The Sigmoid Beverton-Holt Model Revisited

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1 Abstract

We will be examining the Sigmoid Beverton-Holt difference equation. It has been shown that when the Sigmoid Beverton-Holt has a p-periodically-varying growth rate, there exists a p-periodic globally asymptotically stable solution $\{x_n\}$. In this paper we extend this result to include a more general class of Sigmoid Beverton-Holt functions. Furthermore, we consider the case in which the variables of our general class are varied randomly and show that there exists a unique invariant density to which all other densities converge. Lastly, we extend the Beverton-Holt to include a spatial component and show there exists a unique, stable, non-trivial fixed point in this case.

2 Introduction

In this paper, we study the solutions of the Sigmoid Beverton-Holt equation:

$$x_{n+1} = \frac{a_n x_n^{\delta_n}}{1 + x_n^{\delta_n}}, n \in \mathbb{N}$$

with the initial condition

$$x_0 > 0$$

under varying conditions on the parameters a_n and δ_n where $a_n, \delta_n > 0$.

The autonomous case of the Sigmoid Beverton-Holt equation (where $a_n = a$ and $\delta_n = \delta$ are constant) has been introduced by Thompson as a "depensatory generalization of the Beverton-Holt stock-recruitment relationship used to develop a set of constraints designed to safeguard against overfishing." In the case when $\delta_n = 1$ for all $n \in \mathbb{N}$ the model reduces to the well-known Pielou logistic equation

$$x_{n+1} = \frac{a_n x_n}{1 + x_n}, n \in \mathbb{N}$$

which is equivalent to the Beverton-Holt equation:

$$x_{n+1} = \frac{\mu k_n x_n}{k_n + (\mu - 1)x_n}, n \in \mathbb{N}$$

The dynamics and properties of both models have been extensively studied [1][2].

With constant δ, the Sigmoid Beverton-Holt model exhibits different behaviors. In particular, when $\delta > 1$ and $a_n > \delta(\delta-1)^{1/\delta - 1}$ the model exhibits the "Allee effect" first described by W.C. Allee [2][3][4], which models a positive correlation between popoulation density and growth rate at low population densities. Kocic et. al. have proven many results about the behavior of this model with constant δ and a k-periodic sequence $\{a_n\}$ where $a_{k+i} = a_i$ for all $i \in \mathbb{N}$. One goal of this paper is to extend these results to include the case when both δ_n and a_n are varied periodically.

As an extension to the well-studied periodically-varied Beverton-Holt model, Haskell and Sacker studied the behavior of the Stochastic Beverton-Holt Model

$$x_{n+1} = \frac{\mu k_n x_n}{k_n + (\mu - 1)x_n}, n \in \mathbb{N}$$

with $\mu < 1$ and k_n chosen randomly[7]. Haskell and Sacker proved that the distribution of the state variable converges to a unique invariant density. Our second goal in this paper is to extend their result to the Sigmoid Beverton-Holt with varying a and δ.

As a final extension, we examine the Beverton-Holt equation

$$f(x) = \frac{ax}{1+x}$$

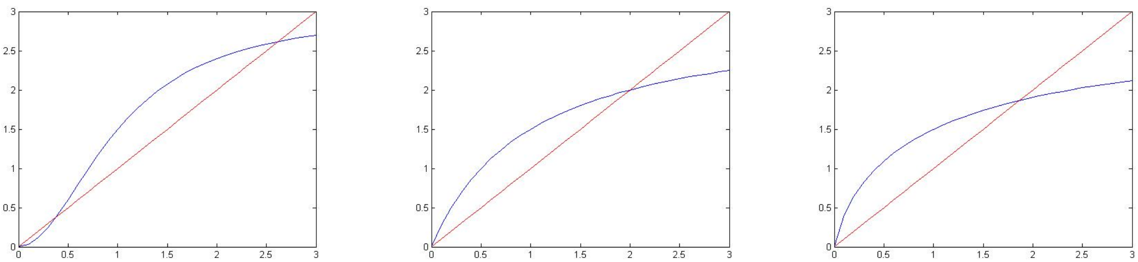
with regards a to spatial component. As a spatial model has not previously existed, we construct a map F_α by considering a one-dimensional case in which we have several populations lying in a line of N boxes. These boxes represent an intial separation between the populations, and, as time progresses, the populations begin to move between boxes according to a constant rate. We show there exists a stable, nontrivial fixed point. We approach this using two methods–the implicit function theorem and the Banach fixed point theorem. With the former, we find that there exists a fixed point in the map F_α. However, we further show F_α is a contraction mapping, and with this we are able to use the latter theorem to show this fixed point is stable.

3 Periodic Orbits of the Periodically Forced Sigmoid Beverton Holt

In this section, we investigate the periodically forced Sigmoid Beverton Holt model:

$$x_{n+1} = \frac{a_n x_n^{\delta_n}}{1 + x_n^{\delta_n}}$$

where $\{a_n\}$ and $\{\delta_n\}$ are postive periodic sequences with period p. We prove that under certain conditions, there exists a stable periodic orbit for sequences of Sigmoid Beverton-Holt equations.



(a) $\delta \in (1, \infty), a > a_{crit}$ (b) $\delta = 1, a > 1$ (c) $\delta \in (0, 1), a \in (0, \infty)$

Figure 1: Sigmoid Beverton-Holts included in $\mathcal{F}$

3.1 The Set $\mathcal{F}$

First, we define the set $\mathcal{F}$ to be the set of all functions that have the following properties:

(i) f is positive, continuous, and increasing everywhere on $\mathbb{R}^+$.

(ii) There exists a number $B_f \geq 0$ such that $f(B_f) > B_f$ and f is concave on (B_f, ∞).

