

North American barren-ground caribou cycles are driven by logistic trophic dynamics

Eric Bongelli¹, Martha Dowsley², Dean Cluff³, Mitch Campbell⁴, and Mitchell Taylor²

¹Lakehead University Faculty of Science and Environmental Studies

²Lakehead University

³Government of the Northwest Territories

⁴Government of Nunavut

June 29, 2022

Abstract

We used the Qamanirjuaq, Bathurst, and George River barren-ground caribou sine cycles to project numbers (N_t), calculate subpopulation annual growth rates (λ_t) and calculate logistic carrying capacity (K_t). Maximum annual growth rate was 1.196 and maximum annual rate of decline was 0.836 for the harvested Qamanirjuaq subpopulation sine cycle. However, the maximum annual subpopulation growth rates for both the harvested Bathurst and George River subpopulation sine cycles were greater than the biologically possible maximum intrinsic rate of increase during the eruption phase. Subpopulation numbers for Qamanirjuaq, Bathurst and George River barren-ground caribou subpopulations all closely tracked carrying capacity for one complete cycle with lag times between N_t and K_t ranging from < 1 -year to approximately 5-years. The short lag times observed indicates that Qamanirjuaq, Bathurst and George River barren-ground caribou subpopulations closely track their range condition. Range condition drives barren-ground caribou subpopulation cycles, but range condition also cycles; presumably because annual barren-ground caribou grazing rates are proportional to barren-ground caribou numbers and eventually exceed range annual growth rates. Immigration from adjacent subpopulations plays a role in the initiation and acceleration of the eruption period in some subpopulations, but not all of them. Numerical synchrony and asynchrony with adjacent subpopulation cycles can affect the timing of the eruption phase through mediation of immigration. Once subpopulation range has recovered, the rapid recovery of subpopulation numbers suggest that subpopulations are not restricted by other factors. The regularity and symmetry of both the increase and decline phases of these cycles suggests that the barren-ground caribou cycle is both stable and resilient. Continuation of barren-ground caribou cycles at historical levels is likely if habitat conservation measures are adopted so that annual migration patterns are not disrupted, summer and winter range remain undisturbed and common-sense harvest management policies are adopted when caribou are at low numbers.

North American barren-ground caribou cycles are driven by logistic trophic dynamics

Bongelli, E.¹, Dowsley, M.², Cluff, H.D.³, Campbell, M.⁴, & Taylor, M.²

Abstract:

We used the Qamanirjuaq, Bathurst, and George River barren-ground caribou sine cycles to project numbers (N_t), calculate subpopulation annual growth rates (λ_t) and calculate logistic carrying capacity (K_t). Maximum annual growth rate during the eruption phase was 1.196 and maximum annual rate of decline was 0.836 for the harvested Qamanirjuaq subpopulation sine cycle. However, the maximum annual subpopulation growth rates for both the harvested Bathurst and George River subpopulation sine cycles were greater than the biologically possible maximum intrinsic rate of increase during the eruption phase. Subpopulation numbers for Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations all closely tracked carrying capacity for one complete cycle with lag times between N_t and K_t ranging from < 1 -year

to approximately 5-years (mean lag times were 2.898, 2.661, and 2.430 years respectively). The short lag times observed indicates that Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations closely track their range condition, and that grazing impacts begin to reduce intrinsic subpopulation growth rates about midway into the increase portion of the cycle. Range condition drives barren-ground caribou subpopulation cycles, but range condition also cycles; presumably because annual barren-ground caribou grazing rates are proportional to barren-ground caribou numbers and eventually exceed range annual growth rates. Barren-ground caribou numbers and their carrying capacity (K_t) sine cycle because state variables in this relatively simple two-level trophic relationship are mutually dependent. Immigration from adjacent subpopulations plays a role in the initiation and acceleration of the eruption period in some subpopulations, but not all of them. Numerical synchrony and asynchrony with adjacent subpopulation cycles can affect the timing of the eruption phase through mediation of immigration. However once subpopulation range has recovered, the rapid recovery of subpopulation numbers suggest that subpopulations are not restricted by other factors. The regularity and symmetry of both the increase and decline phases of these cycles suggests that the barren-ground caribou cycle is both stable and resilient. Continuation of barren-ground caribou cycles at historical levels is likely if habitat conservation measures are adopted so that annual migration patterns are not disrupted, summer and winter range remain undisturbed and common-sense harvest management policies are adopted when caribou are at low numbers.

Key Words: barren-ground caribou, carrying capacity, cyclic species, demography, density effects, management, population cycles, resilience, sine cycle

¹ Faculty of Science and Environmental Studies. Department of Geography and Environment, Lakehead University. 955, Oliver Road, Thunder Bay, ON, Canada P7B 5E1. | KBM Resources Group, 349 Mooney Avenue, Thunder Bay, Canada ON, P7B 5L5. (esbongel@lakeheadu.ca)

² Faculty of Science and Environmental Studies. Department of Geography and Environment, Lakehead University. 955, Oliver Road, Thunder Bay, ON, P7B 5E1

³ Regional Biologist North Slave Region. Department of Environment and Natural Resources, Government of Northwest Territories. 3803 Bretzlaff Drive, Yellowknife, NT. X1A 2P9

⁴ Regional Wildlife Biologist Kivalliq Region. Wildlife Research Division, Department of Environment, Government of Nunavut. PO Box 120, Arviat, NU, X0C 0E0.

DATA ACCESSIBILITY STATEMENT

All the data for this paper were taken from public sources. The compiled dataset used for the analysis described in this manuscript will be publicly accessible through the Dryad data repository. The dataset will be submitted to Dryad upon acceptance of this article.

INTRODUCTION

Subpopulations of mainland migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) are unique among the deer family (Cervidae) because they make annual migrations between the treeless tundra in the summer and the forested taiga in the winter and are typically sine cyclic (Bongelli *et al.*, 2020). Barren-ground caribou are an age-structured, annual birth pulse species (Caughley 1977) whose natural history and ecology are consistent with the assumptions of life table discrete population modeling (Bongelli *et al.* 2020, Gunn & Miller, 1986; Russell *et al.*, 2002; Wilson & Reeder, 2005; Government of Yukon, 2015, and COSEWIC 2016). Ecological circumstances (e.g., the ratio of summer range to winter range, range overlap with adjacent subpopulations, subpopulation exchange rates, harvest removal rates, and the degree of industrial development) can vary between subpopulations. However, Bongelli *et al.*, (2020) showed that 96% of the variation in nine subpopulations of barren-ground caribou sine cycle dynamics could be explained by range area and range productivity.

Barren-ground caribou 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+. 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 subpopulation numbers are ultimately regulated by density-dependent reductions in calf production and/or survival rates (Demerec, 1957; Tanner, 1966; Caughley, 1977; McCullough, 1979; Fowler, 1981; Kie & White, 1985; Skogland, 1985; Clutton-Brock *et al.*, 1987; Messier *et al.*, 1988; Boyce, 1989; McCullough, 1999; Bowyer *et al.*, 2014).

Thomas Malthus (1798) is credited with the first formal proposition that there are natural limitations to population growth. A continuous mathematical formulation of this principle termed the logistic equation was initially formulated by Verhulst (1838) and rediscovered by Pearl and Reed (1920) and Pearl and Reed (1922). An alternative formulation of the discrete logistic equation indicates 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 intrinsic annual growth rate (λ_{\max}) (May, 1976; Renshaw, 1991). We examined the relationship between barren-ground caribou subpopulation growth rate (λ) and K through the cycle by calculating K utilizing the discrete analog of the Verhulst (1838) and Pearl and Reed (1920) formulation of the logistic equation.

The maximum and minimum annual rates of population growth (or decline) reported for barren-ground caribou varies between subpopulations, but typically λ does not exceed 1.17 and is not less than 0.83 (Gunn, 2003). Heard (1980) estimated the maximum stable age population growth rate for barren-ground caribou subpopulations was $\lambda_{\max} = 1.363$, which we confirmed using an independent life table model (Bongelli, 2019). At $\lambda_{\max} [?] 1.363$ the logistic equation suggests that, without lag-times, caribou subpopulations (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 greater than the biologically maximum possible λ for barren-ground caribou.

We chose the Qamanirjuaq, Bathurst, and George River subpopulations for our comparison of barren-ground caribou cycles because they are relatively well-known and have been frequently surveyed. We updated the Bongelli *et al.* (2020) sine model for the Qamanirjuaq subpopulation to include the most recent (2017) abundance estimate. The updated Qamanirjuaq cycle has a period of 58 years ($SE = 5.7$) and an amplitude of 218,431 ($SE = 31,348$). The Bathurst subpopulation sine cycle has a period of 42 years ($SE = 3.4$) and an amplitude of 203,154 ($SE = 23,147$) (Bongelli *et al.*, 2020). The George River subpopulation's sine cycle (Bongelli *et al.*, 2020) was updated to include the 2020 subpopulation estimate of 8,100. The updated George River sine cycle has a period of 52 years ($SE = 2.6$) and an amplitude of 305,000 ($SE = 26,644$).

