Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore

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Abstract

The cumulative effects of climate warming on herbivore vital rates and population dynamics are hard to predict, given that the expected effects differ between seasons. In the Arctic, warmer summers enhance plant growth which should lead to heavier and more fertile individuals in the autumn. Conversely, warm spells in winter with rainfall (rain-on-snow) can cause 'icing', restricting access to forage, resulting in starvation, lower survival and fecundity. As body condition is a 'barometer' of energy demands relative to energy intake, we explored the causes and consequences of variation in body mass of wild female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) from 1994 to 2015, a period of marked climate warming. Late winter (April) body mass explained 88% of the between-year variation in population growth rate, because it strongly influenced reproductive loss, and hence subsequent fecundity (92%), as well as survival (94%) and recruitment (93%). Autumn (October) body mass affected ovulation rates but did not affect fecundity. April body mass showed no long-term trend (coefficient of variation, CV = 8.8%) and was higher following warm autumn (October) weather, reflecting delays in winter onset, but most strongly, and negatively, related to 'rain-on-snow' events. October body mass (CV = 2.5%) increased over the study due to higher plant productivity in the increasingly warm summers. Density-dependent mass change suggested competition for resources in both winter and summer but was less pronounced in recent years, despite an increasing population size. While continued climate warming is expected to increase the carrying capacity of the high Arctic tundra, it is also likely to cause more frequent icing events. Our analyses suggest that these contrasting effects may cause larger seasonal fluctuations in body mass and vital rates. Overall our findings provide an important 'missing' mechanistic link in the current understanding of the population biology of a keystone species in a rapidly warming Arctic.

Keywords: climate change, density dependence, extreme events, icing, nutrition, primary production, *Rangifer*, reindeer, Svalbard, weather

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Introduction

In recent decades, climate warming has been more pronounced in many parts of the Arctic than the global average (IPCC, 2013) with dramatic consequences for tundra ecosystems (Post *et al.*, 2009; Ims & Ehrich, 2013), including impacts on the timing and strength of

seasonality (Ernakovich *et al.*, 2014). In particular, earlier snow melt and warmer summers are associated with greater soil mineralization (Aerts *et al.*, 2006), higher nutrient turnover (Barber *et al.*, 2008) and increases in overall plant productivity (Elmendorf *et al.*, 2012). The resulting increase in available forage for vertebrate herbivores (Hill & Henry, 2011; Van der Wal & Stien, 2014) should enhance body growth, fecundity and survival (Parker *et al.*, 2009), and consequently lead to increases in population size locally (geese: Morrissette *et al.*, 2010; Jensen *et al.*, 2014; musk oxen: Forchhammer *et al.*, 2008; reindeer: Tveraa *et al.*, 2013). As some of these herbivores occur at high densities, changes in their numbers may have profound consequences for tundra plant communities (Van der Wal, 2006), predators (Gilg *et al.*, 2009) and ecosystem processes (e.g. CO_2 flux: Sjögersten *et al.*, 2008) across the Arctic. However, despite earlier springs and longer, warmer summers across much of the Arctic, population declines have been observed for some mammalian herbivores, particularly voles and lemmings (Ims *et al.*, 2008), and also in some populations of caribou/reindeer (Vors & Boyce, 2009). It has been suggested that these declines are due to deteriorating winter conditions but the relative roles of warming winter and summer weather remains unclear. While 'bottom-up' processes may be particularly dominant on Svalbard, elsewhere in the Arctic top-down processes, including predation, may also be changing, especially for small vertebrate herbivores (Legagneux *et al.*, 2012, 2014).

Nonetheless, one common factor emerging from several studies of the population dynamics of Arctic herbivores is the detrimental effect of winter rain, an extreme event which may occur when air temperature is above freezing (Putkonen & Roe, 2003). As the rain percolates through the snow pack it can refreeze, leading to ice layers and ground-fast ice that can cover the tundra with an impenetrable layer, increasing the risk of starvation and population crashes (voles: Aars & Ims, 2002; Stien *et al.*, 2012; lemmings: Kausrud *et al.*, 2008; musk oxen: Forchhammer *et al.*, 2002; caribou/reindeer: Gunn *et al.*, 1981; Kohler & Aanes, 2004; Miller & Barry, 2009; Hansen *et al.*, 2011). Furthermore, on Svalbard synchrony in population fluctuations across the community of resident vertebrate herbivores (ptarmigan, voles and reindeer) has been linked explicitly to variation in 'rain-on-snow' (Hansen *et al.*, 2013). Given that future projections for Svalbard suggest average midwinter temperatures close to 0 °C (Førland *et al.*, 2012), there is likely to be an increase in the frequency of this phenomena (Hansen *et al.*, 2014). However, the extent to which these icing events impact negatively on Rangifer populations over their entire circumpolar range is contested (Tyler, 2010).

Teasing apart the relative influence of summer vs. winter warming on vital rates and population dynamics can be difficult when our mechanistic understanding of the impact of climate warming involves complicated causal chains (Krebs & Berteaux, 2006). However, tundra ecosystems have the advantage that they are comparatively simple, well studied, with low plant and animal diversity, and warming rapidly, yet with great year-to-year variation. For example, on Svalbard, reindeer have no resident grazing competitors, and no predators. In this model system, the positive impact of summer weather on primary production (Van der Wal & Stien, 2014) and reindeer population growth (Aanes *et al.*, 2002; Hansen *et al.*, 2013) is well documented, as is the impact of winter precipitation on fecundity ('rain-on-snow': Stien *et al.*, 2012), mortality (total winter precipitation: Solberg *et al.*, 2001) and population growth (total winter precipitation: Aanes *et al.*, 2000; 'rain-on-snow': Hansen *et al.*, 2013). Nonetheless, the relationships between vital rates and weather in these studies are proximate and overlook the likely importance of body condition as the ultimate determinant of reproduction and survival (Calder, 1984).

Body mass is a convenient measure of body condition which integrates an animal's location-specific energy and protein intake and expenditure (Parker *et al.*, 2009), and which responds continuously to weather and population density through the effects on food availability and energetic costs (Bårdsen & Tveraa, 2012). Therefore, body mass is a 'state' variable suitable for analysing the effects of seasonally varying environmental drivers (Taillon *et al.*, 2011). Thus, one way to improve our mechanistic understanding of the impact of climate warming on the demography of herbivores is to explore the drivers of seasonal variation in body mass, and in turn, the consequences this variation in body mass has on vital rates.

In this study, we begin by analysing the annual variation in body mass of wild female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) using marked individuals, repeatedly sampled each April (i.e. in late winter), as well as data from animals culled in October (i.e. autumn). Second, we investigate how the annual variation in seasonal body mass influences ovulation, fecundity, survival and population growth rates. Third, we explore the effects of summer and winter warming on annual variation in body mass in both October and April, as well as, change in body mass between seasons. Specifically, we predicted that: (i) body mass in autumn, and mass gain over the summer, would increase in association with higher plant productivity in warmer summers (Van der Wal & Stien, 2014); (ii) body mass in April would decline over time, and mass loss over winter increase, because of more frequent

'rain-on-snow' events (Hansen *et al.*, 2014) and the resulting 'icing' restricts access to winter grazing (Hansen *et al.*, 2010). Given the low plant productivity in summer and potential difficulties accessing forage in winter, coupled with an increasing population, we expected density dependence in both October and April body mass (Bonenfant *et al.*, 2009). Our findings are discussed in terms of the likely consequences for the population biology of Arctic herbivores given continued climate warming as projected in many parts of the Arctic.

Materials and methods

Study area and climate

The study was carried out in Nordenskiöldland, Svalbard (77°50′–78°20′N, 15°00′–17°30′E). The generally wide, U-shaped valleys are mostly vegetated (up to about 250 m altitude), although above-ground live vascular plant biomass in vegetated habitats averages only 35 g m^{-2} (annual range 23–46 g m^{-2}: Van der Wal & Stien, 2014). Nonetheless, the area supports a relatively high density of reindeer compared to other parts of Svalbard (Van der Wal & Brooker, 2004). The lower-lying, wetter and more productive, pastures are grazed during summer, but in winter forage tends to be less accessible here because of deep or hard snow, or ice. Therefore, in winter reindeer tend to feed on wind-blown vegetated ridges, and at higher elevations (see also Larter & Nagy, 2001).

