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Understanding Caribou Population Cycles

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Understanding Caribou Population Cycles

Jack St. John

University of Montana

Abstract

The complex population dynamics of caribou (*Rangifer tarandus*) were studied to determine the patterns of their population cycles and the processes driving them. It is well established, via previous archaeological research and Indigenous knowledge, that large migrating caribou herds found in and around the tundra at northern latitudes experience population boom and busts roughly every several decades. However, the processes driving the dynamics of these cycles are relatively unknown, which makes managing caribou herds for recreational and subsistence harvests difficult. It has been hypothesized that a combination of intrinsic and extrinsic factors shape these cycles, with density-dependence, predation, harvest, climate, and others likely all playing a role. I aimed to determine whether caribou herds experience population cycling and, if so, estimate the period and amplitude of their cycles and determine which factors drive them. I collected population data on 43 caribou herds throughout the world, and in doing so, assembled the largest caribou population database to date. I used statistical interpolation to fill in the gaps between available data due to low sampling frequency. I quantified whether herds were cycling by fitting populations to sine waves and using periodograms to distinguish cycling tendencies from white-noise stochasticity. I collected additional information on other factors hypothesized to affect caribou cycles, including predator presence data, climate oscillation data, subspecies and ecotype data, and the latitudes of each herd. I used the interpolated data for each herd to determine the variables influencing the periods and amplitudes of caribou population cycles. The median period length was 40.5 years and the amplitude, standardized about the mean population size, was .871; period length and amplitude were also positively correlated. In addition, cycle amplitude was best predicted by period length, subspecies, biome, and average winter minimum temperature. Period length was best predicted by amplitude, latitude, subspecies, biome, NDVI, and average winter minimums. A better understanding of caribou population dynamics could

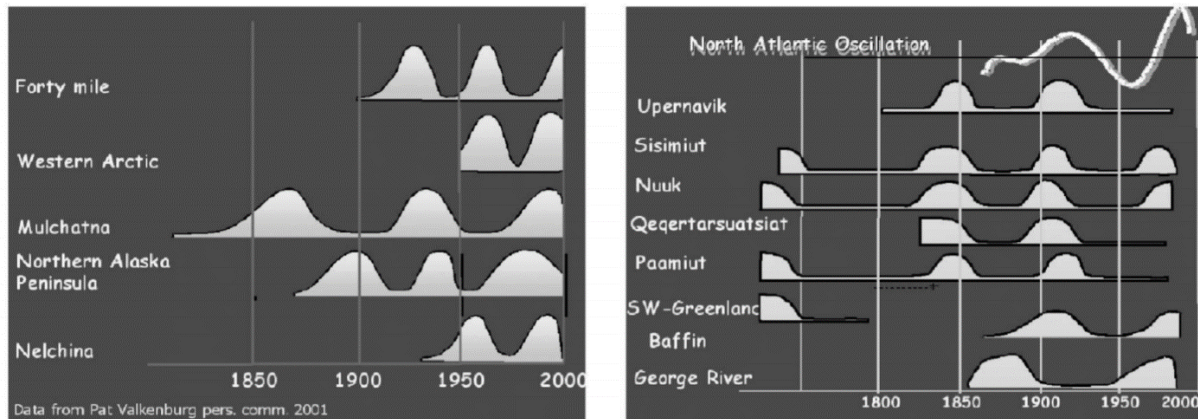
help wildlife professionals and policymakers adapt their caribou management strategies. Climate appears to be a strong driver of these cycles, and with climate change becoming an increasingly apparent reality in the Arctic, cyclic tendencies may prove to disappear, or become amplified and spell disaster for caribou populations. Caribou management strategies will need to adapt to an ever-changing world if we want to preserve natural caribou population cycles—but what that entails remains to be seen.

Introduction

Caribou (*Rangifer tarandus*) are one of the most intensively studied and managed ungulates, yet relatively little is understood about their population dynamics. What can be agreed upon is that many caribou herds, primarily circumpolar herds, experience drastic population fluctuations that span several decades. Gunn (2003) was one of the first to highlight the global nature of these cycles and posture the theory that climate drives changes in caribou body condition and thus reproductive success. The biggest obstacle to fully understanding caribou population cycles is the limits of available data. While Indigenous knowledge illustrates large boom and bust caribou population cycles over the last several centuries—illustrated in Figure 1 below—there are few collected population data from before the mid 20th century, with some herds only receiving closer management attention in recent years.

Figure 1

Standardized fluctuations in caribou abundance in (a) Alaska and (b) Greenland and eastern North America

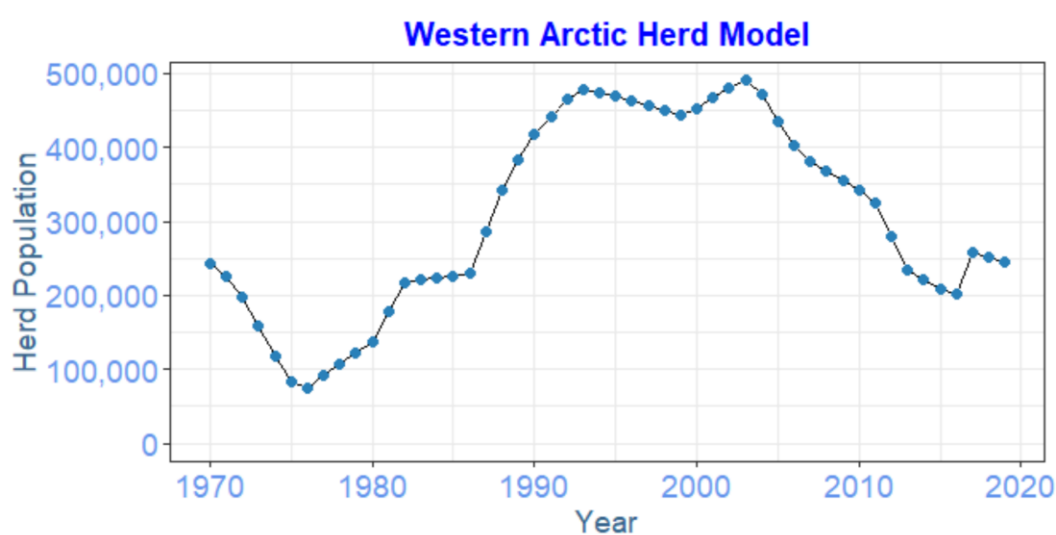


Note. From “Voles, lemmings and caribou – population cycles revisited?,” by A. Gunn, 2003, *Rangifer*, Special Issue No. 14, p. 107.

This paper and accompanying analysis aim to understand caribou population cycles via a spatial approach. While individual herds may have accurate population estimates dating back several decades, often the breadth of available data only captures one “cycle” of the population—see Figure 2 below.

Figure 2

Herd model of the Western Arctic caribou herd with interpolated values



This makes in-depth temporal analysis of population cycles impossible for individual herds. However, by collecting data on 43 caribou herds, I was able to assemble a caribou population database with the goal of analyzing cycles via replication over multiple herds. Additional data were also collected for each herd due to suggestions that they may drive population cycling: number of predators, presence/absence of wolves, latitude, subspecies, ecotype, biome, whether the herd is semi-domestic, NDVI value, average winter monthly minimum temperature, and average winter monthly precipitation. The purpose of collecting these supplementary data was to understand the drivers of these cycles, which has the potential to impact caribou management strategies.

