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INFORMING DECISION-MAKING WITH INDIGENOUS AND LOCAL KNOWLEDGE AND SCIENCE

Research Article

Merging indigenous and scientific knowledge links climate with the growth of a large migratory caribou population

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Abstract

1. Climate change in the Arctic is two to three times faster than anywhere else in the world. It is therefore crucial to understand the effects of weather on keystone arctic species, particularly those such as caribou (*Rangifer tarandus*) that sustain northern communities. Bridging long-term scientific and indigenous knowledge offers a promising path to achieve this goal, as both types of knowledge can complement one another.
2. We assessed the influence of environmental variables on the spring and fall body condition of caribou from the Porcupine Caribou Herd. This herd ranges in the Yukon and Northwest Territories (Canada) and Alaska (USA), and is the only large North American herd that has not declined since the 2000s. Using observations recorded through an indigenous community-based monitoring programme between 2000 and 2010, we analysed temporal trends in caribou condition and quantified the effects of weather and critical weather-dependent variables (insect harassment and vegetation growth), on spring (n = 617 individuals) and fall (n = 711) caribou condition.
3. Both spring and fall body condition improved from 2000 to 2010, despite a continuous population increase of ca. 3.6% per year. Spring and fall caribou condition were influenced by weather on the winter and spring ranges, particularly snow conditions and spring temperatures. Both snow conditions and spring temperatures improved during our study period, likely contributing to the observed caribou population increase. Insect harassment during the previous summer and the frequency of icing events also influenced caribou condition.
4. *Synthesis and applications*. Our study shows how untangling the relative influences of seasonal weather variables allows a much better understanding of variation in seasonal body condition of caribou. It indicates that a large migratory caribou population can grow and improve condition in a global context of caribou decline

and climate warming, thereby warning against generalizations about the influence of climate on all caribou populations. Finally, it testifies how data from indigenous community-based monitoring can remarkably improve ecological understanding of wildlife sustaining human communities. Where possible, we recommend management practices that respectfully engage with indigenous community-based monitoring, as this can enhance knowledge and relationships with communities, both prerequisites of successful resource management.

KEYWORDS

body condition, caribou, community-based monitoring, demography, icing events, indigenous knowledge, seasonal, snow

1 | INTRODUCTION

Climate change has occurred at an unprecedented rate in the circumpolar North (IPCC, 2013). Ecologists and members of northern indigenous communities have thus been increasingly interested in assessing how climate and weather affect the dynamics of arctic animal populations, which are adapted to cold and short growing seasons (Berteaux, Réale, McAdam, & Boutin, 2004). Climate change is expected to greatly affect their population dynamics, but spatial and temporal variations in climate and weather could affect species differently (Mysterud, Yoccoz, Langvatn, Pettorelli, & Stenseth, 2008).

The highly abundant pan-Arctic *Rangifer tarandus* (L., 1758; including caribou and reindeer) is a keystone tundra species (COSEWIC, 2016) at the heart of the cultures and livelihoods of many arctic indigenous peoples (Kofinas et al., 2003). In North America, migratory caribou herds undergo large-scale population fluctuations (Gunn, 2003). However, the accelerated declines observed in most herds since 2000s (CARMA, 2017) raise serious concerns (Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011). Climate change could explain this quasi general decline via a trophic mismatch between plant phenology and caribou needs (Post & Forchhammer, 2008), an increased occurrence of ice-locked winter pastures (Hansen, Aanes, Herfindal, Kohler, & Sæther, 2011), or decreased pasture quality (Fauchald, Park, Tømmervik, Myneni, & Hausner, 2017).

Owing to the ecological and cultural importance of caribou, a detailed understanding of how environmental conditions affect their population dynamics is urgently needed. Body condition is a key variable to understand this link in large herbivores (Barboza, Parker, & Hume, 2009) because it represents the energy reserves that an animal possesses to sustain daily and seasonal activities (Barboza et al., 2009; Schulte-Hostedde, Zinner, Millar, & Hickling, 2005). Therefore, body condition correlates with overwinter survival (Parker, Barboza, & Gillingham, 2009), age at first reproduction (Festa-Bianchet, Gaillard, & Jorgenson, 1998) and pregnancy probability (Russell, Gerhart, White, & Van De Wetering, 1998). Although different measurements are used to assess ungulates' body condition, including body mass, body size and body reserves (e.g. fat and protein; Barboza & Parker, 2008), body mass is best to describe caribou condition (Taillon, Brodeur, Festa-Bianchet, & Côté, 2011).

Environmental impacts of climate change can affect caribou condition in various ways. During winter and spring, snow depth increases costs of locomotion and reduces access to forage (Adams, 2005; Fancy & White, 1987). Likewise, events such as freeze–thaw, freezing rain and rain-on-snow create ice layers and ground ice that impede access to forage (Hansen et al., 2011; Solberg et al., 2001). During summer, low winds and warm temperatures promote insect harassment, leading caribou to expend energy avoiding insects, thus reducing feeding time (Mörschel, 1999; Weladji, Holand, & Almoy, 2003). Yet, high temperatures can enhance plant productivity and quality, improving forage conditions (Lenart, Bowyer, Hoef, & Ruess, 2002). Environmental variables affecting body condition are thus likely to differ across seasons, with different consequences on demography (Albon et al., 2017; Figure 1).

