

Population Viability of Wolves on Isle Royale

A teaching resource developed by Dana Paige Seidel, M.S.

Grade level:	Advanced high school
Estimated time:	1 hour
Objective:	To teach about Population Viability Analysis (PVA) for conservation and wildlife management using the NumerusOL framework and web app. Students will explore the impact of sex ratio, birth rate, density dependence, environmental and demographic stochasticity, and connectivity on the long term existence of small populations. An additional exercise within the NumerusOL web app will allow students to explore how management decisions such as to allow stocking can affect the stability of wolf populations. Although, this lesson is tailored to follow lessons on population dynamics and the unique prey-predator relationships found on Isle Royale, it can be taught entirely on its own.

This handout is meant as an outline and supplement for educators as the exercises and all information is incorporated in the online lesson found <http://www.numerusinc.com/webapps/pva>.

Numerus PVA

The Numerus On Line (NumerusOL) web app, referred to as Numerus PVA, is a flexible, easy to use platform that can be used to introduce students with no prior modelling or coding experience to population viability analysis in its most simplistic form but remains readily adaptable for more complex model structures. Numerus PVA runs directly in a web-browser environment with access via its [URL](#) or a web search using the phrase “Numerus PVA.”

Within the app’s user interface, students can build models with the option to include life stage information for one or both sexes, a variable sex ratio within the population, and three different types of density dependence mechanisms. Additionally models can include either, both, or neither environmental and demographic stochasticity with up to three subpopulations. Migration of individuals among subpopulations incorporates propensity of individuals to move by age and sex, connectivity of regions, and attractivity of regions based on some criterion such as the anticipated fitness of individuals within those regions. Harvesting and stocking management options are also included. In this lesson, students will use the app to build models of wolf populations on Isle Royale with increasing complexity utilizing some of these features within Numerus PVA. The GUI provides data fields that can be entered online and key parameters manipulated using sliders.

Numerus PVA itself was constructed using the Numerus modeling platform and the NumerusOL file conversion technology, for additional information please refer to Salter 2013, Getz et al. 2015, Getz et al. 2016 (*in prep*).

Introduction

The Isle Royale wolf and moose populations have been studied for nearly 60 years as a unique example of a single predator-prey system. But recent changes in climate have initiated cascading changes to this delicate ecosystem - potentially permanently destabilizing the island's populations.

In this lesson, we will focus not on the prey-predator dynamics but instead on the viability of the wolf population on the island given recent conditions, e.g. low birth rate, skewed sex ratios, small populations, low connectivity to mainland populations. In the course of this lesson, students will use the NumerusOL PVA web app to explore the outcomes of different management strategies on the long term probability of wolf extinction in Isle Royale.



Population Viability Analysis

Population viability analysis (PVA) is a common technique for assessing the probability that a biological population will persist for a specified period of time, generally 100 years. These models incorporate population data such as size, age classes, sex structure, and survival and birth rates to predict population size from one time step to another. Additionally these models can incorporate ecological processes through density-dependent reproduction or survival functions, viability thresholds that trigger remedial interventions (e.g. removal of individuals to protected environments), metapopulation structure, stocking, and harvesting of the population.

Exercise 1: Modeling a stable wolf population (deterministic)

What does the population trajectory for population of 300 wolves with no sex and binary age structure (young, mature) and a stable birth and survival rate look like ?

To begin to understand the kinds of population models NumerusPVA can build, we will first build a simple single-sex population model for a hypothetical wolf population.

Direct students to <http://www.numerusinc.com/webapps/pva>

From here click on the 'Viability of Isle Royale' button.

Download all linked .csvs for use in this activity.

When ready to begin, load 'isle_healthy_deterministic.csv' and click 'Parse and Upload CSV'.

Once loaded, the students will see 3 potential sections of inputs, 'Demographic Data', 'Movement and Biomass', and 'Stocking and Harvesting'. Over the course of these exercises, students will get to investigate all three but at first we begin only with the first two.