Population cycles have long been studied in ecology. Cyclic population dynamics have been well-documented and studied in many small mammals such as lynx, snowshoe hares, voles, and lemmings (Barraquand et al., 2017; Gunn, 2003; Post, 2005). Population cycling in ungulates has been observed, however in fewer cases and with less research attached (Post, 2002; Turchin, 2003). Caribou herds have been known to cycle, via knowledge from Indigenous peoples and managers, for the last several centuries (and likely much longer) (Gunn, 2003). Additionally, the strength of density-independent factors such as climate are known to increase in small mammal populations at northern latitudes, a phenomenon that may be driving caribou population cycling at northern latitudes (Post, 2005). For example, in Alaska, large-scale climate oscillation (Arctic and Pacific Decadal) have been related to caribou growth rates (Joly et al., 2011). Top-down and bottom-up factors govern small mammal population cycles, but whether this is the case with caribou remains to be seen (Barraquand et al., 2017; Gunn, 2003). The temporal scale of caribou population cycles, as well as the remote locations of many caribou herds, has made understanding their dynamics difficult.

Caribou are an incredibly valuable resource in the Northern Hemisphere. The several million living caribou are significant both economically and culturally to many countries and peoples. Reindeer husbandry is an important industry and way of life in Eurasia, while Indigenous communities in Alaska and Canada have relied on caribou for millennia (Baskin, 2000; Burch, 1972). Managing caribou in the face of climate change, rapid habitat destruction, and expanding human populations has never been more vital than it is today. By determining the drivers of caribou population cycles, perhaps we can more efficiently manage caribou for both herd health and human benefit. For example, managing for population stability may be advantageous for sustenance and from an economic perspective. Regardless of the outcome, I hope that by fostering a better understanding of caribou population dynamics, caribou can be sustainably managed for the benefit of current and future generations.

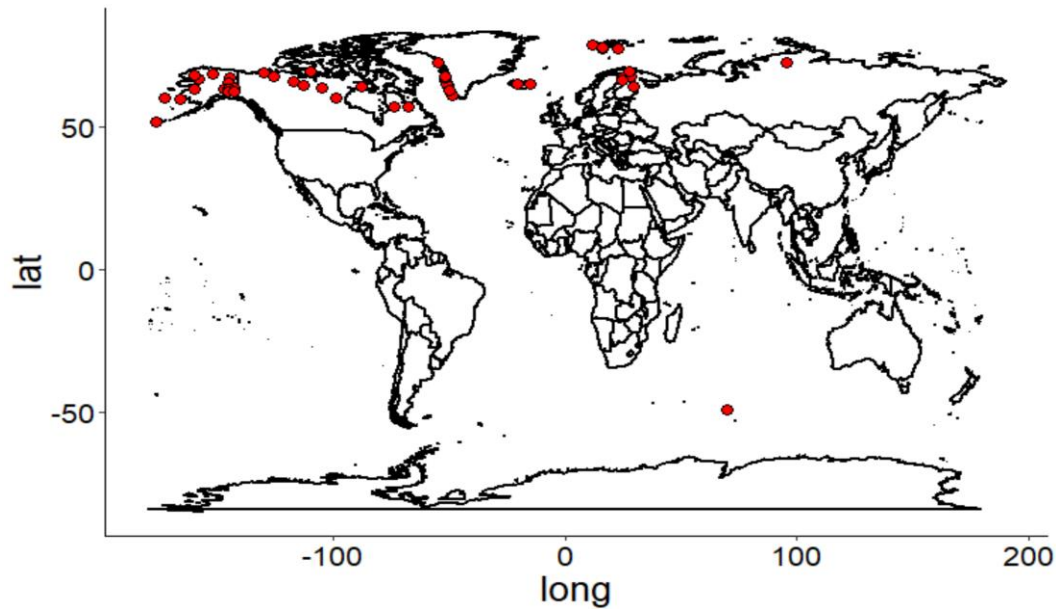
Methods

Data Collection: Herd Estimates

I collected population estimates along with supplementary data for 43 herds. Many of the herds were from Alaska and Canada due to the availability of population estimates, see Figure 3 below. I pulled population estimates from various management reports released by agencies. For herds in Alaska, reports were released by the Department of Fish and Game (ADFG), while in Canada this corresponded to individual providence departments of environment and/or natural resources. An example of estimates compiled in an ADFG management report can be seen in Table 1 below. Herds estimates I obtained for herds found outside of North America were often from scientific papers and government documents.

Figure 3

Map of herds from which population estimates and supplementary data were collected



Note. Red dots correspond to the approximate central distribution of each herd

Table 1

White Mountains caribou herd fall composition counts and estimated population size, 1983-2009

Date	Bulls:100 Cows	Large bulls: 100 Cows	Calves:100 Cows	% Calves	% Cows	% Small bulls	% Medium bulls	% Large bulls	% Total bulls	Composition sample size	Estimate of herd size
9/29/83	44	19	31	18	57	26	29	44	25	135	
10/85	36		31	18	60				22	65	
9/29/88	43	14	33	19	57	51	16	33	24	211	
10/06/89	50	11	36	19	54	46	33	22	27	744	750-1000
10/11/91	23	5	24	16	68	44	35	21	15	312	
10/29/91 ^a				15						324	761 ^b -1000
10/13/92	39	12	23	14	62	52	18	30	24	247	832 ^b -1200
9/27/93	48	21	22	13	59	34	23	43	28	497	
10/04/94	39	16	25	15	61	34	24	42	24	418	
10/16-17/95	36	10	31	19	60	44	27	29	22	418	
10/2/96	44	9	54	27	50	60	20	20	22	513	
10/2/97	34	11	38	22	58	50	19	31	20	341	
10/2/98	50	11	18	11	60	42	37	21	30	759	961 ^b -1100
9/30/99	62	16	39	20	47	33	40	26	31	644	
9/29/00	54	11	13	8	60	40	40	20	32	399	687 ^b -800
9/25/01	57	11	26	14	55	46	36	19	31	441	700-800
9/24/02	34	7	29	18	61	44	35	21	21	405	
10/5/03	30	11	17	11	68	40	22	38	20	308	
10/5/04	35	6	23	15	63	32	49	18	22	321	642 ^b -733
10/6/05	44	18	21	13	61	33	27	40	27	391	514 ^b -600
10/16/06	36	9	20	13	64	43	31	26	23	362	
10/10/07	39	7	37	21	57	54	27	19	22	358	590 ^b -650
10/09/08 ^c	46	12	42	23	53	42	31	27	24	507	677 ^b -762
10/07/09	42	9	15	9	64	44	34	22	27	333	529 ^b -605

^a Conducted with fixed-wing aircraft instead of helicopter.

^b Minimum count from summer census.

^c Some mixing with the Fortymile Caribou herd occurred; therefore this data is less representative of the White Mountains herd alone.

Note. From “Caribou management report of survey-inventory activities 1 July 2008-30 June 2010,” edited by P. Harper, 2011, Alaska Department of Fish and Game.

While herd surveying techniques have improved over the last several decades, there is inherent observation error. To best account for survey errors, the most recent available data took precedent over older data. For example, if a herd was estimated to number 100,000 by a 1970 survey but then listed as 80,000 during the same year in a 2018 management report, I would pick the 80,000 estimate because it was most recent. Population estimates were also prioritized over population (minimum) counts if both were available for the same herd, although not all herds had calculated population estimates. A few of the more closely monitored and smaller herds—such as those found in Finland, on smaller islands, or those that are managed as semi-domestic—had exact population estimates with no observation error. Despite numerous sources of potential error in the population estimates, the reliability of population estimates was not a concern. This study focused on population trends over time, so minute, small-scale population errors are not of concern.

