Norwegian University of Life Sciences

Master's Thesis 2024   60 ECTS
Faculty of Environmental sciences and natural Resource Management

Identifying drivers of calving phenology in Svalbard reindeer

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Acknowledgments

I would boldly like to state that this year has been the most rewarding in terms of learning outcome during my academic career. Whether that is because previous years were mostly spent brewing beer and woodcarving in my cellar, or because this year has forced me through grit and fear to actually sit down an learn through experience, shall remain a mystery to the reader. Nonetheless, the process of writing this master thesis has taught me tons about analysis, working in R, and how to write scientifically, and for that I am grateful.

An important reason why my experience with producing a scientific paper turned out pretty pleasant, is due to my splendid supervisors Leif Egil Loe and Liv Monica Trondrud here at NMBU. When Leif offered me a celery stalk two minutes into our first meeting, I had a feeling this would be an interesting year. The feeling was confirmed when Monica attempted to strength-test the ice of Longyearbreen with her head during a misty descent on our last day of field work. While they both have given me superb guidance when asked for, they have also given me time and space to stumble and work in my own pace. I am very thankful for the time I got to spend on Svalbard during the field work, which certainly made me feel ownership to the project.

I would also like to raise my gratitude and simultaneous apology, to every victim among my friends, family and my partner who has had to endure unprovoked monologue about reindeer during this year. Lastly, I would like to raise many thanks to the rest of the Svalbard reindeer group for giving me feedback and encouragement, and for all the fermented fish I was given at the Christmas table.

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Norges Miljø- og Biovitenskapelige Universitet

May 2024

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Abstract

In seasonal environments, the importance of a well-timed calving that matches spring start and onset of plant growth has resulted in a highly synchronous calving season in large herbivores. Timing is important because it determines both neonatal and parental resource allocation and future reproductive potential. Gestation length is relatively fixed, and mating takes place when no reliable cues about spring conditions are available. Climate change has resulted in earlier spring start. A valid concern is that norther herbivores are not able to follow suit by calving earlier, resulting in an increasing mismatch with annual green up of plants. There is a need for studies investigating environmental and individual drivers of timing of calving.

In this thesis I aimed to investigate the calving phenology of the Svalbard reindeer, a species with a highly synchronized calving season inhabiting a climate change hot spot. I used data from GPS-marked females between 2009-2022 to identify drivers and temporal trends of calving and associated synchrony (i.e. length of calving season). In addition, I added median calving dates from population censuses in the period 1979-1981 and 1996-1998 to identify longer-term temporal trends in calving. I predicted that an advanced spring start would lead to a trend towards earlier calving, and a longer plant growth season would lead to a less synchronous calving season. At the individual level higher body mass, prime age, no cost of reproduction last year and favorable autumn, winter and spring conditions were predicted to cause earlier calving.

Analysis of temporal trends using median calving dates revealed no significant trend for the period 1979-2022. However, when using individual calving dates between 2009-2022 a trend towards delayed calving was identified, despite advancing spring. For every year annual calving happened on average 0.31 days later, causing in total a 4-day delay in the period. There was identified no significant trend for synchrony, which turned out to be driven by annual variation in body mass and spring onset previous year. Late winter maternal body mass was found to be the only individual variable driving timing of calving (-0.37 days/kg). This effect was equally split between interannual differences in mean body mass and individual variation in body mass within years. There was a significant cost of reproduction which led to a 1.7 days delayed calving in the following year. None of the weather variables explained significant variation in calving date.

The population in the study area has seen a threefold increase between 2009-2022. Hence, density dependent factors could be the underlying cause to delayed calving and absence of increased maternal body mass, despite more benign climatic conditions. Maternal body mass is an important driver of both timing of individual calving and calving synchrony, but whether it works through facilitating earlier conception or shortening gestation remains unknown. A lack of response to weather variables suggests that date of calving is less sensitive to weather events than calving loss. A cost of reproduction highlights the trade-of related to reproduction, probably caused by offspring investment delaying ovulation due to delayed buildup of reserves in late summer. To my knowledge this study is the first to report delayed calving for any reindeer subspecies, warning of a potential occurring trophic mismatch. The timing and synchrony of calving is an important metric to continue monitoring for large herbivores subjected to rapid climate change.

Sammendrag

I sesongbaserte miljøer har viktigheten av å sammenfalle kalving med vårstart og planteveksstesongens oppstart ført til at store planteetere kalver svært synkront. Tidspunkt for kalving påvirker kroppskondisjon og fremtidig reproduktivt potensiale hos både mor om avkom. Drektighetslengden kan i liten grad endres, og parring foregår når det ikke foreligger informasjon om vårens forhold. Klimaendringer har medført tidligere vårstart. Dersom planteetere i nordlige strøk ikke klarer å endre kalvingstidpunkt i takt med tidligere vårstart, kan det oppstå et misforhold mellom næringsbehov og ressurstilgjengelighet.

I denne oppgaven ønsket jeg å undersøke tidspunktet for kalving hos Svalbardrein, en art som utviser svært synkron kalving og som befinner seg i en «hot-spot» for klimaendringer. Jeg brukte data fra GPS-merkede simler i årene 2009-2022 for å indentifisere faktorer og trender på kalvingstidspunkt og synkronitet. I tillegg brukte jeg median kalvingsdato fra årene 1979-1981 og 1996-1998 for å avdekke eventuelle trender i et lengre tidsrom. Jeg predikerte at tidligere vårstart ville føre til tidligere kalving, og at lengre planteveksstesong ville føre til mindre synkron kalving. På individnivå predikerte jeg at å ikke ha reprodusert året før, høyrer kroppsvekt, optimal alder og gunstige høst, vinter- og vårforhold ville føre til tidligere kalving.

Bruk av median kalvingsdato avdekket ingen trend for kalvingstidspunkt mellom 1979 og 2022. Ved bruk av individuelle kalvingsdatoer mellom 2009-2022 ble det funnet en trend mot senere kalving. Årlig inntraff kalving 0.31 dager senere, og forårsaket en 4 dagers forsinket kalving i perioden. Det var ingen trend for endret synkronitet, som viste seg å være drevet av innenårsvariasjon i mødres kroppsvekt og tidspunkt for vårstart foregående år. Mors kroppsvekt på senvinteren var enste faktor som påvirket individuelt tidspunkt for kalving (-0.37 dager/kg). Denne effekten skyldtes i like stor grad mellomårvariasjon i gjennomsnittlig kroppsvekt og individuell innenårsvariasjon. I tillegg ble det identifisert at reproduksjon førte til 1,7 dagers senere kalving i påfølgende år. Ingen av værvariablene påvirket kalvingstidspunktet.

Bestanden av Svalbardrein i studieområdet har nesten tredoblet seg mellom 2009-2022. Tetthetsavhengige faktorer kan derfor være med på å forårsake forsinket kalving og

forhindre økt kroppsvekt, tross et mildere klima. Mors kroppsvekt påvirker både enkeltindividers tidspunkt for kalving og synkronitet. Hvorvidt dette skjer ved å avgjøre tidspunkt for eggløsning eller drektighetslengden, er usikkert. Uteblivende respons på inkluderte værvariabler indikerer at tidspunkt for kalving er mindre sensitivt ovenfor været enn hva reproduksjonsraten er. Kostnaden ved å reprodusere tydeliggjør avveiningen som knyttes til reproduksjon, og skyldes muligens at investering i avkom forsinker akkumulering av fettreserver på sensommeren, og medfører senere eggløsning. Så vidt jeg vet, er dette første studie som har identifisert en trend mot senere kalving hos noen underart reinsdyr. Dette roper varsku om en potensielt inntreffende trofisk mismatch. For planteetere som er utsatt for hurtige klimaendringer vil det være viktig å opprettholde kjennskapen til kalvingstidspunkt og synkronitet også i fremtiden.

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1 INTRODUCTION

Timing of reproduction is one of the most important life history traits of animals (Stearns, 1992). In seasonal environments where resource availability is fluctuating, reproductive events tend to be highly time-specific and synchronous across individuals (Bronson, 1989). This has been observed in many taxa; birds (Birkhead, 1977), mammals (Sinclair et al. 2000) and fish (Robertson et al. 1990). The degree of synchrony tends to increase with a latitudinal gradient towards the poles (Burr et al., 2016), even within species (Bronson, 1989). A driving factor is to coincide parturition with seasonally peaking resources to optimize neonatal and perinatal survival- and reproduction rate, while at the same time mitigating risk of predation (Festa-Bianchet, 1988; Guinness et al., 1978; Peláez et al., 2020; Sinclair et al., 2000).

Regardless of a hard selection pressure, ungulates may fail to match parturition with rapidly changing resource peaks. A central problem is that gestation time is relatively fixed (Clements et al., 2011; Matsuura et al., 2004). Hence timing of parturition is largely dependent on the timing of mating in autumn, when individuals have no reliable cues about climate conditions in spring. Shortening gestation at a time when environmental cues about late winter and spring conditions are available is energetically costly, and only possible by a few days (Clements et al., 2011; Mysterud et al., 2009). Adjusting timing of reproductive events in long-lived organisms with long generation times is a slow evolutionary process (Bromham, 2009). The challenges of timing and adjusting parturition combined with advancing plant growth onset, raise concern for a trophic mismatch (Linnell et al., 1998). As the onset of plant growth is richer in energy and proteins compared to later vegetative stages, failing to match the highly energy demanding last stage of gestation and following lactation period with this event, could negatively affect neonatal and parental body condition (Fryxell, 1991; Gittleman et al., 1988; Merkle et al., 2016; Oftedal, 1985). In big horn sheep (*Ovis canadensis*) survival rates among calves dropped from 44% to 5% if born 5 days later than the norm (Festa-Bianchet, 1988), highlighting the importance of reproductive phenology.

Whether to prioritize reproduction or maintain one´s energy allocation, represents a fundamental trade-off, and several constraints have been found. Both age and body mass

determine timing of ovulation (Sadleir, 1987). Individuals of lower body mass may ovulate later than heavier ones, leading to later parturition in the spring (Langvatn et al., 2004). This leaves both calf and mother with less time to acquire resources before the following winter. Reproductive success generally peak around mid-life, termed "prime age" (Rughetti et al., 2015). Involving a considerable cost of energy, reproductive status previous year influences both timing of reproduction and whether it occurs at all (Festa-Bianchet et al., 2019; Hamel et al., 2010). Density dependent factors may also influence timing of reproduction. This is usually observed as a delayed and more synchronous ovulation in line with increasing densities (Langvatn et al., 2004). Other external drivers such as environmental conditions also affect the timing of calving. This works mainly through affecting body condition of individuals, and harsh weather during last stages of gestation tend to delay calving (Adams et al., 1998; Paoli et al., 2018). Thus, calving is a complex phenology with a wide-ranging set of affecting factors.

Populations of reindeer (*Rangifer tarandus)* display highly synchronized calving seasons, with some variation in length between subspecies (Bergerud, 2011; Rowell et al., 2009). With a circumpolar distribution that offers brief plant growth seasons, most subspecies rely on coinciding calving with spring onset to enhance reproductive success (Lent, 1966; Post et al., 2003). Similar to other ungulates, timing of calving is affected by maternal body condition, weather and population densities (Adams et al., 1998; Paoli et al., 2018; Skogland, 1990). Additionally, most subspecies are targeted by predators, and a synchronized calving season could mitigate risk of predation (Kojola et al., 2004; Rivrud et al., 2018; Viejou et al., 2018). Hence, when studying reproductive phenology in reindeer, it becomes difficult to distinguish the effects of annual green up from predation effects. While reproductive phenology in reindeer has received considerable attention, the subspecies differ substantially in morphology and distribution, and thus they have unique reproductive phenology that needs to be studied separately.

The Svalbard reindeer (*Rangifer tarandus* platyrhynchus) constitutes the northernmost cervid, and has practically no predators (Derocher et al., 2000). The latter aspect makes identifying drivers of calving simpler compared to in other subspecies. However, the knowledge of the Svalbard reindeer´s reproductive phenology is limited, despite its potential impact on reproductive success (Feder et al., 2008). Veiberg et al. (2017)

utilized activity data to identify calving dates in Svalbard reindeer and identified a lack of response in median calving dates between 1979-2015, despite spring start advancing by 18 days. This study used median calving dates to investigate temporal trends in calving phenology and the relationship between timing and weather variables. However, using individual calving dates to investigate driving factors of calving phenology in Svalbard reindeer has not been done. Moreover, no study has so far investigated the calving season synchrony in this arctic ungulate.

In this thesis I utilized activity data from 122 adult GPS-marked female reindeer providing a total of 357 individual-years of data across the period 2009-2022. A distinct activity signature during calving enabled determining of exact calving dates at the individual level. I used data on median calving dates originating from field observations of calving events from the years 1979-81(Skogland, 1989; Tyler, 1987), and 1996-98 (Veiberg et al., 2017). At a population level I predicted calving phenology to be driven by a combination of body condition and weather variables. Despite earlier findings of unchanged timing of calving (Veiberg et al., 2017), with seven more years of data I now anticipated seeing some advance in timing of calving. I expected a prolonged plant growth season to release pressure for optimal timing of calving and thus promote a less synchronous calving season. At the individual level, I expected timing of calving to be driven by weather and body condition. Specifically, I predicted that warmer autumns, benign winters, early spring start and higher body mass, no cost of reproduction last year and being in prime age would collectively contribute to earlier calving. By building on the method developed by Veiberg et al. (2017), this thesis is the first to identify the underlying drivers of timing of calving on an individual level and the calving season synchrony in Svalbard reindeer. Additionally, this thesis will reveal any recent development in temporal changes in timing of calving. Continued monitoring of calving phenology is an important component of climate change effect studies of Svalbard reindeer and other northern large herbivores subjected to rapid climate change.

