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# Harvest Rates in a Partially Migrating Moose *Alces alces* Population Relate to Summer but Not Winter Moose Densities

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Animal Biology

# Preface

"To all the educators who have worked tirelessly for quality biology education" (Sadava et al., 2012).

This thesis was completed for Inland Norway University of Applied Sciences (INN) and the GRENSEVILT project. The thesis marks the end of a two-year Master program in Biology at the Norwegian University of Life Sciences (NMBU).

I would like to express gratitude to my supervisors Leif Egil Loe at NMBU, for great tips for succeeding and for invaluable counsel in the writing process, Barbara Zimmermann and Giorgia Ausilio at INN for statistical help and guidance, for structuring and planning the field work and for including me in GRENSEVILT. It´s going to be exciting to follow! To the pellet counting field work group from INN (and all over the world), thank you for the cooperation, for help and for all your time spent in the field. The pellet group count would most definitely not been possible without the joint effort.

I am grateful to my family for encouragements, curiosity and guidance. Thank you for letting me jump between being a 25-year-old master student and a 14-year-old horse girl! Also, for making jokes about my time spent in the forest "playing with moose poop". I think my 3-year-old nephew, Oskar, still calls my name every time he sees a pile of moose pellets in the forest.

Last but not least, to my two fellow thesis writers whom I live and wrote with: thank you and congratulations!! I am ever so thankful for our friendship.

Ås, 31.05.2021

Sara Skybak

# Abstract

Moose *Alces alces* are in many parts of Scandinavia managed at high densities to maximize harvest rates. This comes with benefits for hunters and landowners, but also with costs for forestry, because moose can do considerable browsing damage in young pine stands. The spatial distribution of benefits and costs is a particular challenge for moose management in areas where moose is migratory. When snow falls in high-elevation ranges, increasing movement costs and reducing access to forage, the moose migrates to lower elevations with less snow. If the moose migrates late in, or after the annual moose harvest season, the distribution of cost is be skewed towards management units containing the summer ranges of moose. By comparing summer and winter densities of moose with harvest rates I aimed at explaining how potential costs and benefits of moose are shared among landowners in a partially migrating moose population. My main hypothesis was that moose harvest correlates with the summer density, but not the winter density of moose. As a proxy for moose density, I counted fecal pellet groups during spring 2020 (winter densities 2019-20) and fall 2020 (summer densities 2020) on 1535 sample plots, covering 20 neighboring moose management units in an area of 4544 $km^2$. Data on moose harvest per moose management unit were derived from the official Norwegian and Swedish hunting statistics for the hunting years 2019-20 and 2020-21. As predicted, moose harvest was positively related with summer densities of moose pellet groups but did not correlate with winter densities of pellet groups. The thesis also found that snow depth is an influencing factor for winter distribution. My study substantiates that there is a mismatch between the timing of migration and moose harvest. This can lead to a biased distribution of browsing damage and hunting revenue between the moose management units. As migration is of potential conflicts, I propose a temporal adjustment of the harvest season and collaboration between stakeholders covering the entire range of the studied moose population.

# Sammendrag

Et stort antall elg *Alces alces* forvaltes i Skandinavia med hensikt om størst mulig jaktuttak. Med høy tetthet kommer positive aspekter for jegere og grunneiere, men også negative aspekter for skogbruket da elgen kan gjøre betydelig beiteskade på ung, regenererende furuskog. Disse positive og negative aspektene forstekes ytterligere av det faktum at størsteparten av elg er migrerende. Når det snør i høyereliggende områder, blir bevegelse mer anstrengende og fôrtilgangen reduseres. Dermed vandrer elgen mot lavere liggende områder med mindre snømengde. Hvis elgen migrerer sent i eller etter den årlige elgjakta fordeles kostandene av å ha elg på vinterbeite ujevnt til vinterområdene mens godene av elg på sommerbeite fordeles til sommerområder. Ved å sammenligne tetthet av elg på sommer og vinter med fellingstetthet, belyste dette studiet elgens migrasjonstiming og indirekte hvordan fordeler og ulemper med en migrerende elgbestand fordeles mellom grunneiere i ulike jaktvald. Hypotesen var at størsteparten av elg migrerer etter jaktsesongen med en påfølgende prediksjon om at fellingstettheten kun skal korrelere med sommertetthet og ikke vintertetthet. For å estimere tetthet og fordeling av elg ble møkktaksering benyttet som metode i løpet av våren 2020 (vintertetthet 2019-20) og høsten 2020 (2020-21) på 1535 prøveflater på tvers av 20 ulike jaktvald som grenset til hverandre, på et 4544 km$^2$ stort studieområde. Fellingstall ble hentet for jaktsesongene 2019-20 og 2020-21 fra offisielle kanaler for Norsk og Svensk jaktstatistikk. Som predikert viste det seg at sommertetthet av elg og fellingstetthet samstemte, mens fellingstetthet og vintertetthet ikke hadde noe spesiell sammenheng. Studiet fant også at snødybde er en påvirkningsfaktor for valg av vinterområde. Dette studiet underbygger at det er et romlig misforhold mellom kostnadene av beiteskader og godene som følger elgjakt i de 20 ulike jaktvaldene. Dette kan føre til en uoverensstemmelse når det kommer til beiteskader og jaktinntekter mellom jaktvaldene. Da migrasjonen kan føre til konflikter foreslår jeg en tidsmessig forskyvning av jaktsesongen og et bedre samarbeid mellom ulike forvaltningsenheter på tvers av hele hjemområdet til den migrerende elgbestanden.

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# 1. Introduction

Management of wildlife often follows administrative and political boarders instead of considering the animals ecologically relevant scale (Bischof et al., 2016; Linnell et al., 2001). Migratory species cross many the administrative and political boarders during their seasonal migration, but collaboration of stakeholders and management across these administrative units is often inadequate. Migration can have various motivators, both spatial and temporal, i.e., for resources, reducing predation risks, avoiding parasites or diseases, avoiding early snow at high elevations and high snow accumulation (Gundersen et al., 1998; Rickbeil et al., 2019). Knowing which areas that share a migrating population is difficult, as is knowing when migration happens. Both types of knowledge are crucial for the management of a resource that is harvested only for a small part of the year. Managing a population that between seasons spatially divides over large, administratively divided areas is challenging for moose conservation (Meisingset et al., 2018; Ueno et al., 2014). Optimal management becomes challenging when various managers and moose management units ignore the individual animals space use and treat individuals within their own management area as being part of a homogenous population (Milner-Gulland et al., 2000).

The moose *Alces alces* is considered to be a keystone species and distributed across the wide boreal zone, from North America through Scandinavia and all the way to Siberia (Meiri et al., 2020; Wam & Hjeljord, 2010). Moose are generalist herbivores yet with strong forage selectivity and require large amounts of food (Belovsky, 1981; Wam & Hjeljord, 2010). The ideal moose habitat is described as a mosaic of forest types, with younger and older forests and various other habitats (Nikula et al., 2004). Moose habitat varies with seasons (Bjørneraas et al., 2011) and good summer forage conditions are of major importance for the moose's body growth and fecundity (Wam & Hjeljord, 2010). During summer season moose mostly inhabit fertile habitats dominated by deciduous trees and forbs (Bjørneraas et al., 2011; Nikula et al., 2004). It feeds on deciduous species, especially rowan *Sorbus aucuparia*, aspen *Populus tremula*, willow *Salix caprea* and oak *Quercus sp.*, but at the onset of winter, moose begin to forage on young, thinned forests with coniferous species, like the highly abundant Scots pine *Pinus sylvestris* (Cederlund, 1980; Nikula et al., 2004). Pine browsing damage can incur in significant costs for forestry agencies, because the browsing often happens in highly productive regenerating forests with high potential value (Ball & Dahlgren, 2002).

