Approximating the extinction threshold of spatial dynamics of migratory birds

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(joint work with Jianhong Wu)
Outline

• Introduction

• A simple system without stopovers
  1. Approximate system
  2. Approximate threshold

• A general system with stopovers
  1. Approximate system
  2. Approximate threshold

• Discussion
Introduction

• Threshold theorem: either all solutions converge to the trivial solution, or the system has a positively and globally attractive periodic solution.


• Interesting phenomenon: the bird population is more sensitive to the disease occurring at a stopover during autumn migration than that occurring at a similar stopover during spring migration.

A simple system without stopovers

Denote by $x_s(t)$ and $x_w(t)$ the numbers of birds in the summer and winter sites respectively.

\[
\begin{align*}
\dot{x}_s(t) &= -(m_{sw}(t) + \mu_s(t))x_s(t) + e^{-\mu_{ws}\tau_{ws}}m_{ws}(t - \tau_{ws})x_w(t - \tau_{ws}) \\
&\quad + \gamma_s(t)x_s(t)(1 - x_s(t)/K);
\end{align*}
\]

\[
\begin{align*}
\dot{x}_w(t) &= -(m_{ws}(t) + \mu_w(t))x_w(t) + e^{-\mu_{sw}\tau_{sw}}m_{sw}(t - \tau_{sw})x_s(t - \tau_{sw}).
\end{align*}
\]

Assume the migration rates $m_{sw}$ and $m_{ws}$, the death rates $\mu_s$ and $\mu_w$, and the birth rate $\gamma_s$ are all piecewise constants.
We divide a year by four seasons: $t_0 \xrightarrow{\text{spring}} t_1 \xrightarrow{\text{summer}} t_2 \xrightarrow{\text{autumn}} t_3 \xrightarrow{\text{winter}} t_0 + T$. Suppose

$$m_{ws}(t) = \begin{cases} M_{ws}, & t \in (t_0, t_1); \\ 0, & t \in (t_1, t_0 + T), \end{cases}$$

$$m_{sw}(t) = \begin{cases} M_{sw}, & t \in (t_2, t_3); \\ 0, & t \in (t_0, t_2) \cup (t_3, t_0 + T). \end{cases}$$

Let $\mu_{s}(t) \equiv \mu_{s}$ and $\mu_{w}(t) \equiv \mu_{w}$ be constants independent of $t$. Finally, we assume

$$\gamma_{s}(t) = \begin{cases} \gamma, & t \in (t_0 + \tau_{ws}, t_2); \\ 0, & t \in (t_0, t_0 + \tau_{ws}) \cup (t_2, t_0 + T). \end{cases}$$
Two features of migratory birds

- No migration during summer and winter seasons.
  Convert the system of DDEs into a system of ODEs.

- The vast majority of the migratory birds eventually leave either the summer or the winter patch after the migration.
  Approximate the continuous system by a discrete system.
Dynamics of bird majority

We neglect the birds left behind and consider the dynamic system of bird majority.

- **Spring migration**: birds fly from the winter patch to the summer patch.
- **Summer breeding**: birds give births to newborns.
- **Autumn migration**: birds fly from the summer patch to the winter patch.
- **Winter refuge**: birds live at the summer patch until spring comes.

We introduce a discrete system \( \{X_n\}_{n=0}^\infty \) to approximate the dynamics of bird majority.

\[
X_{4k} \xrightarrow{\text{spring migration}} X_{4k+1} \xrightarrow{\text{summer breeding}} X_{4k+2} \xrightarrow{\text{autumn migration}} X_{4k+3} \xrightarrow{\text{winter refuge}} X_{4k+4}.
\]
Define

\[ g(z) := \frac{\Gamma(-\nu + 1)I_{-\nu-1}(z)(z/2)^{2\nu}}{\Gamma(\nu + 1)I_{\nu+1}(z)}, \]

where \( \nu := (\gamma - \mu_s)/(M_{ws} + \mu_w) \) and

\[ I_p(z) := \sum_{k=0}^{\infty} \frac{(z/2)^{2k+p}}{k!\Gamma(k + p + 1)} \]

