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Density, snow and seasonality lead to variation in muskox habitat selection during summer

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Manuscripts

1 **Density, snow and seasonality lead to variation in muskox habitat selection during summer**

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18

19 Abstract

20 Understanding how environmental conditions influence habitat selection and suitability of free-
21 ranging animals is critical as the outcome may have implications for individual fitness and population
22 dynamics. Density and snow are among the most influential environmental conditions driving
23 habitat selection patterns of northern ungulates. We used two decades of census data from high
24 Arctic Greenland to quantify inter- and intra-annual variation in muskox (*Ovibos moschatus*
25 Zimmermann 1780) habitat selection and suitability during the Arctic summer (July through
26 October). Across years, habitat selection varied considerably, and the strength of habitat selection
27 appeared negatively related to both muskox density and spring snow cover. In early summer,
28 habitat suitability was high and spatially rather uniform. Towards the autumn, suitable habitats
29 contracted to just the lower elevations, when muskoxen exhibited increasingly stronger habitat
30 selection towards low elevations and dense vegetation. This selection strategy clearly reflects the
31 need to build up fat reserves for the upcoming winter, highlighting the energetic importance of the
32 Arctic summer. Extreme climatic events such as freezing rain in autumn are increasing in frequency
33 in Greenland and limit muskox access to high quality forage in fens. Such events may therefore
34 negatively affect the energy acquisition process of muskox with potential cascading consequences
35 on population dynamics.

36

37 Introduction

38 Understanding where and how animals select for habitat and resources therein is a crucial
39 component of ecological research as the outcome of this process can have implications for individual
40 fitness and population dynamics (Krebs 1972; Brown and Rosenzweig 1986a). Extrinsic conditions

41 such as snow depth/cover and population density are well known factors influencing movement,
42 home range size and general space use patterns of free-ranging ungulates (McLoughlin et al. 2006;
43 Hansen et al. 2010; van Beest et al. 2011) but little is known about their influence on habitat
44 selection and suitability of muskoxen roaming the Arctic tundra.

45 The Arctic is characterized by extreme variability in climatic conditions both within and across years
46 (Gilg et al. 2012). While organisms living in this region are well adapted to life under such
47 environmental conditions, climate variability is considered the main determinant of animal
48 population dynamics (Post and Forchhammer 2002). With on-going and future climate change, this
49 variability will likely exacerbate (Saha et al. 2006), putting more pressure on Arctic organisms.

50 Muskoxen are the largest herbivore roaming the Arctic and play a key role in the
51 tundra ecosystem (Kutz et al. 2017). During winter, muskoxen forage on relatively inaccessible, low
52 quality forage (Schmidt et al. 2018). Considering these limitations, muskoxen rely heavily on fat
53 depots built up during the previous short arctic summer for maintenance and reproductive
54 investment in winter (Adamczewski et al. 1998), highlighting the importance of their habitat use
55 during this season. However, due to the large variability in environmental conditions over time,
56 temporal variation in habitat selection patterns (both across and within years or seasons) is to be
57 expected as has been shown for other herbivores (Mobæk et al. 2009; Bjørneraas et al. 2011).
58 Understanding how environmental conditions influence this process is often the overarching goal
59 of habitat selection analyses as the outcome may have implications for individual fitness and thus
60 population dynamics (Brown and Rosenzweig 1986b).

61 Here we capitalize on a long-term monitoring dataset (1996-2016) to assess 1) whether
62 muskox habitat selection differs between years (inter-annual scale) with contrasting snow

conditions and population densities, and 2) whether there is a seasonal trend in muskox habitat selection (intra-annual scale). Based on the ideal-free distribution theorem (Fretwell and Lucas 1969) and related density-dependent habitat selection theory (Rosenzweig 1991), we would expect muskoxen to be less selective as density increases. In contrast, we would expect muskoxen to be more selective as snow cover increases with muskox targeting sites with reduced snow cover more intensively so as to facilitate access to forage.

Materials and Methods

Study area

Field data were collected at Zackenberg research station in high Arctic Greenland (74°28'N, 21°33'W). In 1996, a 47 km² area designated for monitoring the local muskox population was established (Fig. 1). This area extends from sea-level to the top of the mountains (up to app. 800 m a.s.l.). The census area consists of various tundra habitat types, including productive fen habitats, various tundra heath types such as *Cassiope* heath, and almost barren habitats such as abrasion plateaus and fell fields (Elberling et al. 2008). The same habitat types covers the surrounding valleys and mountains. Access to plant forage typically extends from early June when the snow starts melting and until accumulating snow prevents access to forage (Schmidt et al. 2015), usually in November – December (Pedersen et al. 2016). The inter-annual variability on the timing of the snow-free season is however large, and for instance the start date for the snow-free season may vary more than 45 days from year to year (Pedersen et al. 2016).

