

Icing events trigger range displacement in a high-arctic ungulate

AUDUN STIEN,^{1,7} LEIF EGIL LOE,² ATLE MYSTERUD,² TORBJØRN SEVERINSEN,³ JACK KOHLER,⁴ AND ROLF LANGVATN^{5,6}

¹Norwegian Institute for Nature Research (NINA), Arctic Ecology Department, Polar Environmental Centre, N-9296 Tromsø, Norway

²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066, Blindern, N-0316 Oslo, Norway

³Department of Molecular Biosciences, University of Oslo, P.O. Box 1066, Blindern, N-0316 Oslo, Norway

⁴Norwegian Polar Institute, Polar Environmental Centre, N-9296 Tromsø, Norway

⁵The University Centre in Svalbard (UNIS), N-9170 Longyearbyen, Spitsbergen, Norway

⁶Norwegian Institute for Nature Research (NINA), Terrestrial Ecology Department, Tungasletta 2, N-7005 Trondheim, Norway

Abstract. Despite numerous studies of how climate change may affect life history of mammals, few have documented the direct impact of climate on behavior. The Arctic is currently warming, and rain-on-snow and thaw-freeze events leading to ice formation on the ground may increase both in frequency and spatial extent. This is in turn expected to be critical for the winter survival of arctic herbivores. Svalbard reindeer (*Rangifer tarandus plathyrinchus*) have small home ranges and may therefore be vulnerable to local “locked pasture” events (ice layers limit access to plant forage) due to ground-ice formation. When pastures are “locked,” Svalbard reindeer are faced with the decision of staying and live off a diminishing fat store, or trying to escape beyond the unknown spatial borders of the ice. We demonstrate that Svalbard reindeer do the latter, as icing events cause an immediate increase in range displacement between 5-day observations. Population-level responses of previous icing events may therefore not accurately predict future responses if the spatial extent of icing increases. The impact of single events may be more severe if it exceeds the maximum movement distances, so that the spatial displacement strategy reported here no longer buffers climate effects.

Key words: climate change; herbivores; movement; Norway; rain-on-snow; *Rangifer tarandus plathyrinchus*; Svalbard reindeer.

INTRODUCTION

Climate effects on populations and ecosystems are pervasive and well documented (e.g., Stenseth et al. 2002); however, it is still uncertain to what degree innate phenotypic plasticity and/or rapid adaptations will enable animals to cope with rapid climate change (Skelly et al. 2008). For large ungulates, the literature on climate effects is biased toward studies of life-history traits (e.g., Mysterud et al. 2001), demographic rates (e.g., Coulson et al. 2001), and population abundances (e.g., Post 2005). We have limited documentation of behavioral responses to climate, though seeking forest cover for relief (Moen 1976) and migrating to lower elevations to avoid deep snow (Mysterud 1999) are well-known examples from boreal forest ecosystems. Insight into behavioral responses can improve our understanding of what causes nonlinear responses to climatic variables, and is topical since future climatic conditions may be outside the range of conditions observed until recently.

At high latitudes, rain-on-snow (Putkonen and Roe 2003) and thaw-freeze events in the winter are climatic events that can cause extensive ice cover on the ground. Such ice layers limit access to plant forage, a situation often called “locked pastures,” and may cause herbivore populations to crash (Gunn et al. 1989, Gunn 1995, Aars and Ims 2002, Kohler and Aanes 2004). Recent climate scenarios predict an increase, both in the frequency and spatial extent, of conditions that may cause ice formation (Putkonen and Roe 2003, Shabbar and Bonsal 2003, ACIA 2004). The population-level responses of reindeer to previous icing events have been quantified (Kohler and Aanes 2004); however, this may not be sufficient to predict responses to future events if the spatial extent of icing increases. It is therefore important to understand if, and at what spatial scale, herbivores may respond to such challenging climatic conditions by movements. In this paper we investigate the effect of such icing events on timing and scale of movements of Svalbard reindeer.

