ON THE ESTIMATION OF AVERAGES OVER INFINITE INTERVALS WITH AN APPLICATION TO AVERAGE PERSISTENCE IN POPULATION MODELS

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Abstract: We establish a general result for estimating the upper average of a continuous and bounded function over an infinite interval. As an application, we show that a previously studied model of microbial growth in a chemostat with time–varying nutrient input admits solutions (populations) that exhibit weak persistence but not weak average persistence.

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1. Introduction

For a fixed real number b_0 and a function $x : [b_0, \infty) \to \Re$ that is continuous and bounded on $[b_0, \infty)$, the *upper average* of x is defined as

$$A^+(x) = \limsup_{t\to\infty} \frac{1}{t-b_0} \int_{b_0}^{t} x(u)\, du$$

and the *lower average* of x, denoted by $A^-(x)$, is defined as above using the limit inferior instead of the limit superior. Since x is continuous and bounded, $A^+(x)$ and $A^-(x)$ both exist, are finite, and their definitions do not depend on the number b_0 in the sense that if $c_0 > b_0$ then

$$\limsup_{t\to\infty} \frac{1}{t-b_0} \int_{b_0}^{t} x(u)\; du = \limsup_{t\to\infty} \frac{1}{t-c_0} \int_{c_0}^{t} x(u)\; du,$$

and likewise when the limit inferior is used. Furthermore, it is clear that

$$x^- \le A^-(x) \le A^+(x) \le x^+,$$

where

$$x^+ = \limsup_{t\to\infty} x(t)$$

and

$$x^- = \liminf_{t\to\infty} x(t).$$

Our purpose is to establish a general result, Theorem 2.4, that can be used to estimate $A^+(x)$ and to then apply the theorem to a problem involving the question of persistence in a non–autonomous model of microbial growth in a chemostat. In particular, we use the theorem to show that a single species chemostat model with

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time–varying nutrient input that was studied in [5] admits solutions, x, that satisfy $A^+(x) = 0 < x^+$. Such solutions are said to exhibit weak persistence but not weak average persistence. Although Theorem 2.4 is motivated by questions that arise in studies of persistence of solutions of non–autonomous differential equations, the general nature of the threorem suggests that it might be a useful tool in many other applications that require the estimation of time averages over infinite intervals.

The term "persistence" is used in population modelling to describe the idea that a population is in some sense able to survive for an indefinitely long period of time. A function $x : [b_0, \infty) \to [0, \infty)$ that describes the evolution of a population over time is said to exhibit *extinction* if $x^+ = 0$ and is said to exhibit *persistence* otherwise. This basic concept of persistence is adequate for the study of autonomous population models in which it is generally the case that the population (or each of the interacting populations) being modelled either becomes extinct or satisfies $x^- > 0$. However, this is not always the case in non–autonomous population models. Such models require consideration of a more explicit hierarchy of persistence defined as *strong persistence* (SP) meaning that $x^- > 0$, *strong average persistence* (SAP) meaning that $A^-(x) > 0$, *weak average persistence* (WAP) meaning that $A^+(x) > 0$, and *weak persistence* (WP) meaning that $x^+ > 0$. It can easily be seen that SP⇒SAP⇒WAP⇒WP.

For models that take the form of autonomous dynamical systems satisfying certain general conditions that are likely to be present in population models (such as dissipativity and isolated boundary flow), it has been shown in [4] that SP and WP (and consequently all four types of persistence defined above) are equivalent. A similar result given in [6] shows that *uniform* weak and strong persistence are also equivalent in autonomous models. (Uniform weak persistence requires that there exist $M > 0$ such that $x^+ > M$ for all non–trivial solutions, x, of a given system and uniform strong persistence requires that there exist $m > 0$ such that $x^- > m$ for all non–trivial x.) The equivalence of uniform strong and weak persistence was ex-

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tended, under certain additional assumptions, to non–autonomous systems in [11]. In [9], criteria for the equivalence of all four types of persistence (without reference to uniformity) were obtained for a non–autonomous single species chemostat model. Similar criteria were obtained for non–autonomous Kolmogorov–type systems in [1, 8, 12]. However, it is not generally true for non–autonomous systems that the various different types of persistence are equivalent. This is shown to be the case, for example, for the non–autonomous systems studied in [2, 3, 5, 7]. The application of Theorem 2.4 that we provide in Section 3 verifies a claim (that WP does not imply WAP) made in [5, page 143] in reference to a model of a single species in a chemostat with a time–varying nutrient environment.

