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UNIFORM PERSISTENCE IN A MODEL FOR BLUETONGUE DYNAMICS*

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Abstract. Uniform disease persistence is investigated for the time evolution of bluetongue, a viral disease in sheep and cattle that is spread by midges as vectors. The model is a system of several delay differential equations. As in many other infectious disease models, uniform disease persistence occurs if the basic disease reproduction number for the whole system, $\mathcal{R}_0$, exceeds one. However, since bluetongue affects sheep much more severely than cattle, uniform disease persistence can occur in two different scenarios which are distinguished by the disease reproduction number for the cattle-midge-bluetongue system without sheep, $\tilde{\mathcal{R}}_0$. If $\mathcal{R}_0 > 1$ and $\tilde{\mathcal{R}}_0 > 1$, bluetongue persists in cattle and midges even though it may eradicate the sheep, relying on cattle as a reservoir. If $\mathcal{R}_0 > 1 > \tilde{\mathcal{R}}_0$, bluetongue and all host and vector species coexist, and bluetongue does not eradicate the sheep because it cannot persist on midges and cattle alone. The two scenarios require different use of dynamical systems persistence theory.

Key words. bluetongue, delay, persistence, disease reservoir

AMS subject classifications. 34K25, 37C70, 37N25, 92D30

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1. Introduction.

Bluetongue is a viral infection of ruminants, including cattle and sheep, that is spread by biting midges of the *Culicoides* family. The bluetongue virus tends to cause abortion, congenital anomalies, and death in sheep, but mild cases usually recover rapidly and completely [1, 9]. In cattle, bluetongue generally does not cause death [1].

In a previous article [4], a model was presented for bluetongue dynamics that includes cattle and sheep as hosts, and midges with a general incubation period as vectors. We refer to [4] for the detailed explanation of the model and the derivation of the model equations; they can be found in Table 1, while the explanation of the variables, parameters, and parameter functions can be found in Table 2.

Fundamental properties of the model were established such as existence and uniqueness of solutions and their positivity and boundedness. Among other things, necessary and sufficient conditions were obtained for local stability of the disease-free equilibrium (with all host species present) and for uniform weak disease persistence in the midges. The first holds if the basic disease reproduction number $\mathcal{R}_0$ satisfies $\mathcal{R}_0 < 1$, and the second if $\mathcal{R}_0 > 1$. Disease persistence in cattle and sheep was not explicitly addressed. The results in [4] that are relevant here are summarized in sections 2 and 3.

This paper establishes uniform disease persistence in midges and cattle if $\mathcal{R}_0 > 1$.

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TABLE 1
Model equations.

Infective cattle

$$I_c'(t) = \frac{\beta_{mc} S_c(t) I_m(t)}{I_s(t) + S_s(t) + N_c} - \mu_c I_c(t), \qquad S_c(t) + I_c(t) = N_c$$

Susceptible sheep

$$S_s'(t) = b_s(S_s(t)) - \frac{\beta_{ms} S_s(t) I_m(t)}{I_s(t) + S_s(t) + N_c} + \gamma I_s(t) - \mu_s S_s(t)$$

Infective sheep

$$I_s'(t) = \frac{\beta_{ms} S_s(t) I_m(t)}{I_s(t) + S_s(t) + N_c} - \gamma I_s(t) - \mu_{is} I_s(t)$$

Susceptible midges

$$S_m'(t) = e^{-\mu_l \tau} b_m(S_m(t-\tau)) - \mu_m S_m(t) - \frac{\beta_{cm} I_c(t) + \beta_{sm} I_s(t)}{I_s(t) + S_s(t) + N_c} S_m(t)$$

Infective midges

$$I_m'(t) = -\mu_{im} I_m(t) + \int_{-\infty}^{t} \frac{\beta_{cm} I_c(r) + \beta_{sm} I_s(r)}{I_s(r) + S_s(r) + N_c} S_m(r) e^{-\mu_{em}(t-r)} f(t-r)\, dr$$

TABLE 2
Variables and parameters.

t	time
S_c, S_s, S_m	numbers of susceptible cattle, sheep, and midges
I_c, I_s, I_m	numbers of infectious cattle, sheep, and midges
N_c	constant number of cattle
β_{mc}, β_{ms}	per capita transmission rate from midges to cattle, sheep
β_{cm}, β_{sm}	per capita transmission rate from cattle, sheep to midges
μ_c, μ_s, μ_m	per capita mortality rates of susceptible cattle, sheep, and midges
μ_l	per capita mortality rate of midge larvae
μ_{is}, μ_{im}	per capita mortality rates of infectious sheep and midges
μ_{em}	per capita mortality rates of exposed midges
b_s, b_m	birth rate functions of sheep and midges
γ	recovery rate of infectious sheep
τ	mean length of midge larval stage
f	probability density of midge latency period

The disease persists uniformly if the disease prevalence is bounded away from 0 with the lower bound being independent of initial data for sufficiently large times. The disease persists uniformly weakly if its prevalence keeps dropping to arbitrarily low values but always returns to a certain level that does not depend on initial data.

Obviously, the mathematically more desirable property of uniform persistence implies uniform weak persistence. The converse is not true in general, as is shown by the Lotka–Volterra predator–prey system. An elementary epidemic model which illustrates when uniform weak persistence implies uniform persistence, and when it does not, is considered in the introduction of [13]. An epidemic model for which uniform weak disease persistence is shown under rather general conditions, but uniform persistence only under quite restrictive assumptions, is analyzed in [3]. Various general scenarios in which uniform persistence follows from uniform weak persistence are presented in [13, Chap. 4]. In general, the dynamical system in question needs to have compactifying properties for the derivation of uniform persistence from uniform weak persistence. Ideally, the system has a global compact attractor, but weaker compactness properties can be sufficient [14]. Existence of a compact attractor of bounded sets for our differential systems with infinite delays is shown in the appendix. Infinite delays are appropriate because the incubation period of bluetongue in the midge vector is quite variable such that a discrete delay would be too restrictive. While, in reality, there is a maximum length of the incubation period, mathematically one would like the length distribution to include standard infinite distributions like the gamma or the log-normal distribution [11, 12].

In the case of the bluetongue model considered here, the mathematical transition from uniform weak persistence to uniform persistence is difficult because bluetongue affects the livelihoods of the two host species very differently: The cattle's livelihood is affected hardly at all, while the sheep's mortality is increased and their fertility decreased. Cattle may even play the role of a reservoir based on which bluetongue can eradicate the sheep without dying out itself.

As we will show, uniform disease persistence occurs in two different scenarios which are distinguished by the basic disease reproduction number $\tilde{\mathcal{R}}_0$ of the cattle-midge-bluetongue system (without the sheep) and which require different mathematical treatment. If $\mathcal{R}_0 > 1$ and $\tilde{\mathcal{R}}_0 > 1$, bluetongue can persist even though it may eradicate the sheep (section 5). In fact, if $\tilde{\mathcal{R}}_0 > 1$, a disease equilibrium may exist which has no sheep but which is locally asymptotically stable for the whole system [4]. This uniform disease persistence result does not build on the uniform weak persistence result proved in [4].

If $\tilde{\mathcal{R}}_0 \le 1 < \mathcal{R}_0$, bluetongue coexists with both host species and the vector, and the sheep are not eradicated because bluetongue would die out in the absence of the sheep (section 6). This uniform disease persistence result builds on the uniform weak persistence result proved in [4], but uniform persistence of midges and sheep needs to be established first before uniform persistence of bluetongue can be shown. For sheep persistence, a priori estimates of bluetongue prevalence are needed (section 4) that are sharper than those presented in [4].

In general, persistence results for semiflows induced by complex systems (here two hosts, one vector, and one infectious disease agent) can require a delicate interplay between the construction of several compact attractors and the derivation of persistence results for the various system components (here the various species). This interplay must be orchestrated in the right way. For this bluetongue system, first a compact attractor is established for the semiflow on the comprehensive state space which makes it possible to prove uniform persistence for the vector (midges). Since the disease can only persist if the vector is present, the state space for the semiflow must now be restricted to states where the vectors (in one scenario also the sheep) are present. Uniform vector persistence provides a compact attractor for this restricted semiflow which in turn makes it possible to prove uniform persistence of the disease.

2. The model and basic properties of its solutions. The model is a system of three ordinary differential equations and two differential equations with delays, one with discrete and the other with distributed delay (see Table 1). Four components of the solutions need to be prescribed for nonnegative times $t \le 0$, and one component for time $t = 0$, with the following properties:

$$I_m(0) = I_{m0} \geq 0,$$

$$\left.\begin{array}{ll} S_m(\theta) = S_{m0}(\theta) \geq 0, & S_s(\theta) = S_{s0}(\theta) \geq 0 \\ I_s(\theta) = I_{s0}(\theta) \geq 0, & I_c(\theta) = I_{c0}(\theta) \in [0, N_c] \end{array}\right\} \quad \theta \in (-\infty, 0]. \tag{1}$$

For reasons that will become apparent later, in section 5, these initial (or history) functions are chosen from a fading memory space. Let BUC$(-\infty, 0]$ denote the space of bounded uniformly continuous functions from $(-\infty, 0]$ to $\mathbb{R}$. For some $\Delta > 0$ to be chosen, let

$$C_\Delta = \big\{\phi : (-\infty, 0] \to \mathbb{R};\ \ \phi(s)e^{\Delta s} \in \mathrm{BUC}(-\infty, 0]\big\}, \tag{2}$$

which is a Banach space with the norm

$$\|\phi\| = \sup_{s \leq 0} |\phi(s)e^{\Delta s}|. \tag{3}$$

Note that, for any $s \leq 0$, $\phi(s) \leq \|\phi\| e^{-\Delta s}$. Regarding the choice of Δ, we examine the delay term in the right-hand side of the I_m equation in Table 1, and consider the situation at time $t = 0$. At this time, the integral is the sum of two similar terms, the first of which is bounded by

$$\frac{\beta_{cm}}{N_c} \int_{-\infty}^{0} S_{m0}(\eta) I_{c0}(\eta) e^{\mu_{em}\eta} f(-\eta)\, d\eta.$$

For $S_{m0}, I_{c0} \in C_\Delta$, this term is bounded by

$$(\beta_{cm}\|S_{m0}\|\|I_{c0}\|/N_c) \int_{-\infty}^{0} e^{(-2\Delta + \mu_{em})\eta} f(-\eta)\, d\eta. \tag{4}$$

Finiteness of this integral is assured by choosing Δ such that $0 < 2\Delta < \mu_{em}$. Local existence and uniqueness of solutions were obtained in [4] under the stronger condition $0 < 3\Delta < \mu_{em}$.

THEOREM 2.1. *If the initial data have the form* (1), *if b_m and b_s are locally Lipschitz continuous, and if the components $S_{s0}, S_{m0}, I_{c0}, I_{s0}$ each lie in C_Δ, with $0 < 3\Delta < \mu_{em}$, then the model in Table* 1 *has a unique solution defined on an interval $[0, A)$ for some $0 < A \leq \infty$.*

It is reasonable to assume that when the disease remains absent, the numbers of susceptible sheep and midges evolve to constants as $t \to \infty$. These constants are denoted by S_s^0 and S_m^0, and they must satisfy

$$b_s(S_s^0) = \mu_s S_s^0, \qquad e^{-\mu_l \tau} b_m(S_m^0) = \mu_m S_m^0. \tag{5}$$

These values are related to various disease-free equilibria with one, several, or all hosts being present. The existence and uniqueness of $S_s^0 > 0$ and $S_m^0 > 0$ depend very much on the functional forms of the birth functions $b_s(\cdot)$ and $b_m(\cdot)$. We always make the following basic assumptions on these functions and sometimes additional assumptions as needed. For b_s, we assume the following:

(6) $b_s(S_s)$ is nonnegative with $b_s(0) = 0$. Moreover, b_s is locally Lipschitz continuous and there exists $S_s^0 > 0$ such that $b_s(S_s) > \mu_s S_s$ when $0 < S_s < S_s^0$, and $b_s(S_s) < \mu_s S_s$ when $S_s > S_s^0$.