The Svalbard reindeer (*Rangifer tarandus plathyrinchus*) is a subspecies endemic to the arctic archipelago of Svalbard (76–81° N, 10–27° E) where it has adapted

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⁷E-mail: audun.stien@nina.no



PLATE 1. Female Svalbard reindeer grazing on snow- and ice-free patches in the winter. Photo credit: Erik Ropstad.

to a polar, predator-free environment for more than 5000 years (van der Knaap 1989, Loe et al. 2007; see Plate 1). The Svalbard reindeer have no large-scale migrations, relatively small home ranges (Tyler and Øritsland 1989), and occur in small unstable groups throughout the year (Loe et al. 2006). Despite physiological adaptations to the extreme winter, such as building up extensive stores of body fat in summer that potentially meet 25% of the winter energy requirements (Tyler 1987), its survival and reproductive rates are highly variable between years (Solberg et al. 2001, Albon et al. 2002, Tyler et al. 2008). In addition, dispersal rates have been suggested to vary substantially between years (Tyler and Øritsland 1999). Together, the variability in demographic rates causes substantial local population fluctuations that have been correlated to patterns in winter climate (Aanes et al. 2000, Solberg et al. 2001), including variability in the formation of ground ice (Kohler and Aanes 2004).

We use a simple model for ground-ice formation (Kohler and Aanes 2004) to predict the seasonal timing of such icing events. The impact of these icing events on Svalbard reindeer foraging behavior is analyzed using observations of the movement of satellite-collared reindeer over four winters that differed in the predicted timing and extent of icing events. Three alternative hypotheses are evaluated: (H_0) reindeer movement is not affected by the icing events; (H_1) reindeer minimize movement and rely on their fat stores to outlast locked pastures; or (H_2) reindeer increase their movement distances in attempts to escape from locked pastures.

MATERIALS AND METHODS

Study area and the reindeer population

The study was conducted at the Brøgger peninsula (78°50' N, 11°50' E), located on Spitsbergen, Norway in the Arctic archipelago of Svalbard. The terrain is

mountainous and moderately glaciated. In the winter of 1993–1994, the Svalbard reindeer (*Rangifer tarandus plathyrinchus*) population crashed from 360 individuals to ~80 and increased thereafter to ~170 individuals by 1998 (Aanes et al. 2000). There are no roads in the study area, no reindeer hunting, and only a small human settlement (25–150 inhabitants). Hence, human influence on reindeer activity is likely to be minimal.

Reindeer positioning data

We used positioning data from six adult female Svalbard reindeer marked with ARGOS satellite collars (ARGOS, Ramonville Saint-Agnes, France; weight 1.4 kg; ~3% of the winter body mass). The collars recorded the positions of the animals every fifth day from early November 1994 and lasted on average 2.7 years (range 1.0–3.9 years) until batteries failed or the animal died. We analyzed data from the winter months (1 October to 31 March), as we were interested in movement responses to icing. ARGOS positioning data are of three qualities resembling accuracies (radius of one sigma): quality 3, <250 m; quality 2, <500 m; and quality 1, <1500 m. The majority of our data were of the best quality (quality 3, 65%; quality 2, 28%; and quality 1, 6%). We used only data of quality 2 and 3 in analyses. In addition we deleted four obvious outliers (three of quality 2 and one location of quality 3 that were far off the coast). None of the animals were together in the same group when caught and they did not group later (Loe et al. 2007).

Icing events

Daily ground-ice thickness estimates were obtained using the locally parameterized snowpack model of Kohler and Aanes (2004). This model uses temperature and precipitation data from the local weather station in Ny-Aalesund, Norway (78°55' N, 11°56' E) to model temporal variation in snow depth and ground-ice thickness through the winter. The model gives a daily measure of the mean ground-ice thickness in the study area. Modeled ice thickness increases in the case of rain-on-snow events and snow melt, and melts in warm weather when the snow has gone. Annual reindeer population growth-rate estimates, winter snow depth measurements, and direct ground-ice thickness measurements were used to parameterize the model (Kohler and Aanes 2004). While only four years of direct ground-ice thickness measurements were available, the observed mean ice thickness corresponded well with the predicted values for these years ($r = 0.99$). We assume that a thicker mean ice layer corresponds to a more extensive ice cover on the ground and interpret the estimated mean ice thickness as a proxy measure for the spatial extent of icing events.