2 MATERIALS AND METHODS

2.1 Study area

The study area consists of three connected valleys: Reindalen, Semmeldalen and Colesdalen and is located approximately 20 km south of Longyearbyen, Svalbard (Figure 1). Winter is the longest season, with snow cover lasting from September and onwards to at least mid-May (Vickers et al. 2020). Rain-on-snow (ROS) events creating groundice that prevents foraging during winter is expected to increase three folded in frequency by 2100 (Hanssen-Bauer et al., 2019; Vikhamar-Schuler et al., 2016). Onset of plant growth is driven by timing of snowmelt (Semenchuk et al., 2016) and the productive season normally lasts from mid-June to mid-august (Vickers et al., 2016). Plant productivity is strongly determined by summer temperatures and may display a three folded variation between years (Van Der Wal and Stien, 2014).

2.2 Study species

Svalbard reindeer is the only large herbivore on the archipelago (Veiberg, 2007). After heavy exploitation through hunting in the 20th century, the total population now counts 22,000 individuals (Le Moullec et al., 2019; Pedersen et al., 2019). Svalbard reindeer are not harassed by insects, and except for rare occasions of polar bear attacks, they are not prone to predators (Derocher 2000; Staaland 1986). Probability to calf, survival and population growth rate are positively affected by autumn temperatures and delayed snow onset, and negatively affected by ground ice caused by ROS events (Albon et al., 2017; Loe et al., 2020). These effects operate through maternal body mass, which explains approximately 90% of the variation in pregnancy rate, fetal and neonatal loss and calf survival rate over the summer (Veiberg et al., 2016). While most other Rangifer subspecies are facing population declines (Mallory et al., 2018), the Svalbard reindeer population has been growing in both number and distribution (Le Moullec et al., 2019). This is probably a result of increased plant biomass (Hansen et al., 2019; Van Der Wal and Stien, 2014), and that shorter winters surpasses the effect of more frequent ROS events (Loe et al., 2020). In this thesis study area, the population has increased from ca. 1300 individuals to 3500 individuals between 2009 and 2022 (Pigeon. G, unpublished data).
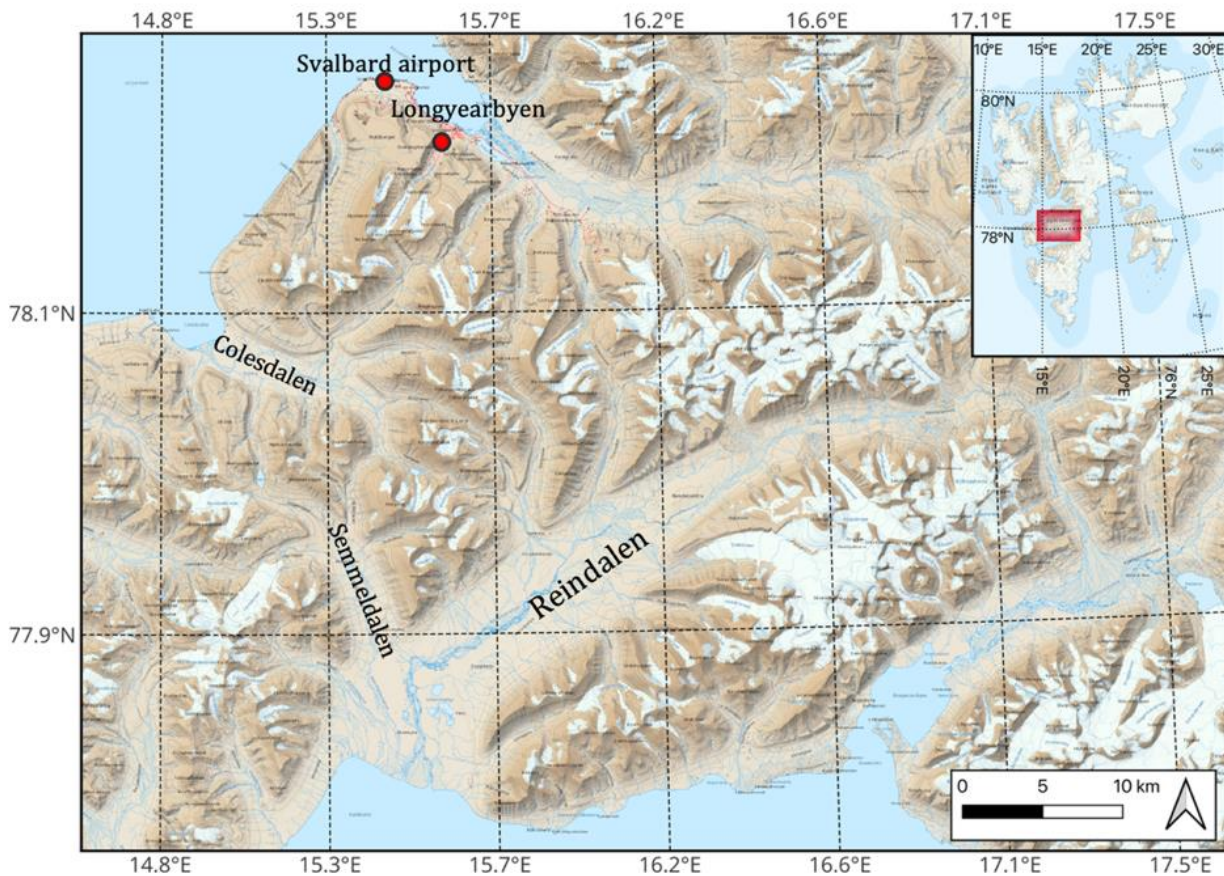
Figure 1. *The study system with Reindalen, Semmeldalen and Colesdalen. Svalbard airport and Longyearbyen are marked with red dots. Longitudes-latitudes are included in both main and overview map (top-right corner). The map was made with QGIS with map layer from the Norwegian Polar Institute ©.*

Most of the year, Svalbard reindeer is loosely organized in groups consisting of a few individuals. However, during the rut in October, females are gathered into harems where they are safeguarded by dominant bucks (Heatta, 2009). Females may ovulate already as yearlings, though with lower probability than adults (Albon et al., 2017). Calving takes place after an approximately 230 days (ca. 8 months) long gestation period. The calving season is normally strongly synchronized and lasts for ca. 10 days in early June (Pedersen et al., 2019; Skogland, 1989; Veiberg et al., 2017).

2.3 Data collection

The data used in this study originated from two annual field work cycles across 14 years (2009-2022). In addition, data from field observations providing median calving dates between 1979-1981 (Skogland, 1989; N. Tyler, 1987), and 1996-1998 (Veiberg et al., 2017) were used. These median calving dates were added to identifying longer-term temporal trends in timing of calving between 1979-2022.

1) The first cycle is carried out in April when presence of snow enables the use of snowmobiles. Annually, since 1995, a capture-mark-recapture (CMR) study has been performed in Reindalen, Semmeldalen, and Colesdalen (Figure 1). During this field work reindeer are caught with the use of nets and snow mobiles (Trondrud et al., 2022) Reindeer are captured and marked as calves and age is therefore known. During capture the female calves are marked with ear tags (Allflex Maxi, Figure 2) and a plastic collar (Figure 2). They are subsequently attempted recaptured each winter throughout their life. Some adult females (>3-year-old) are instrumented with a GPS collar (Vertex Plus, Vectronic Aerospace GmbH), that reports GPS positions and activity (Figure 2). Batteries are replaced upon recapture to ensure continuous data collection and to download the data from the collars as they are "store-on-board". During captures reindeer are weighed to the nearest 0.5 kg and checked for pregnancy status by ultrasound.

2) The second cycle of field work is carried out on foot around the start of August. By using optical aids, marked reindeer are observed to determine whether they have calf at heel or not. This information serves as an important measure of reliability of the estimated calving status from activity data (see below). Moreover, it is an essential part of population monitoring, and provides information regarding over summer calf mortality.

2.4 Activity data

Annually, since 2009, a subset of the marked reindeer has been equipped with GPS collars that also record activity levels. Essentially, activity data is a measure of acceleration in two orthogonal axes, respectively right-left (y)- and back-forward (x) movements, at 4 Hz intervals (Figure 2). A relative measure of activity that ranges from 0 to 255 is calculated as the difference in acceleration between two consecutive measurements. Activity is provided as mean values from 5 min periods, for each axis. (Krop-Benesch et al., 2011). Since 2021, the activity collars also measured acceleration along a vertical (z) axis in addition to the other two. However, the y-axis was used the majority of the time as it displayed calving signatures slightly more clearly. By 2023, a total of 357 individual-years of activity data during calving season were available (Table 1).
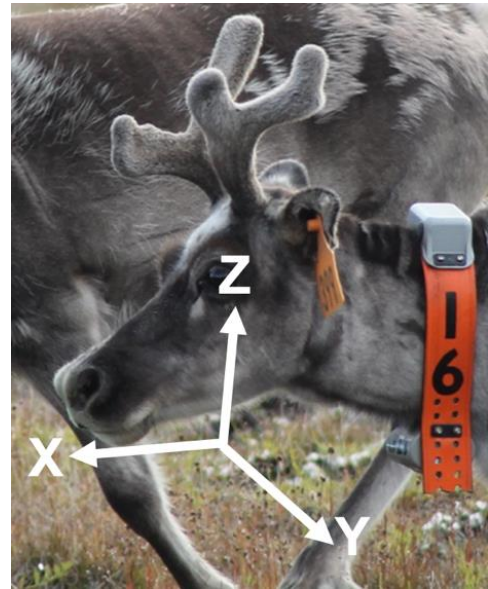
Figure 2. A collard female with GPS-logger and activity sensor on top, measuring activity along three axes. The y-axis was used when plotting activity data. The animal ID is R399 (ear tag) with GPS collar orange 16. (Olvar Skagseth, 2023)

Table 1. Number of females fitted with GPS collars for each calendar year between 2009-2022, and how many out of those whom April capture data was acquired (April data), meaning that body mass and pregnancy status was available.

GPS-collared females per year													
Year	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Females with GPS-activity collar	20	26	25	9	20	19	14	12	29	36	24	19	57	47
April data	17	12	8	3	16	12	10	7	16	26	13	2	42	30

2.5 Identifying calving events from activity data

Veiberg et al. (2017) provided a reliable and verified method for identifying calving by using activity data. The method takes advantage of a distinct change in behavior prior to, and during parturition, as seen in other species (Church et al., 1996; Jensen, 2012). Within one day before calving most individuals display an elevated activity caused by uneasiness, birth streaks, calving and following cleaning of the calf (Figure 3). Post calving, both mother and calf rest. This is visible as a cluster of low activity (Veiberg et al., 2017). This distinct pattern only occurs during calving and thus serves as a reliable cue of the event. If calving does not occur, the pattern remains stable (Figure 4). Although Veiberg et. al. (2017) already estimated calving events for the years 2009-2015, these were re-estimated to ensure continuity and avoid methodological errors. In addition to estimating timing of calving, an effort was made to estimate date of conception and ovulation with activity data and body temperature data. As there was discovered no distinct and reliable pattern related to these events, this approach was abandoned (Appendix 2).

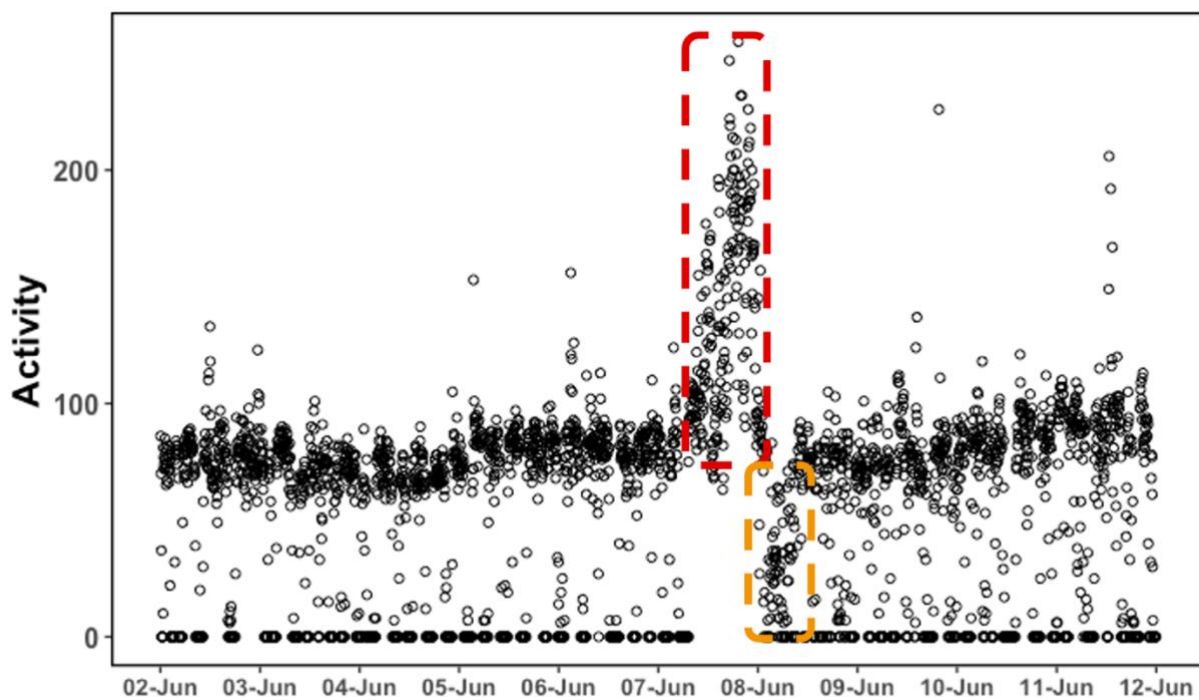***Figure 3.*** *Activity pattern from ID B154 in June 2015. The black open circles are mean values from 5-minute periods of activity data (also in figure 4 and 5). An elevated level of activity (red dashed square) indicates birth streaks, calving and subsequent cleaning of the calf, followed by a period of low activity (orange dashed square) where both mother and calf rest. In this case calving was set to the 7th of June*