We compared cyclic changes in population growth rates (λ_t), carrying capacity (K_t), and lag time required to reach K_t from population numbers (N_t) for our three case studies. When the observed λ_t (N_{t+1}/N_t) is greater than biologically possible, the fraction of population change that is due to extrinsic growth (i.e., immigration) was estimated, and the role of immigration in triggering subpopulation eruption post habitat recovery was examined. Together these summary statistics and comparisons suggest an alternative explanation for barren-ground caribou subpopulation dynamics from those that are strictly intrinsic and drawn from short-term non-cyclic snapshots of the cycle. We considered the implications of viewing barren-ground caribou as a cyclic species for management and status determination.

METHODS

We assumed the published subpopulation estimates varied in quality but were generally accurate because collectively they were a good fit to the sine cycle that is characteristic of barren-ground caribou (Bongelli *et al.*, 2020). The discrete life table model assumes a constant time of census (Birch, 1948; Cole, 1954; Caughley, 1977), which we identified as the calving ground subpopulation surveys. We did not find reliable estimates of age-specific annual survival or of age-specific life table annual recruitment rates that were time-of-census referenced to the subpopulation calving ground survey for any barren-ground caribou subpopulation that extended over more than a fraction of its entire cycle. Consequently, we restricted our consideration of density effects to population growth rate (λ) rather than birth and survival rates.

The sine cycle fit to the subpopulation estimates over time (year) was used to estimate the number at time = t (N_t) for the entire cycle. We estimated annual subpopulation growth rate (λ_t) as: N_{t+1}/N_t . We used the discrete formulation of the Verhulst (1838) logistic equation to calculate carrying capacity (K_t) estimates for each year of the Qamanirjuaq, Bathurst, and George River sine cycles. However, in some cases during subpopulation increase, the observed growth rate was more than the biological maximum rate of increase (λ_{\max} [?] 1.363). We limited the maximum value for intrinsic λ_t to values that were within the biological maximum and realistic. We chose $\lambda_{\text{plausible}} = 1.20$ as our maximum plausible rate of intrinsic increase considering that natural mortality from harvest and predation would never be zero and all cows age 2+ would not calve ($m_x = 1.0$) in a natural subpopulation. We assumed that any subpopulation increase greater than $\lambda_{\text{plausible}}$ was due to immigration. When λ_t values were >1.2 ($\lambda_{\text{plausible}}$) we corrected them to 1.2 for our Verhulst (1838) determinations of K_t because the Verhulst logistic equation does not include a term for immigration. We used the term “eruption period” to describe the time interval when consecutive λ_t values were greater than 1.0 and increasing year over year and/or [?]1.20 (20% increase/year). We calculated K as:

$\lambda_{\max} = 0.363$ (biological maximum intrinsic rate of increase)

$$N_{t+1} - N_t = \lambda_{\max} * N_t * \left(1 - \frac{N_t}{K_t}\right)$$

$$\frac{N_{t+1}}{N_t} = \lambda_t = 1 + \lambda_{\text{intrinsic}}$$

$$\lambda_{\text{intrinsic}} = \left(\frac{N_{t+1}}{N_t}\right) - 1$$

$$K_t = \frac{N_t}{\left(\frac{\lambda_t}{\lambda_{\max}} - 1\right)}$$

We estimated the demographic pressure for increase as the time required for N_t to reach K_t (lag time = L_t) using the uncorrected (intrinsic + immigration) λ_t values:

$$L_t = \ln\left(\frac{K_t}{N_t}\right) / \lambda_t$$

We compared mean lag time values and mean population growth rate values between all three subpopulations using the Kruskal-Wallis non-parametric test (IBM Corp, 2021) for three distinct cycle phases: 1) one complete cycle, 2) one complete cycle excluding the eruption years (i.e., intrinsic growth only) and 3) only the eruption years of the cycle. For all assessments we assumed pairwise comparisons were nonsignificant if the probability of the test statistic was [?] 0.05 using the Bonferroni corrected significance values (IBM Corp, 2021). We used K-means clustering (IBM Corp, 2021) to determine whether subpopulations were grouped or contiguous with respect to lag time values and population growth rate values for the eruption years of the subpopulation cycles.

We calculated the relative contributions of intrinsic growth ($N_t * \lambda_{\text{plausible}}$) and immigration (I_t) to population growth during the eruption period from the following relationship:

$$I_t = (N_{t+1}) - (N_t * \lambda_{\text{plausible}})$$

As per equations above, population growth rate (λ_t), carrying capacity (K_t), and lag time (N_t - K_t) are covariant variables. We used Descriptive Statistics (Correlations) (IBM Corp, 2021) to determine the within-subpopulation bivariate correlation coefficients for these variables.

RESULTS

Sine cycle subpopulation growth rates for the Qamanirjuaq subpopulation (λ_t) varied from a maximum of 1.196 in the increase phase to 0.837 in the decline phase (Table 1; Figure 1). All the sine cycle λ values for the Qamanirjuaq subpopulation were within the maximum plausible rate of increase (i.e., < 1.2). However, calculated sine cyclic estimates of the maximum and minimum rates of annual subpopulation growth were sometimes greater than the maximum biologically possible intrinsic rate of increase ($\lambda_{\max} = 1.363$) during the eruption phase for both the Bathurst ($\lambda_{\max} = 1.47$; $\lambda_{\min} = 0.68$) and George River ($\lambda_{\max} = 2.85$; $\lambda_{\min} = 0.35$) subpopulations (Table 1; Figure 2; Figure 3).

Barren-ground caribou subpopulation numbers (N_t) closely tracked carrying capacity (K_t) for all three subpopulations (Table 1; Figure 1; Figure 2; Figure 3; Figure 4). Mean cycle lag times (years for $N_t - K_t$) at observed λ_t (N_{t+1}/N_t) for the Qamanirjuaq, Bathurst, and George River subpopulations were 2.898 (SE = 0.008), 2.661 (SE = 0.103), and 2.430 (SE = 0.121) respectively (Table 2; Figure 4). Kruskal-Wallis pairwise comparison of the observed mean $N_t - K_t$ lag times of each subpopulation over one complete cycle demonstrated that the mean lag time (intrinsic + immigration) for the George River subpopulation was significantly different from the Qamanirjuaq ($p = 0.018$), but not significantly different from the Bathurst ($p = 0.838$) subpopulation (Table 3). The difference in mean lag times between the Qamanirjuaq and Bathurst subpopulation was also not significant ($p = 0.414$) (Table 3). When the period of eruption years was excluded from the comparison of mean lag time values (i.e., only intrinsic lag times included) there were no significant differences in the projected lag time values between any of the three subpopulations ($p = 0.249$) (Table 3). When pairwise comparisons were restricted to only the eruption period the mean lag time for the George River subpopulation was significantly different from the Qamanirjuaq ($p = 0.013$) but not significantly different from the Bathurst ($p = 0.690$). The difference in mean lag time between the Qamanirjuaq and Bathurst subpopulations was also not significant ($p = 0.221$) (Table 3).

Kruskal-Wallis pairwise comparison of mean population growth rates resulted in no significant difference between subpopulations for one complete cycle ($p = 0.958$) or for one complete cycle excluding eruption years ($p = 0.249$) (Table 4). When only eruption years were considered separately, the mean population growth rate for the George River subpopulation was significantly different than mean population growth rate for the Qamanirjuaq ($p = 0.001$) but not significantly different from the Bathurst mean population growth rate ($p = 0.427$). The difference in mean population growth rate between the Qamanirjuaq and Bathurst subpopulations was also not significant ($p = 0.070$) (Table 4).

Subpopulation annual growth rates during the eruption phase of the sine cycle sometimes exceeded the biologically possible and biologically plausible intrinsic growth rates for barren-ground caribou in both the Bathurst and George River subpopulations (Figure 5). However, the Qamanirjuaq subpopulation growth rates were entirely within the plausible intrinsic value ($\lambda_{\text{plausible}} = 1.2$) (Figure 5). The additional annual increase observed in the George River and Bathurst eruption phase was attributed to extrinsic growth (i.e., immigration) (Figure 6). Immigration rates for the Bathurst subpopulation initially increased, peaked, and then declined (Figure 6). Immigration rates for the George River subpopulation were highest initially then declined throughout the eruption phase (Figure 6).

