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ARTICLE

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Continental synchrony and local responses: Climatic effects on spatiotemporal patterns of calving in a social ungulate

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Abstract

Warming temperatures and advancing spring are affecting annual snow and ice cycles, as well as plant phenology, across the Arctic and boreal regions. These changes may be linked to observed population declines in wildlife, including barren-ground caribou (*Rangifer tarandus*), a key species of Arctic environments. We quantified how barren-ground caribou, characteristically both gregarious and migratory, synchronize births in time and aggregate births in space and investigated how these tactics are influenced by variable weather conditions. We analyzed movement patterns to infer calving dates for 747 collared female caribou from seven herds across northern North America, totaling 1255 calving events over a 15-year period. By relating these events to local weather conditions during the 1-year period preceding calving, we examined how weather influenced calving timing and the ability of caribou to reach their central calving area. We documented continental-scale synchrony in calving, but synchrony was greatest within an individual herd for a given year. Weather conditions before and during gestation had contrasting effects on the timing and location of calving. Notably, a combination of unfavorable weather conditions during winter and spring, including the pre-calving migration, resulted in a late arrival on the calving area or a failure to reach the greater calving area in time for calving. Though local weather conditions influenced calving timing differently among herds, warm temperatures and low wind speed, which are associated with soft, deep snow, during the spring and pre-calving migration, generally affected the ability of female caribou to reach central calving areas in time to give birth. Delayed calving may have potential indirect consequences, including reduced calf survival. Overall, we detected considerable variability across years and across herds, but no significant trend for earlier calving by caribou, even as broad indicators of spring and snow phenology trend earlier. Our results emphasize the importance of monitoring the timing and location of calving, and to examine how weather during summer and winter are affecting calving and subsequent reproductive success.

KEYWORDS
birth location, birth timing, caribou, environmental gradients, migration, parturition, *Rangifer tarandus*, weather

INTRODUCTION

The Arctic is experiencing exceptionally rapid environmental changes (Serreze & Barry, 2011). Temperatures are increasing as much as four times faster than in other parts of the planet (Box et al., 2019; IPCC, 2015; Isaksen et al., 2022), precipitation patterns are changing, perennial sea ice is melting, and snow cover has been greatly reduced (Dore, 2005; Swanson, 2017). Whereas early spring phenology and increased productivity may present a potential benefit for herbivores in the Arctic (Guay et al., 2014; Høye et al., 2007; Zeng et al., 2013), mismatches between life history events and changing forage availability could be detrimental (Parmesan & Yohe, 2003). In addition, increasing temperatures are linked to warmer winters and a higher frequency of rain-on-snow events, which may lead to the formation of an ice layer impeding herbivores' access to vegetation under snow (Albon et al., 2017; Loe et al., 2016; Pan et al., 2018). Additionally, increasing temperatures during summer are known to be linked to a higher insect activity during that season (Hagemoen & Reimers, 2002; Russell et al., 1993; Witter, 2011), which can have a direct effect on the ability of individuals to regain weight during summer. This, in turn, can affect both winter survival and subsequent reproductive success (Weladji et al., 2003; Weladji & Holand, 2003). Because of contrasting effects and the heterogeneity of climate change across the Arctic (Elmendorf et al., 2012), some animal populations may benefit from local changes, whereas others may be disadvantaged (Descamps et al., 2017; Hansen et al., 2019; Joly et al., 2011).

In highly seasonal environments like the Arctic, animal births are often synchronized with the peak of resource availability to allow mothers and their young to exploit high-quality forage during short growing seasons (Parmesan, 2007; Rutberg, 1987; Sinclair et al., 2000). Birth synchrony can therefore emerge at a large scale, with individuals of a particular species or ecotype giving birth within weeks of one another (Davidson et al., 2020). Synchrony can increase even more in response to local conditions to better match births with plant phenology at a local scale (Peláez et al., 2020).

In addition to being synchronized in time, births can be aggregated in space. Access to peak forage quality and shared information about resources are likely evolutionary drivers of aggregated calving in ungulates (Cameron et al., 2020; Sinclair et al., 2000). Spatial aggregation could also act as an anti-predation strategy through shared vigilance and dilution effects, or selection of areas with lower predator density (Bergerud, 1996; Heard et al., 1996; Ims, 1990; Sinclair et al., 2000). These drivers are not necessarily mutually exclusive.

One striking example of a species with highly synchronized calving behavior is the migratory barren-ground caribou (*Rangifer tarandus groenlandicus* and *Rangifer tarandus granti*), the most abundant ungulate in the North American Arctic. Continental barren-ground caribou gregariously migrate hundreds of kilometers to reach calving grounds in the Arctic tundra and typically calve prior to the peak of green-up (Gustine et al., 2017; Joly et al., 2019; Mallory et al., 2020). The calving grounds themselves are characterized by newly emergent, high-quality forage during calving season (Cameron et al., 2020; Gunn et al., 2010; Gustine et al., 2017; Mallory et al., 2020). Both the ability to access preferred calving areas and the ability to synchronize births in time are critical for maintaining high barren-ground caribou abundances, which are orders of magnitude higher than those of nonmigratory caribou ecotypes (Festa-Bianchet et al., 2011). Despite this clearly successful evolutionary strategy and the well-known, cyclic, high-amplitude fluctuations in abundance, many populations of barren-ground caribou have declined precipitously in the past decades (Adamczewski et al., 2019; Festa-Bianchet et al., 2011; Gunn, 2016). These declines have occurred in tandem with rapid climate change and, as such, there has been heightened interest in understanding climate-related drivers of their population dynamics (Davidson et al., 2020; Joly et al., 2011; Laforge et al., 2021).

One plausible mechanism by which climate might be affecting caribou populations is via disruption of pre-calving migration and shifts in the timing of calving. The timing of arrival on calving grounds shows interannual variability (ranging from 18 days for the Western Arctic Herd to 36 days for the Bluenose West Herd, see Gurarie et al., 2019), as well as a weak advance through time and has been shown to depend on weather and climate conditions before and during migration (Gurarie et al., 2019; Le Corre et al., 2017). During migration, hard-packed snow, which can be caused by a combination of strong winds and low temperatures, can facilitate movement and speed up migration in contrast to soft, deep snow that is associated with warm temperatures following snowy winters (Duquette, 1988; Fancy & White, 1987; Leclerc et al., 2021). There is some evidence for large-scale trends toward earlier parturition in barren-ground caribou (Davidson et al., 2020), with uncertain mechanistic links to climate trends. Studies on conception, gestation, and calving timing in caribou and reindeer indicate that better maternal body condition can advance estrus timing and shorten gestation periods (Bergerud et al., 2007; Cameron et al., 1993; McEwan & Whitehead, 1972; Mysterud et al., 2009). Shorter gestation periods may explain why beneficial weather conditions throughout the preceding year, for example, windier and cooler summers preceding conception with less insect harassment and greater female weight gain (Barboza & Parker, 2008), are followed by earlier arrivals at calving grounds (Gurarie et al., 2019; Mallory et al., 2020). It is not, however, known whether these patterns extend to the timing of calving. Birth timing and location may influence early calf survival (Dauphiné & McClure, 1974; Rutberg, 1987), such that any identifiable links between climate and weather and calving timing may have downstream demographic consequences.

We present a comprehensive analysis of caribou calving from over a decade of observations on GPS-collared barren-ground caribou across seven herds from different Arctic climate zones across North America, with an overarching goal of identifying links between climate and calving patterns in space and time (Figure 1). We assessed the level of temporal synchrony and advance in calving timing, predicting that (P1) there would be less variation in calving timing within herds in a given year than across herds and across years, as a response to local conditions, and that (P2) advance in calving timing would be relatively weak, due to substantial interannual variations in weather. We then assessed how weather conditions during the 1-year period preceding calving affected calving date and spatial location. We predicted that (P3a) unfavorable conditions for foraging throughout the year would delay calving date by either delaying estrus timing and/or extending gestation duration. In particular, because caribou acquire much of their body fat late in summer (Barboza & Parker, 2008), we predicted that (P3b) an important portion of the variation in calving timing would be explained by summer conditions prior to conception. With respect to calving locations, we predicted that (P4) a combination of unfavorable weather conditions during winter, spring, and pre-calving migration would hinder pre-calving migration and increase the probability of calving outside the greater calving area (see *Materials and methods*) used by the majority of the herd. Finally, given the high plasticity in migration speed among herds and among years (Gurarie et al., 2019), we were interested in comparing the timing of calving against timing of arrival at the greater calving areas, which we refer to as calving lag. Caribou have evolved with and regularly experience large variability in weather and travel conditions on their way to the calving grounds (Gurarie et al., 2019); thus, we suspected that most caribou would arrive on the calving grounds several days before parturition to account for potential variability en route. We predicted that (P5a), under average conditions, calving lag would be relatively fixed, allowing females to reach the calving area together prior to peak green-up. However, under poor pre-calving migration conditions, we predicted that (P5b) calving lag would be shortened. Because of the wide geographical scope of our study (Figure 2), we expected our results to be consistent across herds, with some variation among herds as a response to local conditions.