Data on muskox numbers and spatial distribution within the census area have been collected as part of the long-term biological monitoring program Biobasis at Zackenberg since 1996. During July and

August, weekly censuses of the area were conducted by foot, and the location and size of all muskox groups registered (Schmidt et al. 2015). In recent years, censuses were also conducted in September and October, but not consistently so (Table S4 in Supplementary Material). Muskoxen move freely in and out of the census area, but stay within app. 40 km from Zackenberg (Schmidt et al. 2016), and frequently return to the census area during the course of the year. While the size of the muskox population in the region is unknown, the censuses conducted at Zackenberg suggest that the population gradually built up from 1996 to a peak in 2007, after which the population declined (Fig. S4 in Supplementary Material).

Environmental variables

We created several environmental predictor raster layers (all with a resolution of 30 x 30 m) describing the muskox census area. The landcover layer included 3 vegetation types; “dense vegetation”, “sparse vegetation” and “bare ground” with the classification based on the normalized differential vegetation index (NDVI) as in Schmidt et al. (2016). The “dense vegetation” includes the productive fen habitats, “sparse vegetation” includes various tundra heath types, whereas “bare ground” includes non-vegetated and almost not vegetated habitats such as fell fields. Dense vegetation covered 4.8%, sparse vegetation 63.7% and bare ground 31.5% of the census area, respectively. We have observed only minor changes in the vegetation composition over the study period (Schmidt et al. 2012), and although our classification is based on a satellite image from 2009 (Schmidt et al. 2016), we are therefore confident that the coarse landcover classification is valid for comparisons both within and between years. As our census data represent temporal snapshots of muskox locations, we created a “distance to”-layer for each landcover type by calculating the Euclidian distance to the nearest cell with the landcover present, rather than including landcover

109 type as a categorical variable in the habitat suitability models. Finally, from a digital terrain model
110 (DEM) we extracted the topographic variables elevation (m), slope (°) and the terrain ruggedness
111 index (Schmidt et al. 2016).

112

113 ***Data analyses***

114 To assess habitat selection patterns of muskox at Zackenberg, we used ecological-niche factor
115 analysis (ENFA) in the R package adehabitatHS (Calenge 2006; Basille et al. 2008). Based on used
116 locations of the study species and raster layers of the root-transformed environmental conditions
117 available in the study area (Fig. 1) ENFA computes two parameters, the marginality and the
118 specialization. Marginality (m^2) can be considered as an index for the rate of the deviation of the
119 used habitat relative to the available habitat. The specialization (γ) expresses the restriction of the
120 used habitat in a particular direction, and higher values indicate greater restriction in habitat
121 selection (Basille et al. 2008). For each scale of analysis, the significance of both the marginality and
122 specialization axes were assessed through a bivariate test using Monte-Carlo simulations. Doing so
123 allows testing the null hypothesis of random habitat selection (Basille et al. 2008).

124 We examined the inter-annual variation in muskox habitat selection by performing ENFA on
125 the data collected in July and August for all years independently (September and October were not
126 considered here as data were not collected in all years). Each muskox group location was weighted
127 by the number of animals in the group. We only considered static environmental conditions at this
128 stage as ENFA requires raster layers to quantify habitat availability. However, we also had point data
129 on dynamic conditions such as the percent spring snow cover in the central part of the census area
130 and annual muskox summer population density (updated from Schmidt et al. 2015). Therefore, and
131 as a second step in the inter-annual-scale analysis, we tested for animal density and snow cover

132 effects on muskox habitat selection in summer. To do so we used the global marginality and
133 specialization values produced by each annual ENFA model as response variables in two separate
134 generalized linear models and including spring snow cover, density, month and their interactions as
135 predictor variables.

136 To examine the intra-seasonal variation in summer habitat selection, we performed ENFA on
137 data for the months July, August, September and October (months lumped together across years),
138 thus arriving at the average seasonal habitat selection for the muskox population. As before, group
139 locations were weighed by the number of animals in the group, and all static environmental
140 conditions were included.