These conditions ensure that the first equation in (5) has zero and S_s^0 as its only solutions. For b_m, the basic assumptions that we always make are the following:

(7) $b_m(S_m)$ is nonnegative with $b_m(0) = 0$. Moreover, b_m is locally Lipschitz continuous and there exists $S_m^0 > 0$ such that $e^{-\mu_l\tau} b_m(S_m) > \mu_m S_m$ when $0 < S_m < S_m^0$, and $e^{-\mu_l\tau} b_m(S_m) < \mu_m S_m$ when $S_m > S_m^0$.

Under these assumptions, the second equation in (5) has zero and S_m^0 as its only solutions. The following results are proved in [4] under more general assumptions.

Proposition 2.2. *Suppose the birth functions b_m and b_s satisfy* (6) *and* (7). *Then each component of any solution of the system in Table* 1 *that satisfies the initial data* (1) *is nonnegative wherever the solution exists. If, in addition, either*

(i) $I_{m0} > 0$*; or*

(ii) $S_{m0}(\eta^*)I_{c0}(\eta^*) > 0$ *or* $S_{m0}(\eta^*)I_{s0}(\eta^*) > 0$ *for some* $\eta^* \in (-\infty, 0]$, *the initial functions are continuous,* $f \in C[0,\infty)$ *and* $f([-\eta^*,\infty)) \neq \{0\}$*; or*

(iii) $I_{c0}(0) > 0$ *or* $I_{s0}(0) > 0$, $S_{m0}(\theta) \not\equiv 0$ *on* $[-\tau, 0]$ *and* $f(\eta) > 0$ *for all* $\eta > 0$,

then $I_m(t)$ *becomes strictly positive at some time, and remains strictly positive as long as the solution exists.*

Differently than [4], Table 1 does not list an equation for the number of exposed midges (midges in the latency period), E_m, because it decouples from the rest of the system. E_m appears in the next result, as do the total numbers of midges, N_m, and the total number of sheep, N_s.

Proposition 2.3. *Suppose the birth functions b_m and b_s satisfy* (6) *and* (7). *Then any solution of the system in Table* 1 *that satisfies the initial data* (1) *is defined for all $t \geq 0$ and is bounded. More precisely, there exist constants $\breve{S}_m > 0$ and $\breve{S}_s > 0$ that do not depend on the solution such that, for $t \geq 0$,*

$$S_m(t) + E_m(t) + I_m(t) = N_m(t) \leq \max\Big\{\breve{S}_m, \sup_{-\tau\leq\theta\leq 0} N_m(\theta)\Big\}$$

and

$$S_s(t) + I_s(t) = N_s(t) \leq \max\{\breve{S}_s, N_s(0)\}.$$

Moreover

$$\limsup_{t\to\infty} N_m(t) \leq \breve{S}_m, \qquad \limsup_{t\to\infty} N_s(t) \leq \breve{S}_s.$$

In addition, if b_s is monotone increasing on $[0, S_s^0]$, then $\breve{S}_s$ can be chosen as S_s^0, and if b_m is monotone increasing on $[0, S_m^0]$, then $\breve{S}_m$ can be chosen as S_m^0.

3. The basic disease reproduction number as threshold.

The system in Table 1 has four disease-free equilibria, all of which have $I_c = I_s = I_m = 0$: the first with $S_m = S_m^0 > 0$, $S_s = S_s^0 > 0$, a second one with $S_m = S_s = 0$, a third one with $S_m = 0$ and $S_s > 0$, and a fourth with $S_m > 0$ and $S_s = 0$. The last three are all unstable if the birth functions satisfy (6) and (7) and b_m is increasing on $[0, S_m^0]$. To obtain a threshold inequality (the weakest possible) for the local asymptotic stability of the first disease-free equilibrium (with susceptible midges, sheep, and cattle positive) in terms of a basic reproduction number, we introduce the following notation for basic disease transmission numbers:

$$\mathcal{R}_{cm} = \frac{1}{\mu_c}\frac{\beta_{cm} S_m^0}{(S_s^0 + N_c)}\hat{f}(\mu_{em}) \qquad \text{(from cattle to midges)}, \tag{8}$$

$$\mathcal{R}_{mc} = \frac{1}{\mu_{im}}\frac{\beta_{mc} N_c}{(S_s^0 + N_c)} \qquad \text{(from midges to cattle)}, \tag{9}$$

$$\mathcal{R}_{sm} = \frac{1}{(\gamma + \mu_{is})}\frac{\beta_{sm} S_m^0}{(S_s^0 + N_c)}\hat{f}(\mu_{em}) \qquad \text{(from sheep to midges)}, \tag{10}$$

$$\mathcal{R}_{ms} = \frac{1}{\mu_{im}}\frac{\beta_{ms} S_s^0}{(S_s^0 + N_c)} \qquad \text{(from midges to sheep)}. \tag{11}$$

Let us focus on (10) to explain these expressions. Here $\frac{1}{\gamma+\mu_{is}}$ is the average sojourn of a sheep in the infectious stage. A typical infectious sheep infects susceptible midges at the rate $\frac{\beta_{sm} S_m^0}{S_s^0 + N_c}$. The quantity

$$\hat{f}(\mu_{em}) = \int_0^\infty e^{-\mu_{em} t} f(t)\, dt$$

is the probability that an infected midge survives the latency period and becomes infectious [15, sect. 13.6]. So $\mathcal{R}_{sm}$ is the average number of infectious midges that is produced by one typical infectious sheep when bluetongue is introduced at the disease-free equilibrium; i.e., it is the basic transmission number of the disease from sheep to midges. Similarly, $\mathcal{R}_{ms}$ is the basic transmission number of the disease from midges to sheep, $\mathcal{R}_{cm}$ is the basic transmission number of the disease from cattle to midges, and $\mathcal{R}_{mc}$ is the basic transmission number of the disease from midges to cattle.

As the joint vector for two hosts, the midges are central for the infection. So let us take the midges' point of view. The product $\mathcal{R}_{mc}\mathcal{R}_{cm}$ is the average number of infectious midges produced via cattle hosts by a typical infectious midge when introduced at the disease-free equilibrium, while $\mathcal{R}_{ms}\mathcal{R}_{sm}$ is the average number of infectious midges produced via sheep hosts. Combining both infection venues, $\mathcal{R}_{mc}\mathcal{R}_{cm} + \mathcal{R}_{ms}\mathcal{R}_{sm}$ is the average number of infectious midges produced via either host by one typical infectious midge. Since this reproduction requires two epidemiological generations, the basic disease reproduction number is given by

$$\mathcal{R}_0 = (\mathcal{R}_{mc}\mathcal{R}_{cm} + \mathcal{R}_{ms}\mathcal{R}_{sm})^{1/2}. \tag{12}$$

The threshold quality of $\mathcal{R}_0$ is manifested by the following two results, which are proven in [4].

Theorem 3.1. *Assume that the birth functions b_s and b_m satisfy* (6) *and* (7) *and are differentiable at S_s^0 and S_m^0, respectively, and that*

$$b_s'(S_s^0) < \mu_s, \qquad -\mu_m \le e^{-\mu_l \tau} b_m'(S_m^0) < \mu_m. \tag{13}$$

Then if $\mathcal{R}_0 < 1$, the disease-free equilibrium

$$(S_s, S_m, I_c, I_s, I_m) = (S_s^0, S_m^0, 0, 0, 0)$$

of the system in Table 1 *is locally asymptotically stable.*

We now introduce the basic reproduction numbers $\mathcal{R}_0^{\mathrm{s}}$ for sheep and $\mathcal{R}_0^{\mathrm{m}}$ for midges, given by

$$\mathcal{R}_0^{\mathrm{s}} = \frac{1}{\mu_s} \liminf_{S\to 0+} \frac{b_s(S)}{S} \tag{14}$$

and

$$\mathcal{R}_0^{\mathrm{m}} = \frac{e^{-\mu_l \tau}}{\mu_m} \liminf_{S\to 0+} \frac{b_m(S)}{S}. \tag{15}$$

The following result concerning uniform weak disease persistence in midges is proved in [4].

THEOREM 3.2. *Assume that the birth functions satisfy* (6) *and* (7) *and that* b_m *is monotone increasing on* $[0, S_m^0]$. *If* $\mathcal{R}_0 > 1$, $\mathcal{R}_0^{\mathrm{m}} > 1$, *and* $\mathcal{R}_0^{\mathrm{s}} > 1$, *then there exists some* $\epsilon > 0$ *such that*

$$\limsup_{t\to\infty} I_m(t) > \epsilon \tag{16}$$

for all solutions of the system in Table 1 *with* $S_s(0) > 0$, $I_m(0) > 0$, *and* $S_m(t) > 0$ *for some* $t \in [-\tau, 0]$.

In particular, if $\mathcal{R}_0 > 1$, the disease-free equilibrium

$$(S_s, S_m, I_c, I_s, I_m) = (S_s^0, S_m^0, 0, 0, 0)$$

is unstable. It is our aim to show uniform disease persistence in midges, i.e., replace lim sup by lim inf in this theorem, and to address disease persistence in cattle and sheep.

To reach this aim, we will also need the disease transmission numbers at the cattle-midge equilibrium without sheep and bluetongue,

$$\tilde{\mathcal{R}}_{cm} = \frac{1}{\mu_c} \frac{\beta_{cm} S_m^0}{N_c} \hat{f}(\mu_{em}), \qquad \text{(from cattle to midges)}, \tag{17}$$

$$\tilde{\mathcal{R}}_{mc} = \frac{\beta_{mc}}{\mu_{im}}, \qquad \text{(from midges to cattle)}, \tag{18}$$

$$\tilde{\mathcal{R}}_{sm} = \frac{1}{\gamma + \mu_{is}} \frac{\beta_{sm} S_m^0}{N_c} \hat{f}(\mu_{em}) \qquad \text{(from sheep to midges)}. \tag{19}$$

Mutatis mutandis, the interpretation is the same as before. The quantity $\tilde{\mathcal{R}}_{cm}$ is the transmission number from cattle to midges, while $\tilde{\mathcal{R}}_{mc}$ is the transmission number from midges to cattle, all taken at the equilibrium with cattle and midges, but no disease and no sheep. The quantity

$$\tilde{\mathcal{R}}_0 = (\tilde{\mathcal{R}}_{mc} \tilde{\mathcal{R}}_{cm})^{1/2} \tag{20}$$

is the basic reproduction number of bluetongue for the system with cattle, midges, and virus only. Moreover, $\tilde{\mathcal{R}}_{sm}$ is the basic transmission number from a sheep to midges if there are no other sheep.

4. Asymptotic estimates of bluetongue prevalence in midges.

Similar estimates were already derived in [4] in order to find a condition for the extinction of bluetongue (see Theorem 4.3 below). However, these are not sharp enough to study persistence of bluetongue in cattle and sheep in the case that bluetongue cannot persist on cattle alone (section 7). We display the new and sharper estimates in a more prominent way than the old ones in [4] because they present information of independent interest.

We will use the superscript infinity to denote the limit superior, as $t \to \infty$, of the variable to which it is attached. The bluetongue reproduction numbers we have just introduced show up in the following estimate for

$$I_m^\infty = \limsup_{t\to\infty} I_m(t), \tag{21}$$

where we consider solutions of the system in Table 1 whose initial data satisfy (1) and have their components in C_Δ with $0 < 3\Delta < \mu_{em}$.

