

Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2015:5

LiDAR, habitat structure and the ecology of ungulates in a landscape of fear

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eit landskap av frykt

Karen Lone

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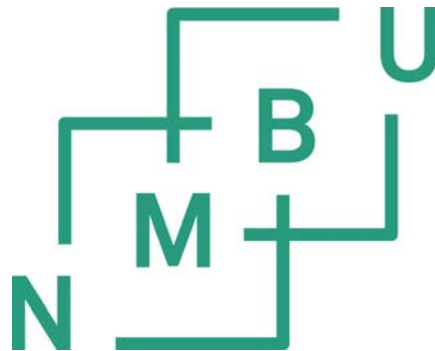
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Ås 2014



Thesis number 2015:5
ISSN 1894-6402
ISBN 978-82-575-1262-0

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Acknowledgements

I would like to thank my three great supervisors Leif Egil Loe, Terje Gobakken and Atle Mysterud for their support and guidance throughout my PhD project in the last three years. Leif Egil, your methodological expertise, scientific insight and enthusiasm make you the perfect collaborator and great mentor. If I had a question or needed to talk through something, your door was always open, and having that support and feedback when I needed it was incredibly important. Terje, thank you for laying the foundation for me to be able to work with LiDAR data in this thesis: getting hold of the datasets I needed, teaching me how to work with this data. Atle, thanks for useful discussions on study designs and research questions, and particularly for helping me develop my writing. Each of you is an inspiration to me.

A big thank you to all my coauthors on the papers included in this thesis. It was a pleasure to collaborate with you. You have willingly shared data, responded quickly and contributed constructively in the publication process. John Odden and John Linnell at NiNA and the project Scandlynx shared data on lynx kill sites, roe deer pellet transects and tracks from GPS-collared roe deer. Jos Milner and Floris van Beest shared forage survey data and moose GPS-tracking data originally collected by the Moose – Forage Project at HiHm, and set up the habitat selection analyses for the moose paper. Thanks to Atle at UiO and Erling Meisingset at Bioforsk Tingvoll for sharing data from GPS-collared red deer from the projects HjortAreal and TickDeer. The LiDAR data used in this study were collected by the Norwegian Mapping Authority for other purposes, and made available for our scientific use free of charge. Thanks to Jørgen Remmen, Tore Olsen, Karen Johanne Gulsvik, Jørgen Kvernhaugen Norum, Hans-Petter Ruud and Inga Stamnes for collecting field data in connection with my project or working with these data as part of their MSc theses.

I would like to thank my fellow PhD-students and other colleagues at INA for creating an open and good learning and working environment, and many useful discussions. I have enjoyed my dual membership of the Ecology and the SkogROVER research groups, which has been socially and academically rewarding. Finally, I would like to thank past and current flat mates and neighbors at Norderås, friends and family for great company and fun during the last three years. Daniel, thank you for being there for me through my PhD-project period in the south.

I gratefully acknowledge that the financial support for my PhD project was provided by my home institution, The Norwegian University of Life Sciences.

Ås, December 2014

Karen Lone

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Papers I to IV

Boxes:

1. A short introduction to LiDAR technology (page 16)
2. Choice and rationale of methods (page 25)

List of original papers:

Paper I

Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Mysterud. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123:641-651. <http://dx.doi.org/10.1111/j.1600-0706.2013.00938.x>

Paper II

Lone, K., A. Mysterud, T. Gobakken, J. Odden, J. D. Linnell, and L.E. Loe. Temporal variation in habitat selection breaks the catch-22 of contrasting predation risk by multiple predators. Manuscript.

Paper III

Lone, K., L. E. Loe, E. L. Meisingset, I. Starnes, and A. Mysterud. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*. <http://dx.doi.org/10.1016/j.anbehav.2015.01.012>

Paper IV

Lone, K., F. M. van Beest, A. Mysterud, T. Gobakken, J. M. Milner, H.-P. Ruud, and L. E. Loe. 2014. Improving broad scale forage mapping and habitat selection analyses with airborne laser scanning: the case of moose. *Ecosphere* 5:144. <http://dx.doi.org/10.1890/ES14-00156.1>

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Abstract

The expression ‘landscape of fear’ describes a situation in which prey behavior and space use across the landscape are shaped by spatial and temporal patterns in predation risk. Yet such behavioral and indirect effects of predation have been much less studied than its numerical and direct effects. One of the challenges in doing so is characterizing habitat at the resolution and extent necessary to effectively study this at the landscape level. In this thesis, I investigated the spatial risk patterns created by natural predators and human hunting and how these two predators influence the habitat selection and ecology of forest ungulates (roe deer, red deer, and moose) across several study systems in Norway.

I used airborne LiDAR (light detection and ranging), an emerging technology, to obtain detailed data on habitat structure over large scales. The three-dimensional LiDAR data were used to 1) elucidate how understory vegetation density, canopy cover, and other habitat characteristics modify predator-prey interactions and 2) predict wildlife forage availability. Whereas structural information from LiDAR was sufficient to model predation risk from lynx and hunters well, it needed to be integrated with auxiliary data, particularly plant species information, to predict forage satisfactorily.

Most studies address a situation with only a single prey-predator pair. Yet, with recolonization of large carnivores, ungulates are frequently facing multiple predators with contrasting hunting styles. An example of such an understudied multiple-predator situation is the roe deer in southern Norway facing two predators (lynx and humans). I documented how these predators create contrasting risk patterns due to their different hunting methods, as lynx risk increased and hunting risk decreased with increasing understory cover. I discussed how this could lead to lower non-consumptive effects of predation in such systems compared to systems with a single predator. Against this background, I investigated dynamic responses in space use to temporally structured predation risk. Diurnal and seasonal variation was studied in roe deer, and adaptive responses to the onset of hunting were studied in a heavily hunted, but otherwise predator-free red deer population. Roe deer shifted their habitat selection towards safer areas during periods of high predator activity, but have a weaker response, possibly no response, to lynx risk during winter. The latter is likely due to harsh winter conditions leading to a more severe trade-off between safety and energetic considerations that constrained roe deer habitat selection during this season. In the study on red deer, deer that were shot during the following hunting season differed from survivors in their habitat use. Whereas all males used similar habitat in the days before the hunting season, the onset of

hunting induced an immediate switch to habitat with more concealing cover in surviving males, but not in males that were later shot. Responding to the onset of hunting appeared to be adaptive, given that it was linked to increased survival, an important fitness component. A final case study expanded habitat characterization to include forage availability and related moose habitat selection to forage and two LiDAR variables capturing variation in concealment and thermal conditions: understory cover and canopy cover. All three functional gradients were important for moose habitat selection on landscape and home range scales, both during winter and summer. Including habitat structural characteristics directly derived from LiDAR datasets in habitat selection studies can be meaningful and successful, while also requiring less effort than alternative predictive approaches.

This thesis elucidates the spatial patterns and temporal nature of spatial antipredator responses in ungulates, and the importance of trade-offs in that regard. My work demonstrates possible applications of LiDAR-derived data on habitat structure to ecological studies at large scales. It establishes that hunters and carnivores impact Norwegian forest ungulates not only numerically, but also behaviorally by creating a 'landscape of fear'. The magnitude of indirect effects of human and natural predators on prey populations and the question of whether predation and hunting cause behaviorally mediated trophic cascades deserve further attention.

Samandrag

Uttrykket «landskap av frykt» skildrar ein situasjon der åtferda og den romlege habitatbruken til byttedyr vert forma av mønster i predasjonsrisiko i tid og rom. Slike åtferdsmessige og indirekte effektar av predasjon har ikkje blitt studert i like stor grad som numeriske og direkte effektar. Ei av utfordringane med å studere dette på landskapsskala har vore evna til å karakterisere habitat over store områder med høg resolusjon. Denne avhandlinga tar for seg dei romlege risikomønstera som skapast av eit naturleg rovdyr og av menneskeleg jakt og korleis desse to funksjonelle predatorane påverkar habitatseleksjonen og økologien til skoglevande hjortevilt (rådyr, hjort og elg) i tre studiesystem i Noreg.

Eg bruka nyvinninga flyboren LiDAR (light detection and ranging) til å samle data om habitatstruktur på stor skala. Dei tredimensjonale LiDAR dataa vart bruka til å 1) belyse korleis tettleiken av undervegetasjon, kronedekke og andre trekk ved eit habitat verkar inn på byttedyr-rovdyr vekselverknader, og 2) predikere beitetilgang for vilt. Strukturinformasjon frå LiDAR var tilstrekkeleg for å modellere predasjonsrisiko frå gaupe og jegerar. Derimot måtte LiDAR brukast i lag med andre datakjelder, fortrinnsvis informasjon om dominerande treslag, i prediksjonen av tilgjengeleg beite.

Dei fleste studiar tek for seg eitt einskild byttedyr-rovdyr par. Når store rovdyr no re-etablerer seg i mange områder vil fleire byttedyr måtte ta stilling til fleire rovdyr som jaktar på dei med ulike taktikkar. Eit eksempel på ein slik understudert multi-predator situasjon er rådyr i Sør-Noreg, der dei har to predatorar (gaupe og menneske). Eg dokumenterte at dei ulike jaktmetodane til desse to rovdyra førte til motstridande risikomønstre for rådyra. Risikoen for å bli drepen av gaupe auka med tettleiken av undervegetasjon, medan risikoen for å bli drepen av jeger minka. Det kan på grunnlag av dette syntest som at indirekte effektar av predasjon vil vere mindre viktig i system med fleire rovdyr, enn i system med færre, eller berre eitt rovdyr. På grunnlag av dei romlege risikomønstra har eg undersøkt dynamiske endringar i habitatbruk som følgje av risikomønstre i tid. Døger- og sesongvariasjonar vart studerte for rådyr og adaptive responsar til starten av jaktseasonen vart studerte i ein hjortebestand som hadde høgt jakttrykk og var praktisk sett fri for anna predasjon. Rådyr endra habitatbruken sin slik at dei bruka områder med låg risiko i den tidsperioden predatoren var mest aktiv. Unntaket var vinterstid, då tilpassa rådyret seg gaupa i mindre grad, kanskje ikkje i det heile. Dette var sannsynlegvis grunna tøffe vinterforhold som førte til at avveginga mellom risikoreduksjon og energetiske omsyn var meir kostbar enn i dei andre sesongane, og dette avgrensa rådyrets habitatseleksjon i denne sesongen. I hjortestudiet vart det klart at habitatbruken til dyr som

overlevde jaktsesongen det året skilde seg frå habitatbruken til dei som vart skotne. Alle bukkane bruka likt habitat i dagane forut for jaktstart, men habitatbruken rett etter jaktstart var ulik: bukkar som overlevde jakta hadde tatt i bruk habitat med meir skjul, medan dei bukkane som seinare vart skotne ikkje hadde endra habitatbruken sin. Denne responsen på jaktstart syntest å vere adaptiv, i og med at det var ein klar samanheng med overleving, som ein saman med reproduksjon er avgjerande for individuell fitness. I det siste studiet utvida eg habitatkarakteristikken til å omfamne også tilgjengeleg mengde beite, og undersøkte korleis habitatbruk hos elg avhenger av beite og to LiDAR variablar som fangar opp variasjon i skjul og temperaturforhold: tettleik av undervegetasjon og kronedekke. Alle desse tre funksjonelle habitatgradientane var viktige for å forklare habitatseleksjonen til elg sommar og vinter, både på heimeområdeskala og landskapsskala. I tillegg til å vere enklare enn å først predikere ein bakkemålt eigenskap, gjev det god meining og gode resultat å inkludere habitatstrukturvariablar som er direkte utrekna frå LiDAR data i studiar av habitatseleksjon.

