

## UNIFORM WEAK IMPLIES UNIFORM STRONG PERSISTENCE FOR NON-AUTONOMOUS SEMIFLOWS

HORST R. THIEME

(Communicated by Hal L. Smith)

ABSTRACT. It is shown that, under two additional assumptions, uniformly weakly persistent semiflows are also uniformly strongly persistent even if they are non-autonomous. This result is applied to a time-heterogeneous model of S-I-R-S type for the spread of infectious childhood diseases. If some of the parameter functions are almost periodic, an almost sharp threshold result is obtained for uniform strong endemicity versus extinction.

### 1. INTRODUCTION

Persistence (or permanence) is an important property of dynamical systems and of the systems in ecology, epidemics, etc. they are modeling. On the one hand it is an important concept in itself addressing the long-term survival of some or all components of a system: see *Hutson, Schmitt* [16] and *Waltman* [26], for reviews and references of the development until the early nineties, and *Zhao* [28] for an update. On the other hand, persistence is also an essential intermediate result leading to more precise statements concerning the systems' qualitative behavior, e.g., the existence or global stability of an equilibrium: see, e.g., *Lin, So* [17], *Feng, Thieme* [8], Section 4, *Zhao* [28, 30], *Smith, Waltman* [21]. Persistence becomes the more relevant, the more complex the systems become, so that little else can be said about its large-time behavior by analytic methods. While this trend can be observed for systems of autonomous partial differential equations (e.g., modeling spatially heterogeneous ecological systems, *Cantrell et al.* [5], or competition of randomly moving microbial species in a flow reactor, *Ballyk et al.* [1], persistence becomes even more important (and difficult) for non-autonomous dynamical systems (semiflows) where obvious candidates for the long-time behavior of the system (equilibria, periodic orbits) are usually missing.

*Freedman, Moson* [10] discovered that uniform weak persistence implies uniform (strong) persistence for autonomous semiflows. *Thieme* [23] elaborates that this is not only an interesting theoretical result, but also a very useful tool to establish uniform persistence because uniform weak persistence can conveniently be shown by the method of fluctuation, by acyclicity of the boundary flow, or by ad hoc methods. Another condition under which (not necessarily uniform) weak persistence implies uniform strong persistence is presented by *Freedman, Ruan, Tang* [11].

---

Received by the editors November 10, 1997.

1991 *Mathematics Subject Classification.* Primary 34C35, 34D05, 92D30.

The author's research was partially supported by NSF grant DMS-9403884.

In this note we show that uniform weak persistence implies uniform strong persistence also for non-autonomous semiflows (Section 2). The result is not so elegant as in the autonomous case, as we will need extra conditions. That such additional conditions, unpleasant as they are, may be natural becomes evident once one tries to reduce the non-autonomous result to the autonomous case by using skew product flows (see *Hale* [13], e.g., for the latter). We do not take this approach here because a general skew product flow acts both on the original space and on translations of the original non-autonomous system, and looking for a useful metric topology on the latter is a hassle we want to avoid. This difficulty does not arise when non-autonomous ordinary differential equations are considered where the skew product flow can operate on translations of the vector field (*Gatica, So*, [12]; *Burton, Hutson* [3]). We prefer to work directly with the non-autonomous semiflow adapting the approach in *Thieme* [23]. This is a topological approach in spirit, an alternative being the use of (vector) Lyapunov-type functions (e.g., *Burton, Hutson* [3]; *Tang, Kuang* [22]). Actually Lyapunov-type functions may also be useful in establishing uniform weak persistence. We hope to narrow the gap between the two approaches by introducing the concept of persistence with respect to a functional  $\rho$ ; traditionally  $\rho(x)$  is the distance of the point  $x$  from the ‘boundary’.