Since the Scandinavian moose utilize different vegetation types in summer and winter, a large proportion of the population migrates in areas with distinct climatic seasonality (Allen et al., 2016) and along predictable gradients, like elevations and snow depths. With winter comes the end of the green season and snowfall. Snow is believed to be an important driver for moose migration and both the depth and density of snow is often suggested as a strong factor for migration (Rivrud et al., 2016). As the snow depth increases, the availability of food is decreased by being buried by snow and the cost of locomotion increases (Ball et al., 2001; Hebblewhite et al., 2008; Lundmark & Ball, 2008; Nikula et al., 2004; Skonhoft & Olaussen, 2005). In snow depths higher than 25 cm winter forage availability is restricted, and in snow deeper than 70 cm studies have shown that the moose´s ability for locomotion is restricted (Allen et al., 2016). Spring migration, from the winter ranges back to the summer ranges, seems to be motivated by extending the period with access to spring greens (the forage maturation hypothesis; Hebblewhite et al. (2008)) and by snow melting (Nikula et al., 2004). During summer the moose is relatively evenly spread in the landscape, often in higher altitudes. As the snow depth increases in these high altitudes in the beginning of the next winter, moose migrate back again to lower altitudes (Gundersen et al., 1998; Gundersen et al., 2004).

Moose hunting is a pilar in Scandinavian culture with long social and cultural traditions and history (Lavsund et al., 2003a; Saether et al., 1996; Skonhoft & Olaussen, 2005). The Scandinavian moose population is managed through age- and sex-specific harvest, making the population to one of the most productive and densest in the world (Ball & Dahlgren, 2002; Lavsund et al., 2003b; Skonhoft & Olaussen, 2005; Wam et al., 2010; Wikenros et al., 2019). Sex and age-specific harvesting was introduced in Norway in the late 1970´s and with this the weight was shifted towards hunting more adult males, yearlings and calves and less adult females. This left a higher part of productive animals for recruitment and led to a growing moose population (Lavsund et al., 2003a; Olaussen & Skonhoft, 2011). In the 1950´s the forestry stand management, with clear-cutting and assisted forest regeneration, was introduced and provided favorable moose habitat (Ball & Dahlgren, 2002; Lavsund et al., 2003b; Nikula et al., 2004). The result of this was improved moose forage availability and together with the sex and age-specific harvest the moose population flourished (Sæther et al., 1992). After these practices with sex- and age-specific harvest and forest stand management began, the number of harvested moose in Norway went from roughly 6000 in the hunting season in 1970/71 to more than 30 000 in 2019/20 (Statistisk sentralbyrå, 2020), dramatically increasing the revenue for hunters and landowners, but also the conflict level.

Browsing damage by moose on young regenerating forest stands causes economic loss for forest owners (Ball & Dahlgren, 2002). Moose can impact the Scandinavian coniferous forest ecosystem in the wintering areas through high browsing pressure on young forest areas and by inhibiting forest rejuvenation (Sæther et al., 1992). Therefore, Scandinavian forestry has a considerable interest in regulating the moose population to limit the browsing damage costs as much as possible (Grensevilt, 2018b). This is in contrast with hunters' interests, which is to have high moose densities and hunting outcomes (Storaas et al., 2001). The different interests between forest owners and hunters can be a cause of conflict, especially in those areas where there is extensive winter browsing damage but local hunters still want high summer densities (Meisingset et al., 2018).

The Norwegian moose harvest is controlled by the municipality through local moose management units and the Swedish moose harvest is controlled by the County governor through local moose management units. Hunting teams in the moose management units manage the moose population across several years to improve monitoring and long-term sustainable harvest of the moose population (Lavsund et al., 2003b; Wikenros et al., 2020). The quotas for the yearly harvest are based on browsing assessments, moose pellet group counts, previous years statistics on seen and shot moose, number of moose killed in traffic the last year and presence of large carnivores (Solberg & Saether, 1999; Wikenros et al., 2019). Presence of wolves is important for setting hunting quotas as wolves can predate a considerable proportion of the moose population, and in particular calves (Ausilio et al., 2021; Gundersen, 2003; Wikenros et al., 2016; Zimmermann et al., 2015; Zimmermann et al., 2019a; Zimmermann et al., 2019b). There are several studies about the wolf's predation on moose inside the same study area (Sand et al., 2019; Wikenros et al., 2019; Wikenros et al., 2020; Zimmermann et al., 2019b), indicating that the hunting pressure of wolves on moose is approximately the same in the entire study area.

Data on moose development (i.e., browsing assessments, moose pellet group counts, observed and harvested moose densities, moose kills in traffic) from previous years are important data for setting area-specific quotas based on moose population structure and density (Skonhoft & Olaussen, 2005; Ueno et al., 2014; Wikenros et al., 2019). If the goal is to keep the population stable, the harvest should balance the annual growth of the population, which means harvest rates between 25-35% of the summer population (Zimmermann et al., 2019b). Harvest quotas set specifically for the different management units are therefore important to regulate the annual growth and to maximize the economic income of the harvest whilst also minimizing the possible forestry browsing damage (Skonhoft & Olaussen, 2005). There is an asymmetry in economic gains and losses for various landowners. Some landowners gain on moose harvest incomes when the moose still roams its summer area, while other landowners only experience economic loss when the moose migrates into their lands after the harvest is over and inflict browsing damage in the forest. Conflicts can emerge when migratory moose cross administrative management boarders and cause economic implications (Mysterud, 2010; Putman, 1996; Sahlsten et al., 2010).

Collecting spatial distribution data over large areas is difficult. For individuals of species living in small groups or that are solitary, a large proportion of the individuals would have to be radio-tagged, which is both costly and highly invasive. For ungulates, fecal sampling has been used to estimate density and habitat use since 1940 (Bennett et al., 1940; Härkönen & Heikkilä, 1999; Neff, 1968). Fecal sampling is a useful proxy for local ungulate density and particularly desirable because it is a non-invasive method of collecting wildlife data (Brinkman et al., 2010; Pfeffer, 2016; Van Vliet et al., 2008; Waits & Paetkau, 2005). I here study the relation between harvest and the seasonally changing moose distribution in northern Finnskog, across the national boarder between Sweden and Norway. Within the framework of the Interreg-funded project GRENSEVILT, I did moose fecal pellet group counts and compiled hunting statistics from hunting seasons 2019-20 and 2020-21 for all moose management units in the study area. For this thesis, I wanted to study if there were a spatial and temporal mismatch between harvest rates and moose distribution across neighboring moose management units.

Firstly, I compared the harvest rates between the two hunting seasons 2019-20 and 2020-21. I predicted that harvest rates were similar for the two hunting seasons for a given moose management unit (hypothesis H1), due to constant harvest quotas and comparable local populations sizes from year to year. Secondly, I compared winter with summer moose densities in the management units. I predicted that the density of fecal pellet groups in a given moose management unit differed between summer and winter (hypotheses H2), due to the migratory behavior of the moose. Thirdly, I compared the harvest densities with the moose densities in the moose management units. I predicted that the harvest in fall/winter 2019-20 and 2020-21 was not related to the density of pellet groups in winter 2019-20 (hypothesis H3), because harvest mostly took place before moose migrated to the wintering areas. I also predicted that the harvest in fall/winter 2020-21 was positively related to the density of summer pellet groups in 2020 (hypothesis H4), because quotas are adjusted to hunter observations and harvest from previous years.

# 2. Method

*2.1. Study area*

The study area is set inside Innlandet county in Norway and the county Värmland in Sweden. Study area ranges across the municipalities Trysil 61°18´36N, 12°18´54Ø, Elverum 60°53´00N, 11°34´00Ø, Våler 60°45´12N, 11°53´51Ø, Åsnes 60°39´13N, 12°09´11Ø and Grue 60°27´02N, 12°12´20Ø in Innlandet and inside the municipality Torsby 60°08´00N, 13°00´00Ø in Värmland. All of the study area is on the east side of the river Glomma and therefore inside the Norwegian wolf zone. As it is of continental climate there is snow cover at least from December to March (Wikenros et al., 2020). Mean snow depth in the study area was estimated at 3-76 cm in 2019-2020 and is highest in the north and lowest in the south (Saloranta, 2014). The total size of the study area is 4544 $km^2$.

Data for the study were collected from a study area set to fit the wolf territories "Varåa", "Juvberget" and "Bograngen". This is part of the study area for the project "GRENSEVILT" (Grensevilt, 2018a). The sampling area is set in the boreal zone. Main tree species in these areas are Norway spruce *Picea abies*, scots pine *Pinus sylvestris,* birch *Betula pubescens,* and some aspen *Populus tremula*, and the understory vegetation is dominated by common grass species, heather species, cowberry *Vaccinium vitis-idaea* and bilberry *Vaccinium myrtillus*. Some sample sites were on mires, on felling areas, on cultivated land and in plots without trees, dominated by heather species. The sample sites located on cultivated land was used for various cereal, potato or grass production. The research area varies in topography. The altitude varies from 148-1077 MASL. The study area is also used by other ungulate species, i.e., roe deer *Capreolus capreolus* and red deer *Cervus elaphus* and predator species wolf *Canis lupus*, brown bear *Ursus arctos*, wolverine *Gulo gulo* and Eurasian lynx *Lynx lynx*.

