Global stability of periodic orbits of nonautonomous difference equations in population biology and the Cushing-Henson conjectures*

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Abstract

Elaydi and Yakubu showed that a globally asymptotically stable(GAS) periodic orbit in an autonomous difference equation must in fact be a fixed point whenever the phase space is connected. In this paper we extend this result to periodic nonautonomous difference equations via the concept of skew-product dynamical systems. We show that for a k-periodic difference equation, if a periodic orbit of period r is GAS, then r must be a divisor of k. In particular sub-harmonic, or long periodic, oscillations cannot occur. Moreover, if r divides k we construct a non-autonomous dynamical system having minimum period k and which has a GAS periodic orbit with minimum period r. Our methods are then applied to prove two conjectures of J. Cushing and S. Henson concerning a non-autonomous Beverton-Holt equation which arises in the study of the response of a population to a periodically fluctuating environmental force such as seasonal fluctuations in carrying capacity or demographic parameters like birth or death rates. We show that the periodic fluctuations in the carrying capacity always have a deleterious effect on the average population, thus answering in the affirmative the second of the conjectures.

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1 Non-autonomous difference equations

A periodic difference equation with period k

$$x_{n+1} = F(n, x_n), \quad F(n+k, x) = F(n, x) \quad x \in \mathbb{R}^n$$

may be treated in the setting of skew-product dynamical systems [10], [9] by considering mappings

$$f_n(x) = F(n, x) \qquad f_i : \mathcal{F}_i \to \mathcal{F}_{i+1 \bmod k}$$

where $\mathcal{F}_i$, the “fiber” over f_i, is just a copy of $\mathbb{R}^n$ residing over f_i and consisting of those x on which f_i acts, fig.1. Then the unit time mapping

$$(x, f_i) \longrightarrow (f_i(x), f_{i+1 \bmod k})$$

generates a semi-dynamical system on the product space

$$X \times Y \quad \text{where} \quad Y = \{f_0, \ldots, f_{k-1}\} \subset \mathbf{C}, \qquad X = \mathbb{R}^n \tag{1.1}$$

where $\mathbf{C}$ is the space of continuous functions, fig.1. We thus study the k-periodic mapping system

$$x_{n+1} = f_n(x_n), \qquad f_{n+k} = f_n \tag{1.2}$$

It is then not difficult to see that an *autonomous* equation f is one that leaves the fiber over f invariant, or put another way, f is a fixed point of the mapping $f_i \longrightarrow f_{i+1 \bmod k}$.

In Elaydi and Sacker [6] the concept of a “geometric r-cycle” was introduced and defined. The definition says essentially that a geometric r-cycle is the projection onto the factor X in the product space (1.1) of an r-cycle in the skew-product flow.

A geometric cycle is called globally asymptotically stable if the corresponding periodic orbit in the skew-product flow is globally asymptotically stable in the usual sense. The example in figure 1 is clearly *not* globally asymptotically stable. Globally asymptotically stable geometric r-cycles may be constructed using the following simple device. On $\mathbb{R}$ define $g(x) = 0.5x$. Then for $r = 3$ any $k \geq 5$ define

$$\begin{aligned} f_0 = f_1 &= \cdots = f_{k-4} \\ f_{k-3} &= g(x) + 1 \\ f_{k-2} &= g(x-1) + 2 \\ f_{k-1} &= g(x-2) \end{aligned}$$

The geometric 3-cycle consists of $\{0, 1, 2\}$. However if one watches the progress of “0” in $\mathbb{R}$ alone one will observe the (minimum period) k-cycle

$$x_0 = 0 \to 0 \to \cdots \to 0 \to 0 \to 0 \to 1 \to 2 \to 0 = x_0,$$

even though “0” seems at first to be fixed (imagine k very large). This can easily be generalized to