MATERIALS AND METHODS

Study areas and GPS data

We analyzed GPS data of female barren-ground caribou in seven herds in western Alaska and northern Canada (Figure 2), with regional and contrasting environmental conditions including climate and vegetation across >3000 km of longitude and >1000 km of latitude (Appendix S1: Figure S1, Table S1; Gould, 2003), and

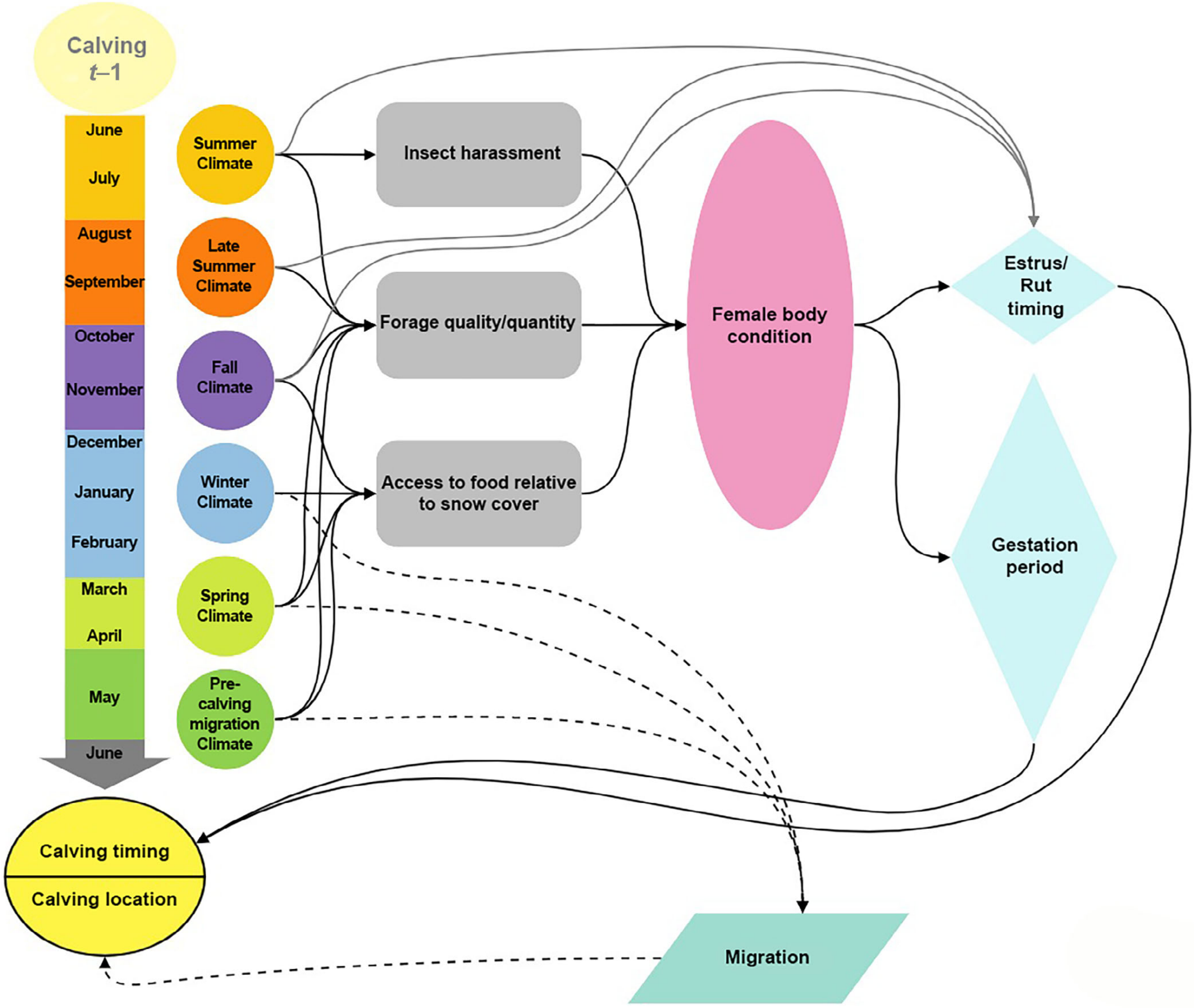

FIGURE 1 Conceptual framework of hypothesized relationships linking seasonal weather conditions to calving timing (plain arrows) and calving location (dashed arrows). Timing may be influenced by insect harassment, vegetation, or access to forage resources, all of which influence body condition, which then influences estrus/rut timing and the gestation period. Calving location is influenced by migration timing, which is influenced by winter and spring snow and weather conditions.

differing population trends. These span the Western Arctic Herd to the west, which ranges over a large area along the Chukchi Sea in western Alaska, USA, to the Qamanirjuaq Herd to the east, which ranges over a large portion of the Canadian Shield, and calves near Hudson Bay. We used data from caribou fitted with GPS collars between 2006 and 2019 by state, federal, and territorial governmental agencies as part of ongoing monitoring efforts, though not all herds were monitored across the entire period (Figure 2). All capture and marking procedures were done in accordance with government animal care committees. The compiled dataset consisted of 747 female caribou, corresponding to 1607 individual-year combinations. We limited the dataset to 15 June of the year preceding calving and 7 July of the year of calving for all individuals. With a fixed schedule of every 8 h, this left 916 ± 663 relocations/individual-year (3 ± 2 relocations/day [mean ± SD]) throughout the study period.

Estimation of calving events

We adapted the individual-based method developed by DeMars et al. (2013) to infer calving events for boreal populations of woodland caribou (*Rangifer tarandus caribou*; Walker et al., 2020, but see Bonar et al., 2018 for contrasting results). Although boreal caribou are nonmigratory and are mostly solitary during calving, this

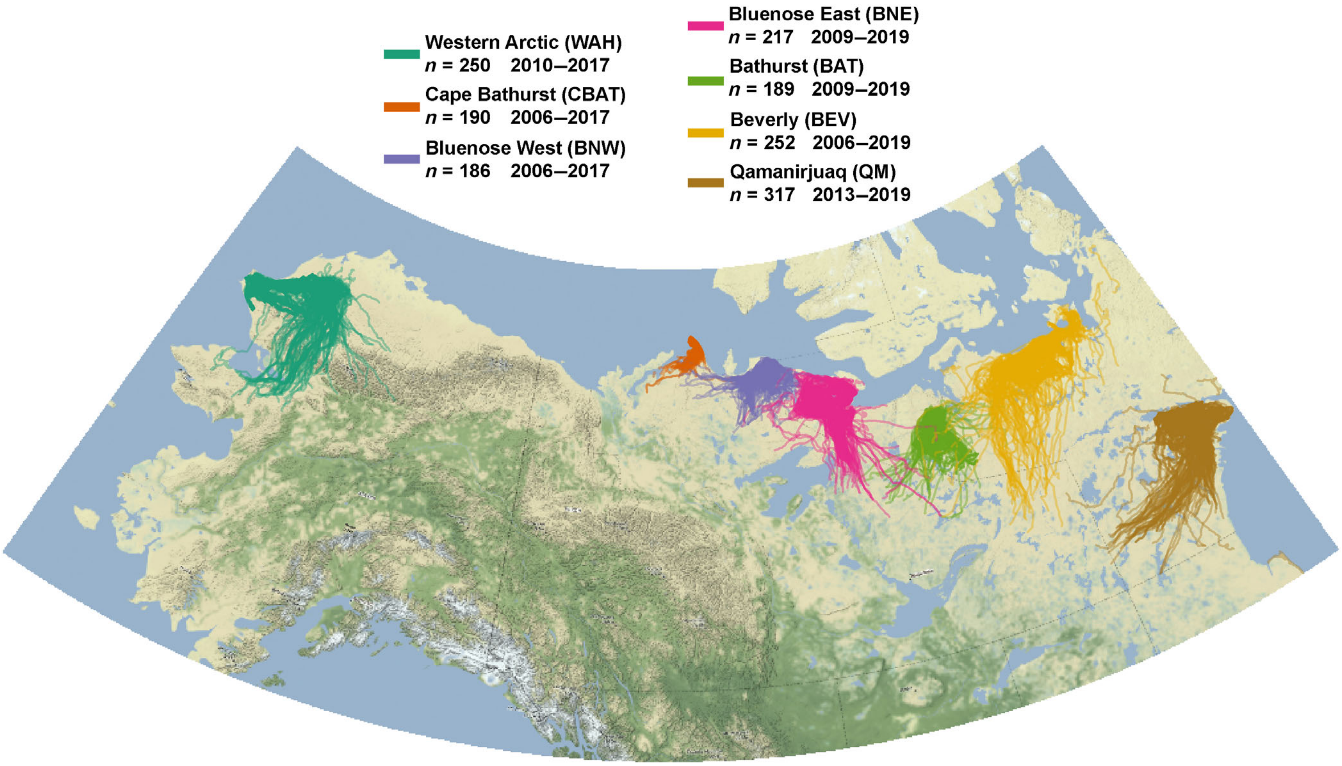

FIGURE 2 Map of the movement tracks of 747 GPS-collared female caribou from seven herds across Alaska and northwestern Canada, between 19 May and 7 July from 2006 to 2019. The annotations correspond to the number of individual-years (*n*; 1607 in total) and the period of monitoring for each herd.

method has been successfully adapted to barren-ground caribou from the Western Arctic Herd, which are also considered in this study, and found to have an overall accuracy of 77% when validating this method against aerial survey data (Cameron et al., 2018). While this difference is nontrivial (23%), there are considerable advantages in terms of time and energy compared with other methods. Indeed, among the existing methods to detect calving events, most are either invasive (e.g., vaginal implants) or require intensive aerial or ground surveys (Adamczewski et al., 2019; Dion et al., 2019).

