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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Response of barren-ground caribou to advancing spring phenology

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Abstract

Phenological shifts are occurring in many ecosystems around the world. The capacity of species to adapt to changing phenology will be critical to their success under climate change scenarios. Failure to adjust migratory and reproductive timing to keep pace with the earlier onset of spring has led to negative demographic effects for populations of species across a variety of taxa. For caribou, there have been concerns that earlier spring green-up on calving areas might not be matched by earlier migration and parturition, potentially leading to a trophic mismatch with nutritional consequences for parturient and lactating caribou cows. However, there is limited evidence supporting these concerns. Here, we investigate the response of barren-ground caribou to changing spring phenology using data from telemetry and satellite imagery. From 2004 to 2016, we found that the average start of green-up on the calving area advanced by 7.25 days, while the start of migration advanced by 13.64 days, the end of migration advanced by 6.02 days, and the date of peak calving advanced by 9.42 days. Despite the advancing onset of green-up, we found no evidence for the development of a trophic mismatch because the advancing green-up coincided with earlier migration and calving by caribou. Changing snow cover on the late winter and migratory ranges was the most supported driver of advancing migratory behavior. The ability of caribou to adjust the timing of migratory and reproductive behavior in response to changing environmental conditions demonstrates the potential resilience of the species to some aspects of climate change.

Keywords Climate change · Migration · Trophic mismatch · *Rangifer tarandus* · Phenology

Introduction

For caribou and other migratory species, the purpose of migration is at least in part to increase fitness by moving to more suitable habitat for birthing and rearing young (Fryxell and Sinclair 1988; Heard et al. 1996; Alerstam et al. 2003). Factors that reduce the quantity and effectiveness of these important habitats or that disrupt important life history stages, such as migration or calving, can have severe negative consequences for wildlife (Brooks et al. 2002; Bolger et al. 2008; Hanski 2011). Although the most imminent threat for many caribou (*Rangifer tarandus*) populations remains anthropogenic disturbance (McLoughlin et al. 2003; Vors et al. 2007; Festa-Bianchet et al. 2011; Uboni et al. 2016), rapid environmental change also can modify habitat and disrupt species behaviors and interactions (Walther et al. 2002; Parmesan and Yohe 2003). A key concern regarding the effects of climate change on ecosystems is the alteration of ecological phenology, or the timing of life history events (Parmesan and Yohe 2003). In many species, the timing of high energetic or nutritional requirements, such as peak lactation in caribou, has evolved to coincide with peak nutrient availability in forage (Klein 1990; Stenseth and Mysterud 2002; Post et al. 2003; Williams et al. 2017). The loss of life history synchrony across trophic levels can result from the unequal response of species to environmental changes, and this deviation from phenological synchrony is often referred to as trophic mismatch (Durant et al. 2007). For caribou, it has been suggested that trophic mismatches could arise if the annual timing of green-up, corresponding to peak nitrogen concentration in forage species (Klein 1970, 1990; Chapin

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1980), advances with increasing temperatures and snowmelt, while the timing of parturition remains consistent or advances more slowly. These mismatches could reduce the temporal overlap between the availability of highly nutritious stages of forage plants and the timing of high-nutritional demands for lactation, potentially resulting in negative effects on body condition and calf survival (Post and Forchhammer 2008). Trophic mismatches, and their negative effects on productivity, have been reported in a wide range of species (Donnelly et al. 2011), including caribou. Post and Forchhammer (2008) reported a trophic mismatch in a caribou population in Greenland and its apparent adverse effects on reproductive success. However, recent studies on Alaskan caribou and reindeer populations in northern Norway and Svalbard have found no evidence of trophic mismatches or negative effects on recruitment and calf survival from earlier springs (Tveraa et al. 2013; Gustine et al. 2017; Veiberg et al. 2017).

In addition to changes in plant community composition and phenology (Myers-Smith et al. 2011; Pearson et al. 2013), climate change is affecting ice formation and breakup (Sharma and Magnuson 2014) and terrestrial snow cover patterns (Barnett et al. 2005; Kunkel et al. 2009; Brown et al. 2010; Kapnick and Hall 2012). Although regional trends are highly variable, earlier spring melt and altered regional snowfall trends are occurring in many locations across the circumpolar world (Xie et al. 2015), and the migratory behavior of species such as caribou might be sensitive to these environmental changes. For example, the amount, duration, and hardness of snow cover affect caribou through reduced access to forage (Collins and Smith 1991; Johnson et al. 2001) and effects on movement. Thick and soft snow requires more time and energy to move through (Fancy and White 1985; Nicholson et al. 2016), and ice crusts can slow caribou and damage their legs when broken through. These factors lead caribou to select areas with less snow for ease of movement and forage accessibility (Duquette 1988; Johnson et al. 2001). However, caribou also benefit from a certain amount of snow and ice along their migratory route, particularly to move across frozen water bodies (Leblond et al. 2016). Although photoperiod is an important cue for migration in many species (Visser et al. 2010), there is evidence to suggest that animals also use local conditions to adjust migratory behavior (Gordo et al. 2005; Caro et al. 2013). Thus, we could expect caribou to time migration in the spring with snow and ice conditions that remain conducive to movement. This reasoning is supported by recent studies that have reported earlier spring migration departure dates following mild winters and delayed migrations when snowfall was abundant in the late winter and early spring (Le Corre et al. 2017; Gurarie et al. 2019).

The Qamanirjuaq barren-ground caribou herd is presently the largest population of caribou in Nunavut, Canada (Campbell et al. 2010). Each year, the herd migrates from its winter range to calving grounds near Qamanirjuaq Lake in Nunavut (Fleck and Gunn 1982). As with many other caribou populations, the Qamanirjuaq herd has recently declined, with surveys indicating that herd abundance has decreased from ~ 496,000 animals in 1994 to ~ 348,000 animals in 2008, and ~ 288,000 animals in 2017 (Boulanger et al. 2018). In this study, we analyzed 12 years of Qamanirjuaq barren-ground caribou telemetry data along with snow and vegetation covariates to investigate whether vegetation and snow phenology are changing on the Qamanirjuaq range, and if so, whether the migratory and calving behavior of the herd is responding to these changes. We further sought to test if there is any evidence to support the development of a trophic mismatch between resource availability and Qamanirjuaq caribou parturition. Based on reports of advancing Arctic vegetation and snowmelt in the literature (Cleland et al. 2007; Brown et al. 2010), we expected to observe some advancement in green-up and snowmelt trends. Recent studies have indicated the *Rangifer* populations can adjust reproductive and migratory behavior in response to environmental conditions (Le Corre et al. 2017; Paoli et al. 2018, 2019; Gurarie et al. 2019), and so we anticipated that some metrics of Qamanirjuaq caribou reproductive and migratory phenology would respond to changes in green-up and snow conditions. Additionally, our own observations during aerial surveys and reports in the literature (Fleck and Gunn 1982) indicate that the Qamanirjuaq herd typically calves before green-up, and so we did not predict that a trophic mismatch, in the sense of vegetation green-up becoming earlier with respect to parturition (e.g., Post & Forchhammer 2008), would have developed over the study period.

Materials and methods

Study area

The annual Qamanirjuaq barren-ground caribou range covers approximately 310,000 km^2 of Canada across two provinces and two territories. Their range extends from northeastern Saskatchewan and the southeastern portion of the Northwest Territories into northern Manitoba and proceeds north along the coast of Hudson Bay into the Kivalliq region of Nunavut, ending near the southern shores of Baker Lake (approximately 56.5° to 64° N, 91° to 106° W). The calving and summer ranges are entirely within the Nunavut territory. During the late spring and summer, areas of continuous permafrost, bedrock outcrops, sandy granitic tills, eskers, and large tracts of wetland characterize the Qamanirjuaq herd's range. The dominant land cover is shrub tundra, with *Betula nana*, *Salix* spp., and *Alnus crispa* occurring in warmer and drier areas, and *Salix* spp., *Sphagnum* spp. and *Carex* spp. found in wetter areas (Campbell et al. 2010).