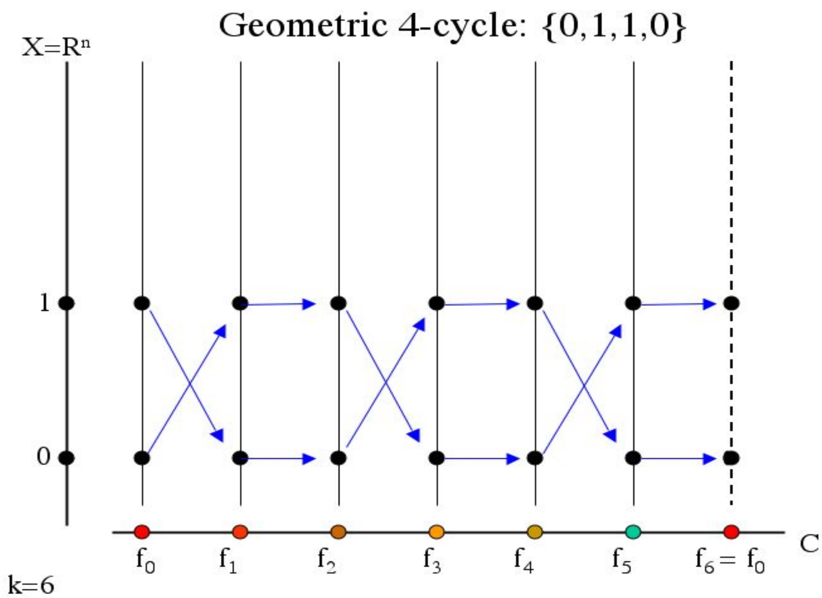

Figure 1: Skew-product flow. Example shown with n=1.

Theorem 1 *Given $r \geq 1$ and $k > r+1$ there exists a k periodic mapping system having a globally asymptotically stable geometric k-cycle one of whose points "appears" fixed, i.e. it is fixed for $k-r$ iterations.*

In general, when we have a geometric r-cycle with $r \leq k$, one has the following

Theorem 2 [**6**] *Assume that X is a connected metric space and each $f_i \in Y$ is a continuous map on X. Let $c_r = \{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{r-1}\}$ be a geometric r-cycle of equation (1.2). If c_r is globally asymptotically stable then $r|k$, i.e. r divides k.*

Thus the geometric 4-cycle in fig.1 cannot be globally asymptotically stable.

The next theorem shows how to construct such a dynamical system given any two positive integers r and k with $r|k$.

Theorem 3 [**6**] *Given any two positive integers r and k with $r|k$ then there exists a non-autonomous dynamical system having minimum period k and which has a globally asymptotically stable geometric r-cycle with minimum period r.*

2 The Beverton-Holt Equation

The Beverton-Holt equation has been studied extensively by Jim Cushing and Shandelle Henson [3, 4]. Also known as the *Beverton-Holt stock-recruitment equation* [1], it is a model for density dependent growth which exhibits *compensation* (Neave [8]) as opposed to *over-compensation* (Clark [2]), see also (Kot [7]). The equation takes the form

$$x_{n+1} = \frac{\mu K x_n}{K + (\mu - 1)x_n}, \qquad x_0 \geq 0 \quad K > 0$$

where μ is the per-capita growth rate and K is the carrying capacity. It is easily shown that for $0 < \mu < 1$ the equilibrium (fixed point) $x = 0$ is globally asymptotically stable whereas for $\mu > 1$ the fixed point K is globally asymptotically stable.
In [3] the authors considered a periodic carrying capacity $K_{n+k} = K_n$ caused by a periodically (seasonally) fluctuating environment

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

Defining

$$f_i(x) \doteq \frac{\mu K_i x}{K_i + (\mu - 1)x}$$

we have an equation of the form (1.2) with period k.

Although this is not always desirable from a qualitative point of view, we will compute a "solution" in closed form of the periodic Beverton-Holt equation.

