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Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Anne Elizabeth Loosen

Spatial ecology of moose (*Alces alces*) in a dynamic world

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PhD Thesis

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Sammendrag

Denne avhandlingen tar for seg noen av de viktigste utfordringene for hovdyrforvaltning i det 21. århundre: arealbruk som bidrar til økt fôrproduksjon, rekolonisering av naturlige predatorer, klimaendringer og utfordringer ved overvåkning av bestander som beveger seg over store områder. Mer spesifikt så har jeg fokusert på beiteøkologi og variasjoner i habitatbruk i tid og rom hos elg (*Alces alces*), vår største herbivor med sirkumboreal utbredelse.

Problemstillingene i avhandlingen var å 1) evaluere hvordan områder med høy predasjonsrisiko, som innenfor ulverevir og nær veier, påvirker beitetrykk fra elg, i tråd med teorier om «fryktens landskap»; 2) evaluere om elgtilpasset skogbruk kan brukes til å redusere konflikter rundt beiteskader; 3) evaluere variasjonen i elgens bruk av ulike områder med varierende vintre over en nord-sør gradient; 4) evaluere kilder til usikkerhet og feil i overvåkningsmetoder av hjortevilt og faktorer som påvirker oppdagbarhet. Jeg brukte data på beitetrykk og møkktellinger samlet inn i felt i en gradient fra nord til sør i Norge og Sverige, til å svare på disse problemstillingene.

Jeg fant at små og store veier var en viktig faktor for å forklare variasjon i elgens beiteøkologi i boreale skoglandskaper, og veier hadde større effekt enn tilstedeværelse av ulv. Sannsynligheten for at elgen beitet nær skogsbilveier, var nesten dobbelt så høy i ungskog, sammenlignet med skogtyper som var eldre eller yngre enn 5-20 år. Et økt beitetrykk nær skogsbilveier kan forverre konflikten rundt beiteskader. Jeg fant også lovende tendenser til at elgtilpasset avvirkning (tilrettelegging av hogstavfall) kan redusere beiteskader. Men her er det også behov for studier over lenger tid. Jeg fant at snødybde og vintertemperatur påvirket elgens brukt av ulike områder, elgen brukte områder med lav temperatur mer enn områder med høy temperatur (over 0°C) om vinteren. Jeg fant også at lav oppdagbarhet under elgmøkktellinger, og forskjeller mellom frivillige observatører, kan underestimere tetthet av elg.

I denne avhandlingen har jeg vist viktigheten av menneskelig forstyrrelser, at menneskelig arealbruk påvirker fôrtilgangen til hjortevilt, og at milde vintre kan påvirke de sørlig og nordlige elgbestandene i Skandinavia ulikt. Jeg har også vist at det er betydelig usikkerhet i overvåkningsdata, og foreslår løsninger for å håndtere observasjonsfeil som kan bidra til å forbedre overvåkingen i fremtiden.

Abstract

This thesis focuses on some of the primary challenges to ungulate management in the 21st century: multiple land uses that provide food subsidies, predator recolonization, climate change, and challenges researchers and managers are faced with when monitoring population trends of wide-ranging animals. Specifically, I focus on the feeding ecology and spatial and temporal patterns of the largest circumboreal herbivore, the moose (*Alces alces*).

The thesis objectives were to: 1) evaluate how browsing was influenced in areas with high predation risk, such as where wolves (*Canis lupus*) are present and areas close to roads, in accordance with a landscape of fear; 2) evaluate if ungulate-adapted forestry can be a human-wildlife conflict mitigation measure to reduce browsing damage; 3) evaluate if there was variation in the intensity of use of moose, in response to variable winters and across a large latitudinal gradient; 4) evaluate sources of error associated with a common deer monitoring method. To meet these objectives, I used field-collected data across a latitudinal gradient in Norway and Sweden, primarily via browsing data and fecal pellet group counts.

I found roads were a major driver of moose browsing ecology within the boreal forest landscape, with seemingly greater effects than wolf occurrence alone. Browsing occurrence was nearly double in young forests along low-traffic roadsides, relative to forests older and young than 5–20 years. This represents an increased browsing risk that could exacerbate the moose-forestry conflict in Scandinavia. I also found promising effects of ungulate-adapted logging to alleviate browsing damage, though I expect that increased monitoring over time could show greater differences. I found that snow depth and winter temperature influenced intensity of use of the landscape, with temperatures above 0°C showing a decline in intensity of use. And last, I found detection errors associated with fecal pellet group counts were largely than previously thought and likely underestimates of moose density and abundance.

This thesis advanced our knowledge of the effects of human disturbances, that humans are an important provider of forage to an abundant large browser via land use changes, and milder winters may disproportionately affect Scandinavia's southern moose populations compared to northern populations. This thesis acknowledges that monitoring data are not perfect, and I provide practical solutions to address detection errors to improve future monitoring programs.

Preface

“Every value I’ve ever held is being questioned, and I’m loving it.”

- Maurice Moss

Keywords: *Alces alces*; boreal; climate; detection error; foraging; forestry; habitat; human-wildlife conflict; landscape of fear; management; moose; roads; scale; ungulate; wolves.

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Loosen, Anne E., Olivier Devineau, Barbara Zimmermann, Joris P. G. M. Cromsigt, Sabine E. Pfeffer, Christina Skarpe, Karen Marie Mathisen. 2021. Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia. Ecosphere 12: e03358. https://doi.org/10.1002/ecs2.3358

Paper 2

Loosen, Anne E., Olivier Devineau, Christina Skarpe, Barbara Zimmermann, Joris P. G. M. Cromsigt, Karen Marie Mathisen. 2021. Ungulate-adapted forestry shows promise for alleviating pine browsing damage. Forest Ecology and Management 482: 118808. https://doi.org/10.1016/j.foreco.2020.118808

Paper 3

Loosen, Anne E., Henrik Andren, Joris P. G. M. Cromsigt, Olivier Devineau, Johan Månsson, Laura Prugh, Håkan Sand, Navinder Singh, Aimee Tallian, Fredrik Widemo, Barbara Zimmermann, Karen Marie Mathisen. 2021. Twenty-three years of monitoring reveal disparate winter conditions between northern and southern moose populations in Scandinavia. *Manuscript*.

Paper 4

Loosen, Anne E., Olivier Devineau, Barbara Zimmermann, Karen Marie Mathisen. 2021. The importance of evaluating standard monitoring methods: Observer bias and detection probabilities for moose pellet group surveys. *Manuscript.*

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Introduction

Humans represent 36% of all mammalian biomass on the globe (Bar-On et al. 2018) and are the primary driver of global environmental change (Rockström et al. 2009). This has wide-reaching consequences, from the induction of global warming to the start of the world's sixth mass extinction (Barnosky et al. 2011). The end of the Holocene (11,650 ybp–1950's) and start of the Anthropocene (1950's–present) has seen the decline of many large-bodied mammals such as large herbivores and carnivores (Ripple et al. 2015, Malhi et al. 2016, Linnell et al. 2020).

In contrast to these declines, in some cases, the densities of modern ungulates (i.e., hooved mammals) have surpassed historical densities (Linnell et al. 2020). The high densities of certain ungulate species can be attributed to the synergistic effects of natural predator extinctions or population reductions and intensified agriculture and forestry providing food subsidies (Apollonio et al. 2010). Conflicting demands of wild ungulates and human interests can intensify human-wildlife conflicts.

This thesis focuses on some of the primary challenges to ungulate management in the 21st century: multiple land uses that provide food subsidies, predator recolonization, climate change, and the precision of monitoring data collected by multiple observers. In the following, I provide background information on these challenges in a global and regional context. Specifically, this thesis focuses on the feeding ecology and spatio-temporal patterns of the largest circumboreal herbivore, the moose (*Alces alces*).

Human land use

The boreal forest is one of the world's largest biomes, spreading across northern latitudes in Asia, Europe, and North America with the majority of the boreal forests occurring in Russia (60%) and Canada (28%) (Brandt et al. 2013). Boreal forests are dynamic systems that are naturally driven by fire, windstorms, mammalian herbivory, insect outbreaks, and the subsequent interactions of these various drivers (Brandt et al. 2013). For example, wildfires can be stand-replacing agents of change that influence forest structure, biodiversity, productivity, and species composition (Weber and Flannigan 1997). Despite being generally of poor productivity, the goods and services provided by boreal forests make them highly valuable for provisioning timber, pulp wood, fresh water, minerals, and wild-harvested food, as well as regulating climate, flood, and disease (Brandt et al. 2013).

But, a global human population of 7.8 billion people places a heavy resource extraction pressure on even remote boreal ecosystems, with about two-thirds of boreal forests under some form of land management, primarily for wood and timber production (Gauthier et al. 2015). This has led to the loss of mature and old growth forests, and the proliferation of young and mid-age forest stands (i.e., contiguous area of trees that are uniform in species composition, structure, and age), which are often low in biodiversity and provide a smaller set of ecosystem services. This also represents a shift from boreal forest structure and diversity being determined by natural drivers such as fire, to anthropogenic drivers such as commercial forestry. The situation in the boreal is likely to become more dire as boreal biomes are undergoing the most rapid land use change second only to the tropics (Soja et al. 2007, Hansen et al. 2013).

Scale

Boreal forests are dynamic, where processes operate at several spatial and temporal scales. Indeed, spatial scale is a critical component to most ecological questions (Johnson 1980, Senft et al. 1987, Boyce 2006). A foraging ungulate, for example, moves within its geographical range (1st order), establishes a home range (2nd order), and within that home range may make seasonal movements, selecting feeding patches (3rd order), individual plants and parts of the plant to eat (4th order; Johnson 1980). Finding the scale at which wildlife behaviors operate has been a primary research topic in ecology for the past decades and remains relevant today.

Indirect effects of predator recolonizations

Throughout the 19th and 20th centuries, many countries eradicated top predators. In North America, the removal of bears (*Ursid* spp.), big cats, and wolves (*Canis lupus*) symbolized the ‘taming’ of the landscape. Throughout the world, it was, and still is, common to place bounties on predators to incentivize the public to eradicate carnivores. This loss of carnivores has resulted in devastating direct and indirect effects: large carnivores remain threatened globally (Ripple et al. 2014) and some ungulate densities have surpassed historical levels. Indeed, humans are the top super-predator (Worm 2015, Smith et al. 2017, Mysterud et al. 2020) and today many ungulate and predator populations are regulated via legal harvest. However, social tolerance for predators is slowly changing as seen with the recovery of wolves (Boyce 2018). In Europe, for example, there are now an estimated 17,000 wolves (Linnell et al. 2020).

Top predators can have direct, lethal consequences (consumptive effects; Figure 1) to prey (Gasaway et al. 1992, Messier 1994). But prey can also perceive predation risk and increasingly, the behavioral effects of predation risk are shown to influence a variety of prey behaviors such as foraging in space and time, vigilance, patch use, diet, and habitat selection (Brown and Kotler 2004, Winnie and Creel 2007, LaManna and Martin 2016). This is commonly termed the 'landscape of fear', which is defined as the spatial variation in prey perception of predation risk (Gaynor et al. 2019) (Figure 1).

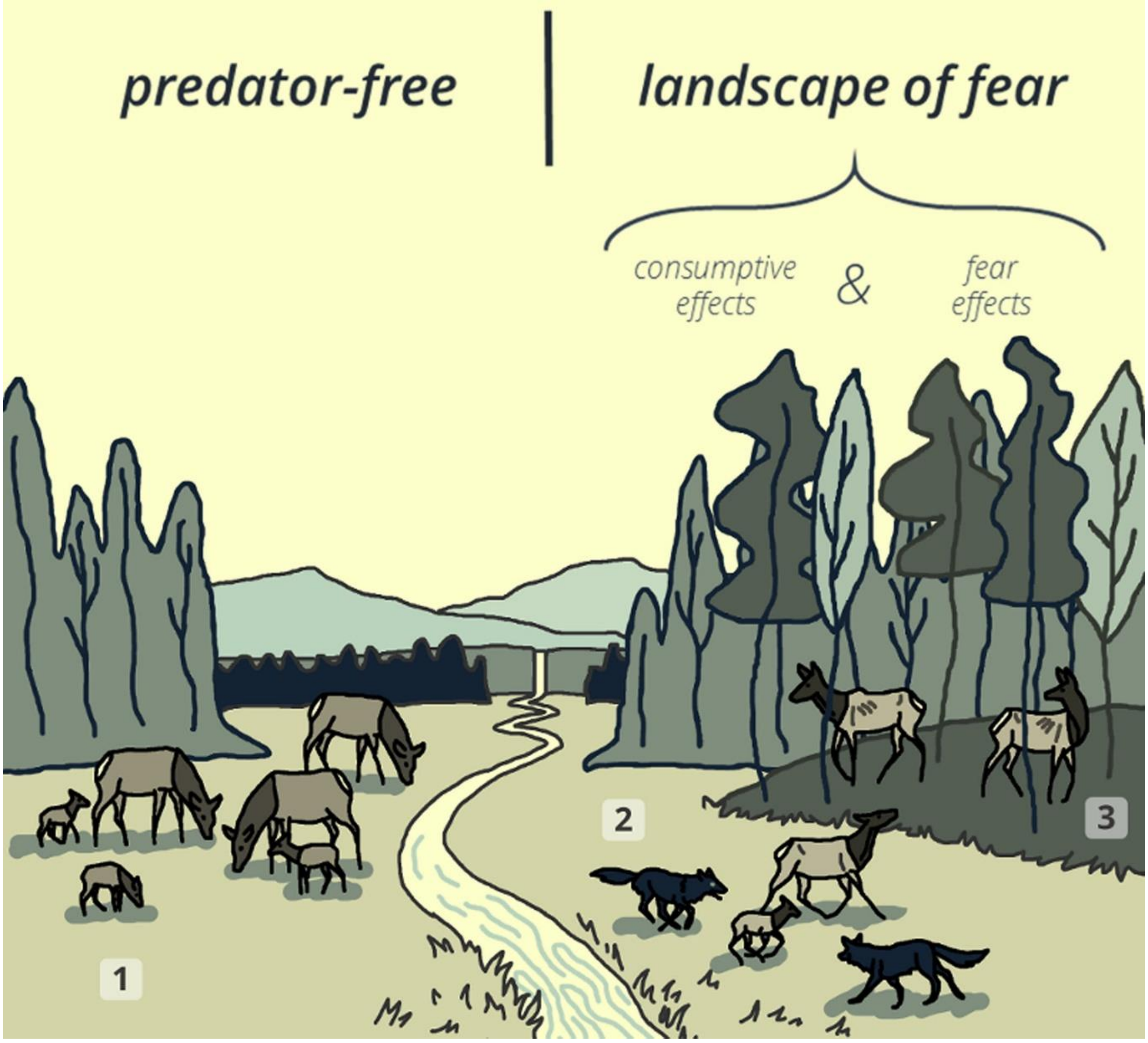


Figure 1. A diagram illustrating the limiting potential of consumptive and fear effects of predation on prey populations; 1) under no predation, prey can select higher quality habitat, forage at higher rates and have lower stress levels which leads to higher reproduction, survival and densities. 2) In the presence of predators, prey suffer higher mortality in high quality habitat and 3) increased fear of predators can result in prey moving to poorer habitat to avoid predators, or increased vigilance and chronic stress levels resulting in higher starvation and/or reduced reproductive output. The net result is reduced prey abundance through decreased survival and reproduction. Figure and caption text is adapted from Peers et al. 2018 and is reused with permission by John Wiley and Sons.

Climate change

Climate change is a threat to biodiversity and ecosystems across the globe (Parmesan et al. 2003). Changing temperatures and precipitation patterns can increase the phenological mismatch between plants and their consumers at multiple trophic levels (Kudo and Ida 2013), can cause shifts in habitat use to accommodate a changing thermal or food landscape (Post and Stenseth 2011, van Beest and Milner 2013, Jennewein et al. 2020), and can even result in altered distribution ranges.

For cold climate adapted species, climate change represents a particular challenge. Moose (*Alces alces*), for example, are a cold climate adapted ungulate species with a global northern distribution (Hundertmark 2016). During winter, moose enter a period of hypometabolism to reduce energy expenditure during a food-limited time of the year (Græsli et al. 2020b). When winter temperatures increase (e.g., > -5°C), moose can go into thermal stress (Renecker and Hudson 1986), which can lead to decreased feeding rates to decrease body temperature (rumination can increase body temperature), or a shift to cooler microhabitats such as mature forests where canopy cover acts a thermal buffer. At larger spatio-temporal scales, climate change will interact with forestry, for example shifting which species can grow when and where, and with forage quality, shifting what forage is available for ungulates. This shift is already occurring with the global “greening” (Boisvenue and Running 2006, Zhu et al. 2016).

Challenges with monitoring data

To manage populations that are subject to the changes described above, we need reliable monitoring data. Methods to calculate density and abundance, for example, have a long history in ecology, such as census counts and distance sampling or capture-mark-recapture methods when the entire population cannot be censused (Witmer 2005). However, calculating density and abundance is expensive, especially for wide-ranging, cryptic, or low-density populations (Woodruff et al. 2018). Instead, population or activity indices are often used whereby indirect observations (e.g., track surveys, pellet counts, food removal) are assumed to be proportional to density or abundance. Too often, population indices are used without validation steps to identify sources of error or bias (Witmer 2005). As well, there is an increased reliance on volunteer-collected data.

Scientific data is increasingly being collected by citizen scientists. Citizen science, the involvement of citizens in scientific research and knowledge production (Cretois et al. 2020), allow researchers and managers to collect data across spatio-temporal domains that would otherwise be too costly to collect (Tulloch et al. 2013, Buesching et al. 2014, Cretois et al. 2020). This is a growing field because of the availability of ‘free’ labor. Yet, these data have trade-offs such as observer bias as a result of (in)experience, the ease of implementing the sampling regime, and the spatial bias of data (i.e., clustering of data around urban areas or in parks and protected areas; Geldmann et al. 2016). There is new emphasis on validating the quality of citizen science data (Clare et al. 2019, Cretois et al. 2020) but this step is not universally applied and not enough is done to quantify potential biases.

Moose in Scandinavia: The role of land use, predator recolonization, climate change, and monitoring challenges

The primary challenges outlined above are important to Scandinavian moose management, which are outlined below.

Human land use

The Scandinavian peninsula, particularly in Sweden, is characterized by widespread and intensive commercial forestry. Until the mid-20th century, selective logging was the primary timber removal method (Berg et al. 2008). Industrialization of commercial forestry in the 1960’s and 70’s changed this, with clearcuts increasing the land surface area affected by timber removal. Forestry has replaced natural disturbances (e.g., fires, windstorms) as the primary driver of land use change. Forestry has thus influenced the age structure of boreal forests in Scandinavia: at the turn of the 20th century older forests dominated, but more recently younger forests dominate (Östlund et al. 1997). This had direct and indirect effects on ungulates. For example, the industrialization of forestry changed the foraging landscape as young pine thrived in newly created clearcuts, and pioneering species like silver birch (*Betula pendula*), downy birch (*Betula pubescens*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) were systematically removed. This increase in forage availability, as well as a shift in moose harvest strategy via sparing of reproductive females, contributed to an increase in moose density in the 1980’s and 1990’s, resulting in some of the highest moose densities across the globe (Lavsund et al. 2003, Jensen et al. 2020). This is a large shift from the early 1900’s in Scandinavia when moose were relatively rare (Figure 2; Dressel et al. 2020). Now the modern management situation in Scandinavia is defined by human-driven land use change, and high ungulate densities which are regulated via human hunting.

Along with high moose densities, however, comes abundant moose-forestry conflicts. Browsing damage is a primary management issue in Scandinavia (Lavsund et al. 2003).

Economic losses because of intensive browsing and subsequent browsing damage have resulted in conflicts between forest owners, who prioritize timber production, and moose hunters, who harvest on average 115,000 moose annually in Norway and Sweden. Efforts to reduce browsing intensity usually involve reducing ungulate densities but the effectiveness of this measure depends on the temporal and spatial scale. If management areas are smaller than an ungulate population, source/sink dynamics, seasonal migration, and compensatory behaviors (e.g., increased fecundity) will counteract intended management goals. I define a population as a group of individuals of one species that occupy a specific area, and where gene flow occurs between individuals (Begon et al. 1996). Other measures to mitigate the negative effects of intensive browsing previously included supplementary and diversionary feeding (van Beest et al. 2010, Mathisen et al. 2014). However, due to the detection of novel diseases in Scandinavia, supplementary feeding becomes a riskier management action. For example, chronic wasting disease was detected in Norway's wild ungulates (Stokstad 2017) and the intentional feeding of ungulates was recently banned (Mysterud et al. 2019).

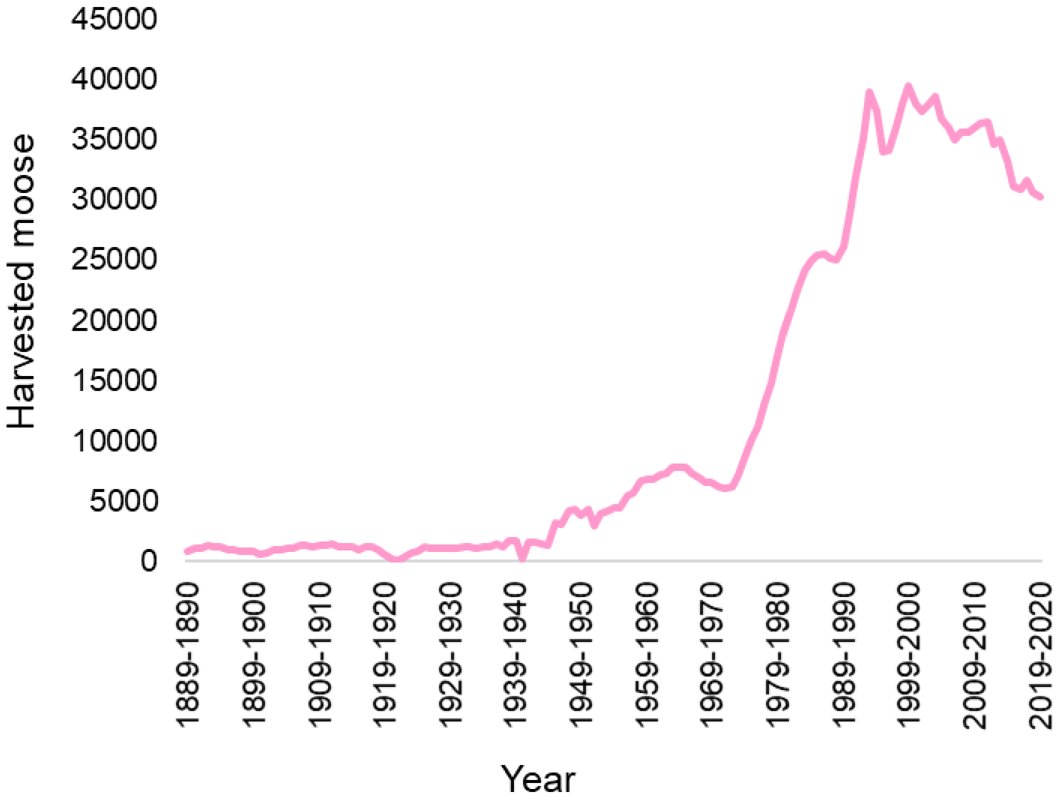


Figure 2. The number of harvested moose by year in Norway. Data were downloaded from Statistics Norway.

Predator recolonization

By the mid-20th century, wolves were functionally extinct in the Scandinavian. With legal protection in 1966 and 1972 in Sweden and Norway, respectively, wolves began to move south and west from Russia. The first reproductions were documented in the 1970's and 80's, signaling the slow return of wolves to Scandinavia (Wabakken et al. 2001). Today, wolves number around 400 (credible intervals 392–412) with 310 individuals in Sweden and 91 individuals in Norway (estimates for autumn 2017; Bischof et al. 2019). Poaching and active management via hunting and culling are the primary mortality factors for wolves (Liberg et al. 2020). Wolves prey on neonate moose calves in the spring and early summer, and moose are the main prey of wolves throughout the year (Swenson et al. 2007, Sand et al. 2008, Zimmermann et al. 2015). Like wolves, brown bears (*Ursus arctos*) have also recolonized Scandinavia after near extinction (Swenson et al. 1995). Bears prey on neonate moose calves in early summer but are not active during winter months (Swenson et al. 2007). Wolverines (*Gulo gulo*) and Eurasian lynx (*Lynx lynx*) also occur in our study area but they rarely prey on moose. Because this thesis focuses on the winter season, I focus on wolves only.

Climate change

In Scandinavia, snow cover duration is projected to decrease by 30–40% by 2050 (Callaghan et al. 2011), the growing period is increasing (Kohler et al. 2006), and surface warming is widely documented (Harris et al. 2003). Warming effects are expected to have greater temperature and precipitation increases during winter compared to summer (Post and Stenseth 2011). Indeed, plant community effects are already being seen: shrubs are expanding northward and upwards in elevation (Bret-Harte et al. 2002, Hallinger et al. 2010, Elmendorf et al. 2012) which could expand moose foods into alpine and northern latitudes, leading to an ecological opportunity for moose in Scandinavia. However, winter warming events can damage shrubs resulting in reduced summer growth (Bokhorst et al. 2009). Of concern, winter warming events are projected to nearly double in northern Scandinavia into the 21st century (Vikhamar-Schuler et al. 2016).

Climate-induced effects on ungulates are already seen in Scandinavia. Warm winter temperatures have been linked with ungulate population declines and reduced body size (Post and Stenseth 2011). For moose, ambient temperatures drive fine-scale habitat selection, and moose must sometimes choose between thermoregulation and forage accessibility (Van Beest et al. 2012), thus providing limitations on individual fitness. Interspecific interactions between expanding ranges of less cold-tolerant ungulates (e.g., fallow deer [*Dama dama*]) are expected to bring novel interactions, particularly regarding disease, which could have negative consequences to moose. Warming winters in Scandinavia could thus have deleterious fitness and demographic consequences to moose.

Challenges with monitoring data

Ungulates are wide-ranging and the data needed to monitor and manage them can be demanding. A simple and 'cheap' method to monitor ungulate populations is via fecal pellet group counts (Neff 1968). Pellet groups are counted at fixed transects or plots, and their relative abundance is monitored over time. This method is widely used in Scandinavia. For example, in central Sweden, pellet group counts (hereafter, pellet counts) are used to supplement observed moose ('sett elg') to help set moose harvest quotas (Bergström et al. 2011). For research, pellet counts are used to estimate relative and absolute density and abundance to relate to relevant research questions (Månsson et al. 2011, Edenius et al. 2015, Zimmermann et al. 2015, Pfeffer et al. 2018). Without known detection errors or habitat biases, estimates based on pellet counts could underestimate density or be biased in certain habitat types. Additionally, many projects rely on volunteers or inexperienced students to collect annual data, which potentially injects additional unknown sources of error.

Thesis objectives

My thesis addressed the following research objectives.

Forestry has created a high-density network of secondary roads. Roads can contribute to a 'landscape of fear' (Laundré et al. 2001) and there is often a trade-off between predation risk and food supply (Schmitz 2005) and ungulate prey move to vegetative cover in response to predators (Mysterud and Østbye 1999, Creel et al. 2005). Thus, we can expect that the spatial effects of predators on ungulate browsing patterns will be altered due to predator movements. In paper one, I asked: ***was moose browsing reduced in areas with high predation risk, such as where wolves were present and areas close to roads, in accordance with a landscape of fear*? *Was the tradeoff between risk and foraging modified by forage value?***

At each stage of intervention in commercial forestry, actions are taken to optimize timber or pulp production. Here I investigated if 'ungulate-adapted forestry' can be an additional step added to optimize ungulate forage availability. I tested two methods which increase forage availability as part of 'ungulate-adapted forestry': ungulate-adapted slash piles (short-term increases) and intensive soil scarification (long-term increases). In paper two, I asked: ***can ungulate-adapted forestry alter moose browsing ecology and forest damage?***

Temperatures are increasing at a faster rate at higher latitudes (Trenberth et al. 2007) and the boreal forest is among the most threatened biomes in response to climate and land use change. We know little about how wildlife in the boreal forest are responding to this change, particularly large herbivores. In paper three, I asked: ***does ambient temperature, snow depth, and forest type drive moose intensity of use across a latitudinal gradient and over time?***

For harvested species, monitoring data are particularly important to assess population trends, yet evaluation of the quality of monitoring methods and data are rare. In paper four, I asked: ***What were the detection probabilities of a common moose density index and what were the primary variables leading to detection errors?***

Methods and results

Study area

The studies in this thesis occurred across a large latitudinal gradient in Norway and Sweden (Figure 3), with elevation ranging from 1–725 m above sea level. The area generally experiences cold, snowy winters and short, cool summers, though winters are less severe in the south relative to the north. Human density also follows a north-south gradient, with southern areas more densely populated relative to the north. Land cover is dominated by boreal forests in the north, and hemiboreal forests in the south (Ahti et al. 1968), both of which are managed for timber and pulp production. Production forests typically undergo one or two thinning events to optimize commercial tree densities. Mature trees are harvested in clearcuts, resulting in a mosaic of even-aged patches or stands of trees (Axelsson and Östlund 2001, Rytter et al. 2014). Regeneration occurs from planted trees or naturally from seed trees. Secondary road density is higher (mean road density 8.5 km/km^2) than primary road density (mean road density 2.7 km/km^2; Sweden road data from lantmateriet.se; Norway data from geonorge.no). Road density is higher in the south.

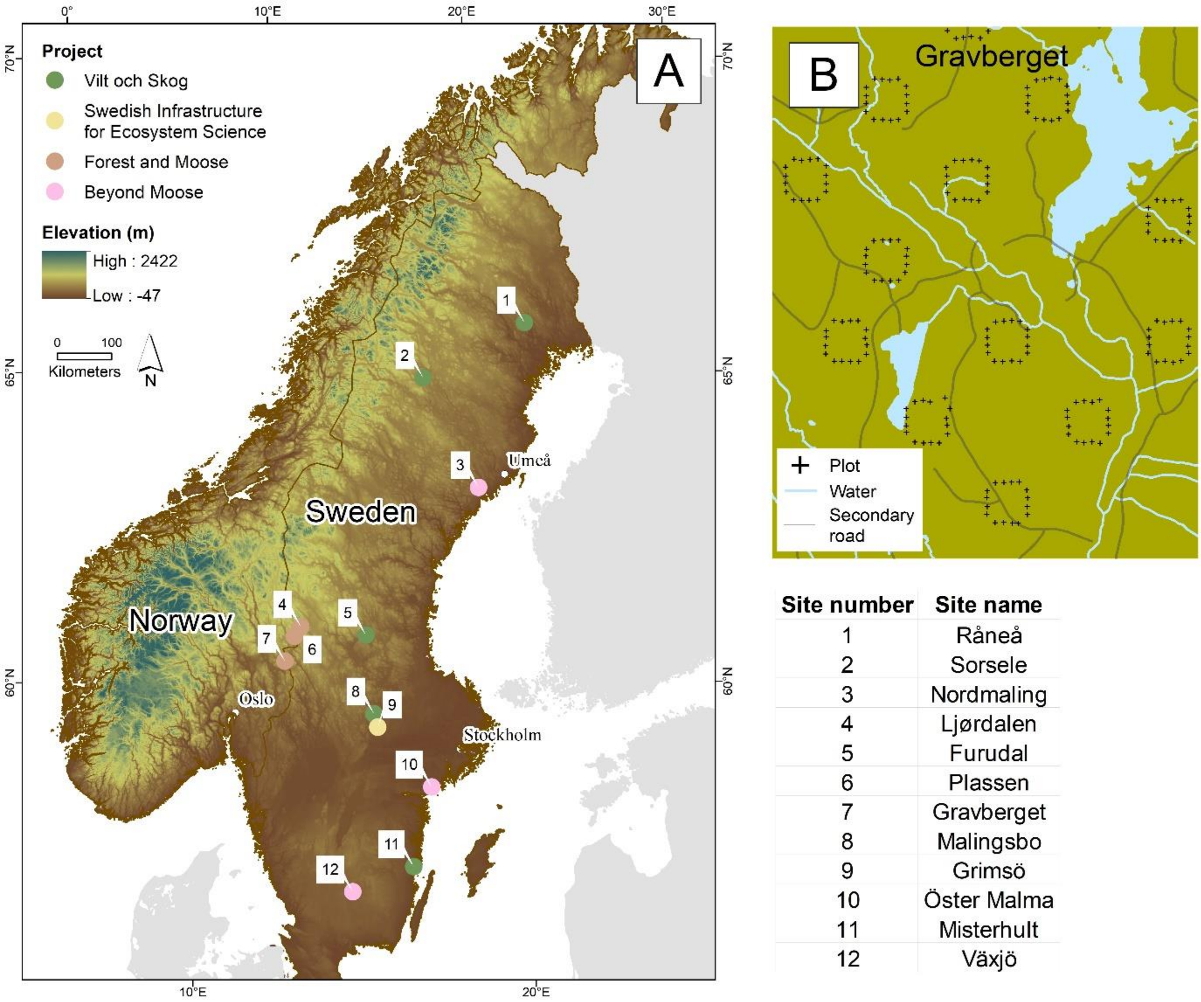
Common tree species include Scots pine (*Pinus sylvestris*), silver birch, downy birch, Norway spruce (*Picea abies*), grey alder (*Alnus incana*), black alder (*Alnus glutinosa*), rowan, goat willow (*Salix caprea*), and aspen. The dwarf-shrub layer is typically dominated by heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), and other Ericaceous species. In boggy areas, *Sphagnum* spp. mosses are dominant (Moen et al. 1998). Generally, rowan, aspen, and willow are highly selected by moose but are rare relative to Scots pine and birch (Shipley et al. 1998, Månsson et al. 2007). Scots pine is a primary food source for moose during winter due to its high abundance whereas spruce is more chemically defended and is rare in moose diets (Cederlund et al. 1980).

Data structure

The data for this thesis were collected during five projects in two countries (Figure 3), span over two decades (1997–2019), and use similar field methods. In Norway, data originated form the project 'Skog og elg' (Forest and Moose). In Sweden, the projects included 'Vilt och Skog' (Game and Forest), 'Swedish Infrastructure for Ecosystem Science' (SITES), 'Fortlöpande Miljöanalys Vilt (FoMa Vilt; Continuous Environmental Analysis of Game)' and 'Beyond Moose' (Figure 3). 'Beyond Moose' was largely an extension of the project 'FoMa Vilt' so we refer only to 'Beyond Moose' for simplicity. The 'Forest and Moose' project adapted their methods from the Swedish methods so data between countries could be compared. Methods used in 'Beyond Moose' and 'FoMa Vilt' were adapted from the 'Game and Forest' project.

Within each project, technicians collected browsing data and deer pellet count data in the spring at systematically placed quadrats (500 x 500 m or 1000 x 1000 m) at 12 sites (Figure 3). Pellet count data have been shown to represent moose habitat use (Månsson et al. 2011), and I use the terms 'habitat use' (papers one to three) or 'intensity of use' (paper four) throughout the thesis. Additionally, because pellet counts are conducted in the spring, they represent winter-time use (i.e., from leaf-fall to snowmelt). Along each quadrat border, four circular plots (100 m^2 each) were positioned every 100 or 200 meters.

The papers included in this thesis cover different spatial extents, from all sites in Norway and Sweden (paper three), all sites except Grimsö (paper one), to only Norwegian sites (papers two and four). We include different aspects of ungulate ecology in each paper.



Site number	Site name
1	Råneå
2	Sorsele
3	Nordmaling
4	Ljørdalen
5	Furudal
6	Plassen
7	Gravberget
8	Malingsbo
9	Grimsö
10	Öster Malma
11	Misterhult
12	Växjö

Figure 3. Map of A) study sites in Norway and Sweden (n = 12) and B) the nested design, where plots are nested within quadrats. Site numbers in the table correspond to site numbers in map A.

Methodology and results: Papers 1–4

Paper 1: Roads, forestry, and wolves interact to drive moose browsing behavior

Methods

For this analysis, I used moose pellet groups counts and browsing pressure at all sites except Grimsö (site number 9; Figure 3). I used the number of pellet groups to represent the time animal(s) spent in a plot (Månsson et al. 2011) and term this ‘habitat use’. I created also the probability of wolf territory and wolf territory presence variables based on snow tracking data, scat/DNA collection, and occasional VHF/GPS tracking (Liberg et al. 2012, Wabakken et al. 2018).

I modeled the presence of browsed trees (browsing occurrence) as well as browsing pressure (ratio of browsed to available shoots per tree) for four browse species: Scots pine, silver birch, downy birch, rowan. I expected moose would browse in areas close to secondary roads due to increased forage quantity and quality. However, because wolves use secondary roads, I expected ungulate browsing occurrence and pressure would decrease close to secondary roads when the probability of wolf territory occurrence was high; I expected highly selected tree species to be of greatest value to ungulates; hence ungulates would accept greater risk to attain them relative to species of lower selectivity. Thus, we expected a weaker effect of roads and wolves when ungulates browse highly selected species, relative to less selected ones. We refer to ‘quality’ as an index based on food selection ranks following Shipley et al. (1998; rowan > silver birch > downy birch ≥ Scots pine).

Results

I found browsing patterns, and their respective drivers, varied by tree species (Figure 4). Wolf territory presence and probability were positively related to an increase in browsing occurrence and pressure for all species. For rowan, the two-way interaction of secondary roads : wolf presence showed that browsing occurrence increased further from secondary roads when wolf territories were present, whereas the opposite occurred when wolf territories were absent (Figure 5). For Scots pine, browsing occurrence was twice as high in young forests relative to non-young forests and decreased with distance from secondary roads. I also found that browsing occurrence decreased closer to primary roads but increased closer to secondary roads. There are many secondary roads in Scandinavia, and even more to be built. I assert that forest and wildlife managers need to consider how an increasing network of secondary roads facilitates intensive moose browsing.

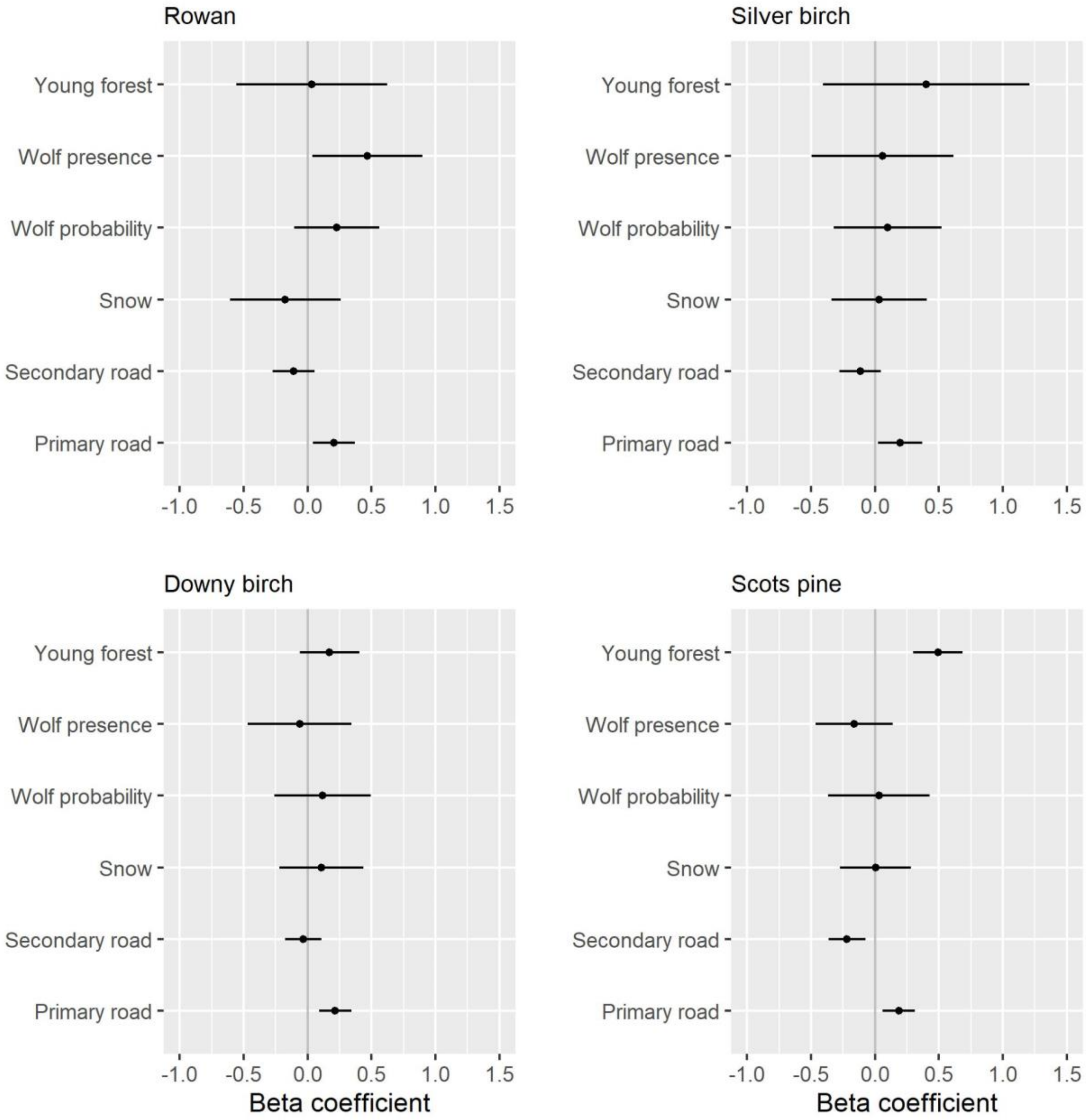


Figure 4. Forest-plots of model-averaged main effect coefficients from browsing occurrence models. Reference categories for binary variables (wolf presence, young forest) are 0. Models were fit with data from Norway and Sweden (2008–2019). Bars represent 95% confidence intervals.

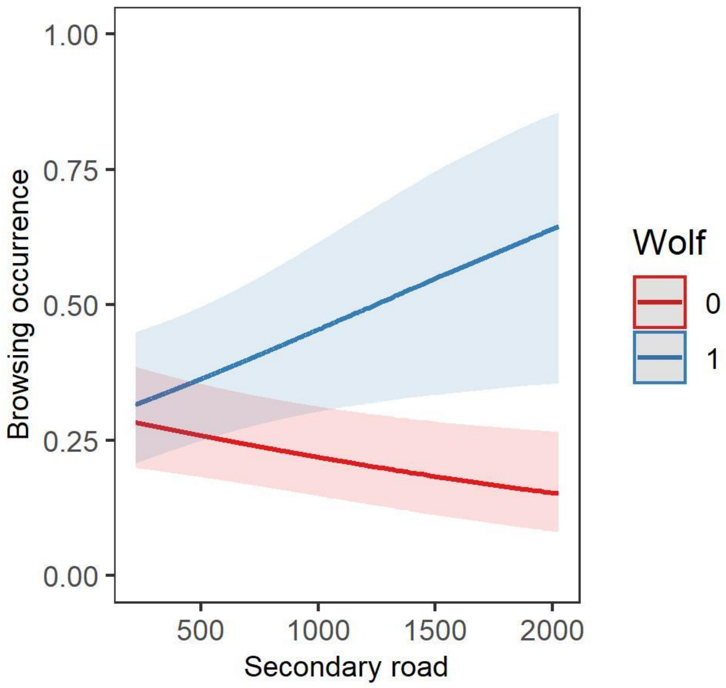


Figure 5. Prediction plot for the interaction secondary road : wolf from the top-ranked rowan browsing occurrence model. Wolf territory absence = 0 and presence = 1. Low road values (in meters) are close to secondary roads while high values are far from secondary roads. Models were fit with data from Norway and Sweden (2008–2019). Ribbons represent 95% confidence intervals.

Paper 2: Ungulate-adapted forestry shows promise for alleviating pine browsing damage

Methods

Formal evaluations of human-wildlife conflict mitigation methods are lacking, especially testing the scale at which mitigation measures are relevant to wildlife. I tested the effect of two mitigation measures on moose browsing behavior and damage to Scots pine: 1) ungulate-adapted slash piles, which included only Scots pine, (Figure 6) created during felling to increase short-term forage availability and 2) intensified soil scarification to increase long-term forage availability (collectively, 'ungulate-adapted forestry'). I evaluated the effects of ungulate-adapted slash piles and intensified scarification on the density of undamaged Scots pine, moose bite diameters, browsing pressure, and moose fecal pellet density. To assess the effect of spatial scale, I created 250 m, 500 m, and 1000-m radius buffers centered on each plot at only the Norway sites (site numbers 4, 6, 7; Figure 3).