Caribou movement behavior and range use

We used an individual-based movement method to estimate key changes in movement behavior for 115 GPS-collared female caribou. For each individual in the year 2004, and from 2006 to 2016, we estimated the beginning and end of spring migration (we considered the end of spring migration to be the start of the calving period), the date of peak calving, and the end of the calving period. Collar data from 2005 were insufficient for our analysis and are not included here. Some animals were collared for multiple years, providing a total of 228 estimated caribou calving periods and 165 estimated spring migrations. Collar deployment was often performed during the spring migration, which reduced the number of caribou used to estimate the start of migration in some years. The number of animals tracked over the study period changed annually: for the calving period estimates, we analyzed a minimum of 5 animals in 2004 and a maximum of 41 animals in 2013 (mean 19, SD 10), and for the start of migration, we analyzed a minimum of 4 animals in 2004 and 32 in 2011 (mean 14, SD 9). The fix rate of collars changed over the study period and included frequencies of 1 day (57 individuals), 12 h (7 individuals), 6 h (13 individuals), and 4 h (50 individuals).

Consistent changes in daily movement rates were used to determine changes in movement behavior (e.g., from migration to calving), and to identify key phenological traits. Following the typically low daily movements of the more sedentary winter period, caribou movement rates increase dramatically at the beginning of migration. Our method estimates the start of migration as the first of three consecutive days of movement rates above 10 km per day. Similarly, movement rates decline at the end of migration when caribou reach their calving area and we estimated the end of migration as the first of three consecutive days with movement rates below 10 km per day. Peak calving is typically defined for barren-ground caribou as the date at which 50% of calves have been born. We did not have calving survey data to identify this date for most years, and so, instead, we estimated peak calving for each individual (reflecting the likely timing of parturition) as the date with the lowest daily movement rate after migration but before the increased movement of the post-calving period (Chen et al. 2018).

A three-day window was chosen to minimize the likelihood that short bursts of high or low movement would be identified as the beginning or end of migration. The threshold of 10 km per day was chosen after considering previous work on Qamanirjuaq movement behavior that found average late-winter movement rates of 4.17 km/day, average spring migration movement rates of 11.98 km/day, average calving movement rates of 8.67 km/day, and average post-calving movement rates of 14.65 km/day (Nagy 2011). After estimating the dates of changes in movement behavior, each individual's movement pattern was visually inspected to assess whether the algorithm had selected unrealistic or erroneous dates. If our method could not clearly identify the changes in movement behavior for an individual in a given year, the individual was excluded from that year's analysis ($n = 19$). We note that we were unable to validate our estimates of peak calving dates or confirm whether a collared female was pregnant due to a lack of corroborating physical or observational data. However, we suggest that the timing of minimum movement of collared cows provides an approximation of peak calving behavior across females due to the usually synchronized calving behavior of barren-ground caribou. As with other cervid species (e.g., moose (*Alces alces*): Bowyer et al. 1999; white-tailed deer (*Odocoileus virginianus*): Carstensen et al. 2003; mule deer (*O. hemionus*): Long et al. 2009), changes in the movement behavior of parturient cows can be used to estimate the timing of calving. Following parturition caribou cows slow for several days when newborn calves restrict movement (Griffith et al. 2002; Nagy 2011; DeMars et al. 2013; Chen et al. 2018), and so this period of depressed movement rates estimates the timing of parturition across pregnant cows within a group. Our experience using collar movement rates to infer parturition to facilitate aerial abundance surveys suggests this method works well and has been successfully deployed during modern mainland migratory calving ground surveys in Nunavut and the Northwest Territories (Campbell et al. 2010; Boulanger et al. 2017). Due to the aggregation of females during this period, a relatively small proportion of collared females represent remarkably well the calving behavior of the herd as a whole (Couturier et al. 1996; Campbell et al. 2010; Nagy and Campbell 2012).

To define the spatial extent of the calving range, we extracted telemetry relocations pooled across individual caribou each year during the estimated calving period. We then calculated the 90% contour of the utilization distribution from these points and used its extent to define an annual calving polygon for each year. For trend analysis, we required a standard area over which to analyze environmental covariates, and so all annual polygons from 2004 to 2016 were combined to determine a total calving range across years. Utilization distributions were calculated using the adehabitatHR package (Calenge 2006) in R (R Core Team 2019). To delineate a winter range polygon, we pooled caribou winter locations across years, with previous work on the Qamanirjuaq herd informing the dates delineating the winter period (Nagy 2011). The 90% contour of the utilization distribution calculated from these locations defined the winter range polygon. The spring migration polygon was defined similarly by the 90% contour of the utilization distribution of caribou locations during the month of May. The average migratory period over the study duration was from the 122nd to the 158th days of the year (~ May 1 to June 6 depending on whether a leap year).

Vegetation phenology

The onset of vegetation green-up is typically associated with peak nitrogen concentration in Arctic plants (Klein 1970, 1990; Chapin 1980). To estimate the beginning of green-up annually on the Qamanirjuaq calving area from 2004 to 2016, we used a documented relationship between remotely sensed normalized difference vegetation index (NDVI) and maximum nitrogen concentration of tundra vegetation, whereby the date at which NDVI reaches half its annual maximum reasonably predicts peak nitrogen concentration, and by association, green-up (Doiron et al. 2013, 2015). NDVI values were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery from the Terra and Aqua platforms (MOD13Q1 and MYD13Q1 version 5) at 250-m spatial and 16-day temporal resolution. The 16-day resolution is offset between Terra and Aqua, allowing an 8-day resolution when combining the data streams. We used cubic spline interpolation to estimate daily NDVI. A snow cover mask was applied when deriving NDVI values. We chose MODIS imagery for analysis because previous studies have identified it as a preferred data source compared to others such as the Advanced Very High Resolution Radiometer for vegetation phenology at northern latitudes (Zeng et al. 2013). To test for relationships between spring temperature and green-up, we accessed daily temperature data for the Qamanirjuaq range from the CircumArctic Rangifer Monitoring and Assessment network's caribou range climate database (Russell et al. 2013). This database is derived from NASA's Modern-Era Retrospective Analysis for Research and Applications (Rienecker et al. 2011).

Snow cover trends

Snow cover data from 2004 to 2016 were produced through the interpretation of MODIS fractional snow cover originating from daily MODIS Terra MOD10A1 version 6, produced at 500-m grid cells. The study area is contained within four MODIS tiles, h12_v02, h12_v03, h13_v02 and h13_v03, which were mosaicked to form single daily snow cover images from April 1 to June 30. Snow cover in MODIS is derived from an algorithm based on the normalized difference snow index (NDSI), NDVI for forested areas, a thermal mask, and a cloud mask (Hall et al. 2002). Fractional snow cover is determined through regression equations for NDSI (Salomonson and Appel 2004) and is reported as values of 0–100% (i.e., the fraction of area covered by snow within a grid cell). MOD10A1 is a semi-classified product; so for grid cells not assigned a fractional snow amount, an ancillary numerical classification between 101 and 254 was assigned for properties such as inland lakes or cloud cover. Fractional snow cover for the study area was determined daily and produced as the average of grid cells, each of which has a snow cover value of 0–100%. We derived snow cover metrics over the winter range polygon in late April (last 2 weeks), the migratory corridor polygon in early May (first 2 weeks) and all of May, and the calving polygon over the average calving period across all years of the study (June 6–26). All spatial manipulations were conducted with ESRI's ArcGIS 10.5 and database manipulation and calculations were conducted with R version 3.4.1 using R Studio (R Core Team 2019).