141 Finally, we used the Mahalanobis distance factor analysis (MADIFA) in the R-package
142 adehabitatHS (Calenge et al. 2008) to produce habitat suitability maps for each scale of analysis. We
143 evaluated the MADIFA habitat suitability maps, using Monte-Carlo simulations and further tested
144 the linkage between MADIFA and ENFA results by correlating their first axes (Calenge and Basille
145 2008). We argue that comparing results of these two methods allows for stronger inference of
146 habitat selection patterns than reporting ENFA results alone.

147

148 Results

149 The ENFAs revealed that habitat selection varied considerably at the inter-annual scale as indicated
150 by a large gradient in global marginality ($m^2_{2012}=0.18$; $m^2_{2004}=3.01$, min and max respectively) and
151 specialization values ($\gamma_{2012}=2.13$, $\gamma_{1996}=11.83$ min max respectively; Table S1 and S2 in
152 Supplementary Material). The importance of the various environmental parameters on habitat
153 selection patterns also differed across years, however with no consistently strong pattern although
154 distance to the various landcover types and elevation appeared the most influential conditions (Fig.

155 S1 and S2 in Supplementary Material). Regardless, some of the variation in marginality and
156 specialization was explained by inter-annual variations in muskox density or spring snow cover (Fig.
157 2). Marginality values from July and August were not related to inter-annual variation in muskox
158 density. Marginality, however, decreased significantly with increasing spring snow cover
159 irrespective of month (Fig. 2, Table 1). In contrast, specialization declined significantly with
160 increasing muskox density, specifically in July, but appeared unrelated to snow cover (Fig. 2, Table
161 1). Re-running the models with only significant marginality and specialization values (Table S1 and
162 S2) revealed qualitatively similar responses to spring snow cover and muskox density as the initial
163 analyses, but for specialization no longer statistically significant (Table S3 and Fig. S3 in
164 Supplementary Material).

165 At the seasonal scale, the ENFA revealed that muskoxen changed their habitat selection
166 pattern as the summer progressed as indicated by the rapidly increasing marginality ($m^2_{Jul}=0.34$,
167 $m^2_{Aug}=0.81$, $m^2_{Sep}=3.05$, $m^2_{Oct}=4.96$; Table 2), suggesting that used habitats were increasingly
168 different from the available habitat over the course of the summer season (Fig. 3). Moreover, the
169 marginality statistic was significant for all months ($p=0.001$). Specialization also increased as
170 summer progressed ($\gamma_{Jul}=1.60$, $\gamma_{Aug}=1.76$, $\gamma_{Sep}=2.62$, $\gamma_{Oct}=4.39$; Table 2), and similar to marginality,
171 was significant for the all months ($p=0.001$). The combined marginality and specialization results
172 suggest that habitat selection was not random and that towards the end of summer, muskoxen
173 increased their selection for specific habitats. Indeed, the ENFA biplot (Fig. 3) clearly showed a
174 gradually increasing deviation of the used habitat space (dark grey convex polygons) relative to the
175 available habitat space (light grey convex polygons in Fig. 3). Over the summer period, marginality
176 and specialization values for the environmental conditions (Table 2) revealed that habitat selection
177 was mostly influenced by elevation (i.e. greater use of low elevation sites towards the end of

summer). Further, there as a simultaneous -increase in global marginality, and increased specialization for densely vegetated sites towards the end of the summer. The intra-annual ENFA results were corroborated by the MADIFA-based habitat suitability maps that also suggested a clear change in habitat suitability over the summer season (Fig. 3). The Monte-Carlo tests revealed that the first MADIFA axis was highly significant ($p < 0.01$) for all the months. Moreover, the first MADIFA axis was highly correlated with the marginality axes and with the first specialization axes of the monthly ENFAs (R^2 between 0.75 and 0.93 and R^2 between 0.21 and 0.60, respectively). Habitat suitability was relatively high and uniform across the study area early in the season (July-August), while high suitability areas were confined to vegetated areas at lower elevations towards the end of the season (September-October).

188

189 Discussion

Both density and spring snow cover influenced muskox habitat selection across years. Based on the ideal-free distribution theorem (Fretwell and Lucas 1969) and related density-dependent habitat selection theory (Rosenzweig 1991), we expected habitat selection to become less strict as muskox density increases. Indeed, our finding that habitat selection changed as a function of both increasing muskox density (i.e. reduced specialization) and increasing spring snow cover (i.e. reduced marginality) supports this expectation. Meanwhile, marginality was not related to variation in muskox density. Further, specialization was not related to variation in spring snow cover. Hence, muskox use a wider variety of habitats as their density increases and also when snow conditions limit accessible foraging sites. The densities of muskox observed at Zackenberg are among the highest reported for the Arctic (Schmidt et al. 2015), and some influence of animal density on habitat selection was therefore to be expected. Snow conditions are known to be a key driver of muskox

