ORIGINAL RESEARCH



Birth date determines early calf survival in migratory caribou

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Abstract

The decline of most caribou (*Rangifer tarandus*) populations underlines the need to understand the determinants of key demographic parameters. In migratory caribou, we have limited information on rates and drivers of pre-weaning mortality. We fitted 60 pregnant females of the Rivière-aux-Feuilles caribou herd with GPS camera collars to track the survival of calves from birth to weaning in 2016–2018. Over the three years, calf survival rate before weaning, i.e. to 01-Sep, approximately three months of age, was 0.63 (CI 0.50–0.77). Summer mortality risk was mainly influenced by calf birth date, with calves born earlier in the calving season having a lower mortality risk than those born later. Mortality also increased when calves experienced low or high temperature during calving. This study provides the first estimates of pre-weaning survival of migratory caribou calves in this herd, illustrating the value of new technologies to collect data otherwise difficult to obtain in widely distributed migratory populations. This approach can easily be extended to other large herbivores and predators. Our study brings new insights on how climate change may affect summer juvenile survival given the increased temperatures and faster changes in plant phenology expected in the future.

Keywords Survival determinants · Pre-weaning survival · Rangifer tarandus · CMR model · Camera collars

Introduction

Reliable estimates of fecundity, survival, and their drivers are needed to better understand population demography (Mace et al. 2010). In ungulates, juvenile recruitment, the product of female fecundity and juvenile survival (Owen-Smith and Mason 2005), is a major driver of population dynamics (Coulson et al. 2001). Several factors such as maternal allocation (Carstensen et al. 2009), weather conditions (Eacker et al. 2016), and predation (Jacques et al.

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2015) can affect juvenile survival. Some of these factors may partially compensate each other, for example predation risk and weather conditions or resource availability (Barber-Meyer et al. 2008). In any cases, juveniles seem particularly at risk before weaning (Gaillard et al. 2000). Monitoring pre-weaning survival presents multiple challenges, such as limited access to birth sites over large remote areas related to field access and cost, and the vulnerability of neonates to manipulation and markers, such as GPS collars, that may affect their survival (Venturato et al. 2009; Roberts 2011).

At birth, survival is influenced by body condition, which is often affected by maternal traits (Wilson and Festa-Bianchet 2009). Lighter mothers give birth to smaller offspring (Robbins and Robbins 1979; Lamb et al. 2023) that have low survival (Keech et al. 2000; Donadio et al. 2012; Otgonbayar et al. 2017). Maternal effects may be reinforced during late gestation, when females have high energy demands but forage abundance and quality are poor (Barboza and Bowyer 2001; Wilson and Festa-Bianchet 2009), potentially reducing fetal growth and birth mass (Parker et al. 2009; Lamb et al. 2023). In their first weeks, juvenile ungulates are completely dependent on maternal milk and will not survive if their mother dies (Landete-Castillejos et al. 2005; Parker et al. 2009). Females in poor body condition may provide less or lower quality milk (Landete-Castillejos et al. 2003; Desforges et al. 2021), which can decrease the growth and survival of juveniles (Tollefson et al. 2011; Scornavacca et al. 2016). Female condition at calving and during lactation is thus a key determinant of offspring condition and survival.

Timing of birth is another key determinant of juvenile survival in ungulates (Bishop et al. 2009; Lee et al. 2017; Thel et al. 2021). Delayed birth may decrease offspring survival due to mismatch in resource availability (Parker et al. 2009), adverse weather conditions (Thel et al. 2021), increased predation risk (Michel et al. 2020) and lower birth mass (Paoli et al. 2019). During early lactation, an early onset of vegetation growth and high productivity allow mothers to improve body condition (Tveraa et al. 2003; Parker et al. 2009) and may have an indirect positive effect on juvenile survival (Landete-Castillejos et al. 2005; Therrien et al. 2008). Inversely, a mismatch between the availability of high-quality food and the peak of lactation can reduce body condition of juveniles (Tveraa et al. 2013; Plard et al. 2014; Stoner et al. 2016). When juveniles are born late in the season, the highest energetic demands of lactation occur after the peak in vegetation availability and quality. Maternal food intake may be insufficient to cover the energetic needs of lactation (Parker et al. 2009; Plard et al. 2014), leading to higher rates of juvenile mortality.

