

## THE BEVERTON–HOLT DIFFERENCE EQUATION

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The Beverton–Holt equation, usually treated as a rational difference equation, is shown in fact to be a logistic difference equation. Based on a crucial transformation connected to logistic equations, an elementary proof of the Cushing–Henson conjectures is given.

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### 1. Introduction

The difference equation

$$x_{n+1} = \frac{\nu K_n x_n}{K_n + (\nu - 1)x_n}, \quad n \in \mathbb{N}_0, \quad (1)$$

where  $\nu > 1$ ,  $K_n > 0$ , and  $x_0 > 0$  is known as the Beverton–Holt equation and has wide applications in population dynamics. The positive sequence  $\{K_n\}$  is the *carrying capacity* and  $\nu$  is the *inherent growth rate*. A periodically forced Beverton–Holt equation is obtained by letting the carrying

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capacity be a periodic positive sequence  $\{K_n\}$  with period  $p \in \mathbb{N}$  so that  $K_{n+p} = K_n$  for all  $n \in \mathbb{N}_0$ .

The Beverton–Holt equation has been treated in the literature as a rational difference equation (see [1–4]). In this paper we show that the Beverton–Holt equation is in fact a logistic difference equation. A simple substitution transforms this equation into a linear difference equation, which can be solved employing the usual variation of parameters formula. This, via an application of the definition of a strictly convex function, also provides an elementary proof of the so-called Cushing–Henson conjecture, which says that *any periodic variation in the carrying capacity of the environment is deleterious to the average population size*. The results in this paper essentially make use of the key ideas in our previous articles [5,6].

## 2. Conversion to a Linear Difference Equation

We begin by introducing

$$\alpha := \frac{\nu - 1}{\nu} \quad \text{so that} \quad \nu = \frac{1}{1 - \alpha}.$$

Suppose  $\{x_n\}$  solves (1). Then we have

$$x_{n+1} = \frac{K_n x_n}{(1 - \alpha)K_n + \alpha x_n}.$$

Now the substitution  $u_n = 1/x_n$  yields the linear difference equation

$$\Delta u_n = -\alpha u_n + \frac{\alpha}{K_n}. \quad (2)$$

We solve the problem (1) with the  $p$ -periodic boundary condition  $\bar{x}_0 = \bar{x}_p$  by solving the equivalent problem (2) with the  $p$ -periodic boundary condition  $\bar{u}_0 = \bar{u}_p$ , where we assume

$$K : \mathbb{Z} \rightarrow \mathbb{R}^+ \quad \text{is } p\text{-periodic,} \quad \text{and} \quad 0 < \alpha < 1, \quad \text{i.e.,} \quad \nu > 1. \quad (3)$$

Using the variation of parameters formula [7, Theorem 3.1 on page 45], the general solution of (2) is

$$u_n = (1 - \alpha)^n u_0 + \sum_{i=0}^{n-1} (1 - \alpha)^{n-(i+1)} \frac{\alpha}{K_i}. \quad (4)$$

(Note here that (4) implies that  $u_n > 0$  provided  $u_0 > 0$ , i.e.,  $x_n > 0$  provided  $x_0 > 0$ .) Then, using  $\bar{u}_0 = \bar{u}_p$  in (4), yields the initial value

$$\bar{u}_0 = \frac{1}{1 - (1 - \alpha)^p} \sum_{i=0}^{p-1} (1 - \alpha)^{p-(i+1)} \frac{\alpha}{K_i}. \quad (5)$$

Plugging the initial value (5) into the general solution (4), we obtain the particular solution (note  $(1 - \alpha)^n(1 - \alpha)^p = (1 - \alpha)^p(1 - \alpha)^n$ )

$$\bar{u}_n = \frac{(1 - \alpha)^p}{1 - (1 - \alpha)^p} \sum_{i=0}^{p-1} (1 - \alpha)^{n-(i+1)} \frac{\alpha}{K_i} + \sum_{i=0}^{n-1} (1 - \alpha)^{n-(i+1)} \frac{\alpha}{K_i}. \quad (6)$$

**Theorem 2.1.** *Assume (3). Then  $\bar{x}_n = 1/\bar{u}_n$  is the only  $p$ -periodic solution to (1), where  $\bar{u}_n$  is given in (6).*

**Proof.** We already showed uniqueness. For  $n \in \mathbb{N}$ , we use again variation of parameters to find another form of the general solution of (2) as

$$u_{n+p} = (1 - \alpha)^n u_p + \sum_{i=p}^{n+p-1} (1 - \alpha)^{n+p-(i+1)} \frac{\alpha}{K_i},$$

which together with (4) and the  $p$ -periodicity of  $\{K_n\}$  yields

$$\bar{u}_{n+p} - \bar{u}_n = (1 - \alpha)^n (\bar{u}_p - \bar{u}_0) = 0.$$

Thus the solution  $\bar{u}_n$  of (2) is  $p$ -periodic.  $\square$

**Remark 2.1.** Note also that, if we assume that  $K_n = K_{n+p}$  for all  $n \in \mathbb{Z}$ , then (2) can be used to define  $\bar{u}_n$  for all  $n \in \mathbb{Z}$  (since  $\alpha \neq 1$ ). Then

$$\bar{u}_{-1} = \frac{\bar{u}_0 - \frac{\alpha}{K_{-1}}}{1 - \alpha} = \frac{\bar{u}_p - \frac{\alpha}{K_{p-1}}}{1 - \alpha} = \bar{u}_{p-1}$$

and it is easy to see that  $\bar{u}_n$  obtained as such satisfies  $\bar{u}_{n+p} = \bar{u}_n$  for all  $n \in \mathbb{Z}$ . Hence there is a unique both-side periodic solution to (2) and consequently to (1).

