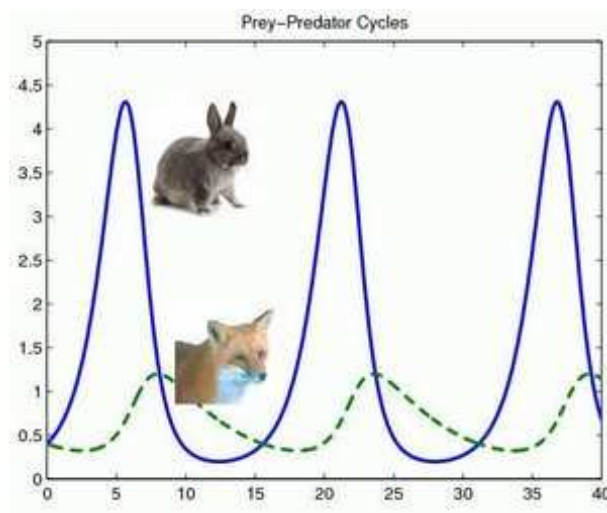


Understanding Population Modeling

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Tutorial 1

Population Dynamics

Contents

1.1	Population Event: Fixed Migration	1
1.2	Population Event: Reproduction and Finite Lifespan	2
1.3	Population Event: Population Migration	3
1.4	Population Event: Predation	4
1.4.1	Effects on Prey	4
1.4.2	Effects on Predators	5
1.5	Example: Lotka-Volterra Population Model	6
1.6	Population Event: Improved Reproduction Model	6
1.7	Population Event: Improved Predation Model	6
1.8	An Improved Predator-Prey Population Model	6
1.9	Homework	7
1.10	Appendix 1: Maple	7
1.11	Appendix 2: Population Event Summary Sheet	7

Assumption(s):

- Homogeneous Populations
- Interactions are Continuous, Not Discrete

We are using Continuous models to represent processes which may be discrete, continuous, or have aspects of both. However, sometimes it is useful to use discrete language in a continuous model. For example, in processes which involve Migration, it may be helpful to think of 5 elephants migrating together on the first Monday of every month, rather than 1 elephant migrating every 1/5th of a month. Of course, that may be more useful than thinking about 1/10th of an elephant migrating every 1/50th of a month! The actual model really represents 1/nth of an elephant migrating every 1/(5n)th of a month as $n \rightarrow \infty$. That is not always the easiest way to think about it!

1.1 Population Event: Fixed Migration

Fixed Migration refers to a constant number of members entering or leaving a population. For example, if a researcher added 3 mice into a larger mouse population every week, then that would constitute a fixed migration.

One should exercise caution when deciding whether to model a given process with Fixed Migration as circumstances leading to it are rare.

Next, we wish to determine the mathematical model which corresponds to Fixed Migration processes. Imagine that after some time period, the population of a given Species was increased by 3 members. We could write that

$$S_{n+1} = S_n + 3 \quad (1.1)$$

We could rearrange that equation and divide both sides by that time interval Δt :

$$\frac{S_{n+1} - S_n}{\Delta t} = \frac{3}{\Delta t} \quad (1.2)$$

We could approximate the left hand side with a derivative:

$$\frac{dS}{dt} = \frac{3}{\text{Time Interval Per Fixed Migration}} \quad (1.3)$$

We could appropriately generalize this to

$$\boxed{\frac{dS}{dt} \Big|_{\text{Fixed Mig.}} = \left(\frac{\Delta n_{FM}}{\Delta t_{FM}} \right) = \frac{\# \text{ Species } S \text{ entering the Population Per Fixed Migration}}{\text{Amount of Time Between Fixed Migrations}}} \quad (1.4)$$

Thus, when the derivative of a population is constant there is a fixed number of members (Δn_{FM}) migrating each time period (Δt_{FM}).

Example 1.1:

A scientist adds 3 mice to a group every 7 days. Determine the mathematical model which governs this process.

