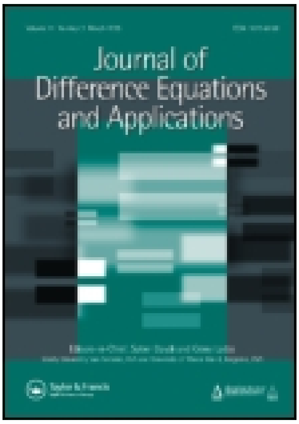

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Resonance and attenuation in the n-periodic Beverton-Holt equation

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Resonance and attenuation in the *n*-periodic Beverton–Holt equation

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With Appendix A by Cymra Haskell[b]

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An exact expression is derived relating the state average of the periodic solution $\{x_j\}$ to the average of the environmental carrying capacities $\{K_j\}$ for the periodic Beverton–Holt equation for arbitrary period. By studying numerically period 3 case, we show that the correlation coefficient of the intrinsic growth rates $\{u_j\}$ and $\{K_j\}$, is not relevant in determining attenuation or resonance. By studying period 4 case, it is shown that if the intrinsic growth rate jumps upward along with steadily increasing carrying capacities, then resonance prevails. A period 7 example using out-of-step step functions is also seen to produce resonance.

Keywords: Beverton–Holt; attenuance; resonance; jump effect

AMS Subject Classification: 39A05; 92D99

1. Introduction

The study of fractional linear maps dates back to August Ferdinand Möbius (1790–1868). The Beverton–Holt map

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

is an example of such a map. By making the substitution $c = (1 - u)/K$, the mapping takes the form

$$f(x) = \frac{uKx}{K + (u - 1)x}, \tag{1}$$

which is the form we wish to study. The only parameters present are significant biological parameters, the *intrinsic growth rate u* and the *carrying capacity K*. This particular *form* of the mapping makes it straightforward to study the evolution of the population x of a species governed by

$$x_{t+1} = f_t(x_t), \quad t = 0, 1, \ldots, \; f_{t+n} = f_t,$$

where environmental fluctuations give rise to periodically varying carrying capacities and

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intrinsic growth parameters with period n. The existence of a globally attracting periodic solution, a qualitative fact, follows just from the concavity of the functions f_t and the semigroup property [4, p. 272]. See [17] for further results following from the semigroup property.

In early papers, 1976 [18] and 1980 [12], it was noted through experimental observation that environmental fluctuations could produce average population densities that were higher than in the case of constant environments, i.e. *resonance* as defined in Section 2. In [3], it was conjectured that for the n-periodic Beverton–Holt equation

$$x_{t+1} = \frac{uK_t x_t}{K_t + (u-1)x_t}, \quad t = 0, 1, \ldots, \tag{2}$$

with constant growth rate $u > 1$ there exists a globally attracting n-periodic solution $\{\bar{x}\} = \{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{n-1}\}$ and *attenuation* takes place. In that paper both questions were answered in the affirmative for period $n = 2$. The complete solution was announced in 2003, and later appeared [5] using an inductive approach and an easily derived formula for the fixed point of two Beverton–Holt maps. There followed other creative solutions [13–15]. In 2004, an exact formula was announced and appeared in [7] and [6] relating the average $\text{av}(\bar{x})$ of the periodic solution and the average $\text{av}(K)$ of the carrying capacities for the 2-periodic case with *both* u and K varying periodically, see (5) where the formula is repeated.

In [10], criteria were given in the 2-periodic case for resonance or attenuation for certain 1D maps near a bifurcation point. In [2] resonance and attenuation were observed in the 2-periodic larvae, pupae, adult (LPA) model and results were compared to the Jillson experiment. See also [1,11]. In [8] several models are studied in which resonance or attenuation is attained with special emphasis on period 2.

In this paper we state and prove a theorem that guarantees attenuance for the case of varying $\{u_j\}$ and $\{K_j\}$ for arbitrary period. We then expand the result obtained in [6,7] by deriving an exact expression relating the state average $\text{av}(\bar{x})$ to the average of the carrying capacities $\text{av}(K)$ for the periodic Beverton–Holt model

$$x_{t+1} = \frac{u_t K_t x_t}{K_t + (u_t - 1)x_t}, \quad t = 0, 1, \ldots \tag{3}$$

for arbitrary period n in Section 3. In Appendix B we state the formula for the 3-periodic case and in Appendix C, the 4-periodic case. In Section 2.1 we put to rest the informal conjecture that the correlation coefficient is the determining factor in whether we have attenuation or resonance. Although no definitive result is achieved, in Section 2.1 we show numerically for period 4 that if the sequences $\{u_0, u_1, \ldots, u_{n-1}\} \subset (1.05, 4)$ and $\{K_0, K_1, \ldots, K_{n-1}\} \subset (3, 5)$ are both increasing (or decreasing) and the variance of u_j is sufficiently close to its theoretical maximum, then from 1.5×10^8 random such samples resonance occurred in 100% of the samples.

Since in period 4 case, the condition on the variance in the increasing case implies u_0, u_1 are near 1 while u_2, u_3 are near 4, we experimented with u_j that 'jump' from a small neighbourhood of the left endpoint 1.05 to a small neighbourhood of 4 but not necessarily a monotone sequence. $\{K_j\}$ were increasing. In all three cases resonance prevailed. A period 7 example employing a step function that jumps at different times is also seen to produce resonance.

2. The Beverton–Holt equation

Consider the following n-periodic Beverton–Holt equation:

$$x_{t+1} = \frac{u_t K_t x_t}{K_t + (u_t - 1)x_t}, \quad t = 0, 1, \ldots, \tag{4}$$

where $u_t > 1$, $x_0 > 0$, $u_{t+n} = u_t$ and $K_{t+n} = K_t$. The following is well established.

THEOREM 2.1. *There is a positive n-periodic solution* $\{\bar{x}\} = \{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{n-1}\}$ *of* (4) *and it globally attracts all solutions with* $x_0 > 0$ [4*, p.* 272].

DEFINITION. *A periodic solution* $\{\bar{x}\}$ *of equation* (4) *is said to be* attenuant *or* resonant *if*

$$\mathrm{av}(\bar{x}) < \mathrm{av}(K) \quad \text{or} \quad \mathrm{av}(\bar{x}) > \mathrm{av}(K),$$

respectively, where 'av' represent the average of any n-periodic sequence $t = \{t_0, t_1, \ldots, t_{n-1}\}$,

$$\mathrm{av}(t) = \frac{1}{n}\sum_{i=0}^{n-1} t_i.$$

In the following sections we will prove the following.

