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

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ABSTRACT. We examined logistic range dynamics of three cyclic subpopulations of migratory barren-ground caribou in northern Canada (Qamanirjuaq, Bathurst, and George River). We used time series census data from each subpopulation cycle to project numbers (N_t), calculate subpopulation annual finite rates of population increase (λ_t), and estimate the corresponding time series of range condition or carrying capacity (K_t) using an algebraically rearranged version of the discrete logistic growth equation. Range condition varied regularly over each cycle, presumably due to seasonal overgrazing and range recovery dynamics. Maximum and minimum annual rates of increase and decline for Qamanirjuaq caribou were 1.196 and 0.836. In contrast, maximum annual subpopulation growth rates for the Bathurst and George River herds were greater than intrinsically possible, indicating that immigration was a component of the irruption period of their recoveries. Subpopulation numbers for Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations closely tracked carrying capacity throughout their cycles, with mean lag times of 3.95 (SE = 0.15), 3.65 (SE = 0.18), and 3.39 (SE = 0.19) years, respectively. Other factors appear to be of relatively minor or transitory importance to population growth for barren-ground caribou if barren-ground caribou are truly a logistic growth species.

Range recovery and population increase did not occur until caribou numbers declined to a recovery threshold number (Qamanirjuaq = 41,971; Bathurst = 18,265; George River = 3141). Predator management and restrictive harvest practices during the low portion of the caribou cycle may unintentionally extend the time required for caribou to decline below the grazing threshold, and thus prolong the period of scarcity. Immigration from adjacent subpopulations played a role in the acceleration of the irruption period in the Bathurst and George River subpopulations, but not the Qamanirjuaq subpopulation. Once the subpopulation range begins to recover, the rapid recovery of subpopulation numbers suggests that other density-dependent and density-independent factors are of relatively minor importance compared to range condition. 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 the natural decline of caribou to the threshold for range recovery is not artificially extended.

Keywords: barren-ground caribou; carrying capacity; cyclic species; demography; density effects; grazing; logistic; management; population cycle; *Rangifer tarandus*; resilience; sine cycle; threshold

RÉSUMÉ. Nous avons examiné la dynamique logistique de l'aire de répartition de trois sous-populations cycliques de caribous de la toundra migrateurs dans le Nord canadien (Qamanirjuaq, Bathurst et rivière George). Nous avons utilisé les données de recensement de séries chronologiques de chacun des cycles de sous-population pour projeter les effectifs (N_t), calculer les taux finis annuels de l'accroissement démographique des sous-populations (λ_t) et estimer les séries chronologiques correspondantes de l'état des aires de répartition ou de la capacité limite (K_t) à l'aide d'une version algébriquement réarrangée de l'équation de croissance logistique discrète. L'état des aires de répartition variait régulièrement pour chaque cycle, vraisemblablement en raison du surpâturage saisonnier et de la dynamique du rétablissement des aires de répartition. Les taux annuels maximaux et minimaux de croissance et de décroissance des caribous de Qamanirjuaq s'établissaient à 1,196 et à 0,836. Par contraste, les taux de croissance maximaux annuels des sous-populations des hardes de Bathurst et de la rivière George étaient plus élevés qu'intrinsèquement possible, ce qui indique que l'immigration constituait une composante de la période de pullulation de leurs rétablissements. Les effectifs des sous-populations de caribous de la toundra de Qamanirjuaq, de Bathurst et de la rivière George suivaient de près la capacité limite tout au long de leurs cycles, avec des temps de réponse moyens de 3,95 (écart-type

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= 0,15), de 3,65 (écart-type = 0,18) et de 3,39 (écart-type = 0,19) années, respectivement. D'autres facteurs semblent avoir une importance relativement mineure ou transitoire en matière de croissance de la population de caribous de la toundra si ces derniers sont vraiment une espèce à croissance logistique.

Le rétablissement des aires de répartition et l'accroissement de la population ne se sont pas produits tant que les effectifs de caribous n'ont pas diminué pour atteindre un seuil de rétablissement (Qamanirjuaq = 41 971; Bathurst = 18 265; rivière George = 3 141). La gestion des prédateurs et les pratiques de récolte restrictive durant la partie basse du cycle des caribous peuvent avoir pour effet involontaire de prolonger le temps nécessaire au décroissement des populations de caribous sous le seuil de pâturage, et, par conséquent, de prolonger la période de rareté des caribous. L'immigration à partir des sous-populations adjacentes a joué un rôle dans l'accélération de la période de pullulation des sous-populations de Bathurst et de la rivière George, mais pas dans celle de la sous-population de Qamanirjuaq. Lorsque l'aire de répartition d'une sous-population commence à se rétablir, le rétablissement rapide des effectifs des sous-populations suggère que d'autres facteurs dépendants et indépendants de la densité revêtent une importance relativement mineure comparativement à l'état de l'aire de répartition. La continuation des cycles de caribous de la toundra à des niveaux historiques est probable si des mesures de conservation de l'habitat sont adoptées, de sorte que les régimes migratoires annuels ne soient pas perturbés, que les aires de répartition estivales et hivernales demeurent non perturbées et que le décroissement naturel des effectifs de caribou jusqu'au seuil de rétablissement pour les aires de répartition visées ne soit pas artificiellement prolongé.

Mots-clés : caribou de la toundra; capacité limite; espèces cycliques; démographie; effets de la densité; pâturage; logistique; gestion; cycle des populations; *Rangifer tarandus*; résilience; cycle sinusoïdal; seuil

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INTRODUCTION

Here we consider what natural forces can cause stable symmetrical barren-ground caribou (*Rangifer tarandus groenlandicus*) population cycles (Bongelli et al., 2020). We use three relatively well-documented examples to explore this question: the Bathurst, Qamanirjuaq, and George River subpopulations of northern Canada (Fig. 1). Our consideration was guided by four observations. First, stable and symmetrical cycles result from reconciliation of two opposing forces that weaken and strengthen over time. Second, barren-ground caribou are ungulates, which are typically regulated by logistic density effects (McCullough, 1979, 1999; Bowyer et al., 2014). Third, 96% of the variance in barren-ground caribou subpopulation population cycles was recently explained by a model employing only range variables (Bongelli et al., 2020). Fourth, caribou numbers and range quality are co-dependent because caribou increase can cause overgrazing, and caribou decline can allow range recovery.

The interdependence between caribou populations and range quality is well documented in ecological research. When caribou numbers increase, their grazing pressure can lead to overgrazing, which depletes vegetation and degrades habitat quality. This dynamic is particularly evident in ecosystems such as Greenland, where population booms of reindeer and caribou, in the absence of natural predators, have been observed to cause habitat degradation followed by population crashes (Meldgaard, 1986). Conversely, when caribou populations decline, the reduced grazing pressure allows for vegetation recovery, improving habitat conditions over time (Ferguson et al., 1998). Similar findings have been reported for boreal woodland caribou, high densities of which can result in significant grazing pressure and limitation of summer forage, while lower densities facilitate habitat regeneration, highlighting the co-dependent relationship between caribou and their range quality (Schaefer and Mahoney, 2013).

To model the suspected co-dependence between caribou population trends and range quality, we employed a discrete version of the continuous logistic population growth model (Verhulst, 1838; Pearl and Reed, 1920, 1922) that is consistent with the conditions identified above and qualitatively different from recently published views of barren-ground subpopulation dynamics. Our discrete logistic model (Supplement S1) assumes that barren-ground caribou are regulated by linear density effects of range condition on caribou rates of recruitment or survival (i.e., logistic growth), but that both subpopulation numbers (N_t) and carrying capacity (K) co-vary over time (Roughgarden, 1974; Boyce and Daley, 1980; Xu et al., 2005; Dose et al., 2015). Typically, the discrete logistic equation is written as a time series of numbers in a given year (N_t) based on the number in the previous year (N_{t-1}), the population growth rate (λ_t), and a constant carrying capacity. Here we view K_t as a proxy for range quality (K units are numbers of individuals). We have the expected N_t time series from the sine cycle period and amplitude estimated by Bongelli et al. (2020) for our focus barren-ground caribou subpopulations. The central purpose of this paper is to rearrange the logistic equation as a solution for the corresponding K_t time series for each subpopulation, then compare and contrast the apparent range condition dynamics for each.