201 population dynamics in the area (Schmidt et al. 2015; Mosbacher et al. 2016b). While spring snow
202 cover was were negatively related to marginality, and thus to habitat selectivity, we had expected
203 snow conditions to be more close linked to the inter-annual habitat selection scale due to the large
204 inter-annual variability in snow conditions in the area (Pedersen et al. 2016). Lack of noticeable
205 effect may have resulted from the large degree of small-scale habitat heterogeneity in the area
206 (Pedersen et al. 2018), allowing muskox to find suitable habitat in most areas irrespective the snow
207 conditions (Beumer et al. 2019). It is likely that this small-scale habitat heterogeneity is also the main
208 driver of the increasing selection for habitat observed at the intra-annual (seasonal) scale. In spring,
209 onset of the snowmelt period varies according to local topography and habitat type (Kankaanpää et
210 al. 2018; Pedersen et al. 2018), which creates a spatially heterogeneous pattern of plant emergence
211 (Pedersen et al. 2016). Hence, in spring muskox likely finds suitable forage resources throughout the
212 census area. In agreement with this, we observed a gradual increase in the strength of the habitat
213 selection from July to October, with increased selection for habitats closer to dense or sparse
214 vegetation, lower elevations and habitats further away from bare grounds. This seasonal pattern in
215 habitat selection was corroborated by the habitat suitability maps, where suitable habitats early in
216 the season are scattered throughout the census area, while the more productive fen habitats in the
217 lowland become increasingly important towards October. The same pattern was also observed in
218 the habitat use of GPS-tracked muskoxen from the Zackenberg area (Beumer et al. 2019). The
219 productive habitats provide abundant forage in summer (Mosbacher et al. 2016a), and muskox
220 obtain the majority of their summer forage there (Kristensen et al. 2011). Marginality and
221 specialization values confirmed this gradual increase in specialization as the season progressed, and
222 particularly in September and October where the areas of the used niche were 2-3 times smaller
223 than the available habitat. Being able to refuel their fat depots over the snow-free period is pivotal

for muskox reproduction (Adamczewski et al. 1998), and ultimately for the survival of individuals. In addition to winter conditions (Schmidt et al. 2015), autumn access to productive habitats, such as fen areas, is therefore a crucial parameter for muskox population dynamics. In the autumn, heavy snow events may preclude muskox from accessing the plant forage in the productive lowland areas. Further, in recent years, autumn rain events at Zackenberg have led to massive flooding in the fen areas. The subsequent ice formation in the fen areas almost completely blocking muskox access to their plant forage even before the snow had accumulated there. Sufficient access to productive habitats (both in time and space) may be another important factor to consider in future studies when examining muskox habitat selection and population dynamics.

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332 **Figure captions**

333

334 **Fig. 1.** The study area and environmental conditions in the muskox (*Ovibos moschatus*) census area.

335 a) Greenland map, with the location of Zackenberg. The environmental conditions in muskox census
336 area, with b) elevation (m), c) slope (°), d) ruggedness (terrain ruggedness index), and e) landcover
337 (3 classes). The star marks the location of Zackenberg research station.

338

339 **Fig. 2.** Inter-annual variation in muskox (*Ovibos moschatus*) habitat selection in relation to muskox
340 density and spring snow cover at Zackenberg in high Arctic Greenland during the period 1996 to
341 2016. Upper panels show ENFA marginality, while lower panel show ENFA specialization. Only
342 significant regression lines for marginality versus spring snow cover ($R^2=0.28$) and specialization
343 versus muskox density ($R^2=0.27$) are shown (see Table 1).

344

345 **Fig. 3.** Muskox intra-annual habitat (*Ovibos moschatus*) selection and suitability at Zackenberg in
346 high Arctic Greenland. Panel A shows the ENFA biplots with convex polygons of available (light grey)
347 and used (dark grey) habitats and the environmental vectors influencing marginality (x-axis) and
348 specialization (y-axis). Red dots correspond to the centroid of the used habitat. The environmental
349 vectors are numbered as 1: elevation; 2: slope; 3: ruggedness; 4: dense vegetation distance; 5:
350 sparse vegetation distance; 6: bare ground distance. Length and direction of vectors indicate the
351 contribution to the axes of the ENFA. Panel B shows the monthly habitat suitability maps, computed
352 with the Mahalanobis distance analysis. The 25% quantiles break the range of values into four
353 classes of suitability. Panel C shows the monthly histograms representing the niche-environment
354 system. Purple histograms show the distribution of the available resource units (the environment),

355 and the white histograms show the distribution of used resource units (the niche), for comparison.
356 Each variable was root-transformed prior to analysis. Panel D shows the corresponding monthly
357 eigenvalues diagrams.

