Adaptations of mobile ungulates in a changing North

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Abstract

The combined effects of global warming and land use changes experienced by animals at high latitudes, are poorly understood. Social and eco-physiological perspectives are therefore necessary to elucidate where and when animals and the ecosystems they represent are most vulnerable to environmental change. This requires integration of multiple disciplines, application of novel and established methods as well as data, to achieve a holistic understanding of accumulating impacts of global change. In this work I investigate the impact of anthropogenic activities and shifting temperatures on keystone ungulates. I studied semi-domesticated reindeer *Rangifer t. tarandus* at the scale of their annual and seasonal pastures and moose *Alces alces* across a large biogeographical gradient across Sweden. Along with herder's knowledge on land use and reindeer herding practices, I utilise an array of biomolecular approaches and sensors that characterise the eco-physiological state of moose. I found that both species are ecologically and physiologically impacted by land use and warming temperatures. Reindeer have lost pastures to the cascading effects of mining, with consequences on herder's livelihood. Moose had higher metabolic expenditure in areas where they encounter increased anthropogenic and thermal stressors, reflected in starvation responses, shortened telomeres and modified behaviour. Overall, this work provides many novel insights into ongoing adaptations of ungulates under global change. My findings are crucial for aiding species and habitat protection across the northern hemisphere.

Keywords: biomarkers, cumulative impacts, eco-physiology, global change, moose, omics, reindeer, resource extraction, ungulates

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Anpassningar hos vandrande klövviltarter i ett föränderligt Norden

Abstract

Det finns fortsatt ett stort kunskapsbehov om hur den kombinerade effekten av global uppvärmning och en förändrad markanvändning påverkar djur på nordliga breddgrader. Både sociala som ekofysiologiska frågeställningar är därför nödvändiga att undersöka för att bättre förstå var och när miljöförändringar påverkar människa, djur och ekosystem. För att få en helhetsbild av den globala förändringens effekt behövs ett tvärvetenskapligt angreppssätt med både nya och väletablerade metoder. I min avhandling undersökte jag effekterna av direkt mänsklig påverkan och av ett förändrat klimat på älg och ren. Jag studerade tamren *Rangifer t. tarandus* över deras års- och säsongsvariationer mellan betesområden, och älg *Alces alces* längs en långsträckt gradient över Sverige. Tillsammans med renskötarnas kunskap om markanvändning och renskötsel, använde jag en uppsättning molekylärbiologiska metoder och sensorer för att beskriva älgens eko-fysiologiska status. Mina resultat visade att både älg och ren påverkas ekologiskt och fysiologiskt av den pågående markanvändningen och av stigande temperaturer. Renen har förlorat betesområden på grund av gruvnäringen, vilket får ekonomiska konsekvenser för rennäringen. Älgen använde mer energi i områden där de påverkades av ökande mänsklig och värmestress, vilket bland annat svält, kortare telomerlängd och ett förändrat beteende visade. Som helhet bidrar mitt arbete till en ökad förståelse för anpassningar i Sverige till globala förändringar i form av markanvändning och klimat kan påverka älgar, renar och ekosystemen. Mina resultat utgör avgörande bidrag till art- och habitatskydd över den norra hemisfären.

Nyckelord: älg, biomarkörer, ekofysiologi, global förändring, klimat, klövvilt, kumulativa effekter, omics, ren, resursutvinning

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Preface

Project director: Don't we already know this?
Me [thinking]**:** Then why did you hire a PhD student?
Me [saying]**:** *...something about adrenal glands in reindeer...*

That was all the motivation I needed to kick my PhD training off. I am truly grateful for the opportunity to have worked within 'Resource Extraction and Sustainable Arctic Communities' and feel privileged to conduct the kind of work I am most passionate about with the bonus of contributing to our understanding of the status and future of northern ecosystems.

Dedication

To **aa_bd_17_007**.
You are part of this study despite tragic circumstances.
You roamed a stunning landscape.
I wish I learnt more about you.

"*Den som går sin egen väg, behöver ingen karta.*"
Drottning Kristina
(1632 - 1654)

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"*Those who go their own way, do not need a map.*"
Christina, Queen of Sweden
(1632 - 1654)

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Fohringer, C.*, Rosqvist, G., Inga, N., and Singh, N. J. (in review). Reindeer husbandry in peril? - How extractive industries exert multiple pressures on an Arctic pastoral ecosystem.

II. Fohringer, C.*, Dudka, I., Spitzer, R., Stenbacka, F., Rzhepishevska, O., Cromsigt, J. P. G. M., Gröbner, G., Ericsson, E., and Singh, N. J. (in press). Integrating omics to characterise eco-physiological adaptations: how moose diet and metabolism differ across biogeographic zones. *Ecology and Evolution*.

III. Fohringer, C.*, Hoelzl, F., Smith, S., Cayol, C., Allen, A. M., Spong, G., Ericsson, G., and Singh N. J. (in review). Large mammal telomere length variation across ecoregions.

IV. Singh, N. J.*, Fohringer, C., Evans, A., Neumann, W., Græsli, A. R., Thiel, A., Malmsten, J., Stenbacka, F., Arnemo, J., Ericsson, G. Temperature-mediated physiological and behavioural adaptations in moose across a latitudinal gradient. (manuscript)

The contribution of Christian Fohringer to the papers included in this thesis was as follows:

I. Main author. Designed the study with co-authors. Collected and integrated the data. Interpreted the data together with NI. Wrote the manuscript with contributions from co-authors.

II. Main author. Conceived the ideas and designed methodology together with NS, RS, ID, and OR. Collected some and processed all serum samples for NMR-analysis. Combined and interpreted data together with ID and RS. Wrote the manuscript with contributions from co-authors.

III. Main author. Conceived the ideas and designed methodology together with GS, and SS. Collected some samples and extracted DNA from all samples. Conducted qPCR assay and bioinformatics together with FH. Carried out statistical analysis together with CC and NS. Wrote the manuscript with contributions from co-authors.

IV. Second author. Designed the study together with NS. Wrote the manuscript with contributions from co-authors.

Abbreviations

DNA	Deoxyribonucleic acid
gHM	Global human modification map
GC-MS	Gas chromatography–mass spectrometry
GIS	Geographic Information System
GPS	Global Positioning System
LC-MS	Liquid chromatography–mass spectrometry
MOTU	Molecular operational taxonomic unit
NMR	Nuclear magnetic resonance
OPLS-DA	Orthogonal partial least squares discriminant analysis
PCA	Principal component analysis
qPCR	Quantitative Polymerase Chain Reaction
RHC	Reindeer herding community (*sameby*)
RTL	Relative Telomere Length
T_b	Body temperature
T_c	GPS-collar temperature
UCT	Upper critical temperature
VFM	Department of Wildlife, Fish and Environmental Studies (Swedish University of Agricultural Sciences)
ZOI	Zone-of-influence

1. Introduction

1.1 Multiple pressures on Northern ecosystems

Warmer temperatures, increased precipitation, increased frequency of weather anomalies (e.g., freeze—thaw cycles or rain-on-snow), and shifts in phenology, are altering the structure and dynamics of sensitive tundra and taiga habitats (Berger *et al.*, 2018; IPCC, 2019). Simultaneously, to meet a growing global demand for energy and other raw materials, anthropogenic activities are increasingly encroaching on critical wildlife habitats (Avango *et al.*, 2013; Davidson, 2020; Tucker *et al.*, 2018). This is because northern ecosystems contain vast deposits of oil, gas, minerals and peat that make them highly attractive for exploitation (UNEP, 2001). The combined effects of climate change and increasing exploitation are exacerbating the already precarious state of animal and pastoral communities that depend upon these ecosystems for forage, cover and livelihoods they contain. Furthermore, this is also challenging their future adaptive potential to persist in these ecosystems.

1.2 The role of large ungulates in Sweden

The focal species of this thesis are moose (*Alces alces*) and reindeer (*Rangifer tarandus*). Both are cold-adapted deer with a circumpolar distribution. According to the ICUN Red List of Threatened Species, both species are of 'least concern' in Europe (Henttonen & Tikhonov, 2007; Hundertmark, 2016), while reindeer are globally listed as 'vulnerable' (Gunn, 2016). Moose occur throughout Sweden (expect on the island of Gotland) at an estimated total number of 350,000 individuals, of which up to

30% are harvested annually (Jägareförbundet, 2015; Wallgren, 2016). There are no wild reindeer in Sweden, as herds are traditionally managed by Sámi reindeer herders across 51 reindeer herding communities (RHCs). Approximately 250,000[1] semi-domesticated reindeer roam the northern half of Sweden and approximately 25% are slaughtered annually.

Moose and reindeer are emblematic of the North and therefore important flagship species that are of high cultural value to society. They attract tourists to high latitudes and their meat is regarded as a provisioning ecosystem service (MA, 2005). Furthermore, reindeer husbandry is a culture-bearing industry that provides livelihood to many Sámi. Reindeer act as ecosystem engineers by keeping the tundra landscape open through grazing. This was shown to increase summer albedo and reduce shrub encroachment (te Beest *et al.*, 2016), which in turn mitigates effects of global heating.

However, moose and reindeer are also involved in several human-wildlife conflicts, including vehicle collisions (approximately 4,500[2] incidents attributed to moose and 3,000[1] to reindeer per year; Seiler, 2005), damage to pastures (grasslands and lichen) and economically valuable timber species as well as general interference with the construction or expansion of industrial land users (Dressel *et al.*, 2018; Klein, 2000; Tyler *et al.*, 2021).

While reindeer are traditionally migrating between seasonal pastures, moose are more flexible regarding their movement strategies. While moose in southern Sweden are more stationary, their propensity to carry out seasonal migrations increases with latitude (Allen *et al.*, 2016; Singh *et al.*, 2012). Moose are therefore regarded as partially migratory and are known to exhibit substantial variation in seasonal home range size (Allen *et al.*, 2016; Cederlund & Sand, 1994). Due to their circumpolar range, requirement for vast areas, and high socio-cultural importance moose and reindeer provide ideal candidates to study the effects of land use and climate change on the landscapes they inhabit.

1.3   Social and eco-physiological indicators of adaptation

The foremost response of an animal to an external stressor is behavioural (Saaristo *et al.*, 2018), e.g., via a change in activity, movement and space

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[1] Recorded by the Sámi Parliament of Sweden: https://www.sametinget.se/

[2] Recorded via https://www.viltolycka.se/

use. For pastoral communities, responses can be similar, such as increased or reduced movement of herds due to loss of pastures, increased artificial provisioning of food and shelter, herding and economic effort resulting ultimately in sedentarisation (Schwartz, 2005). Animal behaviour is a result of interconnected physiological, anatomical and neurological processes, which can therefore act as indicators of an animal's response to environmental changes.

