Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen

Authors: Schmidt, Niels M., Beest, Floris M. van, Mosbacher, Jesper B., Stelvig, Mikkel, Hansen, Lars H., et al.

Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen

Niels M. Schmidt, Floris M. van Beest, Jesper B. Mosbacher, Mikkel Stelvig, Lars H. Hansen, Jacob Nabe-Nielsen and Carsten Grøndahl

N. M. Schmidt (nms@bios.au.dk), F. M. van Beest, J. B. Mosbacher, L. H. Hansen and J. Nabe-Nielsen, and, Dept of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark. NMS, JB and JNN also at: Arctic Research Centre, Aarhus University, Aarhus, Denmark. – M. Stelvig and C. Grøndahl, Copenhagen Zoo, Centre for Zoo and Wild Animal Health, Frederiksberg, Denmark

Detailed knowledge on movement behaviour of free-ranging muskoxen *Ovibos moschatus* is currently lacking. Quantifying variation in individual movement and the variables driving such patterns is important to understand how they meet their basic requirements and to inform management. Because muskoxen exist in nutrient-poor systems with extreme climatic and seasonal variability, individual movement patterns are expected to be largely dependent on environmental conditions and the seasonal variation therein. We analysed high-resolution location data of 14 adult female muskoxen roaming around Zackenberg in northeast Greenland (74°28′N, 20°34′W). We assessed the relative importance (Akaike variable weights) of multiple extrinsic conditions in explaining variation in hourly speed, turning angles, and activity. We found that time of day, ambient temperature, and land cover types were the most important covariates explaining variation in fine-scale movement and activity patterns throughout the year. Movement speeds were consistently lower in land cover types with more dense vegetation. Speed of movement was positively correlated with ambient temperature when the days were long, while negatively related with temperature in periods with few or no hours of daylight. Diurnal peaks in movement and activity patterns were observed most of the year (including mid-winter months with 24-h darkness), except during high-summer (24-h of daylight), when individual movement and activity remained continuously high. The topographic variation (elevation and slope) explained only a small part of the variation in muskox movement patterns in the areas where the muskoxen were observed. Analyses of displacement patterns revealed a mixture of movement behaviours. We conclude that muskoxen in high-arctic Greenland adopt a largely nomadic movement behaviour, but do so within a rather small geographical area (app. 5000 km²), and that their movement and activity patterns are largely directed at finding suitable foraging patches and avoiding cold-stress during harsh winter weather.

Animal movements tie together ecosystem processes, and information about animal movements is thus fundamental to our understanding of general ecosystem functioning (Lundberg and Moberg 2003). In the far north, tundra ecosystems are under severe pressure due to the rapidly changing climate (Post et al. 2009, Gilg et al. 2012). Detailed knowledge about the ecology, including movement patterns, of key species in these ecosystems is required to assess the current and future state of the tundra ecosystem. Yet, data on animal movements from this remote region are scarce.

As one of few large-bodied herbivores, the muskox *Ovibos moschatus*) is a central species in the tundra ecosystem. As the snow melts, muskoxen track the emerging vegetation (Forchhammer et al. 2005). And during the short arctic summer, muskoxen forage intensively in order to build up the fat reserves required for them to gain sufficient body

mass to allow for conception and to sustain foetal growth and vital functions throughout the subsequent snow-covered period (White et al. 1997, Adamczewski et al. 1998). Snow conditions determine access to food in winter (Mosbacher et al. 2016b), and are therefore a major determinant of muskox population dynamics in high-arctic Greenland (Forchhammer and Boertmann 1993, Schmidt et al. 2015). In summer, forage is easily available and more abundant, and muskoxen only consume a negligible fraction of the available plant forage (Mosbacher et al. 2016a).

In contrast to the other true arctic ungulate, the reindeer *Rangifer tarandus*, in which many populations undertake extensive seasonal migrations, the muskox is believed to be rather sedentary. However, only limited data on muskox movements have been published (Reynolds 1998, Reynolds et al. 2002, Danks and Klein 2002, Aastrup 2003). Basic information about the year-round movement behaviour of this tundra key species is scant and detailed information on fine-scale movements is almost completely lacking. Quantifying variation in muskox movements and the

variables driving their movement patterns is thus crucial for our understanding of arctic muskoxen and their environment. Fortunately, recent technical developments in GPS technology have now made it possible to examine the movement patterns of species, even in the most remote parts of the world. The current study therefore aimed at providing basic year-round location data and movement metrics on muskoxen in high-arctic Greenland, and to link these movement patterns to environmental conditions. Living in the nutrient-poor, highly seasonal environment found in the Arctic with short summers and long winters (Callaghan et al. 2013; Fig. 1), we expected individual movement patterns to be largely dependent on the variation in the environmental conditions and to vary among seasons. Specifically, we wanted to examine 1) whether the movement behaviour of muskoxen in high-arctic Greenland can be classified as migration, dispersal, home range or nomadic movement behaviour (following Bunnefeld et al. 2011), and 2) whether muskoxen respond to the varying ambient conditions by altering their fine-scale movement patterns, specifically speed, turning angle, and activity.

Methods

Study site

This study was conducted at Zackenberg in northeast Greenland (74°28′N, 20°34′W). Zackenberg research station hosts one of the most comprehensive ecosystem-based monitoring programs in the Arctic and numerous background data are therefore available from this otherwise remote locality (Forchhammer et al. 2008). The climate at Zackenberg is high-arctic with a mean annual temperature of –9°C (Hansen et al. 2008), and both light regimes, temperature and snow conditions change markedly during the year (Fig. 1). The topography in the region is characterized by mountains up to 1600 m, intercepted by broad valleys (Schmidt et al. 2015). The Zackenberg valley, and the region in general, is covered by a mosaic of tundra habitat types

of varying productivity (Arndal et al. 2009). The growing season typically extends from early June to early September (Tamstorf et al. 2007), but onset may vary several weeks from year to year according to the amount of snow precipitation (Høye et al. 2007).

The muskox is the only large herbivore found in northeast Greenland. The species is numerous around Zackenberg (Schmidt et al. 2015), and in 1990 between 2900 and 4600 muskoxen was estimated to roam in the area around Zackenberg (Boertmann et al. 1990). During summer, most of the habitat types found in the area, and particularly the wet meadows, are utilized by muskoxen for foraging (Berg et al. 2008, Kristensen et al. 2011).

Muskox capture and collaring

In October 2013, a total of 14 adult muskox cows (aged 4 years or more; aged based on horn morphology; Olesen and Thing 1989) with calves were captured and equipped with GPS collars. Presence of a calf was based on observations of the focal individual prior to darting. The sedation and handling of muskoxen in this study followed the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011). Research permits were issued by the Greenland Government (j.no. G13-029).

We approached muskox groups on foot and circled the group to allow the veterinarian to get into close range. The cow was darted from a distance of approximately 30–50 m using a CO_2 driven dart gun (JM Special, DanInject, Denmark). Each cow was immobilized using an anaesthesia mix consisting of 2.0 mg Etorfin (Captivon 9,8 mg ml⁻¹ Wildlife Pharmaceuticals South Africa), 30 mg Xylazine (Rompun dry substance, Bayer Healthcare), 0.3 mg Medetomidine (Zalopine 30 mg ml⁻¹, Orion Pharma) and 40 mg Ketamine (Ketaminol 100 mg ml⁻¹, MDS Animal Health). Upon darting, we withdrew from the group to allow for the anaesthesia to kick in. After about 5 to 8 min, the cow was recumbent and could be approached. After having driven off the group, the immobilized cow was placed in sternal recumbancy to allow for free breathing and belching. To ensure
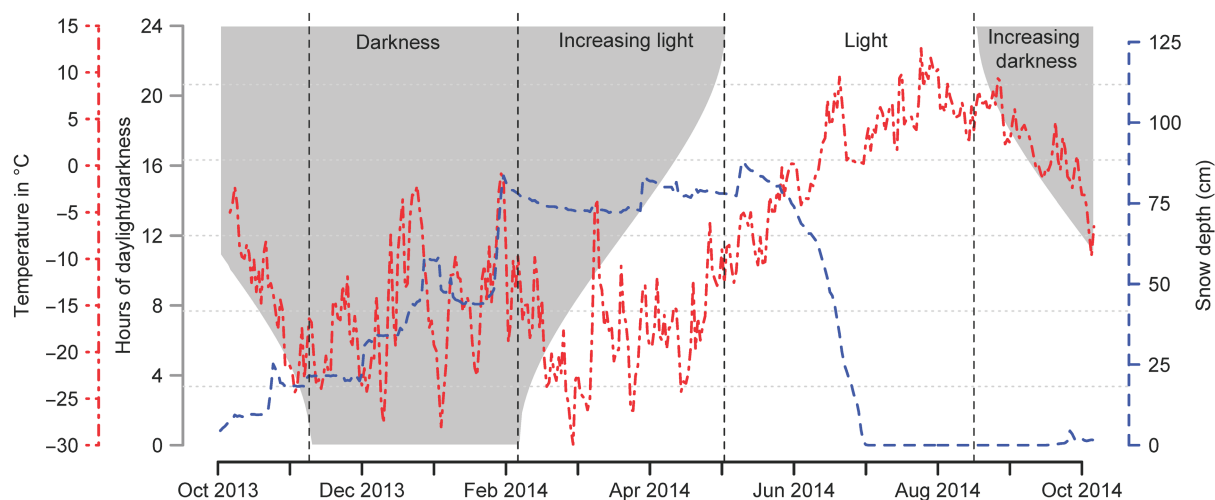

Figure 1. The arctic year visualized using local climate data and light regimes from Zackenberg in high-arctic Greenland during the study period. 'Increasing light' corresponds roughly to spring, 'Light' to summer, 'Increasing darkness' to autumn and 'Darkness' to winter.

