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Range Dynamics of Barren-Ground Caribou Implied by Historical Population Cycles and Logistic Growth

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SUPPLEMENT S1

Logistic Population Growth from Linear Density Effects

Our discrete formulation of the logistic equation is derived for a generalized birth pulse species (Taylor, 1994; Janssens, 2014). We define the per capita birth rate as "B" and the per capita death rate as "D." Assuming there are no density effects on birth or death, and the rates of birth and death are constant (deterministic), 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).

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

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

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

Rewriting Equation 1 yields:

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

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

Equation 4: $\lambda = 1 + \Delta$

Rewriting Equation 3 yields:

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

We see by inspection that when $\Delta = 0$ (or when $\lambda = 1$), then $N_t = N_{t+1} = K$ (constant carrying capacity). We recognize that populations in nature do not usually just decline to extinction or increase to infinity. The number of individuals in a population must cause negative feedback on the per capita rates of birth and death for the population to be regulated. This negative feedback is termed *density effects*. When birth rate or death rate, or both birth rate and death rate are linear functions of population number (N_t), the formulation for population change over time is the discrete logistic equation (Fig. S1).

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

$\Delta_t = (B_t - D_t)$

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

K = Carrying Capacity (K assumed to be constant).

Then $\Delta_t = (-\Delta_{max}/K) * N_t + \Delta_{max}$ (as per: $y = m * x + b$ from Fig. 1).

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

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

Now we rewrite Equation 3 ($N_{t+1} = N_t * (1 + \Delta)$) using the dynamic definition of Δ from Equation 6:

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

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

Divide both sides of above equation by N_t:

$\lambda_t = 1 + \boldsymbol{\Delta}_{max} * (1 - N_t/K)$

Equation 7: $N_{t+1} = N_t * (1 + \boldsymbol{\Delta}_{max} * (1 - N_t/K))$

Our discrete logistic equation is:

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

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The discrete logistic formulation is analogous to the Verhulst (1838) and Pearl and Reed (1920) formulation of the logistic equation, which captures linear density effects to population growth in a continuous context when K (carrying capacity) is constant.

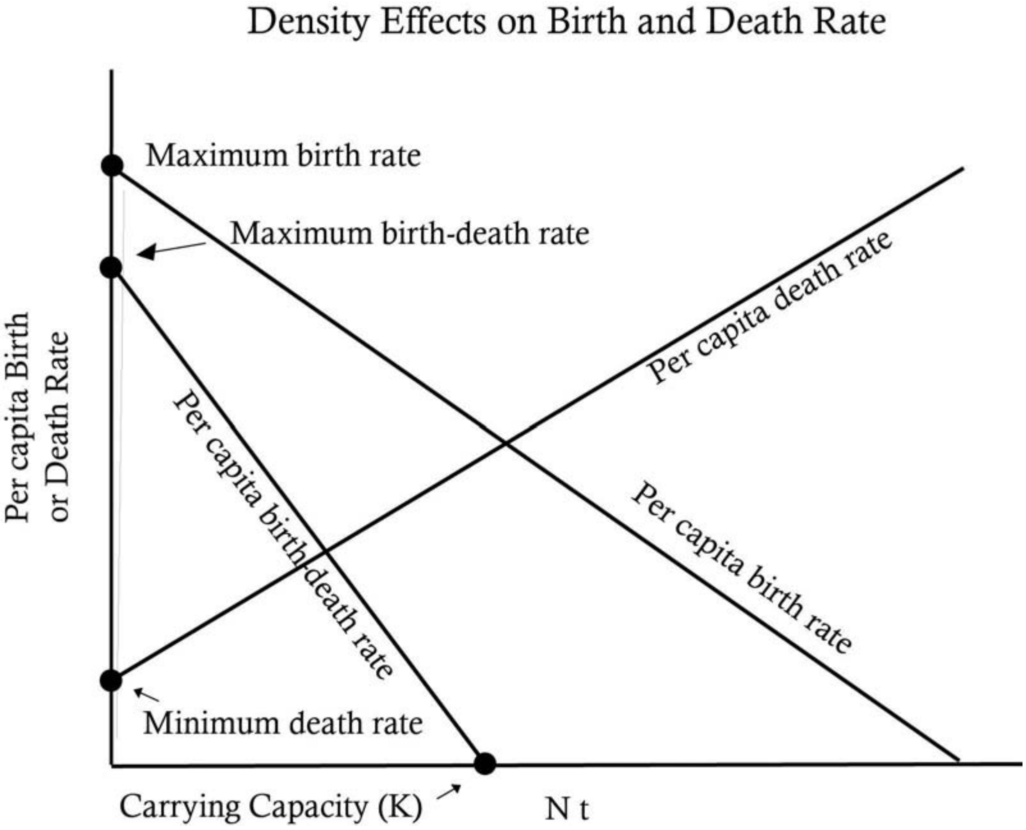

FIG. S1. When birth rate is a declining linear function of N_t, or death rate is an increasing linear function of N_t, or both, then Δ_t is a declining linear function of N_t.