Each of the three subpopulations we considered is unique and distinct with respect to its ecology, management history, and information base. Although our suggestion that barren-ground caribou experience population cycles is not original (e.g., Gunn 2003; Zalatan et al., 2006), we are the

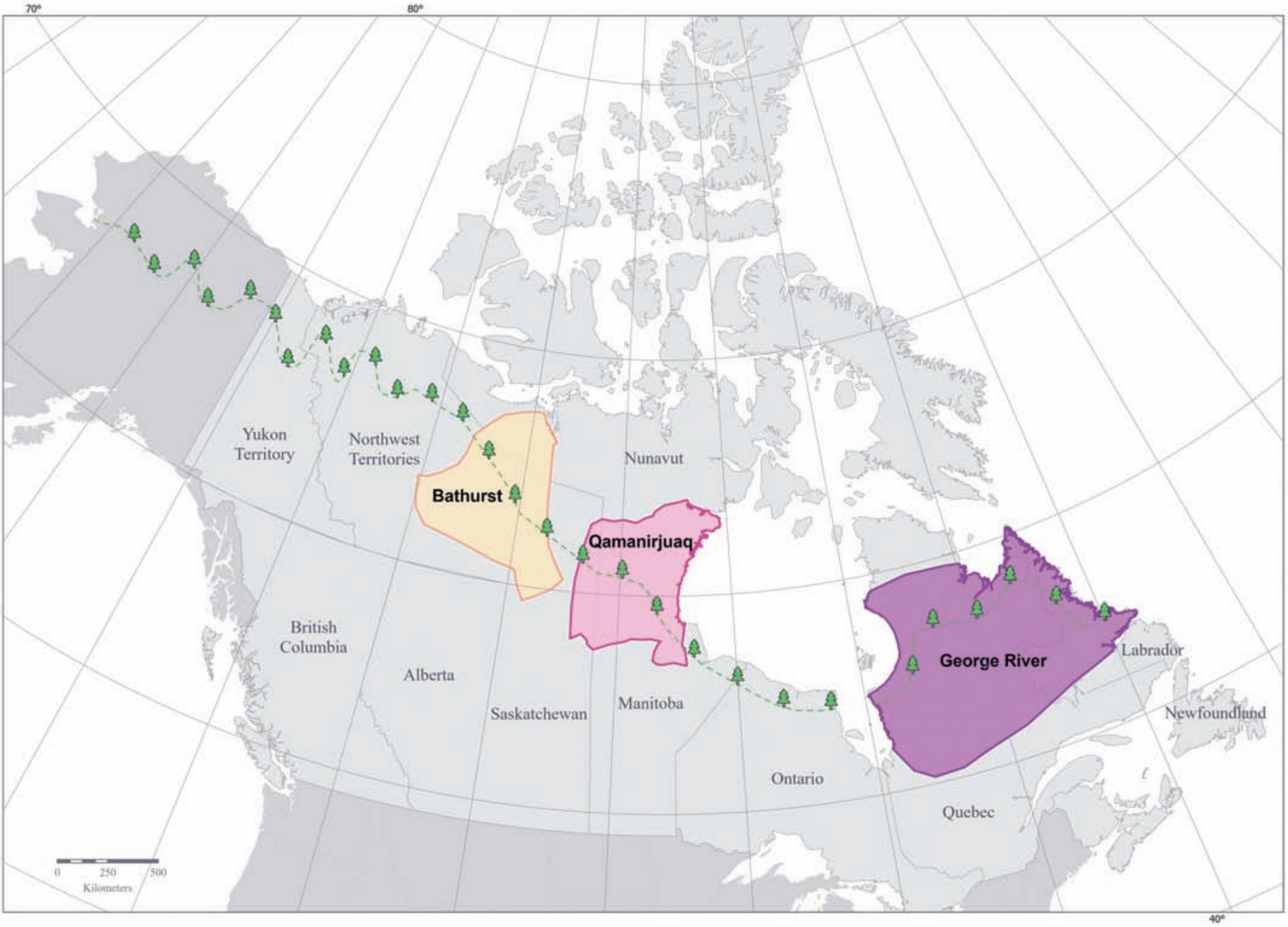

FIG. 1. We chose the Qamanirjuaq, Bathurst, and George River subpopulations of barren-ground caribou as our focus subpopulations because they are both well known and well studied. Although each subpopulation has its own set of unique ecological circumstances (e.g., ratio of summer to winter range, net primary productivity) influencing its cycle dynamics, all three subpopulations were identified as sine cyclic (Bongelli et al., 2020).

first to describe and model a plausible mechanism by which population cycling could occur. We intend this work as a descriptive meta-analysis interpretation of barren-ground caribou census data from a range condition perspective. Assuming caribou are logistically regulated by range condition, we explored what caribou population dynamics infer about range condition dynamics. We examined the evidence for this perspective, particularly with respect to the confounding impacts of exchange between adjacent subpopulations. We considered what this relationship implied regarding management prescriptions during the cycle, and we suggested how this perspective could be tested.

METHODS

Our consideration of barren-ground caribou (*Rangifer tarandus groenlandicus*) population dynamics uses terminology suggested by Cronin (2006) for contiguous wildlife subpopulations as demographically distinct components of the larger North American barren-ground caribou population. Bongelli et al. (2020) used objective th Bayesian information criterion (BIC) to show that the best model to describe the population dynamics for nine of 11 barren-ground caribou subpopulations was the sine cycle. Other time series models ranked in Bongelli et al. (2020) included linear, exponential, logistic, and wavelet (multi-cycle) functions. However, their fit was inferior to the sine cycle model when the BIC penalty for the number of function parameters was considered. Bongelli et al. (2020) also provided a simple linear regression model for subpopulation period and amplitude based on range area and range productivity, which explained 96% of the variation in the pooled (9 sine cyclic subpopulations) census estimates. Two of the 11 subpopulations did not sine cycle, probably because there was too much exchange between adjacent subpopulations (Bongelli et al., 2020). However, the sine cycle function was the best (BIC) model for number of caribou at time = t (N_t) for all three of the subpopulations we considered in this paper, the Qamanirjuaq, Bathurst, and George River herds.

We recommend reading Bongelli et al. (2020) as a companion to the current paper (see Supplement S2 for synopsis). However, the reader does not need to return to that previous paper if they accept its conclusions that the Qamanirjuaq (n = 11 surveys), Bathurst (n = 14 surveys), and George River (n = 14 surveys) time series of surveys are best represented as a sine cycle. The sine cycle is symmetrical along both the x (time) and y (subpopulation numbers) axis. Only three consecutive points are required to calculate both period and amplitude of a sine cycle (Elton and Nicholson, 1942). The sine cycle hypothesis is imminently testable because it repeats itself indefinitely, without the variability seen in most other natural population fluctuations (e.g., hare–lynx cycle) (Elton and Nicholson, 1942).

Discrete (annual) population models assume 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 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 and that extended over more than a fraction of its entire cycle. Consequently, we restricted our consideration of density effects to population growth rate at time = t (λ_t), rather than recruitment or survival rates.

We calculated the expected total number of individuals for each year (N_t) for one full cycle of the Qamanirjuaq, Bathurst, and George River subpopulations from the period and amplitude estimates obtained by fitting the sine function to the subpopulation census data. The respective subpopulation cycle time series are empirical in that they derive from the calving ground census estimates. Thus, our consideration of barren-ground caribou subpopulation cycle dynamics is best regarded as descriptive, not presumptive.

We identified annual subpopulation growth rate (λ_t) as: N_{t+1}/N_t. We assumed that K_t (carrying capacity) changed over time as the result of grazing and recovery. We rearranged the discrete formulation of the Verhulst (1838) logistic equation (Supplement S1) to solve for intrinsic carrying capacity estimates for each year of the Qamanirjuaq, Bathurst, and George River sine cycles.