254

proper oxygenation, oxygen (2 l min⁻¹) was supplied through a nostril to the pharynges via a thin tube. During handling, one person was constantly monitoring the breathing, level of anaesthesia, and belching of the animal.

When the animal was stabilised, a GPS collar (Tellus Large; Followit Lindesberg AB, Sweden) was mounted on the cow. The total weight of the collar was approximately 1.2 kg, corresponding to less than 1% of the muskox cow body mass (Table 1). The collar was programmed to acquire one position every hour. Activity was measured using two standard accelerometers placed perpendicular to each other inside the collar. Collars were also equipped with VHF and UHF modules, as well as a remote drop-off mechanism. All data were received through the FollowIT server via an Iridium satellite communication module in the collar.

Before release, the cow was weighed using a carrying tarpaulin (Daninject, Børkop) and eight standard luggage scales (Korona, max 50 kg, Hans Dinslage GmbH, Germany). Then the cow was given an antidote intramuscularly consisting of 50 mg Naltrexon (Trexonil 50 mg ml⁻¹ Wildlife Pharmaceuticals) and 5 mg Atipamezole (Antisedan 5 mg ml⁻¹ Orion Pharma). Within a few minutes after the antidote was given, the animal stood up and began moving towards its group. The muskox cows seemed unaffected by the handling and collaring, and after release immediately joined the activities of the group.

During the period of GPS collaring, tagged muskox cows were observed moving between groups on several occasions, indicating that group cohesion was low.

GPS data processing

After approximately one year of data collection (30 September 2014), the location data were downloaded for processing. The fix rate of the collars was high and GPS locations were acquired > 99% of the time for all collars. We first removed locations that were acquired before individuals were collared and after an individual had died (date of death was determined based on mortality signals) or the collar had malfunctioned (Table 1). We then filtered the data for large positional outliers acquired while collars were on the animals. Outliers were defined as locations where movement between two successive GPS locations exceeded 10 km h⁻¹ and the angle of the

erroneous location was greater than 166° but less than 194° (i.e. the animal is returning to roughly the same position it came from) (Bjørneraas et al. 2010). With this approach we removed 40 presumed erroneous locations (< 0.02% of the final GPS data set). All GPS positions collected within 24 h of capture were excluded to minimize bias due to tagging and handling in the location data.

We then categorized the location data into four classes according to the light regimes during the arctic year (i.e. 24 h light, increasing darkness, 24 h darkness and increasing light; Fig. 1). These four periods roughly correspond to summer, autumn, winter and spring seasons. Hours of daylight/darkness were obtained using sunrise and sunset times for the study area and period based on the NOAA sunrise sunset calculator (<www.noaa.gov/>). From the GPS data we quantified two movement metrics describing the muskox movements: speed (distance (m) between hourly positions) and turning angle (absolute angle between hourly positions; the lower turning angle, the more successive positions are on a straight line and vice versa). Speed and turning angles between locations were calculated using the package adehabitatLT in the statistical software R (<www.r-project.org>). We also calculated proportional activity for each hour using the registered counts in activity sensors (acquired during satellite communication (lasts up to 60 s; hourly snapshots) with the recursive model developed by Body et al. (2012). By combining these movement and activity metrics, muskox behaviour can be inferred. For example, low speed of movement combined with high turning angles and high activity typically indicates active foraging behaviour, low speed of movement combined with high turning angles and low activity typically indicates resting behaviour, while higher speed and lower turning angles indicates directed travelling movements (van Moorter et al. 2010, Owen-Smith and Martin 2015).

Net squared displacement analyses

The net squared displacement (NSD) measures the straight-line distance between the starting location and each subsequent location within the movement trajectory of a given individual. NSD is often used in ungulate space-use studies to identify the yearly movement behaviour used by

Table 1. Summary table for the muskox cows collared at Zackenberg in northeast Greenland. Movement behaviour was classified based on the individual net squared displacement patterns and the concordance criterion (CC). See text for further explanation.

Collaring date	Muskox ID	Body mass (kg)	Movement behaviour	CC	Days in study	Remarks
04/10/2013	1	180	disperser	0.71	361	alive (30 September 2014)
07/10/2013	2	146	nomad	0.64	154	dead (10 March 2014)
07/10/2013	3	172	disperser	0.53	217	dead (12 May 2014)
07/10/2013	4	193	mixed	0.57	358	alive (30 September 2014)
08/10/2013	5	181	nomad	0.61	357	alive (30 September 2014)
08/10/2013	6	177	mixed	0.81	253	dead (18 June 2014)
09/10/2013	7	195	migrator	0.71	356	alive (30 September 2014)
09/10/2013	8	188	nomad	0.81	250	malfunctioning GPS (16 July 2014)
09/10/2013	9	197	disperser	0.75	245	malfunctioning GPS (11 June 2014)
10/10/2013	10	206	mixed	0.68	355	alive (30 September 2014)
10/10/2013	11	195	disperser	0.80	355	alive (30 September 2014)
10/10/2013	12	201	nomad	0.72	355	alive (30 September 2014)
11/10/2013	13	190	mixed	0.79	354	alive (30 September 2014)
11/10/2013	14	209	mixed	0.81	354	alive (30 September 2014)

individuals, and to classify these as either residency, dispersal, nomadic, migratory, or mixed behaviour (sensu Bunnefeld et al. 2011, Börger and Fryxell 2012, Cagnacci et al. 2016). Each movement behaviour has a distinct NSD curve, which can be estimated using non-linear modelling (see Bunnefeld et al. 2011 for a detailed description of each movement strategy and parameter requirements).

Following Cagnacci et al. (2016), we fitted five, unique non-linear mixed effects models, each corresponding to one of the aforementioned movement strategies, to the yearly trajectories of all individuals. Starting values for the required mixed-model parameters were first estimated using non-linear least-squares analyses. To select the best mixed model, and evaluate its goodness-of-fit for each individual trajectory, we used the concordance criterion (CC; value between 0–1 with 1 being the best fit) (sensu Börger and Fryxell 2012). Although widely used, the NSD approach does have some shortcomings (Singh et al. 2016) and is known to be sensitive to the starting location used in the calculations, which should ideally be selected based on biological–ecological criteria (Cagnacci et al. 2016). Because all individuals in our study were present in the same area around Zackenberg during the collaring period, we used the day following the date of collaring of each individual (Table 1) as the starting location for NSD calculations. This to minimise the risk that any movement bias due to tagging and handling was included in the NSD analyses.

To examine the potential temporal association between the individual muskoxen, and thus the independence of between individuals, we calculated the percentage of simultaneous positions where individuals were less than 100 m apart. The 100 m threshold was based on the group definition provided by Schmidt et al. (2015).

Environmental predictor variables and habitat use

As ambient temperature, we used records of local temperature (°C) obtained from an automatic climate tower located at Zackenberg, in the centre of the Wollaston Forland region (Hansen et al. 2008). Temperature was recorded hourly 2 m above terrain during the study period (Table 2). We used these point measurements of local climate as rough indicators of the climatic conditions throughout the area in which muskoxen roamed. We did therefore not correct the temperatures for wind chill as this effect is highly dependent upon the actual location of the animal.

Topographic variables (i.e. slope, aspect, hill shade, elevation and distance to coast) were derived from a digital terrain model (spatial resolution of 30×30 m). Distance to coast was, however, excluded from further analyses because of collinearity with elevation. We used a Landsat 7 ETM (dated 19 July 2009) satellite image (spatial resolution of 30×30 m) to classify the land cover into three types based on normalized differential vegetation index (NDVI). Based on field measurements from Zackenberg (Tamstorf et al. 2007, Arndal et al. 2009), pixels with NDVI values of 0.35 and above were classified as 'dense vegetation', pixels with values between 0.1 and 0.35 as 'sparse vegetation', while pixels with NDVI values below 0.1 were classified as 'bare ground'. Non-vegetated areas (i.e. perennial snow, water, and glaciers) were grouped into 'snow, water and ice' (Table 2).