According to temperature and precipitation data from Longyearbyen airport (78°25′N, 15°46′E) (http://eklima. met.no), 30 km from the study area, both mean January daily temperature (−10.7 °C, SE = 5.1) and mean July daily temperature (6.7 °C, SE = 0.9) increased linearly between 1994 and 2014 (estimated slope, $\beta = 0.44$ °C, SE = 0.16, $P = 0.01$; and $\beta = 0.073$ °C, SE = 0.027, $P = 0.02$, respectively; Fig. 1a). Over the same period, there was a tendency towards more 'rain-on-snow' (November–March), in later years (Fig. 1b). Five of the six most severe winters (highest 'rain-on-snow') occurred in the second half of the study (Fisher's exact probability test: $P = 0.063$).

Reindeer populations

Although severe winter weather may cause local movement (5–10 km) to seek accessible forage (Stien *et al.*, 2010; Loe *et al.*, 2016), Svalbard reindeer are regarded as sedentary (Tyler & Øritsland, 1989), and populations separated by as little as 40–50 km are genetically distinct (Côté *et al.*, 2002).

Our main study area was centred in *Colesdalen, Semmeldalen* and parts of *Reindalen*, and their side valleys, hereafter referred to as *Semmeldalen* area. Female adults, yearlings and calves of both sexes were caught in winter by net from snow-mobiles, measured, weighed to the nearest 0.5 kg, and
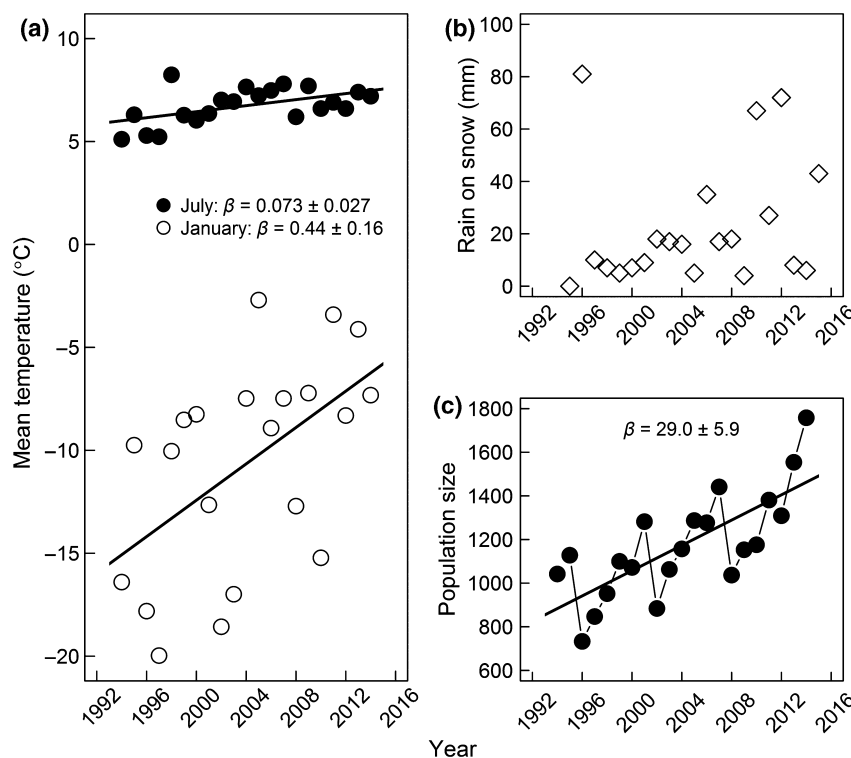
Fig. 1 (a) Mean July daily temperature (solid circles) with fitted linear regression and mean January daily temperature (open circles) with fitted linear regression for 1994–2014, (b) 'rain-on-snow' (November–March) for 1995–2015, (c) population size estimates (females plus calves of both sexes) for Reindalen, Semmeldalen and Colesdalen from the integrated population model from 1994 to 2014 (after Lee *et al.*, 2015; modified by Bjørkvoll *et al.*, 2016), with fitted linear regression.

individually marked with coloured, numbered ear tags and, if female, matching coloured and numbered collars (Milner *et al.*, 2003; Omsjoe *et al.*, 2009). Blood samples were taken for progesterone assay to confirm ultrasound scans of pregnancy status of adult females (Ropstad *et al.*, 1999). Also, the ultra-sound scanner was used to assess whether a foetus was alive or not, based on heart or body-part movements.

Reindeer capture–mark–recapture: winter

Over the 21 years, we made 2786 captures of females in late winter (April–May: median 139 per year: range 84–200) involving 892 individual females, of which 584 were marked for the first time as calves. The mean number of times an individual was caught in April was 3.1 (range 1–11 times), with 17% caught six or more times. Also, between 2007 and 2011, we caught 366 yearling and older females in early winter (February). All capture and live animal handling procedures were performed under licences from the Norwegian Food Inspection Authority and its predecessor the Norwegian National Research Authority.

Calves and yearlings were distinguished from adults on the basis of size and tooth eruption patterns. At the start, adult females marked were of unknown age. However, our focus on marking female calves each year (median 27) resulted in an increasing proportion of known-age animals in the marked population. In the last 3 years of the study, all marked individuals caught were of known age. In total, 704 individuals (79%) of the females marked had known birth years, including 50 animals which were aged when found dead (Reimers & Nordby, 1968). The oldest animal we recaptured was 16 years of age.

Reindeer summer census

In late July and August, observers walked through the *Semmeldalen* study area searching for both marked and unmarked animals, and in particular whether the adult females were accompanied by a calf or not.

Reindeer vital rates and population size estimates

In the *Semmeldalen* study area, annual vital rates were estimated using a modified version (Bjørkvoll *et al.*, 2016) of an integrated population model developed for the female component of the study population (Lee *et al.*, 2015). This model provides a Bayesian state-space framework for obtaining annual estimates of age-specific survival, fecundity and population sizes, based on April capture–mark–recapture data, July–August re-sighting observations (censuses 1996–2014), and independent population structure counts (1993–2007, see Solberg *et al.*, 2001). The model allows for measurement error, as well as demographic stochasticity.

Annual survival estimates were from August$_{t-1}$ to August$_t$. The fecundity estimates were informed by data on the presence of a calf accompanying its marked mother in the July/August census. Annual population size estimates for female adults, female yearlings and calves of both sexes ranged between 733 in 1996 and 1758 in 2014 and increased significantly over the study period by 29 (SE = 5.9) individuals per annum (Fig. 1c).

Reindeer culling

In addition to live capture, we also culled animals in April (1995–2002 and 2009) and October (1994–2007), as part of an investigation of host-parasite interactions (Albon *et al.*, 2002; Stien *et al.*, 2002; Carlsson *et al.*, 2012) in our *Semmeldalen* study area. In addition, there was a licensed hunt in the *Colesdalen* part of our main study area in September. Together, the scientific culling and hunting accounted for 2–4% per annum of the resident population of females. To minimize the impact of these removals on our *Semmeldalen* study population, we also culled animals in *Sassendalen*, another hunting area, approximately 45 km north-east of *Semmeldalen*.

A total of 284 females (135 in *Sassendalen* and 149 in *Semmeldalen*) were shot between 19–27 October and 111 females (47 in *Sassendalen* and 64 in *Semmeldalen*) in April. Age was determined by counting annual growth rings in the first incisor (Reimers & Nordby, 1968). Whole body mass was recorded, before evisceration. The uterus and ovaries were collected for assessment of reproductive status. In October, ovaries were checked for the presence of a primary corpus luteum, indicating ovulation (Langvatn, 1992). Lactation status (lactating or not lactating) was based on the presence of milk in the udder.

