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Research article

The Beverton–Hold model on isolated time scales

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Abstract: In this work, we formulate the Beverton–Holt model on isolated time scales and extend existing results known in the discrete and quantum calculus cases. Applying a recently introduced definition of periodicity for arbitrary isolated time scales, we discuss the effects of periodicity onto a population modeled by a dynamic version of the Beverton–Holt equation. The first main theorem provides conditions for the existence of a unique ω-periodic solution that is globally asymptotically stable, which addresses the first Cushing–Henson conjecture on isolated time scales. The second main theorem concerns the generalization of the second Cushing–Henson conjecture. It investigates the effects of periodicity by deriving an upper bound for the average of the unique periodic solution. The obtained upper bound reveals a dependence on the underlying time structure, not apparent in the classical case. This work also extends existing results for the Beverton–Holt model in the discrete and quantum cases, and it complements existing conclusions on periodic time scales. This work can furthermore guide other applications of the recently introduced periodicity on isolated time scales.

Keywords: Beverton–Holt equation; Cushing–Henson conjecture; isolated time scale; periodicity concept; periodic solutions

1. Introduction

The Beverton–Holt recurrence

$$x_{t+1} = \frac{\eta K x_t}{K + (\eta - 1)x_t}, \tag{1.1}$$

where η is the proliferation rate and K is the carrying capacity, was derived in [1] in the context of fisheries. The solution of the logistic differential equation evaluated at time $T + t_0$ is used to describe the adult fish population (new generation), and the solution at time t_0 represents the juveniles (old generation). The derivation led to a proliferation rate $\eta = e^{rT} > 1$, where $r > 0$ is the growth rate of the underlying continuous model and T is the time span until adulthood. Equation (1.1) for more general parameters is also known as the Pielou equation [2]. For related work on the Beverton–Holt equation, see [3–12], and for other related work, see [13–16].

In [17], Cushing and Henson investigated the effects of a periodically enforced carrying capacity onto flour beetles, which were modeled by the Beverton–Holt recurrence (1.1). Based on their observations, the authors conjectured that the introduction of a periodic environment on populations, modeled by (1.1), results in the existence of a unique periodic solution. Further, the authors predicted that a periodic environment is deleterious to the population, as the average of the unique periodic solution is bounded above by the mean of the periodic environment. These conclusions were formulated as the first and second Cushing–Henson conjectures.

In the case of a two-periodic K_t and constant η, the conjectures have been analytically verified in [18]. For higher-order periodic carrying capacities K_t, the conjectures have been the focus of the works [19, 20]. A discussion assuming additionally time-dependent growth rates can be found in [21]. The extension of the conjectures to periodic time scales was addressed in [22]. Periodic time scales are time domains such that if t is in the time scale, then so is $t + \omega$, hence requiring an additive time structure. The discrete time setting obeys this additive property and is a special case of a periodic time scale, in contrast to the quantum time setting $q^{\mathbb{N}_0}$, which is not periodic. Periodic time scales are a subset of arbitrary time scales, a theory developed by Stefan Hilger in 1988, that unifies the discrete and continuous theories. Studying the Beverton–Holt model on time scales provides a platform to consider time-dependent time spans until adulthood instead of a constant time span T, as assumed in the derivation of the Beverton–Holt model. Due to a lack of existing periodicity definitions for general time domains, the conjectures remained unsolved for this and other examples of nonperiodic time scales. In [23], in order to extend the study to the quantum time scale, the authors defined periodicity in the quantum setting and discussed the Cushing–Henson conjectures. In the quantum time setting, the Beverton–Holt model reads as

$$x(qt) = \frac{\eta K(t)x(t)}{K(t) + (\eta - 1)x(t)}$$

with the carrying capacity $K : q^{\mathbb{N}_0} \to \mathbb{R}^+ := (0, \infty)$ $(q > 1)$ and proliferation rate $\eta > 1$. In [23], the authors proved the existence and global stability of a unique periodic solution for periodic carrying capacities, i.e., for K such that $q^\omega K(q^\omega t) = K(t)$, confirming the first Cushing–Henson conjecture for the q-Beverton–Holt model. In [24], the authors were able to extend this result to time-dependent proliferation rates. The second Cushing–Henson conjecture, however, only remained true in the quantum time scale with a slight modification as follows.

Theorem 1.1 (See [23, Theorem 5.6]). *The average of the ω-periodic solution $\bar{x}$ of the q-Beverton–Holt model is strictly less than the average of the ω-periodic carrying capacity times the constant $\frac{q-\lambda}{1-\lambda}$, i.e.,*

$$\int_1^{q^\omega} \bar{x}(t)\Delta t \le \frac{q - \lambda}{1 - \lambda} \int_1^{q^\omega} K(t)\Delta t,$$

where $\lambda = 1 - (q - 1)A$, $\eta = \frac{1}{1-(q-1)A}$, and $A > 0$.

The multiplicative constant in Theorem 1.1 can be expressed by

$$\frac{q-\lambda}{1-\lambda} = \frac{(q-1)(1+A)}{(q-1)A} = \frac{(q-1)\frac{\eta(q-1)+\eta-1}{\eta(q-1)}}{\frac{\eta-1}{\eta}} = \frac{q\eta-1}{\eta-1}. \tag{1.2}$$

This indicates that the second conjecture does not necessarily hold, and it reveals that the time scale determines the proportionality constant linearly. Given this reformulation of the classical second Cushing–Henson conjecture in the special case of a quantum time scale, we aim to find a general formulation of this conjecture on arbitrary isolated time scales. On any isolated time scale $\mathbb{T}$, we therefore consider the Beverton–Holt model

$$x^\sigma = \frac{\eta K x}{K+(\eta-1)x}, \tag{1.3}$$

where $\eta, K : \mathbb{T} \to \mathbb{R}^+$, $\eta > 1$, and where $\sigma(t)$ is the next time step following t. We can express the recurrence (1.3) as a dynamic equation

$$\frac{x^\sigma - x}{\mu} =: x^\Delta = \alpha x^\sigma\left(1-\frac{x}{K}\right) \quad \text{with} \quad \alpha = \frac{\eta-1}{\mu\eta}, \tag{1.4}$$

where $\mu(t)$ is the distance to the time point following t, formally introduced in Section 2. Equation (1.4) is known as the logistic dynamic equation [25], and it can be transformed equivalently into a linear dynamic equation using the variable substitution $u = 1/x$ for $x \neq 0$, namely

$$u^\Delta = -\alpha u + \frac{\alpha}{K}. \tag{1.5}$$

To study the effects of periodicity on (1.3) on arbitrary time scales, we utilize the recently introduced definition of periodicity in [26]. This new concept was already successfully applied in [27]. This and other useful definitions are stated in Section 2. Section 3 concerns the generalization of the first Cushing–Henson conjecture, discussing the existence of a unique globally asymptotically stable periodic solution. The generalization of the second Cushing–Henson conjecture is addressed in Section 4. The paper is completed in Section 5 with some concluding remarks.

2. Time scales fundamentals

In this section, we introduce some necessary time scales fundamentals. A time scale $\mathbb{T}$ is a closed nonempty subset of $\mathbb{R}$.

Definition 2.1 (See [28, Definition 1.1])**.** For $t \in \mathbb{T}$, the forward jump operator $\sigma : \mathbb{T} \to \mathbb{T}$ is defined by

$$\sigma(t) = \inf\{s \in \mathbb{T} : s > t\}.$$

We adopt the convention that $\inf \emptyset = \sup \mathbb{T}$. If $\sigma(t) > t$, then we say that t is right-scattered. If $\sigma(t) = t$, then we say that t is right-dense. Similarly, left-scattered and left-dense points are defined. The graininess $\mu : \mathbb{T} \to \mathbb{R}_0^+$ is defined by $\mu(t) := \sigma(t) - t$. We define $f^\sigma : \mathbb{T} \to \mathbb{R}$ by $f^\sigma := f \circ \sigma$. If $\mathbb{T}$ has a left-scattered maximum M, then we define $\mathbb{T}^\kappa = \mathbb{T} \setminus \{M\}$; otherwise, $\mathbb{T}^\kappa = \mathbb{T}$.

In this work, we focus on **isolated** time scales, i.e., all points are left-scattered and right-scattered. Hence, in what follows, throughout, $\mathbb{T}$ refers to an **isolated** time scale, and the following definitions and results are taking this special time structure already into account, as well as the entire remainder of this paper.