The individual-based method fits several competing models to the step lengths (the distance between successive GPS locations) of individual females, which are assumed to follow an exponential distribution with a mean parameter. This parameter either drops abruptly at a calving event and then slowly recovers to a pre-calving rate (hereafter the "calf" model), or remains constant throughout the time series if the individual does not have a calf (i.e., from 19 May to 7 July, hereafter the "no calf" model; DeMars et al., 2013). We refined this approach in two ways. First, instead of modeling step lengths, we modeled movement rates (step lengths divided by the corresponding time interval between GPS locations), to account for variability in sampling schedules and missing data across datasets. Second, movement rates were assumed to follow a more flexible gamma distribution specified using two parameters: the shape (which varies from an exponential to a more bell-shaped curve) and scale, which is related to magnitude. The product of these two parameters is the mean movement rate.

In the "no calf" model, the parameters remain constant throughout the entire calving period. In the "calf" model, the mean movement rate ($\overline{R}$) is constant before calving, abruptly drops at the calving date (Table 1), and then increases progressively to the pre-calving level, following this equation:

$$R(t) = \begin{cases} \alpha_m \times \beta_m & \text{when } t < \tau_c \\ \left(\alpha_c + \dfrac{\alpha_m - \alpha_c}{\kappa} t\right)\left(\beta_c + \dfrac{\beta_m - \beta_c}{\kappa} t\right) & \text{when } \tau_c \le t \le \tau_c + \kappa, \\ \alpha_m \times \beta_m & \text{when } t > \tau_c + \kappa \end{cases}$$

where t is time (starting on the first day of the defined period), τ_c is the timing of calving (the main parameter of interest), and κ is the number of days required to recover to the pre-calving movement rate. α_m and β_m are the shape and scale parameters of the gamma distribution that characterizes typical movement before calving and after recovery, and α_c and β_c are the shape and scale

TABLE 1 Definitions—table providing specific meaning for key terms and references.

Term	Level	Definition	References
Arrival date	Individual	Date at which a female entered the greater calving area polygon (95%).	
Calving date	Individual	Individual calving date in a given year estimated by the movement rate parturition analysis (MRPA).	
Calving lag	Individual	Time interval between the arrival date and the calving date.	
Calving location	Individual	Individual calving location in a given year estimated by the MRPA.	Cameron et al. (2020)
Departure date	Population	Average migration departure time of the females of the herd on their calving grounds obtained using the hierarchical range-shift analysis (HRSA).	Gurarie et al. (2019)
Arrival date	Population	Average migration arrival time of the females of the herd on their calving grounds obtained using the HRSA.	Gurarie et al. (2019)
Peak calving	Population	Date by which 50% of the births has occurred (i.e., median calving date).	Rutberg (1987)
Central calving area	Population	Area where 50% of females of a given herd gave birth across all years of observation in this study.	Adapted from Gunn and Miller (1986) and Cameron et al. (2020)
Greater calving area	Population	Area where 95% of females of a given herd gave birth across all years of observation in this study.	Adapted from Gunn and Miller (1986) and Cameron et al. (2020)
Traditional calving ground	Population	The overall area used by the majority of the parturient caribou for calving, including areas occupied during years when cows did not reach more central sections of their traditional calving grounds.	Gunn and Miller (1986)

parameters at calving. Rather than estimate α_c separately, we set it to be equal to the minimum of α_m or 1 if α_m was higher than 1. A shape parameter of 1 corresponds to an exponential distribution, which is an appropriate model for very little movement. In the majority (80%) of cases, α_m was greater than 1. In the "no calf" model, only two parameters were estimated (α_m and β_m), whereas the "calf" model had five (α_m, β_m, β_c, τ_c, and κ). As with previously published methods, we identified whether an animal calved by comparing the two models based on Akaike information criterion (AIC; Cameron et al., 2018; DeMars et al., 2013). We excluded animals that were identified by the movement rate parturition analysis (MRPA) as noncalving from all subsequent analyses. Several additional constraints limited our set of calving events: we constrained the calving date to occur within at least three days on either end of the period of analysis (i.e., no earlier than 22 May and no later than 4 July) and constrained the recovery period to last no less than 5 and no more than 21 days. We refer to this analysis as the MRPA and provide code for performing the analysis in the *TuktuTools* R package (available on GitHub, https://doi.org/10.5281/zenodo.7490164). For this analysis, we limited the dataset to the period from 19 May to 7 July. This left, on average, 162 ± 67 relocations/individual (3 ± 1 relocations/day) throughout the study period.

Migration timing

Because caribou migration is a collective behavior, we were interested in the average migration arrival date of the females of a population (or herd) on their calving grounds. To obtain the average arrival dates, we replicated the hierarchical range-shift analysis (HRSA) following Gurarie et al. (2019). The HRSA estimates the mean and SD of departure and arrival times, as well as pre- and post-migration ranges and the distance between them, thus making herd-year level inferences on the spring migration process (Gurarie et al., 2019). We used the mean departure and arrival date estimates from the HRSA to delineate the "pre-calving migration" seasons (see *Weather covariates* below).

Calving synchrony and trends

We defined peak calving as the median calving date (the date at which 50% of the births had already occurred, Table 1; Rutberg, 1987) and used the interquartile range (IQR; the central span of days during which 50% of calving events occurred) as a measure of variability of calving timing. To examine synchrony in calving timing across our study area, we estimated peak calving and IQR at the herd level (combining all years for each herd), at the annual level (combining all herds for each year), and for each herd-year combination.

We also estimated the pairwise correlation among herds' calving date in order to detect synchrony in calving timing between herds. To do so, we randomly sampled 10 calving dates (with replacement) per year for each herd and calculated the mean calving date per year and per herd. We then estimated the pairwise correlation among herds, repeating the process 10,000 times, and reporting the mean and 95% confidence intervals around those correlation estimates.

To examine temporal trends in calving dates, we reproduced Davidson et al.'s (2020) analysis by regressing calving date against year and used herd as a random intercept and year as a random slope, using a linear mixed-effects model.

Weather covariates

We extracted the weather conditions that individuals experienced throughout the year prior to calving and grouped these into different seasons (hereafter referred to as caribou seasons) based on the annual caribou life history pattern. These were as follows: early summer, the immediate post-calving period of intense insect harassment (15 June–15 August); late summer, when caribou typically take on the most mass (16 August–15 October); fall, roughly beginning with the rutting period (Dauphiné & McClure, 1974; Lent, 1965) and encompassing the migration as caribou shift toward their wintering grounds (16 October–15 December); winter (16 December–15 March); spring (16 March to herd migration departure, estimated by the HRSA); and pre-calving migration period estimated by the HRSA. To standardize caribou location data across different schedules and match the daily resolution of remotely sensed weather data (see next paragraph), we used the average daily location (i.e., the mean of the *x* and *y* coordinates of daily relocations, or centroid) of each individual to attribute weather covariates.

Temperature and precipitation data came from the Daily Surface Weather Data for North America collection (Daymet, spatial resolution = 1000 m, temporal resolution = 24 h), version 3, provided by NASA (Thornton et al., 2016). Wind speed came from the fifth-generation atmospheric reanalysis of global climate (ERA5 daily aggregates, spatial resolution = 27–28 km, temporal resolution = 24 h), provided by the European Centre for Medium-Range Weather Forecasts (ECMWF; Copernicus Climate Change Service [C3S], 2017). We applied the correction from Allen et al. (1998) to estimate wind speed at 2 m above land surface. To aggregate these daily measures to caribou season-specific metrics, we calculated average temperature (in degrees Celsius), cumulative precipitation (in millimeters of all forms of precipitation converted to water equivalent), and average wind speed (in meter per second) experienced by each female during each of the six caribou seasons. As an index of high insect harassment, we also calculated the number of days during which temperature was above 18°C and the number of days during which wind speed was below 6 m/s, during early summer. We summarized the weather conditions experienced by each herd by averaging each metric across individuals and years for each caribou season (Appendix S1: Figure S1). We obtained and preprocessed all weather variables using Google Earth Engine (Gorelick et al., 2017) and standardized by being centered and scaled at the population level, for each analysis (i.e., by removing the mean of each covariate from the value, divided by the SD).