Data Collection: Supplementary Data

In order to understand the underlying mechanisms of caribou population cycles, supplementary data were collected for each herd. These supplementary data consisted of: number of predators, presence/absence of wolves, latitude, subspecies, ecotype, biome, whether the herd is semi-domestic, NDVI, average winter monthly minimum temperature, and average winter monthly precipitation. Predator data were collected due to the known impacts of predation on small mammal population cycles as well as the preliminary evidence that wolves have induced moose population cycling in Isle Royale National Park (Barraquand et al., 2017; Gunn, 2003; Post, 2002).

Caribou genetics and classification is a controversial subject, with numerous governments, management agencies, and researchers using different criteria to differentiate

broad-scale differences in caribou phylogeny. To promote a consistent, reasonable classification of caribou herds, one source was used as the final determination for caribou subspecies and ecotype. Generally, subspecies correlates to genetic differences between caribou herds while ecotype refers to behavioral differences. Each herd was given a subspecies classification, such as *R. t. fennicus* (Eurasian forest reindeer) or *R. t. pearyi* (Peary caribou), as well an ecotype classification, such as insular or montane, according to Mallory & Hillis (1998). Continued refinement of this classification strategy may be necessary for further research conducted on the collected data.

Biome data, defined as “summer range/winter range” was collected using herd management reports which contained details on the migratory patterns of each herd. Each seasonal range was defined as either taiga (boreal forest) or tundra. The herd’s status as either wild or semi-domestic was also collected, although very few herds were semi-domestic. Semi-domestic herds are caribou that are largely free-roaming but are rounded up for harvest yearly and are closely managed.

Latitudinal influences on population cycles have been well documented in small mammals as well, prompting the collection of the approximate central latitude of each herd (Post, 2005). Latitudinal gradients were thought to be an accurate proxy for weather, although this proved to be faulty. While latitude may be an appropriate proxy for climate in certain countries or regions, when dealing with a circumpolar mammal this was not the case. Climate oscillations, broad weather patterns, and geographical factors such as inlets and oceans, render latitude a weaker predictor of climate throughout the Northern Hemisphere. As a result, additional weather/climate data were collected, consisting of NDVI which measures habitat productivity, the average winter monthly minimum temperature, and the average winter monthly

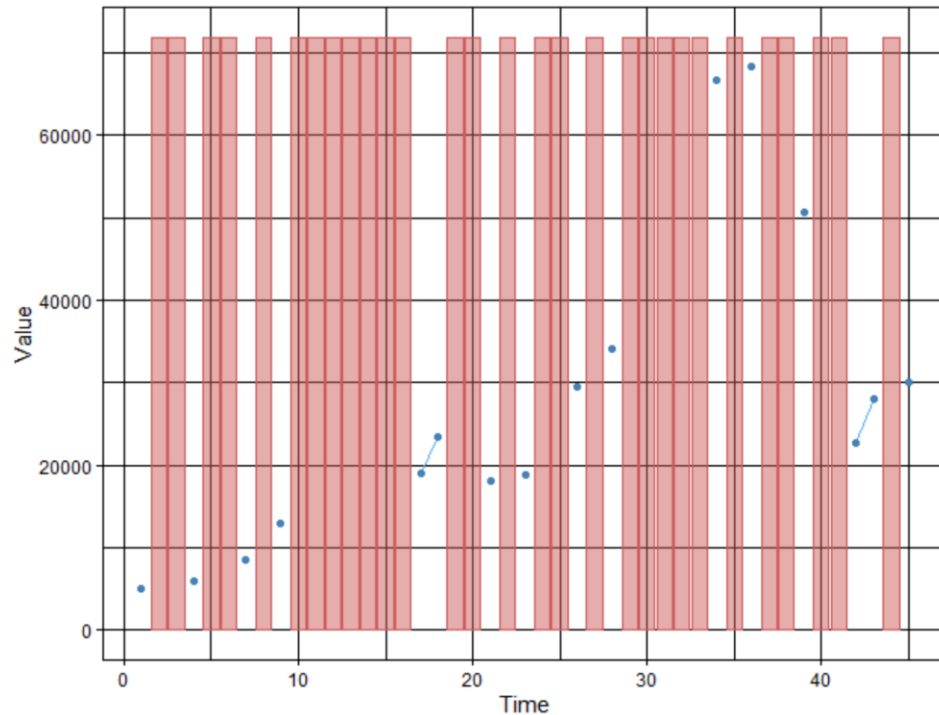
precipitation. For all weather data, a buffer of 10,000 kilometers was incorporated to ensure that local weather conditions of each herd were properly captured. The Normalized Difference Vegetation Index (NDVI) was collected as a dynamic habitat index, measuring the changes in yearlong NDVI values for a region. NDVI values were available from 2003-2014 for each herd and gathered from: <http://silvis.forest.wisc.edu/data/dhis/>. To maintain consistency, temperature and precipitation data were also collected from 2003-2014. Unlike NDVI, precipitation and temperature were only collected and averaged from the winter months (December through March) due to the known strain that winter places on caribou stress, fitness, and pregnancy (Joly et al., 2015; Parker et al., 2005). Winter temperature and precipitation data for each herd were collected from: <http://www.climatologylab.org/terraclimate.htm>.

Data Analysis: Interpolation

Caribou population surveys are not conducted every year for most herds, with many herds not monitored for several years in between population estimates. As a result, the collected herd population estimates were full of gaps, yet oftentimes a clear pattern was obvious—see Figure 4 below. I analyzed the missing data using the “imputeTS” R package developed by Mortiz & Bartz-Bielstein (2017).

Figure 4

Time series model of the Central Arctic caribou herd with missing years highlighted



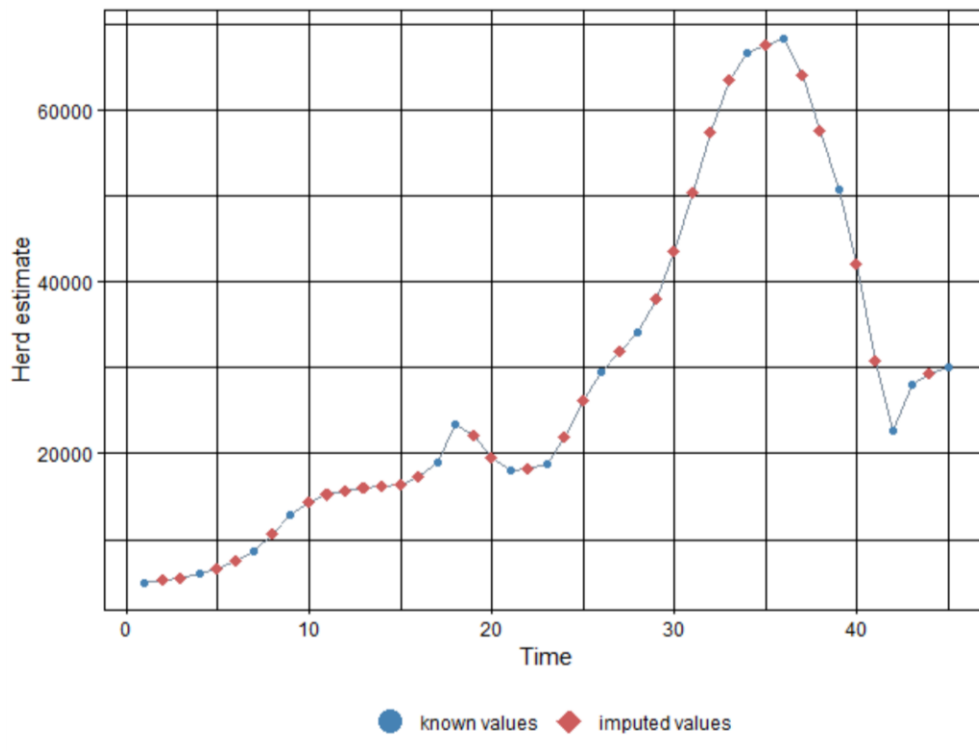
Note. Red bars and blue dots correspond to years with no population estimate and actual surveyed estimates, respectively.

