Fundamental Models in Population Biology

By the end of this practical, you should understand four fundamental models in population biology:

1. Lotka-Volterra model (Manica lectures).
   a) Predator-prey model.
   b) Competition model.
3. SIR model (Russell and Smith lectures).

You should be able to describe the application of each model and understand the important behaviours they exhibit.

To do:
- Download the file “popnBioAllFiles.zip” from the website and unzip the contents to a new folder.
- You will use these MATLAB interfaces to learn about the models.

Background

The response of two populations to each other can take a multitude of forms: ranging from neither population having any significant effect on the other to one eradicating the other, or from independent fluctuations to coupled oscillations. Any external factors influencing the two populations, i.e. the environment, additional predators and competitors, further complicate dynamics thus creating a difficult modelling task. Basic models of isolated interactions between two populations have therefore been developed to help us identify the fundamental patterns and understand the underlying processes behind those observed behaviours.

1. a) Lotka-Volterra predator-prey model

The model

The basic Lotka-Volterra predator-prey model is comprised of a pair of differential equations modelling the number of prey and predator individuals. In the simplest version of the model, the prey population in the absence of predators is assumed to grow exponentially (unbounded); we will call this version model A. A more complex version of the model assumes a logistic growth for the prey (bounded to the carrying capacity), thus accounting for intraspecific competition; we will call this version model B. In both models, the predator population in the absence of prey is assumed to decline exponentially. When both preys and predators are present, the prey are assumed to be removed at a rate proportional to the frequency of encounters between predators and prey, and predator birth rate is dependent on this prey removal term combined with the predator efficiency at converting this food into new offspring.
Model A – exponential growth of the prey population (i.e. no intraspecific competition)

\[
\frac{dH}{dt} = aH - bHL \\
\frac{dL}{dt} = mL - nL
\]

Equilibrium points: (0, 0) and \( \left( \frac{n}{m}, \frac{a}{b} \right) \).

Model B – logistic growth of the prey population (with intraspecific competition)

The addition of the extra term in the prey population equation represents intraspecific density dependence; that is, the prey population will now increase up to a population size of \( k \), at which it is bounded, as a result of within species competition.

\[
\frac{dH}{dt} = aH(1 - \frac{H}{k}) - bHL \\
\frac{dL}{dt} = mL - nL
\]

Equilibrium points: (0, 0), \( (k, 0) \) and \( \left( \frac{n}{m}, \frac{a}{b} \left( 1 - \frac{n}{mk} \right) \right) \).

\( H \) = number of individuals in the prey population.  
\( L \) = number of individuals in the predator population.  
\( a \) = intrinsic prey growth rate.  
\( b \) = attack rate.  
\( n \) = predator mortality rate.  
\( m \) = efficiency rate of conversion of “attacked” prey into new predator offspring.  
\( k \) = carrying capacity of the prey population.

To do:

- Open MATLAB and set the current folder to the folder you extracted the zipped files to.
  - If you are using a university computer, find MATLAB by clicking through: Start > All Programs > Spreadsheets Maths and Statistics > Matlab.
- Double click on “LotkaCycles.m” in the “Current Folder” window. Be sure to click on the .m file rather than the .fig file.
- Once the Editor is open, run the code by clicking on the green play button and wait for the interface to load.

Task

You will use the interface to explore the dynamics of both model A and B by varying the parameter values. The interface will open with model A as fitted to data presented in Elton & Nicholson (1942) on how the lynx
population responds to the hare population in Canada. Note how the initial parameter values provide a model prediction that offers a good estimation of the pattern observed in the data.

To do:

Model A

- Turn Model A “On” under the “Model Selection” section in the top-left of the screen.
  1. Move the “a” slider to vary the hare birth rate.
     a. How does this influence the hare and lynx population sizes?
     b. Why do you think this happens?