(iii) There exists a number $x^* > B_f$ such that $f(x^*) < x^*$.

Claim: There exists a unique fixed point on the interval (B_f, ∞) where $f(x) > x$ for $x \in (B_f, K_f)$ and $f(x) < x$ for $x \in (K_f, \infty)$.

Proof. Since $f(B_f) > B_f$ and f is continuous, there exists an $x_1 > B_f$ such that $f(x_1) > x_1$. Furthermore, there exists, by definiton, $x^* > B_f$ such that and $f(x^*) < x^*$. Thus, by the Intermediate Value Theorem, there exists a fixed point between x_1 and x^*. We look at $\{K_i | f(K_i) = K_i \text{ and } x_1 < K_i < x^*\}$, the set of fixed points between x_1 and x^*. Define $K_f = \min\{K_i | f(K_i) = K_i \text{ and } x_1 < K_i < x^*\}$. Suppose there exists another fixed point $P_f > K_f$. By the intermediate value theorem $\exists\ t_0 \in (0, 1)$ s.t. $t_0 x_1 + (1 - t_0)P_f = K_f$. By concavity $K_f = f(t_0 x_1 + (1 - t_0)P_f) \geq t_0 f(x_1) + (1 - t_0) f(P_f) = t_0 f(x_1) + (1 - t_0)P_f$. But by choice of x_1, $t_0 f(x_1) + (1 - t_0)P_f < t_0 x_1 + (1 - t_0)P_f = K_f$. By contradiction there does not exist a fixed point $P_f > K_f$. Hence K_f is the unique fixed point on (B_f, ∞).

Now we show $f(x) > x$ for $x \in (B_f, K_f)$ and $f(x) < x$ for $x \in (K_f, \infty)$. By (ii), $f(B_f) > B_f$ implies $f(x) > x$ for some $x \in (B_f, K_f)$ since f is increasing. Then $f(x) > x$ until f crosses the diagonal, (ie until $x \geq K_f$). Therefore $f(x) > x$ for all

$x \in (B_f, K_f)$. We know that f crosses the diagonal at K_f by (iii). Once f passes the diagonal, then $f(x) < x$, and since K_f is the unique fixed point on (B_f, ∞), $f(x) < x$ for all $x \in (K_f, \infty)$. □

Claim. K_f is stable on (B_f, ∞).

Proof. By the definition of f, $K_f > f(x) > x$ for $x \in (B_f, K_f)$ and $f(x) < x < K_f$ for $x \in (K_f, \infty)$. Then the sequence $\{a_n\}$ defined by $a_{k+1} = f(a_k)\ \forall\ k \in \mathbb{N}$ is increasing on (B_f, K_f) and is bounded above by K_f. And $\{a_n\}$ is decreasing on (K_f, ∞) and bounded below by K_f. By monotone convergence $\{a_n\}$ has a limit. Denote this limit L. We will show by contradiction that this limit is K_f. Consider first the case when the initial value of the sequence is less than K_f. Then the sequence is bounded above by K_f, so $L \leq K_f$. Now suppose that $L < K_f$, then $L < f(L)$. Choose $\varepsilon = \frac{|f(L)-L|}{2}$. Then $\exists\ \delta$ s.t. $\forall\ x \in (L, K_f)$ if $|x - L| < \delta$ then $|f(x) - f(L)| < \varepsilon$. This implies that $f(x) > L$. Then $L < f(x) < K_f$ and because f is increasing, the $\lim\limits_{x\to\infty} \{a_n\} > L$. By contradiction $L \geq K_f$. A similar proof shows that $L \leq K_f$. Therefore $L = K_f$. □

3.2 Our New Class

Given $l \in \mathbb{R}^+$, define $\mathcal{U}_l = \{f \in \mathcal{F} | B_f < l < K_f\}$.

Claim. $\mathcal{U}_l$ is a semigroup under composition.

Proof. (i) If g is positive for all $x \in \mathbb{R}^+$, then for $f > 0$ for $x \in \mathbb{R}^+$ we clearly have $f \circ g > 0$ for all positive reals. Similarly, if f and g are continuous and increasing on $\mathbb{R}^+$, then it follows $f \circ g$ is continuous and increasing on $\mathbb{R}^+$.

(ii)We show that there exists a $B \geq 0$ such that $f \circ g$ is concave on (B, ∞) and $f(B) > B$.

Assume $B = B_f > B_g \geq 0$. Since $B_g < B < K_g$, $g(B) > B$ which implies that $f \circ g(B) > B$. Then, $\forall x_1, x_2 \in (B, \infty), t \in (0, 1)$, we need to show $f \circ g(tx_1 + (1-t)x_2) \geq tf \circ g(x_1) + (1-t)f \circ g(x_2)$. g is concave in (B, ∞), and by definition of concavity, $g(tx_1 + (1-t)x_2) \geq tg(x_1) + (1-t)g(x_2)$. Then, $f \circ g(tx_1 + (1-t)x_2) \geq f(tg(x_1) + (1-t)g(x_2))$ since f is increasing. Now, since f is also concave in this interval, we apply the definition again to obtain $f(tg(x_1) + (1-t)g(x_2)) \geq tf \circ g(x_1) + (1-t)f \circ g(x_2)$.

If $B_g > B_f$, take $B = B_{f'}$ where $B_{f'}$ is such that $K_g > B_{f'} > B_g > B_f$. This is possible since f, g are continuous. So now $f \circ g(B) > B$, and $f \circ g$ is concave on (B, ∞) by similar reasoning as above.

(iii) We show that there exists an x^* such that $x^* > B$ and $f \circ g(x^*) < x^*$.

