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Parasites and forage as determinants of body condition and population size in an imperiled ungulate.

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Abstract

Rapid environmental changes are resulting in widespread changes in population size, health, and physiology of wildlife, especially at northern latitudes where the impacts of climate change are more pronounced. Barren-ground caribou (*Rangifer tarandus groenlandicus*) have declined across much of their range in recent decades, and while the ultimate causes are unknown, western science and local Indigenous Knowledge both point to changes in body condition and diseases as contributing factors. We used a bioenergetic integral projection model (beIPM) that mechanistically links caribou population dynamics to forage quality, parasitic nematodes, and flying parasitic and biting insects through their effects on body condition. We investigated (i) the effects of parasites on caribou populations and available forage biomass, (ii) the sensitivity of model dynamics to changes in key demographic and physiological parameters, and (iii) modeled how changes in insect harassment, nematode abundance, and forage quality are likely to impact caribou populations. We found that parasites and insects can have substantial impacts on nutritional condition and population dynamics of caribou, and that these impacts can cascade through the ecosystem. In the absence of parasites, caribou numbers were limited by forage resulting in population sizes reaching a stable carrying capacity. Reductions in foraging rate and increased energetic costs associated with parasites lowered caribou population size and increased biomass of available forage. Our study provides a critical contribution toward better understanding of the cumulative effects of multiple stressors on wild populations and outlines a framework for mechanistically evaluating the impacts of energetics, parasites, and disease on wildlife.

Keywords: population dynamics; bioenergetics; integral projection model; caribou; *Rangifer*; parasite; botfly; nematode

Introduction

Developing a mechanistic understanding of the factors that drive the wildlife population dynamics is a central goal of ecology and conservation science (Osada et al. 2015) and imperative for effective conservation and management (Hone and Krebs 2023). Ultimately, population dynamics and demographic rates are the result of individual-level interactions with a suite of environmental and ecological promoters and stressors that scale up to result in population and community level effects (Sibly and Hone 2002, Johnston et al. 2019). Disentangling the impact of multiple interacting stressors on wildlife populations depends on our understanding of how these factors influence individual behavioral and biophysical processes and, subsequently, vital rates and population dynamics. Moreover, rapid and widespread global ecological changes are adding an additional layer of complexity to this challenge by altering the intensity, duration, and suite of those stressors (Smallegange et al. 2017, Plard et al. 2019, Johnston et al. 2019). To avoid the worst ecological and societal effects of global ecosystem change it is important to understand how interacting stressors will impact population dynamics, species communities, and food webs (Tyack et al. 2022).

An individual's physical and nutritional condition (i.e., energetic state) is a significant driver of its survival and reproduction (i.e., fitness) and can be affected by an array of endogenous and exogenous factors including resource availability, inter and intraspecific interactions, and parasites and pathogens. Despite having once been considered relatively benign (Gunn and Irvine 2003), the sublethal effects of parasitism are increasingly recognized as an important driver of wildlife populations though indirect sublethal pathways (Shanebeck et al. 2022). Macroparasites (e.g., helminths, arthropods), are ubiquitous in terrestrial and aquatic ecosystems worldwide and have long been recognized as an important factor affecting hosts at the individual and population levels (Shaw and Dobson 1995). The individual and population level effects of parasitism can be exacerbated when co-occurring with additional biotic and abiotic stressors, such as drought (Aleuy et al. 2024), forage quantity and quality (Wagler et al. 2023), or severe winters (Murray et al. 2006). Due to the significant energetic demands of thermoregulation and lactation coupled with comparatively low energetic content of forage and generally high rates of parasitism, mammalian herbivores, including ungulates, are particularly susceptible to sublethal parasitism (Shanebeck et al. 2022, Murray et al. 2006, Grenfell 1992, Gunn and Irvine 2003). Ungulate species living in highly seasonal alpine or high latitude environments often operate near their physiological and energetic limits, making them highly sensitive to minor changes in factors such as weather, resources, pathogens, or predation risk (Desforges et al. 2021, Tyler 2010, Kutz et al. 2014, Hansen et al. 2020, Aleuy et al. 2022). However, quantifying and comprehending these effects becomes challenging when multiple factors interact simultaneously. In this study we apply a bio-energetic modeling framework (Lachish et al. 2020, Passoni et al. 2024) to better understand how the cumulative effects of multiple stressors influence wildlife populations as mediated through nutrition and body condition using barren-ground caribou (*Rangifer tarandus groenlandicus*) as a model system.

Several herds of barren-ground caribou (hereafter, caribou) have suffered precipitous declines in recent decades, with multiple factors implicated as potential drivers (Vors and Boyce 2009, Boulanger et al. 2011, 2021, Adamczewski et al. 2015, Mallory and Boyce 2018). Caribou inhabit highly seasonal landscapes characterized by long cold winters and short summers (Russell et al. 1993), and undertake the longest migration of any terrestrial mammal (Laforge et al. 2021) with extreme energetic demands and a short vegetative growing season. Spring migration from wintering grounds along the boreal-tundra ecotone to calving grounds on the tundra, a distance that can exceed 1000 km one way (Joly et al. 2019), typically begins in mid- to late-April prior to spring thaw. Females arrive on the calving grounds and give birth in early- to mid-June, prior to spring green up (Barboza et al. 2020). Nutrient rich spring growth is not abundant until several weeks after calving, so the significant nutritional demands of migration, gestation, and lactation are drawn from energetic reserves gained the previous summer (Allaye Chan-McLeod et al. 1999, Parker et al. 2005, White et al. 2013, Barboza et al. 2020). Abundant forage, rich in dietary energy and protein, is critical for caribou to replenish their depleted energy reserves over the brief arctic summer (Figure 1). Accordingly, the probability of successful reproduction in the coming year is a function of fat reserves gained during summer and fall of the previous year and maintained through winter to sustain gestation, migration, parturition, and lactation (Allaye Chan-McLeod et al., 1999; Parker et al., 2005; White et al., 2013). Harassment from biting and parasitic insects (e.g., mosquitoes [*Cuculidae*], blackflies [*Simuliidae*], and warble flies [*Oestridae*]) during a brief 3-6 week summer insect season can limit foraging activity and efficiency while increasing energetic expenditure resulting in marked fitness consequences (Cuyler et al. 2012, Ehlers et al. 2021, Benedict and Barboza 2022). Growth and development of parasitic warble fly larvae also incur substantial energetic costs over winter as they develop subcutaneously. The length and intensity of this Arctic ‘bug season’, and its effects on caribou, can be highly variable from year to year, driven largely by changes in temperature, wind, and precipitation (Witter et al. 2012b).

In contrast to the highly seasonal and variable effects of insects, the impacts of gastrointestinal nematodes on herbivores such as caribou are perhaps less extreme but more insidious, leading to a reduction in foraging activity as a function of parasite intensity, a phenomenon referred to as parasite-induced anorexia (Arneberg et al. 1996, Shanebeck et al.

2022). Internal macroparasites, such as the Trichostrongyle nematode *Ostertagia gruehneri*, can reduce foraging intake year round (Arneberg et al. 1996) and have substantial effects on livestock production (Barone et al. 2020). In wild ungulates, non-lethal effects of parasitism, which are manifest through reduction in body condition, can have significant impacts at individual and population levels (Gunn and Irvine 2003, Murray et al. 2006). The dynamic interaction between physiological energetic demands, forage availability, external stressors of insect harassment and parasitism put caribou on an energetic tightrope where small changes in energy intake or expenditure can have significant consequences on individual fitness (Russell et al. 2005, White et al. 2014).

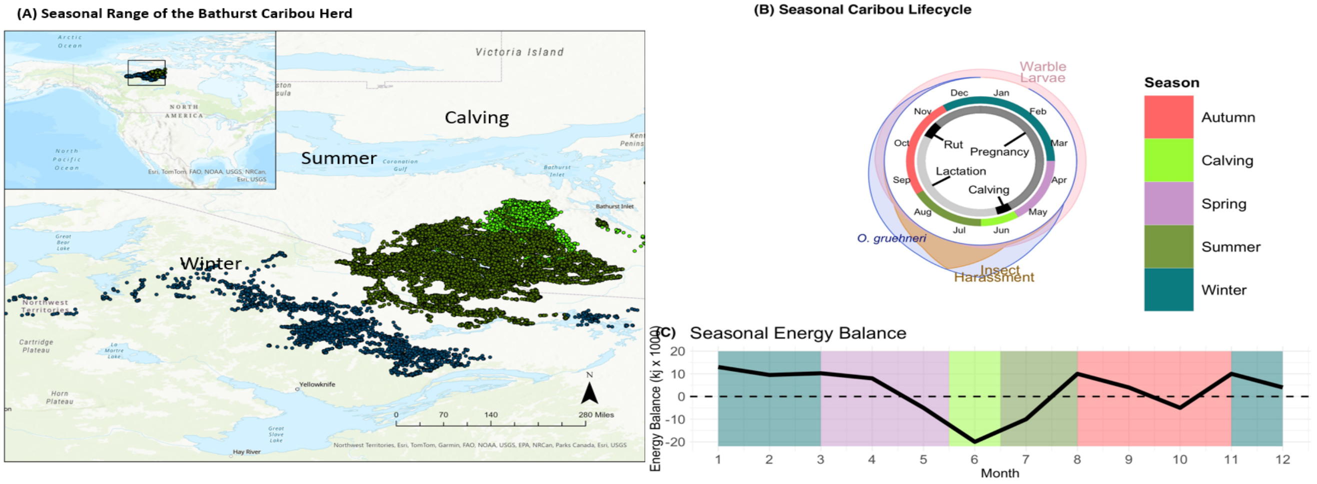

Figure 1: The seasonal distribution and life-cycle of the Bathurst herd of barren-ground caribou. The seasonal range of the Bathurst herd (A) with GPS locations for collared Bathurst caribou in winter, summer, and spring calving (spring and autumn migration omitted). The timing of critical life-history events (B) including rut, pregnancy, and calving as well as the timing of insect harassment, growth of warble larvae, and transmission of the abomasal nematode Ostertagia gruehneri, the most common gastrointestinal parasite of barren-ground caribou. These factors result in highly variable energy balance (C) throughout the year. The accumulated costs of pregnancy, calving, and lactation result in a negative energy balance in spring and early summer. Late summer and autumn foraging is important for restoring energy reserves (Panel C adapted from Russell et al 1993).

The anticipated effects of global climate change on caribou nutrition and energetics are not yet fully understood (Mallory and Boyce 2018). While earlier spring phenology and later autumns lengthen the growing season and increase total forage biomass (Dearborn and Danby

2021), warming temperatures are anticipated to change the timing, availability, and quality of the high-quality forage rich in dietary protein required to restore depleted fat reserves and meet the energetic demands of lactation (Rickbeil et al. 2018, Johnson et al. 2022, Leffler et al. 2022). In addition, changing arctic summers (longer, warmer, drier) are likely to increase the length and intensity of insect activity season (Johnson et al. 2021, Koltz and Culler 2021), reduce the availability of insect refugia (e.g., snow patches), and to facilitate more rapid development and recruitment of gastrointestinal helminths (Hoar et al. 2012). Even small reductions in recruitment or survival though changes in nutrient intake and energy expenditure caused by macroparasites has the potential to drive cascading effects through a population over time (Anderson and May 1978, Irvine 2006). Meanwhile, susceptibility to pathogens increases as body condition and immune function decrease (Shanebeck et al., 2022) resulting in a progressively worsening feedback loop.

Combined insights from western science and Indigenous Knowledge have underscored the critical importance of energetics and nutrition in the population dynamics of barren-ground caribou (Russell et al. 2005, Parker et al. 2009, Jacobsen et al. 2016, Tomaselli et al. 2018). The Bathurst herd of north-central Canada has experienced one of the most significant and sustained declines of barren-ground caribou (Boulanger et al. 2011, Adamczewski et al. 2022). In the early 1980's the Bathurst herd was one of the largest of all barren-ground caribou herds, with an estimated total size greater than 450,000 individuals. It has since declined from 360,000 in 1996, 31,000 in 2009, and 8,200 adults in 2021 (Adamczewski et al. 2022). Declines were steady but slow throughout the 1990s, but reached an inflection point between 1999 and 2000 when rates of decline sharply increased (Boulanger et al. 2011).