By studying animal and human communities in space and time and variation in these biological and socio-economic indicators, one can infer the diversity and potential of their adaptive capacity. Specifically, indicators such as the selection and avoidance of certain key habitats, diet, stress levels, and metabolic state variables, across populations inhabiting a gradient of climatic and human activity, can provide vital cues on the state and dynamics of their adaptations.

1.4 Objectives

Recent advancements in theory and methods of molecular biology, biotelemetry and social-ecological sciences now allow for the quantification of indicators of state dynamics and adaptive capacity. Therefore, I aim to utilise these advancements and combine an array of these novel methods in my thesis to address the cumulative effects of multiple social and environmental pressures that reindeer husbandry and moose encounter across Sweden (Fig. 1).

Despite neither species being under conservation concern in Fennoscandia, generating and combining baseline data to monitor the degree of environmental degradation, metabolic expenditure and shifts thereof in these species could provide an early warning system of changes that affect populations and vulnerable northern ecosystems that they represent. Moose and reindeer could thus serve as 'canaries in a coal mine'.

My main objectives were to:

- Determine where and when cumulative impacts driven by land use and climate change are negatively impacting animal populations.

- Combine novel and established approaches to identify and quantify social and eco-physiological indicators of these impacts.
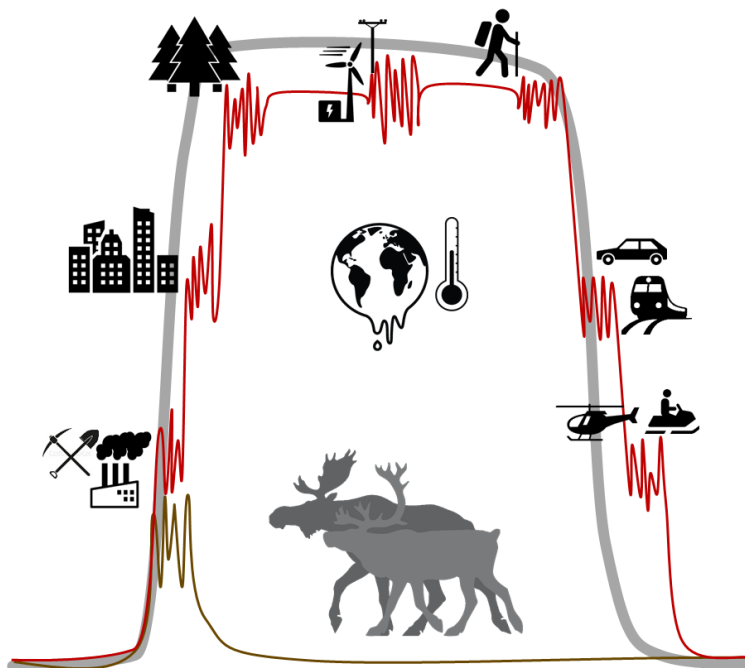
Figure 1. Scenarios of how wide-ranging northern ungulates are impacted across the landscape. The grey line symbolises the idealised animal movement strategy from one range to another (plateau to plateau) and back. If these animals experience one or a series of stressors in their landscape, movement between areas can be repeatedly interruped and delayed (red line) or aborted altogether (brown line). Both adaptations to evade encountered stressors can manifest in increased metabolic expenditure and have consequences on population dynamics.

2. Materials and Methods

2.1 Data collection

2.1.1 Land use and environmental data compilation (*Papers I-III*)

In order to identify the main drivers of anthropogenic change, primary and secondary datasets at multiple spatiotemporal scales were gathered from online sources, by special request from certain land users, and through incorporation of reindeer herder knowledge. The spatial context ranges from the RHC level to county and ecoregion level. Except, for a transnational portion of Laevas RHC extending into Norway, sample and data analysis for this thesis have been restricted to Sweden (Fig. 2). A historical context of intensifying land use is provided in *Paper I*, where the timeframe examined in relation to land use change and reindeer statistics dates back to the turn of the nineteenth century. Specifically, statistical and spatial data on reindeer husbandry and several land use developments were provided by Laevas RHC. Spatial data relating to reindeer husbandry was exported from RenGIS 2.0[3], a common tool for members of Swedish RHC's to digitise the delineation of important grazing lands and spatial developments, to complete our framework with input from herder's perspectives.

Ecoregions, based on Dinerstein *et al.* (2017), explained findings of *Paper II* (where I link diet and metabolism in moose) and provided a key component in explaining the results of *Paper III* (where I measure chronic stress in moose through relative telomere length (RTL)). The three major ecoregions in Sweden are, montane birch forest and grasslands (tundra; Appendix, Fig. A1), boreal forest (taiga), and sarmatic mixed forest. In my analyses, a coastal region was added to highlight contrasting environmental conditions experienced by animals captured around an archipelago in the Bothnian Bay (*Paper II*). These regional categorisations are representing distinct units of biological diversity and its association with climatic conditions across the planet (Olson *et al.*, 2001). Distinct ecoregions also encompass differences in anthropogenic pressures, food availability and weather.

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[3] Swedish Sámi Parliament: https://www.sametinget.se/111684

To illustrate anthropogenic impacts on the landscape the global Human Modification map (gHM), which provides a cumulative measure of human modification of terrestrial lands across the globe at a 1-km resolution (Kennedy *et al.*, 2019), was used.

To characterise habitat selection by moose in response to changes in ambient temperature and body temperature (T_b), the Swedish national land cover data[4] at a resolution of 10 meters was used (*Paper IV*). The land cover in the dataset was classified into 26 broad classes, many of which with relevance for moose biology due to detailed classification of forest types, wetland and open habitats, and human-modified habitats.

All spatial data was compiled in QuantumGIS 3.2.3 (QGIS, www.qgis.org) for visualisation and their spatial extent of this data was determined via Spatial Analysis tools within the software.

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[4]Provided by the Swedish Environmental Protection Agency: https://www.naturvardsverket.se/Sa-mar-miljon/Kartor/Nationella-Marktackedata-NMD/
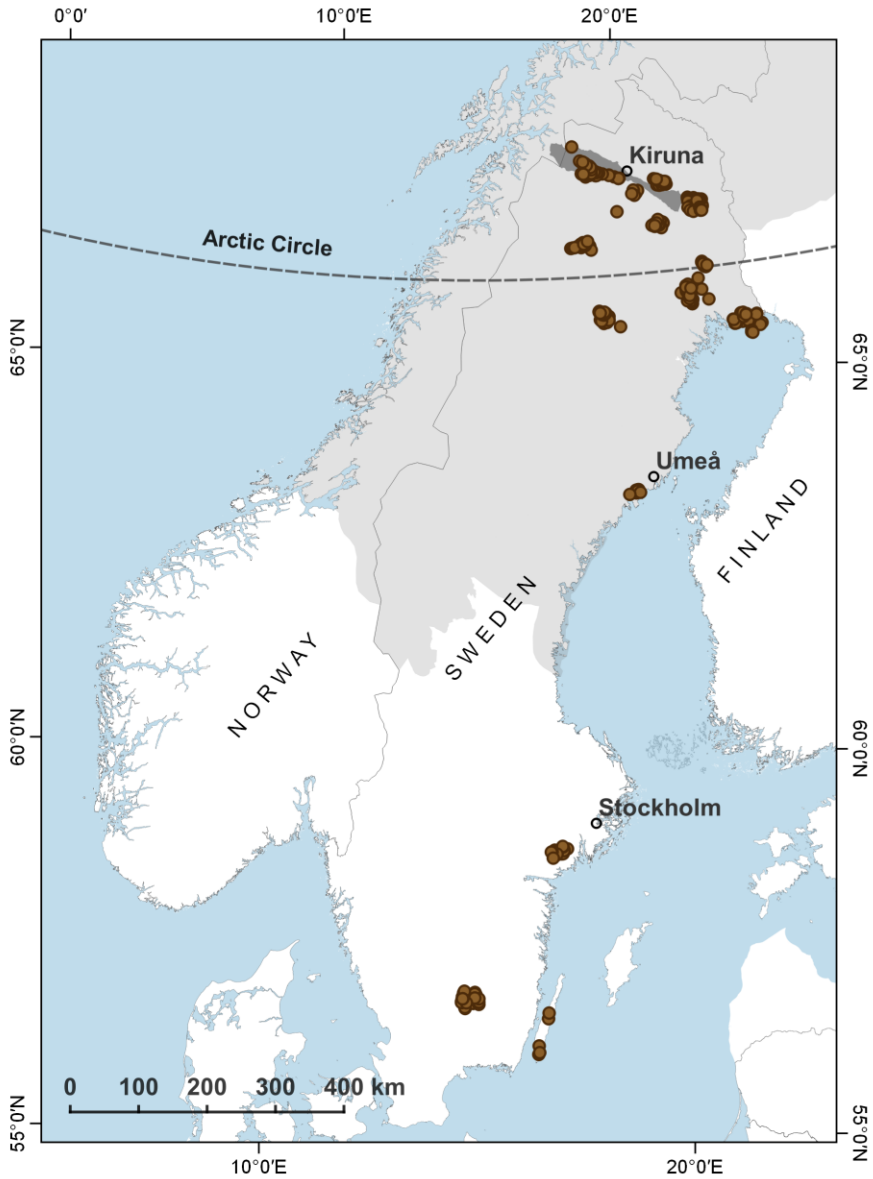
Figure 2. Summary of the spatial coverage examined in this thesis. Capture locations of moose (N=125) are highlighted as brown circles across Sweden and Laevas RHC is highlighted in dark grey within Sápmi, the transnational homeland of the Sámi people (light grey).

