CIS 3130

Modeling Predator-Prey Interactions in Isle Royale National Park

James Singaram

0758172

Dec. 15, 2020

Introduction

The Isle Royale National Park in Michigan, USA has been the site of one of the longest running ecological studies ever conducted. Starting in 1959, moose and wolf population data has been collected and recorded. In the late 1990s and early 2000s inbreeding caused a dramatic decrease in wolf population size. The wolves on Isle Royale are currently threatened with extinction, which would allow the moose population to grow unchecked and further destabilize the ecosystem. In order to counteract the effects of inbreeding and return the wolf population to healthy levels, human intervention is necessary.

Objectives

There are two major hurdles that need to be overcome to salvage the wolf population and restore balance to the ecosystem. First, the population's current genetic makeup is evolutionarily unfit. An increase in genetic diversity will lessen this. Second, the small population is at risk of being wiped out by stochastic environmental effects. Increasing the population size will reduce the population's susceptibility to stochasticity. Both of those problems are remedied by capturing a number of genetically diverse wolves from other habitats and introducing them to Isle Royale.

Introducing too many wolves will cause over-predation and deplenish the moose population. Introducing too few wolves will leave the wolf population susceptible to chance catastrophes and not sufficiently resolve inbreeding. Additionally, if a healthy wolf population will revert to an inbred state if it does not remain above a minimum threshold. In order to determine the optimal number of wolves to introduce, population viability analysis (PVA) will be performed.

Model Conceptualization

A PVA assesses the survival rate for one or more populations over a period of time by simulating the populations repeatedly and returning the probability of critical endangerment for the species. In order to find the optimal number of wolves to introduce, a PVA will be conducted on the populations for several possible numbers of introduced wolves. The number of introduced wolves that yields the lowest critical endangerment rate will offer the greatest likelihood of long-term stability. Additionally, the degree of inbreeding in the wolf population will be estimated for populations that survive the simulation period. In the event that several possible numbers of introduced wolves produce equally viable populations, the one with the lowest degree of inbreeding will indicate the best possible chance of stability beyond the simulated period.

A population is considered to fail upon becoming critically endangered. Critical endangerment refers to a population declining by at least 80% over a period of time (usually three generations). As in the case of the Wolves of Isle Royale, critical endangerment increases the frequency of inbreeding and susceptibility to stochastic events. Each time either the moose or wolf populations become critically endangered, the run will cease and the failure will be recorded. After all runs for a given number of wolves to introduce are complete, the frequency of critical endangerment will be calculated to estimate the probability of each case resulting in extinction.

Moose and wolf populations on Isle Royale define their ecosystem by their predator-prey interactions. Moose are the primary prey species for the wolves, and their consumption defines wolf growth rate. Wolves are the largest source of moose mortality and prevent the moose population from unrestrained growth. Both species will be simulated using Ricker logistic models that account for their interaction. While both species are affected by environmental factors, such as disease, climate, and other species, these can be estimated using historically observed parameters. Stochastic factors will be estimated using a normal distribution and the standard deviation of observed parameters.

The moose population size, N, for year t+1 is based on the moose population in the previous year t. The population will grow logistically based on a maximum growth rate and carrying capacity. The impact of stochastic environmental effects on growth rate will be produced according to a normal distribution and based on the standard deviation historic growth rates. Predation by wolves will reduce the population.

$N_{t+1} = N_t * e^{(rmax(1-Nt/K) + \varepsilon)} - P$

N_t is the moose population size at time t
N_{t+1} is the moose population size at time t+1
r_{max} is the greatest observed growth rate for the moose population
K is the carrying capacity of moose
ε is the stochastic environmental impact on growth rate
P is the number of moose slain by wolf predation

The wolf population size, V, for year t+1 is based on the wolf population in the previous year t. The populations will grow logistically based on the prey-to-offspring conversion factor and predation rate. The impact of stochastic environmental effects on growth rate will be produced according to a normal distribution and based on the standard deviation historic growth rates. Wolf mortality rate will reduce the population

$V_{t+1} = V_t * e^{(c * P/Vt + \varepsilon - D)}$

V_t is the wolf population size at time t
V_{t+1} is the wolf population size at time t+1
c is the prey-to-offspring conversion factor
P is the number of moose slain by wolf predation
ε is the stochastic environmental impact on growth rate
D is the mortality rate

The predation rate for year t, P_t, is based on the average historical kill rate and the relative abundance of moose and wolves. A normally distributed modifier is added based on the standard deviation of historical kill rates.