Model B

- Turn Model B “On” under the “Model Selection” section in the top-left of the screen.
  2. Observe the new behaviour after the addition of bounded prey growth.
     a. How does the introduction of intraspecific density dependence change the dynamics of the model, i.e. how does the behaviour in model B differ from model A?
  3. Play with all of the parameter sliders to explore the changes in the dynamics.
     a. Give a set of parameter values for which the two populations cannot coexist (i.e. there is no positive non-trivial equilibrium).
     b. In this case, where does the population tend to?
     c. Give a set of parameter values which results in the lynx population dying out.
     d. Slowly vary each of the parameter sliders and observe which parameters have a significant effect on returning the system to coexistence.
1. **b) Lotka-Volterra competition model**

*The model*

This model represents two species which are competing for a common resource; an additional term is included within the previous logistic prey growth Lotka-Volterra model to incorporate this interspecific competition. In the absence of the competitive species, the remaining population will eventually grow to be bounded at the carrying capacity.

\[
\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right) \quad \frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2 + \alpha_{21} N_1}{K_2} \right)
\]

Equilibrium points: \((0, 0), (0, K_2), (K_1, 0)\) and \(\left( \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}}, \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}} \right)\).

\(N_1\) = number of individuals in population 1. \(r_1\) = intrinsic growth rate of population 1. \(\alpha_{12}\) = competitive effect of population 2 on population 1. \(K_1\) = carrying capacity of population 1.

*Task*

You will use the interface to explore the dynamics of a system with both intra and interspecific competition. Consider the example system of two parasitoid wasp species *Melittobia digitata* and *Nasonia vitripennis*, which share a host resource in the pupa of flesh fly of the genus, *Sarcophaga*; assume that this is the only suitable host for both species and that the number of available hosts remains constant.
To do:

- Double click on “LotkaCompetition.m” in the “Current Folder” window and run the code.

1. Consider the phase portrait.
   a. Can the long term dynamics of the system be influenced by adjusting the initial numbers of individuals in each population?
   b. Estimate the range of initial conditions where *M. digitata* dominates.
   c. Check your estimate by altering the values in the initial population size boxes.

2. Vary the effect of interspecific competition on both species of wasp by moving the “α_{12}” and “α_{21}” sliders. Keep K_1 and K_2 at the default values 114.8 and 86.8, respectively.
   a. Use the phase portrait to estimate the level of interspecific competition required for *N. vitripennis* to always outcompete *M. digitata*, irrespective of the initial population sizes?
   b. Repeat for when *M. digitata* outcompete *N. vitripennis*.

3. Set α_{12} and α_{21} to a large value so that the situation where interspecific competition has a large effect on both species can be considered.
   a. Vary the effect of intraspecific competition on both species by altering K_1 and K_2, and study the phase plane. Persuade yourself that it is hard for coexistence to exist.
   b. Why does the level of interspecific competition influence coexistence so prominently?

2. **Nicholson-Bailey model**

*The model*

The Nicholson-Bailey model is a fundamental host-parasitoid population dynamics model. In the original form, it is a discrete time model that assumes there is one host population and one parasitoid population; the parasitoids search at random for a host within a closed population; and that the attack rate is driven entirely by the parasitoid population.

The form of the model that you will explore is an extension of the original Nicholson-Bailey model which includes spatial heterogeneity in the model (note that the model is not spatially explicit); the host search is no longer random.

\[
H_{t+1} = bH_t \left(1 + \frac{aP_t}{k}\right)^{-k} \hspace{1cm} P_{t+1} = cH_t \left(1 - \left(1 + \frac{aP_t}{k}\right)^{-k}\right)
\]

- \(H_t\) = host population density at time \(t\).
- \(P_t\) = parasitoid population density at time \(t\).
- \(a\) = searching efficiency of parasitoids.
- \(b\) = rate of host reproduction.
- \(c\) = number of parasitoids that hatch from an infected host.
- \(k\) = measure of the degree of aggregation.