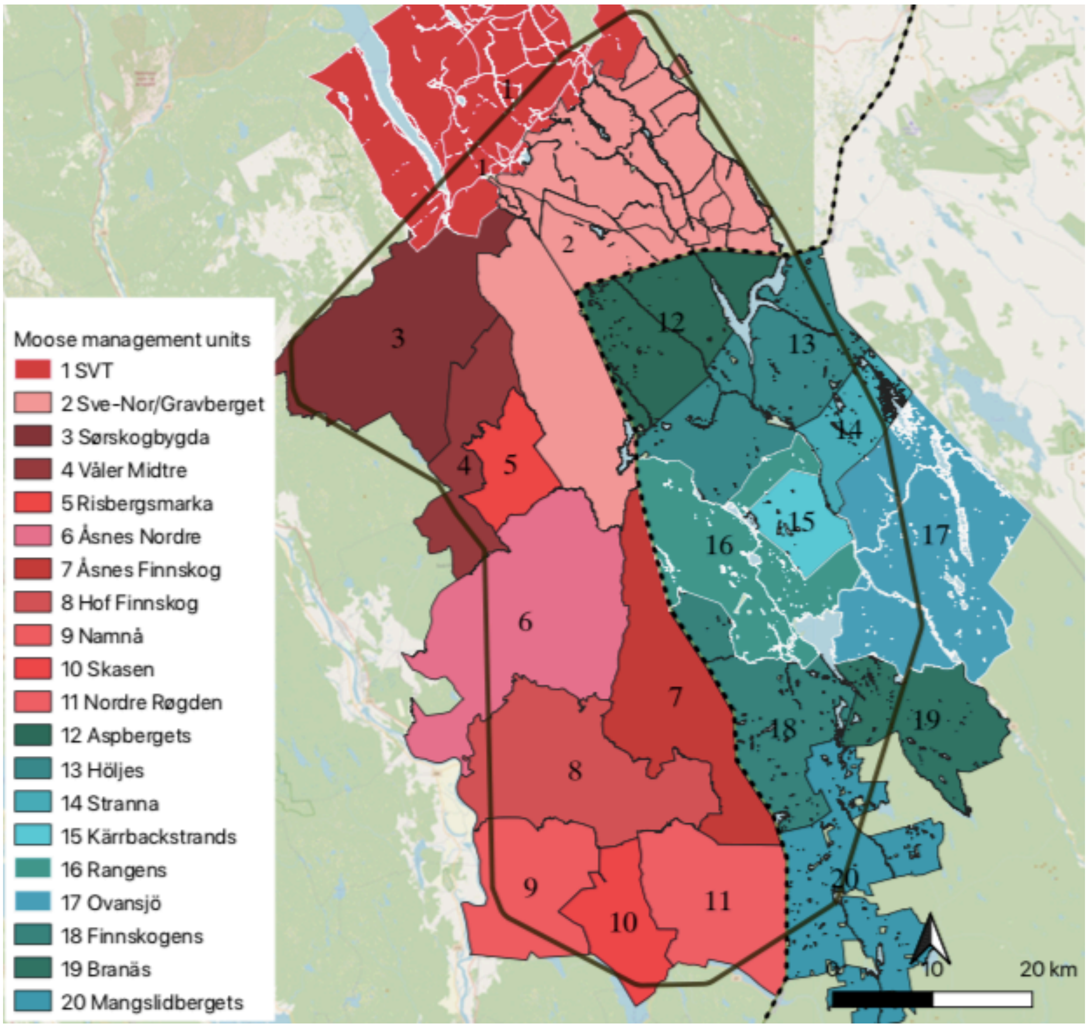


**Figure 1**: Study area map with moose management areas. Black line around shows boarder of study area, plotted line shows national boarder. Moose management units are categorized by color (Norwegian reds/pinks and Swedish blues/greens) and labeled with numbers, explained in the legend. Created with Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019.

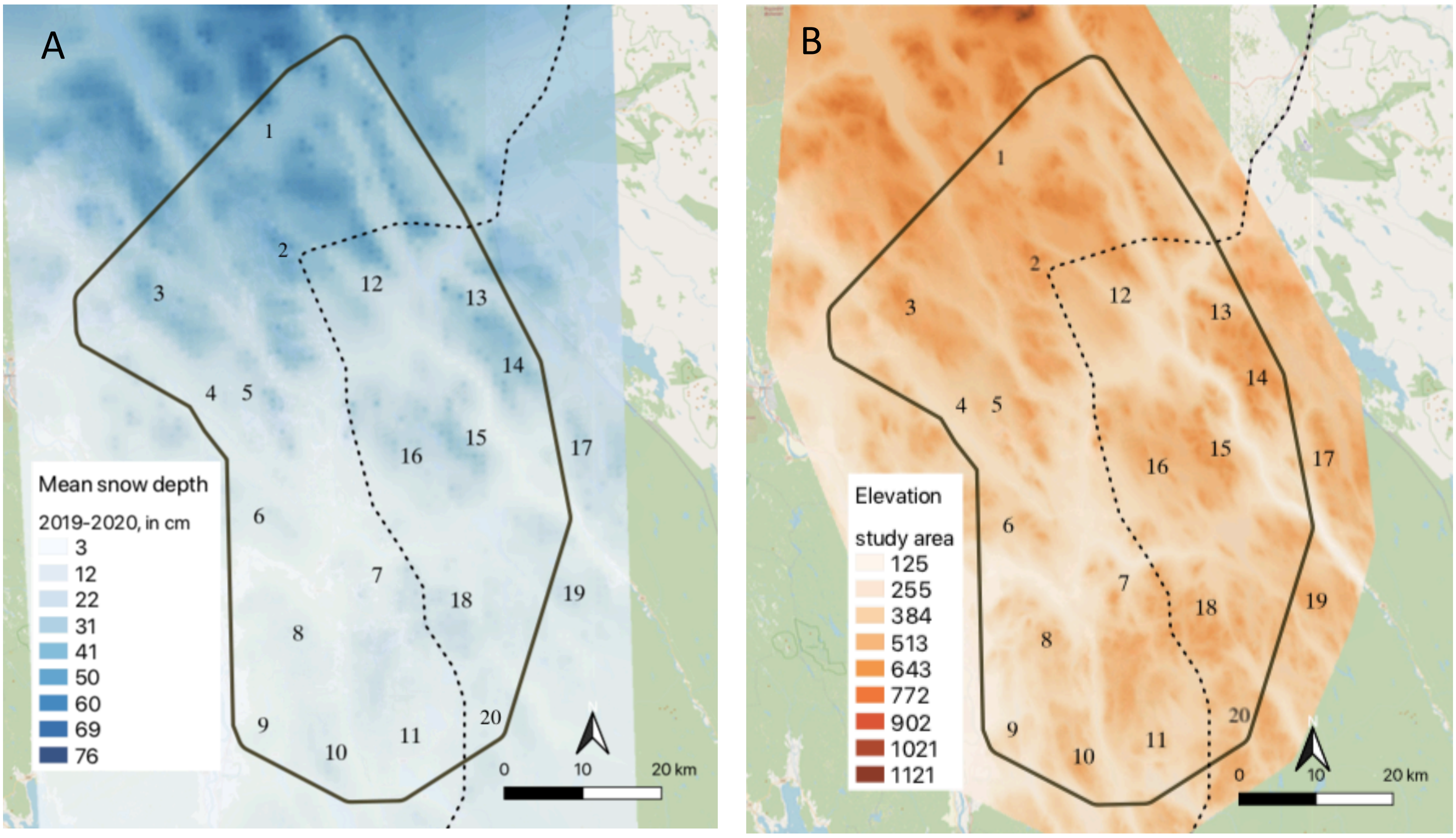


**Figure 2**: **A**: Mean snow depth in the study area from the 2019-20 and 2020-21. Measured in centimeters. **B**: Elevation ranges in the study area, measured in meters above sea level. Numbers inside study area boarder represent the different moose management units. Created with Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019).