Denne avhandlinga belyser romlege mønster og tidsaspekt ved romleg antipredasjonsåtfærd hos hjortevilt, og den viktige rolla avvegingar spelar for dette. Mitt arbeid demonstrerer nokre måtar å bruke habitatstrukturinformasjon frå LiDAR-data i økologiske studiar på stor skala. Det slår fast at jegerar og rovdyr påverkar åtfærd til norsk hjortevilt gjennom «landskap av frykt», og ikkje berre bestandsstorleiken gjennom drap. Storleiken på dei indirekte effektane av menneskeleg jakt og naturlege rovdyr og spørsmålet om predasjon og jakt forårsakar kaskade-effektar i næringskjeda er verdt å forske vidare på.

Synopsis

“During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain mating and thus realize no reproductive success, but in the long term, the day’s shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator; being killed greatly reduces future fitness”

Lima and Dill, 1990

“Whatever else may be said about predation, it does draw attention”

Paul Errington, 1946

Introduction

Indirect effects of predation

Predation is a ubiquitous phenomenon in nature that has been intensively studied. Starting with the work of Lotka and Volterra (Lotka 1925, Volterra 1928), predator-prey interactions have largely focused on consumptive effects. However, predation can have consequences beyond the direct numerical effects on prey populations; prey commonly use behavioral or morphological defenses against predation (Lima and Dill 1990, Bourdeau and Johansson 2012). Prey may reduce or manage risk by adaptations that make them undesirable as prey or less vulnerable to predation, for instance porcupines with their spines, species synthesizing or sequestering toxins, or species mimicking another species that is toxic. Desirable prey can alter their behavior to avoid encounters with predators, or to improve their chances of surviving an encounter with a predator (Lima and Dill 1990, Hebblewhite et al. 2005). Factors influencing the latter would be increasing group size, being more vigilant, and using escape behavior (Roberts 1996, Seamone et al. 2014). Decreasing movement rates can reduce chances of encountering predators (Alós et al. 2012), while habitat selection can influence both stages of the predation process, both encounter rate and survival chances following an encounter (Hebblewhite et al. 2005, Atwood et al. 2009), as it affects the effectiveness of other risk-management behaviors such as vigilance and escape (Heithaus et al. 2009).

Spatial patterns in risk between different habitat types can give rise to ‘landscapes of fear’, if prey detect this variation in risk and modify their behavior in response (Laundré et al. 2001). The term was coined to explain the spatial nature of behavioral changes by elk, *Cervus elaphus canadensis*, in Yellowstone following the reintroduction of wolves, *Canis lupus*. Elk became more vigilant and shifted habitat use away from open areas and into forests, and as a result decreased the quality of their diet (Laundré et al. 2001, Fortin et al. 2005, Hernandez and Laundré 2005). Habitat shifting by a large herbivore redistributes browsing or grazing pressure, and has the potential to result in a behaviorally mediated trophic cascade (BMTC). Mesocosm experiments with insects point to the importance of hunting mode in creating strong spatial contrasts in risk (Schmitz 2008), and the trade-offs made by intermediate species (such as herbivores) in causing a BMTC (Schmitz et al. 2004). In Yellowstone, wolf presence and behavioral changes have been linked to aspen recovery (Ripple et al. 2001, Fortin et al. 2005), but a dispute ensued over the strength of evidence for this BMTC (Kauffman et al. 2010, Beschta and Ripple 2011, Kauffman et al. 2013). Unequivocally testing this on a landscape scale is challenging, and studies investigating how prey space use

is influenced by predators with distinct hunting modes are few (but see Willems and Hill 2009, Thaker et al. 2011).

Habitat selection and trade-offs

Trade-offs between risk-avoidance and forage quality or quantity have been identified in several contexts (Nonacs and Dill 1990, Cowlshaw 1997, Godvik et al. 2009, Christianson and Creel 2010), and animals responding to predation risk by shifting habitat are expected to trade off foraging opportunities against risk avoidance. Prey species must thus undertake a balancing act in their habitat selection, so as to meet the demands they face at short and long time scales; particularly energy intake for growth and reproduction, energy use, and predation risk (Fig. 1). Higher energy use demands larger energy intake, but there can also be more subtle connections and trade-offs between foraging and energy use in a spatial context, for instance through the cost of movement between patches and forage depletion (Holand et al. 1998). Ungulate species such as white-tailed deer, *Odocoileus virginianus*, roe deer, *Capreolus capreolus*, and red deer, *Cervus elaphus elaphus*, tend to use more open habitat during the night and forested habitat during daytime (Beier and McCullough 1990, Mysterud et al. 1999a, Godvik et al. 2009). This differential use of open, good foraging areas and habitat providing cover is commonly interpreted as a trade-off deer face due to predation or human disturbance. Furthermore, in a predator-free, high-density population, deer ceased to select for cover and selected only for forage resources, apparently because they experience a weaker trade-off (Massé and Côté 2009).

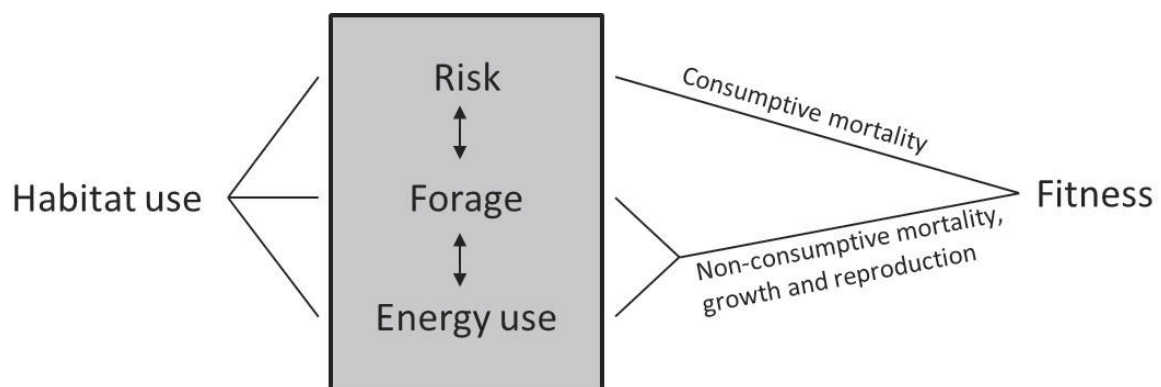


Figure 1: Conceptual model of potentially conflicting factors influencing individual habitat use and their realized fitness consequences. Habitat use by animals can involve a trade-off between exposure to predation risk, foraging needs, and energy use, and the choices made affect survival, growth, and overall fitness.

Many studies have interpreted the use of cover in terms of risk factors and food availability, yet cover can have a plethora of functions for animals (Mysterud and Østbye 1999, Camp et al. 2013, Olsoy et al. 2014). Canopy cover can intercept rain and snow, giving lower snow depth and altered snow conditions underneath dense canopy. It can also alter the thermoregulatory conditions by decreasing radiative transfer and wind speed and intercepting sunlight (Mysterud and Østbye 1999). Horizontal cover from topography or low vegetation can alter visibility and concealment, and affect the efficiency of hunting or the effectiveness of antipredator behavior (Camp et al. 2013, Olsoy et al. 2014). The effects of cover and vegetation structure on animal behavior need to be investigated in more depth since the simple binary classification of open vs. cover does not explain all the effects of vegetation structure on animal behavior.

Ecological processes are inherently scale-dependent (Senft et al. 1987, Wiens 1989). For instance, foraging decisions can be influenced by different factors at the patch, community, landscape and regional levels (Senft et al. 1987). Since patterns do not necessarily scale up or down, a study should be conducted at the temporal and spatial scale thought to reflect the question at hand. Measuring risk landscapes and forage at broad scales is challenging. Studies have typically been constrained by the use of field measurements of cover and forage for fine scale studies, or coarse grain and categorical habitat information for large scale studies. Light detection and ranging (LiDAR) technology can measure vegetation structure with fine grain over broad scales and presents an opportunity to obtain the necessary habitat information to study risk effects on habitat selection across large spatial scales.

