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Climate trends, weather fluctuations and calving phenology in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)

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ABSTRACT

Reproduction is known to be one of the most energetically demanding processes in the life of an organism, and in seasonal environments, vertebrate offspring production is therefore timed to coincide with the annual peak in resource availability. However, the recent advancement of spring phenology due to increased global temperatures may lead to a mismatch between peak resource availability and the high-energy requirements of reproduction. For high Arctic herbivores, such as reindeer, the onset of spring represents the start of a short time window of high resource availability crucial for development and survival, and a trophic mismatch may potentially influence reproductive success. As initiation of reproduction is often determined by cues distant in time of the annual peak in resources, one important question is therefore whether herbivores are able to match the recent advancement of plant phenology. Using data describing the timing of calving in Svalbard reindeer over a time period of 37 years, I here document the lack of changes in calving phenology in this species, despite significant advancement in the onset of spring during the same period. This suggests that the potential development of a trophic mismatch may already be happening, or will happen, but the future consequences are more difficult to predict. Also, my results indicate that the Svalbard reindeer display a certain degree of response in their calving phenology in relation to annual weather fluctuations. My findings suggest that an earlier onset of spring seemed advance calving date when the preceding winter conditions had been severe, whereas this effect was not found when the preceding winters conditions were milder. This interaction effect is possibly due to icing events which decrease forage accessibility in winter, and in turn, reduce body condition of parturient females. Even so, results should be interpreted cautiously due to low sample size and potential confounding factors. Therefore, in future studies, more comprehensive data is needed to adequately address questions about the influential mechanisms on phenology.

Key words: Svalbard reindeer • reproduction • climate change • phenology • trophic mismatch • *Rangifer tarandus*

ABSTRACT IN NORWEGIAN

Reproduksjon er en av de mest krevende prosessene i organismers liv, og i områder med sesongvariasjon er derfor produksjon av nye individer synkronisert til å treffe den årlige toppen i ressurstilgang. Den raske oppvarmingen av det globale klimaet de siste årene har derimot forskjøvet vårfenologien til tidligere tidspunkt, noe som kan lede til en mismatch mellom toppen i ressurstilgang og de store ressurskravene som følger med reproduksjon. For Arktiske herbivorer som reinsdyr er starten på den korte planteveksts sesongen i Arktisk viktig å få med seg for å sikre størst muligheter til vekst og overlevelse. Et trofisk mismatch kan derfor påvirke reproduktiv suksess. Siden reproduksjonsprosessen initieres på et tidspunkt som er langt unna den årlige toppen i ressurstilgang og gjerne bestemmes via mekanismer som ikke er sensitive til temperaturøkninger, er det derfor viktig å se om herbivorer følger etter forskyvningen i plantefenologi. I denne studien bruker jeg data på kalvingstidspunkt av Svalbardrein over en 37 år lang studieperiode for å dokumentere at det ikke eksisterer endringer i kalvingsfenologien til Svalbardreinen, til tross for forskyvninger av vårstarten i samme periode. Dette indikerer at et trofisk mismatch allerede er i utvikling, eller at det vil skje i fremtiden. Konsekvensene av dette er dog vanskeligere å forutse. Resultatene fra studien indikerer også at kalvingsfenologien til Svalbardreinen til en viss grad responderer til årlige fluktuasjoner i værforhold. Mine funn viser at en tidligere vårstart ser ut til å forskyve kalvingsdatoen fremover når det aktuelle året også har hatt harde vinterforhold, men denne effekten sees ikke i år der vinterforholdene har vært mildere. Resultatene må dog sees i lys av liten datamengde og potensielle konfunderende faktorer, og derfor trengs det bedre og mer omfattende data i fremtidige studier for å kunne dra sikre konklusjoner om i hvilken grad ulike faktorer påvirker fenologien i organismer.

Stikkord: Svalbardrein • reproduksjon • klimaendringer • fenologi • trofisk mismatch • *Rangifer tarandus*

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INTRODUCTION

According to life history theory, organisms adapt to their environment through evolutionary mechanisms to maximize their fitness (Stearns 2000). These adaptations may be expressed as behavioral or morphological traits, but also as phenology – the timing of seasonal activities of plants and animals (e.g. bud break, flowering, calving, egg laying, migration; Walther *et al.* 2002). The phenology of reproduction is one of the most important life history traits (Stearns 1992, 2000), but reproduction also represents one of the most energetically demanding processes for an organism (Gittleman & Thompson 1988; Wade & Schneider 1992). In seasonal environments, there is often only a limited time of the year when conditions are favorable enough to support reproduction, and this period is most often determined by the availability of food (Bronson 1989). Therefore, to increase the probability of a successful reproduction, temporal overlap between offspring production and peak resource availability is crucial (Bronson 1989; Visser & Both 2005).

The most favorable time for when to give birth is usually determined by the abundance of focal prey species in lower trophic levels. This principle of phenological synchrony between trophic levels is evident in a broad range of ecosystems in both terrestrial and aquatic systems (see e.g. Visser & Both 2005; Parmesan 2006; Durant *et al.* 2007). However, recent climate change (IPCC 2014) now challenges this relationship, as consumer and prey species display unequal responses to the rapidly increasing temperatures (Walther *et al.* 2002; Visser & Both 2005). Several comprehensive studies show that climate change has already had impacts on a variety of plant and animal life throughout the world in both terrestrial, marine, and freshwater systems (Walther *et al.* 2002; Parmesan & Yohe 2003; Parmesan 2006; IPCC 2014). As temperatures rise, the phenology at lower trophic levels (e.g. plants) is expected to respond strongly to such environmental cues (Menzel *et al.* 2006), with one consequence being that the spring phenology has advanced significantly during the last decades (Cleland *et al.* 2007; Høye *et al.* 2007; Gilg *et al.* 2012; IPCC 2014). Such rapid shifts in phenology may lead to a decoupling of the phenological synchrony and the development of a trophic mismatch, as documented in several bird species (Visser *et al.* 1998; Both & Visser 2001; Storde 2003; Both *et al.* 2006; Visser *et al.* 2006; Both *et al.* 2009; Saino *et al.* 2011), mammals (Inouye *et al.* 2000; Post & Forchhammer 2008; Kerby & Post 2013; Plard *et al.* 2014), as well as in aquatic systems (Edwards & Richardson 2004; Winder & Schindler 2004; Mackas *et al.* 2007; Søreide *et al.* 2010). According to the “match/mismatch

hypothesis” (Cushing 1990; Durant *et al.* 2007), the consequence of a mismatch in phenology between the trophic levels is typically reduced reproductive success and survival of the consumer (Durant *et al.* 2007), especially in seasonal environments (see Durant *et al.* 2005).