Investigating the effects of seasonal meteorological variables on caribou condition over different seasons requires long-term datasets. In the North American Arctic, long-term and uninterrupted scientific data about migratory caribou are mostly lacking (Festa-Bianchet et al., 2011). Monitoring programmes involving observations from northern indigenous hunters, however, hold remarkable potential for mobilizing indigenous knowledge about caribou. Hunters have been looking at the body condition of caribou for their entire life, and for generations. They often live year-round in caribou habitat, spend months in direct contact with the herds and have access to many harvested carcasses. Hunters therefore own a thorough expertise in evaluating the condition of animals. This expertise is exemplified by the indicators of body condition that hunters have developed for evaluating caribou health before and after harvest (Kofinas et al., 2003; Lyver & Lutsël K'é Dene First Nation, 2005).

Here, we worked with a unique long-term dataset from an indigenous community-based monitoring programme that has documented spring and fall body condition annually since 2000 for the Porcupine Caribou Herd (PCH; see Appendix S1). The PCH (Alaska, Yukon and Northwest Territories; *Rangifer tarandus granti*) is one of the largest migratory caribou populations in the world (CARMA, 2017). It occupies a region experiencing amongst the most dramatic climatic changes

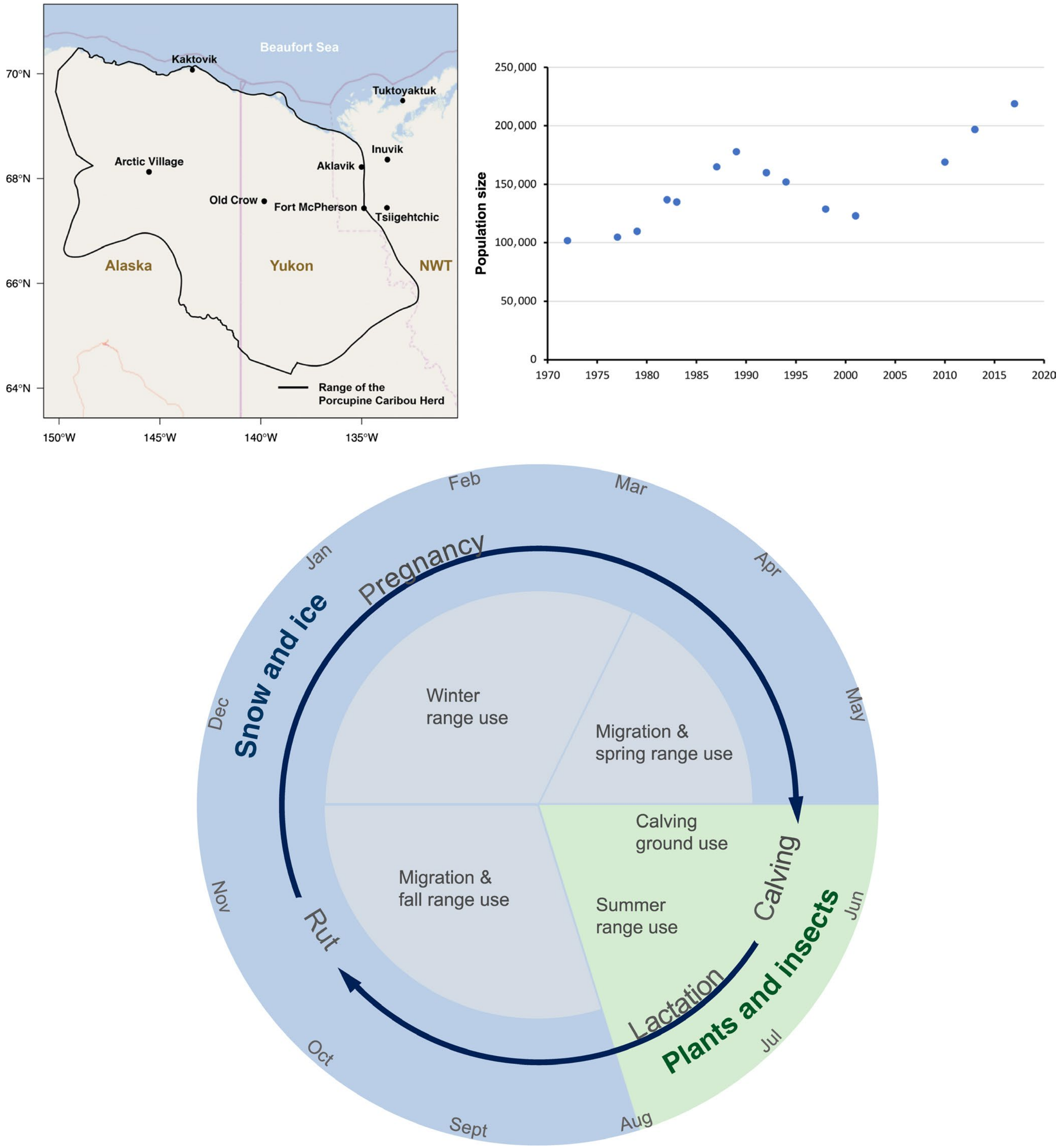

FIGURE 1 Range and population size of the Porcupine Caribou Herd (top), and annual range use, reproductive cycle and environmental factors affecting body condition of migratory caribou (bottom). During fall, winter and early spring (blue), ice and snow impact body condition through their effects on thermoregulation, locomotion and access to forage. During late spring and summer (green), vegetation productivity and insect harassment impact body condition through energy availability and expenditures, respectively

on Earth (IPCC, 2013). Paradoxically, it is the only migratory caribou herd in North America that increased in size over the last two decades (CARMA, 2017). To understand this exceptional case, our aim was first to analyse temporal variations in the annual spring and fall condition of PCH caribou between 2000 and 2010, and then to quantify the influence of local seasonal environmental variables and large-scale climate proxies on spring and fall caribou condition over the same period. We anticipated that spring and fall condition would decrease over time as a response to increase in caribou density (Bonenfant et al., 2009). We also expected spring body condition to be mostly influenced by winter precipitation (Fancy & White, 1987; Hansen et al., 2011) and fall body condition by summer temperature (van der Wal & Stien, 2014).