Definition 2.2 (See [25, Definition 2.25]). A function $p : \mathbb{T} \to \mathbb{R}$ is called regressive, denoted by $\mathcal{R}$, provided

$$1 + \mu(t)p(t) \neq 0 \quad \text{for all} \quad t \in \mathbb{T}.$$

Moreover, p is called positively regressive, denoted by $\mathcal{R}^+$, provided

$$1 + \mu(t)p(t) > 0 \quad \text{for all} \quad t \in \mathbb{T}.$$

Remark 2.3. Assume $f : \mathbb{T} \to \mathbb{R}$ and $t \in \mathbb{T}^\kappa$. Then the delta-derivative of f, denoted by f^Δ (see [25, Definition 1.10]), is

$$f^\Delta(t) = \frac{f(\sigma(t)) - f(t)}{\mu(t)}.$$

For $f, g : \mathbb{T} \to \mathbb{R}$, the product-rule for $t \in \mathbb{T}^\kappa$ (see [25]) reads as

$$(fg)^\Delta = f^\Delta g^\sigma + f g^\Delta = f^\Delta g + f^\sigma g^\Delta, \tag{2.1}$$

and, if $g \neq 0$, the quotient-rule (see [25]) reads as

$$\left(\frac{f}{g}\right)^\Delta = \frac{f^\Delta g - f g^\Delta}{g g^\sigma}.$$

The delta integral is defined for $a, b \in \mathbb{T}$ with $a < b$ by

$$\int_a^b f(\tau)\Delta\tau = \sum_{\tau \in [a,b)\cap\mathbb{T}} \mu(\tau) f(\tau),$$

and consequently,

$$F^\Delta = f, \quad \text{if} \quad F(t) = \int_a^t f(\tau)\Delta\tau.$$

Using the product rule, we get the integration by parts formula (see [25])

$$\int_a^b (f^\Delta g)(t)\Delta t = (fg)(b) - (fg)(a) - \int_a^b (f^\sigma g^\Delta)(t)\Delta t. \tag{2.2}$$

The following circle-plus addition turns $(\mathcal{R}, \oplus)$ into an Abelian group.

Definition 2.4 (See [28, p. 13]). Define circle plus and circle minus by

$$p \oplus q = p + q + \mu pq, \quad p \ominus q = \frac{p - q}{1 + \mu q} \quad \text{for} \quad q \in \mathcal{R}.$$

Theorem 2.5 (See [25, Theorem 2.33]). *Let $p \in \mathcal{R}$ and $t_0 \in \mathbb{T}$. Then the initial value problem*

$$y^\Delta = p(t)y, \quad y(t_0) = 1$$

possesses a unique solution.

The unique solution from Theorem 2.5 is called the dynamic exponential function and is denoted by $e_p(\cdot, t_0)$. On an isolated time scale, the dynamic exponential function for $p \in \mathcal{R}$ is

$$e_p(t, t_0) = \prod_{s\in[t_0,t)\cap\mathbb{T}} (1 + \mu(s)p(s)), \quad t > t_0.$$

Useful properties of the dynamic exponential function follow. Part 6 can easily be shown using parts 4 and 5. Part 8 is the content of [25, Theorem 2.39]. Part 9 is in [25, Theorem 2.48(i)], and the remaining parts are from [25, Theorem 2.36].

Theorem 2.6. *If $p, q \in \mathcal{R}$ and $t, s, r \in \mathbb{T}$, then*

1. $e_0(t, s) = 1$ *and* $e_p(t, t) = 1$,
2. $e_{p\oplus q}(t, s) = e_p(t, s)e_q(t, s)$,
3. $e_{p\ominus q}(t, s) = \frac{e_p(t,s)}{e_q(t,s)}$,
4. $e_{\ominus p}(t, s) = e_p(s, t) = \frac{1}{e_p(t,s)}$,
5. $e_p(\sigma(t), s) = (1 + \mu(t)p(t))e_p(t, s)$,
6. $e_p(t, \sigma(s)) = \frac{e_p(t,s)}{1+\mu(s)p(s)}$,
7. $e_p^\Delta(\cdot, s) = pe_p(\cdot, s)$,
8. $e_p^\Delta(s, \cdot) = -pe_p^\sigma(s, \cdot)$,
9. $p \in \mathcal{R}^+$ *implies* $e_p(t, s) > 0$, *and*
10. *the semigroup property holds:* $e_p(t, r)e_p(r, s) = e_p(t, s)$.

The following result was used in [26, Proof of Theorem 6.2]. A variant of it was also included in [29, Theorem 2.1], see also [30, First formula in the line two lines after (3)]). Here we state it explicitly and include its short proof.

Lemma 2.7. *Let $f : \mathbb{T} \to \mathbb{R} \setminus \{0\}$ be delta-differentiable and $s, t \in \mathbb{T}$. Then*

$$e_{\frac{f^\Delta}{f}}(s, t) = \frac{f(s)}{f(t)}. \tag{2.3}$$

Proof. For fixed $t \in \mathbb{T}$, define $w(s) := \frac{f(s)}{f(t)}$. Since $f \neq 0$, $\frac{f^\Delta}{f} \in \mathcal{R}$ and

$$w^\Delta(s) = \frac{f^\Delta(s)}{f(t)} = \frac{f(s)}{f(t)}\frac{f^\Delta(s)}{f(s)} = w(s)\frac{f^\Delta(s)}{f(s)}, \quad w(t) = 1.$$

By Theorem 2.5, the claim follows. □

Theorem 2.8 (See [31])**.** *If f is nonnegative with $-f \in \mathcal{R}^+$, then*

$$1 - \int_s^t f(\tau)\Delta\tau \le e_{-f}(t, s) \le \exp\left(-\int_s^t f(\tau)\Delta\tau\right). \tag{2.4}$$

Theorem 2.9 (Variation of Constants, see [28, Theorem 2.77])**.** *If $p \in \mathcal{R}$, $f : \mathbb{T} \to \mathbb{R}$, $t_0 \in \mathbb{T}$, and $y_0 \in \mathbb{R}$, then the unique solution of the IVP*

$$y^\Delta = p(t)y + f(t), \quad y(t_0) = y_0$$

is given by

$$y(t) = e_p(t, t_0)y_0 + \int_{t_0}^t e_p(t, \sigma(s))f(s)\Delta s. \tag{2.5}$$

As mentioned in the introduction, the definition of periodicity is crucial in the discussion of effects of periodicity. We refer to our recent work [26], where we introduced periodicity on isolated time sales as follows.

Definition 2.10 (See [26, Definition 4.1])**.** Let $\omega \in \mathbb{N}$. A function $f : \mathbb{T} \to \mathbb{R}$ is called ω-periodic, denoted by $f \in \mathcal{P}_\omega$, provided

$$\nu^\Delta f^\nu = f, \quad \text{where} \quad \nu = \sigma^\omega \quad \text{and} \quad f^\nu = f \circ \nu. \tag{2.6}$$

Example 2.11. If $\mathbb{T} = \mathbb{Z}$, then $\nu(t) = t + \omega$, $\nu^\Delta(t) = 1$, and (2.6) reduces to the known definition of periodicity, $f(t+\omega) = f(t)$.

Example 2.12. If $\mathbb{T} = q^{\mathbb{N}_0}$, then $\nu(t) = q^\omega t$, $\nu^\Delta(t) = q^\omega$, and (2.6) reduces to the known definition of periodicity, $q^\omega f(q^\omega t) = f(t)$, which was introduced in [23].

Now, from our recent paper [26], we collect some results, supplemented by some new tools (substitution rule and change of order of integration formula), that will be used in the remainder of this study.

Lemma 2.13 (See [26, Theorem 5.6 and Corollary 5.8])**.** *If $f, g \in \mathcal{P}_\omega$, then*

$$f + g, f - g, \ominus f, f \oplus g \in \mathcal{P}_\omega.$$

Lemma 2.14 (See [26, Theorem 5.1])**.** *$f \in \mathcal{P}_1$ iff μf is constant.*

Lemma 2.15 (See [26, Lemma 4.6])**.** *We have $\mathcal{P}_1 \subset \mathcal{P}_\omega$ for all $\omega \in \mathbb{N}$.*

Lemma 2.16 (See [26, Lemma 3.1])**.** *We have the formula*

$$\mu\nu^\Delta = \mu^\nu. \tag{2.7}$$

Theorem 2.17 (Chain Rule, Substitution Rule)**.** *For $f : \mathbb{T} \to \mathbb{R}$, we have*

$$F_\nu^\Delta = \nu^\Delta f^\nu - f, \quad \text{if} \quad F_\nu(t) = \int_t^{\nu(t)} f(\tau)\Delta\tau. \tag{2.8}$$

Moreover, if $s, t \in \mathbb{T}$, then

$$\int_{\nu(s)}^{\nu(t)} f(\tau)\Delta\tau = \int_s^t \nu^\Delta(\tau) f(\nu(\tau))\Delta\tau. \tag{2.9}$$

Proof. Equation (2.8) is the content of [26, Lemma 3.8]. Using (2.8), we get

$$\begin{aligned}
\int_{\nu(s)}^{\nu(t)} f(\tau)\Delta\tau &= F_\nu(t) - F_\nu(s) + \int_s^t f(\tau)\Delta\tau \\
&= \int_s^t \left(F_\nu^\Delta(\tau) + f(\tau)\right)\Delta\tau \\
&= \int_s^t \nu^\Delta(\tau) f^\nu(\tau)\Delta\tau,
\end{aligned}$$

i.e., (2.9) holds. □

Theorem 2.18 (See [26, Theorem 4.9]). *If $p \in \mathcal{P}_\omega \cap \mathcal{R}$ and $t, s \in \mathbb{T}$, then*

$$e_p(\nu(t), t) = e_p(\nu(s), s) \quad \text{and} \quad e_p(\nu(t), \nu(s)) = e_p(t, s). \tag{2.10}$$

To conclude this section, we include a result on how to change the order of integration in a double integral. The final formula in the following theorem will be needed in our proof of the second Cushing–Henson conjecture in Section 4, while the other formulas are included for future reference.

