



Preface

This master thesis is the final product of my Master's Degree in Natural Resource Management at the Norwegian University of Life Sciences (NMBU). The work started in the autumn of 2014 and was completed in June 2015. The main objective has been to study how Svalbard reindeer adjust their activity levels under altering weather conditions to better predict how this species will persist in a future with climate change. Working on this thesis has helped me learn about ungulates' thermoregulation, activity levels and temperature range, and Svalbard reindeer ecology. In addition, it has taught me about the process of writing a scientific paper. It has been instructive, challenging and exciting, and this year has increased my interest in natural resource management and ecology.

Several people deserve credit for helping me complete my thesis. I would first like to thank my supervisor professor Leif Egil Loe at NMBU for guidance, encouragement, supplying me with activity - and GPS data, and help with statistical analyses. I would also like to thank researcher Vebjørn Veiberg at the Norwegian Institute for Nature Research for reviewing the methods and results. A special thanks to Martin Gjesdal Bjørndal for supporting me throughout the whole process, for indispensable help with statistical analyses and proofreading. Last but not least, I would like to thank Johanne Rødsvik and Kristel Rødsvik Kolloen for proofreading and my whole family for constructive discussions and loads of motivation.

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Abstract

Animals are evolutionary adapted to certain weather conditions, but as the climate of the earth is changing many species may face new and significant challenges in their environment. The high-Arctic species Svalbard reindeer are living in extreme and unpredictable surroundings with large seasonal changes in their climatic environment. Physiological studies have found that Svalbard reindeer are adapted to low winter temperatures and high wind speeds. However, no long-term studies have investigated the effect of altering weather on the activity level in Svalbard reindeer, or if the animals show signs of cold or heat stress. The latter is of high interest, as the temperature on Svalbard has been rising during the last decades and is expected to continue to do so.

In this study I wanted to reveal how activity levels changed under altering weather conditions, especially under extreme and rare weather events. I specifically wanted to examine whether there were any threshold values where activity abruptly dropped. Adult female reindeer in Nordenskiöld land at Svalbard were equipped with GPS collars with integrated activity sensors during the years 2009-2014 (a total of 108 animal years). Activity levels were recorded continuously and stored in the collars every 5 minutes. Analyses were conducted for the seasons summer (July and August) and winter (December and January), and the included weather variables were temperature (°C), wind speed (m/s), precipitation (mm) and calculated wind chill (perceived temperature in °C).

I found effects of all four weather variables on the activity level of Svalbard reindeer, both during summer and winter. Svalbard reindeer reduced activity levels both at high and low temperatures during summer, potentially indicating both heat stress and cold stress during this season. Both an upper and lower temperature threshold value could be identified. During winter, activity was at its highest at low temperatures, substantiating that Svalbard reindeer are adapted to a cold climate. Activity levels decreased with increasing winter temperatures, but showed no signs of abrupt change and no threshold value could be identified. The same pattern as for temperature could be seen for windchill. With increasing wind speed, activity increased during summer. During winter, however, activity decreased with increasing wind speed. For both seasons, activity levels were reduced when there was precipitation compared to when there was not.

This study contributes to the understanding of activity levels in ungulates under altering weather conditions. In addition, knowing how a high-arctic species like Svalbard reindeer responds to variations in extreme weather events helps us understand how this species will persist in a future with a changing climate.

Sammendrag

Dyr er evolusjonært tilpasset sine normale værforhold, men med dagens klimaendringer opplever mange arter nye, og store, utfordringer i sitt naturlige miljø. Svalbardreinen lever i et ekstremt og uforutsigbart habitat i Arktis, med store sesongmessige endringer i sine klimatiske omgivelser. Fysiologiske studier har vist at Svalbardreinen er tilpasset lave vintertemperaturer og høye vindhastigheter, men ingen studier har undersøkt effekten av vær på aktivitetsnivå hos Svalbardrein over lengre tid, og om dyrene viser tegn til kulde- eller varmessstress. Sistnevnte er av stor interesse, siden temperaturen på Svalbard har vært økende de siste tiårene, og er forventet å fortsatt øke.

I dette studiet ønsket jeg å undersøke hvordan aktivitetsnivå hos Svalbardrein endret seg ved skiftende værforhold, spesielt under ekstreme og sjeldne værhendelser. Jeg ønsket spesielt å undersøke om det var noen terskelverdier der aktiviteten brått ble endret. Voksne simler i Nordenskiöld land på Svalbard ble utstyrt med GPS-halsbånd med integrerte aktivitetssensorer i årene 2009-2014 (totalt 108 dyre-år). Aktivitetsnivå ble registrert kontinuerlig og lagret i halsbåndet hvert 5. minutt. Analysene ble gjort for sommer (juli og august) og vinter (desember og januar) og de inkluderte værvariablene var temperatur (°C), vindstyrke (m/s), nedbør (mm) og beregnet vindavkjølingsindeks (opplevd temperatur i °C).

Jeg fant effekt av alle fire værvariablene på Svalbardreinens aktivitetsnivå, både sommer og vinter. Svalbardreinen reduserte aktivitetsnivå både ved høye og lave temperaturer om sommeren, noe som kan indikere både varmessstress og kuldestress under denne sesongen. Både en øvre og nedre terskelverdi for temperatur kunne identifiseres. Om vinteren var aktiviteten på sitt høyeste ved lave temperaturer, noe som underbygger argumentet om at Svalbardreinen er tilpasset et kaldt klima. Aktiviteten avtok med økende vintertemperaturer, men viste ingen tegn til brå endring og ingen terskelverdi kunne identifiseres. Det samme mønsteret kunne sees for analyser med den kalkulerte vindavkjølingsindeksen. Med økende vindhastighet økte aktiviteten om sommeren. Om vinteren reduserte reinen aktiviteten med økende vindhastighet. For begge sesonger var aktiviteten redusert ved nedbør sammenliknet med perioder uten nedbør.

Denne studien bidrar til forståelsen av hovdyrs aktivitetsnivå under skiftende værforhold. I tillegg gir innsikt i hvordan en kulde-tilpasset art som Svalbardreinen reagerer under ekstreme værhendelser kunnskap om hvordan denne arten vil overleve i en framtid med klimaendringer.

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1. Introduction

Animals are evolutionary adapted to the weather conditions in which they live, and keep their body temperature within narrow limits despite extreme fluctuations in their thermal environment (Irving & Krog 1955; Scholander et al. 1950b). However, as the climate of the earth is changing (IPCC 2014) many species face new and significant challenges with thermoregulation (Boyles et al. 2011; Mysterud et al. 2010). High temperatures, in combination with intense solar radiation and/or little wind, can potentially lead to heat stress, through exceeding an animal's upper critical temperature. Thermal stress can also occur when ambient temperature is low, wind speed is high or precipitation decrease the insulation value of the fur (Hammel 1955), resulting in cold stress. Physiological thermoregulation and changes in behaviour are an animal's primary ways of defence against adverse weather conditions and thermal stress. In addition, behavioural thermoregulation has been found to be less energetically expensive than autonomic thermoregulation (Maloney et al. 2005). Behavioural thermoregulation can include limiting costs of thermoregulation by seeking areas of more favourable microclimate (Mysterud & Østbye 1999) and/or switch activity to more favourable periods of the day (Beier & McCullough 1990).

There is growing evidence of environmental conditions affecting spatial behaviour and activity level of ungulates (Aublet et al. 2009; Bourgoïn et al. 2011; Bowyer & Kie 2009). In a study of grassland herbivores, Belovsky and Slade (1986) found a significant relationship between activity level and average daily temperature in all 14 cases studied. High ambient temperatures, alone or in combination with low wind speed, have been found to lead to heat stress in numerous ungulates (moose (*Alces alces*): (Renecker & Hudson 1986; Van Beest et al. 2012), cow (*Bos taurus*): (Shultz 1984), alpine ibex (*Capra ibex*): (Aublet et al. 2009), black-tailed deer (*Odocoileus hemionus columbianus*): (Bowyer & Kie 2009), wildebeest (*Connochaetes gnou*) (Maloney et al. 2005), and mouflon (*Ovis gmelini musimon*): (Bourgoïn et al. 2011)). As a result, the ungulates may reduce their activity levels (Belovsky & Slade 1986), feed less (Silanikove 2000), spend more time resting and ruminating (Bourgoïn et al. 2008) and/or seek thermal cover (moose: (Demarchi & Bunnell 1995), cow: (Shultz 1984)). Because muscular activity and food intake increase heat production, reduced activity levels in a shaded and cool area will help reduce heat stress (Silanikove 2000). Other ways to deal with heat stress are through reduced heart rate, increased skin circulation, shorter fur insulation, increased radiating surface and increased air movement or convection (Silanikove 2000).

Ungulates inhabiting both temperate and polar environments have also been found to experience cold stress, which normally, as for heat stress, lead to reduced activity levels and increased time spent lying (white-tailed deer (*Odocoileus virginianus*): (Beier & McCullough 1990; Moen 1978), beef cattle: (Graunke et al. 2011), dairy steers: (Redbo et al. 1996), wildebeest (Maloney et al. 2005) and mouflon: (Bourgoin et al. 2008)). Factors decreasing heat loss include internal shift in blood distribution, counter current heat exchange and decreased tissue conductance (Silanikove 2000). To increase heat production over the basal metabolic rate (BMR) an animal may shiver, exercise, tense muscles or chemically increase its metabolic rate (Silanikove 2000). Gates and Hudson (1979), however, discovered that if animals were subjected to cold stress, a strategy of foraging less and restricting activity would be more yielding than a strategy of increasing forage effort and activity levels. In line with what has been observed in previous studies, this means that an animal is expected to restrict activity levels, forage less and lie more when exposed to cold stress.

Activity levels vary throughout the year as a result of the seasonally difference in time necessary for an animal to meet its metabolic needs and the fluctuating forage quantity and quality (Beier & McCullough 1990). Because scarce and low-quality forage takes more time ruminating than abundant and high-quality forage, ruminants usually spend more time ruminating in the winter than during the summer (Jefferies et al. 1994). Both moose and roe deer (*Capreolus capreolus*) have been found to have shorter duration of inactive bouts during summer (Cederlund 1989). This coincides with the findings of Green and Bear (1990), who found that elk (*Cervus canadensis*) fed 55% of the time during summer (July and August), but only 45% of the time during winter (December to March). They explained increased resting in the winter with the increased need for ruminating as forage quality declined (Green & Bear 1990).

Long-term, continuous recording of activity is needed to investigate responses to rare, yet important weather events. The advantage of focal watches, one of the most used ways to study animal behaviour, is that the observer can separate between many activity classes. However, observations depend much on territory, and animals may be disturbed by the approaching observer (Gervasi et al. 2006). In addition, they are time and manpower intensive, thus usually not possible to conduct over longer time periods or with a high number of studied individuals, and may be hard to implement during the night and under harsh weather conditions (Craighead et al. 1973). A continuous, cost- and time effective way of monitoring animal activity is through animal-borne GPS-transmitters with activity loggers (Löttker et al. 2009; Moen et al. 1996). With this equipment disturbing the animal is avoided, and one can record animal locations often, both during day and night, and analyse movement patterns of specific individuals (Beringer et al. 2004) and its relation to activity levels.