THEOREM 2.2. *An n-periodic Beverton–Holt equation* (4) *with* $u_j > 1$ *is attenuant if* $K_s \neq K_{s+1}$ *for at least one* $s \in \{0, 1, \ldots, n-2\}$ *and one of the following two conditions is satisfied:*

(H_1) $u_0 \leq u_1 \leq \cdots \leq u_{n-1}$ *and* $K_0 \geq K_1 \geq \cdots \geq K_{n-1}$,
(H_2) $u_0 \geq u_1 \geq \cdots \geq u_{n-1}$ *and* $K_0 \leq K_1 \leq \cdots \leq K_{n-1}$.

Note: In [6, p. 342] and [7, p. 206] the following was established for $n = 2$:

$$\mathrm{av}(\bar{x}) = \mathrm{av}(K) + \frac{u_0 - u_1}{u_0 u_1 - 1}\frac{K_0 - K_1}{2} - \Delta\frac{(u_0 - 1)(u_1 - 1)}{2(u_0 u_1 - 1)}(K_0 - K_1)^2, \tag{5}$$

where

$$\Delta \doteq \frac{u_0(u_1^2 - 1)K_0 + u_1(u_0^2 - 1)K_1}{u_0(u_1 - 1)^2 K_0^2 + (u_0 - 1)(u_1 - 1)(u_0 u_1 + 1)K_0 K_1 + u_1(u_0 - 1)^2 K_1^2} > 0.$$

In Section 3 we re-derive (5) in a form (24) suitable for generalization and then derive a similar equality for the n-periodic case from which the proof of Theorem 2.2 follows. The derivation is computationally intensive and is carried out in Section 3. The formulas similar to (24) are stated for reference in Appendix B for period 3 and in Appendix C for period 4.

2.1 *Phase as measured by correlation of u and K is not relevant*

It is easily seen from (5) that in period 2 case, resonance is impossible unless the u and K vectors are in 'phase' in the following sense: $u_0 < u_1$ together with $K_0 < K_1$ or $u_0 > u_1$

together with $K_0 > K_1$. The result for period 2 led some, including the second author, to conjecture that resonance occurred due to u_j and K_j being 'in phase'. Since the attenuation result [5] inspired a subsequent similar result in the stochastic case [9], it was natural to ask whether sufficiently high correlation would lead to resonance. For vectors X and Y of length n, the *correlation coefficient* is defined by

$$r = \frac{1}{(n-1)\sigma_X \sigma_Y} \sum_{j=1}^{n} (X_j - \bar{X})(Y_j - \bar{Y}), \tag{6}$$

where $\bar{X}$ is the *mean* or average of X and σ_X is the *standard deviation* of X defined in (9).

The surprise comes when we consider the 3-periodic case where u and K are the first and second rows, respectively, of

$$M = \begin{bmatrix} u_0 & u_1 & u_2 \\ K_0 & K_1 & K_2 \end{bmatrix}.$$

For example if

$$M = \begin{bmatrix} 1.6013 & 1.0407 & 1.8244 \\ 4.2778 & 4.1796 & 4.1321 \end{bmatrix}, \tag{7}$$

the correlation coefficient $r = -0.08155$ while the state average $\mathrm{av}(\bar{x}) = 4.2003$ and $\mathrm{av}(\bar{K}) = 4.1965$, i.e. resonance. However, if we define

$$M_{2,3} = \begin{bmatrix} 1.6013 & 1.8244 & 1.0407 \\ 4.2778 & 4.1321 & 4.1796 \end{bmatrix},$$

which is just M with its last two columns interchanged, we obtain $\mathrm{av}(\bar{x}) = 4.1892$ and $\mathrm{av}(\bar{K}) = 4.1965$, i.e. attenuation. But the correlation coefficient (6) is invariant under permutations of the columns of the matrix having X in row 1 and Y in row 2. Thus *the correlation coefficient can never be the only marker in determining attenuation or resonance*.

From an examination of (B1) in Appendix B and (36) in Section 3 we see that the combinations of u_j multiplying the terms $(K_k - K_{k+1})$ have a special form, e.g.

$$(u_k - u_{n-1}) + (u_{k-1}u_k - u_{n-2}u_{n-1}) + (u_{k-2}u_{k-1}u_k - u_{n-3}u_{n-2}u_{n-1}) + \ldots,$$

that suggests the best chance at observing resonance takes place when u_j and K_j either both increase or both decrease, i.e.

$$\begin{aligned} &u_0 \le u_1 \le \cdots \le n_{n-1} \quad \text{and} \quad K_0 \le K_1 \le \cdots \le K_{n-1}, \quad \text{or} \\ &u_0 \ge u_1 \ge \cdots \ge n_{n-1} \quad \text{and} \quad K_0 \ge K_1 \ge \cdots \ge K_{n-1}. \end{aligned} \tag{8}$$

But this cannot be the whole story since (8) can hold for a sequence u_j with

$$\max_{j,k} |u_j - u_k| < \varepsilon, \quad 0 < \varepsilon \ll 1,$$

and for ε sufficiently small, one simply has an ε-perturbation of the constant u case where attenuation is known to prevail provided K_j are not all the same. Thus we need to establish a criterion that guarantees the elements of the vector $u = \{u_j\}$ are sufficiently *disbursed* on the interval from which they are chosen. If we choose a vector $u = \{u_j\}$ of length n where u_j are chosen randomly from a uniform distribution on (a, b), then the *variance*, $\mathrm{Var}(u)$ and *standard deviation*, $\sigma(u)$ are defined by

$$\sigma^2(u) = \mathrm{Var}(u) \doteq \frac{1}{n}\sum_{0}^{n-1}(u_j - \mu)^2, \tag{9}$$

where μ is the *mean*,

$$\mu \doteq \frac{1}{n}\sum_{0}^{n-1} u_j. \tag{10}$$

Then for $N > 0$, a large integer, and some $\theta \in [0, 1)$, we choose N such vectors u and *discard* all the vectors such that

$$\sigma(u) < \theta\,\sigma_{\max},$$

and set ρ to be the number of remaining vectors. Here $\sigma_{\max}$ is the theoretical maximum standard deviation of n real numbers chosen from a uniform distribution on $[a, b]$. See Appendix A for a derivation:

$$\sigma_{\max} = \begin{cases} \dfrac{\sqrt{n^2-1}}{n}\dfrac{b-a}{2}, & n \text{ is an odd integer,} \\ \dfrac{b-a}{2}, & n \text{ is an even integer.} \end{cases} \tag{11}$$

Then we choose the same number ρ of vectors $K = \{K_j\}$ from a uniform distribution on $[c, d]$. For the kth vector u and the kth vector K, we form the matrix

$$M_k = \begin{bmatrix} u_0 & u_1 & \cdots & u_{n-1} \\ K_0 & K_1 & \cdots & K_{n-1} \end{bmatrix}. \tag{12}$$

The tth column in (12) represents the tth Beverton–Holt function

$$f_t(x) = \frac{u_t K_t x}{K_t + (u_t - 1)x}$$

on the right side of (4). Thus we may establish a one-to-one correspondence

$$M_k \leftrightarrow F_k,$$

where F_k is the composition,

$$F_k(x) \doteq f_{n-1} \circ f_{n-2} \circ \cdots \circ f_1 \circ f_0(x). \tag{13}$$

But the state average along a periodic orbit is invariant under cyclic permutations of the factors in (13), and thus the occurrence of resonance is invariant under cyclic permutations of the columns of M_k. Thus condition (8) may be replaced by the following assumption.