After two iterations

$$x_2 = f_1 \circ f_0(x_0) = \frac{\mu^2 K_1 K_0 x_0}{K_1 K_0 + (\mu - 1)M_1 x_0}.$$

and inductively after k iterations

$$x_k = f_{k-1} \circ f_{k-2} \circ \cdots \circ f_0(x_0) = \frac{\mu^k K_{k-1} K_{k-2} \cdots K_0 x_0}{K_{k-1} K_{k-2} \cdots K_0 + (\mu - 1)M_{k-1} x} \tag{2.1}$$

where M_n satisfies the $2nd$ order *linear* difference equation:

$$M_{n+1} = K_{n+1} M_n + \mu^{n+1} K_n K_{n-1} \ldots K_0, \quad M_0 = 1.$$

Thus

$$M_{k-1} = \prod_{j=0}^{k-2} K_{j+1} + \sum_{m=0}^{k-2} \left(\prod_{i=m+1}^{k-2} K_{i+1} \right) \mu^{m+1} K_m K_{m-1} \cdots K_0.$$

Letting $L_{k-1} = K_{k-1} K_{k-2} \ldots K_0$, we finally obtain (defining H)

$$H(x) \doteq f_{k-1} \circ f_{k-2} \circ \cdots \circ f_0(x_0) = \frac{\mu^k L_{k-1} x_0}{L_{k-1} + (\mu - 1)M_{k-1} x_0}$$

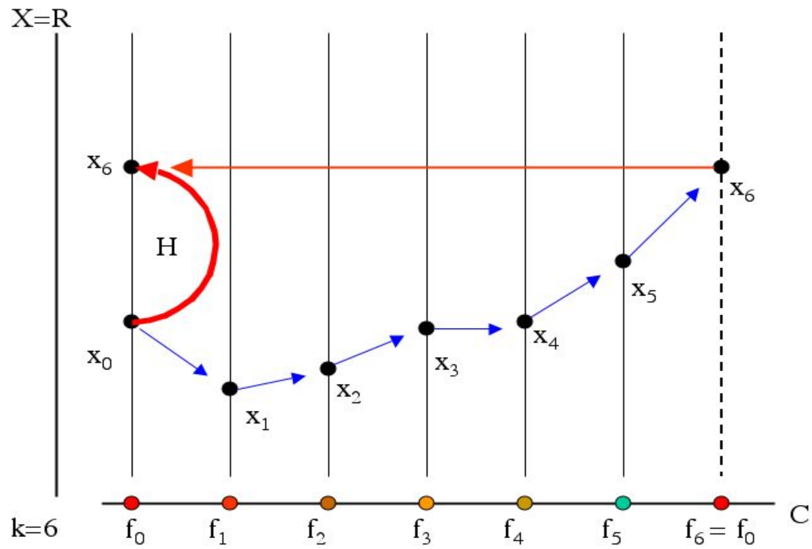

Figure 2:

But then the difference equation, $x_{n+1} = H(x_n)$ leaves the fiber (copy of $\mathbb{R}$) invariant and is thus independent of n, i.e. *autonomous*! (See fig.2 for $k = 6$).

While this may or may not be easy to glean from (2.1) we will nevertheless use (2.1) later, but only in the case $k = 2$:

$$\bar{x} = (\mu + 1)\frac{K_1 K_0}{K_1 + \mu K_0}. \tag{2.2}$$

The mapping $x_{n+1} = H(x_n)$ thus has the unique positive fixed point

$$\bar{x} = \frac{\mu^k - 1}{\mu - 1}\ \frac{L_{k-1}}{M_{k-1}}$$

which is globally asymptotically stable with respect to positive initial conditions. By Theorem 2 we have further that either $\bar{x}$ is of minimal period k or of minimal period r where $r|k$.