The Tłı̨chǫ People who have lived in relationship with the land and with caribou on the Bathurst herd's range for generations report similar trends. Tłı̨chǫ Elders and harvesters reported "good times" in the 1990s, when caribou were fat, abundant, and accessible, but began noticing changes in caribou location, body condition, health, and taste in 1998 and 1999 (Jacobsen et al. 2016). The year 2000 is seen as a turning point, harvesters reported large mortality events which had never been seen before, and by 2005 caribou were very hard to find (Jacobsen et al. 2016). Changes in caribou health were also observed over this time, including skinnier animals, watery bone marrow (indicative of low fat content), white "spots" or cysts in muscles or liver, and "bad tastes" to the meat (Jacobsen et al. 2016). In an effort to better understand why the caribou have not returned to their communities, the Tłı̨chǫ initiated an on the ground monitoring program called *Ekwǫ Nàxoèhde K'è* (ENK) to monitor the caribou, their health, their predators, and their home (Jacobsen et al. 2016). In recent years, as numbers of the Bathurst herd have continued to decline, the Tłı̨chǫ Elders, harvesters, and youth who participate in ENK have reported changes in weather, insect activity, forage quality, relative calf abundance, and caribou body condition (Jacobsen 2022).

Here we evaluate the roles of insect harassments and macro-parasite infection in caribou population dynamics as mediated through nutrition and energetics. To accomplish this, we use a bioenergetic integral projection model (beIPM) informed by western science and Indigenous Knowledge of the Bathurst caribou herd. Our model mechanistically links forage quality, parasitic nematodes, biting flies, and warble flies, to caribou population dynamics through their effects on body condition. Informed and guided by western and Indigenous understandings, we use our beIPM to test the hypothesis that parasitism and insect harassment have contributed to caribou decline and address three key objectives: (i) to investigate the effects of external stressors individually and jointly on caribou populations and forage biomass, (ii) to evaluate the sensitivity of model dynamics to changes in key demographic and physiological parameters, and (iii) model how changes in insect harassment, nematode abundance, and forage quality are likely to impact caribou populations.

Methods

Prior to model development and analysis, we held a Knowledge Sharing workshop with wildlife biologists, wildlife veterinarians, Tłįchǫ Elders, harvesters, and ENK participants to guide the research and modeling process. Tłįchǫ knowledge of changes in caribou and their environment over time, the factors that make a ‘healthy’ or ‘unhealthy’ caribou, and concerns for the future determined the factors included in our model. The goal of this workshop was to engage in conversations about cumulative impacts to and observed changes in the landscape, health, and populations of two barren ground caribou (ekwǫ̀), Kokètì and Sahtı ekwǫ̀ (Bathurst and Bluenose East caribou). Our objectives were to develop a ‘story of change’ that describes relationships between caribou and the environment, to identify factors influencing caribou health, and to brainstorm ideas for improving caribou monitoring field books for Ekwǫ̀ Nàxoèhdee K’è. Following the workshop, we met iteratively to tune model structure and analysis, and to guide interpretation of results.

Bioenergetic Integral Projection Model

Overview

We developed a female-only bioenergetic IPM (beIPM, Figure 2) to reflect the complexity of a highly seasonal host-parasite-resource system through a series of dynamic equations tracking changes in forage biomass, the Trichostrongyle abomasal nematode *Ostertagia gruehneri*, and host body condition and population size at bi-weekly intervals.

Vegetation growth is the foundation of our model. It is limited by caribou consumption and environmental conditions. In each bi-weekly time step, the caribou population consumes available vegetation transforming energy content to body mass which then determines survival and reproduction. Caribou forage intake and energetic expenditure can be reduced by insect harassment and parasitism. We focused on caribou body condition (here quantified as the ratio of reserve mass to total mass) as the critical parameter in our beIPM because it is highly correlated with survival and reproduction in caribou (Parker et al. 2009, Thompson and Barboza 2014); crucially, it is widely recognized by northern Indigenous communities as an important indicator of individual and population level health (Tomaselli et al. 2018, Hanke et al. 2022).

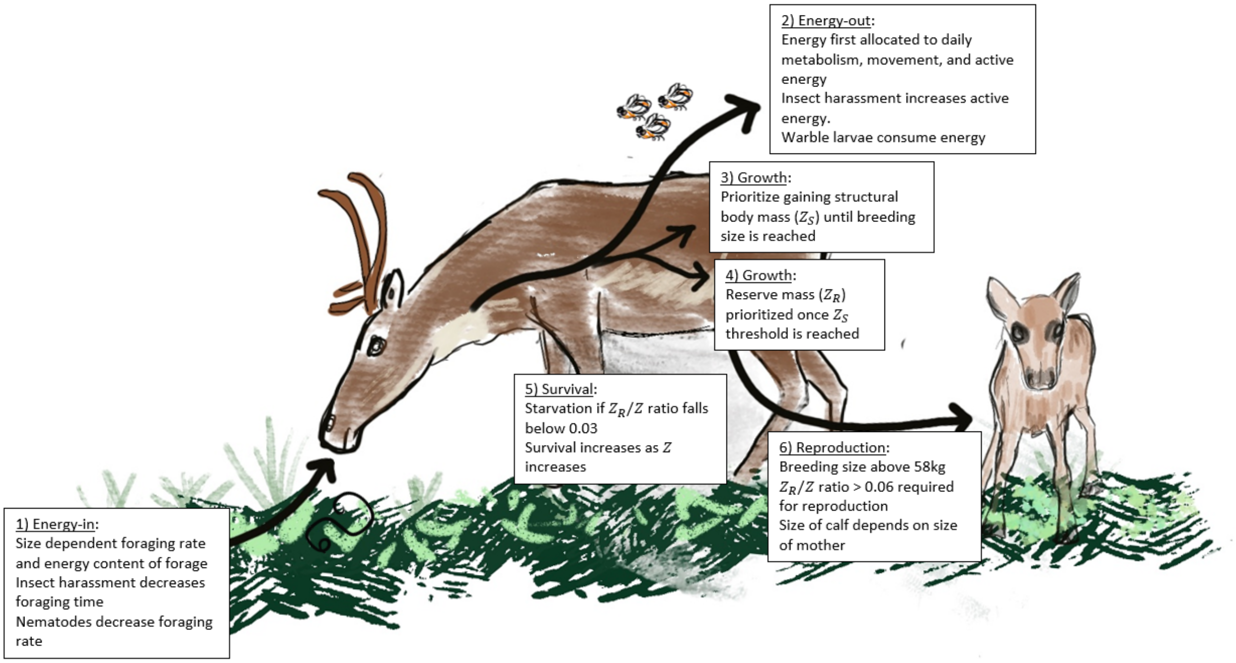

Figure 2: Conceptual diagram of the bioenergetic-IPM model used to explore the effects of forage parasites, insects, and forage resources on total (Z) and reserve (Z_R) body mass, survival, and reproduction of barren-ground caribou. Abomasal nematodes and insects both reduce energy intake by decreasing foraging time (1), while insect harassment and warble fly parasitism increase energy out (2) by increasing active energy and development of warble larvae. Survival and reproduction depend primarily on available reserve mass (Z_R).

To differentiate between total body size and body condition, we broke total body mass (Z) into structural (Z_S) mass, comprised of bones and essential organs, and reserve (Z_R) mass consisting of available fat reserves. Therefore, body size in the caribou population is the sum of structural and reserve mass, $Z = Z_S + Z_R$, and the ratio of reserve to total mass determine critical functions such as survival and reproduction (Lachish et al. 2020). It is important to note that this model does not track individual caribou through time and does not track individual level recruitment or survival. Rather, changes in population size over time are the result of differences in vital rates along the continuum of body mass values in the population (see details on model construction below for more details).

The model is driven by a series of equations that govern: 1) vegetation growth, 2) caribou foraging and energetic expenditure, 3) caribou growth and development, 4) caribou survival and reproduction, and 5) multi-stage development and survival of a helminth parasite. In each 15-day time step, the distribution of body mass in the caribou population at time $t + 1, C(Z', t + 1)$, is a function of mass-dependent (Z, Z_S, Z_R) reproduction, development, survival, and growth at time t. Throughout, Z represents body size distribution in the population at time t, while Z' represents the expected distribution in time $t + 1$ (the same symbology holds true for structural and reserve masses, respectively). In the following paragraphs we describe the fundamental caribou demographic functions and those determining forage availability and rates of parasitism. Table 1 provides a list of model parameters and Figure 2 represents a diagram of energy flow through the model. All parameters in the model were determined from best available estimates in the literature for caribou, or closely related species when caribou-specific estimates were unavailable.

Survival and Recruitment

The survival function, $S(Z, t)$ (eq. 1), determines the probability caribou with a structural mass of Z_S and reserve of Z_R will survive from time t to $t + 1$. Death due to starvation occurs if the ratio of reserve to total mass ($\frac{Z_R}{Z}$) falls below 3%, a value based on measured body fat percentage in caribou suspected to have died from starvation (Cook et al. 2021). For caribou with $\frac{Z_R}{Z} > 0.03$, survival is a logit-linear function of mean survival intercept ($\beta_0 = 0.92$) and slope ($\beta_1 = 0.02$) term for effect of reserve body mass on survival (Johnson et al. 2022).

Age at first reproduction in caribou is determined by time it takes for a female to achieve minimum body size and fat reserves (White et al. 2014). Therefore, only caribou with a structural mass above the breeding threshold ($Z_S > \tau_{Z_S}, \tau_{Z_S} = 58\ kg$) are eligible breeders (Bergerud et al. 2008). The probability of reproduction in breeding intervals for individuals of breeding size depends on the ratio of reserve to total body mass, with breeding occurring only when the ratio of reserve to total mass exceeds a breeding threshold ($\tau_B = 6\%$; Barboza and Parker 2008, Parker et al. 2009). Twinning is relatively uncommon in caribou (3-year mean = 0.5% in Godkin 1986), so we assumed all reproducers would produce a single calf. Because more than 70% of calf mortality occurs in the first week of life (Whitten et al. 1992) we set realized reproduction as $1 - \omega$ where $\omega = 0.4$ to represent realized calf recruitment (Boulanger et al. 2011). This was then halved to account for an even sex ratio of male and female calves in our single-sex model.

$$S(Z,t) = \begin{cases} 0 & \text{if}\left(\frac{Z_R}{Z} < \tau_S\right) \\ \text{logit}(\beta_0 + \beta_1 \times Z_R) & \text{if}\left(\frac{Z_R}{Z} \geq \tau_S\right) \end{cases}$$

Equation 1

$$R(Z,t) = \begin{cases} 0 & \text{if } \ Z_s < \tau_{Z_S}\ |Z_R^{*}\!: Z \leq \tau_B \\ (1-\omega) \times 0.5 & \text{if } \ Z_s > \tau_{Z_S}\ |Z_R^{*}\!: Z > \tau_B \end{cases}$$

Equation 2

Development and Growth

In each breeding interval, a reproducing female allocates a given proportion, γ, of assimilated energy reserves to reproduction, resulting in $\gamma \times Z_R^*$ available for calf growth. Of this a proportion, $\rho = 0.9\%$, is allocated to the calf's structural mass, with the remainder, $(1 - \rho)$, going to offspring's reserves, both of which are converted with a constant energy efficiency, $\varepsilon_r = 0.95$ (Lachish et al. 2020). Therefore, the expected structural and reserve mass of offspring is defined by Equation 3.

$$Z_{S_{calf}} = \rho \times \varepsilon_r \times \gamma \times Z_{R_{mother}}^*$$
$$Z_{R_{calf}} = (1 - \rho) \times \varepsilon_r \times Z_{R_{mother}}^*$$

Equation 3

We incorporate individual variation into expected calf body size (Eq. 3), where calf size $Z'_{R,S}|Z_{R_{mother}}$ is defined by a normal distribution with a mean defined by Eq. 3 and variance $(\sigma_{Z_{R,S}}^2)$ defined as a function of an intercept and slope term.

$$Z'_{R,S} = Normal\left(\mu_{Z_{R,S}}, \sigma_{Z_{R,S}}^2\right)$$

$$where, \sigma_{Z_{R,S}}^2 = \alpha_0 - e^{-\alpha_1 \cdot Z_{R,S}}$$

Equation 4

Growth depends on total energy intake and expenditures with total energy intake depending on the size dependent caribou foraging rate and energy content of the forage. Energy assimilated from forage is first allocated to basal metabolism and maintenance with the remaining energy allocated for growth. Metabolic needs of caribou vary throughout the year and scale according to a three-quarter power law with body size (White et al. 2014). Summer growth of winter coat and antlers, as well as costs of thermoregulation elevate metabolic needs in summer relative to winter (White et al. 2014). During each time interval the metabolic requirements for a caribou of body size Z is defined by Equation 5 where $ndays$ is the number of days in the time interval (*ndays* = 15 in our simulations), δ_b is the baseline metabolic rate, δ_s

is the additional seasonal metabolic rate, and Z is the total body mass. After accounting for metabolism and maintenance, energy available for growth each time step is metabolic needs subtracted from forage intake, scaled for forage availability and snow cover.

