Journal of Difference Equations and Applications,
Vol. 10, No. 8, July 2004, pp. 791–793

A Note on Attenuant Cycles of Population Models with Periodic Carrying Capacity

RYUSUKE KON*

Department of Systems Engineering, Shizuoka University, Hamamatsu, 432-8561, Japan

(Received 24 March 2004; Revised 30 March 2004; In final form 2 April 2004)

In this short note, we consider attenuant cycles of population models. This study concerns the second conjecture of Cushing and Henson [A periodically forced Beverton-Holt equation, *J. Diff. Eq. Appl.*, **8** (2002), pp. 1119–1120], which was recently resolved affirmatively by Elaydi and Sacker [Global stability of periodic orbits of nonautonomous difference equations in population biology and the Cushing-Henson conjectures, *Proc. 8th Inter. Conf. Diff. Eq., Brno*, (in press)]. They showed that the periodic fluctuations in the carrying capacity always reduce the average of population densities in the Beverton-Holt equation. We extend this result and give a class of population models in which the periodic fluctuations in the carrying capacity always reduce the average of population densities.

Keywords: Periodic difference equations; Average population densities; Concave functions; Periodic fluctuations

AMS Classification Codes: 39A11; 92D25

INTRODUCTION

The following non-autonomous difference equation is a population model with periodically fluctuating carrying capacity:

$$x_{n+1} = g\left(\frac{x_n}{K_n}\right)x_n, \quad x_0 \in \mathbb{R}_+ := [0, +\infty), \quad n \in \mathbb{Z}_+ := \{0, 1, 2, \ldots\}, \tag{1}$$

where $g : \mathbb{R}_+ \to \mathbb{R}_+$ is a continuous function which satisfies $g(1) = 1$, $g(x) > 1$ for all $x \in (0, 1)$ and $g(x) < 1$ for all $x \in (1, \infty)$, and $\{K_n\}$ is a periodic sequence such that $K_n > 0$ for all $n \in \mathbb{Z}_+$ and $K_{n+k} = K_n$ for all $n \in \mathbb{Z}_+$ (not necessarily $K_{n+i} \neq K_n$ for all $i, 0 < i < k$). The variable x_n represents a population density at time n and the time dependent parameter K_n is a carrying capacity at time n. By the assumptions of the function g, we see that K_n is a unique positive fixed point of the map $f_n(x) := g(x/K_n)x$. The following (non-autonomous) Beverton-Holt equation is an example of (1):

$$x_{n+1} = \frac{\lambda x_n}{1 + (\lambda - 1)(x_n/K_n)}, \quad \lambda > 1, \quad K_n > 0, \tag{2}$$

where K_n fluctuates with period k.

*Tel./Fax: + 81-53-478-1264. E-mail: kon-r@math.club.ne.jp

Journal of Difference Equations and Applications
ISSN 1023-6198 print/ISSN 1563-5120 online
http://www.tandf.co.uk/journals
DOI: 10.1080/10236190410001703949

Cushing and Henson [1] showed that if $k = 2$ and $K_1 \neq K_2$, then the cycle $\{p_1, p_2\}$ of Eq. (2) attracts all solutions with $x_0 > 0$ and satisfies:

$$\frac{p_1 + p_2}{2} < \frac{K_1 + K_2}{2}.$$

Cushing and Henson [2] also conjectured that even if $k \geq 3$, the situation does not change, i.e. (i) there exists a globally asymptotically stable cycle and (ii) its average is less than the average of carrying capacities. These two conjectures, (i) and (ii), are of ecological interest because they imply that the environmental fluctuation is deleterious to a population in the sense that its time average of the population density in a fluctuating environment is eventually less than that in a constant environment with the same average. The recent studies of Elaydi and Sacker [3,4] resolved these two conjectures affirmatively. Furthermore, they gave a class of periodic difference equations possessing a globally asymptotically stable cycle, which concerns the first conjecture of Ref. [2]. In this short note, we extend the result of Elaydi and Sacker [4] concerning the second conjecture of Ref. [2]. That is, we give a class of population models in which cycles are attenuant.

ATTENUANT CYCLES

We consider the relationship between the time averages of a cycle $\{p_n\}$ and the carrying capacities $\{K_n\}$ of the non-autonomous difference equation (1). A cycle $\{p_n\}$ is said to be *positive* if $p_n > 0$ for all $n \geq 0$. An m-cycle $\{p_n\}$ of Eq. (1) is said to be an *attenuant* if $\bar{p} < \bar{K}$, where $\bar{p} = (p_1 + p_2 + \cdots + p_m)/m$ and $\bar{K} = (K_1 + K_2 + \cdots + K_k)/k$.

Now we introduce two lemmas without proofs, and then obtain the main theorem (Theorem 3) by using these lemmas (see Ref. [5] for the proofs of the lemmas).

