Studying habitat use and behavior of moose (*Alces alces*) by integrating airborne laser scanning and GPS tracking

Markus Melin

School of Forest Sciences

Faculty of Science and Forestry

University of Eastern Finland

Academic dissertation

To be presented, with the permission of the Faculty of Science and Forestry of the University of Eastern Finland, for public criticism in the auditorium BOR100 in Borealis Building of the University of Eastern Finland, Yliopistokatu 7, Joensuu, on December 15th 2015, at 12 o'clock noon.

2

ABSTRACT

Airborne laser scanning (ALS)-based mapping campaigns are expanding in numbers throughout the world. Lands are scanned for the purposes of topography mapping and forestry. Yet, as much of wildlife lives in forests, the data hold accurate information about the structure of wildlife habitats. This is valuable information, because vegetation structure is a key component of habitat suitability.

In this thesis, ALS data were used to analyze habitat use and behavior of moose. The ALS data were integrated into locations of GPS-collared moose. As a consequence, patterns in their habitat use were seen from the ALS point clouds. The types of forests moose used during different seasons, different times of day, or when under thermal stress, were examined in detail. Lastly, ALS data were used to identify moose browsing damages.

The results revealed the usefulness of ALS in wildlife ecology research. It was shown that habitats used during different seasons are significantly different from one another in terms of forest structure, which links to the type of food used during each season and where it exists. Also, the effect of temperature on moose habitat use was revealed: high summer temperatures made moose utilize thermal shelters under high and dense canopies. Views were also gained about the role of forest structure for calving females, who gave birth in open areas (mires) but moved to forests with dense shrub layers shortly after calving: cover and food for the growing calf and the lactating female. Finally, it was shown that differences in forest structure caused by intense moose browsing can be detected from ALS data.

Information about vegetation structure is valuable additional data for wildlife research and can easily be integrated with the existing methods. This thesis gives good examples of how to do this. The approach is applicable to other species as well.

Keywords: ALS, moose, habitat use, vegetation structure, lidar, GPS

TIIVISTELMÄ

Laserkeilausperusteinen metsien inventointi ja -maanpinnan kartoitus ovat tänä päivänä yleisiä menetelmiä joka puolella maailmaa. Tätä aineistoa kerätään yleensä maanmittauksen ja metsätalouden tarpeisiin, mutta se sisältää paljon tietoa, josta voivat hyötyä muutkin toimijat. Eläinten ekologian kannalta metsien ja kasvillisuuden kolmiulotteisen rakenteen tunteminen on tärkeää, koska sen perusteella voidaan arvioida, kuinka hyvän elinympäristön tietty alue voi tietylle lajille tarjota. Laserkeilausaineisto antaa kolmiulotteisen, tarkan ja alueellisesti kattavan kuvauksen tästä rakenteesta.

Tässä väitöskirjatyössä olen yhdistänyt laserkeilausaineistoa GPS-pannoitettujen hirvien sijainteihin. Analysoimalla laseraineistoa näiden sijaintien ympäriltä olen voinut tutkia kuinka metsän rakenne hirvien ympärillä vaihtelee esimerkiksi vuodenaikojen mukaan ja millä tavalla lämpötila vaikuttaa hirven käyttäytymiseen. Lisäksi käytetty aineisto on mahdollistanut sukupuolten sekä mukana kulkevan vasan vaikutusten tutkimisen. Viimeisessä osatutkimuksessa laseraineistoa käytettiin tunnistamaan hirven aiheuttamia metsätuhoja nuorissa taimikoissa.

Saadut tulokset näyttävät selvästi, että laserkeilaus tuottaa tietoa, mistä voi olla suurta hyötyä ekologisessa tutkimuksessa. Tulokset todistivat, että metsän rakenne elinympäristöissä, joita hirvi käyttää vaihtelee merkittävästi eri vuodenaikojen mukaan. Tämä selittyy sillä mitä ravintoa hirvi eri vuodenaikoina käyttää ja millaisissa metsissä tämä ravinto kasvaa. Myös lämpötilan vaikutusta hirvien käyttäytymiseen tutkittiin, ja nämä tulokset näyttivät, että kuumina kesäpäivinä hirvi joutuu hakeutumaan sille epätyypillisiin metsiin saadakseen suojaa lämpöstressiä vastaan. Nämä alueet olivat metsiä, joissa latvusto oli huomattavan korkea ja tiheä. Tulokset antoivat myös uusia näkökulmia metsän rakenteen merkityksestä vasomisaikaan. Tutkitut hirvet synnyttivät avoimilla mailla (suot), mutta pian tämän jälkeen siirtyivät metsiin, joissa oli huomattavan tiheä ja runsas aluskasvillisuus mikä ilmeisesti tarjosi suojaa sekä ruokaa kasvavalle vasalle ja imettävälle emälle. Viimeisessä osatutkimuksessa vakavat hirvituhot pystyttiin onnistuneesti tunnistamaan laserkeilausaineistosta. Tämä väitöskirja antoi esimerkkejä kuinka laserkeilaus- ja GPS-panta-aineiston yhteiskäyttö voidaan toteuttaa ja millaisia tuloksia näin voidaan saavuttaa. Käytetyt menetelmät ovat helposti sovellettavissa muihinkin lajeihin.

Asiasanat: Laserkeilaus, hirvi, ekologia, metsän rakenne, elinympäristö, GPS

ACKNOWLEDGMENTS

LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which in the text are referred to by their Roman numerals (e.g. **Study I**). They were reprinted here with the kind permission of the publishing houses.

I Melin M., Packalen P., Matala J., Mehtätalo L., Pusenius J. (2013). Assessing and modeling moose (*Alces alces*) habitats with airborne laser scanning data. *International Journal of Applied Earth Observation and Geoinformation* 23, 389–396.
doi:10.1016/j.jag.2012.11.004

II Melin M., Matala J., Mehtätalo L., Tiilikainen R., Tikkanen O.-P., Maltamo M., Pusenius J., Packalen P. (2014). Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – An analysis based on airborne laser scanning of the canopy structure at moose locations. Global Change Biology 20(4), 1115–1125
doi: 10.1111/gcb.12405

III Melin M., Matala J., Mehtätalo L., Pusenius J., Packalen P. (2015). Ecological dimensions of airborne laser scanning – Analyzing the role of forest structure in moose habitat use within a year. Remote Sensing of Environment,
doi:10.1016/j.rse.2015.07.025

IV Melin M., Matala J., Mehtätalo L., Suvanto A., Packalen P. (2016). Detecting moose (*Alces alces* L.) browsing damage in young boreal forests from airborne laser scanning data. Canadian Journal of Forest Research 46, 10-19.
doi: 10.1139/cjfr-2015-0326

Mr. Melin was the main author and writer of all the papers. He was also responsible for all the data processing and integration of the data sets with one another and for the analyses and calculations that led to the results. Dr. Packalen provided programs and valuable assistance related to ALS data processing and analysis, Dr. Mehtätalo provided expertise and aid related to modeling and statistics, while Dr. Matala provided expertise related to moose ecology. The studies were planned together by the group described above. All of the co-authors provided valuable comments on and suggestions for the final manuscripts.

The mentioned papers (I–IV) have and will not be used in any other academic works except for this dissertation.

CONTENTS

8

1 INTRODUCTION

1.1 A brief reasoning

The research around airborne laser scanning (ALS) and its use in practical forestry has been very popular in countries such as Finland, Norway, and Sweden. This has resulted in ALS becoming a basic tool for forest inventories. In Finland, for instance, increasing amounts of ALS data are freely available because of the scanning campaigns of the National Land Survey of Finland and Finnish Forest Centre. At the same time, game and wildlife researchers have begun to utilize tracking collars based on the Global Positioning System (GPS). From the point of view of wildlife ecology research, this combination of ALS data and GPS-collared animals has formed a unique set that is very much worthy studying. This is what this PhD thesis focuses on.

1.2 About wildlife-habitat relationships

In its broadest definitions, an animal´s habitat has been simply referred as the area where it lives in, and which offers the basic elements such as food, water and cover, and where animals have adapted to cope with the competitors, predators and climatic variations of that area (Morrison et al. 2006). Habitat selection has then been defined as the process (two- or multi-stage) where animals first look at the general features of a landscape to select broadly from among different environments, after which they respond to more specific characteristics of the habitat when making the decision where to live in (Swardson 1949, Hilden 1965). The decisions about whether the animal stays in that habitat or migrates to somewhere else may then be influenced by, for instance, interspecific competition or predation, but also by features of the environment that are linked to fulfilling the very biological requirements: availability of the resources needed for survival and reproduction (Morrison et al. 2006). The basic assumption here is that animals will select resources that are best in satisfying the basic requirements and that high quality resources are favored over low quality ones. The reasons then why a particular resource is selected or avoided can´t be directly inferred from the amount of used or avoided, because animals exhibit preference over some resources. That is, when offered in equal amounts, animals will select and *prefer* some resources over the other ones (Manly et al. 2002). This creates a link to the term of *habitat use*, which is then the way *how* animals use the resources in their habitats: what are used for foraging, what for cover, denning, bedding etc. (Krausman 1999). This is essentially what this thesis focuses on, studying how forest structure relates to the habitat use of moose under different circumstances.

Often when studying animal's habitat use, we are actually analyzing their behavior, because their behavior is what shows how they actively use their environment. This aspect of behavior is thus important in understanding the distribution, abundance and needs of the animals (Morrison et al. 2006). Here, the behavior of animals is analyzed by looking at what types of habitats/resources they have used during different times or under different circumstances, i.e. how they have behaved. After this is examined, the next step is to dig deeper into these relationship, which typically requires a step towards the world of modeling.

Morrison et al. (2006) define five main goals of why to model the wildlife-habitat relationships: (1) to formalize or describe our current understanding about a species or an ecological system; (2) to understand which environmental factors affect distribution and abundance of a species; (3) to predict future distribution and abundance of a species; (4) to identify weaknesses in and improve our understanding; and (5) to generate testable hypotheses about the species or system of interest. For example, once we have identified key environmental variables (e.g. of forest structure) that account for some observed pattern in the animal´s presence or behavior, we can try and predict the future status of the animal if there, for instance, was an abrupt change in the abundance of a known important structural attribute of vegetation (e.g. forestry operations changing forest structure and thus affecting the abundance of food for moose).

To study the characteristics of the areas occupied by animals we need information about the whereabouts of the animal and about the characteristics of the surrounding landscape. This has, in the past, required extensive field work (both in locating the animals and in estimating the landscape structure) and though field work is still a vital component of many wildlife studies, it has typically been integrated with remote sensing.

1.3 Remote sensing and wildlife ecology

Remote sensing technologies have been used in ecology for decades and they have revolutionized ecological research in many ways. Satellite imagery data sets such as Landsat allow continuous mapping of land and vegetation across the globe. Another frequently used digital product based on satellite imagery is land cover classification, such as CORINE (Co-ORdinated INformation on the Environment), which is a digital raster map of the European environmental landscape that provides comparable data of land cover from each European country (Environmental Protection Agency 2015). In general, remote sensing products such as CORINE have been widely used in ecological research. They allow for monitoring of, for example, environmental changes, the distribution and abundance of vegetation, and are useful for detecting changes in land cover (see, e.g., Holmes et al. 2013, Balmford et. al. 2005, Glenn & Ripple 2004, Ramsey III et al. 2002, Ramsey III et al. 1997). The next step has been to then link this kind of information to the locations and movements of wildlife. In a recent study, Mason et al. (2014) used the CORINE data set to assess the habitat use of an alpine ungulate. In this study, alpine zones were divided into five classes based on CORINE classifications, which, as stated, are based on satellite image interpretation. In another recent study, Michaud et al. (2014) estimated moose occurrence and abundance from a wide set of remote sensing-based environmental indicators. There are hundreds of studies utilizing e.g. digital maps, satellite imagery or related products to assess the habitat use of wildlife. However, as the scope of this thesis is in ALS, these studies are not reviewed here. For more about the use of digital maps and satellite images in wildlife ecology, see e.g. Glenn and Ripple (2004) or Gottschalk et al. (2005).

Despite their usefulness, methods based on satellite imagery lack the ability to produce information about the structure of the study area in three-dimensions (3D). As early as in the 1960s, MacArthur and MacArthur (1961) had acknowledged the importance of 3D vegetation structure in assessing habitat suitability. To measure this at the time was, however, practically impossible. Venier and Pearce (2007) suggested that the lack of detailed information about the structure of vegetation may even pose a challenge to

biodiversity and wildlife habitat management due to the high importance of 3D vegetation structure (such as tree height and density, canopy closure, understory shrubs, etc.) in determining 1) the presence of a wildlife species in an area, 2) the overall usability of an area (nesting, cover, food, etc.), and 3) the overall diversity of wildlife species in the area (Davis 1983, Brokaw & Lent 1999, Clawges et al. 2008). Furthermore, Morrison et al. (2006) synthesize that it is the vegetation structure and configuration in the habitat that most determine patterns of habitat occupancy by animals (see also Hilden 1965, Wiens 1969, James 1971, Rotenberry 1985). Now, as ALS produces detailed 3D data about vegetation structure, its use in ecology was only a matter of time. The range of species that can be studied with ALS ranges from marine to avian species (Vierling et al. 2008). Before going deeper into these studies, however, the technique of ALS must be briefly explained. For an in-depth introduction, see, for example, Wehr and Lohr (1999) or Lefsky et al. (2002).

1.4 Airborne Laser Scanning (ALS) and its use in wildlife ecology

In this thesis, the term ALS is used to refer to the method or the data produced with this method (ALS data). ALS should not be confused with the term LiDAR, which is also used similarly. LiDAR is an acronym for Light Detection And Ranging; this is literally what ALS systems do – detection and ranging using light. Thus, ALS systems use LiDAR to make measurements. Today, there are a variety of LiDAR systems available, including those that can be mounted in a terrestrial unit, or on an airplane, or used as a mobile device onboard a car, for instance.