Weather measures used in the analyses

Weather variables were selected based on both the reproductive cycle and the annual cycle in the seasons (Fig. 2). Calving occurs around snow melt and lactation during the snow-free months when vegetation is accessible. Ovulation occurs in October just after body mass peaks, with gestation lasting throughout the period of snow-lie.

Also, we drew upon studies which have identified relationships between direct and indirect measures of forage availability and weather. For example, above-ground vascular plant biomass measured in *Semmeldalen* in early August (1998–2009) correlated strongly with temperature in midsummer (see Van der Wal & Stien, 2014 for details of both measurement of biomass and the relationships with weather). In particular, plant biomass on ridge habitats supporting dwarf shrubs (*Dryas and Salix*), areas often partially exposed in winter and snow-free early in spring, increased with mean June–July temperature (Van der Wal & Stien, 2014). On *Luzula*-dominated heath and wetter marsh habitats, dominated by mosses with *Alopecurus* and *Dupontia* grasses, snow melt occurred later and mean July temperature was a better predictor of biomass (Van der Wal & Stien, 2014).

Consequently, we consider mean temperature in both June–July and July alone, as potential surrogates of summer forage across all 21 years. In addition, we considered heat sum measures for the snow-free months (June–September degree-days), as an integrated measure of summer temperature and season length. Also, as indicators of the start of summer/end of winter and end of summer/start of winter, we considered log$_e$ transformed May degree-days >0 °C (spring: Pettorelli *et al.*, 2005)
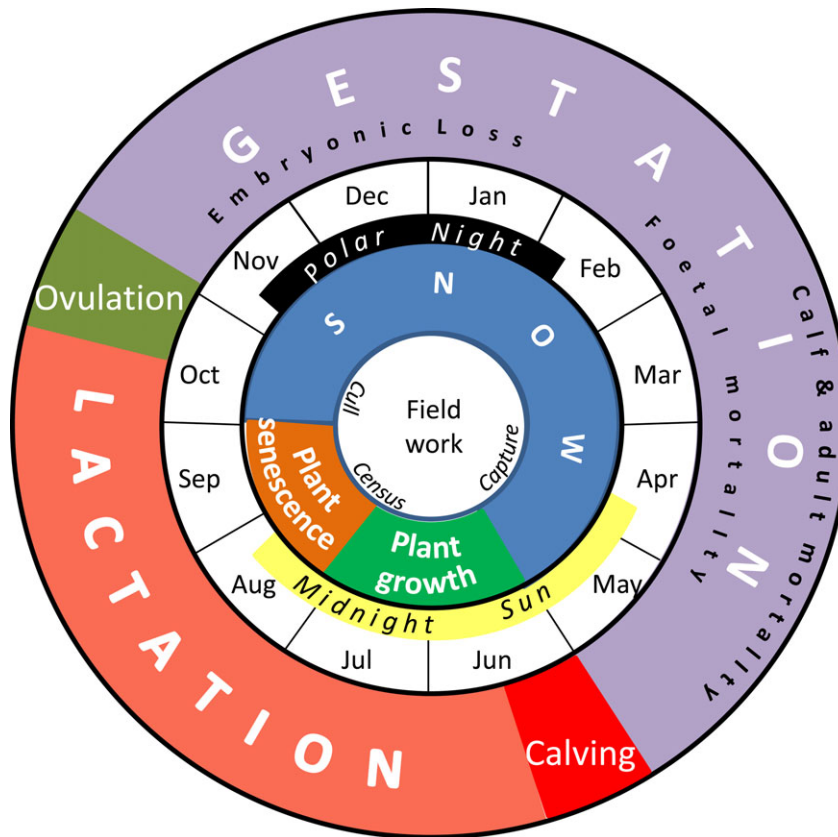
Fig. 2 The Svalbard reindeer year. Showing the major reproductive and survival stages (outer ring) in the annual cycle seasons (inner ring) in terms of winter (snow), summer (plant growth and senescence), the period of 24-h darkness (Polar night) and 24-h light (Midnight sun). The inner circle shows the timing of our main field work activities.

and October degree-days >0 °C (autumn). May degree-days, mean June–July temperature and June–September degree-day all increased over time but October degree-days did not (Table S1). While spring (May degree-days) and summer (June–July) temperatures were positively correlated, there was no significant correlation between autumn temperature and either the preceding spring or summer temperature (Table S1).

For the six most recent winters (2009/10–2014/15), we have undertaken direct field measurements of ice formation in the snow pack and extent of ground-fast ice across a gridded sample of 128 snow pits dug each year at 16 different georeferenced locations (eight pits per site) within the core study area (LE Loe, unpublished). We have correlated the mean ground-ice thickness with a simple index of winter rain-on-snow which can lead to ground-icing (see Appendix S1). Our rain-on-snow index assumes that, when over 24 h, mean air temperature at 2 m is above 0 °C, any precipitation falls as rain (Solberg *et al.*, 2001; Hansen *et al.*, 2011). We used the log$_e$ transformed cumulative precipitation on days with air temperature above 0 °C, over the period November–March (prior to our capture of animals each April) in our analyses. We justify this on the basis of relationships with both historical records of precipitation as rain or sleet made by the Norwegian Meteorological Institute and our recent measurements of ground ice (Figure S1).

Since between November and March, the tundra is almost entirely snow covered, except some wind-blown ridges, and we chose to use the term 'rain-on-snow'. This term is widely used by hydrologists and snow physicists (Harr, 1981; Stimberis & Rubin, 2011), as well as ecologists (Putkonen & Roe, 2003; Rennert *et al.*, 2009; Stien *et al.*, 2010).

In addition to 'rain-on-snow', we investigated the role of ablation – a measure of the processes that remove snow, ice or water from a snowfield or glacier (Paterson, 1999). Tyler *et al.* (2008) developed an ablation index using temperature and wind speed, during the period October–December, when typically there is little snow and the vegetation may be exposed (see Appendix S2 and Fig. S2). The ablation index was significantly correlated with October degree-days and November–March 'rain-on-snow' (Table S1: $r = 0.664$, $P = 0.001$; $r = 0.466$, $P = 0.033$, respectively).

Statistical analyses

The between-year variation in body mass of culled females in October and marked females in April was analysed in GenStat v.18 using linear mixed models where the fit maximizes the restricted log-likelihood (REML – Payne *et al.*, 2015) and one distinguishes between fixed effects and random effects. The fixed effects within models were of two types: those related to

the environment and those related to the reindeer. The environmental variables included weather variables (see above) and population size, all centred with mean zero. In practice because of collinearity, we only fitted one of the possible summer variables at a time. Population size was $\log_e$ transformed. As population size increased significantly over the study (Fig. 1c), we also investigated the effect of detrended population size (the residual from the fitted linear regression in Fig. 1c) with the rationale that carrying capacity may have increased over time. The 'reindeer' variables included: age group and lactation status (lactating or not) for October body mass analysis. For April body mass analysis, age, date of capture and, because there is a 'cost of reproduction', pregnancy in the previous year (pregnant or not, or unknown) were included. As female reindeer grow rapidly during their first 3 years of their lives, and then decline in body mass from about 9 years of age, similar to the pattern found for vital rates (Gaillard *et al.*, 1998; Lee *et al.*, 2015), we distinguished six groups based on known age: calves, yearlings, 2-year-olds, 3- to 8-year-olds, 9- to 11-year-olds, and 12- to 16-year-olds, and a seventh – adults of unknown age. Fitting age in this way significantly reduced the deviance ($\Delta AIC = -43.2$) compared to fitting a quadratic (age + age^2) relationship. In addition, for October body mass, we accounted for where animals were shot and standardized annual estimates, as if all were shot in our core study area, *Semmeldalen*, for subsequent comparison with April mass from captured animals.