Effect of weather conditions on calving date

To examine how calving date was influenced by environmental conditions during the 1-year period preceding calving, we regressed calving date (as Julian date, 1–365) against the additive effect of the weather covariates during all caribou seasons, with year and individual as random effects on the intercept.

Contribution of seasonal weather to calving date variation

To assess the influence of environmental conditions in each of the different caribou seasons on calving date, we quantified the explanatory power of caribou season-specific models. To do this, we first built six sets of linear models explaining variation in calving date against all covariates during all six seasons excluding one "focal season" (i.e., season during which we wanted to quantify the contribution of weather covariates to calving date). Thus, we built one set of models per excluded focal season and retained the covariates in all models with a ΔAIC $\leq$2 in each set.

To capture which period most influenced calving date, we grouped the best performing covariates per season and decomposed the R^2 of the full model (i.e., the model containing all the best covariates). We used Owen values to quantify the contribution of each caribou season to the R^2 of the full model. Owen values are a flexible measure of the contribution of a covariate or set of covariates to explaining observations in a generalized linear modeling framework (Huettner & Sunder, 2012). In this case, it is the average marginal contribution of the set of selected covariates measured in a given season (i.e., the proportion of the explained variance explained by the set of covariates; Huettner & Sunder, 2012). To do so, we built all possible models by changing the order of the caribou seasons in the model (i.e., 720 combinations). For each combination, the reference model contained all seasons without the ones appearing after the focal season (i.e., say we are interested in the effect of spring covariates, if the combination model is $Y \sim X_{\text{summer}} + X_{\text{late summer}} + X_{\text{fall}} + X_{\text{winter}} + X_{\text{spring}} + X_{\text{migration}}$, the reference model would be $Y \sim X_{\text{summer}} + X_{\text{late summer}} + X_{\text{fall}} + X_{\text{winter}} + X_{\text{spring}}$). We then estimated the marginal contribution of the focal period as the difference between the R^2 of the reference model and the R^2 of the same model without the focal period (i.e., in the previous example, we would calculate the difference in the R^2 of the reference model: $Y \sim X_{\text{summer}} + X_{\text{late summer}} + X_{\text{fall}} + X_{\text{winter}} + X_{\text{spring}}$ and the following model: $Y \sim X_{\text{summer}} + X_{\text{late summer}} + X_{\text{fall}} + X_{\text{winter}}$). Finally, we estimated Owen values by taking the mean of the marginal contributions of a given season (i.e., the mean of the marginal contribution of a given season for all combinations) and estimated the bootstrap SE, using 5000 iterations. The outcome of this analysis directly assessed the relative effect of different periods on calving timing, regardless of the strength or the direction of the variable effects, by giving the Owen values corresponding to each period rather than the coefficient corresponding to each covariate.

Delineating calving areas

For each individual that calved, we inferred calving locations as the GPS location corresponding to the estimated calving date. We then used all detected calving locations to estimate calving areas for each herd. We defined "central" and "greater" calving areas as the 50% and 95% contours, respectively, of a bivariate kernel Utilization Distribution (UD) fitted around those sites using the Least-Squares Cross Validation (LSCV) algorithm in adehabitatHR (R package; Calenge, 2006). We note that we make an ecological distinction between calving areas and traditional calving grounds (see Table 1).

Effect of weather conditions on calving location

To examine the effects of environmental conditions on the ability of females to reach the central and greater calving areas, we modeled the effect of weather conditions during winter, spring, and pre-calving migration on the calving location (i.e., individual calved inside the central calving area [50% kernel], inside the greater calving area [95%], or outside both). We fitted a set of cumulative link models (CLMs), with calving location as the ordinal multinomial response variable, using the R package ordinal (Christensen, 2018). Because the interaction among snow depth, temperature, and wind speed determines snow hardness and, consequently, caribou mobility (Duquette, 1988; Fancy & White, 1987), we regressed calving location against three two-way interactions: between winter cumulative precipitation and average spring temperature, between winter cumulative precipitation and average spring wind speed, and between average spring temperature and average spring wind speed. We also regressed calving location against the same three two-way interactions by replacing weather conditions during spring with conditions during migration to capture the potential effect of weather conditions on snow characteristics before and during migration.

Calving lag with respect to arrival on the greater calving area

We defined the individual arrival date on the calving area as the date when a given female entered the greater calving area polygon (Table 1). This value is distinct from the herd arrival time inferred from the HRSA in that the HRSA estimates the average arrival date for all females of the herd rather than the arrival date of a single female. We classified each calving location as being either inside the central calving area, inside the greater calving area, or outside both calving areas. Calving area polygons and calving location maps can be found in Appendix S2.

We estimated the calving lag as the time difference (in days) between the arrival date and calving date for each female. We then fitted a broken-stick regression between the calving lag and arrival date using package nlme (Pinheiro et al., 2006). We expected the relationship to be negative (i.e., when conditions are favorable for migration, females would arrive early on the greater calving area) until reaching a threshold value, at which point the calving lag would be constant, corresponding to the average number of days between arrival and calving on the greater calving area, allowing females to reach the calving area together. We compared this broken-stick model (with three parameters: intercept, slope, and threshold time) with a simpler linear regression (with two parameters: intercept and slope).

Effect of weather conditions on the time interval between arrival and calving

We examined the effect of environmental conditions on the calving lag between individual arrival date and calving date. We regressed calving lag against the same three two-way interactions as the calving location analysis, with year and individual as random effects on the intercept.

To quantify the effect of period-specific weather conditions (i.e., the strength and direction of the variable effects) on calving date, calving location, and calving lag, we fitted models separately for each herd and we report estimates and SEs of the coefficients for the covariates retained in the top-ranked model (i.e., the model with the lowest AIC). All of the analyses were performed in R, version 3.6.2 (R Core Team, 2019).

RESULTS

Detection of calving events

We performed the MRPA on 1607 individual-year combinations from 747 unique adult females. Of these, the analysis estimated calving events for 77% of all individual-years (1255 individual events). This rate ranged from 68% in the Bluenose West Herd to 89% in the Bluenose East Herd (Table 2). Noncalving females ($n = 352$ individual-years) were excluded from subsequent analyses.

Calving synchrony and trend

The overall peak calving date was 5 June and births were similarly synchronized among years and among herds for a given year (Appendix S3: Table S1 for yearly peak of calving by herd). However, we observed a lower interquartile range of calving events within herd-years (IQR = 4 days, SE = 0.2 days; i.e., for a given herd at a given year) than within herds across years (IQR = 6 days, SE = 0.4 days) or within years across herds (IQR = 6 days, SE = 0.5 days). This suggests greater calving synchrony at finer spatial and temporal scales than across herds for a given year, or across years for a given herd, and supports P1.

Neighboring herds had slightly more synchrony in their calving date than more distant herds (Figure 3a). For example, the Cape Bathurst Herd had a higher correlation in its calving dates with the Bluenose West Herd than with other herds ($p = 0.46$, 95% CI = 0.003; see Figure 3a). Similarly, the Bluenose East, Bathurst, and Beverly Herds had a higher calving date correlation with each other than with other herds (mean $p = 0.58$; see Figure 3a). Surprisingly, the Western Arctic Herd had a high calving date correlation with the Bluenose East, Bathurst, and Beverly Herds (Figure 3a).

The overall trend in calving timing as determined from the mixed-effects linear regression was −0.07 days/year (SE = 0.05). The earlier trend was not significant ($p = 0.08$; Figure 3b), providing support for P2.

Effect of weather conditions on calving date

The overall variation in calving date explained by weather covariates during the 1-year period preceding calving varied for all herds, ranging from 27% for the Qamanirjuaq Herd to 50% for the Beverly Herd (Figure 4; see Appendix S4: Table S1 for complete results). Weather conditions before conception (i.e., during early and late summer) explained between 27% of the modeled variation in calving date for the Western Arctic and Bathurst Herds and 48% for the Beverly Herd (Figure 4), providing mixed support for P3b. Of each of the caribou seasons, weather conditions in the early summer (15 June–5 August) and winter (16 December–15 March) periods contributed most to the modeled variation in calving date for all herds, with on average 21% of the explained variation for each herd attributed to each of these periods (Appendix S4: Table S1). However, there were notable exceptions, as only 11% of the explained variation was attributed to winter covariates for the Qamanirjuaq Herd

TABLE 2 Summary table of the number and percentage of female barren-ground caribou for which calving events were estimated, peak calving (median date ± SD), interquartile range (IQR; i.e., the number of days within which 50% of the births occurred).