Lemma 4.1. *Let the birth functions b_s and b_m satisfy assumptions* (6) *and* (7), *and let b_m be increasing on $[0, S_m^0]$. If $I_m^\infty > 0$, then*

$$\frac{I_m^\infty}{N_c} \le (\tilde{\mathcal{R}}_0^2 - 1)\frac{\mu_c}{\beta_{mc}} + \tilde{\mathcal{R}}_{sm}\frac{\beta_{ms}S_s^\infty}{\mu_{im}(S_s^\infty + N_c)}\Big(\frac{\mu_c}{\beta_{mc}} + \frac{I_m^\infty}{N_c}\Big).$$

Proof. We apply the fluctuation method (see [7], [15, Prop. A.22]) to the equation for infective sheep in Table 1. There exists a sequence (t_j) such that $t_j \to \infty$, $I_s(t_j) \to I_s^\infty$, and $I_s'(t_j) \to 0$. It follows that

$$0 = \lim_{j\to\infty} \frac{\beta_{ms}S_s(t_j)I_m(t_j)}{I_s^\infty + S_s(t_j) + N_c} - \gamma I_s^\infty - \mu_{is}I_s^\infty,$$

and therefore that

$$I_s^\infty \le \frac{\beta_{ms}S_s^\infty I_m^\infty}{(\gamma + \mu_{is})(S_s^\infty + N_c)}. \tag{22}$$

Applying the fluctuation method to the equation for infective midges in Table 1, we obtain, after a substitution and some estimates,

$$0 \le -\mu_{im}I_m^\infty + \limsup_{j\to\infty}\int_0^\infty S_m(t_j - r)\frac{\beta_{cm}I_c(t_j - r) + \beta_{sm}I_s(t_j - r)}{N_c}e^{-\mu_{em}r}f(r)\,dr.$$

Recall $\sup_{t\le 0} S_m(t)e^{\Delta t} < \infty$ with $0 < 3\Delta < \mu_{em}$, $I_c \le N_c$, and Proposition 2.3. By Fatou's lemma,

$$\mu_{im}I_m^\infty \le \int_0^\infty \limsup_{j\to\infty} S_m(t_j - r)\frac{\beta_{cm}I_c(t_j - r) + \beta_{sm}I_s(t_j - r)}{N_c}\,e^{-\mu_{em}r}f(r)\,dr.$$

Elementary properties of the limit superior and some algebra yield

$$I_m^\infty \le S_m^\infty\left(\frac{\beta_{cm}I_c^\infty}{N_c} + \frac{\beta_{sm}I_s^\infty}{N_c}\right)\frac{\hat{f}(\mu_{em})}{\mu_{im}}.$$

Since we have assumed that b_m is increasing on $[0, S_m^0]$, $S_m^\infty \le S_m^0$ by Proposition 2.3, and so

$$I_m^\infty \le \frac{S_m^0}{N_c}(\beta_{cm}I_c^\infty + \beta_{sm}I_s^\infty)\frac{\hat{f}(\mu_{em})}{\mu_{im}}. \tag{23}$$

Similarly, the application of the fluctuation method to the equation for infective cattle in Table 1 yields a sequence of times t_j with $t_j \to \infty$, $I_c(t_j) \to I_c^\infty$, and

$$\begin{aligned} 0 = \lim_{j\to\infty} I_c'(t_j) &= \lim_{j\to\infty} \Big(\frac{\beta_{mc}(N_c - I_c(t_j))I_m(t_j)}{I_s(t_j) + S_s(t_j) + N_c} - \mu_c I_c(t_j) \Big) \\ &\leq \frac{\beta_{mc}(N_c - I_c^\infty)I_m^\infty}{N_c} - \mu_c I_c^\infty . \end{aligned}$$

We solve for I_c^∞,

$$I_c^\infty \leq \frac{\beta_{mc} I_m^\infty}{\mu_c + \beta_{mc}(I_m^\infty/N_c)} = \frac{(\beta_{mc}/\mu_c) I_m^\infty}{1 + (\beta_{mc}/\mu_c)(I_m^\infty/N_c)}. \tag{24}$$

We substitute this inequality and inequality (22) into (23),

$$I_m^\infty \leq \frac{S_m^0}{N_c} \left(\frac{\beta_{cm}(\beta_{mc}/\mu_c) I_m^\infty}{1 + (\beta_{mc}/\mu_c)(I_m^\infty/N_c)} + \frac{\beta_{sm}\beta_{ms} S_s^\infty I_m^\infty}{(\gamma + \mu_{is})(S_s^\infty + N_c)} \right) \frac{\hat f(\mu_{em})}{\mu_{im}}. \tag{25}$$

By (19) and (20),

$$I_m^\infty \leq \frac{\tilde{\mathcal{R}}_0^2 I_m^\infty}{1 + (\beta_{mc}/\mu_c)(I_m^\infty/N_c)} + \tilde{\mathcal{R}}_{sm} \frac{\beta_{ms} S_s^\infty I_m^\infty}{\mu_{im}(S_s^\infty + N_c)}.$$

Suppose that $I_m^\infty > 0$. Then

$$1 \leq \frac{\tilde{\mathcal{R}}_0^2}{1 + (\beta_{mc}/\mu_c)(I_m^\infty/N_c)} + \tilde{\mathcal{R}}_{sm} \frac{\beta_{ms} S_s^\infty}{\mu_{im}(S_s^\infty + N_c)},$$

which implies the desired estimate. ▯

If b_s is increasing on $[0, S_s^0]$, then $S_s^\infty \leq S_s^0$ by Proposition 2.3 and, since $x/(x+N_c)$ is increasing, by (11), $I_m^\infty = 0$ or

$$\frac{I_m^\infty}{N_c} \leq (\tilde{\mathcal{R}}_0^2 - 1)\frac{\mu_c}{\beta_{mc}} + \tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms}\Big(\frac{\mu_c}{\beta_{mc}} + \frac{I_m^\infty}{N_c}\Big).$$

We solve this inequality for I_m^∞/N_c and obtain the inequality in the next result.

Proposition 4.2. *Let the birth functions b_s and b_m satisfy assumptions* (6) *and* (7)*, let b_s be increasing on $[0, S_s^0]$, and let b_m be increasing on $[0, S_m^0]$.*

If $\tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms} < 1$, then $I_m^\infty = 0$ or

$$\frac{I_m^\infty}{N_c} \leq \frac{(\tilde{\mathcal{R}}_0^2 + \tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms} - 1)}{1 - \tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms}} \frac{\mu_c}{\beta_{mc}}.$$

As a special case, we obtain the disease extinction result already established in [4].

Theorem 4.3. *Let the birth functions b_s and b_m satisfy assumptions* (6) *and* (7)*, let b_s be increasing on $[0, S_s^0]$, and let b_m be increasing on $[0, S_m^0]$. If $\tilde{\mathcal{R}}_0^2 + \tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms} \leq 1$, then $I_m^\infty = 0$ and the disease dies out.*

Proof. $I_m^\infty = 0$ by the previous proposition. Then $I_c^\infty = 0$ and $I_s^\infty = 0$ by (24) and (22). ▯

We also obtain the following estimate from Lemma 4.1 and Proposition 2.3. It will be used to show uniform sheep persistence if $\tilde{\mathcal{R}}_0 \leq 1$ (Theorem 7.1).

Proposition 4.4. *Let the birth functions b_s and b_m satisfy assumptions* (6) *and* (7)*, and let b_m be monotone increasing on $[0, S_m^0]$.*

If $\tilde{\mathcal{R}}_0 \le 1$*, then*

$$\frac{I_m^\infty}{N_c} \le \tilde{\mathcal{R}}_{sm} \frac{\beta_{ms} S_s^\infty}{\mu_{im}(S_s^\infty + N_c)} \Big(\frac{\mu_c}{\beta_{mc}} + \frac{S_m^0}{N_c} \Big).$$

If there are no sheep at all, we may as well assume that all disease reproduction numbers involving sheep are 0 and so $\tilde{\mathcal{R}}_{sm}\mathcal{R}_{ms} = 0$ in Theorem 4.3.

Corollary 4.5. *Let the birth functions* b_s *and* b_m *satisfy assumptions* (6) *and* (7)*, let* b_m *be monotone increasing on* $[0, S_m^0]$*, and let* $\tilde{\mathcal{R}}_0 \le 1$*. Then the disease dies out in the absence of sheep. If* $\tilde{\mathcal{R}}_0 < 1$*, the equilibrium with* $S_m = S_m^0$ *and* $I_c = I_m = 0$ *is locally stable for the cattle-midge-bluetongue system.*

The local stability statement is proved similarly as for [4, Thm. 3].

5. Uniform persistence of midges. Before we can prove uniform disease persistence, we need to establish uniform persistence of susceptible midges. Recall the basic midge reproduction number, $\mathcal{R}_0^{\mathrm{m}}$, defined by (15).

Theorem 5.1. *Assume that the birth functions satisfy* (6) *and* (7) *and that* b_m *is monotone increasing on* $[0, S_m^0]$*. If* $\mathcal{R}_0^{\mathrm{m}} > 1$*, then there exists some* $\epsilon > 0$ *such that, for all solutions with* $S_{m0}(\theta) \not\equiv 0$ *on* $[-\tau, 0]$*,*

$$\liminf_{t\to\infty} S_m(t) \ge \epsilon. \tag{26}$$

In [4, sect. 3.5], uniform weak persistence of susceptible midges was established, with lim sup replacing lim inf. The transition requires dynamical systems theory.

By the state of the solution at time t, we mean the entity

$$\sigma_t = (S_{s_t}, S_{m_t}, I_{c_t}, I_{s_t}, I_m(t)), \tag{27}$$

where the subscript t means the state at time t; for example, S_{s_t} is the function defined by $S_{s_t}(\theta) = S_s(t+\theta)$, $\theta \in (-\infty, 0]$. Note that the I_m variable differs from the others in that it does not involve delay. When we refer to the actual values of the solution, we write $\sigma(t) \in \mathbb{R}_+^5$, i.e.,

$$\sigma(t) = (S_s(t), S_m(t), I_c(t), I_s(t), I_m(t)) \,. \tag{28}$$

Recall the fading memory space

$$C_\Delta = \big\{\phi : (-\infty, 0] \to \mathbb{R};\ \ \phi(s)e^{\Delta s} \in \mathrm{BUC}(-\infty, 0]\big\}$$

in (2), which is a Banach space with the norm

$$\|\phi\| = \sup_{s\le 0} |\phi(s)e^{\Delta s}|. \tag{29}$$

Initial data are taken from the product space $C_\Delta^4 \times \mathbb{R}$, where the factor of $\mathbb{R}$ relates to the undelayed variable I_m. This space is also a Banach space with the norm

$$|\!|\!|\sigma|\!|\!| = \max\big\{\|S_s\|, \|S_m\|, \|I_c\|, \|I_s\|, |I_m|\big\}. \tag{30}$$

Let X be the nonnegative cone of the product space $C_\Delta^4 \times \mathbb{R}$. X will be the state space for the semiflow T described next. For $t \ge 0$, let $T(t) = T(t, \cdot)$ be the nonlinear transformation that maps the initial data (1) to the state of the solution at time t, i.e., to σ_t in (27).

Proposition 5.2. *Let* $3\Delta < \mu_{em}$*. Then* T *is a continuous semiflow on* X*. Moreover, there exists a compact attractor of bounded sets,* A*; i.e.,* A *is a compact invariant subset of* X *and* $\sup_{x\in U} d(T(t,x), A) \to 0$ *for each bounded subset* U *of* X*.*

Here $d(y,A) = \inf_{a\in A} \|y-a\|$ denotes the distance from a point $y \in X$ to the subset A of X.

Proof of Theorem 5.1. This now follows by combining [13, Thm. 4.5] with the uniform weak persistence of susceptible midges proved in [4]. Use the persistence function $\rho : X \to \mathbb{R}_+$, $\rho(x) = S_m$ for $x = (S_s, S_m, I_c, I_s, I_m)$.