An icing event is dated using the first day in a winter season in which there is a significant increase in model

ground-ice thickness. There was no icing event predicted for the winter of 1994–1995, while the icing event dates for the other winters were 3 December 1995, 25 January 1997, and 14 December 1997. These icing events were all due to rain-on-snow events with >10 mm of precipitation at above 0 temperatures.

Statistical analyses

For each individual reindeer, we calculated displacement, defined as the linear distance between five consecutive day locations (UTM coordinates). Displacement distributions are likely to show seasonal trends, vary among individuals and years, and show temporal autocorrelation for individual reindeer. To enable the statistical modeling of these aspects of the data, we used Generalized Additive Mixed Models (GAMMs), fitted using the *mgcv* package (Wood 2006) for R (R Development Core Team 2008). The displacement observations were assumed to come from a gamma distribution, an assumption supported by residual plots, and the linear predictors were fitted assuming a log link function (Wood 2006). Reindeer identity (ID) was fitted as a random factor and a first-order autoregressive process was assumed for the temporal autocorrelation within individuals. As fixed-effect predictor variables we used (1) days after 1 October modeled using a smoothing spline ($s(\text{Day})$) to model potential trends in displacement distances over the winter season; (2) Winter (coded as 94/95 to 97/98); (3) an indicator variable coded as 0 for dates before and 1 for dates after the date of the icing event of the winter (Ice); and (4) the number of days since the icing event of the winter (Iceday), coded as 0 for days before the date of the icing event (from 1 October). Our a priori hypothesis was that the mean displacement distances differed before and after the icing events and that this effect might decrease with time since the icing event of the winter. We also expected the effect of icing to differ between winters in relation to the extent of the icing events as measured by the estimated ice thickness. Our linear fixed-effect model was therefore $\mu = s(\text{Day}) + \text{Winter} + \text{Ice} + \text{Iceday} + \text{Winter} : \text{Ice} + \text{Winter} : \text{Iceday}$, with “:” indicating interaction terms.

RESULTS

Svalbard reindeer (*Rangifer tarandus plathyrinchus*) responded to icing events by increasing mean displacement distances immediately by two to four times expected levels for the time of year (Ice, Fig. 1a) and a subsequent 25–40% per month decrease in this displacement response (Iceday, Fig. 1a). Most individuals showed long-distance displacement (>7 km per 5-day interval) within the first month after the icing events (Fig. 2). In the case of no icing event, the lowest expected displacement distances occurred in December and January (Fig. 1b), with an increasing trend toward the end of the winter period. Toward the end of the