When estimating calving dates, I plotted activity data for one individual at a time. Both May and June were plotted to capture possible outlying calving events. When a calving signature was identified, date of calving was set to right before the resting period. Some individuals exhibited atypical patterns in relation to calving, which posed challenges to the detection-method. A notable absence of heightened activity levels preceding the resting period occurred in some individuals (Figure 5). This type of activity pattern could be attributed to stillbirth (Veiberg et al., 2017). The estimated status derived from a combination of all aspects mentioned above.
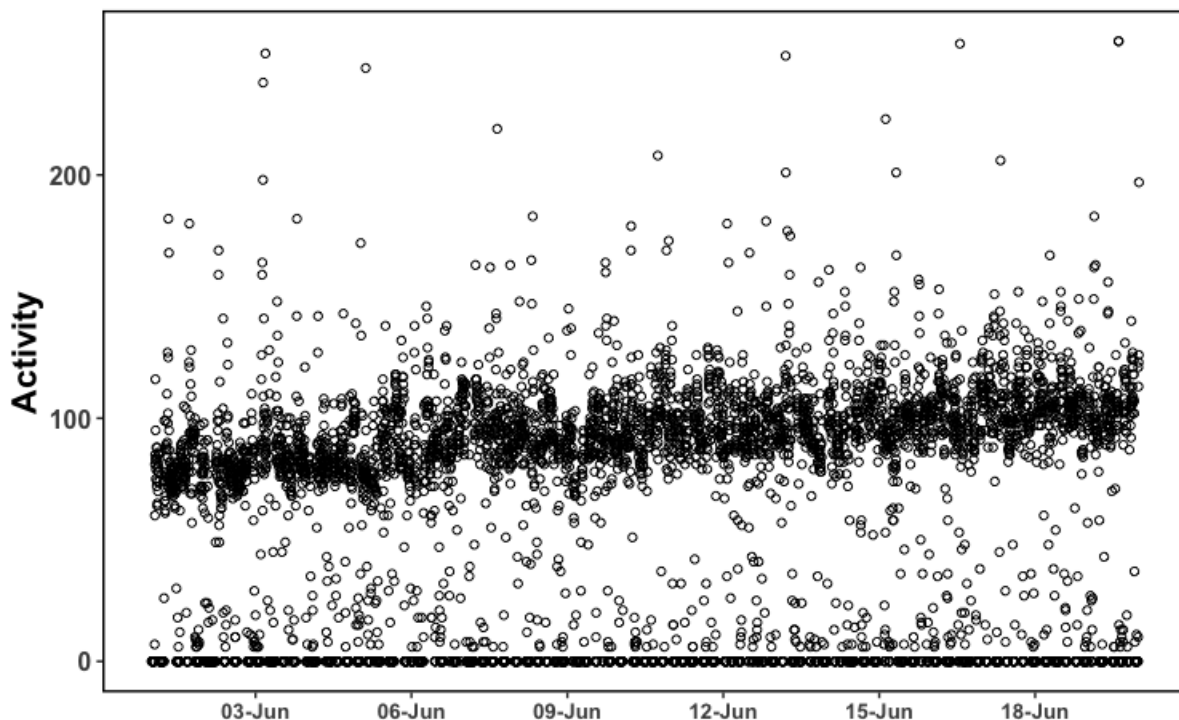
Figure 4. Activity pattern from ID B100 in June 2010 with no clear calving signature, lacking both a period of elevated activity that could originate from birth strokes, calving and cleaning, nor any signs of resting with reduced activity. B100 was estimated not to have calved this year.

2.6 Validation of method

Both the information gained from ultrasound in April (pregnant or not), and from visual observation of calf at heel status in August, provided essential validation criteria to the method. Prior to estimation this information was kept unknown to avoid a potential confirmation bias. However, post estimation, it was used to detect potentially wrongful estimations and subsequently removed, prior to analysis. For instance, if calving was

estimated to have occurred for an individual with absence of fetus in April, the estimation was possibly wrong, and could effectively be excluded from any analyses.

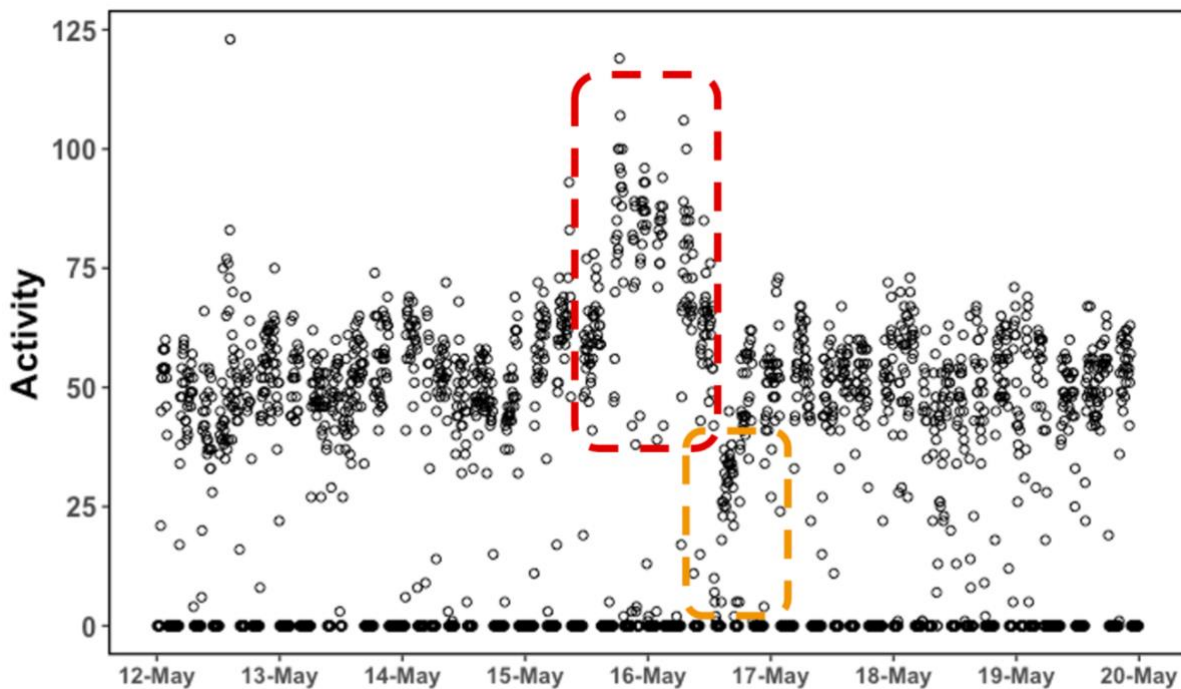***Figure 5.*** *Activity pattern from ID G95 in May 2017, displaying a less obvious calving signature. Both the period of potential birth streaks and cleaning (red dashed square) and the following resting period (orange dashed square) are less distinct. Such a "weak" pattern could be a potential stillbirth (Veiberg et al. 2017). As the only potential signature here was very early (15th – 16th May) combined with unreliable calving signature, this event could not be estimated, and was left out of any analysis.*

In cases where calving had been estimated to occur, while the observed status from August fieldwork was "no-calving" this could be explained by either: (1) The calf died during the summer, before field work was carried out and estimated calving was correct, or (2), calving was wrongfully estimated to have occurred. If the ultrasound detected a fetus in April this would strengthen scenario 1, while if no fetus was detected this would strengthen scenario 2.

2.7 Calculating annual median calving dates and synchrony

Field observations from 1979-1981 and 1996-1998 provided median calving dates, while activity data between 2009-2022 provided individual dates. To check for temporal trends in the period 1979-2022, median calving dates based on individual calving dates had to be calculated. This was done using the same method as Veiberg et al. (2017). A logistic

probit model was used to estimate calving rate (calf per hind) at any given day of the calving season. The calving rate displays a sigmoid curve, and the median calving day was set to the estimated day at which 50% of the parturient reindeer had calved. On the sigmoid curve, which essentially displays the accumulated distribution of calf per hind over time, the median calving day is represented by the turning point of the curve (Appendix 1). It is assumed that calving dates are normally distributed with a standard error σ and mean value μ. Throughout the calving season, the calf per hind index p as a function of time t (julian date), can be calculated as a function of the accumulated distribution of calf per hind ϕ. A scaling parameter q is used to scale the probability by the maximum level of calf per hind the respective year. The following formula was utilized:

$$\rho = q \ * \ \phi \ (\frac{t - \mu}{\sigma})$$

Calculating a measure of calving season synchrony when the sample size (observed calving events) varied across years, and certain years had few individuals with known April capture data, certain considerations needed to be taken. The measure of synchrony, e.g. the length of the calving season, needed to be independent of sample size. If not, the synchrony would tend to be smaller in years of high sample sizes, and vice versa. This would be the case if a 95% confidence interval was utilized and could only be justified if sample size stayed consistent. To avoid such issues, the difference between the 15th and the 85th percentile of annual julian calving day was used as a measure of synchrony. This rather conservative range would leave out at least one potential outlier in either end that could influence the measured synchrony. The years 2012 and 2020 were excluded from analysis on drivers of synchrony because of few estimated calving events where April data was available. The lowest number of calving events in a year that was included in analysis on synchrony was 7 (2016, Appendix 3).

2.8 Environmental data

Environmental data were downloaded for the weather station on Svalbard airport, 20 km north of the study area (www.seklima.met.no). I extracted environmental cues from all periods of the year, to include a variety of potential drivers of calving phenology. Mean monthly air temperature in July previous summer (July_{t-1}) was included as it is known to

influence plant production (Van Der Wal and Stien, 2014). Similarly to Albon et al. (2017) and Loe et al. (2020) annual day-degrees for September and October were calculated as the sum of positive daily mean air temperatures. A proxy for spring start (T50), and spring start previous year (T50$_{t-1}$), were both calculated as the julian day at which the sum of positive daily mean air temperatures (C°), starting from 1st of May, reached 50. Although not being a direct way of detecting onset of plant growth, T50 has proven to be closely correlated (0.66, p = 0.008) to the Global Enhanced Vegetation Index (EVI), for the study site (Veiberg et al., 2017). Rain-on-snow (ROS) was quantified using a well-established indexing method (Albon et al., 2017; Loe et al., 2020; Solberg et al., 2001), and was calculated as the cumulative precipitation from October through March on days when the mean air temperature rose above zero degrees C°. Ground ice thickness was sampled from 128 specific locations during April field work from 2010–2022 (except 2020 due to COVID). While both ground ice and ROS measurements serve as indicators of ice cover, they differ in nature. Ground ice measurements reflect the actual thickness of the ice cover in April, whereas ROS measurements, relying on weather data, provide an estimate and do not specify the actual thickness of the ice layer.

2.9 Individual reindeer variables

Until the start of the plant growth season Svalbard reindeer are living of stored anergy reserves. Thus, the measured late winter body mass is influenced by date of capture, and individuals caught early tend to be heavier than those captured late. A correction method assuming that the individual reindeer experiences a net loss of 170 grams per day from March 1st was therefor used (Loe et al., 2020). The formula for Adjusted late winter body mass is expressed as:

$$Adjusted\ body\ mass = Body\ mass - Capture\ date\ since\ March\ 1st\ x\ 0.170 kg$$

When analyzing synchrony, a variable describing interannual range in late winter body mass variation was established. This range was again measured as the difference between the 15th and the 85th body mass percentile. The purpose of adding this variable, was to include a measure of the annual heterogeneity in body condition, and detect how it potentially affects calving synchrony. Annual mean late winter body mass was also included when analyzing synchrony. The annual calving rate previous year, calculated as

number of reproducing females divided by the total number of females, was included when analyzing synchrony.

For the individual level analysis, both age and body mass were included as numeric variables. A factor variable with estimated reproductive status in year$_{t-1}$ was added to capture cost or reproduction effects on subsequent calving. In later analysis this variable is referred to as "calf last year" and has three levels: Yes (did reproduce last year), no (did not reproduce last year) and not known. "No" was used as the reference level.

2.10 Statistical analysis

All analyses were performed in R version 4.3.1. All dates were converted to julian days (day of the year) prior to analysis. The study consisted of five separate analyses out of which three used calving date as response variable and two used synchrony as response variable. Akaike information criterion for small sample sizes (AIC$_c$) was utilized when evaluating models. This was done following recommended procedures when the ratio of observations to estimated parameters (n/k) is less than 40 (Anderson et al., 2002). The most parsimonious model within 2 ΔAIC$_c$ was considered the best model (Arnold, 2010). In the model selection for drivers of both timing and synchrony null models was added. For timing of calving, the null model included ID and year as random intercepts, while for synchrony only an intercept term was included.

Temporal trends in calving and synchrony

Temporal trend analysis in timing of calving was first performed using median calving dates available for the years 1979-1981, 1996-1998 and 2009-2022 using linear regression. The temporal trends analysis was repeated for the period with activity-derived individual calving dates (2009–2022) using a linear mixed-effects model. In this model, age, late winter body mass and reproductive status last year were included since the same individuals provide calving data over several years. To identify temporal trends in calving, year was added as a numeric variable. Both year (as factor variable) and ID were added to all models as random intercepts. This was done to capture variance that could not be explained by the included variables. Temporal trend analysis on synchrony was performed with a linear regression, and simply included annual synchrony as response and year as predictor.

