Keeping cool in the warming Arctic: Thermoregulatory behaviour by Svalbard reindeer

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Abstract: In animals with long generation times, evolution of physiological and morphological traits may not be fast enough to keep up with the rapid climate warming, but thermoregulatory behaviour can possibly serve as an important buffer mitigating warming effects. In this study, we investigated if the cold-adapted Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) used cool bed sites as a thermoregulatory behaviour in the summer. We recorded habitat variables and ground temperature at 371 bed sites with random 'control' sites 10 and 100 meters distant. Using case-control logistic regression, we found that reindeer selected bed sites on cool substrates (snow and mire) as well as cold, dry ground on days with warm ambient temperatures, while they avoided such sites on cold days. Selection of both cool substrates and cool ground did not depend on age or sex. The study was conducted in an environment where neither predatory threat nor insect harassment influenced bed site selection. Our findings suggest that the thermal landscape is important for habitat selection of cold adapted Arctic ungulates in summer. Thus, behavioural strategies may be important to mitigate effects of climate change, at least in the short-term.

Key words: bed site, behavioural buffering, climate change, habitat selection, snow, ungulates, Svalbard reindeer, Rangifer tarandus platyrhynchus

Introduction

In long-lived organisms with long generation times, the evolution of morphological and physiological traits may not be fast enough to keep up with current climate warming (Parmesan 2006). If the need for thermoregulation change faster than physiological adaptation, thermoregulatory behaviour may be an important mechanism for survival (Boyles et al. 2011). Species vary considerably in their ability to avoid or cope with novel abiotic stressors (Sih et al. 2011). Quantifying species ability for behavioural thermoregulation is therefore important to assess their resilience to climate change.

For large terrestrial mammals in temperate and Arctic regions, the high activity level and food intake during summer (Moen et al. 1996; Loe et al. 2007), results in a higher probability of heat stress at the time of year when conditions are least favourable for heat loss (van Beest and Milner 2013). Because of their low surface area to volume ratio, Arctic terrestrial mammals have less exposed surface area for heat to dissipate passively to the environment (Porter and Kearney 2009). Additionally, they have adapted to cold environment by evolving lower conductance values due to natural selection acting on traits for heat conservation and not heat loss (Scholander et al. 1950). These two traits may render Arctic mammals more susceptible to warming compared to temperate conspecifics. Because of the rapid climate warming, we need to understand how Arctic mammals dissipate excess heat through thermoregulatory behaviour.

Previous research on Arctic ungulates has focused mainly on the effect of climate change during the winter season, as this is the main limiting season due to harsh climate and scarce food availability (Gunn et al. 1989; Forchhammer and Doertmann 1993; Tveraa et al. 2007). During severe rain-on-snow events, many individuals temporally emigrate from ice-covered areas (Stien et al. 2010; Loe et al. 2016), but mortality in such critical winters can still be very high

(Putkonen and Roe 2003; Rennert et al. 2009; Albon et al. 2017). To our knowledge, no study has yet investigated thermoregulatory behaviour of Arctic ungulates in summer. Most animals spend a large part of the day resting, and ruminants in particular spend nearly half of the day bedded during rest and rumination. Selection of resting sites (bed sites) has been suggested as an effective thermoregulatory behaviour across a wide range of taxa like lizards (Bauwens et al. 1996), birds (Ward et al. 2008) and ungulates. Bedding under dense canopy cover for shade (Belovsky 1981; Hetem et al. 2012; van Beest and Milner 2013) reduces the heat load, while resting on cold or wet substrates (Mysterud 1996; McCann et al. 2016) increases conductive heat loss. Other factors can also influence bed site selection, making it difficult to determine the relative importance of cooling. Prey species could select dense microhabitat primarily because it provides protection cover from predators (Mysterud and Østbye 1999), and not to seek shade. Similarly, because insects are more active on warm days, studies have suggested that reindeer (*Rangifer* sp.) aggregate on snow on warm days primarily to avoid insects, and not for thermoregulation (Ion and Kershaw 1989; Hagemoen and Reimers 2002; Vistnes et al. 2008). Studying resting site behaviour of ungulates without the influence of predators and insects would be the ideal situation to elucidate the role of thermoregulation.

The cold-adapted Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) is found in the archipelago of Svalbard, where it has adapted to a high Arctic environment for more than 5000 years (van der Knaap 1989). Compared to other reindeer subspecies, Svalbard reindeer has characteristics that result in the low surface to volume ratio expected for a cold-adapted species (compact body shape, small head, and short legs, ears and muzzle; Banfield 1961). Males are larger than females (90 kg vs. 70 kg in summer; Kovacs and Lydersen 2006). None of the predator species in Svalbard, the polar bear (*Ursus maritimus*, Phipps, 1774) and the Arctic fox