Case 1: Assume there exists an $x > B$ such that $g(x) \geq K_f$. Then pick x^* such that $g(x^*) > K_f$ and $g(x^*) < x^*$. x^* exists since g is increasing everywhere. Then $f \circ g(x^*) < g(x^*) < x^*$.

Case 2: Assume $g(x) < K_f$ for all x. Since $g(x) < K_f$ everywhere, then $f \circ g(x) < f(K_f) = K_f$. Thus, $f \circ g(x) < K_f$ for all x. Take x^* such that $x^* > K_f$. Then $f \circ g(x^*) < K_f < x^*$.

Finally, we show $B < l < K_{f \circ g}$. Since $B = max\{B_f, B_g\}$ and $B_f < l$ and $B_g < l$, $B < l$. Assume first that $K_g > K_f$. Then $f(K_g) < K_g$ which implies $f \circ g(K_g) = f(K_g) < Kg$. Similarly, $g(K_f) > K_f$, which implies $f \circ g(K_f) > K_f$. Thus, we conclude that $K_f < K_{f \circ g} < K_g$, which implies that $K_{f \circ g} > l$. Finally, assume that $K_f > K_g$. Then $f(K_g) > K_g$ which implies that $f \circ g(K_g) = f(K_g) > K_g$. Similarly, since $g(K_f) < K_f$, $f \circ g(K_f) < K_f$. Thus, $K_g < K_{f \circ g} < K_f$. □

3.3 Application to Non-Autonomous Beverton-Holt Model

The forced Sigmoid Beverton-Holt model is described by: $f(x_{n+1}) = \frac{a_n x^{\delta}{}_n}{1+x^{\delta}{}_n}$

Theorem. Suppose we have a sequence $\{(a_n, \delta_n)\}$ such that there exists a number l such that for each n, the Sigmoid Beverton-Holt function f_n with parameters (a_n, δ_n) is contained in $\mathcal{U}_l$.
Then the sequence $\{f_n\}$ has a periodic orbit for any x_0 in the interval (B, ∞), where B is as defined in Claim 1.

Proof. Since each f_n is in $\mathcal{U}$, and $\mathcal{U}$ is a semigroup, if we take f_1, f_2, f_3...,f_n in $\mathcal{U}$ then $g(x) = f_1 \circ f_2 ... \circ f_n \in \mathcal{U}$. Thus, g has a stable fixed point on the interval (B_g, ∞), which implies $f_1 \circ f_2 ... \circ f_n$ has a periodic orbit on (B_g, ∞). □

4 The Stochastic Sigmoid-Beverton Holt Equation

In the next section, we consider the stochastic Sigmoid Beverton Holt model $x_{n+1} = b(a_n, \delta_n, x_n) = \dfrac{a_n x_n^{\delta_n}}{1 + x_n^{\delta_n}}$ with randomly varying carrying capacity. We restrict our considerations to the cases when $\delta_n \in (0, 1), a_n > 0$. Notice that under this restriction, $b(a, \delta, x)$ is increasing and concave on all of $\mathbb{R}^+$. Furthermore, define $k = k(a, \delta)$ to be the carrying capacity of $b(a, \delta, x)$. If we have a sequence of functions, $\{b_n\}$, we will denote the minimum carrying capactiy of the sequence by k_{min}.

We will parallel the methods introduced in Haskell and Sacker to show that for sequences of Sigmoid Beverton Holt equations falling under our restrictions there exists a unique invariant density to which all other density distribtions on the state variable converge. As in Bezandry, Diagana, and Elaydi's paper [8], we have that for all $n \in \mathbb{N}$, (a_n, δ_n) is chosen independently from $((x_0, a_0, \delta_0)......(x_{n-1}, a_{n-1}, \delta_{n-1}))$ from a distribution with density $\Psi(a, \delta)$. Thus, the joint density of x_n, δ_n, and a_n is given by $f_n(x)\Psi(a, \delta)$ where $f_n(x)$ represents the density of x_n. We suppose that the expected value is finite, and that $\Psi(a, \delta)$ is bounded above. Furthermore, we suppose that that Ψ is supported on $[a_{min}, a_{max}] \times [0, 1)$, with $a_{min} > 0$. It follows that $\Psi(a, \delta)$ is supported on $[k_{min}, k_{max})$, where k_{min} represents the minimum carrying capacity of our sequence, and is determined by some $(a^*, \delta^*) \in [a_{min}, a_{max}] \times [0, 1)$. Finally, we suppose that there is some interval (k_l, k_u) such that for all $a, \delta \in [a_{min}, a_{max}] \times [0, 1)$ with $k(a, \delta) \in (k_l, k_u)$, $\Psi(a, \delta)$ is positive everywhere.

Let h be an arbitrary function in $L^\infty(R^+)$. The expected value of h at time $n+1$ is given by

$$E[h(x_{n+1})] = \int_0^\infty h(x) f_{n+1}(x) dx \tag{1}$$

Furthermore, since the joint density of x_n, δ_n, and a_n is given by $f_n(x)\Psi(a, \delta)$, we have that

$$E[h(x_{n+1})] = E[h(b(a, \delta, y))] = \int_0^\infty \int_0^\infty \int_0^1 h(x) f_n(y) \Psi(a, \delta) d\delta da dy$$

We define $a = a(x, \delta, y)$ by the equation

$$x = \frac{a y^\delta}{1 + y^\delta} \tag{2}$$

Solving explicitly for a, one gets that

$$a = \frac{x(1 + y^\delta)}{y^\delta} \tag{3}$$

By making the change of variables $x = b(a, \delta, y)$, we rewrite the expected value as

$$E[h(x_{n+1})] = \int_0^\infty \int_0^\infty \int_0^1 h(x) f_n(y) [\frac{1 + y^\delta}{y^\delta}] \Psi(a, \delta) d\delta dx dy \tag{4}$$

By equations (1) and (2), and using the fact that h is arbitrary, we we get that

$$f_{n+1}(x) = \int_0^\infty \int_0^1 f_n(y) [\frac{1 + y^\delta}{y^\delta}] \Psi(a, \delta) d\delta dy$$

Let $P : L^\infty(R^+) \to L^\infty(R^+)$ be defined by

$$Pf(x) = \int_0^\infty \int_0^1 f_n(y) [\frac{1 + y^\delta}{y^\delta}] \Psi(a, \delta) d\delta dy \tag{5}$$

where $a = a(x, \delta, y)$ is defined by equation (3) .