2.1.2 Collection and storage of biosamples and logger data (*Papers II-IV*)

As part of routine moose monitoring, which has been carried out by the Department of Wildlife; Fish and Environmental Studies (VFM) since the 1980's, moose are captured, sampled and equipped with tracking devices. Samples and data of 125 moose that were (re-)captured across Sweden during winter (Jan–April, 2008–2018) are included in this thesis (Fig. 2 & 3). Standard monitoring during immobilization (Kreeger & Arnemo, 2018) of animals included the collection of blood and faecal pellets, body measurements, and age estimation (based on tooth wear; Ericsson & Wallin, 2001; Rolandsen *et al.*, 2008). In addition to sex, pregnancy status was determined via rectal palpation (Solberg *et al.*, 2003). GPS position of capture location and the number of calves at heel were determined visually from the helicopter. All animals were equipped with GPS-collars including a temperature receiver (Vectronic-Aerospace, Berlin, Germany). The GPS collar was programmed to record positions together with collar temperature (T_c) at 30-minute intervals. Activity sensors in the collar measured acceleration in three orthogonal directions six to eight times per second. For each direction, activity values were averaged for a recording interval of 5 minutes. Additionally, rumen temperature loggers (mortality implant transmitters, Vectronic-Aerospace, Berlin, Germany) to record T_b were deployed in a subset of individuals.). Sensors recorded activity, T_c and T_b at 5-minute intervals and then transmitted information to a collar unit, where it was archived. Data on GPS positions, ancillary T_c, T_b, activity, sex, age, pregnancy status, and number of calves at heel were stored and accessed via the Wireless Remote Animal Monitoring database (Dettki *et al.*, 2014).

Blood samples (used for *Paper II & III*) were collected into 9 ml S-Monovette® Z-Gel collection tubes (Sarstedt, Germany) by jugular venipuncture and stored at -20 °C in VFM's biobank. Faecal samples (used only for Paper II) were stored similarly. After thawing blood samples, 300 µl of the serum fraction in the collection tube was used for NMR-analysis (*Paper II*), while the remaining serum was aliquoted and refrozen at -80 °C for future analysis. After subsequent removal of the gel layer in the tube, approximately 40 mg of the coagulated blood cell fraction was used as the template for DNA-extraction (*Paper III*).
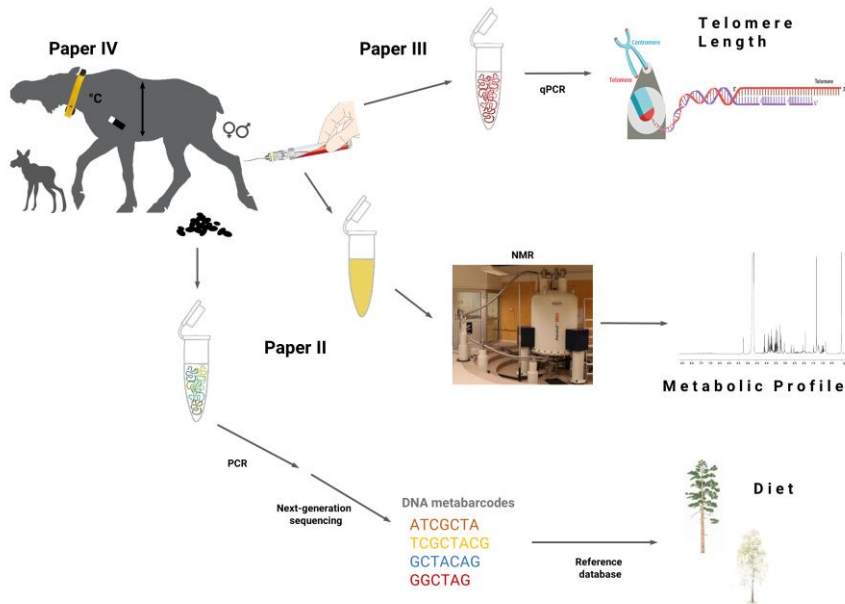
Figure 3. Schematic overview of how samples and data from moose were collected and used and what results were achieved in the respective papers (*II-IV*). The template materials for *Paper II* were serum and faecal samples that were analysed via an NMR to attain information of metabolic profiles and a DNA-metabarcoding approach to attain dietary profiles, respectively. Diets and metabolic profiles were subsequently linked. DNA obtained from white blood cells was the template for the RTL assessment in *Paper III*. Paper IV used biologging data (GPS-position, T_c, and activity measured by the collared unit; Tb measured by an MIT in the rumen) to determine behavioural and physiological effects from exposure to different ambient temperatures. Sex, age, skeletal measurements, pregnancy or calves at heel were integrated when relevant.

2.1.3   DNA metabarcoding (*Paper II*)

DNA from faecal samples was extracted following Spitzer *et al.* (2019) and purification was carried out on a QIASymphony SP platform using the DSP DNA minikit (Qiagen, Hilden, Germany) following the manufacturer's instructions. To determine the diet composition, the universal primer pair Sper01_F & Sper01_R (Taberlet *et al.*, 2018) was used to amplify the P6-loop of the trnL intron of chloroplasts. For each faecal sample, PCR reactions were performed using technical triplicates. All experiments included

extraction controls, PCR negative and positive controls, and PCR blanks. PCR products were purified using the MinElute PCR purification kit and sequenced on an Illumina HiSeq 2500 platform using a paired-end approach (2 x 125 base pairs). Sequence data were then processed using the OBITools software (Boyer *et al.*, 2016) and R. For the taxonomic assignation of sequences, a reference library for the local plant species was built and the final dataset was stored in a relational database using PostgreSQL (https://www.postgresql.org).

2.1.4   Metabolic profiling (*Paper II*)

Prior to analysis, serum samples were mixed with 300 µl 1.5 M deuterated phosphate buffer and transferred into 96-well plates. The ^{1}H NMR spectra were then acquired using a Bruker 600 MHz AVANCE III (Rheinstetten, Germany) spectrometer. Resulting spectra were manually corrected for the phase and the baseline with TopSpin 2.1 (Bruker Biospin, Germany) and subsequently aligned using icoshift 1.2 and manual integration of peaks on all spectra in parallel following a Matlab routine (Dudka *et al.* 2020; Virel *et al.*, 2019). Identification of the metabolites was achieved by assigning their specific resonances according to the chemical shift values and multiplicities using the Chenomx NMR suite professional (version 7.72, Chenomx, Inc., Edmonton, Canada) and the Human Metabolome Database (Wishart *et al.*, 2018).

2.1.5   Relative Telomere Length Assessment (*Paper III*)

For DNA extraction from the coagulated blood fraction, approximately 40 mg of each sample was incubated at 56 °C with 30 µl proteinase K (Qiagen, Germany) for one hour. Through subsequent addition of 190 ml PBS and repeated inverting and vortexing, a liquid state of the sample was attained to perform DNA purification on a QIASymphony SP platform using the DSP DNA minikit (Qiagen, Germany). DNA yield and quality were quantified using a NanoDrop 2000 spectrometer (Thermo Fisher Scientific, USA). Purified DNA was instantly refrigerated at 4 °C until further processing via qPCR.

For measuring RTL, I used the real-time PCR approach (Thomas *et al.*, 2008) adapted for moose. Telomere and non-VCN gene PCRs were carried out in separate runs with 20 ng DNA per reaction, 400 nmol l^{-1} of each primer combination (Tel1b/Tel2b or rt_BLG F/ rt_BLG R) in a final volume of 20

μl containing 10 μl of Master Mix (GoTaq® qPCR, Promega). PCR conditions for telomere and non-VCN runs are described in detail in *Paper III*. Each run contained a negative (non-template) control and two DNA extracts from moose livers as standard samples (to assess inter-run variability). All samples and controls were run in triplicates and cycling was performed on a Rotorgene Q quantitative thermocycler (Qiagen, Germany). We used the software LinRegPCR (2012.0) (Ramakers *et al.*, 2003) for analysis of non-baseline-corrected raw qPCR data. RTL was calculated using the method described by Ruijter *et al.* (2009), modified by Hoelzl *et al.* (2016).

2.2   Data integration and analysis

2.2.1   Integrating spatiotemporal data with herder knowledge (*Paper I*)

Spatial data was compiled, quantified and visualised in QGIS, while trends in human activity and population, reindeer population and demographics, as well as data on reindeer slaughter and predator numbers were summarised in Microsoft Excel. Anthropogenic developments (*i.e.*, trails, railroad, main roads, snow-scooter trails, power lines, mines, quarries, wind farms, settlements, and airports) were buffered by a 'zone of influence' (ZOI) of 500 m as assumedly functionally unavailable to reindeer (Environment Canada, 2011). In addition to mapping and quantifying land use developments on reindeer grazing grounds, a historical context was provided by building a timeline. Herder knowledge was used as an additional data source as well to verify and interpret data.

2.2.2   General statistical analysis (*Papers II-IV*)

Uni- and multivariate analysis were carried out using GraphPad Prism version 8.0.0 (GraphPad Software, San Diego California USA) and SIMCA 14.0 (Umetrics, Umeå, Sweden), respectively (*Paper II*). All other statistical analysis was carried out using R 3.5.2 (R Core Team, 2018) (*Paper II-IV*). All statistical analyses were carried out at a significance level of alpha = 0.05.

2.2.3   Filtering and resampling of logger data (*Papers III & IV*)

GPS and T_c data (used in *Paper III* and *IV*) were filtered to remove outliers and resampled to 1- (*Paper IV*) and 3-hour (*Paper III*) intervals using the R

packages 'amt' (Signer *et al.*, 2019) and 'SDL filter' (Shimada *et al.*, 2012). In order to remove outliers of T_b recordings that derive from drinking and snow intake the R package 'anomalize' (Dancho & Vaughan, 2018) was applied (*Paper IV*).

2.2.4 Combining omics data (*Paper II*)

Molecular operational taxonomic units (MOTUs) that did not represent at least 2.5% in at least one faecal sample were removed from the final dataset (Bison *et al.*, 2015). Because the taxonomic resolution of the trnL P6 barcode varies among plant families (Taberlet *et al.*, 2007), sequences could frequently only be assigned at genus level or higher. The remaining number of MOTUs were subsequently collapsed into the highest taxonomic level detected (e.g., the species *Filipendula ulmaria* and genus *Prunus* were collapsed in the order Rosales) (see *Paper II*, Appendix, Table 1). To determine diet types, we adopted the approach used by Shipley (2010) who defined moose consuming a 'specialist' diet if > 60% of the diet consisted of a single plant genus and, conversely, a 'generalist' moose diet was defined when no plant genus contributed > 60% to the diet. Based on the diet composition, I quantified diet diversity as the Shannon entropy (R package 'vegan'; Oksanen *et al.*, 2017).

Multivariate data analysis methods, PCA and OPLS-DA, were used to reduce dimensionality and to enable the visualisation of the separation of diet types. An unsupervised PCA was performed to obtain a trend of separation of samples according to groups (e.g., sex and diet type) and to identify possible outliers. To maximise the sample group separation and to identify discriminating metabolites, OPLS-DA analysis was carried out. This supervised approach removes the variation that is orthogonal to predefined variables from the models that were calculated for each two-group comparison, making them easier to interpret and thus more informative. All OPLS-DA models were described by the number of principal components. Goodness of fit and the amount of variation predicted by the models was determined using quality parameters (R^2 and Q^2). Important metabolites differentiating selected groups were selected from the respective OPLS-DA model and results of univariate analysis using *t*-tests were used to determine

significantly altered metabolites. A simplified representation of metabolic pathways was based on the KEGG Pathway Database[5].

