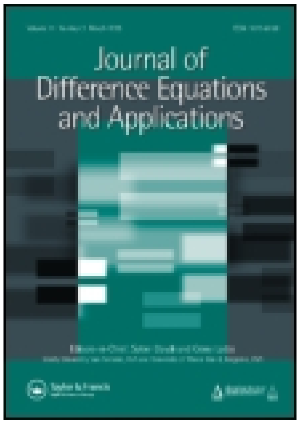

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An extended discrete Ricker population model with Allee effects

Jia Li [a], Baojun Song [b] & Xiaohong Wang [c]

[a] Department of Mathematical Sciences, University of Alabama in Huntsville, Huntsville, AL, 35899, USA

[b] Department of Mathematical Sciences, Montclair State University, Montclair, NJ, 07043, USA

[c] Department of Mathematics and Statistics, Arizona State University, Tempe, AZ, 85287, USA

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An extended discrete Ricker population model with Allee effects

JIA LI†*, BAOJUN SONG‡§ and XIAOHONG WANG¶||

†Department of Mathematical Sciences, University of Alabama in Huntsville, Huntsville, AL 35899, USA
‡Department of Mathematical Sciences, Montclair State University, Montclair, NJ 07043, USA
¶Department of Mathematics and Statistics, Arizona State University, Tempe, AZ 85287, USA

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Based on the classical discrete Ricker population model, we incorporate Allee effects by assuming rectangular hyperbola, or Holling-II type functional form, for the birth or growth function and formulate an extended Ricker model. We explore the dynamics features of the extended Ricker model. We obtain domains of attraction for the trivial fixed point. We determine conditions for the existence and stability of positive fixed points and find regions where there exist no positive fixed points, two positive fixed points one of which is stable and two positive fixed points both of which are unstable. We demonstrate that the model exhibits period-doubling bifurcations and investigate the existence and stability of the cycles. We also confirm that Allee effects have stabilization effects, by different measures, through numerical simulations.

Keywords: Ricker population model; Allee effect; Period-doubling bifurcation; Stabilization

1. Introduction

For modeling fish populations, the classical discrete Ricker model was proposed in Ref. [17]. Since then it has been widely used for other populations [3,9,12–15].

In the classical Ricker model, a density-dependent survival function is assumed, but the birth or growth rate is assumed to be density-independent. While this is a valid assumption in many ecological situations, there are many circumstances which lead to nonconstant density-dependent birth or growth functions, such as species encountering possible mating limitation, inbreeding depression, failure to satiate predators and lack of co-operative feeding, at a lower population level. Such a phenomenon has been observed and is called an Allee affect [1,6,11,18,19]. A typical example came from experiments in which females are forcibly mated to a particular male, which leads to lower fertilization rates, in particular, when the population size is small [16].

To incorporate Allee effects into the population growth, based on the classical Ricker model, we assume that the birth rate is proportional to the population size as the population level is low, but is saturated approximately to be constant when the population size is sufficiently large. We use the rectangular hyperbola, or Holling-II type functional form, for the birth or growth function

*Corresponding author. Email: li@math.uah.edu
§Email: songb@mail.montclair.edu
||Email: xwang@mathpost.la.asu.edu

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for this purpose [6,10,19]. Under these assumptions, we formulate an extended Ricker model in Section 2.

To gain insight into the model behavior and its dynamics, we establish conditions for existence of positive fixed points in Section 3 and investigate the stability of these fixed points in Section 4. The trivial solution $x = 0$ for this extended Ricker model is locally asymptotically stable. We then, in Section 5, explore its domains of attraction. Using the intrinsic growth rate as a bifurcation parameter, we examine that the model exhibits a typical period-doubling bifurcation and study existence and stability of the cycles in Section 6. We provide numerical examples to test stabilization or destabilization effects to the model dynamics that Allee effects may have in Section 7. Finally, brief discussions are given in Section 8.

2. Model formulation

Consider a non-overlapped population. Let x_n be a population at generation n and suppose that the dynamics of the population is governed by

$$x_{n+1} = b(x_n)x_n s(x_n), \tag{2.1}$$

where $b(x_n)$ is the per-capita birth or growth function and $s(x_n)$ is the survival function for generation n.

Based on the classical Ricker population model, we assume that the survival function has the form $\mathrm{e}^{-\mu-kx_n}$, at generation n, where $\mu > 0$ and $k > 0$ are the density-independent death rate and carrying capacity parameter, respectively. We then use a rectangular hyperbola, or Holling-II type functional form, for the birth or growth function such that $b(x_n) = cx_n/(\theta + x_n)$, where $c > 0$ and $\theta \geq 0$ are constant. Note that function b has the following properties

$$b(0) = 0, \quad b(\infty) = c, \quad b'(0) = \frac{c}{\theta}. \tag{2.2}$$

Hence c measures the maximal reproduction or growth rate and the ratio c/θ measures the relative growth rate as the population size is small.

