

APPROXIMATING PERIODIC PATTERNS AND DYNAMIC THRESHOLD FOR PATCHY MODEL OF MIGRATORY BIRDS WITH DELAY

Dedicated to Professor Herb Freedman on his 70th birthday

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ABSTRACT. Based on finite dimensional reduction methods, we approximate the spatial dynamic model of seasonal migration birds with stopovers by a simple discrete periodic system which captures four seasonal activities: spring migration, summer breeding, autumn migration and winter refuging. The transient functions describing the mapping of bird population from one major patch to another are obtained in terms of model parameters such as the migration rate and mortality rate. Using perturbation techniques, we further derive an explicit asymptotic formula for the persistent/extinct threshold of the bird population. Sensitivity analysis shows that this dynamic threshold is more vulnerable to the change of bird death rates at autumn migratory stopovers than that at spring migratory stopovers. We thus conclude that the effect of repeated epizootic (i.e. H5N1) during autumn season is stronger than spring season. This conclusion supports numerical phenomenon simulated in existing literature.

1 Introduction The spread of Highly Pathogenic Avian Influenza (HPAI) virus of type A of subtype H5N1 has been a serious threat to domesticated birds and human beings. It led to the culling of hundreds of millions of domestic poultry [11] and caused more than 400 human death cases worldwide [15, 16]. In 2005, the H5N1 virus brought about mortality of more than 6,000 wild birds in Qinghai Lake, China [4]. Among them were more than 3,000 bar-headed (*Anser indicus*) geese [19]. It was recognized that migratory birds were the source and disseminator of H5N1 [14]. On the other hand, various bird species such as ducks, geese and swans are regarded as the natural reservoir of avian

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influenza virus [13, 8, 6]. It is thus important to investigate potential effects of H5N1 virus on populations of seasonal migratory birds.

Although the outbreak of H5N1 during spring seems more severe than autumn [10], numerical simulations gave an opposite conclusion that for equal duration of residence at two stopovers during spring and autumn migrations respectively, the average number of birds at equilibrium is higher when the disease occurs repeatedly during the spring migration [2]. Here, we intend to provide theoretical support to this numerical observation.

It has been proved that the model system of migratory birds is strongly monotone and strictly sub-homogeneous [5], and hence exhibits threshold dynamics [18]: either the bird population will be extinct, or it will persist in a periodic way. Although the threshold condition can be determined by the spectral radius of a certain monodromy operator, it remains an open problem to tie the spectral radius to the model parameters explicitly.

In a previous paper [12], we made a first attempt to address this problem by studying a simple two-patch migration model. Our approach was based on three assumptions: the migratory activity is insignificant during summer breeding season and winter refuge time; the population left in the winter refuge site (resp. summer breeding site) after spring (resp. autumn) migration is comparably negligible; and the breeding activity does not occur during autumn and winter seasons. Under the first and third assumptions, we may regard the parameters in the system (i.e., migration rates and birth rates) to be piecewise constants. The second assumption ensures us to adopt some perturbation techniques from asymptotic analysis and to derive an asymptotic formula for the threshold parameter explicitly in terms of model parameters.

In this paper, we will continue to investigate the more general case where stopovers during migratory seasons are considered. We make the same assumptions as mentioned above, and then approximate the threshold parameter by the model parameters including the death rates at the stopovers. Sensitive analysis shows that given two similar stopovers during spring and autumn migrations respectively (namely, the migration rates and death rates at these two stopovers are the same), the threshold parameter is more easily affected by the change of death rate at the autumn stopover. This means that repeated occurrence of H5N1 during autumn migration leads to greater loss of bird population than that during spring migration. This coincides with the numerical simulation in [2] and challenges the assertion in [10].

The material of this paper is organized as below. In the following

section, we will describe the migration model as established in [2, 5] and give some basic assumptions on the model parameters. We will then derive an asymptotic formula for the threshold and conduct some sensitivity analysis. Some conclusions will be given in the last section, and the perturbation argument will be described in the Appendix.

2 Migration model and basic assumptions We follow Bourouiba *et al.* [2] and Gourley *et al.* [5] to consider a single species bird population migrating between a summer breeding patch and a winter refuge patch. Suppose there are k stopovers during spring migration and l stopovers during autumn migration. Let $x_{s,0}(t)$, $x_{s,i}(t)$ with $1 \leq i \leq k$, $x_{a,0}(t)$ and $x_{a,j}(t)$ with $1 \leq j \leq l$ be the numbers of birds in winter refuge site, the i -th spring stopover, the summer breeding site, and the j -th autumn stopover respectively (cf. Figure 1). This leads to the following periodic system of delay differential equations

$$\begin{aligned}
 \dot{x}_{s,0}(t) &= -(m_{s,0}(t) + \mu_{s,0})x_{s,0}(t) \\
 &\quad + \alpha_{a,l}m_{a,l}(t - \tau_{a,l})x_{a,l}(t - \tau_{a,l}); \\
 \dot{x}_{s,i}(t) &= -(m_{s,i}(t) + \mu_{s,i})x_{s,i}(t) \\
 &\quad + \alpha_{s,i-1}m_{s,i-1}(t - \tau_{s,i-1})x_{s,i-1}(t - \tau_{s,i-1}), \\
 &\quad 1 \leq i \leq k; \\
 (2.1) \quad \dot{x}_{a,0}(t) &= -(m_{a,0}(t) + \mu_{a,0})x_{a,0}(t) \\
 &\quad + \alpha_{s,k}m_{s,k}(t - \tau_{s,k})x_{s,k}(t - \tau_{s,k}) \\
 &\quad + \gamma(t)x_{a,0}(t)(1 - x_{a,0}(t)/K); \\
 \dot{x}_{a,j}(t) &= -(m_{a,j}(t) + \mu_{a,j})x_{a,j}(t) \\
 &\quad + \alpha_{a,j-1}m_{a,j-1}(t - \tau_{a,j-1})x_{a,j-1}(t - \tau_{a,j-1}), \\
 &\quad 1 \leq j \leq l.
 \end{aligned}$$