At this point it is not clear (except for the special cases of asymptotically autonomous or periodic semiflows) whether the boundary flow analysis (using the *Butler-McGehee* lemma), which can be so powerful in the autonomous or periodic case with its acyclicity conditions (see *Hale, Waltman* [14]; *Thieme* [23]; *Yang, Ruan* [27]; *Zhao* [28], e.g.), can be extended to non-autonomous semiflows. Typically one will rely on an ad hoc proof by contradiction, sometimes supported by the method of fluctuations, to establish uniform weak persistence. What kind of results one may obtain this way is illustrated for a time-heterogeneous S-I-R-S type model for the spread of infectious childhood diseases (Section 3). In the case that some of the parameter functions are almost periodic we establish an almost sharp threshold result for the disease to be uniformly strongly endemic (i.e., to be uniformly strongly persistent in the population). This result involves a threshold parameter which, mathematically, plays the role of a basic replacement ratio, but does not necessarily have the same epidemiologic explanation.

## 2. UNIFORM WEAK IS UNIFORM STRONG

Taking a topological point of view, we let  $(X, d)$  be a metric space,

$$\Delta = \{(t, s); r_0 \leq s \leq t < \infty\}, \quad r_0 \in \mathbf{R}.$$

A mapping  $\Psi : \Delta \times X \rightarrow X$  is called a (*non-autonomous*) *semiflow* on  $X$  (anchored at  $r_0$ ) if

$$\Psi(t, s, \Psi(s, r, x)) = \Psi(t, r, x), \quad \Psi(r, r, x) = x \quad \forall t \geq s \geq r \geq r_0, x \in X.$$

If the mapping  $\Psi$  is continuous and a semiflow, it is called a *continuous semiflow*.  $\Psi$  is called an autonomous semiflow if  $\Psi(t + r, r, x)$  does not depend on  $r \geq r_0$  for  $t \geq 0, x \in X$ . Let

$$\rho : X \rightarrow (0, \infty)$$

be a continuous strictly positive functional on  $X$ . We consider the function

$$\sigma : [0, \infty) \times X \times [r_0, \infty) \rightarrow (0, \infty)$$

defined by

$$(2.1) \quad \sigma(t, x; r) = \rho(\Psi(t + r, r, x)), \quad t \geq 0, x \in X, r \geq r_0.$$

We notice the following relation between  $\sigma$  and  $\Psi$ :

$$(2.2) \quad \begin{aligned} \sigma(t, \Psi(s, r, x); s) &= \rho(\Psi(t + s, s, \Psi(s, r, x))) = \rho(\Psi(t + s, r, x)) \\ &= \sigma(t + s - r, x; r). \end{aligned}$$

We introduce the following notation:

$$\sigma^\infty(x, r) = \limsup_{t \rightarrow \infty} \sigma(t, x; r), \quad \sigma_\infty(x, r) = \liminf_{t \rightarrow \infty} \sigma(t, x; r).$$

**Definition 2.1.**  $\Psi$  is called *weakly  $\rho$ -persistent* if  $\sigma^\infty(x, r) > 0 \quad \forall x \in X, r \geq r_0$ .

$\Psi$  is called *strongly  $\rho$ -persistent* if  $\sigma_\infty(x, r) > 0 \quad \forall x \in X, r \geq r_0$ .

$\Psi$  is called *uniformly weakly  $\rho$ -persistent* if there exists some  $\epsilon > 0$  such that

$$\sigma^\infty(x, r) > \epsilon \quad \forall x \in X, r \geq r_0.$$

$\Psi$  is called *uniformly strongly  $\rho$ -persistent* if there exists some  $\epsilon > 0$  such that

$$\sigma_\infty(x, r) > \epsilon \quad \forall x \in X, r \geq r_0.$$

If no misunderstanding about the functional  $\rho$  is possible, we use *persistent* rather than  $\rho$ -persistent.

$\Psi$  is said to have property **(CA)** if the following holds:

**(CA)** There exists some  $\epsilon_0 > 0$  and a closed subset  $B$  in  $X$  with the following properties:

- For all  $x \in \{\rho \leq \epsilon_0\}, s \geq r_0$ , we have  $\Psi(t, s, x) \rightarrow B, \quad t \rightarrow \infty$ .
- The intersections of  $B$  with the rings  $\{\alpha \leq \rho \leq \beta\}, 0 < \alpha < \beta < \infty$ , have compact closure in  $X$ .

