

Behavioral buffering of extreme weather events in a high-Arctic herbivore

LEIF EGIL LOE,^{1,†} BRAGE B. HANSEN,² AUDUN STIEN,³ STEVE D. ALBON,⁴ RICHARD BISCHOF,¹
ANJA CARLSSON,^{4,5} R. JUSTIN IRVINE,⁴ MORTEN MELAND,¹ INGER MAREN RIVRUD,⁶
ERIK ROPSTAD,¹ VEBJØRN VEIBERG,⁷ AND ATLE MYSTERUD⁶

¹The Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Aas Norway

²Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, NO-7491 Trondheim Norway

³Arctic Ecology Department, Fram Centre, Norwegian Institute for Nature Research, NO-9296 Tromsø Norway

⁴The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH United Kingdom

⁵Department of Ecosystem and Public Health, Faculty of Veterinary Medicine, University of Calgary,
3280 Hospital Dr. NW, Calgary, Alberta T2N 4Z6 Canada

⁶Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES),
University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo Norway

⁷Terrestrial Ecology Department, Norwegian Institute for Nature Research, NO-7485 Trondheim Norway

Citation: Loe, L. E., B. B. Hansen, A. Stien, S. D. Albon, R. Bischof, A. Carlsson, R. J. Irvine, M. Meland, I. M. Rivrud, E. Ropstad, V. Veiberg, and A. Mysterud. 2016. Behavioral buffering of extreme weather events in a high-Arctic herbivore. *Ecosphere* 7(6):e01374. 10.1002/ecs2.1374

Abstract. As global warming advances, there is a growing concern about the impact of extreme weather events on ecosystems. In the Arctic, more frequent unseasonal warm spells and rain-on-snow events in winter cause changes in snow-pack properties, including ground icing. Such extreme weather events are known to have severe effects across trophic levels, for instance, causing die-offs of large herbivores. However, the extent to which individuals and populations are able to buffer such events through behavioral plasticity is poorly understood. Here, we analyze responses in space use to rain-on-snow and icing events, and their fitness correlates, in wild reindeer in high-Arctic Svalbard. Range displacement among GPS-collared females occurred mainly in icy winters to areas with less ice, lower over-winter body mass loss, lower mortality rate, and higher subsequent fecundity, than the departure area. Our study provides rare empirical evidence that mammals may buffer negative effects of climate change and extreme weather events by adjusting behavior in highly stochastic environments. Under global warming, behavioral buffering may be important for the long-term population persistence in mobile species with long generation time and therefore limited ability for rapid evolutionary adaptation.

Key words: Arctic; climate; GPS; ice; ideal-free distribution; migration; movement; *Rangifer tarandus platyrhynchus*; space use; Svalbard; Svalbard reindeer; time-to-event analysis.

Received 1 December 2015; revised 22 February 2016; accepted 7 March 2016. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Loe et al. 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.

† **E-mail:** leif.egil.loe@nmbu.no

INTRODUCTION

Ecological effects of extreme weather events such as summer heat waves (Barriopedro et al. 2011), hurricanes (Gaillard et al. 2003), droughts (Garel et al. 2004), and flooding (Rouse et al.

1997) are expected to increase with global warming. This may threaten the long-term persistence of populations, particularly at the edge of the species range (Easterling et al. 2000, Parmesan 2000, 2006). Our knowledge remains rudimentary about the extent to which different ecosystems

(Knapp et al. 2008) and taxonomic groups (Parmesan 2006) can cope with such extreme events. Although evolutionary adaptations to climate warming have been documented across a range of taxa (Franks et al. 2014, Schilthuizen and Kellermann 2014), there is considerable concern about whether or not the pace of in situ evolutionary adaptations are sufficiently rapid (Parmesan 2006). Phenotypic plasticity can potentially compensate for slow evolutionary change (Boutin and Lane 2014), yet studies investigating the potential for behavioral adaptations to buffer extreme events are still rare, despite being encouraged for nearly a decade (Parmesan 2006).

Global warming is particularly pronounced in the Arctic, a trend which is predicted to continue (IPCC 2013). Here, one consequence of warmer winters is the increased frequency of mild spells and rain-on-snow events (Putkonen and Roe 2003, Shabbar and Bonsal 2003, Rennert et al. 2009). These extreme weather events cause formation of ice layers in the snow-pack or ground-fast ice with far reaching ecosystem consequences (Ims and Fuglei 2005, Gilg et al. 2009, Hansen et al. 2013). In particular, the formation of thick ice layers accentuates the winter food shortage for large herbivores, resulting in starvation-related die-offs and reduced fecundity (Gunn et al. 1989, Solberg et al. 2001, Forchhammer et al. 2002, Hansen et al. 2011, Stien et al. 2012). Warm spells and rain-on-snow events are often linked to large-scale weather systems and may result in spatially extensive ice formation (Rennert et al. 2009, Bartsch et al. 2010). However, local icing events are most common (Wilson et al. 2013) and patches of food may be accessible within the movement range of large herbivores also during large-scale events. A key question for understanding and predicting consequences of climate change is therefore to what degree Arctic ungulates are able to buffer these increasingly common icing events through behavioral plasticity.

The inherent rarity of extreme weather events may explain the general lack of studies addressing the buffering potential of behavioral adaptations. Only a limited number of studies, mainly of birds (Burger and Shisler 1980, Burger 1982, Figuerola 2007, Santoro et al. 2013), have investigated how extreme weather events push individuals out of their original habitat. Similarly, we have previously shown that Svalbard reindeer

(*Rangifer tarandus platyrhynchus*) may display exploratory ranging behavior and move out of their home range when faced with icing (Stien et al. 2010). To the best of our knowledge, however, no studies of any species have examined the consequences of such emigration events, a necessity for identifying behavioral buffering of extreme weather events through movement decisions. Here, we investigate whether wild Svalbard reindeer are able to track landscape-scale variation in ground icing and fitness correlates (reproduction and survival) caused by extreme weather events related to winter climate warming.