### *2.2. Moose harvest*

To compilate hunting statistics from hunting season 2019-20 and 2020-21, statistics has been gathered from all moose management units (MMU´s) in the study area. There were 11 such moose management units in Norway and 9 in Sweden. The moose management units are called “jaktvald” in Norway and “älgskötselsområden” or “jaktområden” in Sweden.

Moose hunting can only be practiced on land authorized as hunting area and within legal hunting season (Lavsund et al., 2003a). The moose hunting season in Norway starts 25$^{th}$ of September and lasts until 23$^{rd}$ of December (Jakt-&fangsttider, 2017). In Sweden the moose hunting season differs a little for different regions. For Värmland moose harvest starts the first Monday in September and ends on the last day of January (Jaktförordning, 1987). The Fennoscandian countries share the goal of having a stable moose population and also maintaining a moose population that is highly productive and therefore allows annual harvesting (Ueno et al., 2014).

The Norwegian moose harvest is controlled by the municipalities, and the municipalities is by the national management authorities encouraged to collaborate with other close by municipalities for optimal moose management over a larger geographical area (Wikenros et al., 2020). Also, several moose management units within the municipalities can cooperate with a joint moose management plan inside a “moose region”. This must be approved by the municipality. Harvest quotas is regularly based on a 3-5-year plan of management. Quotas are set based on indices of moose abundance based on statistics for earlier years. These statistics come from previous harvest data, seen moose density and number of moose-vehicle accidents (Ueno et al., 2014). Same indices are used for setting the Swedish moose harvest quotas.

Sweden got a new moose management system in 2012 after a parliamentary decision (Wikenros et al., 2020). The Swedish moose management is built up my moose management units that can include several municipalities and extend over county borders. Here, the plan of management is based on 3-year periods set by the moose management units. The plan can however be amended if reasoned. The 3-year harvest plans must be accepted by the County Administrative Board.

Recreational hunters are an important part of moose observation monitoring. The hunters report all observed moose during the hunt in a standardized form from the moose observation monitoring program. Sex and age (adult/calf) categories and the hunting effort in form of hours or days hunted (seen per unit effort – SPUE) are reported in to the national deer registers of each country (Hjorteviltregisteret/Älgdata) (Ueno et al., 2014). In Norway the number of observed moose per hunting day is reported throughout the entire moose harvest season, while in Sweden they must only report per hour hunting for the seven first days of the moose harvest season (Wikenros et al., 2019). These direct observation data are important for the wildlife management in use of calculating and predicting density, quality and structure of the moose populations.

**Table 1**: Overview of all moose management units with moose pellet density data for summer and winter pellet counts, harvest data for 2019-20 and 2020-21, and number of sample sites within each moose management unit. Harvest density is calculated through dividing harvest number on respective moose management unit´s area (harvested/$km^2$). Significant numbers from different calculations marked with either orange (highest values) or blue (lowest values) outline.

| Moose management units | Area km^2 | Harvested 2019-20 | Harvest density 2019-20 | Harvested 2020-21 | Harvest density 2020-21 | Summer pellet density | Winter pellet density | Sites |
|---|---|---|---|---|---|---|---|---|
| Åsnes Nordre DPO | 340.05 | 105 | 0.309 | 105 | 0.309 | 0.281 | 0.300 | 20 |
| Åsnes Finnskog DPO | 220.48 | 73 | 0.331 | 68 | 0.308 | 0.364 | 0.351 | 23 |
| Våler Midtre DPO | 114.83 | 69 | 0.601 | 63 | 0.549 | 0.387 | 0.101 | 6 |
| Sørskogbygda jaktvald | 287.14 | 84 | 0.293 | 70 | 0.244 | 0.182 | 0.093 | 26 |
| SVT viltregion | 444.15 | 82 | 0.185 | 108 | 0.243 | 0.088 | 0.025 | 7 |
| Sve-Nor/Gravberget | 695.89 | 114 | 0.164 | 119 | 0.171 | 0.193 | 0.159 | 59 |
| Stranna VVO | 68.91 | 23 | 0.334 | 26 | 0.377 | 0.208 | 0,126 | 5 |
| Skasen elgforvaltning | 93.47 | 22 | 0.235 | 23 | 0.246 | 0.244 | 0.119 | 8 |
| Risbergsmarka V.U. SA | 71.02 | 14 | 0.197 | 13 | 0.183 | 0.156 | 0.159 | 7 |
| Rangens ÄSO | 225.81 | 64 | 0.283 | 77 | 0.341 | 0.264 | 0.179 | 22 |
| Ovansjö ÄSO | 349.76 | 95 | 0.272 | 90 | 0.257 | 0.148 | 0.124 | 7 |
| Nordre Røgden ef. | 179.34 | 27 | 0.151 | 32 | 0,178 | 0.092 | 0.281 | 14 |
| Namnå elgforvaltning | 150.10 | 24 | 0.160 | 27 | 0.180 | 0.176 | 0.200 | 9 |
| Mangslidbergets ÄSO | 252.20 | 73 | 0.289 | 74 | 0.293 | 0.179 | 0.116 | 9 |
| Kärrbackstrands VVO | 59.90 | 18 | 0.301 | 20 | 0.334 | 0.515 | 0.161 | 6 |
| Höljes ÄSO | 242.21 | 69 | 0.285 | 79 | 0.326 | 0.245 | 0.221 | 19 |
| Hof Finnskog DPO | 248.96 | 43 | 0.173 | 53 | 0.213 | 0.046 | 0.142 | 22 |
| Finnskogens ÄSO | 172.83 | 34 | 0.197 | 54 | 0.312 | 0.333 | 0.146 | 16 |
| Branäs-Uggenäs ÄSO | 139.50 | 34 | 0.244 | 50 | 0.358 | 0.316 | 0.027 | 3 |
| Aspbergets ÄSO | 187.45 | 85 | 0.453 | 69 | 0.368 | 0.153 | 0.165 | 19 |

*2.3. Moose pellet group count*

The chosen method for estimating the spatial distribution of moose was counting fecal pellet groups on sample plots inside the field study area. Field studies were conducted in two periods, from May – June 2020 and August – September 2020. Moose pellet group counts were done after snow melt early in the plant growth season in May/June 2020 to count winter pellet groups and right before moose harvest in August/September 2020 to count summer pellet groups. Pellet group counts were done as identically as possible both periods. Plot center marking sticks were put out during the first pellet counting period and tried recovered during the second pellet counting period. In some cases, the marking stick needed to be replaced if the vegetation had grown too high or dense around it or it had been physically removed.

The sample sites were systematically placed 3,5 km between each other (see figure 3) with some deviation to avoid infrastructure or water. Each site consisted of 5 plots arranged as a square of 50 x 50m with one plot in each corner and one in the center. The plots had an area

of 100 m$^2$ and were searched in the inner 10 m$^2$ in clockwise and anti-clockwise direction and did so the same for the outer 90 m$^2$. Old pellet groups from before last leaf fall were not registered during winter pellet group counting, only cleared out of the plot.
Age of pellets was identified by looking at the position of the pellet in relation to the litter and vegetation (on top of and not grown into) and by looking at the color of the pellet (olive green for fresh winter pellets, brown for older pellets) (Neff, 1968). Pellet groups were only registered when there were 20 or more pellets in the groups and when the center of the pile was within the 100 m$^2$ plot. All plots were cleared of pellets after counting to avoid double counting.