(*Vulpes lagopus*, Linnaeus, 1758), are significant predatory threats to the Svalbard reindeer. Although polar bears have been found to prey on reindeer, this rarely happens (only 7 reported cases; Derocher et al. 2000). Attempts of Arctic foxes hunting reindeer calves have been observed (Tyler 1987; Stien pers. obs.), but no confirmed kills have been reported. Mosquitoes (*Culex* sp.) are the only biting insects on Svalbard, but occur only at low abundances (Halvorsen 1986; Coulson 2007). Oestrid flies (*Oestrus tarandi*, Linnaeus, 1758), known to be one of the worst stressors of reindeer and caribou (Morschel and Klein 1997; Morschel 1999), are not present. In Svalbard, there are no trees or erect shrubs casting shade (Brattbakk 1986). Reindeer habitat consists of wide U-shaped valleys with few structures that cast shade. Remaining snow patches, wet substrate, and subsurface ice lenses (Humlum et al. 2003) are on the other hand relatively abundant during summer, and can provide cool bed sites suitable for thermoregulation.

In this study, we therefore sampled microsite characteristics at 371 bed sites of free-ranging Svalbard reindeer. We predicted that: P1) reindeer select cooling substrate and that this selection increases at high ambient temperatures; P2) in the absence of cooling substrate (snow or mire), reindeer will select dry ground with low temperatures for bedding. Finally, we predicted that P3) because of their larger body size adult males select cooling substrates and cool ground to a larger extent than adult females, which in turn are expected to be more selective than the smaller yearlings of either sex. Based on our finding we discuss if bed site selection has a role in thermoregulation of Svalbard reindeer.

Material and methods

Study area

The study was carried out in the high Arctic archipelago of Svalbard. The study area (77°92'N-78°02'N, 15°16'E-15°87'E) is located in central Nordenskiöld Land national park, on Spitsbergen (Fig. 1a-b). The area is characterized by U-shaped valleys and steep mountains that rise to about 600 meters above sea level and used by a population of around 1800 Svalbard reindeer (Albon et al. 2017). 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, and vegetation patches dominated by graminoids, mosses or herbs (Brattbakk 1986). The valley slopes are either vegetated or have non-vegetated scree cover from rock falls, and sand and silt accumulation (Elvebakk 2005) . The light conditions on Svalbard show strong seasonal variation, with midnight sun from 20th April to 22nd August, and a dark season from 26th October to 16th February (Førland 1997). There is very low human activity in this area in summertime. There are no paths and the few cabins in the study area are mainly in use during wintertime.

Mean air temperature for Svalbard (1981-2010) in July, the warmest month, was 5.8°C (Nordli et al. 2014). Over the last century the annual mean temperature has increased by 2.6°C and Svalbard is the location with the greatest temperature increase in Europe during the last 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 per century, while summer has an increase of 1.0°C per century (Nordli et al. 2014).

Svalbard has permafrost that is about 100 meters thick in major valley bottoms and up to 500 meters thick in high mountains (Humlum et al. 2003; Westermann et al. 2011). The top layer of soil that thaws during the summer and freezes again during the autumn is termed the "active

layer". In recent years increasing active-layer depth and rising permafrost temperatures have

been recorded in Svalbard (Christiansen et al. 2010). The topography introduces local and large

variations in ground temperature regimes and permafrost thickness due to variations in slope,

aspect, altitude, topographic shading and redistribution of snow by wind (Westermann et al.

2011). The permafrost can in some areas, typically in large valleys and their valley slopes,

appear closer to the surface 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 (Péwé 1966;

Humlum et al. 2003), but diameters up to 20 meters have been found (Black 1976; Humlum et al.

2003). These wedges of solid ice do not thaw as easily as frozen ground, making the depth of the

active layer patchy during summer (Christiansen 2005).

Sampling design

The data was collected between 9th July and 8th August 2017 (a period of continuous daylight)

between 10 AM and 10 PM (Fig. 1c). Two observers searched the study area on foot and

detected single resting animals or groups with at least one resting animal. The two observers

were always within line of sight from each other and moved in the same general direction. To

optimize daily sample size, the search was neither random nor occurred along fixed transects, but

rather targeted areas with expected high density of reindeer. Most observations occurred in the

valley Semmeldalen (Fig. 1d), due to its high density of reindeer and proximity to the field base.

To minimize repeated observations of the same individuals on the same day, the route was either

one-directional (no observations when returning to base) or consisting of a wide loop to avoid

searching the same area when returning to base.

When larger groups where found, and several animals were bedding in the same area, a maximum of three bed sites where sampled (as a compromise between efficient data sampling while limiting pseudoreplication; sensu Hurlbert 1984). If more than three individuals in a group were bedded, selection of the three candidates followed two rules. First, we attempted to achieve an even distribution of bed sites from adult males, adult females and yearlings, and selected the category with the lowest sample size. Secondly, when several individuals were of the same category, we maximized the distance between observed individuals. When approaching the bedded reindeer it typically stood up and moved at a distance ranging from 20 to 100 meters from the observer. Mean escape distances of reindeer in our study area is 150 meters (Reimers et al. 2011). The most typical behaviour was to resume feeding alone or in a group after the initial escape. The open landscape facilitates visual contact with individuals resulting in low probability of repeated sampling of the same individual the same day. As the reindeer left the bed site, the sex (male/female), age category (adult/yearling) and group size was recorded. Sex and age was determined based on body size, presence/absence of male genitalia and antler characteristics. The animals did not have easily recognizable individual marks, thus the same animal may have been registered on different days in the study period. The exact bed site was identified by flattened vegetation or substrate, shed fur and often warm ground at the site.

