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Maternal winter body mass and not spring phenology determine annual calf production in an Arctic herbivore

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Warming of the Arctic has resulted in earlier snowmelt and green-up of plants in spring, potentially disrupting the synchrony between plant phenology and breeding phenology in herbivores. A negative relationship between offspring survival in West Greenland caribou and the timing of vegetation emergence was the first finding of such a mismatch in Arctic mammals. However, other studies indicate that the energy for foetal growth and early lactation is predominantly drawn from stored energy reserves typical of 'capital' breeders, suggesting that conditions well before spring influence calf production more than the timing of spring onset. Here we use 20 years of observations of marked Svalbard reindeer to evaluate determinants of annual recruitment, as measured by the presence of a calf at foot in mid-summer. Spring temperatures and the enhanced vegetation index were used as proxies for spring onset, while data on body mass and pregnancy rates in late winter allowed us to determine maternal condition and the reproductive status before spring. Pregnancy rate, offspring survival and annual recruitment were all strongly correlated with average late winter adult female body mass ($r = 0.87$; $r = 0.83$; $r = 0.92$, respectively). Contrary to the findings in West Greenland, neither early calf survival nor annual recruitment were correlated with the two measures of annual variation in spring phenology ($r = -0.07$, $p = 0.8$ and $r = -0.15$, $p = 0.6$, respectively). We also revisit the Greenland data and reveal that the pattern of covariance between early and late measures of fecundity, as well as between early measures of fecundity and offspring survival, correspond with the results from Svalbard. Our results emphasize that conditions affecting maternal body mass during winter explain close to all the variation in recruitment, questioning the importance of the role of a mismatch between plant phenology and calving date.

The timing of reproduction and energy allocation to offspring production and provisioning are key life-history traits (Roff 1992, Stearns 1992). Through natural selection the phenology of a species has typically evolved to match environmental conditions and to maximize fitness (Futuyma 1998, Roff 2002). In seasonal environments, the timing of reproduction typically matches peaks in resource availability, and a disruption of this synchrony might have strong implications for population recruitment (Durant et al. 2007). On the other hand, long-lived iteroparous organisms tend to prioritize their own survival at the cost of offspring production (Festa-Bianchet and Jorgenson 1998, Gaillard and Yoccoz 2003). The status of maternal energy reserves well before the birth season is therefore expected to directly influence reproductive output. In this study, we wanted to disentangle the relative effects of variation in spring phenology (onset of vegetation growth) and maternal body condition on offspring production in an Arctic herbivore, the Svalbard reindeer *Rangifer tarandus platyrhynchus*.

The phenology at low trophic levels is often determined by local environmental conditions such as temperature, while the phenology at higher trophic levels often depends on cues distant in space (e.g. long distance avian migrants; Visser and Both 2005) or time (e.g. the condition of birthing habitats at time of parturition in species with over-winter gestation periods). Recent global warming has generated a phenological mismatch between trophic levels in many aquatic and terrestrial systems (reviewed by Donnelly et al. 2011). Such phenological mismatches do not only have the potential to impact strongly on population dynamics, but also ecosystem functioning (Visser et al. 2004, Thackeray et al. 2010, Donnelly et al. 2011, Gilg et al. 2012, Nakazawa and Doi 2012). To what extent a given species' reproductive output is influenced by this asynchrony depends on how much of the energy needed for successful reproduction is covered by current food intake versus energy stores (Stephens et al. 2009).

Global warming is particularly pronounced in the Arctic, resulting in milder winters, warmer summers, higher frequencies of extreme weather events, as well as altered timing of seasonal events such as vegetation green-up (AMAP 2011). Variation in timing of snow melt (Cebrian

et al. 2008, Cooper et al. 2011) and temperature (Turunen et al. 2009, van der Wal and Stien 2014) influence timing of onset of vegetation growth, total forage production, nutritional content and phenological progression. The strong seasonality in the Arctic, and the close relationship between environmental conditions and vegetation development, may represent an adaptive challenge for herbivores if they are sensitive to the timing of forage plant availability (Pettorelli et al. 2005). Studies on Greenland caribou found that advances in the timing of vegetation emergence was negatively correlated with early offspring survival and total calf production, presumably as a consequence of reduced forage quality during early lactation (Post and Forchhammer 2008, Kerby and Post 2013, Post 2013). This is the first empirical evidence of a direct negative effect of a trophic mismatch in an Arctic mammal.