SUPPLEMENT S2

Executive Summary and Readers' Guide to Bongelli et al., 2020

The current range dynamics article, which will challenge the critical reader, builds on earlier results presented in Bongelli et al., (2020). The earlier paper employs frequentist (e.g., regression, hypothesis testing, analysis of variance), Akaike (AIC), and Bayesian (BIC) statistics to show that the time series of subpopulation survey estimates for 9 of 11 North American barren-ground subpopulations are best described as sine cyclic.

Bongelli et al., (2020), hereafter, the sine cycle paper, used AIC and BIC to discriminate between a suite of time-series models using published census data for each barren-ground caribou subpopulation considered. Both AIC and BIC are accepted statistical protocols for model ranking, and the results for AIC and BIC procedures were almost identical. Bongelli et al., (2020) selected BIC model ranking because BIC provides the best model considering the data; and because the parameter penalty for the BIC approach was more suitable for the sample sizes of the subpopulations that the authors considered.

Both AIC and BIC provide an objective (quantitative) way to rank models (including identification of models that have the same support and should be ranked as equal). However, AIC and BIC only rank the models that the analyst considers. If you rank 10 bad models, AIC and BIC will identify the best model of the 10 compared; but what use is the best ranked poorly fit model? For this reason the authors also used regression (frequentist) statistics to determine how well the various models fit the data. They found that the sine cycle was the best model for nine of 11 subpopulations. The sine cycle also fit the census data really well for each of nine subpopulations that tested as sine cyclic (subpopulation R^2 values ranged between 0.770 – 0.999).

A sine cycle is characterized by its period and amplitude. Sine cycles are symmetrical in both the horizontal (time in years) and vertical (numbers) axis. Sine cycle symmetry means that period and amplitude can be estimated with as few as 3 consecutive points, although in practice at least ¼ of the cycle should be sampled for reliable estimates. Once period and amplitude are estimated, the value (expected number) at any given point in the cycle can be determined.

According to calving ground census estimates, most barren-ground caribou (nine of 11 North American subpopulations) are sine cycle, and the sine cycle fits each subpopulation really well. Each subpopulation sine cycle has its own unique period and amplitude, which was estimated by fitting the sine cycle to the census data. The subpopulation estimates of period and amplitude are empirical results based on the census data. The sine cycle paper also looked at how well the sine curve fit the census data considering all 9 subpopulations as a group.

The authors pooled the various census estimates (not expected values from the sine fit, but the actual published census estimates) from all 9 sine cyclic subpopulations into a group called observed. They then compared the observed values to the expected values calculated using the specific subpopulation period and amplitude to calculate expected values that coincided (same year) with the census estimates. The subpopulation-specific period and amplitude generated expected values that explained 96% of the pooled survey variance, with the probability of no relationship at $p < 0.001$. Based on the census data, the sine cycle paper authors concluded that the sine cycle is not only the best time series model for nine of 11 subpopulations examined, but it is also a very good model (meaning the expected sine cycle values are consistently quite close to the actual census estimates). The supplementary data files included with the Bongelli et al., 2020 paper provide period, amplitude, and expected values for all nine of the sine cyclic subpopulations they document.

Hopefully it is clear that the estimates of period and amplitude and the expected values for the number at each year of the cycle (N_t) for each subpopulation are statistical results derived from analysis of the published census data. Another factor relevant to the cycle analysis is sine cycles are symmetrical in both the period and amplitude axes. Sine cycles are not jagged up and down population fluctuations like the lynx-hare cycle. If you have the top half of the cycle, you know the bottom half by definition. If you know the increase half of the cycle, you also know the decline half of the cycle. And if you try to fit a sine cycle to non-cyclic data, the residuals will be asymmetric. Bongelli et al., (2020) tested for asymmetry in the residuals of their sine cycle fit and found that the residuals were symmetrical. While it is preferable to have data for as much of the cycle as possible (or even a time series that spans several cycles), it is not necessary to have sampled 100% of the cycle to accurately estimate the period and amplitude of the cycle. One would not expect to explain 96% of the pooled census data variance using expected values from a function that was inappropriate or was fitted to insufficient data to accurately estimate the function parameters. Inappropriate or poorly supported functions would not be expected to be competitive models in either a BIC or an AIC context.