Influence of phenology on caribou calving

To investigate the influence of climate and environmental conditions on the timing of caribou calving and migration, we built models using snow cover and vegetation covariates collected from satellite imagery (Table 1). We fitted linear mixed-effects models using individual as a random effect to account for inherent differences in movement behavior between individuals that we could not capture otherwise. Model selection was performed with Akaike's Information Criterion corrected for small sample size (AICc), and models within 2 ΔAICc were considered competitive (Burnham and Anderson 2002). To test for potential bias from different radio collar fix rates, we also tested whether including the fix rate of collared individuals improved model fit.

We defined the annual mismatch between caribou and their forage as the number of days between peak nitrogen concentration (green-up) and peak parturition dates for the herd. We calculated the geodesic distance between an individual's location at the beginning and end of their estimated migration. The temporal length of migration was determined by the number of days between the estimated start and end of migration.

We tested models with both the standard deviation in snow cover and mean snow cover to represent snow conditions across the study area. Through our exploratory analysis, we found that standard deviation, reflecting variability in snow cover across the study area, typically performed better than mean snow cover values in our models. Because of this, most of our models include variability in snow cover to provide an index of snow conditions for a given area and time series, where higher variability (standard deviation) reflected patchy or melting snow conditions (increased standard deviation in snow cover was inversely correlated with mean snow cover [$r = -0.88$, $P \ll 0.01$]). In our context of deriving snow cover metrics from satellite imagery, the use of variability (through standard deviation) over mean values is intuitive for two main reasons. A small amount of

Table 1 Comparison of models for the start of migration, end of migration, peak calving dates, and length of migration in 2004, and 2006–2016 of the Qamanirjuaq barren-ground caribou herd using Akaike's Information Criterion corrected for small sample size (AIC_c)

Behavior	Model	ΔAICc	*ωi*
Start of migration	Early May MSC SD + Late April WSC SD + Migration distance + (1∣individual)	0.00	1.00
	Late April WSC SD + Migration distance + (1∣individual)	35.50	0.00
	Early May MSC SD + Migration distance + (1∣individual)	40.56	0.00
	Late April WSC + Migration distance + (1∣individual)	61.33	0.00
	Migration distance + (1∣individual)	78.22	0.00
	(1∣individual)	130.25	0.00
End of migration	May MSC SD + Migration distance	0.00	0.53
	May MSC SD + Migration distance + Calving SC	1.35	0.27
	May MSC SD + Migration distance + Green-up	2.06	0.19
	May MSC SD + Green-up	8.58	0.01
	Green-up	46.43	0.00
	Intercept only	58.24	0.00
	Migration distance	59.50	0.00
Peak calving	May MSC SD + Calving SC + (1∣individual)	0.00	1.00
	May MSC SD + Green-up + (1∣individual)	11.45	0.00
	May MSC SD + (1∣individual)	18.88	0.00
	Calving SC + (1∣individual)	23.89	0.00
	Green-up + (1∣individual)	28.16	0.00
	(1∣individual)	63.73	0.00
Migration length	May MSC SD + Late April WSC SD + Migration distance	0.00	0.79
	Late April WSC SD + Migration distance	2.65	0.21
	May MSC SD + Migration distance	39.95	0.00
	Migration distance	41.16	0.00
	May MSC SD + Late April WSC SD	56.27	0.00
	Intercept only	94.25	0.00

SC snow cover, *MSC* migratory corridor snow cover, *WSC* winter snow cover, *SD* standard deviation

snow in terms of thickness might still provide a relatively high snow cover measure, and remote measures of snow cover are likely to be more variable during periods when snow is melting and bare ground is becoming visible.

We plotted the autocorrelation functions for all time series to identify any significant temporal autocorrelation in the data. We tested for multicollinearity between predictor variables with variance inflation factors. All statistical analyses were performed with R version 3.4.1 (R Core Team 2019).

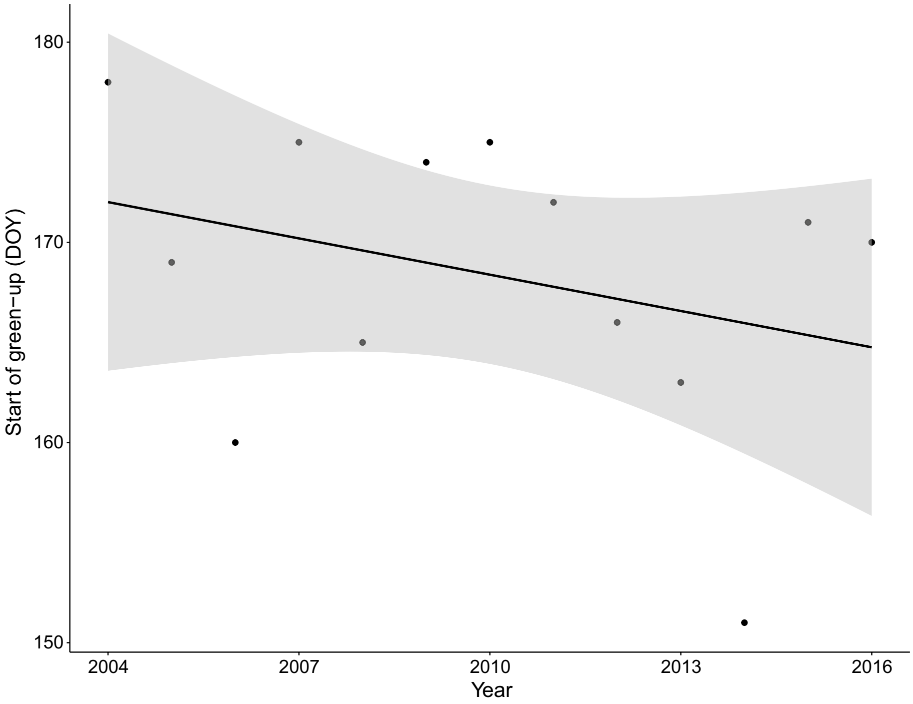
Results

Vegetation and snow phenology

No significant temporal autocorrelation was detected in any of the time series analyzed, and so we report the trends identified using linear regression for statistical inference. Annual estimates of green-up on the Qamanirjuaq calving ground indicated a weak temporally advancing trend over the study period by approximately 7.25 days (year: $\beta = -0.60$, SE = 0.54, 95% CI [− 1.80:0.59]) (Fig. 1). In several years of the study period (e.g., 2006, 2014), estimated green-up occurred much earlier (~ 10 days) than would be predicted by our linear model fit. As would be expected, earlier green-up was strongly correlated with June temperature on the calving range ($r = 0.84$, $P < 0.01$) (temperature data from NASA's Modern-Era Retrospective Analysis for Research and Applications; Rienecker et al. 2011; Russell et al. 2013).

We did not find any meaningful trends in mean snow cover on the three seasonal ranges analyzed (Fig. 2). However by examining statistics other than the mean, it appears that some changes in snow phenology have occurred. During half of the calving periods between 2004 and 2011, mean snow cover on the calving ground was greater than 30%; whereas from 2012 to 2016, the highest mean snow cover was 13.76%. Increased snow cover on the Qamanirjuaq calving range during the calving period was related to later green-up ($r = 0.67$, $P = 0.01$). Over the study period, we also found an increase in snow cover variability during migration (year: $\beta = 0.94$, SE = 0.49, 95% CI [− 0.15:2.02]), particularly from 2011 onward.

