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Generalized periodicity and applications to logistic growth

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ABSTRACT

Classically, a continuous function $f:\mathbb{R}\to\mathbb{R}$ is periodic if there exists an $\omega>0$ such that $f(t+\omega)=f(t)$ for all $t\in\mathbb{R}$. The extension of this precise definition to functions $f:\mathbb{Z}\to\mathbb{R}$ is straightforward. However, in the so-called quantum case, where $f:q^{\mathbb{N}_0}\to\mathbb{R}$ $(q>1)$, or more general isolated time scales, a different definition of periodicity is needed. A recently introduced definition of periodicity for such general isolated time scales, including the quantum calculus, not only addressed this gap but also inspired this work. We now return to the continuous case and present the concept of ν-periodicity that connects these different formulations of periodicity for general discrete time domains with the continuous domain. Our definition of ν-periodicity preserves crucial translation invariant properties of integrals over ν-periodic functions and, for $\nu(t)=t+\omega$, ν-periodicity is equivalent to the classical periodicity condition with period ω. We use the classification of ν-periodic functions to discuss the existence and uniqueness of ν-periodic solutions to linear homogeneous and nonhomogeneous differential equations. If $\nu(t)=t+\omega$, our results coincide with the results known for periodic differential equations. By using our concept of ν-periodicity, we gain new insights into the classes of solutions to linear nonautonomous differential equations. We also investigate the existence, uniqueness, and global stability of ν-periodic solutions to the nonlinear logistic model and apply it to generalize the Cushing–Henson conjectures, originally formulated for the discrete Beverton–Holt model.

1. Introduction

Differential equations are a common tool to describe time-dependent processes mathematically, and various techniques have been developed to investigate their dynamics (e.g., existence, uniqueness, and stability of constant and periodic solutions). Interest to develop such analytical methods for their discrete counterparts, formulated as difference equations, has been increasing, partially due to its computational advantages. More recently, attention has been paid to extending these tools to dynamic equations on time scales, as they can be understood as a unification and generalization of differential and difference equations [1]. Different reasons exist for describing processes either continuously, discretely, or using time scales, including model complexity and computational convenience. Although the available methods to study the dynamics of a model varies with the chosen framework, their underlying ideas are often related. For example, in all three modeling frameworks (continuous, discrete, time scales), one may attempt to derive an explicit solution by making a solution *ansatz*.

With increasing model complexity, however, the available methods to investigate properties of solutions become more framework specific and, in fact, overall reduces. For example, while the subclass of autonomous linear differential equations benefits from specific solution techniques, these tools are generally not applicable to their nonautonomous counterparts such as periodic equations and are often used in applications, e.g., physics and chemistry [2–5], ecology [6–9], and epidemiology [10–12]. Periodic differential equations are characterized by model parameters that are periodic functions. Despite their complexity due to their nonautonomous nature, methods have been developed to study these periodic differential equations, for example, by relating them to a corresponding discrete Poincaré map – an example, where the study of a discrete model aids the analysis of a continuous differential equation.

In these models, periodicity refers to the classical definition by Euler, who described periodic functions with period $\omega>0$ by the property that $f(t+\omega)=f(\omega)$ for all $t\in D_f$, where D_f is the domain of the function f. This definition of periodicity resulted in specific properties of periodic functions such as the *translation invariance of the integral*:

$$\int_a^{a+\omega} f(t)\,\mathrm{d}t=\int_b^{b+\omega} f(t)\,\mathrm{d}t,\qquad \int_a^b f(t)\,\mathrm{d}t=\int_{a+\omega}^{b+\omega} f(t)\,\mathrm{d}t \tag{1}$$

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for $a, b \in D_f$ and any ω-periodic function $f : D_f \to \mathbb{R}$. Both properties in (1) are based on the realization that the area underneath any ω-periodic function is *translation invariant* in the sense that the value of the area for one period is independent of the starting point and the bounds can be shifted by any multiple of the period. Such properties of periodic functions are exploited to derive mathematical methods that aid the analysis of periodic differential equations. Similar analytical simplifications can be obtained in the study of periodic difference equations and periodic dynamic equations on time scales, where periodicity is also defined by $f(t+\omega) = f(t)$ for all $t \in \mathbb{Z}$ and $t \in \mathbb{T}$, respectively. Here, $\mathbb{T} \neq \emptyset$ is an arbitrary closed subset of $\mathbb{R}$, referred to as time scale [1]. In the case of dynamic equations on time scales, this classical definition of periodicity requires the time scale $\mathbb{T}$ to be periodic, that is, $t \pm \omega \in \mathbb{T}$ for all $t \in \mathbb{T}$.

It is exactly this periodic restriction of the time scale that sparked discussions of the generalization of *periodicity*. In [13], the authors partially addressed this question and introduced a concept of periodicity for isolated, not necessarily periodic, time scales. This generalization of periodicity for isolated time scales, i.e., time scales for which every element is isolated, provided a classification of "periodic" functions that satisfy (1). This classification ultimately resulted in new insights of solutions to nonautonomous difference equations that are not periodic in the classical sense [13]. Motivated by these gained insights, we return to the continuous case of differential equations and define a generalization of periodicity that relates periodic functions in the continuous case to these recently developed concepts of periodicity for discrete time spaces such as isolated time scales.

By generalizing the idea of periodicity to preserve the convenient properties (1), we aim to extend results known for periodic differential equations to a broader subclass of nonautonomous differential equations. Since periodic model parameters are often used to represent environmental fluctuations [8,14–16], we explore our new definition in the context of the popular logistic growth model

$$\frac{\mathrm{d}}{\mathrm{d}t}x = rx\left(1 - \frac{x}{K}\right), \qquad t \in \mathbb{R}, \tag{2}$$

where $r > 0$ represents the inherent growth rate and $K > 0$ the carrying capacity. While the autonomous case of (2), that is, $r, K \in \mathbb{R}^+$, implicitly assumes that the growth rate and the environment are time independent, environmental changes that impact the carrying capacity can be captured by considering a time-dependent $K : \mathbb{R} \to \mathbb{R}^+$ instead.

Our study of the logistic model (2) is not only motivated by its popularity and applicability in mathematical population modeling but also due to its vastly different behavior to some of its discrete counterparts. For example, the difference equation $X_{t+1} - X_t =: \Delta X_t = rX_t\left(1 - \frac{X_t}{K}\right)$ is sometimes referred to as "logistic difference equation", but its dynamics is not consistent with the continuous model and can indeed result in negative solutions and chaotic behavior. In contrast, the discrete Beverton–Holt model [17]

$$X_{t+1} = \frac{X_t K}{(1-r)K + rX_t}, \qquad t \in \mathbb{N}_0, \tag{3}$$

exhibits the same monotone dynamics as (2). Hence, one may argue that the Beverton–Holt model should indeed be called the "discrete analogue of the logistic growth model". Thus, the logistic growth model highlights the potential similarities and dissimilarities between differential and difference equations and, therefore, the relevance of the underlying time domain.

In this work, we utilize the relation between the continuous logistic growth model and the Beverton–Holt model to apply our newly introduced concept of periodicity. More precisely, we apply the generalization of periodicity to the continuous logistic growth model to formulate and investigate the Cushing–Henson conjectures that were originally formulated for the discrete Beverton–Holt model. Cushing and Henson conducted experiments with flour beetles that were described using (3), to quantify the effects of periodically varying environmental conditions on the population [18,19]. Based on the experimental observations, the authors formulated two conjectures regarding a periodically forced Beverton–Holt model. The first conjecture guarantees the existence of a unique periodic population level to which the population converges to, while the second conjecture implies a deleterious effect of introducing periodic environmental conditions. These conjectures have been mathematically confirmed for the Beverton–Holt recurrence in [20,21]. In [22], the conjectures have been shown to uphold for the time scales analogue of the Beverton–Holt model on a periodic time scale. Recently, in [23], the condition of a periodic time scale has been relaxed and the conjectures have been discussed for the logistic dynamic equation on isolated time scales. The removal of the rather restrictive condition of a periodic time scale was possible due to a new definition of periodicity that accounted for changes in the underlying time domain. In this work, we will also relax the condition of periodic model parameters and investigate the Cushing–Henson conjectures for the logistic differential equation for a wider class of time-dependent model parameters by applying our generalization of periodicity.

2. Generalization of periodicity

Throughout this work, let $I \subset \mathbb{R}$ be an interval which is unbounded above.

Instead of defining periodicity with respect to a fixed period, we propose the following dynamic definition of periodicity.

Definition 1. Let $\nu : I \to I$ be differentiable and strictly increasing. A function $f : I \to \mathbb{R}$ is called *periodic with respect to* ν (short: ν*-periodic*) provided that

$$\nu'(t) f(\nu(t)) = f(t) \qquad \text{for all } t \in I. \tag{4}$$

The set of functions $f \in C(I, \mathbb{R})$ that satisfy (4), for $\nu \in C^1(I, \mathbb{R})$ strictly increasing, is denoted by $\mathcal{P}_\nu(I)$.

Choosing $\nu(t) = t + \omega$ for $\omega \in \mathbb{R}^+ = (0, \infty)$, Definition 1 collapses to the classical definition of periodicity as (4) then reads: $f(t+\omega) = f(t)$ for all $t \in I \subset \mathbb{R}$. Note that if $\omega \in \mathbb{Q}$, then the Dirichlet function is ν-periodic. Here, the reader is reminded that condition (4) does not impose continuity conditions on f.

Example 2. The constant function $f \equiv C \in \mathcal{P}_\nu(I)$ if and only if $C = 0$ or $\nu(t) = t + c$ for $c \in \mathbb{R}_0^+ = [0, \infty)$.

Example 3. Although $f(t) = e^t$ is not periodic in the classical sense (that is, f is not periodic wrt. $\nu(t) = t + \omega$), $f(t) = e^t \in \mathcal{P}_\nu(\mathbb{R})$ for $\nu(t) = \ln(e^t + \omega)$ for any $\omega \in \mathbb{R}^+$.

Example 4. The trigonometric functions $\cos(t)$ and $\sin(t)$ satisfy (4) for $\nu \in C^2(\mathbb{R}, \mathbb{R})$ only for $\nu(t) = t + 2\pi$, consistent with the classical definition of periodicity. To show that there is no other strictly increasing, twice differentiable $\nu : \mathbb{R} \to \mathbb{R}$ such that

$$\nu'(t)\cos(\nu(t)) = \cos(t), \qquad t \in \mathbb{R}, \tag{5}$$

we note that after integrating (5), we have

$$\sin(\nu(t)) = \sin(t) + D, \qquad D \in \mathbb{R}. \tag{6}$$

Now, differentiating (5) implies

$$\nu''(t)\cos(\nu(t)) - (\nu'(t))^2 \sin(\nu(t)) = -\sin(t),$$

and by using (5) and (6), this is equal to

$$\frac{\nu''(t)}{\nu'(t)}\cos(t) - (\nu'(t))^2(\sin(t) + D) = -\sin(t).$$

Therefore, $w(t) = \nu'(t) > 0$ must satisfy the Bernoulli differential equation

$$w'(t) = (\tan(t) + D\sec(t))w^3(t) - \tan(t)w(t)$$

that has two branches of solutions

$$w(t) = \pm \frac{1}{\sqrt{1 + c_1 \sec^2(t) - 2D\sec(t)\tan(t)}},$$

for $c_1, D \in \mathbb{R}$, whenever the denominator is well-defined. If $c_1, D \neq 0$, then the integral of the positive branch is

$$v(t) = \frac{\tan^{-1}\left(\frac{\sqrt{2}(D+\sin(t))}{\sqrt{m}}\right)\sec(t)\sqrt{m}}{\sqrt{2}\sqrt{1 + c_1\sec^2(t) - 2D\sec(t)\tan(t)}},$$

where $m = 1 + 2c_1 + \cos(2t) - 4D\sin(t)$. This however has a vertical asymptote at $t = \frac{\pi}{2} + 2\pi n$ for any $n \in \mathbb{N}$. Thus, the only positive solution is $w(t) \equiv 1$ (i.e., $c_1 = D = 0$), implying $v(t) = \int w(t)\,\mathrm{d}t = t + C$. Then, (5) determines $C = 2\pi$, resulting in the classical definition of periodicity with period 2π.

