Optimal Control Applied to Wolf and Moose Population Dynamics on Isle Royale

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Abstract

In this work, we formulate a data driven optimal control model involving differential equations to capture the population dynamics of the wolf and moose populations in Isle Royale National Park, Michigan. A numerical solver implemented in the Python language is used to obtain solutions, and these are analyzed to identify optimal strategies for augmentation of the declining wolf population.

1 Introduction

Isle Royale is an archipelago in the northwestern section of Lake Superior where wolf and moose populations have coexisted since at least the 1940s [6]. With the moose comprising 90% of the wolf's diet on Isle Royale, these animals have been the source of many studies over the previous 50 years [7, 12]. Although the wolves and moose have maintained average population sizes of around 25-50 wolves per 1000 square kilometers and 1–2 moose per square kilometer, the wolves have declined to a single pair in recent years due to genetic depression caused by inbreeding [6, 7]. Concerned that the extinction of wolves on Isle Royale would cause the moose to grow too large and negatively impact the archipelago's ecosystem, the National Park Service (NPS) has begun reintroducing wolves to the island, bringing the total wolf count up to 17 wolves by 2020 [6]. Currently, the goal is to add enough wolves to the island to rebuild the wolf population to 20-30 wolves [6]. In this paper, we develop a mathematical model and utilize optimal control theory to determine optimal strategies for the NPS to reintroduce wolves to Isle Royale in order to achieve stable wolf and moose populations. In particular, Section 2 discusses the predator-prey model we used to describe the wolf and moose population dynamics on Isle Royale. Section 3 presents our optimal control problem. Section 4 discusses our numerical simulations and their results, and Section 5 analyzes those results to provide

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insights on successful and unsuccessful augmentation strategies. Ultimately, our results suggest that successful augmentation occurs when the wolves are immediately augmented to a size of 12 and no further augmentation is implemented after the end of the first year of the augmentation period.

2 Establishing the Predator-Prey Model

2.1 Logistic Predator-Prey System

In our work, we used differential equations to model the wolf and moose populations of Isle Royale. Several sources, such as [4, 6], indicated that Isle Royale has limited resources and food for the moose. Prior to the arrival of wolves, the moose became engaged in a cycle of extreme growth followed by heavy death once their food sources became exhausted [4]. The choice to model population dynamics with a predator-prey system came about with the knowledge that the population growth of the wolves is directly tied to the moose population. The moose are such a large part of the wolves diet that their population size directly impacts how large the wolf population can become. The same can be said for the moose whose population growth is dependent on the size of the wolf population, and the amount of resources that the island contains. In order to model this limited amount of available food for the moose, we decided to model the population dynamics via a logistic predator-prey system of differential equations

$$\frac{dM}{dt} = rM(1 - \frac{M}{K}) - cMW \tag{1}$$

$$\frac{dW}{dt} = -eW + fMW, \tag{2}$$

where $r, K, c, e, f > 0$ and W and M are the number of wolves and moose on Isle Royale at time t, respectively. Logistic models utilize a parameter K called the carrying capacity, which in our problem reflects the amount of resources needed to sustain the moose, thereby preemptively incorporating a limit on how large the moose population can become. $rM(1 - \frac{M}{K})$ refers to the growth rate of the moose population that is limited by the carrying capacity. $-cMW$ refers to the death rate of moose caused by wolf and moose interactions. $-eW$ represents the death rate of wolves. Finally, fMW represents the positive effects of wolf and moose interactions for the wolf population.

2.2 Equilibrium Points

Insight into how the logistic predator-prey system behaves locally can be obtained from the system's equilibrium points, the ordered pairs (M, W) for which (1) and (2) are simultaneously 0. Setting (1) and (2) simultaneously equal to 0 and solving for M and W yields that the logistic predator-prey system's equilibrium points are (0,0), $(K, 0)$, and $(e/f, r(1 - e/(fK))/c)$. In order to classify these equilibrium points' stability, we compute the eigenvalues of the

Jacobian of the linearized right hand side of the logistic predator-prey system,

$$DF(M,W) = \begin{bmatrix} r - \frac{2rM}{K} - cW & -cM \\ fW & -e + fM \end{bmatrix},$$

at the equilibrium points. For (0,0), we obtain the eigenvalues r and $-e$. Since $e, r > 0$, one of the eigenvalues of $DF(0,0)$ is positive while the other is negative. Therefore, (0,0) is a saddle point (see Figure 1). This signifies that some nearby solutions to (0,0) will converge to the equilibrium point, thereby modelling the extinction of both populations, while others diverge from 0 in one of the two populations. The equilibrium point $(K, 0)$ has the eigenvalues $-r$ and $-e + fK$. If $e > fK$, then $(K, 0)$ attracts nearby solutions, implying that the wolves will go extinct and the moose will approach Isle Royale's carrying capacity. However, if $e < fK$, then $(K, 0)$ is a saddle point.