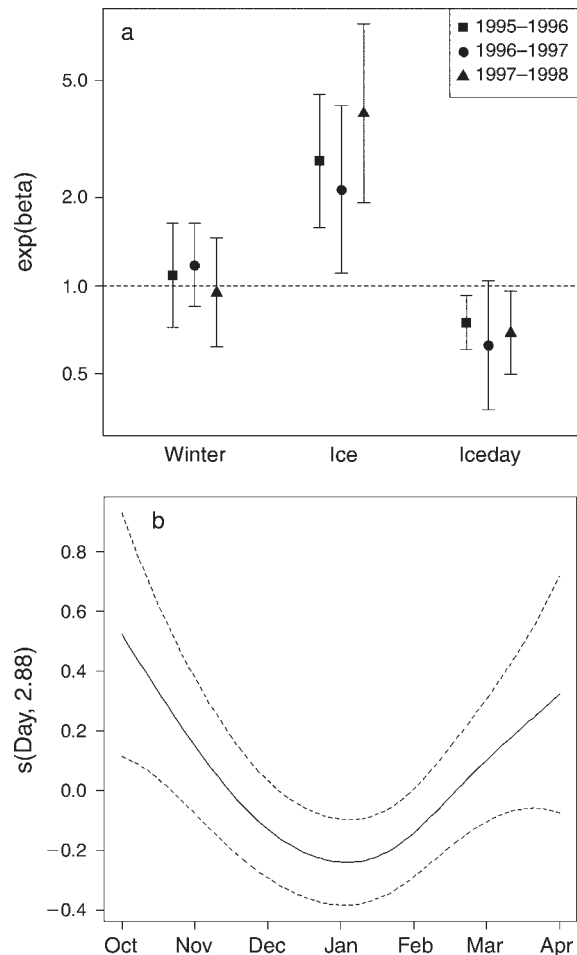


FIG. 1. (a) Estimates of the multiplicative effects on displacement distances [$\exp(\beta)$] of winters (Winter) in relation to the 1994/1995 baseline winter, of the immediate effect of icing within years (Ice), and slope estimates for the decrease in the effect of icing with days after the icing events (Iceday, measured at the scale of months). The dotted line shows the level of no effect [$\exp(\beta) = 1$] and error bars give 95% CI. (b) The seasonal trend in Svalbard reindeer (*Rangifer tarandus plathyrinchus*) displacement distances from 1 October to 31 March (mean \pm SE, dotted lines) as estimated using a smoothing spline with 2.88 degrees of freedom and plotted at the scale of the linear predictor (μ).

winter, this seasonal trend counteracted some of the predicted reduction in displacement distances due to increasing time elapsed since the icing events (Fig. 2). The predicted ice layer was an order of magnitude thicker in the winter 1995/1996 than in 1996/1997 and 1997/1998 (Fig. 2), but there was no evidence for this variation in the severity of the icing events to affect mean displacement distances (Fig. 1a). The increased displacement distances following icing were primarily due to directional movement out of the previously documented winter area (Fig. 3).

