



A nonautonomous Beverton–Holt equation of higher order



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ARTICLE INFO

Article history:

Received 27 April 2017

Available online 4 August 2017

Submitted by J. Shi

Keywords:

Beverton–Holt equation

Periodic environment

Logistic substitution

Matrix difference system

Periodic solution

ABSTRACT

In this paper, we discuss a certain nonautonomous Beverton–Holt equation of higher order. After a brief introduction to the classical Beverton–Holt equation and recent results, we solve the higher-order Beverton–Holt equation by rewriting the recurrence relation as a difference system of order one. In this process, we examine the existence and uniqueness of a periodic solution and its global attractivity. We continue our analysis by studying the corresponding second Cushing–Henson conjecture, i.e., by relating the average of the unique periodic solution to the average of the carrying capacity.

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1. Autonomous Beverton–Holt model

The autonomous Beverton–Holt difference equation is given by [2]

$$z_{n+1} = \frac{\mu K z_n}{K + (\mu - 1)z_n}, \quad n \in \mathbb{N}_0, \quad (1)$$

where $\mu > 1$ and $K > 0$ for all $n \in \mathbb{N}_0$. The constant K represents the carrying capacity, and $\mu > 1$ is the inherent growth rate [7]. The equilibrium point is $\bar{z} = K$, which is globally asymptotically stable. Beverton and Holt introduced their population model in the context of fisheries in 1957, and it still attracts interest in various fields such as biology, economy and social sciences, see [1,2,9,12].

In order to include seasonally changing environments, the periodically forced Beverton–Holt equation was introduced as

$$z_{n+1} = \frac{\mu K_n z_n}{K_n + (\mu - 1)z_n}, \quad n \in \mathbb{N}_0, \quad (2)$$

where the positive carrying capacity K is now assumed to be ω -periodic for some $\omega \in \mathbb{N}$, i.e., $K_{n+\omega} = K_n$ for all $n \in \mathbb{N}_0$.

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In 2002, Cushing and Henson [8] proposed the following two conjectures for (2).

Theorem 1. Equation (2) has a unique positive ω -periodic solution which is globally asymptotically stable on \mathbb{N}_0 .

Theorem 2. The average of the unique ω -periodic solution \bar{z} of (2) is strictly less than the average of the periodic carrying capacity, i.e.,

$$\frac{1}{\omega} \sum_{i=0}^{\omega-1} \bar{z}_i < \frac{1}{\omega} \sum_{i=0}^{\omega-1} K_i. \quad (3)$$

Biologically, Theorem 2 means that the introduction of a periodic environment is deleterious to the population.

In 2004, Kocić [10] proved the Cushing–Henson conjectures for a more general case of (2) with the assumption that K is bounded. In 2005, Kon [11] proved the second conjecture for

$$z(n+1) = z(n)g\left(\frac{z(n)}{K(n)}\right), \quad n \in \mathbb{N}_0,$$

where $z(0) = z_0$ and $g: \mathbb{R}^+ \rightarrow \mathbb{R}^+$ is continuous and satisfies the conditions

- i) $g(1) = 1$,
- ii) $g(z) > 1$ for all $z \in (0, 1)$ and $g(z) < 1$ for all $z \in (1, \infty)$,
- iii) $K_{n+\omega} = K_n > 0$ for some $\omega \in \mathbb{N}$ and all $n \in \mathbb{N}_0$.

In [6], the authors proved the conjectures for a periodic time scales setting, and in [3], the quantum calculus case was presented. In [5], the authors considered the periodically forced Beverton–Holt equation with periodic growth rate. This describes a population with seasonal changing life cycles and reads as

$$z_{n+1} = \frac{\mu_n K_n z_n}{K_n + (\mu_n - 1)z_n}, \quad n \in \mathbb{N}_0, \quad (4)$$

where both the growth rate $\mu > 1$ and the carrying capacity $K > 0$ are assumed to be ω -periodic. The authors provided a proof for the existence and uniqueness of an ω -periodic solution of (4) that is globally attractive. They also provided a counterexample for the classical second Cushing–Henson conjecture, which biologically means that a periodic environment can be beneficial for a population with seasonal life cycles.

2. A higher-order Beverton–Holt model

In this paper, we discuss the Beverton–Holt equation of order $k \in \mathbb{N}$ with periodic coefficients given by

$$z_{n+k} = \frac{\mu_n K_n z_n}{K_n + (\mu_n - 1)z_n}, \quad n \in \mathbb{N}_0, \quad (5)$$

where $\mu > 1$ and $K > 0$ are ω -periodic functions with $\omega > k$, and the initial conditions are

$$z_0 = (z_0, z_1, \dots, z_{k-1})^T, \quad z_i \geq 0.$$

Remark 3. We notice that (5) is not equivalent to

$$z_n = \frac{\mu_n K_n z_{n-k}}{K_n + (\mu_n - 1)z_{n-k}}$$

unless $\omega = k$.

Using the change of variable $\alpha = \frac{\mu-1}{\mu}$ and the substitution $u = 1/z$, we transform (5) into the linear recurrence relation

$$u_{n+k} = (1 - \alpha_n)u_n + \frac{\alpha_n}{K_n}. \quad (6)$$

Since $\mu > 1$, we have $\alpha \in (0, 1)$. We now apply the identity

$$u_{n+k} = \sum_{j=0}^k \binom{k}{j} \Delta^j u_n$$

to see that (6) is the same as the linear difference equation

$$\sum_{j=0}^k \binom{k}{j} \Delta^j u_n = (1 - \alpha_n)u_n + \frac{\alpha_n}{K_n}, \quad (7)$$

i.e.,

$$\sum_{j=1}^k \binom{k}{j} \Delta^j u_n + \alpha_n u_n = \frac{\alpha_n}{K_n}.$$

We introduce $\mathbf{y} = (y_1, y_2, \dots, y_k)^T$, where

$$y_i(n) = \Delta^{i-1} u_n \quad \text{for all } i \in \{1, 2, \dots, k\} \quad \text{and } n \in \mathbb{N}_0.$$

The components of \mathbf{y} satisfy the relation

$$\begin{aligned} \Delta y_i(n) &= y_{i+1}(n) \quad \text{for } i \in \{1, 2, \dots, k-1\}, \\ \Delta y_k(n) &= \Delta^k u_n = -\alpha_n y_1 - \sum_{j=1}^{k-1} \binom{k}{j} y_{j+1}(n) + \frac{\alpha_n}{K_n}. \end{aligned}$$

In vector notation, we arrive at the system

$$\Delta \mathbf{y}(n) = A(n) \mathbf{y}(n) + \mathbf{g}(n), \quad \mathbf{y}(0) = \mathbf{y}_0, \quad (8)$$

where $A(n)$ is the $k \times k$ matrix of the form

$$A(n) = \begin{pmatrix} 0 & 1 & 0 & 0 & \dots & 0 \\ 0 & 0 & 1 & 0 & \dots & 0 \\ 0 & 0 & 0 & 1 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & 1 \\ -\alpha_n & -\binom{k}{1} & -\binom{k}{2} & -\binom{k}{3} & \dots & -\binom{k}{k-1} \end{pmatrix} \quad (9)$$

and

$$\mathbf{g}(n) = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \\ \frac{\alpha_n}{K_n} \end{pmatrix} \quad \text{with initial conditions} \quad \mathbf{y}_0 = \begin{pmatrix} u_0 \\ \Delta u_0 \\ \vdots \\ \Delta^{k-1} u_0 \end{pmatrix}.$$

Before we give the solution of (9), let us first study the matrix $A(n)$ in detail.