In the Arctic, the effects of climate change are expected to exceed those in temperate areas as temperatures rise at almost twice the rate near the poles, as compared to the rest of the world (Overpeck *et al.* 1997; ACIA 2004; IPCC 2014). Moreover, the highly variable weather conditions in the Arctic are likely to escalate with the predicted increase of extreme weather events, such as heat waves and heavy rainfalls (Rennert *et al.* 2009; IPCC 2014). In tundra ecosystems, the effects of climate change are most likely to be associated with a longer and warmer snow-free season (Høye *et al.* 2007; Meltofte *et al.* 2008; Post *et al.* 2009; van der Wal & Stien 2014). One important question in current research on the consequences of Arctic climate change is whether species at higher levels are able to adjust their phenology to track the advancement of the phenology of their prey species (Post & Forchhammer 2008; Gilg *et al.* 2012; Grabowski *et al.* 2013; Kerby & Post 2013; Doiron *et al.* 2015). This can be problematic as the phenology at higher trophic levels is usually determined by environmental cues distant in time (e.g. timing of mating and parturition) or space (e.g. timing of long-distance migration). This is the case for the reproductive phenology of circumpolar ungulates, such as caribou and wild reindeer (both *Rangifer tarandus*), where rut and conception occurs in fall, while parturition is timed to coincide with the favorable conditions at the onset of spring (Skogland 1989; Post *et al.* 2003). At higher latitudes, the nutritional quality and digestibility of plants reach a peak soon after they emerge in spring, followed by a rapid decline (Klein 1990; Post & Klein 1999), and the newly emerged and nutritious plant tissue at the onset of the plant-growing season may therefore be vital after parturition, as the main cost of reproduction is represented by lactation (Gittleman & Thompson 1988; Clutton-Brock *et al.* 1989). Considering the seasonality of circumpolar regions, sufficient time to forage on plant tissue before winter is also important to enhance growth and chances of winter survival of calves (Guinness *et al.* 1978; Festa-Bianchet 1988), as well as to supply energy for the demanding process of lactating (Clutton-Brock *et al.* 1989). Consequently, the spatial variation in calving dates between *R. tarandus* populations highly corresponds to the local onset of the plant-growing season (Skogland 1989; Post *et al.* 2003), with delayed calving at higher latitudes (Skogland 1989).

At the most extreme latitudes in the high Arctic, the plant-growing season is particularly brief (Malnes *et al.* 2010), and with such high seasonality in food availability and quality, one should expect strong selection for females to time parturition to match plant phenology. Indeed, in the high Arctic archipelago of Svalbard, populations of the wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) seem to exhibit a birth-synchrony unparalleled by other *Rangifer* populations (Skogland 1989). The birth-synchrony of *Rangifer* has previously been proposed to be a strategy to avoid predation of newborn calves (e.g. Bergerud 1974), but as predators are virtually absent in Svalbard (only one observation exists in the literature of a Svalbard reindeer calf being killed by predators; Prestrud 1992), the high birth-synchrony is most likely an adaptation to the short plant-growing season (Skogland 1989; Post *et al.* 2003). However, as in other parts of the Arctic, climate is changing and temperatures are rapidly increasing (Forland *et al.* 2011). In an environment with such a brief plant-growing season and rapid advancement of spring (Karlsen *et al.* 2014), there is clearly a potential for the development of a trophic mismatch if the Svalbard reindeer fail to respond to the advancement of plant phenology. Moreover, recent changes in winter climate have already been shown to influence the population dynamics of herbivores (Miller & Gunn 2003; Putkonen & Roe 2003; Hansen *et al.* 2011) and, in turn, higher trophic levels (Hansen *et al.* 2013), due to increased winter rain and the formation of impenetrable snow packs that decrease forage accessibility (Hansen *et al.* 2011). Arctic vertebrates are highly adapted to the extreme conditions of where they reside, but with obvious limitations in migration strategies, circumpolar species are particularly vulnerable in a rapidly changing world.

In this study, I seek to investigate the potential development of a trophic mismatch in the reproductive biology of the Svalbard reindeer in relation to its resources. Being subject to negligible predation, this sub-species of *Rangifer* provides an excellent opportunity for studying phenological effects of climate change. I used calving time data from 13 years, covering a range of 37 years (1979-2015) to generate a time series of population-level estimates of the annual calving date. I expected that, given sufficient phenotypic plasticity and/or adaptation via natural selection, the pronounced advancement of spring in this system (Karlsen *et al.* 2014) would over time lead to earlier calving dates. Furthermore, several studies have recently demonstrated how reindeer behavior and population dynamics are driven by winter climate and, in particular, rain-on-snow (hereafter ROS, also including rain on frozen ground) and icing events (Miller & Gunn 2003; Kohler & Aanes 2004; Hansen *et al.* 2011; Stien *et al.* 2012). Because severe (in this case: rainy) winter conditions lead to

reduced body condition in late winter due to decreased forage accessibility (Albon et al. in revision), I expected that ROS would possibly delay calving dates (cf. Skogland 1989). To evaluate this, I first compared temporal trends in climate covariates (i.e. proxies for spring onset and winter severity) and calving dates, using simple regression techniques. Secondly, I used multiple regressions and model selection to analyze how annual calving dates were related to variation in proxies for the onset of spring and the degree of winter severity.

METHODS

Study system

The study was conducted in the high Arctic archipelago of Svalbard (74–81°N, 10–35°E; Figure 1), situated approximately half way between mainland Norway and the North Pole. Typical features of the islands are long fjords, wide valleys and steep mountains, with glaciers covering about 60% of the total land area (Tyler 1987). The archipelago is inhabited by the endemic Svalbard reindeer, which is found in almost all non-glaciated parts of the islands (Tyler 1987). I studied populations residing in the inner fjord zone of Svalbard's biggest island, Spitsbergen, in the valleys of Adventdalen and Reindalen (including Semmeldalen and Colesdalen; Figure 1). These valleys are in relatively close proximity of the weather station at Svalbard airport, Longyearbyen, and have high densities of reindeer. For the study period of 1979-2015, the mean temperature was $-4.8\text{ }^{\circ}\text{C}$ and the mean precipitation was 0.8 mm.



Figure 1. The study area of Adventdalen and Reindalen (including Semmeldalen and Colesdalen). Red points mark the location of Longyearbyen and Svalbard airport. Longitude–latitude coordinates shown at the map border and map scale in bottom-right corner. The map is made in ArcGIS Rest API 10.11. © Norwegian Polar Institute

The Svalbard reindeer is the only large, terrestrial herbivore in Svalbard. Besides humans, which perform annual low-level reindeer harvest, the only two other mammals that reindeer may encounter are the polar bear (*Ursus maritimus*) and the Arctic fox (*Vulpes lagopus*), but they very rarely prey on reindeer (Prestrud 1992; Derocher *et al.* 2000). Hence, contrary to many other *Rangifer* species, the Svalbard reindeer has no mammal competitors and virtually no natural predators. As a combined effect of the harsh Arctic environment, limited food resources and the absence of predators, the Svalbard reindeer have adapted a somewhat different behavior than most other *Rangifer*. They have a sedentary way of living (Tyler & Øritsland 1989), possibly to reduce energy outputs (Loe *et al.* 2007), and are most often found in small groups rather than large herds (Tyler 1987). As for other ungulates, the annual reproductive cycle is initiated by seasonal changes in day length in fall (in this case October) followed by ovulation and conception (Skogland 1994). During the scarce winter months in Svalbard, forage availability is limited and reindeer are usually found feeding along ridges, mountain slopes, or other places where snow accumulation is low (Bjune *et al.* 2005). At the end of the assumed ~230-day long gestation period (for other species of *R. tarandus*, Leader-Williams 1988; Mysterud *et al.* 2009), a single calf is born, usually in early to mid-June (Tyler 1987; Skogland 1989). The favorable conditions at the onset of the plant-growing season are presumed to provide optimal conditions for growth and development of newborn calves, which suckle for about a month before they are able to also feed on plant tissue (Tyler 1987). This phenological synchrony between plant-growth and calving is also important for females in order to optimize the process of accumulating sufficient fat reserves needed to meet the energetic demands represented by a new reproductive cycle and survival through winter (Clutton-Brock *et al.* 1989; Skogland 1994)