Let (X, A, μ) be an arbitrary measure space and let

$$D(X) := \{f \in L^1(X) : f \geq 0 \text{ and } \int f d\mu = 1\}$$

be the space of all densities on X. A Markov Operator $Q : L^1(X) \to L^1(X)$ is said to be asymptotically stable if there exists $f^* \in D$ for which $Qf^* = f^*$ and for all $f \in D$

$$\lim_{n\to\infty} ||Q^n f - f^*||_{L^1} = 0$$

We would now like to prove that P is asymptotically stable. This can be viewed as the stochatic equivalent to showing that a globally asymptotically stable periodic orbit exists in the periodic case.

Theorem. The Markov operator $P : L^\infty\mathbb{R}^+ \to L^\infty\mathbb{R}^+)$ defined by (5) is asymptotically stable.

First, we prove the following Lemmas about P.

Lemma 1.
(i) P is nonnegative
(ii) P is a Markov Operator
(iii) If f is supported on $[k_{min}, \infty)$ then so is Pf

Proof.
(i) Clearly, P is nonnegative.
(ii) To show that Pf is a Markov operator, we compute $||Pf||$.

$$||Pf|| = \int_0^\infty f(y) \int\int f_n(y)[\frac{1+y^\delta}{y^\delta}]\Psi(a,\delta)dxd\delta dy$$

Let $z = a(x, \delta, y) = \dfrac{x(1+y^\delta)}{y^\delta}$, then

$$||Pf|| = \int_0^\infty f(y) \int\int \Psi(z,\delta)dzd\delta dy = \int f(y) = ||f||$$

Therefore, P is a Markov Operator.

We now define the stochastic kernel corresponding to P. Let $L : \mathbb{R}^+ \times \mathbb{R}^+ \to \mathbb{R}^+$ be defined by

$$L(x,y) = \int \frac{1+y^\delta}{y^\delta}\Psi(a,\delta)d\delta \tag{6}$$

(iii) Note that all the values of Pf will also lie on the interval $[k_{min}, \infty)$. Thus, Pf is also supported on $[k_{min}, \infty)$.

Now, let L_m denote the stochastic kernel of P^m. To obtain an expression for L_m, we first define $b^m : (\mathbb{R}^+)^m \times \mathbb{R}^+ \to \mathbb{R}$ inductively by

$$\begin{gathered} b^1(a_0, \delta_0, x) = b(a_0, \delta_0, x) \\ b^2(a_1, \delta_1, a_0, \delta_0, x) = b(a_1, \delta_1, b^1(a_0, \delta_0, x)) \\ \vdots \\ b^m(a_{m-1}, \delta_{m-1}, \ldots, a_0, \delta_0, x) = b(a_{m-1}, \delta_{m-1}, b^{m-1}(a_{m-2}, \delta_{m-2}, \ldots, a_0, \delta_0, x)) \end{gathered}$$

From the first equations in this section, we have that on the one hand,

$$E[h(x_{n+m})] = \int_0^\infty h(x) f_{n+m}(x) dx \tag{7}$$

while on the other hand,

$$\begin{aligned} &E[h(x_{n+m})] = E[h(b(a_{m-1}, \delta_{m-1}, \ldots, a_0, \delta_0)] = \\ &\int \cdots \int \int \int h(b(a_{m-1}, \delta_{m-1}, \ldots, a_0, \delta_0)) f_n(y) \times \\ &\qquad \Psi(a_{m-1}, \delta_{m-1}) \ldots \Psi(a_0, \delta_0) da_{m-1} d\delta_{m-1} \ldots da_0 d\delta_0 dy \end{aligned} \tag{8}$$

By making the change of variables , we get that

$$\begin{aligned} &E[h(x_{n+m})] = \\ &\int h(x) \int \int \int \frac{1+z^\delta}{z^\delta} f_n(y) \Psi(a, \delta) \ldots \Psi(a_0, \delta_0) d\delta da_{m-2} d\delta_{m-2} \ldots da_0 d\delta_0 dy dx \end{aligned} \tag{9}$$

where $z = b^{m-1}(a_{m-2}, \delta_{m-2}, ...a_0, \delta_0, y)$ and a is given by $x = b^m(a, \delta, \ldots, a_0, \delta_0, y)$.

By equating (8) and (9), we see that

$f_{n+m} = \int \cdots \int \int \frac{1+z^\delta}{z^\delta} f_n(y) \Psi(a, \delta) \ldots \Psi(a_0, \delta_0) da_{m-2} d\delta_{m-2} \ldots da_0 d\delta_0 d\delta dy$ which implies that

$$L_m = \int \cdots \int \int \frac{1+z^\delta}{z^\delta} \Psi(a, \delta) \ldots \Psi(a_0, \delta_0) da_{m-2} d\delta_{m-2} \ldots da_0 d\delta_0 d\delta$$

□

We break up our investigation of how P into two parts. First, we consider how P acts on the parts of the density whose support is in $[k_{min}, \infty)$

Lemma 2. $P : L^1[k_{min}, \infty) \to L^1(k_{min}, \infty)$ is asymptotically stable.