$P_t = (k_{avg} * N_t/K + \varepsilon) * V_t$

P_t is the predation rate at time t
k_{avg} is the average kill rate
N_t is the moose population size at time t
V_t is the wolf population at time t
K is the moose carrying capacity
ε is the stochastic modifier on kill rate

The prey-to-offspring conversion factor and mortality rate for wolves in each run will be a weighted average based on the number of inbred and healthy individuals in the population using the conversion factors and mortality rates for both inbred and healthy wolves.

$c = (V_{sick} * c_{sick} + V_{healthy} * c_{healthy}) / V_t$

c is the prey-to-offspring conversion factor for the population
V_{sick} is the number of inbred wolves in the population
c_{sick} is the prey-to-offspring conversion factor for inbred wolves
$V_{healthy}$ is the number of healthy wolves in the population
$c_{healthy}$ is the prey-to-offspring conversion factor for healthy wolves
V_t is the total number of wolves in the population

$D = (V_{sick} * D_{sick} + V_{healthy} * D_{healthy}) / V_t$

D is the mortality rate for the population
V_{sick} is the number of inbred wolves in the population
D_{sick} is the mortality rate for inbred wolves
$V_{healthy}$ is the number of healthy wolves in the population
$D_{healthy}$ is the mortality rate for healthy wolves
V_t is the total number of wolves in the population

When the wolf population is below the minimum viable population to avoid inbreeding, the prey-to-offspring conversion factor and mortality rate will both be adjusted towards the inbred values based on how far the population is below the minimum viable population size.

$c = c - (V_t / V_{MVP}) * (c - c_{sick}) / G$

- c is the prey-to-offspring conversion factor for the population
- V_t is the total number of wolves in the population
- V_{MVP} is the minimum viable population to avoid inbreeding
- c_{sick} is the prey-to-offspring conversion factor for inbred wolves
- G is the time for one wolf generation, in years

$D = D - (V_t / V_{MVP}) * (D - D_{sick}) / G$

- c is the mortality rate for the population
- V_t is the total number of wolves in the population
- V_{MVP} is the minimum viable population to avoid inbreeding
- c_{sick} is the mortality rate for inbred wolves
- G is the time for one wolf generation, in years

Data Collection

All of the population parameters necessary to construct an accurate model can be extrapolated from population data for moose and wolves. The data that will be used comes from Peterson and Vucetich of the Michigan Technological University. Numbers relating to minimum viable population size to avoid inbreeding are drawn from an article published by Frankham *et al*. in Biological Conservation.

Growth rate and carrying capacity for the moose population will utilize the entire study period. Parameters for native, inbred wolves will be produced using data after inbreeding increased (2000-2018). Parameters for foreign, healthy wolves will use data prior to inbreeding (1959-1999).

Necessary parameters for moose population:

- Maximum growth rate, $r_{max} = 1.2137$
- Growth rate standard deviation, $\sigma_r = 0.210$
- Carrying capacity, $K = 1480$ moose

Necessary parameters for wolf population:

- Prey-to-offspring conversion factor for inbred wolves, $c_{sick} = 0.298$ wolves per moose slain

Prey-to-offspring conversion factor for healthy wolves, $c_{healthy}$ = 0.274 wolves per moose slain
Mortality rate for inbred wolves, D_{sick} = 0.506
Mortality rate for healthy wolves, $D_{healthy}$ = 0.310
Average kill rate, k_{avg} = 8.976 moose per wolf per year
Kill rate standard deviation, σ_k = 3.72 moose per wolf per year
Kill rate was found not to differ significantly between healthy and inbred wolves
Generation time, G = 4 years

Minimum population size to prevent inbreeding, n = 50

Model Translation and Verification

The simulation was written and executed in R. This decision largely rested on the author's experience with modeling populations in R and a number of previously designed scripts that could be used as a starting point in producing the simulation.