Lemma 4. For each $n \in \mathbb{N}_0$, the matrix $A(n)$ is invertible, and

$$\det(A(n)) = (-1)^k \alpha_n.$$

Proof. To see the statement, recall $\alpha(n) \in (0, 1)$ for all $n \in \mathbb{N}_0$. By using a cofactor expansion across the first column, we obtain

$$\det A(n) = (-1)^{k+1} (-\alpha_n) \det I_{k-1} = (-1)^k \alpha_n \neq 0,$$

where I is the identity matrix with the indicated dimension. \square

Lemma 5. $A(n)$ has k distinct eigenvalues, the only real ones being

$$-1 + \sqrt[k]{1 - \alpha_n} \quad \text{if } k \text{ is odd}$$

and

$$-1 - \sqrt[k]{1 - \alpha_n} \quad \text{and} \quad -1 + \sqrt[k]{1 - \alpha_n} \quad \text{if } k \text{ is even.}$$

Moreover,

$$\det(\lambda I_k - A(n)) = (1 + \lambda)^k + \alpha_n - 1. \quad (10)$$

Proof. The matrix $\lambda I_k - A$ is of the form

$$\begin{pmatrix} \lambda & -1 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & \lambda & -1 & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & 0 & \lambda & -1 \\ \alpha_n & \binom{k}{1} & \binom{k}{2} & \binom{k}{3} & \dots & \binom{k}{k-3} & \binom{k}{k-2} & \binom{k}{k-1} + \lambda \end{pmatrix}.$$

Using $k - 1$ row operations, we obtain the corresponding echelon form

$$\begin{pmatrix} \lambda & -1 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & \lambda & -1 & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & 0 & \lambda & -1 \\ 0 & 0 & 0 & 0 & \dots & 0 & 0 & p(n) \end{pmatrix},$$

where

$$p(n) = \binom{k}{k-1} + \lambda + \frac{\alpha_n}{\lambda^{k-1}} + \sum_{i=1}^{k-2} \frac{\binom{k}{i}}{\lambda^{k-(i+1)}}.$$

Hence

$$\begin{aligned}\det(\lambda I_k - A(n)) &= \lambda^{k-1} \left(\lambda + \frac{\alpha_n}{\lambda^{k-1}} + \sum_{i=1}^{k-1} \frac{\binom{k}{i}}{\lambda^{k-(i+1)}} \right) \\ &= \alpha_n + \sum_{i=1}^k \binom{k}{i} \lambda^i = \alpha_n - 1 + \sum_{i=0}^k \binom{k}{i} \lambda^i \\ &= \alpha_n - 1 + (1 + \lambda)^k.\end{aligned}$$

Thus, the eigenvalues of $A(n)$ are the solutions of

$$(1 + \lambda)^k = 1 - \alpha_n,$$

and recalling that $\alpha_n \in (0, 1)$ yields the result. \square

Corollary 6. *The matrix $I_k + A(n)$ is invertible for all $n \in \mathbb{N}_0$.*

Proof. Since, by (10) with $\lambda = -1$,

$$\det(-I_k - A(n)) = \alpha_n - 1 \neq 0,$$

$I_k + A(n)$ is invertible. \square

Lemma 7. *If we put $\mathbf{e}_1 = (1, 0, \dots, 0)^T$, $\mathbf{e}_k = (0, \dots, 0, 1)^T \in \mathbb{R}^k$, then*

$$A^{-1}(n)\mathbf{e}_k = -\frac{1}{\alpha_n}\mathbf{e}_1.$$

Proof. Note that $A^{-1}(n)\mathbf{e}_k$ is the k th column of $A^{-1}(n)$. By Cramer's rule, we have

$$A^{-1}(n)\mathbf{e}_k = \frac{1}{\det A(n)}(C_{k1}, C_{k2}, \dots, C_{kk})^T,$$

where $C_{ki} = (-1)^{k+i}A_{ki}(n)$ and $A_{ki}(n)$ is the determinant of $A(n)$ when the k th row and the i th column are removed. By the construction of A , we see that $C_{ki} = 0$ for $i > 1$ and $C_{k1} = (-1)^{k+1} \det I_{k-1} = (-1)^{k+1}$. By Lemma 4, $\det A(n) = (-1)^k \alpha_n$, and this yields the result. \square

Definition 8. For any matrix sequence B such that $I + B(n)$ is invertible for all $n \in \mathbb{N}_0$, we define the *matrix exponential*

$$e_B(n, m) = \prod_{i=m}^{n-1} (I + B(i)) = (I + B(n-1))(I + B(n-2)) \cdots (I + B(m))$$

if $n > m$, $e_B(n, n) = I$, and $e_B(n, m) = e_B^{-1}(m, n)$ if $n < m$.

The following result will be useful.

Lemma 9 (See [4, Theorem 5.23]). *If B is a matrix sequence such that $I + B(n)$ is invertible for all $n \in \mathbb{N}_0$ and if $a, b, n \in \mathbb{N}_0$ with $a < b$, then*

$$\sum_{i=a}^{b-1} e_B(n, i+1) B_i = e_B(n, a) - e_B(n, b)$$

and

$$\sum_{n=a}^{b-1} e_B(n, i) B_n = e_B(b, i) - e_B(a, i).$$

We will also frequently use the following result.

Lemma 10. *If B is a matrix sequence such that $I + B(n)$ is invertible for all $n \in \mathbb{N}_0$ and such that $B(n + \omega) = B(n)$ for some $\omega \in \mathbb{N}$, then*

$$e_B(n + \omega, m + \omega) = e_B(n, m) \quad \text{for all } m, n \in \mathbb{N}_0. \quad (11)$$

Proof. If $n > m$, then

$$\begin{aligned} e_B(n + \omega, m + \omega) &= \prod_{i=m+\omega}^{n+\omega-1} (I + B(i)) = \prod_{i=m}^{n-1} (I + B(i + \omega)) \\ &= \prod_{i=m}^{n-1} (I + B(i)) = e_B(n, m). \end{aligned}$$

Next, we have $e_B(n + \omega, n + \omega) = I = e_B(n, n)$. If $m > n$, then

$$e_B(n + \omega, m + \omega) = e_B^{-1}(m + \omega, n + \omega) = e_B^{-1}(m, n) = e_B(n, m).$$

The proof is complete. \square

The next result follows immediately from [Definition 8](#).

Lemma 11. *If B is a constant matrix such that $I + B$ is invertible, then*

$$e_B(n + j, n) = \prod_{i=n}^{n+j-1} (I + B) = (I + B)^j = e_B(m + j, m) = e_B(j, 0)$$

for all $m, n, j \in \mathbb{N}_0$.