is the modified Bessel function.
Approximate system

Let $T_1$, $T_2$, $T_3$ and $T_4$ be the time (days) during four seasons (spring, summer, autumn and winter) respectively. For $k \in \mathbb{N}$,

\[
\begin{align*}
X_{4k+1} &:= \frac{(1 - \mu_s/\gamma)K}{1 - \exp[-(\gamma - \mu_s)T_1]} \cdot g\left(\frac{2\sqrt{\gamma/K} \cdot X_{4k}M_{ws} \exp(-\mu_w T_{ws})}{M_{ws} + \mu_w}\right); \\
X_{4k+2} &:= \frac{(1 - \mu_s/\gamma)K \exp[(\gamma - \mu_s)(T_2 - T_{ws})]}{(1 - \mu_s/\gamma)K X_{4k+1} - 1 + \exp[(\gamma - \mu_s)(T_2 - T_{ws})]}; \\
X_{4k+3} &:= \frac{X_{4k+2}}{\exp(\mu_w T_3 + \mu_s T_{sw})} \cdot \frac{M_{sw}}{M_{sw} + \mu_s - \mu_w}; \\
X_{4k+4} &:= \frac{X_{4k+3}}{\exp[\mu_w (T_4 - T_{sw})]}. 
\end{align*}
\]
Approximate extinction threshold

• The threshold parameter of the approximate system

\[
\rho_0 = \frac{\exp[(\gamma - \mu_s)(T_1 + T_2 - \tau_{ws})]}{\exp[\mu_w(T_3 + T_4 - \tau_{sw}) + \mu_{ws}\tau_{ws} + \mu_{sw}\tau_{sw}]}
\times \frac{M_{ws}}{M_{ws} + \mu_w + \gamma - \mu_s} \times \frac{M_{sw}}{M_{sw} + \mu_s - \mu_w}.
\]

• The threshold parameter of the original system

\[
\rho = \rho_0 + O(\varepsilon),
\]

where \(\varepsilon := e^{-M_{ws}T_1} + e^{-M_{sw}T_3}\) is small. In practice, one has \(\varepsilon = O(10^{-4})\); see the references listed in the introduction.
A general system with stopovers

Let $x_{s,i}(t)$ with $1 \leq i \leq k$ be the number of birds in the stopover $s_i$ during spring migration. Let $x_{a,j}(t)$ with $1 \leq j \leq l$ be the number of birds in the stopover $a_j$ during autumn migration.

\[
\begin{align*}
\dot{x}_w(t) &= e^{-\mu_1 \tau_{1w}} m_{1w}(t - \tau_{1w}) x_{a,1}(t - \tau_{1w}) - (m_{w1}(t) + \mu_w(t)) x_w(t); \\
\dot{x}_{s,i}(t) &= e^{-\mu_{i-1,i} \tau_{i-1,i}} m_{i-1,i}(t - \tau_{i-1,i}) x_{s,i-1}(t - \tau_{i-1,i}) \\
&\quad - (m_{i,i+1}(t) + \mu_{s,i}(t)) x_{s,i}(t), \quad 1 \leq i \leq k; \\
\dot{x}_s(t) &= e^{-\mu_{k_s} \tau_{k_s}} m_{k_s}(t - \tau_{k_s}) x_{s,k}(t - \tau_{k_s}) - (m_{s1}(t) + \mu_s(t)) x_s(t) \\
&\quad + \gamma_s(t) x_s(t) (1 - x_s(t)/K); \\
\dot{x}_{a,j}(t) &= e^{-\mu_{j+1,j} \tau_{j+1,j}} m_{j+1,j}(t - \tau_{j+1,j}) x_{a,j+1}(t - \tau_{j+1,j}) \\
&\quad - (m_{j+1,j}(t) + \mu_{a,j}(t)) x_{a,j}(t), \quad 1 \leq j \leq l.
\end{align*}
\]
Approximate system