		Parturient		Nonparturient			
Herd	**Years**	**No.**	**Percentage**	**No.**	**Percentage**	**Peak date**	**IQR**
Western Arctic	2010–2017	200	78	56	22	3 June ±5	7
Cape Bathurst	2006–2017	131	69	59	31	30 May ±6	7
Bluenose West	2006–2017	126	66	60	32	3 June ±6	7
Bluenose East	2009–2019	192	88	25	12	5 June ±6	5
Bathurst	2009–2019	137	72	52	28	2 June ±5	6
Beverly	2006–2019	197	78	55	22	9 June ±5	5
Qamanirjuaq	2013–2019	272	86	45	14	6 June ±5	4.25

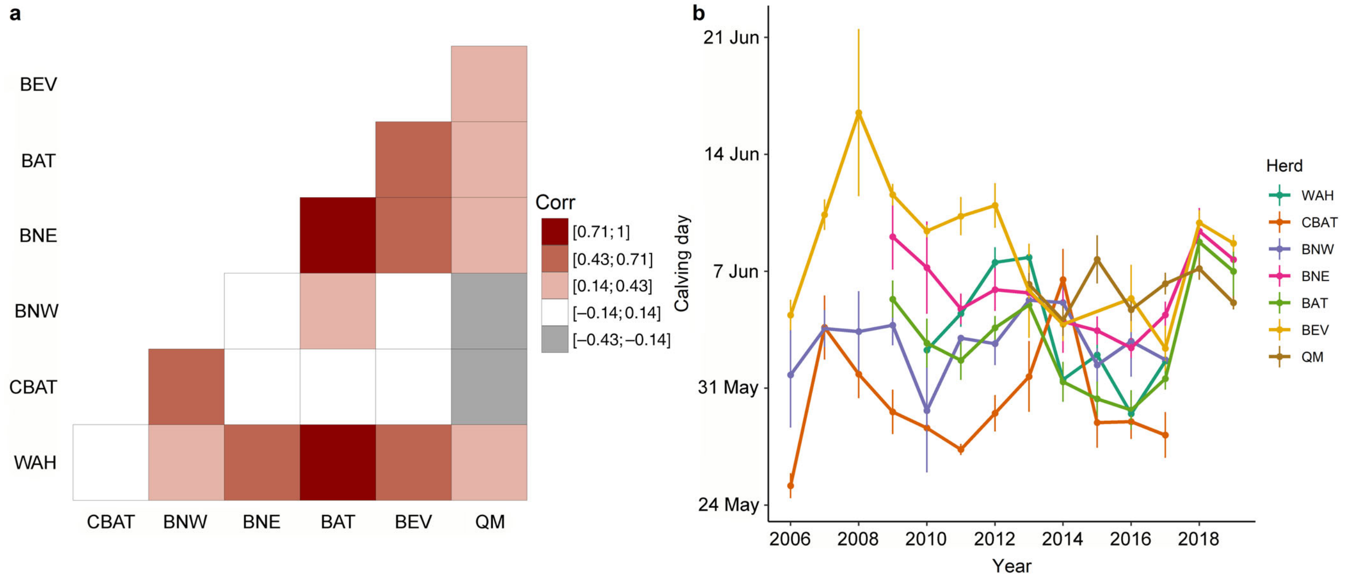

FIGURE 3 Pairwise correlation matrix of the calving timing among herds (sorted from west to east), estimated using the complete set of observations (a) and calving timing of each herd across years (b). Points represent the average calving day for that year and error bars represent the SE. BAT, Bathurst; BEV, Beverly; BNE, Bluenose East; BNW, Bluenose West; CBAT, Cape Bathurst; QM, Qamanirjuaq; WAH, Western Arctic.

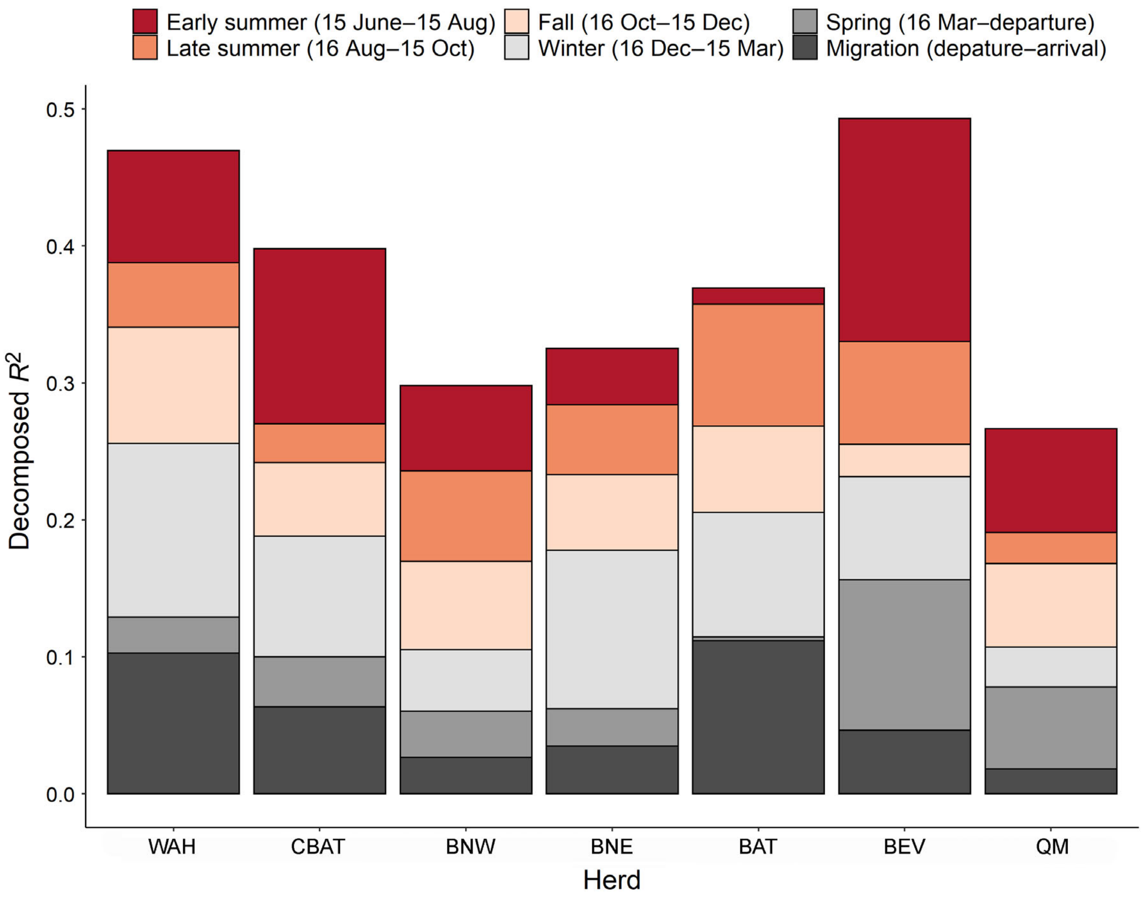

FIGURE 4 Decomposed R^2 of the model explaining variation of the calving date for each herd (sorted from west to east) (see Appendix S4: Table S1 for the covariates in the model for each herd). The R^2 has been decomposed using the Owen values of covariates grouped by periods. BAT, Bathurst; BEV, Beverly; BNE, Bluenose East; BNW, Bluenose West; CBAT, Cape Bathurst; QM, Qamanirjuaq; WAH, Western Arctic.

and only 3% was explained by early summer covariates for the Bathurst Herd (Appendix S4: Table S1).

The particular weather covariates that most influenced calving date differed among herds, with shared covariates sometimes differing in strength and direction of effect, thus not supporting P3a (Table 3). For example, warmer winter temperatures were associated with delayed calving for the Beverly Herd, earlier calving for the Western Arctic and Bluenose West Herds, and had no effect on the four other herds (Table 3).

Effect of weather conditions on calving location

The probability of calving within the greater or central calving area was related to various weather conditions during winter and spring or during winter and pre-calving migration for most herds, supporting P4 (Table 4, Figure 5b,c; Appendices S5, S6, and S11). Factors influencing calving location varied among herds, both in which covariates had an effect and the direction of those effects, but some consistencies across herds were evident. The probability of reaching the central calving area or the greater calving area was higher when wind speed was high during spring and migration for most of the herds, with the exception of the Beverly Herd (Table 4). In addition, high temperatures during spring or migration were associated with an increased probability of calving in the greater calving area for four of seven herds or outside the calving areas altogether for two herds (Table 4).