2 | MATERIALS AND METHODS

2.1 | Study area and caribou population

The PCH ranges over ca. 250,000 km^2 in the northern Yukon and Northwest Territories (Canada) and Alaska (USA; Figure 1). During winter, the herd uses the southern part of its range, where snow is shallower, thus facilitating locomotion and access to lichens, their primary winter forage (Russell, Martell, & Nixon, 1993). During spring, the herd migrates north to reach the calving grounds on the arctic coastal plain of Alaska and northern Yukon (Russell et al., 1993). Common forage plants during spring, calving and summer include mosses, graminoids (especially *Eriophorum* spp.) and deciduous shrubs (Russell et al., 1993). Indigenous communities belonging to the Inupiat, Inuvialuit and Gwich'in cultures are located within or close to the PCH range. These include the communities of Kaktovik and Arctic Village (Alaska), Old Crow (Yukon) and Aklavik, Fort McPherson, Inuvik, Tsiigehtchic and Tuktoyaktuk (Northwest Territories). The PCH has been a central component of the culture and diet of these communities during thousands of years (Pilon, 2017). According to aerial censuses, the size of this herd has fluctuated over time (Figure 1), with an increase since 2001 and spring became earlier and warmer between 2000 and 2010 (see Figure S1).

2.2 | Hunters' monitoring of caribou condition

Seasonal body condition of PCH caribou was monitored through the annual community-based monitoring programme of the Arctic Borderlands Ecological Knowledge Society (ABEKS; ABEKS, 2014). Since 1998, ABEKS has conducted its monitoring programme through a survey questionnaire covering topics such as caribou, berries, birds, weather and fish. This programme involves annually 10 PCH user communities and is conducted by local indigenous monitors trained by experienced community monitors and the ABEKS' coordinator (Appendix S1). Monitors identify annually 15–20 local experts from their community who are active on the land (ABEKS, 2014). Each expert is given a personal identity number allowing anonymous tracking of answers.

We analysed answers to a question asking local experts to report their general impression regarding the average body condition of caribou harvested and/or observed during fall and spring. Respondents chose between 'Poor/skinny', 'Fair/mix of poor and fat', 'Good/excellent' and 'Don't know'. These qualitative categories were developed based on discussions with Porcupine Caribou hunters who use several criteria to assess caribou condition (Appendix S1). In the following, we refer to these categories as poor (a), average (b) and excellent (c), respectively ('Don't know' answers were ignored). During our study, ABEKS data were available for the 2000–2010 period, yielding 711 answers for the fall and 617 answers for the spring, including 10 communities in both seasons. Hunter evaluations were positively correlated with scientific measurements (Appendix S2).

2.3 | Large-scale climate

We used the Arctic Oscillation index (AO; National Weather Service, 2017) to describe broad-scale climate. In our study area, the 'positive' phase of AO corresponds to warmer and wetter winters, with increased snow, whereas the 'negative' phase corresponds to colder, drier and less snowy winters (Thompson & Wallace, 1998). We averaged monthly AO anomalies to obtain an annual AO index for 2000–2010. Because the AO index is most variable during winter (Zhou, Miller, Wang, & Angell, 2001), we also calculated annual winter (January–March) averages (hereafter identified as AOw) using daily AO anomalies for 2000–2010.

2.4 | Local weather over the winter and spring caribou ranges

Weather data from meteorological stations were sparse in our study area. We thus used the CircumArctic *Rangifer* Monitoring and Assessment (CARMA) network's caribou range climate database (https://carma.caff.is/; Russell et al., 2013). The CARMA database was developed using NASA's MERRA database (NASA, 2017), containing remotely sensed daily averaged climate data with a spatial resolution of 0.50° Lat. × 0.66° Long. To construct the CARMA caribou range database, shapefiles of seasonal PCH ranges, estimated through satellite collared animals, were overlapped with MERRA's gridded climate variables using ArcGIS version 10 (ESRI, 2010; Russell et al., 2013). This allowed calculating daily weather variables specific to the range used by the PCH during the fall (16 August–30 November), winter (1 December–31 March), spring (1 April–31 May), calving (1 June–21 June) and summer (22 June–15 August; Cai, Russell, & Whitfield, 2011; Table S1). From the CARMA database, we calculated 19 seasonal weather variables describing snow, temperature and icing conditions susceptible to impact caribou condition (Tables S2 and S3).

The calculated variables were numerous and often correlated. To reduce the number of variables to below the number of years recorded (n = 11), we eliminated variables that were highly correlated (r > .7; Table S2), retaining only one representative variable. We log-transformed the variable 'freezing-rain falling on the ground on the winter range' to meet assumptions of normality and homogeneity of variance. We then pooled remaining variables according to two categories: (a) variables pertaining to snow and temperature, (b) variables pertaining to icing events. We then performed a separate principal component analysis (Jolliffe, 2005) to transform correlated variables into uncorrelated principal components (PCs) for each category. We determined the number of PCs to be used as final variables in each model based on the scree test method (relying on the sharp decline in consecutive eigenvalues (Cattel, 1966) and eigenvalues >1.0 (Jolliffe, 2005)). This resulted in two PCs describing snow/temperature conditions ('PCsnow1' and 'PCsnow2') and one PC describing icing events ('PCice1'; see Table 1 for interpretation of each PC).