Assumption 1. The elements of some cyclic permutation M'_k of the columns of M_k should satisfy (8).

This procedure was then carried out by generating, from a uniform distribution on $[1.05, 4]$, $\rho = 1.5 \times 10^8$ random 4-periodic sequences satisfying (8) for each $\theta = 0, 0.1, 0.2, \ldots, 0.8$. The results are shown in Table 1 where it is easily seen that the number of resonances increases as u_j become more disbursed.

Remark. Regarding formula (11), the variance of each sample of n points is computed relative to the *mean* (10) of the sample rather than the mean of the distribution. It can be shown (see Appendix A) that the maximum variance occurs when $n/2$ points are at each endpoint of the interval $[a, b]$ in the case n is even and when $n = 2k + 1$ for k a positive integer, there are k points at one endpoint and $k + 1$ at the other. Five of the samples of u_j that gave rise to the last row of Table 1 are shown below as the columns $(u_0, u_1, u_2, u_3)^T$ of

$$\begin{bmatrix} 1.2031 & 1.1011 & 1.0972 & 1.1535 & 1.1606 \\ 1.2225 & 1.586 & 1.1293 & 1.9844 & 1.1993 \\ 3.7717 & 3.4647 & 3.6364 & 3.8617 & 3.5366 \\ 3.8856 & 3.9424 & 3.8770 & 3.8737 & 3.8539 \end{bmatrix}.$$

This suggests that if the K_j sequence is increasing while in the sequence $\{u_0, u_1, \ldots, u_{n-1}\}$, the values of u_j with small indices are clustered near the left endpoint of the interval then jump to the remaining values clustered near the right endpoint then resonance will prevail. This was tried with period 4 by artificially creating a jump at indices 1, 2 and 3, i.e. for $u = \{u_0, u_1, u_2, u_3\}$,

$$u \approx \{1, 4, 4, 4\}, \quad u \approx \{1, 1, 4, 4\} \quad \text{and} \quad u \approx \{1, 1, 1, 4\}.$$

The results of running 1.5×10^8 random sets of four increasing $K_j \in (3, 5)$ while choosing the same number of *not-necessarily increasing* $u_j \in (1, 1.1) \cup (3.9, 4)$ with a jump at 1, 2 and 3 are shown in Table 2 together with one sample of the u's for each case. Note that the jump at 1, 2 or 3 all gives rise to 100% resonances. In Figure 1 we give a curious example giving rise to resonance for period 7 using an 'out-of-step' step function.

In the light of formula (B1) and its period-n counterpart (36) in Section 3 plus all that has been said so far, it appears that a practical analytic criterion to determine resonance or

Table 1. Resonances from 1.5×10^8 random 4-periodic increasing sequences.[a]

θ	Resonances[b]	% Resonances
0.0	1.38435429×10^8	92.29029
0.1	1.39241057×10^8	92.82737
0.2	1.42624031×10^8	95.08269
0.3	1.46845425×10^8	97.89695
0.4	1.49199147×10^8	99.46610
0.5	1.49851007×10^8	99.90067
0.6	1.49986898×10^8	99.99127
0.7	1.49999824×10^8	99.99988
0.8	1.50000000×10^8	100.0000

[a] $u_j \in (1.05, 4)$, $K_j \in (3, 5)$.
[b] No rounding took place.

Table 2. Resonances from 1.5×10^8 random 4-periodic sequences.[a]

	Jump = 1	Jump = 2	Jump = 3
% Resonances →	100	100	100
u_0	1.138078	1.191784	1.116634
u_1	3.981959	1.161365	1.165238
u_2	3.910999	3.908413	1.120819
u_3	3.913553	3.918662	3.963425

Notes: The K_j (not shown) are increasing. Jumps are made at various times.
[a] $u_j \in (1.1, 1.2) \cup (3.9, 4)$, $K_j \in (3, 5)$.

attenuation seems elusive and in fact this problem seems destined to become the poster child for numerical explorations.

3. The general case

For completeness we now derive the formula relating the state average and the average of the carrying capacities and prove Theorem 2.2 in the n-periodic case for an arbitrary positive integer. In Appendix C (C1), the 4-periodic case is stated. Let

$$f_0(x) = \frac{u_0 K_0 x}{K_0 + (u_0 - 1)x}, \quad f_1(x) = \frac{u_1 K_1 x}{K_1 + (u_1 - 1)x}, \ldots, f_{n-1}(x) = \frac{u_{n-1} K_{n-1} x}{K_{n-1} + (u_{n-1} - 1)x},$$

and let $\{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{n-1}\}$ be a positive globally asymptotically stable n-periodic solution of (4). Thus, we have

$$\bar{x}_k = f_{k-1} \circ f_{k-2} \circ \cdots \circ f_0 \circ f_{n-1} \circ f_{n-2} \circ \cdots \circ f_k(\bar{x}_k), \quad k = 0, 1, \ldots, n-1. \tag{14}$$

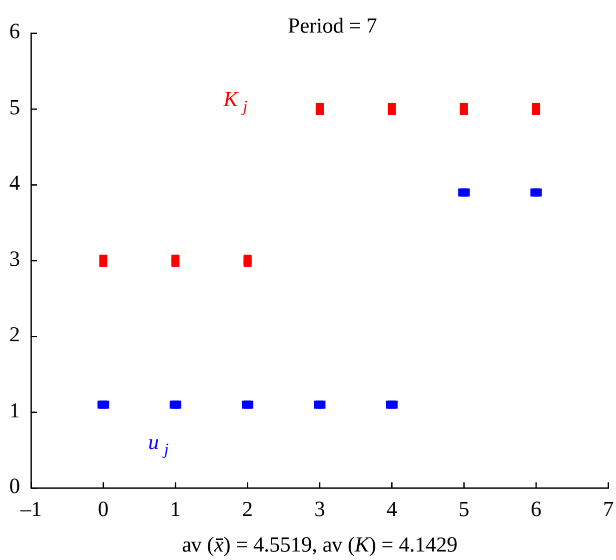

Figure 1. An extreme example showing the jumps need not take place in unison.

