Study of a population model:
the Yoccoz-Birkeland model.

February 26, 2009

Figure: Bank vole (*Clethrionomys glareolus*)
Main reference:

Sylvain Arlot,
*Étude d’un modèle de dynamique des populations*,
http://www.di.ens.fr/~arlot/

Summary:

1. Description of biological characteristics of the population of *Microtus epiroticus* (sibling vole) on Svalbard Isles in the Arctic Ocean.

2. Description of the mathematical model and available theoretical results.

3. Simulations.
Where...?
Biological description

Figure: History
Biological description

- Fertility depends on population density: few good reproduction spots whose quality decreases as the population increases;
- No significant predation, but high oscillations of population: 1 ÷ 100 (not due to lack of food);
- Seasonal factor: harsh and non stable weather conditions;
- High fertility and variable sexual maturation time.

Find a simple deterministic model that includes all these aspects and produces complicated behavior for suitable values of its parameters.
Model description.

- $t$: time measured in years
- $N(t)$: active *female* population at time $t$;
- $A_0$: maturation age;
- $A_1$: maximal age;
- $S(\alpha)$: probability to survive up to $\alpha$ years;
- $m(N)$: annual individual reproduction rate for a population of $N$ individuals;
- $m_\rho(t)$: seasonal factor (reproduction probability at time $t$ of the year).
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\[ N(t - \alpha) \]
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N(t - \alpha) m(N(t - \alpha)) \Delta\alpha
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$$N(t - \alpha)m(N(t - \alpha))\Delta\alpha m_\rho(t - \alpha)S(\alpha)$$

$$N(t) = \int_{A_0}^{A_1} N(t - \alpha)m(N(t - \alpha))m_\rho(t - \alpha)S(\alpha)d\alpha$$
Model description: possible choices

- survival probability: \( S(\alpha) = 1 - \frac{\alpha}{A_1} \)

\( A_1 = 2 \)

\( A_0 = 0.14 \) (50 days)

\( m_0 = 50 \)

\( \rho = 0.7 \) (winter lasts about 8-9 months)
Model description: possible choices

- survival probability: $S(\alpha) = 1 - \frac{\alpha}{A_1}$

- fertility:

$$m(N) = \begin{cases} m_0 & \text{if } N \leq 1 \\ m_0 N^{-\gamma} & \text{if } N > 1 \end{cases} \quad \gamma \geq 1$$

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  \]

- seasonal factor:
  \[
  m_\rho(t) = \begin{cases} 
    0 & \text{if } 0 \leq t < \rho \mod 1 \\
    1 & \text{if } \rho \leq t < 1 \mod 1
  \end{cases}
  \]
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- $A_1 = 2$
- $A_0 = 0.14$ (50 days)
- $m_0 = 50$
- $\rho = 0.7$ (winter lasts about 8-9 months)
Mathematical analysis: first remarks

\[ N(t) = \int_{A_0}^{A_1} N(t - \alpha) m(N(t - \alpha)) m_\rho(t - \alpha) S(\alpha) d\alpha \quad t \geq 0 \]

- the value of \( N \) at time \( t \) depends on which was the situation in \([t - A_1, t - A_0]\)
- if \( N(s) \) is known for \( s \in [-A_1, 0] \), then the equation allows direct computation of \( N(t) \) for \( t \in [0, A_0] \)
- inductively, \( N(t) \) can be computed for \( t \in [(k - 1)A_0, kA_0], \ k \in \mathbb{N} \)
- compatibility condition

\[ N(0) = \int_{A_0}^{A_1} N(-\alpha) m(N(-\alpha)) m_\rho(-\alpha) S(\alpha) d\alpha \]

- non stationary (but 1-periodic in time) equation
Mathematical analysis: towards the dynamical system

Evaluation at integral multiples of the period:

\[ N(k) = \int_{A_0}^{A_1} N(k - \alpha) m(N(k - \alpha)) m_\rho(k - \alpha) S(\alpha) d\alpha \]

\[ = \int_{A_0}^{A_1} N(k - \alpha) m(N(k - \alpha)) m_\rho(-\alpha) S(\alpha) d\alpha \]

In other words, the function \( Y_k(s) = N(k + s), \ s \in [-A_1, 0], \)
satisfies the equation

\[ Y(0) = \int_{A_0}^{A_1} Y(-\alpha) m(Y(-\alpha)) m_\rho(-\alpha) S(\alpha) d\alpha \]

is a reasonable picture of the situation at time \( k \)

is a good choice as a state variable.

in which phase space?
Mathematical analysis: towards the dynamical system

Consider the set \( \mathcal{Y} \) of continuous functions \( Y : [-A_1, 0] \to \mathbb{R} \) such that

\[
Y(0) = \int_{A_0}^{A_1} Y(-\alpha) m(Y(-\alpha)) m_\rho(-\alpha) S(\alpha) d\alpha
\]