Fig. 1 Estimated start of green-up on the Qamanirjuaq barren-ground caribou calving range from 2004 to 2016 (year: $\beta = -0.60$, SE = 0.54, 95% CI [− 1.80:0.59]). DOY: day of year



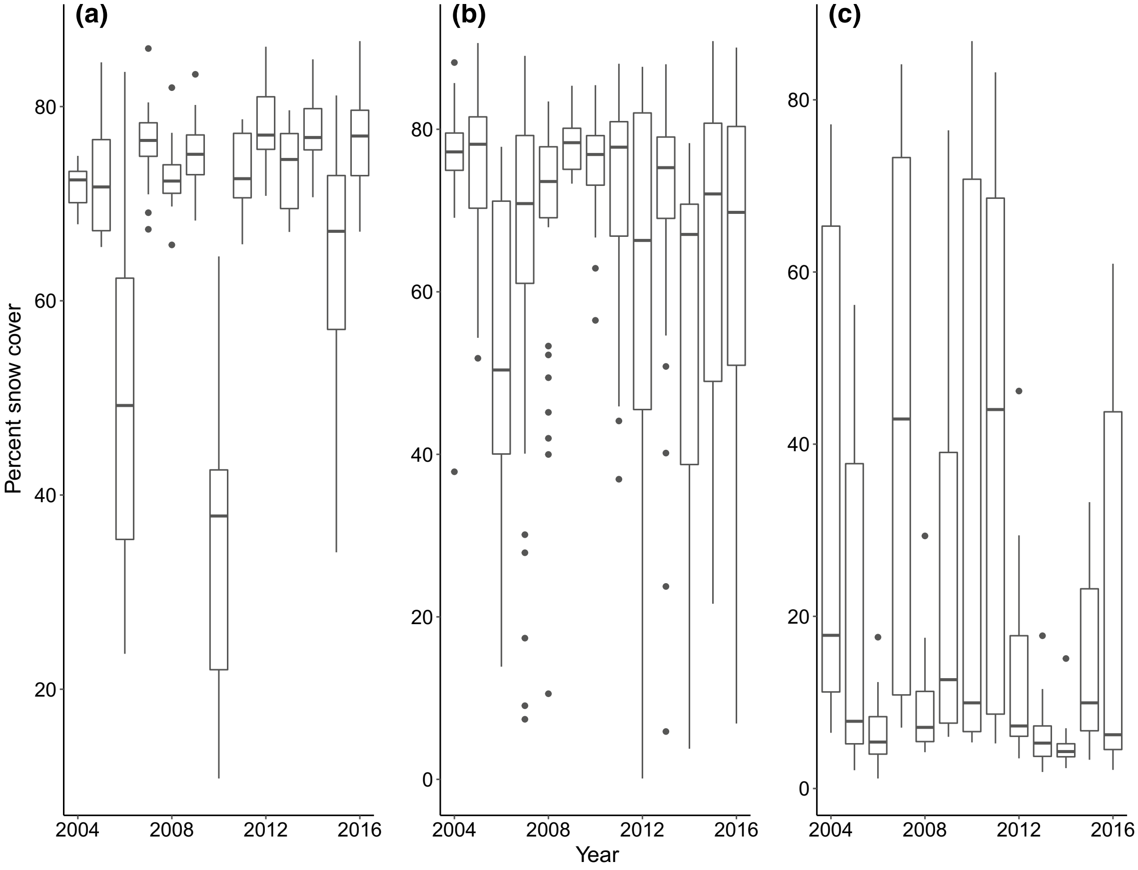


Fig. 2 Percent snow cover from 2004 to 2016 for three seasonal ranges of the Qamanirjuaq caribou herd: **a** Late April (Day of year [DOY] 105–120) winter range, **b** May (DOY 121–153) migratory range, **c** Early June (DOY 158–177) calving range. No significant linear trends exist in the mean values; however, there was an increase in standard deviation of May migratory range snow cover (year: $\beta = 0.94$, SE = 0.49, 95% CI [− 0.15:2.02])

From 2004 to 2010, average standard deviation in snow cover during migration was 10.3%; while from 2011 to 2016, it doubled to 20.6%.

Migratory and calving phenology

All measures of caribou phenology that we estimated (migration start, end, and peak calving) advanced temporally over the study period, although the trends were weak. The average start of spring migration advanced by approximately 13.64 days from 2004 to 2016 (Fig. 3, year: $\beta = -1.14$, SE = 0.25, 95% CI [− 1.62:− 0.65]), the average end of spring migration advanced by approximately 6.02 days (Fig. 3, year: $\beta = -0.50$, SE = 0.12, 95% CI [− 0.75:− 0.26]), and the average date of peak calving advanced by 9.42 days (Fig. 3, year: $\beta = -0.79$, SE = 0.09, 95% CI [− 0.96:− 0.61]).

Influence of environmental phenology on caribou calving

Based on weight of evidence, our models suggested that snow conditions on the Qamanirjuaq winter range provide a cue for the start of migration, and snow conditions during migration influence the time taken to reach the calving ground (Table 1, Fig. 4). Our most supported models indicated that increasing variability in late April snow cover on the winter range, and in May snow cover along the migratory route resulted in earlier arrival on the calving range (Table 2, Fig. 5). The date of peak calving was best explained by snow conditions in May along the migratory route and snow cover on the calving ground during the average calving period (Table 1, Fig. 6). The most supported model for the length of the migration included the distance migrated, snow conditions along the migratory route in May, and late April snow conditions on the winter range (Table 2). Caribou took longer to migrate further distances, and more variable snow conditions increased the length of migration (Fig. 7).