In all linear mixed models, year was included as a random effect. This was to take account of the fact that the repeated measures of individuals were variable over the years and to avoid spurious relationships arising from differences in sample sizes (i.e. in April from 84 to 200). In the analysis of April mass, individual identity was also fitted as a random effect to allow for the fact females were resampled a variable number of times over their lifetime. Also we considered the possibility of temporal correlations by fitting an autoregressive model (AR1). However, this gave no significant improvement (phi = 0.106 ± 0.30; $\Delta AIC = 0.19$).

We report Akaike information criterion (AIC) values, calculated using the total deviance (Shmueli, 2010), to guide model selection. Model comparisons were made using relative differences (ΔAIC) in total deviance by comparison with the 'best' model (lowest AIC). However, even though the additional term may have lowered the deviance we rejected it, if the coefficient was not significant ($P > 0.05$).

Our models of April body mass considered interactions between age groups and all other fixed effects (i.e. both reindeer and environmental covariates). While all the models fitted age in terms of the seven age groups described above, for these interactions, we reduced the number of age groups to four groups [calves, yearlings, 2-year-olds and adults (3 years or older)]. For brevity, we graph relationships between body mass and environmental covariates for adults only, with results for the qualitatively similar relationships in other age groups shown in Table S4. Finally, we considered all two-way interactions between weather covariates and population size.

Ordinary linear models (LMs) were used to (i) analyse the annual variation in both overwinter body mass loss (the difference in the mean adult body mass) between October and April, and recovery of mass (the difference in the mean adult body mass) from April to October (because this is cross-sectional data), as functions of the prevailing weather (see above) and density dependence; (ii) evaluate covariation between and within age classes in fecundity and survival; (iii) analyse the annual population growth rate, calculated as $\log_e (N_t/N_{t-1})$, as a function of body mass.

To analyse survival and fecundity in relation to body mass, we used logistic curves

$$y = A + \frac{C}{1 + e^{-B(x-M)}}$$

in nonlinear regression. In GenStat this is specified as $A + C/(1 + \exp(-B*(X - M)))$, where A is the lower asymptote, $A+C$ is the upper asymptote, B is the slope and M is the x-value for the inflexion point at $A+C/2$. Finally, for the analysis of binomial proportions: ovulation or foetal death, we used generalized linear models with a logit link function.

Results

Annual variation in body mass

October body mass increased significantly (estimated slope, $\beta = 0.34$ kg per annum, SE = 0.12, $P = 0.01$) during the study (Fig. 3). In contrast, and contrary to predicted, there was no systematic temporal change in April body mass of marked adults over the 21 years ($\beta = 0.03$ kg per annum, SE = 0.14, $P > 0.50$). However,
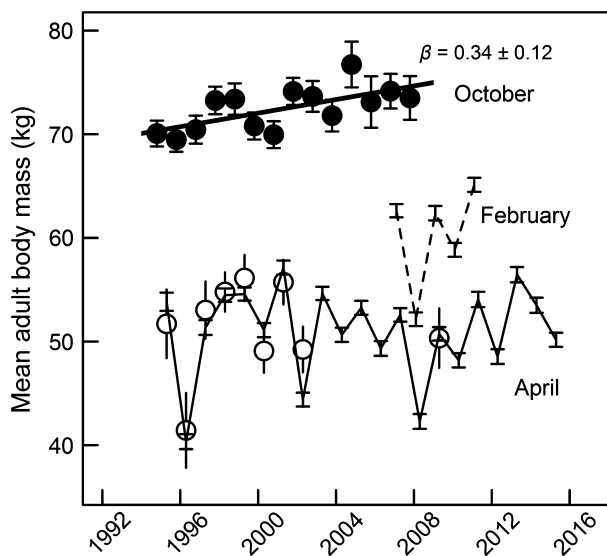
Fig. 3 Annual variation in mean adult body mass (±SE) of female reindeer in October culled animals 1994–2007 (black circles and fitted linear regression); February live-caught animals 2007–2011 (dashed line); April culled animals 1995–2002, and 2009 (open circles); April live-caught animals 1995–2015 (solid line).

the coefficient of variation in average annual April body mass was 8.8%, more than threefold greater than the variation in October body mass [coefficient of variation (CV) = 2.5%; Fig. 3].

There was no significant correlation between mean adult body mass in October and the following April ($r = 0.08$, $N = 14$), nor between April and October in the same year ($r = 0.07$, $N = 13$). However, February and April adult body mass was highly correlated ($r = 0.99$, $P < 0.001$) across the 5 years both were recorded (Fig. 3). There was too little overlap between the October and February body mass time-series to test for a correlation, but the above result suggests that between-year variation in overwinter mass loss was already apparent in February.

Reproduction and body mass

The proportion of adult females that had ovulated by the last week of October was high in most years (mean = 0.92, SE = 0.03). Nonetheless, the relatively small amount of annual variation in adult ovulation rate was positively related to variation in mean October adult body mass ($\chi^2 = 6.5$, df = 1, $P = 0.01$; Fig. 4a).

Females may ovulate for the first time as yearlings, and as yearlings are still growing, their ovulation rates are very variable between years (CV = 115%, compared with 14% in adults). Annual variation in ovulation rates in yearlings was positively correlated to their mean body mass ($\chi^2 = 4.7$, df = 1, $P = 0.03$). Differences in ovulation rate between age classes were a function of differences in body mass, with no additional effect of age *per se* ($\chi^2 = 0.7$, df = 2, $P > 0.7$; Fig. 4a). Therefore, a common logistic regression could be fitted ($y = 0.009 + 0.959/(1 + \exp(-0.30*(X - 57.09)))$: Fig. 4a); subsequent fecundity in late July/early August, estimated from the integrated population model, was substantially lower than the ovulation rate (average for 4- to 9-year-olds: 0.62 ± 0.052, down from an ovulation rate of 0.92), and differed markedly between years (CV = 37%, compared to 14% for ovulation).

Much of this loss of reproductive potential between ovulation (October) and parturition (June) was associated with the severity of the winter, such that there
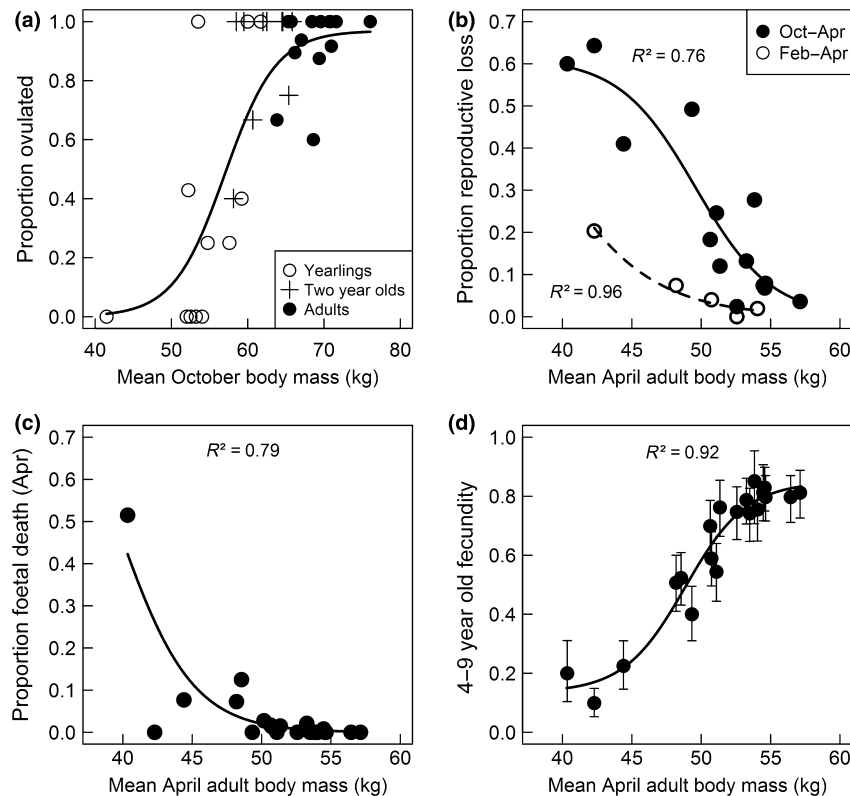
Fig. 4 (a) The age-specific proportions of females ovulating in relation to age-specific body mass each October (1994–2007) with the logistic regression fitted to the binomial proportions for all age/year classes; (b) annual proportion of reproductive loss between October (ovulation) and April (pregnancy) with fitted logistic curve, and February to April with fitted asymptotic curve, plotted against mean April adult body mass; (c) annual proportion of April foetal deaths (number dead/number pregnant) plotted against mean April adult body mass with fitted logistic regression; (d) Annual fecundity of 4- to 9-year-olds plotted against mean April adult body mass ±SE, with fitted logistic curve.