K-means cluster analysis identified three distinct clusters of lag time values and population growth rate values for the eruption years of each subpopulation cycle. Clusters were characterized as: 1) short N-K time lags and high lambda values, 2) intermediate N-K time lags and intermediate lambda values, and 3) long N-K time lags and low lambda values (Figure 7). Cluster 1 was exclusively associated with the George River subpopulation (Figure 7). Cluster 2 was mainly comprised of Bathurst records but also contained George River and Qamanirjuaq records. Cluster 3 was predominantly associated with the Qamanirjuaq subpopulation.

Population growth rate, carrying capacity, and lag time were all correlated ($p[?]0.05$) for each of the three subpopulations (Table 5).

DISCUSSION

Caughley and Gunn (1993), Gunn (2003), Archer and Tieszen (1980), and Payette *et al.* (2001) suggested

that barren-ground caribou fluctuations were mainly caused by the over-grazing of caribou when subpopulation abundance was at high levels, followed by declines to densities sufficiently low that the arctic/subarctic range could recover. Bongelli *et al.*, (2020) provided a quantitative demonstration that most barren-ground caribou subpopulations do not just fluctuate, they cycle in a regular manner (sine cycles). Bongelli *et al.* (2020) found that approximately 96% of the variation in the population cycles of nine sine cyclic North American barren-ground subpopulations could be explained by a relatively simple environmental regression model that considered only the subpopulation range size and range productivity. Recognizing that a sine cycle provides an unambiguous estimate of the N_t for the entire cycle, the Verhulst (1838) equation for logistic growth was employed to show that carrying capacity (K_t) also cycles regularly (Figure 1; Figure 2; Figure 3). Barren-ground caribou logistic carrying capacity (K) is best understood as a dynamic proxy variable (the units for K are subpopulation numbers) for subpopulation range condition.

Subpopulation numbers of Qamanirjuaq, Bathurst, and George River caribou closely tracked their respective carrying capacities (2-3 years) throughout most of their respective cycles (Table 1; Figures 1; Figure 2; Figure 3; Figure 4). However, during the eruption phase of the cycle all three subpopulations required about double the time to reach K_t from intrinsic growth than during the rest of the cycle (Table 1; Figure 4). In these three case studies, barren-ground caribou declined when the range declined due to over-grazing, then increased rapidly once their range had recovered. If some external (perhaps decadal, progressive, catastrophic, or circumstantial) factor were to impact subpopulation numbers, their range, or both there would be a response to the trajectories of both habitat (K) and subpopulation numbers (N). However, Bongelli *et al.*, (2020) showed that the best (Bayesian Information Criteria) mathematical description for barren-ground caribou population trajectories is a sine cycle. The increase phase is symmetrical to the decline phase. Exactly half of the cycle is spent with numbers $> \frac{1}{2}$ the amplitude and exactly half the cycle is spent with numbers $< \frac{1}{2}$ the amplitude. The regularity of barren-ground caribou population dynamics over the history of census data collection for 9 subpopulations suggests a simple and consistent relationship between barren-ground caribou subpopulations and their range. Bongelli *et al.* (2020) suggests that barren-ground caribou population fluctuations are not merely affected by herbivore/range interactions; they are almost entirely determined by this relationship. Other factors may become relevant if those factors are unusually extreme, persistent, or occur at a sensitive time in the cycle (e.g., immigration during eruption or high harvest rates at low numbers). However, Bongelli *et al.*, (2020) suggests that anthropogenic factors at historical levels are unlikely to have any lasting or substantive impact on barren-ground caribou range dynamics. In all three of our case studies, carrying capacity cycled similar to subpopulation numbers.

We defined the eruption phase as consecutive years when annual subpopulation growth rate (λ_t) is greater than 1.0 and increasing each year, and/or λ_t [?] 1.2. Sine cyclic barren-ground caribou subpopulations are gradually increasing for half the cycle period, and gradually declining in the other half. The eruption phase for the Qamanirjuaq, Bathurst, and George River subpopulations ranged from 6 to 9 years or 12-19% of the cycle (Table 1). After the eruption phase, barren-ground caribou subpopulations continue to increase in numbers, but λ_t declines progressively into the low period of the cycle (Figure 1; Figure 2; Figure 3; Figure 4). Post-eruption, the initial decline in λ_t is due to increasing densities of caribou relative to carrying capacity. Once caribou numbers are sufficient to cause carrying capacity to decline, the decline in λ_t is mainly due to declining carrying capacity (Figure 1; Figure 2; Figure 3). The decline in carrying capacity continues until declining caribou numbers are insufficient to cause a continued decline in impacted forage communities (through over-grazing and/or trampling) and habitat recovery can begin. Range recovery is slow initially, prolonging the time when caribou are at low numbers and keeping the rate of caribou recovery sufficiently low that increase is difficult to detect given the variance inherent to standard survey methods. The surge of habitat recovery preceded the surge in caribou numbers by 2-4 years in all three subpopulations.

Population growth rates continued to track K throughout the eruption phase for the Qamanirjuaq subpopulation (Figure 1). The Qamanirjuaq subpopulation appeared to be limited by carrying capacity throughout eruption phase (i.e., $\lambda_t < 1.2$). The maximum and minimum rates of population growth and decline identified for the Qamanirjuaq subpopulation ($\lambda_{\max} = 1.196$; $\lambda_{\min} = 0.837$), align with previously reported (Gunn, 2003) maximum and minimum rates of population growth and decline for barren-ground caribou generally

($\lambda_{\max} = 1.17$; $\lambda_{\min} = 0.830$). The Qamanirjuaq subpopulation increased more slowly and declined more slowly than the Bathurst and George River subpopulations. For the Qamanirjuaq subpopulation our estimates of logistic K_t from sine curve N_t indicated that subpopulation recovery cannot occur faster than habitat regeneration occurs. Once range recovery is well under way, Qamanirjuaq caribou have the potential to double in about 4 years with no immigration under natural conditions. Conversely, the maximum observed rate of decline suggests the half-life of the subpopulation during the cycle period of maximum decline was a little over 3 years. Our results suggest that at any given time in the cycle, the number of caribou in the Qamanirjuaq subpopulation is typically only a few years away from the current carrying capacity of its range (Figure 4).

Both the Bathurst and George River subpopulations increased at rates exceeding the maximum possible intrinsic rates of increase (i.e., $\lambda_t > 1.363$) during the eruption phase of their cycle (Figure 2; Figure 3; Table 1). Population growth rates greater than the maximum plausible rate of increase (> 1.2) during the eruption phase were observed for 9 of 42 years during the Bathurst cycle, and 9 of 52 years for the George River cycle. Observed population growth rates were greater than the intrinsic (or plausible) maximum for the Bathurst and George River subpopulations during the eruption phase, indicating that immigration was contributing to the eruptive increase from low numbers (Figure 5; Figure 6)

The Qamanirjuaq subpopulation did not experience detectable levels of immigration during any part of its cycle. The George River subpopulation experienced the highest observed subpopulation growth rates ($\lambda = 2.85$), the greatest percentage of immigration driven increase (89.2%) and the shortest lag time values (0.765 years) during its eruption period (Figure 5; Figure 6; Figure 7). Immigration during the Bathurst eruption was initially intermediate (~39%), then increased to ~57%, and then gradually declined to about 20% (Figure 6). Net immigration was observed only during the eruption phase for the Bathurst and George River subpopulations. Immigration may be important in initiating and sustaining the eruption phase of barren-ground caribou when immigrants are available from adjacent subpopulations that share the winter range. Our method of calculating immigration assumes net immigration in a given year is a permanent transfer of individuals from an adjacent subpopulation

There were no significant differences between subpopulation cycle mean lag times ($p = 0.249$) or subpopulation cycle mean annual growth rates ($p = 0.249$) when the eruption years were excluded from the cycle samples (Table 3; Table 4). When the eruption years were included in the subpopulation cycle samples, the George River subpopulation had a significantly shorter mean lag time than the Qamanirjuaq ($p = 0.018$), but there were no significant differences between subpopulation annual growth rates ($p = 0.958$) (Table 3). When only the eruption years were considered, the George River subpopulation mean lag time was shorter than the Qamanirjuaq mean lag time ($p = 0.013$) and the George River subpopulation mean annual growth rate was larger than the Qamanirjuaq mean annual growth rate ($p < 0.001$) (Table 3; Table 4). There was no significant difference between the Bathurst mean lag times or the Bathurst mean annual population growth rates when compared to either the George River or the Qamanirjuaq subpopulations (Tables 3; Table 4). The only differences between subpopulation mean lag times and mean annual growth rates were those due to immigration during the eruption phase. Most (89%) of the initial George River eruption increase was due to immigration, while none of the Qamanirjuaq eruption increase was due to immigration (Figure 6). The Bathurst eruption was aided by up to ~50% immigration (Figure 6), but even that contribution was insufficient to cause mean lag times and mean annual subpopulation growth rates during the eruption to be statistically ($p \geq 0.05$) different from the no-immigration Qamanirjuaq eruption phase or high immigration George River phase (Table 3; Table 4).

