



PRIMARY RESEARCH ARTICLE

The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer

Leif Egil Loe^{1,2} | Glen E. Liston³ | Gabriel Pigeon¹ | Kristin Barker² | Nir Horvitz² | Audun Stien⁴ | Mads Forchhammer⁵ | Wayne Marcus Getz^{2,6} | Robert Justin Irvine^{7,8} | Aline Lee⁹ | Lars K. Movik¹ | Atle Myrsterud¹⁰ | Åshild Ø. Pedersen¹¹ | Adele K. Reinking³ | Erik Ropstad¹² | Liv Monica Trondrud¹ | Torkild Tveraa⁴ | Vebjørn Veiberg¹³ | Brage B. Hansen⁹ | Steve D. Albon⁸

¹Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Aas, Norway

²Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA, USA

³Cooperative Institute for Research in the Atmosphere, Colorado State University, Fort Collins, CO, USA

⁴Department of Arctic and Marine Biology, The Arctic University of Norway, Tromsø, Norway

⁵The University Centre in Svalbard, Longyearbyen, Norway

⁶School of Mathematical Sciences, University of KwaZulu-Natal, Durban, South Africa

⁷Frankfurt Zoological Society, Addis Ababa, Ethiopia

⁸The James Hutton Institute, Aberdeen, UK

⁹Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

¹⁰Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Blindern, Oslo, Norway

¹¹Norwegian Polar Institute, Fram Centre, Tromsø, Norway

¹²Faculty of Veterinary Science, Norwegian University of Life Sciences, Oslo, Norway

¹³Norwegian Institute for Nature Research, Trondheim, Norway

Correspondence

Leif Egil Loe, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, NO-1432 Aas, Norway.
Email: leif.egil.loe@nmbu.no

Funding information

Norges Forskningsråd, Grant/Award Number: 267613; Climate-ecological Observatory for Arctic Tundra; US-Norway Fulbright Foundation for Educational Exchange; Svalbard Environmental Fund, Grant/Award Number: 18/9

Abstract

Arctic ungulates are experiencing the most rapid climate warming on Earth. While concerns have been raised that more frequent icing events may cause die-offs, and earlier springs may generate a trophic mismatch in phenology, the effects of warming autumns have been largely neglected. We used 25 years of individual-based data from a growing population of wild Svalbard reindeer, to test how warmer autumns enhance population growth. Delayed plant senescence had no effect, but a six-week delay in snow-onset (the observed data range) was estimated to increase late winter body mass by 10%. Because average late winter body mass explains 90% of the variation in population growth rates, such a delay in winter-onset would enable a population growth of $r = 0.20$, sufficient to counteract all but the most extreme icing events. This study provides novel mechanistic insights into the consequences of climate change for Arctic herbivores, highlighting the positive impact of warming autumns on population viability, offsetting the impacts of harsher winters. Thus, the future for Arctic herbivores facing climate change may be brighter than the prevailing view.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd

KEYWORDS

body mass, climate change, fitness, GPS, movement ecology, plant phenology, *Rangifer*, snow, space use, ungulates

1 | INTRODUCTION

Climate change affects ecosystems and animal populations worldwide via altered temperature and precipitation regimes (Scheffers et al., 2016), causing changes in the timing, duration and characteristics of seasons. Phenological changes due to climate warming, in particular the earlier onset of spring, have received much attention because of a high incidence of asynchrony across trophic levels (Kharouba et al., 2018), where mismatches may have population and evolutionary consequences (Visser & Gienapp, 2019), and potentially disrupt the function, persistence and resilience of ecosystems (Thackeray et al., 2010). In contrast, the effects of delays in the onset of autumn remain understudied (Gallinat et al., 2015), despite their potential importance for population dynamics in a wide range of species (mammalian herbivores: Hurley et al., 2014; insect herbivores: Ekholm et al., 2019; birds: Therrien et al., 2017; bears: Hertel et al., 2018) and ecosystem processes (Piao et al., 2019).

The Arctic is the most rapidly warming biome on the planet (IPCC, 2019; Serreze & Barry, 2011). Summers have become longer, partly driven by the reduction in sea ice cover, which has increased the heat flux from the ocean to atmosphere in autumn and early winter (Vihma, 2014). In recent decades, sea ice formation in the autumn has been delayed more than spring break-up (Bhatt et al., 2017). Despite the changing seasons, the role of autumn warming has received surprisingly little attention given the rapid lengthening of an extremely short growing season (Ernakovich et al., 2014), and shortening of a correspondingly long snow-covered season.

Delayed autumns are likely to enhance the nutritional landscape of herbivores (Hurley et al., 2014; Parker et al., 2009), which may explain why warmer autumns are associated with higher body mass of Svalbard reindeer *Rangifer tarandus platyrhynchus* (Albon et al., 2017). Yet, the focus, both in the scientific literature and in media, has been on the negative effects of winter warming in the Arctic, because conditions are often harsher for resident herbivores due to more extreme 'rain-on-snow' (ROS) events which may encase forage in ice (Putkonen & Roe, 2003; Rennert et al., 2009). These icing events can cause starvation and result in catastrophic die-offs (Gunn, 1995; Hansen et al., 2011; Kohler & Aanes, 2004) and, more generally, ROS reduces population growth rates (Hansen et al., 2013, 2019), through its impact on late winter body mass (Albon et al., 2017). Concerns have even been raised that increased winter severity under current and future global warming can pose a threat to the long-term viability of caribou and reindeer (Mallory & Boyce, 2018; Vors & Boyce, 2009).

Thus, an important but under-studied question is whether warmer autumns, leading to shorter winters, can counteract the effect of harsher winters in the Arctic. Furthermore, the causal mechanism driving the strong association between autumn weather and body mass development remains unknown (Albon et al., 2017). One

possible explanation is that higher autumn temperatures delay the senescence of plants allowing herbivores to access higher-quality forage later into the year (Marchand et al., 2004). Alternatively, delayed onset of snow may allow a higher intake of forage (i.e. more days of unrestricted forage access), regardless of the nutritional quality of those food resources. Either way, given the absence of predation, Svalbard reindeer are very likely regulated 'bottom-up', through their interaction with their food supply.