We call the set  $B$  in **(CA)** an attractor for  $\Psi$ . By  $\Psi(t, s, x) \rightarrow B$  as  $t \rightarrow \infty$ , we mean that for every open set  $U$  containing  $B$ , there exists some  $t_U > 0$  such that  $\Psi(t, s, x) \in U$  for all  $t > t_U$ . Equivalently the distance of  $\Psi(t, s, x)$  from  $B$  tends to 0 as  $t \rightarrow \infty$ .

For every  $x \in B$  we define sets  $\Sigma(x)$  as follows:

$$(2.3) \quad \begin{aligned} \Sigma(x) \quad &\text{consists of functions} \quad \bar{\sigma}_x : [0, \infty) \rightarrow \mathbf{R}, \\ \bar{\sigma}_x(t) &= \lim_{j \rightarrow \infty} \sigma(t, x; s_j) \quad \text{locally uniformly in } t \geq 0, \\ &\text{for some sequence } (s_j) \text{ in } [r_0, \infty) \text{ with } s_j \rightarrow \infty \text{ as } j \rightarrow \infty. \end{aligned}$$

The sets  $\Sigma(x)$  may be empty.

**Theorem 2.2.** *Let  $\Psi$  be a semiflow that is uniformly weakly  $\rho$ -persistent and has the property **(CA)** with attractor  $B$ .*

*Further assume that  $\sigma(\cdot, \cdot; s)$  is continuous on  $[0, \infty) \times B$ , uniformly in  $s \geq r_0$ . Finally assume that*

$$\bullet_1 \quad \liminf_{s \rightarrow \infty} \sigma(t, x; s) > 0 \quad \forall t \geq 0, x \in B,$$

*and that there exists some  $\epsilon > 0$  such that*

$$\bullet_2 \quad \limsup_{t \rightarrow \infty} \bar{\sigma}_x(t) > \epsilon \quad \forall x \in B, \bar{\sigma}_x \in \Sigma(x).$$

*Then  $\Psi$  is uniformly strongly persistent.*

If the semiflow  $\Psi$  is autonomous,  $\sigma(\cdot; s)$  is independent of  $s$  and  $\bar{\sigma}_x(t) = \sigma(t, x; 0)$ . So the two extra assumptions are automatically satisfied.

*Proof.* Assume that  $\Psi$  is uniformly weakly persistent. Then there exists  $\epsilon > 0$  such that

$$\sigma^\infty(x, r) > \epsilon \quad \forall x \in X, r \geq r_0.$$

We can choose  $\epsilon$  smaller than  $\epsilon_0$  in the compactness assumption (CA). We can also arrange that this  $\epsilon$  satisfies the assumption  $\bullet_2$  in the theorem.

*Step 1:* Let  $x \in X$  and  $r \geq r_0$  such that  $\liminf_{t \rightarrow \infty} \rho(\Psi(t, r, x)) < \epsilon_1 < \epsilon$ .

Then there exist sequences  $(s_k)$  in  $[r_0, \infty)$  and  $(t_k)$  in  $(0, \infty)$  such that  $s_k \rightarrow \infty$  ( $k \rightarrow \infty$ ) and

$$\begin{aligned} \rho(\Psi(s_k, r, x)) &= \epsilon, & \rho(\Psi(t_k + s_k, r, x)) &< \epsilon_1 \quad \forall k \in \mathbf{N}, \\ \rho(\Psi(s + s_k, r, x)) &\leq \epsilon, & \text{whenever } 0 \leq s \leq t_k. \end{aligned}$$

Moreover, by the first part of our compactness assumption (CA),

$$\Psi(s_k, r, x) \rightarrow B, \quad k \rightarrow \infty.$$

Hence we find elements  $b_k \in B$  such that

$$d(\Psi(s_k, r, x), b_k) \rightarrow 0, \quad k \rightarrow \infty.$$

Since  $\rho$  is continuous, the elements  $b_k$  are in the intersection of  $B$  with the ring  $\{\epsilon/2 < \rho < \epsilon_0\}$  for sufficiently large  $k$ . After dropping the first elements from the sequence we can assume that

$$b_k \in K := B \cap \{\epsilon/2 \leq \rho \leq \epsilon_0\} \quad \forall k \in \mathbf{N}.$$

The set  $K$  has compact closure by the second part of assumption (CA).

