PERIODIC SYSTEMS OF DELAY DIFFERENTIAL EQUATIONS AND AVIAN INFLUENZA DYNAMICS

X.-S. Wang and J. Wu
<div align="right">UDC 517.929</div>

ABSTRACT. Modelling the spread of avian influenza by migratory birds between the winter refuge ground and the summer breeding site gives rise to a periodic system of delay differential equations exhibiting both the cooperative dynamics (transition between patches) and the predator-prey interaction (disease transmission within a patch). Such a system has two important basic reproductive ratios, each of which being the spectral radius of a monodromy operator associated with the linearized subsystem (at a certain trivial equilibrium): the (ecological) reproduction ratio R_0^c for the birds to survive in the competition between birth and natural death, and the (epidemiological) reproduction ratio R_0^p for the disease to persist. We calculate these two ratios by our recently developed finite-dimensional reduction and asymptotic techniques, and we show how these two ratios characterize the nonlinear dynamics of the full system.

1. Introduction

Periodic systems of delay differential equations arise naturally from modelling the spread of zoonotic diseases such as avian influenza, West Nile virus, and Lyme disease, which are influenced by strong seasonality in temperate climates. For example, describing the spatiotemporal distributions of migrant birds requires a meta-population (patchy) model involving population densities in different (breeding, winter feeding, and stopovers) patches along a particular migration route, where time delays are needed to account for the flight times between patches and periodic coefficients must be used to reflect the seasonality of various biological activities such as birth and migration [2] and [5]. A periodic DDE system was also proposed in [14] for Lyme disease dynamics as a consequence of the interaction of a spirochete with multiple vertebrate hosts and a vector with a two-year life cycle with strong seasonality, where the state variables include tick population sizes at all stages and time lags correspond to the development time of different stages of the vector.

The threshold dynamics of the spatial dynamics model of migrant birds was discussed in [2] and [5]. The threshold is linked to the spectral radius of the monodromy operator associated with the linearized system (at the trivial equilibrium) via a standard application of the Krein–Rutman theorem and some results on discrete monotone dynamical systems. Extensions of this threshold dynamics were also obtained in [1] for the periodic epidemic model that involves the interaction of migrant birds and domestic poultry and the stratification of the bird population by the disease status (susceptible/infected). For the sake of applications, it is very important to develop an approach to calculate/estimate the aforementioned spectral radius when model coefficients are close to step functions with values equal to zero outside corresponding biological activities (for example, the birth rate is zero outside the breeding season, and migration rates are zero outside corresponding migration seasons). This motivated the finite dimension reduction and asymptotic analysis in [11] and [12] for the corresponding bird migration population model. It remains to see how these techniques are related to the approach developed in [7] and [8] that transforms the calculation of the spectral radius of the monodromy operator to a linear ODE boundary value problem.

The purpose of this paper is to show how these finite dimension reduction and asymptotic analysis techniques can be pushed further for the corresponding epidemic models. More precisely, we aim to find an asymptotic formula for the dynamic threshold of a simple two-patch disease model with the patch connected by bird migration.

2. The Model

To state the model, we let S_w and S_b denote the number of susceptible birds at the winter refuge site and the summer breeding site respectively. Here and in what follows, the subscript w indicates a variable associated with the winter refuge site, and the subscript b, for the breeding site. Also, we let I_w and I_b be the number of infected birds at the winter refuge site and summer breeding site respectively. We consider the following periodic system of delay differential equations:

$$S'_w(t) = -[\mu^s_w + m_{wb}(t)]S_w(t) + \alpha^s_{bw}m_{bw}(t - \tau_{bw})S_b(t - \tau_{bw}) - \frac{\beta_w S_w(t)I_w(t)}{S_w(t) + I_w(t)}; \qquad (2.1a)$$

$$I'_w(t) = -[\mu^i_w + m_{wb}(t)]I_w(t) + \alpha^i_{bw}m_{bw}(t - \tau_{bw})I_b(t - \tau_{bw}) + \frac{\beta_w S_w(t)I_w(t)}{S_w(t) + I_w(t)}; \qquad (2.1b)$$

$$S'_b(t) = -[\mu^s_b + m_{bw}(t)]S_b(t) + \alpha^s_{wb}m_{wb}(t - \tau_{wb})S_w(t - \tau_{wb}) - \frac{\beta_b S_b(t)I_b(t)}{S_b(t) + I_b(t)} \qquad (2.1c)$$

$$+ b(t)S_b(t)\left[1 - \frac{S_b(t)}{K}\right];$$

$$I'_b(t) = -[\mu^i_b + m_{bw}(t)]I_b(t) + \alpha^i_{wb}m_{wb}(t - \tau_{wb})I_w(t - \tau_{wb}) + \frac{\beta_b S_b(t)I_b(t)}{S_b(t) + I_b(t)}, \qquad (2.1d)$$

where μ^s_w and μ^s_b are death rates of the susceptible birds, and μ^i_w and μ^i_b are death rates of the infected birds in the respective winter or breeding site. The function m_{bw} (or m_{wb}) is the migration rate from the breeding (or winter) site to the winter (breeding) site. We use constants τ_{bw} and τ_{wb} to denote delays due to migration, namely, the durations for the birds to fly from one site (patch) to another. The coefficients α^s_{bw} and α^s_{wb} are survival probabilities of susceptible birds during migrations, while the constants α^i_{bw} and α^i_{wb} are survival probabilities of the infected birds during migrations. We assume that only the susceptible birds can reproduce and their offsprings are also susceptible, and we assume that the reproduction is described by a logistic function with $b(t)$ being the birth rate and K the capacity. The constants β_w and β_b are disease transmission rates at the winter and the breeding site, respectively, and we use the standard incidence function and assume no infected birds can recover from the infection.

