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Thermoregulatory behavior in a warming Arctic: Bed site selection by Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in summer

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Photo: Linda Williamsen

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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 study was conducted partly at NMBU, and partly at The University Centre in Svalbard (UNIS). It is written as a part of a project supported by The Research Council of Norway: "Trapped in a cold-adapted body: The causes and consequences of phenotypic change in a rapidly warming Arctic".

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Thanks to my fellow NMBU and UNIS students for memorable moments both at the university and in our spare time. A huge thanks to my family for always being supportive, and helping me in any way. And last but not least, a huge thanks to Wilma and Emphie for always taking me out on great hikes and greeting me with such enthusiasm!

Linda Williamsen
Longyearbyen, May 2018

ABSTRACT

Climate change leads to rapidly increasing mean temperatures, and the climate warming is particularly pronounced in the Arctic. In Arctic mammals with long generation times, evolution of physiological and morphological traits may not be fast enough to keep up with the rapid climate warming. However, thermoregulatory behavior can possibly serve as an important buffer for negative effects from climate change, but this is poorly understood. In this study, I investigated if the Arctic, cold adapted, free-ranging Svalbard reindeer (*Rangifer tarandus platyrhynchus*) used cool bed sites as a part of their thermoregulation in summer. I predicted that Svalbard reindeer select cooling substrates, as snow and mire, as bed sites, and increasingly so at high ambient temperatures. I also predicted that they select cool ground as bed sites when cooling substrates are absent, and that the preference increases with ambient temperatures. In addition, I investigated if the bed site selection differed between age and sex of the individuals, as larger individuals are expected to have a higher need to select cooler bed sites compared to smaller individuals during warm ambient temperatures. I visually detected resting reindeer in field and recorded habitat variables and ground temperature both at 371 bed sites and random control sites 10 and 100 meters distant. Bed site selection was analyzed using resource selection functions. I found that the Svalbard reindeer preferred bed sites on cool substrates (snow and mire) as well as cool ground on days with warm ambient temperature. The preference for both cooling substrates and cool ground did not depend on age or sex. This study hence demonstrated that all age and sex categories of Svalbard reindeer used bed sites for thermoregulation, indicating heat stress during warm periods in summer. The study was conducted in an environment where neither predatory threat or insect harassment (monitored, but found insignificant) influenced the bed site selection. As such, this study is among the first to provide conclusive evidence of the use of bed sites as thermal refugee, without confounding factors. It is also the first study to find a selection for ground temperature by a cold adapted ungulate in a habitat where cold and wet cooling substrates and shade from canopy are not involved. The study contributes to the understanding of how a highly cold adapted Arctic ungulate adapt to increasing temperatures, which are expected to continue in the future.

CONTENTS

1 INTRODUCTION

Ambient temperature is considered as a crucial abiotic factor directly influencing animal spatial behavior (Hetem et al. 2007), species distribution (Parmesan 2006) and population dynamics (Post et al. 2009). Endotherms have evolved mechanisms to maintain optimal internal temperature despite seasonal fluctuations in their thermal environment (Folkow & Mercer 1986; Irving & Krog 1955; Scholander et al. 1950). However, as the recent climate change leads to rapidly increasing mean temperatures worldwide (IPCC 2014), many species face great challenges in terms of thermoregulation (Scheffers et al. 2016; Walther et al. 2002). The effect of ambient temperature is likely to become increasingly important for all these processes as the climate deviates from historic norms, causing increased average temperature, as well as more frequent occurrences of extreme temperatures (Hansen et al. 2011; Mysterud & Sæther 2010).

Ungulates have a variety of evolutionarily developed physiological and morphological mechanisms to reduce the impact of changing ambient temperatures (Cain et al. 2006), allowing them to maintain a relatively constant body temperature as ambient temperature varies across seasons (Irving & Krog 1955; van Beest & Milner 2013). When the ambient temperature exceeds an animal's lower or upper critical temperature, the animal will experience greater thermoregulation costs and possibly thermal stress (Boyles et al. 2011; Cain et al. 2006; Folkow & Mercer 1986). Physiological adaptations such as evaporation of water, either through skin or respiratory tract, and changes in blood circulation are used to maintain body temperature balance. Difference in body size and shape, pelage and skin characteristics, and fat deposition are all morphological adaptations to the climate conditions (Cain et al. 2006). For example, large-bodied individuals, which have a lower surface-area-to-volume ratio and higher thermal inertia, will gain and loose heat from the environment at a slower rate than small-bodied individuals (Porter & Kearney 2009). Large individuals should therefore be more sensitive to thermal conditions above their thermoneutral zone than below (Broders et al. 2012; Shrestha et al. 2014). Even though evolutionary adaptations to climate warming have been documented (Schilthuizen & Kellermann 2014), there is a concern that adaptations by morphological and physiological mechanisms to the environment may not be fast enough to keep up with the rapid climate warming (Parmesan 2006). Behavioral adaptations to thermoregulate can compensate for the much slower evolutionary adaptations, and possibly serve as an important buffer for negative effects from climate change (Boutin & Lane 2014; van Beest & Milner 2013).

Thermoregulatory behavior is an efficient way to adapt to the rapidly increasing temperatures, and can reduce the likelihood for heat stress in ungulates, especially during summer (Marchand et al. 2014). Behavioral thermoregulation has also been found to be less energy demanding than autonomic thermoregulation (e.g. involuntary thermoeffector responses, like panting) (Folkow & Mercer 1986; Maloney et al. 2005; van Beest & Milner 2013). Three reported behavioral strategies in which ungulates can avoid thermal stress, and thus lower the energy costs, are modifying activity to more favorable periods of the day (Aublet et al. 2009; Bourgoin et al. 2011), make short-term elevational migrations to escape warm ambient temperatures during summer (Aublet et al. 2009), or do a more fine-scale habitat selection (Mysterud 1996; van Beest et al. 2012), including selection of resting sites.

Ungulates spend several hours of the day bedded during rest and rumination, and selection of bed sites can potentially play an important role in thermoregulation. Bed site selection either by bedding down under dense canopy cover for shade (Belovsky 1981; van Beest & Milner 2013), and/or to find bed sites on cold or wet substrates as snow and mire, which through conduction leads to greater heat loss (McCann et al. 2016; Mysterud 1996), are two strategies by which ungulates can cope with heat stress. Such bed site selection has been shown as an effective thermoregulatory behavior across a wide range of species like lizards (Bauwens et al. 1996), vultures (Ward et al. 2008) and different ungulates; Previous studies show that the cold adapted moose (*Alces alces*) decreases the activity level (Dussault et al. 2004) and increases the selection for thermal covers, such as dense canopy and/or wet bed site substrate during warm summer days (McCann et al. 2016; van Beest et al. 2012; van Beest & Milner 2013) when temperatures exceed their upper critical temperature. Mouflon (*Ovis gmelini*) and roe deer (*Capreolus capreolus*) have also been found to select shaded areas or wet bed sites at high ambient temperatures (mouflon: Marchand et al. 2014; roe deer: Mysterud 1996).

Climate change is particularly severe in Arctic areas (ACIA 2004; Førland et al. 2011; IPCC 2014; Moen 2008; Nordli et al. 2014). In the Arctic, previous research has mainly focused on the effect of climate change on ungulates during the winter season, as this is, in many cases, the limiting season due to harsh climate and scarce food availability (Albon et al. 2017; Tveraa et al. 2007; Weladji et al. 2002). However, following the rapid temperature increase, it is possible that Arctic ungulates will also show thermoregulatory behavior in summer, as found in temperate species (McCann et al. 2016; Mysterud 1996; van Beest & Milner 2013). The high activity level during summer (Loe et al. 2007; Moen et al. 1996), as well as increased metabolism and food intake, result in a higher probability of heat stress at a time of year when the conditions are least favorable for heat loss (van Beest & Milner 2013).

The cold adapted Svalbard reindeer (*Rangifer tarandus platyrhynchus*) can only be found in the archipelago of Svalbard at 74-81° North (Stien et al. 2010), where it has adapted to the extreme polar and predator-free environment for more than 5000 years (Loe et al. 2007; van der Knaap 1989). Reindeer inhabiting this area face an environment with large seasonal changes in their thermal surroundings with a continuous polar night in winter and continuous daylight in summer (Milner et al. 2003). During summer, shedding of their highly insulated fur adjusts their temperature tolerance to summer climate (Scholander et al. 1950). However, body size may affect the temperature tolerance, and large individuals are expected to have a reduced conductance and rate of heat dissipation to the environment compared to smaller conspecifics (Porter & Kearney 2009). Folkow and Mercer (1986) showed that during heat stress situations, due to high ambient temperatures or hard exercise, a high proportion of heat loss occurred through radiant heat exchange from the legs, due to their poor insulation. The convective heat transfer from these body parts are much higher than their relative surface area would indicate. The legs, despite their relatively small diameter, are therefore important for heat dissipation, especially when bedded (Folkow & Mercer 1986).