Under 'Demographic Data', should see the following once the correct .csv is loaded. *For this first exercise, we recommend students run the exercise as is before returning to this page to try some of their own numbers.*

Demographic Data			
Initial Numbers	Survival Rates	Birth Rates	Birth Max
Population 1	Population 1	Population 1	Population 1
<input type="text" value="50"/>	<input type="text" value="0.95"/>	<input type="text" value="0"/>	<input type="text" value="0"/>
<input type="text" value="250"/>	<input type="text" value="0.99"/>	<input type="text" value="5"/>	<input type="text" value="0"/>
	<input type="text" value="0.9"/>		
	Final rate accounts for senescence.		

Below this, click the 'Movement and Biomass' and examine those numbers as well:

Movement and Biomass		
Biomass Weights	Movement Propensity	Connectance
Age-class specific relative biomass.	Age-class specific movement propensity.	The region-to-region connectivity. Ignored if using a single population PVA.
Population 1	Population 1	Connectance applies as a region-to-region attractivity (or propensity). Since there is only 1 region connectivity is ignored. If your simulation has two or three subpopulations there will be entry boxes (forms) where you can enter in relative connectivity from region-to-region. E.g. a two population model has connectivity from regions 1-to-1, 1-to-2, 2-to-1, and 2-to-2.
<input type="text" value="50"/>	<input type="text" value="0"/>	
<input type="text" value="120"/>	<input type="text" value="0"/>	
		Density-dependence Parameters
		The DD parameters are the population levels at which the survival of the corresponding age classes in question are reduced by half.
		Population 1
		<input type="text" value="10000"/>
		<input type="text" value="30000"/>
		<input type="text" value="0"/>

In this exercise, we have a single two-aged single sex population. The first number under Population1 represents the number of individuals in the first age class - in our case, 50 'juvenile' wolves. The number below that represents the number of individuals in the second age class, 250 'mature' wolves.

There are 3 survival rates in the next column describing juvenile survival, mature survival, and senescing survival (survival of those that were mature in the previous time step). We have a pretty healthy population so survival is consistently high.

Birth Rates describe the average number of births per individual in each age class. In our case juvenile wolves on average do not reproduce and mature wolves have average of 5 pups per litter.

