Delay differential equations

Reproduction: \( R(t) = \begin{cases} \gamma & \text{for } a > T \\ 0 & \text{for } a \leq T \end{cases} \)

Mortality: \( \mu(a) = \delta \) for \( a > T \)

(Effectively, we've removed any age-structure among adults.)

\[ \begin{align*}
N(t) &= \int_0^T n(t,a) \, da \quad (\text{pop. dens. adults}) \\
B(t) &= \gamma N(t) \quad (\text{pop. birth rate}) \\
F(a) &= \exp\left\{ -\int_0^a \mu(x) \, dx \right\} \quad \text{for } 0 \leq a \leq T .
\end{align*} \]

Integrate transport equation over \([T, \infty)\):

\[ \dot{N}(t) - N(t,T) + \delta N(t) = 0. \]

From renewal equation:

\[ N(t,T) = B(t-T) F(T) \quad (t > T) \]

\[ \begin{align*}
\dot{N}(t) = \gamma F(T) N(t-T) - \delta N(t) \end{align*} \]

(Delay differential equation)
\[ \dot{N}(t) = \gamma N(t-T) F(T) - \delta N(t) \]

- **birth rate**
- **survival probability**
- **time**
- **units ago**
- **time**
- **T**
- **recruitment rate**
- **at present time**
- **t**

The delay differential equation is complemented by an initial condition which gives \( N \) over an interval of length \( T \):

\[ N(0) \quad \rightarrow \quad t \]

**given initial condition**

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How to "put" a delay in a given ODE like, e.g.,

\[ \dot{N} = r N \left( 1 - \frac{N}{K} \right) \]  
**logistic**

**Example** (Hutchinson 1948; May 1972)

\[ \dot{N} = r N \left( 1 - \frac{N_T}{K} \right) \]  
**delayed logistic**

with \( N_T(t) = N(t-T) \), where does the Hutchinson-May equation come from? What are the underlying i-level processes?
The Hutchinson-May equation is of the form

\[ \dot{N} = aN - bNN_T \] \( (a, b > 0 \text{ constant}) \)

First mechanism:

\[ \begin{aligned}
\text{mortality rate } & \mu(t) \\
0 & \xrightarrow{t} T \\
\text{birth rate } & 2N \\
\end{aligned} \]

Although this mechanism gives a delay-differential equation, it is not of the form of the Hutchinson-May equation 1. Note, however, that without the delay (or \( T=0 \)) both 1 and 2 become the logistic ODE.
Second mechanism.

i-states:

- \( N \): territory owner (adult)
- \( Y \): adult without territory.
- \( X_a \): juvenile of age \( a \in [0,T] \).
- \( S \): free territory.

i-processes:

\[
\begin{align*}
N & \xrightarrow{\lambda} N + X_0 \quad \text{(reproduction)} \\
S + Y & \xrightarrow{\gamma} N \quad \text{(finding territory)} \\
N & \xrightarrow{\delta} S \\
Y & \xrightarrow{\mu(a)} \uparrow \\
X_a & \xrightarrow{\uparrow} \uparrow \\
X_0 & \xrightarrow{\text{delay } T} Y \quad \text{(maturation)}
\end{align*}
\]

i-equations:

\[
\begin{align*}
\dot{N} & = \beta SY - \delta N \\
\dot{Y} & = -\beta SY - \gamma Y + 2N_T F(T) \\
\dot{S} & = -\beta SY + \delta N
\end{align*}
\]

with \( F(T) = \exp\{-\int_0^T \mu(t) \, dt\} \).
Note that $S_0 = S + N$ is constant.
Use this to eliminate $S$ from the equations:

\[
\begin{align*}
\dot{N} &= \beta (S_0 - N) Y - dN \\
\dot{Y} &= -\beta (S_0 - N) Y - \gamma Y + 2N_T F(T)
\end{align*}
\]

Assume that $I$ and $Y$ are large compared with other parameters.

$\implies$ $Y$ fast variable; $N$ slow variable.

**Fast $Y$-dynamics:**

QSS: $\dot{Y} = \frac{I}{\gamma} F(T)$

**Slow $N$-dynamics:**

\[
\dot{N} = \frac{\beta F(T)}{\gamma} (S_0 - N) N_T - dN
\]

Note that this equation is also not the Hutchinson-May equation (1), although without delay (i.e., $T = 0$) both (1) and (3) give the ordinary logistic equation.
Third mechanism.

\[ N \quad \text{territory owner who has}
\text{sufficiently settled down to}
\text{start reproducing.} \]

\[ Y \quad \text{free individuals}
\text{(i.e., without a territory)} \]

\[ S \quad \text{unoccupied territory} \]

\[ Z_a \quad \text{territory owner who is still}
\text{in the phase of preparing}
\text{herself and the territory}
\text{for reproduction, (a \in [0, T])} \]

\[ N \xrightarrow{\lambda} N + Y \quad \text{(reproduction)} \]

\[ S + Y \xrightarrow{\beta} Z_o \quad \text{(occupying territory)} \]

\[ Z_o \xrightarrow{\text{delay } T} N \quad \text{(preparing for repro)} \]

\[ N \xrightarrow{\delta} S \]

\[ Z_a \xrightarrow{\mu} S \quad \text{(death)} \]

\[ Y \xrightarrow{\gamma} t \quad \text{(notice in now age-independent)} \]
\[ \dot{N} = z(t, T) - \delta N \]
\[ \dot{y} = 2N - \beta SY - YY \]
\[ z(t, a) = B(t-a) F(a) \]
\[ B(t) = \beta SY \]
\[ F(a) = e^{-\mu a} \]
\[ s = -\beta SY + \delta N + \mu \int_0^T z(t, a) \, da. \]

Note that \( S_0 = N(t) + \int_0^T z(t, a) \, da \) is constant.

Also define \( z(t) = \int_0^T z(t, a) \, da \).

\[ \Rightarrow \begin{cases} 
    \dot{N} = \beta (S_0 - N - Z) y T F(t) - \delta N \\
    \dot{y} = 2N - \beta (S_0 - N - Z) y - YY 
\end{cases} \]

From the transport equation:

\[ \Rightarrow \dot{z}(t) + z(t, a) \bigg|_0^T + \mu z = 0 \]

\[ \iff \dot{z}(t) + \beta (S_0 - N - Z) y T F(t) - \beta (S_0 - N - Z) y + \mu z = 0 \]
Assume that $I$ and $Y$ are large compared with the other parameters. (Interpret $Y$)

**Fast $Y$-dynamics**

QSS: $Y = \frac{2}{\delta} N$

**Slow $(N,Z)$-dynamics**

\[
\dot{N} = \beta (S_0 - N_T - Z_T) \frac{2}{\delta} N_T F(L) - 8 \delta N
\]
\[
\dot{Z} = -\beta (S_0 - N_T - Z_T) \frac{2}{\delta} N_T F(L) + \beta (S_0 - N - Z) \frac{2}{\delta} N - N Z
\]

There are two equations in an essential way, i.e., we cannot eliminate one or the other by separation of time scales.

Without delay ($T=0$ and hence $Z=0$) system (4) becomes the ordinary logistic equation.

But with the delay, we still don't have recovered the Hutchinson-Verhulst equation.

But we've had some practice with deriving delay diff. equations.