We recall that A defined by [\(9\)](#) is such that $I_k + A(n)$ is invertible for all $n \in \mathbb{N}_0$ (see [Corollary 6](#)), and therefore e_A is well defined (see [Definition 8](#)). In the remainder of this section, we now study the function e_A . Here and in the sequel, by convention, any “empty” sum is zero and any “empty” product is one, i.e.,

$$\sum_{i=a}^b x_i = 0 \quad \text{and} \quad \prod_{i=a}^b x_i = 1 \quad \text{if } a > b.$$

Lemma 12. *For*

$$m = sk + t \quad \text{with } 0 \leq t < k \quad \text{and } s \in \mathbb{N}_0,$$

we have

$$\mathbf{e}_1^T e_A(n+m, n) = \mathbf{b}^T(n, m) \quad \text{for all } n \in \mathbb{N}_0,$$

where \mathbf{e}_1 is as in Lemma 7 and $\mathbf{b} = (b_1, b_2, \dots, b_k)^T \in \mathbb{R}^k$ with

$$b_j(n, m) = \begin{cases} \binom{t}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+n+t}) & \text{if } 1 \leq j \leq t+1 \\ 0 & \text{if } j > t+1. \end{cases}$$

Proof. We prove the statement by induction on m . For $m = 1$, i.e., $s = 0$, $t = 1$, we have

$$\begin{aligned} & \mathbf{e}_1^T e_A(n+1, n) \\ &= (1, 0, 0, \dots, 0) \begin{pmatrix} 1 & 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ -\alpha_n & -\binom{k}{1} & \dots & 0 & -\binom{k}{k-2} & 1 - \binom{k}{k-1} \end{pmatrix} \\ &= (1, 1, 0, \dots, 0, 0) = \mathbf{c}^T, \end{aligned}$$

where

$$\mathbf{c}_j = \begin{cases} \binom{1}{j-1} & \text{if } 1 \leq j \leq 2 \\ 0 & \text{if } j > 2. \end{cases}$$

Therefore $\mathbf{c} = \mathbf{b}(n, 1)$, and the statement holds for $m = 1$. Assume the statement is true for $m \in \mathbb{N}$. First note that

$$\mathbf{e}_1^T e_A(n+m+1, n) = \mathbf{e}_1^T e_A(n+1+m, n+1) e_A(n+1, n).$$

We consider two cases: $m+1 \pmod{k} \neq 0$ and $m+1 \pmod{k} = 0$.

Case 1: Assume $m+1 \pmod{k} \neq 0$, i.e., $t+1 < k$. We have

$$\begin{aligned} & \mathbf{e}_1^T e_A(n+m+1, n) = \mathbf{b}^T(n+1, m) e_A(n+1, n) \\ &= (b_1, \dots, b_{t+1}, 0, \dots, 0) \\ &\quad \times \begin{pmatrix} 1 & 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ -\alpha_n & -\binom{k}{1} & \dots & -\binom{k}{k-3} & -\binom{k}{k-2} & 1 - \binom{k}{k-1} \end{pmatrix} \\ &= (b_1, b_1 + b_2, b_2 + b_3, \dots, b_t + b_{t+1}, b_{t+1}, 0, \dots, 0) = \mathbf{c}^T, \end{aligned}$$

where

$$\mathbf{c}_j = \begin{cases} b_1(n+1, m) & \text{if } j = 1 \\ b_{j-1}(n+1, m) + b_j(n+1, m) & \text{if } 2 \leq j \leq t+2 \\ 0 & \text{if } j > t+2. \end{cases}$$

Note that

$$\begin{aligned}
& b_{j-1}(n+1, m) + b_j(n+1, m) \\
&= \binom{t}{j-2} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) + \binom{t}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) \\
&= \binom{t+1}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+n+(t+1)}).
\end{aligned}$$

Therefore, $\mathbf{c} = \mathbf{b}(n, m+1)$.

Case 2: Assume $m+1 \pmod{k} = 0$, i.e., $t+1 = k$. We have

$$\begin{aligned}
\mathbf{e}_1^T e_A(n+m+1, n) &= \mathbf{b}^T(n+1, m) e_A(n+1, n) \\
&= (b_1, \dots, b_k) \begin{pmatrix} 1 & 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & 1 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ -\alpha_n & -\binom{k}{1} & \dots & 0 & -\binom{k}{k-2} & 1 - \binom{k}{k-1} \end{pmatrix} \\
&= \left(b_1 - \alpha_n b_k, \quad b_1 + b_2 - \binom{k}{1} b_k, \quad \dots, \quad b_{k-1} + b_k - \binom{k}{k-1} b_k \right) \\
&= \mathbf{c}^T,
\end{aligned}$$

where

$$\begin{aligned}
c_1 &= b_1 - \alpha_n b_k \\
&= \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) - \alpha_n \binom{k-1}{k-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) \\
&= \left(\prod_{i=0}^{s-1} (1 - \alpha_{ik+n+k}) \right) (1 - \alpha_n) \\
&= \left(\prod_{i=1}^s (1 - \alpha_{ik+n}) \right) (1 - \alpha_n) = \prod_{i=0}^s (1 - \alpha_{ik+n})
\end{aligned}$$

and, for $j > 1$,

$$\begin{aligned}
c_j &= b_{j-1} + b_j - \binom{k}{j-1} b_k \\
&= \binom{k-1}{j-2} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) + \binom{k-1}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) \\
&\quad - \binom{k}{j-1} \binom{k-1}{k-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) \\
&= \binom{k}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) - \binom{k}{j-1} \prod_{i=0}^{s-1} (1 - \alpha_{ik+(n+1)+t}) \\
&= 0.
\end{aligned}$$

This is equivalent to the entries in \mathbf{b} . The proof is complete. \square

The following corollary follows from the proof of [Lemma 12](#).

Corollary 13. We have $e_1^T e_A(n + sk, n) = \prod_{i=0}^{s-1} (1 - \alpha_{n+ik}) e_1^T$.

3. Periodic solutions

Now we return to (8). Under our conditions, the solution of (8) is given in [4] by

$$\mathbf{y}(n) = e_A(n, 0) \mathbf{y}_0 + \sum_{i=0}^{n-1} e_A(n, i+1) \mathbf{g}(i). \quad (12)$$

Theorem 14 (Existence and Uniqueness). If α and K are ω -periodic and $I_k - e_A(n + \omega, n)$ is invertible for all $n \in \mathbb{N}_0$, then (5) has a unique ω -periodic solution that is globally attracting all positive solutions.

Proof. Assume (5) has an ω -periodic solution \bar{z} with $\bar{z}_0 > 0$. Then $\bar{z}_n > 0$ for all $n \in \mathbb{N}_0$ and $\bar{u} = 1/\bar{z}$ is a positive ω -periodic solution of (6). Then $\bar{\mathbf{y}} = (\bar{u}, \Delta \bar{u}, \Delta^2 \bar{u}, \dots, \Delta^{k-1} \bar{u})$ is an ω -periodic solution of (8). Hence, using (12), we obtain

$$\begin{aligned} \bar{\mathbf{y}}(n) &= \bar{\mathbf{y}}(n + \omega) = e_A(n + \omega, 0) \bar{\mathbf{y}}_0 + \sum_{i=0}^{n+\omega-1} e_A(n + \omega, i+1) \mathbf{g}(i) \\ &= e_A(n + \omega, n) e_A(n, 0) \bar{\mathbf{y}}_0 + \sum_{i=0}^{n-1} e_A(n + \omega, n) e_A(n, i+1) \mathbf{g}(i) \\ &\quad + \sum_{i=n}^{n+\omega-1} e_A(n + \omega, n) e_A(n, i+1) \mathbf{g}(i) \\ &= e_A(n + \omega, n) \bar{\mathbf{y}}(n) + e_A(n + \omega, n) \sum_{i=n}^{n+\omega-1} e_A(n, i+1) \mathbf{g}(i). \end{aligned}$$

Thus,

$$\bar{\mathbf{y}}(n) = [I_k - e_A(n + \omega, n)]^{-1} e_A(n + \omega, n) \sum_{i=n}^{n+\omega-1} e_A(n, i+1) \mathbf{g}(i).$$

Using the identity

$$(I_k - X)^{-1} X = (X^{-1}(I_k - X))^{-1} = (X^{-1} - I_k)^{-1},$$

where X is any invertible matrix, and putting

$$\Lambda_n = [e_A(n, n + \omega) - I_k]^{-1},$$

we have

$$\bar{\mathbf{y}}(n) = \Lambda_n \sum_{i=n}^{n+\omega-1} e_A(n, i+1) \mathbf{g}(i). \quad (13)$$

Thus, $\bar{u}_n = e_1^T \bar{\mathbf{y}}(n)$ and $\bar{z}_n = 1/\bar{u}_n$ for all $n \in \mathbb{N}_0$.