3. Positivity and Boundedness

We assume that all of the parameters in model (2.1) are positive constants or nonnegative and nontrivial periodic functions with the same period T. The appropriate initial conditions for this delay system are

$$S^0_w(\theta) \geq 0 \quad \text{and} \quad I^0_w(\theta) \geq 0 \ \text{ for any } \ \theta \in [-\tau_{wb}, 0];$$
$$S^0_b(\theta) \geq 0 \quad \text{and} \quad I^0_b(\theta) \geq 0 \ \text{ for any } \ \theta \in [-\tau_{bw}, 0]. \qquad (3.1)$$

The corresponding state space is defined as

$$Y := C[-\tau_{wb}, 0] \times C[-\tau_{wb}, 0] \times C[-\tau_{bw}, 0] \times C[-\tau_{bw}, 0] \qquad (3.2)$$

equipped with the usual maximum norm. As in [5], we introduce the subspace

$$M := \{(S^0_w, I^0_w, S^0_b, I^0_b) \in Y : \quad \text{and} \quad S^0_w(0) = I^0_w(0) = S^0_b(0) = I^0_b(0) = 0, \qquad (3.3)$$

$$m_{wb}(\theta)S^0_w(\theta) = m_{wb}(\theta)I^0_w(\theta) = 0 \ \text{ for any } \ \theta \in [-\tau_{wb}, 0], \quad \text{and} \qquad (3.4)$$

$$m_{bw}(\theta)S^0_b(\theta) = m_{bw}(\theta)I^0_b(\theta) = 0 \ \text{ for any } \ \theta \in [-\tau_{bw}, 0]\}. \qquad (3.5)$$

Proposition 3.1. *The solutions of system* (2.1) *subject to the initial conditions are nonnegative for any $t \geq 0$. Moreover, if $(S_w^0, I_w^0, S_b^0, I_b^0) \in Y \setminus M$, then either $(S_w(t), S_b(t)) > 0$ for all $t > t^*$ or $(I_w(t), I_b(t)) > 0$ for all $t > t^*$, where $t^* := \tau_{wb} + \tau_{bw} + T$. Specifically, if $S_w^0(0) > 0$ or $S_b^0(0) > 0$ or $m_{wb}(\theta)S_w^0(\theta) > 0$ for some $\theta \in [-\tau_{wb}, 0]$ or $m_{bw}(\theta)S_b^0(\theta) > 0$ for some $\theta \in [-\tau_{bw}, 0]$, then $(S_w(t), S_b(t)) > 0$ for all $t > t^*$. Similarly, if $I_w^0(0) > 0$ or $I_b^0(0) > 0$ or $m_{wb}(\theta)I_w^0(\theta) > 0$ for some $\theta \in [-\tau_{wb}, 0]$ or $m_{bw}(\theta)I_b^0(\theta) > 0$ for some $\theta \in [-\tau_{bw}, 0]$, then $(I_w(t), I_b(t)) > 0$ for all $t > t^*$.*

Proof. The nonnegativity follows from a standard argument as in [9, Theorem 5.2.1]. The second statement can be obtained by a similar argument as in [5, Proposition 2.1] or [1, Theorem 3.2]. $\square$

Using the argument in [5, Proposition 2.2], we can also show the following result.

Proposition 3.2. *Let $N(t)$ be the total bird population of the system* (2.1) *with initial conditions* (3.1). *Then*

$$\limsup_{t \to \infty} N(t) \leq B/\mu,$$

where $B := \frac{K^2}{4} \max_{0 \leq t \leq T} b(t) < \infty$ and $\mu := \min\{\mu_w^s, \mu_w^i, \mu_b^s, \mu_b^i\} > 0$.

4. Assumption for Migration

As in [11], we will assume that the migratory activity is insignificant during the summer breeding season and the winter refuge time; the population left in the winter refuge site (resp. summer breeding site) after spring (resp. autumn) migration is comparably negligible; and breeding activity does not occur during autumn and winter seasons.

Due to seasonality of bird migration, it is natural to assume that all the nonconstant coefficients in system (2.1) are periodic functions with the period $T = 365$ days. Let $t_0 = nT$, for an arbitrarily fixed $n \in \mathbb{N}$. We shift the time so that t_0 is the starting date when the birds begin to fly to the summer breeding site in a particular year. Denote by t_1 the time when the birds in the winter patch stop their spring migration to the summer breeding site. Assume the birds start their autumn migration at the time t_2 and autumn migration ends at the time t_3. Let $T_1 := t_1 - t_0$, $T_2 := t_2 - t_1$, $T_3 := t_3 - t_2$, and $T_4 := t_0 + T - t_3$ represent the durations of the aforementioned biological activities; we have $T_1 + T_2 + T_3 + T_4 = T$. It is natural to also assume $t_1 + \tau_{wb} < t_2$ and $t_3 + \tau_{bw} < t_0 + T$. In what follows, we assume that the migration rates are piecewise constants:

$$m_{wb}(t) = M_{wb}\, \mathbf{1}_{t_0 < t < t_1} \quad \text{and} \quad m_{bw}(t) = M_{bw}\, \mathbf{1}_{t_2 < t < t_3}, \tag{4.1}$$

where $\mathbf{1}$ is an indicator (characteristic) function of a variable that equals one if the variable is satisfied and zero otherwise. The second assumption we will use is that the migration rates are so large that almost all the birds leave the winter (resp. summer) patch after spring (resp. autumn) migration. Mathematically, this means that the quantity

$$\varepsilon := e^{-M_{wb}T_1} + e^{-M_{bw}T_3} \tag{4.2}$$

is sufficiently small. Finally, we assume that breeding activity does not take place during autumn and winter seasons, namely, the birth function is also a piecewise constant as follows:

$$b(t) = b_0 \cdot \mathbf{1}_{t_0 + \tau_{wb} < t < t_2}. \tag{4.3}$$

In the following sections, we will always assume the three conditions (4.1)–(4.3) are satisfied. Moreover, we will use $O(\varepsilon)$ to denote a quantity that vanishes as $\varepsilon \to 0$. Also, $O(1)$ denotes a bounded quantity.