As mentioned above, a sine cycle is symmetrical and persists unchanged through time unless perturbed. Alternating current occurs as a sine wave. A ball bearing on a spring held by a lab stand exhibits a sine curve through time. The sine cycle paper found no other examples of natural sine cyclic populations for any species (regular fluctuations in numbers yes, but not as sine cycles). Its authors were restricted to published data and open-source data bases, which essentially limited them to georeferenced satellite data that could be summarized as subpopulation specific values for various measures. They developed competing linear regression models for period and amplitude as functions of the various environmental parameters they gleaned from open-source data files and publications mapping the range boundaries of the nine sine cyclic subpopulations. The Regression environmental models for period and amplitude have associated R^2 values of 0.95 and 0.96 respectively. In brief, most of the variance in the period and amplitude for the nine sine cyclic subpopulations could be explained by range size and range productivity. The essential point for the current caribou dynamic paper is that if period and amplitude are best described as functions of range size and range productivity, then it is appropriate to assume that carrying capacity is mainly dependent on range size and range condition. There was no consideration of predation or harvest or development or climate trend in range area or in range productivity in the earlier sine cycle paper's analysis.

Remember the remarkable result from above that 96% of the variation in census estimates could be explained by subpopulation specific estimates of period and amplitude. The sine cycle paper did not use the period and amplitude estimates from their Bayesian sine fit work for this result. Rather, its authors used the period and amplitude expected values from their environmental regression model. The environmental model period and amplitude estimates from range size and range productivity were used to calculate expected subpopulation N_t values corresponding to the observed pooled survey data (included all 9 subpopulations and all survey years). The percent of variance in the pooled survey explained was 96%. Thus, North American barren-ground caribou sine cycle.

In the current range dynamics paper, we used this this conclusion to estimate the time series of population numbers for the three example subpopulation cycles. Furthermore, the period and amplitude of these cycles appear to be mainly a function of range variables (range size and range productivity). The current caribou range dynamics paper uses the logistic growth model to explore what our knowledge about the cycle subpopulation dynamics (N_t) tells us about the subpopulation carrying capacity (K_t) dynamics. Is K_t constant, or does K_t vary randomly, does K_t also sine cycle, does K_t slowly recover during periods of low caribou numbers, or does K_t irrupt once caribou numbers reach a threshold minimum? Logistic K is a proxy for range condition and should provide some insight into the trophic dynamics of barren-ground caribou and its range.

Both the sine cycle and the caribou range dynamics papers are best regarded as empirical (based on data analysis), not theoretical. To those who suggest that the caribou survey data are too variable and uncertain for this type of analysis, we are content to allow the statistics to speak for themselves. We believe our methods are rational and internally consistent. We assume the census data are accurate (if not precise) and that density effects are mainly environmental (range condition) and linear.

Good luck with the caribou range dynamics paper and please accept our apologies if this summary seems pedantic or unnecessary. The idea that caribou cycle as a response to overgrazing and range recovery is not original with us; it has already been suggested in both the scientific literature and traditional knowledge archives. We found that viewing those insights in a mathematical framework not only made the range-caribou dynamics more apparent, but also suggested management changes that could reduce the period of scarcity in barren-ground caribou.

SUPPLEMENT S3

Range Condition Considerations for the Bathurst, George River, and Qamanirjuaq Barren-Ground Subpopulations

Background and Additional Discussion of Main Points: The analysis of historical data on population growth and decline in cyclic animal populations provides valuable insights into the drivers of these patterns, offering a foundation for more effective conservation and management strategies in the present (Stenseth et al., 2002; Brook et al., 2008; Krebs, 2013). Many animal populations exhibit fluctuating patterns of growth and decline, driven by complex interactions among factors such as resource availability, predation, disease, and climate variability (Krebs, 2013). Analyzing historical data on these cycles allows researchers to uncover the underlying mechanisms influencing population trends, providing a foundation for understanding past fluctuations and predicting future changes. For instance, long-term studies of species like snowshoe hares (*Lepus americanus*) and their predators in boreal forests have shown how predator-prey-habitat dynamics might drive multi-year population oscillations (Krebs et al., 2001).