Conversely, define $\bar{\mathbf{y}}$ by (13) and put $\bar{u}_n = \mathbf{e}_1^T \bar{\mathbf{y}}(n)$. Then

$$\begin{aligned}\bar{\mathbf{y}}(n + \omega) &= \Lambda_{n+\omega} \sum_{i=n+\omega}^{n+2\omega-1} e_A(n + \omega, i + 1) \mathbf{g}(i) \\ &= \Lambda_n \sum_{i=n}^{n+\omega-1} e_A(n + \omega, i + 1 + \omega) \mathbf{g}(i + \omega) \\ &= \Lambda_n \sum_{i=n}^{n+\omega-1} e_A(n, i + 1) \mathbf{g}(i) = \bar{\mathbf{y}}(n)\end{aligned}$$

and

$$\begin{aligned}\bar{\mathbf{y}}(n + k) &= \Lambda_{n+k} \sum_{i=n+k}^{n+k+\omega-1} e_A(n + k, i + 1) \mathbf{g}(i) \\ &= \Lambda_{n+k} \sum_{i=n}^{n+\omega-1} e_A(n + k, i + 1) \mathbf{g}(i) + \Lambda_{n+k} \sum_{i=n+\omega}^{n+k+\omega-1} e_A(n + k, i + 1) \mathbf{g}(i) \\ &\quad - \Lambda_{n+k} \sum_{i=n}^{n+k-1} e_A(n + k, i + 1) \mathbf{g}(i) \\ &= \Lambda_{n+k} e_A(n + k, n) \Lambda_n^{-1} \bar{\mathbf{y}}(n) \\ &\quad + \Lambda_{n+k} \sum_{i=n}^{n+k-1} [e_A(n + k, i + 1 + \omega) - e_A(n + k, i + 1)] \mathbf{g}(i) \\ &= \Lambda_{n+k} [e_A(n + k, n + \omega) - e_A(n + k, n)] \bar{\mathbf{y}}(n) \\ &\quad + \Lambda_{n+k} \sum_{i=n}^{n+k-1} [e_A(n + k, i + 1 + \omega) - e_A(n + k, i + 1)] \mathbf{g}(i) \\ &= \Lambda_{n+k} [e_A(n + k, n + k + \omega) e_A(n + k + \omega, n + \omega) - e_A(n + k, n)] \bar{\mathbf{y}}(n) \\ &\quad + \Lambda_{n+k} \sum_{i=n}^{n+k-1} [e_A(n + k, n + k + \omega) e_A(n + k + \omega, i + 1 + \omega) \\ &\quad - e_A(n + k, i + 1)] \mathbf{g}(i) \\ &= \Lambda_{n+k} \Lambda_{n+k}^{-1} e_A(n + k, n) \bar{\mathbf{y}}(n) + \Lambda_{n+k} \sum_{i=n}^{n+k-1} \Lambda_{n+k}^{-1} e_A(n + k, i + 1) \mathbf{g}(i) \\ &= e_A(n + k, n) \bar{\mathbf{y}}(n) + \sum_{i=n}^{n+k-1} e_A(n + k, i + 1) \mathbf{g}(i).\end{aligned}$$

Then, using Lemma 12, we have

$$\begin{aligned}\bar{u}_{n+k} &= \mathbf{e}_1^T \bar{\mathbf{y}}(n + k) = \mathbf{e}_1^T e_A(n + k, n) \bar{\mathbf{y}}(n) + \mathbf{e}_1^T \sum_{i=n}^{n+k-1} e_A(n + k, i + 1) \mathbf{g}(i) \\ &= \mathbf{b}^T(n, k) \bar{\mathbf{y}}(n) + \sum_{i=n}^{n+k-1} \frac{\alpha_i}{K_i} \mathbf{e}_1^T e_A(n + k, i + 1) \mathbf{e}_k\end{aligned}$$

$$\begin{aligned}
&= (1 - \alpha_n)\bar{u}_n + \sum_{i=1}^k \frac{\alpha_{i+n-1}}{K_{i+n-1}} \mathbf{e}_1^T e_A(n+k, i+n) \mathbf{e}_k \\
&= (1 - \alpha_n)\bar{u}_n + \sum_{i=1}^k \frac{\alpha_{i+n-1}}{K_{i+n-1}} \mathbf{b}^T(n+i, k-i) \mathbf{e}_k \\
&= (1 - \alpha_n)\bar{u}_n + \frac{\alpha_n}{K_n}.
\end{aligned}$$

Thus, \bar{u} is an ω -periodic solution of (6), and so $\bar{z} = 1/\bar{u}$ is an ω -periodic solution of (5).

It is left to show that the solution \bar{z} is globally asymptotically stable. Let $\bar{u} = 1/\bar{z}$. Let z be any positive solution of (5) and put $u = 1/z$. We will show that it is enough to prove

$$u_n - \bar{u}_n \rightarrow 0 \quad \text{as } n \rightarrow \infty. \quad (14)$$

Assume (14) holds. Note that

$$|\bar{u}_n| \geq \min_{0 \leq i \leq \omega-1} |\bar{u}_i| =: m > 0 \quad \text{for all } n \in \mathbb{N}_0.$$

Let $\varepsilon > 0$. Because of (14), there exists $N \in \mathbb{N}$ such that

$$|u_n - \bar{u}_n| < \min \left\{ \frac{\varepsilon m^2}{2}, \frac{m}{2} \right\} \quad \text{for all } n \geq N.$$

