

Thesis for Senior Honors Capstone

FORAGE AND PREDATOR DYNAMICS INFLUENCE THE PRESENCE AND INTENSITY
OF CARIBOU POPULATION CYCLES

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ABSTRACT

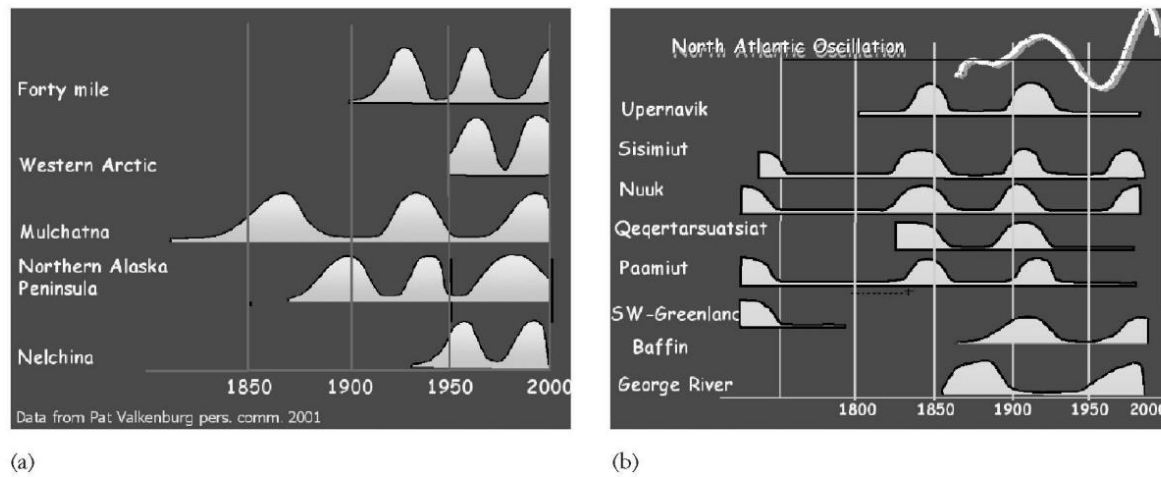
Population cycles, found in small mammals like voles, lemmings, and snowshoe hares, have fascinated ecologists for over a century. More recently, it has been suggested that large mammals like ungulates may have cyclic patterns as well. For example, Indigenous history and paleoecological records show that caribou or reindeer (*Rangifer tarandus*) can have population cycles that last from 50-100 years. Though caribou are well-studied globally, few studies have examined the underlying conditions prompting these dynamics, and so little is known about what causes them. Statistical analysis of caribou population data found that vegetation and climate impacted the period and amplitude of caribou cycles (St. John, 2021). Additionally, I hypothesized that factors such predation, density-dependence, and subsistence harvest are also influential. I aimed to identify which of these factors contribute to population cycling, and better understand how to manage caribou for conservation and management practices. To determine influential factors, I built a tri-trophic mathematical model based on ordinary differential equations representing wolf-caribou-vegetation dynamics. Based on available data, I chose to parameterize my model using existing literature from North American barren-ground caribou herds. I then manipulated parameter values representing forage and predation dynamics to see which factors influenced cycle period and amplitude most significantly. My findings previous results in small mammals on the influence of both vegetation and predation dynamics on population cycling. As predation search rate increased, period and amplitude increased, thus resulting in less frequent but more intense population booms and busts. As forage intrinsic growth rate increased, period and amplitude decreased, which yielded more frequent but less intense booms and busts. The results from these model simulations can better inform future management strategies and policy implementation surrounding sustainable harvest. With a shift

in global climate reducing conditions for caribou forage and causing expanding predator populations, I infer that both the period and amplitude of population cycles will grow larger, potentially leading to more severe population crashes. Thus, adaptive management is crucial to ensure survival for this globally declining species.

1. INTRODUCTION

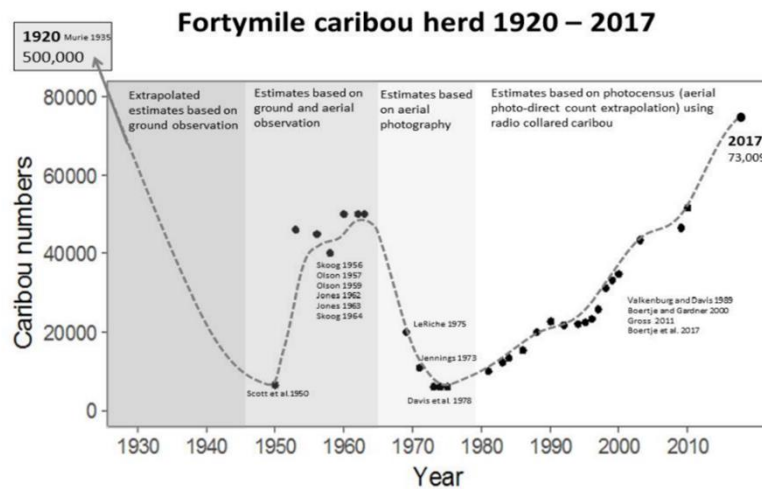
Caribou are one of the most well-studied ungulate species, and population trends have been observed by Indigenous communities for millennia. Though there is far less literature available regarding the presence of cycles in large mammals, paleoecological evidence, coupled with Traditional Ecological Knowledge, suggests that caribou, or reindeer (*Rangifer tarandus*) adhere to cyclic dynamics (Zalatan, 2006; Morneau and Payette, 2000; Gunn, 2003). Traditional Ecological Knowledge indicates that caribou herds have gone through booms and busts over the course of the last two centuries. However, Western science-based population estimates do not extend past the last couple of decades. Gunn (2003), was among the first few Western scientists to acknowledge the scale of caribou cyclicity, and hypothesized that climate was likely an influential factor in determining the intensity of cycles.

Figure 1. *Standardized fluctuations in caribou abundance in (a) Alaska and (b) Greenland and eastern North America (Gunn 2003).*



Therefore, existing temporal data only explains roughly one “cycle”, or even less than one. To summarize population cycles in caribou, data from 43 caribou herds mostly in Alaska and Canada, were compiled and the period and amplitude of the cycle were estimated based on the 19 cyclic populations out of the 43 herds (St. John, 2021). Based on this data, the median period of a single cycle was 40.5 years, with a minimum of 23 years and maximum of 67 years. The calculated median amplitude was 0.87, with a minimum and maximum of 0.406 and 1.570 respectively, implying that the peak or maximum herd population was on average 87% higher than its mean population (St. John, 2021). Although caribou populations cycle over time, little is known about what drives the period and amplitude of population cycles.

Figure 2. *Forty Mile caribou herd population from 1920-2017.* Note. From Forty Mile Caribou Herd Harvest Plan 2019-2023.



There are likely several drivers of caribou population cycles. Based on studies in small mammals which observed population cycling (Krebs et al., 1995), the availability of forage is a significant factor influencing the presence and intensity of cycling. Forage availability, though associated with climate conditions, also poses its own set of drivers. Caribou feed on a variety of plants, with most of their diet composed of lichens (Trudell and White, 1981; Webber et al. 2022). This source of food is especially important in winter months, when accessing forage is difficult due to snow, and nutritious food is not available. Though research indicates that lichen is low in protein, and unsuitable for exclusive consumption, it contains large amounts of carbohydrates and is an important source of energy for caribou (Klein, 1982). Lichen grows remarkably slowly, with an intrinsic growth rate of approximately 0.2 (Gaare, 1997; Yarranton, 1975). Tundra ecosystem dynamics coupled with slow growth make them susceptible to over browsing thus impacting caribou survival and reproductive success. (Joly et al. 2009). As

aforementioned, the average period of a single caribou boom and bust lasts 40.5 years (but can last much longer), which is reasonably close to the growing time for lichen, suggesting that there may be a relationship between the two (Gaare, 1997; Yarranton, 1975). With foreseeable climate changes including warming temperatures, vascular plants with faster growth rates stand to outcompete lichen. Additionally, lichen is at risk of growing even slower due to lacking atmospheric moisture as tundra biomes warm (Klein, 2009). Studies found that caribou avoid areas with low lichen mat coverage, which suggests that as lichen decreases, and vascular plants and shrubs increase, caribou will spend more time searching for optimal resources (Macander et al. 2020). Based on this understanding, I hypothesize that an increase in caribou search rate for forage will result in decreased period and amplitude of population cycles.