Due to seasonality of migration and reproduction, it is natural to set all the coefficients in the system to be periodic functions with the period $T = 365$ days. For more details on migration strategies of migratory birds, please refer to [7, 17] and references therein. Let $t_0 = nT$, for an arbitrarily fixed $n \in \mathbb{N}$. We normalize the time so t_0 is the starting date when the birds begin to fly to the summer breeding site in a particular year. We let t_1 be the time when the birds in the winter patch stop their spring migration to the summer breeding site. Therefore, the time when the last spring migratory bird arrives at the summer site is $t_1 + \tau_s$,

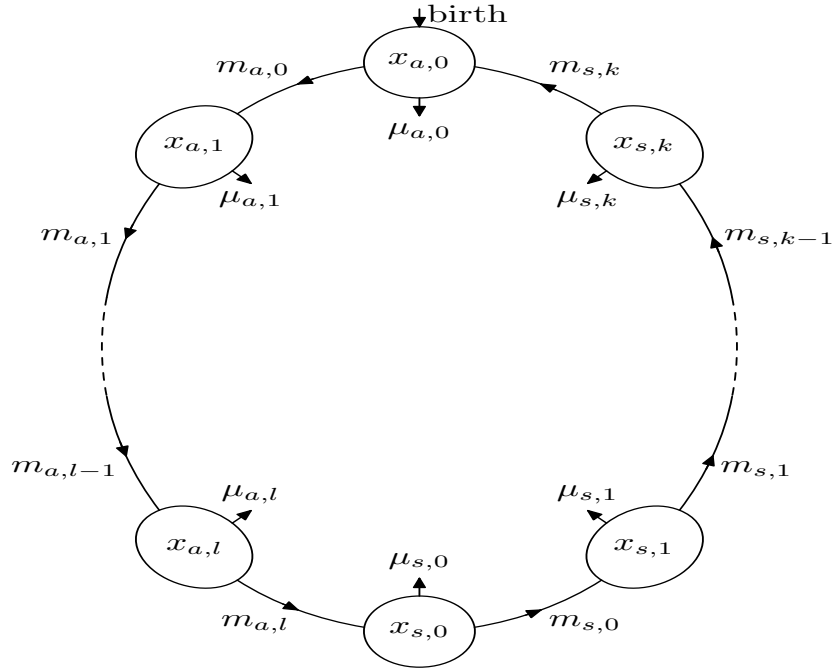


FIGURE 1: Illustration of bird migration and reproduction.

where $\tau_s := \sum_{i=0}^k \tau_{s,i}$ is the durations of spring migration (similarly, we set $\tau_a := \sum_{j=0}^l \tau_{a,j}$ to be the duration of autumn migration). We then assume, after the summer breeding, the birds start their autumn migration at the time t_2 and autumn migration ends at the date t_3 ; see Figure 2.

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 $T_1 + T_2 + T_3 + T_4 = T$, and assume $t_1 + \tau_s < t_2$ and $t_3 + \tau_a < t_0 + T$.

In what follows, we assume the migratory activities only occur during migratory seasons (namely, spring and autumn). Thus, the migration rates are set to be piecewise constants, namely, for t in a period $[t_0, t_0 + T]$, we assume that for $i = 0, 1, \dots, k$,

$$(2.2) \quad m_{s,i}(t) = \begin{cases} M_{s,i}, & t - \sum_{p=0}^{i-1} \tau_{s,p} \in (t_0, t_1); \\ 0, & \text{otherwise,} \end{cases}$$

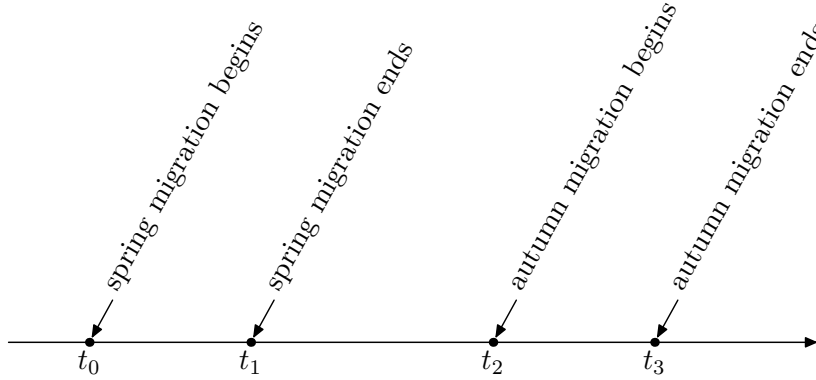


FIGURE 2: Timings when spring or autumn migration starts and ends.

and for $j = 0, 1, \dots, l$,

$$(2.3) \quad m_{a,j}(t) = \begin{cases} M_{a,j}, & t - \sum_{q=0}^{j-1} \tau_{s,q} \in (t_2, t_3); \\ 0, & \text{otherwise.} \end{cases}$$