2.2.5 Telomere length, biogeography and demographics (*Paper III*)

Since land use intensity (measured as gHM) and ambient temperature (measured as T_c) would correlate with each other and with larger geographical delineations, ecoregions were used as an encompassing variable to represent the accumulation of anthropogenic stressors. gHM and T_c were therefore only included to emphasise the degree at which they differ between ecoregions. The mean gHM value was estimated for each individual moose based on its GPS-track collected one year post (re-)capture. The resampled track was used to estimate the mean gHM value from the underlying raster. Similarly, mean annual T_c was based on GPS-locations post capture. In addition to ecoregions, data gathered during moose captures (*i.e.*, sex, pregnancy status, number of calves at heel, and age) were included to explain telomere length.

To explain variation among individuals in RTL, linear mixed-effects models were used (library 'lme4'; Bates, *et al.*, 2015). The initial model contained the two-way interaction between animal age and sex, ecoregion, as well as sample age as explanatory variables. To account for repeated sampling of individuals, individual ID was included as a random effect.

2.2.6 Applying thermal thresholds to logger data (*Paper IV*)

Seasons were defined based on the yearly air temperature estimates made by the Swedish Meteorological and Hydrological Institute[6], for the arrival of spring, autumn, summer and winter, across study locations in Sweden. Considering that the upper critical temperature (UCT) threshold in moose was shown to vary across studies, a threshold of 20 °C (during summer) and 0 °C (during winter) was set as *Hot*, given that moose were observed to be open-mouth panting and to substantially reduce movement at these ambient temperatures (Renecker & Hudson, 1986). Ambient temperatures between 14 and 20 °C as well as -5 and 0 °C were set as the *Summer/Winter Warm*, respectively, given that moose were found to exhibit flexible but significant behavioural responses in this temperature range (McCann *et al.*, 2013;

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[5] Kyoto Encyclopedia of Genes and Genomes Pathway Database: http://www.genome.jp/kegg/pathway.html

[6] http://www.smhi.se/vader/observationer/arstidskarta/

Renecker & Hudson, 1986). Assuming that the thermoneutral zone of moose is below 14 °C in summer and 0 °C in winter, ambient temperatures below this threshold were defined as *Normal*. A *Transition* period was included to exclude the application of thermal thresholds during spring and autumn where thresholds are unknown and moose often shift ranges, for example, through migration. The analysis only focusses on potential heat stress effects, as metabolic rate of moose is assumed to remain constant at ambient temperatures as low as -32 °C (Renecker & Hudson, 1986).

General trends in T_b were estimated by aggregating observations to daily scale across individuals and subsequently tested for differences between seasons, study areas and sexes. To test if T_c and activity explain changes in T_b, generalized additive mixed models (GAMMs) were fitted using library 'mgcv' implemented with moving average correlation structures (Pinheiro & Bates 2000; Wood, 2006). Afterwards, activity and temperature patterns of female moose across study areas during the *Summer hot* versus *Summer normal* and *Winter hot* versus *Winter normal* periods were compared using generalized linear mixed models (Pinheiro & Bates, 2000).

To investigate the thermal responses of moose through habitat selection, step-selection functions were applied to habitat classes encountered by animals during exposure to aforementioned conditions. Habitats in which no moose positions occurred were excluded from the analyses. A positive coefficient indicates selection and negative indicates avoidance.

3. Results and Discussion

3.1 Paper I

By creating a timeline highlighting major land use changes on reindeer pastures of Laevas RHC, I determined that the onset of industrial-scale mining around 1900 triggered a cascade of developments that lead to substantial encroachment (Fig. 4). By applying a 500-m ZOI to all current infrastructural developments interfering with reindeer herding in Laevas RHC, a total extent of 1526.54 km^2 (34% of the total extent of Laevas' pastures) was found to be functionally unavailable on all-year reindeer pasture (*Paper I*, Fig. 3). I estimated that 64% of winter pasture and 21% of summer pasture are impacted (Appendix, Fig. A2). Moreover, I highlighted how the highest intensity of accumulating impacts coincides with Laevas RHC's central geographical bottleneck in the vicinity of the mines around Kiruna (*Paper I*, Fig. 3 and Appendix, Fig. A5).
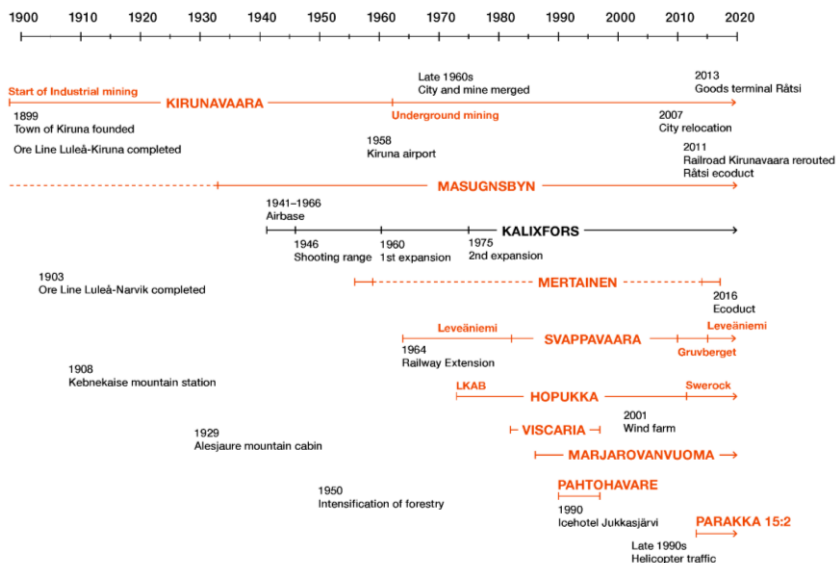
Figure 4. Timeline illustrating the establishment of industrial developments since their onset on Laevas RHC's grazing grounds from 1900 to present. Orange text represents mines and quarries, while black text represents other infrastructural developments associated with mining. Arrows indicate the ongoing operation of mines. Line breaks indicate changes within development and single dates indicate the establishment and gradual build-up of a factor. Gradual changes of land use factors include general dating, e.g., the intensification of forestry or when Kiruna and the Kirunavaara merged.

Reindeer numbers were shown to fluctuate substantially over the last six decades (*Paper I*, Fig. 4). Declines in the total number of animals were attributed to ice-locked pastures and high snow cover caused by weather anomalies, while increases were associated with inverse weather trends (no icing and less snow), the influx of new reindeer, or increased management. The total number of reindeer has remained stable at around 7,000 animals during the last decade, while the number of slaughtered animals has decreased substantially in recent years (*Paper I*, Fig. 4).

Substantially reduced and fragmented pastures, which I found to be particularly high on winter pastures (*Paper I*, Table 1), required increased herding efforts (e.g., supplementary feeding and transportation of reindeer between pastures on trucks) in order to prevent further losses reindeer. With further land loss and fragmentation on top of increasing frequencies of weather anomalies (Rosqvist *et al.*, forthcoming; Turunen *et al.*, 2016), reindeer husbandry as a traditional and sustainable livelihood will be pushed even further to its margins (Persson, 2018). These developments are not restricted to northern Sweden but relevant to many resource rich regions in the Arctic and elsewhere (Tucker *et al.*, 2018). Any assessments of an incoming exploitative land user should consider past developments and local adaptations by herders in order to fully understand the current impacts on system and the consequence of their accumulation. The lack of an interconnected functional ecosystem means that buffering capacity against unfavourable weather via traditional herding strategies will be lost, consequentially preventing sustainable pastoralism to persist.

3.2 Paper II

After filtering DNA-metabarcoding outputs, the resulting 17 MOTUs were collapsed into 7 MOTUs, including the category 'Other', which holds frequencies that were only present at proportions <1% (Fig. 5, Appendix, Fig. A3-5).
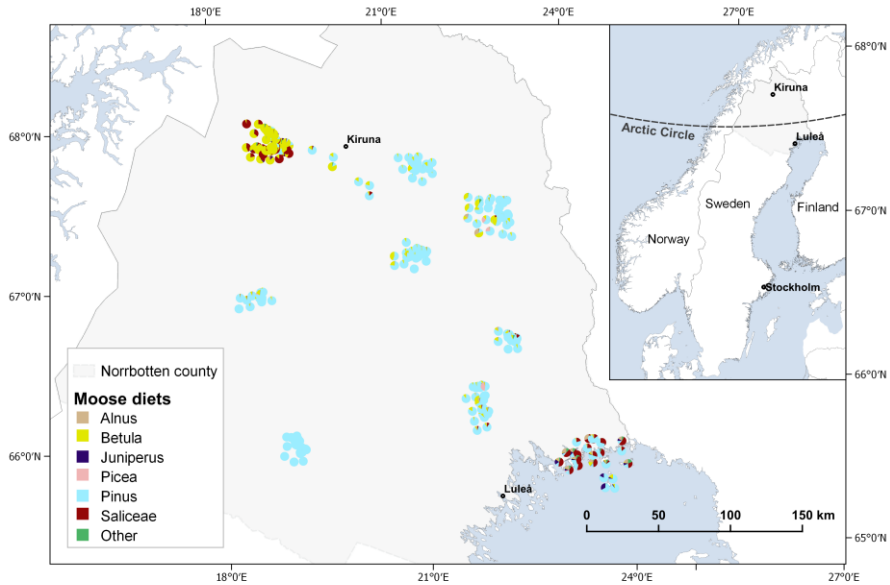
Figure 5. Distribution and composition of 264 moose winter diets across Norrbotten county, northern Sweden. Classification of diet items is based on 7 MOTUs.