If the probability density of the latency period in midges has compact support, Proposition 5.2 readily follows from the well-known theory of functional differential equations with finite delay. For infinite delay, the proof is postponed to section 8 in order not to interrupt the flow of the various persistence results. While one could argue that the compact support case is the only realistic one, there are two good reasons to consider the general case. First, one would like to include models of ordinary differential equations in which the latency period is exponentially distributed. Second, many popular probability densities such as the gamma, normal, and lognormal distributions do not have compact support. The incubation periods of various infectious diseases are often nicely fitted by log-normal distributions, and the fits are better than those by normal distributions [11, 12] (see also [15, sect. 12.8]).

For the various uniform persistence results as formulated in this paper, it is actually sufficient that the semiflow have a compact attractor of points, i.e., $d(T(t,x), A) \to 0$ for each $x \in X$. A compact attractor of bounded sets, however, can be decomposed into a disjoint union of three sets: a compact extinction attractor, a compact persistence attractor, and a set of total orbits connecting the two attractors to each other. See [13, sect. 5.2] for details.

6. Uniform persistence of bluetongue though it may eradicate sheep.

Recall the basic disease reproduction number in the absence of sheep, $\tilde{\mathcal{R}}_0^2 = \tilde{\mathcal{R}}_{mc}\,\tilde{\mathcal{R}}_{cm}$, defined in (20) at the end of section 3, the basic disease reproduction number, $\mathcal{R}_0$, defined in (12), and the basic midge reproduction number, $\mathcal{R}_0^{\mathrm{m}}$, defined in (15).

THEOREM 6.1. *Suppose that the birth functions* b_s *and* b_m *satisfy* (6) *and* (7), *respectively, with* b_m *monotone increasing on* $[0, S_m^0]$. *Assume* $f \in L^1 \cap C[0,\infty)$ *and* $\mathcal{R}_0 > 1$, $\tilde{\mathcal{R}}_0 > 1$, *and* $\mathcal{R}_0^{\mathrm{m}} > 1$.

Then the disease is uniformly strongly persistent in midges and cattle in the sense that there exists $\eta > 0$ *such that* $\liminf_{t\to\infty} I_m(t) \ge \eta$ *for all solutions of the system in Table* 1 *with initial data of the form* (1) *that satisfy* $S_{m0}(\theta) \not\equiv 0$ *on* $[-\tau, 0]$ *and either* (i), (ii), *or* (iii) *of Proposition* 2.2.

Moreover, for the same η,

$$\liminf_{t\to\infty} I_c(t) \ge \frac{\eta \beta_{mc} N_c}{\mu_c(N_c + \breve{S}_s) + \eta\beta_{mc}}, \tag{31}$$

with $\breve{S}_s$ *from Proposition* 2.3. *If there exists some* $c > 0$ *such that* $b_s(x) \le cx$ *for all* $x \ge 0$, *then the disease persists proportionally in the sheep in the sense that*

$$\liminf_{t\to\infty} \frac{I_s(t)}{S_s(t) + I_s(t)} \ge \frac{\beta_{ms}\eta}{(N_c + \breve{S}_s)(\gamma + \delta_s + c) + \beta_{ms}\eta}. \tag{32}$$

Notice that, differently than the uniform weak disease persistence result in Theorem 3.2, taken from [4], this strong disease persistence result does not assume that the basic sheep reproduction number, $\mathcal{R}_0^{\mathrm{s}}$, exceeds 1. In particular, the proof of this theorem does not build on Theorem 3.2.

Proof. To show uniform persistence of the disease in the midges, we use the concept of ρ-persistence for semiflows. For this purpose, we choose the state space

$$Y = \left\{ (S_s, S_m, I_c, I_s, I_m) \in X; \begin{array}{c} S_s \geq 0,\ 0 \leq S_m \not\equiv 0 \\ I_c \geq 0, I_s \geq 0, I_m \geq 0 \end{array} \right\}. \tag{33}$$

Then $Y \subseteq X$ and Y is forward invariant under the semiflow T. Define $\rho : Y \to \mathbb{R}_+$ by

$$\rho(x) = I_m, \qquad x = (S_s, S_m, I_c, I_s, I_m) \in X.$$

Then ρ is uniformly continuous. The existence of a compact point attractor B for T on X follows from Proposition 5.2. Since susceptible midges persist uniformly, the restriction of T to Y also has a compact point attractor.

Since $\rho(T(t,x)) = I_m(t)$, $\rho(x) > 0$ implies $\rho(T(t,x)) > 0$ for all $t \geq 0$. By [13, Thm. 4.5], it is sufficient to show that T is uniformly weakly ρ-persistent. To show the latter, we apply [13, Thm. 8.20].

Notice that $Y_0 = \{x \in Y;\ \forall t \geq 0 : \rho(T(t,x)) = 0\}$ equals

$$Y_0 = \{(S_s, S_m, 0, 0, 0) \in X; S_s \geq 0, 0 \leq S_m \not\equiv 0, I_c = 0, I_s = 0, I_m = 0\},$$

for, if there are infective sheep or infective cattle, our assumptions imply that there will eventually be infective midges as well. Solutions starting in Y_0 converge to $E_1 = (0, S_m^0, 0, 0, 0)$ if $S_s(0) = 0$ and to $E_2 = (S_s^0, S_m^0, 0, 0, 0)$ if $S_s(0) > 0$. These two equilibria are isolated in Y_0 because the first is unstable and the second locally asymptotically stable [13, Lem. 8.22]. In the language of [13, sect. 8.3],

$$\Omega := \bigcup_{x \in Y_0} \omega(x) = M_1 \cup M_2,$$

where $M_1 = \{E_1\}$ and $M_2 = \{E_2\}$. Since E_1 and E_2 are equilibria, M_1 and M_2 are invariant. $\{M_1, M_2\}$ is acyclic because there is no total trajectory from M_2 to M_1 in Y_0. By [13, Thm. 8.20], T is uniformly weakly ρ-persistent, if M_1 and M_2 are uniformly weakly ρ-repelling.

Suppose that $M_1 = \{E_1\}$ is not uniformly weakly ρ-repelling. By [13, Def. 8.15], for all $\epsilon > 0$ there exists some $x \in Y$ such that $\rho(x) > 0$ and

$$\limsup_{t \to \infty}\ d(T(t,x), E_1) < \epsilon.$$

Here d is the metric induced on Y. For the associated solution, $I_m(t) > 0$ for all $t \geq 0$. Shifting forward in time, we can assume that $d(T(t,x), E_1) < \epsilon$ for all $t \geq 0$. In terms of solutions, for each $\epsilon > 0$ there exists a solution such that $I_m(t) > 0$ for all $t \geq 0$ and

$$\max\left\{S_s(t), |S_m(t) - S_m^0|, I_c(t), I_s(t), I_m(t)\right\} < \epsilon, \qquad t \geq 0.$$

We obtain the following differential inequalities from the system in Table 1:

$$\begin{aligned} I_c'(t) \geq & \frac{\beta_{mc}(N_c - \epsilon) I_m(t)}{2\epsilon + N_c} - \mu_c I_c(t), \\ I_m'(t) \geq & -\mu_{im} I_m(t) + \int_0^t \frac{\beta_{cm}(S_m^0 - \epsilon) I_c(r)}{2\epsilon + N_c} e^{-\mu_{em}(t-r)} f(t-r)\, dr. \end{aligned} \tag{34}$$

With λ real and $\lambda > 0$, we apply the Laplace transform $\hat{I}(\lambda) = \int_0^\infty e^{-\lambda t} I(t)\,dt$, which transforms convolutions into products, to obtain

$$\begin{aligned} \lambda \hat{I}_c(\lambda) \geq & \frac{\beta_{mc}(N_c - \epsilon)\hat{I}_m(\lambda)}{2\epsilon + N_c} - \mu_c \hat{I}_c(\lambda), \\ \lambda \hat{I}_m(\lambda) \geq & -\mu_{im}\hat{I}_m(\lambda) + \frac{\beta_{cm}(S_m^0 - \epsilon)\hat{I}_c(\lambda)}{2\epsilon + N_c}\hat{f}(\lambda + \mu_{em}). \end{aligned} \tag{35}$$

We reorganize the first inequality and substitute it into the second,

$$\hat{I}_m(\lambda) \geq \frac{\beta_{mc}(N_c - \epsilon)\hat{I}_m(\lambda)}{(2\epsilon + N_c)(\lambda + \mu_c)} \frac{\beta_{cm}(S_m^0 - \epsilon)}{(2\epsilon + N_c)(\lambda + \mu_{im})}\hat{f}(\lambda + \mu_{em}).$$

Dividing by $\hat{I}_m(\lambda) > 0$,

$$1 \geq \frac{\beta_{mc}(N_c - \epsilon)}{(2\epsilon + N_c)(\lambda + \mu_c)} \frac{\beta_{cm}(S_m^0 - \epsilon)}{(2\epsilon + N_c)(\lambda + \mu_{im})}\hat{f}(\lambda + \mu_{em}).$$

This inequality, which no longer depends on the solution, holds for all $\lambda > 0$ and $\epsilon > 0$, and therefore it also holds in the limit $\lambda \to 0$ and $\epsilon \to 0$. Therefore

$$1 \geq \frac{\beta_{mc}}{\mu_c}\frac{\beta_{cm}S_m^0}{N_c\mu_{im}}\hat{f}(\mu_{em}) = \tilde{\mathcal{R}}_0^2,$$

a contradiction.

Suppose that $M_2 = \{E_2\}$ is not uniformly weakly ρ-repelling. By [13, Def. 8.15], for all $\epsilon > 0$ there exists some $x \in Y$ such that $\rho(x) > 0$ and

$$\limsup_{t\to\infty} d(T(t,x), E_2) < \epsilon.$$

Here d is the metric induced on Y. For the associated solution, $I_m(t) > 0$ for all $t \geq 0$. Shifting forward in time, we can assume that $d(T(t,x), E_2) < \epsilon$ for all $t \geq 0$. In terms of solutions, for each $\epsilon > 0$ there exists a solution such that $I_m(t) > 0$ for all $t \geq 0$,

$$\max\{|S_s(t) - S_s^0|, |S_m(t) - S_m^0|, I_c(t), I_s(t), I_m(t)\} < \epsilon, \qquad t \geq 0.$$

We obtain the following differential inequalities from Table 1:

$$\begin{aligned} I_c'(t) \geq & \frac{\beta_{mc}(N_c - \epsilon)I_m(t)}{2\epsilon + S_s^0 + N_c} - \mu_c I_c(t), \\ I_s'(t) \geq & \frac{\beta_{ms}(S_s^0 - \epsilon)I_m(t)}{2\epsilon + S_s^0 + N_c} - \gamma I_s(t) - \mu_{is}I_s(t), \\ I_m'(t) \geq & -\mu_{im}I_m(t) + \int_0^t \frac{\beta_{cm}I_c(r) + \beta_{sm}I_s(r)}{2\epsilon + S_s^0 + N_c}(S_m^0 - \epsilon) \\ & \qquad \times e^{-\mu_{em}(t-r)}f(t-r)\,dr. \end{aligned}$$

We apply the Laplace transform with λ real and strictly positive. After rearrangement,

$$(\lambda+\mu_c)\hat{I}_c(\lambda) \geq \frac{\beta_{mc}(N_c-\epsilon)\hat{I}_m(\lambda)}{2\epsilon+S_s^0+N_c},$$

$$(\lambda+\gamma+\mu_{is})\hat{I}_s(\lambda) \geq \frac{\beta_{ms}(S_s^0-\epsilon)\hat{I}_m(\lambda)}{2\epsilon+S_s^0+N_c},$$

$$(\lambda+\mu_{im})\hat{I}_m(\lambda) \geq \frac{\beta_{cm}\hat{I}_c(\lambda)+\beta_{sm}\hat{I}_s(\lambda)}{2\epsilon+S_s^0+N_c}(S_m^0-\epsilon)\hat{f}(\lambda+\mu_{em}).$$

We substitute the first and second inequalities into the third, rearrange, and divide by $\hat{I}_m(\lambda)>0$, giving us

$$1 \geq \Big(\frac{\beta_{mc}(N_c-\epsilon)\beta_{cm}}{\lambda+\mu_c}+\frac{\beta_{ms}(S_s^0-\epsilon)\beta_{sm}}{\lambda+\gamma+\mu_{is}}\Big)\frac{S_m^0-\epsilon}{(2\epsilon+S_s^0+N_c)^2}\frac{\hat{f}(\lambda+\mu_{em})}{\lambda+\mu_{im}}.$$

Since this inequality no longer depends on the solution, it holds for all $\lambda>0$ and $\epsilon>0$, and so we may take the limit $\lambda,\epsilon\to 0$ to obtain

$$1 \geq \Big(\frac{\beta_{mc}N_c}{(S_s^0+N_c)\mu_c}\frac{\beta_{cm}S_m^0}{S_s^0+N_c}+\frac{\beta_{ms}S_s^0}{(S_s^0+N_c)(\gamma+\mu_{is})}\frac{\beta_{sm}S_m^0}{S_s^0+N_c}\Big)\frac{\hat{f}(\mu_{em})}{\mu_{im}}=\mathcal{R}_0^2,$$

a contradiction.

