

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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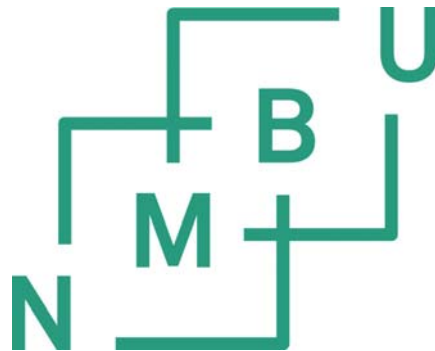
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Ås 2014



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

PhD supervisors

Professor Leif Egil Loe

Department of Ecology and Natural Resource Management

Norwegian University of Life Sciences

Postboks 5003, 1432 Ås, Norway

Professor Terje Gobakken

Department of Ecology and Natural Resource Management

Norwegian University of Life Sciences

Postboks 5003, 1432 Ås, Norway

Professor Atle Mysterud

Centre for Ecological and Evolutionary Synthesis (CEES)

Department of Biosciences

University of Oslo

P.O. Box 1066 Blindern, 0316 Oslo, Norway

Evaluation committee

Associate Professor Kerri Vierling

Fish and Wildlife Resources

University of Idaho

875 Perimeter Drive MS 1136, Moscow, Idaho 83844-1136, USA

Assistant Professor Simone Ciuti

Department of Biometry and Environmental System Analysis

University of Freiburg

Tennenbacher Straße 4, 79106 Freiburg, Germany

Professor Geir Sonerud

Department of Ecology and Natural Resource Management

Norwegian University of Life Sciences

Postboks 5003, 1432 Ås, Norway

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

Contents

Acknowledgements	3
List of original papers	6
Abstract	7
Samandrag	9
Introduction	13
Indirect effects of predation	13
Habitat selection and trade-offs	14
LiDAR.....	15
Objectives	18
Methods	19
Study areas	19
Norwegian forest ungulates and their predators	20
Data	22
Study designs and statistical methods	24
Results and Discussion	27
Functional habitat gradients from LiDAR	27
LiDAR – can it be used to predict risk and forage?	29
Hunting style matters: lynx, hunters and their contrasting risk patterns	31
Responding dynamically to risk in time	32
Shifting habitat is an effective antipredator strategy towards hunting	35
Trade-offs between natural predation, hunting, forage and thermoregulation	36
Are animals responding optimally to current predation patterns?	38
Future perspectives	39
References	42

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).

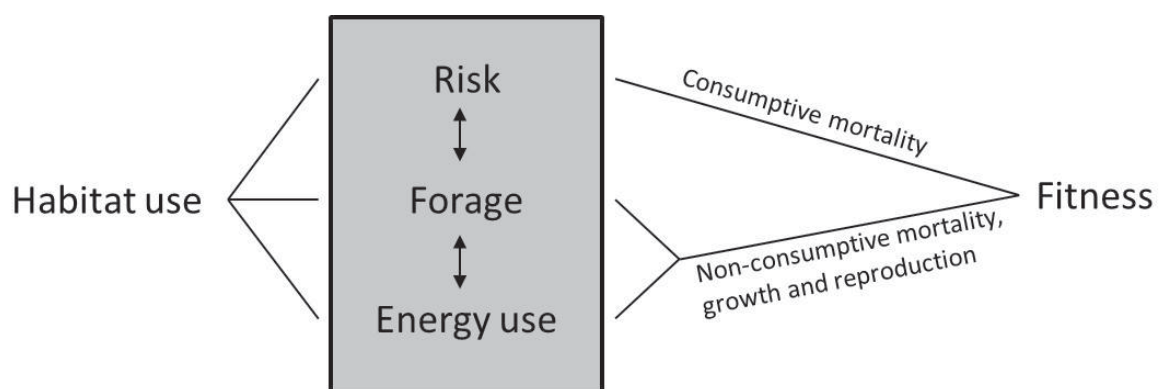


Figure 1: Conceptual model of potentially conflicting factors influencing individual habitat use and their realized fitness consequences. Habitat use by animals can involve a trade-off between exposure to predation risk, foraging needs, and energy use, and the choices made affect survival, growth, and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

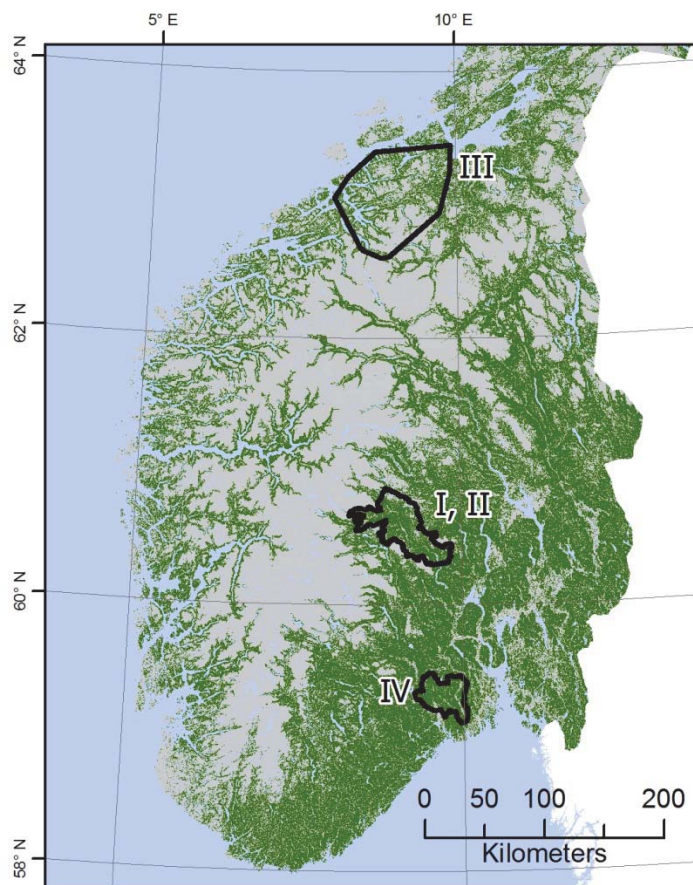


Figure 2: Study areas in southern and central Norway and in which papers (**I-IV**) they were used. Green areas have forest cover.

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 (Myrsterud 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 (Myrsterud 2000). Since red deer and moose diets also overlap by about 30% during winter (Myrsterud 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.

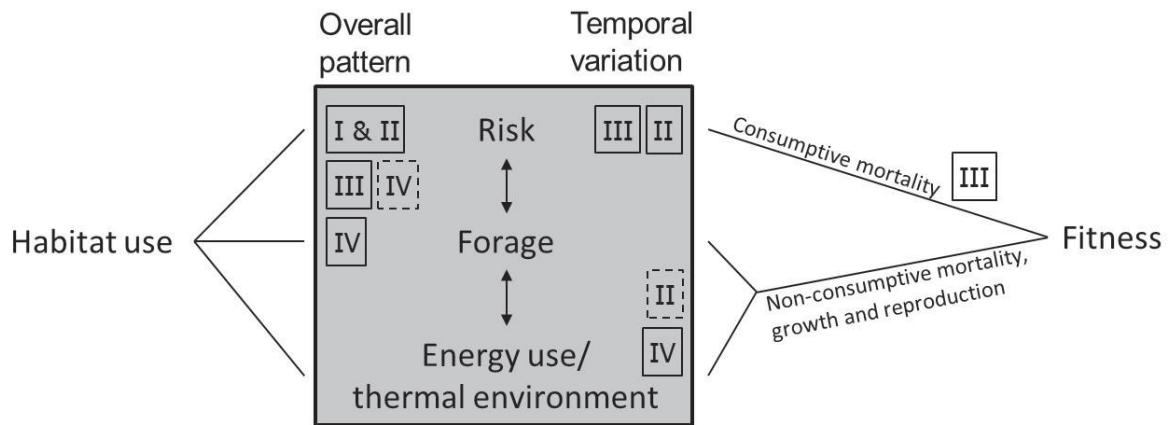


Figure 4: How the four papers are positioned within the conceptual framework of the three interdependent factors influencing habitat use, and whether the studies considered aggregate patterns or temporally dynamic patterns. Roman numerals refer to papers addressing various elements in this framework: 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.

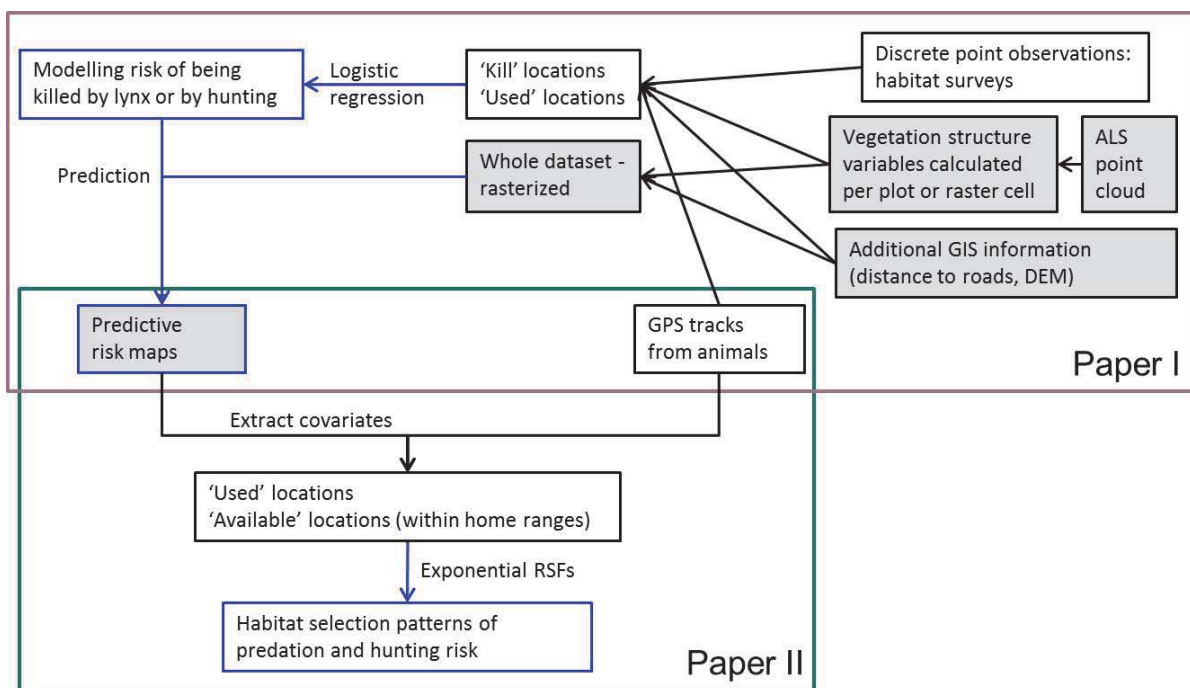


Figure 5: Flowchart of the analyses in **papers I** and **II** together. Blue links and boxes with blue frames are modeling steps and modeling outputs, black links and boxes with black frames are data input and preparatory steps, including modeling input. Grey boxes are data with complete cover over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

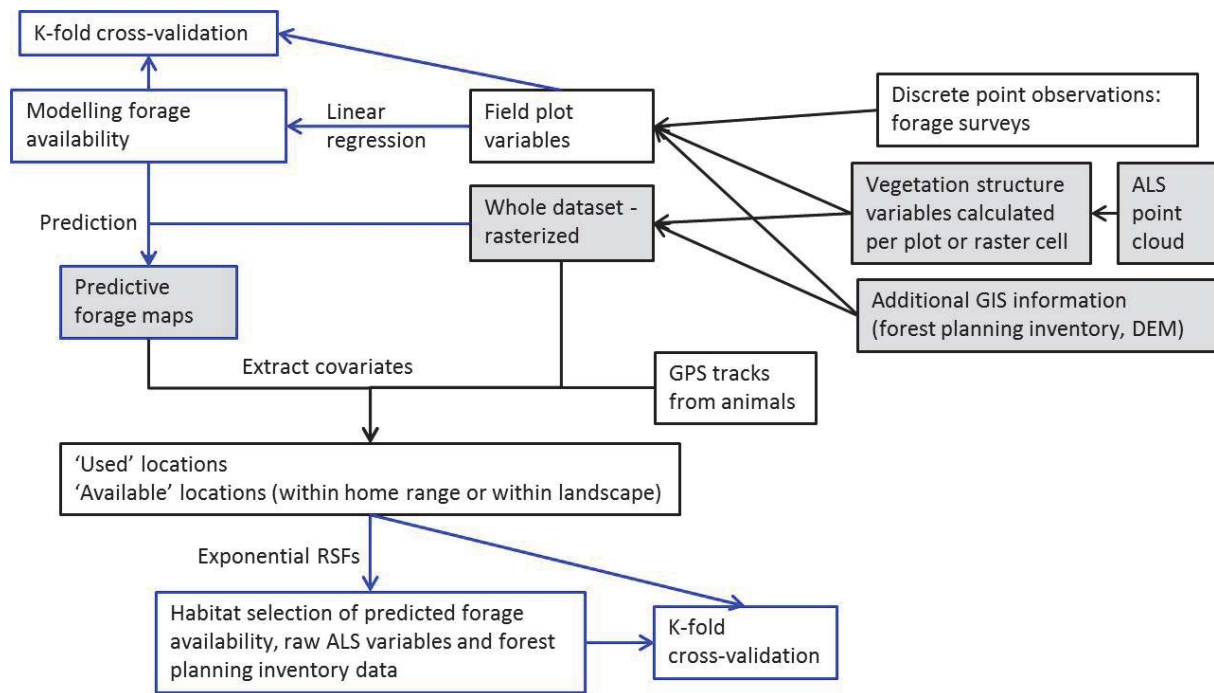


Figure 6. Flowchart of the analysis in **paper IV**. Blue links and boxes with blue frames are modeling steps and modeling outputs, black links and boxes with black frames are data input and preparatory steps, including modeling input. Grey boxes are data with complete cover over the study area (raster 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, Crosmar et al. 2012). Hunters and natural predators could in this way be facilitating each other's hunting success (Kotler et al. 1992).

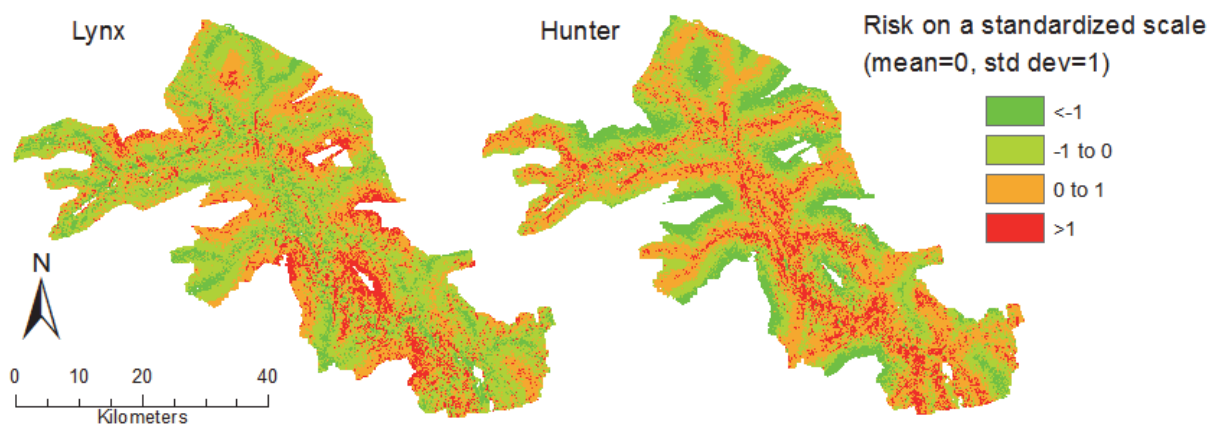


Figure 7: The risk maps from **paper I** form the basis of the habitat selection analysis in **paper II** and were made possible by using LiDAR. Having a reliable risk map with high resolution and large extent that was based on a functional gradient in cover (as well as other important factors) was useful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

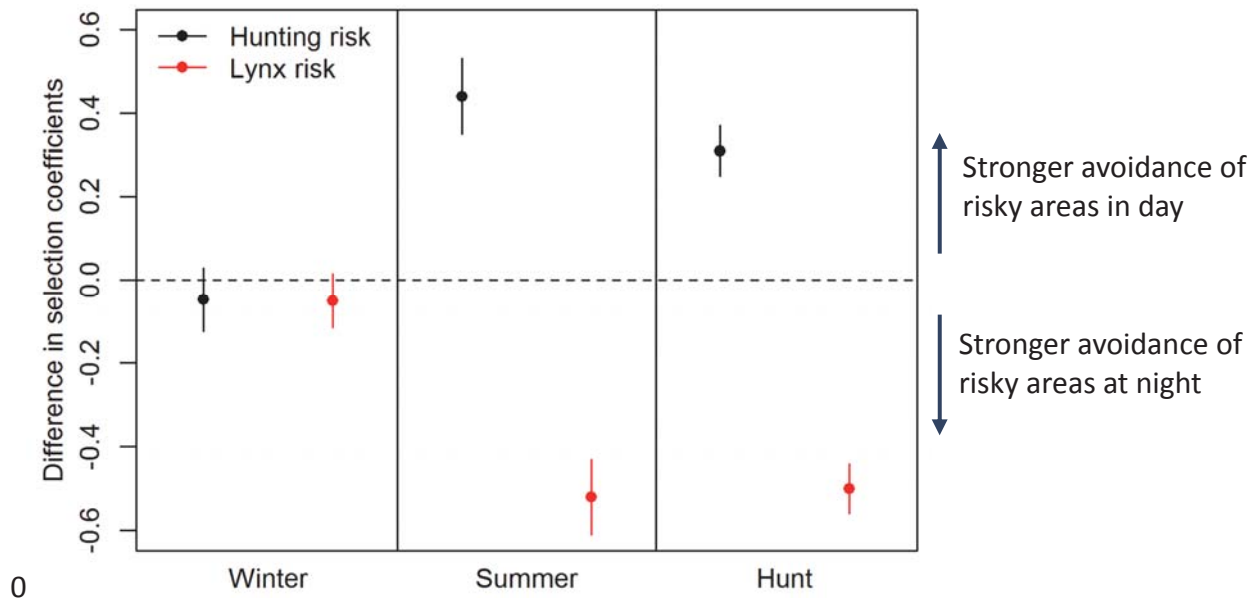


Figure 8: Diel patterns in roe deer selection of habitat that is risky with respect to hunters or with respect to lynx. Plotted values are fitted estimates (\pm SE) of the night vs. day contrast in selection, depending on season.

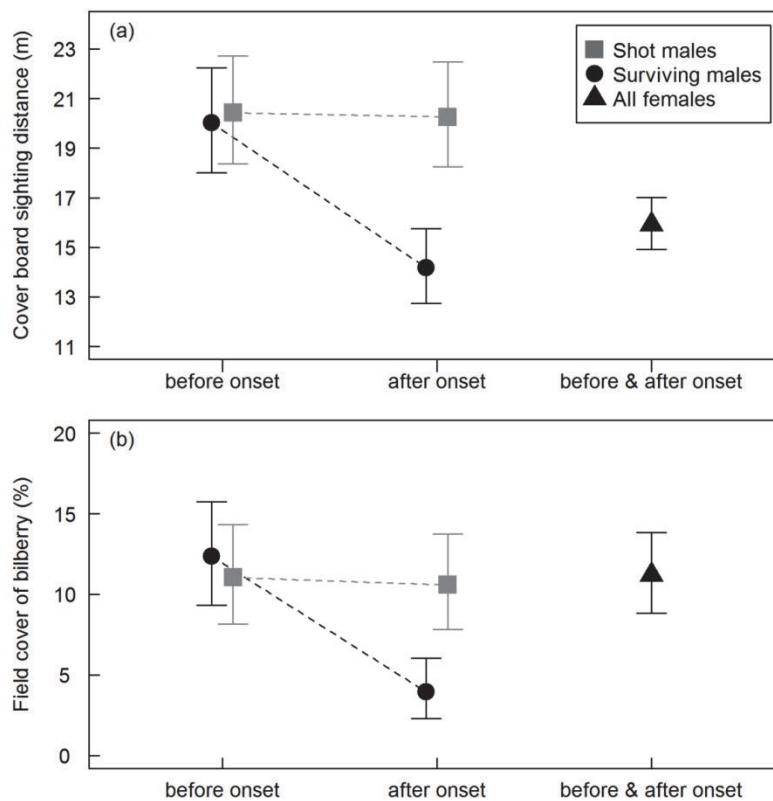


Figure 9: Red deer use of (a) concealment cover (i.e., short sighting distances) and (b) forage habitat depending on sex, whether the animal survived the hunting season or was shot, and time (3 days within the last 9 days before the onset of hunting, and 3 days within 2–8 days after the onset of hunting). 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 (Myserud 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



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

Karen Lone, Leif Egil Loe, Terje Gobakken, John D. C. Linnell, John Odden, Jørgen Remmen and Atle Mysterud

K. Lone (karen.lone@umb.no), L. E. Loe, T. Gobakken and J. Remmen, Dept of Ecology and Natural Resource Management, Norwegian Univ. of Life Sciences, PO Box 5003, NO-1432 Aas, Norway. – J. D.C. Linnell and J. Odden, Norwegian Inst. for Nature Research, PO Box 5685 Sluppen, NO-7485 Trondheim, Norway. – A. Mysterud, Centre for Ecological and Evolutionary Synthesis (CEES), Dept of Biosciences, Univ. of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway.