Proof. To prove that P is asymptotically stable, it suffices to show that there exists an integer m, a function $g \in L^1[k_{min}, \infty)$ and an interval (α, β) such that for all $x, y \in \mathbb{R}^+$, we have that

$$L_m(x, y) \leq g(x)$$

and for all $x \in (\alpha, \beta)$ and $y \in [k_{min}, \infty)$,

$$L_m(x, y) > 0$$

Notice that if $x < k_{min}$, $L_m(x, y) = 0$, and similarly for x if $x > a_{max}$. Thus, we define$g : [k_{min}, \infty)$ as

$$g(x) = \begin{cases} 0 & x < k_{min} \\ \{\sup_{a \in \mathbb{R}^+} \Psi(a, \hat{\delta})\}\{\sup_{a_{m-2}, \delta_{m-2} \ldots a_0, \delta_0, y} \frac{1+z^\delta}{z^\delta}\} & k_{min} < x < a_{max} \\ 0 & x > a_{max} \end{cases}$$

This implies that $L_m(x, y) \leq g(x)$. Furthermore, since the expected value is finite, $g \in L^1[k_{min}, \infty)$. Thus, the first condition is satisfied.

As to the second condition , first notice that for all $a \in \mathbb{R}^+$, $\delta \in (0, 1)$ and $x \in (k_{min}, \infty)$, $b^n(a, \delta, \ldots a, \delta, x) \to k$ as $n \to \infty$, where k is the carrying capacity of the map determined by a and δ.

We choose $a_l, \delta_l, a_u, \delta_u$ such that $\forall\ y \in [k_{min}, \infty)$

$$\lim_{n \to \infty} b^n(a_l, \delta_l, ..., a_l, \delta_l, y) = k_l$$

and

$$\lim_{n \to \infty} b^n(a_u, \delta_u, ..., a_u, \delta_u, y) = k_u$$

Claim: There exists $m \in \mathbb{N}$ large enought such that

$$b^m(a_l, \delta_l, ..., a_l, \delta_l, y) < \frac{k_l + k_u}{2} < b^m(a_u, \delta_u, ..., a_u, \delta_u, y)$$

for all $y \geq k_{min}$.

Proof. Since

$$\lim_{n \to \infty} b^n(a_u, \delta_u, ..., a_u, \delta_u, y) = k_u$$

there exists an $m_1 \in \mathbb{N}$ such that

$$b^{m_1}(a_u, \delta_u, ..., a_u, \delta_u, y) > \frac{k_l + k_u}{2}$$

On the other hand, since

$$\lim_{n \to \infty} b^n(a_l, \delta_l, ..., a_l, \delta_l, y) = k_l$$

there exists an $m_2 \in \mathbb{N}$ such that

$$b^{m_2}(a_u, \delta_u, ..., a_u, \delta_u, a_u) < \frac{k_l + k_u}{2}$$

Since $b(a_u, \delta_u, y)$ is bounded by a_u, this implies that

$$b^{m_2+1}(a_u, \delta_u, ..., a_u, \delta_u, y) < \frac{k_l + k_u}{2}$$

Thus, if we let $m = max\{m_1, m_2 + 1\}$, then we conclude that

$$b^m(a_l, \delta_l, ..., a_l, \delta_l, y) < \frac{k_l + k_u}{2} < b^m(a_u, \delta_u, ..., a_u, \delta_u, y)$$

$\square$

Set $\alpha = \frac{k_l+k_u}{2}$ and $\beta = b^m(a_u, \delta_u, ..., a_u, \delta_u, y)$. If $x \in (\alpha, \beta)$ and $y \in [k_{min}, \infty)$, the inequalities above imply that

$$b^m(a_l, \delta_l, ..., a_l, \delta_l, y) < x < b^m(a_u, \delta_u, ..., a_u, \delta_u, y).$$

Since b^m is continuous in all variables it follows by the implicit function theorem that there exists an open ball $B \subset (k_l, k_u)^{m-1}$ and a function $\kappa : B \to (a_l, a_u)X(\delta_l, \delta_u)$ such that for all $(a_0, \delta_0, ..., a_{m-2}, \delta_{m-2}) \in\ B, (a, \delta) = \kappa(a_0, \delta_0, ..., a_{m-2}, \delta_{m-2})$ is a solution of $x = b^m(a, \delta, a_0, \delta_0, ..., a_{m-2}, \delta_{m-2})$. It follows that $L_m(x, y) > 0$. This completes the proof of the lemma.

$\square$

We now consider how P acts on the parts of the density whose support is in $[0, k_{min}]$.

Lemma 3. If $f \in L^1(\mathbb{R}^+)$ then

$$\lim_{m\to\infty} \int_0^{k_{min}} P^m f(x)dx = 0$$

Proof. Let $\epsilon > 0$. Pick M with $0 < M < k_{min}$ such that

$$\int_0^M f(x)dx < \epsilon$$

Then for all a, δ such that $k(a, \delta) \in (k_l, k_u)$, we know we have $b(a, \delta, M) > M$. Furthermore choose $N > M$ such that the set $A = \{(a, \delta) : k(a, \delta) \geq k_l andb(a, \delta, M) > N\}$ has positive Lebesgue mesaure, q. Consider the straight line $y = g(x)$ from (M, N) to (k_l, k_l). We know that fpr $(a, \delta \in A$ and $x \in (M, k_l)$, $b(a, \delta, x)$ will always lie above this line, due to the fact that b is concave, increasing, and $k(a, \delta) \geq k_l$. Let $y > m$. Then there exists a k such that $b^k(a_k, \delta_k, \ldots, a_0, \delta_0, y) > k_{min}$ where the a_i, δ_i are in A. Thus, after k steps, we have that

$$\int_0^{k_{min}} P^k f(x)dx \leq \int_0^M f(x)dx + (1-q)\int_M^{k_{min}} f(x)dx \leq \epsilon + (1-q)\int_M^{k_{min}} f(x)dx$$

Thus, we have that

$$\int_0^{k_{min}} P^{mk} f(x)dx \leq \epsilon + (1-q)^m \int_M^{k_{min}} f(x)dx$$

So we can conclude that

$$\lim_{m\to\infty} \int_0^{k_{min}} P^{mk} f(x)dx = 0$$

as $m \to 0$
and the proof is complete.