Although Post et al. (2003) reported a match between the progression of the calving season and the progression of plant phenology in one Alaskan and one West Greenland caribou population, the timing of parturition in caribou and reindeer is generally prior to vegetation green-up (Reimers et al. 1983, Crête and Huot 1993, Tveraa et al. 2013). This implies that the energy and nitrogen demands related to foetal development and early lactation is to a large degree drawn from body stores (Chan-McLeod et al. 1999, Barboza and Parker 2008, Taillon et al. 2013). Furthermore, several studies have found that previous summer conditions and autumn/winter body mass has a strong influence on females' subsequent probability of conceiving and carrying a foetus to term (e.g. caribou/reindeer: Cameron et al. 1993, Fauchald et al. 2004; elk *Cervus elaphus*: Gerhart et al. 1996, Cook et al. 2004). Although significant differences in both maternal resource allocation and timing of birth have been documented between *Rangifer* subspecies (Barboza and Parker 2008), body condition of reproducing females is generally at its minimum 2–3 weeks after parturition (Parker et al. 2009). This underlines that early reproductive investment and success in female *Rangifer* is largely influenced by stored energy (Fauchald et al. 2004, Bårdsen et al. 2009).

In semi-domesticated reindeer, female reproductive success has been found to increase with both increased late winter maternal body mass (Lenvik and Aune 1988, Bårdsen and Tveraa 2012) and advanced timing of the onset of spring (Helle and Kojola 2008, Tveraa et al. 2013). The positive effect of advanced spring has in these cases been interpreted as the result of a shorter period with limited food availability and earlier access to fresh and nutrient-rich vegetation, with positive consequences for reindeer in terms of increased dry matter intake and somatic growth (Cebrian et al. 2008). Therefore, in contrast to the West Greenland study (Post and Forchhammer 2008, Kerby and Post 2013, Post 2013), the bulk of the literature suggests that reproduction should be mediated through late winter maternal condition, and that any remaining effect of earlier spring should be positive.

The Svalbard reindeer is known to be strongly food limited in winter, and accumulate extensive fat stores over summer to meet energy requirements during the food-limiting and unpredictable winter (Reimers et al. 1982). In particular, winter rain, causing ground icing, or impenetrable ice layers within the snow-pack, may substantially reduce access to food and over-winter survival in these herbivores (Hansen et al. 2011, 2013). Most of the seasonal variation in body mass of *Rangifer* is associated with changes in body fat (Reimers et al. 1982, Chan-McLeod et al. 1999, Barboza and Parker 2008). Late winter body mass is therefore a measure of the stored energy available for reproductive investment before forage availability and quality rises in spring and calving occurs. Relying heavily on stored resources, at least for their early reproductive investment (Parker et al. 2009), reindeer are closer to the capital breeder than the income breeder side of the continuum (Jönsson 1997, Stephens et al. 2009). This strategy represents both insurance for unpredictable environmental conditions in late gestation (Stephens et al. 2009), and an adaptation to breed ahead of the spring flush so that the calf can benefit directly from grazing high quality plants.

Here, we use 20 years of individual-based data to investigate the effect of late winter maternal body mass and the timing of onset of spring on early calf survival in Svalbard reindeer. Spring temperature in Svalbard has increased resulting in advancement in plant phenology as estimated from NDVI-curves (Karlsen and Hansen unpubl.). Nevertheless because of the dominant role of energy reserves for reproduction in *Rangifer* (Barboza and Parker 2008), we predict that late winter maternal body mass is more important for calf production than the timing of onset of spring (Albon et al. 2016). We also revisit the data from West Greenland (Post and Forchhammer 2008, Post 2013) to compare and contrast patterns of offspring recruitment and early calf survival between Greenland and Svalbard reindeer.