There are no life history limits to the rates at which a subpopulation might decline except those imposed by extirpation. The George River subpopulation had the highest observed λ_{\max} values but also the highest observed rates of decline (λ_{\min}). Bathurst subpopulation maximum rates of increase and decline were intermediate to the George River and Qamanirjuaq subpopulation λ_{\max} and λ_{\min} values. Optimal foraging theory suggests that individuals will shift their habitat to maximize energy intake (Stephens and Krebs, 1986). We suggest that as carry capacity continually declines, individuals may emigrate from their home range to an

adjacent range if greater availability and quality of forage species are available there. Migration to the best range conditions would increase the rate of subpopulation decline in the contributing subpopulation and increase the rate of growth in the adjacent (receiving) subpopulation.

Bathurst and George River eruption patterns suggest that eruption is predicated on habitat recovery but can be accelerated by immigration from adjacent subpopulations. In both cases immigration peaked early in the eruption phase, and then declined as the subpopulation increased. Although substantial net immigration may occur during the eruption phase, these results are most consistent with the view that barren-ground caribou subpopulations may be demographically closed for management purposes. Although immigration may be a factor in triggering the eruption phase, the role of immigration is quickly subordinated by the intrinsic capacity for N_t to quickly close on K_t . Immigration appears to play only a brief and transitory role in barren-ground caribou cycles relative to intrinsic subpopulation growth rates. The main determinant of barren-ground caribou subpopulation numbers and trend is range carrying capacity for all but a few years of the eruption cycle.

George River caribou have one of the largest total ranges and the largest winter ranges of all barren-ground caribou subpopulations (Bongelli *et al.*, 2020; Schmelzer & Otto, 2003). Schmelzer & Otto (2003) found that George River caribou summer range habitat quickly deteriorated during the mid-1980s which corresponds to a period of significant population growth. During this time, George River caribou experienced what Schmelzer & Otto (2003) termed winter range drift. Schmelzer & Otto (2003) suggest that winter range forage allowed George River caribou to delay the effects of density-dependent population decline due to summer forage limitations by expanding their use of the winter range. The ability of George River caribou to shift winter range to provide a compensatory source of forage, delays the density-dependent feedback of range deterioration allowing them to maintain greater numbers, ultimately increasing over-grazing of the summer range before the inevitable decline occurs. Schmelzer & Otto (2003) suggest that the demographic benefits of winter range drift are limited by the cost of lengthier migration to the traditional calving grounds.

Radio collar telemetry data indicated partial overlap between the George River and Leaf River subpopulations during the 1990s and early 2000s (Taillon *et al.*, 2016) which corresponds to a period of growth and peak abundance in the George River subpopulation. However there has been no overlap identified between the two subpopulations since approximately 2006 (Taillon *et al.*, 2016). We speculate that the eruption period of subpopulation growth throughout the 1960s for George River caribou was augmented by immigrants from the adjacent Leaf River subpopulation which was estimated to be at or near its peak during that time (Bongelli *et al.*, 2020). Leaf River caribou are currently declining (CARMA, 2016), so it is unlikely that immigration from the Leaf River subpopulation will contribute substantially (or at all) to the recovery of the George River subpopulation from its current period of low densities. Asynchrony with the Leaf River subpopulation may delay the recovery of the George River subpopulation.

Another possibility to dependency on immigration from the Leaf River subpopulation for eruptive recovery of the George River subpopulation is that some George River caribou have temporarily foregone the annual migration because the summer range was severely over-grazed. As the George River summer range regenerates, the numbers counted (calving ground census) on the summer range could be augmented by a return to annual migration pattern. Still another possibility is that George River caribou may become more aggregated on the calving ground as it increases, and the appearance of immigration during the eruption phase may be due to disaggregation at low densities (resulting in under-estimation) when they are at low numbers. The data available to us were insufficient to limit or discriminate between these or other possibilities for George River caribou recovery scenarios. We do believe that the eruption phase is imminent for the George River caribou, and suggest researchers monitor not only the numerical increase but also determine how the George River subpopulation recovers in the current cycle to guide future management when subpopulation is once again at the low point of its cycle.

Bathurst caribou are intermediate with respect to total range area and the proportion of the total range that is summer range (Bongelli *et al.*, 2020). Like the George River subpopulation, Bathurst caribou can be found further south in the winter range when cycle numbers are high, possibly extending the period

of decline to minimum numbers and thus increasing over-grazing damage to the summer range. Bathurst caribou differ from Qamanirjuaq and George River caribou in that their winter range overlaps with two other barren-ground caribou subpopulations (Bluenose East, and Beverly). The most recent (2021) population abundance estimates for Bathurst and Bluenose-East caribou are 6,240 and 23,200 respectively (Government of Northwest Territories, 2021). The most recent (2018) Beverly population abundance estimate is 103,400 (BQCMB, 2021). The 2021 Bathurst calving ground aerial photo survey and aerial reconnaissance survey found high levels of overlap between Bathurst, Beverly, and Bluenose-East caribou on the calving ground (Government of Northwest Territories, 2021). More recent 2022 telemetry data documents immigration from the Bathurst herd to the Beverly herd. Bathurst spring composition counts appear to contain annually variable fractions of Bluenose-East, and Beverly caribou. Immigration from these adjacent subpopulations could trigger and sustain the eruption phase of the Bathurst subpopulation once its habitat had sufficiently recovered.

Bongelli *et al.* (2020) found that the sine cycle fit for the Bathurst subpopulation was well-supported, but not as definitive as it was for other more demographically segregated subpopulations. Immigration from adjacent subpopulations sufficient to trigger an eruption would be expected to vary from cycle to cycle depending on the degree of synchrony/asynchrony and the degree of overlap with adjacent subpopulations. Predicting precisely when the Bathurst subpopulation will erupt may be more difficult than predicting the eruption phase for a subpopulation that is more demographically segregated and thus mainly driven by intrinsic subpopulation processes (e.g., Qamanirjuaq).

Some subpopulations (e.g., Qamanirjuaq) appear to cycle entirely due to density dependent intrinsic rates of birth and death. Other subpopulations appear to be demographically distinct yet exhibit a dramatic eruption phase that requires substantial immigration or repatriation (e.g., George River). Some subpopulations have overlapping summer and winter ranges with adjacent subpopulations, and inter-subpopulation exchange between these subpopulations is well documented (e.g., Bathurst). Yet all three subpopulations exhibit stable sine cyclic population dynamics rather than converge on some stable equilibrium density or experience periodic extirpation (Bongelli *et al.* 2020).

The λ_t versus lag time phase plane suggests a gradation of barren-ground caribou demographic performance rather than subpopulation specific clusters (Figure, 7). Extremes of eruption periods between mostly immigration (George River) and entirely intrinsic (Qamanirjuaq) were significantly different, but the intermediate immigration eruption subpopulation (Bathurst) was not significantly different from either extreme (Table 2; Figure 7). In all three of our ecologically distinct case studies, N_t closely followed K_t in symmetrical sine cycles. In these three subpopulations, range condition closely moderates caribou numbers except for the eruption phase. Post-eruption phase, range condition is almost immediately reduced by grazing. The N_t - K_t lag time is shortest during the decline portion of the cycle and greatest during the eruption phase that initiates the increase portion of the cycle (Figure 1; Figure 2; Figure 3). The regularity and symmetry of both the increase and decline phases of these cycles suggests that barren-ground caribou cycles are both stable and resilient. Short of extensive range management practices to enhance range productivity and/or availability there is little else managers can do to prevent or mitigate cyclical caribou declines or to speed up recovery.

Our relatively simple view of barren-ground population dynamics has strong quantitative support and is relevant to both wildlife co-management and species status designation. These case studies of the Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations identify both similarities and differences in the ecological circumstances of barren-ground caribou subpopulations. The biggest similarity and the central demographic characteristic of these subpopulations is that they are sine cyclic and N_t closely follows K_t . We suggest that barren-ground caribou subpopulations will cycle indefinitely as a demographic result of herbivore-range dynamics in contiguous tundra/taiga habitat. Barren-ground caribou subpopulations are genetically indistinguishable, but most of them can be regarded as demographically closed for management purposes. Immigration appears to play a role in the initiation and acceleration of the eruption period in some subpopulations, but not all of them. Synchrony and asynchrony with adjacent subpopulations can affect the

timing of the eruption phase but cannot independently initiate the eventual recovery of subpopulations until the range has recovered.