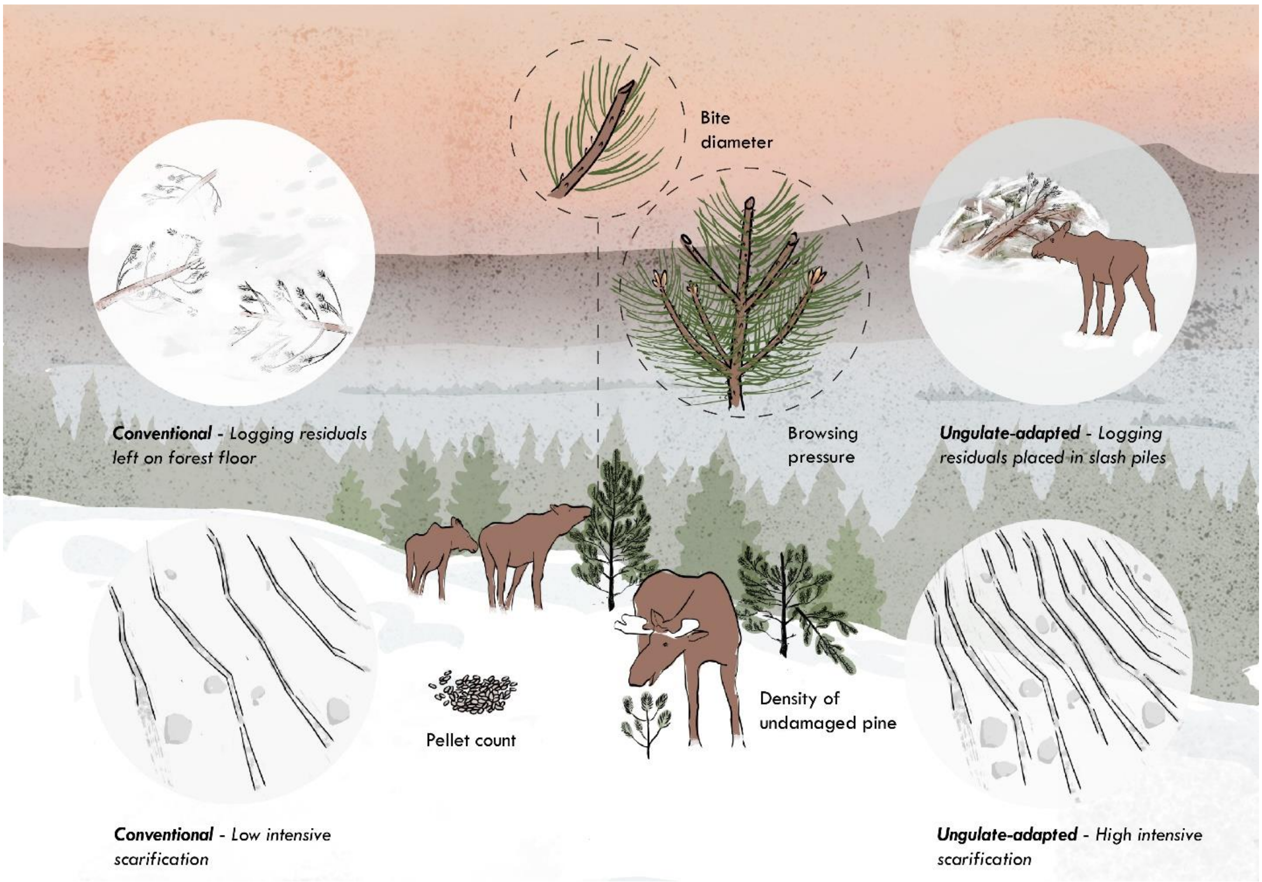


Figure 6. Overview of the experimental study design in paper two. The four response variables (bite diameter, browsing pressure, density of undamaged pine, moose habitat use) are pictured at center. The conventional and ungulate-adapted logging and scarification treatments, which occurred at varying distances from plot centers, are featured at left and right. Illustration by Heidi Loosen (loosenstudio.net).

Results

I found that ungulate-adapted logging increased the density of undamaged pines, as compared to no and conventional logging (Figure 7). I found that logging in general led to smaller bite diameters. I also found that plots near conventional logging had higher browsing pressure, whereas browsing pressure near ungulate-adapted logging was similar to unlogged stands. For scarification, density of undamaged pine increased when the ungulate-adapted stand aged whereas undamaged pine decreased as conventional scarification stands aged. Browsing pressure showed a response at the smallest spatial scale only for ungulate-adapted soil scarification. Peak moose habitat use near conventional and ungulate-adapted scarified stands differed by stand age and distance from scarification. The overall effects of ungulate-adapted forestry were most pronounced at the smallest spatial scale (250 m). My results support ‘ungulate-adapted’ forestry as a practical solution to mitigate browsing damage but uncertainty in some of our estimates suggest further research on the area treated is needed.

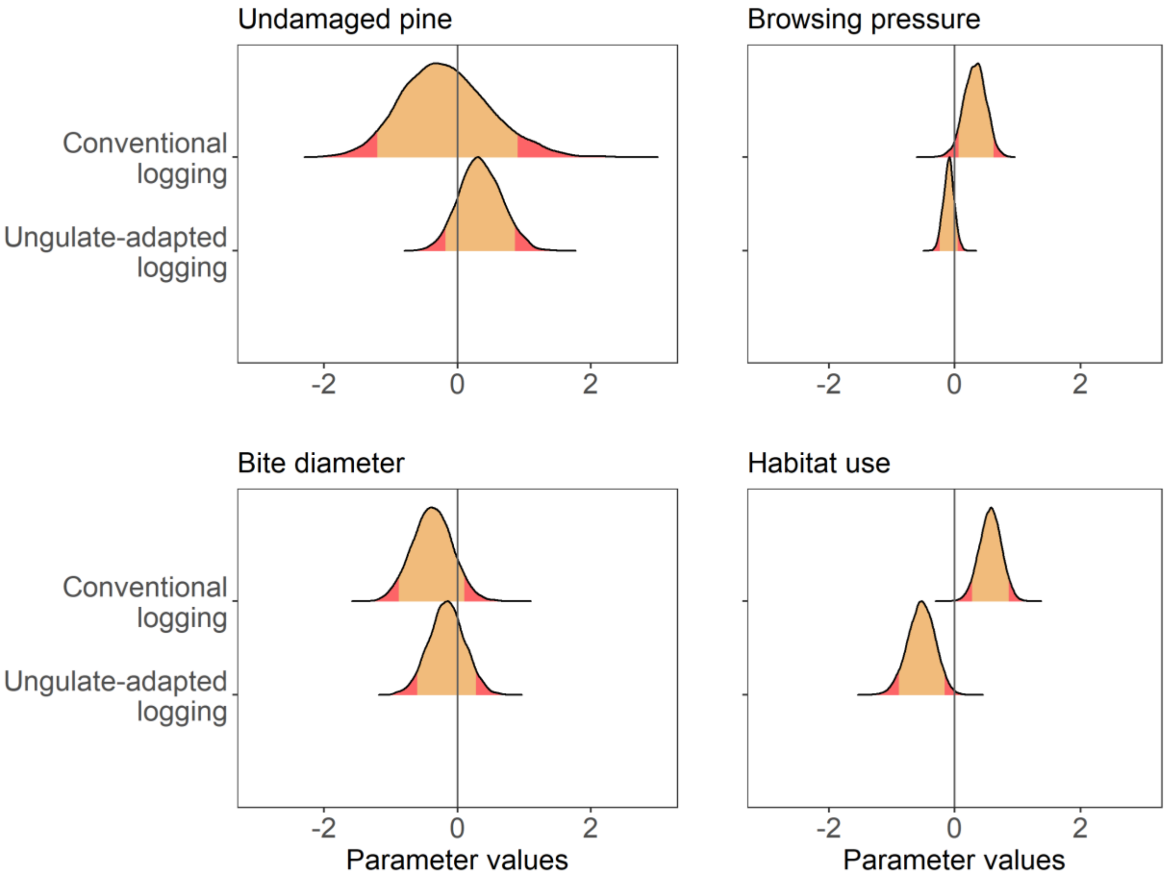


Figure 7. Posterior probability distributions for presence of conventional (top) and ungulate-adapted logging (bottom) across four response variables. Posteriors are from 250-m buffer models. Highest density intervals (HDI) are drawn at 90 (orange) and 100% (red). Models were fit with data from Norway (2011–2019).

Paper 3: Twenty-three years of monitoring reveal disparate winter conditions between northern and southern moose populations in Scandinavia

Methods

I explored trends in two decades (1997–2019) of winter pellet count data. Specifically, I tested the forest maturity hypothesis, whereby mature forests give moose the behavioral flexibility to rest and dissipate heat when ambient temperatures are warm, and avoid deeper snow in open areas. I used data from all sites (Figure 3) to explore if temperature, snow depth, and forest type drive moose intensity of use across a latitudinal gradient. Work by Månsson et al. (2011) showed that pellet counts can be an unbiased representative of moose habitat use when compared with moose GPS collar data. For my study, I adopted similar terminology but utilized ‘intensity of use’ instead as we were not exclusively evaluating habitat. I created annually and spatially varying snow depth and winter temperature covariates and associated these with pellet count data at the quadrat scale (Figure 3). I also extracted moose harvest density the year prior to pellet counts as a proxy for moose density. The tendency to migrate (Singh et al. 2012, Allen et al. 2016), snow depth, and temperature are correlated with latitude. As such, I split the data into northern and southern moose populations to understand how weather influences annual variation in moose intensity of use.

Results

I found snow depth and winter temperature varied by year for northern and southern moose populations. Mean winter temperatures increased over time for both groups, while mean snow depth declined over time only for southern moose populations (Figure 8). For northern and southern populations, I found increases in the intensity of use in response to increasing snow depths, until 20 cm, after which intensity of use declined (Figure 9). Similarly, intensity of use declined as temperatures increased, particularly around 0°C (Figure 9). For the interaction of young forests and temperature, only southern populations showed strong patterns; when the proportion of young forest was high, these quadrats were used more than areas with no or minimal young forest, regardless of temperature. A similar pattern could be seen for the interaction of snow depth and young forests; the intensity of use increased with increasing snow depths at a greater rate when the proportion of young forests was high. I suggest that southern populations may currently be more dependent on thermal cover to withstand to a changing thermal landscape, whereas northern populations might be more flexible in their response to climate change, as they can adjust the timing and duration of migration. However, other studies notes that migration may become a less common strategy for Scandinavian moose as the environment become less seasonal (i.e., smaller differences between winter and summer), more akin to current southern moose population conditions (Allen et al. 2016).

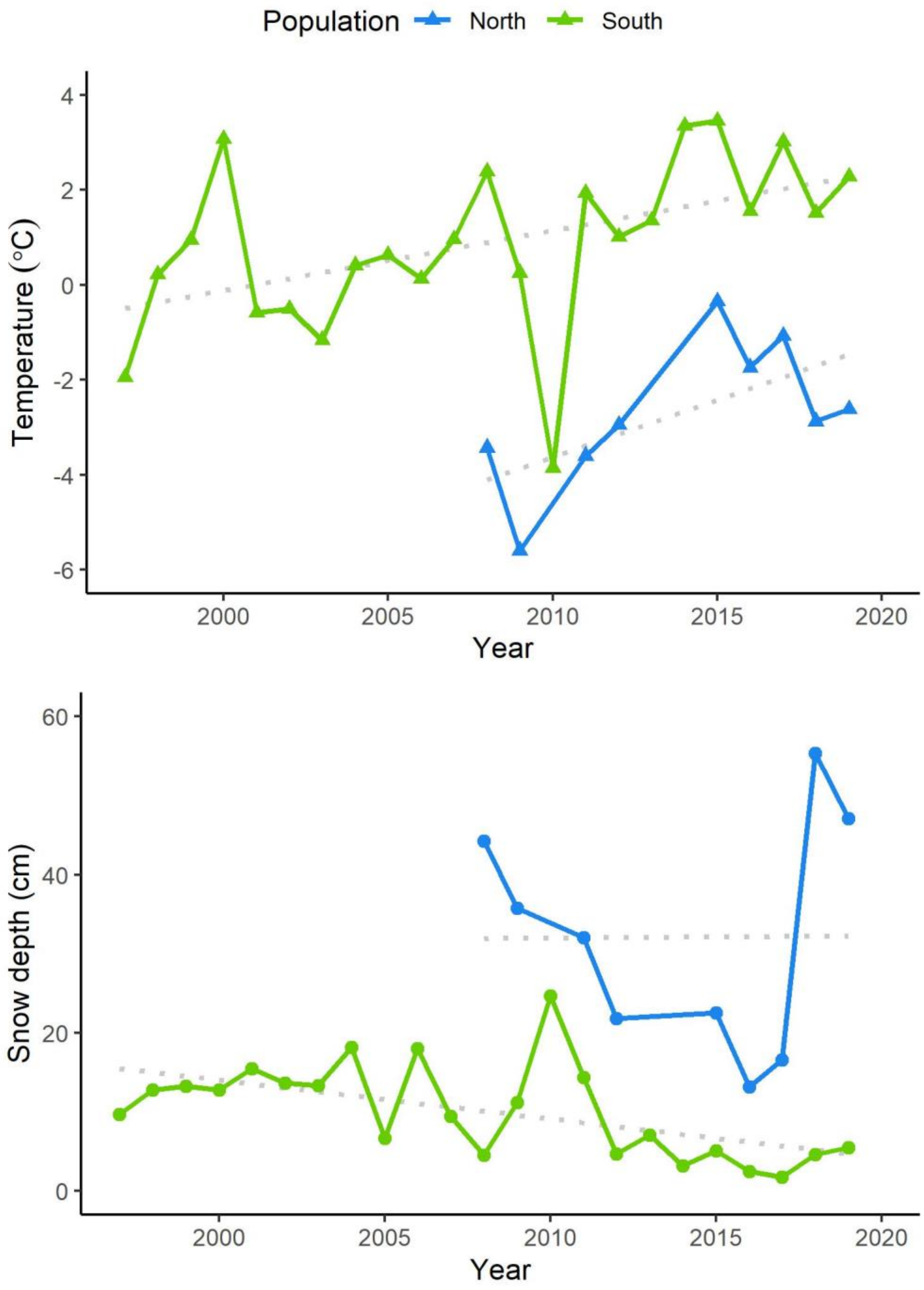


Figure 8. Trends for mean winter temperatures (top) and mean snow depth (bottom) in Scandinavia. The blue and green lines represent data for northern and southern moose populations, respectively. The dotted grey line is a linear trend line. Data were from 1997–2019.

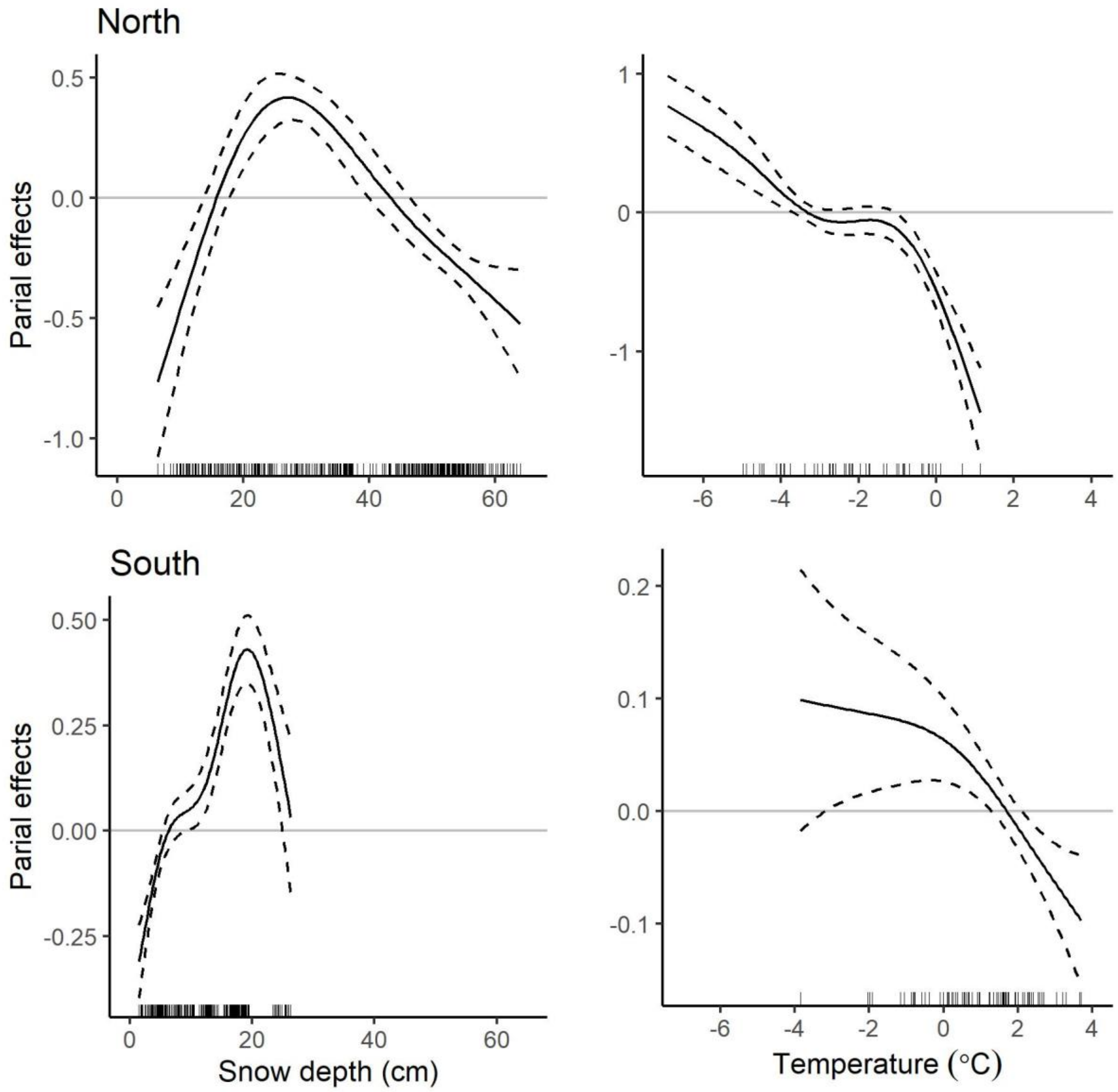


Figure 9. Partial effects of snow depth and temperature on intensity of use for northern (top row) and southern (bottom row) moose populations. Partial effects are the isolated effects of one particular predictor on the response. Dotted lines represent 95% confidence intervals. Hatching (rug) on the x axis represents observed data.

Paper 4: The importance of evaluating standard monitoring methods: Observer bias and detection probabilities for moose pellet group surveys

<u>*Methods*</u>

At a subset of long-term monitoring plots in Norway, I quantified moose pellet group detection errors in Norway using single and dependent double observer survey methods (Jenkins and Manly 2008, Riddle et al. 2010, Powell and Gale 2015). For dependent double surveys, technicians worked in pairs and switched primary and secondary observer roles at every other survey plot. The primary observer surveyed the plot, calling out and pointing to observed moose pellet groups. The secondary observer silently recorded observations. I recorded field variables that could influence detection errors, such as observer experience, weather, and field layer types.

Results

We completed 16% (n = 325) of our long-term monitoring plot as double observer surveys. At these plots, the primary and secondary observers detected the same number of pellet groups in 97% (n = 290) of the plots. However, when pellets were present (e.g., combined observer count > 0) the secondary observer saw additional pellets 42% (n = 40) of the time. Detection probabilities increased with search time and varied by prior observer experience in the field (Figure 10). Detection probabilities were highest for the least and most experienced observers (Figure 10). My results highlight the uncertainties with a standard monitoring method, and I recommend research and management projects complete a subset of plots as double observer surveys to identify and quantify error uncertainties.

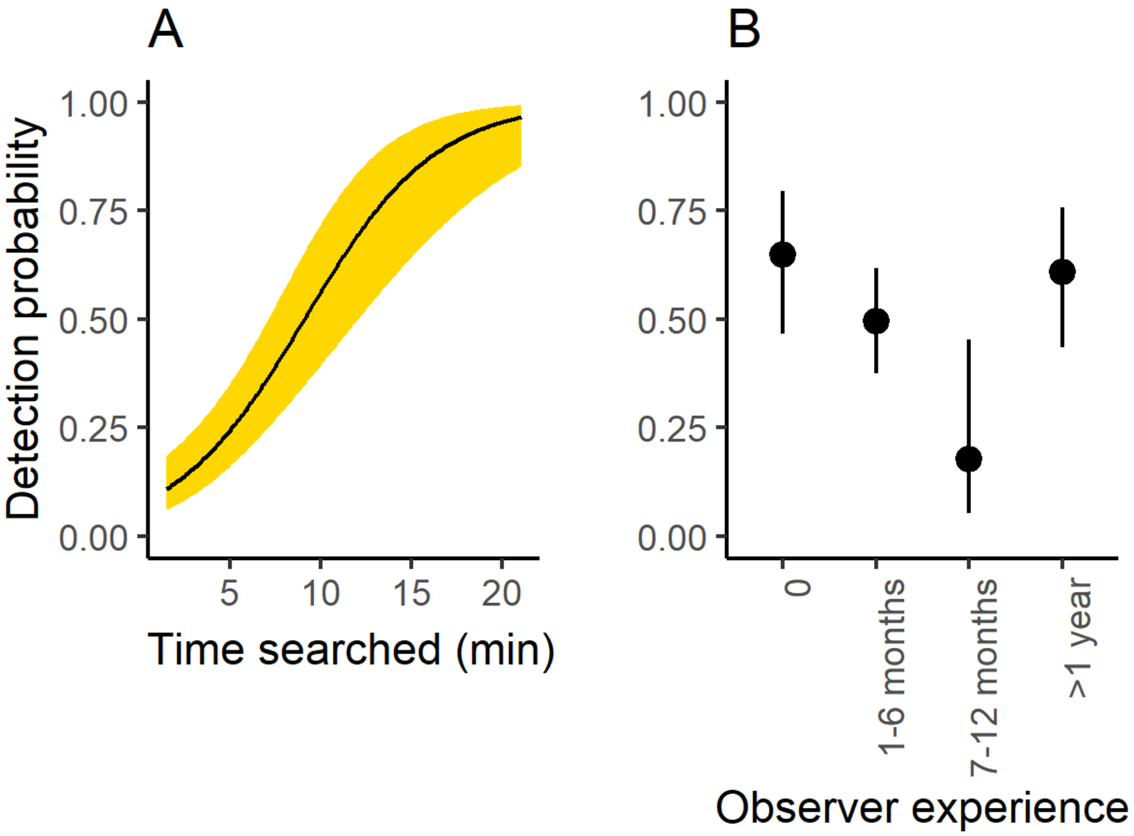


Figure 10. Prediction plots for the effect of A) the time searched in each plot; B) prior observer field experience. Models were fit with data from Norway (2019–2020).

Bringing it all together: A unified discussion

The objectives of this thesis were to evaluate 1) if moose respond to the wolves and roads in accordance with the landscape of fear; 2) if ungulate-adapted forestry can alter moose browsing ecology and forest damage; 3) if ambient winter temperature, snow, and forest type influences moose intensity of use across a latitudinal gradient; and 4) evaluate standard moose monitoring methods. The following discussion attempts to tie these themes and my research findings together.

Land use

Land use changes are projected to be a primary driver of biodiversity loss in the coming decades, with the boreal biome being among the most at-risk across the globe (IPCC 2007). Commercial forestry, one type of land-use change, is a major economy across the boreal. Forage availability, which is highly influenced via different land-use practices, has a strong influence on moose habitat use. Results from my thesis support this. In paper one, I found that browsing occurrence increased closer to secondary roads but decreased closer to primary roads, which might be due to an increased forage availability along secondary roads. Young forests near secondary roads had a browsing occurrence twice as high for Scots pine, compared to other forest ages. In paper two, I found that an increase in forage availability through ungulate-adapted logging increased the density of undamaged stems, decreased habitat use, and decreased browsing pressure on Scots pine.

I showed that forage availability is a strong behavioral driver for moose. This contrasts, however, with how moose are managed, which is primarily via previous years' hunting statistics to mitigate browsing damage levels (Figure 11). Forage availability is often a primary driver of browsing damage whereby with more available food, browsing damage (generally) declines (Pfeffer et al. 2021). If management goals are to maintain high densities of moose for hunting, there should be enough high-quality, natural forage (i.e., the food on the landscape: foodscape) to sustain the high forage demands. A first step to accomplish this would be to monitor foodscape indices and include this in moose management, instead of hunting and browsing damage data only. I propose it is better to manage the ultimate (foodscape), rather than the proximate (browsing damage), drivers for mitigating moose-forestry conflicts (Figure 11). There is currently no system for this in Norway. Sweden uses 'foodpro' (forage prognosis in forestry) but is not well implemented into the management system. This could be improved across both countries.

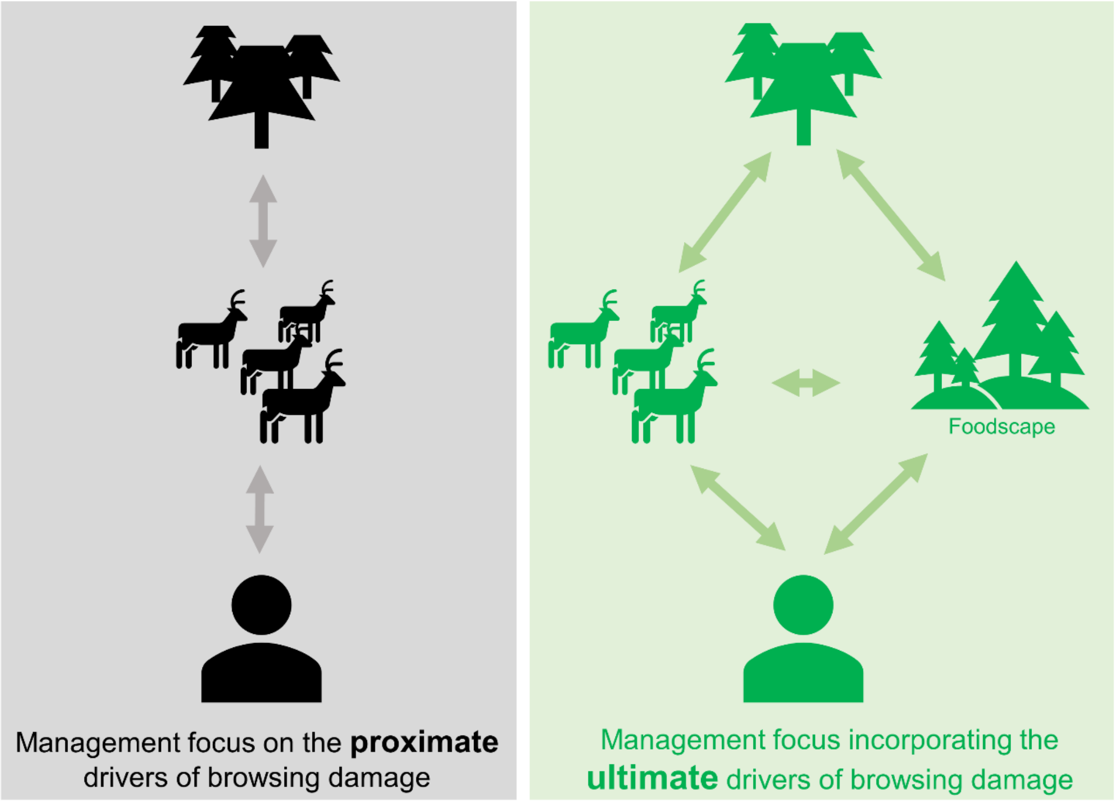


Figure 11. Illustration of the proximate and ultimate drivers of browsing damage. In the grey box, humans directly mediate ungulate densities via hunting. Ungulate browsing may result in browsing damage. I suggest focus should shift to management of food quality and availability (i.e. the foodscape), as this is the ultimate driver of browsing damage (green box). Humans regulate the foodscape via changes in land use (e.g., clearcutting). Increased forage availability generally reduces browsing damage. Note there are two-way arrows since ungulates can shape their foodscape, as well as respond to it. Similarly, humans regulate ungulate densities, but ungulates can influence humans (e.g., disease, human-wildlife conflicts).

While young forests provide high quantities of browse for large browsers like moose, this is a catch-22, as the young forests may then become hot spots for browsing damage. However, there is emerging support for diet complementarity (Simpson et al. 2012, Felton et al. 2016, 2020, Nielsen et al. 2017) where a balanced diet intake of carbohydrates, fiber, and proteins, thus not just quantity, determine fitness. For example, Felton et al. (2020) found that moose calf diets rich in deciduous trees (i.e., higher quality) were associated with higher body mass than a diet dominated by conifers. More research is needed on how the entire food landscape, not just the commercially valuable species, influences moose behavior and fitness.

Historically, one common method to deal with insufficient quantities of natural forage was to provide supplemental food (Geisser and Reyer 2004, Sorensen et al. 2013, Jones et al. 2014, Mathisen et al. 2014, Milner et al. 2014). Diversionary feeding was also used to move animals away from sensitive areas, such as young forests, high traffic roads, or agricultural fields (van Beest et al. 2010, Rogers 2011, Arnold et al. 2018). This type of feeding is increasingly risky, because it promotes concentrated feeding in space and time. Thus, the risk of disease transfer among ungulates is increased (Mysterud et al. 2019). It is important to distinguish between historically common supplementary feeding programs (silage in Norway, silage and sugar beets in Sweden) versus using natural forage in ungulate-adapted forestry. In paper three, I found that ungulate-adapted logging increased the density of undamaged pines. Because ungulate-adapted slash piles provide natural forage in a dispersed manner, the propensity for individuals to congregate is reduced. Ungulate-adapted forestry may be a possible mitigation measure but needs more research to be implemented at larger scales prior.

Mitigating human-wildlife conflicts is challenging since measures do not often occur at large enough spatial and temporal extents (i.e., not big enough, not long enough) (Serrouya et al. 2019). In paper two, while I found hints of a positive effect of our mitigation measures, I suspect our study suffered from this same issue. The possibility of completing an experiment at a larger spatio-temporal extent is only possible with increased collaboration across sectors (research, landowners, forestry, wildlife managers), particularly across administrative and international boundaries. The negative effects of intensive browsing will likely become exacerbated as less cold climate tolerant species move north, increasing competition for forage (Spitzer et al. 2020). This necessitates that wildlife research and management shift from a single species approach (Simberloff 1997), as has been tradition in Scandinavia, towards a multi-species approach (i.e., thinking ‘beyond moose’).

Predator recolonization

Predators can have direct (i.e., mortality) and indirect effects on their prey. This thesis focused on behaviorally mediated indirect effects of recolonizing wolves on moose, their primary prey. I found that moose browsing occurrence increased with an increasing probability of wolf territory occurrence, similar to previous research (van Beeck Calkoen et al. 2018, Ausilio et al. 2021). This counter-intuitive finding could be explained by the fact that wolves align their territories to areas of higher moose densities, or human hunters compensate for wolf presence by reducing moose offtake (Wikenros et al. 2015). Both explanations would result in an associated increase in moose density within wolf territories, which could explain an increased browsing occurrence by moose.

In my research, I primarily detected context-specific behavioral responses of moose to wolves. For example, negative behavioral effects of moose to wolves were only seen away from young forests and secondary roads (Scots pine browsing only). There could be several reasons for finding only context specific responses to wolves. Researchers have suggested that moose may be “naïve” to wolves as predators (Berger et al. 2001, Sand et al. 2006, Nicholson et al. 2014, Månsson et al. 2017). In North America, wolves were never extirpated from the moose’s distribution, or only for short periods (e.g., 40–50 years), whereas moose in Scandinavia have lived without or with very low populations of large carnivores for 120–150 years. Because of this carnivore-free period, moose could have relaxed their aggressive anti-predator response in favor of a flee response (Berger et al. 2001, Sand et al. 2006).

Another explanation for only finding context-specific responses could be as result of the disproportionately large effect of humans on moose mortality. Indeed, annual moose offtake by hunters in wolf territories in Scandinavia is 2.4–3.5 times higher than that from wolves (Zimmermann et al. 2019). Further, moose are hunted with dogs in Scandinavia. Hunting dogs bark at moose, and hunters are more successful at shooting moose that stand their ground, which is an advantageous anti-predator response to wolves. However, it is the fleeing moose that often escape human hunters and may be favored in selection. Further, moose that were experimentally hunted with dogs increased resting time after encounters with dogs, thus decreasing time available for foraging, implying a fitness consequence for moose that escaped harvest (Græsli et al. 2020a).

Climate change

We are seeing a poleward shift in wildlife distributions and shifting movement patterns in response to a changing climate and resource distributions (Parmesan et al. 2003, Hickling et al. 2006). Chen et al. (2011) found a poleward shift of a diversity of taxonomic groups at a median rate of 16.9 kilometers per decade. In Scandinavia, we are seeing a poleward shift of red deer (*Cervus elaphus*) and fallow deer, as winters become warmer and less snowy. This increase in species complexity has resulted in increased interspecific competition for forage such as *Vaccinium* spp., resulting in a more pine-dominant diet for moose. This could exacerbate browsing damage on young pine forests (Spitzer et al. 2020). Results from paper three support findings of Spitzer et al. (2020) where moose intensity of use of young forests was higher in southern Scandinavia, relative to northern populations, which we speculate could be driven by increased competition from smaller deer.

I found snow depths for northern populations were more than four times higher than southern populations, and snow depths saw a decrease over time for southern, but not northern, populations (Figure 8). I also found that southern moose populations experienced very warm mean winter temperatures, which increased over time (Figure 8). Previous research on captive moose indicated that -5C initiated thermal stress for moose in winter. While my study supports recent findings by Thompson et al. (2020) that previous thermal threshold for moose was likely overestimated. Though we cannot link our pellet data to moose fitness consequences, my findings indicate that the winter weather differences between northern and southern populations might become even greater, leading to possible demographic consequences to southern moose populations. Climate change will create opportunities for some species, and dead ends for other species. Future research may be on triaging certain species for management (Gilbert et al. 2020).

Monitoring challenges

Reliable monitoring data are important, particularly for highly valued species such as moose. While counting individual specimens, for example, is thought to be a simple exercise, it is perhaps not as simple as it seems (Elphick 2008). For example, Prater (1979) found observers counting birds from photographs (i.e., true values known) consistently overestimated when counting small groups of birds but underestimated when counting large groups. Pellet counts, a common method for monitoring deer density and population trends, often underestimate density because pellets go undetected due to vegetation and insufficient survey efforts (MacKenzie and Kendall 2002, Buesching et al. 2014).

We completed a subset of long-term monitoring plots as dependent double observer surveys to quantify sources of potential errors. Even though nearly half of the observers did not have prior field experience, similar to citizen science projects, the use of two observers allowed us to quantify detection probabilities. For example, I found that when pellets were detected by the primary observer, the secondary observer saw additional pellets 42% of the time. This has direct management consequences. In central Sweden (Svealand), pellet counts are used to supplement observed moose (‘sett elg’) to help set moose harvest quotas (Bergström et al. 2011). If we indeed underestimate moose density via pellet counts, harvest quotas may be lower than populations can sustain, resulting in a mismatch between actual densities and management goals.

The keen reader might suggest that the findings from paper four negate findings from the previous three papers, which rely heavily on pellet counts. Papers one to three use pellet counts as an index of use, which is a relative measure, rather than an index of abundance or density. In this way, I was 'conservative' in the application of pellet counts since pellet decay, defecation rates, in addition to detection errors, can influence density and abundance. The bigger question is if I found habitat biases that could result in erroneous conclusions about habitat use. The results from double observer surveys were inconclusive (i.e., many overlapping confidence intervals) as to how detection probabilities varied by habitat type (for more details see paper four). I hope continued data collection via double observer surveys in ours, and other projects, elucidates the connection between habitat bias and detection errors.

Management recommendations

The motivation for much of this thesis stemmed from wildlife and land management issues. There are several recommendations I can make:

- I showed roads can exacerbate browsing intensity, especially for Scots pine in young forests. Forest managers could mitigate this by increasing species diversity in young forest stands close to roads, particularly in areas without wolves.
- Develop a method to monitor the foodscape, and test how to use it in moose management.
- Monitoring data should be verified with quality checks such as double-observer surveys, and understand the sources of error especially when there are many (volunteer) observers.
- Certain stands that are heavily browsed and unlikely to be released out of browsing height could be sacrificed as "browsing lawns" (similar to grazing lawns; McNaughton 1984) or "browsing traps" (Bråthen et al. 2017) (Figure 12). These stands could also be manipulated to improve biodiversity, rather than for timber production. In accordance with reducing disease transfer risk (Mysterud et al. 2019), these types of stands should be large and dispersed to not cause individuals to congregate. While I can imagine this is not an economically feasible approach for small forest owners, larger 'owners' (Sveaskog, Statskog) could experiment with this approach.
- Management can make bigger and bolder moves (Serrouya et al. 2019) to use management as real-life experiments. Often, too little is done and only for a short

period. I showed in paper two that ungulate-adapted logging could alleviate some of the negative effects of intensive browsing. However, our results suggest that more experimentation over a larger area, and over longer time periods, needs to be done.

- More coordinated management and research across borders, particularly international borders. Our study stands out because it utilized data from both Norway and Sweden. But more can be done. We can look to other coordinated management, such as polar bears managed by the U.S. and Russia (107th Congress 2002) and transfrontier conservation areas in southern Africa (Munthali 2007), for examples.

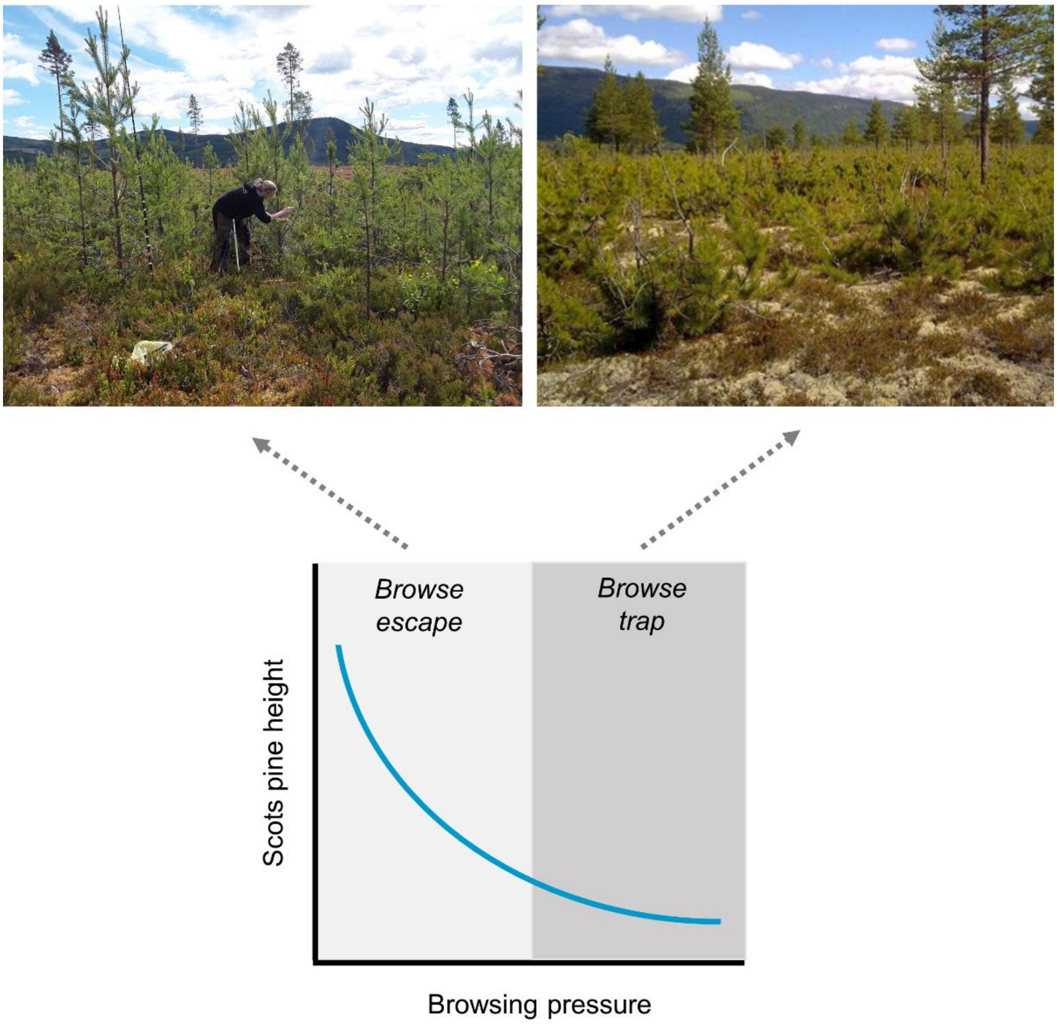


Figure 12. As browsing pressure increases, stands may experience a state shift from 'browse escape', where browse species (e.g., Scots pine) grow beyond moose browsing height (>3 m), to 'browse trap', where browse species remain below browsing height. These areas can also be managed for improved biodiversity. Left photo credit Annie Loosen, right photo credit Floris Smeets. Figure adapted from Bråthen et al. 2017.

Future directions

- This thesis utilized population-level data only, meaning I did not uniquely identify individual moose from pellet counts. While this gives a population ‘average’ and covers a large spatial extent, it is important to understand individual variation within populations (Prokopenko et al. 2016). For example, I recommend exploring the hypotheses in papers one, two and three with GPS collar data.
- More research on how a high-density network of secondary roads influences wildlife in Scandinavia. For example, wind energy development is increasing in Norway and Sweden, but we know little about the multi-scale effects of the turbines and access roads (e.g., habitat fragmentation) on ungulate ecology in Scandinavia.
- Wildlife studies often use satellite-based proxies of food (e.g., Normalized Difference Vegetation Index; NDVI) (Pettorelli et al. 2011) to understand wildlife behaviors. However, these proxies do not work well in boreal systems with dense tree canopies. Future research should focus on creating fine spatio-temporal scale foodscape models incorporating field-collected browsing data, remote sensing data (Kastdalen 2019, Duparc et al. 2020) and fine scale LiDAR data, which can improve estimates of understory cover, which is most important for ungulates (Latifi et al. 2016).
- Browsing pressure can influence standing timber stock. However, longer-term effects of browsing and commercial forestry need to be considered in Scandinavia. For example, how does intensive browsing influence nutrient flows of carbon, nitrogen, and phosphorus? Other studies have shown that large and mega-herbivores can move nutrients against gradients in grazing ‘hot spots’, for example (Le Roux et al. 2020). These will have longer term influences than reduced forage availability or standing timber, particularly in the face of climate change.

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Although I used the pronoun “I” for consistency throughout this thesis, “we” would be more appropriate in all cases.

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Dissertation articles

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esa ECOSPHERE

AGROECOSYSTEMS

Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia

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Abstract. As wild ungulate densities increase across Europe and North America, plant–herbivore interactions are increasingly important from ecological and economic perspectives. These interactions are particularly significant where agriculture and forestry occur and where intensive grazing and browsing by wild ungulates can result in economic losses to growing crops and trees. We studied plant–herbivore interactions in a moose (*Alces alces*)-dominant system where forestry is a primary economy, the primary and secondary road networks are extensive, and wolves (*Canis lupus*) are recolonizing. Wolves and humans use low-traffic, secondary roads, yet roadsides provide high-quality and quantity browse for moose. Foraging theory predicts that moose will respond to riskier landscapes by selecting habitats that reduce predation risk, sacrificing feeding time or food quality. As food becomes limiting, however, animals will accept higher predation risk in search of food. We predicted that road avoidance behavior would be strongest within wolf territories. In areas without wolves, moose should select roadsides for their high forage availability. To test these predictions, we measured moose browsing and counted pellet groups as a proxy for habitat use each spring in Norway and Sweden between 2008 and 2018, in areas with and without wolves and at different distances from primary and secondary roads. We used generalized linear mixed models to evaluate drivers of the probability of browsing occurrence and browsing pressure. We found that browsing occurrence increased closer to secondary roads but decreased closer to primary roads. We also found browsing patterns to vary among tree species. For Scots pine (*Pinus sylvestris*), the browsing occurrence was two times higher in young forests relative to non-young forests and decreased further from secondary roads. Wolf territory presence and probability had neutral or positive effect on browsing occurrence and pressure for all species. However, wolf territory presence had negative effects on browsing occurrence and pressure when interacting with secondary roads, young forest, or snow cover. We showed that roads can influence browsing patterns in Norway and Sweden. However, further research is needed, particularly in the face of continued infrastructure development in Scandinavia.

Key words: *Alces alces*; browsing; forestry; roads; Scandinavia; trophic cascades; ungulates; wolves.

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INTRODUCTION

Predation can have direct, lethal consequences to prey density and abundance (Gasaway et al. 1992, Messier 1994). Prey can also perceive predation risk from predators such as large carnivores and humans. Increasingly, behavioral effects of predation risk are shown to influence a variety of prey behaviors such as foraging, vigilance, patch use, diet, and habitat selection (Brown and Kotler 2004, Winnie and Creel 2007, LaManna and Martin 2016). For prey, there is often a trade-off between predation risk and food supply (Schmitz 2005) and ungulate prey move to vegetative cover in response to predators (Mysterud and Østbye 1999, Creel et al. 2005). Thus, we can expect that the spatial effects of predators on ungulate browsing patterns will be altered due to predator movements (behaviorally mediated trophic cascades; Schmitz et al. 1997).

Predators like wolves (*Canis lupus)* can contribute to the landscape of fear (Beyer et al. 2007, Ripple and Beschta 2012, Kuijper et al. 2013), particularly in protected areas (Hernández and Laundré 2005). However, large carnivores have become threatened globally (Ripple et al. 2014) and humans have a disproportionately large effect (direct and indirect) on wildlife behavior and mortality outside of protected areas. Cascading effects from predators on prey and plant–herbivore interactions (i.e., trophic cascades) have been documented in protected areas (Kuijper et al. 2013). Beyond the boundaries of protected areas, however, humans are the primary mortality factor and long histories of human-managed systems have resulted in reduced spatial landscape heterogeneity (Kuijper et al. 2016). Trophic cascades appear more difficult to elucidate outside protected areas (van Beeck Calkoen et al. 2018), which could have consequences to predator/prey relationships.