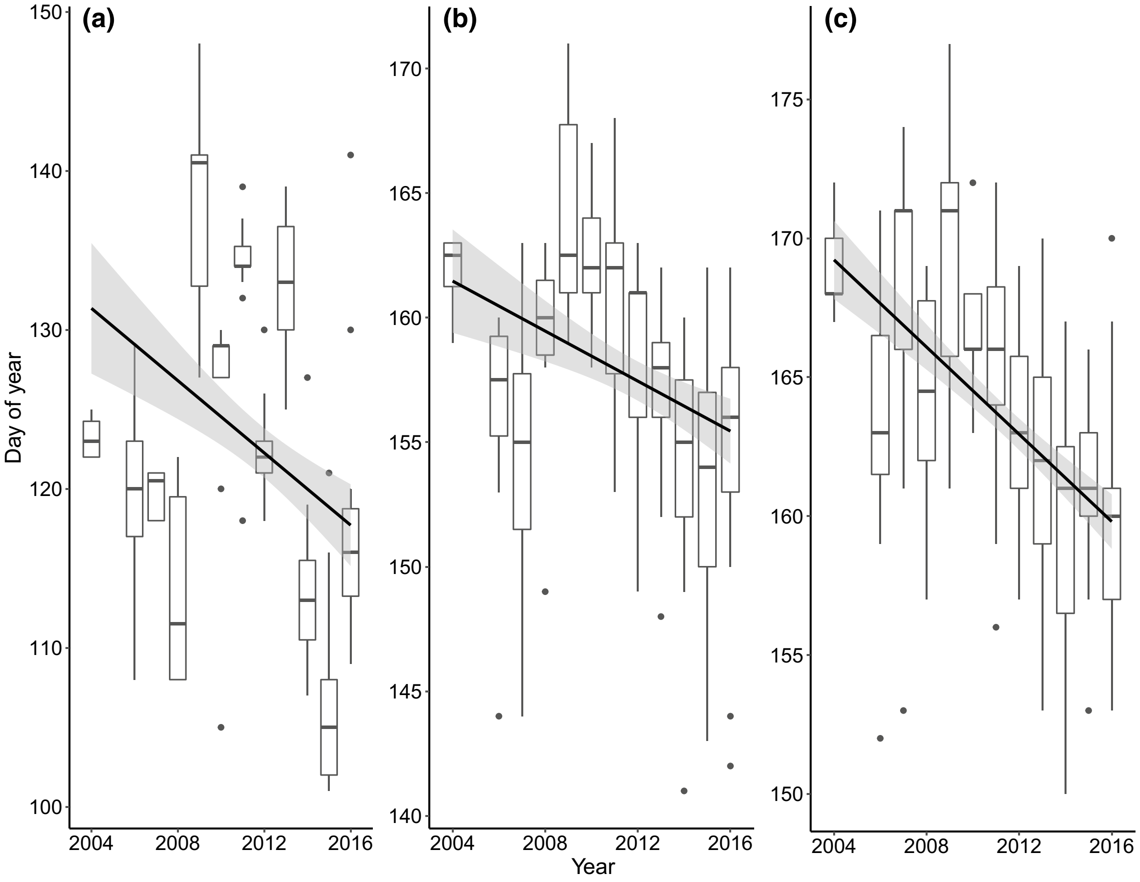


Fig. 3 Annual estimates of three key changes in movement behavior of Qamanirjuaq caribou in 2004 and from 2006 to 2016 with fitted trends and 95% confidence intervals: **a** start of migration (year: $\beta = -1.14$, SE = 0.25, 95% CI [− 1.62:− 0.65]), **b** start of calving (year: $\beta = -0.50$, SE = 0.12, 95% CI [− 0.75:− 0.26]), **c** peak calving (year: $\beta = -0.79$, SE = 0.09, 95% CI [− 0.96:− 0.61])

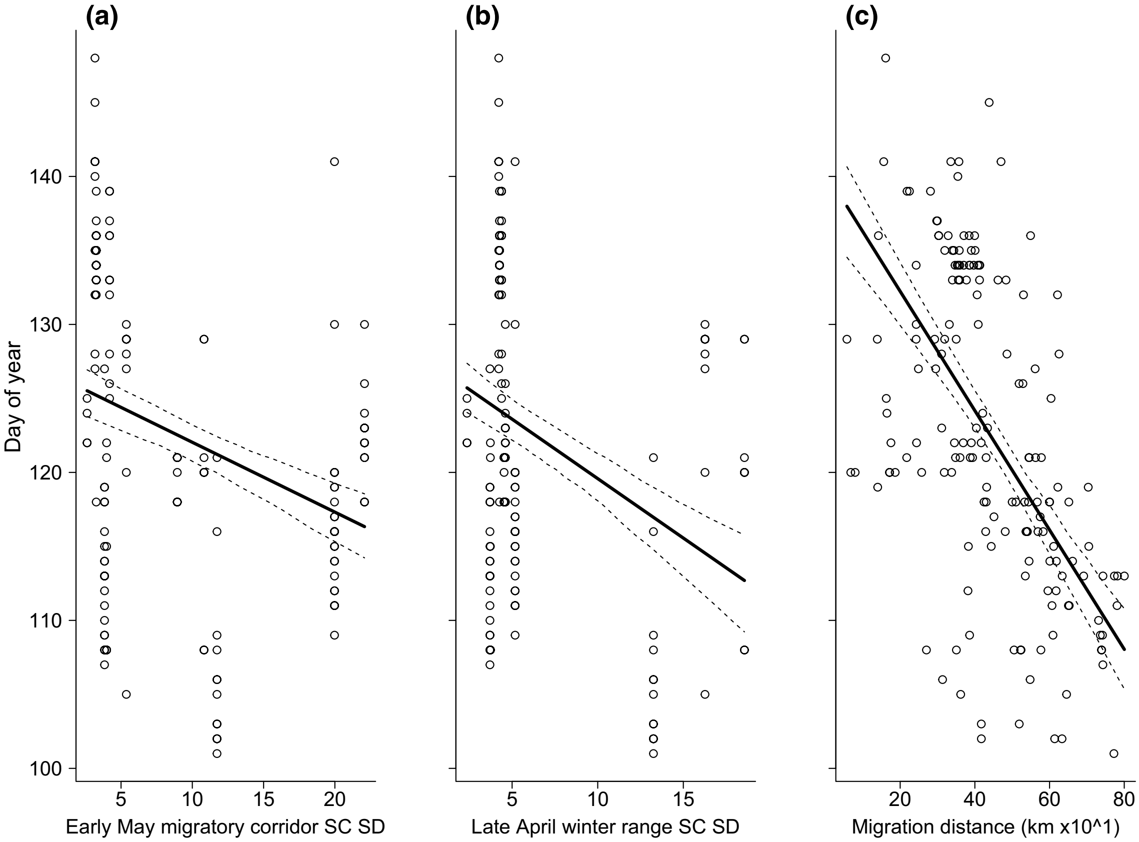


Fig. 4 Predicted linear mixed-effects relationships for covariates in our most supported caribou migration start date model: **a** early May migratory corridor snow cover (SC) standard deviation (SD), **b** late April winter range SC SD, **c** migration distance. Dotted lines represent bootstrapped 95% confidence intervals

There was no discernible trend in the "mismatch" between estimated dates of parturition and green-up over the study period (Fig. 8). The mean date of peak calving occurred an average of 3.32 days (SE = 0.45, 95% CI [− 4.20:− 2.44]) before the start of green-up and the herd typically arrived at the calving area 9.42 days (SE = 0.49, 95% CI [− 10.11:− 8.19]) before green-up began. Green-up began before the mean date of peak parturition in only two of the twelve years considered (2006 and 2014).

Two of our final models (end of migration and length of migration) did not include random effects because they explained little variability in the response (Table 1). For the end of migration, two of the models we compared were within 2 AICc, and so could be considered as competing (Table 1). However, these models differed only by an additional parameter, with the larger model having a ΔAICc of 1.35 over the smaller. Following Arnold (2010), we dismissed the potentially competitive model as containing an additional uninformative (in this case) parameter. Including a fix rate covariate did not improve the fit of any of our models.

Discussion

We evaluated temporal trends in a number of phenological indicators for barren-ground caribou and their habitats. We aimed to understand how barren-ground caribou spring migratory and calving behavior might respond to phenological changes in the environment and to assess the evidence for trophic mismatch development in our study system. From 2004 to 2016, we found advancement in the annual timing of the start and end of migration, and of peak calving. We also found evidence for declining snow cover along the migratory corridor (Fig. 2) and for earlier green-up on the calving ground. These results provided several potential environmental drivers for the observed advancement in migratory and calving behavior, which we evaluated for support using a weight of evidence modeling approach. Our results suggested that snow conditions on the winter range and along the migration route were the primary driver for advancing migratory behavior.

Caribou appeared to use winter range snow conditions as an environmental cue for migration. Late-winter and early-spring conditions seemed to provide some information about

Table 2 Parameter estimates of most supported linear and linear mixed-effects models for the timing of spring movement behavior of the Qamanirjuaq barren-ground caribou herd

Behavior modeled	β	SE
Start of migration		
Intercept	149.67	2.01
Early May MSC SD	− 0.47	0.07
Late April WSC SD	− 0.80	0.11
Migration distance	− 0.40	0.03
End of migraion[a]		
Intercept	163.86	1.11
May MSC SD	− 0.52	0.06
Migration distance	0.07	0.02
Peak calving		
Intercept	166.20	1.16
May MSC SD	− 0.27	0.05
Calving SC	0.10	0.02
Migration length[a]		
Intercept	10.85	2.23
May MSC SD	0.21	0.10
Late April WSC SD	0.90	0.13
Migration distance	0.33	0.04

SC snow cover, *MSC* migratory corridor snow cover, *WSC* winter snow cover, *SD* standard deviation

[a] Fixed effects only

the likely conditions of the calving ground because there was moderate correlation between standard deviation in snow cover along the migratory route and date of green-up on the calving ground ($r = -\ 0.61$, $P < 0.05$). Thus, by timing migrations to conditions that remain amenable to movement, at least at the proximal end of the migratory corridor, caribou might coarsely anticipate the conditions of their destination. Our findings agree with those of other recent publications in which milder winter conditions were correlated with earlier migration departures (Le Corre et al. 2017; Gurarie et al. 2019). However, Le Corre et al. (2017) found that mild spring conditions delayed arrival on the calving range; while in our study, declining snow cover during migration advanced arrival on the calving range (end of migration), although caribou took a longer time to migrate in years with less snow. In our study system, caribou appear to have compensated for the slower pace of migration with earlier departure dates.

