



OPEN

Direct and indirect costs of parasitism preceding a population decline of an Arctic ungulate

Eleanor R. Dickinson^{1✉}, Chinyere Nwafor-Okoli¹, Sylvia L. Checkley¹, Brett Elkin², Marsha Branigan³, Emmanuel Serrano⁴ & Susan J. Kutz¹

Parasites negatively affect the fitness of ungulate hosts directly, and in wild ungulates, these effects may be synzootic with other stressors, such as limited nutritional resources. In the Arctic, muskoxen (*Ovibos moschatus*) occur in a highly seasonal environment and must rely on finite energetic resources for survival and productivity. We investigated the costs of gastrointestinal nematodes on the body condition and reproductive status of 141 muskoxen, on Banks Island, Canada, when the population was at a peak in numbers and density. Using a Partial Least Squares Path Modelling approach, we found that high adult nematode abundance was associated with lower body condition, and high parasite abundance was associated with female reproduction including the indirect effect through on body condition ($n = 87$). These findings suggest that individuals prioritize energetic reserves for reproduction over parasite defence. In fall 2003, a severe icing event that restricted access to forage was associated with high overwinter mortality of muskoxen and a population crash. Through direct and indirect costs of parasite infection on body condition and reproduction, the high abundance of parasites may have contributed to the effects of this extreme weather event. Understanding the mechanisms in which parasites impact fitness can help explain the ecological drivers of ungulate populations and predict the interactions between the environment and populations.

Keywords Reproduction, Body condition, *Ovibos moschatus*, *Marshallagia marshalli*, *Teladorsagia boreoarcticus*, Abomasum, Gastrointestinal nematodes, Fitness

Parasites are important components of ecosystems that can have significant effects on the health of wildlife populations^{1–3}. While some parasites are virulent and have direct deleterious effects on body condition⁴, others have a low or more subtle impact^{5–7}. Gastrointestinal parasites can make individuals more vulnerable to nutritional or environmental stressors^{8,9}, while environmental variation and stressors can increase host susceptibility^{10,11}. At times of low food availability, more energy may be allocated to growth and survival than to reproduction due to the reproduction-survival trade-off⁹. Therefore, in systems where nutritional resources are finite, the impacts of parasites on reproduction and survival may be especially important.

Muskoxen (*Ovibos moschatus*) are culturally important to Indigenous peoples in the Arctic¹² and are a key component of the tundra ecosystem as one of the few large-bodied herbivores^{13,14}. As a non-migratory species, muskoxen experience pronounced seasonal and inter-annual variation in the availability and quality of forage^{15,16}. Population eruptions followed by dramatic declines have occurred in muskox populations in multiple locations across the Arctic^{17–21}, yet there remain significant knowledge gaps in our understanding of the drivers of muskox population change^{22–24}. Muskoxen rely heavily on fat reserves built up through the vegetation growth period as an energy reserve during the winter^{15,25} with limited forage being linked to reduced pregnancy rates and survival^{16,26}. Gastrointestinal nematodes (GINs), present in all wild ruminants, have an energetic cost for their hosts and may contribute to the energetic challenges muskoxen face⁷.

¹Faculty of Veterinary Medicine, University of Calgary, 3280 University Drive, NW, Calgary, AB T2N 1N4, Canada. ²Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NT X1A 1Y3, Canada. ³Environment and Natural Resources, Government of the Northwest Territories, Inuvik, NT X0E 0T0, Canada. ⁴Wildlife Ecology & Health Group (WE&H), Servei d'Ecopatologia de Fauna Salvatge (SEFaS), Departament de Medicina i Cirurgia Animals, Universitat Autònoma de Barcelona, Bellaterra, Spain. ✉email: eleanor.dickinson@ucalgary.ca

The Banks Island muskox population in the Inuvialuit Settlement Region (Northwest Territories), Canada, was the largest in the world in the 1990s, and constituted almost one third of the world's muskoxen population²⁷. This population increased from relatively few animals in the 1950s to 68,500 non-calf animals in the late 1990s and early 2000s^{17,28,29}. By the mid-1980s, 3-year-old cow productivity and calf survival, important indicators of demographics, had decreased^{17,29,30}. Although the population continued to grow until the late 1990s and early 2000s, it subsequently declined following a severe icing event in 2003–2004 and further decline was associated with disease epidemics in 2011–2012^{22,31,32}.

Our aim was to determine whether gastrointestinal parasite abundance was associated with body condition and reproduction in Banks Island muskoxen during the population peak and discuss the potential role of parasites in population dynamics. The objectives of this work were to; (1) describe the gastrointestinal parasite fauna of muskoxen on Banks Island, and (2) determine the association of gastrointestinal parasites on muskox body condition, reproduction and fetus characteristics. We hypothesized that high parasite abundance would be negatively associated with body condition. These costs would also negatively impact the likelihood of pregnancy in female muskoxen and the size of their fetuses. Finally, due to the high energy requirements of lactation and potential trade offs between nutrition and parasite defence, we hypothesized that lactating females would have a higher parasite abundance.

Materials and methods

Study site

We studied the muskox population on Banks Island, Northwest Territories, Canada, which is the fourth largest (70,000 km²) and most western island in the Canadian Arctic archipelago. The population peaked at 68,585 ± 6972 non-calf muskoxen and a density of 97.2 muskoxen per 100 km² in 2001 (a year after this study)²⁹. There is one community on this island, Ikaahuk (or Sachs Harbour), which had a population of 138 people in 1999. Residents of the community harvested muskoxen for subsistence, guided sport hunts and commercial harvests for export¹⁷. Commercial harvests, conducted by the Sachs Harbour Hunters and Trappers Committee and Inuvialuit Development Corporation, occurred annually on Banks Island between 1980 and 2013, and provided employment and income for the community²⁰. Biological samples were collected annually from these harvested animals by biologists in the Government of the Northwest Territories.

To assess parasite diversity and costs, additional samples were collected from 144 muskoxen (n = 89 females, 54 males) during November 1999. This is at a time that follows the principal period (August to October) of body condition gain for muskoxen and is at a time when females with sufficient energy reserves are expected to still be lactating^{33,34}. The abomasum, feces and the left kidney with surrounding fat were collected from each individual and frozen until analysis. As a measure of body condition, the left kidney and its fat were processed to calculate the Kidney Fat Index (KFI)^{35,36}. The sex of individuals was recorded, and age class (calf, yearling, 2-year-old, 3-year-old, and 4-year-old+) was determined by experienced biologists through tooth eruption and horn development as described by Henrichsen and Grue³⁷. Reproduction of females was derived by experienced biologists by visually assessing the uterus for a fetus and expressing the udder for milk. Lactation was defined as whether an animal was producing milk, regardless of quantity, i.e. lactating (no = 0, yes = 1). Reproductive status (i.e. pregnancy status) was defined as whether a fetus was present (no = 0, yes = 1). Fetal characteristics were measured using the length and weight of the fetus as a proxy for fetus size, and fetus sex was defined as whether the fetus was male or female.

Parasitological procedures

Initial analysis of abomasa and faeces was done in Inuvik at Government of the NWT's wildlife laboratory. The abomasal contents were emptied into a 4 L beaker and the mucosal surface was washed three times under slowly running water into the beaker, which was then brought to a total volume of 1.5 L. The solution was mixed well and two 10% (150 mL) subsamples were taken, which were then washed through a #400 sieve. The sieve contents were collected and 10% formalin was added to make 100 ml. Two 5% subsamples (5 ml each) were later extracted from one 100 ml solution per sample, and all larvae and adult parasites were quantified. The remaining 90 ml were examined to quantify adult parasites only. Washed abomasa were frozen at -20 °C until they could be digested. These were digested in 1.5 L of a pepsin and hydrochloric acid solution (0.8% pepsin, 2% HCl, 0.85% NaCl) maintained at 37 °C and agitated until all the tissue was digested³⁸. Two 10% aliquots of the digestion solution (100 ml) were taken and preserved in 10% formalin. Two 5% (5 ml) subsample were taken from each aliquot and examined to quantify larvae. Adult nematodes were identified to species level according to published descriptions of morphological characteristics, including reproductive structures, synlophe and esophageal valve and quantified^{39–44}. Identification of the larvae was not done to the developmental stage nor species taxonomic rank.

Fecal samples were frozen upon collection and eggs and oocysts of gastrointestinal parasites were quantified using a modified double centrifugation Wisconsin sugar flotation technique⁴⁵. Eggs and oocysts were identified to family or genus based on morphology and counted⁴⁶. Eggs that have typical strongyle-type morphology may belong to several different genera. However, they were assumed to primarily represent *Teladorsagia boreoarcticus*, the most common abomasal nematode in muskoxen⁴⁷. Forty-five fecal samples could not be examined in Inuvik and were transported to The University of Saskatchewan, Saskatoon for examination.

Parasite abundance was defined as the number of adult nematodes of each species present in the abomasum (*T. boreoarcticus* and *M. marshalli*), the number of larvae in the lumen and mucosa of the abomasum, and the number of parasite eggs or oocysts of each species counted in feces which included nematodes, protozoa and cestoda (*Strongyle* sp., *Nematodirus* spp., *M. marshalli* and *Eimeria* spp.).

Statistical analysis

All analyses were conducted using R software version 4.1.2⁴⁸. Seven animals were excluded from analysis due to missing information. Univariate comparisons were performed to determine sex, age and reproductive effects on body condition and parasite abundance. Unpaired Student's t-tests were used for the normally distributed variable body condition, KFI, Wilcoxon tests were used for the non-normally distributed variables of parasite abundance, and ANOVA tests were used for the grouped variable, age class. To visualize the relationship between parasite abundance and body condition, a linear regression was used including a fixed effect of reproductive status and lactation status. Model residuals were checked for normality and homoscedasticity.