We make the second assumption that the migration rates are so large that almost all the birds leave the winter (resp. summer) patch after spring (resp. autumn) migration. Mathematically, it means that the quantity

$$(2.4) \quad \varepsilon := \sum_{i=0}^k e^{-M_{s,i}T_1} + \sum_{j=0}^l e^{-M_{a,j}T_3}$$

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:

$$(2.5) \quad \gamma(t) = \begin{cases} \gamma_0, & t \in (t_0 + \tau_s, t_2); \\ 0, & t \in [t_0, t_0 + \tau_s] \cup [t_2, t_0 + T]. \end{cases}$$

Noting that we have assumed there is no birth at the beginning of spring season (namely, on the interval $[t_0, t_0 + \tau_s]$). This is reasonable because

at the time t_0 the number of birds at the summer site is negligible by the second assumption; and due to the time lag, the bird population will not be growing until the first spring migratory bird arrives at the summer site.

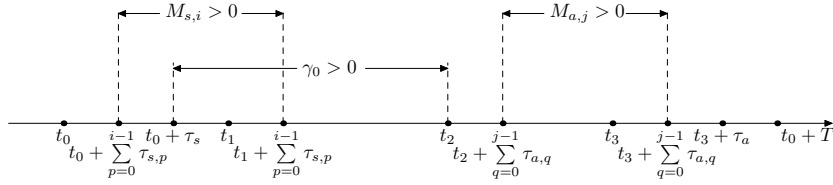


FIGURE 3: Schematic illustrations of migration rates $m_{s,i}(t)$, $m_{a,j}(t)$ and birth rate $\gamma(t)$ in one period $[t_0, t_0 + T]$.

3 Dynamic threshold and sensitivity analysis It has been proved that the model system (2.1) exhibits threshold dynamics: either all solutions converge to the trivial solution, or the system has a positively and globally attractive periodic solution [5]. We follow the perturbation techniques developed in [12] to derive an asymptotic formula for the threshold in terms of model parameters explicitly. Firstly, we approximate the retarded periodic system (2.1) by a simple discrete system which characterizes the dynamics of the bird population. Observing that most of the birds stay at the winter refuge site when the spring migration begins. We denote the number of this majority by A_n (where $n \in \mathbb{N}$ means the number of periods (years) we have counted at this time). When the spring migration ends the birds arrive at the summer breeding site and this population is denoted by B_n . We set C_n to be the bird population at the summer breeding site at the time when autumn migration starts. When autumn migration finishes, the bird majority comes back to the winter site and the population size is denoted by D_n ; see Figure 4.

Similarly to the approach in [12], we derive the following discrete dynamic system from the model system (2.1) and our basic assumptions stated in the previous section (see Appendix for details in deriving this

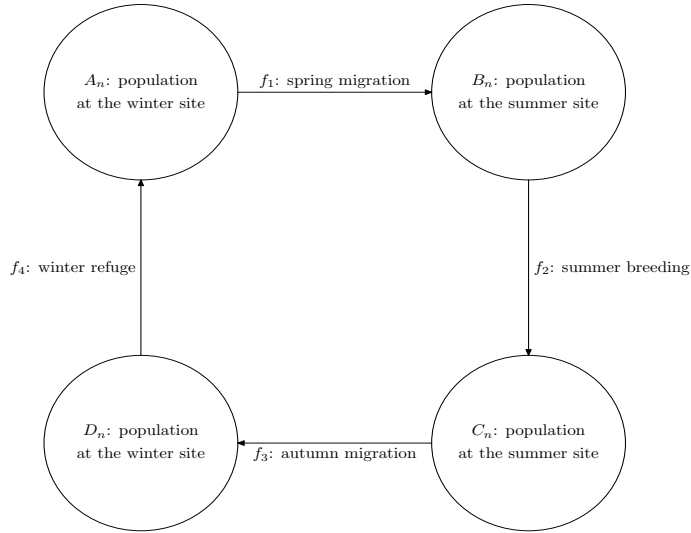


FIGURE 4: The discrete dynamics of the bird population at major patches.

discrete system):

$$\begin{aligned}
 B_n &= f_1(A_n) = A_n e^{(\gamma_0 - \mu_{a,0})T_1} \prod_{i=0}^k \frac{\alpha_{s,i} M_{s,i}}{M_{s,i} + \mu_{s,i} - \mu_{a,0} + \gamma_0} \\
 &\quad + \text{higher order terms of } A_n; \\
 (3.1) \quad C_n &= f_2(B_n) = \frac{(1 - \frac{\mu_{a,0}}{\gamma_0}) K e^{(\gamma_0 - \mu_{a,0})(T_2 - \tau_s)}}{(1 - \frac{\mu_{a,0}}{\gamma_0}) \frac{K}{B_n} - 1 + e^{(\gamma_0 - \mu_{a,0})(T_2 - \tau_s)}}; \\
 D_n &= f_3(C_n) = C_n e^{-\mu_{s,0}T_3} \prod_{j=0}^l \frac{\alpha_{a,j} M_{a,j}}{M_{a,j} + \mu_{a,j} - \mu_{s,0}}; \\
 A_{n+1} &= f_4(D_n) = D_n e^{-\mu_{s,0}(T_4 - \tau_a)}.
 \end{aligned}$$

Here, we remark that the major difference between this discrete system with the one in a previous paper [12] is that the function f_1 here can not be expressed in terms of well-known functions, while Bessel function [9] was used to give an explicit description of the dynamics of spring migration in our early paper. However, to calculate the dynamic threshold of this discrete system, only the first term of f_1 (as given in the formula)

is enough, even though in practise, we can compute recursively as many terms as possible.