Weather conditions may directly affect juvenile survival, particularly immediately after birth, when neonates face a high energy demand for thermoregulation (Knott et al. 2005; Michel et al. 2018). Rain and snow during the first week of life combined with low spring temperatures can increase the risk of hypothermia (Michel et al. 2018; Chinn et al. 2021). Thermoregulatory ability is poor in small or malnourished neonates (Knott et al. 2005; Dion et al. 2020). Vegetation quality and availability may also directly affect growth and survival when juvenile start to feed on forage (Pettorelli et al. 2005b; Garel et al. 2011; Scornavacca et al. 2016). Changes in quality and availability of forage can be induced by temperature and either improve neonatal survival (Therrien et al. 2008; Michel et al. 2018) or deteriorate their physical condition (Pettorelli et al. 2007; Tveraa et al. 2013). Warm summers are also associated with greater insect harassment that can drastically reduce foraging activities (Dussault et al. 2004; Benedict and Barboza 2022) and lower body condition (Hagemoen and Reimers 2002; Benedict and Barboza 2022).

Most research on the drivers of population dynamics in migratory caribou and other ungulates has focused on juvenile recruitment, assessed many months after weaning (Mahoney and Schaefer 2002; Coulson et al. 2005; Serrouya et al. 2017). Pre-weaning survival is expected to vary considerably between years (Gaillard et al. 2000; Harris et al. 2007), but it is rarely studied, notably due to difficulties in obtaining such information in the wild (Duquette et al. 2015; Mumma et al. 2019). Remote data collection using GPS collars and associated devices such as accelerometers and cameras can partly overcome these limitations for monitoring newborns (Lavelle et al. 2012; Brockman et al. 2017), especially in migratory species occupying a very large range (Whitten et al. 1992).

We deployed high-resolution camera collars on pregnant females in the Rivière-aux-Feuilles herd (northern Québec, Canada) to investigate the drivers of pre-weaning survival in migratory caribou. Like most Rangifer populations worldwide (Vors and Boyce 2009), the Rivière-aux-Feuilles herd is in decline and decreased by more than 70% over the last 25 years (see Fig. 2 in Gagnon et al. 2020). During this period, the herd experienced highly variable autumn recruitment, with calves to females ratio ranging from 14:100 in 2014 (Taillon et al. 2016) to 56:100 in 2020 (MFFP, unpubl. data). Calf survival may be a key element explaining the population reduction (Gaillard et al. 1998; White et al. 2011), but no direct information on pre-weaning survival is available for migratory caribou. There are currently no data on newborn survival in barren-ground caribou. Our study aims to fill this gap. To estimate pre-weaning survival, we tracked calf sightings in videos collected by camera collars from birth to weaning (ca. 3 months old, Vuillaume et al. 2021). We then assessed whether maternal body condition prior to calving, calf birth date, resource availability, and weather conditions influenced pre-weaning calf mortality. We expected survival probability to vary yearly and to be explained by both individual and environmental conditions.

Methods

Study area

We monitored caribou on calving and summer ranges of the Rivière-aux-Feuilles herd in Nunavik, northern Québec, Canada (Fig. 1). The calving range covered about 127,000 km² in 2016–2018 and the summer range extended over about 254,000 km² (Fig. 1). According to aerial survey estimates, the herd reached at least 628,000 individuals in 2001 (Couturier et al. 2004), before declining to 199,000 (\pm 15,920, 90% CI) individuals during the latest survey in 2016 (Ministère des Forêts de la Faune et des Parcs 2016).

The Rivière-aux-Feuilles herd migrates ca. 800 km during spring (April–May) from its winter range in the taiga to its calving ground in the tundra (Le Corre et al. 2014). Females usually arrive on the calving ground in early June, where they remain for ca. 35 days (Taillon 2013), before moving to their summer range, where they feed on highquality forage until late September (Taillon et al. 2012; Le Corre et al. 2017). Vegetation in summer includes graminoids, herbaceous, dwarf shrubs (e.g., *Betula* spp., *Salix* spp.), terrestrial lichens, and mosses (Walker et al. 2005).



Fig. 1 Calving and summer ranges (95% kernels) of female migratory caribou (*Rangifer tarandus*) from the Rivière-aux-Feuilles herd, Nunavik, Canada, 2016–2018

The climate of both the calving and summer ranges is characterized by cool summers, with an average maximum temperature of 11.7 °C and an average summer total precipitation of 169.7 kg m⁻² (North American Regional Reanalysis data; Mesinger et al. 2006).

Captures and camera collars

We deployed camera collars on pregnant female caribou to monitor the survival of their calves over the calving and summer seasons. Each year, we located caribou groups based on the recent locations of GPS-collared adult caribou. Groups ranged from a few dozen to several hundred caribou and were several kilometers away from other groups. Groups were spread over ca. 100,000 km² on the winter range, between the 52° and the 55° parallel. We randomly selected a single potentially pregnant female per group sampled.