The theory of predation risk effects predicts behavioral responses in prey when risk of predation is not homogenous in space and time. Prey species are often faced with a tradeoff between food and safety in situations where food availability and predation risk peak in the same habitat type. Determining the optimal strategy becomes more complex if predators with different hunting mode create contrasting landscapes of risk, but this has rarely been documented in vertebrates. Roe deer in southeastern Norway face predation risk from lynx, as well as hunting by humans. These two predators differ greatly in their hunting methods. The predation risk from lynx, an efficient stalk-and-ambush predator is expected to be higher in areas with dense understory vegetation, while predation risk from human hunters is expected to be higher where visual sight lines are longer. Based on field observations and airborne LiDAR data from 71 lynx predation sites, 53 human hunting sites, 132 locations from 15 GPS-marked roe deer, and 36 roe deer pellet locations from a regional survey, we investigated how predation risk was related to terrain attributes and vegetation classes/structure. As predicted, we found that increasing cover resulted in a contrasting lower predation risk from humans and higher predation risk from lynx. Greater terrain ruggedness increased the predation risk from both predators. Hence, multiple predators may create areas of contrasting risk as well as double risk in the same landscape. Our study highlights the complexity of predator–prey relationship in a multiple predator setting.

Synthesis

In this study of risk effects in a multi-predator context, LiDAR data were used to quantify cover in the habitat and relate it to vulnerability to predation in a boreal forest. We found that lynx and human hunters superimpose generally contrasting landscapes of fear on a common prey species, but also identified double-risk zones. Since the benefit of anti-predator responses depends on the combined risk from all predators, it is necessary to consider complete predator assemblages to understand the potential for and occurrence of risk effects across study systems.

Behaviorally responsive prey should maximize fitness by balancing the need for resources and the risk of predation (Lima and Dill 1990). Temporal and spatial variation in the movement, activity and efficiency of predators may give rise to a 'landscape of fear' by affecting prey individuals' decision making and behavior (Laundré et al. 2001). Anti-predator responses decrease prey risk of mortality, but may carry some energetic or physiological cost to the individual. Understanding such non-lethal aspects of predation is critical, since they can have a net effect on populations that sometimes even outweighs the effect of direct predation (Creel and Christianson 2008, but see White et al. 2011, Middleton et al. 2013). Most theoretical and

empirical work has considered a one-predator one-prey case, but more complex cases with multiple predators have received increasing attention, as they more closely reflect reality for most prey species (Lima 1992, Sih et al. 1998). Attributes of the predator, such as their space use and hunting mode determine what kind of prey responses are effective (Schmitz 2008) and thus influence the strength of a prey response when facing a suite of predators (Thaker et al. 2011). Whether prey defenses are synergistic or predator-specific and conflicting may affect both the net predation rate from multiple predators (Sih et al. 1998), as well as the non-lethal effects operating through predator avoidance (Cresswell and Quinn 2013).

The attributes of the physical landscape are the mediators for the spatial 'risk landscape' and the behavioral choices both predators and prey face (e.g. escape tactics, Heithaus et al. 2009). Cover is a key habitat element whose multiple functions depend on the species and context (Mysterud and Østbye 1999, Camp et al. 2013). Cover represents relative safety in a plethora of cases across different systems and species (small mammals; Kotler et al. 1992, freshwater snails; Turner et al. 1999, ungulates; Hernandez and Laundré 2005, carnivores; Ordiz et al. 2011), but its visual and locomotive obstruction can sometimes be to the advantage of the predator, rather than the prey (Camp et al. 2013). There are well established field methods for quantifying horizontal and vertical cover (Mysterud and Østbye 1999), but these are time-consuming and limited to point measurements in the field. Measuring cover with high resolution on a large scale is potentially within reach by use of 3D remote sensing methods providing a much better basis for measuring relevant variables linked to predation risk. Light detection and ranging (LiDAR) data holds information on the three dimensional distribution of vegetation – and can be a source of detailed and continuous information of habitat characteristics across the whole study area (Vierling et al. 2008). The method has been used to estimate forest parameters such as tree height and stem volume successfully (Næsset 2002). Ecological applications include mapping forest structure and habitat quality (Coops et al. 2010, Lesak et al. 2011) and understory vegetation (Martinuzzi et al. 2009, Wing et al. 2012). In the setting of the African savanna, LiDAR based measurements of sighting distance at lion kills have been linked to sex differences in hunting behavior (Loarie et al. 2013). Although the boreal forest interior is a more challenging setting, LiDAR data may hold valuable information on cover and risk also here.

In our study site in Norway, the European roe deer *Capreolus capreolus* face predation from the Eurasian lynx *Lynx lynx* as well as human predation (through regulated hunter harvest). We aim 1) to determine whether these two predators present a case of synergistic or conflicting risks, i.e. whether they impose similar or different risk landscapes on their shared prey. Also, we aim 2) to quantify how the predation risk is related to habitat characteristics, in particular cover, and whether this can be satisfactorily measured using remote sensing LiDAR technology relative to field based measures. We estimate predation risk by using information from roe deer kill sites caused by lynx and humans relative to sites used by GPS-marked roe deer. Lynx and hunters differ greatly in their hunting methods. The Eurasian lynx is a highly efficient stalk-and-ambush predator (Nilsen et al. 2009), which relies on auditory, olfactory and visual cues for detection of their prey, whose predation success should be highest when attacking unaware prey from short distances. Although hunters employ a range of strategies (waiting, calling, stalking), using a gun (mainly rifle, but some also use a shotgun) for shooting is common to all of them and requires high visibility of the target. We expect these differences in hunting methods to link predation risk with habitat characteristics. Within this framework, we make the following predictions:

- P1: Risk-habitats exist for roe deer, i.e. deaths are not distributed proportional to the time roe deer spend in each habitat.
- P2: Landscapes of risk imposed by hunters and lynx differ;
 - 2A) The risk of being killed by lynx increase (providing stalking cover) – while the risk of being shot by a hunter decrease (impedes shooting) with vegetation density.
 - 2B) The risk of being killed by lynx is higher in rougher and steeper terrain (because they prefer and master this habitat) while the risk of being shot by a hunter is highest in smoother and more even terrain (due to human hunter preference).

Material and methods

Study area

The study area was in Hallingdal in Buskerud County, in south-central Norway (8°50'E, 60°40'N, Fig. 1). The landscape is dominated by a forested valley system with high relief, rising steeply from about 200 m a.s.l. at the valley floor up to mountains of subalpine character (>900 m a.s.l.) on either side. It is a multiple-use landscape, with a main road, small towns and agricultural land all along the valley. The forest consists mainly of Scots pine *Pinus sylvestri* and Norway spruce *Picea abies* which is intensively managed using small clear-cuts and a belt of forest dominated by downy birch *Betula pubescence* spp. *tortuosa* at higher elevations.

The average temperature in Nesbyen is –10.5°C in January and 15.2°C in July (<<http://veklima.met.no>>), and snow cover typically lasts from December to April. Supplementary winter feeding (ca January–March) of wild ungulates is a recently adopted practice (the last 10–15 years), but is becoming relatively common in this area. The feeding sites for roe deer are located in habitats that the deer would also otherwise use frequently in winter, often in the transition between forest and agricultural landscape.

The study area hosts a partially migratory roe deer population (Mysterud et al. 2012) occurring at low densities (about 0.1 animals are shot per km²) and a population of Eurasian lynx at intermediate densities (estimate 2006–2011: 90–107 lynx in the 40 000 km² management region; Brøseth and Tovmo 2012). The roe deer population is stable and the offtake by lynx and hunting were of a comparable magnitude in the region at the time of the study. In an area slightly greater than the study area, 65 roe deer were shot annually (source: Statistics Norway), and ca 90 roe deer were estimated killed by lynx annually (Odden unpubl.). The only other notable source of predation is from red foxes *Vulpes vulpes* that may take newborn fawns. Lynx may take a range of different prey species, including red deer *Cervus elaphus*, but roe deer is their most important prey, even at very low roe deer densities (Odden et al. 2006). The lynx population is subjected to quota hunting in a short period in February and March each year. A total of 112 individuals were shot in the lynx management region in the period 2006–2011 (source: Statistics Norway). Roe deer

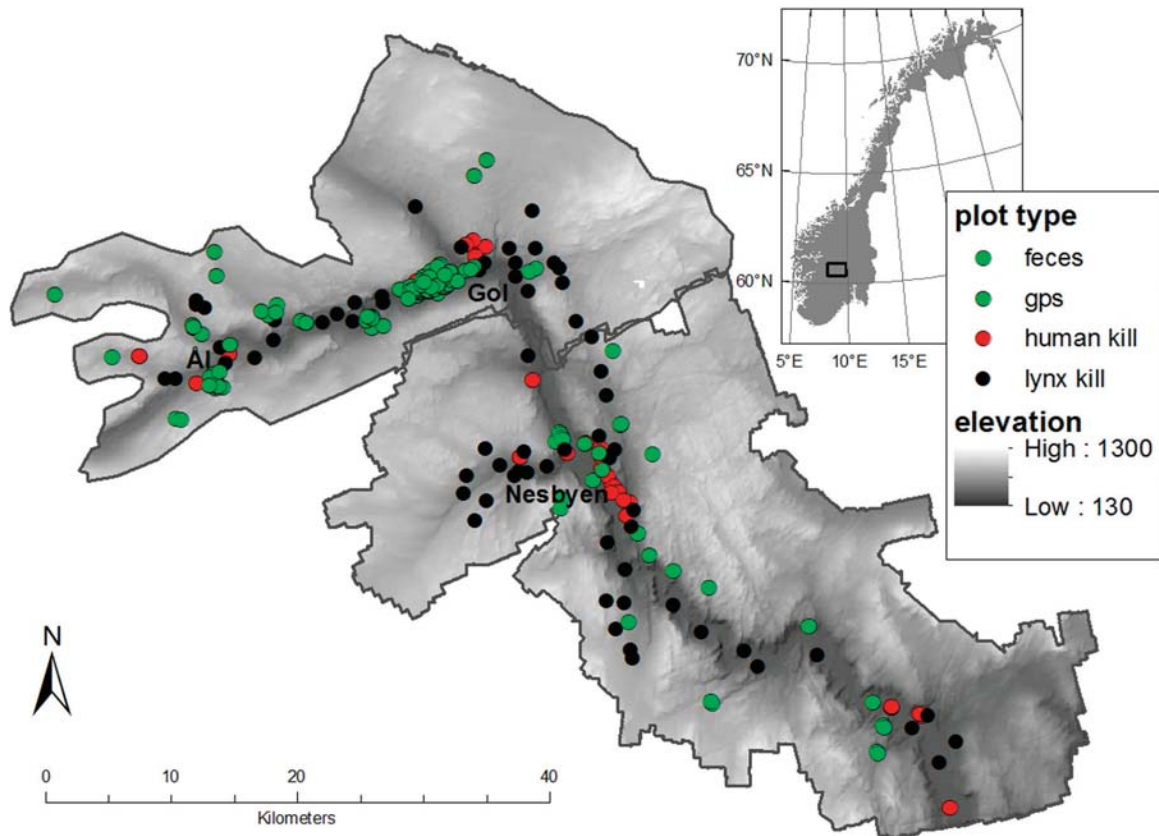


Figure 1. Map of the study area in Buskerud county, Norway, showing the valley topography and the field plots. The extent of the two LiDAR data projects that define the study area are outlined in grey.

hunting is allowed throughout the area and is loosely regulated through quotas, but actual harvest is well below the quota limits. The hunting season for adult males starts 10 August, while all age and sex categories can be harvested in the period 25 September to 23 December. Hunters use either a rifle (most common) or shotgun. The most common hunting tactic is 'sit-and-wait' hunting during the early buck hunting season, both in meadows and in the forest, while drive hunting in teams with or without small barking dogs is the most common tactic during the late hunting season.

Study design

Field plots were established at locations where roe deer had been killed, either by a lynx ($n = 71$) or by a hunter ($n = 53$), at a sample of locations used by GPS-marked roe deer ($n = 132$), and at locations where roe deer fecal pellets had been found in large-scale pellet-count surveys ($n = 36$). All plots ($n = 292$) were within the area of LiDAR data coverage (Fig. 1).

Kill sites

Between 2006 and 2011, nine lynx (four females and five males) were captured and monitored by use of Global positioning system (GPS) collars (Arnemo et al. 2012). Between November and April in winter, and May and September in summer we visited 'clusters' of GPS-locations of the marked lynx, indicative of kill sites. We defined

clusters as a set of at least two locations within 100 m (within the three-to-four week monitoring periods), and visited them to confirm a predation event, identify the prey species if possible, and record the spatial coordinates (see Nilsen et al. 2009 for details on the methodology). The nine lynx individuals killed in total 71 roe deer within the study area restricted by the LiDAR coverage. Through local wildlife managers we got in contact with eight recreational hunters that shared information on where they had shot roe deer in the past five years (2006–2011). They either showed us the locations in situ or shared coordinates they had registered with a hand-held GPS. The hunters contributed 2, 3, 3, 4, 7, 9, 9 and 16 kill sites each: altogether 53 harvest kill sites, roughly one-fifth of all animals harvested in the study period. Since hunting takes place on private property of limited lot-size, there was some clustering of these hunter kill sites, but the clusters are well spread geographically in the area they occur along the valley (Fig. A1 in the online Supplementary material Appendix 1 shows the clustering by field plots by individual). Stalking, sit-and-wait hunting in meadows and in forest, and drive hunting were all represented in the dataset, reflecting the variation in hunting methods practiced in the region.

Locations used by live roe deer

Fifteen roe deer (eight females and seven males, all older than nine months) were captured in box traps at feeding sites close to the villages of Gol and Ål during the winters of

2008–2011. Since most animals use winter feeding sites, we regard the possibility for a biased sampling within the deer population to be low. Since the animals have relatively small home ranges, especially in winter, each deer will often be found close to the site it was captured (Supplementary material Appendix 1 Fig. A1), but we assume their habitat selection represents that of roe deer throughout the study area. The animals were fitted with GPS-collars programmed with several different sampling schedules, but all with at least three positions per day (average GPS fix rate: 95.5%). Out of all recorded positions we randomly selected five May-to-October and five November-to-April locations per individual for field sampling. For the analysis, we discarded plots outside the area of LiDAR coverage, leaving 132 locations, and we defined seasons as the hunting season (10 August – 23 December), winter (24 December – 31 April) and summer (1 May – 9 August). Additional information on sample sizes by season for each individual and individual GPS collar fix rates are available in the Supplementary material Appendix 1, Table A1. To extend roe deer use locations southwards to the same geographical extent as kill sites of lynx and hunters, we also included locations where roe deer pellets were registered as present in a pellet count survey (36 out of 2657 plots) (Fig. 1). The pellet count surveys reflected winter distribution as they were conducted soon after snowmelt during 2007 and 2008. Transects consisting of a triangle of $1 \times 1 \times 1$ km sides were placed randomly, but stratified according to altitude and location of known lynx territories. Ten-m² plots were surveyed for pellets every 100-m interval along each triangle (Torres et al. 2012).

Field data on vegetation characteristics

Field data on vegetation characteristics were collected in the summers of 2011 and 2012. Plots were centered on the known coordinates of kill sites and live sites using a hand held GPS device. Along the four cardinal directions, a 30 cm wide and 80 cm tall cover board (cf Mysterud and Østbye 1999) was used to estimate percent horizontal cover at 10, 20, 30, 40 and 50 m distance, as well as distance at which the cover board was first completely covered (sighting distance; truncated at 50 m). The 40 m and 50 m readings were not used as candidate predictor variables because they had a poor spread in values and contained a high proportion of 100% cover. A concave densiometer was used to estimate canopy cover in the four directions. Relascope counts, development class and general habitat category were registered separately for each quarter-sector of the plot. Horizontal point sampling with relascope by tree species gave us a measure of basal area (m² ha⁻¹) of trees of different species, and hence also tree species proportions of basal area. We registered species as pine, spruce, birch, RAW or 'other'. RAW is an acronym for rowan, aspen and willows, which were grouped because they are high quality forage, and not very abundant. Development class was registered either as 'none' where not applicable, or as a categorical value (1 = forest under regeneration, 2 = regenerated areas and young forest, 3 = young thinning stands, 4 = advanced thinning stands, and 5 = mature forest). Habitat category was registered in more detail, but grouped into three general categories before analysis: coniferous (>80% conifers),

Table 1. Description of field, LiDAR and terrain variables used to assess habitat characteristics for roe deer in Norway.

Variable	Description
<u>Field data</u>	
cov10	% of cover board covered at 10 m from plot center, mean of four cardinal directions
cov20	% of cover board covered at 20 m from plot center, mean of four cardinal directions
cov30	% of cover board covered at 30 m from plot center, mean of four cardinal directions
covgone	sighting distance to cover board at plot center, mean of four cardinal directions
canopy	% canopy cover at plot center, mean of densiometer reading in four cardinal directions
habitat	dominating habitat category – the one registered in most of the four quartiles
devclass	dominating development class – the one registered in most of the four quartiles
RAW.ba	rowan, aspen and willow species basal area (m ² ha ⁻¹) from relascope measure
total.ba	total basal area (m ² ha ⁻¹) from relascope measure
spruce.prop	proportion of total basal area that is spruce
pine.prop	proportion of total basal area that is pine
SP.prop	proportion of total basal area that is spruce or pine
<u>Terrain</u>	
dist.road	euclidian distance (km) to closest public road
elev	height above sea level, based on 100 m DTM
slope	slope of terrain in degrees, based on 100 m DTM, 3 × 3 neighbor cells
slope10	slope of terrain in degrees, based on 10 m DTM, 3 × 3 neighbor cells
vrm	vector ruggedness measure, based on 100 m DTM, using 3 × 3 neighbor cells
vrm10	vector ruggedness measure, based on 10 m DTM, using 3 × 3 neighbor cells
<u>LiDAR data</u>	
ulcd	understorey LiDAR cover density – ratio of understorey returns to the total number of understorey and ground returns ^a
dground	proportion of all returns < 0.5 m
d0.5	proportion of all returns 0.5 < x < 2.5 m
h20	20th height percentile (of all returns > 0.5 m)
h40	40th height percentile (of all returns > 0.5 m)
h60	60th 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	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)

^amodified from Wing et al. (2012). Defined in Methods.

Table 2. Sensor and flight parameters for the airborne scanning LiDAR campaigns.

Parameter	Southern part	Northern part
Instrument	Optech ALTM Gemini	Leica ALS50-II
Aircraft	fixed wing	fixed wing
Date of acquisition	3–4, 25–26 June and 2–3, 10, 22 July (2008)	23, 30, 31 May, and 1 June (2009)
Average flying altitude	1500 m a.g.l.	1550 m a.g.l.
Flight speed	75 m s ⁻¹	70 m s ⁻¹
Pulse repetition frequency	70 kHz	69 kHz
Scan angle	16.0°	17.0°
Pulse density on ground	mean 1.5 m ⁻² range 0.6–4.6 m ⁻²	mean 1.5 m ⁻² range 0.5–4.5 m ⁻²

deciduous (>20% broadleaved, hence also including some mixed forest types) and open. The four directional or sectorial measurements per plot were combined into one value by taking the mean of numerical values and the mode of categorical values. The field derived variables that were considered in the model selection are defined in Table 1.