Converting the model into a functional simulation occurred in several steps. Initial versions simulated the moose population over time using fabricated parameters in order to confirm that the population would grow according to the Ricker logistic model and fluctuate around the carrying capacity. Early versions of the wolf population used a defined growth rate rather than the prey-to-offspring conversion ratio and mortality rates. Predation rate was implemented as a multiplier on growth rate.

Subtracting predation rate from the moose population revealed that the model would extend an instantaneous change across an entire year. This led to dramatic changes in both populations. When a year started with many wolves, the predation rate would remain high for the entire year rather than decreasing as the moose population declined. The end result was wild population fluctuations and frequent extinction within one or two years if the initial populations were not already close to equilibrium. This was remedied by breaking each year into a number of steps. After some testing it was found that using six steps per year, or incrementing the simulation two months at a time, yielded accurate results without increasing execution time an unreasonable amount.

Stochastic variations on the population parameters for each step were added next to produce varied results for each run. The equation for wolf population size was altered to use the prey-to-offspring conversion factor and mortality rate, however those values and initial population sizes were still predefined. Parameters from historical observations were also added at this time.

The program was altered to run for all numbers of wolves to add, run each one multiple times, and identify and count failed runs. While the wolf parameters did not reflect the wolf population composition at this time, early results indicated that the probability of critical endangerment was high at extremely low and high numbers of wolves introduced. This lined up with expectations and reinforced the model's accuracy. The impact of wolf population composition on wolf parameters was added next, along with parameter feedback after each interval of a run to modify population parameters when below the minimum viable population. A sample run for 150 added wolves can be seen in figure 1 (see Sample run for populations.pdf). To assist in readability of the graph, wolf population size was multiplied by ten so that it could be readily compared to moose population size.

Validation

A known weakness of PVAs is that they cannot be easily validated experimentally. Observing the real world environment requires years of study and large financial investment to fund the research. Additionally, it yields only a single result and it cannot be known whether or not that is an outlier. The resource cost of performing a PVA means that they are most often performed on populations and ecosystems that have been observed to be in decline. It is often unreasonable to take no action and observe a failing ecosystem due to the risk of irrevocable damage occurring within that time.

Using scientific data from previous studies on predator-prey interactions allows general trends in the simulation to be tested. Introducing a low number of wolves would be expected to result in the critical endangerment of the wolf population. Introducing an intermediate number of wolves would be expected to result in a stable system, and introducing a large number of wolves would be expected to result in the critical endangerment of the moose population. This trend can be observed in Figure 2 and Figure 3 (see also Fails.pdf, Survival Rate.pdf).

Experimental Design

The PVA simulates a period of 20 years in 120 two-month steps. This ensures that the simulation will monitor survival rates over at least three generations for both wolves and moose.

To ensure that a correct result, all possible numbers of wolves to introduce between 1 and three times the greatest historical wolf population (V = 50) will be used. This yields a range of 1 to 150.

In order to obtain the probability that both species will avoid critical endangerment within 1% of the actual value with a 99% confidence interval, each scenario needs to be run at least 16,589 times. This will be rounded up to 17,000 times to err on the side of caution.

$$z_{\alpha/2} * \sqrt{(pq/n)} \leq 0.01$$
$$2.576 * \sqrt{((0.5)^2/n)} \leq 0.01$$
$$\sqrt{n} \geq (2.576 * \sqrt{(0.5)^2}) / 0.01$$
$$\sqrt{n} \geq 128.8$$
$$n \geq 16589$$

The computer used to run the simulation ran Windows 10 Enterprise with an Intel i5-4670k running at 3.8 GHz. It was run within RGUI 4.0.2. Runtime varied from 30-45 minutes. Termination of other processes could have further reduced runtime.

Implementation

The purpose of this simulation was to find the number of wolves to introduce to Isle Royale in order to maximize long-term stability of wolf and moose populations. Any actions suggested are made with that objective in mind.

Survival rate for both populations exceeds 90% over a 20 year period when anywhere between 11 and 65 wolves are introduced to Isle Royale with a 99% confidence interval. This increases to 98% for 18 to 44 wolves. Survival rates drop off sharply when too few wolves are added and are reduced gradually when too many are added. Dangers associated with introducing foreign individuals, such as disease and conflict between individuals, can reduce the number of wolves that successfully integrate into the environment. While the exact impact that these factors would have cannot be calculated without further experimentation, it is clear that introducing too many wolves is less risky than introducing too few.