Let $T_1$, $T_2$, $T_3$ and $T_4$ be the days during four seasons respectively. For $k \in \mathbb{N}$,

$$
X_{4k+1} := \frac{X_{4k} \exp[(\gamma - \mu_s)T_1]}{\exp[\sum_{i=0}^{k} \mu_{i+1}T_{i+1}]} \prod_{i=0}^{k} \frac{M_{i+1}}{M_{i+1} + \mu_{s,i} - \mu_s + \gamma} + c_2X_{4k}^2 + \cdots;
$$

$$
X_{4k+2} := \frac{\left(1 - \frac{\mu_s}{\gamma}\right)K \exp[(\gamma - \mu_s)(T_2 - \tau_{ws})]}{\left(1 - \frac{\mu_s}{\gamma}\right)X_{4k+1}} - 1 + \exp[(\gamma - \mu_s)(T_2 - \tau_{ws})],
\tau_{ws} := \sum_{i=0}^{k} \tau_{i+1};
$$

$$
X_{4k+3} := \frac{X_{4k+2} \exp[-\mu_wT_3]}{\exp[\sum_{j=0}^{l} \mu_{j+1,j}T_{j+1,j}]} \prod_{j=0}^{l} \frac{M_{j+1,j}}{M_{j+1,j} + \mu_{a,j+1} - \mu_w};
$$

$$
X_{4k+4} := \frac{X_{4k+3}}{\exp[\mu_w(T_4 - \tau_{sw})]},
\tau_{sw} := \sum_{j=0}^{l} \tau_{j+1,j}.
$$
Approximate extinction threshold

- The threshold parameter of the approximate system

\[
\rho_0 = \frac{\exp[(\gamma - \mu_s)(T_1 + T_2 - \tau_{ws})]}{\exp[\mu_w(T_3 + T_4 - \tau_{sw}) + \sum_{i=0}^{k} \mu_{i,i+1} \tau_{i,i+1} + \sum_{j=0}^{l} \mu_{j+1,j} \tau_{j+1,j}]} \times \prod_{i=0}^{k} \frac{M_{i,i+1}}{M_{i,i+1} + \mu_{s,i} - \mu_s + \gamma} \times \prod_{j=0}^{l} \frac{M_{j+1,j}}{M_{j+1,j} + \mu_{a,j+1} - \mu_w}.
\]

- The threshold parameter of the original system

\[
\rho = \rho_0 + O(\varepsilon),
\]

where \( \varepsilon := \sum_{i=0}^{k} e^{-M_{i,i+1}T_1} + \sum_{j=0}^{l} e^{-M_{j+1,j}T_3} \) is small. In practice, one has \( \varepsilon = O(10^{-4}) \); see the references listed in the introduction.
Sensitivity analysis

• Suppose $M_{i,i+1} = M_{j,j-1}$ and $\mu_{s,i} = \mu_{a,j}$ for some $i$ and $j$. We have from the inequality

$$\left| \frac{d\rho_0}{d\mu_{s,i}} \right| < \left| \frac{d\rho_0}{d\mu_{a,j}} \right|$$

that $\rho_0$ is more sensitive to the change of $\mu_{a,j}$ than that of $\mu_{s,i}$.

• Therefore, if there is a serious disease occurring at a stopover during the autumn migration, it will cause more losses to the bird population than that occurring at a similar stopover during the spring migration.

• This provides a mathematical explanation for the phenomenon observed from numerical simulation by Bourouiba et al.
Discussion