Material and methods

Study area

The study was carried out in Nordenskiöld Land, Svalbard. The study area (77°50′–78°20′N, 15°00′–17°30′E) includes three interconnected main valleys with adjoining side valleys in total covering ca 150 km^2. The valleys are generally wide, U-shaped and vegetated up to about 250 m altitude. The vegetation growing season, defined as the time between green-up and 50% senescence, is only 9–10 weeks (Cooper et al. 2011). Across habitats, annual plant biomass production is generally low, but varies twofold (23–46 g m^{-2}) in response to summer temperature (van der Wal and Stien 2014). From November until June, the ground is normally snow covered, but winter weather and snow conditions vary considerably between years (Hansen et al. 2014). Average annual winter (December–February) temperatures during the most recent 30 years 'climate average period' (1981–2010) was –11.7°C (Førland et al. 2011), but, episodes of warm spells with above-zero temperatures occasionally occur. In combination with precipitation as rain, such episodes may lead to formation of ice on the ground or within the snow pack when temperatures return to sub-zero levels. Such icing may substantially restrict access to winter grazing (Hansen et al. 2010), causing reduced survival (Solberg et al. 2001, Albon et al. 2016), fecundity (Stien et al. 2012, Albon et al. 2016), and population growth (Kohler and Aanes 2004, Hansen et al. 2013, Albon et al. 2016) in Svalbard reindeer.

Svalbard reindeer data

We used data from a capture–mark–recapture study (1995–2014) of Svalbard reindeer on Nordenskiöld Land. Individuals were captured in April each year using a net stretched out between two snowmobiles (Milner et al. 2003, Omsjoe et al. 2009). Female calves were marked in their first winter (at ca 10 month age) and fitted with numbered plastic collars and ear tags, and individuals are therefore of known age. In subsequent years, the marked females were recaptured and weighed ($\pm$ 0.5 kg; n = 1786) and pregnancy diagnosis was obtained from blood plasma progesterone (n = 1599) or ultrasound scanning (Ropstad et al. 1999) (n = 187). Variation in capture date within and between years had minimal influence on body mass (estimate = –0.003, SE = 0.039, p = 0.94). Using adjusted mass in analyses gave close to identical results (not reported).

Calving occurs in early June (Tyler 1987, Skogland 1989), but data on calving dates for marked individuals were not available. Marked females were re-sighted in July–August, and the presence of a calf at foot was recorded (n = 1636). Calf survival from April until re-sighting in summer is hereafter referred to as offspring survival (n = 804). Only females two years and older were included in the analyses. Estimates of population size were available for the study period (Lee et al. 2015) but we did not directly include the effect of population density in the analyses. The rationale for this is that annual variation in density and weather are effectively integrated in the annual variation in body mass (Albon et al. 2016), the focal predictor variable of interest in the current study.

Estimating onset of spring

We used two correlated (r = 0.65, p = 0.009) proxies for identification of the timing of onset of spring. First, EVI-spring, the Julian date corresponding to the spring inflection point of the double logistic model fitted to the seasonal pattern of the enhanced vegetation index (EVI) (Ballesteros et al. 2013, Tveraa et al. 2013). For the period 2000–2014, EVI values were available from the MODIS Terra platform as 16-day composites on a spatial resolution of ~250 m (<http://modis-land.gsfc.nasa.gov/vi.html>). Compared to the more widely used normalized difference vegetation index (NDVI), EVI improves monitoring sensitivity in areas with low canopy coverage, like tundra and wetlands, through reducing the effect of background reflection from e.g. geological substrates, snow and water (Huete et al. 2002). Second, our second proxy for timing of onset of spring, T50, refers to the Julian date when the accumulated positive daily temperature means exceeded 50 degree-days (Clausen and Clausen 2013). We used 1 May as the cut-off date since temperatures above zero occasionally occur during late winter, but do not relate to the later progression of spring. Temperatures were measured at Svalbard airport (78°15′N, 15°28′E) by the Norwegian Meteorological Institute (<www.eklima.no>), approximately 20–40 km from the study area. Using T50 as a proxy for onset of spring, allowed us to include reindeer data also from the period 1995–1999, prior to EVI estimates being available.