Rearranging the discrete logistic equation for K_t:

$$\Delta_t = \lambda_t - 1; \Delta_{max} = 0.276$$

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

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

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

$$\Delta_t = \Delta_{max} * (1 - \frac{N_t}{K_t})$$

$$\mathrm{K_t} = \frac{N_t}{\left(1 - (\frac{\Delta_t}{\Delta_{max}})\right)}$$

Logistic carrying capacity is undefined for values of $\Delta_t \geq \Delta_{max}$ because the logistic equation does not anticipate non-intrinsic population growth. Options for an appropriate Δ_{max} for continental subpopulations of barren-ground caribou included the biological Δ_{max} (0.363) (Heard, 1980), the Southampton Island caribou Δ_{max} (0.276) (Heard and Ouellet, 1994), or observed continental caribou Δ_{max} (0.170) (Gunn, 2003). We used the Southampton Island Δ_{max} as a realistic maximum intrinsic growth rate for barren-ground caribou in the absence of predators or anthropogenic impacts. Reflecting that our three subpopulations experience some level of predation and anthropogenic (e.g., harvest) impacts, λ_t values were constrained to 1.2 when calculating intrinsic growth. When expected subpopulation λ_t values (from the sine cycle) were greater than 1.2, the remaining observed increase was attributed to immigration. However, other protocols are possible. We calculated the relative contributions of intrinsic growth ($_t * N_t$) and immigration (I_t) to population growth from the following relationship:

$$I_t = ((N_{t+1}) - N_t) - (\Delta_t * N_t)$$

We used the term "irruption period" to describe the time interval when consecutive λ_t values were greater than 1.0 and increasing each consecutive year. We estimated the demographic pressure for increase as the time required for N_t to reach K_t (lag time = L_t):

$$L_t = \mathrm{In}(K_t / N_t) / \mathrm{In}(N_{t+1} / N_t)$$

We compared mean lag time values and mean intrinsic population growth rate values among the three subpopulations using the Kruskal–Wallis nonparametric test for three distinct cycle phases: 1) one complete cycle, 2) one complete cycle excluding the irruption years, and 3) only the irruption years of the cycle. For all assessments we assumed pairwise comparisons were nonsignificant if the probability of the test statistic was ≥ 0.05. We used K-means clustering to determine whether subpopulations were grouped or contiguous with respect to lag time values and population growth rate values for the irruption years of the subpopulation cycles. We viewed our assumption that barren-ground caribou subpopulations exhibit linear density effects from their range, which varied due to overgrazing and recovery, to be a parsimonious, well-founded, well-supported, and appropriately complex hypothesis that is imminently testable. Our predictions for both population numbers and range quality extend indefinitely into the future or the past.

RESULTS

We found a similar pattern of N and K dynamics in all three subpopulations (Qamanirjuaq, Bathurst, and George

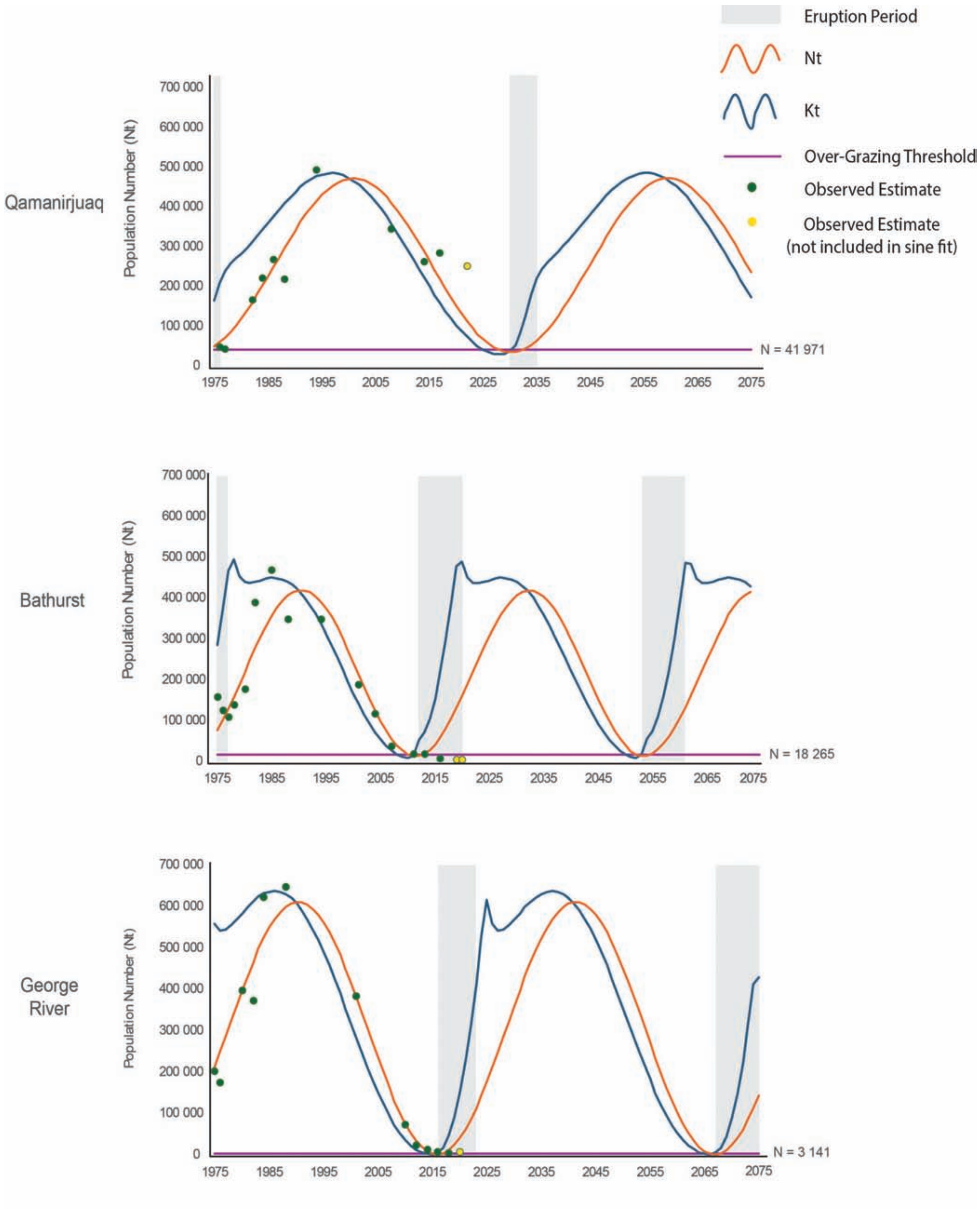

FIG. 2. A sine cycle was the best model to describe the time series of subpopulation estimates for the Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations (Bongelli et al., 2020). The 2022 Qamanirjuaq survey estimate was not available when Bongelli et al. (2020) was published and appears to be an outlier. A rearranged discrete version of the Verhulst logistic equation was used to calculate carrying capacity (K_t) for each year of the subpopulation cycle from the expected N_t. The irruption period was described as years when population growth rate was >1.0 and increasing for consecutive years. The overgrazing threshold is the number of individuals at which grazing intensity is sufficiently reduced so that range recovery can occur.