*Step 2:* Suppose that  $\Psi$  is not uniformly strongly persistent.

Then there exist sequences  $(r_j)$  in  $[r_0, \infty)$  and  $(x_j) \in X$  such that

$$\liminf_{t \rightarrow \infty} \rho(\Psi(t, r_j, x_j)) \rightarrow 0, \quad j \rightarrow \infty.$$

Using step 1 and a diagonalization procedure we obtain sequences  $(r_j)$  and  $(s_j)$  in  $[r_0, \infty)$ , and  $(t_j)$  in  $[0, \infty)$  such that  $s_j > r_j$ ,  $s_j \rightarrow \infty$  as  $j \rightarrow \infty$ , and

$$\begin{aligned} \rho(\Psi(s_j, r_j, x_j)) &= \epsilon, \\ \rho(\Psi(t_j + s_j, r_j, x_j)) &\rightarrow 0, \quad j \rightarrow \infty. \\ \rho(\Psi(s + s_j, r_j, x_j)) &\leq \epsilon, \quad 0 \leq s \leq t_j. \end{aligned}$$

Further we find elements  $b_j$  in the relatively compact set  $K$  such that

$$d(b_j, \Psi(s_j, r_j, x_j)) \rightarrow 0, \quad j \rightarrow \infty.$$

The sequence  $(b_j)$  has an accumulation point  $x \in \bar{K} \subseteq B$ . After choosing subsequences we can assume that

$$\Psi(s_j, r_j, x_j) \rightarrow x, \quad j \rightarrow \infty.$$

We claim:  $t_j \rightarrow \infty$  as  $j \rightarrow \infty$ .

If not,  $t_j \rightarrow t$  after choosing subsequences. Then, by the definition of  $\sigma$  in (2.1),

$$\begin{aligned} 0 &= \limsup_{j \rightarrow \infty} \rho(\Psi(t_j + s_j, r_j, x_j)) = \limsup_{j \rightarrow \infty} \rho(\Psi(t_j + s_j, s_j, \Psi(s_j, r_j, x_j))) \\ &= \limsup_{j \rightarrow \infty} \sigma(t_j, \Psi(s_j, r_j, x_j); s_j). \end{aligned}$$

Since  $\sigma(\cdot; s)$  is continuous uniformly in  $s$ , we have

$$0 = \limsup_{j \rightarrow \infty} \sigma(t, x; s_j)$$

which contradicts  $\bullet_1$  because  $x \in B$ .

Let  $t \geq 0$  now be arbitrary. Since  $t_j \rightarrow \infty$  as  $j \rightarrow \infty$ ,  $t_j > t$  for sufficiently large  $j$ . Hence

$$\epsilon \geq \limsup_{j \rightarrow \infty} \rho(\Psi(t + s_j, r_j, x_j)) = \limsup_{j \rightarrow \infty} \sigma(t, \Psi(s_j, r_j, x_j); s_j).$$

Using again that  $\sigma(\cdot; s)$  is uniformly continuous in  $s \geq r_0$ ,

$$\epsilon \geq \limsup_{j \rightarrow \infty} \sigma(t, x; s_j),$$

where  $x$  is the limit of  $\Psi(s_j, r_j, x_j)$ ,  $x \in B$ . This implies that, for every  $t \geq 0$ , the sequence  $(\sigma(t, x; s_j))$  is bounded. Since  $\sigma(\cdot, x; s)$  is continuous on  $[0, \infty)$  uniformly in  $s$ , by the Arzela-Ascoli theorem, there exists a function  $\bar{\sigma}_x$  on  $[0, \infty)$  such that, after choosing a subsequence,

$$\sigma(t, x; s_j) \rightarrow \bar{\sigma}_x(t), \quad j \rightarrow \infty, \text{ locally uniformly in } t \geq 0.$$

So we have found  $x \in B$  and a function  $\bar{\sigma}_x \in \Sigma(x)$  such that

$$\epsilon \geq \bar{\sigma}_x(t) \quad \forall t \geq 0,$$

which contradicts  $\bullet_2$ .