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2. Estimation of Upper Averages

Throughout, we will assume without loss of generality that $0 \le x(t) \le 1$ for all $t \in [b_0, \infty)$ and hence that

$$0 \le x^- \le A^-(x) \le A^+(x) \le x^+ \le 1.$$

Our main result, Theorem 2.4, provides sufficient conditions for $A^+(x) \le k$ for prescribed $k \in (0,1)$. The proof of Theorem 2.4 is accomplished via three lemmas.

Lemma 2.1. *Suppose that $0 < k < 1$, and suppose that $a_n \to \infty$ and $b_n \to \infty$ are sequences such that*

$$b_0 < a_1 < b_1 < a_2 < b_2 < \cdots$$

and

$$x(t) > k \text{ for all } t \in (a_n, b_n), \quad n = 1, 2, \ldots$$
$$x(t) \le k \text{ for all } t \in [b_{n-1}, a_n], \quad n = 1, 2, \ldots$$

Also, suppose that

$$\lim_{n\to\infty} \frac{1}{b_n - b_0} \sum_{i=1}^{n} (b_i - a_i) = 0. \tag{2.1}$$

Then $A^+(x) \le k$.

Proof. Let $\varepsilon > 0$ be fixed but arbitrary.

Since condition (2.1) is satisfied and since

$$0 < \frac{b_n - a_n}{b_n - b_0} \le \frac{1}{b_n - b_0} \sum_{i=1}^{n} (b_i - a_i)$$

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for all $n \geq 1$, then

$$\lim_{n\to\infty} \frac{b_n - a_n}{b_n - b_0} = 0.$$

Thus, there exists an integer $N \geq 1$ such that both

$$(1-k) \cdot \frac{1}{b_n - b_0} \sum_{i=1}^{n} (b_i - a_i) < \frac{\varepsilon}{2}$$

and

$$\frac{b_n - a_n}{b_n - b_0} < \frac{\varepsilon}{2}$$

for all $n \geq N$.

Let $T = b_N$. Then, clearly, for each $t \geq T$ there exists $n \geq N$ such that $b_n \leq t < b_{n+1}$. We will consider the three cases $t = b_n$, $b_n < t \leq a_{n+1}$, and $a_{n+1} < t < b_{n+1}$ separately. (Note that the result of Case 1 is used in proving Case 2 and that the result of Case 2 is used in proving Case 3.)

Case 1 If $t = b_n$, then

$$\begin{aligned}
\frac{1}{t - b_0} \int_{b_0}^{t} x(u)\ du &= \frac{1}{b_n - b_0} \left(\sum_{i=1}^{n} \int_{b_{i-1}}^{a_i} x(u)\ du + \sum_{i=1}^{n} \int_{a_i}^{b_i} x(u)\ du \right) \\
&\leq \frac{1}{b_n - b_0} \left(\sum_{i=1}^{n} \int_{b_{i-1}}^{a_i} k\, du + \sum_{i=1}^{n} \int_{a_i}^{b_i} 1\, du \right) \\
&= k + (1-k) \cdot \frac{1}{b_n - b_0} \sum_{i=1}^{n} (b_i - a_i) \\
&< k + \frac{\varepsilon}{2}.
\end{aligned}$$

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Case 2 If $b_n < t \le a_{n+1}$, then

$$\begin{aligned}\frac{1}{t-b_0}\int_{b_0}^{t} x(u)\,du &= \frac{1}{t-b_0}\int_{b_0}^{b_n} x(u)\,du + \frac{1}{t-b_0}\int_{b_n}^{t} x(u)\,du \\ &= \frac{b_n-b_0}{t-b_0}\cdot\frac{1}{b_n-b_0}\int_{b_0}^{b_n} x(u)\,du + \frac{1}{t-b_0}\int_{b_n}^{t} x(u)\,du \\ &\le \frac{b_n-b_0}{t-b_0}\left(k+\frac{\varepsilon}{2}\right) + k\cdot\frac{t-b_n}{t-b_0} \\ &= k\left(\frac{b_n-b_0}{t-b_0}+\frac{t-b_n}{t-b_0}\right) + \frac{b_n-b_0}{t-b_0}\cdot\frac{\varepsilon}{2} \\ &< k+\frac{\varepsilon}{2}.\end{aligned}$$