Bed sites are possibly important thermal refuges for Svalbard reindeer during summer. At Svalbard, there are no trees or shrubs (Brattbakk 1986), so to be able to find bed sites in shaded areas on warm, sunny days, the reindeer must find shade from mountains, which can be rare during summer when there is midnight sun (from April 20th to August 22nd) and the sun stands high in the sky. In addition, the most reindeer rich areas are wide U-shaped valleys with few structures causing small-scale variation in shading. Remaining snow patches or wet substrate as mire on the other hand are relatively abundant during summer, and can serve as cooling bed sites for the reindeer. The permafrost can also provide cool bed sites suitable for thermoregulation, by the occurrence of ice lenses or ice wedges close to the surface (Humlum et al. 2003). Previous studies on thermoregulation in ungulates have mainly focused on cases from more temperate regions or thermoregulation during winter (Broders et al. 2012; Cain et al. 2006; Renecker & Hudson 1986). No previous studies have looked into the behavioral adaptations of the Svalbard reindeer to the increasing ambient summer temperatures at Svalbard. Being subject to negligible predation and insect harassment, this *Rangifer* sub-species provides an excellent opportunity for studying their use of bed sites as thermoregulatory behavior in a rapidly changing Arctic. In this study, I sampled microsite characteristics at 371 bed sites of free-ranging Svalbard reindeer, each with two associated control sites, to see whether they specifically selected cold bed sites to cool down on warm summer days. I hypothesized that bed site selection has a role in thermoregulation of Svalbard reindeer, and that there would be a difference in bed site selection between different age and sex categories because of differences in body size (Table 1).

Table 1: An overview of hypotheses (H) and corresponding predictions (a-b) investigated

Hypotheses and predictions
H1: Svalbard reindeer use bed sites as a part of their thermoregulation in summer. a) Svalbard reindeer select for cooling substrates, as snow and mire, and the degree of selection increases with ambient temperature. b) When cooling substrates (snow and mire) are absent, the Svalbard reindeer prefer cool ground as bed sites, and the preference increases with ambient temperature.
H2: Heat stress is body-size dependent, and large individuals will have a stronger preference for cooler bed sites compared to small individuals during warm summer days. a) I expect adult males to select cooling substrates and cool ground to a larger extent than adult females, which in turn are expected to be more selective than yearlings of either sex, and that the difference increases with ambient temperature.

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out in the high Arctic Archipelago of Svalbard (Figure 1), which is located in the Barents Sea, between 74-81°N and 10-35°E. The islands are characterized by long fjords, vide U-shaped valleys and steep mountains that reaches up to about 1000 meters above sea level. Glaciers are covering approximately 60% of the total land area (Tyler 1987). The study area (77°92’N-78°02’N, 15°16’E-15°87’E) is located in central Nordenskiöld Land national park, at the Spitsbergen island, and consists of the three interconnected valleys; Reindalen, Semmeldalen and Istjørndalen.

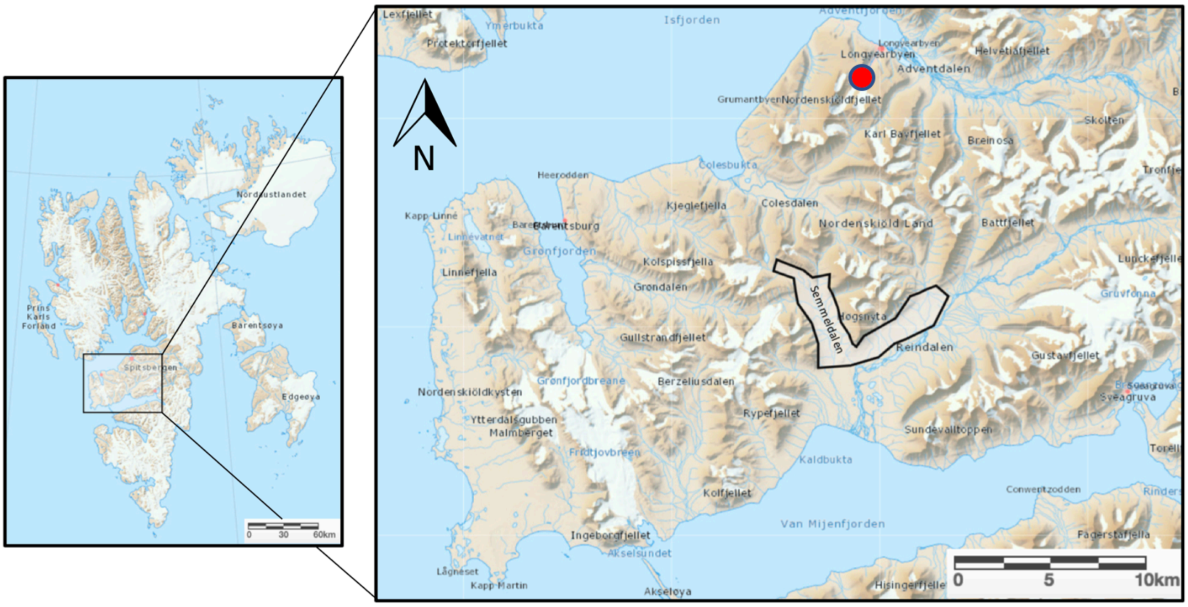

Figure 1: The Svalbard archipelago (left map) and the study area (right map) in Reindalen, Semmeldalen and Istjørndalen (encircled by black lines) at Spitsbergen island. The area is included in Nordenskiöld Land national park. Longyearbyen is marked with a red point north of the study area. The map is collected from http://svalbardkartet.npolar.no/ (The Norwegian Polar Institute).

The vegetation in the area is classified as middle arctic tundra zone (Elvebakk 2005). The valley floors mainly consist of acidic and nutrient-poor mires, graminoids, mosses and herbs (Brattbakk 1986), while the valley slopes are either vegetated or have non-vegetated scree cover from rock-falls, and sand and silt accumulation (Elvebakk 2005). Trees and shrubs are absent, and plants seldom become taller than 5 cm, except for some graminoid species (Hansen 2008). No vegetation is tall enough to create shade for bed sites. Vegetation cover extends from the coastal lines into the valleys and up to 50 meters above sea level (Brattbakk 1986). From 50-200 meters altitude, the vegetation is sparse and sporadic as sand, gravel and rocks become more dominant (van der Wal et al. 2000). The active plant growth season is limited to two - three months (Cooper et al. 2011; Hansen 2008). The onset of growing season is closely linked to the snowmelt (van der Wal et al. 2000), and normally starts in mid-June in the study area (Karlsen et al. 2014). The growing season ends around the beginning of September, as the temperatures drop below zero degrees Celsius (van der Wal et al. 2000). The study area is covered in snow from October/November until mid-June, but varies considerably between years (Hansen et al. 2014). The differences in light conditions on Svalbard are distinct, with midnight sun from April 20th to August 22nd, and dark season from October 26th to February 16th, affecting both the animal life and vegetation in the area (Førland 1997).

Svalbard has large variations in climate elements due to topographical effects and geophysical factors affecting the Arctic climate (Førland et al. 2011; Førland 1997). The west coast of Spitsbergen, and the area of Nordenskiöld Land in particular, is characterized by a relatively temperate but dry climate (Førland 1997). Mean air temperature for Svalbard (1981-2010) was 5.8°C for the warmest month July, and -13°C for the coldest month February (Nordli et al. 2014). For the same period, average annual precipitation was between 190 mm and 440 mm (Nordli et al. 2014). Due to the low temperatures and low amount of precipitation, Svalbard is defined as Arctic desert (Førland et al. 2011). However, Svalbard has relatively high mean winter temperatures compared to other land areas at the same latitudes (Førland 1997). This is caused by the archipelago's relatively small land area and being located near both the northernmost branches of the North Atlantic Current and the southern limit of polar pack ice (Humlum et al. 2003). The West Spitsbergen Current branches off the North Atlantic Current and runs poleward just west of Spitsbergen in the Arctic Ocean (Cokelet et al. 2008) bringing salt and warm water, as well as warm air temperatures (Førland 1997).

Evidence of increased temperatures at Svalbard has been recorded. Throughout the last century, the annual mean temperature has increased by 2.6°C, and Svalbard has experienced the greatest temperature increase in Europe during the latest three decades (Nordli et al. 2014). The largest increase in trends for annual means are detected in spring, with an increase of 3.9°C, while summer has an increase of 1.0°C. For the temperature increase in winter (2.9°C), the trend is much steeper, but with a greater variability than in summer (Nordli et al. 2014), which leads to an increase in frequency of warm periods with temperatures above zero and rain during winter (Albon et al. 2017; Førland et al. 2011; Hansen et al. 2011).