Inbreeding in the surviving population only occurred in significant amounts in populations with less than eight introduced wolves. Given that these populations do not have a significant likelihood of survival, inbreeding is not a significant concern if enough wolves are introduced to ensure high survival rates.

It is assumed that each wolf introduced has the same cost. Introducing 18 wolves would result in a 98.0% chance of the ecosystem remaining stable over 20 years. All comparisons will be made relative to this. Increasing that to 22 wolves increases the probability to 98.5%. This would reduce the likelihood that future human intervention is necessary by 25% while only increasing costs by 22%. The simulation, however, was only accurate to 1%, so it is possible that this approach would not be any more reliable in actuality.

An alternative approach would be to introduce a small number of wolves and reserve funding in case a second group of introductions is required. This assumes that introducing wolves the first time does not significantly alter the ecosystem to the point that this simulation is no longer accurate. Introducing 12 wolves twice yields a 99.5% chance of producing long-term stability in the ecosystem. In the case that the simulation yielded a result more than 1% greater than the actual probability, the chance of yielding long-term stability falls to 99.3%. This still reduces the likelihood that human intervention beyond the second introduction is necessary by 65% while only increasing the costs by 33% in the worst case. There is a 93% chance that the second introduction would not be required, saving 33% compared to introducing 18 wolves once. The average cost of this approach is 71.6% of introducing 18 wolves with only a 0.7% chance of failure.

Author's Commentary

This simulation was designed to mimic efforts made by ecologists in late 2017 to save the wolf population of Isle Royale. Their models indicated that 18 wolves would need to be introduced to restore the population. Those wolves were collected from Michigan, Minnesota, and Ontario in 2018 and introduced to the island. Current estimates place 15 adult wolves on the island plus an additional four pups that they have birthed. While these numbers were known while designing the simulation, no effort was made to guide its results towards them. More than anything, I am surprised that my simulation bore results that match theirs so closely. I made every effort to use scientific sources for the population parameters, however some values were estimated based on studies on wolf populations in different locations and others were deliberately avoided in order to minimize complexity and keep execution time reasonable. The wolf populations during sample runs suggested that the population size would fluctuate around 50-80 in stable situations, roughly doubling historical data. A knock-on effect of this is reduced moose population size. This suggests some flaw in my model regarding either the wolf mortality rate or the prey-to-offspring conversion factor. It is also worth noting that variation in historical moose growth rate was generally small, however sharp declines in two years increased the standard deviation significantly. I could not find a way to model these cataclysmic events in a satisfying fashion. It was my belief that keeping the growth rate standard deviation low and introducing a chance for mortality spikes would cause many artificial critical endangerments due to the nature of the predator-prey interactions. In the future I would make greater efforts to consult experts in the field and implement their feedback.

References

R. Frankham, *et al*. (2014-02-01). "Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses". Biological Conservation. 170: 56–63.

H. Andreassen *et al*. (2014). Predator‐dependent functional response in wolves: from food limitation to surplus killing. Journal of Animal Ecology, 84 (1), 102-112.