LiDAR

In this thesis I use LiDAR to measure functional gradients in cover and vegetation structure with fine grain at a broad scale. LiDAR is an active remote sensing technique that gives detailed information about the three-dimensional (3D) distribution of vegetation and the ground surface by measuring the travel time of an emitted pulse of light that is reflected off an object and back to the sensor (Box 1 gives more technical details, see Wehr and Lohr (1999) for a comprehensive description). The utility of LiDAR as a tool in studies of animal ecology has been recognized and increasingly exploited over the last decade (Lefsky et al. 2002, Vierling et al. 2008, Davies and Asner 2014). Widespread application in other fields of research, most notably geomorphology (Jaboyedoff et al. 2012) and forestry (Hyypä and Inkinen 1999, Næsset and Økland 2002), preceded its application to organism-habitat relationships. Its utility in ecological studies stems from its ability to directly measure

Box 1: A short introduction to LiDAR technology

Laser altimetry, or LiDAR, is to use the travel time of a pulse of light to measure distance. Multiplying the travel time of the light pulse (from emittance to detection after reflection) with the speed of light gives the distance traveled by the light, and dividing this by two gives the distance between the sensor and the object that reflected it. Precise timekeeping is therefore an essential element in LiDAR sensors. When applied over vegetation, LiDAR is able to give information about the three dimensional distribution of biomass well as the ground surface topography, as parts of the laser beam penetrates through gaps in the canopy. The laser pulse has a certain extent or footprint (the size of which varies with type of sensor, flying height, and sensor settings) when it reaches the target where it is reflected, thus parts of the laser beam can be reflected at different distances from the scanner, and this will give several peaks or a spread in the return signal. How the return signal is analyzed and stored is different for the two main classes of LiDAR systems available, full waveform LiDAR and discrete-return LiDAR. While full waveform LiDAR stores the complete signal, discrete-return systems register between one and four peaks in the return signal as echoes returned from point locations. While satellite-borne LiDAR is useful for large-area surveys, airborne laser scanning (ALS) systems are useful at intermediate- to large scales. Airborne systems use GPS, an inertial navigation system that takes account of the pitch, roll and yaw of the plane and the scanning mechanism of the sensor to georeference the position and orientation of the sensor in space. This is necessary to accurately calculate the path of each laser beam and the location of the object (biomass) that reflected it. The scanning mechanism allows the collection of LiDAR data continuously over a large area with a relatively uniform coverage of individual laser echoes in the resulting dataset. The acquired pulse density (and hence, resolution) depends on flying height and sensor settings, and datasets are typically collected to provide a density within the range $0.1\text{--}10\text{ m}^{-2}$, depending on the purpose.

vegetation properties such as canopy height, height variability and foliage density in different height intervals (primary variables) and its demonstrated ability to predicting forest properties such as timber volume, standing dead trees, canopy volume and above-ground biomass (secondary variables) (Lefsky et al. 2002). Studies have used primary or secondary variables to inform how habitat structure relates to habitat quality (Hinsley et al. 2006), species diversity (Müller and Vierling 2014), species distribution/habitat use (Martinuzzi et al. 2009, Zhao et al. 2012), and related management or conservation applications (Vierling et al. 2008, Merrick et al. 2013). Yet it was not until 2010 that the first application to the study of ungulate habitat appeared (Coops et al. 2010)

By now, a plethora of modeling approaches and descriptive variables have been derived from LiDAR data and used in studies of animal ecology or wildlife habitat (Merrick et al. 2013, Davies and Asner 2014). Given that 3D structure is a fundamental aspect of habitat that provides a frame for all biotic and abiotic interactions, it is not surprising that LiDAR can be applied widely and new applications keep appearing. In this thesis I use

airborne LiDAR to study behavioral responses to predation, evaluate its potential for elucidating trophic interactions on a broad scale and to predict the space use of a large ungulate.

I wanted to study indirect effects of predation and hunting on wildlife populations using the forest ungulates of Norway and their predators as the study system. How predation and hunting influence the behavior of large mammals has been largely unknown and thus largely unaccounted for in wildlife management (Solberg et al. 2003). There is a need to investigate this to complete our understanding of predator-prey interactions, especially in light of the return of large carnivores to these ecosystems (Chapron et al. 2014). The study system offers an opportunity to study wildlife responses in a situation with predation from multiple predators, and their responses to a predictable temporal pattern in risk from hunting. At the same time, hunting is a widespread management action, livelihood strategy and recreational activity world-wide. Through hunting, humans might not only influence game populations through numeric control, but also have unintended (or intended: (Cromsigt et al. 2013)) effects on animal behavior that are important to understand.

Objectives

The main objective of this thesis was to study the landscape of risk created by natural predation and human hunting, and consequences for habitat use and survival of Norwegian forest ungulates, using an emerging technology, LiDAR, to characterize habitat structure at a large scale. There were a series of sub-objectives concerning methodology, mechanisms and emerging patterns that were dealt with in one or more papers:

Methodology:

1. Explore the use of LiDAR to quantify habitat structure relevant for forest ungulates, particularly pertaining to predation risk and forage availability (**Papers I, IV**)

Documenting patterns and mechanisms:

2. Characterize spatial patterns in risk imposed by natural and human predators (**Paper I**)
3. Investigate whether animals dynamically adjust their habitat selection to temporal variation in risk (**Papers II, III**)
4. Determine how use of cover and forage habitat relates to survival (**Paper III**)

Trade-off between risk avoidance and other constraining habitat elements:

5. To consider predation risk, forage and implicitly, energetic considerations, as determinants of habitat selection (**Papers II, III, IV**)

Methods

Study areas

The three study areas in Norway (Fig. 2) lie in the boreal vegetation zone and are largely forested mixed-use landscapes with some anthropogenic influence and presence. Within the northern study area there are also several mountainous areas with alpine character. Agricultural areas, paved roads and other anthropogenic developments are mainly restricted to valleys and areas that are relatively flat (Fig. 3). Land cover is dominated by commercially managed coniferous forests composed mainly of Norway spruce, *Picea abies*, and Scots pine, *Pinus sylvestris*. The birch species *Betula pubescens* and *B. pendula* in particular, but also other deciduous species, such as rowan, *Sorbus aucuparia*, willow, *Salix spp.*, aspen, *Populus tremula*, common hazel, *Corylus avellana*, alder, *Alnus spp.*, and elm, *Ulmus glabra*, occur scattered or in small stands. Our southernmost study site (Fritzøe; **paper IV**) also includes deciduous vegetation types of boreonemoral character closer to the coast, and the northernmost study site (Nordmøre; **paper III**) covers a gradient in forests from coast to

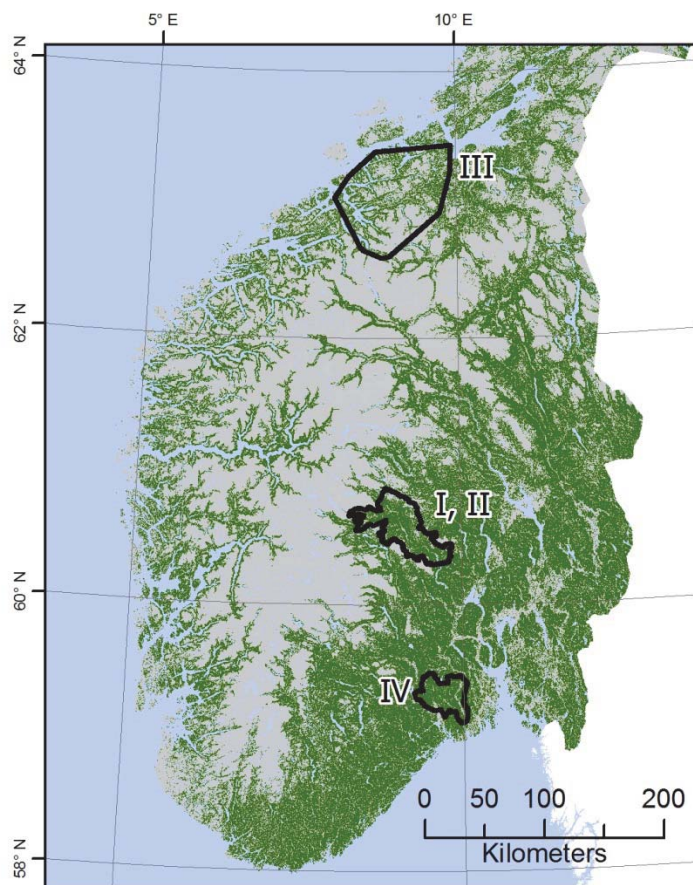


Figure 2: Study areas in southern and central Norway and in which papers (**I-IV**) they were used. Green areas have forest cover.

inland from purely deciduous to coniferous forests. The central and northern study sites (**papers I, II, III**) have one or several pronounced valleys and an altitudinal gradient in vegetation cover, with a transition to only low alpine vegetation occurring at around 1000 m a.s.l. at the inland sites and at lower elevation closer to the coast. All three study areas are large, exceeding 1000 km².



Figure 3: Illustration of a mixed-use landscape in Hallingdal (study area of **papers I and II**) with agricultural areas along the valley bottom and managed coniferous forests.

Norwegian forest ungulates and their predators

There are five wild-living ungulate species in Norway: a single, small population of reintroduced musk ox, *Ovibus moschatus*; wild reindeer, *Rangifer tarandus*, that occur patchily in mountain regions; and roe deer, red deer, and moose, *Alces alces*, all of which are considered forest ungulates and both more abundant and widely distributed than reindeer (Andersen et al. 2010). This thesis concerns roe deer, red deer and moose. These three species have a large spatial overlap in distribution in southern and central Norway. In the western parts, red deer dominate in terms of abundance, whereas moose dominate in the eastern parts. Moose and roe deer are absent from some areas on the West Coast with high population densities of red deer (Andersen et al. 2010).

The three species experience different levels of natural predation from different predators. European lynx, *Lynx lynx*, target all age classes and both sexes of roe deer (Odden et al. 2006). They also kill both young and adult red deer if they are available, but take moose calves only occasionally (Odden et al. 2010). The evolutionary history of predation differs between the three ungulates. Moose and red deer have evolved with pursuit predation from wolf, while roe deer have evolved with stalking predation and experience the same situation today (Nilsen et al. 2009).

At the northern site (**paper III**), red deer is the dominant large ungulate present, but roe deer and moose are also present. Red deer experience high hunting pressure, but very low predation by natural predators as only a few lynx individuals are present in this region. At the central site (Hallingdal; **papers I, II**), roe deer, red deer and moose are all present, but to some degree utilize different areas (Myserud et al. 2012), habitat types and diet types (but with substantial overlap). Lynx is the only large predator that is present in significant numbers as bears or wolves occur only sporadically. All three ungulate species are hunted by humans. At the southern site (**paper IV**) all three ungulate species are present and hunted. Lynx is also present here.

The assemblage of forest-dwelling ungulates in Norway is well distributed along the body weight gradient (female moose = 300 kg, female red deer = 80 kg, adult roe deer = 30 kg). The Jarman-Bell principle contends that small-bodied animals have larger nutritional needs per kg body mass, but the same digestive capacity per kg body mass as larger-bodied animals, leading them to require more easily digestible forage than larger species need (Illius and Gordon 1987). As heat loss rates also scales advantageously with body mass, the overall effect is that roe deer require high quality forage, moose are able to tolerate poorer quality forage, and red deer take an intermediate position between roe deer and moose along a gradient in forage quality. Whereas moose and roe deer are concentrate selectors (i.e., browsers), red deer are intermediate feeders (i.e., mixed feeders) (Hofmann 1989). Even though roe deer are generalists, they are highly selective for high quality forage such as herbs, fruits and grains (Duncan et al. 1998). At the same time, they are selective feeders at the scale of patches, consuming only the best plant parts (Duncan et al. 1998). There is relatively little overlap between diets in sympatric populations. Moose and roe deer diets overlap by about 20% during summer and 30% during winter when they both mainly rely on browse (Myserud 2000). Since red deer and moose diets also overlap by about 30% during winter (Myserud 2000), the species have well separated diet niches, so exploitative competition for forage is mainly against conspecifics.