Understanding the causes of cyclic population dynamics is not merely an academic exercise but has direct implications for conservation and management strategies. Species experiencing extreme population declines or irregular cycles may be more vulnerable to extinction, particularly under the pressures of habitat loss, climate change, and human exploitation (Brook et al., 2008). By identifying historical patterns and their drivers, conservation efforts can be targeted more effectively to mitigate risks and enhance population resilience. For example, management strategies informed by historical data have been employed to stabilize populations of migratory birds and cyclic rodent species, ensuring their persistence despite environmental challenges (Ims and Fuglei, 2005). Analysis of historic data on population growth and decline in expectedly cyclic animal populations can help us to understand the causes of trends and provide focus for contemporary conservation and management strategies.

Comparisons: Bongelli et al., (2020) noted that there can be ecological differences between the subpopulations that can mediate caribou/range interactions (e.g., immigration). The George River subpopulation range appears to be more productive than the Bathurst and Qamanirjuaq range and the Qamanirjuaq subpopulation appears to be more segregated (negligible immigration) from adjacent subpopulations compared to the Bathurst and George River subpopulations. Regardless of these differences, the best model for all three subpopulations is the sine cycle (Bongelli et al., 2020). The time series of census data strongly suggests that barren-ground caribou subpopulations exist in a temporally dynamic equilibrium with their range. Over-grazing eventually results in a caribou decline sufficient to allow the range to escape the effects of over-grazing simultaneously across the range. Range recovery occurs at a faster rate than caribou recovery. Caribou numbers lag carrying capacity numbers during the initial recovery phase because the range recovers as a single range-wide organism while the caribou recover from a small remnant of the previous cycle. The highest annual increments during caribou recovery are half-way into the recovery portion of the cycle.

The range (K) does not slowly recover when caribou densities are low. Even very low numbers of caribou were sufficient to keep K from recovering until the over-grazing threshold was reached in all three subpopulations. Once caribou numbers were reduced to levels insufficient to prevent recovery, range recovery occurred at a faster rate than caribou could respond numerically in all three subpopulations.

At low levels, both K_t and N_t continue a slow decline until a minimum grazing threshold is reached. Once the range is increasing faster than it can be grazed, carrying capacity increases more rapidly than caribou can keep pace. The surge of habitat recovery occurs 1 – 2 years prior to the growth surge in caribou numbers for all three subpopulations. Range conditions start to decline four years prior to the peak in caribou numbers for the Qamanirjuaq subpopulation. Carrying capacity for both the Bathurst and George River subpopulations exhibits a secondary peak after the initial surge, but in both cases the secondary peak in habitat occurs 4–5 years prior to the peak in subpopulation numbers. The irruption phase for the Qamanirjuaq, Bathurst, and George River subpopulations ranged from 6 to 9 years or 12% – 19% of the cycle.

Qamanirjuaq, Bathurst, and George River subpopulations closely tracked their respective carrying capacities with an average lag time of approximately 3.5 years. By comparison, during the initial recovery period all three subpopulations required about double the time to reach K_t from intrinsic growth. In all three cases the maximum lag time occurred at year 12 of the cycle which corresponded to the end of the irruption phase for each subpopulation. In these three case studies, post-irruption barren-ground caribou population growth first slowed and then declined as the range declined due to over-grazing. Once caribou numbers had declined beneath the threshold for recovery, they increased rapidly as their range recovered.

Anthropogenic factors appear not to have had a lasting or substantive impact on barren-ground caribou numbers or range dynamics thus far as evidenced by the symmetry in the residuals from the sine fit (Bongelli et al., 2020) for all three subpopulations. This may change as exploration and industrial development increase across caribou range, and if over-management (harvest restrictions and predator management strategies) are implemented at low densities. In all three subpopulations, carrying capacity was first dramatically reduced by high numbers of caribou, and then repressed by over-grazing even when caribou were at low numbers until the recovery threshold was reached. Paradoxically, current barren-ground caribou management strategies in northern Canada may be extending the period of barren-ground caribou scarcity by increasing the time it takes subpopulations to reach the over-grazing threshold for range recovery.

The recovery thresholds for Qamanirjuaq, Bathurst, and George River subpopulations were 41,971, 18,265, and 3141 respectively. Subpopulation differences in the recovery threshold values would presumably be due to the same factors that determine period and amplitude of the cycles: range size and range productivity (Bongelli et al., 2020); but this line of inquiry was beyond the scope of this study. Each subpopulation has its own set of ecological circumstances (e.g., tundra/forest ratios, annual productivity, immigration potential). The Qamanirjuaq and the Bathurst subpopulations are currently experiencing subsidized wolf control programs, while in the George River subpopulation, predator removals occur as regulated fur harvesting. The timing and magnitude of immigration likely depends on the degree of synchronicity of adjacent subpopulation cycles. In addition to sampling variability there could also be cycle-to-cycle and annual variability (e.g., weather and fire events). Investigation of these potential factors was also beyond the scope of this paper.