Each sampled bed site had two corresponding control sites. The control sites were sampled at 10 meters and 100 meters away from the centre of the bed site along a randomly selected compass course. Based on experience with the species, we assumed a priori that bed site selection would be a relatively small-scale process (that individual rarely move far to bed down). The 10-meter scale was assumed to be an appropriate scale if the reindeer lay down to ruminate

very close to where they cease feeding, while the 100-meter scale would test if individuals visually assess and select from candidate bed sites from a somewhat larger area.

Svalbard reindeer live in small and unstable groups (Loe et al. 2006), with the possible exception of the breeding season (October) when males hold harems. For most of the year, individual behaviour can therefore be assumed to be less dependent on other individuals than for most other *Rangifer* subspecies that undergo long migrations in large herds. Although our study design resulted in some unknown amount of pseudoreplication, it was likely minimal because groups are small, group cohesion is low, and the population size is large. With this rationale, we treated observations as independent and being individual- rather than group level observations.

Substrate, vegetation and ground moisture was registered within one square meter around the centre 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 the eight previously established vegetation types (van der Wal pers. comm.; Table S1 in the Supplementary Material): 1) *Dry Salix* L., *Dryas* Hübner or *Cassiope* D., 2) *Luzula* DC., *Salix* L., *Alopecurus* L., 3) *Phippsia* Stebbing, *Saxifraga hyperborean* R., 4) *Poa* L., *Festuca* L., 5) *Dupontia* R., *Eriophorum* L., 6) *Alopecurus* L., *Equisetum* L., *wet moss,* 7) *Carex lachenalii* Schkuhr, *8) Deschampsia* P., or as 9) "other". In addition we had a tenth category for "non-vegetated" plots. Ground moisture was registered, as either, dry, moist, or wet. This judgement was based on micro topography (convex, concave or flat terrain associated with capacity to hold water) and presence of thick moss layers (indicating dominance of hydrophilic vegetation). The classification should not be affected by short-term precipitation. For example, sparse vegetation cover on convex ridges (facilitating fast water drainage) was classified as dry even if moistened by recent precipitation. Cooling substrates were defined as sites on snow and mire. Mire was

defined as moist or wet vegetation of type 5, 6 or 9, representing what was experienced as mire by a human observer on foot.

Ground temperature was measured at the centre 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 (model TCT013K; Radiant Innovation Inc., China) with a thin (2 mm) type K thermocouple cable. To reduce ground temperature measurements being influenced by the reindeer's body temperature, all registrations of ground temperature were done at least 10 minutes after the reindeer had 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 (Williamsen, unpublished data). The mean ground temperature was 8.6°C (range from -1.1 to 17.6°C).

Air temperature was measured one meter above the ground for each bed site, using the same measuring equipment as used for ground temperature. The tip of the thermocouple cable was exposed to solar radiation and not shaded. Our measure of air temperature is therefore the operative temperature as perceived by the tip of that thermocouple. Air temperature was not measured at control sites, as there was no expected difference in air temperature within the 100 meters from the bed site to the furthest control site. Registrations of sun or shadow at bed sites were not considered, as there was never a contrast in shade between bed sites and control sites due to the short distance, open landscape, and high elevation of the sun. The mean air temperature was 8.9°C (range from 4.5 to 16.2°C).

The Human Landing Catch method was used to estimate mosquito abundance (Krockel et al. 2006). The counting was done by 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. Mosquitos were counted only at the bed sites because 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. Only 51 mosquitos were registered in the 371 sampling sessions in the field, with a maximum of five mosquitos in one five-minute observation period. In analyses, we assumed that the mosquito abundances were similar in bed sites and corresponding controls.

All applicable national and institutional guidelines for the use of animals were followed. More specifically, the study followed ethical requirements in Norway and was approved by the Norwegian Food Safety Authority (permit number 17/237024) and the Governor of Svalbard (permit number 16/01632-15).

Statistical analyses

The statistical analyses were performed using R version 3.4.2 (R Core Team 2017). To investigate bed site selection, a Resource Selection Function approach was used (Manly 2002). Separate analyses were run for 10 meters control sites and 100 meters control sites. In both sets of analyses the dependent variable was site category (bed site=1 and control site=0). The effect of independent variables on bed site selection were then investigated using conditional logistic regression (using the survival package; Therneau 2015) which allowed us to stratify the analysis by control and used bed site pairs. Values of the back-transformed (inverse logit) predicted response higher than 0.5 are interpreted as selected as bed sites and lower than 0.5 as avoided bed sites. Because we adopt a presence-absence design with equally many bed sites (value 1) and

control sites (value 0), a probability value of 0.5 means that a site is as likely to be used as a bed site as to be a randomly selected control site (Manly 2002; Johnson et al. 2006). In contrast to many GPS-studies with presence only data, we can use the term "avoidance" because we have confirmed field observations of true absences (no reindeer on the control sites). We calculated a polyserial correlation (Olsson et al. 1982) between cooling substrate and ground temperature using the function hetcor in the polycor package (Fox 2016). The two variables were moderately correlated (r=0.31) and we opted to analyse them in different models in a sequential manner.