Solution 1.1:

During every Fixed Migration Period 3 mice are added so $\Delta n_{FM} = 3$. The period, Δt_{FM} is 7 days, so

$$\frac{dS}{dt} = \frac{3}{7} \text{ day}^{-1}$$

As a check on the math, we can integrate this and apply the boundary conditions. If we do this, we find

$$S(t) = S_0 + \frac{3}{7}t$$

So, when $t = 7$, we have added 3 mice to the population in agreement with the stated problem. ♣

1.2 Population Event: Reproduction and Finite Lifespan

Similar to Fixed Migration, it readily follows from Eq. (1.4) that for reproduction

$$\frac{dS}{dt} = \frac{\# \text{ Species } S \text{ Born Per Birth Event}}{\text{Time Interval Per Birth Event}} \quad (1.5)$$

For simple reproduction we expect that if we double the population, we should double the number of “babies” born and therefore double the birth rate. Thus, $dS/dt \propto S$.

We can look at this another way. Imagine that all of the members of the group give birth at the same time. In this case the numerator in Eq. (1.5) would depend on the number of members of the group (S). From either point of view, it suggests that we rewrite the numerator so that

$$\frac{dS}{dt} = \frac{\# \text{ Species } S \text{ Born Per Birth Event Per Member of Species } S}{\text{Time Interval Per Birth Event}} \times (\# \text{ of Members of Species } S) \quad (1.6)$$

or

$$\frac{dS}{dt} = \left(\frac{\# \text{ Species } S \text{ Born Per Birth Event Per Member of Species } S}{\text{Time Interval Per Birth Event}} \right) S \quad (1.7)$$

We could rewrite this as

$$\left. \frac{dS}{dt} \right|_{Birth} = \left(\frac{n_{born}}{\Delta t_{born}} \right) S \quad (1.8)$$

if we define

$$\boxed{n_{born} = \# \text{ Species } S \text{ Born Per Birth Event Per Member of Species } S} \quad (1.9)$$

and

$$\boxed{\Delta t_{born} = \text{Time Interval Per Birth Event}} \quad (1.10)$$

In this model, finite lifespan (or Death) should be treated as Negative Birth, so that

$$\left. \frac{dS}{dt} \right|_{Death} = - \left(\frac{n_{died}}{\Delta t_{died}} \right) S \quad (1.11)$$

Many models would include both reproduction and finite lifespan:

$$\boxed{\left. \frac{dS}{dt} \right|_{birth/death} = \left[\left(\frac{n_{born}}{\Delta t_{born}} \right) - \left(\frac{n_{died}}{\Delta t_{died}} \right) \right] S} \quad (1.12)$$

1.3 Population Event: Population Migration

Imagine now that we have two Populations (G and W) of the same species. Here we allow the possibility of G 's to become W 's. When would this happen? Suppose you were disturbed by the assumption that all humans are child bearing. To avoid this assumption you might subdivide the human population into 4 subpopulations:

- Pre-pubescent Girls (G)
- Child-bearing Women (W)
- Post-menopausal women (P)
- Males

As a first and fairly reasonable assumption, you would assume that the percent of girls becoming women every year is the same every year and is approximately 1/16th of the Girl population.

As before the mathematical model is similar to Eq. (1.5):

$$\frac{dG}{dt} = \frac{\# \text{ Species } G \text{ Entering Population Per Population Migration}}{\text{Time Interval Per Population Migration}} \quad (1.13)$$

The number of H 's entering the G population every migration period depends on how many H 's there are to migrate. Thus,

$$\frac{dG}{dt} = \frac{p_0 H}{\text{Time Interval Per Population Migration}} \quad (1.14)$$

where

$$\boxed{p_0 = \text{Fraction of Species } H \text{ Migrating to Species } G \text{ Per Population Migration}} \quad (1.15)$$

$$\boxed{\Delta t_{PM} = \text{Time Interval Per Population Migration}} \quad (1.16)$$

or

$$\boxed{\left. \frac{dG}{dt} \right|_{Pop. Mig.} = \left(\frac{p_0}{\Delta t_{PM}} \right) H} \quad (1.17)$$

For every member that enters population G , that many members must leave population H , so that

$$\boxed{\frac{dH}{dt} = - \left(\frac{p_0}{\Delta t_{PM}} \right) H} \quad (1.18)$$

The number of members of the G-H system does not change so that

$$\frac{d}{dt}(G + H) = 0 \quad (1.19)$$

Example 1.2:

Determine a mathematical model that represents the Population Migration of human Girls (G) into Women (W) and Women into Post-menopausal women (P).

