

**Barren-ground caribou – a cyclic species: The development of a cycle-stratified harvest model and a cycle analysis of North American barren-ground caribou subpopulations**

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## ABSTRACT

Unlike all other members of the deer family, subpopulations of barren-ground caribou (*Rangifer tarandus groenlandicus*) exhibit fluctuations in numbers that have been described as cyclic. We created a cyclic individual-based annual life table harvest model to examine the sustainability and user-benefits of regulating the harvest during the portion of the cycle characterized by low numbers, low unharvested population growth rates, or both for the Qamanirjuaq caribou subpopulation (Chapter 1). Cyclic population dynamics were modeled using density-driven dynamic responses of both per capita survival and calf production to a cyclic carrying capacity function. Model parameters were empirically identified to produce cycles that replicated observed Qamanirjuaq (Nunavut, Canada) subpopulation dynamics, including changes in population numbers, human harvest, calf production and calf survival rates.

We modified the cyclic barren-ground caribou harvest model, developed for the Qamanirjuaq caribou subpopulation, to model the Bathurst and George River subpopulations. We were able to develop models that corresponded to time-series field estimates of population numbers, calf production rates, and calf survival rates of the Bathurst and George River subpopulations, suggesting that the structure of program CARIBOU 1.0 general and robust. We identified three harvest options for the Qamanirjuaq, Bathurst and George River subpopulations: 1) maximized the total number of removals per cycle, 2) minimized the number of years with imposed restrictions, and 3) minimized the degree and frequency of differences between strata harvests (maximized “evenness”). The range of sustainable harvest options was large for all three subpopulations, and thus offers a framework to exploring harvest strategy options in consultations and co-management planning. Deliberate reduction of harvest during the decline and early increase phases of the cycle significantly reduced the period when subpopulations were too small or increasing too slowly to sustain a harvest at basic needs levels.

We fit linear, exponential, logistic, sine and wavelet functions to 14 North American barren-ground caribou subpopulations and found that 11 subpopulations had sufficient data to estimate cyclic function parameters. All 11 subpopulations with sufficient data were best described as sine cyclic. Correlations between subpopulation cycle parameters (period and amplitude) and various range attributes determined independently for the total, summer and winter ranges suggested that subpopulation period was most highly correlated to subpopulation amplitude ( $r = 0.547$ ,  $p = 0.082$ ). Subpopulation amplitude was most highly correlated to subpopulation total range mean temperature ( $r = 0.877$ ,  $p \leq 0.001$ ). Regression modeling of subpopulation amplitude as a function of the subset of biological range attributes suggested that 88.5% of the observed variance in amplitude could be

explained by 2 variables: total range area and the interaction between summer range area and summer range net primary productivity ( $p = 0.006$ ). Regression estimates of subpopulation abundance showed good correspondence to observed population abundance estimates for the 11 subpopulations sampled ( $r = 0.894$ ;  $p < 0.001$ ). Both least squares function fitting and cluster analysis suggested the Porcupine subpopulation was distinct from the other subpopulations. Subsequent investigation revealed a progressive increase in Porcupine subpopulation numbers and a retention of period and amplitude in this subpopulation cycle. We hypothesized the increase might be due to progressive climate warming in this area. We recommend that harvest managers and environmental impact assessments monitor period and amplitude as indicators of direct and cumulative impacts on the population dynamics of individual subpopulations.

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This thesis is comprised of three individual manuscripts. Eric Bongelli is the first author on all three manuscripts, but none of this work would have been possible without the knowledge and assistance of all contributing co-authors. Mitchell Taylor was pivotal in the structure and development of all three manuscripts. Martha Dowsley provided many astute comments during the development and review of all three manuscripts. Discussions with Mitch Campbell were constructive and he provided many insightful comments that were influential in the development of manuscripts 1 and 2. Miroslaw Kuc was enabling in the theoretical and practical development of program CARIBOU 1.0. Finally, Victor Velasco-Herrera contributed greatly to mathematical function fitting throughout manuscript 3.

## THESIS STRUCTURE

This thesis is organized as three individual manuscripts (chapters) that were compiled to form a singular cohesive thesis document. The thesis document is structured as a progressive consideration of barren-ground caribou as a cyclic species.

Census surveys and traditional ecological knowledge agree that barren-ground caribou subpopulations experience fluctuations in abundance that have been qualitatively described as cyclic (Hemming, 1975; Gunn & Miller, 1986; Couturier *et al.*, 1990; Russell *et al.*, 2002; Gunn, 2003; Wilson & Reeder, 2005; Zalatan *et al.*, 2006; Legat *et al.*, 2014; Government of Yukon, 2015; Herbet, 2015). Manuscript 1 develops a cyclic harvest model (CARIBOU 1.0) for the Qamanirjuaq caribou subpopulation. Three harvest scenarios are presented to illustrate the range of sustainable harvest options for Qamanirjuaq barren-ground caribou. In addition, manuscript 1 discusses the possible implications of a cyclic approach to harvest management.

Manuscript 2 modifies program CARIBOU 1.0 to provide harvest simulations for the Bathurst and George River barren-ground caribou subpopulations. Similar to manuscript 1, three harvest simulations are presented to illustrate the range of sustainable harvest options for each subpopulation. Manuscript 2 examines the robustness and generality of program CARIBOU 1.0, and suggests that it may be useful as a decision making support tool for the harvest management for all subpopulations of barren-ground caribou with sufficient data to estimate cycle parameters.

Manuscripts 1 and 2 were developed to describe barren-ground caribou population dynamics as a cyclic phenomenon. Manuscript 3 is a comparative analysis of subpopulation range attributes as possible drivers for barren-ground caribou subpopulation cycles. Manuscript 3 provides empirical evidence for a relatively simple, yet comprehensive explanation for barren-ground caribou subpopulation cycles in North America.

## Cycle stratified harvest policies for a subpopulation of barren-ground caribou

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*Abstract:* The maximum sustainable harvest of barren-ground caribou subpopulations (*Rangifer tarandus groenlandicus*) cycles over time based on the number present and the annual per capita population growth rate. We created a cyclic individual-based annual life table harvest model to examine the sustainability and user-benefits of regulating the harvest during the portion of the cycle characterized by low numbers, low unharvested population growth rates, or both. Cyclic population dynamics were modeled using density-driven dynamic responses of both per capita survival and calf production to a cyclic carrying capacity function. Model parameters were empirically identified to produce cycles that replicated observed Qamanirjuaq (Nunavut, Canada) subpopulation dynamics, including changes in population numbers, human harvest, calf production and calf survival rates. Models based on a cyclic carrying capacity were robust, and were consistent with the observed time-series population abundance, calf production rates, and calf survival estimates of the Qamanirjuaq caribou population.

We identified three harvest strata options: 1) maximize the total number of removals per cycle, 2) minimize the number of years with imposed restrictions, and 3) minimized the degree and frequency of differences between strata harvests (i.e., maximized “evenness”). The maximum removals strategy produced 720,000 removals, 31 years with imposed restrictions, and an evenness index of 0.736 over the 53-year cycle period. The minimum restrictions strategy produced 503,500 removals, 17 years with imposed harvest restrictions, and an evenness index of 0.789 over the 53-year cycle period. The maximized ‘evenness’ strategy produced 407,000 removals, 37 years with imposed restrictions, and an evenness index of 0.930 over the 53-year cycle period. The three harvest options reported were selected from all possible options to provide information regarding the three harvest protocols and also to illustrate the range of sustainable harvest options that could be considered. Status determinations of barren-ground caribou (or other cyclic species) that do not incorporate or consider population cycles may be overly pessimistic during natural declines and low numbers, especially for populations with long cycle periods.

Key Words: barren-ground caribou, cyclic species, demography, density effects, harvest management, simulation model, climate change.

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## INTRODUCTION

Barren-ground caribou (*Rangifer tarandus groenlandicus*) are unique among the deer family (Cervidae) because they make extensive seasonal migrations rather than remain within well-defined home ranges. Barren-ground caribou are also thought to form two differing ecotypes: tundra wintering and mainland migratory (Nagy *et al.* 2011). Of these two ecotypes the mainland migratory display the most extensive migratory behaviour, moving between the treeless tundra (in summer) and the forested taiga (in winter) during their annual migration. All barren-ground caribou population numbers are believed to cycle rather than fluctuate without periodicity around an equilibrium (Gunn & Miller, 1986; Russell *et al.*, 2002; Wilson & Reeder, 2005; Government of Yukon, 2015).

Barren-ground caribou have been and continue to be, a staple food to residents of northern Canada and Alaska, especially First Nations and Inuit peoples (Stenton, 1991; Ashley, 2000; Kendrick, 2003). Archeological analysis of prehistoric North American camp sites documents frequent use of barren-ground caribou for food and tools along the face of retreating glaciers up to 15,000 years ago, within what is now the central range of the Porcupine subpopulation (Kendrick, 2003; COSEWIC, 2016). Barren-ground caribou contribute to the northern economy through meat hunting and guided trophy hunts, while contributing to the food security (Council of Canadian Academies, 2014) and the continuity of cultural traditions held by northern peoples (COSEWIC, 2016; Hummel & Evans, 2017).

Barren-ground caribou are a meta-population with 13-15 relatively discrete North American subpopulations that extend from Alaska, across continental mainland and archipelago Canada from the Yukon to Baffin Island (Nagy, *et al.*, 2011; COSEWIC, 2016; Parlee *et al.*, 2018). All subpopulations spend at least a portion of the year on the barren-lands, with the mainland migratory dividing their time between the tundra and boreal forest (e.g., Qamanirjuaq) and the tundra wintering spending the whole year on the tundra (e.g., Cape Bathurst and Dolphin-Union). The mainland migratory subpopulations

have seasonal ranges associated with their extensive seasonal migration patterns, migrating north in the spring to calve on the snow-covered northern barrens, then south at the end of autumn to winter in the boreal forest (Kelsall, 1968; Skoog, 1968; Hemming, 1971; Fancy *et al.*, 1989; GNWT, 2007). The length and direction of migration routes varies between subpopulations. Barren-ground caribou occur as three distinct genetic clusters (McFarlane *et al.*, 2016). The first cluster consists of fully continental migratory barren-ground caribou, the second cluster consists of Dolphin-Union caribou, and the third cluster consists of Southampton Island (introduced after extirpation from nearby Coats Island) caribou (McFarlane *et al.*, 2016). Subpopulation boundaries are identified by relative fidelity of individuals to their seasonal ranges throughout the annual cycle, especially fidelity to calving regions (Nagy *et al.*, 2011; Nicholson *et al.*, 2016). Fidelity is relative, not absolute; and individuals can shift their calving grounds due to annual variance in ecological conditions (Russell *et al.*, 1993, 2002; GNWT, 2007). Both permanent and temporary migration of individuals between subpopulations have been observed through satellite collar monitoring programs (Nagy *et al.*, 2011).

Barren-ground caribou are a birth-pulse species (Caughley, 1977). The calving period is synchronized for each subpopulation and generally occurs over a 2-week period in June (Nagy, *et al.*, 2011; Nagy & Campbell, 2012; COSEWIC, 2016). Females generally produce one calf annually, usually beginning at age 2+, although reproductive maturity has been observed as early as 16 months (Shefferly, 2000). Poor health or nutrition may cause adult females of any age not to conceive or produce viable calves (COSEWIC, 2016). Like all naturally occurring species, barren-ground caribou population numbers are ultimately regulated by density-dependent reductions in calf production and/or survival rates (Supplementary I; Cold Harbor Spring Symposium, 1957; Tanner 1966; Caughley, 1977; McCullough, 1979; Fowler 1981; Kie & White, 1985; Skogland 1985; Clutton-Brock *et al.*, 1987; Boyce 1989; Messier *et al.*, 1988; McCullough, 1999; Bowyer *et al.*, 2014). The discrete logistic equation suggests that linear density-effects could cause convergence on  $K$  (carrying capacity), converging cycles to  $K$ , stable limit

cycles, increasing oscillations to extinction and even “chaos” depending on the population’s maximum growth rate ( $\lambda_{\max}$ ) (May, 1976; Renshaw, 1991). The maximum and minimum annual rates of population growth (or decline) for barren-ground caribou vary between subpopulations, but typically do not exceed  $\lambda = 1.17$  and are not less than  $\lambda = 0.83$  (Gunn, 2003). At barren-ground caribou  $\lambda_{\max} \leq 1.17$  the logistic equation suggests that, without lag-times, caribou (like other deer species) would converge on carrying capacity (May, 1976; Renshaw, 1991; Vandermeer, 2010). Stable limit cycles are not observed until  $\lambda_{\max} > 2.57$  (May, 1976; Renshaw, 1991) which is more than double the maximum observed annual population growth rate for barren-ground caribou. Both science and TEK (traditional ecological knowledge) agree that barren-ground subpopulations experience regular fluctuations in population abundance (Meldgaard, 1986; Ferguson *et al.*, 1998; Klein, 1991; Russell *et al.*, 2002; Gunn, 2003; Government of Yukon, 2015) that appear to be cyclic.

Research and analysis of barren-ground caribou population dynamics has mainly occurred as trend analysis of single subpopulations during some arbitrary portion of the cycle (i.e., Cr ete & Payette, 1990; Valkenburg *et al.*, 1996; Whitten, 1996). CARMA (2016), Gunn *et al.* (2010), and Sarkadi (2007) suggest the recent (millennial) trend for 12 of 14 barren-ground subpopulations has been negative. This observation suggests synchrony between barren-ground caribou subpopulation cycles. However, differences in the cycle periods of subpopulations would mean that any appearance of synchrony was coincidental. Although there has been considerable speculation on the cause(s) of barren-ground caribou cycles, the impetus of population cycles have not been demonstrated for even the longest and best studied subpopulations (Klein, 1991). Hypotheses for what drives caribou cycles include: predators, pathogens, decadal winter severity, disturbance (development), climate change and forage regeneration rates (Bergerud, 1974; Klein, 1991; Gunn, 2003; Gunn *et al.*, 2010, Bastille-Rousseau *et al.*, 2013). These factors can work independently or in combination on both survival and calf production rates.

Two distinct approaches to modelling population dynamics of species that reproduce in a discrete rather than continuous fashion have been developed: The Leslie (1945) or Leftkovitch (1965) matrix and the life table (Birch, 1948; Cole, 1954; Caughley, 1977). The main difference between the two is the recruitment (calf production) term (Taylor & Carley, 1988). This difference is noteworthy because the Leslie/Leftkovitch matrix recruitment term ( $F_x$ ) includes both recruitment and age class (0) survival information, and thus cannot be directly estimated from a stable standing age distribution unless  $\lambda$  is known. Cole's (1954) life table recruitment term ( $m_x$ ) is simply the number of female offspring produced by females of age  $x$  divided by the number of females of age  $x$  and can be accurately estimated from any accurate census age distribution. Both matrix and life table approaches assume a single time of census within an annual time frame, and that census defines both survival and calf production values (Taylor & Carley, 1988). We employed life table methods to model harvested barren-ground caribou because published calf production estimates were generally life table calf production, not Leslie matrix calf production; and because accompanying estimates of calf survival (age 0) were few and not always referenced to same time of census as the calf production estimate. A variety of modelling approaches have been developed as tools for predicting the varying effects of industrial and resource development, climate change and harvest on barren-ground caribou habitat and subpopulation abundance (i.e., demographic simulation models (Frid *et al.*, 2014), habitat models (Daniel *et al.*, 2016a; Daniel *et al.*, 2016b), cumulative effect models (White *et al.*, 2014) and harvest models (Boulianger & Adamczewski, 2015)). These models include the individual parameters that determine short-term population dynamics, but none have projected stable population cycles.

We constructed and validated a cyclic birth-pulse life table harvest model for barren-ground caribou that could inform relevant jurisdictions and stakeholders regarding likely outcomes for various harvest protocols. The caribou cycle was divided into 6 user-defined abundance-strata with three strata in both the decline and increase phases. As a policy, only long term sustainable options were allowed

because extirpation was not viewed as an acceptable outcome. Harvest policy options associated with periods of increase and decline at high, intermediate, and low densities were identified to explore the effects of differential harvest rates during the cycle in a manner that is both sustainable and negotiable. The number of distinct harvest options that can be specified is unlimited. We examined three options: 1) maximized the number taken per cycle, 2) minimized the number of years when the numbers taken were too few to meet basic user needs, and 3) minimized the degree and frequency of differences between strata harvests (i.e., maximized “evenness”). Harvest strategies that minimize interference with free hunting (both the duration and magnitude of harvest regulations), and also ensure sound conservation practices could be developed through consultation with user-groups, co-management partners, and jurisdictions that share a given subpopulation. Given logistic limitation to human harvesting, periods of great abundance can be exploited to the extent of user-needs. During periods of decline and periods of low numbers, harvest should be regulated to allow optimal recovery of population numbers in a manner that is supported by the user-community and satisfies the conservation mandate of government. Harvest records and consultations with local residents suggest that a harvest of 12,000/year would be required to meet the current minimum needs of aboriginal user-groups of the Qamanirjuaq subpopulation (Priest & Usher, 2004; InterGroup Consultants Ltd, 2008; Campbell *et al.*, 2010, Campbell, pers. comm. 2018).

We chose the Qamanirjuaq subpopulation for our case study because it is relatively well known, and it has a well-established multi-jurisdictional co-management body (The Beverly and Qamanirjuaq Caribou Management Board). The model development strategy was trial and error convergence to a model that mimicked the actual demographic history of the subpopulation cycle. The model validation protocol involved empirical comparison of cyclic changes in model calf production, calf survival, and population numbers to published Qamanirjuaq caribou time-series census estimates of these parameters (Table 1.1).

## METHODS

We identified five functions as null hypotheses for the time-series census population estimates for the Qamanirjuaq caribou subpopulation: linear, exponential, logistic, sine cyclic, and wavelet cyclic. Linear, exponential, logistic and sine cyclic functions were fit using the dynamic fit wizard in program SigmaPlot 14.0. The wavelet function was described by Lau & Weng (1995) and Torrence & Compo (1998). We identified the best function based on the value and statistical significance of the correlation coefficient ( $r$ ) to the time-series estimates. We also used the Shapiro-Wilk method to test the distribution of residuals for normality. Our function validation criteria were statistically significant ( $p \leq 0.05$ ) correlation coefficients of 0.95 or greater from least-squares fitting of the function to the time-series estimates; and a failure to reject the Shapiro-Wilk test for normality of residuals ( $p \leq 0.05$ ).

RISKMAN version 2.0 PVA software (Taylor *et al.*, 2001) was used to explore various harvest options. RISKMAN 2.0 is an individual-based implementation of Cole's (1954) life table mathematics that includes males, has a user-defined sex/age specific harvest selectivity and vulnerability options, and employs a flexible (linear or non-linear) user-defined sex/age specific density-effects option (Taylor *et al.*, 2001). RISKMAN 2.0 code was modified to include a time-lagged density response option, a cyclic carrying capacity option, and to allow six user-defined annual harvest strata (3 abundance-strata during increase phase and 3 abundance-strata during decline phase) of the caribou population cycle. The model protocol required the simulation to develop a stable cycle before the user-defined annual harvest was implemented. Similarly, summary parameters were reported only after the harvested cycle became stable. Starting conditions that did not result in a stable cycle and harvest regimes that were not sustainable were identified with an error condition and summary parameters were not reported. The modified program was named CARIBOU 1.0 and is available with our final project files upon request from the corresponding author (Supplementary IV).

Several general linear and non-linear equations have been proposed to model density-effects (i.e., Eberhardt & Siniff, 1977; Fowler, 1981; Regehr *et al.*, 2015). CARIBOU 1.0 employs a transposed, threshold corrected, Michaelis-Menten function (Taylor, *et al.*, 2001) to model sex/age specific density-effects. This function was chosen because it can be fitted with only two parameters and can describe both linear and non-linear density-effects that dynamically return a fraction of the maximum survival or calf production rate identified by the user based on population numbers (or some user-specified sex/age strata of the total population):

$$\text{equation 1. } R_t = (R_{\max}) \frac{\frac{CC}{N_t} - 1}{\frac{CC}{N_t} - 1 + KS}$$

$R_t$  = survival or calf production rate at time = t.

$R_{\max}$  = maximum survival or calf production rate.

CC = population density index.

$N_t$  = number of animals at time = t.

KS = shape parameter controlling the degree of non-linearity due to density.

We empirically identified CC and KS values for the density-effects function that resulted in annual time-series of model calf survival and calf production rates that were comparable to field estimates of calf survival and calf production rates at the same year of the cycle. The actual rate value employed for any given iteration is some fraction of the maximum rate as determined by the population (or sex/age strata) number, shape factor (KS) and population density index (CC) parameters (Supplementary I). We used total population numbers as the driving variable for density-effects on maximum values for calf (age 0) survival, adult (age 1+) survival of males and females, and calf production rate by mature (age 2+) females (Table 1.2). We assumed adult females had only one calf (sex ratio 0.5 females) when they reproduced because the occurrence of multiple calves per female is rare (COSEWIC, 2016).

Simulation models were developed and refined in stepwise stages, with the simplest models developed and tested first. We identified three families of models: 1) density-effects only, 2) density-effects with time-lags, and 3) density-effects with a sine cyclic carrying capacity option. Time-lags were defined as whole year integers between 1 and 15 years. A time-lagged model looked back in time (lag value) to identify the total population number used to generate the current iteration survival or calf production rate using the user-defined density-effects function. The cyclic carrying capacity option employed a user-specified sine modulated CC value to retain model continuity with the density-effects algorithm. Individual modulation for sex/age strata of survival and calf production rates is possible in CARIBOU 1.0, but we used the same period for the sine modulation for all sex/age strata to retain vital rate synchrony with a single cyclic carrying capacity. Our simulation protocol assumed harvest selectivity was in proportion to abundance (unselective with respect to sex and age). We assumed calves (age 0) were not taken. Using the actual estimated harvest the cycle was allowed to stabilize in order to confirm convergence with the Qamanirjuaq caribou subpopulation cycle.

Our simulation model validation protocol consisted of two steps. The first step was to ensure that the simulation model generated significant ( $p \leq 0.05$ ) positive temporal correlations with correlation coefficients  $r \geq 0.95$  for population numbers, calf production rates and calf survival rates for the portion of the cycle that had available census population, calf production and calf survival estimates. The second step was to test the simulation robustness to environmental variance of model parameters. Final model stochastic simulations using Monte Carlo methods (Taylor, *et al.*, 2001) were run assuming 100% of estimate variance was due to environmental uncertainty. Successful simulations (no error interruption) were accepted as sufficiently robust.

Three harvest strategies were developed to illustrate the range of possible approaches: 1) maximum number of total removals per cycle, 2) minimum number of years with substantial restrictions (defined as the level of harvest that would inhibit users from meeting their minimum needs, assumed to

be approximately 12,000 animals per year) and 3) maximize the “evenness” index, which minimizes the difference between harvest strata. Evenness was evaluated using the Shannon-Weiner Evenness index ( $E_H$ ) (Beals, *et al.*, 2000). Program CARIBOU 1.0 reports summary parameters (i.e., total number of removals, number of removals per cycle strata, and annual values of population number, survival rate and calf production rates).

## RESULTS

Only the sine cyclic function satisfied both validation criteria for the Qaminirjuaq subpopulation. (Table 1.3). The cyclic sine function produced a significant correlation ( $r = 0.961$ ,  $p < 0.001$ ; [Table 1.3]), and produced normally distributed residuals ( $p = 0.530$ ; [Table 1.3]). The sine function produced a cycle with a period of 53 years (SE = 3.3) and an amplitude of 230,897 (SE = 25,872; [Fig. 1.1]). The wavelet function also had a highly significant correlation coefficient ( $r = 0.915$ ,  $p < 0.002$ ) that was just marginally less than our validation criteria, and normally distributed residuals ( $p = 0.351$ ; [Table 1.3]). The logistic function  $r$  value was also relatively high ( $r = 0.891$ ,  $p = 0.01$ ; [Table 1.3]).

The first family of models employed linear and non-linear density effects. There were no combinations of linear or non-linear density-effects identified that were sufficient to produce stable cycles in program CARIBOU 1.0. The best combination of linear and non-linear density-effects in conjunction with lag-times was able to produce a 53-year cycle with an amplitude of 222,078. However, none of the lag-time models met both validation criteria. The second family of models that included a lag-time produced significant temporal correlations of population numbers, calf production rates, and calf survival values, were rejected because they were insufficiently correlated ( $r < 0.95$ ) with census population numbers and calf production values (Table 1.4). All stochastic simulations of lag-time models resulted in an error interruption (i.e., drove the population to extirpation). All lag-time models were rejected as unstable because they were highly sensitive to changes in environmental variability.

The third family of models employed linear and non-linear density effects coupled with a sine-cyclic carrying capacity and was sufficient to meet all validation requirements (Table 1.4). The model produced significant temporal correlations ( $r \geq 0.95$ ) to population numbers, calf survival rates, and calf production rates; however calf production rates were time lagged 27 years (~1/2 cycle period) to produce a positive correlation that met validation requirements (Table 1.4; Fig. 1.2; Fig. 1.3; Fig. 1.4). Stochastic simulations employing a sine-cyclic carrying capacity were viable at sustainable harvest levels, and the final model ran indefinitely in stochastic mode (i.e., was robust).

Our final model coupled linear and non-linear density-effects with a sine-cyclic carrying capacity function and a time lag of 27 years for calf production values. Using trial and error, we identified three harvest-strata options that provided: 1) maximum removals per cycle (Table 1.5), 2) minimum years with imposed restrictions (Table 1.6), and 3) maximized the evenness between cycle segmented harvest levels (Table 1.7). The maximum removals strategy produced 720,000 removals, was insufficient to meet historical basic needs levels for 31 years, and produced an evenness index of 0.736 over the 53-year cycle period (Table 1.5). The minimum restrictions harvest regime produced 503,500 removals, was insufficient to meet historical basic needs levels for 17 years, and produced an evenness index of 0.789 over the 53-year cycle period (Table 1.6). The option that maximized evenness between the six harvest strata resulted in 407,000 removals, was insufficient to meet historical basic needs levels minimum user needs for 37 years, and produced an evenness index of 0.930 over the 53-year cycle period (Table 1.7). The harvest options reported are three examples from all possible scenarios that serve to illustrate the range of sustainable harvest options for Qamanirjuaq caribou subpopulation.

## **DISCUSSION**

Of the five functions (linear, exponential, logistic, sine, and wavelet) we fit to the Qamanirjuaq time-series census data, only the sine function met both of the validation criteria (Table 1.3). Linear,

logistic and wavelet functions also produced significant correlations to the time-series data, but these functions were rejected because their correlation values were less than our validation criteria (Table 1.3). The exponential fit was close to significant ( $p = 0.059$ ), but the exponential  $r$  value ( $r = 0.609$ ) was substantially lower than the minimum identified by our validation criteria (Table 1.3) and the function implies unregulated population growth which is inconsistent with the life history of barren-ground caribou. The five functions fit to the Qamanirjuaq time-series data were limited by the time-frame of the available estimates (only 10 population census estimates over 46 years). Only two of these estimates occurred in the decline phase. We were unable to reject the linear, exponential, logistic, or wavelet functions based on the results of the Shapiro-Wilk test for normality of residual values at  $p \leq 0.05$  (Table 1.3). Our interpretation is that this result occurred because the power of the goodness of fit test is minimal at low sample sizes, especially when the full cycle was not sampled.

Various researchers have concluded that barren-ground caribou subpopulations cycle (i.e., Gunn & Miller, 1986; Russell *et al.*, 2002; Gunn, 2003; Wilson & Reeder, 2005; Government of Yukon, 2015) although, for the most part, these determinations have been qualitative. The sine fit estimated the Qamanirjuaq subpopulation cycle length to be 53 (SE = 3.96) years, however the wavelet function fit suggested a cycle period of 44 years. Chapter 3 evaluates mathematical functions for the 11 barren-ground caribou subpopulations that had sufficient census data. Chapter 3 provides quantitative support for the generality of the sine function to describe barren-ground caribou subpopulation dynamics (Supplementary II). Both the sine and the wavelet functions produced significant correlations ( $p \leq 0.05$ ) for the Qamanirjuaq subpopulation and the residuals of both cyclic functions were sufficiently symmetrical that we could not reject The Shapiro-Wilk test for normality (Table 1.3). The mathematical relationship of the wavelet function to the sine function is beyond the scope of our paper, however it is instructive to note that when a wavelet function is fit to sine generated data, the two functions converge to provide the same estimates of period and amplitude. A wavelet fit to a 50-year time-series

generated by a deterministic sine function produced a correlation coefficient of  $r = 1.0$  ( $p < 0.001$ ), indicating that the wavelet and sine functions will converge on estimates of period and amplitude when the data are sufficient to cover an entire cycle (Fig. 1.5). However, we suggest census data on cyclic populations should be collected throughout the cycle if long-term changes to the cycle period and amplitude are of interest.

Historical archeological information and TEK also support the consensus that barren-ground caribou cycle; however there is little published historic information and TEK that is specific to the Qamanirjuaq subpopulation. Herbert (2015) discusses archeological records that indicate a historical decline in caribou abundance near York Factory First Nation, MB, in the late 19<sup>th</sup> century, which corresponds to the southernmost portion of the present day Qamanirjuaq subpopulation range. The causes of the decline are not implicitly known, but natural population cycles were suggested to be a large contributing factor (Herbert, 2015). Historic information and TEK for barren-ground caribou in the Northwest Territories, corresponding with the range of the present day Bathurst subpopulation, suggests abundance was reduced in the 1920's, near a maximum in the 1940's, declined significantly through the 1950-1970's, and was abundant again in the 1990's (Zalatan, 2006; Legat *et al.*, 2014). Other archeological evidence and TEK suggest that all barren-ground caribou subpopulations have experienced fluctuations in abundance across North America for at least the last 100 years (Zalatan, 2006; Legat *et al.*, 2014), and the last 250 years in Greenland (Meldgaard, 1986).

As anticipated from the behavior of the discrete logistic model (Supplementary I), there was no combination of linear and non-linear density-effects that were sufficient to produce stable 53-year cycles in program CARIBOU 1.0 at estimated historical harvest rates. The introduction of a user-defined lag-time allowed us to produce cycles, but few of these cycles were consistent with Qamanirjuaq caribou field estimates (population numbers, calf production rates and calf survival rates; [Table 1.4]) in all respects. Lag-time models that did produce cycles with close correspondence to estimated

population numbers, calf survival and calf production rates (Table 1.4) were sensitive to small changes in density-effect parameter values, lag-time values, and to environmental variance. Small changes in the values of these parameters caused unexpected and often catastrophic changes in cycle stability, period, and amplitude to models that incorporated lag-time responses to density-effects. Unstable model behavior is inconsistent with archeological information and TEK which suggests robust and regular population cycles (Meldgaard, 1989; Zalatan, 2006; Legat *et al.*, 2014). Conversely, stable cycles that closely matched observed caribou cycles with respect to population numbers, calf survival and calf production rates were easy to identify and parameter variance was robust using the cyclic carrying capacity option (Table 1.4; Fig. 1.1; Fig. 1.2; Fig. 1.3; Fig. 1.4). However, it is important to note that even the best models using the cyclic carrying capacity option did not fit the available census data perfectly (Fig. 1.1; Fig 1.2; Fig 1.3; Fig. 1.4). We were required to introduce a time-lag of 27 years to produce positive temporal correlations of calf production rates that were sufficient to meet our validation requirement for correspondence to observed calf production rates and also generated a cycle that corresponded to the periodic census data. We were unable to explain why calf production response to the population number index (CC) was phase-shifted by  $\frac{1}{2}$  cycle (27) years relative to calf survival. Field estimates of calf production and calf survival were clumped and determined at different times within the Qamanirjuaq cycle and increased monitoring of calf production and calf survival in the same years may suggest an issue with some or all of the historical estimate of these vital rates. We did not evaluate models that employed both time-lags and a cyclic carrying capacity options to model calf survival rates because the additional complexity from adding time-lags was unnecessary to achieve a model that met our validation criteria.