We first consider the case $n = 2$ and re-derive (5) in a form suitable for generalization. From (14), we get

$$\begin{aligned}\bar{x}_0 &= \frac{(u_0u_1 - 1)K_0K_1}{K_1(u_0 - 1) + u_0K_0(u_1 - 1)} \\ &= \frac{1}{(1/K_0)(u_0 - 1)/(u_0u_1 - 1) + (1/K_1)(u_0(u_1 - 1))/(u_0u_1 - 1)},\end{aligned}$$

and

$$\begin{aligned}\bar{x}_1 &= \frac{(u_0u_1 - 1)K_0K_1}{K_0(u_1 - 1) + u_1K_1(u_0 - 1)} \\ &= \frac{1}{(1/K_1)(u_1 - 1)/(u_0u_1 - 1) + (1/K_0)(u_1(u_0 - 1))/(u_0u_1 - 1)}.\end{aligned}$$

Defining

$$r_0^0 = \frac{u_0 - 1}{u_0u_1 - 1}, \quad r_1^0 = \frac{u_0(u_1 - 1)}{u_0u_1 - 1} \quad r_0^1 = \frac{u_1 - 1}{u_0u_1 - 1}, \quad r_1^1 = \frac{u_1(u_0 - 1)}{u_0u_1 - 1}, \tag{15}$$

this simplifies to

$$\bar{x}_0 = \frac{1}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right)} \quad \text{and} \quad \bar{x}_1 = \frac{1}{\left(r_0^1/K_1\right) + \left(r_1^1/K_0\right)}. \tag{16}$$

Obviously,

$$r_0^i + r_1^i = 1, \quad i = 0, 1. \tag{17}$$

By (16) and (17) we have

$$\begin{aligned}\bar{x}_0 &= r_0^0K_0 + r_1^0K_1 + \frac{1 - \left(r_0^0\right)^2 - \left(r_1^0\right)^2 - r_0^0r_1^0((K_0/K_1) + (K_1/K_0))}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right)} \\ &= r_0^0K_0 + r_1^0K_1 + \frac{1 - \left(r_0^0 + r_1^0\right)^2 - r_0^0r_1^0((K_0/K_1) + (K_1/K_0) - 2)}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right)} \\ &= r_0^0K_0 + r_1^0K_1 - \frac{r_0^0r_1^0((K_0/K_1) + (K_1/K_0) - 2)}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right)}.\end{aligned} \tag{18}$$

In a similar fashion we have

$$\bar{x}_1 = r_1^1K_0 + r_0^1K_1 - \frac{r_0^1r_1^1((K_1/K_0) + (K_0/K_1) - 2)}{\left(r_0^1/K_1\right) + \left(r_1^1/K_0\right)}. \tag{19}$$

Define

$$\Delta_0 = \frac{r_0^0r_1^0((K_0/K_1) + (K_1/K_0) - 2)}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right)} \quad \text{and} \quad \Delta_1 = \frac{r_0^1r_1^1((K_1/K_0) + (K_0/K_1) - 2)}{\left(r_0^1/K_1\right) + \left(r_1^1/K_0\right)}. \tag{20}$$

Therefore, if $K_0 \neq K_1$ we obtain

$$\Delta_0 + \Delta_1 > 0. \tag{21}$$

From (18)–(20), we have

$$\mathrm{av}(\bar{x}) = \frac{1}{2}\left(r_0^0 + r_1^1\right)K_0 + \frac{1}{2}\left(r_1^0 + r_0^1\right)K_1 - \frac{1}{2}(\Delta_0 + \Delta_1). \tag{22}$$

By (15), we get

$$r_0^0 + r_1^1 = 1 + \frac{u_0 - u_1}{u_0u_1 - 1} \quad \text{and} \quad r_1^0 + r_0^1 = 1 + \frac{u_1 - u_0}{u_0u_1 - 1}. \tag{23}$$

From (22) and (23), we finally obtain the desired period 2 formula,

$$\begin{aligned} \mathrm{av}(\bar{x}) - \mathrm{av}(K) &= \frac{1}{2}\left(\frac{u_0 - u_1}{u_0u_1 - 1}\right)K_0 + \frac{1}{2}\left(\frac{u_1 - u_0}{u_0u_1 - 1}\right)K_1 - \frac{1}{2}(\Delta_0 + \Delta_1) \\ &= \frac{1}{2}\left(\frac{u_0 - u_1}{u_0u_1 - 1}\right)(K_0 - K_1) - \frac{1}{2}(\Delta_0 + \Delta_1). \end{aligned} \tag{24}$$

Using (21) and either hypothesis (H_1) or (H_2), we get $\mathrm{av}(\bar{x}) < \mathrm{av}(K)$.

In a computation similar to the case $n = 2$, equation (14) implies

$$\bar{x}_k = \frac{1}{\sum_{i=0}^{n-1}\left(r_i^k / K_{i+k}\right)}, \quad k = 0, 1, \ldots, n-1, \tag{25}$$

where

$$r_j^i = \begin{cases} \dfrac{u_i - 1}{u_0u_1\cdots u_{n-1} - 1}, & \text{for } j = 0,\ i \in \{0, 1, \ldots, n-1\}, \\ \dfrac{(u_{i+j} - 1)\prod_{k=i}^{i+j-1} u_k}{u_0u_1\cdots u_{n-1} - 1}, & \text{for } j \neq 0,\ i, j \in \{0, 1, \ldots, n-1\}. \end{cases} \tag{26}$$

Clearly,

$$r_0^i + r_1^i + \cdots + r_{n-1}^i = 1, \quad i = 0, 1, \ldots, n-1. \tag{27}$$

From (25) and (27) we obtain

$$\begin{aligned} \bar{x}_k &= \sum_{j=0}^{n-1} r_j^k K_{j+k} + \frac{1 - \sum_{j=0}^{n-1} (r_j^k)^2 - \sum_{i=0}^{n-2}\sum_{j=i+1}^{n-1}\left((K_{i+k}/K_{j+k}) + (K_{j+k}/K_{i+k})\right) r_i^k r_j^k}{\sum_{j=0}^{n-1}\left(r_j^k / K_{j+k}\right)} \\ &= \sum_{j=0}^{n-1} r_j^k K_{j+k} - \frac{\sum_{i=0}^{n-2}\sum_{j=i+1}^{n-1}\left((K_{i+k}/K_{j+k}) + (K_{j+k}/K_{i+k}) - 2\right) r_i^k r_j^k}{\sum_{j=0}^{n-1}\left(r_j^k / K_{j+k}\right)}, \end{aligned} \tag{28}$$

where $k = 0, 1, \ldots, n-1$.