Solution 1.2:

If we assume that the average child bearing years occur between ages 16 and 40 (these are not biological limits, they are approximate societal norms), then

$$\frac{dG}{dt} = -\left(\frac{1/16}{1 \text{ year}}\right)G \quad (1.20)$$

$$\frac{dW}{dt} = \left(\frac{1/16}{1 \text{ year}}\right)G - \left(\frac{1/(40-16)}{1 \text{ year}}\right)W \quad (1.21)$$

$$\frac{dP}{dt} = \left(\frac{1/(40-16)}{1 \text{ year}}\right)W \quad (1.22)$$

This could be a starting point for a population model for humans. Of course no one dies (or is born) in this model, they merely change categories. Thus, for this beginning stage of a larger model, the total population would be conserved. Thus,

$$\frac{d}{dt}(G + W + P) = 0$$

which can easily be confirmed. From the model it can be seen that all females eventually become post-menopausal women. ♣

It was initially mentioned that the subpopulations should be the same species. The example used different age subgroups of the same group. However, Population Migration models may also apply to populations that are often thought of as different such as *caterpillars* → *chrysalises* → *butterflies*.

1.4 Population Event: Predation

Two Populations: V are Prey (Victims) and P are Predators. Predators eat Prey during “Predation Events.”

1.4.1 Effects on Prey

As before, the analog of Eq. (1.5) for predation is

$$\frac{dV}{dt} = -\frac{\# \text{ Prey Leaving the Population Per Predation Event}}{\text{Time Interval Per Predation Event}} \quad (1.23)$$

The two quantities on the right hand side represent a quotient. Rather than divide, we can invert and multiply as per the rules of basic algebra:

$$\frac{dV}{dt} = -(\# \text{ Prey Leaving the Population Per Predation Event})(\# \text{ Predation Events Per Time}) \quad (1.24)$$

If we define

$$\boxed{n_{\text{killed}} = \# \text{ Prey Leaving the Population Per Predation Event}} \quad (1.25)$$

then

$$\frac{dV}{dt} = -n_{killed} \cdot (\# \text{ Predation Events Per Time}) \quad (1.26)$$

which may be rewritten

$$\frac{dV}{dt} = -n_{killed} \left(\frac{\# \text{ Predation Events}}{\text{Predator} - \text{Prey Encounter}} \right) \left(\frac{\# \text{ Predator} - \text{Prey Encounters}}{\text{Time Interval}} \right) \quad (1.27)$$

If we define

$$\boxed{\eta_{kill} = \frac{\# \text{ Predation Events}}{\text{Predator} - \text{Prey Encounter}}} \quad (1.28)$$

then

$$\frac{dV}{dt} = -n_{killed} \eta_{kill} \left(\frac{\# \text{ Predator} - \text{Prey Encounters}}{\text{Time Interval}} \right) \quad (1.29)$$

which may be rewritten

$$\frac{dV}{dt} = -n_{killed} \eta_{kill} \left(\frac{\# \text{ Predator} - \text{Prey Encounters Per Predator} - \text{Prey}}{\text{Time Interval}} \right) \cdot (\# \text{ Predators} \cdot \# \text{ Prey}) \quad (1.30)$$

If we define

$$\boxed{r_{encounter} = \frac{\# \text{ Predator} - \text{Prey Encounters Per Predator} - \text{Prey}}{\text{Time Interval}}} \quad (1.31)$$

$$\boxed{\left. \frac{dV}{dt} \right|_{killed} = -(n_{killed} \eta_{kill} r_{encounter}) VP} \quad (1.32)$$