We captured 60 pregnant female caribou in March 2016 (n=14), 2017 (n=24), and 2018 (n=22). Captures occurred at least eight weeks before calving, which is usually centered around 09-Jun (1995–2010 average; Taillon et al. 2016). Experienced technicians using a net gun fired from a helicopter captured, restrained, collared, and weighed the

caribou, confirming pregnancy with an ultrasound scanner (ExaGo, ECM Noveko International Inc., Angoulême, France). Camera-GPS collars (model: VERTEX Plus, VECTRONIC Aerospace GmbH, Berlin, Germany) were deployed only on pregnant females. Two models of cameras were used each year: 14 collars had a camera with a resolution of 848×480 pixels and a rate of 60 frames s⁻¹, and 10 had a camera with a resolution of 1280×720 pixels and a rate of 30 frames s⁻¹ (Vuillaume et al. 2021). All collars recorded a 10-s video every 20 min, and a GPS location every hour, from 01-Jun to 01-Sep when they automatically dropped. Collars recorded videos from 05:00 am to 8:00 pm daily, providing a potential of 4426 videos collar⁻¹ over the monitoring period.

Of the 60 collars deployed, 52 were retained for complete analysis. We excluded five collars because they failed to record more than 30% of videos (Lavelle et al. 2015). Three females died before calving. Two females gave birth to stillborn calves which we included only in the estimation of survival. Given the total number of videos (253,920) and the time required to analyse a 10-s video by a trained observer (~1 min), we used a subsample of one video h^{-1} in the analyses. For each day, we randomly selected the time of the first video watched (8:00, 8:20 or 8:40) and then analyzed the videos recorded at hourly intervals for that day. A total of 15 different observers (six each year) worked on the data extraction from the videos. The number of collars assigned to each observer varied from one to seven. To limit the risk of observer influence on the probability of re-sighting, all observers were previously trained for about 10 h with a set of 200 pre-analyzed videos to standardize their interpretation (Vuillaume et al. 2021).

Life history

We built calf life histories to identify which calves survived and which died and when. After the first detected occurrence of the calf, each subsequent video became a re-sighting opportunity. As calves age, the distance between mother and calf increases and the calf should be less likely to be seen in videos (Severud et al. 2019). To overcome this, we computed re-sighting occurrences on a weekly basis to ensure a very high probability of re-sighting (Vuillaume et al. 2021) and to facilitate biological interpretation and comparison with other studies (Kilgo et al. 2012; Monteith et al. 2014).

To ensure that the sighted calf belonged to the monitored mother, observers built an adaptive identity card of each calf with pictures recorded over the weeks (Fig. 1 in ESM 1). This ID card included several phenotypic traits, such as coat color and patterns (Bertulli et al. 2015), to identify the calf with confidence. We also used behaviors, such as affiliative contacts, very close proximity, and calf waiting for the mother to confirm calf identity (Vuillaume et al. 2021). When the identity of the calf could not be confirmed, we considered it not sighted. For each calf, we coded weeks with at least one re-sighting as "1" and weeks without calf re-sighting as "0", regardless of whether the calf was dead or potentially still alive. To account for stillbirths, we included one 'sighting' before birth, representing the living state of the foetus during the ultrasound at capture.

Individual and environmental covariates

We used maternal body mass (kg) at capture, eight weeks before expected calving, as a proxy of maternal body condition during gestation. We estimated calf date of birth (DOB; in Julian day starting on 01-Jan) based on evidence of recent calving in all videos available. Evidence included sighting of a wet newborn, partly covered by the placenta, sometimes with eyes half-opened or showing difficulties to stand.

To have a proxy of resource quality and availability, we built individual curves of the Normalized Difference Vegetation Index (NDVI) for the entire summer to estimate the onset of vegetation growth in June and total vegetation productivity over the summer (Pettorelli et al. 2005a; Hamel et al. 2009; Pettorelli 2013). NDVI values were extracted from a 250 m² 16-day composite IV MODIS, from the National Aeronautics and Space Administration Land Products Distributed Active Archive Center (MOD13Q1 NASA data product; Huete et al. 2002). For each individual, we defined the used area from a simplified trajectory built with the first recorded location each day. We then added a 10 km radius buffer, corresponding to the average daily distance traveled by females during summer $(10.7 \text{ km} \pm 0.2 \text{ km})$ per day; Couturier et al. 2009), around the trajectories. We chose this approach because several individuals had partially straight trajectories, which were incompatible with the use of kernels (loss of the straight segment) and minimum convex polygons (increase in surfaces not used by the caribou).