Since

$$0 < m \leq |\bar{u}_n| \leq |\bar{u}_n - u_n| + |u_n| < \frac{m}{2} + |u_n|,$$

i.e.,

$$|u_n| > \frac{m}{2} \quad \text{for all } n \geq N,$$

we get

$$|z_n - \bar{z}_n| = \left| \frac{1}{u_n} - \frac{1}{\bar{u}_n} \right| = \frac{|u_n - \bar{u}_n|}{|u_n| |\bar{u}_n|} \leq \frac{|u_n - \bar{u}_n|}{\frac{m}{2} \cdot m} < \varepsilon$$

for all $n \geq N$, i.e., $z_n - \bar{z}_n \rightarrow 0$ as $n \rightarrow \infty$. In summary, it is enough to prove (14). Let now $n = sk + t$ for $0 \leq t < k$. Then, using Lemma 12, we have

$$\begin{aligned}
|u_n - \bar{u}_n| &= \|\mathbf{e}_1^T \mathbf{y}(n) - \mathbf{e}_1^T \bar{\mathbf{y}}(n)\|_2 = \|\mathbf{e}_1^T e_A(n, 0)(\mathbf{y}(0) - \bar{\mathbf{y}}(0))\|_2 \\
&\leq \|\mathbf{e}_1^T e_A(n, 0)\|_2 \|\mathbf{y}(0) - \bar{\mathbf{y}}(0)\|_2 \\
&= \|\mathbf{e}_1^T e_A(n, t) e_A(t, 0)\|_2 \|\mathbf{y}(0) - \bar{\mathbf{y}}(0)\|_2 \\
&\leq \|\mathbf{e}_1^T e_A(sk + t, t)\|_2 \|e_A(t, 0)\|_2 \|\mathbf{y}(0) - \bar{\mathbf{y}}(0)\|_2 \\
&= \left\| \left(\prod_{i=0}^{s-1} (1 - \alpha_{ik+t}) \right) \mathbf{e}_1 \right\|_2 \|e_A(t, 0)\|_2 \|\mathbf{y}(0) - \bar{\mathbf{y}}(0)\|_2 \\
&= \prod_{i=0}^{s-1} (1 - \alpha_{ik+t}) \|e_A(t, 0)\|_2 \|\mathbf{y}(0) - \bar{\mathbf{y}}(0)\|_2 \rightarrow 0
\end{aligned}$$

as $n \rightarrow \infty$, i.e., $s \rightarrow \infty$, since $\|e_A(t, 0)\|_2 \leq \max_{0 \leq i \leq \omega-1} \|e_A(i, 0)\|_2$ and $\|\mathbf{y}(0) - \overline{\mathbf{y}}(0)\|_2$ are bounded, and $\alpha_i \in (0, 1)$ for all $i \in \mathbb{N}_0$ implies, together with the ω -periodicity of α , that

$$\prod_{\ell=0}^{(\omega-1)m} (1 - \alpha_\ell) = \left(\prod_{\ell=0}^{\omega-1} (1 - \alpha_\ell) \right)^m \rightarrow 0 \quad \text{as } m \rightarrow \infty.$$

This completes the proof. \square

Remark 15. The second-order Beverton–Holt equation, i.e., (5) with $k = 2$, is a discrete analogue of the second-order nonlinear differential equation

$$z''z = 2z'(z' - z) + \alpha(t)z^2 \left(1 - \frac{z}{K(t)} \right). \quad (15)$$

Note that Theorem 14 provides a method to solve (15), since the transformation $u = 1/z$ yields the second-order linear differential equation

$$u'' + 2u' + \alpha(t)u = \frac{\alpha(t)}{K(t)},$$

which can be solved using the matrix approach discussed in the proof of Theorem 14. The third-order Beverton–Holt equation, i.e., (5) with $k = 3$, is a discrete analogue of the third-order nonlinear differential equation

$$z'''z^2 = -3z^2(z'' + z') + 6(z')^2(z - z') + 6zz'z'' + \alpha(t)z^3 \left(1 - \frac{z}{K(t)} \right)$$

and can be, by applying the transformation $u = 1/z$, transformed into the third-order linear differential equation

$$u''' + 3u'' + 3u' + \alpha(t)u = \frac{\alpha(t)}{K(t)}.$$

Remark 16. It is interesting to note that the average of the periodic solution of the higher-order Beverton–Holt model is not necessarily less than the average of the periodic solution of the classical Beverton–Holt model. To see this, take for example $\alpha = 0.5$ constant, $\omega = 4$, and

$$K_0 = 20, \quad K_1 = 30, \quad K_2 = 40, \quad K_3 = 25.$$

Then the periodic solution in the classical case ($k = 1$) is

$$x_0 = 27.95, \quad x_1 = 23.31, \quad x_2 = 26.69, \quad x_3 = 31.69,$$

which gives an average of $\frac{1}{4} \sum_{i=0}^3 x_i = 27.31$, while the periodic solution for the second-order Beverton–Holt equation is

$$x_0^{(2)} = 30.00, \quad x_1^{(2)} = 26.47, \quad x_2^{(2)} = 24.00, \quad x_3^{(2)} = 28.12,$$

with an average of $\frac{1}{4} \sum_{i=0}^3 x_i^{(2)} = 27.1475$. However, if we change the values slightly to

$$K_0 = 20, \quad K_1 = 10, \quad K_2 = 30, \quad K_3 = 25,$$

then we have

$$\begin{aligned} x_0 &= 21.32, & x_1 &= 20.64, & x_2 &= 13.47, & x_3 &= 18.59, \\ x_0^{(2)} &= 25.71, & x_1^{(2)} &= 16.67, & x_2^{(2)} &= 22.50, & x_3^{(2)} &= 12.50 \end{aligned}$$

with

$$\frac{1}{4} \sum_{i=0}^3 x_i = 18.50 < 19.34 = \frac{1}{4} \sum_{i=0}^3 x_i^{(2)}.$$

It thus depends on K whether or not a delay is beneficial for the population.

4. Constant growth rate

The classical second Cushing–Henson conjecture was formulated for the case $k = 1$ with constant growth and periodic carrying capacity. It says that the average of the periodic solution is less than the average of the carrying capacity, which biologically means that the introduction of a periodic environment is deleterious for the population. In this section, we will show that this is still true if we consider the higher-order Beverton–Holt equation discussed in this paper.

Theorem 17 (*Second Cushing–Henson Conjecture*). *If the growth rate is constant and K is ω -periodic but not constant, then the unique ω -periodic solution \bar{z} of (5) satisfies the second Cushing–Henson conjecture, i.e.,*

$$\frac{1}{\omega} \sum_{i=0}^{\omega-1} \bar{z}_i < \frac{1}{\omega} \sum_{i=0}^{\omega-1} K_i. \quad (16)$$

Equality holds if and only if K is constant.

Proof. We recall that $\bar{z} = 1/\bar{u}$. We also recall that the ω -periodic solution \bar{y} is given by

$$\bar{y}(n) = \Lambda_n \sum_{i=n}^{n+\omega-1} e_A(n, i+1) g(i),$$

with (see Lemma 11)

$$\Lambda_n = [e_A(n, n+\omega) - I_k]^{-1} = [e_A(0, \omega) - I_k]^{-1} =: \Lambda.$$

Note first (use Lemma 11, Lemma 4, Lemma 9, and Cramer’s rule)

$$\begin{aligned} e_1^T \Lambda \sum_{i=n}^{n+\omega-1} e_A(n, i+1) e_k &= e_1^T \Lambda \left(\sum_{i=n}^{n+\omega-1} e_A(n, i+1) A \right) A^{-1} e_k \\ &= e_1^T \Lambda (e_A(n, n) - e_A(n, n+\omega)) A^{-1} e_k \\ &= e_1^T \Lambda (I_k - e_A(0, \omega)) A^{-1} e_k \\ &= -e_1^T \Lambda \Lambda^{-1} A^{-1} e_k \\ &= -e_1^T A^{-1} e_k = -\frac{(-1)^{k+1}}{\det A} = \frac{1}{\alpha}. \end{aligned}$$