Svalbard has permafrost all year round, meaning that the ground temperature is not exceeding 0°C for two consecutive years (Humlum et al. 2003). The permafrost in Svalbard is about 100 meters thick in major valley bottoms, but extends up to 400-500 meters thickness in the high mountains (Humlum et al. 2003; Westermann et al. 2011). The mountain topography introduces local and large variations in ground temperature regime and permafrost thickness due to variations in slope, aspect, altitude, topographic shading and redistribution of the winter snow cover by wind (Westermann et al. 2011). This, in addition to the archipelago being located close to the West Spitsbergen Current, causes the permafrost in Svalbard to be more sensitive to changes in temperature and thickness than the permafrost of extensive lowlands in Siberia, northern Canada and Alaska (Humlum et al. 2003). Due to warmer summer and winter temperatures on Svalbard (Førland et al. 2011; Nordli et al. 2014), a trend of increasing thawing of permafrost is observed in summer as well as decreasing freezing indices during winter (Humlum et al. 2003). In recent years, the upper 1-2 meters thaw during summer, depending on the area, creating an active layer. The permafrost can in some areas, typically in large valleys and their valley slopes, appear closer to the surface than other parts of the landscape due to formation of ice lenses or wedges (Black 1976; Hinkel et al. 2001; Humlum et al. 2003). Ice wedges are formed by ice growth in thermal contraction cracks in the permafrost and are typically between 1 centimeter and 5 meters wide and close to the surface (Humlum et al. 2003; Péwé 1966), although diameters up to 20 meters have been found (Black 1976; Humlum et al. 2003). These lenses or wedges of solid ice do not thaw as easily as frozen ground, making the permafrost patchy during summer (Christiansen 2005).

2.2 Study species

The Svalbard reindeer is a subspecies of reindeer (*Rangifer tarandus*), and can only be found at the archipelago of Svalbard (Stien et al. 2010). The overall population of Svalbard reindeer was estimated at 11’000 animals in the mid 1980’s (Øritsland & Alendal 1986), and there is no recent total count. The reindeer population within the Colesdalen-Semmeldalen-Reindalen valley system of Nordenskiöld Land (covering the study area) is estimated at about 1500 reindeer (Governor of Svalbard 2009). Svalbard reindeer is classified as a high-arctic tundra reindeer, and it has several unique adaptations to the harsh environment and large seasonal variability found in the Arctic. Compared to other reindeer subspecies, Svalbard reindeer is characterized by a small and compact body shape, small head, short legs, ears and muzzle (Banfield 1961). The summer weight of Svalbard reindeer is about 90 kg for adult males and 70 kg for adult females (Kovacs & Lydersen 2006), while the late summer weight for yearlings (1 year, either sex) is approximately 50 kg (Albon et al., unpublished data). They are able to accumulate a large amount of fat reserves (Reimers et al. 1982; Tyler 1987), and both adult females and males show seasonal changes in body mass of 40%-50%, which is extreme compared to other ungulates (Reimers & Ringberg 1983). The body temperature of reindeer does not vary more than about 2°C (Irving & Krog 1955), even when exposed to a 60°C range of ambient temperature (Johnsen et al. 1985). A variety of physiological, morphological and behavioral mechanisms help them to regulate the body temperature, and reindeer can lose heat to the environment passively by radiation, convection, and conduction. Heat dissipation by the legs and through the respiratory tract, due to a highly efficient counter-current heat exchange mechanism, are two of the main mechanisms by which reindeer dissipate excess heat (Blix & Johnsen 1983). The upper critical temperature for Svalbard reindeer is not known.

Due to the short summers, when the grazing facilities have the highest quality and quantity, undisturbed grazing is important in order to maximize growth and fattening before the long winter. Loe et al. (2007) found that the Svalbard reindeer had season-dependent feeding-rumination intervals, with no distinct peaks in activity at sunrise and sunset. The activity level was in general much higher during summer (June to September) than the rest of the year, with a periodicity of five hours during summer, and approximately seven hours for the remaining months. The actual time spent foraging in summer is about 70% of the day, leaving 30% for resting and rumination (Kastnes 1979). Calving takes place in the beginning of June, and the calves suckle for about a month before they are able to feed on plant tissue (Tyler 1987).

The Svalbard reindeer differ largely from other reindeer species, as the Svalbard reindeer live in small groups with no more than two to four animals (Loe et al. 2006). Individual behavior can therefore be assumed to be less dependent on other individuals than for most other *Rangifer* subspecies. Although reindeer and caribou (*Rangifer tarandus granti*) are known to be nomadic within seasons, and implement long seasonal migrations, the Svalbard reindeer show no such behavior, and are a more sedentary species with relatively small home ranges (Tyler & Øritsland 1989).

Only two other large mammals are present on Svalbard; the arctic fox (*Vulpes lagopus*) and the polar bear (*Ursus maritimus*). Even though polar bears have been found to prey on reindeer, this rarely happens (Derocher et al. 2000), and neither them, nor the arctic foxes are considered a predatory threat to the Svalbard reindeer (Derocher et al. 2000; Staaland 1986). Insect harassment normally increases with increasing ambient temperatures, and have been found to affect reindeer through reduced grazing time and increased energy expenditure in semi-domestic reindeer in Finland (Weladji et al. 2003). Oestrid flies (*Hypoderma tarandi*), known to be the worst stressors of reindeer and caribou (Mörschel & Klein 1997; Mörschel 1999), are not present on Svalbard, but mosquitos (*Culex* spp.) are locally abundant for a limited period during summer (Coulson 2007; Halvorsen 1986). Hunting is legal in the study area in the period from August 20th to September 10th, but the hunting pressure is generally low and restricted to an annual cull of 150-200 reindeer at the whole archipelago (Governor of Svalbard 2009).

2.3 Sampling of data

Sampling of data was conducted over a period of 24 field days between 9th of July and 8th of August 2017. In total, 371 bed sites and two associated control sites per bed site were sampled. I attempted to achieve a fairly even distribution of bed sites from adult males, adult females and yearlings, and ended up with a sample size of 118 adult males, 157 adult females and 96 yearlings (both gender). Registrations of sun or shadow at bed sites were not considered as there was never a contrast between bed sites and control sites due to the open landscape. The animals are unmarked, thus the same animal may have been registered several times. With the rationale that groups are small and unstable, I interpret my observations as individual- rather than group level observations.

2.3.1 Identification of bed sites and control sites

Bed sites and associated control sites were registered mainly in Semmeldalen due to its high density of reindeer and proximity to field base, but also in Reindalen and Istjørndalen. Two or three observers searched the study area on foot and detected single resting animals or groups with at least one resting animal. Often there were several individuals to choose from within visual range. By closing up on the resting reindeer, it moved (often at a range of 20 to 100 meters from the observers), and the exact bed site was identified by flattened vegetation or substrate, shed fur and often warm ground at the site. The center of the bed site was marked, and the GPS coordinates in that spot registered using a Garmin GPSmap 62s. To determine the control sites, a random compass course was selected, using a premade sheet with randomly selected numbers between 1 and 360. This set the direction in which to walk to the control sites, using a Silva Expedition S compass. Control sites where found at 10 meters and 100 meters away from the center of the bed site, measured by the GPS.

2.3.2 Sampling at bed sites and control sites

Thermal factors

Ground temperature was measured at the center of the bed site and at the associated control sites. Measurements were done in the upper layer of the substrate, 1 cm below the surface, using a ZyTemp Thermocouple Thermometer (Radiant Innovation Inc., China). To avoid ground temperature measurements that were influenced by the reindeer's body temperature, all registrations of ground temperature were done no earlier than 10 minutes after the reindeer departed. Tests of how long it took for the ground temperature to stabilize after a reindeer rested at a site, were done the first field day (16 registrations at different substrates), and 10 minutes was set as a limit throughout the rest of the study, because the temperature stabilized well before that (results not shown). Air temperature was measured 1 meter above the ground for each bed site, but not for the control sites, as there was no expected difference between the 100 meters from bed site to the furthest control site.

Animal specifications

As the reindeer left the bed site, the sex (male/female) and age category (adult/yearling) was noted. Bed sites from calves are not a part of this study, as it is expected that the calves choose bed site as a function of where their mother chooses to rest. Further, the number of animals in the group was counted. When larger groups were found, and several animals were resting in the same area, a maximum of 3 registrations of bed sites and their associated control sites were sampled to limit pseudoreplication.