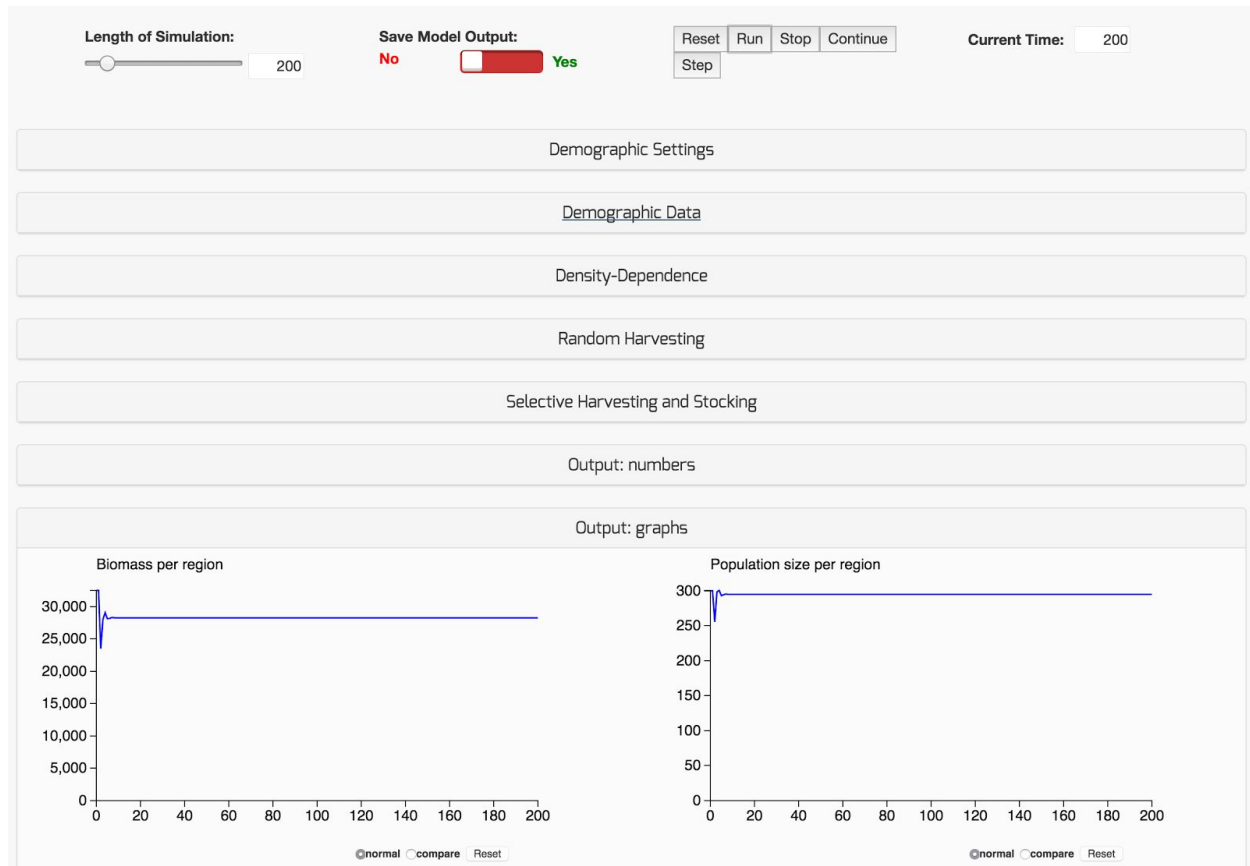
Biomass Weights refer to the specific or relative weights you expect each individual in each age class to weigh on average. Since we are talking about wolves, we chose specific weights of 50 lbs for a juvenile and 120 pounds for adults.

In a realistic environment, population levels are controlled by the carrying capacity of a landscape - in other words, the amount of live (wolf) biomass the region can support. We enter these limits as the Density-dependence parameters.

NumerusPVA can implement density dependence in 3 different ways: 1) by affecting survivorship of the youngest age classes, 2) by the oldest age classes, and/or 3) by affecting specifically mature male age-classes. In our case, we are interested in a very productive and healthy environment so our biomass weights are high (10,000 lbs for juveniles, and 30,000 lbs for adults) and we only expect density dependence to affect young and old age classes - not mature males specifically since we are not modelling a two-sex population (this is why the third value is left at 0).

Some columns like Birth Max and Movement Propensity default to 0 and are not discussed here -- these sections are not used in the current model and we will describe them as needed in later exercises. For now we are ready to click 'Generate Model' at the bottom of the page.

Once the model has been generated, students will be taken to the model page. Here, students should click run.



Given our parameters, students should see the above graphs. If they clicked the dropdown - 'Output: numbers' - students would see the final population stabilized at roughly 102 juveniles and 193 adults.



Question: What's unrealistic about these graphs? Do populations ever stay that stable from year to year? What might we be missing in our model?

The world has a level of randomness - weather, acts of god, survival, birth rates, etc all may fluctuate from year to year - we need to account for this in our simulations.

This randomness is called stochasticity, and our models can account for two types of it:

Demographic stochasticity: Random fluctuations arising from the probabilistic nature of applying vital rates to individuals at every life stage in both sexes. E.g. birth rates may vary year to year.

Environmental stochasticity: Random, environmentally-induced fluctuations, which have been applied to survivorship of the first life stage only (i.e. environmentally-induced juvenile mortality) in NumerusPVA. environmental stochasticity is an option for survivorship .

Do you think stochasticity will affect some populations more than others? Why? What type of populations?