In this study, we used late winter body mass data of known-aged female Svalbard reindeer from 1995 to 2019, to test the two hypotheses posited above to explain the positive relationship between higher autumn temperatures and increased late winter body mass. Specifically, we predicted that variation in late winter body mass was explained by an index of plant senescence (derived from the Enhanced Vegetation Index—EVI: Huete et al., 2002), if the relationship between autumn temperature and body mass was driven by prolonged access to high-quality forage (Livensperger et al., 2019). Alternatively, or in addition, late winter body mass could be explained by onset of snow, if the relationship was driven by availability of forage later into the autumn, rather than strictly by forage quality (i.e. a shortening of winter). We extracted environmental information from the habitat used by a subset of GPS individuals, based on detailed location data (hereafter referred to as tracks), to test the relative importance of shared environmental effects (weather) and conditions on individual tracks. Upon identifying snow-onset as an important autumn variable, we analysed the relative importance of snow-onset and ROS for the full 25-year dataset to evaluate if later autumns counteract the effect of more frequent icy winters, which could explain the observed population increase. By evaluating the effects of changes in autumn snow and forage conditions on Arctic ungulates, our study contributes to our understanding of the impact of continued climate warming on these keystone species.

2 | MATERIALS AND METHODS

2.1 | Study area, vegetation and climate

The study area is located in Nordenskiöld Land, Svalbard (78°N, 15°E; 150 km²). Although the mountains rise above 1000 m, there is little vegetation above 250 m, vascular plants mostly grow interspersed in moss carpets and except in the valley bottoms do not generally reach >35% ground cover (Van der Wal & Stien, 2014). The plant growing season typically lasts from the start of June to mid-August, but with large year-to-year variation caused by variation in temperature (Vickers et al., 2016).

Mean daily July temperature was 6.7 °C ± 0.9 SE in the first two decades of the study, and then increased (Albon et al., 2017).

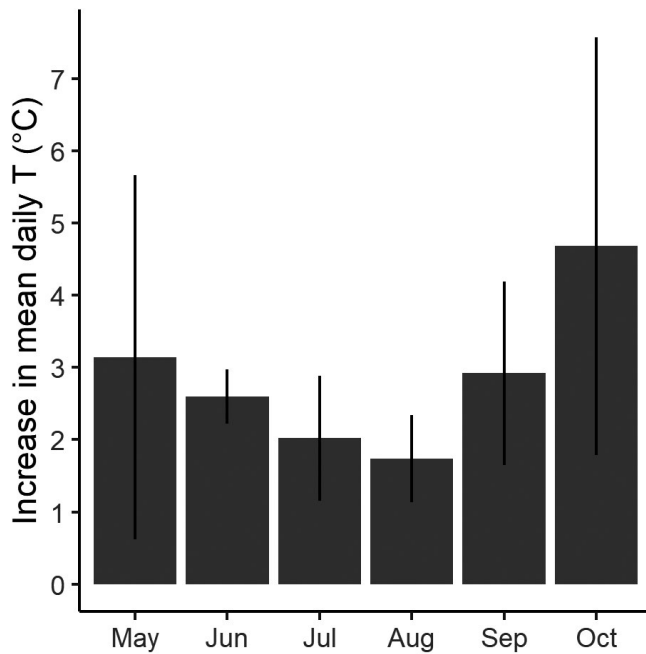


FIGURE 1 2010–2019 increase in monthly mean temperature above climate standard period 1961–1990. Temperatures are measured at Svalbard airport, 20 km from the study area

Over the same period (1994–2014), mean daily January temperature was $-10.7^{\circ}\text{C} \pm 5.1$ SE, and, also increased significantly (Albon et al., 2017). Snow typically covers most of the ground from October to June, with some windblown ridges remaining partially snow-free year-round (Hansen et al., 2010). The onset of winter snow fall has been delayed more than spring-melt has advanced (van Pelt et al., 2016): changes associated with the greater warming in autumn than spring, or summer (Figure 1).

2.2 | Reindeer

The non-migratory Svalbard reindeer live in small groups often consisting of two to five individuals (Loe et al., 2006) in an almost predator-free environment (only seven documented kills made by polar bears [*Ursus maritimus*] including two in our study area; Derocher et al., 2000). Movement decisions are likely made at the individual level and driven primarily by the search for food (Loe et al., 2016), although with greater snowmobile traffic associated with increasing winter tourism, there could be locally increased disturbance from some feeding sites (Reimers et al., 2003; Tyler, 1991).

Female reindeer were initially captured and marked as calves in April (Omsjø et al., 2009), hereafter referred to as 'late winter'. They were subsequently recaptured and weighed in late winter throughout their lives (Figure 2a). Between 1995 and 2019, 2875 captures were made of 839 known age individuals. Since 2009, a subset of 65 adults (3–13 years of age, mean 7.3) have been tagged with GPS-collars (Vectronic Aerospace), giving positions in the landscape at 2- or 8-h intervals (total 152 reindeer-years). The capturing followed ethical requirements in Norway and was approved by the