Calving lag with respect to arrival on the greater calving area

The average date of arrival on the greater calving area was 23 May (±10 days) and the calving lag ranged from

TABLE 3 Coefficients and SEs of the best performing covariates (i.e., covariates in the top-ranked model, based on AIC) explaining variation in the calving date for each herd.

Period	Covariate	WAH	CBAT	BNW	BNE	BAT	BEV	QM
Early summer	No. days with temperature >18°C							*2.68 ± 0.37*
	No. days with wind speed <6 m/s						*−1.18 ± 0.41*	
	Precipitation	*0.78 ± 0.34*	*−2.20 ± 0.61*					
	Temperature		*2.33 ± 0.65*					*−2.68 ± 0.69*
	Wind speed				0.67 ± 0.41			
Late summer	Precipitation					*−2.27 ± 0.68*	*1.12 ± 0.47*	
	Temperature				*−0.86 ± 0.42*			
	Wind speed			−1.34 ± 0.71			*−1.79 ± 0.46*	
Fall	Precipitation		*1.95 ± 0.69*	1.77 ± 0.96	−0.79 ± 0.42			
	Temperature					1.19 ± 0.69		
	Wind speed					−1.77 ± 0.48		
Winter	Precipitation		*−1.70 ± 0.58*		*−1.50 ± 0.41*			
	Temperature	*−2.54 ± 0.33*		*−1.98 ± 0.87*			*1.90 ± 0.53*	
	Wind speed				0.75 ± 0.40			
Spring	Precipitation							
	Temperature							
	Wind speed							*−1.27 ± 0.39*
Migration	Precipitation							
	Temperature	*2.02 ± 0.34*	*1.36 ± 0.59*					
	Wind speed					*−1.43 ± 0.49*	*1.19 ± 0.50*	

Note: Positive values indicate a later date of calving with an increasing value of the corresponding covariate, whereas negative values indicate the reverse. Values in italics are significant.

Abbreviations: AIC, Akaike information criterion; BAT, Bathurst; BEV, Beverly; BNE, Bluenose East; BNW, Bluenose West; CBAT, Cape Bathurst; QM, Qamanirjuaq; WAH, Western Arctic.

TABLE 4 Coefficients and SEs of the best performing covariates (i.e., covariates in the top-ranked model, based on AIC) explaining variation in the calving location for each herd.

Period	Covariate	WAH	CBAT	BNW	BNE	BAT	BEV	QM
Spring	Winter precipitation	*0.37 ± 0.20*				*−0.58 ± 0.40*		0.19 ± 0.31
	Spring temperature	0.10 ± 0.18			0.21 ± 0.23	*0.66 ± 0.65*	0.17 ± 0.21	
	Spring wind speed	*−0.41 ± 0.23*			*−0.30 ± 0.22*	*−0.94 ± 0.49*	*0.34 ± 0.20*	−0.28 ± 0.28
	Winter precipitation × spring temperature	*−0.46 ± 0.23*						
	Winter precipitation × spring wind speed	*0.77 ± 0.30*						−0.11 ± 0.39
	Spring temperature × spring wind speed	*−0.40 ± 0.13*				*−1.31 ± 0.41*	*−0.30 ± 0.14*	
Migration	Winter precipitation	*−0.61 ± 0.29*	*0.32 ± 0.21*		*0.33 ± 0.23*			
	Migration temperature	*1.15 ± 0.25*						*0.90 ± 0.26*
	Migration wind speed	*−1.14 ± 0.25*	*−0.70 ± 0.25*		*−0.33 ± 0.21*			*−0.67 ± 0.25*
	Winter precipitation × migration temperature	*0.52 ± 0.27*						
	Winter precipitation × migration wind speed				*−0.51 ± 0.23*			
	Migration temperature × migration wind speed	*0.77 ± 0.28*						*0.86 ± 0.24*

Note: Positive values indicate a higher probability of calving in the greater calving area (95%) or outside the calving area versus in the central calving area (50%), for a high value of the corresponding covariate, whereas negative values indicate the reverse. Values in italics are significant.
Abbreviations: AIC, Akaike information criterion; BAT, Bathurst; BEV, Beverly; BNE, Bluenose East; BNW, Bluenose West; CBAT, Cape Bathurst; QM, Qamanirjuaq; WAH, Western Arctic.

0 to 50 days (13 ± 8 days [mean ± SE]). Our broken-stick linear model relating calving lag and date of arrival on the greater calving area outperformed the linear model (ΔAIC ≥2) for four of six herds and did not converge for the Qamanirjuaq Herd (Appendix S7: Table S1), partially supporting P5a. The broken-stick model indicated that after around 30 May (SD = 6 days), the average calving lag was constant at five days (ranging from three days [Bluenose West and Beverly] to nine days [Bluenose East], Appendix S7: Table S1). Before 30 May, the estimated slope was on average −0.9 (from −1.18 for the Bluenose East Herd to −0.72 for the Western Arctic Herd; Figure 5d; Appendix S7: Table S1). In addition, for four of seven herds (Cape Bathurst, Bluenose East, Bluenose West, and Bathurst), there were no annual trends in calving lag, whereas the other three (Western Arctic, Beverly, and Qamanirjuaq) exhibited greater calving lags in more recent years (Appendix S10: Table S1, Figure S1).

Effect of weather conditions on calving lag

Weather conditions did not affect the calving lag the same way in all herds (Table 5; Appendices S8 and S9), but there were some consistent trends across herds, lending some support to P5b. When temperature during spring or migration was high, calving lag consistently decreased. In addition, an increase in wind speed during spring had a positive effect on the calving lag (i.e., females arrived earlier before calving on the greater calving area) in the majority of herds (Figure 5e, Table 5).

DISCUSSION

Timing and location of calving, through their effects on juvenile survival, are important drivers of ungulate population dynamics (Bunnell, 1982; Gaillard et al., 1998, 2000). For social, migratory ungulates, simultaneous pressures exist for both temporal synchrony and spatial aggregation of births (Cote et al., 2017; Estes, 1976; Gunn & Miller, 1986; Sinclair et al., 2000). By estimating 1255 calving events across seven herds over a 15-year period—an unprecedentedly large dataset—we examined timing of calving, calving synchrony, and aggregation as well as the influence of climatic factors on spatiotemporal variations in barren-ground caribou calving across a wide swath of northern North America (Figure 4). Despite the