**Theorem 2.2.** *Assume (3). The solution  $\{\bar{x}_n\}$  of (1) is globally attractive.*

**Proof.** Let  $\{x_n\}$  be an arbitrary solution of (1) with  $x_0 > 0$  and consider  $u_n = 1/x_n$ . Define

$$\gamma = \gamma(u) := \min \left\{ u_0, \min_{0 \leq i \leq p-1} \frac{1}{K_i} \right\} > 0.$$

By (4) we have

$$u_n \geq (1 - \alpha)^n \gamma + \sum_{i=0}^{n-1} (1 - \alpha)^{n-(i+1)} \alpha \gamma = \gamma$$

so that, again by (4),

$$|x_n - \bar{x}_n| = \frac{(1 - \alpha)^n |u_0 - \bar{u}_0|}{u_n \bar{u}_n} \leq \frac{(1 - \alpha)^n |u_0 - \bar{u}_0|}{\gamma(u) \gamma(\bar{u})},$$

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which tends to zero as  $n$  tends to infinity.  $\square$

**Remark 2.2.** Although it was not necessary here to use the fact that the Beverton–Holt equation is a logistic difference equation, this observation was the idea for the key substitution  $u_n = 1/x_n$ . In fact, by letting in turn  $x_n = 1/u_n$  in (2), one can easily see that the resulting equation is

$$\Delta x_n = \alpha x_{n+1} \left( 1 - \frac{x_n}{K_n} \right),$$

which is the natural discrete analogue of the logistic equation, and which therefore should be called the *logistic difference equation*.

### 3. The Cushing–Henson Conjecture

Let  $\chi_{\{m < n\}}$  be 1 if  $m < n$  and 0 otherwise. Define

$$h_{nm} := \alpha(1 - \alpha)^{n-(m+1)} \left( \frac{(1 - \alpha)^p}{1 - (1 - \alpha)^p} + \chi_{\{m < n\}} \right),$$

where  $h_{nm} > 0$  since  $0 < \alpha < 1$ . Then from (6) we obtain for  $n < p$

$$\begin{aligned} \bar{u}_n &= \frac{(1 - \alpha)^p}{1 - (1 - \alpha)^p} \sum_{i=0}^{p-1} (1 - \alpha)^{n-(i+1)} \frac{\alpha}{K_i} + \sum_{i=0}^{p-1} (1 - \alpha)^{n-(i+1)} \frac{\alpha}{K_i} \chi_{\{i < n\}} \\ &= \sum_{i=0}^{p-1} (1 - \alpha)^{n-(i+1)} \left( \frac{(1 - \alpha)^p}{1 - (1 - \alpha)^p} + \chi_{\{i < n\}} \right) \frac{\alpha}{K_i} = \sum_{i=0}^{p-1} \frac{h_{ni}}{K_i}. \end{aligned}$$

**Lemma 3.1.** For all  $0 \leq j \leq p - 1$ , we have  $\sum_{i=0}^{p-1} h_{ij} = \sum_{i=0}^{p-1} h_{ji} = 1$ .

**Proof.** We have

$$\sum_{i=0}^{p-1} h_{ji} = \frac{\alpha(1 - \alpha)^j}{1 - (1 - \alpha)^p} \sum_{i=0}^{p-1} (1 - \alpha)^{p-1-i} + \alpha \sum_{i=0}^{j-1} (1 - \alpha)^{j-1-i} = 1$$

and

$$\sum_{i=0}^{p-1} h_{ij} = \frac{\alpha(1 - \alpha)^{p-(j+1)}}{1 - (1 - \alpha)^p} \sum_{i=0}^{p-1} (1 - \alpha)^i + \alpha \sum_{i=j+1}^{p-1} (1 - \alpha)^{i-(j+1)} = 1,$$

which concludes the proof.  $\square$

**Remark 3.1.** In the one-line proof of the Cushing–Henson conjecture below we use the (consequence of the) definition of a strictly convex function  $f : (0, \infty) \rightarrow \mathbb{R}$  which says that for any  $m \in \mathbb{N}$ ,

$$\left\{ \begin{array}{l} f\left(\sum_{k=1}^m \lambda_k x_k\right) < \sum_{k=1}^m \lambda_k f(x_k) \quad \text{for all } \lambda_k, x_k > 0, 1 \leq k \leq m, \\ \text{where } \sum_{k=1}^m \lambda_k = 1 \quad \text{and there exist } 1 \leq i < j \leq m \text{ with } x_i \neq x_j. \end{array} \right.$$

**Theorem 3.1.** Assume (3). If  $\{K_n\}$  is not constant, then

$$\frac{1}{p} \sum_{i=0}^{p-1} \bar{x}_i < \frac{1}{p} \sum_{i=0}^{p-1} K_i.$$

**Proof.** Using Remark 3.1 for  $f(x) = 1/x$ , Lemma 3.1, and  $h_{ij} > 0$  gives

$$\sum_{i=0}^{p-1} \bar{x}_i = \sum_{i=0}^{p-1} \frac{1}{\bar{u}_i} = \sum_{i=0}^{p-1} \frac{1}{\sum_{j=0}^{p-1} \frac{h_{ij}}{K_j}} < \sum_{i=0}^{p-1} \sum_{j=0}^{p-1} h_{ij} K_j = \sum_{j=0}^{p-1} K_j.$$

Dividing by  $p$  yields the final result.  $\square$

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