## Appendix D

## Computational Projects

These projects are designed around the computational implementation of one or more mathematical models and the use of that implementation to explore the properties of the model, and are intended to be done individually, rather than in groups. The projects should be treated as a computational experiments, with results written in the style of a lab report that is aimed at a third party with little background in the subject. The results thus need to be fully explained with such an audience in mind. A recommended structure would include:

Title: Project title, author and date.

**Abstract:** A *brief* summary of the key questions, results and conclusions. In general this should not be longer than a half page, double spaced.

Introduction: A description of the problem(s) under consideration, and any relevant background information. This section should include both a summary of the biological problem(s) being considered, as well as the mathematical modeling frameworks that will be used.

**Results and Discussion:** An integrated presentation of the results of each "experiment" and any relevant discussion. This should be written in narrative prose (that is, complete sentences that walk the reader through everything that was done), with any generated graphics and code inserted at the appropriate location.

**Conclusion:** A brief summary of the key insights obtained, and perhaps any unanswered questions that remain.

**References:** A list of all resources used in completion of the project. If a resource is used in generating a specific result or in support of specific point made in the introduction or discussion, this should be noted with a citation at the appropriate place in the report text. A specific format for citations/references is not required, but the format used should be consistent.

Note that the projects were created with the use of MATLAB in mind, and in my classes this is expected. However, the projects are not dependent on this choice, and could be handled equally well with other programming languages.

## D.3 Snowshoe hares and the Canadian Lynx

The Canada lynx (*Lynx canadensis*) — a mid-sized wild cat — is a specialist predator that preys upon the snowshoe hare (*Lepus americanus*) as a primary food source; reciprocally, the lynx is the foremost predator of the snowshoe hare. Both these species inhabit the boreal forest of northern North America and have nearly perfectly overlapping ranges of native presence. The populations of both species have been observed to oscillate with a cycle of about 10 years, making them literally a "textbook example" of cyclic predator-prey interactions and a natural test case of the Lotka–Volterra model:

$$\frac{dU}{dt} = \alpha U - \gamma UV \quad \frac{dU}{dt} = 0 \rightarrow V = \frac{\alpha}{\gamma} \quad or \quad U = 0$$

$$\frac{dV}{dt} = \epsilon \gamma UV - \beta V \quad \frac{dV}{dt} = 0 \rightarrow U = \frac{\beta}{\epsilon \gamma} \quad or \quad V = 0$$

More "correct" models may be proposed that account for intraspecies competition between prey (using the Logistic equation) and a saturated predator-response function (for example, the Holling's disk model):

- Single species exponential growth,  $\frac{dN}{dt} = kN$ , has an analytical solution of  $N(t) = N(0)e^{kt}$ . Show that this leads to a conversion of  $k = ln(R_a)$ , where  $R_a$  is an annual per capita rate and t is measured in years.
- If under optimal conditions female hares bear an average of 18 young a year, 33% of which survive the first month, the monthly survival rate of all hares more than a month old is 95%, and sexual maturity is reached at one year, compute the annual per capita reproduction rate, as measured in terms of survival to reproductive age. Also compute the per capita annual death rate of adults and the overall optimal net annual per capita growth rate. Use the latter to find  $\alpha$ .
- If 30% of lynx die per month in the absence of hares, compute an annual per capita death rate for the lynx, and use this to find  $\beta$ .
- If each lynx consumes 1 hare per day when there are 1000 hares present per square kilometer, the mass of lynx and hares are 10 kg and 1.5 kg respectively, and 10% of consumed prey mass goes towards reproduction and rearing of kittens, the annual per capita predation rate,  $\gamma$ , and the conversion (efficiency) factor for predator growth,  $\epsilon$ .
- Implement a simulation of the Lokta–Volterra model using the parameters found above; use the Forward Euler update rule of  $x(t + \Delta t) = x(t) + \frac{dx(t)}{dt} \Delta t$  with a time step of 0.001 years. Run a simulation for 40 years from a starting density of 400 hares and 1 lynx per km<sup>2</sup>, and plot the populations versus time. Additionally plot the populations on the Lynx–Hare phase plane, and add all null clines and stationary points.
- Discuss your observations, including: the amplitude and period of any observed cycles; the minimum and maximum population densities reached for each species; the

maximum rate of change of population density observed for each species; the relative timing of the peak population for each species; and the length of time that any species spends at below 1 individual per  $100 \text{ km}^2$ .

- Repeat your simulation with starting densities of (i) 800 hares and 2 lynx and (ii) 200 hares and .5 lynx per km<sup>2</sup> and discuss the similarities and differences you observe.
- Implement a modified model where the constant per capita (Malthusian/exponential) prey growth model is replaced with logistic growth; the evolution rules should be:

$$\begin{array}{rcl} \frac{dU}{dt} & = & \alpha U \left( 1 - \frac{U}{K} \right) & - & \gamma U V \\ \frac{dV}{dt} & = & \epsilon \gamma U V & - & \beta V \end{array}$$

Repeat the simulations done with the Lotka–Volterra model, using the same parameters as above and a hare carrying capacity of 3000 per  $\rm km^2$ , repeat the simulations. Discuss any similarities and differences you observe.

• Next, implement a modified model where prey have constant per capita growth, but the predator response follows the Holling's disk equation; the evolution rules should be:

$$\frac{dU}{dt} = \alpha U - \left(\frac{\gamma U}{1 + \gamma \kappa U}\right) V 
\frac{dV}{dt} = \epsilon \left(\frac{\gamma U}{1 + \gamma \kappa U}\right) V - \beta V$$

Repeat the simulations done with the Lotka–Volterra model, using the same parameters as above and a prey handling time of 4 hours. Note: for consistency with other parameters, you must convert this to be in units of *years*. Discuss any similarities and differences you observe.

• Finally, combine the above, implementing a modified model where prey follow a logistic growth model and the predator response follows the Holling's disk equation; the evolution rules should be:

$$\begin{array}{rcl} \frac{dU}{dt} & = & \alpha U \left( 1 - \frac{U}{K} \right) & - & \left( \frac{\gamma U}{1 + \gamma \kappa U} \right) V \\ \frac{dV}{dt} & = & \epsilon \left( \frac{\gamma U}{1 + \gamma \kappa U} \right) V & - & \beta V \end{array}$$

Repeat the simulations, using the same parameters as above, and discuss any similarities and differences you observe.

- Given the totality of your observations, discuss to what degree you think these model justify an interpretation that predator-prey dynamics dominate the observed 10-year cyclic variations in lynx and rabbit populations, noting that:
  - A 10-year cycle in populations has been consistently observed throughout northern North America for more than 200 years.
  - The cycles over large swaths of the continent are synchronized, but there are multiple subregions out of phase with each other.
  - Islands from which lynx have been extirpated (i.e. gone locally extinct) preserve the 10 year cycle for hares.