5.   Basic Reproductive Ratios

We start with the disease-free subsystem

$$S_w'(t) = -[\mu_w^s + m_{wb}(t)]S_w(t) + \alpha_{bw}^s m_{bw}(t - \tau_{bw})S_b(t - \tau_{bw}) \tag{5.1}$$

$$S_b'(t) = -[\mu_b^s + m_{bw}(t)]S_b(t) + \alpha_{wb}^s m_{wb}(t - \tau_{wb})S_w(t - \tau_{wb})$$
$$+ b(t)S_b(t)\left[1 - S_b(t)/K\right], \tag{5.2}$$

which is exactly the same as the one studied in [11]; see also [2]. By [11, Theorem 4.1] we obtain an asymptotic formula for the (ecological) basic reproductive ratio:

$$R_0^c \sim \frac{\exp[(b_0 - \mu_b^s)(T_1 + T_2 - \tau_{wb})]}{\exp[\mu_w^s(T_3 + T_4 - \tau_{bw})]} \times \frac{\alpha_{wb}^s \alpha_{bw}^s M_{wb} M_{bw}}{(M_{wb} + b_0 + \mu_w^s - \mu_b^s)(M_{bw} + \mu_b^s - \mu_w^s)}. \tag{5.3}$$

The above subsystem is cooperative and we can apply the well-studied theory on monotone dynamic systems (cf. [15]) to obtain the following results.

Proposition 5.1. *If $R_0^c < 1$, then the zero equilibrium in system (2.1) is globally asymptotically stable.*

Proof. By [5, Theorem 3.2], if $R_0^c < 1$, then the solutions of the subsystem (5.1) will tend to zero as $t \to \infty$. Since the components $(S_w(t), S_b(t))$ of the solutions to the original system (2.1) are bounded by the solutions of the subsystem (5.1) by the comparison principle [9, Theorem 5.1.1], we obtain the global asymptotic stability of the trivial equilibrium. $\square$

Therefore, if $R_0^c < 1$, then $(S_w(t), S_b(t)) \to 0$ for the original system (2.1) by using a standard comparison argument, from which we can also conclude that $(I_w(t), I_b(t)) \to 0$ as $t \to \infty$.

We now consider the case where $R_0^c > 1$. First of all, we consider the linearized system for the infected birds at the disease-free nontrivial equilibrium $(S_w^*(t), 0, S_b^*(t), 0)$:

$$I_w'(t) = [\beta_w - \mu_w^i - m_{wb}(t)]I_w(t) + \alpha_{bw}^i m_{bw}(t - \tau_{bw})I_b(t - \tau_{bw}); \tag{5.4a}$$

$$I_b'(t) = [\beta_b - \mu_b^i - m_{bw}(t)]I_b(t) + \alpha_{wb}^i m_{wb}(t - \tau_{wb})I_w(t - \tau_{wb}). \tag{5.4b}$$

In the same way as we did in [11, Theorem 4.1], we obtain the (epidemiological) basic reproductive ratio:

$$R_0^p \sim \exp[r_b(T_1 + T_2 - \tau_{wb}) + r_w(T_3 + T_4 - \tau_{bw})]$$
$$\times \frac{\alpha_{wb}^i \alpha_{bw}^i M_{wb} M_{bw}}{(M_{wb} - r_w + r_b)(M_{bw} - r_b + r_w)}, \tag{5.5}$$

where

$$r_w := \beta_w - \mu_w^i \quad \text{and} \quad r_b := \beta_b - \mu_b^i \tag{5.6}$$

are infection rates at two patches.

Proposition 5.2. *If $R_0^c > 1$ and $R_0^p < 1$, then the disease-free nontrivial equilibrium $(S_w^*(t), 0, S_b^*(t), 0)$ in system (2.1) is globally asymptotically stable.*

Proof. By [5, Theorem 3.2], if $R_0^p < 1$, then the solutions of the subsystem (5.4) will tend to zero as $t \to \infty$. Since the components $(I_w(t), I_b(t))$ of the solutions to the original system (2.1) is bounded by the solutions of the subsystem (5.4), we conclude that $I_w(t) \to 0$ and $I_b(t) \to 0$ as $t \to \infty$. Thus, the system (2.1) is reduced to the subsystem (5.1) (in the sense of being asymptotically periodic), which possesses a global asymptotic stable periodic equilibrium $(S_w^*(t), S_b^*(t))$ by the condition $R_0^c > 1$ and [5, Theorem 3.2]. $\square$

6. Finite-Dimensional Reduction

Numerical simulation shows that if both R_0^c and R_0^p are greater than one, then the endemic equilibrium is unstable when R_0^p is small compared with R_0^c, and the trivial equilibrium is stable when R_0^p is large compared with R_0^c. This suggests that there should be another threshold value, denoted by R_0^e, that characterizes the asymptotic stability of the trivial equilibrium. In order to find an asymptotic formula for R_0^e, we need to apply the method of finite-dimension reduction introduced in [11] to reduce the DDE system (2.1) to an ODE system.

Recall that the interval of one year $[t_0, t_0 + T]$ is divided into four seasons separated by t_1, t_2, and t_3. First, we consider the spring time at the winter patch. For $t \in [t_0, t_1]$, we obtain from (2.1) and (4.1) that

$$S_w'(t) = -(\mu_w^s + M_{wb})S_w(t) - \frac{\beta_w S_w(t)I_w(t)}{S_w(t) + I_w(t)}; \tag{6.1}$$

$$I_w'(t) = -(\mu_w^i + M_{wb})I_w(t) + \frac{\beta_w S_w(t)I_w(t)}{S_w(t) + I_w(t)}. \tag{6.2}$$

Define $P_w(t) := S_w(t)/[S_w(t) + I_w(t)]$ to be the proportion of susceptible birds in the total population. A simple calculation gives

$$\frac{P_w'(t)}{P_w(t)} = \frac{S_w'(t)}{S_w(t)} - \frac{S_w'(t) + I_w'(t)}{S_w(t) + I_w(t)} = -(r_w + \mu_w^s)[1 - P_w(t)],$$

where $r_w := \beta_w - \mu_w^i$ is the infection rate defined in (5.6). This is a logistic equation, and the solution is given by

$$P_w(t) = \frac{\exp[-(r_w + \mu_w^s)(t - t_0)]}{\exp[-(r_w + \mu_w^s)(t - t_0)] - 1 + 1/P_w(t_0)}. \tag{6.3}$$