The association of parasites with body condition and reproduction in muskoxen was examined using a Partial Least Squares Path Modelling (PLS-PM) approach using the package "plspm"⁴⁹. PLS-PM uses parameters that have been directly measured, known as manifest variables (MV) to form unobservable latent variables (LV) and quantifies the network between them⁵⁰. This enables assessment of direct and indirect pathways between latent variables, as well as the contribution of MV's to the LV⁵¹. A single MV can be used to form an LV. Path coefficients (β) and effects determine links between LV's, while weights, loadings and communality determine the contribution of a MV to the LV⁵². The PLS-PM approach allows us to examine the relationships between multiple components and works with non-normally distributed data because it does not depend on distributional assumptions.

Three PLS-PM analyses were conducted with the function *plspm()* to investigate the effects of parasites on muskox life history traits using a bootstrapping procedure. The first analysis used all individuals separated by sex (n = 86 females, 49 males) to determine the relationship between age, parasite burden and body condition, had three LVs; (i) age class, (ii) parasite abundance and (iii) body condition (KFI) (Fig. 1a). The parasite abundance LV consisted of 8 reflective MVs; *T. boreoarcticus* and *M. marshalli* adults, lumen and mucosal larvae, *Strongyle* spp., *Marshallagia* and *Nematodirus* spp. eggs, and *Eimeria* spp. oocysts. A group comparison was conducted with a global model including all individuals using the function *plspm.groups()*, allowing us to investigate the effects for all individuals and the effects separated by sex⁵⁰. To determine the relationship between parasite abundance and reproduction, a second analysis using only female muskoxen of reproductive age (3 years and older; n = 56) was used with five LVs; (i) age class, (ii) lactation status, (iii) parasite abundance, (iv) body condition and (v) reproductive status (pregnancy status; Fig. 1b). To determine the relationship with fetus characteristics, a third analysis using only pregnant female muskoxen (n = 26) was used with four LVs; (i) age class, (ii) parasite abundance, (iii) body condition and (iv) fetus characteristics (Fig. 1c). Fetus characteristics were defined as fetus size

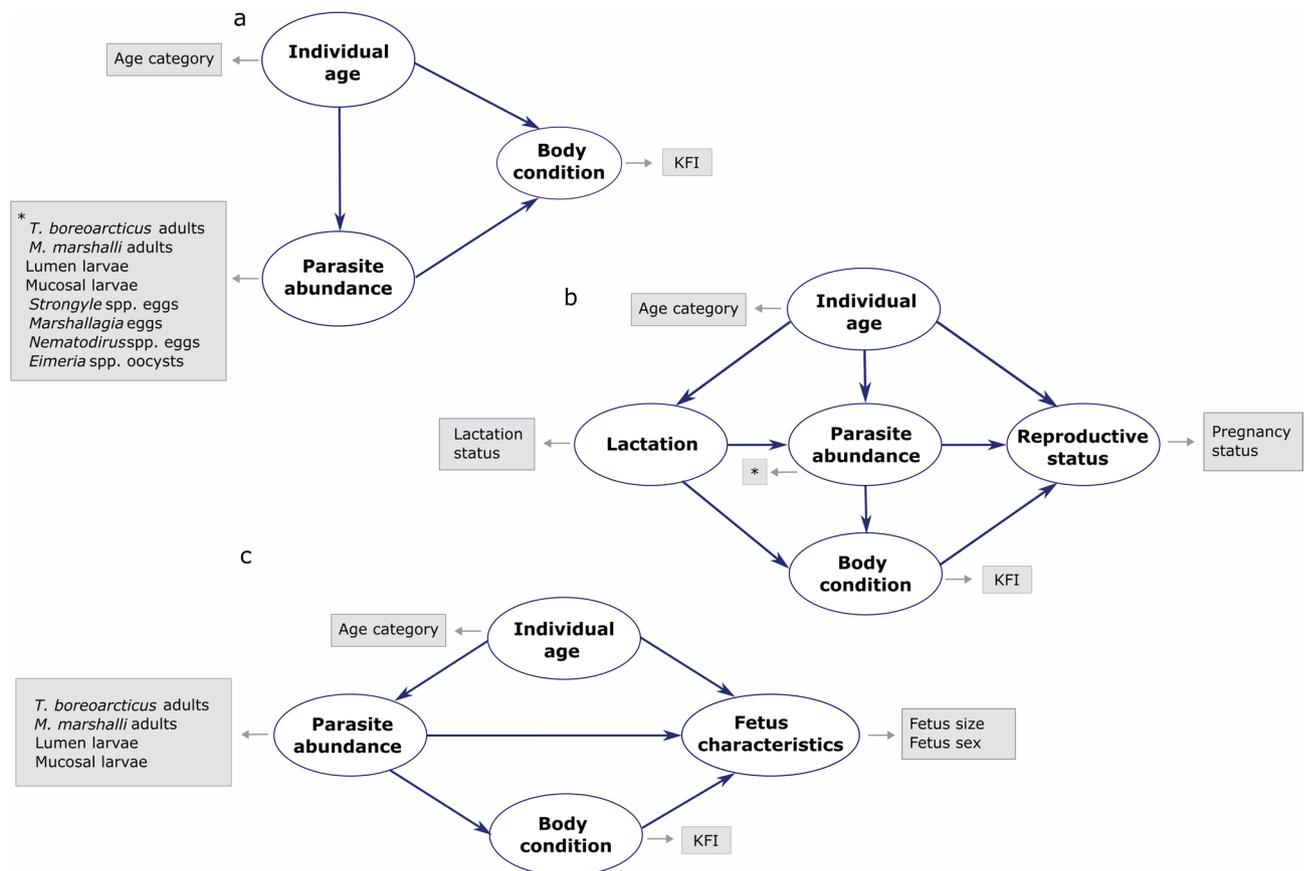


Figure 1. The path models describing; (a) the relationship between age class, parasite abundance and body condition using a group comparison between males and females, (b) the relationship between age class, lactation status, parasite abundance, body condition and reproduction in female muskoxen, and (c) the relationship between age class, parasite abundance, body condition and fetus characteristics in pregnant female muskoxen.

(fetus length/fetus weight) and fetus sex. Due to low prevalence of eggs or oocysts in pregnant females, fecal egg counts were excluded from the third analysis.

Loadings represent the outer model coefficients for each MV, and communalities are squared loadings, which represent the amount of variation of the LV explained by the MV⁵⁰. Average variance extracted (AVE) is used to assess the amount of variance captured by the LV and is measured as the mean communality or mean squared loadings⁵⁰. A loading of more than 0.6 was taken to mean that the MV was moderately correlated to its LV, i.e. more than $0.6^2 \approx 36\%$ of the variation in the MV was captured by the LV. An AVE of more than 0.5 was taken to mean that the variance of the MVs was adequately captured by the LV, i.e. more than 50% of variance was explained. Model simplification was conducted by removing MVs with loadings that were poorly correlated to the LV, i.e. less than 0.6, or that did not sufficiently contribute to the variance explained by the MVs, i.e. AVE less than 0.5. Model quality was additionally validated using redundancy and unidimensionality measures, including Cronbach's Alpha with a threshold of 0.7⁵². Path coefficients (β) indicate the size of the relationship between two LVs, calculated by linear ordinary least squares regressions between the LVs. The coefficient of determination (R^2) is estimated for each LV and goodness of fit is estimated as the average R^2 for all of the LV's. A bootstrap validation was used to obtain confidence intervals for evaluating the precision of the PLS parameter estimation (e.g. path coefficients, fit indices and total effects).

Ethical approval

Sampling protocols were approved by the Government of NWT, and sampling was conducted in agreement with Government of NWT guidelines. None of the samples included in this study were derived from animals purposely sourced or killed for the study.

Results

Age, body condition, female reproduction and parasite diversity and intensity were analysed for 135 muskoxen ($n = 86$ females, 49 males; Table 1). In total, 26 adult (3-year-old and above) female muskoxen were pregnant (29.0%) and 23 were lactating (26.4%). Only animals 3-year-old and older were reproducing, and only those 4-year-old and older were both pregnant and lactating.

Variable	Total (n = 135)	Females (n = 86)	Males (n = 49)	Comparison
Age	n	n	n	
Calf (0 years)	22	11	11	
Yearling (1 year)	19	9	10	
2 years	20	10	10	
3 years	32	23	9	
4 + years	42	33	9	
Body condition	Mean (\pm SE)	Mean (\pm SE)	Mean (\pm SE)	Student's t-test
KFI	0.99 (\pm 0.33)	1.05 (\pm 0.33)	0.88 (\pm 0.31)	t = 3.09, P = 0.0025
Reproduction		% of adults (n = 56)		
% Pregnant		45.6 (n = 26)		
% Lactating		40.4 (n = 23)		
% Pregnant and Lactating		17.5 (n = 10)		
% Not Pregnant		54.4 (n = 30)		
Abomasal parasite abundance	Prevalence % (95% CI)	Median (range)	Median (range)	Wilcoxon test
<i>T. boreoarcticus</i> adults	94.2 (0.87–0.98)	305 (10–9520)	1045 (20–10,690)	W = 1673, P = 0.016
<i>M. marshalli</i> adults	85.5 (0.78–0.92)	120 (10–2020)	200 (10–1710)	W = 1679, P = 0.015
<i>Nematodirus</i> spp. adults	8.0 (0.04–0.15)	10 (10–60)	–	
Lumen larvae	97.1 (0.91–0.99)	12,600 (1200–57,100)	14,650 (2600–68,800)	W = 2086, P = 0.93
Mucosal larvae	90.6 (0.84–0.96)	5600 (200–40,600)	8300 (6000–36,600)	W = 1475, P < 0.01
Fecal parasite eggs	Prevalence % (95% CI)	Median (range)	Median (range)	Wilcoxon test
Strongyle spp.	33.3 (0.24–0.43)	0.63 (0.25–46.50)	0.63 (0.25–5.75)	W = 2056, P = 0.47
<i>Marshallagia</i> spp.	55.1 (0.45–0.65)	1.50 (0.25–12.00)	2.50 (0.25–11.75)	W = 0.56, P < 0.001
<i>Nematodirus</i> spp.	72.5 (0.63–0.81)	1.75 (0.25–18.00)	8.50 (0.25–48.80)	W = 1673, P = 0.015
<i>Moniezia</i> spp.	1.5 (0.00–0.07)	–	0.63 (0.50–0.75)	
<i>Eimeria</i> spp.	94.5 (0.89–0.98)	120.00 (1.50–500.00)	154.00 (9.50–1000.00)	W = 1971, P = 0.27

Table 1. Summary of the demographic, reproduction and parasite infection data for all muskoxen sampled on Banks Island, Northwest Territories. Mean Kidney Fat Index (KFI) with standard error (SE) is reported as the measure of body condition. Abomasal parasite abundance is measured by the number of adults, and fecal parasite eggs are measured in eggs (or oocysts) per gram (EPG).