Estimates of offspring production and survival from West Greenland and Svalbard

The West Greenland data was extracted from existing publications (Post and Forchhammer 2008, Post 2013). In the most recent publication of the West Greenland data series (Post 2013), offspring production and offspring mortality is provided for the period 2002–2010. The measure of offspring production (PC) used in the West Greenland study was calculated as $PC = n_{calves}/(n_{calves} + n_{adult\ females})$, where n_{calves} is the number of calves observed in the study area in a given day, and $n_{adult\ females}$ is the number of adult, unmarked females observed the same day. They repeated observations of PC over the reindeer calving season and used the maximum estimate of PC, PC_{max}, as their measure of the calf production immediately after calving in early June, and before significant calf mortality had occurred. They used PC towards the end of their field campaigns in late June to early July, PC_{final}, as an estimate of calf production after early calf mortality (Post and Forchhammer 2008). Relative calf mortality was estimated as $M = (PC_{max} - PC_{final})/PC_{max}$. Female reindeer have at most one calf, and the proportion of females with a calf, $pc = n_{calves}/n_{adult\ females}$, is the most commonly used measure of calf production for reindeer. We have therefore transformed the estimates to this scale using the relationship: $pc = PC/(1 - PC)$. In the latest presentation of the West Greenland data (Post 2013, p. 198), only offspring mortality, M and PC_{final} are presented. PC_{max} was calculated as $PC_{final}/(1 - M)$.

For Svalbard, we use the proportion of marked, adult females pregnant in April (p_p) as our early fecundity measure. Greenland equivalent: $pc_{max} = PC_{max}/(1 - PC_{max})$. The late fecundity measure in Svalbard was given as the proportion of adult marked females with a calf at foot in July–August (p_c). Greenland equivalent: $pc_{final} = PC_{final}/(1 - PC_{final})$. Finally we calculated offspring survival as $s_o = p_c/p_p$ for Svalbard and as $s_c = pc_{final}/pc_{max}$ for Greenland.

A full overview of the annual estimates from Svalbard and West Greenland is given in Supplementary material Appendix 1 Table A1.

Statistical analyses

We report the correlation coefficient r in cases where we are interested in testing for a relationship between independent variables, while we use R^2-values as an estimate of how much early fecundity and calf survival contribute to the final measures of calf production. Thus, we provide Pearson's correlation (r) to quantify correlation between proxies for spring onset, as well as between annual means of body mass, pregnancy rate (p_p), summer calf rate (p_c) and offspring survival (s_o) in Svalbard. The relative impact of pregnancy rate and offspring survival on summer calf rate, were evaluated using R^2-values obtained from simple linear regression on annual estimates of pregnancy rates and proportional reduction due to offspring mortality ($p_{reduction} = p_c - p_p$). Similarly, we used R^2-values to evaluate the impact of the early measure of fecundity (pc_{max}), and subsequent offspring survival (s_c) on summer calf rates (pc_{final}) in West Greenland. Furthermore, for the Svalbard reindeer data the effects of individual maternal body mass, as well as spring onset, on offspring survival

were modelled using generalized linear mixed-effects models with the glmer-function in the R package lme4 (Bates et al. 2015, <www.r-project.org>). Using a binomial error structure and a logit link function, we investigated the effect of maternal body mass and 1) EVI-spring (2000–2014), and 2) T50 (1995–2014), including their interaction, on offspring survival. Presence of a calf at foot was the response variable and only individuals with a confirmed pregnancy in April were included. In these analyses, year and individual were modelled as crossed random factors. Values of body mass, EVI-spring and T50 were standardized (mean = 0, variance = 1) prior to analysis. Age category (2, 3, 4–9, 10–12 and 13 years or older; Lee et al 2015) was included as a fixed effect to account for age effects on calf survival that are independent of body mass. The effects of body mass, EVI-spring and T50 are qualitatively very similar in models excluding the effect of age.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.qt5bd> (Veiberg et al. 2016).