Insect harassment

Mosquitos, being the only insect stressor of reindeer on Svalbard (Coulson 2007), were counted only at the bed sites due to time consuming registration, and the fact that the same mosquitos followed us from the bed sites to the control sites (but generally not between different bed site registrations due to longer distances). The Human Landing Catch method was used to estimate mosquito abundance (Kroeckel et al. 2006). The counting was carried out holding out one hand and counting the number of mosquitos landing on the back of the hand over a time span of five minutes. No insect repellent was used, and the mosquitos that landed and sucked blood from the hand were not removed before the five minutes time was up.

Substrate and topography

At both bed sites and control sites, substrate, vegetation and ground moisture was registered within one square meter around the center of the bed sites and control sites. Substrate was divided into the following categories; rocks, gravel, vegetation, snow and other. Vegetation was recorded as one of eight known vegetation types (van der Wal pers.comm.; Table 2), or as "other" or "non-vegetated". Ground moisture was registered as either dry, moist or wet, and the classification should not be affected by short-term precipitation.

Table 2: Description of vegetation categories, developed by René van der Wal (pers.com.), used to classify the vegetation at bed sites and control sites in Reindalen, Semmeldalen and Istjørndalen.

Vegetation category	Vegetation classification	Dominant species	Associated species	Characteristics
1	*Dry Salix, Dryas* or *Cassiope*	*Salix Polaris* or *Dryas octopetala*	-	Common dry ridge vegetation, dominated by dry *Salix*
2	*Luzula, Salix, Alopecurus*	*Luzula confusa*	*Salix polaris, Alopecurus borealis*	Common vegetation type. Dry tussocks in the valley bottoms and lower valley slopes
3	*Phippsia, Saxifraga hyperborea*	*Phippsia algida*	*Saxifraga hyperborea*	Rare vegetation type. Wet, graminoid community
4	*Poa, Festuca*	*Poa sp., Festuca sp.*	*Oxyria digyna, Polygonum viviparum*	Common vegetation type. Green areas dominated by graminoids in valley slopes
5	*Dupontia, Eriophorum*	*Dupontia pelligera*	*Eriophorum scheuchzeri*	Rare vegetation type. Typical in flat valley bottoms close to the shore
6	*Alopecurus, Equisetum,* Wet moss	*Alopecurus borealis, Equisetum arvense*	-	Common vegetation type. Moist/wet, tussocks vegetation at valley bottoms. Rich in graminoids
7	*Carex lachenalii*	*Carex lachenalii*	-	Rare vegetation type. Dense cover of *Carex*-tussocks in medium wet areas
8	*Deschampsia*	*Deschampsia alpina*	-	Tall grass in tussocks. Normally in riverbed gravel
9	Non-vegetated	-	-	Exposed ground, not vegetated
10	Other	-	-	-

2.4 Statistical analysis

The statistical analysis was performed using R version 3.4.2 for Mac (R Core Team 2017). All data used in the analysis were sampled during the fieldwork, and no external data were utilized. Cooling substrates are defined as sites on mire and on snow. The combination of registrations made on wet, vegetated areas with vegetation category 6 and 10, as well as moist, vegetated areas with vegetation category 6, all together define mire in the analysis. Vegetation category 10 (other) was included if consisting of wet moss (because wet moss alone did not have a separate category). The age/sex explanatory variable consists of the three levels; male adults, female adults and yearlings of both genders combined.

To investigate the probability of a site being used by reindeer as a bed site, a resource selection function approach was used. The approach provides values proportional to the probability of use of a resource unit (Boyce et al. 2002), and is widely used in spatial use-availability designs (Johnson et al. 2006). Bed sites (used) and control sites (not used) were redefined as categorical variables (usage) with bed sites = 1 and control sites = 0. The effect of explanatory variables on usage were then investigated using generalized linear model with binomial distribution. This allowed me to test if the variables describing used bed site were used more than expected from their availability.

First, the preference for cooling substrates was investigated through model selection (Model 1: Appendix 1; Table A1). Usage (bed site = 1, control site = 0) was used as the response variable. Candidate explanatory variables were: air temperature, mosquito abundance, cooling substrates and age/sex as well as selected interactions. The full models with the different interactions for all analyses the can be seen in Appendix 1 and 2. The model was then simplified using stepwise backward model selection, starting off with a full model containing all factors and interactions of interest (Crawley 2007), and then simplifying it until the simplest model explaining the bed site selection was retained. An analysis of variance was used to determine which variable was the least significant and a candidate for model simplification. Likelihood Ratio Tests (LRT) were used to compare the more complex model to a simpler version (Pinheiro 2000) with one less interaction or main variable. If the simpler model did not differ significantly from the more complex one, meaning little information was lost in the process, the simpler model was retained. These steps were repeated until only significant variables remained, being the final model. Bed sites were tested against both 10 meters control sites and 100 meters control sites in separate models.

It was then tested if ground temperature could be a better explanatory variable than cooling substrates. In the final model (Appendix 3; Table A3) from this first model selection, cooling substrates was replaced by ground temperature as an explanatory variable in the interactions and as a main variable. Akaike's Information Criterion (AIC) was used to compare the final model with cooling substrates against the final model with ground temperature, to find the most parsimonious model (Crawley 2007). In this case, ANOVA LRT could not be used due to the fact that both models had the same number of degrees of freedom and the models are not nested. To investigate whether the reindeer selected for cool ground independent of the cooling substrates snow and mire, the model was re-run on a data subset where all bed- and control sites on cooling substrates were excluded. The new model (Model 2: Appendix 2; Table A2) consisted of usage as response variable, and air temperature, ground temperature, mosquito abundance and age/sex as candidate explanatory variables. Stepwise backward model selection was performed as previously described.

3 RESULTS

All results were qualitatively similar using 10 meters and 100 meters as control sites. To avoid repetitions, results on the 10 meters scale are presented in the main text, whereas results from the 100 meters scale can be found in Appendix 5.

3.1 Selection for cooling substrates

Altogether 34.2% of bed sites and 32.4% of control sites were classified as cooling substrates. The Svalbard reindeer showed a strong preference for cooling substrates on warm days (Figure 2). Using the backward stepwise model selection for model 1 (Appendix 1; Table A1), only the interaction between air temperature and cooling substrates (and by default also the two main effects) were retained in the final model (LRT p-value of 0.021: Appendix 3; Table A3). On days when the air temperature was high, represented by an air temperature of 11.4°C (being the 90th percentile of the measured air temperature range), the reindeer showed a moderate preference for using cooling substrates as bed sites. On the contrary, they preferred the non-cooling substrates on cold days represented by air temperature of 6.7°C (10th percentile of the air temperature range). This supports prediction H1a stating that Svalbard reindeer select for cooling substrates, and that the selection increases with the ambient temperature.

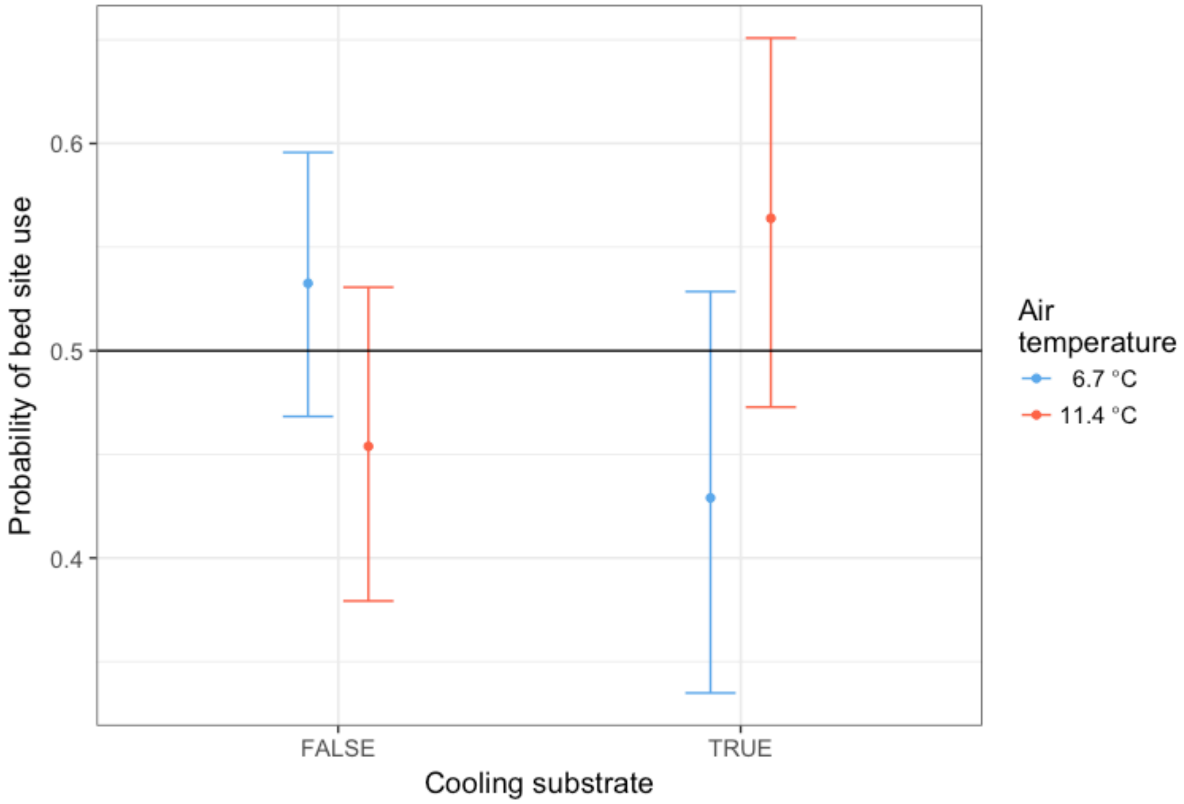

Figure 2: The probability of a site being used as bed site as a function of the presence of cooling substrates (snow and mire), at cold (blue lines) and warm (red lines) air temperatures. Air temperatures are represented by 6.7°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. Values are shown with their respective 95% confidence interval. Values above the 0.5 line (black) indicate preference for the substrate, while values below the 0.5 line indicate avoidance of the substrate.