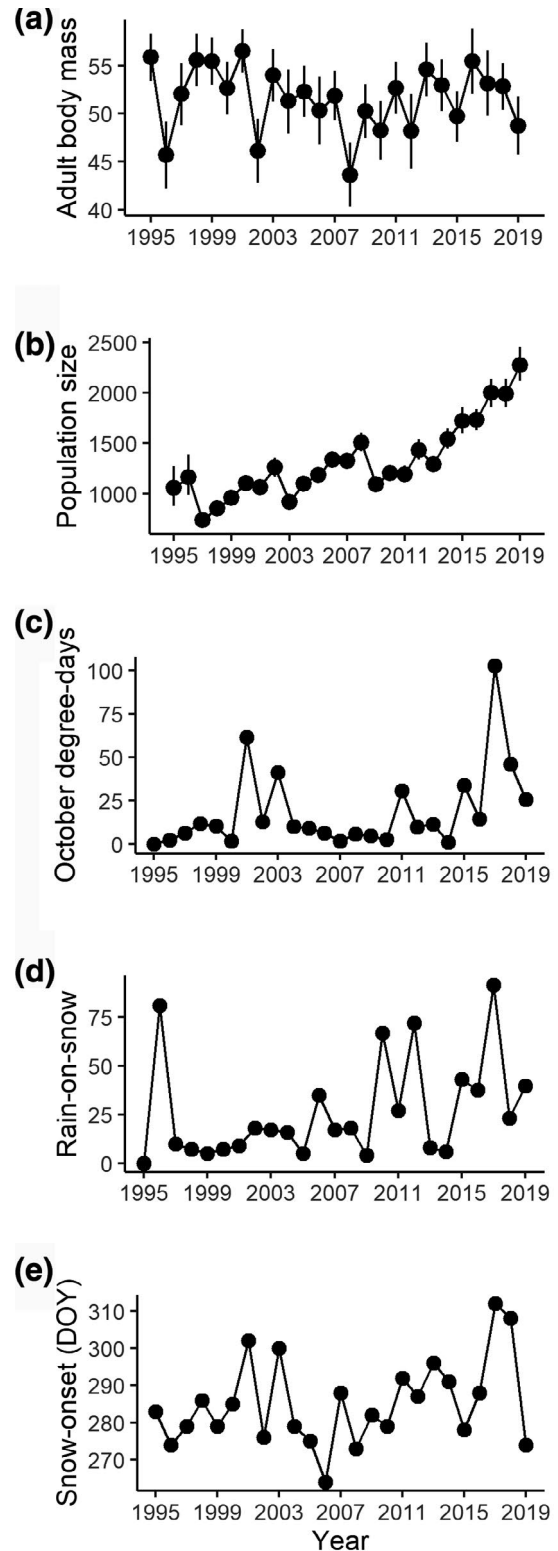


FIGURE 2 Time series of (a) late winter body mass of Svalbard reindeer in the Colesdalen-Semmeldalen-Reindalen study area (b) population size estimated by capture-recapture methods, (c) October degree-days at Svalbard airport, (d) amount of rain-on-snow (mm) falling from November through March, and (e) day of year of snow-onset date in autumn. Note that the year provided on the x-axis are aligned according to impact on reindeer April mass in year t . Autumn effects are from year $t - 1$ and ROS from November $t - 1$ through March year t

Norwegian Food Safety Authority (permit number 17/237024) and the Governor of Svalbard (permit number 16/01632-9).

Reindeer population size was estimated using capture–mark–recapture methods from both the April capture and count data from a survey conducted over c. 10 days in late July/early August each year (Lee et al., 2015). The population estimate includes females and calves of both sexes. During the 25-year study, the population has increased markedly varying from a low of 768 in summer 1996 to a high of 2266 in summer 2018 (Figure 2b). Although some animals are shot each year in Colesdalen and Reindalen by local hunters (mean = 30 females and calves per year), this is too few to substantially affect the population growth.

2.3 | Environmental data

We extracted daily temperature and precipitation from a nearby (20 km) weather station (Svalbard airport; <http://www.eklima.met.no>). Following Albon et al. (2017), we calculated annual measures of October degree-days (sum of all positive daily mean temperatures; Figure 2c) and ROS (defined as the sum of precipitation in mm that fell on days with mean air temperature above 0°C; Figure 2d) from November through March. We utilized a spatially distributed snow-evolution modelling system, SnowModel (Liston & Elder, 2006), to simulate snow depth (m) and snow density (kg/m^3) within grid increments of 100×100 m at daily intervals. In situ snow depth and density were extracted for all reindeer GPS-locations, ensuring matching of reindeer use and snow characteristics in space and time (i.e. along the track). For each individual's autumn track, we (1) calculated the snow-water-equivalent (SWE) depth (mm; $\text{SWE} = \text{snow depth} \times \text{snow density} / \text{water density}$, and converted that from m to mm); (2) identified the day-of-year (DOY; 1–365 or 366 for leap years) when the SWE exceeded 15 mm for the first time in autumn (with typical snow densities, this equates to snow approximately 5 cm deep); and (3) defined this DOY to be the 'snow-onset' date (Figure 2e). The threshold value of 15 mm was selected because the resulting snow-onset dates centred around mid-October (median: 19 October, 95% quantiles 22 Sep–7 Nov), thus matching the period of the previously reported October degree-day effect (Albon et al., 2017).

Ground ice thickness was measured at 128 fixed locations once, each April between 2010 and 2019. Continuous spatial ice thickness maps were developed by creating nearest-neighbour polygons (Hijmans et al., 2017). Exploration of ground temperature data substantiates ground ice developing in January and early February in most years; ground ice thickness established during this time remains consistent through March and April (Loe et al., 2016). Therefore, we felt that our application of April ice measurements to previous time periods was appropriate. As a measure of individual variation in exposure to ground ice, we extracted estimated ground ice thickness on individual tracks from February 1st through March 31 to capture the typical time period during which animals are exposed to this phenomenon.

Finally, to represent plant senescence, we used the autumn inflection point for the annual EVI curve (the point where the function

changes from being convex to concave) following the protocol developed by Beck et al. (2006; the point A in their figure 3). Across all years, the median date for the autumn inflection point was 21st September (95% quantiles 7 Sep–7 Oct).

2.4 | Statistical analyses

We conducted all statistical analyses using R software version 3.6.2 (R Core Team, 2019). We first focussed on the subset of GPS-animals, because it enabled detailed assessment on the effect of on-track environment, and also, to tease apart between and within-year effects of the environment on late winter body mass. Upon finding evidence for strong between-year effects of autumn and winter conditions in step 1, we tested the relative importance of autumn and winter effects on body mass for all marked adult females collected 1995–2019.

2.4.1 | Models using the subset of GPS-individuals in years 2010–2019

Prior to model selection, we adjusted the response variable, late winter body mass of GPS-tagged females, by removing the effects of cost-of-reproduction (i.e. calf at heel the year before; two-level factor variable), age (as a spline function to capture growth and senescence of individuals) and capture date (linear negative effect) in a generalized additive model (Wood, 2006). In the process of removing these three effects and generating an adjusted mass value, we took advantage of the larger dataset of all adult female body masses (including non-GPS-tagged individuals), because these well-known effects are more robustly estimated for a large dataset spanning more years and individuals. Effect sizes of these three covariates are presented as part of the global model using all individuals (see description below and Table 2).

Using adjusted mass of GPS-tagged females as the response variable, we subjected a limited set of candidate variables (see Table S1 for a correlation matrix) to model selection and used the corrected Akaike information criterion (AICc) to rank models (Burnham & Anderson, 2002). We tested a combination of population-level variables (population size, ROS and October degree-days) and individual-level variables extracted along GPS-tracks of individual reindeer (plant senescence, autumn snow-onset and ground ice thickness). Note that population size and the autumn covariates (plant senescence date, snow-onset and October degree-days) reflect values occurring immediately before the effect of winter covariates (ROS and ground ice) and the response variable, late winter body mass, because we are evaluating the influence of autumn in year $t - 1$, on subsequent body mass in year t . ROS, ground ice thickness, October degree-days and snow-onset were all log+1 transformed to reduce heteroscedasticity, before they were scaled (to zero mean and unit variance) to facilitate comparison of effect sizes. To account for repeated observations across years, we included individual as a random

factor. All models were fitted using the function 'lmer' in the lme4 R package (Bates et al., 2015) and predicted confidence intervals were estimated using 'predictInterval' in the 'merTools' R package (Knowles & Frederick, 2019). Correspondence between predicted and observed fit was plotted for the final model (Figure S1).