Parasite diversity and intensity

Teladorsagia boreoarcticus and *Marshallagia marshalli* were present in the abomasa at a high prevalence of 94% (95% CI = 0.79–1.12) and 85% respectively (95% CI = 0.71–1.02). Infection intensity of *T. boreoarcticus* was higher than *M. marshalli*. The intensity of adult nematode infections (median) was significantly higher in male muskoxen compared to females of all ages for both *T. boreoarcticus* and *M. marshalli* (Table 1). Nematode intensities were highest in yearlings and decreased with age for both *T. boreoarcticus* ($F = 56.41$, $df = 4$, $P < 0.001$) and *M. marshalli* ($F = 13.87$, $df = 4$, $P < 0.001$) (Fig. 2). The prevalences of lumen and mucosal larvae were high, at 97.1% and 90.6%, respectively. Male muskoxen had higher intensities of mucosal larvae than female muskoxen, but there was no significant difference in lumen larvae intensity (Table 1).

Parasite eggs found in the fecal samples were strongyle type (presumably primarily *T. boreoarcticus* based on abomasal examination), *Marshallagia* sp., *Nematodirus* spp., and *Moniezia* sp., and *Eimeria* spp. oocysts. Fecal egg counts (FEC) were higher in male muskoxen for *Marshallagia* sp. and *Nematodirus* spp., but not for strongyle type eggs and *Eimeria* spp. oocysts (Table 1). *Moniezia* sp. eggs were only detected in two male muskoxen at low intensity (< 1 eggs per gram) and this parasite was not included in any further analysis. FEC for all parasite species were higher in calves and yearlings and decreased with age: Strongyle type ($F = 3.73$, $df = 4$, $P = 0.007$), *Marshallagia* sp. ($F = 10.96$, $df = 4$, $P < 0.001$), *Nematodirus* spp. ($F = 47.67$, $df = 4$, $P < 0.001$) and *Eimeria* spp. ($F = 8.62$, $df = 4$, $P < 0.001$) (Fig. 2).

Parasite infection and body condition

Body condition (i.e. KFI) was inversely related to parasite infection intensity for both male and female muskoxen (Fig. 3). For the PLS-PM model for all individuals describing body condition using parasite abundance and individual age, the goodness of fit was 0.45 and the model explained 25% of the variation in body condition and retained *T. boreoarcticus* and *M. marshalli* adults, *Marshallagia* and *Nematodirus* spp. eggs (Fig. 3; Tables 2, 3). Parasite abundance generally decreased with age class, and body condition decreased with increasing parasite abundance. Age class did not have a significant direct effect on body condition. In the group comparison, there were no significant differences between the male and female models for the effects between age and parasite abundance ($t_{1,32} = 1.08$, $P = 0.14$), parasite abundance and body condition ($t_{1,32} = 0.11$, $P = 0.47$), and age and body condition ($t_{1,32} = 0.76$, $P = 0.22$).

Parasite infection and reproduction

Females were less likely to be pregnant if they had higher parasite infection intensity (*T. boreoarcticus*, $W = 281$, $P < 0.001$; *M. marshalli*, $W = 260$, $P < 0.001$). Additionally, females that were lactating likely have higher parasite

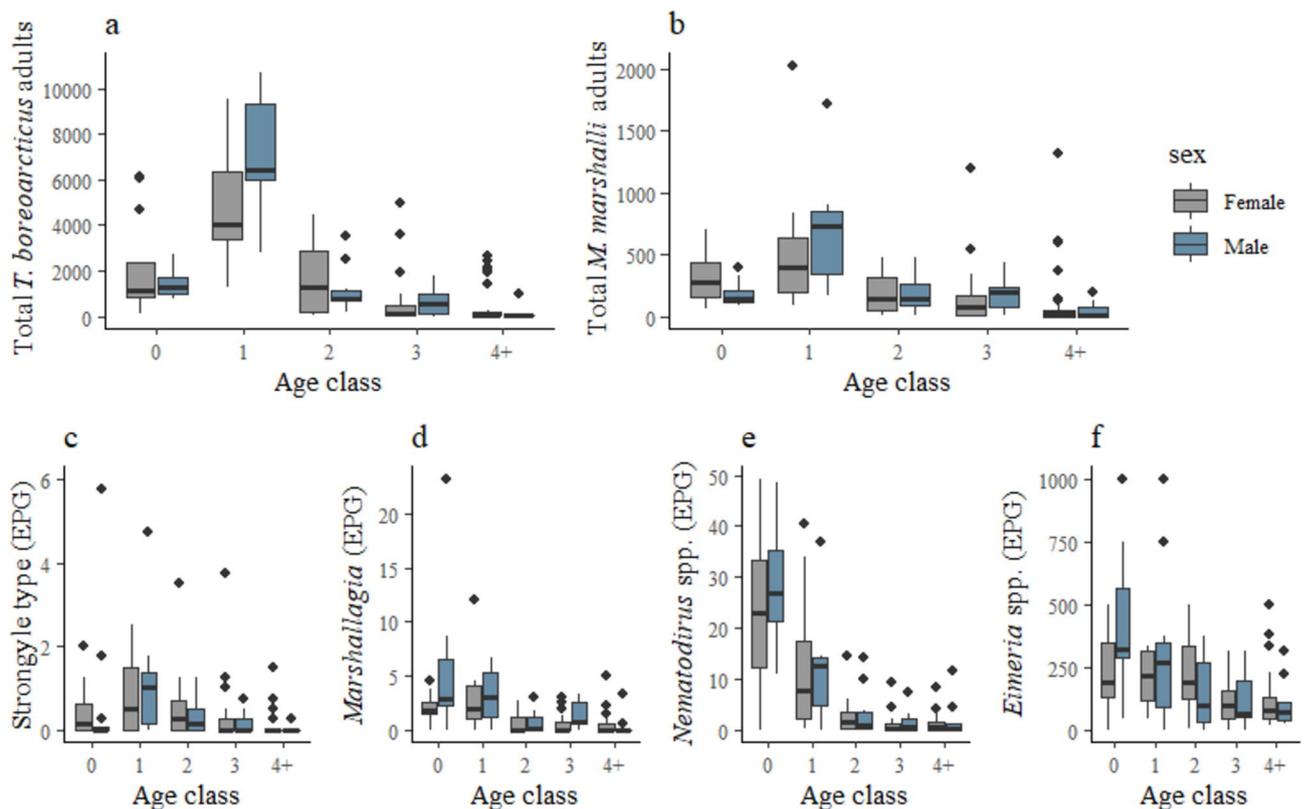


Figure 2. Age and sex specific parasite abundance of adult abomasal nematodes; (a) *T. boreoarcticus* and (b) *M. marshalli*, and parasite eggs or oocysts in feces measured by eggs per gram (EPG); (c) Strongyle type, (d) *Nematodirus* spp., (e) *Marshallagia*, and (f) *Eimeria* spp. in muskoxen.

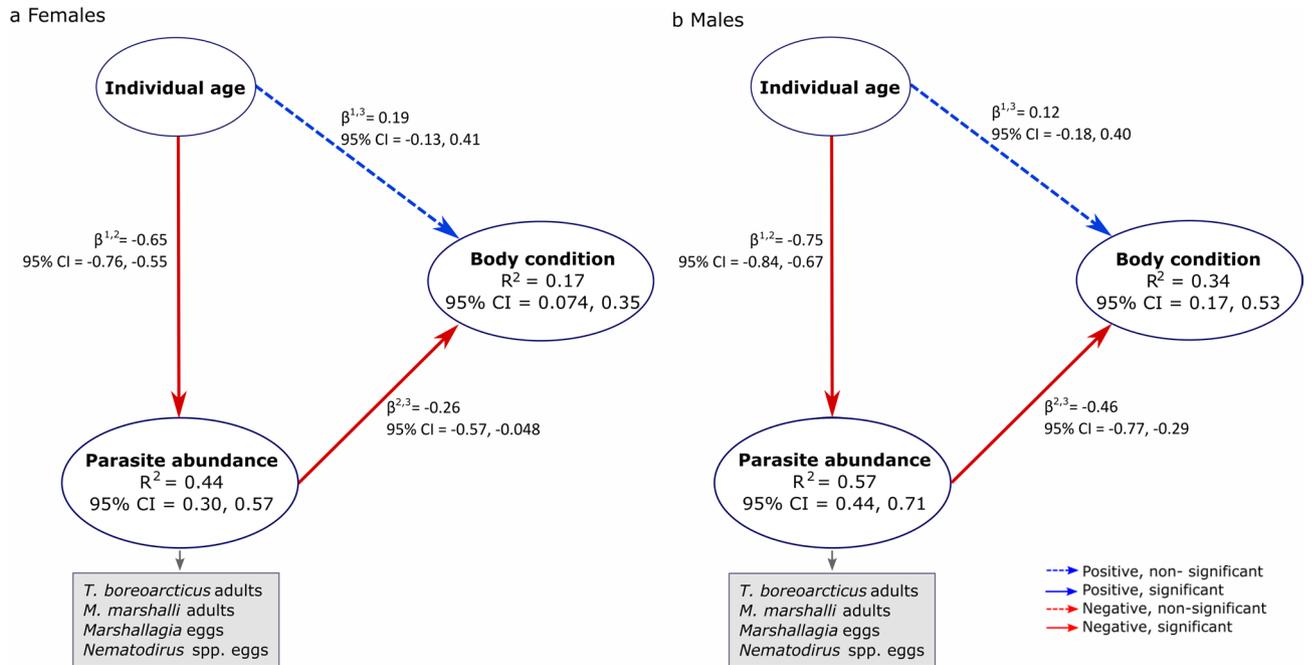


Figure 3. The path model describing the relationship between age class, parasite abundance and body condition for male and female muskoxen. The grey boxes show the retained manifest variables and the open circles show the latent variables (LVs). β is the path coefficient, while R^2 represents how much variation of the LV was explained by the preceding LVs.