3 The Ricatti equation

We next consider the more general autonomous Ricatti equation

$$x_{n+1} = f(x_n), \qquad f(x) \doteq \frac{ax + b}{cx + d}$$

where we assume the following conditions

$$\begin{array}{ll} 1. & a,c,d>0,\ \ b\geq 0 \\ 2. & \quad ad-bc\neq 0 \\ 3. & bc>0 \quad \text{or} \quad a>d \end{array} \tag{3.1}$$

$$\begin{array}{lll} 1 & \Longrightarrow & f:\mathbb{R}^+\to\mathbb{R}^+ \\ 2 & \Longrightarrow & f \quad \text{not a constant function} \\ 3 & \Longrightarrow & f \quad \text{has a positive fixed point (Bev.-Holt if } b=0) \end{array}$$

Under composition, letting

$$g(x)=\frac{\alpha x+\beta}{\gamma x+\delta}\ ,$$

one easily obtains

$$g\circ f(x)=\frac{(a\alpha+c\beta)x+(b\alpha+d\beta)}{(a\gamma+c\delta)x+(b\gamma+d\delta)}$$

from which 1,2 and 3 in (3.1) easily follow.

The following change of variables, Elaydi [5, p.87]

$$cx_n+d=\frac{y_{n+1}}{y_n}$$

reduces the Ricatti equation to a $2nd$ order *linear* equation

$$y_{n+2}-py_{n+1}-qy_n=0$$

where $p=a+d$ and $q=bc-ad$. The general solution is then

$$y_n=c_1\lambda_{max}^n+c_2\lambda_{min}^n$$

where λ_{max} and λ_{min} are the roots of the characterstic equation $\lambda^2-p\lambda-q=0$,

$$\lambda_{max}=\frac{a+d+\sqrt{(a-d)^2+4bc}}{2}, \tag{3.2}$$

$$\lambda_{min}=\frac{a+d-\sqrt{(a-d)^2+4bc}}{2} \tag{3.3}$$

One can show that $c_1\neq 0$ for solutions through $x_0>0$ from which it follows that

$$\frac{y_{n+1}}{y_n}\to\lambda_{max}.$$

From this it follows that

$$x_n\to x^*\doteq\frac{\lambda_{max}-d}{c},$$

and therefore x^* is a globally asymptotically stable fixed point in $\mathbb{R}^+$.

We now consider the **periodic Ricatti equation**

$$x_{n+1} = f_n(x_n) \doteq \frac{a_n x_n + b_n}{c_n x_n + d_n}$$

where the coefficients satisfy 1, 2 and 3 in (3.1) and have period $k > 0$. Again, the function H defined by

$$H(x) \doteq f_{k-1} \circ f_{k-2} \circ \cdots \circ f_1 \circ f_0$$

has the same Ricatti form and satisfies 1, 2 and 3 in (3.1). Thus we conclude that the periodic Ricatti equation has a globally asymptotically stable geometric r-cycle and by Theorem 2, $r|k$.

4 The General Case

In the previous sections we based our analysis on the special form the difference equations had. In this section we extract the salient properties that makes it all work. Recall that $h : \mathbb{R}^+ \to \mathbb{R}^+$ is **concave** if

$$h(\alpha x + \beta y) \geq \alpha h(x) + \beta h(y) \qquad \text{for all } x, y \in \mathbb{R}^+$$

where $\alpha, \beta \geq 0, \alpha + \beta = 1$. The following property is easily verified: **If f, g are concave and f is increasing then $f \circ g$ is concave**. Note however that by requiring our maps to take values in $\mathbb{R}^+$ *and* to be defined on *all* of $\mathbb{R}^+$, a concave function is automatically increasing.

Define the class $\mathcal{K}$ to be all functions which satisfy

(1) $f : \mathbb{R}^+ \to \mathbb{R}^+$ is continuous

(2) f is concave (and therefore increasing)

(3) There exist x_1 and x_2 such that $f(x_1) > x_1$ and $f(x_2) < x_2$, i.e. the graph of f crosses the "diagonal".

$\mathcal{K}$ generalizes the class "A1" of Cushing and Henson [3].

Properties of $\mathcal{K}$.

(a) $\mathcal{K}$ is closed under the operation of composition, i.e. $f, g \in \mathcal{K}$ implies $f \circ g \in \mathcal{K}$. Thus $\mathcal{K}$ is a semi-group under composition.