Physiological adaptations of reindeer (*Rangifer tarandus*) are well known, and this arctic species is excellently adapted to a cold climate (Blix & Johnsen 1983; Irving & Krog 1955). Reindeer are able to reduce respiratory heat and water loss through their nasal structures, where heat exchange is actively regulated (Blix & Johnsen 1983) through a highly efficient counter-current heat exchange mechanism (Johnsen et al. 1985a). Conservation of heat and decreased tissue thermal gradients are also achieved by counter-current heat exchange in the lower legs (Irving & Krog 1955). Heat loss from the extremities differs very little from that of the trunk per unit area, despite the fact that the legs are much less insulated (Johnsen et al. 1985b). During heat stress situations in the winter, reindeer can lose some heat through the body surface, but most important are the legs (Johnsen et al. 1985b). However, reindeer's most effective way of losing heat, both during summer and winter, is through the respiratory tract (Folkow & Mercer 1986; Johnsen et al. 1985a; Johnsen et al. 1985b).

Behaviour and activity level of reindeer should be adapted to the thermal conditions of the environment for the individual to be able to maintain its core body temperature (Randall et al. 2002). On hot, sunny days, reindeer may enhance heat dissipation by increasing respiratory frequency and exhaled air temperature (Blix & Johnsen 1983; Folkow & Mercer 1986), or by behavioural actions like standing on snow patches, in shady or windy areas, or in cool water (Anderson & Nilssen 1998). Reindeer have been found to respond directly to high temperatures by decreasing feeding time (Mörschel & Klein 1997) or altering habitat use by moving to snow patches of higher elevations (Anderson & Nilssen 1998; Skarin et al. 2004). In regards to cold stress, reindeer have developed a highly cold-tolerant behaviour, with reduced activity levels for reduced energy costs (Cuyler & Øritsland 1993). Winter activity budget for reindeer is dominated by lying, and an animal may spend as much as 45 – 47 % of their time resting, and each resting bout can last up to 5-6 hours (Tyler 1987). When lying in a closed curl, reindeer may have only one-fifth of the surface area of the standing animal, and this preserves heat in an extraordinary way, as it covers all the short-haired body surfaces (Morrison 1966). This lying posture, with lower conductance, may significantly reduce the heat loss of the animal and save energy when maintained for longer periods (Cuyler & Øritsland 1993).

Svalbard reindeer (*Rangifer tarandus platyrhynchus*) are the most northerly living ungulate, inhabiting the islands of Svalbard. Animals in the Arctic live in an extreme and unpredictable environment, with large seasonal changes in their thermal surroundings. At present, climate change is rapidly altering the environment of reindeer, threatening the persistence of this arctic species (Vors & Boyce 2009). Temperature is presently rising and precipitation is increasing for all seasons of the year (Førland et al. 2012). As homeotherms maintain their body temperature stable during the cold winters and the warmer summers, they need to sustain an extreme flexibility in the variable physiological functions

concerned with the regulation of heat (Irving & Krog 1955). Svalbard reindeer seem to be better insulated against wind than any other reindeer or caribou subspecies and have not been found to be affected by low amounts of precipitation (Cuyler 1992). The winter fur of Svalbard reindeer has been found to be so well insulated that their deep body temperatures are higher during winter compared to summer (Cuyler & Øritsland 1986). In adult Svalbard reindeer a steady resting metabolic rate has been found to remain down to -50°C during winter (Blix 2005; Cuyler & Øritsland 2002a; Nilssen et al. 1984). This lower critical temperature threshold is the lowest temperature that an animal can stand without losing body temperature (Scholander et al. 1950b). The thermoneutral zone for winter is likely to extend up to 10°C (Nilssen et al. 1984). During the summer, arctic mammals adjust their temperature tolerance through shedding (Scholander et al. 1950a) which changes fur insulation due to reduced fur depth (Moote 1955). The lower critical temperature threshold increases to -15°C for Svalbard reindeer in the summer (Nilssen et al. 1984). Upper critical temperature threshold for the summer is not known.

Knowing how an arctic species like Svalbard reindeer responds to altering weather conditions is of high interest for understanding its future prospects, especially as the current climate change leads to rapid changes in the animals' environment. Previous studies on weather effects on reindeer have been focal studies over short time spans or experiments with reindeer's physical adaptations to thermoregulation (i.e. fur insulation value and counter-current heat exchange in the nasal region and lower legs). Physiological studies on metabolic rate and autonomic responses have also revealed how well-adapted to a cold climate the Svalbard reindeer is. However, no long term studies with continuous and quantitative data collection of weather and activity levels have been conducted. Therefore, the objective of this study was to examine how altering weather conditions affect activity levels of free-ranging female Svalbard reindeer during the seasons: summer and winter. This included detection of potential threshold values where reindeer activity changed abruptly and specifically analysing what patterns reindeer activity showed during rare weather events.

As most ruminants have been found to be more active during summer compared to winter I predict that **P1**) Svalbard reindeer activity levels will be higher during summer than during winter. Most previous studies on ungulate behaviour have reported reduced activity levels and increased time spent resting and ruminating as a result of heat stress (Aublet et al. 2009; Bourgoin et al. 2011; Bowyer & Kie 2009; Renecker & Hudson 1986; Shultz 1984; Van Beest et al. 2012), and I therefore predict that **P2**) Svalbard reindeer will reduce activity when temperature increase, due to heat stress, both in summer (**P2a**) and winter (**P2b**). The same pattern as for temperature (but with different threshold values) is predicted for wind chill, as wind chill is the combined effect of temperature and wind speed measured

as effective temperature in degrees Celsius. The dominant activity response to cold stress has been found to be a limit in activity level and a decrease in exposed body surface, by seeking favourable microclimates and lying at rest (Beier & McCullough 1990; Graunke et al. 2011; Moen 1978; Redbo et al. 1996). However, previous physiological experiments have demonstrated that Svalbard reindeer are resilient to temperatures down to -50°C in the winter and -15°C in the summer (Blix 2005; Cuyler & Øritsland 2002a; Nilssen 1984) whereas temperatures in Svalbard rarely drop below -40°C during winter and 0°C in the summer (Meteorologisk institutt 2015). I therefore predict that **P3**) there will be no reduction in activity levels due to cold stress, neither as a result of low ambient temperatures nor high wind speed during summer (**P3a**) or winter (**P3b**). Precipitation has only been found to affect reindeer when it occurs in large amounts and pelts get soaked (Cuyler 1992). I therefore predict that **P4**) precipitation, either falling as rain or snow, will not affect reindeer activity levels, neither during summer (**P4a**) nor winter (**P4b**).

meters may thaw during summer. The growing season is short (usually about 6-8 weeks), as plant growth is closely linked to the disappearance of snow (Kudo 1991). Growing season in the valleys of Reindalen, Colesdalen and Semmeldalen usually starts around the middle of June, but there is large variability between years due to fluctuations in precipitation during winter, and temperature and solar radiation during spring (Karlsen et al. 2014). The end of the growing season is usually in the beginning of September (Van der Wal et al. 2000b).

The annual variation in light conditions on Svalbard is distinct, with midnight sun from April 20th to August 22nd, and dark season from October 26th to February 16th (Førland et al. 1997). There are no roads in the area, and human presence is rare. During winter time there is some travelling along a snowmobile track, but as reindeer have been found to rapidly habituate to snowmobiles (Tyler 1991), the effect on reindeer activity is probably minimal.

According to Köppens system of climate classification, Svalbard has a polar tundra climate (ET), with mean air temperature of the warmest month under 10°C (polar), and more than one month has mean air temperature above 0°C (tundra). The coldest month is March, with mean values at -16.2°C, and the warmest month July, with mean values at 5.9°C (Meteorologisk institutt 2015). However, Svalbard has relatively high winter temperatures compared to other areas of the Arctic. This is due to oceanic influence, as the West Spitsbergen Current is a warm, salty current bringing water from the Atlantic into the Arctic creating the northernmost area of open water and thus bringing warm air temperatures with it (Førland et al. 1997). Winter weather is highly variable between years and months. Historically, there has been as much as 25°C between the highest and lowest monthly mean in December to March (Meteorologisk institutt 2015). Short periods of temperatures above zero are relatively normal, and as the mean winter temperature in the Arctic is increasing such periods are increasing in frequency and duration (Førland et al. 2012).

The prevailing winds on Svalbard are from the northeast-southeast sector and there are often strong winds during winter (Hanssen-Bauer et al. 1990). The most common wind direction is however along valleys or fjords from the inland to the coast (Førland et al. 1997). Winds are normally transporting mild air from lower latitudes, and as Svalbard is lying in a border zone between cold Arctic air from the north and mild maritime air from the south, unstable and stormy weather is common in winter (Førland et al. 1997).

Precipitation in the area is low, with mean annual precipitation at 190 mm/year (recorded at the weather station at Svalbard airport) (Meteorologisk institutt 2015), the lowest normal value recorded at any Norwegian station (Førland et al. 1997). Mean monthly precipitation is at its minimum during

the period of April to June (Meteorologisk institutt 2015). The study area is covered in snow from October to mid-June, but snow may occur at any time of the year (Meteorologisk institutt 2015). During the last few decades temperature, especially in the winter, and precipitation, have been increasing on Svalbard (Førland et al. 2012). This leads to the warming of permafrost and changing hydrological processes (Hinzman et al. 2005).

Reliable measurements of precipitation can be difficult to obtain under certain weather conditions, and blowing and drifting of snow may cause substantial problems for accurate data recording (Førland et al. 1997). In addition, the topography of Svalbard causes large local differences in precipitation and wind (Førland et al. 1997).

2.2. Study Species

Svalbard reindeer is a subspecies of reindeer that are only found on the archipelago of Svalbard (Banfield 1961). This species have several unique adaptations making them well equipped for a life as the world's most northerly living herbivore. Svalbard reindeer is a high-arctic tundra reindeer characterized by a small body size, short legs, ears and muzzle compared to other reindeer subspecies (Banfield 1961). The small body size has been thought to be the outcome of the generally low levels of plant biomass in the high Arctic (Van der Wal et al. 2000b), but the body shape of Svalbard reindeer is also in agreement with Allen's rule of species, stating that organisms in cold climates should have low ratios of surface area to volume. Despite the low levels of plant biomass (Brattbakk 1986) the vegetation utilized by reindeer in the high Arctic is known to be of high digestibility and nutritional content (Staaland et al. 1983). In addition, Svalbard reindeer have no natural predators and can store large amounts of body fat (Reimers et al. 1982). In fact they have higher amounts of body fat than any other cervid species, including domestic reindeer (Reimers et al. 1982).

Reindeer on the Svalbard archipelago face an extreme climate with polar night, cold temperatures and strong winds in winter, and continuous daylight, and a short growing season in summer. The high seasonality in the Arctic means that undisturbed grazing is crucial in order to maximize growth and fattening. Energy and protein stores need to be replenished in spring, and females need additional protein for lactation (Van der Wal et al. 2000b). During summer, energy is deposited as fat to survive the winter, and males need energy for the energetic demands of the rut (breeding season) (Van der Wal et al. 2000b), which is in October - November (Skogland 1989). The majority of the calves are born

in the first two weeks of June (Tyler 1987). Recruitment of calves varies widely between years, as harsh weather conditions during winter leads to larger die-off of calves in the spring (Solberg et al. 2001).

The Svalbard reindeer is the only large herbivore on Svalbard, and thus it is not exposed to any interspecific competition. Only two other large mammals are present; the arctic fox (*Alopex lagopus*) and polar bear (*Ursus maritimus*). Polar bears are opportunistic and can potentially prey on ungulates, but this rarely happens (Derocher et al. 2000). Insect harassment, which increases with increasing temperature, affect reindeer through reduced grazing time and increased energy expenditure (Weladji et al. 2003). Several studies point to oestrid fly (skin warble flies (*Hypoderma tarandi*) and nasal bot flies (*Cephenemyia trompe*)) harassment as the main cause of insect-related behavioural alterations (Anderson et al. 2001; Mörschel & Klein 1997; Reimers 1997) and mosquitos have been found to have little effect (Witter et al. 2012). As there are only mosquitos on Svalbard, insect harassment is unlikely to affect Svalbard reindeer activity to any large extent. Part of the study area (Colesdalen and part of Reindalen) is included in the area where hunting of reindeer is legal. Hunting pressure is generally low, and is restricted to an annual cull of 150-200 reindeer in the period of August 20th to September 10th (Syssemmannen på Svalbard 2009).