LiDAR and terrain variables

The LiDAR data in this study are a composite of two projects that were originally acquired for other purposes under leaf-on conditions (Table 2). The two projects are from different dates that can potentially influence the LiDAR variables due to differences in plant phenology. Regarding the early 23 May flight, we assume leaves were sprung out, since the data was intended and used for forest inventory purposes. Moreover, we found a close to 1:1 relationship and a strong correlation in two focal LiDAR variables in a 9.5 km² overlap zone (Supplementary material Appendix 1, Fig. A2). The initial processing of the data was done by the contractors and datasets were delivered as points clouds with planimetric coordinates and ellipsoidal height, with ground returns classified. A ground surface was created as a triangular irregular network (TIN) of the echoes classified as ground returns. Height above the ground (dz) was calculated for all echoes by subtracting the height of the ground surface TIN. Two digital terrain models (DTMs) were derived from the TIN, one with 100 m cell size, and one with 10 m cell size. For each DTM, we calculated slope and vector ruggedness measure (VRM) (Sappington et al. 2007) using a 3 × 3 cell neighborhood; thus providing measures of topography at two different scales (30 m and 300 m). Values for elevation, slope and VRM were extracted for the raster cell that the plot center fell within. Distance to the closest public road was calculated and included as a proxy for hunter accessibility and/or human activity.

Accurate coordinates for the plot centers (kill sites and live roe deer sites) were acquired with a differential GPS system and post-processing of the GPS signal using base stations of the Norwegian Mapping Authority. When available (250 out of 292 plots), the accurate plot center coordinates (software estimated average SE = 0.3 m) were used in the extraction of LiDAR and terrain variables. LiDAR data were extracted from 2500-m² circular areas centered on each plot. The sensors were capable of recording up to four echoes per pulse. All echoes were used in the analysis, as it yielded better results than splitting the dataset into first and last echoes did. Various variables describing the vertical distribution of the echoes (Table 1) were calculated for each plot. Three variables were aimed at quantifying the amount of understory vegetation. The understory LiDAR cover density (ulcd) variable is defined as the ratio of understory returns to the total number of understory and ground returns (Wing et al. 2012). Our variable is a simplification of that used by Wing et al. (2012) because we lacked calibrated intensity measures, thus we defined the returns only based on height (ground: dz < 0.5 m, understory: 0.5 < dz < 2.0 m). The two other understory metrics were dground, the proportion of all returns with dz < 0.5 m, and the variable d0.5, the proportion of all returns with 0.5 < dz < 2.5 m.

Statistical analyses

Logistic regression was used to relate habitat characteristics to predation risk. The response variable (y) represented relative predation risk: plots where roe deer had been killed had y = 1, plots from GPS marked animals or registered feces had y = 0. In this way, kill sites were compared with the plots assumed to represent the proportional time use of the habitat by roe deer. Predictor variables in this model quantify the change in predation risk (on logit scale) per unit predictor variable of a location being a kill site instead of a live site. Risk of predation from humans and lynx were carried out as two separate analyses, with different sets of kill sites, but with the same set of used locations (y = 0). All statistical analyses were performed with the software R ver. 2.14.1.

Logistic regression models were grouped in three sets: first using only field registered vegetation information as predictor variables; second adding LiDAR data in addition to field data; and third using LiDAR data alone. Terrain variables were always included. To avoid problems of multicollinearity, highly correlated variables (r > 0.5) were identified and only the variable with the lowest AIC in a univariate regression was kept (results of the univariate modeling and variable selection: Supplementary material Appendix 1 Table A2). To allow comparison between the lynx and hunting models the same cover board variable and understory LiDAR metric was included in both. These two variables were chosen so as to minimize the sum of the AIC of both models. The final model selection made use of the stepAIC forward selection, which ends when it cannot reduce the AIC value any further by adding a new variable. In the lynx predation model, potential interactions between season and selected variables (canopy cover, basal area of RAW, habitat, cov20 and ulcd) were also considered. If no interactions with season were included in the model, the main effect of season was not kept either, as it would only reflect different proportions of kill- and live sites by season, an effect which is dominated by variable sampling intensity of kill sites by field personnel (Table 3). For the hunting risk model, interactions with season were not considered since there were no hunting kills outside the hunting season. The final models were checked against hunting season data only, and also against a dataset excluding southern geographical outliers, and found to provide qualitatively similar estimates (model estimates in the Supplementary material Appendix 1 Table A3, A4). A multivariate analysis was also explored, indicating relative consistency in grouping patterns of lynx kill sites, hunter kill sites and used kill sites in multivariate space across individuals and across seasons (Supplementary material Appendix 2).

Table 3. Seasonal distribution of roe deer live-sites (feces and GPS) and kill-sites from Hallingdal, Norway. Number of sites (independent observations) in each category is listed.

	Hunt	Winter	Summer
Feces	0	36	0
GPS	47	45	40
Hunter kill	53	0	0
Lynx kill	20	40	11

The predictive ability of the models was evaluated using the area under the ROC curve (AUC), which compares true vs. false positives for a range of discrimination values. When reporting results of the models, we define values for AUC of 0.5 to 0.6 as no evidence of predictive ability, 0.6 to 0.7 as poor predictive ability, 0.7 to 0.8 as fair predictive ability, 0.8 to 0.9 as good predictive ability, while an AUC above 0.9 indicate excellent predictive ability.

Based on the best LiDAR and terrain variable models for lynx and hunters, we created spatial maps of the predicted predation risk. To stay within the range of the variables used in the models, we restricted the spatial prediction to areas within 4500 m from a public road. Because the number of roe deer shot by hunters and killed by lynx does not reflect absolute risk levels, we standardized the raster values in each map individually, with a mean of zero and standard deviation of 1. For each map, a pixel value higher than zero mean a higher than average risk of being killed by that predator. We define 1 and -1 as cut off values for high and low predation risk (which give a theoretic expectation of ca 16% of pixel values beyond the cut off values in each tail of the distribution). After standardizing it is possible to identify 'safe zones' where both predators have lower predation risk, contrasting areas where one predator has high risk and the other low, and areas with 'double predation'.

Results

The best model predicting lynx predation risk using only terrain variables and field data included basal area of RAW, proportion of spruce, distance to road, and terrain ruggedness both at 30 m and 300 m scale (Table 4). All variables were positively correlated with predation risk. Interactions with season were not included in the best

model. The model had an AUC of 0.763, indicating a fair predictive ability of the model. When adding LiDAR variables, the lynx predation model became more complex. In addition to slope entering the model, one LiDAR variable was included: understory cover (ulcd), which was positively correlated with predation risk (Table 4). The performance of the model improved slightly with an increase in AUC from 0.763 to 0.785, and a 4.0 unit improvement in AIC.

The best model predicting predation risk from hunting using only terrain variables and field based measures contained horizontal cover at 20 m, canopy cover, habitat type, proportion of pine, distance to road, slope, and terrain ruggedness at 30 m scale (Table 5). An increase in distance to road, horizontal cover and canopy cover was associated with a decrease in predation risk by humans. Steeper slope, a greater proportion of pine, and more rugged topography led to greater risk. Open habitats were most risky, followed by coniferous, while deciduous were the least risky. The AUC statistic for this model was 0.796. The best model considering also LiDAR variables differed by including the LiDAR metric hcv (the coefficient of variation of echo heights), and excluding canopy cover and ruggedness (Table 5). Field measured horizontal cover remained in the model, while LiDAR measured understory (ulcd) was not included. Overall, the inclusion of LiDAR measures made only slight improvements on this model also. AUC remained similar (increased from 0.796 to 0.798), and there was a 2.2 unit improvement in AIC.

Compared to the field based and the combined models, a model with only remotely sensed terrain- and LiDAR variables performed nearly equally well for lynx predation (Table 4). The model's AUC statistic of 0.756 indicates fair predictive power. The hunting risk is captured less well by the LiDAR-only model, the model's AUC of 0.713 indicates a notable drop in predictive performance relative

Table 4. The best models for lynx predation risk using field data only, LiDAR data only and both types of data together (combined model). Significant effects ($p < 0.05$) are in bold. Lynx kill sites ($n = 71$) are compared to all used sites (GPS and feces) ($n = 168$).

	FIELD model			LiDAR model			COMBINED model		
	β	SE	p	β	SE	p	β	SE	p
(intercept)	-2.72	0.37	<0.001	-2.16	0.39	<0.001	-2.89	0.47	<0.001
<u>Field data</u>									
cov20	-	-	-	-	-	-	-	-	-
canopy	-	-	-	-	-	-	-	-	-
habitat ^a									
deciduous	-	-	-	-	-	-	-	-	-
open	-	-	-	-	-	-	-	-	-
RAW.ba	0.118	0.052	0.024	-	-	-	0.0964	0.054	0.075
spruce.prop	1.98	0.49	<0.001	-	-	-	1.84	0.51	<0.001
pine.prop	-	-	-	-	-	-	-	-	-
<u>LiDAR</u>									
ulcd	-	-	-	12.6	3.6	<0.001	10.0	3.8	0.008
hcv	-	-	-	-	-	-	-	-	-
<u>Terrain</u>									
dist.road	0.499	0.22	0.021	0.604	0.22	0.005	0.580	0.22	0.008
slope10	-	-	-	-0.0394	0.025	0.11	-0.0429	0.025	0.090
vrn	67.6	32	0.033	93.0	35	0.008	82.6	36	0.021
vrn10	108	44	0.013	112	43	0.009	121	45	0.008
AUC	0.763			0.756			0.785		
AIC	253.9			260.6			249.9		

^areference = coniferous.

Table 5. The best models for hunter predation risk using field data only, LiDAR data only and both types of data together (combined model). Significant effects ($p < 0.05$) are in bold. Hunter kill sites ($n = 53$) are compared to all used sites (GPS and feces) ($n = 168$). Running the model on data from the hunting season only (total $n = 99$) yielded qualitatively similar estimates.

	FIELD model			LiDAR model			COMBINED model		
	β	SE	p	β	SE	p	β	SE	p
(intercept)	0.927	0.96	0.33	-1.82	0.57	0.001	-0.557	0.90	0.54
<u>Field data</u>									
cov20	-0.0279	0.0087	0.001				-0.0338	0.0093	<0.001
canopy	-0.0128	0.0058	0.026				-	-	-
habitat ^a									
deciduous	-1.24	0.61	0.043				-1.31	0.62	0.034
open	-0.168	0.60	0.78				0.464	0.49	0.35
RAW.ba	-	-	-				-	-	-
spruce.prop	-	-	-				-	-	-
pine.prop	0.980	0.54	0.072				1.32	0.53	0.013
<u>LiDAR</u>									
ulcd				-17.6	5.3	<0.001	-	-	-
hcv				0.0158	0.0090	0.080	0.0244	0.0094	0.009
<u>Terrain</u>									
dist.road	-1.09	0.56	0.050	-1.13	0.49	0.020	-1.06	0.56	0.058
slope10	0.0665	0.027	0.015	0.0441	0.029	0.12	0.0692	0.027	0.009
vrn	-	-	-	80.0	44	0.026	-	-	-
vrn10	95.4	63	0.13	131	59	0.026	-	-	-
AUC	0.796			0.713			0.798		
AIC	212.8			231.6			210.6		

^areference = coniferous.

to the two models including field data (Table 5). In the LiDAR-only models there was a contrasting effect of understory cover on the risk of lynx predation versus human harvesting (Fig. 2) supporting prediction 2A. When it comes to terrain, effects differed notably from our predictions. Ruggedness was associated with higher risk in all three top models for lynx, and with higher risk in two of the models for hunting (Fig. 2). In the models where slope was included, there was a contrasting effect of slope from the two predators, but the negative effect on lynx risk

and positive effect on hunter risk were the reverse of what we predicted (P2B). There were strong spatial contrasts in the risk patterns for both lynx and hunters (Fig. 3a–b). When combined (Fig. 3c), there tended to be a spatial relationship with the distance to roads where strong contrasting predation risk occurred close to roads and far away from roads. Additionally, there was a patchy distribution in valley sides with ‘double high’ predation risk from lynx and hunters, and a few scattered small patches with double low predation risk. With our defined threshold

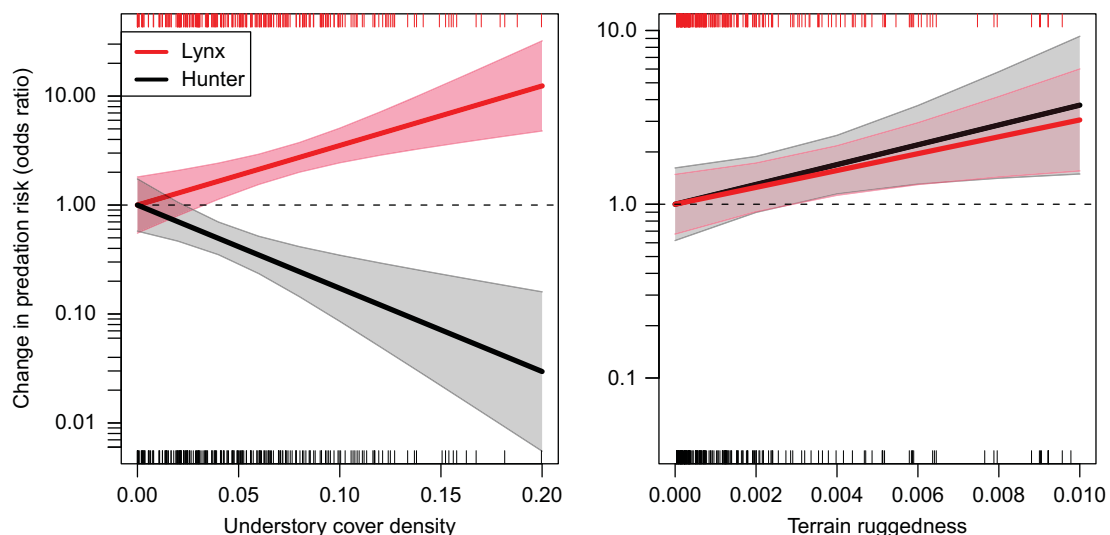


Figure 2. Odds ratio ($\pm 95\%$ CI) of predation risk of lynx and humans with respect to change in two selected habitat attributes: understory cover density and terrain ruggedness on 30 m scale, based on the best models using LiDAR and terrain variables. The odds ratios are relative to the case of no understory cover, or even terrain ($x = 0$). Distribution of data points is shown as rug plots along the top and bottom of each graph for lynx and hunter models separately.

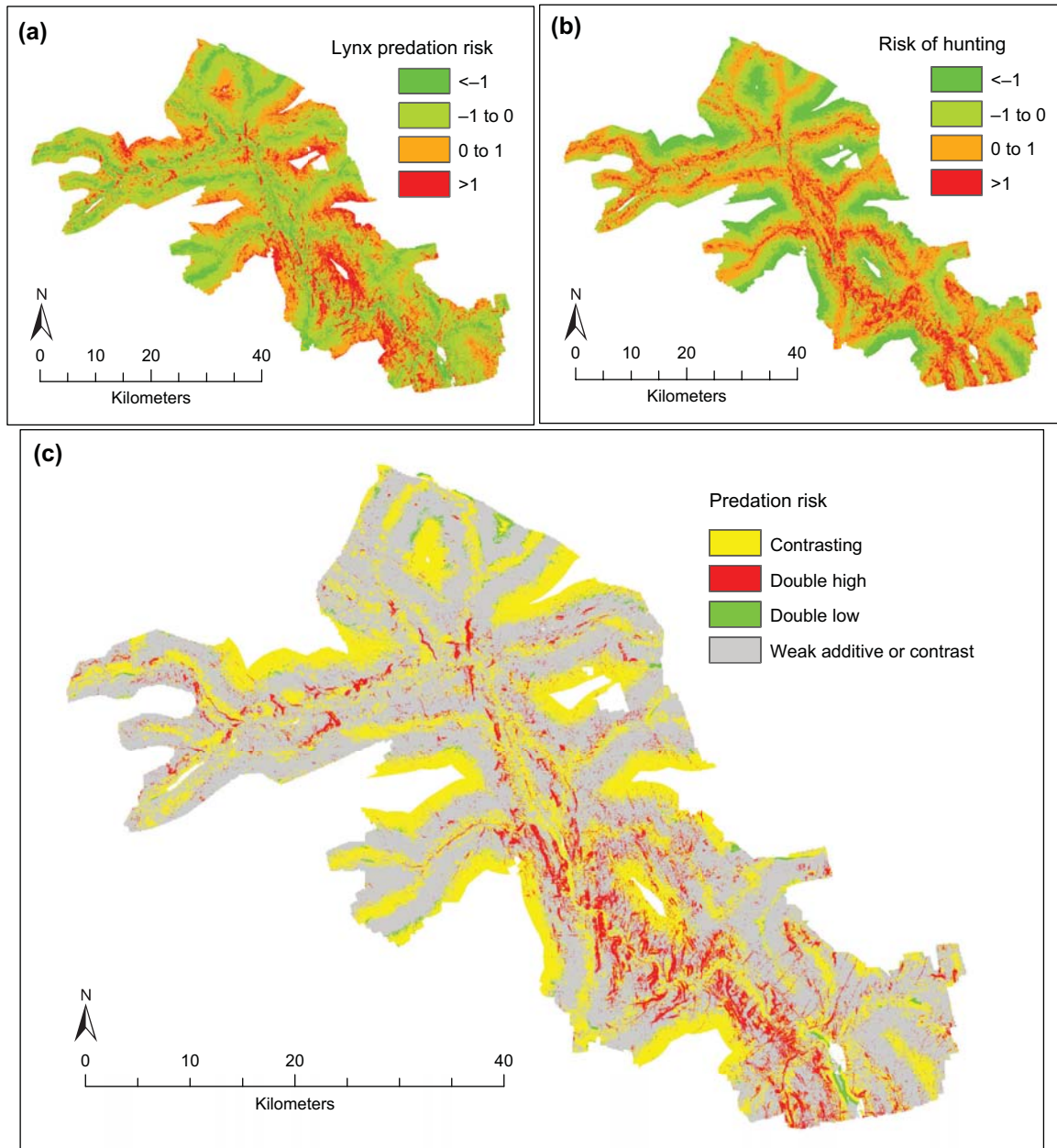


Figure 3. Predicted risk map for (a) lynx and (b) hunters and (c) combined based on normalized values (mean = 0, standard deviation = 1) from predictions on the logit scale. In (a) and (b), pixels with higher than mean risk will get positive values while pixels with lower than mean risk will get negative values. The combined risk map (c), display areas with ‘contrasting’ risks (one predator > 1 and the other < 0 , or one predator < -1 and the other > 0), ‘double high’ indicate additive high risk (one predator > 1 , the other > 0), while ‘double low’ indicate safe areas with low risk from both predators (one predator < -1 , the other < 0). The remaining category “weak additive or contrast” indicate areas with no strong pattern of risk (absolute value between 0 and 1 for both predators; i.e. both are within 1 SD from the mean risk).

of high risk, 31% of the total area had large contrast in predation risk, 8% double high risk, and 1% double low risk.

Discussion

Many ungulates now experience a situation in which large carnivores such as wolves, bears and lynx have recolonized former ranges, thus adding a new potential risk in addition to

human hunting (Berger et al. 2001). However, even though large habitat differentiation among large carnivores is documented (May et al. 2008), ungulates risk landscapes in a multiple predator setting has been explored only in a few carnivore–ungulate systems (Atwood et al. 2007, 2009, Proffitt et al. 2009, Thaker et al. 2011). Understanding this is particularly important in multi-use landscapes where human hunting is a major cause of death. For roe deer in southern Norway, we found evidence that the risk landscape imposed by humans and lynx differed. The risk of

lynx predation increased with LiDAR understory cover, while the risk of hunting mortality decreased with LiDAR understory cover. However, there were also 'double risk' areas, as for example rugged terrain increased risk of predation from both. Refuge areas with low predation from both predators were rare. Our study thus highlights how multiple predators may squeeze prey from two sides, making it difficult to single out one simple strategy to avoid predation.