Energy available for growth is prioritized to structural mass (Z_S) with a smaller proportion going to reserve mass (Z_R). When the breeding size threshold is reached ($Z_S \geq \tau_{Z_S}, \tau_{Z_S} = 58\ kg$), all available energy following metabolism and maintenance is allocated to reserve mass, Z_R. When $Z_S < \tau_{Z_S}$, a proportion of assimilated energy reserves ($\varphi_S = 40\%$) to structural mass with a conversion efficiency (ε=0.95), with $1 - \varphi_S$ going to reserve mass, Z_R (White et al. 2014). Finally, as with calf body size, we assume that the probability distribution of body size (Z_S or Z_R) in time $t + 1$ follows a Gaussian distribution. So, probability of reserve (or structural) mass $Z'_{R,t+1}$ given $Z_{R,t}$ is a normally distributed random variable with a mean of μ_{Z_R} and standard deviation $\sigma^2_{Z_R}$ (Equation 6).

$$M(Z) = ndays \cdot (\delta_b + \delta_s) \cdot Z^{\frac{3}{4}}$$

Equation 5

$$G(Z_{R,t+1}) = Normal(\mu_{Z_R}, \sigma^2_{Z_R})$$

$$where, \sigma^2_{Z_R} = \beta_0 - e^{-\beta_1 \cdot Z_R}$$

Equation 6

Breeding females allocate a proportion of their reserve mass ($\gamma = 60\%$) for reproduction, of which a proportion ($\rho = 90\%$) is allocated to the structural mass of the calf with the remainder going to reserves. The energetic requirements of gestation and lactation are the most significant costs in a female caribou's annual life cycle. Because the majority of the costs of gestation occur during the last few weeks of pregnancy (White et al. 2014), all costs of gestation are incurred during the breeding interval. However, the timing and duration of lactation, which overlaps the brief Arctic summer and insect harassment season is important. Therefore, for caribou of breeding size and appropriate reserve mass, the energetic costs of lactation were spread out over a 3-month period based on an average daily cost for lactation of approximately 4.5 MJ day^{-1} (Boertje 1985). As noted above, potential breeders ($Z_S > \tau_{Z_S}$) will reproduce if the ratio of reserve to total mass exceeds the minimum breeding threshold (τ_B). Change in reserve mass through the breeding interval is defined by Equation 7.

$$Z_R(t) = \begin{cases} (1-\varphi_S) \cdot Z_R^* & \text{if } (Z_S < \ \tau_{Z_S}) & \text{non-breeder} \\ Z_R^* & \text{if } (Z_s < \tau_{Z_{S)}} \mid Z_R^*: Z \leq \tau_B & \text{non-breeder} \\ (1-\gamma) \cdot Z_R^* & \text{if } Z_s > \tau_{Z_S} \,\&\, Z_R^*: Z > \tau_B & \text{breeder} \end{cases}$$

Equation 7

Together, the survival, reproduction, growth, and development functions form the IPM kernel (Equation 8). At each time step four matrices are generated from the survival, reproduction, growth, and development functions which predict the transition rate of individuals for every possible value of Z_R and Z_S. These are then combined with the population vector, which represents the distribution of body mass in the caribou population at time t, through matrix multiplication to determine mass distribution in *t+1*. Population size is determined by the frequency of individuals of every possible body mass value along a discretized gridded kernel. Therefore, abundance at each time step is equal to the sum of all values in the population vector.

$$C(Z', t+1) = \int [D(Z' \vee Z, t)R(Z, t) + G(Z' \vee Z, t)S(Z, t)] \cdot C(Z, t)dZ$$

Equation 8

Forage Biomass Dynamics

Our model replicates an environment with long frigid winters and a short growing season. For each 15-day time step, change in forage biomass is determined by seasonal growth rate

($\alpha_t = 0.1 - 0.5$), the current vegetation biomass V_t, vegetation carrying capacity V_{max}, and herbivore foraging F_H.

$$V_{t+1} = (1 - \alpha_t) \cdot V_{max} + \alpha_t \cdot V_t - s_v \cdot F_H$$

Equation 9

As vegetation biomass increases, whenever $V_{t-1} < V_{max}$ growth will asymptotically converge to vegetation carrying capacity. Meanwhile, caribou reduce vegetation biomass through foraging behavior which depends on body mass and snow cover s_v.

Caribou Foraging

We assumed the maximum consumption rate of a caribou is proportional to body size such that foraging rate scales according to a three-quarter power law with total body mass ($Z^{3/4}$; White & Trudell, 1980). Consumption was then assumed to follow a Holling type-II functional response with forage biomass such that forage intake slowed as availability decreased (Owen-Smith et al. 2010). Finally, to approximate satiation and rumen handling time, foraging rate slowed as caribou reserve mass approached a theoretical maximum value of reserve mass of 40% total mass (Lachish et al. 2020). This results in 15-day forage intake as defined by equation 9.

$$F_H(Z) = f \times Z^{\frac{3}{4}} \times \left(\frac{V_t}{\theta + V_t}\right)\left(\frac{1}{1 + exp\left(-\eta \times (\tau_F \cdot Z - Z_R)\right)}\right)$$

Equation 10

where $f = 6.2$ is the slope of the foraging power function, $\theta = 10{,}000\ kg$ is the half-saturation forage biomass of foraging rate, $\eta = 15\ kg^{-1}$ is the steepness parameter determining satiation scaling of consumption such that forage intake decreases as reserve mass increases, and τ_F is a threshold reserve mass at which forage intake slows. Total forage intake across the entire caribou population is determined by the distribution of body mass in the population as $\int C(Z,t) \times$

$F_H(Z) \times dZ$. To ensure that the population did not reduce forage biomass to zero we set a minimum biomass limit that scales foraging to ensure that V_{t+1} does not fall below V_{min}:

$$p = \begin{cases} 0 & \text{when } (V_t \leq V_{min}) \\ 1 & \text{when } \left(V_t - \int C(Z,t) \cdot F_H(Z) \cdot dZ > V_{min}\right) \\ \dfrac{V_t - V_{min}}{\int C(Z,t) \cdot F_H(Z) \cdot dZ} & \text{when } \left(V_t - \int C(Z,t) \cdot F_H(Z) \cdot dZ < V_{min}\right) \end{cases}$$

Equation 11

Snow and ice are present for much of the year in caribou habitat. For time steps when snowfall was present, we reduced caribou forage intake by a constant, ς, drawn from a uniform distribution between 0.4 and 0.6. This results in the final change in resource availability per 15-day time step as defined by equation 11.

$$V_{t+1} = (1 - \alpha_t) \cdot V_{max} + \alpha_t V_t - \varsigma \cdot p \int C(Z,t) \cdot F_H(Z) dZ$$

Equation 12

Parasite Dynamics

We designed our model to account for the energetic costs of common parasites on barren-ground caribou. One internal macroparasite represented by an abomasal strongyle nematode, *Ostertagia gruehneri*, and external macroparasites in the form of dipterid flies including mosquitoes (*Aedes spp.*), black flies (*Simulium spp.*), and warble flies (*Hypoderma tarandi*).

Insects impact caribou behavior and movement which increases energetic expenditures and reduces forage intake (Johnson et al. 2022, Benedict and Barboza 2022). Additionally, larvae of parasitic warble flies, which develop under the host's skin during winter, incur significant energetic costs (Cuyler et al. 2012). We incorporated behavioral impacts of insect harassment into the model through increased metabolic costs and decreased forage intake during bug-season (June through mid-August). Activity and abundance of biting flies and warble flies on the landscape (i.e., insect harassment) is tightly linked to temperature and wind speed (Witter et al. 2012b), so, we quantified insect activity during each time step using indices developed for mosquitos and Oestrids that estimate insect activity based on surface temperature and wind speed (Russell et al. 2013). We estimated insect harassment indices for mosquito index (MI) and Oestrid index (OI) based on the equations of Russell et al. (Russell et al. 2013). These unitless indices range from 0, no insect activity, and 1, extreme activity. We randomly generated monthly insect harassment scores based on the mean and standard deviation of monthly MI and OI scores in the Bathurst range from 1980 through 2020 using monthly temperature and wind speed data obtained from the NASA MERRA database (Global Modeling And Assimilation Office 2015). Recent work in Alaska has shown that foraging activity during periods of insect harassment is reduced by more than 25%, with similar increases in energetically costly behaviors such as running (Ehlers et al. 2021). We set maximum possible values for reduced foraging activity and increased energetic costs associated with insect harassment in each 15-day time step at 60% to ensure that we did not underestimate the effects of insects on caribou populations. At each time step, the realized effect of insect harassment was the maximum value ($i_h = 0.6$) multiplied by the insect activity scores for that time step. Similarly, we set a maximum value for mean warble larval burden at 600 larvae per caribou based on data from the Bathurst herd's range (Hughes et al. 2008), with monthly values determined by the product of this maximum and OI score for that time step. Total energetic costs of larval parasitism is a function of the energy required for growth for warble fly larvae, the number of larvae, and the daily basal metabolic rate of the larvae, BMR (Eq 13).

$$E_{costs} = \frac{E_g \cdot N_{WF}}{0.98} + \frac{BMR}{0.85}$$

$$BMR = 0.05 \cdot 70 \cdot 4.187 \cdot (\text{kg} \cdot \text{WF}^{-1})^{0.75}$$

Equation 13

The abomasal nematode *O. gruehneri* has been empirically shown to reduce pregnancy and reproduction in *Rangifer*, an effect that is mediated through reduced body condition (Albon et al. 2002, Stien et al. 2002, Dickinson et al. 2023). Reduced condition is caused by a combination of inflammation and nutrient loss due to adult worms in the abomasal lining, and parasite induced anorexia, where infected individuals spend less time foraging and have reduced overall forage intake than non-infected individuals (Arneberg et al. 1996). In the absence of nematodes, size dependent caribou foraging is a function of the maximum foraging rate, f. At each time interval, we modified f to $\hat{f}$ to incorporate per-parasite reduction in foraging as:

$$\hat{f} = f \cdot \frac{K \cdot N_C}{\alpha_{forage} \cdot P + K \cdot N_C}$$

Equation 12

where N_C is the caribou population size, P is the adult parasite population, $K = 0.994$ is an aggregation parameter, and $\alpha_{forage} = 0.00001$ is a parameter for the per-parasite reduction of foraging (Koltz et al. 2022). To better reflect the complexity of host-parasite dynamics with multiple free-living life stages, we explicitly modeled the lifecycle of *O. gruehneri* through two free-living stages, non-infective eggs, L1 and L2 considered jointly as non-infective, and infective L3, and two host stages, L4 (arrested and developing) and adults. Critically, parasite egg production is highly seasonal, and survival and development of free-living stages is temperature dependent, resulting in strong annual cycles of transmission (Hoar et al. 2012b, Molnár et al. 2013, Peacock et al. 2022). Eggs produced by adult parasites residing in the abomasum are shed into the environment through the host's feces hatch into first stage, L_1 larvae and develop in the external ecosystem through non-infective L_2 to the infective third larval stage, L_3. Infective larvae then migrate vertically on vegetation where they are ingested by foraging hosts. Once ingested by the caribou host, larvae may enter a period of arrested development in the lining of the mucosa as non-infective arrested larvae, $L_{4.A}$. Ingested L_3 either enter arrested development, $L_{4.A}$, or direct development, L_4 before becoming adults in the abomasal lining. Equations for the full *O. gruehneri* model are in Supplementary Materials.

Our aim was to parameterize the simulation model to reflect the environmental and ecological factors experienced by the Bathurst herd while being applicable to barren-ground caribou more broadly. Seasonal barren-ground caribou ranges overlap with muskoxen (*Ovibos moschatus*), moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*), however, barren-ground caribou are by far the most abundant ungulate in the tundra-tussock ecosystems. Therefore, we did not consider intra-specific resource competition in our model.

Our model is inherently non-spatial and was parameterized to encompass a herd's entire annual range (Figure 1.A). However, because the region is vast and remote, accurate field-based estimates of forage biomass in Canadian barren-ground caribou herd's ranges are not available. Advances in spatial imagery and remote-sensing analysis have improved estimates of the distribution and biomass of vegetation in a changing arctic (Johnson et al. 2018, Rickbeil et al. 2018, Dearborn and Danby 2021), allowing for estimation of forage quality (energy and protein content) and quantity (biomass) in the summer range of the Central Arctic caribou herd of Alaska (Johnson et al. 2018). While the ecology and forage conditions in north central Alaska differ substantially from those experienced by caribou on the Canadian shield including the Bathurst, we used the field-based estimates of forage biomass (mean = 22.5 $g \times m^{-2}$, range = 0.0 – 63.9 $g \times m^{-2}$) by Johnson et al. to estimate potential total forage biomass in the herd's annual range ($kg \times km^{-2}$) because these represent the most rigorous empirical estimates of caribou forage biomass available. We set the maximum forage biomass (i.e., vegetation carrying capacity) as the estimated biomass based on mean values of Johnson et al plus 75%, and the minimum forage biomass as 10% of the maximum (Table 1). Growth of vegetation occurred during a short growing season of up to 4 months, with a maximum growth rate, α_t. We assumed snow covered a herd's range for between 7 and 9 months with stochastic variation between years. Caribou diets vary throughout the year in response to changes in nutritional needs, forage availability, and snow cover. In summer, when fat reserves are depleted and energetic needs are high, caribou take advantage of high-quality new growth of herbaceous graminoids and deciduous shrubs (Adamczewski et al. 1993, Leffler et al. 2022, Webber et al. 2022). By late fall quality and availability of herbaceous forage and deciduous shrubs has declined, so caribou shift to a diet composed almost exclusively of lichens and mosses, which are relatively rich in dietary energy, but almost devoid of dietary protein (Joly et al. 2007). To represent seasonal shifts in caribou diet, we allow forage energy content to vary to reflect differences in protein content in varied summer diets (ve_summer $= 12\ MJ \times kg^{-1}$) and lichen-dominated winter diets (ve_winter = 9.5 $MJ \times kg^{-1}$).