Data

All four papers are observational studies using tracking data from GPS-collared animals. Lynx and roe deer were collared by NiNA and the project Scandlynx. The group also periodically monitored lynx movements intensively to document predation events, generating a set of locations of kill sites of roe deer. Locations where hunters had killed roe deer were obtained by asking local hunters to share this information. The red deer were collared by Bioforsk Tingvoll for the projects HjortAreal and TickDeer, and the moose were collared by HiHM for the Moose – Forage Project. All animal handling procedures were approved by the Norwegian Animal Research Authority and permission to capture wild animals was granted by the Norwegian Directorate for Nature Management (FOTS IDs: 1428, 2827, 1391, 4863).

Habitat was characterized using field-based surveys in **paper III**, and by a combination of LiDAR data, field data and other GIS map data (always including a digital elevation model, DEM) for **papers I, II** and **IV**. In my thesis I relied on six LiDAR datasets collected for other purposes but made available to me. Two datasets were used together in **paper I**, and four datasets were used together in **paper IV**. Although not collected during the same year, as would have been ideal, the datasets used together in the papers are all within a timeframe of a few years (Table 1).

Table 1: When the data used in this thesis were collected.

Data type	Papers I, II	Paper III	Paper IV
Animal data (GPS data, kill sites)	2007–2012	2007–2012	2007–2008
Field data (habitat or browse survey)	2011–2012	2013	2007
LiDAR data	2008–2009	Not used	2008–2010

Specifically, the LiDAR datasets were collected using discrete-return scanning instruments (Optech ALTM Gemini and Leica ALS50-II) mounted on airplanes. These ALS datasets are ‘point clouds’ consisting of millions of individually registered echoes (return signals) with the x, y, and z coordinates of locations where the laser beam was reflected. Ground points were classified by the contractor, and from these I constructed a ground surface model that was subtracted from the height (z) of the point cloud to yield a point cloud with height above ground (dz). The ground surface model was also exported to yield an accurate DEM.

There are seemingly endless possibilities for calculating variables describing the distribution of echoes (a set of commonly used variables are reviewed in Merrick et al. 2013,

Hill et al. 2014). Although variables can be used in a purely exploratory manner, it is a general goal for ecologists employing these tools to develop and use variables with ecological and functional rationales. I calculated LiDAR variables that described the vertical distribution of echoes, within circular areas centered on the center coordinates of each field plot and for raster cells of the same size in a grid covering the entire dataset (Table 2). Many of these variables are commonly used in area-based modeling of forest characteristics. Additional variables describe understory vegetation and density within absolute height intervals. Many of the LiDAR variables were highly correlated and hence many were excluded during pre-screening of variables to avoid collinearity in the models. I retained the variables with the best explanatory power (**paper I**) or with the clearest ecological interpretation (**paper IV**).

Several types of field data were collected either to be used directly in ecological analyses relating risk to habitat use (**papers I, III**), or as ground reference values to be modeled using LiDAR (**paper IV**). Habitat surveys were concentrated on quantifying concealment cover, collected using a 30 cm wide and 80 cm tall coverboard that was placed in the center of the plot (Mysterud et al. 1999b). As the viewer moved away from the

Table 2: LiDAR variables used in **papers I** and **IV** describing the vertical distribution of laser echoes in a plot or raster cell (2500 m²) based on their height above ground (dz).

Variable	Description
ulcd ^a , understory cover ^b	proportion: $n_{\text{understory}} / (n_{\text{understory}} + n_{\text{ground}})$, where ground: ≤ 0.5 m and understory: $0.5 < dz \leq 2.0$ m
dground	proportion of all returns ≤ 0.5 m
d0.5	proportion of all returns $0.5 \leq dz \leq 3.0$ m ^a (or $0.5 \leq dz \leq 2.5$ m ^b)
canopy cover ^b	proportion of all returns > 3.0 m
h10 ^b	10th height percentile (of all returns > 0.5 m)
h20	20th height percentile (of all returns > 0.5 m)
h30 ^b	30th height percentile (of all returns > 0.5 m)
h40	40th height percentile (of all returns > 0.5 m)
h50 ^b	50th height percentile (of all returns > 0.5 m)
h60	60th height percentile (of all returns > 0.5 m)
h70 ^b	70th height percentile (of all returns > 0.5 m)
h80	80th height percentile (of all returns > 0.5 m)
h90	90th height percentile (of all returns > 0.5 m)
hmean	mean height (of all returns > 0.5 m)
hqmean ^a	quadratic mean height (of all returns > 0.5 m)
hsd	standard deviation in height (of all returns > 0.5 m)
hcv	coefficient of variation of height (of all returns > 0.5 m)

^a Used in **paper I**

^b Used in **paper IV**

coverboard, the distance at which the coverboard disappeared from view was recorded, and the mean of the four cardinal directions was used as the habitat ‘sighting distance’. In one study an observer also stood back first 10 m, then 20 m, and counted how many of the 80 squares drawn on the board were visible (i.e., not obstructed by vegetation or the ground). Canopy cover was registered with a densiometer. Habitat type, forest development class, and basal area of the main tree species were also registered. Plots were centered on a single point, and many of the measurements had a variable radius (e.g. sighting distance and basal area registrations with a relascope), but for other measurements the plot was considered to extend to a 20 m (**paper III**) or 50 m (**paper I**) radius. Additionally, forage resources were characterized as percent ground cover in three 2×2 m plots for the study in **paper III**. The forage survey used as ground reference data in **paper IV** consisted of estimates of available browse forage biomass of six tree species eaten by moose in 153 plots. Each plot consisted of five 50-m^2 subplots, the average value of which was taken to represent the 2500 m^2 area within which they were measured. Note that this was opportunistic use of an extensive, existing dataset and the use of LiDAR was not considered in the sampling design at the time of collection (van Beest et al. 2010).

Study designs and statistical methods

In each paper, I investigated one or more elements or relations in the habitat use-risk-forage-energy use-survival complex (Fig. 4). I drew inferences on the basis of a series of statistical comparisons (Box 2), relating the outcome to specific expectations, specified in each paper, to test hypotheses. The main statistical procedures used were logistic regression (Hosmer and Lemeshow 2000), linear regression, mixed effects linear regression (Zuur et al. 2009), and exponential resource selection functions (RSFs; Manly et al. 2002) estimated with mixed effects logistic regression (Gillies et al. 2006). The performance of predictive models was evaluated using AUC (the area under the ROC curve) (risk model, **paper I**), K-fold cross-validation with root-mean-square-error measures (browse model, **paper IV**), or K-fold cross-validation with spearman rank correlation (RSF models (Boyce et al. 2002), **paper IV**). RSF models in **paper II** were not evaluated as they were used to identify patterns in the selection, and not used predictively.

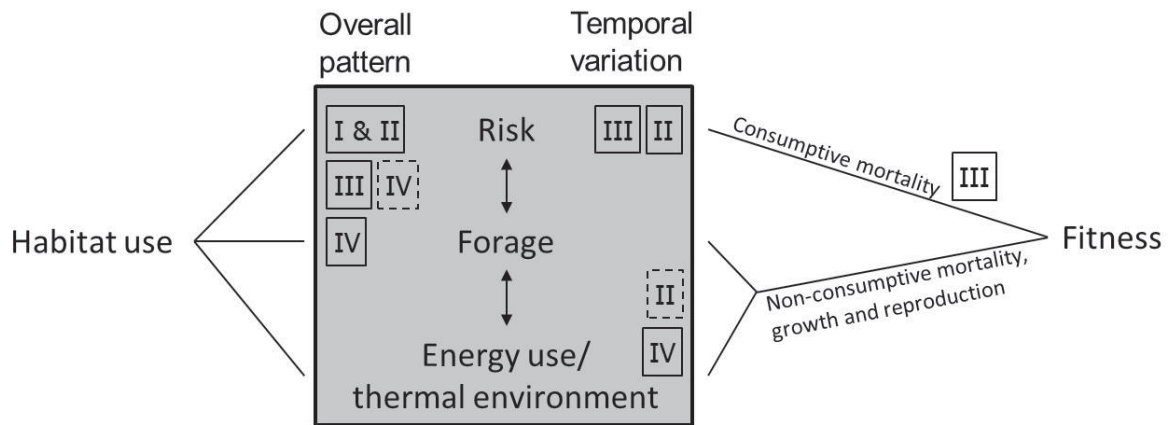


Figure 4: How the four papers are positioned within the conceptual framework of the three interdependent factors influencing habitat use, and whether the studies considered aggregate patterns or temporally dynamic patterns. Roman numerals refer to papers addressing various elements in this framework: the spatial distribution of animals and selection of safe locations (**I, II, III**) or forage resources and energetically favorable environments (**IV**); trade-offs or constraints between these (**III, II, and IV**); consequences of habitat use with respect to mortality (**III**). Dashed frames indicate elements which were studied implicitly.

Box 2: Choice and rationale of methods

In this thesis, I made extensive use of comparisons, through logistic regressions, exponential RSFs, and linear regressions to test the predictions regarding animal habitat use in a rigorous manner, and identify statistically significant relationships and their ecological relevance. Here follows a list of the main comparisons made, what they yield information about, and in which paper each was used.

Kill sites vs. sites used by living prey	identifies factors influencing RISK	I
Used locations vs. available locations	identifies factors SELECTED on this scale	II, IV
Selection at t_1 vs. selection at t_2	identifies temporal change in selection: the RESPONSE to factors changing between t_1 and t_2 , indicative of a trade-off	II
Use at t_1 vs. use at t_2	identifies temporal change in use: the RESPONSE to factors changing between t_1 and t_2 , indicative of a trade-off	III
Use by survivors vs. use by shot animals	identifies how use CORRELATES with survival (either directly or indirectly)	III
Performance of LiDAR-enhanced models vs. LiDAR-less models	evaluates whether LiDAR captures additional variation that is important in the studied process	I, IV
Performance of LiDAR-only models vs. LiDAR-less models	evaluating the performance of stand-alone LiDAR in comparison to alternative/traditional data	I, IV

Figures 5 and 6 show the general analysis framework used in **papers I, II** and **IV**. **Paper III** was methodologically simpler as I used only field data on cover and forage collected at a systematic sample of locations used by 40 GPS-collared animals known to have been shot or survived the hunting season that year. Here, I compared the habitat characteristics at six sites used by survivors and shot animals shortly (1–9 days) before the onset of hunting and six sites used shortly (2–8 days) after the onset of the hunting season. I refer the reader to the specific papers for sample sizes and more details on the auxiliary data types and analyses.