Define

$$\Delta_k = \frac{\sum_{i=0}^{n-2}\sum_{j=i+1}^{n-1}\left((K_{i+k}/K_{j+k}) + (K_{j+k}/K_{i+k}) - 2\right)r_i^k r_j^k}{\sum_{j=0}^{n-1}\left(r_j^k/K_{j+k}\right)}, \quad k = 0, 1, \ldots, n-1. \tag{29}$$

Therefore, if $K_s \neq K_{s+1}$ for at least one $s \in \{0, 1, \ldots, n-2\}$, we get

$$\frac{1}{n}\sum_{i=0}^{n-1}\Delta_i > 0. \tag{30}$$

3.1 Calculation of av($\bar{x}$)

From (28) and (29), we have

$$\mathrm{av}(\bar{x}) = \sum_{k=0}^{n-1}\left(\sum_{i=0}^{n-1} r^i_{(n+k-i)\,\mathrm{mod}(n)}\right)\frac{K_k}{n} - \frac{1}{n}\sum_{i=0}^{n-1}\Delta_i. \tag{31}$$

By comparing (27) with (31), we see immediately that

$$\mathrm{av}(\bar{x}) - \mathrm{av}(K) = \sum_{k=0}^{n-1}\sum_{i=0}^{n-1}\left(r^i_{(n+k-i)\,\mathrm{mod}(n)} - r^{(k+1)\mathrm{mod}(n)}_{(n+k-i)\,\mathrm{mod}(n)}\right)\frac{K_k}{n} - \frac{1}{n}\sum_{i=0}^{n-1}\Delta_i. \tag{32}$$

To keep notation manageable we shall not repeat the 'mod(n)' below. Define

$$\mu = \frac{1}{u_0 u_1 \cdots u_{n-1} - 1}. \tag{33}$$

Clearly, $\mu > 0$ and by (26) and (32) we obtain

$$\begin{aligned}\mathrm{av}(\bar{x}) - \mathrm{av}(K) &= \sum_{k=0}^{n-1}\left(u_k + (u_k - 1)\sum_{j=1}^{n-2}\prod_{i=1}^{j} u_{n+k-i} - \prod_{i=1}^{n-1} u_{n+k-i}\right)\mu\frac{K_k}{n} - \frac{1}{n}\sum_{i=0}^{n-1}\Delta_i \\ &= \sum_{k=0}^{n-1}\left(\sum_{j=0}^{n-2}\prod_{i=0}^{j} u_{n+k-i}\right)\mu\frac{K_k - K_{k+1}}{n} - \frac{1}{n}\sum_{i=0}^{n-1}\Delta_i.\end{aligned} \tag{34}$$

Clearly,

$$K_{n-1} - K_0 = -\sum_{i=0}^{n-2}(K_k - K_{k+1}).$$

This plus (34) leads to the desired formula:

$$\mathrm{av}(\bar{x}) - \mathrm{av}(K) = \sum_{k=0}^{n-2}\sum_{j=0}^{n-2}\left(\prod_{i=0}^{j} u_{n+k-i} - \prod_{i=0}^{j} u_{n-1-i}\right)\mu\frac{K_k - K_{k+1}}{n} - \frac{1}{n}\sum_{i=0}^{n-1}\Delta_i. \tag{35}$$

Writing out the first few terms, we have

$$\begin{aligned}
&\mathrm{av}(\bar{x}) - \mathrm{av}(K) \\
&= \Bigg((u_0 - u_{n-1}) + (u_0 - u_{n-2})u_{n-1} + (u_0 - u_{n-3})u_{n-2}u_{n-1} + \cdots \\
&\quad + (u_0 - u_1)\prod_{i=2}^{n-1} u_i \mu \Bigg) \frac{K_0 - K_1}{n} \\
&\quad + \Bigg((u_1 - u_{n-1}) + (u_0 u_1 - u_{n-2}u_{n-1}) + (u_0 u_1 - u_{n-3}u_{n-2})u_{n-1} + \cdots \\
&\quad + (u_0 - u_2)u_1 \prod_{i=3}^{n-1} u_i \mu \Bigg) \frac{K_1 - K_2}{n} \\
&\quad \vdots
\end{aligned} \tag{36}$$

From (30), it follows that if one of conditions (H_1) and (H_2) is satisfied,

$$\mathrm{av}(\bar{x}) < \mathrm{av}(K),$$

and the proof of Theorem 2.2 is completed.

4. Conclusion

For the Beverton–Holt difference equation

$$x_{t+1} = \frac{u_t K_t x_t}{K_t + (u_t - 1)x_t}, \quad t = 0, 1, \ldots$$

with both parameters u_t and K_t periodic with arbitrary period n, we prove a theorem guaranteeing attenuation and also provide numerical evidence guaranteeing resonance for period $n = 4$. We show attenuance, if $u = \{u_1, u_2, \ldots, u_{n-1}\}$ is an increasing sequence while $K = \{K_1, K_2, \ldots, K_{n-1}\}$ is decreasing (or u decreasing and K increasing) and $K_i \neq K_j$ for some pair.

For resonance the story is more complicated. We chose 1.5×10^8 random (uniform) sequences $u \in [1.1, 4]$ and $K \in [3, 5]$. If the sequences u and K are both increasing or both decreasing, without further restriction, then $\approx$92.3% of the pairs yielded resonance. The percentage of resonances increased as we required u_j to be more and more disbursed on $[1.1, 4]$ as measured by the standard deviation of the samples. When the standard deviation exceeded 80% of its theoretical maximum, all 1.5×10^8 samples yielded resonance. Since this theoretical maximum is achieved when the u_j are evenly divided between the endpoints of the interval $[1.1, 4]$, it was apparent that the resonance was caused when u_j *jump* from a small neighbourhood of the left endpoint to a small neighbourhood of the right endpoint. Further explorations determined that the jump was the determining factor rather than the even distribution of u_j near the endpoints. A period 7 example using a step function with jumps at differing times is also seen to produce resonance.

All this seems to indicate that in a steadily improving environment (K_j increasing), a sudden increase in the growth rates u_j is more effective in creating a resonant outcome than a steadily increasing sequence.

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Note

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Appendix A: A variance lemma

Lemma A.1. (Cymra Haskell).

Consider the function V that is defined on $\mathbb{R}^n$ where $n \geq 2$ and is given by

$$V(x_1, x_2, \ldots, x_n) = \frac{1}{n}\sum_{i=1}^{n} x_i^2 - \left(\frac{1}{n}\sum_{i=1}^{n} x_i\right)^2. \tag{A1}$$

On the set $U = \{(x_1, \ldots, x_n) : 0 \leq x_i \leq 1, 1 \leq i \leq n\}$, V attains a maximum $V_{\max}$ that is equal to

$$V_{\max} = \begin{cases} \dfrac{1}{4}, & n = 2k \text{ is even,} \\ \left(\dfrac{k}{n}\right)\left(1 - \dfrac{k}{n}\right), & n = 2k+1 \text{ is odd.} \end{cases}$$

Moreover, when $n = 2k$ is even this maximum is attained when k of the x_i's are equal to 0 *and the other k are equal to* 1, *and when $n = 2k + 1$ is odd this maximum is attained when $k + 1$ of the x_i's are equal to* 0 *and the other k are equal to* 1 (*or when k of them are equal to* 0 *and the other $k + 1$ are equal to* 1).