I identified 4 main diet types in moose: pine-, birch-, and willow/aspen-'specialists' as well as 'generalists' that did not consume items that amounted to more than 60% of a single MOTU. The majority (73%) of moose were categorised as pine 'specialists', followed by 12% of animals that had a diets dominated by birches and 4% that consumed predominantly willow and aspen (see Appendix Fig. 5-6 for examples of heavily browsed winter diet items). The remaining 11% of animals had 'generalist' diets, which were also found to be most diverse, while pine-rich diets were the least diverse (see *Paper II*, Fig. 2). I found that diet types reflected ecozonation and the land use intensity that moose were exposed to (*Paper II*, Appendix, Fig. A1). Even though diets reflected the climatic coast-to-mountain gradient, they were also affected by intensive forestry practices manipulating the supply of

forage species to moose, especially the quantity of Scots pine (*Pinus sylvestris*) which is the major timber species (Appendix, Fig. A5-6). Moreover, I found that female moose exhibited a higher winter diet diversity than males (*Paper II*, Appendix Fig. A3), who consumed a higher mean proportion of *Pinus*. This difference follows the Jarman-Bell principle (Geist, 1974) enabling the generally larger sized males to rely less on quality but rather on abundant diet items during winter. Moose males generally enter winter with lower energy reserves as they spend less time foraging, especially during the rutting period (late September to mid-October) compared to females. Hence, males should typically maximise their instantaneous rate of food intake to sustain them through the winter (Du Toit, 2006).

Similar to the separation in diet types, I found differences in energy metabolism of individuals based on the biomarkers observed across ecoregions. In total, 55 metabolites were identified and quantified (complete list of identified metabolites is provided in *Paper II* Appendix, Table A2). In addition to differences in diets between sexes, I also found that their metabolic profiles differed. Specifically, concentrations of creatinine and albumin lysyl were significantly decreased in males compared to females. To investigate the metabolic variations correlated with four diet types, a two-way comparison of each diet type was conducted. A pathway network map of significantly altered metabolites corresponding to diet types, summarises the key significant metabolites that are major intermediates of pathways involving amino acid, lipid and gut microbiota metabolism (Fig. 6).
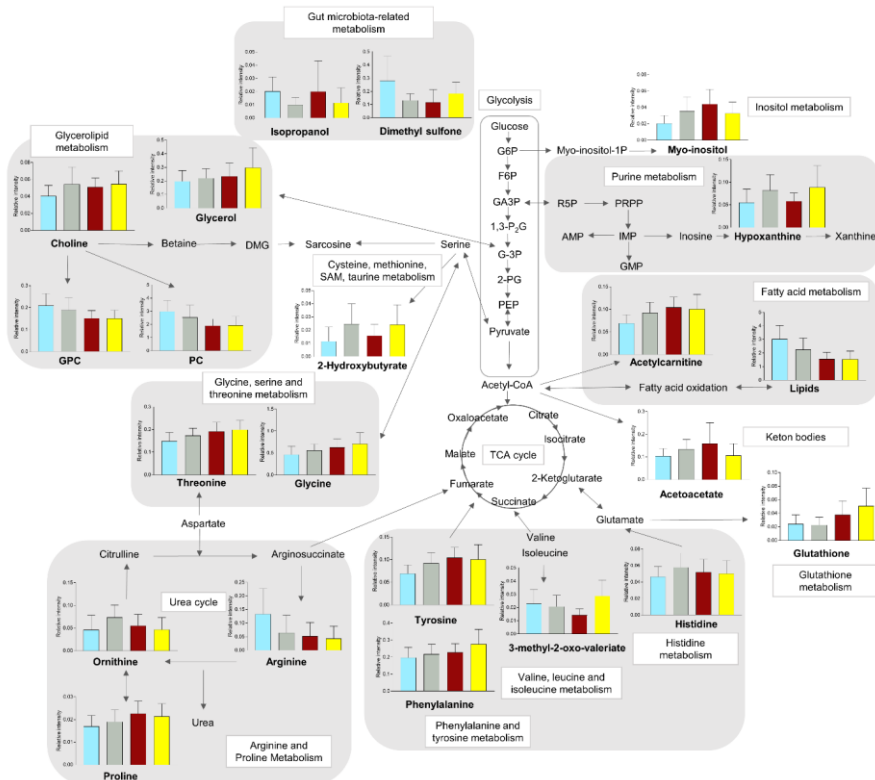
Figure 6. Simplified representation of metabolic pathways showing significantly altered metabolites in four categories based on moose diet types: *Pinus* (turquoise bars), 'generalist' (grey bars), Saliceae (burgundy bars), *Betula* (yellow bars).

I identified several molecular markers indicating metabolic constraints linked to diet constraints in terms of food availability during winter. While animals consuming pine had higher concentrations of fatty acids, phospocholine and glycerophosphocholine concentrations in their serum than other diet types, birch- and willow/aspen-rich diets exhibit elevated concentrations of several amino acids (glutathione, threonine, proline, phenylalanine, tyrosine, glycine, histidine, and ornithine). Moreover, differences in gut microbiota were directly reflected by a significant increase of dimethyl sulfone in moose with pine-rich diets compared to all other types

of diet. This compound is derived from dietary sources, and high concentrations thereof were shown to be the result of enhanced intestinal fermentation activity due to fiber consumption (He & Slupsky, 2014). This suggests that even though moose in pine dominated areas are limited in diet diversity, they may still be able to cope well due to high dimethyl sulfone promoting fermentation. Pine may therefore serve as a bulk item that is 'good enough', providing endosymbiotic bacteria with sufficient amounts of cellulose to keep beneficial dimethyl sulfone at a comparatively higher level. Moreover, I found that individuals with highest diet diversity had increased levels of ketone bodies, indicating extensive periods of starvation for animals in the coastal region.

My results show how the adaptive capacity of moose at the eco-physiological level varies over a large eco-geographic scale. In light of extensive ongoing climate and land use changes, these findings pave the way for future scenario building for their adaptive capacity.

3.3 Paper III

I found that in the boreal ecoregion, RTL was on average significantly longer than in a northern (montane) and southern (sarmatic) ecoregion *(Paper III*: Fig. 2, Table 1). Mean annual temperature (based on T_c) was 5.44 ± 4.08 °C in the montane, 9.80 ± 2.71 °C in the boreal and 14.16 ± 2.10 °C in the sarmatic ecoregion (*Paper III*: Fig. 1). Land use intensity follows a similar trend with low mean gHM values encountered by moose in the montane (0.06 ± 0.05) and boreal (0.05 ± 0.02) but high mean values (0.34 ± 0.08) encountered in the sarmatic ecoregion (*Paper III*: Fig. 1). These findings suggest that animals in the northern boreal forests, with relatively homogenous land use (*i.e.*, large stands of monoculture), are less disturbed by environmental and anthropogenic stressors. In contrast, animals in areas experiencing a higher rate of anthropogenic and environmental change, in the montane and sarmatic region, experience increased stress. As ecoregions are encompassing differences in anthropogenic pressures, food availability and weather, they differ in degree of exposure to different environmental conditions (including an array of stressors). Due to repeated triggering of the hypothalamic-pituitary-adrenal axis beyond full recovery, animals are chronically stressed, and RTL is therefore shorter, in regions where stressful conditions prevail.

Sex and age of animals did not influence RTL significantly; neither did pregnancy and the number of calves at heel when only females where considered (*Paper III*: Appendix, Table A1, Fig. A1-4). The age of the sample was negatively correlated with RTL and likely the result of varying storage durations of blood causing different degrees of DNA-degradation. However, the effect of storage duration did not impact our study as storage time was randomly distributed throughout ecoregions and among the other variables.

By measuring telomeres in moose for the first time, *Paper III* provides valuable insights towards our current understanding of telomere biology in free-ranging wildlife and telomere length variation across large spatial scales in human-modified ecosystems.

3.4 Paper IV

In general, I show that there is a spatial and temporal variation in moose T_b patterns and a positive $T_c – T_b$ relationship (*Paper IV*, Fig. 2, 3 and 5). Males had significantly lower average T_b ($\bar{x}_m$=38.06 °C) than females ($\bar{x}_f$=38.29 °C), which is likely due to their sexual size dimorphism (Paper IV, Fig. 2). Ambient temperature experienced by moose in its microclimate drove changes in T_b and behaviour, specifically through changes in activity patterns to cope with thermal stress. Moose were able to maintain their T_b better during winter than in summer (Fig. 7). The proportion of time during which moose exceeded their UCT was variable across a latitudinal gradient. However, the proportion of time exposed to *Hot* conditions was always higher than *Warm* or *Normal* conditions during summer in all three study areas (*Paper IV*, Fig. 4). Most strikingly, however, I found that moose in the southernmost study area (Öland) do not encounter thermoneutral, *i.e.*, *Normal*, conditions during winter (Fig. 7). Moose in this area are known to be suffering from low recruitment and reports on ambient temperature trends suggest a steep rise in spring temperatures in the region over the last three decades (Allen *et al.*, 2017). Activity was generally higher in summer than in winter and highly variable across individuals (*Paper IV*, Fig. 6).

The strategies to cope with thermal exposure were primarily reflected in the selection for wetland type habitats over other habitat types during stressful conditions (*Paper IV*, Fig. 7). This, however, occurred in parallel with the

selection for foraging habitats, which may provide thermal shelter simultaneously.
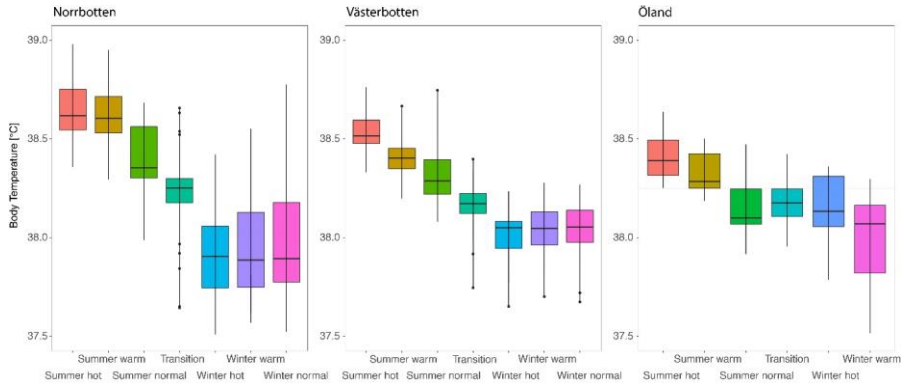

Figure 7. Mean T_b (±S.E.) of female moose (N= 29) in each study area when T_c in each study area was within predefined temperature categories during summer and winter. *Summer Hot*: T_c >20 °C, *Summer Warm*: T_c 14-20 °C, *Summer Normal*: T_c <14 °C, *Winter Hot*: T_c >0 °C, *Winter Warm*: T_c -5-0 °C, *Winter Normal*: T_c <0 °C, *Transition*: during spring and autumn. Note the absence of *Winter Normal* conditions in Öland.