Then:

- take any initial condition \( Y_0 \in \mathcal{Y} \)
- find the unique solution \( N \) of the model equation such that \( N(s) = Y_0(s) \) for \( s \in [-A_1, 0] \)
- the functions \( Y_k(s) = N(k + s) \), \( s \in [-A_1, 0] \), belong to \( \mathcal{Y} \) for all \( k \in \mathbb{N} \)
- obtain the 1-period map \( T : \mathcal{Y} \to \mathcal{Y} \), \( T(Y_0) \) := \( Y_1 \)
- observe that \( Y_k = T^k(Y_0) \)
- \( Ym(Y) = m_0 \min\{Y, Y^{1-\gamma}\} \) is \( L \)-Lipschitz continuous \( \Rightarrow T \) is Lipschitz continuous with constant \( (A_1 - A_0) L \).
Mathematical analysis: global attractor?

Some assumptions:

- $\gamma \geq 1$
- $A_1 \geq \max\{2A_0, A_0 + 1\}$
- $m_0c_0 := m_0 \int_{A_0 + \rho}^{A_0 + 1} S(\alpha) d\alpha > 1$

The last condition is a worst case condition: a single female ($N = 1$) that becomes fertile at the beginning of winter (so that it can proliferate only at the age of $A + \rho$) will give birth in the following summer to more than one baby that will survive.

Indeed it is used to exclude extinction:

- for every initial condition $Y_0 \neq 0$, if $k$ is sufficiently large, then

$$\frac{c_0 m_0}{2} \left( 1 - A_0 \right)^2 \leq T^k(Y_0)(s) \leq N_{\text{max}} \quad \forall s \in [-A_1, 0]$$

where $N_{\text{max}} = m_0 \frac{A_1}{2} \left( 1 - \frac{A_0}{A_1} \right)^2$
Mathematical analysis: global attractor?

Moreover, the solutions $N(t)$ of our integral equation becomes Lipschitz continuous as soon as they leave the initial interval:

- $|N(t_1) - N(t_2)| \leq L |t_1 - t_2|$ if $t_1, t_2 \geq 0$ with
  \[ L := m_0 \left( 3 - \frac{A_0}{A_1} \right) \]

Define the set $\mathcal{K} \subset \mathcal{Y}$ of functions $Y$ such that

- $\frac{c_0 m_0}{2} N_{max}^{1-\gamma} \leq Y(s) \leq N_{max}$ for $s \in [-A_1, 0]$
- $Y$ is $L$-Lipschitz continuous

Then $\mathcal{K}$:

- is compact w.r.t. the uniform convergence
- is invariant $T(\mathcal{K}) \subset \mathcal{K}$
- is eventually absorbing: $T^k(Y) \in \mathcal{K}$ if $k$ is large enough and $Y \not\equiv 0$
Let
\[ \Lambda := \bigcap_{k \in \mathbb{N}} T^k(K) \]
then
- \( \Lambda \) is a compact subset of \( \mathcal{Y} \)
- \( T(\Lambda) = \Lambda \)
- for every neighborhood \( U \) of \( \Lambda \) and every initial datum \( Y \in \mathcal{Y} \) we have that \( T^k(Y) \in U \) for every \( k \) large enough
- \( \Lambda \) is a global attractor for the dynamical system \( (T^k)_{k \in \mathbb{N}} \) on \( \mathcal{Y} \).
Simulations: discretization of the model

- divide each year into \( p = 100 \) intervals of length \( h = 1/p \)
- \( n_i \): number of births in the interval \( I_i := [(i-1)h, ih] \)
- \( N_i \): mean value of mature population in \( I_i \)
- \( e_i \): mean value of the seasonal factor \( m_\rho \) in \( I_i \)
- \( s_i \): fraction of surviving mature females that were born \( i \) time intervals before

then

\[
\begin{align*}
n_i &= N_i \times m(N_i) \times e_i \times h \\
N_i &= \sum_{k=1}^{2p} s_k \times n_{i-k}
\end{align*}
\]

Given the initial condition \( (n_i)_{1 \leq i \leq 2p} \), the system allows to compute \( n_i \) for all \( i > 2p \).
Simulations: initial conditions

Figure: initial condition 1
Simulations: initial conditions

Figure: initial condition 2
Simulations: bifurcation diagrams

- fix $A_1 = 2$ and $m_0 = 50$
- play with $A_0$, $\rho$, $\gamma$
- calculate $N_i$ up to $i = 20000$ and plot $(N_i)_{19001 \leq i \leq 20000}$ for different values of the parameters