$\square$

5 Spatial Considerations

We now consider a spatial component in our study of the Beverton-Holt model

$$f(x) = \frac{ax}{1+x}$$

In particular, we find that, under certain conditions of α, there exists a stable, non-trivail fixed point for our map.

Consider a one-dimensional case where the populations lie in a line of boxes from 1 to N and move between boxes at rate α. We can model this behavior by $\mathbf{x_{j+1}} = \mathbf{F}_\alpha(\mathbf{x_j})$ where $\mathbf{F}_\alpha : \mathbb{R}^\mathbf{N} \to \mathbb{R}^\mathbf{N}$ is defined by

$$\mathbf{F}_\alpha(x_1, x_2, \cdots, x_N) = (y_1, y_2, \cdots, y_3)$$

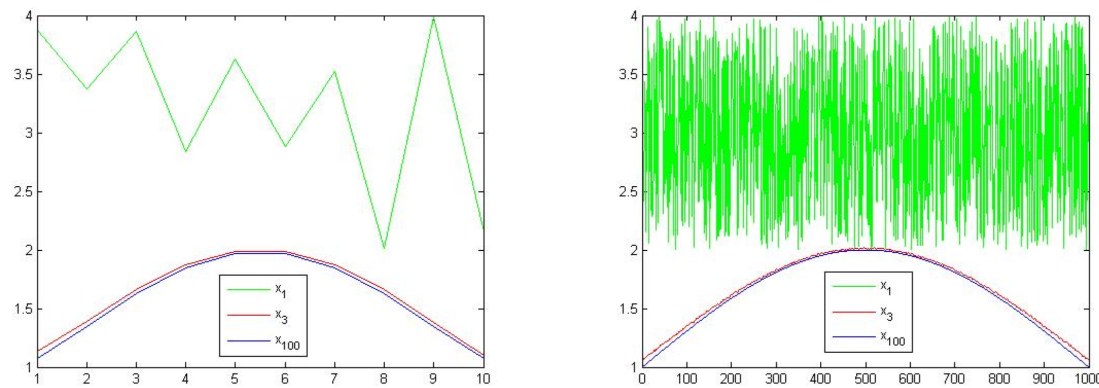
where

$$y_1 = f_1((1-\alpha)x_1 + \alpha x_2)$$
$$y_i = f_i(\alpha x_{i-1} + (1-2\alpha)x_i + \alpha x_{i+1}), i = 2, \cdots, N-1$$
$$y_N = f_N(\alpha x_N - 1 + (1-\alpha)x_N)$$

where $f_i(x) = \frac{a_i x}{1+x}$, and $a_i > 1$.

Notice if $\alpha = 0$, our system is uncoupled, with a non-trivial fixed point at $(a_1 - 1, a_2 - 1, \cdots, a_N - 1)$.

From Figure 2, F_α seems to converge to a fixed point of the mapping. We will use the implicit function theorem to show there exists a non-trivial fixed point when α is close to 0. Also, we will give an alternative proof using the Banach fixed point



(a) 100 Iterations of 5 Populations

(b) 100 Iterations of 1000 Populations

Figure 2: Fixed point iteration where $\alpha = .3$; $a_i = \sin(\frac{(i-1)\pi}{N-1}) + 2$

theorem from which we can deduce this fixed point is stable, depending on certain conditions on α. We have included in this section statements of both theorems as a reminder for the reader.

5.1 Implicit Function Theorem

Let $g : \mathcal{R}^{n+m} \to \mathcal{R}^m$ be a continuously differentiable function, with $\mathcal{R}^{n+m}$ having coordinates $(\mathbf{x}, \mathbf{y})$ and let $(\mathbf{a}, \mathbf{b})$ satisfy $g(\mathbf{a}, \mathbf{b}) = \mathbf{c}$, where $\mathbf{c} \in \mathcal{R}^m$. If the matrix $[\frac{\partial g_i}{\partial y_j}(\mathbf{a}, \mathbf{b})]$ is invertible, then there exists an open set $\mathcal{U}$ containing $\mathbf{a}$, an open set V containing $\mathbf{b}$, and a unique continuously differentiable function $\phi : \mathcal{U} \to \mathcal{V}$ such that

$$\{(\mathbf{x}, \phi(\mathbf{x}) | \mathbf{x} \in \mathcal{U}\} = \{\mathbf{x}\mathbf{,y} \in \mathcal{U} \times \mathcal{V} | g(\mathbf{x}\mathbf{,y}) = \mathbf{c}\}.$$

5.2 Application to Spatial Beverton-Holt Model

Let

$$g(\alpha, x_1, x_2, \cdots, x_N) = F_\alpha(x_1, x_2, \cdots, x_N) - (x_1, x_2, \cdots, x_N).$$

Notice $g : \mathbb{R}^{1+N} \to \mathbb{R}^N$, and $g(0, a_1 - 1, \cdots, a_N - 1) = (0, 0, \cdots, 0)$.