Remote sensing techniques that are dependent on sunlight (e.g., satellite imagery) are referred to as passive techniques. ALS is an active remote sensing system, because it produces the light itself and is not dependent on the availability of sunlight. ALS systems are normally carried by a fixed-wing airplane. The measurements made by the ALS system are measurements of the distance between the device and the target. The device measures this by submitting pulses of laser light in the form of a fan perpendicular to the plane's line of flight. The pulse itself can be thought of as a clump of photons. As the pulse hits a target, the photons reflect back and the device recognizes these incoming photons. The device then measures the time between the emission of the pulse and the arrival of the reflection (echo). Next, it calculates the location where the echo came from, which is possible because the speed of light, the direction in which the pulse was shot, and the location where the pulse was shot from are known. The location of the ALS device is determined continuously by a Global Navigation Satellite System (GNSS) and an inertial measurement unit (IMU), which takes into account the effects of the tilting airplane (roll, pitch, and yaw). What must be noted is that one pulse can give many echoes, because when it hits a non-solid target, such as a tree canopy, not all the photons are reflected back. Instead, some continue the journey before hitting another target further down and giving another echo. The first echo is reflected from the highest surface intersected by the laser pulse and the last echo is reflected from the lowest intersection, where complete extinction occurs. In the end, the device produces point cloud data in which the X-, Y-, and Z-coordinates of every received echo, as well as the intensity at which they were received, are known. The modern systems submit as many as 800,000 pulses per second, resulting in a dense point cloud of data.
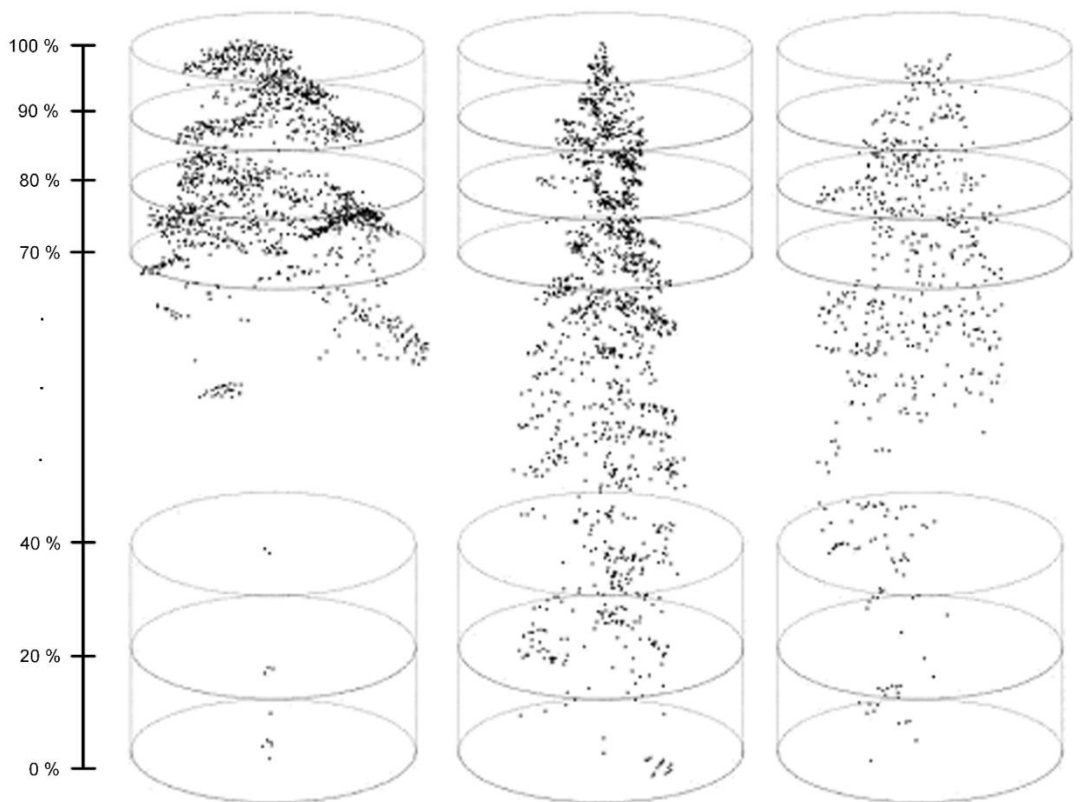
Figure 1. ALS data visualized (Vauhkonen et al. 2009). The black points illustrate the locations where an echo was received (i.e., a location that was hit by a pulse).

The analyses of this thesis were done with low pulse density data that were collected from an altitude of 1500–2000 meters (m) above ground level. This resulted in a pulse density of ca. 0.84 pulses/m^2. The data in **figure 1** were collected from 200 m above ground level, which consequently led to higher pulse density and even allowed for identification of the tree species. The pulse densities vary according to the intended purpose, but for mapping terrain metrics such as topography or for generating area-based estimates of forestry attributes, a data set such as the one used in this thesis (the National Land Survey data set) is detailed enough.

ALS is highly applicable in forestry, because the height distribution of the data is related to the vertical structure of the tree canopy (Packalen et al. 2008) and so variables calculated from the point cloud can be linked to attributes such as tree height, basal area, and volume, or to attributes of the canopy structure and leaf area indices (Naesset 2002, Maltamo et al. 2006, Packalen & Maltamo 2006, Vauhkonen et al. 2009, Korhonen et al. 2011). Now, when thinking about forest wildlife, attributes that are crucial for survival (such as the availability of food, shelter, and cover) are also very often determined by the structure of the surrounding forest. Furthermore, it has been suggested that knowledge

about the presence and abundance of understory vegetation and its vertical structure in general is necessary for predicting wildlife–habitat relationships accurately (MacArthur & MacArthur 1961, James 1971, Dueser & Shugart Jr. 1978). This is what makes ALS useful in wildlife ecology too. ALS has been used to study the habitat use of marine, avian and terrestrial species. As this thesis focuses on a large forest herbivore, only the key past studies focusing on forest species are reviewed here. For thorough reviews on the use of ALS in wildlife ecology see Davies and Asner (2014), Hill et al. (2014) or Müller and Vierling (2014).

Birds as a species are highly dependent on the structure of forest canopy and so they have been a common target for ALS based habitat studies. In a pioneering work in UK, Hill et al. (2004) predicted habitat quality for Great Tits (Parus major) from ALS data. The rationale here was that vegetation structure was known to be a key determinant of nesting and foraging habitat quality. Hill et al. (2004) modeled the nestling body mass of birds against mean canopy height derived from ALS data for 54m x 54m grids in their study area and in the end, the potentials of ALS to predict habitat quality was clearly demonstrated. In Switzerland, Graf et al. (2009) used ALS to estimate the suitability of different areas for capercaillie (*Tetrao urogallus*) habitats. They calculated ALS metrics that described the horizontal and vertical structure of the vegetation and used logistic regression to model them against capercaillie absence/presence from field data. The bird data was collected in 125 x 125m grids, for which the ALS metrics were aggregated using a 125m moving window. Their two final models were able to predict capercaillie presence/absence with an AUC values of 0.71 and 0.77 (see section 4.4 from this thesis for explanation of the term AUC). For birds in Northern Idaho (US), Martinuzzi et al. (2009) used ALS to map the abundance and presence of understory layers and snags, which were known to be important attributes of habitat suitability. They first used ALS and field inventory data to predict the presence of understory species and snags for the study area (with 83 − 88% classification accuracies). Next they aggregated these (and other) ALS metrics to 1 hectare (ha) grids that were then used to model habitat suitability index (HS) for four different bird species (i.e. how suitable each of the 1 ha grid cells are for each of the bird species). The final accuracies of their HSI models ranged between 79 and 91% depending on the bird species.

Tree canopies host also other species than just birds. In UK, Flaherty et al. (2014) modeled ALS derived vegetation metrics (mean tree height, canopy closure, stem count) against squirrel presence/absence also using the generalized linear model (logistic regression). They created a habitat suitability map with 14 m cell size. Finally, their ALS based predictions of squirrel presence had a 59% correlation against predictions made in field. Work has also been done with larger mammals occupying the canopy: Palminteri et al. (2012) predicted the abundance of a bald faced Saki monkey (*Pithecia irrorata*) with ALS variables describing the canopy structure. They first used logistic regression to predict the probability of the animals using a certain site based on the structure of its canopy. They then assessed the intensity at which each sites were used with quantile regression. They received information about the animal´s (bald-faced Saki monkey) habitat use that had not been assessed before and concluded that ALS is an emerging tool for ecologists and conservation planners.

ALS has also been used for studying ungulates and their habitats. Coops et al. (2010) showed that ALS can identify characteristics of forest stands that are known attributes of mule deer (*Odocoileus hemionus*) winter habitats. Lone et al (2014) showed that the inclusion of ALS can improve the performance of models predicting moose habitat suitability and the availability of browse biomass. They concluded this to be the case

because ALS can identify structural attributes of vegetation that are important for wildlife. In sum, although the target species of the cited studies were very different, the basic idea was the same: the 3D vegetation structure of an area affects its suitability for a species, and ALS yields information about this structure.

In many of the studies, ALS data was used as additional data where its purpose was to bring information about the vegetation structure into the models. It is thus obvious that ALS data alone can´t describe the full spectrum of animal´s relationship with its habitat, but the data is rather unique in how accurately it can describe the structural features of the habitat and that is why its incorporation improved the predictive power of the models in the cited studies. The mentioned studies made breakthroughs in the sense that they proved that ALS does have the potential to identify attributes that are important for wildlife. Yet, in order to directly analyze what kind of a forest the animals have occupied at a given time, accurate data are needed about their locations. This has also been a challenge in the past; however, in the same way that ALS made it possible to analyze forests in 3D, GPS collars revolutionized the way in which wildlife can be tracked and located.

1.5 Studying animal movements with GPS-collars

Understanding how and why animals move are the goals of mechanistic approaches to animal ecology, including how and why animals use specific resources, how and why animals interact with conspecifics, and how and why they compete and reproduce (Cagnacci et al. 2010). The reasons behind animal movements and migrations are linked to the very basics of their biology: finding food, gaining energy, avoiding predation, increasing survival, reproduction etc. (Nathan et al. 2008). However, behind these reasons are causes such as climate, predation risk, competition or food availability that may ultimately force animals to move or to migrate in order to fulfill their basic biological goals (Jachowski and Singh 2015, Fryxell and Sinclair 1988). Jachowski and Singh (2015) suggested that ultimately it is the internal physiological status of the animal that drives it to move and migrate in order to, for instance, find better sources of food. Furthermore, it was shown in Singh et al. (2012) that the patterns and scale of moose movements (migration, nomadism, dispersal, sedentary) were affected by factors such as climate and presence of humans. It is thus evident that movement plays a vital role in animal ecology. Fortunately, the introduction of tracking techniques such as very high frequency (VHF) telemetry and especially GPS collars overcome many of the problems associated with discovering precisely where target animals had been. Nowadays, GPS collars can be seen as standard monitoring equipment of animal populations throughout the world. Cagnacci et al. (2010) mention that GPS technology was pioneered on large vertebrates, such as elephants (Douglas-Hamilton 1998), bears (Schwartz & Arthur 1999), and moose (Rodgers et al. 1996, Edenius 1997), although nowadays the range of target animals covers aquatic, terrestrial, arboreal and aerial species throughout the world.

GPS collars measure their positions using satellites. Typically, GPS collars record animal locations on a regular basis, for example, hourly or daily. They also record auxiliary data about the accuracy of the positioning itself and the date and time of the positioning. Some collars also store data about temperature and about the status of the animal (moving, staying still, etc.) at the time of positioning. Some collars store the data in the collar unit itself, where the data are then collected when the collar automatically drops after a predefined period of time. Typically (as in this thesis), the collar is also connected to a

GSM-network, via which the positioning data are sent to an external storage system, such as a database. Naturally, every technology comes with its limitations. Hebblewhite and Haydon (2010) provide a critical review of the use of GPS in ecology, pointing out the benefits and possible sources of bias. Still, in order to link animal locations to their surroundings and to analyze this information, the location data need to be accurate and need to be available for the entire study area, both in space and time. GPS tracking, despite its flaws, provides a good basis for this.

In the past decade, moose in particular have been a common target for GPS tracking in Finland and elsewhere (see, e.g., Dettki et al. 2003, Dussault et al. 2004, Lowe et al. 2010, van Beest et al. 2012, Singh et al. 2012, van Beest and Milner 2013).

1.6 Moose in Fennoscandia

In Finland (and in the whole Fennoscandia), the moose has a dualistic nature. On the one hand it is the most important and valuable game species, but on the other hand it causes great damage to society through browsing of young seedling stands and through traffic accidents. Moose (*Alces alces*) is also an important keystone species in boreal forest ecosystems as it modifies the tree species composition of its environment by browsing (McInness et al. 1992, Kielland and Bryant 1998). It is thus an important animal no matter the point of view and therefore its ecology and behavior have been studied for decades (see, e.g., Hjeljord et al. 1990, Dettki et al. 2003, Nikula et al. 2004). Often, the moose has separate summer and winter habitats between which it migrates. The migratory distance can extend as far as 200 km (Pulliainen 1974, Singh et al. 2012). It has been assumed that this migratory behavior is related to, for example, finding proper food sources, escaping from predators, or avoiding extreme snow depths (Singh et al. 2012). Moose are thermally very sensitive. They can withstand extremely cold temperatures, but get stressed very easily during warm temperatures, which may have an effect on habitat use and behavior, especially during the summer (van Beest et al. 2012, Dussault et al. 2004). Their habitat use is also known to be affected by human presence and human related architecture (roads, railways) (Lykkja et al. 2009, Neumann 2009). It is also commonly suggested that during different seasons the habitat selection of moose is a result of trade-offs between maximizing energy-gains (food), minimizing energy costs (movement) and avoiding predation (cover) (Dussault et al. 2005a,b).

In the summer, a generalist herbivore such as moose is faced with a dilemma of having vast amounts of food to eat, but having a digestive organ of a limited size. Moose should thus select only the high-quality and energy-rich food (Westoby 1974, Hjeljord 1990). Summer provides plenty of easy sources of food (both from trees and green plants) and so during summer, it is the quality of the food that is seen as a limiting factor rather than quantity. The consequence of this quality-induced selection is that there is a pattern in selective feeding from the scale of the whole landscape (deciduous forest, bogs etc.) to the decision about which parts of the plant are ultimately eaten (Hjeljord 1990). These patterns also vary according to the progress of seasons from spring to autumn (Hjeljord et al. 1990). Hjeljord et al. 1990 discovered that from May to October moose used 31 different species for food, but from these only nine accounted for more than 1% of the total forage. Main species for food between late spring and autumn are grasses, deciduous trees, shrubs and water plants. This list includes species such as birch (*Betula spp.*), willows (*Salix spp.*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), raspberry (*Rubus idaeus*), fire weed

(*Epilobium angustifolium*), blueberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitsidaea*), bog whortleberry (*Vaccinium uliginosum*), common heather (*Calluna vulgaris*), wavy hair grass (*Deschampsia flexuosa*), bogbean (*Menyanthes trifoliata*), the water horsetail (*Equisetum fluviatile*) and the yellow water-lily *(Nuphar lutea)* (Hjeljord et al. 1990). Saether and Andersen (1990) concluded that the interaction between moose and their food is strongly dependent on factors that influence the digestibility of forage. They noted that in areas with poor-quality food, moose moved within a smaller area, spend more time foraging and ate larger proportion of the available biomass. On contrary, in areas with high-quality food the diet was more versatile, moose moved within larger areas and had a longer defecation rate (produced less pellets) (Saether and Andersen 1990). No plant seems to dominate moose diet in mid-summer (Hjeljord et al. 1990) and Nikula et al. (2004) suggest that there is no, or only a slight, difference between the summer habitat and the overall landscape.

Another factor that is limiting, or affecting, the movements of moose during summer is temperature. As moose can´t tolerate high summer temperatures they do most of their feeding during night (in young forests and cultivated lands), while the daytimes are spent in more mature forest (which also offer protection against the heat) (Dussault et al. 2004, Bjorneraas et al. 2011, van Beest et al. 2012). In addition, Bjorneraas et al. (2011) noted that moose took advantage of the variations in food-cover caused by agriculture and forestry: they used agricultural lands more during the times when crop biomass was the highest. As summer turns to autumn, the effects of thermal stress disappear, fields have been harvested and moose diet gets narrower with plants such as blueberry in particular and common heather, as well as mushrooms, start to dominate the diet (Hjeljord et al. 1990). Consequently, the selection of habitats during this time favors areas that offer more of these types of food sources (more mature forests) (Bjorneraas et al 2011).