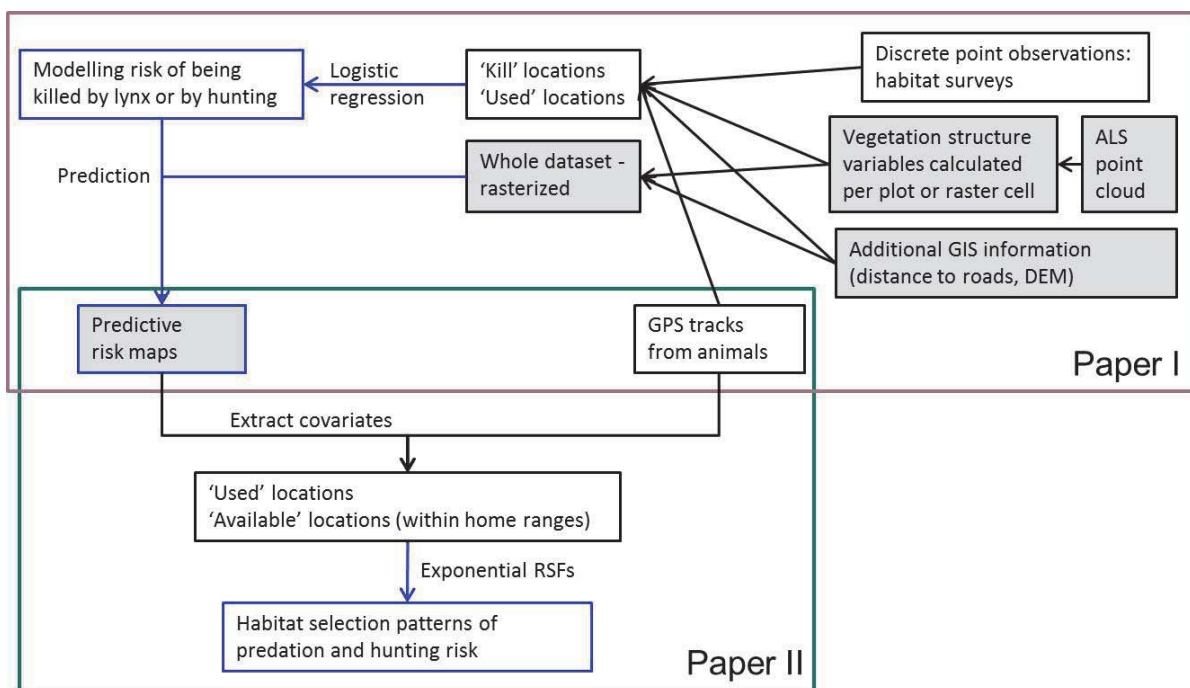


Figure 5: Flowchart of the analyses in **papers I** and **II** together. Blue links and boxes with blue frames are modeling steps and modeling outputs, black links and boxes with black frames are data input and preparatory steps, including modeling input. Grey boxes are data with complete cover over the study area (raster or point cloud).

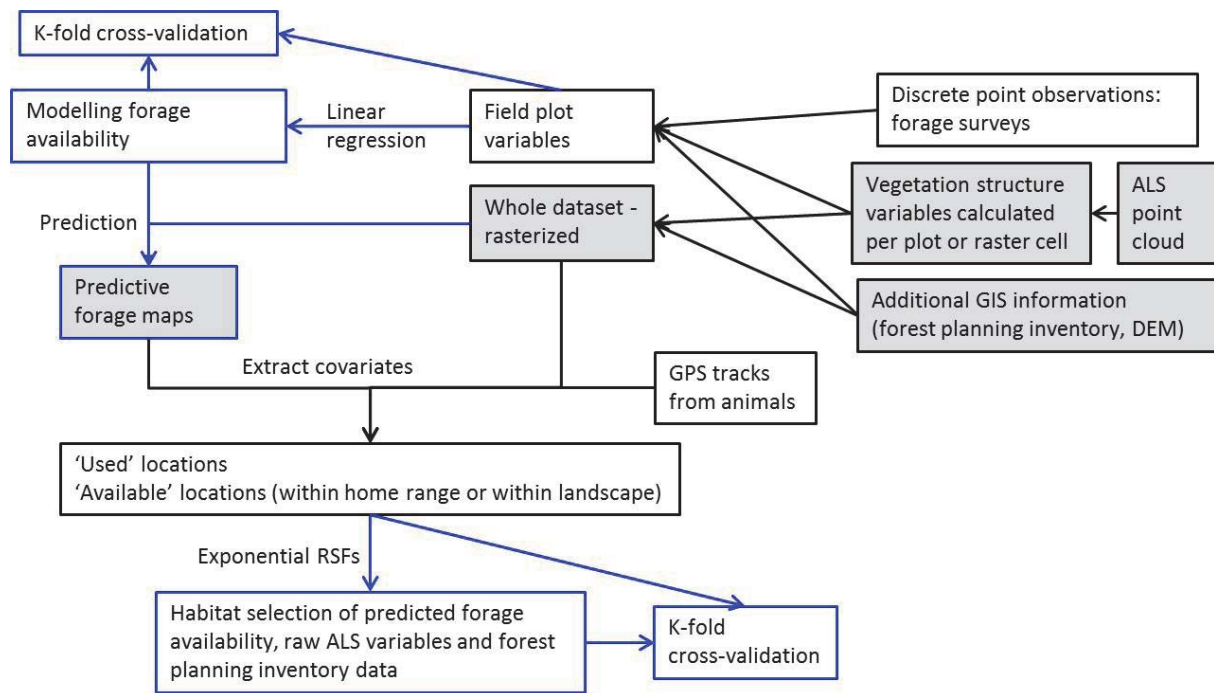


Figure 6. Flowchart of the analysis in **paper IV**. Blue links and boxes with blue frames are modeling steps and modeling outputs, black links and boxes with black frames are data input and preparatory steps, including modeling input. Grey boxes are data with complete cover over the study area (raster or point cloud).

Results and Discussion

Functional habitat gradients from LiDAR

LiDAR can describe physical properties of the habitat and vegetation structure that are directly linked to ecological function. To study the importance of risk, forage and energetic considerations for ungulate habitat selection, I attempted to derive measures related to amount of concealment cover in a habitat and the modification of the thermal- and light- environment, and to quantify available browse in a modeling approach. Quantifying habitat gradients in this way is an alternative to inferring relative forage and concealment cover from habitat classification, which disregards variation within habitat classes (Blix et al. 2014).

Variables such as canopy cover, coefficient of variation of height (vegetation height heterogeneity), and understory cover are primary variables directly derived from the remote sensing data. Not using a predictive model can be an advantage because there are no errors attributable to the modeling step and there is no need for ground reference data for prediction and estimation, but a primary variable should always be interpreted with its technical definition in mind. Regardless, field validation is useful, and demonstrating the validity of the functional interpretation empirically can only strengthen the claim set forth. For instance,

others have demonstrated that several differently formulated canopy cover variables related to understory light conditions (Alexander et al. 2013), an interpretation I rely on to explain the relationship between canopy cover and browse biomass (**paper IV**).

The understory cover variable was derived to describe the ability of the habitat to conceal a prey or predator. However, the correlations between LiDAR-derived understory cover and concealment as estimated by field based methods are low (Table 3). Several things could cause a poor correlation: imprecision in the LiDAR measurements, the relationship between amount of understory and concealment being noisy or non-linear, and imprecision of the ground reference data. Others using a similarly defined (differing by also incorporating intensity information) LiDAR measure of understory cover found that it was strongly related to field measured understory cover (R^2 of 0.74 in ponderosa pine forest (Wing et al. 2012)).

Imprecise ground reference data explain a larger part of the poor correlation. Concealment is a concept and a process involving an object and a viewer, one or both of which are moving, so defining what quantity to measure is a matter of debate and depends on the question being posed. Quantifying the concealment of a coverboard or an object of a certain size and shape is an established field method that has effectively been used to demonstrate habitat use patterns relating to visual exposure and predation risk (Myserud 1996, Ordiz et al. 2009, Ordiz et al. 2011, Camp et al. 2012). These sampling methods are powerful and easily interpretable because they functionally mimic prey concealment in the field, but they are imprecise, as is manifested in the low correlation between the three coverboard measurements: sighting distance and horizontal cover at 20 m and 10 m (Table 3).

When evaluating the interpretation of LiDAR data in this way, there should ideally be a one-to-one relationship with little noise between a ground reference value and the LiDAR variable. I showed a positive correlation between understory cover as measured by airborne LiDAR and field measured concealment, but not a strong enough relationship to support interpreting one directly as a proxy for the other. However, proposing a few hypotheses and finding compliance with one of them, as I did in **papers I** and **II** regarding the concealing function of understory cover as measured by LiDAR, is also a strong indication that LiDAR is picking up the intended ecological signal.

Table 3: Pearson cross-correlation between LiDAR understory cover and measurements of cover and visibility using a 30 × 80 cm coverboard, in the 292 field plots from **paper I**.

	Understory cover	Sighting distance of coverboard	% horizontal cover at 20 m
Sighting distance of coverboard	-0.41		
% horizontal cover at 20 m	0.40	-0.84	
% horizontal cover at 10 m	0.31	-0.77	0.73

LiDAR – can it be used to predict risk and forage?

In this thesis, I made several types of predictive models using LiDAR, with different purposes. Firstly, I modeled predation and hunting risk, aiming to identify the underlying causes of risk patterns (**paper I**), in addition to using the risk models predictively as the basis for understanding habitat selection (**paper II**). Secondly, I modeled browse forage availability, with the aim of predicting this across a larger area, and using it in a habitat selection study alongside primary LiDAR variables (**paper IV**). Both risk and browse were modeled as a function of vegetation structural variables derived from LiDAR, together with auxiliary data sources. Two of the key questions (Box 2) were whether LiDAR captured relevant habitat information for predicting risk and forage, and whether LiDAR data could complement or replace the auxiliary habitat data, to yield reliable predictions over large spatial scales.

In **paper I**, LiDAR and terrain variables performed well on their own (and nearly as well as field data and terrain variables on their own), indicating that they had captured the relevant habitat variation influencing risk. LiDAR data did not greatly improve predictive ability of models when they were included together with field data, and can therefore best be described as a replacement rather than a complement of the field data. This supports the notion that understory cover from LiDAR likely captures some of the same variation in concealment cover as the field measurement with coverboard. The lynx models were practically equally good between LiDAR and field data, whereas the hunting models had a somewhat lower predictive ability, but still within the range considered ‘good’. Again, our measure of understory cover was the main variable that was positively correlated with risk from lynx and negatively correlated with risk from hunters. The importance and success of the understory cover variable (particularly in the lynx model) nonetheless emphasizes the usefulness of this variable as it pertains to risk.