Predators, including wolves and bears, are present in many caribou systems in the Northern hemisphere. There is reason to believe that predators impose top-down population control on these ungulates given historical caribou-wolf relations. Spatial dynamics appear to play a role in determining the presence and magnitude of cycling in small mammals, which may be applicable to similar research on large mammals. Vole population cycle period increases in northern latitudes, and Hanski et al. (1991) concluded that there was a relationship between the presence of generalist and specialist predator species and the intensity of cycling at varying latitudes. Northern areas on average had far fewer generalists when compared to southern regions. As a result, cyclicity of populations in the South had shorter periods and smaller amplitudes, implying that generalist predators consumed prey items based on their abundance. This essentially creates density-dependent predation, allowing for more regulated prey populations. Wolves act as a shared predator for moose and woodland caribou in Alberta and British Columbia, Canada (Serrouya et al., 2019). The density-dependent predator-prey

relationship suggests that wolves will eat caribou when herds are large in number. Likewise, when caribou densities are lower, wolves are more likely to prey switch to moose, their preferred prey item (Dale, 1994). Habitat fragmentation and increased global climate change has prompted regime shifts in moose populations, leading to higher densities of moose in primarily caribou habitat. Based on this understanding, I hypothesize that increased predation pressure on caribou will result in a larger period, and smaller amplitude.

2. METHODS

2.1 The Vegetation – Caribou Model

The Michaelis-Menten type of equation, which is a first-order differential equation, can broadly describe populations with varying phenomenality. The models based on this type of equation, which is what I will be relying on, are based on the Rosenzweig MacArthur predator-prey models Turchin (2003) used to represent the relationships between vegetation, moose, and wolf predation. The Rosenzweig MacArthur model is an adaptation of the Lotka-Volterra model and integrates density-dependent prey growth, as well as a type II functional and numerical response (Stevens, 2009). Turchin's (2003) model describing the relationship between vegetation, moose, and wolves, has been re-parameterized to describe caribou dynamics. I used three separate models to describe the relationship between vegetation, caribou, and predators. The first equation models vegetation density and the second equation describes how many caribou are in a given population that are consuming the vegetation. The equations describing this interaction is as follows:

$$\frac{dV}{dt} = u_0 \left(1 - \frac{V}{m}\right) - \frac{aVN}{b+V} \quad \text{Equation 1}$$

$$\frac{dN}{dt} = \Sigma N \left(\frac{aV}{b+V} - \eta\right) \quad \text{Equation 2}$$

In equation 1, V represents the vegetation biomass density, u_0 is the intrinsic growth rate of vegetation, which in this case encompasses lichen and some vascular plants, and m is the vegetation carrying capacity. To factor in caribou, I have included a which denotes caribou search rate on vegetation, and b which denotes caribou handling time on vegetation.

In equation 2, N represents the number of caribou in a population, η denotes the limiting factor to caribou population growth which in this case is vegetation availability. Σ is a type II response for caribou and describes how many caribou are produced per unit of vegetation consumed. Conversion efficiency can be solved for by using factors closely related to the intrinsic growth rate of caribou as well as the handling time, maximum intake rate, and carrying capacity of vegetation. Thus, Σ can be solved for by using this equation:

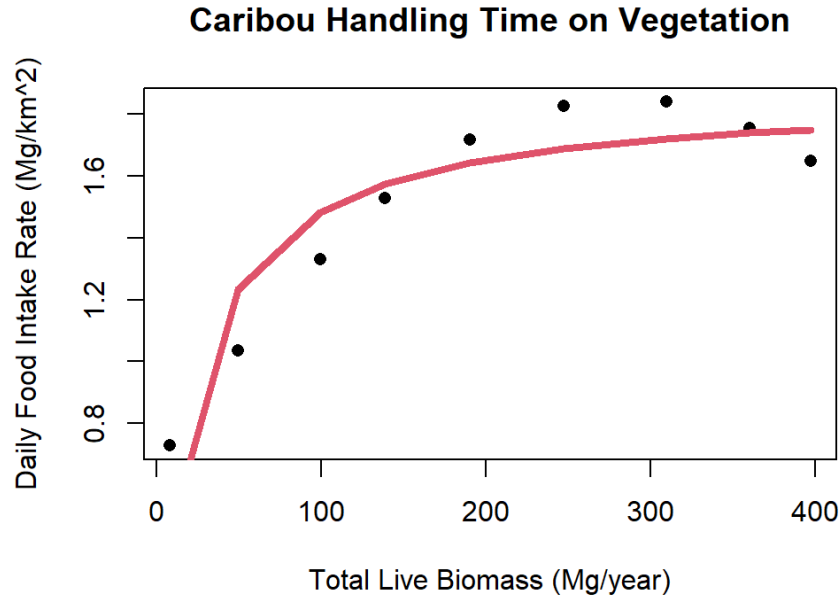
$$\Sigma = \frac{r_0}{\frac{am}{b+m} - \eta} \quad \text{Equation 3}$$

Where variable r_0 is the intrinsic growth rate of caribou.

Parameterization

All parameter units were standardized according to Turchin's model (2003). Vegetation is in Mg (dry weight), area is in km^2 , time is in years, and the density of caribou is in individuals per km^2 . Parameter m is set as $100 \text{ Mg}/\text{km}^2$ (Turchin, 2003). All other literature estimates yielded abnormally high amplitudes, and unrealistic periods, while Turchin's value yielded an appropriate period and amplitude, so we can assume that his value is reasonable. Caribou functional parameters, a and b , were far less extensively researched than anticipated, and I chose to set a equal to $1.78 \text{ Mg}/\text{individual}/\text{year}$, as documented by Klein's study (Klein, 1982). Though this paper is nearly 40 years old, Klein's observations yielded important results, and thus I was confident in his estimation of caribou search rate. There was no existing literature providing caribou handling time, however, and I calculated b by fitting a curve to data provided by Trudell (Trudell and White, 1981). I chose to include points along the dashed line Trudell estimated, and then converted the units provided into units that fit my model. I created a model for my data and took the coefficient for handling time, which was approximated at $25.4 \text{ Mg}/\text{individual}/\text{year}$, with a standard error value of 9.44 and a p-value of 0.03. The high standard error value suggests that this may not be certain estimate of handling time and should be kept in mind when analyzing my results.

Figure 3. *Functional response of caribou on lichen (Trudell and White, 1981).*



I set η equal to 0.89 Mg/individual/year, which Turchin (2003) estimated is equivalent to half of the maximum intake rate (search rate), and in my model is equivalent to 1.78 Mg/individual/year. Σ relies on several other parameters, including the intrinsic growth rate of caribou (r_0). Using $r_0 = 0.26$ (Serrouya 2020, D.C. Heard, Fryxell) in equation 3, I calculated Σ as 0.3. There were several reputable estimations of vegetation regrowth rate (u_0), however, most only accounted for lichen, which grows incredibly slowly. Most evaluated the intrinsic growth rate of lichen to be 0.3 (Gaare, 1997; Yarranton, 1975), but to account for vascular plant intake, 0.8 was the value I ultimately landed on. Vascular plant growth, though highly variable depending on size and species, I approximated around 1 for fast growing tundra species. Therefore, 0.8 yielded appropriate cycles in accordance with existing literature (St. John, 2021). Starting state values for V and N are 50 and 0.1 respectively.

2.2 The Caribou – Wolf Model

The second set of equations, representing the number of caribou and the number of wolves in a population, can be used to describe the relationship between caribou and their primary predator without the constraints of vegetation. Many cyclic populations adhere to classic density-dependent time lags, where as the number of prey increase, the number of predators increase as well, consuming more prey. However, when predator population numbers reach carrying capacity they consume too many individuals, yielding a decline in prey. Some time - steps later, depending on the prey and predator species, the predator population will no longer have enough food to sustain their population size, and thus will also crash. This dynamic can be represented by this set of equations:

$$\frac{dN}{dt} = \Sigma N \left(\frac{aV}{b+V} - \eta \right) - \frac{cPN}{d+N} \quad \text{Equation 4}$$

$$\frac{dP}{dt} = X \left(\frac{cN}{d+N} - \mu \right) P - \frac{s_0}{k} P^2 \quad \text{Equation 5}$$

In equation 4, Σ , N , a , b , and η are the same as they were in equations 1 and 2.

Parameters c and d are wolf search rate and handling time, and P is the number of predators in each area.