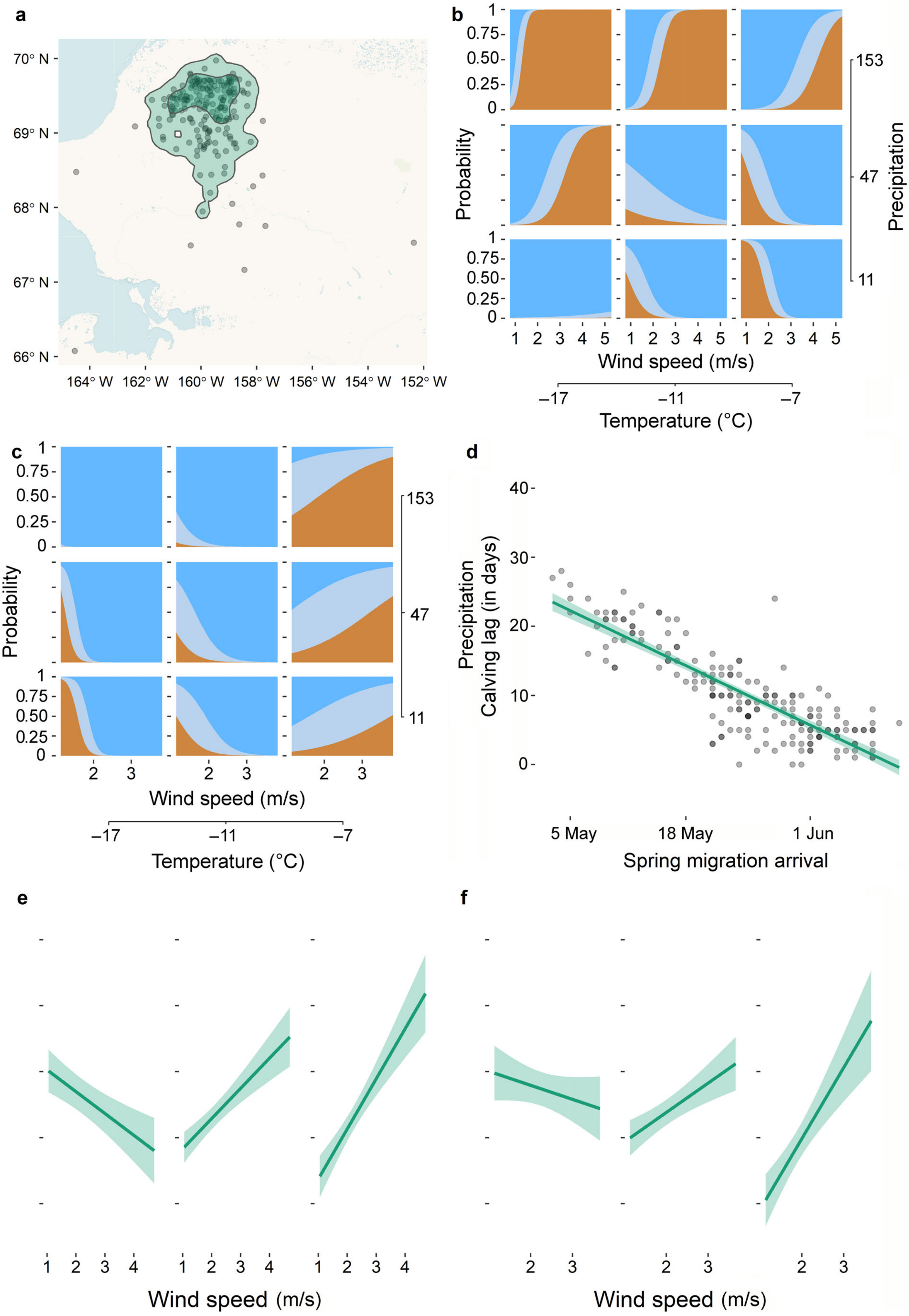

FIGURE 5 Legend on next page.

large amount of environmental variability that occurs across the span of the continent, we documented widespread synchrony in the timing of calving. As expected, synchrony increased with decreasing spatial scale, likely related to individual responses to local conditions and perhaps the social nature of this gregarious animal. We found that conditions associated with deep, soft snow affected the ability of all herds to reach their respective calving areas prior to parturition. Calving lag (the time between arrival on the calving grounds and parturition) can be considered a behavioral adaptation to buffer annual environmental variation, ensuring that individuals are within the greater calving area prior to parturition. While climate change has brought significantly earlier springs to the Arctic, we did not detect a corresponding change in calving date in caribou across northern North America. However, we found that the calving lag increased for some of the herds and remained constant for others (Appendix S10), suggesting an adaptation to interannual climate variability in the Arctic.

Effect of weather conditions on calving location

We found that weather conditions in winter and spring can directly impact the ability of caribou to reach their calving grounds. Warm temperatures and low wind speed (i.e., conditions leading to deep, soft, melting snow; Collins & Smith, 1991; Eira et al., 2013) directly led to a higher probability of females calving outside the central or even greater calving areas, or led to females arriving with very little time before calving. Deep soft snow is known to hamper caribou movements and delay pre-calving migration departure (Gurarie et al., 2019; Le Corre et al., 2017; Leclerc et al., 2021), whereas ice and hard snow can facilitate movement (Duquette, 1988; Leblond et al., 2016). These patterns were consistent across all herds. Notably, those herds for which weather conditions had the least influence on calving ground arrival (Cape Bathurst and the Bluenose West) also had the shortest migration distances (Gurarie et al., 2019). Failure to reach calving areas, as we document here, has also been reported for the Porcupine Herd in 2000 and 2001 (Griffith et al., 2002).

The high fidelity that caribou exhibit to particular calving areas (Cameron et al., 2020; Gunn & Miller, 1986; Joly, Gurarie, et al., 2021), as well as the high level of temporal synchrony of calving timing revealed by our analysis, reflects the importance of spatiotemporal aggregation of births as an evolutionary strategy to increase neonatal survival (Bekenov et al., 1998; Estes, 1976; Sinclair et al., 2000). Calves born outside of the calving area are more susceptible to predation or have access to poorer quality forage (Bergerud et al., 2007; Cameron et al., 2020; Griffith et al., 2002). Thus, opportunities for climate-related disruption of access to calving grounds may have important demographic consequences.

Calving synchrony

Parturition timing has likely evolved as a response to seasonality, resource availability, and predation (Ims, 1990; Rutberg, 1987), with each factor exerting selective pressure for synchronous births. We documented continental-scale (across >3000 km of longitude, >1000 km of latitude) synchrony in calving timing over almost two decades and a wide range of environmental conditions: Peak calving for each herd and year occurred within a 3-week window (25 May–16 June; see Appendix S3: Table S1). Our results support our prediction (P1) that herds exhibited substantial synchrony with neighboring herds, even though geographically distant herds had synchronous calving timing, hypothetically led by weather conditions occurring similarly at distant locations. P1 was also supported

FIGURE 5 Spatiotemporal parturition analyses for the Western Arctic Herd, as an example. Corresponding summary figures for all the herds can be found in Appendix S11. (a) All calving locations and the central (dark green) and the greater calving areas (light green), determined as the 50% and 95% kernel Utilization Distribution (UD), respectively. (b) Predictions of the cumulative link model of calving location (i.e., inside the central calving area—blue; inside the greater calving area—gray; or outside the calving area—orange) against the two-way interactions between the total amount of precipitation during winter (panels going up), temperature during spring (panels going right), and wind speed during spring (*x*-axis). Thus, for example, warm, wet conditions are represented in the upper right subpanel with a high probability of not reaching calving grounds, while cold, dry conditions are represented in the lower left subpanel. (c) Predictions of the cumulative link model of calving location against the two-way interactions between the total amount of precipitation during winter (panels going up), temperature during migration (panels going right), and wind speed during migration (*x*-axis). (d) Linear regression between calving lag (i.e., the number of days between arrival on the greater calving area and calving) and date of arrival on the greater calving area. (e) Predictions of the generalized linear model of the calving lag against the two-way interaction between wind speed during spring and temperature during spring. (f) Predictions of the generalized linear model of the calving lag against the two-way interaction between wind speed during migration and temperature during migration.

TABLE 5 Coefficients and SEs of the best performing covariates (i.e., covariates in the top-ranked model, based on AIC) explaining variation in the calving lag for each herd.

Period	Covariate	WAH	CBAT	BNW	BNE	BAT	BEV	QM
Spring	Winter precipitation				*−1.01 ± 0.76*		0.80 ± 1.30	*2.01 ± 0.99*
	Spring temperature	*−1.06 ± 0.57*	−1.31 ± 1.65		*−2.42 ± 0.83*	*−3.72 ± 0.90*	*−2.81 ± 1.69*	*−3.12 ± 0.73*
	Spring wind speed	*2.43 ± 0.85*	*−5.63 ± 1.08*	*3.17 ± 1.44*	*0.99 ± 0.65*	*−1.65 ± 1.00*		*2.11 ± 1.00*
	Winter precipitation × spring temperature				*−1.38 ± 0.88*		*4.29 ± 2.14*	
	Winter precipitation × spring wind speed				*−1.59 ± 0.78*			*1.49 ± 0.79*
	Spring temperature × spring wind speed	*1.13 ± 0.32*	*−3.23 ± 1.10*			*2.58 ± 0.84*		
Migration	Winter precipitation				*−2.29 ± 1.13*			
	Migration temperature	*−1.75 ± 0.79*			*−5.04 ± 1.05*	*−2.93 ± 1.04*	*−2.70 ± 1.09*	*−5.57 ± 1.07*
	Migration wind speed	*1.63 ± 0.79*			*−1.55 ± 0.75*			
	Winter precipitation × migration temperature				*2.77 ± 0.98*			
	Winter precipitation × migration wind speed				*−1.77 ± 0.84*			
	Migration temperature × migration wind speed	*1.08 ± 0.47*						

Note: Positive values indicate a longer calving lag, for a high value of the corresponding covariate, whereas negative values indicate the reverse. Values in italics are significant.

Abbreviations: AIC, Akaike information criterion; BAT, Bathurst; BEV, Beverly; BNE, Bluenose East; BNW, Bluenose West; CBAT, Cape Bathurst; QM, Qamanirjuaq; WAH, Western Arctic.

by the even greater synchrony at the intra-herd level. This suggests that herds have adapted calving timing to their local conditions (i.e., the environmental conditions specific to the area where the herd is located), as seen in other ungulates such as bighorn sheep (*Ovis canadensis*; Whiting et al., 2012) and roe deer (*Capreolus capreolus*; Peláez et al., 2020). The observation that synchrony was highest within a given herd-year further supports the assertion that specific shared conditions preceding year influence calving timing.

Integrated effects of weather conditions

We found that no less than 15% (Bluenose West and Qamanirjuaq) and as much as 40% (Western Arctic and Beverly) of the variation in calving timing could be explained by seasonal weather conditions. Considering the complexity and indirect links among weather and behavioral and physiological constraints of calving, as well as the imprecision and coarse scale with which weather covariates were estimated and included in our models, this is a surprisingly high amount of variation explained by weather. Furthermore, more than one third of the modeled variation was explained by weather conditions preceding the rut, during the early and late summer periods (i.e., more than 8 months before calving; Appendix S4: Table S1).