My colleagues and I hereby demonstrate the intricate linkages between external environment and internal state of a wild endotherm and the trade-offs made between selecting forage and thermoregulation. Overall, our results show the adaptive behaviour of moose to regulate T_b against a varying external environment over a large biogeographic scale. Nevertheless, I found that moose are exposed to thermally stressful conditions even at the northern extent of their range. I suggest that long-term physiological and behavioural consequences that heat-sensitive endotherms, such as moose, will be facing with the ongoing increase in ambient temperature will vary across areas differently. In areas where their adaptive potential is limited, population dynamics and long-term fitness may be negatively impacted in the future.

4. Reflections

The initial plan for my PhD project called for an investigation of the combined effects of land use and climate change at northern latitudes by studying animal movements in response to environmental changes. Both, reindeer and moose were initially targeted as sources of data and later biosamples that would offer insights into where and when animals and pastoralist were most vulnerable to accumulating land use and extreme weather conditions. Unfortunately, my plans of studying reindeer in the same detail as moose had soon to be abandoned. Ownership and close human-animal contact that reindeer husbandry implies, made access to animals and samples more complicated than foreseen. It would have required additional time – years in fact – to establish sufficiently deep understanding, collaboration and trust from the RHC to be able to disentangle management strategies from anthropogenic disturbance and to set up purposeful scientific experiments. *Paper I* was therefore designed as social-ecological study that relied on data collation and integration by focussing on issues faced by a RHC that is facing extreme land degradation. Nevertheless, I was able to transfer the analysis that was intended to be carried out on both species simultaneously to moose only by conducting empirical eco-physiological studies (*Papers II-IV*).

Most approaches in this thesis have previously not been applied in either the study species or at the spatial scale (small: RHC level - *Paper I*; large: ecoregion level – *Paper II & III*; latitudinal/national – *Paper IV*). Therefore, several considerations and caveats are necessary to discuss at this point.

4.1 Representation of a case study (*Paper I*)

Population dynamics in relation to land use and climate change effects in reindeer and caribou are often assessed at large scales. For example, Uboni *et al.* (2016) and Bårdsen *et al.* (2017) did not detect evidence for population declines of semi-domesticated reindeer in relation to climate and land use change at the national (Swedish) level. This might be because the examined scales does not align with the necessary details needed to detect case-specific mechanisms influencing herd dynamics. Providing a historical context and detailed examination of land-use developments through a participatory approach, were key additions for a holistic assessment of the current baseline

of pressures faced by Laevas RHC (Bull *et al.*, 2015). Animal population dynamics are known to be more affected by local factors such as human disturbance, food availability, predation and weather (Benton *et al.*, 2006; Coulson *et al.*, 2000). Analysis at the scale of annual pastures at the RHC level might actually be an ideal prerequisite to study herd dynamics, given that herd management is relatively similar within the RHC and comprehensible when herder knowledge is included. One might even argue that the RHC level is too coarse to determine conclusive interpretations of reindeer herd dynamics due to potentially varying management strategies between *siidas* (traditional management units for a herd) within the RHC.

I have only examined a single mountain RHC in Sweden but there are other herding styles, for example forest RHC's (*skogsamebyar*), as well as different community structures and policies in different countries that would influence the outcome of a similar assessment. Other communities might face different challenges and geographies, e.g., scenarios where other forms of land use are more dominating and problematic. However, by examining an 'extreme' case of extractive violence (Sehlin McNeil, 2019), I was able to highlight what scenarios other communities with similar preconditions might face in the future, if current trends of land use intensification continue and impact assessments fail to fully realise their purpose.

4.2 Zone-of-Influence (*Paper I*)

To determine the extent of land loss and habitat fragmentation within Laevas RHC, anthropogenic developments were buffered by a ZOI of 500 m as assumedly functionally unavailable to reindeer (Environment Canada, 2011; Rudolph *et al.*, 2017). The choice of using a conservative buffer of fixed size, is based on the relatively high spatiotemporal plasticity that reindeer and caribou exhibit towards different types of human activity and infrastructure. I justify the applicability of Environment Canada's model (based on wild caribou) to semi-domesticated reindeer in a pastoral system because undisturbed home ranges are essential for the welfare of both *Rangifer* subspecies and the people that culturally and economically depend on them. I assumed that pastures within the ZOI become less suitable or not suitable for reindeer grazing due to the reindeers' avoidance behaviour and a reduced pasture quality in addition to general land loss and habitat fragmentation.

The ZOI for reindeer and caribou was shown to vary both annually and spatially because of the location of infrastructural developments and human activities to habitat selection and seasonal range size (Plante *et al.*, 2019; reviewed by Skarin & Åhman, 2014). Among the latest research on the ZOI of caribou in relation to mines, Boulanger *et al.* (2021) estimated an average distance of 7.2 km via state-of-the-art methodology. Few ZOI estimates generate a more conservative estimate then 500-m for individual disturbances, suggesting that my application of Environment Canada's model resulted in an underestimation of the actual scale of functionally unavailable reindeer grazing grounds in the Fennoscandia context. Moreover, my decision to not attribute a ZOI to clear cuts or mineral exploration, *i.e.*, factors we were uncertain of having a similarly adverse impact in the Fennoscandian context, likely added to this underestimation. Despite this risk, I determined that available undisturbed pastures in Laevas RHC are only 1 % above the threshold of minimum area required to sustain viable caribou herds (Environment Canada, 2011). Were one to apply a less conservative (*i.e.*, ungeneralised and likely more generous) ZOI's to various stressors, Laevas RHC would be in even worse situation.

4.3 Herder Knowledge (*Paper I*)

Herder's knowledge (also referred to as local and indigenous knowledge or traditional ecological knowledge) was an integral part of the analysis of spatiotemporal trends of all land use concerning Laevas RHC. Incorporating their knowledge was critical to holistically assess accumulating impacts on land that is traditionally used by pastoralists. Therefore, without the inclusion of herder knowledge, impact assessments may fail to fully realise their purpose when conducted on pastoral landscapes. Moreover, herder knowledge is too often dismissed by exclusionary agencies (including scientist) that choose to only accept empirical expert knowledge that risks lacking invaluable context when impact assessments (or social-ecological research) is conducted (Baker & Westman, 2018; Larsen *et al.*, 2017).

Including herder's knowledge is unique but also challenging. If different or more community members within Laevas or other/additional RHC's had been interviewed, it could have potentially influenced my analysis but the overall outcome may still hold. Despite relying on a single informant for the integration of herder knowledge in *Paper I*, I want to emphasise that Niila

Inga's contribution goes beyond personal opinion. He was chosen as the representative chair and spokesperson by and for the community.

4.4 Sensitivity of omics approaches (*Paper II*)

A distinct advantage of the DNA metabarcoding approach is its independence from observer bias, accurate identification of species and efficiency when handling large sample sizes, compared to alternative methods, such as microhistology (Spitzer *et al.*, 2021). However, challenges arising through the application of DNA metabarcoding include marker limitations (Taberlet *et al.*, 2007) and PCR amplification bias (Pawluczyk *et al.*, 2015, Nichols *et al.*, 2018), which may affect the quantities of sequence reads and lead to under- or overestimations of diet components (Spitzer *et al.*, 2021). Quantity and quality of DNA in faecal samples of herbivores, in particular ruminants, may also be affected by differences in digestibility or variation in chlorophyll concentrations across plant species and tissues (Spitzer *et al.*, 2021). Nevertheless, such biases can be expected to be consistent if standardised sampling and downstream processing of template material (*i.e.*, faecal pellets in our case) are being maintained across experiments. As faecal samples were sampled directly from the rectum and frozen immediately afterwards, the introduction of bias from environmental contamination or various degrees of microbial degradation was highly unlikely. Consequently, the relative differences in diet compositions should constitute true ecological signals that reflect changes in consumption even if the proportions consumed and the proportions detected may not be an exact match (Spitzer *et al.*, 2021).

Despite being a feasible, rapid and easily reproducible metabolic profiling method, NMR is a relatively less sensitive and specific than other analytical techniques, including both LC- and GC-MS. Compared to LC- and GC-MS, NMR spectroscopy is often 10 to 100 times less sensitive. This means that a typical NMR-based metabolomic study usually only returns information on 50–200 identified metabolites with concentrations >1 µM, while a typical LC-MS study can return information on 1000+ identified metabolites with concentrations of >10 to 100 nM (Emwas *et al.*, 2019). Therefore, the NMR approach used in *Paper II*, may have missed to identify other biomarkers of animal health, behaviour and fitness. Nevertheless, this was the first application of NMR and its combination with another omics approach in this

species provided valuable results contributing to our understanding of eco-physiology in light of starvation.

4.5 Population effects (*Papers II-IV*)

I did not account for population effects (*i.e.*, different phenotypes based on regional adaptations) that could potentially bias results derived from measuring diet composition, metabolic shifts or RTL within similar latitudes. In fact, I assumed that moose within counties in Sweden (*Papers II & IV*) are genetically similar. Studies have shown that moose in Sweden are only genetically distinct via a north-south gradient, e.g., Blåhed *et al.* (2018), Niedzialkowska *et al.* (2016), and Wennerstrom *et al.* (2016). In support of these studies, Singh *et al.* (2012) and Allen *et al.* (2016) have found that moose in northern Sweden exhibit a higher propensity for migration than conspecifics in southern latitudes. Migration occurs typically within the same latitude, across a large spatial scale (30-100 km; Singh *et al.* 2012), making genetic admixture for animals examined in this study likely (and population effects unlikely). Metabolic shifts detected in *Paper II* are therefore unlikely attributed to genetic differences among animals.

   The function of telomeres is highly conserved, as they are evolutionarily ancient and consistent across eukaryotes (Gomes *et al.*, 2010). Therefore, despite known genetic differences between moose in northern compared to southern Sweden, I assumed that these differences are unlikely manifested in telomere length (*Paper III*). However, telomere restoration mechanisms, e.g., telomerase activity, is known to be variably active in different species, cell types and life stages (Monaghan & Ozanne, 2018). Comparison of RTL across populations should therefore be less big of a concern than doing so across taxa, somatic tissues and different age classes.

   Additionally, I accounted for area effects on biomarkers (*Papers II & III*) and T_b (Paper *IV*) by testing if animals exhibited similar patterns within or beyond capture areas (*Paper II*). When cohorts were compared across larger (*i.e.,* a national) scale (*Papers III & IV*), I included capture area, ecoregion or county as an explanatory variable in statistical models.