A multiple predator squeeze – being 'food for the many'

It is suggested that large carnivores may create a landscape of fear for ungulates. The most famous example being wolf-elk in Yellowstone National Park, USA (Laundré et al. 2001), where a behavioral shift of elk has been claimed to cause a trophic cascading effect in the ecosystem (argued by Ripple et al. 2001, but contested by Kauffman et al. 2010). Similarly, it has been shown that elk using more open habitat are at higher risk of being killed by human hunters (Ciuti et al. 2012). The smaller roe deer is in a parallel manner subject to spatially heterogeneous and habitat dependent predation risk. With a contrasting effect of two predators, avoiding predation by one can lead to increased exposure to the other predator, i.e. risk enhancement (Sih et al. 1998). A similar conflict with regards to habitat use was documented by (Atwood et al. 2007, 2009) who found that avoidance of wolf predation by moving into denser cover left elk at greater risk of cougar predation. If the roe deer in our study area use more open habitat they are at greater risk of being shot; if they use habitat with denser understory they are at greater risk of being killed by lynx. Contrasting spatial patterns in risk from two predators could therefore result in higher net predation rates, but lower non-lethal effects (Cresswell and Quinn 2013) and lower potential for behaviorally mediated trophic cascades than would be predicted considering only one predator. This is because when gradients in predation risk get flatter by considering several predators, the potential gain of shifting habitat is smaller. Thus the optimal response from prey would be weaker, implying also weaker overall risk effects and ecosystem effects. On the other hand, synergistic spatial patterns in risk may strengthen anti-predator behavior. When relative predation risks align, prey may be able to take one unified strategy to reduce risk, implying potentially greater overall risk effects or ecosystem effects. This is particularly true if the double predation risk has a strong trade off against important resources, meaning that double predation will be costly. Studies on elk–wolf–cougar have documented contrasting, habitat specific differences in predation risk from two predators, and an explicit (Atwood et al. 2007, 2009) tradeoff in risk associated with shifting habitat use. Proffitt et al. (2009) also found contrasting risk with habitat and habitat modulated strength of anti-predator responses. A wintertime study on roe deer in southern Norway found that roe deer did not shift away from dense forest habitat (Ratikainen et al. 2007) probably because they were constrained by other factors such as food and thermoregulation. In addition, encounters with lynx may be rare while the risk of starvation is a constant threat, possibly exerting pressures strong enough to subvert any risk response.

In addition to understory cover, terrain attributes and tree species composition modified predation risk. That tree species composition affected predation risk can also be due to lateral cover. For instance, mature spruce stands are generally much more visually dense in the horizontal plane than mature pine stands, making the first a good hunting site for lynx and the second a better hunting site for humans. The terrain effects did not follow the expectation of human preference of 'easy' terrain and lynx preference of 'difficult' terrain. More rugged terrain increased the risk of hunting mortality from both – creating 'double risk' areas. It is possible that steeper and more rugged terrain can give hunters an advantage in locating and stalking up to roe deer during a hunt, or in predicting animal movement during drive hunts if deer are more prone to follow paths in difficult terrain. That lynx predation risk increases with ruggedness is as expected for an agile stalking felid that can use also topography as stalking cover while the reduction in predation risk in steep slopes may be associated with risks of injury during attack.

Two components of predation risk can differ according to habitat: encounter rate and hunting success (Hebblewhite et al. 2005). If lynx exactly matched the habitat specific time use of roe deer and were equally successful in all habitat types there would be no effect of habitat characteristics on predation risk. The presence of such effects documented here means that lynx either spend more time than roe deer in dense, rugged habitat (increase encounter rate) or that hunting success increased in such habitat. We invoke both mechanisms in our explanations, but stress our main hypothesis that hunting modes of lynx and human hunters influence predation risk through hunting success. For human hunters, the need for high visibility when using a gun may both affect hunting success and, indirectly, hunter habitat preference. For lynx, the positive association between cover and hunting success is corroborated by snow-tracking data from southeastern Norway (Odden unpubl.). Other studies that have analytically decomposed risk into encounter rate and hunting success for wolves and cougar, found that habitat affected both processes (Hebblewhite et al. 2005, Atwood et al. 2009). Lynx select for suitable roe deer habitat (Odden et al. 2008), but may select for denser habitat than roe deer due to secondary factors, such as exposure to humans. Lynx are attracted to human-disturbed areas due to the high density of roe deer on agricultural fields and feeding sites in winter, but avoid the areas with most human activity, which could potentially function as refuges for roe deer from lynx (Basille et al. 2009), but not from human hunting, as seen by the contrasting effect of distance from public roads.

Measurement of cover and scale

Resource selection functions and habitat suitability modeling are frequently used in management. In some cases, such maps provide very broad descriptions limited by the lack of a link between habitat categories and resource levels (Loe et al. 2012). This is where LiDAR holds promise for bridging the gap of spatial scales, and allows for analysis on a range of scales. Terrain characteristics on 30 and 300 m scale were both relevant for predation risk. With coverage of LiDAR in our study area, it is possible to extend the

prediction of risk on the basis of our models using only LiDAR and terrain data beyond the plots with field data (Fig. 3). Although the LiDAR models performed poorer than the models based on field measured data, the LiDAR model for lynx suffered only a minor reduction in predictive ability while the model for hunting deteriorated more. One limitation is probably the lack of information about tree species composition, a notorious challenge to extract from LiDAR data except at very high resolution (Turner et al. 2003, Brandtberg 2007), but available from other remote sensing data such as optical information (Ørka et al. 2013). The second issue is that it is challenging to measure and predict understory cover with laser scanning, and the explanatory power of the models tends to be low (Martinuzzi et al. 2009, Wing et al. 2012). However, LiDAR captures some of the key variability and could be used together with additional data (forest inventory maps, aerial photos, or other land use maps) for the gain of making a high-resolution map visualizing in detail the risk landscapes over large areas.

Conclusion and perspectives

We have demonstrated that risk habitats exist for roe deer, and that two predators impose contrasting risk along habitat gradients, in particular cover and distance to roads, but aligning risk with respect to another habitat gradient, terrain ruggedness. Considering the two landscapes of risk together revealed a strong reduction in refuge habitats with low risk of predation. As more predators with sufficiently different landscapes of risk are added to an assembly, opportunities to escape predation will be lower and anti-risk behavior is expected to bring less benefit at the same cost, yielding lower net risk effects. We thus provide one important step forward in understanding how the landscapes of risk from multiple predators with elements of contrast and similarity may combine to affect the spatial ecology of prey. Whether the landscape of risk induces a habitat dependent landscape of fear depends on whether deer are able to perceive and predict the risk and how they respond to it, if at all (Cromsigt et al. 2013). The higher temporal predictability of human hunting pressure makes it both easier, and more cost-efficient, to respond to than predation from natural predators (Proffitt et al. 2009). If roe deer are able to assess temporal distribution of risk, responses to humans should be limited to the four month long hunting season (Sonnichsen et al. 2013), while lynx should elicit responses year round. As for diurnal patterns in risk, we did not have fine-scale temporal information on kill sites to determine this, but generally, lynx are active during nighttime and hunters during daytime. Because of the short temporal overlap in risk, temporal discrimination in prey response may reduce the tradeoff inherent in the contrasting risk landscapes of lynx and humans. On the other hand, areas that are risky with regards to both predators but have important resources can become the premises of a temporal tradeoff between exposure to the two predators (cf Crosmary et al. 2012). Recolonizing large carnivore populations add considerable complexity to ecosystems, and understanding functioning of multiple predator and prey landscapes yields a new array of ecological challenges.

Acknowledgements – This study is based on GPS data from collared lynx and roe deer, kill sites data, and fecal pellet surveys collected by the project Scandlynx (<<http://scandlynx.nina.no/>>), and was supported by the Research Council of Norway, the Norwegian Directorate for Nature Management (DN), the Norwegian Inst. for Nature Research (NINA), the Nature Protection Division of the County Governor's Office for Buskerud counties, and the municipalities of Flå, Gol, Nes and Ål as well as by the large carnivore management board for region 2. We would like to thank the hundreds of people who have helped us in the field during the years of this study, in particular Tore Olsen and Karen Johanne Gulsvik who collected field data specifically for this paper and the hunters who shared information with us. The primary author was funded by a doctoral scholarship from the Norwegian University of Life Sciences. We wish to thank Nicolas Morellet who greatly improved an earlier version of the manuscript.

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Supplementary material (available online as Appendix oik-00938 at <www.oikosjournal.org/readers/appendix>). Appendix 1.

Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J. and Mysterud, A. 2013. 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 doi: 10.1111/j.1600-0706.2013.00938.x

Appendix 1

Table A1. Detailed sample sizes for individuals by season for individual GPS marked roe deer, lynx providing kill-sites and hunters providing kill-sites. Sex of roe deer and lynx, and GPS collar fix success rate for roe deer.

individual	hunt	summer	winter	total	sex	fix rate (%)
<u>Roe deer</u>	47	40	45	132		
6212	3	0	0	3	female	99.8
6214	3	2	4	9	female	99.1
6216	0	0	5	5	male	99.5
6219	4	2	4	10	male	99.2
6221	6	2	2	10	male	99.0
62242	2	3	4	9	male	99.5
6480	4	4	2	10	male	98.8
6484	3	5	2	10	male	99.2
6485	3	4	2	9	female	98.6
8001	4	3	3	10	male	99.1
8003	1	4	4	9	female	95.0
8004	3	3	4	10	female	77.2
8005	3	3	3	9	female	86.8
8006	5	3	2	10	female	91.8
8007	3	2	4	9	female	89.7
<u>Lynx</u>	20	11	40	71		
F189	8	5	4	17	female	
F218	5	1	14	20	female	
F228	1	0	5	6	female	
F237	1	1	7	9	female	
M187	0	1	0	1	male	
M209	3	1	2	6	male	
M263	2	1	6	9	male	
M273	0	0	2	2	male	
M275	0	1	0	1	male	
<u>Hunters</u>	53			53		
EK	3			3		
GRAN	2			9		
HT	9			4		
JA	7			3		
JN	4			2		
KHJ	3			7		
KPR	16			16		
ODE	9			9		

Table A2. Results of the univariate modeling for variable selection (included variables for lynx models and hunting models are in bold). Variables denoted with the same letter (a–g) were correlated $\rho > 0.5$. In some of the groups it was possible to include several variables because only some of the variables were correlated $\rho > 0.5$, within these groups, the lowest AIC variable was chosen first, highly correlated variables were excluded, and again the lowest AIC variable was chosen. From groups denoted with a * (a, f) one variable measuring cover was chosen by minimizing overall AIC in both analyses. Variables AICs marked with ** were chosen out of their groups prioritizing ease of interpretation, as there was only very minor differences in AIC. Δ AIC values are relative to the constant model.

Variable	Comparison	AIC _{lynx}	Δ AIC _{lynx}	AIC _{hunt}	Δ AIC _{hunt}
constant	0	292.8	0.0	245.5	0.0
cov10	a*	294.6	1.8	240.9	-4.6
cov20	a*	294.2	1.4	229.3	-16.2
cov30	a*	292.8	0.0	237.7	-7.8
covgone	a*	294.8	2.0	237.3	-8.1
canopy	b	289.1	-3.7	244.8	-0.7
total.ba	b	288.8	-4.0	247.2	1.7
habitat	c	277.4	-15.4	234.2	-11.3
SP.prop	c	279.1	-13.7	246.2	0.7
spruce.prop	c	272.1	-20.7	245.1	-0.4
devclass	c	-	-	240.3	-5.2
pine.prop	c	-	-	240.9	-4.6
total.ba	c	-	-	247.2	1.7
slope	d	294.5	1.7	242.2	-3.2
slope10	d**	293.4	0.6	242.4	-3.1
elev	e	288.4	-4.4	246.7	1.2
dist_road	e	286.0	-6.8	245.1	-0.4
ulcd	f*	284.1	-8.7	242.9	-2.6
dground	f*	288.5	-4.3	241.4	-4.1
d0.5	f*	282.6	-10.2	245.6	0.1
h20	g	294.2	1.4	247.2	1.7
h40	g	294.6	1.8	247.1	1.6
h60	g	294.8	2.0	247.1	1.6
h80	g	294.5	1.7	247.1	1.6
h90	g**	293.5	0.7	247.1	1.6
hmean	g	294.8	2.0	247.1	1.6
hqmean	g	294.6	1.8	247.1	1.6

Table A3. Model estimates for the LiDAR data model of lynx predation risk applied to subsets of the data: hunting season only and geographical subset excluding the southernmost points (south of UTMN 32V N6708000, south of the cluster of points close to Nesbyen). The model estimates from the full dataset are the same as presented in Results and are included here for ease of comparison. Sample sizes differ between the three: The full dataset compares 71 lynx kill sites to year round used sites (132 GPS + 36 feces), hunting season dataset compares 20 lynx kill sites to 47 used sites (all GPS). In Nesbyen and north dataset, 56 lynx kill sites are compared to year round used sites (131 GPS + 25 feces).

	full dataset		Hunting season dataset		Nesbyen and north dataset				
	β	SE	p	β	SE	p			
(intercept)	-2.16	0.39	<0.001	-2.03	0.78	0.009	-2.66	0.46	<0.001
<u>ALS data</u>									
ulcd	12.6	3.6	<0.001	20.6	7.5	0.006	11.5	4.0	0.004
hcv	-	-	-	-	-	-	-	-	-
<u>Terrain</u>									
dist.road	0.000604	0.00022	0.005	-0.0000792	0.00040	0.84	0.000757	0.00025	0.002
slope10	-0.0394	0.025	0.11	-0.0221	0.048	0.64	-0.0179	0.028	0.53
vrn	93.0	35	0.008	153	81	0.060	156	52	0.002
vrn10	112	43	0.009	-236	188	0.21	93.4	49	0.057
AUC	0.756			0.784			0.802		

Table A4. Model estimates for the LiDAR data model of hunter risk, using only subsets of the data to test its robustness: hunting season only and geographical subset excluding the southernmost points (south of UTMN 32V N6708000, south of the cluster of points close to Nesbyen). The model estimates from the full dataset are the same as presented in Results and are included here for ease of comparison. Sample sizes differ between the three: The full dataset compares 53 hunter kill sites to year round used sites (132 GPS + 36 feces), hunting season dataset compares 53 hunter kill sites to 47 used sites (all GPS). In Nesbyen and north dataset, 46 hunter kill sites are compared to year round used sites (131 GPS + 25 feces).

	full dataset	Hunting season dataset			Nesbyen and north dataset				
	β	SE	p	β	SE	p	β	SE	p
(intercept)	-1.82	0.57	0.001	-1.73	0.85	0.040	-2.62	0.64	<0.001
<u>ALS data</u>									
ulcd	-17.6	5.3	<0.001	-23.7	7.7	0.002	-17.7	5.8	0.002
hcv	0.0158	0.0090	0.080	0.0409	0.016	0.012	0.0151	0.0095	0.11
<u>Terrain</u>									
dist.road	-0.00113	0.00049	0.020	-0.00156	0.00063	0.012	-0.000757	0.00047	0.11
slope10	0.0441	0.029	0.12	0.0540	0.039	0.17	0.0797	0.031	0.011
vrn	80.0	44	0.026	234	87	0.022	138	64	0.030
vrn10	131	59	0.026	149	87	0.087	155	64	0.015
AUC	0.714			0.775			0.769		

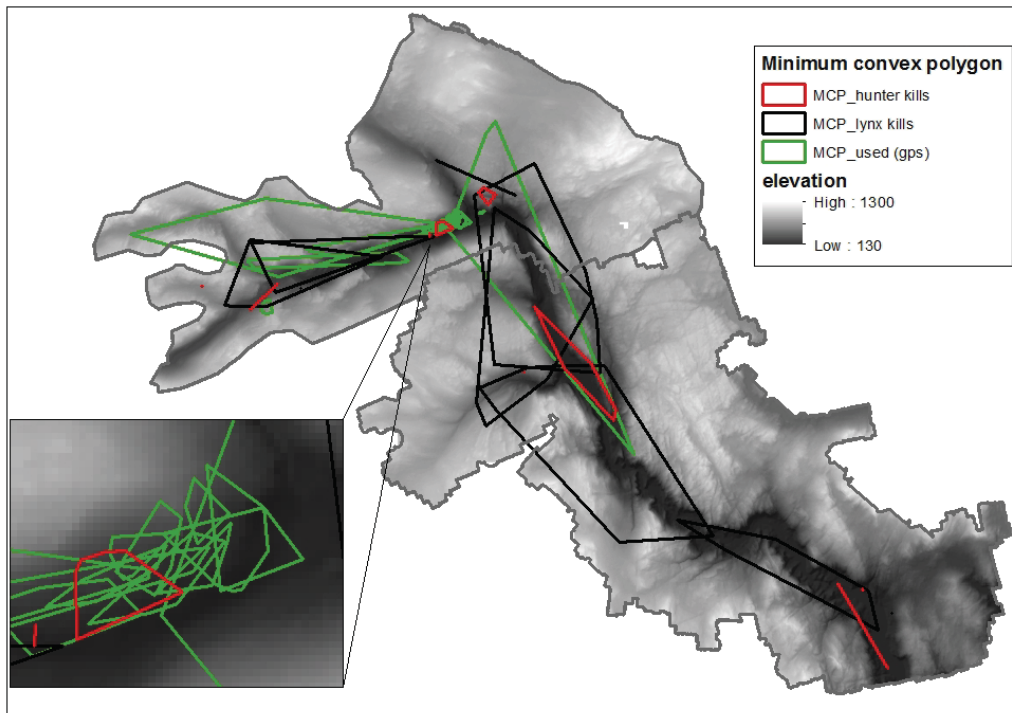


Figure A1. Distribution of individuals across the landscape shown by minimum convex polygons (MCPs) of the plots associated with unique individuals: hunters contributing kill sites, marked lynx contributing kill sites and marked roe deer contributing used sites.

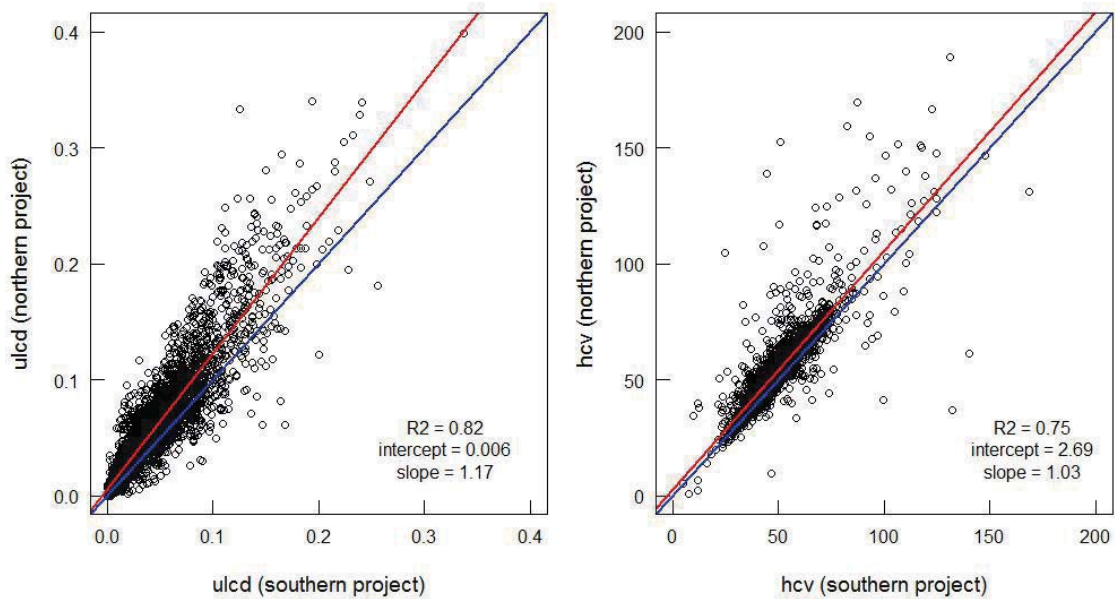


Figure A2. Correlation between LiDAR variables understory LiDAR cover density (ulcd) and coefficient of variation of non-ground echoes (hcv) calculated for the same cells in an area of overlap of the two LiDAR scanning projects. All ulcd values are shown ($n = 3906$), while only hcv values < 200 are used in the comparison ($n = 3839$). The blue line shows the ideal 1:1 relationship between the two variables, the red line is the estimated slope; coefficients are given in the plot panels.

Appendix 2

Explorative multivariate analysis

To identify differences between the groups of plots belonging to used sites, lynx kill sites and hunter kill sites, we performed a between-class principal component analysis. The three groups can be separated in multivariate space, but not fully, as the region of overlap is substantial (Fig. A3). We can assess which variables capture differences between the groups by looking at their contribution to the principal components (PC) in the loading plot (Fig. A4). PC1 (x-axis) is an axis representing a gradient from more open to more closed, left to right, and separates lynx kills from hunter kills with used sites in the middle. PC2 (y-axis) separates both types of kill sites from used sites, and aligns with the contrast between deciduous and coniferous habitat, ruggedness measures, laser height measurements, and slope. How different individuals are placed in the multivariate space is shown in Fig. S5. Here, we see that there is some inter-individual variation, and it is the greatest in hunters where some individuals (HPR and GRAN) lean into the region typical of lynx kill sites, while other individuals (e.g. JN, KHJ) are farther to the right on PC1, and hunt in terrain characterized by openness. This is as expected, and shows that the data spans a range of methods known to be used in hunting. Differences between seasons are also present in lynx kill sites (Fig. A6), but the kill sites from the hunting season represent the centre of mass of year-round lynx-kill sites.