Precautionary harvest management at low numbers prior to the eruption phase will likely shorten the recovery time from low numbers. Once habitat has recovered the need for harvest management measures will diminish then disappear because it will become logistically impossible to stop barren-ground caribou from increasing to the point that they over-graze their range. Over-grazing begins and rapidly increases well before subpopulation numbers peak (Figure 1; Figure 2; Figure 3). Given the fundamental importance of the range to barren-ground caribou, wildlife co-managers could consider a “No Net Loss” policy requiring viable habitat replacement and/or critical habitat protection measures (e.g., calving, and calving migrations routes) for commercial developments on caribou range that cause harmful alteration, disruption, or destruction of caribou habitat. The utility of precautionary up-listing the conservation status of barren-ground caribou during the portion of their cycle when they are declining and at low numbers is unclear and appears inconsistent with their natural history. Species status determination could employ fidelity to an historical cycle as an alternative to generation-based designation criteria for cyclic species.

The underlying assumption of these findings is that the census estimates for these subpopulations of barren-ground caribou were accurate. Our results are empirical, not simulation model results. We are describing the demographic consequences of Bongelli et al. (2020) finding that the Qamanirjuaq, Bathurst, and George River (and most barren-ground caribou subpopulations) are sine cyclic. Our paper is fundamentally descriptive, not theoretical. Population growth rate (λ_t), carrying capacity (K_t), and lag time ($N_t - K_t$) are highly correlated (Table 5) because of how these variables are calculated. The axes of Figure 7 are population growth rate (λ_t) and lag time ($N_t - K_t$), and obviously we find that shorter lag times are associated with higher population growth rates for all three subpopulations. It is also apparent that there is a geometric relationship between (λ_t) and ($N_t - K_t$). We use these axes to define a phase plane useful in determining if there are subpopulation eruption clusters. The apparent geometric relationship between population growth rate and lag time is due to autocorrelation. The linear correlation measures between (λ_t), (K_t), and lag time ($N_t - K_t$) (Table 7) are highly significant but imperfect because the relationship between these two variables is geometric not linear; and because immigration rates between these subpopulations during the eruption phase were different. Population growth rate (λ_t), carrying capacity (K_t), and lag time ($N_t - K_t$) are descriptive summary statistics that derive from the sine cycles of the three subpopulations considered.

ACKNOWLEDGEMENTS:

We acknowledge Lakehead University and the Government of Nunavut for financial and logistic support. Troy Hegel and the *Rangifer* editorial board and reviewers contributed useful comments to an earlier version of this paper. The results, interpretations, opinions, conclusions, and any errors are entirely our own; and do not necessarily represent the views of any other individual, agency, or institution. All the data for this paper were taken from public sources or are acknowledged in the text. We acknowledge the hard work and professionalism of those who collected these data and made them open-source available.

LITERATURE CITED

- Archer, S., & Tieszen, L.L.** 1980. Growth and physiological responses of tundra plants to defoliation. - *Arctic and Alpine Research* . 12(4):531-552.
- Beverly Qamanirjuaq Caribou Management Board (BQCMB).** 2021. 2020/21 Annual Report. 46pp.
- Birch, L.C.** 1948. The intrinsic rate of natural increase of insect population. - *Journal of Animal Ecology* 17 (1): 15-26.
- Bongelli, E., Dowsley, M., Velasco-Herrera, V.M., & Taylor, M .** 2020. Do North American migratory barren-ground caribou subpopulations cycle? - *Arctic*. 73 (3): 326-346.

- Bongelli, E.** 2019. 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. Masters Thesis. Lakehead University. Department of Geography. 133pp.
- Bowyer, T.R., Bleich, V.C., Stewart, K.M., Whiting, J.C. & Monteith, K.L.** 2014. Density-dependence in ungulates: A review of causes and concepts with some clarifications. - *California Fish and Game*. 100 (3): 550-572.
- Boyce, M.S.** 1989. The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, Cambridge, United Kingdom.
- CARMA (CircumArctic Rangifer Monitoring and Assessment Network).** 2016. Interactive map. <http://carma.caff.is/index.php/carma-interactive-map>
- Caughley, G.** 1977. *Analysis of vertebrate populations*. John Wiley & Sons, London. 234pp.
- Caughley, G. & A. Gunn.** 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. *Oikos* 67:47-55.
- Clutton-Brock, T.H., Major, M., Albon, S.D. & Guinness, F.E.** 1987. Early development and population dynamics in Red Deer. I. density-dependent effects on juvenile survival. - *Journal of Animal Ecology*. 56 (1): 53-67.
- Cole, L.C.** 1954. Population consequences of life history phenomena. - *Quarterly Review of Biology* 29 (2): 103-134.
- COSEWIC**. 2016. COSEWIC assessment and status report on the Caribou *Rangifer tarandus*, Barren-ground population, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 123 pp.
- Demerec, M., Organizer.** 1957. Population studies: Animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology 22. Cold Spring Harbor, New York: The Biological Laboratory
- Fowler, C. W.** 1981. Density-dependence as related to life history strategy. - *Ecological Society of America*. 62 (3): 602-610.
- Government of Northwest Territories.** 2021. 2021 Survey Results for the Bathurst and Bluenose-East Barren-ground Caribou Herds. 9pp.
- Government of Yukon.** 2015. Barren-ground caribou. – Environment Yukon. Electronically available at: <http://www.env.gov.yk.ca/animals-habitat/mammals/barrengroundcaribou.php>
- Gunn, A.,** 2003. Voles, lemmings, and caribou - population cycles revisited? - *Rangifer*. 23 (2003): Special Issue No. 14: 105-112.
- Gunn, A, and Miller, F. L.** 1986. Traditional behavior and fidelity to caribou calving grounds by barren-ground caribou. *Rangifer*. 6 (1986): Special Issues No. 1: 151-158.
- Heard, D.C.** 1980. The intrinsic rate of increase of reindeer and caribou populations in arctic environments. -*Rangifer*. 1990: Special Issue No. 3, 169-173.
- IBM Corp.** Released 2021. IBM SPSS Statistics for Windows, Version 28.0. Armonk, NY: IBM Corp.
- Kie, J.G., & White, M.** 1985. Population dynamics of white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge, Texas. - *The Southwestern Naturalist* 30 (1): 105-118.
- May, R.** 1976. Simple mathematical models with very complicated dynamics. - *Nature*. 261: 459-467.
- McCullough, D.R.** 1979. The George Reserve deer herd: Population ecology of a K-selected species. University of Michigan Press, Ann Arbor, USA.

- McCullough, D.R.** 1999. Density-dependence and life-history strategies of ungulates. - *Journal of Mammalogy*. 80 (4): 1130-1146.
- Messier, F., Huot, J. Henaff, D., & Luttich, S.** 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. - *Arctic* 41 (4): 279-297.
- Nagy, J. A., Johnson, D. L., Larter, N. C., Campbell, M. W., Derocher, A. E., Kelly, A., Dumond, M., Allaire, D., & Croft, B.** 2011. Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. - *Ecological Applications*. 21 (6): 2334-48.
- Nagy, J.A., & Campbell, M.** 2012. Herd structure, movements, calving grounds, activity periods, home range similarity, and behaviours of migratory and tundra-wintering barren-ground caribou on mainland Nunavut and eastern mainland Northwest Territories, Canada. Manuscript report Prepared for the Beverly and Qamanirjuaq Caribou Management Board. 155 pp.
- Payette, S., Fortin, M.J., & Gamache, I.** 2001. The Subarctic forest – Tundra: The structure of a biome in a changing climate: The shifting of local Subarctic tree lines throughout the forest-tundra biome, which is linked to ecological processes at different spatiotemporal scales, will reflect future global changes in climate. - *BioScience* 51(9):709 – 718.
- Pearl, R. and Reed, L. J.** 1920. On the Rate of Growth of the Population of the United States and its Mathematical Representation. Proceedings of the National Academy of Sciences. 6: 275-288.
- Pearl, R., Reed, L. J.** 1922. A Further Note on the Mathematical Theory of Population Growth. Proceedings of the National Academy of Sciences, 8: 365-368.
- Renshaw, E.** 1991. *Modelling biological populations in space and time*. Cambridge University Press, New York, NY. 350pp.
- Russell, D.E., Kofinas, G., & Griffith, B.** 2002. Barren-ground caribou calving ground workshop: Report of proceedings. Technical report series no. 390. Canadian Wildlife Service, Ottawa, Ontario.
- Schmelzer, I., & Otto, R.** 2003. Winter Ranger drift in the George River Caribou Herd: a response to summer forage limitation? - *Rangifer*. Special Issue No. 14: 113-122.
- Skogland, T.** 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. - *Journal of Animal Ecology* 54 (2): 359-374.
- Stephens, D.W., and Krebs, J.R.** 1986. Foraging Theory. Princeton University Press. Princeton, New Jersey.
- Taillon, J., Brodeur, V., & Rivard, S.** 2016. Biological status of migratory caribou, Leaf River herd, ministère des Forêts, de la Faune et des Parcs, Québec, 67 p.
- Tanner, J.T.** 1966. Effects of population density on growth rates of animal populations. - *Ecology*. 47 (5): 733-745.
- Vandermeer, J.** 2010. How populations grow: The exponential and logistic equations. - *Nature Education Knowledge*. 3(10):15
- Verhulst, P.F.** 1838. Notice sur la loi que la population poursuit dans son accroissement. *Correspondance Mathématique et Physique*. 10: 113-121
- Wilson, D., E. and Reeder, D., M.** (editors) (2005). *Rangifer tarandus*. Wilson and Reeder's Mammal Species of the World — A Taxonomic and Geographic Reference 3rd ed. Baltimore, Maryland: Johns Hopkins University Press/Bucknell University. 2,142 pp.
- Table 1. Summary statistics for the Qamanirjuaq, Bathurst, and George River barren-ground caribou cycles. The sine cycle maximum and minimum annual subpopulation growth rates (λ_t) were updated from Bongelli *et al.* 2020. Sine cycle estimates of λ_t greater than the biologically plausible were limited to 1.2 ($\lambda_{\text{plausible}}$)

with the remainder of population growth for those years attributed to immigration. Subpopulation growth that was partially immigration (intrinsic + immigration) occurred only during the eruption phase.