were significantly greater losses in winters with low April body mass (Fig. 4b). For example, there was on average a 54% loss of reproductive potential between ovulation in October and pregnancy in April in the 4 years when April adult body mass was <50 kg (Fig. 4b). In comparison, the average loss was just 6% in 4 years when April body mass was >54 kg (Fig. 4b). The logistic curve relating annual variation in the reproductive loss between October and April to mean April body mass explained 76% of the variance ($y = 0.0103 + 0.596/(1 + \exp(0.387*(X − 49.6)))$: $F_{3,10} = 14.7$, $P < 0.001$; Fig. 4b). Also, in the five winters we captured females in both February and April, the proportional reduction in the pregnancy rate over the 8-week interval was significantly related to April body mass (exponential curve $y = −0.052 + 51.0*\exp(−0.125*X)$: $F_{2,2} = 47.8$, $P = 0.02$; Fig. 4b).

Furthermore, our ultrasonography data show that the proportion of foetal death recorded in April is higher in winters when body mass is low (fitted logistic regression: $y = 0 + 1.0/(1 + \exp(0.369*(X − 39.467)))$; $\chi^2 = 88.40$, $P < 0.001$; Fig. 4c). There was a marked increase in the incidence of foetal death in years when

mean adult body mass was below ca. 50 kg (Fig. 4c). Overall the annual variation in 4- to 9-year-old fecundity (measured as 'calves-at-foot' in summer) was strongly correlated with mean April adult body mass (fitted logistic regression $y = 0.135 + 0.714/(1 + \exp(−0.453*(X − 48.85)))$; Fig. 4d).

Survival and body mass

Like fecundity, survival estimated from the integrated population model was very variable between years, particularly in calves and the oldest individuals (Fig. 5a). For example, the coefficient of variation was 32% in calves and 27% in females aged 12 years and older, but only 3% in 3- to 8-year-olds. Across age classes, the fluctuations in survival were highly concordant (Fig. 5a; see also Lee *et al.*, 2015). Even between calves and 3- to 8-year-olds the correlation across years was high ($r = 0.96$, $P < 0.001$; Fig. 5b). The annual estimates of April adult female body mass were a good predictor of annual survival rates, for example, with the fitted logistic regression (Fig. 5c) explaining 94% of the variance in 3- to 8-year-old survival.
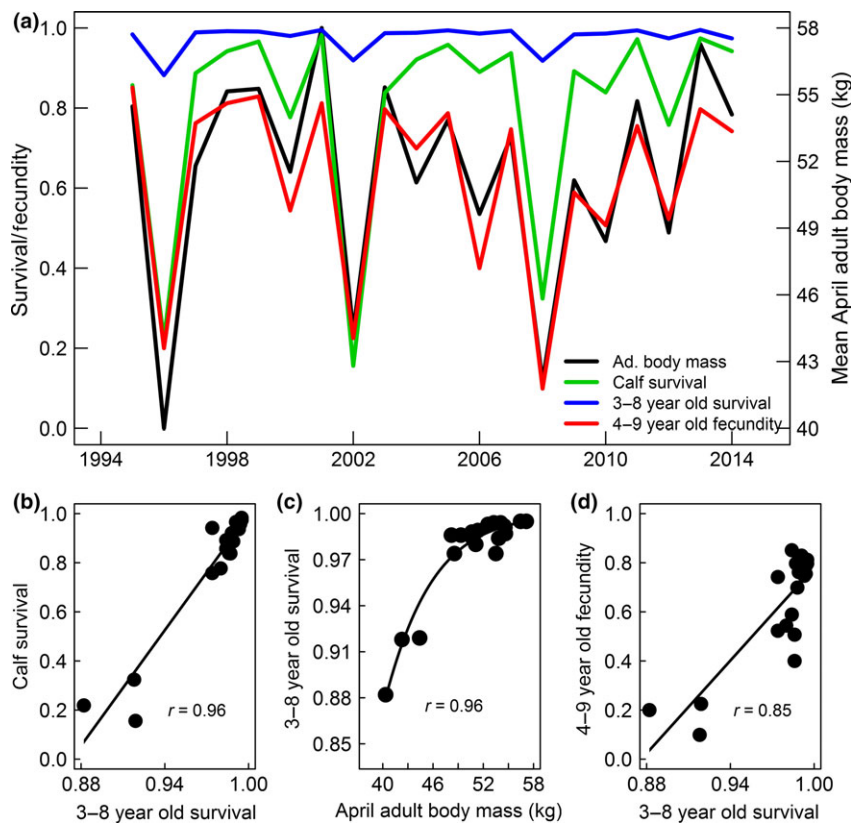

Fig. 5 (a) Annual variation in April adult body mass (black line), survival of calves (green line) and 3- to 8-year-olds (blue line), and subsequent fecundity in 4- to 9-year-olds (red line); (b) calf survival plotted against 3- to 8-year-old survival; (c) 3- to 8-year-old survival plotted against April adult body mass with fitted logistic curve; (d) the subsequent fecundity of 4- to 9-year-olds plotted against 3- to 8-year-old survival.

Population growth rate and body mass

Annual variation in fecundity and survival in prime-aged females was highly correlated (Fig. 5d), and both vital rates were correlated with April adult body mass (Figs 4d and 5c, respectively). Accordingly, April body
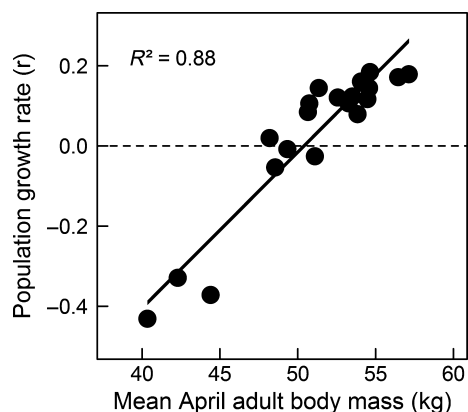

Fig. 6 The intrinsic population growth rate, r, plotted against April adult body mass (linear regression: $y = -1.96 + 0.039x$).

mass explained 88% of the variance in the instantaneous population growth rate between summers (Fig. 6). In five of 6 years when mean adult body mass was <50 kg, the population declined. Whereas in 13 of 14 years, when body mass was >50 kg, the population increased.

Collectively, these findings demonstrate the importance of body mass in mediating reproduction, survival and, in turn, population growth. In the subsequent sections, we explore the environmental factors which could be driving variation in annual body mass.