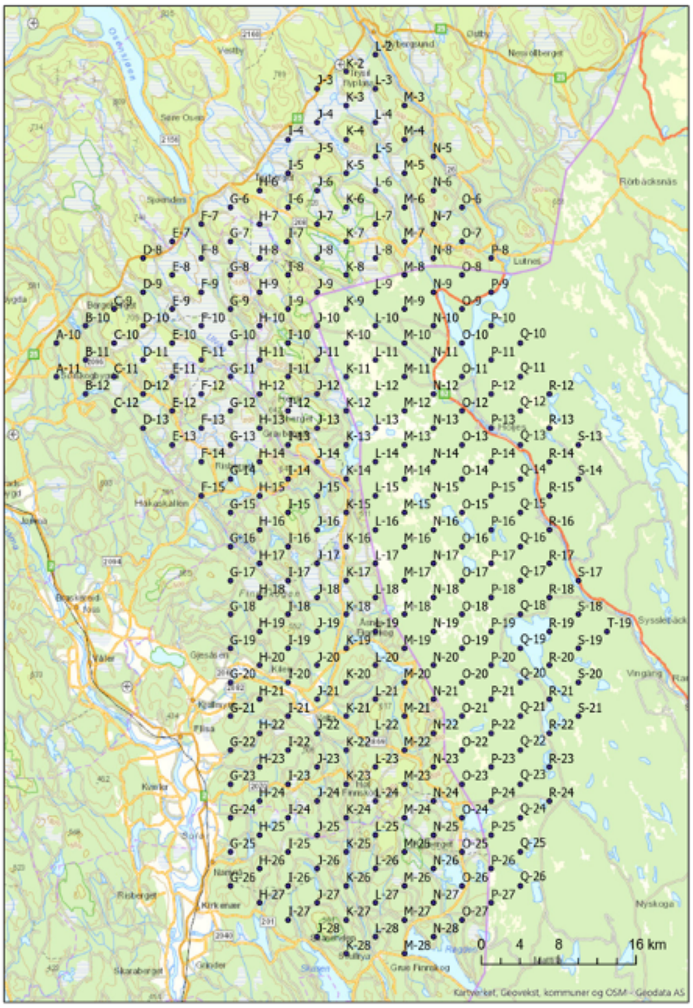


**Figure 3**: Study area map with all 307 pellet group count sites

Plots were located with a digital map (Norgeskart) on a tablet or GPS and were identified with plot and square ID. Waypoint GPS-coordinates were also saved on each plot. Centre of each plot were marked with a blue/white marked bamboo stick. All ungulate feces were sampled in plastic bags with waypoint-ID and species names labeled on the bag. These bags were frozen and saved for possible DNA-testing in the near future. Variables like forest development class, area vegetation, dominating tree species and other type of animal feces found inside the plots were also registered for further use. A larger number of sample sites could have provided greater security in the data, but the moose pellet group count sample sites were placed in the exact system to include the three wolf territories ("Varåa", "Juvberget" and "Bograngen") inside the study area.

*2.4. Data analyses*

Statistical analyses were conducted in R version 4.0.4 (2021-02-15) with Rstudio version 1.1.463 (2018). All data were managed in Microsoft Excel for Mac 2020 version 16.43. Maps were made in Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019).

To calculate the average moose density index per moose management unit for a given season, I first summed the pellet groups per site before dividing this sum with the length of the survey period. This was important because the counting dates (numbers of days feces accumulated per site) varied between sites. For the winter pellet group count, the counting dates was the number of days from leaf fall (set to 10.10.2020 for the whole study area) until the date of summer pellet group count. For summer, the survey period was the number of days between spring and fall count. Secondly, I adjusted the pellet group density (groups/day/500m$^2$) to groups/day/ha by multiplying the site estimate with 20. I then calculated the mean density across all sites within a given moose management unit.

In Q-GIS I merged the moose management unit of the different municipalities into one vector file. Moose management unit that only existed on paper maps were digitalized before merging. Moose harvest densities and pellet group densities were added to the attribute table of the respective moose management unit and later exported to Excel and RStudio. Snow depth map and elevation map was made by merging moose management units and snow depth map or elevation map into one vector file.

To test whether the moose harvest density was similar in 2019-20 and 2020-21 (H1), I used a linear regression model, with moose harvest density in 2020-21 as response and harvest density in 2019-20 as independent variable. To test if the moose pellet group densities differed between winter and summer (H2), I used a linear regression model with summer density as response and winter density as independent variable. To test if the harvest density was correlated with winter (H3) or summer (H4) moose pellet group density, I used a generalized linear model (GLM). I entered the number of shot moose as response variable, the moose density index as independent variable, and the area ($km^2$) of the moose management area as a log-transformed offset variable. Due to overdispersion I used a Quasipoisson link to model the error term. The moose management units varied in size and some were only partly within the area of the pellet count. These moose management units had few sample sites compared to moose management units that were fully inside the study area, so I therefore added a weight variable to all models that included moose density. The weight variable had a value between 0 and 1, depending on the number of pellet count sites within the moose management unit. Scatter plots were made for each of the hypothesis with the ggplot2 package (Wickham, 2016). I added a regression line with 95 % confidence interval for significant relationships.

# 3. Results

*3.1 Harvest densities*

Within our study area, 657 and 495 moose were harvested in the 2019-20 in Norway and Sweden, respectively. In the 2020-21 hunting season, 681 and 539 moose were harvested in Norway and Sweden, respectively. Harvest rates were slightly higher in 2020-21 than in 2019-20, with 0.254 moose/$km^2$ in 2019-20 and 0.268 moose/$km^2$ in 2020-21. In 2019, harvest density was highest in the moose management unit "Våler Midtre" (0.60 moose/$km^2$) and was lowest in "Nordre Røgden" (0.15 moose/$km^2$) (Table 1). In 2020, "Våler Midtre" was again the moose management unit with the highest harvest density (0.55 moose/$km^2$), while "Sve-Nor/Gravberget" had the lowest (0.17 moose/$km^2$) (Table 1). The Swedish moose management units generally had higher harvest densities than Norwegian moose management units in both years (Figure 4 C, Figure 4 D). Moose management unit-specific harvest rates were strongly correlated between 2019-20 and 2020-21 (H1), (Figure 7 A, Table 2).

*3.2 Moose pellet group density*

A total of 307 sites (107 in Sweden and 200 in Norway) with 5 sample plots per site (1535 plots) were surveyed during our two-season pellet group count in 2020. In total, 962 moose pellet groups were counted in the study area, 597 winter pellet groups and 365 summer pellet groups. Within our study area, 45% of the sites had no moose pellet groups, 20% had 1 moose pellet group, 26% had between 2-4 moose pellet groups, 7% had between 5-10 and 2% of the sites had more than 10 moose pellet groups.

Maps are used to illustrate seasonal differences in moose pellet density (Figure 4 A, Figure 4 B, Figure 5) and moose harvest density (Figure 4 C, Figure 4 D, Figure 6) on moose management unit level. Pellet group density maps showed that there was a tendency of a more centered pellet density in summer compared to winter (Figure 5), as the moose pellet group density was more evenly distributed throughout the moose management units in the study area during summer than during winter (Figure 4 A, Figure 4 B).

Average moose pellet group density (± SE) across all sites in the study area was 0.160 ± 0.082 groups/ha/day in winter and 0.228 ± 0.114 groups/ha/day in summer. Generally, moose pellet group density was higher during winter than summer in the south-west portion of the study area, except for one moose management unit ("Nordre Røgden", Figure 1). Swedish moose management units, located on the eastern part of study area, overall had higher summer pellet densities than the Norwegian moose management units (Figure 5). The moose management units with the highest winter pellet density are also of lower average elevation and with the lower average snow depth 2019-2020, (Figure 4 A, Figure 4 B, Figure 2A, Figure 2B). The highest mean snow depths and the highest elevation were found in the northernmost moose management units in the study area (Figure 2A, Figure 2B). The moose pellet group density for summer 2020 and winter 2019-20 did not show any correlation (H2) (Figure 7 B, Table 2). The Swedish moose management units generally had higher summer pellet densities than the Norwegian moose management units (Figure 5).

The harvest density maps show that some moose management units have approximately equal harvest densities in 2020-21 as in 2019-20, but most have either a little higher or lower in one of the years (Figure 4 C, Figure 4 D, Figure 6). The Swedish moose management units generally had higher harvest densities than Norwegian moose management units in both of the studied years (Figure 4 C, Figure 4 D). The difference between hunting seasons is evenly distributed between Norwegian and Swedish moose management units and harvest densities does not seem to have any gradient specifics (Figure 4 C, Figure 4 D, Figure 6).