Claim: F_α has a non-trivial fixed point.

Proof. To use the implicit function theorem, we need to show the Jacobian matrix

$\frac{\partial g_i}{\partial x_j}(\alpha, x) =$

$$\begin{pmatrix} \frac{a_1(1-\alpha)}{d_1}-1 & \frac{a_1\alpha}{d_1} & 0 & \cdots & \cdots & 0 \\ \frac{a_2(\alpha)}{d_2} & \frac{a_2(1-2\alpha)}{d_2}-1 & \frac{a_2(\alpha)}{d_2} & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \ddots & \ddots & 0 \\ \vdots & & & & & \vdots \\ 0 & \cdots & & & \frac{a_N(\alpha)}{d_N} & \frac{a_N(1-\alpha)}{d_N}-1 \end{pmatrix}$$

where $d_1 = (1+(1-\alpha)x_1+\alpha x_2)^2, d_2 = (1+\alpha x_1+(1-2\alpha)x_2+\alpha x_3)^2, ..., d_N = (1+\alpha x_{N-1}+(1-\alpha)x_N)^2$.

evaluated at $(0, a_1-1, ..., a_N-1)$ is invertible, i.e. we need to show the determinant is not equal to 0. Evaluation of the Jacobian at this point gives us

$$\frac{\partial g_i}{\partial x_j}(0, a_1-1, ..., a_N-1) = \begin{pmatrix} \frac{1}{a_1}-1 & 0 & & \cdots & 0 \\ 0 & \frac{1}{a_2}-1 & 0 & \cdots & 0 \\ \vdots & & \ddots & \ddots & \vdots \\ 0 & & & \frac{1}{a_{N-1}}-1 & 0 \\ 0 & \cdots & & 0 & \frac{1}{a_N}-1 \end{pmatrix}$$

We see that

$$\det\left(\frac{\partial g_i}{\partial x_j}(0, a_1-1, ..., a_N-1)\right) = \left(\frac{1}{a_1}-1\right) \times \left(\frac{1}{a_2}-1\right) \times \cdots \times \left(\frac{1}{a_N}-1\right)$$

which is non-zero because the a_i's are greater than one. Therefore, the implicit function theorem is satisfied, and by this we have an open set $\mathcal{U} \subset \mathbb{R}$ that contains 0, an open set $\mathcal{V} \subset \mathbb{R}^N$ that contains $(a_1-1, \cdots, a_N-1)$, and a map $\phi : \mathcal{U} \to \mathcal{V}$ such that

$$\{(\alpha, \phi(\alpha)) : \alpha \in \mathcal{U}\} = \{(\alpha, \mathbf{x}) \in \mathcal{U} \times \mathcal{V} : g(\alpha, \mathbf{x}) = (0, 0, \cdots, 0)\}$$

In other words, for all α sufficiently close to 0, the map F has a fixed point.

$\square$

5.3 Banach Fixed Point Theorem

Let (X, d) be a non-empty complete metric space. Let $T : X \to X$ be a contraction mapping on X, i.e. there is a $q \in \mathbb{R}^+$, where $q < 1$, such that

$$d(T(x), T(y)) \leq q \cdot d(x, y)$$

for all $x, y \in X$. Then T has a unique, stable fixed point in X.

5.4 Application to Spatial Beverton-Holt Model

Claim: F_α has a stable, non-trivial fixed point.

Proof. We need to show F_α is a contraction mapping. Notice that $|F_\alpha(x_1, \cdots, x_N) - F_\alpha(y_1, \cdots, y_N)|$ equals

$|(\frac{a_1[(1-\alpha)x_1+\alpha x_2]}{1+(1-\alpha)x_1+\alpha x_2} - \frac{a_1[(1-\alpha)y_1+\alpha y_2]}{1+(1-\alpha)y_1+\alpha y_2}, \frac{a_2[\alpha x_1+(1-2\alpha)x_2+\alpha x_3]}{1+\alpha x_1+(1-2\alpha)x_2+\alpha x_3} - \frac{a_2[\alpha y_1+(1-2\alpha)y_2+\alpha y_3]}{1+\alpha y_1+(1-2\alpha)y_2+\alpha y_3}, \cdots,$

$\frac{a_N[\alpha x_{N-1}+(1-\alpha)x_N]}{1+\alpha x_{N-1}+(1-\alpha)x_N} - \frac{a_N[\alpha y_{N-1}+(1-\alpha)y_N]}{1+\alpha y_{N-1}+(1-\alpha)y_N})|$

$\leq \frac{a_1(1-\alpha)+a_2\alpha}{(1+(1-\alpha)x_1+\alpha x_2)(1+(1-\alpha)y_1+\alpha y_2)}|x_1 - y_1|$
$+ \frac{a_1\alpha+a_2(1-2\alpha)+a_3\alpha}{(1+\alpha x_1+(1-2\alpha)x_2+\alpha x_3)(1+\alpha y_1+(1-2\alpha)y_2+\alpha y_3)}|x_2 - y_2| +$
$\cdots + \frac{a_{N-1}(1-\alpha)+a_N\alpha}{(1+(1-\alpha)x_{N-1}+\alpha x_N)(1+(1-\alpha)y_{N-1}+\alpha y_N)}|x_N - y_N|$

$< \frac{a_1(1-\alpha)}{(1+(1-\alpha)x_1+\alpha x_2)(1+(1-\alpha)y_1+\alpha y_2)}|x_1 - y_1|$
$+ \frac{a_2(1-2\alpha)}{(1+\alpha x_1+(1-2\alpha)x_2+\alpha x_3)(1+\alpha y_1+(1-2\alpha)y_2+\alpha y_3)}|x_2 - y_2|$
$+ \frac{a_N(1-\alpha)}{(1+(1-\alpha)x_{N-1}+...+\alpha x_N)(1+(1-\alpha)y_{N-1}+\alpha y_N)}|x_N - y_N|$