Warmer summers result in higher October body mass

As predicted, female reindeer were on average heavier in October following warm summer weather. Mean June–July temperature, an index of summer forage biomass, accounted for 36% of the variance in October body mass, with a 1 °C increase resulting in a 1.41 ± 0.65 kg increase in average body mass ($P = 0.04$; Fig. 7a). After accounting for summer temperature, there was no effect of the previous spring or winter
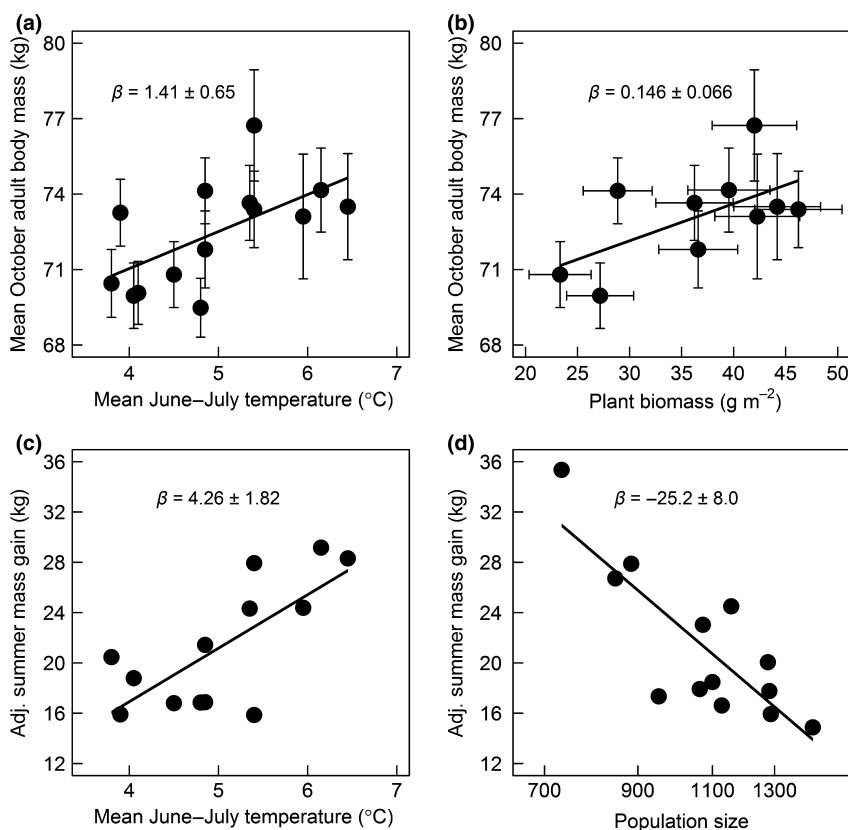
Fig. 7 Mean October body mass ($\pm$SE) of females aged 3- to 8-year-olds, standardized for valley and reproductive status, plotted against (a) mean June–July temperature (1994–2007) with fitted regression line, and (b) vascular plant biomass measurements ($\pm$SE) for 1998–2007 (after Van der Wal & Stien, 2014) with fitted regression line. Also, illustrated is summer mass gain plotted against (c) mean June–July temperature, and (d) $\log_e$ population size. Plot (c) shows the mean body mass adjusted for population size and plot (d) the mean body mass is adjusted for mean June–July temperature. The fitted partial regression lines are shown.

climate variables on October body mass. Although the mixed model with the lowest AIC included $\log_e$ population size in addition to June–July temperature (Table S2), we rejected it because the density dependence was not significant (-2.2 ± 3.6). Thus, the most parsimonious model of variation in October body mass suggests that only the immediate growing season is important, with no detectable 'carry-over' effect of the previous winter conditions. Accordingly, over the 10 years for which we had both October body mass data and direct measures of plant biomass in midsummer, there was a strong tendency for heavier reindeer in years of high plant biomass ($P = 0.059$; Fig. 7b).

Summer mass gain

Summer mass gain from April to October varied twofold (15.6–30.1 kg: mean 21.3 ± 1.4 kg). After accounting for a positive effect of mean June–July mean temperature ($t_{10} = 2.34$, $P = 0.041$; Fig. 7c), mass gain was negatively related to $\log_e$ population size ($t_{10} = -3.14$, $P = 0.01$: Fig. 7d). Together, summer temperature and population density explained 40% of the variance in summer mass gain. Also, modelling relative mass gain, rather than absolute mass gain, increased the variance explained by the model to 48%. Overall the implication is that population size relative to the changing resource base influences the summer recovery of body mass.

Icy winters depress April body mass

As expected, over the six most recent years for which we had 'ground-ice' field measurements, April adult body mass declined with increasing ground-ice thickness (Fig. 8). Furthermore, over the entire 21-year study April body mass declined significantly with 'rain-on-snow' (Table S1 and S3; see also Fig. 9a).

The mixed model of April body mass with the lowest AIC included $\log_e$ October degree-days (Fig. 9b), in addition to $\log_e$ 'rain-on-snow' (Table S3: Model 1). The next 'best' model included the detrended population size (ΔAIC = 4.5; Table S3: Model 2). Although 'rain-on-snow', October degree-days and the detrended population size all significantly influenced adult April body mass, the fit of this model was poor compared with just using rain-on-snow and October degree-days. Adding the detrended population size appeared to be associated with a reduction in the variance explained (shallower slopes and little or no change in the standard error) by both 'rain-on-snow' ($\beta = 2.79 \pm 0.59$ vs. 3.09 ± 0.58) and October degree-days ($\beta = -1.90 \pm 0.65$ vs. -2.30 ± 0.63). The respective coefficients and SEs for all age classes in the 'best' model are shown in Table S4.

There were no significant effects of either the ablation index, or June–July temperature in the previous summer on April body mass (Table S3). Also, there were no significant interactions between population size and either 'rain-on-snow' or October degree-days, irrespective of whether or not population size was detrended.

Overwinter mass loss

Mass loss between October and April over the 14 winters for which we had both measurements varied more than twofold (12.8–31.2 kg; mean = 21.8 ± 1.41 kg). Overwinter mass loss was significantly greater in winters with high 'rain-on-snow' and was significantly reduced following warm October weather ($F_{2,11} = 7.18$, $P = 0.01$). These effects mirrored the 'best' model explaining variation in April body mass (Fig. 9a, b), and together explained 48.6% of the variance. Although population size and October degree-days were not significantly correlated over the 14 winters ($r = -0.31$, $P > 0.25$), a model with $\log_e$ 'rain-on-snow' and $\log_e$ population size provided an alternative model (Fig. 9c, d). In this model, $\log_e$ 'rain-on-snow' and $\log_e$ population size were both independently significant ($t_{11} = 2.20$, $P = 0.050$, and $t_{11} = 2.29$, $P = 0.043$, respectively), and together explained 48.7% of the variance.

As the ablation index was significantly correlated with $\log_e$ October degree-days ($r = 0.76$, $P < 0.001$) over the 14 years we were able to estimate overwinter mass loss, the ablation index could potentially be substituted into the model with 'rain-on-snow'. However, this model explained less of the variance (42% compared with 49%) and the ablation index was not independently significant ($t_{11} = -1.89$, $P = 0.09$).
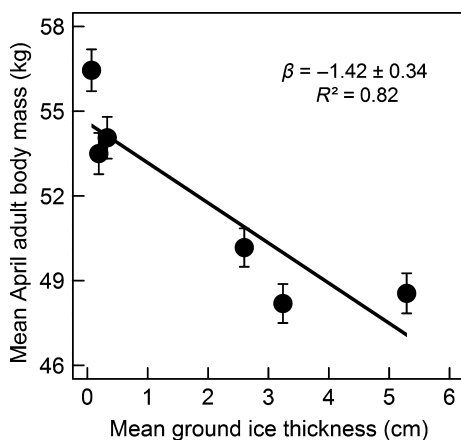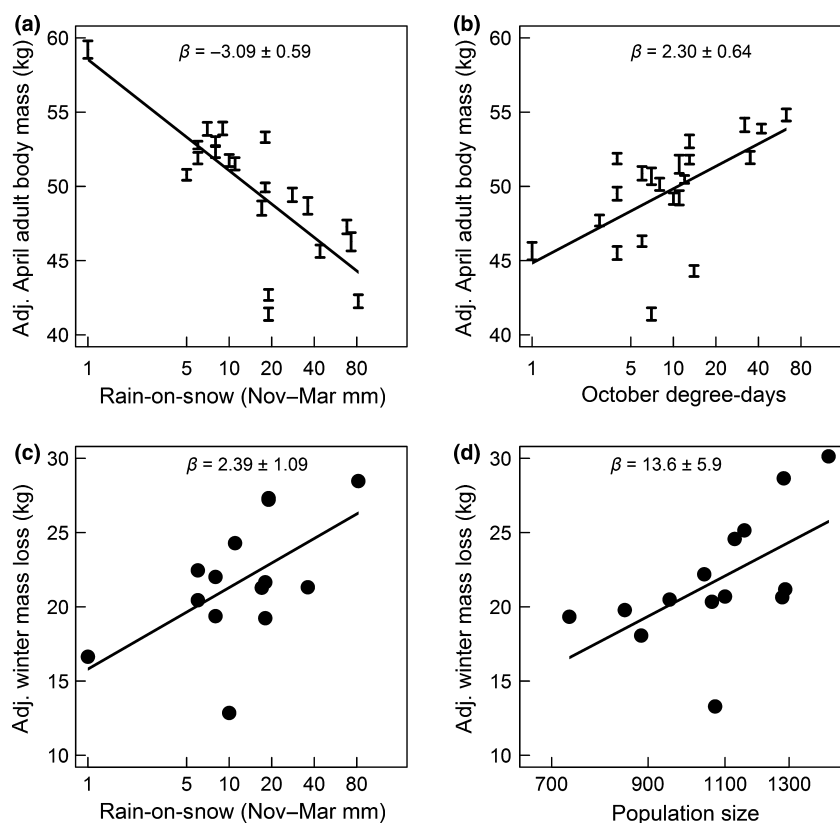