With these assumptions, model equation (2.1) becomes

$$x_{n+1} = \frac{cx_n}{\theta + x_n} x_n \,\mathrm{e}^{-\mu-kx_n}. \tag{2.3}$$

Let $r = c\mathrm{e}^{-\mu}$. We rewrite model equation (2.3) as

$$x_{n+1} = \frac{rx_n^2}{\theta + x_n} \mathrm{e}^{-kx_n}. \tag{2.4}$$

Rescaling equation (2.4) by letting $y_n := kx_n$, we have equation

$$y_{n+1} = \frac{r\,y_n^2}{k\theta + y_n} \mathrm{e}^{-y_n}. \tag{2.5}$$

For simplifying expressions without confusion, we keep using x_n as the state variable and rewrite $\alpha := k\theta$. Then we study the following extended Ricker model

$$x_{n+1} = \frac{rx_n^2}{\alpha + x_n} \mathrm{e}^{-x_n} := F(x_n). \tag{2.6}$$

Function $F(x)$ has properties similar to the nonlinear unimodal function in the classical Ricker model. That is, $F(x) \geq 0$ for all $x \geq 0$, $F(0) = 0 = F(\infty)$ and there is a unique positive point C such that $F(x) < F(C)$ for all $x \geq 0$ and $x \neq C$ [3,17]. Moreover, since $F'(0) = 0$, the origin is a trivial fixed point and is locally asymptotically stable.

3. Existence of positive fixed points

Positive fixed points correspond to the steady states of the model population which are an important part for the population dynamics. To find positive fixed points, we consider the equation

$$\frac{rx}{\alpha + x} \mathrm{e}^{-x} = 1,$$

or, equivalently,

$$x + \ln(\alpha + x) - \ln x = \ln r, \tag{3.1}$$

for $x > 0$.

Define function $H(x) := x + \ln(\alpha + x) - \ln x$. We have

$$H'(x) = 1 + \frac{1}{\alpha + x} - \frac{1}{x} = \frac{x(\alpha + x) - \alpha}{x(\alpha + x)}, \tag{3.2}$$

and

$$H''(x) = \frac{1}{x^2} - \frac{1}{(\alpha + x)^2} > 0.$$

Solving $H'(x) = 0$ from (3.2), we have a unique positive critical point

$$x_\mathrm{c} := \frac{\sqrt{\alpha^2 + 4\alpha} - \alpha}{2}. \tag{3.3}$$

Hence, if $H(x_\mathrm{c}) = \ln r$, there exists a unique positive solution, $x = x_\mathrm{c}$, to (3.1) and if $H(x_\mathrm{c}) < \ln r$, there exist two positive solutions to (3.1).

Note that the equation $H(x_\mathrm{c}) = \ln r$, with x_c given in (3.3), is equivalent to

$$\ln \frac{\sqrt{\alpha^2 + 4\alpha} + \alpha}{\sqrt{\alpha^2 + 4\alpha} - \alpha} + \frac{1}{2}\left(\sqrt{\alpha^2 + 4\alpha} - \alpha\right) = \ln r.$$

Define function $P_1(\alpha)$ as

$$P_1(\alpha) := \frac{\sqrt{\alpha^2 + 4\alpha} + \alpha + 2}{2} \mathrm{e}^{\frac{\sqrt{\alpha^2+4\alpha}-\alpha}{2}}. \tag{3.4}$$

Then we have the following existence result.

THEOREM 3.1. *For model* (2.6)*, there exist two positive fixed points if* $r > P_1(\alpha)$*, a unique positive fixed point if* $r = P_1(\alpha)$ *and no positive fixed points if* $r < P_1(\alpha)$*.*

4. Stability of the positive fixed points

We investigate the stability of the positive fixed points, if they exist, in this section.

For function $F(x)$ defined in (2.6), we have

$$F'(x) = \frac{rx\mathrm{e}^{-x}}{(\alpha+x)^2}(x + 2\alpha - x(\alpha + x)).$$

If x is a positive fixed point, it satisfies $rx = (\alpha + x)\mathrm{e}^x$. Then it follows that

$$F'(x) = \frac{1}{\alpha+x}(x + 2\alpha - x(\alpha + x)) = 1 - \frac{x(\alpha+x) - \alpha}{\alpha+x}.$$

Hence x is locally asymptotically stable if

$$0 < \frac{x(\alpha+x) - \alpha}{\alpha+x} < 2, \tag{4.1}$$

and is unstable if

$$x\frac{(\alpha+x) - \alpha}{\alpha+x} < 0, \quad \text{or} \quad \frac{x(\alpha+x) - \alpha}{\alpha+x} > 2. \tag{4.2}$$

Suppose that there exist two positive fixed points, denoted $x^{\{1\}}$ and $x^{\{2\}}$. It follows from Section 3 that $x^{\{1\}} < x_c < x^{\{2\}}$ and

$$H'(x^{\{1\}}) < 0 = H'(x_c) < H'(x^{\{2\}}).$$

Then it follows from (3.2), which is equivalent to

$$\frac{(x\alpha+x) - \alpha}{\alpha+x} = xH'(x),$$

that

$$\frac{x^{\{1\}}(\alpha+x^{\{1\}}) - \alpha}{\alpha+x^{\{1\}}} = x^{\{1\}}H'(x^{\{1\}}) < 0.$$