In order to “fill in” these gaps, Stineman (stine) interpolation as described by Stineman (1980) was used. This method of interpolation was favored over other interpolation methods due to its ability to produce reasonable population outputs. Caribou, being large mammals with slow gestation periods and little year-over-year population fluctuations, were a perfect fit for an interpolation method that produces no new inflection points or “wild’ points” (Stineman, 1980). Stine interpolation has been used in other ecological research with success and appears to be suited well for datasets with abrupt changes in slope, which is necessary when considering the drastic population cycles being studied (Perillo & Piccolo, 1991). The method worked well with

my dataset, providing realistic population estimates for years without available data as seen in Figure 5 below.

Figure 5

Time series model of the Central Arctic caribou herd with interpolated herd estimates



Note. Red dots and blue dots correspond to stine interpolated population estimates and actual, surveyed population estimates, respectively.

Each herd with at least one missing population estimate within their dataset underwent stine interpolation to fill in each gap. The final dataset included these interpolated values for further analysis.

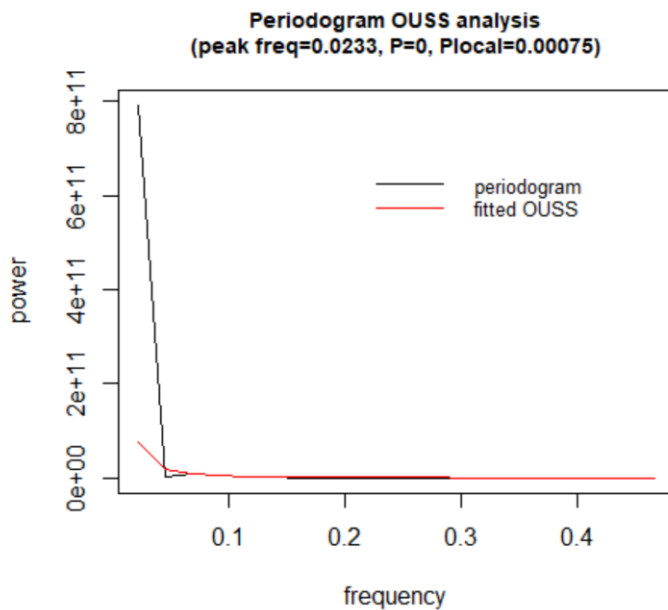
Data Analysis: Period and Amplitude

After each of the 43 herds were compiled with supplementary data and missing years were interpolated, I utilized cyclic analysis to determine the cyclicity of individual herds. I then

estimated the period and amplitude of those herds deemed cyclic. Cyclic analysis was completed following the procedure for ecological time series data, “peacots,” developed by Louca & Doebeli (2015). Herds were considered cyclic if their periods were statistically different ($p < .05$) than normal stochasticity, more specifically an Ornstein-Uhlenbeck state space (OUSS) null model. Periods were determined by fitting sine waves to each of the herds and finding the frequency that minimized the residuals between the wave and the interpolated data. Each optimized frequency was computed using spectral density, determining the dominant frequencies of a time series. An example periodogram, which is an estimate of the spectral density of a time series, is provided in Figure 6 below. Period length, which is the time in years between population cycles, was calculated by dividing 1 by the optimized frequency. The optimized frequency was determined based on the power of the periodogram, which measures its predictive strength at a given frequency.

Figure 6

Periodogram of the Leaf River caribou herd

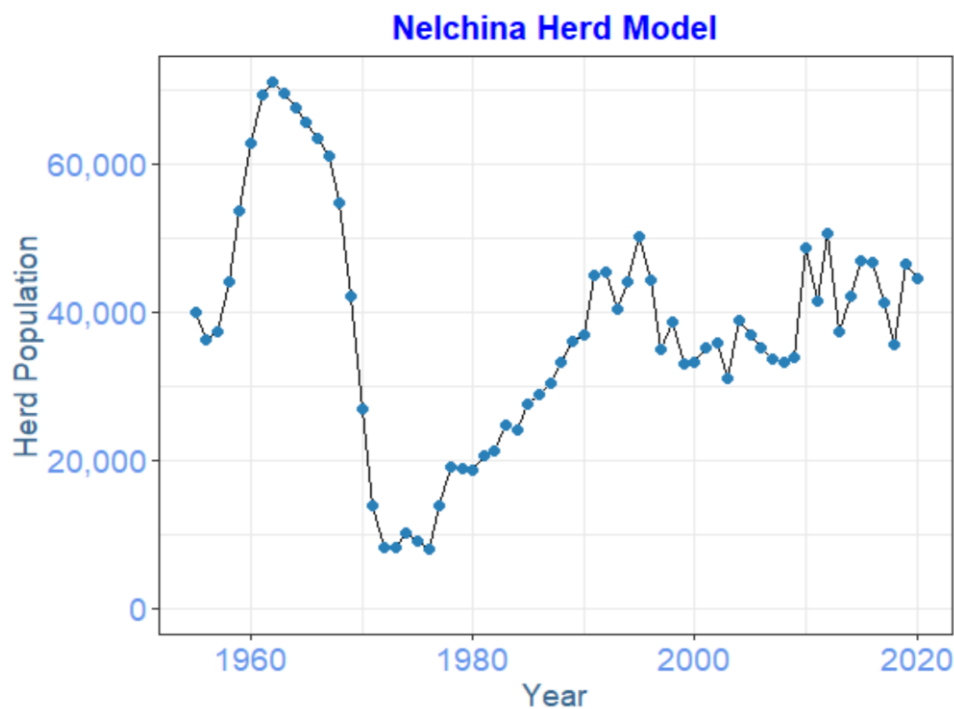


Note. Power vs frequency with accompanying periodogram and null OUSS models

While some herds, such as the Central Arctic herd depicted in Figure 5, are clearly cyclic, many were not. Limited data and stringent statistical requirements left many herds out of period and amplitude analysis despite some of them possibly being cyclic herds. As a result, of the 43 herds, I only 19 were deemed cyclic via periodogram analysis. Some herds, such as the Nelchina herd shown in Figure 7 below, did not have enough statistical evidence to be considered cyclic despite Indigenous and management knowledge that the herd has cycled for centuries.