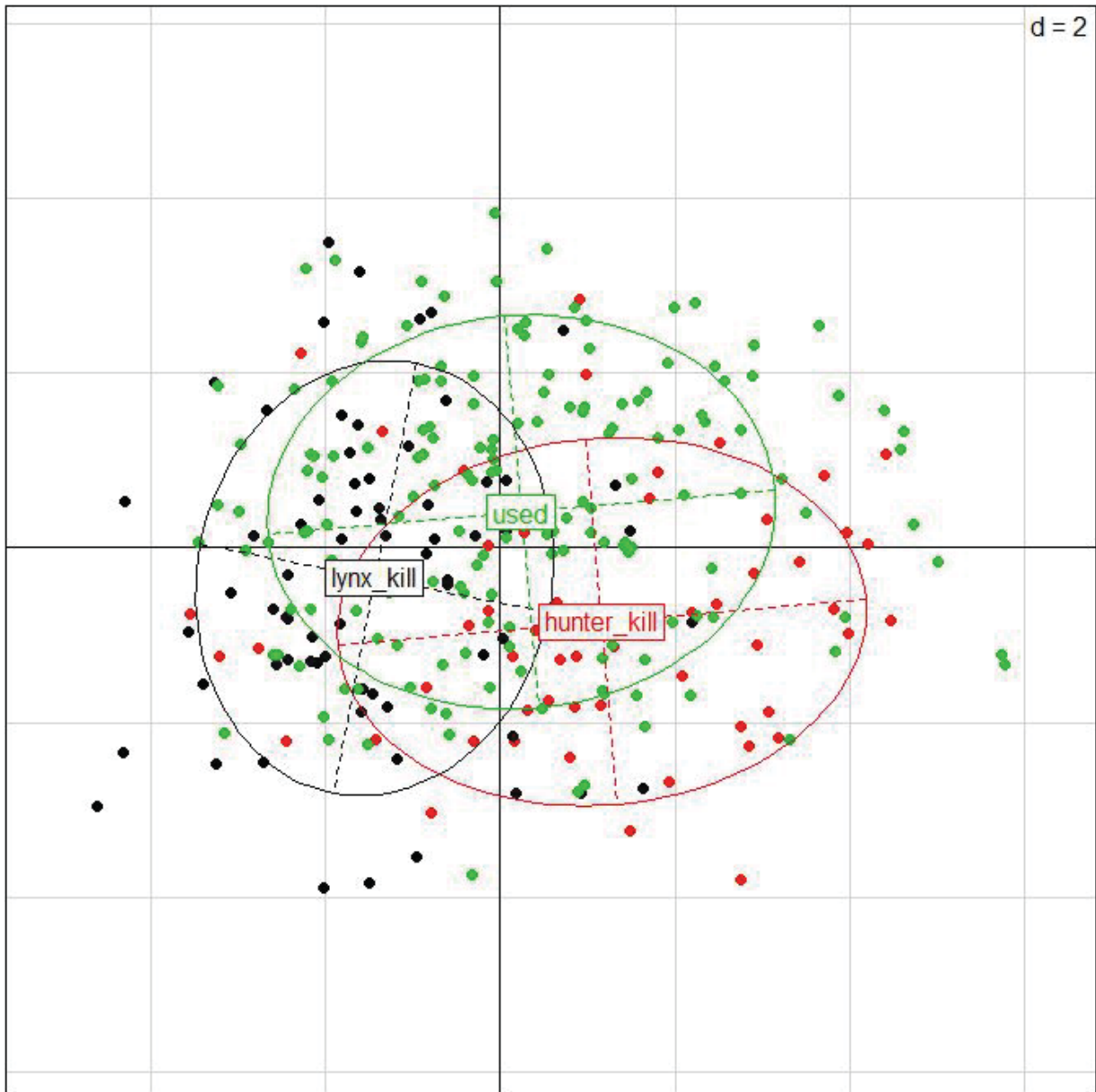


Figure A3. Observations and their group membership (used, lynx kill or hunter kill) shown on the principal component axis 1 (x) and 2 (y).

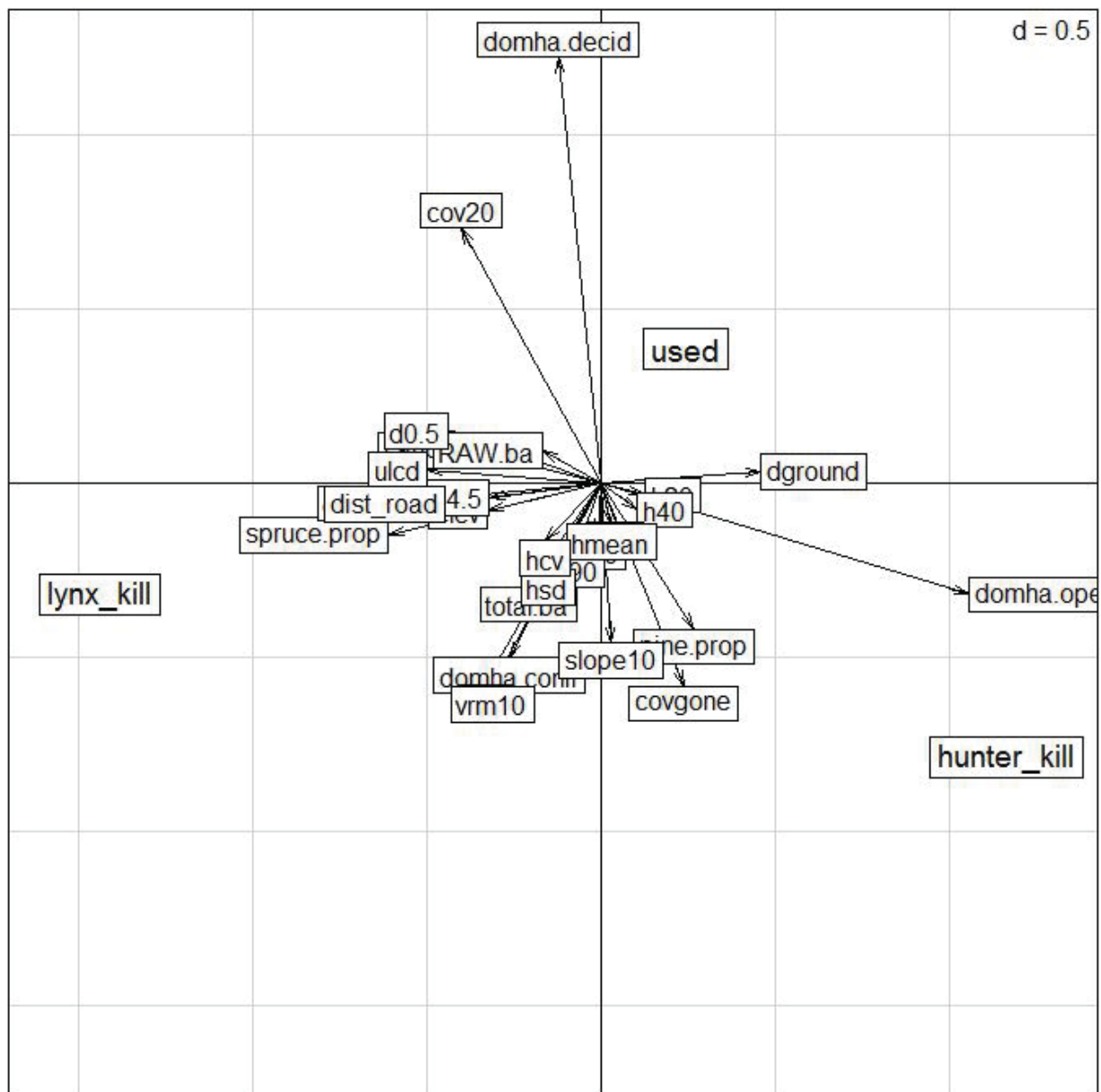


Figure A4. Loadingplot of the contribution of the variables to the principal components axis 1 (x) and 2 (y). The centers of the three groups of observations (used, lynx kill and hunter kill) are shown.

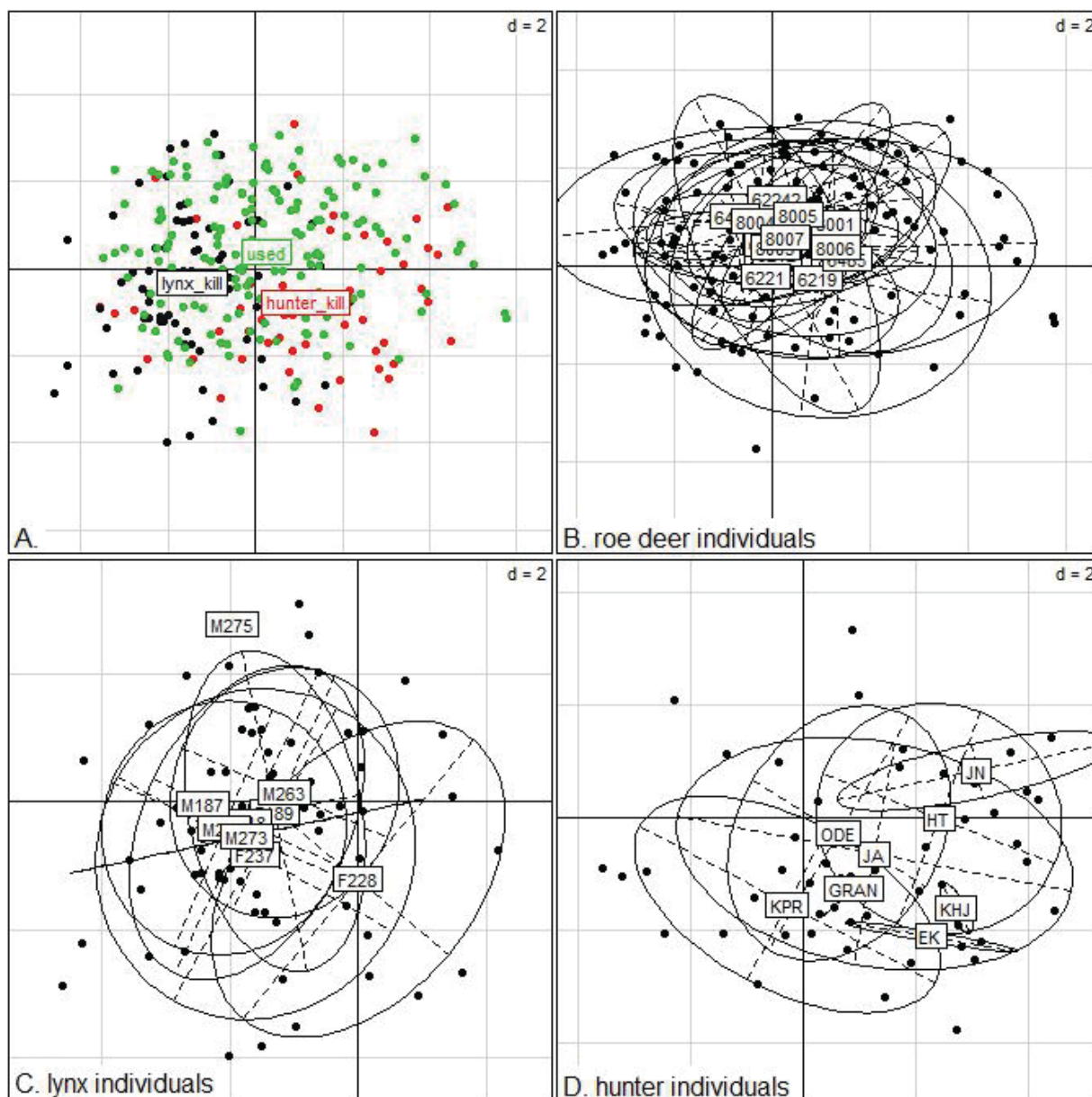


Figure A5. Panel A: Observations and their group membership (used, lynx kill or hunter kill) shown on the principal component axis 1 (x) and 2 (y). Panels B, C, D: Observations are grouped by individuals on the same scales (PC1 and PC2). Lynx M275 contributed only a single point, and has no associated ellipse.

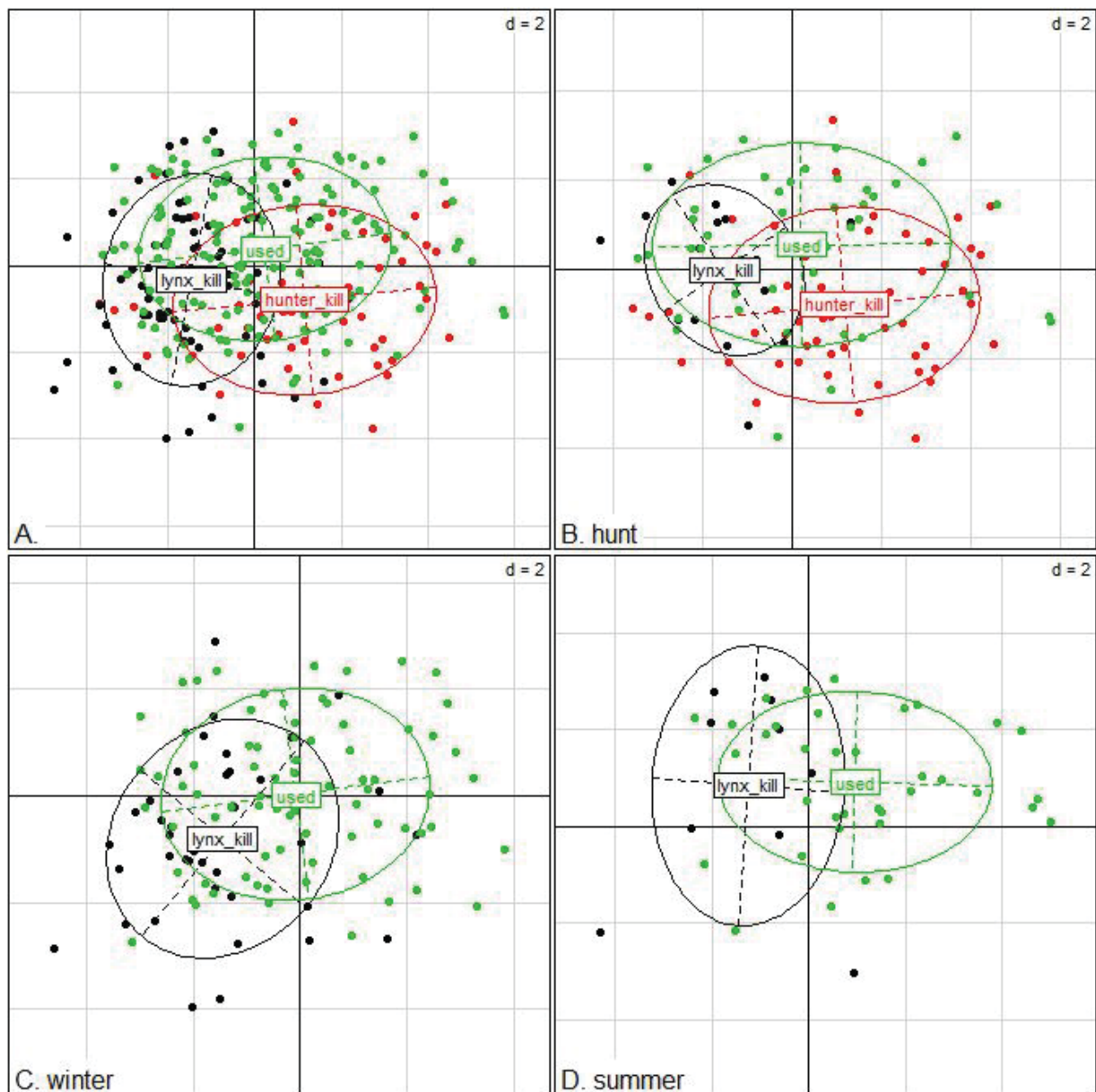


Figure A6. Observations and their group membership (used, lynx kill or hunter kill) shown on the principal component axis 1 (x) and 2 (y). Panel A shows all data together, while it is split by season in panels B through D.

PAPER II

**Temporal variation in habitat selection breaks the catch-22 of contrasting predation risk
by multiple predators**

Karen Lone¹, Atle Mysterud², Terje Gobakken¹, John Odden³, John Linnell³, and Leif Egil
Loe¹

¹ Department of Ecology and Natural Resource Management, Norwegian University of Life
Sciences, P.O. Box 5003, NO-1432 Aas, Norway

² Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences,
University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

³ Norwegian Institute for Nature Research, P. O. Box 5685 Sluppen, NO-7485 Trondheim,
Norway.

ABSTRACT

Predator avoidance depends on prey being able to discern temporal and spatial distribution patterns of risk, but this is made considerably more complicated if risk is presented by multiple predators. This scenario describes the current situation for many prey species, and the future situation for an increasing number of mammalian prey species as large carnivores recover or are reintroduced in ecosystems on several continents. Roe deer, *Capreolus capreolus*, in southern Norway illustrate the case in which prey face two predators with contrasting patterns of predation risk. They face a catch-22; spatially avoiding the risk from one predator implies exposure to the other. We tested for daily and seasonal variation in roe deer selection for habitat with respect to its year-round average risk level. Generally, roe deer increased their avoidance of risk from the nocturnal lynx, *Lynx lynx*, during night and increased avoidance of diurnal hunting risk during day. Seasonal variation matched only partially with the known variation in risk. Whereas roe deer avoided areas with high risk of hunting more strongly during hunting season than in other seasons, as expected, there was a lack of response to the risk of lynx predation during winter. We explain this by risk of starvation constraining roe deer habitat selection during this energetically challenging season with snow cover and limited natural forage. Our study demonstrates that roe deer adjust habitat selection in response to two documented risk gradients that in turn integrate several gradients in habitat characteristics. Adjusting risk-avoidance behavior temporally can be an optimal response in the case of several predators whose predation patterns differ in space and time.

Keywords: antipredator strategy, *Capreolus capreolus*, day vs. night, diel pattern, dynamic risk responses, European roe deer, European lynx, habitat selection, hunting, *Lynx lynx*, Norway, trade-off.

INTRODUCTION

Predation is a ubiquitous phenomenon in nature and many organisms have developed chemical, morphological or behavioral adaptations to predation (Lima and Dill 1990, Bourdeau and Johansson 2012). In this way, prey can influence their desirability as a prey (Mukherjee and Heithaus 2013) or their vulnerability in the predation process. Vulnerability can be decomposed into the encounter rate with predators and the probability of surviving an encounter with a predator (Lima and Dill 1990, Hebblewhite et al. 2005). Prey species can reduce the encounter rate with predators by decreasing movement rates (Alós et al. 2012). Survival on encounter is affected by a range of behavioral mechanisms, such as increasing group size, being more vigilant, ‘freezing,’ fighting or using escape behavior upon detecting a predator (Roberts 1996, Stevens et al. 2011, Mukherjee and Heithaus 2013). Habitat selection can influence both encounter rate and chance of survival following an encounter, thus relating both to the space use of predators and their hunting success in different habitats. Habitat characteristics affect the effectiveness of other risk-management behaviors such as vigilance and escape. Spatial variation in predation risk can be large, and one of the most common responses of prey is to alter habitat selection toward use of safer areas (Werner et al. 1983, Laundré et al. 2001, Hebblewhite et al. 2005, Heithaus et al. 2009, Willems and Hill 2009).

Most studies of habitat selection trade-offs between foraging and predator avoidance consider a simple one prey-one predator situation. However, prey often face contrasting spatial risk patterns from multiple predators (Moreno et al. 1996, Cresswell and Quinn 2013, Lone et al. 2014). Under such conditions, prey can spatially avoid only one predator at a time and when doing so they increase their exposure to the other predator. This double predation trade-off is what we call their ‘catch-22’ as it precludes simple strategies in predator avoidance and habitat selection. Different predators not only differ in their spatial predation pattern, but also in their diel activity pattern when they occur in sympatry (Monterroso et al. 2014). Therefore, contrasting risk in both space and time is a general expectation for

increasing numbers of coexisting predators segregating across temporal and spatial niches (Monterroso et al. 2014).