In order to become more familiar with the role of the set  $\Sigma$  in (2.3) we consider asymptotically autonomous semiflows. We recall that a semiflow  $\Psi$  is called *asymptotically autonomous* if there exists an autonomous semiflow  $\Phi$  such that, for all sequences  $t_j \rightarrow t$ ,  $s_j \rightarrow \infty$ ,  $x_j \rightarrow x$  as  $j \rightarrow \infty$ ,

$$\Psi(t_j + s_j, s_j, x_j) \rightarrow \Phi(t, x), \quad j \rightarrow \infty.$$

$\Phi$  is called the *limit flow* associated with  $\Psi$ .

First, this implies that  $\sigma(t, x; s) = \rho(\Psi(t, s, x))$  is continuous in  $(t, x)$  uniformly in  $s \geq r_0$ . Secondly, since, for any sequences  $t_j \rightarrow t$ ,  $x_j \rightarrow x$ ,  $s_j \rightarrow \infty$  as  $j \rightarrow \infty$ , we have

$$\sigma(t_j, x_j; s_j) \rightarrow \rho(\Phi(t, x)), \quad j \rightarrow \infty,$$

for every  $x \in X$ ,  $\Sigma(x)$  has exactly one element  $\bar{\sigma}_x$ , namely  $\bar{\sigma}_x(t) = \rho(\Phi(t, x))$ .  $\square$

The following result is now immediate from Theorem 2.2.

**Corollary 2.3.** *Let  $\Psi, \Phi$  be continuous semiflows on  $X$  that are uniformly weakly  $\rho$ -persistent. Let (CA) holds for  $\Psi$  with an attractor  $B$ . Further assume that  $\Phi$  is autonomous,  $\Psi$  is asymptotically autonomous, and  $\Phi$  the limit semiflow of  $\Psi$ . Then  $\Psi$  is uniformly strongly  $\rho$ -persistent.*

We remark that uniform strong  $\rho$ -persistence of the limit flow  $\Phi$  is not sufficient even for weak  $\rho$ -persistence of the asymptotically autonomous semiflow  $\Psi$ . (See Section 2.1 of Thieme [24].)

Similarly, one can explicitly determine  $\Sigma(x)$ , if the semiflow  $\Psi$  is periodic or asymptotically periodic. We leave it to the reader to derive corollaries like Corollary 2.3 for these special non-autonomous semiflows from Theorem 2.2. For related material we refer to Zhao ([28, 29, 30]).

Traditionally, the topologically oriented school of persistence theory assumes that  $X$  is the open subset of a larger metric space  $Z$  and that  $\rho(x), x \in X$ , is the distance of  $x$  from  $Z \setminus X$ . Looking at some general functional  $\rho$  earns us some extra flexibility as demonstrated by the following Corollary which, for simplicity, we only state in the special case of an asymptotically autonomous semiflow in a finite dimensional space.

**Corollary 2.4.** *Let  $X$  be a closed subset of  $\mathbf{R}^n$  and  $\Psi, \Phi$  be continuous semiflows on  $X$ . Further assume that  $\Phi$  is autonomous,  $\Psi$  is asymptotically autonomous, and  $\Phi$  the limit semiflow of  $\Psi$ .*

*Finally assume that there exists some  $c > 0$  such that*

$$\liminf_{t \rightarrow \infty} \|\Phi(t, x)\| < c \quad \forall x \in X$$

and

$$\liminf_{t \rightarrow \infty} \|\Psi(t, s, x)\| < c \quad \forall x \in X, s \geq r_0.$$

*Then there exists some  $c > 0$  such that*

$$\limsup_{t \rightarrow \infty} \|\Psi(t, s, x)\| < c \quad \forall x \in X, s \geq r_0.$$