Figure 7

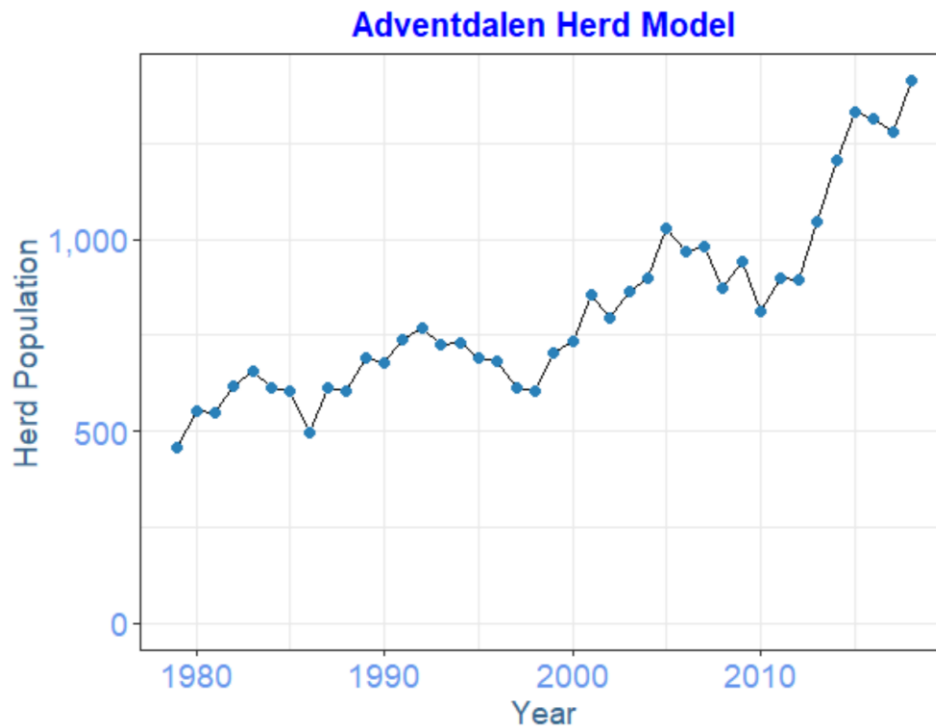
Interpolated model of the Nelchina caribou herd in Alaska from 1955-2020



The Nelchina herd appears to have lost its cyclic population tendencies in the last several decades, possibly due to intense predator (wolf) control (Boertje et al., 2017). I eliminated other herds from period and amplitude analysis for a more straightforward reason, such as the Adventdalen herd shown in Figure 8 below, that being obvious non-cyclic population dynamics.

Figure 8

Interpolated model of the Adventdalen caribou herd in the Svalbard Islands from 1979-2018



I also calculated amplitudes for each of the 19 cyclic herds, albeit with some modifications. While amplitude is traditionally the distance between the mean of a wave and its peak or trough, I had to adjust this procedure to account for herds of various sizes. While sine waves are on a standardized scale, caribou population cycles are not. To prevent larger herds numbering in the hundreds of thousands from skewing the results, I standardized each amplitude about the mean. Otherwise, large herds would have proportionately large amplitudes. As a result, relative amplitudes for each herd were calculated as follows:

$$\frac{(\text{Maximum Herd Population} - \text{Minimum Herd Population})/2}{\text{Mean Herd Population}}$$

Data Analysis: Model Selection

Upon the completion of preliminary period and relative amplitude analysis, I built generalized linear models (GLMs) using Gaussian errors and an identity link function to explain these variables. GLMs for period length and relative amplitude were completed in the same fashion and utilizing backwards stepwise elimination (Burnham & Anderson, 2003). I removed model components based on Akaike information criterion (AIC), but certain colinear variables were removed outright before stepwise elimination began. In both cases, the indicator variables for semi-domesticity and ecotype were removed due to high collinearity. Once those were removed, both the number of predators and the average winter precipitation were also removed due to their high collinearity with the presence/absence of wolves and the average winter temperature, respectively.

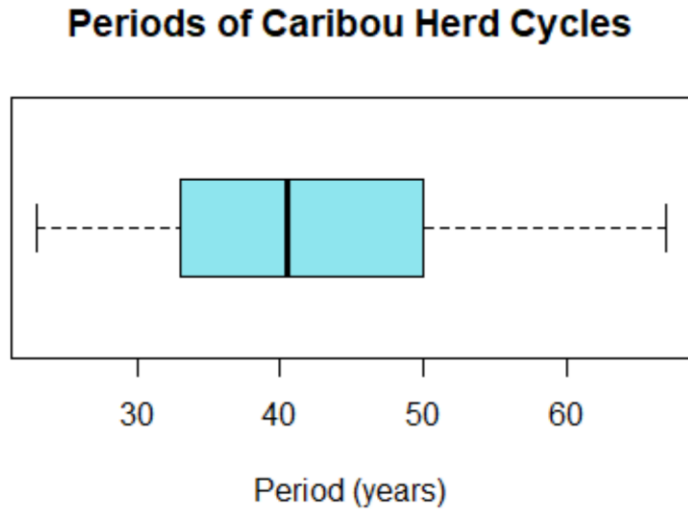
Although it is generally accepted that model variables are to be removed if they incur a decline in AIC of at least 2, the removal of many period and amplitude model components resulted in an AIC drop of very close to, but not quite, 2. As a result, I decided to remove all variables, in a backwards, stepwise fashion, that caused any drop in AIC regardless of the magnitude. This process may be refined for further analysis. I confirmed model assumptions of normality and homoscedasticity of residuals by examining normal quantile-quantile plots and residuals vs. fitted values, respectively.

Results*Period and Amplitude*

The median period length of the cyclic caribou herds was 40.5 years while the median relative amplitude was 0.87. See Figure 9 and Figure 10 below for boxplot visualizations of these data. Figure 11 is a display of the positive relationship between the two variables.

Figure 9

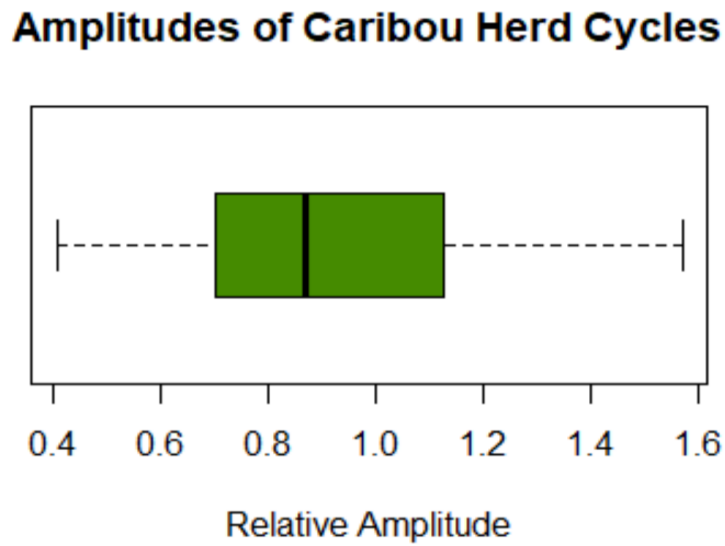
Period lengths of the 19 cyclic caribou herds