Several studies have shown the importance of both spatial and temporal patterns for risk avoidance behavior (Creel et al. 2008, Latombe et al. 2014). Deer that are able to discriminate on the basis of instantaneous risk level or predictable temporal patterns in predation risk can restrict costly behaviors to the times when this actually pays off in increased survival. Diel patterns in activity levels and habitat selection have been linked to mortality risks in a range of species (Pizzatto et al. 2008, Aumack et al. 2011, Kadye and Booth 2014, Marchand et al. 2014), as have diel patterns in risk-avoidance behaviors such as vigilance, reduced movement rates and group size (Crosmarj et al. 2012, Ordiz et al. 2012, Sönnichsen et al. 2013). Avoiding predators typically come with increased energetic costs in terms of reduced foraging opportunities (Nonacs and Dill 1990, Cowlshaw 1997, Christianson and Creel 2010). During periods of energetic stress, such as during winter for deer, antipredator behavior might be too costly to apply over longer periods. The strength of the trade-off against foraging opportunities or thermoregulation could in this way influence the selection of riskier or safer areas. The resource situation and animals' internal states (e.g. reproductive state and energy reserves) do not vary between night and day, but they do vary between seasons and could thus influence the strength of selection of riskiness between seasons (Fig. 1).

Distribution of risk is often coarsely defined and inferred from habitat characteristics or animal behavior. Deer species such as white-tailed deer, *Odocoileus virginianus*, roe deer, *Capreolus capreolus*, and red deer, *Cervus elaphus*, tend to use more open habitat during the night and forested habitat during daytime. This difference in the 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 (Beier and McCullough 1990, Mysterud et al. 1999a, Godvik et al. 2009). Agile mountain ungulates modify their behavior depending on distance to steep

slopes, presumably because predators have limited access to or poor predation success in steep ‘escape terrain’ (Risenhoover and Bailey 1985). Such findings are valuable, yet behavioral adaptations to risk should also be supported by empirical evidence of predation risk patterns, such as that presented by Hebblewhite et al. (2005) and Atwood et al. (2009).

Predation from lynx and hunting from humans represent the largest sources of mortality for European roe deer, *Capreolus capreolus*, in a region in southern Norway (Melis et al. 2013). Hunters and lynx, *Lynx lynx*, impose contrasting spatial patterns of predation risk on roe deer (Lone et al. 2014), but the ways in which contrasting temporal patterns in predation risk affect roe deer habitat selection have not been quantified. Hunter activity and hunting risk is greatest during daytime, whereas risk from the nocturnal lynx is likely higher during night (Schmidt 1999, Podolski et al. 2013). While hunting only takes place in fall, lynx prey on roe deer year round, yet with higher kill rates during winter (Nilsen et al. 2009, Gervasi et al. 2014).

In this paper we investigate whether roe deer adjust their selection of habitat to temporally avoid the predator most active in a given season or time of day. We hypothesize that prey track the temporal variation in predation risk, due to predator activity, and dynamically adjust their habitat selection away from areas that are risky at a given time. Specifically, we make predictions (P1–4) concerning the diel and seasonal patterns observed. We predict diel patterns in which lynx risk is avoided more during night than day during all seasons (P1), and hunting risk is avoided more during day than during night during the hunting season (P2). Seasonal variability in selecting for or against risk is expected to match the predator’s seasonal activity pattern (Fig. 1). Specifically, avoidance of lynx risk at night was expected to be of similar strength during all seasons (no significant seasonal contrasts; P3a) or possibly strongest during winter when lynx kill most roe deer (Nilsen et al. 2009, Gervasi et al. 2014). Avoidance of hunting risk in daytime was expected to be greater during hunting season than during summer and winter (P4).

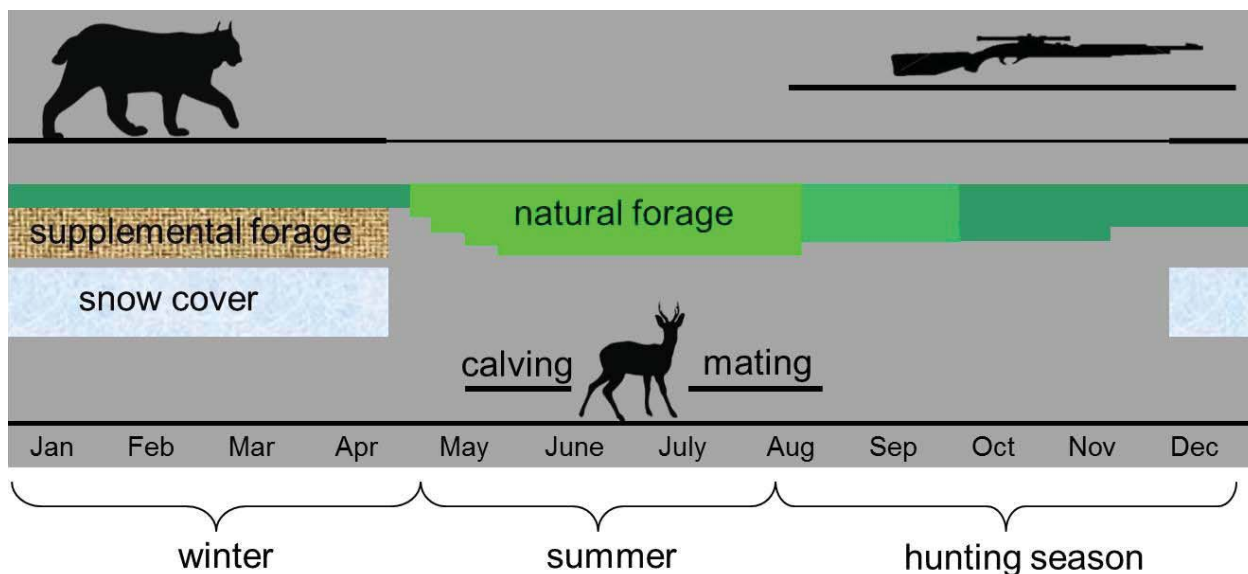


Figure 1: Seasonal variation in important factors influencing roe deer ecology and habitat selection: predation pressure from lynx and hunters, forage availability and quality, snow cover (influencing energy use, predation risk from lynx and forage availability) and reproductive events.

METHODS

Study area

The study was conducted in Hallingdal in Buskerud County, in south-central Norway (60° 40' N; 8° 50' E). The study area is a large valley system with high relief, with steep valley sides rising up from the valley floor at around 200 m a.s.l. to mountains of subalpine character (> 900 m a.s.l.) on either side. It is a multiple-use landscape, in which a main road, small towns and agricultural land are situated along the length of the valley, mainly at low elevation. The forest cover is mainly the managed species Scots pine, *Pinus sylvestris*, and Norway spruce *Picea abies*, and, in a transitional zone before alpine vegetation takes over at high elevations, downy birch, *Betula pubescence* spp. *tortuosa*. The average temperature in measured at the meteorological station Nesbyen at 167 m a.s.l. in the valley floor, is -10.5°C

in January and 15.2°C in July (<http://eklima.met.no>), and snow cover typically lasts from December to April.

The study area hosts a partially migratory roe deer population (Mysterud et al. 2012) occurring at low densities (0.1 animals are shot per km² annually (Statistics Norway 2014)) and a population of Eurasian lynx at intermediate densities (estimate 2006–2011: 90–107 lynx in the 40 000 km² management region (Brøseth and Tovmo 2012)). The roe deer population is stable and losses to lynx and hunting were of a similar magnitude in the region at the time of the study. Annually, around 65 roe deer were shot (Statistics Norway 2014) and ca. 90 roe deer were estimated killed by lynx (John Odden, unpublished data) in the study area. The only other notable source of predation is newborn fawns being lost to red foxes, *Vulpes vulpes*. Hunting is allowed throughout the area at the discretion of landowners under a formal quota system. The hunting season for adult males starts 10 August, and after the 25 September all age and sex categories can be harvested until the hunting season ends on 23 December.

GPS-collared deer and analysis of habitat selection

We studied whether habitat selection of roe deer differed between different times of day and different seasons using data from GPS-collared roe deer in Hallingdal valley in southern Norway and previously developed risk maps for lynx predation and hunting for the same region (Lone et al. 2014). Roe deer (n = 30) were captured in box-traps at 13 established supplementary feeding stations in the period January – April in years 2008–2010. All animal handling procedures were approved by the Norwegian Animal Research Authority (FOTS ID: 2827 & 1391) and permits to capture wild animals were provided by the Norwegian Directorate for Nature Management. Adult deer (>1.5 years old) were equipped with ear tags and fitted with a GPS collar (VECTRONIC Aerospace GmbH, Berlin, Germany; Followit Lindesberg, Sweden; ATS, Isanti, MN, USA), providing wireless data download over the GSM telecommunications network. A variety of sampling schedules were used, all of them

recording three positions per day or more during the first year of operation. Most collars were programmed to drop off after one or two years, but the length of data collection was often shorter due to collar malfunction, limited battery life or roe deer mortality. Details on data collection for each individual are available in Table A1. GPS data were screened for errors with a method excluding unrealistic movements, removing less than 0.05% of the data (Bjørneraas et al. 2010). Timing of migration or dispersal was classified by visual inspection (Bischof et al. 2012) and GPS positions on migration or dispersal routes were excluded from the dataset used in analysis. We defined the seasons as winter, summer and hunting season (August 10 – December 23). The division between winter and summer season was defined individually by the time of migration or dispersal, for migrating ($n = 5$) and dispersing ($n = 6$) deer, and by the median date of spring migration (May 3) for stationary animals ($n = 18$). The small fraction of the population that was migratory moved to winter ranges during the hunting season (median date October 21). Positions were excluded if they lay outside the risk map, as was the case for some deer that dispersed out of the study area and for some migrating deer whose summer ranges were around the outskirts of the study area. If a deer was represented with fewer than 80 different Julian dates from one season (60 for summer), all data from that season were excluded for that deer. This screening left data from 23 individuals in the habitat selection analysis, with 16 or 17 individuals contributing data in any given season (more information on the contribution of each collared animal in Appendix 1).

A resource selection function (RSF) is any function proportional to the probability of use of a resource by an animal (Manly et al. 2002). In our use-availability design (design III data; Thomas and Taylor 2006), we defined resources within seasonal home ranges as available (third selection order of Johnson 1980). Seasonal home ranges were delineated as the 100% minimum convex polygons (MCPs) of the animal relocations, with a lower threshold for calculating a MCP of one hundred relocations. We chose 100% MCPs so the home ranges would not only consider the most intensively used areas, but also include the

relevant variability in resources on the outskirts of the core home range. The hunting season home ranges of migrating deer consisted of two areas (those used before and after fall migration), for which we calculated separate home ranges. Within each seasonal home range, we sampled randomly the same number of available locations as the number of animal relocations within that home range to achieve a 1:1 ratio of used vs. available positions for each id, season, and time of day considered.

We have previously developed standardized relative risk maps specific to roe deer in Hallingdal, Norway based on kill sites of deer and sites used by live roe deer (Lone et al. 2014). The maps reflect the overall (year-round) risk of being killed by lynx and by humans as a function of terrain characteristics (i.e. elevation, slope and ruggedness), understory density, and anthropogenic influence (i.e. distance to roads) (Lone et al. 2014). In the current study we extracted the relative risk of being killed by lynx and the relative risk of being killed by human hunters from these maps for all locations (both used and available). We estimated the coefficients of an exponential RSF using a mixed-effect logistic regression analysis using package lme4 in R (R Development Core Team 2011, Bates et al. 2012).

To test the hypothesis that avoidance of risk (i.e., negative selection of risk) differed between day and night and between different seasons, we fit a model in which used or available location was the response variable and day/night/twilight, season and risk level (including all two-way interactions and the three-way interaction) were fixed effects. A random intercept for each individual was incorporated to adjust both for unbalanced sampling between individuals and for dependence among positions originating from the same animal (Gillies et al. 2006). Light conditions (daylight/darkness/twilight) were defined using tables for sunrise, sunset and civil twilight at a location central with respect to all GPS tracks within the study area (60° 35' N; 9° 4' E) (<http://aa.usno.navy.mil>). Risk from hunting and risk from lynx were treated in separate models, as there were signs of collinearity in a model including

both. The two variables were also relatively strongly correlated in the set of used positions ($\rho = 0.57$), indeed much more than in the set of available positions ($\rho = 0.29$).

As the risk maps (Lone et al. 2014) were based on a subsample of GPS positions from the same animals whose habitat selection we investigate here, the derivation of risk in Lone et al. (2014) could possibly influence our habitat selection analysis towards selection against risky habitat in absolute terms. Risk was defined as the relative probability of being killed in a unit time spent in a certain habitat and derived from the distribution of predator kill sites relative to year-round positions used by marked roe deer, as a function of habitat characteristics. If the distribution of sampled positions of the marked animals differs from the proportional time use of the roe deer population, it could result in bias towards lower risk defined for the positions used by the sample deer. We therefore frame our investigation around the contrast between day and night and among seasons: comparisons in which the expected pattern following our hypotheses cannot arise from the sampling and our definition of overall risk.

RESULTS

Roe deer tended to select similarly for risk levels during night and twilight, and both night and twilight were significantly different from daylight (Appendix 2). We present results based on pooling the categories ‘dark’ and ‘twilight’, thus separating only between ‘night’ and ‘day’ positions based on sunrise and sunset. A positive difference in the selection coefficient between night and day indicates that deer shift towards selecting riskier areas during night relative to day (or, equivalently, shifting towards selecting safer areas during day than night). Negative differences indicate a shift in the opposite direction, towards selecting safer areas during night relative to day. Roe deer showed diel differences in selection of risky habitat between night and day in summer and during hunting season, but not in winter (Fig. 2). The patterns in the selection of risk went in the expected direction (P1, P2), as roe deer selected

relatively riskier areas at night with regards to spatial hunting risk, and relatively safer areas at night with respect to spatial lynx risk (Fig. 2). Yet, day vs. night differences diverged from the predicted seasonal pattern (P1, P2) in two ways. First, there was no diel response to lynx risk during winter, and second, a diel response to hunting risk was present during summer when no hunting occurred (Fig. 2). In contrast, the pattern of seasonal differences in selection during daytime did not involve a strong response to hunting risk during summer, but followed our expectations (P4a). The differences in selection coefficient of risk between seasons reveal that animals shifted towards selecting safer areas during hunt and summer compared to winter (Fig. 3). Responses to hunting were highest during hunting season and no differences between summer and winter, and the strongest responses to lynx occurred during summer (Fig. 3). Deer avoided risky areas more strongly during the hunt than during winter or during summer (Fig. 3; hunt vs. summer difference in selection coefficient = -0.52 ; 95% CI: $[-0.58, -0.46]$). Roe deer avoided lynx risk more strongly during hunting season and summer than during winter (Fig. 3), and also more strongly during hunting season than during summer (Fig. 3; hunt vs. summer difference in selection coefficient = 0.25 ; 95% CI: $[0.16, 0.34]$). This contradicted P3a and P3b, which postulated equal selection through the year because deer are exposed to lynx predation throughout the year, or possibly stronger responses during winter when predation rates are highest.

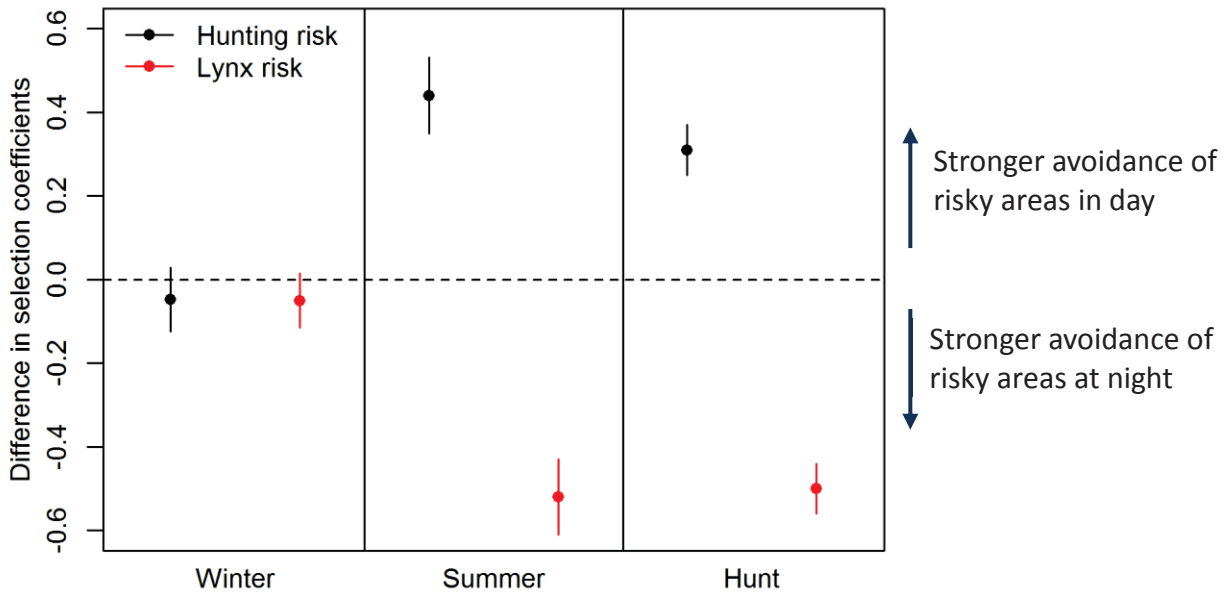


Figure 2: Change in the selection coefficient (with 95% CI) for lynx risk or hunting risk between night and day. Day is the reference.

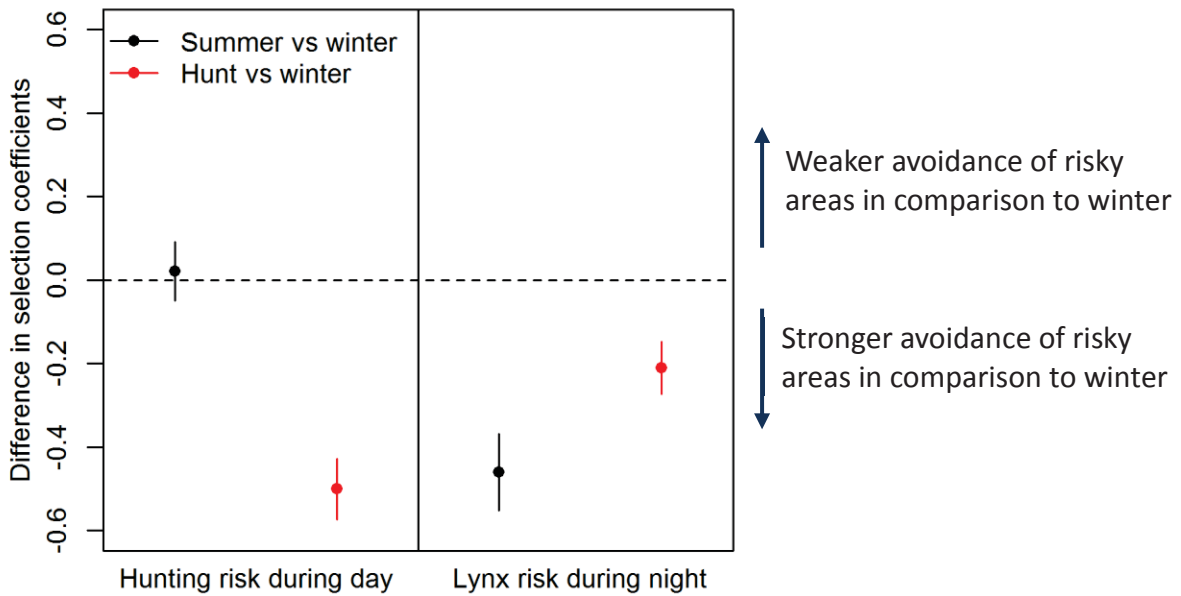


Figure 3: Change in the selection coefficient (with 95% CI) for lynx risk and hunting risk during the relevant time of day for risk exposure (day or night) between seasons, where winter is used as the reference level.

DISCUSSION

Prey responses to multiple predators may involve complex trade-offs between spatial and temporal risk. We have shown that roe deer selected habitat in a manner that reduced their predation risk to hunters in daytime and lynx at night, during the relevant risk seasons. In this manner, deer were to some degree able to avoid both lynx risk and hunting risk, even though the two contrast strongly spatially with respect to habitat features such as distance to roads and understory density (Lone et al. 2014). Winter represented a discrepancy in the pattern because roe deer lacked a response to lynx during winter, when their predation rates are high. We suggest that this seeming anomaly can be due to risk of starvation which might constrain behavior during this energetically demanding season (Holand et al. 1998). Increased exposure to lynx risk may explain the higher predation during this period (Gervasi et al. 2014). It is recognized that both spatial and temporal structure of risk is important to prey (Valeix et al. 2009, Laundré 2010). We demonstrate that roe deer respond dynamically to their mortality risk, and adjust their habitat selection to match the activity pattern of their predators for large parts of the year.