| | Barren-Ground Caribou Subpopulation | Barren-Ground Caribou Subpopulation |
|--|-------------------------------------|-------------------------------------|
| Cycle Parameter | Qamanirjuaq | Bathurst |
| Sine Cycle Period | 58 | 42 |
| Cycle λ_{\max} | 1.196 | 1.469 |
| Cycle λ_{\min} | 0.837 | 0.680 |
| Cycle $\lambda_{\text{plausible-max}}$ | 1.196 | 1.2 |
| Max N-K Lag Time | 4.333 | 4.238 |
| Min N-K Lag Time | 2.086 | 1.640 |
| Eruption Phase Duration | 6 | 9 |
| Years of Partial Immigration | 0 | 8 |

Table 2. Mean lag time (years) values and the mean population growth rate values associated with three unique phases (complete cycle, complete cycle excluding eruption years, and eruption years only) of the Qamanirjuaq, Bathurst and George River subpopulation cycles. Uncorrected values of annual population growth rate were used to account for both intrinsic growth and extrinsic growth attributed to immigration.

| Subpopulation | Cycle Phase | Mean Lag Time (SE) | Mean λ_t (SE) |
|---------------|------------------------------------|--------------------|-----------------------|
| Qamanirjuaq | Complete cycle | 2.898 (0.008) | 1.006 (0.013) |
| | Complete cycle (no eruption years) | 2.805 (0.079) | 0.992 (0.013) |
| | Eruption years only | 3.693 (0.2555) | 1.127 (0.031) |
| Bathurst | Complete cycle | 2.661 (0.103) | 1.027 (0.032) |
| | Complete cycle (no eruption years) | 2.611 (0.118) | 0.942 (0.025) |
| | Eruption years only | 2.85 (0.222) | 1.312 (0.047) |
| George River | Complete cycle | 2.430 (0.121) | 1.126 (0.072) |
| | Complete cycle (no eruption years) | 2.571 (0.116) | 0.921 (0.029) |
| | Eruption years only | 2.125 (0.375) | 1.74 (0.192) |

Table 3. Pairwise comparison of mean lag time values associated with three unique phases (complete cycle, complete cycle excluding eruption years, and eruption years only) of the Qamanirjuaq, Bathurst and George River subpopulation cycles. We used a confidence level of $p \leq 0.05$ and significance values were adjusted by the Bonferroni correction for multiple tests. Mean lag times for one complete cycle for the Qamanirjuaq subpopulation were significantly different than the George River subpopulation, but the difference was not significant between the Qamanirjuaq and Bathurst or Bathurst and George River subpopulations. Mean lag times for the entire population cycle, excluding eruption years (intrinsic growth only) were not significantly different between any of the subpopulations. Lag time values associated with only the eruption years for the Qamanirjuaq subpopulation were significantly different than the George River subpopulation, but the difference was not significant between the Qamanirjuaq and Bathurst or Bathurst and George River subpopulations.

| Subpopulation | Pairwise Comparison | One Complete Population Cycle: sig. value |
|-----------------------------------|-----------------------------------|---|
| Qamanirjuaq | George River | 0.018* |
| Bathurst | Qamanirjuaq | 0.414 |
| George River | Bathurst | 0.838 |
| Hypothesis Test Summary Statistic | Hypothesis Test Summary Statistic | 0.022* |

*Denotes SPSS Kruskal-Wallis comparison that is significant at $p \leq 0.05$.

Table 4. Mean population growth rate values associated with three unique phases (complete cycle, complete cycle excluding eruption years, and eruption years only) of the Qamanirjuaq, Bathurst and George River subpopulation cycles. We compared the uncorrected values for population growth rate (i.e., intrinsic + immigration). We used a confidence level of $p \leq 0.05$ and significance values were adjusted by the Bonferroni correction for multiple tests. Mean population growth rates for one complete cycle for were significantly not different between any of the subpopulations. Mean population growth rates for the entire population cycle, excluding eruption years (intrinsic growth only) were not significantly different between any of the subpopulations. Mean population growth rates associated with only the eruption years for the Qamanirjuaq versus George River pairwise comparison was significant, but the Qamanirjuaq and Bathurst pair and the Bathurst and George River pair were not significantly different.

| Subpopulation | Pairwise Comparison | One Complete Population Cycle: sig. value |
|-----------------------------------|-----------------------------------|---|
| Qamanirjuaq | George River | 1.000 |
| Bathurst | Qamanirjuaq | 1.000 |
| George River | Bathurst | 1.000 |
| Hypothesis Test Summary Statistic | Hypothesis Test Summary Statistic | 0.958 |

*Denotes SPSS Kruskal-Wallis comparison that is significant at $p \leq 0.05$.

Table 5. Bivariate correlations between population growth rate (λ_t), carrying capacity (K_t), and lag time ($N_t - K_t$) for the Qamanirjuaq, Bathurst and George River barren-ground caribou subpopulations during the eruption phase (IBM Corp, 2021). The within-subpopulation bivariate correlation coefficients for these variables are significant ($p \leq 0.05$) for all three subpopulations.

| Subpopulation | $\lambda_t \text{ vs } K_t$ | $\lambda_t \text{ vs } N_t - K_t$ | $K_t \text{ vs } N_t - K_t$ |
|---------------|-----------------------------|-----------------------------------|-----------------------------|
| Qamanirjuaq | 0.435 ($p = 0.001$) | 0.982 ($p < 0.001$) | 0.279 ($p = 0.043$) |
| Bathurst | 0.885 ($p < 0.001$) | 0.973 ($p < 0.001$) | .0778 ($p < 0.001$) |
| George River | 0.827 ($p < 0.001$) | 0.954 ($p < 0.001$) | 0.743 ($p < 0.001$) |

Figure 1. The Qamanirjuaq subpopulation numbers (N_t) tracked carrying capacity (K_t) throughout its subpopulation cycle. Maximum and minimum rates of population growth ($\lambda_{\max} = 1.19$; $\lambda_{\min} = 0.83$) closely align with the maximum reported rates of barren-ground caribou population growth ($\lambda = 1.17$) and population decline ($\lambda = 0.83$) (Gunn, 2003). The eruption period (i.e., $\lambda > 1.0$ and increasing over consecutive years) lasted for approximately 6-years. N_t closely tracked K_t throughout the cycle with the maximum lag time over one complete cycle (1971-2030) being 4.33-years.