Calving time data

I used calving time data from three different time periods: 1979-1981 (Tyler 1987), 1996-1998 (R. J. Irvine *et al.* unpubl.) and 2009-2015 (L.E. Loe unpubl.), which provided temporal distributions of calving dates for 13 years in total. Until 1998, the calving time data are based on *in situ* observations made in the calving areas (see Appendix, Table A1 for a summary), whereas calving time data for years 2009-2015 were obtained by activity data recorded by GPS-collars (see below). Observations in 1979-1981 were recorded at irregular intervals along a predetermined route in Adventdalen (Tyler 1987). The frequency of observations differed between years, but generally covered the range from June 1st to the middle of July, at the time of the main summer census. For these years, the number of observed adult females

ranged from 10–244 per day (mean±SD = 85±76), and the number of observed calves ranged from 0–171 per day (mean±SD = 32±48). Observations in 1996-1998 were recorded in Reindalen on a daily or close-to-daily basis (R. J. Irvine *et al.* unpubl). The frequency of observations differed between years, but generally covered the range from the first days of June to the 1st of July, with the exception being 1997, when observations started the 24th of May. For these years, the number of observed adult females ranged from 5–164 per day (mean±SD = 46±35), and the number of observed calves ranged from 0–123 per day (mean±SD = 20±25). Despite the spatial distance between Adventdalen and Reindalen (Figure 1), the two studied populations fluctuate in synchrony and are shaped by similar environmental drivers (Aanes *et al.* 2003), which are also highly correlated in space (B.B Hansen, pers.comm.) Furthermore, in 1979, independent calves per female observations were done in both Adventdalen (Tyler 1987) and Reindalen (Skogland 1989), with approximately the same estimates of calving phenology (see Appendix, Figure A1), suggesting that valley differences are negligible.

Since 2009, about 30 adult females in Reindalen have carried GPS-collars as part of a long-term capture-mark-recapture project (see Loe *et al.* In press). In addition to tracking the location of the animals, the GPS-collars also record and store activity data for individual reindeer. Records from pregnant females show unusually high levels of activity during a short time interval of the day in periods when calving is expected to occur, i.e. mainly early to mid-June, which is typically followed by a long resting period lasting for several hours. The increased activity around parturition is probably related to a general restlessness prior and during birth, as well as intensive licking of the newborn calf. When analyzing the activity data (V. Veiberg & L.E. Loe, unpubl), the peak activity followed by an extended resting period is seen as a clear anomaly from the normal activity pattern, and this characteristic signature can thus be used as an estimate for the individual calving date without observing the actual calving itself (Vebjørn Veiberg, pers. comm.). This assumption is supported both by studies on other species (Langbein *et al.* 1998; Jensen 2012), as well as in *in situ* field observations (see below).

Each April since 2009, as many GPS-collars as possible have been retrieved during fieldwork and their data analyzed, generating a series of calving time data from 2009-2015. Activity data from 12 collars retrieved in April 2016 were compared to *in situ* observations of calving

in 2015 (V. Veiberg, unpubl) and the high match in estimated calving date gave strong support for using the indirect method of estimating calving date (see Appendix, Figure A2).

Climate proxies for spring onset and winter severity

In the absence of data on the timing of spring onset and winter severity covering the entire study period, I used proxies based on weather data. It has been shown that the timing of spring onset (Karlsen *et al.* 2014) is closely related to the heat sum in May-June and, in particular, from the second half of May (Karlsen *et al.* In prep). Furthermore, the amount of winter ROS is strongly correlated with icing extent (Kohler & Aanes 2004; Hansen *et al.* 2011; Hansen *et al.* 2014; Albon *et al.* unpubl.), and reflects feeding conditions in winter well. I therefore used spring heat sum as proxy for spring onset, and amounts of ROS as proxy for winter severity. I downloaded data containing measurements of daily mean temperature and daily precipitation from Svalbard airport (Figure 1, 78.25°N, 15.50°E), available through the Norwegian Meteorological Institute, for all years in the study period (1979-2015). To estimate spring heat sum, I used the sum of all above-zero temperatures from 15th of May to 30th of June. Note that this heat sum was almost perfectly correlated with heat sum for May plus first half of June ($r = 0.88$, $P < 0.01$), and also with the entire May-June period ($r = 0.99$, $P < 0.01$). To estimate ROS for year t , I used the sum of daily precipitation at above -1°C temperatures from November _{$t-1$} to April _{t} . November–April was chosen because the soil usually freezes in late October (Roth & Boike 2001) and the snow starts melting in early May.

Statistical analyses

The statistical analyses consisted of (1) estimating annual population-level calving dates, (2) investigating temporal trends in climate and calving data, and (3) investigating potential correlations between variation in climate proxies and annual variation in calving dates.

To obtain population-level estimates of the annual calving date, I used calving time data containing the number of calves and adult females observed (until 1998; Table A1), as well as individual calving time data based on activity levels (2009-2015). I chose the point at which 50% of the parturient females had given birth as my estimate of the annual calving date. At any given observational day, the number of observed calves and adult females yields a proportion of calves per female. However, this proportion also includes observations of non-parturient females. This can be accounted for by using a scaling parameter, and thus the

point at which 50% of parturient females can be estimated. In the analyses, I assumed the proportion of parturient females giving birth a certain day to be normally distributed around the 50%-calving date for each year. Thus, the proportion of parturient females that have given birth follows a cumulative normal distribution, with mean μ and standard deviation σ , where the mean μ is equal to the 50%-calving date (Garel *et al.* 2009). The proportion of parturient females that have calved p is given by

$$p = q \cdot \Phi \frac{x-\mu}{\sigma} \quad (1)$$

where Φ denotes the cumulative distribution, and x = Julian date (i.e. day of year) and q is the scaling parameter. Equation (1) displays a sigmoid relationship between p and x , leveling off at the scaling parameter q (Garel *et al.* 2009). If $q = 1$ (i.e. a population with only parturient females), the proportions of observed calves per female could have been used directly to estimate the sigmoid curve. Equation (1) can after re-parameterization be written as

$$\text{probit} \frac{p}{q} = \beta_0 + \beta_1 x \quad (2)$$

where the probit link function is the inverse of the cumulative standard normal density Φ and the new parameters, the regression coefficients

$$\beta_0 = \frac{\mu}{\sigma}, \quad \beta_1 = \frac{1}{\sigma} \quad (3)$$

Using the probit link function, I estimated the date where 50% of the parturient females had given birth (Garel *et al.* 2009), giving a time series of calving dates for all years.

Based on the time series of the climate proxies (spring heat sum and ROS), I used simple linear regression models with each proxy as the response variable against year to examine climatic trends during the study period (1979-2015). Then, I used the time series of annual calving dates as the response variable against year to investigate for any potential long-term trend in calving phenology.

To investigate for potential effects of variation in weather on the annual calving date, I used the climate proxies as covariates in multiple linear regression models (assuming Gaussian

distribution). *A priori*, either variable could possibly affect calving date (see above, Introduction). In addition, it is not unlikely that the effect of one climate variable is influenced by the level of the other variable (i.e. an interaction effect). Thus, starting with a global model that included annual calving date as the response variable, and spring heat sum, ROS and an interaction between the two as explanatory variables, I ran all possible subsets of this model, including the null model, giving a total of five candidate models.