*Proof.* Set  $\rho(x) = (1 + \|x\|)^{-1}$ . The compactness condition (CA) is trivially satisfied by choosing  $B = X$  because the  $\rho$ -shells are compact. Obviously  $\Phi$  and  $\Psi$  are weakly uniformly  $\rho$ -persistent. So  $\Psi$  is strongly uniformly  $\rho$ -persistent by Corollary 2.3.  $\square$

### 3. THE TIME-HETEROGENEOUS S-I-R-S MODEL

As an application of the theory developed in the previous section, we consider a model for the spread of infectious childhood diseases. It has been argued that the school system induces a time-heterogeneity in the per capita/capita infection rate,  $\alpha$ , because the chain of infections is interrupted or at least weakened by the vacations and new individuals are recruited into a scene with higher infection risk at the beginning of each school year (*Schenzle* [18]; *Dietz, Schenzle* [7]). Here we consider a model without exposed period; the total population, with size  $N$ , is divided into its susceptible,  $S$ , infective,  $I$ , and recovered,  $R$ , parts, and the contraction of the disease is modeled by the law of mass action involving susceptibles and infectives:

$$(3.1) \quad \begin{aligned} N &= S + I + R, \\ \frac{d}{dt}I &= -\mu(t)I + \alpha(t)SI - \gamma(t)I, \\ \frac{d}{dt}R &= -\mu(t)R + \gamma(t)I - \eta(t)R. \end{aligned}$$

We assume that the disease causes no fatalities and that the population size  $N(t)$  is a given function of time  $t$ .  $\mu(t)$  is the instantaneous per capita mortality rate.  $\gamma(t)$  and  $\eta(t)$  are the instantaneous per capita rates of leaving the infective stage or removed stage, respectively.

The case that  $\alpha$  is a periodic function and that  $N, \mu, \gamma$  and  $\eta$  are constant has been extensively studied, see *Dietz, Schenzle* [7] and *Hethcote, Levin* [15] for reviews and references. We mention that periodic solutions can exist whose periods

are integer multiples of the period of  $\alpha$  and that co-existence of stable periodic solutions with different periods is possible (*Smith* [19, 20]).

Here we assume that  $N, \mu, \alpha, \gamma$ , and  $\eta$  are non-negative bounded continuous functions. Further we assume that  $N, \mu, \alpha$  and  $\gamma$  are strictly positive and almost periodic.  $\eta$  is not assumed to be almost periodic and the solutions of (3.1) will not necessarily be almost periodic as a consequence (cf. *Gatica, So* [12]). We will state an almost sharp threshold result for uniform strong persistence of the disease versus disease extinction. Detailed proofs will be given elsewhere (*Thieme* [25]), here we will only give some explanations. Unfortunately our approach does not seem to extend to the S-E-I-R-S model.

We introduce

$$\mathcal{R}_\diamond = \frac{\overline{\alpha N}}{\overline{\mu} + \overline{\gamma}}, \quad \overline{\alpha N} = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \alpha(s)N(s)ds, \quad \overline{\gamma} = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \gamma(s)ds,$$

and  $\overline{\mu}$  analogously to  $\overline{\gamma}$ . The limits of the time averages exist because the integrands are almost periodic. The following threshold result has been phrased in terms of the number  $\mathcal{R}_\diamond$  which formally plays the role of a basic replacement ratio without having this interpretation. Notice that in general  $\mathcal{R}_\diamond$  is not the asymptotic time average of the instantaneous basic replacement ratios

$$\mathcal{R}_0(t) = (\alpha(t)N(t))/(\mu(t) + \gamma(t)).$$

**Theorem 3.1.** (a) *If  $\mathcal{R}_\diamond < 1$ , the disease dies out, i.e., for every solution of (3.1) we have  $I(t), R(t) \rightarrow 0$  as  $t \rightarrow \infty$ .*

(b) *If  $\mathcal{R}_\diamond > 1$ , the disease persists uniformly strongly in the population in the sense that there exists some  $\epsilon > 0$  such that  $\liminf_{t \rightarrow \infty} I(t) > \epsilon$  for all solutions of (3.1) with  $I(0) > 0, R(0) \geq 0$ .*