Relationship	Direct	Indirect	Total	SE	95% CI	
Females						
Age → Parasites	-0.65		-0.65	0.053	-0.75	-0.54*
Age → Body condition	0.19	0.17	0.37	0.086	0.18	0.52*
Parasites → Body condition	-0.26		-0.27	0.14	-0.55	-0.0063*
Males						
Age → Parasites	-0.77		-0.76	0.036	-0.85	-0.69*
Age → Body condition	0.096	0.37	0.37	0.11	0.24	0.68*
Parasites → Body condition	-0.49		-0.49	0.14	-0.78	-0.22*

Table 2. Direct, indirect and total effects between latent variables in the final PLS-PM explaining body condition in muskoxen. Standard error (SE) and 95% confidence intervals (CI) were estimated by bootstrapping. Star (*) indicates a significant effect.

Manifest variable	Male and female body condition			Female body condition and reproduction			Fetus characteristics		
	Loading	95% CI		Loading	95% CI		Loading	95% CI	
<i>T. boreoarcticus</i> adults	0.75*	0.66	0.84	0.88*	0.66	0.96	0.86*	-0.26	0.98
<i>M. marshalli</i> adults	0.63*	0.51	0.75	0.89*	0.71	0.96	0.95*	-0.30	0.98
Lumen larvae	-0.0011	-0.20	0.23	0.53	0.15	0.76	0.54	-0.43	0.90
Mucosal larvae	-0.034	-0.24	0.23	0.29	-0.16	0.63	0.12	-0.46	0.89
Stronglye type eggs	0.47	0.24	0.63	0.44	0.20	0.71			
<i>Marshallagia</i> eggs	0.77*	0.66	0.85	0.70*	0.28	0.93			
<i>Nematodirus</i> spp. eggs	0.72*	0.63	0.79	0.57*	0.15	0.87			
<i>Erimeria</i> spp. oocysts	0.58	0.43	0.70	0.31	-0.18	0.65			
Cronbach's Alpha	0.73			0.70			0.85		
AVE	0.55			0.60			0.51		

Table 3. The manifest variable (MV) loadings for the parasite abundance latent variable (LV) in the PLS-PM analyses describing the effect of parasite infection intensity on muskox body condition, reproduction and fetus characteristics, including the 95% confidence intervals. The asterisk shows the MVs retained in the final model. Cronbach's Alpha and average variance extracted (AVE) were calculated using the retained MVs.

infection intensity of *T. boreoarcticus* ($W = 549$, $P = 0.070$) but not *M. marshalli* ($W = 597$, $P = 0.18$; Fig. 4). Pregnant individuals had higher KFI compared to not pregnant individuals (*T. boreoarcticus*, $F_{53,54} = 10.03$, $P = 0.0026$; *M. marshalli*, $F_{53,54} = 11.34$, $P = 0.0014$), and lactating individuals had lower KFI compared to individuals that were not lactating (*T. boreoarcticus*, $F_{53,54} = 9.64$, $P = 0.0031$; *M. marshalli*, $F_{53,54} = 10.51$, $P = 0.0026$; Fig. 5). For the second PLS-PM analyses for adult female muskoxen, goodness of fit was 0.37 and the model explained 35.9% of variation in reproduction. Parasite MV's retained in the model included *T. boreoarcticus* adults, *M. marshalli* adults and *Marshallagia* and *Nematodirus* spp. eggs (Table 3). The loading for *Nematodirus* spp. eggs was below the threshold, but the variable was retained due to acceptable Cronbachs Alpha and AVE values. Body condition (i.e. KFI) decreased with increasing parasite abundance and, when body condition was lower, individuals were less likely to be pregnant (Table 4, Fig. 6). The observed effect of parasites on reproduction was significant when including the indirect effect through body condition (Table 4, Fig. 6). Individuals that were lactating were more likely to have higher parasite infection intensities and lower body condition (Table 4, Figs. 4, 6).

Effect on fetus size and sex

In the 24 pregnant muskoxen, 19 individuals were infected with *T. boreoarcticus* and ten were infected with *M. marshalli*. Parasite infection intensity in pregnant muskoxen was generally low for both *T. boreoarcticus* (median = 30) and *M. marshalli* (median = 25) adult nematodes. In the fecal samples, only three individuals had *Marshallagia* eggs, two had strongyle type eggs and ten had *Nematodirus* spp. eggs. For the PLS-PM model including fetus characteristics, goodness of fit was 0.26 and the model explained 12.5% of variation in fetus characteristics. There was no effect of age, parasite infection intensity and body condition on fetus size (KFI, $F_{20,21} = 0.27$, $P = 0.61$; *T. boreoarcticus*, $F_{20,21} = 0.54$, $P = 0.47$; *M. marshalli*, $F_{20,21} = 0.0025$, $P = 0.96$) or fetus sex (KFI, $t = -0.32$, $P = 0.75$; *T. boreoarcticus*, $W = 69$, $P = 0.90$; *M. marshalli*, $W = 69.5$, $P = 0.93$; Fig. 7; Table 5). The model retained both *T. boreoarcticus* and *M. marshalli* adult nematodes (Table 3).

Discussion

We have described the gastrointestinal parasite fauna of muskoxen, and the associated direct and indirect costs on muskox fitness during a population peak, which preceded a substantial population decline. The parasite diversity reported here was typical of that described for muskoxen^{47,53}. It was dominated by *Teladorsagia boreoarcticus*, a common abomasal nematode of muskoxen in the North American Arctic^{44,47}. *Marshallagia marshalli*, another commonly reported abomasal nematode of muskoxen, was also abundant. The occurrence of *M. marshalli* in muskoxen is more variable and it is generally less abundant than *T. boreoarcticus*^{47,54,55}. The intestinal parasites detected through the fecal egg counts, *Nematodirus* spp. (nematode), *Eimeria* spp. (protozoan) and *Moniezia* sp. (tapeworm), have been frequently reported in muskoxen⁴⁷. The parasite intensities and age class relationships were typical of that seen for the parasite taxa in northern and Arctic ungulates^{1,56,57}. Lower exposure and ingestion rates by calves, and arrested development typical of *Teladorsagia*, and perhaps *Marshallagia*, may account for the lower intensity in calves followed by the peak abundance in yearlings when hypobiotic larvae mature^{47,58,59}. In contrast, *Nematodirus* spp. and *Eimeria* spp. develop directly and are common in young ungulates^{47,60}.

We found a direct negative association between parasitism and body condition in muskoxen and an effect of parasitism on female reproduction. Females were more likely to be pregnant if they had lower parasite infection intensities, which included a direct effect and an indirect effect through the negative effect of parasites on body condition. While the costs of parasitism have not previously been explored in muskoxen, the link between

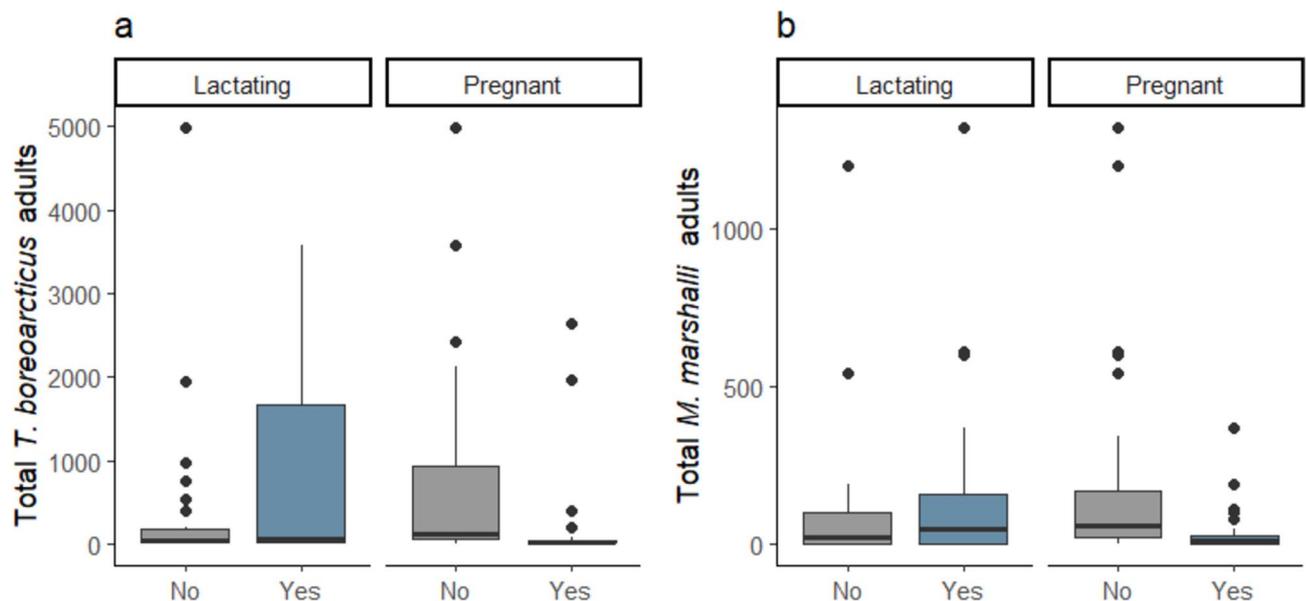


Figure 4. Association between median adult parasite intensity and adult female muskox reproductive status, pregnancy and lactation, for adult abomasal nematodes: (a) *Teladorsagia boreoarcticus* or (b) *Marshallagia marshalli*.