1.4.2 Effects on Predators

The analog of Eq. (1.32) for predators is

$$\left. \frac{dP}{dt} \right|_{kill} = (\# \text{ Predators Entering the Predator Population Per Predation Event}) (\eta_{kill} r_{encounter}) VP \quad (1.33)$$

however the

$$\begin{aligned} & \# \text{ Predators Entering the Predator Population Per Predation Event} \\ &= \left(\frac{\text{Starvation Time} \cdot n_{born}}{\text{Reproduction Time}} \right) (\# \text{ Meals per Predation Event}) \end{aligned} \quad (1.34)$$

The idea behind the last equation is a little subtle. When Predators eat their prey, the prey population does not increase, directly. The meal only allows the predator to continue living. However, if the predator lives long enough, it will reproduce. As an example, suppose that the predator reproduces 1 time each year producing 1 child, and that a full meal will last 1 week. If the prey represents 1 full meal, then the predator needs 52 kills to live a year and produce a single offspring. In this scenario, 1/52 predators are entering the predator population each predation event. These numbers would be altered if the prey represent multiple number of predator meals, or if the number of predators born per birth event was more than 1.

Combining the previous equations yields

$$\boxed{\left. \frac{dP}{dt} \right|_{kill} = \left(\frac{\Delta t_{starvation}}{\Delta t_{reproduction}} n_{born} n_{meals} \eta_{kill} r_{encounter} \right) VP} \quad (1.35)$$

where

$$\boxed{\Delta t_{starvation} = \text{Mean time after last full meal before Predator starves to death}} \quad (1.36)$$

$$\boxed{\Delta t_{reproduction} = \text{Mean time between birth events}} \quad (1.37)$$

$$\boxed{n_{meals} = \# \text{ meals produced per predation event}} \quad (1.38)$$

1.5 Example: Lotka-Volterra Population Model

The Lotka-Volterra Predator-Prey Population Model is

$$\frac{dV}{dt} = b_g V - a_{hg} PV \quad (1.39)$$

$$\frac{dP}{dt} = -b_h P + a_{gh} VP \quad (1.40)$$

Fixed points/stability

Time Series

Phase Plots

Maps?

Bifurcation Diagrams?

Linearize system/find eigenvalues/evaluate eigenvalues

Two criticisms: exponential V, VP model not valid for large V

Analysis of Lotka-Volterra The Lotka-Volterra model is one of the earliest predator-prey models to be based on sound mathematical principles. It forms the basis of many models used today in the analysis of population dynamics. Unfortunately, in its original form Lotka-Volterra has some significant problems. As you may have noted in your experiments, neither equilibrium point is stable. Instead the predator and prey populations seem to cycle endlessly without settling down quickly. It can be shown (see any undergraduate differential equations book for details) that this behavior will be observed for any set of values of the model's four parameters. While this cycling has been observed in nature, it is not overwhelmingly common. It appears that Lotka-Volterra by itself is not sufficient to model many predator-prey systems. Context specific information must be added.

1.6 Population Event: Improved Reproduction Model

$$\frac{dS}{dt} = b_g S \left(1 - \frac{S}{S_{eq}} \right) \quad (1.41)$$

1.7 Population Event: Improved Predation Model

$$\left. \frac{dP}{dt} \right|_{kill} = \left(\frac{a_{gh} V}{1 + \frac{a_{gh}}{b_h} V} \right) P \quad (1.42)$$

$$\left. \frac{dP}{dt} \right|_{kill} = \left(\frac{a_{gh} V}{\sqrt{1 + \frac{a_{gh}^2}{b_h^2} V^2}} \right) P \quad (1.43)$$

$$\left. \frac{dP}{dt} \right|_{kill} = \left(\frac{a_{gh} V}{\left[1 + \frac{a_{gh}^n}{b_h^n} V^n \right]^{1/n}} \right) P \quad (1.44)$$

$$\left. \frac{dP}{dt} \right|_{kill} = \begin{cases} a_{VP} V P & : V < \frac{b_P}{a_{VP}} \\ b_P P & : V \geq \frac{b_P}{a_{VP}} \end{cases} \quad (1.45)$$