In equation 5, X is the conversion efficiency for caribou, and describes how many wolf offspring are produced per caribou eaten. The limiting factor to wolf populations growth is often space and is represented by μ . $\frac{s_0}{k} P^2$ describes wolf population self-regulation, where s_0 is the maximum rate of wolf population increase, k is the maximum wolf population density (carrying capacity), and P^2 is the number of wolves in a population at any time. Turchin switched from the

Rosenzweig-MacArthur model to this Bazykin model including self-regulation to account for wolf population dynamics. At high densities, wolf populations will compete with one another, regulating their size without other constraints like climate or lack of food.

Parameterization

All parameter units were standardized according to Turchin's model (2003), where area is in km^2 , time is in years, the density of caribou is in individuals per km^2 , density of wolves is in wolves per km^2 , and functional parameters are in caribou per wolf per year. I set c to 18.5 caribou/wolf/year, which is an average of three values: 29.9 (Hayes, 2000), 8.03 (Lake, 2013), and 17.5 (Holleman and Stephenson, 1981). Similar to the caribou-vegetation model, there was limited literature on wolf handling time, and estimated d at the very end, once all of my other parameters were established. Due to lacking data, I varied values of d between 0 and 2, keeping all other parameters constant, and established that 0.5 provided modeled cycles with an appropriate period and amplitude. For this model $d = 0.5$ caribou/ km^2 . X is 0.114 (Serrouya et al., 2019), μ is 9.25 wolves/ km^2 and was calculated by averaging three estimates of maximum wolf densities: 15, 4, and 8.75 (Mech, 2003). These values are on the higher end of wolf densities. Both s_0 and k were adopted from Turchin's model, where $s_0 = 0.3$ and $k = 0.1$ wolves/ km^2 (Turchin, 2003). The starting state values for P and N are 0.025 and 0.1 respectively.

2.3 The Tri-trophic model

I combined all three equations to identify the relationships between vegetation, caribou, and wolves to determine whether vegetation and predation both play a role in the presence and intensity of caribou population cycling. The tri-trophic model is as follows:

$$\frac{dV}{dt} = u_0 \left(1 - \frac{V}{m} \right) - \frac{aVN}{b+V} \quad \text{Equation 1}$$

$$\frac{dN}{dt} = \Sigma N \left(\frac{aV}{b+V} - \eta \right) - \frac{cPN}{d+N} \quad \text{Equation 4}$$

$$\frac{dP}{dt} = X \left(\frac{cN}{d+N} - \mu \right) P - \frac{s_0}{k} P^2 \quad \text{Equation 5}$$

This model can be used to describe caribou population dynamics when vegetation and predation are both present. Therefore, we can control vegetation availability, while altering predation pressure to see if our results are different from the first two models, which only consider a bi-trophic relationship. Likewise, we can control predation, while altering vegetation growth rate and standing crop, and determine whether vegetation is an important factor even when predation pressure is evidently influential.

3. Parameters

Table 1. Estimated parameter values for modelling.

Variable	Parameter Description	Estimate	Source
$u0$	Intrinsic vegetation regrowth rate	0.8	estimated in R
m	Maximum vegetation coverage	100 Mg/km ²	Turchin, 2003
a	Caribou forage efficiency	1.78 Mg/ind/yr	Klein,1982
b	Handling time of caribou with lichen	25.4 Mg/km ²	Estimated using R and data from Trudell and White, 1981
r_0	Intrinsic Caribou growth rate	0.26	Heard, 1990, Serrouya et al.,2019, and Turchin, 2003
η	Caribou limiting factor (food availability)	0.89 Mg/ind/yr	half of maximum intake rate
c	Forage search rate- average of caribou search rates	18.5 caribou/wolf/yr	29.9 + 8.03 + 17.5 (Source: Mech, 2003)
d	Handling time	0.5caribou/km ²	Estimated using R
ε	Conversion factor	0.3	Turchin, 2003
X	Conversion efficiency (number of wolf offspring produced per caribou eaten)	0.114	Serrouya et al., 2019
μ	Wolf limiting factor	9.25 wolves/km ²	Average of: 15+ 4 + 8.75 (Source: Mech, 2003)
S_0	Maximum wolf population rate of increase	0.3	Turchin, 2003
k	Maximum wolf density	0.1 wolves/km ²	Turchin, 2003

3.1 Sensitivity Analysis

For each of the three models I created a function using respective equations, provided initial starting states and parameter values, ran the ordinary differential equations, and visually examined the plotted model. I ran the models over 200 years, 500 years, and 1000 years. I created functions to calculate period and amplitude to assess how reasonably my model fits historical estimates. Using the “peacots” package in RStudio 4.0.4 (Louca & Doebeli, 2015), sine waves were fitted to the modeled cycles. The frequencies of the sine waves was determined by spectral density analysis, which can be displayed in a periodogram (St. John, 2021). The period of this time series was then calculated by dividing one by the peak frequency of the sine waves. Amplitude was calculated using this equation:

$$\frac{(\text{Maximum herd population} - \text{Minimum herd population})/2}{\text{Mean herd population}}$$

This equation was used to provide a standardized population amplitude for varying population sizes (St. John, 2021).

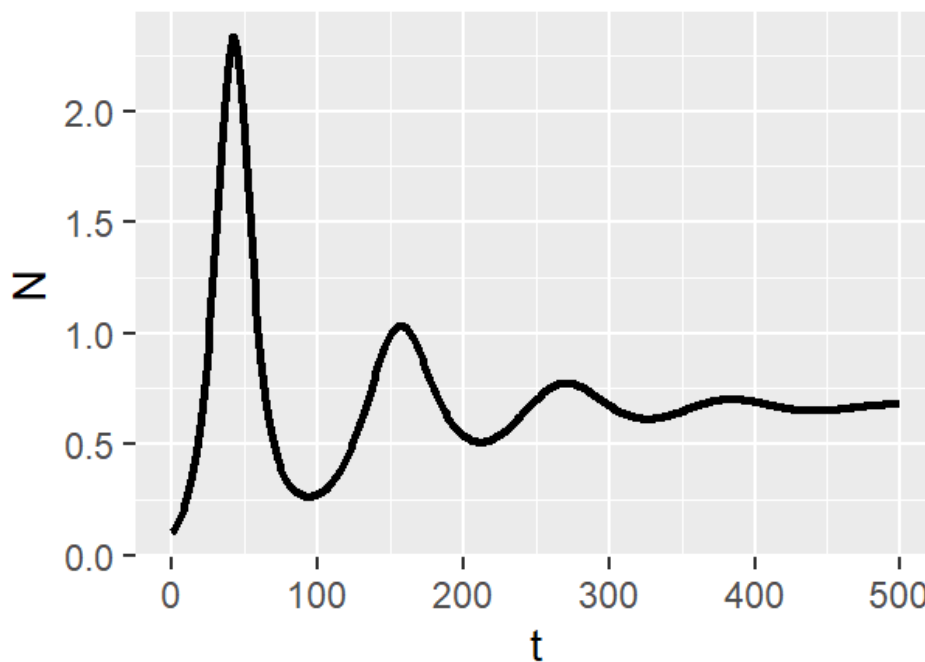
I varied 6 different parameter values based on my understanding of predator-prey dynamics and trophic interactions. I anticipated that these parameters would have the greatest impact on the population cycling based on my knowledge of snowshoe hare and vole cyclic dynamics. Depending on the model being utilized, I varied u_0 (vegetation intrinsic growth rate), m (maximum vegetation standing crop) a (search rate of caribou on vegetation), b (handling time of caribou with vegetation), to understand the impact of vegetation dynamics, and c (search rate of wolves on caribou), and d (handling time of wolves on caribou) to assess the influence of predator dynamics. With all functions created, I created a for loop for each parameter which cycled through a series of 10 values ranging 100% below and above my estimated value. I

plotted the series of values against the period and amplitude individually to determine whether the parameter influenced changes in caribou population dynamics. The visual representations were compared to my initial hypotheses.