Drivers of synchrony

Linear regression models were used when analyzing drivers of synchrony. The number of observations used to calculate synchrony varied across years(Appendix 3). Thus, a weight term constituted of the square root of observed calving events each year was added to the models to account for each observation´s reliability.

Drivers of calving on an individual level

Drivers of individual timing of calving were analyzed using linear mixed-effects models. Again, ID and year were included as random intercepts in all models. Model selection was carried out in a two-stage process. First, candidate models were established separately for weather variables and individual body condition variables (Table 2). This was done because weather variables are expected to work mainly through individual body condition. Then candidate models from both selections were combined to arrive at the best model. The non-linear effect of age was also tested for with a generalized additive model. However, for the age span of individuals used here the relationship between age and calving date was near-linear. A linear mixed-effects model could therefore be used. Collared reindeer that were not captured in April lacked data on body mass. This led to 52 calving events being removed prior to analysis.

When testing for the effect of body mass on timing of calving it is beneficial to identify whether the effect arises from interannual differences in average body mass, or from differences between individuals within the same year. The effect of body mass was therefore split into two effects: in general termed *within subject* and *between subject* effects (van de Pol et al., 2009). *Between subject centering* was calculated as the mean body mass of each year while the *within subject centering* was calculated as the difference between each individual's body mass from the annual mean (van de Pol et al., 2009). No other variables (except for random intercepts) were included when testing the effects of *within subject* and *between subject* on timing of individual calving day.

Table 2. *Overview of variables included in the model selection on timing of calving and synchrony. The mean value and corresponding standard deviation and temporal trends with estimated effects (analyzed with linear regression) is provided for all variables (except calf last year) between 2009-2022. Trends for reindeer data is not provided between 1979-2022 as data is not available for the whole period. The first six upper variables are related to reindeer attributes on population or individual level, while the seven bottom variables are related to weather. Significant trend effects are in bold. The significant increase in age is due to individuals retaining GPS-collars throughout their life, misleadingly suggesting that the population is aging.*

variable characteristics overview							
	Mean ± SD	**2009-2015**		**1979-2022**		**Timing**	**Synchrony**
		slope	p-value	slope	p-value		
Body mass (kg)	53.8 ±5.1	-0.09	0.548			x	
Annual mean Body mass	54.8±2.4	-0.13	0.447				x
Variability body mass (kg)	8.1±2.3	-0.08	0.675				x
Age	7.0±2.2	0.14	**0.007**			x	
Calving rate previous year	0.82±0.15	0.01	0.17				x
Calf last year	No:39					x	
	Yes: 179						
	NA: 139						
Day degrees October	28.5±29.4	0.11	0.13	0.57	**0.03**	x	x
Day degrees September	100±26	0.86	0.66	1.51	**<0.001**	x	x
T50	161±7.7	-0.86	0.07	-0.54	**<0.001**	x	x
T50$_{t-1}$	162±7	-0.78	0.09	-0.50	**<0.001**	x	x
July$_{t-1}$	7.6±1.3	0.11	0.13	0.05	**<0.001**	x	x
ROS (mm)	23.8 ±24	-0.39	0.84	0.65	**0.02**	x	x
Groundice	1.5±1.2	-0.10	0.43	-	-	x	

3 RESULTS

A total of 357 individual-years of activity data resulted in 266 estimated calving events. The median date of calving was julian day 158 (7th June) and on average 70% of annual calving events occurred within 8 days (3.June-11.June). The equivalent number for 90% was 14 days (31.May-14.June).

3.1 Description of raw data

Calving status was estimated (did/did not calve) for 326 out of 357 reindeer-years (Table 3). Among these, 266 were recognized as calving while 58 were deemed not calving. A total of 33 individuals were classified as not available or uncertain, and ended in the

category "could not be decided". Out of these, nine were due to malfunctioning collars with incomplete data, 20 because the activity pattern was ambiguous, and four because estimation status was in conflict with fetus/calf-at-heel status (elaborated in next paragraph).

Table 3. Distribution of estimated calving statuses for 357 individual-years of activity data between 2009–2022. The table includes the total number in each estimation category and provides information on how many of those had a fetus in April and a calf at heel in August.

Overview of estimated calving events			
Estimate status	Number	Fetus/no fetus/NA	Calf/no calf/NA
Did calve	266	206/0/60	115/42/109
Did not calve	58	14/32/12	0/33/25
Could not be decided	33	13/7/13	8/11/14

Out of the 266 animals with estimated calving, 206 had a fetus during ultrasound in April, while 60 lacked data on April pregnancy status. Two individuals with absence of fetus in April, were first estimated to have calved. In absence of fetus, but with a clear calving signature, these events were relocated to the category "could not be decided". Out of the 58 females with estimated *no calving* 13 had a fetus in April, and two were recorded with a calf at heel in August. The two individuals with calf at heel in August were also relocated to "could not be decided". Among the individuals that could not be decided, 13 were present with a fetus and eight were observed with a calf at heel in August.

3.2 Temporal trends in calving date and synchrony, 1979 – 2022

The median annual calving day varied by 12 days, spanning from the earliest occurrence on May 31st in 2016 (leap year), to the latest on July 12th in 1996 (leap year) (Figure 6). When using median calving days from 1979-81 (Skogland, 1989; N. Tyler, 1987) , 1996-1998 and 2009-2022, no significant temporal trend was detected (slope = -003, p = 0.49, Figure 6). Over the same period, T50 significantly advanced by 24 days (slope = -0.54, p<0.001, Figure 6).

When using individual calving dates between 2009 and 2022 as response variable, I identified a trend towards delayed timing of calving (slope = 0.29, p=0.004, Figure 7), despite controlling for age, reproduction status last year, and body mass. This resulted in a predicted effect of a 4-day delayed calving over the 14-year period. Data on synchrony were only available for 2009-2022, and there was identified no significant trend (slope = 0.02, p = 0.87).
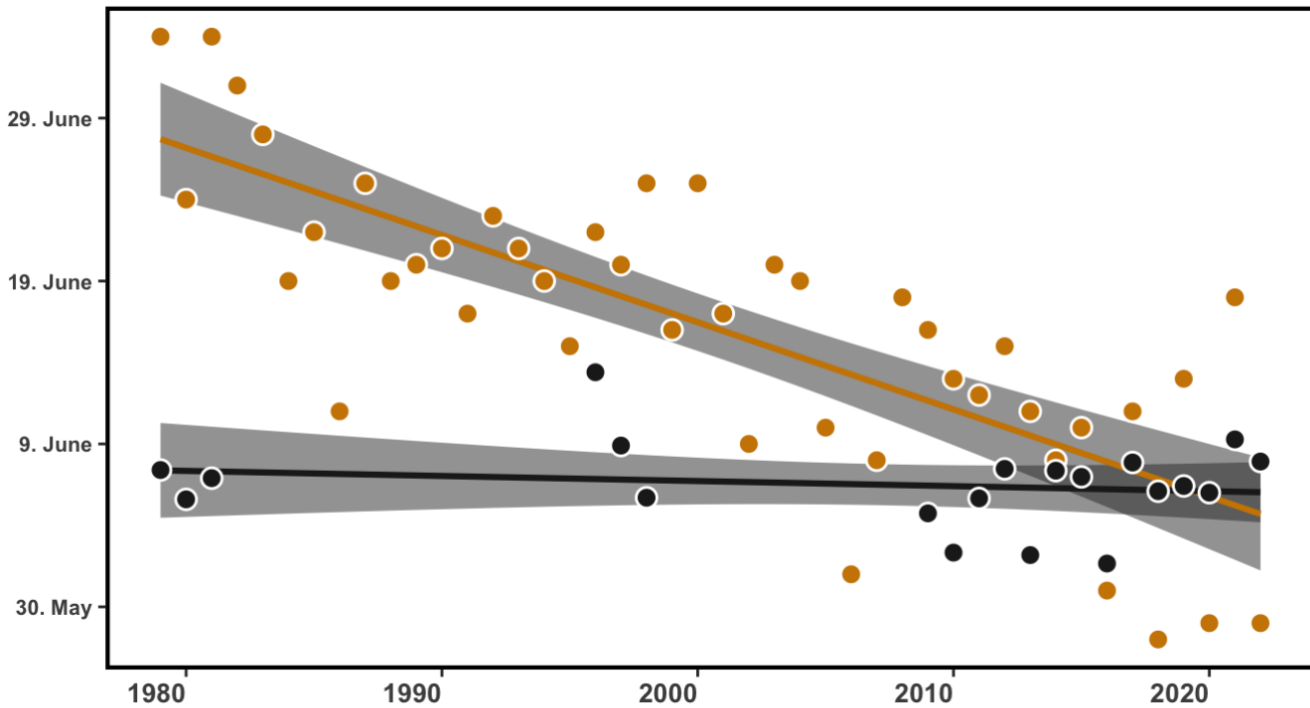

Figure 6*. Annual spring start (T50) between 1979 and 2022 in orange and median calving dates for the years 1979-1981, 1996-1998 and 2009-2022 in black. Both spring start and median calving dates have a predicted line and a 95% confidence interval included, but only spring start showed a significant trend in the period.*
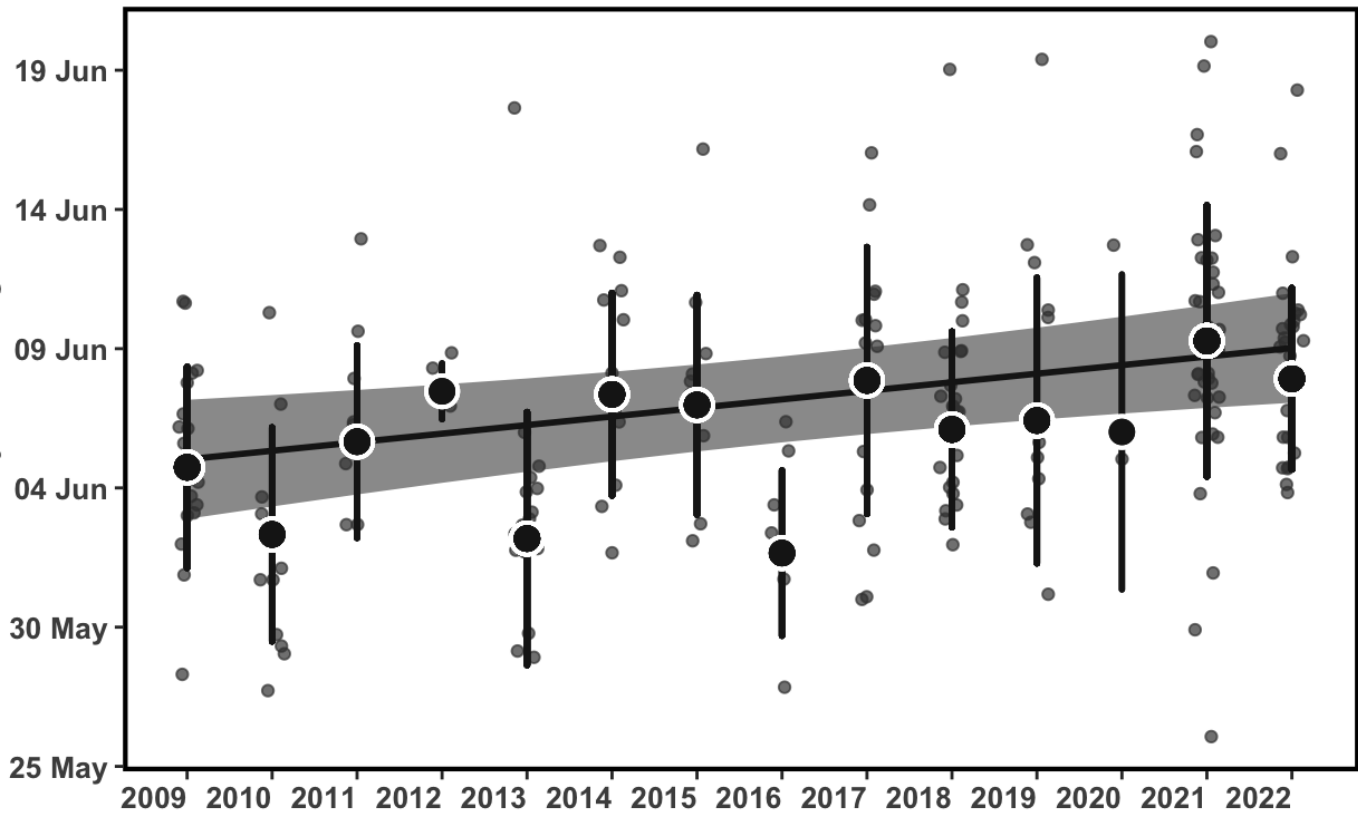
Figure 7. *Temporal trend in calving across the study period with calendar day on the y-axis and years along the x-axis. Individual calving dates estimated from inspection of activity data are plotted as small, grey dots. The predicted response and associated 95% confidence interval are displayed as a black line and grey band, respectively. The larger black dots represent the annual median calving day, while the black vertical lines are the associated standard deviation.*

3.3 Model selection on drivers of synchrony

The model selection on synchrony indicated that annual variation in body mass (slope=0.44, p=0.003) and $T50_{t-1}$ (slope=-0.09, p=0.013) had the strongest effect on calving season length (Model 1, Table 4). Reduced synchrony was observed in years when variation in late winter body mass was greater (Figure 8, panel A), and in years following an early spring start (Figure 8, panel B).

Table 4. Model selection on synchrony arranged by descending AICc score. The models were fitted with linear regression. VBM is variability in annual late winter body mass, (length of 15th to 85th percentile), MBM is annual mean body mass, $T50_{t-1}$ is spring start previous year, $July_{t-1}$ is mean monthly air temperature the year before calving.