*Note that as \(k \to \infty, \left(1 + \frac{aP_t}{k}\right)^{-k} \to e^{-\alpha P_t} \). This retrieves the original Nicholson-Bailey with the parasitoids randomly searching for the host: \(H_{t+1} = bH_t e^{-aP_t}\) and \(P_{t+1} = cH_t (1 - e^{-aP_t})\).*
**Task**

You will use this interface to explore the dynamics of a host-parasitoid interaction between greenhouse whiteflies and the parasitoid wasp *Encarsia formosa*. The default parameter values are based on the fit to experimental data for this system (Burnett 1958).

### To do:

- Double click on “NicholsonBailey.m” in the “Current Folder” window and run the code.

1. Consider a scenario when the level of aggregation is high by setting $k$ to a very small value.
   a. Slowly increase $k$ up to $k \approx 0.8$ and comment on how increasing aggregation influences the time it takes for the populations to reach stability.
   b. How does the long-term outcome of the populations change if $k \geq 1$?
2. Set $k$ to approximately 0.8 thus assuming some aggregation.
   a. Slowly decrease the birth rate of the whiteflies by moving the “b” slider and comment on how this affects the dynamics of both populations.
3. Set $k$ to approximately 0.4, thus assuming a high level of aggregation, and set $b$ to approximately 2.
   a. Does varying the initial population sizes have any effect on the eventual stable population sizes?

### 3. SIR model

**The model**

The SIR model is a compartmental model used in epidemiology to model the spread of a disease within a population. Any individual in a population is considered to be in one of three states: susceptible to infection, infected or recovered from the infection and therefore immune. This model assumes that: the birth and death rates are equal, the infection is not fatal and that individuals move homogeneously through the population which allows disease transmission to follow mass-action (**i.e. the rate of infection is proportional to the product of the number of susceptibles and the number of infected**).
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\[
\begin{align*}
\frac{dS}{dt} &= b(1 - p)N - \beta IS - bS \\
\frac{dI}{dt} &= \beta IS - vI - bI \\
\frac{dR}{dt} &= vI - bR + bpN
\end{align*}
\]

- \( S \) = number of susceptibles.
- \( I \) = number of infecteds.
- \( R \) = number of recovereds.
- \( N \) = total population size.
- \( \beta \) = transmission rate.
- \( v \) = recovery rate.
- \( b \) = birth and death rate.
- \( p \) = proportion vaccinated at birth.

**Task**

You will use this interface to explore the dynamics of the three compartments (S, I and R) in this model. The example scenario is based on an outbreak of influenza in a boys’ boarding school in 1978 in which one boy introduced the infection and all others had previously not been infected or vaccinated (Keeling and Rohani 2007). The default values in the interface represent the parameterised model for this example.
To do:

- Double click on “SIR.m” in the “Current Folder” window and run the code.

1. Keep the default values fixed whilst increasing the recovery rate.
   a. How does this affect the number of boys that caught influenza?
   b. Explain why this is the case.

- Return to the default values.

2. Suppose the school was smaller, try incrementally decreasing the population in the “Total number of boys” box. Remember to take the new N and then enter N-1 into the “Number initially susceptible” box.
   a. How does a smaller school size influence the proportion of boys that became infected? (Note: the graph axis scale will alter according to the initial conditions).

- Return to the default values.

3. Consider the phase plane whilst varying the birth/death rate and recovery rate (b and ν sliders).
   a. How do both of these influence the equilibrium value?

- Return to the default values.

4. Increase the rate of recovery to approximately 1. Suppose that a number of boys returned to school infected. Vary the “Number initially infected”, remembering that the “Number initially susceptible” is the new number of infected subtracted from the total number of boys.
   a. How does the increased number of initially infected boys affect the proportion of boys that become infected?

- Return to the default values.

5. Suppose we are now considering the dynamics of the infection over a long period of time and therefore births are significant.
   a. How does increasing the birth rate affect the long term dynamics of the disease?
   - Fix the birth rate at approximately 0.08.
   b. Estimate the proportion of the population that you would need to vaccinate for the disease to be eradicated.
   c. How does varying the birth rate affect this proportion?

References

