Journal of Biological Dynamics
Vol. 00, No. 00, February 2012, 1–12

Difference Equations with the Allee Effect and the Periodic Sigmoid Beverton-Holt Equation Revisited

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(*Received 00 Month 200x; revised 00 Month 200x; in final form 00 Month 200x*)

In this paper we investigate the long term behavior of solutions of the periodic Sigmoid Beverton-Holt equation

$$x_{n+1} = \frac{a_n x^{\delta_n}}{1 + x^{\delta_n}}, \quad x_0 > 0, \quad n = 0, 1, 2, \dots,$$

where the a_n and δ_n are p-periodic positive sequences. Under certain conditions there are shown to exist an asymptotically stable p-periodic state and a p-periodic Allee state that repels nearby states. This appears to be the first study of the equation with variable δ.

Keywords: Periodic difference equation, global stability, Sigmoid Beverton-Holt, Allee states

AMS Subject Classification: 39A11, 92, 92D, 92D25

1. Introduction

In this paper we investigate the long term behavior of solutions of the periodic Sigmoid Beverton-Holt (or Holling Type III, [8]) equation

$$x_{n+1} = \frac{a_n x^{\delta_n}}{1 + x^{\delta_n}}, \quad x_0 > 0, \quad n = 0, 1, 2, \dots, \tag{1.1}$$

where the a_n and δ_n are p-periodic positive sequences. In a recent groundbreaking publication by Harry, Kent and Kocic [7] an extensive study was made in the case δ =constant and a rich source of references on the subject were presented. Technically, the term "Sigmoid" applies only to the case in which $\delta > 1$ where the graph of what we call the Sigmoid Beverton-Holt function,

$$f_{a,\delta}(x) = \frac{a x^{\delta}}{1 + x^{\delta}}, \quad a > 0,$$

has the characteristic "S" shape, the slow rise from zero, a rapid rise then flattening out for large x. This shape is especially interesting in discrete dynamics when for 'a' sufficiently large it gives rise to the famous Allee effect in which small populations are driven to extinction. This is of paramount importance in the management of fisheries and establishment of safeguards against overfishing [1], [12]. In [17], Stephens and Sutherland described several scenarios that cause the Allee effect in both animals and plants. For example, cod and many freshwater fish species have high juvenile mortality when there are fewer adults. Fewer red sea urchin give rise to worsening feeding conditions of their young and less protection from predation. In some mast flowering trees, such as *Spartina alterniflora*, low population density results in lower probability of pollen grains finding stigma [17]. See [4] for a discussion of some new examples of models exhibiting the

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Journal of Biological Dynamics
ISSN: 1751-3758 print/ISSN 1751-3766 online © 2012 Taylor & Francis
http://www.tandf.co.uk/journals
DOI: 10.1080/1751375YYxxxxxxxx

Allee effect and, similar to the Beverton-Holt model, having important biological quantities as parameters, e.g. intrinsic growth rate, carrying capacity and Allee threshold. Further references pertaining to the Allee effect can be found in [11], [2], [18], [9], [10], [15], [19], [20], [5], [6].

Throughout the paper we use the notation $\mathbb{R}^+ = [0, \infty)$ and $\mathbb{R}_0^+ = (0, \infty)$. Also "increasing" shall always mean strictly increasing and similarly for decreasing. Also, by $C^1(\mathbb{R}^+, \mathbb{R}^+)$ we mean the space of continuously differentiable functions from $\mathbb{R}^+$ to $\mathbb{R}^+$.

2. Stable Periodic Orbit

The model we consider is the p-periodic iterated mapping

$$x_{n+1} = f_n(x_n), \quad n = 0, 1, \ldots \tag{2.1}$$

on $\mathbb{R}^+$ where $f_n = f_{n+p}$, $n = 0, 1, \ldots$. In particular we are interested in the case when $f_n = f_{a_n,\delta_n}$ are Sigmoid Beverton-Holt functions although we will also have occasion to consider other functions f_n. We are interested in establishing the existence of a positive periodic orbit

$$\{s_0, s_1, \ldots, s_{p-1}\}, \tag{2.2}$$

that is asymptotically stable and attracts all orbits for which x_0 lies in some interval (B, ∞). It is well known that this is equivalent to showing the existence of a fixed point s_0 of the mapping $F : \mathbb{R}^+ \to \mathbb{R}^+$ given by

$$F \doteq f_{p-1} \circ \cdots \circ f_0.$$

that has the same stability properties.

It is also known [3], [13], but not fully appreciated, that the concept of a *semigroup* plays a key role in the study of periodic difference equations. To illustrate this fact we begin by disposing of the case in which *all* $\delta_n \le 1$ in (1.1).

THEOREM 2.1 *Suppose in (2.1) that $f_n = f_{a_n,\delta_n}$ with $\delta_n \le 1$ and $\{a_n\} \subset \mathbb{R}_0^+$ has the property that $a_n > 1$ whenever $\delta_n = 1$. Then there is a periodic orbit (2.2) that is asymptotically stable and attracts any orbit for which $x_0 \in \mathbb{R}_0^+$.*

Proof: It is shown in [3, p. 272] that the set of all functions from $\mathbb{R}^+$ to $\mathbb{R}^+$ that are continuous, non-decreasing, concave, and whose graph crosses the diagonal on $\mathbb{R}_0^+$, forms a semigroup under composition. Moreover, for any function f in this set, the value of $x \in \mathbb{R}_0^+$ where the graph crosses the diagonal is a fixed point of the iterated mapping $x_{n+1} = f(x_n)$ that attracts any orbit for which $x_0 \in \mathbb{R}_0^+$. It is easy to see, under the hypotheses of the theorem, the functions f_n belong to this set, so, by the semigroup property, their composition $F = f_{p-1} \circ \cdots \circ f_0$ must also belong to this set. The positive fixed point of F corresponds to a periodic orbit of (2.1) that is asymptotically stable and attracts any orbit for which $x_0 \in \mathbb{R}_0^+$.