Although reindeer are known as migratory, seasonally nomadic animals, Svalbard reindeer seem neither to undertake long seasonal migrations nor to be nomadic within seasons (Tyler & Øritsland 1989). However, recent studies have suggested that poor winter foraging conditions may induce range expansion (Hansen et al. 2010a; Stien et al. 2010) and partial seasonal migration across natural barriers (Hansen et al. 2009). Patch choice for Svalbard reindeer has also been found to be influenced by the timing of snowmelt, and reindeer selectively forage in areas with early snowmelt and high plant biomass (Van der Wal et al. 2000b). The observed patterns of partial seasonal migration seems to be a combined result of density-dependent migration, learned behaviour, and trade-offs between access to high-quality forage (higher probability for successful calving) and avoiding the risk of crossing barriers (higher survival probability) (Hansen et al. 2010b). The dispersion pattern and the size of the individual home ranges of Svalbard reindeer are also different from other reindeer species, as Svalbard reindeer live in small groups (consisting of two to four individuals) without any other permanent social bonds than female and their calf (Loe et al. 2006), and on much smaller home range sizes than other reindeer species (Tyler & Øritsland 1989). This may suggest that feeding patches on Svalbard are smaller, but more widely spaced out than in continental habitats of other reindeer species (Tyler & Øritsland 1989).

Krüll et al. (1985) suggested that most animals have an intrinsic, regular, cyclic rhythm (called Zeitgebers) functioning as a physiological clock affected by changing environmental stimuli (e.g. sunrise, sunset and day length) and linked to internal psychological processes (e.g. feeding, digestion and rumination). However, continuous light in summer and darkness in winter have been found to cause a loss in daily rhythmic activity in reindeer living far above the Arctic circle (Maier & White 1998). Van Oort et al. (2005) found that reindeer showed alternating bouts of activity and inactivity typical of ruminants, but with cycles substantially shorter than 24 hours (ultradian) as would be expected. This coincided with the results of Loe et al. (2007), who also found that arctic reindeer showed season-specific feeding-rumination intervals, but with no distinct peak in activity at sunrise nor sunset and hence exhibiting nyctothermal activity. This loss of Zeitgebers is expected from animals who attempt to maximize energy intake rates in environments without predators (Loe et al. 2007).

Population estimates from capture-recapture modelling suggests that the study area has a population of about 800 adult female reindeer (Lee et al. 2015).

2.3. Activity Data

In total, 36 adult female reindeer were caught and equipped with GPS collars with integrated activity sensors. The catch was conducted with two snowmobiles and a net, and the reindeer were manually restrained (see Omsjoe et al. (2009) for more details on the method of capture). Collars were retrieved and returned each April from 2009 to 2014, and in February in the years 2010 and 2011. In addition, the collar of a single dead animal found during the summer of 2012, was retrieved in August 2012. Collars recorded location and activity in the time period between 22nd of April 2009 and 8th of April 2014, but not all 36 reindeer individuals were equipped with a collar every year (n = 16 in 2009, n = 25 in 2010, n = 33 in 2011, n = 23 in 2012, n = 8 in 2013 and n = 3 in 2014). In total 108 animal-years represented the data for the study.

The collars used were GPS Plus collars from VECTRONIC Aerospace (Berlin, Germany) equipped with a dual-axis motion sensor recording activity levels. The weight of the collar is approximately 650 gram, which is 1-2% of the winter body mass of adult female Svalbard reindeer. The activity sensor is composed of two perpendicular cylinders, giving activity on two different axes; horizontally and vertically. The sensor register a count each time a captive ball contacts a pin at each end of the cylinder, resulting in aggregated "hits" saved on intervals of 5 minutes. This is registered on a scale from 0 to 255, indicating numbers of hits per 5 minutes. The horizontal sensor is oriented perpendicular to the

animals' spine, and measures activity from left to right, generating X-values. The vertical sensor is oriented parallel to the spine of the animal and records the movement back and forth, generating Y-values. Activity is stored in the collar as activity on the X-axis (sideward; defined as activity X) and Y-axis (forward/backward; defined as activity Y).

Activity patterns from GPS-collars clearly separate active behaviour from resting (Godvik et al. 2009), but it is harder to separate between different types of active behaviour (Gervasi et al. 2006). However, due to reindeer spending 90% of their time either grazing or lying down (Skogland 1984), the biphasic categorisation (active and inactive) seems legitimate for the study of activity response to alternating weather conditions.

Location of the reindeer was recorded by the GPS unit every two hours. All GPS-coordinates and activity values were saved in the collar and downloaded after the recapture of the animal.

2.4. Weather Data

Weather data is available from the Norwegian Meteorological Institute (www.eklima.no). The data used in this study were recorded at the weather station at Svalbard airport (78° 15' N, 15° 28' E) at 28 m. a. s. l., located north of the study area (figure 1). This weather station shares similar environmental conditions as the study area, although there are some local topographic effects, especially on wind. Included weather variables from this weather station were temperature, wind speed and precipitation. Average temperature and wind speed were recorded four times a day (at hours 01.00, 07.00, 13.00, and 19.00) for the full study period (table 1) from 2009 to 2014. Accumulated precipitation was recorded twice a day (at hours 07.00 and 19.00) as precipitation over the last 12 hours (table 1).

In addition to analysing the weather variables recorded at Svalbard airport I included wind chill, the perceived decrease in air temperature felt by the body due to the flow of air (table 1). Standard wind chill index (T_{WC}), presented here as effective temperature in °C, is calculated by combining temperature and wind speed (Osczevski 1995). The formula I have used for this calculation is the enhanced formula Environment Canada together with other countries developed as the international standard for wind chill index in 2000 (Osczevski & Bluestein 2005), and the formula the Norwegian Meteorological institute use in their calculations (Meteorologisk institutt 2010). It gives standard wind chill index (T_{WC}) in °C from the following formula:

$$T_{WC} = 13.12 + 0.6215TA - 11.37(3.6 \times WS)^{0.16} + 0.3965TA (3.6 \times WS)^{0.16}$$

where WS is wind speed (recorded 10 m above ground) in m/s and TA is average temperature (recorded 2 m above ground) in °C. The equation is only valid for temperatures below 10 °C and wind speed above 3 m/s. Only valid temperature and wind speed recordings are included in the analysis, for both summer and winter.

Table 1. The four weather variables included in the study were temperature, precipitation, wind speed and wind chill. Here presented with units and description (Meteorologisk institutt 2015).

| Weather variable | Unit | Description |
|------------------|------|--|
| Temperature | °C | As measured 2 meter above ground level |
| Precipitation | mm | Precipitation accumulated last 12 hours |
| Wind speed | m/s | As measured 10 meter above ground level |
| Wind chill | °C | Calculated effective temperature, as perceived by the animal |

2.5. Statistical Analyses

Analyses were done for two homogenous bimonthly periods in terms of weather regime, the summer season defined as July and August, and the winter season defined as December and January. Contrast in seasonality is at its maximum between these two periods. In addition, the subdivision of summer and winter was based on light conditions, as there is midnight sun between April 20th and August 22nd and dark season between October 26th and February 16th (Førland et al. 1997). I also wanted to exclude the confounding effect of calving and rut on activity patterns.

Activity distribution and differences in activity level between the summer- and winter season was studied on 5-minute intervals, as stored in the collars. Activity X and activity Y showed significant and almost perfect positive correlation (p -value < 0.001, correlation coefficient = 0.96). Randomly chosen, activity Y was used in all further analyses.

For analyses with the weather variables, activity data was aggregated for each individual (taking the sum of all 5-minute aggregated activity values during each period) to two times a day (at hours 07.00 and 19.00), to match with precipitation, the weather variable on lowest temporal resolution.

Although initially continuous, precipitation was redefined as a categorical variable: precipitation (1) and no precipitation (0). This was due to a strong dominance of 0 mm precipitation recordings. Analyses were carried out for the effect of precipitation as a categorical variable. A separate analysis (for each season) was conducted for the continuous effect of precipitation, using only the subset of data where precipitation was recorded.

Candidate predictor variables were checked for co-linearity, by performing a correlation test using the cor-function in R (R Core Team 2014). Correlation between the weather variables and time of day was checked using the hector-function in the package polycor (Fox 2010). During summer (July and August), all correlation coefficients were far below the critical threshold value of 0.5 (Zuur et al. 2009). Correlation coefficients between the weather variables were below 0.1 and correlation coefficients between the weather variables and time of day were below 0.22 (table 2). However, all values had significant p-values ($p < 0.001$), but note the large amounts of data in the data set.

Table 2. Correlation coefficients for weather variables, and weather variables and time of day during summer (July and August). All correlation coefficients were below the critical value of 0.5 and all the predictor variables could thus be included in the same model. However, p-values were significant ($p < 0.001$) for all variables (both correlation between weather variables and correlation between weather variables and time of day), but note the large amounts of data in the data set.

| | Wind speed | Precipitation | Time of day |
|---------------|------------|---------------|-------------|
| Temperature | 0.04 | - 0.098 | 0.22 |
| Wind speed | - | 0.05 | 0.15 |
| Precipitation | - | - | 0.11 |

During winter (December and January), all the weather variables, and weather variables and time of day had correlation coefficients below 0.2 (table 3), thus below the critical threshold of 0.5 (Zuur et al. 2009). All p-values were significant for correlation between the three weather variables ($p < 0.001$), but for correlation between the weather variables and time of day, temperature had insignificant p-value ($p = 0.19$), and wind speed ($p = 0.01$) and precipitation were significant ($p < 0.001$). However, there were large amounts of data in my data set.

Table 3. Correlation coefficients for weather variables, and weather variables and time of day, during winter (December and January). Correlation coefficients were below the threshold value 0.5 and could thus be included

in the same model. All p-values were significant for correlation between the three weather variables ($p < 0.001$), but not for the weather variables and time of day, where temperature had insignificant p-value ($p = 0.19$), wind speed had slightly significant p-value ($p = 0.01$) and precipitation had significant p-value ($p < 0.001$).

| | Wind speed | Precipitation | Time of day |
|---------------|------------|---------------|-------------|
| Temperature | 0.12 | 0.17 | - 0.01 |
| Wind speed | - | 0.12 | - 0.02 |
| Precipitation | - | - | 0.11 |

Co-linearity was thus no restriction for including all predictor variables in the same model. In the analyses with temperature, wind speed and precipitation, the outcome of a predictor variable's effect on activity level was interpreted as the effect after accounting for the influence of the two other variables (a "Type 3" test approach). In the analysis with wind chill, only precipitation category was accounted for as wind chill is the combined effect of temperature and wind speed. Precipitation was included as a categorical variable (precipitation/no precipitation) in all analyses, except for the analyses where the continuous effect of precipitation was studied.

To explore the relationship between activity and the weather variables (see above) we fitted Generalized Additive Mixed Models (GAMMs) using the *mgcv* package in R (Wood 2006). Effect of individual was included as a random intercept to account for the combined effect of individual and collar differences in activity. Time of day was included as a categorical fixed-effect covariate (at the same temporal resolution as the weather data) to account for any diurnal variation in activity pattern (although no strong patterns are expected in continuous daylight (summer) and continuous darkness (winter) (Loe et al. 2007)). GAMMs are used to fit non-linear relationships between the predictor variables and the response variable (Hastie & Tibshirani 1990), and in this case GAMMs were used to analyse the non-linear effect of weather variables (predictors, fitted with spline functions) on the level of activity (response variable).