METHODS

Study area and model species

The study was conducted in Nordenskiöldland (78° N, 15° E), Svalbard. The study area (~150 km²) is dominated by two large valleys: Colesdalen in the northwest (NW area) and Reindalen in the southeast (SE area), located approximately 20 km apart. The main valleys are interconnected by several smaller valleys, all with higher elevation passes with little or no accessible food in winter. Annual winter weather fluctuations on Svalbard are large. While most winters are virtually without rain-on-snow events, others are characterized by warm spells, heavy rainfall and extensive icing, causing reduced survival (Solberg et al. 2001), fecundity (Stien et al. 2012), and population growth in Svalbard reindeer (Kohler and Aanes 2004, Hansen et al. 2011, 2013). Svalbard reindeer are non-territorial and movement is therefore unlikely to be affected by social barriers. They do not migrate long distances (Tyler and Øritsland 1989) and movement decisions are likely taken at the individual level as Svalbard reindeer occur alone or in small groups (Tyler 1987, Loe et al. 2006). Predation is negligible (only a handful of observations; Derocher et al. 2000) and no interspecific foraging competition (with other large herbivores) or insect harassment occur. Selection of forage is likely to be a main behavioral driver in movement decisions aside from range use during calving in the first 2 weeks of June (Tyler 1987, Skogland 1989) and rut in October (Skogland 1989). The population size of females increased steadily over the course of the study (Lee et al. 2015).

Spatiotemporal variation in snow and ice

Air temperature and precipitation data used to quantify the amount of rain-on-snow in winter (November–April) were measured at Svalbard airport (~20 km from the study area) by the Norwegian Meteorological Institute (www.eklima.no). Rain-on-snow is defined as the amount of precipitation falling when air temperature exceeds 0°C between 1 November and 30 April.

Ground temperature loggers (ibuttons DS1921G; Maxim Integrated, San Jose, California, USA) were placed in the soil surface in ridge (*Salix polaris*) and sub-ridge vegetation (*Luzula confusa* or *Poa* sp.) at 128 locations throughout the study area. Ridge and sub-ridge vegetation types were selected because they constitute the main feeding habitat for reindeer in winter (Hansen et al. 2010). Each logger recorded soil surface temperature every sixth hour throughout the year. Periods in winter when ground temperature is equal to or exceeds zero lead to melting and ground ice formation when temperature subsequently drops. Adjacent to the 128 sites, we excavated snow pits with snow shovels and axes one time per year in February and/or April and measured snow depth and ground ice thickness to the nearest 0.5 cm. We used the mean ice thickness per year and area (SE and NW) as our measure for annual and spatial variation in ground ice formation. The rationale of this setup is that the continuous monitoring of ground temperature will detect periods of melting and refreezing while the field measurements of ground ice is used to calculate annual and spatial variation in icing.

Reindeer data

Between April 2009 and April 2013, 41 adult Svalbard reindeer females were fitted with store-on-board GPS-collars (Vectronic Aerospace, Berlin, Germany). Together they contribute 102 individual years. The GPS-marked individuals are a subsample of a much larger population of female reindeer captured each year using a net from a pair of snowmobiles and weighed to the nearest 0.5 kg (Omsjø et al. 2009). All animals were of known age having been marked with conventional ear tags and plastic collars at 10 months of age as part of a capture–mark–recapture study (Lee et al. 2015). The mean age of GPS-marked females was 6.8 yr (range: 3–11). GPS data were

downloaded during recapture events in February and/or April from 2010 to 2014. All locations obtained during the capture periods were removed. GPS-collars recorded a location every second hour. We used bihourly step length (in meters) as a measure of movement rate.

For each animal-year, we calculated the net displacement (ND) curve from 1 July in year t to 1 July in year $t + 1$ using the function `ltraj` in the R package “`adehabitat`” (Calenge 2006). We classified movement phenotypes as either “stationary” or “mobile” following the methodology of Bunnefeld et al. (2011), modified by Bischof et al. (2012). This approach fits different functions to the profile of the net-squared displacement (NSD) of sequential relocations from the origin, including logistic, double logistic, and intercept-only models. The ND pattern of individuals defined as “mobile” (with range displacement in winter) had the best fit to either a logistic function, as it moved away from summer site in spring and stayed in one winter area for an extended period of time (without return to the original range within the observed time period), or double logistic curve (hat-shaped) if the deer returned to the original summer site next spring (see Appendix S1). Stationary individuals had the best fit to an intercept-only model, as the NSD did not change over time (they stayed close to the origin). Automatic designations of phenotype (“stationary” or “mobile”) were confirmed, and when necessary, adjusted by inspecting plots of spatial relocation pattern (Bischof et al. 2012; Appendix S1). For the “mobile” phenotype, departure locations were defined as the last coordinate prior to, and arrival locations as the first coordinate after, the transition period. The transition period was defined as the date of the inflection point ± 2.5 times the scale value of the logistic curve (Bischof et al. 2012; Appendix S1). If departure and arrival location were situated in different areas (NW and SE), this was termed “displacement.”

In August each year, field personnel on foot conducted a population survey. The reproductive status of marked females (i.e., calf at heel or not) was observed and their spatial location was recorded. Similarly, the spatial location of carcasses of all age and both sexes (both marked and unmarked) were recorded. Carcasses from the preceding winter are normally detectable from long distances as distinct patches of white

fur contrasting the color of rocks and vegetation. Carcasses from previous years are normally at a more advanced stage of decomposition. Annual carcass numbers (of marked and unmarked individuals) and proportion of adult (>2 yr old) marked females with calf was calculated for each area and used as proxies for spatial contrasts in fitness. Carcass numbers were standardized (to mean = 0, variance = 1) separately for each area, and positive values represent higher mortality while negative values represent lower area-specific mortality than normal for the time period 1995–2014.

Statistical analyses

Area differences in ground ice thickness and snow depth (continuous response variables) were analyzed using linear models (LM) with sampling month (February or April) and area (SE or NW) as two-level categorical predictor variables.