TABLE 1 Description of the principal components (PCs) used as climate indices

Variable	Description	Meaning of component	% of variance explained	Cumul. % of variance explained
PCsnow1	Temperature and early melt	Greater scores represent years with a longer snow season (late melting date), deeper snow in winter and spring, and colder temperatures	61.5	61.5
PCsnow2	Variability in snow depth	Greater scores represent years with more variability in snow depth during winter, as well as shallower snow on the winter range	24.5	86.0
PCice1	Icing events	Greater scores represent years with more icing events in general and especially more freeze–thaw events on the winter range	48.0	48.0

2.5 | Proxies of vegetation and insect conditions on the calving and summer ranges

Temperature is a strong driver of plant growth in the Arctic. We used effective growing degree-days (GDD; cumulative values above 5°C, available from CARMA; Table S1) as a proxy to capture variability in vegetation productivity and phenology (e.g. Albon et al., 2017; Gamon, Huemmrich, Stone, & Tweedie, 2013). To reflect differential forage availability across periods, we used cumulative GDD from 1 January to 31 May (when caribou leave the spring range; 'GDDMay'), from 1 January to 21 June (plant productivity on the calving range; 'GDDJune') and from 1 January to 15 August (plant productivity over the entire summer; 'GDDAugust'). GGDJune and GDDAugust were strongly positively correlated ($r = .86$); thus, we only retained GDDMay and GDDJune in further analyses. To measure the level of insect harassment during calving and summer, we used the daily oestrid harassment index from 1 June to 15 August (available from CARMA; Table S1). This insect harassment index (IHI) is a proxy of insect harassment calculated from temperature and wind data (Mörschel, 1999; Weladji et al., 2003).

Since IHI was positively correlated with GDDJune ($r = .77$), we never used both variables in the same model. Both GDD and IHI were measured in the summer prior to measures of body condition, meaning that both variables were measured at t−1 for the spring condition (see Table S4). Both GDD and IHI were standardized to be comparable with the PCs scores (Schielzeth, 2010).

2.6 | Statistical analyses

We used R software version 3.4.2 (R Development Core Team, 2017). To investigate temporal trends in the spring and fall caribou condition, we used Pearson's product-moment correlations for normally distributed samples (cor.test function) to test for association between years and both spring and fall annual average body condition. To assess the effects of large-scale climate, local weather, vegetation productivity and insect harassment on spring and fall caribou condition, we used cumulative link mixed models (function clmm2, ordinal package; Christensen, 2015a). CLMMs, also known as 'ordinal regression models', allow for analysis of ordered categorical response variables. They calculate the probability of an observation to fall into a certain category according to variations in explanatory variables, while considering the effects of random factors (Christensen, 2015b). We included 'community' as a random intercept to control for repeated observations within a community each year. A CLMM assumes proportional odds or equal slopes, meaning that the slope estimate representing the probability of passing from one category to another with changes in an explanatory variable is held constant (Christensen, 2015b). We used the 'nominal' option to relaxes this assumption when it was violated, allowing slope estimates to vary according to response categories (Christensen, 2015b). Thus, the model estimated two slopes instead of one, one for the probability of changing from condition '1' to '2' and one for changing from '2' to '3'.

Because we were dealing with numerous explanatory variables, we developed candidate models using a distinctive step approach using four steps for both spring and fall. In all steps, we excluded variable combinations with correlations of $r > .50$. In step I, we built candidate models assessing the effect of large-scale climate on body condition (Tables S4 and S5). In step II, we built models assessing the influence of locomotion and thermoregulation costs during winter/spring season on body condition (PCsnow1, PCsnow2 and PCice1). In step III, we built models assessing impacts of environmental conditions reflecting vegetation productivity and insect harassment during calving/summer season on body condition (GDDMay, GDDJune and IHI). For these three steps, we used an Akaike information criterion approach, considering models with $\Delta\text{AIC} \le 2$ as equivalently supported (Burnham & Anderson, 2002). In step IV, we built final candidate models with variables from all the supported models in steps I to III and again considered final models with $\Delta\text{AIC} \le 2$ as supported. Parameter estimates and 95% confidence intervals (CIs) for the final equivalent models are in Tables S6 and S7.

3 | RESULTS

3.1 | Variation in caribou condition over time

Despite the increase in population size with time, spring and fall caribou condition increased significantly during the study period (Pearson's r [95% CI]: spring = 0.86 [0.54; 0.96], $n = 11$; fall = 0.84 [0.48; 0.96], $n = 11$; Figure 2).

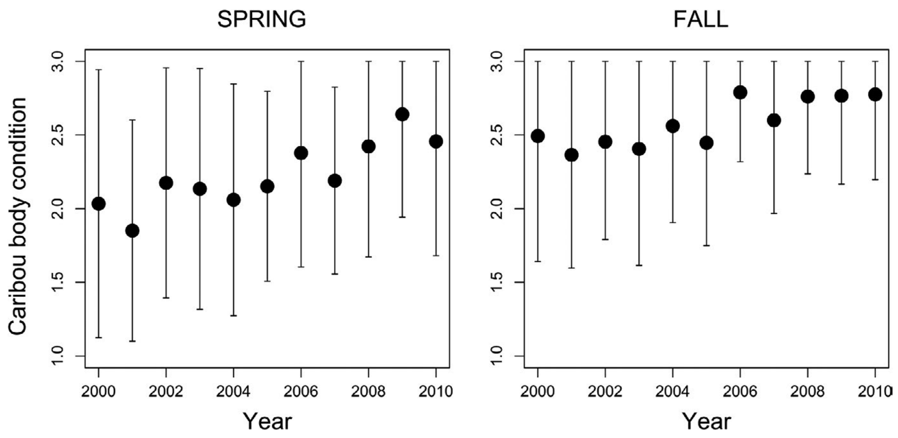

FIGURE 2 Changes in the average spring and fall caribou condition of the Porcupine Caribou Herd between 2000 and 2010