4. RESULTS

4.1 Caribou-Vegetation Model

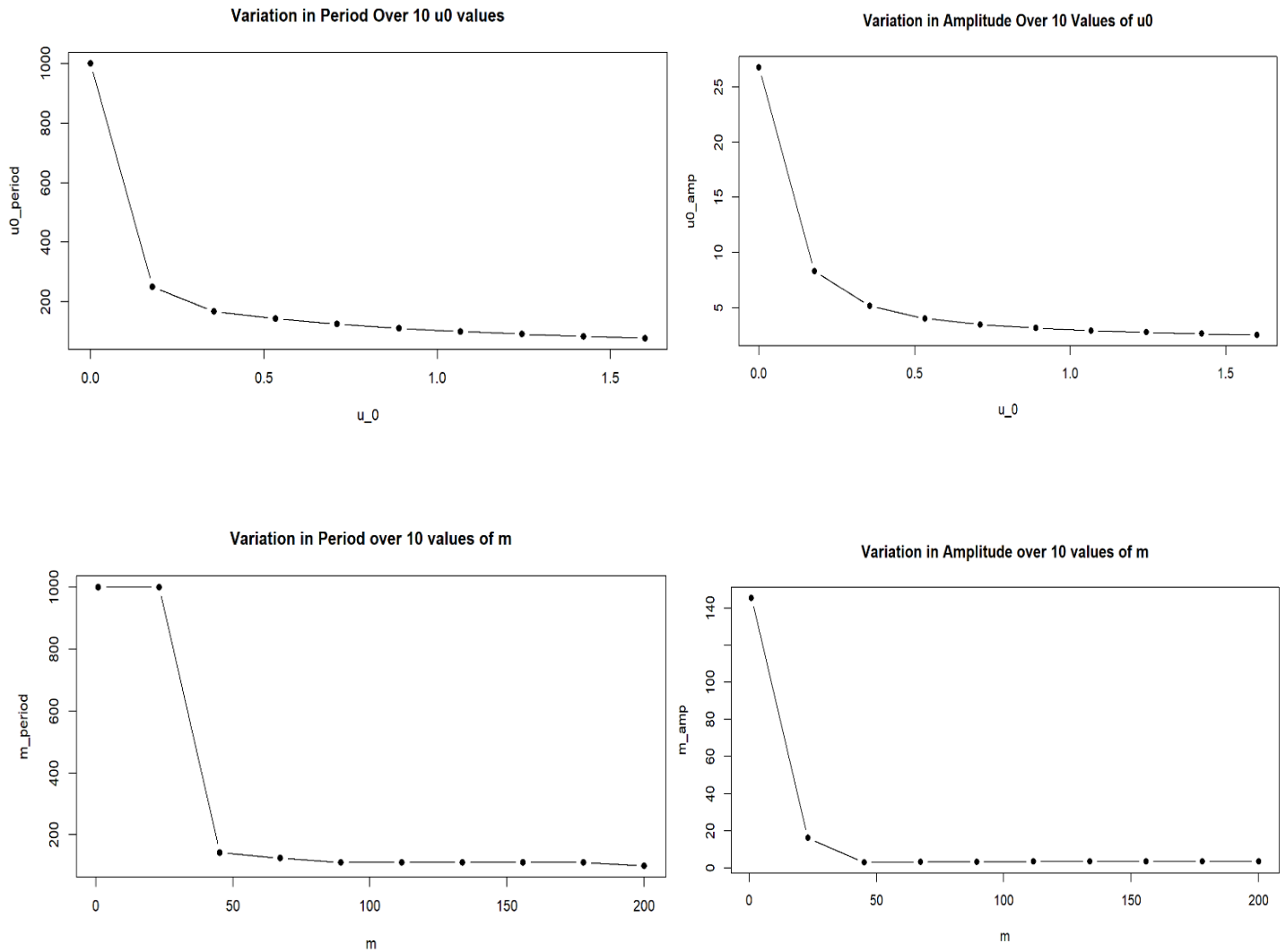
Figure 6. *Modeled caribou population over 500 years.*



The caribou-vegetation model predicts that over 500 years, caribou populations will cycle for nearly 350 years before stabilizing. In the absence of predators, caribou populations still cycle due to the growth rate and availability of vegetation. I calculated the period to be 125.25

years, which is longer than hypothesized. The amplitude for this model is 3.22. Thus, at its peak, caribou populations are on average 322% higher than their mean population.

Figure 7 *Change in period and amplitude for varied values of u_0 and m .*

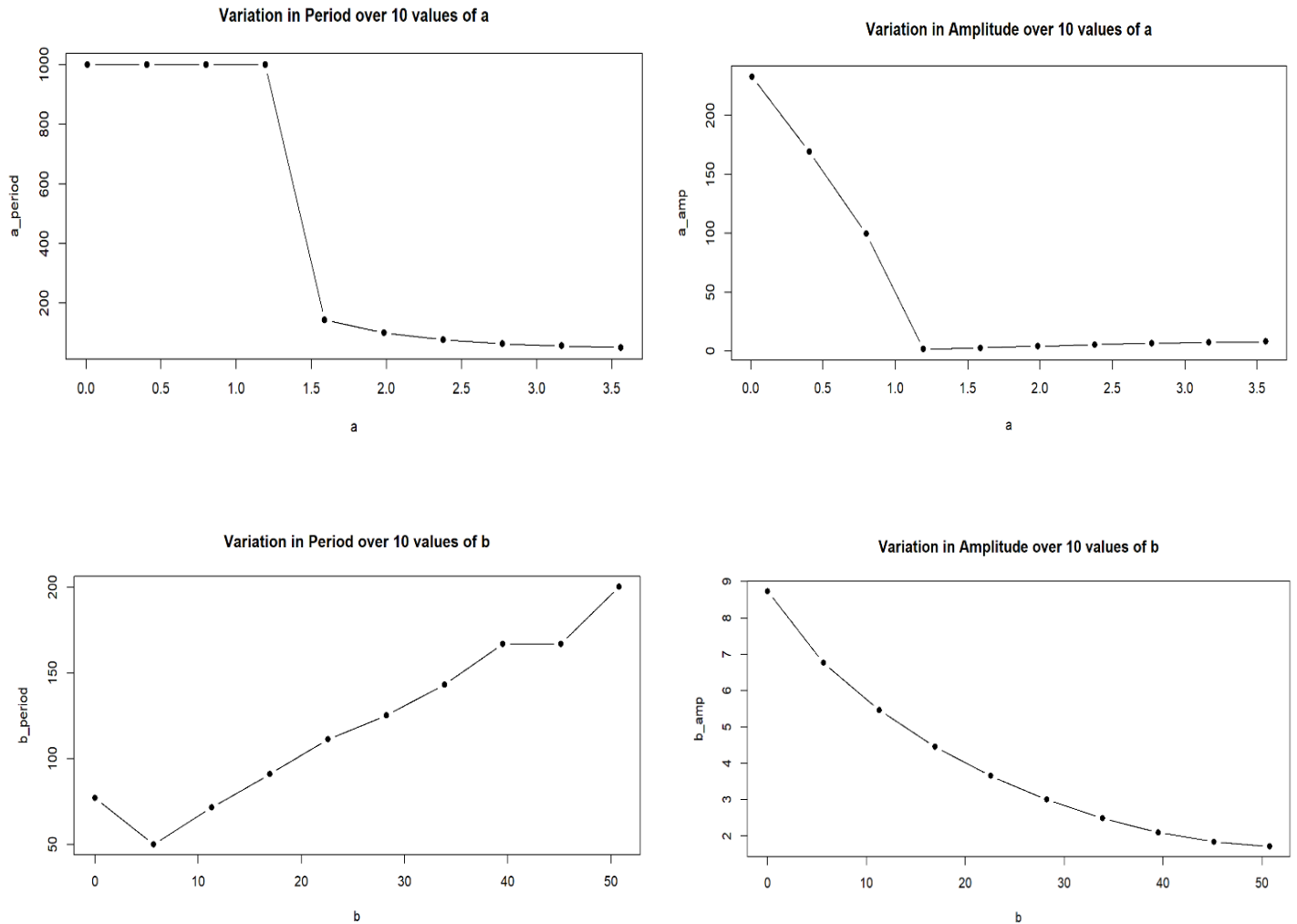


When we varied the values of u_0 between 0 and 1.6, we found that both period and amplitude decreased as u_0 increased. This aligns with our assumptions, as when vegetation grows faster, and caribou eat more quickly, populations grow at an increased pace. However,

populations will not reach high amplitudes, and will decrease in numbers when vegetation availability decreases, thus yielding shorter periods of cyclicity at lower amplitudes.

As we varied values of m from 0 to 200, we found that similarly to u_0 in the absence of predators, period and amplitude both decreased as m increased, meaning that as the amount of available standing crop increases, the time it takes for one boom and bust to occur is much shorter, but the amplitude at peak population is lower than under normal conditions. This outcome deviates from our hypothesis which assumed that as available food and energy increased, population cycles would become more chaotic, and amplitude at the very least would increase. We hypothesized that as caribou ate more food and populations grew faster, they would reach a much higher peak, and thus crash equally as hard when individuals ate all available standing crop. The caribou-vegetation model in the absence of predators describes the opposite interaction.