The trade-off between predation avoidance and foraging has long been recognized (Sih 1980, McNamara and Houston 1987). Predation and foraging are dynamic processes that vary in time and space, and their effects are context and scale-dependent (Oates et al. 2019). The risk allocation hypothesis states that predation risk and food availability interact: under food-limited conditions, animals will lose fat faster and enter risky areas earlier than in areas with abundant food (Lima and Bednekoff 1999). Thus, as available food declines, animals will accept a higher predation risk in search of food (Sinclair and Arcese 1995). For browsing and grazing ungulates, however, only a small fraction of plant biomass is palatable and easily digested, and there is often a trade-off between food quantity and quality (Felton et al. 2018). Optimal foraging theory predicts that a foraging ungulate aims to maximize net energy consumption (Pyke et al. 1977). Consequently, food items with high nutrient or energy concentration or digestibility (i.e., high quality) would be of greater value to food-limited ungulates relative to low-quality food items. Seasonal constraints such as winter snow cover can drive changes in food availability, which can be population bottlenecks (Nordengren et al. 2003, Wiegand et al. 2008, Coltrane and Barboza 2010). Snow can also increase wolf predation risk because wolves have light foot loads relative to many ungulates, so they are able to catch ungulate prey easier in deep snow (Fuller 1991, Mech et al. 2001). As a result, we can expect ungulates to accept higher predation risk to obtain higher-quality items or seasonally during periods of food limitation.

Roads are among the most pervasive forms of human disturbance on the globe (Fahrig and Rytwinski 2009). Roads can increase habitat fragmentation, reduce gene flow, change species composition, facilitate the spread of invasive and exotic species, and increase wildlife mortality due to vehicle collisions (Pauchard and Alaback 2004, Fahrig and Rytwinski 2009, Holderegger and Di Giulio 2010). For ungulates, roads can also alter predator–prey relationships by increasing predator movements, encounter rates with prey, and prey vigilance levels (Eriksen et al. 2009, Dickie et al. 2017). High-traffic road sides also increase mortality risk from vehicle collisions (Seiler 2005, Laurian et al. 2008*a*, Eldegard et al. 2012). Thus, roads can contribute to a landscape of fear (Laundré et al. 2001), which is defined as the spatial variation in prey perception of predation risk (Gaynor et al. 2019). Yet, roads and road sides are attractive to ungulates because they can provide a human-shield from predators (Berger 2007), create nutrient pools (Laurian et al. 2008*b*), reduce movement costs especially during winter (Parker et al. 1984), and increase access to high-quality food such as young, deciduous trees (Bowman et al. 2010). Because roads represent a trade-off between predation risk and food, we used primary (high-traffic, generally paved roads) and secondary roads (low-traffic, gravel roads) to test the risk allocation hypothesis. We predicted that, in areas with wolves, moose should avoid secondary roads under conditions where food is not limiting. In areas without wolves, moose should select roadsides for their high forage availability. Primary roads should be avoided due to collision risks.

We tested these predictions using a predator–ungulate–forest system in Sweden and south-central Norway where moose (*Alces alces*) are the dominant browsers, wolves are recolonizing portions of their former range (Wabakken et al. 2001), and commercial forestry is the primary land use. Forestry is the primary driver of landscape change in Scandinavia (Swedish Forest Agency 2014), and forest access roads occur at high densities (Sand et al. 2006*a*). Humans are the primary cause of annual moose mortality during a fall hunt (Sæther et al. 1996, Stubsjøen et al. 2000) but moose are the primary prey of wolves year-round (Sand et al. 2008, Wikenros et al. 2009). Interestingly, previous studies have not found a cascading effect of wolves through affecting moose browsing behavior (Nicholson et al. 2014, Wikenros et al. 2016, Månsson et al. 2017).

Moose can damage young commercial trees in the form of apical shoot browsing, bark browsing and rubbing, and stem breakage, which can negatively affect tree growth and morphology (Danell et al. 1994, Bergström and Danell 1995, Wallgren et al. 2013). Browsing damage is largely concentrated during winter when moose may congregate, food availability is reduced, and winter diets are dominated by young Scots pine (*Pinus sylvestris*). Browsing damage has resulted in conflicts between forest owners, who want to sell commercial timber, and moose hunters, who harvest over 115,000 moose annually in Norway and Sweden combined (harvest data from www.ssb.no and www.algdata.se). Here, we investigate how forestry, predators, and roads influence moose browsing behavior, which could have consequences to moose-forestry conflicts.

We aimed to answer two research questions: (1) Is moose browsing reduced in areas with high predation risk, such as where wolves are present and areas close to primary roads, in accordance with a landscape of fear? (2) Is the trade-off between risk and foraging modified by forage value, that is, tree species of different selectivity? We used browsing selectivity rankings from previous literature (Shipley et al. 1998) as a proxy for food quality, and as the basis for our predictions (below) on browsing pressure and occurrence. Previous research has suggested that fine-scale evaluation may reveal a behavioral response by moose to recolonizing wolves (Nicholson et al. 2014). We thus evaluated these questions at the tree level, which corresponds to the fine-scale food selection an animal makes within a foraging patch and represents the fourth order of selection in the hierarchy of selection processes (Johnson 1980). Moose may browse one or two shoots on a tree and continue searching until they find a suitable tree to feed on (Shipley et al. 1998). Thus, we modeled the presence of browsed trees (browsing occurrence) as well as browsing pressure (ratio of browsed to available shoots per tree). We predicted the following: (P1) Moose will browse in areas close to secondary roads due to increased forage quantity and quality. However, because wolves use secondary roads, we expect ungulate browsing occurrence and pressure to decrease close to secondary roads when the probability of wolf territory occurrence is high; (P2) primary roads offer foraging opportunities but they represent an increased mortality risk. Thus, we expect that ungulates will avoid primary roads and browsing occurrence and pressure will decrease closer to primary roads; (P3) we expect browsing occurrence and pressure will increase with increasing snow coverage as the field layer and shrubs are concealed; (P4) we expect highly selected tree species to be of greatest value to ungulates; hence, ungulates would accept greater risk to attain them relative to species of lower selectivity. Thus, we expect a weaker effect of roads and wolves when ungulates browse highly selected species, relative to less selected ones.

METHODS

Study area

Our study area lies between 57.0°–66.4° N and 12.2°–22.2° E in Norway and Sweden (hereafter, Scandinavia; Fig. 1), with elevation ranging from

1 to 725 m above sea level. The area experiences cold, snowy winters (January average temperature −1.9°C; average snow depth 0.2 m; Swedish Meteorological and Hydrological Institute) and short, cool summers, though winters are less severe in the south relative to the north. Land cover is dominated by boreal and hemiboreal forests (Ahti et al. 1968), which are managed for timber and pulp production. Production forests, which are largely coniferous, typically undergo one or two thinning events to optimize commercial tree densities. Mature trees are harvested in clear-cuts up to 1000 ha, resulting in a mosaic of even-aged patches or stands of trees (Axelsson and Östlund 2001, Rytter et al. 2014). Regeneration occurs from planted trees or naturally from seed trees. Forestry has created a high-density network of secondary roads (mean road density 8.5 km/km^2) whereas primary roads are less common (mean road density 2.7 km/km^2; Sweden road data from www.lantmateriet.se; Norway data from www.geonorge.no). Road density is higher in the south (Fig. 1).

Common tree species include Scots pine, silver birch (*Betula pendula*), downy birch (*Betula pubescens*), Norway spruce (*Picea abies*), gray alder (*Alnus incana*), black alder (*Alnus glutinosa*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula*). The dwarf-shrub layer is typically dominated by heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), and other Ericaceous species. In boggy areas, Sphagnum spp. mosses are dominant (Moen et al. 1998). Generally, rowan, aspen, and willow are highly selected by moose but are rare relative to Scots pine and birch (Shipley et al. 1998, Månsson et al. 2007). Scots pine is a primary food source for moose during winter due to its high abundance whereas spruce is more chemically defended and is rare in moose diets (Cederlund et al. 1980).

Since the industrialization of forest management in the 1960s, combined with changes in moose harvest strategies, moose densities peaked in the 1980s and 1990s with local winter densities of 5–6 individuals per km^2 (Lavsund et al. 2003). Average annual moose densities have since decreased and vary across our study area (0.50–2.6 moose/km^2; Sand et al. 2006*b*, Mattisson et al. 2013, Zimmermann et al. 2015, Pfeffer et al. 2018). Moose typically migrate from high-elevation mountainous areas to low-elevation valley bottoms to over-winter, where snow depths are reduced (Sweanor and Sandegren 1988, Bunnefeld et al. 2011, Singh et al. 2012). Assemblages of other ungulates vary across our study area. Roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and red deer (*Cervus elaphus*) have higher densities in the south and along the coast (based on hunting statistics; www.algdata.se and www.viltdata.se). Carnivores include wolves, brown bears (*Ursus arctos*), wolverines (*Gulo gulo*), and Eurasian lynx (*Lynx lynx*). Wolves and bears prey on neonate calves in the spring and early summer, and moose are the main prey of wolves throughout the year (Swenson et al. 2007, Sand et al. 2008, Zimmermann et al. 2015). Wolf density in Scandinavia is lower (0.154 wolves/100 km^2; 95% credible intervals 0.151–0.159; Bischof et al. 2019) than in North America (0.3–5.4 wolves/100 km^2; Mech and Barber-Meyer 2015), yet wolf hunting success of moose is substantially higher in Scandinavia than in North America (Sand et al. 2006).

Data collection

Our data were collected during four projects: Forest and Moose (2012, 2015, and 2018) in Norway, and Vilt och Skog (2008–2009, 2011), Fortlöpande Miljöanalys (2012–2015), and Beyond Moose (2015–2018) in Sweden. All projects had common methods for counting ungulate pellet groups and assessing browsing at fixed monitoring plots. We systematically placed quadrats (500 × 500 m or 1000 × 1000 m) at 11 sites (Fig. 1). Within sites, quadrats were placed at minimum 1 km and maximum 3 km apart. Along each quadrat's border, we placed 16 circular plots every 100 m (Norway and Sweden) or 200 m (Sweden; Fig. 1).

Browsing surveys.—We assessed browsing from circular plots in the spring. Starting with the tree closest to the plot center, we identified the tree species, and counted the number of browsed and unbrowsed shoots from the previous growing season. We defined a shoot as woody tissue >1 cm long. We considered shoots <1 cm to be unavailable to moose because they are too small for processing. The number of available shoots is the sum of browsed and unbrowsed shoots. We registered browsing from the current winter season where browsed shoots were still wet with

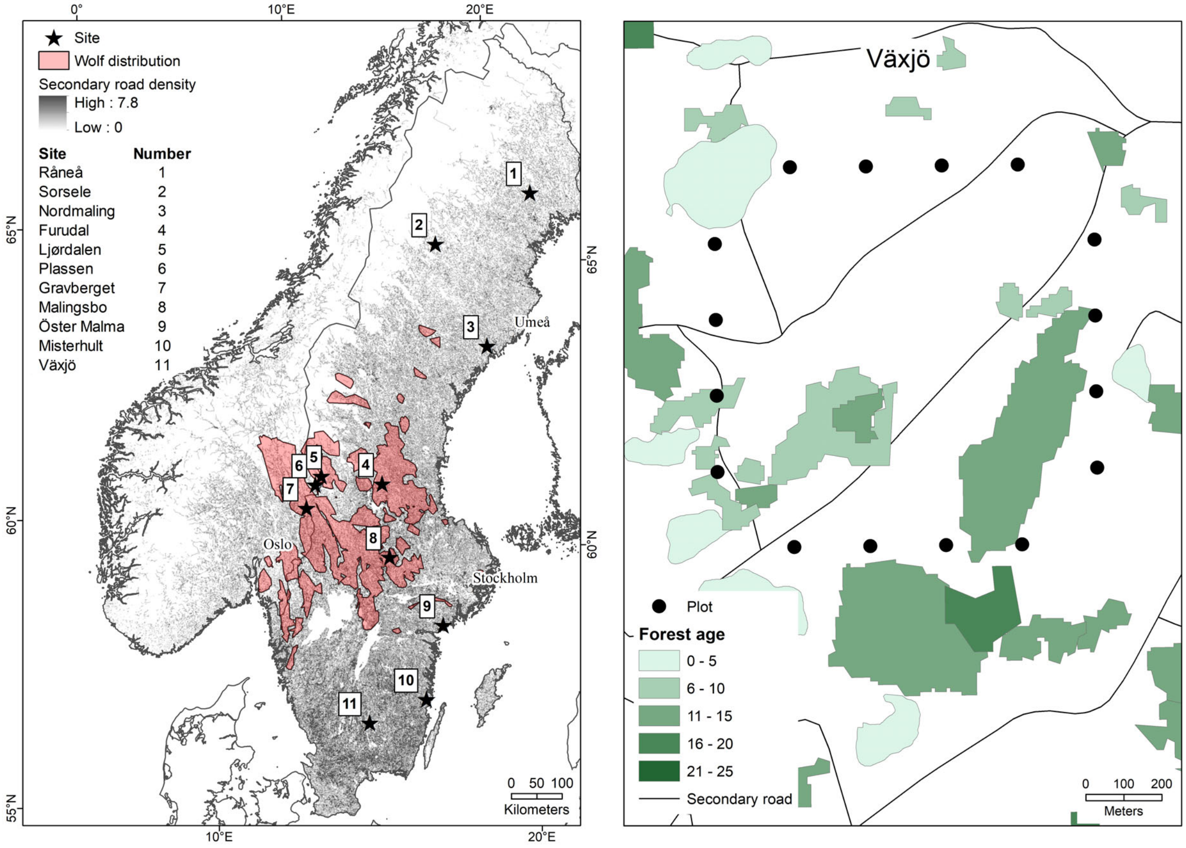

Fig. 1. Our study included 11 sites across a gradient of human-use, predator occurrence (left), and forestry activities (right) in Norway and Sweden. At right, 16 plots lie along the quadrat boundary. Wolf distribution data were derived from annual monitoring surveys (Wabakken et al. 2018). Secondary road density units are km/km^2.

resin, and the wood had not died or become gray (Ball and Dahlgren 2002). We restricted our analysis to trees ≥30 cm and ≤3 m tall to be consistent with field protocols across projects. The lower height represented average winter snow levels below which trees were not available for browsing during winter. The upper height represented the maximum browsing height for moose (Nichols et al. 2015). For the Forest and Moose project, we assessed browsing on up to 10 trees per species in 50-m^2 plots. For Swedish projects, we assessed browsing on one tree per species in 100-m^2 plots. In both cases, we chose trees closest to the plot center. The four common tree species to all project protocols were rowan, downy birch, silver birch, and Scots pine.

Pellet counts.—Because browsing pressure is highly correlated with animal abundance, we counted ungulate pellet groups (Neff 1968) in 100-m^2 circular plots during late spring. We used the number of pellet groups to represent the time animal(s) spent in a plot which Månsson et al. (2007) identified as an unbiased estimator of habitat use. Pellet counts occurred at the same plot center as browsing surveys. Although we were primarily interested in moose habitat use, we counted pellets for all ungulate species present. We identified ungulate species by morphological characteristics of the pellets and the number of pellets per group (Spitzer et al. 2019). To register a pellet group, >50% of the group needed to fall within the plot (Norway) or the center of the group was within the plot (Sweden). A minimum number of 20 moose pellets were required to register pellets as a group. We distinguished between fresh (current winter) and old (prior to current winter) pellets. Typically, winter pellets were brown, in pellet form, and positioned on top of leaf litter and forest debris. Summer pellets were often in patty form, had leaf litter on top of pellets, or had mold or fungus growth (Zimmermann et al. 2015). For this analysis, we were only interested in winter pellets, which corresponded to winter browsing.

Wolf data.—Wolves in Scandinavia have been monitored annually with snow tracking, scat/DNA collection, and occasional VHF/GPS tracking (Liberg et al. 2012, Wabakken et al. 2018), with the goal to monitor reproduction events and breeding pairs. Despite extensive tracking efforts (mean km tracked annually = 3011.2 km; SD 1394.8; Milleret et al. 2017), data per territory were sparse for the spatio-temporal extent of our study (3–21 individual wolves collared each year in Sweden and Norway). Because home range estimators are biased at low spatial and temporal sampling (Burgman and Fox 2003, Börger et al. 2006, Mattisson et al. 2013), territory centers and boundaries were inestimable or unreliable for most packs (Appendix S1: Figs. S1, S2, S3). We instead used all available data to compute a centroid point location for each territory and year. We then used that centroid to rebuild the pack's territory by buffering each annual centroid by 18 km, which is the average radius of a wolf territory (1000 km^2) in Scandinavia (Mattisson et al. 2013). Because territory size is influenced by prey density, population density, intra- and interspecific competition, and habitat characteristics (McNab 1963, Mattisson et al. 2013, Allen et al. 2016), we accounted for density-dependence by not allowing territory boundaries to overlap (see description in Appendix S1). We created a wolf territory presence variable (Table 1), which was the presence of a wolf territory created from the above steps (Appendix S1: Fig. S4).

Due to limited tracking data, however, there was uncertainty in the territory boundary (see Milleret et al. 2017 for details). Therefore, we created a second wolf variable (probability of wolf territory occurrence; Table 1) by assigning a decreasing probability of territory occurrence as distance from the centroid increased. We used a probability because we were more confident that the areas closer to the centroid contained a wolf territory, compared to the areas far from a centroid. We assumed a parabolic decrease in probability of wolf territory occurrence from the centroid to the buffer edge (Appendix S1: Fig. S2, S3). The probability stayed high in the first 9-km radius from the centroid but uncertainty increased further out. We based this assumption on the non-linear use of their territory by wolves, where they concentrate on a small core area and use the rest of the territory less intensely (Ciucci et al. 1997, Zimmermann et al. 2019). For example, Ciucci et al. (1997) found core territory use represented only 15% of the MCP home range. We extracted raster values (probability values 0–1) for each plot in each study year in Norway and Sweden at a 1000-m resolution, which represents a coarse-scale variable. Areas outside a wolf territory were assigned a null probability. Both wolf variables (wolf territory presence, probability of wolf territory occurrence) were calculated for the winter prior to browsing surveys from 08/2007 to 08/2017. Wolf territory presence was described previously in Milleret et al. (2017). Both wolf variables are described in full in Appendix S1.

Environmental data.—We extracted additional spatial data known to influence moose habitat use and selection (Table 1). We expected the number of days with snow coverage to correlate with winter severity (Foster et al. 1982), which would influence food availability and predation risk. The spatial coverage of weather stations was insufficient to interpolate snow depth for our study area, so we calculated the number of days per year per plot with snow cover from the Normalized Difference Snow Index from MODIS (500 m; Hall et al. 2006). The spatial resolution of the snow cover variable matches the quadrat, and we interpret this variable as such. We extracted elevation because it is negatively correlated with productivity (Danell et al. 1991*b*). We extracted percent canopy cover because open areas increase predation risk by wolves (Creel et al. 2005, Gervasi et al. 2013) and human hunters (Lone et al. 2014) but often provide the most food resources (Mysterud and Østbye 1999). Young forests provide high quantity and quality food for moose (Wallgren et al. 2013). We created a binary young forest (5–20 yr old) variable based on field-collected data in Norway, and national forest inventory data in Sweden. We included the presence of downy and silver birch, Scots pine, and rowan in the plot, as we could expect the presence of other browse

Table 1. Explanatory variables used in browsing occurrence and browsing pressure models.

Variable	Abbreviated name	Units	Scale	Data source
Base model covariates				
Available shoots	Available	Number of browsed and unbrowsed shoots	Tree	field collected
Downy birch presence	Downy birch	Presence (1)/absence (0) of downy birch	Plot	field collected
Silver birch presence	Silver birch	Presence (1)/absence (0) of silver birch	Plot	field collected
Scots pine presence	Pine	Presence (1)/absence (0) of Scots pine	Plot	field collected
Rowan presence	Rowan	Presence (1)/absence (0) of rowan	Plot	field collected
Moose pellet group counts	Moose	Number of moose pellet groups	Plot	field collected
Canopy cover	Canopy	0 (no forest)–1 (full canopy)	25 m	Copernicus Land Monitoring Service
Elevation	Elevation	m	25 m	Copernicus Land Monitoring Service
Hypothesis-driven covariates				
Euclidian distance to nearest primary road	Primary road	m	Vector†	National road inventory (SWE: Lantmäteriet; NOR: Geonorge)
Euclidian distance to nearest secondary road	Secondary road	m	Vector	National road inventory (SWE: Lantmäteriet; NOR: Geonorge)
Young forest	Young forest	Presence (1)/absence (0) of young forest	Vector	SWE: Swedish Forest Agency (Skogsstyrelsen); NOR: field collected
Snow cover	Snow	Number of snow days/year	500 m	MODIS (Hall et al. 2006)
Probability of wolf territory occurrence	Wolf probability	0 (low probability)–1 (high probability)	1000 m	Wabakken et al. 2018
Presence of wolf territory	Wolf presence	Presence (1)/absence (0) of wolf territory	1000 m	Wabakken et al. 2018

† Vectors are spatial features that represent points, polygons, or lines. The spatial resolution is defined by the precision of the x, y coordinates, but the original resolution of these coordinates is often not preserved.

species could alter browsing behavior (Danell et al. 1991*a*). Last, we calculated the distance to roads in meters as the Euclidian distance to nearest primary and secondary roads. See Table 1 for variable details. Spatial extractions were done in ArcMap version 10.3.1 (Environmental Systems Research Institute 2011).

Statistical analysis

Browsing occurrence

We modeled tree browsing occurrence with a logistic regression (0, unbrowsed; 1, browsed) separately for the four species: silver birch, downy birch, rowan, and Scots pine. It was important to separate browse species because forage mass differs between species. For example, Scots pine in winter has up to 20 times the mass of the other browse species (Shipley et al. 1998). It is difficult to define forage quality based on a single metric of digestibility, nutrient content, or defense compounds (Bergström and Danell 1987). Instead, we refer to quality as an index based on food selection ranks following Shipley et al. (1998; rowan > silver birch > downy birch ≥ Scots pine).

We included the presence of other palatable species, elevation, canopy cover, and moose pellet group counts in all candidate models. We refer to these as “base model covariates.” We then added up to three variables per model related to our research questions (young forest, secondary road, primary road, wolf) as additive or interactive terms, resulting in 25 candidate models (Table 2). Hereafter, we refer to moose pellet group counts as “habitat use” (see definition above in pellet counts subsection). To account for differences in study design structure and sampling years, we included two random intercepts: plot nested within site (site/plot) and year. We mean-centered and scaled continuous predictor variables to SD = 2 so scaled coefficients from continuous variables are comparable to unscaled binary predictor coefficients (Gelman and Hill 2006). We checked for collinearity using Pearson correlation coefficients. All values > 0.7 were considered correlated and were not included in the same model (Dormann et al. 2013).

We used generalized linear mixed models (GLMM) with a binomial family (logit link) in package glmmTMB (Brooks et al. 2017). We used Akaike information criteria (AIC) to identify the most parsimonious model(s) and model-averaged parameter effect sizes based on AIC weights (Burnham et al. 2011) using the modavg function in package AICcmodavg (Mazerolle 2019). We excluded models with interaction terms from model averaging (Cade 2015). Prediction curves were created from top-ranked models only. We evaluated model fit by visualizing the scaled residuals simulated from the fitted model with package DHARMa (Hartig 2020). All analyses were completed in program R version 3.6.1 (R Core Team 2018). We report results by tree species in the ranked order of selectivity.

Table 2. Candidate models for evaluating browsing occurrence and browsing pressure.

Model number	Description
1	Young forest × wolf probability
2	Young forest + wolf probability
3	Young forest × secondary road
4	Young forest + secondary road
5	Young forest + primary road
6	Wolf probability × secondary road
7	Wolf probability + secondary road
8	Wolf probability + primary road
9	Snow × secondary road
10	Snow + secondary road
11	Snow + primary road
12	Snow × wolf probability
13	Snow + wolf probability
14	Wolf probability × secondary road × young forest
15	Wolf probability × secondary road × snow
16	Young forest × wolf presence
17	Young forest + wolf presence
18	Wolf presence × secondary road
19	Wolf presence + secondary road
20	Wolf presence + primary road
21	Snow × wolf presence
22	Snow + wolf presence
23	Wolf presence × secondary road × young forest
24	Wolf presence × secondary road × snow
25	Null model (base model covariates only)

Notes: Browsing occurrence is the probability of a tree being browsed (0, unbrowsed; 1, browsed). Browsing pressure is the number of browsed shoots per tree with the log-transformed number of available shoots as an offset. In addition to the listed variables below, all models included base model covariates moose pellet groups, elevation, canopy cover, and the presence of other palatable species. See Table 1 for variable definitions.

Browsing pressure

We modeled browsing pressure by using the number of browsed shoots per tree as our response variable and the log-transformed number of available shoots per tree as an offset. We used zero-inflated negative binomial models (logit link binomial, log-link count) with the identical fixed (Table 1) and random effect variables as the model for browsing occurrence for the conditional count and zero-inflated process models. The zero-inflation formula describes the probability of excess zeros (Brooks et al. 2017), which differs from the logistic regression. We followed the same variable standardizing, model fitting, selection, averaging, and diagnostics described above for browsing occurrence models. We did not include an offset for the binomial model.

RESULTS

From 2012 to 2018, we visited 51,527 plots to count pellet groups and assess browsing. Most plots (78%) had no pellets present (median = 0). On average, moose pellet group counts were highest among ungulate species (mean = 0.004, SE = 5.9e-05) but pellet counts varied strongly by site (Appendix S1: Fig. S5). Fallow deer were present in our study area, but inconsistencies in field data collection across years resulted in an excess of NA values. Because roe deer and red deer detections were constrained to three sites, and model fitting was difficult, moose were the only ungulate species included as explanatory variables. Distances from plots to the nearest secondary (min = 0 m, max = 2248 m) and primary roads (min = 1 m, max = 5929 m) varied. Across years, 17% of plots on average intersected with wolf territories.

We recorded 29,314 individual tree measurements. Deciduous species occurred less frequently in plots than Scots pine (in order of selectivity): rowan (14%; *n* = 4,235), silver birch (13%; *n* = 3,740), downy birch (37%; *n* = 10,800), and Scots pine (36%; *n* = 10,539). Overall browsing pressure was low (mean = 0.06; SD = 0.18). Mean browsing pressure was highest for rowan (Fig. 2). Minimum and maximum distance to nearest secondary and primary roads did not vary substantially between species: rowan (secondary 1–2040 m; primary 1–5700 m), downy birch (secondary 1–2248; primary 0–5928 m), silver birch (secondary 1–1869; primary 4–5578 m), and Scots pine (secondary 0–2248 m; primary 1–5794 m).

Statistical analysis

Rowan.—The top-ranked browsing occurrence model included the interaction snow:wolf presence:secondary road and was 2.7 times more supported by the data (based on AIC weights) than the next-ranked model (Appendix S1: Table S1). The interaction showed that with a higher number of snow days and wolf territory presence, browsing occurrence increased further from secondary roads. With lower snow coverage days and wolf territory presence, browsing occurrence decreased further from secondary roads. The two-way interaction of secondary roads:wolf presence showed that browsing occurrence increased further from secondary roads when wolf territories were present, whereas the opposite occurred when wolf territories were absent (Fig. 3). Model-averaged parameter estimates indicated that moose habitat use (β = 0.33; 95% CI = 0.19, 0.47), wolf territory presence (β = 0.23; 95% CI = −0.12, 0.59; Fig. 4), presence of silver birch (β = 0.17; 95% CI = −0.01, 0.34), and secondary roads (β = −0.11, 95% CI = −0.27, 0.06; Figs. 4, 5) had a positive effect on browsing occurrence on rowan. The presence of Scots pine (β = −0.17; 95% CI = −0.34, −0.01), elevation (β = −0.46; 95% CI = −0.83, −0.09), and distance to primary road (β = 0.21; 95% CI = 0.04, 0.37; Figs. 4, 5) had a negative effect on rowan browsing occurrence. Rowan browsing occurrence was 2.3 times higher and 1.5 lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5). For all models, no variables were correlated above |0.7|. All correlation coefficients are presented in Appendix S1: Fig. S6.

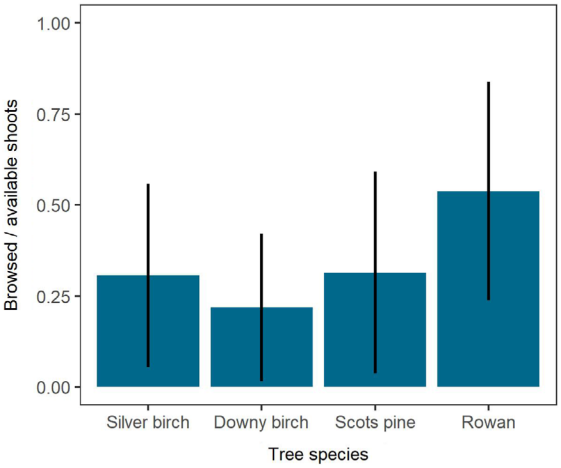

Fig. 2. Bar chart showing mean browsing pressure across all tree species for Norway and Sweden (2008–2018). We calculated browsing pressure as the number of browsed shoots divided by the number of available shoots per individual tree. For visualization, we excluded unbrowsed trees. Bars represent standard error.

There were no clear top models for rowan browsing pressure (Appendix S1: Table S2). Model-averaged parameter estimates showed moose habitat use had a positive effect (β = 0.19; 95% CI = 0.10, 0.28) and downy birch presence (β = −0.14; 95% CI = −0.25, −0.03) had a negative effect on rowan browsing pressure.

Silver birch.—For silver birch browsing occurrence, there were no clear top models (Appendix S1: Table S1). Model-averaged parameter estimates indicated a positive effect of moose habitat use (β = 1.03; 95% CI = 0.83, 1.23) and secondary roads (β = −0.12; 95% CI = −0.28, 0.05; Figs. 4, 5), and a negative effect of primary roads (β = 0.20; 95% CI = 0.02, 0.37; Figs. 4, 5) and downy birch presence (β = −0.27; 95% CI = −0.44, −0.10) on browsing occurrence. Browsing occurrence was 1.26 times higher at the highest probability of wolf territory occurrence relative to a zero probability. Silver birch browsing occurrence was 1.4 times higher and 1.6 times lower along secondary and primary roadsides,

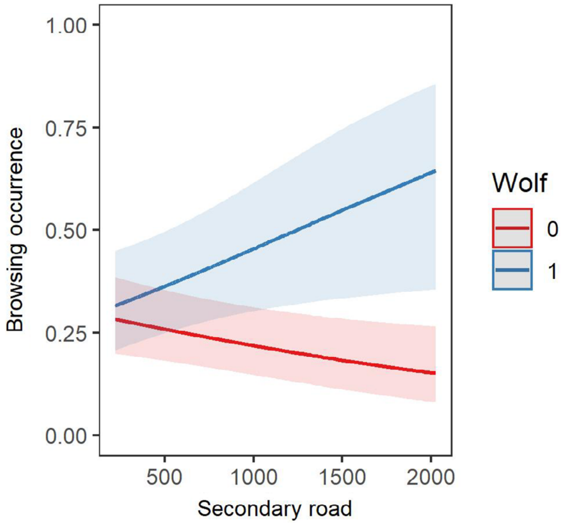

Fig. 3. Predictive plot for the interaction secondary road:wolf from the top-ranked rowan browsing occurrence model. Wolf territory absence = 0 and presence = 1. Low road values (in meters) are close to secondary roads, while high values are far from secondary roads. Predictions were from the top-ranked browsing occurrence model. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

respectively, relative to the maximum distance from each road type (Fig. 5).

For silver birch browsing pressure, the top model was 2.6 times more likely than the second-ranked model (Appendix S1: Table S2). Model-averaged parameter estimates indicated a strong positive effect of moose habitat use (β = 0.15; 95% CI = 0.05, 0.24) and a negative effect of young forests (Fig. 6) on browsing pressure.

Downy birch.—The top downy birch browsing occurrence model was 2.3 times more likely than the next-ranked model (Appendix S1: Table S1). This model contained the additive terms young forest and primary roads. Model-averaged parameter estimates indicated a positive effect of moose habitat use (β = 0.47; 95% CI = 0.37, 0.57) and secondary roads (β = −0.03, 95% CI = −0.17, 0.11; Figs. 4, 5), but a negative effect of primary roads (β = 0.22; 95% CI = 0.09, 0.34; Figs. 4, 5) and elevation (β = −0.54; 95% CI = −0.89, −0.20) on browsing occurrence. Browsing occurrence was 1.37 times higher at the highest probability of wolf territory occurrence relative to a zero probability. Downy birch browsing occurrence was 1.1 higher and 1.8 times lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5).

There were no clear top models for downy birch browsing pressure (Appendix S1: Table S2). Model-averaged covariates included negative effect of elevation (β = −0.46; 95% CI = −0.71, −0.20) and Scots pine presence (β = −0.11; 95% CI = −0.25, 0.04) on browsing pressure.

Scots pine.—The top Scots pine browsing occurrence model was two times more likely than the second-ranked model (Appendix S1: Table S1). This model included interaction terms young forest:secondary road where browsing occurrence was higher in young forests but declined further from secondary roads. Outside young forests, browsing occurrence on Scots pine was lower and the road effect was dampened (Appendix S2: Fig. S4). Model-averaged parameter estimates showed a positive effect of moose habitat use (β = 0.77; 95% CI = 0.67, 0.87), the presence of young forest (β = 0.49; 95% CI = 0.30, 0.69; Fig. 4), silver birch (β = 0.38; 95% CI = 0.24, 0.51), and downy birch (β = 0.42; 95% CI = 0.29, 0.54) on Scots pine browsing occurrence (Fig. 4). Browsing occurrence increased closer to secondary roads (β = −0.22; 95% CI = −0.36, −0.08) but decreased closer to primary roads (β = 0.19; 95% CI = 0.06, 0.31; Figs. 4, 5). Pine browsing occurrence was 1.6 times higher and 1.9 times lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5).

The top browsing pressure model was 10 times more likely than the second-ranked model (Appendix S1: Table S2). This model included the interaction of wolf presence:secondary road: young forest. Browsing pressure outside wolf territories was relatively unchanged whether close to or far from secondary roads, or in young forests or not. Inside wolf territories, browsing pressure decreased in young forests when further from secondary roads. Browsing pressure increased further from secondary roads when outside young forests (Fig. 7). Model-averaged parameter estimates showed a positive effect of the presence of silver birch (β = 0.14; 95% CI = 0.002, 0.29) and a negative effect of

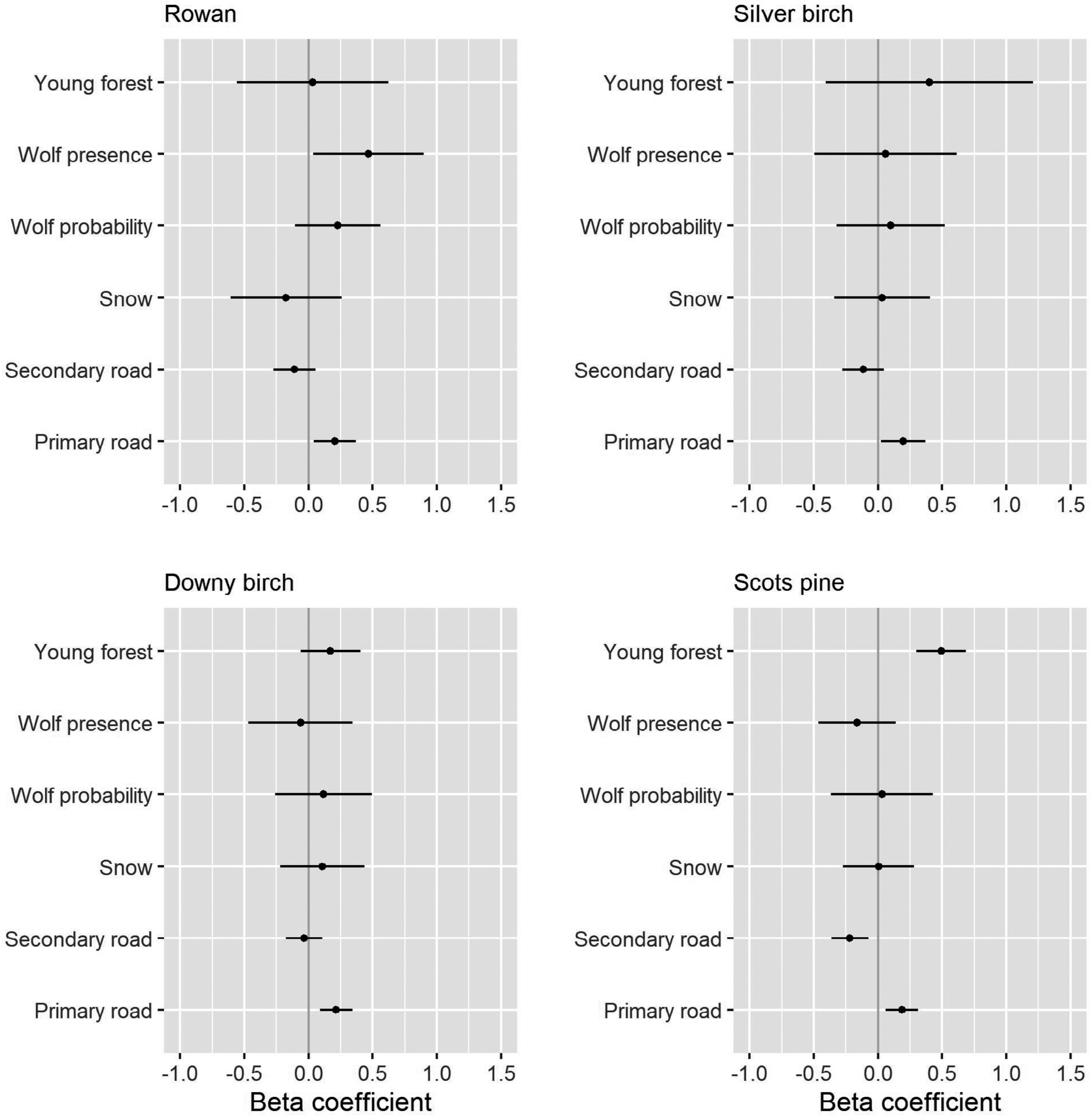

Fig. 4. Forest plots of model-averaged main effect coefficients from browsing occurrence models. Estimates are from binomial models. Reference categories for binary variables (wolf presence, young forest) are 0. Bars represent 95% confidence intervals.

elevation (β = −0.58; 95% CI = −0.92, −0.24) on Scots pine browsing pressure.

DISCUSSION

We tested the importance of roads, young forests, and wolves on moose browsing occurrence and browsing pressure at a fine spatial scale and large spatial extent. Primary and secondary roads were important explanatory variables for moose browsing occurrence and pressure on all tree species. Generally, for all tree species, browsing occurrence and pressure decreased close to primary roads but browsing occurrence

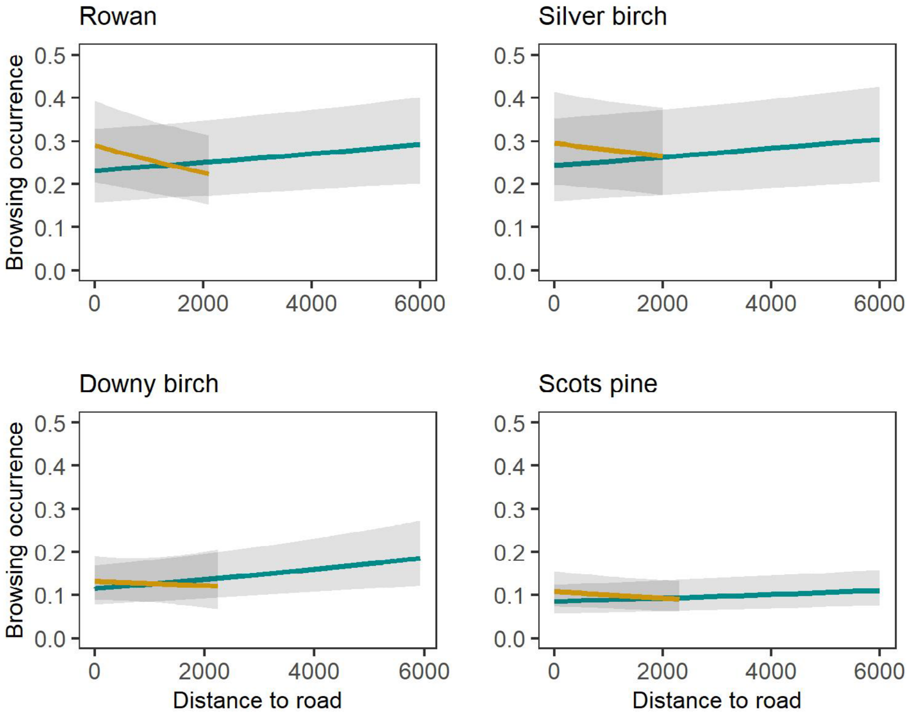

Fig. 5. Predictive plots for the relationship between browsing occurrence and distance to secondary (yellow line) and primary roads (green line) for all four tree species. Low road values (in meters) are close to roads, while high values are far from roads. Plots are from highest ranked models that contain secondary and primary roads for each species. See Appendix S1: Table S1 for model rankings. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

increased close to secondary roads (P1, P2). We also found a neutral to positive effect of wolf territory presence and probability on browsing occurrence and pressure. However, wolf effects became negative when they interacted with food and risk variables like snow cover, distance to roads, and presence of young forest (P1). We found little support for days with snow cover increasing browsing occurrence and pressure (P3) and tree species with differing selectivity rankings explaining differences in road and wolf effects (P4).

Our results showed reduced browsing occurrence close to primary roads and increased browsing occurrence close to secondary roads, as expected. Primary roads can increase chances of moose-vehicle collisions and are barriers to moose migration (Ball et al. 2001, Seiler et al. 2003), with vehicle speed, traffic volume, and fencing being primary deterrents (Seiler 2005). For all tree species, we found browsing occurrence was 1.6–1.9 times lower along primary roadsides relative to the furthest point from primary roads. This supports a behavioral response from moose to avoid risky primary roads. Indeed, road avoidance behavior results in indirect habitat loss, which can often be a bigger driver than direct habitat loss (Dwinnell et al. 2019). This can reduce nutritional carrying capacity, reduce fitness, and lead to population declines (McLoughlin et al. 2006). While Scandinavian moose densities are among the highest in the world (Lavsund et al. 2003), little emphasis is placed on the fitness consequences of road development in Scandinavia.