TABLE 2 Model selection to explain variation in spring body condition of the Porcupine Caribou Herd (2000–2010)

	Models	K	AIC	ΔAIC	AICweight
1	*PCsnow1* + PCsnow2 + PCice1 + IHI$_{yr-1}$**	*9*	*1,096.91*	*0.00*	*0.32*
2	**PCsnow1* + PCsnow2 + IHI$_{yr-1}$***	**8**	**1,096.98**	**0.07**	**0.31**
3	*AO + PCsnow1* + PCsnow2 + PCice1 + IHI$_{yr-1}$**	*10*	*1,098.63*	*1.72*	*0.14*
4	AO + PCsnow1* + PCsnow2 + IHI$_{yr-1}$*	9	1,098.96	2.05	0.12
5	AO + GDDMay$_{yr-1}$ + PCsnow2 + PCice1 + IHI$_{yr-1}$*	9	1,100.47	3.56	0.05
6	AO + GDDMay$_{yr-1}$ + PCsnow2 + IHI$_{yr-1}$*	8	1,101.46	4.55	0.03
7	GDDMay$_{yr-1}$ + PCsnow2 + PCice1 + IHI$_{yr-1}$*	8	1,103.70	6.79	0.02
8	AO + GDDMay$_{yr-1}$ + IHI$_{yr-1}$*	7	1,104.19	7.27	0.01
9	GDDMay$_{yr-1}$ + PCsnow2 + IHI$_{yr-1}$*	7	1,105.79	8.88	0.00
10	GDDMay$_{yr-1}$ + IHI$_{yr-1}$*	6	1,109.10	12.18	0.00
11	PCsnow1* + PCsnow2 + PCice1	7	1,112.21	15.30	0.00
12	PCsnow1* + PCsnow2	6	1,112.44	15.53	0.00
13	AO + PCsnow1* + PCsnow2 + PCice1	8	1,114.21	17.29	0.00
14	AO + PCsnow1* + PCsnow2	7	1,114.28	17.37	0.00
15	AO	4	1,144.53	47.62	0.00
16	Null	3	1,149.47	52.56	0.00

Note: The selected model is indicated in bold; equivalently supported but less parsimonious models are in italic (based on difference in Akaike information criterion [AIC]).

Abbreviations: AO, annual Arctic Oscillation index; GDDMay, cumulative growing degree-days on 31 May; GDDJune, cumulative growing degree-days on 21 June; IHI, insect harassment index; PCsnow1, PCsnow2, PCice1, see Table 1; yr-1, variable measured the previous year; *, variables with a nominal effect (see Section 2).

3.2 | Spring body condition

According to the most parsimonious model selected (#2, Table 2), spring body condition was correlated to the IHI during the previous summer (IHI$_{yr-1}$) and winter severity (PCsnow1 and PCsnow2). When IHI$_{yr-1}$ more than tripled, the probability of caribous' being rated in 'excellent' condition declined by 44% (from 0.45 to 0.25), 'average' increased by 44% (from 0.45 to 0.65) and 'poor' remained constant at about 0.10 (Figure 3a). High PCsnow1 scores also reduced the probability of caribou being rated in good condition. When cumulated snow doubled, average temperature in spring dropped from −2°C to −10°C, and spring was delayed by 28 days, the probability of caribous' being rated in 'excellent' condition decreased by 64% (from 0.55 to 0.20), 'average' increased by 40% (from 0.43 to 0.60) and 'poor' rose by a factor 10 (from 0.02 to 0.20; Figure 3b). High PCsnow2 scores also reduced the probability of caribous' being rated in good condition, but to a lesser extent than insect harassment and harsh winters (Figure 3). When the coefficient of variation in winter snow depth almost tripled, the probability of caribou's being rated 'excellent' declined by 25% (from 0.40 to 0.30), 'poor' tripled (ca. 0.05 to 0.15) and 'average' remained relatively constant at 0.55 (Figure 3c). Equivalent but