Remark 5. It is worth noting that ν-periodic functions relate to solutions of the Schröder equation [24]:

$$\psi(\nu(t)) = \nu'(z_0)\psi(t), \tag{7}$$

where $\nu : \mathbb{R} \to \mathbb{R}$ and $z_0 \in \mathbb{R}$ is a fixed point of ν, i.e., $\nu(z_0) = z_0$, and $\nu'(z_0) \neq 0$. The Schröder equation is, for example, used in dynamical systems to study chaos and to discuss renormalization groups [25,26]. We now show that this equation is also related to the set of ν-periodic functions. Let $\psi(t) \neq 0$ be a solution to the Schröder equation (7). Then, differentiating (7) implies that $\psi'(\nu(t))\nu'(t) = \nu'(z_0)\psi'(t)$ and therefore, for $f(t) = \frac{\psi'(t)}{\psi(t)}$,

$$\nu'(t)f(\nu(t)) = \nu'(t)\frac{\psi'(\nu(t))}{\psi(\nu(t))} = \nu'(t)\frac{\frac{\nu'(z_0)\psi'(t)}{\nu'(t)}}{\nu'(z_0)\psi(t)} = \frac{\psi'(t)}{\psi(t)} = f(t).$$

Thus, a ν-periodic solution can be constructed from a solution to the Schröder equation and vice versa. Works that have addressed the existence of solutions to the Schröder equation are [27–29].

In contrast to the classical definition of periodicity, where derivatives and anti-derivatives of periodic functions remain periodic, (4) does not have to hold for derivatives or anti-derivatives of ν-periodic functions. Thus, ν-periodicity is not necessarily invariant with respect to the functional operators of differentiation and integration. However, Definition 1 assures a fundamental property of periodic functions, that is, the area under a periodic function over its period is translation invariant in the sense of (1). To prove this crucial aspect, we first define, for $f \in C(I, \mathbb{R})$,

$$F_\nu(t) := \int_t^{\nu(t)} f(\tau)\,\mathrm{d}\tau, \qquad t \in I. \tag{8}$$

Lemma 6. *If $f \in C(I, \mathbb{R})$ and F_ν is as defined in (8) for $\nu \in C^1(I, \mathbb{R})$, then*

$$F_\nu' = \nu' f^\nu - f, \qquad t \in I,$$

where $f^\nu = f \circ \nu$.

Proof. With $H(t) := \int_{t_0}^t f(\tau)\,\mathrm{d}\tau$, $t_0 \in I$, we have

$$F_\nu(t) = H(\nu(t)) - H(t).$$

Hence, by the chain rule,

$$F_\nu'(t) = \nu'(t)H'(\nu(t)) - H'(t) = \nu'(t)f(\nu(t)) - f(t) = \nu'(t)f^\nu(t) - f(t),$$

confirming the claim. □

Theorem 7. *If $f \in \mathcal{P}_\nu(I)$, then*

$$\int_t^{\nu(t)} f(\tau)\,\mathrm{d}\tau = \int_{t_0}^{\nu(t_0)} f(\tau)\,\mathrm{d}\tau, \qquad t, t_0 \in I. \tag{9}$$

Proof. By Lemma 6 and (4), $F_\nu' = \nu' f^\nu - f = 0$, so F_ν defined in (8) is constant. □

Example 8. By Example 3, $f(t) = e^t \in \mathcal{P}_\nu(\mathbb{R})$ for $\nu(t) = \ln(e^t + \omega)$ and $\omega \in \mathbb{R}^+$. Then, we have for $t, s \in \mathbb{R}$,

$$\begin{aligned}\int_t^{\nu(t)} e^\tau\,\mathrm{d}\tau &= \int_t^{\ln(e^t+\omega)} e^\tau\,\mathrm{d}\tau = e^t + \omega - e^t = \omega = e^s + \omega - e^s \\ &= \int_s^{\ln(e^s+\omega)} e^\tau\,\mathrm{d}\tau = \int_s^{\nu(s)} e^\tau\,\mathrm{d}\tau,\end{aligned}$$

as predicted in (9).

Theorem 9. *If $f \in \mathcal{P}_\nu(I)$, then*

$$\int_a^b f(\tau)\,\mathrm{d}\tau = \int_{\nu(a)}^{\nu(b)} f(\tau)\,\mathrm{d}\tau, \qquad a, b \in I. \tag{10}$$

Proof. Since $f \in \mathcal{P}_\nu(I)$, we have

$$\int_{\nu(a)}^{\nu(b)} f(\tau)\,\mathrm{d}\tau = \int_a^b \nu'(\tau)f(\nu(\tau))\,\mathrm{d}\tau = \int_a^b f(\tau)\,\mathrm{d}\tau,$$

completing the proof. □

Although the definition of ν-periodicity via (4) may seem, at first glance, unrelated to our classical understanding, Theorems 7 and 9 confirm that the crucial properties of translation invariance, summarized in (1), remain true for our extension of periodicity. Another relation to the classical formulation of periodicity can be identified by considering the class of anti-derivatives of ν-periodic functions. Consider $\mathcal{F}(t) = \int f(s)\mathrm{d}s$. Then, if $F(\nu(t)) = F(t)$ for all $t \in I$, $f \in \mathcal{P}_\nu(I)$. Note however that the set of derivatives of continuously differentiable functions that satisfy $F(\nu(t)) = F(t)$ is only a subset of ν-periodic functions because even if $F(\nu(t)) = F(t) + C$ for $C \neq 0$, F' still satisfies (4).

Some other useful properties known from the classical definition of periodicity that also hold for ν-periodicity are formulated in Lemmas 10–11.

Lemma 10. *We have $\mathcal{P}_\nu(I) \subseteq \mathcal{P}_{\nu\circ\nu}(I)$.*

Proof. Assume $\nu'(t)f(\nu(t)) = f(t)$ for all $t \in I$ and define $\tilde{\nu}(t) = (\nu\circ\nu)(t) = \nu(\nu(t))$. Then

$$\tilde{\nu}'(t)f(\tilde{\nu}(t)) = \nu'(t)\nu'(\nu(t))f(\nu(\nu(t))) = \nu'(t)f(\nu(t)) = f(t).$$

Hence, f is $(\nu\circ\nu)$-periodic. □

Lemma 11. *If $f, g \in \mathcal{P}_\nu(I)$ and $\alpha, \beta \in \mathbb{R}$, then $\alpha f + \beta g \in \mathcal{P}_\nu(I)$.*

Proof. We have

$$\nu'(t)(\alpha f + \beta g)(\nu(t)) = \alpha\nu'(t)f(\nu(t)) + \beta\nu'(t)g(\nu(t)) = \alpha f(t) + \beta g(t),$$

completing the proof. □

Remark 12. Lemmas 10–11 remain true for discontinuous $f : U \to \mathbb{R}$ for $U \subseteq \mathbb{R}$ that are ν-periodic, that is, f satisfies the identity (4).

Remark 13. Note that the product of two ν-periodic functions is not necessarily ν-periodic. However, if $f \in \mathcal{P}_\nu(I)$ and $g(\nu(t)) = g(t)$ for all $t \in I$, then $f \cdot g \in \mathcal{P}_\nu(I)$ and, if $g \neq 0$, $\frac{f}{g} \in \mathcal{P}_\nu(I)$.

Remark 14. Given a function $f \in C(I, \mathbb{R})$, (4) identifies the family of functions ν such that $f \in \mathcal{P}_\nu(I)$. More precisely, ν can be obtained by solving a differential equation. Alternatively, integrating (4) with respect to t yields $\widetilde{F}(\nu(t)) = \widetilde{F}(t) + C$, for $t \in I$, $C \in \mathbb{R}$, and $\widetilde{F}(t) := \int_{t_0}^t f(s)\,ds$ for some $t_0 \in I$. If f does not change sign on I, then $\widetilde{F}$ is monotone and an explicit expression for ν can be obtained via $\nu(t) = \widetilde{F}^{-1}(\widetilde{F}(t) + C)$.

Remark 15. The description of the set $\mathcal{P}_\nu(I)$, for a given ν, is directly linked to solving a functional equation. Assume that ν is continuously differentiable, strictly increasing and there exists $\xi \in I$ such that $\nu'(\xi) < 1$ and, additionally, the following two properties hold:

(a) $(\nu(t) - t)(\xi - t) > 0$ for $t \in I, t \neq \xi$,
(b) $(\nu(t) - \xi)(\xi - t) < 0$ for $t \in I, t \neq \xi$.

Then, the only continuous function f that is ν-periodic is the trivial function $f \equiv 0$. This can be shown by applying [30, Theorem 2 (p. 6)]. Consequently, the only continuous function that is ν-periodic, where $\nu(t) = \sqrt{t}$, and $I = \left(\frac{1}{2}, \infty\right)$ is the trivial function.

3. Periodic solutions to first-order linear differential equations

In this section, we apply the definition of periodicity to study the existence of periodic solutions to first-order linear differential equations. We are specifically interested in the conditions to guarantee the existence and uniqueness of ν-periodic solutions to a given nonautonomous linear differential equation. For the remainder of this manuscript, we let $\nu : I \to I$ be a twice differentiable, strictly increasing function.

To simplify our notation, we define for $f \in C(I, \mathbb{R})$,

$$e_f(t,s) := \exp\left\{\int_s^t f(\tau)\,\mathrm{d}\tau\right\}, \qquad s,t \in I \tag{11}$$

and

$$E_f(\nu(t),t) := \nu'(t) e_f(\nu(t),t), \qquad t \in I. \tag{12}$$

By the properties of exponential functions, we immediately have for $f \in C(I, \mathbb{R})$,

$$e_f(t,s) = e_{-f}(s,t) = \frac{1}{e_f(s,t)}, \qquad \frac{\mathrm{d}}{\mathrm{d}t} e_f(t,s) = f(t) e_f(t,s),$$

$$e_f(t,s) e_f(s,r) = e_f(t,r),$$

for $r, s, t \in I$.

Theorem 16. *If $f \in \mathcal{P}_\nu(I)$, then*

$$e_f(\nu(t),t) \qquad \text{is independent of } t \in I$$

and

$$e_f(\nu(t),\nu(s)) = e_f(t,s) \qquad \text{for all } t,s \in I.$$

Proof. The first statement is true due to Theorem 7 and the definition of $e_f(t,s)$. From

$$e_f(\nu(t),\nu(s)) = e_f(\nu(t),t) e_f(t,s) e_f(s,\nu(s)) = \frac{e_f(\nu(t),t)}{e_f(\nu(s),s)} e_f(t,s) = e_f(t,s),$$

we see that the second statement holds as well. □

Lemma 17. *For $f \in C(I, \mathbb{R})$, we have*

$$E_f(\nu(t),t) \qquad \text{is independent of } t \in I$$

if and only if

$$\frac{\nu''}{\nu'} + \nu' f^\nu = f \qquad \text{on } I. \tag{13}$$

Proof. Using Lemma 6, we get

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}\left(E_f(\nu(t),t)\right) &= \frac{\mathrm{d}}{\mathrm{d}t}\left(\nu'(t) e_f(\nu(t),t)\right)\\ &= \nu''(t) e_f(\nu(t),t) + \nu'(t)\left\{\nu'(t) f(\nu(t)) - f(t)\right\} e_f(\nu(t),t)\\ &= \left\{\nu''(t) + (\nu'(t))^2 f(\nu(t)) - \nu'(t) f(t)\right\} e_f(\nu(t),t),\end{aligned}$$

and thus, $E_f(\nu(t),t)$ is independent of $t \in I$, i.e., $\frac{\mathrm{d}}{\mathrm{d}t}\left(E_f(\nu(t),t)\right) = 0$, iff f satisfies (13). □

Note that if $e_f(t,t_0)$ is ν-periodic for some $t_0 \in I$, then $E_f(\nu(t),t)$ is independent of t because

$$E_f(\nu(t),t) = \nu'(t) e_f(\nu(t),t_0) e_f(t_0,t) = (\nu'(t) e_f(\nu(t),t_0))(e_f(t,t_0))^{-1} = 1.$$

3.1. Homogeneous differential equations

We consider the homogeneous first-order linear differential equation

$$x' = a(t)x, \tag{14}$$

where $a \in C(I, \mathbb{R})$ and $I \subseteq \mathbb{R}$ unbounded from above. The solution is given by

$$x(t) = \exp\left\{\int_{t_0}^t a(s)\,\mathrm{d}s\right\} x(t_0) = e_a(t,t_0) x(t_0), \qquad t_0 \in I.$$

We are specifically interested in the existence and uniqueness of ν-periodic solutions of (14). The next theorem provides sufficient conditions for a solution to be ν-periodic.