Remark. The value of V is, of course, the variance of the data $x_1, x_2, \ldots, x_n$. The function V also attains a minimum on U though this is of less interest. The minimum is 0 and is attained on the hyperplane $\{(x_1, \ldots, x_n) \in U : x_1 = x_2 = \cdots = x_n\}$. It is well known and not hard to see that V can also be written as

$$V(x_1, x_2, \ldots, x_n) = \frac{1}{n}\sum_{i=1}^{n}\left(x_i - \frac{1}{n}\sum_{i=1}^{n} x_i\right)^2.$$

By scaling and shifting, the lemma can be stated on the interval $[a, b]$ as follows.

Corollary A.2. *The maximum of the function V in* (A1) *on the set $\{(x_1, x_2, \ldots, x_m) : a \leq x; \leq b, 1 \leq b \leq m\}$ is*

$$V_{\max} = \begin{cases} \dfrac{(b-a)^2}{4}, & n = 2k \text{ is even,} \\ \dfrac{k}{n}\left(1 - \dfrac{k}{n}\right)(b-a)^2 = \dfrac{n^2-1}{4n^2}(b-a)^2, & n = 2k+1 \text{ is odd.} \end{cases}$$

The maximum is attained for $n = 2k$ when there are k points at each endpoint and for $n = 2k + 1$ when there are k points at one endpoint and $k + 1$ at the other.

Proof. Before embarking on the proof we make the following observation which is well known to probabilists and statisticians. Let $X = (x_1, x_2, \ldots, x_n)$ be the data and let $Y = \{I, J\}$ be any partition of the indices $\{1, 2, \ldots, n\}$ into two subsets I and J. Let n_I be the number of elements in the set I and let n_J be the number in J. Of course, $n_I + n_J = n$. Let $E(X|Y) = (M_I, M_J)$ be the average of all those x_i's for which $i \in I$ and the average of all those for which $i \in J$, respectively. In other words

$$M_I = \frac{1}{n_I}\sum_{i \in I} x_i$$

and

$$M_J = \frac{1}{n_J}\sum_{i\in J} x_i.$$

Similarly, let $\mathrm{Var}(X|Y) = (V_I, V_J)$ be the variance of all those x_i's for which $i \in I$ and the variance of all those for which $i \in J$, respectively. In other words

$$V_I = \frac{1}{n_I}\sum_{i\in I} x_i^2 - \left(\frac{1}{n_I}\sum_{i\in I} x_i\right)^2 = \frac{1}{n_I}\sum_{i\in I}(x_i - M_I)^2$$

and

$$V_J = \frac{1}{n_J}\sum_{i\in J} x_i^2 - \left(\frac{1}{n_J}\sum_{i\in J} x_i\right)^2 = \frac{1}{n_J}\sum_{i\in J}(x_i - M_J)^2.$$

If $n_I = 0$, then we define $M_I = V_I = 0$. Similarly if $n_J = 0$. Now define

$$E(E(X|Y)) = \left(\frac{n_I}{n}\right)M_I + \left(\frac{n_J}{n}\right)M_J,$$
$$E(\mathrm{Var}(X|Y)) = \left(\frac{n_I}{n}\right)V_I + \left(\frac{n_J}{n}\right)V_J$$

and

$$\begin{aligned}\mathrm{Var}(E(X|Y)) &= \left(\left(\frac{n_I}{n}\right)M_I^2 + \left(\frac{n_J}{n}\right)M_J^2\right) - \left(\left(\frac{n_I}{n}\right)M_I + \left(\frac{n_J}{n}\right)M_J\right)^2 \\ &= \left(\frac{n_I}{n}\right)(M_I - E(E(X|Y)))^2 + \left(\frac{n_J}{n}\right)(M_J - E(E(X|Y)))^2.\end{aligned}$$

The important observation is the following [16, p. 348]:

$$\begin{aligned}&E(\mathrm{Var}(X|Y)) + \mathrm{Var}(E(X|Y)) \\ &= \left(\frac{1}{n}\sum_{i=1}^{n} x_i^2 - \frac{1}{nn_I}\left(\sum_{i\in I} x_i\right)^2 - \frac{1}{nn_J}\left(\sum_{i\in J} x_i\right)^2\right) \\ &\quad + \left(\frac{1}{nn_I}\left(\sum_{i\in I} x_i\right)^2 + \frac{1}{nn_J}\left(\sum_{i\in J} x_i\right)^2\right) - \left(\frac{1}{n}\sum_{i=1}^{n} x_i\right)^2 \\ &= V(x_1, \ldots, x_n).\end{aligned}$$

To prove the lemma, notice first that V is continuous and U is compact, so V attains a maximum on U. Let $(x_1, \ldots, x_n) \in U$ be given. Let

$$I = \{i : x_i = 0 \ \text{ or } \ x_i = 1\},$$
$$J = \{i : 1 \le i \le n \ \text{ and } \ i \notin I\}.$$

Suppose that $J \neq \emptyset$. In this case we shall construct $X^* = (x_1^*, x_2^*, \ldots, x_n^*) \in U$ such that $V(x_1^*, \ldots, x_n^*) > V(x_1, \ldots, x_n)$. Let $x_i^* = x_i$ for all $i \in I$. Let

$$\alpha = \min_{i\in J} x_i$$

and

$$\beta = \max_{i \in J} x_i.$$

Notice that $0 < \alpha \leq \beta < 1$. Suppose first that $\alpha < \beta$. In this case $\alpha < M_J < \beta$. To construct the x_i^*'s we take all the x_i's with $i \in J$ and stretch them about their mean M_J as far as we can without letting them leave the interval $[0, 1]$. In particular, let

$$\gamma = \min\left\{\frac{M_J}{M_J - \alpha}, \frac{1 - M_J}{\beta - M_J}\right\}.$$