The third family of models that coupled linear and non-linear density effects with a cyclic carrying capacity produced robust and stable population cycles. The cyclic carrying capacity models have the flexibility to fit barren-ground caribou cycles, but do not depend on a mechanistic

understanding of the drivers of the cycles. Barren-ground caribou migrate north to calve on the barren lands in the spring (Kelsall, 1968; Skoog, 1968; Hemming, 1971; Fancy *et al.*, 1989; GNWT, 2007). Slower regeneration rates of critical forage on summer pastures at northern latitudes during the calving period could be the main driver for population cycling. The observation that other members of the deer family are non-cyclic (e.g., white tail deer, moose, woodland caribou, etc.) and stay within relatively defined home ranges as opposed to partake in annual seasonal migrations to ranges with slower forage regeneration rates is consistent with this hypothesis.

A qualitative comparison of the CARIBOU 1.0 cycle model to previous models can be made by considering the range of complexity of caribou simulation models that have been developed (Fig. 1.6). Simple demographic models that do not consider carrying capacity, age structure, trophic structure, or harvest are unsatisfying because the simulations from these models do not correspond to caribou population ecology. At the other end of the model spectrum, there are complex models that employ mechanistic links between other trophic levels by considering forage availability, caribou local and migratory movements, foraging strategies, nutritional physiology, energetics, disease, parasites, predators, and disturbance and denial of habitat from development activities. Retroactive simulations that have been user-tuned to replicate past conditions correspond well to historical data, but retroactive comparisons of model output are not a valid test of a model's capacity to provide accurate projections. Program CARIBOU 1.0 is less mechanistic than these complex models (e.g., energy balance or energy simulation models [White *et al.*, 2013]) and more developed than simulation models that project the population in a linear or exponential trajectory for short time intervals (e.g., Leader-Williams, 1980). We suggest that program CARIBOU 1.0 may provide more realistic and reliable predictions because it is intermediate in terms of complexity with respect to currently available demographic models for barren-ground caribou, and can be empirically customized to specific subpopulations based on census and demographic rate estimates (e.g., the Qamanirjuaq subpopulation; [Fig. 1.6]). Models of the

Qamanirjuaq subpopulation in program CARIBOU 1.0 are highly correlated with historical data (Table 1.4; Fig. 1.1; Fig. 1.2; Fig. 1.3; Fig. 1.4), however, the test of any model's utility for management is its ability to generate reliable predictions of future outcomes. The reliability of this model to predict future cycles accurately for various harvest regimes will only become apparent with subsequent demographic census and surveys.

The CARIBOU 1.0 simulations presented in this paper are deterministic. Sensitivity to environmental and parameter variance were considered in our model validation protocol; however, only deterministic harvest simulations were considered because stochastic simulations imply knowledge about the variance of projected results that we felt were inappropriate given uncertainties about model structure. Density-effect parameters were developed empirically to drive a simulation that mimicked the observed cycles in calf survival rates, calf production rates, and population numbers, not estimated from data. Only a fraction of the estimate parameters from field studies reported an associated variance estimate. Simulation through the 53-year cycle period assumes seasonality but does not incorporate (or appear to require) a function to model progressive change (e.g., climate warming or development) that could cause deviations from the predicted outcomes.

Program CARIBOU's primary purpose is to support harvest co-management decisions. There are unlimited combinations of sustainable harvest options associated with separating the cycle into 6 user-defined abundance strata (Table 1.5; Table 1.6; Table 1.7). Other options for dividing the cycle into more or fewer segments were not considered. This exercise was meant to provide harvest management options that were simple enough to be captured with regulations that remained consistent over a reasonable time interval. The maximum number of removals per cycle, minimum number of years with imposed restrictions, and minimizing the difference between harvest strata (Table 1.5; Table 1.6; Table 1.7) are intended to illustrate a range of possible harvest options as well as the long-term effect of varying the harvest on population abundance. We did not attempt to identify a single or optimal

harvest policy. What is deemed best depends on the goals and values of the various stakeholders and the conservation mandates of the relevant management agencies. What is viewed as optimal can change as the number of northern residents increases and as perspectives on conservation governance evolve. The CARIBOU 1.0 model could be used to facilitate consultations towards a whole-cycle harvest management plan that would key on population numbers and population trends to identify management regimes. Program CARIBOU 1.0 could be employed to explore sustainable harvest options collectively and identify a sustainable harvest policy that best satisfies the needs and preferences of hunters and also meets the conservation mandates of the various responsible agencies.

The cyclic nature of barren-ground caribou has significant implications to harvest management. Increased access and better harvesting technology has led to a greater capacity for today's modern hunters, which has changed the feedback between harvest and effort. Payette *et al.* (2004) identified a correlation between the introduction of rifles in the late 1800's and the decline of the present day Rivière-aux-Feuilles caribou herd. Bergerud *et al.* (2008) noted that the disappearance of the small Harp Lake caribou herd in Québec, coincided with the introduction of snow machines in the late 1970's. When large caribou subpopulations, such as the Qamanirjuaq are increasing or at peak abundance, all caribou user-groups (i.e., aboriginal, non-aboriginal, commercial meat sales, sport hunts, and tourism) can likely be accommodated without conservation concern. Conversely, increased hunting, due to increased access and availability leave barren-ground caribou vulnerable to modern caribou hunters when the cycle begins to decline. The co-management system must eventually coordinate harvest restrictions during times of decline and scarcity to avoid severe reductions in numbers that extend the period of low numbers and reduce the overall value of the subpopulation to all user-groups.

Co-management of a mainland migratory barren-ground subpopulation is difficult for several reasons. Their geographic range is so large that it typically overlies multiple jurisdictions. Inter-jurisdictional co-management requires consultation and research collaboration, making rapid unilateral

decisions ineffective at managing the subpopulation as a whole. Wide-ranging species like mainland migratory barren-ground caribou that have seasonally overlapping ranges with other subpopulations make it difficult, or even impossible, to identify functional harvest regulations when there are multiple demographic units (subpopulations) in the same seasonal range at the same time. Harvest policies must be evaluated in a manner that is consistent with the natural dynamic changes in subpopulation numbers and productivity associated with their ecology and distribution in all seasons. Harvest policies identified on a cycle basis are objective and can be negotiated in a co-management setting that meet both user-needs and government conservation mandates.

Equilibrium concepts such as MSY (maximum sustained yield) and TAH (total allowable harvest) are difficult to apply for species that cycle naturally (e.g., barren-ground caribou). The decline phase of the cycle provides no MSY or TAH in the classical sense because the subpopulation declines whether it is harvested or not. Qamanirjuaq caribou have been and can continue to be harvested throughout the cycle without causing extirpation, permanently reducing numbers, or compromising the ecosystem they inhabit. Current federal and provincial species-at-risk criteria for barren-ground caribou use a threshold of percent reduction in pooled subpopulation numbers as one of several indicators for status assessments. Status criteria for cyclic species such as barren-ground caribou should consider the potential for asynchronous relationships between subpopulation cycles and recognize that periods of decline and low abundance are a natural part of some species' life history biology.

# Cycle stratified harvest policies for the Bathurst and George River barren-ground caribou subpopulations

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*Abstract:* The maximum sustainable harvest of barren-ground caribou subpopulations (*Rangifer tarandus groenlandicus*) cycles over time based on the number present and the annual per capita population growth rate. We modified CARIBOU 1.0, a cyclic barren-ground caribou population harvest model developed for the Qamanirjuaq subpopulation (Chapter 1), to model the Bathurst and George River barren-ground caribou subpopulations. We were able to develop models that corresponded to time-series field estimates of population numbers, calf production rates, and calf survival rates of the Bathurst and George River subpopulations, suggesting that the structure of CARIBOU 1.0 is general and robust.

We identified three harvest options for both subpopulations: 1) maximized the total number of removals per cycle, 2) minimized the number of years with imposed restrictions, and 3) maximized the “evenness” between cycle segmented harvest levels. The maximum removals strategy for the Bathurst subpopulation produced 533,500 removals per cycle, 8 years when the harvest was insufficient to meet basic user needs, and an evenness index of 0.795. The minimum restrictions strategy for the Bathurst subpopulation produced 428,650 removals per cycle, 6 years when the harvest was insufficient to meet basic user needs, and produced an evenness index of 0.725. The evenness strategy for the Bathurst subpopulation produced 464,500 removals per cycle, 13 years when the harvest was insufficient to meet basic user needs, and an evenness index of 0.882. The maximum removals strategy for the George River subpopulation produced 978,000 removals per cycle, 9 years when the harvest was insufficient to meet basic user needs, and an evenness index of 0.770. The minimum restrictions strategy for the George River subpopulation produced 748,000 removals per cycle, 6 years when the harvest was insufficient to meet basic user needs, and produced an evenness index of 0.712. The ‘evenness strategy for the George River subpopulation produced 776,500 removals per cycle, 17 years when the harvest was insufficient to meet basic user needs, and an evenness index of 0.865. The range of sustainable harvest options was large for both subpopulations, and thus offers a framework to exploring harvest strategy options in consultations and co-management planning.

Key Words: barren-ground caribou, cyclic species, demography, density-effects, harvest management, simulation model.

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## INTRODUCTION

Migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) are unique among the deer family (Cervidae) because they make regular seasonal migrations rather than remain within well-defined home ranges. Barren-ground caribou are also thought to form two differing ecotypes: tundra-wintering and mainland migratory (Nagy *et al.* 2011, Nagy & Campbell, 2012). Mainland migratory subpopulations display the most extensive seasonal migratory behaviour, moving between the treeless tundra in summer and the forested taiga in winter. Barren-ground caribou population numbers cycle rather than fluctuate around an equilibrium number, but the factors that drive the cycle are poorly understood (Gunn & Miller, 1986; Russell *et al.*, 2002; Wilson & Reeder, 2005; Government of Yukon, 2015). Chapter 1 and COSEWIC (2016) provide a summary of the relevant natural history, ecology of barren-ground caribou, and the rationale for modeling the population dynamics of this species using life table methods.

We re-parameterized the same cyclic birth-pulse life table harvest model that was employed to model Qamanirjuaq barren-ground caribou population dynamics (Chapter 1) for Bathurst and George River subpopulations to evaluate the generality of program CARIBOU 1.0. We chose the Bathurst and George River subpopulations because they are sine cyclic (Chapter 3; Fig. 2.1a; Fig. 2.1b), relatively well known, and thus provide more robust tests of the generality of CARIBOU 1.0 than subpopulations with fewer data. The caribou cycle was stratified into 6 user-defined abundance-strata with three strata in both the decline and increase phases. Only long term sustainable options were allowed because extirpation was not viewed as an acceptable outcome. Harvest policy options associated with periods of increase and decline at high, intermediate, and low densities were identified to explore the effects of differential harvest rates during the cycle. The number of distinct harvest options that can be specified is unlimited. We examined three options: 1) maximized the number taken per cycle, 2) minimized the number of years when the numbers taken were too few to meet subsistence needs, and 3) minimized

the degree and frequency of differences between strata harvests (i.e., maximized evenness). Harvest strategies that minimize interference with free hunting (both the duration and magnitude of any harvest restrictions) and also insure sound conservation practices could be developed through consultation with user-groups, co-management partners, and jurisdictions that share a given subpopulation. During periods of abundance, barren-ground caribou subpopulations can be exploited to the extent of user-needs due to logistic limitations in human harvesting. During periods of decline and periods of low numbers, harvest should be regulated to allow optimal recovery of population numbers and productivity in a manner that is supported by the user-community and satisfies the conservation mandate of government. There are few available harvest records for the Bathurst caribou subpopulation, however, Nesbitt & Adamczewski (2009), and Boulanger & Adamczewski (2015) suggest a current minimum basic needs level of approximately 7,000/year for the Bathurst subpopulation. Newfoundland and Labrador (2010) report suggest that an annual take of 9,000 would be required to meet the current minimum basic needs of harvesting from the George River subpopulation.

The model development strategy was trial and error convergence to a model that mimicked the actual demographic history of the subpopulation cycle as closely as possible (Chapter 1). The model validation protocol involved empirical comparison of cyclic changes in model population numbers, calf production rates and calf survival rates to published Bathurst and George River caribou time-series census estimates of these parameters (Table 2.1a; Table 2.1b).

## **METHODS**

RISKMAN version 2.0 PVA software (Taylor *et al.*, 2001) was modified to include a time-lagged density response option, a cyclic carrying capacity option, and to allow six user-defined annual harvest strata (3 abundance-strata during increase phase and 3 abundance-strata during decline phase) of the caribou population cycle (Chapter 1). The model protocol required the simulation to develop a stable

cycle before the user-defined annual harvest was implemented. Similarly, summary parameters were reported only after the harvested cycle became stable. Starting conditions that did not result in a stable cycle and harvest regimes that were not sustainable were identified with an error condition and summary parameters were not reported. The modified program was named CARIBOU 1.0 and is available with our final project files upon request from the corresponding author (Supplementary IV).

The harvest mortality rate estimates for the George River and Bathurst subpopulations were determined from available harvest records for each of the six population strata identified (Table 2.2a; Table 2.2b). Bergerud *et al.* (2008) identified historical harvest estimates for the George River subpopulation of 1,000-2,000 (1957-1967) corresponding to the lower decline region of the cycle, 2000+ (1967-1972) corresponding to the lower increasing region of the cycle, 9,000-10,000 (1972-1982) corresponding to the middle increasing region of the cycle, and 15,000-25,000 (1982-1992) corresponding to the upper increasing and upper decreasing regions of the cycle. Harvest estimates for the middle decreasing region of the George River subpopulation cycle were unavailable.

The Dogrib Harvest Study (unpublished) and Boulanger & Gunn (2007) suggested an average annual harvest of 15,864 for the Bathurst caribou subpopulation between 1988-1993, which corresponds to the upper increasing and upper decline regions of the population cycle. Nesbitt & Adamczewski (2009) reported a harvest between 5000-7000 in 2008 which corresponds to the middle decreasing region of the Bathurst subpopulation cycle. The BGTWG (2015) report, identified a harvest of 300 Bathurst caribou in Northwest Territories with an additional 70 commercial tags for Nunavut outfitters in 2013/2014 corresponding to the lower declining region of the population cycle. We rounded the 370 known removals to 500 to subjectively include unreported removals. Harvest estimates for the Bathurst subpopulation that corresponded to the lower increasing and middle increasing regions of the cycle were unavailable.

Available harvest strata estimates from the Qamanirjuaq subpopulation (Chapter 1; Table 1.2), and George River subpopulations were close to equal between adjacent strata regions (i.e., the George River subpopulation lower decline region harvest estimate 1,000-2,000, and the lower increasing region harvest estimate was 2000+). We estimated the harvest for the missing population strata (i.e., lower and middle increasing regions for the Bathurst subpopulation and middle decreasing region for the George River subpopulation) based on the proportionality pattern of available harvest records, assuming that missing harvest strata values would be equal to the adjacent harvest strata value that had an available harvest record (Table 2.2a; Table 2.2b). We estimated the lower and middle increasing harvest regions of the Bathurst subpopulation cycle to be 500 and 6,000 removals annually, corresponding to available harvest records from the lower and middle decreasing harvest regions (Table 2.2a). We estimated the middle decreasing harvest region for the George River subpopulation to be 9,000 annually, corresponding to available harvest record for the middle increasing harvest region (Table 2.2b).

We empirically identified population density index (CC) and shape factor (KS) values for the density-effects function (Chapter 1; Fig. 2.2) that resulted in annual time-series of model calf survival and calf production rates that were comparable to field estimates of natural calf survival and calf production rates at the same year of the cycle for each subpopulation. The actual rate value employed for any given iteration is some fraction of the maximum rate as determined by the population (or sex/age strata) number, KS and CC parameters (Chapter 1; Fig. 2.2). We used total population numbers as the driving variable for density-effects on maximum values for calf (age 0) survival, adult (age 1+) survival of males and females, and calf production rate by mature (age 2+) females (Table 2.1a; Table 2.1b). We assumed adult females had only one calf (sex ratio 0.5 females) when they reproduced because the occurrence of multiple calves per female is rare (COSEWIC, 2016).

Our simulation model validation protocol consisted of two steps (Chapter 1). The first step was to ensure that the simulation model generated significant ( $p \leq 0.05$ ) temporal correlations with correlation coefficients  $r \geq 0.7$  for population numbers, calf production rates and calf survival rates for the portion of the cycle that had available census population, calf production and calf survival estimates. The second step was to test the simulation robustness to environmental variance of model parameters. Final model stochastic simulations using Monte Carlo methods (Taylor, *et al.*, 2001) were run assuming 100% of estimate variance was due to environmental uncertainty. Successful simulations (no error interruption) were accepted as sufficiently robust.

Three harvest strategies were developed to illustrate the range of possible approaches: 1) maximum number of total removals per cycle, 2) minimum number of years with substantial restrictions (defined as the level of harvest that would inhibit users from meeting their minimum needs), and 3) maximize the evenness index, which minimizes the difference between harvest strata. Evenness was evaluated using the Shannon-Weiner Evenness index ( $E_H$ ) (Beals, *et al.*, 2000). Program CARIBOU 1.0 reports summary parameters (i.e., total number of removals, number of removals per cycle strata, and annual values of population number, survival rate and calf production rates).

## **RESULTS**

The sine cyclic harvest models for both the Bathurst and George River subpopulations (Table 2.2a; Table 2.2b) we developed were sufficient to meet our validation criteria in terms of population numbers, calf production and calf survival temporal correlations (Fig. 2.3a; Fig. 2.3b; Fig 2.3c; Fig. 2.4a; Fig 2.4b; Fig.2.4c) and were considered sufficiently robust. We identified three harvest-strata options that provided: 1) maximum removals per cycle (Table 2.3a, Table 2.4a), 2) minimum years with imposed restrictions (Table 2.3b; Table 2.4b), and 3) maximized the evenness between cycle segmented harvest levels (Table 2.3c; Table 2.4c) for both the Bathurst and the George River subpopulations.

The maximum removals strategy for the Bathurst subpopulation produced 533,500 caribou over the 42-year period but the harvest was insufficient to meet basic user needs for 8 years and produced an evenness index value of 0.795 (Table 2.3a). The minimum restrictions harvest regime yielded a total harvest of 428,650 Bathurst caribou over the cycle period, but the strategy resulted in 6 years where harvest was insufficient to meet the basic user needs and produced an evenness index value of 0.725 (Table 2.3b). The option that maximized 'evenness' between the six harvest strata resulted in a total harvest of 464,500 Bathurst caribou over the cycle period, was insufficient to meet basic user needs for 13 years and produced an evenness index value of 0.882 (Table 2.3c).

The maximum removals strategy for the George River subpopulation produced 978,000 caribou over the 45-year period, but was insufficient to meet basic user needs for 9 years and produced an evenness index of 0.770 (Table 2.4a). The minimum restrictions strategy for the George River subpopulation resulted in a total harvest of 748,000 over the cycle period, but the strategy resulted in 6 years where the harvest was insufficient to meet basic user needs, and produced an evenness index value of 0.712 (Table 2.4b). The option that maximized evenness for the George River subpopulation between the six harvest strata resulted in a total harvest of 773,000 caribou over the cycle period, was insufficient to meet basic user needs for 17 years, and produced an evenness index value of 0.865 (Table 4c). The harvest options reported are not exhaustive and were selected both to provide information regarding the three harvest protocols and also to illustrate the range of sustainable harvest options.

## **DISCUSSION**

Various researchers have concluded that barren-ground caribou subpopulations cycle (i.e., Gunn & Miller, 1986; Russell *et al.*, 2002; Gunn, 2003; Wilson & Reeder, 2005; Government of Yukon, 2015), although, for the most part, these determinations have been qualitative. CARIBOU 1.0 was able to simulate the Qamanirjuaq (Chapter 1), Bathurst and George River subpopulation cycles in a manner that

was consistent with the available time-series census data (Fig. 2.3a; Fig. 2.3b; Fig. 2.3c; Fig. 2.4a; Fig. 2.4b; Fig. 2.4c). However, the demographic rate correlations were lower for the Bathurst and George River subpopulations than the Qamanirjuaq subpopulation (Chapter 1). To compensate, we reduced our model validation criteria of population number and demographic rate correlations to census data from  $r \geq 0.95$  ( $p \leq 0.05$ ) for the Qamanirjuaq subpopulation (Chapter 1) to  $r \geq 0.7$  ( $p \leq 0.05$ ) for the Bathurst and George River subpopulations. CARIBOU 1.0 can be generalized to other barren-ground caribou subpopulations and perhaps to other cyclic birth-pulse species where there is sufficient time-series data to develop and validate the model. However, both the simulation model and the validation protocol are empirical, and do not explain the mechanism for the observed cycles.

Program CARIBOU's primary purpose is to support harvest co-management decisions. Harvest policies specifying the maximum number of removals per cycle (Table 2.3a; Table 2.4a), minimum number of years with imposed restrictions (Table 2.3b; Table 2.4b), and minimizing the difference between harvest strata (Table 2.3c; Table 2.4c) were intended to illustrate a range of possible harvest options for each subpopulation, as well as illustrate the long-term effects of varying the harvest on subpopulation abundance. We did not attempt to identify a single "best" harvest policy for any of the subpopulations investigated, because what is deemed to be best depends on the goals and values of the various stakeholders and the conservation mandates of the relevant management agencies. Program CARIBOU 1.0 could be employed to explore sustainable harvest options in order to identify a sustainable harvest policy that best satisfies the needs and preferences of hunters and also meets the conservation mandates of the various responsible agencies (Chapter 1). Although the numerical results differed between subpopulations, the qualitative results were the same for both subpopulations.

When large caribou subpopulations, such as the George River, are increasing or at peak abundance all caribou user-groups (i.e., aboriginal, non-aboriginal, commercial, sport hunts, and tourism) can be accommodated without conservation concern. However, high exploitation rates from

commercial harvesting initiatives, increased access and availability from development and improved technology can make barren-ground caribou vulnerable to over-hunting when the cycle enters its decline phase. The various co-management systems should coordinate harvest restrictions during times of decline and scarcity to avoid severe reductions in numbers that extend the period of low numbers and thus reduce the overall value of the subpopulation to all user-groups. These results were consistent and general for the Qamanirjuaq, Bathurst, and George River subpopulations. Reducing the number removed when barren-ground caribou are declining rapidly or are at low numbers will reduce the length of time for any barren-ground caribou subpopulation to recover and will thus increase the benefits from caribou harvesting to all stakeholders.

## A cycle analysis of North American migratory barren-ground caribou subpopulations

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Abstract: Unlike all other members of the deer family, subpopulations of barren-ground caribou (*Rangifer tarandus groenlandicus*) exhibit fluctuations in numbers that have been described as cyclic. We fit linear, exponential, logistic, sine, and wavelet functions to 14 of these subpopulations and found that 11 subpopulations had sufficient census data to estimate cyclic function parameters. All 11 subpopulations were best described as sine cyclic with periods ranging from a minimum of 26 years (Porcupine) to a maximum of 59 years (Western Arctic); and amplitudes ranging from a minimum of 8,455 (Cape Bathurst) to a maximum of 329,886 (George River). The Porcupine subpopulation was the only subpopulation sampled that did not produce a cyclic function fit that was sufficient to meet out validation criteria. Porcupine caribou have shown a long-term progressive (annual) increase in abundance between consecutively sampled cycles, but have also maintained consistent period and amplitude values.

Although the total number of the barren-ground caribou (meta-population) is currently declining, the decline is an artifact of the trend analysis, which fails to consider the natural damping and resonance of subpopulation cycles. We did not find support for the view that some progressive general factor or factors are currently affecting all barren-ground caribou subpopulations. Comparison of the pooled estimate in 2015 from the 6 subpopulations that had both an exponential fit (COSEWIC, 2016) and sine cyclic fit (this paper) showed that the our 2015 meta-population cycle-based estimate (517,137) closely corresponded to COSEWIC's 2015 meta-population exponential fit estimate (537,549). The trend from the pooled exponential fit was negative, however, the long term trend of the cycle is no trend.

Correlations between subpopulation cycle parameters (period and amplitude) and various range attributes determined individually for the total range, summer range and winter ranges suggested that subpopulation period was most correlated to subpopulation amplitude ( $r = 0.547$ ,  $p = 0.082$ ). Subpopulation amplitude was most highly correlated to subpopulation total range mean temperature ( $r = 0.877$ ,  $p \leq 0.001$ ). Regression modeling of subpopulation amplitude as a function of the subset of biological range attributes suggested that 88.5% ( $p = 0.006$ ) of the observed variance in amplitude could be explained by 2 variables: total range area and the interaction between summer range area and summer range net primary productivity. Inclusion of the interaction term was significant ( $p = 0.036$ ), and was the only main or interaction term that resulted in a significant improvement in the correlation

after total range area. Subpopulations with large ranges and greater summer range net primary productivity experienced the greatest fluctuations in numbers. Regression estimates of subpopulation amplitude showed good correspondence ( $r = 0.918$ ,  $p \leq 0.001$ ) to census (sine fit) estimates of amplitude, and the regression estimates of population abundance showed good correspondence to observed population abundance estimates for all subpopulations ( $r = 0.894$ ;  $p < 0.001$ ).

Key Words: Barren-ground caribou, species designations, COSEWIC, IUCN, cyclic species, cycle analysis, cycle analysis, climate change

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## INTRODUCTION

Census surveys have documented that barren-ground caribou (*Rangifer tarandus groenlandicus*) herds exhibit regular fluctuations in population abundance that are believed to be cyclic (Gunn & Miller, 1986; Couturier *et al.*, 1990; Russell *et al.*, 2002; Gunn, 2003; Wilson & Reeder, 2005; Government of Yukon). Traditional ecological knowledge (TEK) also confirms regular periodic changes in abundance are characteristic of this species (Hemming, 1975; Zalatan *et al.*, 2006; Legat *et al.*, 2014; Herbet, 2015). The factors that regulate barren-ground caribou population dynamics are not well understood (Messier *et al.*, 1988, Klien, 1991), but forage availability, predators, pathogens, decadal winter severity, habitat disturbance (development and forest fires), and climate change are all known to influence population dynamics in other species, and could also drive barren-ground caribou population cycles (Kelsall, 1968; Skoog, 1968; Hemming, 1971; Fancy *et al.*, 1989; GNWT, 2007).

Barren-ground caribou are a meta-population with 13-15 relatively discrete North American subpopulations that extend from Alaska, across continental mainland and archipelago Canada (Nagy, *et al.*, 2011; COSEWIC, 2016; Parlee *et al.*, 2018). All subpopulations spend at least a portion of the year on the barren-lands, with mainland migratory herds dividing their time between the tundra and boreal forest (e.g., Qamanirjuaq) and tundra wintering herds spending the entire year on the tundra (e.g., Cape Bathurst and Dolphin-Union). Barren-ground caribou partake in regular seasonal migrations, rather than remaining within a single well-defined home range that is used throughout the year (Fancy *et al.*, 1989; Royal Canadian Geographic Society, 2010; COSEWIC, 2016; Nicholson *et al.*, 2016). Mainland migratory barren-ground caribou generally migrate north towards the Arctic coast to calve on the barren-lands and occur throughout the summer and early autumn on the tundra in the Southern Arctic ecozone (COSEWIC, 2016). Mainland populations usually winter in the boreal forest within the Taiga Cordillera, Taiga Plains or Taiga Shield ecozones (Kelsall, 1968; Skoog, 1968; Hemming, 1971; Fancy *et al.*, 1989; GNWT, 2007; COSEWIC, 2016). Fluctuations in abundance influence the size of seasonal ranges and the

length of migration patterns (COSEWIC, 2016). As subpopulation abundance increases, seasonal ranges expand. Conversely, as subpopulation abundance declines seasonal ranges contract towards the traditional calving areas (Hemming, 1975). The contraction of the home range allows for the recovery of previously overused seasonal pastures (Hemming, 1975).

Barren-ground caribou forage on a variety of plants such as: willows, grasses, dwarf birch, mountain avens, arctic sorrel, mushrooms, moss campion and berries (Thorpe *et al.*, 2001; Dumond 2007; Environment and Climate Change Canada, 2017) on the summer range, but lichen (dominated by *Cladina sp.*) is the primary forage for barren-ground caribou on the winter range (Thomas & Hervieux, 1986; Théau *et al.*, 2005; Collins, 2006; Andersen & Johnson, 2014; Rickbeil *et al.*, 2017), constituting approximately 60-80% of their diet (Thomas & Hervieux, 1986; Jandt *et al.*, 2003; Andersen & Johnson, 2014). Manseau *et al.* (1996) suggest that quality and volume of available forage on summer pastures is the primary regulator of physical body condition and population abundance. Others (e.g., Klein, 1970; Klein 1986; Parker *et al.*, 2005) suggest barren-ground caribou abundance can be attributed to winter foraging conditions. The availability and volume of forage is influenced by grazing intensity, trampling, and forest fires (winter range only) (Ahti, 1959; Scotter, 1964; Zalatan *et al.*, 2006; Collins *et al.*, 2011; Andersen & Johnson, 2014).

Direct weather events, such as snow depth and icing, can affect barren-ground caribou's ability to access vegetation (Weladji & Holand, 2003). The frequency and severity of direct weather events is influenced by large-scale patterns in climatic activity such as El Niño Southern Oscillation (ENSO) events, the Atlantic Multidecadal Oscillation (AMO) the Arctic Oscillation (AO), Pacific Decadal Oscillation (PDO), and longer-term progressive climate trends (COSEWIC, 2016). The AO has a strong negative correlation with population trends for the Porcupine and Central Arctic subpopulations (Joly *et al.*, 2011).

North America's barren-lands are comprised of 5 main biome types: alpine tundra, shrub tundra, herb tundra, forest tundra and boreal forest (Dyke, 2005). These five biomes are characterized by relatively low temperatures, short growing seasons, acidic nutrient-poor soils with patchy vegetation and slow vegetation regeneration rates (Archer & Tieszen, 1980; Payette & Gamache, 2001). The western Arctic of Alaska and the Yukon is predominantly characterized by boreal forest and alpine tundra, while the eastern Canadian Arctic is predominantly shrub, herb and forest tundra at similar latitudes (Dyke, 2005). Ecological productivity follows a SW to NE gradient of decreasing net primary productivity (NPP) in northern North America (Qian, 1999; Hicke, *et al.* 2002; Gillman *et al.* 2015). The gradient of NPP is driven by regional temperature trends and is clearly illustrated by the treeline isopleth. The mechanisms responsible for regional temperature trends are marine in origin and include sea surface temperature as mediated by ENSO events, the PDO, and the AMO (Liu, *et al.*, 2015).

Many barren-ground caribou subpopulations have experienced declines in abundance over approximately the last two decades (Gunn *et al.*, 2010; CARMA, 2016; COSEWIC, 2016). Both COSEWIC (Committee on the Status of Endangered Wildlife in Canada) and the IUCN (International Union for Conservation of Nature) has responded to the declines in subpopulation abundance by assigning respective barren-ground caribou species designations of threatened and vulnerable (COSEWIC, 2016; IUCN, 2016). Present trends in subpopulation abundance suggest barren-ground caribou subpopulation cycles are either synchronized or are currently influenced by a common factor that has interrupted their natural cycle (COSEWIC 2016). Alternatively, differences in subpopulation cycle periods could cause apparent meta-population trends that were only damping and resonance of the pooled subpopulation natural cycles. Periods of synchrony might be coincidental rather than caused by some factor that was affecting all barren-ground caribou subpopulations simultaneously.

We identified 14 North American barren-ground caribou subpopulations that had a time-series of census estimates, and attempted to characterize their population dynamics as linear, exponential, logistic, sine cyclic or wavelet cyclic. We estimated the period and amplitude (with associated SE estimates) for subpopulations that were found to be cyclic based on comparisons with other time-series functions. We examined the effects of damping and resonance on total barren-ground caribou population numbers by extrapolating the subpopulation cycles forward and pooling those estimates for a meta-population time-series estimate.

We explored the relationships between selected subpopulation seasonal range attributes (total range area, tundra range area, forest range area, tundra percentage, mean land surface temperature (LST), net primary productivity (NPP), and normalized difference vegetation index (NDVI) and subpopulation cycle characteristics (cycle period length and amplitude).

## **METHODS**

We identified five functions as potential descriptions for the time-series of population census estimates for each of the 14 subpopulations we considered: linear, exponential, sigmoidal (logistic density effects), sine cyclic and wavelet cyclic. We identified the best function based on the value and statistical significance of the function correlation coefficient ( $r$ ), and also employed the Shapiro-Wilk test to determine the normality of residual values. Our validation criteria for the best supported functions were statistically significant ( $p \leq 0.05$ ) correlation coefficients of 0.95 or greater from least squares fitting of the function to available time-series census estimates; and a failure to reject the Shapiro-Wilk test for normality of residuals ( $p \leq 0.05$ ). We created a time-series estimate of total caribou numbers (i.e., sum of all subpopulations) by extrapolating the best function fit for each subpopulation from herds with a sufficient amount of census data to compare function fits. We explored the temporal variation in

pooled subpopulation (meta-population) numbers to assess if cyclic characteristics of the meta-population were evident.