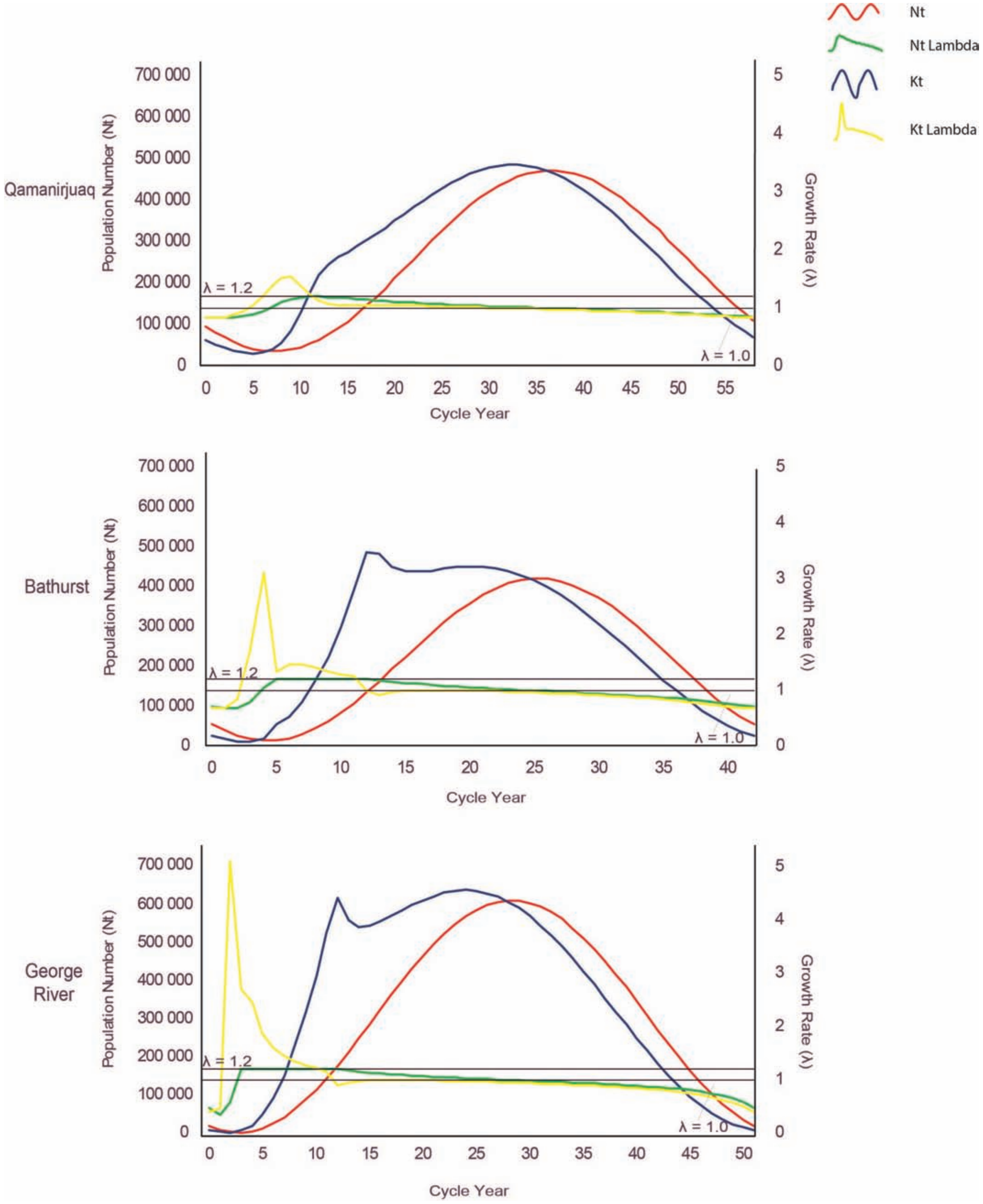

FIG. 3. A sine cycle was the best model to describe the time-series of estimates of observed population estimates for the Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations (Bongelli et al., 2020). A rearranged discrete version of the Verhulst logistic equation was used to calculate carrying capacity (K_t) for each year of the subpopulation cycle. Annual growth rates for both population numbers and carrying capacity were defined as N_{t+1}/N_t and K_{t+1}/K_t respectively. In all cases eruptive growth of carrying capacity preceded the eruptive growth of population numbers by several years, but the decline in carrying capacity was closely tracked by a decline in population numbers. Black lines indicate lambda thresholds (λ=1.0 and λ=1.2, respectively).

TABLE 1. Descriptive statistics associated with the Qamanirjuaq, Bathurst, and George River population cycles. The cycle period was determined by the sine cycle fit to the population numbers (Qamanirjuaq = 58 years, Bathurst = 42 years, and George River = 51 years). In this example, one complete cycle began and ended at the minimum carrying capacity growth rate. The threshold value for range recovery is defined as the population number (Nt) associated with the minimum K-value.

	Qamanirjuaq		Bathurst		George River	
Variable	Cycle year	Value	Cycle year	Value	Cycle year	Value
K λ_{min}	0	0.833	0	0.674	0	0.406
K λ_{max}	9	1.537	4	3.102	2	5.311
K_{min}	5	30,844	3	10,416	2	1245
N_t (at K_{min}): Threshold value for range recovery	5	41,971	3	18,265	2	3141
K_{max}	33	486,183	12	487,210	24	638,682
N_t (at K_{max})	33	457,460	12	134,159	24	569,975
N_{min}	7	36,093	4	14,466	3	1821
N_{max}	37	472,647	25	420,179	28	611,509

River) considered (Figs. 2, 3). Subpopulation numbers closely tracked carrying capacity throughout all three cycles, except for the period just after the subpopulation minimum, when K increased more rapidly than N in all three subpopulations (Table 1, Fig. 2). Minimum subpopulation thresholds that were required to initiate *K* increase for the Qamanirjuaq, Bathurst, and George River subpopulations were 8.8%, 4.35%, and 0.51% of maximum numbers, respectively (Table 1, Fig. 3). During the low portion of the cycle, relatively low numbers of caribou were able to prevent range recovery until they were extremely scarce. However, once caribou numbers had declined beneath the threshold required to initiate range recovery, the rate of range recovery outstripped the concurrent rate of caribou recovery by a substantial margin (Fig. 3). Overgrazing (progressive reduction to carrying capacity) was initiated at intermediate and increasing caribou densities that continued to increase, peaked, then declined to low numbers, as *K* was progressively reduced to the cycle minimum in all three subpopulations (Fig. 3).

Sine cycle subpopulation growth rates for the Qamanirjuaq subpopulation varied from a maximum of 1.195 in the increase phase, to 0.837 in the decline phase of the cycle (Table 2). All the sine cycle λ_t values for the Qamanirjuaq subpopulation were within the Southampton Island rate of intrinsic increase (i.e., < 1.276). However, calculated sine cyclic estimates of the maximum and minimum rates of annual subpopulation growth were sometimes greater than the island maximum rate of intrinsic increase and the maximum biologically possible intrinsic rate of increase ($\lambda_{max} = 1.363$) during the irruption phase for both the Bathurst ($\lambda_{max} = 1.473$; $\lambda_{\min} = 0.678$) and George River ($\lambda_{max} = 2.810$; $\lambda_{\min} = 0.347$) subpopulations (Fig. 4, Table 2). The additional (i.e., observed $\lambda > 1.2$) annual increase in the Bathurst and George River irruption phase was attributed to extrinsic growth (i.e., immigration) (Fig. 4). Immigration rates for the Bathurst subpopulation initially increased, peaked, then declined. Immigration rates for the George River subpopulation, as a percentage of total growth, were highest initially, then declined throughout the irruption phase (Fig. 4).

Mean cycle lag times (years for N_t to equal K_t) for the Qamanirjuaq, Bathurst, and George River subpopulations were 3.946 (SE = 0.151), 3.649 (SE = 0.184), and 3.389 (SE = 0.188) respectively (Tables 1, 2). Kruskal–Wallis pairwise comparison of the observed immigration mean lag times of each subpopulation over one complete cycle demonstrated that the mean lag time for the George River subpopulation was significantly different from the Qamanirjuaq lag time ($p = 0.032$), but not significantly different from the Bathurst lag time ($p = 0.339$) subpopulation (Table 3). The difference in mean lag times between the Qamanirjuaq and Bathurst subpopulation was also not significant ($p = 0.216$) (Table 3). When the period of irruption years was excluded from the comparison of mean lag time values (i.e., intrinsic growth only), there were no significant differences in the projected lag time values between any of the three subpopulations (Table 3). When pairwise comparisons were restricted to only the irruption period (i.e., period of immigration for both the Bathurst and George River subpopulations), the mean lag time for the George River subpopulation was significantly different from the Qamanirjuaq lag time ($p = 0.025$) but not significantly different from the Bathurst lag time ($p = 0.145$). The difference in mean lag time between the Qamanirjuaq and Bathurst subpopulations was also not significant ($p = 0.077$) (Table 3).