R. Peterson *et al*. (2002). The effect of prey and predator densities on wolf predation. Ecology, 83 (11), 3003-3013.

S. Hoy *et al*. (2020). Ecological studies on wolves on Isle Royale. Annual Report 2019-2020. Houghton, Michigan. 1-24.

J. Fryxell *et al*. (2014). Wildlife Ecology, Conservation, and Management.

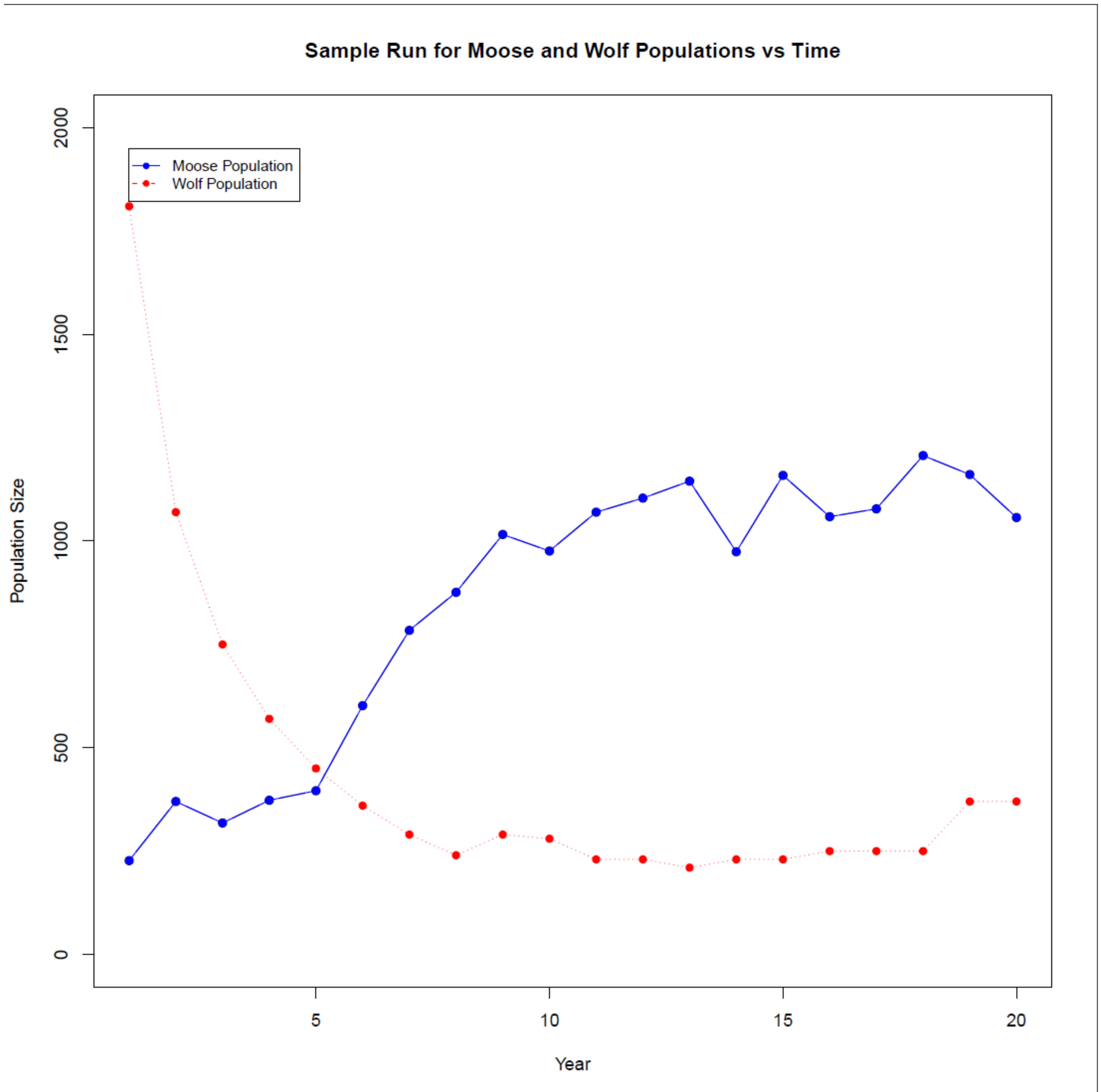

Figure 1. Sample run for moose and wolf populations vs time

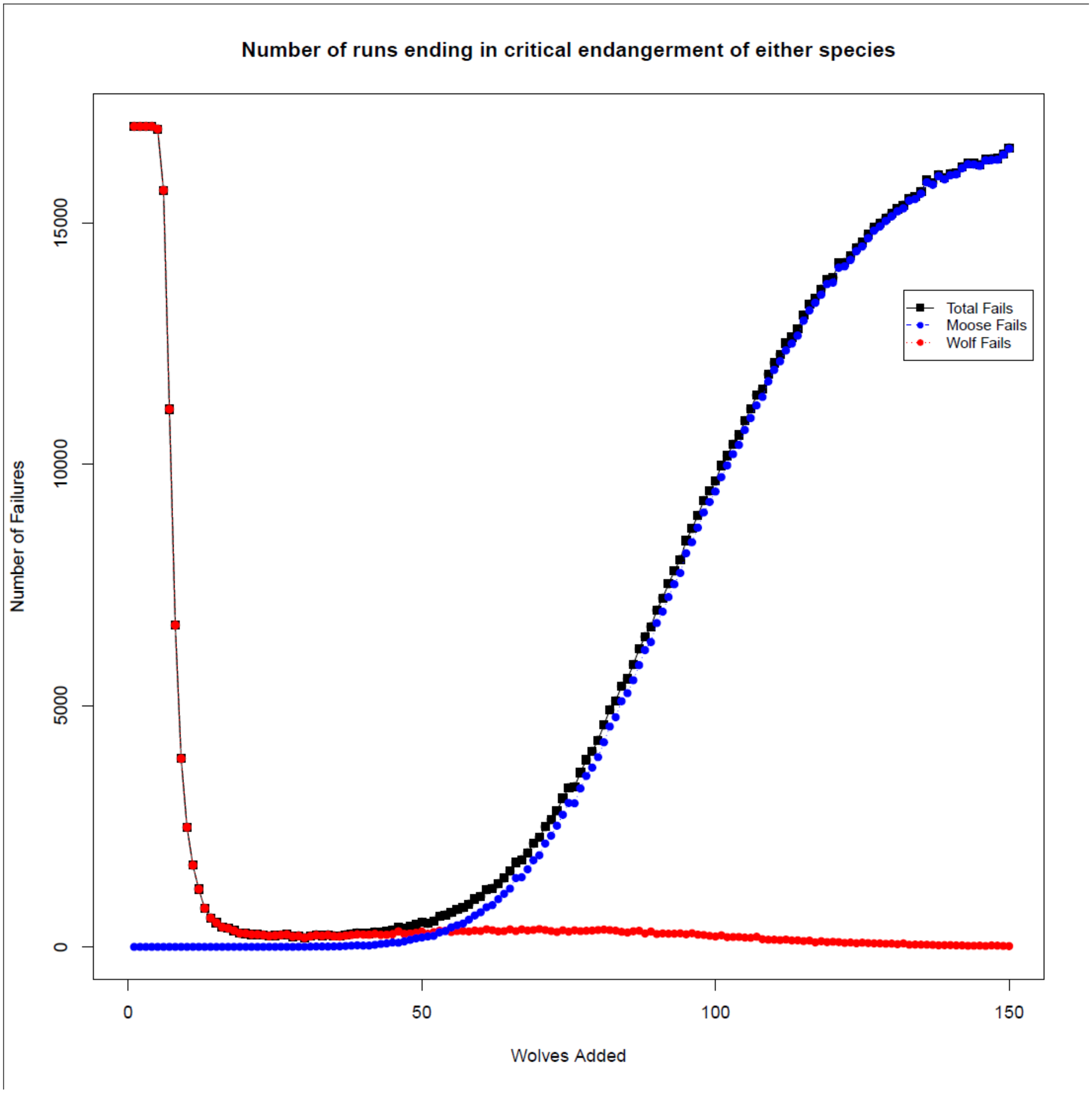