Theorem 2.19. *Let $f, g : \mathbb{T} \to \mathbb{R}$ and $a, b, c \in \mathbb{T}$. For $\Phi(t, s) := f(t)g(s)$, we have*

$$\int_a^b \int_c^t \Phi(t, s)\Delta s\Delta t = \int_a^b \int_c^a \Phi(t, s)\Delta t\Delta s + \int_a^b \int_{\sigma(s)}^b \Phi(t, s)\Delta t\Delta s, \tag{2.11}$$

$$\int_a^b \int_c^{\nu(t)} \Phi(t, s)\Delta s\Delta t = \int_a^b \int_c^{\nu(a)} \Phi(t, s)\Delta t\Delta s + \int_{\nu(a)}^{\nu(b)} \int_{\nu^{-1}(\sigma(s))}^b \Phi(t, s)\Delta t\Delta s, \tag{2.12}$$

$$\int_a^b \int_t^{\nu(t)} \Phi(t, s)\Delta s\Delta t = \int_a^b \int_a^{\nu(a)} \Phi(t, s)\Delta t\Delta s - \int_a^b \int_{\sigma(s)}^b \Phi(t, s)\Delta t\Delta s + \int_{\nu(a)}^{\nu(b)} \int_{\nu^{-1}(\sigma(s))}^b \Phi(t, s)\Delta t\Delta s, \tag{2.13}$$

$$\int_a^{\nu(a)} \int_t^{\nu(t)} \Phi(t, s)\Delta s\Delta t = \int_a^{\nu(a)} \int_a^{\sigma(s)} \Phi(t, s)\Delta t\Delta s + \int_{\nu(a)}^{\nu(\nu(a))} \int_{\nu^{-1}(\sigma(s))}^{\nu(a)} \Phi(t, s)\Delta t\Delta s. \tag{2.14}$$

Proof. In what follows, we use the notation

$$F(t) := -\int_t^b f(s)\Delta s, \quad G(t) := \int_c^t g(s)\Delta s,$$
$$G_\nu(t) := \int_t^{\nu(t)} g(s)\Delta s, \quad \psi(t) := g(t)F^{\nu^{-1}}(\sigma(t)),$$

which imply

$$F(b) = 0, \quad F^\Delta = f, \quad G^\Delta = g, \quad G_\nu^\Delta \overset{(2.8)}{=} \nu^\Delta g^\nu - g.$$

First,

$$\begin{aligned}\int_a^b \int_c^t \Phi(t, s)\Delta s\Delta t &= \int_a^b F^\Delta(t)G(t)\Delta t \\ &\overset{(2.2)}{=} F(b)G(b) - F(a)G(a) - \int_a^b F(\sigma(s))G^\Delta(s)\Delta s,\end{aligned}$$

so (2.11) holds. Next,

$$\begin{aligned}\int_a^b \int_t^{\nu(t)} \Phi(t,s)\Delta s\Delta t &= \int_a^b F^\Delta(t)G_\nu(t)\Delta t\\ &\overset{(2.2)}{=} F(b)G_\nu(b) - F(a)G_\nu(a) - \int_a^b F(\sigma(s))G_\nu^\Delta(s)\Delta s\\ &= -F(a)G_\nu(a) - \int_a^b \nu^\Delta(s)\psi^\nu(s)\Delta s - \int_a^b F(\sigma(s))g(s)\Delta s\\ &\overset{(2.9)}{=} -F(a)G_\nu(a) - \int_{\nu(a)}^{\nu(b)} \psi(s)\Delta s - \int_a^b F(\sigma(s))g(s)\Delta s\end{aligned}$$

shows (2.13). Finally, (2.12) follows by adding (2.11) and (2.13), while (2.14) is the same as (2.13) with $b = \nu(a)$. □

3. First Cushing–Henson conjecture

Recall that throughout, $\omega \in \mathbb{N}$ and $\nu = \sigma^\omega$. Recall also that $\eta > 1$ and

$$\alpha := \frac{\eta - 1}{\mu\eta} = -\left(\ominus\frac{\eta-1}{\mu}\right), \quad \text{i.e.,} \quad \eta = 1 + \mu(\ominus(-\alpha)) = \frac{1}{1-\mu\alpha}. \tag{3.1}$$

Throughout the remainder of this paper, we assume

$$\eta : \mathbb{T} \to (1,\infty), \quad \alpha, K : \mathbb{T} \to (0,\infty), \quad -\alpha \in \mathcal{R}^+.$$

We formulate some assumptions.

(A_1) $\left(\sigma^\Delta\eta\right)^\nu = \sigma^\Delta\eta$,
(A_2) $\frac{K}{\eta-1} \in \mathcal{P}_\omega$.

Theorem 3.1 (First Cushing–Henson Conjecture)**.** *Let* $t_0 \in \mathbb{T}$. *Assume* (A_1) *and* (A_2). *Define*

$$\lambda := \nu^\Delta(t_0)e_{\ominus(-\alpha)}(\nu(t_0), t_0) - 1. \tag{3.2}$$

If $\lambda \neq 0$, *then* (1.4) *has a unique* ω*-periodic solution* $\bar{x}$, *given by*

$$\bar{x}(t) = \frac{\lambda}{\displaystyle\int_t^{\nu(t)} e_{\ominus(-\alpha)}(\sigma(s),t)\frac{\alpha(s)}{K(s)}\Delta s}. \tag{3.3}$$

If additionally, $\mathbb{T}$ *is unbounded above,* $\int_{t_0}^\infty \alpha(s)\Delta s = \infty$, *and* $\bar{x}$ *and* K *are bounded above, then* $\bar{x}$ *is globally asymptotically stable for solutions with positive initial conditions.*

Given the structure of (1.3), we immediately obtain that solutions remain positive for positive initial conditions, i.e., for $x_0 > 0$, the solution x satisfies $x(t) > 0$ for all $t \in \mathbb{T}$, $t \geq t_0$.

Before proving Theorem 3.1, we give a series of auxiliary results.

Lemma 3.2. *Consider*

(A_3) $\frac{-\alpha+\frac{1}{\mu}}{\sigma^\Delta} \in \mathcal{P}_\omega$,
(A_4) $\left(\frac{\ominus(-\alpha)}{K}\right)^\nu = \frac{\ominus(-\alpha)}{K}$.
(A_5) $\varphi := (-\alpha) \ominus \frac{\mu^\Delta}{\mu} \in \mathcal{P}_\omega$.

Then (A_1) *holds iff* (A_3) *holds iff* (A_5) *holds, and* (A_2) *holds iff* (A_4) *holds.*

Proof. The three calculations

$$\begin{aligned}
&\mu\left\{\nu^\Delta\left(\frac{-\alpha+\frac{1}{\mu}}{\sigma^\Delta}\right)^\nu - \frac{-\alpha+\frac{1}{\mu}}{\sigma^\Delta}\right\} \\
&= \mu\left\{\nu^\Delta\left(\frac{1-\mu\alpha}{\mu\sigma^\Delta}\right)^\nu - \frac{1-\mu\alpha}{\mu\sigma^\Delta}\right\} \\
&\overset{(2.7)}{=} \left(\frac{1-\mu\alpha}{\sigma^\Delta}\right)^\nu - \frac{1-\mu\alpha}{\sigma^\Delta} \overset{(3.1)}{=} \frac{1}{(\sigma^\Delta\eta)^\nu} - \frac{1}{\sigma^\Delta\eta},
\end{aligned}$$

$$\begin{aligned}
&\mu\left\{\nu^\Delta\left(\frac{K}{\eta-1}\right)^\nu - \frac{K}{\eta-1}\right\} \\
&\overset{(3.1)}{=} \mu\left\{\nu^\Delta\left(\frac{K}{\mu(\ominus(-\alpha))}\right)^\nu - \frac{K}{\mu(\ominus(-\alpha))}\right\} \\
&\overset{(2.7)}{=} \left(\frac{K}{\ominus(-\alpha)}\right)^\nu - \frac{K}{\ominus(-\alpha)},
\end{aligned}$$

and (using $1 + \mu^\Delta = \sigma^\Delta$ and Lemmas 2.13, 2.14, and 2.15)

$$\frac{-\alpha+\frac{1}{\mu}}{\sigma^\Delta} - \varphi = \frac{1}{\mu} \in \mathcal{P}_1 \subset \mathcal{P}_\omega \tag{3.4}$$

complete the proof. □

Lemma 3.3. *Let* $t, s \in \mathbb{T}$. *For* $\varphi \in \mathcal{R}$ *defined in* (A_5),

$$e_\varphi(t,s) = e_{-\alpha}(t,s)\frac{\mu(s)}{\mu(t)} \tag{3.5}$$

and

$$e_{\ominus\varphi}(\nu(t),t) = \nu^\Delta(t)e_{\ominus(-\alpha)}(\nu(t),t). \tag{3.6}$$