Results

In Svalbard, average body mass, proportion of pregnant females and proportion of females with a calf in summer, all varied substantially between years (Fig. 1a). Between year variation in the proportion of pregnant females and offspring survival were both strongly correlated with annual average female body mass ($r = 0.87$, $p < 0.001$; $r = 0.83$, $p < 0.001$, Fig. 1b–c respectively), consequently causing a high correlation between body mass and overall calf production (proportion of females with a calf in summer; $r = 0.92$, $p < 0.001$, Fig. 1d). There was no correlation between offspring survival and either EVI-spring ($r = -0.07$, $p = 0.81$; Fig. 2a) or T50 ($r = -0.06$, $p = 0.79$; Fig. 2b), and no significant effect of these predictors when the effect of age and individual female body mass was controlled for (either alone, or in interaction with body mass; Table 1). Furthermore, in Svalbard there was no correlation between the annual proportion of marked, adult females with a calf at foot and either EVI-spring ($r = -0.15$, $p = 0.59$) or T50 ($r = 0.13$, $p = 0.57$).

In both Svalbard and West Greenland, there were strong correlations between the measures of early fecundity and the final measures of calf production (Svalbard: $r = 0.86$ $p < 0.001$; West Greenland: $r = 0.96$, $p = 0.002$, Fig. 3). Variation in factors affecting early fecundity proved more important to overall annual calf production than the measures of offspring survival. In Svalbard, April pregnancy rates explained more than twice as much of the variation in annual calf production ($R^2 = 0.73$, Fig. 3) than early calf survival ($R^2 = 0.27$). The relationship between early and late fecundity measures were even stronger in the West Greenland