Kruskal–Wallis pairwise comparison of mean population growth rates resulted in no significant difference between subpopulations for one complete cycle or for one complete cycle excluding irruption years (Table 4). When only irruption years were considered separately, the mean population growth rate for the George River subpopulation was significantly different than the mean population growth rate for the Qamanirjuaq ($p = 0.001$) but not significantly different from the Bathurst mean population growth rate ($p = 0.085$). The difference in mean population growth rate between the Qamanirjuaq and Bathurst irruption years was also significantly different ($p = 0.010$) (Table 4).

K-means cluster analysis identified three distinct clusters of lag time values and population growth rate values for the irruption years of each subpopulation cycle. Clusters were characterized as: 1) short N_t to K_t lag times

TABLE 2. The Qamanirjuaq subpopulation experienced maximum and minimum rates of population growth that aligned with previously reported rates (λ_{max} = 1.17; λ_{min} = 0.83) of maximum and minimum rates of population growth and decline for continental subpopulations of barren-ground caribou (Gunn, 2003). The Bathurst and George River subpopulations both experienced maximum rates of population growth that were greater than biologically possible (λ_{max} = 1.363). We assumed that all continental subpopulations experience varying levels of harvest, predation, and other forms of natural mortality. Any subpopulation growth rates >1.2 were constrained to λ = 1.2 to account for these natural conditions. Any growth exceeding this was attributed to immigration from adjacent subpopulations. Lag times were calculated as the time (in years) for population numbers (N_t) to reach carrying capacity (K_t).

	Subpopulation		
Cycle parameter	Qamanirjuaq	Bathurst	George River
Cycle period	58	42	51
λmax (uncorrected)	1.195	1.473	2.810
λmin (uncorrected)	0.837	0.679	0.347
Maximum lag time (cycle year)	6.895 (12)	6.672 (12)	6.934 (12)
Minimum lag time (cycle year)	2.608 (2)	1.993 (0)	1.146 (0)
Average lag time	3.946	3.649	3.389
Irruption duration	6	9	9
Years of immigration	0	8	9

and high lambda values; 2) intermediate N_t to K_t lag times and intermediate lambda values; and 3) extended N_t to K_t lag times and intermediate lambda values (Fig. 5). Cluster 1 was exclusively associated with George River estimates from the beginning of the irruption phase. Cluster 2 was comprised of a mix of Bathurst and Qamanirjuaq records from the start of their respective irruptions and the latter half of the George River irruption phase. Cluster 3 was predominantly associated with the Qamanirjuaq subpopulation, but also included records from the latter portions of both the Bathurst and George River irruptions (Fig. 5).

DISCUSSION

For brevity, we have restricted the discussion to the more germane aspects of these results with respect to barren-ground caribou ecology. Supplement S3 includes a more developed range-specific discussion.

Range Dynamics Implied by Caribou Cycles (Logistic Narrative)

The expected values for the Qamanirjuaq, Bathurst, and George River N_t sine cycles are empirical in that they derive from the best Bayesian model for the respective census data time series for these barren-ground caribou subpopulations (Bongelli et al., 2020). In contrast, our logistic perspective of the corresponding dynamics of range quality (K_t) derives from two assumptions: 1) range condition varies annually due to the opposing forces of caribou overgrazing and range recovery; and 2) barren-ground caribou population dynamics are logistic depending only on range condition (and sometimes immigration). Field studies have documented that periods of barren-ground caribou decline coincide with overgrazed range (Archer and Tieszen, 1980; Caughley and Gunn, 1993; Payette et al., 2001; Gunn, 2003; Payette et al., 2004; Zalatan et al., 2006). However, we found no published estimates or indices of range condition that extended for a substantial fraction of any subpopulation cycle period. We were thus unable to compare our range condition proxy values to independent measures or indices of range quality for any barren-ground caribou subpopulation. The following discussion of barren-ground caribou subpopulation regulation due to range condition dynamics is presumptive, rather than descriptive.

Most barren-ground caribou subpopulations do not just fluctuate over time; they cycle in a regular manner (Bongelli et al., 2020). We show that logistic carrying capacity (range condition) also increases and declines in a regular manner that was similar for all three subpopulations, but does not specifically sine cycle like subpopulation numbers (Figs. 2, 3). Range condition time series dynamics were similar for the Qamanirjuaq, Bathurst, and George River subpopulations, but subpopulation range dynamics were also unique in important ways.

All three range condition time series were asymmetrical. The asymmetry in K_t dynamics derived from the period of slow decline during the lowest part of the cycles until the threshold number that allowed range recovery to be initiated was reached (Figs 2, 3). Once range recovery was initiated, range condition increased faster than caribou numbers increased until the range was no longer a limiting factor in caribou population increase. Erupting subpopulations of caribou rapidly became abundant across their range. However, before caribou subpopulations had recovered to even half of their maximum population numbers, the rate of caribou population growth was already declining from ecological maximum values due to reduced range condition recovery rates caused by the increased grazing (Table 1; Fig. 3).

By the time caribou reached their maximum numbers, range condition was already reduced due to overgrazing that had been occurring from intermediate numbers well before the peak in caribou was reached (Figs. 3, 4). Before any management concerns were apparent, it was already too late to prevent an overgrazing decline that