Following centuries of human persecution, many large carnivores are now returning to their former ranges across Europe and North America (Swenson et al. 1995, Wabakken et al. 2001, Fortin et al. 2005, Linnell et al. 2009). During the period of absence, many deer populations have exploded due to a number of coinciding factors (McShea et al. 1997, Apollonio et al. 2010). Animals' behavioral response to the presence of both human hunting and returning large carnivores has become a topical issue.

Our analyses show that roe deer responded dynamically to temporal variability in predation risk by altering their habitat selection diurnally and from season to season. The contrast between day and night matched our expectations. Deer avoided risky habitat with respect to either predator at the times of day when they are active: night for lynx and during the day for hunters. Still, the interpretation of the patterns and their causes requires some

caution because lynx risk and hunting risk depend on the same habitat variables, but are inversely related. The inherent correlation between the two kinds of risk means that the diel response to hunting risk during summer can be explained as a response to lynx. It follows that the risk of lynx alone could explain the diel pattern in which deer select areas with thick understory vegetation or far from roads in daytime and areas that are open or closer to people in nighttime. Human disturbance (rather than only human hunting) in daytime is another possible explanation for the diel patterns in hunting risk (and possibly also lynx risk) during summer and hunting season. Yet, we judge this mechanism as less likely, as other studies have shown that animals are acutely aware of the onset of hunting, and respond specifically at times of risk (Ordiz et al. 2012, Lone et al. in press), and that human activity can instead cause habituation (Stankowich 2008, but see Ciuti et al. 2012). Diel patterns of vigilance have been seen in roe deer in Germany, where deer were more vigilant during day than during night and increased their level of vigilance during the hunting season (Sönnichsen et al. 2013). The dynamic habitat selection we documented is thus largely consistent with vigilance behavior with respect to the spatio-temporal variation in risk presented by hunters and one or more natural predators, and is further evidence of the behavioral plasticity of roe deer as described by Sönnichsen et al. (2013).

Many ecological factors change across seasons (Fig. 1). Seasonal differences in resource availability, calf vulnerability and energy budget constraints could interplay with predation risk and cause weaker responses to risk in winter, stronger responses due to calf vulnerability or either weaker or stronger responses due to a positive or negative correlation with resources to risk in summer. Nonetheless, we found that the deer habitat selection behavior could be explained on the basis of daytime hunting risk alone, without invoking other factors.

In some seasons roe deer behavior did not conform to our expectations on the basis of predation risk alone. Directly opposing prediction P3b, the seasonal response to lynx was

lowest during the winter and there was no diel pattern in risk avoidance during this season. Winter is a challenging season for roe deer across their geographical range, and especially in Norway which lies at the northern edge of their distribution range (Holand et al. 1998). Roe deer have limited fat reserves and therefore depend on continuous energy intake through the winter, a season when forage availability and quality is low (Holand 1992). Maintaining body temperature in low temperatures and moving in snow are energetically demanding, so conserving energy and obtaining sufficient food are critical for survival (Holand et al. 1998). Nutritional and thermoregulatory constraints are thus likely reasons for reduced ability to respond to predation risk during the winter. Another investigation in southern Norway (Ratikainen et al. 2007) found similar results. In that study, roe deer resting sites and feeding sites were both located in denser vegetation than random sites and selection of canopy cover depended on weather, indicating selection of thermal shelter even if it implied a higher risk of lynx predation. We also know that there is much less food in open areas during winter (Mysterud et al. 1999b), effectively forcing roe deer to select closed vegetation both day and night.

Understory cover contributed strongly to the contrast in risk gradient in our study, and was included because we could quantify it across the study area using LiDAR (laser scanning) data (Lone et al. 2014). Cover affects both concealment and visibility. Depending on the hunting style of the predator, this confers some advantage to the prey or leaves them at a disadvantage (Camp et al. 2013). The interplay between cover, predation risk and time of day may differ between predator-prey assemblages; in our case, cover was safe habitat during day and risky during night. In other species as well, cover has been linked to differing risk levels during day and night depending on the function of the predators and their activity pattern, with animals alternating preference and avoidance in a diel cycle, e.g. in hares (Moreno et al. 1996). Another LiDAR-based study on roe deer in the Bavarian forest in Germany found that animals did discriminate in their use of areas depending on understory density in winter.

These roe deer selected high density understory during active bouts, and low density during resting periods (Ewald et al. 2014). This suggests the existence of dynamic patterns of selection against lynx predation risk correlating with cycles of activity and rest, in agreement with the diurnal pattern found in our study.

Conclusion and Perspectives

Populations of wild ungulates are often subject to harvesting, and game species have learned to avoid hunters in space and time. As large carnivores recover in Europe and North America, an increasing number of prey populations return to a more natural state in which they face multiple predators. In many cases, such as the human and lynx predators in our study, the predation risk patterns contrast in either space or time (Crosmarty et al. 2012, Cresswell and Quinn 2013), as can be expected due to predator niche differentiation. This reduces the possibility for the prey to adapt through risk avoidance (Lone et al. 2014). We demonstrate here that in cases where temporal variation in risk and spatial variation both are contrasting, prey can get out of a spatial catch-22 by dynamically adjusting their behavior in response to the seasonal and diurnal variation in risk posed by their suite of predators (Monterroso et al. 2014).

It is important to understand how prey respond to the presence of large carnivores, as it can have large impacts on ecosystems through cascading effects (Schmitz et al. 1997, Werner and Peacor 2003, Beschta and Ripple 2009, Ripple et al. 2014). Yet the evidence base for the prime example from terrestrial systems involving large mammals is heavily debated (Kauffman et al. 2010, Beschta and Ripple 2011, Kauffman et al. 2013). The predation of lynx seems to shape roe deer habitat selection more during summer and fall than during winter, and any cascading effects from lynx predation mediated through altered browsing patterns by deer are unlikely during the energy-restricted period with snow cover. We suggest that in the case of predators who present a set of risks contrasting in space and time, optimal

habitat selection shifts temporally, making strong predator-induced patterns in overall browsing pressure less likely than in a case with a single predator. Our study also indicates that large costs of responding to predation can limit prey responses, opening up for a discussion on whether strong trade-offs can lead to weaker rather than stronger indirect effects.

ACKNOWLEDGMENTS

This study and the underlying risk map is based on GPS data from collared lynx and roe deer, kill sites data, and fecal pellet surveys collected by the project Scandlynx (<http://scandlynx.nina.no/>), and was supported by the Research Council of Norway, the Norwegian Directorate for Nature Management (DN), the Norwegian Institute for Nature Research (NINA), the Nature Protection Division of the County Governor's Office for Buskerud counties, and the municipalities of Flå, Gol, Nes, and Ål as well as by the large carnivore management board for region 2. We would like to thank the hundreds of people who have helped us in the field during the years of this study. K. Lone was funded by a doctoral scholarship from the Norwegian University of Life Sciences.

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Appendix 1: *Roe deer GPS data*

Table A1: Number of GPS-marked roe deer contributing to the analyses in different seasons and years and average home range sizes

	winter	summer	hunt
Distinct individuals (n)	17	16	17
Distinct id-season-year (n)	30	21	21
Size of 100% MCP home range (km ²)			
median	1.5	1.8	1.6
mean	3.4	14.1	7.5
range	0.4-21.7	0.7-105	0.3-88

Table A2: The 30 collared individuals, their migratory status and the number of used points considered for each id-season-year (data from multiple years separated by commas). Individual fates and movement pattern cause data to be imbalanced across seasons at the individual level, but all three seasons are well represented in the aggregate by 16 (summer) or 17 (winter and hunt) individual roe deer whose data were weighted so each individual contributed equally at the within-season level. Collared animals were monitored for a mean of 337 days, with the range 16-901 days.

individual	migratory status	reason for partial representation	Used points from different years		
			winter	summer	hunt
6212	migratory	migration ^a	831,202		
6214	dispersal	dispersal out	1103		
6215	stationary		877,682,246	763,194	1082,268
6216	dispersal	dispersal out	787		
6217	stationary	killed by car	670		
6219	stationary		714,666	768,194	1079,271
6221	migratory		1010,699,191	450,171,103	1051,268
6224B	stationary		239,584	780	1080
6480	migratory	collar failure		1485	1601
6482	migratory	collar failure		1206	
6483	stationary	killed by lynx		1166	1113
6484	stationary		495,485	1147	1498
6485	stationary	killed by car		1161	1603
B2008001	stationary		712,665	774,196	1079,206
B2008003	migratory		355,335	536	745
B2008004	stationary		316,179	503	604
B2008005	stationary		286,407	491	682
B2008006	migratory	migration ^a	305,439		500
B2008007	dispersal				489
R3055	stationary		277	257	318
R3056	stationary		188	287	350
R3059	stationary			219	338
R3066	dispersal	dispersal out	452		
B2008002		starvation			
6224		killed by lynx			
6227		hit by car			
R3046		hit by car			
R3063		killed by lynx			
R3064		killed by train			
R3067		dispersal out			

Note: ^a summer home range outside risk map

APPENDIX 2: Additional results from the modelling

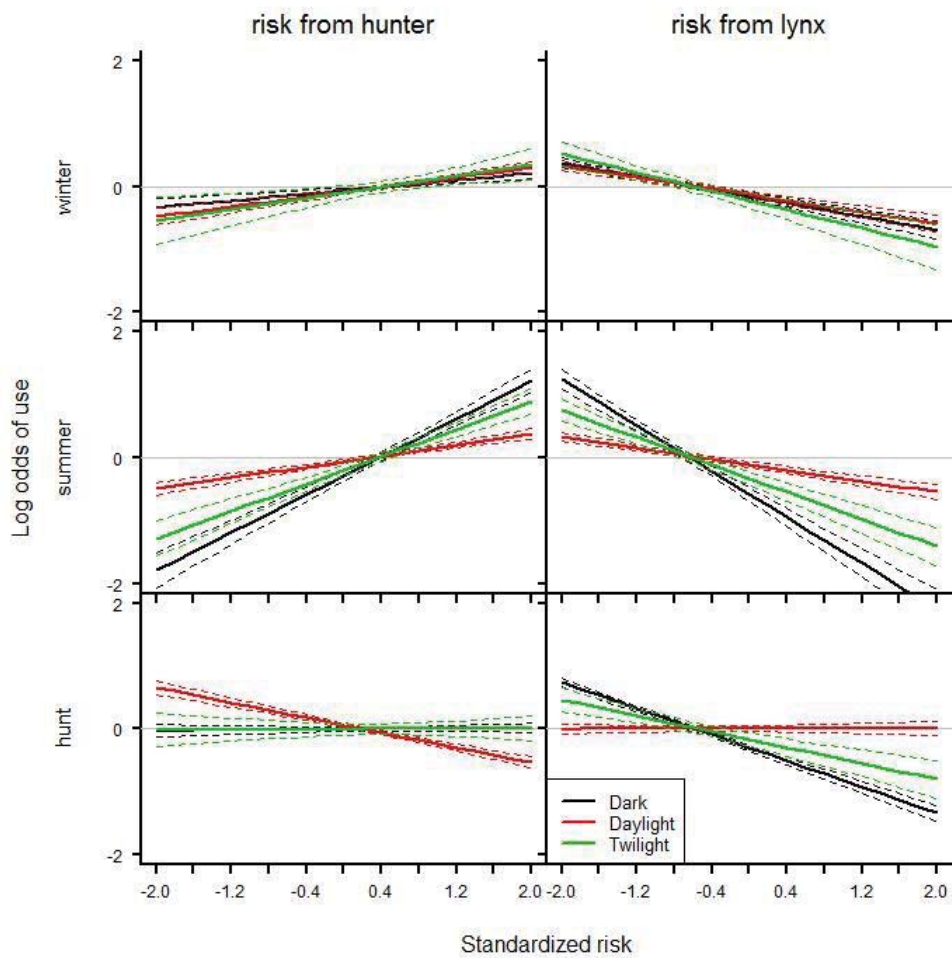


Figure A1: Roe deer habitat selection with regards to relative risk depending on time of day and season. Absolute selection for risk could be influenced by our definition of risk, and therefore requires cautious interpretation, while contrasts (changes in slope) among seasons and time of day are unaffected by this

PAPER III

**An adaptive behavioural response to hunting: surviving male red deer shift
habitat at the onset of the hunting season**

Karen Lone^{a*}, Leif Egil Loe^a, Erling L. Meisingset^b, Inga Stamnes^a, Atle Mysterud^c

^a Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences

^b Norwegian Institute for Agricultural and Environmental Research, Organic Food and Farming Division

^c Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Norway

*Corresponding author: Karen Lone, email: karen.lone@nmbu.no, phone no: (+47) 64965723, fax no: (+47) 64965801, postal address: Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Aas, Norway

Animal Behaviour, in press

ABSTRACT

Human hunting can be a potent driver of selection for morphological and life history traits in wildlife populations across continents and taxa. Few studies, however, have documented selection on behavioural responses that increase individual survival under human hunting pressure. Using habitat with dense concealing cover is a common strategy for risk avoidance, with a higher chance of survival being the pay off. At the same time, risk avoidance can be costly in terms of missed foraging opportunities. We investigated individual fine-scale use of habitat by 40 GPS-marked European red deer, *Cervus elaphus*, and linked this to their survival through the hunting season. 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. This habitat switch also involved a trade-off with foraging opportunities on bilberry, *Vaccinium myrtillus*, a key forage plant in autumn. Moreover, deer that use safer forest habitat might survive better because they make safer choices in general. The lack of a corresponding pattern in females can be because females were already largely using cover when hunting started, as predicted by sexual segregation theory and the risk of losing offspring. The behavioural response of males to the onset of hunting appears to be adaptive, given that it is linked to increased survival, an important fitness component. We suggest that predictable harvesting regimes with high harvest rates could create a strong selective pressure for deer to respond dynamically to the temporal change in hunting risk. Management should consider the potential for both ecological and evolutionary consequences of harvesting regimes on behaviour.

Keywords: behavioural plasticity, cover, fitness, food, forage, risk-avoidance, safety, survival, trade-off, wildlife management.

INTRODUCTION

Human harvesting is a major source of mortality and potent force of ‘unnatural’ selection in many wildlife populations (Darimont et al., 2009). The pattern of mortality from harvesting is rarely random and often differs from patterns of natural mortality (Allendorf & Hard, 2009). Thus, recently, there has been much interest in potential evolutionary effects of harvesting on life history attributes and morphological traits such as horns, antlers and body size (Allendorf & Hard, 2009; Festa-Bianchet, 2003). Systems dominated by human harvesting outpace systems dominated by natural selection or other anthropogenic agents in the rate of phenotypic change (Darimont et al., 2009). Harvested populations have shown substantial alteration of morphological and life history traits with net documented changes in these types of traits averaging 18% and 25%, respectively (Darimont et al., 2009). Yet, discerning between ecological and evolutionary causes is neither a trivial nor a simple matter (Bunnefeld & Keane, 2014; Fenberg & Roy, 2008) and, in one recent study, demographic changes resulting from hunting explained observed phenotypic changes that were earlier attributed to evolution (Traill, Schindler, & Coulson, 2014). Still, potential evolutionary impacts of harvesting deserve consideration in applied management and conservation efforts, not least because they can be difficult to reverse (Bunnefeld & Keane, 2014; Coltman et al., 2003; Darimont et al., 2009; Fenberg & Roy, 2008). ‘Unnatural’ selection from hunting can potentially also affect heritable behavioural traits (Allendorf & Hard, 2009), but there is still limited knowledge of the link between human harvesting and animal behaviour.

Behavioural responses to human or natural predators are widespread, diverse and generally carry some cost (Lima & Dill, 1990; Peacor, Peckarsky, Trussell, & Vonesh, 2013). One widespread response to reduce predation risk is to shift habitat use away from areas with high predation risk (Creel, Winnie Jr, Maxwell, Hamlin, & Creel, 2005; Valeix et al., 2009). Across a range of taxa, such a habitat shift involves a trade-off between access to resources

and safety (Breviglieri, Piccoli, Uieda, & Romero, 2013; Embar, Raveh, Burns, & Kotler, 2014; Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009; Nonacs & Dill, 1990). A typical situation for large grazing mammals is that individuals have to choose between open habitats with good foraging opportunities, but where they are visible to predators, and habitats that provide more cover from potential dangers but which might limit foraging efficiency (Godvik et al., 2009; Werner, Gilliam, Hall, & Mittelbach, 1983). Individuals can differ substantially in how they respond to such a trade-off (Bonnot et al., 2014). The shy–bold continuum is one of the most studied personality axes in animals and characterizes inherent tendencies in how an individual responds to novelty, innovation and risk-taking (Quinn & Cresswell, 2005; Wolf & Weissing, 2012). Nevertheless, there has been less focus on individual differences in behaviour and trade-offs in situations where humans are the predator (Ciuti et al., 2012; Madden & Whiteside, 2014).

Risk varies in space and time, and studies should ideally incorporate both elements (Creel, Winnie Jr, Christianson, & Liley, 2008; Latombe, Fortin, & Parrott, 2014). Prey responses can be constant (also called ‘chronic’ (Latombe et al., 2014); e.g. as assumed in Laundré, Hernández, and Ripple (2010)), or temporary, varying at characteristic spatio-temporal scales in response to cues (Latombe et al., 2014; Valeix et al., 2009). North American wapiti, *Cervus elaphus canadensis*, respond to wolf, *Canis lupus*, predation by a combination of constant and temporary responses at different scales (Latombe et al., 2014). Whether animals tend to respond constantly or temporarily, and at what temporal and spatial scales, depends on the context, with the costs and benefits of alternative strategies varying with factors such as predator mobility, resource needs, risk patterns and the ability of prey to assess risk reliably (Brilot, Bateson, Nettle, Whittingham, & Read, 2012; Lima & Bednekoff, 1999; Lone et al., 2014). A constant response could be favoured if prey have incomplete knowledge of the whereabouts of predators or if switching between behaviours is costly or

simply not feasible. Conversely, if risk varies strongly at certain time scales (such as between seasons or between day and night), temporary behavioural responses during high-risk periods could be favoured. Human hunting is often strongly structured temporally (Cromsigt et al., 2013), and can elicit behavioural shifts in game species between the open and closed hunting seasons (Proffitt et al., 2010; Tolon et al., 2009). Nevertheless, although hunting is an ideal and controlled way to test for dynamic responses, few studies have examined immediate responses to the onset of the hunting season (Ciuti et al., 2012; Ordiz et al., 2012).

By definition, anti-predator behaviour should be effective in reducing mortality, but few empirical studies have explicitly linked individual behaviour with survival (DeCesare et al., 2014; Leclerc, Dussault, & St-Laurent, 2014; Van Moorter et al., 2009). Previous studies have found that higher hunting pressure and hunter accessibility negatively affect wapiti survival at the scale of seasonal home ranges, but that there are no significant associations between cover and survival at this scale (McCorquodale, Wiseman, & Marcum, 2003; Unsworth, Kuck, Scott, & Garton, 1993). Nor are there significant associations between wapiti survival and the amount of cover at the scale of weekly home ranges (Webb et al., 2011). In contrast, a finer-scale analysis has revealed that bold wapiti individuals, with higher rates of movement, weaker response to human activity and greater use of open terrain, are more likely to be harvested than shy individuals (Ciuti et al., 2012).

To determine if and how behaviour influences hunting-season survival, and to identify potential trade-offs, we investigated habitat use by European red deer, *Cervus elaphus elaphus*, at spatial and temporal scales likely to shape their responses to hunting. Red deer populations in central Norway occur at high densities and are heavily hunted by humans; there are no other major predators present (Langvatn & Loison, 1999). We compared the use of fine-scale cover and forage habitat between ten surviving and ten shot deer of each sex shortly before and soon after the onset of the hunting season. We tested four competing

hypotheses (Table 1) to identify whether individual differences in habitat use affects survival (H2, H3 or H4); whether deer respond dynamically to the onset of the hunting season (H1, H3 or H4); and whether the strength of these dynamic responses influences survival (H4). We expected differences in the use of cover because it presents a gradient of risk, and differences in the use of forage habitat as this would arise from spatial behaviour that traded off the risk of mortality against access to food.

Table 1: Null and alternative hypotheses relating the fate of red deer during the hunting season to their risk-avoidance behaviour, along with associated predictions about the individuals' habitat use with respect to sighting distance (and the inverse pattern expected for concealment cover) and forage availability (forage opportunities forgone, a potential cost of responding spatially to predation).