Applying this to the equations of $S_w(t)$ and $I_w(t)$ yields

$$S_w(t) = S_w(t_0) \exp[-(\mu_w^s + M_{wb} + \beta_w \bar{P}_w(t))(t - t_0)]; \tag{6.4}$$
$$I_w(t) = I_w(t_0) \exp[-(\mu_w^i + M_{wb} - \beta_w \bar{P}_w(t))(t - t_0)], \tag{6.5}$$

where

$$\begin{aligned}
\bar{P}_w(t) &:= \frac{1}{t - t_0} \int_{t_0}^{t} P_w(s)ds = \frac{1}{t - t_0} \int_{t_0}^{t} \left[1 + \frac{P_w'(s)}{(r_w + \mu_w^s)P_w(s)}\right] ds \\
&= -\frac{\log[P_w(t_0)e^{-(r_w + \mu_w^s)(t - t_0)} - P_w(t_0) + 1]}{(r_w + \mu_w^s)(t - t_0)}.
\end{aligned}$$

Note that the average $\bar{P}_w(t)$ remains in the interval $[0, 1]$ and equals 0 (resp. 1) if and only if $P(t_0)$ equals 0 (resp. 1). Now we investigate the bird population at the birth site during the spring migration. For $t \in [t_0 + \tau_{wb}, t_1 + \tau_{wb}]$, where τ_{wb} is the time lag, we obtain from (2.1), (4.1), and (4.3) that

$$S_b'(t) = \alpha_{wb}^s M_{wb} S_w(t - \tau_{wb}) - \frac{\beta_b S_b(t)I_b(t)}{S_b(t) + I_b(t)} - \mu_b^s S_b(t) + b_0 S_b(t)[1 - S_b(t)/K]; \tag{6.6}$$

$$I_b'(t) = \alpha_{wb}^s M_{wb} I_w(t - \tau_{wb}) + \frac{\beta_b S_b(t)I_b(t)}{S_b(t) + I_b(t)} - \mu_b^i I_b(t). \tag{6.7}$$

The above system is integrable even though a closed form of the solution seems impossible to obtain. Also note from (4.2) and (6.4)-(6.5) that $S_w(t_1) = O(\varepsilon)S_w(t_0)$ and $I_w(t_1) = O(\varepsilon)I_w(t_0)$ as $\varepsilon \to 0$. It then follows from (2.1) and (4.1) that

$$S_w(t) = O(\varepsilon)S_w(t_0) \quad \text{and} \quad I_w(t) = O(\varepsilon)I_w(t_0) \tag{6.8}$$

for all $t \in [t_1, t_2 + \tau_{bw}]$. As mentioned earlier, $O(\varepsilon)$ denotes a quantity that vanishes as ε defined in (4.2) tends to zero.

697

Now, we study the bird population at the birth site during the summer. For $t \in [t_1 + \tau_{wb}, t_2]$, it is readily seen from (2.1) and (4.1) that

$$S_b'(t) = -\frac{\beta_b S_b(t) I_b(t)}{S_b(t) + I_b(t)} - \mu_b^s S_b(t) + b_0 S_b(t)[1 - S_b(t)/K]; \tag{6.9}$$

$$I_b'(t) = \frac{\beta_b S_b(t) I_b(t)}{S_b(t) + I_b(t)} - \mu_b^i I_b(t). \tag{6.10}$$

The above system is also integrable.

In the next step we consider the dynamics of autumn migration. For $t \in [t_2, t_3]$, we obtain from (2.1), (4.1), and (4.3) that

$$S_b'(t) = -(\mu_b^s + M_{bw}) S_b(t) - \frac{\beta_b S_b(t) I_b(t)}{S_b(t) + I_b(t)}; \tag{6.11}$$

$$I_b'(t) = -(\mu_b^i + M_{bw}) I_b(t) + \frac{\beta_b S_b(t) I_b(t)}{S_b(t) + I_b(t)}. \tag{6.12}$$

This is similar to the system (6.1)-(6.2), and we have the following closed form:

$$S_b(t) = S_b(t_2) \exp[-(\mu_b^s + M_{bw} + \beta_b \bar{P}_b(t))(t - t_2)]; \tag{6.13}$$

$$I_b(t) = I_b(t_2) \exp[-(\mu_b^i + M_{bw} - \beta_b \bar{P}_b(t))(t - t_2)], \tag{6.14}$$

where

$$\bar{P}_b(t) := \frac{1}{t - t_2} \int_{t_2}^t P_b(s) ds = -\frac{\log[P_b(t_2) e^{-(r_b + \mu_b^s)(t-t_2)} - P_b(t_2) + 1]}{(r_b + \mu_b^s)(t - t_2)}$$

with

$$P_b(t) := \frac{S_b(t)}{S_b(t) + I_b(t)} = \frac{\exp[-(r_b + \mu_b^s)(t - t_2)]}{\exp[-(r_b + \mu_b^s)(t - t_2)] - 1 + 1/P_b(t_2)} \tag{6.15}$$

being the proportion of susceptible birds. It is noted from (4.2) and (6.13)-(6.14) that $S_b(t_3) = O(\varepsilon) S_b(t_2)$ and $I_b(t_3) = O(\varepsilon) I_b(t_2)$. Consequently, we obtain from (2.1), (4.1), and (4.3) that

$$S_b(t) = O(\varepsilon)[S_b(t_0) + S_w(t_0)] \quad \text{and} \quad I_b(t) = O(\varepsilon)[I_b(t_0) + I_w(t_0)] \tag{6.16}$$

for any $t \in [t_3, t_0 + T + \tau_{wb}]$. Recall that $O(\varepsilon)$ denotes a quantity that vanishes as ε defined in (4.2) tends to zero.