Environmental conditions were linked to each individual muskox based on the GPS coordinates (in case of topographic and land cover variables) or the date–time stamp of the GPS coordinates (in case of temperature). Two successive GPS locations are needed to calculate speed and three successive GPS locations are needed to calculate turning angles. In our analyses we considered the environmental conditions observed at the 2nd or 3rd location (for speed and turning angle analyses respectively) and did not consider the environmental conditions that may have been encountered along the step, as we could not be certain of the exact movement path taken by an individual between successive GPS locations. Habitat use of muskoxen was calculated as the proportion of GPS locations in different land cover types for each light regime separately.

Modelling of variation in movement and activity patterns across temporal scales

To examine the temporal variation in movement and activity patterns of muskoxen, we employed generalised additive mixed models (GAMMs) in the R package mgcv. We expected movement and activity patterns of muskoxen to change non-linearly over time (i.e. hours of the day and seasonally) and GAMMs provide a suitable framework to model such changes in behaviour because explanatory variables with expected non-linear effects, can be fitted as

Table 2. Explanatory variables used in the generalized additive models.

Explanatory variable	Biological effect	Unit	Data source
Time of day	diurnal rhythm	UTC time	modelled using a spline function
Slope	associated with cost of movement as well as snow accumulation	radians	calculated from a digital elevation model (raster layer 30×30 m)
Hillshade	associated with incoming radiation and thus local temperature	radians	combines slope and aspect. Calculated from the digital elevation model above
Elevation	associated with plant productivity and snow accumulation	meters	calculated from the digital elevation model above
Land cover type	associated with plant productivity	4 classes	categorized based on NDVI raster layer (30×30 m) into 'Bare ground' (48.0% of study area), 'Sparse vegetation' (8.4%), 'Dense vegetation' (0.3%) and 'Snow, water and ice' (43.3%)
Temperature	associated with energetic losses	degrees C	hourly data available from the climate towers at Zackenberg, located centrally in the study area
Body mass	associated with animal condition	kg	measured in the field

parametric or non-parametric smoothing terms (Wood 2006). Moreover, variables can be modelled as random effects and any residual dependence among observations can be modelled using autocorrelation structures (Pinheiro and Bates 2000, Wood 2006). We constructed three sets of models with log-transformed speed (m h⁻¹), linearity (absolute value of turning angles) or logit-transformed proportion of activity as the response variables. We were interested in determining the relative importance of each predictor variable ($N_{predictors} = 6$; Table 2) in explaining variation in muskox movement and activity patterns. To do so we used a multi-model inference technique based on model averaging (Burnham and Anderson 2002). To obtain robust results, we did not consider interactions between covariates due to our limited sample size of N = 14. As we limited our analyses to a minimum number of non-correlated covariates (Spearman correlation (r_s) < 0.5 and variance inflation factor < 3) to reduce collinearity, our set of candidate models consisted of all possible combinations of predictor variables. Hour of the day was included as a cyclic cubic regression spline, with the optimal smooth curve estimated by the generalized cross-validation procedure (Wood 2006). In addition, hour of the day was forced into all models, as quantifying diurnal variation in movement patterns was an important aim, leaving a total of 6 predictor variables on which to base all possible combinations ($N_{model} = 64$). We calculated model averaged coefficients and unconditional standard errors for covariates using the R package MuMIn. Models were fitted using the maximum-likelihood estimation, which is necessary when comparing mixed-effects models or models with correlation structures with different fixed effects (Pinheiro and Bates 2000). Finally, we calculated the relative variable importance [$w+(j)$] for each fixed effect by summing the Akaike's weights (w) across all the models in the set where variable j occurred. The larger the $w+(j)$, the more important variable j is (Burnham and Anderson 2002). A summary of model autocorrelation functions and random intercepts is given in Supplementary material Appendix 1 Table A1.

Results

Upon filtering, a total of 97 089 locations were available for modelling the movement patterns of the 14 muskox cows during the first year following collar deployment. During that period, three of the muskox cows were confirmed dead, while two collars malfunctioned (Table 1). Basic metrics for the 14 cows handled in this study are shown in Table 1.

During the year, all 14 muskox cows moved extensively, but stayed within the region Wollaston Forland and Clavering Island, and within approximately 40 km from the collaring location at Zackenberg (Fig. 2). The average distance covered by an individual within a year was 780 km (std = 230 km). No clear seasonal pattern in area use was evident from the individual movement tracks (Fig. 2), and muskoxen seemed to follow coastlines and valleys throughout the year. On a few occasions, individuals were observed crossing frozen fjords up to 8 km wide (3 occasions; individuals no. 8, no. 10 and no. 13; Fig. 2) and climbing mountains and glaciers up to more than 1000 m a.s.l. (one occasion; individual no. 13; Fig. 2) during winter.

The NSD analysis revealed a mixture and large individual variation of annual movement behaviours employed by the muskox cows. Indeed, the results of fitting the five different statistical models (residency, dispersal, nomadic, migratory or mixed behaviour) to the muskox movement trajectories showed that four individuals (29% of tagged animals) were best classified as dispersers, four individuals (29%) as nomads, one individual (7%) as a migrator, five individuals (35%) as mixed, and none (0%) as residents (Fig. 3). Although the goodness-of-fit of the selected models was adequate with CC values > 0.5 for all individuals (Table 1), the migration model did not fit the NSD data for individual no. 7 very well (Fig. 3). Individual muskoxen generally exhibited only very limited temporal association (Supplementary material Appendix 1 Table A2).

The muskoxen exhibited a clear diurnal movement pattern with increased activity and movement speeds and less convoluted movements between 4 a.m. and 8 p.m. throughout the year, except under continuous light where there was no diurnal variation in the three movement metrics (Fig. 4). The pattern was bimodal under increasing light and increasing darkness, whilst during the periods of continuous light and darkness the pattern was flat and mostly unimodal, respectively. Moreover, the main peak of movement activity at around 10 a.m. in the increasing light and darkness periods seems to be shifted to around noon during the period of darkness. Figure 4 also suggests a tight coupling between speed of movement and activity, whereas turning angle was not directly coupled to the other two metrics. Moreover, muskox activity in periods of continuous light was continuously high, while speed of movement and turning angle also were stable throughout the day, and at a relatively low level, indicating more extensive foraging while moving steadily forward in this season compared to other seasons (Fig. 4). Across the year, muskoxen were mainly found on 'bare ground', while the vegetated areas, and in particular the densely vegetated (highly productive) ones, were increasingly used from spring and into autumn (Fig. 5).

Relating the three movement metrics to the environmental predictors showed that movement patterns varied mostly with ambient temperature and across land cover type (Table 3). For example, speed of movement decreased with increasing ambient temperature when daylight was short or absent, while movement speed increased with increasing ambient temperature when light during the day was long (Fig. 6). Moreover, variations in muskoxen movement and activity patterns varied among land cover types throughout the year (Table 3). Topographic features of the landscape, such as elevation and slope, were of moderate importance in explaining movement and activity patterns, likely because rugged areas were largely unused (Table 3). Speed of movement was highest in non-vegetated areas, and generally decreased in land cover types with more vegetation (Fig. 7).