3.1.1 Harassment from mosquitos

In total, only 51 mosquitos were registered in field (maximum of 5 for a 5-minutes observation). Model 1 (Appendix 1; Table A1), including the full dataset, was used for this analysis. Mosquito abundance was included as an explanatory variable and in interaction with cooling substrates in the full model, to see if they contributed to the reindeer's selection of bed sites. Using LRT, the interaction between cooling substrates and mosquitos fell out of the model selection with a p-value of 0.470 (Appendix 1; Table A1). Mosquitos as a main variable was highly non-significant, with a p-value of 0.942. This suggests that mosquitos did not affect the selection for cooling substrates as bed sites for the reindeer in this study.

3.1.2 The impact of ambient temperature on different age and sex categories

In order to test the effect of age and sex on the bed site selection, model 1 was used. The age/sex category was included in the model as explanatory variable, both as main effect and in interactions (Appendix 1; Table A1) to test if the different age and sex categories had different preferences in selection of bed sites at different ambient temperatures. All interactions that included age/sex fell out early in the model selection. This meaning that there was no significant difference between age and sex categories in how they selected the bed sites. Hence, no support for hypothesis H2 and prediction H2a was found in this study.

3.2 Selection for cool ground

3.2.1 Ground temperature as an explanatory variable

Replacing cooling substrates with ground temperature as an explanatory variable in the best model from model selection of model 1 (Appendix 3; Table A3), improved significantly the fit of the model (dAIC = 11). Thus, ground temperature was hereafter used as an explanatory variable in the investigation of the reindeer's selection for cool ground.

The mean temperature of the bed sites was 8.5°C while it was 9.9°C on control sites (median: 8.7°C vs 9.8°C respectively). Using ground temperature as an explanatory variable clearly showed that the reindeer preferred different ground temperatures at different ambient temperatures (Figure 3). When the air temperature was high (represented by 11.4°C), a preference for bed sites on cool ground, and an avoidance of bed sites on warm ground were found, but with relatively large confidence limits. When the air temperature was low (represented by 6.7°C), bed site selection depended much less on ground temperature (Figure 3).

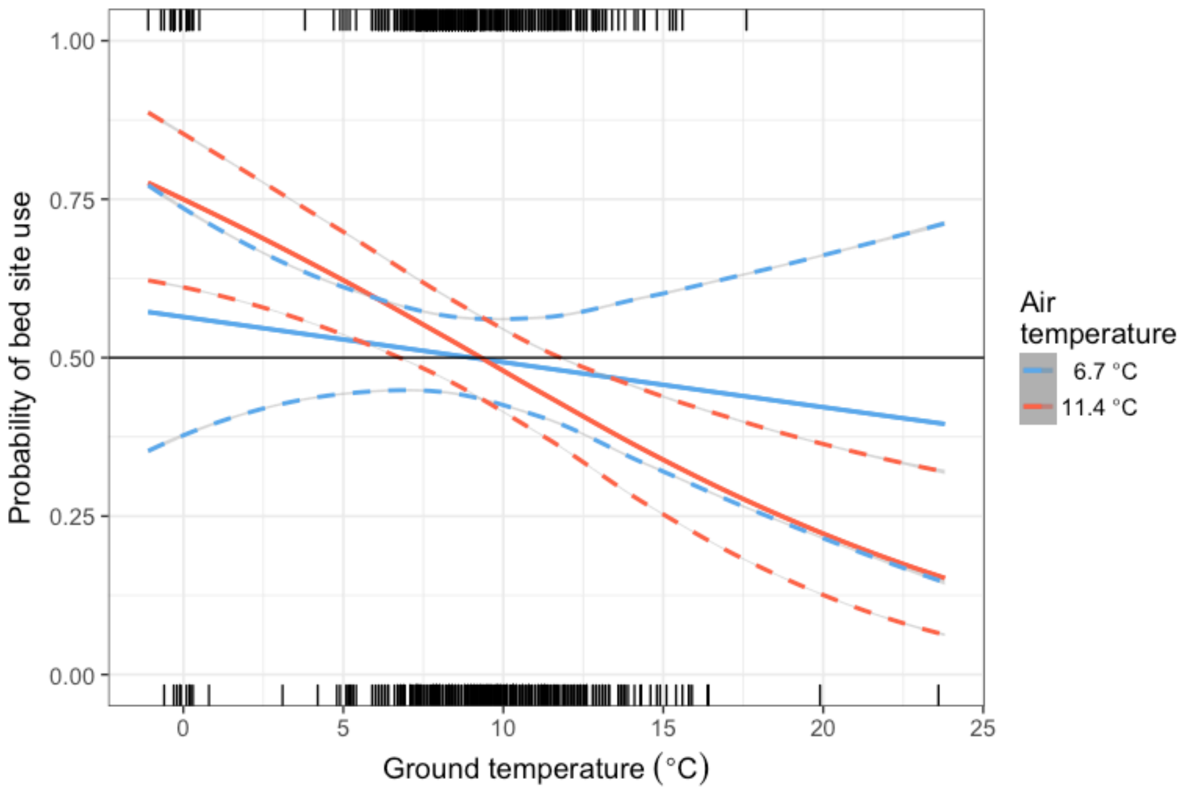

Figure 3: The probability of a site being used as bed site as a function of ground temperature. The predicted cold (blue solid line) and warm (red solid line) air temperatures are represented by 6.7°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. The dashed lines represent 95% confidence interval. Values above the 0.5 line (black) indicate a preference for the given ground temperatures, while values below the 0.5 line indicate avoidance of the given ground temperatures. Tick marks along the top display ground temperatures registered at the bed sites, while tick marks along the bottom display ground temperatures registered at the control sites (10 meters).

3.2.2 Selection for cool ground when excluding cooling substrates

To further explore the selection for cool ground, all data registrations containing cooling substrates was excluded from the dataset, and a backward stepwise model selection for model 2 (Appendix 2; Table A2) was done. Only the interaction between ground temperature and air temperature (and by default also the two main effects) was retained in the final model (Table 3). This indicates that the reindeer preferred cool ground as bed sites even though typical cooling substrates as snow and mire were absent. The preference for cool ground increased with the ambient temperature (Appendix 4; Figure A1). This supports prediction H1b.

Table 3: Regression coefficients (β), standard errors (SE) and p-values after implementation of the model selection for registrations of bed sites without cooling substrates. Usage is the response variable.

Explanatory variables	**β**	**SE**	**P-value**
Intercept	-2.47	1.65	0.133
Ground temp.	0.28	0.18	0.116
Air temp.	0.40	0.19	0.036
Ground temp. x air temp.	-0.04	0.02	0.027

4 DISCUSSION

In this study, I addressed the selection of bed sites as thermoregulatory behavior for the Svalbard reindeer during summer. Svalbard reindeer is a suitable species to study concerning this, because their habitat selection is not affected by the presence of predators and they experience limited insect harassment. Analyzing bed site selection during one summer season, I documented that the Svalbard reindeer select cooling substrates, as snow and mire, and that the degree of selection increases with ambient temperature. In addition, I demonstrated a selection for cool ground even when cooling substrates such as snow and mire are absent. No difference in bed site selection between different age and sex categories were found. My study is the first to document that Svalbard reindeer actively seek cold sites to rest, a finding compatible with the view that bed sites play a role in thermoregulation of Svalbard reindeer. It is also the first study to find selection for cool ground temperature by an ungulate in habitat without available shade from canopy cover or cooling substrates. My findings are particularly relevant as the Arctic is rapidly warming and adds general knowledge of behavioral buffering of climate change.