We now consider $(e/f, r(1 - e/(fK))/c)$. For the rest of this subsection, we will assume that $1 - e/(fK)$ is positive so that we can prescribe physical meaning to this equilibrium point's stability. $(e/f, r(1 - e/(fK))/c)$ has the eigenvalues $\left(-er \pm \sqrt{e^2r^2 - 4fK(erfK - e^2r)}\right)/(2fK)$. Since $e, r > 0$, $-er < 0$. Thus, if

$$e^2r^2 - 4fK(erfK - e^2r) < 0,$$

then $(e/f, r(1 - e/(fK))/c)$ is a spiral attractor (see Figure 2), signifying that, for nearby solutions, the sizes of the wolf and moose populations will oscillate as they eventually converge to $R(1 - e/(fK))/c$ and e/f, respectively. If

$$\sqrt{e^2r^2 - 4fK(erfK - e^2r)} < er,$$

then the equilibrium point is an attractor; nearby solutions will converge to the equilibrium point without undergoing the oscillations of the spiral attractor case. Finally, if

$$\sqrt{e^2r^2 - 4fK(erfK - e^2r)} > re,$$

then the equilibrium point is a saddle point.

Since the wolf and moose population sizes from the data have been oscillating over time, and since $(e/f, r(1 - e/(fK))/c)$ is the only equilibrium point that does not involve the extinction of either population when

$$r(1 - e/(fK))/c > 0,$$

it is desirable for $(e/f, r(1 - e/(fK))/c)$ to be a spiral attractor after we apply optimal control theory to logistic predator-prey system. Therefore, to help us determine when $(e/f, r(1 - e/(fK))/c)$ is a spiral attractor, we will rewrite

$$e^2r^2 - 4fK(erfK - e^2r) < 0$$

so that this criterion can be computed with fewer operations. We will accomplish this by rewriting the inequality so that K is expressed in terms of the other three

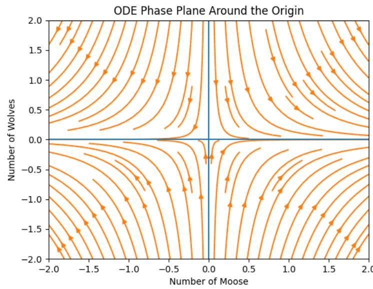

Figure 1: Example phase plane of the system centered around the EP (0,0).

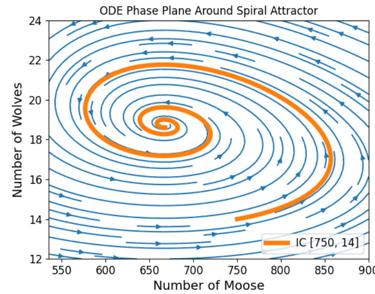

Figure 2: Example phase plane of a spiral attractor and solution curve with initial condition (750,14).

variables. Rewriting the inequality, it follows that $(e/f, r(1-e/(fK))/c)$ is a spiral attractor if

$$4f^2K^2 - 4efK - er > 0.$$

The left hand side of this inequality is a quadratic in terms of K whose vertex is $(e/(2f), -e^2 - er)$. Although $-e^2 - er < 0$, since $4f^2 > 0$, this quadratic is positive if K lies outside of the closed interval between the quadratic's zeros

$$K = \frac{e \pm \sqrt{e^2 + er}}{2f}.$$

Thus, $(e/f, R(1-e/(fK))/c)$ is a spiral attractor if

$$K > \frac{e + \sqrt{e^2 + er}}{2f} \text{ or } K < \frac{e - \sqrt{e^2 + er}}{2f}.$$

However, the right side of the second inequality is negative. Therefore, since $K > 0$, the equilibrium point is a spiral attractor when

$$K > \frac{e + \sqrt{e^2 + er}}{2f} > \frac{e}{f}.$$

2.3 Parameter Values for the Model

Following the utilization of a logistic model, literature reviews were conducted to ascertain ranges for the parameter values to fall within. Our value for r ($r = 0.371$) was based on [8]. An approximation for K ($K = 2753$) was obtained by averaging the moose carrying capacities of Isle Royale computed in simulations from [5]. The values of c, e, and f did not have direct parallels in literature; they were fit t o t he w olf a nd m oose p opulation d ata from [11] between 2004 and 2018. A copy of this data is included in Table 2 in Appendix A. A Python algorithm was created to solve the system of differential equations and which used a minimization function to fit the data via the

Relative Error		
	2004-2011	2012-2018
Moose	0.20904	0.12527
Wolves	0.13150	0.35172

Table 1: Table containing the relative ℓ_2 errors of our best fit parameters.

Levenberg-Marquardt method. This worked by minimizing the least squares error, in other words, minimizing the squared difference between the model solution and the data. Accuracy was determined by the relative error as well as visual confirmation that the general trends of the fit solution were aligning with the measured data.

The decision was made to incorporate piecewise dynamics for our e and f values because the dynamics of the wolf population changed during the final years of our time interval, largely due to inbreeding in the wolf population [6]. Since the shift in dynamics occurred only in the wolf population, the conditions for the different piecewise components were based on the value of W. The particular W value that marked the shift in the wolf population dynamics was determined by calculating the inbreeding effective population size. The inbreeding effective population size relates to "the rate of decrease in heterozygosity" across generations, and therefore provides information about "the short term survival of the population" [13]. An upper bound for the inbreeding effective population size can be computed with the formula

$$N_e = \frac{T-1}{\frac{1}{N(0)} + \frac{1}{N(1)} + \frac{1}{N(2)} + \dots + \frac{1}{N(T-1)}}, \tag{3}$$

where T is the number of years a population has existed and $N(t)$ is the population size in year t [13]. Using the data from [11], we computed that the upper bound is approximately 13.688. Moreover, according to the data from [11], the wolf population never rebounded in size when the total number of wolves was below 12. Combining this fact with the upper bound, we concluded that the inbreeding effective population size is 12 wolves. Since the wolf population dropped below 12 in 2012, we broke up our time interval from 2004-2018 into 2004-2011 (before inbreeding) and 2012-2018 (with inbreeding).