Discussion

We present the first direct year-round high-resolution measurements of female muskox movement patterns in the high-arctic. On average, the muskoxen travelled approximately 800 km per year, and all muskox cows stayed within
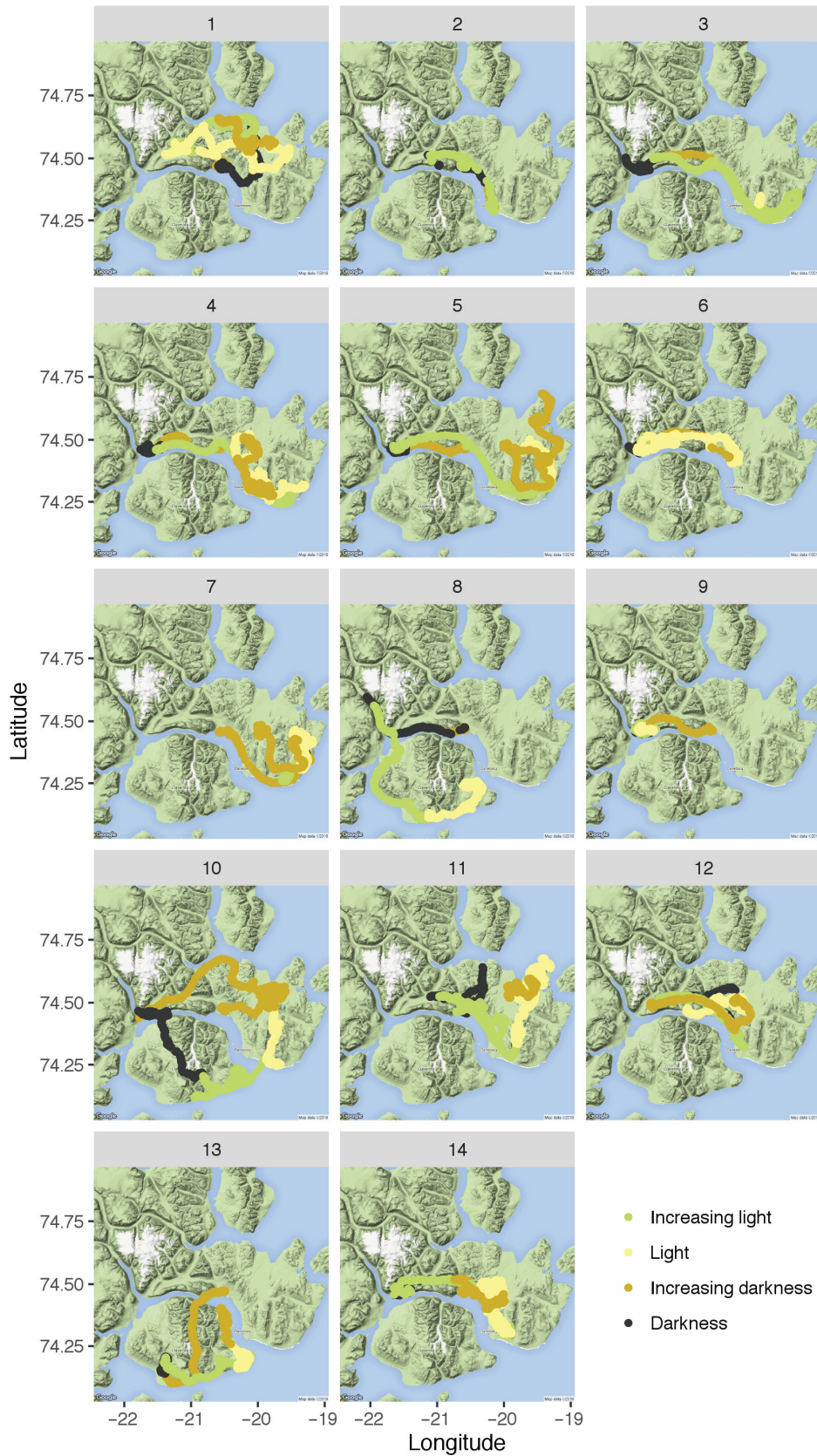
Figure 2. Overview of GPS locations for each of the 14 adult female muskoxen collared at Zackenberg in high-arctic Greenland during a full year. Numbers above panels refer to the identification numbers. Location data are broken down into four periods according to the light regime.
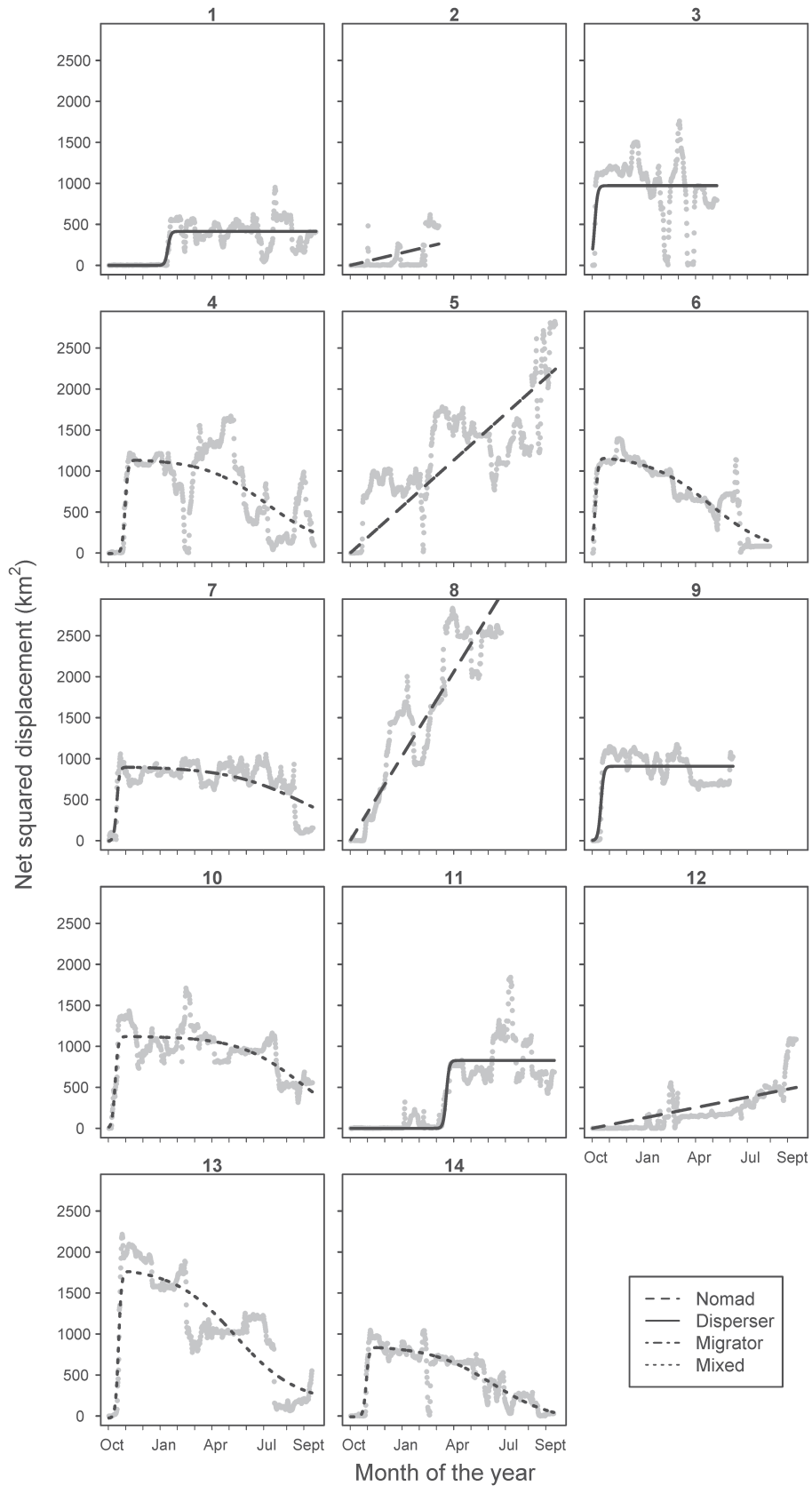
258