If (A_5) *holds, then*

$$\nu^\Delta(t)e_{\ominus(-\alpha)}(\nu(t),t) = \nu^\Delta(s)e_{\ominus(-\alpha)}(\nu(s),s) \tag{3.7}$$

and

$$\nu^\Delta(t)e_{\ominus(-\alpha)}(\nu(t),\nu(s)) = \nu^\Delta(s)e_{\ominus(-\alpha)}(t,s). \tag{3.8}$$

Proof. By Theorem 2.6 (part 3) and (2.3), we get (3.5). Using (3.5) with (2.7) yields (3.6). If $\varphi \in \mathcal{P}_\omega$, then $\ominus\varphi \in \mathcal{P}_\omega$ by Lemma 2.13. Employing (3.5) and (3.6) together with (2.10) (applied to $p = \ominus\varphi$) implies (3.7). Theorem 2.6 and (3.7) result in (3.8). □

Lemma 3.4. *Assume* (A_3) *and* (A_4)*. Let* $t_0 \in \mathbb{T}$ *and define*

$$H_\nu(t) := \int_t^{\nu(t)} h(s)\Delta s \quad \text{with} \quad h(t) := e_{\ominus(-\alpha)}(\sigma(t), t_0)\frac{\alpha(t)}{K(t)}. \tag{3.9}$$

Then, for λ *defined in* (3.2)*, we have*

$$H_\nu^\Delta(t) = \lambda h(t) \tag{3.10}$$

and

$$H_\nu^\nu(t) = (\lambda + 1)H_\nu(t). \tag{3.11}$$

Proof. First, by Theorem 2.6 (part 5), we have

$$h(t) = \frac{e_{\ominus(-\alpha)}(t, t_0)\alpha(t)}{(1 - \mu(t)\alpha(t))\,K(t)} = \left(\frac{\ominus(-\alpha)}{K}\right)(t)e_{\ominus(-\alpha)}(t, t_0),$$

and hence

$$\begin{aligned} h^\nu(t) &= \left(\frac{\ominus(-\alpha)}{K}\right)^\nu (t)e_{\ominus(-\alpha)}(\nu(t), t_0) \\ &\overset{(A_4)}{=} \left(\frac{\ominus(-\alpha)}{K}\right)(t)e_{\ominus(-\alpha)}(\nu(t), t_0) = e_{\ominus(-\alpha)}(\nu(t), t)h(t). \end{aligned}$$

Thus,

$$H_\nu^\Delta(t) \overset{(2.8)}{=} \nu^\Delta(t)h^\nu(t) - h(t) \overset{(3.7)}{=} (\lambda + 1 - 1)h(t) = \lambda h(t),$$

which shows (3.10). Next,

$$\begin{aligned} H_\nu^\nu(t) &= H_\nu(\nu(t)) = H_\nu(t) + \int_t^{\nu(t)} H_\nu^\Delta(s)\Delta s \\ &\overset{(3.10)}{=} H_\nu(t) + \lambda \int_t^{\nu(t)} h(s)\Delta s \\ &= H_\nu(t) + \lambda H_\nu(t) = (\lambda + 1)H_\nu(t) \end{aligned}$$

proves (3.11). □

With Lemmas 3.3 and 3.4, we now have sufficient machinery to prove Theorem 3.1.

Proof of Theorem 3.1. In a first step, we show that $\bar{x}$ given by (3.3) is an ω-periodic solution of (1.4). Note that

$$\bar{x}(t) \overset{(3.9)}{=} \frac{\lambda}{e_{-\alpha}(t, t_0)H_\nu(t)},$$

and thus,

$$\begin{aligned} \nu^\Delta(t)\bar{x}^\nu(t) &= \frac{\lambda \nu^\Delta(t)}{e_{-\alpha}(\nu(t), t_0)H_\nu^\nu(t)} \\ &\overset{(3.11)}{=} \frac{\lambda \nu^\Delta(t)}{e_{-\alpha}(\nu(t), t_0)(\lambda + 1)H_\nu(t)} \end{aligned}$$

$$
\begin{aligned}
&= \frac{\nu^{\Delta}(t)}{e_{-\alpha}(\nu(t), t)(\lambda+1)\bar{x}(t)} \\
&\overset{(3.7)}{=} \bar{x}(t)
\end{aligned}
$$

(use also (3.2) in the last equality), so $\bar{x}$ is ω-periodic. With $\bar{u} = 1/\bar{x}$, we get

$$
\bar{u}(t) = \frac{1}{\lambda} e_{-\alpha}(t, t_0) H_{\nu}(t),
$$

and thus,

$$
\begin{aligned}
\bar{u}^{\Delta}(t) &\overset{(2.1)}{=} \frac{1}{\lambda} \left\{ e_{-\alpha}(\sigma(t), t_0) H_{\nu}^{\Delta}(t) - \alpha(t) e_{-\alpha}(t, t_0) H_{\nu}(t) \right\} \\
&\overset{(3.10)}{=} e_{-\alpha}(\sigma(t), t_0) h(t) - \alpha(t) \bar{u}(t) \\
&\overset{(3.9)}{=} \frac{\alpha(t)}{K(t)} - \alpha(t) \bar{u}(t),
\end{aligned}
$$

so $\bar{u}$ solves (1.5), and thus $\bar{x} = 1/\bar{u}$ solves (1.4). Altogether, $\bar{x}$ is an ω-periodic solution of (1.4).

Conversely, we assume that $\tilde{x}$ is any ω-periodic solution of (1.4). Then $\tilde{u} = 1/\tilde{x}$ satisfies (1.5), i.e., $\tilde{u}^{\Delta}(t) = -\alpha(t)\tilde{u}(t) + \frac{\alpha(t)}{K(t)}$. Hence,

$$
\begin{aligned}
\nu^{\Delta}(t) \tilde{u}(t) &= \frac{\nu^{\Delta}(t)}{\tilde{x}(t)} = \frac{1}{\tilde{x}^{\nu}(t)} = \tilde{u}^{\nu}(t) \\
&= \tilde{u}(\nu(t)) \overset{(2.5)}{=} e_{-\alpha}(\nu(t), t) \tilde{u}(t) + \int_t^{\nu(t)} e_{-\alpha}(\nu(t), \sigma(s)) \frac{\alpha(s)}{K(s)} \Delta s \\
&= e_{-\alpha}(\nu(t), t) \left\{ \tilde{u}(t) + e_{-\alpha}(t, t_0) \int_t^{\nu(t)} e_{\ominus(-\alpha)}(\sigma(s), t_0) \frac{\alpha(s)}{K(s)} \Delta s \right\} \\
&= e_{-\alpha}(\nu(t), t) \left\{ \tilde{u}(t) + e_{-\alpha}(t, t_0) H_{\nu}(t) \right\}
\end{aligned}
$$

(note that (2.5) was applied with t_0 replaced by t and t replaced by $\nu(t)$), so

$$
\begin{aligned}
(1+\lambda)\tilde{u}(t) &\overset{(3.7)}{=} \nu^{\Delta}(t) e_{\ominus(-\alpha)}(\nu(t), t) \tilde{u}(t) \\
&= \tilde{u}(t) + e_{-\alpha}(t, t_0) H_{\nu}(t),
\end{aligned}
$$

which, upon solving for $\tilde{u}(t)$, results in

$$
\tilde{u}(t) = \frac{e_{-\alpha}(t, t_0) H_{\nu}(t)}{\lambda},
$$

i.e.,

$$
\tilde{x}(t) = \frac{1}{\tilde{u}(t)} = \frac{\lambda}{e_{-\alpha}(t, t_0) H_{\nu}(t)} = \bar{x}(t).
$$

To prove the global asymptotic stability of $\bar{x}$, let x be the unique solution of (1.4) with initial condition $x_0 > 0$, and let $\bar{x}_0 := \bar{x}(t_0)$. Since $1/x$ solves (1.5), using (2.5), we get

$$
x(t) = \frac{x_0}{e_{-\alpha}(t, t_0) \left(1 + x_0 \int_{t_0}^{t} h(s) \Delta s \right)}.
$$