4.1 Bed sites have a role in thermoregulation

In support of hypothesis H1, Svalbard reindeer were found to use bed sites for thermoregulation in summer. By selecting cooler microclimates for bed sites, reindeer can accelerate the rate of heat loss, without having to engage as much in more energy demanding autonomic thermoregulation. This is in line with previous bed site studies on ungulates from tropical deserts to temperate environments (Marchand et al. 2014; McCann et al. 2016; Mysterud 1996; van Beest et al. 2012; van Beest & Milner 2013). Desert ungulates like eland (*Taurotragus oryx*), desert mule deer (*Odocoileus hemionus eremicus*) and springbok (*Antidorcas marsupialis*) have been found to frequently use shaded microhabitat when temperature is at its warmest during the day (Bigalke 1972; Taylor & Lyman 1967; Tull et al. 2001). In the open valleys of Svalbard habitat, small-scaled thermal variation is provided by the substrate rather than shade from trees or other structures. As predicted by H1a, the Svalbard reindeer preferred to bed down on cooling substrates, as snow and mire, and the degree of selection increased with the ambient temperature (Figure 2). Several studies, including for example mouflon, roe deer, moose and caribou, have found that bed site selection on wet substrate increases during warm ambient temperatures (Marchand et al. 2014; McCann et al. 2016; Mysterud 1996; Mörschel & Klein 1997; van Beest et al. 2012; van Beest & Milner 2013). Similarly, in a study on free-ranging reindeer (*Rangifer tarandus tarandus*) from mainland Norway, Anderson and Nilssen (1998) concluded that reindeer aggregate on snow patches to thermoregulate as they were observed standing still or bedded on snow during warm ambient temperatures in summer. A wet bed will help the reindeer dissipate more heat than a dry bed (Cosenza et al. 2003; Gatenby 1977) because the substrate water content is positively correlated with thermal conduction (Cosenza et al. 2003). Since the legs are important for heat dissipation (Folkow & Mercer 1986), reindeer may possibly lose a significant amount of heat through conduction when bedded. Registered wet substrates in this study consist of snow and mire, where the latter contains a high percentage of moss. A study by van der Wal et al. (2001) reported that soil temperature correlated with moss thickness, and that a thick moss layer insulates the soil and limits the extent to which the permafrost thaws during summer, hence the soil temperature in these areas is colder. The combination of permafrost beneath, and wet moss and mire on top, as well as snow, provide favorable microclimates for the Svalbard reindeer to cool down during adverse thermal conditions.

Previous studies on bed site selection in conjunction with thermoregulation, have focused on bed sites on wet substrate and with canopy cover. I found that Svalbard reindeer were able to detect cold ground temperatures also independent of the visual cues of snow and wet ground, supporting prediction H1b under hypothesis H1. The utilization of nearby cold ground for cooling down is much less energetically costly than moving longer distances for either shade from mountains or take altitudinal migrations or even for snow that diminishes throughout summer. The ability to detect and utilize such patches probably arises from a combination of small home ranges of the reindeer (enabling learning) and the stable nature of such cold patches. These cold patches are possibly caused by ice wedges, which is a common feature related to permafrost at Svalbard (Humlum et al. 2003). Sargeant et al. (1994) showed that mule-deer scraped the bed site in dry areas before bedding, and increasingly so on clear, warm days. Mysterud (1996) on the other hand, found no difference in scraping activity between warm and cold ambient temperatures for roe deer before bedding. Scraping of dry areas before bedding exposes more humid substrate, but can possibly also be used to come closer to the permafrost in Arctic regions where permafrost is present. Registrations of depth down to the permafrost, or searching for ice lenses and wedges, as well as bed site scraping, were unfortunately not performed in this study, however reindeer were observed scraping ground on several occasions.

4.2 Selection of snow despite no insect harassment

Many previous studies from lower latitudes have investigated and found that during summer, parasitic insects periodically harass *Rangifer* spp. and disturb their activity patterns (Colman et al. 2001; Downes et al. 1986; Mörschel & Klein 1997). Several studies have suggested that reindeer aggregate on snow as a behavioral adaptation primarily to avoid insects, and not to thermoregulate (Hagemoen & Reimers 2002; Ion & Kershaw 1989; Vistnes et al. 2008). Mosquitoes, being the only possible insect stressor to reindeer present on Svalbard, have previously been registered at low abundance at the archipelago (Coulson 2007; Halvorsen 1986). Kastnes (1979) found no sign of the Svalbard reindeer being harassed by any parasitic insects, although the mosquito abundance may have increased over the last three decades due to warmer summers. Nonetheless, a very low abundance of mosquitoes was recorded, and variation in abundance did not influence on the probability to select a bed site with snow (Appendix 1; Table A1). CO_2-baited traps would perhaps have registered higher mosquito abundance than the method used in this study, but the overall results would likely have been similar due to generally low abundance of mosquitoes at Svalbard. A previous study conducted in northern Norway, where insects are very abundant, also suggests that the reindeer aggregate on patches of snow to thermoregulate rather than seek relief from parasitic insects (Anderson & Nilssen 1998), but hard conclusion is hampered by correlation between insect activity and warm weather. As such, my study is the first *Rangifer* study to find selection of snow and other cold substrates in an area virtually free of harassing insects.

4.3 Similar bed site selection for all age and sex categories

Thermal sensitivity is influenced by body size as large bodied individuals have a lower surface area to volume ratio and a higher thermal inertia than smaller individuals, and therefore a reduced heat dissipation capacity (Porter & Kearney 2009). Based on such theoretical expectations of larger individuals to be more heat stressed than smaller conspecifics, and increasingly so at warm ambient temperatures (hypothesis H2), adult males were expected to show a stronger preference for cold bed sites compared to adult females, which in turn were expected to be more selective than yearlings of either sex (prediction H2a). In this study, no significant difference between age and sex categories of Svalbard reindeer was found, hence rejecting hypothesis H2. Few studies of cold adapted ungulates have investigated how different age and sex categories within the same species respond to warm summer conditions. Contrary to my results, research by Marchand et al. (2014) on the Mediterranean mouflon (*Ovis gmelini musimon*) found that males selected habitat that provided thermal refuge when the ambient temperature increased in summer, while selection by females was largely driven by habitat that should protect their lamb against predators, despite their poor thermal cover. A different study performed on Alpine ibex (*Capra ibex*) in alpine regions in Italy, found that older and larger individuals spent less time grazing and more time resting as the solar radiation and ambient temperature increased, and showed a steeper decrease in grazing time than younger and smaller ibex (Aublet et al. 2009). The study was conducted only on males as their weight range extends from 45 to 110 kg. This range somewhat exceeds the weight span between the smallest (yearlings) and the largest (adult male) Svalbard reindeer, which may contribute to the contrasting findings. The results in my study indicate that a selection for cold bed sites to dissipate excess heat in summer was beneficial for all age and sex categories in an environment with continuous daylight, generally increased locomotor activity and no activity shifts between day and night. It is possible that the weight difference between adult males and females, and yearlings is not large enough for the reindeer to have distinguished preferences. It is also possible that living in small and mixed groups may have an impact on the bed site selection to a larger extent than expected for the Svalbard reindeer. The effects of one animal laying down can affect the group decision, resulting in bedding by several animals, even though the groups are unstable.

5 CONCLUSION

Behavioral adaptations are important to buffer climate change, as evolutionary adaptations are not likely to keep pace with the ongoing rapid warming of the climate. There are few other studies addressing the use of behavioral adaptations as buffer against warmer climate, especially in the Arctic where the climate changes are most pronounced. This study was conducted in an environment where neither predatory threat, insect harassment or the presence of canopy cover influenced the bed site selection. As these factors occur in most other studies concerning bed site selection, this study is unique in that way as well as being the first to examine the use of bed sites as thermal refugee by Svalbard reindeer.

This study contributes to the understanding of how a highly cold adapted Arctic ungulate adapt to increasing temperatures which are expected to continue in the future. It demonstrated that Svalbard reindeer used bed sites as a part of their thermoregulation in summer. The preference for cooling substrates, as snow and mire, as well as the preference for cool ground, increased equally for all age and sex categories as the ambient temperature increased. These results show that Svalbard reindeer implement behavioral thermoregulation and use bed sites to compensate for adverse thermal conditions, thus indicating heat stress in this cold adapted species during warm periods in summer. I found a ground temperature threshold of approximately 10°C dividing preference from avoidance of cooling bed sites. As the upper critical temperature for Svalbard reindeer is not known, future studies could investigate if this threshold is expected from physiological theory. The sampling performed in this study, was carried out during a limited time within one year. It would be interesting to investigate if there is a difference between years, especially since the climate warming is expected to increase in Arctic regions in particular. Gaining more knowledge about behavioral adaptations used to buffer against climate change is crucial to determine future consequences of global warming.