Fig. 8 Mean adult April body mass (kg) plotted against mean ice thickness (cm) measured at 128 sites in April in each of 6 years between 2010 and 2015 (LE Loe, unpublished).

Fig. 9 Adjusted mean April adult body mass (±SE) each year from 1995 to 2015 plotted against, (a) 'rain-on-snow' ($\log_e$ Nov–Mar mm), (b) previous October degree-days ($\log_e$). Also illustrated is an alternative model for winter mass loss plotted against, (c) 'rain-on-snow' and (d) population size ($\log_e$). Each pair of plots, (a/b) and (c/d), show the annual means adjusted for the other explanatory variable and the fitted partial regressions lines.

Discussion

Our findings of how body mass determines vital rates and, in turn, how weather influences body mass provide an important 'missing' mechanistic link in our current understanding of the population biology of a keystone species in a rapidly warming Arctic. Two findings are of particular note. First, the incidence of 'rain-on-snow' in warmer winters which leads to starvation due to ice-locked pastures (Hansen *et al.*, 2010) depresses late winter body mass. The weather prevailing in this 'bottle-neck' not only influenced the immediate late winter survival of adults and recruitment of young, but also the subsequent fecundity of survivors, because body mass in later winter determines the degree of reproductive loss throughout gestation. No previous study of a wild Arctic herbivore has systematically quantified annual variation in loss of reproductive potential. As the changes in vital rates are concordant, late winter body mass is an excellent predictor of annual population growth rate, accounting for almost 90% of the variance. Only one other study of a

large herbivore has related population growth to winter body condition and that was mule deer in a variable semi-arid environment (see Monteith *et al.*, 2014). Second, the negative effects of warmer winter weather were ameliorated by warmer autumns, presumably because it extended the period of snow-free grazing.

As predicted, warmer weather in summer, and the associated increase in primary production (Van der Wal & Stien, 2014), enhanced the recovery of body mass, leading to higher autumn body mass and ovulation rates, confirming results from other studies of caribou/reindeer (Thomas, 1982; Cameron *et al.*, 1993; Pachkowski *et al.*, 2013) and mammals, in general (Bronson, 2009). However, despite the higher plant biomass associated with warmer summer weather, we did not detect any 'carry-over' effect of this weather on the subsequent mean April body mass, 9 months later. Also, like some other studies of northern ungulates (Pettorelli *et al.*, 2005; Mysterud *et al.*, 2008), we did not detect any residual effect of the previous winter weather on October body mass after accounting for summer temperature. This may be due to correlation

across seasons between phenological measures and the weather driving them. The effect of winter weather could then be masked by its potential impact on the timing of spring 'green-up', and/or the relationships could be shifting due to climate change (Christianson *et al.*, 2013). However, we found correlations between spring/summer weather variables and the previous winter weather were not significant. The limited 'carry-over' effects suggest that currently Svalbard reindeer are well adapted to cope with the vagaries of the different seasons (Huôt, 1989), although this might change (Betini *et al.*, 2013). Currently, whatever their condition at the end of winter Svalbard reindeer appear able to regain mass over the summer, and reset their reproductive potential.

Given climate warming is projected to continue, we now discuss our findings on the influence of winter severity (Campbell *et al.*, 2005; Cooper, 2014), and the ameliorating effects of warmer autumns (see Gallinat *et al.*, 2015), which either change our perceptions, and/or have implications, for how we might study the consequences of future climate change on Arctic herbivores more generally (see also Berteaux *et al.*, 2006). And, also, we discuss two findings, weak density dependence (see Post, 2005), and the consequences of likely increased variability in vital rates (see Tews *et al.*, 2007a), which substantially reinforce our current understanding of their population biology.

Winter severity, April body mass and population demography

Although caribou in West Greenland (*Rangifer tarandus groenlandicus*) have been described as 'income' breeders when compared to sympatric musk ox (Kerby & Post, 2013), a comparative physiological study of reindeer and caribou estimated that 96% of foetal growth in reindeer (*R. t. tarandus*) came from stored maternal reserves, compared to 84% in the later calving caribou (*R. t. granti*) (Barboza & Parker, 2008). This suggests that reindeer are very much 'capital' breeders (Stephens *et al.*, 2009). As almost all the allocation to reproduction in reindeer is from body reserves laid down in the summer, the environmental factors influencing body condition of mothers later in winter are likely to be critically important to fitness.

When body reserves are severely depleted, an individual may terminate the current pregnancy to stop investing in reproduction, in order to minimize the risk to its own survival (Stearns, 1992; Festa-Bianchet & Côté, 2008). Thus, while summer conditions on Svalbard influence autumn body mass and ovulation rate, it is winter conditions, and the degree of mass loss, that are likely to influence whether a female retains her

pregnancy and calves successfully in June (Milner *et al.*, 2013; Monteith *et al.*, 2014). Among adult females, there was on average a 30% reduction in reproductive potential between ovulation rates in late October and the proportion of females that have a calf in August (fecundity). Between-year differences in ovulation rates were small compared to variation in fecundity the subsequent summer. Not only was the proportion of females with a calf strongly related to April body mass, but the loss of reproductive potential during the winter was also negatively related to April body mass. In particular, in winters when body mass was less than ca. 50 kg, we observed high rates of reproductive loss including an elevated proportion of dead foetuses recorded at capture in April. Information on prenatal losses is scarce (Russell *et al.*, 1998; Langvatn *et al.*, 1999; Milner *et al.*, 2013), but in white-tailed deer deep snow depressed female body condition (Garroway & Broders, 2005) and led to the differential loss of male foetuses (Garroway & Broders, 2007).

After severe winters, recovery over the summer is likely to be enhanced by not undergoing the energetic demands of lactation (Bårdsen & Tveraa, 2012; Bårdsen *et al.*, 2014), which are greater than the demands of foetal growth (Loudon & Racey, 1987). Indeed, in October nonlactating females were significantly heavier (ca. 5%) than lactating females, suggesting that not lactating enables more energy to be redirected into their own body reserves. Our findings are consistent with risk minimization, but without examining the subsequent survival of individual adults, we cannot determine whether this is an adaptive strategy, or simply an energetic cost saving (Milner *et al.*, 2013).

Other studies of northern ungulates have reported poor survival in harsh winter conditions, particularly in young and old individuals (Loison & Langvatn, 1998; Coulson *et al.*, 2001; Garrott *et al.*, 2003; Keech *et al.*, 2011; Willisch *et al.*, 2013). We found that survival in calves, and thus the recruitment rate, as well as adult survival, was strongly correlated with mean adult body mass in April, and therefore was influenced, in particular, by the severity of the winter.