Theorem 18. *Let $a \in C(I, \mathbb{R})$ satisfy (13) and x be a solution of (14). If there exists $t_0 \in I$ such that*

$$\nu'(t_0) x(\nu(t_0)) = x(t_0),$$

then x is ν-periodic.

Proof. Let $g(t) := \nu'(t) x(\nu(t)) - x(t)$. Then $g(t_0) = 0$ and

$$\begin{aligned} g'(t) &= \nu''(t) x(\nu(t)) + (\nu'(t))^2 x'(\nu(t)) - x'(t)\\ &= \left[\nu''(t) + (\nu'(t))^2 a(\nu(t))\right] x(\nu(t)) - a(t)x(t)\\ &\overset{(13)}{=} a(t) g(t),\end{aligned}$$

so $g(t) = e_a(t,t_0) g(t_0) = 0$ for all $t \in I$. □

Theorem 19. *Let $a \in C(I, \mathbb{R})$ satisfy (13). If there exists $t_0 \in I$ such that*

$$E_a(\nu(t_0), t_0) = 1,$$

then all solutions of (14) are ν-periodic. In all other cases, (14) has no nontrivial ν-periodic solution.

Proof. The solution to (14) is ν-periodic iff $\nu'(t) x(\nu(t)) = x(t)$, i.e.,

$$\nu'(t) e_a(\nu(t),t_0) x(t_0) = e_a(t,t_0) x(t_0), \quad \text{i.e.,} \quad \nu'(t) e_a(\nu(t),t) x(t_0) = x(t_0), \tag{15}$$

i.e., $E_a(\nu(t),t) x(t_0) = x(t_0)$. Clearly, $x(t_0) = 0$ satisfies this equation so that the trivial solution is always ν-periodic. For $x(t_0) \neq 0$, $x(t) \neq 0$, and (15) is satisfied iff $E_a(\nu(t),t) = 1$. Since a satisfies (13), $E_a(\nu(t),t) = E_a(\nu(t_0),t_0)$, by Lemma 17, and the claim follows. □

Example 20. For the classical definition of periodicity, i.e., $\nu(t) = t + \omega$, $\omega \in \mathbb{R}^+$, a function f satisfies (13) if and only if $f(t+\omega) = f(t)$ for all $t \in I$. Thus, Theorem 19 coincides with the classical result: If $a \in C(I, \mathbb{R})$ and $a(t+\omega) = a(t)$ for all $t \in I$, then either all solutions to $x'(t) = a(t)x(t)$ are periodic or the only periodic solution is the trivial solution. More precisely, if there exists $\tilde{t} \in I$ such that $\int_{\tilde{t}}^{\tilde{t}+\omega} a(t)\,\mathrm{d}t = 0$, then all solutions to $x'(t) = a(t)x(t)$ are ω-periodic. If no such $\tilde{t} \in I$ exists, then the only periodic solution is the trivial one.

Example 21. If $I = (0, \infty)$ and $\nu(t) = 3\sqrt{t}$, then $a(t) = -\frac{1}{t} \in C(I, \mathbb{R})$ satisfies (13) and

$$E_a(\nu(t),t) = \nu'(t) e_a(\nu(t),t) = \frac{3}{2\sqrt{t}} e^{\int_t^{3\sqrt{t}} \frac{-1}{\tau}\,\mathrm{d}\tau} = \frac{1}{2} \neq 1.$$

By Theorem 19, only the trivial solution is ν-periodic. Instead, considering now $\nu(t) = 3t$, (13) still holds but

$$E_a(\nu(t),t) = \nu'(t) e_a(\nu(t),t) = 3 e^{\int_t^{3t} \frac{-1}{\tau}\,\mathrm{d}\tau} = 1.$$

Hence, by Theorem 19, all solutions are ν-periodic. Note that in both cases, the differential equation is $x'(t) = -t^{-1} x(t)$ and its solution on I is $x(t) = \frac{x(t_0) t_0}{t}$ for $t_0 \in I$.

Example 22. The constant function $a(t) \equiv a \in \mathbb{R}^+$ satisfies (13) for $v(t) = \frac{\log(ae^{at}+D)}{a}$ for any $D \in \mathbb{R}^+$. Note that $v'(t) = \frac{ae^{at}}{ae^{at}+D} > 0$ so that

$$E_a(v(t), t) = v'(t)e_a(v(t), t) = \frac{ae^{at}}{ae^{at} + D} e^{av(t)-at} = a.$$

By Theorem 19, if $a = 1$, then all solutions are v-periodic. Else, if $a \neq 1$, then no nontrivial solution is v-periodic.

Remark 23. In the classical theory of periodic linear differential equations, there exists a ω-periodic solution to $x' = a(t)x$ if $a(t+\omega) = a(t)$ for all $t \in I$. The corresponding result for the generalization of periodicity is however not necessarily true. That is, if $a \in \mathcal{P}_v(I)$, then $x' = a(t)x$ does not necessarily have a nontrivial v-periodic solution. More precisely, suppose $a \in \mathcal{P}_v(I)$ and there exists a nontrivial solution x to $x' = a(t)x$. Then, by the same argument as in (15), $E_a(v(t), t) = 1$ for all $t \in I$. By Lemma 17, this necessarily implies (13), that is,

$$v''(t) + (v'(t))^2 a(v(t)) = v'(t)a(t).$$

However, since a is v-periodic, $v'(t)a(v(t)) = a(t)$, so that (13) implies $v''(t) \equiv 0$ for all $t \in I$. Consequently, if $v''(t_0) \neq 0$ for some $t_0 \in I$, then $x' = a(t)x$ with $a \in \mathcal{P}_v(I)$ does not have a nontrivial v-periodic solution. Moreover, if $v''(t) \equiv 0$ for all $t \in I$, then any v-periodic $a \in C(I, \mathbb{R})$ also satisfies (13) and Theorem 19 applies.

3.2. Nonhomogeneous differential equations

We now bring our attention to nonhomogeneous first-order linear differential equations. For that, we consider

$$x' = a(t)x + b(t), \qquad t \in I, \tag{16}$$

where $a, b \in C(I, \mathbb{R})$ and, as before, I is an interval in $\mathbb{R}$, unbounded from above. Its solution is given by

$$x(t) = e_a(t, t_0)x(t_0) + \int_{t_0}^{t} e_a(t, s)b(s)\,\mathrm{d}s, \qquad t_0 \in I. \tag{17}$$

First, we provide a sufficient condition for a given solution to be v-periodic.

Theorem 24. *Let $a \in C(I, \mathbb{R})$ satisfy (13) and let $b \in C(I, \mathbb{R})$ satisfy*

$$(v')^2 b^v = b. \tag{18}$$

If x solves (16) with

$$v'(t_0)x(v(t_0)) = x(t_0)$$

for some $t_0 \in I$, then x is v-periodic.

Proof. Define $g(t) := v'(t)x(v(t)) - x(t)$. Then

$$\begin{aligned} g'(t) &= v''(t)x(v(t)) + v'(t)x'(v(t))v'(t) - x'(t) \\ &\overset{(16)}{=} v''(t)x(v(t)) + (v'(t))^2 a(v(t))x(v(t)) + (v'(t))^2 b(v(t)) - a(t)x(t) - b(t) \\ &\overset{(18)}{=} v''(t)x(v(t)) + (v'(t))^2 a(v(t))x(v(t)) - a(t)x(t) \\ &\overset{(13)}{=} v'(t)a(t)x(v(t)) - a(t)x(t) = a(t)g(t). \end{aligned}$$

Since $g(t_0) = 0$, $g(t) \equiv 0$, which completes the proof. □

Note that (18) is satisfied if b can be written as a product of two v-periodic functions.

Example 25. In the classical case when $v(t) = t + \omega$ for $\omega \in \mathbb{R}^+$, condition (13) reads as $a(t+\omega) = a(t)$ and condition (18) collapses to $b(t+\omega) = b(t)$ for all $t \in \mathbb{R}$. Thus, Theorem 24 states that if a and b are ω-periodic (in the classical sense), and there exists a solution x such that $x(t_0 + \omega) = x(t_0)$ for some $t_0 \in I$, then x is ω-periodic. This is consistent with the classical theory of linear periodic differential equations.

Lemma 26. *Let $a \in C(I, \mathbb{R})$ satisfy (13) and let $b \in C(I, \mathbb{R})$ satisfy (18). Define, for $t_0 \in I$,*

$$H(t; t_0) := \int_t^{v(t)} e_a(t_0, s)b(s)\,\mathrm{d}s \tag{19}$$

then, for $t \in I$,

$$\frac{\mathrm{d}}{\mathrm{d}t} H(t; t_0) = \left(\frac{1}{E_a(v(t_0), t_0)} - 1 \right) b(t)e_a(t_0, t).$$

Proof. Assume H is defined as in (19) for $t \in I$. By Lemma 6, we have for $H'(t) := \frac{\mathrm{d}}{\mathrm{d}t} H(t; t_0)$,

$$\begin{aligned} H'(t) &= v'(t)e_a(t_0, v(t))b(v(t)) - e_a(t_0, t)b(t) \\ &= v'(t)e_{-a}(v(t), t)e_a(t_0, t)b(v(t)) - e_a(t_0, t)b(t) \\ &\overset{(18)}{=} \left(\frac{e_{-a}(v(t), t)}{v'(t)} - 1 \right) b(t)e_a(t_0, t) = \left(\frac{1}{E_a(v(t), t)} - 1 \right) b(t)e_a(t_0, t). \end{aligned}$$

By Lemma 17, $E_a(v(t), t) = E_a(v(t_0), t_0)$, completing the claim. □

Theorem 27. *Let $a, b \in C(I, \mathbb{R})$ satisfy (13) and (18), respectively. If $E_a(v(t_0), t_0) \neq 1$ for some $t_0 \in I$, then (16) has a unique v-periodic solution $\bar{x}$ given by*

$$\bar{x}(t) = \lambda e_a(t, t_0) \int_t^{v(t)} e_a(t_0, s)b(s)\,\mathrm{d}s, \tag{20}$$

where

$$\lambda := \frac{E_a(v(t_0), t_0)}{1 - E_a(v(t_0), t_0)}.$$

Proof. The solution of (16) is given by (17) and

$$x(v(t)) = e_a(v(t), t)x(t) + \int_t^{v(t)} e_a(v(t), s)b(s)\,\mathrm{d}s.$$

If $\bar{x}$ is a v-periodic solution, then

$$\bar{x}(t) = v'(t)\bar{x}(v(t)) = v'(t)e_a(v(t), t)\bar{x}(t) + v'(t) \int_t^{v(t)} e_a(v(t), s)b(s)\,\mathrm{d}s,$$

i.e.,

$$\bar{x}(t) = \frac{E_a(v(t), t)}{1 - E_a(v(t), t)} \int_t^{v(t)} e_a(t, s)b(s)\,\mathrm{d}s = \lambda e_a(t, t_0)H(t; t_0), \tag{21}$$

where

$$\lambda \overset{\text{Lem 17}}{=} \frac{E_a(v(t_0), t_0)}{1 - E_a(v(t_0), t_0)} \quad \text{and} \quad H(t; t_0) \overset{(19)}{=} \int_t^{v(t)} e_a(t_0, s)b(s)\,\mathrm{d}s.$$