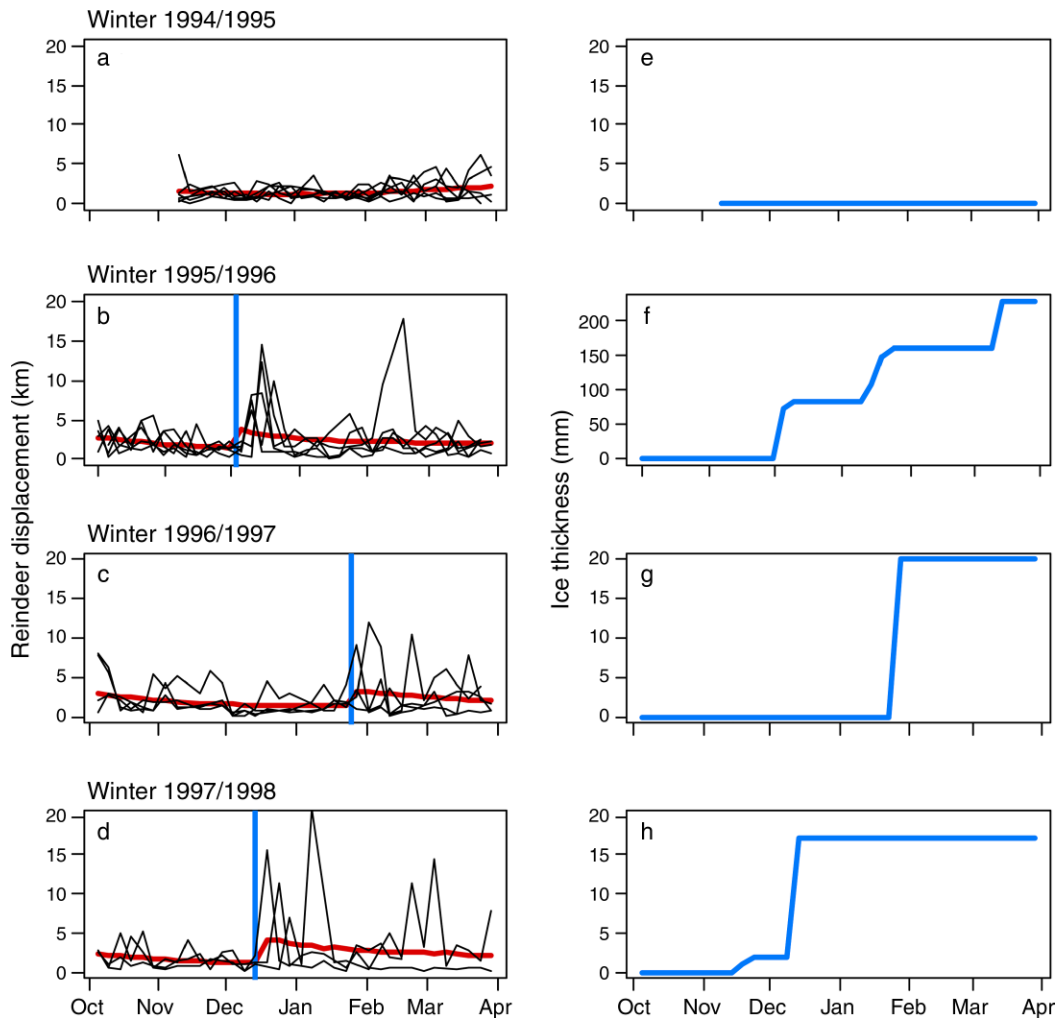


FIG. 2. Movement of female Svalbard reindeer related to icing events during four consecutive winters. Panels (a)–(d) show reindeer displacement (km) per 5-day interval (the black lines give the observations for each individual; the red line gives mean predicted displacement based on the GAMM model, while blue lines identify the estimated date of the icing event). Panels (e)–(h) show predicted ice thickness (mm) through the winters. Note that the ice layer was predicted to be an order of magnitude thicker in winter 1995/1996 than in other winters.

DISCUSSION

We demonstrate that Svalbard reindeer (*Rangifer tarandus plathyrinchus*) respond immediately to icing by increasing their displacement distances (Figs. 1 and 2). This suggests that the reindeer alter their behavior in an attempt to buffer the effect of extreme winter climate by opportunistically searching for new and more favorable wintering grounds (Fig. 3).

Nonlinear responses to climate have received much attention in the literature on trophic match–mismatch (Visser and Holleman 2001, Stenseth and Myrseth 2002, Post and Forchhammer 2008). We predict nonlinear responses to future icing events, since the predicted increased frequency of icing events may be accompanied with increased spatial extent (Putkonen and Roe 2003,

Shabbar and Bonsal 2003). The effect of the spatial displacement strategy on population dynamics is likely to depend on the spatial scale of the icing events. In many cases, dispersal and exploration distances of mammals are limited (e.g., Andreassen et al. 1998), so with increasing scale of icing we may predict nonlinear effects on survival. If the icing events are large scale, the search for better sites may fail and result in mass mortalities (Gunn 1995) or cause high emigration rates; both processes would cause large local population fluctuations. However, with smaller scale extent of locked pastures, the strategy of searching for ice-free ground is likely to buffer some of the effects of these climate events. The predicted increase in the spatial extent of icing in the future may therefore be disturbing news for the reindeer on Svalbard.