A primary objective of the study was to identify changes in activity levels during extreme and rare weather events, and whether there was a threshold value where activity levels changed abruptly. For this reason I needed the flexibility offered by the GAMM approach, instead of using a simple linear trend model.

To investigate whether changes in reindeer activity levels were related to movement I fitted GAMMs (Wood 2006) to identify the relationship between step length and activity. Step length, measured as distance moved in meter over a two-hour period, was calculated from the GPS coordinates by use of the *ltraj* function in the R-package *adehabitat* (Calenge 2006).

All statistical analyses were performed using R x64 3.1.1 (R Core Team 2014). For analyses on wind speed, wind chill and the continuous effect of precipitation recordings (for both summer and winter), degrees of freedom were restricted to 5. This was to prevent fitting too complex relationships that are not biologically realistic. When interpreting the results from a GAMM, a p-value is provided for the estimated degrees of freedom (edf) for the spline function (the higher the edf, the more complex is the spline function). When $p < 0.05$, this was interpreted as significant non-linearity. Detection of positive and negative effects, as well as thresholds, are visually detected based on plots of predicted effects with associated 95% confidence limits.

3. Results

3.1. Activity Distribution

The frequency distribution of activity counts of both axes (X and Y) showed a bimodal distribution with a distinct spike at 0 hits per five minutes (inactive behaviour), with one minimum around 20 and a less defined peak between 50 and 100 hits per five minutes (indicating different levels of active behaviour) (figure 2). I defined 20 as the threshold between inactive and active. The biphasic categorisation of active and inactive is supported by the bimodal frequency distribution of logger values (figure 2). Activity is recorded above 20 hits per five minutes (active) 56.2% of the time throughout the year.

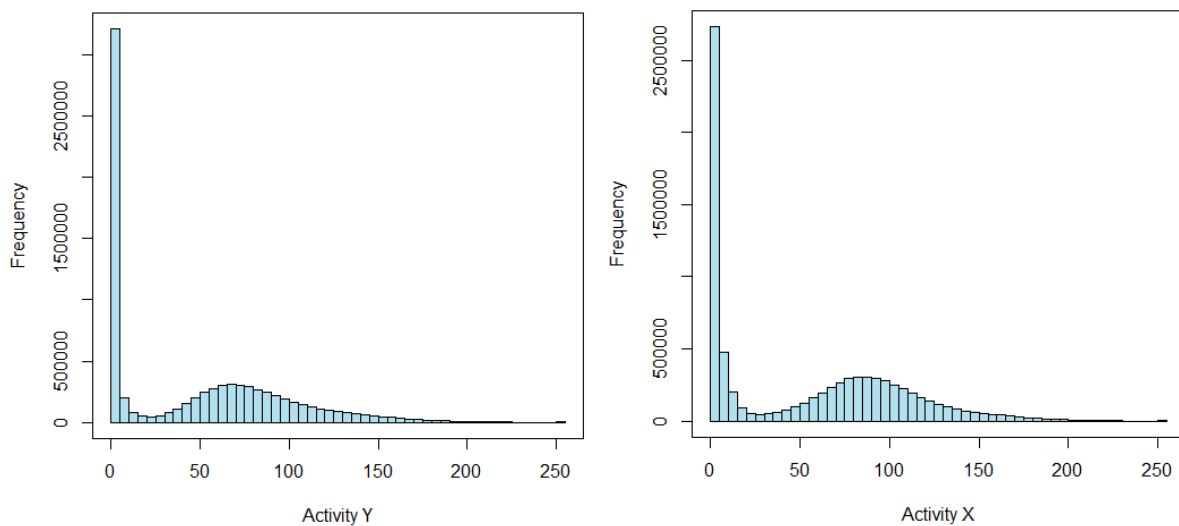


Figure 2. Frequency distribution for the activity counts for the year as a whole, for movements backwards/forwards (activity Y; left) and sideward (activity X; right). Activity is recorded as amounts of “hits” per five minutes (as stored in the collars), on an interval between 0 and 255 hits per five minutes. Animals were active (activity levels recorded above 20) 56.2% of the time during the year.

Coinciding with previous studies’ results and my predictions (P1), the probability of being active was higher in summer than in winter (estimate = -0.71, SE = 0.002, $z = -297.59$, $p < 0.001$). Mean activity level of recordings above 20 for summer was 113 hits per five minutes (of a maximum hit capacity of 255) and the mean for winter was 78 hits per five minutes. During summer reindeer were active 65.7% of the time, and during winter reindeer were active 48.6 % of the time.

3.2. Summer

Temperature during the summer ranged from 0.1°C to 16.8°C, with a mean of 6.6°C (figure 3B). The relationship between temperature and activity level in summer was significantly non-linear (estimated degrees of freedom of the spline, edf = 7.8, $p < 0.001$). Predicted activity increased steeply from a minimum at 0.1°C to about 5°C where it increased moderate, but steadily until a maximum at about 12°C where it again dropped sharply to the maximum temperature of 16.8°C (figure 3A). The threshold temperature of 12°C corresponded to the 97th percentile (only 3% of observations are warmer) of long-term observations (1984-2014) of summer temperature at Svalbard airport (Meteorologisk institutt 2015). The threshold temperature of 5°C corresponded to the 75th percentile (25% of observations are colder) of the long-term weather observations (Meteorologisk institutt 2015). As expected of P2a, but conflicting with predictions in P3a, Svalbard reindeer activity was low at both high and low ambient temperatures. Reindeer showed highest activity levels in the range of 5 – 12°C.

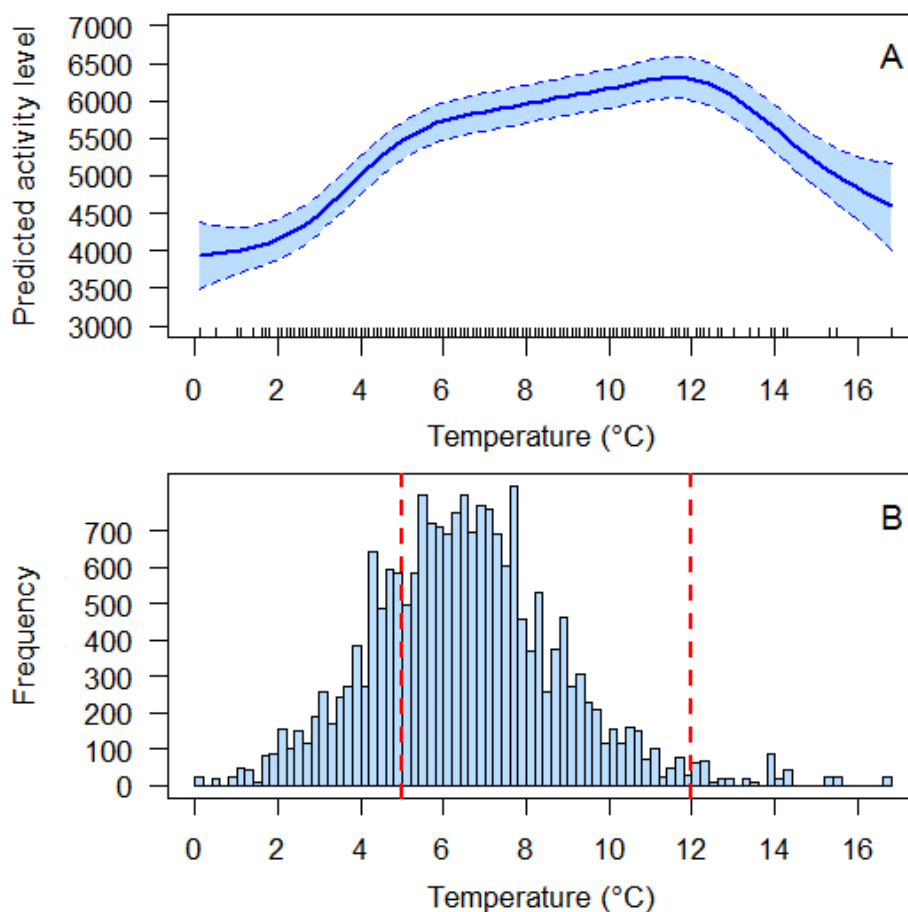


Figure 3A: Predicted mean activity level per 12 hour period as a function of temperature (°C) (when controlled for wind speed and precipitation) during summer. The dashed lines represent 95% confidence limits. **3B:** The distribution of temperature (°C) during summer, recorded at the weather station at Svalbard Airport. The vertical,

dashed lines indicate the threshold values where activity abruptly decreased. The lower value was at 5°C and the higher value at 12°C.

Wind speed during summer ranged from a minimum of 0 m/s to a maximum of 14.6 m/s, with a mean of 4.24 m/s (figure 4B). Although the effect of wind speed on predicted activity level was significantly non-linear (edf = 2.66, $p < 0.001$) the effect was close to linear (figure 4A). Because the relationship was so close to linear, I repeated the GAMM-analysis with a linear effect of wind speed. The result was significant (estimate = 60.43, SE = 4.44, $t = 13.6$, $p < 0.001$) and the total increase in activity was 12% from a minimum at 0 m/s to a maximum at 14.6 m/s. In accordance with P3a there was no reduction in activity levels when wind speed increased.

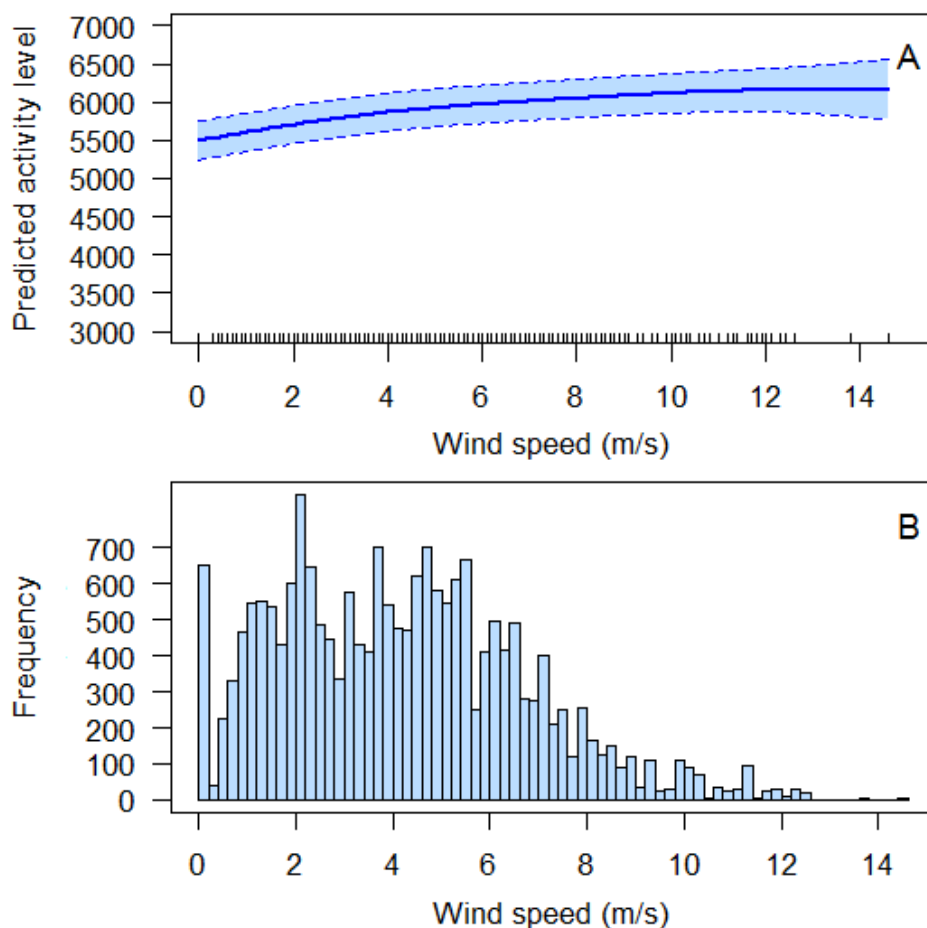


Figure 4A: Predicted mean activity level per 12 hour period as a function of wind speed in m/s (when controlled for precipitation and temperature) during summer. Dashed lines represent 95% confidence limits. **4B:** The distribution of wind speed (m/s) during summer, recorded at the weather station at Svalbard Airport.