The inclusion of LiDAR data moderately improved models of browse biomass available to moose (**paper IV**) because LiDAR captured additional habitat variation that explained browse availability. Increasing understory cover and decreasing canopy cover was associated with a higher amount of browse, probably relating to biomass in the browsing height range and more light reaching the understory (Alexander et al. 2013). However, some important habitat characteristics were evidently described better in the alternative data (forest management inventory maps with stand-level information on species composition, development stage and productivity), as models based only on LiDAR data performed poorly (best R^2 attained was 0.24) in comparison with models based only on inventory data. I was not able to demonstrate an adequate method for predicting browse using only data on vegetation and terrain structure from LiDAR. LiDAR provides structural information and can thus complement, but not easily replace, species information. The performance of the LiDAR variables also likely suffered from the non-optimal matching between laser data and field data. The ground reference data incorporated a large random error, as the field survey of browse only covered 10% of the field plot area and a handheld GPS was used for georeferencing. Inaccurate matching between LiDAR data and ground data deteriorates the predictive ability of LiDAR (Gobakken and Næsset 2009). Therefore, the performance of LiDAR in this study should be thought of as a minimum estimate that would improve if the method was applied to ground data whose sampling was better designed for this purpose.

The performance of the models was very different in **paper I** and in **paper IV**, but so were the quantities and processes modeled. Modeling risk has less in common with modeling a physical quantity such as browse than with modeling habitat selection, for which there is no real ground reference value, just plots classified as one or zero. LiDAR measurements and field measurements captured important habitat variation with regards to risk in similar ways. In contrast, in the prediction of browse, the relevant information captured by LiDAR was complementary to that captured by inventory data. In the former case, LiDAR data provided an alternative to field data, allowing extrapolation across the entire area of LiDAR coverage. In the latter case, LiDAR data were used together with the auxiliary data to extrapolate predictions, since the auxiliary data were also available on a large scale. Also others have highlighted the utility of combining structural information from LiDAR with other remote sensing or survey data to yield overall better habitat characterizations (Swatantran et al. 2012). Modeling browse is a challenging exercise using remote sensing, as it depends both on plant species and structure, and while waiting for better tools for mapping it in greater spatial detail, extensive field surveys are the norm for moose (i.e. as in Massé and Côté 2009,

Månsson et al. 2012). LiDAR improved on the habitat selection analysis of moose through the inclusion of cover variables directly, not through improved browse predictions. This demonstrates the utility of primary LiDAR variables, which have also been used in other recent studies on roe deer and moose (Melin et al. 2013, Ewald et al. 2014).

In my work I opportunistically paired LiDAR datasets collected for a different purpose with existing GPS data and available ground reference data. The modest results for browse forage prediction in **paper IV** is a reminder of the importance of using appropriate ground referencing data when predicting secondary variables. In essence, that means appropriately defining the quantities one measures, using accurately georeferenced plots, for instance using differential GPS, that are large enough that the point cloud is not too strongly influenced by randomness, and surveying a large portion of each plot, ideally 100%. I expect the results of both studies could be somewhat improved by using LiDAR datasets with higher point density or full waveform, as these will have more information from the understory height segment. Future studies could be improved by using the same settings for data collection across the whole study area, collecting field data and LiDAR data at the same time if predicting a ground referenced quantity, and collecting LiDAR data during both leaf-on and leaf-off conditions. Nonetheless, this is not always possible, and my work demonstrates the added value of analyzing existing data and applying it in new context – particularly using primary variables from LiDAR with existing, extensive GPS tracking datasets.

Hunting style matters: lynx, hunters and their contrasting risk patterns

Hunting mode matters for the spatial structure of risk, predictability of risk in space, and the type of antipredator response used by prey (Schmitz 2008, Thaker et al. 2011). Furthermore, hunting methods whose effectiveness varies between habitats will give rise to a spatial pattern in risk. In **paper I**, I investigated how predation risk from lynx and hunters was related to terrain attributes and vegetation classes or structure. The predation risk from lynx is expected to be higher in areas with dense understory vegetation because they stalk and ambush their prey. In contrast, predation risk from human hunters was expected to be higher where visual sight lines were longer. Increasing understory cover resulted in a contrasting lower predation risk from humans and higher predation risk from lynx. Predation risk was also contrasting with respect to distance to roads (a proxy for human activity and accessibility) and slope, while risk of being killed by both lynx and humans increased with increasing terrain ruggedness. Extrapolated risk maps showed that multiple predators can create areas of contrasting risk and areas of double risk in the same landscape (Fig. 7;

paper I). In this context it is not possible to avoid both predators by using a single behavioral rule for habitat selection; it requires a combination of behaviors or a temporal habitat shift. Most prey face multiple predators, yet many study the interactions of a single prey and single predator. As several predators are added to an assemblage, and these differ in their habitat use (May et al. 2008) or hunting methods (Thaker et al. 2011), one can expect the degree of complementarity to increase, and that there are fewer areas with low overall risk of being killed. The assemblage of large natural predators in Norway has been recovering over the last decades (Chapron et al. 2014). Although there are some areas with overlap between multiple large predators, up to four, the dominating pattern is that large carnivores in Norway currently have a very limited degree of sympatry (May et al. 2008), and therefore a limited ability to impose contrasting risk patterns on a spatial scale relevant for prey populations or individuals. Human hunters, on the other hand, overlap with all the natural predators. Indeed, several studies have shown an inherent conflict between responding to human hunting and natural predation (Ciuti et al. 2012b, Crosmarj et al. 2012). Hunters and natural predators could in this way be facilitating each other's hunting success (Kotler et al. 1992).

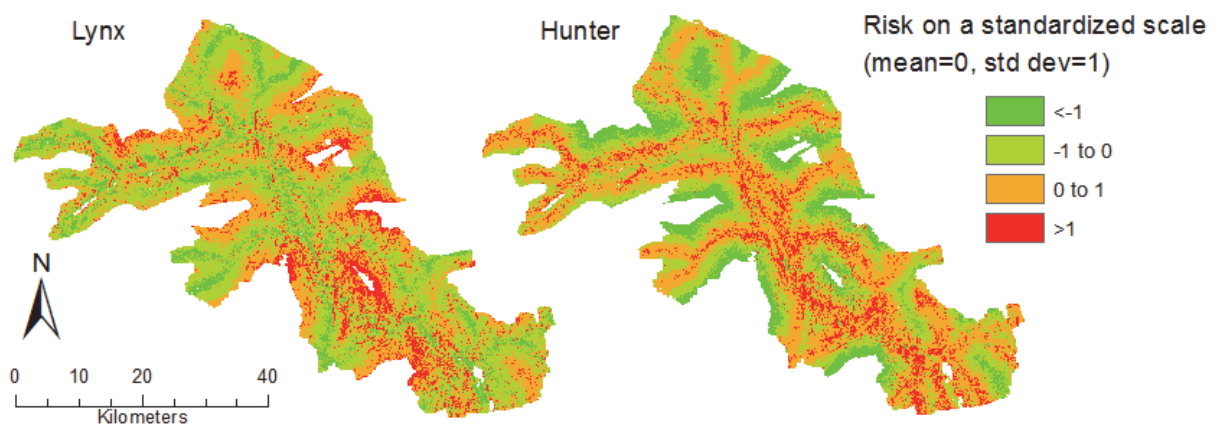


Figure 7: The risk maps from **paper I** form the basis of the habitat selection analysis in **paper II** and were made possible by using LiDAR. Having a reliable risk map with high resolution and large extent that was based on a functional gradient in cover (as well as other important factors) was useful because it enabled asking questions directly about how animals relate to risk.

Responding dynamically to risk in time

Risk varies in space, but also in time. Discerning at what times a predator presents a risk and restricting responses to these times can be an advantageous strategy, because it changes the inherent trade-off rates between risk-avoidance, foraging and conserving energy

(Creel et al. 2008). Animals could then respond effectively to risk when it pays off, without giving up foraging or energetically favorable conditions when risk is low. Not only does the spatial risk pattern of these lynx and hunters contrast, their temporal risk pattern is also strongly contrasting between day and night. Human hunting is typically strongly temporally structured (Cromsigt et al. 2013), making it an ideal candidate for a temporally dynamic response in habitat selection. Do deer exploit this and adjust their habitat selection to match variation in risk at different time scales? In **papers II** and **III**, I investigated temporal variation in habitat selection, with respect to risk maps for roe deer and with respect to field-measured cover and forage for red deer. I expected that deer responded to the onset of the hunting season within a few days, and that they selected risk habitat differently between night and day and among seasons, matching the activity pattern of hunters and lynx.

Daily and seasonal changes in the use of risky habitat by roe deer reflected to a large extent the relative risk levels as gauged from temporal activity patterns of lynx and humans (**paper II**). Indeed, roe deer avoided areas with hunting risk more strongly during day than during night, and conversely avoided areas with lynx risk more strongly during night than day during summer and hunt (Fig. 8; **paper II**). The roe deer also appeared to adjust to the hunting season with stronger hunting risk avoidance during that season, whereas the seasonal pattern for lynx risk avoidance did not correspond to the expectations based on relative risk levels alone, as the weakest avoidance of lynx risk occurred during winter, the season in which their kill rates are highest (Gervasi et al. 2014). In **paper III**, I focused on the onset of the hunting season and identified a clear response by a subset of the animals (surviving males; Fig. 9) that shifted to using safer cover habitat within a few days of it. It is not clear whether this represented a permanent shift sustained throughout the hunting season or a behavioral response on a finer temporal scale to hunter activity and disturbance, which is particularly high during the first week of hunting, but either would represent an ability to detect and respond to hunting. Yet, females and the males that were shot later in the same hunting season did not change their habitat use at the onset of hunting.