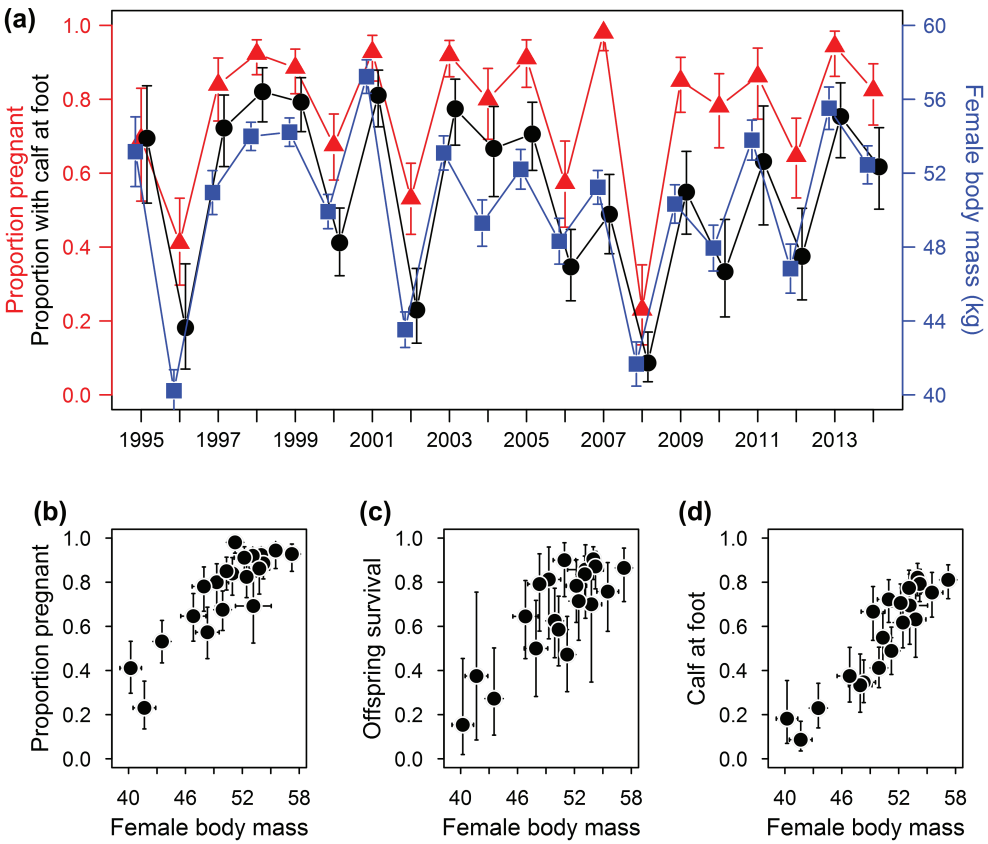

Figure 1. (a) Estimates (± 95% CI) of annual proportions of adult Svalbard reindeer females pregnant in April (red triangles) and seen with a calf in summer (black circles), as well as April body mass (blue squares). Relationship between estimated annual April female body mass and (b) the proportion of females pregnant in April, (c) offspring survival from April to summer and d) proportion of females with a calf in summer.

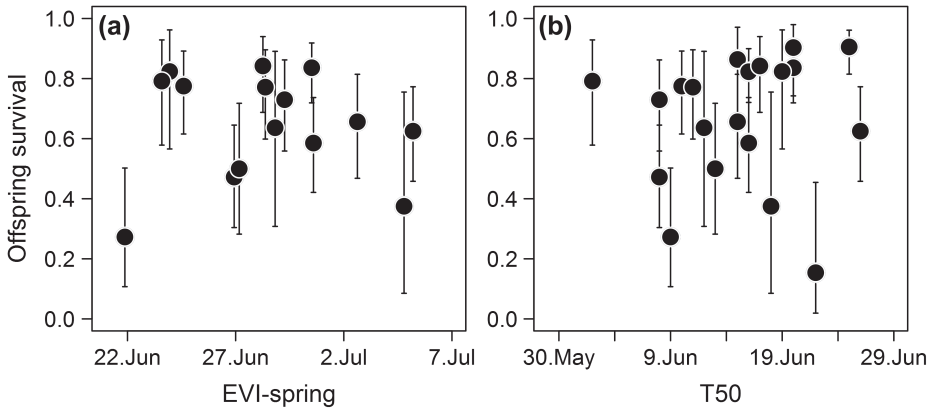

Figure 2. The relationship between Svalbard reindeer offspring survival (± 95% CI), and our two proxies for timing of onset of spring based on (a) the enhanced vegetation index (EVI-spring) and (b) the date in spring when accumulated degree-days exceed 50 (T50).

data ($R^2_{pc.max} = 0.93$, Fig. 3), and accordingly early calf survival affected the final measure of annual production to a lesser degree ($R^2_{pc.final\text{-}pc.max} = 0.07$).

Discussion

As predicted, maternal April body mass was the main predictor of calf production in Svalbard reindeer. In contrast, we found no effect of the timing of onset of spring on any of the calf production variables. This is consistent with the hypothesis that Svalbard reindeer rely on body stores to secure reproduction and that environmental conditions experienced well before spring dominate between-year variation in calf production. In both Svalbard and West Greenland, early measures of calf production were more important for the final estimates of calf production than offspring survival between these measurements of fecundity. These results support the view that species relying mainly on stored energy for reproduction, 'capital' breeders, are less vulnerable to phenological mismatch than species relying on an 'income' strategy (Stephens et al. 2009).

Table 1. Generalized linear mixed-effects model of offspring survival in Svalbard reindeer as function maternal April body mass and the estimated timing of spring onset based on (a) EVI-spring (2000–2014), and (b) T50 (1995–2014), controlled for the effect of age class (2, 3, 4–9, 10–12 and 13 years or older). Values of body mass, EVI-spring and T50 were standardized (mean = 0, variance = 1) prior to analysis. Age class 4–9 is the reference level for the age effect.