Notice that $\gamma > 1$. For $i \in J$ define

$$x_i^* = M_J + \gamma(x_i - M_J).$$

Notice that $x_i^* \geq M_J + \gamma(\alpha - M_J) = M_J - \gamma(M_J - \alpha) \geq 0$ and $x_i^* \leq M_J + \gamma(\beta - M_J) \leq 1$. Moreover,

$$M_I^* = \frac{1}{n_I}\sum_{i \in J} x_i^* = M_I,$$

$$V_I^* = \frac{1}{n_I}\sum_{i \in I}\left(x_i^* - M_I^*\right)^2 = V_I,$$

$$M_J^* = \frac{1}{n_J}\sum_{i \in J} x_i^* = \frac{1}{n_J}\sum_{i \in J}(M_J + \gamma(x_i - M_J)) = M_J + \frac{\gamma}{n_J}\sum_{i \in J} x_i - \gamma M_J = M_J$$

and

$$V_J^* = \frac{1}{n_J}\sum_{i \in J}\left(x_i^* - M_J^*\right)^2 = \gamma^2\frac{1}{n_J}\sum_{i \in J}(x_i - M_J)^2 = \gamma^2 V_J > V_J.$$

It follows that

$$E(\mathrm{Var}(X^*|Y)) > E(\mathrm{Var}(X|Y))$$

and

$$\mathrm{Var}(E(X^*|Y)) = \mathrm{Var}(E(X|Y)),$$

so

$$V\left(x_1^*, \ldots, x_n^*\right) > V(x_1, \ldots, x_n).$$

Now suppose that $\alpha = \beta$. Then $x_i = \alpha$ for all $i \in J$, so $M_J = \alpha$ and $V_J = 0$. To construct the x_i^*'s we move all the x_i's for $i \in J$ so that they are as far away from M_I as possible. In particular, for $i \in J$ we define

$$x_i^* = \begin{cases} 1, & \text{if } M_I \leq \frac{1}{2}, \\ 0, & \text{if } M_I > \frac{1}{2}. \end{cases}$$

Now $V_I^* = V_I$ and $V_J^* = 0 = V_J$ so $E(\mathrm{Var}(X^*|Y)) = E(\mathrm{Var}(X|Y))$. Moreover, $M_I^* = M_I$ and if $M_I \leq 1/2$ then $M_J^* = 1$ and if $M_I > 1/2$ then $M_J^* = 0$. In particular, since $0 < \alpha < 1$, $|M_I - \alpha| < |M_I - M_J^*|$. Thus, the conditional distribution $E(X^*|Y) = (M_I, M_J^*)$ is more spread out than the original conditional distribution $E(X|Y) = (M_I, \alpha)$.

Without any calculation, it is easy to see that

$$\mathrm{Var}(E(X^*|Y)) = \left(\frac{M_I - M_J^*}{M_I - \alpha}\right)^2 \mathrm{Var}(E(X|Y)) > \mathrm{Var}(E(X|Y)).$$

(If $M_I = \alpha$, then $\mathrm{Var}(E(X|Y)) = 0$ and $\mathrm{Var}(E(X^*|Y)) > 0$, so the inequality still holds.) It follows that

$$\begin{aligned} V\left(x_1^*, \ldots, x_n^*\right) &= E(\mathrm{Var}(X^*|Y)) + \mathrm{Var}(E(X^*|Y)) \\ &> E(\mathrm{Var}(X|Y)) + \mathrm{Var}(E(X|Y)) = V(x_1, \ldots, x_n). \end{aligned}$$

Thus, the maximum of V must occur at a point $(x_1, \ldots, x_n)$ where $J = \emptyset$. Now it is a simple calculation to get the result. Let $(x_1, \ldots, x_n)$ be such a point and let p be the number of x_i's that are equal to 1. Then

$$V(x_1, \ldots, x_n) = \frac{p}{n} - \frac{p^2}{n^2} = \frac{p}{n}\left(1 - \frac{p}{n}\right).$$

The quadratic function $f(x) = x(1 - x)$ is symmetric about $x = 1/2$ and increases from $x = 0$ to $x = 1/2$ and decreases from $x = 1/2$ to $x = 0$. It follows that the maximum of f along $x = 0, 1/n, 2/n, \ldots, 1$ is equal to $1/4$ and is attained at $x = 1/2$ when n is even and is equal to $(k/n)(1 - k/n)$ and is attained at $p = k$ or $p = k + 1$ when $n = 2k + 1$ is odd. □

Appendix B: Period 3 formula

In this appendix we write formula (36) for the 3-periodic case.

$$\begin{aligned} \mathrm{av}(\bar{x}) - \mathrm{av}(K) = {} & \frac{1}{3(u_0u_1u_2 - 1)}(u_2(u_0 - u_1) + (u_0 - u_2))(K_0 - K_1) \\ & + \frac{1}{3(u_0u_1u_2 - 1)}(u_1(u_0 - u_2) + (u_1 - u_2))(K_1 - K_2) \\ & - \frac{1}{3}(\Delta_0 + \Delta_1 + \Delta_2), \end{aligned} \tag{B1}$$

where

$$\Delta_0 = \frac{r_0^0r_1^0((K_0/K_1) + (K_1/K_0) - 2) + r_0^0r_2^0((K_0/K_2) + (K_2/K_0) - 2) + r_1^0r_2^0((K_1/K_2) + (K_2/K_1) - 2)}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right) + \left(r_2^0/K_2\right)},$$

$$\Delta_1 = \frac{r_0^1r_1^1((K_1/K_2) + (K_2/K_1) - 2) + r_0^1r_2^1((K_1/K_0) + (K_0/K_1) - 2) + r_1^1r_2^1((K_2/K_0) + (K_0/K_2) - 2)}{\left(r_0^1/K_1\right) + \left(r_1^1/K_2\right) + \left(r_2^1/K_0\right)},$$

$$\Delta_2 = \frac{r_0^2r_1^2((K_2/K_0) + (K_0/K_2) - 2) + r_0^2r_2^2((K_2/K_1) + (K_1/K_2) - 2) + r_1^2r_2^2((K_0/K_1) + (K_1/K_0) - 2)}{\left(r_0^2/K_2\right) + \left(r_1^2/K_0\right) + \left(r_2^2/K_1\right)}$$

and

$$r_0^0 = \frac{u_0 - 1}{u_2u_1u_0 - 1}, \quad r_1^0 = \frac{u_0(u_1 - 1)}{u_2u_1u_0 - 1}, \quad r_2^0 = \frac{u_0u_1(u_2 - 1)}{u_2u_1u_0 - 1},$$

$$r_0^1 = \frac{u_1 - 1}{u_2u_1u_0 - 1}, \quad r_1^1 = \frac{u_1(u_2 - 1)}{u_2u_1u_0 - 1}, \quad r_2^1 = \frac{u_1u_2(u_0 - 1)}{u_2u_1u_0 - 1},$$

$$r_0^2 = \frac{u_2 - 1}{u_2u_1u_0 - 1}, \quad r_1^2 = \frac{u_2(u_0 - 1)}{u_2u_1u_0 - 1}, \quad r_2^2 = \frac{u_0u_2(u_1 - 1)}{u_2u_1u_0 - 1}.$$