Hence the fixed point $x^{\{1\}}$ is always unstable. Similarly, we have that the fixed point $x^{\{2\}}$ is asymptotically stable if

$$\frac{x^{\{2\}}(\alpha+x^{\{2\}}) - \alpha}{\alpha+x^{\{2\}}} < 2, \tag{4.3}$$

or equivalently,

$$x^{\{2\}}((\alpha + x^{\{2\}}) - 2) < 3\alpha.$$

Consider the inequality

$$x((\alpha + x) - 2) < 3\alpha. \tag{4.4}$$

It is easy to see that any solution x to inequality (4.4) satisfies

$$s_- < x < s_+,$$

where

$$s_\pm = \frac{2-\alpha \pm \sqrt{\alpha^2+8\alpha+4}}{2}. \tag{4.5}$$

Since $s_- < 0 < x^{\{2\}}$, the only condition that leads to local stability of $x^{\{2\}}$ is $x^{\{2\}} < s_+$.

Notice that for all $x > x^{\{2\}}$, we have $H'(x) > 0$. Hence $H(x)$ is a monotone increasing function on interval $(x^{\{2\}}, \infty)$. Then the condition for $x^{\{2\}}$ to be stable is equivalent to $H(x^{\{2\}}) < H(s_+)$, that is,

$$r < \mathrm{e}^{s_+}\frac{s_+ + \alpha}{s_+}. \tag{4.6}$$

Substituting (4.5) into (4.6) yields

$$r < \frac{2+\alpha+\sqrt{\alpha^2+8\alpha+4}}{2-\alpha+\sqrt{\alpha^2+8\alpha+4}}\mathrm{e}^{\frac{2-\alpha+\sqrt{\alpha^2+8\alpha+4}}{2}} := P_2(\alpha). \tag{4.7}$$

Hence, if condition (4.7) is satisfied, $x^{\{2\}}$ is locally asymptotically stable.

In the case of there existing a unique positive fixed point $x = x_{\mathrm{c}}$, simple calculation yields

$$F''(x) = \frac{r\mathrm{e}^{-x}}{(\alpha+x)^3}(((1-x)(\alpha+x)-2x)(x+2\alpha-x(\alpha+x))+x(\alpha+x)(1-\alpha-2x)). \tag{4.8}$$

Then, it follows from $H'(x_{\mathrm{c}}) = 0$ that

$$\begin{aligned} F''(x_{\mathrm{c}}) &= \frac{r\mathrm{e}^{-x_{\mathrm{c}}}}{(\alpha+x_{\mathrm{c}})^3}((\alpha-x_{\mathrm{c}}-\alpha)(x_{\mathrm{c}}+2\alpha-\alpha)+\alpha(1-\alpha-2x_{\mathrm{c}})) \\ &= -\frac{r\alpha(\alpha+2x_{\mathrm{c}})\mathrm{e}^{x_{\mathrm{c}}}}{(\alpha+x_{\mathrm{c}})^3} < 0. \end{aligned} \tag{4.9}$$

Hence the unique positive fixed point $x = x_{\mathrm{c}}$ is unstable [8].

We summarize these stability results for positive fixed points in Theorem 4.1 and illustrate them in Figure 1.

THEOREM 4.1. *If $r = P_1(\alpha)$, where P_1 is defined in* (3.2)*, then there exists a unique positive fixed point $x = x_{\mathrm{c}}$ with x_{c} given in* (3.3) *and it is unstable. If $r > P_1(\alpha)$, there exist two positive fixed points $x^{\{1\}} < x^{\{2\}}$. The positive fixed point $x^{\{1\}}$ is unstable and $x^{\{2\}}$ is locally asymptotically stable if $r < P_2(\alpha)$ and is unstable if $r > P_2(\alpha)$, where $P_2(\alpha)$ is defined in* (4.7)*.*

5. Global stability and domains of attraction of the trivial fixed point $x = 0$

The trivial fixed point $x = 0$ is always locally asymptotically stable. We can further show that it is globally asymptotically stable if there exist no positive fixed points. If there exist positive fixed points, the dynamics for the trivial fixed point $x = 0$ can be complex [19].

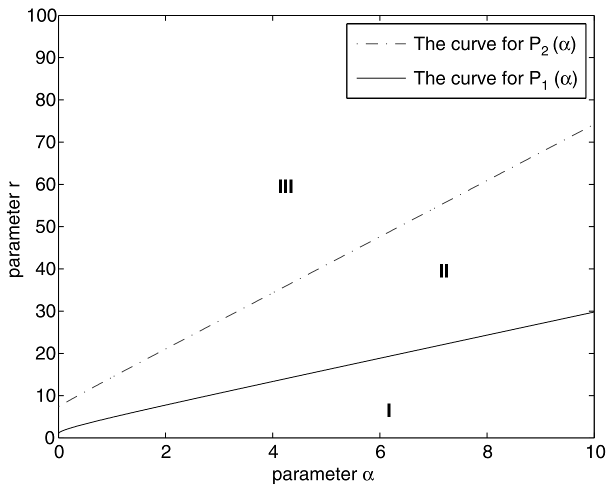

Figure 1. No positive fixed points exist in region I. There exist two positive fixed points $x^{\{1\}} < x^{\{2\}}$ in region II. The positive fixed point $x^{\{1\}}$ is unstable and $x^{\{2\}}$ is locally asymptotically stable in this region. There exist two positive fixed points in region III and both are unstable.