Later in the autumn, as the twigs of dwarf shrubs become covered by snow, there is a need to change diet, which in many cases lead also to change in habitat: migration begins and the moose turn toward winter habitats. Depending on the landscape, the winter habitats may occur in the same area or may require an extensive migration to be reached by moose (Pulliainen 1974). The winter home-range size of moose have been documented to decrease in accordance to deep snow (van Beest et al. 2011). The wintering habitats of moose in Finland are typically characterized by Scots pine (*Pinus sylvestris*) dominated forests, peatlands, or shrub lands, which, compared to the surrounding landscape, include more forests in young successional stages (Nikula et al. 2004). Forestry and the increase of clear-cuts have made life in winter easier for moose, because clear-cuts eventually grow to provide plenty of easy food sources (pine and birch stands). In Finland, pine is the most consumed source of food during winter due to its high availability in the seedling stands, which can be seen annually from the extensive browsing damage. The browsing is extensive, because Scots pines have lower nutrient quantities when compared to e.g. birch and so moose needs to browse high amounts in order to meet with the daily energy requirements of winter (Heikkilä 1990,1994). In an area with large young pine stands the browsing damage is typically repeated year-after-year; moose favors the same areas for winter habitats. It is known that the presence of other favored food species (such as rowan, birch, or aspen) may increase the browsing pressure on pine (Löyttyniemi & Piisilä 1983, Lääperi & Löyttyniemi 1988, Heikkilä 1990). Heikkilä (1994) also noted that having a number of mature spruce forests in the same area seemed to increase browsing on pine, while Parker and Morton (1978) concluded that young stands under the height of four meters can be considered as the most important food source for moose.

As spring approaches and the fresh green plants and leaves start to emerge, the migration towards summer habitats begins. For some females, the migration goes towards calving sites. Calving takes typically place in May or early June, but the exact timing varies (Bogomolova & Kurochkin 2002, Bertram & Vivion 2002, Haydn 2012) due to factors such as the timing of the previous autumn's rut, the progress of spring, the availability of food, and the condition of the mother (Bowyer et al. 1998, Keech et al. 2000). Just as forest damage can occur in the same area year-after-year, so can moose calving. Fidelity to calving sites have been documented especially in areas with no natural predators (Tremblay et al. 2007), but the selection of the actual calving site is still highly varied depending on the landscape; factors such as elevation, slope, and the structure of vegetation affect calving site selection because they provide differing amounts of cover/visibility, for instance, against predators (Addison et al. 1990, Chekchak et al. 1998, Bowyer et al. 1998, Poole et al. 2007). Females typically give birth to one or two calves and a calf at heel has been documented to affect female´s habitat selection. Females with calves have been noted to select areas with low predation risk, for instance avoiding cultivated lands and open areas during summer (Bjorneraas et al. 2011). van Beest et al. (2011) saw the effect of calf on female vanish as autumn progressed, yet in winter, the effect is seen again by the avoidance to open areas that would have deep snow cover (hard for the calf to move).

In general, the seasonal habitat use of moose in Finland (and in Fennoscandia) is rather well known. However, the methods this has been studied with have not been able to accurately characterize the 3D structure of forests. Yet, as forest animals, moose are affected by this structure. Therefore, due to the ongoing changes that, for example, forestry causes in landscapes (thinning, clear-cutting), it is important to understand the habitat requirements of moose in relation to forest structure. This thesis aims to describe the forest structure at moose habitats and how this changes under different circumstances. According to Saveraid et al. (2001), studies that utilize spatially and temporally accurate data (such as GPS tracking data) should also utilize more accurate habitat data. In this thesis, GPS collars have been used to gain this more intensive and accurate tracking of moose and ALS has been used to collect more accurate habitat data. Moreover, as moose browsing damage is the most significant source of damage in pine and birch seedling stands, and as the inspection of the damage requires intensive field work, it is worth testing whether the damaged areas could be detected from ALS data

1.7 Objectives

The overall aim of the thesis is to study the applicability of ALS data and animal location data obtained from GPS collars in wildlife research. The combined use of these data sources is expected to reveal patterns about how the behavior and habitat use of moose is related to forest structure. In addition, the thesis aims to show that ALS data can be used to describe ecologically important attributes of vegetation and forest structure that may define how suitable a given area is for a given species. Thus, the thesis aims to show that ALS data could bring vital additional value to wildlife ecology research, in particular to the study about animal´s habitat use and preferences. The aims of the individual articles that this thesis is based on (**Study I–IV**) were:

Study I. To test the potential of ALS in moose habitat analysis. To characterize and map suitable moose winter and summer habitats with a pervasive method that covered the entire study area. To examine can ALS data be used to differentiate summer and winter habitats from one another based on the structure of vegetation.

Study II. To identify the use and the structure of potential thermal shelters that moose use during thermal stress. Additionally, to more accurately determine the threshold of temperature at/after which behavior shows favoring toward thermal shelters and to gain new information about how moose may react to changing climate. The inclusion of ALS data was assumed to bring more insights into the structure of these thermal shelters.

Study III. To describe the year-round habitat use of moose in relation to forest structure and to see how sex and especially the presence of calves affect it. Special attention was given to winter and calving period to study the time of winter when browsing damage might mostly occur, and to study if calving females show differing patterns of habitat use during and after calving when compared to the other moose.

Study IV. To study if the differences in stand structure caused by moose browsing can be detected using ALS data, and to test how accurately the moose damage can be mapped based on ALS data.

2   MATERIALS

2.1 Study areas

Two study areas were used in this thesis. Study Area I (**Studies I–III**) is located on the west coast of Finland and Study Area II (**Study IV**) is located in northeast Finland (**figure 2**).
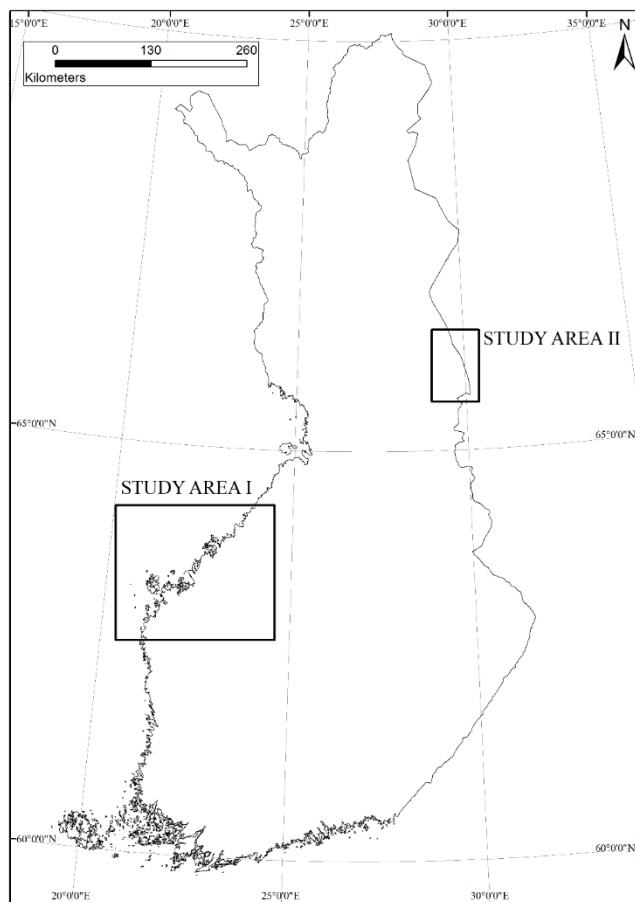
Figure 2. A map of Finland illustrating the locations of the study areas.

Study Area I covers an area of 2,000 km^2 and is characterized by agricultural fields and forests, many of which are located on peatland. Typical of western Finland, Study Area I is extremely flat with an overall topographical variation of less than 10 m in most parts of the study area. In the forests, Scots pine is the most common species, although Norway spruce (*Picea abies*) and downy birch (*Betula pubescens*) are also present (METLA 2013), and the proportions of downy birch can be relatively high in peatlands. The inland waters of the area are characterized by small lakes, ponds, and rivers. A total of 48% of the inland water bodies are less than 1 hectare in size and 94% are less than 10 hectares. The rivers flow steadily without any large rapids and the majority are less than 20 m wide. The density of the moose population (after the hunting period) in the study area is around 3.5 moose per 1,000 hectares (RKTL 2011), which is a typical density in the area.

Study Area II is located in the municipality of Kuusamo (66° 08' N, 29° 41' E). The area is at an altitude of around 280 m above sea level and the topography is characterized by slopes and small hills with rivers and small lakes scattering the landscape. The study area's forests belong to a jointly owned forest, Kuusamon Yhteismetsä. The forests consist of pine, spruce, and birch forests. In Study Area II, pines were the dominant species in the

majority of the stands (73%), followed by spruce (14%) and birch + other deciduous trees (13%). Of the pine stands, 58% were seedling stands or young forests. The forests in the area are intensively managed with silvicultural operations being conducted in a timely manner (regeneration, thinning, etc.). The forests have an evenly aged stand structure and the forest classes range from clear-cuts to mature forests. For **Study IV**, the studied forests were seedling stands with and without moose browsing damage. Seedling stands here mean forests that contain trees that are less than 8 centimeters in diameter or less than 8 m in height.

2.2 Moose data

The moose location data were provided by Natural Resources Institute Finland (Luke) and they were used in **Studies I–III**. The GPS collars (Vectronic) used stored positions on an hourly basis, together with the date, time, temperature, and other auxiliary information about positioning. Every fourth hour, the collars sent the collected information to a WRAM database (Swedish University of Agricultural Sciences 2011) via a GSM-network (Global System for Mobile Communications). The collars were installed in the winter of 2009 by the Finnish Game and Fisheries Research Institute, in co-operation with the Finnish Food Safety Authority, Evira. Moose location data in the study area were collected between January 2009 and August 2010.

Moose data for **Study I** consisted of 18 moose individuals. The study periods were summer (June, July, August) and winter (January, February, March). The selected winter months are when permanent snow cover exists in the study area (true winter) and when migration to winter habitats is usually complete. In June, on the other hand, the most common summer food of moose has emerged (green leaves and plants) and moose have already migrated to their summer habitats. In addition, in September leaves are beginning to lose their green and moose start to use other, more autumnal sources of food. In addition, moose hunting begins in September and may continue until December. This period was excluded because we wanted to examine moose's behavior without hunting pressure. Data were analyzed at the level of the individual moose, and sex was not taken in account.

Study II used also 18 moose, but this time sex was noted and therefore the data consisted of 11 females and 7 males. **Study II** focused on thermal stress during summer and so the study period covered the summer months (June, July, and August) in 2009 and 2010.

In **Study III**, moose were followed for a full year, which reduced the number of individuals, because a 365-day period during which most of the moose were tracked with functioning collars was the requirement. Finally, the moose data for **Study III** consisted of 15 moose. Here, sex and reproductive stage were both noted and so the final data consisted of 6 non-calving females, 5 calving females and 4 males. The study period was a 365-day period from April 10, 2009 onwards. This meant that the mothers and their calves born in the spring of 2009 were followed for one year (via their mother's GPS collar).

2.3 ALS data

ALS data for Study Area I were provided by the National Land Survey of Finland (License no. TIPA/517/10-M) and were collected between April 24 and May 5, 2009 with a Leica

ALS50 laser scanning system. For Study Area II, the ALS data were collected by Blom Kartta Oy between July 24 and August 4 in 2009 with an Optech ALTM Gemini ALS device. The technical details of the ALS surveys are provided in the articles (**Studies I–IV**).

2.4 Temperature data

Temperature data were used in **Study II**. The data set was downloaded from the Topographic Database of the National Land Survey of Finland. Originally, it was measured and provided to the database by the Finnish Meteorological Institute (FMI). The data set is a grid where the distance between each point is 10 km and where each point contains information about the temperature at the corresponding location. The data used in **Study II** contained the minimum, maximum, and average daily temperatures for every point between 2009 and 2011. The temperatures represent air temperatures.

2.5 Moose browsing damage data

Forest damage data were used in **Study IV**. The damage was moose browsing damage in the forests of Kuusamon Yhteismetsä in Study Area II. The study area had already had moose browsing damage in the past, but in 2007 and 2009 damage was extremely severe. Altogether, the stands of the study area formed a holding of 8,288 hectares, from which 565 hectares were damaged. This amounted to 1,847 healthy and 56 damaged stands. The damage was inspected by the Finnish Forest Centre according to the official regulations for compensation of moose damage (Ministry of Agriculture and Forestry 2009). The data set held information about the location of the damaged stand, the area of the damage, the severity of the damage (four classes), the number of damaged seedlings in each severity class, and the general state of the stand (dominant species, height, basal area or stem count, site type, and soil type). In the end, we only used a binary coding to indicate the presence (1) or absence (0) of moose browsing damage.

3   METHODS

3.1 Preprocessing

3.1.1 Processing the ALS data

The ALS data contained the following information for each received echo: $X, Y, Z, I, N, R,$ and C. XYZ represent the XYZ-coordinates of an echo. I represents the intensity at which the reflected echo was received. N represents the number of echoes received from a pulse, and R represents the ordering of the received echoes, that is, if N is 2 and R is 1 then two echoes ($N = 2$) were received from this pulse and this was the first one of them ($R = 1$). C represents classification. Here, the pulses were pre-classified as ground points and other points using the method of Axelsson (2000). The laser scanners used in these studies capture a maximum of four echoes for each submitted pulse. The echo categories are *first of*

many, *last of many*, *only*, and *intermediate*. *first of many* means that the device received many echoes from a pulse, from which the current echo was the first one. Correspondingly, *only* means that only one echo was detected. In **Studies I–III**, only the echo categories *first of many* and *only* were used, because they represent surface hits. From now on, these are referred as surface echoes. In **Study IV**, the other echo categories were also utilized, because we wanted to examine whether browsing affects the amount of received *intermediate* echoes. Also, if the vegetation becomes less dense, the site could provide more *only* echoes.

In the preprocessed data sets, the Z-coordinate stood for height above the geoid, which needed to be transformed into height above ground level. For this purpose, a digital terrain model was interpolated from the ground echoes using inverse distance-weighted (IDW) interpolation method (Shepard 1968). The result was a raster, a digital terrain model (DTM), where the value of each cell depicts its height above the geoid. Next, this DTM was subtracted from the echoes. The result was now a data set containing the same echoes, but now with a Z-coordinate that stood for height above ground level. From now on, all the mentioned heights refer to the height above ground level.