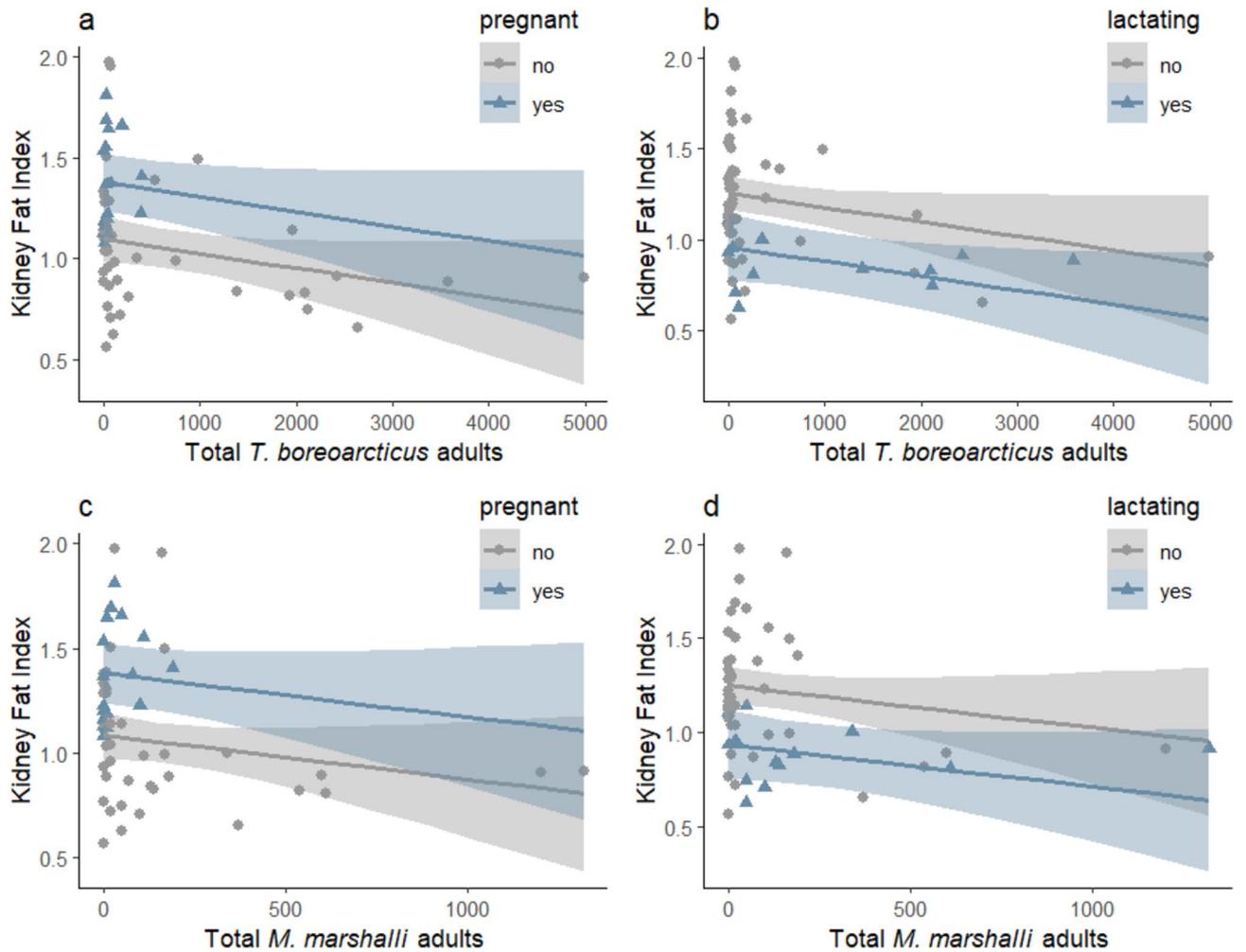


Figure 5. The relationship between body condition, measured by Kidney Fat Index, and adult abomasal nematode abundance of *Teladorsagia boreoarcticus* (a, b) and *Marshallagia marshalli* (c, d) in female muskoxen when individuals are either pregnant (a, c) or lactating (b, d).

Relationship	Direct	Indirect	Total	SE	95% CI	
Age→ Lactation	0.50		0.50	0.12	0.28	0.72*
Age→ Parasites	-0.26	0.18	-0.078	0.14	-0.28	0.24
Age→ Body condition		-0.17	-0.17	0.085	-0.35	-0.021*
Age→ Reproduction	0.33	-0.051	0.28	0.13	0.0094	0.54*
Lactation→ Parasites	0.37		0.37	0.13	0.16	0.65*
Lactation→ Body condition	-0.38	-0.096	-0.48	0.095	-0.63	-0.28*
Lactation→ Reproduction		-0.24	-0.24	0.090	-0.46	-0.11*
Parasites→ Body condition	-0.26		-0.26	0.093	-0.44	-0.086*
Parasites→ Reproduction	-0.17	-0.10	-0.27	0.11	-0.50	-0.097*
Body condition→ Reproduction	0.38		0.38	0.16	0.071	0.67*

Table 4. Direct, indirect and total effects between latent variables in the final PLS-PM explaining reproduction in female muskoxen. Standard error (SE) and 95% confidence intervals (CI) of the total effect were estimated by bootstrapping. Star (*) indicates a significant effect.

reproduction, body condition and parasite abundance has been found in other studies, e.g. caribou^{55,57}, Svalbard reindeer^{61,62}, and Dall’s sheep (*Ovis dalli dalli*)¹. Similar to the findings reported in this study, *M. marshalli* has previously been associated with body condition and reproduction in caribou and Dall’s sheep^{1,57}. However, an association between *T. boreoarcticus* and host fitness has not previously been demonstrated in caribou or reindeer^{55,57}. This is likely because this parasite species is generally present at low prevalence and intensity in

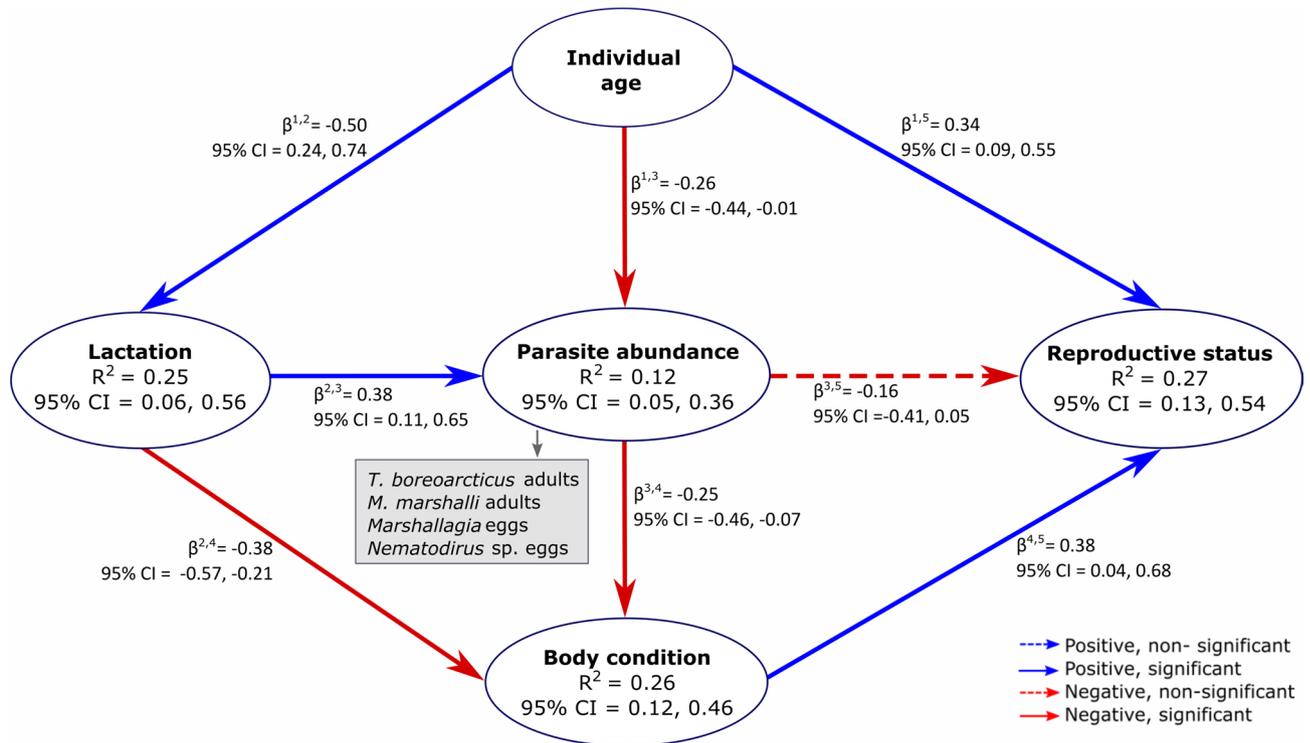


Figure 6. The path model describing the relationship between female age class, parasite abundance, lactation, body condition and reproductive status in female muskoxen. The grey boxes show the retained manifest variables and the open circles show the latent variables (LVs). β is the path coefficient, while R^2 represents how much variation of the LVs were explained.

these ungulate species, whereas it is the dominant abomasal nematode in muskoxen⁴⁷. Although *Nematodirus* spp. are widespread intestinal parasites, the costs in wild ungulates are unknown⁴⁷. Our results suggest that *Nematodirus* spp. may contribute to the cost of parasitism and targeted studies on intestinal parasitism could explain these effects.