In contrast to the response to primary roads, we found browsing occurrence was 1.1–2.3 times higher along secondary roadsides relative to the furthest point from the road. Moose could use secondary roads for travel but often these linear features are perceived as risky, especially when predators are present (Dickie et al. 2020), so we

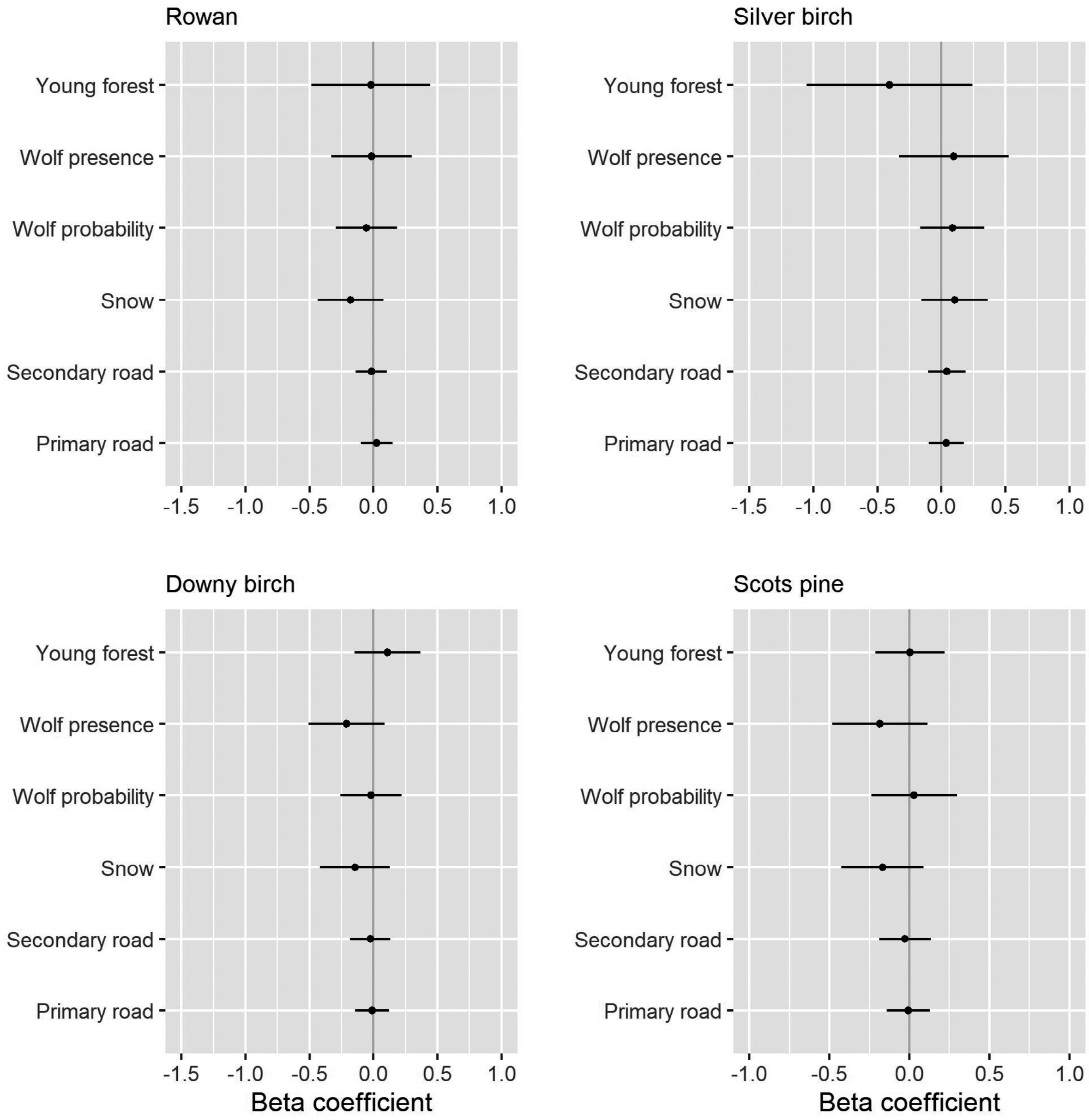

Fig. 6. Forest plots of model-averaged main effect coefficients from browsing pressure models. Estimates are from the conditional part of zero-inflated negative binomial models. Reference categories for binary variables are 0. Bars represent 95% confidence intervals.

would expect some degree of road avoidance behavior. A more plausible explanation for the positive effect of secondary roads is that roads change an herbivore's food landscapes without adding the burden of high vehicle traffic. For example, roadside mowing and ditching can increase plant diversity, specifically birch density (Zielińska et al. 2013, Jakobsson et al. 2018). Forests in Scandinavia are typically low in structural and species diversity because deciduous tree densities are reduced during pre-commercial thinning. Roads and clear-cuts offer one of the few disturbance events to stimulate early successional deciduous tree growth. We could thus

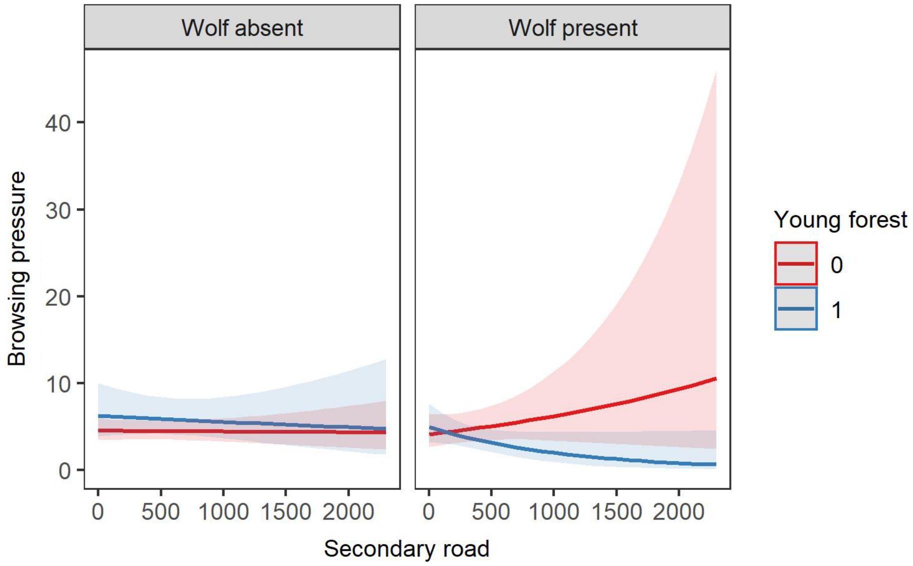

Fig. 7. Predictive plot for the interaction between secondary road:young forest:wolf territory presence from the top Scots pine browsing pressure model. Low road values (in meters) are close to secondary roads, while high values are far from secondary roads. Young forest presence = 1 and absence = 0. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

expect a relationship between roads and deciduous tree density, which could positively influence browsing occurrence and pressure. This is a plausible explanation for the positive main effect of secondary roads, though we could not detect any trend between tree density and distance to roads in Norway (Appendix S1: Fig. S7). Tree density data were not available for Sweden.

While secondary roadsides can offer food subsidies and easy travel routes, they also represent a spatial mortality risk to moose because they are also used by predators and humans. This could result in temporal or spatial road avoidance under certain situations (Mathisen et al. 2018). Indeed, we found rowan browsing occurrence increased further from secondary roads where wolf territories were present (Fig. 3), which suggests that secondary roadsides could be perceived as risky when predators are present. Globally and locally, roads increase the distance and speed at which wolves travel (Zimmermann et al. 2014, Dickie et al. 2017); in Scandinavia, wolves travel almost twice as fast on roads versus off roads. This could increase detection rates of prey and motivate moose to spend time away from roads despite roadsides offering attractive foods. Additionally, multi-predator systems (including humans as predators) could have contrasting, additive, or multiplicative effects on the ungulate prey. For example, Lone et al. (2014) found that roe deer predation risk was greatest in rugged terrain where lynx and human hunters overlapped, creating areas of additive predation risk. Similarly, because secondary roads are used by wolves and humans, they could also be areas of additive (or additional) moose predation risk.

While browsing occurrence increased close to secondary roads for most tree species (except downy birch; Fig. 4), young forests intensified the positive effect of secondary roads for Scots pine (Fig. 7). For the commercially valuable Scots pine, the presence of young forest stands alongside secondary roads nearly doubled Scots pine browsing occurrence (*P* = 0.20) compared with a recently clear-cut, or forests older than 20 yr (*P* = 0.11; Appendix S2: Fig. S4). Much of Scandinavia's productive areas are used for agriculture and forestry. During winter, young pine forests are selected by moose for the abundance of high quantity and quality foods. However, intensive browsing can lead to a delay in stand maturity, irregular growth, or tree death (Wallgren et al.

2013, Herfindal et al. 2015). This is the center of the conflict between forest owners who want commercially valuable timber, and moose hunters, who want to sustain high harvest rates. Many forest roads in Scandinavia are being upgraded to allow for larger machinery (Flisberg et al. 2014), and new roads are being built for access to wind turbines, a growing energy source in Scandinavia (IEA Wind TCP 2018). While overall browsing occurrence along roadsides was low, the high-density secondary road network in Scandinavia could be facilitating intensive moose browsing. This could have long-term consequences to forestry and moose-forestry conflicts by intensifying moose browsing along roadsides.

Our browsing pressure estimates were comparable to previous Scandinavian studies. For example, browsing pressure estimates 1–10 km from supplemental feeding stations (where they did not find effects of feeding stations) from Mathisen et al. (2014) were 44% for rowan (2 SE = 9.0; 1.5 times higher than our average), 34% for silver birch (2 SE = 9.0; 1.3 times higher than our average), 27% for downy birch (2 SE = 6.0; 1.3 times higher than our average), and 33% for Scots pine (2 SE = 7.0; 1.2 times higher than our average). For both their study and ours, rowan experienced the highest browsing pressure (Fig. 2). Rowan is highly selected by moose, and high browsing impacts on rowan may have strong negative effects on plant and animal biodiversity (Shipley et al. 1998, Månsson et al. 2007). Indeed, Speed et al. (2013*a*, *b*) found height growth was restricted when 20–45% of rowan shoots and 30% of Scots pine shoots were browsed. For our study, 42% (*n* = 740) of Scots pine measured had ≥30% of shoots browsed. For rowan, 89% (*n* = 1,077) had ≥20% of shoots browsed and 57% (*n* = 691) had ≥45% of shoots browsed. We note the effect of browsing pressure on individual tree growth and development depends on many factors such as site productivity, tree species, or predation pressure, which make browsing pressure estimates difficult to generalize and compare. While our study was designed to quantify changes in moose browsing, and not changes in the plant community in relation to the presence of wolves, we recommend future research in Scandinavia to focus on the cascading effects of carnivores on plant biomass or recruitment.

Browsing occurrence and pressure represent different aspects of ungulate ecology but are poorly differentiated in the browsing literature. Given the data and our models, we found much clearer signals for browsing occurrence relative to browsing pressure. According to Shipley et al. (1998), moose utilize only 20% of available bites along a foraging path, taking only one or two bites per tree. In this case, we can think of browsing occurrence as one of many steps in the forage selection process: First, the moose needs to be present, then it encounters a tree, takes a bite or two, but may later reject the tree from further browsing. In contrast, browsing pressure reflects that moose have sampled the tree and chose to continue feeding on it. Browsing pressure is perhaps the more ecologically meaningful metric, as we can estimate the amount of forage removed from a tree/patch/landscape. However, browsing pressure had a low signal-to-noise ratio in our study. There were multiple potential sources of variation, including differences in tree morphology or uncertainty in our count estimates. For example, maximum counts for the number of browsed and available shoots reached 250 and 1028, respectively. These are high values, and although we used clicker-counters, human error likely contributed to some of this unknown error. For example, Prater (1979) found observers counting birds from photographs (i.e., true values known) consistently overestimated when counting small groups of birds but underestimated when counting large groups. For counting shoots on a tree, this could result in the systematic underestimation of the number of shoots on larger trees and overestimation of smaller trees. Shoot counting could be improved by using double observer surveys to quantify and correct for the uncertainty (Morrison 2016). Feedback sessions where all technicians count the same tree and learn from the group average could also be useful (Wintle et al. 2013).

Similar to Ausilio (2018) and van Beeck Calkoen et al. (2018), we found browsing occurrence increased with increasing probability of wolf territory occurrence (Fig. 4): For downy and silver birch, browsing occurrence was 1.37 and 1.26 times higher at the highest probability of wolf territory occurrence relative to a zero probability. This counterintuitive finding could result from wolves and moose being displaced by humans to less productive areas, which results in high wolf-utilization areas having lower tree densities, or wolves aligning their territories with areas of higher moose densities. Unlike previous studies, however, we found that for rowan, browsing occurrence decreased close to secondary roads when wolf territories were present and the number of snow days were high. With a lot of snow, wolves may be more likely to use forest roads; alternatively, it may be easier for moose to move in the forest rather than on unplowed forest roads with deep snow. Similarly, browsing pressure was three times higher away from secondary roads when wolves were present and browsing occurred in clear-cut, or forests older than 20 yr. In contrast, browsing pressure was 1.4 times higher close to secondary roads when browsing occurred in young forests and wolves were present (Fig. 7). This finding lends tentative support for the risk allocation hypothesis that given roads represent a mortality risk, as we have shown above, moose are still attracted to roadsides when food sources are abundant. However, moose are less willing to accept this level of risk if the food reward is diminished, as is typically the case in mature forests. We note the high uncertainty with these estimates and are cautious in our interpretation.

Overall, however, wolf effects were lower than we expected. Part of this uncertainty could be because the wolf territory variable represents a coarser resolution (500 and 1000 m) than all other variables. At finer spatial resolutions, we would expect a stronger effect with reduced uncertainty. Another explanation for uncertain wolf effects is that our dataset is biased toward areas without wolves, so an excess of zeros in our wolf variables could mask underlying patterns. Post hoc, we ran browsing occurrence and pressure models with data only from sites within wolf distribution. Wolf effects become stronger (Appendix S2: Figs. S1, S2) but most other variables increased in uncertainty. Important interactions, such as the interaction of wolf territory presence and distance to secondary roads, remained present but estimates became more uncertain (Appendix S2: Figs. S3, S4). See Appendix S2 for post hoc results.

Our results of weak wolf effects are consistent with other European studies where the effects of wolves have been more difficult to elucidate than in North America, possibly because of reduced landscape heterogeneity and dampened effects of predators relative to the effects of humans (Schmidt and Kuijper 2015). In Scandinavia, previous research has also suggested that moose may be naïve to wolves as predators. Sand et al. (2006) found wolf hunting success of moose to be 2–9 times higher in Scandinavia relative to North America, which they argue is an artifact of mortality contributions from humans (high) and large carnivores (low). In North America, wolves were never extirpated from the moose's distribution (or only for short periods; e.g., 40–50 yr) whereas moose in Scandinavia have lived without large carnivores for 120–150 yr. Because of this carnivore-free period, Sand et al. (2006) and others (Berger et al. 2001) argue that moose have relaxed their aggressive anti-predator response in favor of a flee response. Last, another possible reason for a weak wolf effect could be because moose are widely hunted with dogs in Scandinavia. Hunting dogs bark at moose, and hunters are more successful at shooting moose that stand their ground, which is an advantageous anti-predator response to wolves. However, it is the fleeing moose that often escape human hunters and may thus be favored in selection. Hunting is a widely popular activity in Scandinavia with almost 115,000 moose shot annually, so human hunters potentially exert a stronger selection pressure relative to wolves.

To conclude, we found browsing occurrence and pressure effects varied by tree species. We found neutral to positive effects of wolves. Wolf effects became more certain and positive when they interacted with other factors such as snow cover, young forests, and roads. Whether these effects are large enough to shape tree recruitment or community patterns remains unknown. We found browsing occurrence increased close to secondary roads but decreased close to primary roads. The presence of young forests near secondary roads nearly doubled moose browsing occurrence for Scots pine, which could have consequences for moose-forestry conflicts. There are many secondary roads in Scandinavia, and even more to be built. We assert that forest and wildlife managers need to consider how an increasing network of secondary roads facilitates intensive moose browsing.

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Ungulate-adapted forestry shows promise for alleviating pine browsing damage

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ABSTRACT

High densities of ungulates can increase human-wildlife conflicts. Where forestry is an important economy, intensive browsing can lead to browsing damage, resulting in volume losses, poor stand regeneration, and reduced timber quality. The forestry industry thus looks for practical, long-term measures to mitigate browsing damage. We tested the effect of two mitigation measures on moose (*Alces alces*) browsing behaviour and damage to Scots pine (*Pinus sylvetris*): (1) ungulate-adapted slash piles (i.e., palatable species only) created during felling to increase short-term food availability and (2) intensified soil scarification to increase long-term food availability (collectively, 'ungulate-adapted forestry'). Our study occurred in southern Norway where we established fixed vegetation and moose faecal pellet plots at varying distances from conventional and ungulate-adapted slash piles and scarified stands. We evaluated the effects of ungulate-adapted slash piles and intensified scarification on the density of undamaged Scots pine, moose bite diameters, browsing pressure, and moose faecal pellet density. To assess the effect of spatial scale, we created 250 m, 500 m, and 1000-m radius buffers centered on each plot. We found that ungulate-adapted logging near our plots increased the density of undamaged pines, as compared to no and conventional logging. We found that logging in general led to smaller bite diameters. We also found that plots near conventional logging had higher browsing pressure, whereas browsing pressure near ungulate-adapted logging was similar to unlogged stands. For scarification, density of undamaged pine increased when the ungulate-adapted stand aged whereas undamaged pine decreased as conventional scarification stands aged. Browsing pressure showed a response at the smallest spatial scale only for ungulate-adapted scarification. Peak moose habitat use near conventional and ungulate-adapted scarified stands differed by stand age and distance from scarification. The overall effects of ungulate-adapted forestry were most pronounced at the smallest spatial scale (250 m). Our results support 'ungulate-adapted' forestry as a practical solution to mitigate browsing damage but uncertainty in some of our estimates suggest further research on the area treated is needed.

1. Introduction

Food subsidies from agriculture and forestry, selective ungulate harvests, and loss of large carnivores have resulted in an increase in certain wild ungulate species' distribution, abundance, and density (Apollonio et al. 2010). An increase in ungulate densities represents a challenge economically (Putman 1996, Putman et al. 2011) because ungulates are often the main drivers of plant population dynamics, forest structure, and ecosystem processes (Danell et al. 2003, Ross et al. 2016, Speed et al. 2019). Intensive browsing can reduce forest regeneration or cause shifts in plant species composition (Gill 1992, Rooney and Waller 2003, Schütz et al. 2003). As a result, forest owners and forestry planners look for practical, long-term measures to mitigate consequences of intensive browsing.

Measures to mitigate browsing damage include intentional feeding of ungulates away from critical areas such as young forest stands (diversionary feeding; Geisser and Reyer 2004), intentional feeding to increase food availability (supplemental feeding; Milner et al. 2014),

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exclusionary fences or deterrents, and/or changes to ungulate harvest strategies (Putman et al. 2011). The efficacy of each method is scale and context dependent (Boyce et al. 2017). Further, measures are often difficult to successfully implement because they are costly, ungulates cross jurisdictional boundaries, and researchers often work at fine spatial scales (Hobbs 2003) whereas wildlife management occurs at broader scales (Weisberg and Bugmann 2003), thus creating a mismatch between wildlife movement and management boundaries (Meisingset et al. 2018).

Spatial scale is a critical component to most ecological questions because resource selection occurs at different hierarchical orders, or scales (Johnson 1980, Senft et al. 1987, Boyce 2006) yet studies linking hierarchical scales of foraging to mitigation measures are rare. A foraging ungulate, for example, moves within its geographical range (1st order), establishes a home range (2nd order), and within that home range may make seasonal movements, selecting feeding patches (3rd order), individual plants and which parts of the plant to eat (4th order; Johnson 1980). Similarly, mitigation measures can operate at multiple spatial scales: coarse scales, where seasonal ungulate movements are altered by winter feeding stations (Jones et al. 2014), or fine scales, where resident ungulates are diverted away from high-traffic roads during winter (Milner et al. 2014). However, the scale at which ungulates respond to resources depends on multiple factors including temporal scale, physiology, life history traits, and habitat (Gaillard et al. 2010).

Northern latitudes experience strong seasonality in ungulate food availability and habitat conditions (Dussault et al. 2005), and functional responses to food availability and food quality are scale dependent. Moose (*Alces alces*), for example, the largest member of the deer family (Cervidae), select for abundant browse irrespective of quality at large spatial scales, but select for higher quality browse at finer scales (van Beest et al. 2010b). However, experimental increases in food availability do not necessarily increase food consumption (Edenius et al. 2014) and large scale selection could constrain available forage at a finer spatial scale (Wilmshurst et al. 1999).

Our study system is in the boreal forests of Scandinavia where forestry is a primary economy, moose have a high recreational and economical value, and moose-forestry conflicts are abundant (Lavsund et al. 2003). Industrialization of commercial forestry in the 1960s, combined with concurrent changes in moose harvest strategies, caused local moose densities to spike in the 1980s and 1990s (e.g., local winter densities of 5–6 moose per km^2; Lavsund et al. 2003, Speed et al. 2019). While moose densities have slowly declined over the past twenty years (Speed et al. 2019), as has food availability (Milner et al. 2013), moose continue to negatively affect tree growth and survival by browsing the bark or apical shoot, or by breaking the tree stem. Subsequent tissue damage and changes to growth morphology can reduce the economic value of growing trees and forest stands, resulting in what is commonly termed ‘browsing damage’ (Hörnberg 2001, Lavsund et al. 2003). In this study, we instead focus on the density of undamaged trees, as it is the density of unaffected trees that result in adequate stand regeneration rather than the damaged trees. We considered a tree ‘undamaged’ if the tree did not have top-shoot browsing, bark browsing, main stem breakage, or if <60% of a tree’s shoots have been browsed (Hårstad 2008). In Scandinavia, browsing damage is primarily applied to Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) because they hold commercial value. Scots pine is a primary moose food in winter and browsing damage most commonly occurs in young Scots pine forests (5–20 years old) during winter when food is limited and where moose congregate at lower elevations (van Beest et al. 2010b).

Economic losses as a result of browsing damage have resulted in conflicts between forest owners, who prioritize timber production, and moose hunters, who harvest on average 196,000 moose annually in Norway and Sweden (for study years 2011/12–2014/15; public data from www.ssb.no and www.älgdata.se). Wildlife managers have used moose population reduction via harvest as the primary strategy to decrease intensive moose browsing. However, since young pine forests are highly selected by moose, moose population reduction does not consistently reduce browsing damage (Reimoser and Gossow 1996). Diversionary or supplemental feeding (typically with silage) are other mitigation strategies, but feeding wild ungulates was recently banned in Norway due to the detection of chronic wasting disease (Stokstad 2017). Managers thus need to be creative in designing alternative, effective, long-term mitigation strategies in Scandinavia.

One mitigation strategy that has been minimally studied is the modification of conventional forestry practices during felling and site preparation to increase available forage. Branches and tree stems <5 cm in diameter from felled trees are left on site because they have low commercial value (Månsson et al. 2010). Conventional logging uses some of the branches as “slash mats” to reduce the compaction of underlying vegetation and soils from the heavy machinery. However, branches are crushed and become inaccessible to moose after snowfall, and shoots no longer have the biting resistance necessary for browsers because they are not attached to a tree (Månsson et al. 2010). A single mature Scots pine in Sweden holds on average 29 kg dry weight of moose forage (Månsson et al. 2010), yet only about 5% of potential forage remains available after the trees are felled and cleaned for hauling. Heikkilä and Härkönen (2000) found that residual Scots pine tree-tops raised above the snow, what we term ungulate-adapted slash piles, were utilized four times more than treetops lying on the ground. Machine operators can thus create ungulate-adapted slash piles with palatable species (e.g., Scots pine, birch; Shipley et al. 1998). This contrasts with traditional slash piles that include all felled species. Despite the increase in food availability, the use of ungulate-adapted slash piles (hereafter, slash piles) have not clearly mitigated browsing damage and require further research (Heikkilä and Härkönen 2000, Edenius et al. 2014).

In addition to slash piles, soil scarification is a common site preparation method in Scandinavia whereby the top organic layer is overturned to expose mineral soil, with the aim to improve seed establishment and increase soil temperature (Örlander et al. 1996, Béland et al. 2000, Berg et al. 2008). An increase in soil scarification intensity can increase Scots pine seedling establishment (Saursaunet et al. 2018), thus increasing Scots pine density and food availability when trees are within browsing height and before stand thinning (Örlander et al. 1996). While soil scarification can have many deleterious ecological effects (Atlegrim and Sjöberg 1996a, Örlander et al. 1996), previous research in our study area found pine seedling density increased with mineral soil exposure (Saursaunet et al. 2018). Thus, intensive scarification could increase food availability during early-to-mid successional stages, creating a forage-rich landscape and reducing browsing damage via resource dilution (Tscharntke et al. 2012).

At each stage of intervention in commercial forestry, actions are taken to optimize timber or pulp production, as described above. We propose ‘ungulate-adapted forestry’ be an additional step added to this process to optimize ungulate forage production. Here, we test two methods that can be part of ‘ungulate-adapted forestry’: ungulate-adapted slash piles and intensive scarification. Our objective was to examine if ungulate-adapted forestry via slash piles and intensified soil scarification can alter ungulate browsing ecology and forest damage (Fig. 1). We tested if conventional and ungulate-adapted forestry influenced: (1) browsing damage; (2) moose habitat use; (3) bite size; (4) browsing pressure near treatment stands; and (5) whether these changes were similar at different spatial scales. Long-term monitoring plots were placed at varying distances from stands that were logged and scarified, rather than placed directly in logged and scarified stands. Current work (Mathisen et al. unpublished results) addressed the within-stand changes whereas our study investigated responses outside the stands.

Rarely is browsing damage connected to browsing ecology in the literature, yet it could explain many of the mechanisms influencing damage. For example, browsing damage could depend on the abundance of preferred species in the same plot. We expected a diversionary effect

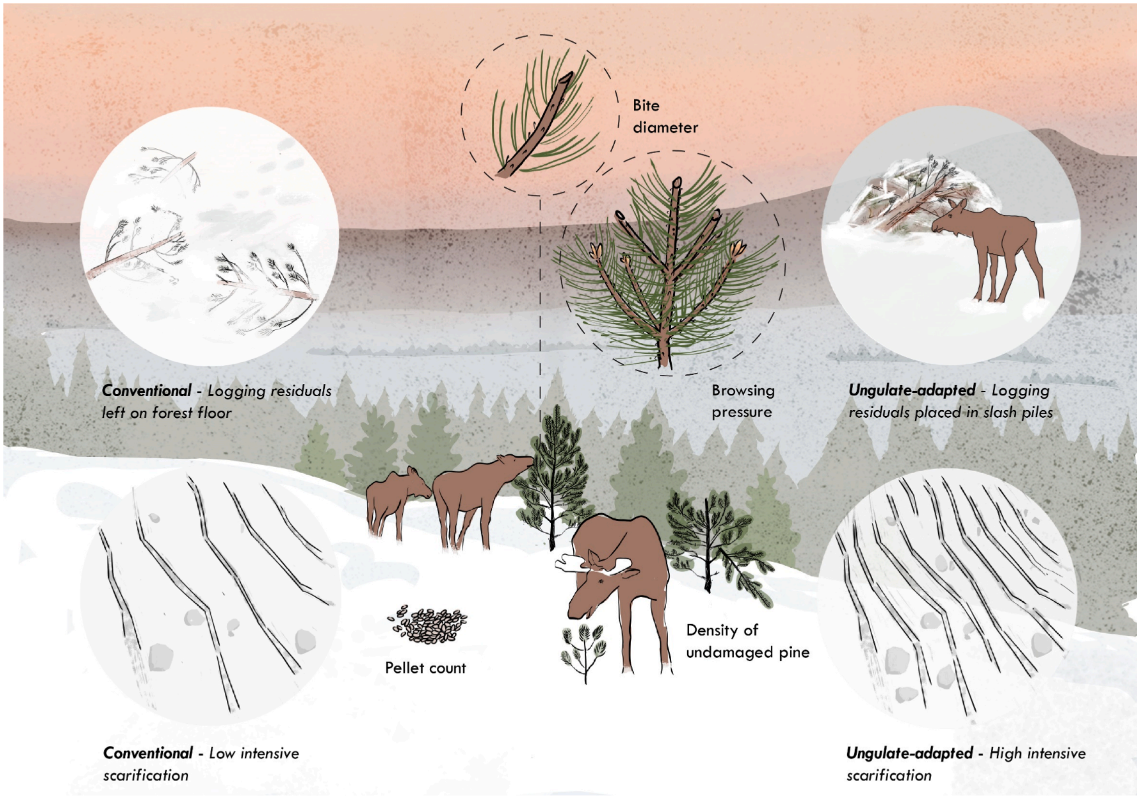

Fig. 1. Overview of the experimental study design. The four response variables (bite diameter, browsing pressure, density of undamaged pine, moose habitat use) are pictured at center. The conventional and ungulate-adapted logging and scarification treatments, which occurred at varying distances from plot centers, are featured at left and right. Response variables are described in Sections 2.4.2–2.4.5 and in Table 2. Illustration by Heidi Loosen (loosenstudio.net).

of the experiment to lead moose away from young stands, but also a supplementary effect to increase overall food availability, both leading to a decrease in browsing on Scots pine in the studied stands. We focused our analyses on Scots pine since it is a bulk winter food for moose in Scandinavia and has high economic value (Shipley et al. 1998). Our data were collected at the plot scale, which corresponds to the patch selection scale in hierarchical forage selection (3rd order; Herfindal et al. 2015), and at the tree and shoot scale, which corresponds to food selection (4th order; Senft et al. 1987).

Research suggests that pine damage decreases with an increase in pine forage availability (Bergqvist et al. 2014, Herfindal et al. 2015, Pfeffer et al. 2021). We thus hypothesized the density of undamaged pine stems would be higher in the areas close to slash piles (H1). Bite size, which is an index of forage intake (Gordon 2003), can reflect available forage. For example, moose select larger bites as browse density and quality decline, and as distance between patches increases (Vivas and Sæther 1987, Shipley and Spalinger 1995, Shipley et al. 1998). Large bites require less handling time per unit biomass consumed, but result in a greater intake of fiber, which increases mastication, rumination, and digestion time. Small bites have less fiber, but require greater handling time per unit biomass consumed (Palo et al. 1992, Shipley 2007). Thus, bite size is a trade-off between food intake and quality. Because ungulate-adapted forestry increases availability of Scots pine (Mathisen et al. unpublished results), we hypothesized bite size to decrease near ungulate-adapted stands due to increased food availability (H2).

We hypothesized ungulate-adapted forestry would decrease browsing pressure (H3) because of the increase in alternative forage via slash piles and intensive scarification (Månsson et al. 2010, Edenius et al. 2014). Further, we assumed that consuming pine shoots from concentrated slash piles would be more efficient than browsing on dispersed trees. We hypothesized ungulate-adapted forestry to increase habitat use (H4) because of the creation of a forage-rich landscape and spill-over effects on surrounding stands, as was found with moose habitat use close to supplemental feeding stations (Gundersen et al. 2004, van Beest et al. 2010a). Based on research from supplemental feeding stations in Norway (van Beest et al. 2010a, Mathisen et al. 2014), we hypothesized stronger effects at smaller spatial scales for all response variables (H5).

2. Methods

2.1. Study area

Our study area lies between 60.8°–61.4°N and 12.2°–12.7°E in Innlandet County (Fig. 2; Fig. S1). Elevation ranges from 265 to 750 m above sea level. The area experiences cold, snowy winters (mean January temperature 2011–2018: −9.3 °C; Norwegian Meteorological Institute) and short, cool summers. Land cover is dominated by boreal forests, which are managed for timber and pulp production. Production forests, which are largely coniferous, typically undergo one pre-commercial thinning at 10–20 years to remove competing deciduous shrubs and trees. Stands undergo 1–2 thinning events at 40–50 years and 70–80 years to optimize commercial tree density. All time estimates are dependent on site productivity. Natural regeneration from seed trees is most common for pine, whilst spruce are often planted.

Common tree species include Scots pine, silver birch (*Betula pendula*), downy birch (*Betula pubescens*), Norway spruce, grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula*). The shrub layer is dominated by bilberry (*Vaccinium myrtillus*), heather (*Calluna vulgaris*), and other Ericaceous dwarf shrubs. In boggy areas, *Sphagnum* spp. mosses are dominant. Generally, rowan, aspen, and willow (*Salix* spp.; RAW) are rare relative to Scots pine and birch, and are highly selected by moose (Shipley et al. 1998, Månsson

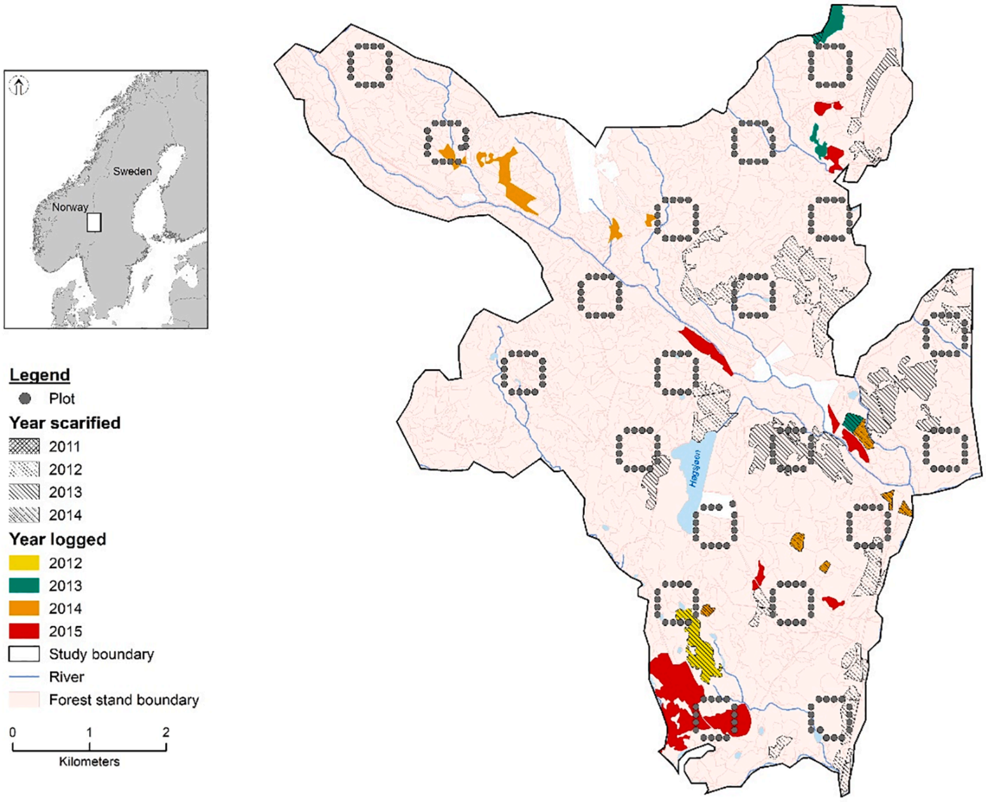

Fig. 2. Map of forestry activities from 2011 to 2015 at one of our three study sites (Gravberget). Scarification occurred from 2011 to 2014 and logging occurred from 2012 to 2015. Scarification occurred one to two years after logging. Only winter logging stands are pictured here. Inset map shows our study area (white rectangle) in southern Norway. Each site contained 20–22 quadrats. Each quadrat contained 16 plots (grey circle). At each plot we measured the density of undamaged pine, browsing pressure, bite diameters, and moose pellet groups. See Fig. S2 for a map of all study sites.

et al. 2007). Still, Scots pine is a primary food source for moose during winter due to its high abundance whereas spruce are well-defended chemically and rare in moose diets (Cederlund et al. 1980).

In winter, moose typically migrate from summer ranges in high-elevation mountainous areas to low-elevation valley bottoms where snow depths are reduced (Sweanor and Sandegren 1988, Bunnefeld et al. 2011, Singh et al. 2012). Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are present in our study area but occur at low densities. Large carnivores include wolves (*Canis lupus)*, brown bears (*Ursus arctos*), wolverines (*Gulo gulo*), and Eurasian lynx (*Lynx lynx*). Wolves and bears prey on neonate calves in the spring and early summer, and moose are the main prey of wolves throughout the year (Swenson et al. 2007, Sand et al. 2008, Zimmermann et al. 2015). However, annual moose offtake by hunters, which only occurs in the autumn, is 2.4–3.5 times higher than that from wolves, where predation occurs year-round (Zimmermann et al. 2019).

2.2. *Forestry activities*

Our study had three forestry activity levels; no forestry actions, conventional forestry, and ungulate-adapted forestry. Conventional stands had conventional logging (no slash piles) and low intensity soil scarification (see Section 2.2.2). Ungulate-adapted stands had ungulate-adapted logging (ungulate-adapted slash piles) and high intensity soil scarification (see Section 2.2.2).

2.2.1. *Logging*

Conventional logging does not make residual forest materials available for moose. In ungulate-adapted stands, harvester operators created slash piles from discarded Scots pine branches and tree-tops (stem diameters <5 cm) (Fig. 1). From November to March between 2012 and 2015, slash piles were created during felling. Slash piles varied in size and frequency by stand, particularly with available forage. In our study area slash piles doubled the amount of Scots pine biomass available, on average, compared to conventional logging (Mathisen et al. unpublished results). Harvester time spent in conventional and ungulate-adapted logging stands did not differ (Mathisen et al. unpublished results). Ungulate-adapted logging occurred in 46 stands (268 ha) while 32 stands (204 ha) received conventional logging (Table S1). While we aimed for an equal number of conventional and ungulate-adapted stands, previous research has shown that many factors influenced when, where, and why small private Norwegian landowners harvested timber (Bashir et al. 2020) and these may not align with forest research goals.

Logging occurred at varying distances to plot centers (Fig. 2). To assess how spatial scale influenced our response variables, we created 250 m, 500 m, and 1000-m radius buffers centered on each monitoring plot in ArcMap (Environmental Systems Research Institute 2011). We limited our distance to 1000 m to reflect the maximum distance at which feeding stations have an effect on browsing and moose density in Norway (Mathisen et al. 2014). For each buffer size we created three unique logging variables: (1) a 4-level factor with 4 treatment levels (absence of logging, presence of conventional logging, presence of ungulate-adapted logging, and presence of both conventional and ungulate-adapted logging), (2) the area (m^2) with conventional logging; and (3) the area (m^2) with ungulate-adapted logging. All variables refer to logging that occurred the winter prior to spring data collection. See Table 1 for details.

2.2.2. *Scarification*

Scarification occurred during the summer from 2011 to 2014, one to two years after logging. Ungulate-adapted scarification occurred in 22 stands (306 ha) while 47 stands received conventional scarification (390 ha; Table S1). Conventional scarification practices in Norway typically expose 13–20% mineral soil to improve seedling regeneration (Øyen 2002). We classified 0–20% mineral soil exposure as low intensity (conventional) and >20% as high intensity (ungulate-adapted) (Øyen 2002).

Table 1

Forestry variables used for modeling. Each variable was extracted using 250, 500, and 1000-m buffers, which were centered on each plot. Scarification age refers to time since scarification (in years).

Variable	Description
Logging type	4-level factor indicating the presence of logging in buffered areas 0: no logging 1: conventional logging 2: ungulate-adapted logging 3: both conventional and ungulate-adapted logging
Area conventional logged	Area (m^2) within each buffer size that had conventional logging
Area ungulate-adapted logged	Area (m^2) within each buffer size that had ungulate-adapted logging
Conventional scarification age	5-level factor indicating the presence of conventional scarification age in buffered areas 0: no scarification 1: 1-year old scarification stand 2: 2-year old scarification stand 3: 3-year old scarification stand 4: 4-year old scarification stand
Ungulate-adapted scarification age	5-level factor indicating the presence of ungulate-adapted scarification age in buffered areas 0: no scarification 1: 1-year old scarification stand 2: 2-year old scarification stand 3: 3-year old scarification stand 4: 4-year old scarification stand
Area conventional scarification 1–2 yr	Area (m^2) within buffers containing 1–2-year-old conventional scarification stands
Area conventional scarification 3–4 yr	Area (m^2) within buffers containing 3–4-year-old
Area ungulate-adapted scarification 1–2 yr	Area (m^2) within buffers containing 1–2-year-old ungulate-adapted scarification stands
Area ungulate-adapted scarification 3–4 yr	Area (m^2) within buffers containing 1–2-year-old conventional scarification stands

Using the same buffer sizes as for logging, we created six scarification variables for each buffer size: variables (1) and (2) were 5-level factor variables indicating no scarification or the presence of 1–4 year old (time since scarification) conventional and ungulate-adapted scarification; variables (3) and (4) represented the area with ungulate-adapted scarification 1–2 and 3–4 years old in each buffer; and variables (5) and (6) represented the area with conventional scarification 1–2 and 3–4 years old in each buffer (Table 1). For the area scarified variables, we grouped stands by age because we would expect younger stands to have lower browsing biomass relative to older scarification stands.

2.3. *Plots*

We established long-term plots at varying distances from conventional and ungulate-adapted stands where we counted moose pellet groups and measured browsing metrics. We had three unique sites (site area: Gravberget = 47.4 km^2; Ljørdalen = 55.6 km^2; Plassen = 38.7 km^2; Fig. 2). Sites were on average 30 km apart (SD = 17.8; Fig. S1). Within each of the three sites, we systematically placed 20–21 quadrats of 500 × 500 m. Along each quadrat border, we placed four circular plots every 100 m, resulting in 16 plots per quadrat (Fig. 2).

2.3.1. *Pellet counts*

We counted ungulate pellet groups (Neff 1968) in 100-m^2 circular plots during late spring each year from 2012 to 2015. Pellet groups represent habitat use, or the time animal(s) spent in a plot (Månsson et al. 2007). Although moose were the dominant browser, we counted pellets for all ungulates present. We identified ungulate species by morphological characteristics of the pellets (Spitzer et al. 2019). To include a pellet group in our counts, >50% of the pellets from an individual group had to fall within the plot. Only piles with ≥20 pellets for moose and red deer, and ≥10 pellets for roe deer were counted. We visually distinguished between current winter and old (prior to winter) pellets. Typically, winter pellets were brown, in pellet form, and positioned on top of leaf litter and forest debris, while summer pellets were often in patty form, had leaf litter on top, or had mold or fungus growth (Zimmermann et al. 2015). We counted only current winter pellets, which corresponded to the winter browsing period. Pellets were removed from the plot each spring to avoid double counting the following year, except for the year prior to the start of our study.

2.3.2. *Browsing surveys*

In 2012 and 2015, we assessed browsing from the same plot centers as those where we conducted pellet counts but used 50-m^2 plots. We identified the tree species and counted the number of browsed and unbrowsed shoots from the previous growing season. A shoot was defined as live, woody growth ≥1 cm long. We registered browsing from only the current winter season (i.e., "fresh") where browsed shoots were still wet with resin and the wood had not died nor become grey (Ball and Dahlgren 2002). We counted browsed and unbrowsed shoots between 30 cm and 3 m above ground. The lower height represents average snow depth, below which trees are not available for browsing during winter, and the upper height represents the maximum browsing height for moose (Nichols et al. 2015). We counted browsed and unbrowsed shoots on up to 10 trees per species, working from the plot center to the edge in a spiral pattern. On each browsed tree, we used digital and manual calipers to measure twig diameter (to the nearest 0.1 mm) just below the bite for up to five bite diameters. When >5 browsed shoots were present, which was rare, technicians closed their eyes and grabbed shoots to measure. We also assessed browsing damage but only in young forests (cutting class 2; Table 2). See Table 2 for a summary of field measurements.

2.4. *Statistical analysis*

We used four response variables: density of undamaged Scots pine, bite diameters, browsing pressure, and moose habitat use (Fig. 1, Table 2). Browsing response variables were for Scots pine only. Undamaged pine were assessed only in young forests whereas the other three response variables represent forests of all age classes.

2.4.1. *Model fitting*

Model formulation differed by response variable. We defined *a priori* models using hierarchical regression models in a Bayesian framework (Gelman et al. 2013a). We fit presence of treatment (logging and scarification) and area of treatment in different models, resulting in four models per response variable per buffer size (48 models total). All logging and scarification models included additional habitat variables which were standard across each response variable (Tables 3 and 4). We fit logging and scarification models separately due to different expected temporal responses. With logging, we would expect slash piles to offer food only during the winter of logging and thus included data from all

Table 2
Field measurements used for modeling. The plot area was 50 m^2 for browsing variables and 100 m^2 for pellets. All variables were measured in each plot, except undamaged pine, which was assessed only in young forests (cutting class two). Response variables are indicated with a 'Y'.

Variable	Description	Scale measured	Response variable
Bite diameters	Diameter (mm) of Scots pine shoot measured below the point of browsing	Shoot	Y
Browsed	Number of browsed shoots per tree	Tree	
Unbrowsed	Number of unbrowsed shoots per tree	Tree	
Browsing pressure	Number browsed shoots per tree / number available shoots per tree	Tree	Y
Accumulated browsing	Measure of how the growth form of a tree has been affected by browsing during its lifetime 0: no old browsing 1: old browsing visible but growth form not changed 2: old browsing visible and growth form of tree changed. Examples include crooked stem or increased branching likely caused by one browsing event 3: old browsing visible and growth form strongly changed by repeated browsing	Tree	
Height	Height of the tree above ground (m)	Tree	
Undamaged pine	Binary variable indicating Scots pine damage (0) / non-damage per plot (1)	Tree	
Undamaged pine sum	Number of undamaged Scots pine per plot	Plot	Y
Pine density	Number of Scots pine per plot	Plot	
Moose	Number of moose pellet groups per plot	Plot	Y
Birch density	Number of birch (*B. pubescens* and *B. pendula*) per plot	Plot	
RAW density	Number of rowan, aspen, willow per plot	Plot	
Available shoots summed	Number of available (browsed + unbrowsed) Scots pine shoots summed per plot	Plot	
Cutting class	6-level factor of forest maturity 1: clear cut; no regeneration 2: visible regeneration, tree height <10 m 3: tree height >10 m 4: forest mature for logging, 55–75 years depending on productivity 5: old growth forest. Could include dead trees, deadwood 0: Non-commercial forest, open, tree crowns do not touch	Stand	

years. In contrast, scarification offers increasing amounts of food with age. We therefore used browsing data only for 2015 for scarification models, since we would not expect sufficient regrowth to occur shortly after scarification.

All continuous predictor variables were mean-centered and scaled to one standard deviation. We did not include correlated (Pearson $r > |0.7|$) variables in the same models (Dormann et al. 2013). We included spline-based smoothers ($k = 5$) on all continuous variables, as we expected non-linear responses.

We built hierarchical models (Tables 3 and 4) by including different spatial scales (shoot, tree, plot; Table 2) in different sub-models (Szewczyk and McCain 2019). For example, we included variables measured at the tree-level as 'fixed effects' (population level) and variables measured at the plot level as 'random effects' (group level). For model fitting, we used weakly informative (default) priors on all parameters (Appendix III) and randomly generated initial values. We fit all models using package *brms* (Bürkner 2017, 2018) which uses the Stan programming language (Stan Development Team 2018). We ran 4 chains with 2000 iterations with 1000 warmup each, which resulted in 4000 posterior samples. We checked parameter convergence by visual inspection of the chains and with the Gelman-Rubin diagnostic (Gelman et al. 2013a). We evaluated model fit of the top model with posterior predictive checks.

Our interests with model fitting were two-fold: first, we wanted to compare conditional effects of logging and scarification across buffer sizes to identify scale-specific responses. We thus interpret all models. Second, we did model selection to identify the scale explaining the most variation for each response variable. We did separate model selection for logging and scarification models since the datasets were different. We determined the most parsimonious model using Watanabe-Akaike information criterion (WAIC) weights. WAIC weights (w_i) can be interpreted similar to the more familiar Akaike information criterion (AIC) as the relative support for the model, given the data (Gelman et al. 2013a). WAIC is appropriate for Bayesian approaches as it averages over the posterior distribution rather than conditioning on a point estimate (Gelman et al. 2013b). All models were fit in program R version 3.6.1 (R Core Team 2018).