Note. Min=23, Q1=33, Median=40.5, Q3=50, Max=67

Figure 10

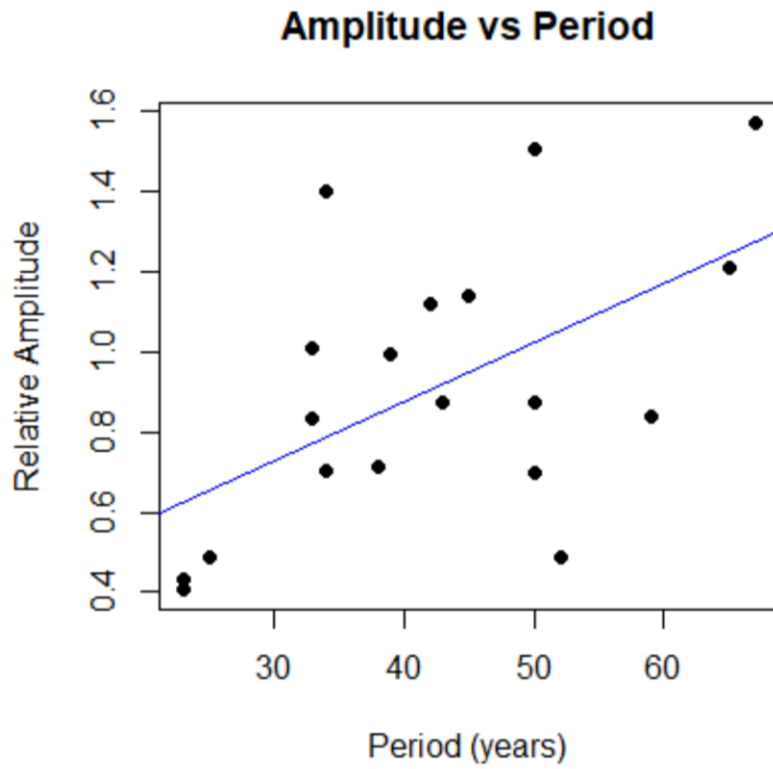
Relative Amplitudes of the 19 cyclic caribou herds



Note. Min=.406, Q1=.700, Median=.871, Q3=1.126, Max=1.570

Figure 11

Amplitude vs Period for the 19 cyclic caribou herds



Note. Line of best fit shown in blue. Cor=.550, p=.015

Period and Amplitude vs Latitude

Amplitude and period were plotted against latitude with no significant correlation—
 p=.227 and p=.220, respectively—between the variables (Figures 12 and 13 below).

Figure 12

Amplitude vs Latitude for the 19 cyclic caribou herds

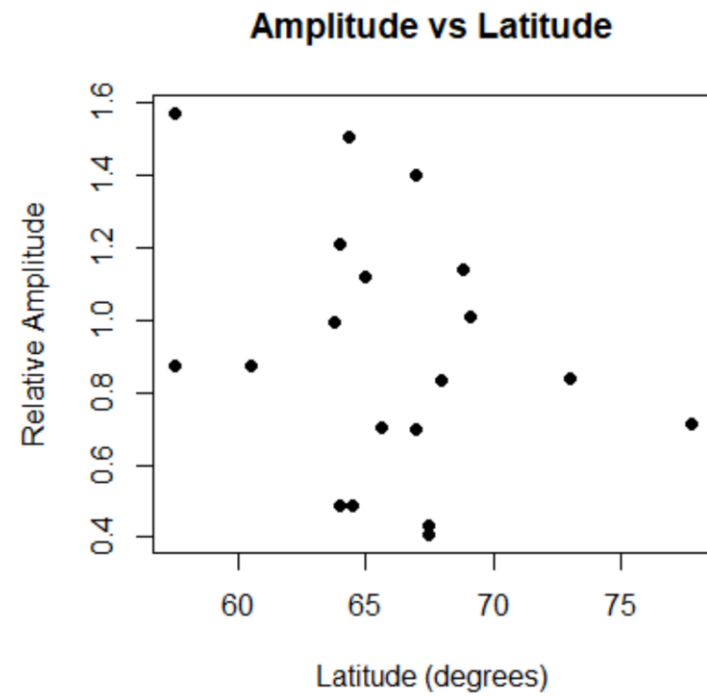
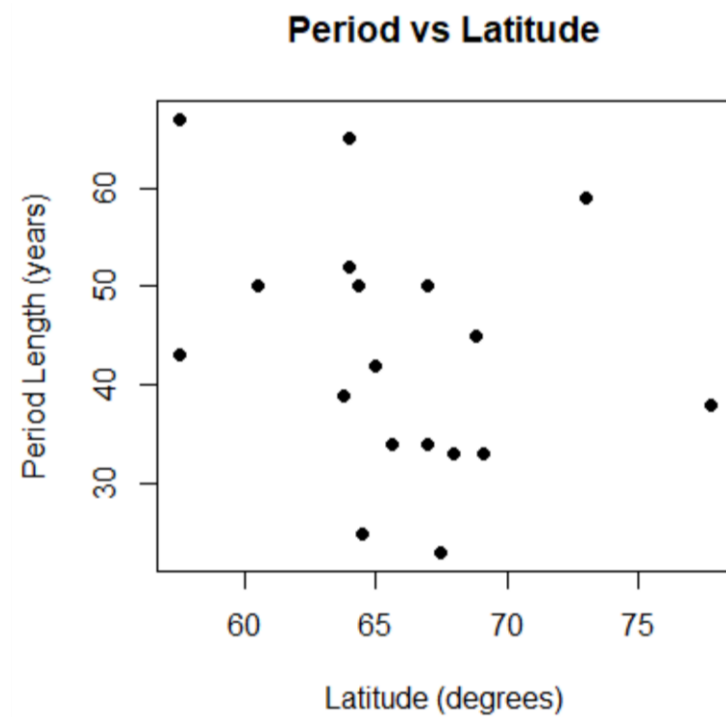