1.8 An Improved Predator-Prey Population Model

$$\frac{dV}{dt} = b_g V \left(1 - \frac{V}{V_{eq}} \right) - \left(\frac{a_{hg} V}{\sqrt{1 + \frac{a_{hg}^2}{b_g^2} V^2}} \right) P \quad (1.46)$$

$$\frac{dP}{dt} = -b_{h2}P + \left(\frac{a_{gh}V}{\sqrt{1 + \frac{a_{gh}^2}{b_h^2}V^2}} \right) P \quad (1.47)$$

1.9 Homework

P1.1. The dependent variables are number of servings of food, $G(t)$ (Grass), the number of herbivores, $H(t)$, and the number of carnivores, $C(t)$. As initial conditions, we will imagine that there are 1000 servings of Grass, 200 Herbivores, and 25 Carnivores.

$$\frac{dG}{dt} = -a_{hg}HG + b_gG \left(1 - \frac{G}{G_{eq}} \right) \quad (1.48)$$

$$\frac{dH}{dt} = -a_{ch}CH + \left(\frac{a_{gh}G}{1 + \frac{a_{gh}}{b_h}G} \right) H - b_{h2}H \quad (1.49)$$

$$\frac{dC}{dt} = a_{hc}HC - b_cC \quad (1.50)$$

1.10 Appendix 1: Maple

1.11 Appendix 2: Population Event Summary Sheet

See the Table on the next page.

Event	Diff. Eq.	Constant	Meaning
Fixed Migration	$\frac{dG}{dt} = f_0$	$f_0 = \frac{n_{FM}}{\Delta t_{FM}}$	$n_{FM} = \# \text{ Species } G \text{ entering the Population Per Fixed Migration}$ $\Delta t_{FM} = \text{Amount of Time Between Fixed Migrations}$
Natality/Mortality	$\frac{dG}{dt} = b_G G$	$b_G = \left(\frac{n_{born}}{\Delta t_{born}} \right) - \left(\frac{n_{died}}{\Delta t_{died}} \right)$	$n_{born} = \# \text{ Species } G \text{ Born Per Birth Event Per Member of Species } G$ $\Delta t_{born} = \text{Time Interval Per Birth Event}$ $n_{died} = \# \text{ Species } G \text{ Died Per Death Event Per Member of Species } G$ $\Delta t_{died} = \text{Time Interval Per Death Event}$
Population Migration	$\frac{dG}{dt} = c_H H$ $\frac{dH}{dt} = -c_H H$	$c_H = \frac{p_0}{\Delta t_{PM}}$	$p_0 = \text{Fraction of Species } H \text{ Migrating to Species } G \text{ Per Pop. Mig.}$ $\Delta t_{PM} = \text{Time Interval Per Pop. Mig.}$
Predation	$\frac{dG}{dt} = -a_H H G$ $\frac{dH}{dt} = a_G G H$	$a_H = n_{killed} \eta_{kill} r_{encounter}$ $a_G = \frac{\Delta t_{starvation}}{\Delta t_{reproduction}} \times n_{born} n_{meals} \eta_{kill} r_{encounter}$	$n_{killed} = \# \text{ Prey Leaving the Population Per Predation Event}$ $\eta_{kill} = \frac{\# \text{ Predation Events}}{\text{Predator-Prey Encounter}}$ $r_{encounter} = \frac{\# \text{ Predator-Prey Encounters Per Predator-Prey}}{\text{Time Interval}}$ $\Delta t_{starvation} = \text{Mean time after last full meal before Predator starves to death}$ $\Delta t_{reproduction} = \text{Mean time between Predator birth events}$ $n_{meals} = \# \text{ meals produced per predation event}$
Improved Nat./Mort.	$\frac{dG}{dt} = b_G G \left(1 - \frac{G}{G_{eq}} \right)$	G_{eq}	$G_{eq} = \text{Equilibrium Population (Carrying Capacity)}$
Improved Predation	$\frac{dG}{dt} = - \left(\frac{a_H G}{\sqrt{1 + \frac{a_G^2}{b_{G,max}^2} G^2}} \right) H$ $\frac{dH}{dt} = \left(\frac{a_G G}{\sqrt{1 + \frac{a_G^2}{b_{G,max}^2} G^2}} \right) H$	$b_{G,max}$	$b_{G,max} = b_G \text{ when there is an abundant food supply}$