Exercise 1A: Adding realism - understanding stochasticity

On the model page, click the drop down 'Demographic Settings' and switch on 'Demographic Stochasticity' like shown below.

Demographic Settings

Adult Female Pseudo-Extinction:

Adult Male Pseudo-Extinction:

Demographic Stochasticity: ☒ Off ☐ On

Engage Metapopulation Migration: ☒ Off ☐ On

Migration with Relative Fitness: ☒ Off ☐ On

Env. Stochasticity of Pop1:

Next, click to dropdown the 'Demographic Data' and find the 'Birth Max' fields. In our previous model, they were left at default '0' but when demographic stochasticity is turned on, birth rates can vary from year to year. The birth rates given before (0 & 5) are taken as means of a distribution ranging from zero to the Birth Max value entered. For our purposes, enter here '3' and '10' like shown below. This will mean that, in our model, juveniles still on average have 0 babies per year, but they could have up to 3 babies (a relatively small litter). Adults now have an average of 5 babies per year but could have a litter of up to 10 babies!

Demographic Data

Initial Numbers

Population 1

50

250

Birth Rates

Population 1

0

5

Survival Rates

Population 1

0.95

0.99

0.9

Final rate
accounts for
senescence.

Max Births

Population 1

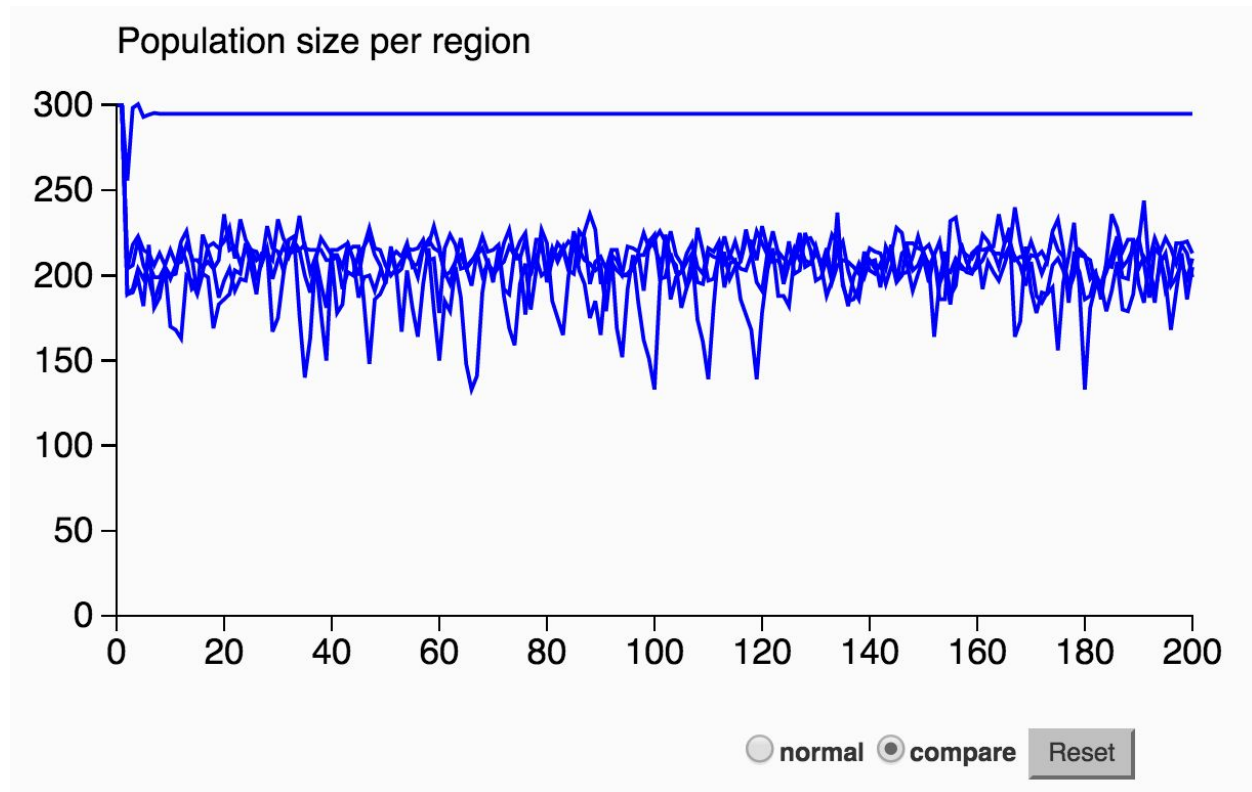
0

0

Scroll now to the top of the model page, click 'Reset' and then 'Run'.

Question: What does demographic stochasticity do to the model output? Does it seem to be incorporating realistic randomness?

Try clicking plots into the "Compare" mode and running the model with and without demographic stochasticity or with changing values of 'Environmental Stochasticity' (also found under the 'Demographic Settings' dropdown on the model page).



Question: What sorts of patterns do you see? What does environmental stochasticity do to the population level on average? Can you see a difference between graphs including the different types of stochasticity?

Note: For reference, the inputs for exercise 1A (with stochasticity) are included in the 'isle_healthy_stochastic.csv' downloaded at the beginning of this resource.

Exercise 2: Case Study, Isle Royale

So although wolves on Isle Royale have been studied for nearly 60 years, the population has been dwindling recently due to a combination of problems including inbreeding, a shortage of females, and collapse of prey populations due to climate change. How might we include these factors into our model?