3.1.2 Linking ALS data to targets

In **Studies I–III** the aim was to see the types of forests moose occupied at different times or under different circumstances. Thus, data describing the forests around the moose locations were needed. Based on earlier experience, it was concluded that a circle with a 25-meter radius is sufficient to describe the structure of forests and the vegetation in the near vicinity of moose. In addition, the accuracy of GPS-collar positioning is only around 10 m and so the buffer helped to reduce the effects of positioning error. Therefore, a circular buffer with a 25-meter radius was created around each moose location and ALS data were extracted from these buffers (**figure 3**). In **Study I** additional analysis was done by creating a set of ringed buffers around the moose locations. The ringed buffers (six of them) covered the area within 150 m of the moose and they provided information about how the structure of the forest varies within different distances from the moose. The reason for this analysis was to acknowledge the fact that moose habitat use may have multiple scales even at the local scale (Dettki et al. 2003, Nikula et al. 2004) and the ringed buffers were assumed to give indications about the existence of this pattern.
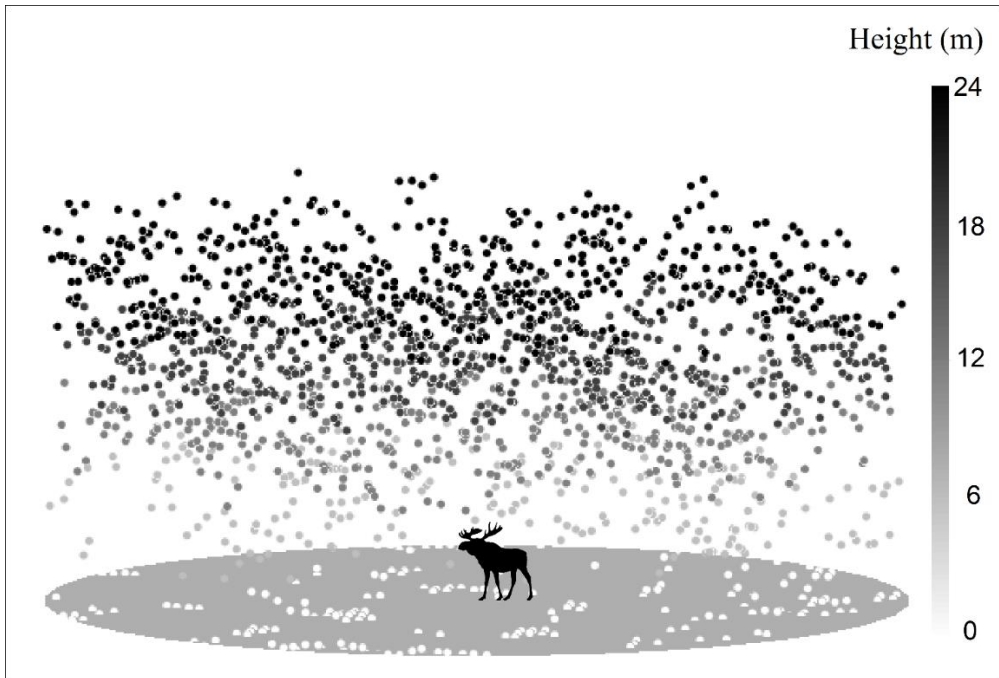
Figure 3. ALS data extracted and visualized around a moose. The grey circle has a radius of 25 m.

Moose location data were not used in **Study IV,** where the targets were seedling stands with and without moose damage. Here, a regular grid with a 15-m cell size was created in the study area and the cells that fell completely within the borders of the target stands (**Figure 4**) were the ones from which the ALS metrics were extracted and analyzed.
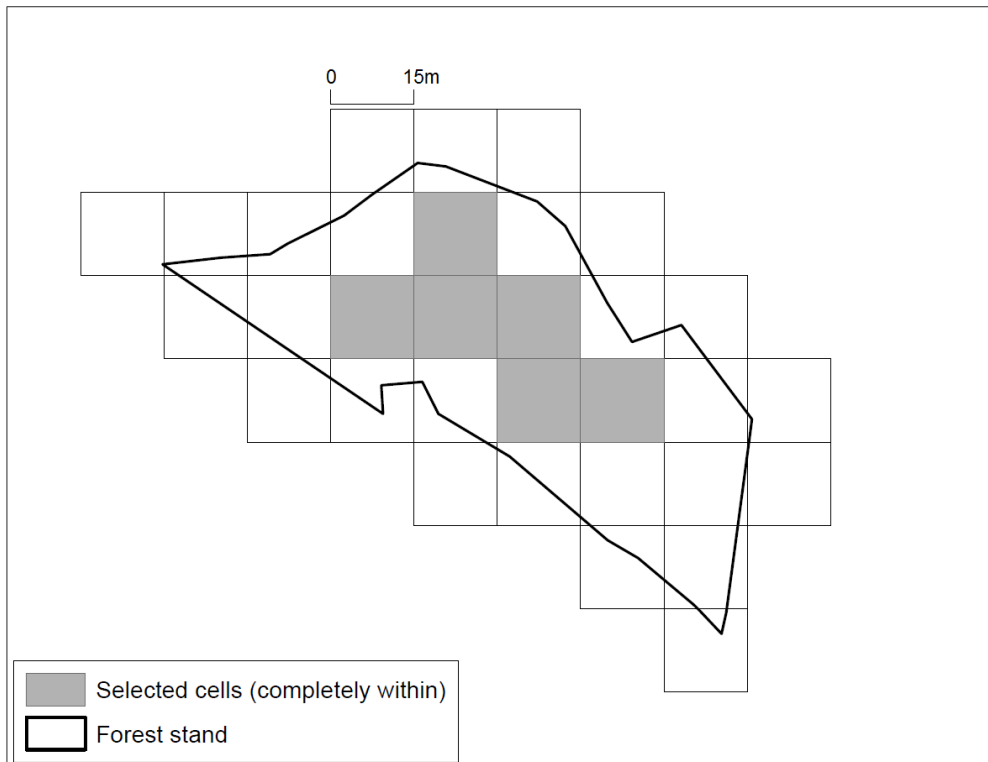
Figure 4. The setting showing the selection procedure of cells inside target stands in **Study IV**.

3.2 Analysis

3.2.1 ALS metrics

As each of the articles (**Studies I–IV**) had a different aim, there was no uniform way of analyzing the ALS data. Instead, the calculated point cloud variables were tailored to fit the research question at hand. Common height percentiles were used in **Study I** and **IV**. Height percentiles (*h5...h100*) indicate how the echoes distribute vertically. For instance, an *h80* value of 13.5 indicates that 80% of all the echoes came from below 13.5 m. In addition, a set of *p*-variables were used that describe the proportion or frequency of echoes at a certain height class (e.g., *p3_5* is the percentage of echoes between 3 and 5 m) or above a certain height (e.g., *p7* is the percentage of echoes above 7 m). For instance, a *p7* value of 0.6 means that 60% of the echoes came from above 7 m. The *p*-variables were used in **Studies II–IV**. In **Studies I–III**, the variables were calculated from ALS data extracted around moose (**Figure 3**). In **Study IV**, the same was done to the target cells (**figure 4**).

3.2.2 The modeling

Chapter 1.2 outlined the background why to model wildlife-habitat relationships. The core here was in modeling moose-forest structure relationship (**figure 3**): the species data here is recorded observations of presence and the ALS data tells the about the forest structure around the observation. The modeling task was then to describe the relationships between the two. The idea was the same when the relationships of forest structure at the animal location was modeled, for instance, against temperature. The scope changed, but the concept stayed the same. The modeling techniques used in this thesis involve logistic regression (**Study I** and **IV**) and linear mixed-effects modeling (**Study II** and **III**). These techniques were also used in some of the studies cited in **section 1.4**.

Logistic regression is a special case of the generalized linear model, where the dependent variable is binary (0 or 1). In **Study I**, the binary coding represented moose absence or presence and in **Study IV**, the presence of moose browsing damage. The models in both of the papers followed the basic form of logistic regression:

$$ln\left(\frac{p_i}{1-p_i}\right) = \beta_1 + \beta_2 X_2 + \cdots + \beta_i X_i \qquad (1)$$

where ln is a natural logarithm, X´s are the variables and the *betas* are the regression coefficients to be estimated. In the data, the presence and absence of moose (**Study I**) or moose browsing (**Study IV**) were coded as binary (0 or 1) and so their distribution is defined by the Bernoulli distribution (p_i), where p_i indicates the probability of a case where presence (*Y*) in a location is 1. In general, logistic regression defines that the expected value of *Y* is *p*, where *p* is the probability that *Y* = 1. In the end, logistic models (**Study I** and **IV**) can be regarded as classifiers. Here, the performance of these classifiers was assessed with Cohen´s Kappa, Overall Accuracy and ROC (Receiver Operating Characteristics) analysis. The model structures (what was the response and what were the predictors) and the analysis of their performance are described in detail in the next chapters.

The modeling technique used in **Study II** and **III**, linear mixed-effects modeling, extends the basic linear regression model so that it acknowledges the possible grouping of the data (by e.g. moose individuals). The term 'mixed' is used, because a mixed model constitutes of two parts: fixed effects and random effects. The fixed part is the basic linear model, while the random part takes into account the mentioned grouping (random effect). In its simplest form, a linear mixed-effects model can be expressed as:

$$y = X\beta + Zb + \varepsilon \qquad (2)$$

where *X* is the design matrix for fixed effects and β is the vector for fixed effects, *Z* is the design matrix for random effects and *b* is the vector for random effects, while ε is the vector for observation errors (Pinherio & Bates 2004).

The next chapters describe, in more detail, the ways the models were formulated and evaluated in each of the papers. All the modeling in this thesis was conducted in R (R Development Core Team 2015).

3.2.3 Winter and summer habitats of moose (Study I)

To see how the used winter and summer habitats differed from their surrounding landscapes in terms of forest structure, a set of random points was created in both, moose winter and

summer areas. These points were forced to be at least 50 m away from any observed moose location. The ALS data were then extracted around both, the random locations (assumed no-moose locations) and the moose locations. Next, the ALS data in areas occupied and not occupied by moose were analyzed for summer and winter separately. This gave information about how the forest structure at moose location differed when compared to the assumed no-moose locations.

The modeling part of **Study I** aimed to predict the probability of moose presence in a given location. This was predicted with logistic regression. The explanatory variables were ALS metrics that were extracted from the areas near moose (25m buffer) and from an area away from moose (125-150 meters away from moose). The reason for this was that we wanted to test does the outer buffer bring any additional value to the models, because it is known that moose habitat use may have multiple scales even at the local level. The outcome of the modeling was a prediction of probability of moose occurrence. This prediction was then compared with actual moose occurrences and through this, the model performances were assessed with Cohen´s Kappa and the overall accuracy of correctly predicting moose absence or presence.

The variable selection procedure was done exhaustively from a set of variables that, based on prior analysis and earlier studies, were assumed to be the most significant for moose during the given seasons. The following tables illustrate the models and their variables.

Table 1. The model of predicting probability of moose occurrence during winter.

Variable*	Estimate	Std. error	t-value	p-value
Intercept	0.0349	0.0217	1.612	0.107
veg_i	0.014	0.0004	32.047	<2e-16
h30_i	-0.1692	0.0038	-44.769	<2e-16
h100_i	0.0142	0.0017	8.193	<2.55e-16

*veg = proportion of echoes above 0.5 meters, see section 3.2.1 for h30 and h100
* i = variable was from the area near moose. o = variable was from the area away from moose.

Table 2. The model of predicting probability of moose occurrence during summer.

Variable	Estimate	Std. error	t-value	p-value
Intercept	-1.939	0.044	-43.92	<2e-16
h30_i	-0.111	0.006	-19.05	<2e-16
h70_i	-0.156	0.005	-34.48	<2e-16
log(h100_i)	1.459	0.023	64.63	<2e-16
veg_o	0.028	0.001	39.63	<2e-16
h30_o	-0.230	0.006	-41.03	<2e-16

* i = variable was from the area near moose. o = variable was from the area away from moose.

3.2.4 Moose response to thermal stress (Study II)

Here, the main aim was the identification of potential thermal shelters. For this purpose, a variable named *p10* was created. *p10* accounts for the proportion of echoes that come from above 10 m, and its values indicate how much shelter an area can offer: a high *p10* value indicates a high and dense canopy, which in turn offers cover during the periods of the most intense solar radiation. Other metrics were tested too, but *p10* proved to be the best one in describing both, the height and density of the canopy. In order to see what kinds of habitats moose used under different temperatures, the information about vegetation structure was linked with temperature. This was achieved by combining temperature data from the FMI data grid with the moose locations. The temperature values to moose locations were interpolated from four nearest neighbors (the four nearest temperature points in the FMI data grid; **Study II, Section 2.5**). Now, the temperature at the moose location on the day of positioning was known, as well as the structure of the vegetation at that same location (**Study II**, **p. 1119**).

The responses of moose individuals to temperature were then analyzed with linear mixed-effects modeling with random, individual-level moose effects. The analysis was conducted on moose locations in the summer months between 9 a.m. and 6 p.m., as these are the hours with the most intense solar radiation (highest temperatures) and thus were those most likely to show the possible changes in moose behavior due to thermal stress. The final model quantified the effect of temperature on the structure of vegetation (the dependent variable) at moose locations and allowed for interactions between temperature and individuals, as well as temperature and month. This meant that the model allowed testing of whether the effect of temperature varied between summer months and how this differed between individuals. The model was formulated as:

$$y_{mi} = \beta_1 + \sum_{s=2}^{3} \beta_s I(s) + \beta_4 + \sum_{s=2}^{3} \beta_{3+s} I(s) t_{mi} + u_m + v_m t_{mi} + e_{mi} \qquad (3)$$

where y_{mi} is the daily mean value of the ALS variable *y* around moose *m* on day *i*, $I(s)$ indicates the months June(1), July(2) or August (3), β indicates a constant, t_{mi} indicates the

temperature around moose m on day i, u_m and v_m are the random moose effects $(u_m \sim N(0, \delta_u^2) \; v_m \sim N(0, \delta_u^2), \; \text{cov}(u_m, v_m) \neq 0)$, and e_{mi} is a normally distributed residual.

The hypothesis was that as temperature increases the value of the ALS variable (*p10*) also increases: the higher the temperature, the denser and higher the canopy at moose locations. The temperature used here was the daily maximum temperature, because: 1) we assumed that the maximum temperature occurred between the selected time span (from 9 a.m. to 6 p.m.); and 2) the daily maximum temperature was assumed to more clearly reveal the effect of temperature than the average temperature would.

3.2.5 The role of forest structure in year-round habitat use (Study III)

In **Study III**, the focus was on analyzing differences in habitat use caused by season and individuals. The structure of the used habitats was analyzed with three ALS variables: *p_canopy*, *p_ground*, and *p_shrub*. The variables described the proportions of echoes above 5 m (*p_canopy*), the proportion of pulses that hit the ground (*p_ground*), and the proportion of echoes that came from between 0.5 m and 5 m (*p_shrub*). These three variables were chosen after a thorough investigation of ALS metrics and how they were linked to moose habitat use. In the end, *p_ground* was an obvious choice since its value directly (inversely) describes the amount of vegetation in the target area, which is linked to, for instance, the availability of food and shelter. The other two variables are related to the vertical profile of the vegetation. Here, the main point was to distinguish the canopy and shrub layers from one another so that their structures could be analyzed separately. The height limit of five meters was assumed to be valid for this purpose. In Dettki et al. (2003), for instance, vegetation below five meters was considered as a food source for moose. Furthermore, with the limit of five meters, some pulses were certain to hit shrub vegetation, if it existed. If we had cut the limit to 2 meters then the probability of catching the understorey layer would have also been very low. With the canopy layer above five meters, we did not make further vertical divisions (e.g., 5–10 m) and so anything above five meters was considered as the canopy layer. Other p-variables (p4, p7 etc.) and the height percentiles were tested also, but the three variables (*p_ground, p_shrub, p_canopy*) proved to be a combination, which performed rather well in describing different aspects of the forest structure with minimum amount of variables. Main criteria in testing and selecting variables for modeling was in keeping the amount of predictor variables reasonably low, but still maintaining the ones that matter the most. The final three metrics now contained information about the openness of the forest, about the amount of food or the cover it could provide, and about canopy density and height, which can be linked to the age of the forest.

Similarly to the thermal responses in **Study II**, the habitat preferences of individuals were analyzed with linear mixed-effects models. Here, the random effects were the individuals; grouping was according to sex and, additionally for females, the presence of a calf, because the interest was also in seeing differences between males, females, and calving females in particular. The periods of interest were the entire year, winter, and the calving period. In order to study the habitat use during the calving period, the period needed to be located in time and in space (i.e., the calving sites). This was done by analyzing the movement patterns of the pregnant females between April and July, because the movements of moose cows are known to substantially decrease just prior to giving birth (Poole et al. 2007). Hour-by-hour tracking revealed a significant period of diminishing movement between May 3 and May 10. This pattern was seen for all the pregnant females. After this period, the movements began to rise and were never as low again. Therefore, it was

concluded that the calves were born somewhere between May 3 and May 10, most probably between May 3 and May 6, as these were the days with least movement.