Model selection on synchrony					
Model	Variables	AICc	ΔAICc	Df	R^2
1	VBM + $T50_{t-1}$	37.2	0.0	4	0.79
2	VBM	41.1	3.95	3	0.58
3	VBM + MBM	44.3	7.2	4	0.62
4	$T50_{t-1}$	44.4	7.3	3	0.44
5	MBM	45.8	8.6	3	0.37
6	Null model	47.7	10.6	2	0.0
7	ROS	48.1	10.9	3	0.24
8	Calving rate	48.4	11.2	3	0.05
9	T50	48.4	11.2	3	0.22
10	$July_{t-1}$	49.2	12.1	3	0.16
11	Day degrees September	50.8	13.7	3	0.05
12	Day degrees October	51.2	14.0	3	0.02

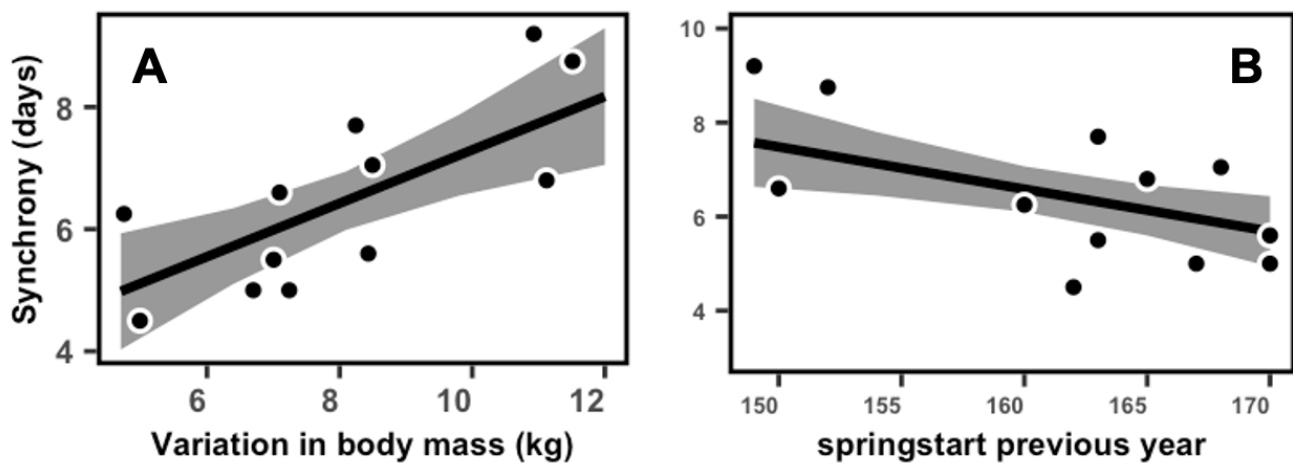**Figure 8** The plots display the predicted effect of the variables included in the best ranked model on describing variance in calving season length (synchrony). Panel A shows the effect of annual variation in late winter maternal body mass, and panel B shows the effect of spring start previous year ($T50_{t-1}$). The predicted effect and its associated 95% confidence interval are shown with a black line and grey band, respectively.

3.4 Model selection on drivers of individual timing of calving

When running a model selection on weather variables only, the null model was best at describing variance in timing of individual calving (Table 5). Groundice and $July_{t-1}$ were respectively second and third best models, but the parameter estimates were not significant for these, or any of the other weather variables.

Table 5. Model selection with only weather variables included. Models are listed by descending AICc score. Df is the degrees of freedom and variance explained by respectively fixed effects and the total variance including random effects are listed in the R^2 column. All models include ID and year as random intercepts.

	Weather variables only				
Model	Variables	AICc	ΔAICc	Df	R^2
1	Null model	1085.5	0.0	4	0.00/0.42
2	Groundice	1086.0	0.5	5	0.02/0.43
3	$July_{t-1}$	1086.2	0.8	5	0.01/0.44
4	$T50_{t-1}$	1088.1	2.6	5	0.01/0.44
4	T50	1089.9	4.5	5	0.01/0.44
5	Day degrees September	1092.3	6.9	5	0.02/0.43
6	ROS	1092.5	7.0	5	0.01/0.43
7	Day degrees October	1093.1	7.6	5	0.01/0.43

In the model selection with only individual variables, body mass alone was the best model (Table 6). Combining calf last year status and body mass resulted in a slightly lower AICc score. Adding the interaction effect of body mass and calf last year status resulted in a relatively high AICc score. The effect of age did worse than the null model.

Table 6. Model selection with only individual variables included. Models are listed by descending AICc score. Df is the degrees of freedom and variance explained by respectively fixed effects and the total variance including random effects are listed in the R^2 column. All models include ID and year as random intercepts.

	Individual variables only				
Model	Variables	AICc	ΔAICc	Df	R^2
1	Body mass + Calf last year	1060.6	0.00	7	0.16/0.47
2	Body mass	1061.0	0.4	5	0.15/0.47
3	Body mass * calf last year	1067.5	6.9	9	0.16/0.47
4	Calf last year	1083.4	22.8	6	0.02/0.43
5	Null model	1085.9	24.9	4	0.00/0.42
6	Age	1088.5	27.9	5	0.01/0.42

As expected, in the combined model selection, the best model was again a model only including body mass and random intercepts (Table 7). No other model with the same simplicity were within 2 ΔAICc of this model.

Table 7. Full model selection with both weather and individual variables included. Models are listed by descending AICc score. Df is the degrees of freedom and variance explained by respectively fixed effects and the total variance including random effects are listed in the R^2 column. All models include ID and year as random intercepts.

	Combined variables only				
Model	Variables	AICc	ΔAICc	Df	R^2
1	Groundice + Calf last year + Body mass	1060.6	0.00	8	0.17/0.47
2	Calf last year + Body mass	1061.6	0.03	7	0.16/0.47
3	Groundice + Body mass	1061.9	0.4	6	0.17/0.46
4	Body mass	1061.0	0.5	5	0.15/0.47
5	Body mass + Calf last year + July mean	1061.5	0.9	8	0.16/0.48
6	July mean + Body mass	1061.8	1.2	6	0.15/0.48
7	Groundice + July mean + Body mass	1061.9	1.3	7	0.17/0.48
8	Body mass * T50	1074.7	14.1	7	0.14/0.48
9	Null model	1085.2	24.9	4	0.00/0.42

The effect of body mass was highly significant (slope = -0.37, p <0.001, Table 8 model 1, Figure 9). This implies that heavier reindeer tend to calve earlier than lighter ones, with a predicted 2.7 kg body mass increase causing a one-day advance in estimated timing of calving. The carry over cost of reproduction, when considered alone, was not among the best models (Table 6), but its effect was significant with an effect of 1.7 days delay (Table 8, model 2). As expected, the significance disappeared when body mass was added to the model (Table 8, model 3), signifying that cost of reproduction operates through body mass. The category "not known" also had a delaying effect on timing of calving (Table 8). This is most likely due to the high reproductive rate in the study period (82%, Table 2), and thus the category mostly contains individuals who reproduced last year.

Once body mass was identified as the predictor most suitable for prediction of calving day, within-subject centering was utilized to distinguish between year and within year effects. Both within and between year effects contributed to explaining variation in timing of calving. While the individual variation within year was significant with an effect size of 0.34 days earlier calving per kg, the between year variation were only close to significant with an effect size of 0.5 day per kg.

Table 8. Effect estimates for variables in respectively the most parsimonious model within 2 ΔAICc of the model with lowest AIC, cost of reproduction model, cost of reproduction when body mass is accounted for, and the within-subject centering model. CI is the 95% confidence interval of the estimated effect. Significant variables are in bold.

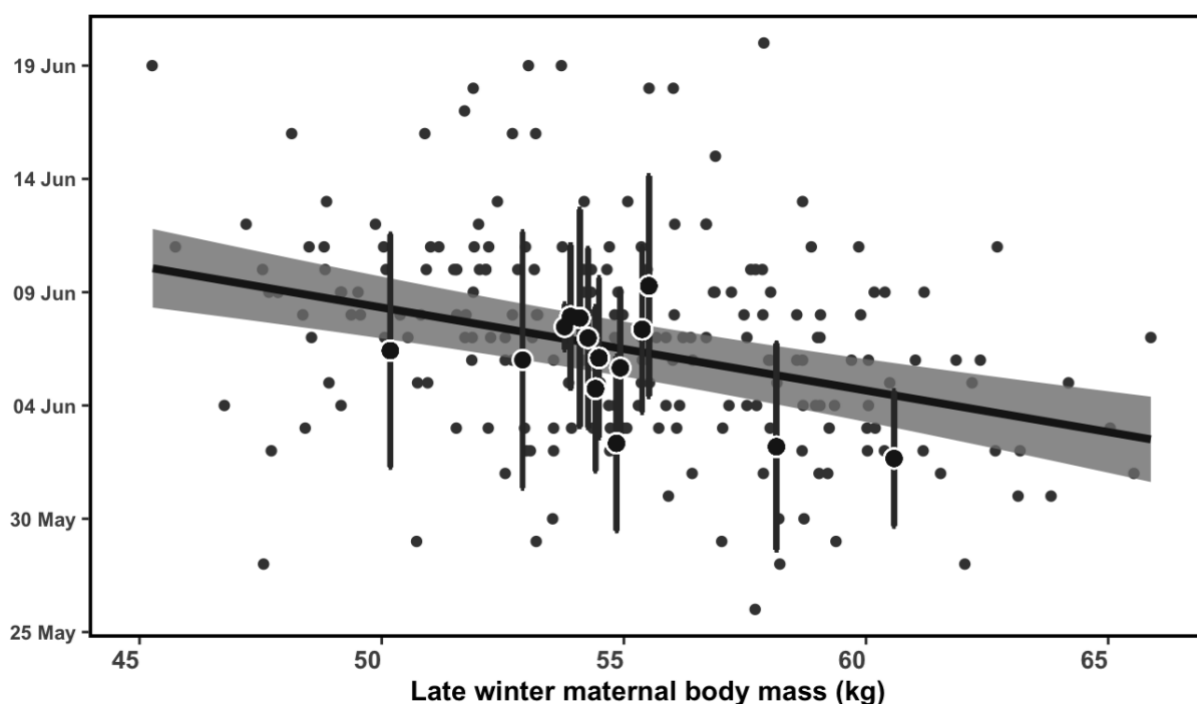| Variable effect estimates				
Model	**Variables**	**effect estimates**	**95% CI**	**p-value**
1	**Body mass**	**-0.37**	**[-050, -0.24]**	**<0.001**
2	Calf last year			
	yes	**1.69**	**[0.13, 3.26]**	**0.034**
	Not known	1.48	[0.19, 3.16]	0.082
3	**Body mass**	**-0.36**	**[-0.49, -0.22]**	**<0.001**
	Calf last year			
	yes	1.35	[-0.40, -3.11]	0.13
	Not known	1.27	[-0.55, -3.08]	0.17
4 - Within subject centering model	**Body mass within year**	**-0.34**	**[-0.48,-0.19]**	**<0.001**
	Body mass between year	-0.49	[-0.99,-0.001]	0.053

Figure 9: The relationship between calving day and late winter body mass (kg), with calendar day on the y-axis and body mass along the x-axis. The calving dates estimated from inspection of activity data are plotted as small grey dots while the predicted response and the associated 95% confidence interval are shown with a black line and grey band, respectively. The larger black dots represent the annual median calving day, while the black vertical lines are ± 1 SD of the mean.

4. DISCUSSION

In this study I used 266 individual calving events between 2009 – 2022 and median calving dates from 1979 – 81 and 1996-1998 to investigate reproduction phenology of the Svalbard reindeer. Although timing of spring start, here represented by T50, advanced by 24 days, there was no temporal change in median calving dates between 1979-2022. However, when focusing solely on individual calving dates from the period 2009 – 2022 there was a tendency towards later calving. I identified no trend for season synchrony, which turned out to be driven mainly by annual variation of body mass, with $T50_{t-1}$ and $July_{t-1}$ providing some additional explanatory power. Individual calving day was mostly driven by late winter body mass, with no weather variables constituting reliable predictors. When separating between annual and interannual effects of body mass, both were equally important. Lastly, individuals who had a calf previous year were delayed by an average of 1.7 days the following year, indicating a carry-over cost of reproduction on timing of calving, an effect that operated through body mass. The results in this study emphasizes the importance of body condition on timing of reproduction in this highly seasonal ungulate. As a consequence, both negative and positive effects of climate change is expected to impact body condition and thus calving phenology.

4.1 Temporal trends in timing of calving

Populations may adjust reproductive phenology over time in response to changing conditions (Langvatn et al., 2004; Paoli et al., 2018; Visser, 2013). Advancing spring start in response to climate warming has shown to impact reproductive phenology in seasonal environments (Hagen et al., 2021; Paoli et al., 2018). Yet, for reindeer, a highly seasonal ungulate, responses to climate change differ among subspecies. Both semi-domesticated reindeer in Finland, and populations of caribou in Canada has been displaying earlier calving dates in recent decades (Davidson et al., 2020; Paoli et al., 2018). Other populations, however, display a lack of response to advancing spring, and one caribou population exhibited later calving dates, though not significantly (Davidson et al., 2020). Veiberg et al. (2017), replicated in Tyler et al. (2024), identified no advance in calving for Svalbard reindeer between 1979-2015. The lack of a long-term trend holds even after I have added seven more years to the time series. Despite being the same species and experiencing advancing spring start and an overall warming climate, their timing of

reproduction responds differently. This suggests that there exist diverging constraints between subspecies affecting the requirement for, and potential, to alter timing of calving.