Figure 3. Analyses of the net squared displacement of female muskoxen in high-arctic Greenland during a full year. Panels show the classification of the individual movement trajectories into either migration, dispersal, home range or nomadic movement behaviour. Numbers above panels refer to the identification numbers. See Table 1 for additional information.
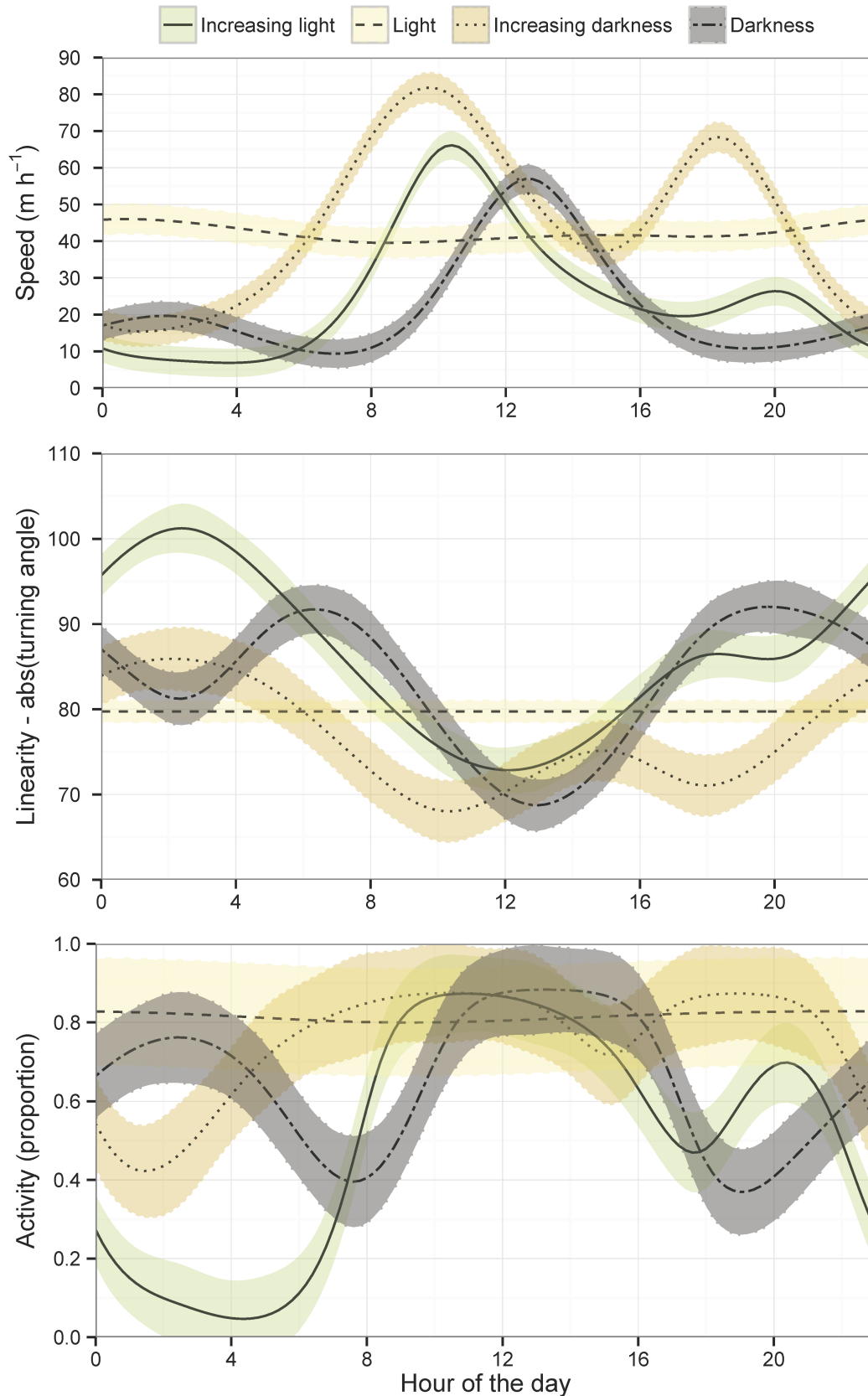
Figure 4. Main effect of hour of the day on movement and activity patterns of female muskoxen in high-arctic Greenland. Panels show the mean (and 95% confidence intervals) predicted level of speed, linearity and activity for each season. Predictions were made while keeping other variables in the models constant at their mean value.
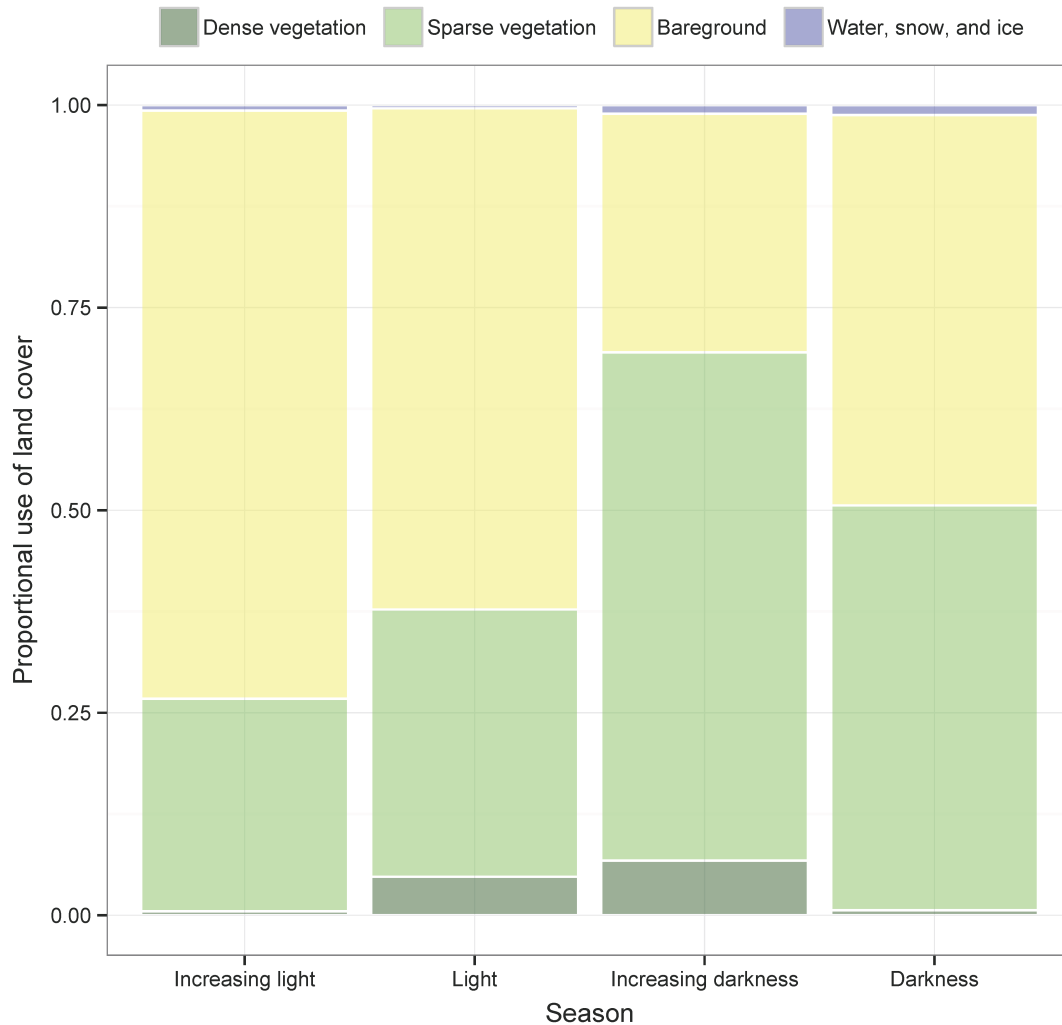
Figure 5. Seasonal variation in the proportional use of different land cover types by female muskoxen in high-arctic Greenland.

approximately 40 km from the collaring site, roughly corresponding to an area of approximately 5000 km². Our study thus confirms the notion of muskoxen being rather sedentary (Reynolds et al. 2002, Gustine et al. 2011). Our results thus seem to contradict the study by Aastrup (2003) who concluded that muskoxen were highly mobile and may disperse more than 100 km, and thus exhibited low site fidelity. However, the study by Aastrup (2003) was based on resightings of ear-marked animals collected over several years, and even though the muskoxen in that study moved a lot (as in our study) they still stayed within an area only about twice the area muskoxen stayed within in our study.

Compared to reindeer, muskoxen exhibit a completely different movement pattern, particularly in winter, most likely reflecting the degree to which the two species rely on energy acquisition or energy reserves in winter. Hence, while reindeer rely on continuous supply of forage even in winter (Tyler 1986), muskoxen rely largely on their body stores acquired during the previous summer and autumn (White et al. 1997, Adamczewski et al. 1998). Also, as capital breeders, muskoxen do not need to match their calving with the emerging vegetation in both space and time as reindeers, that often are income breeders (Kerby and Post 2013), do. This allows muskoxen to stay within a smaller area year-round,

but also to be more flexible in the movement behaviours as evident from the displacement analyses. We observed a mixture of movement behaviours. All five individuals classified with the mixed movement behaviour category dispersed away from the collaring site at Zackenberg within a few weeks, yet as time progressed they gradually moved back towards the collaring site. As such, this behaviour could be considered a mixture of dispersal and nomadism with the valley around Zackenberg as an attraction/focal area. In winter, when the fjords and ground are frozen, muskoxen are capable of crossing fjords and mountains, and are as such not confined to Wollaston Forland. Nonetheless, the muskoxen remained within the region year-round. As the Zackenberg valley holds some of the highest densities of muskoxen reported for the Arctic (Schmidt et al. 2015), we expected that muskoxen would have either stayed or at least returned to the valley during the year, for instance in summer to forage on the lush vegetation there. This, however, was not the case, and the muskoxen collared at Zackenberg moved independently of each other and exhibited a mix of movement behaviours while roaming over a rather limited area during the year. As such, we posit that muskoxen in the area adopt a largely nomadic movement behaviour, but is constrained to a rather small geographical area.

261

Table 3. Summary of the mixed-effects generalized additive models predicting variability in muskox movement and activity patterns for each season. Regression estimates and unconditional standard errors (SE) are based on a model averaging procedure using all possible models. The relative variable importance (Imp.) is provided for each predictor variable and calculated by summing the Akaike's weights (*w*) for that variable from all possible models. The spline function was included in all models, leaving a total of 6 covariates in a total of 64 model candidates. The output forms the analytical basis for Fig. 4, 6 and 7.