First let's consider the **sex imbalance**. Recent publications have highlighted the limited number of surviving females in the population: this can be implemented into our model by our starting values for a two sex model. *Although not necessary in our case, the NumerusPVA framework can also account for sex ratio differences in the birth probability - this is the input called 'Sex Ratio'.*

For our example Isle Royale Population, which will have 2 sexes and 2 age classes: let's begin with the following numbers for male and female wolves to more accurately model the sex imbalance in the current population.

	juvenile	adult
males	5	17
females	5	8

Second, on our island where wolf populations have been ravaged by disease and their prey is dwindling we will want to adjust both the **carrying capacity of the region (density dependence parameters)** and the **survival parameters themselves**.

Return to the input page now, and load a new .csv 'isle_realwolves.csv'. Students should note that there are additional inputs because we have added a second sex to the population model. Additionally, the density dependence parameters and survival rates have been lowered to reflect the harsh life on Isle Royale.

A couple more things have changed on this page now that we have included a sex population, notably an entry field for 'Female Sex Ratio' and 'Male Maturity Age'. Both can be left at their defaults: .5 and 0 respectively.

<h2>Female Sex Ratio</h2> <p>Value from 0 to 1.</p> <h3>Population 1</h3> <div style="border: 1px solid #ccc; border-radius: 10px; padding: 10px; width: 280px; margin: 10px auto; text-align: center;">0.5</div>	<h2>Male Maturity Age</h2> <p>Integer index of first <i>mature-male</i> age class.</p> <h3>Population 1</h3> <div style="border: 1px solid #ccc; border-radius: 10px; padding: 10px; width: 280px; margin: 10px auto; text-align: center;">0</div>
---	--

Despite the imbalance in adult sex ratio, we have no evidence that conditions have changed the wolves ratio of males to females in their litters so we leave this at 0.5 -- meaning that overall, each year will bring an equal number of male and female juveniles. Since our model does not use mature male density dependence, the Male Maturity Age can be left at 0 and will have no effect in our model.