2.4.2. Density of undamaged pines

The number of undamaged pine trees per 50 m^2 was calculated as:

$$y_i = \frac{a_i}{b_i} \times c_i$$

where $a_i$is the number of undamaged pine assessed in plot i (field protocols capped this at 10), b_i is the number of pine assessed (capped at 10), and $c_i$is the total count of pine. This measurement is used to assess national forest regeneration regulations (Regulation of Sustainable Forestry: https://lovdata.no/dokument/SF/forskrift/2006–06-07–593). We excluded trees >10 m to be consistent with the definition of a young forest (Table 2).

We used a gamma distribution y_i $Gamma(n_i, \alpha)$ with a log link where n_i are the combination of predictor variables for each plot-level observation i and α is the shape parameter. We added 1e-5 to our response variable, as zeros were present (Zuur et al. 2009). We included fixed effect variables collected at the plot level: moose pellet counts, available shoots summed, birch density, and RAW density (Tables 3 and 4). Year was included as a fixed effect parameter because it had only two levels (2012, 2015) and would be difficult to estimate variance if included as a random effect. Pine density was excluded as a predictor variable as it was included in the response. To account for the nested sampling design, our grouping structure was an intercept of quadrat nested within site (Tables 3 and 4).

2.4.3. Bite diameter

We used a gaussian distribution $gaussian(\mu_f, \sigma)$ with an identity link where μ_f is the linear combination of predictors for the tree-level observation f and$\sigma$is standard deviation. A gaussian is appropriate to use on strictly positive values when the tail of the distribution has a low likelihood of overlapping zero, which is the case for bite diameters (Zuur et al. 2009). For fixed effect variables collected at the tree level, we included year, tree height, number of browsed shoots, number of unbrowsed shoots, damage presence, and accumulated browsing (Tables 3 and 4). Moose and pine density were collected at the plot scale and were used as slope terms, with the plot as the intercept. Because bite sizes are a trade-off between food intake and quality, we expected bite

Table 3
Candidate logging models for the four response variables density of undamaged pines, bite diameters, browsing pressure, and moose habitat use. Each model was run with 250-m, 500-m, and 1000-m buffer data. Subscripts refer to the level at which data were collected (i = plot, site = j, k = quadrat, f = tree). For random effect variables, values on the left of the | are used as slope terms and values on the right are intercept terms. Nested random effect terms are represented by /. Variables are defined in Tables 1 and 2.

Response variable	Model number	Years	Population level forestry variables	Population level habitat variables	**Group**
Density of undamaged stems	1	2012, 2015	logging type$_i$	year$_i$, moose$_i$, available shoots summed$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2012, 2015	area ungulate-adapted logged$_i$, area conventional logged$_i$	year$_i$, moose$_i$, available shoots summed$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
Bite diameters	1	2012, 2015	logging type$_f$	year$_f$, height$_f$, browsed$_f$, unbrowsed$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$ 1 $\mid$ treeID$_f$
	2	2012, 2015	area ungulate-adapted logged$_f$, area conventional logged$_f$	year$_f$, height$_f$, browsed$_f$, unbrowsed$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$ 1 $\mid$ treeID$_f$
Browsing pressure	1	2012, 2015	logging type$_f$	year$_f$, height$_f$, species$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2012, 2015	area ungulate-adapted logged$_f$, area conventional logged$_f$	year$_f$, height$_f$, species$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
Habitat use	1	2012–2015	logging type$_i$	year$_i$, cutting class$_i$, pine$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2012–2015	area ungulate-adapted logged$_i$, area conventional logged$_i$	year$_i$, cutting class$_i$, pine$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$

Table 4
Candidate scarification models for response variables density of undamaged pines, bite diameters, browsing pressure, and moose habitat use. Each model was run with 250-m, 500-m, and 1000-m buffer data. Subscripts refer to level at which data were collected (i = plot, site = j, k = quadrat, f = tree). For random effect variables, values on the left of the | are used as slope terms and values on the right are intercept terms. Nested random effect terms are represented by /. Variables are defined in Table 1.

Response variable	Model number	Years	Population level forestry variables	Population level habitat variables	Group
Density of undamaged stems	1	2015	ungulate-adapted scarification age$_f$, conventional scarification age$_f$	year$_i$, moose$_i$, available shoots summed$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2015	area ungulate-adapted scarification 1–2yr$_f$, area conventional scarification 1–2yr$_f$, area ungulate-adapted scarification 3–4yr$_f$, area conventional scarification 3–4yr$_f$	year$_i$, moose$_i$, available shoots summed$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
Bite diameters	1	2015	ungulate-adapted scarification age$_f$, conventional scarification age$_f$	year$_f$, height$_f$, browsed$_f$, unbrowsed$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$ 1 $\mid$ treeID$_f$
	2	2015	area ungulate-adapted scarification 1–2yr$_f$, area conventional scarification 1–2yr$_f$, area ungulate-adapted scarification 3–4yr$_f$, area conventional scarification 3–4yr$_f$	year$_f$, height$_f$, browsed$_f$, unbrowsed$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$ 1 $\mid$ treeID$_f$
Browsing pressure	1	2015	ungulate-adapted scarification age$_f$, conventional scarification age$_f$	year$_f$, height$_f$, species$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2015	area ungulate-adapted scarification 1–2yr$_f$, area conventional scarification 1–2yr$_f$, area ungulate-adapted scarification 3–4yr$_f$, area conventional scarification 3–4yr$_f$	year$_f$, height$_f$, species$_f$, undamaged$_f$, accumulated browsing$_f$	moose$_i$, pine$_i$ $\mid$ plot$_i$ 1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
Habitat use	1	2015	ungulate-adapted scarification age$_f$, conventional scarification age$_f$	year$_i$, cutting class$_i$, pine$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$
	2	2015	area ungulate-adapted scarification 1–2yr$_f$, area conventional scarification 1–2yr$_f$, area ungulate-adapted scarification 3–4yr$_f$, area conventional scarification 3–4yr$_f$	year$_i$, cutting class$_i$, pine$_i$, birch$_i$, RAW$_i$	1 $\mid$ site$_{ij}$ / quadrat$_{ijk}$

sizes to increase where habitat use was high and decrease with increasing pine density. We included quadrat and tree ID separately as intercepts. We included a unique tree identifier as we have repeated measures per tree (Tables 3 and 4).

2.4.4. Browsing pressure

We restricted analyses to Scots pine <10 m to be consistent with the density of undamaged pine analysis ($n_{removed} = 70$; $n_{total} = 8067$) and excluded trees where the number of available shoots was zero (i.e., no browse available; n = 2735 removed). We used a beta regression y_f $beta(\mu_f, \varphi)$with an identity link forφ and a logit link for u_f where f is the tree-level observation. We transformed the response variable to exclude zero and one:

$$y_{adjusted} = \frac{(bp_{tree} * (n-1) + 0.5)}{n}$$

where n is the number of observations (Smithson and Verkuilen 2006, Cribari-Neto and Zeileis 2010). We initially modeled browsing pressure with a binomial distribution, but the extreme tail led to poor model convergence and fit. We used a nested grouping structure to account for the design and repeated measures of multiple trees per plot. We included moose pellet counts and pine density as random slopes. Candidate models are presented in Tables 3 and 4.

2.4.5. Moose habitat use

We used the number of pellet groups as the response variable, which represents the time animal(s) spent in a plot. Månsson et al. (2007) identified pellet counts as an unbiased estimator of habitat use. We used a Poisson distribution y_i $Poisson(\lambda_i)$ with a log link, for each plot-level observation *i*. We included five plot-level population variables: year, pine density, birch density, and RAW density (Tables 3, 4). We lacked tree density data in years 2013 and 2014, when only pellet counts were conducted. Rather than excluding 2013 and 2014, which represented 45% of the full dataset, we imputed missing tree densities separately for each species (pine, silver birch, downy birch, rowan, aspen, willow spp.). Tree density in Scandinavia does not change substantially between years unless forestry activities occur (Hedwall et al. 2019). We used two complementary datasets to identify if a stand had forestry activities: (1) field data set (see Table 2) and (2) spatial dataset (i.e., boundaries of forestry activities in our study area; see Fig. 2). We used multiple imputation as a robust means to impute missing data (Sterne et al., 2009; White et al., 2011). Multiple imputation creates several imputed data sets based on other variables in the dataset. We created 10 different datasets (i.e., multiple imputation) and fit models separately to each dataset. This practice does have pitfalls (Rubin, 1996) but is becoming standard in the field of medicine, for example (Azur et al., 2011). We used multiple imputation by chained equations using the random forest algorithm from package *mice* (van Buuren and Groothuis-Oudshoorn 2011). We compared distributions of the univariate and multivariate datasets for each variable to evaluate prediction accuracy. Each model was fitted to the 10 datasets separately and posteriors were pooled across models. We evaluated sub-model convergence via r-hat values.

3. Results

3.1. Density of undamaged pine

We registered browsing damage in 424 young forest plots (Table S2, Fig. S3). There were no ungulate-adapted scarification stands older than two years within the 250-m buffers. From the hierarchical models, the density of undamaged pine was highest near ungulate-adapted logging and where both conventional and ungulate-adapted logging occurred, regardless of buffer size (Figs. 3 and 4). The area logged had minimal effect on the density of undamaged pine (Fig. S4). The most parsimonious logging model was logging presence within 1000 m ($w_i = 0.82$).

Plots near conventional and ungulate-adapted scarification stands showed contrasting relationships with the density of undamaged pine: plots close to one and four-year-old conventional scarification stands had the highest and lowest density of undamaged stems, though we note there was high uncertainty (Fig. 3). The area scarified had minimal effects on the density of undamaged pine (Fig. S5). The most parsimonious scarification model was scarification presence within 250 m ($w_i = 1$). From the top model, an increase in moose habitat use increased the density of undamaged pine from 13.9 to 21.2 undamaged pine per 50 m^2 when moose pellet group counts changed from 0.4 to 4.1 (Fig. S6). All

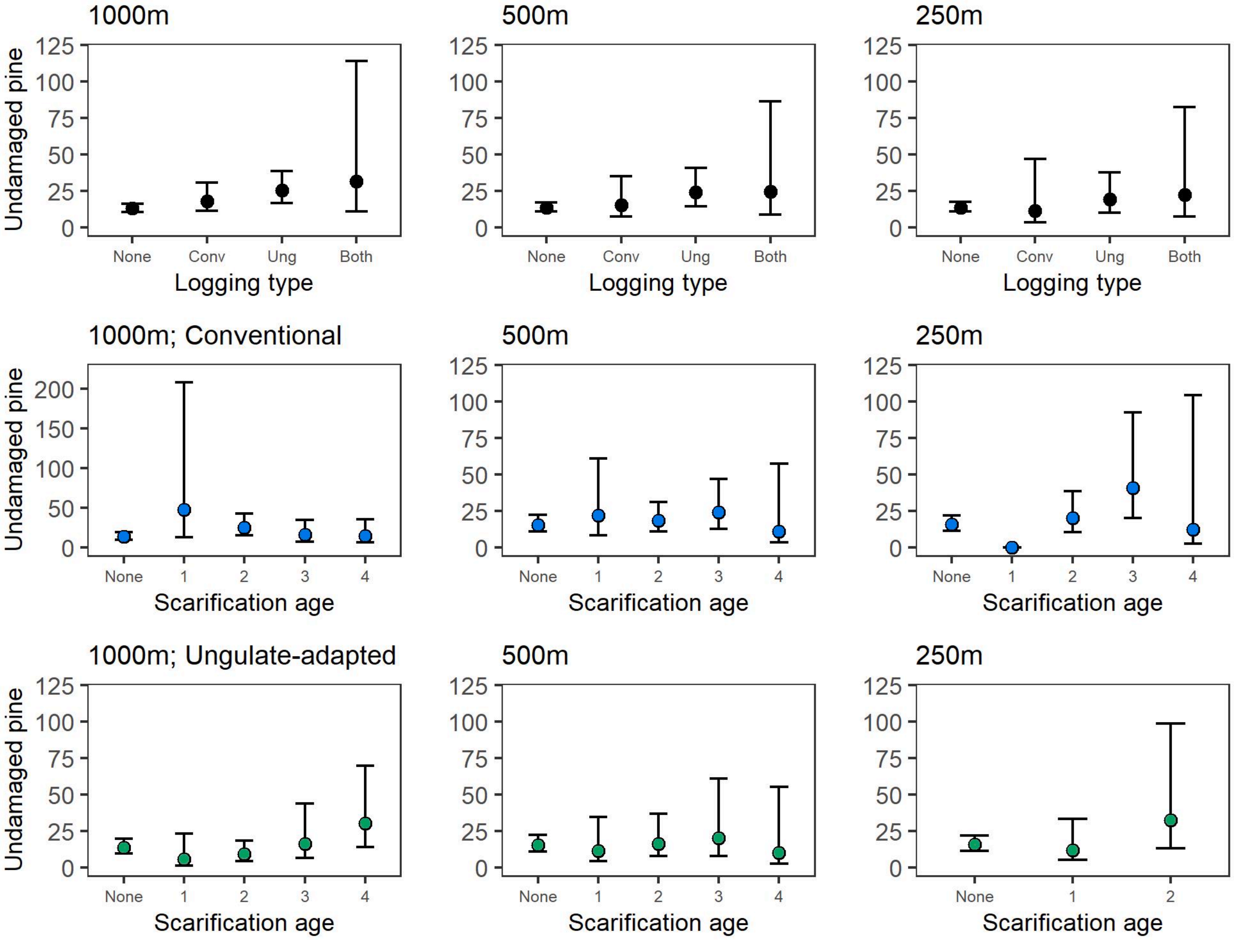

Fig. 3. Conditional effects of the presence of logging (top row) and scarification (middle and bottom rows) in 1000 m, 500 m, and 250-m buffers on the density of undamaged pine per 50 m^2. Logging data were from Norway in 2012 and 2015 (n = 424). Scarification data were from 2015 (n = 177). Bars represent 90% credible intervals. Scarification age represents time (in years) since scarification. Note the different y-axis limits for the middle row, left panel and lack of scarified stands >2 years of age in the lower right panel. In the top row of panels, ‘conv’ stands for conventional and ‘ung’ stands for ungulate-adapted logging.

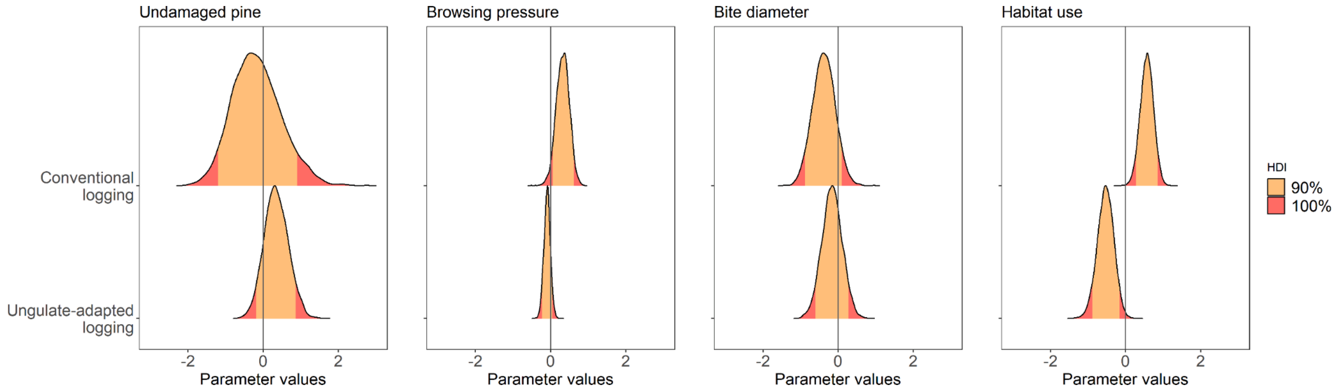

Fig. 4. Posterior probability distributions for presence of conventional and ungulate-adapted logging across four response variables. Posteriors are from 250-m buffer models. Highest density intervals (HDI) are drawn at 90 (orange) and 100% (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

logging and scarification models suffered from relatively poor model fit for large values of the response (Fig. S7).

3.2. Bite diameter

We registered 2620 individual bite diameters on 757 individual Scots pine (Table S2, Fig. S8). From the hierarchical models, the presence of logging within 250-m buffers decreased bite diameters in the plots (no logging = 3.61 mm, 90% CI = 3.34–3.89; conventional logging = 3.24 mm, 90% CI = 2.67–3.79; ungulate-adapted logging = 3.45 mm, 90% CI = 2.94–3.95) (Fig. 4, Fig. S9). Bite diameters were smallest where both ungulate-adapted and conventional logging occurred (3.04 mm, 90% CI = 2.40–3.67) which suggests that more logging decreased bite diameters. The area logged had a negative to neutral effect on bite diameters across buffers (Fig. S10). The most parsimonious logging model was the area logged within 1000 m ($w_i = 0.88$). From the top model, the

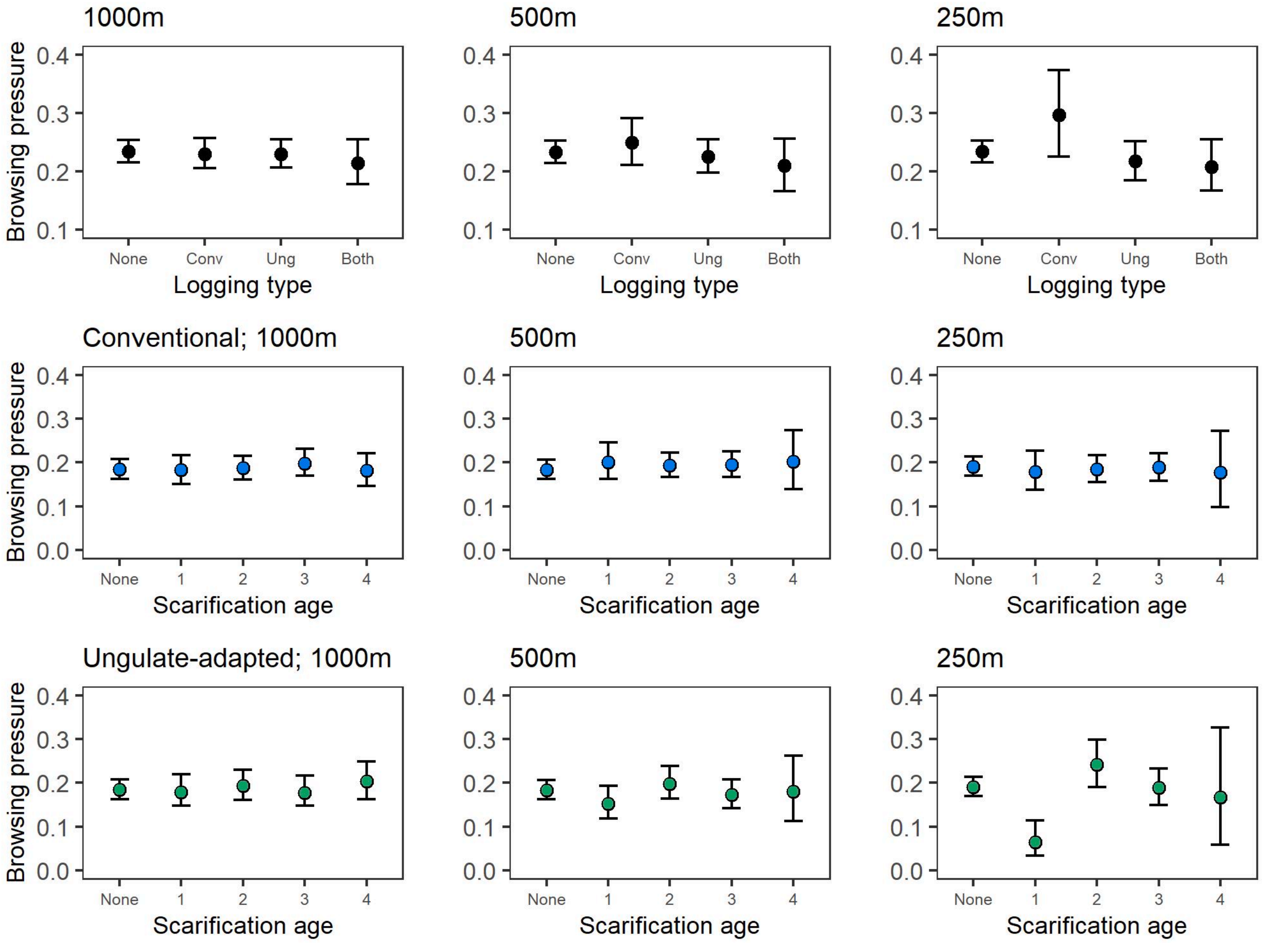

Fig. 5. Conditional effects of the presence of logging (top row) and scarification age (middle and bottom rows) on browsing pressure. Logging data were collected in 2012 and 2015 in Norway (n = 5262). Scarification data were from 2015 only (n = 2820). Error bars represent 90% credible intervals. Scarification age represents time (in years) since scarification. In the top row, 'conv' stands for conventional and 'ung' stands for ungulate-adapted logging.

presence of ungulate-adapted and conventional logging showed a decreasing trend of bite diameters until age four (Fig. S9). Bite diameters were largest at intermediate tree heights (Fig. S11), damaged trees had larger bites relative to undamaged trees (Fig. S11), and bites were largest when accumulated browsing levels were low (accumulated browsing 1: 3.92 mm, 90% CI = 3.58–4.30) and smallest when accumulated browsing levels were moderate (accumulated browsing 2: 3.58 mm, 90% CI = 3.27–3.92).

For scarification analyses, bite diameter data were restricted to 2015 (n = 1111 bites). From the data, maximum bite diameters were highest where scarification did not occur regardless of scarification type (Fig. S9). From the hierarchical models, bite diameters did not decrease as the scarified stand aged as expected (Fig. S9). The area scarified had minimal effects on bite diameters (Fig. S12). The most parsimonious scarification model was scarification presence, but weights were split among buffer sizes (500 m: $w_i = 0.30$; 1000 m: $w_i = 0.30$; 250 m: $w_i = 0.20$).

3.3. *Browsing pressure*

We assessed browsing pressure on 5252 Scots pine (Table S2, Fig. S13). From the hierarchical models, the area with conventional logging within 250 m had the highest browsing pressure at intermediate stand area treated (4.8 ha). The area with ungulate-adapted logging had a weak negative effect on Scots pine browsing pressure (Fig. S14). Parameter uncertainty increased as the buffer size decreased. The presence of logging had the strongest effect on browsing pressure at 250 m, where areas near ungulate-adapted logging stands had 27% lower browsing pressure than conventional logged stands (Fig. 5). The most parsimonious model was the area logged within 250 m ($w_i = 0.95$).

The area scarified had no apparent effects on browsing pressure, except for young ungulate-adapted scarified stands (1–2 years old) within 250 and 500 m where browsing pressure spiked at intermediate stand area (Fig. S15). The presence of scarification stands had the greatest effect at 250 m where browsing pressure was lowest at age one (0.06, 90% CI = 0.04–0.10) and highest at age two (0.24, 90% CI = 0.20–0.29) (Fig. 5). The most parsimonious model was the area scarified within 250 m ($w_i = 1$).

3.4. *Moose habitat use*

We registered moose pellet groups in 3630 plots (Table S2). Mean pellet groups were higher where logging occurred (logging = 0.43, SD = 1.09; no logging = 0.29, SD = 0.77) within 250 m (Fig. S16). From the hierarchical models, habitat use within 250 m was 67% lower near ungulate-adapted logged stands relative to conventional stands (Figs. 4 and 6). The area logged had minimal effect on habitat use (Fig. S17). The most parsimonious model was logging presence within 250 m ($w_i = 0.87$). From the top model, predicted habitat use was 1.8 times as high in young (cutting class two) and mature forests (cutting class five) relative to clear cuts (cutting class one), and habitat use peaked with an optimal pine density (Fig. S18).

For scarification models, habitat use declined as the conventional scarification stand aged whereas habitat use increased as ungulate-

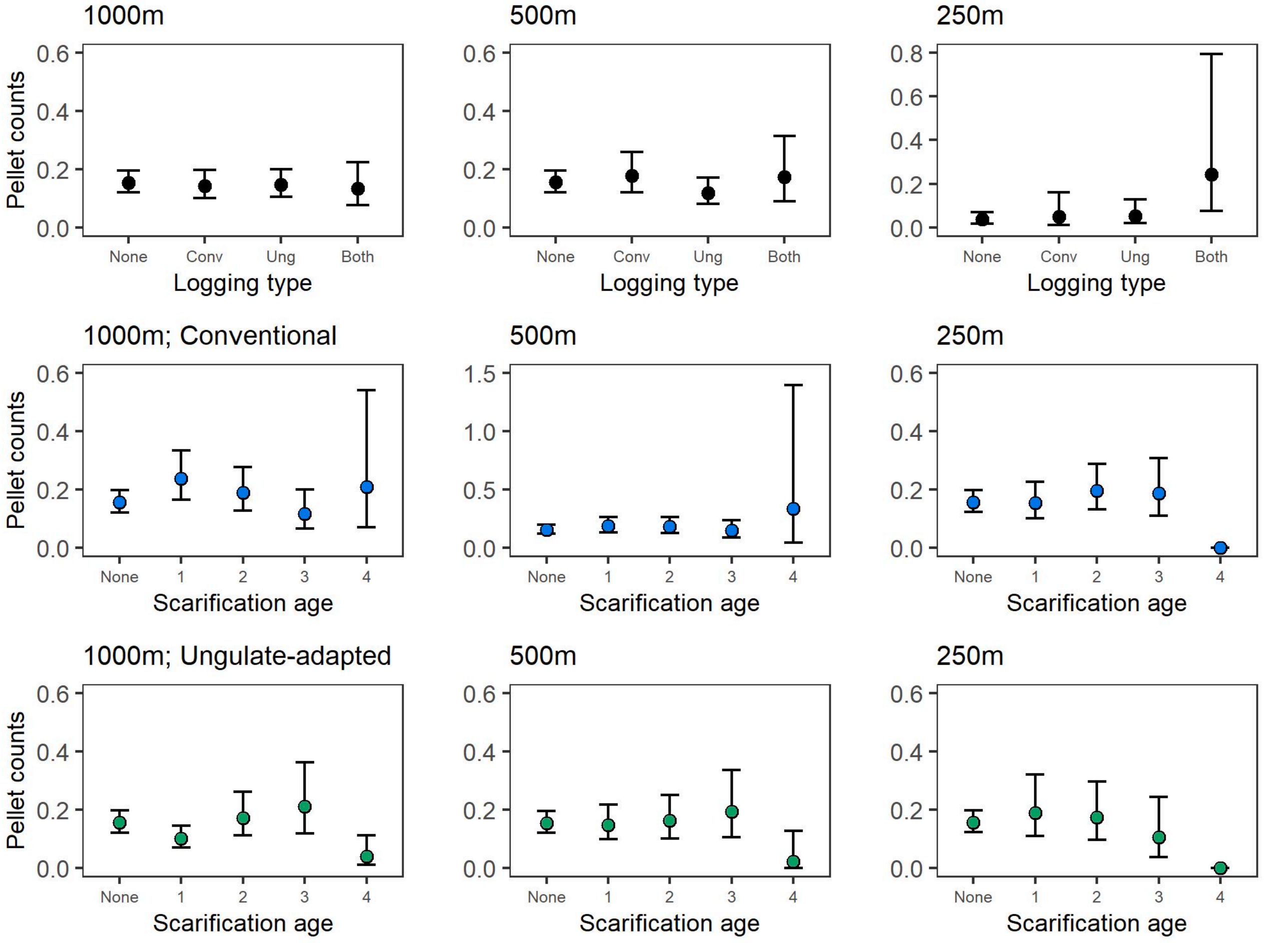

Fig. 6. Conditional effects of the presence of logging (top row) and scarification age (middle and bottom rows) on moose pellet counts. Data were collected from 2012 to 2015. Error bars represent 90% credible intervals. Scarification age represents time (in years) since scarification. Note the different y-axis limits for the upper right and center panels. In the top row, ‘conv’ stands for conventional and ‘ung’ stands for ungulate-adapted logging.

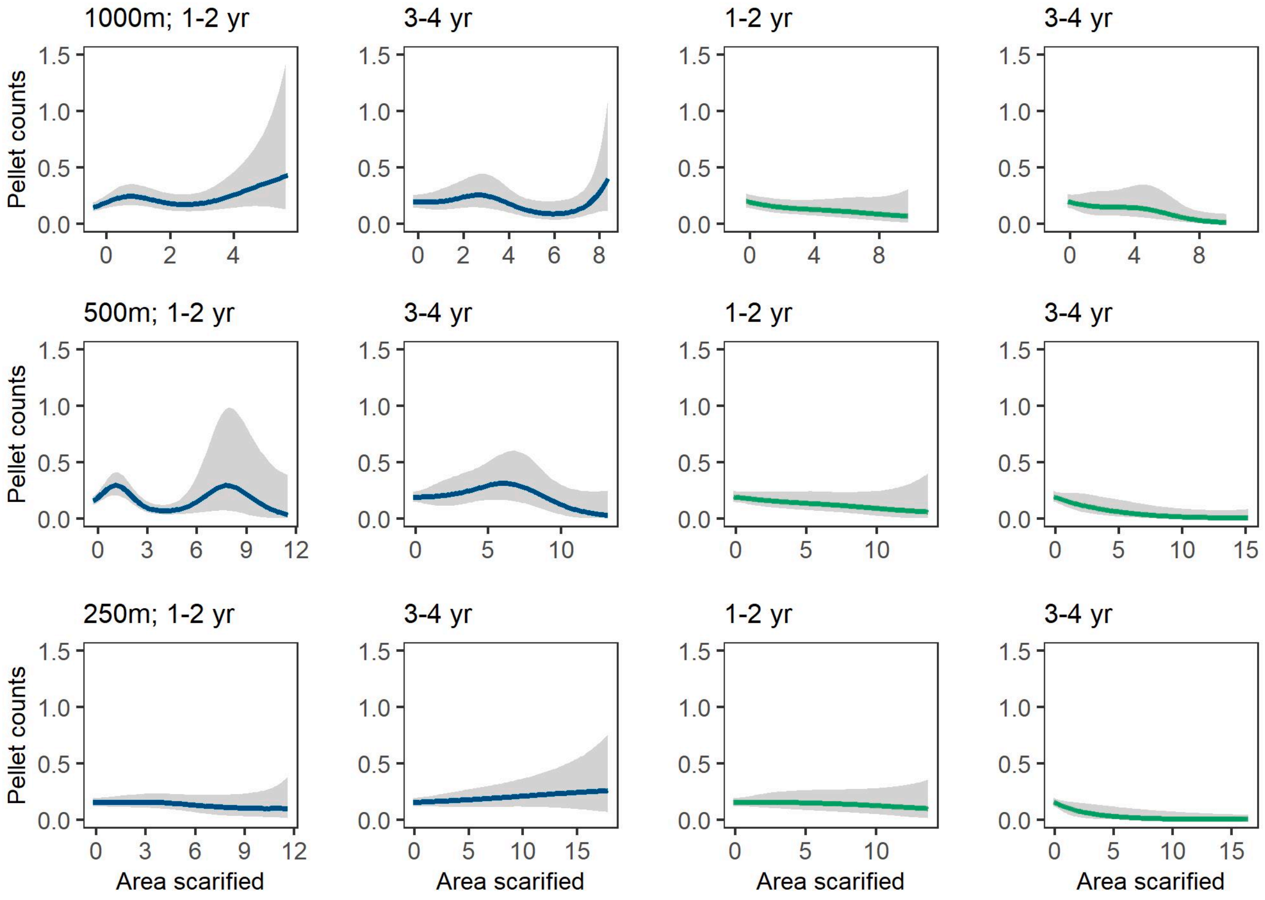

Fig. 7. Conditional effects of area scarified on moose pellet counts by conventional (blue line) and ungulate-adapted (green line) logging. Data were collected in Norway, with 3630 plots in 2012 (n = 976), 2013 (n = 670), 2014 (n = 992), and 2015 (n = 992). Grey ribbons represent 90% credible intervals. Scarification age (1–2 yr; 3–4 yr) represents time (in years) since scarification. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adapted scarification stand aged (Fig. 6). This effect was most pronounced at 1000 m. Moose habitat use decreased with the area of ungulate-adapted scarification, with strong non-linearities for plots near conventional scarification (Fig. 7). The top model was scarification presence within 250 m ($w_i = 1$).

4. Discussion

We tested whether ungulate-adapted forestry changed browsing damage, bite diameters, browsing pressure, and moose habitat use across three spatial scales. For logging, the density of undamaged pine increased near ungulate-adapted stands (supporting H1), bite diameters increased where logging did not occur (not supporting H2), and browsing pressure (supporting H3) and habitat use (supporting H4) decreased near ungulate-adapted logged stands. For scarification, results were more equivocal, but habitat use decreased over time near conventionally scarified stands but increased near ungulate-adapted stands (not supporting H4). Conditional effects of logging and scarification across response variables were most pronounced at 250 m (H5).

As expected, the density of undamaged pines was highest near ungulate-adapted logging, and where both conventional and ungulate-adapted logging occurred, regardless of buffer size (H1). The density of undamaged pine in plots was 1.4–1.7 times higher near ungulate-adapted relative to conventional logging stands across buffer sizes (Fig. 3). The mechanism for the damage decreases near ungulate-adapted stands could be explained by the concurrent decrease in browsing pressure and habitat use (i.e., pellet counts). A previous stand-level analysis found that available forage biomass doubled and mean biomass removed was higher in our ungulate-adapted logged stands (available biomass: 98 kg per ha) relative to conventional logged stands (available biomass 53 kg per ha; Mathisen et al. unpublished results). This would suggest that moose were able to maintain intake rates of Scots pine from slash piles, while concurrently reducing time spent feeding in the surroundings (H4).

Our results show promise for ungulate-adapted logging as a measure to increase the density of undamaged pine stems. Most of our study area occurs in forest productivity zones (site index) F6–8 and F11–14 (Astrup et al. 2019). According to the National Norwegian Regulation of Sustainable Forestry, F11–14 areas should have a minimum of 1900 pines per hectare, but 2280 to 4560 are recommended. F6–8 areas should have a minimum of 950 pines per hectare, but 1520 to 2470 are recommended (https://lovdata.no/dokument/SF/forskrift/2006–06-07–593). From our hierarchal models, conventional logging within 250 m reduced densities of undamaged pine (2254 pine per ha, 90% CI = 718–9394) outside the recommended range. However, ungulate-adapted logging increased densities (3882 pine per ha, 90% CI = 2048–7582) to within the recommended tree density. These results show strong support for ungulate-adapted logging as a mitigation measure against moose browsing damage.

While we found that the presence of logging treatments had a positive effect on the density of undamaged pine, the area treated rarely affected undamaged pine densities (Fig. S4). It is possible that we did not treat large enough areas, as has been suggested by other studies where extensive feeding is necessary to see any effects (Putman and Staines 2004). We suggest however that more research is required. For example, we expect forage saturation would occur (e.g., type II functional response) assuming many new individual moose do not move into the study area. Future research should focus on treating a range of stand sizes, particularly above our maximum ungulate-adapted logged stand size of 57 ha, to identify optimal stand sizes for specific contexts and scales.

We found browsing pressure was 27% lower near ungulate-adapted logged stands relative to conventionally logged stands (H3; Fig. 5). This was as expected due to the doubling in forage biomass via slash piles (Mathisen et al. unpublished results), increased browsing efficiency from slash piles versus dispersed trees, and potentially reduced plant secondary metabolites of slash contents because most shoots developed above moose browsing height. However, chemical responses to browsing remains poorly understood; for example, Burney and Jacobs (2012) found only one tree species (*Thuja plicata*) of a multi-species study that increased terpene production in response to simulated browsing. For unbrowsed trees, secondary metabolites differed by tree height and species: Nordengren et al. (2003) found secondary metabolites from field-collected tree samples (152–727 cm in height) increased with height for willows but decreased for birch. Our generalized understanding of tree chemical defenses in response to browsing remains limited. Despite the support of our hypothesis that browsing pressure decreased near ungulate-adapted stands, we should expect a two-fold decrease in browsing pressure relative to conventional stands if moose foraging matched the doubling in forage biomass. Our results did not support this. This mismatch could be because food availability is not the limiting factor in browsing damage. Our hierarchical models indicated food availability had a strong positive effect on the density of undamaged stems only when food availability was low. When food was highly abundant, there was no apparent effect on undamaged pine.

Another explanation for the mismatch is that slash pile contents are of lower quality than shoots available within browsing height, not higher quality as we suggested earlier. If this is the case, digestion of slash pile contents would take longer, thus limiting intake rates (Belovsky 1984). Moose may also require complementary diets (Felton et al. 2016, 2020; but see Hjeljord and Histøl 1999), which additional pine browse would not facilitate. The complementary diet approach contrasts with typical supplementary or diversionary feeding designs, where the goal is often to maximize energy intake or assumes that food is the limiting agent, without regard to balanced diets. For example, moose that eat carrots and potatoes in supplemental feed may be fiber deficient. This may increase their propensity to browse tree bark, which is high in fiber (Felton et al. 2020). We suggest that diet mixing and alternative forage in supplemental feed requires further research.

Our study design contrasts with many typical supplemental and diversionary feeding studies. First, slash piles and scarification stands resulted in dispersed resources, rather than few point locations where only the most dominant individuals can feed (Ozoga 1972, Putman and Staines 2004). Dispersed resources should also decrease time spent at the feeding site, as moose could avoid intense competition for resources. This would also reduce risk of disease transmission since individuals can avoid overcrowding (Mysterud et al. 2019). This is pertinent in Norway, where chronic wasting disease was recently detected in moose (Stokstad 2017). Second, the 'feed' in our study is a natural part of a moose's winter diet so the potential for individuals to suffer from pH imbalances or insufficient fiber are reduced (Mysterud 2010). This also reduces the potential of affecting behavioral traits or 'natural' selection of fed individuals or populations (Mysterud 2010).

As expected, we found logging and scarification effects on browsing pressure, and logging effects on moose habitat use, were strongest at the smallest spatial scale (250 m; H5). This corresponds to third-order patch selection whereby moose adjust movements within their winter home range to feed or rest near recently modified stands. Similar feeding patterns have been found for white-tailed deer (*Odocoileus virginianus*) (Ozoga and Verme 1970) and migratory moose in Sweden (Sahlsten et al. 2010). This makes sense both from a movement and energy maximization standpoint. On average, moose move very little while on their winter range (on average 2 km per day in winter in Scandinavia; Pfeffer et al. 2018). We would thus not expect moose to make long-distance winter movements 'in search' of our treatment areas; rather, they would adjust patch selection from within their seasonal home range. From an energy maximization standpoint, moose could feed in logged or scarified stands, which are on average quite small in our study (133 ha for conventional and ungulate-adapted logging and scarification stands) and still be close to resting sites in mature forest stands where this is protective cover. Based on our results, we cannot identify at what distances moose are influenced by our treatments and therefore cannot suggest at which distances ungulate-adapted stands should be placed from young forests. To help answer this question, we suggest future studies use concurrent GPS-collar data to evaluate multi-scale responses to ungulate-adapted forestry.

One unexpected result was the difference in peak habitat use by time since scarification: habitat use near conventional stands increased over time whereas habitat use near ungulate-adapted scarified stands decreased (Fig. 6). One explanation for this could be that both conventional and ungulate-adapted stands attract moose, but because ungulate-adapted stands have more forage, moose spend more time in the scarified stands. Because there is less forage in conventionally scarified stands, moose instead forage more in the surrounding scarified stands. Indeed, pioneering trees such as birch, which are attractive browse for moose, dominate regrowth in Scandinavian boreal forests (Wam et al. 2010). Another explanation for the decrease in habitat use over time near ungulate-adapted stands could reflect nutrient loss, which is facilitated by intensive mineral soil exposure from ungulate-adapted scarification. Nutrient loss could result in a slower regrowth period (Bergquist and Örlander 1998, Knudsen 2014). This is supported by an analysis in our study area: Saursaunet et al. (2018) found current annual growth of Scots pine and downy birch declined as soil scarification intensity increased. Slower regrowth in ungulate-adapted stands could influence not only the biomass available but feeding preferences by moose: previous research has shown that moose browsing increases as the plant reaches moose chest height (Bobrowski et al. 2015), so older stands (e.g., four versus one-year-old stands) may offer not only more abundant browse, but that which has lower handling time.

Despite the possible benefits of soil scarification to increasing ungulate food availability, it has extensive negative ecological effects: it facilitates soil carbon release, intensive site preparation may increase nutrient loss and decrease long-term site productivity, and is detrimental to understory species like bilberry, which are an important food source for herbivores (Atlegrim and Sjöberg 1996b, Jandl et al. 2007, Bergstedt et al. 2008, Maillard et al. 2010). Thus, the possible benefits of increased food availability of Scots pine must be weighed against the many detrimental effects for intensive soil scarification to be justified. For our study, we had more ambiguous signals from scarification effects on increasing the density of undamaged pine. As such, we recommend ungulate-adapted forestry should focus more on creating slash piles versus extensive implementation of intensive scarification.

Regardless of the benefits of feeding as discussed above, there are certainly risks associated with supplemental and diversionary feeding. Previous research has shown that feeding can change foraging patterns (van Beest et al. 2010a), restrict movement (Guillet et al. 1996), change the amount of time spent on seasonal ranges (Jones et al. 2014), increase the risk of disease transmission (Sorensen et al. 2013), and increase population productivity (Milner et al. 2014). A study reviewed by Putman and Staines (2004) found that the only variable correlated with red deer browsing damage was the presence of supplementary feeding: aggregations of deer around feeding stations produced high local densities, resulting in a significant increase in forest damage. Similarly, Mathisen et al (2014) found browsing pressure increased over time, likely due to an increase in carrying capacity from supplemental feeding. Feeding programs thus often require a simultaneous increase in ungulate harvest with concurrent population and forage monitoring. Feeding is also associated with a poor mismatch with the timing of migration and plant phenology (Jones et al. 2014): movements of migrating elk that did not use winter feed grounds in Wyoming, USA closely matched spring green-up. In contrast, fed elk stayed longer on stop-over locations resulting in a poor mismatch of green-up and later arrival to summer ranges. Fed elk also departed summer ranges early, resulting in fed elk spending nearly a month less on summer ranges than unfed elk. Migratory moose in Scandinavia (Singh et al. 2012) could display similar patterns, and the extended period on winter and transitional ranges could thus intensify browsing on the natural forage before winter feeding starts, thus counteracting the intended effects of supplemental feeding.

There are of course challenges in doing large-scale, long-term forestry experiments such as coordinating among different land tenures, having protocols followed at all levels of operation, and changing timber prices which make meeting forestry research goals unrealistic (Bashir et al. 2020). For example, we attribute much of our model uncertainties to few non-zero data points, meaning less logging and scarification occurred than we expected. In total, only 4.72 km^2 was logged during our study. Other items which researchers may consider in future research include how sawmills purchase timber (e.g., continuous supply, so forest owners are motivated to log both in the summer and not just the winter) as well as reduced costs with logging larger, continuous stands rather than more smaller, dispersed stands, which we had hoped for in our study. Despite these shortcomings, our data suggest that larger logged stands could increase density of undamaged pines. While beyond the range of our data, perhaps even larger ungulate-adapted logging stands would illicit a stronger positive effect on undamaged pine. While large-scale experiments are difficult, they are important since we will experience large scale habitat and wildlife range shifts with climate change, which will influence wildlife ecology, agriculture, and forestry.

4.1. Conclusions

Our results suggest that ungulate-adapted forestry can reduce browsing damage, but more work is needed to determine how the area logged can produce detectable effects on browsing damage and at what spatial scale we can see moose movement is affected. We found that the intensive scarification can reduce browsing damage as the stand ages, but this comes at a cost as soil scarification can have strong negative effects. We suggest that supplementary feeding should be followed by careful population and forage monitoring. Provided that feeding is dispersed, natural forage from adapted forestry could be a better alternative to silage feeding. Future research should focus on whether feeding ungulates with mixed forage (e.g., deciduous and coniferous) could better account for a complementary diet.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Christina Skarpe and Karen Marie Mathisen conceived of the research idea and study design. Anne Loosen and Karen Marie Mathisen contributed to data collection. Anne Loosen performed the statistical analyses with input from Olivier Devineau. Anne Loosen wrote the manuscript, and all authors contributed significantly to the final draft.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118808.

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3

Title: Twenty-three years of monitoring reveal disparate winter conditions between northern and southern moose populations in Scandinavia

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Abstract

Climate change is a threat to biodiversity and ecosystems across the globe. Changing temperatures and precipitation patterns can cause wildlife to shift landscape use to accommodate a changing thermal or food landscape. We studied landscape use patterns of a cold climate adapted species, the moose (*Alces alces*), in the boreal forests of Scandinavia where snow cover duration is projected to decrease by 30–40% by 2050 and winter warming events are projected to nearly double into the 21st century. We explored trends of winter moose pellet count data, a proxy for intensity of landscape use (hereafter, intensity of use), over two decades (1997–2019). We tested if ambient winter temperature, snow depth, and forest type drive moose intensity of use across a latitudinal gradient. We tested the 'forest maturity hypothesis' in northern and southern moose populations in Norway and Sweden, whereby mature forests give moose the behavioral flexibility to dissipate heat when ambient temperatures are warm, and to use areas with lower snow depths that may otherwise conceal low-growing foods and impede movement. We found mean winter temperatures increased over time for northern and southern populations, but mean snow depth declined over time only for southern moose populations. For both populations, we found intensity of use decreased once snow depths reached 20–30 cm and temperatures exceeded 0°C, suggesting a shift in landscape use in response to the snow and thermal landscape. In southern populations, moose used areas with a high proportion of young forests regardless of temperature. Similarly, the intensity of use increased with increasing snow depths at a greater rate when the proportion of young forests (i.e., not mature forests) was high. Our results suggest that moose regularly tolerate winter temperatures that exceed those previously thought to initiate thermal stress in moose (-5°C). We suggest that northern populations might be more flexible in their response to climate change, as they can adjust migration depending on autumn conditions, and that southern populations may currently be more dependent on thermal cover to withstand to a changing thermal landscape. In a changing climate, wildlife and forest managers must emphasize the conservation of high-quality habitats that can sustain moose to support both foraging and thermoregulatory requirements.