Part (a) can be proved in a straightforward way by considering  $\ln I(t)$ . In part (b) uniform weak persistence can be shown by a contradiction argument again considering  $\ln I(t)$ . For both disease extinction and uniform weak disease persistence, the almost periodicity of the various functions is only needed in so far as it guarantees the convergence of the time averages. Almost periodicity or a similar property is needed, however, to satisfy condition  $\bullet_2$  in Theorem 2.2 from which Theorem 3.1 will follow. In order to find a sufficient condition for uniform strong persistence, the combination of almost periodicity with  $\mathcal{R}_\diamond > 1$  can be replaced by a condition similar to *Burton, Hutson* [3]), Theorem 4.2. In order to apply Theorem 2.2, we choose as metric space  $X = \{(I, R); I > 0, R \geq 0\}$  and  $\rho(I, R) = I$  as functional. Property (CA) is satisfied because  $I^\infty \leq \sup N$  and  $R^\infty \leq \frac{\sup \gamma}{\inf \mu} I^\infty$  with  $I^\infty, R^\infty$  denoting the limit superior of  $I, R$  respectively.

In order to keep the illustration short, we have chosen an ODE model, and Theorem 3.1 can presumably be also proved using an average Lyapunov function like in *Burton, Hutson* [3] where average type conditions guarantee predator persistence in a prey predator system. However, since Theorem 2.2 does not only hold for ordinary differential equations, but for general semiflows, Theorem 3.1 holds under the same assumptions for  $N, \mu, \alpha, \gamma$ , if the exponential distribution of the length of the removed stage, described by  $\eta$ , is replaced by an arbitrary distribution. Details will be presented elsewhere (*Thieme* [25]); see *Castillo-Chavez, Thieme* [6] for the model modification.

## ACKNOWLEDGEMENT

Thanks to Hal Smith for rekindling my interest in persistence and to Xiao-Qiang Zhao for bibliographic hints.