Calving timing, by definition, is the sum of conception date (which is tied to estrus timing) and gestation period; with the former being potentially more plastic than the latter (Clements et al., 2010; Matsuura et al., 2004). In many ungulates, including reindeer and caribou, females that are fatter at conception calve earlier (Adams & Dale, 1998; Brown & Mallory, 2007; Keech et al., 2000; Skogland, 1984), potentially due to earlier conception (Bergerud et al., 2007; Mysterud et al., 2009; Rowell & Shipka, 2009) or shorter gestation period (Aikens et al., 2021; Asher et al., 2005; Bergerud et al., 2007; McEwan & Whitehead, 1972).

Separating the effects of conception timing and gestation period is difficult without developing approaches to estimate conception date at a large scale. While inferring conception timing directly from movement data poses a greater challenge than estimating parturition timing, it is an important line of research that warrants additional attention. While caribou are generally considered to be "capital" breeders (Taillon et al., 2013), it is worth noting that a substantial variation in calving timing is explained by conditions after the rut (in fall, winter, and spring): places them on a continuum between "capital" and "income" breeders (Jönsson, 1997). This is consistent with the observation by Loe et al. (2021) that late winter body condition explains 90% of the variation in population growth rates for wild reindeer in Svalbard.

Local variation due to local adaptation?

Despite the strong linkages between calving and weather in a general sense, there was wide variability in both the particular weather conditions that influenced calving timing as well as the direction and magnitude of those effects across herds. For example, warmer winter temperatures were associated with earlier calving dates in some herds (Western Arctic and Bluenose West), had no relationship with other herds, and were even associated with delayed calving for one herd (e.g., Beverly). These differences likely reflect strong local effects (e.g., habitat suitability), but can be challenging to interpret. The Western Arctic Herd typically overwinters in a coastal tundra environment, with a relatively mild winter climate and where snowy, cold, and windy winters might make food difficult to access. Conversely, the Bluenose West and Beverly herds both overwinter south of, or at the edge of, the boreal forest tree line (albeit in different ecozones), but these two herds had opposite responses to winter temperature conditions.

The local specificity of these relationships is an important aspect to consider when generalizing across caribou populations. Although there is some overlap among herds, particularly in the winter months when the animals are most dispersed and movement rates are the lowest, summering ranges and migration pathways tend to be distinct for most herds, and the weather conditions and biotic environments that they experience can be similarly unique, promoting local adaptations as suggested by the high levels of genetic variations in barren-ground caribou populations (McFarlane et al., 2016). In other words, each herd may be adapted to specific local conditions and therefore may have specific optimal conditions, such that the absolute values of such conditions may matter less than deviations from local norms. Similarly, localized responses to environmental conditions have been reported in multipopulation studies of reindeer (Hansen et al., 2019) and wild boar (*Sus scrofa*, Vetter et al., 2015).

Previous work by Davidson et al. (2020) reported an overall trend toward earlier calving for a subset of herds, at a rate of −0.4 days/year. Our more extensive analyses showed an overall trend toward earlier calving times (P2), but it was not significant. The discrepancy between the two studies is mainly explained by later calving dates in the most recent years (Figure 3b). While the aggregated dataset analyzed here is perhaps unprecedented in its sample size for large, free-ranging mammals, the complete calving time series are, in fact, rather short (7–14 years), highly variable across years and herds, and sensitive to outlying years. Trends in birth timing and opportunities for mismatches between birth timing and resource availability will be better understood as high-quality movement data continue to be collected with the help of consistently applied analysis tools such as the ones presented here.

Methodological robustness and caveats

An important methodological question is the ability of parturition models to estimate the timing of calving. We estimated that calving occurred in 77% of the individual-years studied here, with relatively consistent results across herds. This value is lower than typically reported pregnancy rates and female:calf ratios (Adamczewski et al., 2019; Cameron et al., 1993; Dauphiné & McClure, 1974) and there is, inevitably, uncertainty and error in this individual movement method (true-positive rate: 0.85, false-positive rate: 0.84; Appendix S12). Many of those nonpregnant females misidentified as pregnant females displayed the stereotypical profile of a sudden drop in movement rate, followed by a gradual increase that was similar to the movement profile of calving females. This result points to the influence that collective, social behavior may have on individual movements, such that some pregnant and nonpregnant females may have similar movements at the scale we considered, owing to the social grouping of individuals in the calving areas. We recommend further improvements to the methodology to target the short window of isolation at calving when the mother and calf establish pair bonds prior to joining larger nursery bands (Lent, 1966), such as methods leveraging higher frequency GPS data (Hepler, 2019). However, given the highly collective behavior exhibited by barren-ground caribou, especially during their migrations, summer, and the reproductive period (Dalziel et al., 2015; Skoog, 1968), both nonpregnant and pregnant females mostly experience similar environmental conditions throughout the year and along migration routes. Even in winter, pregnant and nonpregnant female caribou can be found sympatrically (Joly et al., 2015). Thus, we expect the conclusions made about calving ecology to be robust, even when including the false-positive calving events (see Appendix S12).

CONCLUSIONS

Climate change scenarios for the Arctic predict continuing trends of advancing spring, warming, changes in vegetation phenology, and greater frequency and intensity of precipitation (Box et al., 2019; IPCC, 2015). We did not detect a significant advance of calving dates corresponding to large-scale climate trends. Consequences related to phenological mismatch for caribou have been debated (Gustine et al., 2017; Kerby & Post, 2013; Mallory et al., 2020; Post et al., 2008). As caribou calving in the Arctic takes place in advance of green-up, we concur with Joly, Gunn, et al. (2021) that mismatch impacts will be subtle at first and that monitoring parturition timing will remain an important task going forward.

On the other hand, other climate-change-related impacts may immediately impact caribou as our results do suggest that the combined effects of increased precipitation and warming temperatures could be leading to later arrivals on the calving grounds. This, in turn, could lead to more calving events occurring outside of traditional calving grounds following pre-calving migration, with potential for reduced reproductive output. A worst-case scenario is one in which conditions that push calving timing earlier (e.g., good summer foraging conditions leading to earlier rut and good winter conditions leading to a shorter gestation) coincide with conditions that make pre-calving migration difficult (e.g., wet and heavy snow), in which case many calves could be born outside the calving areas. Alternatively, enough warming in winter and spring may reduce snow depth and/or increase snow hardness (via thaw–freeze cycling), allowing for increased movement rates during pre-calving migration. The rather broad range in calving lag that we documented, however, reinforces the notion that caribou display plasticity in migrations (i.e., their astonishing ability to move across the landscape, even under dynamic and unpredictable spring conditions). Under most conditions, caribou were able to arrive at the calving ground well in time to calve, with a typical lag of five to nine days.

Although our results and the relative short duration of our time series limit general conclusions on how caribou will respond to future broadscale trends in climate, our findings contribute to a better understanding of factors influencing calving timing and location, which is an important characteristic of population dynamics of caribou. In addition, because timing and location of calving are likely to affect juvenile survival, which is a factor driving population dynamics in many species, our work demonstrates the range of ecological insights that can be gained when large-scale, comparative analyses incorporate information on local conditions. With almost all large northern caribou herds in decline across the Arctic, we recommend not just intensifying efforts to monitor the timing and location of calving, but also examining how changing weather patterns during summer and winter are affecting calving in terms of impacts on the herd declines via productivity and juvenile survival.

AUTHOR CONTRIBUTIONS

Ophélie H. Couriot and Eliezer Gurarie conceived the ideas and designed the study. Kyle Joly, Jan Adamczewski, Mitch W. Campbell, Tracy Davison, Allicia P. Kelly, Matthew D. Cameron, and Judy Williams provided the data. Ophélie H. Couriot and Eliezer Gurarie carried out the statistical analyses with the help of Matthew D. Cameron. Ophélie H. Couriot and Eliezer Gurarie took the lead in writing the manuscript. All authors contributed to the interpretation of the results, provided critical feedback on the manuscript, and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Western Arctic Herd caribou location data used in this manuscript are available from the National Park Service DataStore: https://irma.nps.gov/Datastore/Reference/Profile/2260262. Caribou data from the Northwest Territories (Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Beverly) are available from the Wildlife Management Information System database: https://www.enr.gov.nt.ca/en/services/research-and-data-nwt/wildlife-management-information-system. Qamanirjuaq caribou data can be available upon request by contacting the Department of Environment, Government of Nunavut, Arviat, Nunavut, Canada. However, access to the data is restricted due to the sensitivity of a harvestable species' location data and applicable laws and policies of the United States and Canada. The code used to perform the movement rate parturition analysis is available in the TuktuTools R package, available from Zenodo: https://doi.org/10.5281/zenodo.7490164.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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