Wind chill, the perceived air temperature due to wind (presented as effective temperature in °C), ranged from a minimum of -4.8°C to a maximum of 8.1°C with a mean of 2.6°C during summer (figure 5B). Wind chill numbers are always lower than air temperature for the range where the wind chill formula is valid (for temperatures below 10°C and wind speed above 3 m/s). The effect of wind chill was very similar to the effect of ambient temperature at temperatures below 10°C and showed a significant non-linear effect on predicted activity levels (edf = 5.5 and $p < 0.001$). There was a steady increase in activity level from a minimum at -4.8°C until about 2.5°C, where it levels out (figure 5A). The threshold value of 2.5°C corresponded to the 47th percentile, meaning that 47% of observations of calculated wind chill (from long-term observations (1984-2014) of temperature and wind speed at Svalbard airport) were lower than 2.5 effective °C (Meteorologisk institutt 2015). Contradicting to predictions in P2a reindeer activity was lowered at low wind chill values, potentially indicating signs of cold stress.

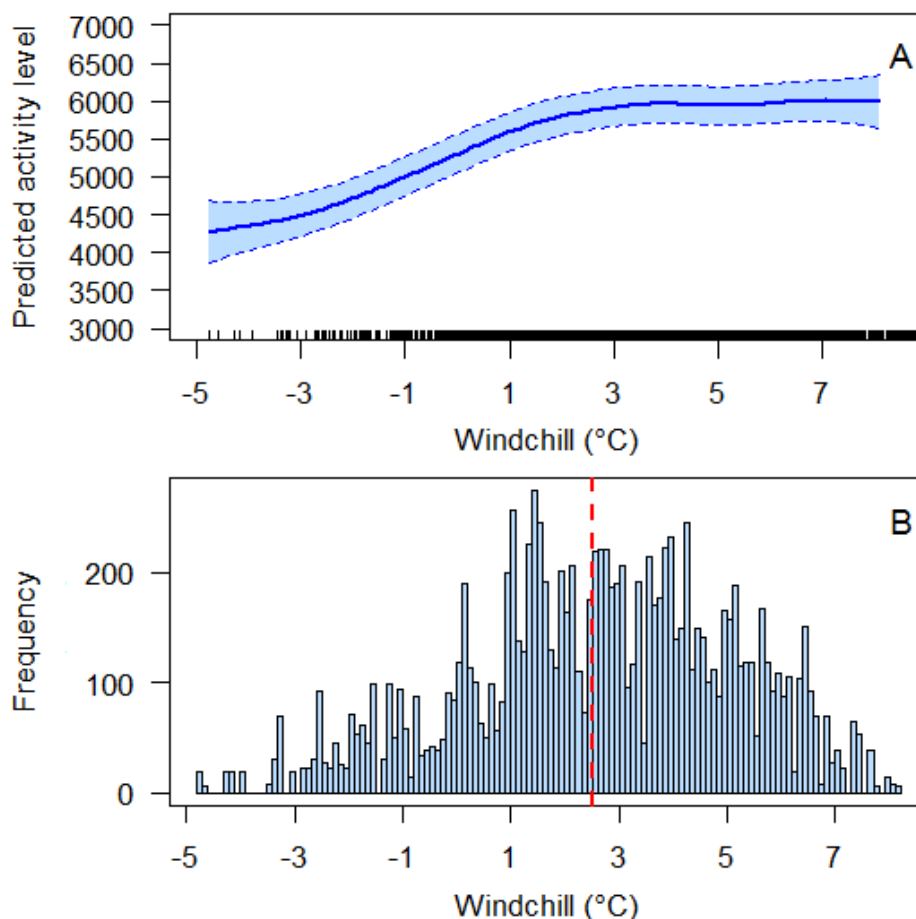


Figure 5A: Predicted mean activity level per 12 hour period as a function of wind chill, presented as effective temperature in °C (when controlled for precipitation) during summer. Dashed lines represent 95% confidence

limits. **5B**: The distribution of wind chill (presented as effective temperature in °C) during summer. The vertical, dashed line indicates the lower threshold value for high activity levels, at 2.5 effective °C.

Precipitation was recorded at 0 mm (no precipitation during the last 12 hours) 86.4% of the time during summer and below 1 mm was recorded 96% of the time (figure 6B). The maximum value for the precipitation recordings was 9.4 mm per 12 hours, however above 9 mm was only recorded 0.08% of the time during July and August 2009-2014. Mean value of precipitation recordings was 0.13 mm. When only including recordings of precipitation, the mean was 1.01 mm.

When analysed as a factor variable (1 for precipitation registrations and 0 for no precipitation), the effect of precipitation on activity level was non-significant (estimate = 48.1, SE = 34.0, $t = 1.41$, $p = 0.16$). When analysed as a continuous variable, only including observations with precipitation, the effect was significantly non-linear (edf = 3.76, $p < 0.001$). Activity level was stable until about 4 mm, where it dropped (figure 6A). However, at about 6.5 mm the activity level tended to increase rapidly again, to the maximum recorded precipitation value of 9.4 mm. However, there are very few observations above 3mm. Above 3 mm is recorded 1% of the time, and above 6.5 mm is recorded only 0.16% of the time. As high precipitation registrations were recorded rarely, predicted activity at these values are more uncertain than predicted activity at precipitation registrations closer to 0 mm.

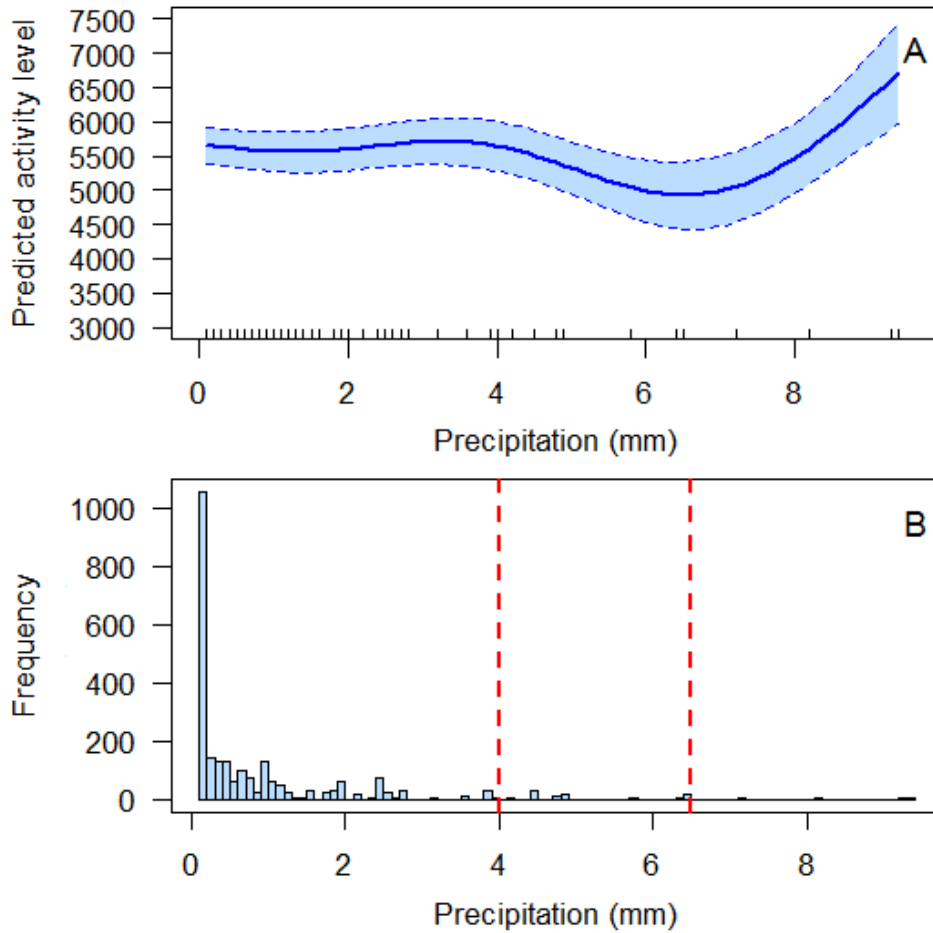


Figure 6A: Predicted mean activity level per 12 hour period as a function of precipitation, when only including recordings with precipitation (controlled for wind speed and temperature) during summer. Dashed lines represent 95% confidence limits. **6B:** The distribution of non-zero precipitation registrations (mm) during summer, recorded at the weather station at Svalbard Airport with a mean of 1.01 mm and a maximum of 9.4 mm. The two vertical dashed lines indicate the precipitation values where activity levels abruptly changed, at 4 mm and 6.5 mm.

Thus, my prediction (P4a) received little support. When analysed as a categorical variable, precipitation did not affect activity levels, but when analysed as a continuous variable, the result was significant. When precipitation reached about 4 mm precipitation per 12 hours, activity tended to decline, but a probable spurious, later increase in activity levels leaves this pattern inconclusive.

3.3. Winter

Temperature during winter (December and January) ranged from -29.9°C to 5.1°C with a mean of -8.23°C (figure 7B). The result of temperature's effect on predicted activity levels was significantly non-linear (edf = 2.62, $p < 0.001$). Activity levels decreased steadily from a maximum level at a temperature of -29.9°C to a minimum level at 5.1°C , showing a close to linear relationship between predicted activity level and temperature (figure 7A). I repeated the GAMM-analyses with a linear effect of temperature and the result was significant (estimate = -14.70 , SE = 1.08 , $t = -13.62$, $p < 0.001$). The total decrease in activity was 44% from a maximum at -29.9°C to a minimum at 5.1°C . Conflicting with my prediction (P2b), reindeer did not seem to be affected by heat stress as there was no threshold value where activity levels abruptly decreased. In accordance with my prediction on cold stress (P3b) low temperatures did not lead to decreased activity levels.