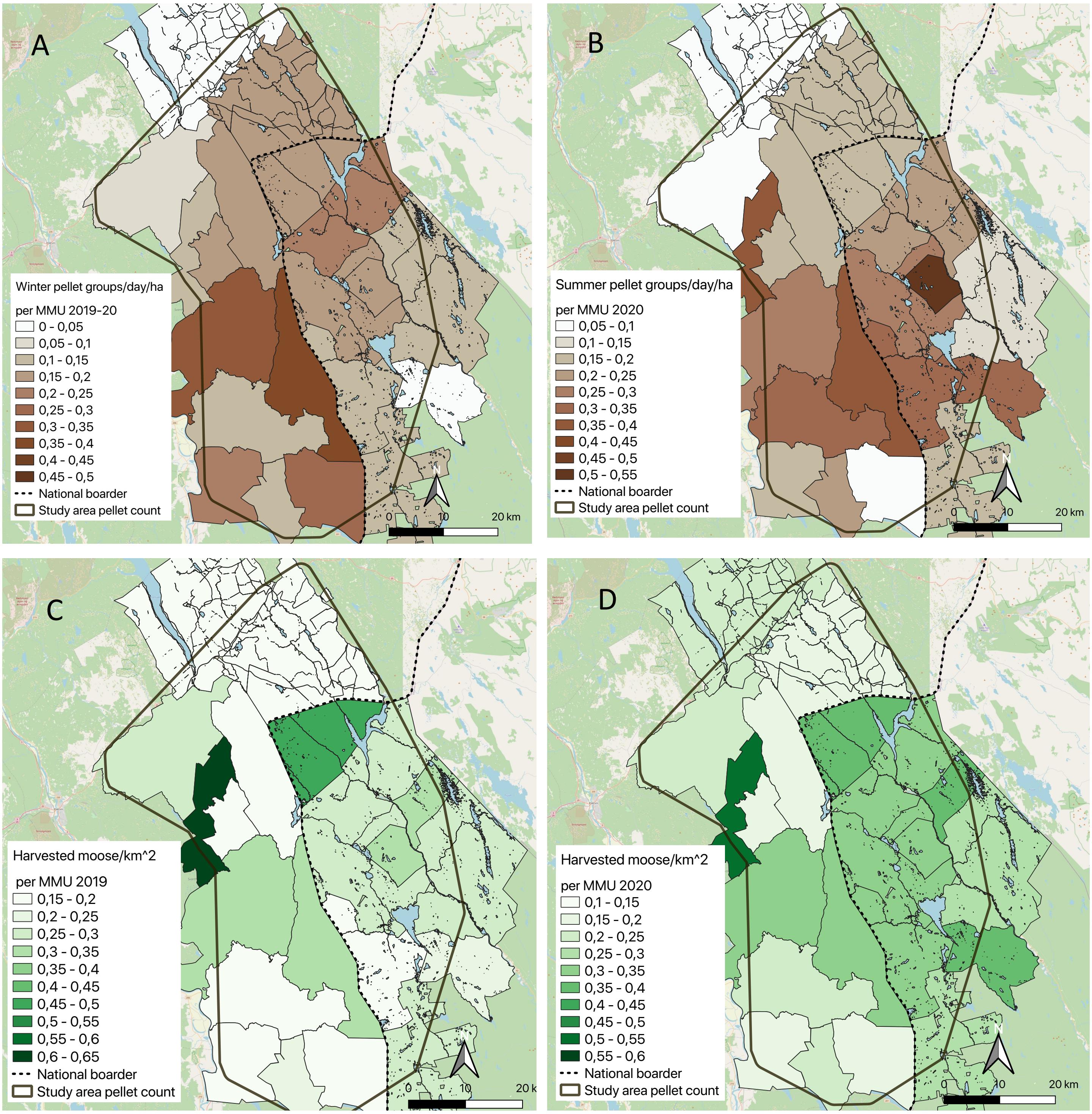


**Figure 4**: Maps showing pellet densities and moose harvest densities per moose management unit (MMU) **A:** Winter pellet group density/day/ha 2019-20. **B:** Summer pellet group density/day/ha 2020. **C**: Harvest density/km$^2$ 2019-20 hunting season. **D**: Harvest density/km$^2$ 2020-21 hunting season**.** Maps created with Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019).

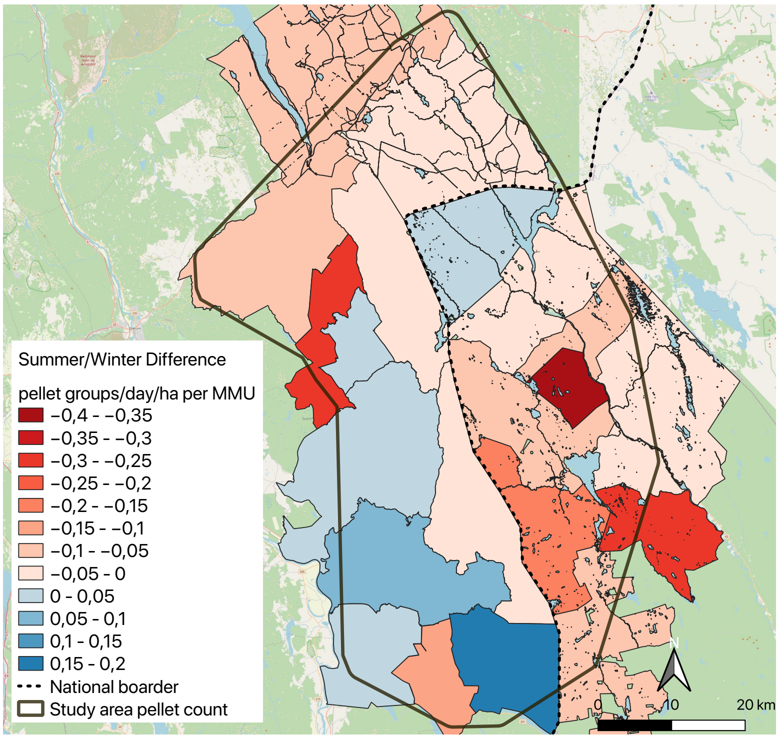


**Figure 5**: Map showing difference between summer pellet density 2020 and winter pellet density 2019/20. Blues indicates moose management units with higher densities of winter pellets, reds indicates moose management units with higher densities of summer pellets. Created with Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019).

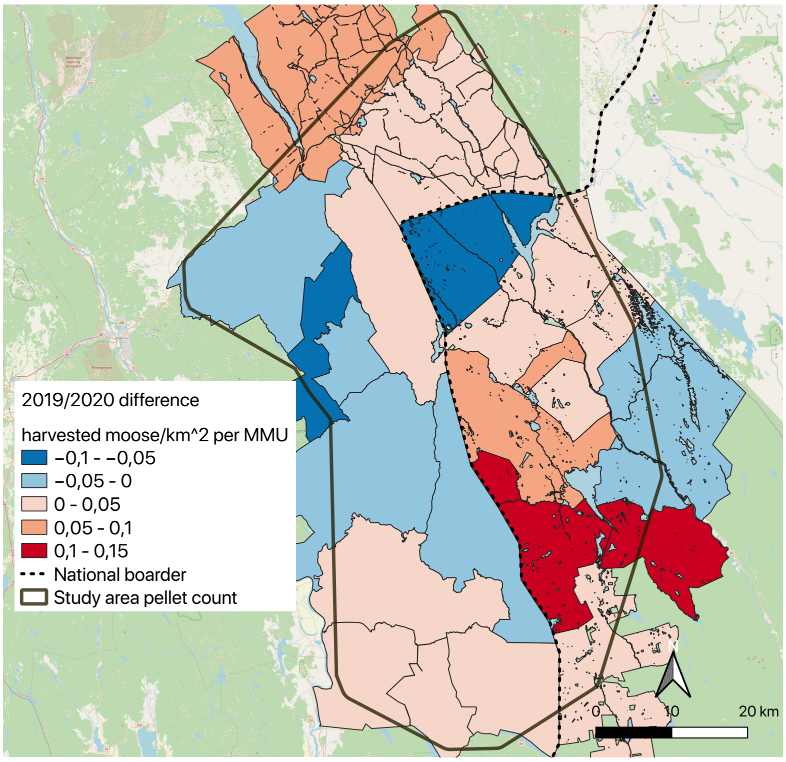


**Figure 6**: Map showing difference in moose harvest density/km$^2$ between hunting seasons 2019-20 and 2020-21. Blues indicate moose management units with lower harvest densities in 2020 than 2019, reds indicate moose management units with higher harvest densities in 2020 than 2019. Created with Q-GIS version 3.10.11-A Coruña (Quantum GIS Develop team 2019).

*3.3 Harvest rates compared to pellet group densities*

The harvest density per moose management unit in 2019-20 did not correlate with the winter moose pellet group density of 2019-20 (H3, Table 2, Figure 7 C). The same was the case for the harvest densities in 2020-21, when related to the winter pellet group density of 2019-20 ($p$=0.298). However, the harvest rate in 2020-21 was correlated with the pellet group density of summer 2020 (H4, Table 2, Figure 7 D). The harvest density was higher in moose management units with high summer pellet group density. The regression model predicted that the harvest density doubled with an increase in pellet group density of 0.35 groups/day/ha.