NDVI is a commonly used remote sensing method for assessing and monitoring ecological productivity. NDVI has been used to monitor ecosystem health, faunal habitat, faunal distribution and condition, forage quality and disease risk (Leyequien, *et al.*, 2007). NDVI is an index that is calculated from satellite-monitored ground pixel radiance in specific spectral bands visible (VIS) (0.4 to 0.7  $\mu\text{m}$ ) light and near-infrared (NIR) (0.7 to 1.1  $\mu\text{m}$ ) (Schmid, 2017). NDVI provides an estimation of the density of vegetation within a given pixel based on the reflectance of VIS and NIR light. NDVI is calculated as:  $\text{NDVI} = (\text{NIR} - \text{VIS}) / (\text{NIR} + \text{VIS})$  (Weier & Herring, 2000). NDVI values for individual pixels range from 0.1 (stone, sand and snow), 0.3 (sparse vegetation), 0.6 (temperate forests) to 0.8-1.0 (the highest possible density of vegetation, [e.g., rainforest]). Negative values indicate the presence of water or ice (Schmid, 2017). We used NDVI as an indicator of ecological productivity on barren-ground caribou summer ranges, producing a monthly summer range index (2000-2016) by averaging the time-referenced values of all pixels georeferenced to the summer range.

NPP (net primary productivity) is a fundamental measure of annual change in terrestrial biological activity (NEO, 2018). Regional NPP has been used to define the carrying capacity of a specific region (Gonsamo & Chen, 2017). The spatial variability of NPP ranges from approximately 1000 grams of carbon per cubic meter per year (evergreen tropical rainforests) to less than 30 grams of carbon per cubic meter per year (deserts) (NEO, 2018). NPP is equal to carbon uptake by vegetation through photosynthesis (Gross Primary Productivity [GPP]) minus carbon lost to respiration (RE) and is calculated as:  $\text{NPP} = \text{GPP} - \text{RE}$  (GLOBE, 2012; NEO, 2018). NPP is designed to produce an accurate regular measure of terrestrial vegetation growth (NEO, 2018). Annual NPP data (2000-2014) was retrieved from Moderate Resolution Imaging Spectroradiometer (MODIS), aboard NASA's Terra and Aqua satellites

(NEO, 2018). We used NPP as an additional indicator of ecological productivity on barren-ground caribou subpopulation seasonal ranges.

Google Earth Engine (GEE) is a web-based remote sensing platform that is able to carry out spatial and temporal aggregations of satellite imagery (Sidhu, et al., 2018). GEE provides public access to satellite archives from Landsat 4-8, Sentinel 1-2, MODIS to Aster, and World Health Indicators System (WHIS) providing climate, land cover and topographic data (Schmid, 2017). GEE allows for the spatial and temporal manipulation of these datasets using a JavaScript and Python application programming interface. We used ArcMap 10.4.1 to visualize, transform, and map spatial data. We geo-referenced the home ranges based on the COSEWIC map of barren-ground caribou subpopulations (COSEWIC, 2016) using the Lambert Conformal Conic projected coordinate system. We classified the summer range as the proportion of the range north of the treeline, and winter range as the proportion of the range south of the treeline. We used GEE to query LST, NDVI and NPP data for the seasonal ranges (and total range) of 11 discrete barren-ground caribou subpopulations (Supplementary III). We filtered the data by date to retain only data from May-August which we assumed would correspond to the main portion of the growing season on both the barren-lands and forested areas (Post, *et al.*, 2009). LST and NPP data were acquired from MODIS satellite imagery at a 1km pixel resolution from 2000-2018 and 2000-2014 respectively. NDVI data was acquired from Landsat 7 at a 30m pixel resolution from 2000-2016.

We generated a correlation matrix of range attributes and subpopulation cycle characteristics (period and amplitude) using IBM SPSS statistics. We identified physical and biological range attributes that were significantly correlated ( $p \leq 0.05$ ) to period and to amplitude independently. Considering the results of the correlation matrix, we employed multiple linear regression analysis to evaluate models of period and amplitude based on a subset of physical and environmental variables on subpopulation total, summer and winter ranges. We required models to explain a significant ( $p \leq 0.05$ ) proportion of the

variation in period and amplitude as well as produce regression estimates that produced a significant ( $p \leq 0.05$ ) correlation of 0.90 or greater to census estimates of period and amplitude.

We employed the “two-step” cluster analysis method in SPSS (SPSS, 2001) to create an empirical clustering of subpopulations using the environmental and physical variables that explained the greatest amount of variation in amplitude as our discriminate axes. The two-step method partitions the data set into a set of “ $k$ ” groups, where  $k$  represents the number of clusters. Clusters were identified by assigning subpopulation variables into one of  $k$  clusters by minimizing intra-cluster variation based on Euclidean distance (Norusis, 2010). The two-step method allows the user to identify the optimal number of clusters based on Schwarz Bayesian Criterion (SBC), Akaike’s Information Criterion (AIC), or specify a fixed number of clusters (Norusis, 2010). We employed the fixed number of clusters method based on the silhouette measure of cohesion and separation (Norusis, 2010) because our sample size (i.e., number of subpopulations; [n=11]) limits the power of both the SBC and AIC methods. The silhouette measure ranges from -1 to +1 where a higher value indicates that samples are well matched to their own cluster and poorly matched to neighbouring clusters. We identified the optimal number of clusters as the fewest number of clusters that produced a silhouette value  $> 0$  (Norusis, 2010).

## RESULTS

Of the 14 discrete North American subpopulations (Nagy, *et al.*, 2011; COSEWIC, 2016; Parlee *et al.*, 2018), 11 subpopulations (George River, Leaf River, Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine, Central Arctic, Teshekpuk Lake, and Western Arctic) had sufficient census data (i.e.,  $\geq 6$  population abundance estimates) for a time-series function analysis and three subpopulations (Ahiak/Beverly, Dolphin-Union, and Tuktoyaktuk Peninsula) did not. Cyclic (sine or wavelet) function fits to the time-series census data met our validation criteria for 10 of the 11 subpopulations, and 1 (Porcupine) did not (Table 3.1). The wavelet function provided the best fit of temporal

correlations of  $r \geq 0.95$  to 4 subpopulations (Table 3.1). The sine function provided the best fit of temporal correlations of  $r \geq 0.95$  to 6 subpopulations (Table 3.1). The sine function provided the best fit to the Porcupine time-series census data ( $r = 0.868$ ,  $p < 0.001$ ; [Table 3.1]). All sine and wavelet functions produced normally distributed residuals for each subpopulation (Table 3.1). Using the sine function fits of the 11 subpopulations that had sufficient census data we produced estimates of period and amplitude (Table 3.2), and extrapolated those estimates to produce a meta-population time-series estimate (Fig. 3.1; Fig. 3.2). We describe total barren-ground caribou population numbers (meta-population) as irregular fluctuations between limits depending on resonance-damping harmonics of the pooled subpopulation cycles (Fig. 3.2).

The correlation matrix between subpopulation seasonal range attributes and cycle characteristics identified significant ( $p \leq 0.05$ ) correlations between amplitude and tundra percentage, total range area, summer range area, winter range area, and total range mean LST (Table 3.3). There were no individual variables that were significantly correlated with period, but amplitude was most highly correlated with period ( $r = 0.547$ ,  $p = 0.082$ ; [Table 3.3]). Total range LST (a physical variable) was the best single variable predictor of subpopulation amplitude ( $r = 0.877$ ,  $p \leq 0.001$ ; [Table 3.3]). There were several other biological variables that were significantly correlated with amplitude and also significantly correlated with total range LST: tundra percentage, total range area, summer range area, and winter range area (Table 3.3). The multiple regression model that explained the greatest amount of variation in amplitude included total range area, summer range area, summer range NPP and the interaction of summer range area x summer range NPP ( $R^2 = 0.885$ ,  $p = 0.006$ ; [Table 3.4]). Summer range area and summer range NPP main effects contributed little to the final model, and but were necessary to include because the interaction effect (summer range area X summer range NPP) was significant ( $p = 0.036$ ; [Table 3.4]). Comparison of regression estimates of subpopulation amplitude produced a correlation coefficient of  $r = 0.918$  ( $p < 0.001$ ) to census (sine function fits) estimates of

amplitude (Fig. 3.3a). Comparison of regression estimates of subpopulation period produced a correlation coefficient of  $r = 0.519$  ( $p = 0.102$ ) to census estimates of period (Fig. 3.3b). Comparison of regression estimates of subpopulation abundance produced a significant positive correlation of  $r = 0.894$  ( $p < 0.001$ ) to observed population abundance estimates for the set of eleven subpopulations considered (Fig. 3.3c).

Cluster analysis was based on total range area, and the interaction of summer range area x summer range NPP. The optimal number of clusters identified was two (silhouette measure= 0.7). Cluster 1 (i.e., George River, Leaf River and Porcupine) was characterized by large total areas and high values summer range area x summer range NPP (Table 3.5; Fig. 3.4). Cluster 2 (i.e., Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Central Arctic, Teshekpuk Lake, and Western Arctic) was characterized by small total range areas and low values of summer range area x summer range NPP (Table 3.5; Fig. 3.4).

## **DISCUSSION**

Of the five functions (linear, exponential, logistic, sine cyclic and wavelet cyclic) fit to the time-series census data of the 11 subpopulations, the sine cyclic or wavelet cyclic functions produced the greatest correlation coefficients to all subpopulations (Table 3.1). The wavelet function was only fit to 6 of the 11 subpopulations due to data limitations (Table 3.1). The wavelet function provided the greatest correlation coefficients to 4 (George River, Bathurst, Central Arctic and Western Arctic) subpopulations (Table 3.1), and the sine function provided the greatest correlation coefficients to 7 (Leaf River, Qamanirjuaq, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine and Teshekpuk Lake) subpopulations (Table 3.1). The wavelet and sine functions produced different estimates of both period and amplitude. However, the wavelet estimate of cycle period length and amplitude value converges on a sine cycle estimate of period length and amplitude value when a true sine curve is sampled

symmetrically for at least one complete cycle ( $r = 1.0, p < 0.001$ ; [Fig. 1.4]). However, the converse is not always true because the wavelet function can fit other cycles including time-series data that is comprised of several simultaneous cycles (Zhang *et al.*, 2000). We suggest increasing the monitoring frequency of barren-ground subpopulations to ensure the entire cycle period is sampled symmetrically so that progressive changes to period length and amplitude value can be identified, and to facilitate the discrimination between competing cyclic functions.

None of the five functions we employed were able to produce a correlation coefficient  $r \geq 0.95$  to the time-series population census estimates of the Porcupine subpopulation (Table 3.1). The observation that the most recent population abundance estimate of 218,000 (2017) was greater than the maximum of the previous cycle, 177,000 (1990) suggests barren-ground caribou cycles may change over time. The sine cyclic function produced the best fit ( $r = 0.868, p < 0.001$ ) to the time-series census data for the Porcupine subpopulation. (Table 3.1). Our validation criteria was deliberately stringent, but essentially arbitrary. Discrimination between sine cyclic and wavelet cyclic function fits based on statistical significance and observed correlations were difficult because there was little difference between the sine and wavelet function fits (Table 3.1; Fig. 1.4). We classified all 11 subpopulations as sine cyclic to increase consistency in period and amplitude estimates used in the correlation, multiple linear regression, and cluster analyses.

The COSEWIC (2016) barren-ground caribou meta-population estimate included seven subpopulations that we did not have a sufficient amount of census data to fit a sine function to: Tuktoyaktuk Peninsula, Beverly/Ahiak, Lorillard + Wager Bay, Boothia Peninsula, Southampton Island, Coats Island and Baffin Island subpopulations (Fig. 3.1). The COSEWIC (2016) report also excluded the George River, and Leaf River subpopulations as well as the three Alaskan (Central Arctic, Teshekpuk Lake, and Western Arctic) subpopulations (Fig. 3.1; Fig. 3.2). A comparison between the COSEWIC

(2016) exponential fit and our sine cycle extrapolations that included only the six subpopulations that were sampled in common (Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst and Porcupine; [Fig. 3.1; Fig. 3.2]) yielded almost the same 2015 meta-population abundance estimate (COSEWIC estimate = 537,549, sine cyclic estimate = 517,317). The close correspondence between qualitatively distinct methods emphasizes the difficulty in discriminating between population functions over a short time-frame (Fig. 3.2).

The COSEWIC (2016) pooled subpopulation extrapolation trend estimates are an exponential fit to the 13 subpopulations they included in their trend analysis (Fig. 3.1). Both COSEWIC and the IUCN determine status based on trends in population abundance over a 3-generation period. Barren-ground caribou have a generation time of 7-9 years (COSEWIC, 2016; IUCN, 2016), meaning a 3-generation period would be approximately 21-27 years. Our cycle analysis indicates some subpopulations (e.g., Qamanirjuaq and Western Arctic) can have cycle period lengths greater than 50 years (Table 3.2). This would mean periods of increase or decline could last longer than a 3-generation time period for some subpopulations. Cyclic barren-ground caribou subpopulations neither increase exponentially, nor decline exponentially to extirpation unless they are perturbed. Status determinations based on exponential or linear 3-generation period trends may be inappropriate for cyclic species that can have periods of growth or decline longer than the 3-generation period.

Both the IUCN and COSEWIC use a threshold of  $\geq 50\%$  reduction in total mature individuals (when the causes of the decline are known, understood and reversible) as one of the criteria for threatened or vulnerable species designations (COSEWIC, 2016, IUCN, 2016). Our meta-population abundance estimate suggests that barren-ground numbers experience natural fluctuations in abundance that can result in prolonged ( $\geq 3$  generation) periods of growth or decline, including declines greater than 50%. Sine cyclic subpopulations by definition spend half of their cycle at numbers  $< 50\%$  of maximum

levels. Periods of growth and decline are asynchronous between different subpopulations which is apparent by the observed differences in cycle period lengths (Table 3.2). Subpopulations with larger amplitudes and greater maximum numbers (e.g., George River or Qamanirjuaq; Table 3.2) can dominate meta-population dynamics, obscuring any progressive changes to smaller subpopulations and imply a synchronous decline across all subpopulations when no such synchrony exists.

In addition to population abundance criteria, COSEWIC and the IUCN Redbook system may incorporate other information before making final status assessments (COSEWIC, 2016). Disturbance and habitat loss (from industrial exploration and development), over-hunting, climate change and contaminants may present a risk to barren-ground subpopulations (Adamczewski, *et al.*, 2013). For example, there is evidence that the introduction of mining roads can affect the seasonal distribution patterns and movements of barren-ground caribou, and improve access for hunters (Campbell, pers. comm., 2018). Discussing the impacts of these direct and cumulative effects in the context of species status designation for barren-ground caribou is beyond the scope of our work.

Each subpopulation has a unique combination of period and amplitude values (Table 3.2) which formed a general NW-SE gradient of increasing cycle period length and amplitude value. This trend was unexpected given the SW-NE gradient of decreasing NPP running perpendicular to the treeline (Fig. 3.6a; Fig. 3.6b). Subpopulations experiencing relatively more climate amelioration due to marine effects (e.g., Western Arctic, Qaminirjuaq, and George River subpopulations) had longer periods and greater amplitudes than more continental subpopulations (e.g., Bluenose-East, Bluenose-West and Bathurst subpopulations; [Table 3.2]).

There were no individual variables or two-way interactions of variables (subpopulation range attributes) that were correlated to subpopulation period at  $p \leq 0.05$ . Period was most correlated with amplitude ( $r = 0.547$ ;  $p = 0.082$ ; [Table 3.3]). The maximum and minimum rates of population growth (or

decline) for barren-ground caribou vary between subpopulations but typically do not exceed  $\lambda = 1.17$  and are not less than  $\lambda = 0.83$  (Gunn, 2003). Subpopulations with large amplitudes require more time for the subpopulation to increase to levels where density effects reduce vital rates causing the subpopulation to decline. Similarly, the declines take longer to occur, perhaps delaying vegetation recovery which would also extend high amplitude cycles. Our data was insufficient to propose a specific demographic herbivore-vegetation hypothesis. The relatively low correlation of period with amplitude suggests that ecological circumstances vary between subpopulations.

Many researchers (e.g., Klein, 1970; Klein 1986; Parker *et al.*, 2005; Manseau *et al.*, 1996) have suggested that the quality and volume of forage availability on the seasonal ranges of barren-ground caribou subpopulations drive population cycling. Our regression model suggested that total range and the interaction between summer range area and summer range NPP were sufficient to explain 88.5% ( $p = 0.006$ ) of the variation in amplitude for the subpopulations we considered (Table 3.4). This result supports the hypothesis that forage availability drives barren-ground caribou subpopulation cycling, but additionally suggests the forage productivity on the summer ranges is of particular importance. Ecological productivity drives barren-ground caribou cycles by setting the upper limits to amplitude and period, and also by determining recovery times through forage regeneration rates. Subpopulations with larger seasonal range areas, and higher values of ecological productivity (i.e., summer range area x summer range NPP) tend to have longer population cycles and larger amplitude values (Table 3.6; Fig. 3.4). We recommend further research into the regeneration rates of barren-ground caribou forage species on both winter and summer ranges to better understand the role of northern forage regeneration rates as the driver of barren-ground caribou subpopulation cycles.

The Porcupine subpopulation was a notable outlier with respect to the sine fit (Table 3.1; Fig 3.7) and the cluster analysis (Fig. 3.4). The Porcupine subpopulation is characterized by relatively large

total and summer range areas, and high values of summer range NPP and summer range area x summer range NPP, but has a comparatively low amplitude value (Table 3.6; Fig. 3.4). The Porcupine subpopulation was the only subpopulation sampled that did not produce a cyclic function fit that was sufficient to meet our validation criteria (Table 3.1). Porcupine caribou have shown progressive increase in abundance between consecutively sampled cycles (Fig. 3.7), but have also maintained consistent period and amplitude values (Fig. 3.7). A sine function fit with a linear increase term to the Porcupine subpopulation time-series census data produced a greater correlation coefficient ( $r = 0.944$ ,  $p < 0.01$ ) compared to the sine function fit alone ( $r = 0.868$ ,  $p < 0.01$ ). The contribution of the linear term to the regression was also significant ( $p \leq 0.01$ ). Annual increases in abundance in addition to cyclic fluctuations in numbers could be a response climate warming induced increases in annual net productivity across the Porcupine range. Alternatively, the apparent increase in maximum population abundance of Porcupine caribou may have resulted from increased selection for males in the harvest beginning in 2010 (Hegel, pers. comm. 2018).

Regional differences in ecological productivity perhaps related to local climate conditions; may influence subpopulation cycle characteristics. Each barren-ground caribou subpopulation may have (or may develop) a unique set of ecological circumstances that determine (or can modify) the period and amplitude of its individual cycle. We recommend that harvest managers and environmental impact assessments monitor period and amplitude as indicators of direct and cumulative effects impacts in the population dynamics of individual subpopulations. Additionally, perspectives on northern aboriginal food security may wish to consider that caribou abundance will fluctuate regionally due to a cyclic over-grazing, and the harmonics of relevant (local) caribou subpopulation cycles. Northern management agencies are limited in their ability to reduce the amplitude of caribou cycles by the logistic limitations to increased harvesting that are imposed by the vast and sparsely populated migratory ranges of barren-ground caribou. Reduced harvest and male-selective harvests when subpopulation numbers are low

and declining can reduce the number of years that the harvest of barren-ground is less than basic needs levels.

## CONCLUSIONS

This thesis explores what can be learned from choosing to look at barren-ground caribou population dynamics as cycles. Chapters 1 and 2 developed and tested the generality of a cycle stratified harvest model focusing on the Qamanirjuaq, Bathurst and George River subpopulations as case studies. The first manuscript developed the harvest model (program CARIBOU 1.0) using Qamanirjuaq caribou as the focal subpopulation. The second manuscript focused on examining the generality of program CARIBOU 1.0 by modifying the harvest model to fit the census demographic information of the Bathurst and George River barren-ground caribou subpopulations. The observation that we were able to produce successful models for both the Bathurst and George River subpopulations suggests that the structure of program CARIBOU 1.0 is general and robust. The third manuscript was an exploratory cycle analysis of 11 discrete migratory barren-ground caribou subpopulations that had sufficient census data to fit cyclic functions. The period of subpopulation cycles was best described by subpopulation amplitude ( $r = 0.547, p = 0.082$ ). Amplitude was best described by a subset of four biological attributes: total range area, summer range area, summer range NPP and the interaction between summer range area and summer range NPP ( $r = 0.885, p = 0.006$ ). Summer range area and summer range NPP were necessary to include because the interaction of summer range area X summer range NPP was significant. The biological range of attribute regression estimates of subpopulation amplitude showed good correspondence ( $r = 0.918, p \leq 0.001$ ) to census sine fit estimates of amplitude, and the regression estimates of population abundance showed good correspondence to observed population abundance estimates for all subpopulations ( $r = 0.894; p < 0.001$ ).

## MAJOR CONTRIBUTIONS OF EACH MANUSCRIPT

Census surveys and TEK have documented that barren-ground caribou (*Rangifer tarandus groenlandicus*) herds exhibit regular fluctuations in population abundance that we believed to be cyclic (Hemming, 1975; Couturier *et al.*, 1990; Gunn & Miller, 1986; Russell *et al.*, 2002; Gunn, 2003; Wilson & Reeder, 2005; Zalatan *et al.*, 2006; Legat *et al.*, 2014; Government of Yukon, 2015; Herbet, 2015). When subpopulations are abundant, the magnitude of the harvest is of little concern. When subpopulations begin to decline the magnitude of the harvest can extend the period of time that the subpopulation is too few to provide harvest at basic needs levels without declining further. The central contribution of the first manuscript is the development of a cycle stratified harvest model, known as program CARIBOU 1.0, that could be empirically fit to any barren-ground caribou subpopulation with sufficient data. Program CARIBOU 1.0 allows for the development of stratified (by number and trend) harvest policies that are objective and can be negotiated in a co-management setting that meet both user-needs and government conservation mandates. The second manuscript demonstrates the generality of program CARIBOU 1.0. The program can be modified to model any subpopulation of barren-ground caribou provided there is sufficient data on population numbers, harvest removals and rates of survival and calf production to validate model performance.

The third manuscript documents and quantifies barren-ground subpopulation cycles for the first time. Although the total number of barren-ground caribou (meta-population) is currently declining over a three generation period, we show that the decline is an artifact of the time interval considered for the trend analysis. A longer-term perspective that considers the natural damping and resonance of subpopulation cycles shows no trend in barren-ground caribou numbers. We did not find support for the view that some progressive general factor or factors are currently affecting all barren-ground

caribou subpopulations, but we did find evidence of a positive linear trend in the Porcupine subpopulation cycle. Comparison of the pooled estimate in 2015 from the 6 subpopulations that had both an exponential fit (COSEIC, 2016) and a sine cyclic fit (Chapter 3) showed that our 2015 meta-population cycle based estimate (517,137) closely corresponded to COSEWIC's 2015 meta-population exponential fit estimate (537,549). The short-term (3 generation) trend from the pooled exponential fit was negative, however the long-term trend of the meta-population cycle is no trend.

Correlations between subpopulation cycle parameters (period and amplitude) and various range attributes determined individually for the total range, summer range and winter ranges suggested that subpopulation period was most correlated to subpopulation amplitude ( $r = 0.547, p = 0.082$ ). Subpopulation amplitude was most highly correlated to subpopulation total range mean temperature ( $r = 0.877, p \leq 0.001$ ). Regression modeling of subpopulation amplitude as a function of the subset of biological range attributes suggested that 88.5% of the observed variance in amplitude could be explained by two variables: total range area and the interaction between summer range area and summer range net primary productivity ( $p = 0.006$ ). Inclusion of the interaction term was significant ( $p = 0.036$ ), and summer range area X summer range NPP was the only main or interaction term that resulted in a significant improvement in the correlation after total range area. Subpopulations with large range areas and greater summer range annual net primary productivity experienced the greatest fluctuations in numbers (cycle amplitude). For barren-ground caribou, population growth and population decline takes time; so larger amplitudes require longer periods. A sine curve is symmetrical, but we were not able to explain why the barren-ground caribou subpopulation decline phase was sine symmetrical to its increase phase. The biological range of attribute regression estimates of subpopulation amplitude showed good correspondence ( $r = 0.918, p \leq 0.001$ ) to census sine fit estimates of amplitude, and the regression estimates of population abundance showed good correspondence to observed population abundance estimates for all subpopulations ( $r = 0.894; p <$

0.001). The unexplained variance (especially for period) suggest that other ecological factors also play a significant role in population dynamics. It seems likely that each subpopulation would be influenced by the unique ecological circumstances of its range.

The third manuscript made the observation that the Porcupine caribou subpopulation cycle is an outlier compared to the 10 other subpopulations that were examined. The Porcupine subpopulation was the only subpopulation sampled that did not produce a cyclic function fit ( $r = 0.868$ ,  $p < 0.01$ ) that was sufficient to meet our validation criteria ( $r \geq 0.95$ ,  $p \leq 0.05$ ). The Porcupine subpopulation was also a notable outlier in terms of our cluster analysis. The Porcupine clustered together with the George River and Leaf River subpopulations, which were all characterized by relatively large total and summer range areas, and high values of summer range NPP and summer range area x summer range NPP, but the Porcupine subpopulation has a comparatively low amplitude value compared to the George River and Leaf River subpopulations. Porcupine caribou have shown a progressive increase in abundance between consecutively sampled cycles, but have also maintained consistent period and amplitude values. A sine function fit with a linear increase term to the Porcupine subpopulation time-series census data produced a greater correlation coefficient ( $r = 0.944$ ,  $p < 0.01$ ) compared to the sine function fit alone ( $r = 0.868$ ,  $p < 0.01$ ). The contribution of the linear term to the regression was also significant ( $p \leq 0.01$ ). Annual increases in abundance in addition to cyclic fluctuations in numbers could be a response climate warming induced increases in annual net productivity across the Porcupine range.

## **FUTURE RESEARCH**

A time-lag of 27 years (~1/2 cycle period) was required to sufficiently model calf production values for the Qamanirjuaq subpopulation only. We were unable to come up with a biological explanation for this. The calf survival and calf production estimates from field data do not overlap much, so some of the answer may be problems with the historical estimates. However, that view is not

consistent with the high correlations currently estimated between not-lagged model generated values and field estimates of calf production for the Bathurst and George River subpopulations.

Program CARIBOU 1.0 could be modified for other barren-ground caribou subpopulations and sustainable harvest options could be developed for those subpopulations as a decision support tool to assist co-management decisions. Consultations between communities and/or jurisdictions that have stakeholder or management authority responsibilities for barren-ground subpopulations might be facilitated through exploring the long-term implications of various harvest options for subpopulation dynamics including sustainable removal rates. The hypothesis that slow forage regeneration rates on the summer ranges of barren-ground caribou subpopulations are the main driver for population cycling could be tested through field studies on summer range forage communities, or the development and analysis of a more targeted set of remotely sensed data. Our analysis of the range attributes that influence barren-ground caribou subpopulation cycles was descriptive rather than mechanistic. It is curious that only the Porcupine subpopulation showed a progressive change in population numbers. If this increase in numbers is related to climate warming, comparisons to other subpopulations that continue to cycle without any apparent change in mean numbers might provide some insight into how climate warming affects barren-ground caribou population dynamics. Continued and improved monitoring of period and amplitude by increased frequency of census estimates may prove to be useful as an indicator of the direct and cumulative impacts to individual barren-ground caribou subpopulations. We identified but were unable to explain an observed half-cycle time-lagged relationship for Qamanirjuaq calf production relative to Qamanirjuaq calf survival. We described but could not explain the sine symmetry for the increase and decline phases of barren-ground caribou cycles.

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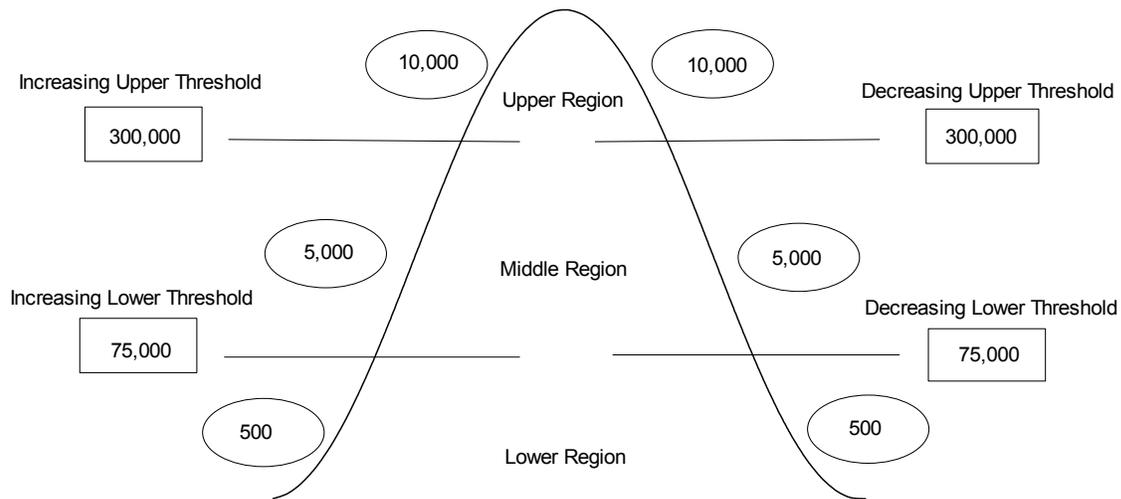
## TABLES

Table 1.1. Census estimates for the Qamanirjuaq caribou total subpopulation numbers, calf production rates, and calf (age 0) survival rates are time referenced to the calving ground census in early June and reported by year. Calf production rates were calculated as number of calves divided by the total number of adult (age 2+) females. Survival estimates from 1979-1985 were referenced only as “personal communications” and not included because the reliability of the estimates is uncertain.

Year	Pop. Estimate (N)	SE	Calf Production	Calf Survival
1968	60,000 <sup>3</sup>		0.545 <sup>2</sup>	
1976	50,000 <sup>3</sup>		0.546 <sup>2</sup>	
1977	44,000 <sup>1</sup>		0.523 <sup>2</sup>	
1980			0.521 <sup>2</sup>	
1982	170,000 <sup>3</sup>			
1984	225,000 <sup>3</sup>	65,000 <sup>3</sup>		
1985			0.557 <sup>2</sup>	
1986	270,000 <sup>3</sup>	140,000 <sup>3</sup>		
1988	221,000 <sup>4</sup>	72,000 <sup>4</sup>		
1993				0.47 <sup>2</sup>
1994	495,665 <sup>4</sup>	105,426 <sup>4</sup>	0.679 <sup>2</sup>	0.49 <sup>2</sup>
1995				0.48 <sup>2</sup>
1996				0.42 <sup>2</sup>
1999				0.3 <sup>2</sup>
2003				0.27 <sup>2</sup>
2006				0.17 <sup>2</sup>
2007				0.19 <sup>2</sup>
2008	348,661 <sup>4</sup>	44,861 <sup>4</sup>	0.701 <sup>2</sup>	0.18 <sup>2</sup>
2014	264,718 <sup>4</sup>	44,084 <sup>4</sup>		

<sup>1</sup>Heard, 1981; <sup>2</sup>Cambell *et al.*, 2010; <sup>3</sup>BQCMB, 2014; <sup>4</sup>Campbell *et al.*, 2015

Table 1.2. The final cyclic CC model parameter inputs for Qamanirjuaq caribou harvest simulations project file using program CARIBOU 1.0. The maximum survival and calf production rates for the Qamanirjuaq barren-ground caribou subpopulation are reduced by density-effects as modulated by the CC and KS parameters in program CARIBOU 1.0. A sine cyclic population density index (CC) is specified with a period of 53-years. The density modified demographic rates are limited to no less than 0.1 of the maximum value specified. All harvest simulations assume cows produce a single calf annually and begin producing at adult rates by age 2. The maximum age for these simulations is 16.