Parasites may have differing effects depending on their life history strategies and relative abundance in the host population^{57,62,63}. In this study we found similar effects of both species of adult abomasal nematodes despite differences in overall abundance and life history strategies. The peak period of larval exposure and parasitism by adult *T. boreoarcticus* is during the summer where vegetation growth and resource intake is highest for muskoxen. The costs of developing larvae and adult parasitism at this time may affect the ability of individuals to build energy reserves⁴⁷. Conversely, adult intensities of *M. marshalli* peak during the winter when muskoxen are experiencing limited forage and possibly cold-induced energetic stress^{16,64}. Thus, both parasite species have potentially additive effects on host fitness through differing timing of infestations dependant on parasite life-history strategies^{47,65}.

Parasites may also impact hosts differently depending on the conditions of the host population, including environmental dynamics and individual characteristics⁸. Male-biased parasitism is common in wild ungulates and has been linked to high testosterone and the physiological costs of rutting^{5,66}. Although we did not find a significant effect of sex on the relationship between parasites and body condition, our results suggest there may be subtle effect of increased parasite infection intensity in males. Infection intensity in pregnant females was lower than both non-pregnant females and males, suggesting that reproduction is suppressed in females facing high parasite infection intensities because they are less likely to have enough energy reserves required to support reproductive costs^{15,16,25,26,61}. Parasites generally impact ungulates through the energetic burden that they impose, which can have additional effects such as reduced feeding rates, which further exacerbates nutritional imbalance^{6,7}. The effect of parasites may be augmented when the nutritional status of the host is compromised because energy reserves may be traded off between body condition, immunity and reproduction^{8,67,68}. This can impact energy reserves that are important for survival during the winter, maintenance of pregnancy and lactation early the following spring^{15,25}.

Higher energetic costs have been attributed to lactation compared to pregnancy in mammals^{69–71}. We found that lactating female muskoxen were more likely to have higher parasite infection intensities and lower body condition than females that were not lactating. Due to the costs associated with lactation, lactating females will have had a higher energetic demand since parturition, making them more vulnerable to parasites and depleting their energy reserves. Our results showed that lactating females had a larger range of parasite infection intensities than pregnant females, which generally had low infection intensities. Prior reproduction (i.e. lactating females) may impact subsequent fecundity (i.e. pregnant females), because females may not have sufficient energy reserves for future reproduction^{71,72}. Females may only become pregnant if they have low infection intensities. Additionally,

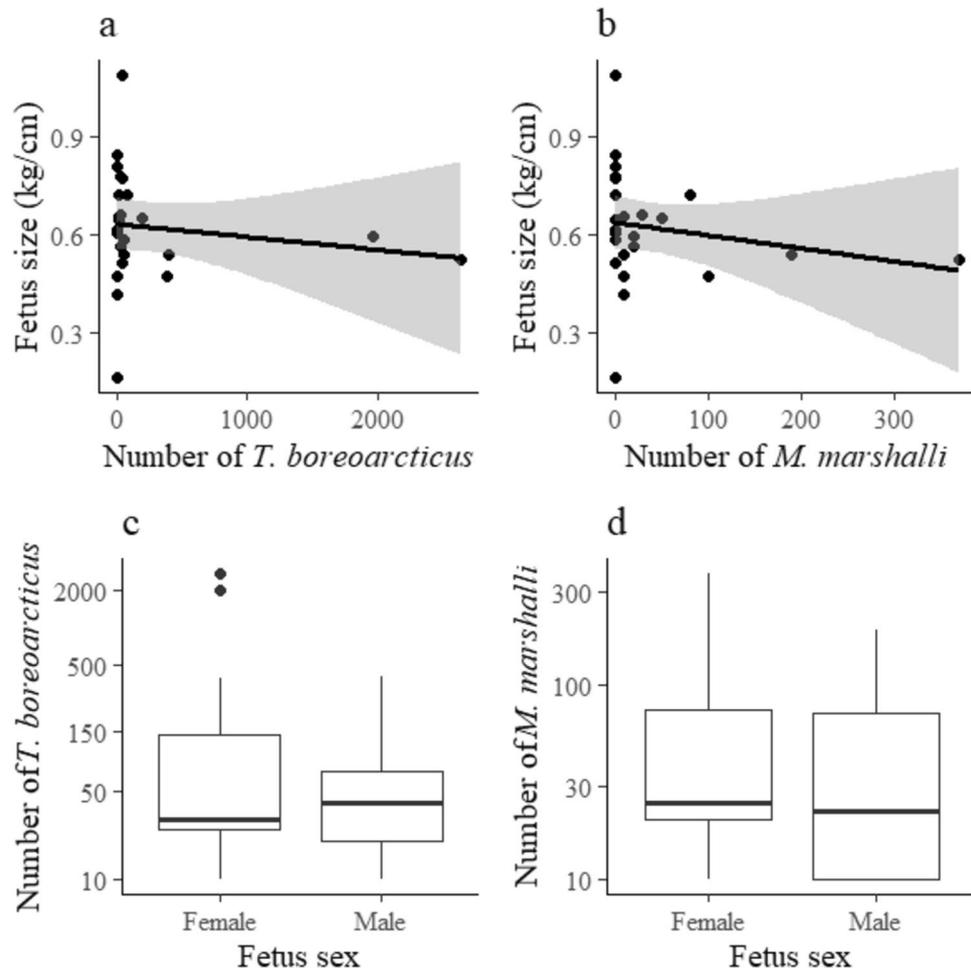


Figure 7. The effect of adult abomasal nematode infection intensity of *Teladorsagia boreoarcticus* or *Marshallagia marshalli* on fetus characteristics in pregnant female muskoxen including fetus size (weight divided by length) (a, b), and fetus sex (c, d).

Relationship	Direct	Indirect	Total	SE	95% CI
Age -> Parasites	- 0.051		- 0.051	0.37	- 0.81 0.61
Age -> Body condition		0.020	0.020	0.095	- 0.25 0.073
Age -> Fetus characteristics	- 0.32	0.014	0.31	0.39	- 0.66 0.68
Parasites -> Body condition	- 0.39		- 0.39	0.34	- 0.70 0.33
Parasites -> Fetus characteristics	- 0.27	- 0.050	- 0.22	0.21	- 0.53 0.27
Body condition -> Fetus characteristics	- 0.13		- 0.13	0.28	- 0.56 0.52

Table 5. Direct, indirect and total effects between latent variables in the PLS-PM explaining fetus characteristics in pregnant female muskoxen (n = 24). Standard error (SE) and 95% confidence intervals (CI) were estimated by bootstrapping. Star (*) indicates a significant effect.

survival of females may be compromised by reproduction due to the energetic investment of lactation⁷¹. These effects are likely to be exacerbated by the costs of parasites and the associated energetic demands for females.

Low virulence parasites can affect fetus size through delayed conception or fetal development due to suboptimal nutrition to the fetus and can be associated with fetus sex due to sex-dependant fetal energetic costs^{51,73-75}. We did not find any association between parasite burden and fetus development or sex. Although this suggests that there may not be an association between parasite burden and fetus characteristics, the data available for pregnant females is not adequate to support a conclusion. The pregnant females generally had the lowest parasite burdens found in this study, and our sample size of pregnant females was relatively small, even though PLS-PM models can handle small sample sizes⁷⁶. Additionally, the lack of association found with fetal size may be due to the time of sampling, which occurred in November and was early in muskox fetal development.

At the time of this study, the population of muskoxen on Banks Island was the largest in the world^{17,20,27,32}. A severe icing event during winter 2003–2004 resulted in a thick layer of ice across the landscape that restricted access for muskoxen to winter forage^{31,77}. The population subsequently declined by more than 30% by 2005 and to 50% of its 2001 peak by 2010. This decline was largely attributed to winter mortality directly associated with the icing event and sustained multigenerational effects of malnutrition on reproduction and survival^{20,26,31}. Studies on Soay sheep (*Ovis aries*) have demonstrated how parasitism can exacerbate the effects of severe weather events and food shortage, leading to higher mortality rates of heavily infected hosts⁸. The high population density of muskoxen in the late 1990s and early 2000s, and high levels of parasitism, may have increased their vulnerability to the icing event. Thus, parasites may play a role in population declines associated with restricted access to forage. Weather events, such as the icing event of 2003 and 2004, are becoming more common due to climate change, increasing the urgency of understanding and mitigating their impacts⁷⁷, and understanding how parasite dynamics may shift⁷⁸.

Ungulate population dynamics, especially for species in extreme environments such as the Arctic, are sensitive to multiple stressors from their biological and physical environment, and from their relationships with humans⁷⁹. Therefore, observing relatively small effect sizes or explained variance is likely when multiple stressors are not accounted for^{6,80}. The cross-sectional nature of this study and low variation explained in the modelling approach means that causality or directionality of relationships must be interpreted with caution. However, longitudinal experimental studies in *Rangifer* sp. where reindeer body condition improved after anthelmintic treatment⁶², supports a causal nature to this relationship despite low effect sizes. Additionally, the directionality assigned between variables, required by the PLS-PM approach, was based on the strongest expected effect based on known interactions between parasites and hosts. However, the direction of these effects may be reciprocal rather than unidirectional and could be interpreted as such.