IPM Kernal and Starting Values

Body size, our phenotypic trait of interest, is inherently continuous. However, the beIPM kernel (Eq 8) is a complex integral that cannot be estimated analytically. To circumvent this we used the mid-point method which instead uses a range of possible values (i.e., mid-points) that are discretized to create a gridded kernel that can be analyzed numerically (Rees et al. 2014). Total body mass of adult female barren-ground caribou typically ranges between 100 and 125 kg (Barboza and Parker 2008, Cook et al. 2021), with percent body fat varying significantly throughout the year from less than 5% in June and July to between 10 and 15% in early winter (Adamczewski et al. 1993, Allaye Chan-McLeod et al. 1999, Cook et al. 2021). We constructed a vector of structural body mass (Z_S) values ranging from 0.1 to 115 kg, each of which was associated with a value in a vector of reserve mass (Z_R) values ranging from 0.1 to 35 kg, resulting in 2,500 possible body mass (Z) values for the IPM kernel. These values were set well outside the observed values for barren-ground caribou in order to ensure that no possible phenotypes were excluded (Lachish et al. 2020) and unrealistic values will represent an insignificant portion of the simulated population. All parameters in the model were determined from best available estimates in the literature for caribou, or closely related species when caribou-specific estimates were unavailable (Table 1). Sensitivity of model output to input values was tested for parameters with uncertain estimates in the literature by varying one parameter at a time by ± 20 and 10% from baseline values (Lachish et al. 2020) (Appendix B). We used our model to evaluate four alternative scenarios: (i) no parasites, (ii) nematodes only, (iii) insects only, and (iv) both nematodes and insects. For all simulation scenarios at each time step, we tracked vectors for total (Z), reserve (Z_R), and structural (Z_S) mass, forage biomass, and population size of all *Ostertagia* life stages. All simulations were run in R (Team 2019). Model simulation code is available at https://zenodo.org/records/8322457.

Results

Knowledge Sharing Workshop

The goal of this workshop was to engage in conversations about cumulative impacts to and observed changes in the landscape, health, and populations of two barren ground caribou (ekwǫ̀), Kokètì and Sahtı ekwǫ̀ (Bathurst and Bluenose East caribou). Our objectives were to develop a ‘story of change’ that describes relationships between caribou and the environment, to identify factors influencing caribou health, and to brainstorm ideas for improving caribou monitoring field books for Ekwǫ̀ Nàxoèhdee K’è. Tłı̨chǫ Elders at the workshop made it clear that mining, insect harassment, and parasites have stressed caribou populations. When asked how scientific and Indigenous knowledge could be used to research and monitor caribou health, Elders pointed to coat condition, timing of when caribou fatten up, and caribou behavior as traits that tell them caribou are healthy. August and September are the “fat days” for caribou according to Elders; this is when the caribou should be fat and healthy, especially females to get ready for breeding and calving. To better understand the effects of health stressors (i.e., parasites and insects) on caribou populations and to guide future monitoring, we built on these conversations and the observations of Ekwǫ̀ Nàxoèhdee K’è to guide our model development. A full summary of the workshop is available in Appendix C.

Model Output

No Parasites

Under the no parasites scenario, model predicted caribou populations quickly increased from a starting value of 55,000 individuals to reach a carrying capacity just under 250,000 (Figure 3.a). Excluding a 12,000 iteration (approximately 500 simulation years) burn-in phase, the simulated caribou population remained at the vegetative carrying capacity with minimal inter-annual variation (Figure 3.a). Mean reserve mass (Z_R) was 32.99 kg (sd=3.73) with lower reserve mass following periods of reduced forage availability (Figure 4, Figure 5).

Ostertagia Only

The addition of the abomasal nematode *O. gruehneri* to the model substantially reduced caribou population size resulting in a mean 23.1% reduction in population size when compared to the No Parasites scenario. The ratio of reserve to total body mass was similar to the No Parasites though less variable, with a mean reserve mass of 33.1 kg (sd=2.5).

Insects Only

Parasitic biting insects and Oestrid flies had a more substantial effect on the simulated caribou population than abomasal parasites alone, resulting in a 36.9% mean reduction in population size relative to the No Parasites scenario (Figure 3). The addition of insects also led to significant cycles in caribou population size from a maximum annual population size around 225,000 to a minimum around 75,000 and an estimated period of approximately 281 simulation years. Mean reserve mass was similar to the No Parasites and Ostertagia Only scenarios (mean=33.6 kg, sd=2.4). However, like population size, reserve mass cycled, with the lowest reserve mass observed when population size was at the peak amplitude.

Ostertagia and Insects

Including both abosmasal nematodes and flying biting and parasitic insects resulted in cyclic population dynamics similar to the Insects Only scenario but with a substantial reduction in overall caribou population size (Figure 3). Mean burden of abomasal parasites (total adult *O. gruehneri* divided by total host numbers) was significantly lower in the two-parasite scenario than when nematodes alone were included (Appendix A.4).

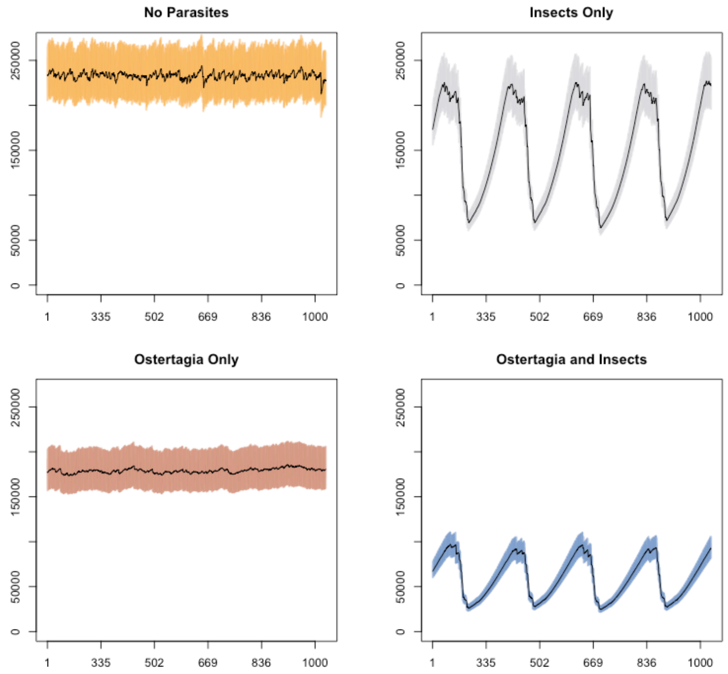

Figure 3: Caribou population trends of four baseline scenarios over a 1500-year simulation (36,000 15-day iterations) with a 12,000 iteration (~500 year) burn-in period removed. In each panel the total population size (colored line) reflects seasonal pulses in birth and death with the annual mean shown as a solid black line. The No Parasites scenario (i, orange, top-left) resulted in the largest population which was ultimately limited by forage availability. Populations in the Insects Only (grey, top-right) scenario showed eruptive population cycles, while Oster Only scenario (dark red, bottom-left) experienced reduced recruitment and lower overall population size. Finally, the multi-parasite Oster Insects scenario (blue, bottom-right) saw the reduced overall population size and population cycles resulting in the lowest overall population size the four scenarios.

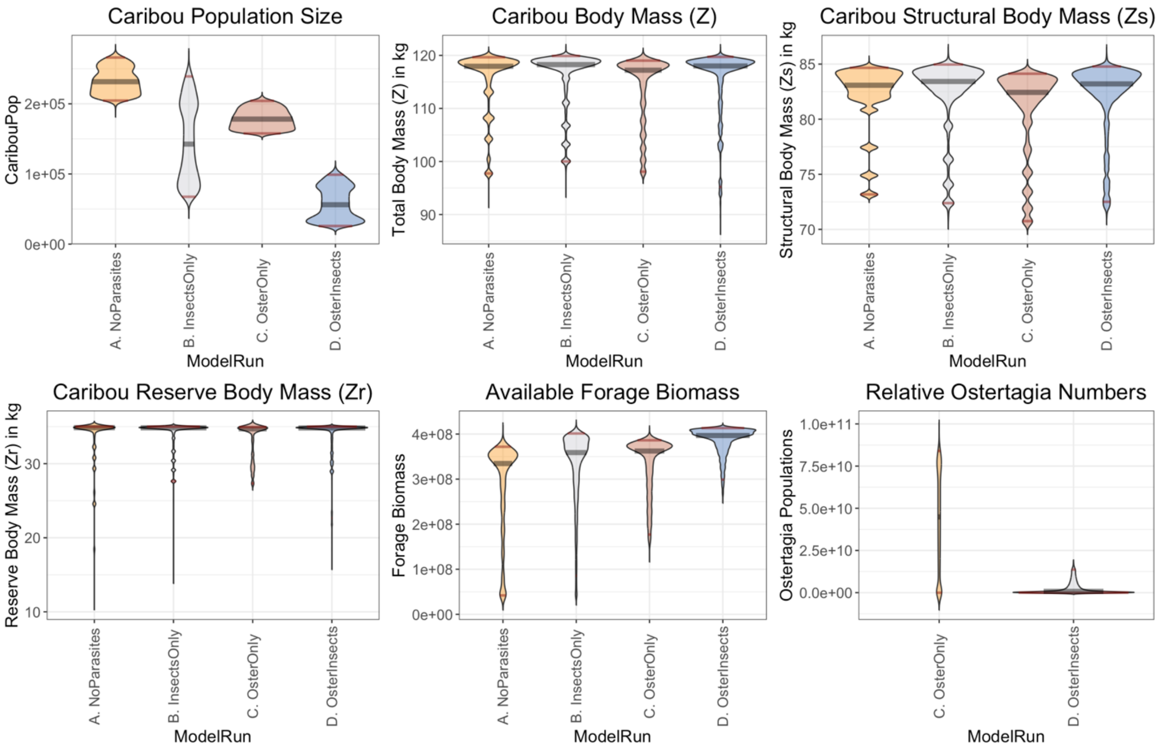

Figure 4: Key model output from the four baseline scenarios. While mean total (A), reserve (B) and structural (C) body mass did not vary significantly between simulation scenarios, there was variation in the distribution of these. Population size (D) was substantially lower when O. gruehneri was present (Baseline-ii and Baseline-iv) while forage biomass (F) was greater.

Parameter Sensitivity

Parameter sensitivity analyses showed that changes in parameters that influenced reserve body mass (Z_R) and the degree of maternal investment in calves had the most significant changes on population size and body mass (Appendix B). The parameter γ (Z_R to Z for reproduction) controls percentage of a female's reserve mass (Z_R) that is allocated for reproduction, which directly influences maternal investment in the calf. A 20% increase in this parameter from 0.60 to 0.72 doubled caribou population size, while a 20% decrease to 0.48 reduced caribou population size by 50% (Appendix B Figures 1, 2). Similarly, decreasing the breeding Z_R threshold (τ_B) by 20% from 0.06 to 0.048 allows females in poorer body condition to reproduce resulting in lower quality calves and higher risk of maternal mortality (Appendix B Figures 21, 22). Similarly, parameters that influence timing of first reproduction had a large influence on population size. For example, τ_{Z_S} is the threshold structural mass required for reproduction. Changing this parameter by ±20% both led to decreases in caribou population size when compared to the insects and Ostertagia simulation. A 20% decrease allowed smaller females to attempt reproduction before they had amassed sufficient reserve mass, while a 20% increase led to fewer females reproducing in a given year as more time was needed to reach a sufficient body size (Appendix B Figures 29, 30). Likewise, increases in δ_S, which governs the amount of available reserve mass that is allocated to structural growth for sub-adults, led to decreases in caribou population size despite lowering the age at first reproduction (Appendix B Figures 9, 10). While population models suggest that lowering age at first reproduction should increase population growth rate (Hone et al. 2010), for species in highly seasonal environments with high maternal investment such as caribou, there is a tradeoff between early reproduction and storing reserve mass to increase probability of calf survival and decrease cow mortality risk (Allaye Chan-McLeod et al. 1999).