The final models in **Study III** now quantified the effects of different time, sex, and the presence of a calf on the structure of the forest at moose locations. The models were formulated as:

$$y_{mi} = f(time_{mi}, sex_m, calf_m) + b_m + e_{mi} \tag{4}$$

where y_{mi} is the value of the ALS metric *y (p_shrub, p_canopy or p_ground)* around moose *m* on day *i*. $time_{mi}$ indicates the period that was used to distinguish between different times of the year (either month or week), sex_m indicates sex (male or female), $calf_m$ indicates the presence of a calf (calf or no calf), b_m is the random moose effect with variance δ_b^2 and e_{mi} is a normally distributed residual with variance δ^2 and where *cor(e_{mi},* $e_{mi'}$) = $\rho^{(time_{mi} - time_{mi'})}$. For obvious practical reasons, males were not allowed to have calves. The models also included interactions between the variables (time of year, calf, sex). Through this, the possibility that the effects of sex and/or a calf were stronger or weaker at certain times of year was examined. In addition, the contrasts of the models were redefined so that the responses of consecutive months/weeks were compared against one another (i.e., April to March, May to April, June to May, etc.). This was done to see whether the possible differences in habitat use are statistically significant between different months and especially to see when the significant changes in habitat use occurred and in particular, toward what kinds of forests.

3.2.6 Detecting moose browsing damage from ALS data (Study IV)

Moose browsing may cause structural abnormalities in tree seedlings and forest stands, which in severe cases can lead to economic losses. The major differences in the structure of a damaged stand should thus be detectable from ALS data. When compared to a no-damage reference stand, a damaged stand should have decreased canopy cover since moose have eaten the branches and needles. These were the hypothesis with which the issue was studied.

In **Study IV**, a set of both *p*-metrics and height percentile metrics were calculated. Here, the variables were those that were best in describing the loss of needles and branches. In addition to point cloud metrics, the information about the intensities of the received echoes as well as their echo category (*first of many*, *intermediate*, *last of many*, or *only*) were used. All the metrics were cell-specific (**Figure 4**). A complete listing of the computed metrics is provided in **Study IV (Table 1)**.

In order to conduct the comparison of browsing and no-browsing sites properly, the assumption that healthy and damaged cells had a similar forest structure needed to be confirmed (so that cells from mature forests would not be compared with cells from young seedling stands). This was achieved by excluding all the cells that had more than 2.5% of the ALS echoes coming from above 7 m. In practice, this delineation excluded mature forests. Now, the final data set consisted of damage (n = 18,630) or no-damage (n = 96,628) cells which were located in similar forests, but with different browsing impact.

As with **Study I**, the modeling for **Study IV** was also done with logistic regression. Here, the model inputs were remote sensing metrics from a cell and the output was a prediction about the probability of moose browsing damage in this cell (from 0 to 1). Since many cells can belong to the same stand, the models were ultimately created (as well as

used for prediction) with leave-one-stand-out cross validation. This meant that no cells belonging to a stand were used when building the model and when conducting the prediction phase for the other cells belonging to the same stand. Similarly to **Study I**, the model's performance was analyzed with the Kappa coefficient and overall accuracy, but also with receiver operating characteristics (ROC) analysis, which is a convenient method for analyzing classifier performance. Details of this are provided in **Study IV (Section 2.2.4)**. The variables used in the model were selected exhaustively from the set given in **Study IV (Table 1)**. Here, variables were removed and/or interchanged with one another until a point was reached where the inclusion or removal of a variable did not improve the model's performance. The variables were selected with this approach instead of statistical testing because all of the cells of a stand were either damage or no-damage and there were no variations inside a stand. This makes statistical testing unreliable, because the standard error estimates of the model's coefficients would be underestimations. Therefore, p-values are not presented as they were in **Table 1**.

The final model consisted of the following variables: proportion of ground echoes (*p_ground*), proportion of echoes coming from above one meter (*p1*), and average echo intensity (*ave_intens*). The model was then formulated as:

$$ln(\frac{p_i}{1-p_i}) = \beta_1 + \beta_2 p\_ground_i + \beta_3 p1_i + \beta_4 p1^2{}_i + \beta_5 ave\_intens_i \qquad (5)$$

where the *betas* are the regression coefficients to be estimated. *p_ground* was included as a dummy variable divided into five classes with equal amounts of cells in each. This was done because the *p_ground* value is distinctly linked to the amount of vegetation in the cell and showed significant non-linearity.

In the end, each cell had a predicted probability of browsing damage on a scale ranging from 0 to 1. The classifying performance of the model was examined with ROC analysis (Receiver Operating Characteristics), which is a commonly used method for analyzing and visualizing classifier performance and the trade-off between different types of prediction errors (false positive, false negative). The classifier here is the model and its damage predictions. For an in-depth overview of ROC analysis, see Fawcett (2006). The ROC analysis was done with the pROC package (Robin et al. 2011).

In addition to modeling, the differences in the ALS variables were analyzed directly by comparing their values and their distributions (with histograms) in the damage and no-damage cells. For instance, if a seedling stand had lost most of its branches, the first echoes would come mostly from the ground instead of the vegetation. Furthermore, their intensity values would also differ as a result. In addition, if the vegetation is less dense, the number of intermediate echoes might differ, as well as the height from which the last echo comes from (ground vs. vegetation).

4   RESULTS

4.1 Characterization of summer and winter habitats

The first task (**Study I**) of detecting differences between moose summer and winter habitats from ALS data was completed successfully and the results were in line with previous knowledge about the issue. When analyzing the vertical distributions of ALS echoes from the moose and no-moose areas, it was noted that when compared to winter habitats, summer habitats were characterized by more mature forests. The no-moose areas in summer then differed from corresponding moose areas in that they had even more echoes coming from high canopies (more mature forest) and less echoes coming from heights below 10 m. Thus, the summer habitats of moose seemed to be in mature forests, although in ones with shrubs and an understory layer.

In winter, the differences between moose and no-moose areas were clearer: the moose areas were characterized by younger forests (with a height below 8 m) and fewer mature forests than no-moose areas. These results are presented in **Study I (Section 3.2, Figure 3)**. The analysis from the ringed buffers that extended further away from moose showed that as the distance from the moose increased, the surrounding areas became more heterogeneous in terms of, for instance, canopy height. In summer, it was seen that the areas around the moose had large variations in canopy height. In winter, the areas furthest away from moose had, on average, higher canopies than immediately around the moose locations. This phenomenon resembles that seen by Heikkilä (1994) who noted that the presence of mature spruce forests in the area increased browsing on pine.

The analysis described above constituted the basis for modeling how suitable certain locations would then be. The accuracy of the summer model by means of the Kappa value was 0.21 and the accuracy of predicting moose presence or absence was 0.607, which means that 61% of moose/no-moose cases were correctly classified. The winter model performed with a Kappa value of 0.41 and an overall accuracy of 71%. **Table 3** lists the model performance.

Table 3. Performance of the summer and winter models of **Study I.** Error matrix showing the amounts of correct and incorrect classifications of moose presence or absence.

Error Matrix	SUMMER		WINTER	
	No-moose	Moose	No-moose	Moose
No-moose	17195	17859	19582	10524
Moose	10315	21739	7173	22933

The modeling was easier for winter, because the areas used by moose during winter areas were clearly different from the no-moose areas in terms of forest structure. A visual example of the habitat suitability model's performance in winter is given in **Study I** (**Section 3.3, Figure 4**). The figure shows the phenomenon were moose seem to prefer younger forests (seedling stands) instead of the nearby mature forests.

4.2 Behavioral response to thermal stress

The results of **Study II** suggested that increasing temperatures caused significant shifts in moose habitat use toward areas with higher and denser canopies (i.e., areas offering shelter): as temperatures increased, the value of the variable *p10* also increased. In addition to this phenomenon, a circadian pattern where moose clearly used thermal shelters during the daytime of the hottest days was also observed. This pattern was not present in lower temperatures; it only became significant during the hottest hours of the hottest days. A textbook example of this is shown in **figure 5**.
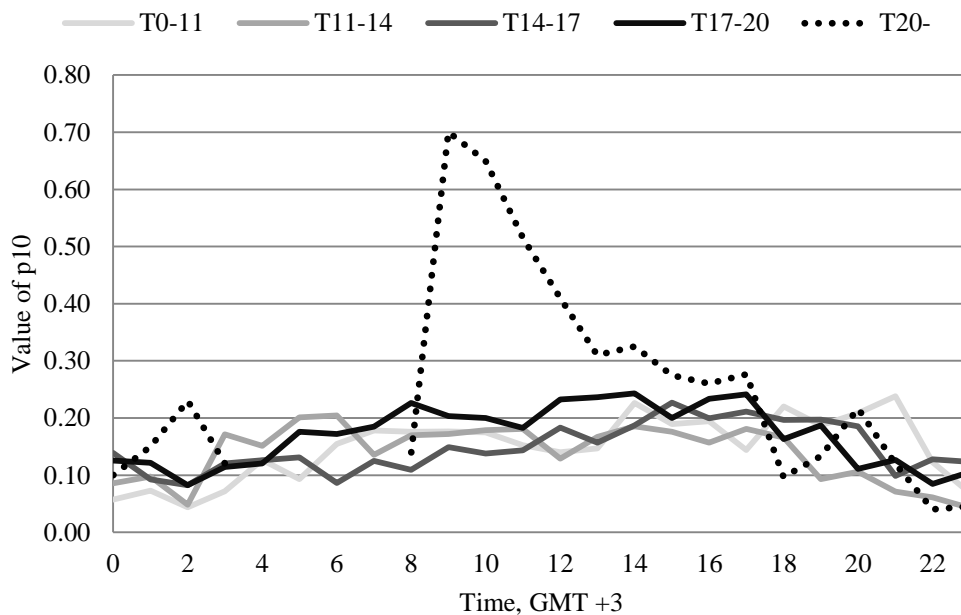

Figure 5. Behavior of moose 4497 in relation to varying temperatures in different temperature classes. For instance, T17-20 accounts for locations positioned during days when the temperature was between 17°C and 20°C.

As seen from the image, moose individual 4497 clearly favored the thermal shelters from 8 a.m. until 1 p.m. during the hottest days (**Figure 5, series T20-**). The value of p10 in its locations increases dramatically when compared to the locations where it was during the times with lower temperatures.

These results gave clear evidence that moose do react to extreme temperatures, but here detectable (significant) changes in behavior were noted only when temperatures rose to 20°C and beyond. In addition, it was noted that the moose living near to the sea had no need for thermal shelters from high and dense forests; they instead moved to the coastal forests and even took frequent swims. The most important finding was that the thermal shelters were found in forests that were not generally favored. Thus, the animals were forced to select sheltering from heat over habitat suitability. The euclidean distance from the moose to the nearest inland waterbody was also tested as an additional variable in the modeling, but it was not significant. **Figure 6** shows, based on the modeling, the average relationship between increasing temperature and canopy density at moose locations:
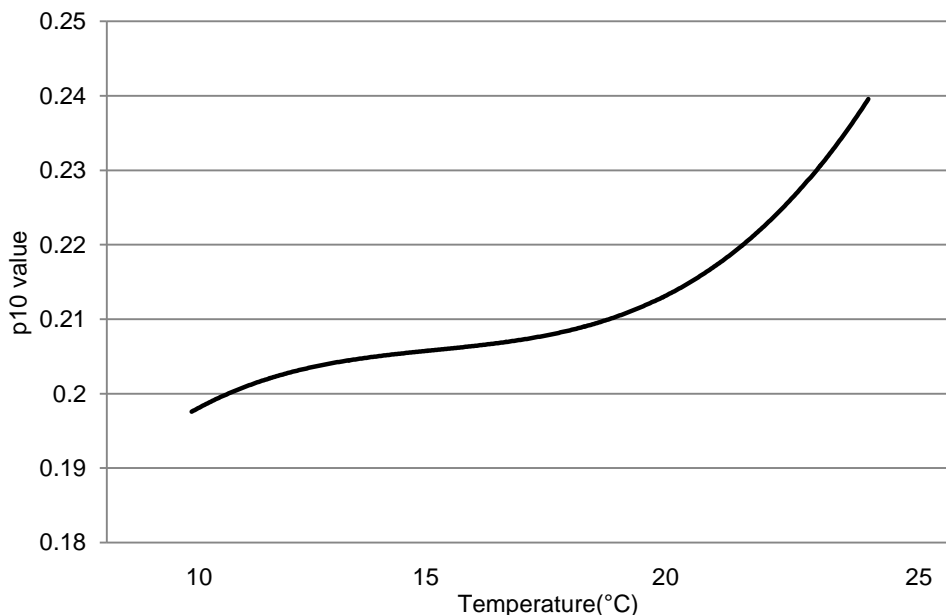

Figure 6. The average effect of temperature on the value of p10 at moose locations. As temperatures reach 20°C and beyond, the effect of temperature becomes stronger. More detailed results are presented in **Study II** (**pp. 1120–1123**).

4.3 Forest structure and moose habitat use during different seasons

Habitat use of moose covers a large variety of forests: from seedling stands favored in winter to mature stands favored in summer. The reasons behind this are linked to, for example, finding food and shelter. Acknowledging this, and the results of **Study I**, the phenomenon was now studied on a year-round basis while also noting the differences in habitat use between males and females with and without calves.

Results showed that there are significant differences in what types of forests moose are found in during different times of year. Moreover, this seems to vary between males and females, with females' whereabouts further being affected by the presence of a calf. The noted pattern was that moose went to mature forests as summer turned to autumn, and eventually to young forests/seedling stands as snow and winter came in (**Study III, Figure 2**). This is linked to forest structure and to where food is found during each season: during summer, moose can utilize dozens of food plants growing in various types of forest and so it moves a lot in search for the best quality food (Hjeljord et al. 1990). During autumn their diet mainly consists of the berry plants, heather and mushrooms that are mostly found in mature forests. As for winter, their main sources of food are birch and pine seedlings or young trees, which consequently means that they are mostly found in younger forests and seedling stands (Nikula et al. 2004). During winter, the shift to younger forests occurred as early as in January, but the use of young forests peaked in March when all moose groups were found in areas with areas having high amounts of vegetation below five meters (**Study III, Figure 4**).

Interesting patterns were also found from the more detailed analysis conducted during the calving period and winter. Calves were born in areas with practically no vegetation below five meters, but a few days after calving, the mother and the calf moved to areas with most (and lots of) vegetation below five meters. This was very different from where they were before or where the other females or males were (**Study III, Figure 3**).