Because the selected model of late winter body mass variation of GPS-tagged females included only variables with individual-level information (snow-onset and ground ice thickness), we could tease apart between-year vs. within-year variation in a subsequent step. We computed annual means, and individual deviations from annual means, for snow-onset and ground ice thickness. We then tested their relative contribution in explaining variation in body mass in a mixed model using year as random effect, following van de Pol and Wright (2009).

2.4.2 | Models using all individuals in years 1995–2019

Finally, we tested the effect of snow-onset on late winter body mass for the extended dataset of all marked animals dating back to 1995, using an additive mixed-effects model fitted with the function 'gamm4', using unadjusted body mass as response variable and individual and year as random intercepts. Predictor variables consisted of cost-of-reproduction, age, capture date and ROS (as specified above). Additionally, the effects of October degree-days and snow-onset were fitted in two competing models and the most parsimonious model selected based on AIC (Burnham & Anderson, 2002). A main aim was to compare the relative effects of later snow-onset and harsher winters (ROS) on body mass. We based the comparison on the scaled effect sizes which estimate the change in one mass unit when increasing the predictor variable by one SD unit. To obtain estimates of snow-onset from years pre-dating GPS-tagging (1995–2009), we pooled all GPS-data sampled between 15 September and 15 November from all available years (2010–2019) and all marked reindeer. Our assumption was that this is a better representation of locations likely to be used in autumn, in years where GPS-data were not available, instead of extracting snow from the entire study area that would also include unused areas. After extracting the snow-onset date on all these locations we computed the annual means, which was used as the estimate of annual snow-onset.

3 | RESULTS

The 10-year subset of GPS-tagged individuals enabled the extraction of plant phenology, snow-onset and empirically measured ground ice on the maximum level of detail (individual tracks) and was used to test the plant senescence versus snow-onset hypothesis. The positive effect of October degree-days, and negative effects of ROS and population density (Albon et al., 2017; Hansen et al., 2019) on late winter body mass was significant also for this 10-year subset (M1; Table 1). Variation in the apparent date of plant senescence did

TABLE 1 Model selection of candidate predictor variables explaining variation in late winter body mass (April) of female GPS-tagged Svalbard reindeer. Body mass was adjusted for the effect of age, cost-of-reproduction and capture-date prior to analyses. An individual effect was included as a random factor in all models (SD = 2.3 in the most parsimonious model). All variables except plant senescence were log-transformed. All variables (including those log-transformed) were subsequently scaled to zero mean and unit variance. Bold parameter estimates (with SE in brackets) are significant at $p < 0.05$ level

Model	Predictions	Population-level variables			Individual-level variables			AICc	ΔAICc
		October degree-days	ROS	Population density	Plant senescence	Snow-onset	Ground ice		
M1	Original ROS and October degree-days model (Albon et al., 2017) plus density dependence (Hansen et al., 2019)	1.40 (0.44)	-2.01 (0.38)	-1.21 (0.46)			899.9	3.6	
M2	October degree-days effect better represented by timing of on-track plant senescence		-1.36 (0.37)	-0.59 (0.42)	0.40 (0.38)		909.1	12.8	
M3	October degree-days effect better represented by snow-onset		-1.45 (0.36)	-0.68 (0.41)		1.16 (0.37)	900.1	3.8	
M4	October degree-days effect better represented by snow-onset and ROS effect better represented by on-track ground ice thickness			-0.65 (0.41)		1.26 (0.36)	896.3	0	

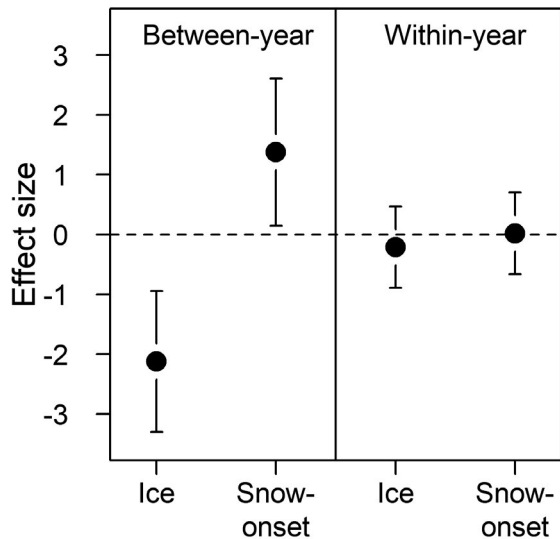


FIGURE 3 Separating the effects of ground ice and snow-onset into between-year and within-year effects on variation in late winter body mass of 65 GPS-marked female Svalbard reindeer from 2009 to 2019, by using a mixed effects variance partitioning approach. Error bars are 95% confidence limits

TABLE 2 Variation in late winter body mass (kg) of female Svalbard reindeer captured between 1995 and 2019 (including non-GPS-tagged individuals; $n = 2875$) as a function of age, capture date, cost of reproduction, snow-onset and rain-on-snow (ROS). Age was fitted using a spline function and individual and year was included as random intercepts. Snow-onset and ROS were scaled after log-transformation to a mean of zero and unit variance allowing direct comparison of the effects of warmer autumns with delayed snow-onset versus harsher winters with higher ROS. Adjusted R^2 was 0.86

Parametric coefficients	Estimate	SE	T	p
Intercept	48.5	0.871	55.65	<0.001
Capture date (days)	-0.096	0.0150	-6.42	<0.001
Calf last year (Yes vs. No)	-3.55	0.246	-14.41	<0.001
Calf last year (Unknown vs. No)	-1.76	0.20	-8.98	<0.001
Snow-onset (log-transformed and scaled)	1.92	0.51	3.75	<0.001
ROS (mm; log-transformed and scaled)	-1.49	0.53	-2.83	0.005
Population size (log-transformed and scaled)	-0.614	0.574	-1.07	0.285
Random effects (intercepts)		Variance	SD	
Individual		6.89	2.62	
Year		5.87	2.42	
Approximate significance of smooth terms		edf	F	p
Age (years)		8.48	2411	<0.001

not improve model fit, neither when fitted additionally, nor when replacing October degree-days (M2; Table 1). However, replacing October degree-days and ROS with on-track measures of snow-onset and ground ice thickness resulted in a more parsimonious model ($\Delta\text{AICc} = -3.6$; M4; Table 1), in support of the snow-onset hypothesis. Because both snow-onset and ground ice are spatially explicit variables and show individual variation within year, we teased apart the relative effect sizes of between-year and within-year (individual tracks) variation on body mass. For both ground ice and snow-onset, the effect on late winter body mass occurred mainly through between-year variation, with effect sizes of within-year variation close to zero (Figure 3), implying that the positive effect of a delayed winter and negative effect of an icy winter is shared among all individuals in a given year.