First, we investigated if reindeer selected cooling substrates as bed sites. Candidate models included as independent variables, in addition to an additive effect of cooling substrates (yes or no), its interaction with: air temperature (continuous), mosquito abundance (continuous), and age/sex category (the three levels male adults, female adults and unsexed yearlings). We also tested for the three-way interaction of air temperature, age/sex and cooling substrate. The candidate models were then compared based on the principle of parsimony with the models, with the lowest corrected Akaike information criterion considered to be best (AICc; Table 1; Burnham and Anderson 2002). In addition, AIC weights were used to quantify the support of the best model relative to lower ranked models.

Second, to investigate whether the reindeer selected for cool ground also when not using the cooling substrates snow and mire, we re-ran the analyses on the subset of data where all bed and control sites on cooling substrates were excluded. Candidate models included as independent variables ground temperature and its interaction with air temperature and age/sex category, and were compared on the basis of their AICc and AICc weights (Table 2).

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

the 10 meters scale can be found in the Supplementary Material (Tables S2, S3 and S4; Fig. S1

and S2). Including several individuals from the same group could result in pseudoreplication. We

therefore repeated the model selection and tested the final models on a data set where only one

randomly selected individual was included from each group. The same models were selected as

top models and all effects remained significant with similar parameter estimates (Table S5).

Results

In total, we observed 371 bed sites (118 adult males, 157 adult females and 96 yearlings of both

sexes). Altogether 35 % of bed sites and 31 % of control sites were classified as being on the

cooling substrates snow and mires. The model with the lowest AICc (Table 1a; AICc

weight=0.87), included only the effect of cooling substrates and the interaction between air

temperature and cooling substrates (Table 1b). On days when the air temperature was high, the

reindeer showed a strong selection for using cooling substrates as bed sites, whereas, they

avoided the cooling substrates on the coldest days (Fig. 2). Selection for cooling substrates

changed from preference to avoidance below a threshold air temperature of approximately 9°C

(95% confidence interval [7.9, 9.5]; Fig. 2).

When all data from cooling substrates (snow and mire) were excluded from the dataset,

the model with the lowest AICc included ground temperature as the only variable (Table 2; AICc

weight=0.72). Reindeer showed a strong selection for bed sites with low ground temperature and

avoided warm ground even in the absence of snow and mire (β=-0.348, SE=0.078, p<0.001; Fig.

3). Investigating the pair-wise difference in ground temperatures across all substrate types

(including cooling substrate) corroborated this finding. Bed sites tended to be cooler than their

corresponding controls (mean difference =-1.8°C; 95% CIs [-2.3, -1.4]). The temperature

difference between bed sites and controls was larger on warmer than average (Fig. 4a; mean difference=-3.2°C; 95% CIs [-3.9, -2.4]) compared to colder than average days (Fig. 4b; mean difference=-0.8°C; 95% CIs [-1.3, -0.3]).

Mosquito densities were very low. Accordingly, we found no evidence for mosquito abundance to affect reindeer bed site selection of cooling substrates (ΔAICc=4.05; Table 1a).

There was also no evidence for significant differences between age and sex categories in their temperature dependent bed site selection (ΔAICc=11.9 and 17.4 in Table 1 and 2). Predicted values from a model allowing for differential responses of age and sex categories supports that they all start to select for cooling ground around the same air temperature threshold (Fig A3).

Discussion

Understanding how animals cope with high temperatures is needed to predict consequences of climate change. Behavioural thermoregulation is expected to play an increasingly important role in a warmer environment. Many animals select for dense habitat and cold sites when resting, but the role of thermoregulation in bed site selection is often hard to separate from other confounding factors such as predator avoidance and insect harassment. Ruling out confounding factors, we demonstrated that Svalbard reindeer started to select for cool substrates at an ambient temperature threshold reached on average every second day in summer. These findings are particularly relevant as the Arctic is rapidly warming.