LEMMA 1 *If $g(z)z$ is concave on some interval (a, b), $0 < a < b$, then $f(x, y) := g(x/y)x$ is concave on the convex set $\{(x, y) \in \mathbb{R}_+^2 : ay < x < by\}$.*

LEMMA 2 *Let $\{p_n\}$ be a positive m-cycle of Eq.* (1). *Suppose that $K_s \neq K_{s+1}$ for some $s \in \{1, 2, \ldots, k\}$. Then $p_i/K_i \neq p_j/K_j$ for some $i, j \in \{1, 2, \ldots, mk\}$.*

THEOREM 3 *Let $\{p_n\}$ be a positive m-cycle of Eq.* (1). *Suppose that $K_s \neq K_{s+1}$ for some $s \in \{1, 2, \ldots, k\}$. Assume that $g(z)z$ is strictly concave on an interval (a, b), $0 < a < b$ containing all points $p_i/K_i \in (a, b)$, $i \in \{1, 2, \ldots, mk\}$. Then the cycle $\{p_n\}$ is attenuant.*

Proof By Lemma 2, there exist $i, j \in \{1, 2, \ldots, mk\}$ such that $p_i/K_i \neq p_j/K_j$. Then, by the strict concavity of $g(z)z$, we have the following:

$$\begin{aligned} g\left(\frac{(p_i/2) + (p_j/2)}{(K_i/2) + (K_j/2)}\right)\left(\frac{p_i}{2} + \frac{p_j}{2}\right) &= g\left(t\frac{p_i}{K_i} + (1-t)\frac{p_j}{K_j}\right)\left(t\frac{p_i}{K_i} + (1-t)\frac{p_j}{K_j}\right)\frac{K_i + K_j}{2} \\ &> \left\{tg\left(\frac{p_i}{K_i}\right)\frac{p_i}{K_i} + (1-t)g\left(\frac{p_j}{K_j}\right)\frac{p_j}{K_j}\right\}\frac{K_i + K_j}{2} \\ &= \frac{1}{2}g\left(\frac{p_i}{K_i}\right)p_i + \frac{1}{2}g\left(\frac{p_j}{K_j}\right)p_j, \end{aligned}$$

where $t = K_i/(K_i + K_j)$. Hence,

$$\frac{1}{2}f(p_i, K_i) + \frac{1}{2}f(p_j, K_j) < f\left(\frac{1}{2}(p_i + p_j), \frac{1}{2}(K_i + K_j)\right). \tag{3}$$

By Lemma 1, we see that $f(x, y) = g(x/y)x$ is concave on $\{(x, y) \in \mathbb{R}^2_+ : ay < x < by\}$. Since $\{p_n\}$ is a solution of System (1), the following equation holds for all $n \in \mathbb{Z}_+$:

$$p_{n+1} = f(p_n, K_n).$$

Hence, by the concavity of $f(x, y)$ and Eq. (3), we have

$$\begin{aligned}
\frac{1}{mk}\sum_{n=1}^{mk} p_{n+1} &= \frac{1}{mk}\left\{\sum_{\substack{n=1\\ n\neq i,j}}^{mk} f(p_n, K_n) + 2\left(\frac{1}{2}f(p_i, K_i) + \frac{1}{2}f(p_j, K_j)\right)\right\} \\
&< \frac{1}{mk}\left\{\sum_{\substack{n=1\\ n\neq i,j}}^{mk} f(p_n, K_n) + 2f\left(\frac{1}{2}(p_i + p_j), \frac{1}{2}(K_i + K_j)\right)\right\} \\
&\leq f\left(\frac{1}{mk}\sum_{n=1}^{mk} p_n, \frac{1}{mk}\sum_{n=1}^{mk} K_n\right).
\end{aligned}$$

Furthermore, since $\{p_n\}$ and $\{K_n\}$ are periodic with periods m and k, respectively, we have $\bar{p} < f(\bar{p}, \bar{K})$, where $\bar{p} = \sum_{n=1}^{m} p_n/m$ and $\bar{K} = \sum_{n=1}^{k} K_n/k$. Since $f(x, \bar{K}) = g(x/\bar{K})x$, the assumptions of g implies that $f(x, \bar{K}) > x$ for all $x \in (0, \bar{K})$ and $f(x, \bar{K}) < x$ for all $x \in (\bar{K}, \infty)$. Hence, we have $\bar{p} < \bar{K}$. □

By this theorem, we easily see that a cycle of the Beverton-Holt equation (2) is attenuant since $g(z)z = \lambda z/\{1 + (\lambda - 1)z\}$ is concave. Since the monotonicity of $g(z)z$ is not assumed in Theorem 3, it is also applicable to population models without monotone $g(z)z$ (note that $g(z)z$ of Eq. (2) is monotone increasing). For example, the function $g(z)z$ of the Ricker equation is not monotone but concave on some interval. An example of application of Theorem 3 to the Ricker equation is found in Ref. [5] (see Refs. [3–5] for the stability of the attenuant cycles).

Acknowledgements

The author thanks Professor Robert J. Sacker for suggesting writing this short note.

References

[1] J. M. Cushing and S. M. Henson, Global dynamics of some periodically forced monotone difference equations, *J. Diff. Eq. Appl.*, **7** (2001), 859–872.
[2] J. M. Cushing and S. M. Henson, A periodically forced Beverton-Holt equation, *J. Diff. Eq. Appl.*, **8** (2002), 1119–1120.
[3] S. Elaydi and R.J. Sacker, Global stability of periodic orbits of non-autonomous difference equations and population biology, *J. Diff. Eq.*, (in press).
[4] S. Elaydi and R.J. Sacker, Global stability of periodic orbits of nonautonomous difference equations in population biology and the Cushing-Henson conjectures, *Proc. 8th Int. Conf. Diff. Eq., Brno*, (in press).
[5] R. Kon, Attenuant cycles of population models with periodic carrying capacity, *J. Diff. Eq. Appl.*, (in press).