The threshold of this discrete system (3.1) is easily calculated as

$$(3.2) \quad R := r_s \cdot p_s \cdot t_r,$$

where

$$r_s := e^{\gamma_0(T_1+T_2-\tau_a)}$$

is the reproduction ratio in the summer,

$$p_s := \left(\prod_{i=0}^k \alpha_{s,i} \right) \times e^{-\mu_{a,0}(T_1+T_2-\tau_a)} \times \left(\prod_{j=0}^l \alpha_{a,j} \right) \times e^{-\mu_{s,0}(T_3+T_4-\tau_a)}$$

is the survival probability during four seasons, and

$$t_r := \left(\prod_{i=0}^k \frac{M_{s,i}}{M_{s,i} + \mu_{s,i} - \mu_{a,0} + \gamma_0} \right) \times \left(\prod_{j=0}^l \frac{M_{a,j}}{M_{a,j} + \mu_{a,j} - \mu_{s,0}} \right)$$

is the transition rate during spring and autumn migrations. Consequently, we have a clear ecological interpretation of R as the annual reproduction rate.

The discrete system (3.1) approximates the original dynamic system (2.1) if ε defined in (2.4) is small. We thus obtain an asymptotic formula for the threshold of the model system (2.1):

$$(3.3) \quad r = R + O(\varepsilon),$$

where $O(\varepsilon)$ is a small perturbation which tends to zero as $\varepsilon \rightarrow 0$. The threshold is defined as the spectral radius of the monodromy operator of system (2.1) linearized at the zero solution. A rigorous proof of this formula is given later in Appendix.

We are now ready to carry out sensitivity analysis. Suppose there are two similar stopovers during spring and autumn migrations respectively. Similarity means migration rates and death rates are the same, namely, $M_{s,i} = M_{a,j} = M$ and $\mu_{s,i} = \mu_{a,j} = \mu$ for some i in $1, 2, \dots, k$ and j in $1, 2, \dots, l$. Now we assume there is repeated deadly epizootic of H5N1 at spring migration stopovers, namely, $\mu_{s,i} = \bar{\mu} > \mu$. Consequently, the threshold R in (3.2) decreases by

$$\beta_{s,i} = \frac{\bar{\mu} - \mu}{M + \bar{\mu} - \mu_{a,0} + \gamma_0}.$$

On the other hand, when there are repeated H5N1 outbreaks at autumn migration stopovers, the corresponding decreasing rate of the threshold is

$$\beta_{a,j} = \frac{\bar{\mu} - \mu}{M + \bar{\mu} - \mu_{s,0}}.$$

Since $\gamma_0 > \mu_{a,0}$ (birth rate is greater than death rate at the summer site) and $\mu_{s,0} > 0$, it is easily seen that

$$\beta_{s,i} < \beta_{a,j},$$

which implies that epizootic of H5N1 during spring migration has greater impact reducing the bird population than that during autumn migration. This gives a mathematical verification of the simulated results in [2].

4 Conclusion Based on the finite dimensional reduction method developed in our early paper [12], we approximated the continuous dynamic system for migratory birds by a simple discrete system. Consequently, an asymptotic formula for the threshold of spatial dynamic model was derived. Sensitivity analysis on this explicit formula shows that deadly H5N1 outbreaks at autumn stopovers will influence more on the bird population than the disease during spring migration.

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A The discrete system (3.1) Here, we provide some details in deriving the discrete system (3.1) from the original system (2.1) and our basic assumptions (2.2), (2.3), (2.4) and (2.5). For simplicity, we only consider the case when $k = l = 1$; the case with general k and l can be studied similarly. Firstly, in view of the assumptions (2.2), (2.3) and

(2.5), we obtain from (2.1) that (noting $\tau_s := \tau_{s,0} + \tau_{s,1}$)

$$\begin{aligned}
\dot{x}_{s,0}(t) &= -(M_{s,0} + \mu_{s,0})x_{s,0}(t), \quad t \in [t_0, t_1]; \\
\dot{x}_{s,1}(t) &= -(M_{s,1} + \mu_{s,1})x_{s,1}(t) + \alpha_{s,0}M_{s,0}x_{s,0}(t - \tau_{s,0}), \\
&\quad t \in [t_0 + \tau_{s,0}, t_1 + \tau_{s,0}]; \\
\dot{x}_{a,0}(t) &= -\mu_{a,0}x_{a,0}(t) + \alpha_{s,1}M_{s,1}x_{s,1}(t - \tau_{s,1}) \\
&\quad + \gamma_0x_{a,0}(t)(1 - x_{a,0}(t)/K), \\
&\quad t \in [t_0 + \tau_s, t_1 + \tau_s]; \\
\dot{x}_{a,0}(t) &= -\mu_{a,0}x_{a,0}(t) + \gamma_0x_{a,0}(t)(1 - x_{a,0}(t)/K), \\
&\quad t \in [t_1 + \tau_s, t_2].
\end{aligned}
\tag{A.1}$$