Conversely, $\bar{x}$ given in (21) solves (16), because, by Lemma 26,

$$\begin{aligned} \bar{x}'(t) &= \lambda \left\{ a(t)e_a(t, t_0)H(t; t_0) + e_a(t, t_0)\frac{\mathrm{d}}{\mathrm{d}t} H(t; t_0) \right\} \\ &= \lambda \left\{ a(t)e_a(t, t_0)H(t; t_0) + e_a(t, t_0) \left(\frac{1}{E_a(v(t_0), t_0)} - 1 \right) b(t)e_a(t_0, t) \right\} \\ &= \lambda \left\{ a(t)e_a(t, t_0)H(t; t_0) + \frac{1}{\lambda} b(t) \right\} = a(t)\bar{x}(t) + b(t), \end{aligned}$$

and $\bar{x}$ is v-periodic, since

$$\begin{aligned} v'(t)\bar{x}(v(t)) &= v'(t)\lambda e_a(v(t), t_0)H(v(t); t_0) = E_a(v(t), t)\lambda e_a(t, t_0)H(v(t); t_0) \\ &= E_a(v(t), t)\lambda e_a(t, t_0) \left\{ H(t; t_0) + \int_t^{v(t)} \frac{\mathrm{d}}{\mathrm{d}\tau} H(\tau; t_0)\,\mathrm{d}\tau \right\} \\ &\overset{\substack{\text{Lem 17} \\ \text{Lem 26}}}{=} E_a(v(t_0), t_0)\lambda e_a(t, t_0) \left\{ H(t; t_0) + \int_t^{v(t)} \frac{1}{\lambda} e_a(t_0, \tau)b(\tau)\,\mathrm{d}\tau \right\} \\ &= E_a(v(t_0), t_0)\lambda e_a(t, t_0) \left\{ H(t; t_0) + \frac{1}{\lambda} H(t; t_0) \right\} \\ &= \frac{\lambda}{1 + \lambda} \lambda e_a(t, t_0) \left\{ H(t; t_0) + \frac{1}{\lambda} H(t; t_0) \right\} = \lambda e_a(t, t_0)H(t; t_0) = \bar{x}(t), \end{aligned}$$

completing the proof. □

Example 28. In the classical case when $v(t) = t + \omega$ for $\omega \in \mathbb{R}^+$, Theorem 27 states that if a and b are ω-periodic (in the classical sense) and $\int_{t_0}^{t_0+\omega} a(s)\,\mathrm{d}s \neq 0$ for some $t_0 \in I$, then there exists a unique ω-periodic solution $\bar{x}$ of (16), given by

$$\overline{x}(t) = \lambda \int_t^{t+\omega} e^{\int_s^t a(\tau)\,\mathrm{d}\tau} b(s)\,\mathrm{d}s$$

with $\lambda = \left(e^{-\int_{t_0}^{t_0+\omega} a(s)\,\mathrm{d}s} - 1\right)^{-1}$. This is again consistent with the classical result for nonhomogeneous linear periodic differential equations.

The analogous result of Theorem 19 for the nonhomogeneous linear differential equation is formulated as follows.

Theorem 29. *Let $a, b \in C(I, \mathbb{R})$ satisfy (13) and (18), respectively. If*

$$E_a(\nu(t_0), t_0) = 1 \tag{22}$$

and

$$\int_{t_0}^{\nu(t_0)} e_a(t_0, s) b(s)\,\mathrm{d}s = 0 \tag{23}$$

for some $t_0 \in I$, then all solutions of (16) are ν-periodic. Otherwise, no nontrivial solution of (16) is ν-periodic.

Proof. Let x be a solution of (16). By (20),

$$x(\nu(t)) = e_a(\nu(t), t)x(t) + \int_t^{\nu(t)} e_a(\nu(t), \tau) b(\tau)\,\mathrm{d}\tau$$

and

$$\begin{aligned} \nu'(t)x(\nu(t)) &= \nu'(t) e_a(\nu(t), t)x(t) + \nu'(t) \int_t^{\nu(t)} e_a(\nu(t), \tau) b(\tau)\,\mathrm{d}\tau \\ &\overset{\text{Lem 17}}{=} E_a(\nu(t_0), t_0) \left\{ x(t) + \int_t^{\nu(t)} e_a(t, \tau) b(\tau)\,\mathrm{d}\tau \right\} \\ &\overset{(22)}{=} x(t) + \int_t^{\nu(t)} e_a(t, \tau) b(\tau)\,\mathrm{d}\tau = x(t) + e_a(t, t_0) H(t; t_0), \end{aligned}$$

where H is defined in (19) and $t_0 \in I$. Note that (22) implies $\frac{\mathrm{d}}{\mathrm{d}t} H(t; t_0) = 0$ in Lemma 26. We therefore have

$$\nu'(t)x(\nu(t)) = x(t) + e_a(t, t_0) H(t_0; t_0)$$

and by (23), $H(t_0; t_0) = 0$. Hence x is ν-periodic and the proof is complete. □

4. Application to the logistic differential equation

Consider the nonautonomous logistic growth model

$$x'(t) = r(t)x(t)\left(1 - \frac{x(t)}{K(t)}\right) \tag{24}$$

with time-dependent carrying capacity $K \in C(I, \mathbb{R}^+)$, time-dependent growth rate $r \in C(I, \mathbb{R}^+)$, and positive initial condition $x(t_0)$ for $t_0 \in I$. Then, $x(t) > 0$ for all $t \in I$ and the substitution $u = \frac{1}{x}$ transforms (24) into the linear differential equation

$$u'(t) = -r(t)u(t) + \frac{r(t)}{K(t)}. \tag{25}$$

In the case when $r > 0$ and K is periodic in the classical sense with period $\omega > 0$, then (24) has a unique ω-periodic solution $\bar{x}$ that is globally attractive [22]. In fact, this result, which corresponds to the so-called first Cushing–Henson conjecture, originally formulated for the discrete Beverton–Holt model, was proven in [22] to uphold for the time-scales analogue of (24). More precisely, the authors showed that the dynamic equation

$$x^{\Delta} = r x^{\sigma}\left(1 - \frac{x}{K(t)}\right) \tag{26}$$

with $r > 0$ and $K(t + \omega) = K(t)$ for $t \in \mathbb{T}$, where $\mathbb{T}$ is an ω-periodic time scale, has a unique ω-periodic solution. Furthermore, the average of this ω-periodic solution is strictly smaller than the average of the ω-periodic carrying capacities, implying a deleterious effect of a periodically forced environment [22]. This is also known as the second Cushing–Henson conjecture.

Although these conjectures were originally formulated for the discrete Beverton–Holt model, they also remain true for the continuous logistic growth model. That is, if K is ω-periodic (in the classical sense) and r is constant, then there exists a unique ω-periodic solution that is globally attractive for positive initial conditions. Furthermore, the introduction of a periodic environment is deleterious for the species. These results immediately follow from (26), which contains (24) if $\mathbb{T} = \mathbb{R}$ and the Beverton–Holt model if $\mathbb{T} = \mathbb{Z}$. Note that (26) allows the construction of the logistic dynamic equation on the quantum time scale, $\mathbb{T} = q^{\mathbb{N}_0} = \{1, q, q^2, \dots\}$ for $q > 1$. However, the result in [22] cannot be readily applied since $q^{\mathbb{N}_0}$ is not a periodic time scale. Thus, the formulation of the Cushing–Henson conjectures on quantum calculus required already a nonstandard definition of periodicity [31–33]. More recently, equipped with a definition of periodicity for isolated time scales introduced in [13], the interplay between the discrete and continuous logistic model was able to be continued. More precisely, in [23], the Cushing–Henson conjectures were extended to a general discrete space, so-called isolated time scales. With our introduction of ν-periodicity, we return to the continuous case and advance the discussion of the Cushing–Henson conjectures on the continuous time domain.

4.1. First Cushing–Henson conjecture

To extend the first Cushing–Henson conjecture to (24), we consider (24) with the additional assumptions:

$$\frac{\nu''}{\nu'} + \nu' r^{\nu} = r, \tag{H1}$$

$$\left(\frac{r}{K}\right)^{\nu} = \frac{r}{K}. \tag{H2}$$

Theorem 30 (*Existence of a unique ν-periodic solution*)**.** *Consider (24) with (H1) and (H2) on I. If $E_r(\nu(t_0), t_0) > 1$ for $t_0 \in I$, then there exists a unique positive ν-periodic solution of (24), given by*

$$\overline{x}(t) = \lambda \left(\int_t^{\nu(t)} e_r(s, t) \frac{r(s)}{K(s)}\,\mathrm{d}s \right)^{-1}, \tag{27}$$

where $\lambda = E_r(\nu(t_0), t_0) - 1 > 0$.

Proof. Note that, by Lemma 17 and the assumption (H1), $E_r(\nu(t_0), t_0) > 1$ implies $E_r(\nu(t), t) > 1$ for all $t \in I$. Since $x(t) > 0$ for all $t > t_0$, whenever $x(t_0) > 0$, we may apply the transformation $u = \frac{1}{x}$ to (24), to obtain (25) with its solution given by

$$u(t) = e_{-r}(t, t_0) u(t_0) + \int_{t_0}^t \frac{r(s)}{K(s)} e_{-r}(t, s)\,\mathrm{d}s, \qquad t_0 \in I. \tag{28}$$

If $\bar{x} > 0$ is a ν-periodic solution of (24), then $\bar{u} = \frac{1}{\bar{x}}$ satisfies

$$\begin{aligned} \nu'(t)\bar{u}(t) = \bar{u}(\nu(t)) &= e_{-r}(\nu(t), t_0) u(t_0) + \int_{t_0}^{\nu(t)} \frac{r(s)}{K(s)} e_{-r}(\nu(t), s)\,\mathrm{d}s \\ &= e_{-r}(\nu(t), t)\bar{u}(t) + e_{-r}(\nu(t), t) \int_t^{\nu(t)} \frac{r(s)}{K(s)} e_{-r}(t, s)\,\mathrm{d}s. \end{aligned}$$

Solving for $\bar{u}(t)$ yields

$$\bar{u}(t) = \frac{1}{\lambda} \int_t^{\nu(t)} \frac{r(s)}{K(s)} e_{-r}(t, s)\,\mathrm{d}s, \tag{29}$$

where

$$\lambda = \frac{\nu'(t) - e_{-r}(\nu(t), t)}{e_{-r}(\nu(t), t)} = E_r(\nu(t), t) - 1 \overset{\text{(H1)}}{=} E_r(\nu(t_0), t_0) - 1 > 0. \tag{30}$$

It is left to show that (29) satisfies (i) $\bar{u}'(t) = -r(t)\bar{u}(t) + \frac{r(t)}{K(t)}$ and (ii) $\nu'(t)\bar{u}(t) = \bar{u}(\nu(t))$.

Claim (i) follows after recalling that $E_r(\nu(t),t) = \lambda + 1$ and therefore

$$\begin{aligned}\overline{u}'(t) &= \frac{1}{\lambda}\left\{\frac{r(\nu(t))}{K(\nu(t))}e_{-r}(t,\nu(t))\nu'(t) - \frac{r(t)}{K(t)}e_{-r}(t,t) + \int_t^{\nu(t)} \frac{r(s)}{K(s)}\left(\frac{\mathrm{d}}{\mathrm{d}t}e_{-r}(t,s)\right)\mathrm{d}s\right\}\\ &\overset{\text{(H2)}}{=} \frac{1}{\lambda}\left\{\frac{r(t)}{K(t)}(\lambda+1) - \frac{r(t)}{K(t)}\right\} - r(t)\frac{1}{\lambda}\int_t^{\nu(t)}\frac{r(s)}{K(s)}e_{-r}(t,s)\,\mathrm{d}s\\ &= \frac{r(t)}{K(t)} - r(t)\overline{u}(t).\end{aligned}$$

To show (ii), we calculate

$$\begin{aligned}\frac{1}{\nu'(t)}\overline{u}(\nu(t)) &= \frac{1}{\lambda\nu'(t)}\int_{\nu(t)}^{\nu\circ\nu(t)}\frac{r(s)}{K(s)}e_{-r}(\nu(t),s)\,\mathrm{d}s\\ &= \frac{1}{\lambda\nu'(t)}\int_t^{\nu(t)}\frac{r(\nu(s))}{K(\nu(s))}e_{-r}(\nu(t),\nu(s))\nu'(s)\,\mathrm{d}s\\ &= \frac{1}{\lambda\nu'(t)}\int_t^{\nu(t)}\frac{r(\nu(s))}{K(\nu(s))}e_r(\nu(s),s)e_r(s,t)e_r(t,\nu(t))\nu'(s)\,\mathrm{d}s\\ &\overset{\text{(H2)}}{=} \frac{1}{\lambda}\int_t^{\nu(t)}\frac{r(s)}{K(s)}E_r(\nu(s),s)e_r(s,t)\frac{1}{E_r(\nu(t),t)}\,\mathrm{d}s\\ &= \frac{1}{\lambda}\int_t^{\nu(t)}\frac{r(s)}{K(s)}e_r(s,t)\,\mathrm{d}s = \overline{u}(t),\end{aligned}$$

because $E_r(\nu(t),t)$ is independent of $t \in I$. □

Although the Cushing–Henson conjectures were originally formulated for the discrete Beverton–Holt model based on experimental data [19], we may still fit the provided discrete data to its continuous analogue that we, as argued earlier, consider to be the logistic differential equation. Moreover, our generalization of periodicity allows us to study the existence of ν-periodic solutions even in the case when the coefficients are seemingly constant, which would have previously been referred to as 1-periodic. As an example, we fit the parameters r and $x(0)$ to the experimental data set (Replicate [19, Culture #13 in Table 1]). The fitted solution is, see Appendix A.1,

$$\hat{x}(t) = \frac{e^{\hat{r}t}\hat{K}\hat{x}(0)}{\hat{K} - \hat{x}(0) + e^{\hat{r}t}\hat{x}(0)}, \qquad \hat{x}(0) = 191.3611, \quad \hat{r} = 0.0163, \quad \hat{K} = 729.$$

By choosing

$$\nu(t) = \nu_0 - \log\left(1 + \nu_1(e^{\hat{r}t} - 1)\right) \tag{31}$$

with

$$\nu_0 = 25, \qquad \nu_1 = e^{-\hat{r}\nu_0}\left(\frac{\hat{x}(0)}{\hat{K}}(e^{\hat{r}\nu_0} - 1) + 1\right) \approx 0.7527, \tag{32}$$

we can show that the fitted solution $\hat{x}$ is also the unique ν-periodic solution given in (27). If we had chosen different ν_0 and ν_1, then another solution would have been the corresponding ν-periodic solution, see $\bar{x}_1$ and $\bar{x}_2$ in Fig. 1(a) for such examples.