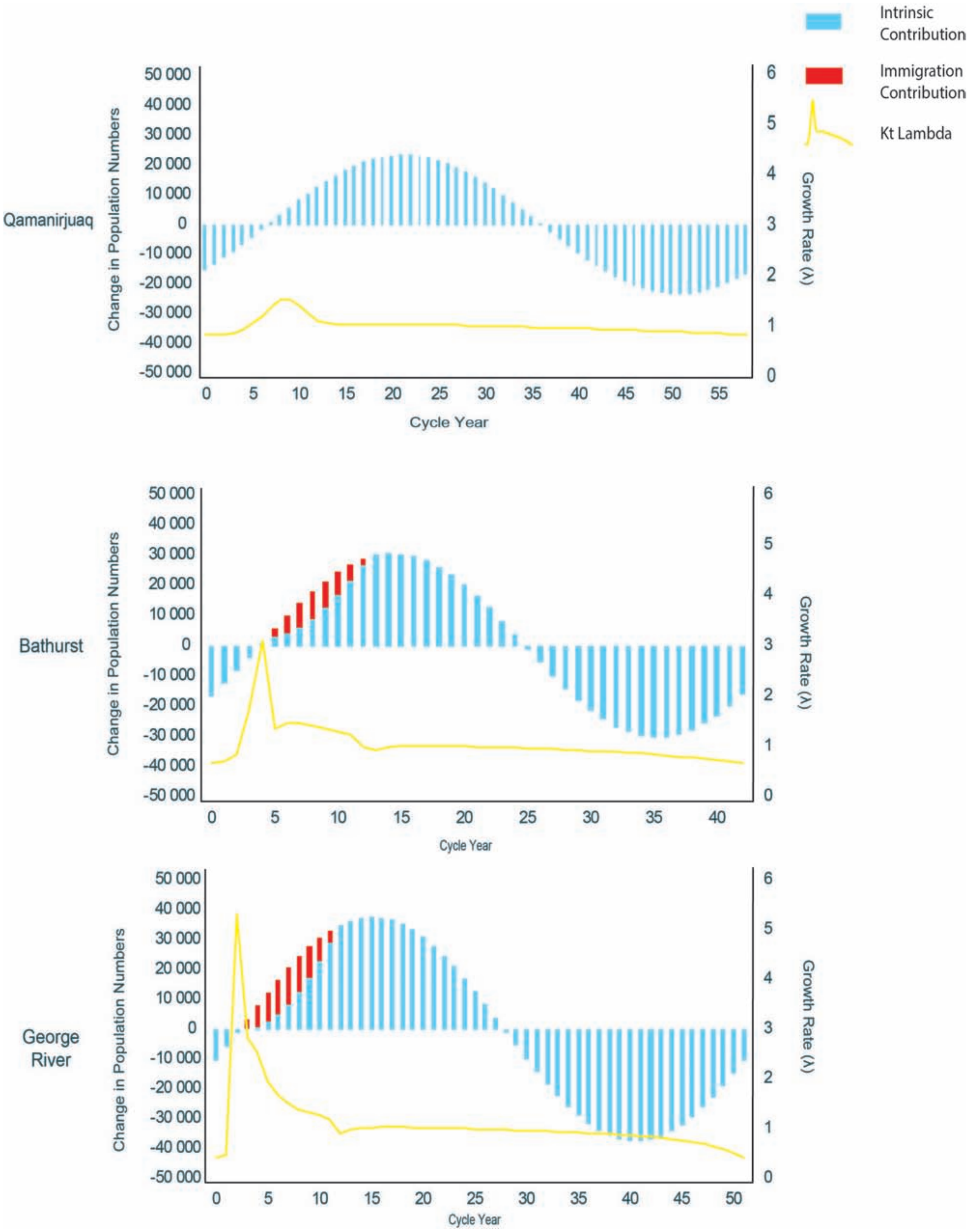

FIG. 4: Barren-ground caribou subpopulations are limited to a biological maximum population growth rate of 1.363. All continental subpopulations of barren-ground caribou will experience some combination of harvest, predation, and other forms of natural mortality that reduce annual population growth rates. We identified λ = 1.2 as realistic maximum population growth rates for subpopulations of barren-ground caribou under natural conditions. Population growth above this rate was attributed to immigration. The Qamanirjuaq subpopulation did not experience population growth rates greater than 1.2, while the Bathurst and George River subpopulations experienced population growth rates > 1.2 for eight years and nine years of their respective cycles. High rates of subpopulation growth and immigration were preceded by eruptive growth in carrying capacity in both the Bathurst and George River subpopulations. Immigration rates were initially low, increased, and slowly declined into strictly intrinsic subpopulation growth in both cases.

TABLE 3. The irruption phase of the population cycle was defined as the number of years that population growth rate was >1.0 and increasing in consecutive years. The duration of the irruption period was six years, eight years, and nine years for the Qamanirjuaq, Bathurst and George River subpopulations respectively. Lag times (time required for N_t to equal K_t in years) were compared for three unique phases of the population cycles: 1) one complete population cycle; 2) one complete population cycle excluding the irruption period; and 3) only years associated with the irruption period of each subpopulation. Pairwise comparisons were considered significant at $p < 0.05$.

Subpopulation	Pairwise comparison	One complete population cycle: sig. value	One complete population cycle excluding irruption: sig. value	Only irruption years: sig. value
Qamanirjuaq	George River	0.032*	0.142	0.025*
Bathurst	Qamanirjuaq	0.216	0.093	0.077
George River	Bathurst	0.339	0.984	0.145

* denotes those pairwise comparisons are significant at $p < 0.05$.

TABLE 4. The irruption phase of the population cycle was defined as the number of years that population growth rate was >1.0 and increasing in consecutive years. The duration of the irruption period was six years, eight years, and nine years for the Qamanirjuaq, Bathurst, and George River barren-ground caribou subpopulations respectively. Uncorrected (for immigration) population growth rates were compared for three unique phases of the population cycles: 1) one complete population cycle; 2) one complete population cycle excluding the irruption period; and 3) only years associated with the irruption period of each subpopulation. Pairwise comparisons were considered significant at $p < 0.05$.

Subpopulation	Pairwise comparison	One complete population cycle: sig. value	One complete population cycle excluding irruption: sig. value	Only irruption years: sig. value
Qamanirjuaq	George River	0.822	0.142	0.001
Bathurst	Qamanirjuaq	0.831	0.093	0.010
George River	Bathurst	0.946	0.984	0.085

resulted in a prolonged period of caribou scarcity. A key prediction of this hypothesis is that once range condition has been reduced to low levels by overgrazing, relatively low densities of caribou are sufficient to keep range from recovering until a minimum threshold of caribou density has been reached (Table 1; Fig. 2). Range recovery does not occur gradually over the portion of the cycle when caribou numbers are at low numbers; rather, range recovery is delayed until caribou numbers (grazing impacts) have declined below the threshold required for range recovery.

These results assume logistic (linear) density dependence for barren-ground caribou relative to a carrying capacity (range quality) that varies as a function of range grazing and range recovery rates. Non-linear density effects models, or more complex ecological models, would result in a plethora of currently indistinguishable alternative range condition dynamics, all based on the empirical observation that these subpopulations cycle. However, assuming that carrying capacity is non-variant is mathematically inconsistent with logistic population cycles for populations with a maximum annual growth rate < 2.6 (May, 1976). The absolute biological maximum population growth rate for barren-ground caribou is: $\lambda_{max} = 1.363$ (Heard, 1980). Ungulates may fluctuate in numbers, but do not cycle when range condition remains approximately constant or fluctuates around some average value (May, 1976; Renshaw, 1991; Vandermeer, 2010).

Bongelli et al. (2020) noted that ecological difference can exist between the subpopulations that can mediate caribou-range interactions. Qualitative differences were observed in the K_t dynamics of these three sine cyclic subpopulations. These differences are most apparent (Table 1, Fig. 3) when the time series for the three subpopulation cycles is indexed to the year that range recovery begins, rather than indexed to the actual census time frames.

At low caribou numbers, both K_t and N_t continue a slow decline until a minimum grazing threshold is reached (Table 1, Fig. 2). Once the threshold minimum N_t is reached, range quality increases faster than it can be grazed, so carrying capacity increases more rapidly than caribou numbers can keep pace (Figs. 2, 3, 4). The surge of habitat recovery occurs one to two years prior to positive intrinsic growth in caribou numbers for all three subpopulations (Table 1). The irruption phase for the Qamanirjuaq, Bathurst, and George River subpopulations ranged from 6 to 9 years, or 12%–19% of their respective cycle periods (Tables 1, 2). Range conditions began to decline four years prior to the peak in caribou numbers for the Qamanirjuaq subpopulation (Table 1). 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 range quality occurs four to five years prior to the peak in subpopulation numbers (Fig. 3). The Qamanirjuaq range recovery rate of increase was more gradual than the Bathurst and George River range recovery rate profiles. The hump (Qamanirjuaq) or spike (Bathurst and George River) in range recovery rates (Fig. 3) is the inflection point at which grazing intensity first arrests then reduces the range recovery rate until range recovery becomes range decline due to overgrazing.