Here, we mention that $x_{s,1}(t_0 + \tau_{s,1})$ is fully determined by $x_{s,1}(t_0)$ since there is only natural death at the first stopover during spring migration for t in the interval $[t_0, t_0 + \tau_{s,1}]$. Similarly, $x_{a,0}(t_0 + \tau_s)$ is fully determined by $x_{a,0}(t_0)$. This observation, together with the one to be remarked in the paragraph before equation (A.6), demonstrate that the solutions to the system (2.1) can be fully determined as long as the initial values at time t_0 is known. Solving the above equations (A.1) one-by-one, we have

$$\tag{A.2} \quad x_{s,0}(t) = x_{s,0}(t_0)e^{-(M_{s,0} + \mu_{s,0})(t - t_0)}$$

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

$$\begin{aligned}
\tag{A.3} \quad x_{s,1}(t) &= x_{s,1}(t_0 + \tau_{s,0})e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_{s,0})} \\
&\quad + \int_{t_0 + \tau_{s,0}}^t e^{-(M_{s,1} + \mu_{s,1})(t - s)} \alpha_{s,0}M_{s,0} \\
&\quad \times x_{s,0}(t_0)e^{-(M_{s,0} + \mu_{s,0})(s - t_0 - \tau_{s,0})} ds \\
&= x_{s,1}(t_0 + \tau_{s,0})e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_{s,0})} \\
&\quad + \alpha_{s,0}M_{s,0}x_{s,0}(t_0) \\
&\quad \times \frac{e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_{s,0})} - e^{-(M_{s,0} + \mu_{s,0})(t - t_0 - \tau_{s,0})}}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})}
\end{aligned}$$

for $t \in [t_0 + \tau_{s,0}, t_1 + \tau_{s,0}]$, and

$$\tag{A.4} \quad x_{a,0}(t) = x_{a,0}(t_0 + \tau_s)e^{(\gamma_0 - \mu_{a,0})(t - t_0 - \tau_s)}$$

$$\begin{aligned}
 & + \int_{t_0+\tau_s}^t e^{(\gamma_0-\mu_{a,0})(t-s)} \alpha_{s,1} M_{s,1} x_{s,1}(s-\tau_{s,1}) ds \\
 & + \text{higher order terms} \\
 = & x_{a,0}(t_0 + \tau_s) e^{(\gamma_0-\mu_{a,0})(t-t_0-\tau_s)} \\
 & + \alpha_{s,1} M_{s,1} x_{s,1}(t_0 + \tau_s, 0) \\
 & \times \frac{e^{(\gamma_0-\mu_{a,0})(t-t_0-\tau_s)} - e^{-(M_{s,1}+\mu_{s,1})(t-t_0-\tau_s)}}{(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})} \\
 & + \frac{\alpha_{s,1} M_{s,1} \alpha_{s,0} M_{s,0} x_{s,0}(t_0)}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})} \\
 & \times \frac{e^{(\gamma_0-\mu_{a,0})(t-t_0-\tau_s)} - e^{-(M_{s,1}+\mu_{s,1})(t-t_0-\tau_s)}}{(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})} \\
 & - \frac{\alpha_{s,1} M_{s,1} \alpha_{s,0} M_{s,0} x_{s,0}(t_0)}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})} \\
 & \times \frac{e^{(\gamma_0-\mu_{a,0})(t-t_0-\tau_s)} - e^{-(M_{s,0}+\mu_{s,0})(t-t_0-\tau_s)}}{(M_{s,0} + \mu_{s,0}) + (\gamma_0 - \mu_{a,0})} \\
 & + \text{higher order terms}
 \end{aligned}$$

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

$$(A.5) \quad x_{a,0}(t) = \frac{(1 - \mu_{a,0}/\gamma_0)K \exp[(\gamma_0 - \mu_{a,0})(t - t_1 - \tau_s)]}{\frac{(1-\mu_{a,0}/\gamma_0)K}{x_{a,0}(t_1+\tau_s)} - 1 + \exp[(\gamma_0 - \mu_{a,0})(t - t_1 - \tau_s)]}$$

for $t \in [t_1 + \tau_s, t_2]$. The above four equations characterize dynamics of bird population during spring and summer time $[t_0, t_2]$. Similarly, during autumn and winter time $[t_2, t_0 + T]$, we have from (2.1), (2.2), (2.3) and (2.5) that

$$\begin{aligned}
 \dot{x}_{a,0}(t) &= -(M_{a,0} + \mu_{a,0})x_{a,0}(t), \quad t \in [t_2, t_3]; \\
 \dot{x}_{a,1}(t) &= -(M_{a,1} + \mu_{a,1})x_{a,1}(t) + \alpha_{a,0}M_{a,0}x_{a,0}(t - \tau_{a,0}), \\
 & \quad t \in [t_2 + \tau_{a,0}, t_3 + \tau_{a,0}]; \\
 \dot{x}_{s,0}(t) &= -\mu_{s,0}x_{s,0}(t) + \alpha_{a,1}M_{a,1}x_{a,1}(t - \tau_{a,1}), \quad t \in [t_2 + \tau_a, t_3 + \tau_a]; \\
 \dot{x}_{s,0}(t) &= -\mu_{s,0}x_{s,0}(t), \quad t \in [t_3 + \tau_a, t_0 + T].
 \end{aligned}$$