Although the experiments in [19] did not consider the case of decreasing resources, we could now use simulations to study the effect on this (fitted) species if resources continuously decrease. We assume that such decrease results in a corresponding continuous decline of the carrying capacity, i.e., $K(t) = \frac{\widetilde{K}}{t\cdot\sigma_K}$ for $t \geq 1$, where $\sigma_K \in (0,1]$ captures the speed of decline. We choose the constant $\widetilde{K}$ such that on average (over the time frame of collected data), the average of $K(t)$ for $\sigma_K = 1$ is identical to the optimized K-value $\hat{K} = 729$, i.e., $\frac{1}{70}\int_1^{71}\frac{\widetilde{K}}{t}\,dt = \hat{K} = 729$. Similarly, we assume that a decline in resources also results in a corresponding decrease in the inherent growth rate r so that $r(t) = \frac{\widetilde{r}}{t\cdot\sigma_r}$, where again $\sigma_r \in (0,1]$ determines the speed of decrease due to reduced resources, $t \geq 1$, and $\widetilde{r}$ is chosen such that the average of $r(t)$ over the data set corresponds to the previously fitted constant $\hat{r} = 0.0163$, i.e., $\frac{1}{70}\int_1^{71}\frac{\widetilde{r}}{t}\,dt = 0.0163$. The solution to (24) for $t \geq 1$ is then given by

$$x(t) = \frac{t^{\sigma_r^{-1}\widetilde{r}}x_1}{1 + x_1\frac{\widetilde{r}\sigma_K}{\widetilde{K}\sigma_r(\widetilde{r}\sigma_r^{-1}+1)}(t^{\widetilde{r}\sigma_r^{-1}+1} - 1)},$$

where $x_1 = x(1) = X(0)$ is the initial population size. The solutions for two different choices of σ_K and σ_r are plotted in black in Fig. 1(b). We note that although the behavior of the two solutions is similar, the slowing down of the impact of decreasing resources (i.e., $\sigma_r = \sigma_K = 0.8$) results in higher population levels.

The corresponding ν-periodic solutions for these two parameter sets, where $\nu(t) = 2(t^{1+\widetilde{r}\sigma_r^{-1}} + 1)^{\frac{1}{1+\widetilde{r}\sigma_r^{-1}}}$ is motivated by Example 33, are plotted with their respective shapes in red. For small t-values, these solutions exceed 1000 but decrease monotonically. It would be interesting to investigate experimentally how fast populations, that can be modeled using the logistic differential equation, converge to this ν-periodic solution in the case of such decreasing resources. This would require an experimental set-up in which the resources are continuously decreasing.

Our new formulation of periodicity can also be exploited to relax the condition of constant coefficients. To account however for some of the observed variation (see orange data points in Fig. 1a), one can relax the conditions of constant model parameters. Consider for example a constant K but a piece-wise linear growth function, to account for example for a specie's intrinsic evolutionary trait processes. That is, we consider $r(t) = r_n + \frac{(r_{n+1}-r_n)}{2}(t - \lfloor t \rfloor)$ for $t \in (t_{n-1}, t_{n+1})$. This choice of growth rate allows, for example, to perfectly describe the observed date by choosing $\mathbf{r} = (r_1, \ldots, r_N)$ such that it solves the matrix equation,

$$\begin{bmatrix} 1 & 1 & 0 & 0 & \ldots & 0 & 0\\ 0 & 1 & 1 & 0 & \ldots & 0 & 0\\ \vdots & \vdots & \vdots & \vdots & \vdots\vdots\vdots & \vdots & \vdots\\ 0 & 0 & 0 & 0 & \ldots & 0 & 1\end{bmatrix}\mathbf{r} = \begin{pmatrix}\ln\left(\frac{(K-X_0)X_1}{X_0(K-X_1)}\right)\\ \ln\left(\frac{(K-X_1)X_2}{X_1(K-X_2)}\right)\\ \vdots\\ \ln\left(\frac{(K-X_{N-1})X_N}{X_{N-1}(K-X_N)}\right)\end{pmatrix}, \tag{33}$$

where X_i are the observed (biweekly) data points for $i \in \{0, 1, \ldots, N-1\}$, representing the population at time t_{2i} (see details in Appendix A.2). Alternatively, one may determine values for $r_1, \ldots, r_N$ using an optimization problem that minimizes the error to the data points, i.e., minimizes $\sum_{i=0}^{N-1}(x(t_{2i};\mathbf{r}) - X_i)^2$, subject to conditions (H1) and (H2) to ensure the existence of a ν-periodic solution. Note that for constant K, (H2) reads as $r^\nu = r$, so that if (H2) holds, (H1) can be written as

$$\frac{\nu''}{\nu'} + \nu' r = r, \qquad \text{i.e.,} \qquad \nu'' = r\nu'(1-\nu').$$

Solving this differential equation for ν' for a piece-wise linear r as described above, gives, for $t \in (t_{n-1}, t_{n+1})$,

$$\nu(t) = \nu(t_{n-1}) + \int_{t_{n-1}}^t \frac{\upsilon'(t_{n-1})}{e^{-(s-t_{n-1})(r_n + \frac{r_{n+1}-r_n}{4}(s+t_{n-1}))}(1 - \upsilon'(t_{n-1})) + \upsilon'(t_{n-1})}\,\mathrm{d}s,$$

where $\upsilon(t_{n-1})$ and $\upsilon'(t_{n-1})$ are obtained inductively and $\upsilon(t_0) = \upsilon(0)$ and $\upsilon'(t_0) = \upsilon'(0)$ can be chosen freely. Details of this calculation are provided in Appendix A.3.

Other functional forms of r could have been considered. As long as K is constant, a suitable ν can be found in the same way, that is, by solving the $y' = r(t)y(1-y)$, where $y = \nu'$, and then integrating the solution to obtain $\nu(t) = \int y(s)\mathrm{d}s$. Although beyond the scope of this manuscript, exploring computationally and analytically the existence of such functional forms remains an interesting future avenue.

Lemma 31. *Consider (24) with (H1) and (H2) on I. Suppose there exists $t_0 \in I$ such that $E_r(\nu(t_0), t_0) > 1$. If $\limsup_{s\in I} K(s) < \infty$, then the unique positive ν-periodic solution of (24) is bounded.*

Proof. The unique ν-periodic solution $\overline{x}$ of (24) can be expressed as the reciprocal of (28), that is,

$$\overline{x}(t) = \frac{\overline{x}(t_0)}{e_{-r}(t,t_0) + \overline{x}(t_0)\int_{t_0}^t \frac{r(s)}{K(s)}e_{-r}(t,s)\,\mathrm{d}s}.$$

Since $\overline{x}(t_0) \in (0,\infty)$ and $e_{-r}(t,t_0) \geq 0$, it suffices to show that $\lim_{t\to\infty}\int_{t_0}^t \frac{r(s)}{K(s)}e_{-r}(t,s)\,\mathrm{d}s > 0$. Let $K^M := \limsup_{s\in I} K(s)$. Then

$$\int_{t_0}^t \frac{r(s)}{K(s)}e_{-r}(t,s)\,\mathrm{d}s \geq \frac{1}{K^M}\int_{t_0}^t r(s)e_r(s,t)\,\mathrm{d}s = \frac{1}{K^M}(1 - e_r(t_0,t)),$$

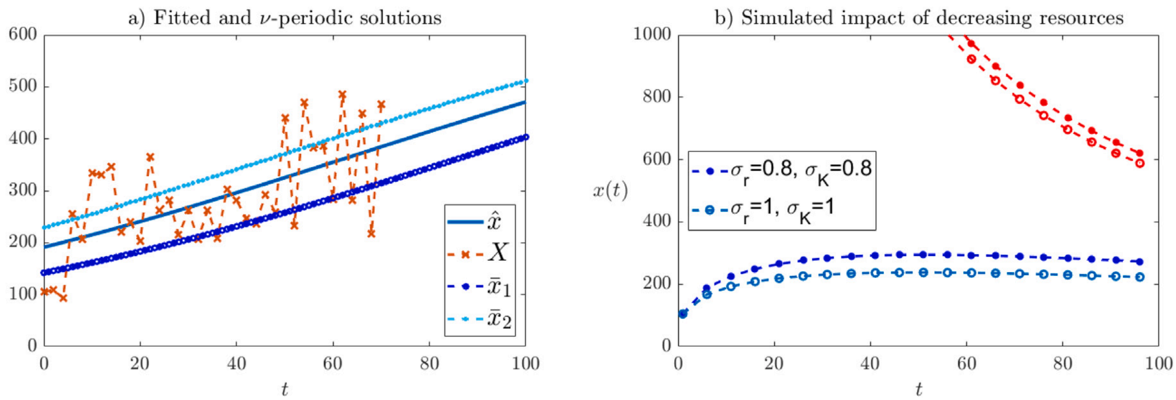

Fig. 1. (a) The orange dots refer to the data points given in [19, Table 1]. The fitted solution $\hat{x}$ with constant parameters is also the ν-periodic solution $\bar{x}$ given by (31) with (32). If we chose $\nu_0 = 25$ and $\nu_1 = 0.73$ in (31), then the unique ν-periodic solution is $\bar{x}_1$ and for $\nu_1 = 0.77$, the unique ν-periodic solution is $\bar{x}_2$. Note that the curvature is not identical for these ν-periodic solutions. (b) The solution x of (24) for $r = \frac{\tilde{r}}{\sigma_r t}$ and $K = \frac{\tilde{K}}{\sigma_K t}$ are plotted in blue. The red curves are the associated ν-periodic solutions $\bar{x}$ with $\nu(t)$ given in Example 34 for $D_1 = 2$ and $D_2 = 1$. Curves with open circles correspond to the pair $(\sigma_r, \sigma_K) = (1, 1)$ and filled circles correspond to the pair $(0.8, 0.8)$, representing a reduced speed of decline, hence higher population levels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

which is positive because $e_r(t_0, t) = e_{-r}(t, t_0) < 1$ for $t > t_0$, completing the proof. $\square$

Theorem 32 (*Global Asymptotic Stability*). *Consider (24) with (H1) and (H2) on I. Suppose there exists $t_0 \in I$ such that $E_r(\nu(t_0), t_0) > 1$. If $\limsup_{s\in I} K(s) < \infty$, then the unique ν-periodic solution $\bar{x}$ of (24) is globally asymptotically stable for solutions with positive initial conditions.*

Proof. After resubstituting $u = x^{-1}$ in (28), a solution to (24) can be expressed as

$$x(t) = \frac{x_0}{e_{-r}(t, t_0) + x_0 \int_{t_0}^{t} e_{-r}(t, s) \frac{r(s)}{K(s)} \, ds},$$

with initial value $x(t_0) = x_0 > 0$. The ν-periodic solution can be expressed equivalently with the initial condition

$$\bar{x}_0 = \bar{x}(t_0) = \lambda \left(\int_{t_0}^{\nu(t_0)} \frac{r(s)}{K(s)} e_r(s, t) \, ds \right)^{-1}.$$