Changes in parameters that influenced foraging rate, energy output, or forage quality all had effects on model output. Decreasing maximum foraging rate (f) or the foraging fat threshold (τ_F) both caused caribou populations do decline to near zero (Appendix B Figures 15, 19). Sensitivity analyses also showed that changes in the energy content of winter forage (VE_{wint}) had more significant impacts on population size than changes in summer forage quality with a 20% reduction in winter forage quality causing populations to decline to zero while a 20% increase in winter forage quality increased maximum population size to 250,000.

Finally, altering the severity of insect harassment through its influence on foraging efficiency or increasing energy expenditure was significant, with the effects of insect harassment on forage intake most significant (Appendix B Figures 25, 26). See Appendix B for full sensitivity analysis results.

Discussion

Evaluating cumulative effects on caribou health and population trends

Our study provides an important contribution toward understanding how multiple interacting ecological stressors can influence herbivore populations by demonstrating the significant role that individual level parasitism, insect harassment, and energy balance have at population level. Results from our four simulation scenarios demonstrate the extent to which internal and external macroparasites can impact nutritional condition and population dynamics of caribou, and how these impacts can subsequently reverberate through the ecosystem. Furthermore, our results show the variable ways in which energetic stressors, such as parasites, can cause cyclic population dynamics in the host species.

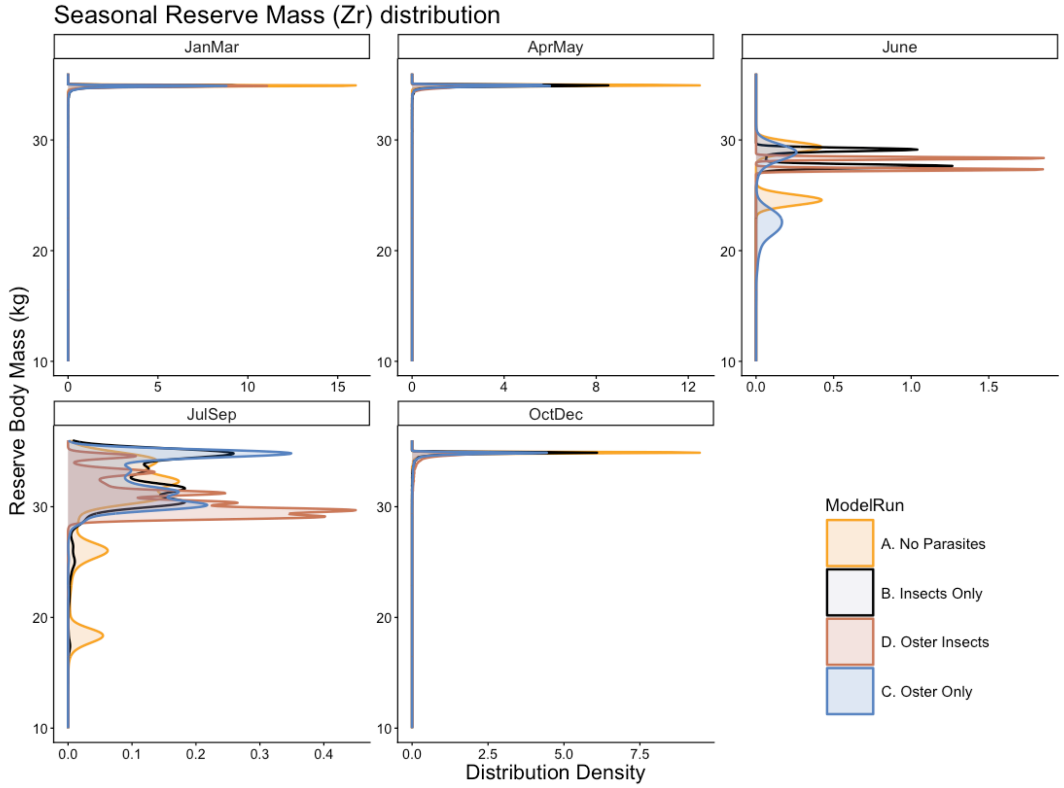

Figure 5: Seasonal distribution of reserve body mass (Z_R) in the four baseline scenarios. In all cases, variation in reserve mass is most present in the spring and summer when reproduction, lactation, and insect harassment incur significant energetic costs. The costs of insects and lactation on reserve mass is visible in summer (Jul-Sep, bottom left) in the Oster Insects scenario when reserve mass for a large proportion of the population is at or below 30 kg.

In the absence of stressors (i.e., insects and parasites), the simulated caribou population size was limited only by available forage and quickly rose to a carrying capacity. And as expected, sensitivity analyses showed that changes in forage quality resulted in proportional changes in caribou population size (Appendix B, Figures 7, 8). The addition of energetic stressors in the form of a gastrointestinal nematode, insect harassment, and warble flies, had substantial, though varied, effects on caribou energetics and caribou populations. The gastrointestinal nematode *O. gruehneri* caused a chronic low intensity reduction in forage intake that lowered caribou population size and limited reduction of available forage. The effects of insect harassment and warble fly parasitism were more dynamic, resulting in seasonal reduction in forage intake combined with increased energy expenditure that caused significant cycling in the simulated caribou population (Figure 3). The effects of abomasal nematodes, *Oestrid* larval growth, and insect harassment have been well studied in *Rangifer*, with each stressor shown to have a demonstrated ability to regulate caribou demography and population dynamics and reduce abundance on its own (Supplement A.1 and A.4). However, wild caribou populations are unlikely to be exposed to these stressors in isolation. Hence, exploring the joint influence of these multiple stressors is critical for understanding and predicting caribou population trajectories.

The mechanism by which warble flies, biting insects, and nematodes impact caribou differ. In addition to the brief and variable insect harassment season, growth and development of warble fly larvae incur energetic costs over winter as the larvae develop, but the larval burden in a given year is dependent on insect activity the prior summer. In our model, inter-annual variability and seasonality of insect harassment and warble larvae burden led to cyclic population dynamics caused by the significant energetic costs associated with insects. The extreme nutritional costs due to energy increased expenditure and decreased foraging associated insect harassment resulted in significant population cycling with peaks of approximately 220,000 caribou and troughs of less than 70,000 (Figure 3). The population cycling caused by insects reflects the significant effect harassment can have on the growth rate of caribou populations and the nutritional resources in the form of forage required to overcome the losses sustained. When populations are near the cycle's peak, reduced forage quantity reduces the ability of simulated caribou to recoup the nutritional losses of insects. At lower population size, however, the short but intense insect season can be mitigated through increased foraging when resources are abundant. Nevertheless, individuals that start the year in poorer body condition are less likely to overcome the effects of insects, leading to the increased variability in demographic rates when insects are present.

The energetic impacts the gastrointestinal nematodes *Ostertagia gruehneri* was modeled as a reduction in foraging activity as a function of parasite intensity (Arneberg et al. 1996, Shanebeck et al. 2022). Despite some seasonality in adult worm burden caused by development of arrested L4 larva during spring (Hoar et al. 2012b, Peacock et al. 2022), *O. gruehneri* infection can reduce foraging intake year round (Arneberg et al. 1996). Model output from the *Ostertagia* Only scenario reflected this sustained energetic drain in the reduced population level carrying capacity relative to the No Parasites scenario but without the population cycles seen in the Insects Only or Oster Insects scenarios. This population level impact of nematodes was caused less by an increase in mortality associated with parasite induced starvation, but rather by lower recruitment in females without sufficient reserve mass during breeding (Figure 5). In the full *Ostertagia* and Insects scenario, the total population size was reduced relative to all three other scenarios with significant population cycling, however, the amplitude of these cycles was less extreme than the Insects Only scenario (Figure 3). Overall, the results from these four modeling scenario clearly demonstrate that insect harassment and endoparasitism can be a significant driver of caribou demographic rates and thereby regulate populations, a process that is mediated by reduction in energetic reserves that are critical for survival and reproduction in caribou (Allaye Chan-McLeod et al. 1999, Barboza and Parker 2008, Denryter et al. 2020).

Changing Climate and Caribou Energetics

The rapidly changing Arctic climate is altering environmental conditions with significant implications for the caribou-parasite-energetics system. As small flying ectotherms, biting insects and *Oestrid* flies are highly sensitive to weather conditions, particularly temperature and wind speed (Witter et al. 2012b, Russell et al. 2013, Koltz and Culler 2021), which has historically limited their activity to a relatively short, though intense, insect season in early summer. As temperatures warm the insect harassment season is anticipated to lengthen and become more severe, while higher temperatures will likely facilitate faster development time of aquatic (*Cuculidae* and *Simuliidae*) and terrestrial (*Oestridae*) larvae leading to greater density and intensity of active insects (Koltz and Culler 2021). Using our model, we varied the intensity with which insect harassment reduced forage intake and increased energy expenditure. As little as a 5 percent increase in the severity of insect harassment (i.e., reduction in foraging and increase in energy expenditure) was sufficient to reduce simulated caribou population size by half (Figure 7).

Warming temperatures are also expected to influence mortality rates and development times of parasite eggs and free-living larval stages for species with complex life cycles like *O. gruehneri* (Molnár et al. 2013, Dobson et al. 2015). In addition to lower mortality rates and shorter development times, warming climate is also expected to change the behavior of *O. gruehneri* development. After being ingested by a caribou host, infectious L3 larvae may begin direct development into adult worms or they may enter a stage of arrested development where they remain in the lining of the mucosa until the following spring when development to adult worms begins (Hoar et al. 2012b, Peacock et al. 2022). Under current climatic conditions almost all ingested larvae arrest for a period of several months over winter to reduce unnecessary reproduction when eggs would not survive in sub-zero conditions (Hoar et al. 2012a). This effectively slows the rate of infection and parasite reproduction (i.e., R_0), however, as climate warms a higher percentage of ingested larvae may undergo direct development in a single summer leading to a faster completion of the parasite life cycle and amplification of parasite infection (Hoar et al. 2012b, Dobson et al. 2015). Conversely, some experimental warming studies suggest that the optimum temperatures for *O. gruehneri* development will likely be exceeded in warmer conditions, thereby decreasing development rates (Hoar et al. 2012b).

Perhaps the most significant effects of warming climate on northern herbivores such as caribou will be changes in timing of green-up, peak forage quality, insect harassment, and parasite eruption. Caribou migration and parturition is timed to allow females to exploit high quality new plant growth that is rich in dietary protein prior to significant insect harassment begins. However, earlier plant growth in the spring is resulting in a "trophic mismatch" and reduced reproductive success (Post and Forchhammer 2008, Gustine et al. 2017). With warming temperatures simultaneously shifting plant phenology earlier in the spring and increasing the rate at which forage quality is lost (Zamin et al. 2017, Richert et al. 2021, Leffler et al. 2022), increasing the duration and intensity of insect harassment (Witter et al. 2012b, Koltz and Culler 2021, Benedict and Barboza 2022), and increasing development rates of internal macroparasites (Hoar et al. 2012b, Molnár et al. 2013, Peacock et al. 2022) populations of caribou, and other northern herbivores, will be under extreme energetic stress with serious population level implications. Mechanistic bioenergetic population models such as that developed here are an ideal tool to explore and understand how resource availability, behavior, and pathogens will impact energy balance and demography in a changing climate.

Role of Parasites in Ecosystems

Our model demonstrates that insects and internal macro parasites can have significant effects on the trophic dynamics and food webs at an ecosystem scale. In the absence of parasites, herbivore populations suppressed forage biomass resulting in density dependent population regulation (Figure 4). In the presence of parasites, however, per capita forage intake as well as total herbivore numbers were reduced due to insect harassment and parasite infection which led to greater forage biomass available on the landscape.