These case studies of the Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations identify both similarities and differences in the ecological circumstances of distinct 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 (i.e., short lag times). We suggest that barren-ground caribou subpopulations will cycle indefinitely as a demographic result of the herbivore-range dynamics in contiguous tundra/taiga habitat if their range remains predominantly intact and they are not over-managed.

Subpopulation Specific Considerations

George River: 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 and Otto, 2003). Schmelzer and Otto (2003) found that George River caribou summer range habitat quickly deteriorated during the mid-1980s which corresponded to a period of significant population growth. During this time, George River caribou experienced what Schmelzer and Otto (2003) termed winter range drift. Schmelzer and 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 delayed 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 and Otto (2003) suggest that the demographic benefits of winter range drift are limited by the cost of lengthier migration to the traditional calving grounds.

The Leaf River and George River subpopulations are genetically indistinct (Boulet et al., 2007). 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. Boulet et al., (2007) found that permanent dispersal between George River and Leaf River was low in most years (< 6%) but approximately 35% in 1996. We speculate that the irruption 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). Even a low permanent dispersal rate (~6%) could result in a substantial increase to the receiving subpopulation if the receiving subpopulation was at low numbers and the contributing subpopulation was abundant. However there has been no overlap identified between the two subpopulations since approximately 2006 (Taillon et al., 2016). Leaf River caribou are currently in decline from a maximum of about 630,000 to 187,000 estimated in 2018 (Taillon et al., 2016). It appears unlikely that immigration from the Leaf River subpopulation has contributed substantially (or perhaps at all) to the recent (2020 and 2022) initial recovery of the George River subpopulation from cycle lows (Government of Newfoundland and Labrador, 2022).

Another possibility to explain the previous and potential irruptive 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 recovers, 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 irruption 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. The most recent (2022) population estimate for George River caribou (7200) is close to our estimate of the minimum grazing threshold (3141) and we suggest that the irruption phase is imminent or already occurring. A recommendation for future research for George River caribou is to monitor both the numerical increase in caribou and the recovery of its range.

Bathurst: 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 population abundance estimates for Bathurst (2022) and Bluenose-East (2021) caribou are 6,800 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 augment the irruption phase of the Bathurst subpopulation once its range has begun to recover. Current Bathurst population numbers are below the grazing threshold identified (18,265) to allow for range recovery. We suggest a recovery of the Bathurst subpopulation is imminent.

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 significantly augment an irruption would be expected to vary from cycle to cycle depending on the degree of cycle synchrony or asynchrony and overlap with adjacent subpopulations. Predicting precisely when the Bathurst subpopulation will erupt may be more difficult than predicting the irruption phase for a subpopulation that is more demographically segregated and thus mainly driven by intrinsic subpopulation processes (e.g., Qamanirjuaq).

Qamanirjuaq: Qamanirjuaq caribou appear to cycle entirely due to density dependent intrinsic rates of birth and death. The Qamanirjuaq subpopulation is relatively more segregated throughout their cycle than the Bathurst and George River subpopulations. Other subpopulations (e.g., George River) appear to be demographically distinct at low densities yet exhibit a dramatic irruption phase that could only be possible if augmented with significant immigration. Some subpopulations (e.g., Bathurst) have overlapping summer and winter ranges with adjacent subpopulations throughout their cycle, and inter-subpopulation exchange between these subpopulations is well documented. Yet all three subpopulations exhibit stable sine cyclic population dynamics rather than converge on some stable equilibrium density or experience periodic extirpation.

The recent (2022) calving ground census estimate was not included in the sine cycle fit to observed estimates, but it provides a sine cycle anomaly in the current Qamanirjuaq decline. The 2022 Qamanirjuaq estimate indicates a larger than expected number of caribou for that subpopulation. Nunavut currently has a territory-wide wolf bounty program that is actively pursued by Inuit hunters. Has reduced wolf predation allowed Qamanirjuaq caribou to maintain high numbers and high grazing rates? Is the 2022 survey a statistical anomaly? Or is this a reason to question the sine cycle hypothesis for this subpopulation? The grazing-driven sine cycle hypothesis predicts a precipitous decline over the next 5 years for this subpopulation due to increased grazing from the artificially enhanced (mortality reduced) numbers. Based on current conditions, we anticipate this decline to be apparent by the next scheduled survey. Subsequent monitoring of the Qamanirjuaq subpopulation (among all other subpopulations) will allow objective evaluation of the role of grazing in barren-ground subpopulation cycle dynamics.

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