Contrary to what was expected, a trend towards later calving was found between 2009-2022 in the Svalbard reindeer. In ungulates, delayed parturition could be caused by less hospitable conditions, such as unfavorable weather or increased population density (Langvatn et al., 2004; Paoli et al., 2018). However, environmental conditions have improved during the study period, with earlier spring start, warmer summers (Table 2) and a delayed onset of snow in the autumn (Loe et al., 2020). This disfavors weather as underlying cause. Density dependence has been found to drive population dynamics in interaction with ROS events in Svalbard reindeer (Hansen et al., 2019). Since the population in the study area has been increasing (Pigeon. G. unpublished data), density dependent factors could delay calving by enhancing foraging competition (Langvatn et al., 2004; Skogland, 1983). Whether Svalbard reindeer exhibit this mechanism remains unknown, but could explain delayed calving despite advancing spring start.

Late winter body mass, which this study has found to drive timing of calving, has not improved despite more favorable climatic conditions (Table 2). While the Svalbard reindeer population increased in the study period, the semi-domesticated reindeer in Finland were kept rather constant at 100 individuals, possibly hindering increased intraspecific competition (Paoli et al., 2018). This could partly explain the diverging trends in in timing of calving between the two studies. In present study, body mass was included in the model when testing for temporal trends in timing of calving. Hence, density dependence affecting timing of calving is arguably not operating through maternal body mass. Albon et al. (1983) found that reproductive investment per unit body mass was reduced with increased population densities in red deer (*Cervus elaphus*). If Svalbard reindeer exhibit the same mechanism, increased densities could lead to later calving despite unchanged body mass in late winter and increasing October body masses (Albon et al., 2017). Long lived iteroparous animals are expected to prioritize own energy allocation before reproduction (Festa-Bianchet 2019; Hamel 2010). Hence density dependence may affect timing of calving through altered life history strategies reflected as delayed timing of calving.

In addition to warming climate in Arctic regions, global warming is resulting in more variability (Schmidt et al., 2023). The onset of spring start could potentially vary substantially between years, regardless of a trend towards advancement. This seems to have happened in the past 43 years on Svalbard too (Figure 6). Increased weather variability could complicate timing of parturition for organisms in seasonal environments and perhaps counteract benefits of early calving. This could explain lacking response in median calving between 1979-2022. As Svalbard reindeer partly rely on built up fat reserves during the last stages of gestation and first stages of lactation, they are not totally dependent on the availability of food shortly after calving (Veiberg et al., 2016). Subspecies of reindeer differ in location on the capital-to-income breeder continuum, and reproductive success of capital breeders has been found to be less affected by spring conditions than income breeders (Kerby et al., 2013). Hence, natural selection could with varying force , depending on each subspecies location on the capital-to-income continuum, advance calving. Put in other word, income breeders should have more incentive to advance calving in line with spring start than capital breeders. Conversely, early calf survival and annual recruitment of Svalbard reindeer correlates with late winter body mass, while spring phenology does not (Veiberg et al., 2016). It could be that the risk imposed by increased weather variability, combined with reliance on body reserves during the last stages of gestation and early lactation, mitigates potential benefits of advancing calving.

4.2 Temporal trend and drivers of synchrony

How synchronous a population exhibits parturition in a predator free environment reflects the importance of matching parturition with annually peaking resources (Bronson, 1989; Linnell et al., 1998). For Svalbard reindeer, the degree of synchrony remained unchanged between 2009-2022 despite improved climatic conditions (Table 2). This is partly contradictory to the responses reported on reindeer in Finland by Paoli et al. (2018) where favorable weather tended to weaken calving synchrony. On the other hand, density may also affect calving synchrony as ovulation in red deer is found to be more synchronous during high densities, potentially leading to a shorter calving season (Langvatn et al., 2004). Hence, more favorable weather and increased population densities could be functioning as opposite forces in driving the degree of calving synchrony; Increased density facilitating a shorter calving season while more hospitable

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climate facilitating a longer calving season. It could be that these two effects balance each other, resulting in unchanged synchrony.

The present study has found late winter body mass to drive individual timing of calving. Naturally, an increase in variability of this attribute leads to a longer calving season (i.e. less synchrony), and has also been documented as a driver of synchrony in red deer (Loe et al., 2005). Studies has found that body mass as adult is partly determined by body mass at birth (Feder et al., 2008; Festa-Bianchet et al., 2000; Keech et al., 1999; Plard et al., 2015), which again is affected by timing of parturition (Côté and Festa-Bianchet., 2001a). Hence, variance in body mass is a driver of synchrony, which again drives variance in offspring body mass. Through this mechanism, synchrony and variability in body mass is connected and could cause delayed effects through cohort and maternal effects.

$T50_{t-1}$ was the only weather variable which yielded a significant effect on synchrony, and was part of the best model. Early spring start entails a prolonged plant growth season and could lead to females being heavier by the end of summer (Albon et al., 2017; Van Der Wal and Stien, 2014). Because an early spring start led to less synchrony the following year, it could be argued that it operates by causing heterogeneity in body condition among female reindeer. The effect of $T50_{t-1}$ is in line with findings in other ungulates where less synchrony tends to follow favorable conditions (Langvatn et al., 2004; Paoli et al., 2018). Since late winter body mass was included in the same model, the effect of $T50_{t-1}$ does not operate through late winter body mass. However, the underlying mechanisms in how spring start affect synchrony of the following calving season, remains unclear.

4.3 Drivers of individual timing of calving

None of the weather models performed better than the null model which only assumed an intercept. This is contradictory to previous studies where both October degree-days and ROS has proven to affect late winter body mass in Svalbard reindeer (Loe et al., 2020), which again, as this study has found, affects timing of calving (Table 7). Late winter body mass explains about 90% of variance in pregnancy rates (Veiberg et al., 2016), as opposed to the 15% explained on timing of calving (Table 6/7). Arguably, body mass has a stronger effect on pregnancy rates than on timing of calving. This could explain why there

is an observed effect of ROS on pregnancy rates (Hansen et al., 2019), but not on timing of calving.

In addition, July temperatures has been increasing in the study period (Table 2), promoting plant productivity and increasing resource availability (Van Der Wal and Stien, 2014). This has led to increasing population densities, which could cause enhanced foraging competition, possibly counteracting the effects of more favorable climatic conditions. Hence density dependence could mask the effect of climatic variables. Similar to present study, Bowyer et. al (1998) found no effect of spring and winter conditions on timing of calving on moose (*Alces alces)* in Alaska. They suggested that this derived from timing of calving being an adaptation to long-term patterns in climate. There is high inter-annual variability in onset of plant growth in Arctic regions (Schmidt et al., 2023), and a "bet-hedging" strategy would suggest that in the long run organisms would benefit from coincide parturition with average annual green up, as opposed to the riskier opportunity of calving earlier, but also potentially too early (Meltofte et al., 2007; Seger et al., 1987). Such a theory would suggest that the timing of calving in Svalbard reindeer should not be affected by annual variability in weather conditions. In summary, the findings in the present study do not support the hypothesis of weather variables driving individual timing of calving.

Reproduction in large herbivores is costly and represents a trad off between investment in current and future reproduction (Stearns, 1992). A cost of reproduction has been identified in several seasonal ungulates, such as big horn sheep, mountain goat (*Oreamnos americanus*) (Festa-Bianchet et al., 2019), and also in the Svalbard reindeer, observable as a mean of 5.8 kg body mass reduction 8 months post calving (Pigeon et al., 2022). According to the effect of body mass on timing of calving (Table 8), this should translate into a 2-day delay, very close to the 1.7 days delay found in present study. Pigeon et al. (2022) demonstrated that interannual body mass changes, independent of previous year reproduction state, varies greatly, while the body mass cost of reproduction varies little between years. Whether cost of reproduction on timing of following calving also displays little interannual variation is hard to tell. Though not significant, the effect of having reproduced previous year was not totally removed when body mass was included in the model (Table 8, model 3). This could imply that cost of

reproducing is delaying calving through other mechanisms apart from reducing body mass.

While body mass is but one out of several measures of body condition in ungulates, it is considered an important feat as it reflects stored energy (Wilder et al., 2016). In ungulates, increased body mass is associated with elevated reproductive potential and survival (Côté and Festa-Bianchet, 2001b; Gaillard et al., 2000; Plard et al., 2015). The present study result of late winter body mass being a driver of timing of calving is in line with findings in other ungulates, such as bighorn sheep (Feder et al., 2008), Caribou (Adams et al., 1998; Cameron et al., 2011), roe deer (*Capreolus capreolus*) (Plard et al., 2014) and reindeer (Holand et al., 2004). Svalbard reindeer display high interannual variation in body mass (Pigeon et al., 2022), ultimately causing interannual variability to timing of calving. Within subject centering revealed that females that are relatively heavier than their conspecifics within a year calves earlier even during harsh winters with generally lower body mass. This imply that body mass affect timing of calving both through annual averages, and by individual differences. Maternal body mass is indeed an important driver of calving phenology and arguably made more important because of its great interannual variability.

There are several potential ways in which maternal body mass potentially could affect timing of parturition in ungulates. Firstly, heavier females could tend to ovulate earlier, ultimately leading to earlier calving (Mysterud et al., 2009). By back extrapolating embryo-size based on assumed growth rate, Tyler et al. (2024) estimated conception dates in Svalbard reindeer. It was identified that the connection between maternal body mass in October and date of conception was weak. It should be noted that because Svalbard reindeer is very synchronous in its reproductive phenology (Skogland, 1989), a small error when estimating conception date could make for relatively large impact and possibly mask the effect of body mass. Nonetheless, mean October body mass is not correlated to late winter body mass in Svalbard reindeer (Albon et al., 2017). Hence, it cannot be assumed that heavy individuals in late winter also were heavy in October and thus ovulated early.

Secondly, heavy individuals could calve earlier by exhibiting shorter gestation length. If this is how body mass operates on timing of calving in Svalbard reindeer, it would be contradictory to findings in both red deer and reindeer where early conceiving females display a longer gestation period (Mysterud et al., 2009; Shipka et al., 2010). Another option is that heavy females have the opportunity to adjust gestation length to coincide calving with spring start. However, this is not supported either as there was identified no interaction effect of body mass and T50 (Table 7). An alternative explanation is that body mass drive timing of calving through a combination of regulating timing of conception and advancing calving through phenotypic plasticity. While it remains unvalidated just how late winter body mass affect timing of calving, it should be emphasized that the effect is clear and robust.

4.4 Weaknesses of identifying calving events with activity data

While identifying calving events with activity data is a tried and verified method, estimation errors could occur. There are some differences in present study estimated median calving dates (Appendix 1) and the results in Veiberg et al. (2017), which used the same method. This implies diverging estimation for some individuals and also highlights possible weaknesses of the method. It is especially challenging to decide date of calving when the calving signature is located close to midnight as this causes two days to seem likely.

Out of the 266 individuals with estimated calving, 42 were seen without a calf (Table 3). This is not alarming as calves could die over the summer (Veiberg et al., 2016). The two individuals who were originally estimated with calving, but which did not have a fetus in April, indicate that mistakes can occur. If fetus status had not been available, these two events would have been included in the analysis. For the individuals with estimated calving where fetus status is unavailable, validation of estimation status cannot be provided. Out of the 58 individuals with estimated "no calving", 14 had a fetus in April. As late winter abortions occur regularly (Albon et al., 2017), this does not necessarily imply wrongful estimation.

Eight of the individuals who could not be estimated due to ambiguous calving signature (Figure 5), were observed with a calf at heel in August. Hence, a possible systematic error

may occur as females with this type of "unclear calving signature" are discarded. However, these instances are relatively few, and there are no apparent reasons to believe that these individuals are in systematically different body condition from those with clear signature. While assumed to be less detectable than successful births when using activity data, stillbirths could potentially be falsely recognized as successful calving events (Veiberg et al., 2017). Although not documented, both maternal body condition and timing of calving related to stillbirths could be expected to differ from cases of successful reproduction. Thus, including stillbirths could affect the result in my study, but most likely only to a lesser degree.

Concluding remarks

My study consolidates to maternal body mass being an important driver of calving phenology and contribute to establish GPS activity data as a reliable source of individual calving dates. Using activity data to estimate calving dates is both labor efficient and accurate. To my knowledge, this study is the first to report delayed timing of calving in any Rangifer subspecies. The delayed calving is seemingly contradictory to what should be expected considering recent climate change with advancing spring start. This illuminates the complexity and challenges of understanding and predicting species development when both climate and population dynamics are changing. Moreover, this study demonstrates that other mechanisms apart from climate, such as population density, could drive calving phenology with forces of equal magnitude. That fact that spring start and timing of calving moves in opposite directions raises both concern about the future of this Arctic herbivore and a valuable opportunity to monitor the effects of an accelerated trophic mismatch in real time.