We summarize our results and describe the domains of attraction for the trivial fixed point $x = 0$ as follows.

THEOREM 5.1. *If there are no positive fixed points, the trivial solution $x = 0$ is globally asymptotically stable. If there exist two positive fixed points $x^{\{1\}} < x^{\{2\}}$, there exists a unique $x^* > C$ such that $x^{\{1\}} = F(x^*)$, where C is the critical point with $F(x) < F(C)$ for all $x \geq 0$ and $x \neq C$. If $F(C) < x^*$, the set $[0, x^{\{1\}}) \bigcup (x^*, \infty)$ is the domain of attraction for the locally asymptotically stable trivial solution $x = 0$. If $F(C) > x^*$, the set $[0, x^{\{1\}}) \bigcup (x^*, \infty)$ is contained in the domain of attraction for the trivial solution $x = 0$.*

Proof. Rewrite model (2.6) as

$$x_{n+1} = x_n \frac{r x_n}{\alpha + x_n} \mathrm{e}^{-x_n} := x_n g(x_n). \tag{5.1}$$

Suppose no positive fixed points exist. Then it follows from $F'(0) = 0$ that $F(x) = xg(x) < x$, that is, $g(x) < 1$, for all $x > 0$. Hence, any solution $\{x_n\}$ of (2.6) is a monotone decreasing sequence, which implies that the limit of x_n, as $n \longrightarrow \infty$, must be a fixed point of model (2.6). The uniqueness of the only trivial fixed point then leads to $\lim_{n\to\infty} x_n = 0$ for all solution with any initial values. Therefore the trivial solution $x = 0$ is globally asymptotically stable.

Suppose that there exist two positive fixed points $x^{\{1\}} < x^{\{2\}}$. We first show the existence and uniqueness of x^* with $F(x^*) = x^{\{1\}}$.

It is easy to see that $x^{\{1\}} < C$. Indeed, it follows from $F'(C) = 0$ and the fact that $x^{\{1\}}$ is unstable (from Theorem 4.1) that $x^{\{1\}} \neq C$. If $x^{\{1\}} > C$, then $F(x) > x$, for $x \in (0, x^{\{1\}})$, which implies that the trivial fixed point $x = 0$ is unstable, a contradiction. Hence $x^{\{1\}} < C$. Then it follows from $x^{\{1\}} < C$ and $F(\infty) = 0$ that there exists $x^* > C$ such that $F(x^*) = x^{\{1\}}$. Moreover, since function $F(x)$ is unimodal (one hump), x^* is unique.

Next, we suppose $F(C) < x^*$. If $\{x_n\}_{n=1}^{\infty}$ is a solution of (2.6) with $0 < x_0 < x^{\{1\}}$, then it follows from the property of $F(x)$, as shown in the left figure in figure 2, that $F(x_0) < x_0$, that is, $g(x_0) < 1$. Then it follows from the same argument above that the solution $\{x_n\}_{n=1}^{\infty}$ is a monotone decreasing sequence and $\lim_{n\to\infty} x_n = 0$. Hence the set $[0, x^{\{1\}})$ is contained in the domain of attraction for $x = 0$.

If $\{x_n\}_{n=1}^{\infty}$ is a solution of (2.6) with $x_0 > x^*$, then it again follows from the property of $F(x)$ that $x_1 = F(x_0) < x^{\{1\}}$ and hence the solution sequence $\{x_n\}_{n=2}^{\infty}$ is a monotone decreasing sequence which implies that all solutions with $x_0 > x^*$ approach the origin as $n \to \infty$. Therefore interval (x^*, ∞) is contained in the domain of attraction for $x = 0$.

Notice that interval $[x^{\{1\}}, x^*]$ is invariant for (2.6) since $x^{\{1\}} \le x \le x^*$ implies $x^{\{1\}} \le F(x) \le F(C) \le x^*$. Hence, it is excluded from the domain of attraction for $x = 0$. Therefore, we conclude that the domain of attraction for $x = 0$ is $[0, x^{\{1\}}) \bigcup (x^*, \infty)$.

In the case of $F(C) > x^*$, it follows from the property of $F(x)$ that there exist two points $x^{\{3\}} < C < x^{\{4\}}$ such that $F(x^{\{3\}}) = F(x^{\{4\}}) = x^*$ and $F(x) > x^*$, for $x \in (x^{\{3\}}, x^{\{4\}})$ and $x^{\{1\}} < F(x) < x^*$, for $x \in (x^{\{1\}}, x^{\{3\}}) \bigcup (x^{\{4\}}, x^*)$. (See the right figure in figure 2). Following the same argument above, we conclude that $[0, x^{\{1\}}) \bigcup (x^{\{3\}}, x^{\{4\}}) \bigcup (x^*, \infty)$ is contained in the domain of attraction for the trivial solution $x = 0$. □

Remark 5.1. The description for the domains of attraction of the trivial fixed point $x = 0$ for the case of $F(C) > x^*$ in Theorem 5.1 is not complete. It can be complex. We briefly illustrate as follows.