■

When at least one of the δ_n's is greater than 1 the existence of a positive asymptotically stable periodic orbit (2.2) is more subtle. In order to state conditions on the parameters under which such an orbit is guaranteed to exist we first explore the nature of the autonomous iterated mapping $x_{n+1} = f_{a,\delta}(x_n)$ for different values of the parameters (see also [7]).

It is clear that every Sigmoid Beverton-Holt function $f_{a,\delta}$ is increasing, goes through the origin, and $\lim_{x\to\infty} f_{a,\delta}(x) = a$. When $0 < \delta < 1$ and a has any value and when $\delta = 1$ and $a > 1$, the graph is concave everywhere and there is a unique fixed point $K_f \in (0, \infty)$ that is asymptotically stable on $\mathbb{R}_0^+$. When $\delta = 1$ and $0 < a \le 1$ the graph is concave everywhere but lies below the diagonal so $x = 0$ is the only fixed point and it is globally asymptotically stable. When $\delta > 1$ the function is convex on $(0, x^{\text{infl}})$ and concave on

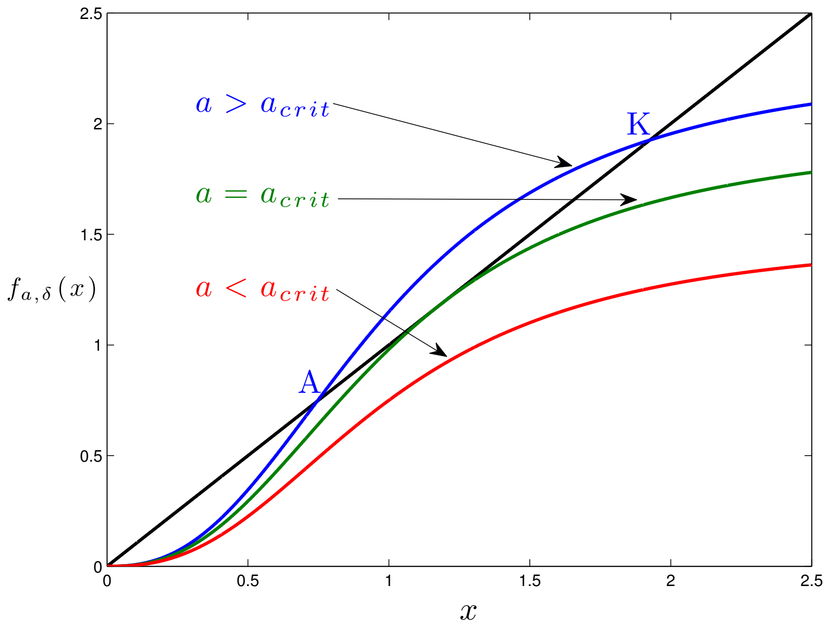

Figure 1. Bifurcation as a increases for fixed $\delta > 1$

$(x^{\text{infl}}, \infty)$ where the inflection point is given by

$$x^{\text{infl}}(\delta) = \left(\frac{\delta - 1}{\delta + 1}\right)^{\frac{1}{\delta}}.$$

Notice that x^{infl} depends on δ alone. Also, $x^{\text{infl}}(\delta) < 1$ and $x^{\text{infl}}(\delta) \to 1$ as $\delta \to \infty$. It is shown in [7] that there is a critical value of a given by

$$a^{\text{crit}}(\delta) \doteq \frac{\delta}{(\delta - 1)^{1-\frac{1}{\delta}}}$$

at which a saddle-node bifurcation takes place. Namely,

(i) for $a < a^{\text{crit}}$ the entire graph of $y = f_{a,\delta}(x)$, $x \in \mathbb{R}_0^+$, lies under the diagonal $y = x$ so the origin is globally asymptotically stable, while
(ii) for $a = a^{\text{crit}}$ the graph of $y = f_{a,\delta}(x)$ is tangent to the diagonal at a semi-stable fixed point, and
(iii) for $a > a^{\text{crit}}$ the graph of $y = f_{a,\delta}(x)$ intersects the diagonal in two fixed points: the Allee threshold A_f and the carrying capacity K_f. The origin is exponentially asymptotically stable and attracts all orbits for which $x_0 \in [0, A_f)$, the Allee threshold A_f is unstable, and K_f is exponentially asymptotically stable and attracts all orbits for which $x_0 \in (A_f, \infty)$.

The graphs of $f_{a,\delta}$ when $\delta > 1$ are illustrated in Figure 1.

Also of significance is the x value of the bifurcation point as a function of δ, $x^{\text{bif}}(\delta)$. At the bifurcation point the graph of f intersects and is tangent to the diagonal. Thus x^{bif} is the solution to the simultaneous equations

$$a^{\text{crit}} \frac{x^\delta}{1 + x^\delta} = x, \quad \text{and} \quad a^{\text{crit}} \delta x^{\delta - 1} = (1 + x^\delta)^2.$$

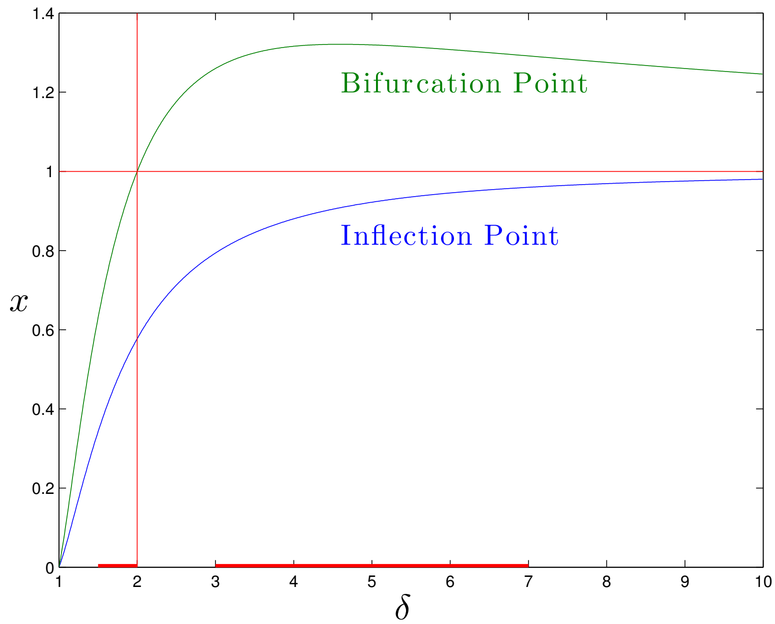

Figure 2. Bifurcation and inflection points as a function of δ

Dividing the first by the second and simplifying, we obtain the rather simple expression