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APPENDICES

Appendix 1 – Model 1; model selection including cooling substrates, full dataset, 10 meters scale

Table A1: Model selection when including cooling substrates (snow and mire) as an explanatory variable in both main effect and in interactions, and usage being the response variable. Explanatory variables are presented in chronological order for when they fall out of the model selection as non-significant, and with their respective deviances (X^2), degrees of freedom (DF) and p-values. The grey rows show the significant variables, representing the final model. Values for the final model are found in Appendix 3; Table A3.

Explanatory variables	**X^2**	**DF**	**P-value**
Cooling substrates x agesex x air temp.	0.25	2	0.883
Air temp. x agesex	0.21	2	0.901
Cooling substrates x agesex	0.90	2	0.637
Cooling substrates x mosquitos	0.52	1	0.470
Agesex	0.00	2	0.999
Mosquitos	0.01	1	0.942
Air temp.			
Cooling substrates			
Air temp. x cooling substrates			

Appendix 2 – Model 2; model selection using ground temperature, excluding cooling substrates, 10 meters scale

Table A2: Model selection using registrations without cooling substrates (snow and mire), and usage being the response variable. Explanatory variables are presented in chronological order for when they fall out of the model selection as non-significant, and with their respective deviances (X^2), degrees of freedom (DF) and p-values. The grey rows show the significant variables, representing the final model. Values for the final model are found in Table 3 (main text).

Explanatory variables	**X^2**	**DF**	**P-value**
Ground temp. x agesex x air temp.	2.59	2	0.273
Ground temp. x mosquitos	0.04	1	0.836
Ground temp. x agesex	0.55	2	0.761
Air temp. x agesex	1.49	2	0.473
Agesex	0.08	2	0.963
Mosquitos	0.28	1	0.596
Ground temp.			
Air temp.			
Ground temp. x air temp.			

Appendix 3 – Model 1; final model of selection for cooling substrates, 10 meters scale

Table A3: Regression coefficients (β), standard errors (SE) and p-values after implementation of the model selection for registrations of bed sites including cooling substrates on a 10 meters scale. Usage is the response variable.

Explanatory variables	**β**	**SE**	**P-value**
Intercept	0.58	0.42	0.171
Air temp.	-0.07	0.05	0.158
Cooling substrates	-1.64	0.73	0.025
Air temp. x cooling substrates	0.18	0.08	0.021

Appendix 4 – Selection for cool ground when excluding cooling substrates, 10 meters scale

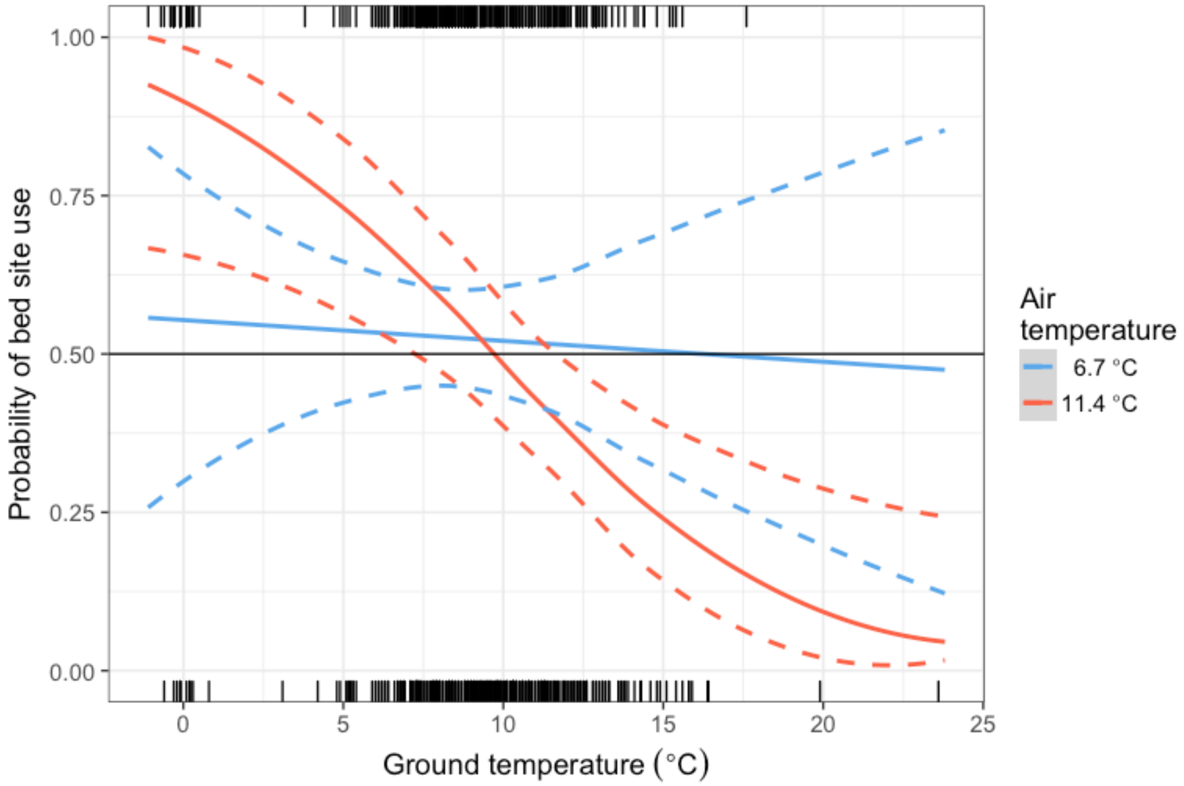

Figure A1: The probability of a site being used as bed site as a function of ground temperature when registrations with cooling substrates, as snow and mire, are excluded from the data set. The predicted cold (blue solid line) and warm (red solid line) air temperatures are represented by 6.6°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. The dashed lines represent 95% confidence interval. Values above the 0.5 line (black) indicate a preference for the given ground temperatures, while values below the 0.5 line indicate avoidance of the given ground temperatures. Tick marks along the top display ground temperatures registered at the bed sites, while tick marks along the bottom display ground temperatures registered at the control sites (10 meters).

Appendix 5 – Results for 100 meters control points

Final model of selection for cooling substrates, 100 meters scale

Table A4: Regression coefficients (β), standard errors (SE) and p-values after implementation of the model selection for registrations of bed sites including cooling substrates on a 100 meters scale. Usage is the response variable.

Explanatory variables	**β**	**SE**	**P-value**
Intercept	0.87	0.42	0.036
Air temp.	-0.10	0.04	0.024
Cooling substrates	-2.75	0.77	<0.001
Air temp. x cooling substrates	0.32	0.08	<0.001

Selection for cooling substrates, 100 meters scale

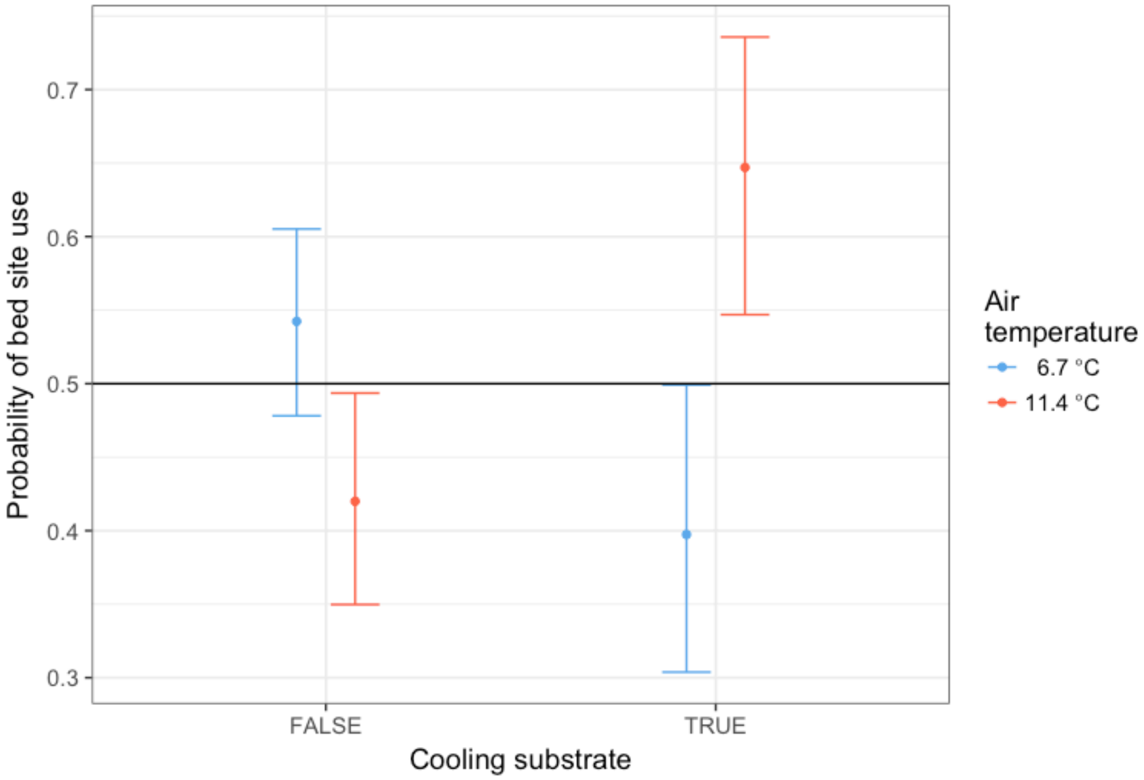

Figure A2: The probability of a site being used as bed site as a function of the presence of cooling substrates (snow and mire), at cold (blue lines) and warm (red lines) air temperatures. Air temperatures are represented by 6.7°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. Values are shown with their respective 95% confidence interval. Values above the 0.5 line (black) indicate preference for the substrate, and values below the 0.5 line indicate avoidance of the substrate.