Note that if $K_i \neq K_{i+1}$ for at least $i \in \{0, 1\}$, we have

$$\Delta_0 + \Delta_1 + \Delta_2 > 0.$$

Appendix C: Period 4 formula

In this appendix we write formula (36) for the 4-periodic case.

$$\begin{aligned} &\mathrm{av}(\bar{x}) - \mathrm{av}(\bar{K}) \\ &\quad = \frac{1}{4(u_0u_1u_2u_3 - 1)}((u_0 - u_3) + (u_0u_3 - u_2u_3) + (u_0 - u_1)u_2u_3)(K_0 - K_1) \\ &\quad + \frac{1}{4(u_0u_1u_2u_3 - 1)}((u_1 - u_3) + (u_0u_1 - u_2u_3) + (u_0 - u_2)u_1u_3)(K_1 - K_2) \\ &\quad + \frac{1}{4(u_0u_1u_2u_3 - 1)}((u_2 - u_3) + (u_1u_2 - u_2u_3) + (u_0 - u_3)u_1u_2)(K_2 - K_3) \\ &\quad - \frac{1}{4}(\Delta_0 + \Delta_1 + \Delta_2 + \Delta_3), \end{aligned} \tag{C1}$$

where

$$\begin{aligned} \Delta_0 &= \frac{((K_0/K_1) + (K_1/K_0) - 2)r_0^0r_1^0 + ((K_0/K_2) + (K_2/K_0) - 2)r_0^0r_2^0 + ((K_0/K_3) + (K_3/K_0) - 2)r_0^0r_3^0}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right) + \left(r_2^0/K_2\right) + \left(r_3^0/K_3\right)} \\ &+ \frac{((K_1/K_2) + (K_2/K_1) - 2)r_1^0r_2^0 + ((K_1/K_3) + (K_3/K_1) - 2)r_1^0r_3^0 + ((K_2/K_3) + (K_3/K_2) - 2)r_2^0r_3^0}{\left(r_0^0/K_0\right) + \left(r_1^0/K_1\right) + \left(r_2^0/K_2\right) + \left(r_3^0/K_3\right)}, \\ \Delta_1 &= \frac{((K_1/K_2) + (K_2/K_1) - 2)r_0^1r_1^1 + ((K_1/K_3) + (K_3/K_1) - 2)r_0^1r_2^1 + ((K_1/K_0) + (K_0/K_1) - 2)r_0^1r_3^1}{\left(r_0^1/K_1\right) + \left(r_1^1/K_2\right) + \left(r_2^1/K_3\right) + \left(r_3^1/K_0\right)} \\ &+ \frac{((K_2/K_3) + (K_3/K_2) - 2)r_1^1r_2^1 + ((K_2/K_0) + (K_0/K_2) - 2)r_1^1r_3^1 + ((K_3/K_0) + (K_0/K_3) - 2)r_2^1r_3^1}{\left(r_0^1/K_1\right) + \left(r_1^1/K_2\right) + \left(r_2^1/K_3\right) + \left(r_3^1/K_0\right)}, \\ \Delta_2 &= \frac{((K_2/K_3) + (K_3/K_2) - 2)r_0^2r_1^2 + ((K_2/K_0) + (K_0/K_2) - 2)r_0^2r_2^2 + ((K_2/K_1) + (K_1/K_2) - 2)r_0^2r_3^2}{\left(r_0^2/K_2\right) + \left(r_1^2/K_3\right) + \left(r_2^2/K_0\right) + \left(r_3^2/K_1\right)} \\ &+ \frac{((K_3/K_0) + (K_0/K_3) - 2)r_1^2r_2^2 + ((K_3/K_1) + (K_1/K_3) - 2)r_1^2r_3^2 + ((K_0/K_1) + (K_1/K_0) - 2)r_2^2r_3^2}{\left(r_0^2/K_2\right) + \left(r_1^2/K_3\right) + \left(r_2^2/K_0\right) + \left(r_3^2/K_1\right)}, \\ \Delta_3 &= \frac{((K_3/K_0) + (K_0/K_3) - 2)r_0^3r_1^3 + ((K_3/K_1) + (K_1/K_3) - 2)r_0^3r_2^3 + ((K_3/K_2) + (K_2/K_3) - 2)r_0^3r_3^3}{\left(r_0^3/K_3\right) + \left(r_1^3/K_0\right) + \left(r_2^3/K_1\right) + \left(r_3^3/K_2\right)} \\ &+ \frac{((K_0/K_1) + (K_1/K_0) - 2)r_1^3r_2^3 + ((K_0/K_2) + (K_2/K_0) - 2)r_1^3r_3^3 + ((K_1/K_2) + (K_2/K_1) - 2)r_2^3r_3^3}{\left(r_0^3/K_3\right) + \left(r_1^3/K_0\right) + \left(r_2^3/K_1\right) + \left(r_3^3/K_2\right)}. \end{aligned} \tag{C2}$$

and

$$
\begin{aligned}
r_0^0 &= \frac{u_0 - 1}{u_0u_1u_2u_3 - 1}, & r_1^0 &= \frac{(u_1 - 1)u_0}{u_0u_1u_2u_3 - 1}, & r_2^0 &= \frac{(u_2 - 1)u_0u_1}{u_0u_1u_2u_3 - 1}, & r_3^0 &= \frac{(u_3 - 1)u_0u_1u_2}{u_0u_1u_2u_3 - 1}, \\
r_0^1 &= \frac{u_1 - 1}{u_0u_1u_2u_3 - 1}, & r_1^1 &= \frac{(u_2 - 1)u_1}{u_0u_1u_2u_3 - 1}, & r_2^1 &= \frac{(u_3 - 1)u_1u_2}{u_0u_1u_2u_3 - 1}, & r_3^1 &= \frac{(u_0 - 1)u_1u_2u_3}{u_0u_1u_2u_3 - 1}, \\
r_0^2 &= \frac{u_2 - 1}{u_0u_1u_2u_3 - 1}, & r_1^2 &= \frac{(u_3 - 1)u_2}{u_0u_1u_2u_3 - 1}, & r_2^2 &= \frac{(u_0 - 1)u_3u_2}{u_0u_1u_2u_3 - 1}, & r_3^2 &= \frac{(u_1 - 1)u_0u_3u_2}{u_0u_1u_2u_3 - 1}, \\
r_0^3 &= \frac{u_3 - 1}{u_0u_1u_2u_3 - 1}, & r_1^3 &= \frac{(u_0 - 1)u_3}{u_0u_1u_2u_3 - 1}, & r_2^3 &= \frac{(u_1 - 1)u_0u_3}{u_0u_1u_2u_3 - 1}, & r_3^3 &= \frac{(u_2 - 1)u_1u_0u_3}{u_0u_1u_2u_3 - 1}.
\end{aligned}
$$