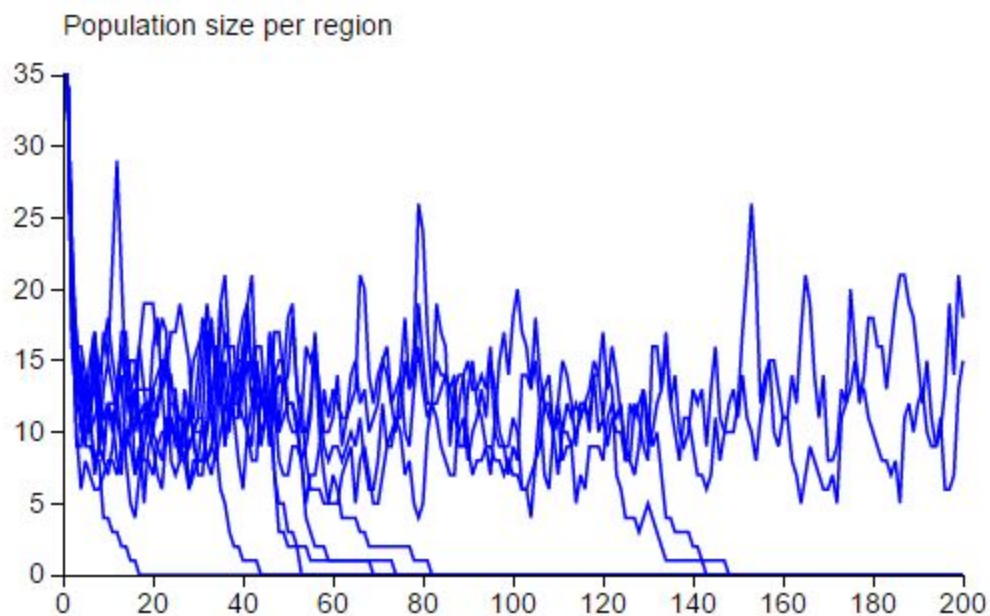
Students, feel free to try out your own parameters in this exercise, keeping in mind the real conditions that wolf populations face on such a small island.

Click 'Generate Model' again and before running the model, return to the 'Demographic Settings' tab to ensure that 'Demographic Stochasticity' is turned on, and take a moment to set 'Environmental Stochasticity' to some value - in the following plots, I have chosen a value of 0.7. Note that you can also change the Density Dependence parameters we entered earlier - representing the age-specific carrying capacity of the island.

Click plots into 'Compare' mode and run the model 10 times. Record the resulting population levels and when/if the population went extinct. For how long on average do we expect the population to persist?

Try increasing the environmental stochasticity -- what happened?

Question: Does climate change increase or decrease environmental stochasticity? Why is that bad for small populations such as ours?



Exercise 3: Can we save Isle Royale's wolves?

NumerusPVA can help managers understand the impact of potential conservation efforts or other management decisions by incorporating stocking and harvest levels as well as modelling the impact of connectivity and movement between different regions and populations.

Because of the extreme inbreeding in the Isle Royale populations threatens the population's survival, some managers might suggest stocking (periodically bringing in new animals) as a measure for

ensuring the long term survival of the island population. Others recognize that much of the population's problems come from their isolation and would like to consider means of increasing connectivity between the island population and the main land.

Consider both these possibilities with models in the NumerusPVA app.

Option 1, Stocking:

Scroll down on the model page to the 'Selective Harvesting and Stocking' Tab. Enter in the number of males or females, you want to stock to the population and at what frequency. Since we don't want to hunt or harvest any of the animals in our endangered population, leave the harvest values at 0. In the example below, we have instrumented a stocking regime of 4 animals being stocked every 10 years.

Selective Harvesting and Stocking		
Stocking Amounts	Harvesting Amounts	Frequency of Application
Population 1	Population 1	
Males	Males	Selective stocking and harvesting are applied every i^{th} and j^{th} time increment, respectively. Note: default to 1.
<input type="text" value="0"/>	<input type="text" value="0"/>	
<input type="text" value="0"/>	<input type="text" value="0"/>	
Females	Females	
<input type="text" value="0"/>	<input type="text" value="0"/>	Population 1
<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="1"/>
		<input type="text" value="1"/>

Scroll up, hit 'Reset' and then 'Run' to see how stocking influences the population levels. Feel free to go back to the inputs and try different stocking levels at different frequencies. How often would we have to stock the population to have it stabilize for 100 years?