As is shown in Theorem 5.1, the set $[0, x^{\{1\}}) \bigcup (x^{\{3\}}, x^{\{4\}}) \bigcup (x^*, \infty)$ is contained in the domain of attraction for $x = 0$. Hence whenever $x_i \in (0, x^{\{1\}})$, $i \ge 0$, $x_i \in (x^{\{3\}}, x^{\{4\}})$, or $x_i \in (x^*, \infty)$, the solution $\{x_n\}_{n=1}^{\infty}$, containing this x_i, converges to $x = 0$.

Then what can it happen if $x_0 \in (x^{\{1\}}, x^{\{3\}})$ or $x_0 \in (x^{\{4\}}, x^*)$? We assume $x_0 \in (x^{\{1\}}, x^{\{3\}})$. It can be discussed similarly if $x_0 \in (x^{\{4\}}, x^*)$.

For $x_0 \in (x^{\{1\}}, x^{\{3\}})$, it follows from

$$x^{\{1\}} < x_0 < x_1 = F(x_0) < x^*$$

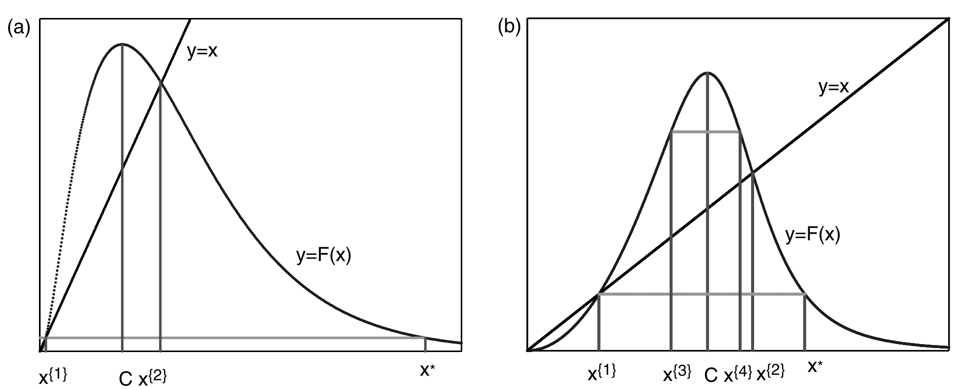

Figure 2. The two intersection points between the curve for $y = F(x)$ and the straight line for $y = x$ are the fixed points, $x^{\{1\}}$ and $x^{\{2\}}$. The point x^* is the unique point with $F(x^*) = x^{\{1\}}$. The left figure is for $F(C) < x^*$ where the domain of attraction for the trivial solution $x = 0$ is $[0, x^{\{1\}}) \bigcup (x^*, \infty)$. The right figure is for $F(C) > x^*$. The two points $x^{\{3\}} < C < x^{\{4\}}$ are from $F(x^{\{3\}}) = F(x^{\{4\}}) = x^*$ and the set $[0, x^{\{1\}}) \bigcup (x^{\{3\}}, x^{\{4\}}) \cup (x^*, \infty)$ is contained in the domain of attraction for the trivial solution $x = 0$.

that the following three possible cases can happen: (1) $x_1 \in (x^{\{1\}}, x^{\{3\}})$ again, (2) $x_1 \in (x^{\{3\}}, x^{\{4\}})$, or (3) $x_1 \in (x^{\{4\}}, x^{\{2\}})$.

In case (2), that is, $x_1 \in (x^{\{3\}}, x^{\{4\}})$, it follows from the argument above, the solution goes to zero.

In case (1), it follows from $F(x) > x$, for x in $(x^{\{1\}}, x^{\{3\}})$, that the sequence is an increasing sequence. Its components will enter $(x^{\{3\}}, x^{\{4\}})$, or $(x^{\{4\}}, x^{\{2\}})$, at a finite time. If its term enters interval $(x^{\{3\}}, x^{\{4\}})$, the solution goes to zero. If its term enters interval $(x^{\{4\}}, x^{\{2\}})$, its following term will enter the interval $(x^{\{2\}}, x^*)$. Then it follows from $F(x) < x$, for $x > x^{\{2\}}$, that its following terms enter either interval $(x^{\{1\}}, x^{\{3\}})$, $(x^{\{3\}}, x^{\{4\}})$, or $(x^{\{4\}}, x^{\{2\}})$. As a consequence, possible circulative iterations occur. The solution may or may not converge to $x = 0$.

The discussion of case (3) is similar to those for case (2).

6. Existence and stability of cycles

Model (2.6) exhibits typical period-doubling bifurcations as shown in figure 3. We investigate the existence and stability of the cycles analytically in this section.

We first establish the following lemma.

Lemma 6.1. *Let $F^1(x) = F(x)$ and define $F^k(x) := F(F^{k-1}(x))$, for $k \geq 2$. Let $\bar{x}$ be a 2^j-cycle, $j \geq 1$. Then*

$$\left(F^{2^i}\right)'(\bar{x}) = \left(\left(F^{2^j}\right)'(\bar{x})\right)^{2^{i-j}}, \quad \text{for all } \; i \geq j. \tag{6.1}$$

Proof. We prove (6.1) by induction.