Case 3 If $a_{n+1} < t < b_{n+1}$, then

$$\begin{aligned}\frac{1}{t-b_0}\int_{b_0}^{t} x(u)\ du &= \frac{1}{t-b_0}\int_{b_0}^{a_{n+1}} x(u)\ du + \frac{1}{t-b_0}\int_{a_{n+1}}^{t} x(u)\ du \\ &\le \frac{1}{a_{n+1}-b_0}\int_{b_0}^{a_{n+1}} x(u)\ du + \frac{t-a_{n+1}}{t-b_0} \\ &\le k+\frac{\varepsilon}{2}+\frac{b_{n+1}-a_{n+1}}{b_{n+1}-b_0} \\ &< k+\varepsilon.\end{aligned}$$

We have shown that for arbitrary $\varepsilon > 0$ there exists $T > b_0$ such that

$$\frac{1}{t-b_0}\int_{b_0}^{t} x(u)\ du < k+\varepsilon$$

for all $t \ge T$. This establishes the stated result. $\square$

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Lemma 2.2. *Let c_n and d_n be sequences such that $0 < c_n < d_n$ for all n and such that $c_n/d_n \to 0$. Also, suppose that there exists $\eta > 0$ such that*

$$d_{n+1} > \eta \sum_{i=1}^{n} d_i \quad \text{for all } n$$

and let r_n be the sequence

$$r_n = \frac{\sum_{i=1}^{n} c_i}{\sum_{i=1}^{n} d_i}.$$

Then $r_n \to 0$.

Proof. First we note that $0 \le L \equiv \limsup_{n\to\infty} r_n \le 1$.

Also, for each $n \ge 1$ we have

$$\frac{\sum_{i=1}^{n+1} c_i}{\sum_{i=1}^{n+1} d_i} < \frac{\sum_{i=1}^{n} c_i}{\sum_{i=1}^{n} d_i + d_{n+1}} + \frac{c_{n+1}}{d_{n+1}} = \frac{r_n}{1 + \frac{d_{n+1}}{\sum_{i=1}^{n} d_i}} + \frac{c_{n+1}}{d_{n+1}},$$

which shows that

$$r_{n+1} < \frac{r_n}{1+\eta} + \frac{c_{n+1}}{d_{n+1}}$$

for each $n \ge 1$. Taking the limit superior as $n \to \infty$ yields $L \le L/(1+\eta)$ from which we conclude that $L = 0$ and hence that $r_n \to 0$. $\square$

Lemma 2.3. *Let a_n and b_n be sequences such that*

$$b_0 < a_1 < b_1 < a_2 < b_2 < \cdots$$

and such that

$$\frac{b_n - a_n}{b_n - b_{n-1}} \to 0.$$

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Also suppose that there exists $\eta > 0$ *such that*

$$b_{n+1} - b_n > \eta\left(b_n - b_0\right) \quad \textit{for all } n.$$

Then

$$\lim_{n\to\infty} \frac{1}{b_n - b_0} \sum_{i=1}^{n} \left(b_i - a_i\right) = 0.$$

Proof. If we define $c_n = b_n - a_n$ and $d_n = b_n - b_{n-1}$, then the stated result follows immediately from Lemma 2.2. □

By combining Lemmas 2.1 and 2.3, we obtain our main result.

Theorem 2.4. *Suppose that* $0 < k < 1$ *and suppose that* $a_n \to \infty$ *and* $b_n \to \infty$ *are sequences such that*

$$b_0 < a_1 < b_1 < a_2 < b_2 < \cdots$$

and

$$x\left(t\right) > k \textit{ for all } t \in \left(a_n, b_n\right), \quad n = 1, 2, \ldots$$
$$x\left(t\right) \leq k \textit{ for all } t \in \left[b_{n-1}, a_n\right], \quad n = 1, 2, \ldots$$

Also suppose that

$$\frac{b_n - a_n}{b_n - b_{n-1}} \to 0$$

and that there exists a $\eta > 0$ *such that*

$$b_{n+1} - b_n > \eta\left(b_n - b_0\right) \quad \textit{for all } n.$$

Then $A^+\left(x\right) \leq k$.

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As a remark, we note that the idea underlying Lemma 2.1 is that condition (2.1) implies that the percentage of the interval $[b_0, T]$ on which $x(t) > k$ becomes increasingly negligible as $T \to \infty$. If condition (2.1) can be verified, then Lemma 2.1 can be applied directly to obtain the estimate $A^+(x) \leq k$. However, condition (2.1) is difficult to verify directly in many cases of interest.