We have demonstrated a strong link between parasitism, body condition and reproduction in an Arctic ungulate using a cross-sectional study. Climate change is occurring in the Arctic at an accelerated rate, meaning that species are facing increasing stressors⁸¹. This includes shifting phenology and weather events which are impacting the accessibility and quality of forage^{77,82,83}. If energetic resources are limited, for example during increasingly frequent icing events, reproducing females will be vulnerable to higher parasite burdens while also having fewer energy reserves for subsequent reproduction and survival. Additionally, climate change may have significant effects on host-parasite dynamics and the costs associated with parasitism, with consequences for population dynamics and ecosystem function^{6,78}. Understanding the mechanisms in which nutritional resources and parasites influence wildlife populations will contribute to a holistic understanding of ungulate population dynamics and ecosystem health.

Data availability

Data and code is available via https://github.com/ERDickinson0/muskox_parasites.

Received: 8 January 2024; Accepted: 17 July 2024

Published online: 25 July 2024

References

1. Aleuy, O. A. *et al.* Diversity of gastrointestinal helminths in Dall's sheep and the negative association of the abomasal nematode, *Marshallagia marshalli*, with fitness indicators. *PLoS ONE* **13**, e0192825 (2018).
2. Altizer, S. *et al.* Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. Syst.* **34**, 517–547 (2003).
3. Hudson, P. J., Rizzoli, A. P., Grenfell, B. T., Heesterbeek, J. A. P. & Dobson, A. P. *Ecology of Wildlife Diseases* (Oxford University Press, 2002).
4. Carvalho, J. *et al.* Sarcoptic mange breaks up bottom-up regulation of body condition in a large herbivore population. *Parasit. Vectors* **8**, 1–9 (2015).
5. Oliver-Guimerá, A. *et al.* The physiological cost of male-biased parasitism in a nearly monomorphic mammal. *Parasit. Vectors* **10**, 1–7 (2017).
6. Koltz, A. M. *et al.* Sublethal effects of parasitism on ruminants can have cascading consequences for ecosystems. *Proc. Natl. Acad. Sci.* **119**, e2117381119 (2022).
7. Shanebeck, K. M., Besson, A. A., Lagrue, C. & Green, S. J. The energetic costs of sub-lethal helminth parasites in mammals: A meta-analysis. *Biol. Rev.* **97**, 1886–1907 (2022).
8. Gulland, F. M. D. The role of nematode parasites in Soay sheep (*Ovis aries* L.) mortality during a population crash. *Parasitol.* **105**, 493–503 (1992).
9. Leivesley, J. A. *et al.* Survival costs of reproduction are mediated by parasite infection in wild Soay sheep. *Ecol. Lett.* **22**, 1203–1213 (2019).
10. Ezenwa, V. O. Interactions among host diet, nutritional status and gastrointestinal parasite infection in wild bovids. *Int. J. Parasitol.* **34**, 535–542 (2004).
11. Murray, D. L. *et al.* Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildl. Monogr.* **166**, 1–30 (2006).
12. Tomaselli, M., Gerlach, S. C., Kutz, S. J., Checkley, S. L., Community of Iqaluktuqiaq. Iqaluktuqiaq voices: Local perspectives about the importance of muskoxen, contemporary and traditional use and practices. *Arctic* **71**, 1–14 (2018).
13. Post, E. & Pedersen, C. Opposing plant community responses to warming with and without herbivores. *Proc. Natl. Acad. Sci.* **105**, 12353–12358 (2008).
14. Falk, J. M., Schmidt, N. M., Christensen, T. R. & Ström, L. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. *Environ. Res. Lett.* **10**, 045001 (2015).
15. Mosbacher, J. B., Michelsen, A., Stelvig, M., Hendrichsen, D. K. & Schmidt, N. M. Show me your rump hair and I will tell you what you ate—The dietary history of muskoxen (*Ovibos moschatus*) revealed by sequential stable isotope analysis of guard hairs. *PLoS ONE* **11**, e0152874 (2016).
16. Desforges, J. P. *et al.* Quantification of the full lifecycle bioenergetics of a large mammal in the high Arctic. *Ecol. Model.* **401**, 27–39 (2019).

17. Gunn, A., Shank, C. & McLean, B. The history, status and management of muskoxen on Banks Island. *Arctic* **44**, 188–195 (1991).
18. Reynolds, P. E. Dynamics and range expansion of a reestablished muskox population. *J. Wildl. Manag.* **62**(2), 734–744 (1998).
19. Schmidt, N. M., Pedersen, S. H., Mosbacher, J. B. & Hansen, L. H. Long-term patterns of muskox (*Ovibos moschatus*) demographics in high arctic Greenland. *Polar Biol.* **38**, 1667–1675 (2015).
20. Davison, T.M., Williams, J., & Adamczewski, J. Aerial survey of Peary caribou (*Rangifer tarandus pearyi*) and muskoxen (*Ovibos moschatus*) on Banks Island, July 2014. Environment and Natural Resources, Government of the Northwest Territories, 270 (2017).
21. Tomaselli, M., Kutz, S., Gerlach, C. & Checkley, S. Local knowledge to enhance wildlife population health surveillance: Conserving muskoxen and caribou in the Canadian Arctic. *Biol. Conserv.* **217**, 337–348 (2018).
22. Kutz, S. *et al.* *Erysipelothrix rhusiopathiae* associated with recent widespread muskox mortalities in the Canadian Arctic. *Can. Vet. J.* **56**, 560–563 (2015).
23. Afema, J. A., Beckmen, K. B., Arthur, S. M., Huntington, K. B. & Mazet, J. A. Disease complexity in a declining Alaskan muskox (*Ovibos moschatus*) population. *J. Wildl. Dis.* **53**, 311–329 (2017).
24. Kutz, S. Muskox health ecology symposium 2016: gathering to share knowledge on “umingmak” in a time of rapid change. *Arctic* **70**, 225–236 (2017).
25. White, R. G., Rowell, J. E. & Hauer, W. E. The role of nutrition, body condition and lactation on calving success in muskoxen. *J. Zool.* **243**, 13–20 (1997).
26. Adamczewski, J. Z., Fargey, P. J., Laarveld, B., Gunn, A. & Flood, P. F. The influence of fatness on the likelihood of early-winter pregnancy in muskoxen (*Ovibos moschatus*). *Theriogenology* **50**, 605–614 (1997).
27. Larter, N. C. & Nagy, J. A. Calf production, calf survival, and recruitment of muskoxen on Banks Island during a period of changing population density from 1986–1999. *Arctic* **54**, 394–406 (2001).
28. Barr, W. The commercial trade in muskox hides in the Northwest Territories 1860–1916. *Rangifer* **11**, 81–82 (1991).
29. Nagy, J.A., Larter, N., & Wright, W.H. Population estimates for Peary caribou and muskox on Banks Island, NT, July 2001. Department of Environment and Natural Resources, Government of the Northwest Territories, 199 (2006).
30. Jingfors, K. T. & Klein, D. R. Productivity in recently established muskox populations in Alaska. *J. Wildl. Manag.* **46**, 1092–1096 (1982).
31. Nagy, J.A., & Gunn, A. Productivity of Peary caribou and muskoxen on Banks and Melville Islands, NT, July 2005. Department of Environment and Natural Resources, Government of the Northwest Territories, 200 (2009).
32. Davison, T.M., & Baryluk, S. Aerial Survey of Muskoxen (*Ovibos moschatus*) and Peary Caribou (*Rangifer tarandus pearyi*) on Banks Island, July and August 2019. Department of Environment and Natural Resources, Government of the Northwest Territories, 295 (2021).
33. White, R. G., Holleman, D. F. & Tiplady, B. A. Seasonal body weight, body condition, and lactational trends in muskoxen. *Can. J. Zool.* **67**, 1125–1133 (1989).
34. Adamczewski, J., Gunn, A., Laarveld, B. & Flood, P. F. Seasonal changes in weight, condition and nutrition of free-ranging and captive muskox females. *Rangifer* **12**, 179–183 (1992).
35. Huot, J., 1988. Review of methods for evaluating the physical condition of wild ungulates in northern environments. Centre d'études nordiques, Université Laval, Laval, **32**, (1988).
36. Riney, T. Evaluating condition of free-ranging red deer (*Cervus elephas*), with special reference to New Zealand. *Trans. R. Soc. New Zeal.* **36**, 429–463 (1955).
37. Henrichsen, P. & Grue, H. Age criteria in the musk ox (*Ovibos moschatus*) from Greenland [horn, tooth, skull, eruption, attrition]. *Dan. Rev. Game Biol.* **11**, 3–18 (1980).
38. Herlich, H. A digestion method for post-mortem recovery of nematodes from ruminants. *Proc. Helminthol. Soc. Wash.* **23**, 102–103 (1956).
39. Skrjabin, K. I., Shikhobalova, N. P. & Schulz, R. S. Trichostrongylids of Animals and Man. *Acad. Sci. USSR.* **3**, 704 (1954).
40. Lichtenfels, J. R., Pilitt, P. A. & Lancaster, M. B. Cuticular ridge patterns of seven species of Ostertagiinae (Nematoda) parasitic in domestic ruminants. *Proc. Helminthol. Soc. Wash.* **55**, 77–86 (1988).
41. Lichtenfels, J. R. & Pilitt, P. A. Cuticular ridge patterns of *Marshallagia marshalli* and *Ostertagia occidentalis* (Nematoda: Trichostrongyloidea) parasitic in ruminants of North America. *Proc. Helminthol. Soc. Wash.* **56**, 173–182 (1989).
42. Lichtenfels, J. R. & Pilitt, P. A. A redescription of *Ostertagia bisonis* (Nematoda: Trichostrongyloidea) and a key to species of Ostertagiinae with a tapering lateral synlophe from domestic ruminants in North America. *Proc. Helminthol. Soc. Wash.* **58**, 231–244 (1991).
43. Lichtenfels, J. R. & Hoberg, E. P. The systematics of nematodes that cause ostertagiasis in domestic and wild ruminants in North America: An update and a key to species. *Vet. Parasitol.* **46**, 33–53 (1993).
44. Hoberg, E. P., Monsen, K. J., Kutz, S. & Blouin, M. S. Structure, biodiversity, and historical biogeography of nematode faunas in holarctic ruminants: morphological and molecular diagnoses for *Teladorsagia boreoarcticus* n. sp. (Nematoda: Ostertagiinae), a dimorphic cryptic species in muskoxen (*Ovibos moschatus*). *J. Parasitol.* **658**, 910–934 (1999).
45. Egwang, T. G. & Slocombe, J. O. Evaluation of the Cornell-Wisconsin centrifugal flotation technique for recovering trichostrongylid eggs from bovine feces. *Can. J. Comp. Med.* **46**, 133 (1982).
46. Foreyt, W. J. *Veterinary Parasitology: Reference Manual* 5th edn, 235 (Blackwell Publishing, 1997).
47. Kutz, S. J. *et al.* Parasites in ungulates of Arctic North America and Greenland: a view of contemporary diversity, ecology, and impact in a world under change. *Adv. Parasitol.* **79**, 99–252 (2012).
48. R core team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
49. Sanchez G., Trinchera L., & Russolillo G. plsmpm: Partial Least Squares Path Modeling (PLS-PM). R package version 0.5.1, <https://CRAN.R-project.org/package=plsmpm> (2024).
50. Sanchez, G. PLS Path Modeling with R. (Trowchez Editions, Berkeley). <http://www.gastonsanchez.com/PLSPathModelingwithR.pdf> (2023)
51. Aleuy, O. A., Serrano, E., Ruckstuhl, K. E., Hoberg, E. P. & Kutz, S. Parasite intensity drives fetal development and sex allocation in a wild ungulate. *Sci. Rep.* **10**, 1–10 (2020).
52. Tenenhaus, M., Vinzi, V. E., Chatelin, Y. M. & Lauro, C. PLS path modeling. *Comput. Stat. Data Anal.* **48**, 159–205 (2005).
53. Korsholm, H. & Olesen, C. R. Preliminary investigations on the parasite burden and distribution of endoparasite species of muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus groenlandicus*) in West Greenland. *Rangifer* **13**, 185–189 (1993).
54. Samuel, W. M. & Gray, D. R. Parasitic infection in muskoxen. *J. Wildl. Manag.* **38**, 775–782 (1974).
55. Hughes, J., Albon, S. D., Irvine, R. J. & Woodin, S. Is there a cost of parasites to caribou?. *Parasitology* **136**, 253–265 (2009).
56. Davidson, R. K. *et al.* Sentinels in a climatic outpost: Endoparasites in the introduced muskox (*Ovibos moschatus wardi*) population of Dovrefjell. *Norway. Int. J. Parasitol. Parasites Wildl.* **3**, 154–160 (2014).
57. Dickinson, E. R., Orsel, K., Cuyler, C. & Kutz, S. J. Life history matters: Differential effects of abomasal parasites on caribou fitness. *Int. J. Parasitol.* **53**, 221–231 (2023).
58. Hoar, B. M., Eberhardt, A. G. & Kutz, S. J. Obligate larval inhibition of *Ostertagia grueneri* in *Rangifer tarandus*? Causes and consequences in an Arctic system. *Parasitology* **139**, 1339–1345 (2012).
59. Nazarbeigy, M., Yakhchali, M. & Pourahmad, F. First molecular characterization and seasonality of larvae of trichostrongylid nematodes in arrested development in the abomasum of Iranian naturally infected sheep. *Acta Parasitol.* **66**, 193–198 (2021).