	Estimate	SE	Z	p
(a) Intercept	0.76	0.16	4.8	< 0.001
Age class (2 vs 4–9 years)	2.11	0.79	2.66	0.007
Age class (3 vs 4–9 years)	0.71	0.36	1.95	0.051
Age class (10–12 vs 4–9 years)	0.22	0.41	0.53	0.59
Age class (13 + vs 4–9 years)	–1.15	0.72	–1.6	0.11
Body mass	1.08	0.16	6.9	< 0.001
EVI-spring	–0.030	0.13	–0.23	0.82
Body mass × EVI-spring	–0.019	0.15	–0.13	0.90
Individual random effect (SD)	0.73			
Year random effect (SD)	2.3×10^{-6}			
(b) Intercept	1.0	0.16	6.1	< 0.001
Age class (2 vs 4–9 years)	1.28	0.55	2.3	0.020
Age class (3 vs 4–9 years)	0.67	0.34	1.96	0.050
Age class (10–12 vs 4–9 years)	0.089	0.36	0.25	0.81
Age class (13 + vs 4–9 years)	–1.44	0.68	–2.1	0.034
Body mass	1.05	0.15	7.0	< 0.001
T50	0.17	0.14	1.2	0.22
Body mass × T50	0.099	0.14	0.67	0.49
Individual random effect (SD)	0.65			
Year random effect (SD)	0.30			

Variation in maternal late winter energy reserves determine annual recruitment

In a study of maternal allocation of resources to neonatal calves of reindeer and caribou, Barboza and Parker (2008) compared the importance of maternal versus dietary sources of nitrogen for calf protein production from birth until three weeks old. Whereas maternal stored protein was used for 96% of foetal growth in reindeer, 84% of the protein needed for foetal growth in caribou came from stored maternal resources. Both subspecies relied on maternal stored body protein for 91% of the protein, assimilated by calves, through lactation over the first three weeks. This clearly shows that both caribou and reindeer rely heavily on maternal protein sources, rather than on dietary nitrogen sources

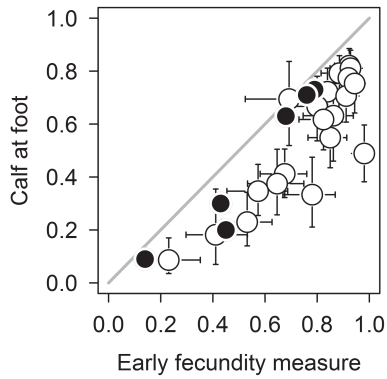

Figure 3. The proportion of female Svalbard reindeer with a calf in summer (1995–2014) plotted against the proportion of females pregnant in April (open circles, ± 95% CI). Late calf proportion for West Greenland (pc_{final}, 2002–2010) is plotted against the early calf proportion (pc_{max}) (filled circles). The grey line illustrates the 1:1 relationship, i.e. no mortality.

for both foetal development and milk production during the early neonatal phase.

Body mass is well known to be an integrator of the long-term nutritional situation of large ungulates, affected by both density dependence and stochastic weather events (Douhard et al. 2014). The close correlation between average late winter body mass of adult Svalbard reindeer females and the simultaneously measured pregnancy rates, as well as with the subsequent calf production and survival, support the interpretation that stored energy is a main determinant of successful reproduction in this subspecies. These results correspond well with findings from other *Rangifer* populations (Barboza and Parker 2008, Taillon et al. 2013).

Annual variation in winter weather and population density are the main drivers of population dynamics of Svalbard reindeer (Stien et al. 2012, Hansen et al. 2013), mediated through their impact on forage availability, body mass and subsequent influence on survival and reproductive success (Albon et al. 2016). Although less pronounced than in our case, carry-over effects from maternal winter condition to offspring survival have also been reported for other northern ungulates, including moose *Alces alces* (Milner et al. 2013), red deer *Cervus elaphus* (Kruuk et al. 1999) and bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 1998). This strong link between maternal energy stores and reproductive output contrasts the findings in typically income dependent species like roe deer *Capreolus capreolus* (Andersen et al. 2000, Plard et al. 2014) and goats *Capra hircus* (Hempson et al. 2015), where annual recruitment is highly dependent upon resource availability during the postnatal period.