If the initial data satisfy one of the assumptions in Proposition 2.2 rather than $I_m(0)>0$, then $I_m(t_0)>0$ for some $t_0\geq 0$, and the same conclusion holds after a shift in time.

This concludes the proof that the disease persists uniformly in the midges.

To show (31), uniform disease persistence in cattle, consider the equation for infected cattle in Table 1 in the form

$$I_c'(t)=\frac{\beta_{mc}(N_c-I_c(t))I_m(t)}{I_s(t)+S_s(t)+N_c}-\mu_c I_c(t).$$

By the fluctuation method (see [7], [15, Prop. A.22]), there exists a sequence of times (t_j) such that

$$t_j\to\infty,\quad I_c(t_j)\to I_{c\,\infty}=\liminf_{t\to\infty}I_c(t),\quad I_c'(t_j)\to 0,\qquad j\to\infty.$$

Since $I_s(t)+S_s(t)=N_s(t)$,

$$0\geq\frac{\beta_{mc}(N_c-I_{c\,\infty})\eta}{N_s^\infty+N_c}-\mu_c I_{c\,\infty}$$

with $N_s^\infty=\limsup_{t\to\infty}N_s(t)\leq\breve{S}_s$ (see Proposition 2.3). Solving this inequality for $I_{c\,\infty}$ gives (31).

To show proportional disease persistence in the sheep we introduce the proportion of infected sheep:

$$p_s(t)=\frac{I_s(t)}{N_s(t)},\qquad N_s(t)=S_s(t)+I_s(t).$$

We add the differential equations for susceptible and infective sheep and express the equation for the sum in terms of the new variables N_s and p_s,

$$N_s'(t) = b_s(N_s(t)(1-p_s(t))) - (\mu_s + \delta_s p_s(t))N_s(t),$$

where $\delta_s = \mu_{is} - \mu_s$. By the quotient rule,

$$\begin{aligned} p_s'(t) = {} & \frac{\beta_{ms}(1-p_s(t))I_m(t)}{N_s(t)+N_c} - \gamma p_s(t) - \mu_{is} p_s(t) \\ & - p_s(t)\bigg(\frac{b_s(N_s(t)(1-p_s(t)))}{N_s(t)} - (\mu_s + \delta_s p_s(t))\bigg). \end{aligned}$$

By assumption, there exists some $c > 0$ such that $b_s(x) \le cx$ for all $x \ge 0$. Also, since $\mu_{is} = \mu_s + \delta_s$, the following differential inequality is obtained:

$$p_s'(t) \ge \frac{\beta_{ms}(1-p_s(t))I_m(t)}{N_s(t)+N_c} - \gamma p_s(t) - \delta_s p_s(t)(1-p_s(t)) - c p_s(t). \tag{36}$$

We apply the fluctuation method [15, Prop. A.22] to this inequality and find a sequence (t_j) such that

$$t_j \to \infty, \quad p_s(t_j) \to p_{s\infty} = \liminf_{t\to\infty} p_s(t), \quad p_s'(t_j) \to 0, \qquad j \to \infty.$$

By (36),

$$\begin{aligned} 0 \ge {} & \liminf_{j\to\infty} \Big(\frac{\beta_{ms}(1-p_s(t_j))I_m(t_j)}{N_s(t_j)+N_c} - \gamma p_s(t_j) - \delta_s p_s(t_j)(1-p_s(t_j)) - c p_s(t_j)\Big) \\ \ge {} & \frac{\beta_{ms}(1-p_{s\infty})I_{m\infty}}{N_c + N_s^\infty} - \gamma p_{s\infty} - \delta_s p_{s\infty}(1-p_{s\infty}) - c p_{s\infty}. \end{aligned}$$

Since $p_{s\infty} \le 1$, $I_{m\infty} \ge \eta$, and $N_s^\infty \le \breve{S}_s$ (Proposition 2.3),

$$0 \ge \frac{\beta_{ms}(1-p_{s\infty})\eta}{N_c + \breve{S}_s} - \gamma p_{s\infty} - \delta_s p_{s\infty} - c p_{s\infty}.$$

We solve this inequality for $p_{s\infty}$ and obtain

$$p_{s\infty} \ge \frac{\beta_{ms}\eta}{(N_c + \breve{S}_s)(\gamma + \delta_s + c) + \beta_{ms}\eta}. \qquad \square$$

7. Uniform disease persistence if sheep persist.

We first show that susceptible sheep persist uniformly when bluetongue cannot persist in the absence of sheep; i.e., $\tilde{\mathcal{R}}_0 \le 1$ for the disease reproduction number in the absence of sheep defined in (20). As in Theorem 3.2, taken from [4], but differently than Theorem 6.1, we also assume that the basic reproduction number of sheep, defined in (14), satisfies $\mathcal{R}_0^{\mathrm{s}} > 1$.

THEOREM 7.1. *Suppose that the birth functions* b_s *and* b_m *satisfy* (6) *and* (7) *with* b_m *increasing on* $[0, S_m^\circ]$. *Suppose* $f \in L^1 \cap C[0,\infty)$. *Assume also that* $\mathcal{R}_0^{\mathrm{s}} > 1 \ge \tilde{\mathcal{R}}_0$. *Then susceptible sheep persist uniformly: There exists some* $\epsilon > 0$ *such that* $\liminf_{t\to\infty} S_s(t) \ge \epsilon$ *for all solutions of the system in Table* 1 *for which* $S_s(0) > 0$.

Proof. We first show that the susceptible sheep persist uniformly weakly; i.e., the statement holds with the limit inferior being replaced by the limit superior. We use a proof by contradiction and assume that for each $\epsilon > 0$ there exists a solution of the system in Table 1 such that $S_s(0) > 0$ and $S_s^\infty = \limsup_{t\to\infty} S_s(t) < \epsilon$. By Proposition 4.4, there exists $M > 0$ that is independent of $\epsilon > 0$ and $I_m^\infty < M\epsilon$.

After a shift in time, we can assume that $0 < S_s(t) < \epsilon$ and $I_m(t) < M\epsilon$ for all $t \geq 0$. So the susceptible sheep satisfy the following inequality:

$$S_s'(t) \geq \inf_{0<S<\epsilon} \frac{b_s(S)}{S} S_s(t) - \frac{\beta_{ms} S_s(t) M\epsilon}{N_c} - \mu_s S_s(t).$$

We apply the Laplace transform to this inequality, with the transform variable λ being real and strictly positive,

$$\lambda \hat{S}_s(\lambda) \geq \inf_{0<S<\epsilon} \frac{b_s(S)}{S} \hat{S}_s(\lambda) - \frac{\beta_{ms} \hat{S}_s(\lambda) M\epsilon}{N_c} - \mu_s \hat{S}_s(\lambda).$$

We divide by $\hat{S}_s(\lambda) > 0$ and rearrange,

$$1 \geq \frac{1}{\lambda + \mu_s}\bigg(\inf_{0<S<\epsilon} \frac{b_s(S)}{S} - \frac{\beta_{ms} M\epsilon}{N_c} \bigg).$$

This inequality holds for all $\lambda > 0$ and $\epsilon > 0$, and therefore also in the limits $\lambda \to 0$ and $\epsilon \to 0$,

$$1 \geq \frac{1}{\mu_s} \liminf_{S\to 0} \frac{b_s(S)}{S} = \mathcal{R}_0^{\mathrm{s}},$$

a contradiction. This proves uniform weak persistence of susceptible sheep.

In order to show uniform persistence of susceptible sheep, we use [13, Thm. 4.5]. We choose the state space X, the closed nonnegative cone of $C_\Delta^4 \times \mathbb{R}$. By Proposition 5.2, T has a compact set B that attracts all points in X. Further we choose the persistence function $\rho : X \to \mathbb{R}_+$ as

$$\rho(x) = S_s(0), \qquad x = (S_s, S_m, I_c, I_s, I_m) \in X.$$

Then ρ is uniformly continuous and $\rho \circ T$ is continuous. Since $\rho(T(t,x)) = S_s(t)$ for solutions of the system in Table 1, $\rho(x) > 0$ implies $\rho(T(t,x)) > 0$ for all $t > 0$.

In the language of [13, Thm. 4.5], we have shown before that T is uniformly weakly ρ-persistent. So T is uniformly ρ-persistent, which implies the uniform persistence of susceptible sheep. ▯

The next uniform disease persistence result builds on Theorem 3.2, taken from [4], but can only do so in combination with the uniform persistence results for midges and sheep in Theorems 5.1 and 7.1. The reason is that, for the transition from uniform weak to uniform disease persistence, we need a compact attractor for the restriction of the semiflow to a state space in which both midges and sheep are present. Recall the basic disease reproduction numbers with and without sheep, $\mathcal{R}_0$ and $\tilde{\mathcal{R}}_0$, defined in (12) and (20), and the basic reproduction numbers for midges and sheep, $\mathcal{R}_0^{\mathrm{m}}$ and $\mathcal{R}_0^{\mathrm{s}}$, defined in (15) and (14).

THEOREM 7.2. *Suppose that the birth functions* b_s *and* b_m *satisfy* (6) *and* (7), *respectively, with* b_m *monotone increasing on* $[0, S_m^0]$. *Assume* $f \in L^1 \cap C[0,\infty)$ *and* $\mathcal{R}_0 > 1 \geq \tilde{\mathcal{R}}_0$ *and* $\mathcal{R}_0^{\mathrm{m}} > 1$ *and* $\mathcal{R}_0^{\mathrm{s}} > 1$.

Then the susceptible sheep persist uniformly, and the disease is uniformly persistent in the midges, cattle, and sheep in the sense that there exist $\epsilon > 0$ *and* $\eta > 0$ *such that*

$$S_{s\infty} := \liminf_{t\to\infty} S_s(t) \geq \epsilon, \qquad I_{m\infty} := \liminf_{t\to\infty} I_m(t) \geq \eta$$

for all solutions of the system in Table 1 *with initial data of the form* (1) *that satisfy* $S_{m0}(\theta) \not\equiv 0$ *on* $[-\tau, 0]$*,* $S_s(0) > 0$ *and* (i) *or* (ii) *or* (iii) *of Proposition* 2.2*. Moreover,*

$$\begin{aligned} &\liminf_{t\to\infty} I_c(t) \geq \frac{I_{m\infty}\beta_{mc}N_c}{\mu_c(N_c + \breve{S}_s) + \beta_{mc}I_{m\infty}}, \\ &\liminf_{t\to\infty} I_s(t) \geq \frac{\beta_{ms}S_{s\infty}I_{m\infty}}{(\gamma + \mu_{is})(\breve{S}_s + N_c)}, \end{aligned} \tag{37}$$

with $\breve{S}_s$ *from Proposition* 2.3*.*

Proof. We choose the state space as

$$Z = \left\{ (S_s, S_m, I_c, I_s, I_m) \in X; \begin{array}{c} S_s \geq 0, S_s(0) > 0,\ 0 \leq S_m \not\equiv 0, \\ I_c \geq 0, I_s \geq 0, I_m \geq 0 \end{array} \right\}.$$

Notice that Z is a proper subset of $Y \subseteq X$ in (33) and that Z is forward invariant under T. Z needs to be chosen with $S_s(0) > 0$ because, since $\tilde{\mathcal{R}}_0 \leq 1$, bluetongue cannot persist without sheep.