Figure 8 *Change in period and amplitude for varied values of a and b .*



When we varied values of a between 0 and 3.7 we found that both period and amplitude decreased as values of a increased. I hypothesized that increasing search rate would increase period, since caribou would take longer to find their food, and thus would reproduce at a slower rate, ultimately reaching their peak population size later. However, my hypothesis regarding amplitude was confirmed by our output. Increasing search rate for vegetation decreases amplitude, allowing caribou populations to maintain more steady cyclic dynamics rather than eating all the available forage, reaching high numbers, and then crashing dramatically.

When we varied the handling time of caribou with vegetation (b) between 0 and 50.8, we found that period increased. This aligns with our initial hypothesis which inferred that when caribou took longer to eat and digest their food, their population would grow slower because individuals would reproduce at slower rates. Thus, it would take longer for caribou populations to reach their peak. However, as we increased handling time, amplitude decreased, which conflicts with our initial assumption that period and amplitude are positively correlated. A decrease in amplitude suggests that because caribou take longer to eat, vegetation has more time to grow and thus does not get depleted as quickly. This results in a lower peak population size, and overall, more stable population cycles.

4.2 Caribou- Wolf Model

Figure 9 *Modelled caribou population dynamics over 500 years in the presence of wolves.*

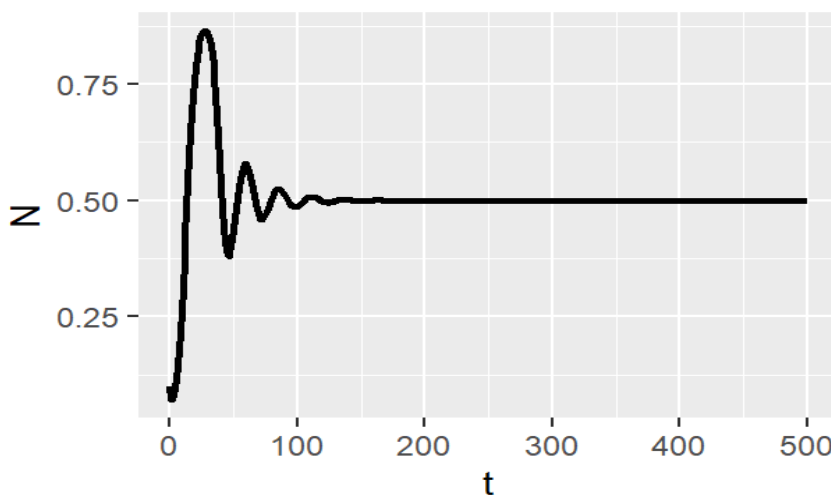
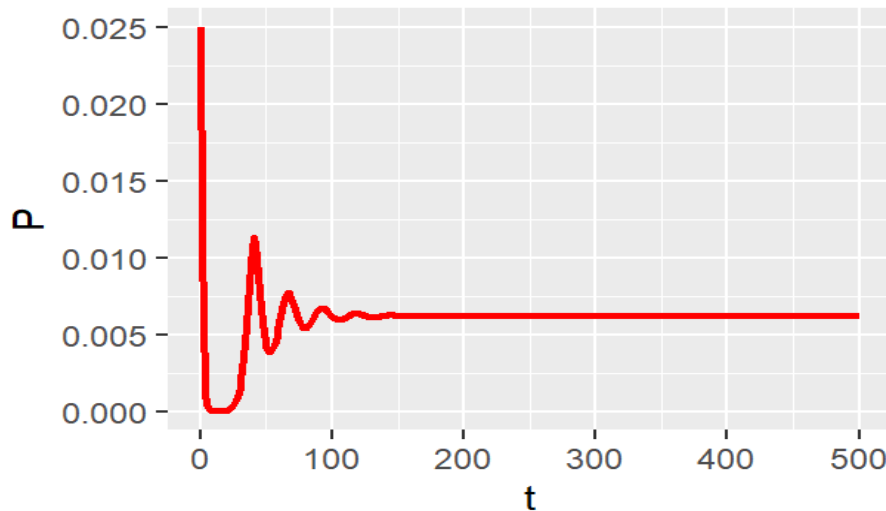
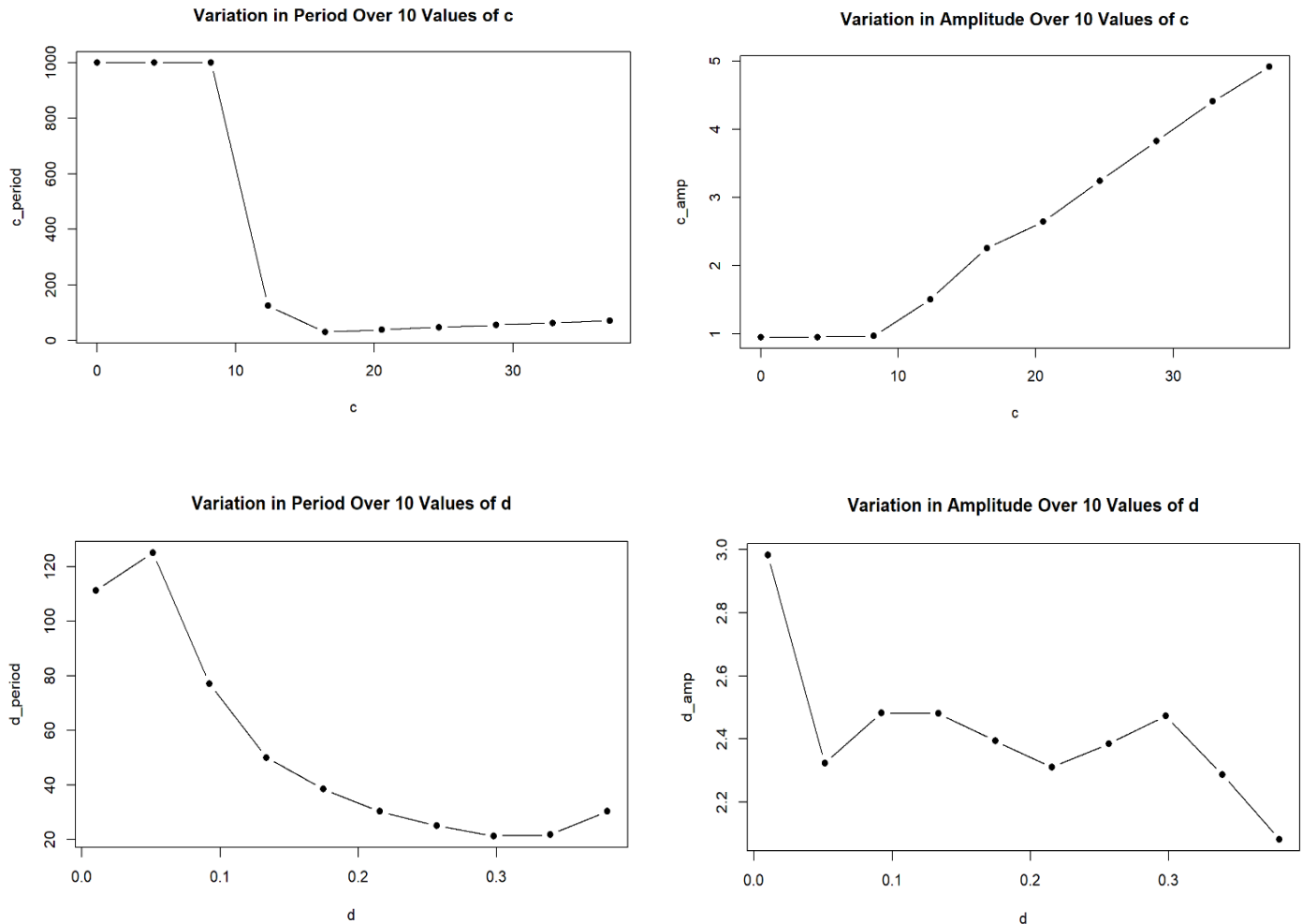


Figure 10 *Modelled wolf population dynamics over 500 years in the presence of caribou.*



Based on our caribou-wolf bi-trophic model, caribou populations (figure 9) will increase and decrease with varying amplitude and period for nearly 100 years before stabilizing in the absence of vegetation. At the same time wolves will initially decrease, and then increase as caribou populations increase as well. Wolf populations, pictured in figure 10, follow opposite boom and bust patterns to caribou due to the presence of a time lag. I calculated the period to be 45.5 years, which is comparable to St. John's calculated period of 40.5 years (2021). The amplitude for this model is 1.64, meaning the peak population size is 164% higher than the mean population.