Upon identifying snow-onset as the key autumn variable in the subset of GPS-individuals, we tested this effect for the full dataset spanning 25 years. Females had higher body mass in years following later snow-onset (scaled effect size = 1.92; SE = 0.51) and replacing the effect of October degree-days (see Albon et al., 2017) with snow-onset resulted in a more parsimonious model of late winter body mass ($\Delta\text{AIC} = -4.8$). For this full dataset, the positive effect of late snow-onset more than offset the negative effect of ROS on mass (scaled effect size = -1.49, SE = 0.53; see Table 2 for the full model). A 6-week delay in snow-onset, that is, the approximate data range, enhanced late winter body mass by around 5 kg (Figure 4).

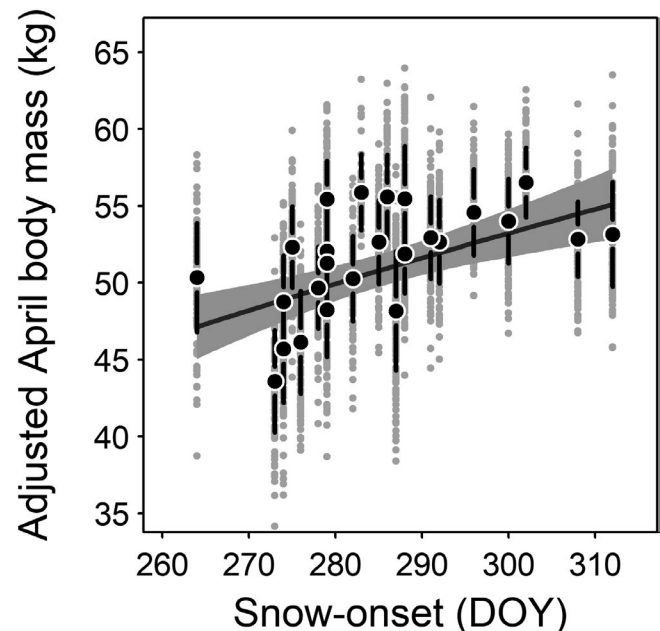


FIGURE 4 Late winter body mass (April) of adult female Svalbard reindeer (adjusted for variation in age, cost-of-reproduction, capture-date and rain-on-snow) as a function of snow-onset date (in day of year; DOY) in the years 1995–2019. The solid black line represents the predicted regression line and the polygon represents the 95 CI. Grey dots are individual body mass values ($n = 2875$), black large points are annual means and black bars are ± 1 SD of the mean

4 | DISCUSSION

An extended snow-free season is a key element of climate change in many temperate and Arctic ecosystems (Piao et al., 2019). Combining rare long-term life-history data of an Arctic herbivore with a spatially explicit snow modelling approach, we demonstrated that the positive effect of delayed snow on late winter body mass, to a large extent counteracts the negative effects of harsher, icy winters and higher population densities. Our study enhances the mechanistic understanding of the ecological impacts of climate change (Morales et al., 2010; Tomkiewicz et al., 2010).

In contrast to many other *Rangifer* populations (Mallory & Boyce, 2018; Vors & Boyce, 2009), Svalbard reindeer are increasing throughout the archipelago (Le Moullec et al., 2019). However, in contrast to many *Rangifer* populations, especially in North America, there is virtually no predation because there are no wolves on Svalbard, and polar bear attacks are rare (Derocher et al., 2000). Also, hunting accounts for a mere 2% reduction in numbers. Thus, the most likely explanation for the population growth is that a delay in snow-onset provides a mechanism by which a warmer climate could enhance the plane of nutrition. Predicted late winter body mass increased by 5 kg (10%) over the observed 6-week variation in snow-onset, an effect size which would raise the population growth rate (r) by 0.20 (figure 6 in Albon et al., 2017). Our finding aligns with research in other ecosystems and suggests that the length of winter is a key driver of fitness in ungulates. For instance, Grøtan et al. (2005) found that population growth of roe deer (*Capreolus capreolus*) in Norway was higher in years with low snow depth in early winter, while Hurley et al. (2014) found that body mass of mule deer (*Odocoileus hemionus*) fawns in Idaho, USA was more strongly influenced by autumn foraging conditions than by spring foraging conditions. Our study suggests that the quantity of available forage that remains accessible later in the season plays a key role in allowing ungulates to accrue additional body mass prior to the forage-limited winter months.

Mechanistically, the effect of snow-onset on herbivore fitness has been explained by a range of factors. In prey species, off-season snow may reduce survival because of poorer camouflage (snowshoe hare *Lepus americanus*; Zimova et al., 2016) or reduced ability to escape predators in deep snow (Lendrum et al., 2018; Nilsen et al., 2009). For the predator-free environment of Svalbard reindeer, reduced late winter body mass could either result from increased energy expenditure or from reductions in energy intake. The added energy cost of moving in up to 30 cm of snow (the highest mean SnowModel snow depth estimate on any October GPS-track) is expected to result in only a marginal increase in locomotion cost in *Rangifer* spp (Fancy & White, 1987). Instead, the positive effect of delayed snow-onset was most likely associated with higher energy intake afforded by extended periods of snow-free grazing, which increased late winter body mass in Svalbard reindeer.

The between-year variation in snow-onset and ground ice thickness explained much more of the variation in body mass than did the conditions experienced on individual tracks (within-year

variation). First, snow accumulation ultimately results from synoptic-scale weather conditions (Sturm et al., 1995), so while snow distributions and properties across our study area varied in space and time, the relative annual characteristics (e.g. snow-rich or snow-poor year, early or late snow-onset) were widespread, meaning that animals experienced comparable winter conditions in a given year. In simple terms, it was probably impossible to entirely escape from an early winter within our relatively small study area of 150 km². The annual variation in snow-onset was also very large, spanning 6 weeks over our 25-year study period. Second, behavioural responses to local spatial variation in early snow accumulation (i.e. moving from areas with early to areas with late snow accumulation) may be shared by most individuals, further diminishing individual variation. Previous research has demonstrated a shared rapid behavioural response to ROS-events in an earlier set of GPS-tagged individuals that were included in this study (Loe et al., 2016). Most population studies do not use GPS-collars and must rely on environmental data at the study area level and not from individual tracks. Our study suggests that, as with other meteorological measurements, environmental data at the study area level may often suffice as explanatory variables of individual fitness.