Figure 13

Amplitude vs Latitude for the 19 cyclic caribou herds

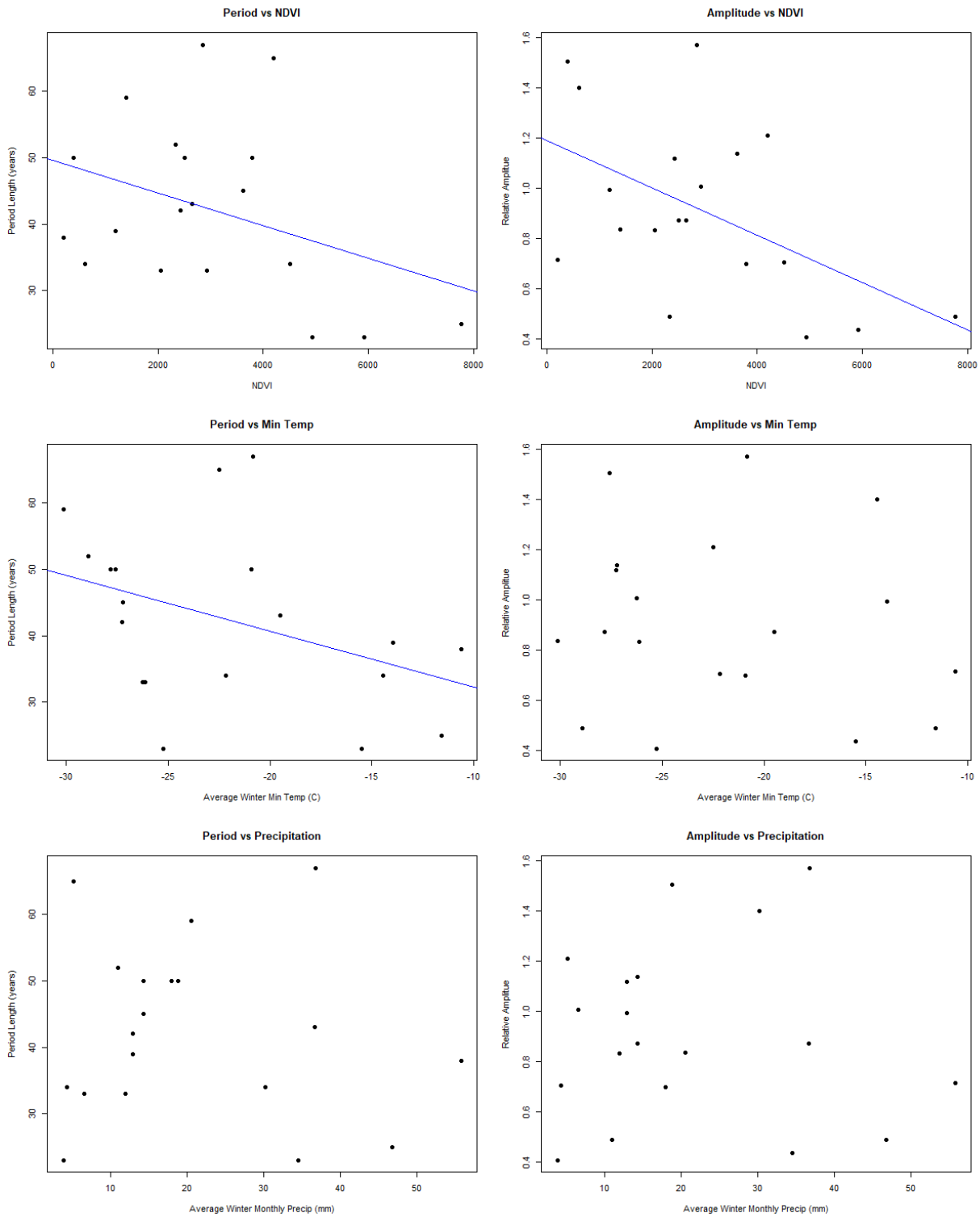


Period and Amplitude vs Weather Data

Period and amplitude were plotted against each of the three weather data metrics: NDVI, average winter minimum temperature, and average winter monthly precipitation. Lines of best fit were plotted on the scatterplots with a p-value between the variables less than .15. See Figure 14 below for the six correlation plots

Figure 14

Period and Amplitude vs Weather Data for the 19 cyclic caribou herds



Note. Period vs NDVI: Cor=-.366, p=.12; Amplitude vs NDVI: Cor=-.522, p=.022; Period vs Min Temp: Cor=-.397, p=.093

*Period Model Selection***Table 2***Stepwise, backwards selection of period length explanatory model*

Model	ΔAIC
Amp+Latitude+Wolves+Predators+Subspecies+Biome+NDVI+Temp+Precip	5.66
Amp+Latitude+Wolves+Predators+Subspecies+Biome+NDVI+Temp	3.67
Amp+Latitude+Wolves+Subspecies+Biome+NDVI+Temp	1.93
Final: Amplitude+Latitude+Subspecies+Biome+NDVI+Temp	0

Note. AIC increased after NDVI was removed from the model. As a result, it was not removed from the final model

Table 3*Model components of the period length explanatory model*

Variable	Coefficient	2.5%	97.5%	p-value
Amplitude	20.563	6.114	35.013	.027
Latitude	-1.989	-4.413	43.467	.152
Subspecies: <i>R. t. fennicus</i>	31.222	-1.893	64.337	.107
Subspecies: <i>R. t. granti</i>	21.612	-.209	43.433	.093
Subspecies: <i>R. t. groenlandicus</i>	6.405	-12.833	25.643	.535
Subspecies: <i>R. t. platyrhynchus</i>	50.434	1.238	99.630	.085
Subspecies: <i>R. t. tarandus</i>	30.568	-2.520	63.658	.113
Biome: Tundra/Taiga	16.778	2.522	31.033	.054
Biome: Tundra/Tundra	4.297	-12.343	20.937	.628
NDVI	-.002	-.005	.002	.387
Temperature	-.900	-1.842	.0419	.103
Intercept	114.042	-27.478	255.562	.158

*Relative Amplitude Model Selection***Table 4***Stepwise, backwards selection of period length explanatory model*

Model	ΔAIC
Period+Latitude+Wolves+Predators+Subspecies+Biome+NDVI+Temp+Precip	7.67
Period+Latitude+Wolves+Subspecies+Biome+NDVI+Temp+Precip	5.67
Period+Latitude+Wolves+Subspecies+Biome+NDVI+Temp	3.95
Period+Latitude+Wolves+Subspecies+Biome+Temp	2.13
Period+Latitude+Subspecies+Biome+Temp	.50
Final: Period+Subspecies+Biome+Temp	0

Note. AIC increased after Biome was removed from the model. As a result, it was not removed from the final model

Table 5*Model components of the relative amplitude explanatory model*

Variable	Coefficient	2.5%	97.5%	p-value
Period	.025	.012	.037	.003
Subspecies: <i>R. t. fennicus</i>	-.445	-1.093	.203	.211
Subspecies: <i>R. t. granti</i>	-.241	-.618	.135	.241
Subspecies: <i>R. t. groenlandicus</i>	.091	-.285	.467	.647
Subspecies: <i>R. t. platyrhynchus</i>	-.777	-1.451	-.103	.050
Subspecies: <i>R. t. tarandus</i>	-.289	-.764	.186	.264
Biome: Tundra/Taiga	-.253	-.750	.243	.343
Biome: Tundra/Tundra	.213	-.233	.659	.374
Temperature	.025	-.004	.053	.127
Intercept	.601	-.093	1.295	.124

Discussion

Period and Amplitude

The median period length of the 19 cyclic caribou herds was 40.5 years, with the minimum and maximum lengths being 23 and 67 years, respectively. While it has been observed that many caribou herds cycle over the course of several decades, there has been little analysis completed to better understand the length of these cycles. One notable exception, Bongelli et al. (2020) found that nine of the North American barren-ground caribou herds' cycles lasted between 26 and 55 years, similar to the span of lengths I found. The distribution of caribou population cycle lengths appears to be unimodal and possibly skewed slightly right, indicating that the 20-some year range of caribou population cycles may be the lower biological limit of these cycles. This solidifies evidence that caribou experience the longest-known population cycles of any species.

Much like the period lengths, amplitudes of caribou population cycles have not been extensively studied. The relative amplitude of herd population cycles, which involved a standardization about the mean, was calculated as opposed to the traditional amplitude for reasons described previously. This means that unlike the period length, interpreting the relative amplitude is less straightforward. A proper interpretation of relative amplitude is best explained with an example. A herd with a relative amplitude of .5 indicates that the maximum (peak) herd population is 50% higher than its baseline (mean) population. Likewise, its minimum (trough) herd population is half the size of its baseline population. The median relative amplitude of the 19 cyclic caribou herds was .871, with the minimum and maximum amplitudes being .406 and 1.570, respectively.

There was a moderate, positive, statistically significant correlation between period length and relative amplitude (Figure 11) with $r = .550$ and $p = .015$. This indicates that caribou population cycles tend to increase in magnitude as the period length increases. Therefore, herds with extremely long population cycles also have the most drastic boom and busts, albeit spread out. On the other hand, this also means that caribou herds that experience shorter population cycles tend to have less drastic peaks and troughs relative to their mean population.