(b) Each f has a unique globally asymptotically stable fixed point $x_f > 0$

(c) If $f, g \in \mathcal{K}$ with $x_f < x_g$ then $x_f < x_{f\circ g} < x_g$ and $x_f < x_{g\circ f} < x_g$

Thus, for the k-periodic difference equation

$$x_{n+1} = F(n, x_n), \qquad x \in \mathbb{R} \tag{4.1}$$

if for all n, $f_n \in \mathcal{K}$, where $f_n(x) = F(n, x)$ then g defined by

$$g(x) \doteq f_{k-1} \circ f_{k-2} \circ \cdots \circ f_1 \circ f_0 \in \mathcal{K}$$

represents an autonomous equation

$$x_{n+1} = g(x_n)$$

having a unique globally asymptotically stable fixed point. Therefore the difference equation (4.1) has a globally asymptotically stable geometric r-cycle and by Theorem 2, $r|k$.

5 The Cushing and Henson Conjectures

In [4], Cushing and Henson conjectured that for the periodic k-Beverton-Holt equation, $k \geq 2$

$$x_{n+1} = \frac{\mu K_n x_n}{K_n + (\mu - 1)x_n}, \quad \mu > 1, \; K_n > 0,$$

1. **[Conj.1]** There is a positive k-periodic solution $\{\bar{x}_0 . \ldots, \bar{x}_{k-1}\}$ and it globally attracts all positive solutions
2. **[Conj.2]** The average over n values $\{y_0, y_1, \ldots, y_{n-1}\}$, $av(y_n) \doteq \frac{1}{k}\sum_{i=0}^{k-1} y_i$ satisfies

$$av(\bar{x}_n) < av(K_n)$$

In Conj.2 it is implicit that the minimal period of the cycle $\{\bar{x}_0 . \ldots, \bar{x}_{k-1}\}$ exceeds one, i.e. it is not a fixed point. The truth of Conj.2 implies that a fluctuating habitat has a deleterious effect on the population in the sense that the average population is less in a periodically oscillating habitat than it is in a constant habitat with the same average. Earlier [3] they proved both statements for $k = 2$. By our remarks in the previous section, Conj.1 is now completely solved: There exists a positive r-periodic globally asymptotically stable solution, with respect to $(-\infty, \infty)$, and moreover $r|k$.

We now answer Conj.2 in the affirmative for all $k \geq 2$ and in the process give a much simpler proof in the $k = 2$ case.

Comment: Without loss of generality we will now assume that k is the *minimal* period. Then for the periodic sequence $\{K_0, K_1, \ldots, K_{k-1}, K_k = K_0\}$, it follows that $K_i \neq K_{i+1}$ for at least one $i \in \{0, 1, \ldots, k-2\}$.
Everything then follows from an elementary algebraic lemma:

Lemma 4 *Define, for $\alpha, \beta, x, y \in (0, \infty), \alpha + \beta = 1$,*

$$g(x, y) = \frac{xy}{\alpha x + \beta y} - \beta x - \alpha y.$$

Then $g(x, y) \leq 0$ with "$=$" $\iff$ $x = y$.

Equivalently,

$$\frac{xy}{\alpha x + \beta y} < \beta x + \alpha y, \quad \iff x \neq y.$$

Proof

$$\begin{aligned} & (\alpha x + \beta y) g(x, y) \\ = \;& \{(1 - \alpha^2 - \beta^2) xy - \alpha\beta(x^2 + y^2)\} \\ = \;& -\alpha\beta(x - y)^2. \end{aligned} \qquad QED$$