Then,

$$\begin{aligned} |x(t) - \bar{x}(t)| &= \left| \frac{x_0 e_{-r}(t, t_0) - \bar{x}_0 e_{-r}(t, t_0)}{(e_{-r}(t, t_0) + x_0 \int_{t_0}^{t} e_{-r}(t, s) \frac{r(s)}{K(s)} \, ds)(e_{-r}(t, t_0) + \bar{x}_0 \int_{t_0}^{t} e_{-r}(t, s) \frac{r(s)}{K(s)} \, ds)} \right| \\ &= \left| \frac{e_{-r}(t, t_0)(x_0 - \bar{x}_0)}{(e_{-r}(t, t_0) + x_0 \int_{t_0}^{t} e_{-r}(t, s) \frac{r(s)}{K(s)} \, ds)} \cdot \frac{\bar{x}(t)}{\bar{x}_0} \right| \\ &\le \left| \frac{1}{1 + x_0 \int_{t_0}^{t} e_{-r}(t_0, s) \frac{r(s)}{K(s)} \, ds} \right| \cdot \left| \frac{\bar{x}(t)}{\bar{x}_0} \right| \cdot |x_0 - \bar{x}_0|, \end{aligned}$$

where the right-hand side can be made arbitrarily small for sufficiently large t because

$$\int_{t_0}^{t} e_{-r}(t_0, s) \frac{r(s)}{K(s)} \, ds = \int_{t_0}^{t} e_r(s, t_0) \frac{r(s)}{K(s)} \, ds \ge \frac{1}{K^M} \left(e_r(t, t_0) - 1 \right).$$

This completes the proof. $\square$

Theorems 30 and 32 confirm the *First Cushing–Henson Conjecture* for the nonautonomous model (24) with the generalization of periodicity defined in (4). Theorems 30 and 32 are consistent with the results obtained in [22] for periodic time scales, after choosing the specific time scale $\mathbb{T} = \mathbb{R}$ and $\nu(t) = t + \omega$.

Example 33. Consider the logistic model

$$x' = r(t) x \left(1 - \frac{x}{K(t)} \right), \qquad t \ge t_0 > 0, \tag{34}$$

with

$$r(t) = \frac{r_0}{t}, \qquad K(t) = \frac{K_0}{t},$$

for $r_0, K_0 > 0$ and $t \in I = [t_0, \infty)$. By construction, $r, K \in C(I, \mathbb{R})$ and (H2) is satisfied for any $\nu : I \to I$. It is not hard to show that (H1) is satisfied for $\nu(t) = D_1 \left(t^{1+r_0} + D_2 \right)^{\frac{1}{1+r_0}} > 0$ for any $D_1, D_2 > 0$, where $\nu'(t) = \frac{D_1^{1+r_0} \nu(t)}{\nu^{1+r_0}(t)} t^{r_0} = D_1^{1+r_0} \left(\frac{t}{\nu(t)} \right)^{r_0} > 0$ for $t \in I$. Furthermore,

$$E_r(\nu(t), t) = D_1^{1+r_0} \left(\frac{t}{\nu(t)} \right)^{r_0} e^{\int_t^{\nu(t)} \frac{r_0}{s} \, ds} = D_1^{1+r_0} \left(\frac{t}{\nu(t)} \right)^{r_0} \left(\frac{\nu(t)}{t} \right)^{r_0} = D_1^{1+r_0}.$$

For $D_1 > 1$, there exists, by Theorem 30, a unique positive ν-periodic solution of (34) that is given by (27). Furthermore, since $\limsup_{s\in I} K(s) = \frac{K_0}{t_0} < \infty$, the unique ν-periodic solution $\bar{x}$ is globally attracting solutions with positive initial conditions, by Theorem 32. Fig. 2(a) visualizes the behavior of solutions for different initial conditions, as well as their convergence to $\bar{x}$ (see red curve). Although $\bar{x}(t)$ is decreasing in t, see Fig. 2(a), $\bar{x}$ is ν-periodic. Fig. 2(b) and (c) visualize the property of ν-periodic functions of translation invariance of integration. More precisely, (b) shows that only for the ν-periodic solution, the integral function κ increases to the same value (namely 1, due to the normalization constant C) in each interval $(\nu^k(1), \nu^{k+1}(1))$ for all $k \in \mathbb{N}_0$ and where ν^k denotes the composition of ν with itself k-times. This behavior implies that $\int_{\nu^k(1)}^{\nu^{k+1}(1)} \bar{x}(s) ds$ remains constant, i.e., the area underneath the curve from $\nu^k(1)$ to $\nu^{k+1}(1)$ remains constant. This is highlighted in (c), where, despite the decrease of the ν-periodic function, the area underneath $\bar{x}$ remains the same across different k (here: $k = 0, 1, 2, 3$; colored in different shades).

4.2. Second Cushing–Henson conjecture

We define $H \in C^1(I, \mathbb{R})$ to be the solution to the linear functional equation

$$H(\nu(t)) + \ln(\nu'(t)) = H(t). \tag{35}$$

By [34, Theorem 2.1], see also [30, Theorem 2], if ν satisfies additionally that there exists $\xi \in I$ such that

$$\begin{aligned} (\nu(t) - t)(\xi - t) &> 0, \qquad t \in I, t \ne \xi \\ (\nu(t) - \xi)(\xi - t) &< 0, \qquad t \in I, t \ne \xi, \end{aligned}$$

then there exists a unique $H \in C(I, \mathbb{R})$ to (35). Note that if H is differentiable, then $h(t) := H'(t)$ satisfies $E_h(\nu(t), t) = 1$, where E_h is defined in (12), i.e.,

$$E_h(\nu(t), t) = \nu'(t) e_h(\nu(t), t) = \nu'(t) e^{\int_t^{\nu(t)} h(s) \, ds} = 1. \tag{36}$$

If there exists $h \in C^1(I, \mathbb{R})$ that satisfies (36), then, by Lemma 17, h satisfies (H1).

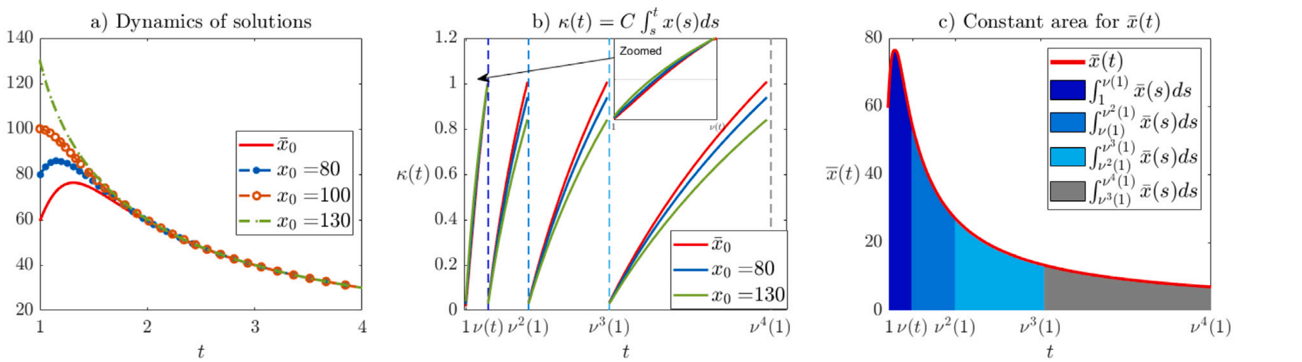

Fig. 2. Plots are based on (34) with $r_0 = 5$, $K_0 = 100$, $D_1 = 2$, $D_2 = 1$. (a) Dynamics of the solution to (34) for different initial conditions x_0. All solutions, as predicted in Theorem 32, converge to the ν-periodic solution $\bar{x}$ (red solid curve). (b) Visualization of the periodic property (9) using the function $\kappa(t) := C\int_s^t f(\tau)\mathrm{d}\tau$ for $t \in (s, \nu(s)]$, where $s = \nu^k(1)$ for some $k \in \mathbb{N}_0$ and $C = \int_1^{\nu(1)} f(\tau)\mathrm{d}\tau$. If f is ν-periodic, then κ is strictly increasing with $\kappa(\nu^k(1)) = 0 < \kappa(t) < \kappa(\nu^{k+1}(1)) = 1$. Note that only $\bar{x}$ (red curve) satisfies this condition. (c) Visualization of the area preserving property of ν-periodic functions. Since $\bar{x}$ (red solid curve) is ν-periodic, $\int_{\nu^k(1)}^{\nu^{k+1}(1)} \bar{x}(s)\,\mathrm{d}s$ is constant for all $k \in \mathbb{N}$. That is, the areas highlighted in shades of blue have all the same value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Note that if $\nu(t) = t+\omega$, then (36) reads as $e_h(t+\omega, t) = 1$, requiring h to be an ω-periodic function such that $\int_{t_0}^{t_0+\omega} h(s)\,\mathrm{d}s = 0$ for $t_0 \in I \subset \mathbb{R}$.

Example 34. Let $I = (0,\infty) \subset \mathbb{R}$. If $\nu(t) = t + D\sqrt{1+t} + \left(\frac{D}{2}\right)^2 > 0$ for $D > 0$, then ν satisfies

$$\left(\nu'(t)\right)^2 = \frac{1+\nu(t)}{1+t} > 0. \tag{37}$$

Since

$$\frac{\sqrt{1+\nu(t)}}{\sqrt{1+t}} = \nu'(t) = \exp\left\{\frac{1}{2}\int_t^{\nu(t)} (1+s)^{-1}\,\mathrm{d}s\right\} = \exp\left\{\int_{\nu(t)}^t h(s)\,\mathrm{d}s\right\} = e_h(t, \nu(t)),$$

for $h(t) = \frac{-1}{2(1+t)}$. Thus, $h < 0$ satisfies (36).

Changing $\nu(t) = ((1+t)^{\frac{3}{2}}+3)^{\frac{2}{3}} - 1$, then $\nu'(t) = \frac{\sqrt{1+t}}{((1+t)^{\frac{3}{2}}+3)^{\frac{1}{3}}} = \frac{\sqrt{1+t}}{\sqrt{1+\nu(t)}} > 0$. Now, (36) is satisfied for $\widetilde{h} = \frac{1}{2(1+t)} > 0$.

To formulate an analogue of the second Cushing–Henson conjecture, we strengthen our assumption (H1) on r by assuming that

$$(r-h)(s)e_h(t,s) = (r-h)(t), \qquad \text{for all } s,t \in I, \tag{H1*}$$

where h is given by (36).

