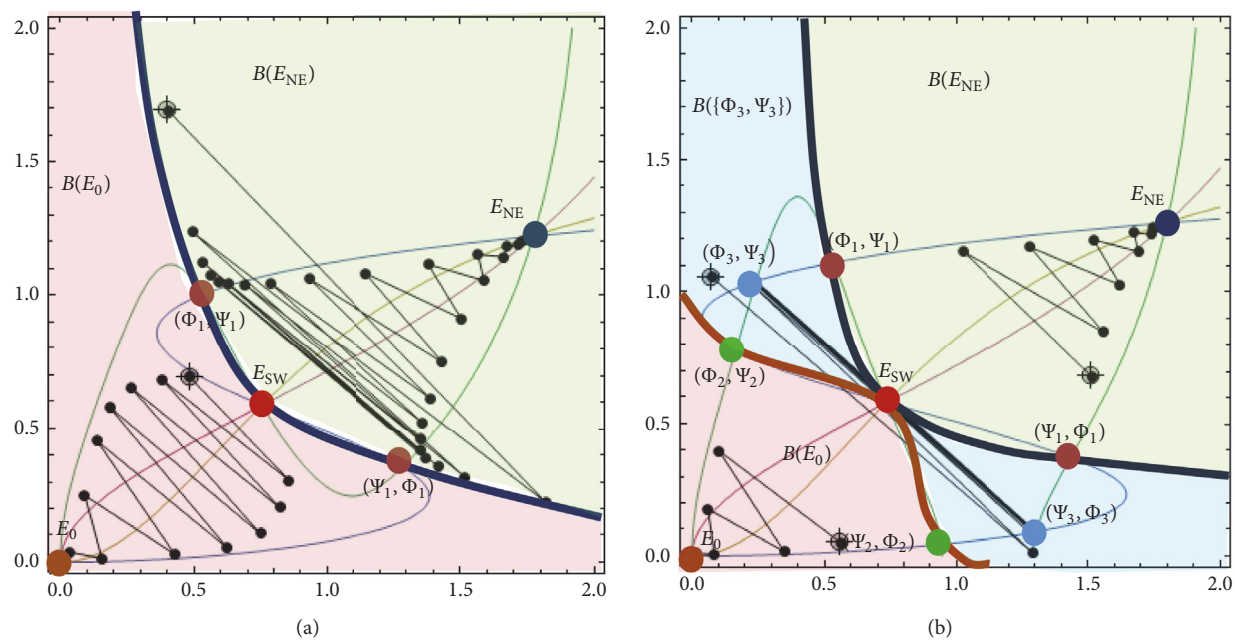

FIGURE 2: (a) Visual illustration of Theorem 34, case (e), where larger period-two solution is a saddle point. (b) Visual illustration of Theorem 34, case (e), where smaller period-two solution is a saddle point.

condition for (131) to have three equilibrium points $\overline{x}_0 = 0$, $\overline{x}_- = (1/2)(a_0 + a_1 - \sqrt{(a_0 + a_1)^2 - 4})$, $\overline{x}_+ = (1/2)(a_0 + a_1 + \sqrt{(a_0 + a_1)^2 - 4})$ is $a_0 + a_1 > 2$. When $a_0 + a_1 > 2$ the direct calculation shows that $\overline{x}_-$ is a saddle point and $\overline{x}_+$ is locally asymptotically stable.

As a consequence of the results in [38] every solution $\{x_n\}$ of (131) has two eventually monotone subsequences $\{x_{2n}\}$ and $\{x_{2n+1}\}$, which in view of the boundedness of solutions of (131) implies that all solutions of (131) converge either to the equilibrium or to period-two solutions.

When $a_0 + a_1 < 2$ (131) has only the zero equilibrium and can be linearized as

$$\begin{aligned} x_{n+1} &= a_0 \frac{x_n}{1 + x_n^2} x_n + a_1 \frac{x_{n-1}}{1 + x_{n-1}^2} x_{n-1} \\ &= g_0 x_n + g_1 x_{n-1}, \quad n = 0, 1, \ldots. \end{aligned} \tag{134}$$

Since $u/(1 + u^2) \leq 1/2$ for every u we have

$$g_0 + g_1 = a_0 \frac{x_n}{1 + x_n^2} + a_1 \frac{x_{n-1}}{1 + x_{n-1}^2} \leq \frac{a_0}{2} + \frac{a_1}{2} < 1, \quad n = 0, 1, \ldots \tag{135}$$

which by Theorem 2 in [29] or Theorem 27 implies that the zero equilibrium is globally asymptotically stable.

The cases $a_0 + a_1 = 2$ and $a_0 + a_1 > 2$ are explained in great details in [37]. □

Remark 35. The algebraic conditions on the coefficients a_0, a_1 for having 1, 2, or 3 period-two solutions for model (116) are given in [37]. We have also shown in [37] that another feasible model

$$x_{n+1} = A x_n + \frac{B x_{n-1}^2}{1 + x_{n-1}^2}, \quad n = 0, 1, \ldots, \tag{136}$$

where $A, B > 0$ and the initial conditions x_{-1}, x_0 are nonnegative, has similar dynamic scenarios as well as the combination of Beverton-Holt and sigmoid Beverton-Holt model:

$$x_{n+1} = A \frac{x_n}{1 + x_n} + \frac{B x_{n-1}^2}{1 + x_{n-1}^2}, \quad n = 0, 1, \ldots, \tag{137}$$

where $A, B > 0$ and the initial conditions x_{-1}, x_0 are nonnegative. In both cases the conditions for existence of period-two solutions are rather complicated.

The biological implications of models (116), (136), and (137) are that for some values of parameters of these models period-two behavior emerges with substantial basin of attraction.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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