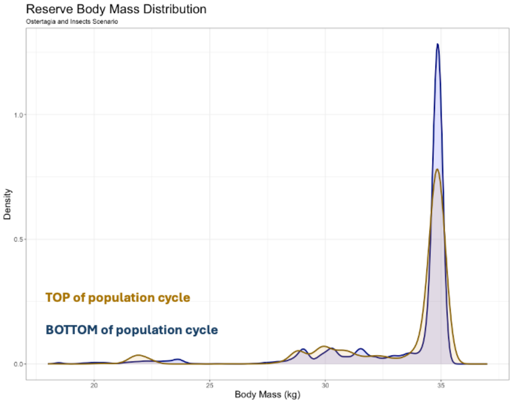

Figure 6: *Reserve body mass (Z_R) at the in the 2,000 15-day iterations centered on the peak of the population cycle (yellow) vs the same time period at the bottom of the population cycle (blue). The range of reserve mass in the period preceding population decline (cycle peak) is lower with a substantially smaller proportion of the population with high reserve mass over 30 kg.*

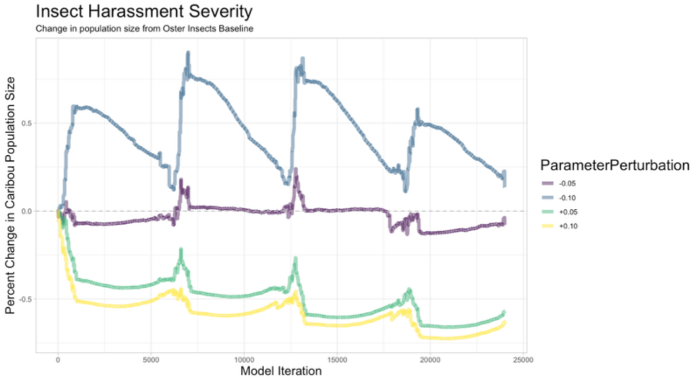

Figure 7: *Percent change from baseline (Oster-Insects Scenario) for four different levels of insect harassment severity. Small changes in the overall severity of insect harassment can have significant implications for caribou populations. As small as a 5% increase in the reduction in foraging time and excess energy expenditure caused by insect harassment can reduce caribou populations by nearly 50%.*

It is well known that predators can influence trophic dynamics in terrestrial and marine ecosystems through lethal (Pace et al. 1999) or sub-lethal (Fortin et al. 2005) effects. However, pathogens have also been shown to influence food webs. For example, eradication of the highly contagious and lethal rinderpest virus in wildebeest (*Connochaetes taurinus*) in the Greater Serengeti ecosystem caused a rapid increase in herbivore populations and subsequent decrease in forage biomass and fire frequency (Holdo et al. 2009). In contrast to microparasites such as rinderpest, evidence for the role of macroparasites in influencing trophic dynamics are comparatively rare in the literature (Buck and Ripple 2017). Recent theoretical work has shown the potential for gastrointestinal nematodes to exert top-down control on herbivore-forage dynamics (Koltz et al. 2022). Using a dynamic mathematical model to simulate a caribou-forage-nematode system, Koltz et al. (2022) showed that non-lethal infection of macroparasites could initiate trophic cascades. Our work confirms and extends the findings of Koltz et al. by showing that sub-clinical infection of abomasal nematodes, non-lethal insect harassment and warble fly parasitism can have meaningful effects on forage biomass by reducing population size and forage intake of herbivores. Importantly, our results reveal that the combined impacts of biting insects, parasitic insects and abomasal nematodes on caribou physiology resulted in a greater reduction in forage biomass than did any individual stressor in isolation.

In addition to the effects on forage biomass, our model showed that parasite presence can lead to cyclic dynamics in host populations. Demographic cycles in northern species, caribou included, are well recognized. However the drivers of these cycles are still disputed (Gunn 2003, Clark-Wolf et al. 2025), but parasites have been shown to cause population cycles in some species. Experimental removal of the parasitic nematode *Trichostrongylus tenuis* from a red grouse (*Lagopus lagopus scoticus*) population in Scotland, for example, prevented population cycles in the host population (Hudson et al. 1992, 1998). A mathematical evaluation of the host-parasite system suggested that parasite-induced population cycles were likely when parasite induced reductions in host recruitment where greater than increases in host mortality (Dobson and Hudson 1992). In contrast to the model of Dobson and Hudson (1992), our model had no direct per-parasite effect on host mortality or recruitment, rather, changes in vital rates were caused by changes in body condition and energy budgets. The substantial energetic costs of insect harassment affect both survival and recruitment in caribou, however, the effects on reproduction are stronger (Johnson et al. 2022). The inability to gain sufficient body fat during summer insect season due to harassment and warble fly parasitism will reduce the likelihood that a female will breed that fall, or that it will successfully produce and rear a calf the following spring (Cuyler et al. 2012, Witter et al. 2012a). While insect harassment and parasitism are unlikely to cause population cycles observed in caribou, when coupled with additional energetic stressors and other direct sources of mortality such as predation, it is likely that parasitism plays a role in the caribou population cycle. Most critically, our model captured differences in caribou body condition between cycle peaks and troughs through reserve mass (Z_R). When the caribou population is at its peak preceding a significant decline, the distribution of reserve mass in the population is lower than when the population size is lowest prior to increase (Figure 6). This underscores the importance of monitoring body condition, particularly in populations prone to cycling or eruptive dynamics. Populations showing a sustained reduction in body condition should be monitored closely for signals of decline, such as depressed recruitment, lower survival, or an increase in age at first reproduction. In these populations, managers can work to lessen the significance of declines by reducing energetic impacts of external stressors such as roads, industry, or hunting and recreation (Johnson et al. 2005)

Model Assumptions and Limitations

It is important to remember that all models are imperfect. Here, we attempted to balance increasing model complexity while maintaining model adaptability (i.e., generalizability to other systems) and interpretability. As a result, our model makes several simplifying assumptions and does not fully capture the true complexity of the caribou-forage-parasite system. First, our model was non-spatial, which essentially assumes that caribou, parasites, and forage are uniformly distributed across the landscape. In reality, barren-ground caribou undergo extended seasonal migrations between wintering range and calving grounds, and large post-calving / summer foraging grounds where groups of animals move frequently in search of high-quality forage and relief from biting insects (Rickbeil et al. 2015, 2018, Johnson et al. 2021, Boulanger et al. 2021). Migrations between and within seasonal ranges has significant implications for both host-parasite and herbivore-forage dynamics which are not fully captured with our model (Rickbeil et al. 2015, Teitelbaum et al. 2018, Peacock et al. 2022). Capturing the fine scale dynamism of forage quantity/quality, insect harassment, areas of insect relief, and external nematode transmission would have required significant assumptions in to parameterize the model due to lack of sufficient data. Our model does account for the broad spatial and temporal patterns of caribou-parasite overlap and changes in forage quality. However, further exploration of these effects in the model is warranted, as changing climate is expected to alter the spatial and temporal patterns of forage quality and quantity (Dearborn and Danby 2021, Leffler et al. 2022), life history of *O. gruehneri* (Molnár et al. 2013)*,* insect activity (Witter et al. 2012b, Koltz and Culler 2021), and caribou movements (Theoret et al. 2022).

Caribou diets can be quite variable, and individuals are known to seek out specific forage items according to state-dependent nutritional needs, forage conditions, and environmental factors (e.g., insects; Denryter et al. 2020, Ehlers et al. 2021, Johnson et al. 2022). Our model made two relevant simplifications in this regard: first, we did not track biomass and energy content for different forage types (e.g., shrubs, lichen, sedges, etc.), and second, we did not distinguish between dietary energy and dietary protein or digestibility of plant matter. Caribou forage quality depends not only on the energy content, but also digestibility (determined by fiber content, cell wall thickness, and secondary compounds), and, critically, dietary protein (White et al. 2014, Leffler et al. 2022). Winter diets, composed primarily of lichen (*Cladonia spp.*) are high in dietary energy, but almost devoid of dietary protein, which is critical for successful growth and reproduction (Barboza and Parker 2008, Barboza et al. 2020). In summer, however, diets switch to focus on new growth of shrubs including dwarf birch (*Betula nana*) and willows (*Salix spp.*) which are rich in energy and protein needed to restore depleted fat reserves (White et al. 2014), but decline in quality throughout the growing season (Zamin et al. 2017, Richert et al. 2021, Leffler et al. 2022). The complex interplay of forage digestibility, energy, protein content, and environmental conditions are known to affect caribou physiology and vital rates (White et al. 2014, Johnson et al. 2021). Future extensions of this modeling framework should work to explicitly model the variability of these aspects of forage quality.

For generations, Indigenous cultures have understood that caribou experience significant cycles in population size (Beaulieu 2012, Dokis-Jansen et al. 2021). More recently, western science suggests that cycles may be driven by climate induced changes in forage driven by the North Atlantic Oscillation and Pacific Decadal Oscillation (Gunn 2003, Joly et al. 2011, Mallory and Boyce 2018), however the specific factors at play are still unclear. Forage quality and availability in our model was a stochastic process driven by annually variable snowfall and caribou foraging rate, as such, we did not incorporate a mechanism for decadal variation in large scale climatic patterns to influence vegetation. Because the multi-decade period of caribou cycles would make experimental manipulation difficult, our model is an ideal framework to evaluate how various factors including parasites, climate, and predation impact the period and amplitude of caribou population cycles.

Finally, our model did not consider how inter-specific interactions such as predation and iter-specific competition for forage would impact demography of parasite dynamics of caribou. Studies examining the potential for competition between muskoxen and caribou have generally found little evidence of competition, citing niche separation and spatio-temporal habitat partitioning (Brodeur et al. 2023, Post et al. 2023). However, it is possible that growing populations of muskoxen along the boreal-tundra ecotone is resulting in changes in how and when caribou use the landscape. Indeed, competition from expanding muskox populations has been reported as a cause for caribou declines by Indigenous communities across the arctic, including by Tłı̨chǫ Elders (Appendix B). In addition to competing for resources, sympatric muskox populations could alter the caribou-parasite dynamics both positively and negatively. Muskox and caribou share a number of parasite species, including *O. gruehneri* (Kutz et al. 2012). By acting as an additional host species, muskox could reduce parasite burdens in caribou in a phenomena known as the dilution effect (Ostfeld and Keesing 2000, Keesing et al. 2006). Alternatively, they could amplify the abundance of infective larvae in the grazing areas. The long seasonal migrations undertaken by caribou allow for some seasonal reprieve from parasite infection through migratory escape (Hoar et al. 2012b, Kutz et al. 2014). Increasing populations of muskoxen and other expanding ungulates such as moose may act as reservoir hosts that maintain high levels of parasites in the environment year round, disrupting the partial escape currently experienced by caribou (McCallum and Dobson 1995). Each of these warrants further research, and our forage-host-parasite modeling framework could be extended to include additional herbivore species and test the effects of multiple herbivores on forage and parasite dynamics.

Conclusions

Our bio-energetic IPM illustrates several important messages with implications for future research, monitoring, and management of herbivores in seasonal environments. First, our models showed that the cumulative energetic costs of insect harassment, warble flies, and abomasal nematodes are significant enough to alter caribou reproduction, survival, and population dynamics. These findings underscore the importance of understanding host-parasite dynamics and how these systems may change as climate warms. Furthermore, our model represents a robust framework for mechanistically evaluating the impacts of parasitism and environmental stressors through the lens of energetic physiology. Teasing out mechanistic pathways in wild populations is often impossible because of the difficulty in experimentally manipulating wild systems. Ecological bio-energetic models such as ours are ideal tools for identifying ecological mechanisms which can then be tested through targeted observational or experimental field studies. Second, our results suggest that parasites and insects are important members of Arctic food webs by altering foraging behavior of herbivores. Finally, these findings underscore the importance of individual-level health metrics such as body condition and parasite burden in determining how populations respond to future environmental stressors. Accordingly, monitoring efforts should attempt to collect individual health data whenever possible through non-invasive observations, scientific captures, hunter-based sampling, and Indigenous Knowledge. These data could then be used to inform model parameterization by providing information on the distribution of body mass or parasite burden in the population, which could be used to forecast future populations under varying climate conditions to facilitate proactive management and conservation. For example, hunter-based sampling efforts can be used at large (e.g., state or provincial) and small (e.g., community based) scales to collect health metrics from harvested ungulates, such as estimated kidney or back fat. Over time, changes in the distribution of these metrics can serve as early warning signals that the population may be at risk of decline. Similarly, tracking the intensity and frequency of sublethal stressors, such as insect harassment or extreme heat, can further improve anticipation of changes in demographics of at-risk populations. Lastly, this model can be used as a framework to evaluate mechanistic drivers of population dynamics through an energetic lens, with wide applicability to improve conservation and management efforts in various ecosystems.

References

Adamczewski, J., J. Boulanger, J. Williams, D. Cluff, K. Clark, J. Nishi, S. Goodman, K. Chan, and R. Abernethy. 2022. ESTIMATES OF BREEDING FEMALES & ADULT HERD SIZE AND ANALYSES OF DEMOGRAPHICS FOR THE BATHURST HERD OF BARREN-GROUND CARIBOU: 2021 CALVING GROUND PHOTOGRAPHIC SURVEY. Population Survey, Government of Northwest Territories.

Adamczewski, J., A. Gunn, K. G. Poole, A. Hall, J. Nishi, and J. Boulanger. 2015. What Happened to the Beverly Caribou Herd after 1994? Arctic 68:407–421.

Adamczewski, J. Z., R. J. Hudson, and C. C. Gates. 1993. Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. Canadian Journal of Zoology 71:1221–1229.