Now we apply the Jensen inequality to arrive at

$$\begin{aligned}
\sum_{n=0}^{\omega-1} \bar{z}_n &= \sum_{n=0}^{\omega-1} \frac{1}{e_1^T \bar{y}(n)} = \sum_{n=0}^{\omega-1} \frac{1}{e_1^T \Lambda \sum_{i=n}^{n+\omega-1} e_A(n, i+1) g(i)} \\
&= \frac{1}{\alpha} \sum_{n=0}^{\omega-1} \frac{1}{\sum_{i=n}^{n+\omega-1} \frac{1}{K_i} e_1^T \Lambda e_A(n, i+1) e_k} \\
&< \frac{1}{\alpha} \sum_{n=0}^{\omega-1} \frac{\sum_{i=n}^{n+\omega-1} e_1^T \Lambda e_A(n, i+1) e_k K_i}{\left(e_1^T \Lambda \sum_{i=n}^{n+\omega-1} e_A(n, i+1) A A^{-1} e_k \right)^2} \\
&= \alpha \sum_{n=0}^{\omega-1} \sum_{i=n}^{n+\omega-1} e_1^T \Lambda e_A(n, i+1) e_k K_i \\
&= \alpha \left\{ \sum_{i=0}^{\omega-1} K_i e_1^T \Lambda \sum_{n=0}^i e_A(n, i+1) e_k + \sum_{i=\omega}^{2\omega-2} K_i e_1^T \Lambda \sum_{n=i+1-\omega}^{\omega-1} e_A(n, i+1) e_k \right\} \\
&= \alpha \left\{ \sum_{i=0}^{\omega-1} K_i e_1^T \Lambda [I_k - e_A(0, i+1)] A^{-1} e_k \right. \\
&\quad \left. + \sum_{i=\omega}^{2\omega-2} K_i e_1^T \Lambda [e_A(\omega, i+1) - e_A(i+1-\omega, i+1)] A^{-1} e_k \right\} \\
&= \alpha \left\{ \sum_{i=0}^{\omega-1} K_i e_1^T \Lambda [I_k - e_A(0, i+1)] A^{-1} e_k \right. \\
&\quad \left. + \sum_{i=0}^{\omega-1} K_i e_1^T \Lambda [e_A(\omega, i+1+\omega) - e_A(i+1, i+1+\omega)] A^{-1} e_k \right\} \\
&= \alpha e_1^T \Lambda [I_k - e_A(0, \omega)] A^{-1} e_k \sum_{i=0}^{\omega-1} K_i \\
&= -\alpha e_1^T A^{-1} e_k \sum_{i=0}^{\omega-1} K_i = \sum_{i=0}^{\omega-1} K_i.
\end{aligned}$$

Dividing this inequality by ω shows (16). \square

Example 18. Let $\omega = 4$, $k = 2$, and let the periodic carrying capacity be given by

$$K_0 = 20, \quad K_1 = 40, \quad K_2 = 30, \quad K_3 = 25.$$

The average of the carrying capacity is then 28.7500. If we choose the growth rate $\alpha = 0.5$, then we obtain the periodic solution \bar{z} as

$$\bar{z}_0 = 25.7143, \quad \bar{z}_1 = 28.5714, \quad \bar{z}_2 = 22.5000, \quad \bar{z}_3 = 33.3333,$$

which gives an average of $27.5298 < 28.7500$, see Fig. 1. The dark dots represent the values for the periodic solution, the dark line the average of the periodic solution, and the light line the average of the carrying capacity.

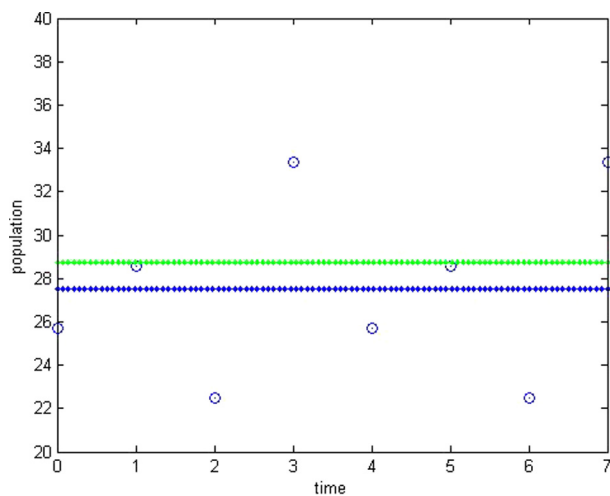


Fig. 1. The periodic solution in Example 18.

Example 19. If we change the growth rate to $\alpha = 0.2$, then we obtain the periodic solution \bar{z} as

$$\bar{z}_0 = 24.5455, \quad \bar{z}_1 = 30.0000, \quad \bar{z}_2 = 23.4783, \quad \bar{z}_3 = 31.5789,$$

which gives an average of $27.4007 < 28.7500$. Fig. 2 contains the values of this example.

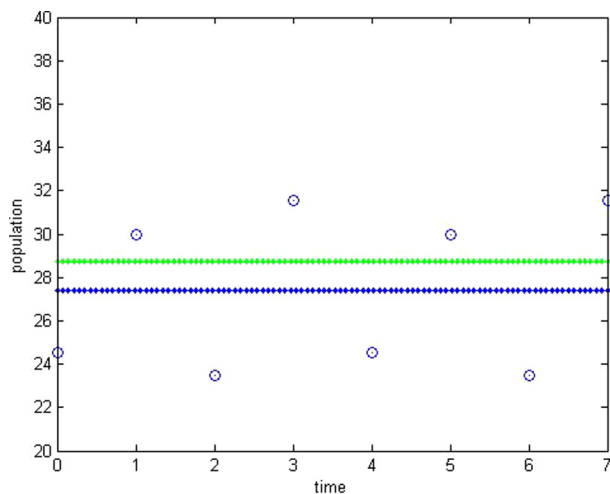


Fig. 2. The periodic solution in Example 19.

Example 20. Fig. 3 contains the information for $\alpha = 0.7$. The carrying capacity is as in Example 19. The values for the periodic solution \bar{z} are

$$\bar{z}_0 = 26.8966, \quad \bar{z}_1 = 27.3684, \quad \bar{z}_2 = 21.6667, \quad \bar{z}_3 = 35.1351,$$

which gives an average of 27.7667. This is again less than the average of the carrying capacity.

We conclude this section with the following equality.

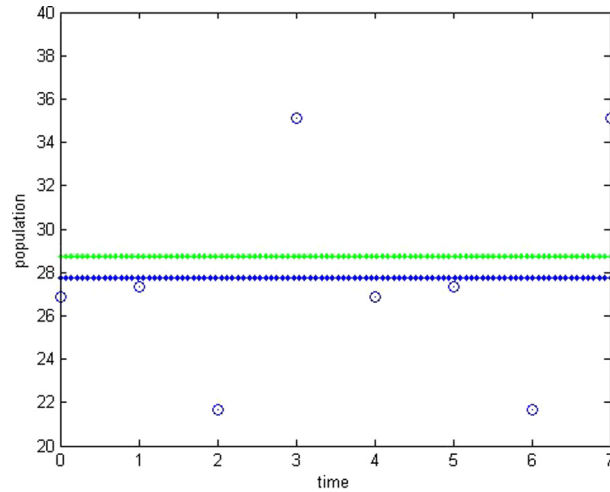


Fig. 3. The periodic solution in Example 20.