We first derive a formula for a fixed point, $x_{f \circ g}$ of the composition of 2 Beverton-Holt functions using the formula (2.2):

$$\begin{aligned} f(x) &= \frac{\mu K x}{K + (\mu - 1)x}, \quad g(x) = \frac{\mu L x}{L + (\mu - 1)x} \\ x_{f \circ g} &= (1 + \mu)\frac{KL}{K + \mu L} = \frac{KL}{\alpha K + \beta L} = \frac{x_f x_g}{\alpha x_f + \beta x_g} \end{aligned} \tag{5.1}$$

where $\alpha = 1/(\mu + 1)$ and $\beta = \mu/(\mu + 1)$. From the previous comment and the lemma it follows that

$$x_{f \circ g} = \frac{x_f x_g}{\alpha x_f + \beta x_g} \leq \beta x_g + \alpha x_f, \tag{5.2}$$

with strict inequality for at least one pair $f = f_i,\ g = f_{i+1},\ i \in \{0, 1, \ldots, k-2\}$.

Proof of Conj.2 for k=2:

$$f_0(x) = \frac{\mu K_0 x}{K_0 + (\mu - 1)x}, \quad f_1(x) = \frac{\mu K_1 x}{K_1 + (\mu - 1)x}$$

$$\begin{aligned} f_1 \circ f_0(x_0) &= x_0 = x_{f_1 \circ f_0} = \frac{K_1 K_0}{\alpha K_1 + \beta K_0} \\ f_0 \circ f_1(x_1) &= x_1 = x_{f_0 \circ f_1} = \frac{K_0 K_1}{\alpha K_0 + \beta K_1} \end{aligned}$$

Now add and use (5.2) and $\alpha + \beta = 1$,

$$\begin{aligned} x_0 + x_1 &= \frac{K_1 K_0}{\alpha K_1 + \beta K_0} + \frac{K_0 K_1}{\alpha K_0 + \beta K_1} \\ &< \alpha K_0 + \beta K_1 + \alpha K_1 + \beta K_0 \\ &= K_0 + K_1. \qquad QED \end{aligned}$$

Proof for k $>$ 2:
I. **For** k **odd**, assume, inductively that Conj.2 is true for $(k+1)/2$.

Take **k=3**. Then

$$f_2 \circ (f_1 \circ f_0)(x_0) = x_0, \qquad f_0 \circ (f_2 \circ f_1)(x_1) = x_1$$
$$f_1 \circ (f_0 \circ f_2)(x_2) = x_2.$$

Using the period 2 result,

$$\begin{aligned} 1. \quad f_1 \circ f_0(x_0) &= x_2, \quad \text{and} \quad f_2(x_2) = x_0 \implies \\ x_0 + x_2 &\leq x_{f_1 \circ f_0} + x_{f_2} = \frac{K_1 K_0}{\alpha K_1 + \beta K_0} + K_2 \\ &\leq \alpha K_0 + \beta K_1 + K_2 \\ 2. \quad f_2 \circ f_1(x_1) &= x_0, \quad \text{and} \quad f_0(x_0) = x_1 \implies \\ x_0 + x_1 &\leq x_{f_2 \circ f_1} + x_{f_0} \leq \alpha K_1 + \beta K_2 + K_0 \\ 3. \quad f_0 \circ f_2(x_2) &= x_1, \quad \text{and} \quad f_1(x_1) = x_2 \implies \\ x_1 + x_2 &\leq x_{f_0 \circ f_2} + x_{f_1} \leq \alpha K_2 + \beta K_0 + K_1 \end{aligned}$$

where at least one of the inequalities is strict. Adding, using (5.2) and $\alpha + \beta = 1$ we get

$$2(x_0 + x_1 + x_2) < 2(K_0 + K_1 + K_2).$$

Sketch for k=5:(fig.3)

$$f_1 \circ f_0(x_0) = x_2, \quad f_3 \circ f_2(x_2) = x_4,$$
$$f_4(x_4) = x_0 \implies$$
$$x_0 + x_2 + x_4 \leq x_{f_1 \circ f_0} + x_{f_3 \circ f_2} + x_{f_4}$$