Albon, S. D., A. Stien, R. J. Irvine, R. Langvatn, E. Ropstad, and O. Halvorsen. 2002. The role of parasites in the dynamics of a reindeer population. Proceedings of the Royal Society B: Biological Sciences 269:1625–1632.

Aleuy, O. A., M. Anholt, K. Orsel, F. Mavrot, C. A. Gagnon, K. Beckmen, S. D. Côté, C. Cuyler, A. Dobson, B. Elkin, L. Leclerc, J. Taillon, and S. Kutz. 2022. Association of Environmental Factors with Seasonal Intensity of Erysipelothrix rhusiopathiae Seropositivity among Arctic Caribou. Emerging Infectious Diseases 28.

Allaye Chan-McLeod, A. C., R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and nonbreeding female caribou. Canadian Journal of Zoology 77:1901–1907.

Anderson, R. M., and R. M. May. 1978. Regulation and Stability of Host-Parasite Population Interactions. Journal of Animal Ecology 47:249–267.

Arneberg, P., I. Folstad, and A. J. Karter. 1996. Gastrointestinal nematodes depress food intake in naturally infected reindeer. Parasitology 112:213–219.

Barboza, P. S., and K. L. Parker. 2008. Allocating protein to reproduction in arctic reindeer and caribou. Physiological and Biochemical Zoology 81:835–855.

Barboza, P. S., R. D. Shively, D. D. Gustine, and J. A. Addison. 2020. Winter Is Coming: Conserving Body Protein in Female Reindeer, Caribou, and Muskoxen. Frontiers in Ecology and Evolution 8.

Barone, C. D., J. Wit, E. P. Hoberg, J. S. Gilleard, and D. S. Zarlenga. 2020. Wild ruminants as reservoirs of domestic livestock gastrointestinal nematodes. Veterinary Parasitology 279:109041.

Beaulieu, D. 2012. Dene traditional knowledge about caribou cycles in the Northwest Territories. Rangifer 32:59.

Benedict, B. M., and P. S. Barboza. 2022. Adverse effects of Diptera flies on northern ungulates: *Rangifer* , *Alces* , and *Bison*. Mammal Review.

Bergerud, A. T., S. N. Luttich, and L. Camps. 2008. Return of Caribou to Ungava. McGill-Queens University Press.

Boertje, R. D. 1985. An Energy Model for Adult Female Caribou of the Denali Herd, Alaska. Journal of Range Management 38:468.

Boulanger, J., A. Gunn, J. Adamczewski, and B. Croft. 2011. A data-driven demographic model to explore the decline of the Bathurst caribou herd. The Journal of Wildlife Management 75:883–896.

Boulanger, J., K. G. Poole, A. Gunn, J. Adamczewski, and J. Wierzchowski. 2021. Estimation of trends in zone of influence of mine sites on barren-ground caribou populations in the Northwest Territories, Canada, using new methods. Wildlife Biology 2021.

Brodeur, A., M. Leblond, V. Brodeur, J. Taillon, and S. D. Côté. 2023. Investigating potential for competition between migratory caribou and introduced muskoxen. The Journal of Wildlife Management 87:e22366.

Buck, J. C., and W. J. Ripple. 2017. Infectious Agents Trigger Trophic Cascades. Trends in Ecology & Evolution 32:681–694.

Clark-Wolf, T. J., J. St. John, C. A. Rajesh, and M. Hebblewhite. 2025. Caribou and Reindeer Population Cycles Are Driven by Top-Down and Bottom-Up Mechanisms Across Space and Time. Ecology and Evolution 15:e71348.

Cook, J. G., A. P. Kelly, R. C. Cook, B. Culling, D. Culling, A. Mclaren, N. C. Larter, and M. Watters. 2021. Seasonal patterns in nutritional condition of caribou (Rangifer tarandus) in the southern Northwest Territories and northeastern British Columbia, Canada. Canadian Journal of Zoology 858:845–858.

Cuyler, C., R. R. White, K. Lewis, C. Soulliere, A. Gunn, D. E. Russell, and C. Daniel. 2012. Are warbles and bots related to reproductive status in West Greenland caribou? Rangifer:243–257.

Dearborn, K. D., and R. K. Danby. 2021. Remotely sensed trends in vegetation productivity and phenology during population decline of the Bathurst caribou (Rangifer tarandus groenlandicus) herd. Arctic Science 24:1–24.

Denryter, K., R. C. Cook, J. G. Cook, K. L. Parker, and M. P. Gillingham. 2020. State-dependent foraging by caribou with different nutritional requirements. Journal of Mammalogy 101:544–557.

Desforges, J., G. M. Marques, L. T. Beumer, M. Chimienti, L. H. Hansen, S. H. Pedersen, N. M. Schmidt, and F. M. Beest. 2021. Environment and physiology shape Arctic ungulate population dynamics. Global Change Biology 27:1755–1771.

Dickinson, E. R., K. Orsel, C. Cuyler, and S. J. Kutz. 2023. Life history matters: Differential effects of abomasal parasites on caribou fitness. International Journal for Parasitology.

Dobson, A. P., and P. J. Hudson. 1992. Regulation and Stability of a Free-Living Host-Parasite System: Trichostrongylus tenuis in Red Grouse. II. Population Models. The Journal of Animal Ecology 61:487.

Dobson, A. P., P. K. Molnár, and S. J. Kutz. 2015. Climate change and Arctic parasites. Trends in Parasitology 31:181–188.

Dokis-Jansen, K. L., B. L. Parlee, Ł. K. D. F. Nation, D. S. Hik, B. G. Berthiaume, E. Macdonald, and C. Stinn. 2021. “These trees have stories to tell”: Linking dënesǫ́łıné oral history of caribou use with trample scar frequency on black spruce roots at ʔedacho kué. Arctic 74:290–305.

Ehlers, L., G. Coulombe, J. Herriges, T. Bentzen, M. Suitor, K. Joly, and M. Hebblewhite. 2021. Critical summer foraging tradeoffs in a subarctic ungulate. Ecology and Evolution 00:1–38.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Global Modeling And Assimilation Office. 2015. MERRA-2 tavg1_2d_slv_Nx: 2d,1-Hourly,Time-Averaged,Single-Level,Assimilation,Single-Level Diagnostics V5.12.4. [object Object].

Godkin, G. F. 1986. Fertility and twinning in Canadian reindeer. Rangifer:145–150.

Gunn, A. 2003. Voles, lemmings and caribou - population cycles revisited? Rangifer 23:105.

Gunn, A., and R. J. Irvine. 2003. Subclinical parasitism and ruminant foraging strategies-a review. Wildlife Society Bulletin 31:117–126.

Gustine, D., P. Barboza, L. Adams, B. Griffith, R. Cameron, and K. Whitten. 2017. Advancing the match-mismatch framework for large herbivores in the Arctic: Evaluating the evidence for a trophic mismatch in caribou. PLOS ONE 12:e0171807.

Hanke, A. N., M. Angohiatok, L.-M. Leclerc, C. Adams, and S. Kutz. 2022. A Caribou Decline Foreshadowed by Inuit in the Central Canadian Arctic: A Retrospective Analysis. Arctic 74:437–455.

Hansen, B. B., V. Grøtan, I. Herfindal, and A. M. Lee. 2020. The Moran effect revisited: spatial population synchrony under global warming. Ecography 43:1591–1602.

Hoar, B. M., A. G. Eberhardt, and S. J. Kutz. 2012a. Obligate larval inhibition of *Ostertagia gruehneri* in *Rangifer tarandus* ? Causes and consequences in an Arctic system. Parasitology 139:1339–1345.

Hoar, B. M., K. Ruckstuhl, and S. Kutz. 2012b. Development and availability of the free-living stages of Ostertagia gruehneri , an abomasal parasite of barrenground caribou (Rangifer tarandus groenlandicus), on the Canadian tundra. Parasitology 139:1093–1100.

Holdo, R. M., A. R. E. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A Disease-Mediated Trophic Cascade in the Serengeti and its Implications for Ecosystem C. PLoS Biology 7:e1000210.

Hone, J., R. P. Duncan, and D. M. Forsyth. 2010. Estimates of maximum annual population growth rates (rm) of mammals and their application in wildlife management: Estimating maximum population growth rate. Journal of Applied Ecology 47:507–514.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of Population Cycles by Parasite Removal. Science 282:2256–2258.

Hudson, P. J., D. Newborn, and A. P. Dobson. 1992. Regulation and Stability of a Free-Living Host-Parasite System: Trichostrongylus tenuis in Red Grouse. I. Monitoring and Parasite Reduction Experiments. Journal of Animal Ecology 61:477–486.

Hughes, J., S. D. Albon, R. J. Irvine, and S. Woodin. 2008. Is there a cost of parasites to caribou? Parasitology 136:253–265.

Irvine, R. J. 2006. Parasites and the dynamics of wild mammal populations. Animal Science 82:775–781.

Jacobsen, P. 2022. Ekwǫ̀ Nàxoèhdee K’è: 2021 Results. Pages 1–45. Dedats’eetsaa: Tłı̨cho Research and Training Institute.

Jacobsen, P., R. Wetrade, G. Chocolate, M. Birlea, and Dedats’eetsaa. 2016. Ekwò zò gha dzô nats’êdè “We Live Here For Caribou”: Cumulative Impacts Study on the Bathurst Caribou. Pages 1–54. Dedats’eetsaa: Tłı̨cho Research and Training Institute.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative Effects of Human Developments on Arctic Wildlife. Wildlife Monographs 160:1–36.

Johnson, H. E., T. S. Golden, L. G. Adams, D. D. Gustine, E. A. Lenart, and P. S. Barboza. 2021. Dynamic selection for forage quality and quantity in response to phenology and insects in an Arctic ungulate. Ecology and Evolution 11:11664–11688.

Johnson, H. E., D. D. Gustine, T. S. Golden, L. G. Adams, L. S. Parrett, E. A. Lenart, and P. S. Barboza. 2018. NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity. Ecosphere 9:e02461.

Johnson, H. E., E. A. Lenart, D. D. Gustine, L. G. Adams, and P. S. Barboza. 2022. Survival and reproduction in Arctic caribou are associated with summer forage and insect harassment. Frontiers in Ecology and Evolution 10.

Johnston, A. S. A., R. J. Boyd, J. W. Watson, A. Paul, L. C. Evans, E. L. Gardner, and V. L. Boult. 2019. Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach. Proceedings of the Royal Society B: Biological Sciences 286:20191916.

Joly, K., M. J. Cole, and R. R. Jandt. 2007. Diets of Overwintering Caribou, Rangifer tarandus, Track Decadal Changes in Arctic Tundra Vegetation. The Canadian Field-Naturalist 121:379–383.

Joly, K., E. Gurarie, M. S. Sorum, P. Kaczensky, M. D. Cameron, A. F. Jakes, B. L. Borg, D. Nandintsetseg, J. G. C. Hopcraft, B. Buuveibaatar, P. F. Jones, T. Mueller, C. Walzer, K. A. Olson, J. C. Payne, A. Yadamsuren, and M. Hebblewhite. 2019. Longest terrestrial migrations and movements around the world. Scientific Reports 9:15333.

Joly, K., D. R. Klein, D. L. Verbyla, T. S. Rupp, and F. S. Chapin. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34:345–352.

Keesing, F., R. D. Holt, and R. S. Ostfeld. 2006. Effects of species diversity on disease risk. Ecology Letters 9:485–498.

Koltz, A. M., D. J. Civitello, D. J. Becker, S. L. Deem, A. T. Classen, B. Barton, M. Brenn-White, Z. E. Johnson, S. Kutz, M. Malishev, D. L. Preston, J. T. Vannatta, R. M. Penczykowski, and V. O. Ezenwa. 2022. Sublethal effects of parasitism on ruminants can have cascading consequences for ecosystems. Proceedings of the National Academy of Sciences 119:1–10.

Koltz, A. M., and L. E. Culler. 2021. Biting insects in a rapidly changing Arctic. Current Opinion in Insect Science 47:75–81.

Kutz, S. J., J. Ducrocq, G. G. Verocai, B. M. Hoar, D. D. Colwell, K. B. Beckmen, L. Polley, B. T. Elkin, and E. P. Hoberg. 2012. Parasites in Ungulates of Arctic North America and Greenland. Pages 99–252 Advances in Parasitology. Elsevier.

Kutz, S. J., E. P. Hoberg, P. K. Molnár, A. Dobson, and G. G. Verocai. 2014. A walk on the tundra: Host–parasite interactions in an extreme environment. International Journal for Parasitology: Parasites and Wildlife 3:198–208.

Lachish, S., E. E. Brandell, M. E. Craft, A. P. Dobson, P. J. Hudson, D. R. MacNulty, and T. Coulson. 2020. Investigating the Dynamics of Elk Population Size and Body Mass in a Seasonal Environment Using a Mechanistic Integral Projection Model. The American Naturalist 196:E23–E45.