The system for the birds at the winter site also follows from (2.1) and (4.1):

$$S_w'(t) = \alpha_{bw}^s M_{bw} S_b(t - \tau_{bw}) - \frac{\beta_w S_w(t) I_w(t)}{S_w(t) + I_w(t)} - \mu_w^s S_w(t); \tag{6.17}$$

$$I_w'(t) = \alpha_{bw}^i M_{bw} I_b(t - \tau_{bw}) + \frac{\beta_w S_w(t) I_w(t)}{S_w(t) + I_w(t)} - \mu_w^i I_w(t). \tag{6.18}$$

Finally, we consider the bird population during the winter. On account of (6.16), we only need to study the equations of birds at the winter site. For $t \in [t_3 + \tau_{bw}, t_0 + T]$, it is easily seen from (2.1) and (4.1) that

$$S_w'(t) = -\mu_w^s S_w(t) - \frac{\beta_w S_w(t) I_w(t)}{S_w(t) + I_w(t)}; \tag{6.19}$$

$$I_w'(t) = -\mu_w^i I_w(t) + \frac{\beta_w S_w(t) I_w(t)}{S_w(t) + I_w(t)}. \tag{6.20}$$

Similar to (6.4)-(6.5), the explicit solution of above system is given by

$$S_w(t) = S_w(t_3 + \tau_{bw}) \exp[-(\mu_w^s + M_{wb} + \beta_w \bar{P}_w(t))(t - t_3 - \tau_{bw})]; \tag{6.21}$$

$$I_w(t) = I_w(t_3 + \tau_{bw}) \exp[-(\mu_w^i + M_{wb} - \beta_w \bar{P}_w(t))(t - t_3 - \tau_{bw})], \tag{6.22}$$

where

$$\bar{P}_w(t) \ := \ \frac{1}{t - t_3 - \tau_{bw}} \int_{t_3+\tau_{bw}}^{t} P_w(s)ds$$

$$= \ -\frac{\log[P_w(t_3 + \tau_{bw})e^{-(r_w+\mu_w^s)(t-t_3-\tau_{bw})} - P_w(t_3 + \tau_{bw}) + 1]}{(r_w + \mu_w^s)(t - t_3 - \tau_{bw})}$$

and the proportion

$$P_w(t) = \frac{\exp[-(r_w + \mu_w^s)(t - t_3 - \tau_{bw})]}{\exp[-(r_w + \mu_w^s)(t - t_3 - \tau_{bw})] - 1 + 1/P_w(t_3 + \tau_{bw})}. \tag{6.23}$$

In conclusion, we have used the method of finite-dimension reduction (cf. [11]) to show that given nonnegative initial value $(S_w(t_0), I_w(t_0), S_b(t_0), I_b(t_0))$ at the beginning of the spring, the DDE system (2.1) is reduced to four successive ODE systems (cf. [11]): (6.1)-(6.2) and (6.6)-(6.7) for the spring migration; (6.9)-(6.10) for the summer breeding; (6.11)-(6.12) and (6.17)-(6.18) for the autumn migration; and (6.19)-(6.20) for the winter refuge.

7.   The Threshold for Disease Persistence

With the aid of the above reduced ODE systems, we are now ready to define and calculate the dynamic threshold R_0^e. Due to the nonlinearity of the standard incidence function, it seems impossible to linearize the ODE system with respect to S_w, I_w, S_b, I_b. However, we could view the system as equations of S_w, I_w, S_w/I_w, S_b, I_b and S_b/I_b and linearize it at $S_w(t_0) = 0$, $I_w(t_0) = 0$, $S_w(t_0)/I_w(t_0) = 0$, $S_b(t_0) = 0$, $I_b(t_0) = 0$ and $S_b(t_0)/I_b(t_0) = 0$. For $t \in [t_0, t_1]$, we have from (6.1)-(6.2) that

$$S_w'(t) \ = \ -(\mu_w^s + M_{wb})S_w(t) - \beta_w S_w(t); \tag{7.1}$$
$$I_w'(t) \ = \ -(\mu_w^i + M_{wb})I_w(t). \tag{7.2}$$

For $t \in [t_0 + \tau_{wb}, t_1 + \tau_{wb}]$, we have from (6.6)-(6.7) that

$$S_b'(t) \ = \ \alpha_{wb}^s M_{wb}S_w(t - \tau_{wb}) - \beta_b S_b(t) + (b_0 - \mu_b^s)S_b(t); \tag{7.3}$$
$$I_b'(t) \ = \ \alpha_{wb}^s M_{wb}I_w(t - \tau_{wb}) - \mu_b^i I_b(t), \tag{7.4}$$

For $t \in [t_1 + \tau_{wb}, t_2]$, we have from (6.9)-(6.10) that

$$S_b'(t) \ = \ (b_0 - \mu_b^s)S_b(t) - \beta_b S_b(t); \tag{7.5}$$
$$I_b'(t) \ = \ -\mu_b^i I_b(t). \tag{7.6}$$

For $t \in [t_2, t_3]$, we have from (6.11)-(6.12) that

$$S_b'(t) \ = \ -(\mu_b^s + M_{bw})S_b(t) - \beta_b S_b(t); \tag{7.7}$$
$$I_b'(t) \ = \ -(\mu_b^i + M_{bw})I_b(t). \tag{7.8}$$

For $t \in [t_3 + \tau_{bw}, t_0 + T]$, we have from (6.17)-(6.18) that

$$S_w'(t) \ = \ \alpha_{bw}^s M_{bw}S_b(t - \tau_{bw}) - \beta_w S_w(t) - \mu_w^s S_w(t); \tag{7.9}$$
$$I_w'(t) \ = \ \alpha_{bw}^i M_{bw}I_b(t - \tau_{bw}) - \mu_w^i I_w(t). \tag{7.10}$$

For $t \in [t_3 + \tau_{bw}, t_0 + T]$, we have from (6.19)-(6.20) that

$$S_w'(t) \ = \ -\mu_w^s S_w(t) - \beta_w S_w(t); \tag{7.11}$$
$$I_w'(t) \ = \ -\mu_w^i I_w(t). \tag{7.12}$$

Let F be the Poincaré map F of the reduced ODE system, namely,

$$F: \begin{pmatrix} S_w(t_0) \\ I_w(t_0) \\ S_w(t_0)/I_w(t_0) \\ S_b(t_0) \\ I_b(t_0) \\ S_b(t_0)/I_b(t_0) \end{pmatrix} \rightarrow \begin{pmatrix} S_w(t_0+T) \\ I_w(t_0+T) \\ S_w(t_0+T)/I_w(t_0+T) \\ S_b(t_0+T) \\ I_b(t_0+T) \\ S_b(t_0+T)/I_b(t_0+T) \end{pmatrix} \tag{7.13}$$

Denote by $DF(0)$ the linearized operator DF value taken at the trivial equilibrium, i.e., $DF(0)$ is a 6×6 square matrix obtained by integrating the above linear system. Now we define R_0^e to be the spectral radius (principle eigenvalue) of the linear operator (matrix) $DF(0)$.