Since susceptible midges and susceptible sheep are uniformly persistent by Theorems 5.1 and 7.1, respectively, T has a compact attractor of points on Z by Proposition 5.2.

Define $\rho : Z \to \mathbb{R}_+$ by

$$\rho(x) = I_m, \qquad x = (S_s, S_m, I_c, I_s, I_m) \in X.$$

Then ρ is uniformly continuous. Notice that $\rho(T(t, x)) = I_m(t)$. By Theorem 3.2, bluetongue persists uniformly weakly in midges. In the language of [13, Thm. 4.5], T is uniformly weakly ρ-persistent and thus uniformly ρ-persistent. So, there exists some $\eta > 0$ such that $I_{m\infty}$ for all solutions with $I_m(0) > 0$. Applying the fluctuation method to the equation for infective sheep in Table 1 yields

$$0 \geq \frac{\beta_{ms}S_{s\infty}I_{m\infty}}{\breve{S}_s + N_c} - (\gamma + \mu_{is})I_{s\infty}.$$

This implies the inequality for $I_{s\infty}$. The inequality for infective cattle follows similarly. ☐

Appendix. A semiflow with global compact attractor. A framework for proving the existence of a global compact attractor for semiflows induced by functional differential equations with infinite delay can be found in [6, sect. 12.9] (page 411 has references to other works on infinite delays). This framework comes with a lot of notation and assumptions, and quite a few details are left to the reader. We feel more comfortable proving a couple of fading memory results from scratch and using the attractor existence results from [13].

In order to prove Proposition 5.2, we write the system in Table 1 in the compact form

$$\sigma'(t) = \Psi(\sigma_t), \tag{38}$$

where the map $\Psi : X \to \mathbb{R}^5$ is defined by the right-hand side of the model and the notation in (27) and (28) is used. Recall the fading memory space C_Δ in (2) with norm $\|\cdot\|$ in (3) and the product space $C_\Delta^4 \times \mathbb{R}$ with norm $|\!|\!|\cdot|\!|\!|$ in (30). The state space X is the nonnegative cone of $C_\Delta^4 \times \mathbb{R}$.

LEMMA A.1. *Let* $3\Delta < \mu_{em}$ *and* $K > 0$*. Let* D *be the set of initial data in the state space* X *defined by the inequalities* $\|S_{m0}\| < K$*,* $\|S_{s0}\| < K$*,* $\|I_{s0}\| < K$*,*

$\|I_{c0}\| < K$, and $I_{m0} < K$. Then Ψ is Lipschitz continuous on D and thus locally Lipschitz continuous on X.

Proof. We focus our attention on the most difficult term, the integral term on the right-hand side of the I_m equation in Table 1. After a substitution and employing the notation involving the subscript t, this term becomes

$$\int_{-\infty}^{0}\left(\frac{\beta_{cm}S_{m_t}(r)I_{c_t}(r)}{I_{s_t}(r)+S_{s_t}(r)+N_c}+\frac{\beta_{sm}S_{m_t}(r)I_{s_t}(r)}{I_{s_t}(r)+S_{s_t}(r)+N_c}\right)e^{\mu_{em}r}f(-r)\,dr=\mathcal{H}(\sigma_t).$$

This expression acts on the state σ_t defined by (27) and indicates how to define a functional $\mathcal{H}: X\to\mathbb{R}$ that needs to be locally Lipschitz, namely,

$$\mathcal{H}(\sigma)=\int_{-\infty}^{0}H(S_s(r),S_m(r),I_c(r),I_s(r))e^{\mu_{em}r}f(-r)\,dr. \tag{39}$$

Here $\sigma=(S_s(\cdot),S_m(\cdot),I_c(\cdot),I_s(\cdot),I_m)\in X$, and $H:\mathbb{R}^4_+\to\mathbb{R}$ is defined as

$$\begin{aligned} H(S_s,S_m,I_c,I_s)&=\beta_{cm}\tilde{H}(S_m,I_c,I_s+S_s)+\beta_{sm}\tilde{H}(S_m,I_s,I_s+S_s),\\ \tilde{H}(z)&=\frac{z_1z_2}{z_3+N_c},\qquad z=(z_1,z_2,z_3)\in\mathbb{R}^3_+.\end{aligned} \tag{40}$$

For $z,\tilde{z}\in\mathbb{R}^3_+$,

$$\begin{aligned}\tilde{H}(z)-\tilde{H}(\tilde{z})&=\frac{z_1z_2-\tilde{z}_1\tilde{z}_2}{z_3+N_c}+\tilde{z}_1\tilde{z}_2\Big(\frac{1}{z_3+N_c}-\frac{1}{\tilde{z}_3+N_c}\Big)\\ &=\frac{(z_1-\tilde{z}_1)z_2+\tilde{z}_1(z_2-\tilde{z}_2)}{z_3+N_c}+\frac{\tilde{z}_1\tilde{z}_2(\tilde{z}_3-z_3)}{(z_3+N_c)(\tilde{z}_3+N_c)}.\end{aligned}$$

Let $|z|_\infty=\max|z_j|$ and $|z|_1=\sum|z_j|$ be the maximum and sum norms on a Euclidean vector space. For $z,\tilde{z}\in\mathbb{R}^3_+$,

$$|\tilde{H}(z)-\tilde{H}(\tilde{z})|\le\max\Big\{\frac{|z|_\infty}{N_c},\frac{|\tilde{z}|_\infty}{N_c},\frac{|z|^2_\infty}{N_c^2},\frac{|\tilde{z}|^2_\infty}{N_c^2}\Big\}|z-\tilde{z}|_1.$$

By (40), there exists some constant $c>0$ such that, for all $y,\tilde{y}\in\mathbb{R}^4_+$,

$$|H(y)-H(\tilde{y})|\le c\max\Big\{|y|_\infty,|\tilde{y}|_\infty,|y|^2_\infty,|\tilde{y}|^2_\infty\Big\}|y-\tilde{y}|_\infty.$$

Let

$$\begin{aligned}\sigma&=(S_s(\cdot),S_m(\cdot),I_c(\cdot),I_s(\cdot),I_m)\in X,\\ y(r)&=(S_s(r),S_m(r),I_c(r),I_s(r))\in\mathbb{R}^4_+,\qquad r\ge0,\end{aligned}$$

and let $\tilde{\sigma}\in X$ and $\tilde{y}\in\mathbb{R}^4_+$ be analogous. Further let $K>0$ and $\|\sigma\|,\|\tilde{\sigma}\|\le K$ with $\|\cdot\|$ defined in (30). Since $\|\sigma\|=\sup_{s\le0}|\sigma(s)|_\infty e^{\Delta s}$, $|y(r)|_\infty\le\|\sigma\|e^{-\Delta r}$ and

$$\begin{aligned}|H(y(r))-H(\tilde{y}(r))|&\le c\max\Big\{\|\sigma\|,\|\tilde{\sigma}\|,\|\sigma\|^2_\infty,\|\tilde{\sigma}\|^2_\infty\Big\}e^{-2\Delta r}\|\sigma-\tilde{\sigma}\|_\infty e^{-\Delta r}\\ &\le c\max\big\{K,K^2\big\}\,\|\sigma-\tilde{\sigma}\|_\infty e^{-3\Delta r}.\end{aligned}$$

By (39),

$$|\mathcal{H}(\sigma)-\mathcal{H}(\tilde{\sigma})|\le c\max\big\{K,K^2\big\}\hat{f}(\mu_{em}-3\Delta)\|\sigma-\tilde{\sigma}\|.$$

This confirms that $\mathcal{H}$ is Lipschitz continuous on D, provided $\hat{f}(\mu_{em} - 3\Delta) < \infty$, which is true because of the assumption $0 < 3\Delta < \mu_{em}$.

Verifying that the other terms on the right-hand sides of the system in Table 1 satisfy Lipschitz conditions is similar, but simpler. For the terms involving the contact rates, one can make use of the function H using ideas similar to those just presented. For the delay term $e^{-\mu_l \tau} b_m(S_m(t-\tau))$, a new functional $\mathcal{J} : C_\Delta^4 \times \mathbb{R} \to \mathbb{R}$ can be defined as $\mathcal{J}(S) = e^{-\mu_l \tau} b_m(S_m(-\tau))$. Estimation of $|\mathcal{J}(\sigma) - \mathcal{J}(\tilde{\sigma})|$ using local Lipschitz continuity of b_m gives rise to the quantity $|S_m(-\tau) - \tilde{S}_m(-\tau)|$, which is bounded by $e^{\Delta\tau}\|S_m - \tilde{S}_m\|$ and therefore by a constant times $\|\sigma - \tilde{\sigma}\|$. ∎

LEMMA A.2. *Let* $\Delta > 0$*. For a continuous function* $g : \mathbb{R} \to \mathbb{R}$ *and* $t \in \mathbb{R}$*, we define functions* $g_t : \mathbb{R}_- \to \mathbb{R}$ *by* $g_t(\theta) = g(t+\theta)$*,* $\theta \le 0$*. Assume that* $g_0 \in C_\Delta$*. Then, for all* $t \ge 0$*,* $g_t \in C_\Delta$*,*

$$\|g_t\| \le \max\Big\{\|g_0\| e^{-\Delta t}, \sup_{0 \le r \le t} |g(r)|\Big\}. \tag{41}$$

If, in addition, g *is bounded on* $\mathbb{R}_+$*,*

$$\|g_t\| \le \max\Big\{\|g_0\|, \sup_{r \ge 0} |g(r)|\Big\}, \qquad t \ge 0,$$

and

$$\limsup_{t\to\infty} \|g_t\| = \limsup_{t\to\infty} |g(t)|. \tag{42}$$

Finally g_t *is a continuous function of* $t \ge 0$ *with values in* C_Δ*.*

Proof. Let $t \ge 0$. We first check that $\theta \mapsto g(\theta + t)e^{\Delta\theta} \in \mathrm{BUC}(-\infty, 0]$. Notice that

$$\sup_{\theta \le 0} |g_t(\theta) e^{\Delta\theta}| = \max\Big\{ \sup_{\theta \le -t} |g_t(\theta)e^{\Delta\theta}|, \sup_{-t < \theta \le 0} |g_t(\theta)e^{\Delta\theta}| \Big\}.$$

We have

$$\sup_{\theta \le -t} |g_t(\theta)e^{\Delta\theta}| = \sup_{\theta + t \le 0} |g_0(t+\theta)e^{\Delta(t+\theta)}| e^{-\Delta t} = \|g_0\| e^{-\Delta t}$$

and

$$\sup_{-t<\theta\le 0} |g_t(\theta)e^{\Delta\theta}| = \sup_{0<\theta+t\le t} |g(t+\theta)e^{\Delta\theta}| \le \sup_{0\le r\le t} |g(r)|,$$

so the boundedness of $\theta \mapsto g(\theta+t)e^{\Delta\theta}$ and the estimate (41) follow.