Bed sites have a role in thermoregulation

In support of prediction P1, Svalbard reindeer selected cool bed sites on warm summer days. At the opposite temperature extreme, desert ungulates like Arabian oryx (*Oryx leucoryx*, Link, 1795), sand gazelles (*Gazella subgutturosa marica*, Thomas, 1897), springbok (*Antidorcas marsupialis*, Zimmermann, 1780), and desert mule deer (*Odocoileus hemionus eremicus*, Mearns, 1897), have been found to frequently use shaded microhabitats when temperature peak during the day (Bigalke 1972; Tull et al. 2001; Hetem et al. 2012). In these studies the temperatures that induced behavioural responses were close to (Hetem et al. 2012) or even exceeded 30°C (Tull et al. 2001). Our results for Svalbard reindeer indicate a gradual response in bed site selection in response to ambient temperature. At low ambient temperatures cool substrates were avoided, while they were increasingly selected when ambient temperature exceeded 9°C. Other studies have also found that behaviour linked to heat stress occurs at surprisingly low temperatures. Renecker and Hudson (1986) found that moose were heat stressed at temperatures as low as zero degrees in winter, but that they had a much higher heat tolerance in summer (threshold at 14-20°C). Our study demonstrates that cold-adapted, just like heat-adapted ungulates (Bigalke 1972; Tull et al. 2001; Hetem et al. 2012), display behavioural responses to ambient temperatures in the upper range of what they normally experience.

Animals cope physiologically with excess heat by autonomic thermoregulation such as panting or sweating. However, heat loss through these pathways is energetically costly and cause loss of water and minerals too (West 1999). To start behavioural thermoregulation before physiological thermoregulation is a good strategy to conserve water and energy (Fuller et al. 2014). Physiological thermoregulation starts at the upper critical temperature (T_{uc} sensu Bligh and Johnson 1973). Behavioural thermoregulation is consequently expected to occur before their

T_{uc}. It is the energetic cost of active heat dissipation which produces the increase in metabolic rate at T_{uc}. Nilssen et al. (1984) observed the relationship between metabolic rate and ambient temperature in Svalbard reindeer under controlled indoor conditions. In their study, metabolic rate did not increase for temperatures up to 15°C (which was the maximum temperature tested), indicating that T_{uc} is even higher. Although we cannot rule out that the operative environmental temperature (Huey 1991) experienced by the reindeer is higher than the air temperature we measured on days with high solar radiation, our finding suggests that behavioural thermoregulation starts at temperatures well below their T_{uc}. In support of this, we never observed obvious heat stress behaviour, such as panting, during our field work.

In the open valleys of Svalbard, small-scaled thermal variation is provided by the substrate rather than shade from trees or other structures. We found wet terrain to be an important cooling substrate for Svalbard reindeer. This is in line with previous studies that documented bed site selection for wet substrates at warm ambient temperatures in mouflon *(Ovis aries* Linnaeus, 1758; Marchand et al. 2014), roe deer (*Capreolus capreolus*, Linnaeus, 1758; Mysterud 1996), moose (*Alces alces*, Linnaeus, 1758; van Beest et al. 2012; van Beest and Milner 2013; McCann et al. 2016) and caribou (*Rangifer* sp.; Morschel and Klein 1997). As observed in sheep (*Ovis aries*, Linnaeus, 1758; Gatenby 1977), a wet bed may help the reindeer dissipate more heat than a dry bed, because the substrate water content is positively correlated with thermal conduction (Cosenza et al. 2003). Since the legs are important for heat dissipation (Folkow and Mercer 1986), reindeer may possibly lose a significant amount of heat through conduction when bedded. A wet substrate would also increase evaporate heat dissipation from the animals surface. Wet substrates in our study consist of mire, containing a high percentage of moss. A thick moss layer insulates the soil and limits the extent to which the permafrost thaws

during summer (van der Wal et al. 2001). The combination of permafrost beneath, and wet moss and mire on top, as well as snow, seems to provide favourable microclimates for the Svalbard reindeer to cool down during adverse thermal conditions. However, in support of prediction P2, Svalbard reindeer were also able to detect cold ground temperatures independent of the visual cues of snow and wet ground. The use of nearby cold ground for cooling down is less energetically costly than moving longer distances for shade from mountains, to cooler altitudes or to find snow, as it diminishes throughout summer.

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 and Kearney 2009). However, we found no differences in bed site selection between age and sex categories. This suggests that the mass difference between adult males, adult females, and yearling reindeer is not large enough to cause substantial differences in bed site selection. Even small-sized individuals selected cool bed sites on warm days, and they all avoided resting on snow and in mire on cold days.

Selection of snow despite no insect harassment

Previous studies from lower latitudes have found that parasitic and/or biting insects periodically harass *Rangifer* spp. and disturb their activity patterns (Downes et al. 1986; Morschel and Klein 1997; Colman 2000). With only mosquitos present at low abundances, Kastnes (1979) found no sign of the Svalbard reindeer being harassed by any parasitic insects. Nearly four decades later, we still record very low abundances of mosquitoes. Furthermore, contrary to predicted (P3), variation in mosquito abundances did not influence the selection of cooling substrate as bed site. As such, our study is the first *Rangifer* study to find selection of snow and other cold substrates

independent of insect harassment, which lend support to the view that thermoregulation plays a role in bed site selection.