Running our least squares algorithm on these two time intervals with a variety of starting points, we obtained that the best parameter values are

$$r = 0.371;\ K = 2753;\ c = 0.015;$$
$$e(W) = \begin{cases} 0.2 & W \geq 12 \\ 0.59999 & W < 12 \end{cases};\ f(W) = \begin{cases} 0.0003 & W \geq 12 \\ 0.000217 & W < 12 \end{cases}.$$

The relative ℓ_2 error for these fits are given in Table 1 . Graphs of our best fit solutions can be found in Figures 3 and 4.

We now evaluate the locations and types of our logistic predator-prey system's equilibrium points when the model uses our best fit parameters. When

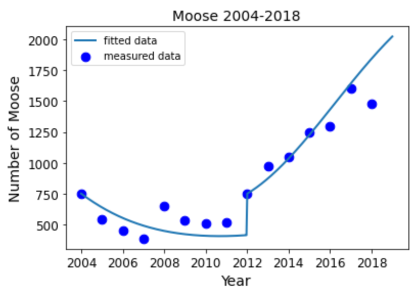

Figure 3: Model $M(t)$ solution using our best fit parameters.

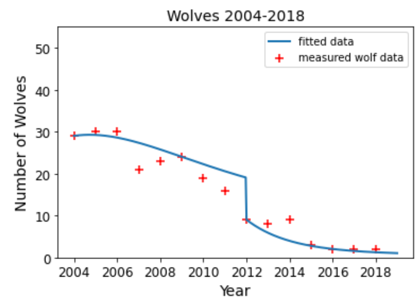

Figure 4: Model $M(t)$ solution using our best fit parameters.

$W < 12$, the equilibrium points are (0,0), (2753,0), and approximately (2764, -0.103). As stated earlier, (0,0) is a saddle point. Since $0.5999 > (0.000217)(2753) = 0.597$, (2753,0) is an attractor. Finally,

$$
\begin{aligned}
&e^2r^2 - 4fK(erfK - e^2r) \\
&\approx (0.6)^2(0.371)^2 - 4(0.0003)(2753)((0.6)(0.371)(0.0003)(2753) - (0.6)^2(0.371)) \\
&\approx 0.051 > 0.0495 \approx e^2r^2 > 0.
\end{aligned}
$$

Therefore, (2764,-0.103) is a saddle point. Extending our logistic predator-prey system in time using our best fit parameters (see Figure 5), we can see that the wolf and moose populations are converging to (2753,0), so the wolves are headed to extinction while the moose are growing to our approximated moose carrying capacity of Isle Royale. Moreover, since the W value for the equilibrium point (2765,-0.103) is negative, the logistic system has no equilibrium points in which M and W are both positive. Thus, the wolf and moose populations cannot both converge to stationary, non-extinct population sizes when $W < 12$.

When $W \geq 12$, the equilibrium points are (0,0), (2753,0), and approximately (667,18.7); (0,0) is still a saddle point. Since $0.2 > (0.0003)(2753) = 0.8259$, (2753,0) is a saddle point. Finally, since

$$\frac{e + \sqrt{e^2 + er}}{2f} = \frac{0.2 + \sqrt{(0.2)^2 + (0.2)(0.371)}}{2(0.0003)} \approx 896.6 < 2753 = K,$$

(667,18.7) is a spiral attractor. Therefore, when $W \geq 12$, it follows that the wolf and moose populations will oscillate in size over time; as long as W never drops below 12, both populations will converge to stationary, non-extinct population sizes of approximately 667 moose and 19 wolves (see Figure 6 for an example).

These computed values for the equilibrium points and the nature of the wolf and moose population dynamics described by our model capture the trends of the population dynamics and are suitable for augmentation study for multiple reasons. First, as described by our inbreeding coefficient, when the wolf population is less than 12 in size, genetic inbreeding prevents the wolf population from

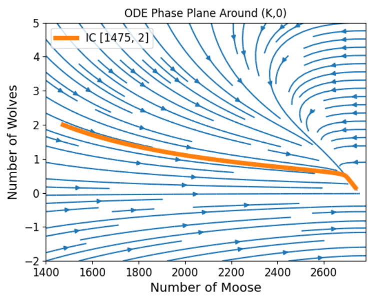

Figure 5: Phase plane around $(K, 0)$ with $W < 12$ and initial condition (2,1475).

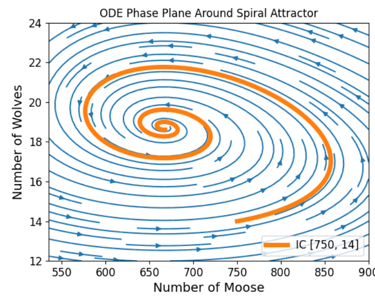

Figure 6: Phase plane around (667,19) with $W \geq 12$ and example initial condition (750,14).

successfully sustaining itself on Isle Royale, thereby causing the wolves to reach extinction and enabling the moose population to grow to the carrying capacity. On the other hand, if the wolf population does not drop below 12 in size, then genetic inbreeding does not take over the population, thereby enabling the wolves to maintain stable population dynamics. The value of $W \approx 18.7$ is an appropriate value for the spiral attractor equilibrium point because the median wolf population size before 2012 was 19.5 wolves and $18.7 > 12$. Although the value $M \approx 667$ differs from the median moose population size before 2012 (951 moose) by approximately 284 moose, this value still lies within the range of the number of moose typically observed on Isle Royale (see [6]). Moreover, our model's ability to capture the general trends in the moose population with a sufficiently small relative ℓ_2 error and accurately describe the wolf population dynamics also minimizes the significance of this difference.