Figure 2. Number of runs ending in critical endangerment of either species

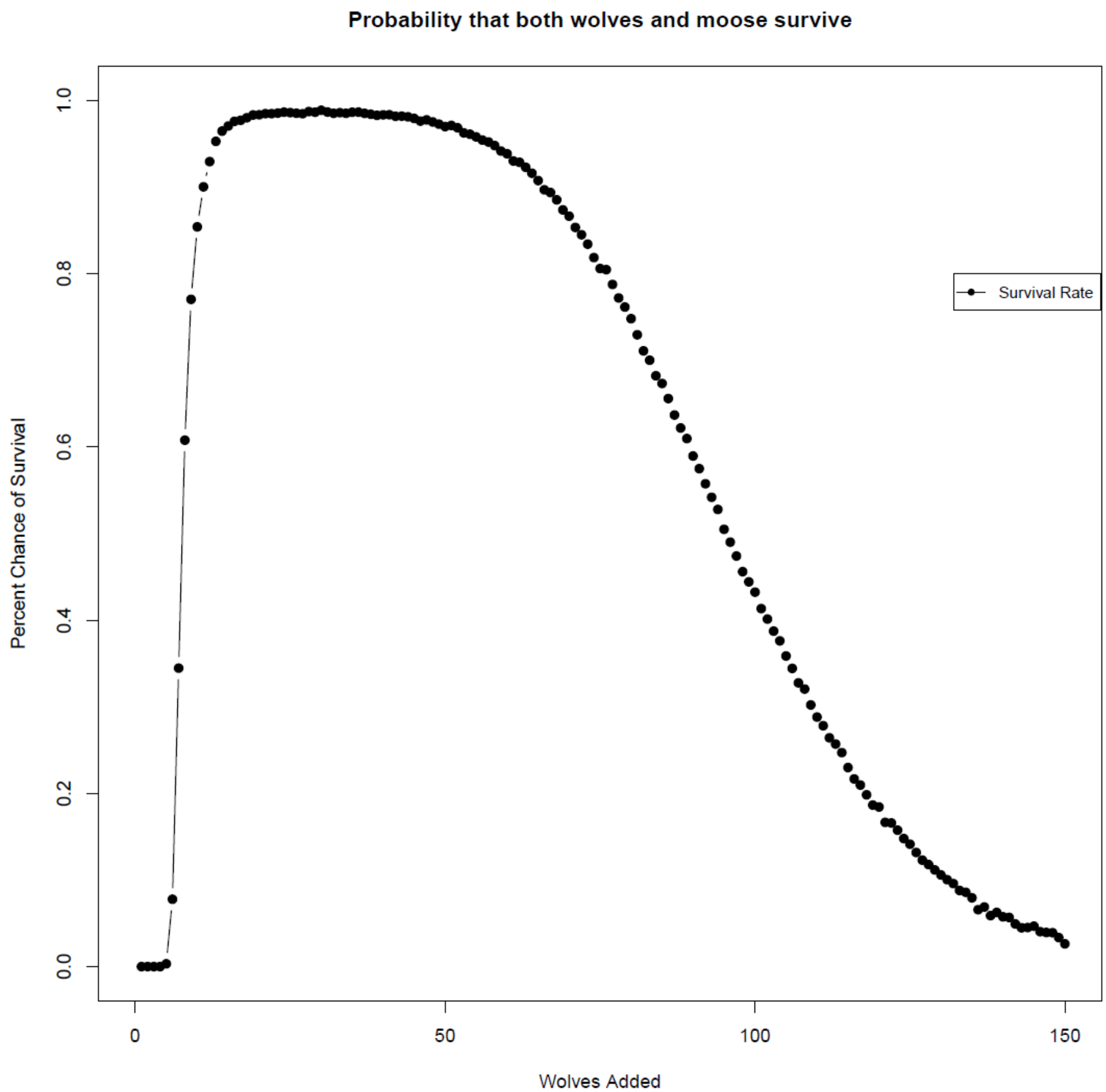

Figure 3. Probability that both wolves and moose survive

Table 1. Sample of output results (see output.csv for full results)

wolves.added	wolf.failures	moose.failures	total.failures	survival.rate
1	16999	0	16999	0.000
2	16998	0	16998	0.000
3	16999	0	16999	0.000
4	16999	0	16999	0.000
5	16944	0	16944	0.003
6	15677	0	15677	0.078
7	11141	0	11141	0.345
8	6666	0	6666	0.608
9	3902	0	3902	0.770
10	2479	0	2479	0.854
11	1692	1	1693	0.900
12	1197	1	1198	0.930
13	801	0	801	0.953
14	600	0	600	0.965
15	500	0	500	0.971
16	408	0	408	0.976
17	387	0	387	0.977
18	337	1	338	0.980
19	282	1	283	0.983
20	278	1	279	0.984
21	257	0	257	0.985
22	257	0	257	0.985
23	246	0	246	0.986
24	226	2	228	0.987
25	236	1	237	0.986
26	246	3	249	0.985
27	257	2	259	0.985
28	216	0	216	0.987
29	226	3	229	0.987
30	188	3	191	0.989