Consistent with some studies on long-distance avian migrants (Cotton 2003; Gordo et al. 2005), our results support the importance of winter range conditions as a driver for the timing of spring migration and ultimately arrival on the calving or breeding grounds. Snow conditions, icing conditions, and lake and river ice formation and quality are critical to barren-ground caribou migration. Ease of movement and energy expenditure during this period are largely determined by snow conditions, with thick soft snow, ice crusts, and slush hindering movement (Fancy and White 1987; Nicholson et al. 2016). Sufficient ice thickness on water bodies along the migratory route allows caribou to make crossings safely (Miller and Gunn 1986). Caribou are known to wait for adequate ice conditions before making crossings (Poole et al. 2010) and to skirt or avoid water bodies with thin or no ice (Leblond et al. 2016). Sharp ice crusts from rain-on-snow or thaw–freeze events also can cause damage to the lower legs of caribou when they break through to the softer snow underneath, leading not only to pain and discomfort but also to rapid transmission of diseases such as hoof-rot (Valkenburg et al. 2003). These snow conditions are more likely during warmer weather and when snow is melting, providing a possible mechanism for the observed increase in migration time in years with earlier snow melt. Along with our findings, these examples support the importance of snow and ice conditions during spring caribou migrations and the adaptive value for barren-ground caribou to use local snow conditions on the winter and early migratory ranges as a cue for migration.

We found that peak calving occurred earlier in years with less snow on the calving area and along the migratory route. Although the timing of parturition in caribou is primarily related to the timing of the rut and the length of gestation, some plasticity in the length of gestation could be selectively advantageous and allow otherwise underweight fetuses longer developmental periods to increase the likelihood of survival (Bergerud et al. 2008). Plasticity in the length of gestation might then allow for some modification of the timing of parturition depending on annual conditions on the calving area. We would not expect this effect to dramatically override nutritional effects throughout gestation or female condition coming out of the previous summer (Cameron et al. 1993; Gerhart et al. 1997; Pachkowski et al. 2013), and the lesser influence of calving area conditions on peak calving can be seen in the smaller effect sizes of environmental predictors on peak calving than the other behaviors modeled (Table 2). Chen et al. (2018) found that peak calving dates of the Bathurst barren-ground caribou herd were altered by both the previous year's conditions and the start of the growing season in the current year, and Paoli et al. (2018) documented earlier reindeer calving dates in response to reduced April snow cover. Both of these examples support our findings that spring conditions can alter the timing of calving in the same year.

Whereas there have been some reports of advancing breeding phenology in response to changing environmental conditions in avian and ungulate species (e.g., Moyes et al. 2011; Dunn and Møller 2014), very few studies have reported climate-mediated advancement in the breeding phenology of an Arctic ungulate (Paoli et al. 2018, 2019). Le Corre et al. (2017) recently investigated the effects of climate

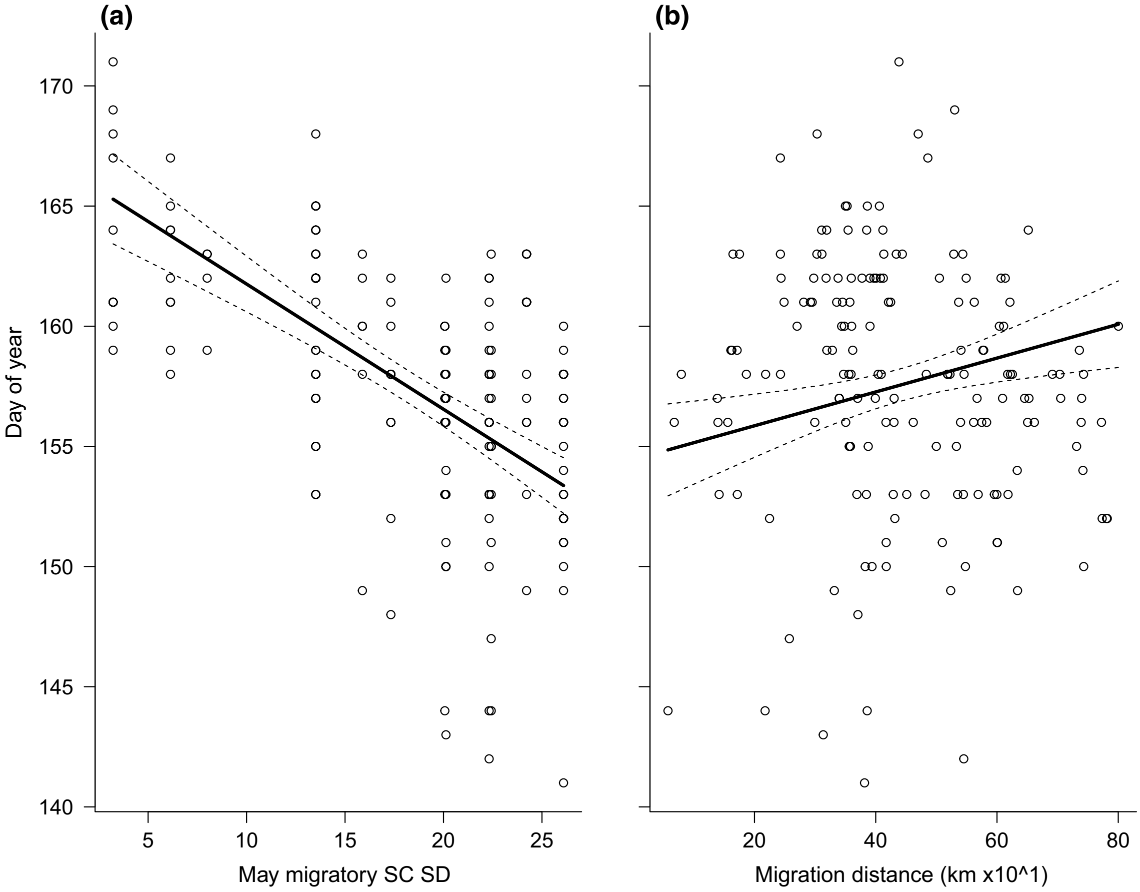


Fig. 5 Predicted linear relationships for covariates in our most supported end of spring migration model: **a** May migratory corridor snow cover (SC) standard deviation (SD), **b** migration distance. Dotted lines represent 95% confidence intervals

conditions on migration phenology of caribou in northern Quebec and Labrador, Canada. Although they observed an advancement of spring migration departure dates, they found no trend in dates of arrival on the calving area, which suggested deteriorating conditions for movement during migration in the spring. Chen et al. (2018) reported that peak calving dates in the Bathurst barren-ground caribou herd likely resulted from cumulative climate-driven habitat changes across multiple years, but did not find a temporal trend in the timing of parturition. Paoli et al. (2018) found that the calving of a population of reindeer in Finland had advanced by around 7 days between 1970 and 2016 in response to reduced April snow cover and warmer spring temperatures.