Again, we have to remark that $x_{a,1}(t_2 + \tau_{a,0})$ is fully determined by $x_{a,1}(t_0)$ and $x_{s,0}(t_2 + \tau_a)$ is fully determined by $x_{s,0}(t_1)$. This, together

with the observation mentioned after the equation (A.1) indicate that the system (2.1) is fully determined by the initial values at one single time t_0 . Solving the above equations one-by-one, we obtain

$$(A.6) \quad x_{a,0}(t) = x_{a,0}(t_2)e^{-(M_{a,0}+\mu_{a,0})(t-t_2)}, \quad t \in [t_2, t_3];$$

$$(A.7) \quad x_{a,1}(t) = x_{a,1}(t_2 + \tau_{a,0})e^{-(M_{a,1}+\mu_{a,1})(t-t_2-\tau_{a,0})} \\ + \alpha_{a,0}M_{a,0}x_{a,0}(t_2) \\ \times \frac{e^{-(M_{a,1}+\mu_{a,1})(t-t_2-\tau_{a,0})} - e^{-(M_{a,0}+\mu_{a,0})(t-t_2-\tau_{a,0})}}{(M_{a,0} + \mu_{a,0}) - (M_{a,1} + \mu_{a,1})}, \\ t \in [t_2 + \tau_{a,0}, t_3 + \tau_{a,0}];$$

$$(A.8) \quad x_{s,0}(t) = x_{s,0}(t_2 + \tau_a)e^{-\mu_{s,0}(t-t_2-\tau_a)} \\ + \alpha_{a,1}M_{a,1}x_{a,1}(t_2 + \tau_{a,0}) \\ \times \frac{e^{-\mu_{s,0}(t-t_2-\tau_a)} - e^{-(M_{a,1}+\mu_{a,1})(t-t_2-\tau_a)}}{(M_{a,1} + \mu_{a,1}) - \mu_{s,0}} \\ + \frac{\alpha_{a,1}M_{a,1}\alpha_{a,0}M_{a,0}x_{a,0}(t_2)}{(M_{a,0} + \mu_{a,0}) - (M_{a,1} + \mu_{a,1})} \\ \times \frac{e^{-\mu_{s,0}(t-t_2-\tau_a)} - e^{-(M_{a,1}+\mu_{a,1})(t-t_2-\tau_a)}}{(M_{a,1} + \mu_{a,1}) - \mu_{s,0}} \\ - \frac{\alpha_{a,1}M_{a,1}\alpha_{a,0}M_{a,0}x_{a,0}(t_2)}{(M_{a,0} + \mu_{a,0}) - (M_{a,1} + \mu_{a,1})} \\ \times \frac{e^{-\mu_{s,0}(t-t_2-\tau_a)} - e^{-(M_{a,0}+\mu_{a,0})(t-t_2-\tau_a)}}{(M_{a,0} + \mu_{a,0}) - \mu_{s,0}}, \\ t \in [t_2 + \tau_a, t_3 + \tau_a];$$

$$(A.9) \quad x_{s,0}(t) = x_{s,0}(t_3 + \tau_a)e^{-\mu_{s,0}(t-t_3-\tau_a)}, \quad t \in [t_3 + \tau_a, t_0 + T].$$

On account of (2.4), it follows from (A.2)–(A.9) that as $\varepsilon \rightarrow 0$,

$$x_{a,0}(t_1 + \tau_s) = \frac{\alpha_{s,1}M_{s,1}\alpha_{s,0}M_{s,0}x_{s,0}(t_0)e^{(\gamma_0-\mu_{a,0})T_1}}{[(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})] \cdot [(M_{s,0} + \mu_{s,0}) + (\gamma_0 - \mu_{a,0})]} \\ + O(\varepsilon) + \text{higher order terms of } x_{s,0}(t_0); \\ x_{a,0}(t_2) = \frac{(1 - \mu_{a,0}/\gamma_0)K \exp[(\gamma_0 - \mu_{a,0})(T_2 - \tau_s)]}{\frac{(1 - \mu_{a,0}/\gamma_0)K}{x_{a,0}(t_1 + \tau_s)} - 1 + \exp[(\gamma_0 - \mu_{a,0})(T_2 - \tau_s)]};$$

$$x_{s,0}(t_3 + \tau_a) = \frac{\alpha_{a,1}M_{a,1}\alpha_{a,0}M_{a,0}x_{a,0}(t_2)}{[(M_{a,1} + \mu_{a,1}) - \mu_{s,0}] \cdot [(M_{a,0} + \mu_{a,0}) - \mu_{s,0}]} + O(\varepsilon);$$

$$x_{s,0}(t_0 + T) = x_{s,0}(t_3 + \tau_a)e^{-\mu_{s,0}(T_4 - \tau_a)}.$$

For any $t_0 := nT$, we let $A_n := x_{s,0}(t_0)$ be the bird population in the winter site at the beginning of spring migration; $B_n := x_{a,0}(t_1 + \tau_s)$ be the bird population in the summer site at the end of spring migration; $C_n := x_{a,0}(t_2)$ be the bird population in the summer site at the beginning of autumn migration; $D_n := x_{s,0}(t_3 + \tau_a)$ be the bird population in the winter site at the end of autumn migration. The approximating discrete system (3.1) follows immediately from the four equations given above.

Remark A.1. In view of (2.4), we observe from (A.3) and (A.7) that as $\varepsilon \rightarrow 0$, $x_{s,1}(t_1 + \tau_{s,0}) = O(\varepsilon)$ and $x_{a,1}(t_3 + \tau_{a,0}) = O(\varepsilon)$, which imply that the bird population at the stopovers is small after migrations.