First, it is easy to see that

$$F^{2^n}(x) = \underbrace{F\left(F\left(\ldots F\left(F^{2^{n-1}}(x)\right)\right)\right)}_{2^{n-1}+1 \;\; \text{times}}, \quad \text{for all } \; n \geq 1.$$

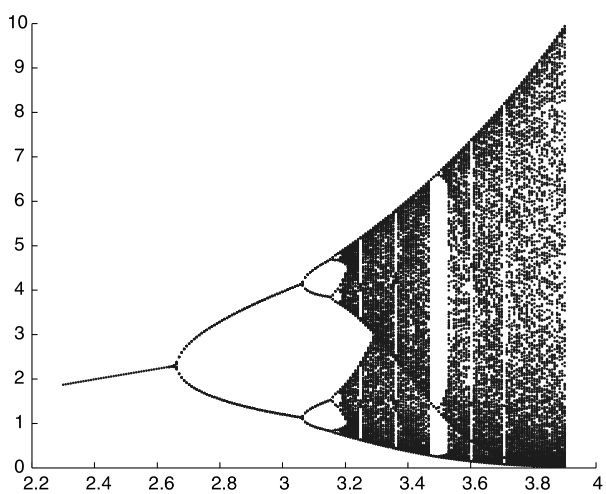

Figure 3. A bifurcation diagram for the model (2.6). Here $\alpha = 1$. The asymptotic values of x_n are plotted as a function of r.

Then, for $i = j + 1$, let $\bar{x}$ be a 2^j-cycle such that $F^{2^j}(\bar{x}) = \bar{x}$. It follows from

$$\left(F^{2^{j+1}}\right)'(\bar{x}) = F'\underbrace{\left(F\left(\ldots F\left(F^{2^j}(\bar{x})\right)\right)\right)}_{2^j+1 \text{ times}} \underbrace{F'\left(F\left(\ldots F\left(F^{2^j}(\bar{x})\right)\right)\right)}_{2^j \text{ times}} \ldots F'\left(F^{2^j}(\bar{x})\right)\left(F^{2^j}\right)'(\bar{x})$$

$$= \underbrace{F'(F(\ldots F(\bar{x})))}_{2^j \text{ times}} \underbrace{F'(F(\ldots F(\bar{x})))}_{2^j-1 \text{ times}} \ldots F'(\bar{x})\left(F^{2^j}\right)'(\bar{x}) = \left(\left(F^{2^j}\right)'(\bar{x})\right)^2$$

that (6.1) holds for $i - j = 1$.

Suppose (6.1) holds for $i - j = k - 1$. Notice that if $\bar{x}$ is a 2^j-cycle, it is also 2^{j+l}-cycle, for all $l > 1$, such that $F^{2^{j+l}}(\bar{x}) = F^{2^j}(\bar{x}) = \bar{x}$, for all $l > 1$. Then if follows that

$$\begin{aligned}\left(F^{2^{j+k}}\right)'(\bar{x}) &= \underbrace{F'\left(F\left(\ldots F\left(F^{2^{j+k-1}}(\bar{x})\right)\right)\right)}_{2^{j+k-1}+1 \text{ times}} \underbrace{F'\left(F\left(\ldots F\left(F^{2^{j+k-1}}(\bar{x})\right)\right)\right)}_{2^{j+k-1} \text{ times}} \\ &\quad \ldots F'\left(F^{2^{j+k-1}}(\bar{x})\right)\left(F^{2^{j+k-1}}\right)'(\bar{x}) \\ &= \underbrace{F'(F(\ldots F(\bar{x})))}_{2^{j+k-1} \text{ times}} \underbrace{F'(F(\ldots F(\bar{x})))}_{2^{j+k-1}-1 \text{ times}} \ldots F'(\bar{x})\left(F^{2^{j+k-1}}\right)'(\bar{x}) \\ &= \left(\left(F^{2^{j+k-1}}\right)'(\bar{x})\right)^2 = \left(\left(\left(F^{2^j}\right)'(\bar{x})\right)^{2^{k-1}}\right)^2 = \left(\left(F^{2^j}\right)'(\bar{x})\right)^{2^k}.\end{aligned}$$

That is, (6.1) holds for $i - j = k$.

By induction, (6.1) holds for all $i \geq j$. □

We hence have results for the existence and stability of the cycles as follows.

Theorem 6.2. *If all 2^i-cycles, $i = 0, \ldots, n-1$, become unstable as the parameter r varies, there exist at least 2^n locally asymptotically stable 2^n-cycles.*

Proof. We again prove this theorem by induction.

Define $G_i(x) := F^{2^i}(x) - x$, for all $i \geq 0$. Then there exists a 2^i-cycle if and only if there exists a positive solution to $G_i(x) = 0$.

First, we suppose that the two fixed points $x^{\{i\}}$, $i = 1, 2$, exist and both are unstable. Then it follows from Lemma 6.1 that

$$G_1'(x^{\{i\}}) = (F'(x^{\{i\}}))^2 - 1 > 0, \quad i = 1, 2,$$

and hence $G_1(x)$ is increasing at $x = x^{\{i\}}$, $i = 1, 2$.