$$x^{\text{bif}}(\delta) = (\delta - 1)^{\frac{1}{\delta}}. \tag{2.3}$$

Clearly $x^{\text{infl}}(\delta) < x^{\text{bif}}(\delta)$ for all $\delta > 1$ and $A_f < x^{\text{bif}}(\delta) < K_f$. However, the relative sizes of $x^{\text{infl}}(\delta)$ and A_f depend on the size of a. We denote by $a^{\text{allee}}(\delta)$ the value of a where $A_f = x^{\text{infl}}(\delta)$. At this value we have

$$f_{a,\delta}(x^{\text{infl}}(\delta)) = x^{\text{infl}}(\delta).$$

Solving yields

$$a^{\text{allee}}(\delta) = \left(\frac{2\delta}{(\delta - 1)^{1-\frac{1}{\delta}}(\delta + 1)^{\frac{1}{\delta}}} \right). \tag{2.4}$$

Notice that $a^{\text{crit}}(\delta) < a^{\text{allee}}(\delta)$ for all $\delta > 1$. If $a^{\text{crit}}(\delta) < a < a^{\text{allee}}(\delta)$ then $x^{\text{infl}}(\delta) < A_f < x^{\text{bif}}(\delta) < K_f$ and if $a > a^{\text{allee}}(\delta)$ then $A_f < x^{\text{infl}}(\delta) < x^{\text{bif}}(\delta) < K_f$. Figure 2 shows plots of x^{infl} and x^{bif} as functions of δ and Figure 3 shows plots of a^{allee} and a^{crit} as functions of δ.

In all of our theorems we will only be concerned with those Sigmoid Beverton-Holt functions that have a positive asymptotically stable fixed point, in other words those for which $\delta < 1$ and a has any value, or $\delta = 1$ and $a > 1$, or $\delta > 1$ and $a > a^{\text{crit}}$. To specify these concisely we define $a^{\text{crit}}(\delta) \doteq 0$ for $\delta < 1$ and $a^{\text{crit}}(\delta) \doteq 1$ for $\delta = 1$. The maps we are interested in are then those $f_{a,\delta}$ for which $a > a^{\text{crit}}(\delta)$.

In [7], Harry, Kent and Kocic obtained the following result concerning the existence of a positive asymptotically stable periodic orbit of (2.1) in the δ_n =constant case.

Theorem 2.2 (A. J. Harry, C. M. Kent and V. L. Kocic, [7, Thm. 8]) *Let $\delta_n = \delta > 1$ be fixed and $\{a_n\} \subset \mathbb{R}^+$ be a p-periodic sequence satisfying $a_n > a^{crit}(\delta)$, $0 \le n \le p-1$. Suppose*

$$A_{max} \doteq \max\{A_{f_0}, \ldots, A_{f_{p-1}}\} < K_{min} \doteq \min\{K_{f_0}, \ldots, K_{f_{p-1}}\}. \tag{2.5}$$

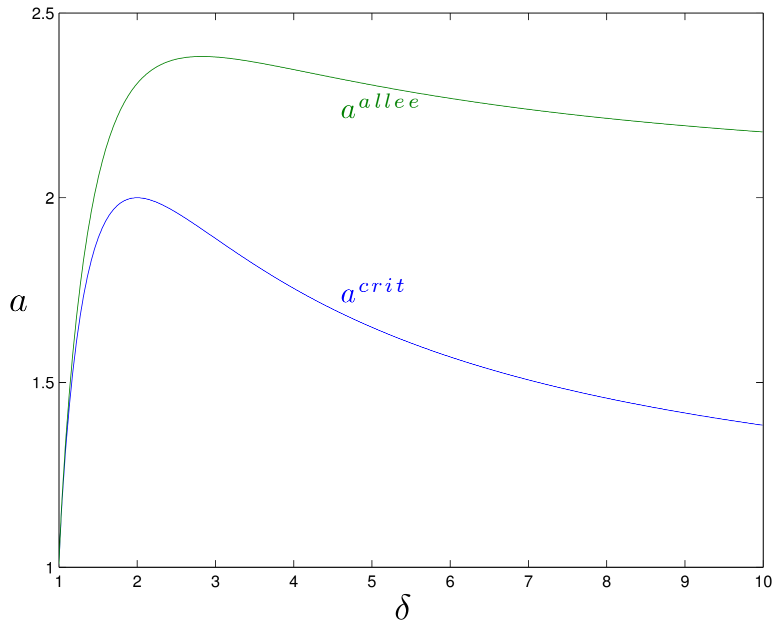

Figure 3. a^{allee} versus a^{crit} curves

Then there exists $A \in (A_{max}, K_{min})$ *and a periodic orbit (2.2) that is asymptotically stable and attracts all orbits for which* $x_0 \in (A, \infty)$.

Since $\delta > 1$ is constant in this theorem and $A_f < x^{\mathrm{bif}}(\delta) < K_f$, hypothesis (2.5) is unnecessary. In addition, we will show in Theorem 2.4 that any orbit for which $x_0 > A_{max}$ is asymptotic to the periodic orbit. Thus, the theorem can be restated as follows.

Theorem 2.3 *Let* $\delta > 1$ *be fixed and* $\{a_n\} \subset \mathbb{R}^+$ *be a p-periodic sequence satisfying* $a_n > a^{crit}(\delta)$, $0 \le n \le p-1$. *Then there is a periodic orbit (2.2) that is asymptotically stable and attracts all orbits for which* $x_0 \in (A_{max}, \infty)$.