   The presumed bias in latitudinal effects on T_b found in female moose (*Paper IV*) can potentially be attributed to a sampling bias of animals related to body mass (as per Kleiber's law, heavier animals should have lower metabolic rate and therefore possibly lower T_b), which should otherwise

conform with Bergman's rule (*i.e.*, larger body size corresponding to higher body mass and therefore lower T_b; Sand *et al.*, 1995).

Due to the lack of samples of moose from central Sweden, I was not able to conduct a more complete assessment along a gradient of environmental changes that moose experience across the landscape. Having this data would have also enabled a better accounting for potential population effects.

4.6 Mammalian blood as a template for telomere length assessment (Paper *III*)

Unlike other vertebrate groups, mammalian red blood cells do not have a nucleus and thus DNA extracted from their blood reflects only leucocyte telomere length (Watson *et al.*, 2017). Granulocytes and lymphocytes are known to differ in telomere length and replication rate (Aubert *et al.*, 2012; Baerlocher *et al.*, 2007; Kimura *et al.*, 2010). The proportion of circulating white blood cell types may also shift during immune responses (Beirne *et al.*, 2014; Davis *et al.*, 2008; Weng, 2012) and is known to differ between age and sex groups (Linton & Dorshkind, 2004; Watson *et al.*, 2017). Despite these known caveats in quantifying telomere length from white blood cells, our general hypotheses were confirmed and the results align with those found in several other studies (see *Paper III*). However, if possible, alternative tissues with high cell turn-over rate would be a better choice for RTL assessments in mammals. Mucosal cells, as used by Hoelzl *et al.* (2016), provide such an alternative and their sampling is less invasive than blood extraction. Moreover, adequate sample and DNA storage are invaluable prerequisites for analysis that - like RTL assessment - is sensitive to DNA degradation effects. To assure best DNA quality, it should be extracted as soon as possible after sample collection and subsequently stored at -80 ˚C. DNA used for moose RTL assessment in *Paper III* was of relatively poor quality that resulted in relatively low qPCR efficiencies (76.9% and 86.7% for the non-VCN gene and telomere reactions, respectively), likely due to the aforementioned constraints.

4.7 Ambient temperature and thresholds (*Paper IV*)

The temperature thresholds used for data analysis in *Paper IV* are based on a relatively dated study and behavioural observations of only few individuals

(Renecker & Hudson, 1986). While several studies have applied these thresholds (Lowe *et al.*, 2010; van Beest *et al.*, 2012), others have determined slightly different thermal thresholds for moose (McCann *et al.*, 2013), or even discourage the application of static thresholds of ambient air temperature altogether (Thompson *et al.*, 2020). However, by acknowledging that heat-stress thresholds of moose are potentially higher than -5 (in winter) and 14 °C (in summer) across areas with different environmental conditions, I assumed UCT to be 0 and 20 °C (categorised as *Summer* and *Winter Hot*, respectively), which was when moose were observed to be open-mouth panting and to substantially reduce movement (Renecker & Hudson, 1986).

The use of T_c as a proxy for ambient temperature instead of nearest weather station temperature data implies a trade-off. While studies have suggested (Ericsson *et al.*, 2015) and applied (Græsli *et al.*, 2020) a correction of T_c to account for the potential bias deriving from solar radiation and/or emitted body heat, nearest weather station data might not be the ideal alternative source of ambient temperature as station might be far away and therefore exposed to different microclimatic conditions than the animals themselves. The choice of using uncorrected T_c as proxy for ambient temperature is based on van Beest *et al.* (2012), who experimentally validated high T_c and ambient temperature correlation. Moreover, using T_c corresponding to directly to GPS-, activity-, and T_b-data generated on and from within the moving animal was a more logical choice than relying on relatively weather-station data that is decoupled from the body of interest.

Additional data on animal demographics population dynamics as well as would have greatly benefitted the analysis of *Papers I-IV*. In particular, body mass or other fitness proxies, true age (instead of age estimates based on tooth wear), or disease status of individual moose were not available for my analyses. Moreover, including longitudinal aspects of the examined biomarkers would have been a valuable addition to better understand the intricate physiological response to environmental change (see Appendix Fig. 3 for an example of diet analysis of a recaptured individual). However, by acknowledging certain caveats encountered in *Papers I-IV*, I want to highlight the critical reflections that, nonetheless, provided scientifically robust insights across disciplines. Future studies can benefit from this discussion if similar experimental set-ups and methods are considered.

5. Conclusions

In this thesis I was able to show the breadth of the adaptive capacity of reindeer husbandry and moose. The results of *Papers I-IV* indicate that animals under certain conditions might face limits in their adaptive potential in the future.

I show:
1. Where and why reindeer husbandry is most vulnerable due to cumulative impacts triggered by the onset of industrialisation in the Arctic (*Paper I*)
2. Using biomarkers, where and when moose face starvation during winter (*Paper II*)
3. Shorter telomeres as an indicator of stress in regions where moose faced energetically limiting climatic conditions and/or high degrees of human disturbance (*Paper III*)
4. Moose body temperature varies between sexes and across areas, and they modified their habitat selection in response to seasonal exposure to heat stress (*Paper IV*)

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Popular science summary

As northern ecosystems across the globe experience changes in land use and climate at accelerated rates, it becomes crucial to understand how animals and communities that depend on them will adapt in the future. For example, what will animals eat and how will they cope with harsh conditions, and how are food and energy balance linked? What is the current status of pastoralism and how vulnerable are animal populations that indigenous and local communities depend on? How do we best determine how impacted the rapidly changing ecosystems, that moose and reindeer represent, are?

Until now, it has been difficult to study how wild animals across different habitats respond to rapidly changing environments in fine detail due to the lack of suitable and feasible technology, methods, enough data and spatial and temporal coverage of data. Using several new molecular methods to study diets (metabarcoding) and physiology (metabolomics and telomere length), I investigated the adaptations of moose across Sweden. By applying these methods, I analysed a large number of blood and dung samples of wild moose, acquired during multiple winters. By using sensors, I studied habitat use based on interplay between the temperature surrounding moose and their body temperature. I included perspectives of a local reindeer herding community as well as industries, for information on past developments. This was fundamental for understanding the current status and trends that are threating the space required for sustainable and undisturbed reindeer herding and moose migration.

By examining accumulating land use pressures faced by a reindeer herding community that is in particular peril, I highlighted where reindeer herding and grazing is hindered or impossible (on 34 % of the communities total area). I identified, mining as the main driver of land use change in the area as its impacts go beyond the 'hole in the ground' because mining has

triggered the build-up of multiple pressures (e.g. forestry, tourism, roads and railway, city growth and relocation) that followed since the turn of the 19th century. Reindeer herders only manage to keep the number of reindeer at present stable because fewer animals are slaughtered and sold or are supplementary fed and herded more intensively.

I also found many new insights into moose biology using new methods. 1) Moose adapt their diet to what is available. For example, moose can specialise on eating pine, birch, willow/aspen or a mixture and these specialisations have consequences on the concentration of different key metabolites that indicate well-being. 2) Moose in mountainous, coastal and southern regions of Sweden starved more and were more stressed than their counterparts in heavily managed pine forests. 3) I was also able to distinguish metabolites that differ between moose males and females, and could prove that males enter the harsh winter with fewer energy stores than females because of the rut. 4) Moose body temperature response to the surrounding temperature, and moose change their habitat use and activity in response. Their body temperature differs between sexes, areas and seasons, with most pronounced differences in northern Sweden where seasonal changes are dramatic. In particular, moose in the south are facing temperatures that suggest that they are hot for extensive periods of time, upon which they make trade-offs between getting suitable food to not overheat.

I was able to highlight areas where animals are particularly vulnerable as my analysis focused on scales (both small and large) that have not been examined before. My results indicate that, if the environment of moose and reindeer continues to change at the current rate, they may suffer increased stress and starvation. Unpredictable individual and population level effects can be expected if northern ecosystems continue to change as rapidly as now. With this study I provide new insights that inspire the development of scientifically robust impact assessments through a combination of tools allowing us to assess the full impact and current status of multiple pressures affecting wildlife beyond my study area. My approach is geared to aid decision-making processes of land-use conflicts between industries and pastoralists facing multiple pressures.

Populärvetenskaplig sammanfattning

När nordliga ekosystem genomgår allt snabbare förändringar i markanvändning och klimat är det avgörande att förstå hur djur, och de samhällen som är beroende av dem, kommer att anpassa sig till framtida förhållanden. Vi måste ta reda på vad som kommer finnas för djuren att äta, hur de kommer att hantera stränga förhållanden och hur deras födoresurser är sammankopplade med deras energibalans. I denna avhandling har jag fokuserat på älg och tamren och kartlagt de olika former av påverkan som deras livsmiljöer är utsatta för. Jag har också utvecklat metoder som kan hjälpa oss förutsäga möjliga konsekvenser av förändringar i dessa ekosystem.

Fram tills nu har det varit svårt att i detalj studera hur vilda djur i olika miljöer reagerar på snabba miljöförändringar. Det har inte funnits lämplig teknologi, anpassade metoder eller tillräcklig mängd av data över tid och platser. Genom att använda flera nya molekylära metoder för att studera djurs diet (metabarkodning) och fysiologi (metabolomik och telomerlängd) har jag undersökt älgens anpassningar till sin omgivande miljö över Sverige. Detta har jag gjort genom att analysera ett stort antal blod- och spillningsprover från älg som samlats in under flera vintrar. Jag har också studerat älgars val av livsmiljöer kopplat till temperatur med hjälp av rörelsesensorer som också registrerat älgens kroppstemperatur.

Genom att inkludera perspektiv från Sveriges urfolk samerna, lokalsamhällen och industrier har information om tidigare mänsklig påverkan som förändrat ekosystemen samlats in. Detta har varit grundläggande för att förstå de hot som renskötsel och älgars vandring står inför i dag.

Genom att studera det ökade trycket på markanvändning som särskilt påverkar en sameby kunde jag se att renskötsel och renbete hindras eller är

omöjligt på 34 procent av samebyns totala yta. Jag identifierade gruvdrift som den huvudsakliga orsaken till den förändrade markanvändningen i området. Gruvdriften var starten för en rad olika faktorer som påverkat området; skogsbruk, turism, vägar, järnväg, stadsbyggnad och omlokaliseringar som följt efter 1900-talets början. För att kunna hålla antalet renar på en jämn nivå får renskötare i dag slakta och sälja färre djur, stödutfodra och sköta sin hjord mer intensivt än de historiskt gjort.