**Table 2:** Results from linear models (hypotheses 1 and 2) and Quasipoisson regression models (hypotheses 3 and 4) with intercept values on moose harvest density of harvest seasons 2019-20 and 2020-21 and winter- and summer moose pellet density of respectively 2019-20 and 2020. Statistical tests were performed in RStudio. Significant values in bold.

| **Hypothesis/tested variables** | **Est.** | **SE** | **t-value** | ***p*** |
|---|---|---|---|---|
| H1: Harvest density 2020~Harvest density 2019 | | | | |
| Intercept | 0.087 | 0.027 | 3.239 | **<0.01** |
| Slope | 0.742 | 0.092 | 8.052 | **<0.001** |
| H2: Summer moose density 2020~Winter moose density 2019-20 | | | | |
| Intercept | 0.137 | 0.053 | 2.557 | **<0.05** |
| Slope | 0.446 | 0.275 | 1.619 | 0.123 |
| H3: Harvest density 2019~Winter moose density 2019-20 | | | | |
| Intercept | -1.701 | 0.224 | -7.599 | **<0.001** |
| Slope | 1.269 | 1.157 | 1.097 | 0.287 |
| H4: Harvest density 2020~Summer moose density 2020 | | | | |
| Intercept | -1.854 | 0.183 | -10.117 | **<0.001** |
| Slope | 1.976 | 0.802 | 2.464 | **<0.05** |

Significance levels: *$p$<0.05, **$p$<0.01, ***$p$<0.001

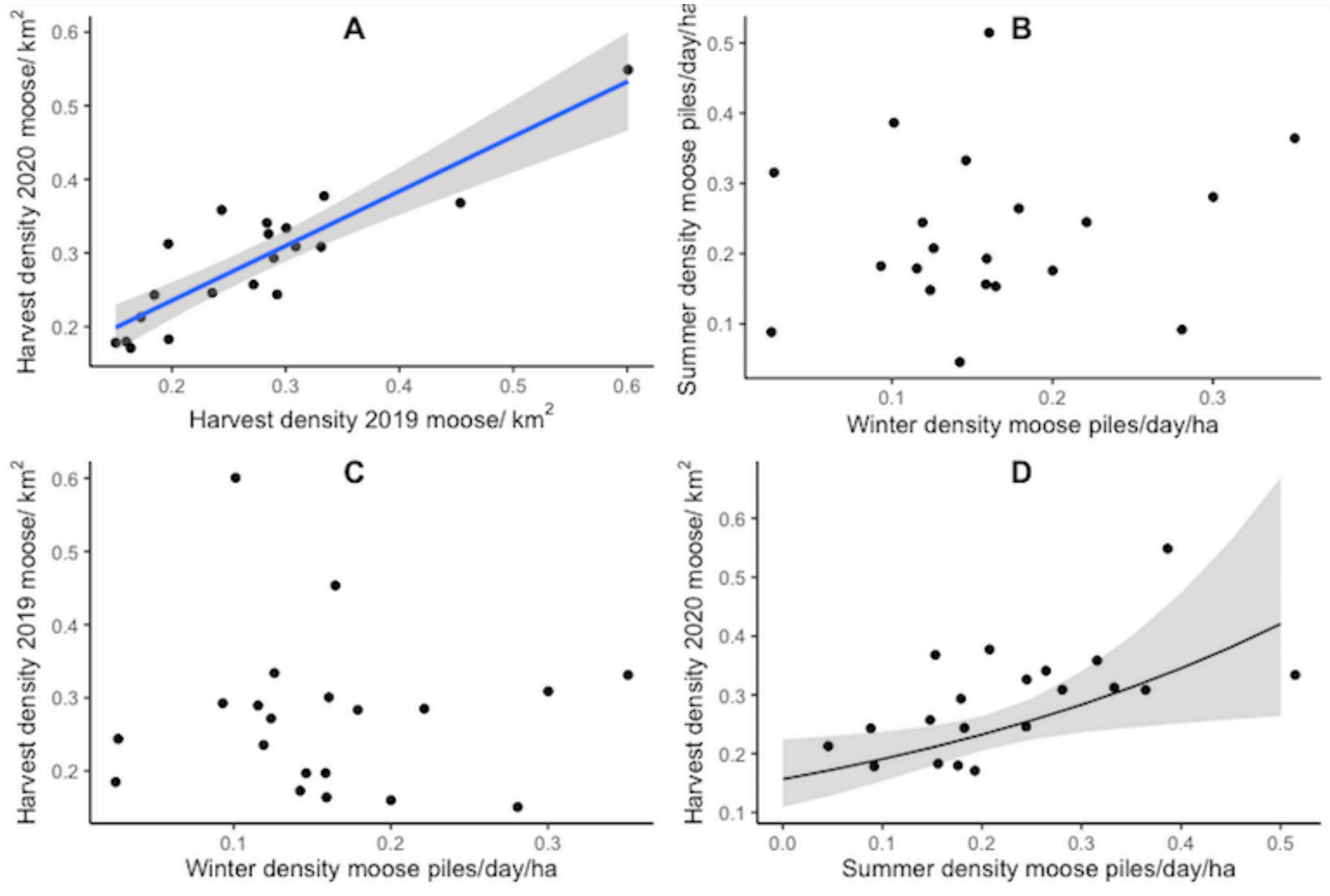


**Figure 7**: Scatter plot of the four tested hypotheses. Predicted lines with confidence limits are added for significant relationships. **A:** Correlation between harvest density in MMU´s in 2019 with harvest density in MMU´s in 2020. Black dots are values for average harvest density/km$^2$ in the moose management units in 2019 and 2020. The predictions are from a linear model and show average with the blue line and 95% confidence intervals with the grey span. **B:** Correlation between summer moose density 2020 and winter moose density 2019-20. Black dots show values of average density in the MMU´s in summer and winter. **C:** Correlation between winter moose density 2019/20 and 2020 harvest density. Black dots show values of average harvest density and winter moose density in the MMU´s. **D:** Correlation between harvest density 2020 and summer moose density 2020. Black dots show values for average summer moose density and harvest density of the summer 2020 in the moose management units.

# 4. Discussion

The harvest density in the studied moose management units did not differ greatly between 2019-20 and 2020-21, suggesting that the moose harvest and truly also the population within our study area was relatively stable between those years (hypothesis H1). There was no correlation between the estimated moose pellet group density in winter 2019-20 and summer 2020, indicating a significant difference in the seasonal distribution of moose, which means that either the whole population or a part of it migrated between winter and summer (hypothesis H2). Several studies show that moose can follow a migration pattern and use the same summer and winter ranges through generations (Andersen, 1991; Borowik et al., 2020; Bunnefeld et al., 2011). The moose redistributes more evenly in the summer range than in the winter range. In the winter range the moose often stands very concentrated and a concentrated winter population of moose can cause substantial browsing damage on regenerating forest stands (Loosen et al., 2021).

My findings shed light on the timing of migration. In accordance with my prediction of hypothesis H3, the moose pellet group density in winter 2019-20 did not explain the observed variation in harvest densities, neither for the hunting period preceding nor following the winter moose pellet count. During the 2019-20 harvest season, the migrating moose population had not yet migrated into winter areas and therefore the harvest targeted moose in their summer ranges. These may have been both moose that were stationary in a given moose management unit and those having migrated from a different winter range to their summer range during spring 2019. Similarly, moose shot in 2020-21 included moose that had returned to their summer ranges after spring migration in 2020. This pattern is supported by the positive correlation between harvest density in 2020-21 and the moose pellet group density during summer 2020, in accordance with hypothesis H4 that migratory moose are shot most often in their summer range. Several red deer and elk populations (Bocci et al., 2010; Loe et al., 2016; Meisingset et al., 2018; Rivrud et al., 2016) show migration timing that opposes the moose's timing. Bocci et al (2010) found that red deer hinds showed a clear tendency of migrating back to protected winter ranges from the summer ranges, where they were exposed to hunting, before or during the first week of hunting season. Loe et al. (2016) and Rivrud et al. (2016) show that the largest part of red deer hunting happens in the wintering area because the red deer migrates much earlier towards winter ranges than moose does. So, in the case of these studies on red deer, the connection between summer-/winter density and harvest density provides opposite results of the results found in this thesis. In addition to sensitivity to hunting, foraging ecology may play a role as moose feed more in the tree layer and may be less sensitive to the first shallow snow cover compared to other species.