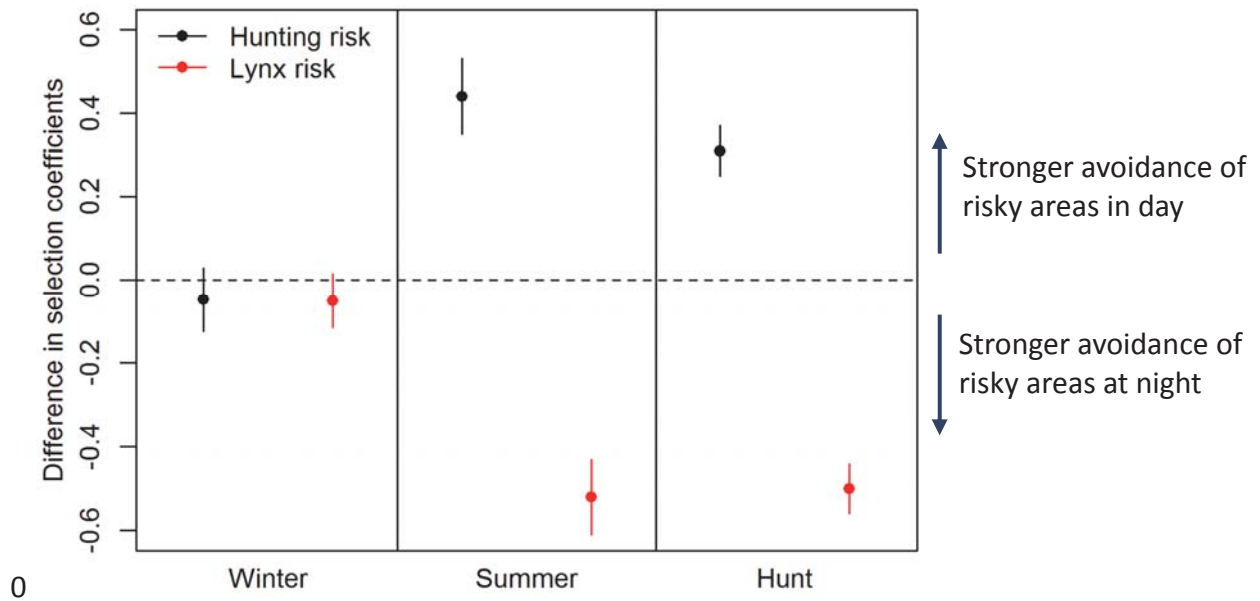


Figure 8: Diel patterns in roe deer selection of habitat that is risky with respect to hunters or with respect to lynx. Plotted values are fitted estimates (\pm SE) of the night vs. day contrast in selection, depending on season.

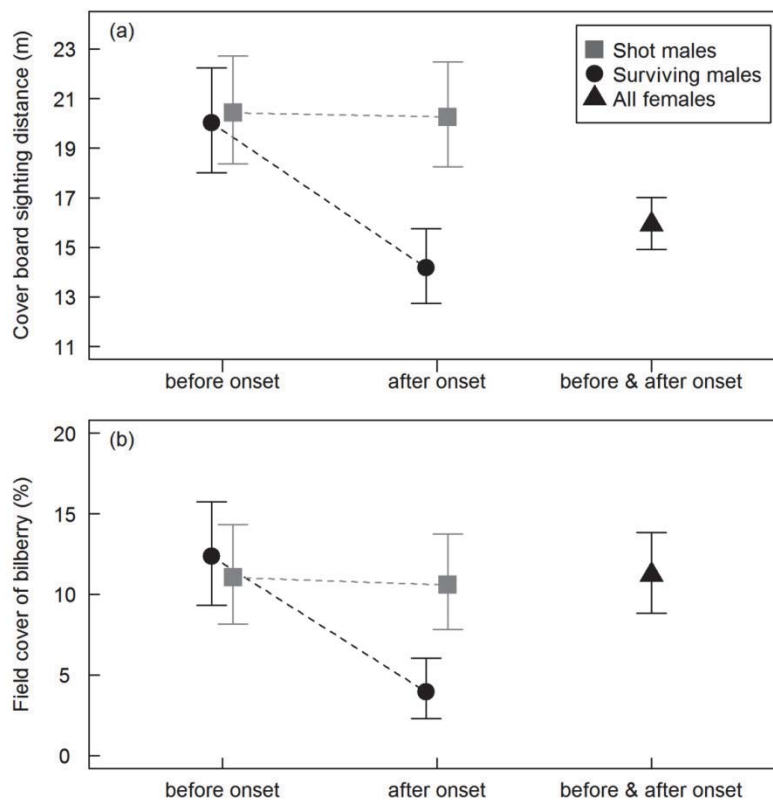


Figure 9: Red deer use of (a) concealment cover (i.e., short sighting distances) and (b) forage habitat depending on sex, whether the animal survived the hunting season or was shot, and time (3 days within the last 9 days before the onset of hunting, and 3 days within 2–8 days after the onset of hunting). Fitted estimates (\pm SE) from the best models for males and females, for females this was the intercept-only null model.

Temporal patterns in risk alter the outcome of the habitat-specific trade-offs between risk, resources and energetics. Responding to the temporal pattern in risk from lynx and humans could also be a way for roe deer to respond to each predator at the times when it is active, thus reducing their exposure to both predators overall. It is not clear from my study to what extent the documented patterns in **paper II** show actual flexibility and behavioral plasticity in responding to current risk patterns, or if some of these patterns would persist in a predator-free population or in response to human disturbance without hunting. These issues are better resolved in **paper III**, where I also discuss human off-track activity and gunshots as possible cues used by deer to gauge risk.

Shifting habitat is an effective antipredator strategy towards hunting

Paper I demonstrated that hunting risk varied spatially depending on habitat characteristics for roe deer. It is generally expected to depend on cover and exposure for other ungulates as well (Godvik et al. 2009, Massé and Côté 2009). **Paper III** was an explicit investigation of whether individual differences in habitat use were linked with survival. In other words – is avoiding risk habitat an effective strategy against hunting? I found that male survivors had shifted to using forest habitat with 29% shorter sighting distance and 68% less bilberry cover within a week after the onset of hunting. In contrast, males that later in the hunting season were shot had, as a group, not changed their use of forest habitat at the onset of hunting.

This indicated that animals that shifted to using cover habitat and less good foraging habitat, experienced higher survival rates as a result. This is evidence that habitat use matters for survival, but as this was an observational study that only looked at habitat use during a short period at the onset of hunting, it can only demonstrate correlation, not causation in a strict sense. It is possible that responding to the onset of hunting could be part of a behavioral syndrome of risk averseness, for which there is some evidence in several ungulate species (Ciuti et al. 2012a, Bonnot et al. 2014). As an example, a shift to denser habitat could be correlated with increased use of vigilance in a hunting situation, with vigilance ultimately being the factor causing higher survival.

Hunting pressure is high in this population, with male mortality at around 45% annually (Veiberg et al. 2010). With such high probability of being shot, there can be a sizable negative fitness consequence of not responding to hunting. Alternatively, a large offset is required in non-consumptive mortality, growth or reproductive output (see Fig. 1). It is clear

that human harvesting can exert a selective pressure on morphological and life history traits exceeding the rate of phenotypic change in natural systems (Allendorf and Hard 2009), and several studies have identified possible consequences of selective harvesting on behavior also (Biro and Post 2008, Ciuti et al. 2012a, Madden and Whiteside 2014). Given that the shift in habitat appears to be an adaptive response to hunting, and contingent on the trait being heritable, there could be selection on behavioral plasticity in responding to hunting in our study system.

Trade-offs between natural predation, hunting, forage and thermoregulation

The existence of trade-offs is central to whether antipredator behavior has a cost to the animal performing the behavior. The strength of the trade-off will also determine whether an antipredator activity is worthwhile based on the costs and benefits of that behavior and alternative behaviors. If the trade-off is steep, the optimal response to predation can be no response. In this thesis I have sought to identify directly or elucidate indirectly some of the main trade-offs ungulates in Norway make in their habitat selection.

The clearest evidence of a trade-off between hunting risk and forage was the decreased use of sites with bilberry cover by male red deer that survived the hunting season (Fig. 9; **paper III**). Surprisingly, the link between bilberry cover and concealment cover was not very strong, so it is not obvious what was the proximate reason survivors decreased their use of good foraging habitat. Also there can be a trade-off between avoiding two risk factors, as demonstrated in **paper I**, and one solution for resolving such a trade-off is to vary habitat selection temporally (**paper II**). Additional trade-offs were indirectly inferred in or from the four papers. The lack of diurnal responses to lynx during winter (**paper II**), can be explained by roe deer behavior being constrained by a steep trade-off against thermoregulation and forage benefits.

Although I in **paper II** did not account for other ecological factors known to vary seasonally, such as forage quantity, quality and energy use, it is well known that Scandinavian habitats are considered to present extremely challenging environments for roe deer during winter (Holand et al. 1998). Snow is important in the habitat selection of ungulates, both on seasonal scales driving fall migration to lower elevations (Mysterud et al. 1997, Lundmark and Ball 2008), and within home ranges (Dussault et al. 2005). Two recent studies highlight the importance of recently fallen snow (Richard et al. 2014) and snow sinking depth (Ossi et al. 2014) on the habitat selection and behavior of mountain goats, *Oreamnos americanus*, and roe deer, respectively. These studies show the spatial and energetic constraints imposed by

this environmental factor, which can increase the cost of movement, constrain space use, reduce forage availability, and render animals more vulnerable to predation. Additionally, low wintertime temperatures increase the cost of thermoregulation. As roe deer have a limited ability to store energy, their principal source of energy during winter is their food supply (Holand et al. 1998). In the balance between energy use, foraging and predator avoidance, it seems that predator avoidance is down-prioritized. It is clear that responding to predation from lynx is more costly for roe deer during winter; the ultimate cost being dying from starvation. Lynx have large territories (Herfindal et al. 2005). While the threat of starvation is constant, encounters with lynx are expected to occur only rarely. Habitat shifting at other time scales in response to predator presence could still be possible, as for instance caribou and moose alter their habitat selection for some days following the passage of grey wolf, *Canis lupus* (Latombe et al. 2014).

From a comparison of the patterns presented in **papers I and IV**, I indirectly infer that there is no trade-off between browse availability and avoiding hunting risk, as browse availability increased and hunting risk decreased with increased understory cover. This is assuming that the documented relationship in roe deer and red deer also holds for moose. Yet moose actually avoided understory cover, at the same time as they selected forage as it varied along other gradients. It is not clear why this is so, but perhaps a functional aspect of understory cover other than concealment cover (such as impeding overview (Camp et al. 2013)) is of importance to moose. However, the study was conducted outside the hunting season, so avoidance of cover could not be due to the actual risk from hunting, although it could still be related to perceived risk from humans. The greater use of canopy cover during day than during night was especially pronounced in summer, and could be related to its function as shelter against high summer temperatures and insolation (Melin et al. 2014) during daytime or avoidance of human disturbance during daytime. Thermal shelter and human disturbance would be another set of factors that align rather than impose a trade-off for moose in their habitat selection.

It is clear that the presence and strength of trade-offs between the three factors risk, forage and energy use identified in the introduction (Fig. 1) are resource- and predator-specific and temporally changing. Canopy- and understory openness can be related to summer forage availability for roe deer and red deer that preferably forage in the field layer during summer, while the same deer rely on browse during winter, which has the inverse relationship to canopy and understory. Since lynx predation risk increases with understory density, there could be a trade-off between avoiding lynx predation and gaining access to preferred forage

during winter, but not during summer. Instead, during summer the trade-off may be between avoiding hunter or human disturbance and access to preferred forage. A spatial trade-off between thermal shelter and a risk factor exists if risk increases with higher understory cover or canopy cover. It does so for lynx in my study, but not for hunting. The strength of the trade-off against thermal shelter is expected to be most important during winter and vary as a function of temperature and snow depth, since the cost of movement and thermoregulatory functions depends on these factors. In short, what species incur trade-offs and when is not a trivial question. It is a question that deserves further investigation, as it can be key to determining when animals respond to predation, and perhaps even more importantly, how costly it is for them.