Season/photoperiod	Covariate	Speed (log[m h⁻¹])			Linearity (abs(turning angle [°]))			Activity (logit[proportion])		
		Estimate	SE	Imp.	B	SE	Imp.	B	SE	Imp.
Increasing light	land cover			1			0.79			0.22
	bareground	2.905	0.335	–	69.978	11.891	–	0.784	1.052	–
	sparsely vegetated	2.662	0.045	–	71.371	1.229	–	0.566	0.125	–
	densely vegetated	2.818	0.278	–	68.360	8.251	–	0.252	0.774	–
	water/snow/ice	3.390	0.185	–	53.782	6.145	–	0.892	0.524	–
	elevation (m)	–0.0002	0.0002	0.38	0.006	0.003	0.62	0.0001	0.0004	0.27
	slope (°)	–0.009	0.004	0.91	0.145	0.088	0.59	0.013	0.010	0.46
	temperature (°C)	–0.021	0.004	1	0.223	0.093	0.87	–0.051	0.011	1
	hillshade	–0.243	0.229	0.4	5.955	5.242	0.42	–1.596	0.611	0.91
	body weight (kg)	–0.002	0.002	0.35	0.109	0.045	0.8	–0.002	0.009	0.28
	spline(hour of the day)	7.661	–	1	6.018	–	1	7.685	–	1
Light	land cover			1			0.59			1
	bareground	3.020	1.232	–	89.930	12.940	–	1.037	3.341	–
	sarsely vegetated	2.806	0.035	–	92.582	1.072	–	1.689	0.120	–
	densely vegetated	2.778	0.080	–	93.087	2.414	–	2.535	0.269	–
	water/snow/ice	3.047	0.221	–	89.840	7.266	–	–0.567	0.774	–
	elevation (m)	0.0003	0.0001	0.96	–0.004	0.003	0.5	0.001	0.0004	0.99
	slope (°)	–0.009	0.003	0.98	0.156	0.075	0.77	–0.016	0.009	0.65
	temperature (°C)	0.049	0.003	1	–0.131	0.078	0.6	0.151	0.009	1
	hillshade	–0.184	0.169	0.4	2.602	4.723	0.31	–0.646	0.546	0.43
	body weight (kg)	0.009	0.007	0.44	–0.099	0.059	0.58	0.020	0.025	0.34
	spline(hour of the day)	3.189	–	0.72	0.943	–	0.27			0.85
Increasing darkness	land cover			1			1			0.16
	bareground	3.875	0.282	–	70.800	9.771	–	4.250	1.629	–
	sparsely vegetated	3.590	0.090	–	7.455	1.367	–	4.469	0.150	–
	densely vegetated	3.430	0.046	–	9.434	2.653	–	4.548	0.292	–
	water/snow/ice	4.353	0.181	–	–2.795	5.780	–	4.731	0.601	–
	elevation (m)	0.001	0.0002	0.94	–0.001	0.006	0.27	–0.0001	0.001	0.28
	slope (°)	–0.012	0.004	0.94	0.055	0.109	0.3	–0.018	0.014	0.47
	temperature (°C)	0.033	0.003	1	–0.086	0.068	0.45	0.071	0.008	1
	hillshade	0.247	0.312	0.34	–5.065	7.326	0.32	–1.390	0.957	0.52
	body weight (kg)	–0.001	0.002	0.3	0.068	0.047	0.51	–0.011	0.009	0.42
	spline(hour of the day)	7.394	–	1	5.509	–	1	7.405	–	1
Darkness	land cover			1			1			0.28
	bareground	2.365	0.276	–	87.511	6.507	–	0.936	1.234	–
	sparsely vegetated	2.127	0.037	–	93.596	1.168	–	0.326	0.127	–
	densely vegetated	1.886	0.186	–	97.325	5.839	–	0.814	0.615	–
	water/snow/ice	2.811	0.137	–	92.618	4.735	–	1.173	0.458	–
	elevation (m)	–0.0008	0.0001	0.28	0.008	0.003	0.93	–0.001	0.0005	0.88
	slope (°)	–0.002	0.003	0.54	0.252	0.081	0.97	–0.028	0.011	0.91
	temperature (°C)	–0.019	0.003	1	0.202	0.078	0.92	–0.048	0.011	1
	hillshade	0.307	0.257	0.73	–9.491	5.460	0.63	0.043	0.740	0.27
	body weight (kg)	0.001	0.001	0.39	–0.019	0.046	0.29	0.006	0.010	0.31
	spline(hour of the day)	7.663	–	1	6.667	–	1	7.636	–	1

Whether this mixed pattern of movement behaviours was induced by several rain-events on frozen ground observed in autumn 2013 at Zackenberg (Mylius et al. 2014) or the close to record-high amounts of snow at Zackenberg during the winter 2013–2014 (GeoBasis Zackenberg unpubl.) is currently unknown, but ungulates in other arctic regions have previously been reported to shift to other locations following icing events (Stien et al. 2010). Longer studies on muskox movement patterns across multiple years with contrasting environmental conditions are needed to confirm this.

The most productive land cover types in the region were important, particularly in summer and autumn when plant biomass has accumulated there during the snow-free period and muskox individuals prepare for winter by consuming large quantities of forage. The utilization of these highly productive areas, dominated by graminoids (Falk et al. 2015), in summer and autumn, agrees with current knowledge on muskox summer diets (Kristensen et al. 2011). In the snow-covered period, most of these low-lying, productive areas are covered by a thick layer of snow, preventing the muskoxen from accessing the vegetation there (Kazmin and Abaturov 2009). This forces muskoxen to move to more wind-exposed, less productive areas (Nellemann 1998, Gustine et al. 2011), as also observed in this study. In mountainous regions, such as Northeast Greenland, the availability of suitable summer and winter habitats in close proximity may indeed be an
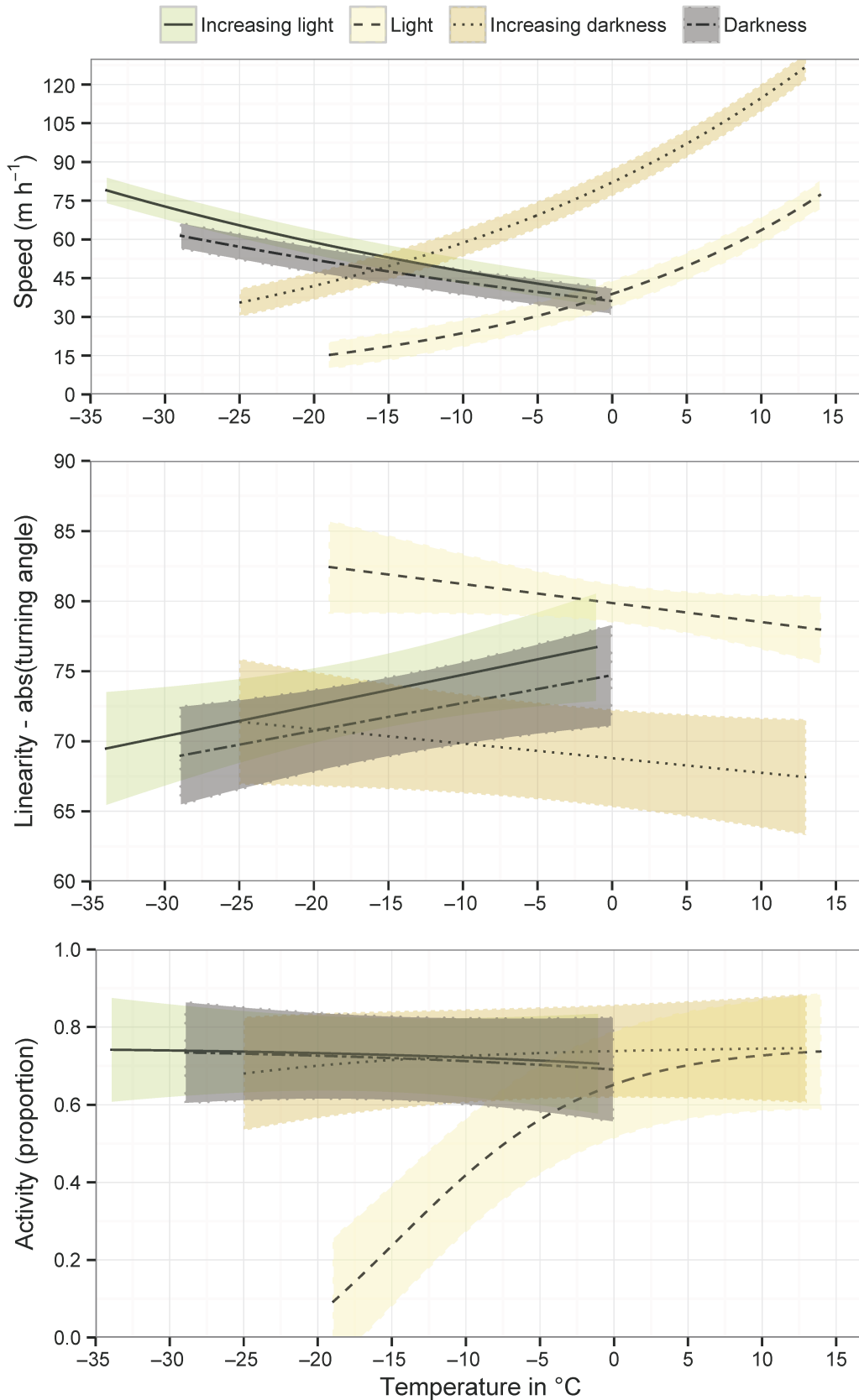
Figure 6. Main effect of temperature on movement and activity patterns of female muskoxen in high-arctic Greenland. Panels show the mean (and 95% confidence intervals) predicted level of speed, linearity and activity for each season. Predictions were made while keeping other variables in the models constant at their mean value.
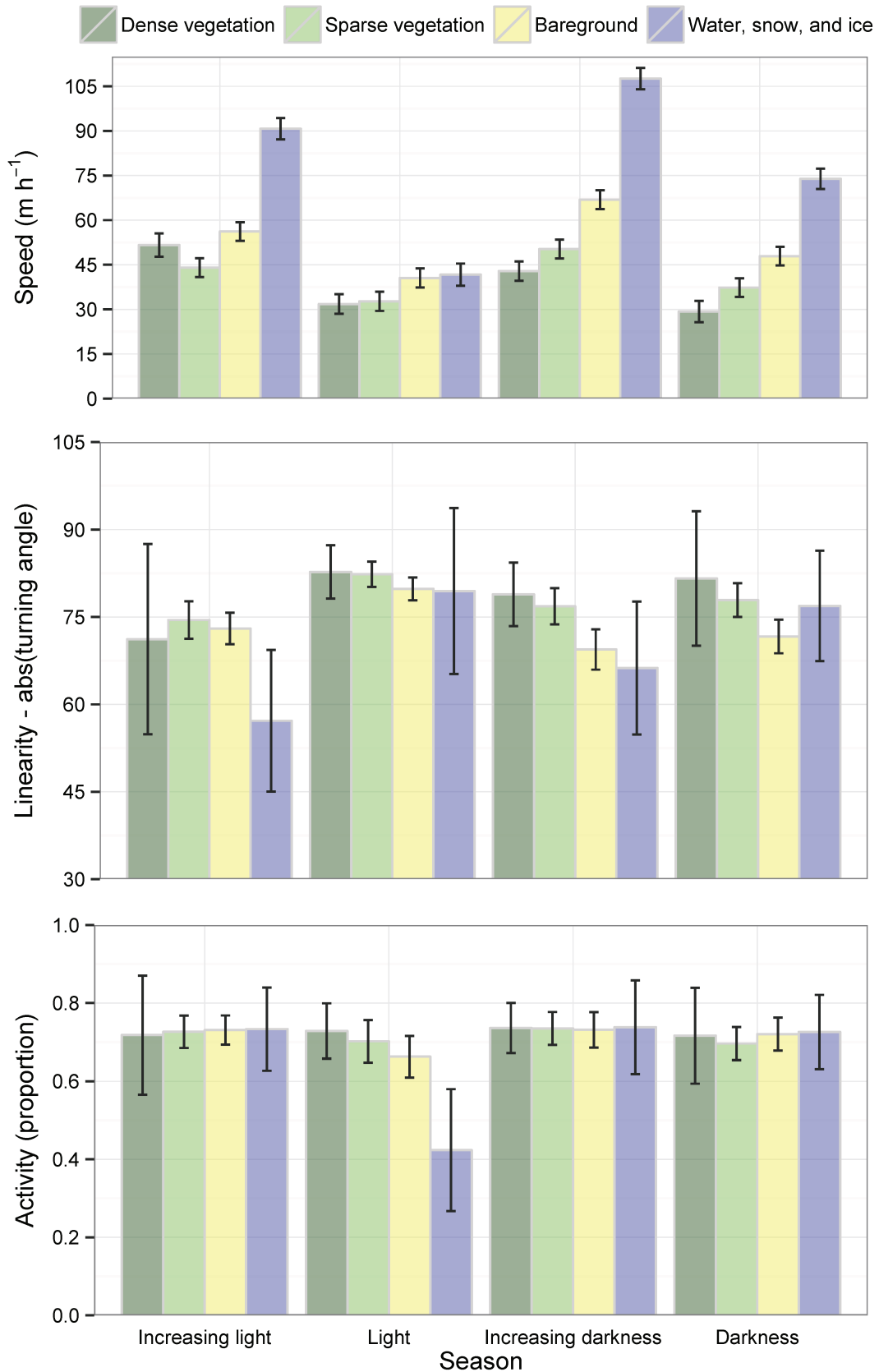
Figure 7. Main effect of land cover type on movement and activity patterns of female muskoxen in high-arctic Greenland. Panels show the mean (and 95% confidence intervals) predicted level of speed, linearity and activity for each season. Predictions were made while keeping other variables in the models constant at their mean value.