Genom att använda nya metoder har jag också tagit fram ny kunskap om älgens biologi. Jag fann att: 1) Älgen anpassar sin diet efter vad som finns tillgängligt. Till exempel kan älgen specialisera sig på att äta tall, björk, sälg/asp, eller en blandning. Dessa specialiseringar påverkar koncentrationen av olika nyckelmetaboliter som indikerar hur älgen mår. 2) Älgar i fjäll- och kustlandskap och i södra delar av Sverige svälter mer och är mer stressade än älgar som lever i brukade tallskogar. 3) Jag kunde också urskilja metaboliter som skiljde sig åt mellan könen hos älg, och kunde visa att älgtjurar börjar den stränga vinterperioden med mindre energireserver än älgkorna på grund av brunsten. 4) Älgens kroppstemperatur är kopplad till aktivitet och omgivande temperatur. Kroppstemperaturen varierar mellan kön, områden och säsonger, med de mest uttalade skillnaderna i norra Sverige, där säsongsvariationerna är dramatiska. Älgar i sydliga områden utsätts för varma temperaturer under långa perioder, något som leder till att de tvingas göra avvägningar mellan att hitta lämplig föda och att inte bli överhettade.

I min forskning har jag kunnat peka ut områden där djuren är särskilt sårbara, då jag i min analys fokuserat på både små och stora skalor (över tid och platser) som inte tidigare undersökts. Mina resultat tyder på att älg och ren kan drabbas av ökad stress och svält om deras livsmiljöer fortsätter att förändras i nuvarande hastighet. Oförutsägbara effekter på både individ- och populationsnivå kan förväntas om våra nordliga ekosystem fortsätter att förändras i samma takt.

Denna studie bidrar med ny kunskap till utvecklingen av robusta vetenskapliga konsekvensanalyser. Den kombination av verktyg som jag använt möjliggör en bedömning av både nuläge och den påverkan som finns på djurs livsmiljöer, även utanför mitt studieområde. Detta angreppssätt är anpassat för att underlätta beslutsprocesser i konflikter kring markanvändning mellan industri och nomadiserande boskapsskötsel som globalt står inför många utmaningar.

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♡

Umeå, 1 February, 2021.

Appendix

Figure A1. GPS-collared moose (top; photo credit: Navinder J. Singh) and dead moose in the regionally typical mountain birch (*Betula pubescens*) forest of the montane capture area close to Nikkaluokta, Sweden, in late February.

Figure A2. Top: Laevas RHC's summer pasture in Alesjaure in the Kiruna Mountains, Sweden. The Sámi village of Alesjaure and an associated pen for reindeer round-ups are visible in the distance. Bottom: A group of Laevas RHC's reindeer are walking across a waste rock pile of the Kirunavaara mine next to the town of Kiruna, Sweden (photo credit: Niila Inga).
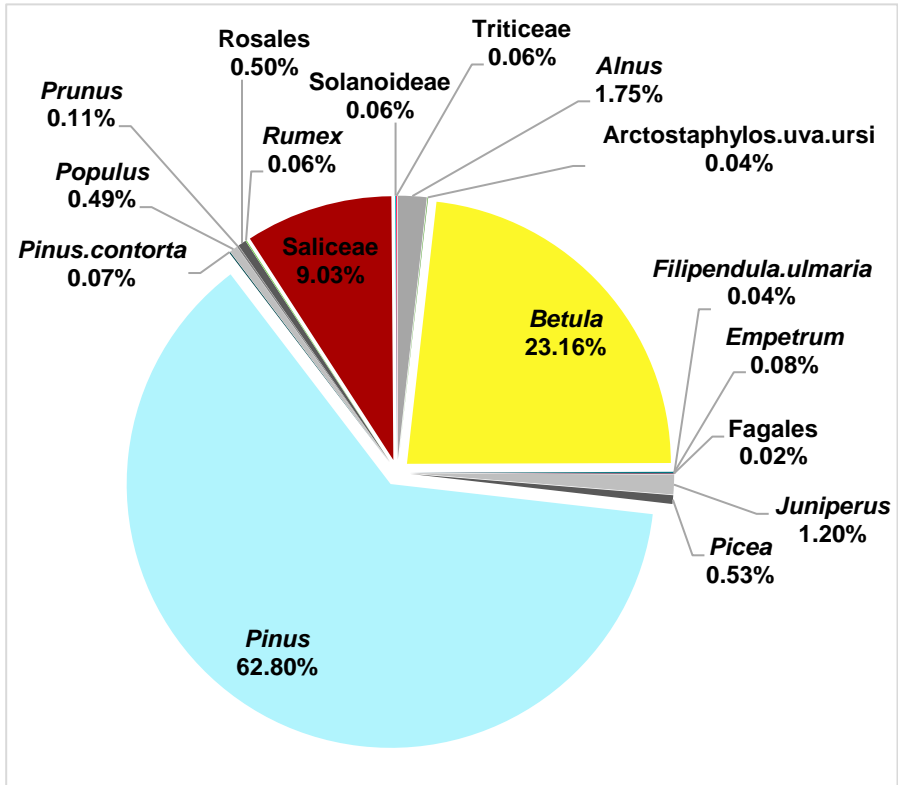
Figure A3. Total number of winter diet items (17 MOTUs) and their proportion determined via DNA-metabarcoding from moose faecal pellets across northern Sweden.
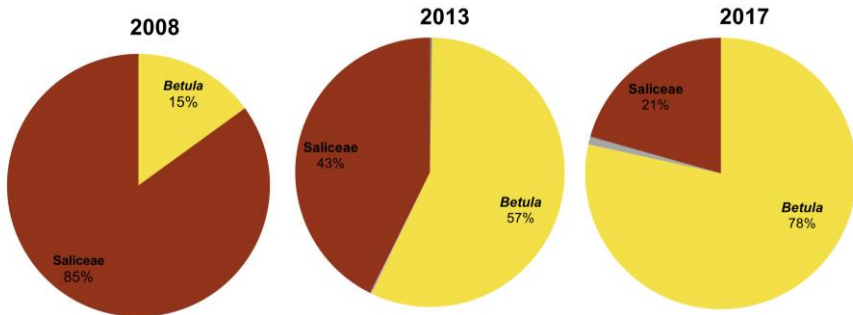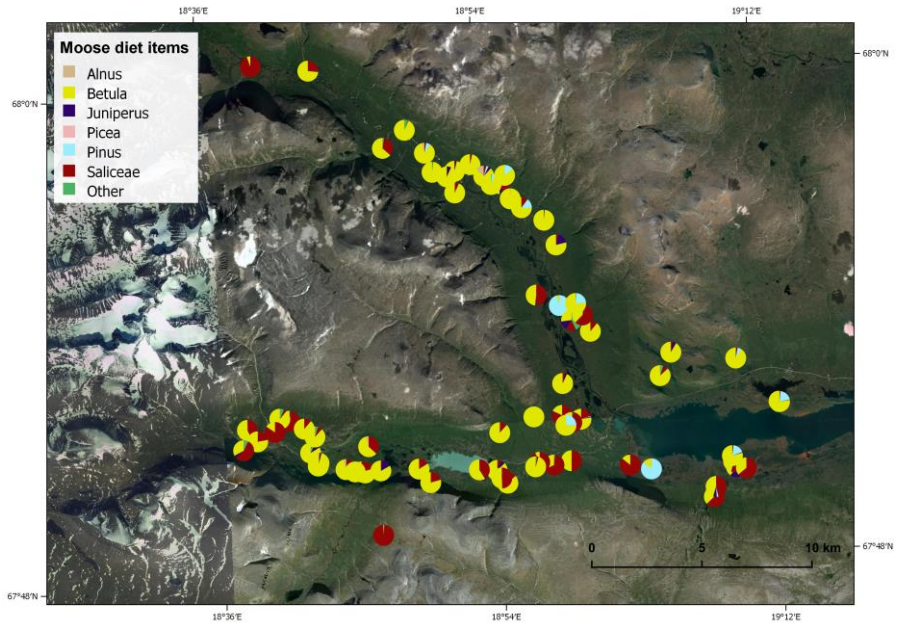
Figure A4. Top: Moose winter diets in two mountain valleys in the montane ecoregion of northern Sweden. Diet composition is based on capture locations across multiple years. Bottom: Winter diet of an individual female from this montane capture area that was sampled in 2008, 2013 and 2017.
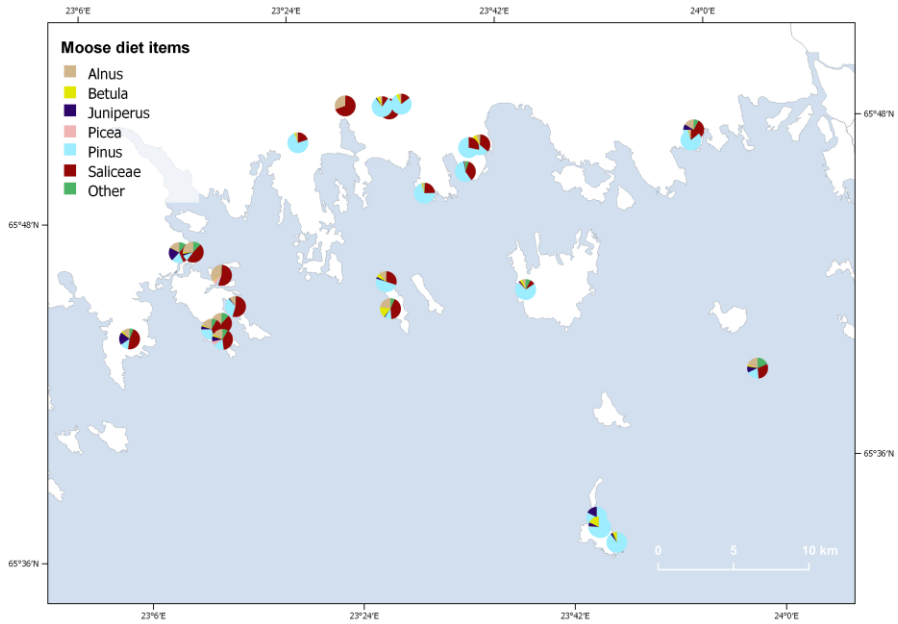
Figure A5. Moose winter diet compositions in the coastal capture area with highest diet diversity (top) and a boreal capture area inland with lowest diet diversity (bottom).

Figure A6. Moose browsing damage documented in early March on Scots pine (*Pinus sylvestris*) in the boreal ecoregion in northern Sweden (top) and on willow (*Salix* sp.) within mountain birch (*Betula pubescens*) forest in the montane ecoregion (bottom).