Let X be that subset of $\mathcal{R}^N$ where $(x_1, \cdots, x_N) \in X)$ if and only if

$$(1 + (1-\alpha)x_1 + \alpha x_2) \geq \sqrt{a}_1$$
$$(1 + \alpha x_{i-1} + (1-2\alpha)x_i + \alpha x_{i+1}) \geq \sqrt{a}_i \quad i = 2, \cdots, N-1$$
$$(1 + (1-\alpha)x_{N-1} + \alpha x_N) \geq \sqrt{a}_N$$

Then, if **x**,**y** $\in X$ we see from above that

$|$**F(x) - F(y)**$| < (1-\alpha)|x_1 - y_1| + (1-2\alpha)|x_2 - y_2| + \cdots + (1-\alpha)|x_N - y_N| \leq (1-2\alpha)|\mathbf{x} - \mathbf{y}|$.

Now it is left to show F_α maps X to itself. Let $\mathbf{x} \in X$ be given. Let $\mathbf{y} = \mathbf{F}_\alpha(\mathbf{x})$. Recall that

$$y_1 = \frac{a_1[(1-\alpha)x_1 + \alpha x_2]}{1 + (1-\alpha)x_1 + \alpha x_2}$$

$$y_i = \frac{a_i[(\alpha x_{i-1} + (1-2\alpha)x_i + \alpha x_{i+1}]}{1 + \alpha x_{i-1} + (1-2\alpha)x_i + \alpha x_{i+1}}, i = 2, ..., N-1$$

$$y_N = \frac{a_N[(1-\alpha)x_{N-1} + \alpha x_N]}{1 + (1-\alpha)x_{N-1} + \alpha x_N}$$

Thus,

$$\begin{aligned} 1 + (1-\alpha)y_1 + \alpha y_2 &= (1-\alpha)\frac{a_1[(1-\alpha)x_1 + \alpha x_2]}{1 + (1-\alpha)x_1 + \alpha x_2} + \alpha\frac{a_1[(1-\alpha)x_1 + \alpha x_2]}{1 + (1-\alpha)x_1 + \alpha x_2} \\ &> (1-\alpha)\frac{a_1[(1-\alpha)x_1 + \alpha x_2]}{1 + (1-\alpha)x_1 + \alpha x_2}. \end{aligned}$$

Consider g such that $g(x) = \frac{x}{1+x}$. Notice g is positive and increasing for $x > 0$. We see we have $(1-\alpha)(a_1)g((1-\alpha)x_1+\alpha x_2)$. Since $x \in X$, we know $g((1-\alpha)x_1+\alpha x_2) > g(\sqrt{a}_1 - 1) = 1 - \frac{1}{\sqrt{a}_1}$. Thus,

$$1 + (1-\alpha)y_1 + \alpha y_2 > (1-\alpha)(a_1)(1 - \frac{1}{\sqrt{a}_1}) = (1-\alpha)\sqrt{a_1}(\sqrt{a_1} - 1)$$

which is greater than $\sqrt{a}_1 - 1$ when $(1-\alpha)\sqrt{a}_1 > 1$ or $\alpha < 1 - \frac{1}{\sqrt{a}_1}$.

Similarly, we can show that

$$(1 + \alpha x_{i-1} + (1-2\alpha)x_i + \alpha x_{i+1}) \geq \sqrt{a}_i \quad i = 2, \cdots, N-1$$

$$(1 + (1-\alpha)x_{N-1} + \alpha x_N) \geq \sqrt{a}_N$$

provided $\alpha < \frac{1}{2}(1 - \frac{1}{\sqrt{a}_i}), i = 2, ..., N-1$ and $\alpha < 1 - \frac{1}{\sqrt{a}_N}$, respectively.

Therefore, F_α is a contraction mapping in X when

$$\alpha < \min \begin{pmatrix} 1 - \frac{1}{\sqrt{a}_1} & i = 1 \\ \frac{1}{2}(1 - \frac{1}{\sqrt{a}_i}) & i = 2, \cdots, N-1 \\ 1 - \frac{1}{\sqrt{a}_N} & i = N \end{pmatrix}$$

and therefore has a unique, stable fixed point in X. □

6 Conclusion

In this paper, we found that previous results for the Sigmoid Beverton-Holt with a periodically-varying growth rate could be extended to a general class of functions. In particular, we constructed a class $\mathcal{U}_l$ such that for all sequences of functions in $\mathcal{U}_l$, there exists a periodic orbit for any x_0 in the interval (B, ∞). This class includes periodically forced Sigmoid Beverton-Holt functions with certain parameters. In particular, it includes not only Sigmoid Beverton-Holts with one non-trivial fixed point, often known as the carrying capacity, but also includes those that exhibit an Alle effect as well.

As extensions, we first considered the case of a randomly-varying environment, in which a_n and δ_n were taken from a random distribution. We discovered that there exists a unique invariant density to which all other density distributions on the state variable converge. This extended results proven by Sacker and Haskell [7] and Bezandry, Diagana and Elaydi [8].

We also noted spatial considerations, and seeing as none had previously existed, constructed a Sigmoid Beverton-Holt model with $\delta = 1$ with regards to a spatial component. To achieve this we looked at a one-dimensional case in which the populations lie in a line of boxes and move between boxes according to a constant rate α. We first used the implicit function theorem to show there exists a non-trivial fixed point. We then followed with the stronger Banach fixed point theorem and showed that this non-trivial fixed point is unique and stable.

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