Laforge, M. P., M. Bonar, and E. Vander Wal. 2021. Tracking snowmelt to jump the green wave: phenological drivers of migration in a northern ungulate. Ecology 102:1–11.

Leffler, A. J., H. A. Becker, K. C. Kelsey, D. A. Spalinger, and J. M. Welker. 2022. Short-term effects of summer warming on caribou forage quality are mitigated by long-term warming. Ecosphere 13:e4104.

Mallory, C. D., and M. S. Boyce. 2018. Observed and predicted effects of climate change on Arctic caribou and reindeer. Environmental Reviews 26:13–25.

McCallum, H., and A. P. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. Trends in Ecology & Evolution 10:190–194.

Molnár, P. K., A. P. Dobson, and S. J. Kutz. 2013. Gimme shelter - the relative sensitivity of parasitic nematodes with direct and indirect life cycles to climate change. Global Change Biology 19:3291–3305.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, Nutritional Deficiency, and Climate Influences on a Declining Moose Population. Wildlife Monographs 166:1–30.

Osada, Y., T. Kuriyama, M. Asada, H. Yokomizo, and T. Miyashita. 2015. Exploring the drivers of wildlife population dynamics from insufficient data by Bayesian model averaging. Population Ecology 57:485–493.

Ostfeld, R. S., and F. Keesing. 2000. Biodiversity series: The function of biodiversity in the ecology of vector-borne zoonotic diseases. Canadian Journal of Zoology 78:2061–2078.

Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. Foraging theory upscaled: The behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2267–2278.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23:57–69.

Parker, K. L., P. S. Barboza, and T. R. Stephenson. 2005. PROTEIN CONSERVATION IN FEMALE CARIBOU (RANGIFER TARANDUS): EFFECTS OF DECREASING DIET QUALITY DURING WINTER. Journal of Mammalogy 86:610–622.

Passoni, G., T. Coulson, F. Cagnacci, P. Hudson, D. R. Stahler, D. W. Smith, and S. Lachish. 2024. Investigating tritrophic interactions using bioenergetic demographic models. Ecology 105:e4197.

Peacock, S. J., S. J. Kutz, B. M. Hoar, and P. K. Molnár. 2022. Behaviour is more important than thermal performance for an Arctic host – parasite system under climate change. Royal Society Open Science 9:220060.

Plard, F., D. Turek, M. U. Grüebler, and M. Schaub. 2019. IPM2: toward better understanding and forecasting of population dynamics. Ecological Monographs 89:1–18.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2367–2373.

Post, E., E. Kaarlejärvi, M. Macias-Fauria, D. A. Watts, S. Bøving, S. Cahoon, R. C. Higgins, C. John, J. Kerby, C. Pedersen, M. Post, and P. F. Sullivan. 2023. Large herbivore diversity slows sea ice–associated decline in arctic tundra diversity. Science 380:1282–1287.

Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: a user's guide. Journal of Animal Ecology 83:528–545.

Richert, J. C., A. J. Leffler, D. E. Spalinger, and J. M. Welker. 2021. Snowier winters extend autumn availability of high-quality forage for caribou in Arctic Alaska. Ecosphere 12:e03617.

Rickbeil, G. J. M., N. C. Coops, and J. Adamczewski. 2015. The grazing impacts of four barren ground caribou herds (Rangifer tarandus groenlandicus) on their summer ranges: An application of archived remotely sensed vegetation productivity data. Remote Sensing of Environment 164:314–323.

Rickbeil, G. J. M., T. Hermosilla, N. C. Coops, J. C. White, M. A. Wulder, and T. C. Lantz. 2018. Changing northern vegetation conditions are influencing barren ground caribou (Rangifer tarandus groenlandicus) post-calving movement rates. Journal of Biogeography 45:702–712.

Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. Range Ecology of the Porcupine Caribou Herd in Canada. Rangifer 13:1.

Russell, D. E., R. G. White, and C. J. Daniel. 2005. Energetics of the Porcupine Caribou Herd: a computer simulation model. Technical Report 431:64.

Russell, D. E., P. H. Whitfield, J. Cai, A. Gunn, R. G. White, and K. Poole. 2013. CARMA's MERRA-based caribou range climate database. Rangifer 33:145.

Shanebeck, K. M., A. A. Besson, C. Lagrue, and S. J. Green. 2022. The energetic costs of sub-lethal helminth parasites in mammals: a meta-analysis. Biological Reviews 2.

Sibly, R. M., and J. Hone. 2002. Population growth rate and its determinants: an overview. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357:1153–1170.

Smallegange, I. M., H. Caswell, M. E. M. Toorians, and A. M. Roos. 2017. Mechanistic description of population dynamics using dynamic energy budget theory incorporated into integral projection models. Methods in Ecology and Evolution 8:146–154.

Stien, A., R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, and S. D. Albon. 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. Journal of Animal Ecology 71:937–945.

Team, R. C. 2019. R: A language and environment for statistical computing.

Teitelbaum, C. S., S. Huang, R. J. Hall, and S. Altizer. 2018. Migratory behaviour predicts greater parasite diversity in ungulates. Proceedings of the Royal Society B: Biological Sciences 285.

Theoret, J., M. Cavedon, T. Hegel, D. Hervieux, H. Schwantje, R. Steenweg, M. Watters, and M. Musiani. 2022. Seasonal movements in caribou ecotypes of Western Canada. Movement Ecology 10:1–14.

Thompson, D. P., and P. S. Barboza. 2014. Nutritional implications of increased shrub cover for caribou (Rangifer tarandus) in the Arctic. Canadian Journal of Zoology 92:339–351.

Tomaselli, M., S. C. Gerlach, S. J. Kutz, and S. L. Checkley. 2018. Iqaluktutiaq Voices : Local Perspectives about the Importance of Muskoxen, Contemporary and Traditional Use and Practices. Arctic 71:1–14.

Tyack, P. L., L. Thomas, D. P. Costa, A. J. Hall, C. M. Harris, J. Harwood, S. D. Kraus, P. J. O. Miller, M. Moore, T. Photopoulou, E. Pirotta, R. M. Rolland, L. H. Schwacke, S. E. Simmons, and B. L. Southall. 2022. Managing the effects of multiple stressors on wildlife populations in their ecosystems: developing a cumulative risk approach. Proceedings of the Royal Society B: Biological Sciences 289:20222058.

Tyler, N. J. C. 2010. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (Rangifer tarandus L.). Ecological Monographs 80:197–219.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626–2633.

Webber, Q. M. R., K. Ferraro, J. Hendrix, and E. Vander Wal. 2022. What do caribou eat? A review of the literature on caribou diet. Canadian Journal of Zoology 206:197–206.

White, R. G., C. J. Daniel, and D. E. Russell. 2013. CARMA's integrative modeling: historical background of modeling caribou and reindeer biology relevant to development of an energy/protein model. Rangifer 33:153.

White, R. G., D. E. Russell, and C. J. Daniel. 2014. Simulation of maintenance, growth and reproduction of caribou and reindeer as influenced by ecological aspects of nutrition, climate change and industrial development using an energy-protein model. Rangifer 34:1–126.

White, R. G., and J. Trudell. 1980. Habitat Preference and Forage Consumption by Reindeer and Caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511.

Whitten, K. R., G. W. Garner, F. J. Mauer, and R. B. Harris. 1992. Productivity and Early Calf Survival in the Porcupine Caribou Herd. The Journal of Wildlife Management 56:201–212.

Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and M. P. Gillingham. 2012a. Behavioural trade-offs in response to external stimuli: Time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. Journal of Animal Ecology 81:284–295.

Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and L. M. Poirier. 2012b. Gauging climate change effects at local scales: Weather-based indices to monitor insect harassment in caribou. Ecological Applications 22:1838–1851.

Zamin, T. J., S. D. Côté, J. P. Tremblay, and P. Grogan. 2017. Experimental warming alters migratory caribou forage quality: Ecological Applications 27:2061–2073.

Table 1: Model parameters, their interpretation, and baseline values.

Parameter	Name	Units	Description	Value	Source
State Variables					
Z		kg	Total body mass	0.2 - 135	
Z_R		kg	Reserve body mass	0.1 - 35	Lachish et al. 2020
Z_S		kg	Structural body mass	0.1 - 115	Lachish et al. 2020
V_{max}		kg	Maximum vegetation biomass	221197500	Johnson et al. 2018
V_{min}		kg	Minimum vegetation biomass	6635925	Johnson et al. 2018
Vegetation Parameters					
α_τ	veg growth rate		Vegetation growth rate during the 4-month growing season. Values α_t varied each time step during the growing season to reflect weather variation.	0.1 - 0.5	Lachish et al 2020
Θ	half saturation biomass	kg	The biomass of vegetation at which intake rate is half of the maximum. Low value relative vegetation biomass keeps forage intake at or near realized maximum rate	10,000	Owen-Smith 2002
η	steepness	kg^{-1}	Steepness parameter in satiation of intake rate.	15	De Roos et al. 2009 (this value was assumed in the study by De Roos for a large ungulate model)
VE_{SUMMER}	summer energy	MJ kg^{-1}	Energy content of caribou forage during summer months (mid-May through August). Here, 'energy is all encompassing, and includes both dietary energy and dietary protein.	12	Russell et al. 1993, Leffler et al. 2022, White et al. 2014

VE_{WINTER}	winter energy	MJ kg^{-1}	Energy content of caribou forage during non-summer months. Here, ‘energy is all encompassing, and ’ includes both dietary energy and dietary protein.	9.5	Russell et al. 1993, Leffler et al. 2022, White et al. 2014
ς	snow effect	%	Percent reduction in foraging efficiency caused by snow cover during the non-summer months.	$N(0.6,0.1)$	White et al. 2014
Caribou Demography					
τ_{Z_S}	Z_S breeding threshold	kg	Structural mass (Z_S) at which structural growth stops (i.e., adulthood), and minimum structural mass required for reproduction.	58	White et al. 2014, Bergerud et al. 2008
τ_B	Z_R breeding threshold	%	Minimum ratio of reserve to total body mass (Z_R/Z) required for reproduction	0.06	Barboza and Parker 2008; Parker et al. 2009
τ_S	starvation threshold	%	Ratio of reserve to total body mass (Z_R/Z) below which an individual dies of starvation	0.03	Cook et al. 2021
β_0	survival intercept		Intercept of logit function relating survival to total body mass.	0.92	Johnson et al 2020
β_1	survival slope		Slope of logit function relating survival to mass	0.02	
ω	neonate mortality		Constant mortality rate of newborn calves, incurred during breeding interval.	0.4	Boulanger et al. 2011; Adamczewski et al. 2021
Bioenergetic Parameters					
f	maximum foraging rate	kg kg$^{-3/4}$ timestep^{-1}	Scalar constant of foraging rate per 15-day interval	6.2	White and Trudell 1980 (observed values range 2.4-3.3 kg kg$^{-3/4}$ day^{-1})
δ_b	baseline metabolism	MJ kg$^{-3/4}$ day^{-1}	Baseline constant basal metabolic rate	0.293	White et al. 2014

$\delta_{S.s}$	summer metabolism	MJ kg$^{-3/4}$ day^{-1}	Summer addition to basal metabolic rate	0.300	White et al. 2014
$\delta_{S.w}$	winter metabolism	MJ kg$^{-3/4}$ day^{-1}	Winter addition to basal metabolic rate	0.150	White et al. 2014
$\boldsymbol{\kappa}$	active energy	MJ day^{-1}	Daily energetic costs of activity and movement	4.0 - 6.0	Adamczewski and Hudson 1993 (...)
m	anabolic / catabolic	MJ kg^{-1}	Coefficient for anabolic / catabolic conversion between assimilated energy and energy reserves	54 / 39.3	Illius and O'Connor 2000
φ_S	Z_R to Z_S	%	proportion of available reserve energy converted to structural mass	0.40	White et al. 2014
ε_r	energy conversion efficiency	%	Efficiency with which reserve mass is converted to structural mass, or, a mother's reserve mass is converted to offspring mass (reserve and structural)	0.95	Lachish et al. 2020
γ	Z_R for Reproduction	%	Proportion of reserve mass allocated for reproduction and provisioning (e.g., fetal growth and lactation) by breeders	0.6	Lachish et al. 2020
ρ	Z_R to offspring Z_S	%	Proportion of allocated reserve mass (γ) that is converted to offspring's structural mass	0.9	Lachish et al. 2020
Parasite Parameters					
α_{forage}	forage reduction		Per parasite reduction in foraging rate caused by *O. gruehneri*	0.00001	Koltz et al. 2022
K	aggregation		Parasite aggregation term	0.994	Estimated from 2009 data in Bathurst caribou
i_F	ins_harr_max	%	Maximum percent reduction in foraging activity caused by insect harassment	0.6	Ehlers et al. 2021