Model selection was done using an information-theoretic approach according to the Akaike Information Criteria corrected for small sample size (AIC_c ; Anderson & Burnham 2002), available through the “MuMIn” package (Barton 2016). The model with lowest AIC_c score was considered as the best-fitted model, given the data and the candidate models. As a rule of thumb, and in accordance with Burnham & Anderson (2002), models with $\Delta AIC_c < 2$ were considered to have substantial support. Natural log-transformation of the covariates was done to see if this yielded a better fit, but it did not. Note that the sample size was low, hence, the full model should be cautiously interpreted. All statistical analyses were done in R version 3.2.4 (R Core Team 2016)

RESULTS

Temporal trends in climate proxies

During the study period, spring heat sum ranged from 20.2–171.4 °C (mean±SD = 100.5±34.3) and increased by an average of 2.2 °C per year (Figure 2a). Notably, the ten years with highest spring heat sum all occurred from 2002 and onwards, while the five years with lowest spring heat sum all occurred before 1988. Even though there were strong inter-annual fluctuations indicating variable weather conditions, the trend of an increasing spring heat sum across the study period is highly significant ($\beta = 2.23$, $SE = 0.38$, $t = 5.86$, $P < 0.01$; Figure 2a).

The amount of ROS ranged from 0–66.2 mm (mean±SD = 15.5±19.1; Figure 2b). Many years show zero, or close to zero ROS, while certain years show high amounts of ROS relative to adjacent years. 1996, 2010 and 2012 represent the rainiest winters with 62–66 mm of ROS. Note that the eight winters with lowest amounts of ROS (< 1.5 mm) all occurred before 1999, whereas all winters after 1999 have ROS amounts above 3 mm. Even so, annual fluctuations were high, with no statistically significant linear trend of change in the amount of ROS during the study period ($\beta = 0.28$, $SE = 0.29$, $t = 0.96$, $P = 0.34$; Figure 2b)

Calving phenology

For years 1979–1981, 1996–1998 and 2009–2015, the earliest calving date was Julian date 154 (3rd June) in 2013, and the latest calving date was Julian date 164 (12th June) in 1996 (mean±SD = 158±9.5; Figure 2c & Figure 3). The three earliest calving dates all occurred late in the study period (2009, 2010 and 2013), but there was no statistically significant linear trend of change in the calving dates over the course of the study ($\beta = -0.048$, $SE = 0.058$, $t = -0.830$, $P = 0.424$; Figure 2c)

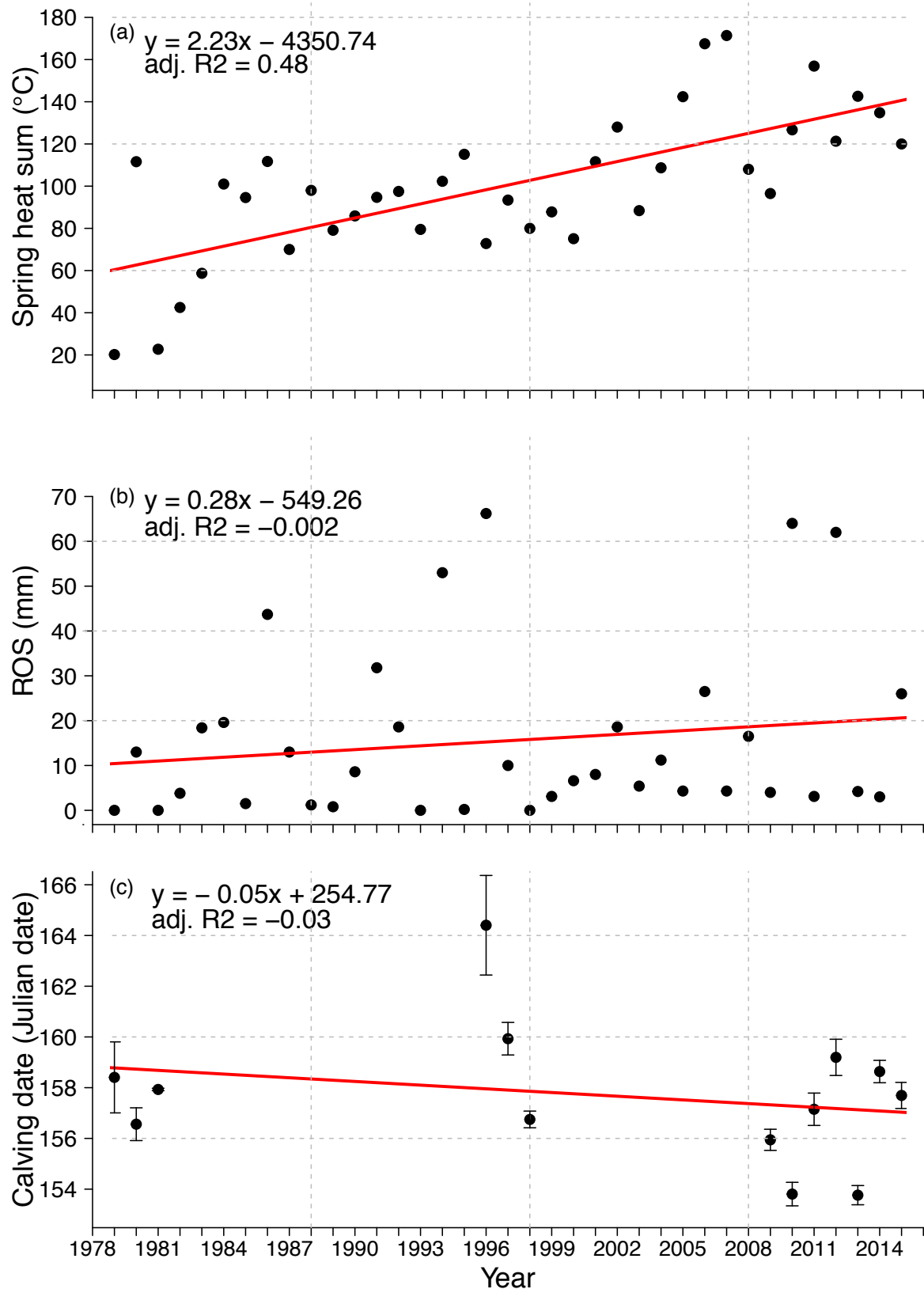


Figure 2: Time series (1979-2015) showing the annual (a) spring heat sum, (b) rain-on-snow (ROS), and (c) calving date \pm standard errors. Calving date is reported as Julian date (mean = 158, corresponding to June 7th [6th in leap years])