Figure 11 *Change in period and amplitude for varied values of c and d .*



Search rate (c) and handling time (d) are the two most important parameters related to caribou and wolf dynamics. When we varied search rate between 0 and 37 we found that as search rate increased, period decreased. This suggests that as wolves take longer to find and kill caribou, caribou populations have a better opportunity to reproduce without the constraints of predation. Thus, populations reach their peaks faster when there is less regulation from wolves. By the same token, amplitude increases when there is less predation pressure, and the booms and busts experienced by caribou populations are more drastic.

4.3 Tri-trophic Model

Figure 12 *Modelled caribou population dynamics over 500 years in the presence of vegetation and predation by wolves.*

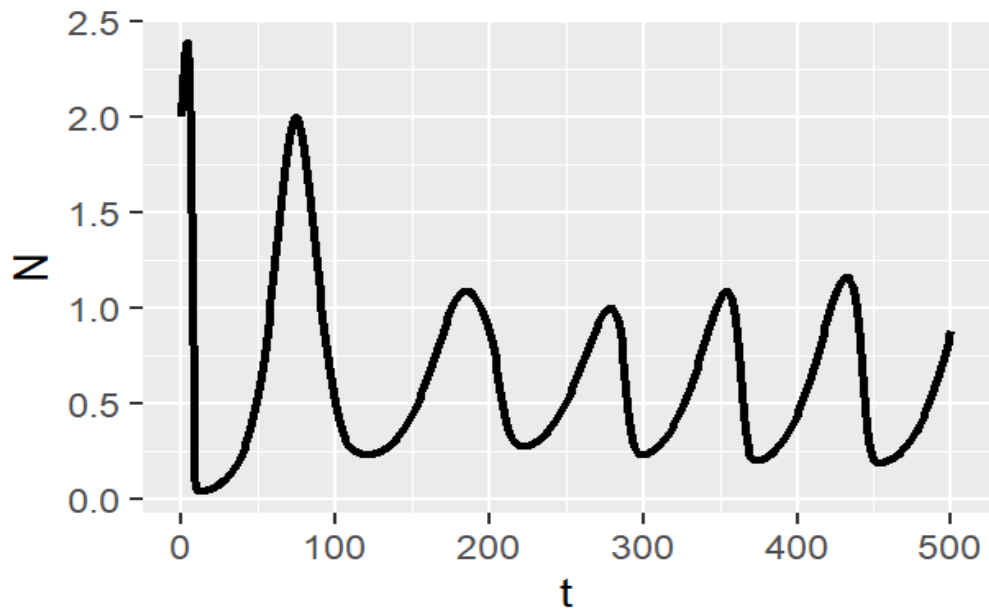
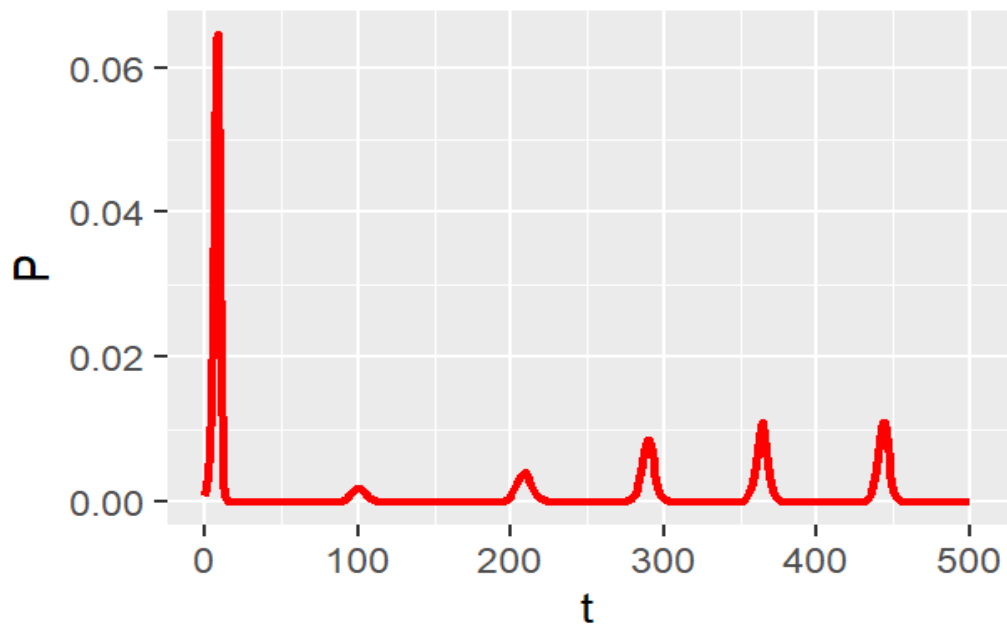
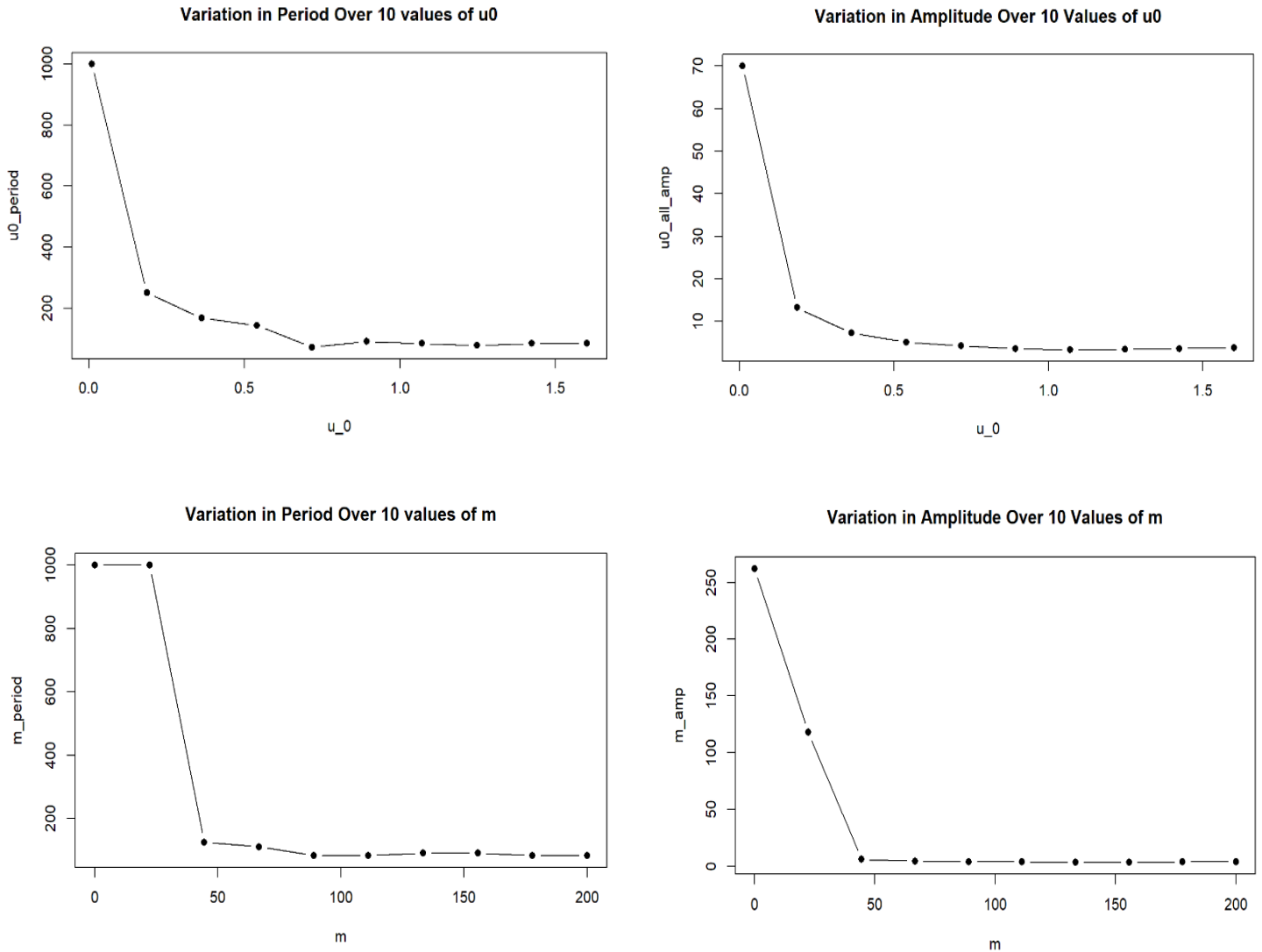


Figure 13 *Modelled wolf population dynamics over 500 years in the presence of vegetation and caribou.*



The tri-trophic model takes into consideration the impacts of vegetation dynamics and predation pressure. Figure 12 illustrates that when vegetation and predation are both present, caribou populations follow relatively consistent cycles over the course of 500 years unlike the other two bi-trophic models, which only show cycling for the first few hundred years. This is important because in reality it is rare to find instances where one of these factors is removed. There are exceptions to this of course: island populations void of predators. However, this model is most closely related to existing ecological processes. The calculated period for caribou cycles is 83.5 years, and the amplitude is 3.79, which means at its peak the population is 379% greater than when the population is at its mean.