Notice that since fixed points are also trivial 2-cycles, we have $G_1(x^{\{i\}}) = 0$, $i = 1$, 2 and $G_1(x) < 0$ for x sufficiently large. Then $G_1(x)$ changes its sign from negative to positive when x crosses $x = x^{\{i\}}$, for $i = 1$, 2. Hence, $G_1(x)$ changes its sign at least once in each of the intervals $(x^{\{1\}}, x^{\{2\}})$ and $(x^{\{2\}}, \infty)$, which implies that there exist at least two positive solutions to $G_1(x) = 0$, or two 2-cycles of equation (2.6), that are different from $x^{\{i\}}$, $i = 1, 2$. Moreover, as x passes through these two positive solutions of $G_1(x) = 0$ along the x-axis, $G_1(x)$ changes from positive to negative; that is, $G_1'(x)$ is negative at these two points. It then follows from Lemma 6.1 that $|F^{2'}(x)| < 1$ at these two points. Therefore the two fixed points of $F^2(x)$, that is, the 2-cycles of (2.6), are asymptotically stable.

Next, suppose that all 2^i-cycles, $i = 0, \ldots, n-1$, become unstable. Since for each $1 \le i \le n-1$, there are 2^i unstable 2^i-cycles and there are also two unstable fixed points, there are totally $2 + 2 + 2^2 + \cdots + 2^{n-1} = 2^n$ trivial fixed points to $F^{2^n}(x)$, or positive solutions to $G_n(x) = 0$. List these points as $\{x_n^{\{i\}}\}_{i=1}^{2^n}$. Then we have $G_n(x_n^{\{i\}}) = 0$ and hence $|(F^{2^i})'(x_n^{\{i\}})| > 1$, for $i = 1, \ldots, 2^n$, since all these fixed points to $F^{2^n}(x)$ are unstable. Therefore, it follows from Lemma 6.1 again that $G_n'(x)$ are positive at $x_n^{\{i\}}$, for $i = 1, \ldots, 2^n$. As a consequence, $G_n(x)$ crosses the x-axis at least 2^n times from above between two adjacent points in $\{x_n^{\{i\}}\}_{i=1}^{2^n}$, which implies that there exist at least 2^n positive solutions to $G_n(x) = 0$, that is, 2^n 2^n-cycles of (2.6). Moreover, at these points, we have $G_j'(x) < 0$, or, equivalently, $|(F^{2^j})'(x)| < 1$ from Lemma 6.1. Hence, there are 2^n asymptotically stable 2^n-cycles for (2.6).

By induction, the proof is complete. □

Remark 6.1. We did not use any particular formulas for function $F(x)$ in the proof of Theorem 6.2. Hence, this theorem can be applied to more general bounded smooth maps with bifurcation parameters.

7. Stabilization effects of the Allee effects

Stabilization or destabilization effects on population dynamics are an important subject in population studies and have been intensively investigated for various models from different perspectives (see, e.g. Refs. [2,4,5,7,18]). In particular, it has been shown that Allee effects increase the stability of the stable fixed point for a broad class of one-dimensional discrete models in Ref. [18].

Stabilization or destabilization effects on population dynamics can be also determined by different measures.

Consider two models and compare solutions starting with same initial points for the two models. We define the model with solutions going to stable fixed points to be more stable than the model with oscillatory solutions. If the two models both exhibit sustained oscillations, we define the model having oscillatory solutions with smaller periods or with smaller amplitude (oscillating "less") to be more stable.

Using these measures and through numerical simulations, we show that Allee effects have stabilizing effects on the dynamics of model (2.6).

As is shown in figure 4, we compare the dynamics of the classical Ricker model, where the birth function $b(x_n) = r$ is constant, with the dynamics of the extended Ricker model (2.6). We let $\alpha = 0.5$ and vary the parameter r. When $r = 5$, the classical Ricker model has a stable 2-cycle, whereas model (2.6) has a stable fixed point, as shown in the upper left figure. As we increase r to 8.1, a 4-cycle appears for the classical Ricker model, but there is only a stable 2-cycle with much smaller amplitude for model (2.6), shown in the upper right figure. For $r = 13.5$, the classical Ricker model seems to have a stable cycle with period 24, but model (2.6) has only a stable 4-cycle, shown in the lower right figure. When $r = 35$, both models show chaotic behavior, but model (2.6) has oscillations with smaller amplitude, compared to the oscillations created by the classical Ricker model, as in the lower right figure. Then, it is demonstrated that the Allee effects have stabilizing effects on the model dynamics using the measures stated above.