Generalized additive mixed models (GAMM; Wood 2006), fitted with the function “*gamm*” in the R-package “*mgcv*” were used to analyze temporal variation in movement. Models were fitted separately for each winter, using a log link function and a gamma error distribution (Stien et al. 2010). Movement rate of the GPS-marked reindeer was used as a continuous response variable. Days since 15 October, fitted as a spline function, was used as the single predictor variable. Individual was fitted as a random intercept to account for individual variation in mean step length. We defined a winter to last from 15 October to 1 May in the following calendar year, and used the notation “winter 2009/2010” to refer to the winter lasting from 15 October 2009 to 1 May 2010.

The probability of individual reindeer being classified as “mobile” vs. stationary in response to icing was analyzed with a logistic mixed model using the function “*glmer*” in the R-package “*lme4*” (Bates et al. 2014). Movement category (mobile = 1, stationary = 0) was fitted as a binomially response variable, and annual ice classification (ice: winter 2009/2010 and 2011/2012; no ice: remaining years) and area (NW or SE) as a two-level factorial predictor variables. Individual was fitted as a random intercept to account for repeated decisions for the same individuals across years. To test individual flexibility in

movement strategy between consecutive icy and non-icy winters, we ran a chi-square test on a 2×2 contingency table of movement phenotype and ice condition.

To relate timing of range displacement to timing of icing events, we used time-to-event models (Hosmer et al. 2008). We first ran a model to investigate if the overall potential of displacement was associated with ground temperature in winter. In this analysis, we included both stationary and mobile individuals in all years of study. All individuals had one entry per day; zero if no displacement occurred on that day, and 1 if a displacement event occurred. For mobile individuals, entries after the date of the displacement event were removed. Stationary individuals had only zero entries up to 1 May. In these analyses, ground temperature was used as a continuous predictor variable. The second analysis attempted to investigate if there was a direct response or a delay between ground temperature warm spells in mid-winter and displacement events. In these analyses, only individuals classified as mobile in icy winters were included. Individual data was organized in the same way as in the first analysis (zeros leading up to a 1 identifying the day of displacement), but ground temperature was treated differently. We defined the date in mid-winter (after December) with the highest proportion of ground temperature loggers $\geq 0^\circ\text{C}$, to be the center date of each winters mild spell event. We fitted six models for each predictor, where the period of the event was coded 1, and remaining days coded 0: the week centered on the mild spell, the week before, the week after, the two weeks centered on the event, the two weeks before, and the two weeks after. Models with finer or coarser temporal resolution failed because too few or too many of the displacement events, respectively, coincided with the events, causing singularity. The fit of the models were compared based on the log likelihood.

Area-specific winter body mass loss was estimated from all marked individuals captured in the same area both in February and in April the same year, in one icy winter (2009/2010) and one non-icy winter (2010/2011), the two years when biannual captures were conducted. In a linear mixed model, body mass was used as response variable, age (fitted as a quadratic term), month (February and April), area (SE and NW), and the

interaction between month and area, all as fixed effects, and individual as a random intercept. A significant interaction implies different winter weight loss between the areas. Separate models were run for the icy (2009/2010) and the non-icy (2010/2011) winter. In this subsample of individuals with biannual weights ($n = 64$), only one individual was caught in different areas in February and April (because the majority of range displacement occur before February). To compare body mass of displaced and stationary individuals, we used the GPS individuals with known movement phenotype and fitted a linear model with April body mass as response variable, movement class (stationary NW, stationary SE, relocating from SE to NW), and annual ice classification (ice: winter 2009/2010 and 2011/2012; no ice: remaining three winters) as predictor variables.

Differences in calf/female ratio and standardized carcass numbers in departure and arrival areas (SE and NW) were analyzed using paired t -tests. Calf/female ratio was never close to the boundaries (0 and 100%) and was in addition arcsine square root transformed to meet the criteria of normality. All analyses were conducted in R version 3.2.0 (R Core Team 2015).

RESULTS

Spatiotemporal variation in icing

In two of the five winters (2009/2010 and 2011/2012), a large proportion of the precipitation fell as rain-on-snow (Fig. 1A). While a thick ground ice layer covered most of the vegetation in these two winters, ground ice was virtually absent in the remaining three study winters (2010/2011, 2012/2013, and 2013/2014; Fig. 1B). In icy winters, mean ice thickness was higher in the SE area (5.2 ± 0.26 cm) than in the NW area (3.6 ± 0.27 cm; $P < 0.001$; Fig. 1B; see Appendix S1: Fig. S4 for the spatial pattern of icing). Snow depth was less variable among years but on average thicker in the SE area (35 ± 1.2 cm) than NW (19 ± 1 cm; $P < 0.001$).

Movement responses to the ground ice gradient

Bihourly movement rates of GPS-marked reindeer declined from mid-October to January in all winters (Fig. 2A). In all three non-icy winters, movement rates remained low from December to April. In contrast, in the icy

winters reindeer increased their movement rate in mid-winter (Fig. 2A, B).

Accounting for repeated observations of individuals, the odds of being classified as “mobile” was 55 times higher in icy winters compared to non-icy winters (log odds ratio = 4.0, SE = 1.2, $P < 0.001$) and was 25 times higher in the SE area than in NW (log odds ratio = 3.4, SE = 1.1, $P = 0.002$). The displacement potential was positively affected by ground temperature (time-to-event analysis: estimate = 0.459, SE = 0.112, $z = 4.1$, $P < 0.001$) and was highest in the 2-week-period following the peak in ground temperature (Table 1), suggesting that reindeer moved as a response to refreezing of the ground. In icy winters, 80% ($n = 16$) of individuals in the SE area moved to the NW area (Figs. 1C and 3A). The relocation was temporary as nearly all of the individuals that left SE had returned by next August (93%). Between consecutive years, 40% of individuals switched their movement strategy between “mobile” in icy years and remaining stationary in non-icy years. In contrast, no individuals switched strategy in the opposite direction ($\chi^2 = 19$, $df = 1$, $P < 0.001$). Other individuals did not change strategy, that is, they remained stationary (41%) or were always “mobile” (19%).

Spatial variation in fitness components

There was a temporal correlation of all fitness proxies between the SE and NW area in the study period (body mass: $r = 0.89$, $P = 0.04$; calf/female ratio: $r = 0.85$, $P = 0.07$; carcass numbers: $r = 0.98$, $P = 0.002$; Fig. 1D–F). However, all fitness components suggested spatial differences related to icing.