No consequences of the timing of the onset of spring

In contrast to the findings on West Greenland (Post and Forchhammer 2008, Kerby and Post 2013, Post 2013), advances in the timing of spring have been found to positively influence both reproductive success (Helle and Kojola 2008, Tveraa et al. 2013) and calf growth (Pettorelli et al. 2005, Couturier et al. 2009, Tveraa et al. 2013). This suggests that advancing spring phenology has a positive impact on energy availability around the period of calving and early lactation. These results are supported by both experimental (Cebrian et al. 2008), and observational (Mårell et al. 2006) studies, which have showed that advances in flowering phenology can have a substantial influence on resource availability and increased nitrogen intake in reindeer. Calf production in Svalbard reindeer was, on the other hand, neither positively nor negatively affected by the timing of spring (Fig. 2).

A potential complicating factor is that spring phenology may be partly determined by winter weather (Pettorelli et al. 2005, Mysterud et al. 2008). Depending on the pattern of co-variation between important aspects of winter weather, maternal condition and spring phenology, this could cause, both negative and positive, spurious correlations between the timing of the onset of spring and reindeer fecundity (see Herfindal et al. 2006 for a similar example in moose). On Svalbard, the winter weather factor of major importance for population dynamics of reindeer is the amount 'rain-on-snow' during winter (Stien et al. 2012, Hansen et al. 2013). We found no correlation between this measure of winter severity and our two proxies for onset of spring (EVI-spring: $r = 0.003$, $p = 0.99$; T50: $r = 0.05$, $p = 0.84$).

Are West Greenland caribou more dependent on spring phenology than Svalbard reindeer?

In Arctic and alpine areas, advanced timing of vegetation emergence is expected to lead to increased resource availability and subsequent increased maternal energy gain (Cebrian et al. 2008). The findings of a decreasing reproductive output in caribou with advanced timing of the onset of spring in West Greenland (Post and Forchhammer 2008, Post 2013), is therefore somewhat surprising. Compared to other small to moderate sized ungulates, caribou produce offspring that are small relative to maternal body mass (Robbins and Robbins 1979, Oftedal 1985). This life-history strategy is likely an adaptation to life in stochastic environments through minimizing the reproductive investment before parturition (Adams 2005). In this way, unfavourable conditions during gestation and the postnatal period will affect juvenile survival substantially more than adult survival (Gaillard et al. 1998, Adams 2005).

Analysing the West Greenland data, we found that most of the variation in the final numbers of calves recorded was determined at the time of their early measure of fecundity; i.e. at the time of calving, and not by subsequent calf mortality. In addition, there was a strong positive relationship between Post and co-workers early measure of fecundity and early calf survival (Fig. 3). The studies from West Greenland did not present any information about female age distribution, maternal condition or population density over the study period. These factors are known to be of primary importance to reproductive output in large ungulates (Bonenfant et al. 2009), and could provide alternative explanations to the reported reduction in both calf production and early offspring survival (Supplementary material Appendix 1 Table A1). The Greenland Institute of Natural Resources have been monitoring the Kangerlussuaq Sisimiut herd by aerial surveys for many years. In 2011 they reported that the caribou population density had been increasing rapidly during the last 10 years period (Cuyler et al. 2011). At that time, the counted population was more than three times the population density that the management authorities regarded as sustainable. The institute emphasized that neither the population counts, nor knowledge about carrying capacity was perfect. Nonetheless, they expected that the reported declines in offspring production were at least partly due to density-dependent factors (Cuyler et al. 2011). Our study supports the assumption that between year variation in early recruitment in West Greenland, as well as on Svalbard, is primarily determined by processes taking place before parturition.

In conclusion, the effect of climate change on reindeer population dynamics is likely to depend on effects of food availability throughout the year (Tews et al. 2007, Parker et al. 2009, Hansen et al. 2013), mediated through the effect on maternal mass (Albon et al. 2016). To reveal how breeding phenology and population dynamics in Arctic ungulates are influenced by stochastic variation, as well as trends in environmental conditions and plant phenology, additional

long-term studies from populations experiencing contrasting environmental conditions are required.

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Supplementary material (available online as Appendix oik-03815 at <www.oikosjournal.org/appendix/oik-03815>). Appendix 1.