Theorem 7.1. *The threshold R_0^e has the following asymptotic formula*:

$$\begin{aligned} R_0^e \quad \sim \quad & \frac{\exp[(b_0 - \mu_b^s - \beta_b + \mu_b^i)(T_1 + T_2 - \tau_{wb})]}{\exp[(\beta_w + \mu_w^s - \mu_w^i)(T_3 + T_4 - \tau_{bw})]} \\ & \times \frac{\alpha_{wb}^s (M_{wb} + \mu_w^i - \mu_b^i)}{\alpha_{bw}^i (M_{wb} + b_0 + \mu_w^s - \mu_b^s + \beta_w - \beta_b)} \\ & \times \frac{\alpha_{bw}^s (M_{bw} + \mu_b^i - \mu_w^i)}{\alpha_{bw}^i (M_{bw} + \mu_b^s - \mu_w^s + \beta_b - \beta_w)}. \end{aligned} \tag{7.14}$$

Proof. Solving the linear system (7.1)-(7.12), we obtain

$$\begin{aligned} S_w(t) &= S_w(t_0)e^{-(\mu_w^s + M_{wb} + \beta_w)(t-t_0)}; \tag{7.15} \\ I_w(t) &= I_w(t_0)e^{-(\mu_w^i + M_{wb})(t-t_0)} \tag{7.16} \end{aligned}$$

for $t \in [t_0, t_1]$, and

$$\begin{aligned} S_b(t) &= S_b(t_0 + \tau_{wb})e^{(b_0 - \mu_b^s - \beta_b)(t-t_0-\tau_{wb})} \\ &\quad + \frac{\alpha_{wb}^s M_{wb} S_w(t_0)}{M_{wb} + b_0 + \beta_w - \beta_b + \mu_w^s - \mu_b^s} \\ &\quad \times [e^{(b_0 - \mu_b^s - \beta_b)(t-t_0-\tau_{wb})} - e^{-(\mu_w^s + M_{wb} + \beta_w)(t-t_0-\tau_{wb})}] \tag{7.17} \\ I_b(t) &= I_b(t_0 + \tau_{wb})e^{-\mu_b^i(t-t_0-\tau_{wb})} + \frac{\alpha_{wb}^s M_{wb} I_w(t_0)}{M_{wb} + \mu_w^i - \mu_b^i} \\ &\quad \times [e^{-\mu_b^i(t-t_0-\tau_{wb})} - e^{-(\mu_w^i + M_{wb})(t-t_0-\tau_{wb})}] \tag{7.18} \end{aligned}$$

for $t \in [t_0 + \tau_{wb}, t_1 + \tau_{wb}]$, and

$$\begin{aligned} S_b(t) &= S_b(t_1 + \tau_{wb})e^{(b_0 - \mu_b^s - \beta_b)(t-t_1-\tau_{wb})}; \tag{7.19} \\ I_b(t) &= I_b(t_1 + \tau_{wb})e^{-\mu_b^i(t-t_1-\tau_{wb})} \tag{7.20} \end{aligned}$$

for $t \in [t_1 + \tau_{wb}, t_2]$, and

$$\begin{aligned} S_b(t) &= S_b(t_2)e^{-(\mu_b^s + M_{bw} + \beta_b)(t-t_2)}; \tag{7.21} \\ I_b(t) &= I_b(t_2)e^{-(\mu_b^i + M_{bw})(t-t_2)} \tag{7.22} \end{aligned}$$

for $t \in [t_2, t_3]$, and

$$
\begin{aligned}
S_w(t) &= S_w(t_2 + \tau_{bw})e^{-(\beta_w + \mu_w^s)(t - t_2 - \tau_{bw})} + \frac{\alpha_{bw}^s M_{bw} S_b(t_2)}{M_{bw} + \beta_b - \beta_w + \mu_b^s - \mu_w^s} \\
&\quad \times \left[e^{-(\beta_w + \mu_w^s)(t - t_2 - \tau_{bw})} - e^{-(\mu_b^s + M_{bw} + \beta_b)(t - t_2 - \tau_{bw})} \right];
\end{aligned}
\tag{7.23}
$$

$$
\begin{aligned}
I_w(t) &= I_w(t_2 + \tau_{bw})e^{-\mu_w^i(t - t_2 - \tau_{bw})} + \frac{\alpha_{bw}^i M_{bw} I_b(t_2)}{M_{bw} + \mu_b^i - \mu_w^i} \\
&\quad \times \left[e^{-\mu_w^i(t - t_2 - \tau_{bw})} - e^{-(\mu_b^i + M_{bw})(t - t_2 - \tau_{bw})} \right]
\end{aligned}
\tag{7.24}
$$

for $t \in [t_2 + \tau_{bw}, t_3 + \tau_{bw}]$, and

$$
\begin{aligned}
S_w(t) &= S_w(t_3 + \tau_{bw})e^{-(\beta_w + \mu_w^s)(t - t_3 - \tau_{bw})}; &\tag{7.25} \\
I_w(t) &= I_w(t_3 + \tau_{bw})e^{-\mu_w^i(t - t_3 - \tau_{bw})} &\tag{7.26}
\end{aligned}
$$

for $t \in [t_3 + \tau_{bw}, t_0 + T]$.