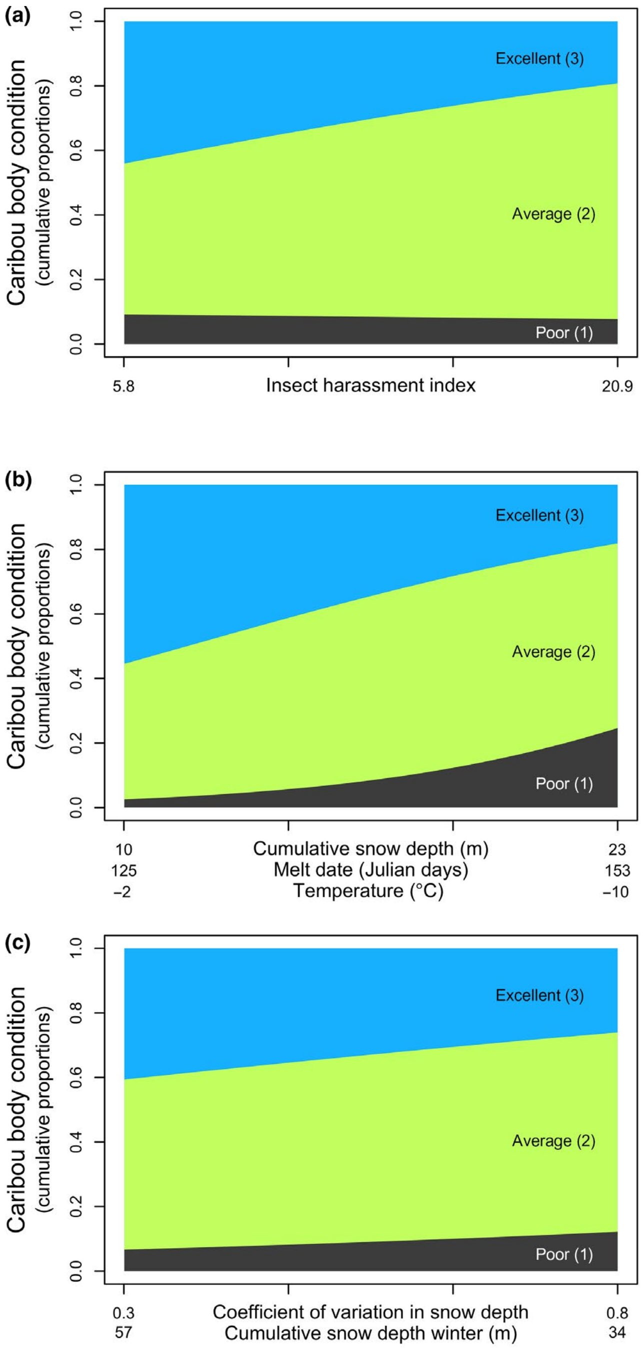

FIGURE 3 Relationship between weather conditions occurring on the range of the Porcupine Caribou Herd, and local experts' body condition assessment during spring, 2000–2010. Panels show the cumulative probabilities (proportion) of experts rating caribou as being in excellent, average or poor condition in relation to a proxy of insect harassment index (a), cumulative snow depth on the spring range, melt date and temperature (b) and variation in snow depth and cumulative snow depth on the winter range (c)

less parsimonious models identified icing events occurring during winter and spring (PCice1) and the AO has having a potential influence on spring body condition (Table 2), but estimates for these variables were small and imprecise, with their 95% CI overlapping 0 (Table S6).

3.3 | Fall body condition

According to the most parsimonious model selected (Table 3), fall body condition was also influenced by winter severity. The probability of caribous' being rated in good condition was affected by PCice1, PCsnow1 and PCsnow2 (Figure 4; Table S7). When the number of days with freeze–thaw events recorded on the winter range increased from 12 to 34, the probability of caribous' being rated 'excellent' declined by 25% (from 0.73 to 0.55), 'average' increased by 60% (from 0.25 to 0.40) and 'poor' increased by 150% (0.02 to 0.05; Figure 4a). When cumulated snow doubled on the spring range, average temperatures in the spring dropped from −2°C to −10°C, and spring was delayed by 28 days, the probability of caribous' being rated 'excellent' declined by 25% (from 0.73 to 0.55), 'average' increased by 60% (from 0.25 to 0.40) and 'poor' increased by 150% (0.02 to 0.05; Figure 4b). Finally, when the coefficient of variability in snow depth tripled over the previous winter, the probability of caribous' being rated 'excellent' decreased by 31% (from 0.75 to 0.52), 'average' increased by 54% (from 0.24 to 0.37) and 'poor' increased by a factor of 10 (0.01 to 0.11; Figure 4c).

Two equivalent models also presented support to the data, with model 1 having almost twice greater support than model 2 (Table 3). Model 1 differed by including GDDMay instead of PCsnow1 and was less parsimonious simply because GDDMay had a nominal effect, increasing by 1 the number of parameters estimated. GDDMay and PCsnow1 were highly negatively correlated with (*r* = −.90), suggesting these two variables have a similar influence on fall condition. Indeed, GDDMay had a strong influence (Table S7): with an increase of 58 GDD in May, the probability of caribous' being rated 'excellent' increased by 55% (from 0.55 to 0.85), 'average' decreased by 70% (from 0.43 to 0.13) and 'poor' remained relatively constant (0.02; Figure 4d).

4 | DISCUSSION

Our findings show that bridging long-term indigenous observations about caribou condition with climate data can considerably improve our understanding of the ecology of a growing migratory caribou herd. Two results are of particular interest. First, though we expect body condition to decrease with increasing density (Bonenfant et al., 2009), spring and fall caribou condition improved over time despite population growth. Second, both spring and fall caribou condition were influenced by weather on the winter and spring ranges, particularly snow conditions and spring temperatures. Most importantly, our results reiterate how indigenous knowledge can provide reliable data on caribou at temporal and spatial scales that are not easily monitored by scientists. In northern Canada, numerous studies have documented traditional knowledge about caribou that contributed to a wealth of detailed descriptions about caribou distribution, movement and population fluctuations (e.g. Ferguson, Williamson, & Messier, 1998; Parlee, Manseau, & Lutsël K'é Dene First Nation, 2005). Our study takes a different approach that is less descriptive, but nevertheless based on one important strength of indigenous knowledge: repeated observations

TABLE 3 Model selection to explain variation in fall body condition of the Porcupine Caribou Herd (2000–2010)

	Models	K	AIC	ΔAIC	AICweight
1	*GDDMay* + PCsnow2* + PCice1*	*8*	*1,020.30*	*0.00*	*0.40*
2	**PCsnow1 + PCsnow2* + PCice1**	**7**	**1,021.27**	**0.97**	**0.24**
3	*AO + GDDMay* + PCsnow2* + PCice1*	*9*	*1,021.70*	*1.40*	*0.20*
4	AO + PCsnow1 + PCsnow2* + PCice1	8	1,023.17	2.87	0.09
5	AO + GDDMay* + PCsnow2* + GDDJune	9	1,025.69	5.39	0.03
6	GDDMay* + PCsnow2* + GDDJune	8	1,025.85	5.55	0.03
7	PCsnow1 + PCsnow2* + GDDJune	7	1,027.91	7.61	0.01
8	AO + PCsnow1 + PCsnow2* + GDDJune	8	1,029.81	9.52	0
9	GDDMay* + GDDJune	6	1,033.79	13.49	0
10	AO + GDDMay* + GDDJune	7	1,035.43	15.14	0
11	AO	4	1,048.86	28.56	0
12	Null model	3	1,050.71	30.42	0

Note: See Table 2 for notations.