First, April body mass was always higher in the NW area in icy winters and in the SE area in non-icy winters (Fig. 1D). In the two study years when winter body mass loss could be estimated, individuals in the most icy area (SE) were already 3.6 kg lighter than NW individuals in February (effect size of area in February = -3.6 [95% CI: -6.1 , -1.0]), and the body mass difference doubled from February to April (Fig. 4; effect size of month \times area interaction = -3.5 [95% CI: -5.6 , -1.3]). Notably, the body mass pattern was reversed in the following non-icy winter, with individuals in SE being 4 kg heavier than in NW both in February and April (Fig. 4; main effect of area = 4.0 [95% CI: 1.3, 6.8]). This may

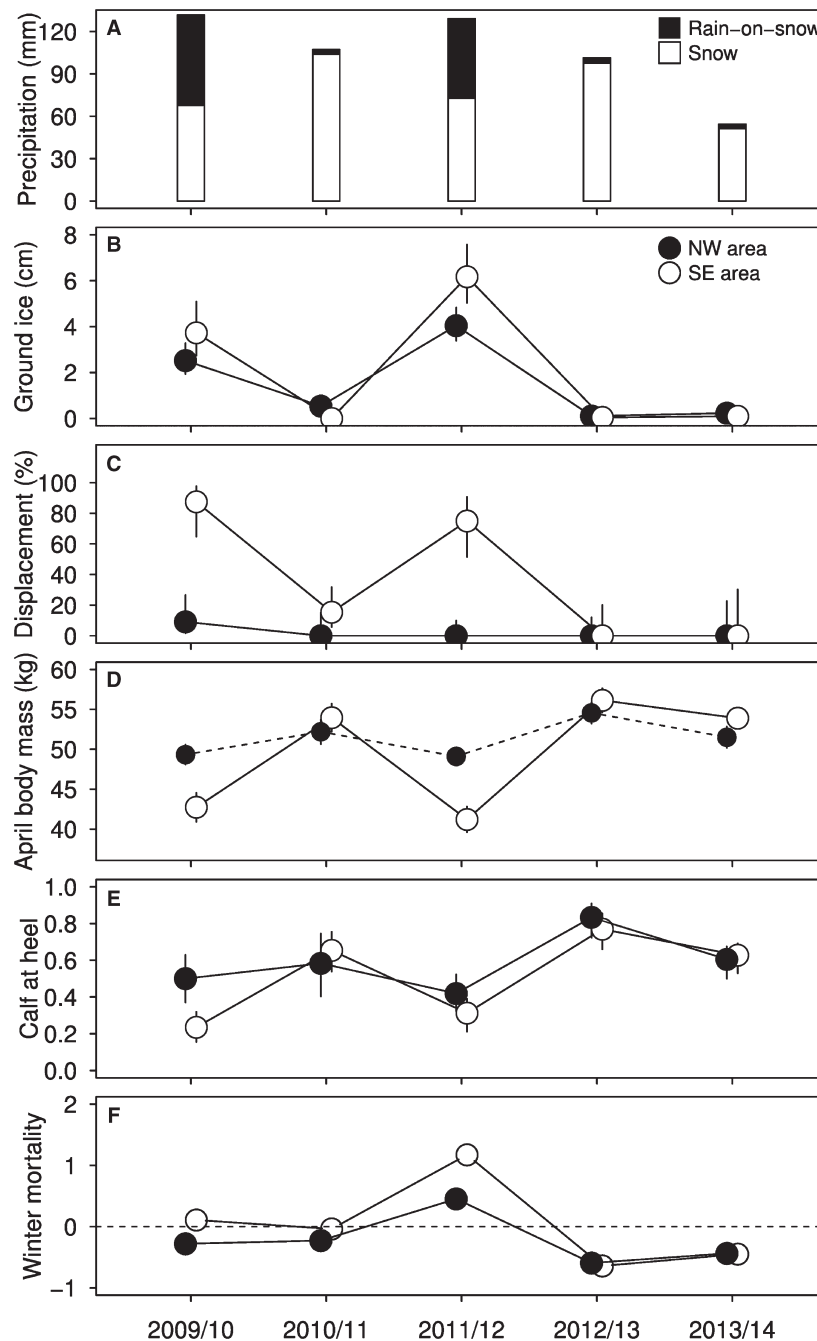


Fig. 1. (A) Annual variation in winter precipitation (November–April) falling as snow and rain in winter (rain-on-snow: defined as precipitation falling at temperatures $\geq 0^{\circ}\text{C}$). (B–F): Annual and area differences in (B) predicted mean ground ice thickness, (C) percentage of female GPS-marked reindeer showing displacement behavior, (D) predicted mean adult female body mass in April accounting for age, (E) proportion of adult marked females (≥ 3 yr old) with a calf at heel in August, and (F) a winter mortality index measured as the standardized number of carcasses of all ages and both sexes, relative to the long-term (1995–) mean annual carcass number for each area. Error bars are ± 1 SE.