Qamanirjuaq

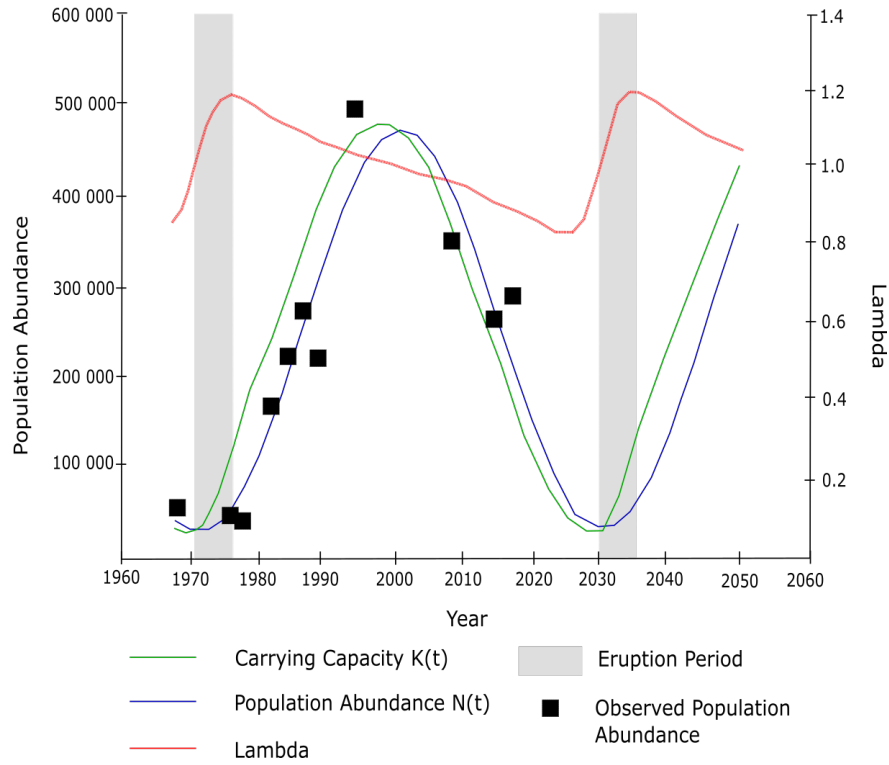


Figure 2. The Bathurst subpopulation tracked carrying capacity (K) throughout its population cycle. Maximum and minimum rates of annual (intrinsic + immigration) population growth ($\lambda_{\max} = 1.469$; $\lambda_{\min} = 0.68$) were greater than the biological maximum annual population growth rate ($\lambda_{\max} = 1.363$; Heard, 1980) during the eruption phase. The eruption period ($\lambda > 1.0$ and increasing over consecutive years or $\lambda > 1.20$) last for approximately 9-years. When λ_t values were $[\geq] 1.2$ we limited them to 1.2 for calculation of the associated Verhulst (1838) carrying capacity (K_t) because the Verhulst logistic equation is specific for intrinsic λ only (no immigration). We choose $\lambda [\geq] 1.2$ as the threshold because natural populations experience both natural and harvest mortality and not every reproductive age female would produce viable offspring each year. N_t closely tracks K_t throughout the cycle with the maximum lag time over one complete cycle (1978-2020) being 4.238-years.

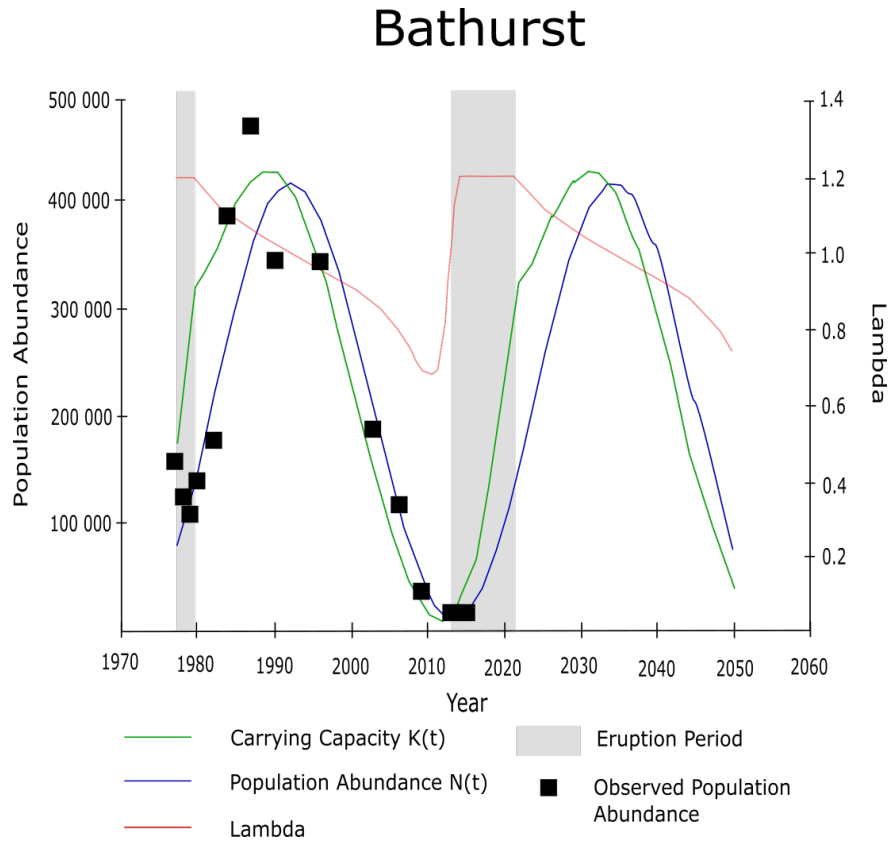


Figure 3. The George River subpopulation tracked carrying capacity (K) throughout its population cycle. Maximum and minimum rates of annual (intrinsic+ immigration) population growth ($\lambda_{\max} = 2.848$; $\lambda_{\min} = 0.345$) were greater than the biological maximum annual intrinsic population growth rate ($\lambda_{\max} = 1.363$; Heard, 1980) during the eruption phase. The eruption period ($\lambda > 1.0$ and increasing over consecutive years or $\lambda > 1.20$) lasted for approximately 9-years. When λ_t values were ≥ 1.2 we limited them to 1.2 for calculation of the associated Verhulst (1838) determination of K_t because the Verhulst logistic equation is specific for intrinsic λ only (no immigration). We choose $\lambda \geq 1.2$ as the threshold because natural subpopulations experience some natural and harvest mortality; and because not every reproductive age female produces viable offspring in every year. N_t closely tracked K_t throughout the cycle with the maximum lag time over one complete cycle (1965-2017) being 4.334-years.

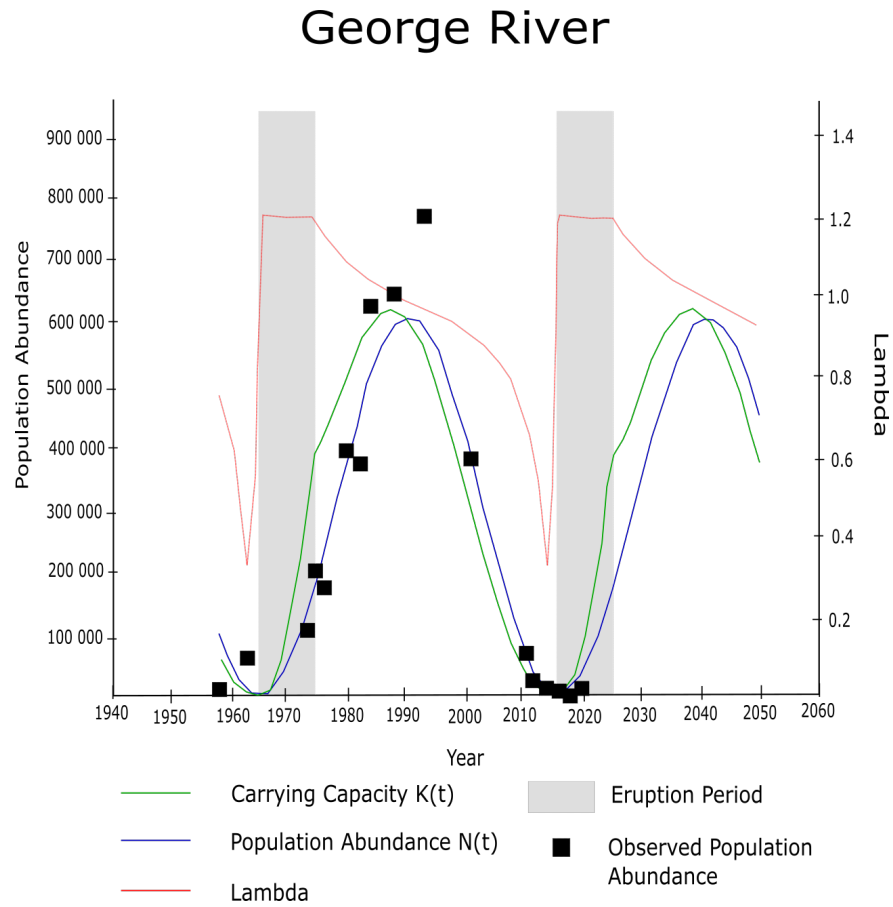


Figure 4. Lag time as the number of years for N_t to reach K_t for the Qamanirjuaq, Bathurst and George River caribou subpopulations considering both intrinsic and extrinsic population growth over one complete cycle period. All three subpopulations closely track carrying capacity during the decline phase of the cycle with the largest deviations occurring the eruption years.