Figure 14 *Change in period and amplitude for varied values of u_0 and m .*

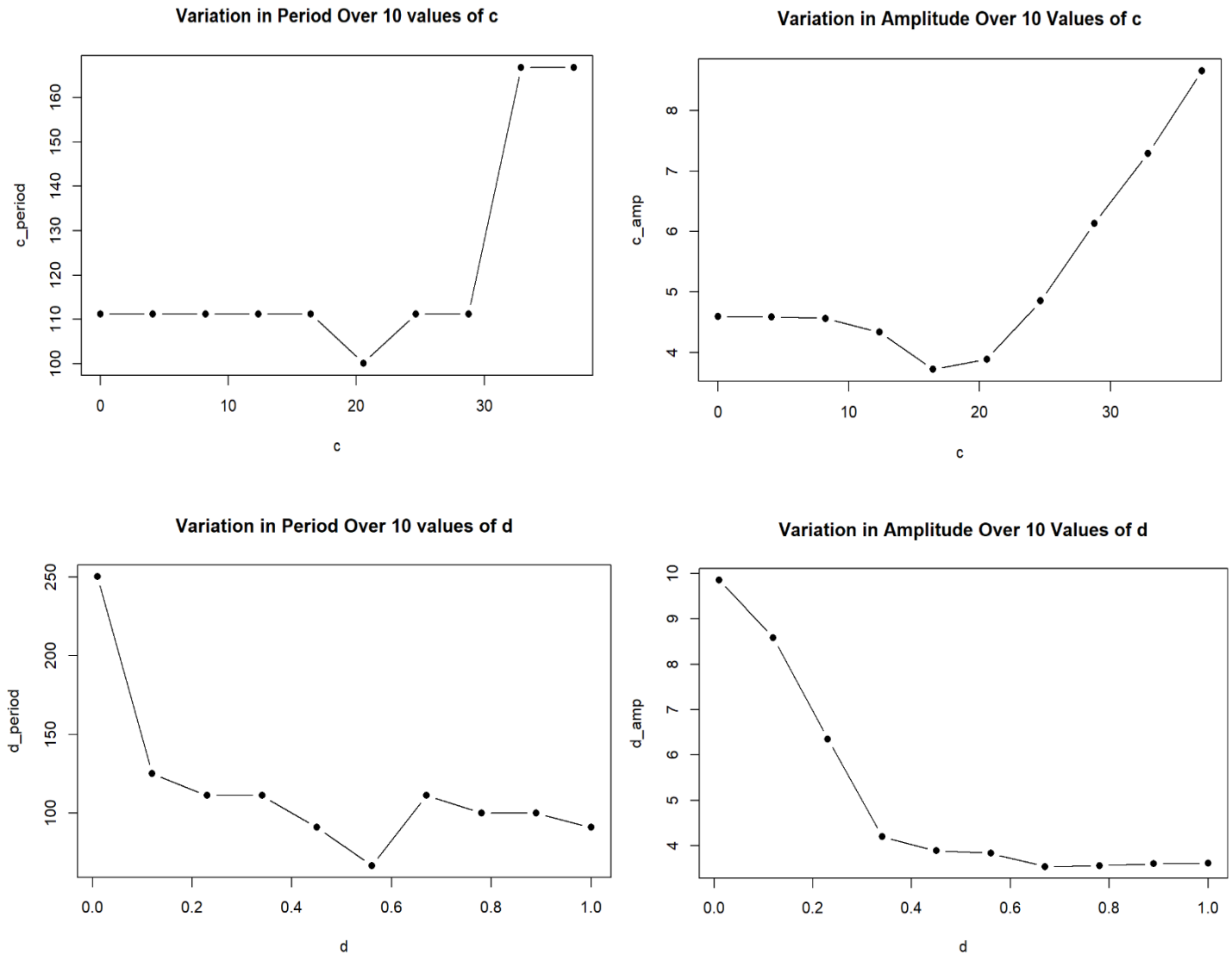


When we varied values of u_0 between 0 and 1.6 for the tri-trophic model, we found that both period and amplitude decreased, similar to our results for the bi-trophic caribou-vegetation model. This suggests that even when predators are present, changes in vegetation growth rate impact the cyclicity of caribou populations. When predation occurs at a fixed rate and vegetation

growth rate increases, caribou populations reach their peak size faster, but in general reach a lower peak value due to the fast regeneration of forage.

When we varied values of m between 0 and 200, we found that period and amplitude also decreased, which is concurrent with our findings in the caribou-vegetation model. Thus, revealing that when vegetation carrying capacity is higher, it is easier for caribou populations to reach carrying capacity as well, but carrying capacity is lower since more vegetation is available for consumption. This is contrary to our initial hypothesis, which inferred that caribou dynamics would be more chaotic when we increased the amount of energy input into the system. We anticipated a decrease in period, but an increase in amplitude because with greater available forage, in theory populations would increase to much higher peak sizes.

Figure 15 *Change in period and amplitude for varied values of c and d .*



When we varied c between 0 and 37 for the tri-trophic model, we found that both period and amplitude increased as c increased. This suggests that when we increase the amount of time it takes for wolves to find and kill prey, caribou populations have more time to grow in size because they are not being as heavily impacted by predation pressure. In the face of lower predation regulation, populations will also reach much higher carrying capacities.

When we varied d between 0 and 1 we found that period and amplitude decreased as d increased. This is concurrent with our results from the caribou-wolf model, which means that with consistent vegetation availability, when it takes longer for wolves to eat and digest caribou, caribou populations will increase much faster but reach lower peak sizes. This is because wolves take longer to digest their prey, so they reproduce at lower rates. Therefore, the number of wolves is not increasing at an alarming rate. However, with search rate constant, caribou are still being predated on, and therefore they do not reach higher amplitudes.

5. DISCUSSION

5.1 Major Findings

The median period of a single cycle was calculated to be 40.5 years, while the calculated median amplitude was 0.87, implying that the peak or maximum herd population was on average 87% higher than its mean population (St. John, 2021). However, based on my third model, including vegetation, caribou, and wolves, the period was 83.5, which is not unlikely considering caribou have the longest known cyclic periods of any species (St. John, 2021). The corresponding calculated amplitude was 3.79.

Impacts of vegetation on caribou population dynamics

As I varied vegetation dynamics, I found that both period and amplitude, which are positively correlated (St. John, 2021), decreased. This suggests that as vegetation increases and carrying capacity increases, there will be shorter periods of cyclicity, but less drastic booms and busts. I hypothesized that an increase in growth rate and carrying capacity would yield more chaotic dynamics, aligning with McArthur's theory of the paradox of enrichment (1971).

However, while shorter periods may correspond with less stability, a decrease in amplitude offsets the turbulence caused by the increase in energy into the system.

With climate change and global temperature increases, “It is well established that the greening of the Arctic is mainly attributed to the expansion of tall erect deciduous shrubs in the Arctic tundra biome (12–15). In North America, expanding shrubs such as birch and alder (that is, *Betula nana* exilis *Betula glandulosa*, and *Alnus viridus*) contain antibrowsing toxins (resins) that deter browsing from mammals (22, 29). These shrubs respond readily to climate warming, and because the antibrowsing defense gives them a competitive advantage over the more edible *Salix* (willow) species (22), they dominate the shrub expansion in several areas, replacing moss-, grass-, and herb-dominated vegetation [see the review by Myers-Smith et al. (13)]. Moreover, the expansion of shrubs reduces the lichen cover (15), which is an important winter forage for caribou. In summary, the current shift to a shrub-dominated tundra might therefore reduce the availability of high-quality caribou forage” (Fauchald et al., 2017).