important factor allowing muskoxen to be rather sedentary (Gustine et al. 2011).

In winter and autumn, muskoxen responded to the ambient temperatures by increasing their speed of movement as temperatures dropped, while the opposite was true for the summer and spring seasons. Linearity of movements exhibited the opposite pattern. Hence, muskoxen seemingly avoid thermal stress when exposed to very low winter temperatures by moving faster but apparently while foraging. In summer, declining temperatures resulted in muskoxen moving more slowly and less direct, thus indicating an increase in foraging activities. The activity measure in this study was, however, based on 1-hourly snapshots, and may hence have failed to capture behaviours too infrequent to be reflected in the modelling, and can therefore be only regarded as a rough index of true activity. Nonetheless, combined with the location data, the activity data revealed some strong patterns. Firstly, the importance of the summer and autumn seasons for restoring body reserves was also reflected in the daily movement and activity patterns of the high-arctic muskoxen, and in the behaviour inferred from these. Hence, during summer, muskoxen seemed to forage continuously while moving slowly and steadily forward, whereas other seasons were characterized by more variation in these movement metrics. Outside the summer season, muskoxen mostly foraged early and late in the 'day', while undertaking more directional movements around noon. Outside the periods of continuous light or darkness, muskox movement activity exhibited a bimodal pattern, a phenomenon well-known under day/night periodicity (Aschoff 1966). Interesting is also that even during the dark period, muskoxen did exhibit a clear diurnal pattern, though shifted from around 10 AM in the increasing light and darkness periods to around noon during the dark period. As a predator-avoidance tactic, ungulates are most active during the daylight hours (Richard et al. 2014), but in the almost predator-free northeast Greenland (Marquard-Petersen 2011) these seasonal differences in foraging activities likely reflect the seasonal changes in the abundance and quality of plant forage. Hence, outside the summer season, accumulation of snow and senescence of plant material result in a patchy distribution of resources, whereas in summer resources are more easily accessible and more evenly distributed (Nellemann 1997). The consistent, forward moving foraging behaviour of the muskoxen throughout the day and 'night' in summer, and the presence of foraging bouts outside the summer season intercepted by fast, directional movements are consistent with the expected patchy distribution of resources outside the summer season. Indeed, muskox food intake increases markedly from spring to autumn, which ensures sufficient fat depots before the lean period (Barboza et al. 2006). Not being able to replenish the fat reserves may result in low pregnancy rates, loss of foetus, and ultimately the death of the cow. Interesting is therefore that the muskoxen that died during the first year were among the cows with lowest body masses, and thus poorest body condition. Three cows dying out of 14 may be seen as a relatively high mortality rate. However, the large amounts of snow at Zackenberg during the winter 2013–2014 mentioned above, and the concomitant reduced access to the limited forage, is a likely determinant of the observed mortality (Gunn et al. 1989, Schmidt

et al. 2015). Consistent with this is also the general reduction in muskox abundance within the designated muskox census area at Zackenberg observed in summer 2014 (BioBasis Zackenberg unpubl.), suggesting that mortality during the proceeding winter was generally high. Comparing the movement behaviour of muskox cows that died to those that lived during the study period did not yield indications of changes in movement behaviour that could be linked to the fate of the individual, because of the large variation in movement behaviour among individuals.

High forage intake in summer and autumn also aids preparing the essential rumen microflora for the upcoming period of hypophagia (Barboza et al. 2006), and rumen microbes are dramatically suppressed by starvation (Aagnes et al. 1995). Thus, the surprisingly high level of activity and likely foraging observed in this study, even in midwinter, may reflect the need for some energy acquisition as well as the need for sustaining a functional rumen microflora throughout the snow-covered period until fresh plant material is accessible again. Other ungulates usually cope with low availability of food by lowering the level of activity (Loe et al. 2007). Apparently, in winter muskoxen only do so in areas or periods with access to good quality forage (Schaefer and Messier 1996), and the high level of activity we observed in winter suggests that the winter forage available at Wollaston Forland may be limited or of rather poor quality.

The present study has provided the first year-round, high-resolution location data for muskoxen in the high-arctic. We conclude that muskox cows in northeast Greenland exhibited a mixture of movement behaviours, whilst moving within a rather small geographical area. Their movement and activity patterns varies across the year, and seems largely directed at finding patches with available forage throughout most seasons and at avoiding cold-stress during harsh winter weather. Muskoxen are mostly found in mixed-sex groups (Reynolds 1993), typically led by adult females (Ihl and Bowyer 2011), and group cohesion is low (Reynolds 1993, Aastrup 2003, this study). From the individual tracks it was clear that during the course of the year, individuals occasionally teamed up with other tagged cows, but these bonds were short-term and often replaced by bonds with other tagged animals. This dynamic group structure, combined with the lack of small-scale site fidelity observed, suggests that the 14 individuals collared in the present study constitute a representative sample of the muskox population in the Wollaston Forland region in high-arctic Greenland. Our study thus provides novel insight into important, yet largely unknown, aspects of the ecology of this tundra key species.