358

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Fig. 1. The study area and environmental conditions in the muskox (*Ovibos moschatus*) census area. a) Greenland map, with the location of Zackenberg. The environmental conditions in muskox census area, with b) elevation (m), c) slope (°), d) ruggedness (terrain ruggedness index), and e) landcover (3 classes). The star marks the location of Zackenberg research station.

Fig. 2. Inter-annual variation in muskox (*Ovibos moschatus*) habitat selection in relation to muskox density and spring snow cover at Zackenberg in high Arctic Greenland during the period 1996 to 2016. Upper panels show ENFA marginality, while lower panel show ENFA specialization. Only significant regression lines for marginality versus spring snow cover ($R^2=0.28$) and specialization versus muskox density ($R^2=0.27$) are shown (see Table 1).

159x179mm (300 x 300 DPI)

Fig. 3. Muskox intra-annual habitat (*Ovibos moschatus*) selection and suitability at Zackenberg in high Arctic Greenland. Panel A shows the ENFA biplots with convex polygons of available (light grey) and used (dark grey) habitats and the environmental vectors influencing marginality (x-axis) and specialization (y-axis). Red dots correspond to the centroid of the used habitat. The environmental vectors are numbered as 1: elevation; 2: slope; 3: ruggedness; 4: dense vegetation distance; 5: sparse vegetation distance; 6: bare ground distance. Length and direction of vectors indicate the contribution to the axes of the ENFA. Panel B shows the monthly habitat suitability maps, computed with the Mahalanobis distance analysis. The 25% quantiles break the range of values into four classes of suitability. Panel C shows the monthly histograms representing the niche-environment system. Purple histograms show the distribution of the available resource units (the environment), and the white histograms show the distribution of used resource units (the niche), for comparison. Each variable was root-transformed prior to analysis. Panel D shows the corresponding monthly eigenvalues diagrams.

Table 1. Summary statistics for the analyses of ENFA output (global marginality and specialization) and inter-annual variation in muskox (*Ovibos moschatus*) density and spring snow cover. Significant P-values are shown in bold.

	Estimate	SE	F value	P value	Model R ²	Model P
<i>Marginality</i>					0.36	0.005
Month (July)	0.202	0.801	1.234	0.274		
Muskox density	0.446	0.256	2.084	0.156		
Month*Muskox density	-0.370	0.362	1.045	0.573		
Spring snow cover	-0.011	0.006	15.542	0.001		
Month*Spring snow cover	0.002	0.362	0.323	0.314		
<i>Specialization</i>					0.28	0.033
Month (July)	5.166	2.687	2.083	0.158		
Muskox density	-0.102	0.859	5.456	0.025		
Month*Muskox density	-2.633	1.214	4.701	0.037		
Spring snow cover	0.011	0.019	1.531	0.224		
Month*Spring snow cover	-0.021	0.027	0.062	0.805		

Table 2. Results of the intra-annual ENFA analysis for muskoxen (*Ovibos moschatus*) of Zackenberg Valley. The value for marginality (m) and the specialization (γ) are reported for the global model and for each environmental variable for each month. Note that global marginality is reported as m^2 while marginality for variables is reported as m . “ N ” indicates the number of muskox locations included in the analysis.

	July		August		September		October	
Locations (N)	1354		1692		719		428	
Measure	m	γ	m	γ	m	γ	m	γ
Global	0.34	1.60	0.81	1.76	3.05	2.62	4.96	4.39
P value	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Variables								
Elevation	-0.06	0.02	-0.30	-0.04	-0.42	0.01	-0.42	0.73
Slope	-0.16	0.62	-0.36	-0.64	-0.45	-0.06	-0.43	-0.22
Ruggedness	-0.16	-0.77	-0.35	0.76	-0.43	-0.32	-0.42	0.02
Distance to dense vegetation	-0.91	0.04	-0.68	-0.07	-0.51	-0.30	-0.52	-0.34
Distance to sparse vegetation	-0.18	-0.10	-0.22	0.05	-0.12	-0.50	-0.08	-0.54
Distance to bBare ground	0.30	-0.01	0.38	-0.02	0.41	-0.09	0.43	-0.01