For example, fix also $A_0 = 0.18$ and $\rho = 0.41$, while moving $\gamma$ in $[2, 16]$
Simulations: bifurcation diagrams

\[ A_1 = 2 \ ; \varepsilon = 0 \ ; m_0 = 50 \ ; \text{m(N) C}^1 \ ; 100 \text{ pas de temps par an} \]

\[ A_0 = 0.18 \ ; \rho = 0.41 \ ; \gamma \text{ variable} \ ; 19000 \leq t \leq 19999 \]
Simulations: bifurcation diagrams

...or fix $A_0 = 0.18$ and $\gamma = 8.25$ and move $\rho$ in $[0, 0.5]$...
Simulations: bifurcation diagrams

\[ A_1 = 2; \, \varepsilon = 0.1; \, m_0 = 50; \, m(N) \, C^1; \, 100 \text{ pas de temps par an} \]

\[ A_0 = 0.18; \, \rho \text{ variable}; \, \gamma = 8.25; \, 19001 \leq t \leq 20000 \]
Simulations: visualization of an attractor

The discretized phase space is a point in $\mathbb{R}^{201}$

$$Y_k^{(201)} = (N_i)_{100k \leq i \leq 100k+200} \in \mathbb{R}^{201}$$

Instead, project $\pi : \mathbb{R}^{201} \to \mathbb{R}^3$ by taking only

$$Y_k^{(3)} = (N_{100k}, N_{100(k+1)}, N_{100(k+2)}) \in \mathbb{R}^3.$$ 

It is like considering only the values $(N(t), N(t+1), N(t+2))$ in the continuous time model for $t \in \mathbb{N}$ and, actually, $10002 \leq t \leq 19998$.

Example: $A_0 = 0.18$, $\rho = 0.30$, $\gamma = 8.25$
Simulations: visualization of an attractor

\[ A_0 = 0.1800, A_1 = 2; \rho = 0.300, \varepsilon = 0.1; m_0 = 50, \gamma = 8.25 \ m(N) \ C^1 \]

\[ 10002 \leq t \leq 19998; \ 1.1933 \leq N \leq 6.0547; \ 100 \text{ pas de temps par an ; } i_0 \text{ non-entier} \]
Simulations: injectivity of $\pi : Y^{(201)}_k \mapsto Y^{(3)}_k$

Are distant points on the attractor in $\mathbb{R}^{201}$ mapped to sufficiently distant points in $\mathbb{R}^3$?

- suitably choose a set of times $h$ (in our case they are 80) and a radius $r$ ($= 0.1$)
- for each time $h$ evaluate the supremum of the quotients

$$\frac{\| Y^{(201)}_k - Y^{(201)}_h \|_{\mathbb{R}^{201}}}{\| Y^{(3)}_k - Y^{(3)}_h \|_{\mathbb{R}^3}}$$

on all the points $Y^{(201)}_k$ that falls into the ball $B$ centered at $Y^{(201)}_h$ with radius $r$ (with respect to some $p$-norm in $\mathbb{R}^{201}$).

- plot
Simulations: injectivity of $\pi : \mathcal{Y}_k^{(201)} \hookrightarrow \mathcal{Y}_k^{(3)}$

Test de l'injectivité de la projection $L^{\infty}(\mathbb{R}^{201}) \rightarrow L^{\infty}(\mathbb{R}^3) ; \delta_t = 0$
Simulations: fractal dimension of the attractor

If $K$ is a compact set of a metric space, the fractal dimension of $K$ is the number

$$D(K) = \limsup_{r \to 0^+} \frac{\log N_r(K)}{-\log r}$$

where $N_r(K)$ is the minimum number of balls of radius $r$ that is needed to cover $K$.

Here the cubes

$$C_{ijk} = [ir, (i + 1)r] \times [jr, (j + 1)r] \times [kr, (k + 1)r]$$

are considered and $N_r(K)$ is the number of cubes containing at least a point of the attractor.

The slope of the graph of $\log r$ versus $\log N_r(K)$ gives the fractal dimension.
Simulations: fractal dimension of the attractor

$A_0 = 0.15 \; \rho = 0.3 \; \gamma = 8.25$; dimension fractale de l'attracteur

$log_{10}(N(r)) = -1.3289 \times log_{10}(r) + 1.1915$
Simulations: fractal dimension of the attractor

\[ D(K) \simeq \frac{4}{3} < 1.5 \]

It suggests an *a posteriori* justification of the visualization of the attractor in \( \mathbb{R}^3 \) by invoking the extension of Whitney’s theorem to compact sets of fractal dimension \( d \):

they can be visualized in \( \mathbb{R}^n \) with \( n > 2d \)

And what about the fluctuations of the population of *Microtus epiroticus* in Svalbard Isles?
Simulations: solution behavior on attractor