The individual 16-day composite values of NDVI were extracted for each corresponding segments of all trajectories. For each 16-day period, we computed the mean of all pixels in each segment. We then computed the integrated NDVI in June (iNDVI) by adding the mean NDVI for the two 16-day periods in June (01-Jun–15-Jun and 16-Jun–30-Jun, Hamel et al. 2009; Garel et al. 2011) and used it as a proxy of the onset of vegetation growth (Garel et al. 2011; DeMars et al. 2017). We then built NDVI curves for the summer by fitting a loess curve to NDVI values from 01-Jul to 01-Sep and used these curves to compute the cumulative NDVI (TiNDVI), calculating the area under the NDVI curve over the summer and using it as a proxy of total vegetation productivity during summer (Campeau et al. 2019; Mahoney et al. 2021).

To define local weather conditions encountered by each mother-calf pair, we used data from the North American Regional Reanalysis (NARR), provided by the National Oceanic and Atmospheric Administration's National Center for Atmospheric Prediction (NCEP; Mesinger et al. 2006). The NARR data are projections based on the pre-existing NCEP Eta model and the Regional Data Assimilation System estimating precipitation and temperature data. The available data covers North America with a Northern Lambert Conformal Conic grid of 349×277 pixels and a resolution of 32 km², which we centered over the province of Québec using a Québec Lambert projection (epsg:32,198). These projections are predicted over North America from data collected at weather stations and are the most accurate available for Nunavik (Mesinger et al. 2006). We validated the accuracy of the NARR projections by assessing the correlation between NARR data and data available from 14 Nunavik weather stations. During the summer (01-Jun-31-Aug), we found a strong positive correlation for mean daily temperature (r = 0.81 [0.80–0.82], n = 4792, from 2006 to 2019) and a moderate positive correlation for precipitation (r = 0.56[0.54–0.58], n = 3559, from 2006 to 2019; ESM 2).

We extracted weather conditions predicted at the first GPS location each day. Based on data resolution of the data and caribou speed, we expected all locations of an individual to be within the same pixel for a given day. We extracted daily total precipitation (kg m^{-2}) and daily local mean and maximum temperatures (°C) from the NARR database. We considered weather conditions to be relevant for calf survival at three temporal scales. First, we computed the total precipitation on the day of calf birth. Second, we calculated the mean daily precipitation and mean daily temperature (in °C) in June, which roughly corresponds to the calving season. Third, we computed the mean daily precipitation and mean daily temperature (in °C) in summer (July and August), which corresponds to the conditions experienced by calves during their development.

Statistical analyses

We estimated the probability of calf survival during the calving season, i.e. in June, which represented survival to one month for a calf born the first week of June. We also estimated calf survival probability before weaning, i.e. to 01-Sep, which represented survival from birth to three months. Following the methodology presented in Vuillaume et al. (2021), we used a capture-mark-recapture approach based on calf sightings on videos as recaptures to estimate calf survival (Mackey et al. 2008). We used Cormack-Joly-Seber models (Lebreton et al. 1992) implemented in MARK (v. 9.0, Cooch and White 2013) through the R statistical software (R Core Team 2020) with the package RMark (Laake 2013) to assess survival estimates and the probability of calf re-sighting for all calves including stillborns. To test the general fit of the model with the data, we first fitted a general season-dependent model, i.e.

 ϕ (~season)p(~Time), where the season covariate constrained ϕ (survival probability) to vary between calving and summer season (~ season) and the probability of detection (p) was a continuous variable representing the time in weeks. We used the U-care software (Choquet et al. 2001, 2009) with the R package R2ucare (Gimenez et al. 2018) to compute the Goodness-of-fit of the general model, which adequately fitted the data (P values > 0.05). In addition to the general model, we then built two other models including different covariates for the detection probability: a model including only a continuous covariate representing the age of the calf varying each week, i.e. ϕ (~season)p(~Age), and a model constraining p to be fixed for the 3 months of the study, i.e. $\phi(\sim \text{season})p(\sim 1)$. To evaluate the best model for the probability of detection, we compared these three candidate models (i.e. ~ Time, ~ Age, and ~ 1) based on the Akaike Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002), retaining the model with the lowest AIC_c value and equivalent models ($\Delta AIC_c < 2$). Because the general model and the model with constant detection were equivalently supported ($\Delta AIC_c < 2$, Table 1 in ESM 1), we pursued with the general model for evaluating survival probability ϕ , keeping the temporal effect of Time on p to ensure to account for this influence. We used this model to estimate calf survival during calving season and before weaning including stillborns.