In 2018, there were less than twelve wolves on Isle Royale [11]. According to our model, the wolf population is headed for extinction; in order to avoid the extinction of the wolves, it is necessary for humans to help the wolf population grow via a process like augmentation. In order for any wolf augmentation to be successful, it is necessary for the National Park service to bring the wolf population up to at least 12 wolves in such a way that the wolf population never oscillates below 12 wolves in size.

3 Optimal Control Model

Having developed a model that describes the wolf and moose population dynamics on Isle Royale, we are now ready to cast our augmentation problem as an optimal control problem. To do so, we let the term $u(t)W(t)$ represent the rate at which wolves are added to Isle Royale on a yearly basis, where $u(t)$ is our control function and $\int_0^t u(s)W(s)\,ds$ represents the number of wolves that have been added to Isle Royale by time t. We chose our augmentation term to be of this form since it reflects how the augmentation rate will depend on how many wolves are on Isle Royale at time t. Since the rate of augmentation will directly impact the growth rate of the wolves, we rewrote our logistic model as

$$\frac{dM}{dt} = rM(1 - \frac{M}{K}) - cMW \tag{4}$$
$$\frac{dW}{dt} = -eW + fMW + uW. \tag{5}$$

Also, since wolves will not be removed from Isle Royale, we imposed the restriction that $u(t) \geq 0 \; \forall \; t$.

According to [9, 10], the NPS is planning on adding 20-30 wolves to Isle Royale over a 3 year period, potentially introducing more wolves over the following 2 years if necessary, and refraining from further augmentation after then. Since wolves will be added for at most 5 years, we set our final time T to be 5 years. To represent how the NPS is wanting to initially add at most 30 wolves before evaluating if further augmentation is necessary, we imposed that

$$\int_0^T uW \, dt \leq 30.$$

We considered two initial conditions to see how different initial wolf and moose population sizes would impact our simulations. For the first case, we set $M(0) = 975$ and $W(0) = 8$, the recorded population sizes in 2013. Since the data from Isle Royale did not have any entries that had between 3 to 8 wolves, and since an initial population size of 2 to 3 wolves is not very realistic under our differential equations model's assumptions about well mixing, we used our differential equations model to compute the initial conditions $M(0) = 932$ and $W(0) = 5$.

For our problem, we considered two separate sets of performance measures. For the first one, we sought to maximize the number of wolves and moose at the end of the augmentation period while simultaneously minimizing the number of wolves that had to be augmented onto Isle Royale. In equation form, this performance measure was written as

$$\max_u W(5) + BM(5) - A\int_0^5 u^2(t) \, dt - C\int_0^5 uW \, dt, \tag{6}$$

where $A \in \{1, 20, 100\}$, $B \in \{0, 0.25, 0.5, 0.75, 1, 2\}$, and $C \in \{0, 0.5, 1, 20, 100\}$ are constants representing the weight factors of each of the terms. Our values for A were taken from the values Bodine et al used for their A weight factor in [3]. Portions of performance measures deemed more important are given higher weight values. Since the wolf augmentation plan is largely concerned with preventing the wolf population from going extinct, we evaluated that it was of greater importance to maximize the final number of wolves than the final number of moose. This was reflected by the values chosen for B (the moose weight factor) that are less than 1.

For our second performance measure, we sought to minimize the squared difference between the number of wolves present at the end of the augmentation period and 19 wolves, the approximate W value of the equilibrium point $(e/f, r(1-e/(fK))/c)$ when $W \geq 12$, in conjunction with minimizing the number of wolves that were added to Isle Royale. We prioritized getting the final wolf population as close as possible to the equilibrium point value to test whether or not that would lead to successful augmentation. In addition, although the NPS is planning on a five year augmentation phase (see [9]), we wanted to see how adjusting the length of the augmentation period would impact how the wolves are augmented. Due to this, we set our final time T to be either 5, 10, or 15 years rather than only 5 years. In equation form, this objective functional was

$$\min_u (W(T)-19)^2 + A\int_0^T u^2(t)\,dt + C\int_0^T uW\,dt, \tag{7}$$

where $A \in \{1, 20, 100, 1000\}$, $C \in \{0, 0.5, 1, 20, 100, 1000\}$, and $T \in \{5, 10, 15\}$ are constants.

In summary, our optimal control problem sought to find a function $u(t)$ that satisfied either (6) or (7) subject to the constraints

$$\begin{aligned}
&\frac{dM}{dt} = rM(1-\frac{M}{K}) - cMW \\
&\frac{dW}{dt} = -eW + fMW + uW \\
&\int_0^T uW\,dt \leq 30 \\
&u(t) \geq 0
\end{aligned}$$

and exactly one of the following initial conditions: $M(0) = 975$ and $W(0) = 8$, and $M(0) = 932$ and $W(0) = 5$.