Lemma 35. *Let h be given by (36). If r satisfies (H1*), then r satisfies (H1).*

Proof. Let $r \in C(I,\mathbb{R})$ satisfy (H1*) on I. Then, for $s = \nu(t)$,

$$(r-h)(\nu(t))\underbrace{e_h(t,\nu(t))}_{\nu'(t)} = (r-h)(t)$$

so that $\varphi = r-h$ is ν-periodic. Thus, by Theorem 16, $e_\varphi(\nu(t),t)$ is independent of t and, therefore,

$$e_\varphi(\nu(t_0),t_0) = e_\varphi(\nu(t),t) = e_r(\nu(t),t)e_{-h}(\nu(t),t) \overset{(36)}{=} e_r(\nu(t),t)\nu'(t) = E_r(\nu(t),t).$$

Hence, by Lemma 17, r satisfies (13) and therefore (H1), completing the claim. □

Proposition 36. *Suppose there exists $h \in C(I,\mathbb{R})$ satisfying (36). If (H2) holds on I, then, $\beta(t) := \frac{K(t)}{r(t)}e_h(t,t_0) \in \mathcal{P}_\nu(I)$.*

Proof. We have

$$\nu'(t)\beta(\nu(t)) = \nu'(t)\frac{K(\nu(t))}{r(\nu(t))}e_h(\nu(t),t_0) \overset{(H2)}{=} \frac{K(t)}{r(t)}\nu'(t)e_h(\nu(t),t)e_h(t,t_0) \overset{(36)}{=} \frac{K(t)}{r(t)}e_h(t,t_0) = \beta(t),$$

completing the claim. □

Proposition 37. *Suppose there exists $h \in C(I,\mathbb{R})$ satisfying (36). Let $r \in C(I,\mathbb{R})$ satisfy (H1). Then, for $\varphi := r-h$,*

$$e_\varphi(\nu(s),\nu(t_0)) = e_\varphi(s,t_0). \tag{38}$$

Proof. We calculate

$$\begin{aligned} e_\varphi(\nu(s),\nu(t_0)) &= e_\varphi(\nu(s),s)e_\varphi(s,t_0)e_\varphi(t_0,\nu(t_0)) \\ &= e_r(\nu(s),s)e_h(s,\nu(s))e_\varphi(s,t_0)e_r(t_0,\nu(t_0))e_h(\nu(t_0),t_0) \\ &\overset{(36)}{=} e_r(\nu(s),s)\nu'(s)e_\varphi(s,t_0)e_r(t_0,\nu(t_0))\frac{1}{\nu'(t_0)} \\ &= E_r(\nu(s),s)e_\varphi(s,t_0)\frac{1}{E_r(\nu(t_0),t_0)} \\ &\overset{(H1)}{=} e_\varphi(s,t_0), \end{aligned}$$

completing the claim. □

Theorem 38 (*Second Cushing–Henson Conjecture*)**.** *Consider (24) with (H1*) and (H2) on I. Suppose there exists $h \in C(I,\mathbb{R})$ satisfying (36) such that $\varphi(t) := r(t)-h(t) > 0$ for all $t \in I$. Assume that there exists $t_0 \in I$ such that $E_r(\nu(t_0),t_0) > 1$. Then, the unique positive ν-periodic solution $\bar{x}$ of (24) obeys*

$$\frac{1}{|\nu(t)-t|}\int_{t_0}^{\nu(t_0)} \bar{x}(s)\,\mathrm{d}s \le \frac{1}{|\nu(t)-t|}\int_{t_0}^{\nu(t_0)} G(s)K(s)\,\mathrm{d}s, \tag{39}$$

where

$$G(s) = \frac{\varphi(t_0)}{\varphi(t_0)+h(s)e_h(t_0,s)} > 0.$$

Equality in (39) holds if and only if $\frac{r}{K}$ is constant.

Proof. We will apply the weighted Jensen inequality to the concave function $F(z) = z^{-1}$, that is,

$$\frac{1}{\int_a^b w(s,t)y(s,t)\mathrm{d}s} \le \frac{1}{\left(\int_a^b w(s,t)\,\mathrm{d}s\right)^2}\int_a^b \frac{w(s,t)}{y(s,t)}\mathrm{d}s,$$

for weights $w(s,t) > 0$. Here, we choose

$$w(s,t) := e_\varphi(s,t)\varphi(s) > 0, \qquad y(s,t) = e_r(s,t)e_\varphi(t,s)\frac{r(s)}{\varphi(s)K(s)}$$

for $\varphi = r-h > 0$. By this choice of $w(s,t)$ and $y(s,t)$, we have

$$\int_t^{\nu(t)} w(s,t)\,\mathrm{d}s = \int_t^{\nu(t)} e_\varphi(s,t)\varphi(s)\,\mathrm{d}s = e_\varphi(\nu(t),t) - 1 \overset{(36)}{=} \nu'(t)e_r(\nu(t),t) - 1 \overset{(30)}{=} \lambda$$

and

$$\frac{w(s,t)}{y(s,t)} = \frac{e_h(t,s)e_\varphi(s,t)\varphi^2(s)}{r(s)}K(s) \overset{(H1^*)}{=} \frac{\varphi(t)e_\varphi(s,t)\varphi(s)}{r(s)}K(s)$$
$$= \frac{\varphi(t)e_\varphi(s,t)}{r(s)}K(s)\cdot\frac{\varphi(s)e_h(t_0,s)}{e_h(t_0,s)} \overset{(H1^*)}{=} \frac{\varphi(t)e_\varphi(s,t)}{r(s)}K(s)\cdot\frac{\varphi(t_0)}{e_h(t_0,s)}$$
$$= \varphi(t_0)\beta(s)\varphi(t)e_\varphi(s,t),$$

where $\beta(s) := \frac{K(s)}{r(s)}e_h(s,t_0)$. Note that by Proposition 36, $\beta \in \mathcal{P}_\nu(I)$. The application of the weighted Jensen inequality gives then

$$\int_{t_0}^{\nu(t_0)} \bar{x}(t)\,\mathrm{d}t \overset{(27)}{=} \int_{t_0}^{\nu(t_0)} \lambda \frac{1}{\int_t^{\nu(t)} e_r(s,t)\frac{r(s)}{K(s)}\,\mathrm{d}s}\,\mathrm{d}t$$
$$= \lambda \int_{t_0}^{\nu(t_0)} \frac{1}{\int_t^{\nu(t)} w(s,t)y(s,t)\,\mathrm{d}s}\,\mathrm{d}t$$
$$\le \lambda \int_{t_0}^{\nu(t_0)} \frac{1}{(\int_t^{\nu(t)} w(s,t)\,\mathrm{d}s)^2} \int_t^{\nu(t)} \frac{w(s,t)}{y(s,t)}\,\mathrm{d}s\,\mathrm{d}t$$
$$= \frac{\varphi(t_0)}{\lambda} \int_{t_0}^{\nu(t_0)} \int_t^{\nu(t)} \beta(s)\varphi(t)e_\varphi(s,t)\,\mathrm{d}s\,\mathrm{d}t$$
$$= \frac{\varphi(t_0)}{\lambda} \left\{ \int_{t_0}^{\nu(t_0)} \beta(s) \int_{t_0}^{s} \varphi(t)e_\varphi(s,t)\,\mathrm{d}t\,\mathrm{d}s + \int_{\nu(t_0)}^{\nu^2(t_0)} \beta(s) \int_{\nu^{-1}(s)}^{\nu(t_0)} \varphi(t)e_\varphi(s,t)\,\mathrm{d}t\,\mathrm{d}s \right\}$$
$$= \frac{\varphi(t_0)}{\lambda} \left\{ \int_{t_0}^{\nu(t_0)} \beta(s)(e_\varphi(s,t_0)-1)\,\mathrm{d}s + \int_{\nu(t_0)}^{\nu^2(t_0)} \beta(s)(e_\varphi(s,\nu^{-1}(s)) - e_\varphi(s,\nu(t_0)))\,\mathrm{d}s \right\}$$
$$= \frac{\varphi(t_0)}{\lambda} \left\{ \int_{t_0}^{\nu(t_0)} \beta(s)(e_\varphi(s,t_0)-1)\,\mathrm{d}s + \int_{t_0}^{\nu(t_0)} \beta(\nu(s))(e_\varphi(\nu(s),s) - e_\varphi(\nu(s),\nu(t_0)))\nu'(s)\,\mathrm{d}s \right\}$$
$$\overset{(38)}{=} \frac{\varphi(t_0)}{\lambda} \left\{ \int_{t_0}^{\nu(t_0)} \beta(s)(e_\varphi(s,t_0)-1) + \beta(\nu(s))\nu'(s)(e_\varphi(\nu(s),s) - e_\varphi(s,t_0))\,\mathrm{d}s \right\}$$
$$\overset{\beta\in\mathcal{P}_\nu}{=} \frac{\varphi(t_0)}{\lambda} \int_{t_0}^{\nu(t_0)} \beta(s)\underbrace{(-1+e_\varphi(\nu(s),s))}_{\lambda}\,\mathrm{d}s$$
$$= \varphi(t_0)\int_{t_0}^{\nu(t_0)} \beta(s)\,\mathrm{d}s = \int_{t_0}^{\nu(t_0)} G(s)K(s)\,\mathrm{d}s,$$

where

$$G(s) := \frac{\varphi(t_0)}{r(s)e_h(t_0,s)} = \frac{\varphi(t_0)}{(\varphi(s)+h(s))e_h(t_0,s)} \overset{(H1^*)}{=} \frac{\varphi(t_0)}{\varphi(t_0)+h(s)e_h(t_0,s)}.$$

Note that $0 < r(s)e_h(s,t_0), \varphi(t_0)$ implies $G(s) > 0$ for all $s \in I$. To show the second statement, we recall that the Jensen inequality is an equality if and only if $y(s,t)$ is s-independent. Since

$$y(s,t) = e_r(s,t)e_\varphi(t,s)\frac{r(s)}{\varphi(s)K(s)} = e_r(s,t)e_{r-h}(t,s)\frac{r(s)}{\varphi(s)K(s)} = \frac{r(s)}{\varphi(s)e_h(t,s)K(s)}$$
$$\overset{(H1^*)}{=} \frac{r(s)}{\varphi(t)K(s)},$$

the claim follows and the proof is complete. □

Example 39. In the classical case, i.e., $\nu(t) = t + \omega$, $f \in \mathcal{P}_\nu(I)$ implies $f(t+\omega) = f(t)$ for $t \in I$ and $h \equiv 0$ satisfies (36). Then, condition (H1*) requires r to be constant and (H2) implies K to be ω-periodic in the classical sense. Thus, $r \in \mathbb{R}^+$ and $K \in C(I,\mathbb{R})$ with $K(t+\omega) = K(t)$ for all $t \in I$ satisfy the conditions of Theorem 38 and we can conclude, by Theorem 38 and (39),

$$\frac{1}{\omega}\int_{t_0}^{t_0+\omega} \bar{x}(s)\,\mathrm{d}s \le \frac{1}{\omega}\int_{t_0}^{t_0+\omega} K(s)\,\mathrm{d}s, \tag{40}$$

where we used that $G(s) = \frac{\varphi(t_0)}{\varphi(t_0)+h(s)e_h(t_0,s)} = 1$ since $h \equiv 0$. Thus, for $\nu(t) = t+\omega$, Theorem 38 collapses to the continuous analogue of the second Cushing–Henson conjecture. Equality then only holds if K is constant, again implying a deleterious impact of a periodic environment. This is consistent with the results in [22] for the periodic time scale $\mathbb{T} = \mathbb{R}$.

Remark 40. It is worth noting that the second Cushing–Henson conjecture for our general concept of periodicity is formulated using weighted averages rather than averages, that is, "the average of the periodic solution is at most equal to the average of the *weighted* average of the carrying capacity", where the weight function is given by the function G that depends on the value $r(t_0)$ and the function ν through h. Furthermore, if $h = 0$, then $G(s) = 1$ and if $h<0$, then $G(s) > 1$, allowing for beneficial effects on the population after introducing periodicity. Else, for $h > 0$, $G < 1$ so that the upper bound is even smaller as in the traditional formulation suggesting an even stronger deterioration. In fact, Fig. 3 illustrates an example where the moving average of the ν-periodic solution (dashed orange curve) remains above the moving average of the carrying capacities (dotted purple curve) in the left panel or intersects, on the right panel. Note that since $\frac{r}{K}$ is constant, equality holds in (39). Thus, the orange dashed curve equivalently represents $\frac{1}{|\nu(t)-t|}\int_t^{\nu(t)} G(s)K(s)\mathrm{d}s$. Since the dashed curve is the (non-weighted) average of K, the comparison of the dashed orange and the dotted purple curves reveal the relevance of the underlying time domain. The classical description of the second Cushing–Henson Conjecture would have predicted that the average of the periodic solution (orange curve) would always remain below the average of the purple curve.