4.4 Browsing damage is detectable from remote sensing data

Many of the ALS metrics behaved differently in damage and no-damage cells. **Figures 7** and **8** show the histograms of four selected metrics.
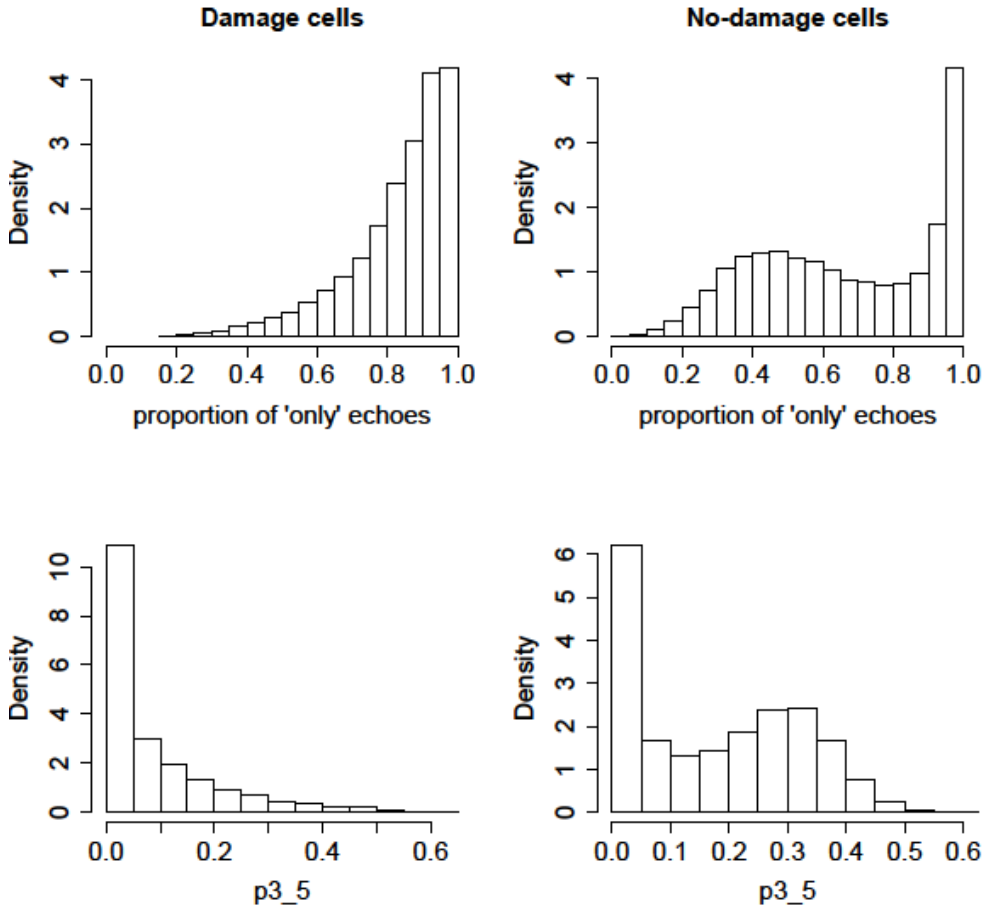
Figure 7. Histograms of selected ALS metrics in cells with (left column) and without (right column) moose damage. *p3_5* stands for the proportion of echoes that came between the heights of 3 m and 5 m.
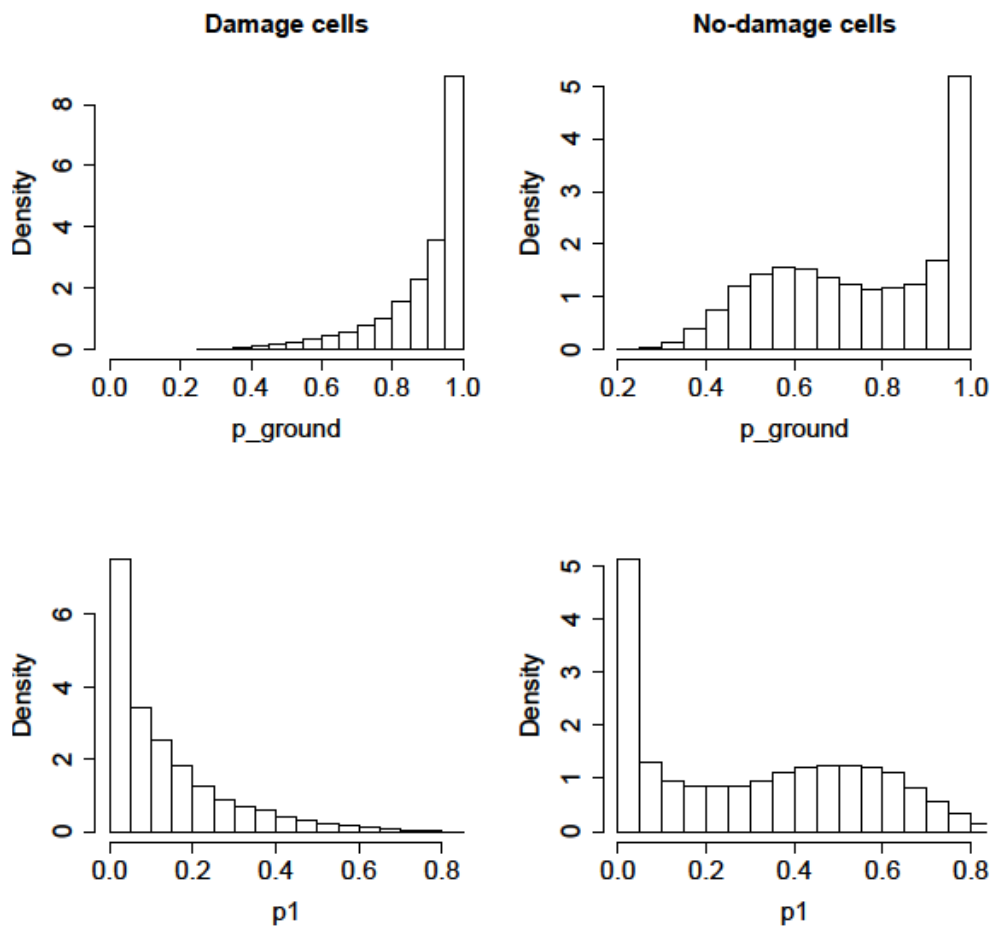
Figure 8. Histograms of selected ALS metrics in cells with (left column) and without (right column) moose damage. *p_ground* stands for proportion of ground echoes and *p1* for the proportion of echoes that came from above 1 m.

As the figures show, the ALS variables between the damage and no-damage cells differ in many ways. The damage cells have less vegetation in the displayed heights of above one meter, but in particular between the heights of 3–5 m. In addition, the proportions of ground hits and *only* echoes are clearly higher in the cells with moose damage. These types of differences were found from many other metrics, as well (see the results section of **Study IV**). However, when the ALS metrics were used to predict the level of browsing damage, the models suffered from false predictions. **Figure 9** shows an example of mapped predicted damage in relation to locations of confirmed damage.
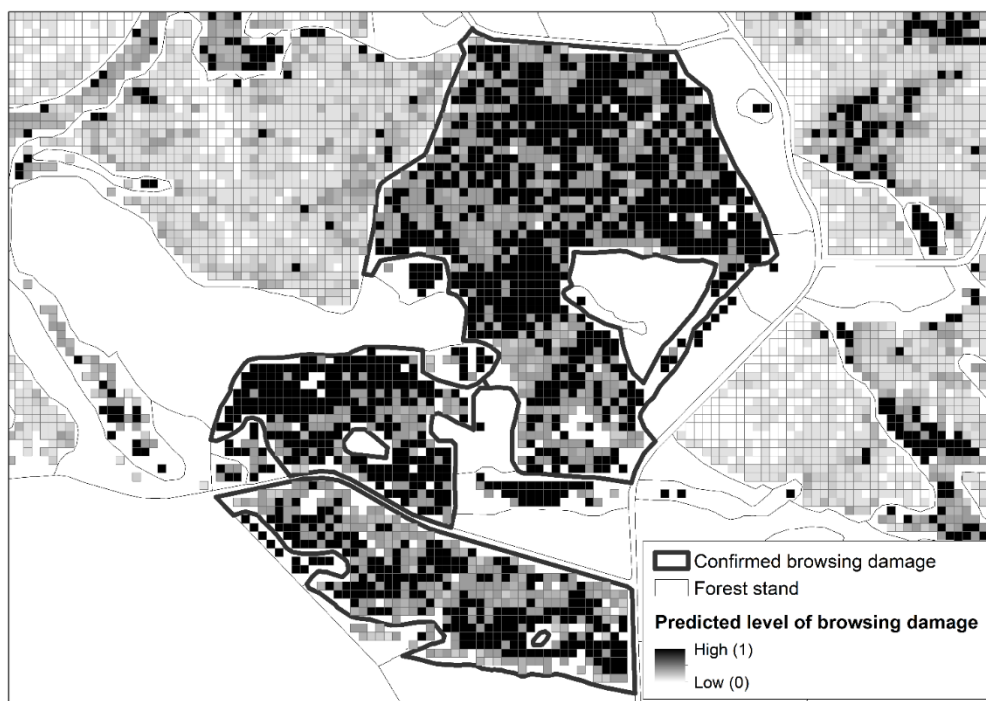
Figure 9. Predictions of moose damage overlaid with forest stands with and without damage. The predictions were the outcomes of the logistic regression; the values were converted to a scale of 0–1.

As seen from the image, the model was capable of finding "hotspots" of browsing damage, but the predictions were not this successful in other regions of the study area. The final model performed with a Kappa value of 0.28 and with an overall accuracy of 76%, which means that when classifying a damage/no-damage case, the model was correct 76% of the time.

Overall accuracy, however, does not indicate anything about what went wrong with the predictions: did the model predict healthy forests as damaged or vice versa? This question was answered by the ROC analysis. **Figure 10** shows the result of this analysis: the ROC curve. In this figure, the diagonal black line ($y = x$) represents random guessing; any point on its right-hand side (the lower-right triangle) is a result from a prediction that is worse than a random guess. Points in the upper-left triangle indicate performance that is better than a random guess. If they appear closer to the top-right corner, they can be thought of as "liberal": they make positive classifications with weak evidence (damage is predicted more easily). These kinds of cases would classify almost all the positives correctly (the actual damage), but they also have a high false positive rate (predicting damage where there is no damage). The points closer to the bottom-left corner are then "conservative": they only make positive classifications (damage predictions) with very strong evidence. Thus, they don't predict many false positives, but they also have a low true positive rate, as they may only catch a tiny percentage of the actual damage. A point exactly in the top-left corner would represent a perfect case with no errors on either side (see Fawcett 2006)
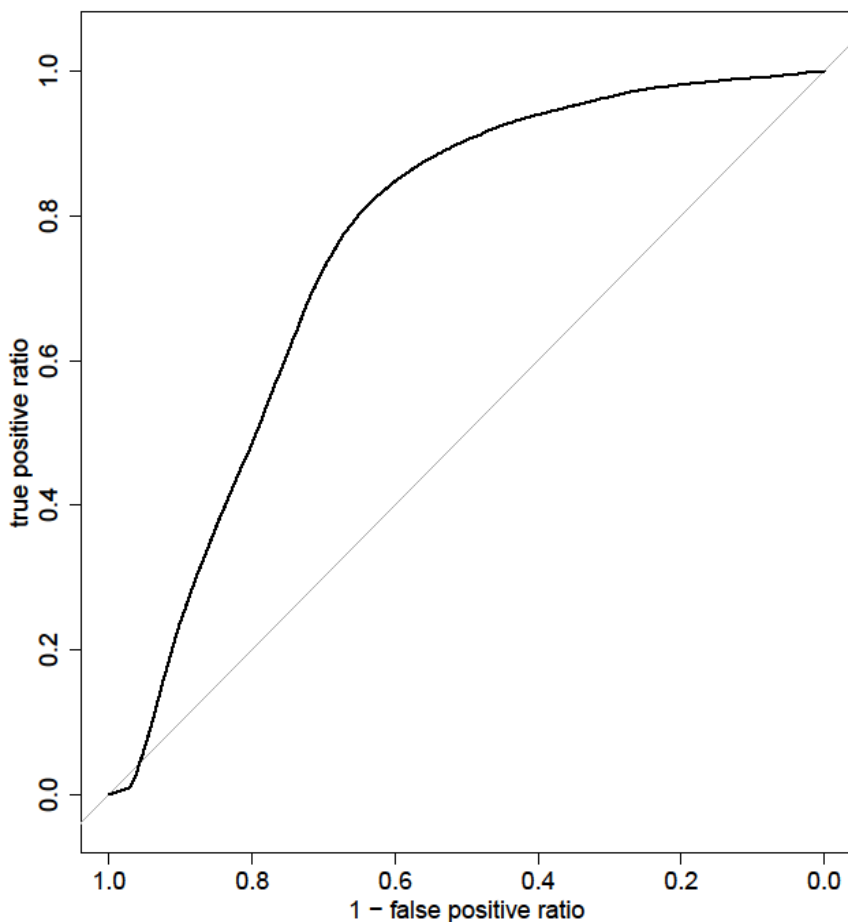
Figure 10. An image from the ROC analysis; the ROC curve.

One derivative of the ROC curve (**Figure 10**) is the AUC value. The AUC (area under a ROC curve) value indicates the probability that the classifier will rank a randomly chosen positive instance higher than a randomly chosen negative instance (Fawcett 2006). In this study, this means the probability of predicting damage in a damage cell instead of predicting it in a no-damage cell. The AUC value is always between 0 and 1. However, as the black "random guess" line has an AUC value of 0.5, a prediction is only worth something if it has an AUC > 0.5. Our classifier (the model) performed with an AUC value of 0.76 and a Cohen´s Kappa of 0.28. **Table 4** summarizes the model performance with some key figures.

Table 4. Performances of the model in **Study IV**. Error matrix showing the correct and incorrect classifications of a damage or no-damage cell.

Error Matrix	Damage	No-damage
Damage	6005	12625
No-damage	12625	83998

In the end, ROC analysis revealed the weakness of the model: predicting too many false positives. Although cases such as those in **Figure 9** showed that the model has potential, too many false positives are still being produced. **Figure 10** shows that if the false positive rate is reduced (moving to the left-hand side), prediction power for true positives is also lost, because when moving left along the ROC curve the values on the *y*-axis decrease (true positive rate). Consequently, maximizing the true positive rate is followed by a higher false positive rate.

5   DISCUSSION

5.1 Intro

The research for this thesis began in 2010 and at the time, the ALS data from National Land Survey was not freely available. This limited our study area to the west coast of Finland where we had also a small sample of GPS-collared moose. These moose were the only ones that at the time were occupying an area within the ALS coverage. This posed some limitations as the *n* of individuals was rather small (18). In addition, west Finland´s topography and landscape is highly different from the rest of the country and the area practically lack´s true natural predation. This makes it hard to generalize the results, but this is not a serious problem since the focus of this thesis was to test how well can moose behavior and habitat use be analyzed from ALS data and then to show that the data could be of additional value for moose- and wildlife research in general.

It is also known that many other attributes such as human presence, amount of mires and agriculture lands, roads etc. affect moose habitat use. It was a deliberate choice that these were left out from, for instance, the models of **Study III**. This decision may seem irrational at the first glance, because it obviously affected the performances of the models, which in many cases were only moderate (for instance the summer model of **Study I**) but the justification to do this was that we wanted to examine how well can ALS data describe and reveal known patterns in moose habitat use (for instance, thermal stress in **Study II**) and what kind of an additional value it could bring to the analysis. If we had chosen to build models including every possible variable about the landscape and human presence, the results would surely have been better and the models more accurate, but then the actual focus and aim of the thesis, to test and develop the use of ALS data, would have been left in the background. It is the work for the future, to incorporate ALS data in the habitat

suitability studies of moose and other wildlife species as this thesis now showed that the data holds significant information, definitely worthy of taking in account.