Similarly to the proof of [11, Theorem 4.1], we obtain from (4.2), (6.8), and (6.16) that $S_b(t_0 + T) = O(\varepsilon)$, $I_b(t_0 + T) = O(\varepsilon)$, $S_b(t_0 + T)/I_b(t_0 + T) = O(\varepsilon)$ and

$$
\begin{aligned}
S_w(t_0 + T) &= (DF)_{11}(0)S_w(t_0) + O(1)S_b(t_0); &\tag{7.27} \\
I_w(t_0 + T) &= (DF)_{22}(0)I_w(t_0) + O(1)I_b(t_0); &\tag{7.28} \\
\frac{S_w(t_0 + T)}{I_w(t_0 + T)} &= (DF)_{33}(0)\frac{S_w(t_0)}{I_w(t_0)} + O(1), &\tag{7.29}
\end{aligned}
$$

where $O(1)$ denotes a bounded quantity and

$$
\begin{aligned}
(DF)_{11}(0) &\sim \frac{\exp[(b_0 - \mu_b^s - \beta_b)(T_1 + T_2 - \tau_{wb})]}{\exp[(\beta_w + \mu_w^s)(T_3 + T_4 - \tau_{bw})]} \\
&\quad \times \frac{\alpha_{wb}^s M_{wb}}{M_{wb} + b_0 + \mu_w^s - \mu_b^s + \beta_w - \beta_b} \\
&\quad \times \frac{\alpha_{bw}^s M_{bw}}{M_{bw} + \mu_b^s - \mu_w^s + \beta_b - \beta_w},
\end{aligned}
\tag{7.30}
$$

$$
\begin{aligned}
(DF)_{22}(0) &\sim \exp[-\mu_b^i(T_1 + T_2 - \tau_{wb}) - \mu_w^i(T_3 + T_4 - \tau_{bw})] \\
&\quad \times \frac{\alpha_{wb}^i \alpha_{bw}^i M_{wb} M_{bw}}{(M_{wb} + \mu_w^i - \mu_b^i)(M_{bw} + \mu_b^i - \mu_w^i)},
\end{aligned}
\tag{7.31}
$$

and

$$
\begin{aligned}
(DF)_{33}(0) &\sim \frac{\exp[(b_0 - \mu_b^s - \beta_b + \mu_b^i)(T_1 + T_2 - \tau_{wb})]}{\exp[(\beta_w + \mu_w^s - \mu_w^i)(T_3 + T_4 - \tau_{bw})]} \\
&\quad \times \frac{\alpha_{wb}^s(M_{wb} + \mu_w^i - \mu_b^i)}{\alpha_{bw}^i(M_{wb} + b_0 + \mu_w^s - \mu_b^s + \beta_w - \beta_b)} \\
&\quad \times \frac{\alpha_{bw}^s(M_{bw} + \mu_b^i - \mu_w^i)}{\alpha_{bw}^i(M_{bw} + \mu_b^s - \mu_w^s + \beta_b - \beta_w)}.
\end{aligned}
\tag{7.32}
$$

It follows from the definition of R_0^e that

$$
R_0^e = \max\{(DF)_{11}(0), (DF)_{22}(0), (DF)_{33}(0)\} = (DF)_{33}(0).
$$

This proves the theorem. $\qquad\square$

Remark 7.2. *It is readily seen from (5.3), (5.5), and (7.14) that if $r_w = r_b$, then*

$$R_0^e \sim \frac{R_0^c}{R_0^p}.$$

The locally asymptotic stability of the trivial equilibrium follows from the definition of R_0^e and the fact that system (2.1) is reduced to a finite-dimensional periodic system whose Poincaré map is F.

Theorem 7.3. *If $R_0^c > 1$, $R_0^p > 1$, and $R_0^e < 1$, then the trivial equilibrium of system (2.1) is locally asymptotically stable. If $R_0^c > 1$, $R_0^p > 1$, and $R_0^e > 1$, then the trivial equilibrium of system (2.1) is locally asymptotically unstable.*

Proof. If $R_0^e < 1$, then by definition, the spectral radius of the linearized Poincaré map at $S_w(t_0) = 0$, $I_w(t_0) = 0$, $S_w(t_0)/I_w(t_0) = 0$, $S_b(t_0) = 0$, $I_b(t_0) =$, and $S_b(t_0)/I_b(t_0) = 0$ is less than one. Hence, the trivial equilibrium is locally asymptotically stable. If $R_0^e > 1$, then we have to linearize the system at $S_w(t_0) = 0$, $I_w(t_0) = 0$, $I_w(t_0)/S_w(t_0) = 0$, $S_b(t_0) = 0$, $I_b(t_0) =$, and $I_b(t_0)/S_b(t_0) = 0$. A similar approach as in the derivation of the asymptotic formula for R_0^e shows that the corresponding spectral radius is equal to $\max\{R_0^c, R_0^p, 1/R_0^e\}$, which is again larger than one. Therefore, the trivial equilibrium is locally asymptotically unstable. $\square$

Remark 7.4. *We use the following simple SIR model with periodic logistic birth to illustrate our idea of linearizing the standard incidence function.*

$$S'(t) = b(t)S(t)[1 - S(t)/K] - \frac{\beta S(t)I(t)}{S(t) + I(t)} - \mu^s S(t);$$

$$I'(t) = \frac{\beta S(t)I(t)}{S(t) + I(t)} - \mu^i I(t).$$

The ecological basic reproductive ratio is

$$R_0^c = e^{(\bar{b} - \beta - \mu^s)T},$$

where

$$\bar{b} = \frac{1}{T} \int_0^T b(t)dt$$

is the average of birth rate during the period T. The epidemiological basic reproductive ratio is

$$R_0^p = e^{(\beta - \mu^i)T}.$$

Now we introduce a new function $T(t) := S(t)/I(t)$ and linearize the above system at $S(0) = 0$, $I(0) = 0$, and $T(0) = 0$ to obtain

$$S'(t) = [b(t) - \beta - \mu^s]S(t);$$
$$I'(t) = -\mu^i I(t);$$
$$T'(t) = [b(t) - \beta - \mu^s + \mu^i]T(t).$$

Integrating this linear system during a given period gives the dynamic threshold

$$R_0^e := \max\{e^{(\bar{b} - \beta - \mu^s)T}, e^{-\mu^i T}, e^{(\bar{b} - \beta - \mu^s + \mu^i)T}\} = e^{(\bar{b} - \beta - \mu^s + \mu^i)T} = \frac{R_0^c}{R_0^p}.$$

We further introduce a function $V(t) := I(t)/S(t)$ and linearize the system at $S(0) = 0$, $I(0) = 0$, and $V(0) = 0$:

$$S'(t) = [b(t) - \mu^s]S(t);$$
$$I'(t) = (\beta - \mu^i)I(t);$$
$$T'(t) = -[b(t) - \beta - \mu^s + \mu^i]T(t).$$

The spectral radius of the corresponding linearized Poincaré map is the maximum of R_0^c, R_0^p, and $1/R_0^e$; see also the proof in the previous theorem.