We will prove the following theorem in Section 3; it will be a direct consequence of a more general theorem that we prove there. It is considerably stronger than Theorem 2.3, since it allows δ_n to vary.

Theorem 2.4 *Let* $\{\delta_n\}$ *and* $\{a_n\}$ *be p-periodic sequences in* $\mathbb{R}_0^+$ *such that* $a_n > a^{crit}(\delta_n)$, *for* $0 \le n \le p-1$. *Let* $\mathcal{N} = \{n \,|\, \delta_n > 1\}$ *and define*

$$x^{infl}_{max} = \max_{n\in\mathcal{N}} x^{infl}(\delta_n), \quad A_{max} = \max_{n\in\mathcal{N}} A_{f_n}, \quad K_{min} = \min_{0\le n\le p-1} K_{f_n}, \quad K_{max} = \max_{0\le n\le p-1} K_{f_n},$$

and suppose

$$\max\{x^{infl}_{max}, A_{max}\} < K_{min}. \tag{2.6}$$

Then there is a periodic orbit (2.2) that is asymptotically stable and attracts all orbits for which $x_0 \in (A_{max}, \infty)$. *In addition the entire orbit (2.2) lies in the interval* $[K_{min}, K_{max}]$.

Since we don't have simple formulae for A_f and K_f, the hypotheses in the theorem above may need to be verified numerically. The following corollary is weaker than the theorem but the hypotheses are easily verifiable analytically, since we have formulae for all of the relevant quantities in terms of a_n and δ_n.

Corollary 2.5 *Let* $\{\delta_n\}$ *and* $\{a_n\}$ *be p-periodic sequences in* $\mathbb{R}_0^+$ *such that* $\delta_n > 1$ *and* $a_n > a^{allee}(\delta_n)$, *for* $0 \le n \le p-1$. *Define*

$$x^{bif}_{min} = \min_{0 \le n \le p-1} x^{bif}(\delta_n),$$

and assume

$$x^{infl}_{max} < x^{bif}_{min}. \tag{2.7}$$

Then there is a periodic orbit (2.2) that is asymptotically stable and attracts all orbits for which $x_0 \in (A_{max}, \infty)$.

Proof: Since $\delta_n > 1$ and $a_n > a^{\text{allee}}(\delta_n)$ we know that $A_{f_n} < x^{\text{infl}}(\delta_n) < x^{\text{bif}}(\delta_n) < K_{f_n}$ for all n. It follows that

$$\max\{x^{infl}_{max}, A_{max}\} = x^{infl}_{max}$$

and

$$x^{infl}_{max} < K_{min}.$$

Thus, by the hypothesis of the corollary, $\max\{x^{infl}_{max}, A_{max}\} < K_{min}$, and the result follows by the theorem. ∎

Remark 1 Condition (2.7) in the corollary is a condition on the δ's alone. This condition says that the δ's must lie in an interval in which the highest point on the inflection point graph is lower than the lowest point on the bifurcation graph. For example, it is clear from Figure 2 that this condition is satisfied if $\delta_n \ge 2$ for all n. As another example, if $1.5 \le \delta_n \le 2$ for all n then the highest point on the inflection point graph is ≈ 0.5774 and the lowest point on the bifurcation graph is ≈ 0.6300, so again this condition is satisfied.

Remark 2 Condition (2.6) in the theorem is needed. For $a_0 = 1.2$, $\delta_0 = 50$ and $a_1 = 1.1$, $\delta_1 = 1.01$ the condition $a_n > a^{\text{crit}}(\delta_n)$ holds but the composition $f_1 \circ f_0$ has only one fixed point at $x = 0$ and all solutions are attracted to it.

3. A General Theorem

In this section we prove a general theorem that will have Theorem 2.4 as a corollary.

Given $r \ge 0$, define $\mathcal{F}_r$ as the set of all continuous functions $f : \mathbb{R}^+ \to \mathbb{R}^+$ that have the following properties:

(i) $f : [r, \infty) \to [r, \infty)$.
(ii) There exists a number $B \ge r$ such that $f(B) > B$ and f is increasing and concave on (B, ∞),
(iii) There exists a number $x^* > B$ such that $f(x^*) < x^*$.

For $f \in \mathcal{F}_r$ define $B_f = \inf\{B\}$, where the infimum is taken over all B satisfying (ii). Notice that $B_f \ge r$, $f(B_f) \ge B_f$, and f is increasing and concave on (B_f, ∞).

Lemma 3.1 *For each function* $f \in \mathcal{F}_r$ *the iterated mapping given by*

$$x_{n+1} = f(x_n) \tag{3.1}$$

has a unique fixed point K_f *on the interval* (B_f, ∞). *This point is asymptotically stable and attracts all orbits for which* $x_0 \in (B_f, \infty)$.

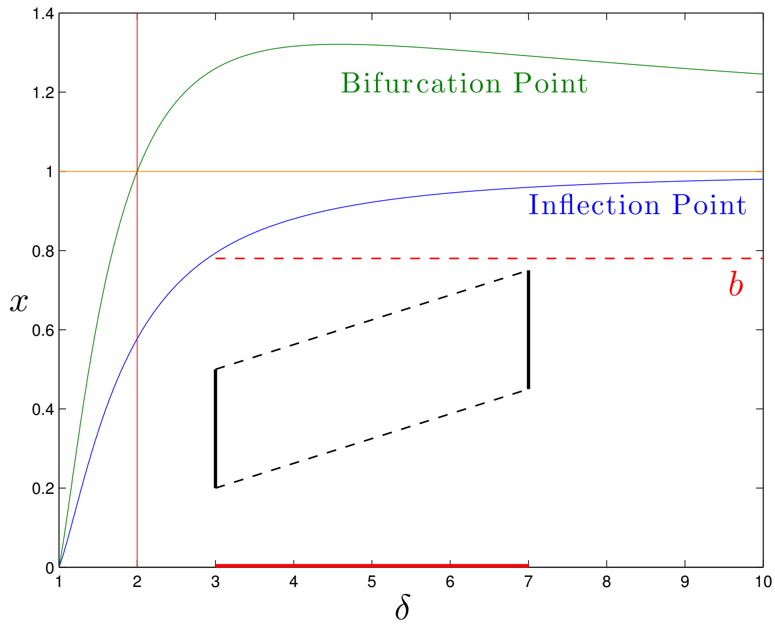

Figure 4. Allee thresholds shown below the inflection curve

Proof: We first prove uniqueness. Suppose $x_1 < x_2$ are fixed points on (B_f, ∞). Choose B such that $B_f < B < x_1$ and $f(B) > B$. Choose t such that $x_1 = tB + (1-t)x_2$. Since f is concave on (B, x_2),