Thus, we obtain

$$\begin{aligned} x(t)-\bar{x}(t) &= \frac{x_0}{e_{-\alpha}(t,t_0)\left(1+x_0\int_{t_0}^t h(s)\Delta s\right)} - \frac{\bar{x}_0}{e_{-\alpha}(t,t_0)\left(1+\bar{x}_0\int_{t_0}^t h(s)\Delta s\right)} \\ &= \frac{x_0-\bar{x}_0}{e_{-\alpha}(t,t_0)\left(1+x_0\int_{t_0}^t h(s)\Delta s\right)\left(1+\bar{x}_0\int_{t_0}^t h(s)\Delta s\right)} \\ &= \frac{(x_0-\bar{x}_0)\,\bar{x}(t)}{\bar{x}_0\left(1+x_0\int_{t_0}^t h(s)\Delta s\right)}, \end{aligned}$$

which tends to zero as $t \to \infty$ because $\alpha > 0$ and $-\alpha \in \mathcal{R}^+$ so that

$$\begin{aligned} 1+x_0\int_{t_0}^t h(s)\Delta s &\geq 1+\frac{x_0}{\|K\|_\infty}\int_{t_0}^t e_{-\alpha}(t_0,\sigma(s))\alpha(s)\Delta s \\ &= 1+\frac{x_0}{\|K\|_\infty}(e_{-\alpha}(t_0,t)-1) \\ &= 1-\frac{x_0}{\|K\|_\infty}+\frac{x_0}{\|K\|_\infty}e_{-\alpha}(t_0,t) \\ &\overset{(2.4)}{\geq} 1-\frac{x_0}{\|K\|_\infty}+\frac{x_0}{\|K\|_\infty}\left(1-\int_t^{t_0}\alpha(s)\Delta s\right) \\ &= 1+\frac{x_0}{\|K\|_\infty}\int_{t_0}^t \alpha(s)\Delta s \to \infty \quad \text{as} \quad t\to\infty, \end{aligned}$$

completing the proof. □

Example 3.5. If $\mathbb{T} = \mathbb{Z}$, then

$$\sigma(t) = t+1, \quad \sigma^\Delta(t) = 1, \quad \nu(t) = t+\omega, \quad \nu^\Delta(t) = 1,$$
$$\mu(t) = 1, \quad \mu^\Delta(t) = 0$$

and, as noted in Example 2.11, periodicity defined in (2.6) is consistent with the classical periodicity definition, i.e., f is ω-periodic if $f(t+\omega) = f(t)$ for all $t \in \mathbb{Z}$. In this case, (A_1) states that

$$\eta(t+\omega) = \eta(t),$$

and (A_2) says that

$$\frac{K(t+\omega)}{\eta(t+\omega)-1} = \frac{K(t)}{\eta(t)-1}.$$

Together, (A_1) and (A_2) are equivalent to

$$\eta(t+\omega) = \eta(t) \quad \text{and} \quad K(t+\omega) = K(t),$$

i.e., both η and K are ω-periodic. Next, (A_3) says that

$$-\alpha(t+\omega)+1 = -\alpha(t)+1,$$

and (A_4) states that

$$\frac{\alpha(t+\omega)}{1-\alpha(t+\omega)}\cdot\frac{1}{K(t+\omega)}=\frac{\alpha(t)}{1-\alpha(t)}\cdot\frac{1}{K(t)}.$$

Together, (A_3) and (A_4) are equivalent to

$$\alpha(t+\omega)=\alpha(t) \quad \text{and} \quad K(t+\omega)=K(t),$$

i.e., both α and K are ω-periodic. We also note that $\varphi=(-\alpha)\ominus 0=-\alpha$, and so φ is ω-periodic if and only if α is ω-periodic. If $\alpha>1$ is constant and K is ω-periodic, then (A_3) and (A_4) are satisfied, and $\bar{x}$ from (3.3) is consistent with the unique ω-periodic solution derived in [22]. In that case, $\bar{x}$ and K are bounded, as any periodic function on $\mathbb{Z}$ is bounded, and

$$\int_{t_0}^{t}\alpha\Delta s=\alpha(t-t_0)\to\infty \quad \text{as} \quad t\to\infty.$$

Hence, the ω-periodic solution is globally asymptotically stable for solutions with positive initial conditions. The classical first Cushing–Henson conjecture is therefore a special case of Theorem 3.1. Further, Theorem 3.1 for $\mathbb{T}=\mathbb{Z}$ also contains an extension of the classical first Cushing–Henson conjecture as presented in [21], where the authors considered both K and α to be ω-periodic. Again, in this case, all assumptions of Theorem 3.1 are satisfied, and the unique ω-periodic solution is globally asymptotically stable.

Example 3.6. If $\mathbb{T}=q^{\mathbb{N}_0}$, then

$$\sigma(t)=qt,\quad \sigma^{\Delta}(t)=q,\quad \nu(t)=q^{\omega}t,\quad \nu^{\Delta}(t)=q^{\omega},$$
$$\mu(t)=(q-1)t,\quad \mu^{\Delta}(t)=q-1$$

and, as noted in Example 2.12, periodicity defined in (2.6) is consistent with the periodicity definition from [23], i.e., f is ω-periodic if $q^{\omega}f(q^{\omega}t)=f(t)$ for all $t\in q^{\mathbb{N}_0}$. In this case, (A_1) states that

$$q\eta(q^{\omega}t)=q\eta(t),$$

and (A_2) says that

$$q^{\omega}\frac{K(q^{\omega}t)}{\eta(q^{\omega}t)-1}=\frac{K(t)}{\eta(t)-1}.$$

Together, (A_1) and (A_2) are equivalent to

$$\eta(q^{\omega}t)=\eta(t) \quad \text{and} \quad q^{\omega}K(q^{\omega}t)=K(t),$$

i.e., both η/μ and K are ω-periodic. Next, (A_3) says that

$$q^{\omega}\frac{-\alpha(q^{\omega}t)+\frac{1}{(q-1)q^{\omega}t}}{q}=\frac{-\alpha(t)+\frac{1}{(q-1)t}}{q},$$

and (A_4) states that

$$\frac{\alpha(q^{\omega}t)}{1-(q-1)q^{\omega}t\alpha(q^{\omega}t)}\cdot\frac{1}{K(q^{\omega}t)}=\frac{\alpha(t)}{1-(q-1)t\alpha(t)}\cdot\frac{1}{K(t)}.$$

Together, (A_3) and (A_4) are equivalent to

$$q^{\omega}\alpha(q^{\omega}t) = \alpha(t) \quad \text{and} \quad q^{\omega}K(q^{\omega}) = K(t),$$

i.e., both α and K are ω-periodic. We also note that

$$\varphi(t) = \frac{-\alpha(t) - \frac{1}{t}}{1 + \frac{(q-1)t}{t}} = -\frac{\alpha(t) + \frac{1}{t}}{q},$$

and so φ is ω-periodic if and only if α is ω-periodic. Since these assumptions coincide with the assumptions in [24], [24, Conjecture 1] is the same as Theorem 3.1 if $\mathbb{T} = q^{\mathbb{N}_0}$. We would like to remind the reader that Theorem 3.1 is therefore also a generalization of [23, Conjecture 1] that assumes α to be 1-periodic.

Examples 3.5 and 3.6 show that assumptions (A_4) and (A_5) are equivalent to α and K being ω-periodic, in the sense of (2.6), if $\mathbb{T} = \mathbb{Z}$ or $\mathbb{T} = q^{\mathbb{N}_0}$. One might wonder for which other time scales this observation is true.

Theorem 3.7. *Assume* $\mathbb{T}$ *is such that*

$$\frac{\mu^{\Delta}}{\mu} \in \mathcal{P}_{\omega}, \quad \textit{i.e.,} \quad \mu^{\Delta\nu} = \mu^{\Delta}. \tag{3.12}$$

Then (A_4) *and* (A_5) *hold if and only if both* α *and* K *are* ω*-periodic.*

Proof. Assume (3.12). First, assuming (A_4) and (A_5) hold, we get from (A_5) that

$$-\alpha = \varphi \oplus \frac{\mu^{\Delta}}{\mu} \in \mathcal{P}_{\omega}$$

due to (3.12) and Lemma 2.13. Hence, using again Lemma 2.13, we obtain $\alpha \in \mathcal{P}_{\omega}$. Then, by ($A_4$),

$$\frac{\ominus(-\alpha)}{K} = \left(\frac{\ominus(-\alpha)}{K}\right)^{\nu} = \frac{\nu^{\Delta}}{\nu^{\Delta}}\left(\frac{\ominus(-\alpha)}{K}\right)^{\nu} = \frac{\nu^{\Delta}(\ominus(-\alpha))^{\nu}}{\nu^{\Delta}K^{\nu}} = \frac{\ominus(-\alpha)}{\nu^{\Delta}K^{\nu}},$$

so K is ω-periodic. Conversely, assuming both α and K are ω-periodic, we get by Lemma 2.13 that $-\alpha \in \mathcal{P}_{\omega}$, and hence

$$\varphi = (-\alpha) \ominus \frac{\mu^{\Delta}}{\mu} \in \mathcal{P}_{\omega}$$

due to (3.12) and Lemma 2.13. Hence, (A_5) holds. Moreover,

$$\left(\frac{\ominus(-\alpha)}{K}\right)^{\nu} = \frac{\nu^{\Delta}}{\nu^{\Delta}}\left(\frac{\ominus(-\alpha)}{K}\right)^{\nu} = \frac{\nu^{\Delta}(\ominus(-\alpha))^{\nu}}{\nu^{\Delta}K^{\nu}} = \frac{\ominus(-\alpha)}{K},$$

showing (A_4). □

However, if (3.12) does not hold, then, assuming α and K are ω-periodic instead of (A_4) and (A_5), there does not even exist an ω-periodic solution of (1.4) in general. This can be verified easily with $\omega = 1$ according to the following example.