Our findings suggest the existence of two phenomena. First, it appears that changes to spring phenology, at least in terms of snowmelt and vegetation green-up, have occurred across the Qamanirjuaq herd's range. Second, it appears that over the study period, phenological changes on the herd's winter and migratory ranges have allowed caribou to keep pace with changes occurring on the calving range. Because of this, we observed no trend in the temporal separation between green-up and calving over the study period, and, therefore, no support for the development of a trophic mismatch (Fig. 8). This lack of trend results from the similar magnitude in advancement of snowmelt, green-up, and calving. We must note that although we are confident that in general a small number of collared cows can reflect the spatial distribution of larger numbers female caribou during the calving period, as sample size decreases, the chance of not capturing behavior representative of the entire herd increases. In some years, our sample size is relatively low (i.e., 5 tracked animals in 2004, 9 tracked animals in 2010), and so some degree of caution is necessary in our results and interpretation.

The vulnerability of a species to the effects of trophic mismatch depends partly on their life history strategies. For example, animals that undertake long-distance migrations might be more susceptible to trophic mismatches than non-migratory species (Both et al. 2009). Species with more proximate seasonal ranges, such as the caribou in this study, may be better positioned to adjust to phenological changes that arise at comparable rates across their total annual range. Both Veiberg et al. (2017) and Gustine et al. (2017) suggested that because caribou and reindeer are

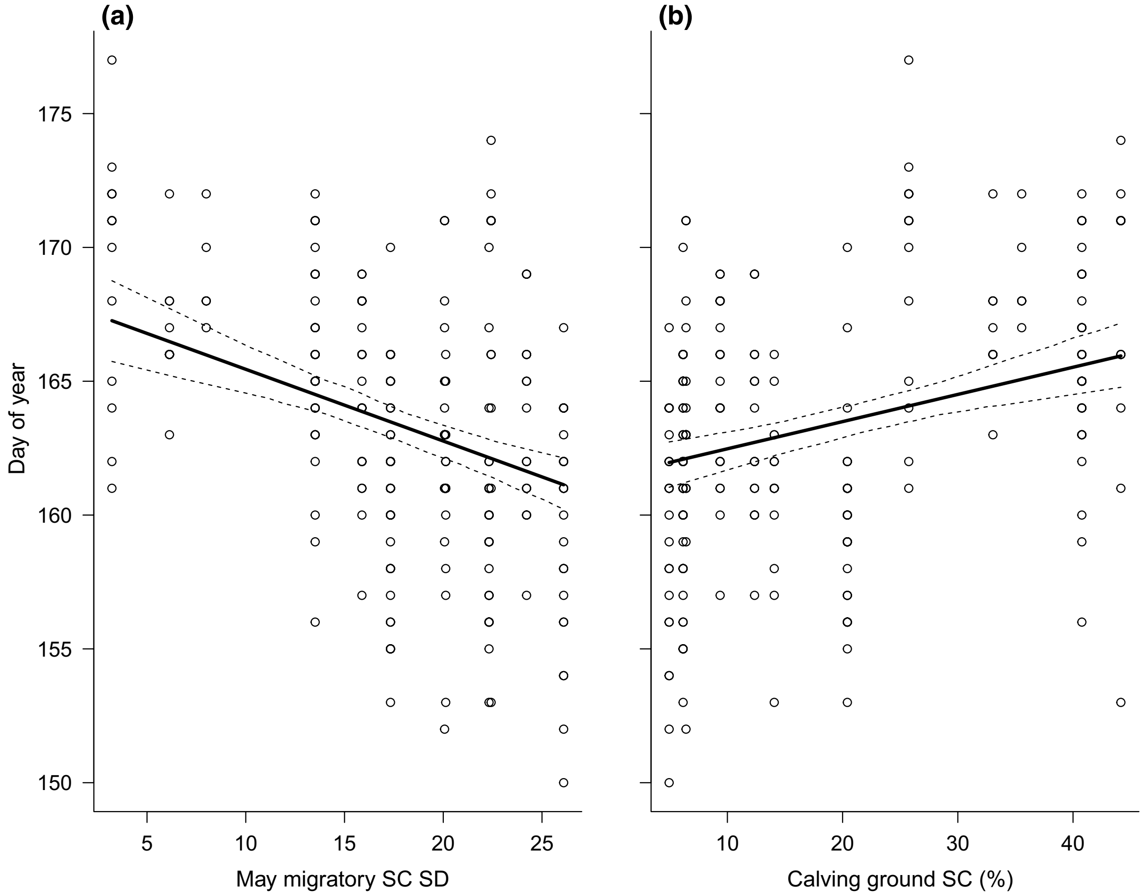


Fig. 6 Predicted linear mixed-effects relationships for covariates in our most supported caribou peak calving date model: **a** May migratory corridor snow cover (SC) standard deviation (SD), **b** calving ground snow cover. Dotted lines represent bootstrapped 95% confidence intervals

primarily capital breeders (Taillon et al. 2013), the influence of spring phenology should be less important than that of maternal winter body condition on reproductive success, and this strategy for financing reproduction could mitigate the effects of changing or variable spring phenology (Williams et al. 2017). Substantial evidence, including from this study, indicates that many barren-ground caribou populations often calve well in advance of green-up (Fleck and Gunn 1982; Reimers et al. 1983; Crête and Huot 1993; Bergerud et al. 2008; Gustine et al. 2017; Veiberg et al. 2017; see review by Mallory and Boyce 2018), reducing the potential importance of concurrent timing of these events. Although barren-ground caribou are well-adapted to highly variable and often difficult conditions during parturition, cows and calves certainly benefit from earlier access to high-quality forage and improved nutritional income at this time of year. In fact, the early onset of spring can benefit caribou cows and calves by providing earlier access to high-quality forage that supplements the nutritional costs of lactation (Pettorelli et al. 2005; Cebrian et al. 2008; Helle and Kojola 2008; Couturier et al. 2009; Tveraa et al. 2013). For example, Paoli et al. (2019) reported that reindeer calves in northern Finland were born heavier and had higher over-summer survival in years with an earlier onset of vegetation growth. Accessible and nutritious forage near parturition and during lactation remains important, and it stands to reason that caribou which can maintain calving behavior that keeps pace with changes to forage phenology might have better reproductive success than those which do not. Although the evidence for the possible development of a true “trophic mismatch” for most *Rangifer* populations examined is scant, the timing of the onset of vegetation growth can have consequences for calf and cow nutrition, and phenological changes that reduce either the availability or quality of forage at this time of year will still have some implications for these northern ungulates (Couturier et al. 2009; Tveraa et al. 2013; Paoli et al. 2019).

Though we have insufficient data to investigate links between advancing reproductive and migratory phenology with demographic parameters, studies of other species provide basis for speculation. Analysis by Møller et al. (2008) revealed that European bird species with migratory behavior that had not advanced in response to changing climate