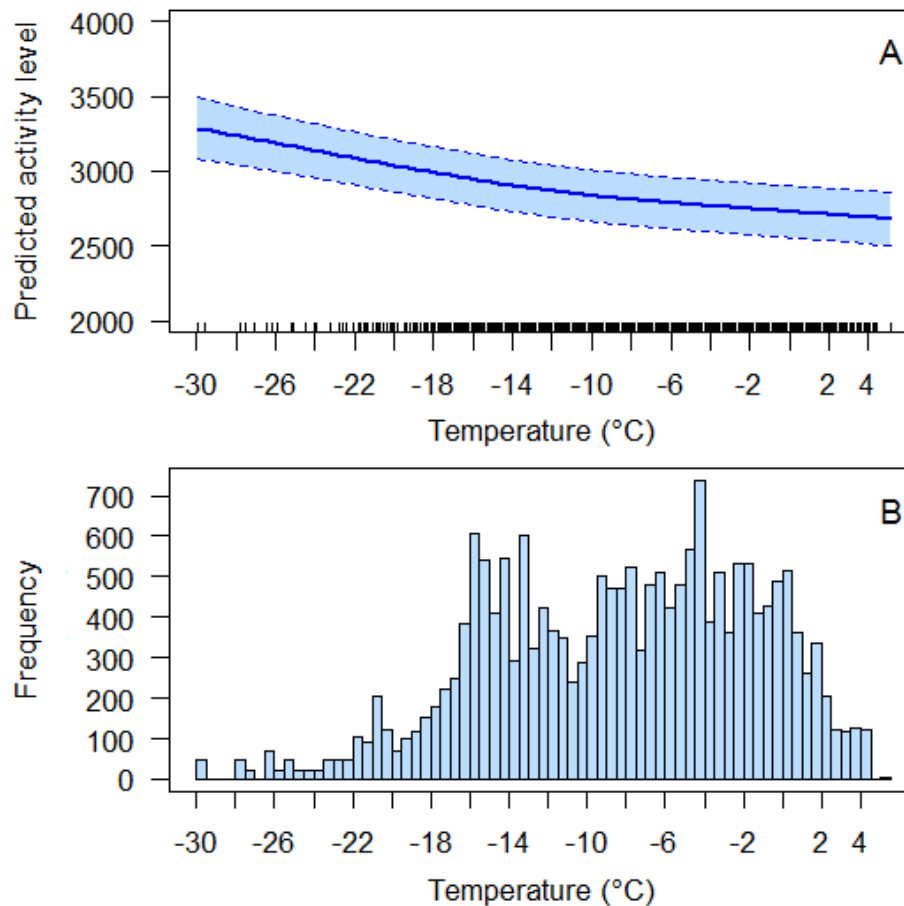


Figure 7A: Predicted mean activity level per 12 hour period as a function of temperature ($^{\circ}\text{C}$) (when controlled for wind speed and precipitation) during winter. The dashed lines represent 95% confidence limits. **7B:** The

distribution of temperature (°C) during winter, recorded at the weather station at Svalbard Airport with a minimum of -29.9°C and a maximum at 5.1°C.

Wind speed during winter ranged from 0 m/s to 23.5 m/s with a mean of 5.96 m/s (figure 8B). Effect of wind speed on predicted activity levels during winter was significantly non-linear (edf = 3.68, $p < 0.001$). Activity steadily declined from a maximum at 0 m/s to a minimum at 23.5 m/s (figure 8A). When repeating the analysis with a linear effect of wind speed the decrease was significant (est = -10.32, SE = 2.03, $t = -5.08$, $p < 0.001$) with a total decrease of 13% from a maximum activity level at wind speed at 0 m/s to a minimum activity level at 23 m/s. Thus, conflicting with my predictions (P2b) reindeer activity seemed to be affected by increased wind speed during winter, as predicted activity levels declined with increasing wind speed.

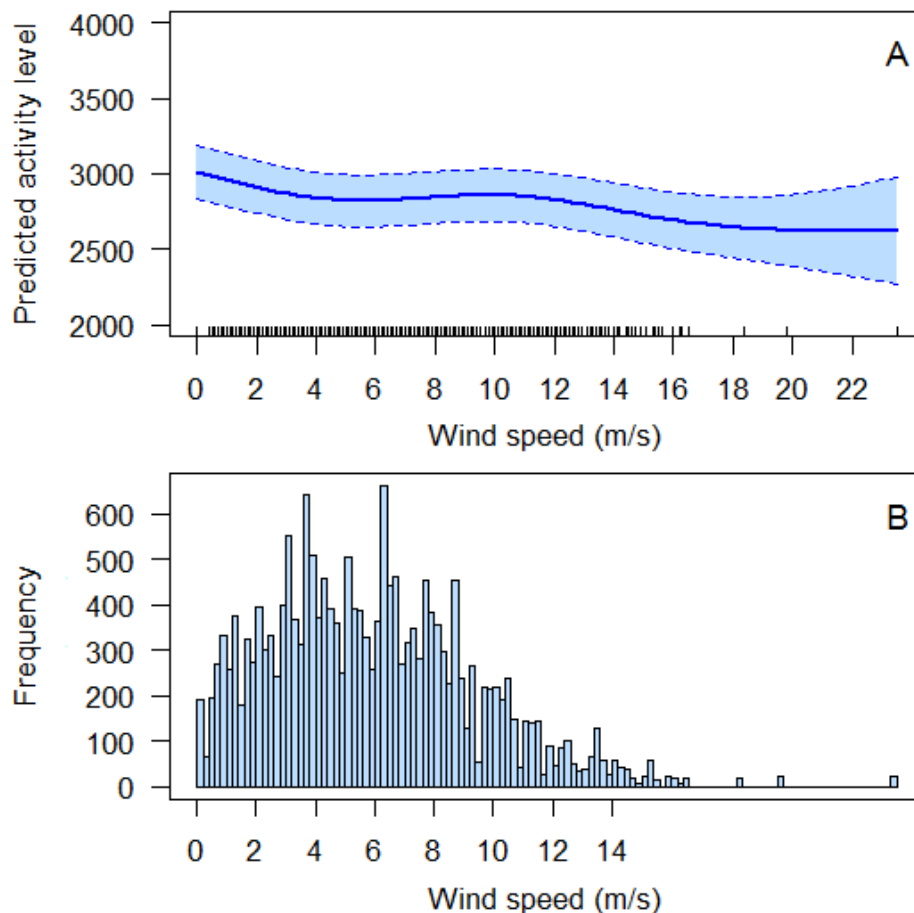


Figure 8A: Predicted mean activity level per 12 hour period as a function of wind speed (m/s) during winter, controlled for precipitation and temperature. The dashed lines represents 95% confidence limits. **8B:** Distribution

of wind speed (m/s) during winter, recorded at the weather station at Svalbard Airport with a minimum of 0 m/s and a maximum of 23.4 m/s.

Wind chill distribution, reported as the effective temperature, ranged from -40.2°C to 0°C with a mean of -16.2°C during winter (figure 9B). With a pattern similar to temperature, predicted activity level significantly decreased with increasing effective temperature (edf = 1, $p < 0.001$; figure 9A), in a significantly linear relationship. When replaced with a linear effect, the result was also significant (estimate = -10.8, SE = 0.9, $t = -11.5$, $p < 0.001$) and the decrease was 14% in total, from a maximum at -40°C to a minimum at 0°C. Giving no support to prediction P2b, there are no signs of heat stress, but in line with prediction P3b there are no signs of cold stress either.

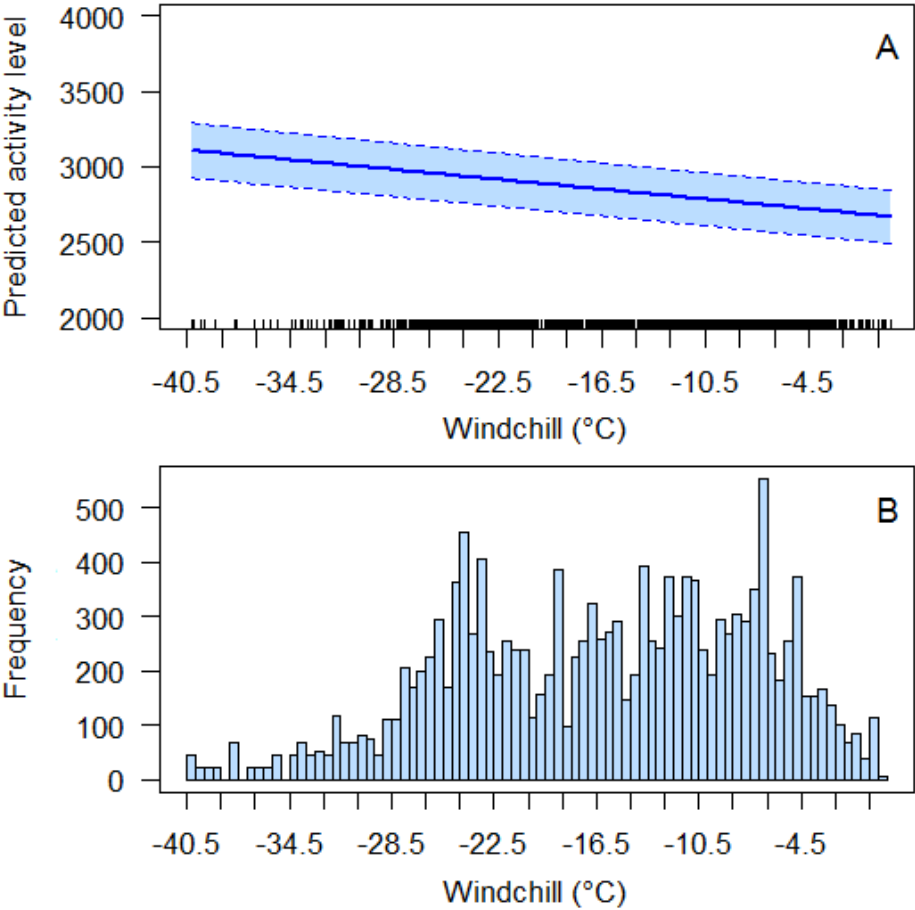


Figure 9A: Predicted mean activity level per 12 hour period as a function of wind chill (effective temperature in °C) during winter, controlled for precipitation. The dashed lines represents 95% confidence limits. **9B:** Distribution of wind chill (effective temperature in °C) during winter, recorded at the weather station at Svalbard Airport with a minimum of -40°C and a maximum at 0°C.

Precipitation was recorded at 0 mm 84.1% of the time during winter. The maximum recorded precipitation was 21.2 mm and mean was 0.2 mm. With only non-zero precipitation recordings, mean precipitation was 1.26 mm (Figure 11B).

When precipitation was categorised into precipitation (1) and no precipitation (0) the result of the variable and its effect on activity level was significant (est = -79.1, SE = 19.4, t = -4.1, p < 0.001). The animals were thus significantly more active when there was no precipitation compared to when there was (figure 10).

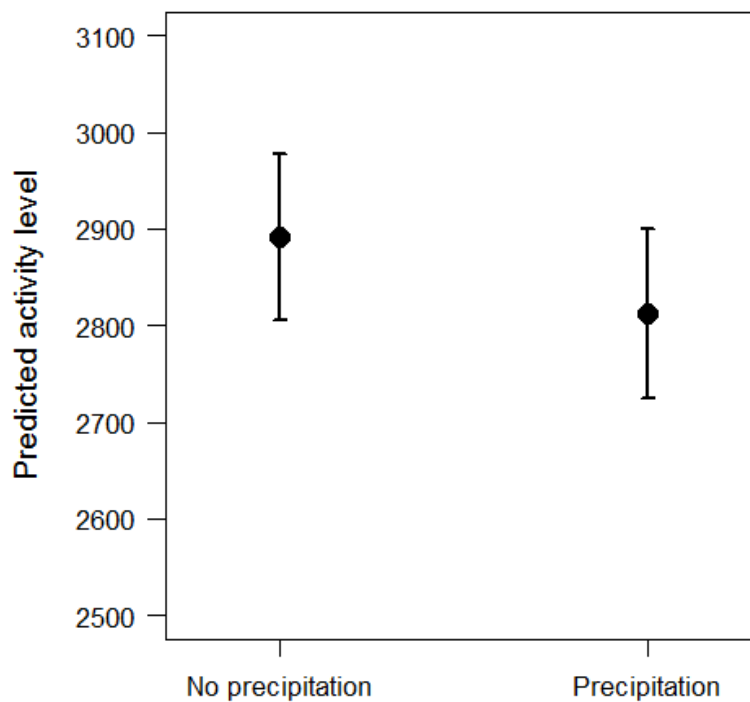


Figure 10: Predicted mean activity level per 12 hour period in winter as a function of precipitation category (no precipitation and precipitation) during winter, when controlled for wind speed and temperature. Error bars represents 95% confidence limits.

