Kelp and seaweed feeding by high-arctic wild reindeer under extreme winter conditions

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Abstract

One challenge in current arctic ecological research is to understand and predict how wildlife may respond to increased frequencies of "extreme" weather events. Heavy rain-on-snow (ROS) is one such extreme phenomenon associated with winter warming that is not well studied but has potentially profound ecosystem effects through changes in snow-pack properties and ice formation. Here we document how ice-locked pastures following substantial amounts of ROS forced coastal Svalbard reindeer (*Rangifer tarandus platyrhynchus*) to use marine habitat in late winter 2010. A thick coat of ground ice covered 98% of the lowland ranges, almost completely blocking access to terrestrial forage.

Accordingly, a population census revealed that 13% of the total population (n = 26 out of 206 individuals) and as much as 21% of one sub-population were feeding on washed-up kelp and seaweed on the sea-ice foot. Calves were overrepresented among the individuals that applied this foraging strategy, which probably represents a last attempt to avoid starvation under particularly severe foraging conditions. The study adds to the impression that extreme weather events such as heavy ROS and associated icing can trigger large changes in the realised foraging niche of arctic herbivores.

Keywords

climate change, ground-ice, High Arctic, marine algae, terrestrial herbivore, ungulate

Introduction

Current and future climate trends in most of the Arctic include rising temperatures, changing precipitation patterns and more frequent extreme weather events (ACIA 2004). The ecological effects of extreme weather phenomena are potentially large yet poorly explored (Post et al. 2009). For instance, heavy rain-on-snow (ROS) events, which are expected to become more frequent across the Arctic (Rennert et al. 2009), may strongly alter the snow-pack properties and even generate thick ice layers on the frozen ground when followed by sub-zero temperatures (Putkonen & Roe 2003; Kohler & Aanes 2004; Grenfell & Putkonen 2008; Rennert et al. 2009; Bartsch et al. 2010; Hansen et al. 2010a). There are indications that such ground-icing may have negative implications across trophic levels, including effects on plants (Robinson et al. 1998; Bjerke in press), microbiota (Coulson et al. 2000), and small (Kausrud et al. 2008; Gilg et al. 2009) and large herbivores (e.g. Kohler & Aanes 2004; Hansen et al. 2010a; Stien et al. 2010; Hansen et al. in press).

Despite its circumpolar relevance, our empirical knowledge of the ecological responses to heavy ROS events is limited to a few “early warning” systems, particularly the Ny-Ålesund area on the coast of Svalbard (Rennert et al. 2009). Here, heavy ROS and ground-icing occur rather regularly and have been shown to strongly reduce the population growth rates of the local meta-population of wild Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Kohler & Aanes 2004; Hansen et al. in press). Despite a remarkable ability to locate ice-free microhabitat beneath the snow-pack (Hansen et al. 2010a), ground-icing can generate large changes in the reindeer's behaviour, including exploratory movements across natural barriers (Stien et al. 2010) and range expansion to steep mountainous habitat (Hansen et al. 2010a). The present study documents how reindeer facing particularly icy conditions may further expand their niche to include washed-up kelps and seaweed (hereafter collectively referred to as kelp), a food source that is only occasionally included as a subsidy in the diets of large terrestrial herbivores (Carlton & Hodder 2003).

Materials and methods

Study area and species

The study area is located at Brøggerhalvøya, Sarsøyra and Kaffiøyra on the north-western coast of Spitsbergen (see e.g. Hansen et al. 2010b). Except for a small research settlement on Brøggerhalvøya (Ny-Ålesund), there is low human activity, and no hunting. The climate is oceanic and mild for this latitude (79°N), with average temperature of -11.1°C and average total precipitation of 229 mm during November-April 1979-2010. The plant cover is scarce and dominated by mosses, lichens, the dwarf willow *Salix polaris*, the purple saxifrage *Saxifraga oppositifolia* and graminoids. The vegetation rarely becomes taller than ~3-5 cm (except some graminoids) and is mainly confined to low altitudes.

Reindeer had been extinct in the area for almost a century due to past hunting, when 15 wild animals were transferred from Adventdalen to Brøggerhalvøya in 1978 (Aanes et al. 2000). The population irrupted and then crashed from ~360 to ~80 individuals during the extremely icy winter of 1994 (Kohler & Aanes 2004), when ~40 individuals migrated to Sarsøyra and established a new population (N.A. Øritsland, pers.comm.). The population on Kaffiøyra further south was in turn established during ~1996-97.