Permits – The sedation and handling of muskoxen in this study followed the guidelines of the American Society of Mammalogists (Sikes and Gannon 2011). Research permits were issued by the Greenland Government (j.no. G13-029).

References

Aagnes, T. H. et al. 1995. Ruminal microbial digestion in free-living, in captive lichen-fed, and in starved reindeer (*Rangifer tarandus tarandus*) in winter. – Appl. Environ. Microb. 61: 583–591.

Aastrup, P. 2003. Muskox site fidelity and group cohesion in Jameson Land, east Greenland. – Polar Biol. 27: 50–55.

Adamczewski, J. Z. et al. 1998. The influence of fatness on the likelihood of early-winter pregnancy in muskoxen (*Ovibos moschatus*). – Theriogenology 50: 605–614.

Arndal, M. F. et al. 2009. Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. – Arct. Antarct. Alp. Res. 41: 164–173.

Aschoff, J. 1966. Circadian activity pattern with two peaks. – Ecology 47: 657–662.

Barboza, P. S. et al. 2006. Ruminal fermentation and fill change with season in an Arctic grazer: responses to hyperphagia and hypophagia in muskoxen (*Ovibos moschatus*). – Physiol. Biochem. Zool. 79: 497–513.

Berg, T. B. et al. 2008. High-Arctic plant–herbivore interactions under climate influence. – Adv. Ecol. Res. 40: 275–298.

Bjørneraas, K. et al. 2010. Screening global positioning system location data for errors using animal movement characteristics. – J. Wildl. Manage. 74: 1361–1366.

Body, G. et al. 2012. The recursive model as a new approach to validate and monitor activity sensors. – Behav. Ecol. Sociobiol. 66: 1531–1541.

Boertmann, D. et al. 1990. The Greenland muskox population status 1990. – Rangifer 12: 5–12.

Börger, L. and Fryxell, J. M. 2012. Quantifying individual differences in dispersal using net squared displacement. – In: Dispersal and spatial evolutionary ecology. Oxford Univ. Press, pp. 222–228.

Bunnefeld, N. et al. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. – J. Anim. Ecol. 80: 466–476.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference – a practical information-theoretic approach, 2nd edn. – Springer.

Cagnacci, F. et al. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. – J. Anim. Ecol. 85: 54–68.

Callaghan, T. V. et al. 2013. Arctic terrestrial ecosystems. – In: Encyclopedia of biodiversity, Volume 1. Academic Press, pp. 227–244.

Danks, F. S. and Klein, D. R. 2002. Using GIS to predict potential wildlife habitat: a case study of muskoxen in northern Alaska. – Int. J. Remote Sens. 23: 4611–4632.

Falk, J. M. et al. 2015. Large herbivore grazing affects the vegetation structure and greenhouse gas balance in a high arctic mire. – Environ. Res. Lett. 10: 045001.

Forchhammer, M. C. and Boertmann, D. 1993. The muskoxen *Ovibos moschatus* in north and northeast Greenland: population trends and the influence of abiotic parameters on population dynamics. – Ecography 16: 299–308.

Forchhammer, M. C. et al. 2005. Local-scale and short-term herbivore-plant spatial dynamics reflect influences of large-scale climate. – Ecology 86: 2644–2651.

Forchhammer, M. C. et al. 2008. Zackenberg in a circumpolar context. – Adv. Ecol. Res. 40: 499–544.

Gilg, O. et al. 2012. Climate change and the ecology and evolution of Arctic vertebrates. – Ann. N. Y. Acad. Sci. 1249: 166–190.

Gunn, A. et al. 1989. Evidence for and possible causes of increased mortality of bull muskoxen during severe winters. – Can. J. Zool. 67: 1106–1111.

Gustine, D. D. et al. 2011. Characteristics of foraging sites and protein status in wintering muskoxen: insights from isotopes of nitrogen. – Oikos 120: 1546–1556.

Hansen, B. U. et al. 2008. Present-day climate at Zackenberg. – Adv. Ecol. Res. 40: 111–149.

Høye, T. T. et al. 2007. Rapid advancement of spring in the High Arctic. – Curr. Biol. 17: R449–R451.

Ihl, C. and Bowyer, R. T. 2011. Leadership in mixed-sex groups of muskoxen during the snow-free season. – J. Mammal. 92: 819–827.

Kazmin, V. D. and Abaturov, B. D. 2009. Mechanical properties of the snow cover and availability of forage for reindeer (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) on pastures of Wrangel Island. – Zool. Zh. 88: 990–1000.

Kerby, J. and Post, E. 2013. Capital and income breeding traits differentiate trophic match-mismatch dynamics in large herbivores. – Phil. Trans. R. Soc. B 368: 20120484.

Kristensen, D. K. et al. 2011. Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C_3 plants, faeces and wool. – Can. J. Zool. 89: 892–899.

Loe, L. E. et al. 2007. Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm. – Oecologia 152: 617–624.

Lundberg, J. and Moberg, F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. – Ecosystems 6: 87–98.

Marquard-Petersen, U. 2011. Insular and disjunct distribution of the Arctic wolf in Greenland, 1978–1998. – Polar Biol. 34: 1447–1454.

Mosbacher, J. B. et al. 2016a. Quantifying muskox biomass and nitrogen removal and deposition in a high arctic tundra ecosystem. – Arct. Antarct. Alp. Res. 48: 229–240.

Mosbacher, J. B. et al. 2016b. Show me your rump hair and I will tell you what you ate – the dietary history of muskoxen (*Ovibos moschatus*) revealed by sequential stable isotope analysis of guard hairs. – PloS ONE 11: e0152874.

Mylius, M. R. et al. 2014. Zackenberg basic – the ClimateBasis and GeoBasis programmes. – In: Jensen, L. M. et al. (eds), Zackenberg ecological research operations, 19th Annu. Rep. 2013. DCE - Danish Centre for Environment and Energy, pp. 14–30.

Nellemann, C. 1997. Grazing strategies of muskoxen (*Ovibos moschatus*) during winter in Angujaartorfiup Nunaa in western Greenland. – Can. J. Zool. 75: 1129–1134.

Nellemann, C. 1998. Habitat use by muskoxen (*Ovibos moschatus*) in winter in an alpine environment. – Can. J. Zool. 76: 110–116.

Olesen, C. R. and Thing, H. 1989. Guide to field classification by sex and age of the muskox. – Can. J. Zool. 67: 1116–1119.

Owen-Smith, N. and Martin, J. 2015. Identifying space use at foraging arena scale within the home ranges of large herbivores. – PloS ONE 10: e0128821.

Pinheiro, J. C. and Bates, D. M. 2000. Mixed-effects models in S and S-Plus: statistics and computing. – Springer.

Post, E. et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. – Science 325: 1355–1358.

Reynolds, P. E. 1993. Dynamics of muskox groups in northeastern Alaska. – Rangifer 13: 83–89.

Reynolds, P. E. 1998. Dynamics and range expansion of a reestablished muskox population. – J. Wildl. Manage. 62: 734–744.

Reynolds, P. E. et al. 2002. Muskoxen. – In: Douglas, D. C. et al. (eds), Arctic refuge coastal plain terrestrial wildlife research

summaries. US Geological Survey, Biol. Resour. Div., pp. 54–64.

Richard, J. H. et al. 2014. The effect of snow on space use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. – Can. J. Zool. 92: 1067–1074.

Schaefer, J. A. and Messier, F. 1996. Winter activity of muskoxen in relation to foraging conditions. – Ecoscience 3: 147–153.

Schmidt, N. M. et al. 2015. Long-term patterns of muskox (*Ovibos moschatus*) demographics in high arctic Greenland. – Polar Biol. 38: 1667–1675.

Sikes, R. S. and Gannon, W. L. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. – J. Mammal. 92: 235–253.

Singh, N. J. et al. 2016. Quantifying migration behaviour using net squared displacement approach: clarifications and caveats. – PloS ONE 11: e0149594.

Stien, A. et al. 2010. Icing events trigger range displacement in a high-arctic ungulate. – Ecology 91: 915–920.

Tamstorf, M. et al. 2007. Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in high arctic Greenland. – BMC Ecol. 7: 9.

Tyler, N. J. C. 1986. The relationship between the fat content of Svalbard reindeer in autumn and their death from starvation in winter. – Rangifer 6: 311–314.

van Moorter, B. et al. 2010. Identifying movement states from location data using cluster analysis. – J. Wildl. Manage. 74: 588–594.

White, R. G. et al. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. – J. Zool. 243: 13–20.

Wood, S. N. 2006. Generalized additive models: an introduction with R. – Chapman and Hall/CRC.

Supplementary material (available as Appendix wlb-00219 at < www.wildlifebiology.org/appendix/wlb-00219 >). Appendix 1.