Option 2, Increased connectivity:

Isle Royale is an island that originally had no large mammals. Moose swam over in the early 1900s and a single pair of wolves inhabited the island during the winter of 1949 after crossing an ice bridge from Ontario, Canada. At its shortest distance, the mainland is just over 14 miles from the southern tip of the island -- too far for most terrestrial mammals to cross by swimming -- resulting in very isolated populations. What if we could change this just the slightest, could that help save the wolves?



In NumerusPVA, connectivity between different regions is modeled as implicit movement of individuals along vertices of a weighted node network - each individual population being a node. Movement propensity is an age- and sex-based demographic state specifying the likelihood of emigration to another area (independent of destination). Regional connectivity is represented as an underlying matrix with entries, scaled to take values on the interval $[0,1]$, that represent the relative ease-of-transition among different nodes in the metapopulation. In other words, this parameter could represent the geographic ease of interregional migration.

Go to the input page and load the provided .csv: 'isle_twopop.csv'. Scroll down and note the new fields.

We must now enter data for a second two sex, two age population, plus there are now we want to provide inputs for the movement propensity and connectance fields.

Demographic Data					
Initial Numbers		Survival Rates		Female Sex Ratio	
Population 1	Population 2	Population 1	Population 2	Value from 0 to 1.	
				Population 1	
Males	Males	Males	Males	<input type="text" value="0.5"/>	
<input type="text" value="5"/>	<input type="text" value="50"/>	<input type="text" value="0.75"/>	<input type="text" value="0.9"/>		
<input type="text" value="17"/>	<input type="text" value="150"/>	<input type="text" value="0.9"/>	<input type="text" value="0.99"/>		
		<input type="text" value="0.85"/>	<input type="text" value="0.95"/>		
		Final rate accounts for senescence.	Final rate accounts for senescence.	Population 2	
Females	Females	Females	Females	<input type="text" value="0.5"/>	
<input type="text" value="5"/>	<input type="text" value="50"/>	<input type="text" value="0.75"/>	<input type="text" value="0.9"/>		
<input type="text" value="8"/>	<input type="text" value="200"/>	<input type="text" value="0.9"/>	<input type="text" value="0.99"/>		
		<input type="text" value="0.85"/>	<input type="text" value="0.95"/>		
		Final rate accounts for senescence.	Final rate accounts for senescence.		
Birth Rates		Max Births		Male Maturity Age	
Population 1	Population 2	Population 1	Population 2	Integer index of first mature-male age class.	
				Population 1	
<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="4"/>	<input type="text" value="4"/>	<input type="text" value="0"/>	
<input type="text" value="5"/>	<input type="text" value="5"/>	<input type="text" value="10"/>	<input type="text" value="10"/>	Population 2	
				<input type="text" value="0"/>	

In our case, interregional migration is pretty hard, so we might set this regional connectivity between population 1 and 2 to a very small value, here .05. Additionally, by coding the movement propensity with 1s and 0s, we have identified that only juvenile female and male wolves from the mainland population (population2) will be able to move between populations. *Students can adjust these values as they are curious.*