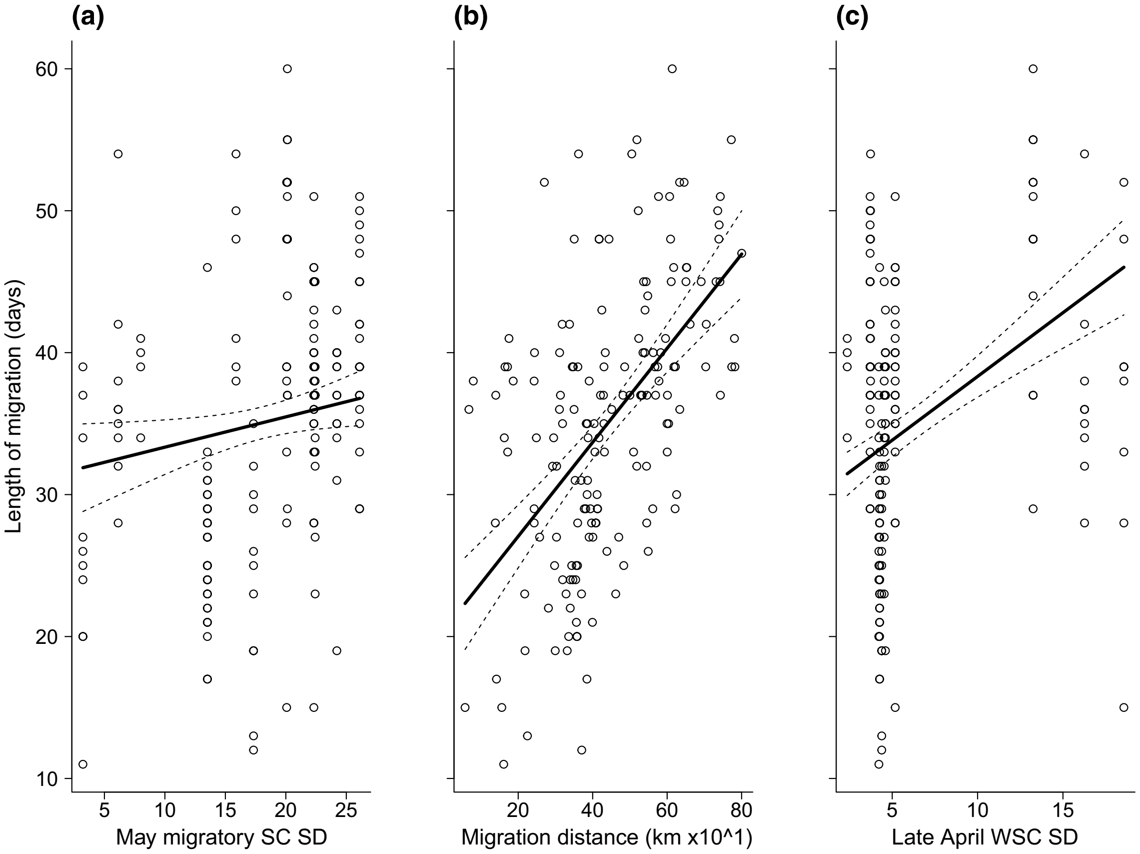
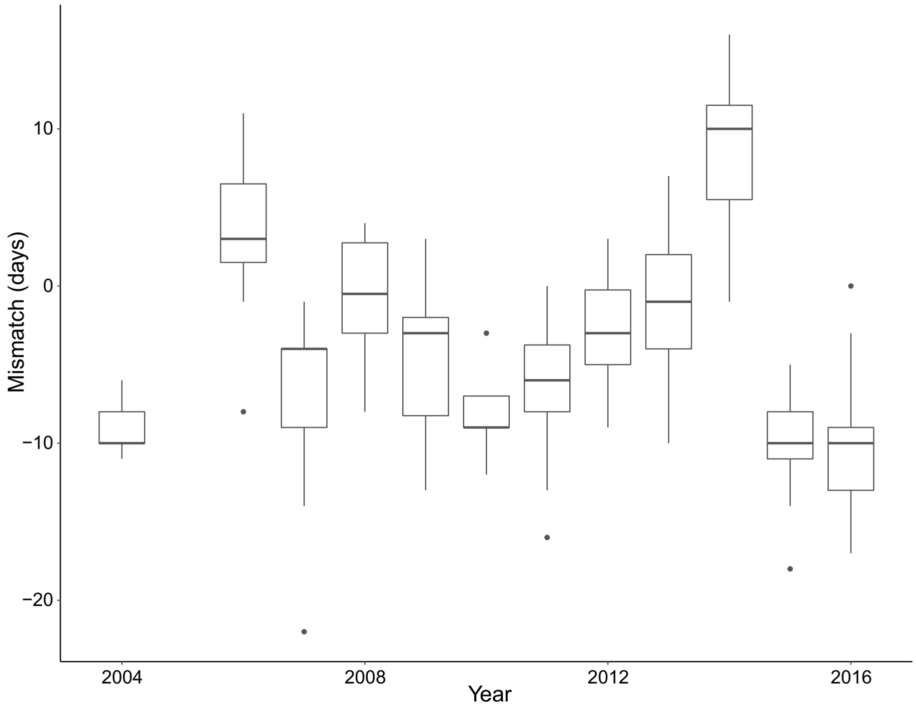


Fig. 7 Predicted linear relationships for covariates in our most supported caribou migration length model: **a** May migratory corridor snow cover (SC) standard deviation (SD), **b** migration distance, **c** late April winter range snow cover (WSC) SD. Dotted lines represent bootstrapped 95% confidence intervals

Fig. 8 Estimated mismatch, defined as the difference (in days) between the date of caribou peak parturition and estimated start of green-up on the Qamanirjuaq calving range in 2004 and from 2006 to 2016. Peak parturition occurred an average of 3.32 days (SE = 0.45, 95% CI [− 4.20:− 2.44]) before the start of green-up over this period



conditions experienced stronger population declines than species that had advanced the timing of their migrations. Similarly, the inability of roe deer (an income breeder) in France to adjust their breeding phenology to cope with earlier spring onset resulted in negative demographic effects in the population (Plard et al. 2014). In contrast, the reproductive phenology of some northern mammals such as red deer (*Cervus elaphus*; Moyes et al. 2011) has responded strongly to changing climate conditions, with advancing parturition dates and other phenological traits. These examples suggest that the apparent ability of barren-ground caribou to adjust their migratory and reproductive phenology in response to the earlier onset of spring could provide resilience to climate change. However other factors, such as anthropogenic disturbance, can also disrupt caribou migratory and calving behavior. Caribou have been widely reported to avoid anthropogenic disturbance and negatively respond to human activity (Cameron et al. 2005; Johnson et al. 2005; Vistnes and Nellemann 2008; Festa-Bianchet et al. 2011; Boulanger et al. 2012; Johnson and Russell 2014), and in some cases, these disturbances have disrupted the migratory behavior of individuals (Mahoney and Schaefer 2002; Vistnes et al. 2004; Wilson et al. 2016). The potential for caribou to adjust migratory behavior in response to changing environmental cues could be hampered by novel disturbances along their migratory routes, and it is, therefore, imperative that decision makers give adequate weight to these effects when considering human activities on caribou ranges.

Our analysis indicates that in years with more variable snow conditions and earlier snowmelt, caribou spend longer periods migrating (Fig. 7). At some point, longer periods spent migrating could have negative implications for caribou. Barren-ground caribou expend substantial resources during migration at a time when forage resources are poor. Longer durations spent in poor forage conditions during spring migration could negatively affect the condition of cows and calves, potentially reducing calf survival (Crête and Huot 1993; Gerhart et al. 1996; Sharma et al. 2009).

Conclusions

Our study reports climate-mediated advancement in the reproductive phenology of an Arctic ungulate. This advancement results from changing spring snow conditions on the caribou herd's winter and migratory range that provide earlier cues for migration and calving. Earlier calving and migratory behavior have allowed caribou to keep pace with earlier green-up, and we found no evidence to suggest the development of a detrimental trophic mismatch. In fact, as shown by their life history characteristics and empirical evidence (Taillon et al. 2013; Gustine et al. 2017), *Rangifer* populations appear unlikely to be broadly susceptible to trophic mismatches at the timing of parturition.

Caribou and reindeer have huge socioeconomic importance across the circumpolar world and the ways in which a changing climate might affect the conservation of these populations has become an important area of research (e.g., Sharma et al. 2009; Turunen et al. 2009; Uboni et al. 2016). Although the potential consequences of climate change for *Rangifer* populations are many (Mallory and Boyce 2018), we suggest that the ability of caribou to adjust calving and migratory behavior in response to shifting environmental cues could be a critical behavior for climate change adaptation.

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Author contribution statement All authors contributed to the design of this study. CDM and SNW analyzed the data and wrote the manuscript. MWC and MSB provided editorial advice.

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