$$x_1 = f(tB + (1-t)x_2) \geq tf(B) + (1-t)f(x_2) > tB + (1-t)x_2 = x_1,$$

a contradiction. The existence follows from (ii) and (iii) and the intermediate value theorem. To show the asymptotic stability of K_f, notice that $x < f(x) < K_f$ for $x \in (B_f, K_f)$ and $K_f < f(x) < x$ for $x \in (K_f, \infty)$. Thus the sequence $\{x_n\}$ defined by (3.1) is increasing and bounded above by K_f when $x_0 \in (B_f, K_f)$ and decreasing and bounded below by K_f when $x_0 \in (K_f, \infty)$. It follows that the sequence converges. By continuity, the limit is a fixed point and by uniqueness it must be K_f.

■

There are two important observations to be made about $\mathcal{F}_r$. The first is the role of the number r. Since every function in $\mathcal{F}_r$ maps the interval $[r, \infty)$ into itself the autonomous iterated mapping (3.1) can be restricted to the set $[r, \infty)$. Moreover, because this interval is common to all the functions in $\mathcal{F}_r$, the p-periodic iterated mapping (2.1) where $f_n \in \mathcal{F}_r$, can also be restricted to $[r, \infty)$. Each function $f \in \mathcal{F}_r$ also has other intervals that map to themselves, namely $[B, \infty)$ for any number B satisfying (ii). However, the p-periodic iterated mapping cannot necessarily be restricted to any subset of $[r, \infty)$, since there may not be a number B that is common to all of the f_n's.

The second observation already came out in the proof of Lemma 3.1 but it will be used again, so we point it out explicitly. Given any function $f \in \mathcal{F}_r$, $x < f(x) < K_f$ for $x \in (B_f, K_f)$ and $K_f < f(x) < x$ for $x \in (K_f, \infty)$.

3.1. *A New Class of Mappings*

Given $r \geq 0$ and $\ell \in [r, \infty)$ we define the class

$$\mathcal{U}_{r,\ell} \doteq \{f \in \mathcal{F}_r \,|\, B_f \leq \ell < K_f\}. \tag{3.2}$$

THEOREM 3.2 *$\mathcal{U}_{r,\ell}$ is a semigroup under the operation of composition of maps. Moreover, for any $f, g \in \mathcal{U}_{r,\ell}$, $B_{f\circ g} \leq \max\{B_f, B_g\}$ and $K_{f\circ g}$ lies on the closed interval with endpoints K_f and K_g.*

Proof: Let $f, g \in \mathcal{U}_{r,\ell}$ be given. We first show that $f \circ g$ lies in $\mathcal{F}_r$.

(i) Since f and g both map $[r, \infty)$ to itself, $f \circ g$ does as well.

(ii) Let B be any number such that $\max\{B_f, B_g\} < B < \min\{K_f, K_g\}$. Since $B \in (B_g, K_g)$, $g(B) > B$, and, since f is increasing on $[B, \infty)$ it follows that $f \circ g(B) = f(g(B)) > f(B)$. Now, since $B \in (B_f, K_f)$, $f(B) > B$. Thus $f \circ g(B) > B$. Moreover, f and g are both increasing and concave on (B, ∞) and, since $g(B) > B$, this interval is invariant under g, so $f \circ g$ is also increasing and concave on this interval.

(iii) We show that there exists a number $x^* > B$ such that $f \circ g(x^*) < x^*$.
Case 1: Suppose there exists $x > B$ such that $g(x) > K_f$. Since g is increasing on (B_g, ∞) this will be true for all sufficiently large x. Choose x^* so that $g(x^*) > K_f$ and $x^* > K_g$. Then $x^* > B$ and, since $g(x^*) > K_f$, $f \circ g(x^*) = f(g(x^*)) < g(x^*)$ which, in turn, is less than x^*, since $x^* > K_g$.
Case 2: Suppose $g(x) \leq K_f$ for all $x > B$. In this case, choose x^* to be any number larger than K_f. Then $x^* > B$ and, since $g(x^*) \leq K_f$ and f is increasing on (B, ∞), $f \circ g(x^*) = f(g(x^*)) \leq f(K_f) = K_f < x^*$.

Thus, $f \circ g$ lies in $\mathcal{F}_r$. Once we have established that $B_{f \circ g} \leq \max\{B_f, B_g\}$ and that $K_{f \circ g}$ lies between K_f and K_g it will follow immediately that $f \circ g \in \mathcal{U}_{r,\ell}$. The former is immediate because we have seen that *any* number B that lies between $\max\{B_f, B_g\}$ and $\min\{K_f, K_g\}$ has the properties in (ii). To show the latter there are three cases.
Case 1: Suppose $K_f < K_g$. Then $K_g \in (K_f, \infty)$ so $f \circ g(K_g) = f(K_g) < K_g$. Similarly, $K_f \in (B_g, K_g)$ so $g(K_f) > K_f$ and f is increasing on (B_f, ∞) so $f \circ g(K_f) = f(g(K_f)) > f(K_f) = K_f$. Thus, $K_f < K_{f \circ g} < K_g$.
Case 2: Suppose $K_f > K_g$. Then $K_g \in (B_f, K_f)$ so $f \circ g(K_g) = f(K_g) > K_g$. Similarly, $K_f \in (K_g, \infty)$ so $g(K_f) < K_f$ and f is increasing on (B_f, ∞) so $f \circ g(K_f) = f(g(K_f)) < f(K_f) = K_f$. Thus $K_g < K_{f \circ g} < K_f$.
Case 3: Suppose $K_f = K_g$. In this case $f \circ g(K_g) = f(g(K_g)) = f(K_g) = f(K_f) = K_f$. Thus, $K_f = K_g$ is a fixed point of $f \circ g$, so by uniqueness it must be $K_{f \circ g}$.