Example 41. Let $I = (0,\infty)$. Consider $\nu(t) = t + D\sqrt{1+t} + \left(\frac{D}{2}\right)^2$ for $D > 0$ and $t \in I$. Then, by (37), ν is strictly increasing for $t \in I$. By Example 34, $h(t) = \frac{-1}{2(1+t)}<0$ satisfies (36) and

$$e_h(t,s) = \exp\left\{\frac{1}{2}\int_t^s (1+\tau)^{-1}\,\mathrm{d}\tau\right\} = \frac{\sqrt{1+s}}{\sqrt{1+t}}, \qquad s,t \in I.$$

Choosing $r(t) = \frac{2r_0}{\sqrt{1+t}} - \frac{1}{2(1+t)} = \frac{2r_0}{\sqrt{1+t}} + h(t)$, then $r(t) > 0$ for $r_0 > \frac{1}{4}$ and $\varphi(t) > 0$ and we get for $s,t \in I$,

$$(r-h)(s)e_h(t,s) = \frac{2r_0}{\sqrt{1+s}}\frac{\sqrt{1+s}}{\sqrt{1+t}} = 2r_0\frac{1}{\sqrt{1+t}} = (r-h)(t),$$

so that r satisfies (H1*). Choosing $K(t) = K_0 r(t)$ satisfies (H2). By Theorem 38, (39) holds for

$$G(s) = \frac{\varphi(1)}{\varphi(1)+h(s)e_h(1,s)} = \frac{\sqrt{2}r_0}{\sqrt{2}r_0 - \frac{1}{2(1+s)}\frac{\sqrt{1+s}}{\sqrt{2}}} = \frac{4r_0\sqrt{1+s}}{4r_0\sqrt{1+s}-1} > 1, \quad s \in I.$$

Fig. 4 illustrates (39) for different values of r_0, comparing the upper bounds of the weighted average $\int_t^{\nu(t)} G(s)K(s)\,\mathrm{d}s$ to the classical average $\int_t^{\nu(t)} K(s)\,\mathrm{d}s$. Note that since $G(s) > 1$, the weighted moving average on the right-hand side of (39) (black curve with stars) is bigger than the traditional average (green dotted curve). Furthermore, since $K(t) = K_0 r(t)$, $\frac{r}{K}$ is constant, so that Theorem 38 predicts that the moving average of $\bar{x}$ (left-hand side of (39)) is indeed equal to the moving weighted average. This is visualized by the fact that the dark red solid curve is equal to the dashed curve with black stars.

5. Discussion

In this work, we introduced a novel definition of periodicity with respect to a strictly increasing and differentiable function $\nu \in C(I,\mathbb{R})$. We say a function f is ν-periodic provided it satisfies the functional equation (4). The set of ν-periodic functions, for given ν, can be determined by solving a functional equation that is related to the known Schröder equation. Instead, the function ν, with which respect a given function f

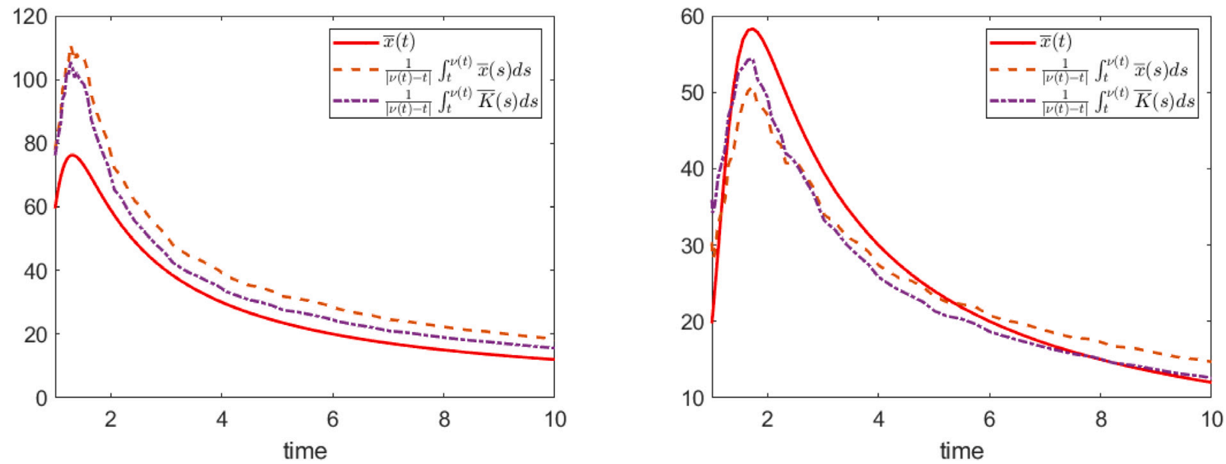

Fig. 3. Behavior of the ν-periodic solution and moving averages for (34) with $r_0 = 5$, $K_0 = 100$, $D_1 = 2$. Left: $D_2 = 1$, consistent with the parameters in Fig. 2. The moving average of the ν-periodic solution remains above the moving average of the carrying capacities, indicating a beneficial impact of a ν-periodic environment. Right: $D_2 = 5$. The effect of introducing a ν-periodic environment changes over time, indicating however eventually a positive impact. Note that since $K(t) = c \cdot r(t)$ for constant $c > 0$, equality holds in (39).

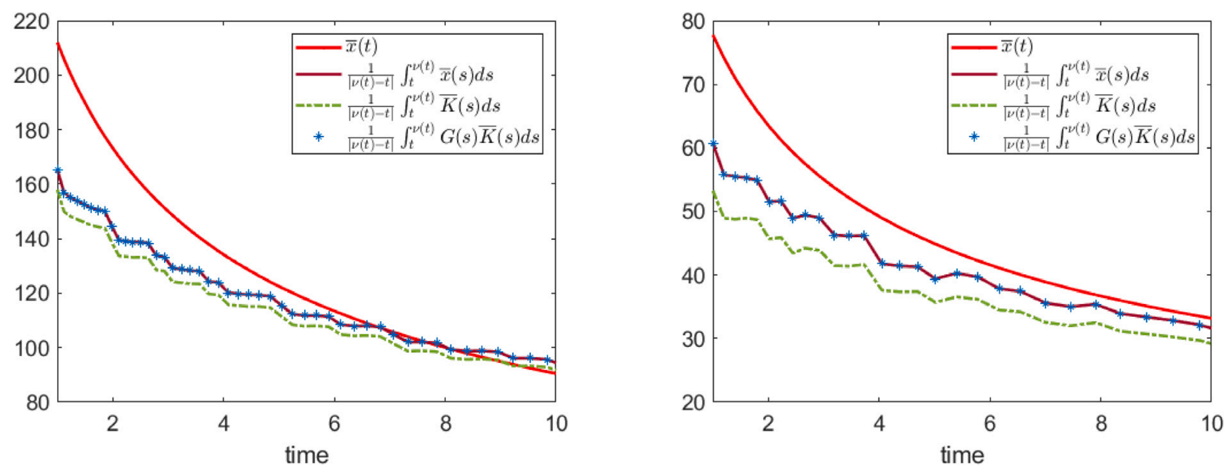

Fig. 4. Behavior of $\overline{x}$ and the weighted and nonweighted moving averages based on Example 41 with $K_0 = 50$, $D_1 = 2$. Left: $r_0 = 3$; Right: $r_0 = 1.1$. By (39), the moving average of $\overline{x}$ is equal to the moving weighted average since equality holds in (39). For $r_0 = 1.1$, right panel, the traditional nonweighted average is not an upper bound, justifying the necessity of the weighted upper bound with weights $G(s)$.

is periodic to, is obtained by solving a first-order differential equation. If $\nu(t) = t + \omega$, the definition coincides with the classical definition of ω-periodicity, that is, $f(t+\omega) = f(t)$ for all $t \in I$, where $f : I \to \mathbb{R}$. Our definition of ν-periodicity guarantees the classical translation invariant property of integrals of periodic functions, formulated in Theorems 7 and 9. In Section 3, we investigated the existence and uniqueness of ν-periodic solutions to linear homogeneous and nonhomogeneous differential equations. For $\nu(t) = t + \omega$, our obtained results are consistent with the classical theorems for periodic differential equations. More specifically, we identified conditions that guarantee the unique existence of a ν-periodic solution for a nonautonomous differential equation. In Section 4, we applied the concept of ν-periodicity to the logistic growth model. We formulated and proved the Cushing–Henson conjectures that address the impacts of a periodically forced environment for the logistic differential equation. Our formulated first Cushing–Henson conjecture provides conditions for the time-dependent model parameters to guarantee the existence, uniqueness, and positivity of a globally attracting ν-periodic solution. This implies, that even though the model parameters may not be periodic in the classical sense, one may still be able to classify the global attracting solution using the generalization of periodicity. We also extended the second Cushing–Henson conjecture that, originally, identified a deleterious effect of introducing a periodic environment for the discrete Beverton–Holt model. For model parameters satisfying the modified conditions using ν-periodicity, the average of the globally attracting ν-periodic solution is bounded by a weighted average of the carrying capacities, so that the effect of the introduction of a time-dependent environment depends on ν and may potentially be beneficial.

We also highlighted the relevance of ν-periodic functions in the context of the Cushing–Henson conjectures by revealing the existence of a ν-periodic function despite a constant environment that was modeled with constant coefficients. Interesting, but beyond the scope of this manuscript, would be to experimentally explore the impact of a ν-periodically changing environment on a population that grows logistically. For example, the Cushing–Henson conjectures were originally formulated for the discrete Beverton–Holt model and were based on collected data of a flour beetle population that was exposed to a periodically changing environment. Our new periodicity concept would now allow for the set-up of a ν-periodically changing environment, where $\nu(t) \neq t + \omega$, that is, ν-periodic functions are not periodic in the classical sense.

CRediT authorship contribution statement

Martin Bohner: Writing – review & editing, Validation, Investigation, Formal analysis, Conceptualization. **Jaqueline Mesquita:** Writing – review & editing, Validation, Investigation, Formal analysis, Conceptualization. **Sabrina Streipert:** Writing – review & editing, Writing –

original draft, Visualization, Validation, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors report no conflict of interest.

Data availability

Reference of the article containing the data is included in the manuscript and clearly referenced.

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Appendix

A.1. Data fitting

Consider [19, Culture #13 in Table 1] and let $X(i)$ be its data points for the population at week i ($i = 0,\dots,34$). Using "fminsearch" in Matlab, we find the value $\hat{x}(0)$ and $\hat{r}$ that reduce the residual, defined by

$$\text{res} := \omega \sum_{i=0}^{35} (X(i) - x(t_i))^2,$$

where x is the solution to the logistic differential equation, $t_i = i + 2$ (to match the biweekly recorded data points). The optimization-weight ω was chosen to be 0.8 to aid the fminsearch-algorithm in finding reasonable parameter values. For the same reason, we chose $K = 1.5 \max_i X(i)$. Despite these choices, similar values are obtained after relaxing these constraints.

A.2. Special case of a piecewise linear growth rate

Consider $r(t) = r_n + \frac{(r_{n+1}-r_n)}{2}(t - \lfloor t \rfloor)$ for $t \in (t_n, t_{n+2})$, where t_n are the observed table points for $n = 0, 1, \dots, N$. For [19, Culture #13 in Table 1], $N = 34$. Then the solution to the logistic differential equation $x' = r(t)x\left(1 - \frac{x}{K}\right)$ with constant K can be expressed for $t \in [t_n, t_{n+2})$ as

$$\begin{aligned} x(t) &= \frac{Kx(t_n)}{e^{-\int_{t_n}^{t} r(s)\,ds}(K - x(t_n)) + x(t_n)} \\ &= \frac{Kx(t_n)}{e^{-\int_{t_n}^{t} r_n + \frac{(r_{n+1}-r_n)}{2}(s-t_n)\,ds}(K - x(t_n)) + x(t_n)}. \end{aligned}$$

Thus, for $t = t_{n+2}$, we have

$$x(t_{n+2}) = \frac{Kx(t_n)}{e^{-(r_1+r_2)}(K - x(t_n)) + x(t_n)}.$$

Hence, we could choose r_i such that $x(t_{n+2})$ matches the observation for all n. Then,

$$X_k = \frac{KX_{k-1}}{e^{-(r_{k-1}+r_k)}(K - X_{k-1}) + X_{k-1}},$$

which can now be solved for $r_{k-1} + r_k$, resulting in

$$r_{k-1} + r_k = \ln\left(\frac{(K - X_{k-1})X_k}{(K - X_k)X_{k-1}}\right),$$

resulting in the matrix structure (33).

A.3. Calculations to determine v for constant K

Let K be constant. Then, (H2) is satisfied if $r^v = r$, which allows to rewrite (H1) as

$$\frac{v''}{v'} + v'r = r,$$

i.e., a logistic differential equation in v',

$$v'' = rv'(1 - v').$$

The solution is therefore

$$v'(t) = \frac{y_0}{e^{-\int_{t_0}^{t} r(s)\,ds}(1 - y_0) + y_0}, \qquad y_0 = v'(t_0).$$

Integrating this expression gives

$$v(t) = v(t_0) + \int_{t_0}^{t} \frac{y_0}{e^{-\int_{t_0}^{s} r(\tau)\,d\tau}(1 - y_0) + y_0}\,ds.$$

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