Period and Amplitude vs Latitude

As aforementioned, latitudinal gradients in caribou population dynamics were anticipated due to the known impacts of latitudinal effects on small mammal population density dependence (Post, 2005). Additionally, climate is thought to be a driving force behind mammal population cycles (Barraquand et al., 2017; Gunn, 2003). While latitude may be a great predictor of weather/climatic conditions in certain areas, as previously explained this is not necessarily the case when looking at a species with a large circumpolar distribution. As a result, I expected to not see a significant correlation between either amplitude or period and latitude, which is exactly what was observed (Figure 12 and Figure 13).

Period and Amplitude vs Weather Data

While latitude was not significantly correlated with period length or relative amplitude, some climatic data were. Period and amplitude were plotted against each of the three weather data metrics: NDVI, average winter minimum temperature, and average winter monthly precipitation in Figure 14 above. Period length and relative amplitude both had a moderate, negative relationship with NDVI. However, the presence of some influential points with high NDVI values may be portraying that the relationship is stronger than in reality. Regardless, the

relationship between amplitude and NDVI was statistically significant ($p = .022$) while the relationship between period and NDVI was not, yet low enough to be convincing ($p = .12$). The only other observed relationship was between period and the average winter minimum temperature. Again, this moderate relationship was negative and somewhat statistically justifiable ($p = .093$).

NDVI, which is an index measuring ecosystem productivity, had a negative relationship with both period length and relative amplitude. The more productive a landscape, the less caribou herds fluctuated over time. This would indicate that density-dependent population factors, which are more prevalent under favorable environmental conditions (higher NDVI values), promote shorter, smaller amplitude caribou cycles (Post, 2005). Poor environmental conditions (lower NDVI values), on the other hand, tend to be indicative of longer and more drastic caribou population cycles. As a result, the effect of density-dependence on caribou population cycles seems to increase as NDVI increases, a similar phenomenon observed in small mammals (Post, 2005).

The negative relationship between the period length and the average winter minimum temperature may be providing insight into the same conclusion. Herds in habitats with colder winter temperatures tend to have longer population cycles. Extremely cold winters may decrease the availability of non-lichen forage, be indicative of longer winters, and overall lead to a more hostile living environment. As a result, density-independent factors may be more of a driving force for caribou population dynamics in those areas and thus extending population cycles. Interestingly, relative amplitude did not have a similar relationship with the winter temperatures. While caribou may avoid deeper snow when foraging, this behavior—and the impact of snow

depth across a herd's range—on caribou population dynamics appears to be either complex or non-existent (Tucker et al., 1991; Tyler, 2010).

Climate as a whole, including climatic oscillations, is known to impact caribou populations, however, how this impact will change (and is changing) in the face of global warming is complex and requires further research (Gunn, 2003; Joly et al., 2011).

Period and Relative Amplitude Models

Both the period and relative amplitude models were remarkably similar (Table 3 and Table 5). It is interesting to note that the model coefficients for period length and relative amplitude were statistically significant in the opposite model. This relationship is evident by the strong, positive correlation between the variables illustrated in Figure 11 above. Both models incorporated the indicator variables for subspecies and biome of the herd, yet not ecotype (due to high collinearity). It seems that biome and subspecies information sufficiently explain behavior, which is represented by ecotype.

The relative amplitude model was slightly smaller, with both NDVI and latitude excluded. It is intriguing to see the positive coefficient of temperature in this model despite the lack of a relationship between the two apparent in Figure 14. On the other hand, amplitude and NDVI were strongly correlated (Figure 14) yet this relationship was not significant to the explanatory model. Refer to Table 5 for the complex relationship between amplitude and caribou herds of different subspecies and biomes.

Future Improvements

There are a number of areas within this project that would benefit from further refinement and consideration. A number of these issues have previously been highlighted, including the

need for more accurate and up-to-date ecotype and subspecies classifications. Relative amplitude measurements will need to be re-worked for future research because the data constraints of each herd resulted in relative amplitudes above 1 for some herds, which is technically not impossible. A hybrid of Barraquand et al.'s (2017) amplitude measurement, which is the amplitude of the fitted sine wave, with a standardization is a possible solution. Regardless, a more readily interpretable method of amplitude measurements is desired. I believe the period length measurements to be sound, but further population estimates over the coming decades will strengthen these estimates. Herds were deemed cyclic if their period lengths were statistically significant, but this is a flawed method when considering the constraints of available data. Multiple herds that have been known to cycle for centuries were excluded from cyclic analysis due to limited data. Data limitations also dampen the significance of our results because in most cases we only have information pertaining to one caribou population cycle per herd. Ideally, having multiple cycles per herd would not only strengthen the results statistically but also make them more accurate.

Climate is known to play an important role in governing caribou population dynamics—and therefore cycles (Gunn, 2003). Because of this reality, it is imperative that more climatic data are collected to help explain this relationship. My preliminary findings seem to suggest that certain climatic aspects, such as vegetation and temperatures, do play a large role in shaping caribou population cycles. However, the interconnectedness of climate and caribou population cycling is not necessarily straightforward; many influences likely shape this intricate relationship.

Management Implications

Proper, institutional caribou management has never been more important than it is today. A vulnerable species on the IUCN Red List with a declining population of less than 3 million left globally, caribou are faced with a multitude of conservation threats (Gunn, 2016). Climate change and habitat loss via logging and oil extraction paint a bleak picture for the future of caribou—especially woodland caribou—highlighting the need for proactive conservation actions and proper management strategies. However, appropriate management can only stem from an abundance of accurate knowledge about the species. At the moment, the mechanics of caribou population cycles are poorly understood—an issue I aimed to tackle with my research.

Many different management strategies have been tried to boost dwindling caribou herds, some options being predator control and conservative/restricted harvests. Despite the popularity of wolf control efforts, the results are not overwhelmingly positive. Research shows “no convincing support” for lower levels of wolf predation on caribou during nonlethal control and “no support” for improved caribou survival when either lethal or nonlethal wolf control is implemented (Boertje et al., 2017). While there is little evidence that wolf control is effective at increasing caribou numbers at the moment, more case studies are needed to accurately evaluate the effectiveness of this method. The Nelchina caribou herd of the southcentral region of Alaska is an example of a herd that has experienced drastic predator management. The population dynamics of the herd (Figure 7) illustrate the complicated nature of wolf control. While the herd (like many others) has been known to cycle, the subpopulation appears to have stopped cycling in the last several decades (Gunn, 2003). It would seem that predator control, along with intense harvest pressure, has prevented the herd from continuing its cyclic tendencies (Boertje et al.,

2017). If the Nelchina herd is any indication, it may be possible to stop caribou population cycles as long as intense population management practices are in place.

Less controversial, yet still equally vital, is determining not only how to effectively manage caribou, but also the end goal of said management. Do we want caribou herds to continue experiencing population cycles or do we want to manage for stable populations? The answer, from an economic and subsistence standpoint, is likely the latter. Stable caribou populations will provide consistent food and financial benefit to local communities and industries, but we do not know the prolonged ecological effects of “losing” cycles. Disrupting caribou population cycles may prove to have a negative impact on the flora and fauna communities in the area. After all, population cycles are an evolutionary construct and serve a purpose in food webs and ecological processes.

My research suggests that periods and amplitudes of caribou population cycles are heavily intertwined, and the positive correlation between the two indicates that managing for stable populations may be difficult. Managing for high periods and low amplitudes, which would likely lead to more stable population cycles, could be impossible (Figure 11). However, managing for low period lengths and low amplitudes seems more feasible. How to do this, and whether it would lead to high enough, consistent caribou population numbers, remains to be seen.

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