Then, we assessed the influence of individual and environmental covariates (Table 1) on pre-weaning survival probability of calves. This second step only considered live-born calves. Using the same approach described above, we modeled ϕ with different covariate combinations, again

keeping p modelled as a function of Time. We assessed the influence of individual traits and environmental conditions encountered during two biological seasons, calving and summer. All individual and environmental covariates were centered and scaled. Because calves that died during the calving season (n=5) did not experience summer conditions, our design matrix applied effects of summer covariates (temperature, precipitation, and TiNDVI) only at the time occasion within the summer season. We used the binary variable "Summer" to stratify time: weeks in the calving season were coded 0 and weeks in the summer were coded 1. This variable was in interaction with the summer covariates. We tested the influence of the different covariates, including birthdate because birthdate has been shown to be associated with survival in some ungulates (Bishop et al. 2009; Kilgo et al. 2012) and raw data suggested an effect of this variable (Fig. 2A). We only tested two covariates per candidate model to avoid overparameterization with a maximum number of parameters of 6 (4 for Φ and 2 for p), leading to 21 candidate models including the null model (Table 2).

We evaluated the relevance of including year as a categorical covariate in all models, comparing the model including only the year to a null model. Because the model including year had a $\Delta AIC_c > 4$ (Table 2) and yearly estimates confirmed similar survival among the 3 years (confidence intervals overlapping 0; see R code), we did not include year as a covariate to avoid overparameterization. For all precipitation and temperature covariates, we tested the relevance of fitting a quadratic effect using a likelihood ratio test. These tests supported the inclusion of a quadratic effect for covariates: mean daily precipitation during calving season (χ^2

Model	Covariate	Туре	Description
р	Time	Continuous	Time in weeks since 01-June
$\boldsymbol{\Phi}$ and \boldsymbol{p}	Age	Continuous	Age in weeks
Φ	Summer	Categorical	Binary variable (0-1) to call summer covariates only during summer weeks
	Season	Categorical	Binary variable (1-2) to identify calving and summer seasons
	Year	Categorical	2016, 2017, and 2018
	DOB	Continuous	Date of birth in Julian day starting on 01-Jan
	mass	Continuous	Mass of the mother at capture, ca. 8 weeks before calving (kg)
	pcpbirth	Continuous	Total precipitation the day of birth (kg m^{-2})
	tcalv	Continuous	Mean daily temperature during the calving season (°C)
	pcpcalv	Continuous	Mean daily precipitation during the calving season (kg m ⁻²)
	iNDVI	Continuous	Vegetation growth index during the calving season-integrated NDVI in June
	tsum ^a	Continuous	Mean daily temperature in summer (°C)
	pcpsum ^a	Continuous	Mean daily precipitation in summer $(kg.m^{-2})$
	TiNDVI ^a	Continuous	Productivity index—cumulated NDVI in summer

 Table 1
 Individual and environmental variables to evaluate the determinants of survival and detection probability for migratory caribou calves during the first 3 months of life, from 2016 to 2018, from the Rivière-aux-Feuilles herd in Nunavik, Canada

Most variables were tested in separate models (see Table 2)

^aVariables tested on a reduced sample for calves present in summer only (n=45, see "Methods")

Fig. 2 Relationship between the birth date and the survival of calves monitored by camera collars during the calving and summer seasons of 2016, 2017 and 2018 from the Rivière-aux-Feuilles migratory caribou herd (Nunavik, Canada). a Distribution of birth dates: gray circles represent calves alive at the end of the study period, black crosses calves that died during the study period. **b** Calf survival probability before weaning (2016–2018) as a function of their birth date. The line is the mean prediction for the median summer temperature (13.5 °C), and the gray zone is the 95%confidence interval



Date of birth

Table 2Model selection resultsfor the analyses evaluatingthe effects of individual andenvironmental variablesmeasured during the calvingseason (June) and the summerseason (01-July to 01-Sep)on the pre-weaning survivalprobability of migratory cariboucalves