Key words

Alces alces; boreal forest; climate change; deer; habitat; moose; pellets; snow; temperature; ungulate.

Introduction

Winter can be a nutritional and energetic bottle-neck for many wildlife species (Bowman et al. 2005, Coltrane and Barboza 2010). At northern latitudes, cold temperatures require sufficient body insulation (Scholander et al. 1950) while deep snow often decreases food availability (Rominger and Oldemeyer 1990, Hovey and Harestad 1992) and can be energetically costly to move through (Parker et al. 1984). Mammalian behavioral strategies to cope with winter are diverse, ranging from hibernation, migration, seasonal use of marginal areas (e.g., wind-swept ridges and plateaus), reduced movement, and habitat selection for thermal cover or reduced snow depth (Mysterud 1999, Mysterud and Østbye 1999, Hall et al. 2016). Understanding how and when certain landscapes or habitats are used during this limiting season is critical for wildlife management and conservation, because it is may result in important fitness-related behaviors that affect wildlife populations (McLoughlin et al. 2006).

Climate change is a pervasive phenomenon causing poleward shifts in wildlife distributions and altered movement patterns in response to changing, and sometimes unpredictable, resource distributions (Parmesan et al. 2003, Hickling et al. 2006). This poses a challenge to wildlife in coping with increased environmental and climatic variation, as well as managers tasked with monitoring wildlife movements and population vital rates. The boreal, which spreads across high northern latitudes, is one of the world's largest biomes and has been identified as among the most vulnerable ecosystems to climate change, with species extinctions and biome shifts (e.g., permafrost melting, increased fire frequency and intensity, insect outbreaks) expected (IPCC 2007, Soja et al. 2007). We know little about how wildlife in the boreal biome are responding to warmer and more variable winters, particularly large herbivores, which can act as a keystone species (Danell et al. 2006). This is especially important because large herbivores can alter carbon stores and have a 'cooling effect' by constraining shrub and tree growth (Leroux et al. 2020, Vuorinen et al. 2020).

While climate change is expected to govern terrestrial biodiversity loss, land use change is expected to be a similarly important driver of biodiversity loss, especially in boreal forests (IPCC 2007). In the 20th century, the industrialization of commercial forestry in the boreal caused a shift from selective logging to clearcutting. This meant that many forested regions, which were formerly mixed-age and mixed-species forest stands, are now dominated by single-species and single-aged stands (Östlund et al. 1997). Today, about two-thirds of boreal forests under some form of land management, primarily for wood and timber production (Gauthier et al. 2015), and the boreal forest is expected to undergo the most rapid land use change in the coming decades, second only to the tropics (Soja et al. 2007, Hansen et al. 2013). This has direct and indirect effects on ungulates. For example, the industrialization of forestry in Scandinavia changed the foraging landscape as young pine (*Pinus sylvestris*) thrived in newly created clearcuts. Scots pine is a primary food source for moose during winter (Cederlund et al. 1980). This increase in food availability for moose (*Alces alces*), as well as a shift in hunter harvest strategy via sparing of reproductive females, contributed to an increase in moose densities in the 1980's and 1990's, resulting in some of the highest moose densities across the globe (Lavsund et al. 2003, Jensen et al. 2020).

Moose, the largest boreal herbivore, are well-adapted to the boreal biome. With an average chest height of one meter, large hoof surface area and dew claws which help distribute body weight, long winter guard hairs, and a dense undercoat, they are able to adeptly handle severe winters (i.e., low temperatures and deep snow; Kelsall 1969, Telfer and Kelsall 1984, Renecker and Hudson 1986). Although severe winters can reduce overwinter survival and recruitment of young moose (Turner et al. 1994, Hegel et al. 2010), the warmer, highly variable winters associated with climate change have been partially attributed to drastic moose population declines, particularly across their southern North American distribution (Monteith et al. 2015, Hoy et al. 2017, Shively et al. 2019). Variable winters can also result in moose space use shifts. For example, shallow snow depths (e.g., 30 cm) can cover low-growing foods like bilberry (*Vaccinium* spp.) whereas snow depths of 40–70 cm can begin to impede moose movement (Kelsall 1969, Rounds 1982), thus increasing locomotion costs (Lundmark and Ball 2008). Previous work has shown closed-canopy areas hold less snow compared to open areas (Mysterud and Østbye 1999) so use of mature forests may be a strategy to find low-growing foods and deal with increased locomotion costs. As well, moose often migrate from summer ranges in high-elevation mountainous areas to low-elevation valley bottoms in winter where snow depths are reduced (Sweanor and Sandegren 1988, Bunnefeld et al. 2011, Singh et al. 2012). Singh et al. (2012) found the tendency to migrate was related to variation in snow depth and road density, with migration increasing with latitude.

In addition to winter snow depth, air temperature can also directly influence moose. Thompson et al. (2020) found that in summer, as ambient air temperature increased so did respiration rates, which increased metabolic rates and energetic demands. Rumination can increase internal body temperature, and reduced intake rates have also been correlated with warm air temperatures during the growing season (Shively et al. 2019). This trade-off could result in reduced physical condition, and ultimately reduced fitness (Renecker and Hudson 1986, van Beest and Milner 2013). This trade-off could also result in the increased use of cooler areas within the landscape on warm winter days to increase heat dissipation. For example, young forests provide high quantity and quality food (Wallgren et al. 2013) but provide minimal thermal cover in winter (Mysterud and Østbye 1999). On warm winter days, moose seek thermal cover in mature forests to rest, at the cost of diminished food availability and time spent feeding (Mysterud and Østbye 1999, Dussault et al. 2004, Van Beest et al. 2012, Street et al. 2015, Ditmer et al. 2018, Arsenault et al. 2019, Jennewein et al. 2020, Thompson et al. 2021). Thus, moose may trade-off foraging for resting to mitigate against warm ambient temperatures.

Scandinavia is part of the boreal biome and is an ideal study area to evaluate spatial shifts of moose in response to changing winters; recent winters have been highly variable and mean winter temperature has shown an upward trend (Hallinger et al. 2010). Climate change scenarios in Scandinavia predict increasingly warm winter temperatures (smhi.se) and a 30–40% decrease in snow cover duration by 2050 (Callaghan et al. 2011). Extrinsic factors such as winter severity (snow depth, air temperature) could also have a strong influence on moose space use, specifically local aggregations of moose (Figure 1), and this may vary from year-to-year. The largest impacts of climate change to the forestry industry are expected to be felt earliest in boreal systems (IPCC 2007). This inter-annual variation presents an obstacle to successful forest management and mitigation to moose-forestry conflicts remains a knowledge gap.

We explored trends in two decades (1997–2019) of moose winter moose pellet count data in Norway and Sweden (Neff 1968, Månsson et al. 2011). We then analyzed how weather and environmental factors affected these trends. Work by Månsson et al. (2011) showed that pellet counts can be an unbiased representative of moose habitat use when compared with moose GPS collar data. For our study, we adopted similar terminology but utilized ‘intensity of landscape use’ (hereafter, intensity of use) instead as we were not exclusively evaluating habitat. Specifically, pellet group counts were a measure of the intensity of use for an entire winter (i.e., from leaf-fall to snowmelt; Zimmermann et al. 2015). With these data, we asked if ambient air temperature, snow depth, and forest type drive moose intensity of use across a latitudinal gradient. We tested the forest maturity hypothesis, whereby mature forests give moose the behavioral flexibility to rest and dissipate heat when ambient temperatures are warm, and provides areas of reduced snow depth. We predicted: 1) the interaction between temperature and young forests will decrease intensity of use in young forests during warm winters, where there is low thermal cover (P1); 2) the interaction between snow depth and young forests will decrease intensity of use in young forests with deep snow, but increase as snow depth declines (P2). We tested our predictions across a latitudinal gradient, which was correlated with snow depth, temperature, and migration strategy. Generally, the tendency to migrate increases with latitude (Singh et al. 2012, Allen et al. 2016). We also predicted: 3) a dampened response to snow in northern moose populations as result of migration (P3). Late-season snows on moose summer ranges could delay moose migration onto their winter range. Thus, thus the link between snow depth and intensity of use may be decoupled in northern populations, as we could not accurately define summer range conditions. In contrast, southern moose tend to migrate less, so we expected a decrease in intensity of use of quadrats with higher snow depths.

Figure 1. Moose, which are typically solitary animals, congregate in a young forest during winter in Scandinavia. Photo credit: Jon Martin Arnemo

Study area

Our study area is situated between 57.0° and 66.3° N and 12.2°–22.2° E in Norway and Sweden (Figure 2). The area is characterized by cold, snowy winters and short, cool summers. Winters are colder and have higher snow depths in the north relative to the south. The landscape is dominated by boreal and hemiboreal forests (Ahti et al. 1968), which are managed for timber and pulp production. Production forests, which are dominated by coniferous trees, typically undergo 1–2 pre-commerical thinnings and another 1–2 thinnings to optimize commercial tree density. Mature trees are harvested in clear-cuts, resulting in a mosaic of even-aged patches or stands of trees (Andren and Angelstam 1993, Axelsson and Östlund 2001, Rytter et al. 2014). Regeneration occurs from planted trees or naturally from seed trees. Forestry has created a high-density network of low-traffic gravel roads, hereafter called secondary roads. High-traffic paved roads (hereafter, primary roads) are less common. Densities of both road types are higher in the south relative to the north.

Common tree species include Scots pine, silver birch (*Betula pendula*), downy birch (*Betula pubescens),* Norway spruce (*Picea abies*), grey alder (*Alnus incana*), black alder (*Alnus glutinosa*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula).* The frequency of tree species varies by site. The dwarf-shrub layer is typically dominated by heather (*Calluna vulgaris*), lingonberry (*Vaccinium vitis-idaea*), bilberry, and other shrubs (*Ericaceae* spp.). In boggy areas, *Sphagnum* spp. mosses are dominant (Moen et al. 1998). Generally, rowan, aspen, and willow are rare relative to Scots pine and birch, and are highly selected by moose (Shipley et al. 1998, Månsson et al. 2007). Spruce is rare in moose diets (Cederlund et al. 1980).

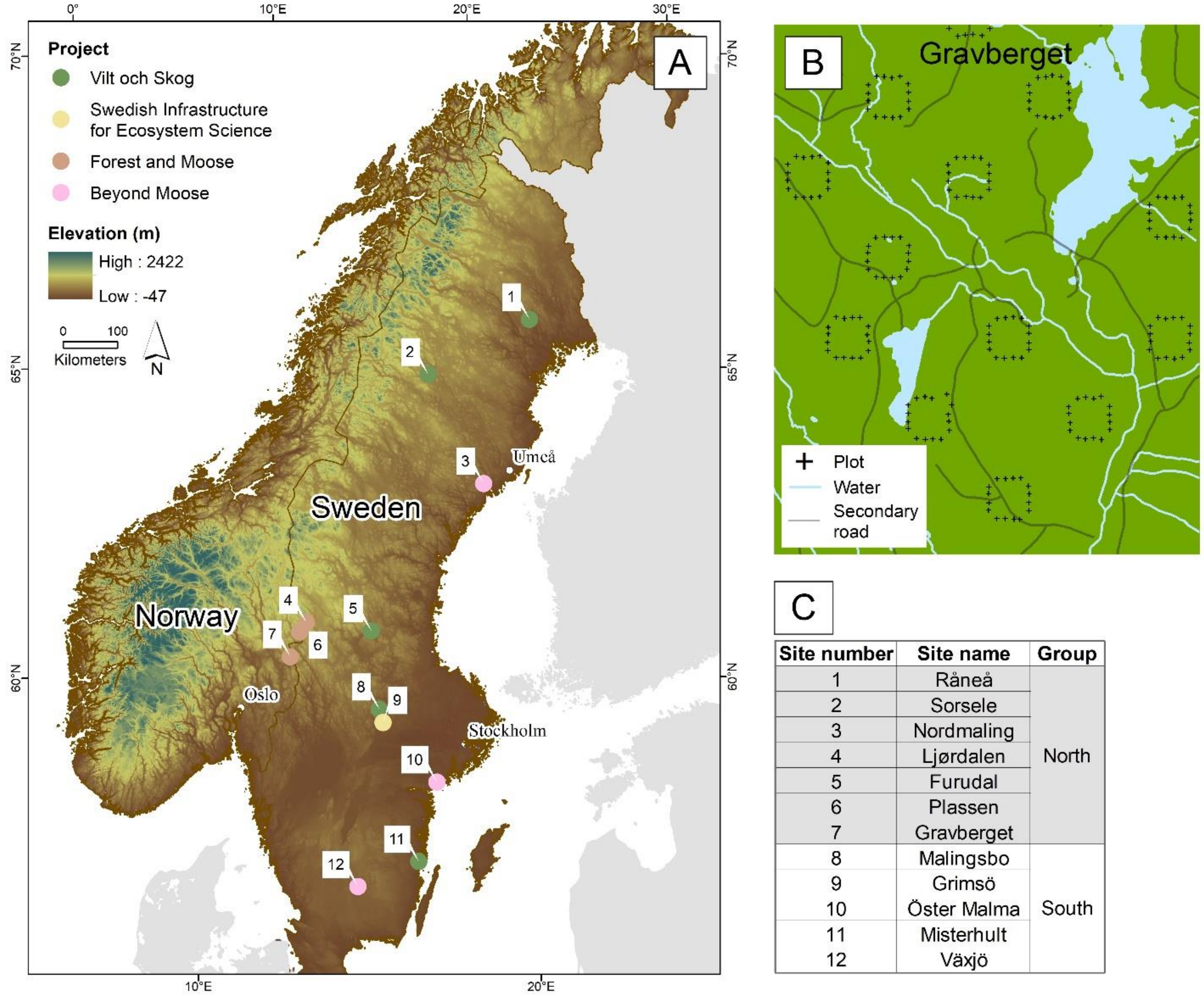
The intensification of clear-cut practices in the 1970's and sex-specific harvest led to an increase in moose densities, which peaked in the 1980's and 1990's. Local winter densities reached 5–6 moose per km^2 (Lavsund et al. 2003, Milner et al. 2013), though numbers have since declined. Average annual moose densities vary across our study area (0.50–2.6 moose per km^2; Sand et al. 2006b, Mattisson et al. 2013, Zimmermann et al. 2015, Pfeffer et al. 2018), as do assemblages and abundances of other deer species. Roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and red deer (*Cervus elaphus*) have higher densities in the south and along the coast (based on hunting statistics; älgdata.se and viltdata.se). Carnivores include wolves (*Canis lupus*), brown bears (*Ursus arctos*), wolverines (*Gulo gulo*), and Eurasian lynx (*Lynx lynx*). Carnivore and their relative densities and distributions are unevenly distributed across Scandinavia (Bischof et al. 2019). Wolves and bears prey on neonate moose calves in the spring and early summer, and moose are the main prey of wolves throughout the year (Swenson et al. 2007, Sand et al. 2008, Zimmermann et al. 2015). Despite this, moose have shown a weak habitat selection response to the recolonization of wolves (Sand et al. 2006b, Månsson et al. 2017, van Beeck Calkoen et al. 2018). Bears are not active during winter.

Data

Pellet data

Pellet group data were collected during four research project periods between 1997 and 2019. In Norway, the ‘Forest and Moose’ project monitored 992 plots annually from 2012–2019 (except 2016). In Sweden, ‘Vilt och Skog’ monitored 3285 plots annually in 2008, 2009, and 2011, ‘Beyond Moose’ monitored 2832 plots annually from 2012–2019, and ‘Swedish Infrastructure for Ecosystem Science’ monitored 551 plots annually from 1997–2019. For populations classified as partially migratory in central and northern Scandinavia (Supplementary information: Figure S 3), sites were chosen because they were wintering areas for moose. We assumed each site represented a unique moose population, as sites were at a minimum 20 km apart. The combined data resulted in 12 unique sites, spanning 23 years (Figure 2). The area of each site varied (min area = 38.7 km^2; max area = 1330.0 km^2), but all projects used similar methods for counting moose pellet groups at fixed monitoring plots, which followed a nested design. Quadrats (Norway: 500 x 500 m; Sweden: 1000 x 1000 m) were systematically placed within each site (Figure 2). Along each quadrat's border, circular plots were distributed every 100 meters (Norway) or 200 meters (Sweden), resulting in 16 plots per quadrat for all sites except Grimsö, where there were up to 23 plots per quadrat.

We counted moose pellet groups in 100-m^2 circular plots during late spring just after snowmelt. Although moose are the dominant browser in most sites, we counted pellets for all deer species because the presence of other deer could influence moose space use. We identified deer species by morphological characteristics of the pellets and the number of pellets per group (Spitzer et al. 2019). To register a pellet group, > 50% of the group needed to fall within the plot (Norway) or the center of the group was within the plot (Sweden). A minimum number of 20 moose pellets were required to register pellets as a group. We distinguished between fresh (current winter) and old (prior to current winter) pellets. Typically, winter pellets were brown, in pellet form, and positioned on top of leaf litter and forest debris. Summer pellets were often in patty form, had leaf litter on top of pellets, or had mold or fungus growth (Zimmermann et al. 2015). We were only interested in winter pellets for this analysis. Site numbers 4, 6, 7, and 9 (Figure 2) were cleaned each year to avoid double counting pellet counts the following spring (Månsson et al. 2011).



Site number	Site name	Group
1	Råneå	North
2	Sorsele	
3	Nordmaling	
4	Ljørdalen	
5	Furudal	
6	Plassen	
7	Gravberget	
8	Malingsbo	South
9	Grimsö	
10	Öster Malma	
11	Misterhult	
12	Växjö	

Figure 2. Map of A) twelve study sites in Norway and Sweden where we conducted moose pellet group counts. Sites colors represents different projects; B) plots nested within quadrats at each site, which were placed at varying distances from roads; C) a table listing the site number, site name, and latitudinal grouping. Site numbers in the table correspond to numbers mapped in 'A'.

Weather variables

We downloaded snow depth and temperature data from all available weather stations in Sweden (smhi.se) and eastern Norway (met.no) for the duration of our study. From the point location datasets, we extracted mean annual snow depth (cm) and mean annual winter temperature (°C) (Table 1). We used winter means, as this matched the temporal resolution of our pellet counts. For winter temperature, we defined 'winter' as Oct 1–April 30 (Zimmermann et al. 2015). We used co-kriging to create continuous surfaces from the point data. We co-kriged using spatial variables elevation (m, 25-m spatial resolution, European Digital Elevation Model, version 1.1), latitude, and longitude. This resulted in separate continuous surfaces for snow depth and winter temperature for each year from 1997 to 2019. Co-kriging was done in ArcMap version 10.3.1 (Environmental Systems Research Institute 2011). We validated each kriging model by correlating observed with predicted values (Supplementary information: Table S 2).

Moose harvest density

Hunter harvest plays a strong role in moose population dynamics, where on average 196,000 moose are shot each year in Norway and Sweden (statistics for years 2011/12–2014/15 from ssb.no and älgdata.se). In Norway, time-lagged hunter harvest data (t – 1 year) is correlated with moose density (Ueno et al. 2014). We acknowledge different management objectives could de-couple the moose density/ harvest density relationship, but these are the only reliable moose density indices available at national extents that are common to both Norway and Sweden. We used the number of moose shot per km^2 the year prior to pellet counts as a proxy for moose harvest density (Tallian et al. 2017). We used moose harvest data from both Norway (ssb.no/en/elgjakt; hjortevilt.no/) and Sweden (algdata.se). We first related the average weighted mean harvest density to each hunting district (mean area = 150,928 ha, SD = 251,423 ha) in Sweden and the municipality in Norway (mean area = 109,838 ha; SD = 110,935). This resulted in spatial data of moose harvest densities from 1996–2019. The harvest variable represents a coarse scale process (i.e., site scale). To intersect harvest densities with our sites, we created minimum convex polygons around the plots at each site to define 12 unique ‘site’ geometries. We then did a spatial intersection to relate moose harvest density to our site polygons. Intersections were done in program R version 4.0.3 (R Core Team 2020)

Other covariates

Secondary roads provide food benefits to moose, but also increase predation risk (Bowman et al. 2010, Eldegard et al. 2012, Loosen et al. 2021). Thus, secondary roads present a foraging/predation tradeoff. We excluded primary roads because they are consistently avoided by moose (Seiler et al. 2003, Eldegard et al. 2012, Loosen et al. 2021). We calculated the Euclidian distance (m) from the quadrat centroid to the nearest secondary road. Road data were from national road inventories (Norway: Geonorge; Sweden: Lantmäteriet). Young forests provide abundant winter forage for moose (Shipley et al. 1998), so we created an annually varying ‘young forest’ (5–20 years old) variable based on stand maturity data in Norway, which was collected in the field, and national forest inventory data in Sweden (Skogsstyrelsen). Because latitude was highly correlated with many of our variables, and we expected differing responses by latitude due to migration, we created a site-level variable distinguishing between northern and southern moose populations. Latitudinal groupings were based on snow depth, temperature, and migration strategy (Figure 3). Migration strategies were assigned based on GPS collar data, annual project reports, and primary literature. See the Supplementary information for classifications and supporting literature (Table S 1). We included the sampling day of the year as this influences the accumulation period during which pellets are deposited (Table 1). Spatial extractions of covariates were done in either ArcMap and R. Covariates are summarized in Table 1.

Statistical methods

Intensity of use

We tested our hypotheses by looking at moose intensity of use over time. Intensity of use (i.e., the number of moose pellet groups per quadrat per year) was our response variable. We aggregated the data to the quadrat level, which corresponds to the 3^{rd} order scale, the scale described by Johnson (1980) as the selection of feeding sites within the home range. This scale is relevant to forest owners because it can result in large economic losses from intensive browsing. Thus, we refer to pellet groups as intensity of use at the quadrat level. We used a Poisson distribution with a log link and two offsets: 1) sampling day of year, assuming a longer window would allow for more pellet group depositions; 2) the number of plots per quadrat, which varied by site. We assumed the higher number of plots per quadrat could result in higher pellet group counts. We split our dataset into northern (n = 877) and southern (n = 1490) populations. We did this for two reasons: 1) to avoid 3-way interactions, which are difficult to interpret; 2) because we expected different responses to snow in northern and southern populations due to migration, as explained above. For each dataset, we defined two candidate models using generalized additive mixed models (GAMM): 1) temperature * young forest; 2) snow depth * young forest. Interactions were included as tensor smoothers, which are recommended if the covariates are in different units/scales. For all models, we also included distance to secondary roads, young forest, and moose harvest density as smooths (i.e., non-linear functions), as these are known to influence moose intensity of use. Variables are described in Table 1.

All models included site as a random intercept to account for site-level differences. Thus, we discuss within-site, rather than between-site, variation. Because we used moose harvest density to account for moose density, and this represents annual changes in a biologically meaningful way more so than just ‘year’ (i.e., year was a nuisance variable), we excluded ‘year’ as an explicit time predictor variable. Snow depth and temperature were correlated (Pearsons correlation coefficient > 0.7) and were not included in the same models. All other variables had correlation coefficients < 0.7 (Supplementary information: Table S 3).

To account for temporal autocorrelation in our data, we fit each model with an autoregressive moving-average model (ARMA) correlation structure. In the autoregressive portion (AR) of the model, the response variable is regressed on previous (lagged) values. The length of lag is defined by '*p*'. The moving-average (MA) portion of the model is a defined by '*q*', the size of the moving window. We allowed *p* and *q* values from range one to three. We chose three as the maximum value as this was the maximum duration of most of our study projects. Varying *p* and *q* values resulted in nine candidate correlation structures. We chose the best autocorrelation structure based on AIC values from the linear model component of the GAMM. We considered models < 2 AIC apart to be equally supported, and chose the simpler (i.e., smaller *p* and *q* values) model. From this final model, we evaluated model fit two ways; we visualized residual autocorrelation across temporal lags, and we performed a Ljung-Box test (Ljung and Box 1978) for examining the null hypothesis of independence of observations, where p-values > 0.05 indicated lack of autocorrelation of the time series (i.e., good model fit). We fit models with R package 'mgcv' (Wood 2011).

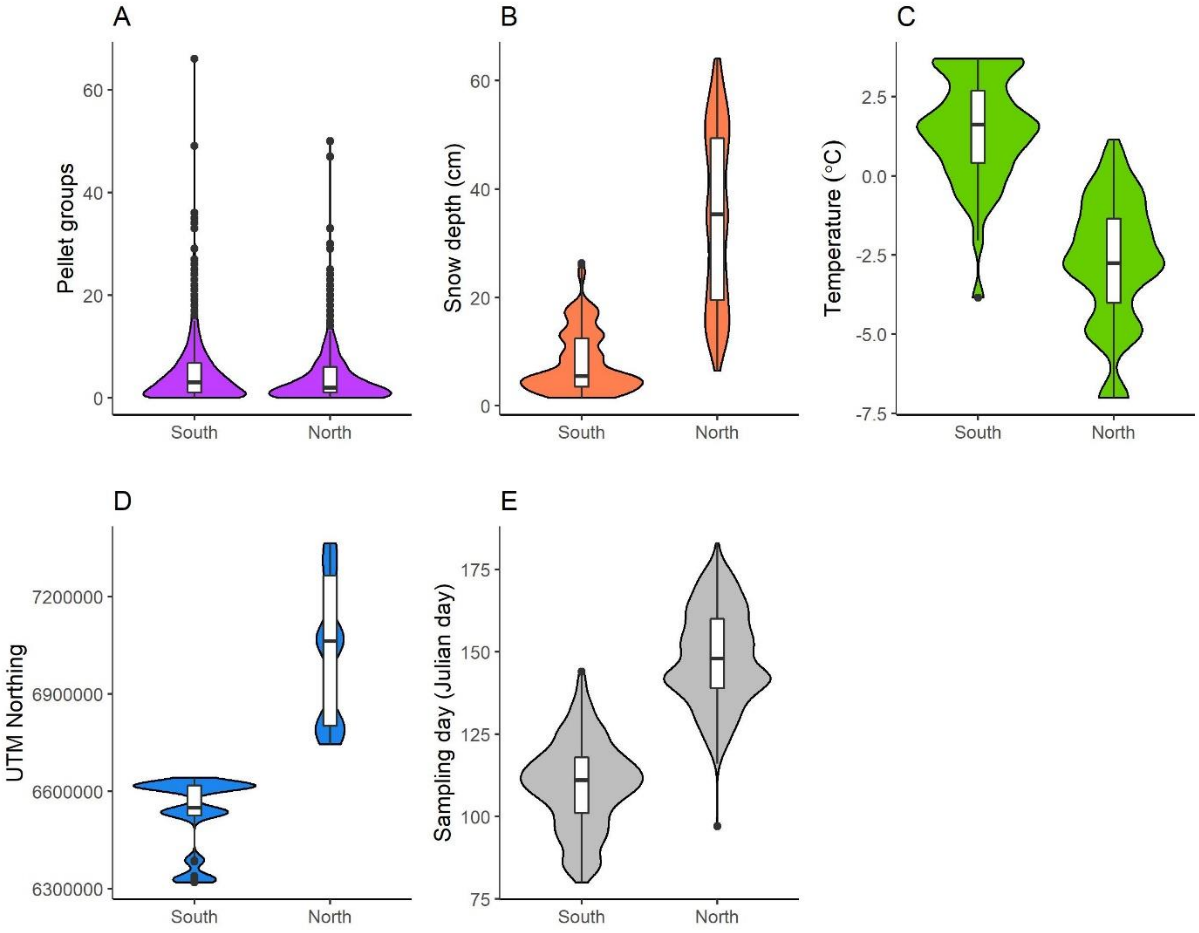


Figure 3. Violin and boxplots of A) moose pellet group counts per quadrat; B) snow depth; C) temperature; D) UTM northing; E) sampling day of the year per quadrat. Data were split into northern and southern groups. Data were from Norway and Sweden (1997–2019).

Table 1. Covariates included in statistical modeling.

Covariate	**Description**	**Temporally varying**	**Resolution**
Distance to secondary roads	Euclidian distance (m) of the quadrat centroid to the nearest secondary road.	n	Quadrat level
Young forest	The proportion of plots within a quadrat that were classified as young forest (aged 5–20 year).	y	Quadrat level
Sampling day of year	Mean day of the year that pellet group counts occurred in the quadrat. Each year, values started from January 1st (DOY = 1).	y	Quadrat level
Snow depth	Mean winter (Oct 31–April 30) snow depth (cm). Original point data were from weather stations across Norway and Sweden. We used kriging to create continuous surfaces of mean snow depth for each sampling year.	y	Quadrat level
Winter temperature	Mean winter (Oct 31–April 30) temperature (°C). Original point data were from weather stations across Norway and Sweden. We used kriging to create continuous surfaces for each sampling year.	y	Quadrat level
Moose harvest density	Mean annual harvest density (# shot moose per km^2). Values represent hunting the autumn prior to spring sampling and are an index of moose density.	y	Site level
Latitudinal group	A 2-level factor indicating if the site was a northern or southern moose population.	n	Site level

Results

Mean moose pellet group counts for the entire study area were 0.31 (SD = 0.90) pellets per 100 m^2. Counts varied by site with the highest mean counts in Råneå (mean = 0.58; SD = 1.35), the furthest north site, and the lowest in Furudal (mean = 0.07; SD = 0.38) (Figure 2). Counts also varied by year (Supplementary information: Figure S 1). Snow depth and winter temperature varied by year for northern and southern moose populations. Mean winter temperatures increased over time for both groups, while mean snow depth declined over time only for southern moose populations (Figure 4).

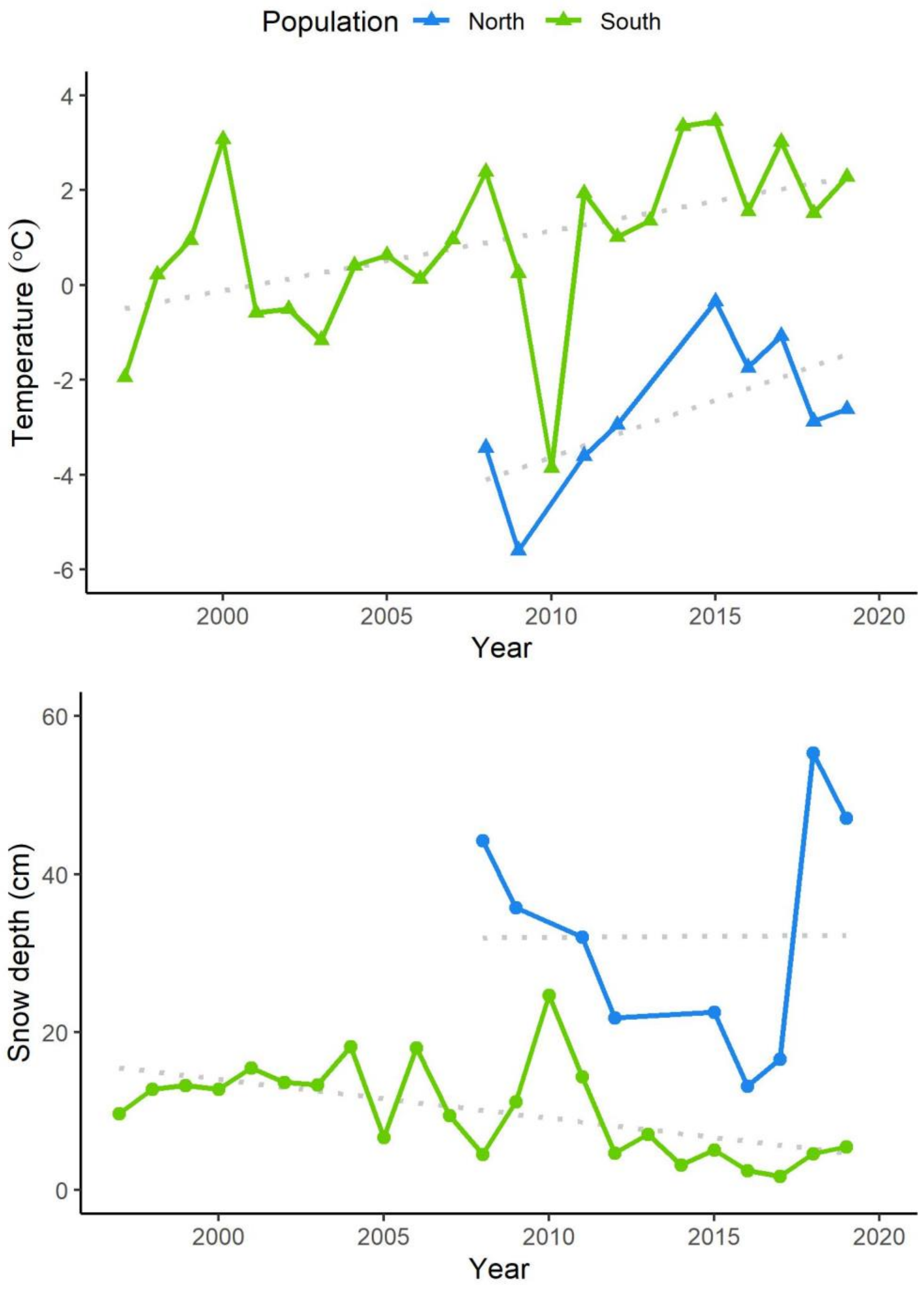


Figure 4. Trends for mean winter temperatures (top) and mean snow depth (bottom) in Scandinavia. The blue and green lines represent data for northern and southern moose populations, respectively. The dotted grey line is a linear trend line. Data were from 1997–2019.

Intensity of use

For northern and southern populations, we found similar increases in the intensity of use in response to increasing snow depths, until 20 cm, after which intensity of use declined (Figure 5).

Similarly, intensity of use of quadrats within sites declined as temperatures increased, particularly above 0°C (Figure 5).

For the interaction of young forests and temperature, southern populations showed strong patterns. Quadrats with a high proportion of young forests (0.9) were used more than areas with no or minimal young forest (0, 0.2) regardless of temperature (Figure 6). The distribution of young forests within quadrats was nearly double for southern (mean proportion of young forests = 0.14, SD = 0.22) relative to northern (mean proportion of young forests = 0.05, SD = 0.14) populations. A similar pattern could be seen for the interaction of snow depth and young forests in both moose populations; the intensity of use of quadrats increased with increasing snow depths at a greater rate when the proportion of young forests was high (0.9) (Figure 6).

For other effects, intensity of use declined precipitously when quadrats were greater than 1 km from secondary roads in southern populations (Supplementary information: Figure S 2). For both northern and southern populations, moose harvest density had a positive relationship with intensity of use up to 0.25 shot moose per km^2 (Supplementary information: Figure S 2). However, southern populations saw an additional peak in intensity of use around 0.5 shot moose per km^2.

For the ARMA correlation structure, *p* and *q* varied by model and population (Supplementary information: Table S 4). For model fit, all models suffered from persistent autocorrelation (Supplementary information: Figure S 3) and poor model fit (Supplementary information: Table S 4). However, northern populations experienced better model fit than southern populations, as seen with the reduced autocorrelation at all lags.

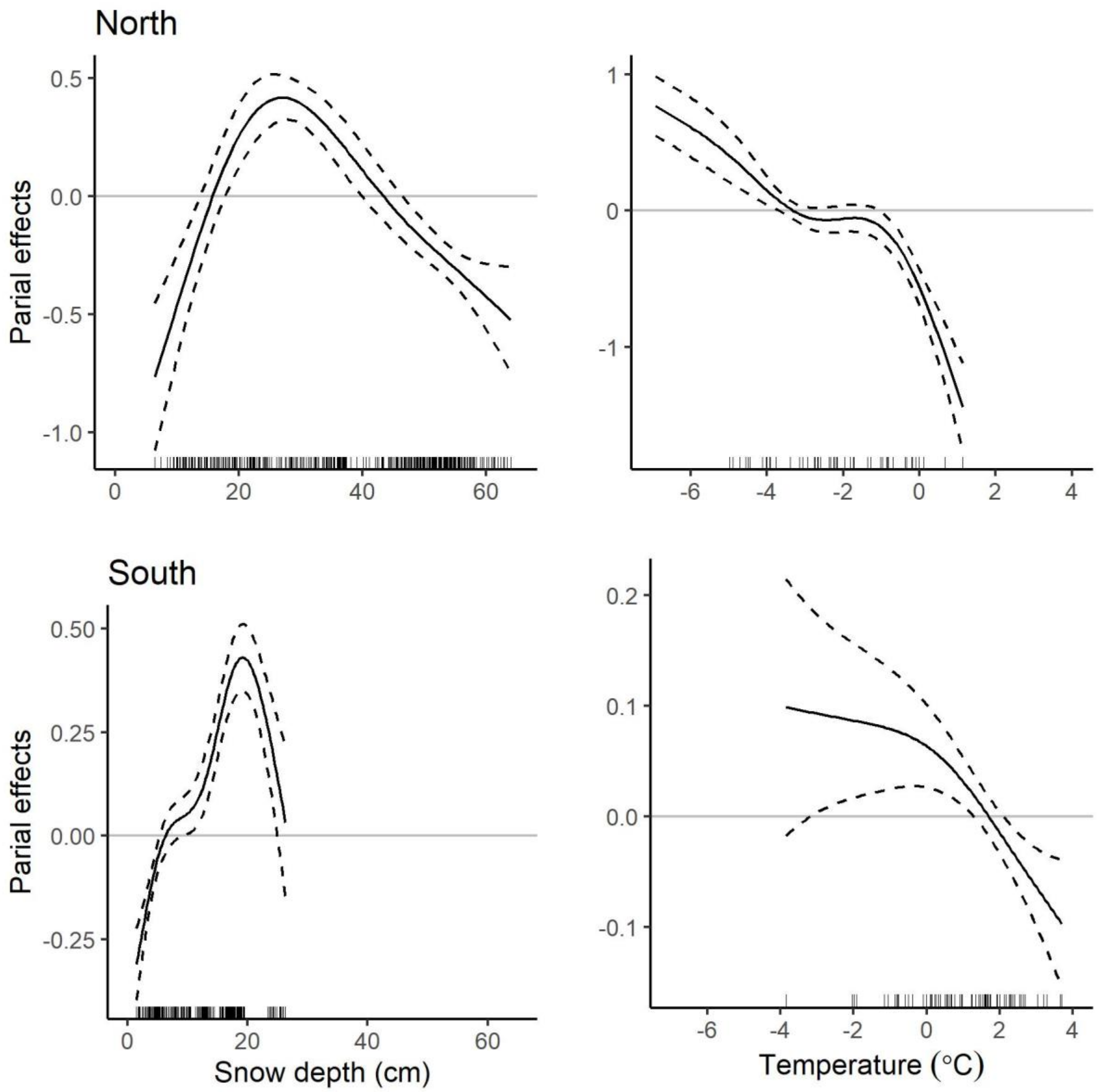


Figure 5. Partial effects of snow depth and temperature on intensity of use for northern (top row) and southern (bottom row) moose populations. Partial effects are the isolated effects of one particular predictor on the response. Dotted lines represent 95% confidence intervals. Hatching (rug) on the x axis represents observed data.

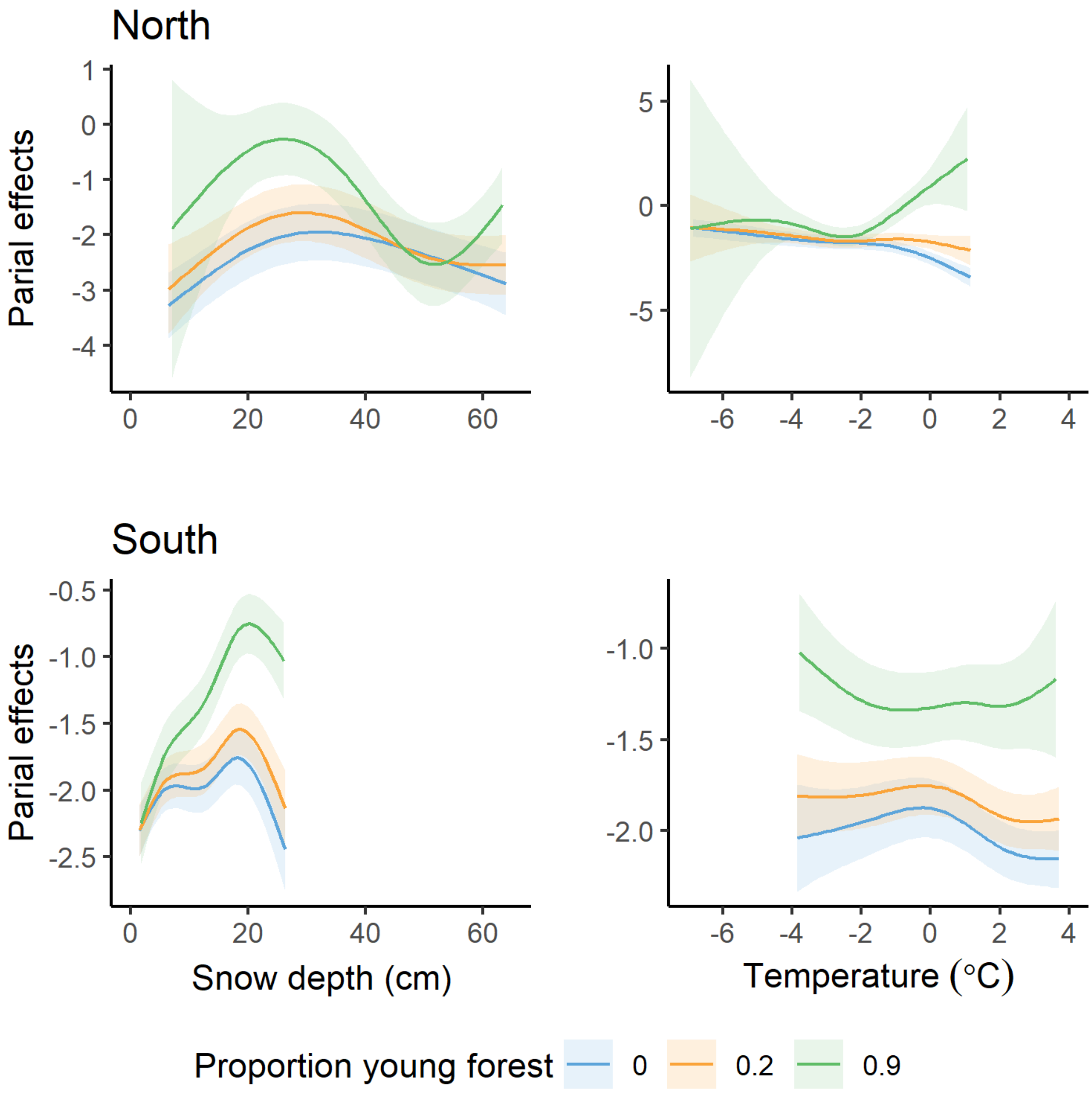


Figure 6. Partial effects of the interaction of temperature and the proportion of young forest on intensity of use in northern (top row) and southern (bottom row) moose populations. Proportions of young forest visualized here represent the median (0), third quantile (0.2), and maximum (0.9) value of the observed values. Partial effects are the isolated effects of one particular predictor on the response. Colored ribbons represent 95% confidence intervals.

Discussion

We analysed moose pellet group count data from 1997 to 2019 across a latitudinal gradient in Norway and Sweden. Generally, we found that for both northern and southern populations, intensity of use of quadrats declined precipitously when winter temperatures became warmer than 0°C. Intensity of use of quadrats peaked with snow depths of between 20–30 cm for both northern and southern populations. We tested three predictions regarding the interactions of weather (temperature, snow) and forest types in northern and southern moose populations. First, we predicted that intensity of use will decrease in young forests during warm winters, where there is low thermal cover (P1). Second, we predicted that intensity of use will decrease in young forests with deep snow but increase as snow depth declines (P2). Third, we predicted that there will be a dampened snow response in northern populations (P3).

For prediction one, we found the intensity of use declined after 0°C when the proportion of young forests in the quadrat was low (0, 0.2). This was found only in southern populations. This indicates that moose sought thermal shelter (i.e., used young forests less) either to avoid peak daytime temperatures, or to rest and dissipate heat (Thompson et al. 2021). This pattern was not supported, however, when young forests were abundant (i.e., proportion young forest = 0.9); intensity of use declined towards 0°C but remained stable as temperatures increased. This indicates that when there was no thermal shelter available nearby, which would be the case if much of a quadrat contained young forests, moose cannot shelter in other forest types simply because they were unavailable. Or, use could have remained high because moose shifted to foraging during night, as has been supported by other studies (Ditmer et al. 2018, Thompson et al. 2021). While Ditmer et al. (2018) found that moose rested more frequently at night and traveled/foraged during the day, van Beest and Milner (2013) found moose foraged more at twilight in response to warm air temperatures. However, because we had data only at the temporal resolution of a winter season, we could not tease apart diel patterns but expect this is an important part of the response of moose to warm thermal conditions.