Our different optimal control simulations were solved numerically through the GEKKO Optimization Suite, "a Python package for machine learning and optimization of mixed-integer and differential algebraic equations" ([1]). We refer the interested reader to [2] for an in depth description of GEKKO. In addition to solving our optimal control problem, we sought to determine which optimal control strategies would successfully prevent the wolf populations from going extinct. Therefore, after finding the optimal solution u^*, we solved (4)-(5) from $t = 0$ to $t = 80$ with the wolf and moose population sizes at $t = 0$ being their respective sizes at the end of the augmentation period in order to predict whether or not the wolves would go extinct after augmentation.

4 Results

For this section of our paper, we first focus on our simulations with (6) as our performance measure and then present our results using (7). The value of the objective functional for each of the following simulations is given in Table 3 in Appendix A.

4.1 Performance Measure (6)

4.1.1 Case 1: A=1; B=0,0.25,0.5; & C=1

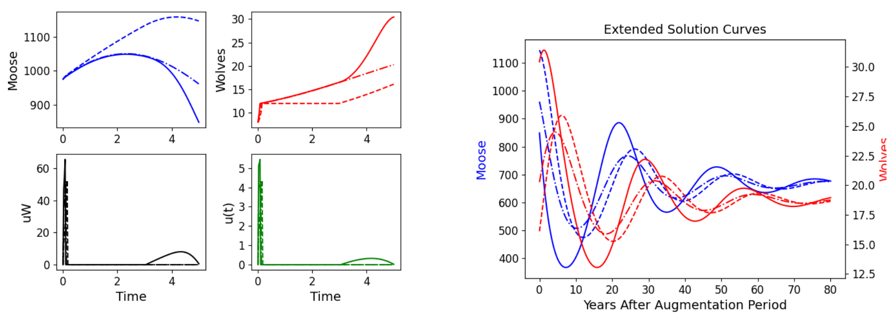

Figure 7: Simulations with performance measure (7), $A = C = 1$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, and dashed lines correspond to $B = 0$, $B = 0.25$, and $B = 0.5$, respectively.

We begin by fixing A and C and allowing B to vary, reflecting how a change in the importance of maximizing the number of moose will impact augmentation. When $A = C = 1$, we assigned little importance to the cost of wolf augmentation while varying the importance of maximizing the number of moose. Figure 7 shows our results for all values of B that yielded an optimal solution $u(t)$ when using the initial conditions $M(0) = 975$ and $W(0) = 8$. In all simulations, wolves were immediately added to obtain a population size of around 12 wolves; in the $B = 0$ simulation, the wolves underwent another augmentation that began around the start of the third year of the augmentation phase. The wolves never went extinct in any simulation. The results of the simulations with $M(0) = 932$ and $W(0) = 5$ were similar to the simulations with $M(0) = 975$ and $W(0) = 8$.

4.1.2 Case 2: A=20; B=0,0.5,1,2; & C=20

For the case of $A = C = 20$, we assigned some importance to the cost of wolf augmentation and continued to vary B. Figure 8 shows the results when $M(0) = 975$ and $W(0) = 8$. Each case avoided wolf extinction. The first three cases had immediate augmentation to bring the wolf population to around 12 in size and afterwards ceased augmentation. The $B = 2$ case was similar except the augmentation occurred later and over a longer time period. The trials when $M(0) = 932$ and $W(0) = 5$ behaved similarly except the augmentation occurred more gradually over longer time intervals. Nevertheless, all of those trials except the $B = 2$ case had all of the augmentation occur within year one.

4.1.3 Case 3: A=100; B=0,0.25,0.5,0.75; & C=100

Next, we performed the same trials with $A = C = 100$. Figure 9 shows the results for $B = 0, 0.75, 1, 2$ when $M(0) = 975$ and $W(0) = 8$. For both sets

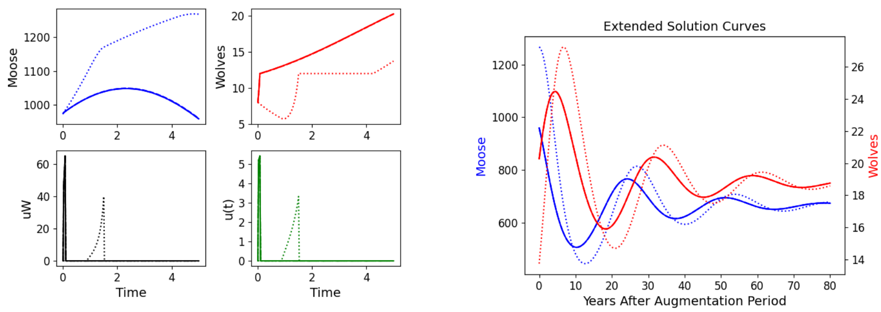

Figure 8: Simulations with performance measure (7), $A = C = 20$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $B = 0$, $B = 0.5$, $B = 1$, and $B = 2$, respectively.

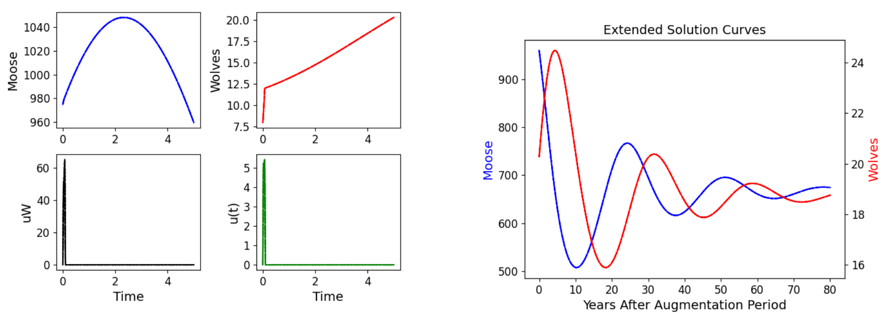

Figure 9: Simulations with performance measure (7), $A = C = 100$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $B = 0$, $B = 0.25$, $B = 0.5$, and $B = 0.75$, respectively.

of initial conditions, wolves were immediately augmented to about 12 in size; augmentation ceased after that. Wolf extinction was always avoided.