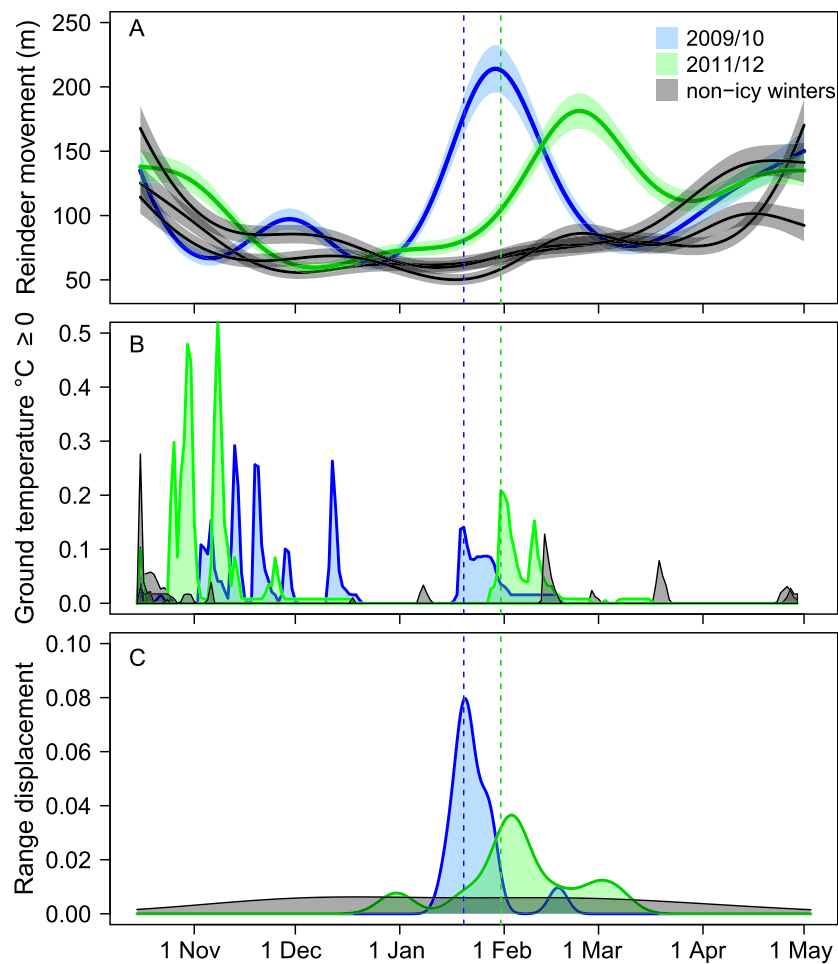


Fig. 2. (A) Predicted reindeer movement (bihourly step lengths \pm 95% CI) by date in the two icy (2009/2010 and 2011/2012) and the three non-icy winters (data pooled), (B) the daily proportion of temperature loggers measuring temperature above freezing in five winters (2009/2010 to 2013/2014), and (C) a kernel density plot of range displacement events by date. Blue (2009–2010) and green (2011–2012) lines represent values in the icy winters, while black is used commonly for all three non-icy winters. Vertical dotted lines represent the date for the peak mid-winter mild spells in each of the two icy winters, indicating onset of refreezing.

be caused by a reduction in population size and thus competition in the SE area after icing events (Appendix S1: Fig. S5). In the smaller subset of GPS-marked animals, where spatial strategy could be determined, April body mass differences between SE and NW were similar to the larger sample of all marked deer, both in icy and non-icy winters (Appendix S1: Fig. S6). In addition, GPS-marked individuals moving from SE to NW in icy winters had April body mass comparable to stationary GPS-marked individuals in NW (Appendix S1: Fig. S6), suggesting that range displacement reduced body mass loss.

Second, the proportion of adult females with calf was markedly higher in NW than in SE in the summers following icy winters (Fig. 1E). Thus, as displaced individuals almost exclusively moved from SE to NW, there was a substantial difference in population-level calf/female ratio between the departure and arrival locations ($t = 3.3$, $df = 11$, $P = 0.008$; Fig. 5). The difference between the two areas was much smaller or even with opposite sign after non-icy winters (Fig. 1E).

Third, carcass numbers after icy winters were higher in SE than in NW (Fig. 1F), and the standardized carcass numbers were, hence, on

Table 1. Time-to-event analyses relating the timing of mild spell to the potential of performing a displacement event.

Time period	Coefficient	Hazard ratio	SE	z	P	logLik
1 week centered on mild spell†	0.40	1.50	0.55	0.73	0.467	-57.7
1 week before	-0.99	0.37	0.77	-1.27	0.203	-57.2
1 week after	2.15	8.58	1.05	2.04	0.042	-54.5
2 weeks centered on mild spell	0.56	1.74	0.54	1.04	0.300	-57.4
2 weeks before	-2.10	0.12	0.78	-2.68	0.007	-52.9
2 weeks after‡	2.87	17.71	1.05	2.74	0.006	-50.4

† Timing of mild spells is taken as the date when the highest proportion of temperature logger exceeded 0°C in mid-winter (see vertical lines in Fig. 2B). Only individuals with displacement were included and only for the two icy winters (2009–2010 and 2011–2012).

‡ The model with the highest likelihood is presented in bold.

average higher in departure than arrival locations for relocating individuals ($t = 5.3$, $df = 11$, $P < 0.001$; Fig. 5). There was no area difference in carcass numbers in non-icy winters (Fig. 1F). The higher mortality in the second compared to the first icy winter (Fig. 1B) corresponds with the observed difference in ice thickness (Fig. 1F).

DISCUSSION

Organisms may respond to climate change by both evolutionary adaptations and phenotypic plasticity (Parmesan 2006, Boutin and Lane 2014). While evolutionary adaptation in animals with long generation times is not likely to keep pace with the ongoing rapid warming of the Arctic (Parmesan 2006), our study demonstrates that Arctic ungulates are capable of behaviorally buffering climate related changes in their habitat. Individual variation in the spatial response to extreme weather events may have important implications for variation in fitness. Icing events triggered an immediate increase in Svalbard reindeer movement rates with displacement toward less icy ranges with less severe feeding conditions, lower body mass loss, lower mortality index, and higher fecundity. Since the vast majority of individuals in the more icy range displaced and successfully tracked these gradients, our results suggest that behavioral buffering of such extreme events may counteract population decline following critical winters. However, it is also important to acknowledge the strong annual correlation in all fitness proxies between the good and bad winter range,

suggesting that the spatial heterogeneity in the climate impacts is too small for full behavioral compensation.