Remotely sensed vegetation indices have been found to correlate well with ground-truth measures of green-up and peak vegetation productivity (Pettorelli et al., 2011), including in polar environments (Karlsen et al., 2018; Santin-Janin et al., 2009). However, to our knowledge, no one has explicitly investigated remotely sensed vegetation senescence (browning) in the Arctic. Conditional that our EVI-based measurements provided a reliable metric, annual variation in plant senescence did not affect late winter body mass in the period EVI was available (autumn 2000 onwards). Autumn warming effects on plant senescence are highly complex. In temperate trees, it has recently been shown that the effect is nonlinear and that night-time warming delayed plant senescence while daytime warming advanced senescence by causing drought (Chen et al., 2020). Also, it is possible that autumn warming results in more efficient nutrient resorption in plants (Estiarte & Penuelas, 2015), retarding the decline in quality of the forage remaining available on winter pastures. Furthermore, timing of autumn phenology is in some cases positively correlated with spring phenology (Keenan & Richardson, 2015; Liu et al., 2016), but in many other cases, ambiguous (Menzel et al., 2006). For the 'bottom-up' regulated Svalbard reindeer, it is likely that large changes in plant phenology will ultimately impact on body mass and population dynamics, but the directionality of the putative impact requires research on the link between warming and phenology of key forage plants. More generally, our findings support the importance of ecologists studying the impacts of climate change in the autumn window (Gallinat et al., 2015).

In conclusion, we have demonstrated that warmer autumns compensate for winters being warmer and icier. Although most North-American caribou populations are sampled at multi-year intervals, hampering detailed studies of population dynamics, it is likely that

many of the apparent long-term population declines attributed to climate change are caused, at least partly, by factors related to change in human land use (Uboni et al., 2016), rather than climate change per se. In addition to the short-term gain of higher plant productivity, we anticipate two other positive warming effects. First, vegetation communities are predicted to change from moss-dominated, to graminoid-dominated swards, where the reduction in moss layer reinforces soil warming and mineralization, to further increase productivity (Ravolainen et al., 2020). This process is driven partly by positive feedback mechanisms from the greater density of reindeer (Van der Wal & Brooker, 2004). Second, a positive effect of continued winter warming may arise when reaching the temperature threshold where ROS results in exposure of pastures, rather than ground ice formation (Tyler, 2010). Thus, the future for Arctic herbivores facing climate change may be brighter than the prevailing view in the scientific literature (Mallory & Boyce, 2018; Vors & Boyce, 2009) and media.

ACKNOWLEDGEMENTS

This work was supported by the Norwegian Research Council (grant number 267613), Svalbard Environmental Fund (grant 18/19), US-Norway Fulbright Foundation for Educational Exchange and the Climate-ecological Observatory for Arctic Tundra (COAT; www.coat.no). We thank the Governor of Svalbard for permission to undertake the research and technical staff at the University Centre in Svalbard (UNIS) for supporting the field campaigns. Thanks to numerous field assistants for help during field work, and to the Norwegian Polar Institute Svalbard for the use of the cabin 'Tarandus' during the field season, and to two anonymous referees that improved an earlier version of the manuscript.

AUTHOR CONTRIBUTIONS

Leif Egil Loe conceived the idea. Leif Egil Loe, Kristin Barker, Steve D. Albon, Brage B. Hansen and Lars Kvam Movik wrote the first version of the manuscript. Steve D. Albon, Robert Justin Irvine, Vebjørn Veiberg, Audun Stien, Leif Egil Loe, Erik Ropstad, Monica Trondrud Gabriel Pigeon, Åshild Ø. Pedersen, Lars Kvam Movik, Mads Forchhammer and Brage B. Hansen collected the data. Glen E. Liston did the snow modelling. Torkild Tveraa and Nir Horvitz extracted the EVI data. Gabriel Pigeon, Nir Horvitz and Audun Stien assisted Leif Egil Loe with statistical analyses. All authors commented on the manuscript before submission.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request and permission of the third parties (i.e. the data holders for the long-term Svalbard reindeer project; Steve D. Albon, Erik Ropstad, Robert Justin Irvine, Vebjørn Veiberg and Audun Stien).

ORCID

Leif Egil Loe  <https://orcid.org/0000-0003-4804-2253>

Brage B. Hansen  <https://orcid.org/0000-0001-8763-4361>

REFERENCES

- Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., Veiberg, V., Wal, R., Bjørkvoll, E. M., Duff, E. I., Hansen, B. B., Lee, A. M., Tveraa, T., & Stien, A. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, 23(4), 1374–1389. <https://doi.org/10.1111/gcb.13435>
- Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Beck, P. S. A., Atzberger, C., Høgda, K. A., Johansen, B., & Skidmore, A. K. (2006). Improved monitoring of vegetation dynamics at very high latitudes: A new method using MODIS NDVI. *Remote Sensing of Environment*, 100(3), 321–334. <https://doi.org/10.1016/j.rse.2005.10.021>
- Bhatt, U. S., Walker, D. A., Reynolds, M. K., Bieniek, P. A., Epstein, H. E., Comiso, J. C., Pinzon, J. E., Tucker, C. J., Steele, M., Ermold, W., & Zhang, J. (2017). Changing seasonality of panarctic tundra vegetation in relationship to climatic variables. *Environmental Research Letters*, 12(5), 17. <https://doi.org/10.1088/1748-9326/aa6b0b>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and inference: A practical information-theoretic approach* (2nd ed.). Springer.
- Chen, L., Hänninen, H., Rossi, S., Smith, N. G., Pau, S., Liu, Z., Feng, G., Gao, J., & Liu, J. (2020). Leaf senescence exhibits stronger climatic responses during warm than during cold autumns. *Nature Climate Change*, 10(8), 777–780. <https://doi.org/10.1038/s41558-020-0820-2>
- Derocher, A. E., Wiik, O., & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, 23(10), 675–678. <https://doi.org/10.1007/s003000000138>
- Ekholm, A., Tack, A. J. M., Bolmgren, K., & Roslin, T. (2019). The forgotten season: The impact of autumn phenology on a specialist insect herbivore community on oak. *Ecological Entomology*, 44(3), 425–435. <https://doi.org/10.1111/een.12719>
- Ernakovich, J. G., Hopping, K. A., Berdanier, A. B., Simpson, R. T., Kachergis, E. J., Steltzer, H., & Wallenstein, M. D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, 20(10), 3256–3269. <https://doi.org/10.1111/gcb.12568>
- Estiarte, M., & Penuelas, J. (2015). Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: Effects on nutrient proficiency. *Global Change Biology*, 21(3), 1005–1017. <https://doi.org/10.1111/gcb.12804>
- Fancy, S. G., & White, R. G. (1987). Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*, 65(1), 122–128. <https://doi.org/10.1139/z87-018>
- Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30(3), 169–176. <https://doi.org/10.1016/j.tree.2015.01.004>
- Grøtan, V., Sæther, B.-E., Engen, S., Solberg, E. J., Linnell, J. D. C., Andersen, R., Brøseth, H., & Lund, E. (2005). Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. *Ecology*, 86(6), 1472–1482. <https://doi.org/10.1890/04-1502>
- Gunn, A. (1995). Responses of arctic ungulates to climatic change. In D. L. Peterson & D. R. Johnson (Eds.), *Human ecology and climate change* (pp. 90–104). Taylor and Francis.
- Hansen, B. B., Aanes, R., Herfindal, I., Kohler, J., & Sæther, B.-E. (2011). Climate, icing, and wild arctic reindeer: Past relationships and future prospects. *Ecology*, 92(10), 1917–1923. <https://doi.org/10.1890/11-0095.1>
- Hansen, B. B., Aanes, R., & Sæther, B. E. (2010). Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Canadian Journal of Zoology*, 88(2), 170–177. <https://doi.org/10.1139/z09-130>