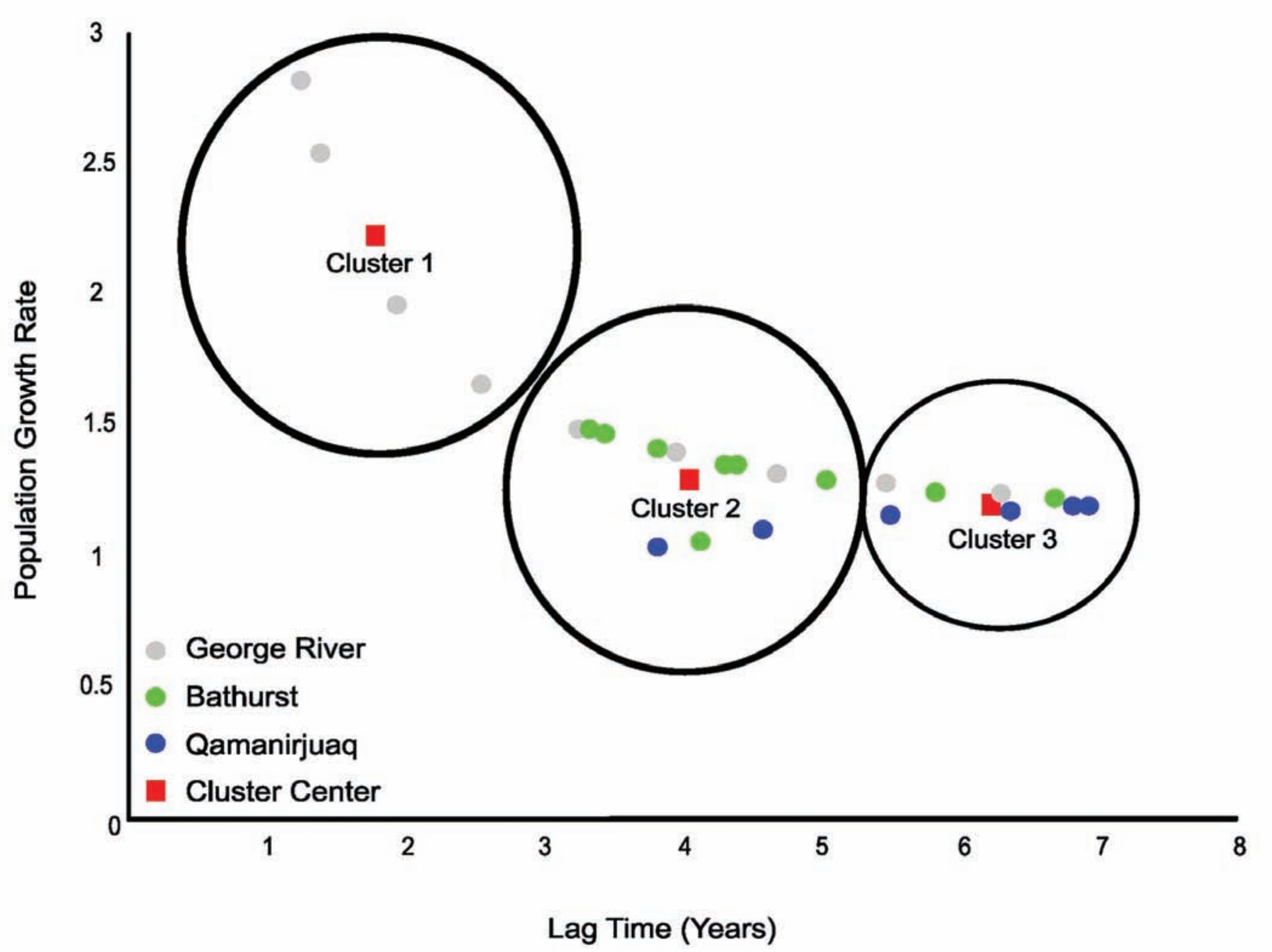

FIG. 5: We defined the irruption phase of the population cycle as the number of years that population growth rate was >1.0 and increasing in consecutive years. K-means cluster analysis identified three unique clusters associated with the population growth rates and lag time values during the irruption years of Qamanirjuaq, Bathurst, and George River subpopulation cycles.

In the initial irruption period, both carrying capacity and caribou numbers are simultaneously increasing. Range condition is limited by total range area and maximum range productivity. As caribou numbers increase, net range productivity is reduced by grazing. Consequently, the rate of N_t growth begins to decline as N_t approaches K_t.

The difference between maximum range condition (K_{max}) and maximum population numbers (N_{max}) for the Qamanirjuaq, Bathurst, and George River subpopulations was four, 13, and four years, respectively (Table 1, Figs. 1, 2). The dip in the K_t curve for the Bathurst and George River subpopulations is consistent with a surge of immigration observed in those two subpopulations (Fig. 4). No dip in the K_t curve or immigration was observed for the Qamanirjuaq subpopulation, where all subpopulation growth could be attributed to intrinsic growth.

Irruption

Including immigration, the George River subpopulation had the highest observed λ_{max} values and the highest observed rates of decline (λ_{min}). Including immigration, the Bathurst subpopulation maximum rates of increase and decline were intermediate to the George River and Qamanirjuaq subpopulation λ_{max} and λ_{min} values (Table 2). Optimal foraging theory suggests that individuals will shift their home range to maximize energy intake (Stephens and Krebs, 1986). We suggest that as range condition declines due to overgrazing, individuals may explore adjacent ranges and sometimes remain there if the adjacent range condition is better than the individuals' original subpopulation range. Migration to improved range conditions would increase the rate of subpopulation decline in the contributing subpopulation and increase the rate of growth in the adjacent receiving subpopulation.

Both the Bathurst and George River subpopulations increased at rates exceeding maximum continental intrinsic rates of increase (i.e., $\lambda_t > 1.363$) during the irruption phase of their cycle. The George River subpopulation experienced the highest observed total subpopulation growth rate ($\lambda = 2.810$), the greatest percentage of immigration driven annual increase (89%), and the shortest lag time value (1.146 years) just prior to its irruption period (Table 2). Immigration contributions to growth during the Bathurst irruption were initially intermediate (~42%), increased to ~57%, then gradually declined to about 6% of annual increase (Fig. 4). Population growth rates greater than the continental maximum rate of increase during the irruption phase were observed for nine of 42 years during the Bathurst cycle, and nine of 51 years for the George River cycle. Our method of calculating immigration assumes net immigration in a given year is a permanent transfer of individuals from an adjacent subpopulation. However, both permanent and temporary exchange between adjacent subpopulations has been documented for most subpopulations of barren-ground caribou (McFarlane et al*.*, 2016; Environment and Climate Change Canada, 2017). Cycle synchrony (or asynchrony) of adjacent subpopulations could affect the timing and magnitude of net immigration to barren-ground caribou subpopulations. Additionally, the calculation of immigration depends on our assumption of the maximum intrinsic growth rate given predation and human harvest. Assuming a larger maximum intrinsic growth rate ($\lambda > 1.2$) would cause less of the irruption increase to be attributed to immigration.

The Qamanirjuaq subpopulation appeared to be limited to intrinsic population growth throughout its irruption phase (i.e., $\lambda_t \leq 1.2$). The maximum and minimum rates of population growth and decline estimated for the Qamanirjuaq subpopulation ($\lambda_{max} = 1.196$; $\lambda_{\min} = 0.837$; Table 2), align with previously reported (Gunn, 2003) maximum and minimum rates of population growth and decline for continental subpopulations of 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. Once range recovery was well under way, Qamanirjuaq caribou were able to double in about four years, with no immigration under natural (i.e., predators and harvest) conditions. Conversely, the maximum observed rate of decline suggests the half-life of the Qamanirjuaq subpopulation during the cycle period of maximum decline was a little over three 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 number identified by the current carrying capacity of its range.

Bathurst and George River irruption patterns suggest that although irruption is predicated on habitat recovery, it can be accelerated by immigration from adjacent subpopulations. In both cases, immigration peaked early in the irruption phase, then declined as the subpopulation increased. Although substantial net immigration may occur during the irruption phase, these results are most consistent with the view that overall barren-ground caribou subpopulations may be considered demographically closed for management purposes. Immigration did not appear to be a factor in triggering the irruption phase of the Qamanirjuaq subpopulation (Fig. 4). Immigration is not required for initial subpopulation increase because the range can apparently increase faster than the caribou once the minimum threshold of caribou has been reached (Fig. 3). Immigration appears to play only a transitory and relatively minor role in barren-ground caribou cycles relative to intrinsic subpopulation growth.

Range recovery rate exceeds population recovery rate once the threshold for recovery is reached. In our formulation, carrying capacity increases or declines as a range-wide unit, rather than as patches of distinct winter/summer units. Caribou numbers lag behind range recovery resulting in low (perhaps negligible) grazing rates during the initial recovery period. In the Bathurst and George River examples, range quality does not appear to limit caribou population growth rates during the initial portion of the irruption phase (Table 2, Fig. 4). Qamanirjuaq subpopulation growth rates appeared to be range limited throughout their cycle.