Model for Φ	K	AIC _c	ΔAIC_{c}	AIC _c Wt	Deviance
~DOB + Summer:tsum + Summer:tsum ²	6	178.83	0.00	0.92	166.64
\sim DOB + pcpcalv + pcpcalv ²	6	186.04	7.21	0.02	173.85
~DOB + Summer:TiNDVI	5	187.39	8.56	0.01	177.26
~DOB	4	187.44	8.62	0.01	179.36
~DOB+iNDVI	5	188.39	9.56	0.01	178.26
~DOB + mass	5	189.31	10.49	0.00	179.18
~DOB+pcpbirth	5	189.37	10.54	0.00	179.23
~DOB+tcalv	5	189.41	10.58	0.00	179.28
~DOB+Time_sum:pcpsum	5	189.45	10.63	0.00	179.32
~ Summer:tsum + Summer:tsum ²	5	189.80	10.97	0.00	179.66
~Summer:TiNDVI	4	194.82	15.99	0.00	186.73
\sim pcpcalv + pcpcalv ²	5	196.23	17.40	0.00	186.09
~1	3	197.36	18.54	0.00	112.10
~tcalv	4	198.24	19.41	0.00	190.15
~iNDVI	4	198.82	19.99	0.00	190.73
~ Summer:pcpsum	4	198.96	20.13	0.00	190.87
~ Age	4	199.09	20.26	0.00	111.79
~ pcpbirth	4	199.33	20.50	0.00	191.24
~mass	4	199.33	20.51	0.00	191.25
~ Season	4	199.40	20.57	0.00	112.10
~ Year	5	201.40	22.57	0.00	112.06

Covariates in the models were centered and scaled. In all models, the detection probability was a function of Time as a continuous variable. See Table 1 for variable description

K number of parameters, AIC_c Akaike criterion for small sample size, ΔAIC_c AIC_c – the lowest AIC_c, AIC_c , AIC_c , AIC_c , AIC_c weight, *covariate*² squared covariate

=4.88, df = 1, p = 0.03) and mean daily temperature during summer (χ^2 =4.64, df = 1, p = 0.03), which we fitted using a polynomial function of degree 2. We identified the best models based on the AIC_c as described above, and used the function *covariates.predictions* from the *Rmark* package to predict survival estimates with the covariates included in the selected models.

Results

Birthdates ranged from 01-Jun to 04-Jul, with a median of 12-Jun [80% confidence interval (CI) = 07-Jun–18-Jun] (Fig. 2A). Of the 52 calves monitored, 2 were stillborn and 16 disappeared and were considered dead, including five that disappeared during the calving season (June). Calf survival [95% CI] during the calving season was 0.86 [0.77–0.96] and pre-weaning survival, from birth to 01-Sep, was 0.63 [0.50–0.77]. The survival estimates were similar when stillbirths were excluded from the analysis (Table 1 and Fig. 1 in ESM 3).

For the analysis evaluating the effect of individual and environmental covariates on pre-weaning survival, one model stood out with an AIC_c weight of 0.93 (Table 2). This model indicated a linear negative effect of birthdate and a quadratic effect of mean daily temperature during summer (Table 3). Based on this model, the mean [95% CI] calf survival before weaning was 0.67 [0.53–0.80]. When accounting for birthdate, pre-weaning survival probability decreased for calves born late (Fig. 2B). Mean [95% CI] calf survival probability before weaning was 0.99 [0.97–1.00] for a calf born on 01-Jun and 0.58 [0.24–0.85] for one born around 01-Jul. Calf survival probability also varied with mean daily summer temperature (Fig. 3). Mean [95% CI] calf survival probability before weaning was highest during summers with moderate mean daily temperature (13.5 °C), at about

Table 3 Effect sizes (on the logit scale) of the covariates included in the most supported model (Table 2) describing survival (Φ) and detection probabilities (p) of migratory caribou calves during the first three months of life (n=50; 2016–2018), from the Rivière-aux-Feuilles herd (Nunavik, Canada)

Parameter	Beta	Estimate	SE	LCI	UCI
Φ	Intercept	3.46	0.32	2.83	4.09
	DOB	- 0.98	0.25	- 1.48	- 0.48
	Summer:tsum	18.08	5.22	7.84	28.31
	Summer:tsum ²	- 17.44	5.17	- 27.57	- 7.32
р	Intercept	3.75	0.87	2.06	5.45
	Time	0.11	0.18	- 0.23	0.46

See Table 1 for variable description

SE standard error, LCI lower 95% confidence interval, UCI upper 95% confidence interval, *covariate*² squared covariate



Fig. 3 Calf survival probability before weaning as a function of the mean daily temperature during summer (°C) for migratory caribou from the Rivière-aux-Feuilles herd (2016–2018, Nunavik, Canada). The line is the mean prediction for the median date of birth (12-Jun), and the gray zone is the 95% confidence interval

0.99 [0.97–1.00]. It slightly decreased to 0.94 [0.84–0.98] in warm summers with temperature around 14.8 °C, but decreased to 0.69 [0.34–0.90] in cool summers with a mean daily temperature of 11.4 °C (Fig. 3).