Example 3.8. Let $\omega = 1$ and assume α and K are ω-periodic. Let $\tilde{x}$ be an ω-periodic solution of (1.4). Let $\tilde{u} = 1/\tilde{x}$. By Lemma 2.14, $\tilde{c} := \alpha/K$ is constant. Moreover, since $\tilde{x} = 1/\tilde{u}$ satisfies (2.6), we get

$$\sigma^{\Delta}\tilde{u} = \tilde{u}^{\sigma}. \tag{3.13}$$

Thus,

$$\tilde{u}^{\Delta} = \frac{\tilde{u}^{\sigma} - \tilde{u}}{\mu} \overset{(3.13)}{=} \frac{\sigma^{\Delta}\tilde{u} - \tilde{u}}{\mu} = \frac{\mu^{\Delta}}{\mu}\tilde{u},$$

and hence, due to

$$0 \overset{(1.5)}{=} \tilde{u}^{\Delta} + \alpha\tilde{u} - \tilde{c} = \left(\frac{\mu^{\Delta}}{\mu} + \alpha\right)\tilde{u} - \tilde{c},$$

we obtain

$$\tilde{u} = \frac{\mu\tilde{c}}{\mu^{\Delta} + \mu\alpha}. \tag{3.14}$$

Hence,

$$\tilde{u}^{\sigma} \overset{(3.14)}{=} \frac{\mu^{\sigma}\tilde{c}}{\mu^{\Delta\sigma} + \mu^{\sigma}\alpha^{\sigma}} \overset{(2.7)}{=} \frac{\mu\sigma^{\Delta}\tilde{c}}{\mu^{\Delta\sigma} + \mu\sigma^{\Delta}\alpha^{\sigma}} \overset{(2.6)}{=} \frac{\mu\sigma^{\Delta}\tilde{c}}{\mu^{\Delta\sigma} + \mu\alpha}$$

and

$$\sigma^{\Delta}\tilde{u} \overset{(3.14)}{=} \frac{\mu\sigma^{\Delta}\tilde{c}}{\mu^{\Delta} + \mu\alpha}.$$

Thus, with (3.13), we obtain (3.12).

Example 3.9. Let $\omega = 4$. For $q > 0$, consider

$$\mathbb{T} = \{t_m : \; m \in \mathbb{N}_0\}, \quad \text{where} \quad t_m = \sum_{i=0}^{m-1} q^{(-1)^i} \quad \text{for} \quad m \in \mathbb{N}_0,$$

where the "empty sum" is by convention zero, i.e., $t_0 = 0$. Then

$$\begin{aligned} \sigma(t_m) = t_{m+1}, \quad \mu(t_m) = t_{m+1} - t_m = q^{(-1)^m}, \\ \sigma^{\Delta}(t_m) = \frac{\sigma(t_{m+1}) - \sigma(t_m)}{\mu(t_m)} = \frac{\mu(t_{m+1})}{\mu(t_m)} = q^{2(-1)^{m+1}}, \\ \mu^{\Delta}(t_m) = \sigma^{\Delta}(t_m) - 1 = q^{2(-1)^{m+1}} - 1. \end{aligned}$$

Hence (3.12) holds. Let $K_0, K_1, K_2, K_3 > 0$, $\bar{K}_i = K_{i \bmod 4}$, $a \neq 1$ and define

$$\eta(t_m) = aq^{2(-1)^m}, \quad K(t_m) = q^{(-1)^{m+1}}\bar{K}_m.$$

Clearly, $K \in \mathcal{P}_{\omega}$ by design, and since $\eta^{\nu} = \eta$, we have $\alpha \in \mathcal{P}_{\omega}$. By Theorem 3.7, ($A_3$) and ($A_5$) hold, so that by Theorem 3.1, the unique 4-periodic solution is given by

$$\bar{x}(t_m) = \frac{\lambda}{(\eta(t_m) - 1)\frac{\bar{K}_m + \bar{K}_{m+2}}{\bar{K}_m\bar{K}_{m+2}} + \eta(t_m)(\eta(\sigma(t_m)) - 1)\frac{\bar{K}_{m+1} + \bar{K}_{m+3}}{\bar{K}_{m+1}\bar{K}_{m+3}}},$$

where $\lambda = a^4 - 1 \neq 0$.

4. Second Cushing–Henson conjecture

We now bring our attention to the second Cushing–Henson conjecture, which reads for the Beverton–Holt difference equation as follows. If $\eta > 1$ is constant, $K : \mathbb{Z} \to \mathbb{R}^+$ is ω-periodic, i.e., $K(t+\omega) = K(t)$ for all $t \in \mathbb{Z}$, then the average of the unique periodic solution $\bar{x}$ of (1.1) is less than or equal (equal iff K is constant) the average of the periodic carrying capacity, i.e.,

$$\frac{1}{\omega}\sum_{t=0}^{\omega-1} \bar{x}(t) \leq \frac{1}{\omega}\sum_{t=0}^{\omega-1} K(t).$$

Biologically, this inequality is interpreted as deleterious effect of a periodic environment to the population. In order to extend this result to isolated time scales, we aim to find an upper bound for the average of the unique periodic solution. Similar to the discrete case, where the second Cushing–Henson conjecture assumed a constant proliferation rate, we adjust (A_1) accordingly for $\omega = 1$. More specifically, we consider the assumptions

(A_6) $\left(\sigma^\Delta \eta\right)^\sigma = \sigma^\Delta \eta$,
(A_7) $\frac{-\alpha+\frac{1}{\mu}}{\sigma^\Delta} \in \mathcal{P}_1$,
(A_8) $\varphi = (-\alpha) \ominus \frac{\mu^\Delta}{\mu} \in \mathcal{P}_1$.

Remark 4.1. According to Lemma 3.2, we have

(A_6) holds iff (A_7) holds iff (A_8) holds,

and, by Lemma 2.15,

any of (A_6), (A_7), (A_8) implies any of (A_1), (A_3), (A_5).

Assume now any of the conditions (A_6), (A_7), and (A_8). By Remark 2.14,

$$C := \mu\frac{-\alpha + \frac{1}{\mu}}{\sigma^\Delta} = \frac{1-\mu\alpha}{\sigma^\Delta} \quad \text{is constant.} \tag{4.1}$$

Moreover, due to (3.4), we have

$$\mu\varphi = C - 1 \quad \text{and thus} \quad \mu(\ominus\varphi) = \frac{-\mu\varphi}{1+\mu\varphi} = \frac{1-C}{C} =: D. \tag{4.2}$$

Because of

$$e_{\ominus\varphi}(\nu(t_0), t_0) = \prod_{\tau\in[t_0,\nu(t_0))\cap\mathbb{T}} (1 + \mu(\tau)(\ominus\varphi)(\tau)) = \left(1 + \frac{1-C}{C}\right)^\omega = \frac{1}{C^\omega},$$

and thus, we get that

$$\lambda \overset{(3.2)}{=} \nu^\Delta(t_0) e_{\ominus(-\alpha)}(\nu(t_0), t_0) - 1 \overset{(3.6)}{=} e_{\ominus\varphi}(\nu(t_0), t_0) - 1 = \frac{1}{C^\omega} - 1.$$

Theorem 4.2 (Second Cushing–Henson Conjecture)**.** *Assume* (A_4), (A_8), *and* $C < 1$, *where* C *is defined in* (4.1). *Then the average of the unique* ω*-periodic solution* $\bar{x}$ *of* (1.4) *is bounded above by*

$$\frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \bar{x}(t)\Delta t \le \frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{1-C}{\frac{1}{\sigma^{\Delta}(t)} - C} K(t)\Delta t, \tag{4.3}$$

and equality holds iff $\frac{K}{\ominus(-\alpha)}$ *is constant.*

The central tool in the proof of Theorem 4.2 is the following generalized Jensen inequality from [32, Theorem 2.2], which reads for the strictly convex function $1/z$ as follows:

$$\frac{\displaystyle\int_a^b w(s)\Delta s}{\displaystyle\int_a^b w(s)v(s)\Delta s} \le \frac{\displaystyle\int_a^b \frac{w(s)}{v(s)}\Delta s}{\displaystyle\int_a^b w(s)\Delta s} \quad \text{with} \quad w > 0. \tag{4.4}$$

We apply (4.4) with

$$w_t(s) := -\varphi(s)e_{\varphi}(t, \sigma(s)) > 0 \quad \text{and} \quad v_t(s) := \mu(t)\frac{\tilde{\beta}(s)}{(\ominus\varphi)(s)},$$

where we also put

$$\tilde{\beta} := \frac{\ominus(-\alpha)}{\mu K} \quad \text{and} \quad \beta := \frac{1}{\mu^2\tilde{\beta}} = \frac{K}{\mu(\ominus(-\alpha))}.$$

Note that (A_4) implies (use (2.7))

$$\beta, \tilde{\beta} \in \mathcal{P}_{\omega}. \tag{4.5}$$

Before proving Theorem 4.2, we offer the following auxiliary result.