5.2 Forest structure and moose habitat use (Studies I–III)

The results of **Study I** were important, because they showed that ALS data can be used to analyze moose habitat use in the first place. In **Study I**, a basic method for studying this was developed and tested by integrating moose location data with ALS data. The research questions at this point were simple and aimed more at testing the capabilities of the method rather than gaining breakthroughs in moose ecology research. It was shown that moose select different habitats according to season (summer or winter) and that these habitats are distinguishable from one another through analysis based on ALS data. In addition, it was shown that even simple knowledge about the importance of forest structure (related to habitat use) can be used to model suitable areas in a given space, again with only ALS data. The habitat suitability modeling in **Study I** was more successful in winter, which is a direct consequence of moose ecology: during summer, moose move in larger areas and the used habitats do not differ significantly from the surrounding landscape (Nikula et al. 2004). During winter, however, clear differences were already noted when contrasting the structure of forests from moose locations to that of random locations. Here it was seen that the areas used by moose had significantly more ALS echoes coming from heights between two and eight meters, which is in line with the findings of previous studies (Cassing et al. 2006, Parker 2003). These are also the heights that provide the most winter food for moose (Parker & Morton 1978). In **Study I**, the analysis was done using all individuals, regardless of sex. The method that was used to model how suitable certain areas in landscape are (logistic regression) was commonly used in other ALS-ecology studies as well (**section 1.4**). Naturally, the predictive performance of the models would have been better if other features of the landscape would have been included in the models, but the point of **Study I** was to test whether data about forest structure alone can be used to identify patterns in moose habitat use. The answer seems to be yes, but the fact that ALS data alone can´t describe all the patterns in moose habitat use must be acknowledged.

In **Study II**, temperature was the factor assumed to affect moose behavior. The role that temperature plays in actual habitat use had not been studied with data sets holding information about the 3D structure of forests. The temperature data provided by FMI formed a unique study design in which the locations where the animals were during different temperatures were known along with information about the 3D structure of forests around these locations. The thresholds of thermal stress for moose, as suggested by Renecker and Hudson (1986), are −5°C during winter and 14°C during summer. Even the Finnish summers exceed this temperature throughout the day, so it is fair to assume that a thermoregulatory response of some sort takes place during the hottest days. According to the modelling, this was the case: moose did alter their behavior due to thermal stress, which was seen from the favoring of areas with high and dense canopies (thermal shelter). Van Beest et al. (2012) used 50 m × 50 m satellite image-based land cover maps and noted a temperature-induced trade-off in habitat use where moose searched for thermal shelters in mature coniferous forests and avoided open areas. The results of **Study II** supported this view, but the results also showed that the change in behavior happened only when air temperatures exceeded 20°C. The used thermal shelters were then characterized by high and dense canopies, the structure of which was assessed with sub-meter accuracy. In

addition, the results showed that the reaction to temperature was practically absent from moose living near the sea. Van Beest et al. (2012) discovered that the responses to thermal stress were strongest during daytime and twilight time. The results of **Study II** showed that the strongest favoring of thermal shelters happened during daytime, which means the hours of intense sunshine and highest temperatures. Similar results were also received by Dussault et al. (2004). The finding that the distance to nearest inland waterbody was insignificant could be explained by the fact that the inland waters of the study area are small ponds and in most cases located near mires, which means that their ability to offer cooling effect would not be good: when compared to e.g. mature spruce forests with significant shading effect the mires and mire ponds are hot environments especially during sunshine and were thus not used by moose for purposes of cooling. **Study II** proved that ALS data can be linked with different kinds of data sets in a useful manner. Given the current climate change scenarios, the results are very topical. The results should now be expanded to other locations to see how moose behave under thermal stress in different landscapes. This is vital, since the sea was noted to have an effect already in here. So, in order to thoroughly estimate the effects of temperature, data about moose habitat use would be needed from landscapes with more complex topography and with large lakes. Here, this was not a possible research question due to the data limitations (**section 5.1**).

In **Study III**, the external factor that ALS was linked to was not temperature, but time. Its effects on habitat use were analyzed throughout the whole year and separately during winter and the calving period. Moreover, the responses of males and females with and without calves were analyzed separately. This was necessary since many authors have noted differing patterns between the habitat use of males and females (Cederlund & Sand 1994, Nikula et al. 2004). Past studies have suggested that in different seasons, moose select habitats that are best at offering food or shelter against deep snow (Månsson 2009, Kittle et al. 2008). In **Study III**, this was proven by analyzing the structure of habitats used in different seasons (for instance, mature forests offering berries during autumn and seedling stands and young forests offering easy food in winter). The structural analysis of forests together with time also provided interesting insights into when the movements toward the next area happen. For instance, it was seen that the shift toward wintering areas in the study area began in November, which was proven by the clear change in the types of forests the animals were found in. The results also showed that the habitat use in mid-winter was a mixture of favoring both, food and shelter against deep snow (**Study III, Figure 5**). This was in accordance with the findings of Dussault (2002) and Dussault et al. (2005a,b), who found that moose increased their use of stands offering shelter, which were located in forest edges. The change from the wintering areas then seemed to take place in late March/early April.

As other moose went for their summer ranges, some were looking for calving grounds, which was the topic of greatest interest in **Study III** (the effect that newborn calves had on females' choice of habitat). Related to this, the timing of calving was also studied with results showing that females in the study area gave birth during the first half of May, most probably between May 3 and May 6, during which they favored areas without shrubs and understory vegetation. A week after calving, the areas with high amounts of shrubs were the ones mostly favored, which is linked to the growing need for food of both the mother (lactation) and the calf. This issue had not been studied before with an approach that can quantify the vegetation structure around the target animals. Past studies on this issue have been contradicting: views have been gained for both the use of open areas and the use of closed areas with more vegetation. For instance, Poole et al. (2007) found elevation to have

the biggest effect on calving site selection. The moose who climbed higher then selected areas with low amounts of vegetation and good visibility, whereas the moose who did not climb were selecting calving sites with dense vegetation. In Alaska, under heavy predation, the moose according to Bowyer et al. (1999) were selecting calving sites that had high variability in overstorey cover. They also noted that the number of various *Salix* species was almost twice as high in the calving sites than in the landscape in general. In a recent study, McGraw et al. (2014) noted that calving sites were more often (40%) located in bogs than in other soil types. The analysis of forest structure in our calving sites suggested the same, since a typical bog in the study area has practically zero shrubs, although the bogs do contain occasional pines to account for the very small canopy that was noted (**Study III, Figure 3**). In our study area, there is practically no predation and the bogs are also the areas that are the furthest away from roads, human settlements, or humans, which supports the view of McGraw et al. (2014). Furthermore, Thompson and Stewart (1998) suggested that cows apparently choose their calving site to avoid detection of their calves during and briefly after parturition. The sites where calving occurred in our study area would be ideal for this kind of a strategy.

In general, the results from **Studies I–III** showed that ALS can give more insights about animals' behavior and habitat use, because of the accurate descriptions of forest structure. The research questions posed in **Study III** can be definitely addressed more thoroughly in the fiture by incorporating ALS data with existing models about moose habitat use.

5.3 Moose browsing changing the forest structure (Study IV)

Study IV turned the scope away from how moose interact with their environment and focused instead on revealing how they affect their environment. However, before discussing the results, it is important to acknowledge that the damage in the study area was unusually severe, which made the research setting possible. Basically, the detected structural differences between the damage and no-damage areas could have been caused by three cases: 1.) Moose habitat selection: it selects habitats for winter that are, by default, different from the other areas. 2.) Moose modifies the structure of its winter habitat through browsing. 3.) Both of these cases.

Here, the cause can be reliably expected to be case nro 3: moose has preferred the areas, but the detected differences in structure were due to browsing. This is because of many reasons: the damage here was very severe and the ALS data was collected right after the damage. This means that the observed differences were very probably caused by moose browsing. After all, the areas after damage are not suitable winter habitats; they were suitable when the pines of the areas had the needles, the shoots, the twigs and the tree tops still attached. The preference was most likely related to the fact that the damage stands formed a large enough area that was able to offer enough food for the whole winter. The study area has very deep snow cover, which means that by favoring large seedling stands moose can minimize moving during winter and conserve energy, which they have been assumed to do (Singh et al. 2012, Pulliainen 1974). Also, it is very unlikely that the compared forests (damage and no-damage) were significantly different in structure before the browsing, because they are growing on similar soil types, are of similar site types and have been regenerated and maintained with similar methods throughout their history.

The results then clearly showed that by analyzing various ALS metrics, the loss of branches and twigs due to moose browsing can be detected (**Figures 7 and 8**). However,

the model performances in predicting the level of damage were modest: map-based analysis showed that the model was able to identify 'hotspots' of browsing, which in many cases agreed well with the locations of inspected damage. Similarly, many large areas without moose damage were clearly identified as no-damage areas. Yet, the model was only able to identify most of the actual damage when it was forced to overestimate the numbers of damage cells. This meant that as the model's performance in detecting actual damage increased, its rate of predicting false damage increased as well, which can be seen in the ROC curve (**Figure 10**). The model performance might have been weakened by the fact that the known browsing was counted as inspected damage only when it was severe enough. Thus, the model might have inputted no-damage cells that were actually damaged to some degree, but just not enough to be counted as 'damaged' by the authorities.

Future work in this area would require accurate field data taken from areas with various levels of damages and from areas with zero damage. The potential of using ALS and small field training data in detecting moose damage seems to be promising, especially since ALS-based forest inventories are being conducted in growing numbers. Each year, moose damage inventories are conducted by the authorities. These inventories consist of manual field work and manual estimations of the magnitude and extent of the damage. As was shown here, ALS data could be useful in identifying "hot-spots" of moose damage, which could then serve as indicators about the locations with definite large-scale and severe damage.

6   CONCLUSIONS

There is no doubt about the usefulness of ALS data in wildlife research. The data are practically unattainable by other means and hold detailed information about a target area's suitability for wildlife. In this thesis, ALS data were linked with the locations of a nationally important game species moose. It was shown that the habitat requirements of moose show significant variations according to season, although it was also shown that the patterns in habitat use differed between males and females. Furthermore, factors such as temperature or calving were shown to have additional effects on the favoring of certain types of forests. In addition, it was also shown that the known effect of moose on forest structure (browsing damage) can also be detected from ALS data. What is important is that this thesis used solely ALS data, but still significant patterns in habitat use were detected. This suggests that the possible co-use of ALS data with other datasets about the landscape could take the analysis of wildlife ecology a step or two forwards. Work et al. (2011) concluded that "*the utility of lidar will be borne out when the force of this data is realized through mechanistic hypotheses related to habitat requirements of plants and animals*". To fully analyze the habitat requirements, multiple data sources would definitely be required.

At the time of writing this paragraph, around 80% of Finland's land is covered in ALS data. Eventually, the coverage will include the whole country and the data will be re-collected in 10-year cycles. In Finland, many other ungulate species as well as their predators have already been equipped with GPS collars and the numbers are increasing. This makes the situation excellent for further research. Without a doubt, the combination of animal location data with 3D descriptions of the landscape and its vegetation will bring new information for wildlife research and management.

REFERENCES

Addison E. M., Smith J. D. McLaughlin R. F., Fraser D. J. H., Joachim, D. G. (1990). Calving sites of moose in central Ontario. Alces 26: 142–153.

Axelsson P. (2000). DEM generation from laser scanning data using adaptive TIN models. International Archives of Photogrammetry and Remote Sensing 33(B4): 110–117.

Balmford A., Bennun L., Brink B. T., Cooper D., Côté I. M., Crane P., Dobson A., Dudley N., Dutton I., Green R. E., Gregory R. D., Harrison J., Kennedy E. T., Kremen C., Leader-Williams N., Lovejoy T. E., Mace G., May R., Mayaux P., Morling P., Phillips J., Redford K., Ricketts T. H., Rodríguez J. P., Sanjayan M., Schei P. J., van Jaarsveld A. S., Walther B. A. (2005). Ecology: The Convention on Biological Diversity's 2010 target. Science 307: 212–213. doi: 10.1126/science.1106281

Bertram M. R., Vivion M. T. (2002). Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66(3): 747–756. doi: 10.2307/3803140

Bjorneraas K , Solberg E.J., Herfindal I., Van Moorter B., Rolandsen C.M., Tremblay J.P., Skarpe C., Saether B.E., Eriksen R., Astrup, R. (2011). Moose (Alces alces) habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17: 44-54. doi: http://dx.doi.org/10.2981/10-073

Bogomolova E. M., Kurochkin Y. A. (2002). Parturition activity of moose. Alces, Suppl. 2: 27–31.

Bowyer T. B., Kie J. G., van Ballenberghe V. (1998). Timing and synchrony of parturition in Alaskan moose: Long-term versus proximal effects of climate. Journal of Mammalogy 79(4): 1332–1344. doi: 10.2307/1383025

Bowyer T. B., van Ballenberghe V., Kie J. G., Maier A. K. (1999). Birth-site selection by Alaskan moose: Maternal strategies for coping with a risky environment. Journal of Mammalogy 80(4): 1070–1083. doi: 10.2307/1383161

Brokaw N., Lent R. (1999). Vertical structure. In M. L. Hunter Jr. (Ed.), Maintaining Biodiversity in Forest Ecosystems (pp. 373–399). Cambridge University Press, Cambridge.

Cagnacci F., Boitani L., Powell R. A., Boyce M. S. (2010). Animal ecology meets GPS-based radio telemetry: A perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society of London B 365: 2157–2162. doi: 10.1098/rstb.2010.0107

Cassing G., Greenberg L. A., Mikusiński G. (2006). Moose (Alces alces) browsing in young forest stands in central Sweden: A multiscale perspective. Scandinavian Journal of Forest Research 21(3): 221–230. doi: 10.1080/02827580600673535

Cederlund G., Sand H. (1994). Home-range size in relation to age and sex in moose. Journal of Mammalogy 75(4): 1005–1012. doi: 10.2307/1382483

Chekchak T., Courtois R., Ouellet J. P., Breton L., St-Onge S. (1998). Caractéristiques des sites de mise bas de l'orignal (Alces alces) [Characteristics of moose (Alces alces) calving sites]. Canadian Journal of Zoology 76(9): 1663–1670. doi: 10.1139/z98-096

Clawges R., Vierling K., Vierling L., Rowell E. (2008). The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen forest. Remote Sensing of Environment 112(5): 2064–2073. doi:10.1016/j.rse.2007.08.023

Coops N. C., Duffe J., Koot C. (2010). Assessing the utility of lidar remote sensing technology to identify mule deer winter habitat. Canadian Journal of Remote Sensing 36(2): 81–88. doi: 10.5589/m10-029

Davis J. W. (1983). Snags are for wildlife. In J. W. Davis, G. A. Goodwin, and R. A. Ockenfels (Eds.), Snag Habitat Management: Proceedings of the Symposium on (pp. 4–9). USDA Forest Service General Technical Report, RM-99.

Davies A. B., Asner G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology & Evolution 29(12): 681–691. doi: http://dx.doi.org/10.1016/j.tree.2014.10.005

Dettki H., Löfstrand R., Edenius L. (2003). Modeling habitat suitability for moose in coastal northern Sweden: Empirical vs process-oriented approaches. Ambio 32(8): 549–556.

Douglas-Hamilton I. (1998). Tracking African elephants with a global positioning system (GPS) radio collar. Pachyderm 25: 81–92.

Dueser R. D., Shugart Jr. H. H. (1978). Microhabitats in a forest-floor small mammal fauna. Ecology 59(1): 89–98.

Dussault C. (2002). Influence des Contraintes Environnementales sur la Sélection de l'Habitat de l'Orignal (Alces alces). Ph.D. thesis, Université Laval, Québec, Canada.

Dussault C., Oullet J.-P., Courtois R., Huot J., Breton L., Larochelle J. (2004). Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11(3): 321–328.

Dussault C., Ouellet J.-P. Courtois R., Huot J., Breton L., Jolicoeur H. (2005a). Linking moose habitat selection to limiting factors. Ecography 28(5): 619–628.

Dussault C., Courtois R., Ouellet J.P., Girard I. (2005b). Space use of moose in relation to food availability. Canadian Journal of Zoology 83:1431–1437. doi:10.1139/z05-140.