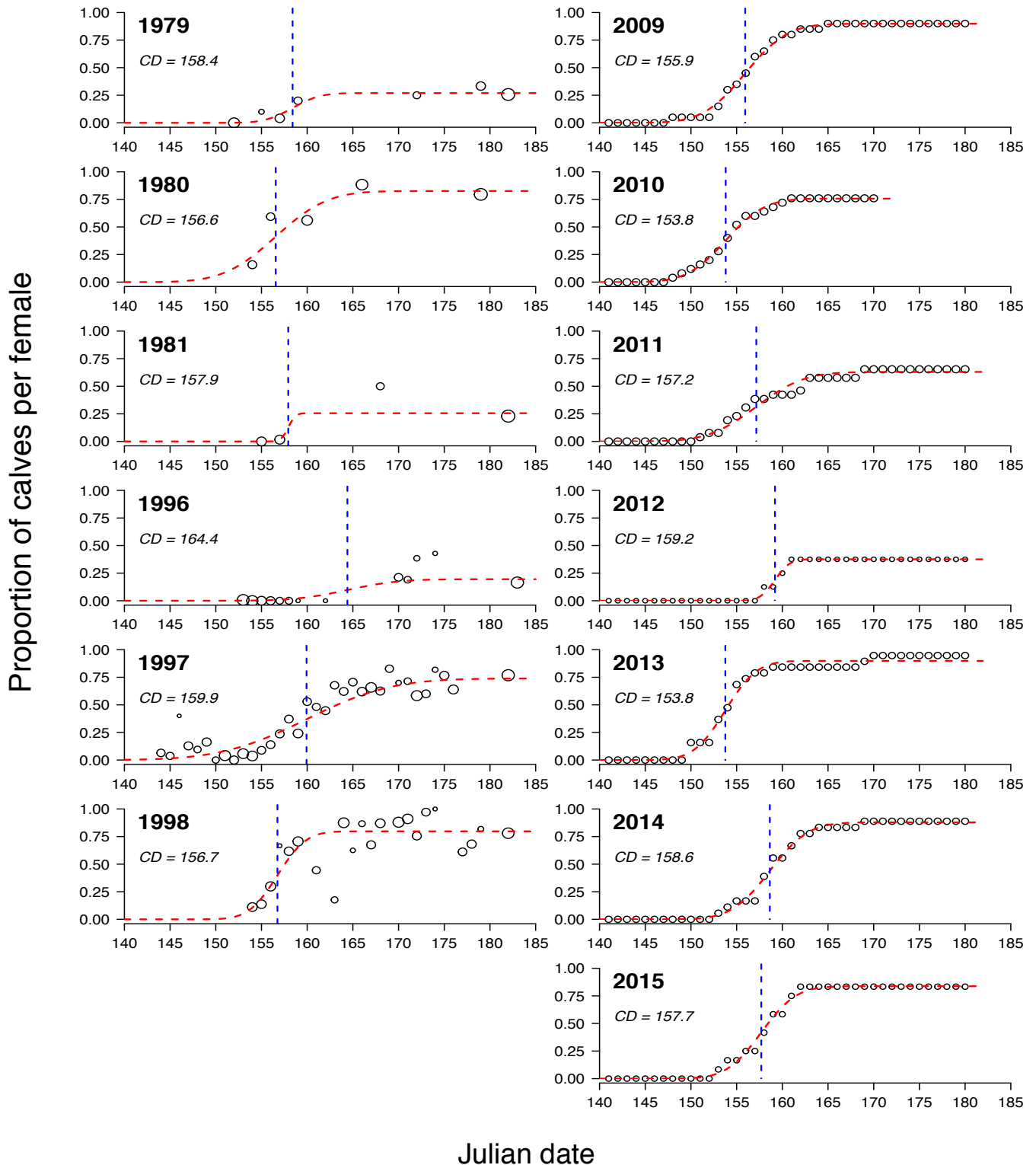


Figure 3: Estimates of annual calving date (blue vertical line) based on observational data (1979-1998, left side) and activity data (2009-2015, right side). The x-axis displays Julian date and the y-axis display the proportion of calves per adult female. The annual calving date is estimated to the date where 50% of the parturient females have calved. The size of the data points is proportional to the sample size.

Effects of climate proxies

Based on five candidate models, the variation in annual calving dates was best explained by the global model, including spring heat sum, ROS, and the interaction between them as explanatory variables (Table 1; Model 1; $AIC_c = 66.53$). Note that the null model was ranked second in the model selection process (Table 1; Model 2; $AIC_c = 67.22$, $\Delta AIC_c < 2$). The global model indicated a significant positive effect of ROS on calving date (i.e. a delaying effect) at low (zero) spring heat sum, with a negative interaction effect suggesting that the effect of ROS decreased and became non-significant at higher spring heat sum (Table 1). The negative interaction term indicates an advance in calving dates with increasing spring heat sum, but only when the amount of ROS is high (Figure 4). Thus, an earlier onset of spring seem to advance the timing of calving when winter conditions have been severe (i.e. rainy), but this is not the case when winter conditions have been less severe. To evaluate whether the spring heat sum effect was simply an effect of time (i.e. a confounding factor, due to the linear trend displayed in Figure 2a), the global model was tested with year as a covariate instead of spring heat sum. This alternative model yielded a less good fit ($AIC_c = 73.64$), but, although non-significant, it showed the same tendency (**Intercept:** $\beta = 181.644$, $SE = 122.917$, $t = 1.478$, $P = 0.174$; **Year:** $\beta = -0.012$, $SE = 0.062$, $t = -0.200$, $P = 0.846$; **ROS:** $\beta = 11.150$, $SE = 6.250$, $t = 1.79$, $P = 0.110$; **Year:ROS:** $\beta = -0.006$, $SE = 0.003$, $t = -1.777$, $P = 0.109$)

Table 1. Models included in the analysis of how annual weather fluctuations correlated with variation in calving dates. Models are ranked 1 to 5 based on the Akaike Information Criterion model selection corrected for sample size (AIC_c). The AIC_c, AIC and adjusted R² scores are included. Calving date (in Julian date) is the response variable, with spring heat sum and rain-on-snow (ROS) as explanatory variables. Standard errors (\pm SE) reported for intercept and explanatory variables.

Model	<u>Explanatory variables</u>				<u>Model selection</u>			
	Intercept	Spring heat sum	ROS	Spring heat sum:ROS	AIC _c	Δ AIC _c	AIC	R ²
1	158.300 \pm 1.428	-1.156 \cdot 10 ⁻² \pm 1.366 \cdot 10 ⁻²	2.769 \cdot 10 ⁻¹ \pm 7.653 \cdot 10 ⁻² **	-2.290 \cdot 10 ⁻³ \pm 7.135 \cdot 10 ⁻⁴ *	66.53	0.00	57.96	0.548
Null model	157.705 \pm 7.589 \cdot 10 ⁻¹				67.22	0.69	66.02	
3	160.012 \pm 196.377 \cdot 10 ⁻²	-2.316 \cdot 10 ⁻² \pm 1.820 \cdot 10 ⁻²			68.90	2.37	66.24	0.049
4	157.063 \pm 95.361 \cdot 10 ⁻²		3.264 \cdot 10 ⁻² \pm 2.979 \cdot 10 ⁻²		69.34	2.81	66.68	0.016
5	159.657 \pm 189.806 \cdot 10 ⁻²	-2.744 \cdot 10 ⁻² \pm 1.769 \cdot 10 ⁻²	4.021 \cdot 10 ⁻² \pm 2.847 \cdot 10 ⁻²		70.88	4.35	65.86	0.127