■

3.2. *Proof of Theorem 2.4*

It is easy to see that every Sigmoid Beverton-Holt function $f = f_{a,\delta}$ with $a > a^{\text{crit}}(\delta)$ lies in $\mathcal{F}_0$ and $B_f = 0$ if $\delta \leq 1$ and $B_f = \max\{x^{\text{infl}}(\delta), A_f\}$ if $\delta > 1$. Choose l so that $\max\{x^{\text{infl}}_{max}, A_{max}\} < l < K_{min}$. This is possible by the hypothesis of the theorem. Then $f_n \in \mathcal{U}_{0,l}$ for all n. It follows by Theorem 3.2 that $F = f_0 \circ f_1 \circ \ldots f_{p-1} \in \mathcal{U}_{0,l} \subset \mathcal{F}_0$ and that $B_F \leq \max\{x^{\text{infl}}_{max}, A_{max}\}$. Thus, by Lemma 3.1, F has a unique fixed point on the interval (B_F, ∞) that is asymptotically stable and attracts all orbits for which $x_0 \in (B_F, \infty)$. This fixed point corresponds to a periodic orbit of the non-autonomous system (2.1) with the same stability properties.

Since $B_F \leq \max\{x^{infl}_{max}, A_{max}\}$, it follows immediately that this periodic orbit attracts all orbits for which $x_0 \in (\max\{x^{infl}_{max}, A_{max}\}, \infty)$. However, if $A_{max} < x^{infl}_{max}$ we still need to show that the periodic orbit attracts all orbits for which $x_0 \in (A_{max}, x^{infl}_{max}]$. To this end, let such a point x_0 be given and let $\{x_i\}_{i=0}^{\infty}$ denote its orbit under (2.1). To show that this orbit is attracted to the periodic orbit it suffices to show that there exists $k \in \mathbb{N}$ such that $x_{kp} > x^{infl}_{max}$.

Notice first that if $x_n > K_{min}$ then $x_{n+1} > K_{min}$ since, if $x_n \leq K_n$ then $x_{n+1} = f_n(x_n) \geq x_n > K_{min}$ and if $x_n > K_n$ then $x_{n+1} = f_n(x_n) > K_n \geq K_{min}$. Moreover, if $x_n \in (A_{max}, K_{min})$ then $A_n < x_n < K_n$, so $x_{n+1} = f_n(x_n) > x_n$. Thus there are two possibilities; the first is that there exists $n \in \mathbb{N}$ such that $x_n > K_{min}$ and the second is that $x_n \leq K_{min}$ for all n. In the former case, $x_m > K_{min} > x^{infl}_{max}$ for all $m \geq n$ so the result follows. In the latter case, $\{x_i\}_{i=0}^{\infty}$ is an increasing sequence that is bounded above and therefore has a limit. By continuity the limit is a fixed point of F. But the observations that we have just made show that for any $x \in (A_{max}, K_{min})$, $F(x) > x$, so the limit must be $K_{min} > x^{infl}_{max}$ and the result follows.

To show the entire orbit lies in $[K_{min}, K_{max}]$ we use induction. From Theorem 3.2,

$$\min\{K_{f_1}, K_{f_0}\} \leq K_{f_1 \circ f_0} \leq \max\{K_{f_1}, K_{f_0}\}.$$

Assume, as an induction hypothesis,

$$\min_{0 \leq j \leq m} \{K_{f_j}\} \leq K_{f_m \circ \cdots \circ f_0} \leq \max_{0 \leq j \leq m} \{K_{f_j}\}.$$

Applying Theorem 3.2 to f_{m+1} and $f_m \circ \cdots \circ f_0$ we get

$$\min\{K_{f_{m+1}}, K_{f_m \circ \cdots \circ f_0}\} \leq K_{f_{m+1} \circ \cdots \circ f_0} \leq \max\{K_{f_{m+1}}, K_{f_m \circ \cdots \circ f_0}\}.$$

From the inductive hypothesis it follows that

$$\min_{0 \leq j \leq m+1} \{K_{f_j}\} \leq K_{f_{m+1} \circ \cdots \circ f_0} \leq \max_{0 \leq j \leq m+1} \{K_{f_j}\}.$$

This shows that $s_0 = K_{f_{p-1} \circ \ldots \circ f_0} \in [K_{min}, K_{max}]$. To show that the entire periodic orbit lies in $[K_{min}, K_{max}]$ notice that $s_i = K_{f_{i-1} \ldots f_0 \circ f_{p-1} \ldots \circ f_{i+1} \circ f_i}$ and apply a similar argument.

■

4. Allee Periodic Orbit

We saw in Theorem 2.4 that inside the envelope $[K_{min}, K_{max}]$ of the carrying capacities there is an asymptotically stable periodic state. A similar result obtains for the Allee thresholds. For $b > 0$, define

$$\begin{aligned} \mathcal{X}_b \doteq \{ f \in C^1(\mathbb{R}^+, \mathbb{R}^+) \mid f(0) = 0, f \text{ increasing and convex on } [0, b], \\ f(b) > b, \text{ and there exist } x_1 \in [0, b) \ni f(x_1) < x_1 \}. \end{aligned} \tag{4.1}$$

Notice that each function $f \in \mathcal{X}_b$ has a unique unstable fixed point $A_f \in [0, b)$ such that any orbit of the autonomous iterated mapping $x_{n+1} = f(x_n)$ for which $x_0 \in [0, A_f)$ converges to 0.