## REFERENCES

1. Ballyk, M.; Dung, L.; Jones, D.A.; Smith, H.L. (to appear): Effect of random motility on microbial growth and competition in a flow reactor. *SIAM J. Appl. Math.*
2. Bremermann, H.J.; Thieme, H.R. (1989): A competitive exclusion principle for pathogen viruses. *J. Math. Biol.* **27**, 179-190 MR **90d**:92021
3. Burton, T.A.; Hutson, V. (1991): Permanence for non-autonomous predator-prey systems. *Diff. Integral Equations* **4**, 1209-1280 MR **93f**:34019
4. Busenberg, S.; Cooke, K.L.; Thieme, H.R. (1991): Demographic change and persistence of HIV/AIDS in a heterogeneous population. *SIAM J. Appl. Math.* **51**, 1030-1052 MR **92j**:92016
5. Cantrell, R.S.; Cosner, C.; Hutson, V. (1996): Ecological models, permanence and spatial heterogeneity. *Rocky Mountain J. Math* **26**, 1-35 MR **97g**:92011
6. Castillo-Chavez, C.; Thieme, H.R. (1995) Asymptotically autonomous epidemic models. *Mathematical Population Dynamics: Analysis of Heterogeneity I. Theory of Epidemics* (O. Arino *et al.*, eds.) Wuerz, 33-50.
7. Dietz, K.; Schenzle, D. (1985): Mathematical models for infectious disease statistics. *A Celebration of Statistics. The ISI Centenary Volume* ed. by A.C. Atkinson, S.E. Fienberg, 167-204. Springer MR **87h**:92054
8. Feng, Z.; Thieme, H.R. (1995): Recurrent outbreaks of childhood diseases revisited: the impact of isolation. *Math. Biosci.* **128**, 93-130 MR **96b**:92010
9. Fernandes, M.L.C. (1990): Uniform repellers for processes with applications to periodic differential systems. *J. Diff. Equations* **86**, 141-157 MR **91g**:58165
10. Freedman, H.I.; Moson, P. (1990): Persistence definitions and their connections. *Proc. AMS* **109**, 1025-1032 MR **90k**:34054
11. Freedman, H.I.; Ruan, S.; Tang, M. (1994): Uniform persistence and flows near a closed positively invariant set. *J. Dynamics Diff. Equations* **6**, 583-600 MR **95i**:34080
12. Gatica, J.A.; So, J. W.-H. (1988): Predator-prey models with almost periodic coefficients. *Appl. Anal.* **27**, 143-152 MR **89a**:92057
13. Hale, J.K. (1989): *Asymptotic Behavior of Dissipative Systems*. AMS MR **89g**:58059
14. Hale, J.K.; Waltman, P. (1989): Persistence in infinite-dimensional systems. *SIAM J. Math. Anal.* **20**, 388-395 MR **90b**:58156
15. Hethcote, H.W.; Levin, S.A. (1989): Periodicity in epidemiological models. *Applied Mathematical Ecology* (S.A. Levin, T.G. Hallam, L.J. Gross; eds.), 193-211. Biomathematics **18**, Springer CMP 90:04
16. Hutson, V.; Schmitt, K. (1992): Permanence in dynamical systems. *Math. Biosci.* **111**, 1-71 MR **93d**:92003
17. Lin, X.; So, J. W.-H. (1993): Global stability of the endemic equilibrium and uniform persistence in epidemic models with subpopulations. *J. Austral. Math. Soc., Ser. B*, **34**, 282-295 MR **93k**:92010
18. Schenzle, D. (1984): An age-structured model of pre- and postvaccination measles transmission. *IMA J. Math. Appl. Med. Biol.* **1**, 169-191 CMP 18:16
19. Smith, H.L. (1983a): Subharmonic bifurcation in an SIR epidemic model. *J. Math. Biol.* **17**, 163-177 MR **85d**:92033a
20. Smith, H.L. (1983b): Multiple stable subharmonics for a periodic epidemic model. *J. Math. Biol.* **17**, 179-190 MR **85d**:92033b
21. Smith, H.L.; Waltman, P. (to appear): Perturbation of a globally stable steady state. *Proc. Amer. Math. Soc.* CMP 98:05
22. Tang, B.; Kuang, Y. (1996): Permanence in Kolmogorov-type systems of nonautonomous functional differential equations. *J. Math. Anal. Appl.* **197**, 427-447 MR **96k**:34164
23. Thieme, H.R. (1993): Persistence under relaxed point-dissipativity (with applications to an epidemic model). *SIAM J. Math. Anal.* **24**, 407-435 MR **94a**:34055
24. Thieme, H.R. (1994): Asymptotically autonomous differential equations in the plane. *Rocky Mountain J. Math.* **24**, 351-380 MR **96a**:34095
25. Thieme, H.R. (preprint): Persistence and permanence for non-autonomous semiflows

26. *Waltman, P.* (1991): A brief survey of persistence in dynamical systems. *Delay Differential Equations and Dynamical Systems* (S. Busenberg and M. Martelli, eds.), 31-40. Lecture Notes in Mathematics **1475**. Springer MR **92j**:34093
27. *Yang, F.; Ruan, S.* (1996): A generalization of the Butler-McGehee lemma and its applications in persistence theory. *Diff. Integral Equations* **9**, 1321-1330 CMP 97:01
28. *Zhao, X.-Q.* (1995): Uniform persistence and periodic coexistence states in infinite-dimensional periodic semiflows with applications. *Canad. Appl. Math. Quart.* **3**, 473-495 MR **96k**:58188
29. *Zhao, X.-Q.* (1996): Asymptotic behavior for asymptotically periodic semiflows with applications. *Comm. Appl. Nonl. Anal.* **3**, 43-66 MR **97i**:58150
30. *Zhao, X.-Q.* (1997): Global asymptotic behavior in a periodic competitor-competitor-mutualist parabolic system. *Nonlinear Anal., TMA* **29**, 551-568 CMP 97:13

DEPARTMENT OF MATHEMATICS, ARIZONA STATE UNIVERSITY, TEMPE, ARIZONA 85287-1804  
E-mail address: [h.thieme@asu.edu](mailto:h.thieme@asu.edu)