For the uniform continuity in θ, we will show that for any $\epsilon > 0$ and any $t_0 > 0$ there exists $\delta > 0$ such that

$$\begin{aligned} &\text{if } |\theta_1 - \theta_2| < \delta,\ \theta_1 \le 0 \text{ and } \theta_2 \le 0, \text{ and } t \in [0, t_0], \\ &\text{then} \qquad \big| g_t(\theta_1)e^{\Delta\theta_1} - g_t(\theta_2)e^{\Delta\theta_2} \big| < \epsilon. \end{aligned} \tag{43}$$

This is more than is needed at this point but will facilitate later arguments.

Let us fix $\epsilon > 0$ and $t_0 > 0$. Define

$$c_0 = \max\Big\{\|g_0\|, \sup_{0\le r\le t_0} |g(r|\Big\}. \tag{44}$$

By (41),

$$\|g_t\| \le c_0, \qquad 0 \le t \le t_0. \tag{45}$$

Let $t \in [0, t_0]$. We distinguish three cases.

First, suppose that $\theta_1 \le -t$ and $\theta_2 \le -t$. By assumption, $u \mapsto g_0(u)e^{\Delta u}$ is uniformly continuous on $(-\infty, 0]$, so there exists a $\delta_1 > 0$ such that

$$\big|g_0(u_1)e^{\Delta u_1} - g_0(u_2)e^{\Delta u_2}\big| < \frac{\epsilon}{2}$$

whenever $|u_1 - u_2| < \delta_1$, $u_1 \le 0$, $u_2 \le 0$. Then, if $|\theta_1 - \theta_2| < \delta_1$,

$$\big|g_t(\theta_1)e^{\Delta\theta_1} - g_t(\theta_2)e^{\Delta\theta_2}\big| = \Big|g_0(\theta_1 + t)e^{\Delta(t+\theta_1)} - g_0(\theta_2 + t)e^{\Delta(t+\theta_2)}\Big| e^{-\Delta t} < \frac{\epsilon}{2}.$$

Second, suppose that $0 \ge \theta_1 \ge -t$ and $0 \ge \theta_2 \ge -t$, or equivalently $(\theta_1 + t) \in [0, t]$ and $(\theta_2 + t) \in [0, t]$. Since g is uniformly continuous on $[0, t_0]$, there exists some $\delta_2 > 0$ such that $|g(u_1) - g(u_2)| < \epsilon/2$ whenever $u_1, u_2 \in [0, t_0]$, $|u_1 - u_2| < \delta_2$. Further, it can be arranged that $e^{\Delta\delta_2} - 1 < \epsilon/(2c_0 + 1)$. If $|\theta_1 - \theta_2| < \delta_2$, then $|(\theta_1 + t) - (\theta_2 + t)| < \delta$ and, by (45),

$$\begin{aligned}
&\big|g_t(\theta_1)e^{\Delta\theta_1} - g_t(\theta_2)e^{\Delta\theta_2}\big| \\
&\le \big|g(\theta_1 + t)e^{\Delta\theta_1} - g(\theta_2 + t)e^{\Delta\theta_1}\big| + \big|g(\theta_2 + t)e^{\Delta\theta_1} - g(\theta_2 + t)e^{\Delta\theta_2}\big| \\
&\le \big|g(\theta_1 + t) - g(\theta_2 + t)\big| + \|g_t\|(e^{\Delta|\theta_1 - \theta_2|} - 1) < \frac{\epsilon}{2} + \frac{\epsilon}{2} = \epsilon.
\end{aligned}$$

Third, suppose that $\theta_1 \le -t < \theta_2$ (the case $\theta_1 > -t \ge \theta_2$ is the same). Then $\theta_1 + t < 0$ and $\theta_2 + t \in [0, t]$. Combining the triangle inequality with the arguments of the first two cases, we obtain

$$\begin{aligned}
&\big|g_t(\theta_1)e^{\Delta\theta_1} - g_t(\theta_2)e^{\Delta\theta_2}\big| \\
&\le \big|g_t(\theta_1)e^{\Delta\theta_1} - g_t(-t)e^{-\Delta t}\big| + \big|g_t(-t)e^{-\Delta t} - g_t(\theta_2)e^{\Delta\theta_2}\big| < \epsilon
\end{aligned}$$

whenever $|\theta_1 + t| < \delta_1$ and $|\theta_2 + t| < \delta_2$. Choose $\delta := \min\{\delta_1, \delta_2\}$. Observe that $|\theta_1 + t| = -(\theta_1 + t) < \theta_2 - \theta_1$ and $|\theta_2 + t| = \theta_2 + t < \theta_2 - \theta_1$. Hence

$$\big|g_t(\theta_1)e^{\Delta\theta_1} - g_t(\theta_2)e^{\Delta\theta_2}\big| < \epsilon$$

if $|\theta_2 - \theta_1| < \delta$. This completes the proof of (43).

To show that g_t is a continuous function of $t \ge 0$ with values in C_Δ, let $\epsilon > 0$, $t_0 > 0$, and $0 \le r < t \le t_0$. By (43), there exists $\delta_1 > 0$ such that, for $\theta \le 0$ (then also $r - t + \theta \le 0$),

$$\Big|g_t(r - t + \theta)e^{\Delta(r-t+\theta)} - g_t(\theta)e^{\Delta\theta}\Big| < \frac{\epsilon e^{-\Delta t_0}}{2} \le \frac{\epsilon e^{\Delta(r-t)}}{2}$$

whenever $|(r - t + \theta) - \theta| = |r - t| < \delta_1$. Therefore it is also true that if $|r - t| < \delta_1$,

$$\Big|g(r + \theta)e^{\Delta\theta} - g(t + \theta)e^{\Delta(t-r+\theta)}\Big| < \epsilon/2.$$

Furthermore, there is a $\delta_2 > 0$ such that, with c_0 from (44),

$$c_0\big(e^{\Delta\delta_2} - 1\big) < \frac{\epsilon}{2}.$$

For $|r-t|<\delta_1$, the triangle inequality gives

$$\begin{aligned}\big|(g(r+\theta)-g(t+\theta))e^{\Delta\theta}\big| &\le \Big|g(r+\theta)e^{\Delta\theta}-g(t+\theta)e^{\Delta(t-r+\theta)}\Big|\\ &\quad+\Big|g(t+\theta)e^{\Delta(t-r+\theta)}-g(t+\theta)e^{\Delta\theta}\Big|\\ &< \frac{\epsilon}{2}+\big|g(t+\theta)e^{\Delta\theta}\big|\big(e^{\Delta(t-r)}-1\big).\end{aligned}$$

If $|r-t|<\delta:=\min\{\delta_1,\delta_2\}$, taking the supremum over all $\theta\le 0$ and using (45) yields

$$\|g_r-g_t\|\le\frac{\epsilon}{2}+\|g_t\|(e^{\Delta(t-r)}-1)\le\frac{\epsilon}{2}+c_0\big(e^{\Delta\delta_2}-1\big)<\epsilon.$$

This shows that g_t is a continuous function of $t\ge 0$.

To show (42), we define $g^t(r)=g(t+r)$ for $t,r\in\mathbb{R}$. Then $g_{t+s}=(g^t)_s$ for $t,s\ge 0$. Notice that $(g^t)_0=g_t$. By (41),

$$\|g_{t+s}\|\le\max\Big\{e^{-\Delta s}\|(g^t)_0\|,\sup_{0\le r\le s}|g^t(r)|\Big\}\le\max\Big\{e^{-\Delta s}\|g_t\|,\sup_{r\ge t}|g(r)|\Big\}.$$

So, for every $t\ge 0$,

$$\limsup_{s\to\infty}\|g_s\|=\limsup_{s\to\infty}\|g_{t+s}\|\le\sup_{r\ge t}|g(r)|.$$

We take the limit as $t\to\infty$ and obtain (42) with $\le$ instead of $=$. Equality follows because $\|g_t\|\ge|g(t)|$. ▯

Lemma A.3. *The vector space* $\mathrm{BC}(\mathbb{R}_-)$ *of bounded continuous functions on* $\mathbb{R}_-=(-\infty,0]$ *is a subspace of* C_Δ*. Furthermore, every equicontinuous and equibounded subset of* $\mathrm{BC}(\mathbb{R}_-)$ *has compact closure in* C_Δ*.*

Recall that $\mathcal{M}\subseteq\mathrm{BC}(\mathbb{R}_-)$ is called equibounded if $\bigcup_{f\in\mathcal{M}}f(\mathbb{R}_+)$ is a bounded subset of $\mathbb{R}$. The set $\mathcal{M}\subseteq\mathrm{BC}(\mathbb{R}_-)$ is called equicontinuous if for each $\epsilon>0$ and $\theta\le 0$ there exists some $\delta>0$ such that $|f(\theta)-f(\eta)|<\epsilon$ whenever $f\in\mathcal{M}$, $\eta\le 0$, and $|\theta-\eta|<\delta$.

Proof. Let $g\in\mathrm{BC}(\mathbb{R}_-)$ and $|g(\theta)|\le c$ for all $\theta\le 0$. Then $g(\theta)e^{\Delta\theta}$ is a bounded function of $\theta\le 0$.

Let $\eta,\theta\le 0$. By the triangle inequality,

$$|g(\theta)e^{\Delta\theta}-g(\eta)e^{\Delta\eta}|\le|g(\theta)-g(\eta)|e^{\Delta\theta}+c\Delta|\theta-\eta|. \tag{46}$$

Let $\epsilon>0$. Choose $L>0$ such that $2ce^{-\Delta L}<\epsilon/4$. Then g is uniformly continuous on $[-L-1,0]$. Choose $\delta\in(0,1]$ such that $|g(\theta)-g(\eta)|<\epsilon/4$ whenever $\theta,\eta\in[-L-1,0]$, $|\theta-\eta|<\delta$. Furthermore, choose δ small enough that $c\Delta\delta<\epsilon/4$.

Now let $\theta,\eta\le 0$ and $|\theta-\eta|<\delta$.

Case 1. $\theta\ge -L$. Then $\eta\ge -L-1$ and

$$|g(\theta)e^{\Delta\theta}-g(\eta)e^{\Delta\eta}|\le\frac{\epsilon}{4}+c\Delta\delta<\epsilon.$$

Case 2. $\theta\le -L$. Then

$$|g(\theta)e^{\Delta\theta}-g(\eta)e^{\Delta\eta}|\le 2ce^{-\Delta L}+c\Delta\delta<\epsilon.$$

The two cases show that $g(\theta)e^{\Delta\theta}$ is a uniformly continuous function of $\theta\le 0$.

Now let $\mathcal{M}$ be an equibounded and equicontinuous subset of $\mathrm{BC}(\mathbb{R}_-)$, and let (g_k) be a sequence in $\mathcal{M}$. Let $c > 0$ be such that $|g_k(s)| \le c$ for all $k \in \mathbb{N}$ and $s \le 0$. By the Arzelà–Ascoli theorem [8, Thm. 8.5], there exists a subsequence (h_j) of (g_k) that converges uniformly on every set $[-L, 0]$, $L > 0$. Set $g(\theta) = \lim_{j\to\infty} h_j(\theta)$, $\theta \le 0$. Then $g \in\mathrm{BC}(\mathbb{R}_-)$ and $|g(s)| \le c$ for all $s \le 0$. Let $L > 0$. Then

$$\begin{aligned}\|h_j - g\| =& \sup_{s\le 0} |h_j(s) - g(s)|e^{\Delta s}\\ \le& \sup_{s\le -L} |h_j(s) - g(s)|e^{\Delta s} + \sup_{-L\le s\le 0} |h_j(s) - g(s)|e^{\Delta s}\\ \le& 2ce^{-\Delta L} + \sup_{-L\le s\le 0} |h_j(s) - g(s)|.\end{aligned}$$

Since $h_j(s) \to g(s)$ uniformly for $s \in [-L, 0]$,

$$\limsup_{j\to\infty} \|h_j - g\| \le 2ce^{-\Delta L}.$$

This holds for any $L > 0$, and thus $\limsup_{j\to\infty} \|h_j - g\| = 0$. $\square$

Proof of Proposition 5.2. Let $3\Delta < \mu_{em}$.