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3. An Application

As an application of Theorem 2.4, we verify a claim made in [5] regarding a family of non–autonomous systems

$$
\begin{aligned}
s'(t) &= D(q(t) - s(t)) - s(t)\,x(t), \\
x'(t) &= (s(t) - D)\,x(t),
\end{aligned}
\tag{3.1}
$$

that models the growth of a microbial culture in a chemostat. In these equations, x denotes the microbial population in the chemostat culture vessel and s denotes the concentration of a particular nutrient that the microorganisms must have in order to survive and reproduce. The family of systems (3.1) is parameterized by the controls $D > 0$ and $q : [b_0, \infty) \to [0, \infty)$ which signify, respectively, the dilution rate of the chemostat and the concentration of fresh nutrient that is being supplied to the culture vessel. For the interested reader, an exposition on the theory of chemostats that begins from first principles can be found in [10].

A pair of functions (s, x) is termed to be *admissible* with respect to system (3.1) if $s(t)$, $x(t) > 0$ for $t \in [b_0, \infty)$ and there exist controls $D > 0$ and $q : [b_0, \infty) \to [0, \infty)$ continuous and bounded on $[b_0, \infty)$, such that (D, q, s, x) satisfies system (3.1) for all $t \geq b_0$. It was claimed but not proved in [5, page 143] that there exists an admissible pair, (s, x), for which

$$
x(t) = \exp(-t - t\sin(\ln t))
\tag{3.2}
$$

and that the function (3.2) satisfies $A^+(x) = 0 < x^+$, thus demonstrating that the family (3.1) admits solutions that exhibit weak persistence but not weak average persistence. The existence of an admissible pair with x component as defined in (3.2) is easily verified via a criterion given in [5, Eq. (9)] . It is also clear that $x^+ = 1 > 0$. In what follows, we will use Theorem 2.4 to show that $A^+(x) = 0$,

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thus completing the verification of the claim. Our strategy in applying Theorem 2.4 to the function (3.2) will be to show that

$$A^{+}(x)=\limsup_{t\to\infty}\frac{1}{t-e^{2k\pi}}\int_{e^{2k\pi}}^{t}x(u)\,du\leq\exp\left(-e^{2k\pi}\right)$$

for each integer $k\geq 0$. Once this has been established, the fact that $A^{+}(x)=0$ will follow from the fact that $\exp\left(-e^{2k\pi}\right)\to 0$ as $k\to\infty$.

In order to construct the sequences a_n and b_n needed in Theorem 2.4, we will need the following facts about the behavior of x on the interval $\left[e^{2(m-1)\pi},e^{2m\pi}\right]$ for each integer $m\geq 1$:

1. $x(t)$ decreases from $\exp\left(-e^{2(m-1)\pi}\right)$ at $t=e^{2(m-1)\pi}$ to $\exp\left(-e^{2\left(m-\frac{1}{2}\right)\pi}\right)$ at $t=e^{2\left(m-\frac{1}{2}\right)\pi}$.
2. $x(t)$ increases from $\exp\left(-e^{2\left(m-\frac{1}{2}\right)\pi}\right)$ at $t=e^{2\left(m-\frac{1}{2}\right)\pi}$ to 1 at $t=e^{2\left(m-\frac{1}{4}\right)\pi}$.
3. $x(t)$ decreases from 1 at $t=e^{2\left(m-\frac{1}{4}\right)\pi}$ to $\exp\left(-e^{2m\pi}\right)$ at $t=e^{2m\pi}$.

The properties of x given above can be deduced using elementary calculus and the fact that

$$x'(t)=-x(t)\left(1+\cos(\ln t)+\sin(\ln t)\right)=-x(t)\left(1+\sqrt{2}\sin\left(\ln t+\frac{\pi}{4}\right)\right).$$

To define the sequences a_n and b_n, we first let $k\geq 0$ be a fixed but arbitrary integer and define $b_0=e^{2k\pi}$. Next, for each integer $n\geq 1$ we define a_n to be the unique point in the interval $\left(e^{2\left(k+n-\frac{1}{2}\right)\pi},e^{2\left(k+n-\frac{1}{4}\right)\pi}\right)$ such that $x(a_n)=\exp(-b_0)$ and we define b_n to be the unique point in the interval $\left(e^{2\left(k+n-\frac{1}{4}\right)\pi},e^{2(k+n)\pi}\right)$ such that $x(b_n)=\exp(-b_0)$.