Our knowledge on the thermal requirements of moose have changed substantially in the last few years. First, we now know that moose enter a period of hypometabolism (lower body temperature and heart rate) to deal with limited food availability and to reduce energy expenditure during winter (Græsli et al. 2020). This ‘walking hibernation’ has been found in other mammals, such as polar bears during food limited summers (Walford and Spindler 1997). Second, it was also previously thought that moose enter thermal stress once winter temperatures exceed -5°C (Renecker and Hudson 1986), though they only studied captive individuals. Thermal stress can increase respiration, heart rate, and energy expenditure and could result in weight loss, leading to reduced fitness (Renecker and Hudson 1986, Thompson et al. 2019). Many of the individual moose in both populations, but in particular the southern populations, likely experienced days with winter temperatures warmer than -5°C, given the mean winter temperatures were 1.5°C (SD = 1.65) and -2.75°C (SD = 1.99), respectively. Despite this, pellet group counts remained similar between both populations (Figure 3), indicating that moose were able to effectively use landscape features to buffer against warm winter temperatures. Recent work found that this -5°C threshold is overestimated, and body condition, sex, pregnancy status, and the relative change in temperature are greater drivers of thermal stress than air temperature alone (Thompson et al. 2020). Our study supports recent findings by Thompson et al. (2020) that previous winter thermal threshold for moose were likely overestimated.

The trend of southern populations experiencing higher winter temperatures could have fitness consequences, however. We know moose will reduce dry matter intake under warm conditions to reduce heat generated from feeding and rumination (Beatty et al., 2008), which could result in increased resting periods and decreased movement. We might expect more spatial clustering of moose pellet groups, particularly in cool, damp forests or bogs in response to warming. Warm weather can also shorten the period of high forage quality with early or fast spring green-up (Monteith et al. 2015), leading to reduced body mass (Post and Stenseth 1999, van Beest and Milner 2013). Moose found at the southern range limit, where temperatures are warm, also have shorter life spans (Hoy et al. 2017). As well, Post and Stenseth (1999) found that northern ungulates showed population declines following increasingly warmer winters. Warmer winters can also cause shifts in distributional ranges, allowing animals which are less adapted to the cold to move northward, such as white-tailed deer (*Odocoileus virginianus*) in North America, and roe, red, and fallow deer in Europe, bringing with them novel diseases and pathogens (Murray et al. 2006). Recent work has found that increased interspecific competition between moose and growing densities of roe, fallow, and red deer in southern Sweden was linked to an increased prevalence of Scots pine in moose diets. This implies a space use shift as well, though this was not explicitly tested (Spitzer et al. 2020). On this basis, we could expect more southern populations to be more susceptible to climate change as the thermal, disease, and food landscapes change. Though we cannot link our pellet data to moose fitness consequences, we recommend this be a priority for future research.

In addition to temperature effects, we found northern and southern moose experienced vastly different snow conditions. Mean snow depths for northern populations (mean = 34.80 cm, SD = 15.70) were more than four times higher than southern populations (mean = 8.02 cm, SD = 5.61) (Figure 3). Further, snow depths saw a decrease over time for southern, but not northern, populations (Figure 4), indicating the differences between the north and south might become even greater. However, common to both northern and southern populations was that intensity of use peaked around 20–30 cm of snow, followed by a precipitous decline (Figure 5). This was true in areas where young forests were both rare and abundant (Figure 6). These results did not support our predictions that there would be an interaction of snow depth and young forests driving intensity of use (P2), and that northern moose would show a dampened snow response (P3). However, we did find that once low-growing foods were concealed by snow, moose shifted intensity of use within their winter home ranges. If snow was only a movement impediment, we would expect a response a negative response only at snow depths known to increase locomotion costs (40–70 cm).

The difficulty with this analysis was understanding the effects of moose harvest density and migration strategy on our response variable. We can see from long-term trends in moose pellet group count data, particularly from Grimsö as this represents the longest dataset, that pellets count and moose harvest density trends were strongly related (Figure 7). This patterns was also found by Ueno et al. (2014). While harvest can be correlated with density, it could simply reflect management goals. For example, if two neighboring hunting districts had similar moose densities but one had a large commercial forestry industry, the hunting district’s management goal may be to reduce moose densities to reduce browsing damage (Wallgren et al. 2013). The two districts would thus have a high and low moose harvest densities, but we would (falsely) have interpreted low harvest densities as a low moose density. Despite these issues, harvest data remain one of the few national scale datasets that are common across countries, so their use continues (Cretois et al. 2020), despite these uncertainties. Migration can also cause confusion in our analysis, primarily because of events that occurred outside the temporal window of our pellet counts. For example, early season snow in a summer area (e.g., nearby mountains) could trigger early migration of moose onto their winter range (Sandegren et al. 1985). This could increase the number of “moose days” spent on a wintering area, and thereby increase the number of pellet groups. We could not fully capture the non-winter story as we do not know where all summer ranges were from which the moose came, nor was this was the goal of our study. In contrast, a late season snow could result in a later migration. We suspect this was one of the drivers of the hump-shaped curve seen in Figure 5, as snow accumulated outside the study area in the mountains, covering up food or making travel difficult. As snow depths increased above 30 cm, moose used areas with reduced snow depth, or it is possible they moved to other wintering areas. As such, migration presents a challenge in interpreting pellet count data, as moose can trickle in during autumn migration and trickle out again during spring migration, and the proportion of the population that migrates may vary by year.

In Scandinavia, snow cover duration is decreasing, and the growing period is increasing. Warming effects are expected to have greater temperature and precipitation increases during winter compared to summer (Post and Stenseth 2011). Indeed, plant community effects are already being seen. For example, shrubs are expanding northward and upwards in elevation (Bret-Harte et al. 2002, Hallinger et al. 2010, Elmendorf et al. 2012) which could expand moose foods into alpine and northern latitudes, leading to an ecological opportunity for moose in Scandinavia, particularly northern populations where there is a large elevational gradient. However, winter warming events can damage shrubs resulting in reduced summer growth (Bokhorst et al. 2009). Of concern, winter warming events are projected to nearly double in northern Scandinavia into the 21st century (Vikhamar-Schuler et al. 2016).

The different thermal landscapes across this study's latitudinal gradient highlights a reoccurring issue for cold-adapted species as winters continue to warm; that there may be a range contraction of the southern limit, and an expansion of the northern limit. The contraction of moose southern range limits are already being seen in places such as Minnesota, USA, where disease, land use, and warmer winters are interacting to cause drastic declines in moose body condition, survival, and abundance (Murray et al. 2006). We suggest that southern populations may currently be more dependent on thermal cover to withstand to a changing thermal landscape, based on the available geography with minimal topographical relief. We suggest that northern populations might be more flexible in their response to climate change, as they can adjust migration depending on autumn conditions. However, other studies notes that migration may become a less common strategy for Scandinavian moose as the environment become less seasonal (i.e., smaller differences between winter and summer), more akin to current southern moose population conditions (Allen et al. 2016). Wildlife and forest managers must emphasize the protection and creation of high-quality habitats that can sustain moose not just from a foraging perspective, but also from a thermal perspective, such that they can thermoregulate via landscape use during increasingly warmer winters.

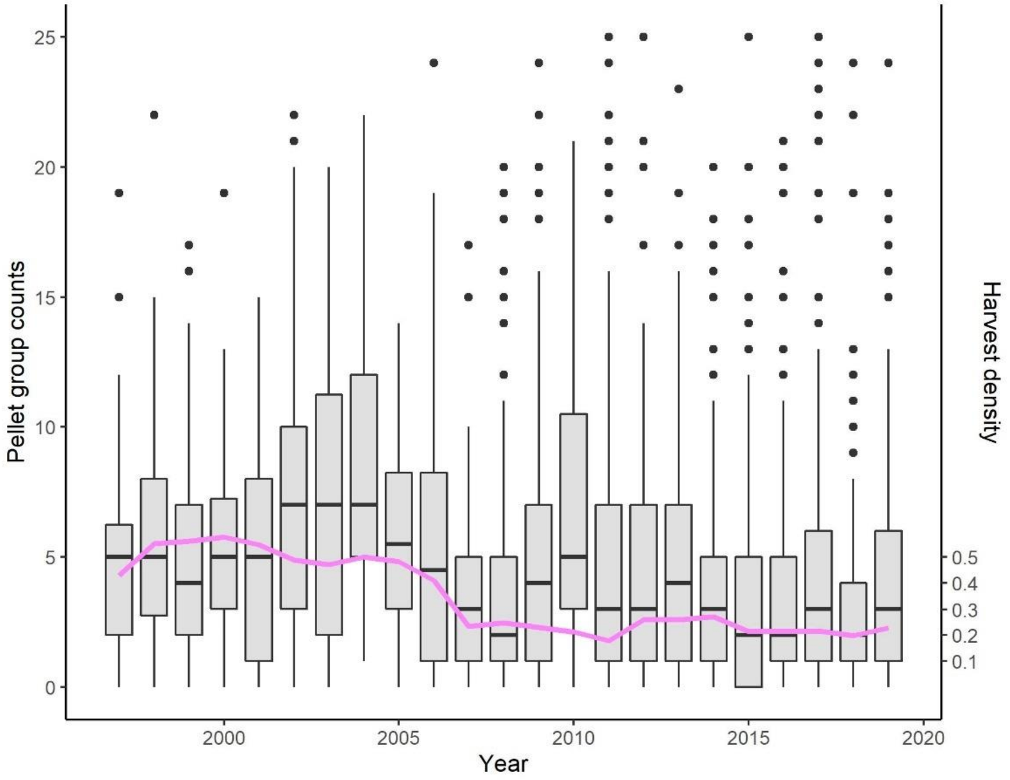


Figure 7. Boxplots of observed pellet group counts per quadrat (left y axis; black line), mean moose harvest density (right y axis; purple line; number of shot moose per km^2), and year (x axis). Data were from Grimsö, Sweden 1997–2019. The left y axis was truncated at 25 pellet groups for visualization purposes (max = 66).

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Supplementary information

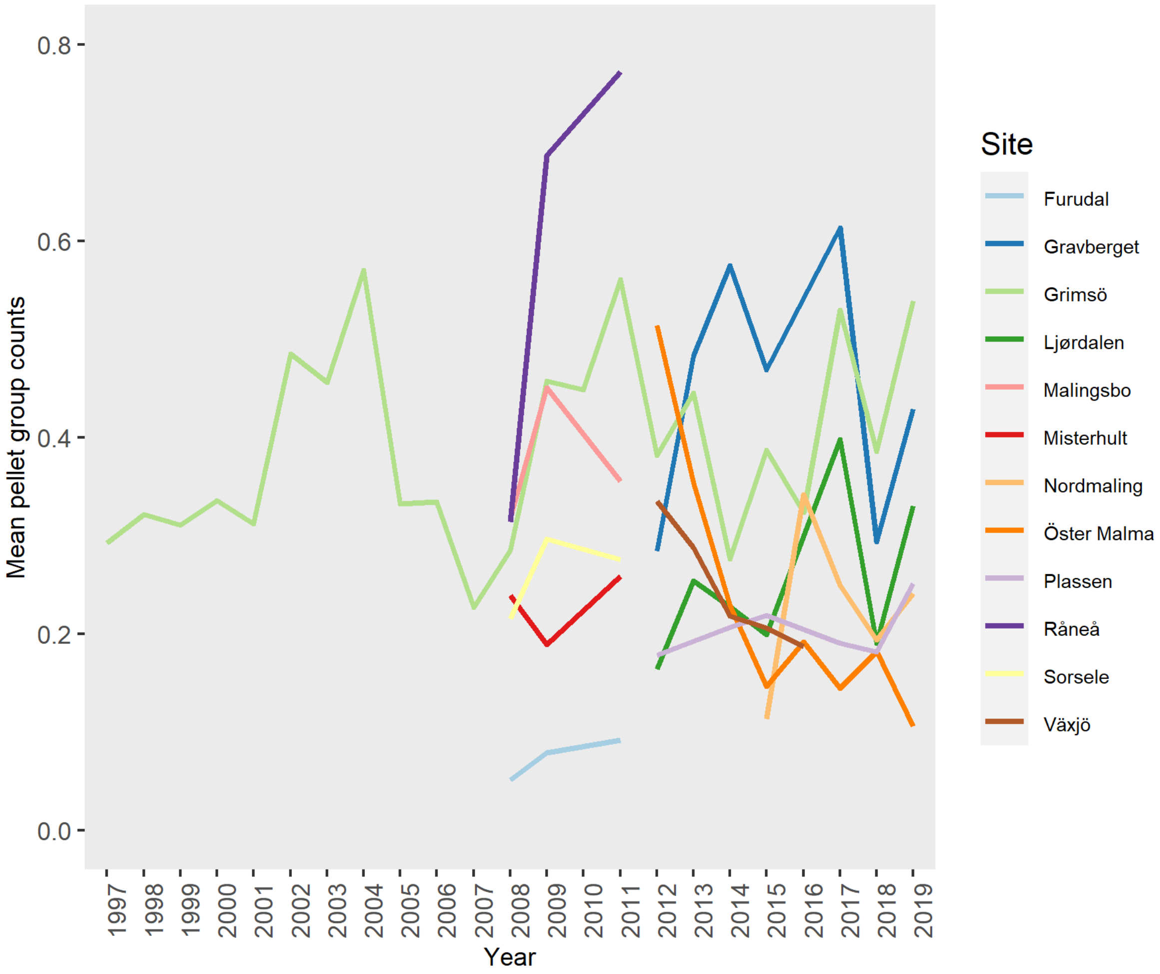

Figure S 1. Mean moose pellet group counts varied by time (1997–2019) for each of the 12 study sites in Norway and Sweden.

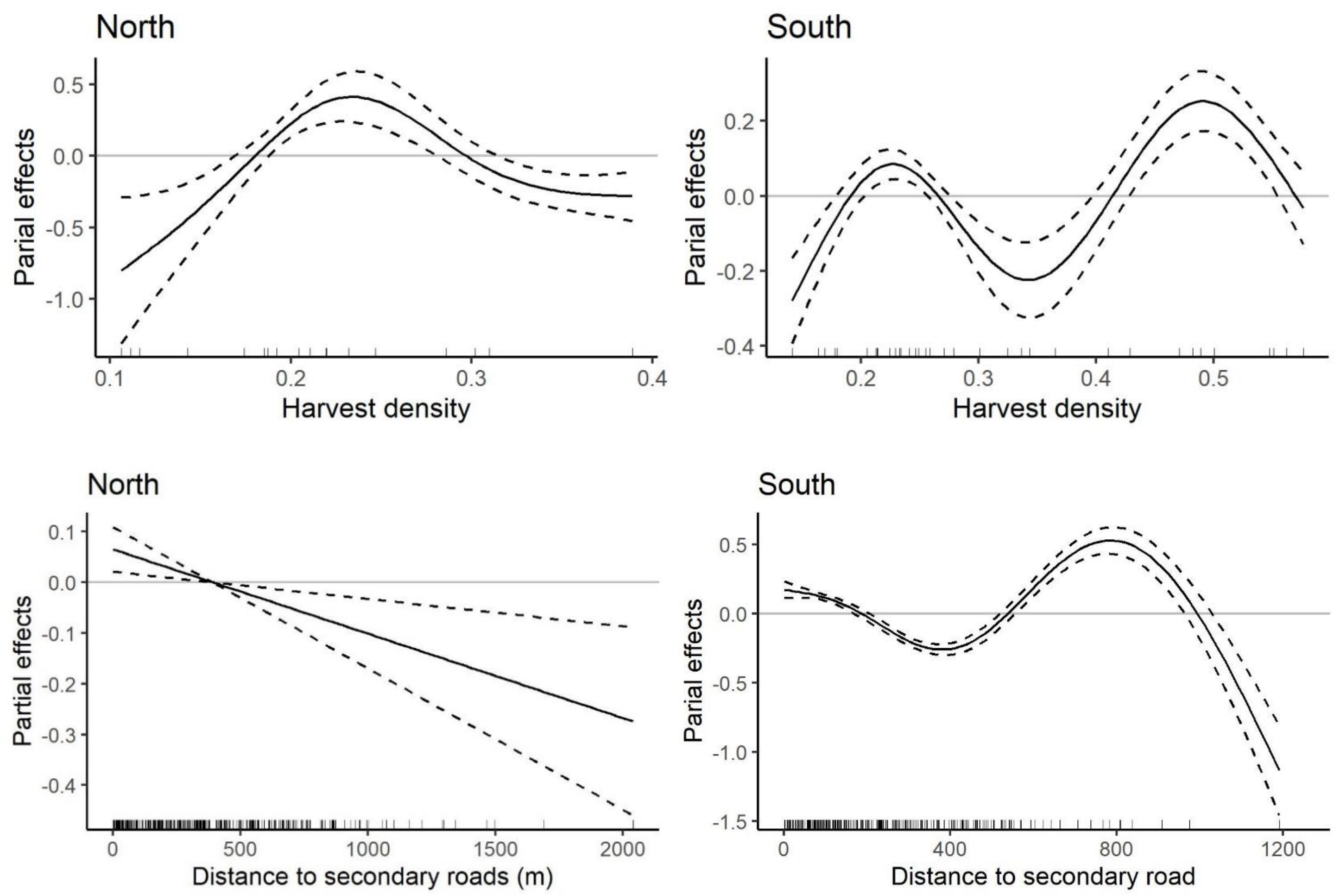

*Figure S 2. Partial effects of moose harvest density and distance to secondary roads (m) on moose intensity of use. Dotted lines represent 95% confidence intervals. Rug represents observed data. Predictions were from the snow depth * young forest models.*

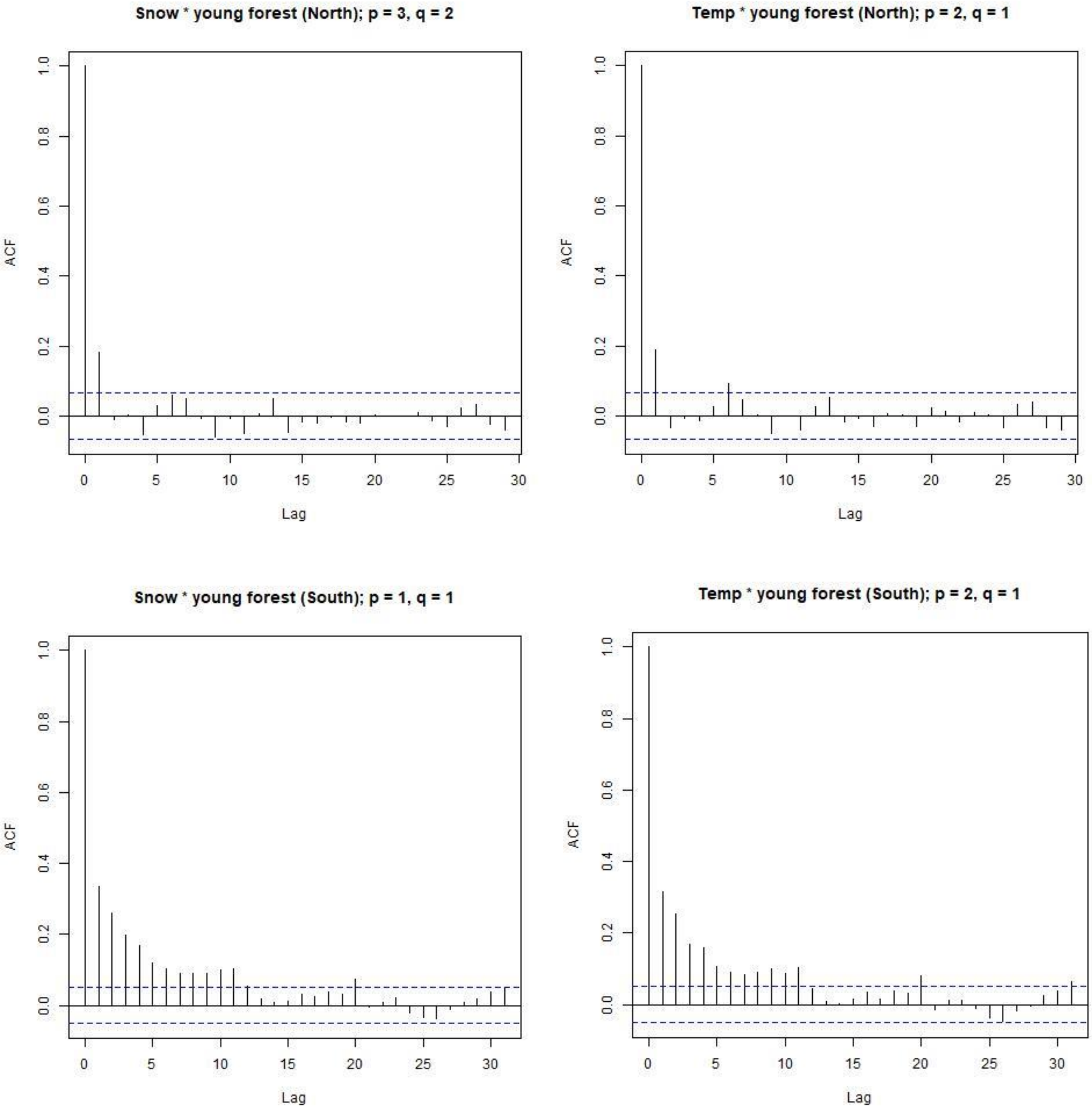

Figure S 3. Residual temporal autocorrelation from GAMMs for northern (top row) and southern (bottom row) moose populations. We tested two interactions; temperature and young forest and snow depth and young forest. The graphs show the autocorrelation function (acf) over varying lags (x axis) for top-ranked ARMA correlation structures.

Table S 1. Classifications of movement strategies of Scandinavian moose populations at each of the 12 study sites in Norway and Sweden.

Site	**Movement strategy**	**Reference**
Råneå, Sweden	Partially migratory	(Singh et al. 2012, Allen et al. 2016)
Sorsele, Sweden	Partially migratory	(Singh et al. 2012, Allen et al. 2016)
Furudal, Sweden	Partially migratory	(Sweanor and Sandegren 1988)
Nordmaling, Sweden	Partially migratory	(Neumann et al. 2018a)
Ljørdalen, Norway	Partially migratory	(Bramorska 2020)
Plassen, Norway	Partially migratory	(Bramorska 2020)
Gravberget, Norway	Partially migratory	(Bramorska 2020)
Malingsbo, Sweden	Non migratory	(Singh et al. 2012, Allen et al. 2016)
Grimsö, Sweden	Non migratory	(Cederlund and Sand 1994)
Öster Malma, Sweden	Non migratory	(Neumann et al. 2018b)
Misterhult, Sweden	Non migratory	(Singh et al. 2012, Allen et al. 2016)
Växjö, Sweden	Non migratory	(Neumann et al. 2019)

Table S 2. Pearson correlation coefficients comparing observed and predicted values from co-kriging models for snow depth and winter temperature in Norway and Sweden.

Year	Snow depth	Temperature
1997	0.91	0.98
1998	0.90	0.99
1999	0.88	0.99
2000	0.90	0.98
2001	0.87	0.99
2002	0.87	0.99
2003	0.89	0.99
2004	0.83	0.99
2005	0.91	0.98
2006	0.78	0.97
2007	0.89	0.99
2008	0.91	0.99
2009	0.88	0.99
2010	1.00	0.96
2011	0.75	0.98
2012	0.87	0.99
2013	0.86	0.97
2014	0.87	0.99
2015	0.84	0.98
2016	0.90	0.99
2017	0.89	0.99
2018	0.88	0.97
2019	0.90	0.97

Table S 3. Pearson correlation matrix of numeric covariates used in generalized additive mixed modelling. Data were aggregated at the quadrat level. Cells highlighted in orange had absolute values greater than 0.70. Values along the diagonal should be ignored.

	Sampling day of year	**Snow depth**	**Winter temperature**	**Moose harvest density**	**Distance to secondary roads**	**Young forest**	**UTM Easting**	**UTM Northing**
Sampling day of year	1.00							
Snow depth	0.72	1.00						
Winter temperature	-0.80	-0.81	1.00					
Moose harvest density	-0.23	-0.20	0.17	1.00				
Distance to secondary roads	0.36	0.34	-0.32	-0.08	1.00			
Young forest	0.11	0.03	-0.10	0.33	0.04	1.00		
UTM Easting	0.16	0.10	-0.19	-0.27	-0.04	-0.30	1.00	
UTM Northing	0.82	0.73	-0.82	-0.30	0.30	-0.02	0.55	1.00

Table S 4. Table of autoregressive moving average (ARMA) structures and results from Ljung-Box tests for northern and southern moose populations.

Model	**Population**	**ARMA structure**	**Ljung-Box test**		
			X-squared	**Degress of freedom**	**p-value**
Temperature * young forest	North	p = 2, q = 1	52.19	1	< 0.001
	South	p = 2, q = 1	242.8	1	< 0.001
Snow depth * young forest	North	p = 3, q = 2	114.27	1	< 0.001
	South	p = 1, q = 1	252.32	1	< 0.001

4

Title: The importance of evaluating standard monitoring methods: Observer bias and detection probabilities for moose pellet group surveys

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Abstract

Counting is not always a simple exercise. Specimens can be misidentified or not detected when they were present, giving rise to unidentified sources of error. Deer pellet group counts are a common method to monitor absolute or relative abundance, density, and population trend. Yet, detection errors and observer bias could introduce error into sometimes very large (spatially, temporally) datasets. For example, in Scandinavia, moose (*Alces alces*) pellet group counts are conducted by volunteer hunters and students, but it is unknown how much uncertainty observer error introduces into these datasets. Our objectives were to 1) estimate the detection probability of moose pellet groups; 2) identify the primary variables leading to detection errors including prior observer experience; and 3) compare density estimates using single and double observer counts. We selected a subset of single observer plots from a long-term monitoring project to be conducted as dependent double observer surveys, where primary and secondary observers work simultaneously in the field. We did this to quantify detection errors for moose pellet groups, which were previously unknown in Scandinavia, and to identify covariates which introduced variation into our count estimates. Our study area was in the boreal forests of southern Norway where we had a nested grid of 100-m^2 plots that we surveyed each spring. Our observers were primarily inexperienced observers. We found that when pellet groups were detected by the primary observer, the secondary observer saw additional pellet groups 42% (n = 40) of the time. We found search time was the primary covariate influencing detection. We also found density estimates from double observer counts were 1.4 times higher than single observer counts, for the same plots. This density underestimation from single observer surveys could have consequences to managers, who sometimes use pellet counts to set harvest quotas. We recommend specific steps researchers and managers can take to improve future moose pellet counts.

Key words

Alces alces; deer; detection error; double observer; monitoring; moose; multinomial-Poisson mixture models; fecal pellets.

Introduction

Sign surveys have a long tradition in the field of ecology, such as counting the number of birds seen from a point location, the number of frogs heard during a set time interval, or the number of carnivore scats seen along a transect line. The number of specimens observed can be used as an index of abundance, density, or population trend. However, counting is perhaps not as simple as it seems (Elphick 2008). For example, Prater (1979) found that observers counting birds from photographs (i.e., with true values known) consistently overestimated the number of individuals when counting small groups of birds, but underestimated their numbers when counting large groups. Errors associated with sign surveys, such as observation (e.g., species misidentification) or detection error (e.g., animal was present but went undetected) lead to biased estimates of occupancy, density, or abundance (Lele et al. 2012, Royle et al. 2014, Burton et al. 2015) Recently, statistical advances have attempted to account for these errors (MacKenzie et al. 2002, Royle and Nichols 2003). For example, the advent of methods to account for differences in detection and movement skyrocketed with the use of camera traps (Burton et al. 2015). Yet, certain sign survey methods lag in widespread methodological advancements and acceptance.

A common sign survey for monitoring deer (Cervidae) is counting their feces (i.e., pellet group counts) as a proxy for animal distribution, abundance, and population trend (Bennett et al. 1940, Neff 1968, Patterson et al. 2002, Theuerkauf et al. 2012). The primary issue with counting pellet groups, as with any sampling method, is identifying the sources of error (Neff 1968, Forcey et al. 2006, Riddle et al. 2010). For example, pellets may be removed or made less visible through heavy rain events or trampling (Harstad and Bunnell 1987, Woodruff et al. 2015), or decompose quickly if the habitat is damp or if there is insect activity (Van Vliet et al. 2009). Additionally, if pellet groups are present, there is a possibility they may not be detected (i.e., the detection probability). Detection probabilities of deer pellet groups can vary widely, especially based on pellet size, environmental conditions, weather, and observer experience. In a study of Columbian black-tailed deer (*Odocoileus hemionus*) and Roosevelt elk (*Cervus elaphus roosevelti*) in a temperate coniferous rainforest, pellet detection probabilities (defined as 'p') ranged from < 0.2 to 1.0, depending upon observer and distance of the pellet group from the transect line (Jenkins and Manly 2008). In another study, pellet groups from the muntjac (*Muntiacus muntjac*), a small deer resident to tropical forests of India, had very low detection probabilities of $p = 0.03$ (SE = 0.02; Gopalaswamy et al. 2012), meaning they were almost impossible to detect when present. Pellet group counts (hereafter, pellet counts) continue to be extensively used because they do not require expensive equipment, technicians can be trained quickly, and surveys can be done across relatively large areas. However, methods to quantify and account for sampling and detection errors are not widely implemented.

Moose (*Alces alces*) are the largest member of the deer family with comparatively large fecal pellets (2–3.5 cm; Spitzer et al. 2019). Moose pellet groups are typically identified by a single observer, and surveys are often repeated annually or semi-annually (Snaith et al. 2002, Rea et al. 2010, Månsson et al. 2011, Zimmermann et al. 2015). However, habitat heterogeneity, environmental conditions, and observer skill level introduce variation in the accuracy and precision of pellet counts (Persson 2003, Jung and Kukka 2016, Spitzer et al. 2019). For example, immediately after snow melt and before spring green-up, moose pellets are highly visible (Persson 2003). However, early green-up, late-season snow, or inexperienced observers can lead to imperfect detections (Persson 2003, Kéry and Royle 2015, Spitzer et al. 2019).

Despite the widespread use of moose pellet counts as a direct index of moose density or population trend, few studies incorporate detection error because it is largely assumed to be negligible since moose pellets are so large. In Scandinavia, for example, moose density (D) is calculated as the number of observed pellet groups divided by the average defecation rate of 14 pellet groups per day for an accumulation period (Cederlund and Liberg 1995, Rönnegård et al. 2008, Månsson 2009, Zimmermann et al. 2015, Pfeffer et al. 2018). This formulation, however, assumes perfect detection and minimal pellet decay during the winter period, which could lead to underestimates of moose abundance if these assumptions are incorrect. For a heavily hunted species such as moose, where between 18–35% of the population are harvested each autumn in Norway (Sand et al. 2011, Jonzén et al. 2013), any systematic bias in population estimates could lead to a mismatch between population goals and management strategies.

Pellet counts are conducted by volunteer hunters in Sweden to track moose density and population trends, and by research projects in Scandinavia. Thus, pellet count datasets are formed from volunteer contributions, which we loosely term ‘citizen scientists’. Citizen science, the involvement of citizens in scientific research and knowledge production (Cretois et al. 2020), allow researchers and managers to collect data across spatio-temporal domains that would otherwise be too costly to collect (Tulloch et al. 2013, Buesching et al. 2014, Cretois et al. 2020). This is a growing field because of the availability of ‘free’ labor. Yet, these data have trade-offs such as observer bias as a result of (in)experience, the ease of implementing the sampling regime, and the spatial bias of data (i.e., clustering of data around urban areas; Geldmann et al. 2016). There is new emphasis on validating the quality of citizen science data (Clare et al. 2019, Cretois et al. 2020) but this step is not universally applied and not enough is done to quantify potential biases.

We designed a study using single and double observer survey methods to count moose pellet groups in southern Norway. Our objectives were to 1) estimate the detection probability of moose pellet groups; 2) identify the primary variables leading to detection errors including prior observer experience; and 3) compare density estimates using single and double observer counts. We predicted higher detection probabilities with double observer compared to single observer surveys, with more search time, for more experienced observers, and higher density estimates with double observer counts.

Study area

Our study area lies between 60.8° and 61.4° N and 12.2°–12.7° E in Innlandet County in southern Norway (Figure 1). Elevation ranges from 265–750 m above sea level. The area experiences cold (mean January temperature 2011–2018: -9.3 Cº) and snowy (mean winter snow depth 2011–2018: 39.0 cm; Norwegian Meteorological Institute) and short, cool summers. Land cover is dominated by boreal forests (Ahti et al. 1968), which are managed for timber and pulp production based on even-aged forest management. Production forests, which are largely coniferous, typically undergo one pre-commercial thinning at 10–20 years to remove competing deciduous shrubs and trees. Stands undergo 1–2 thinning events at 40–50 years and 70–80 years to optimize commercial tree density. Moose prefer young forests for the high food availability (Shipley et al. 1998).

Common tree species include Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*), downy birch (*Betula pubescens*), Norway spruce (*Picea abies*), grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula*). The shrub layer is dominated by bilberry (*Vaccinium myrtillus*), heather (*Calluna vulgaris*), and other dwarf shrubs (*Ericaceae* spp.). In boggy areas, *Sphagnum* spp. mosses are dominant (Moen et al. 1998). In winter, moose typically migrate from summer ranges in higher elevation areas to low-elevation valley bottoms where snow depths are reduced (Sweanor and Sandegren 1988, Bunnefeld et al. 2011, Singh et al. 2012). Moose are the dominant deer species. Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are present in the area but occur at low densities.

Methods

Pellet counts

As part of a long-term monitoring project (Loosen et al. 2021a, 2021b), we have plots (n = 992) nested within quadrats at three sites. Within each site, we systematically placed 20–21 quadrats of 500 x 500 m. Each quadrat contained 16 100-m^2 circular plots (Figure 1) where we counted pellet groups. All plot centers were marked with a pole. Observers used a rope, which was marked at 5.64 m and 3.99 m, to measure the plot radii. Observers walked in the inner circle (radius = 3.99 m), zig-zagging within the circle to ensure the area was properly surveyed. Once the smaller circle was surveyed, observers moved to the outer circle (radius = 5.64 m) and searched in the opposite direction to ensure pellet groups obscured by vegetation could be seen (Figure 2). We counted deer pellet groups in late spring, shortly after snow melt (May or early June). We identified deer species according to morphological characteristics of the pellets (Spitzer et al. 2019). Roe and red deer pellets are smaller and easily differentiated from moose pellets (Spitzer et al. 2019). To include a pellet group in our counts, >50% of the pellets had to fall within the plot. Only piles with ≥20 pellets for moose and red deer and ≥10 pellets for roe deer were counted. We visually distinguished between fresh (current winter) and old (prior to winter) pellets. Winter pellets were typically brown, in pellet form, and positioned on top of leaf litter and forest debris, while summer pellets were often in patty form, covered by leaf litter, or had mold or fungus growth (Zimmermann et al. 2015). We included only winter pellets in this analysis. Pellets were removed from the plot each spring to avoid double counting the following year. One full day each field season (i.e., year), we trained observers in the field. Observers then worked independently for the duration of the field season. All observers were students enrolled in an educational program at the authors' institution.

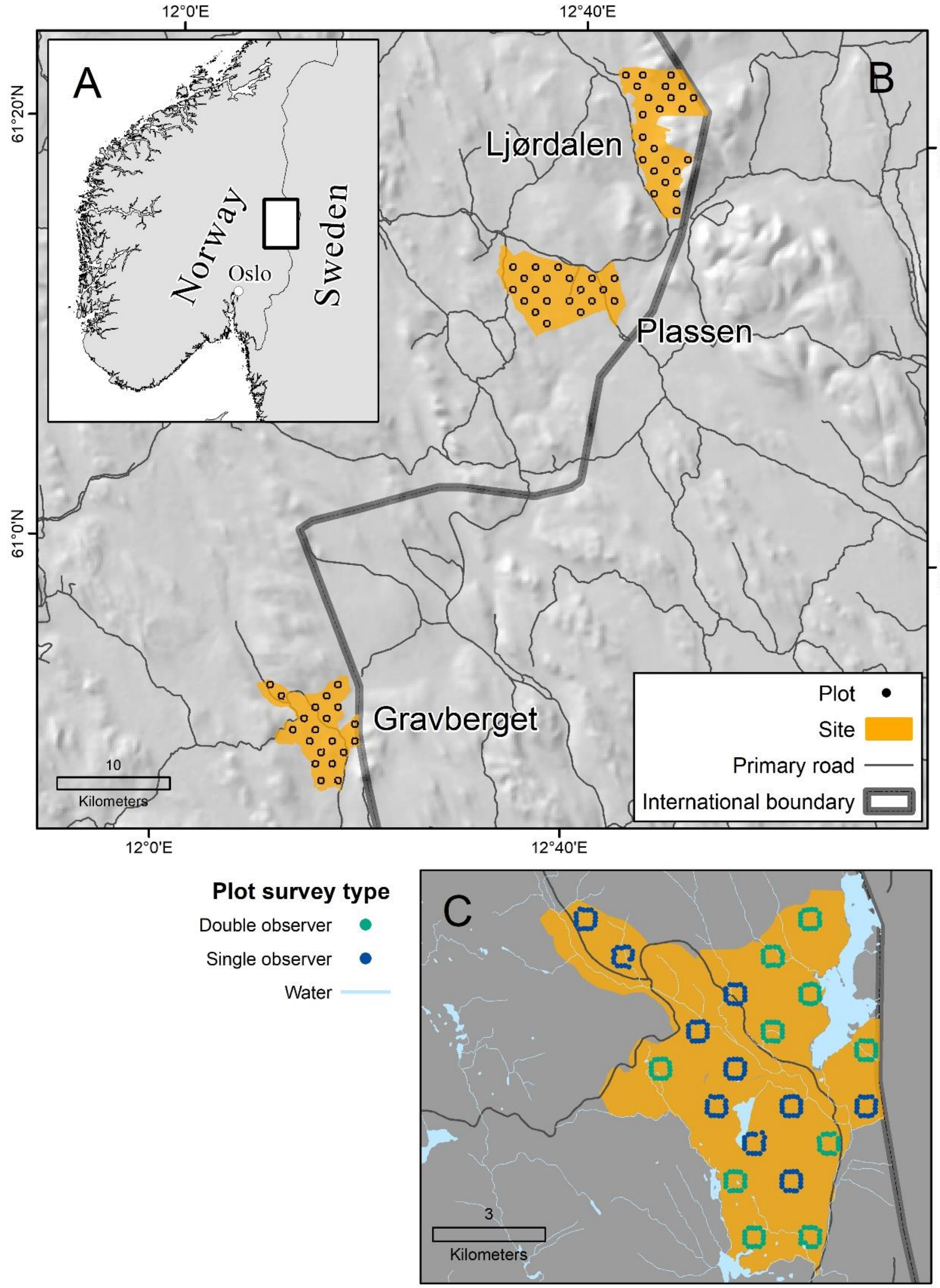

Figure 1. Maps of A) our study area in southern Norway; B) each of the three sites (Gravberget, Plassen, Ljørdalen) which contained 20–21 quadrats. Background map is a 20-m digital elevation map; C) each quadrat contained 16 plots. A subset of long-term monitoring plots were completed as double observer surveys. Gravberget is shown as an example.

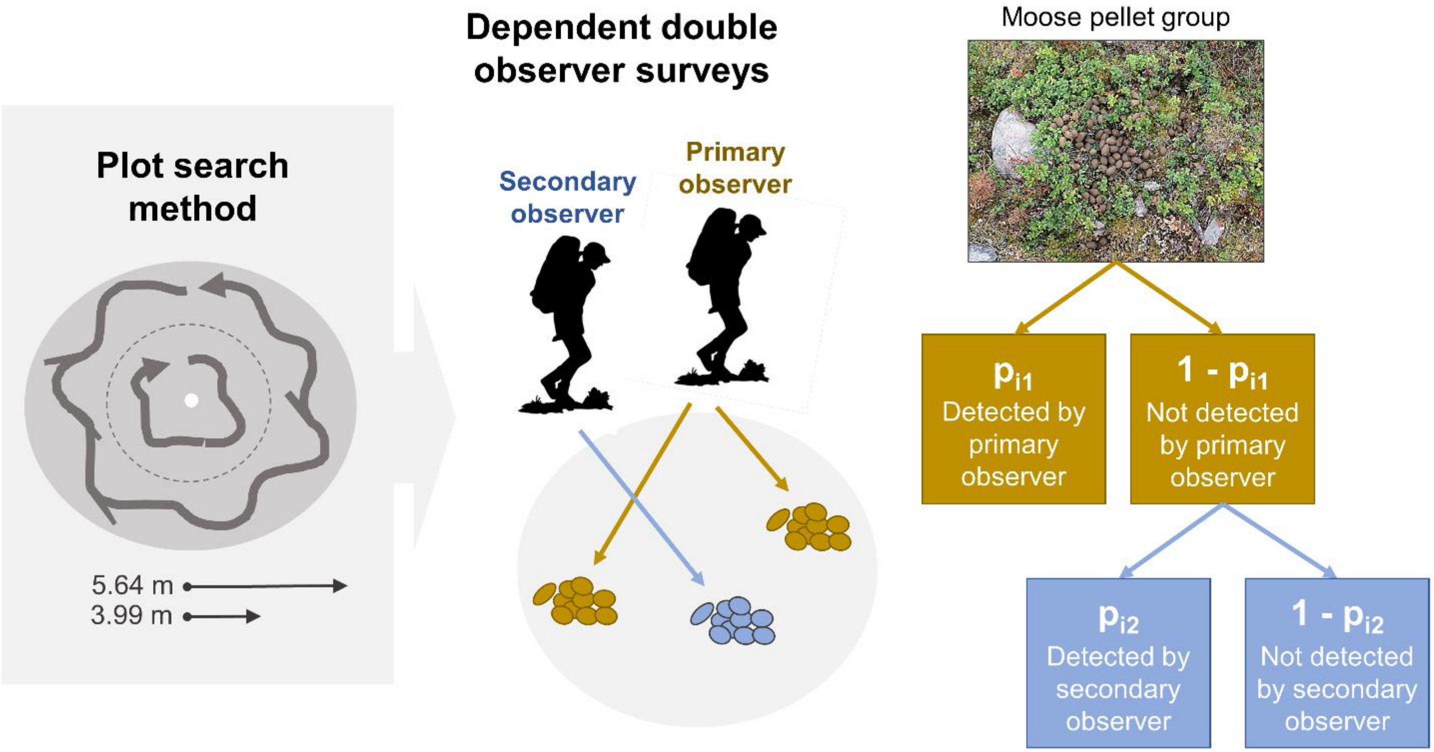

Figure 2. In the grey box at left, a diagram showing how each 100-m2 circular plot was searched. Observers first walked the 'inner circle' (the 3.99-m radius, indicated by the dotted grey line) in a zig-zag fashion to identify pellet groups. Once the inner circle was surveyed, the observer moved to the outer circle (5.64-m radius) and surveyed in the opposite direction. Each plot center was marked with a white pole. At center, a diagram showing the data collected during dependent double observer surveys. The primary observer (in brown) communicated the pellet groups seen to the secondary observer, who recorded the observations (here, two pellet groups). The secondary observer (in blue) recorded additional pellet groups the primary observer missed (here, one pellet group). At right, a diagram showing the three probabilities (p) estimated with dependent double observer surveys. Figure adapted from Powell and Gale 2015. Photo credit: Roos Ahlers.

Double observer surveys

To estimate detection error, we counted pellet groups using a dependent double observer survey method (Riddle et al. 2010, Powell and Gale 2015). Dependent double surveys have higher precision and are more time efficient in the field than independent double observer methods (Forcey et al. 2006). The primary observer surveyed the plot, pointing to and verbalizing observed pellet groups (Figure 2). The secondary observer recorded observations made by the primary observer while simultaneously searching for and recording additional pellet groups that the primary observer did not detect (Figure 2). Thus, the secondary observer counts are ‘dependent’ on the primary observer counts. All pellet group locations were drawn by hand on a data sheet in the field to ensure double counting did not occur (Supplementary information: Figure S 1). Observers switched primary and secondary observer roles between each plot (Jenkins and Manly 2008, Riddle et al. 2010, Powell and Gale 2015). These surveys resulted in two counts per plot: one count for the pellet groups seen by the primary observer and a second count for the additional pellet groups seen by the secondary observer. This method did not require observers to match or reconcile individual observations. Observers did not discuss their results. Double observers switched partners every day for the duration of the field season to increase knowledge ‘mixing’ between all observers.

We aimed to complete 30% (n = 297) of the plots each year as dependent double observer surveys, based on previous years’ time effort and available observers. We used a random number selector to select 30% of the quadrats. We selected entire quadrats rather than single plots to minimize travel time between plots (i.e., a pair of observers could travel together to quadrats rather than meeting up after single observer surveys).

Covariates

We recorded covariates which could increase variation in detectability (Table 1). At each plot, we recorded weather conditions, visually estimated the percent cover of snow or standing water, visually estimated the percent cover of forestry residues (i.e., branches), time of day, Julian day, and forestry actions (see Table 1). We included also the total time spent searching for pellet groups in the plot (minutes; primary and secondary observer time combined). There was no search time cut-off. The observer-level covariates we included in our models were ‘observer experience’, an index of prior field research experience, and ‘prior pellet counting experience’ (Table 1; see survey questions sent to observers in Supplementary Information: Figure S 2).