Discussion

We assessed calf survival during the first three months of life and identified its main determinants. Early calf survival is crucial to understand variations in population dynamic but was poorly documented for barren ground caribou. Juvenile ungulates are at high risk of dying soon after birth (Bishop et al. 2009; Kilgo et al. 2012). Our results concur with these studies as one third (5/16) of live-born calves that disappeared died within the first 2 weeks of life. Survival during calving season (June), up to 1 month old, was consistent with calf survival rates observed in the Porcupine migratory caribou herd and boreal caribou (Gustine et al. 2006; Porcupine Caribou Technical Committee 2017). In our study, the number of calves that died shortly after birth (n=4), i.e. within the first week, was twice as high as in the study by Gustine et al (2006) based on 50 boreal caribou calves. Unlike most studies on ungulates that focus on survival during the calving season or to recruitment (6-12 months old, Coulson et al. 2005; Owen-Smith and Mason 2005), we also assessed pre-weaning survival. We estimated pre-weaning survival, i.e. to 01-Sep, at 0.63, which was similar to survival at 3 months old (93 days) in elk (Cervus canadensis, Griffin et al. 2011). During the same years as our study, recruitment rate at 6 months old varied substantially for the Rivière-aux-Feuilles herd (18% in 2016, 52% in 2017, 33% in 2018; MFFP unpubl. data) with variable winter pregnancy

rates (55% in 2016, 70% in 2017 and 2018; MFFP unpubl. data). The 15% difference in pregnancy rates between 2016 and 2017/2018 likely contributed to the lower recruitment in 2016. Considering that our analyses suggested similar estimates of pre-weaning survival among these years, the difference in recruitment rates could also be partly related to calf survival in autumn. Mahoney et al. (2016) estimated 6-month survival probability of boreal caribou in Newfoundland at $35.0 \pm 4.0\%$ during a population decline, confirming that survival to recruitment may often be low. For migratory populations, survival from weaning to recruitment, here September to October, may be reduced by the onset of fall migration and associated costs (Malpeli 2022). A full understanding of annual variations in calf survival will require a consideration of pregnancy rates, survival to fall recruitment and overwinter survival.

The risk of mortality during summer was mainly influenced by the covariate "date of birth", with pre-weaning survival decreasing by 11% per week of delay in birthdate since 01-Jun. The date of birth might have been correlated with calf body condition at birth, or even predation risk. Negative effects of birthdate on juvenile survival are common in temperate and arctic ungulates (Clutton-Brock et al. 1987; Bishop et al. 2009; Kilgo et al. 2012). When calves are born early in the season, the peak of lactation is more likely to match the peak of vegetation growth associated with the disappearance of snow (Pettorelli et al. 2007; Stoner et al. 2016). The mismatch between these two peaks may lead to higher mortality rates in juvenile ungulates (Tveraa et al. 2013; Plard et al. 2014). Although we could not assess calf body condition, birthdate could be correlated with calf birth mass if it was primarily determined by conception date, as demonstrated for several ungulate populations (Clements et al. 2010). During the breeding season, female ungulates in poor body condition might mate later (Cook et al. 2004). Given the expected relationship between female and calf body condition at birth, late-born calves could have been lighter and have a lower survival probability to weaning (Paoli et al. 2019). Early birth may also improve survival because predation risk could be lower at the beginning of the calving season due to lower predator density prior to peak births (Kilgo et al. 2012; Jacques et al. 2015). Moreover, female with enhanced nutrition may better detect predators and successfully defend their calf, while well-fed calves might be in better condition and less susceptible to predation (Bishop et al. 2009; Buuveibaatar et al. 2013).

Weather conditions at calving and during the summer can influence resource availability and thermoregulation costs. Our results suggest survival decreases when summer temperatures are cooler, potentially reflecting thermoregulation challenges for newborns. Low temperature associated with precipitation could increase the risk of calf mortality by hypothermia (Michel et al. 2018; Dion et al. 2020). Lower temperature in summer might also reflect late snow melting and vegetation onset during spring, implying limited vegetation resources for females at calving and potentially lower quality milk in early lactation (Scornavacca et al. 2016). All these conditions could affect early growth of calves and their survival to weaning (Tollefson et al. 2011; Scornavacca et al. 2016; Nord and Giroud 2020).