- Hansen, B. B., Gamelon, M., Albon, S. D., Lee, A. M., Stien, A., Irvine, R. J., Sæther, B.-E., Loe, L. E., Ropstad, E., Veiberg, V., & Grøtan, V. (2019). More frequent extreme climate events stabilize reindeer population dynamics. *Nature Communications*, *10*. <https://doi.org/10.1038/s41467-019-09332-5>
- Hansen, B. B., Grotan, V., Aanes, R., Saether, B.-E., Stien, A., Fuglei, E., Ims, R. A., Yoccoz, N. G., & Pedersen, A. O. (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science*, *339*(6117), 313–315. <https://doi.org/10.1126/science.1226766>
- Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2018). Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos*, *127*(2), 197–207. <https://doi.org/10.1111/oik.04515>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). *dismo: Species distribution modeling*. R package version 1.1-4. Retrieved from <https://CRAN.R-project.org/package=dismo>
- Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, *83*(1–2), 195–213. [https://doi.org/10.1016/s0034-4257\(02\)00096-2](https://doi.org/10.1016/s0034-4257(02)00096-2)
- Hurley, M. A., Hebblewhite, M., Gaillard, J.-M., Dray, S., Taylor, K. A., Smith, W. K., Zager, P., & Bonenfant, C. (2014). Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1643). <https://doi.org/10.1098/rstb.2013.0196>
- IPCC. (2019). *IPCC special report on the ocean and cryosphere in a changing climate* [H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegria, M. Nicolai, A. Okem, J. Petzold, B. Rama, & N. M. Weyer (eds.)]. In press. <https://www.ipcc.ch/srocc/cite-report/#:~:text=Schuur%2C%202019%3A%20Polar%20Regions.,%C3%B6rtner%2C%20D.C.%20Roberts%2C%20V>
- Karlsen, S. R., Anderson, H. B., Van der Wal, R., & Hansen, B. B. (2018). A new NDVI measure that overcomes data sparsity in cloud-covered regions predicts annual variation in ground-based estimates of high arctic plant productivity. *Environmental Research Letters*, *13*(2). <https://doi.org/10.1088/1748-9326/aa9f75>
- Keenan, T. F., & Richardson, A. D. (2015). The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Global Change Biology*, *21*(7), 2634–2641. <https://doi.org/10.1111/gcb.12890>
- Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., & Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(20), 5211–5216. <https://doi.org/10.1073/pnas.1714511115>
- Knowles, J., & Frederick, C. (2019). *merTools: Tools for analyzing mixed effect regression models*. R package version 0.5.0. <https://CRAN.R-project.org/package=merTools>
- Kohler, J., & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snow-pack model. *Arctic, Antarctic, and Alpine Research*, *36*(3), 333–341. [https://doi.org/10.1657/1523-0430\(2004\)036%5B0333:EOWSA G%5D2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036%5B0333:EOWSA G%5D2.0.CO;2)
- Le Moullec, M., Pedersen, A. Ø., Stien, A., Rosvold, J., & Hansen, B. B. (2019). A century of conservation: The ongoing recovery of svalbard reindeer. *Journal of Wildlife Management*, *83*(8), 1676–1686. <https://doi.org/10.1002/jwmg.21761>
- Lee, A. M., Bjørkvoll, E. M., Hansen, B. B., Albon, S. D., Stien, A., Saether, B.-E., Engen, S., Veiberg, V., Loe, L. E., & Grøtan, V. (2015). An integrated population model for a long-lived ungulate: More efficient data use with Bayesian methods. *Oikos*, *124*, 806–816. <https://doi.org/10.1111/oik.01924>
- Lendrum, P. E., Northrup, J. M., Anderson, C. R., Liston, G. E., Aldridge, C. L., Crooks, K. R., & Wittemyer, G. (2018). Predation risk across a dynamic landscape: Effects of anthropogenic land use, natural landscape features, and prey distribution. *Landscape Ecology*, *33*(1), 157–170. <https://doi.org/10.1007/s10980-017-0590-z>
- Liston, G. E., & Elder, K. (2006). A distributed snow-evolution modeling system (SnowModel). *Journal of Hydrometeorology*, *7*(6), 1259–1276. <https://doi.org/10.1175/jhm548.1>
- Liu, Q., Fu, Y. H., Zhu, Z., Liu, Y., Liu, Z., Huang, M., Janssens, I. A., & Piao, S. (2016). Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. *Global Change Biology*, *22*(11), 3702–3711. <https://doi.org/10.1111/gcb.13311>
- Livensperger, C., Steltzer, H., Darrouzet-Nardi, A., Sullivan, P. F., Wallenstein, M., & Weintraub, M. N. (2019). Experimentally warmer and drier conditions in an Arctic plant community reveal microclimatic controls on senescence. *Ecosphere*, *10*(4), e02677. <https://doi.org/10.1002/ecs2.2677>
- Loe, L. E., Hansen, B. B., Stien, A., D. Albon, S., Bischof, R., Carlsson, A., Irvine, R. J., Meland, M., Rivrud, I. M., Ropstad, E., Veiberg, V., & Mysterud, A. (2016). Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere*, *7*(6). <https://doi.org/10.1002/ecs2.1374>
- Loe, L. E., Irvine, R. J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S. D., Mysterud, A., & Stenseth, N. C. (2006). Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology*, *75*(2), 485–496. <https://doi.org/10.1111/j.1365-2656.2006.01069.x>
- Mallory, C. D., & Boyce, M. S. (2018). Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews*, *26*(1), 13–25. <https://doi.org/10.1139/er-2017-0032>
- Marchand, F. L., Nijs, I., Heuer, M., Mertens, S., Kockelbergh, F., Pontailier, J. Y., & Beyens, L. (2004). Climate warming postpones senescence in High Arctic tundra. *Arctic, Antarctic, and Alpine Research*, *36*(4), 390–394. [https://doi.org/10.1657/1523-0430\(2004\)036%5B0390:Cwpsih%5D2.0.Co;2](https://doi.org/10.1657/1523-0430(2004)036%5B0390:Cwpsih%5D2.0.Co;2)
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Á., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H., & Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2289–2301. <https://doi.org/10.1098/rstb.2010.0082>
- Nilsen, E. B., Linnell, J. D. C., Odden, J., & Andersen, R. (2009). Climate, season, and social status modulate the functional response of an efficient stalking predator: The Eurasian lynx. *Journal of Animal Ecology*, *78*(4), 741–751. <https://doi.org/10.1111/j.1365-2656.2009.01547.x>
- Omsjoe, E. H., Stien, A., Irvine, J., Albon, S. D., Dahl, E., Thoresen, S. I., Rustad, E., & Ropstad, E. (2009). Evaluating capture stress and its effects on reproductive success in Svalbard reindeer. *Canadian Journal of Zoology*, *87*(1), 73–85. <https://doi.org/10.1139/z08-139>
- Parker, K. L., Barboza, P. S., & Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, *23*(1), 57–69. <https://doi.org/10.1111/j.1365-2435.2009.01528.x>
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research*, *46*(1), 15–27. <https://doi.org/10.3354/cr00936>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X. U., Shen, M., & Zhu, X. (2019). Plant phenology and global climate