B Asymptotic formula of dynamic threshold (3.3) As mentioned in the previous section, we observe that the system is fully determined by the initial values at t_0 . Let $F : \mathbb{R}^{k+l+2} \rightarrow \mathbb{R}^{k+l+2}$ be the Poincaré mapping which describes the evolution of system (2.1) after one period, namely, F maps the initial values of $x_{s,i}(t_0)$ with $i = 0, \dots, k$ and $x_{a,j}(t_0)$ with $j = 0, \dots, l$ to $x_{a,i}(t_0 + T)$ with $0 \leq i \leq k$ and $x_{a,j}(t_0 + T)$ with $0 \leq j \leq l$. It has been proved [5] that F is a monotone mapping, and hence the dynamic threshold of the original system (2.1) is characterized by $r := \rho(DF(0))$, the spectral radius of linear operator $DF(0)$; see also [18]. Under assumption (2.4), we intend to prove the asymptotic formula for this threshold (3.3). Firstly, we consider the linearization of system (2.1) at the zero equilibrium:

$$\begin{aligned} \dot{x}_{s,0}(t) &= -(m_{s,0}(t) + \mu_{s,0})x_{s,0}(t) \\ &\quad + \alpha_{a,l}m_{a,l}(t - \tau_{a,l})x_{a,l}(t - \tau_{a,l}); \\ \dot{x}_{s,i}(t) &= -(m_{s,i}(t) + \mu_{s,i})x_{s,i}(t) \\ (B.1) \quad &\quad + \alpha_{s,i-1}m_{s,i-1}(t - \tau_{s,i-1})x_{s,i-1}(t - \tau_{s,i-1}), \\ &\quad 1 \leq i \leq k; \\ \dot{x}_{a,0}(t) &= -(m_{a,0}(t) + \mu_{a,0})x_{a,0}(t) \\ &\quad + \alpha_{s,k}m_{s,k}(t - \tau_{s,k})x_{s,k}(t - \tau_{s,k}) + \gamma(t)x_{a,0}(t); \end{aligned}$$

$$\begin{aligned}
\text{(B.1)} \quad \dot{x}_{a,j}(t) &= -(m_{a,j}(t) + \mu_{a,j})x_{a,j}(t) \\
&\quad + \alpha_{a,j-1}m_{a,j-1}(t - \tau_{a,j-1})x_{a,j-1}(t - \tau_{a,j-1}), \\
&\quad 1 \leq j \leq l.
\end{aligned}$$

Without loss of generality, we may assume that $k = l = 1$. On account of (2.2), (2.3) and (2.5), it can be obtained from (B.1) that

$$\begin{aligned}
\dot{x}_{s,0}(t) &= -(M_{s,0} + \mu_{s,0})x_{s,0}(t), \quad t \in [t_0, t_1]; \\
\dot{x}_{s,1}(t) &= -(M_{s,1} + \mu_{s,1})x_{s,1}(t) + \alpha_{s,0}M_{s,0}x_{s,0}(t - \tau_{s,0}), \\
&\quad t \in [t_0 + \tau_{s,0}, t_1 + \tau_{s,0}]; \\
\text{(B.2)} \quad \dot{x}_{a,0}(t) &= -\mu_{a,0}x_{a,0}(t) + \alpha_{s,1}M_{s,1}x_{s,1}(t - \tau_{s,1}) \\
&\quad + \gamma_0x_{a,0}(t)(1 - x_{a,0}(t)/K), \\
&\quad t \in [t_0 + \tau_s, t_1 + \tau_s]; \\
\dot{x}_{a,0}(t) &= -\mu_{a,0}x_{a,0}(t) + \gamma_0x_{a,0}(t), \quad t \in [t_1 + \tau_s, t_2].
\end{aligned}$$

The above equations can be solved one-by-one, and the solutions are given by

$$x_{s,0}(t) = x_{s,0}(t_0)e^{-(M_{s,0} + \mu_{s,0})(t - t_0)}$$

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

$$\begin{aligned}
x_{s,1}(t) &= x_{s,1}(t_0 + \tau_{s,0})e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_{s,0})} + \alpha_{s,0}M_{s,0}x_{s,0}(t_0) \\
&\quad \times \frac{e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_{s,0})} - e^{-(M_{s,0} + \mu_{s,0})(t - t_0 - \tau_{s,0})}}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})}
\end{aligned}$$

for $t \in [t_0 + \tau_{s,0}, t_1 + \tau_{s,0}]$, and

$$\begin{aligned}
x_{a,0}(t) &= x_{a,0}(t_0 + \tau_s)e^{(\gamma_0 - \mu_{a,0})(t - t_0 - \tau_s)} + \alpha_{s,1}M_{s,1}x_{s,1}(t_0 + \tau_{s,0}) \\
&\quad \times \frac{e^{(\gamma_0 - \mu_{a,0})(t - t_0 - \tau_s)} - e^{-(M_{s,1} + \mu_{s,1})(t - t_0 - \tau_s)}}{(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})} \\
&\quad + \frac{\alpha_{s,1}M_{s,1}\alpha_{s,0}M_{s,0}x_{s,0}(t_0)}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})}
\end{aligned}$$

$$\begin{aligned}
& \times \frac{e^{(\gamma_0 - \mu_{a,0})(t-t_0-\tau_s)} - e^{-(M_{s,1} + \mu_{s,1})(t-t_0-\tau_s)}}{(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})} \\
& - \frac{\alpha_{s,1} M_{s,1} \alpha_{s,0} M_{s,0} x_{s,0}(t_0)}{(M_{s,0} + \mu_{s,0}) - (M_{s,1} + \mu_{s,1})} \\
& \times \frac{e^{(\gamma_0 - \mu_{a,0})(t-t_0-\tau_s)} - e^{-(M_{s,0} + \mu_{s,0})(t-t_0-\tau_s)}}{(M_{s,0} + \mu_{s,0}) + (\gamma_0 - \mu_{a,0})}
\end{aligned}$$