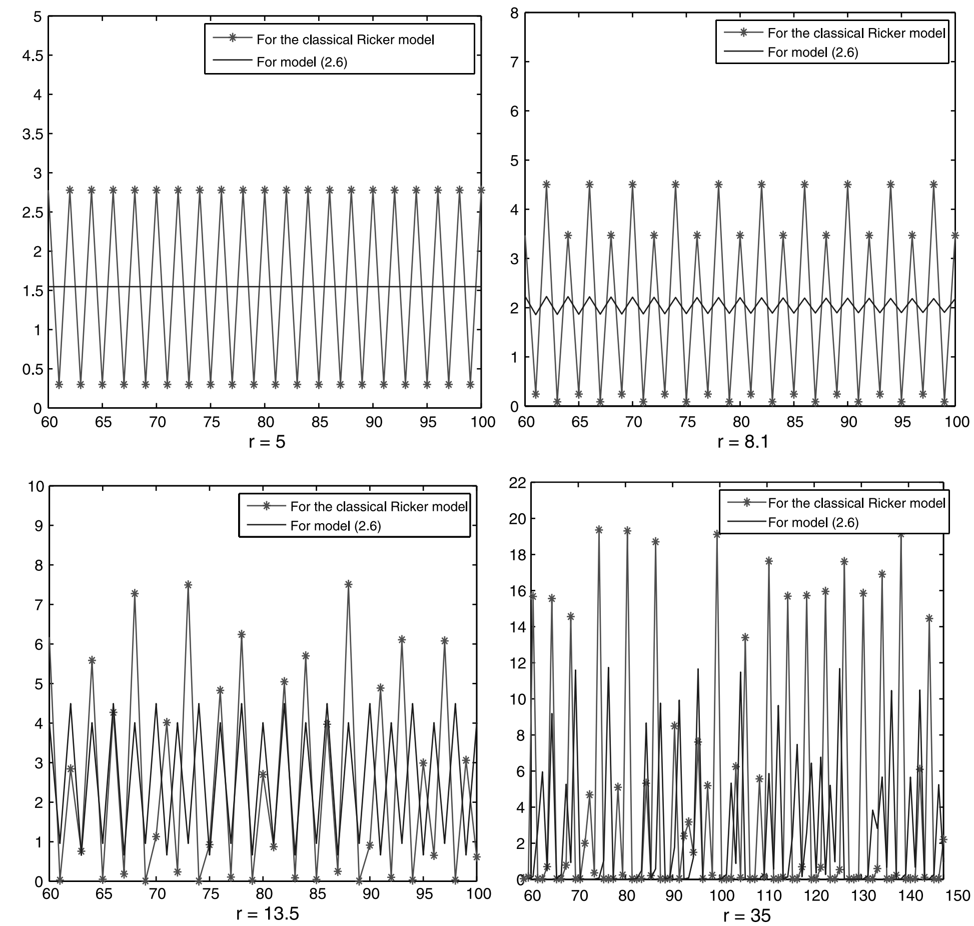

Figure 4. Parameter $\alpha = 0.5$ is fixed. We then vary r from 5, 8.1, 13.5, to 35, in the figures from the upper left to the right and the lower left to the right, respectively.

8. Concluding remarks

In this paper, we incorporate Allee effects into the classical Ricker model by assuming rectangular hyperbola, or Holling-II type functional form, for the birth or growth function and formulated an extended Ricker model (2.6). To explore dynamics features of this extended Ricker model, we established existence and local stability of positive fixed points and found regions where there exist no positive fixed points, two positive fixed points only one of which is stable and two positive fixed points both of which are unstable, shown in figure 1.

The trivial solution $x = 0$ for the extended Ricker model (2.6) is locally asymptotically stable. We showed that it is also globally stable if there exist no positive fixed points. Moreover, if there is a stable fixed point, there exists an attracting region for the trivial fixed point such that all solutions starting in this region approach the trivial solution $x = 0$. Notice that, however, the domains of attraction can be complex, depending on the properties of the growth rate of the population, namely, $F(x)$. We gave a complete description for the case of $F(C) < x^*$, whereas the description for the case of $F(C) > x^*$ is still incomplete.

Using the intrinsic growth rate r as a bifurcation parameter, we showed that the model exhibits typical period-doubling bifurcations. We then investigated the existence and stability of the cycles analytically. We first established Lemma 1 which can be, indeed, applied to more general discrete models with a bifurcation parameter. Using this lemma, we showed that as the fixed points loss their stability, at least two stable 2-cycles appear. As the fixed points and 2-cycles loss their stability, at least four stable 4-cycles appear. This continues on that as all 2^i, $i \geq 0$, cycles loss their stability, at least 2^{i+1} stable 2^{i+1}-cycles appear. This confirmed the typical period-doubling bifurcations, not only numerically, but also analytically.

It has been shown that Allee affects increase the dynamical stability of populations by decreasing the spectral radius at the fixed points [18]. By numerical simulations and using different measures, we also illustrated that Allee affects have stabilization effects for model populations. We compared the dynamics of the extended Ricker model with the classical Ricker model and showed that while solutions start exhibiting sustained oscillations for the classical Ricker model, solutions with the same initial values still approach the stable positive fixed point for a certain parameter setting. While solutions exhibit sustained oscillations for both models, the solutions for the extended Ricker model always have smaller periods and smaller amplitude. We conclude that, in all aspects, Allee effects do have stabilizing effects on population dynamics.

It is worth to point out that the trivial solution $x = 0$ is always locally asymptotically stable for the extended Ricker model, whereas the trivial solution for the classical Ricker model is unstable. If a population starts with a very large initial size, the density-dependent death rate plays a determining role to drive the population size low in the next generation. Then due to Allee effects, the population may not be able to survive. This agrees with what is pointed out in Ref. [19] due to mating limitation. Nevertheless, this may need to be further justified since most species are able to perform their self-adjustment to the environment to survive.

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