7. REFERENCES

Adams, L. G., & Dale, B. W. (1998). Timing and synchrony of parturition in Alaskan caribou. *Journal of Mammalogy*, *79*(1), 287–294. doi: 10.2307/1382865

Albon, S., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., Veiberg, V., van der Wal, R., Bjørkvoll, E. M., Duff, E. I., Hansen, B. B., Lee, A. M., Tveraa, T., & Stien, A. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, *23*(4), 1374–1389. doi: 10.1111/GCB.13435

Albon, S., Mitchell, B., & Staines, B. W. (1983). Fertility and Body Weight in Female Red Deer: A Density-Dependent Relationship. *The Journal of Animal Ecology*, *52*(3), 969. doi: 10.2307/4467

Anderson, D. R., & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management*, *66*(3), 912. doi: 10.2307/3803155

Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*(6), 1175–1178. doi: 10.2193/2009-367

Bergerud, A. T. (2011). The reproductive season of Newfoundland caribou. *Https://Doi.Org/10.1139/Z75-145*, *53*(9), 1213–1221. doi: 10.1139/Z75-145

Birkhead, T. R. (1977). The Effect of Habitat and Density on Breeding Success in the Common Guillemot (Uria aalge). *The Journal of Animal Ecology*, *46*(3), 751. doi: 10.2307/3638)

Bowyer, R. T., & Kie, J. G. (1998). *Timing and synchrony of parturition in Alaskan moose: Long term versus proximal effects of climate*. Retrieved from https://academic.oup.com/jmammal/article/79/4/1332/846057

Bromham, L. (2009). Why do species vary in their rate of molecular evolution? *Biology Letters*, *5*(3), 401. doi: 10.1098/RSBL.2009.0136

Bronson, F. H. (1989). Mammalian reproductive biology. *University of Chicago Press*.

Burr, Z. M., Varpe, Ø., Anker-Nilssen, T., Erikstad, K. E., Descamps, S., Barrett, R. T., Bech, C., Christensen-Dalsgaard, S., Lorentsen, S. H., Moe, B., Reiertsen, T. K., & Strøm, H. (2016). Later at higher latitudes: large-scale variability in seabird breeding timing and synchronicity. *Ecosphere*, *7*(5), e01283. doi: 10.1002/ECS2.1283

Cameron, R. D., Smith, W. T., Fancy, S. G., Gerhart, K. L., & White, R. G. (2011). Calving success of female caribou in relation to body weight. *Https://Doi.Org/10.1139/Z93-069*, *71*(3), 480–486. doi: 10.1139/Z93-069

Church, J. S., & Hudson, R. J. (1996). Calving behaviour of farmed wapiti (Cervus elaphus). *Applied Animal Behaviour Science*, *46*(3–4), 263–270. doi: 10.1016/0168-1591(95)00604-4

Clements, M. N., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M., & Kruuk, L. E. B. (2011). Gestation length variation in a wild ungulate. *Functional Ecology*, *25*(3), 691–703. doi: 10.1111/J.1365-2435.2010.01812.X

Côté, S. D., & Festa-Bianchet, M. (2001a). Birthdate, mass and survival in mountain goat kids: Effects of maternal characteristics and forage quality. *Oecologia*, *127*(2), 230–238. doi: 10.1007/S004420000584

Côté, S. D., & Festa-Bianchet, M. (2001b). Reproductive success in female mountain goats: The influence of age and social rank. *Animal Behaviour*, *62*(1), 173–181. doi: 10.1006/ANBE.2001.1719

Davidson, S. C., Bohrer, G., Gurarie, E., LaPoint, S., Mahoney, P. J., Boelman, N. T., Eitel, J. U. H., Prugh, L. R., Vierling, L. A., Jennewein, J., Grier, E., Couriot, O., Kelly, A. P., Meddens, A. J. H., Oliver, R. Y., Kays, R., Wikelski, M., Aarvak, T., Ackerman, J. T., … Hebblewhite, M. (2020). Ecological insights from three decades of animal movement tracking across a changing Arctic. *Science*, *370*(6517), 712–715. doi: 10.1126/SCIENCE.ABB7080/SUPPL_FILE/ABB7080_MDAR_REPRODUCIBILITY_CHECKLIST.PDF

Derocher, A. E., Wiig, Ø., & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, *23*(10), 675–678. doi: 10.1007/S003000000138/METRICS

Feder, C., Martin, J. G. A., Festa-Bianchet, M., Bérubé, C., & Jorgenson, J. (2008). Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia*, *156*(4), 773–781. doi: 10.1007/S00442-008-1035-9

Festa-Bianchet, M. (1988). Birthdate and survival in bighorn lambs (Ovis canadensis). *Journal of Zoology*, *214*(4), 653–661. doi: 10.1111/J.1469-7998.1988.TB03764.X

Festa-Bianchet, M., Côté, S. D., Hamel, S., & Pelletier, F. (2019). Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. *Journal of Animal Ecology*, *88*(8), 1118–1133. doi: 10.1111/1365-2656.13002

Festa-Bianchet, M., Jorgenson, J. T., & Réale, D. (2000). Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, *11*(6), 633–639. doi: 10.1093/BEHECO/11.6.633

Fryxell, J. . (1991). Forage Quality and Aggregation by Large Herbivores. *Https://Doi.Org/10.1086/285227*, *138*(2), 478–498. doi: 10.1086/285227

Gaillard, J. M., Festa-Bianchet, M., Delorme, D., & Jorgenson, J. (2000). Body mass and individual fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1442), 471. doi: 10.1098/RSPB.2000.1024

Gittleman, J. L., & Thompson, S. D. (1988). Energy Allocation in Mammalian Reproduction. *Integrative and Comparative Biology*, *28*(3), 863–875. doi: 10.1093/ICB/28.3.863

Græsli, A. R., Thiel, A., Fuchs, B., Stenbacka, F., Neumann, W., Malmsten, J., Singh, N. J., Ericsson, G., Arnemo, J. M., & Evans, A. L. (2022). Body temperature patterns during pregnancy and parturition in moose. *Journal of Thermal Biology*, *109*. doi: 10.1016/J.JTHERBIO.2022.103334

Guinness, F. E., Albon, S. D., & Clutton-Brock, T. H. (1978). Factors affecting reproduction in red deer (Cervus elaphus) hinds on Rhum. *Reproduction*, *54*(2), 325–334. doi: 10.1530/JRF.0.0540325

Hagen, R., Ortmann, S., Elliger, A., & Arnold, J. (2021). Advanced roe deer (Capreolus capreolus) parturition date in response to climate change. *Ecosphere*, *12*(11), e03819. doi: 10.1002/ECS2.3819

Hamel, S., Côté, S. D., & Festa-Bianchet, M. (2010). Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology*, *91*(7), 2034–2043. doi: 10.1890/09-1311.1

Hansen, B. B., Pedersen, Å. Ø., Peeters, B., Le Moullec, M., Albon, S. D., Herfindal, I., Sæther, B. E., Grøtan, V., & Aanes, R. (2019). Spatial heterogeneity in climate change effects decouples the long-term dynamics of wild reindeer populations in the high Arctic. *Global Change Biology*, *25*(11), 3656–3668. doi: 10.1111/GCB.14761

Hanssen-Bauer, I., Førland, E. J., Hisdal, H., Mayer, S., Sandø, A. B., Sorteberg, A., Adakudlu, M., Andresen, J., Bakke, J., Beldring, S., Benestad, R., Bilt, W., Bogen, J., Borstad, C., Breili, K., Breivik, Ø., Børsheim, K. Y., Christiansen, H. H., Dobler, A., … Wong, W. K. (2019). *Climate in Svalbard 2100 – a knowledge base for climate adaptation*. Retrieved from https://munin.uit.no/handle/10037/18819

Heatta, M. J. (2009). *The mating strategy of female Svalbard reindeer (Rangifer tarandus platyrhynchus)*.

Holand, Ø., Weladji, R. B., Gjøstein, H., Kumpula, J., Smith, M. E., Nieminen, M., & Røed, K. H. (2004). Reproductive effort in relation to maternal social rank in reindeer (Rangifer tarandus). *Behavioral Ecology and Sociobiology*, *57*(1), 69–76. doi: 10.1007/S00265-004-0827-0/FIGURES/1

Høy-Petersen, J., Lemière, L., Thompson, D. P., Thiel, A., Crouse, J. A., Ropstad, E., Græsli, A. R., Arnemo, J. M., & Evans, A. L. (2023). Vaginal temperature and collar activity variations in relation to fecal progestagens of captive moose. *Animal Biotelemetry*, *11*(1), 1–13. doi: 10.1186/S40317-023-00345-Y/FIGURES/3

Jensen, M. B. (2012). Behaviour around the time of calving in dairy cows. *Applied Animal Behaviour Science*, *139*(3–4), 195–202. doi: 10.1016/J.APPLANIM.2012.04.002

Keech, M. A., Boertje, R. D., Terry Bowyer, R., & Dale, B. W. (1999). Effects of birth weight on growth of young moose: Do low-weight neonates compensate? *ALCES*, *35*, 51–57.

Kerby, J., & Post, E. (2013). Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1624). doi: 10.1098/RSTB.2012.0484

Kojola, I., Huitu, O., Toppinen, K., Heikura, K., Heikkinen, S., & Ronkainen, S. (2004). Predation on European wild forest reindeer (Rangifer tarandus) by wolves (Canis lupus) in Finland. *Journal of Zoology*, *263*(3), 229–235. doi: 10.1017/S0952836904005084

Krop-Benesch, A., Berger, A., Streich, J., & Scheibe, K. (2011). *Activity Pattern - User's Manual VECTRONIC Aerospace.*

Langvatn, R., Mysterud, A., Stenseth, N. C., & Yoccoz, N. G. (2004). Timing and synchrony of ovulation in red deer constrained by short northern summers. *American Naturalist*, *163*(5), 763–772. doi: 10.1086/383594/ASSET/IMAGES/LARGE/FG6.JPEG

Le Moullec, M., Pedersen, Å. Ø., Stien, A., Rosvold, J., & Hansen, B. B. (2019). A century of conservation: The ongoing recovery of Svalbard reindeer. *The Journal of Wildlife Management*, *83*(8), 1676–1686. doi: 10.1002/JWMG.21761

Lent, P. C. (1966). Calving and Related Social Behavior in the Barren-Ground Caribou. *Zeitschrift Für Tierpsychologie*, *23*(6), 701–756. doi: 10.1111/J.1439-0310.1966.TB01707.X

Linnell, J. D. C., & Andersen, R. (1998). Timing and synchrony of birth in a hider species, the roe deer Capreolus capreolus. *Journal of Zoology*, *244*(4), 497–504. doi: 10.1111/J.1469-7998.1998.TB00055.X

Loe, L. E., Bonenfant, C., Mysterud, A., Gaillard, J. M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N., & Stenseth, N. C. (2005). Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *Journal of Animal Ecology*, *74*(4), 579–588. doi: 10.1111/J.1365-2656.2005.00987.X

Loe, L. E., Liston, G. E., Pigeon, G., Barker, K., Nir, H., Stien, A., Forchhammer, M., Getz, W. M., Robert, J. I., Lee, A., Movik, L., Mysterud, A., Åshild, P., Reinking, A., Ropstad, E., Trondrud, L. M., Tveraa, T., Veiberg, V., Hansen, B., & Albon, S. (2020). The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer. *Glob Change Biol*, *00*, 1–10. doi: 10.1111/gcb.15458

Mallory, C. D., & Boyce, M. S. (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews*, *26*(1), 13–25. doi: 10.1139/ER-2017-0032/ASSET/IMAGES/LARGE/ER-2017-0032F2.JPEG

Matsuura, Y., Sato, K., Suzuki, M., & Ohtaishi, N. (2004). The effects of age, body weight and reproductive status on conception dates and gestation periods in captive sika deer. *Mammal Study*, *29*, 15–20.

Meltofte, H., Piersma, T., Boyd, H., McCaffery, B., Ganter, B., Golovnyuk, V. V., Graham, K., Gratto-Trevor, C. L., Morrison, R. I. G., Nol, E., Rösner, H.-U., Schamel, D., Schekkerman, H., Soloviev, M. Y., Tomkovich, P. S., Tracy, D. M., Tulp, I., & Wennerberg, L. (2007). Effects of climate variation on the breeding ecology of Arctic shorebirds. *Meddelelser Om Grønland. Bioscience*, *59*. doi: 10.7146/MOGBIOSCI.V59.142631

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1833). doi: 10.1098/RSPB.2016.0456

Mysterud, A., Røed, K. H., Holand, Ø., Yoccoz, N. G., & Nieminen, M. (2009). Age-related gestation length adjustment in a large iteroparous mammal at northern latitude. *Journal of Animal Ecology*, *78*(5), 1002–1006. doi: 10.1111/J.1365-2656.2009.01553.X

Oftedal, O. T. (1985). Pregnancy and Lactation. In R. J. Hudson & R. G. White (Eds.), Bioenergetics of wild herbivores (pp. 215–238). Boca Raton: CRC.

Paoli, A., Weladji, R. B., Holand, Ø., & Kumpula, J. (2018). Winter and spring climatic conditions influence timing and synchrony of calving in reindeer. *PLOS ONE*, *13*(4), e0195603. doi: 10.1371/JOURNAL.PONE.0195603

Pedersen, Å. Ø., Paulsen, I. M. G., Albon, S., Arntsen, G. B., Hansen, B. B., Langvatn, R., Loe, L. E., Le Moullec, M., Overrein, Ø., Peeters, B., Ravolainen, V., Ropstad, E., Stien, A., Tyler, N. J. C., Veiberg, V., Wal, R. van der, Andersen, R., Beumer, L. T., Eischeid, I., … Trondrud, L. M. (2019). Svalbard reindeer (Rangifer tarandus platyrhynchus): a status report. *58*, 54. Retrieved from https://brage.npolar.no/npolar-xmlui/handle/11250/2629207

Peláez, M., Gaillard, J. M., Bollmann, K., Heurich, M., & Rehnus, M. (2020). Large-scale variation in birth timing and synchrony of a large herbivore along the latitudinal and altitudinal gradients. *Journal of Animal Ecology*, *89*(8), 1906–1917. doi: 10.1111/1365-2656.13251

Pigeon, G. (2024). *Personal communication*.