Timing of migration can have various drivers. Studies on elk *Cervus canadensis* in Yellowstone national park (Rickbeil et al., 2019) and red deer *Cervus elaphus* in Norway (Rivrud et al., 2016) suggested that the timing of spring migration was fairly synchronous throughout the population and that the most important drivers of migration were snow melting and the spring green-up. The same studies imply that there was less synchrony in the timing of migration to wintering areas. In my study, snow seems to be an important driver for ungulate migration in this study area as has been shown for both red deer (Rivrud et al., 2016) and previously for moose by use of GPS-data (Bunnefeld et al., 2011). Based on this, it is natural to predict that the timing of migration for the studied moose population will be affected by snowfall, particularly by high snow depths.

The moose management unit with the largest drop from summer to winter pellet density is Swedish “Kärrbackstrands VVO”, which is a moose management unit with high elevations and high mean snow depth (MMU 15, Figure 2, Table 1). “Sørskogbygda jaktvald” is another moose management unit with the same pattern of density drop from summer to winter, possibly also affected by high mean snow depth (MMU 3, Figure 2). A typical pattern for temperate ungulates (Mysterud, 1999) is to migrate from high-elevation summer ranges to low-elevation winter ranges, and high-elevation coincides with high precipitation and early snowfall (Rivrud et al., 2016). The Norwegian moose management unit “Nordre Røgden elgforvaltning” (Figure 1) has the highest increase in density from summer to winter and fairly low harvest rates and also low mean snow depth (Table 1, MMU 11Table 2 A). The sudden spike in pellet density from summer to winter in this moose management unit implies that this is a popular winter range. Sve-Nor/Gravberget is the largest moose management unit (696 $km^2$, Table 1) with minor changes in data output from season to season. As this moose management unit is of large size, it varies in mean snow depth and elevation range. The northernmost part of the moose management unit is of both higher altitude and of higher mean snow depth than the southern part (MMU 2, Figure 2). The differences in fecal pellet density found in my study support that moose utilize the elevation gradient and that summer ranges are abandoned due to deep snow.

The moose inhabits dense forest areas and because of this it can be difficult to observe and count moose directly for population density estimates. Pellet group counts can be a useful method to see how the moose distributes in the landscape both before and after the harvest, and is recognized as a method that can give similar outputs as those achieved from GPS-tracking and direct observations (Månsson et al., 2011; Rönnegård et al., 2008). For this thesis the pellet group counts were completed immediately before the moose hunt began and in the early spring after the hunt was over. The pellet group count method is an easy to learn, and easy to use method. Thus, the method can be a cost-effective way to estimate ungulate habitat use and density in a specific area, and has shown to be successful for several species (Månsson et al., 2011). For this thesis, the use of pellet group counts as the population estimation method was sufficient to establish seasonal variation in moose density within the study area. There can potentially be many sources of errors in pellet group counts, like incorrect ageing of the feces or missing abilities to separate different species from each other (Spitzer et al., 2019), poor visibility due to vegetation, weather factors like heavy rain or direct sunlight, or high temperatures leading to increased decomposition rate (Månsson et al., 2011). Moose pellet group counts from several years would have provided a clearer and more detailed picture on eventual patterns of distribution throughout the migration and throughout the year in general, and with data from several years it could also be possible to look for variation between years.

Combining pellet group counts, harvest density and seen moose-density would give a detailed picture on distribution and density of the moose population with several sources to look to. In this study, harvest values were gathered from the 20 moose management units inside the study area. For a more detailed image of the distribution of moose inside each of the moose management units, harvest data could have been compiled from the hunting areas that the moose management units contain of. It was decided to go with the coarse scale, to stay on moose management unit level, because of possible inaccuracy as hunters, for the simplicity, have a tendency to register harvest data from a number of hunting areas onto one single hunting area. In this case there is large potential for improvement and data compiled from a finer scale would have provided more exact data on moose distribution within the moose management units. Despite their limitations, the combination of the fecal pellet group method and harvest data at a relatively course scale proved sufficient to conclude on timing of migration in my study, possibly helped by a large spatial and temporal variation in the real moose density in the study area.

For some areas in Sweden, winter hunting is used to limit the moose population that heavily damages the regenerating forests. With winter ranges losing out to summer ranges, the management options of delaying a fixed length hunting season or extending it into winter are relevant also in Norway. Winter hunts have been practiced in Norway in areas with particular increase in winter moose density and therefore also large browsing damage (Härkönen & Heikkilä, 1999). Shifting the hunting season has earlier been tested out with success. Loe et al. (2016) reported from his study that a nine day postponement of the red deer hunting season gave a higher harvest density in the inland areas of their study area. Their study found that adjusting the harvest season could contribute to a more even distribution of harvest revenues for the moose management units and landowners. The skew could however have several constraints. Tradition and habit is a big motivation for the recreational hunter that expect high success rate to the hunting effort, and a study by Andersen et al. (2014) proclaimed that Norwegian willow ptarmigan hunters rather restricted their hunting quotas than alter their harvest season. Likely would having to hunt in deep snow be of the biggest constraints for the hunters. Another aspect of the timing of harvest is the risk of orphaned calves. Shooting the mother from the offspring is not regulated in law but considered highly unethical among hunters. The animal is in this case mainly is shot in its summer range and mostly applies browsing damage in the winter ranges, it would probably be more logical and natural to eventually postpone the start of hunting season towards winter rather than towards early fall. Postponing the start of hunting season for a period of time towards the winter and rather start when the migration has taken place to a greater extent, could be a possible solution in moose management units that suffer from high browsing damage and has a significant moose density increase from summer to winter.

My results underline the importance of knowledge around migratory hunting resources and uneven distribution of damages and benefits inside our study area. Several studies have shown how a temporal mismatch between hunting season and migration can lead to conflict (Meisingset et al., 2018; Mysterud, 2010; Putman, 1996; Sahlsten et al., 2010; Sandström et al., 2013). Hunting revenue is in several cases considered as compensation for landowners inside heavily browsed moose management units and based on this, the conflict generally is about uneven distributions of damage by browsing and these revenues (Loe et al., 2016).

Härkönen & Heikkilä (1999) found in their research that pellet density correlated positively with browsing intensity. As hunting revenue often is considered compensation for browsing damage (Loe et al., 2016), "Nordre Røgden" is likely a moose management unit with high contribution to the conflict regarding benefits and costs with moose, and might be a good candidate for a delayed hunting season (allowing for winter hunting). This should however be researched closer and with more accuracy as this thesis only has data from a very short period of time (2019-2020) which must be taken in consideration when it comes to such a long-lived animal as the moose. On basis of what I have found, there is reason to believe that a part of the hunting income is disconnected from the browsing damage the following winter. A deciding factor of hunting quotas are the amount of browsing damage in the moose management unit (Ball & Dahlgren, 2002; Grensevilt, 2018b; Skonhoft & Olaussen, 2005) and so, the quotas of the harvest is affected by summer moose pellet density and based on browsing damage done by the winter moose population. If the winter population and the browsing damage is low while the summer population is high, then high harvest quotas in moose management units with high moose densities will equal high harvest densities. If, however, the winter damage is greater than the summer population, then the harvest outcomes might be too low to match the outcomes of the browsing damage. In this case there would be an uneven distribution within the affected moose management unit.

## 4.1 Concluding remarks

My results show that there is spatial disconnection between areas with high density of moose feces in summer and winter, substantiating that the moose in my study area is, at least, a partially migrating moose population. I further found correlation between summer moose density and harvest density but no relationship between winter moose density and harvest density. This shows that the largest part of the annual moose harvest happens before the moose migrates to winter range. I also found a connection between snow depth and winter moose density as the winter pellet group density seemed to be most dense in areas with low mean snow depth. I conclude that pellet group count was a cost-effective method that enabled us to conclude on the effect of timing of seasonal harvest on offtake. I have substantiated that there is a mismatch in the outcomes of the moose migration. Allowing for winter hunting could facilitate a fairer distribution of the yearly surplus of moose because they are to a larger degree shot in areas where they do browsing damage in winter. Recognizing the seasonally changing spatial structure of a harvested population will be important, both for the sustainability of the moose population, for longtime profitable harvests and for minimizing conflict in the moose management units.

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