Theorem 21. If α is constant and K is ω -periodic, then the ω -periodic solution \bar{z} of (5) satisfies

$$\sum_{i=0}^{\omega-1} \frac{1}{\bar{z}_i} = \sum_{i=0}^{\omega-1} \frac{1}{K_i}.$$

Proof. We use Lemma 9, Lemma 11, and Lemma 7 to calculate

$$\begin{aligned} \sum_{i=0}^{\omega-1} \frac{1}{\bar{z}_i} &= \sum_{i=0}^{\omega-1} e_1^T \bar{y}(i) = \sum_{i=0}^{\omega-1} e_1^T \Lambda \sum_{j=i}^{i+\omega-1} e_A(i, j+1) g(j) \\ &= \alpha \sum_{i=0}^{\omega-1} \sum_{j=i}^{i+\omega-1} \frac{1}{K_j} e_1^T \Lambda e_A(i, j+1) e_k \\ &= \alpha \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda \sum_{i=0}^j e_A(i, j+1) A A^{-1} e_k \\ &\quad + \alpha \sum_{j=\omega}^{2\omega-2} \frac{1}{K_j} e_1^T \Lambda \sum_{i=j+1-\omega}^{\omega-1} e_A(i, j+1) A A^{-1} e_k \\ &= \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda \left(- \sum_{i=0}^j e_A(i, j+1) A \right) e_1 \\ &\quad + \sum_{j=\omega}^{2\omega-2} \frac{1}{K_j} e_1^T \Lambda \left(- \sum_{i=j+1-\omega}^{\omega-1} e_A(i, j+1) A \right) e_1 \\ &= \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda (e_A(0, j+1) - I_k) e_1 \\ &\quad + \sum_{j=\omega}^{2\omega-2} \frac{1}{K_j} e_1^T \Lambda (e_A(j+1-\omega, j+1) - e_A(\omega, j+1)) e_1 \\ &= \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda (e_A(0, j+1) - I_k) e_1 \end{aligned}$$

$$\begin{aligned}
& + \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda (e_A(j+1, j+1+\omega) - e_A(\omega, j+1+\omega)) e_1 \\
& = \sum_{j=0}^{\omega-1} \frac{1}{K_j} e_1^T \Lambda (e_A(0, \omega) - I_k) e_1 = \sum_{j=0}^{\omega-1} \frac{1}{K_j},
\end{aligned}$$

which completes the proof. \square

5. Periodic growth rate

Now we investigate (16) for the higher-order Beverton–Holt equation in the case when the growth rate is not constant. In this case, the classical conjecture is already not satisfied for $k = 1$, see [5, Example 3.1]. However, for $k = 1$, the following two modifications were presented in [5].

Theorem 22 (See [5, Conjecture 3.2]). *The weighted average of the ω -periodic solution \bar{z} of (4) is strictly less than the weighted average of the nonconstant ω -periodic carrying capacity K , i.e.,*

$$\frac{1}{a} \sum_{n=0}^{\omega-1} \alpha_n \bar{z}_n < \frac{1}{a} \sum_{n=0}^{\omega-1} \alpha_n K_n, \quad \text{where } a = \sum_{n=0}^{\omega-1} \alpha_n. \quad (17)$$

If the carrying capacity K is constant, then we have equality in (17).

Theorem 23 (See [5, Theorem 3.3]). *The average of the ω -periodic solution \bar{z} of (4) is strictly less than the average of the “surrounded” nonconstant ω -periodic carrying capacity K , i.e.,*

$$\frac{1}{\omega} \sum_{n=0}^{\omega-1} \bar{z}_n < \frac{1}{\omega} \sum_{n=0}^{\omega-1} K_n (1 + \delta_n), \quad (18)$$

where

$$\delta_n = \frac{\lambda + 1}{\lambda} \sum_{i=1}^{\omega-1} (\alpha_n - \alpha_{n+i}) \prod_{j=n+1}^{n+i-1} \frac{1}{\mu_j}, \quad \lambda = \prod_{j=0}^{\omega-1} \mu_j - 1.$$

If the carrying capacity K is constant, then we have equality in (18).

If $k \geq 1$ and the growth rate is periodic, then we can provide the following inequality, which yields a new relation even for the case of $k = 1$.

Theorem 24. *The average of the ω -periodic solution \bar{z} of (5) is less than the average of a function times the carrying capacity, namely*

$$\frac{1}{\omega} \sum_{i=0}^{\omega-1} \bar{z}_i \leq \frac{1}{\omega} \sum_{i=0}^{\omega-1} \frac{Q_i}{\alpha_i} K_i,$$

where

$$Q_i = \sum_{n=0}^{\omega-1} \frac{S_{ni}}{\left(\sum_{i=0}^{\omega-1} S_{ni} \right)^2}$$

with

$$S_{ni} = \mathbf{e}_1^T \Lambda_n [\Lambda_n^{-1} (1 - \chi_{i \geq n}) + I_k] e_A(n, i+1) \mathbf{e}_k$$

and

$$\Lambda_n = [e_A(n, n+\omega) - I_k]^{-1}, \quad \chi_{i \geq n} = \begin{cases} 1 & \text{if } i \geq n \\ 0 & \text{else.} \end{cases}$$

Equality holds if and only if there exists a constant C such that $C\alpha_i = K_i$ for all $i \in \mathbb{N}_0$.

Proof. We apply the Jensen inequality to obtain

$$\begin{aligned} \sum_{i=0}^{\omega-1} \bar{z}_i &= \sum_{i=0}^{\omega-1} \frac{1}{\mathbf{e}_1^T \bar{\mathbf{y}}(i)} = \sum_{i=0}^{\omega-1} \frac{1}{\mathbf{e}_1^T \Lambda_i \sum_{j=i}^{i+\omega-1} e_A(i, j+1) \mathbf{g}(j)} \\ &= \sum_{i=0}^{\omega-1} \frac{1}{\mathbf{e}_1^T \Lambda_i \left\{ \sum_{j=i}^{\omega-1} e_A(i, j+1) \mathbf{g}(j) + \sum_{j=0}^{i-1} e_A(i, j+1+\omega) \mathbf{g}(j+\omega) \right\}} \\ &= \sum_{i=0}^{\omega-1} \frac{1}{\mathbf{e}_1^T \Lambda_i \sum_{j=0}^{\omega-1} e_A(i, j+1) [\Lambda_{j+1}^{-1} + I_k - \Lambda_{j+1}^{-1} \chi_{j \geq i}] \mathbf{g}(j)} \\ &= \sum_{i=0}^{\omega-1} \frac{1}{\mathbf{e}_1^T \Lambda_i \sum_{j=0}^{\omega-1} e_A(i, j+1) [\Lambda_{j+1}^{-1} (1 - \chi_{j \geq i}) + I_k] \mathbf{e}_k \frac{\alpha_j}{K_j}} \\ &\leq \sum_{i=0}^{\omega-1} \frac{\sum_{j=0}^{\omega-1} \mathbf{e}_1^T \Lambda_i e_A(i, j+1) [\Lambda_{j+1}^{-1} (1 - \chi_{j \geq i}) + I_k] \mathbf{e}_k \frac{K_j}{\alpha_j}}{\left(\sum_{j=0}^{\omega-1} \mathbf{e}_1^T \Lambda_i e_A(i, j+1) [\Lambda_{j+1}^{-1} (1 - \chi_{j \geq i}) + I_k] \mathbf{e}_k \right)^2} \\ &= \sum_{j=0}^{\omega-1} \frac{K_j}{\alpha_j} Q_j, \end{aligned}$$

where

$$Q_j = \sum_{i=0}^{\omega-1} \frac{S_{ij}}{\left(\sum_{j=0}^{\omega-1} S_{ij} \right)^2}$$

and

$$\begin{aligned} S_{ij} &= \mathbf{e}_1^T \Lambda_i e_A(i, j+1) [\Lambda_{j+1}^{-1} (1 - \chi_{j \geq i}) + I_k] \mathbf{e}_k \\ &= \mathbf{e}_1^T \Lambda_i [\Lambda_i^{-1} (1 - \chi_{j \geq i}) + I_k] e_A(i, j+1) \mathbf{e}_k. \end{aligned}$$