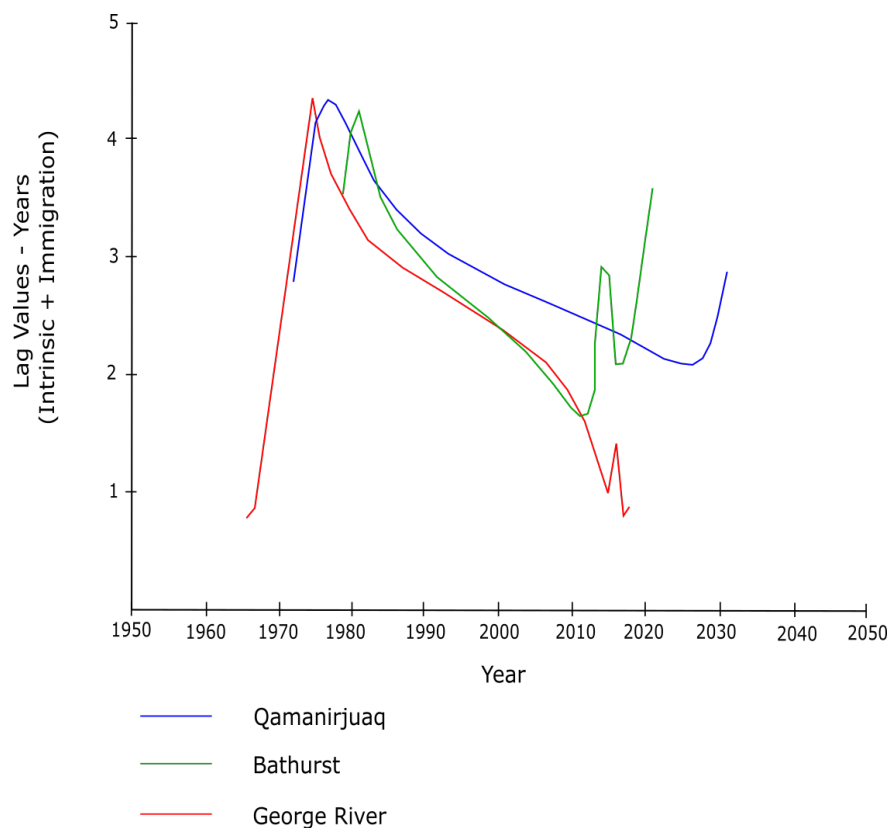


Figure 5. The Qamanirjuaq, Bathurst and George River subpopulations experience varying levels of population growth during the eruption periods of their respective cycles. The Qamanirjuaq subpopulation eruption period lasts approximately 6-years, and the maximum subpopulation growth rate was well within plausible intrinsic limits. The Bathurst and George River subpopulations experience rates of subpopulation growth during a portion of the eruption period (9-years respectively) that exceed biologically possible intrinsic rates of growth (i.e., included immigration).

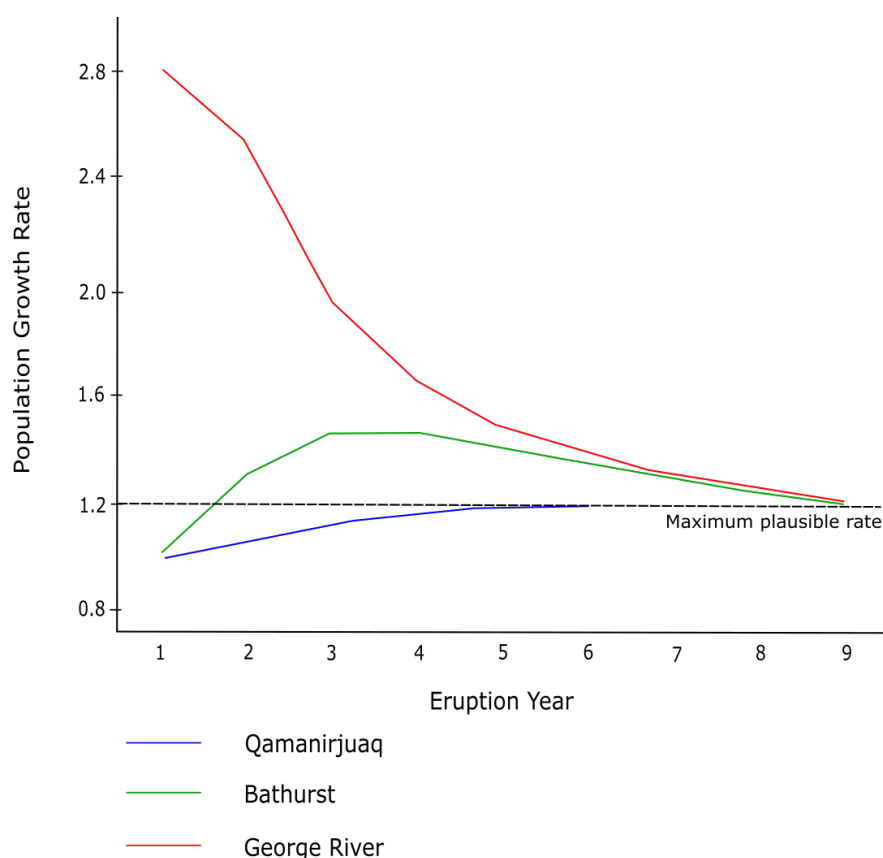


Figure 6. Eruption phase relationship with immigration for the Qamanirjuaq, Bathurst and George River subpopulation cycles. Biologically plausible maximal intrinsic growth rates ($\lambda_{\text{plausible}}$) of 1.2 were substituted for the sine-cycle projected rates providing a measure of maximum intrinsic growth potential. The remaining increase was ascribed to extrinsic growth (i.e., immigration) providing a measure of relative contribution to annual growth. The Qamanirjuaq subpopulation did not experience any additional population growth due to immigration. Both the Bathurst and George River subpopulation experienced varying levels of immigration driven population growth. The maximum contribution of immigration to total population growth was ~57% and ~89% for the Bathurst and George River subpopulations, respectively.

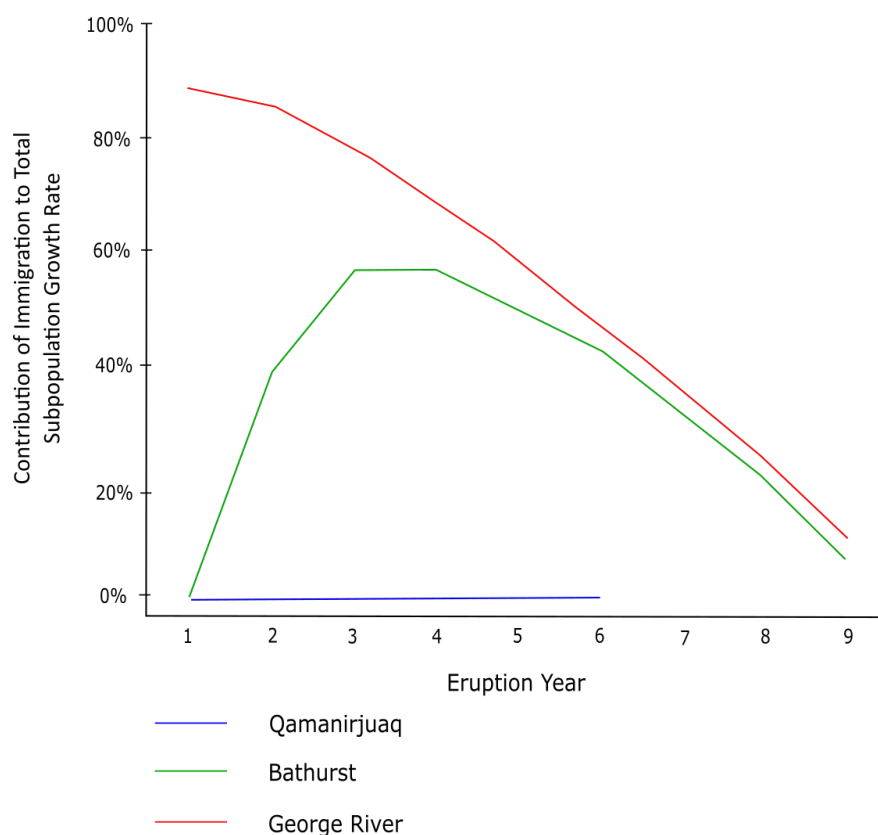


Figure 7: Comparison of lag times (years to reach K_t from N_t) and mean population growth rates from the eruption years only for the Qamanirjuaq, Bathurst, and George River subpopulations. Three clusters were identified: 1) short lags and high lambda values, 2) intermediate lag time and intermediate lambda values, and 3) long lag time and low lambda values. Cluster 1 was associated with only three George River eruption year records, all of which had over 70% immigration. Most (7/9) eruption year records for the Bathurst subpopulation were associated with intermediate cluster 2. Intermediate cluster 2 also contained two Qamanirjuaq eruption year records, and four George River eruption year records. Most (4/6) eruption year records for the Qamanirjuaq subpopulation were associated with cluster 3.