Lemma 4.3. *Assume* (A_4) *and* (A_5). *Define* λ *by* (3.2). *We have*

$$\int_t^{\nu(t)} w_t(s)\Delta s = \lambda \tag{4.6}$$

and

$$w_t(s)v_t(s) = e_{\ominus(-\alpha)}(\sigma(s), t)\frac{\alpha(s)}{K(s)}. \tag{4.7}$$

Moreover, if (A_8) *holds, then*

$$\frac{w_t(s)}{v_t(s)} = -D\beta(s)\varphi(t)e_{\varphi}(t, \sigma(s)), \tag{4.8}$$

where D *is defined in* (4.2).

Proof. First, we use Theorem 2.6 (part 8) to integrate

$$\int_t^{\nu(t)} w_t(s)\Delta s = -\int_t^{\nu(t)} \varphi(s)e_{\varphi}(t, \sigma(s))\Delta s = e_{\varphi}(t, \nu(t)) - 1 = \lambda,$$

where we also used (3.6), (3.7), and (3.2). This proves (4.6). Next, using (3.5), we get

$$\begin{aligned}w_t(s)v_t(s) &= -\varphi(s)e_\varphi(t,\sigma(s))\mu(t)\frac{\tilde\beta(s)}{(\ominus\varphi)(s)}\\&= e_\varphi(t,s)\mu(t)\tilde\beta(s) = e_{-\alpha}(t,s)\mu(s)\tilde\beta(s)\\&= e_{-\alpha}(t,s)\frac{(\ominus(-\alpha))(s)}{K(s)} = e_{\ominus(-\alpha)}(\sigma(s),t)\frac{\alpha(s)}{K(s)},\end{aligned}$$

which shows (4.7). Finally, assuming (A_8), we have (4.1) and (4.2). Then

$$\begin{aligned}\frac{w_t(s)}{v_t(s)} &= \frac{-\varphi(s)e_\varphi(t,\sigma(s))}{\mu(t)\frac{\tilde\beta(s)}{(\ominus\varphi)(s)}} = \frac{-\varphi(s)(\ominus\varphi)(s)}{\mu(t)}\mu^2(s)\beta(s)e_\varphi(t,\sigma(s))\\&= -\mu(s)\varphi(s)\mu(s)(\ominus\varphi)(s)\beta(s)\frac{e_\varphi(t,\sigma(s))}{\mu(t)}\\&= -\mu(t)\varphi(t)\mu(s)(\ominus\varphi)(s)\beta(s)\frac{e_\varphi(t,\sigma(s))}{\mu(t)}\\&= -\mu(s)(\ominus\varphi)(s)\beta(s)\varphi(t)e_\varphi(t,\sigma(s))\\&= -D\beta(s)\varphi(t)e_\varphi(t,\sigma(s))\end{aligned}$$

shows (4.8). □

We can now bring our attention to the proof of the second Cushing–Henson conjecture on isolated time scales.

Proof of Theorem 4.2. We apply the generalized Jensen inequality (4.4) on time scales in the single forthcoming calculation to estimate

$$\begin{aligned}\int_{t_0}^{\nu(t_0)}\bar x(t)\Delta t &\overset{(3.3)}{=} \int_{t_0}^{\nu(t_0)}\frac{\lambda}{\int_t^{\nu(t)}e_{\ominus(-\alpha)}(\sigma(s),t)\frac{\alpha(s)}{K(s)}\Delta s}\Delta t\\&\overset{(4.6)}{=}\int_{t_0}^{\nu(t_0)}\frac{\int_t^{\nu(t)}w_t(s)\Delta s}{\int_t^{\nu(t)}e_{\ominus(-\alpha)}(\sigma(s),t)\frac{\alpha(s)}{K(s)}\Delta s}\Delta t \overset{(4.7)}{=}\int_{t_0}^{\nu(t_0)}\frac{\int_t^{\nu(t)}w_t(s)\Delta s}{\int_t^{\nu(t)}w_t(s)v_t(s)\Delta s}\Delta t\\&\overset{(4.4)}{\le}\int_{t_0}^{\nu(t_0)}\frac{\int_t^{\nu(t)}\frac{w_t(s)}{v_t(s)}\Delta s}{\int_t^{\nu(t)}w_t(s)\Delta s}\Delta t \overset{(4.6)}{=}\frac{1}{\lambda}\int_{t_0}^{\nu(t_0)}\int_t^{\nu(t)}\frac{w_t(s)}{v_t(s)}\Delta s\Delta t\\&\overset{(2.14)}{=}\frac{1}{\lambda}\left\{\int_{t_0}^{\nu(t_0)}\int_{t_0}^{\sigma(s)}\frac{w_t(s)}{v_t(s)}\Delta t\Delta s + \int_{\nu(t_0)}^{\nu(\nu(t_0))}\int_{\nu^{-1}(\sigma(s))}^{\nu(t_0)}\frac{w_t(s)}{v_t(s)}\Delta t\Delta s\right\}\\&\overset{(4.8)}{=}\frac{-D}{\lambda}\left\{\int_{t_0}^{\nu(t_0)}\beta(s)\int_{t_0}^{\sigma(s)}\varphi(t)e_\varphi(t,\sigma(s))\Delta t\Delta s\right.\end{aligned}$$

$$
\begin{aligned}
&+\int_{\nu(t_0)}^{\nu(\nu(t_0))}\beta(s)\int_{\nu^{-1}(\sigma(s))}^{\nu(t_0)}\varphi(t)e_\varphi(t,\sigma(s))\Delta t\Delta s\Big\}\\
&=\frac{D}{\lambda}\Big\{\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\sigma(s))-1\right)\Delta s\\
&\quad+\int_{\nu(t_0)}^{\nu(\nu(t_0))}\beta(s)\left(e_\varphi(\nu^{-1}(\sigma(s)),\sigma(s))-e_\varphi(\nu(t_0),\sigma(s))\right)\Delta s\Big\}\\
&\overset{(2.9)}{=}\frac{D}{\lambda}\Big\{\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\sigma(s))-1\right)\Delta s\\
&\quad+\int_{t_0}^{\nu(t_0)}\nu^\Delta(s)\beta^\nu(s)\left(e_\varphi(\sigma(s),\sigma(\nu(s)))-e_\varphi(\nu(t_0),\sigma(\nu(s)))\right)\Delta s\Big\}\\
&\overset{(2.10)}{=}\frac{D}{\lambda}\Big\{\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\sigma(s))-1\right)\Delta s\\
&\quad+\int_{t_0}^{\nu(t_0)}\nu^\Delta(s)\beta^\nu(s)\left(e_\varphi(t_0,\nu(t_0))-e_\varphi(t_0,\sigma(s))\right)\Delta s\Big\}\\
&\overset{(4.5)}{=}\frac{D}{\lambda}\Big\{\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\sigma(s))-1\right)\Delta s\\
&\quad+\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\nu(t_0))-e_\varphi(t_0,\sigma(s))\right)\Delta s\Big\}\\
&=\frac{D}{\lambda}\int_{t_0}^{\nu(t_0)}\beta(s)\left(e_\varphi(t_0,\nu(t_0))-1\right)\Delta s\\
&\overset{(3.6)}{=}D\int_{t_0}^{\nu(t_0)}\beta(s)\Delta s=\int_{t_0}^{\nu(t_0)}\frac{1-C}{\frac{1}{\sigma^\Delta(s)}-C}K(s)\Delta s,
\end{aligned}
$$

where the last equality holds because

$$
D\beta(s)\overset{(4.2)}{=}\frac{(1-C)(1-\mu(s)\alpha(s))K(s)}{C\mu(s)\alpha(s)}\overset{(4.1)}{=}\frac{(1-C)\sigma^\Delta C}{C(1-\sigma^\Delta C)}.
$$