- change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Putkonen, J., & Roe, G. (2003). Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophysical Research Letters*, 30(4). <https://doi.org/10.1029/2002GL016326>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Version 64 x 3.6.2.
- Ravolainen, V., Soininen, E. M., Jónsdóttir, I. S., Eischeid, I., Forchhammer, M., Van der Wal, R., & Pedersen, Å. Ø. (2020). High Arctic ecosystem states: Conceptual models of vegetation change to guide long-term monitoring and research. *Ambio*, 49(3), 666–677. <https://doi.org/10.1007/s13280-019-01310-x>
- Reimers, E., Eftestøl, S., & Colman, J. E. (2003). Behaviour responses of wild reindeer to direct provocation by a snowmobile or a skier. *Journal of Wildlife Management*, 67(4), 747–754. <https://doi.org/10.2307/3802681>
- Rennert, K. J., Roe, G., Putkonen, J., & Bitz, C. M. (2009). Soil thermal and ecological impacts of rain on snow events in the circumpolar arctic. *Journal of Climate*, 22(9), 2302–2315. <https://doi.org/10.1175/2008jcli2117.1>
- Santin-Janin, H., Garel, M., Chapuis, J. L., & Pontier, D. (2009). Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: A case study on the Kerguelen archipelago. *Polar Biology*, 32(6), 861–871. <https://doi.org/10.1007/s00300-009-0586-5>
- Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, 354(6313), 11. <https://doi.org/10.1126/science.aaf7671>
- Serreze, M. C., & Barry, R. G. (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, 77(1–2), 85–96. <https://doi.org/10.1016/j.gloplacha.2011.03.004>
- Sturm, M., Holmgren, J., & Liston, G. E. (1995). A seasonal snow cover classification system for local to global applications. *Journal of Climate*, 8(5), 1261–1283. [https://doi.org/10.1175/1520-0442\(1995\)008%3C1261:Assccs%3E2.0.Co;2](https://doi.org/10.1175/1520-0442(1995)008%3C1261:Assccs%3E2.0.Co;2)
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
- Therrien, J.-F., Lecomte, N., Zgirski, T., Jaffré, M., Beardsell, A., Goodrich, L. J., Bêty, J., Franke, A., Zlonis, E., & Bildstein, K. L. (2017). Long-term phenological shifts in migration and breeding-area residency in eastern North American raptors. *The Auk*, 134(4), 871–881. <https://doi.org/10.1642/auk-17-5.1>
- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2163–2176. <https://doi.org/10.1098/rstb.2010.0090>
- Tyler, N. J. C. (1991). Short-term behavioral responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. *Biological Conservation*, 56, 179–194. [https://doi.org/10.1016/0006-3207\(91\)90016-3](https://doi.org/10.1016/0006-3207(91)90016-3)
- Tyler, N. J. C. (2010). Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus* L.). *Ecological Monographs*, 80(2), 197–219. <https://doi.org/10.1890/09-1070.1>
- Uboni, A., Horstkotte, T., Kaarlejärvi, E., Sévêque, A., Stammer, F., Olofsson, J., Forbes, B. C., & Moen, J. (2016). Long-term trends and role of climate in the population dynamics of Eurasian reindeer. *PLoS One*, 11(6), e0158359. <https://doi.org/10.1371/journal.pone.0158359>
- van de Pol, M. V., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, 77(3), 753–758. <https://doi.org/10.1016/j.anbehav.2008.11.006>
- Van der Wal, R., & Brooker, R. W. (2004). Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18(1), 77–86. <https://doi.org/10.1111/j.1365-2435.2004.00820.x>
- Van der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass. *Ecology*, 95(12), 3414–3427.
- van Pelt, W. J. J., Kohler, J., Liston, G. E., Hagen, J. O., Luks, B., Reijmer, C. H., & Pohjola, V. A. (2016). Multidecadal climate and seasonal snow conditions in Svalbard. *Journal of Geophysical Research: Earth Surface*, 121(11), 2100–2117. <https://doi.org/10.1002/2016jfr003999>
- Vickers, H., Hogda, K. A., Solbo, S., Karlsen, S. R., Tommervik, H., Aanes, R., & Hansen, B. B. (2016). Changes in greening in the high Arctic: Insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters*, 11(10), 9. <https://doi.org/10.1088/1748-9326/11/10/105004>
- Vihma, T. (2014). Effects of Arctic sea ice decline on weather and climate: A review. *Surveys in Geophysics*, 35(5), 1175–1214. <https://doi.org/10.1007/s10712-014-9284-0>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Vors, L. S., & Boyce, M. S. (2009). Global declines of caribou and reindeer. *Global Change Biology*, 15(11), 2626–2633. <https://doi.org/10.1111/j.1365-2486.2009.01974.x>
- Wood, S. (2006). *Generalized additive models: An introduction with R*. Taylor & Francis, CRC Press.
- Zimova, M., Mills, L. S., & Nowak, J. J. (2016). High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters*, 19(3), 299–307. <https://doi.org/10.1111/ele.12568>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Loe LE, Liston GE, Pigeon G, et al.

The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer.

Glob Change Biol. 2020;00:1–10. <https://doi.org/10.1111/gcb.15458>