Additionally, we assigned a forest maturity index (cutting class), field-layer composition (Fremstad 1997), tree density, and dominant canopy species from a separate dataset, which was collected in 2018 (Loosen et al. 2021b). These covariates should not change within one or two years unless the area was clearcut or thinned, which was indicated in the ‘forestry actions’ variable collected in 2019 and 2020 (Table 1). In this case, clearcut or thinned plots were dropped from the dataset.

Table 1. Table of plot-level and observer-level covariates used in modeling.

Covariate	Description	Plot-level	Observer-level
Weather	Weather conditions: foggy; rainy; cloudy (≥50%); partly cloudy (<50%); sunny/clear	X	
Snow cover	Percent cover of snow or standing water in the plot (0–100%). Visually estimated.	X	
Residual cover	Percent cover of forestry residues (i.e., branches) in the plot (0–100%). Visually estimated.	X	
Time of day	Time of day survey was started	X	
Search time	Time spent searching for pellet groups in the plot	X	
Julian day	Julian day of the year sampling occurred	X	
Forestry actions	Forestry activity: clearcut; thinned; scarified; clearcut and scarified; none of the above	X	
Field layer[1]	Dominant field layer: dwarf shrub; grass; fen; bog; lichen; small fern	X	
Tree density[1]	Number of trees ≥ 0.3 m tall	X	
Dominant tree[1]	Dominant tree species in the forest canopy	X	
Cutting class[1]	Forest maturity index: 0: forestry not present (i.e., barren rock or bog); 1: clear cut; no regeneration; 2: visible regeneration, tree height < 10 m; 3: tree height > 10 m; 4: forest mature for logging, age of tree 55–75 years depending on productivity; 5: old growth forest	X	
Observer experience	Prior general field research experience: no experience; 1–6 months; 7–12 months; >1 year		X
Pellet counting experience	Prior pellet counting experience: no experience; 1–6 months; 7–12 months; >1 year		X

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[1] Extrapolated from 2018 dataset.

Density estimates

We calculated density separately for each year and for single and double observer counts. We compared counts from single observer surveys (i.e., primary observer counts only) and double observer surveys (i.e., primary and secondary observer counts summed), assuming the counts from double observer surveys were closer to 'truth'. We did this only for plots where double observer surveys occurred. We estimated moose density (D) as:

Equation 1

$$D = \frac{n}{a * t * d}$$

where n is the number of detected pellet groups, a is the area sampled, t is the accumulation period in days (usually based on time elapsed since first snow fall), and d is the daily defecation rate (Cederlund and Liberg 1995, Rönnegård et al. 2008, Månsson 2009, Zimmermann et al. 2015, Pfeffer et al. 2018). Following standard methods we assumed an average defecation rate of 14 pellet groups per day for moose (Zimmermann et al. 2015, Pfeffer et al. 2018) and an accumulation period of 183 days (30 October –30 April). We calculated density ranges based on minimum and maximum defecation rates (min. 13 and max. 23 moose pellet groups per day; Andersen et al. 1992, Persson et al. 2000, Matala and Uotila 2013). We defined the effective sampling area as the number of plots multiplied by the plot area (100 m^2).

Multinomial-Poisson mixture models

We estimated detection probabilities for only double observer survey data. For this we used multinomial-Poisson mixture models (Royle 2004, Royle and Dorazio 2006). We used a multinomial distribution for the observation state (i.e., the observed counts), and a Poisson distribution became the latent (i.e., unobserved) variable. We used a structure for dependent double observer surveys by specifying multinomial cell probabilities according to (i) the probability observer 1 but not observer 2 detected the pellet group (column 1; Figure 2); (ii) the probability that observer 2 but not observer 1 detected the pellet group (column 2); and (iii) the probability that both detected the pellet group (column 3). We included a single covariate on detection probability (*p;* all covariates described in Table 1) and cutting class as a single covariate on abundance (Edenius et al. 2015). We also specified a null model (~1 on *p*, ~1 on abundance), resulting in 12 candidate models. We calculated density by dividing abundance by the effective sampling area (see above). We used only moose pellet counts for this analysis. We used Akaike's Information Criterion corrected for small sample sizes (AICc) and model weights (w_i) for model selection. We considered models <2 ΔAIC to be equally supported and chose the simpler model (Burnham and Anderson 2002). We ran models using package 'unmarked' (Fiske and Chandler 2011) in program R (R Core Team 2020).

Results

Pellet counts

We completed 19% (n = 192) and 15% (n = 145) of all plots as double-observer surveys in 2019 and 2020, respectively. Seven plots were clearcut and five had missing data from 2018 so we could not reliably assign tree density, field layer, and dominant tree species. These plots were dropped from the analysis (new sample size = 325). Across years, most double observer surveys occurred among two sites (Gravberget: n = 161; Ljørdalen: n = 123; Plassen: n = 41). Of the 325 plots, we counted 230 moose pellet groups with a mean count of 0.68 pellet groups per plot (SD = 1.55). We did not detect pellet groups in 70% (n = 229) of the plots. Pellet counts were highest among dwarf shrub (mean pellet counts per plot = 0.52, SD = 1.24) and lichen (mean pellet counts per plot = 0.53, SD = 0.99) field layer types. Forty-eight percent (n = 13) of our observers had no prior field experience, 31% (n = 8) had 0–6 months experience, 12% (n = 3) had 6–12 months experience, and 8% (n = 2) had >1 year of experience. Single observers spent less time surveying (Figure 3A). Mean pellet group counts were similar for observer experience levels

(Figure 3C), but observers with 7–12 months prior field experience spent more time searching (Figure 3D). For double-observer surveys, the second observer detected additional pellet groups (mean = 0.20, SD = 0.67) not seen by the first observer (mean = 0.48, SD = 1.12), indicating a potential source of detection error (Figure 3B). The primary and secondary observers detected the same number of pellet groups in 88% (n = 285) of the plots. However, when pellet groups were present (e.g., combined observer count > 0; n = 96) the secondary observer saw additional pellet groups 42% (n = 40) of the time (Figure 3D). See Table 2 for the distribution of pellet group counts by primary and secondary observer.

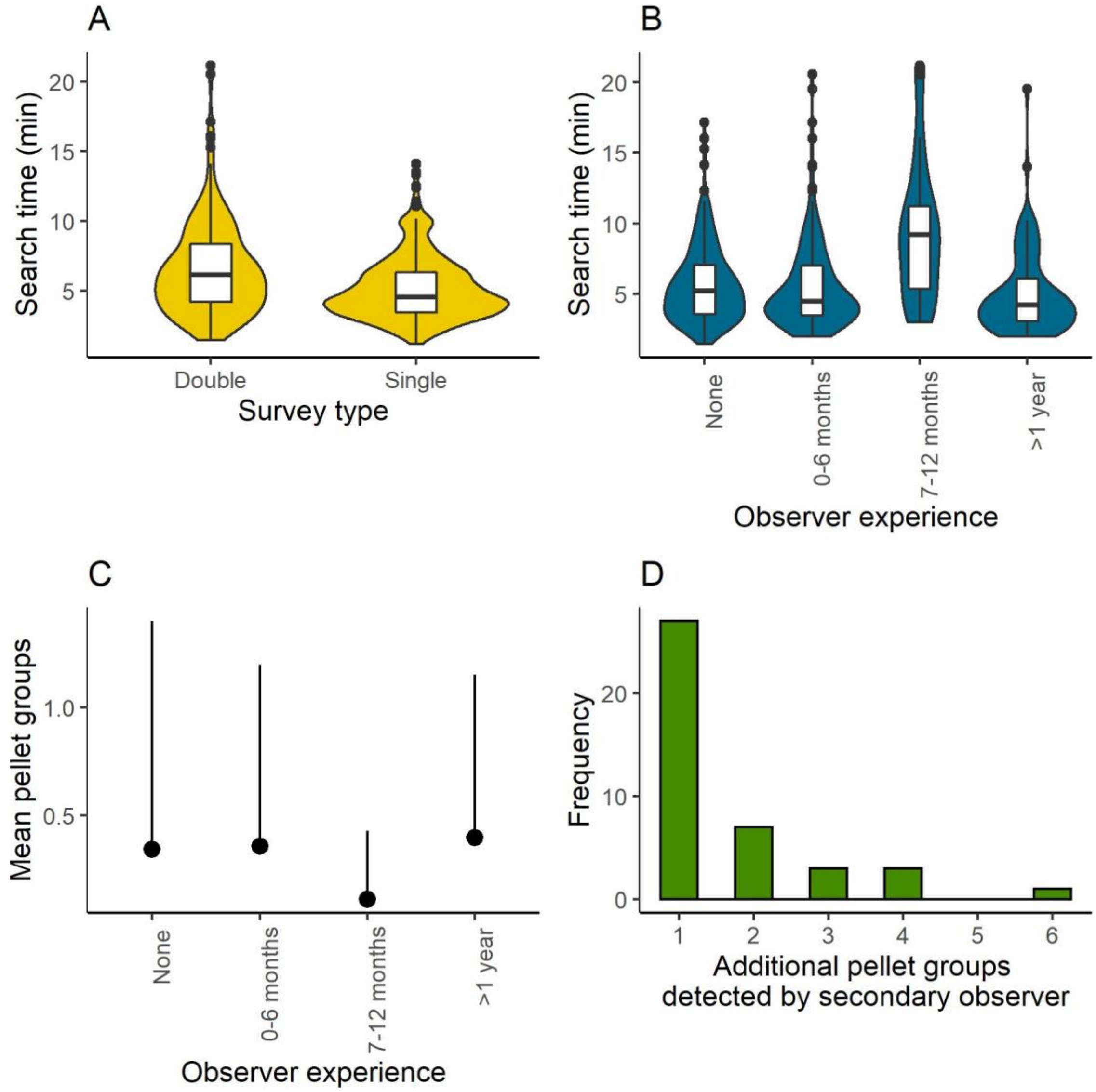

Figure 3. A) Box and violin plot of search time by survey type; B) box and violin plots of the search time (by both primary and secondary observers) in minutes by observer experience; C) the mean number of pellet groups detected by observer experience, which is a general field research experience index. We used mean values as the data are very zero-biased, thus it is difficult to visualize many zeros in boxplots. Error bars represent standard deviation; D) distribution of additional pellet groups detected by the secondary observer. Surveys were conducted in Norway 2019–2020.

Table 2. The distribution of moose pellet group counts by primary and secondary observers. The first row under the primary observer column means observer one did not detect pellets in 233 plots. For the second row under the secondary observer column, observer two detected one additional pellet group in 26 plots. We denoted the gap between 6 and 13 pellet group counts with an empty row. Data were from 325 plots in Norway (2019–2020).

Pellet group count	**Primary observer**	**Secondary observer**
0	233	285
1	64	26
2	15	7
3	5	3
4	5	3
5	1	0
6	1	1
…	…	…
13	1	0
Total	325	325

Density estimates

We calculated density estimates separately for 2019 and 2020. In 2019, double and single observer density estimates were 2.0 (min–max: 1.2–2.1) and 1.4 (min–max: 0.9–1.5) moose per km^2, respectively. In 2020, double and single observer density estimates were 2.7 (min–max: 1.7–2.9) and 1.9 (min–max: 1.2–2.0) moose per km^2, respectively.

Multinomial-Poisson mixture models

The top-ranked model included time searched (Table 3). Detection probabilities increased with search time (Figure 4A). At 10 minutes search time, detection probability was 0.60 (95% CI = 0.42–0.75). At 20 minutes search time, detection probability was 0.94 (95% CI = 0.81–0.99). Looking at lower-ranked models (

Table 3), *p* increased with tree density (Figure 4B), *p* was highest for experienced observers (Figure 4C), and *p* decreased slightly as Julian day increased (Figure 4D). Interestingly, field layers ranked low (

Table 3) in relative parsimony but they are important from a possible habitat bias perspective. Detection probabilities were highest in field layers dominated by dwarf shrubs (Figure S 3) but this was also the most common field layer type (Figure S 4). Uncertainties (i.e., wide 95% confidence intervals) in field layer estimates, however, precluded any strong conclusions. We back-transformed estimates of p for the null model: $p = 0.56$ (SE = 0.06) and abundance = 0.84 (SE = 0.08). This suggests that when a pellet group was present, it went undetected 44% of the time by the first observer. Moose density was highest in cutting class two (Figure 5).

Table 3. Model selection table from multinomial Poisson mixture models. Covariates were used only on detection probability (p). Cutting class was the sole covariate used on abundance and is not listed in the table.

Model	**K**	**AICc**	**ΔAICc**	**w_i**	**LL**
Time searched	8	948.65	0.00	1.00	-466.10
Tree density	8	963.48	14.83	0.00	-473.51
Observer experience	10	977.34	28.69	0.00	-478.32
Julian day	8	978.07	29.42	0.00	-480.81
Snow cover	8	980.99	32.34	0.00	-482.27
Dominant tree	10	981.42	32.77	0.00	-480.36
Residual cover	8	982.00	33.35	0.00	-482.77
Time of day	8	982.71	34.05	0.00	-483.13
Field layer	12	983.69	35.04	0.00	-479.35
Weather	12	983.75	35.10	0.00	-479.38
Pellet counting experience	9	983.89	35.24	0.00	-482.66
Null model	2	1077.19	128.54	0.00	-536.58

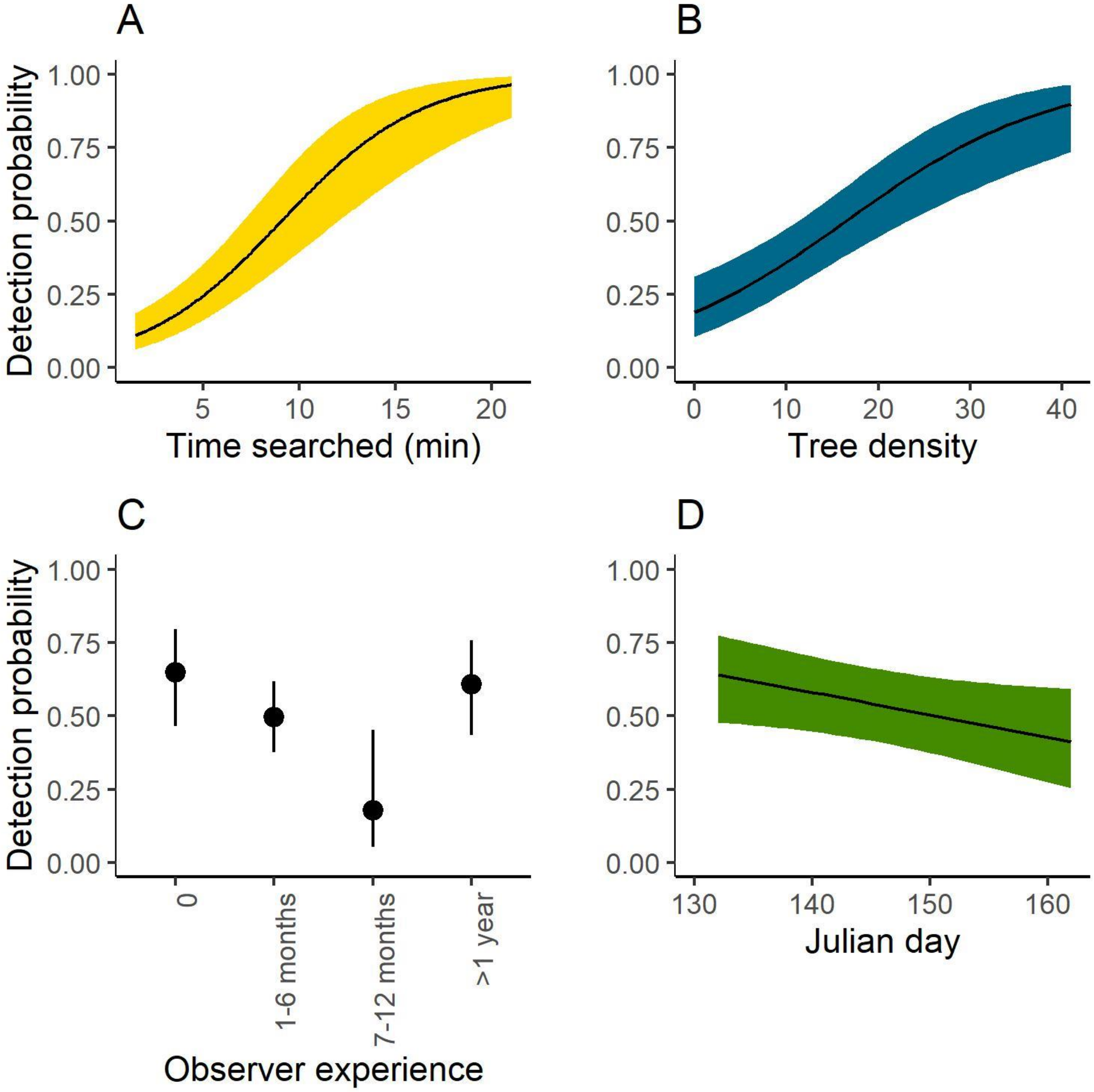

Figure 4. Prediction plots showing detection probabilities for A) the time searched in minutes; B) number of trees taller than 0.30 cm in the plot; C) prior observer experience in field research; D) Julian day that sampling occurred. Ribbons and error bars represent 95% confidence intervals. Predictions were made from models listed in Table 3.

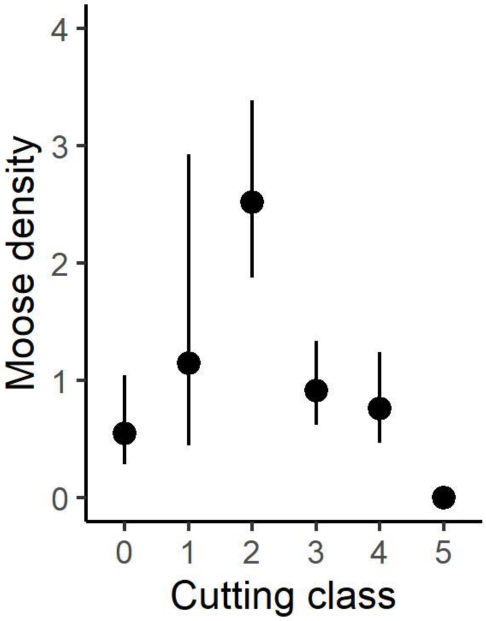

Figure 5. Predicted moose density (number of moose per km^2) by cutting class, which are graphed in order of maturity (1 = clearcut, 5 = old-growth forest; see Table 1 for the variable description). Predictions taken from top-ranked multinomial-Poisson mixture model. Error bars represent 95% confidence intervals.

Discussion

Pellet counts are a commonly used method to monitor ungulates because they are relatively cheap, it is easy to train inexperienced workers, and pellet counts do not require expensive field equipment. There are known issues, however, such as uncertainties with pellet decay and incomplete observations (Alves et al. 2013). We completed 16% of our annual plot surveys across two years as double observer surveys, a method common to avian point counts. Use of double observer methods allowed us to provide detection probabilities for moose pellet groups. This was important especially for our work, as we relied heavily on volunteers, many of whom had no prior field experience. We believe our results also provide valuable knowledge for other studies relying on fecal count estimates.

It should be no surprise that we found more pellet groups when two instead of one observer looked for pellets. Indeed, rarely are counts without error (MacKenzie and Kendall

2002, Elphick 2008). Generally, pellet counts underestimate density because pellets go undetected due to vegetation, decay, and insufficient survey efforts (MacKenzie and Kendall 2002). Results from our modeling indicate that overall, we detected 56% of pellet groups when they were present. This matches what was seen in the observed data as well. While our estimates indicate we missed pellets, and may be cause for concern, they were similar to estimates of *p* in other deer studies. For example, in one study, teams of inexperienced observers detected on average 68% of the deer (fallow deer [*Dama dama*], roe deer, white-tailed deer [*Odocoileus virginianus*]) pellet groups detected by professional biologists (i.e., experienced observers; Buesching et al. 2014), meaning they missed 32% of the known pellet groups. The consequences of missing pellet groups could be small if the spatial and temporal scale of the estimates are also small, as was the case in our study. Indeed, the scale of our study was small relative to moose distributions in Scandinavia (Figure 1), and one could argue that our sites were too small (minimum site area = 38.68 km^2; maximum site area = 55.57 km^2) to estimate moose density, relative to an average moose winter home range (across Sweden 10.81 km^2; SD = 6.55; Allen et al. 2016; specific to our study region in Norway 42.15 km^2; SE = 8.55; Bramorska 2020). Yet, if we think of our density estimates as simply a mathematical exercise, and we assume our double observer counts represent “true” values, the moose density would be 1.4 larger than if we had estimated using single observer counts only.

In Scandinavia, hunting is a primary driver of moose mortality (Zimmermann et al. 2019), where between 18 and 35% of the population is harvested each autumn (Sand et al. 2011, Jonzén et al. 2013). Pellet counts are used by both researchers and managers as indices of absolute and relative abundance, density, or population trend (Cederlund and Liberg 1995, Rönnegård et al. 2008, Månsson 2009, Zimmermann et al. 2015, Pfeffer et al. 2018). For a research example, Zimmermann et al. (2015) used pellet counts to estimate the relative density of moose and other deer species to understand functional responses of wolves to their prey. For a management example, in central Sweden (Svealand), pellet counts are used to supplement observed moose ('sett elg') to help set moose harvest quotas (Bergström et al. 2011), though the use of pellet counts may decline in the future (F. Widemo, pers. comm.). If we indeed underestimate moose density, harvest quotas may be lower than populations can sustain. More importantly, this could result in a mismatch between on-the-ground moose densities and management objectives.

Our detection probability covariates provided insights into our sampling biases. First, detection probabilities were highest for the least and most experienced observers. While this is not an intuitive result, it is supported by findings from other studies where inexperienced observers performed better than experienced observers. For example, technicians new to the sampling protocol in a non-invasive genetic sampling study in the USA collected more scats, were more accurate in identifying the target species, and collected more high-quality samples for genetic amplification relative to technicians familiar with the protocol (Soller et al. 2020). The authors attributed these findings to inexperienced observers being choosier, meaning they likely sampled from higher-quality scats, and experienced observers possibly became bored or fatigued. This could certainly be the case in our study, where the same protocols are completed multiple times per day. Interestingly, observers with 6–12 months prior experience searched the longest but had the lowest detection probability. We collected the observer experience data as a binned category. In hindsight, we should have collected continuous data since our binned categories may have been inappropriate (i.e., is there a different between 1–5 months and 6–12 months experience?). However, our findings indicate that it is important to properly define prior observer experience. Second, we also found that detection probability increased with increasing tree density. Given this counterintuitive result, we suspected this was a result of increased search time in plots with more trees. However, our data do not support this (Figure 6). More likely, high tree densities may reduce field layer complexity due to canopy shading. Likely there are interactions present, which we did not test in this paper. Third, we found that *p* decreased with Julian day; an increase by one week (7 days) decreased *p* by 0.9. This makes sense as green-up of the field layer can conceal pellets, as confirmed by previous studies (Persson 2003).

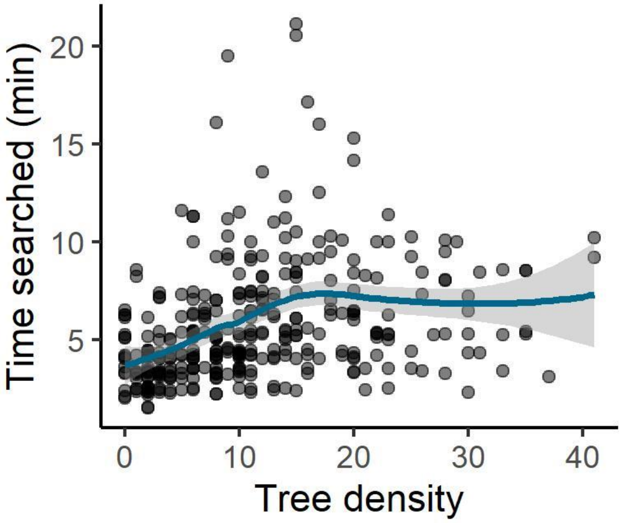

Figure 6. Scatter plot and loess smoother (green line) of tree density and time spent searching the plot. Tree density was number of trees taller than 0.30 cm per plot. Grey ribbon represents 95% confidence interval. Data were from Norway 2019–2020.

Given our study, how can pellet count methods be improved? We provide three recommendations. First, we recommend that projects relying on pellet counts do a subset of plots as double observer surveys to identify sources of error or bias. While we implemented a dependent double observer method because it has higher precision and is more time efficient in the field than independent double observer methods (Forcey et al. 2006), projects could modify our methods to do independent double counts. For example, the Scandinavian Wolf Research Project (SKANDULV; e.g. Zimmermann et al. 2015, Sand et al. 2016) conducts deer pellet counts by surveying the plot in a similar manner as described in Figure 2. However, they have a single observer walk the inner and outer circles twice, walking each circle first clockwise and then counter-clockwise (i.e., they make four ‘rounds’). This is an intensive searching method that could be easily changed to estimate detection rates: the first walk around could be recorded as a ‘first count’ and the second walk would be the ‘second count’.

A second recommendation for improving pellet counts is that once sources of error are identified, they can be accounted for in the field and in modeling. In our case, search time was an important variable for detection. In the field, minimum search times could be implemented based on desired detection probabilities, and ‘time searched’ should be recorded. At the office, ‘time searched’ could be included in models and future single-observer counts could be adjusted based on the known detection probabilities. Third, we recommend doing a subset of single observer plots as double observer surveys for several years. The data collected for this study only represented two years. In this time, we relied on large groups (> 16 observers) of inexperienced observers. However, every third year (e.g., 2018, 2021) we have smaller groups (4–8 observers) who spend up to two months in the field. Observers thus get more experience within the field season, versus only a few days where observers have only a short ‘learning window.’ We might see even stronger trends in p based on prior observer experience.

Another recommendation from this study is improving the sampling design to match scales of movement relevant to moose. During winter, moose move on average 3 km per day (Pfeffer et al. 2018). Thus, 100m^2 (5.6–m radius) plots represent a very small total sampled area for a moose. Other methods, such as distance sampling with transects (Alves et al. 2013) might allow researchers to cover more ground with equivalent effort. As well, this could increase habitat representation along a gradient (e.g., a transect could cover a range of distances to an open forest). The choice of methods, however, depends on the goals of the monitoring project.

While not a direct result from our study, we recommend regular feedback sessions with observers throughout the field season, rather than train them only one day at the beginning.

Previous work has shown that data collected by volunteers increases in accuracy with consistent supervision and training (Foster-Smith and Evans 2003, Buesching et al. 2014). Feedback sessions could be useful, where all observers count the same plots and learn from the group average (Wintle et al. 2013). For large-scale efforts like those in Svealand, Sweden, pellet counts are completed mostly by volunteer hunters (‘citizen scientists’). This represents an excellent database, but the numerous observers with differing prior field experience levels likely introduces additional variation into the observed pellet groups.

The future of population monitoring is changing. Advances in non-invasive genetic techniques have made individual assignment of moose from pellets possible (Blåhed et al. 2019). While more costly for the same spatial extent, this may represent a possibility for future moose population monitoring, as is the case for other wide-ranging mammals (Proctor et al. 2015, Loosen et al. 2019). One of the take-homes from this study is that large uncertainties exist in management decisions and being able to identify sources of error can help reduce those uncertainties. We maintain that pellet counting is an important tool for monitoring, as it is an easy method to implement across large areas. However, our results highlight the uncertainties with a standard method and recommend research and management projects complete a subset of plots as double observer surveys to identify and quantify uncertainties.

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Barbara Zimmermann: Writing – review & editing

Karen Marie Mathisen: Funding acquisition; Investigation; Project administration; Supervision; Writing – review & editing

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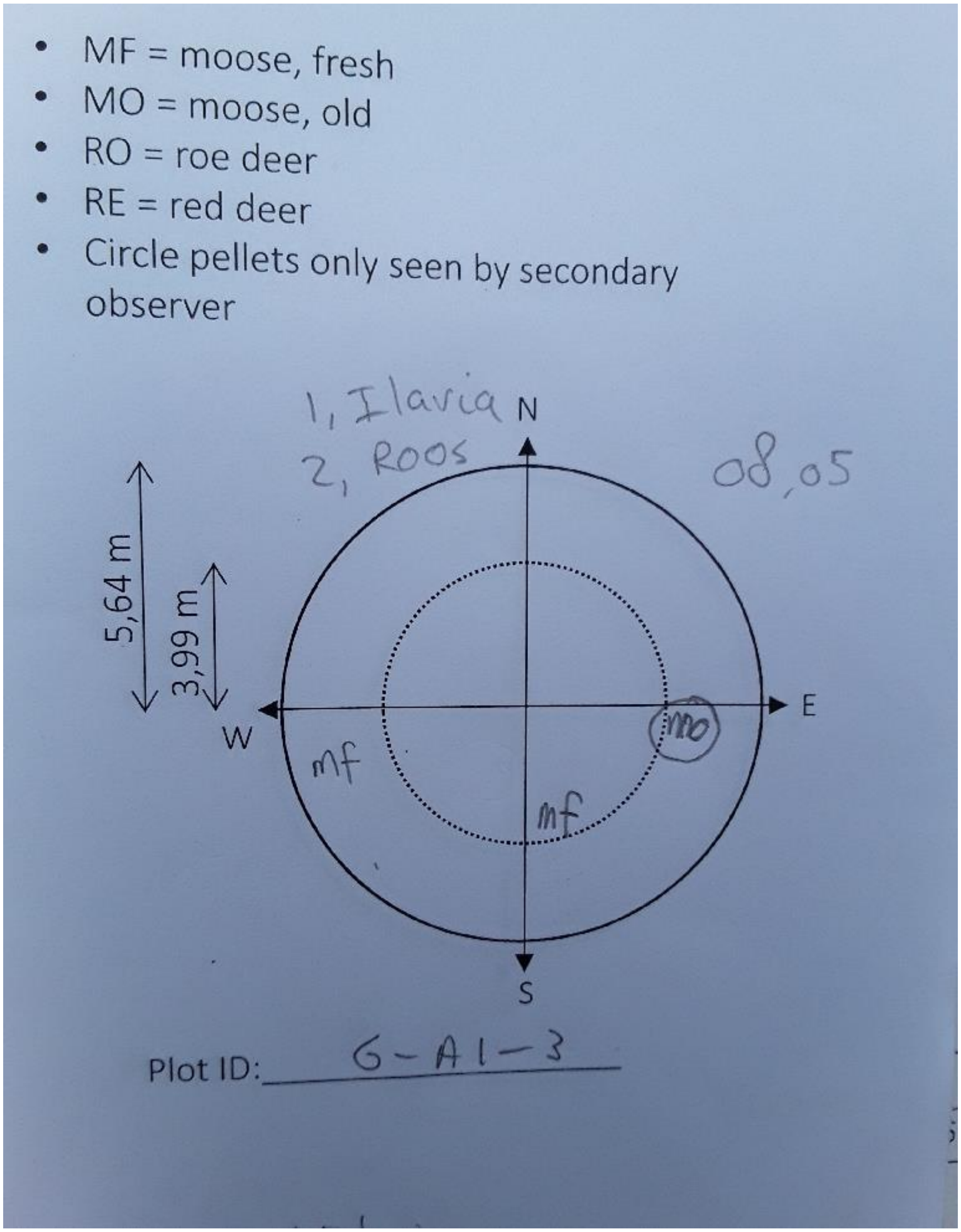
Supplementary information



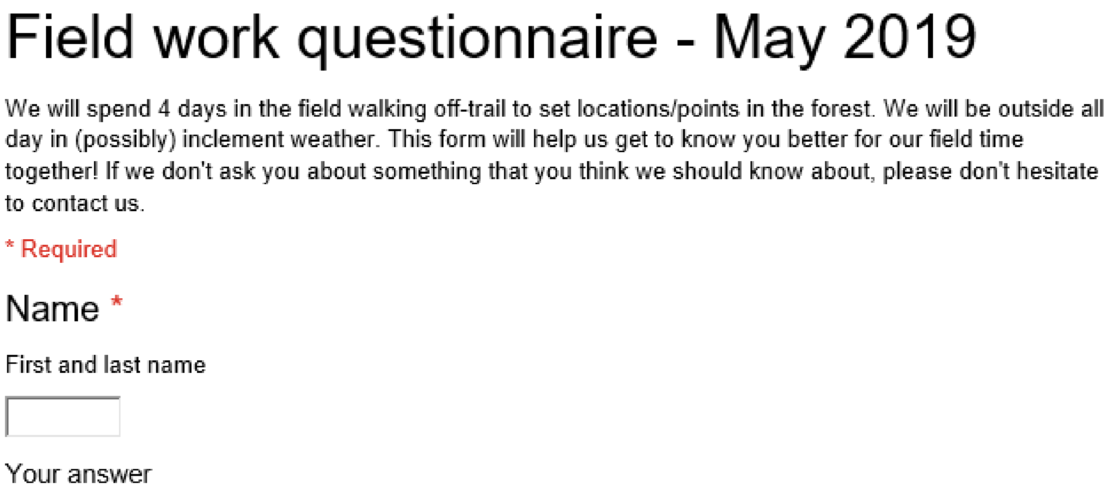
- MF = moose, fresh
- MO = moose, old
- RO = roe deer
- RE = red deer
- Circle pellets only seen by secondary observer

1, Ilavia
2, Roos

08,05

Plot ID: G-A1-3

Figure S 1. Example of a double observer diagram completed in the field.



Field work questionnaire - May 2019

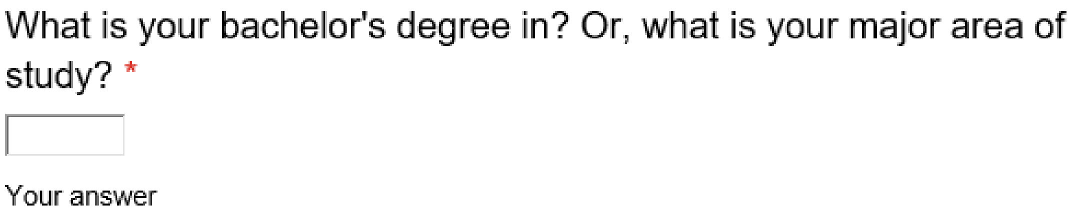
We will spend 4 days in the field walking off-trail to set locations/points in the forest. We will be outside all day in (possibly) inclement weather. This form will help us get to know you better for our field time together! If we don't ask you about something that you think we should know about, please don't hesitate to contact us.

* Required

Name *

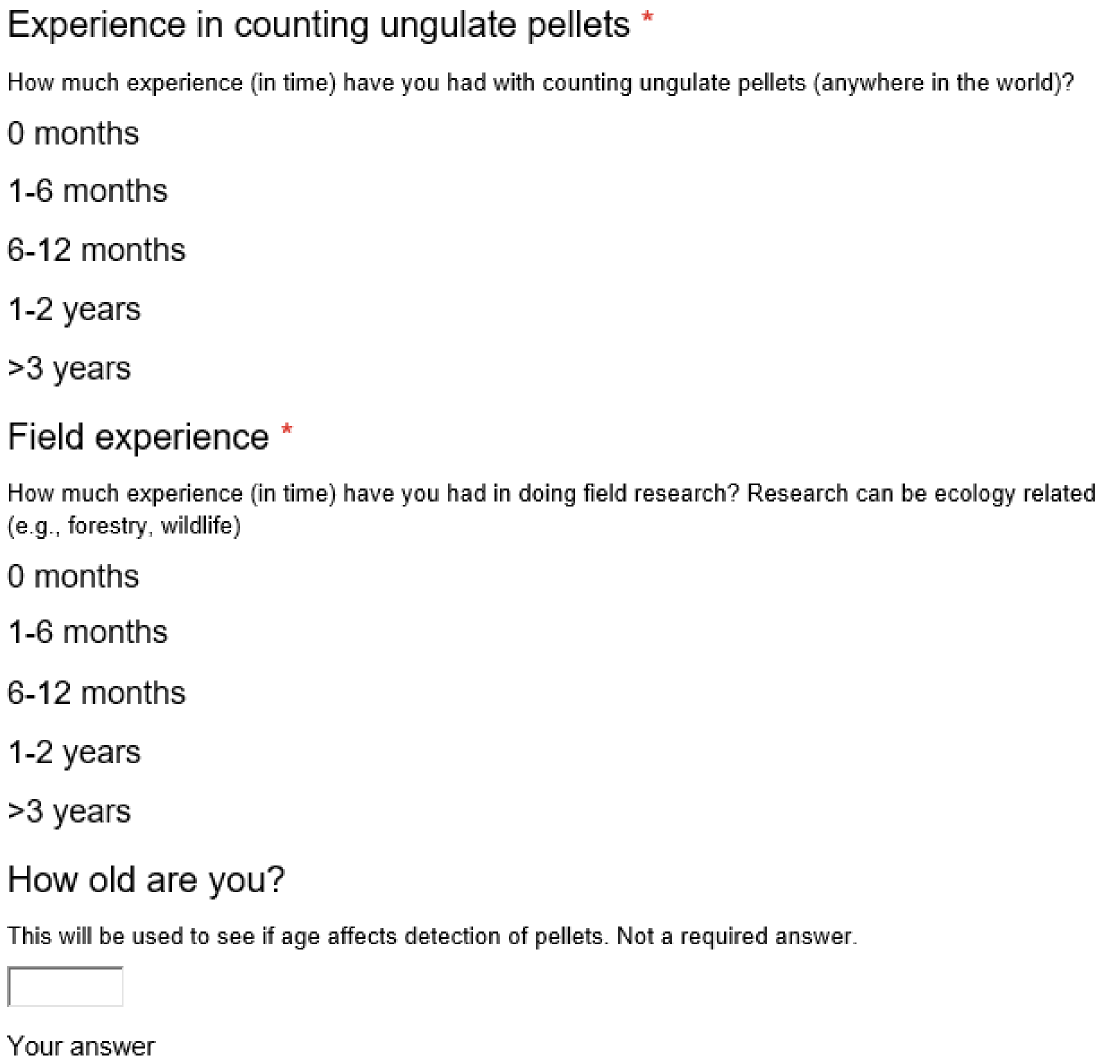
First and last name

Your answer



What is your bachelor's degree in? Or, what is your major area of study? *

Your answer



Experience in counting ungulate pellets *

How much experience (in time) have you had with counting ungulate pellets (anywhere in the world)?

0 months

1-6 months

6-12 months

1-2 years

>3 years

Field experience *

How much experience (in time) have you had in doing field research? Research can be ecology related (e.g., forestry, wildlife)

0 months

1-6 months

6-12 months

1-2 years

>3 years

How old are you?

This will be used to see if age affects detection of pellets. Not a required answer.

Your answer

Figure S 2. Survey questions completed by each observer.

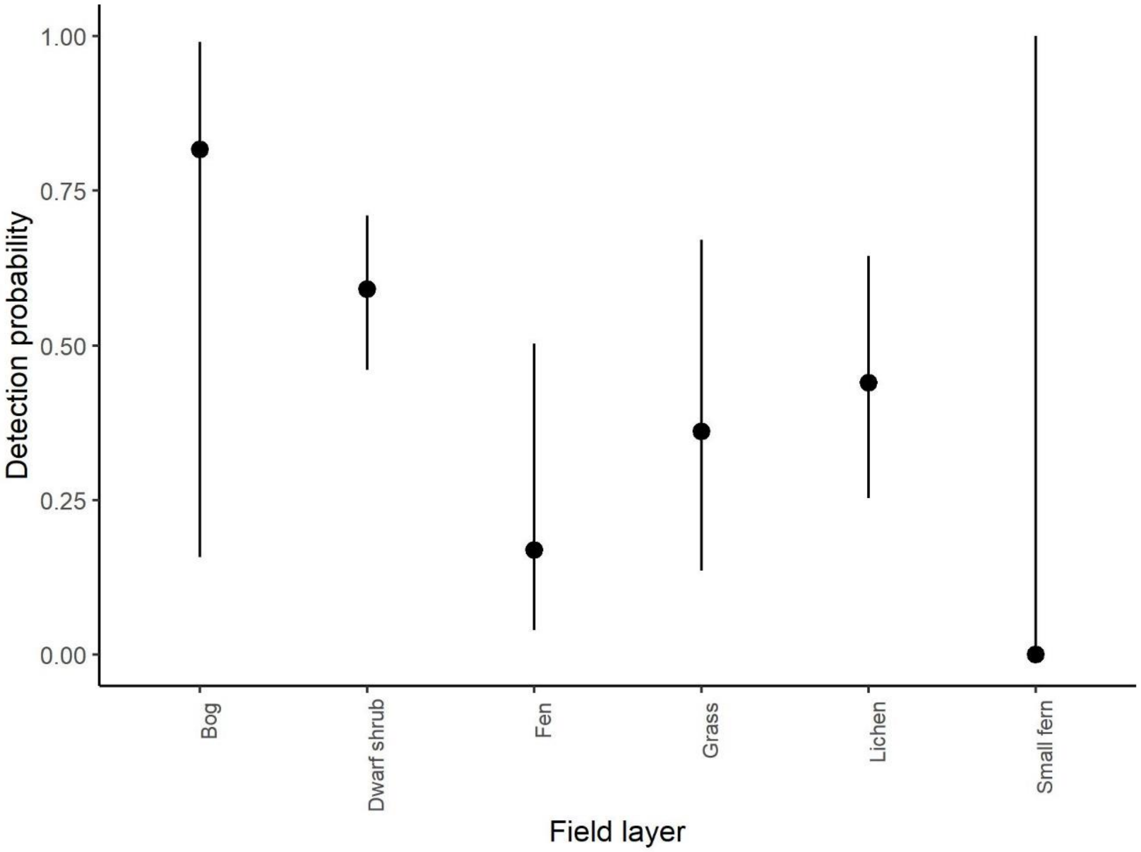


Figure S 3. Detection probabilities by field layer type. Error bars represent 95% confidence intervals. Data were from Norway 2019–2020.

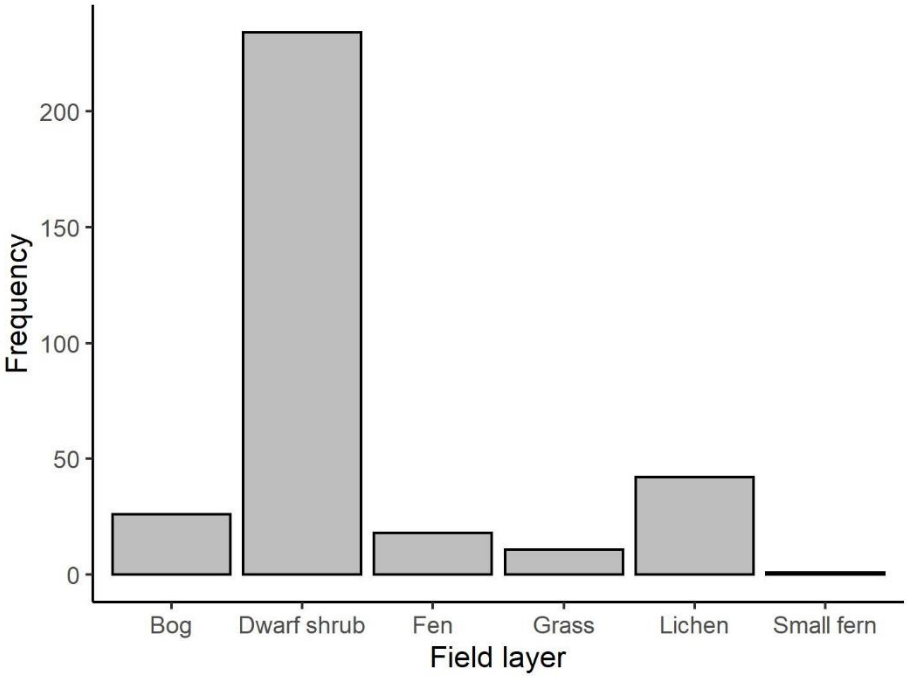


Figure S 4. The distribution of field layer classifications in our data. Data were from Norway 2019–2020.

Inland Norway
University of
Applied Sciences

This thesis focuses on the primary challenges to ungulate management in the 21st century: multiple land uses that provide food subsidies, predator recolonization, climate change, and monitoring population trends of wide-ranging animals. I focus on the feeding ecology and spatio-temporal patterns of the largest circumboreal herbivore, the moose (*Alces alces*).

The thesis objectives were to evaluate: 1) how browsing was influenced in areas with high predation risk, such as areas close to roads and with wolves (*Canis lupus*), in accordance with a landscape of fear; 2) whether ungulate-adapted forestry can be used to mitigate and reduce browsing damage; 3) if there was variation in the intensity of landscape use of moose, in response to variable winters; 4) sources of error associated with a common monitoring method for cervids.

I found that roads are a major driver of moose browsing ecology, with a greater effect than wolf occurrence alone. Browsing occurrence was nearly double in young forests along low-traffic roadsides, relative to forests older and younger than 5–20 years, which could exacerbate moose-forestry conflicts. I also found promising effects of ungulate-adapted logging to alleviate browsing damage, although monitoring over a longer period would likely show greater differences. I found that snow depth and winter temperature influenced intensity of use of the landscape by moose, with temperatures above 0°C showing a decline in intensity of use. And last, I found evidence that the detection errors associated with fecal pellet group counts were larger than previously thought.

This thesis advanced our knowledge of the effects of human disturbance on moose ecology. It highlights that humans are an important provider of forage via land use changes, and that milder winters may disproportionately affect Scandinavia's southern moose populations compared to northern populations. I provide practical suggestions to address detection errors to improve monitoring.