Theorem 4.1 *Consider a finite collection of functions $f_0, f_1, \ldots f_{p-1} \in \mathcal{X}_b$. Define*

$$A_{min} = \min_{0 \leq n \leq p-1} A_{f_n} \qquad \text{and} \qquad A_{max} = \max_{0 \leq n \leq p-1} A_{f_n}.$$

The periodic iterated mapping (2.1) has a positive unstable p-periodic orbit $\alpha = \{\alpha_0, \alpha_1, \ldots, \alpha_{p-1}\} \subset [A_{min}, A_{max}]$ such that all orbits for which $x_0 \in [0, \alpha_0)$ are attracted to 0. We call this orbit the Allee periodic orbit of the iterated mapping.

Proof: Define

$$F_n(x) = \begin{cases} f_n(x) & x \in [0, b] \\ f_n(b) + f_n'(b)(x - b) & x > b \end{cases}$$

and let $\phi_n = F_n^{-1}$. Notice that $\phi_n \in U_{0,0}$ for all n and recall that $U_{0,0}$ is a semigroup under composition. (See Section 3.1 for the definition and properties of $U_{0,0}$.) Moreover, $B_{\phi_n} = 0$ and $K_{\phi_n} = A_{f_n}$. It follows that the iterated mapping $x_{n+1} = \phi_{p-1-n}(x_n)$ has a unique stable periodic orbit $\beta = \{\beta_0, \beta_1, \ldots, \beta_{p-1}\}$ that attracts all orbits for which $x_0 \in (0, \infty)$. The fact that $\beta \subset [A_{min}, A_{max}]$ follows by an induction argument similar to that used in the proof of Theorem 2.4. Thus $\alpha_0, \alpha_1, \ldots, \alpha_{p-1}$ where $\alpha_n = \beta_{p-1-n}$ is an unstable p-periodic orbit of the iterated mapping $x_{n+1} = F_n(x_n)$ and any orbit for which $x_0 \in [0, \alpha_0)$

is attracted to 0. Since $f_n = F_n$ on $[0, b]$ and $\alpha_n \in [A_{min}, A_{max}] \subset [0, b]$ for all n, α is also a periodic orbit of $x_{n+1} = f_n(x_n)$ and any orbit of this iterated mapping for which $x_0 \in [0, \alpha_0)$ is attracted to 0.

■

4.1. *Application to the Sigmoid Beverton-Holt Equation*

Recall the definition of a^{allee} in (2.4), the value of a as a function of δ at which the inflection point and Allee threshold coincide. Its graph is shown in Figure 3. If $a_n > a^{\text{allee}}(\delta_n)$ for $n = 0, 1, \ldots, p-1$, each Allee threshold lies on an interval of convexity of the graph of f_n. Thus if we assume

$$A_{max} < x_{min}^{infl} \doteq \min_{0 \le n \le p-1} x^{infl}(\delta_n),$$

then each $f_n \in \mathcal{X}_b$ where $b = x_{min}^{infl}$, see Figure 4. Thus we have the following

THEOREM 4.2 *Let $\{\delta_n\}$ and $\{a_n\}$ be p-periodic sequences in $\mathbb{R}_0^+$ such that $\delta_n > 1$ and $a_n > a^{allee}(\delta_n)$, for $0 \le n \le p-1$. Assume*

$$A_{max} < x_{min}^{infl}.$$

Then the periodic iterated mapping (2.1) has a positive unstable p-periodic orbit $\alpha = \{\alpha_0, \alpha_1, \ldots, \alpha_{p-1}\} \subset [A_{min}, A_{max}]$ such that all orbits for which $x_0 \in [0, \alpha_0)$ are attracted to 0.

Remark 3: As a increases through $a^{\text{crit}}(\delta)$ with δ fixed, $K_{f_{a,\delta}}$ moves upward from the bifurcation graph and $A_{f_{a,\delta}}$ moves downward. The trapezoidal region in Figure 4 shows a typical containment region for all the A_{f_n} satisfying the hypotheses of the theorem.

5. A New Look in the Skew-Product Space

Certain refinements to the above results can be realized by studying the problem in the Skew-Product setting. In the 1970s the Skew-Product Dynamical System was introduced and developed by R. J. Sacker and G. R. Sell as a means to analyze time varying differential equations in a more geometric setting (see [14] and references therein). The concept sprung from an idea in [16] in which the evolution in time of the function on the right hand side of

$$x'(t) = f(t, x), \qquad x \in \mathbb{R}^n, \tag{5.1}$$

is considered along with the evolution of a solution. This is accounted for by embedding f in a certain function space $\mathfrak{F}$ and introducing the *shift flow* σ in $\mathfrak{F}$ whereby the function f, after τ units of time evolves to $\sigma(f, \tau) = f_\tau$, where $f_\tau(t, x) = f(t + \tau, x)$. In this setting, the orbit under the action of σ of a periodic f in (5.1) is a closed Jordan curve in $\mathfrak{F}$. Then an *enlarged phase space* $\mathbb{R}^n \times \mathfrak{F}$ is introduced and the skew-product flow

$$\pi : \mathbb{R}^d \times \mathfrak{F} \times \mathbb{R} \to \mathbb{R}^d \times \mathfrak{F} \quad \text{with} \quad \pi(x_0, g, \tau) = (\varphi(x_0, g, \tau), g_\tau), \quad \forall g \in \mathfrak{F} \tag{5.2}$$

where $\varphi(x_0, g, \tau)$ is the solution, evaluated at τ, of $x'(t) = g(t, x)$, $\varphi(x_0, g, 0) = x_0$. It is readily verified that π is indeed a *flow* in the enlarged state space $\mathbb{R}^d \times \mathfrak{F}$ and thus all the theory of *autonomous* dynamical systems can be brought to bear.