After one cyclic permutation:

$$x_1 + x_3 + x_0 \leq x_{f_2 \circ f_1} + x_{f_4 \circ f_3} + x_{f_0}.$$

After 3 **more cyclic permutation:**

$$\begin{aligned} x_2 + x_4 + x_1 &\leq x_{f_3 \circ f_2} + x_{f_0 \circ f_4} + x_{f_1} \\ x_3 + x_0 + x_2 &\leq x_{f_4 \circ f_3} + x_{f_1 \circ f_0} + x_{f_2} \\ x_4 + x_1 + x_3 &\leq x_{f_0 \circ f_4} + x_{f_2 \circ f_1} + x_{f_3} \end{aligned}$$

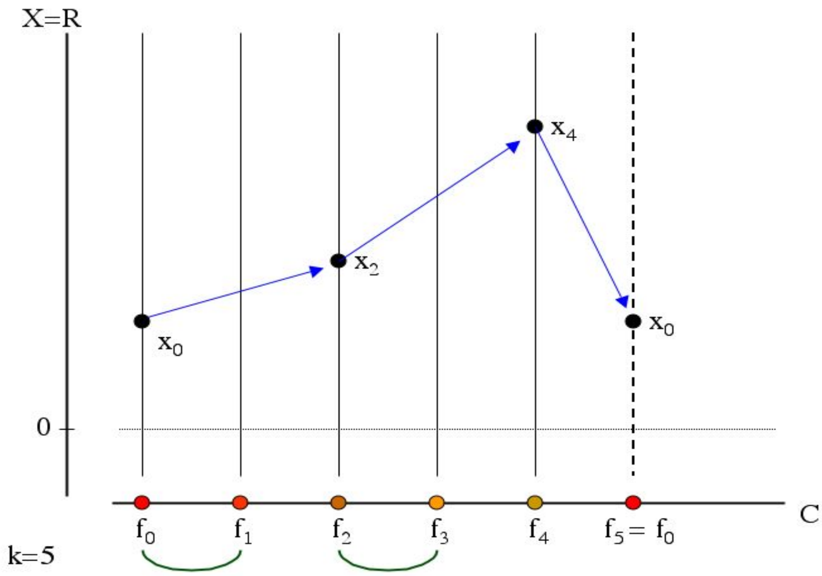

Figure 3:

where at least one of the inequalities is strict. Adding gives the result

$$3(x_0 + x_1 + \cdots + x_4) < 3(K_0 + K_1 + \cdots + K_4).$$

Sketch for k even, k=6: (fig.4) Inductively assume the conjecture true for $k/2$.

$$\begin{aligned} f_1 \circ f_0(x_0) &= x_2, \quad f_3 \circ f_2(x_2) = x_4, \quad f_5 \circ f_4(x_4) = x_0 \\ &\Longrightarrow \quad x_0 + x_2 + x_4 \leq x_{f_1 \circ f_0} + x_{f_3 \circ f_2} + x_{f_5 \circ f_4} \\ &\leq \quad \alpha K_0 + \beta K_1 + \alpha K_2 + \beta K_3 + \alpha K_4 + \beta K_5 \end{aligned} \tag{5.3}$$

After one (and only one) cyclic permutation: (fig.5)

$$\begin{aligned} f_2 \circ f_1(x_1) &= x_3, \quad f_4 \circ f_3(x_3) = x_5, \quad f_0 \circ f_5(x_5) = x_1 \\ &\Longrightarrow \quad x_1 + x_3 + x_5 \leq x_{f_2 \circ f_1} + x_{f_4 \circ f_3} + x_{f_0 \circ f_5} \\ &\leq \quad \alpha K_1 + \beta K_2 + \alpha K_3 + \beta K_4 + \alpha K_5 + \beta K_0 \end{aligned} \tag{5.4}$$

where at least one of the inequalities is strict. Adding (5.3) and (5.4), we obtain the result.