Behavioural adaptations are important to buffer climate change, as evolutionary adaptations are not likely to keep pace with the ongoing rapid warming of the climate. This study contributes to the understanding of how cold adapted ungulates select bed sites to compensate for warm summer temperatures. The percentage of summer days (July to mid-August) with maximum daily temperatures exceeding 9°C has increased from 37% in 1977 to 52% in 2017 (prediction from a linear model estimated with data Svalbard airport), a trend which is predicted to increase in the future (Nordli et al. 2014). As a consequence of warmer temperatures, accessibility to summer snow patches and near-surface permafrost will be reduced (Vaughan et al. 2013). Increased movement costs and loss of foraging time could be a consequence if future warming result in scarcity of suitable bed sites close to where individuals cease their foraging bouts. Dry sites without snow currently compose 65% of the bed sites. If these sites become less suitable, proximity to cold substrates may restrict ranging behaviour. This could result in increased density-dependent forage competition close to mire and other cold substrates, a general phenomenon seen in central place foragers (feral horses *Equus ferus caballus*, Linnaeus, 1758, restricted by proximity to water holes; Rozen-Rechels et al. 2015). If cold patches are small and as such possible to monopolize, they could also become a source for interference competition. The energetic cost of thermoregulation in a warming world has been shown to affect body condition (du Plessis et al. 2012) and breeding success (Cunningham et al. 2013). In Svalbard reindeer, a fitness cost from lack of cooling substrate would likely occur through reduced feeding efficiency and body fat deposition in summer, in turn affecting recruitment rates next spring. We conclude that while the need may increase, cool bed sites may be increasingly hard to find on a

warmer Arctic tundra. Future studies could investigate if cool bed sites under some conditions are sufficiently rare to be a source for competition and if individual variation in ability to detect and occupy such sites lead to variation in fitness traits.

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Table 1. a) Ranking of Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) bed site selection models when including cooling substrates (snow and mire) as an explanatory variable in both main effect and in interactions. Candidate models are presented with their respective number of parameters (*K*), AICc, ΔAICc and AICc weight. b) Parameter estimates of the most parsimonious model with its regression coefficients (*β*), standard errors (SE) and *p*-values.

a) Model	*K*	AICc	ΔAICc	AICc wt
Cooling substrate + Air temperature x Cooling substrate	3	504.6	0.00	0.87
Cooling substrate + Air temperature x Cooling substrate + Mosquito abundance x Cooling substrate	5	508.6	4.05	0.11
Cooling substrate + Air temperature x Cooling substrate + Age/Sex category x Cooling substrate	9	514.8	10.25	0.01
Cooling substrate	1	515.2	10.61	0
Cooling substrate + Air temperature x Cooling substrate + Age/Sex category x Cooling substrate + Age/Sex category x Air temperature x Cooling substrate	11	516.5	11.90	0
Cooling substrate + Air temperature x Cooling substrate + Age/Sex category x Cooling substrate + mosquito abundance x Cooling substrate	11	518.9	14.34	0
Cooling substrate + Air temperature x Cooling substrate + Age/Sex category x Cooling substrate + mosquitos x Cooling substrate + Age/Sex category x Air temperature x Cooling substrate	13	520.6	15.99	0
Cooling substrate + Age/Sex category x Cooling substrate	6	524.7	20.07	0
b) parameter estimate for the best model	*β*	SE	*p*	
Cooling substrate	-2.79	0.84	<0.001	
Air temperature x Cooling substrate	0.32	0.090	<0.001	

Table 2. Ranking of Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) bed site selection models when excluding cooling substrates (snow and mire), but adding ground temperature as a candidate explanatory variable. Candidate models are presented with their respective number of parameters (*K*), AICc, ΔAICc and AICc weight.

Model	*K*	AICc	ΔAICc	AICc wt
Ground temperature	1	215.2	0	0.72
Ground temperature + Age/Sex category x Ground temperature	3	217.9	2.7	0.18
Ground temperature + Air temperature x Ground temperature	3	219.2	4.0	0.10
Ground temperature + Air temperature x Ground temperature + Age/Sex category x Ground temperature	9	230.2	15.0	0
Ground temperature + Air temperature x Ground temperature + Age/Sex category x Ground temperature + Age/Sex category x Air temperature x Ground temperature	11	232.6	17.4	0

Figure legends

Fig. 1. The study was conducted in Svalbard (a), around 20 km south of the main settlement Longyearbyen in Nordenskiöld land (b). All data were sampled between 10 AM and 10 PM (c). The majority of the 371 bed sites (red points) were recorded in the valley Semmeldalen, where our field base was located in the southern end (black circle; c). Grey contour lines represents 50-meter increments in elevation. Coordinates on *x* and *y*-axes are in UTM 33.

Fig. 2. The probability of cooling substrates (snow and mire) being selected for bed sites as a function of air temperature. The line shows the model prediction with the shaded region representing the 95% confidence interval. Dots show mean (±SE) use according to air temperature separated in 1°C bins. Values above 0.5 indicate selection for the cooling substrate, and values below 0.5 indicate avoidance.