Shrubification of the Arctic will increase forage competition between caribou and other ungulates (Lemay et al. 2021). Moose are well-adapted to eating shrubs and other types of vegetation that caribou are mal adapted to consume. With increasing temperatures, shrubs will grow readily, while lichen and other caribou vegetation will decrease. Thus, my model suggests that if climate trends continue, and vegetation persists slowly, caribou populations will face higher amplitudes and longer periods, which some herds may not be able to recover from

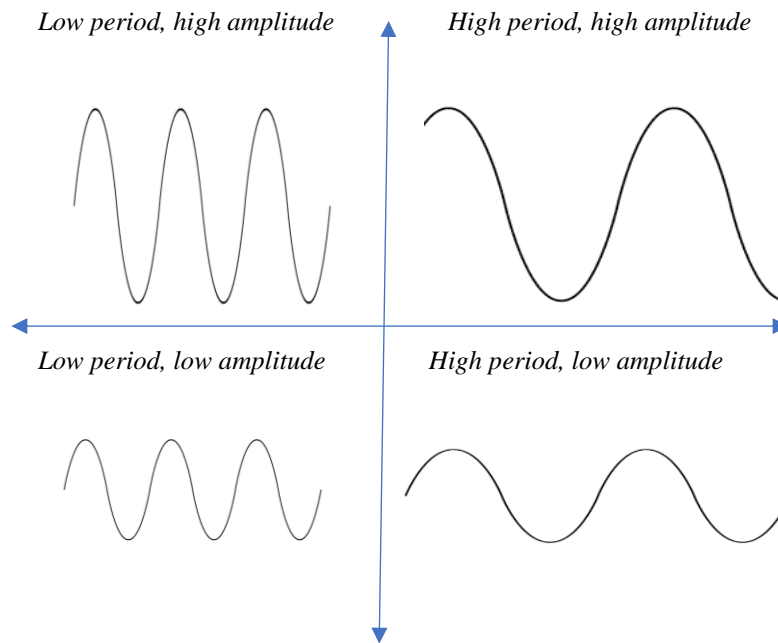
Impacts of predation on caribou population dynamics

Unlike Jack St. John’s findings, likely due to a lack of data on predators globally, my results indicate that there is a relationship between predation pressure and caribou population

stability (St. John, 2021). When I increased predator search rate, I found that period and amplitude increased. However, when I increased handling time, both period and amplitude decreased. These are consistent with what the literature predicted. This suggests that the longer it takes for wolves to find caribou, the more time caribou populations must increase in size, and thus the higher their population peaks become. Furthermore, when I increase the amount of time it takes for wolves to eat and digest caribou, period decreased, as did amplitude, which is not what I expected. I assumed that as wolves ate and digested their food faster, amplitude and period would have increased, leading to more booms and busts.

In the face of climate change, Wolves act as a shared predator for moose and caribou, inducing apparent competition between the two ungulate species. Habitat fragmentation and increased global climate change has prompted regime shift in moose populations, leading to higher densities of moose in primarily caribou habitat. Predation pressure is not high on the list of reasons for caribou population decline likely due to seasonal overlap with predators (Messier et al., 1988). However, “predation may negatively affect migratory caribou abundance when forage resources are not sufficient to maintain high caribou densities to swamp predators on calving grounds (Dale et al., 1994) and loss of lichen as a winter-food resource is likely as the treeline advances northward (Cornelissen et al., 2001). Repercussions of climate warming for migratory caribou thus might include increased predation pressure. Moose, being the preferred prey item, encourage wolves to follow them into caribou habitat as well, resulting in increased predation on both moose and caribou (Serrouya et al., 2019). With increasing temperatures, and increasing wolf populations, caribou herds may be at risk of further decline.

Figure 16 *Cyclic tendencies based on period and amplitude*



From a management perspective, ideally caribou cyclic periods are longer, and amplitudes are lower. This is the most stable outcome and would require the least dynamic management strategies for harvest. I achieved this goal when I increased handling time of caribou on vegetation (Figure 8). However, it is unrealistic to increase caribou handling time of vegetation and does not provide management boards with much insight. On the other hand, I found that in Figure 11, when I increased search rate of wolves on caribou, period decreases, and amplitude increases. This is the most chaotic outcome, considering more cycles occur within a shorter amount of time. Moreover, amplitude increases, which means caribou reach higher peak population sizes, and thus crash more intensely. If wolves move further north and predation rates

increase on caribou improve their hunting skills, this could be detrimental to caribou survivability and herd management. At this time, organizations like the Porcupine Caribou Management Board or U.S. Fish and Wildlife may see it fit to implement stricter wolf management policies to decrease the amount of predation pressure on caribou populations. Predator control studies in Alaska indicate that increased lethal wolf regulation may prompt an increase or stability in caribou populations. The Forty Mile Caribou herd has seen more stability over the last several decades, and a reduction in amplitude due to increased management and strict harvest controls. Other herds on the decline may be able to expand on their mission and incorporate similar tactics to ensure lower cyclic amplitudes. Expanded wolf harvest surrounding the Delta caribou herd, located in Central Alaska, led to increased caribou density the following 14 years (Beortje, 1990). However, wolf management is not the only solution, as climate is playing an increasingly important role in caribou regime shifts, and vegetation availability. More integrative solutions will be necessary to prevent further global decline. Currently, caribou management and policy are widespread, but more consistent data and population modelling is necessary to determine the impacts of vegetation, predation, and harvest on the species' global decline.

Caribou are known to have some of the largest population cycles among mammals. The relationship between snowshoe hares and lynx is the predominant example of mammalian population cycling. As an r-selected species, hares reproduce quickly, exceeding carrying capacity in almost 3 years (Krebs et al., 1995). While hare populations grow, the primarily predator—lynx—grow at a slower rate. Once hares exceed carrying capacity and resources like forage and space are limited, predation rates increase significantly, and snowshoe hare populations rapidly decline in approximately 2 years (Krebs et al., 1995). For the following 5

years both hare and lynx populations are low, allowing forage to regenerate before the increasing phase of this cycle restarts (Boonstra et al., 1998). This example of population cycles can be applied to several mammals, not just those similar in size to hares, but 10-year periods support more data availability when compared to multi-decade cycle periods. Caribou, which cycle over a period anywhere between 40-80 years roughly, may be more difficult to study for that reason. However, my results provide us with a broad understanding of the species' population dynamics, and support the idea that well-studied cyclic species and larger less-studied mammals may adhere to similar processes.

4.2 Limitations and Future Aims

The parameterization process for all three models gave insight into available research and resources regarding caribou and wolf functional responses. Though caribou are extensively studied, there is little understanding about forage search rates and handling times. Furthermore, I was unable to find estimates for search and rate and handling time for wolves as well and had to calculate these parameters using limited information. Thus, it was difficult to find estimates for these two parameters, which may have skewed the period and amplitude of our predictive model and influenced our results. However, our model yielded insightful results regarding the relationship between caribou, wolves, and vegetation, that were seemingly unknown prior to this modelling process. While we gained a better understanding of what drivers impact caribou population cycling, there are limitations to my model and the validity of my results. Furthermore, I did not find accurate estimates for several parameters, and thus had to interpolate based on other parameter values, which may not have yielded the most intuitive or sensible estimates. I tested one parameter at a time, rather than multiple parameters. There are likely several

parameters directly influencing the presence of cycles, but due to limitations on time I was unable to test for compounding affects.

Future research is necessary to confirm our findings and provide scientists and managers with a better understanding of caribou dynamics in the short and long term. I chose to use the Michaelis-Menten discrete stochastic model, but it may be worth trying different discrete or continuous models to describe caribou cyclicity. Inverse modeling can be used to simulate population dynamics, and fit parameters according to appropriate simulations. Furthermore, it is fundamental that multiple parameters are varied at the same time to check for changes in period and amplitude. Due to time constraints, I was unable to incorporate harvest in our model. Harvest impacts caribou populations directly, and organizations like the Porcupine Management Board aim to track caribou population dynamics to better inform harvest policy. Caribou are globally declining (Vors & Boyce, 2009), and it is important to recognize that we fully understand how factors like climate, forage, predation, and harvest interact to drive this decline (. There is reason to believe that increased climate change and increased predation pressures will only add to this global decline, so scientists and managers will need to consider the tradeoff between saving caribou in the short term or trying to predict population tendencies in the future.

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