Model Parameter	Maximum Rate ( $R_{max}$ )	Carrying Capacity (CC)	Minimum CC Proportion	Shape Factor (KS)	Period	Min. Proportion Generated by Density-Effects	Lag-Time (Years)
Calf Production	0.98	800,000	0.35	0.7	53	0.1	27
Calf Survival	0.96	575,000	0.055	0.4	53	0.1	-
Adult Survival	0.97	6,750,000	0.055	0.25	53	0.1	-

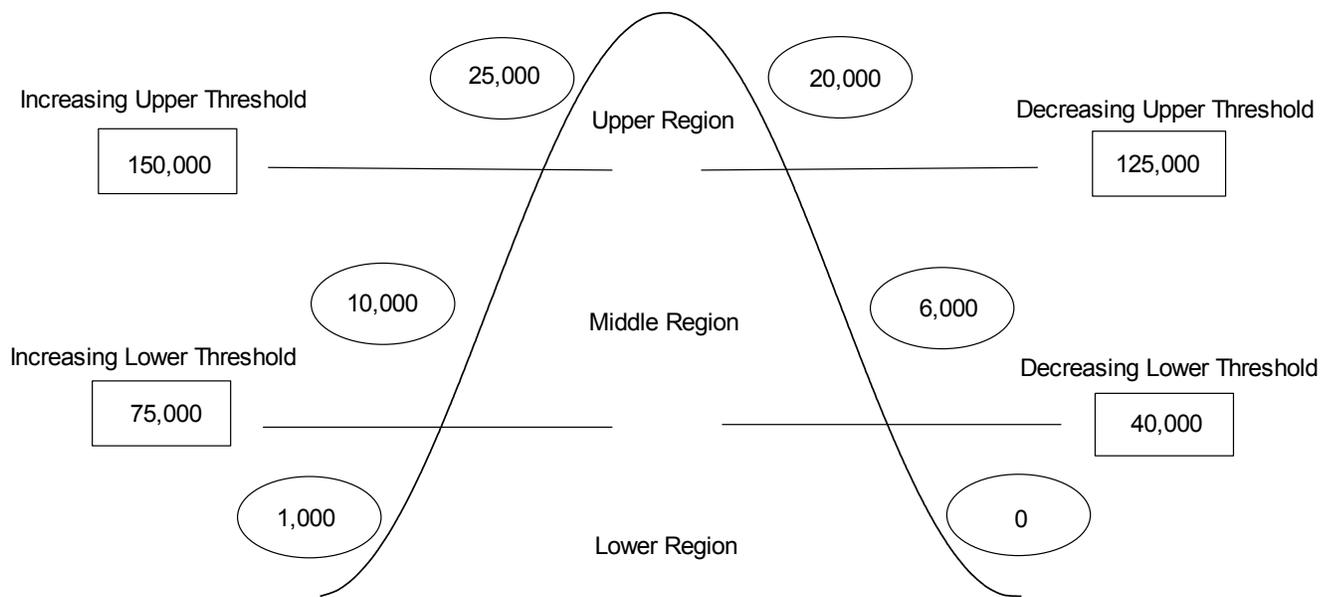
Table 1.3. Linear, exponential, logistic, sine and wavelet functions were fit to Qamanirjuaq time-series census population estimates. Our validation criteria required the functions to produce statistically significant ( $p \leq 0.05$ ) correlation coefficients ( $r$ ) of 0.95 or greater and a failure to reject the Shapiro-Wilk (S-W) test for normality of residuals ( $p \leq 0.05$ ). Only the sine function met the required validation criteria. The sine function produced a cycle with a period of 53 years (SE = 3.3) and an amplitude of 230,897 (SE = 25,872).

Function	Correlation Coefficient ( $r$ )	Significance ( $p$ )	S-W test ( $p$ )
Linear	0.692	0.027	0.217
Exponential	0.609	0.059	0.103
Logistic	0.891	0.01	0.082
Sine	0.961	<0.001	0.530
Wavelet	0.915	0.002	0.351

Table 1.4. Temporal correlations between Qamanirjuaq caribou census population numbers, calf survival rates, and calf production rates to model output population numbers, calf survival rates, and calf production rates from the lag-time and sine cyclic population density index (CC) models. The best lag-time model did not meet our specified validation criteria ( $r \geq 0.95$ ) in terms of significant ( $p \leq 0.05$ ) temporal correlations to both population numbers and calf production rates. The cyclic CC model produced acceptable ( $r \geq 0.95$ ) significant temporal correlations to population numbers, calf survival, and calf production rates. However the relationship of calf production was time lagged 27 years (~1/2 cycle period) to generate correspondence to estimated (field data) calf production rates. We employed the cyclic CC model for all harvest simulations.

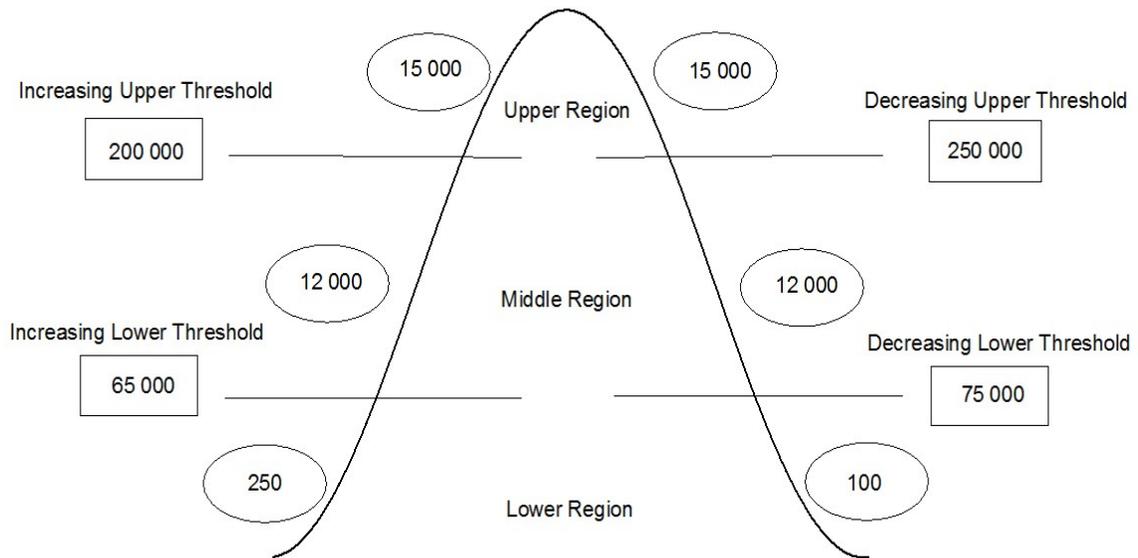
<b>Model</b>	<b>Population N</b>	<b>Calf Survival</b>	<b>Calf Production</b>
Lag-time	0.904 ( $p < 0.001$ )	0.958 ( $p < 0.001$ )	0.794 ( $p = 0.033$ )
Cyclic CC	0.950 ( $p < 0.001$ )	0.962 ( $p < 0.001$ )	0.964 ( $p < 0.001$ )

Table 1.5. The maximum removals harvest strategy developed for the Qamanirjuaq caribou subpopulation using program CARIBOU 1.0. The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the total number of harvest removals over the 53-year cycle period.



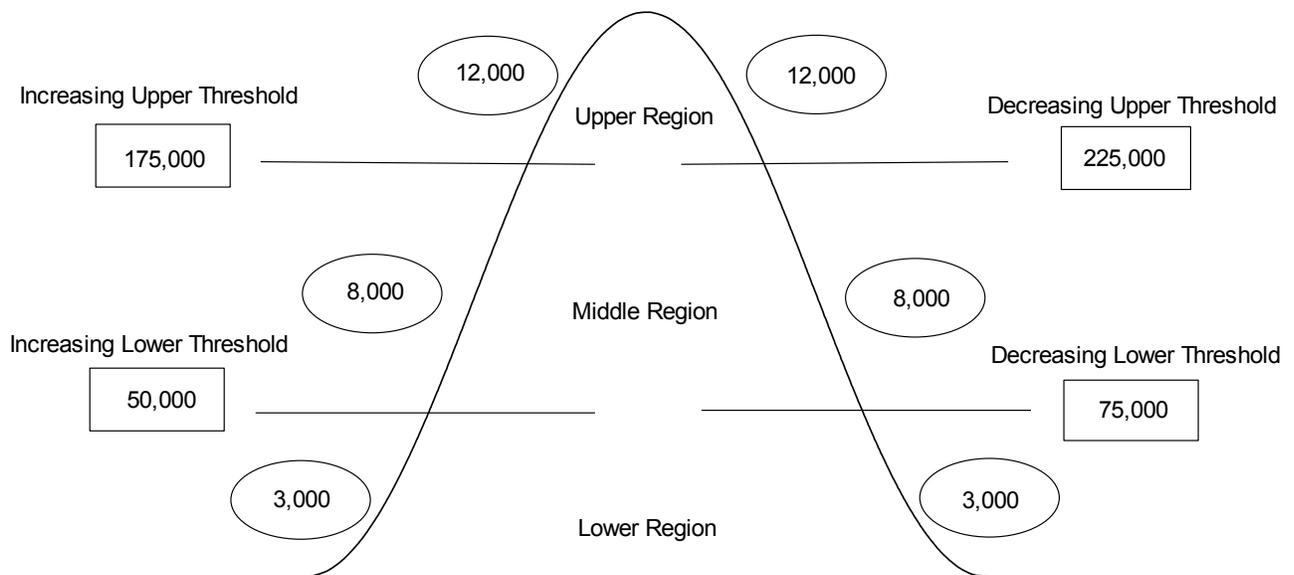
Summary Parameter	Value
Simulated Cycle Minimum	30,764
Simulated Cycle Maximum	428,801
Total Harvest Removals per Cycle	720,000
# of Years < 12,000 removals/year	31
Shannon-Weiner Evenness Index	0.736

Table 1.6. The minimum restrictions harvest strategy developed for the Qamanirjuaq caribou subpopulation using program CARIBOU 1.0. Restrictions are defined as the level of annual harvest that would inhibit users from meeting their basic minimum needs (i.e., 12,000/year). The four threshold values (boxes) are given in population numbers. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. The user-defined harvest removal strata and threshold values were optimized using trial and error to minimize the number of years with a harvest less than 12,000/year.



Summary Parameter	Value
Simulated Cycle Minimum	36,369
Simulated Cycle Maximum	491,896
Total Harvest Removals per Cycle	503,500
# of Years < 12,000 removals/year	17
Shannon-Weiner Evenness Index	0.789

Table 1.7. The evenness harvest strategy developed for the Qamanirjuaq caribou subpopulation using program CARIBOU 1.0. 'Evenness' aims to minimize the difference between the six annual harvest strata and was evaluated using the Shannon-Weiner Evenness Index (Beals, *et al.*, 2000). The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the evenness index.



Summary Parameter	Value
Simulated Cycle Minimum	22,835
Simulated Cycle Maximum	446,292
Total Harvest Removals per Cycle	407,000
# of Years < 12,000 removals/year	37
Shannon-Weiner Evenness Index	0.930

Table 2.1a. Census estimates for the Bathurst caribou total subpopulation numbers, calf production rates, and calf (age 0) survival rates are time-referenced to the calving ground census in early June and reported by year. Calf production was defined as the number of breeding females \* 0.72 (assumed pregnancy rate) divided the total number of females in the subpopulation (Boulanger *et al.*, 2017) The sine function fit to the population estimates produced a cycle with a period of 42 (SE = 3.43) years and an amplitude of 203,081 (SE = 24,520).

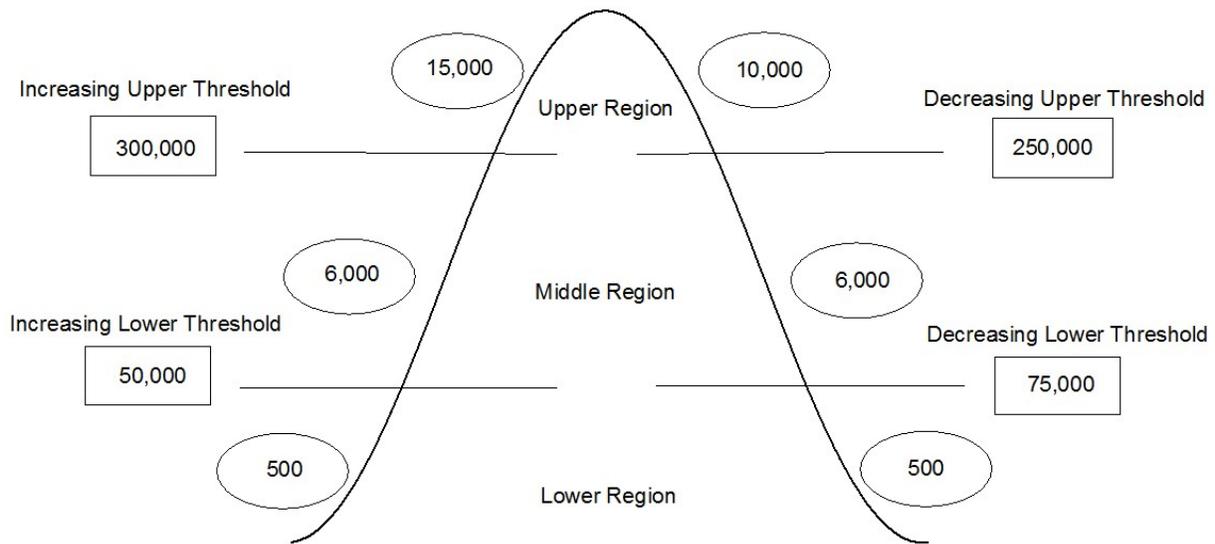
Year	Pop. Estimate (N)	SE	Calf Production	Calf Survival
1977	160,000 <sup>2</sup>			
1978	127,000 <sub>2</sub>			
1979	110,000 <sup>2</sup>			
1980	140,000 <sup>2</sup>			
1982	180,000 <sup>2,3</sup>			
1984	390,000 <sup>2,3</sup>	60,000 <sup>2,3</sup>		
1985				0.32 <sup>1</sup>
1986			0.516 <sup>4</sup>	
1987	472,000 <sup>2,3</sup>	70,000 <sup>2,3</sup>		0.37 <sup>1</sup>
1989				0.34 <sup>1</sup>
1990	350,000 <sup>2,3</sup>	70,000 <sup>2,3</sup>		0.32 <sup>1</sup>
1991			0.519 <sup>4</sup>	0.44 <sup>1</sup>
1992				0.25 <sup>1</sup>
1993				0.44 <sup>1</sup>
1994				0.25 <sup>1</sup>
1995				0.18 <sup>1</sup>
1996	350,000 <sup>2,3</sup>	70,000 <sup>2,3</sup>	0.517 <sup>4</sup>	
2001				0.25 <sup>1</sup>
2002				0.16 <sup>1</sup>
2003	190,000 <sup>2,3</sup>	30,000 <sup>2,3</sup>	0.507 <sup>4</sup>	0.22 <sup>1</sup>
2004				0.16 <sup>1</sup>
2006	120,000 <sup>2,3</sup>	20,000 <sup>2,3</sup>	0.554 <sup>4</sup>	
2009	40,000 <sup>1,2</sup>		0.614 <sup>4</sup>	
2012			0.574 <sup>4</sup>	
2013	20,000 <sup>2</sup>			
2015	20,000 <sup>3</sup>			

<sup>1</sup>Gunn *et al.*, 2005; <sup>2</sup>Gunn *et al.*, 2010; <sup>3</sup>GNWT, 2015; <sup>4</sup>Boulanger *et al.*, 2017

Table 2.1b. Census estimates for the George River caribou total subpopulation numbers estimates, calf production rates, and calf (age 0) survival rates are time-referenced and reported by year. Population estimates, calf production estimates and calf survival estimates were taken from Bergerud *et al.*, (2008). The sine function fit to the population estimates produced a cycle with a period of 45 (SE = 2.4) years and an amplitude of 354,413 (SE = 21,653.5).

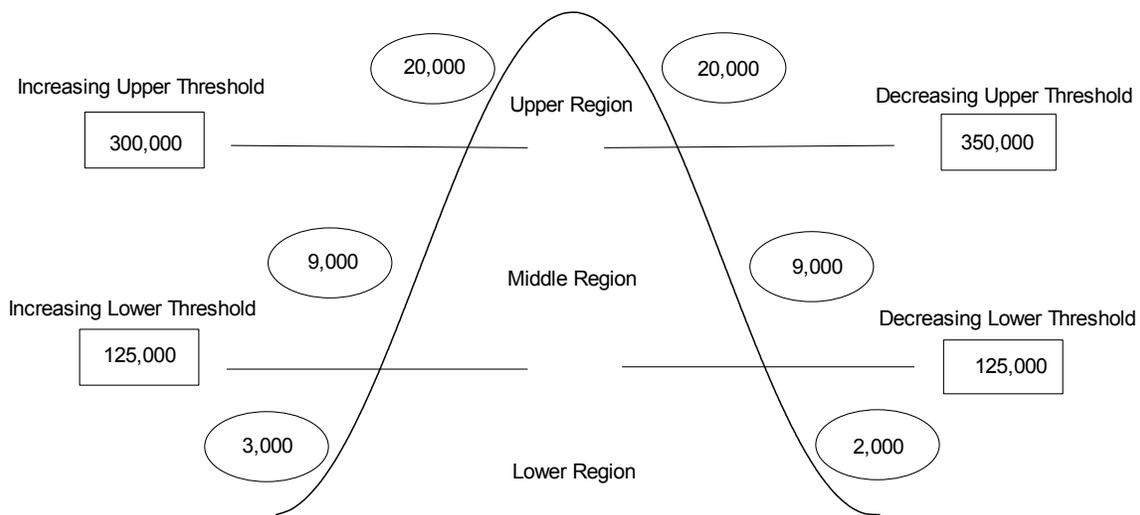
Year	Pop. Estimate (N)	SE	Calf Production	Calf Survival
1973	105,000			0.6
1974				0.338
1975	205,000			0.28
1976	176,000	52,800	1.0	0.414
1977			0.943	0.36
1978			0.889	0.308
1979				0.293
1980	400,000	100,000	0.863	0.172
1981				0.339
1982	375,000	80,000	0.935	0.442
1983				0.321
1984	625,000	150,000	0.684	
1985			0.856	0.211
1986			0.6	0.182
1987			0.755	0.157
1988	650,000	200,000	0.625	0.169
1989			0.612	0.114
1990			0.591	0.095
1991			0.783	0.124
1992			0.755	0.94
1993	775,000		0.664	
2001	385,000			
2010	74,000			
2012	27,000	10,000		
2014	14,200	700		
2016	8,938			

Table 2.2a. The final cyclic CC and KS model parameter and harvest inputs for Bathurst caribou harvest simulations project file using program CARIBOU 1.0. Simulation model validation protocol consisted of two steps discussed in Chapter 1. The maximum survival and calf production rates for the Bathurst barren-ground caribou subpopulation are reduced by density-effects as modulated by the CC and KS parameters in program CARIBOU 1.0. A sine cyclic population density index (CC) is specified with a period of 42-years. The density modified demographic rates are limited to no less than 0.1 of the maximum value specified. All harvest simulations assume cows produce a single calf annually and begin producing at adult rates by age 2+. The maximum age for these simulations is 16.



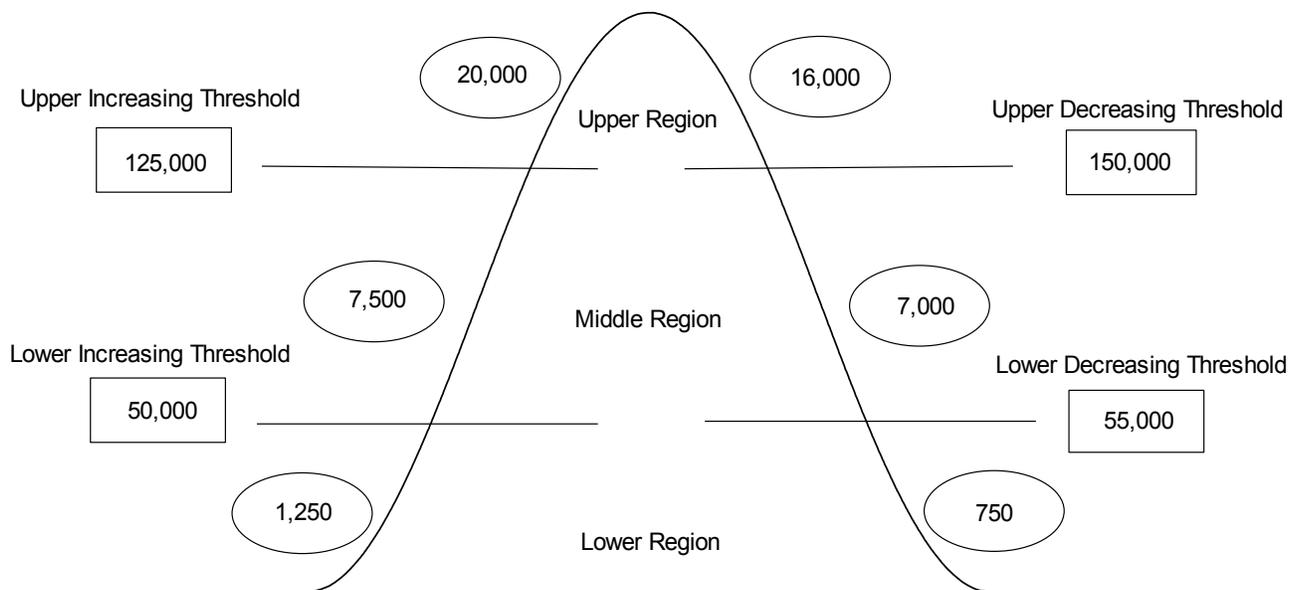
Model Parameter	Maximum Rate ( $R_{max}$ )	Carrying Capacity (CC)	Minimum CC Proportion	Shape Factor (KS)	Period	Min. Proportion Generated by Density-Effects
Calf Production	0.97	1,000,000	0.35	0.85	42	0.1
Calf Survival	0.9	800,000	0.05	0.45	42	0.15
Adult Survival	0.98	3,750,000	0.05	0.4	42	0.15

Table 2.2b. The final cyclic CC and KS model parameter and harvest inputs for George River caribou harvest simulations project file using program CARIBOU 1.0. Simulation model validation protocol consisted of two steps discussed in Chapter 1. The maximum survival and calf production rates for the George River barren-ground caribou subpopulation are reduced by density-effects as modulated by the CC and KS parameters in program CARIBOU 1.0. A sine cyclic population density index (CC) is specified with a period of 45-years. The density modified demographic rates are limited to no less than 0.05 of the maximum value specified. All harvest simulations assume cows produce a single calf annually and begin producing at adult rates by age 2. The maximum age for these simulations is 16.



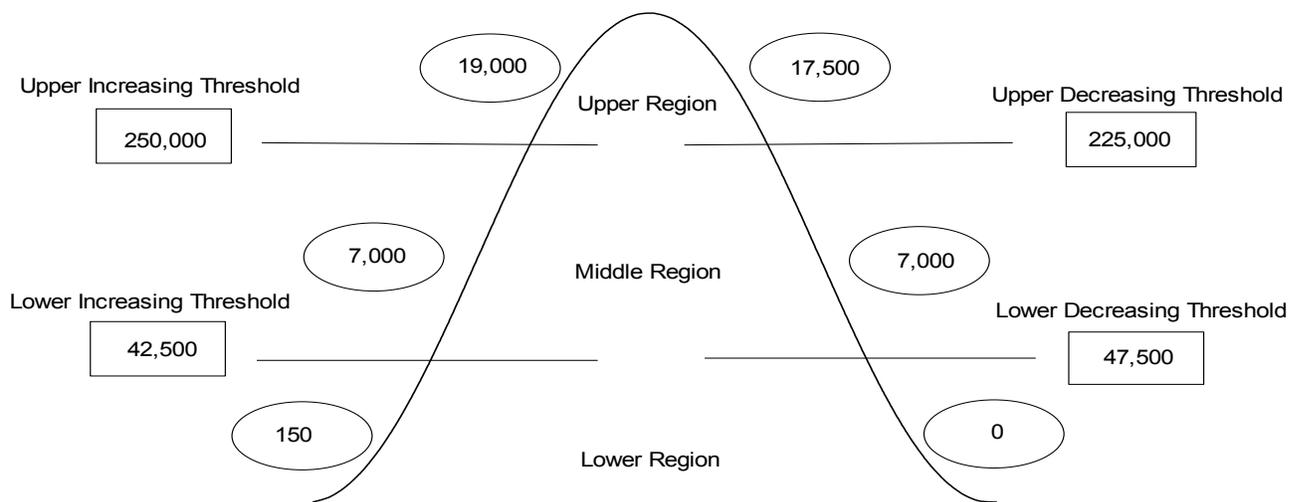
Model Parameter	Maximum Rate ( $R_{max}$ )	Carrying Capacity (CC)	Minimum CC Proportion	Shape Factor (KS)	Period	Min. Proportion Generated by Density-Effects
Calf Production	0.96	4,000,000	0.85	0.45	45	0.15
Calf Survival	0.95	1,000,000	0.055	0.55	42	0.05
Adult Survival	0.98	5,500,000	0.055	0.45	42	0.05

Table 2.3a. The maximum removals harvest strategy developed for the Bathurst caribou subpopulation using program CARIBOU 1.0. The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the total number of harvest removals over the 42-year cycle period.



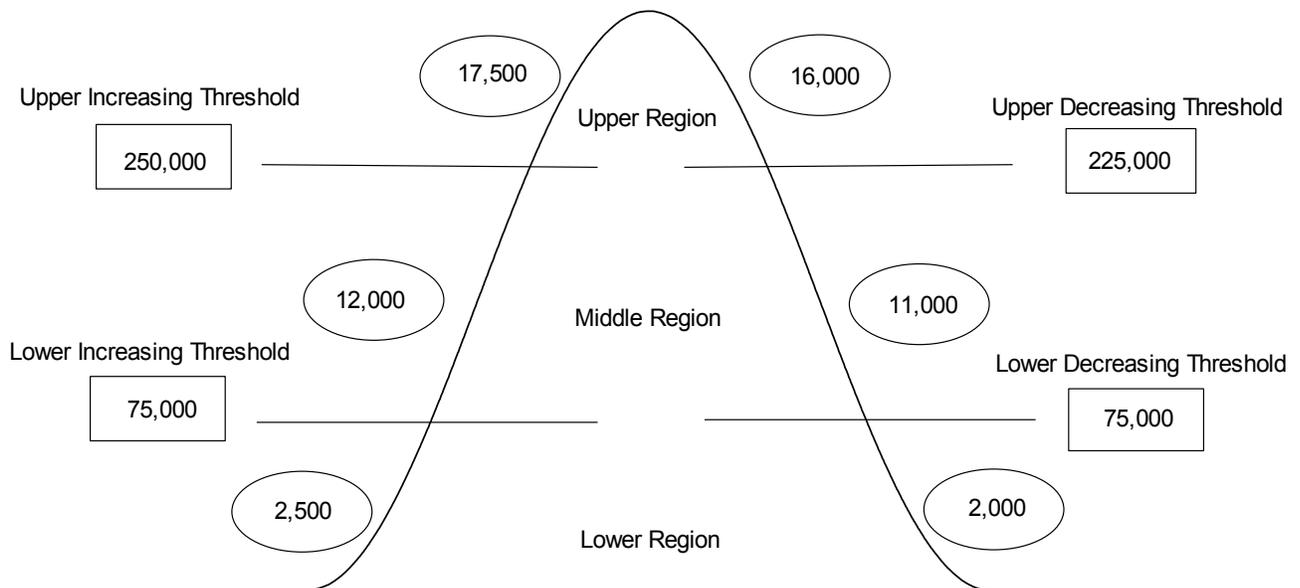
Summary Parameter	Value
Simulated Cycle Minimum	35,848
Simulated Cycle Maximum	325,435
Total Harvest Removals per Cycle	533,500
# of Years < 7,000 removals/year	8
Shannon-Weiner Evenness Index	0.795

Table 2.3b. The minimum restrictions harvest strategy developed for the Bathurst caribou subpopulation using program CARIBOU 1.0. Restrictions are defined as the level of annual harvest that would inhibit users from meeting their basic needs (i.e., >7,000/year). The four threshold values (boxes) are given in population numbers. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. The user-defined harvest removal strata and threshold values were optimized using trial and error to minimize the number of years with a harvest less than 7,000/year.



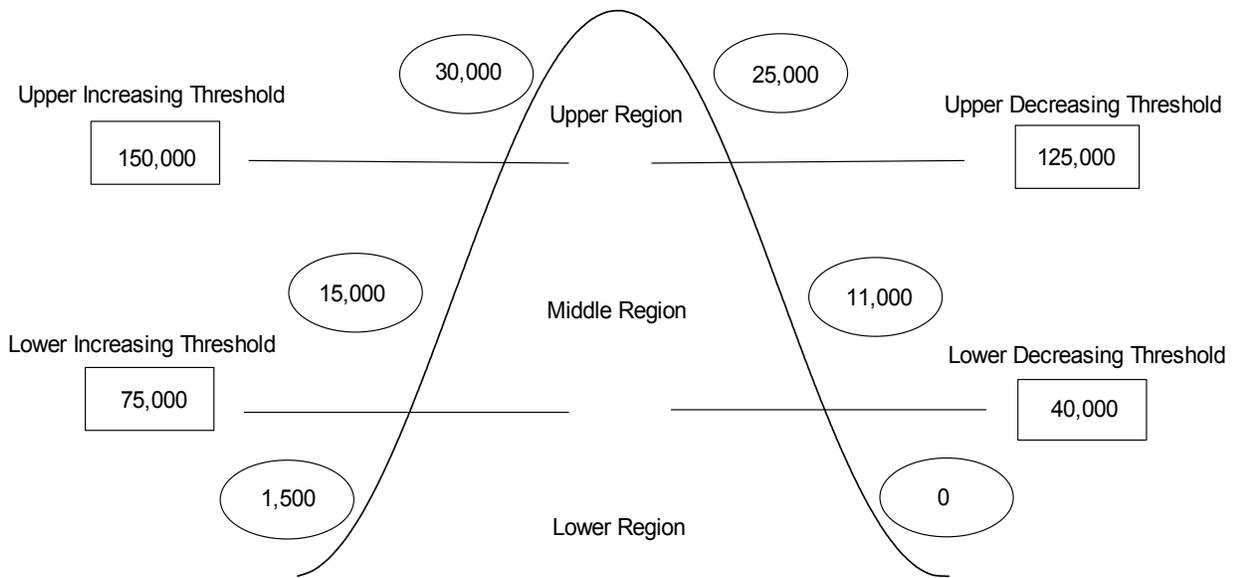
Summary Parameter	Value
Simulated Cycle Minimum	35,994
Simulated Cycle Maximum	407,148
Total Harvest Removals per Cycle	428,650
# of Years < 7,000 removals/year	6
Shannon-Weiner Evenness Index	0.725

Table 2.3c. The evenness harvest strategy developed for the Bathurst caribou subpopulation using program CARIBOU 1.0. 'Evenness' aims to minimize the difference between the six annual harvest strata and was evaluated using the Shannon-Weiner Evenness Index (Beals, *et al.*, 2000). The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the evenness index.