Pigeon, G., Albon, S., Loe, L. E., Bischof, R., Bonenfant, C., Forchhammer, M., Irvine, R. J., Ropstad, E., Veiberg, V., & Stien, A. (2022). Context-dependent fitness costs of reproduction despite stable body mass costs in an Arctic herbivore. *Journal of Animal Ecology*, *91*(1), 61–73. doi: 10.1111/1365-2656.13593

Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. J. M., Delorme, D., Warnant, C., Nilsen, E. B., & Bonenfant, C. (2014). Long-lived and heavier females give birth earlier in roe deer. *Ecography*, *37*(3), 241–249. doi: 10.1111/J.1600-0587.2013.00414.X

Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. J. M., Douhard, M., Klein, F., Delorme, D., Warnant, C., & Bonenfant, C. (2015). The influence of birth date via body mass on individual fitness in a long-lived mammal. *Ecology*, *96*(6), 1516–1528. doi: 10.1890/14-0106.1

Post, E., Bøving, P. S., Pedersen, C., & MacArthur, M. A. (2003). Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Canadian Journal of Zoology*, *81*(10), 1709–1714. doi: 10.1139/Z03-172

Rivrud, I. M., Sivertsen, T. R., Mysterud, A., Ahman, B., Støen, O.-G., & Skarin, A. (2018). *Reindeer green-wave surfing constrained by predators*. doi: 10.1002/ecs2.2210

Robertson, D. R., Petersen, C. W., & Brawn, J. D. (1990). Lunar reproductive cycles of benthic-brooding reef fishes: Reflections of larval biology or adult biology? *Ecological Monographs*, *60*(3), 311–329. doi: 10.2307/1943060

Rowell, J. E., & Shipka, M. P. (2009). Variation in gestation length among captive reindeer (Rangifer tarandus tarandus). *Theriogenology*, *72*(2), 190–197. doi: 10.1016/J.THERIOGENOLOGY.2009.01.022

Rughetti, M., Dematteis, A., Meneguz, P. G., & Festa-Bianchet, M. (2015). Age-specific reproductive success and cost in female Alpine ibex. *Oecologia*, *178*(1), 197–205. doi: 10.1007/S00442-014-3192-3/TABLES/3

Sadleir, R. M. F. S. (1987). *Reproduction of female cervids*.

Schmidt, N. M., Kankaanpää, T., Tiusanen, M., Reneerkens, J., Versluijs, T. S. L., Hansen, L. H., Hansen, J., Gerlich, H. S., Høye, T. T., Cirtwill, A. R., Zhemchuzhnikov, M. K., Peña-Aguilera, P., & Roslin, T. (2023). Little directional change in the timing of Arctic spring phenology over the past 25 years. *Current Biology*, *33*(15), 3244-3249.e3. doi: 10.1016/J.CUB.2023.06.038

Seger, john, & Brockmann, J. (1987). *What is Bet-Hedging?* Retrieved from https://www.researchgate.net/publication/248421021_What_is_Bet-Hedging

Semenchuk, P. R., Gillespie, M. A. K., Rumpf, S. B., Baggesen, N., Elberling, B., & Cooper, E. J. (2016). High Arctic plant phenology is determined by snowmelt patterns but duration of phenological periods is fixed: An example of periodicity. *Environmental Research Letters*, *11*(12). doi: 10.1088/1748-9326/11/12/125006

Shipka, M. P., & Rowell, J. E. (2010). *Gestation length in farmed reindeer*.

Sinclair, A. R. E., Mduma, S. A. R., & Arcese, P. (2000). What Determines Phenology and Synchrony of Ungulate Breeding in Serengeti? *Ecology*, *81*(8), 2100. doi: 10.2307/177099

Skogland, T. (1983). The effects of density dependent resource limitation on size of wild reindeer. *Oecologia*, *60*(2), 156–168. doi: 10.1007/BF00379517/METRICS

Skogland, T. (1989a). *Comparative Social Organization of Wild Reindeer in Relation to Food, Mates and Predator Avoidance*.

Skogland, T. (1989b). Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology*, *29*, 1–74.

Skogland, T. (1990). Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. *Oecologia*, *84*(4), 442–450. doi: 10.1007/BF00328158/METRICS

Solberg, E. J., Jordhøy, P., Strand, O., Aanes, R., Loison, A., Sæther, B. E., & Linnell, J. D. C. (2001). Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography*, *24*(4), 441–451. doi: 10.1111/J.1600-0587.2001.TB00479.X

Staaland, H. , and K. H. R. (1986). *Om Svalbardreinens slektskaps- forhold og opprinnelse*.

Stearns, S. C. (1992). *The Evolution of Life Histories*. New York: Oxford University Press Inc.

Trondrud, L. M., Ugland, C., Ropstad, E., Loe, L. E., Albon, S., Stien, A., Evans, A. L., Thorsby, M., Veiberg, V., Irvine, R. J., & Pigeon, G. (2022). Stress responses to repeated captures in a wild ungulate. *Scientific Reports |*, *12*. doi: 10.1038/s41598-022-20270-z

Tyler, N. (1987). Natural limitation of the abundance of the High Arctic Svalbard reindeer. *PhD Thesis, Cambridge University*.

Tyler, N. J. C., Post, E., & Hazlerigg, D. G. (2024). Weak coupling between energetic status and the timing of reproduction in an Arctic ungulate. *Scientific Reports*, *14*(1). doi: 10.1038/S41598-024-56550-Z

van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, *77*(3), 753–758. doi: 10.1016/J.ANBEHAV.2008.11.006

Van Der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. *Ecology*, *95*(12), 3414–3427. doi: 10.1890/14-0533.1

Veiberg, V. (2007). *Patterns, causes and consequences of tooth wear in cervids*.

Veiberg, V., Danielsen, P., Loe, L. E., Stien, A., Peeters, B., Hansen, B. B., Irvine, R. J., Ropstad, E., Albon, S. D., Tveraa, T., & Varpe, Ø. (2017). Klimaeffektar på svalbardreinens kalvingstidspunkt. In 33 s. Norsk institutt for naturforskning (NINA). Retrieved from https://brage.nina.no/nina-xmlui/handle/11250/2447479

Veiberg, V., Loe, L. E., Albon, S. D., Irvine, R. J., Tveraa, T., Ropstad, E., & Stien, A. (2016). Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore. *Oikos*, *126*(7), 980–987. doi: 10.1111/OIK.03815

Vickers, H., HØgda, K. A., SolbØ, S., Karlsen, S. R., TØmmervik, H., Aanes, R., & Hansen, B. B. (2016). Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters*, *11*(10), 105004. doi: 10.1088/1748-9326/11/10/105004

Vickers, H., Karlsen, S. R., & Malnes, E. (2020). A 20-Year MODIS-Based Snow Cover Dataset for Svalbard and Its Link to Phenological Timing and Sea Ice Variability. *Remote Sensing*. doi: 10.3390/rs12071123

Viejou, R., Avgar, T., Brown, G. S., Patterson, B. R., Reid, D. E. B., Rodgers, A. R., Shuter, J., Thompson, I. D., & Fryxell, J. M. (2018). Woodland caribou habitat selection patterns in relation to predation risk and forage abundance depend on reproductive state. *Ecology and Evolution*, *8*(11), 5863. doi: 10.1002/ECE3.4124

Vikhamar-Schuler, D., Isaksen, K., Haugen, J. E., Tømmervik, H., Luks, B., Schuler, T. V., & Bjerke, J. W. (2016). Changes in Winter Warming Events in the Nordic Arctic Region. *Journal of Climate*, *29*(17), 6223–6244. doi: 10.1175/JCLI-D-15-0763.1

Visser, M. E. (2013). Phenological Shifts in Animals Under Contemporary Climate Change. *Encyclopedia of Biodiversity: Second Edition*, 716–727. doi: 10.1016/B978-0-12-384719-5.00376-2

Wilder, S. M., Raubenheimer, D., & Simpson, S. J. (2016). Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. *Functional Ecology*, *30*(1), 108–115. doi: 10.1111/1365-2435.12460

8. Appendix

Appendix 1 Calculation of annual median calving dates
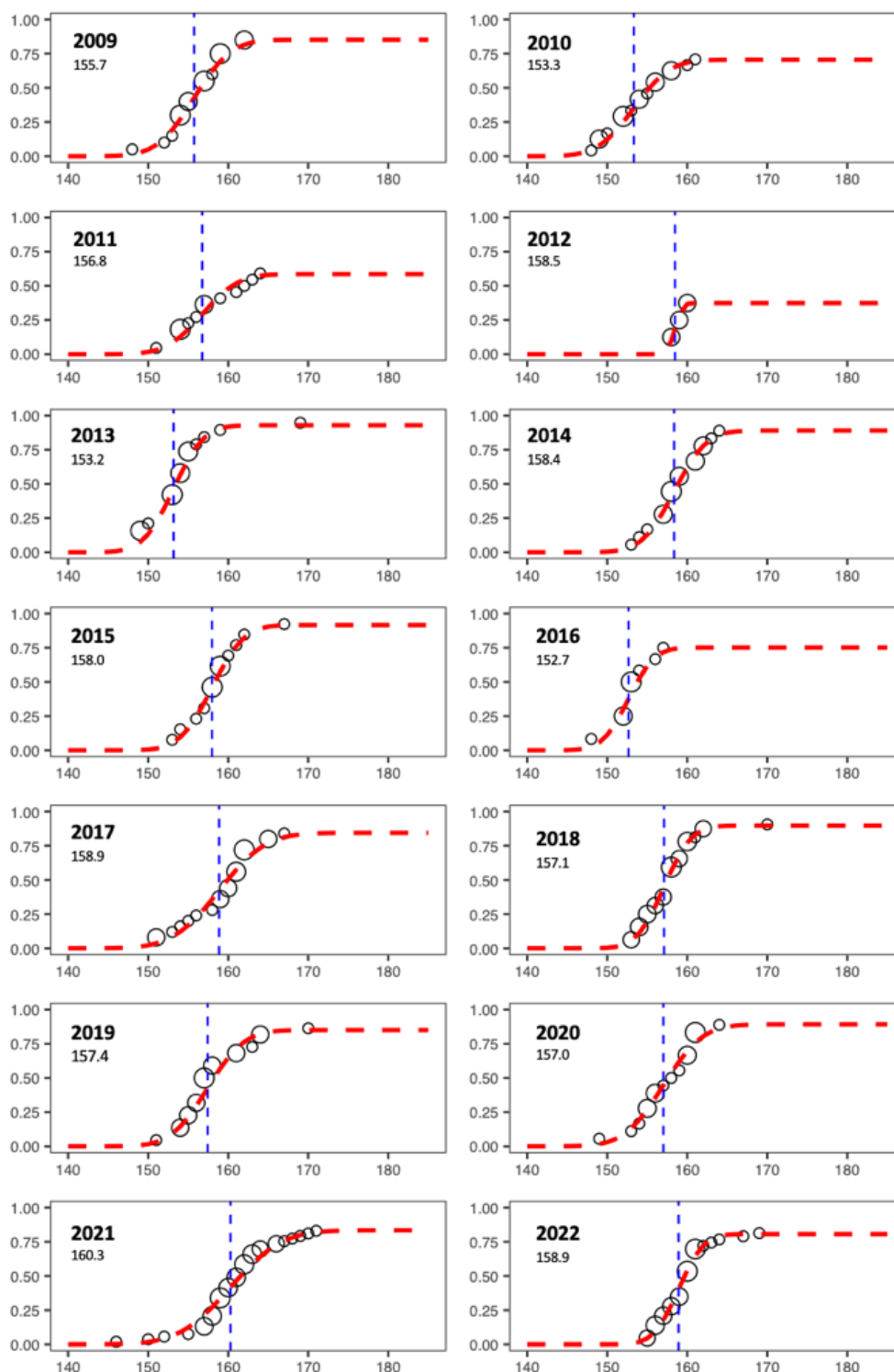
Appendix 1: *The sigmoid curve in red dashed line shows the relation between accumulated calving rate (calf per hind) and julian day of the year through the calving season. The blue dashed line indicates the point at which the sigmoid curve is the steepest. The annual estimated calving day is shown beneath the year label for each graph.*

Appendix 2 Attempt at identifying conception

While identification of calving with the use of activity data has already been successfully performed , identifying events of rutting remains unaccomplished for Svalbard reindeer. Due to the highly limited knowledge concerning behavior during mating periods, an exploratory approach that combines activity- and temperature data was adopted when looking for a potential pattern that could reveal ovulation or conception. Using body temperature data to identify ovulation has previously been done on moose *Alces alces*, while using activity data was not successful (Græsli et al., 2022; Høy-Petersen et al., 2023). To give sufficient strength to a potential method of detecting rutting would require that there exists a temperature and/or activity related pattern that only occurs when this event (rutting) takes place. Preferably, there would exist a pattern that aligns activity and temperature data. Because of this, the year 2018, where both activity and temperature data are available for seven individuals, was the initial target. However, the females do not go through ovulation simultaneously. When one or several of the females in a harem become fertile (ovulates) it is reasonable to assume that these individual experiences an increase in attention from nearby bucks. It could be chased by both its preferred mating partner and newcomers. As the females tends to stay together in a herd during the rut, such chasing could cause the whole herd of females to display similar activity patterns, despite only some or just one of them having ovulation (Heatta, 2009). This challenges the task of confidently detection rutting patterns in the activity data. It was decided that estimating conception and ovulation from activity and temperature data would be abandoned.

Appendix 3 Overview of estimated calving events per year

Appendix 3: *Number of estimated calving events per year by using activity data, and the number of calving events where capture data from April is also available. The years 2020 and 2012 were excluded from analysis on drivers of synchrony due to low sample sizes.*

						Observed calving events							
2009	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**
17	16	13	3	18	16	12	9	20	29	19	16	43	35
					Observed calving events per year where capture data is also available								
17	12	8	3	16	12	10	7	16	26	13	2	42	30