8. Discussion

In this paper, we have used the method of finite-dimensional reduction and some asymptotic techniques to derive asymptotic formulas for two basic reproductive ratios (R_0^c and R_0^p) and the threshold (R_0^e) of a patch disease model for avian influenza transmitted by migratory birds in patches. The two basic reproductive ratios R_0^c and R_0^p characterize the ecological and epidemiological dynamics respectively, and the competition between R_0^c and R_0^p is determined by a threshold R_0^e as follows:

- $R_0^c < 1$: the trivial equilibrium is globally asymptotically stable.
- $R_0^c > 1$ and $R_0^p < 1$: the disease-free positive periodic solution is globally asymptotically stable.
- $R_0^c > 1$, $R_0^p > 1$, and $R_0^e < 1$: the trivial equilibrium is locally asymptotically stable.
- $R_0^c > 1$, $R_0^p > 1$, and $R_0^e > 1$: the trivial equilibrium is locally asymptotically unstable.

It would be interesting to prove that in Case 3, the trivial equilibrium is globally asymptotically stable and that in Case 4, there exists an endemic periodic solution that is globally asymptotically stable. The main difficulty arises from the fact that the full model is a coupled system combining a cooperative system and a predator-prey subsystem, and the theory for monotone dynamic systems ([15]) no longer applies.

We would also like to mention that our definition of basic reproductive ratios for periodic systems is the reproductive ratio after one period with a small perturbation of zero equilibrium. Mathematically, it is defined as the spectral radius of the linearized Poincaré map. This is slightly different with the definition of the basic reproduction number by using the next generation matrix/operator [3, 4, 6, 10], and [13].

Acknowledgments

REFERENCES

1. L. Bourouiba, S. Gourley, R. Liu, and J. Wu, "The interaction of migratory birds and domestic poultry and its role in sustaining avian influenza," *SIAM J. Appl. Math.* **71**, 487–516 (2011).
2. L. Bourouiba, J. Wu, S. Newman, J. Takekawa, T. Natdorj, N. Batbayar, C. M. Bishop, L. A. Hawkes, P. J. Butler, and M. Wikelski, "Spatial dynamics of bar-headed geese migration in the context of H5N1," *J. R. Soc. Interface* **7**, 1627–1639 (2010).
3. O. Diekmann, J. A. P. Heesterbeek, and J. A. J. Metz, "On the definition and the computation of the basic reproduction ratio R_0 in models for infectious diseases in heterogeneous populations," *J. Math. Biol.*, **28**, 4, 365–382 (1990).
4. O. Diekmann, J. A. P. Heesterbeek, and M. G. Roberts, "The construction of next-generation matrices for compartmental epidemic models," *J. R. Soc. Interface*, **47**, 873–885 (2010).
5. S. Gourley, R. Liu, and J. Wu, "Spatiotemporal distributions of migratory birds: patchy models with delay," *SIAM J. Appl. Dyn. Syst.*, **9**, 589–610 (2010).
6. J. M. Heffernan, R. J. Smith, and L. M. Wahl, "Perspectives on the basic reproductive ratio," *J. R. Soc. Interface*, **47**, 873–885 (2005).
7. A. L. Skubachevskii and H.-O. Walther, "On the spectrum of the monodromy operator for slowly oscillating periodic solutions of functional differential equations," *Dokl. Acad. Nauk*, **384**, 442–445 (2002).
8. A. L. Skubachevskii and H.-O. Walther, "On Floquet multipliers for slowly oscillating periodic solutions of nonlinear functional differential equations," *Tr. Mosk. Mat. Obshch.*, **64**, 3–54 (2002).

9. H. L. Smith, 1995. *Monotone Dynamical Systems. An Introduction to the Theory of Competitive and Cooperative Systems*, AMS, Providence, RI (1995).

10. P. Van den Driessche and J. Watmough, Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission. *Math. Biosci.*, **180**, 29–48 (2002).

11. X.-S. Wang and J. Wu, "Seasonal migration dynamics: periodicity, transition delay, and finite-dimensional reduction," *Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci.*, **468**, No. 2139, 634–650 (2012)

12. X.-S. Wang and J. Wu, "Approximating periodic patterns and dynamic threshold for patchy model of migratory birds with delay," *Can. Appl. Math. Q.*, to appear.

13. W. Wang and X.-Q. Zhao, Threshold dynamics for compartmental epidemic models in periodic environments. *J. Dynam. Differ. Equ.*, **20**, no. 3, 699–717 (2008).

14. X. Wu, V. Duvvuri, Y. Lu, N. Ogden, and J. Wu, "Investigation of the use of Fourier analysis to estimate development rates and seasonal activity of the tick vector of Lyme Disease Ixodes scapularis," *submitted* (2012).

15. X.-Q. Zhao, *Dynamical Systems in Population Biology*, CMS Books in Math., Springer-Verlag, New York (2003).

Xiang-Sheng Wang
Centre for Disease Modelling,
Laboratory for Industrial and Applied Mathematics,
York University, Toronto, Canada M3J 1P3
Jianhong Wu
Centre for Disease Modelling,
Laboratory for Industrial and Applied Mathematics,
York University, Toronto, Canada M3J 1P3
E-mail: `wujh@mathstat.yorku.ca`