Step 1. *The semiflow T is well-defined and time continuous.*

By Proposition 2.2, solutions with initial data in X exist for all times, and are bounded. We show that the state σ_t of the solution at time t evolves in the space $C^4_\Delta \times \mathbb{R}$ and is a continuous function of $t \ge 0$. Obviously $I_m(t) \in \mathbb{R}$ and is a continuous function of $t \ge 0$. The other four components of the state are in C_Δ and continuous functions of $t \ge 0$ by Lemma A.2. So, for every $t \ge 0$, the definition $T(t)\sigma_0 = \sigma_t$ defines a map $T(t)$ on X such that $T(t)\sigma_0$ is a continuous function of t. The semiflow property $T(t) \circ T(s) = T(t + s)$, $t, s \ge 0$, follows from the uniqueness and the translation invariance of the solutions to the model equations in Table 1. In this appendix, we write $T(t)\sigma_0$ instead of $T(t, \sigma_0)$, as we did in the main body of the paper.

Step 2: *The semiflow T is continuous.*

We show that $T(t)$ is state-continuous, uniformly in finite time; that is, for every $\sigma_0 \in X$, $u \ge 0$, $\epsilon > 0$, there exists some $\delta > 0$ such that $\|T(t)\sigma_0 - T(t)\widehat{\sigma}_0\| < \epsilon$ whenever $t \in [0, u]$ and $\|\sigma_0 - \widehat{\sigma}_0\| < \delta$. Suppose the contrary of this claim holds. Then there is a $\sigma_0 \in X$, $u > 0$, $\epsilon > 0$ such that for each $n \in \mathbb{N}$, there are $t_n \in [0, u]$ and $\sigma^n_0 \in X$ with $\|T(t_n)\sigma^n_0 - T(t_n)\sigma_0\| \ge \epsilon$ and $\|\sigma^n_0 - \sigma_0\| < \frac{1}{n}$. Fix such σ_0, u, ϵ, and sequence (σ^n_0). By definition of T, there are solutions $\sigma^n : \mathbb{R}_+ \to \mathbb{R}^5_+$ of (38) such that $T(t)\sigma^n_0 = \sigma^n_t$. By Proposition 2.3, for all $t \ge 0$,

$$\sigma^n(t) \le K := \max\Big\{\breve{S}_m, \breve{S}_s, \sup_{\theta\in[-\tau,0],n\in\mathbb{N}} N^n_m(\theta), \sup_{n\in\mathbb{N}} N^n_s(0)\Big\} < \infty.$$

That K is finite follows from $\|\sigma^n_0 - \sigma_0\| < \frac{1}{n}$. Thus the set

$$Q := \big\{\sigma^n_t \in X;\ n \in \mathbb{N}, t \in [0, u]\big\}$$

is bounded by some constant C^Q. It has been established in Lemma A.1 that if $3\Delta < \mu_{em}$, then Ψ in (38) is locally Lipschitz continuous, with some Lipschitz constant C^Q_L valid in the set $X \cap B_{C^Q}$ where B_{C^Q} is the ball with center 0 and radius C^Q in $C^4_\Delta \times \mathbb{R}$. Since $Q \subseteq X \cap B_{C^Q}$, there is a uniform bound for $\frac{d}{dt}\sigma^n(t)$, because the values of derivatives are given by Ψ on the set Q. Specifically, for any $\xi \in Q$, we have

$$|\Psi(\xi)| \le |\Psi(\xi) - \Psi(\sigma_0)| + |\Psi(\sigma_0)| \le C^Q_L C^Q + |\Psi(\sigma_0)|.$$

We can apply the Arzelà–Ascoli theorem to conclude that there exists a subsequence (σ^{n_k}) that converges uniformly on $[0,u]$ to some function $\bar{y}:[0,u]\to\mathbb{R}^5_+$. Solutions of (38) satisfy the integral relation

$$\sigma^n(t)=\sigma^n(0)+\int_0^t \Psi(\sigma^n_s)\,ds.$$

Let $\overline{\sigma}:(-\infty,u]\to\mathbb{R}^5$ be the function that coincides with σ_0 on $(-\infty,0)$ and coincides with $\bar{y}$ on $[0,u]$, and let $t\in[0,u]$. The straightforward estimate

$$\|\sigma^{n_k}_t-\overline{\sigma}_t\|\le\|\sigma^{n_k}_0-\overline{\sigma}_0\|+\sup_{t\in[0,u]}|\sigma^n(t)-\bar{y}(t)|$$

shows that $\|\sigma^{n_k}_t-\overline{\sigma}_t\|\to 0$ uniformly for $t\in[0,u]$, and by the local Lipschitz continuity of Ψ the limit $\overline{\sigma}_t$ satisfies the integral relation above. From the uniqueness of solutions we obtain that $\overline{\sigma}_t\equiv\sigma_t=T(t)\sigma_0$. The convergence $\|T(t)\sigma^{n_k}_0-T(t)\sigma_0\|\to 0$, which is uniform for $t\in[0,u]$, contradicts $\|T(t_n)\sigma^n_0-T(t_n)\sigma_0\|\ge\epsilon$, which was supposed to hold for all $n\in N$. Thus we obtain that T is state-continuous, uniformly in finite time.

Time continuity and state continuity uniformly in finite time imply that T is a continuous semiflow in the product topology of $\mathbb{R}_+\times X$ (see Lemma 1.34 in [13]).

Step 3: *The semiflow T is asymptotically smooth.*

It is sufficient to check that for any bounded subset U of X for which $T(t)U\subseteq U$ for all $t\ge 0$, there exists a compact subset $\mathcal{M}$ of X such that $d(T(t)U,\mathcal{M})\to 0$ as $t\to\infty$. Here $d(y,\mathcal{M})=\inf_{x\in\mathcal{M}}\{\|y-x\|; x\in\mathcal{M}\}$ is the distance from the point y to the set $\mathcal{M}$, and $d(U,\mathcal{M})=\sup_{y\in U}d(y,\mathcal{M})$ is the distance from the set U to the set $\mathcal{M}$. Notice the asymmetry between U and $\mathcal{M}$.

So let U be a bounded subset of X such that $T(t)U\subseteq U$ for all $t\ge 0$. Then there exists some $A>0$ that depends only on U such that for each component ϕ of (S_s,S_m,I_c,I_s,I_m) of a solution starting in U we have $0\le\phi(t)\le A$ for all $t\ge 0$. Furthermore, $\|\phi_t\|\le A$ for all $t\ge 0$ and each component $\phi\in\{S_s,S_m,I_c,I_s\}$.

Following [2], we define sets $\mathcal{M}_1,\mathcal{M}_2,\mathcal{M}_3,\mathcal{M}_4$ related to S_s,S_m,I_c,I_s, respectively, by

$$\mathcal{M}_i=\bigl\{\phi\in\mathrm{BC}(\mathbb{R}_-);\ 0\le\phi(\theta)\le A, |\phi(\theta)-\phi(\eta)|\le\omega_i|\theta-\eta|\bigr\},\quad i=1,2,3,4,$$

with the Lipschitz constants ω_i still to be determined. Each $\mathcal{M}_i$ is a subset of $\mathrm{BC}(\mathbb{R}_-)$ and equibounded and equicontinuous and thus a compact subset of C_Δ by Lemma A.3.

We set $\mathcal{M}=\mathcal{M}_1\times\cdots\times\mathcal{M}_4\times[0,A]$ with properly chosen constants ω_i. Then $\mathcal{M}$ is a compact subset of X. We show that $d(T(t)U,\mathcal{M})\to 0$ by proving for each component $\phi\in\{S_s,S_m,I_c,I_s\}$, of a solution starting in U, that $d(\phi_t,\mathcal{M}_j)\to 0$ (with appropriate j), with convergence holding uniformly for initial data in U.

Recall that $S_s(t)\le A$, $S_m(t)\le A$ and similar inequalities hold for the other components as well for all $t\ge 0$. Furthermore, $\|\phi_t\|\le A$ for all $t\ge 0$ and $\phi\in\{S_s,S_m,I_c,I_s\}$.

Then we find the Lipschitz constants ω_i as bounds for the derivatives of S_s, S_m, I_c, I_s for $t\ge 0$. For example, from Table 1 we can find that

$$|S_s'(t)|\le\max_{y\in[0,A]}b(y)+\frac{\beta_{ms}A^2}{N_c}+\gamma A+\mu_s A,\qquad t\ge 0,$$

and we define ω_1 as the right-hand side of this inequality. Notice that ω_1 can be chosen uniformly for all solutions starting in U.

We find $\omega_2, \omega_3, \omega_4$ analogously from the equations for S_m, I_c, I_s, respectively.

Let ϕ be the jth component of $(S_s, S_m, I_c, I_s, I_m)$ for a solution starting in U, $j = 1, \dots, 4$. Following [10], we let

$$\psi^t(\theta) := \left\{ \begin{array}{cc} \phi(t+\theta), & -t \le \theta \le 0 \\ \phi(0), & \theta \le -t \end{array} \right\}, \quad t \ge 0.$$

Then $\psi^t \in \mathcal{M}_j$, and

$$\begin{aligned} d(\phi_t, \mathcal{M}_j) &\le d(\phi_t, \psi^t) = \sup_{\theta \le 0} |\phi(t+\theta) - \psi^t(\theta)| e^{\Delta\theta} \\ &= \sup_{\theta \le -t} |\phi(t+\theta) - \phi(0)| e^{\Delta\theta} \\ &\le \sup_{\theta \le -t} |\phi(t+\theta)| e^{\Delta\theta} + \sup_{\theta \le -t} |\phi(0)| e^{\Delta\theta} \\ &\le \|\phi_t\| e^{-\Delta t} + \phi(0) e^{-\Delta t} \le 2A e^{-\Delta t}. \end{aligned}$$

Hence $d(\phi_t, \mathcal{M}_j) \to 0$, with the convergence being uniform for all solutions starting in U.

As for I_m, $I_m(t) \in [0, A]$ for all $t \ge 0$ and all solutions starting in U.

Thus $d(T(t)U, \mathcal{M}) \to 0$ as $t \to \infty$, and T has been shown to be asymptotically smooth.

Step 4: *The semiflow T is eventually bounded on bounded sets.*

We will prove a stronger result: for every bounded set U of initial data in X there exists some $\bar{A} > 0$ such that $\|T(t)x\| \le \bar{A}$ for all $t \ge 0$, $x \in U$.

Let U be a bounded subset of X. Then there exists some $A > 0$ that depends only on U such that, for each component ϕ of $(S_s, S_m, I_c, I_s, I_m)$ of a solution starting in U, we have $0 \le \phi(0) \le A$. Furthermore $\|\phi_0\| \le A$ for each component $\phi \in \{S_s, S_m, I_c, I_s\}$.

By Proposition 2.3, there exists some $\tilde{A} > 0$ which also depends only on U such that, for each component ϕ of $(S_s, S_m, I_c, I_s, I_m)$ of a solution starting in U, we have $0 \le \phi(t) \le \tilde{A}$ for all $t \ge 0$. By Lemma A.2, for each component $\phi \in \{S_s, S_m, I_c, I_s\}$, $\phi_t \in C_\Delta$ and $\|\phi_t\| \le \max\{A, \tilde{A}\} =: \bar{A}$ for all $t \ge 0$. Then $\|T(t)x\| \le \bar{A}$ for all $x \in U$.

Finally, we combine Proposition 2.3 and Lemma A.2 and obtain that T is point-dissipative. Existence of a compact attractor of bounded sets now follows from [5, Thm. 2.4.6], [13, Thm. 2.33].

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