Theorem 5 *For a k-periodic Beverton-Holt equation with minimal period $k \geq 2$*

$$x_{n+1} = \frac{\mu K_n x_n}{K_n + (\mu - 1)x_n}, \quad \mu > 1, \; K_n > 0$$

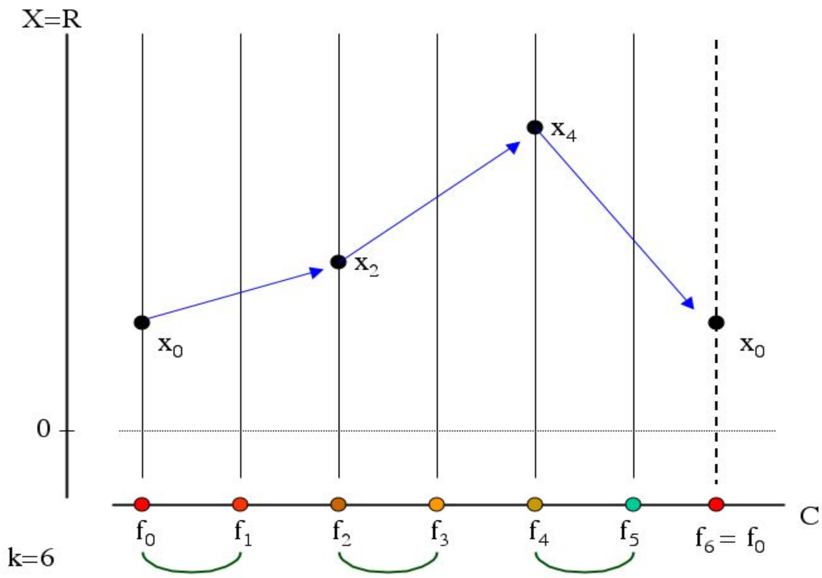

Figure 4:

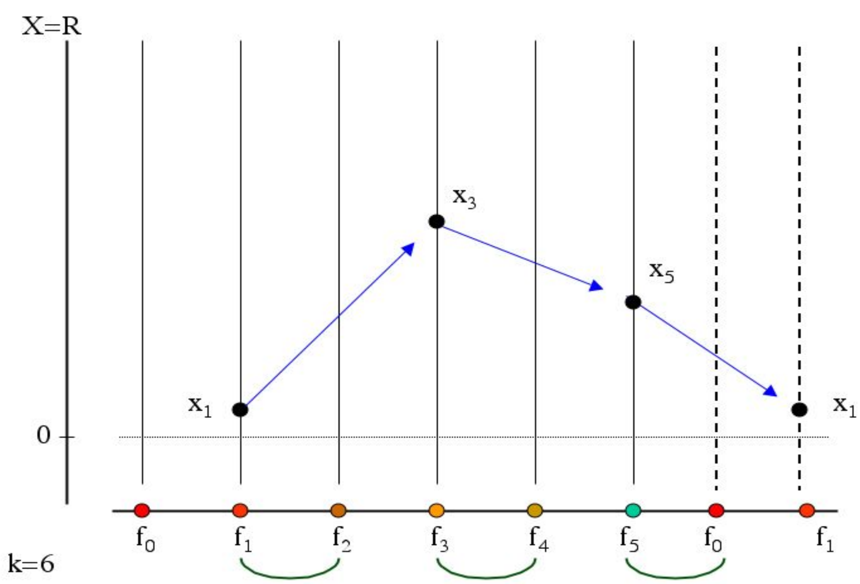

Figure 5:

there exists a unique globally asymptotically stable k-cycle, $C = \{\xi_0, \xi_1, \ldots, \xi_{k-1}\}$ *and*

$$\mathrm{av}(\xi_n) < \mathrm{av}(K_n)$$

Summary of proof: **Zig-zag induction**

1. Prove it directly for $k = 2$,
2. k odd: True for $(k+1)/2 \implies$ True for k,
3. k even: True for $k/2 \implies$ True for k.

By judiciously pairing and permuting the maps and using only the formula for the fixed point of 2 maps, (5.1), it is straightforward to write down the complete proof for any $k > 2$.

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