Recovery Thresholds

The recovery thresholds for Qamanirjuaq, Bathurst, and George River subpopulations were 41,971 ($0.080 * N_{max}$), 18,265 ($0.044 * N_{max}$), and 3141 ($0.005 * N_{max}$), respectively. Statistical comparisons were not determined for subpopulation recovery threshold numbers, but it is clear that the threshold number for range recovery is a very small proportion of the number present at the height of the cycle. Subpopulation differences in the recovery threshold values would presumably be due to the same factors that determine period and amplitude of the cycles (i.e., range size and range productivity) (Bongelli et al., 2020). However, each subpopulation has its own unique set of ecological circumstances (e.g., tundra/forest ratios, annual productivity, migration corridors, immigration potential). The Qamanirjuaq and the Bathurst subpopulations are currently experiencing subsidized wolf control (removal) programs, while in the George River subpopulation, predator removals are limited to seasonal fur harvesting. The timing and magnitude of immigration would depend 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). We found the existing data to be insufficient to evaluate demographic impacts of non-range factors. However, Bongelli et al. (2020) were able to explain 96% of the variability in the pooled census data for nine cyclic subpopulations using a linear regression model that employed only range size and range productivity as independent variables. Non-range factors appear to be relatively unimportant compared to range dynamics in driving barren-ground caribou cycles.

The recent (2022) Qamanirjuaq calving ground census estimate was not available for the Bongelli et al. (2020) sine cycle fit estimate, but it appears to be an 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. Reduced wolf predation may have allowed Qamanirjuaq caribou to maintain higher than expected numbers and grazing rates. Conversely, the 2022 survey result could be nothing more than a statistical anomaly. In either event, our grazing-driven sine cycle hypothesis predicts a precipitous decline over the next five years for this subpopulation due to increased grazing from the artificially enhanced (mortality reduced) numbers, or perhaps a trajectory correction to the 2022 census anomaly. Continued monitoring of the Qamanirjuaq subpopulation (and other cyclic subpopulations) will allow objective evaluation of the role of grazing in barren-ground caribou cycles.

The Bathurst and George River caribou recoveries are currently somewhat behind the anticipated schedule according to the timing predicted from their sine cycle. Several explanations are possible. The variance in recent calving ground census estimates may be sufficient to mask subpopulation trends early in the recovery period. The caribou cycle may vary from cycle to cycle more than our single cycle sample suggests. Range overlap with adjacent subpopulations may mean the effective number of caribou on the range is still greater than the minimum threshold required for range recovery. Harvest restrictions and predator control activities may have increased caribou survival rates and reduced caribou declines at low densities sufficient to keep caribou numbers above threshold recovery levels for these subpopulations.

Cycle Lag Times

When comparing mean cycle lag times only the Qamanirjuaq and George River subpopulations were significantly different ($p = 0.032$) (Table 3). There were no significant differences between mean annual population growth rates for any pairwise comparisons of these three subpopulations (Tables 3, 4). K-means cluster analysis (Fig. 5) suggests that the irruption period of the subpopulations is the main contributor to the differences in lag times between the subpopulations. The Qamanirjuaq and George River subpopulation mean lag times were different, but the Bathurst mean lag time was intermediate and not significantly different (Fig. 5). The N_t to K_t lag time is shortest when population growth rates are at or near their minimum and greatest at the end of the irruption phase of the cycle. The regularity and symmetry of both the increase and decline phases of these cycles suggest that barren-ground caribou cycles were historically stable and resilient.

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. We suggest that barren-ground caribou subpopulations will cycle indefinitely as a demographic result of herbivore-range dynamics in contiguous tundra/taiga habitat if their range remains predominantly intact and they are not over-managed.

Testing the Hypothesis

Although we are currently unable to compare our proxy variable for range condition with actual field measures of range condition or other proxy variables of range condition due to data limitations, we can evaluate our model in two ways. The first test is to project the expected subpopulation sine cycles forward in time and compare the expected estimates with the future census estimates. We suggest that the decline of Qamanirjuaq caribou will continue and accelerate, followed by a decade or more of relative scarcity. The N_t sine cycles and K_t profiles of the Bathurst and George River subpopulations suggest that the irruption phase is imminent or already occurring in those subpopulations. A surge in Bathurst and George River subpopulation numbers can be expected and may already be occurring at levels too low to be reliably detected by surveys over their vast ranges.

The second prediction is that range conditions in the Bathurst and George River subpopulations are either close to the lowest levels observed for these ranges or are currently recovering at a rapid rate from those lows. We suggest that the Qamanirjuaq range is currently declining rapidly due to overgrazing. Range condition studies or documentation of relevant traditional ecological knowledge on range condition will be required to evaluate these range predictions. Based on our study, we predict that all of our focus subpopulations are in a period of rapid range quality change.

Barren-ground caribou are an International Union for Conservation of Nature and Committee on the Status of Endangered Wildlife in Canada (COSEWIC) threatened species because of observed declines in some subpopulations over three generations. A threatened species is presumed to be in decline. If not arrested, the decline will eventually result in the species being declared endangered. If the cause of the decline is still not addressed, the species will eventually become extirpated or extinct. Many reasons have been suggested for these declines, but none of the proposed causes have been unambiguously documented by any direct or experimental evidence. Even human harvest mortality may be additive, compensatory, or some combination of both. For example, Parlee et al. (2018) argued that the subsistence hunt could not have been responsible for the population declines in the subpopulations that they studied. Bongelli et al. (2020) suggested that most barren-ground subpopulations rise and fall according to the period and amplitude of their cycles. Gunn (2003) suggested that caribou's regular population fluctuations are synchronized on a subcontinental scale, implying an external factor, such as climate. The 2016 COSEWIC status report noted that seven of nine (78%) of the subpopulations considered were declining, and two were increasing (COSEWIC, 2016). Gunn (2023) identified a current continental trend, with seven of 14 herds declining, and seven of 14 herds increasing. Fisher's exact test indicates that the probability of the 2016 and 2023 trends being the same is: $p = 0.0457$. We suggest that neither the 2016 decline nor the 2023 stable/increase are meaningful without considering the state of the natural cycles of the individual subpopulations considered. Bongelli et al. (2020) showed that when the nine cyclic subpopulations were considered as a group, they sometimes appeared to have declined as a group and sometimes appeared to have increased as a group, based only on the degree of synchrony or asynchrony of these zero-trend cycles.

Management Implications

Precautionary management actions that retard the rate of decline when caribou subpopulations are at low numbers (e.g., harvest restrictions and wolf control) could extend the time required for the decline to reach the threshold minimum for recovery. Short of extensive range management practices to enhance range productivity, the only apparent management strategy to reduce the period of low caribou numbers appears to be to allow caribou hunters to continue their subsistence harvest practices and to prohibit subsidized predator harvests. Once the range begins to recover, there is no practical management strategy that can prevent or mitigate the natural barren-ground caribou cycle that eventually results in overgrazing the range and subsequent decline to lower numbers. In our view, barren-ground caribou population dynamics are inextricably bound to range depletion and range recovery cycles, and vice versa.

Sine cycles have no long-term trend. A rationale for identifying the conservation status of barren-ground caribou that fails to consider subpopulation synchrony and asynchrony is unreliable at best and can be misleading. Most barren-ground caribou subpopulations cycle with distinct periods and amplitudes (Bongelli et al., 2020). Fidelity of current barren-ground caribou subpopulation dynamics to previous cycles could be considered as an alternative to the generation-referenced trend criteria currently used to determine barren-ground caribou status. Given the apparent importance of range quality to barren-ground caribou, wildlife co-managers could consider precautionary policies requiring seasonal range protection (e.g., calving range, spring migratory corridors, summer range, winter range) for areas associated with commercial developments, and transportation corridors to ensure caribou habitat remains predominantly intact. Our hypothesis to explain barren-ground caribou cycles as the result of logistic growth throughout the overgrazing and recovery dynamics presumes retention of the essential qualities of their historically pristine range.

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DATA ACCESSIBILITY STATEMENT

All data used in this paper were taken from public sources and are available from the corresponding author.

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