4.1.4 Case 4: A=1,20,100; B=0; & C=1

After Cases 1-3, we fixed B and C and varied A to see how the cost of augmentation shaped the augmentation. Figure 10 shows the results when $M(0) = 8$ and $W(0) = 975$. These simulations behaved similarly to the simulations with $M(0) = 975$ and $W(0) = 8$ in Case 1 in Subsection 4.1.1. In each trial, the wolf population was immediately augmented to about 12 wolves; further augmentation ceased except for the $A = 1$ case when wolves were added toward the end of the augmentation phase. All trials avoided wolf extinction. The case when $M(0) = 5$ and $W(0) = 932$ behaved similarly.

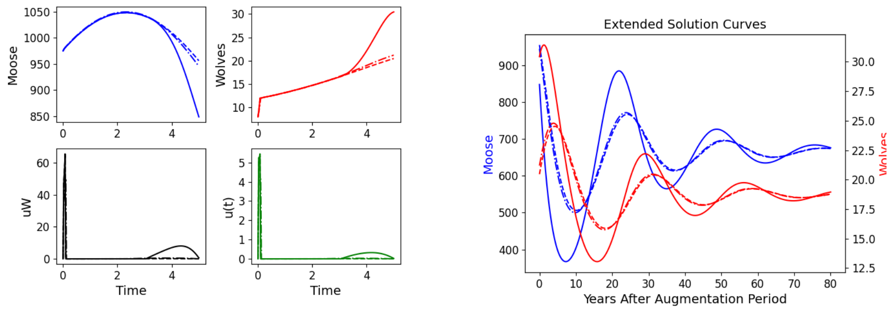

Figure 10: Simulations with performance measure (7), $B = 0$, $C = 1$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, and dashed lines correspond to $A = 1$, $A = 20$, and $A = 100$, respectively.

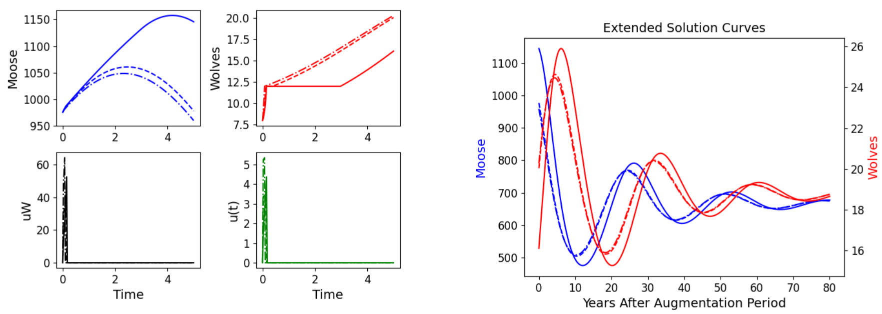

Figure 11: Simulations with performance measure (7), $B = 0.5$, $C = 1$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $A = 1$, $A = 20$, and $A = 100$, respectively.

4.1.5 Case 5: A=1,20,100; B=0.5; & C=1

Figure 11 shows when $M(0) = 8$ and $W(0) = 975$. For both initial conditions, the trials behaved similarly to the simulations in Subsection 4.1.4 except that the second augmentation phase did not occur when $A = 1$ and the augmentation was more gradual when $A = 20$, $M(0) = 932$, and $W(0) = 5$.

4.1.6 Case 6: A=20; B=0; & C=0,1,20,100

Figure 12 shows the trials when $M(0) = 975$ and $W(0) = 8$. The wolves went extinct only when $C = 0$. In that case, the wolves had immediate augmentation and a later augmentation, causing the wolves to grow to about 45 wolves by the end of the five y ears. As revealed by the extended solution curves in Figure 12, the extinction resulted from the wolves overeating the moose and then not having enough moose to sustain themselves. In the other solutions, the later augmentation did not take place; the resulting smaller wolf populations did not overeat the moose. The trials when $M(0) = 932$ and $W(0) = 5$ were similar.

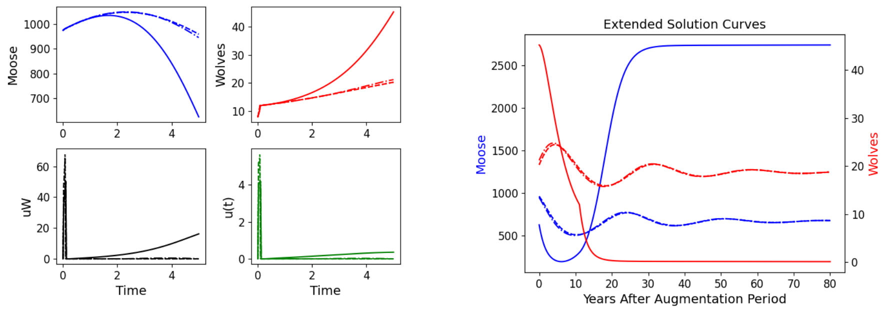

Figure 12: Simulations with performance measure (7), $A = 20$, $B = 0$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $C = 0$, $C = 1$, $C = 20$, and $C = 100$, respectively.