* P < 0.05, ** P < 0.01, *** P < 0.001

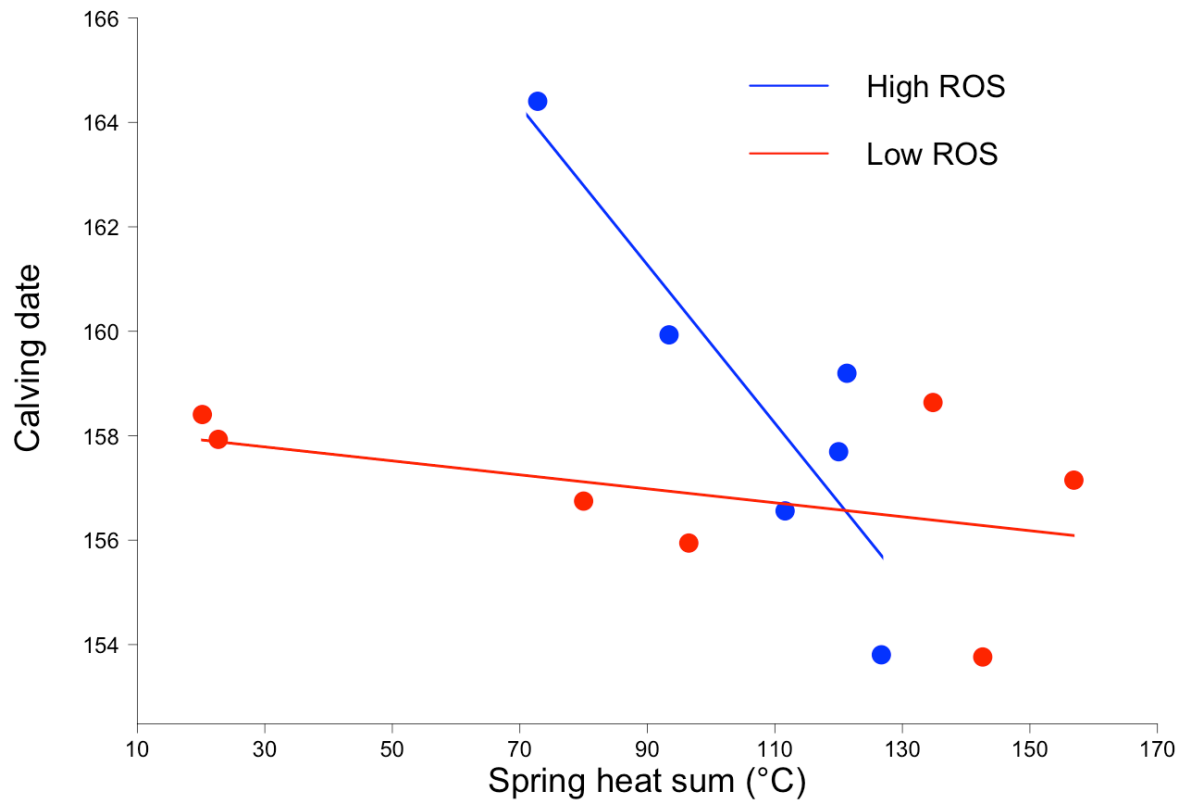


Figure 4. Visualization of the interaction effect in the global model, showing how the relationship between calving date and spring heat sum is dependent on the amounts of ROS. ROS is here categorized as either high (six years with highest ROS, blue) or low (seven years with lowest ROS, red).

DISCUSSION

In the present study I addressed potential changes in the reproductive phenology of a high Arctic herbivore in relation to climate change. I here document that the Svalbard reindeer display no significant changes in calving phenology over the course of 37 years (Figure 2c), despite significant warming (Figure 2a) and advancement of spring onset in the same period. To my knowledge, this is the first study to document temporal patterns and the lack of a response in calving dates of the Svalbard reindeer in relation to climate change. My results suggest that the development of a trophic mismatch may already be happening, or will happen in this system. However, my results indicated an advance in calving dates when spring was warm, but this apparent effect depended on the preceding winter conditions (Figure 4), suggesting a possible interaction effect with reduced body condition due to decreased forage accessibility in severe winters. Even though the relatively consistent of calving dates over the study period suggests no long-term directional response to advanced spring onset, my findings indicate that the Svalbard reindeer display a certain degree of plasticity in calving phenology in response to their environment (Table 1).

Calving phenology and long-term changes in climate

Like in other parts of the Arctic, temperatures are rising in Svalbard (Figure 2a; Forland *et al.* 2011) and the onset of spring has advanced (Clausen & Clausen 2013). Given the assumption that timing of reproduction in relation to resources is important for fitness (Durant *et al.* 2007), addressing whether consumers adequately match the phenological shifts of their focal prey species is crucial (Visser & Both 2005). Over evolutionary time spans, the Svalbard reindeer have apparently been under a strong selection pressure for the timing of calving, indirectly evident by their high population-level synchrony in births. Having been shaped by the environment in Svalbard for at least 4000 (Van der Knaap 1986) and possibly as long as 20000-40000 years (Hakala *et al.* 1986), the high inter-annual variation in the onset of the plant-growing season in the Arctic (Meltotte 2007; Malnes *et al.* 2010; Gilg *et al.* 2012) would suggest a “bet-hedging” calving strategy where parturition is timed to coincide with the long-term average onset of spring (Seger 1978). Assuming a constant selection pressure, the Svalbard reindeer should in theory track the recent advancement of plant phenology, given sufficient time and additive genetic variation. In contrast, this study demonstrates the lack of long-term changes in calving phenology over the course of the study (Figure 2c & 3).

One possible explanation for this may be that the present study encompasses the calving phenology over a period not sufficiently long to see enough to see any response even if evolutionary mechanisms are presently operating. As evidence suggests that calving date is genetically determined (Plard *et al.* 2013), adaptation by the differential selection of certain genotypes may be a slow process for ungulates, who are long-lived animals with long generation times (Gilg *et al.* 2012). However, the magnitude of recent climate change and the rapid advancement in the onset of spring clearly demonstrates the potential for the development of a trophic mismatch. The Svalbard reindeer reside in an environment with particularly strong seasonality in resources and the development of a trophic mismatch is therefore expected to decrease reproductive success and survival (Durant *et al.* 2007). Accordingly, it has been showed that a trophic mismatch caused by advancement of plant phenology has lead to reduced survival of calves and reduced offspring production in caribou in another high Arctic system (Post & Forchhammer 2008; Kerby & Post 2013). In this view, the rapidly changing climate may also have similar effects on the Svalbard reindeer.

While the global climate is certainly changing, the biological consequences are very difficult to predict (see e.g. Mustin *et al.* 2007; Wookey *et al.* 2009; Gilg *et al.* 2012). For Arctic herbivores, such as the Svalbard reindeer, the increased temperatures in the snow-free season may be beneficial in such a low-productivity environment. Studies show how Svalbard reindeer selectively choose food abundance rather than food quality when given a choice, possibly due to the low productivity and the general high quality of plants in the Arctic (Van der Wal *et al.* 2000). With increasing temperatures, biomass production (van der Wal & Stien 2014) and the length of the snow-free season in the Arctic is expected to increase. Thus, contrary to the effects on e.g. birds, where warming-induced shifts in spring phenology leads an advancement of peak resource availability relative to the peak resource requirements of offspring (Visser *et al.* 2006), Arctic herbivores may experience a general increase in food abundance and/or availability that at least partly may counteract potentially negative effects of a trophic mismatch in the breeding phenology. An earlier spring advances the accessibility of vegetation, shortening the period of winter starvation for parturient females, in turn benefiting the fetus and/or calf. As capital breeders, this is clearly beneficial as the energetic demands represented by lactation are very high (Clutton-Brock *et al.* 1989). Also, newborn calves should benefit from a longer plant-growing season and higher biomass production by increasing their chances of winter survival. This then, could seemingly ease the selection pressure on timing of calving. Thus, increased food abundance and availability from warmer

summers suggest enhanced reproductive success and population growth (Hansen et al. 2013, especially in a bottom-up controlled system such as is the case with the Svalbard reindeer.

Although there are, arguably, positive effects of increased biomass and a prolonged length of the plant-growing season, the expected increase in the frequency of extreme weather events, such as ROS (Hansen *et al.* 2011; Hansen *et al.* 2014; IPCC 2014), may act in the opposite direction. As herbivores must face the harsh winter months of the high Arctic where food is limited, ROS may cause massive ice blocking of vegetation and, in turn, reduce population growth rates (Putkonen & Roe 2003; Kohler & Aanes 2004; Hansen *et al.* 2011; Hansen *et al.* 2014). Also, ROS may have more complex effects on herbivores than previously acknowledged, as icing can damage vegetation (Milner *et al.* 2016) and thereby influence the herbivores indirectly and with a delay. This then, suggests that the negative effects of ROS may potentially counteract any positive effects by increased plant biomass and a longer plant-growing season. Despite this high Arctic system being relatively simple, there are clearly several influential mechanisms on population dynamics and, though out of scope for this study, this illustrates the difficulties of predicting the ecological consequences of climate change.