Note also, that due to the strict convexity of $1/z$ (see [32, Theorem 2.2]), equality holds in (4.4) if and only if $v_t(s)$ is independent of s, which means $\beta\in\mathcal{P}_1$. □

Remark 4.4. If (A_4) and $\beta\in\mathcal{P}_1$ hold, then the unique periodic solution of (1.4) is $D\beta$, where D is given by (4.2). In detail, the unique periodic solution is

$$
\frac{cD}{\mu(t)},\quad\text{where}\quad c:=\left(\frac{K}{\ominus(-\alpha)}\right)(t)\quad\text{is constant.}\tag{4.9}
$$

We can check (4.9) in two simple ways, namely by calculating it from (3.3), i.e.,

$$
\bar{x}(t)\overset{(3.3)}{=}\frac{\lambda}{\displaystyle\int_t^{\nu(t)}e_{\ominus(-\alpha)}(\sigma(s),t)\frac{\alpha(s)}{K(s)}\Delta s}
$$

$$
\begin{aligned}
&= \frac{\lambda}{\displaystyle\int_t^{\nu(t)} e_{-\alpha}(t,s)\left(\frac{\ominus(-\alpha)}{K}\right)(s)\Delta s} = \frac{\lambda c}{\displaystyle\int_t^{\nu(t)} e_{-\alpha}(t,s)\Delta s} \\
&\overset{(3.5)}{=} \frac{\lambda c}{\displaystyle\int_t^{\nu(t)} e_{\varphi}(t,s)\frac{\mu(t)}{\mu(s)}\Delta s} = \frac{\lambda c}{\displaystyle\int_t^{\nu(t)} e_{\varphi}(t,s)\frac{\mu(t)(\ominus\varphi)(s)}{\mu(s)(\ominus\varphi)(s)}\Delta s} \\
&\overset{(4.2)}{=} \frac{\lambda c D}{\mu(t)\displaystyle\int_t^{\nu(t)} e_{\ominus\varphi}(s,t)(\ominus\varphi)(s)\Delta s} \overset{(3.6)}{=} \frac{cD}{\mu(t)},
\end{aligned}
$$

or by directly checking that it is 1-periodic (this is clear from Lemma 2.14) and verifying that it solves (1.4), i.e.,

$$
\begin{aligned}
&\alpha\left(\frac{cD}{\mu}\right)^{\sigma}\left(1-\frac{cD}{\mu K}\right)-\left(\frac{cD}{\mu}\right)^{\Delta} \\
&= \frac{\alpha c D}{\mu^{\sigma}}\left(1-\frac{D(1-\mu\alpha)}{\mu\alpha}\right)+\frac{cD\mu^{\Delta}}{\mu\mu^{\sigma}} \\
&= \frac{cD}{\mu\mu^{\sigma}}\left(\mu\alpha - D(1-\mu\alpha)+\sigma^{\Delta}-1\right) \\
&= \frac{cD}{\mu\mu^{\sigma}}\left((\mu\alpha-1)(1+D)+\sigma^{\Delta}\right) \\
&= \frac{cD}{\mu\mu^{\sigma}}\left(-C(1+D)+1\right)\sigma^{\Delta} \overset{(4.2)}{=} 0.
\end{aligned}
$$

It can also be verified easily that for (4.9), the inequality (4.3) becomes an equality with cD on both sides:

$$
\frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{cD}{\mu(t)}\Delta t = cD
$$

and

$$
\begin{aligned}
&\frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{1-C}{\frac{1}{\sigma^{\Delta}(t)}-C}K(t)\Delta t \\
&= \frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{(1-C)c\alpha(t)}{\left(\frac{1}{\sigma^{\Delta}(t)}-C\right)(1-\mu(t)\alpha(t))}\Delta t \\
&= \frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{(1-C)c\alpha(t)}{\left(\frac{1}{\sigma^{\Delta}(t)}-C\right)C\sigma^{\Delta}}\Delta t = \frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{(1-C)c\alpha(t)}{C-C^2\sigma^{\Delta}(t)}\Delta t \\
&= \frac{1}{\omega}\int_{t_0}^{\nu(t_0)} \frac{(1-C)c\alpha(t)}{C\mu(t)\alpha(t)}\Delta t = \frac{cD}{\omega}\int_{t_0}^{\nu(t_0)} \frac{\Delta t}{\mu(t)} = cD.
\end{aligned}
$$

Remark 4.5. For all isolated time scales such that $\sigma^{\Delta} = c$ is constant for some $c \in \mathbb{R}$, Theorem 4.2 implies that the average of the unique periodic solution is less than or equal to the average of the carrying capacity multiplied by the constant $\frac{\eta c-1}{\eta-1}$. If $\mathbb{T} = \mathbb{Z}$, then $c = 1$, and the classical second

Cushing–Henson conjecture is retrieved. If $\mathbb{T} = q^{\mathbb{N}_0}$, then $c = q$, and Theorem 4.2 is consistent with the second Cushing–Henson conjecture formulated in [23], see also (1.2). The inequality (4.3) reveals that the upper bound is increasing in σ^Δ. Since

$$\frac{1-C}{\frac{1}{\sigma^\Delta}-C} = 1 + \frac{1-\frac{1}{\sigma^\Delta}}{\frac{1}{\sigma^\Delta}-C} = 1 + \frac{\sigma^\Delta - 1}{1 - C\sigma^\Delta} \overset{(4.1)}{=} 1 + \frac{\mu^\Delta}{\mu\alpha},$$

we can write (4.3) also as

$$\int_{t_0}^{\nu(t_0)} \bar{x}(t)\Delta t \leq \int_{t_0}^{\nu(t_0)} \left(1 + \frac{\mu^\Delta(t)}{\mu(t)\alpha(s)}\right) K(t)\Delta t.$$

Hence if $\mu^\Delta(s) < 0$ for all $s \in [t_0, \nu(t_0))$, then the upper bound for the average periodic solution is smaller than the average of the carrying capacities, suggesting an even stronger negative effect of periodicity onto the population compared to the classical case. If $\mu^\Delta(s) > 0$ for all $s \in [t_0, \nu(t_0))$, then the second Cushing–Henson conjecture does not necessarily hold as the multiplicative factor exceeds one. The inequality (4.3) exposes the effects of the time structure onto the upper bound of the mean periodic population.

5. Conclusion

In this work, we studied the Beverton–Holt model on arbitrary isolated time scales with time-dependent coefficients. Using the recently formulated periodicity concept for isolated time scales allows to address the Cushing–Henson conjectures for nonperiodic time scales. After an introduction in Section 1 and some preliminaries in Section 2, in Section 3, we provided conditions for the existence and uniqueness of a globally asymptotically stable periodic solution. This generalizes the first Cushing–Henson conjecture to an arbitrary isolated time scale. The provided theorem, when applied to the special case of the discrete time domain $\mathbb{Z}$, coincides with results in existing literature. The presented conditions for existence and uniqueness of the periodic solution and its global asymptotic stability are equivalent to the conditions in the first conjecture presented in [21]. It therefore generalizes the classical formulation of the first Cushing–Henson conjecture. We also showed that our result is consistent [24, Conjecture 1] in the special case of a quantum time scale. A special subcase in this time scale was discussed in [23]. As we outlined, Theorem 3.1 contains these works as special cases. In Section 4, we focused on the discussion of the second Cushing–Henson conjecture on arbitrary isolated time scales. In the classical case, when $\mathbb{T} = \mathbb{Z}$, the conjecture concerns the effects of a periodic environment under constant proliferation rate, mathematically formulated by an upper bound of the average periodic solution. The derived upper bound in Theorem 4.2 is, in contrast to the classical case, a weighted average dependent on changes of the time scale. This highlights that the second Cushing–Henson conjecture does not necessarily hold in general, and its statement depends on the change of the time scale. If the time scale changes with a constant rate, that is, σ^Δ is constant, then the average of the periodic solution is bounded by a factor times the average of the carrying capacity. Examples of this special case contain the discrete and the quantum time scale. For both of these time scales, Theorem 4.2 is consistent with existing formulations of the second Cushing–Henson conjecture in [18, 21, 23]. Our results complement work in [22], where the authors consider the Cushing–Henson conjectures for the Beverton–Holt model on periodic time scales. In contrast to isolated time scales, ω-periodic time scales assume $t + \omega \in \mathbb{T}$ for all $t \in \mathbb{T}$. Since periodic and isolated time scales intersect but neither is a subset of the other, modifications of the conjectures remain unknown on arbitrary time scales. We highlight that this work is an application of the new definition of periodicity on isolated time scales, defined in [26]. The introduced method of the application of periodicity on isolated time scales can now be extended to other models, such as delay Beverton–Holt models. In fact, in [33–35], the Cushing–Henson conjectures for different delay Beverton–Holt models in the discrete case are discussed. The tools used in this paper can be used to establish these results on an arbitrary isolated time scale.

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Conflict of interest

The authors declare there is no conflict of interest.

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