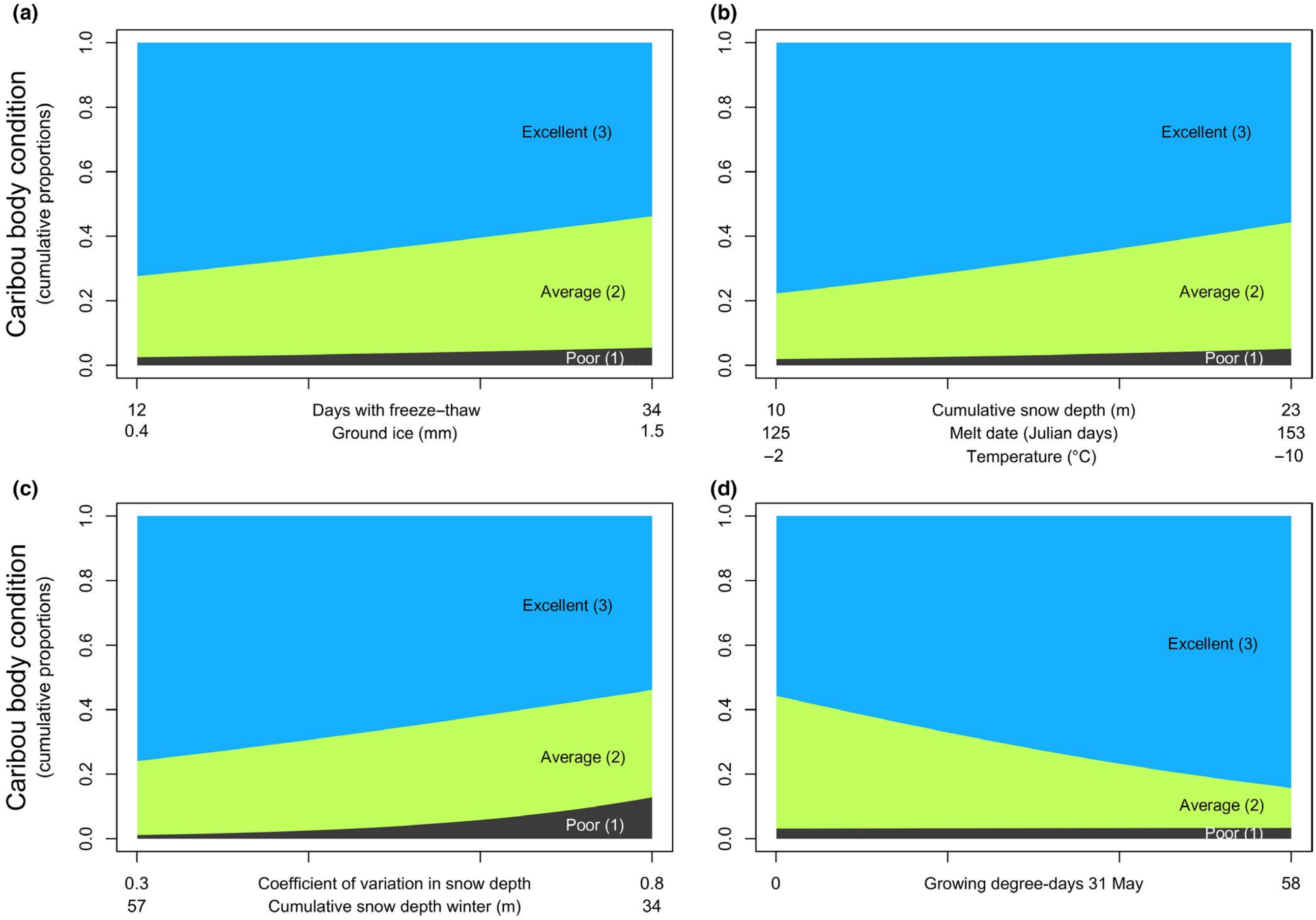

FIGURE 4 Relationship between weather conditions occurring on the range of the Porcupine Caribou Herd, and local experts' body condition assessment during fall, 2000–2010. Panels show the cumulative probabilities (proportion) of experts rating caribou as being in excellent, average or poor condition in relation to number of days with freeze–thaw events on the winter range and quantity of ground ice (a), cumulative snow depth on the spring range, melt date and temperature (b), variation in snow depth and cumulative snow depth on the winter range (c) and cumulative growing degree-days in May (d)

and evaluation of the surrounding environment. This approach allowed us to merges two very different long-term datasets using novel analytical tools.

Earlier studies of the PCH showed that parturition rate, calving rate and net calf production were not affected by population size (Griffith et al., 2002). Our results also suggest that density dependence might not be the main driving factor of body condition, at least for population sizes encountered during the decade studied. Because the PCH inhabits one of the northernmost ranges occupied by migratory caribou herds (CARMA, 2017), this finding supports the suggestion that negative density dependence declines with latitude (Bjørnstad, Falck, & Stenseth, 1995; Post, 2005). Nevertheless, we observed strong temporal trends during that decade towards warmer springs, earlier snow melt and shallower snow depths (see Figure S1). These weather trends are likely responsible for the improvement in spring and fall caribou condition in the PCH during that time period, and perhaps its population growth, and thereby could have compensated for density dependence (Albon et al., 2017).