Disease at one stopover (ongoing work joint with Yijun Lou and Jianhong Wu)

\[ \dot{S}_{b1} = \sigma_b R_{b1} - (m_{1w}(t) + m_{1s}(t) + d_b + \theta_b)S_{b1} - \left( \beta_b S_{b1}I_{b1} + \beta_{pb}S_{b1}I_{p1} \right)/N_1 \]
\[ + \alpha s_1 m_{s1}(t - \tau_{s1})S_{bs}(t - \tau_{s1}) + \alpha w_1 m_{w1}(t - \tau_{w1})S_{bw}(t - \tau_{w1}); \]

\[ \dot{I}_{b1} = \left( \beta_b S_{b1}I_{b1} + \beta_{pb}S_{b1}I_{p1} \right)/N_1 - (m_{1w}(t) + m_{1s}(t) + d_b + \gamma_b + \varepsilon_b)I_{b1} \]
\[ + \alpha s_1 m_{s1}(t - \tau_{s1})I_{bs}(t - \tau_{s1}) + \alpha w_1 m_{w1}(t - \tau_{w1})I_{bw}(t - \tau_{w1}); \]

\[ \dot{R}_{b1} = \gamma_b I_{b1} + \theta_b S_{b1} - (m_{1w}(t) + m_{1s}(t) + d_b + \sigma_b)R_{b1} \]
\[ + \alpha s_1 m_{s1}(t - \tau_{s1})R_{bs}(t - \tau_{s1}) + \alpha w_1 m_{w1}(t - \tau_{w1})R_{bw}(t - \tau_{w1}); \]

\[ \dot{S}_{p1} = (1 - p_p)b(t, N_{p1}) + \sigma_p R_{p1} - (d_p + \theta_p)S_{p1} - \left( \beta_p S_{p1}I_{p1} + \beta_{bp}S_{p1}I_{b1} \right)/N_1; \]

\[ \dot{I}_{p1} = \left( \beta_p S_{p1}I_{p1} + \beta_{bp}S_{p1}I_{b1} \right)/N_1 - (d_p + \gamma_p + \varepsilon_p)I_{p1}; \]

\[ \dot{R}_{p1} = p_p b(t, N_{p1}) + \gamma_p I_{p1} + \theta_p S_{p1} - (d_p + \sigma_p)R_{p1}. \]
\[ \dot{S}_{bw} = \sigma_b R_{bw} - (m_{w1}(t) + d_b + \theta_b)S_{bw} - \beta_b S_{bw}I_{bw}/N_{bw} \]
\[ + \alpha_{1w} m_{1w}(t - \tau_{1w})S_{b1}(t - \tau_{1w}); \]
\[ \dot{I}_{bw} = \beta_b S_{bw}I_{bw}/N_{bw} - (m_{w1}(t) + d_b + \gamma_b + \varepsilon_b)I_{bw} \]
\[ + \alpha_{1w} m_{1w}(t - \tau_{1w})I_{b1}(t - \tau_{1w}); \]
\[ \dot{R}_{bw} = \gamma_b I_{bw} + \theta_b S_{bw} - (m_{w1}(t) + d_b + \sigma_b)R_{bw} \]
\[ + \alpha_{1w} m_{1w}(t - \tau_{1w})R_{b1}(t - \tau_{1w}); \]
\[ \dot{S}_{bs} = (1 - p_b)b(t, N_{bs}) + \sigma_b R_{bs} - (m_{s1}(t) + d_b + \theta_b)S_{bs} - \beta_b S_{bs}I_{bs}/N_{bs} \]
\[ + \alpha_{1s} m_{1s}(t - \tau_{1s})S_{b1}(t - \tau_{1s}); \]
\[ \dot{I}_{bs} = \beta_b S_{bs}I_{bs}/N_{bs} - (m_{s1}(t) + d_b + \gamma_b + \varepsilon_b)I_{bs} \]
\[ + \alpha_{1s} m_{1s}(t - \tau_{1s})I_{b1}(t - \tau_{1s}); \]
\[ \dot{R}_{bs} = p_b b(t, N_{bs}) + \gamma_b I_{bs} + \theta_b S_{bs} - (m_{s1}(t) + d_b + \sigma_b)R_{bs} \]
\[ + \alpha_{1s} m_{1s}(t - \tau_{1s})R_{b1}(t - \tau_{1s}). \]
Discussion

• Pioneering work.

• Threshold parameter?

• Reproductive ratio?

• Approximate system?

• Sensitivity analysis?

• Disease control?
Thank you!