Fig. 3. Bed site selection of Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) as a function of ground temperature. The *y*-axis is interpreted as the probability of a site being a bed site instead of a control site. Predicted values above the 0.5 indicate that it is more likely that a site is a bed site than a control (selection) and below 0.5 conversely indicate avoidance. The shaded regions represent 95% confidence intervals. Points show raw data being the proportion of sites consisting of bed sites in 2°C ground temperature increments. Error bars are ±1SE.

Fig. 4. The relationship between ground temperatures of Svalbard reindeer (*Rangifer tarandus platyrhynchus*, Vrolik, 1829) bed sites and their corresponding controls located 100 meters distant in a random direction (*n*=371 pairs; including sites with cooling substrates snow and mire). Values

below the diagonal line implies that the bed site was colder than the control. Panel (a) is for air temperatures above and panel (b) for air temperature below average for our recorded air temperatures. Open circles are used when neither the bed site nor control site are located in cooling substrate, x is used when both are in cooling substrate, plus sign (+) when only bed site is in cooling substrate and open triangle when only control site is in cooling substrate.
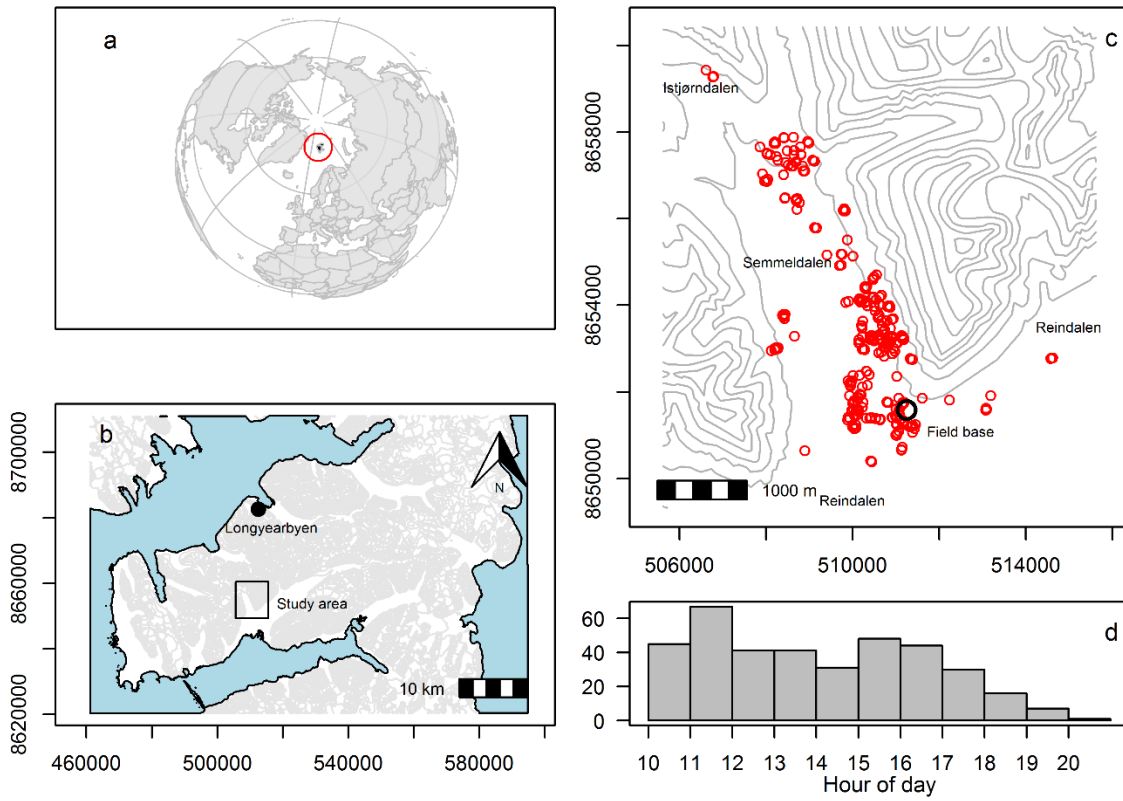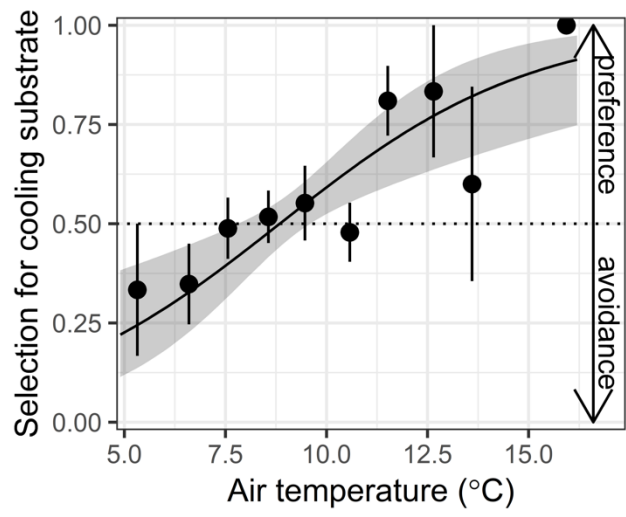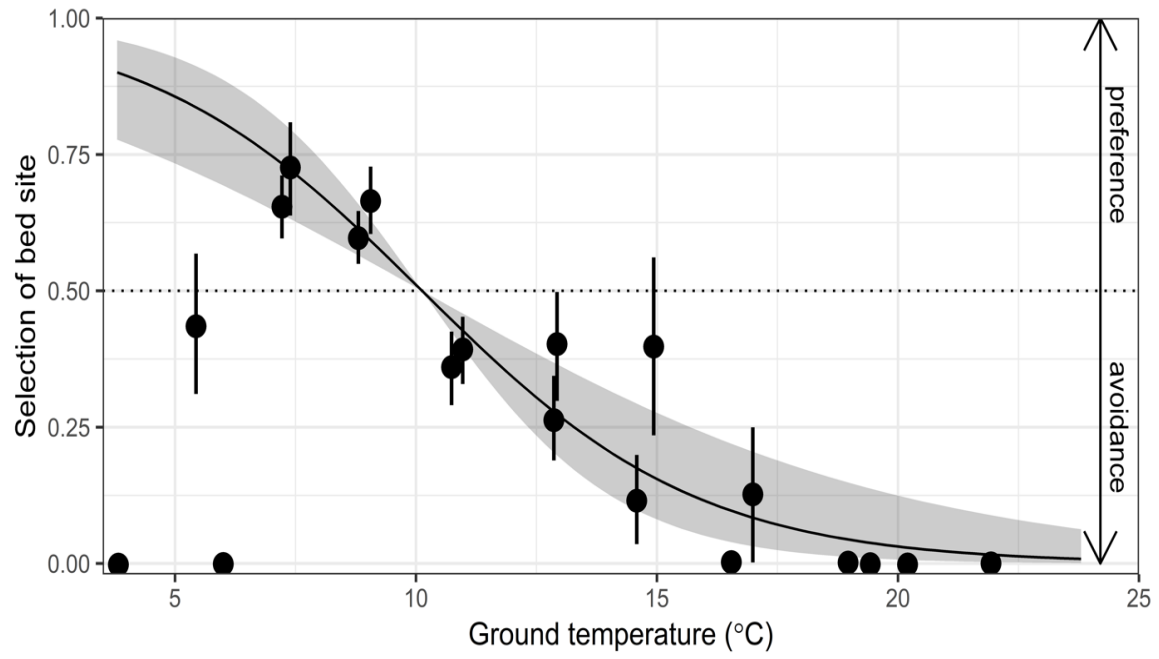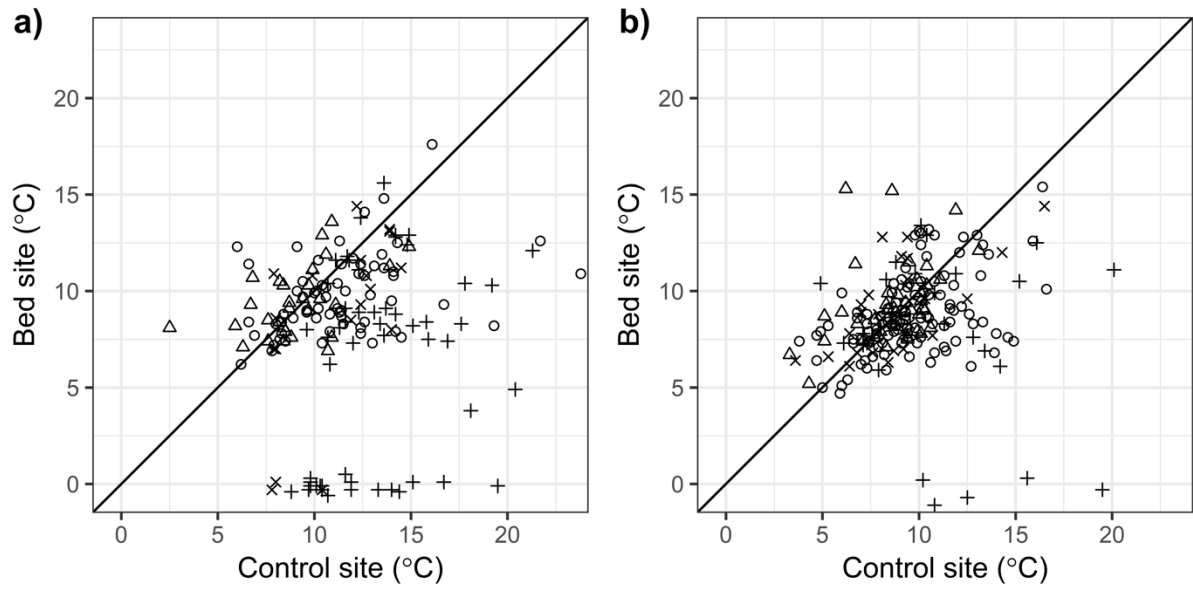
Figures

Fig 1

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