

Periodically Fluctuating Carrying Capacity in the Beverton–Holt Equation

J.M. CUSHING^{a,*} and SHANDELLE M. HENSON^b

^a*Department of Mathematics, Arizona State University, Tempe, AZ 85721, USA;*
^b*Department of Mathematics, Arizona State University, Sunnyvale, CA 94085, USA*

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For $r > 1$ and $K > 0$ the difference equation

$$x_{n+1} = \frac{rx_n}{K + (r-1)x_n}, \quad n = 0, 1, 2, \dots$$

has a unique positive equilibrium K and all solutions with $x_0 > 0$ approach K as $n \rightarrow \infty$. This equation (known as the Beverton–Holt equation) arises in applications to population dynamics, and in that context K is the “carrying capacity” and r is the “inherent growth rate”. A modification of this equation that arises in the study of populations living in a periodically (seasonally) fluctuating environment replaces the constant carrying capacity K by a periodic sequence K_n of positive carrying capacities.

*Corresponding author. E-mail: cushing@math.arizona.edu
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Thus, we have a periodically forced Beverton–Holt equation

$$K_{t+1} = \frac{rK_t}{K_t + (r-1)} \quad (1)$$

in which the sequence K_0, K_1, \dots of positive numbers is periodic with a base period p , i.e. $K_{t+p} = K_t > 0$ for all $t \geq 0$ and a (minimal) integer $p \geq 1$. Keep the inherent growth rate $r > 1$ constant and consider the following assertions.

- (a) Equation (1) has a positive p -periodic solution $K^* > 0$, and it is globally attracting for $K_0 > 0$.
- (b) If $p > 2$, the strict inequality $a_p(K^*) < a_p(K)$ holds. Here a_p denotes the average of a periodic cycle, e.g.

$$a_p(K) = \frac{1}{p} \sum_{i=0}^{p-1} K_i.$$

These assertions are of ecological interest because they imply a fluctuating habitat is deleterious to a population in the sense that the average population size, in the long run, is less in a periodically oscillating habitat than it is in a constant habitat with the same average.

As pointed out above, (a) holds when $p = 1$ (i.e. $K_t = K$ is a constant). However, when $p = 1$ assertion (b) is false, since in that case $K_t = K$ and hence $a_p(K) = a_p(K)$. On the other hand, it is known that both (a) and (b) are true for $p = 2$ [1]. We conjecture (a) and (b) are in fact true for all periods $p \geq 2$. However, it remains an open problem to prove (or disprove) these assertions for $p \geq 3$.

References

- [1] Cushing, J.M. and Shandelle M., Henson, Global dynamics of some periodically forced, monotone difference equations, *Journal of Difference Equations and Applications* 7 (2001), 859–872.

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