Documenting the cost of a trade-off or the non-consumptive effects (NCE) of responding to predation is not very easy in free-living vertebrates. However, some antipredator behaviors that were assumed to be costly have been shown to have limited effects on condition and reproduction (Creel et al. 2007, White et al. 2011, Middleton et al. 2013). One reason for this can be that animals are able to compensate for the behavior. For instance, if foraging deer are limited by handling time, they can increase vigilance while they are chewing, and in this way keep up their foraging efficiency completely or partially while improving their chance of detecting a predator (Illius and Fitzgibbon 1994, Fortin et al. 2004). Other possible compensatory mechanisms when giving up good foraging habitats (as red deer did in **paper III**), could be greater selectivity at the bite level, increased time spent foraging, increased forage intake or increased the rumination time. In future studies, an attempt should be made to quantify trade-offs, either in terms of energy intake rates, physiological effects, or ultimate effects on growth and reproduction, if the aim is to document the indirect impact of predators (Creel 2011).

Are animals responding optimally to current predation patterns?

Predator-prey interactions are a classic example of co-evolution. The tight feedback loop to fitness via mortality and energy intake has spurred arms races leading to a wide diversity in how predators and prey interact, including behavioral adaptations by both. Evaluating trade-offs may be a useful tool for understanding the factors influencing habitat selection, but making the assumption that animals behave optimally, i.e., in a way that maximizes fitness, is risky. Recent work has nicely demonstrated cases in which animals select habitat non-optimally (DeCesare et al. 2014), or even have maladaptive behavior so they are caught in an ecological trap (Robertson et al. 2013). I have also identified some cases

in my studies where habitat use or selection did not follow my expectation based on optimal behavior relative to current differences in risk. For instance, red deer females did not shift habitat at the onset of the hunting season (Fig. 9). However, they were already using more cover habitat than males before the onset of hunting. This seems not to be the optimal response to current hunting patterns and low or no natural predation, and could be a lingering behavioral pattern that evolved under past patterns of predation risk from wolves or human hunting. The use of safer habitat throughout the summer season, a period during which they have a young and hence vulnerable calf at heel, is common in many ungulates, also in populations not currently subjected to predation (Ruckstuhl and Neuhaus 2005), including Norwegian red deer (Bonenfant et al. 2004).

Conclusions and future perspectives

Behavioral responses are studied for several reasons. Behavioral adaptations and -mechanisms are interesting in themselves, they can impact the population dynamics of the prey species through NCEs manifested through reduced growth and reproduction, and they can have consequences for other segments of the food web or ecosystem. Such consequences could include altered prey availability for the predator and alternative predators (Kotler et al. 1992, Atwood et al. 2007) or trophically cascading effects from changed patterns of foraging and trampling (Beschta and Ripple 2009, Kuijper et al. 2013). This thesis is focused on the behavioral phenomena themselves as they relate to habitat use. I have found that risk has strongly contrasting spatial patterns between two predators, that the dynamic responses of prey can be attributed to changing levels of risk, and that hunting has ecological and potentially evolutionary consequences on behavior. I have also shown some ways in which predation risk, forage and thermal shelter act together in shaping the habitat selection of forest-dwelling ungulates in Norway. Based on the findings I have attempted to extract some insights related to the potential for indirect effects and cascading effects of predation in my study systems. NCEs are likely to be less under predation risk from multiple predators, but this depends on predator hunting methods and the degree to which animal responses are constant through the year. The ungulates studied altered their space use in response to variability in predation risk. This means that there is a potential for trophic cascading effects through changing browsing patterns as a response to hunting or the natural predator lynx.

The invention of remote sensing, particularly satellite-based and airborne, has opened a large toolbox to wildlife researchers and managers who need information across large extents (Kuenzer et al. 2014). LiDAR is uniquely suited to investigate species-habitat

interactions relating to the physical structure of the habitat. Although the technology has existed for five decades, it is still developing rapidly. Current development trends include higher point densities and full-waveform storage capacities increasing the resolvable structural detail, lighter sensor systems and cheaper data acquisition and development of methods to fuse LiDAR with other data sources to better characterize habitats. Terrestrial laser scanning (TLS) systems, a ground-based LiDAR, have in particular become cheaper, lighter and more user-friendly over the last few years. They could have many applications in ecology, replacing manual collection of data on vegetation structure of small areas (Olsoy et al. 2014). TLS gives a very dense scan of the vegetation in a small area, and can be used to model the obstruction of any hypothetical visual sight line, giving a better classification of general (or particular) concealment characteristics over a ground reference plot (Olsoy et al. 2014). From my work, understory cover stands out as a key habitat characteristic quantifiable with LiDAR that is likely to be relevant to most animals that spend their lives on the ground. An improved ground measurement of concealment cover with TLS could be very helpful in confirming or modeling the relationship understory cover and other structural metrics from LiDAR and concealing properties of the vegetation.

Work et al. (2011) have pointed out that the strength of LiDAR comes evident when testing mechanistic hypotheses regarding plant and animal habitat associations. What sets it apart from field techniques is the possibility of testing such hypotheses over a range of scales. As this thesis exemplifies, the fine-grain and broad scale of LiDAR data collection also fills a specific need in wildlife management and conservation to expand our knowledge of processes at broad scales and develop tools to perform analyses at these scales. I have explored issues of scale in my thesis and there is potential to study these in even greater depth. One analysis that could be feasible using LiDAR data is to vary grain size to determine whether different habitat elements are selected at different ‘patch’ sizes or whether spatial antipredator responses occur on a characteristic scale.

It is up to society and wildlife managers to consider how to apply new insights on the behavioral effects of hunting and human disturbance. In some cases, the management goal might be to preserve areas in as natural a state as possible, and behavioral responses to management actions such as artificial feeding sites, hiking trails and hunting could directly counter these goals (Möst et al. 2015). In other contexts it has been suggested that behavioral effects could be deliberately exploited. ‘Hunting for fear’ is a proposed management framework in which hunting is intentionally structured so as to elicit a desired behavioral response, such as avoiding damages to crops or vulnerable nature types (Cromsigt et al.

2013). Based on theoretical and empirical considerations, the idea needs further testing concerning applicability (Le Saout et al. 2014). ‘Hunting for fear’ could potentially be a successful management strategy in our study system to increase deer avoidance of pastures, as I have shown that roe and red deer respond spatially to temporally predictable risk. From a purely practical viewpoint (there are also ethical considerations to be made) the temporal pattern of hunting could be altered to make it unpredictable over the growing season or over the whole year. However, altering the temporal predictability also alters trade-offs, and as I have highlighted before, if trade-offs are sufficiently steep, as they might be for roe deer and also red deer during the winter, the result might be that deer do not respond at all.

Observational studies on mammals are increasing the knowledge base regarding behavioral impacts of predation and hunting (DeCesare 2012, Kuijper et al. 2013, Sönnichsen et al. 2013, Rivrud et al. 2014), bringing new perspectives into the discourse regarding management of ungulates, carnivores and ecosystems. One thing that could have a direct application is quantified NCEs. We have a good understanding of the net consumptive effect of our large carnivores (Nilsen et al. 2009, Gervasi et al. 2012). Coupled with knowledge of how indirect effects impact population growth rate, one could estimate the total impact on prey populations and the proportion of the population that could sustainably be harvested. However, little is known about the strength of indirect effects of predation in the case of large mammals. One reason for this is that to measure the effect of predation, a case with no predation should ideally be available for comparison. Predation risk experiments are often able to manipulate the lethality of predators and in this way very elegantly measure the indirect effect on population growth caused solely by predator presence (Preisser et al. 2005), demonstrating that these can be large, in some cases even outweighing the direct effect of predation (Preisser et al. 2005, Creel and Christianson 2008). Such experiments are clearly intractable at large scales and there are few ‘natural experiments’ of predator removal and/or reintroduction that have been studied where direct and indirect effects have been teased apart (Fortin et al. 2005). The current trend of carnivore recovery in Scandinavia offers a rich opportunity to study behavioral effects of predation (Sand et al. 2006), but also for quantifying NCEs and ecosystem impacts from potentially altered browsing patterns. Recolonization of large carnivores provides an ideal study system in which prey species growth rates, reproductive rates, habitat use, predation rates and overall mortality could be monitored over time.

Antipredator responses have been shown to be exhibited by naïve prey after only short exposure to their ‘old’ predators who have been absent for about a century (Berger et al.

2001). Thus a study could be designed in which one compared communities across the expansion front of recolonization (either in time or in space), documenting behavioral adjustments to risk made by prey as the predator community becomes more diverse. Potentially one could test whether the impact through BMTCs and prey NCEs is smaller or larger in a more diverse predator community. An increase could arise through animal responding incrementally more to each predator added to the assemblage. A decrease could come about if predators are largely complementary and facilitate the hunting success of the other. As a new predator is added to the assemblage, the overall spatial distribution of risk in the landscape would become more even and the ‘landscape of fear’ less pronounced. Interactions within the predator guild are likely important for the outcome (Elbroch et al. 2014, Monterroso et al. 2014). Schmitz (2008) proposes that strength of BMTCs is strongly influenced by whether a predator hunts actively or is a sit-and-wait predator. It would be particularly interesting to compare data on impacts of hunting by wolves, lynx, and perhaps human hunters using different hunting styles to test these and similar predictions about the role of ‘landscapes of fear’ using the ungulate community in Scandinavia. Such a study could increase our general knowledge of the importance of predator identity and hunting mode for spatial risk patterns, NCEs and BMTCs.

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Paper I

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Paper II

Lone, K., Mysterud, A., Gobakken, T., Odden, J., Linnell, J.D. & Loe, L.E. Temporal variation in habitat selection breaks the catch-22 of contrasting predation risk by multiple predators.

(Manuscript)

Paper III

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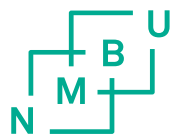
DOI: [10.1016/j.anbehav.2015.01.012](https://doi.org/10.1016/j.anbehav.2015.01.012)

Paper IV

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DOI: [10.1890/ES14-00156.1](https://doi.org/10.1890/ES14-00156.1)

ISBN: 978-82-575-1262-0
ISSN: 1894-6402



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