In the present setting of p-periodic difference equations in one dimension the situation is much simpler, $\mathfrak{F} = \{f_0, f_1, \ldots, f_{p-1}\}$, $\sigma(f_k, m) = f_{k+m}$ and (5.2) becomes

$$\pi : \mathbb{R}^+ \times \mathfrak{F} \times \mathbb{Z}^+ \to \mathbb{R}^+ \times \mathfrak{F} \quad \text{with} \quad \pi(x_0, f, n) = (\varphi(x_0, f, \tau), f_n). \tag{5.3}$$

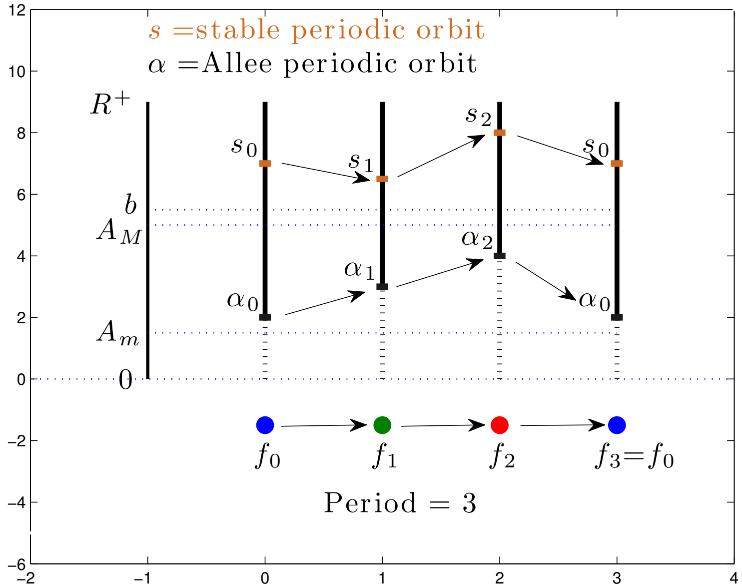

Figure 5. The stable periodic orbit and the Allee periodic orbit in the Skew-Product space, $A_M = A_{max}, A_m = A_{min}$

In Figure 5 the skew-product space is shown for period $p = 3$ along with the stable periodic orbit $s = \{s_0, s_1, s_2\}$ and the Allee periodic orbit $\alpha = \{\alpha_0, \alpha_1, \alpha_2\}$. The following theorem is obtained by a more careful analysis of this figure.

Theorem 5.1 *Let $\{\delta_n\}$ and $\{a_n\}$ be p-periodic sequences in $\mathbb{R}_0^+$ such that $\delta_n > 1$ and $a_n > a^{allee}(\delta_n)$, for $0 \le n \le p-1$. Suppose that*

$$A_{max} < x_{min}^{infl} \le x_{max}^{infl} < x_{min}^{bif}$$

Then there are a stable periodic orbit $s = \{s_0, s_1, \ldots, s_{p-1}\} \subset [K_{min}, K_{max}]$ and an Allee periodic orbit $\alpha = \{\alpha_0, \alpha_1, \ldots, \alpha_{p-1}\} \subset [A_{min}, A_{max}]$. Moreover, we have the following.

i) For all $n \in \mathbb{N}$, the interval $(0, \alpha_n)$ maps homeomorphically onto $(0, \alpha_{n+1})$, and any orbit for which $x_0 \in (0, \alpha_0)$ approaches 0 asymptotically.

ii) For all $n \in \mathbb{N}$, the interval (α_n, s_n) maps homeomorphically onto (α_{n+1}, s_{n+1}), and any orbit for which $x_0 \in (\alpha_0, \infty)$ is attracted to the stable periodic orbit s.

Proof: The existence of the stable and Allee periodic orbits and their containments within $[K_{min}, K_{max}]$ and $[A_{min}, A_{max}]$ respectively follows directly from Theorems 2.4 and 4.2. Moreover, any orbit for which $x_0 \in (A_{max}, \infty)$ is attracted to the stable periodic orbit and any orbit for which $x_0 \in (0, \alpha_0)$ approaches 0 asymptotically. That $(0, \alpha_n)$ maps homeomorphically to $(0, \alpha_{n+1})$ and (α_n, s_n) maps homeomorphically to (α_{n+1}, s_{n+1}) follows from the fact that f_n is increasing.

It only remains to show that any orbit for which $x_0 \in (\alpha_0, A_{max}]$ is attracted to the stable periodic orbit s. For this we look more carefully at the proof of Theorem 4.1. The orbit β is globally asymptotically stable under the iterated mapping $x_{n+1} = \phi_{p-1-n}(x_n)$. In particular, any orbit under this mapping for which $x_0 \in (A_{max}, b)$, where $b = x_{min}^{infl}$, is attracted to the periodic orbit β. It follows that there are points arbitrarily close to α_n that are ultimately mapped into the interval (A_{max}, b) under the mapping $x_{n+1} = F_n(x_n)$. Since $F_n = f_n$ on $[0, b)$ this is also true under the mapping $x_{n+1} = f_n(x_n)$. Since (α_n, s_n) maps homeomorphically to (α_{n+1}, s_{n+1}), all points arbitrarily close and greater than α_0 are ultimately mapped to points greater than A_{max}. The result follows since (A_{max}, ∞) has already been shown to lie in the basin of attraction of the stable periodic orbit. ∎

6. Conclusions

An investigation is conducted into the long term behavior of solutions of the periodic Sigmoid Beverton-Holt equation

$$x_{n+1} = \frac{a_n x^{\delta_n}}{1 + x^{\delta_n}}, \quad x_0 > 0, \quad n = 0, 1, 2, \ldots,$$

where the a_n and δ_n are p-periodic positive sequences. Under certain conditions on the parameters a_n and δ_n there are shown to exist an asymptotically stable p-periodic state to which all nearby as well as large initial populations approach and a p-periodic Allee state that drives all initially small states to extinction.

For δ_n independent of n we obtain a previous result in [7] with fewer conditions.

Acknowledgements

Authors GG, KG, FG and CH were supported by NSF grant DMS-1045536 as part of the California Research Training Program in Computational and Applied Mathematics. The authors thank Andrea Bertozzi for organizing the Summer Research Experience for Undergraduates.

RJS is supported by University of Southern California, Dornsife School of Letters Arts and Sciences Faculty Development Grant.

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