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It can be verified that a_n and b_n satisfy the equations

$$a_n = \exp\left(2\left(k+n-\frac{1}{2}\right)\pi + \arcsin\left(1-\frac{b_0}{a_n}\right)\right), \tag{3.3}$$

$$b_n = \exp\left(2\left(k+n\right)\pi - \arcsin\left(1-\frac{b_0}{b_n}\right)\right), \tag{3.4}$$

that $a_n, b_n \to \infty$, and that

$$b_0 < a_1 < b_1 < a_2 < b_2 < \cdots .$$

Also, it follows from equations (3.3), (3.4) that

$$e^{-2n\pi} a_n \to e^{2\left(k-\frac{1}{4}\right)\pi}, \tag{3.5}$$

$$e^{-2n\pi} b_n \to e^{2\left(k-\frac{1}{4}\right)\pi}. \tag{3.6}$$

Furthermore, for each $n \geq 1$, we have

$$\begin{aligned} x(t) &> \exp(-b_0) \text{ for all } t \in (a_n, b_n), \\ x(t) &\leq \exp(-b_0) \text{ for all } t \in [b_{n-1}, a_n], \end{aligned}$$

and by using (3.5), (3.6) and the fact that

$$\frac{b_n - a_n}{b_n - b_{n-1}} = \frac{e^{-2n\pi} b_n - e^{-2n\pi} a_n}{e^{-2n\pi} b_n - e^{-2\pi} \cdot e^{-2(n-1)\pi} b_{n-1}}, \quad n \geq 1,$$

we obtain

$$\lim_{n\to\infty} \frac{b_n - a_n}{b_n - b_{n-1}} = 0.$$

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Finally, for each $n \geq 1$ we have

$$\begin{aligned}\frac{b_{n+1}-b_n}{b_n-b_0} &= \frac{\frac{b_{n+1}}{b_n}-1}{1-\frac{b_0}{b_n}} \\ &> \frac{b_{n+1}}{b_n}-1 \\ &= \exp\left(2\pi - \arcsin\left(1-\frac{b_0}{b_{n+1}}\right) + \arcsin\left(1-\frac{b_0}{b_n}\right)\right) - 1 \\ &> \exp\left(2\pi - \frac{\pi}{2} + 0\right) - 1 \\ &= e^{\frac{3\pi}{2}} - 1,\end{aligned}$$

which shows that

$$b_{n+1} - b_n > \left(e^{\frac{3\pi}{2}} - 1\right)(b_n - b_0) \qquad \text{for all } n \geq 1.$$

Theorem 2.4 thus yields the conclusion that $A^+(x) \leq \exp\left(-e^{2k\pi}\right)$ and, since the integer $k \geq 0$ is arbitrary, we conclude that $A^+(x) = 0$.

As a concluding remark, we note that the construction used in defining the sequences a_n and b_n in the above argument can also be used to show that the integral $\int_1^\infty x(u)\, du$ diverges. If we take $k = 0$, then $b_0 = 1$ and

$$b_n = \exp\left(2n\pi - \arcsin\left(1 - \frac{1}{b_n}\right)\right) \qquad \text{for all } n \geq 1.$$

We then define

$$c_n = \exp\left(2\left(n - \frac{1}{2}\right)\pi + \arcsin\left(1 - \frac{1}{b_n}\right)\right).$$

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and observe that $a_n < c_n < b_n$ and that

$$b_n - c_n = \frac{1}{e^{-2n\pi} b_n} \cdot \frac{\exp\left(-\arcsin\left(1 - \frac{1}{b_n}\right)\right) - \exp\left(-\pi + \arcsin\left(1 - \frac{1}{b_n}\right)\right)}{\frac{1}{b_n}}$$

for each $n \geq 1$.

Using (3.6), we obtain

$$\lim_{n\to\infty} \frac{1}{e^{-2n\pi} b_n} = e^{\frac{\pi}{2}}$$

and L'Hôpital's Rule yields

$$\begin{aligned}
&\lim_{s\to 0^+} \frac{\exp\left(-\arcsin\left(1-s\right)\right) - \exp\left(-\pi + \arcsin\left(1-s\right)\right)}{s} \\
&= \lim_{s\to 0^+} \frac{\exp\left(-\arcsin\left(1-s\right)\right) + \exp\left(-\pi + \arcsin\left(1-s\right)\right)}{\sqrt{2s - s^2}} \\
&= \infty,
\end{aligned}$$

which shows that

$$\lim_{n\to\infty} \frac{\exp\left(-\arcsin\left(1 - \frac{1}{b_n}\right)\right) - \exp\left(-\pi + \arcsin\left(1 - \frac{1}{b_n}\right)\right)}{\frac{1}{b_n}} = \infty$$

and hence that $\lim_{n\to\infty} \left(b_n - c_n\right) = \infty$. Divergence of the integral $\int_1^\infty x\left(u\right)\, du$ then follows from the fact that $x\left(t\right) > e^{-1}$ for all $t \in \left(c_n, b_n\right)$, $n \geq 1$.

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