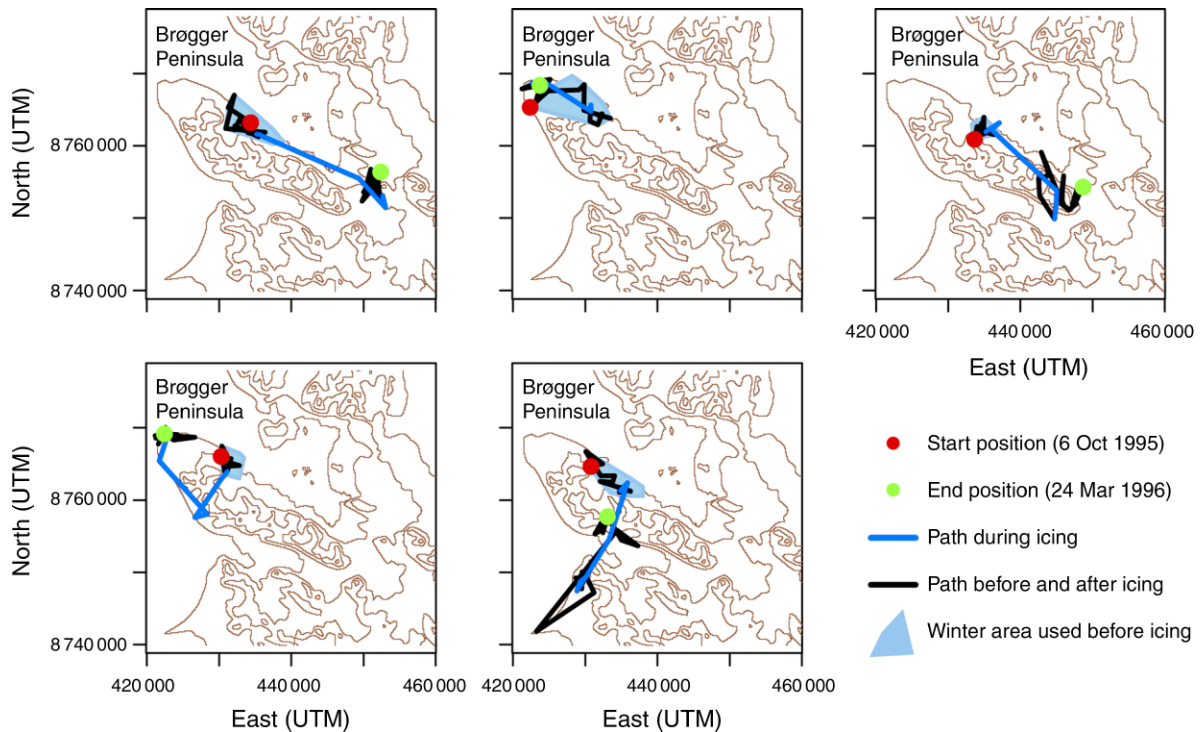


FIG. 3. Spatial trajectories of the five satellite-collared female Svalbard reindeer during the 1995/1996 winter. The red points are locations at the start (6 October 1995) and the green points are locations at the end (24 March 1996) of the observation period. The blue lines show the trajectories of individuals from 25 November to 29 December 1995, and therefore start just before the icing event on 3 December 1995. The black lines show movements before and after this period, and the light blue polygons represent the 100% minimum convex polygon of the winter area used prior to the icing event, including the previous winter.

Calves and old senescing individuals are the age classes typically most sensitive to environmental stress in ungulates (Gaillard et al. 2000), and opportunistic ranging in extreme winters do not seem to prevent mass mortalities of these age classes of Svalbard reindeer (Solberg et al. 2001). In addition, extreme winters affect the fecundity of all age classes of female Svalbard reindeer (Albon et al. 2002). While the high prime-age survival of Svalbard reindeer (Albon et al. 2002) will buffer some demographic effects of climate change (Morris et al. 2008), an increase in the frequency of icing events may potentially push the Svalbard reindeer into persistent population decline. The hypothesis that the spatial scale of both the climate effects and the available behavioral strategies determine the outcome for this endemic *Rangifer* subspecies is likely to be applicable also to other large herbivores living in temperate and arctic regions. Models or detailed monitoring of the spatial distribution of ice combined with extensive individual-based studies of space use and survival are needed to evaluate this hypothesis empirically.

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