Calving phenology and annual weather fluctuations

To what degree an organism is able to display a short-term response to changes in the environment (i.e. phenotypic plasticity) is highly relevant for whether there is a potential for the development of a trophic mismatch (Visser 2008). Interestingly therefore, my results suggest that annual weather fluctuations may influence the annual calving date (Table 1, Model 1). The negative interaction term in the best-fitted model suggests that an earlier onset of spring may advance calving date when the preceding winter has been severe (i.e. rainy; Figure 4). For instance, in 1996, the onset spring was relatively late and the preceding winter was severe, resulting in the latest calving in the study period (Figure 2c). Winters in 2010 and 2012 were also severe, but the earlier spring seemingly advanced calving. Noting the low sample size and the fact the null model gained substantial support as the best fitted (Table 1; $AIC_c < 2$), results should be cautiously interpreted, but presumably, in winters with high levels of ROS, the forage accessibility is reduced due to icing (Putkonen & Roe 2003; Hansen *et al.* 2011; Hansen *et al.* 2014), and hence, body condition of parturient females is poor (Albon *et al.* unpubl). Accordingly, studies on the Svalbard reindeer show correlations between high amounts of ROS and a lower April body mass (Albon *et al.* unpubl; Loe *et al.*

In press). On the individual level, low April body mass is furthermore associated with late calving dates (Leif Egil Loe pers comm.) In theory then, a warm spring with early snowmelt may at least partly counteract the reduced body condition due to increased forage accessibility, enhancing the fetal growth rate (Clements *et al.* 2011), as shown in studies where captive red deer (*Cervus elaphus*) calve earlier with increased nutrition in late gestation (Asher *et al.* 2005).

However, there is also a possibility that the effect of spring heat sum is actually an effect of time (i.e. a confounding factor due to the significant increase in temperature displayed in Figure 2a). This was tested for and, although the results were non-significant (see Results), the trend remained the same, indicating that the general trend of increasing temperatures might counteract the apparent delaying effect of ROS on calving date. ROS is known to influence population dynamics, also indirectly indicated in this study, as the poor conditions in 1996 (i.e. the year with highest amounts of ROS, Figure 2b) was associated with a very low proportion of calves per female in the population (see Table A1; Solberg *et al.* 2012). Furthermore, in 2012 (i.e. the year the third-highest amount of ROS, Figure 2b), a high number of Svalbard reindeer carcasses were recorded despite favorable winter-feeding conditions before the ROS events (Hansen *et al.* 2014). However, the possibility that the advancing effect of spring heat sum is an effect of time once again illustrates that one should be cautious to regard the results as conclusive.

Most studies on reproductive phenology address the effects of shifts in spring plant phenology, but when discussing the timing of parturition, an inevitable question is to what extent autumn affects the process of phenological synchronization. In very simple terms, two factors are decisive in determining the date of parturition: (1) the date of conception and (2) the species-specific length of the gestation period. Adjusting the date of conception in autumn obviously has implications on the range of possible parturition dates in spring if the gestation period is relatively fixed (which is the case for ungulates; Clements *et al.* 2011). In some ungulates it has been shown that the date of conception may influence the timing of calving to a larger extent than spring phenology (Clutton-Brock *et al.* 1982; Kourkgy *et al.* 2016) However, in lack of data on conception dates, this is impossible to account for in the present study. Moreover, factors such as age (Clutton-Brock *et al.* 1992; Langvatn *et al.* 2004; Mysterud *et al.* 2009), previous reproductive history (Guinness *et al.* 1978), and offspring sex (Clutton-Brock *et al.* 1982; Holand *et al.* 2006; Mysterud *et al.* 2009) may also

affect gestation length, further increasing the complexity of the question. Due to the low sample size of this study then, one should be cautious to be conclusive, as extreme years may also have impacted the results, especially 1996, with high ROS and late calving. Furthermore, there is some uncertainty around the estimated calving dates, with 1996 having the highest standard error (Julian date = 164, Figure 2c). Nevertheless, no calves were observed up until day 162 (Figure 3; 1996), so it might be plausible to suggest the true calving date to occur, if not after, then at least not before day 164, and thus this would have had minimal impacts on the results. Moreover, excluding 1996 (or 2010 or 2012) from the analyses did not qualitatively influence the results from the model selection (analyses not presented). However, this clearly demonstrates the need of quality data when addressing complex questions regarding to phenological studies to determine to what extent different factors are influential.

Concluding remarks

The present study gives an insight of the past and the present situation of the reproductive phenology of a high Arctic herbivore in relation to climate change. This study is to my knowledge the first to document long-term temporal patterns in the calving dates of the Svalbard reindeer, and this during a period with significant changes in climate. The expected continuation of global warming indicates that a trophic mismatch has, or will, develop in this system, but the consequences are more difficult to predict. Despite no long-term directional response, however, my results indicate that the Svalbard reindeer show some response to fluctuations (or possibly long-term changes) in spring onset, but only when winter conditions, and hence, body condition, are poor. However, phenology is a complex area of study and more comprehensive data sets are needed to adequately address questions regarding the influential mechanisms. Nevertheless, gaining more knowledge about such mechanisms is crucial to determine potential future consequences in a rapidly changing world, especially for the vulnerable organisms in the Arctic.

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APPENDIX

Table A1. A summary of the *in situ* observations included in this study, showing the temporal range of the census, the frequency of observations in the census, and the total number of observed adult females and calves during the census, reported for years 1979-1981 (Tyler, 1989) and 1996-1998 (R. J. Irvine unpubl.) For 2009-2015, GPS-collars were used to give individual estimates of calving date (see methods). The ratio of calves per female is reported for all years, based on *in situ* observations during the annual main summer census (Solberg *et al.* 2012).

Year	Census range	Observations (days)	Observed adult females	Observed calves	Calves per female
1979	1 st June – 1 st July	7	474	87	0.26
1980	2 nd June – 27 th June	5	498	357	0.73
1981	4 th June – 1 st July	4	388	70	0.24
1996	1 st June – 1 st July	13	628	47	0.16
1997	24 th May – 1 st July	34	1531	628	0.77
1998	3 rd June – 1 st July	22	1016	685	0.78
2009	10 th May – 29 th June	-	-	-	0.54
2010	10 th May – 19 th June	-	-	-	0.49
2011	10 th May – 29 th June	-	-	-	0.68
2012	10 th May – 28 th June	-	-	-	0.47
2013	10 th May – 29 th June	-	-	-	0.65
2014	10 th May – 29 th June	-	-	-	0.61
2015	10 th May – 29 th June	-	-	-	0.83