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

$$x_{a,0}(t) = x_{a,0}(t_1 + \tau_s) e^{(\gamma_0 - \mu_{a,0})(t-t_1-\tau_s)}$$

for $t \in [t_1 + \tau_s, t_2]$. In view of (2.4), we have

(B.3)

$$x_{s,0}(t_1) = O(\varepsilon) x_{s,0}(t_0);$$

$$x_{s,1}(t_1 + \tau_{s,0}) = O(\varepsilon) x_{s,0}(t_0) + O(\varepsilon) x_{s,1}(t_0);$$

$$x_{a,0}(t_1 + \tau_s) = O(1) x_{a,0}(t_0) + O(1) x_{s,1}(t_0)$$

$$+ \frac{\alpha_{s,1} M_{s,1} \alpha_{s,0} M_{s,0} x_{a,0}(t_0) e^{(\gamma_0 - \mu_{a,0})T_1}}{[(M_{s,1} + \mu_{s,1}) + (\gamma_0 - \mu_{a,0})] \cdot [(M_{s,0} + \mu_{s,0}) + (\gamma_0 - \mu_{a,0})]};$$

$$x_{a,0}(t_2) = x_{a,0}(t_1 + \tau_s) e^{(\gamma_0 - \mu_{a,0})(T_2 - \tau_s)}.$$

Here, we have made use of $x_{s,1}(t_0 + \tau_{s,0}) = x_{s,1}(t_0) e^{-\mu_{s,1}\tau_{s,0}}$ and $x_{a,0}(t_0 + \tau_s) = x_{a,0}(t_0) e^{-\mu_{a,0}\tau_s}$. Similarly, on account of (2.2), (2.3), (2.4) and (2.5), it follows from (B.1) that

$$x_{a,0}(t_3) = O(\varepsilon) x_{a,0}(t_2);$$

$$x_{a,1}(t_3 + \tau_{a,0}) = O(\varepsilon) x_{a,0}(t_2) + O(\varepsilon) x_{a,1}(t_2);$$

$$(B.4) \quad x_{s,0}(t_3 + \tau_a) = O(1) x_{s,0}(t_2) + O(1) x_{a,1}(t_2)$$

$$+ \frac{\alpha_{a,1} M_{a,1} \alpha_{a,0} M_{a,0} x_{a,0}(t_2) e^{-\mu_{s,0}T_3}}{[(M_{a,1} + \mu_{a,1}) - \mu_{s,0}] \cdot [(M_{a,0} + \mu_{a,0}) - \mu_{s,0}]};$$

$$x_{s,0}(t_0 + T) = x_{s,0}(t_3 + \tau_a) e^{-\mu_{s,0}(T_4 - \tau_a)}.$$

Since

$$x_{s,0}(t_2) = x_{s,0}(t_1) e^{-\mu_{s,0}T_2};$$

$$x_{s,1}(t_0 + T) = x_{s,1}(t_1 + \tau_{s,0}) e^{-\mu_{s,1}(T - T_1 - \tau_{s,0})};$$

$$x_{a,0}(t_0 + T) = x_{a,0}(t_3) e^{-\mu_{a,0}T_4};$$

$$\begin{aligned}x_{a,1}(t_2) &= x_{a,1}(t_0)e^{-\mu_{a,1}(T_1+T_2)}; \\x_{a,1}(t_0 + T) &= x_{a,1}(t_3 + \tau_{a,0})e^{-\mu_{a,1}(T_4-\tau_{a,0})},\end{aligned}$$

we have from (B.3) and (B.4) that (recall the formula of R in (3.2))

$$\begin{aligned}x_{s,0}(t_0 + T) &= [R + O(\varepsilon)]x_{s,0}(t_0) + O(1)x_{s,1}(t_0) \\&\quad + O(1)x_{a,0}(t_0) + O(1)x_{a,1}(t_0); \\x_{s,1}(t_0 + T) &= O(\varepsilon)x_{s,0}(t_0) + O(\varepsilon)x_{s,1}(t_0); \\x_{s,0}(t_0 + T) &= O(\varepsilon)x_{s,0}(t_0) + O(\varepsilon)x_{s,1}(t_0) + O(\varepsilon)x_{a,0}(t_0); \\x_{a,1}(t_0 + T) &= O(\varepsilon)x_{s,0}(t_0) + O(\varepsilon)x_{s,1}(t_0) \\&\quad + O(\varepsilon)x_{a,0}(t_0) + O(\varepsilon)x_{a,1}(t_0).\end{aligned}$$

This implies that

$$DF(0) = \begin{pmatrix} R + O(\varepsilon) & O(1) & O(1) & O(1) \\ O(\varepsilon) & O(\varepsilon) & 0 & 0 \\ O(\varepsilon) & O(\varepsilon) & O(\varepsilon) & 0 \\ O(\varepsilon) & O(\varepsilon) & O(\varepsilon) & O(\varepsilon) \end{pmatrix}.$$

Finally, we obtain $r := \rho(DF(0)) = R + O(\varepsilon)$. This proves (3.3).

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