4.1.7 Case 7: A=20; B=0.5; & C=0.5,1,20,100

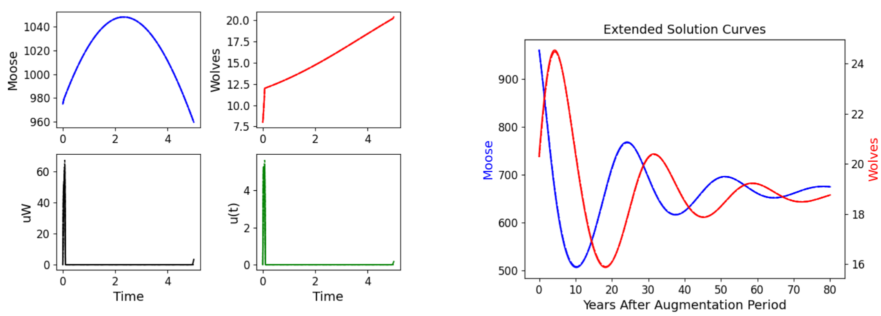

Figure 13: Simulations with performance measure (7), $A = 20$, $B = 0.5$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $C = 0.5$, $C = 1$, $C = 20$, and $C = 100$, respectively.

Figure 13 considers when $M(0) = 975$ and $W(0) = 8$. For both sets of initial conditions, the main augmentation occurred within year one; the wolves avoided extinction.

4.2 Performance Measure (7)

4.2.1 Case 8: A=1,20,100,1000; C=1; & T=5

We now consider objective functional (7). Our first trials kept C and T fixed and varied A. Figure 14 shows the results when $M(0) = 975$ and $W(0) = 8$. Similar to previous cases, both initial conditions had the augmentation occurring within the first y ear t o g et t he w olves t o a round 1 2 i n s ize; t he w olves never went extinct.

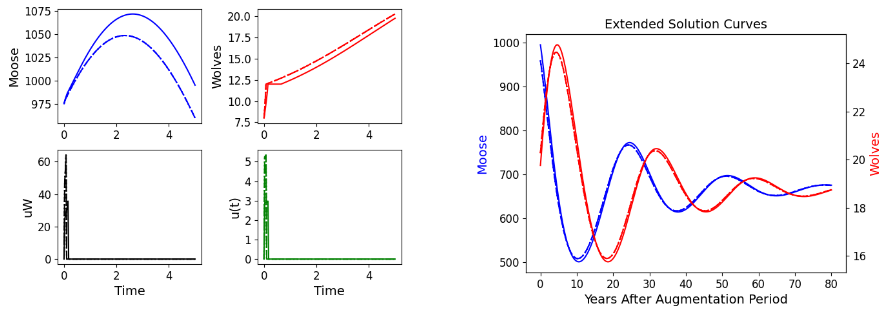

Figure 14: Simulations with performance measure (7), $C = 1$, $T = 5$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $A = 1$, $A = 20$, $A = 100$, and $A = 1000$, respectively.

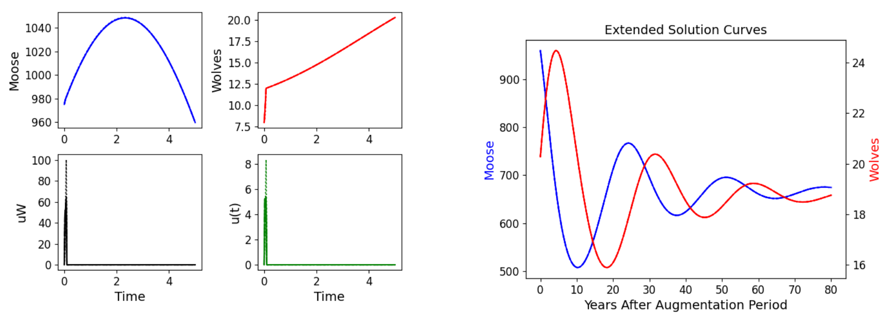

Figure 15: Simulations with performance measure (7), $A = 20$, $T = 5$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, dashed, and dotted lines correspond to $C = 0.5$, $C = 1$, $C = 20$, and $C = 1000$, respectively.

4.2.2 Case 9: A=20; C=0,0.5,1,20,100,1000; & T=5

Figure 15 displays many of the trials when $M(0) = 975$ and $W(0) = 8$. Both initial conditions had similar augmentation results to the previous cases: augmentation occurred within the first year to reach 12 wolves and then largely stopped for the rest of the five years.

4.2.3 Case 10: A=20; C=1; & T=5,10,15

Finally, we fixed A and C and varied T to see how the length of the augmentation phase impacted the augmentation. Figure 16 displays the trials when $M(0) = 975$ and $W(0) = 8$. Wolf extinction never occurred; outside of some augmentation toward the end of the augmentation period when $T = 15$, all augmentation occurred in the first 2 years. For the $M(0) = 932$ and $W(0) = 5$ case, the $T = 10$ trial had no solution; no analysis was performed on these initial conditions.