To realize the last equality, note that

$$\begin{aligned} &e_A(i, j+1) [\Lambda_{j+1}^{-1} (1 - \chi_{j \geq i}) + I_k] \\ &= e_A(i, j+1) [(e_A(j+1, j+1+\omega) - I_k) (1 - \chi_{j \geq i}) + I_k] \\ &= [(e_A(i, j+1+\omega) - e_A(i, j+1)) (1 - \chi_{j \geq i}) + e_A(i, j+1)] \\ &= [(e_A(i, i+\omega) e_A(i+\omega, j+1+\omega) - e_A(i, j+1)) (1 - \chi_{j \geq i}) + e_A(i, j+1)] \end{aligned}$$

$$= [(e_A(i, i + \omega) - I_k)(1 - \chi_{j \geq i}) + I_k]e_A(i, j + 1),$$

which completes the claim. Equality holds if and only if K/α is constant. \square

From [Theorem 24](#), we obtain immediately the following corollary.

Corollary 25. *If $Q_i \leq \alpha_i$ for all $i = 0, 1, \dots, \omega - 1$, then*

$$\frac{1}{\omega} \sum_{i=0}^{\omega-1} \bar{z}_i \leq \frac{1}{\omega} \sum_{i=0}^{\omega-1} K_i.$$

Remark 26. If $k = 1$, then

$$S_{ij} = e_{-\alpha}(i, j + 1) \left(\frac{e_{-\alpha}(0, \omega)}{e_{-\alpha}(0, \omega) - 1} - \chi_{j \geq i} \right).$$

Remark 27. If $\alpha_i = \alpha$ is constant, then $Q_i = \alpha$ and the second Cushing–Henson conjecture is satisfied. We have

$$\begin{aligned} \sum_{j=0}^{\omega-1} S_{ij} &= \sum_{j=0}^{\omega-1} e_1^T \Lambda [\Lambda^{-1} (1 - \chi_{j \geq i}) + I_k] e_A(i, j + 1) e_k \\ &= e_1^T \Lambda e_A(0, \omega) \sum_{j=0}^{i-1} e_A(i, j + 1) A A^{-1} e_k + e_1^T \Lambda \sum_{j=i}^{\omega-1} e_A(i, j + 1) A A^{-1} e_k \\ &= e_1^T \Lambda e_A(0, \omega) [e_A(i, 0) - I_k] A^{-1} e_k + e_1^T \Lambda [I_k - e_A(i, \omega)] A^{-1} e_k \\ &= e_1^T \Lambda [e_A(i, \omega) - e_A(0, \omega) + I_k - e_A(i, \omega)] \left(-\frac{1}{\alpha} \right) e_1 \\ &= e_1^T \Lambda (-\Lambda^{-1}) \left(-\frac{1}{\alpha} \right) e_1 = \frac{1}{\alpha} \end{aligned}$$

and the condition of [Corollary 25](#) is satisfied.

We can also generalize the equality discussed in [Theorem 21](#).

Theorem 28. *If α and K are ω -periodic, then the unique ω -periodic solution \bar{z} satisfies*

$$\sum_{i=0}^{\omega-1} \frac{\alpha_i}{\bar{z}_i} = \sum_{i=0}^{\omega-1} \frac{\alpha_i}{K_i}.$$

Proof. The periodic solution \bar{z} of (5) satisfies the transformed equation (6), i.e.,

$$\bar{u}_{i+k} = (1 - \alpha_i) \bar{u}_i + \frac{\alpha_i}{K_i},$$

where $\bar{u} = 1/\bar{z}$. This can be rewritten as

$$\sum_{j=1}^k \binom{k}{j} \Delta^j \bar{u}_i + \alpha_i \bar{u}_i = \frac{\alpha_i}{K_i}.$$

Summing both sides of this equation yields

$$\sum_{i=0}^{\omega-1} \sum_{j=1}^k \binom{k}{j} \Delta^j \bar{u}_i + \sum_{i=0}^{\omega-1} \alpha_i \bar{u}_i = \sum_{i=0}^{\omega-1} \frac{\alpha_i}{\bar{K}_i},$$

which gives the desired equality provided $\sum_{i=0}^{\omega-1} \sum_{j=1}^k \binom{k}{j} \Delta^j \bar{u}_i = 0$. Note that

$$\sum_{i=0}^{\omega-1} \sum_{j=1}^k \binom{k}{j} \Delta^j \bar{u}_i = \sum_{j=1}^k \binom{k}{j} \sum_{i=0}^{\omega-1} \Delta^j \bar{u}_i,$$

and $\sum_{i=0}^{\omega-1} \Delta^j \bar{u}_i = 0$ due to the periodicity of \bar{u} . The proof is complete. \square

References

- [1] Leonid Berezensky, Elena Braverman, On impulsive Beverton–Holt difference equations and their applications, *J. Difference Equ. Appl.* 10 (9) (2004) 851–868.
- [2] Ray J.H. Beverton, Sidney J. Holt, On the Dynamics of Exploited Fish Populations, *Fish. Invest.* (Great Britain, Ministry of Agriculture, Fisheries, and Food), vol. 19, H. M. Stationery Off., London, 1957.
- [3] Martin Bohner, Rotchana Chieochan, The Beverton–Holt q -difference equation, *J. Biol. Dyn.* 7 (1) (2013) 86–95.
- [4] Martin Bohner, Allan Peterson, *Dynamic Equations on Time Scales*, Birkhäuser Boston, Inc., Boston, MA, 2001. An introduction with applications.
- [5] Martin Bohner, Sabrina Streipert, The Beverton–Holt equation with periodic growth rate, *Int. J. Math. Comput.* 26 (4) (2015) 1–10.
- [6] Martin Bohner, Howard Warth, The Beverton–Holt dynamic equation, *Appl. Anal.* 86 (8) (2007) 1007–1015.
- [7] Jim M. Cushing, Shandelle M. Henson, Global dynamics of some periodically forced, monotone difference equations, *J. Difference Equ. Appl.* 7 (6) (2001) 859–872. On the occasion of the 60th birthday of Calvin Ahlbrandt.
- [8] Jim M. Cushing, Shandelle M. Henson, A periodically forced Beverton–Holt equation, *J. Difference Equ. Appl.* 8 (12) (2002) 1119–1120.
- [9] Matthew H. Holden, Jon M. Conrad, Optimal escapement in stage-structured fisheries with environmental stochasticity, *Math. Biosci.* 269 (2015) 76–85.
- [10] Vlajko L. Kocić, A note on the nonautonomous delay Beverton–Holt model, *J. Biol. Dyn.* 4 (2) (2010) 131–139.
- [11] Ryusuke Kon, A note on attenuant cycles of population models with periodic carrying capacity, *J. Difference Equ. Appl.* 10 (8) (2004) 791–793.
- [12] Tahvonen Olli, Optimal harvesting of age-structured fish populations, *Mar. Resour. Econ.* 24 (2009) 147–169.