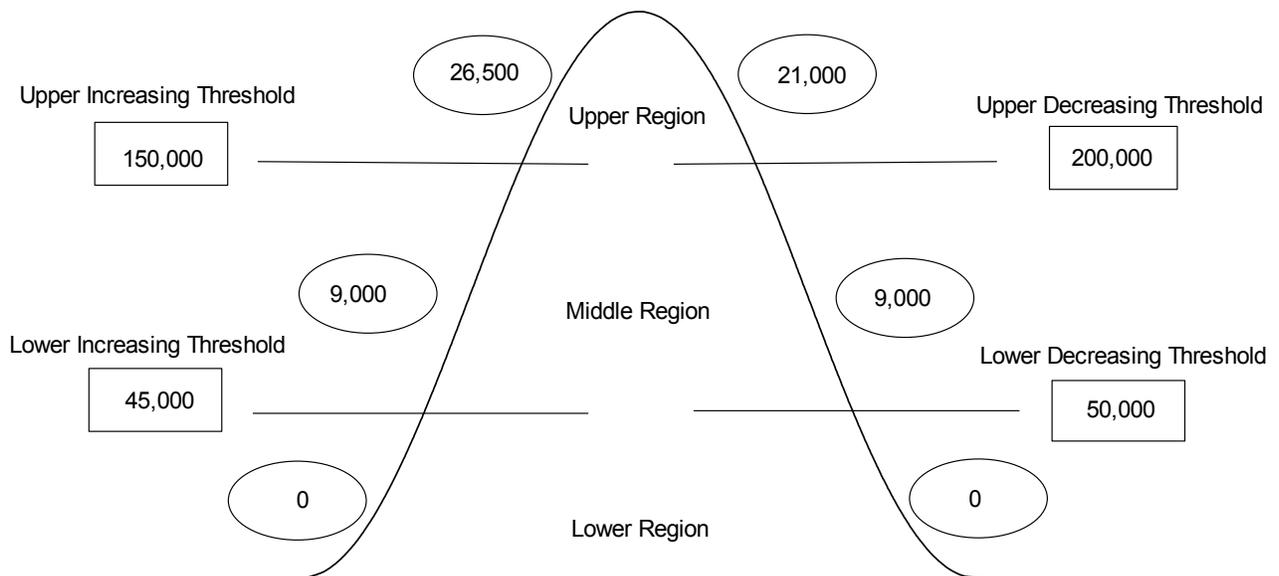
Summary Parameter	Value
Simulated Cycle Minimum	31,571
Simulated Cycle Maximum	397,955
Total Harvest Removals per Cycle	464,500
# of Years < 7,000 removals/year	13
Shannon-Weiner Evenness Index	0.882

Table 2.4a. The maximum removals harvest strategy developed for the George River caribou subpopulation using program CARIBOU 1.0. The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the total number of harvest removals over the 45-year cycle period.



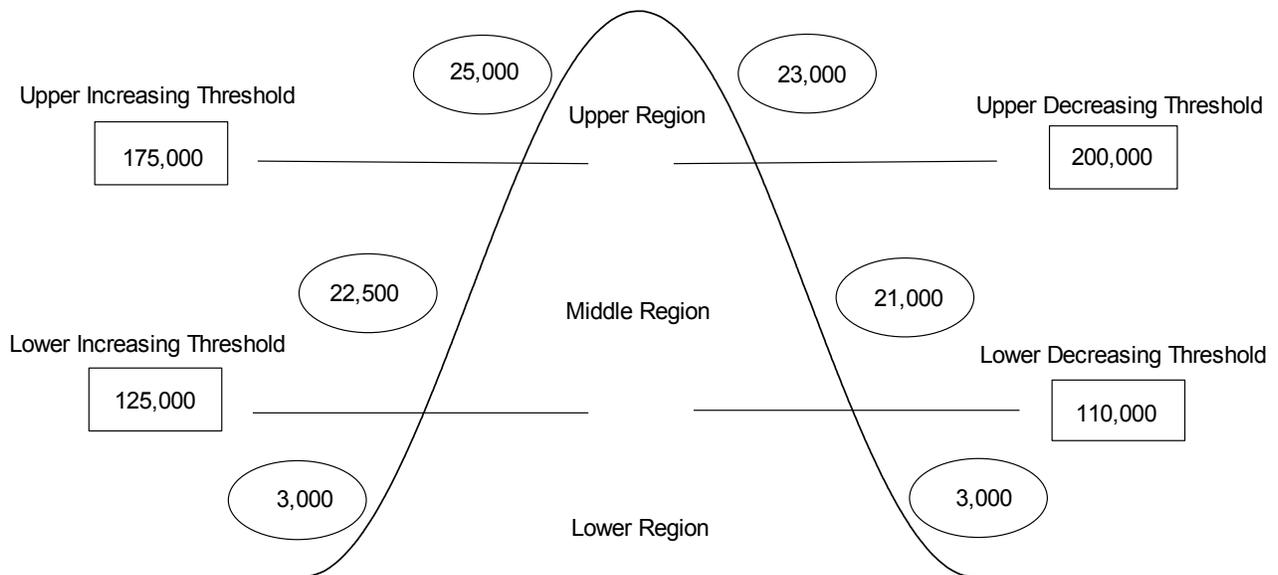
Summary Parameter	Value
Simulated Cycle Minimum	30,313
Simulated Cycle Maximum	520,619
Total Harvest Removals per Cycle	978,000
# of Years < 9,000 removals/year	9
Shannon-Weiner Evenness Index	0.770

Table 2.4b. The minimum restrictions harvest strategy developed for the George River caribou subpopulation using program CARIBOU 1.0. Restrictions are defined as the level of annual harvest that would inhibit users from meeting their basic needs (i.e., >9,000/year). The four threshold values (boxes) are given in population numbers. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. The user-defined harvest removal strata and threshold values were optimized using trial and error to minimize the number of years with a harvest less than 9,000/year.



Summary Parameter	Value
Simulated Cycle Minimum	38,028
Simulated Cycle Maximum	603,938
Total Harvest Removals per Cycle	748,000
# of Years < 9,000 removals/year	6
Shannon-Weiner Evenness Index	0.712

Table 2.4c. The evenness harvest strategy developed for the George River caribou subpopulation using program CARIBOU 1.0. 'Evenness' aims to minimize the difference between the six annual harvest strata and was evaluated using the Shannon-Weiner Evenness Index (Beals, *et al.*, 2000). The four threshold values (boxes) are given in population numbers. Threshold values and the number of annual removals per cycle segment (ovals) are user-defined. Summary parameters were reported only after the harvested cycle became stable. If the specified harvest regime was not sustainable (i.e., collapsed the cycle) an error condition was returned and summary parameters were not reported. The user-defined harvest removal strata and threshold values were optimized using trial and error to maximize the 'evenness' index.



Summary Parameter	Value
Simulated Cycle Minimum	35,589
Simulated Cycle Maximum	634,915
Total Harvest Removals per Cycle	776,500
# of Years < 9,000 removals/year	17
Shannon-Weiner Evenness Index	0.865

Table 3.1. Linear, exponential, logistic, sine, and wavelet functions were fit to the 11 barren-ground subpopulation with  $\geq 6$  census population abundance estimates using program SigmaPlot 14.0. Our validation criteria required the functions to produce statistically significant ( $p \leq 0.05$ ) correlation coefficients ( $r$ ) of 0.95 or greater to either the sine or wavelet functions and a failure to reject the Shapiro-Wilk (S-W) test for normality of residuals ( $p \leq 0.05$ ). The Leaf River, Bluenose-East, Bluenose-West, Cape Bathurst and Teshekpuk Lake subpopulations did not have a sufficient number of time-series population number estimates to provide a wavelet function fit ( $\geq 8$  population abundance estimates). Only the Porcupine subpopulation did not meet our validation criteria, however the sine function did produce the greatest correlation coefficient to the Porcupine time-series census data. We accepted each subpopulation as sine cyclic because of the minimal difference between correlation coefficients of the sine and wavelet functions, and to increase the consistency of period and amplitude estimates.

Function	George River			Leaf River			Qamanirjuaq			Bathurst		
	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )
Linear	0.148	0.613	0.189	0.579	0.173	0.359	0.692	0.027	0.217	0.409	0.147	0.025
Exponential	0.514	0.06	0.157	0.037	0.937	0.697	0.614	0.059	0.103	0.553	0.040	0.258
Logistic	0.554	0.04	0.457	0.795	0.33	0.132	0.891	0.01	0.082	0.685	0.202	0.955
Sine	0.859	<0.001	0.657	0.987	<0.001	0.446	0.961	<0.001	0.530	0.934	<0.001	0.143
Wavelet	0.957	<0.001	0.689	-	-	-	0.915	0.002	0.351	0.958	<0.001	0.483
Function	Bluenose-East			Bluenose-West			Cape Bathurst			Porcupine		
	$R$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )
Linear	0.269	0.662	0.187	0.911	0.002	0.562	0.996	<0.001	0.405	0.868	<0.001	0.974
Exponential	0.356	0.556	0.612	0.552	0.156	0.139	0.569	0.183	0.112	0.704	0.007	0.001
Logistic	0.685	0.202	0.955	0.987	<0.001	0.182	0.992	<0.001	0.705	0.759	0.003	0.688
Sine	1.0	<0.001	0.520	0.991	<0.001	0.754	0.996	<0.001	0.405	0.868	<0.001	0.974
Wavelet	-	-	-	-	-	-	-	-	-	0.820	0.001	0.224
Function	Central Arctic			Teshekpuk Lake			Western Arctic					
	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )	$r$	$p$	S-W ( $p$ )			
Linear	0.734	0.002	0.008	0.858	<0.001	0.334	0.303	0.314	0.087			
Exponential	0.202	0.471	0.058	0.324	0.304	0.722	0.273	0.367	0.399			
Logistic	0.805	<0.001	0.188	0.895	<0.001	0.284	0.772	0.002	0.404			
Sine	0.798	<0.001	0.653	0.919	<0.001	0.696	0.972	<0.001	0.062			
Wavelet	0.960	<0.001	0.609	-	-	-	0.986	<0.001	0.744			

Table 3.2. The period and amplitude estimates of 11 barren-ground caribou subpopulations based on the equations of the sine cycle fits. The sine function produced the greatest correlation coefficient to 7 subpopulations. The wavelet function produced the greatest correlation coefficient to 4 subpopulations. Discrimination between the sine and wavelet function fits based on statistical significance and observed correlations was difficult because the difference between function fits was minimal. We classified all 11 subpopulations as sine cyclic to increase the consistency of period and amplitude estimates.

<b>Subpopulation</b>	<b>Period</b>	<b>SE</b>	<b>Amplitude</b>	<b>SE</b>
George River	45	2.4	354,413	21,653.5
Leaf River	46	2	297,784	26,124.2
Qamanirjuaq	53	3.3	230,897	25,872.4
Bathurst	42	3.4	203,081	24,520.3
Bluenose-East	26	0.13	71,723	354.8
Bluenose-West	34	1.9	52,408	3,942
Cape Bathurst	30	1.7	8,394	447.5
Porcupine	26	1.5	42,795	7,255.6
Central Arctic	49	10	21,400	5,084.5
Teshkepkuk Lake	43	8.3	20,905	3,260.2
Western Arctic	59	16.3	240,953	85,188

Table 3.3. A correlation matrix of cycle characteristics (period length and amplitude) and subpopulation range attributes. Our criteria described significant correlations as  $p \leq 0.05$ . Period was not significantly correlated with any range attributes, but amplitude was the best single predictor of period ( $r = 0.547$ ;  $p = 0.082$ ). Amplitude was significantly correlated to tundra percentage, total range area, summer range area, winter range area, and total range LST, with total range LST being the single best predictor of amplitude ( $r = 0.877$ ;  $p < 0.001$ ).

		Period	Amplitude	<sup>1</sup> NDVI	Tundra %	Total Range Area	Summer Range Area	Winter Range Area	<sup>2</sup> Total Range NPP	Summer Range NPP	Winter Range NPP	<sup>3</sup> Total Range LST	Summer Range LST	Winter Range LST
Period	<b>R</b>	1	.547	-.009	-.098	.246	.181	.224	.185	-.048	.237	.353	-.203	.010
	<b>Sig.</b>	-	.082	.978	.774	.466	.594	.507	.587	.888	.483	.287	.549	.976
Amplitude	<b>r</b>	.547	1	.531	-.705	.860	.698	.819	.495	.067	.386	.877	.482	.560
	<b>Sig.</b>	.082	-	.093	.015	.001	.017	.002	.122	.844	.242	.000	.133	.073
NDVI	<b>r</b>	-.009	.531	1	-.190	.428	.530	.335	-.022	-.239	.118	.358	.028	.224
	<b>Sig.</b>	.978	.093	-	.575	.189	.093	.314	.948	.478	.730	.280	.934	.508
Tundra %	<b>r</b>	-.098	-.705	-.190	1	-.764	-.473	-.793	-.588	-.203	-.394	-.773	-.547	-.609
	<b>Sig.</b>	.774	.015	.575	-	.006	.142	.004	.074	.550	.231	.005	.082	.047
Total Range Area	<b>r</b>	.246	.860	.428	-.764	1	.807	.967	.535	.174	.379	.872	.621	.448
	<b>Sig.</b>	.466	.001	.189	.006	-	.003	.000	.090	.608	.250	.000	.041	.167
Summer Range Area	<b>r</b>	.181	.698	.530	-.473	.807	1	.633	.475	.290	.466	.790	.637	.568
	<b>Sig.</b>	.594	.017	.093	.142	.003	-	.036	.140	.387	.148	.004	.035	.068
Winter Range Area	<b>r</b>	.224	.819	.335	-.793	.967	.633	1	.466	.080	.262	.792	.538	.335
	<b>Sig.</b>	.507	.002	.314	.004	.000	.036	-	.149	.815	.437	.004	.088	.314
Total Range NPP	<b>r</b>	.185	.495	-.022	-.558	.535	.475	.466	1	.809	.940	.763	.618	.519
	<b>Sig.</b>	.587	.122	.948	.074	.090	.140	.149	-	.003	.000	.006	.043	.102
Summer Range NPP	<b>r</b>	-.048	.067	-.239	-2.03	.174	.290	.080	.809	1	.785	.422	.635	.438
	<b>Sig.</b>	.888	.844	.478	.550	.608	.387	.815	.003	-	.004	.197	.036	.178
Winter Range NPP	<b>r</b>	.237	.386	.118	-.394	.379	.466	.262	.940	.785	1	.675	.521	.533
	<b>Sig.</b>	.287	.242	.730	.231	.250	.148	.437	.000	.004	-	.023	.100	.092
Total Range LST	<b>r</b>	.353	.877	.358	-.773	.872	.790	.792	.793	.422	.675	1	.675	.680
	<b>Sig.</b>	.287	.000	.280	.005	.000	.004	.004	.006	.197	.023	-	.023	.021
Summer Range LST	<b>r</b>	-.203	.482	.028	-.547	.621	.637	.538	.618	.635	.521	.675	1	.785
	<b>Sig.</b>	.549	.133	.934	.082	.041	.035	.088	.043	.036	.100	.023	-	.004
Winter Range LST	<b>r</b>	.010	.560	.224	-.609	.448	.568	.335	.519	.438	.533	.680	.785	1
	<b>Sig.</b>	.976	.073	.508	.047	.167	.068	.314	.102	.178	.092	.021	.004	-

<sup>1</sup>NDVI (Normalized Difference Vegetation Index), <sup>2</sup>NPP (Net Primary Production), <sup>3</sup>LST (Land Surface Temperature)

Table 3.4. Amplitude was best described by a subset of biological range attributes that included total range area, summer range area, summer range net primary production, and the interaction of summer range area x summer range net primary production. The model explained 88.5% of the variation in amplitude, was significant ( $p = 0.006$ ) and was able to produce regression estimates of amplitude that met our required criteria producing a significant correlation coefficient to census sine fit estimates of amplitude ( $r = 0.918$ ,  $p \leq 0.001$ ). Summer range area and summer range NPP main effects contributed little to the final model, and were only included because the interaction effect (summer range area X summer range NPP) was significant. There was no subset of range attributes that could significantly model period.

<b>Effect</b>	<b>R<sup>2</sup></b>	<b>Sig.</b>	<b>R<sup>2</sup> Change</b>	<b>Sig. of Change</b>
Total Range Area	0.739	0.001	-	-
Total Range Area + Summer Range Area	0.739	0.005	0	0.975
Total Range Area + Summer Range Area + Summer Range NPP	0.747	0.017	0.008	0.656
Total Range Area + Summer Range Area + Summer Range NPP + Summer Range Area x Summer Range NPP	0.885	0.006	0.138	0.036

Table 3.5. We employed the two-step cluster analysis method in IBM SPSS statistics to cluster subpopulations based on values of total range area, and the interaction of summer range area x summer range NPP. Cluster #1 consisted of the George River, Leaf River and Porcupine subpopulations and was characterized by larger total range areas and higher values of summer range area x summer range NPP. Cluster #2 consisted of the Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Central Arctic, Teshekpuk Lake and Western Arctic subpopulations and was characterized by smaller total range areas and lower values of summer range area x summer range NPP values.

<b>Range Attribute</b>	<b>Cluster #1 mean value</b>	<b>Cluster #2 mean value</b>
Total Range Area (km <sup>2</sup> )	620,907.33	233,742.62
Summer Range Area x Summer Range Net Primary Production	463,547,415.45	172,619,276.85

Table 3.6. Discrete values of subpopulation total range area (km<sup>2</sup>), summer range area (km<sup>2</sup>), summer range net primary production (kg\*C/m<sup>2</sup>) (NPP) and summer range area x summer range NPP for each subpopulation. The inclusion of these four variables in the multiple linear regression model explained 88.5% of the variation in amplitude ( $p = 0.006$ ). Subpopulations with larger total and summer range areas and greater ecological productivity tend to have greater amplitude values. The Porcupine subpopulation is a unique outlier to this relationship.

<b>Herd</b>	<b>Amplitude</b>	<b>Total Range Area (km<sup>2</sup>)</b>	<b>Summer Range Area (km<sup>2</sup>)</b>	<b>Summer Range NPP (kg*C/m<sup>2</sup>)</b>	<b>Summer Range Area x Summer Range NPP</b>
George River	329,886	933,826	271,427	1675.22	454,699,938
Leaf River	298,168	559,628	293,874	1544.54	453,900,148
Qamanirjuaq	228,685	342,687	186,544	1591.08	296,806,428
Bathurst	203,081	496,626	124,837	1467.77	183,232,003
Bluenose-East	71,893	269,346	93,462	1474.34	137,794,765
Bluenose-West	52,408	126,730	94,458	1527.81	144,313,877
Cape Bathurst	8,445	27,469	27,469	1612.82	44,302,553
Porcupine	41,942	369,268	242,884	1984.66	482,042,159
Central Arctic	21,227	82,553	82,553	1165.37	96,204,790
Teshekpuk Lake	20,838	184,396	123,741	1890.64	233,949,684
Western Arctic	219,831	340,044	155,600	1974.69	307,261,764

## FIGURES

Figure 1.1. The population trajectory of the Qamanirjuaq caribou subpopulation is cyclic and approximates a sine wave with a period of 53 years (SE = 3.96) and amplitude of 230,897 (SE = 25,872). Harvest program CARIBOU 1.0 models this cycle using a sine cyclic population density index set to a period of 53 years, user-defined density-effects on survival and calf production rates, and 6 abundance-stratified user-defined harvest removal rates. The sine function, and program CARIBOU 1.0 provide a good approximation of the Qamanirjuaq caribou subpopulation cycle.

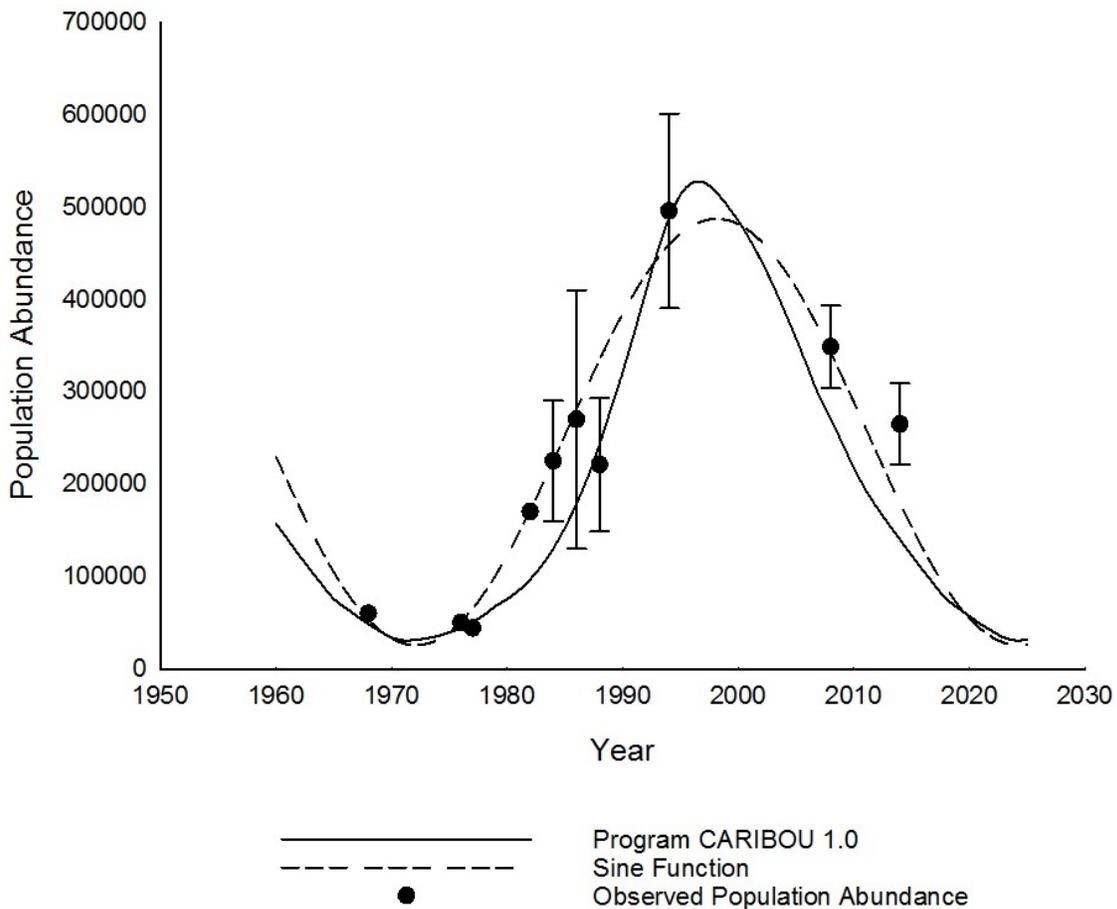


Figure 1.2. We defined calf production as the number of breeding females divided by the total number of females in the subpopulation. All breeding females were assumed to produce a single calf. The calf production rates generated from the cyclic CC model using program CARIBOU 1.0 are compared to the observed calf production rates by referencing points to the 53-year cycle that were common to both. A lag-time of 27 years (1/2 cycle period) was required to produce model generated calf production rates that corresponded to estimated calf production rates. Linear regression between census Qamanirjuaq caribou calf production and modeled calf production rates produced a significant correlation  $r = 0.964$  ( $p < 0.001$ ).

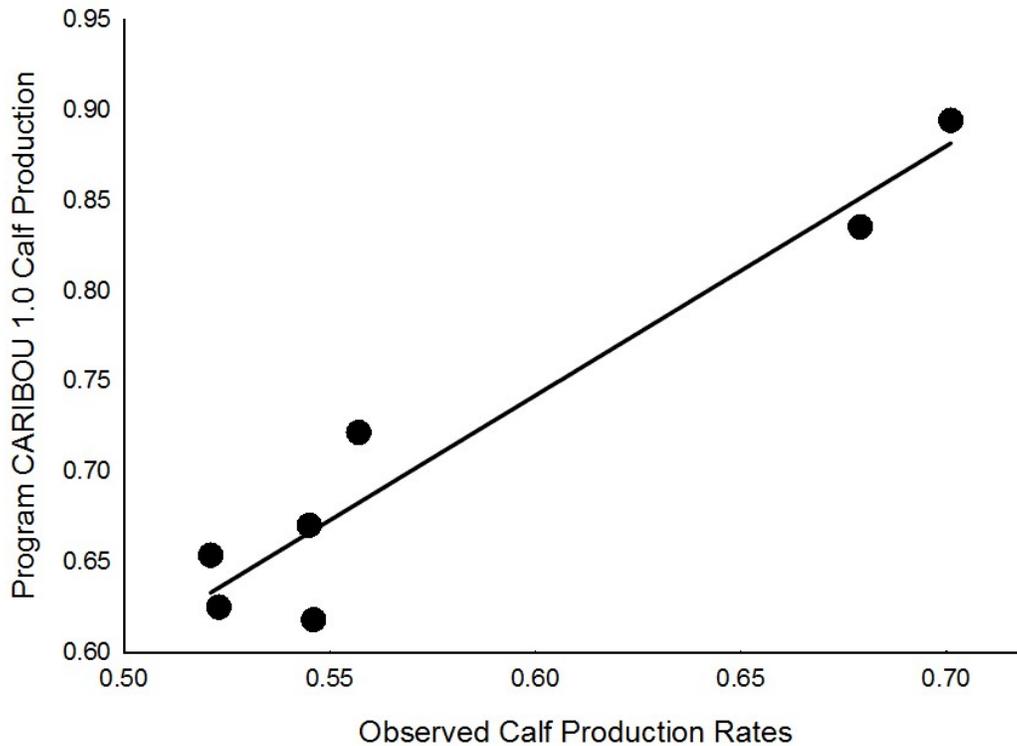


Figure 1.3. Calf Survival rates were obtained from Campbell, *et al.* (2010). The calf survival rates generated from cyclic CC model in program CARIBOU 1.0 are compared to the observed calf survival rates by time referencing points across the 53-year cycle. Linear regression between census Qamanirjuaq caribou calf survival and modeled calf survival were strongly correlated  $r = 0.962$  ( $p < 0.001$ ).

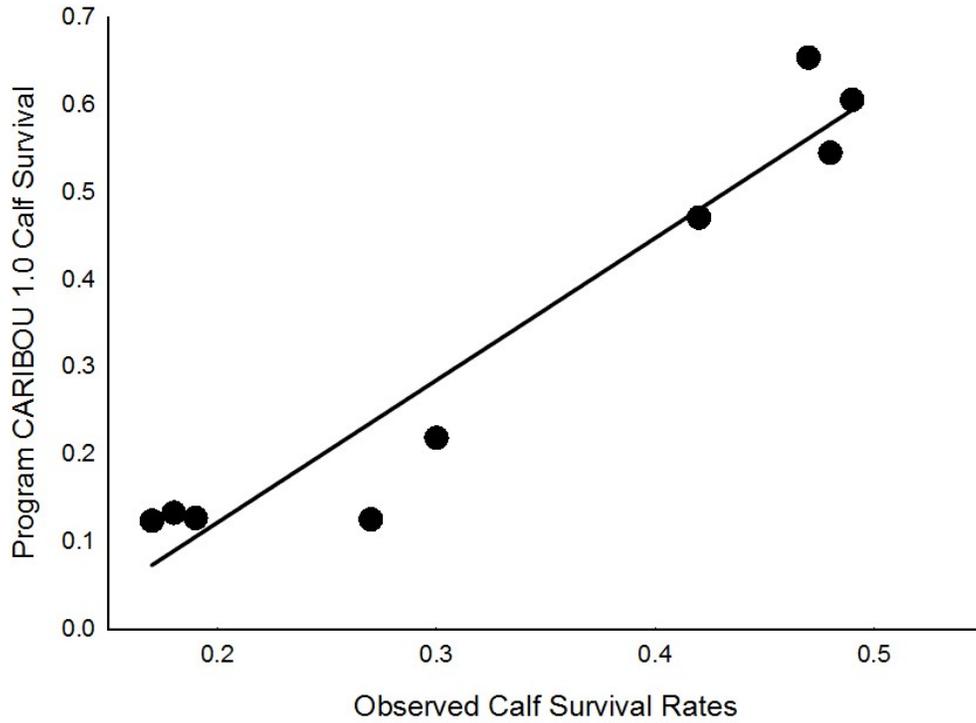


Figure 1.4. The population abundance estimates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model in program CARIBOU 1.0 are compared to the census population abundance estimates of the Qamanirjuaq subpopulation by time referencing points across the 53-year cycle. Qamanirjuaq caribou population abundance estimates and model generated population estimates were positively correlated  $r = 0.950$  ( $p < 0.001$ ).

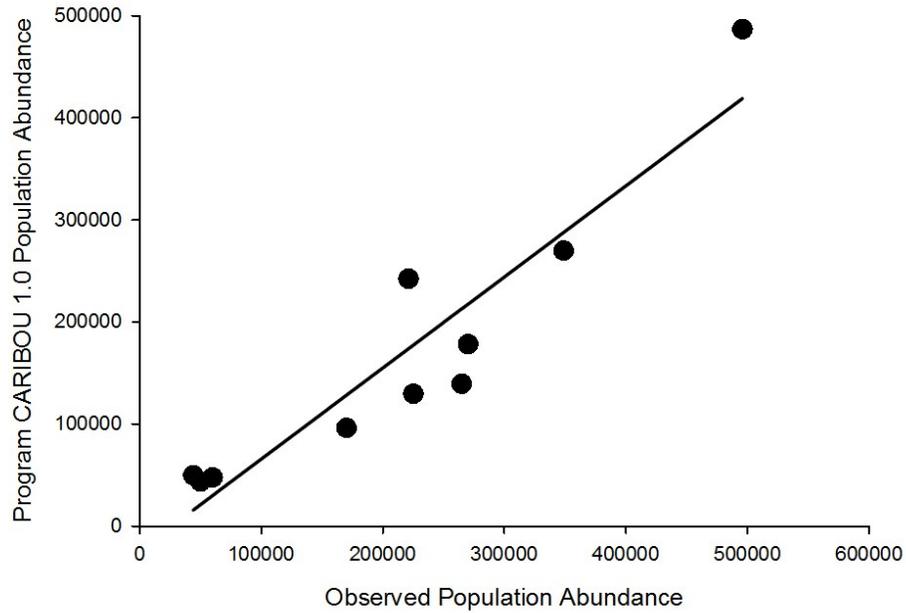


Figure 1.5. Wavelet and sine functions produced differing estimates of period and amplitude for all subpopulations that had a sufficient number of time-series census population number estimates. A wavelet function fit to a sine generated time-series produced a correspondence of  $r = 1.0$  ( $p < 0.001$ ). This implies that given a sufficient amount of census data, wavelet and sine functions will converge on estimates of period and amplitude if the cycle is a sine cycle. Discriminating between the two functions to describe the time-series population estimates of all barren-ground caribou subpopulations was arbitrary. We chose to describe all subpopulations as sine cyclic to increase consistency between subpopulation period and amplitude estimates.

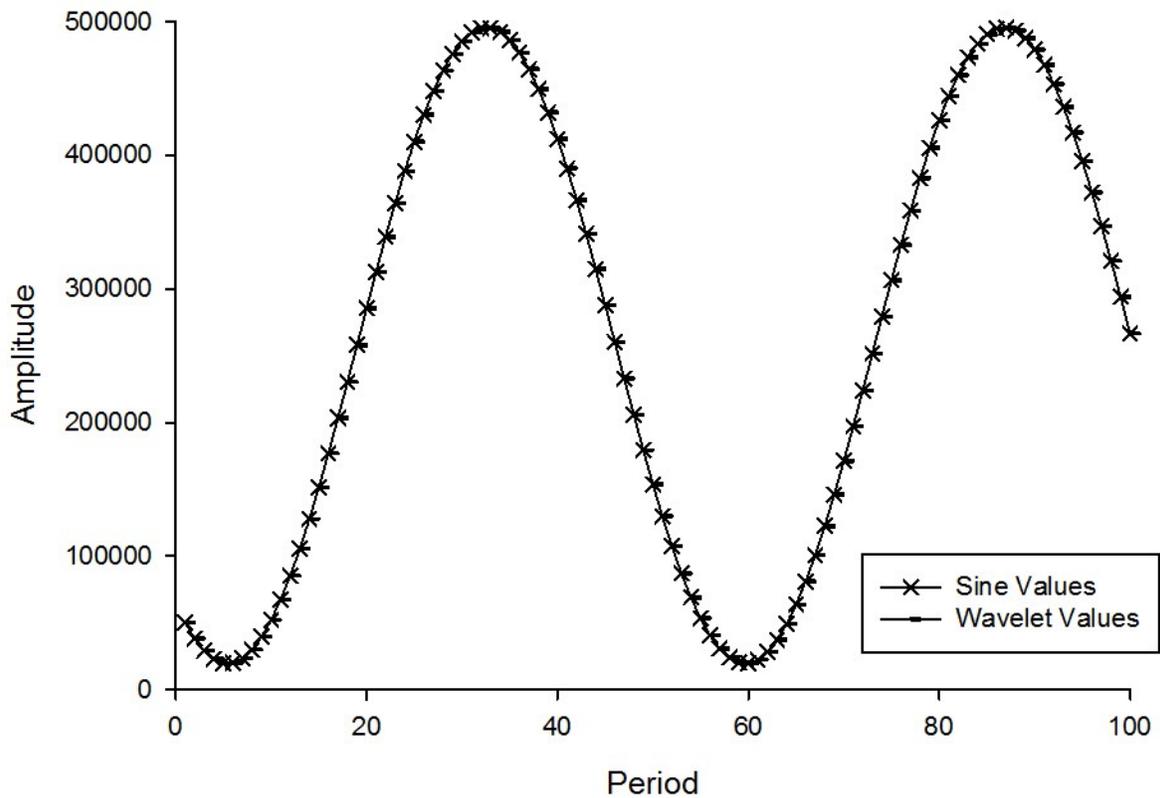


Fig. 1.6. Models that are too simple are unrealistic because they fail to capture essential elements of the modeled system. Models that are too complex require invalidated assumptions regarding model structure and functional relationships; and often the input data required to run them are unavailable. Models of moderate complexity are more likely to provide accurate projections of future conditions. Our intention was to position program CARIBOU 1.0 at an appropriate level of complexity to be useful as a decision support tool of barren-ground caribou harvest co-management. This figure was adapted from Bunnell (1989).