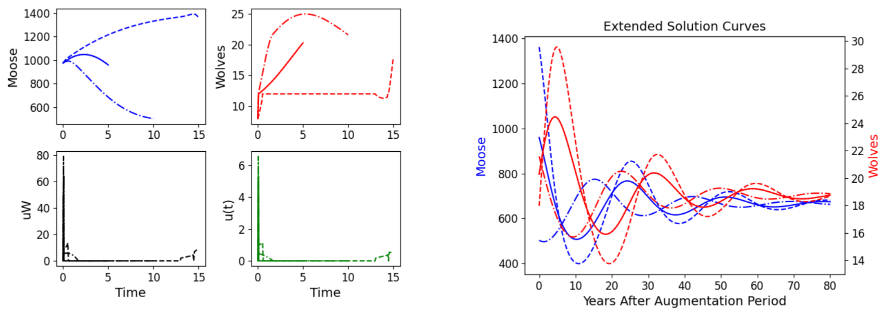

Figure 16: Simulations with performance measure (7), $A = 20$, $C = 1$, $M(0) = 975$, and $W(0) = 8$. The solid, dash-dot, and dashed lines correspond to $T = 5$, $T = 10$, $T = 15$, respectively.

5 Conclusions

In our studies, we have performed many simulations pertaining to wolf augmentation on Isle Royale. Although these simulations are not meant to be prescriptive, they were accurately based on data from Isle Royale and thus provide general insights into successful and unsuccessful augmentation strategies. When the augmentation was delayed, the moose population often grew too large and caused the wolf population size to undergo high amplitude oscillations that led to wolf extinction. However, when wolves were immediately augmented, this phenomena was avoided. Hence, these trends imply that the wolf augmentation should be immediate rather than delayed. For our trials with immediate augmentation, successful augmentation typically occurred when the wolf population size was immediately augmented to around twelve wolves and further augmentation stopped by the end of year one. This reveals that the wolf population should be mainly augmented within the first year of the augmentation period.

Despite its many strengths, this model also had limitations. In particular, the small number of wolves, which reached a total of two in 2016, diminishes the efficacy of our ordinary differential equation model which assumes well mixing. Though the wolves belong to the same pack and are likely to interact, a much larger population size is typical of the assumptions embedded within this model. Nevertheless, the strategies detailed above which saw success, namely the immediate addition of wolves to Isle Royale within one year, were replicated in all of our simulations.

Acknowledgements

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A Supplemental Materials

Year	Wolf Population Size	Moose Population Size	Year	Wolf Population Size	Moose Population Size
2004	29	750	2012	9	750
2005	30	540	2013	8	975
2006	30	450	2014	9	1050
2007	21	385	2015	3	1250
2008	23	650	2016	2	1300
2009	24	530	2017	2	1600
2010	19	510	2018	2	1475
2011	16	515			

Table 2: This table contains the recorded wolf and moose population sizes on Isle Royale from 2004 to 2018. This data is taken from [11].

Case Number and Performance Measure	A	B	C	Objective Functional Values
Case 1 (PM 6)	1	0, 0.25, 0.5	1	$M(0) = 975$ and $W(0) = 8$: 14.2, 254, 583 $M(0) = 932$ and $W(0) = 5$: -1.92,285,572
Case 2 (PM 6)	20	0, 0.5, 1, 2	20	$M(0) = 1475$ and $W(0) = 2$: 299, 575, 696, 263 $M(0) = 975$ and $W(0) = 8$: -105, 135, 375, 615 $M(0) = 932$ and $W(0) = 5$: -194, 356, 907, 2360
Case 3 (PM 6)	100	0, 0.25, 0.5, 0.75	100	$M(0) = 975$ and $W(0) = 8$: -605, -365, -125, 114 $M(0) = 932$ and $W(0) = 5$:-1717, -1427,-1133,-862
Case 4 (PM 6)	1, 20, 100	0	1	$M(0) = 975$ and $W(0) = 8$: 14.2, -17.9, -193 $M(0) = 932$ and $W(0) = 5$: -1.92, -128, -1021
Case 5 (PM 6)	1,20,100	0.5	1	$M(0) = 975$ and $W(0) = 8$: 583, 454, 359 $M(0) = 932$ and $W(0) = 5$: 572, 514, -439
Case 6 (PM 6)	20	0	0, 1, 20, 100	$M(0) = 975$ and $W(0) = 8$: 6.47, -17.9, -105 $M(0) = 932$ and $W(0) = 5$: -173,-128,-194
Case 7 (PM 6)	20	0.5	0.5, 1, 20, 100	$M(0) = 975$ and $W(0) = 8$: 456, 454, 375, 42.2 $M(0) = 932$ and $W(0) = 5$: 518, 514, 356, -319
	A	**T**	**C**	
Case 8 (PM 7)	1, 20, 100, 1000	5	1	$M(0) = 975$ and $W(0) = 8$: 6.31, 47.6, 215, 2099 $M(0) = 932$ and $W(0) = 5$: 12.6, 216, 1043, 6631
Case 9 (PM 7)	20	5	0, 0.5, 1, 20, 100, 1000	$M(0) = 975$ and $W(0) = 8$: 43.5, 45.6, 47.6, 126.7, 459,4196 $M(0) = 932$ and $W(0) = 5$: 162, 167, 216, 215, 939, 7290
Case 10 (PM 7)	20	5, 10, 15	1	$M(0) = 975$ and $W(0) = 8$: 47.6, 63.8, 32.4 $M(0) = 932$ and $W(0) = 5$: No solution

Table 3: The above table details values obtained from the recorded simulations using performance measures 6 and 7 (PM 6 & PM 7). Each case corresponds to the subsections in our results, and in each simulation, one of the values is varied. These values consist of A,B,C, and T.