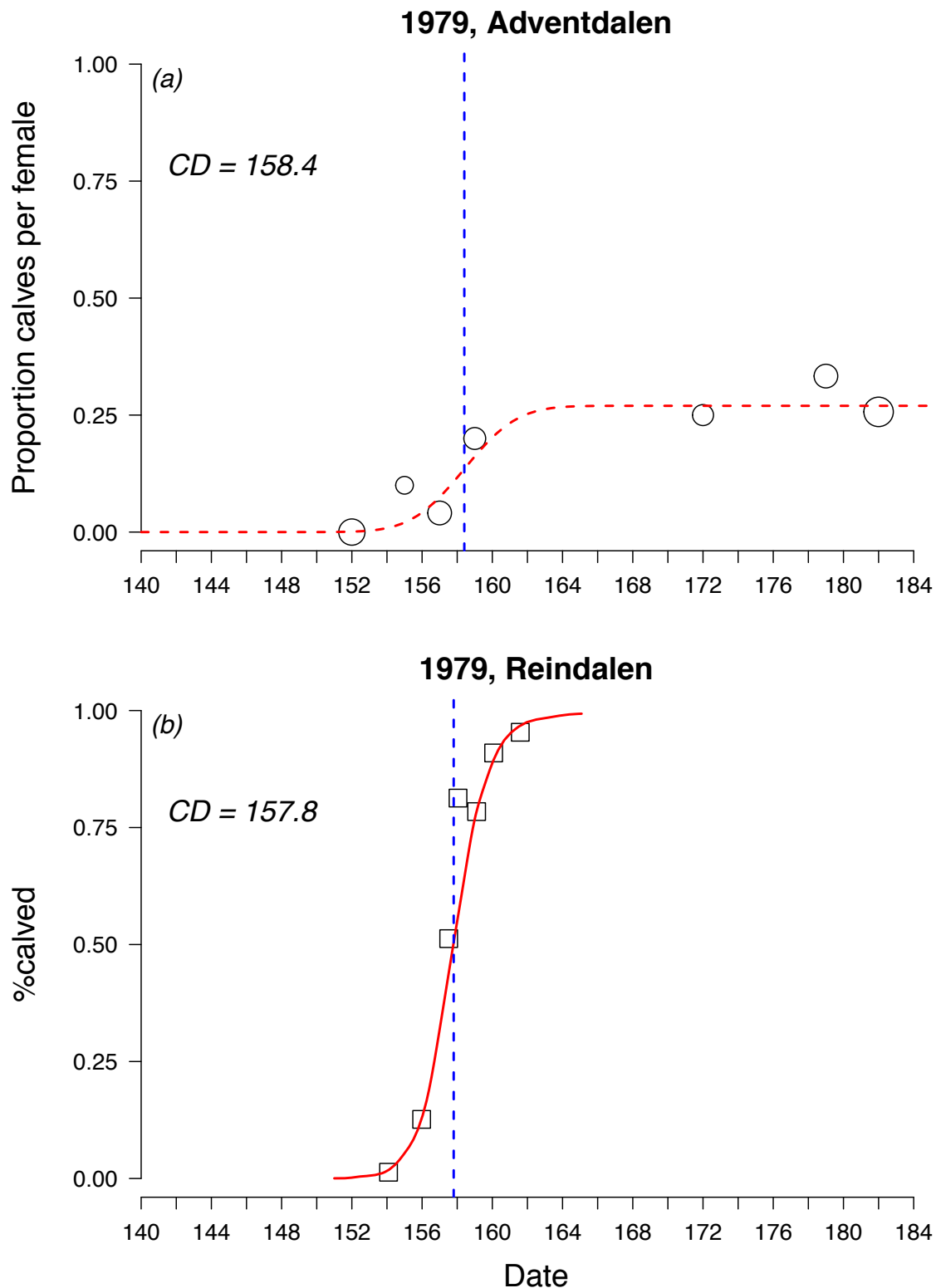


Figure A1. The estimated calving date in 1979 based on observations in (a) Adventdalen (Skogland 1989) and (b) Reindalen (Tyler 1978). Despite spatial differences between valleys (see Figure 1), the estimated calving dates are nearly identical (blue vertical lines). The x-axis displays Julian date and the y-axis display (a) the proportion of calves per female, and (b) the percentage of females that have calved. Due to lack of raw data, (b) was copied from Skogland (1989, p 31) by using PlotDigitizer 2.6.8 and R studio 10.11.

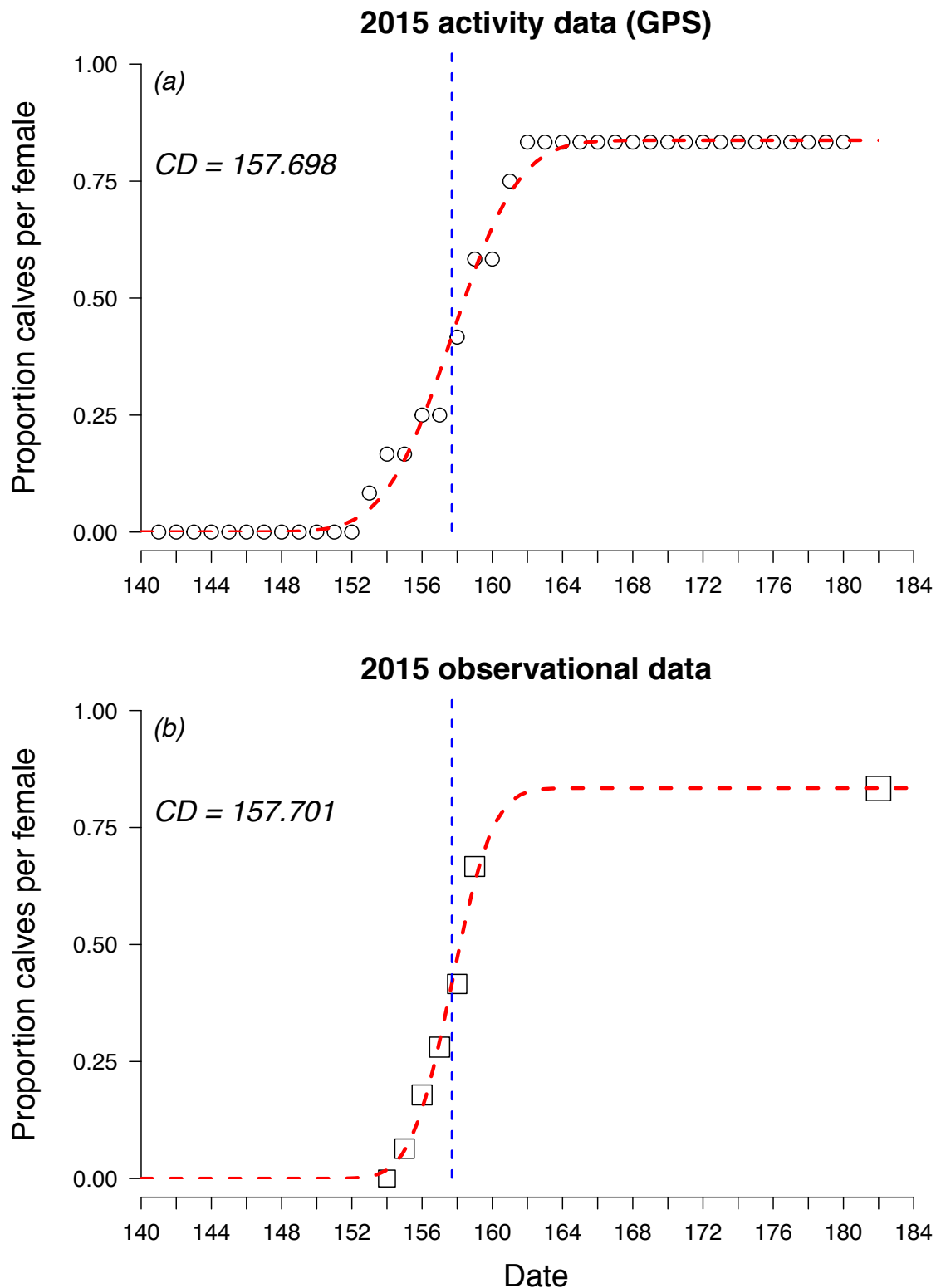


Figure A2. The estimated calving date in 2015 based on (a) records of activity data from GPS-collared females (Loe et al. unpubl), and (b) *in situ* observations of calving (V. Veiberg unpubl). Despite different methods of calving detection, the estimated calving dates are virtually identical (blue vertical lines). The x-axis displays Julian date and the y-axes display the proportion of calves per female. Data points are proportional to sample size.