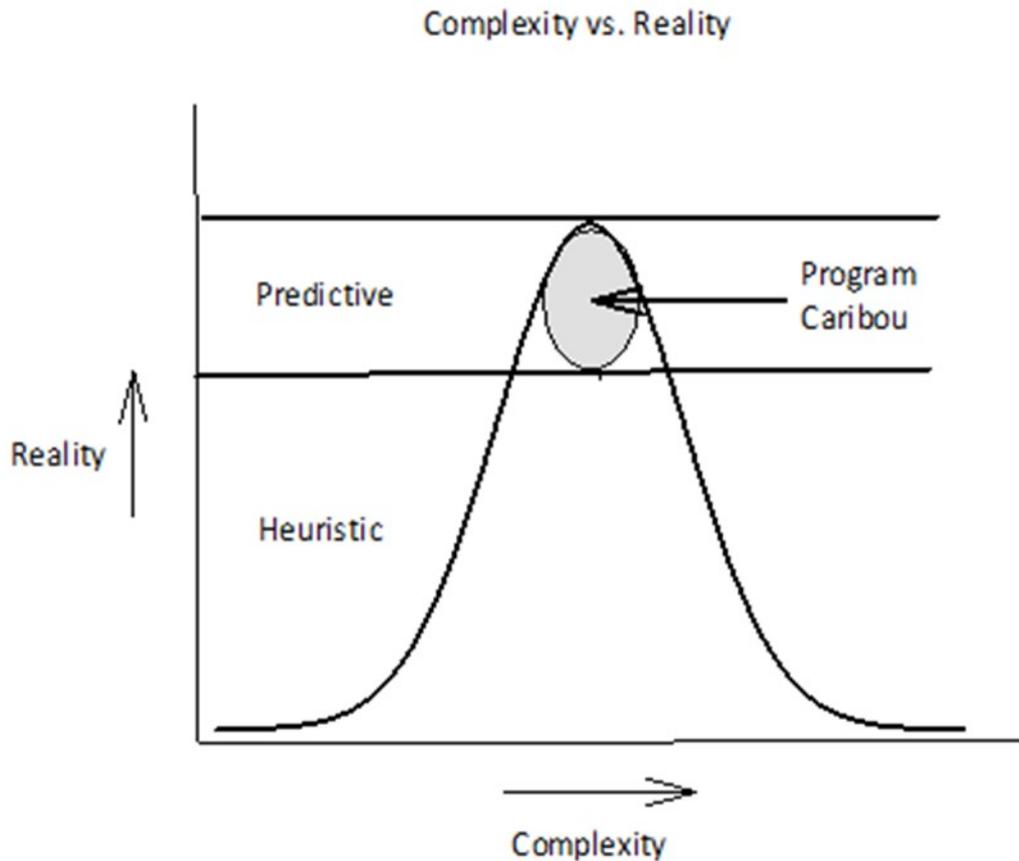


Figure 2.1a. The sine fit to the time-series census population estimates of the Bathurst barren-ground caribou subpopulation. The Bathurst subpopulation approximates a sine wave ( $r = 0.934$ ,  $p < 0.001$ ) with a period of 42 (SE = 3.43) years and an amplitude of 203,081 (SE = 24,520).

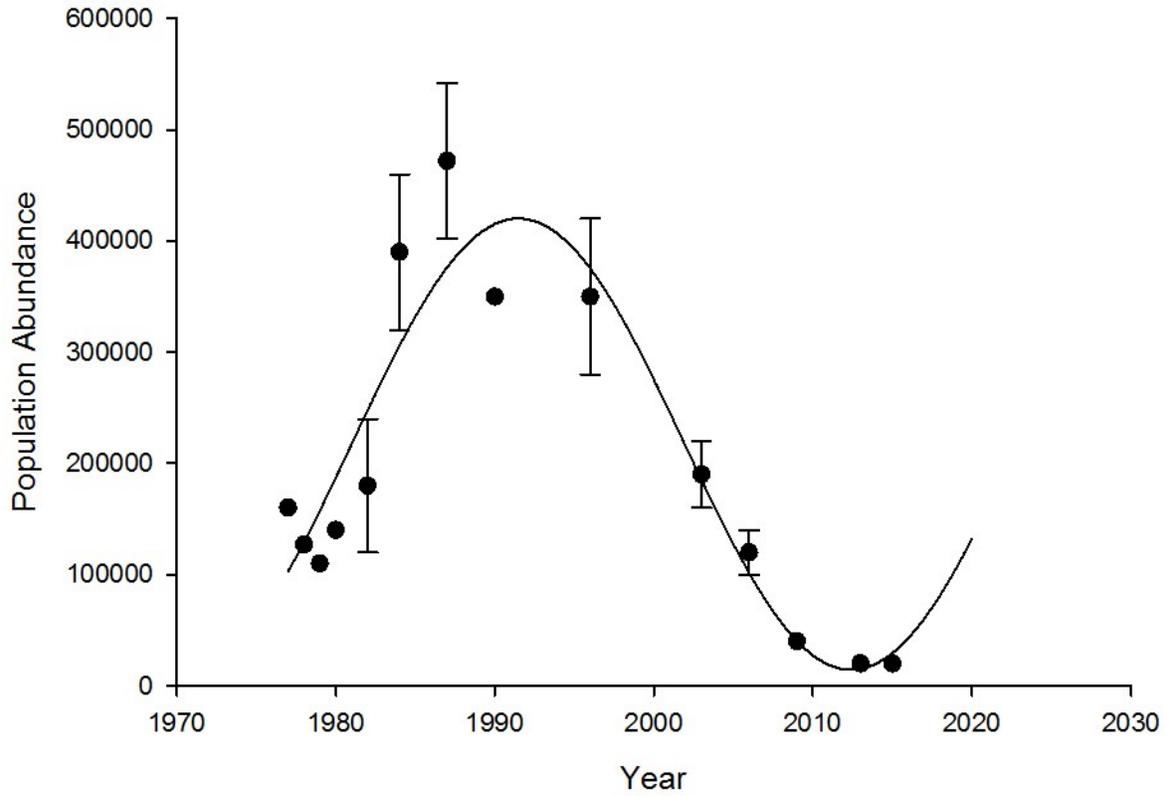


Figure 2.1b. The sine fit to the time-series census population estimates of the George River barren-ground caribou subpopulation. The George River subpopulation approximates a sine wave ( $r = 0.859$ ,  $p < 0.001$ ) with a period of 45 (SE = 2.4) years and an amplitude of 354,413 (SE = 21,653).

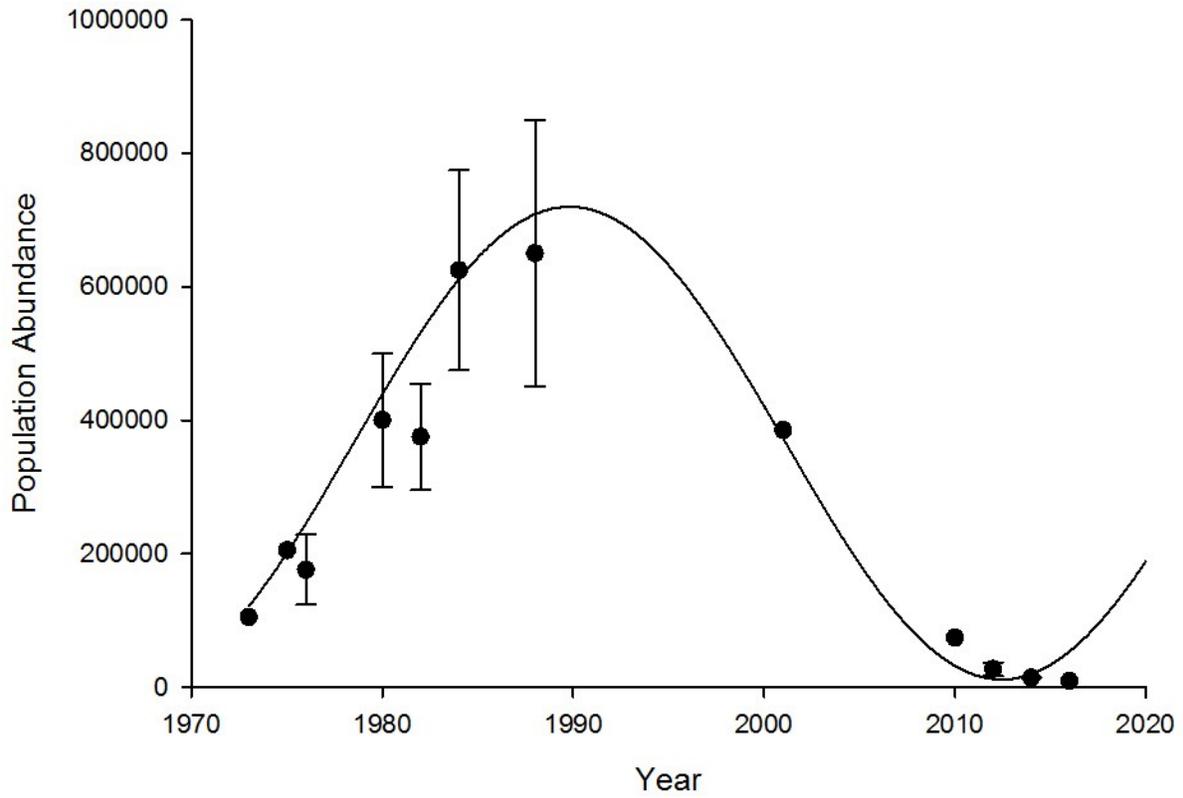


Figure 2.2. The threshold corrected Michaelis-Menton function employed in CARIBOU 1.0 is used to model sex and age specific density-effects. It illustrates how a varying shape parameter (KS) or carrying capacity (CC) controls the degree of linearity or non-linearity.

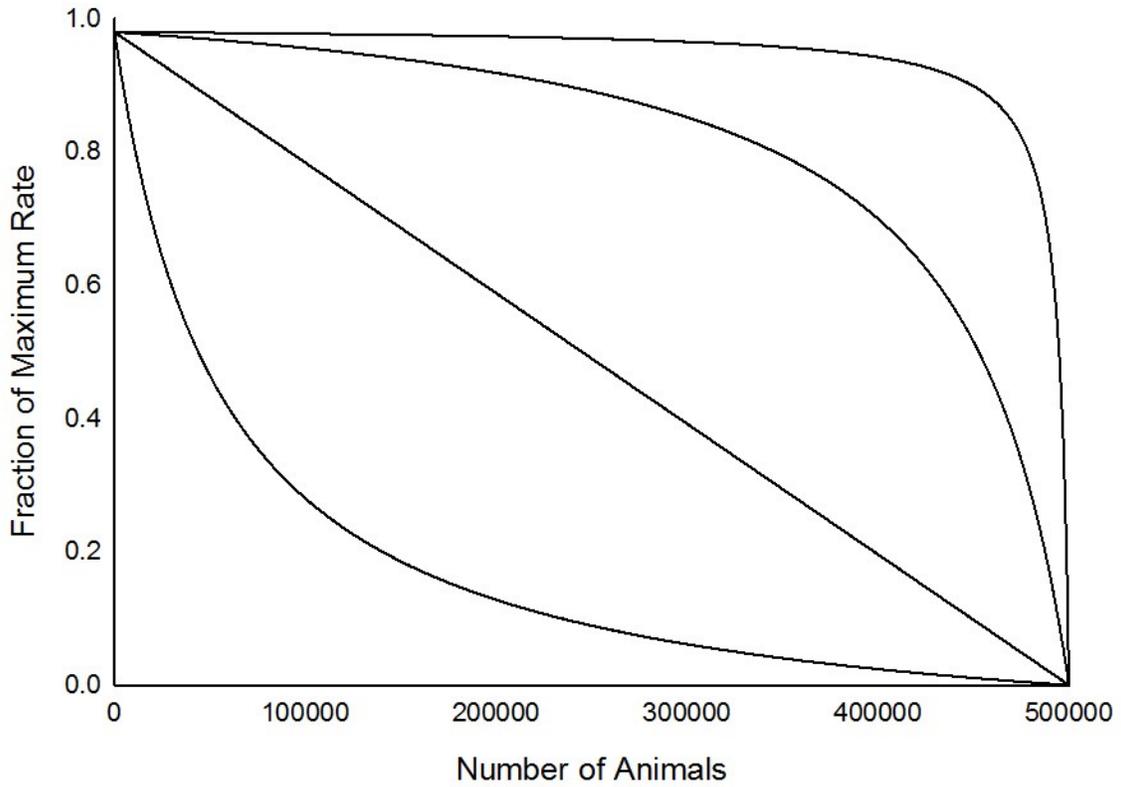


Figure 2.3a. The population abundance estimates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model in program CARIBOU 1.0 are compared to the census population abundance estimates of the Bathurst subpopulation by time referencing points across the 42-year cycle. Bathurst caribou population abundance estimates and model generated population estimates were positively correlated  $r = 0.871$  ( $p < 0.001$ ).

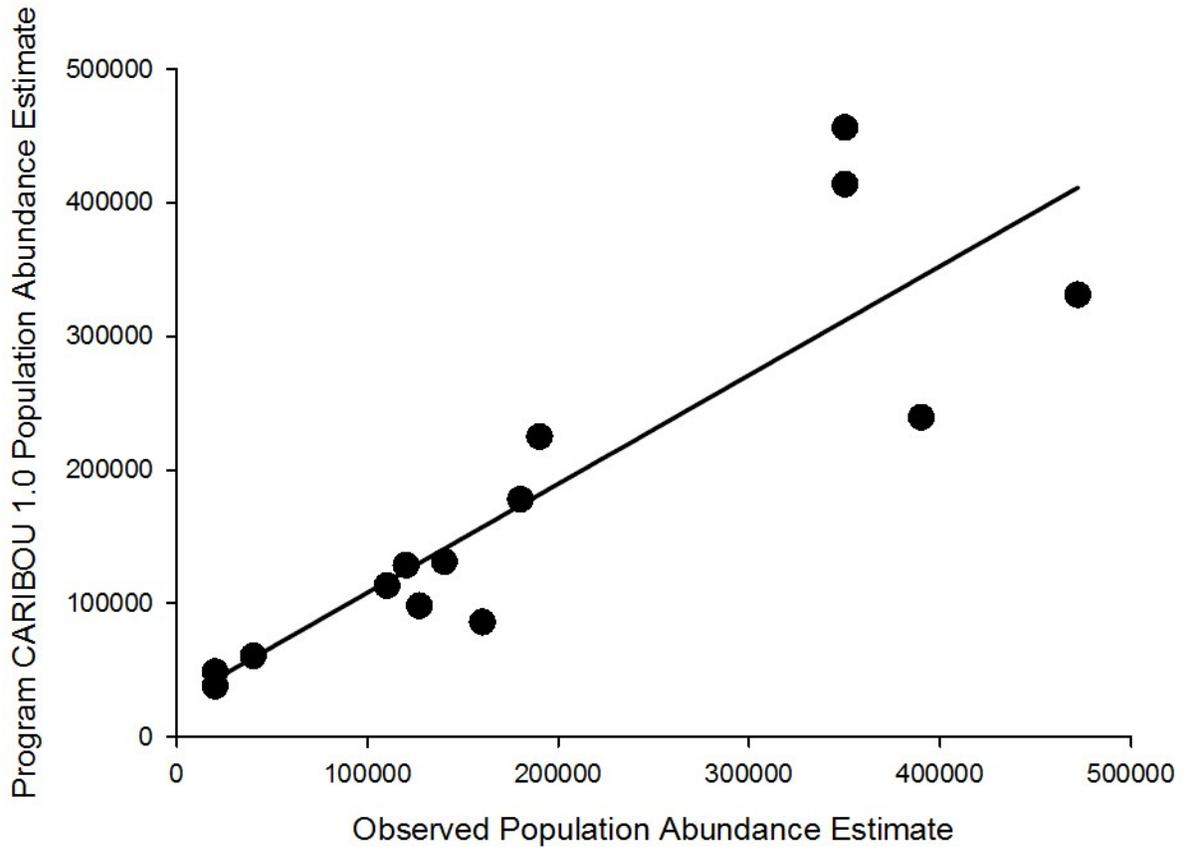


Figure 2.3b. The calf production rates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model using program CARIBOU 1.0 are compared to the observed calf production rates for the Bathurst subpopulation by referencing points to the 42-year cycle that is common to both. Linear regression between census Bathurst caribou calf production and modeled calf production rates produced a significant correlation  $r = 0.819$  ( $p = 0.024$ ).

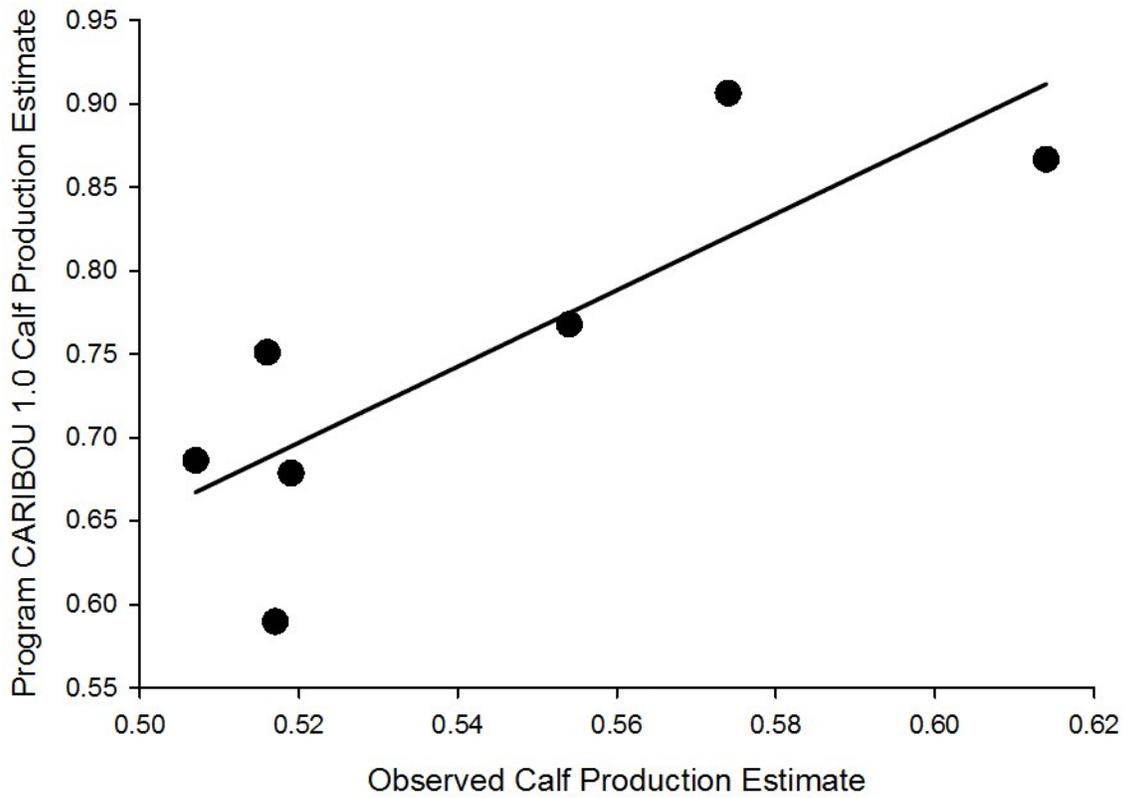


Figure 2.3c. The calf survival rates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model in program CARIBOU 1.0 are compared to the observed calf survival rates for the Bathurst subpopulation by time referencing points across the 42-year cycle. Linear regression between census Bathurst caribou calf survival and modeled calf survival were positively correlated  $r = 0.702$  ( $p = 0.007$ ).

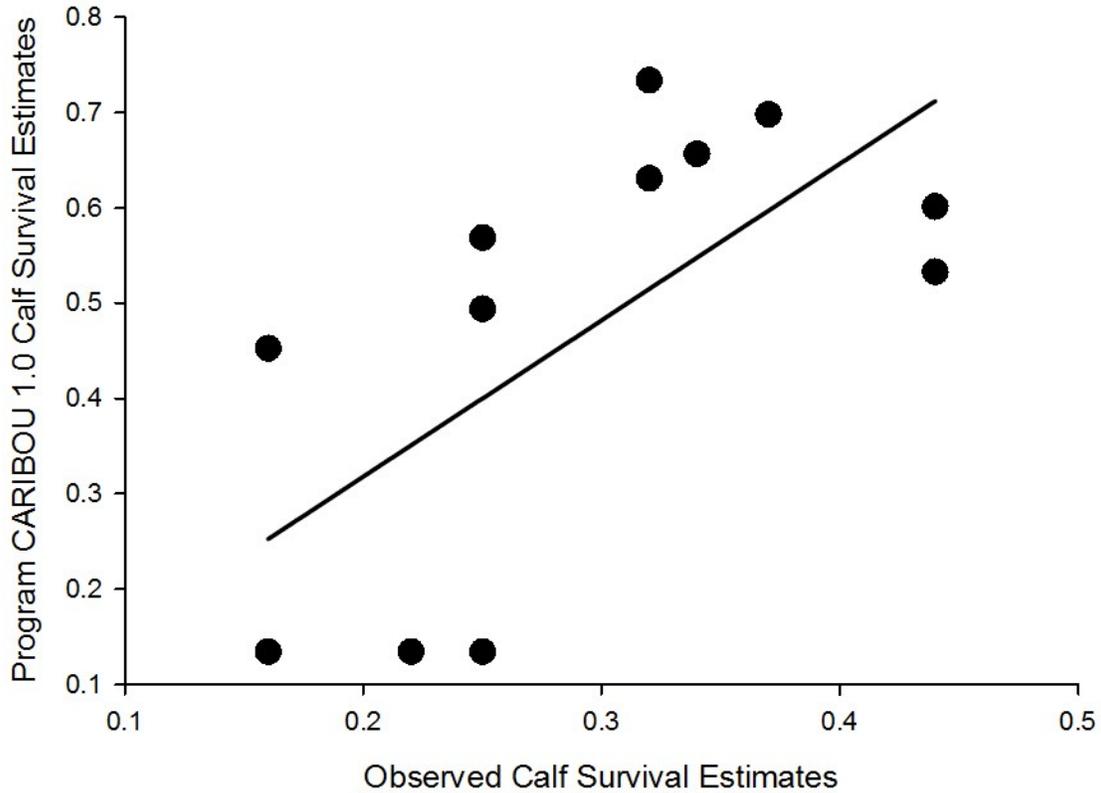


Figure 2.4a. The population abundance estimates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model in program CARIBOU 1.0 are compared to the census population abundance estimates of the George River subpopulation by time referencing points across the 45-year cycle. Linear regression between census George River caribou population abundance estimates and modeled population abundance were positively correlated  $r = 0.944$  ( $p < 0.001$ ).

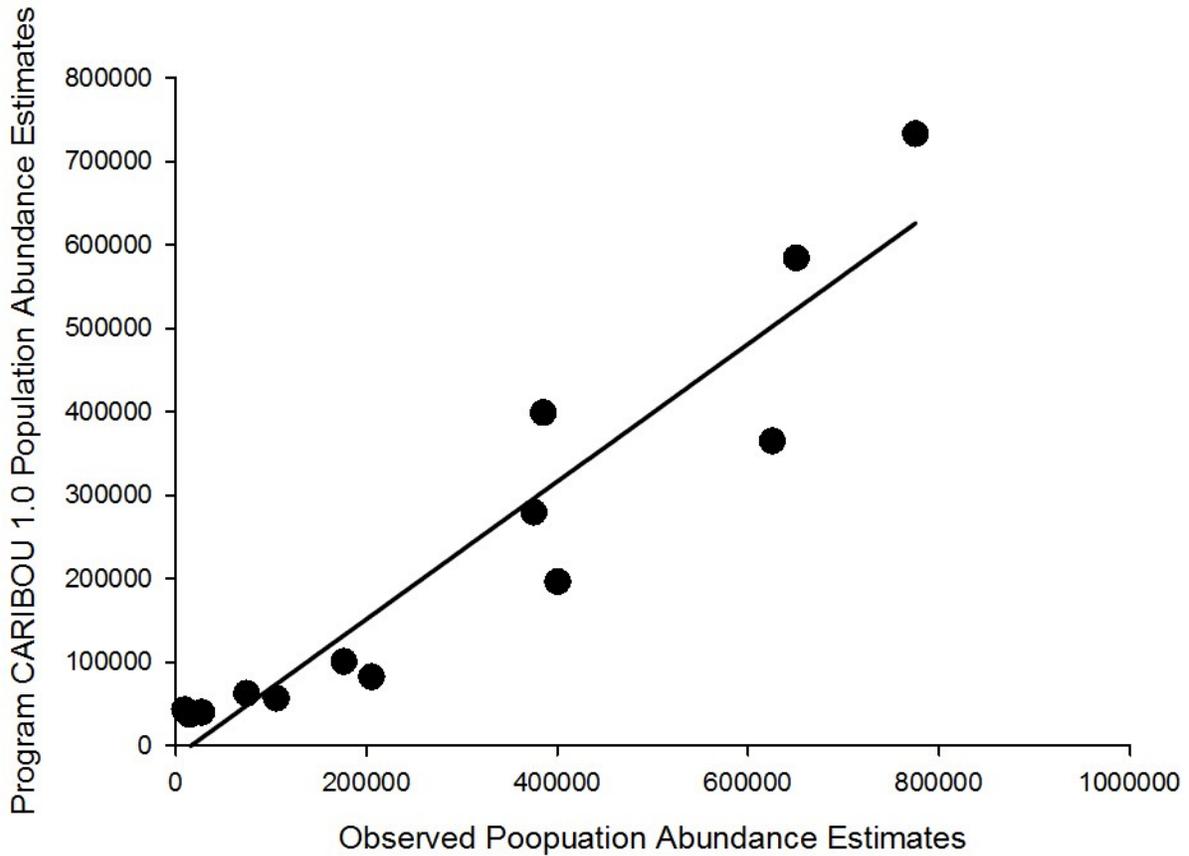


Figure 2.4b. The calf production rates generated from the non-linear density function (KS) and the sine cyclic population density index (CC) model using program CARIBOU 1.0 are compared to the observed calf production rates for the George River subpopulation by referencing points to the 45-year cycle that is common to both. Linear regression between census George River caribou calf production and modeled calf production rates produced a significant correlation  $r = 0.769$  ( $p < 0.001$ ).

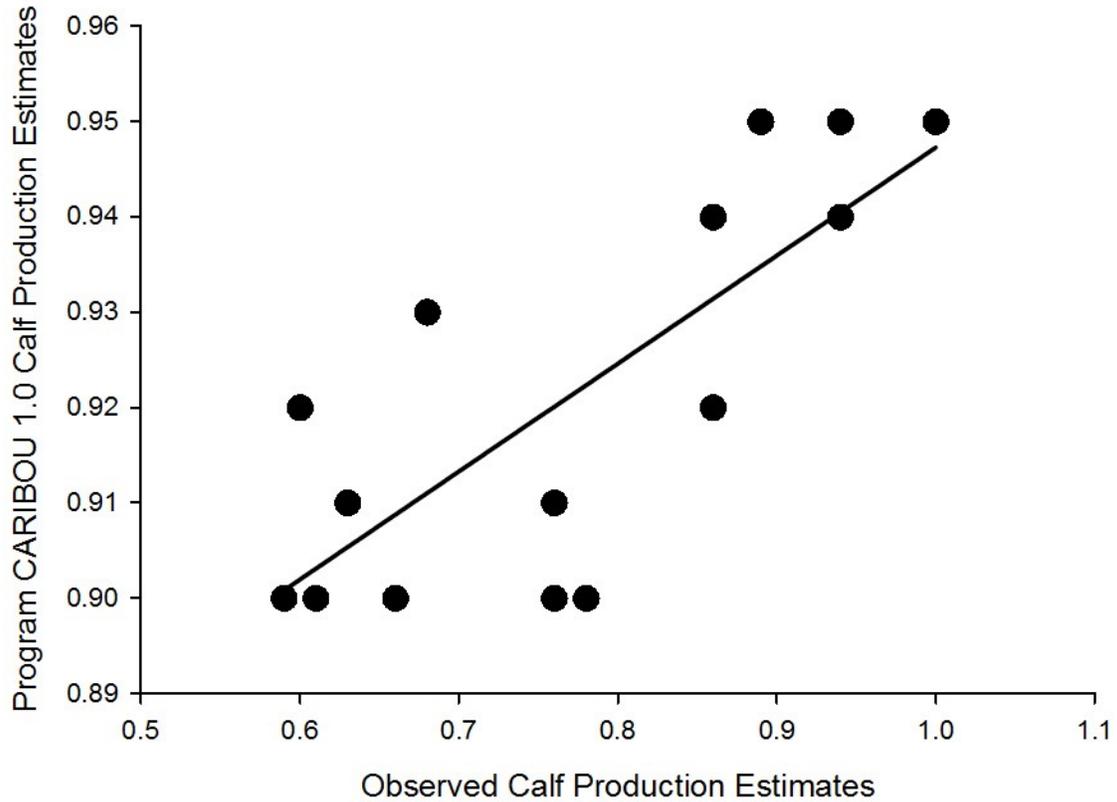


Figure 2.4c. The calf survival rates generated from the non-linear density effects function (KS) and the sine cyclic population density index (CC) model in program CARIBOU 1.0 are compared to the observed calf survival rates for the George River subpopulation by time referencing points across the 45-year cycle. Linear regression between census George River caribou calf survival and modeled calf survival were positively correlated  $r = 0.702$  ( $p = 0.001$ ).

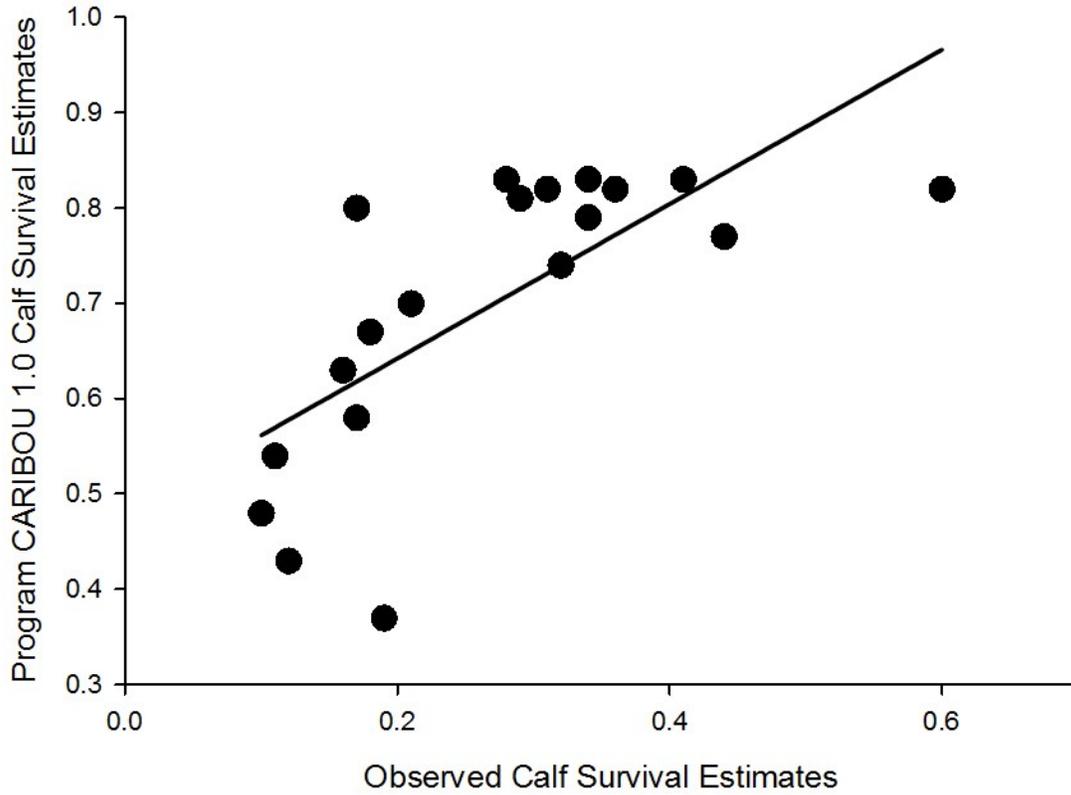


Figure 3.1. We had a sufficient amount of census data to fit a sine function to 11 subpopulations of North American barren-ground caribou (i.e., George River, Leaf River, Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine, Central Arctic, Teshekpuk Lake, and Western Arctic). The COSEWIC (2016) report extrapolated estimates for 13 subpopulations of barren-ground caribou (Tuktoyaktuk Peninsula, Beverly/Ahiak, Lorrillard + Wager Bay, Boothia Peninsula, Southampton Island, Coats Island, Baffin Island, Qamanirjuaq, Bathurst, Cape Bathurst, Bluenose-East, Bluenose-West, Porcupine) based on linear or exponential trends over a 3-generation period. We compared our sine cyclic extrapolation to COSEWIC's 3-generation trend extrapolation based on 6 subpopulations that we both sampled.