Selection for ground temperature when including cooling substrates, 100 meters scale

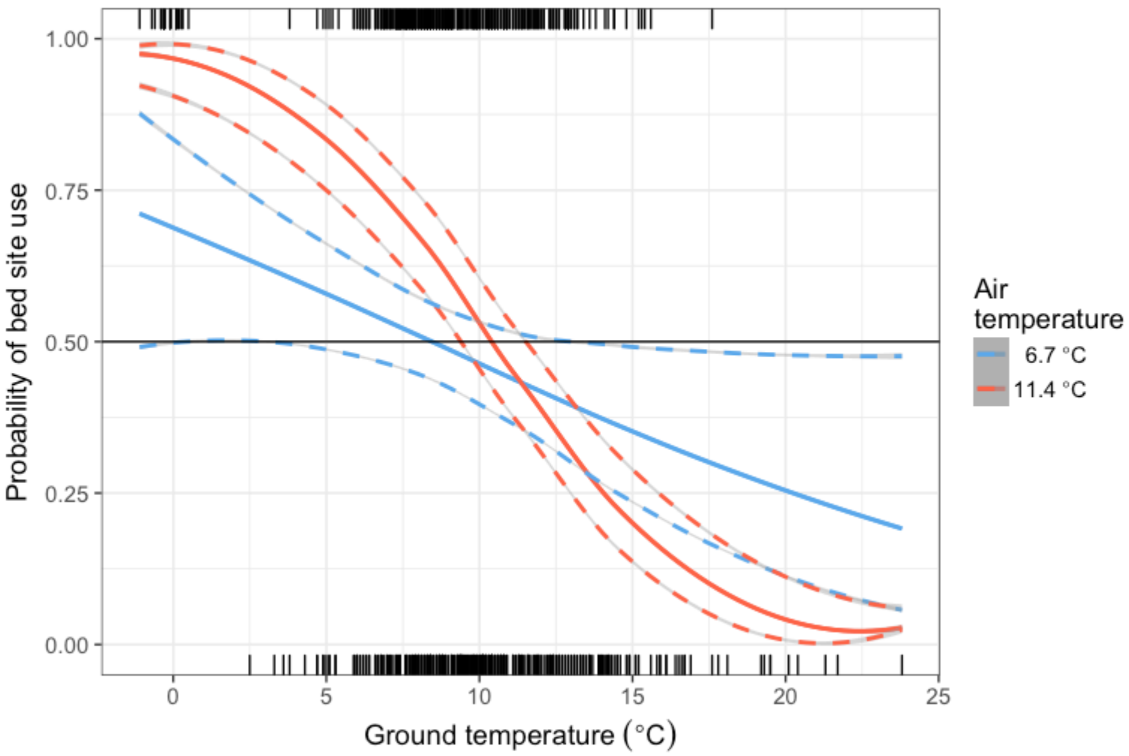

Figure A3: The probability of a site being used as bed site as a function of ground temperature. The predicted cold (blue solid line) and warm (red solid line) air temperatures are represented by 6.7°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. The dashed lines represent 95% confidence interval. Values above the 0.5 line (black) indicate a selection for the given ground temperatures, while values below the 0.5 line indicate avoidance of the given ground temperatures. Tick marks along the top display ground temperatures registered at the bed sites, while tick marks along the bottom display ground temperatures registered at the control sites (100 meters).

Final model of selection for cool ground when excluding cooling substrates, 100 meters scale

Table A5: Regression coefficients (β), standard errors (SE) and p-values after implementation of the model selection for registrations of bed sites without cooling substrates. Usage is the response variable.

Explanatory variables	**β**	**SE**	**P-value**
Intercept	-2.81	1.73	0.103
Ground temp.	0.23	0.18	0.184
Air temp.	0.64	0.21	0.002
Ground temp. x air temp.	-0.06	0.02	0.004

Selection for cool ground when excluding cooling substrates, 100 meters scale

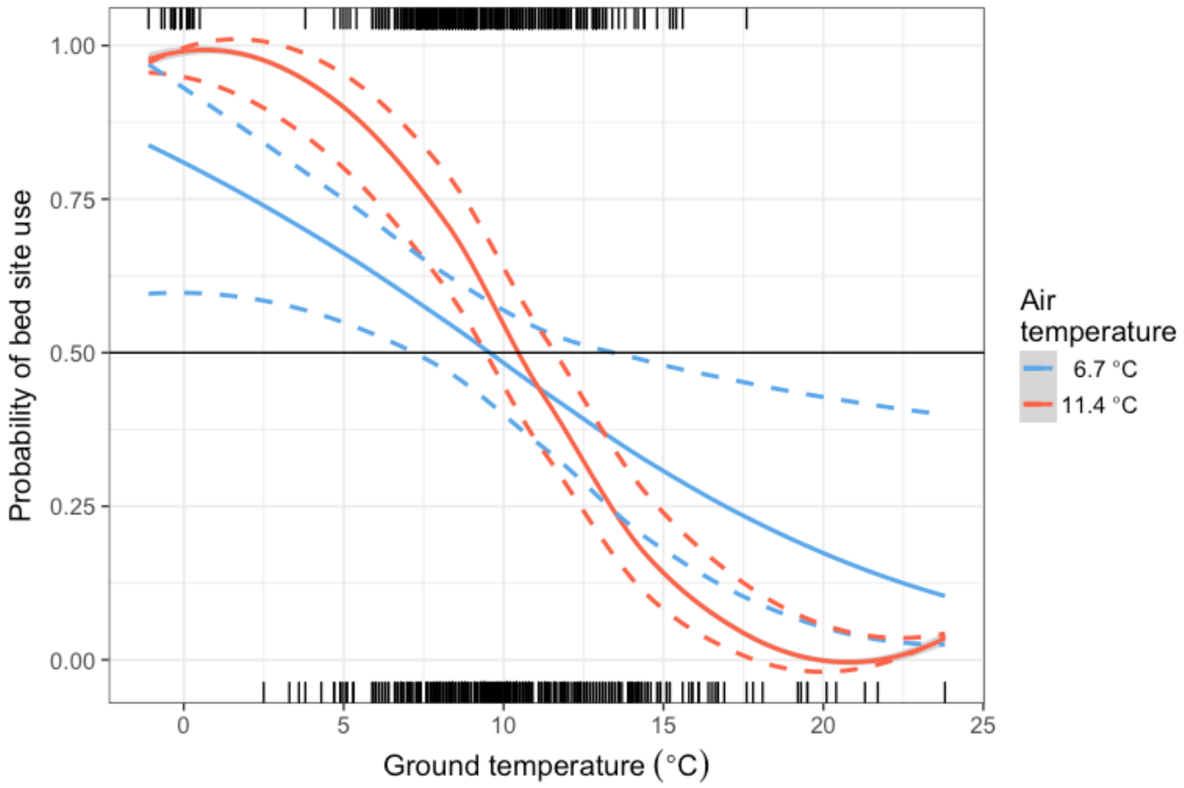

Figure A4: The probability of a site being used as bed site as a function of ground temperature when registrations with cooling substrates, as snow and mire, are excluded from the data set. The predicted cold (blue solid line) and warm (red solid line) air temperatures are represented by 6.6°C and 11.4°C, being respectively the 10th and 90th percentile of the registered air temperature range. The dashed lines represent 95% confidence interval. Values above the 0.5 line (black) indicate a selection for the given ground temperatures, while values below the 0.5 line indicate avoidance of the given ground temperatures. Tick marks along the top display ground temperatures registered at the bed sites, while tick marks along the bottom display ground temperatures registered at the control sites (100 meters).

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