When analysing the continuous effect of precipitation, and only including observations with precipitation, the result was not significant (edf = 1, p = 0.45; figure 11A). Activity seemed therefore not to be affected by increasing amounts of precipitation.

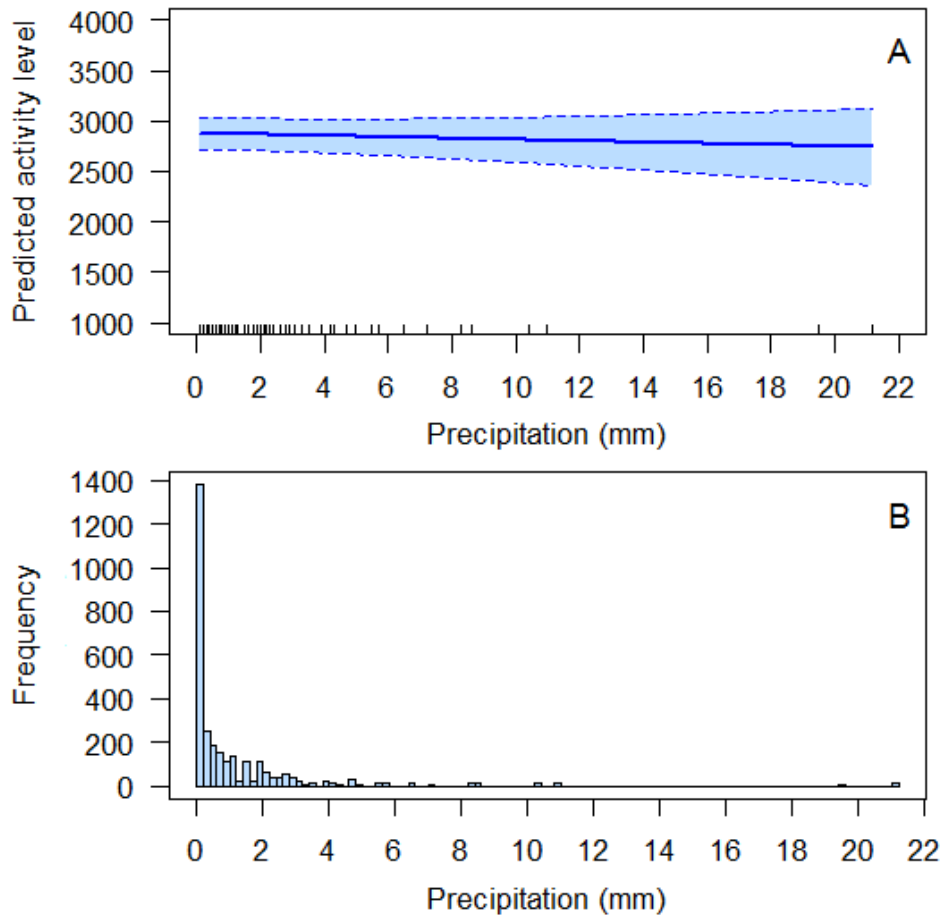


Figure 11A: Predicted mean activity level per 12 hour period as a function of precipitation (controlled for temperature and wind speed) during winter. The dashed lines represents 95% confidence limits. **11B:** Distribution of non-zero precipitation registrations (mm) during winter.

Conflicting with my prediction (P4b), and contrary to the summer season, activity levels seem to be affected by precipitation (activity levels are significantly higher when there is no precipitation), but unaffected by an increase in amount of recorded precipitation per 12 hours.

3.4. Step Length as a Function of Activity Level

In order to facilitate interpretation of increased and decreased activity, I investigated how activity level was related to movement distance. An increase in activity was found to be associated with an increase in step length (figure 12). When the activity level (aggregated on a two-hour period) was low, the step

length (measured as distance moved in meter over a two-hour period) was low, and with increasing activity step length also increased, in an almost perfect linear relationship.

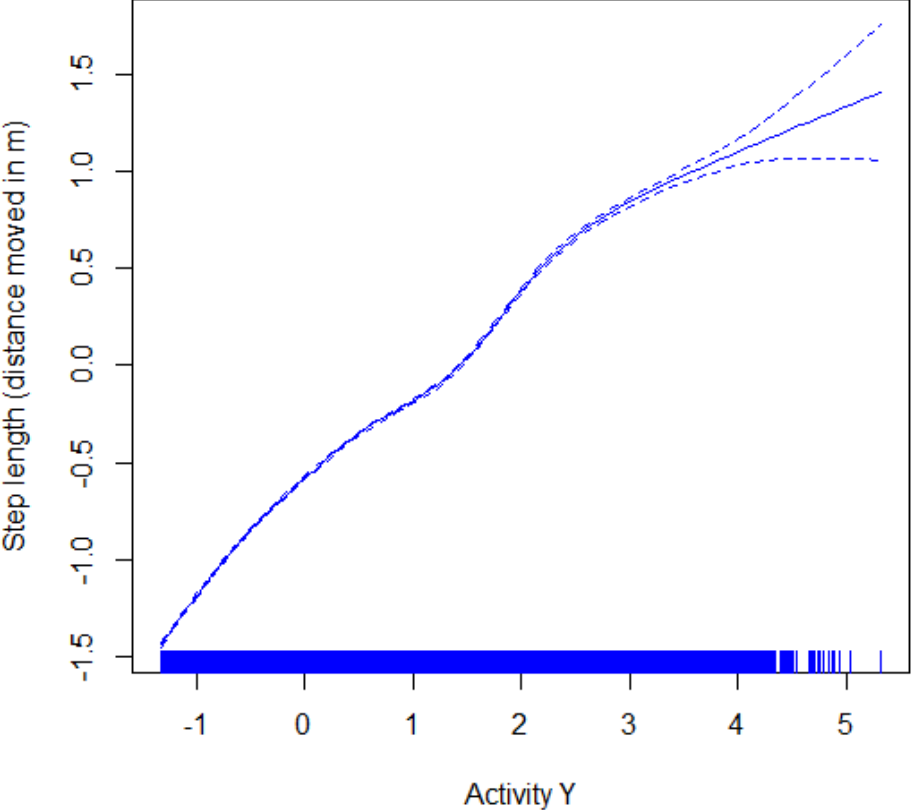


Figure 12. Step length (distance moved in meter over two hours; plotted at the scale of the predictor) as a function of scaled activity (aggregated at two hour level) shows that step length increases when activity increases, in an almost perfect relationship.

4. Discussion

This study is the first to demonstrate that free-ranging Svalbard reindeer adjust their activity levels with altering weather conditions. While a change in predicted activity level was evident for all weather parameters both during summer and winter, the effects of temperature and wind chill were stronger than the effects of wind speed and precipitation. Through reduced predicted activity levels, reindeer showed indications of heat stress during summer, but not during winter. The upper temperature value where reindeer activity abruptly declined was at abnormally high temperatures for Svalbard during the summer, which is as expected since animals are adapted to the weather they normally experience. In addition, presumably indicating cold stress, activity levels abruptly decreased at a certain lower threshold value during summer. This abrupt change was, however, at a normal temperature value for Svalbard during the summer. There was no indication of cold stress during winter, as activity levels were steady when ambient temperatures were high. Somewhat surprising was the significant increase in activity levels with decreasing temperatures during winter, and the discovery of the maximum activity level at the lowest recorded temperature.

This thesis support the view that large Arctic herbivores respond to their thermal environment by altering their activity levels. As predicted activity levels showed a decline at both a lower and upper threshold value during summer, reindeer seemed to be affected by both heat stress and cold stress during this season. However, during winter, Svalbard reindeer showed a different pattern than any other ungulate studied, as activity levels increased with decreasing temperatures. This study is the first to reveal this activity pattern at low temperatures during winter.

4.1. Seasonal Differences in Activity Levels

In accordance with my predictions (P1) and in line with previous studies on activity levels in ungulates (Beier & McCullough 1990; Georgii 1981; Kammermeyer & Marchinton 1977; Loe et al. 2007; Tyler & Blix 1990), activity of Svalbard reindeer was higher during summer than winter. In the summer reindeer were active 66% of the time, whilst during winter they were active 49% of the time. This supports the findings of Tyler (1987), who reported that Svalbard reindeer spent 68% of their time grazing in the summer, against 53% during the winter. When inactive, animals may be ruminating in addition to resting (Gross et al. 1995). Low-quality vegetation takes more time to ruminate than high-quality forage (Jefferies et al. 1994). During spring and summer, higher diet quality permits more rapid

processing of forage and thus increasing the opportunity to feed more frequently (Green & Bear 1990). The low activity level during winter may also indicate conservation of energy by the animal, through utilizing patches with relatively dense, but low quality forage (Cederlund 1989). During summer, emphasis may be shifted towards high quality, but widespread patches (Cederlund 1989). Underlying is the assumption that an animal is maximizing the net intake of energy, and that activity levels fluctuate as a result of the time necessary for an animal to meet seasonally changing metabolic needs and the shifts in forage quantity and quality (Beier & McCullough 1990).

4.2. Indications of Heat Stress During Summer

Svalbard reindeer showed signs of heat stress through reduced activity levels at high temperatures during summer, with a pronounced upper temperature value where activity levels declined sharply (in accordance with prediction P2a). In a previous study, Anderson and Nilssen (1998) concluded that reduced activity levels were a sign of thermoregulation as reindeer were observed lying down or standing still on the snow, and standing with the muzzle just above the snow surface (presumably to inhale cool air), when ambient temperatures reached a certain high level. Several studies in the past, including species such as caribou (*Rangifer tarandus granti*), mouflon, and cow have found decreased animal activity levels with increasing temperatures, and concluded that this is evidence of heat stress (mouflon: (Bourgoin et al. 2008), cow: (Shultz 1984) and caribou: (Mörschel & Klein 1997)). Moose, who are extremely well adapted to cold climates (and can tolerate temperatures down to -32°C without a change in their metabolic rate), suffer from heat stress during warm periods in both summer and winter (Renecker & Hudson 1986) and have been found to reduce activity levels and seek thermal cover when weather conditions are adverse (Demarchi & Bunnell 1995).

Activity levels in the summer showed a marked maximum activity level at a temperature of 12°C followed by a sharp decline with increasing temperatures. This can be interpreted as a sign of thermal stress through overheating, as an adult reindeer can experience heat stress even at moderate temperatures during summer due to their very effective fur and skin insulation (Irving & Krog 1955). In addition, reindeer do not sweat significantly even under heavy exercise (Irving & Krog 1955) and heat dissipation through the fur is rather scanty, thus making it hard for reindeer to cope with high temperatures. Coinciding with my results, previous studies have also found signs of heat stress in ungulates when temperatures exceed an upper threshold value (Aublet et al. 2009; Renecker & Hudson 1986; Van Beest et al. 2012). For example, white-tailed deer reduced their activity levels when

temperatures exceeded 16°C during spring, summer and fall (Beier & McCullough 1990). 12°C is hot for summers on Svalbard as temperatures above 12°C are only recorded 3% of the time during July and August in the years 1984-2014 (Meteorologisk institutt 2015). It therefore looks as if Svalbard reindeer cope with temperatures up to abnormally high levels before they reduce activity levels at what seems to be their upper critical threshold value, which I would suggest based on my results is at about 12°C in the summer. This is in line with what is expected, as animals are evolutionary adapted to their normal temperature range, but may show thermal stress at extremely high temperature values (Boyles et al. 2011).

As a potentially corroborative sign of heat stress in the summer season, reindeer activity levels increased with increasing wind speed. As activity levels were highest at high wind speed I speculate whether this is a sign of animals utilizing winds for cooling, as has been found for white-tailed deer (Beier & McCullough 1990). Coinciding with my results, Cuyler (1992) found that wind speed did not affect Svalbard reindeer to any large extent during summer. There is, however, no threshold value and no indication of distinct or abrupt changes in activity levels with altering wind speed and as I have not studied effect of wind speed under high temperatures separately a conclusion is hard to draw.