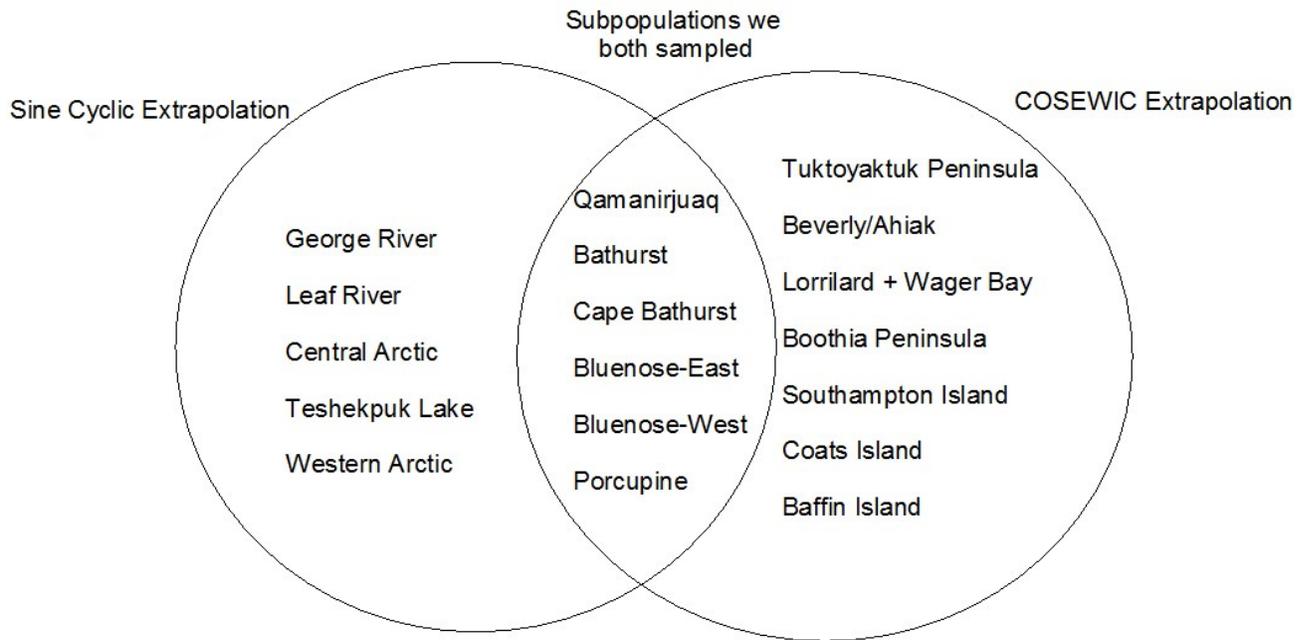


Figure 3.2. The time-series of pooled estimates of North American barren-ground caribou subpopulations based on our sine cyclic extrapolation for the George River, Leaf River, Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine, Central Arctic, Teshekpuk Lake and Western Arctic subpopulations is charted. We also produced a sine cyclic extrapolation based on 6 subpopulations that were sampled in common with the COSEWIC (2016) report (Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst and Porcupine). Our sine cyclic estimate 517,137 was in close correspondence to COSEWIC's 2015 estimate of 537,549 for common subpopulations. By definition, the long term population growth rate mean of both sine cyclic extrapolated curves is 1.0.

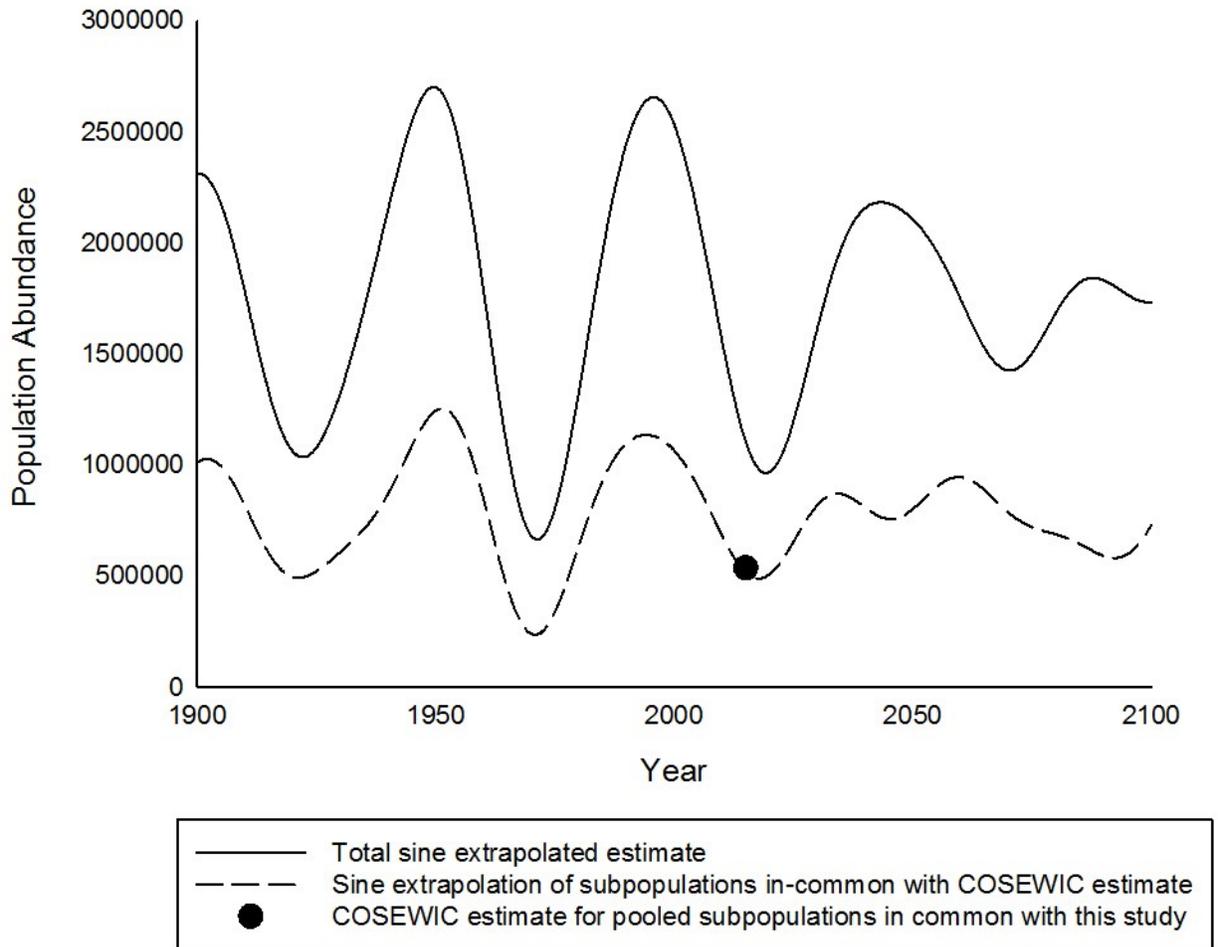


Figure 3.3a. The best multiple linear regression model for amplitude included total range area, summer range area, summer range net primary production and the interaction of summer range area x summer range net primary production. Summer range area and summer range NPP were only included in the model because the interaction effect (summer range area x summer range NPP) was significant. A comparison of regression model estimates of amplitude and census estimates (sine function fits) of amplitude produced a correlation coefficient of  $r = 0.918$  ( $p < 0.001$ ).

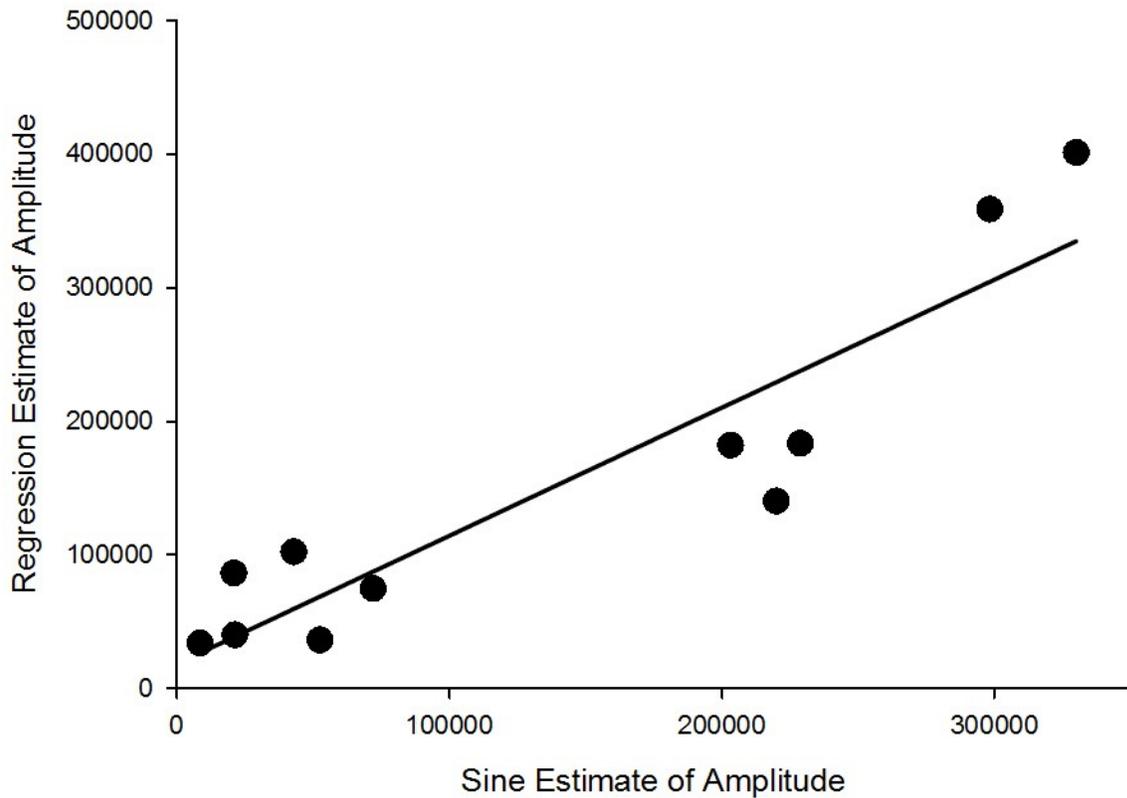


Figure 3.3b. Amplitude alone was the best predictor of period. A comparison of regression estimates of subpopulation period and census estimates of period (sine function fits) produced a correlation coefficient of  $r = 0.519$  ( $p = 0.102$ ). Our data was insufficient propose a specific demographic herbivore-vegetation hypothesis. The relatively low correlation of period with amplitude suggests that ecological circumstances vary between subpopulations.

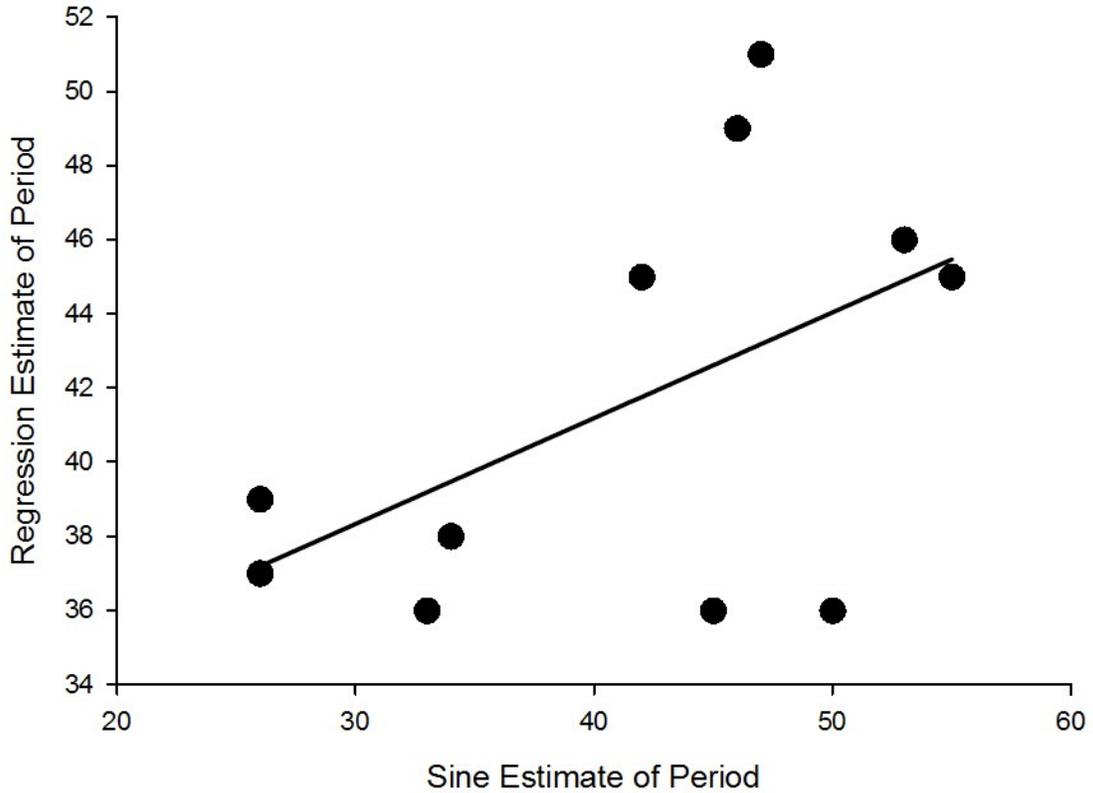


Figure 3.3c. The best multiple linear regression model for amplitude included total range area, summer range area, summer range net primary production and the interaction of summer range area x summer range net primary production. Amplitude alone was the best predictor of period. Using the regression estimates of period and amplitude, a comparison of regression model estimates of subpopulation abundance and census estimates of subpopulation abundance produced a correlation coefficient of  $r = 0.894$  ( $p < 0.001$ ) for all 11 subpopulations.

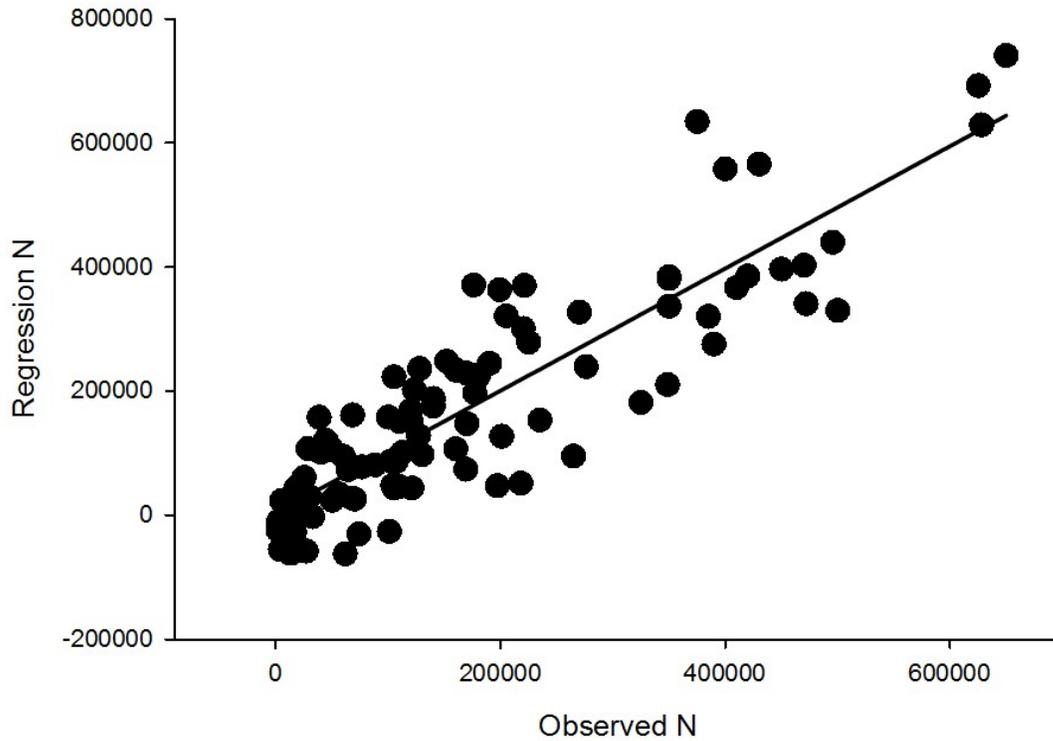


Figure 3.4. The optimal number of clusters for cluster analysis based on the total range area, the interaction of summer range area x summer range NPP was two. We normalized and plotted the values against amplitude to illustrate the distribution of clusters. Cluster 1 (George River, Leaf River and Porcupine) was characterized by larger total range areas, and high values of summer range area x summer range NPP. Cluster 2 (Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Central Arctic, Teshekpuk Lake, and Western Arctic) was characterized by smaller total range areas, and lower values of summer range area x summer range NPP. The observation that the Porcupine herd is an outlier based on relatively low amplitude value, suggests other variables besides seasonal range areas and ecological productivity influence the amplitude of individual subpopulations.

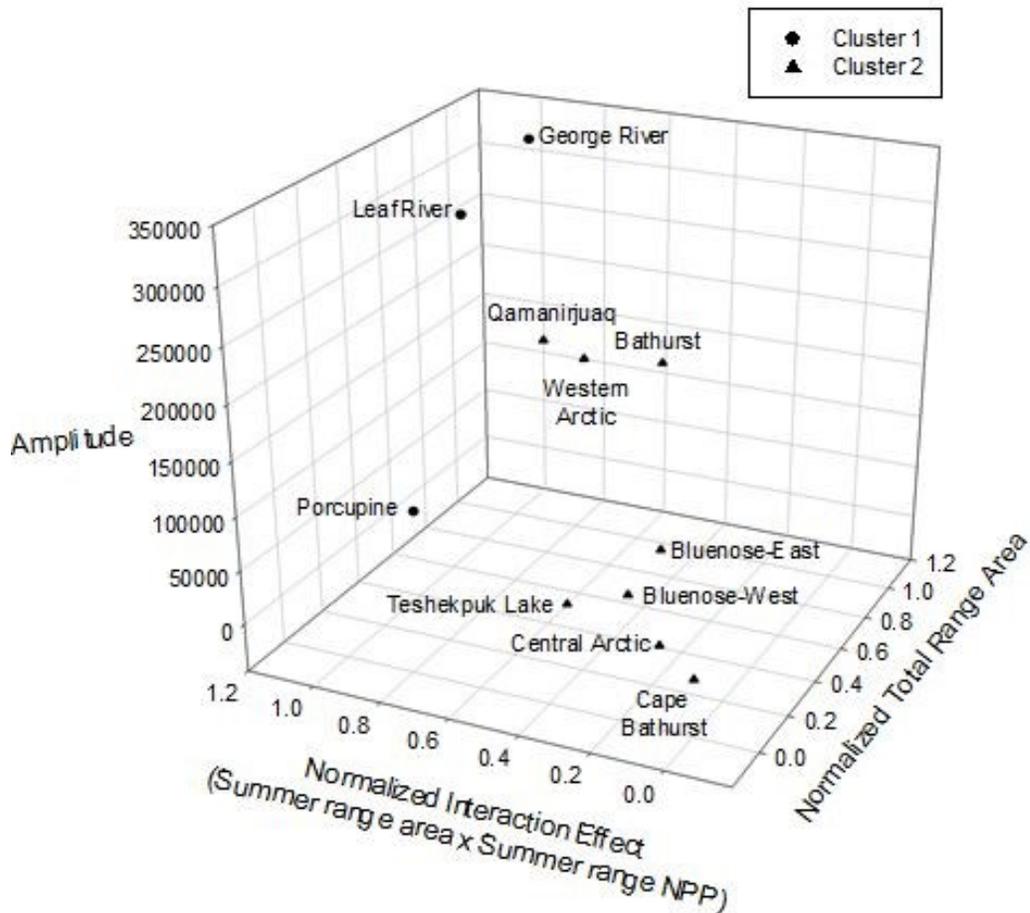


Figure 3.6a. Ecological productivity follows a SW to NE gradient of decreasing net primary productivity (NPP) in northern North America. The gradient of NPP is driven by regional temperature trends and is clearly illustrated by the treeline isopleth. Each subpopulation has a unique combination of period and amplitude values which seemed to follow a NW-SE gradient of increasing cycle period length and amplitude value. Subpopulations experiencing relatively more climate amelioration due to marine effects (e.g., Western Arctic, Qaminirjuaq, and George River subpopulations) had generally longer periods and greater amplitudes than more continental subpopulations (e.g., Bluenose-East, Bluenose-West and Bathurst subpopulations).

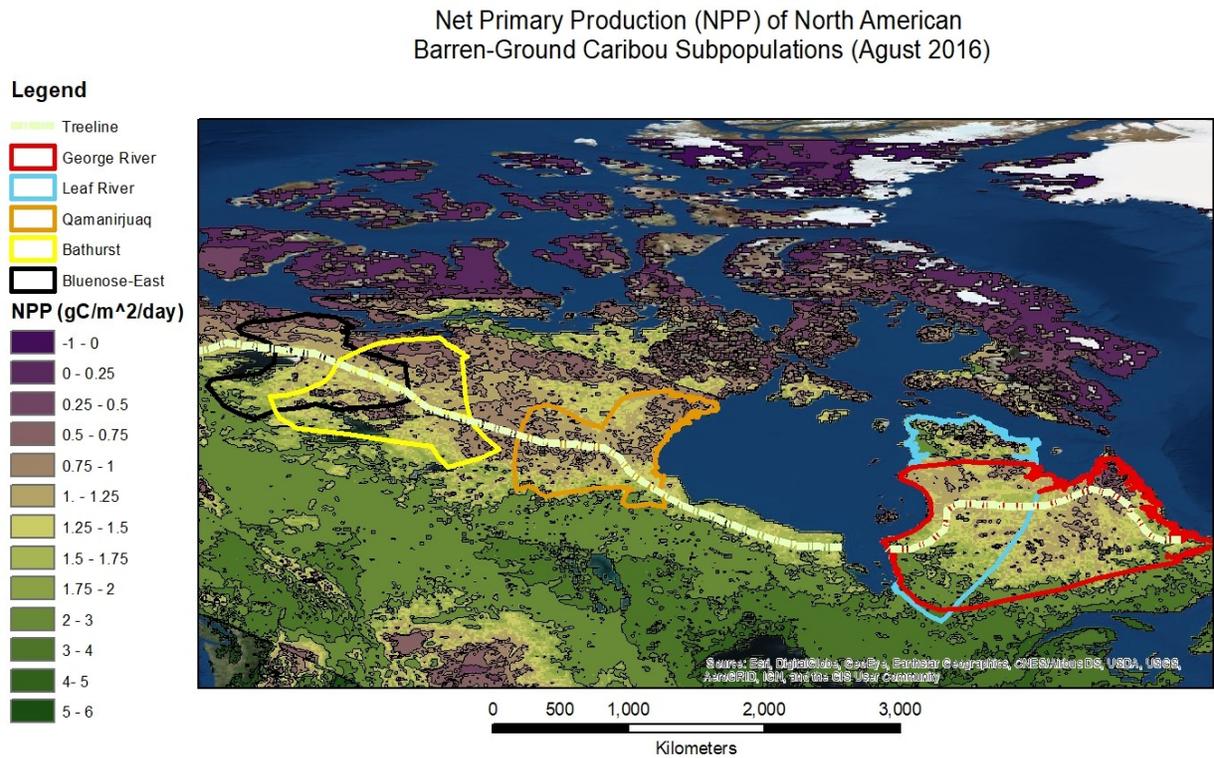


Figure 3.6b. Ecological productivity follows a SW to NE gradient of decreasing net primary productivity (NPP) in northern North America. The gradient of NPP is driven by regional temperature trends and is clearly illustrated by the treeline isopleth. Each subpopulation has a unique combination of period and amplitude values which seemed to follow a NW-SE gradient of increasing cycle period length and amplitude value. Subpopulations experiencing relatively more climate amelioration due to marine effects (e.g., Western Arctic, Qaminirjuaq, and George River subpopulations) had generally longer periods and greater amplitudes than more continental subpopulations (e.g., Bluenose-East, Bluenose-West and Bathurst subpopulations).

Net Primary Production (NPP) of North American Barren-Ground Caribou Subpopulations (August 2016)

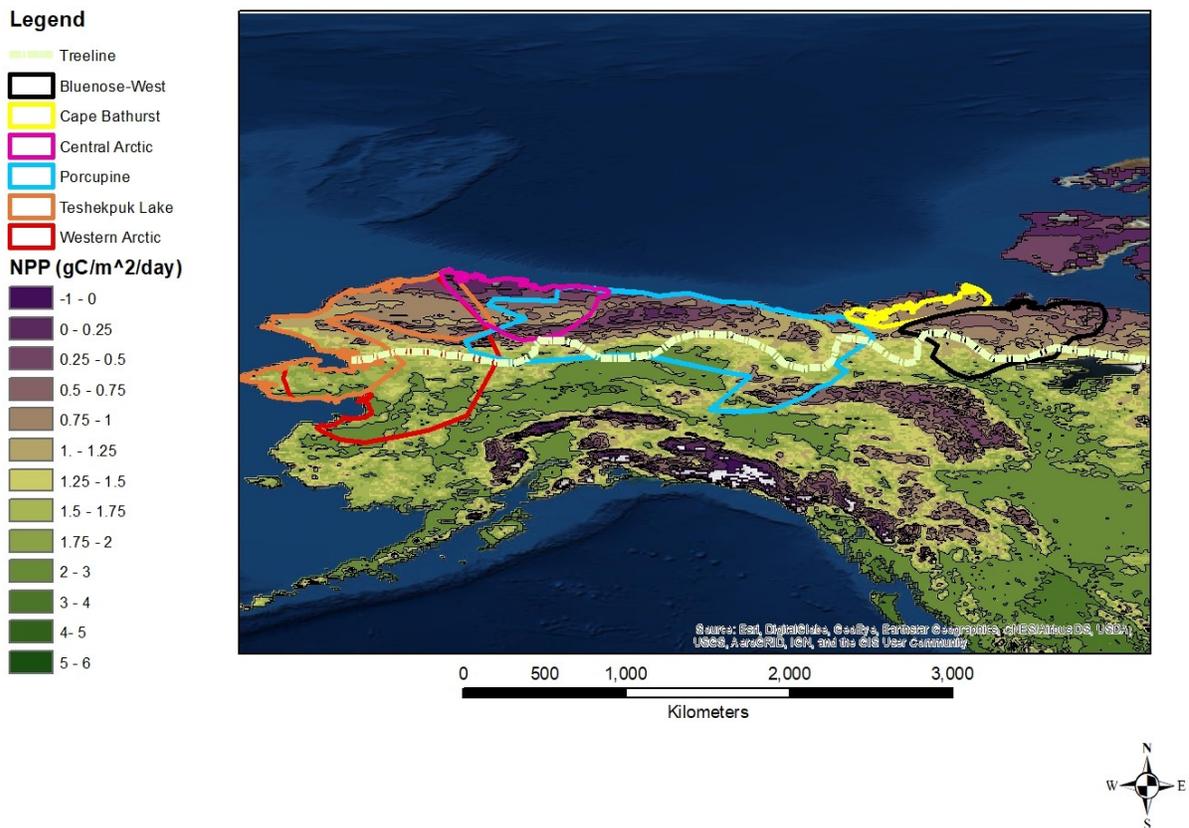
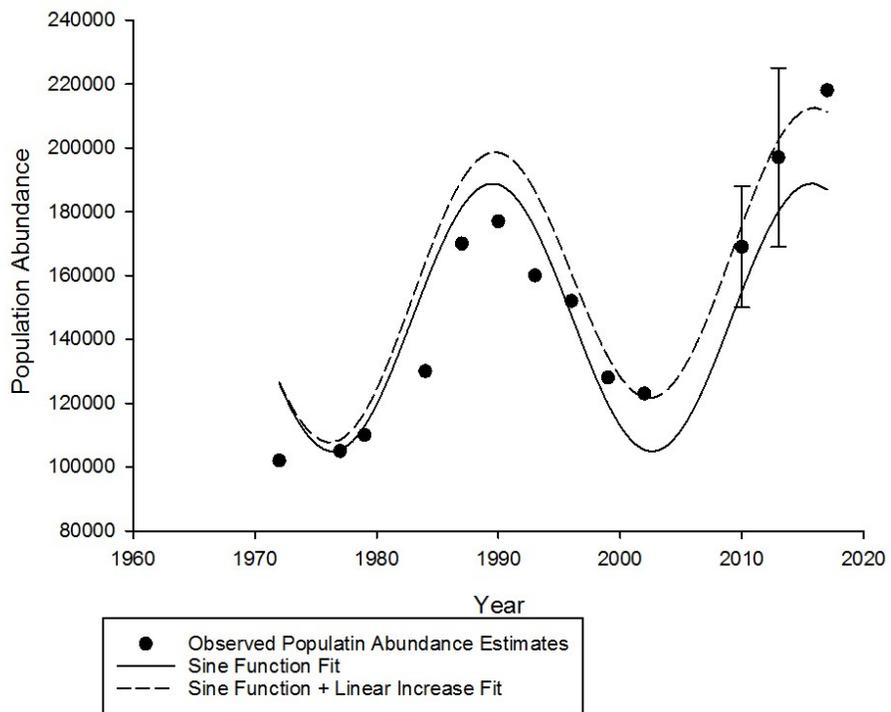


Figure 3.7. The Porcupine subpopulation census estimates from 1972 to 2018 approximate a sine wave ( $r = 0.868$ ,  $p < 0.01$ ) with a period of 26 years ( $SE = 1.67$ ) and an amplitude of 42,795 ( $SE = 7,255$ ). The minimum and maximum values of the second cycle appear to have increased over time. A sine function with a linear increase term was fit to the Porcupine time-series census data. The sine function plus linear term fit was significantly better ( $r = 0.944$ ,  $p < 0.01$ ) and contribution of the linear term was also significant ( $p < 0.01$ ). Increases in abundance between consecutive cycles could be a response to increasing productivity associated with climate warming on the Porcupine subpopulation range.