Svalbard reindeer are more or less solitary and, in contrast to most other *Rangifer*, they are highly sedentary and do not undertake long-distance migrations. Movement between the study ranges is restricted by glaciers, steep mountains and open sea or thin sea-ice, but spatiotemporal variation in foraging conditions may induce shorter migrations (Hansen et al. 2010b; Stien et al. 2010). Svalbard reindeer also differ from most other wild ungulates in that they are not subject to predation (only a handful of killings by polar bear *Ursus maritimus* are reported; Derocher et al. 2000; Sandal 2009), insect harassment (in our study area) or significant interspecific competition. The population dynamics are shaped by variation in climate and food availability (Reimers 1977, 1983; Aanes et al. 2000, 2002, 2003; Solberg et al. 2001; Kohler & Aanes 2004; Hansen et al. 2007; Tyler et al. 2008; Hansen et al. in press), particularly during winter. Individual behaviour and range use are closely related to the distribution of food plants, both during summer (Hansen et al. 2009b) and winter (Hansen et al. 2009a).

Data collection and analyses

As part of an annual monitoring programme, we surveyed the three sub-populations in late winter (1-8 April) 2010 from two snow mobiles crossing the landscape. Because of the open landscape and calm and stationary reindeer behaviour (see Hansen et al. 2009a), the animals can be approached at rather short distances (typically 100-200 m in winter), and census errors are assumedly small. Each separate sub-population was surveyed during one day, except for Brøggerhalvøya (two days).

Following standard procedures (see Hansen et al. 2010a), we performed snow profile transects distributed in a 900 x 1800 m grid system below 120 m a.s.l., providing a total of 57 snow profiles that reached the ground or, if present, ground-ice (profiles were not completed when the snow-pack was >100 cm deep, n = 1). We performed ground-ice measurements in n = 20 sites on Brøggerhalvøya, n = 22 sites on Sarsøyra, and n = 15 sites on Kaffiøyra. Altitudes above 120 m a.s.l. were not examined as they are generally not accessible on snow mobiles. Note that the ground-ice thickness was usually only measured down to 14-15 cm depth for logistical reasons, but this did not influence our estimate of central tendency (i.e. the median, see Results). Analyses were performed in R for Windows versions 2.12.0 (R Development Core Team 2010).

Results

Winter 2010 was the fourth mildest (-8.9°C) and the fourth wettest ever recorded (326 mm precipitation), with several heavy ROS events occurring during November-January (Fig. 1). Ground-ice (Fig. 2a) was present in 98% (n = 56 out of 57) of the snow profiles (median thickness 11 cm), and 89% of the profiles had ≥5 cm ground-ice. Under these severe foraging conditions, the population survey revealed that 13% of the total reindeer meta-population (Table 1) was feeding on washed-up kelps on the sea-ice foot (Fig. 2b,c). The proportion kelp feeders during this population "snap-shot" was 0% on Brøggerhalvøya, 12% on Kaffiøyra, and 21% on Sarsøyra, of which the latter area provided the best access to this type of habitat. The demographic composition among kelp feeders (Table 1) differed significantly from the non-kelp feeders (Fisher's exact test: $P < 0.01$), and the few calves alive at this point in winter were overrepresented (Fisher's exact test: $P < 0.01$). The adult (>1 yr) male segment ($X^2 = 0.066$, df = 1, $P = 0.797$), adult female segment ($X^2 = 2.494$, df = 1, $P = 0.114$), and unknown sex and age segment (Fisher's exact test: $P \approx 1$) were neither overrepresented nor underrepresented among the kelp feeders.

Discussion

The present study has documented how parts of a coastal Svalbard reindeer meta-population used kelp as food during a winter with extremely poor foraging conditions due to heavy ROS and extensive ground-icing. To our knowledge, such use of non-terrestrial food has neither been demonstrated nor quantified previously in Svalbard reindeer. Likewise, non-anecdotal reports of other large terrestrial herbivores feeding on marine algae are few (Carlton & Hodder 2003) and largely limited to introduced reindeer (*R. tarandus*) on South-Georgia (Leader-Williams et al. 1981) and red deer (*Cervus elaphus*) on the Isle of Rum (Conradt 2000), which occasionally fed on washed-up seaweed at low tide in winter.