On Svalbard, the consequences of low body mass in April are two consecutive cohorts with few individuals recruited. The former, born the year before the severe winter, suffer high mortality as calves in the first winter of life. The latter because the high reproductive losses due to low foetal/neonatal viability mean, very few are born or survive the first week of life. This causes large fluctuations in the population age structure (Lee *et al.*, 2015).

Our study emphasizes that one of the main challenges in current Arctic ecosystem research is to obtain a better mechanistic understanding of the

environmental changes occurring outside the growing season, such as those related to snow and icing (Post *et al.*, 2009). It is noteworthy that our simple measure of 'rain-on-snow' was a good predictor of mean ground-ice thickness, and other more complex indices, such as weighting for the timing of winter rain events, did not improve the model fit (Hendrichsen & Tyler, 2014). This may reflect that the formation of ground ice is likely dependent on an interaction between the intensity of 'rain-on-snow' events and snow depth. Unfortunately, snow depth is poorly documented in the meteorological records and also highly variable in space because of topography (Loe *et al.*, 2016). Remote-sensed measures corroborated by field sampling and geophysical modelling may be necessary to inform better spatio-temporal models of icing. Likewise, how icing affects herbivore food plants *per se* is not well known. There is, however, some evidence from the sub-Arctic (reviewed in Cooper, 2014), and an experiment from our study area (Milner *et al.*, 2016) that the growth and reproduction of some plants can be severely affected by ice encasement, suggesting a delayed indirect effect on herbivores, as well as the direct effect that icing has on restricting access to forage in winter.

Warmer autumns: longer summers and shorter winters

After accounting for the effects of 'rain-on-snow', we found a positive effect of October degree-days on the subsequent April body mass. Most likely, this reflects a delay in the onset of winter snow cover and thus an extended period of unrestricted grazing. This could explain why a study of reindeer population growth in the neighbouring Adventdalen (Tyler *et al.*, 2008) found a positive effect of ablation, that is snow melt, in the last quarter of the year. Conditions favouring ablation, notably above-zero temperatures, are much more common in October than November/December.

In general, the effect of warmer autumn weather seems to have attracted little attention compared to the widely documented impact of warmer springs on phenology (Gallinat *et al.*, 2015). Over much of Europe, including boreal regions, remote-sensed NDVI measures indicate lengthening growing seasons, due to delays in the timing of senescence, as much as advances in spring 'green-up' (Garonna *et al.*, 2014). A recent study of mule deer in semi-arid Idaho found a twofold greater effect-size of autumn forage, compared to spring forage, on body mass at 6 months of age, which in turn influenced overwinter survival (Hurley *et al.*, 2014). However, for most study systems, including in the Arctic, estimates of both the quantity and quality of forage remaining at the end of summer, and thereby, potentially available to herbivores in winter, are currently not available.

The strength of density dependence

Density-dependent effects were most strongly revealed in the overwinter mass loss and the summer mass gain, measured over the first 14 years. In contrast, over the entire 21-year study, when the population more than doubled, density dependence was only detected in April body mass using the detrended population size, and not at all in October body mass.

The somewhat inconsistent detection of density dependence lends support to Haldane's (1956) argument that one might expect density independent factors to predominate at the edge of the species' range, where conditions are suboptimal. Our observations are thus confirmatory of the observed tension between strengthening density independence and weakening density dependence with increasing latitude, widely recognized in Fennoscandinavian rodents (Gilg *et al.*, 2009) and also found across reindeer/caribou populations (Post, 2005). Together with Peary caribou on the Canadian Arctic islands, Svalbard reindeer are at the northern edge of the species' range and may therefore be much more influenced by stochastic weather effects (Miller & Barry, 2009), than population density, *per se*. However, a model of Peary caribou population dynamics has demonstrated that, while extreme winter conditions may be a dominant factor in their population dynamics, without density dependence operating, populations would be much larger than observed (Tews *et al.*, 2007b).

On Svalbard density dependence has been described in earlier studies of population growth rate (Solberg *et al.*, 2001; Aanes *et al.*, 2002; Hansen *et al.*, 2011, 2013), and also in body mass over the first 18 years of our study (M Douhard, unpublished). The apparent recent absence of density dependence may be due to temporal covariation between population size and warmer summers (June–July temperature: $r = 0.707$, $P < 0.001$), with the implication that the higher productivity in the warmer summers raised the carrying capacity (Marino *et al.*, 2014). Unfortunately, we were not able to statistically separate out these confounding effects, but the increase in productivity could well account for the steady increase in the reindeer population size. A similar lack of density dependence has been witnessed in at least one expanding Arctic goose population (Morrissette *et al.*, 2010).

An alternative, yet not 'mutually exclusive' explanation is that, at high densities increased grazing pressure can lead to increased productivity of tundra vegetation, because the thickness of moss layer is reduced, thereby

increasing soil temperature (Van der Wal & Brooker, 2004), and enhancing soil mineralization (Aerts *et al.*, 2006) and nutrient turnover (Barber *et al.*, 2008). This, coupled with increased nutrient returns from faeces (Van der Wal *et al.*, 2004), stimulates greater growth of vascular plants. Consequently this may counteract an increased competition for food due to larger population size, and thus might obscure the expected density dependence (Bêty *et al.*, 2014).

Amplitude of seasonal cycle in body mass and demographic consequences

The trend for warmer summers and the resulting increase in plant biomass (Van der Wal & Stien, 2014) led to a steady increase in autumn body mass. In contrast, there has been no trend in late winter body mass. The expected increase in the incidence and/or magnitude of 'rain-on-snow' (Rennert *et al.*, 2009; Hansen *et al.*, 2011, 2014) may, however, be expected to induce low body masses more frequently, potentially increasing the amplitude of the annual body mass cycle. Surprisingly, none of the empirical literature we reviewed appears to have explored the possibility of changes in the amplitude of the annual cycle of body mass, explicitly in relation to climate warming. Most studies report body mass data in a single season and typically autumn. However, a study of semidomesticated reindeer in Finnmark, Norway (Bårdsen *et al.*, 2010), showed a temporal decline in spring adult body mass in relation to increasing density and winter weather, but no consistent trend in average autumn body mass. Although these reindeer were able to regain increasing amounts of mass in successive years, their reproductive rate declined as resources became limited.

While the likelihood and consequences of an increasing annual fluctuation in body mass have not been investigated explicitly, the potential net effects of warmer summers with higher primary productivity and more winters with 'rain-on-snow' on future population dynamics have been modelled for Peary caribou (Tews *et al.*, 2007b). This simulation suggests significantly lower population die-offs during extreme winters, if summer forage biomass increases by 50%, as projected within the next 100 years. However, if over the same period, forage accessibility in poor winters, decreases by more than 30%, because 'rain-on-snow' increases in magnitude or frequency, caribou may experience negative net effects of climate (Tews *et al.*, 2007b).

Our results suggest that, while the tundra in some parts of the Arctic may support larger populations of large herbivores, their numbers may be much more variable because of the greater variability in their vital rates, driven by the stochastic effects of 'icing' on winter food availability, and consequently on late winter body mass. As such, the demographic consequences of climate change may differ in Rangifer populations from that already witnessed in cyclic small Arctic herbivores (invertebrates, grouse and rodents), where the trend is towards collapsing cycles (Ims *et al.*, 2008).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Correlation coefficients between body mass and weather variables.

Table S2. Comparison of linear mixed models using environmental covariates to explain variation on October body mass.

Table S3. Comparison of linear mixed models using environmental covariates to explain variation on April body mass.

Table S4. The most parsimonious model for April body mass, giving the estimates of environmental covariates for all age classes.

Appendix S1. 'Rain-on-Snow' indices in the models of April body mass.

Appendix S2. The ablation index and its relationship with October degree-days.

Figure S1. Our simple winter 'rain-on-snow' index plotted against precipitation recorded as rain and sleet (Nov–Mar, 1994/5 – 2003/4).

Figure S2. The ablation index plotted against $\log_e$ October degree-days.