Our results suggest that snow depth and its variation, temperature and melt date are fundamental drivers of spring and fall caribou condition in the PCH. Early calf survival and recruitment correlate with female caribou condition in late winter (Veiberg et al., 2017). By increasing by as much as 10 times the probability of caribou being in poor condition in spring, harsh snow conditions likely have large impacts on the PCH, as reported in other northern ungulates (Post & Stenseth, 1999; Solberg et al., 2001). The negative effects of a long snow season with deep snow during spring also had a carry-over effect on the subsequent fall. This supports previous evidence that PCH females could not compensate during summer for poor spring condition (Russell & McNeil, 2005), affecting fecundity rates in the fall (Russell et al., 1993). Furthermore, our study indicated that greater GDD in May increased the probability that caribou were in excellent fall condition. GDDMay was highly negatively correlated with the principal component representing snow depth, spring melting date and spring temperatures. Together, the influence of these two variables demonstrates that spring weather is a crucial determinant of fall caribou condition in the PCH, as shown in other ungulates (Couturier, Côté, Otto, Weladji, & Huot, 2009; Mysterud et al., 2008; Pettorelli et al., 2005).

While snow depth is a major determinant of caribou winter survival (Weladji, Klein, Holland, & Mysterud, 2002), the density, layering and hardness of snow can also affect forage availability by impeding digging and changing diet composition (Tyler, 2010). In our study, variability in snow depth was inversely correlated with cumulative snow depth and was one of the main variables negatively affecting caribou condition. Caribou overwinter in areas with shallower snow (Russell et al., 1993), but select habitat based on both snow depth and hardness (LaPerriere & Lent, 1977). We thus hypothesize that years with high snow variability represent years with hardest snow and perhaps greater snow density, resulting in a more difficult access to forage.

Icy conditions reducing or impeding access to forage will increase winter mortality and reduce fecundity (Hansen et al., 2013; Solberg et al., 2001). In the PCH, icing events affected fall body condition, with condition being reduced mostly by an increase in the number of freeze–thaw events occurring on the winter and spring ranges and in the amount of ground ice before snow arrival. Icing was included as a variable influencing spring condition in an equivalent but less parsimonious models, but this effect was weak and imprecise compared with winter severity and insect harassment (Tables S1 and S7). It is possible that the strong influence of these variables overrode the weaker influence of icing events, or that the power to detect this effect was reduced in the spring models because it included more parameters.

A combination of early spring and cool summer temperatures is optimal for reindeer juveniles as this increase vegetation quality and reduce insect harassment (Finstad & Prichard, 2000). Increased insect harassment due to climate warming was suggested as a cause of the PCH decline in the 1990s (Griffith et al., 2002). We found that summer insect harassment did not reduce the proportion of caribou found in excellent condition in the fall, but did so the following spring. This may seem surprising but could be explained by methodology. Our study focused on adult condition, whereas insect harassment mostly reduces fall condition in reindeer calves (Weladji et al., 2003). While calves were unlikely to be included in the fall data, we hypothesize that some soon-to-be yearlings might have been considered in hunters' evaluation in spring, as they are very similar to adults in size and appearance.

5 | CONCLUSIONS

Much remains to be understood about the direct and indirect effects of climate and weather on the dynamics of migratory caribou populations. Our study demonstrates how body condition at a seasonal scale provides a mechanistic link between weather and demography (Albon et al., 2017; Veiberg et al., 2017). While climate change was shown to have detrimental effects on *Rangifer* populations (Hansen et al., 2013), our results suggest these detrimental impacts are not ubiquitous (Uboni et al., 2016). Given that human disturbances can impact *Rangifer* populations more heavily than climate (Parlee, Sandlos, & Natcher, 2018; Uboni et al., 2016), population models including the cumulative impacts of weather and human development are much needed. This is very challenging considering that data on North American migratory caribou are riddled with gaps (Festa-Bianchet et al., 2011; Kofinas et al., 2003).

We hope our study will trigger broader interest in community-based monitoring of caribou. Engaging with indigenous resource users has broader implications than just additional data collection. This underlines the differences between scientific and traditional knowledge systems, and the persistent power dynamics in the natural resource management sector, where indigenous knowledge is prone to be co-opted (Nadasdy, 1999). These challenges, however, must not lead resource managers and communities to isolate themselves from each other. In this regard, community-based monitoring programmes, if truly inclusive of indigenous communities, offer opportunities to move forward. They can act as venues for scientists and land users to co-produce knowledge and to build long-term relationships based on trust and respect, the latter being a prerequisite for successful caribou conservation in northern Canada (Parlee et al., 2018).

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AUTHORS' CONTRIBUTIONS

C.A.G., S.H., D.B. and D.E.R. conceived the ideas; C.A.G. and S.H. designed and performed the analysis, with access to databases and new analytical ideas being provided by M.Y.S., D.E.R., T.P. and J.A.; C.A.G., S.H. and D.B. led the writing of the manuscript. All authors contributed critically to drafts and approved the final manuscript for publication.

DATA AVAILABILITY STATEMENT

All climate and climate-related environmental data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.wpzgmsbh4 (Gagnon et al., 2019). The authors were not allowed to publicly archive survey data from the ABEKS due to its sensitive nature relating to endangered species and human identity. Access to ABEKS data requires consent from indigenous communities involved in the project and the completion of a data request form which can be accessed via https://www.arcticborderlands.org/services. If you have any question, please contact the corresponding author at catherinealexandra.gagnon@erebia.ca

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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