There is a general lack of studies addressing the buffering potential of behavioral adaptations. Extreme events are likely to change animals' behavior and range use, such as in the laughing gull *Larus atricilla* (Burger and Shisler 1980) and black skimmers *Rynchops niger* (Burger 1982), where both species changed breeding grounds following a year with flooding and unsuccessful breeding. Likewise, it has recently been suggested that droughts are the main driver of long-distance dispersal in Glossy ibis *Plegadis falcinellus* (Santoro et al. 2013) and black-winged stilts *Himantopus himantopus* (Figuerola 2007). To the best of our knowledge, only two studies demonstrate similar patterns in mammals. Juvenile northern fur seal (*Callorhinus ursinus*) responded to Arctic storms by immediate dispersal (Lea et al. 2009) and in a previous study, we demonstrated that the usually sedentary Svalbard reindeer moved out of their home range as a response to icing (Stien et al. 2010). While the aforementioned studies have demonstrated that extreme events push individuals out of their original habitat, our study is the first to link movement decisions to fitness correlates, which is required for understanding and predicting both individual and population-level consequences of behavioral buffering.

The impact of animal range use on fitness components provides an important link between individual behavior and population dynamics (Gaillard et al. 2010). The ideal-free distribution (IFD) theory (Fretwell and Lucas 1970) is a common theoretical framework to address this.

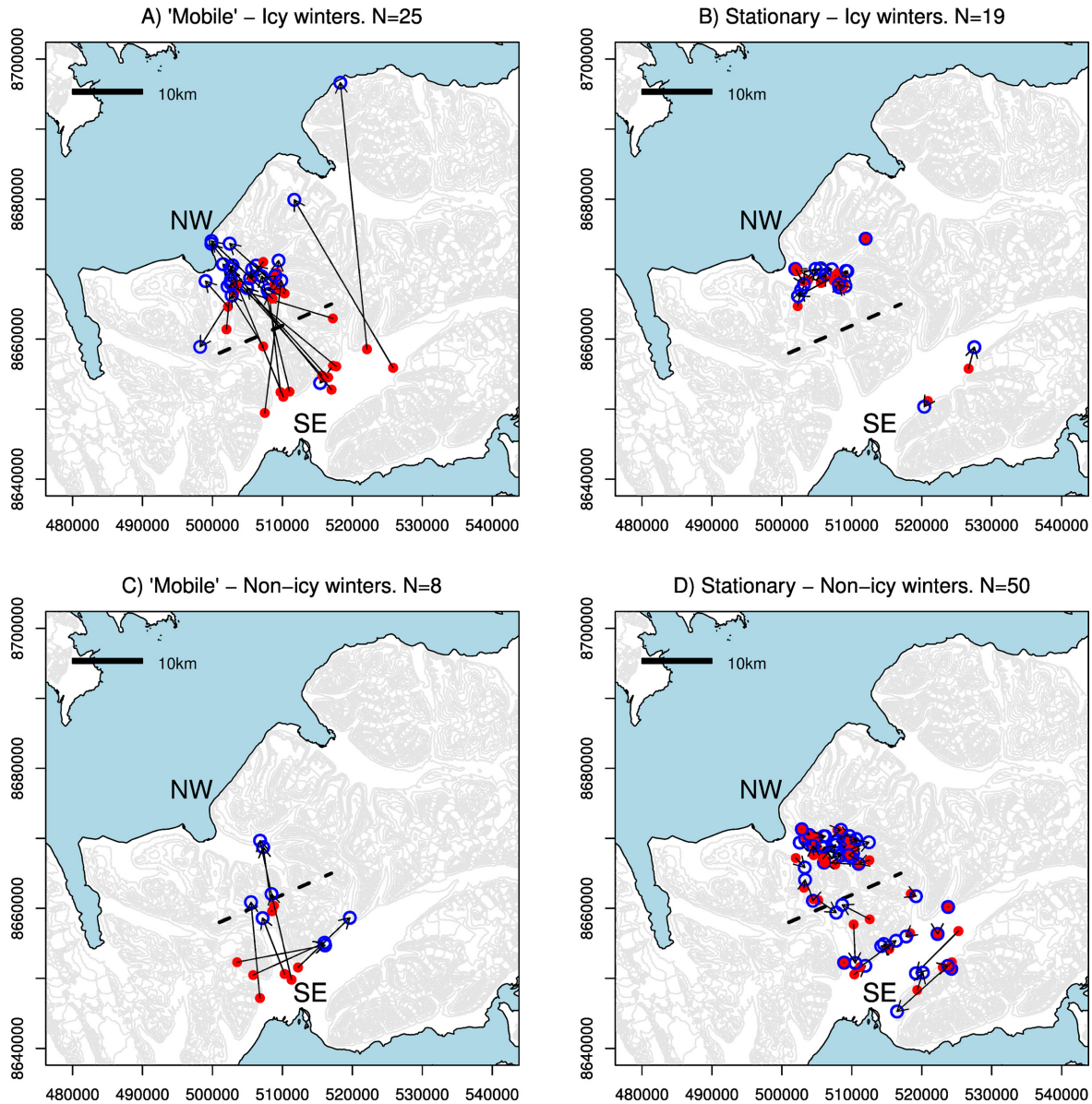


Fig. 3. Movement of GPS-marked reindeer for all four combination of winter condition (icy vs. non-icy winters) and movement strategy (“mobile” vs. stationary). For “mobile” individuals, departure locations (red dot) is defined as the last position occupied before winter movement, and arrival location (blue circles) is the first location recorded after ending winter movement. Black lines connect the departure and arrival location of each individual. For stationary individuals, start and end dates are defined as the locations used on the median departure and arrival dates for “mobile” individuals in the same observation year. Note that displacement occurs over longer distances and is more systematically occurring in icy winters (A) compared to non-icy winters (C). The dashed black lines show the separation between SE and NW area corresponding approximately to the three movement corridors between the two areas.

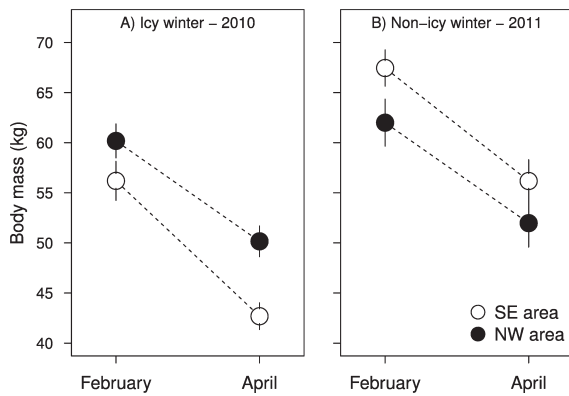


Fig. 4. Area-specific body mass of female Svalbard reindeer in February and April in (A) icy winters and (B) non-icy winters. Biannual captures (in both February and April) were only conducted in 2010 and 2011. Only individuals captured in the same area in both February and April are included. Point values represent mean body mass of adult individuals (≥ 2 yr old) and error bars represent 95% CI.