In ungulates, resource availability can improve calf condition and survival (Garel et al. 2011; Bonar et al. 2016). We found no evidence that forage availability affects pre-weaning survival, but other research showed that summer forage productivity can have delayed effects on winter calf survival (Hurley et al. 2017). Furthermore, while earlier onset of vegetation growth in spring could lead to a mismatch between vegetation quality and lactation peaks (Gauthier et al. 2013; Renaud et al. 2022), it could also increase the temporal availability of high-quality forage ("slow start hypothesis"; Christianson et al. 2013) and indirectly enhance calf survival. Despite the large variability in spring green-up among the years of our study (ESM 3), we did not detect an impact of spring onset on calf pre-weaning survival.

Maternal mass is strongly and positively related to the ability to provide milk and improve offspring mass gain (Dobson et al. 1999; Skibiel et al. 2009; Macdonald et al. 2020). Offspring body mass is positively related to juvenile survival in ungulates (Keech et al. 2000; Griffin et al. 2011; Dion et al. 2020). Smaller juveniles and juveniles from mothers with limited body reserves are more likely to die earlier (Keech et al. 2000; Lamb et al. 2023). Influence of maternal body mass on calf body mass has been previously documented in the Rivière-aux-Feuilles herd for females and calves measured at calving in 2007-2009 (Taillon et al. 2012). However, we did not find an effect for body mass of adult females in spring on calf survival. Females in poor condition might have been underrepresented in our sample because larger females with a round belly, suggesting pregnancy, were targeted for capture. Mothers captured for this study appeared heavier (96.5 kg, range 84-121 kg) than females of this herd captured in February-March from 2010 to 2017 and for which pregnancy was not assessed (91.7 kg, range 70.0-114.2 kg; MFFP unpubl. data). Moreover, females were captured prior to spring migration, eight weeks before calving. Harsh environmental conditions during migration can increase migration costs (Leblond et al. 2016; Le Corre et al. 2017) and deplete maternal body reserves. The females were also not necessarily at the same stage of pregnancy. Thus, mass recorded in March may not indicate adequately the body condition of a female at calving.

Using a novel observational method, our results show that birthdate and mean daily temperature during summer are the predominant factors linked to pre-weaning survival for migratory caribou of the Rivière-aux-Feuilles herd. Several studies found similar relationships in other taxa such as birds for which these variables are well-known determinants of juvenile survival (Dunn 2004; Sauve et al. 2021). Small sample size and the strong influence of calf birthdate may have limited our ability to detect small environmental effects such as forage productivity and precipitation, which require further investigation. In addition, we were unable to account for predation or determine the causes of calf death from videos. We were neither able to investigate the influence of body condition of calves and their mothers at calving because we could not measure individuals at that time.

Despite these limitations, our study provides cues on how calf survival might be affected by climate change in future years. Warmer temperatures are expected to occur, affecting ungulates worldwide (Malpeli 2022; Zhou et al. 2022), as well as increased precipitation in the Arctic. These conditions should provide more abundant resources during summer, through earlier snowmelt and vegetation onset, as well as longer growing seasons (Hassol 2004; Gauthier et al. 2013; Ciach and Peksa 2018). Conversely, warmer summers may increase insect harassment (Benedict and Barboza 2022). Faster change in plant phenology, however, is likely to increase the risk of mismatch between vegetation and lactation peaks, which will reduce calf survival if mothers cannot adjust calving dates accordingly (Post and Forchhammer 2008; Lee et al. 2017). Moreover, environmental conditions that will increase the cost and length of spring migration (Bekenov et al. 1998; Robinson et al. 2009; Le Corre et al. 2017), may limit the potential for females to adjust their arrival date on calving ground and exacerbate the mismatch by increasing calving delay. Therefore, rates of pre-weaning survival and recruitment of ungulate calves in the coming years will depend, at least partly, on the capacity of mothers to adapt their migration and/or habitat selection behaviors to the changing climate.

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Author contribution statement SDC, MFB and JT originally formulated the idea and obtained funding for the study, BV, SDC, JHR and JT developed the methodology and BV, JHR and JT conducted fieldwork, BV and SH collaborated in designing the analyses and developed the models, BV performed statistical analyses, BV wrote the manuscript and all the authors provided editorial advice.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All animal handling and experiments followed standards approved by the Animal Care Committees of the Ministère des Forêts, de la Faune et des Parcs du Québec (Certificate No. CPA-FAUNE-16-05) and Université Laval (Certificate No. #2018033).

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