**SUPPLEMENTARY I:** Logistic Population Growth from Linear Density-Effects (Taylor, 1994; Janssens, 2014).

The discrete formulation of the logistic equation is derived for a generalized birth pulse species. We define the per capita birth rate as “B” and the per capita death rate as “D” if there are no density-effects on birth or death, and the rates of birth and death are constant (no environmental variance), and there is no sex or age structure. The number of individuals at time (t+1) in the population ( $N_{t+1}$ ) is a function of the number of individuals at time (t).

$$\text{Equation 1: } N_{t+1} = N_t + N_t * (B-D)$$

We can define a term  $\Delta$  as the per capita difference between birth rate and death rate.

$$\text{Equation 2: } \Delta = (B - D)$$

Rewriting eq. 1 yields:

$$\text{Equation 3: } N_{t+1} = N_t * (1 + \Delta)$$

We can define a term called population growth rate ( $\lambda$ ) as  $1+\Delta$

$$\text{Equation 4: } \lambda = 1 + \Delta$$

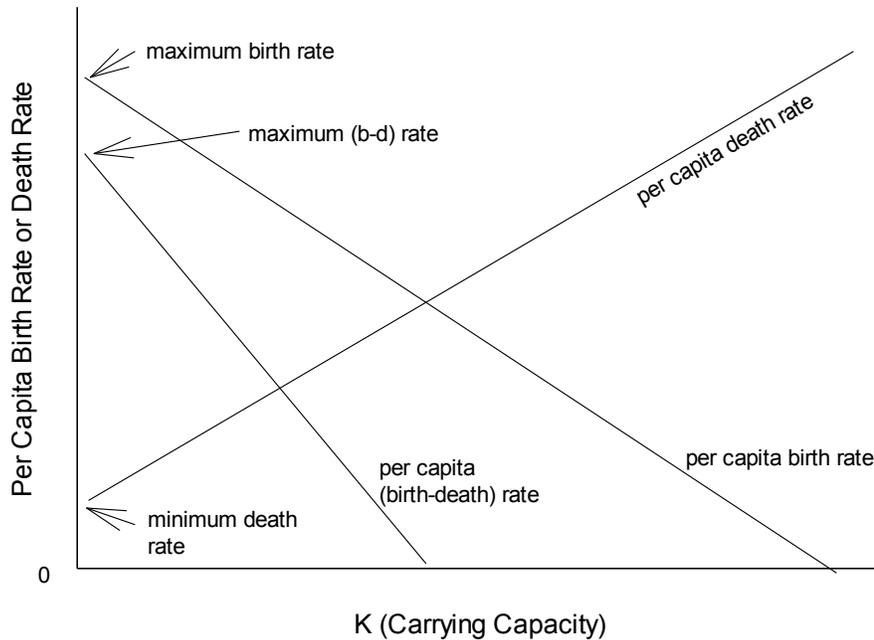
Rewriting eq. 3 yields:

$$\text{Equation 5: } N_{t+1} = N_t * \lambda$$

We see by inspection that when  $\Delta = 0$  or when  $\lambda=1$  then  $N_t = N_{t+1} = K$ . But the chance that B-D equals exactly 0 is infinitely small. We also recognize that populations in nature do not usually just decline to extinction or increase to enormous numbers. The number of individuals in a population must feedback on the per capita rates of birth and death. This negative feedback we term “density-effects”. The simplest way to model density-effects is a model that represents birth rate or death rate or both birth rate and death rate as a linear function of population number ( $N_t$ ).

Figure below shows that if birth rate is a declining function of  $N_t$ , or death rate is an increasing function of  $N_t$ , or both; then  $\Delta_t$  is a declining function of  $N_t$ .

## Density Effects on Birth and Death Rates



Using the standard equation for a linear relationship (e.g.,  $y = mx + b$ ), we can write an equation for  $\Delta$  as a function of  $N_t$ . Recalling the definitions above:

$$\Delta_t = (B - D)$$

$$\Delta_{\max} = (B_{\max} - D_{\min})$$

$K$  = Carrying Capacity

Then  $\Delta_t = (-\Delta_{\max}/K) * N_t + \Delta_{\max}$  (using  $y = m*x + b$  from the preceding figure).

$$\Delta_t = \Delta_{\max} - [\Delta_{\max} * (N_t/K)] \text{ (linear density-effects).}$$

$$\text{Equation 6: } \Delta_t = \Delta_{\max} * (1 - N_t/K)$$

Now we rewrite eq. 3 using the dynamic definition of  $\Delta$  from eq. 6:

$$N_{t+1} = N_t * \lambda$$

$$N_{t+1} = N_t * (1 + \Delta)$$

$$N_{t+1} = N_t * (1 + \Delta_{\max} * (1 - N_t/K))$$

Divide both sides by  $N_t$ :

$$\lambda = 1 + \Delta_{\max} * (1 - N_t/K)$$

Equation 7:  $N_{t+1} = N_t(1 + \Delta_{\max} *(1-N_t/K))$  (discrete logistic equation)

As discussed in Methods, CARIBOU 1.0 models density-effects on age (x) specific survival ( $p_x$ ) and age specific calf production (recruitment) rate ( $m_x$ ), CARIBOU 1.0 also allows a user-specified density function that can identify both linear and non-linear responses:

$$\text{Equation 8: } R_t = (R_{\max}) \frac{\frac{CC}{N_t} - 1}{\frac{CC}{N_t} - 1 + KS}$$

Where  $R_t = p_x$  or  $m_x$  (annual life-table survival and recruitment rate parameters).

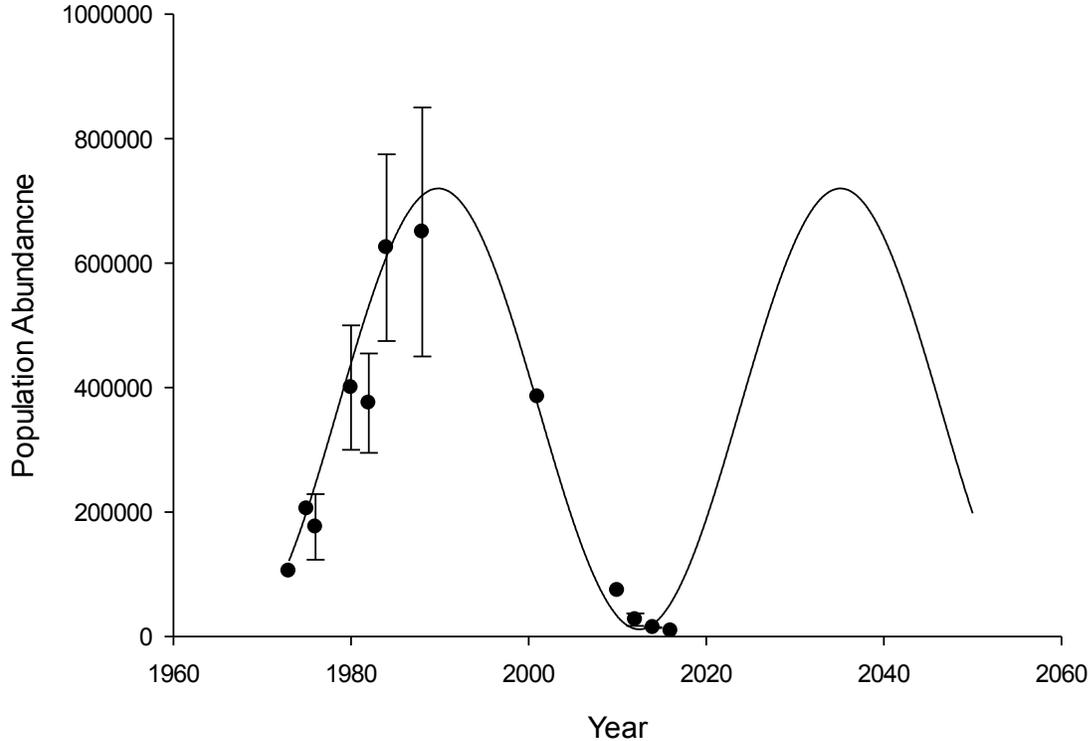
## SUPPLEMENTARY II: SUBPOPULATION SINE FUNCTION FITS + CENSUS DATA

Sine functions were fit to the available census data for 11 subpopulations that had a sufficient number of subpopulation abundance estimates (i.e., George River, Leaf River, Qamanirjuaq, Bathurst, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine, Central Arctic, Teshekpuk Lake and Western Arctic). Graphical representation, period lengths, amplitude values, correlation coefficients, and significance of the fits are provided below.

The population abundance estimates, calf production (recruitment), calf survival and harvest estimates for the Qamanirjuaq, Bathurst and George River subpopulations (Chapter 1; Chapter 2) in addition to the population abundance census estimates for the Leaf River, Bluenose-East, Bluenose-West, Cape Bathurst, Porcupine, Central Arctic, Teshekpuk Lake, and Western Arctic subpopulations (Chapter 3) are archived under the file name "Barren-ground Caribou Subpopulation Census Data + Sine Function Fits.xlsx" and is available upon request to the corresponding author.

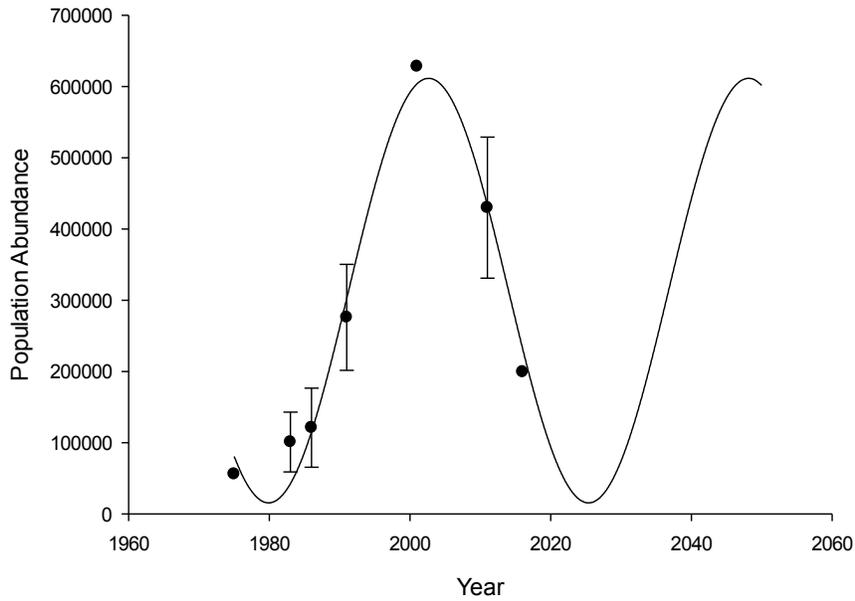
The George River subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.859$ ,  $p < 0.01$ ) with a period 45 years ( $SE = 2.4$ ) and an amplitude of 354,413 ( $SE = 21,653$ ).

George River Sine Function Fit



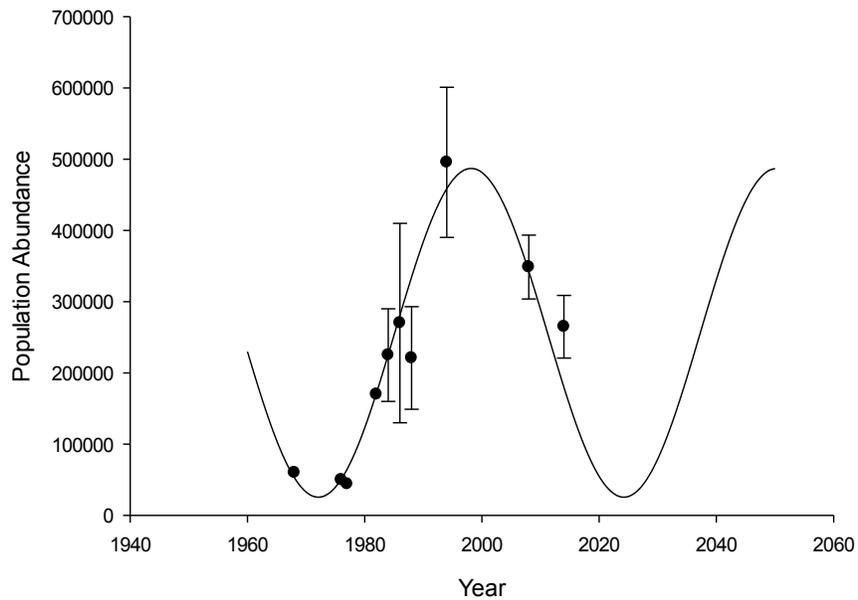
The Leaf River subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.987$ ,  $p < 0.01$ ) with a period of 46 years (SE = 2.0) and an amplitude of 297,784 (SE = 26,142).

Leaf River Sine Function Fit



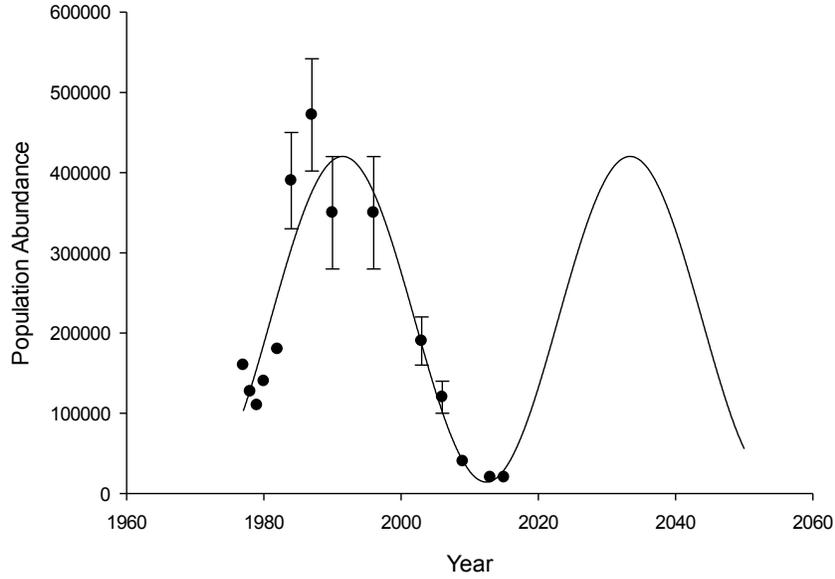
The Qamanirjuaq subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.961$ ,  $p < 0.01$ ) with a period of 53 years (SE = 3.3) and an amplitude of 230,897 (SE = 25,872).

Qamanirjuaq Sine Function Fit



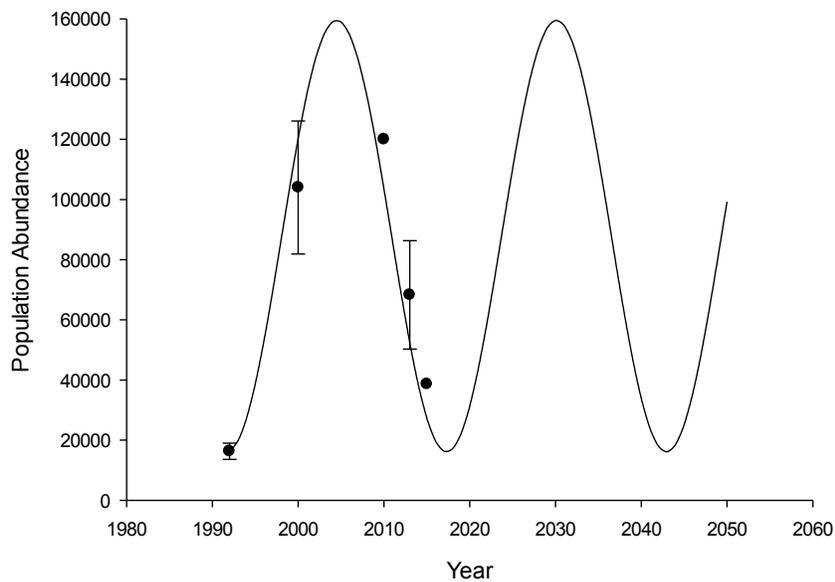
The Bathurst subpopulation time-series census population estimates approximate a sine wave ( $r = 0.934$ ,  $p < 0.01$ ) with a period of 42 years (SE = 3.4) and an amplitude of 203,081 (SE = 24,520).

Bathurst Sine Function Fit

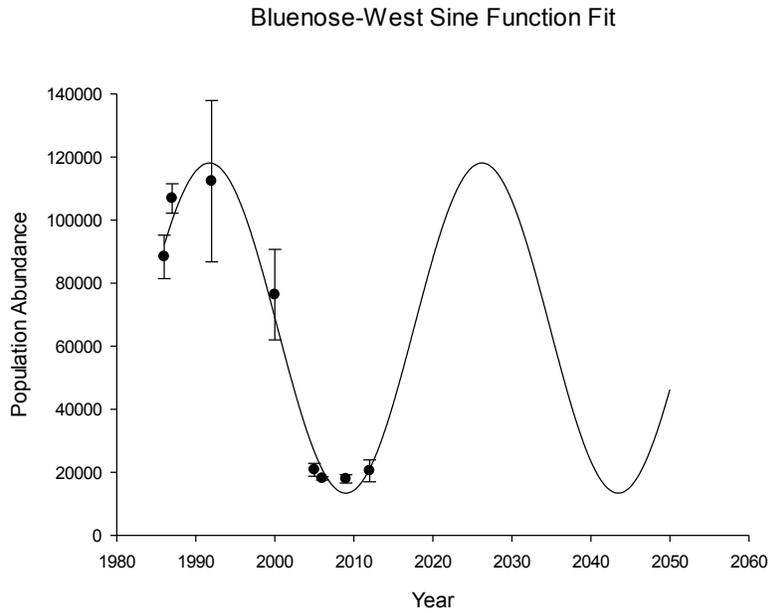


The Bluenose-East subpopulation time-series population abundance estimates approximate a sine wave ( $r = 1.0$ ,  $p < 0.01$ ) with a period of 26 years (SE = 0.13) and an amplitude of 71,723 (SE = 354).

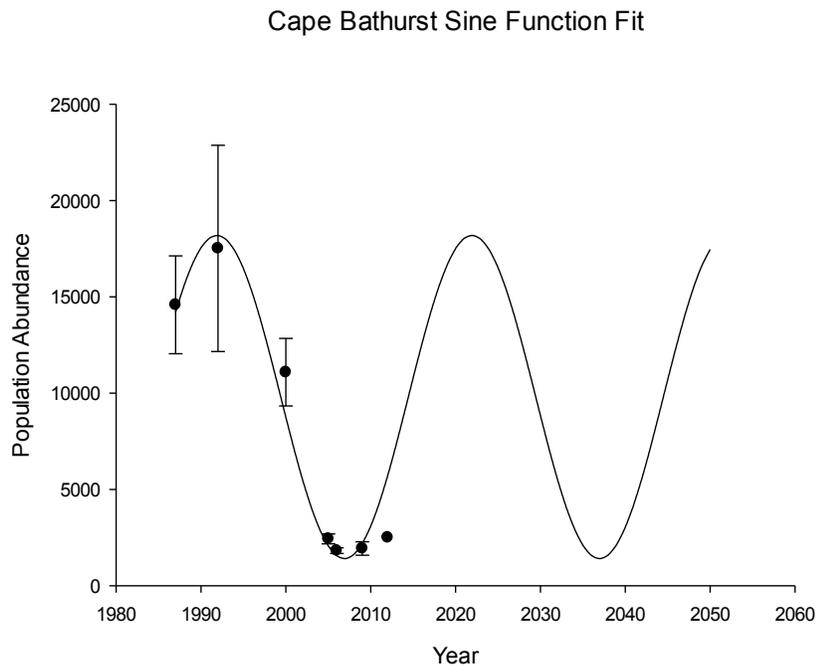
Bluenose-East Sine Function Fit



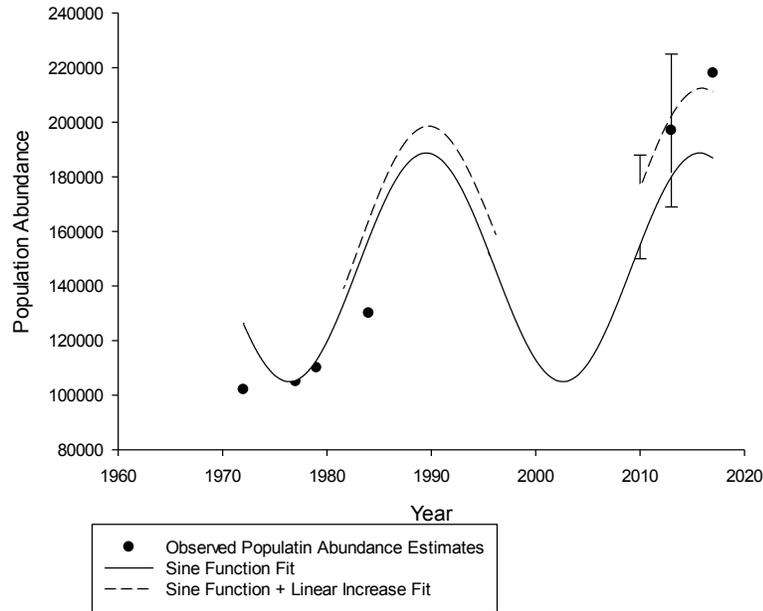
The Bluenose-West subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.991$ ,  $p < 0.01$ ) with a period of 34 years ( $SE = 1.9$ ) and an amplitude of 52,408 ( $SE = 3,942$ ).



The Cape Bathurst subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.996$ ,  $p < 0.01$ ) with a period of 30 years ( $SE = 1.7$ ) and an amplitude of 8,394 ( $SE = 447$ ).

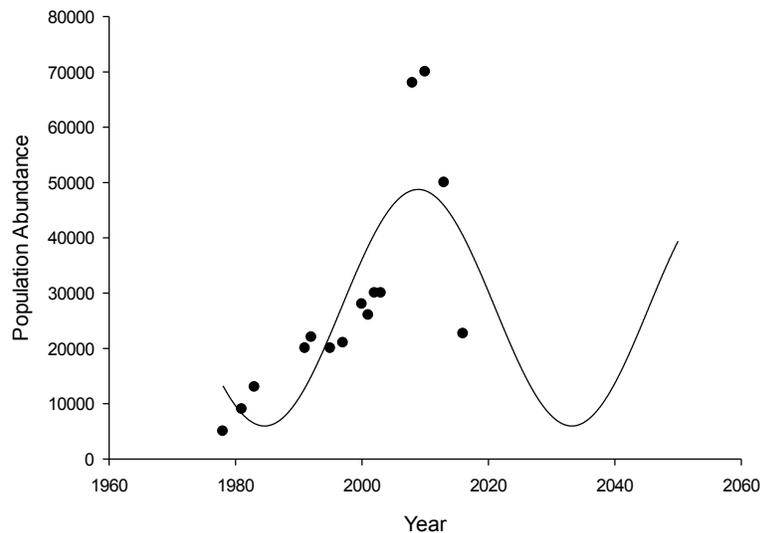


The Porcupine subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.868$ ,  $p < 0.01$ ) with a period of 26 years ( $SE = 1.5$ ) and an amplitude of 42,795 ( $SE = 7,255$ ). A sine function with a linear increase term improved the fit ( $r = 0.944$ ,  $p < 0.01$ ) to the Porcupine time-series census population abundance estimates.



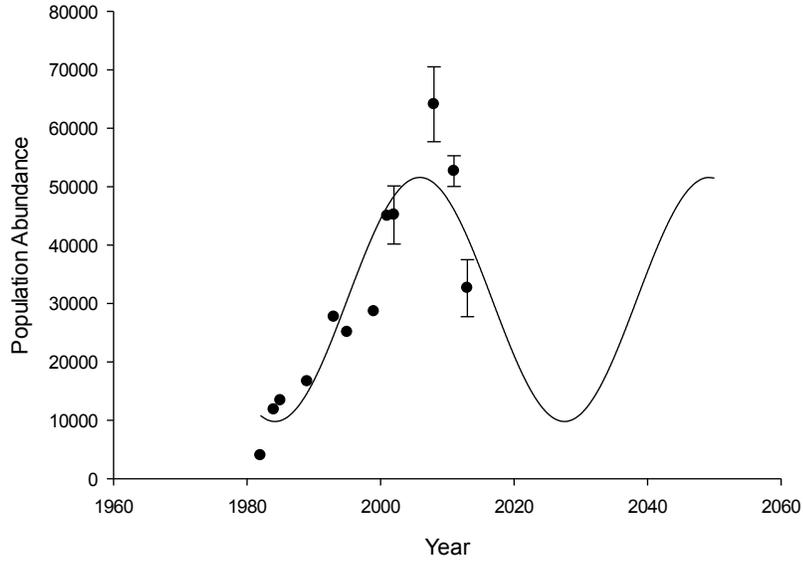
The Central Arctic subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.798$ ,  $p < 0.01$ ) with a period of 49 years ( $SE = 10$ ) and an amplitude of 21,400 ( $SE = 5,084$ ).

Central Arctic Sine Function Fit



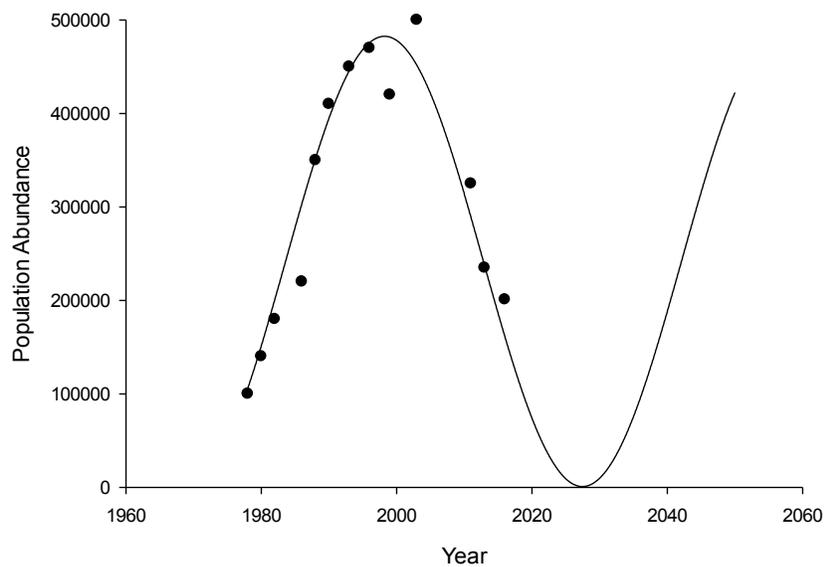
The Teshekpuk Lake subpopulation time-series population abundance estimates approximate a sine wave ( $r = 0.919$ ,  $p < 0.01$ ) with a period of 43 years ( $SE = 8.3$ ) and an amplitude of 20,905 ( $SE = 3,260$ ).

Teshekpuk Lake Sine Function Fit



The Western Arctic subpopulation time-series census population abundance estimates approximate a sine wave ( $r = 0.972$ ,  $p < 0.01$ ) with a period of 59 years ( $SE = 16.3$ ) and an amplitude of 240,953 ( $SE = 85,188$ ).

Western Arctic Sine Function Fit



### SUPPLEMENTARY III: SUBPOPULATION RANGE ATTRIBUTE METADATA

Normalized difference vegetation index (NDVI), net primary production (NPP) and mean land surface temperature (LST) were obtained for each subpopulation range using Google Earth Engine. The scripts identified (below) are examples. Each script was slightly modified to select the specified attribute on a subpopulation by subpopulation basis.

Subpopulation ranges were identified and georeferenced based on the COSEWIC (2015) report map of barren-ground caribou designatable units. The ranges used in conjunction with the Google Earth Engine script were archived in KML and KMZ file formats under the file name “Google Earth Engine – Barren-ground Caribou Subpopulation Range Files”. The NDVI, NPP and LST metadata obtained from Google Earth Engine was organized by subpopulation archived under the file name “Barren-ground Caribou Subpopulation LST, NPP and NDVI meta-data.xlsx”. Both the range files and meta-data file are available upon request to the corresponding author.

**Normalized Difference Vegetation Index (NDVI):** NDVI data was obtained from the USGS Landsat 7 TOA Reflectance (Orthorectified) image collection.

```
//Import Barrenland Herd KML ranges
var range = ee.FeatureCollection('ft:1Eugplvi9_n2CCoXJyPb5feDmenjGx0egXFJwhEbn');
Map.addLayer(range);

//Function for collection of images minimizing cloud cover
var rgb_vis = {min: 0, max: 0.3, bands:['B4', 'B3', 'B2']};
function addNDVI(image) {
  var ndvi = image.normalizedDifference(['B4', 'B3']);
  return image.addBands(ndvi);
}
var filtered = L7.filterDate('2000-01-01', '2017-12-31')
  .filterBounds(ROI);
var with_ndvi = filtered.map(addNDVI);
Map.addLayer(filtered.median(), rgb_vis, 'RGB');
Map.addLayer(with_ndvi.median(), {bands: 'nd', min: 0, max: 1}, 'NDVI');

//Print time series chart
```

```
print(Chart.image.series(with_ndvi.select('nd'), ROI));
```

**Net Primary Production (NPP):** NPP data was obtained from the MOD17A3.055: Terra Net Primary Production Yearly Global 1km image collection.

```
//Import Barrenland Herd KML ranges
```

```
var range = ee.FeatureCollection('ft:1Eugplvi9_n2CCoXJyPb5feDmenjGx0egXFJwhEbn');
```

```
Map.addLayer(range);
```

```
// Extract NPP band
```

```
var NPP = MODIS.select('Npp');
```

```
//Clip image to polygon geometry
```

```
var NPP_roi = MODIS.map(function(image) { return image.clip(WA_Total); });
```

```
Map.addLayer(NPP_roi);
```

```
//Print NPP time-series
```

```
print(Chart.image.series(NPP_roi.select('Npp'), WA_Total));
```

**Mean Land Surface Temperature (LST):** LST data was obtained from the MOD11A2.006 Terra Land Surface Temperature and Emissivity 8-Day Global 1km image collection.

```
//Import Barren-ground caribou KML Herd Ranges
```

```
var range = ee.FeatureCollection('ft:1Eugplvi9_n2CCoXJyPb5feDmenjGx0egXFJwhEbn');
```

```
Map.addLayer(range);
```

```
//Import LST and convert from Kelvin to Celcius
```

```
var modisLSTday = ee.ImageCollection('MODIS/006/MOD11A2').select('LST_Day_1km');
```

```
var modLSTday = modisLSTday.map(function(img) {
```

```
  return
```

```
  img.multiply(0.02).subtract(273.15).copyProperties(img,['system:time_start','system:time_end']);
```

```
});
```

```
//Clip LST to barren-ground polygons
var LST_roi = modLSTday.map(function(image) { return image.clip(WA_Total); });
Map.addLayer(LST_roi);

//Chart LST Time-series
var time_series = Chart.image.series(LST_roi, WA_Total, ee.Reducer.mean(), 1000, 'system:time_start');
print(time_series);
```

## **SUPPLEMENTARY IV: PROGRAM CARIBOU 1.0**

This Supplementary contains an email address for the following digital materials. First is a ReadMe.doc text file that describes how to install program CARIBOU 1.0. Program CARIBOU 1.0 is written in the Visual Basic program language. The second file is titled: VisualBasicPowerPacksSetup.exe. This file needs to be installed before program CARIBOU will run. Third is a zipped file containing Program CARIBOU 1.0 and associated install files including the usual setup.exe that automates the installation. Fourth, is a folder containing three “project files”. Program CARIBOU 1.0 can read and save subpopulation-specific project files. The three project files included are for the Qamanirjuaq, Bathurst, and George River subpopulations. One can load and modify them using program CARIBOU 1.0, which means you can create entirely new project files for other subpopulations or change the harvest and demographic values described in Chapters 1 and 2 to explore the response space, conduct sensitivity analyses, or correct our simulations if you disagree with our input values or density effects settings. The fifth file is the user manual for Visual Basic program RISKMAN, which was the life table model that program CARIBOU 1.0 was created from. The RISKMAN user manual provides information on conventions for entering and modifying the input variables, modifying the density effect functions, and viewing/saving the output data.

There is currently no website or journal archive address where these files can be obtained. The files are available upon request from Mr. Eric Bongelli at: [esbongel@lakeheadu.ca](mailto:esbongel@lakeheadu.ca). The steps to install PROGRAM caribou on an IBM PC with Windows 10 operating system are as follows:

- 1) Run VisualBasicPowerPacksSetup.exe .
- 2) Click on the CARIBOU zipped file, and run setup.exe .
- 3) Open one of the project files using the CARIBOU 1.0 file tab.
- 4) Run the program.

Questions on how to load and run the program are welcome. The program is written as an expert simulation system for barren-ground caribou. It is intended for people with a population dynamics background, and does require some time to learn before it can be used effectively. It is recommended that new users read the RISKMAN manual to become familiar with the structure and the terminology used in the program. A program CARIBOU 1.0 manual is planned, but has not been completed.