Even in habitat with more predictable distribution of resources, deviations from IFD are common (Gaillard et al. 2010) and several studies of temperate large herbivores have thus repeatedly rejected the IFD model, including studies of red deer *Cervus elaphus* (McLoughlin et al. 2006), roe deer *Capreolus capreolus* (Pettorelli et al. 2001), and Soay sheep *Ovis aries* (Jones et al. 2006). Deviation from a perfect IFD is expected (Arlt and Part 2007, DeCesare et al. 2014), particularly in stochastic environments (Gaillard et al. 2010). In

our study, 20% of the GPS-marked female reindeer deviated from IFD by remaining stationary in the area with the most severe feeding conditions during icy winters. Accordingly, they faced greater body mass loss and reduced population-level vital rates compared with the less icy area. More surprisingly, however, was the higher body mass in the SE area in non-icy winters, suggesting spatiotemporal fluctuations in the deviation from IFD also in non-icy winters. In Svalbard reindeer, range displacement is a flexible strategy that varies between individuals and according to conditions (see also Hansen et al. 2010). Yet, this study suggests that limited range perception (Gray and Kennedy 1994, Lima and Zollner 1996) and a temporal lag or inertia in movement strategies (Jackson et al. 2004) contribute to a suboptimal distribution of animals across the landscape. Thus, a quarter of the individuals that displaced in the first icy winter repeated their strategy in the subsequent non-icy winter, thereby contributing to increased competition and reduced vital rates compared with their departure range (Appendix S1: Fig. S5; Bonenfant et al. 2009). However, the spatial differences in body mass in non-icy winters were not accompanied by substantial differences in calf ratio or mortality implying that individuals in both areas were above the body mass threshold for successful survival (Gaillard et al. 2000) and reproduction (Festa-Bianchet et al. 1998).

Ecological effects of extreme weather events are a growing concern in the face of global warming (Easterling et al. 2000, Smith 2011, Diffenbaugh et al. 2013), and may be just as important as effects related to long-term trends (Parmesan 2000). Although populations of long-lived animals and plants have a higher ability to buffer climatic variability than short-lived ones (Morris et al. 2008), long generation time is a hindrance for rapid evolutionary adaptation to entirely new climate regimes (Berteaux et al. 2004, Parmesan 2006). Our study has demonstrated that by temporarily relocating to better habitat, individuals may increase their chances of survival and reproduction, suggesting adaptive buffering behavior. This may suggest that behavioral buffering is an understudied mechanism that can potentially mitigate the negative effects of climate change and extreme events on the population dynamics of long-lived species.

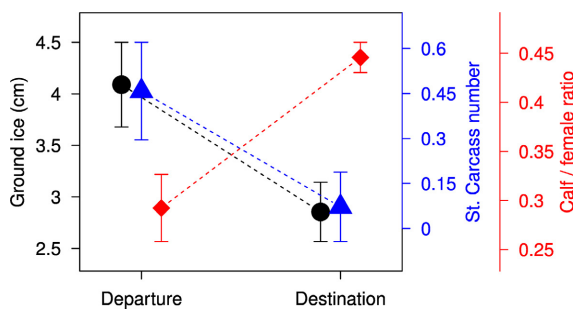


Fig. 5. Ground ice thickness (black circles), mortality index (blue triangles), and calf/female ratio (red diamonds) at departure and arrival locations for GPS-marked individuals with range displacement in icy winters (2009/2010 and 2011/2012).

ACKNOWLEDGMENTS

Thanks to Rolf Langvatn and Odd Halvorsen who initiated the long-term individual-based study of the Svalbard reindeer together with SA. The UK Natural Environment Research Council, the Research Council of Norway (project number 216051), Svalbard Environmental Protection Fund (project number 12/115 and 13/74) and Svalbard Science Forum (Arctic Field Grants to LEL, VV, AS, and MM) and Macaulay Development Trust funded the study. We greatly acknowledge the support of Centre for Advanced Study in Oslo, Norway that funded and hosted our research project (“Climate effects on harvested large mammal populations”) during the academic year of 2015/2016. Thanks to Roy Andersen and numerous field assistants for contributing to the field campaigns.

LITERATURE CITED

- Arlt, D., and T. Part. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology* 88:792–801.
- Barriopedro, D., E. M. Fischer, J. Luterbacher, R. Trigo, and R. Garcia-Herrera. 2011. The hot summer of 2010: redrawing the temperature record map of Europe. *Science* 332:220–224.
- Bartsch, A., T. Kumpula, B. C. Forbes, and F. Stammer. 2010. Detection of snow surface thawing and refreezing in the Eurasian Arctic with QuikSCAT: implications for reindeer herding. *Ecological Applications* 20:2346–2358.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.
- Berteaux, D., D. Réale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change: can arctic life count on evolution? *Integrative and Comparative Biology* 44:140–151.
- Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Myrsterud. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *American Naturalist* 180:407–424.
- Bonenfant, C., et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.
- Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications* 7:29–41.
- Bunnfeld, N., L. Börger, B. Van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80:466–476.
- Burger, J. 1982. The role of reproductive success in colony-site selection and abandonment in black skimmers (*Rynchops niger*). *Auk* 99:109–115.
- Burger, J., and J. Shisler. 1980. Colony and nest site selection in laughing gulls in response to tidal flooding. *Condor* 82:251–258.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology* 83:343–352.
- Derocher, A. E., O. Wiik, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. *Polar Biology* 23:675–678.
- Diffenbaugh, N. S., M. Scherer, and M. Ashfaq. 2013. Response of snow-dependent hydrologic extremes to continued global warming. *Nature Climate Change* 3:379–384.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- Festa-Bianchet, M., J. M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* 152:367–379.
- Figueroa, J. 2007. Climate and dispersal: Black-winged Stilts disperse further in dry springs. *PLoS ONE* 2:e539.
- Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology* 44:113–120.
- Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications* 7:123–139.
- Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Gaillard, J.-M., P. Duncan, D. Delorme, G. V. Laere, N. Pettorelli, D. Maillard, and G. Renaud. 2003. Effects of Hurricane Lothar on the population dynamics of European roe deer. *Journal of Wildlife Management* 67:767–773.
- Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding

- the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B* 365:2255–2265.
- Garel, M., A. Loison, J. M. Gaillard, J. M. Cugnasse, and D. Maillard. 2004. The effects of a severe drought on mouflon lamb survival. *Proceedings of the Royal Society B* 271:S471–S473.
- Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. *Global Change Biology* 15:2634–2652.
- Gray, R. D., and M. Kennedy. 1994. Perceptual constraints on optimal foraging – a reason for departures from the ideal free distribution. *Animal Behaviour* 47:469–471.
- Gunn, A., F. L. Miller, and B. McLean. 1989. Evidence for and possible causes of increased mortality of bull muskoxen during severe winters. *Canadian Journal of Zoology* 67:1106–1111.
- Hansen, B. B., R. Aanes, and B. E. Saether. 2010. Feeding-crater selection by high-arctic reindeer facing ice-blocked pastures. *Canadian Journal of Zoology* 88:170–177.
- Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B.-E. Saether. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology* 92:1917.
- Hansen, B. B., V. Grøtan, R. Aanes, B. E. Saether, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and A. O. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science* 339:313–315.
- Hosmer, D. W., S. Lemeshow, and S. May. 2008. *Applied survival analysis: regression modeling of time to event data*. Second edition. Wiley, New York, New York, USA.
- Ims, R. A., and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *BioScience* 55:311–322.
- IPCC. 2013. *The physical science basis. Working group 1 contribution to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, UK.
- Jackson, A. L., S. Humphries, and G. D. Ruxton. 2004. Resolving the departures of observed results from the ideal free distribution with simple random movements. *Journal of Animal Ecology* 73:612–622.
- Jones, O. R., J. G. Pilkington, and M. J. Crawley. 2006. Distribution of a naturally fluctuating ungulate population among heterogeneous plant communities: ideal and free? *Journal of Animal Ecology* 75:1387–1392.
- Knapp, A. K., et al. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience* 58:811–821.
- Kohler, J., and R. Aanes. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: results of a simple snowpack model. *Arctic, Antarctic, and Alpine Research* 36:333–341.
- Lea, M.-A., D. Johnson, R. Ream, J. Sterling, S. Melin, and T. Gelatt. 2009. Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters* 5:252–257.
- Lee, A., E. Bjørkvoll, B. B. Hansen, S. D. Albon, A. Stien, B. E. Saether, S. Engen, V. Veiberg, L. E. Loe, and V. Grøtan. 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos* 124:806–816.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–135.
- Loe, L. E., R. J. Irvine, C. Bonenfant, A. Stien, R. Langvatn, S. D. Albon, A. Mysterud, and N. C. Stenseth. 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. *Journal of Animal Ecology* 75:485–496.
- McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B* 273:1449–1454.
- Morris, W. F., et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89:19–25.
- Omsjø, E. H., A. Stien, J. Irvine, S. D. Albon, E. Dahl, S. I. Thoresen, E. Rustad, and E. Ropstad. 2009. Evaluating capture stress and its effects on reproductive success in Svalbard reindeer. *Canadian Journal of Zoology* 87:73–85.
- Parmesan, C. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* 81:443–450.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Pettorelli, N., J. M. Gaillard, P. Duncan, J. P. Ouellet, and G. Van Laere. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* 128:400–405.
- Putkonen, J., and G. Roe. 2003. Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophysical Research Letters* 30:1188.
- R Core Team. 2015. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rennert, K. J., G. Roe, J. Putkonen, and C. M. Bitz. 2009. Soil thermal and ecological impacts of rain

- on snow events in the circumpolar Arctic. *Journal of Climate* 22:2302–2315.
- Rouse, W. R., et al. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11:873–902.
- Santoro, S., A. J. Green, and J. Figuerola. 2013. Environmental instability as a motor for dispersal: a case study from a growing population of glossy ibis. *PLoS ONE* 8:12.
- Schilthuizen, M., and V. Kellermann. 2014. Contemporary climate change and terrestrial invertebrates: evolutionary versus plastic changes. *Evolutionary Applications* 7:56–67.
- Shabbar, A., and B. Bonsal. 2003. An assessment of changes in winter cold and warm spells over Canada. *Natural Hazards* 29:173–188.
- Skogland, T. 1989. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology* 29:1–74.
- Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology* 99:656–663.
- Solberg, E. J., P. Jordhoy, O. Strand, R. Aanes, A. Loison, B. E. Sæther, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* 24:441–451.
- Stien, A., L. E. Loe, A. Mysterud, T. Severinsen, J. Kohler, and R. Langvatn. 2010. Icing events trigger range displacement in a high-arctic ungulate. *Ecology* 91:915–920.
- Stien, A., et al. 2012. Congruent responses to weather variability in high arctic herbivores. *Biology Letters* 8:1002–1005.
- Tyler, N. J. C. 1987. Natural limitation of the abundance of the high arctic Svalbard reindeer. Dissertation. University of Cambridge, Cambridge, UK.
- Tyler, N. J. C., and N. A. Øritsland. 1989. Why don't Svalbard reindeer migrate? *Holarctic Ecology* 12:369–376.
- Wilson, R. R., A. Bartsch, K. Joly, J. H. Reynolds, A. Orlando, and W. M. Loya. 2013. Frequency, timing, extent, and size of winter thaw-refreeze events in Alaska 2001–2008 detected by remotely sensed microwave backscatter data. *Polar Biology* 36:419–426.
- Wood, S. 2006. Generalized additive models: an introduction with R. Taylor & Francis, CRC Press, London, UK.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1374/supinfo>