As Svalbard reindeer have been found to have trouble thermoregulating during warm periods during both summer and winter (Johnsen et al. 1985b), I would expect Svalbard reindeer to show signs of heat stress during winter (P2b) as well. Surprisingly, and contrary to this, there were no indications of Svalbard reindeer experiencing heat stress during winter. Activity levels decreased slowly with increasing temperature, but with no abrupt change in activity at higher temperatures. This is contradictory to the results of numerous previous studies on thermal stress in ungulates during winter (Beier & McCullough 1990; Graunke et al. 2011), but in line with the result from a study on moose (Van Beest et al. 2012). In addition, in accordance with my results, the thermoneutral zone for Svalbard reindeer during winter has been found to extend up to 10°C (Nilssen 1984), thus suggesting that Svalbard reindeer can cope with the high temperatures (up to 5°C in this study) that can occur during the arctic winter.

4.3. Signs of Cold Stress During Summer?

Contradictory to my predictions (P3a), Svalbard reindeer reduced activity levels when temperatures, both recorded ambient temperature and calculated effective temperature (wind chill), reached a certain low value during the summer. This coincides with the result of Beier and McCullough (1990),

who found that the activity of white-tailed deer declined when ambient temperatures were below their lower critical temperature threshold in the summer, at 10°C. Skarin et al. (2004) also found signs of animals experiencing cold stress in their study, as reindeer moved towards lower regions when ambient temperature was low and the wind speed was strong, clearly to utilize the favourable environmental conditions of warmer temperatures and less wind at lower elevations. In my results, activity declined from about 5°C down to 0°C, potentially indicating that animals experience cold stress at these temperature, and as a result of this move and forage less, stand still or lie down in areas with a favourable microclimate. Nilssen et al. (1984) reported that the lower critical temperature threshold for Svalbard reindeer during summer was -15°C. This is a much lower temperature value than the threshold value at 5°C which, based on this analysis looks like a lower critical temperature for high reindeer activity levels during summer. A threshold value of 5°C, however, seems abnormally high for reindeer in Svalbard, as temperatures below this point are recorded 25% of the time during the summer (Meteorologisk institutt 2015). In regards to wind chill, activity levels showed a distinct drop at 2.5 effective °C. This does, however, also seem like an unlikely high value for reindeer activity to decline, as 47% of long term wind chill observations (1984-2014) were below this point (Meteorologisk institutt 2015).

4.4.A Species Adapted to Low Temperatures During Winter

This study is the first to demonstrate that Svalbard reindeer activity increases with falling temperatures during the winter. In line with my predictions (P3b), Svalbard reindeer does not seem to be negatively affected by low ambient temperatures in the winter, in fact they seem to increase their activity levels with decreasing ambient temperature. The effect of wind chill showed the same pattern on activity levels as temperature: increasing activity levels with decreasing effective temperatures (wind chill factor). This is a surprising result in regards to previous studies' results on ruminant activity, as almost all of them report the opposite: a decrease in activity when temperature declines during winter (Beier & McCullough 1990; Bourgoin et al. 2011). Both Graunke et al. (2011) and Redbo et al. (1996) observed that beef cattle and outdoor-wintered dairy steers, respectively, were lying more during cold periods during the winter and increased amount of activity with increasing temperature. Beier and McCullough (1990) found that white-tailed deer shifted their activity to periods when weather conditions were more favourable for thermoregulation and selected habitats with reduced wind speeds and/or better solar exposure on cloudless days.

Homeothermic animals maintain their body temperature by balancing heat production and heat dissipation (Scholander et al. 1950a). If heat generated by activity substitutes the heat required for thermoregulation, increased activity levels with decreasing temperatures could be an energetically rewarding strategy (Gates & Hudson 1979). However, as numerous researchers have reported a decrease in activity during periods of low temperatures and cold stress, it seems unlikely that the observed increase in activity level in this study reflect an increase in physical activity for the matter of heat production. In addition, previous studies on physical adaptations of Svalbard reindeer have found this species to be well adapted to a cold climate (Cuyler & Øritsland 1993; Tyler 1987). Tyler (1987) predicted that Svalbard reindeer would not be distinctly cold stressed during winter, due to their fur's high insulation value. Several studies have shown that heat loss in Svalbard reindeer is low even at very low ambient temperatures, both during rest (Blix & Johnsen 1983) and during short periods of exercise (Folkow & Mercer 1986; Johnsen et al. 1985b; Nilssen et al. 1990). Based on these results and the result in this study, it seems likely that Svalbard reindeer may be practically unaffected by low winter temperature. In addition, the lower critical temperature threshold for Svalbard reindeer during winter, at -50°C (Nilssen et al. 1984), is far lower than normal temperature values reported at Svalbard in December and January (Meteorologisk institutt 2015). I speculate if snow conditions tend to be better during the periods with low temperature (possibly improving foraging conditions) thus making it more profitable for the animals to maintain high activity levels, and even increase their activity level, during cold time periods.

Although adapted to a cold winter season, activity steadily declined with increasing wind speed during the winter. This result is somewhat surprising when Svalbard reindeer withstand low temperatures so well, and contradicts my prediction in P3b. In addition, Svalbard reindeer fur has been found to have high insulation value and be more or less unaffected by high wind speeds (Cuyler & Øritsland 2002b) and individuals are able to seek favourable microclimates when wind speed is high and wind direction unfavourable (Cuyler 1992). However, the decrease in activity levels with increasing wind speed could be a sign of cold stress, potentially indicating that animals can withstand low temperatures, but not high wind speed during winter. This coincides with the results of Henshaw (1968), who found that caribou in north western Alaska were affected by wind speed during the winter, as movement normally ceased once wind speed exceeded levels of about 4.5 m/s and feeding ceased when wind speeds rose above 11 m/s. Continuing high wind speed caused caribou to change territories, lie down in areas with less wind speed, thus conserve energy and then resume feeding during calm periods again (Henshaw 1968). As Henshaw (1968) found that caribou would feed when ambient temperatures dropped as far down as -50°C, but would limit movements and feeding with increasing wind speed I speculate if

Svalbard reindeer show the same pattern, and seek shelter, stand still or lie down to reduce heat loss when wind speed is high.

4.5. Reduced Activity Levels With Precipitation?

My predictions (P4) for continued activity with precipitation received little support, as precipitation seemed to affect activity levels to a certain degree both during summer (P4a) and winter (P4b). This is consistent with the findings of Graunke et al. (2011), who studied the effect of weather (temperature, wind speed, precipitation, solar radiation and wind chill) and available protection on the behaviour of outdoor-wintered beef cattle, and found that during precipitation (i.e. rain, snow and hail) the animals sought shelter and protection in the forest. Horses (*Equus ferus caballus*) have also been found to seek shelter more frequently in rainy conditions (Heleski & Murtazashvili 2010). In this analysis, activity level during summer seemed to be steady for precipitation values up to 4 mm, but then activity levels declined. This is in accordance with the results of Cuyler (1992), who found that limited precipitation did not affect Svalbard reindeer's thermoregulation to any extent, and thus would not alter their activity levels, but when pelts got soaked the fur insulation dropped significantly. However, there are few observations above 3 mm in the data set during the summer (only 1% of the recordings) and this makes the relationship between precipitation and activity levels hard to interpret. An increase in predicted activity levels when precipitation exceeds 6 mm (as can be seen in the results) seems unlikely and may indicate randomness in the data. A certain conclusion is thus difficult to provide in terms of precipitation's effect on summer activity levels. During winter, predicted activity level was lower when there was precipitation compared to when there was not. Loe et al. (2007) also found negative effects of precipitation on activity levels during winter and suggested that the effect of precipitation (mainly as snow) may be linked to reduced forage availability. In addition, reduced activity levels may be a result of increased energy expenditure through locomotion in snow, as this increases with increasing snow depth (Parker et al. 1984). If precipitation during winter fall as rain, reduced activity levels could be due to the reduced insulation value of wet fur (Cuyler 1992), leading to cold stress.

4.6. Considerations in Regards to the Analyses

It can be stated that an increase in activity level is related to animal movement, as the results indicated that increased activity levels was correlated to distance moved in meter. This coincides with the results of Risenhoover (1986), who found that the amount of time moose were active per day was correlated to animal movements and the distance the animal moved during the day. In addition to connecting

activity to movement, Risenhoover (1986) could, through his additional direct observations of moose, report that the distance travelled increased exponentially as the duration of foraging periods increased. Thus, the more time an animal was active the more time it spent foraging and the further it moved during the day (Risenhoover 1986).

Interpreting the results of activity change due to altering weather must be done with caution and there may be potential sources of error. If there are temporal trends in weather, and temporal trends in activity caused by other factors than weather, this could result in confounded effects between weather and other, unknown drivers of activity. In the analyses, time of day is included as a covariate to account for diurnal variation, but apart from that I have not accounted for the temporal sequence of the activity data. I have assumed that the bimonthly periods of summer and winter are uniform, in the sense that day to day variation in weather and activity is much larger than any temporal trends within the season.

GAMMs were chosen for the flexibility they provide and because I wanted to find threshold values (if there were any) where activity abruptly changed. They do however have certain restrictions. Only additive differences can be studied, and not the interactions between the weather variables. I have thus not been able to study how reindeer activity is altered by one weather variable coinciding with another.

5. Conclusion and Future Perspectives

This study contributes to the understanding of activity levels in ungulates under altering weather conditions during summer and winter. It supports the view that ungulates respond to their thermal environment by altering their activity levels, probably due to individuals experiencing thermal stress. It is the first study to demonstrate how long-term recorded, free-ranging Svalbard reindeer adjust their activity levels with changes in temperature, wind speed, wind chill and precipitation. While a change in activity level was evident for all weather parameters both during summer and winter, the effect of temperature and wind chill was stronger than the effect of wind speed and precipitation. Reindeer showed signs of heat stress through reduced predicted activity levels during summer, but not winter. The upper temperature value where reindeer activity abruptly declined was at abnormally high temperatures for Svalbard during the summer, which is as expected since animals are adapted to the weather they normally experience. In addition, presumably indicating cold stress, activity levels abruptly decreased at a certain lower threshold value during summer. This abrupt change was, however, at a more normal temperature value for Svalbard, which makes it harder to conclude whether this is a lower critical threshold value or coincidences in the data. There was no sign of cold stress during winter. In fact, surprisingly and for the first time, a pattern of increased activity levels with decreasing temperatures was found. The increase in activity levels with decreasing temperatures in the winter was significant, and maximum activity level was at the lowest recorded temperature during December and January.

Knowing how the high-arctic Svalbard reindeer responds to variations in extreme weather events may increase our knowledge on how this species will persist in the. At present, climate change is rapidly altering the surroundings of this arctic species, and threatens the persistence of both reindeer and caribou populations in the Arctic (Vors & Boyce 2009). Temperatures have been rising steadily for the last decades and average winter temperature at Svalbard airport is projected to be around 10°C higher at the end of this century (Førland et al. 2012). In addition, the annual amount of precipitation is expected to further increase (Førland et al. 2012). Svalbard reindeer are well adapted to low temperatures (Cuyler & Øritsland 1986), and in this study show highest predicted activity levels at the lowest recorded ambient temperature during winter. Climate change with subsequent rising of temperature, altered atmospheric circulation and increased precipitation could thus be severe for this cold-adapted arctic species. Continued monitoring is necessary to be able to study Svalbard reindeer survival and foresee its persistence into the future.

6. References

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