Edenius L. (1997). Field test of a GPS location system for moose (Alces alces) under Scandinavian boreal conditions. Wildlife Biology 3: 39–43.

Environmental Protection Agency. 2015. CORINE (Co-ORdinated INformation on the Environment). Available at: http://www.epa.ie/soilandbiodiversity/soils/land/corine/#. VBFTTWPisik (Accessed September 11, 2014).

Fawcett T. (2006). An introduction to ROC analysis. Pattern Recognition Letters, 27(8), 861–874. doi:10.1016/j.patrec.2005.10.010

Flaherty S., Lurz P., Patenaude G. (2014). Use of LiDAR in the conservation management of the endangered red squirrel (Sciurus vulgaris L.). Journal of Applied Remote Sensing (8)1. http://dx.doi.org/10.1117/1.JRS.8.083592

Fryxell J.M, Sinclair A.R.E. (1988). Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3: 237-241. doi: 10.1016/0169-5347(88)90166-8

Glenn E. M., Ripple W. J. (2004). On using digital maps to assess wildlife habitat. Wildlife Society Bulletin 32(3): 852–860.

Gottschalk T.K., Huettmann F., Ehlers M. (2005). Thirty years of analyzing and modeling avian habitat relationships using satellite imagery data: a review. International Journal of Remote Sensing 26: 2631-2656. doi:10.1080/01431160512331338041

Graf R. F., Mathys L., Bollmann K. (2009). Habitat assessment for forest dwelling species using LiDAR remote sensing: Capercaillie in the Alps. Forest Ecology and Management 257(1): 160–167. doi:10.1016/j.foreco.2008.08.021

Haydn A. (2012). Calving site selection by moose (Alces alces) along a latitudinal gradient in Sweden. Master's thesis. University of Natural Resources and Life Sciences (BOKU), Vienna, Austria.

Hebblewhite M., Haydon D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society of London B 365: 2303–2312. doi: 10.1098/rstb.2010.0087

Heikkilä R. (1990). Effect of plantation characteristics on moose browsing on Scots pine. Silva Fennica 24(4): 341–351.

Heikkilä R. (1994). Moose (Alces alces) feeding in relation to the characteristics of winter habitats and the damage in young stands. The Finnish Forest Research Institute, Research Paper No. 486.

Hilden O. (1965). Habitat selection in birds. Annales Zoologici Fennici 2: 53-75.

Hill R.A., Hinsley S.A., Gaveau D.L.A., Bellamy P.E. (2004). Predicting habitat quality for Great Tits (Parus major) with airborne laser scanning data. International Journal of Remote Sensing 25(22). doi:10.1080/0143116031000139962

Hill R. A., Hinsley S. A., Broughton R. K. (2014). Assessing habitats and organism–habitat relationships by airborne laser scanning. In M. Maltamo, E Næsset, and J. Vauhkonen (Eds.), Forestry Applications of Airborne Laser Scanning: Concepts and Case Studies (pp. 335–356). Springer Netherlands, Dordrecht, The Netherlands.

Hjeljord O., Hövik N., Pedersen H. B. (1990). Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Ecography 13(4): 281–292.

Holmes K. R., Nelson T. A., Coops N. C., Wulder M. A. (2013). Biodiversity indicators show climate change will alter vegetation in parks and protected areas. Diversity 5(2): 352–373. doi:10.3390/d5020352

Jachowski D.S., Singh N.J. (2015). Toward a mechanistic understanding of animal migration: incorporating physiological measurements in the study of animal movement. Conservation Physiology 3: doi:10.1093/conphys/cov035.

James F. C. (1971). Ordinations of habitat relationships among breeding birds. The Wilson Bulletin 83(3): 215–236.

Keech M. A., Bowyer R. T., Ver Hoef J. M., Boertje R. D., Dale B. W., Stephenson T. R. (2000). Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64(2): 450–462.

Kielland K., Bryant J. P. (1998). Moose herbivory in taiga: effects on biochemistry and vegetation dynamics in primary succession. Oikos 82: 377–383.

Kittle A. M., Fryxell J. M., Desy G. E., Hamr J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157(1): 163–175. doi: 10.1007/s00442-008-1051-9

Korhonen L., Korpela I., Heiskanen J., Maltamo M. (2011). Airborne discrete-return LiDAR data in the estimation of vertical canopy cover, angular canopy closure and leaf area index. Remote Sensing of Environment 115(4): 1065–1080. doi:10.1016/j.rse.2010.12.011

Krausman P. (1999). Some Basic Principles of Habitat Use. In 'Grazing Behavior of Livestock and Wildlife.' (Eds K Launchbaugh, K Sanders and J Mosley) pp. 85-90. University of Idaho: Moscow, USA.

Lääperi A., Löyttyniemi K. (1988). Moose (Alces alces) damage in pine plantation established during 1973–1982 in the Uusimaa-Häme Forestry Board District. Folia Forestalia 719.

Lefsky M. A., Cohen W. B., Parker G. G., Harding D. J. (2002). Lidar remote sensing for ecosystem studies. Bioscience 52(1): 19–30. doi: 10.1641/0006-3568(2002)052[0019:LRSFES]2.0.CO

Lone K., van Beest F.M., Mysterud A., Gobakken T., Milner J. M., Ruud H.-P., Loe L. E. (2014). Improving broad scale forage mapping and habitat selection analyses with airborne laser scanning: The case of moose. Ecosphere 5(11): art144.

Lowe S.J., Patterson B.R., Schaefer J.A. (2010) Lack of behavioral responses of moose (Alces alces) to high ambient temperatures near the southern periphery of their range. Canadian Journal of Zoology, 88, 1032‑1041. doi: 10.1139/Z10-071

Löyttyniemi K., Piisilä N. (1983). Moose (Alces alces) damage in young pine plantations in the Forestry Board District Uusimaa-Häme. Folia Forestalia 553.

Lykkja O.N., Solber E.J., Herfindal I., Wright J., Rolandsen C.M., Hanssen M.G. (2009). The effects of human activity on summer habitat use by moose. Alces 45: 109-124.

MacArthur R. H., MacArthur J. W. (1961). On bird species diversity. Ecology 42(3): 594–598.

Maltamo M., Eerikäinen K., Packalén P., Hyyppä J. (2006). Estimation of stem volume using laser scanning-based canopy height metrics. Forestry 79(2): 217–229. doi: 10.1093/forestry/cpl007

Manly B.F.J., McDonald L.L., Thomas D.L. (2002). Resource selection by animals: statistical design and analysis for field studies. Secaucus, NJ, USA. Kluwer Academic Publishers.

Martinuzzi S., Vierling L. A., Gould W. A., Falkowski M. J., Evans J. S., Hudak A. T., Vierling K. T. (2009). Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. Remote Sensing of Environment 113(12): 2533–2546. doi:10.1016/j.rse.2009.07.002

Mason T.H.E., Stephens P.A., Apollonio M., Willis S.G. (2014). Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. Global Change Biology 20(12): 3872–3882. doi: 10.1111/gcb.12641

McGraw A.M., Terry J., Moen R. (2014). Pre-parturition movement patterns and birth site characteristics of moose in northeast Minnesota. Alces 50, 93–103.

McInnes P. F., Naiman R. J., Pastor J., Cohen Y. (1992). Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royal, Michigan USA. Ecology 73: 2059–2075. http://dx.doi.org/10.2307/1941455

METLA. (2013). Finnish National Forest Inventory. Available at: http://www.metla.fi/ ohjelma/vmi/vmi-moni-en.htm (Accessed January 1, 2013).

Michaud J.-S., Coops N. C., Andrew M. E., Wulder M. A., Brown G. D., Rickbeil G. J. M. (2014). Estimating moose (Alces alces) occurrence and abundance from remotely derived environmental indicators. Remote Sensing of Environment 152: 190–201. doi:10.1016/j.rse.2014.06.005

Ministry of Agriculture and Forestry. 2009. Game Animal Damages Act. 105/2009. Available at: http://www.finlex.fi/en/laki/kaannokset/2009/en20090105 (Accessed June 1, 2015).

Morrison M.L., Marcot B.G., Mannan W.R. (2006). Wildlife-Habitat Relationships: concepts and applications. Washington, DC, USA: Island Press.

Månsson J. (2009). Environment variation and moose Alces alces density as determinants of spatio-temporal heterogeneity in browsing. Ecography 32(4): 601–612. doi: 10.1111/j.1600-0587.2009.05713.x

Müller J., Vierling K. (2014). Assessing biodiversity by airborne laser scanning. In M. Maltamo, E Næsset, and J. Vauhkonen (Eds.), Forestry Applications of Airborne Laser Scanning: Concepts and Case Studies (pp. 357–374). Springer Netherlands, Dordrecht, The Netherlands.

Næsset E. (2002). Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. Remote Sensing of Environment 80(1): 88–99. doi:10.1016/S0034-4257(01)00290-5

Nathan R., Getz W.M., Revilla E., Holyoak M., Kadmon R., Saltz D., Smouse P.E. (2008). A movement ecology paragidm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105: 19052-19059. doi: 10.1073/pnas.0800375105

Neumann W. (2009). Moose Alces alces behavior related to human activities. PhD Thesis, Swedish University of Agricultural Sciences, Umeå.

Nikula A., Heikkinen S., Helle E. (2004). Habitat selection of adult moose Alces alces at two spatial scales in central Finland. Wildlife Biology 10(2): 121–135.

Packalén P., Maltamo M. (2006). Predicting the plot volume by tree species using airborne laser scanning and aerial photographs. Forest Science 52(6): 611–622.

Packalén P., Maltamo M., Tokola, T. (2008). Detailed assessment using remote sensing techniques. In K. von Gadow and T. Pukkala (Eds.), Designing Green Landscapes, Managing Forest Ecosystems Series, Volume 15, Part 2 (pp. 53–77). Springer Netherlands, Dordrecht, The Netherlands.

Palminteri S., Powell G.V.N., Asner G.P., Peres, C.A. (2012). LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate. Remote Sensing of Environment 127: 98-105. doi:10.1016/j.rse.2012.08.014

Parker G. (2003). Status report on the Eastern Moose (Alces alces americana Clinton) in mainland Nova Scotia. Report for Nova Scotia Department of Natural Resources, Nova Scotia, Halifax, Canada.

Parker G. R., Morton L. D. (1978). The estimation of winter forage and its use by moose on clearcuts in northcentral Newfoundland. Journal of Range Management 31(4): 300–304.

Pinherio J. C., Bates D. M. (2004). Mixed-Effects Models in S and S-PLUS, Statistics and Computing Series. Springer, New York, NY.

Poole K. G., Serrouya R., Stuart-Smith K. (2007). Moose calving strategies in interior Montane ecosystems. Journal of Mammalogy 88(1): 139–150. http://dx.doi.org/10.1644/06-MAMM-A-127R1.1

Pulliainen E. (1974). Seasonal movements of moose in Europe. Naturaliste Canadien, 101, p. 379–392.

R Core Team. (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramsey III E. W., Chappell D. K., Baldwin D. G. (1997). AVHRR imagery used to identify hurricane damage in a forested wetland of Louisiana. Photogrammetric Engineering & Remote Sensing 63(3): 293–297.

Ramsey III E. W.m, Sapkota S. K., Barnes F. G., Nelson G. A. (2002). Monitoring the recovery of Juncus roemerianus marsh burns with the normalized difference vegetation index and Landsat Thematic Mapper data. Wetlands Ecology and Management 10(1): 85–96.

Renecker L. A., Hudson R. J. (1986). Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64(2): 322–327. doi: 10.1139/z86-052

RKTL (2011). Data about Finland's moose populations. Available at: http://www.rktl.fi/riista/riistavarat/hirvi_vuonna.html (accessed January 2013).

Rodgers A. R., Rempel R. S., and Abraham K. F. (1996). A GPS-based telemetry system. Wildlife Society Bulletin 24(3): 559–566.

Rotenberry J. T. (1985). The role of habitat in avian community composition: Physiognomy or floristics? Oecologia 67:213–17.

Sæther B.-E., Andersen R. (1990). Resource limitation in a generalist herbivore, the moose Alces alces: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68, 993-999. doi: 10.1139/z90-143

Saveraid E. H., Debinski D. M., Kindscher K., Jakubauskas M. E. (2001). A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA. Landscape Ecology 16(1): 71–83.

Schwartz C. C., Arthur S. M. (1999). Radiotracking large wilderness mammals: Integration of GPS and Argos technology. Ursus 11: 261–273.

Shepard D. (1968). A two-dimensional interpolation function for irregularly-spaced data. In Proceedings of the 23rd ACM National Conference (ACM '68), August 27–29, 1968, New York, NY, USA, pp. 517–524.

Singh N. J., Börger L., Dettki H., Bunnefeld N., Ericsson G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22(7): 2007–2020. doi: http://dx.doi.org/10.1890/12-0245.

Swardson G. (1949). Competition and habitat selection in birds. Oikos 1: 157-174.

Swedish University of Agricultural Sciences. (2011). WRAM (Wireless Remote Animal Monitoring). Available at: http://www.slu.se/WRAM/ (Accessed September 21, 2010).

Thompson I.D., Stewart R.W. (1998). Management of moose habitat. In Ecology and management of the North American moose. Edited by A.W. Franzmann and C.C. Schwartz. Smithsonian Institution Press, Washington, D.C. pp. 173–221.

Tremblay J-P., Solberg E.J., Saether B-E., Heim M. (2007). Fidelity to calving areas in moose (Alces alces) in the absence of natural predators. Canadian Journal of Zoology 85(8): 902-908. doi: 10.1139/Z07-077

van Beest F. M., Milner J. M. (2013). Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. PLoS ONE 8(6): e65972. doi: 10.1371/journal.pone.0065972

van Beest F. M., Van Moorter B., Milner J. M. (2012). Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84(3): 723–735. doi:10.1016/j.anbehav.2012.06.032

van Beest F.M., Rivrud I.M., Loe L.E., Milner J.M., Mysterud A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology, http://dx.doi.org/10.1111/j.1365-2656.2011.01829.x.

Vauhkonen J., Tokola T., Packalén P., Maltamo M. (2009). Identification of Scandinavian commercial species of individual trees from airborne laser scanning data using alpha shape metrics. Forest Science 55(1): 37–47.

Venier L. A., Pearce J. L. (2007). Boreal forest landbirds in relation to forest composition, structure, and landscape: Implications for forest management. Canadian Journal of Forest Research 37(7): 1214–1226. doi: 10.1139/X07-025

52

Vierling K. T., Vierling L. A., Gould W. A., Martinuzzi S., Clawges R. M. (2008). Lidar: Shedding new light on habitat characterization and modeling. Frontiers in Ecology and the Environment 6(2): 90–98. http://dx.doi.org/10.1890/070001

Wehr A., Lohr U. (1999). Airborne laser scanning—An introduction and overview. ISPRS Journal of Photogrammetry and Remote Sensing 54(2–3): 68–82. doi:10.1016/S0924-2716(99)00011-8

Westoby M. (1974). An analysis of diet selection by large generalist herbivores. American Naturalist 112: 627-631.

Wiens J. A. (1969). An approach to the study of ecological relationships among grassland birds. Ornithological Monographs no. 8. Lawrence, KS: Allen Press.

Work T. T., St Onge B., Jacobs J.M. (2011). Response of female beetles to LIDAR derived topographic variables in Eastern boreal mixedwood forests (Coleoptera, Carabidae). ZooKeys, 147, 623–639. doi: 10.3897/zookeys.147.2013