Movement and Biomass

Biomass Weights	Movement Propensity	Connectance
<p>Age-class specific relative biomass.</p> <p>Males 1</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="25"/></div> <div><input style="width: 100px;" type="text" value="70"/></div> <p>Females 1</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="20"/></div> <div><input style="width: 100px;" type="text" value="55"/></div> <p>Males 2</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="25"/></div> <div><input style="width: 100px;" type="text" value="70"/></div> <p>Females 2</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="20"/></div> <div><input style="width: 100px;" type="text" value="55"/></div>	<p>Age-class specific movement propensity.</p> <p>Males 1</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="0"/></div> <div><input style="width: 100px;" type="text" value="0"/></div> <p>Females 1</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="0"/></div> <div><input style="width: 100px;" type="text" value="0"/></div> <p>Males 2</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="1"/></div> <div><input style="width: 100px;" type="text" value="0"/></div> <p>Females 2</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="1"/></div> <div><input style="width: 100px;" type="text" value="0"/></div>	<p>The region-to-region connectivity. Ignored if using a single population PVA.</p> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="1"/></div> <div><input style="width: 150px;" type="text" value="0.05"/></div> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="0.05"/></div> <div><input style="width: 150px;" type="text" value="1"/></div> <p>Density-dependence Parameters</p> <hr/> <p>The DD parameters are the population levels at which the survival of the corresponding age classes in question are reduced by half.</p> <p>Population 1</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="500"/></div> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="1500"/></div> <div><input style="width: 100px;" type="text" value="0"/></div> <p>Population 2</p> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="15000"/></div> <div style="margin-bottom: 10px;"><input style="width: 100px;" type="text" value="50000"/></div> <div><input style="width: 100px;" type="text" value="0"/></div>

Generate the model, set the Environmental Stochasticity, AND in the same drop down click to turn 'Engage Metapopulation Migration' to ON.

Demographic Settings

<p>Adult Female Pseudo-Extinction:</p> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="0"/></div> <p>Demographic Stochasticity:</p> <p>Off <input checked="" type="checkbox"/> On</p> <p>Env. Stochasticity of Pop1:</p> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="0.7"/></div>	<p>Adult Male Pseudo-Extinction:</p> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="0"/></div> <p>Engage Metapopulation Migration:</p> <p>Off <input checked="" type="checkbox"/> On</p> <p>Env. Stochasticity for Pop2:</p> <div style="margin-bottom: 10px;"><input style="width: 150px;" type="text" value="0"/></div>	<p>Migration with Relative Fitness:</p> <p>Off <input type="checkbox"/> On</p>
--	---	---

Hit run and consider the population and movement graphs. What is going on? Can such a small amount of connectivity save the wolf population on Isle Royale?

Question: Which of the two management options would you chose if you were a manager, why? Can you think of any others?

Citations and Additional Resources

Primary Literature:

Getz et al. In Prep. A Numerus Population Viability and Harvesting Analyses Web App.

Salter, R. M. 2013. Nova: A modern platform for system dynamics, spatial, and agent-based modeling. *Procedia Computer Science* **18**:1784-1793.

Secondary Sources:

Flesher, J. (2008, April 19). Watching wolves, moose -- and heat -- on Michigan island. Retrieved August 16, 2016, from

http://usatoday30.usatoday.com/tech/science/2008-04-19-2372941962_x.htm

Flesher, J. (2011, March 29). Female shortage endangers wolves on Isle Royale. Retrieved August 16, 2016, from <http://www.mprnews.org/story/2011/03/29/wolves-isle-royale>

Hadhazy, A. (2009, April 7). Gene pool jeopardy: Can Isle Royale's wolves be saved? Retrieved August 16, 2016, from

<http://blogs.scientificamerican.com/news-blog/wolf-packs-in-jeopardy-2009-04-07/>

Mlot, C. (2016, April 18). Extreme inbreeding likely spells doom for Isle Royale wolves. Retrieved August 16, 2016, from

<http://www.sciencemag.org/news/2016/04/extreme-inbreeding-likely-spells-doom-isle-royale-wolves>

Repanshek, K. (2011, April 24). How Stable Is The Future Of Isle Royale National Park's Wolf Population? Retrieved August 16, 2016, from

<http://www.nationalparkstraveler.com/2011/04/how-stable-future-isle-royale-national-parks-wolf-population7994>

Wolves and moose on Isle Royale. (2016, June 12). Retrieved August 16, 2016, from

https://en.wikipedia.org/wiki/Wolves_and_moose_on_Isle_Royale