Why should the reindeer use marine algae as food? Carlton & Hodder (2003) suggested that terrestrial mammals may utilize the intertidal zone as a seasonal food subsidy during resource-restricted periods of the year. Although quantitative data on kelp feeding are not available from other years, we have only observed this foraging strategy during winters when the accessibility of terrestrial forage has been particularly limited due to icing (R. Aanes, pers.obs.). The nutritional value of kelp and seaweed for terrestrial herbivores is largely unknown, but the *in vitro* digestibility of seaweed in the Isle of Rum system was comparable to terrestrial forage (Conradt 2000), and high mineral contents may possibly also have a significant nutritional value. On the other hand, roughly one fourth of the kelp feeders in our study apparently had diarrhoea (R. Aanes, pers.obs.). This was observed only occasionally among animals utilizing terrestrial foraging sites and could thus be associated with e.g. high salt intake from marine algae. The overrepresentation of calves among the kelp feeders further indicates that kelp is not a high-quality food source, as this demographic group has the poorest ability to compete for (or dig their way down to) the few ice-free terrestrial feeding sites.

Our results confirm that heavy ROS and icing can block access to winter forage (Hansen et al. 2010a) and thereby generate important changes in the realised foraging niche of arctic herbivores. In the Ny-Ålesund area, icing has been shown to induce sudden range displacements (Stien et al. 2010) and force parts of the population to seek steep mountainous habitat (Hansen et al. 2010a) or alternative marine food sources (this study). These refuges are unlikely to provide resources sufficient to maintain the population in the long-term, and icing has been shown to strongly suppress the reindeer population growth rates (Kohler & Aanes 2004; Hansen et al. in press). This was also confirmed during winter 2010 when there was an 18% reduction in population size (from summer 2009 to summer 2010) despite initially very low animal densities (R. Aanes, unpubl.). Whether the reindeer can dig their way out of the expected future increase in heavy ROS and icing (Rennert et al. 2009) is thus highly uncertain (Hansen et al. in press). Nevertheless, the behavioural plasticity demonstrated in the rapidly warming Ny-Ålesund area may serve as a bellwether of changes in range use and foraging niche expansion in arctic herbivores facing an increase in extreme weather (such as heavy ROS) or climate change in general. Furthermore, the present study adds to the impression that warmer and wetter winters may reduce forage accessibility and have overall negative implications for herbivore populations across the Arctic (Forchhammer and Boertmann 1993; Aanes et al. 2000, 2003; Solberg et al. 2001; Miller and Gunn 2003; Kohler and Aanes 2004; Tews et al. 2007; Hansen et al. 2010a; Stien et al. 2010; Hansen et al. in press).

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Tables

Table 1. Distribution of kelp-feeders versus non-kelp feeders across populations and demographic groups in a Svalbard reindeer meta-population during a “snap-shot” (population survey) in late winter 2010. Total estimated population size was 206 animals.

Population	Males (>1 yr)		Females (>1 yr)		Calves (<1 yr)		Unknown		Total	
	Kelp feeders	Non-kelp feeders	Kelp feeders	Non-kelp feeders	Kelp feeders	Non-kelp feeders	Kelp feeders	Non-kelp feeders	Kelp feeders	Non-kelp feeders
Brøggerhalvøya (n)	0	9	0	21	0	3	0	15	0	48
Sarsøyra (n)	6	16	4	46	6	2	1	1	17	65
Kaffiøyra (n)	2	26	5	33	0	1	2	7	9	67
Total (n)	8	51	9	100	6	6	3	23	26	180

Figure legends

Figure 1. The weather in Ny-Ålesund during winter 2010. Bars represent daily total precipitation (measured between 06 hrs day t-1 and 06 hrs day t), solid line indicates fluctuations in daily average temperature (00-24 hrs day t). Arrows indicate when major precipitation events (i.e. > 10 mm daily precipitation measured in day t) occurred at above-zero temperatures (measured in day t-1), i.e. on 11-12 November (total 43 mm), 11 December (17 mm), and 17-19 January (total 55 mm). Source: The Norwegian Meteorological Institute.

Figure 2. (a) Ridge habitat coated with ground-ice on Sarsøyra during April 2010. (b) Reindeer feeding on kelps on the beaches of Sarsøyra, with blocks of sea-ice in the background. (c) Reindeer feeding craters with kelp fragments on Sarsøyra. Photos: B. B. Hansen (the Norwegian Polar Institute).