60. Idland, L. *et al.* Occurrence of faecal endoparasites in reindeer (*Rangifer tarandus*) in two grazing areas in northern Norway. *Acta Vet. Scand.* **63**, 1–12 (2021).
61. Albon, S. D. *et al.* The role of parasites in the dynamics of a reindeer population. *Proc. R. Soc. B* **269**, 1625–1632 (2002).
62. Stien, A. *et al.* The impact of gastrointestinal nematodes on wild reindeer: Experimental and cross-sectional studies. *J. Anim. Ecol.* **71**, 937–945 (2002).
63. Aleuy, O. A., Peacock, S. J., Molnár, P. K., Ruckstuhl, K. E. & Kutz, S. J. Local thermal adaptation and local temperature regimes drive the performance of a parasitic helminth under climate change: The case of *Marshallagia marshalli* from wild ungulates. *Glob. Change Biol.* **29**, 6217–6233 (2023).
64. Carlsson, A. M. *et al.* Little impact of over-winter parasitism on a free-ranging ungulate in the high Arctic. *Funct. Ecol.* **32**, 1046–1056 (2018).
65. Johnson, P. T. & Hoverman, J. T. Parasite diversity and coinfection determine pathogen infection success and host fitness. *Proc. Natl. Acad. Sci.* **109**, 9006–9011 (2012).
66. Ezenwa, V. O., Stefan Ekernas, L. & Creel, S. Unravelling complex associations between testosterone and parasite infection in the wild. *Funct. Ecol.* **26**, 123–133 (2012).
67. Murray, D. L., Cary, J. R. & Keith, L. B. Interactive effects of sublethal nematodes and nutritional status on snowshoe hare vulnerability to predation. *J. Anim. Ecol.* **66**, 250–264 (1997).
68. Garnier, R. *et al.* Joint associations of blood plasma proteins with overwinter survival of a large mammal. *Ecol. Lett.* **20**, 175–183 (2017).
69. Adamczewski, J. Z., Flood, P. F. & Gunn, A. Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). *J. Zool.* **241**, 245–269 (1997).
70. Clutton-Brock, T., Albon, S. & Guinness, F. Fitness costs of gestation and lactation in wild mammals. *Nature* **337**, 260–262 (1989).
71. Froy, H., Walling, C. A., Pemberton, J. M., Clutton-Brock, T. H. & Kruuk, L. E. B. Relative costs of offspring sex and offspring survival in a polygynous mammal. *Biol. Lett.* **12**, 20160417 (2016).
72. Albery, G. F. *et al.* Fitness costs of parasites explain multiple life-history trade-offs in a wild mammal. *Am. Nat.* **197**, 324–335 (2021).
73. Robbins, C. T. & Robbins, B. L. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *Am. Nat.* **114**, 101–116 (1979).
74. O’Callaghan, D. & Boland, M. P. Nutritional effects on ovulation, embryo development and the establishment of pregnancy in ruminants. *Anim. Sci.* **68**, 299–314 (1999).
75. Douhard, M. *et al.* Maternal longevity and offspring sex in wild ungulates. *Proc. R. Soc. B* **286**(1896), 20181968 (2019).
76. Chin, W. W. & Newsted, P. R. Structural equation modeling analysis with small samples using partial least squares. *Stat. Strateg. Small Samp. Res.* **1**, 307–341 (1999).
77. Hansen, B. B. *et al.* Warmer and wetter winters: Characteristics and implications of an extreme weather event in the High Arctic. *Environ. Res. Lett.* **9**, 114021 (2014).
78. Peacock, S. J., Kutz, S. J., Hoar, B. M. & Molnár, P. K. Behaviour is more important than thermal performance for an Arctic host-parasite system under climate change. *R. Soc. Open Sci.* **9**, 220060 (2022).
79. Di Francesco, J. *et al.* Documenting indigenous knowledge to identify and understand the stressors of muskoxen (*Ovibos moschatus*) in Nunavut, Canada. *Arctic* **74**, 418–436 (2021).
80. Rempel, R. S. *et al.* Modeling cumulative effects of climate and development on moose, wolf, and caribou populations. *J. Wildl. Manag.* **85**, 1355–1376 (2021).
81. Post, E. *et al.* Ecological dynamics across the Arctic associated with recent climate change. *Science* **325**, 1355–1358 (2009).
82. Mallory, C. D. & Boyce, M. S. Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environ. Rev.* **16**, 13–25 (2018).
83. Van Beest, F. M., López-Blanco, E., Hansen, L. H. & Schmidt, N. M. Extreme shifts in habitat suitability under contemporary climate change for a high-Arctic herbivore. *Clim. Change* **176**, 31 (2023).

Acknowledgements

Sachs Harbour Hunters and Trappers Committee and the Inuvialuit Development Corporation supported the collection of information and samples during the commercial harvests. John Nagy was instrumental in initiating this work, planning and coordinating sample collection, and in the overall monitoring of this muskox population. Lizz Gordon, Brent Wagner, Nic Larter and Rehkah Trembath for the many hours they spent digesting the abomasa and counting parasites. Lydden Polley and Eric Hoberg for their support during data collection. Funding for this research was provided by Inuvialuit Final Agreement Implementation Funds, GNWT. Environment and Climate Change Canada (ECCC) supported ED.

Author contributions

M.B, S.J.K, and B.E conceived the study design. S.J.K, B.E conducted the data collection. E.R.D, C.N.O, E.S and S.J.K designed and performed the data analysis and interpretation of the results. E.R.D wrote the first draft of the manuscript. All authors contributed critically to the final draft.

Funding

Funding for this research was provided by Inuvialuit Final Agreement Implementation Funds, GNWT. Environment and Climate Change Canada (ECCC) supported ED.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to E.R.D.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2024