Alternative hypotheses	Temporal pattern	Pattern of survivors vs shot individuals	Model structure
<i>H0: No response to onset of the hunting season and survivors and shot individuals use habitat with the same characteristics</i>	<i>No</i>	<i>No</i>	<i>~1 (intercept only)</i>
H1: Dynamic response to onset of the hunting season that either is exhibited by all animals equally, or does not affect survival	Yes, decreasing	No	Period
H2: No dynamic response to onset of the hunting season, but individual differences in habitat use affect survival	No	Survivors have lower mean values than shot animals	Fate
H3: All individuals respond dynamically to the onset of hunting, but survival is determined by pre-existing and ongoing individual differences	Yes, decreasing by similar amounts for both groups	Survivors have lower mean values than shot animals	Period + Fate
H4: Individuals differ in their dynamic response to the onset of hunting, and the strength of this response influences survival	Yes, decreasing by different amounts	Survivors respond more strongly than shot animals	Period × Fate

Note: The males in our study were found to conform to the model in bold and the females to the model in italics.

METHODS

Ethical Note

Permits to capture and mark animals were granted by the Norwegian Animal Research Authority (NARA) (ref no. s-2006/28799; permit no. FOTS ID 4863), and the Norwegian Environment Agency (ref no. 2006/5393). Three veterinarians, assisted by eight other field personnel approved by NARA, marked the animals. Animals were captured under cover of darkness using spot lights at feeding sites from January to early April each year. Deer were immobilized by dart injection of xylazine-tiletamine-zolazepam from a distance of 10–30 m, in accordance with standard procedures (Sente et al., 2014). When animals were recumbent, they were approached slowly, blindfolded and kept lying down. The main physiological side effects of immobilization were mild hypoxemia and hypercapnia. Animals were closely monitored during immobilization and through recovery (12 ± 7 min) after drug reversal with atipamezole (Sente et al., 2014). Out of the 132 captures, there were two capture-related mortalities. One female died within a few days of marking and one male became asphyxiated during weighing, after which safer specialized weighing equipment was developed and used to avoid a recurrence. All animals were marked with ear tags (Allflex Super Maxi Tag, 75 x 97 mm, Allflex, Denmark) in one of the ears, and were fitted with GPS collars suitable for red deer females and males, respectively (Tellus from Followit, Sweden, and GPS ProLite from Vectronic, Germany; collar weight: ca. 850 g, 0.5–1.0% of animal body weight). Collars were set to provide one location every hour for up to two years and most collars supported wireless download of data over the GSM telecommunications network, thus not requiring collar recovery. Nonetheless, many collars had the capacity to drop off when data collection ended. Two collars malfunctioned at the time of deployment, and some others stopped collecting data prematurely. Animals whose collars were not designed to drop off, or which malfunctioned or stopped working, were recaptured whenever possible to remove the collars. These animals

were either shot as normal during the hunting season, shot during winter (under special permit from municipalities), or recaptured by darting at a feeding site during winter. This collar-retrieval could take between one and four years, and some collared deer were never recovered. The collars caused minor hair loss or slight chafing around the neck in some deer, but no severe adverse effects of the tags or collars were observed during the study.

Study Area

The study was carried out on a partially migratory population of red deer in central Norway (62° 36'–63° 30'N; 8° 48'–10° 6' E). The study area was approximately 6000 km² and included coastal to inland areas with diverse topography, land use and cover (Fig. 1). The

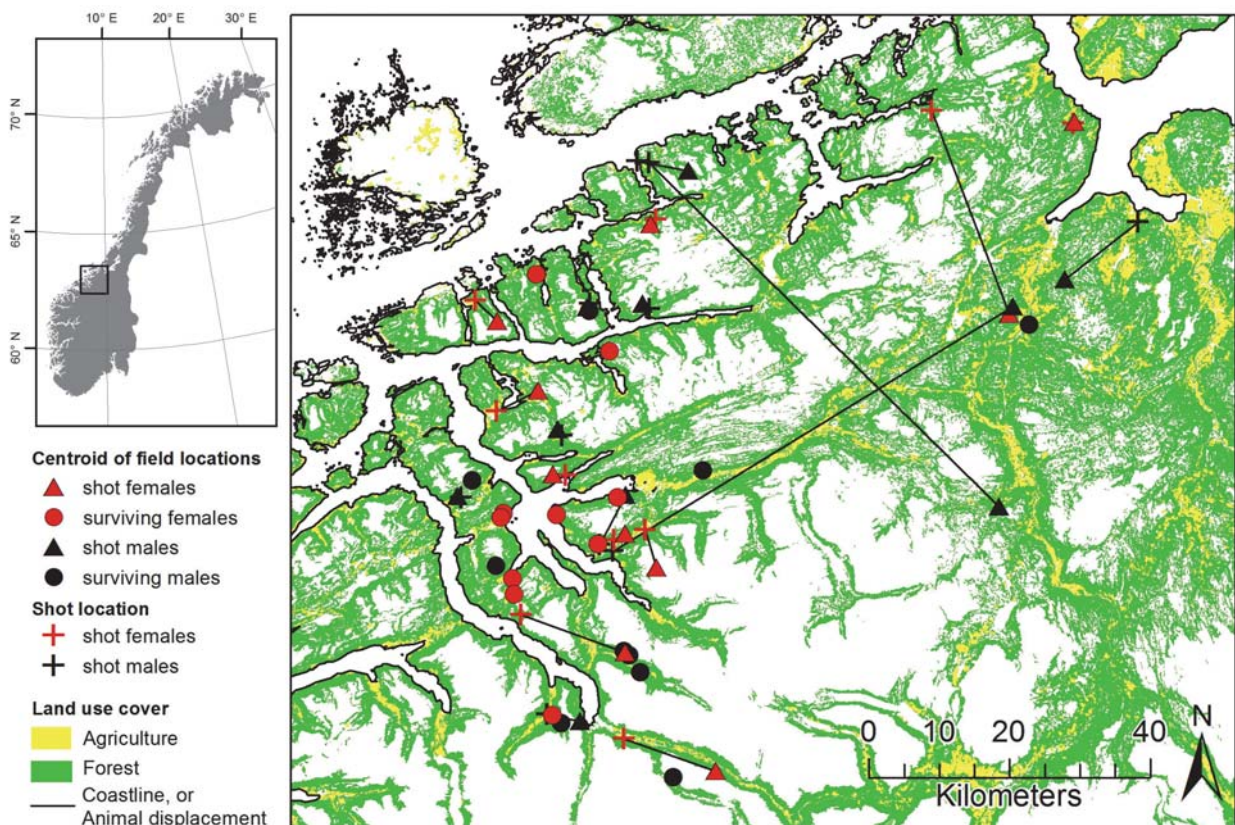


Figure 1: Study area and spatial distribution of studied red deer (centroid position of the 12 field plots for each individual). Black lines connect the centroids of the field plots with the location where each individual was shot. In some cases, deer were shot close to the areas used at the onset of hunting; in other cases they were shot some distance away.

landscape included agricultural areas in the valleys, but was dominated by forested and montane areas. Natural forests that were not intensively managed, but where some harvesting occurred, were dominated either by deciduous species (mainly *Betula pubescens*, *Betula pendula*, *Salix caprea*, *Alnus incana*, *Alnus glutina* and *Sorbus aucuparia*) or by Scots pine, *Pinus sylvestris*. Dense plantations of Norway spruce, *Picea abies*, were scattered across the study area. The patchy mixtures of dense spruce plantations and other forest types of varying age and density of understory created strong heterogeneity in sighting distance within the forests.

Red Deer Population

Absolute density estimates were not available, but from hunting statistics we know that, on average across the study area, 6.2 deer were harvested annually per 10 km² during the study period (Statistics Norway, 2014). Red deer are the dominant large mammal in the region. Their primary habitat is forest, but they also use agricultural areas intensively for foraging, mainly during the night (Godvik et al., 2009). Red deer associate in small matrilineal family groups (2–7 individuals) during most of the year, whereas juvenile and older males are generally solitary (Bonenfant et al., 2004). During the rutting season, however, animals form mixed-sex groups and males compete for the right to defend a harem of females. Males defend a group of females and not a territory. Young or otherwise subordinate males are typically found nearby the harems and are, on occasion, able to secure a mating undetected by the dominant male (Clutton-Brock, Guinness, & Albon, 1982). In winter, deer occur in larger groups because they congregate at food sources. The hunting season coincides with the rutting season, which peaks in early- to mid-October (Loe et al., 2005). The rutting season begins gradually. The sexes generally start associating around 19 September (95% CI: 14–23 September), with the earliest roaring male being heard on 17 September (305 instances of

roaring males across 16 years (Loe et al., 2005)). Females that are two years or older typically reproduce every year (Langvatn, Bakke, & Engen, 1994; Langvatn, Mysterud, Stenseth, & Yoccoz, 2004). The migratory segment of the population move between their summer and winter ranges at some point during the hunting season, usually in September (Meisingset et al. in prep).

Hunting Regime

Hunters hunt for meat and recreation rather than for trophies (Milner et al., 2006); offtake is limited by locally-set age- and sex-specific quotas (Andersen, Lund, Solberg, & Saether, 2010). Harvest mortality has been strongly male biased for many years (1977–1995), with the risk of mortality to males increasing slightly during the 1980s, before stabilizing in the 1990s (Langvatn & Loison, 1999). Recent cohort modelling of data from three areas in Norway (one of them within our study area) confirmed this pattern and quantified the annual mortality risk from harvesting to be around 45% for adult males (≥ 2 years old) and around 15% for adult females (Veiberg, Nilsen, & Ueno, 2010). The strong male bias contrasts with harvesting practices in the rest of Europe, where there is generally low or no sex bias, and if anything, a slight female bias (Milner et al., 2006). Note, however, that females typically have a calf at heel, and calves are also targeted by hunters (annual mortality risk around 15%: (Veiberg et al., 2010)). For several decades up until 2011, the hunting season started on 10 September, but in 2012 it was advanced to 1 September. During our study (2007-2012, Table A1), the hunting season was open until 23 December. Deer are harvested throughout, but there is a strong burst of hunting activity when the season opens, with around 27% of all animals being shot during the first week (www.hjorteviltregisteret.no). Both adult males and females are targeted with similar proportions of the total harvest for each sex, 23% and 26% respectively, being taken during the first week. Hunters access all parts of the red deer's habitat and use a

variety of hunting methods (stand hunting, still hunting, call hunting and drive hunting with and without dogs) to target all ages and sexes, although call hunting is used mainly for males during the rutting season and comprises a small percentage of the total harvest. Although open agricultural land makes up only a small proportion of the landscape, it is the riskiest per unit area, with around 50% of all hunting mortality occurring there (Rivrud, 2013). Hunting occurs around the clock, with distinct peaks during twilight hours at dusk and dawn. Night hunting is only undertaken during strong moonlight. All hunting is done with rifles, requiring a free line of sight between the hunter and the animal. The spatial distribution of risk should thus be directly related to vegetation density and sighting distance.

During the study, hunters and local residents were informed that there were no restrictions on harvesting marked deer. In other populations, harvest rates of radio-collared deer were found to be representative of the population, despite differing hunter attitudes towards shooting radio-collared animals (Buderman, Diefenbach, Rosenberry, Wallingford, & Long, 2014). We therefore assume that marked deer were subject to a similar pattern of risk as unmarked deer, and because we compared across marked animals, any slight bias would likely be similar among them. Nevertheless, any discrimination against marked animals should favour the survival of marked deer in open areas, where they can be observed for longer and the collar noticed. A tendency to move in groups could cause the same pattern, because marked deer could be spared at the expense of another group member in open environments, whereas in denser forest a hunter might not even realize that the deer is member of a group. Neither of the two potential sources of bias would predict a lower probability of an individual being shot when using denser habitat. On the contrary, both these relationships could be expected to weaken (or reverse) the predicted relationship between sighting distance and survival hypothesized in Table 1. Because we predict the opposite patterns to those expected from hunter bias, our analysis is therefore a conservative test of the

hypotheses about how individual behaviour influences survival. Furthermore, it is difficult to see how this potential hunting bias could account for the predicted shift to using habitat with denser cover once hunting begins.

GPS-tracking Data and Selection of Animals

This study is based on an existing dataset of 130 GPS-collared red deer (82 females, 48 males) marked and monitored during 2007–2012 in Møre-og Romsdal and Sør-Trøndelag counties in central Norway (Bischof et al., 2012, unpubl.; Mysterud et al., 2011). Hourly GPS position data were screened for outliers visually and with an automated technique based on movement characteristics (Bjørneraas, Moorter, Rolandsen, & Herfindal, 2010), removing less than 0.05% of the locations. Median location error had earlier been calculated to be 12 m (Godvik et al., 2009). Limited by logistics and time, we restricted field investigations to locations from 40 adult deer (≥ 2.5 years old) with sufficiently complete track logs during the period of interest and known either to have been shot by hunters or to have survived the entire hunting season. We chose 10 animals of each sex and fate because a balanced sampling design maximises the statistical power for a given sample size. Further details of how these animals were selected and what efforts were taken to avoid biases in this are given in Appendix 1. The estimated ages of shot and surviving deer were similar (female means 6.8 and 5.2 years, respectively, unpaired t test: $t_{18} = 1.43$, $P = 0.17$; male means 4.2 and 4.9 years, respectively, unpaired t test: $t_{18} = 0.66$, $P = 0.52$). Age is closely connected to social status in males, thus there is no indication of any systematic differences in social status between shot and surviving males. Shooting dates for the females ranged from 24 September – 11 December with a mean date of 8 November; shooting dates for the males ranged from 25 September – 15 November (mean date: 15 October).

Study Design

This field study compares habitat use between 10 surviving and 10 shot deer of each sex in a short period around the start of the hunting season. For each individual, we surveyed the habitat at six locations it had visited before, and six locations it had visited after the onset of the hunting season. The twelve locations for each animal were selected as follows. We sampled the last Monday–Wednesday (3 days) before the hunt started ('before onset', 1–9 days before the onset, depending on the year concerned), and the first Monday–Wednesday after the first weekend of the hunting season ('after onset', 2–8 days after onset), so we could expect some hunting to have taken place in all hunting areas. The sample periods were selected to be as close together in time as possible (consecutive weeks for two-thirds of the animals) to identify immediate responses and to minimize any confounding effect of season on our results. Importantly, all points were sampled before the rutting season so any change in habitat use could not be attributable to rutting activities rather than behavioural responses to hunters.

Within each sampled day two positions were selected: the first position after sunrise and the first position before sunset, times when deer are expected to be active and the light levels are sufficient for hunting. The motivation for restricting the locations to two times of day was to ensure that the deer had moved some distance between the positions and to avoid diurnal patterns in habitat use inflating the variance when comparing shot and surviving animals. Our data do not show habitat use throughout the 3-month long hunting season, but are a snapshot of what happens at the start of the hunting season in early- to mid-September. Locations on pastures were excluded so as to focus on within-forest variation in habitat use. The use of different habitat types by red deer has been contrasted in other studies (Godvik et al., 2009). Gaps in the GPS track logs and the exclusion of pasture locations (initially thought to be in forest, based on GIS maps) caused some individuals to be represented by fewer than

12 but never less than 10 locations. The final dataset consisted of 458 surveyed deer locations. Only two of the females and five of the males in our study were shot in forest; the remaining eight females and five males were shot on agricultural land (based on locations reported by hunters and GIS maps).

Habitat Surveys

To characterize the habitats used by deer before and after the onset of hunting, we surveyed habitat cover and forage availability at the deer locations between 18 June and 20 August 2013. An individual had used a given location up to six years prior to the habitat survey, but the habitats were likely to have remained similar throughout this period. In the field we evaluated whether any changes in habitat state had occurred since the year when the animal used that location – tree harvests, avalanches, recent drought, or successional stages or young plantations likely to have grown radically in few years – but did not find grounds for excluding any plots. We measured the distance at which a 30 cm wide, 80 cm high cover board could be sighted in all four cardinal directions at a single point at the GPS location; the mean value reflected the visual screening provided by cover at the plot as a function of topography and vegetation (Lone et al., 2014). A concave densiometer was used to estimate the proportional canopy cover directly above the plot, as an average of four measurements in the cardinal directions. Available forage was characterised in three 2 x 2 m quadrats located 10 m apart. Percentage ground cover was calculated as the mean of the three quadrats for each of three functional groups, the three potentially important forage resources for red deer in September: grasses, herbs, and the ericoid species bilberry, *Vaccinium myrtillus*. Of these, bilberry has the highest quality this late in the growing season (Albon & Langvatn, 1992).

Statistical Analysis

We modelled these field-measured habitat characteristics as responses to the crossed effects of fate (shot or surviving) and period (before or after the onset of hunting) in a linear mixed model with a random intercept for animal identity. This was to identify the relationship between survival and habitat use, and to test for expected differences between deer that were shot and those that survived, including different temporal patterns (Table 1). Separate mixed models were constructed for each sex for each of the response variables: (1) sighting distance of cover board; (2) canopy cover; and forage availability measured as percent cumulative cover of (3) grasses, herbs and bilberry, (4) grasses and herbs, or (5) bilberry alone. Because preliminary data analysis showed that males and females differed in their responses, we chose to analyse male and female data separately so the alternative scenarios could be tested for each sex. All proportions were arcsine-square root transformed and sighting distance was log transformed to meet the assumption of a homogeneous and normal error structure when modelled using the function `lme` from the package `nlme` (Pinheiro, 2014) in the software R 2.14.1 (R Development Core Team, 2011). For each response variable, the five candidate models corresponding to the alternative scenarios in Table 1 were compared on the basis of AIC (Burnham & Anderson, 2002). All models with $\Delta\text{AIC} \leq 2$ and lower AIC than simpler nested models (thereby avoiding uninformative parameters), were considered to have some support (Arnold, 2010). We report Ω^2 and Ω_0^2 as measures of explained variation by the fixed effects and fixed and random effects, respectively (Xu, 2003). They give the proportional reduction in residual sum of squares of the model compared with the residual sum of squares of a null model that included only random effects (Ω^2) or a fixed intercept (Ω_0^2).

RESULTS

The best models, based on AIC, differed for males and females (Table 2). With respect to habitat openness and forage availability, the contrast between survivors and shot individuals was in line with H4 for males (Table 1). Hypothesis H4 states that there are individual differences in the dynamic response to onset of hunting, and the strength of this response influences survival. The males that ultimately survived the hunting season had shifted to using areas with 29% shorter sighting distances after the onset of hunting compared with those used before the hunt, whereas the males that ended up being shot during the hunting season did not change their use of concealing cover (Table 3, Fig. 2a). The male patterns were also similar when the analysis was run using only individuals shot in forests or on agricultural land, and were actually stronger when considering only the males shot on agricultural land. In males, there was support for the hypothesis of a trade-off between forage availability and survival (Table 2). In line with H4, surviving males switched to areas with an average 68% less bilberry cover after the onset of the hunting season compared with the pre-hunting season, and in contrast to shot males (Fig. 2b). Lower bilberry cover was the main contributor to the

Table 2: Summary of Δ AIC values for the candidate models fitted to male and female data.

Model	DF	Sighting distance	Canopy cover	Grasses and herbs	Grasses, herbs, and bilberry	Bilberry
Males						
~1	3	12.6	1.9	0.2	2.3	9.3
Period	4	6.0	0.0	0.0	4.0	3.5
Fate	4	12.5	3.9	2.2	4.1	10.4
Period + Fate	5	5.9	2.0	2.0	5.8	4.5
Period \times Fate	6	0.0	1.8	1.2	0.0	0.0
Females						
~1	3	0.2	0.4	0.0	0.0	0.0
Period	4	2.2	2.8	2.0	2.0	1.4
Fate	4	0.0	0.0	2.0	1.8	2.0
Period + Fate	5	1.9	2.0	3.9	3.8	3.3
Period \times Fate	6	3.4	3.3	3.3	4.5	5.3

Note: Models with Δ AIC \leq 2 without uninformative parameters are shown in bold.

reduced cover of grasses, herbs and bilberry combined in habitats used by surviving males (Table 3, Fig. A2). Neither canopy cover nor the cover of grasses and herbs alone differed statistically between sites used by shot and surviving deer (Table 2). The patterns identified are also visible in the raw data despite wide variation in habitat used by different individuals as well as large heterogeneity between sites used by the same individual (Fig. A2).

Table 3: Parameter estimates from the best models relating red deer use of cover and forage (cover of grasses (G), herbs (H), and/or bilberry (B)) to hunting-season fate and time period (before and after the onset of hunting).

Sex	Response	Fixed effect	Estimate	SE	Ω^2	Ω_0^2	Random intercept SD	Residual SD
Male	Sighting distance	(Intercept)	0.19	0.20	0.07	0.36	0.51	0.83
		Survive vs. Shot	-0.04	0.28				
		After vs. Before	-0.02	0.16				
		Survive vs. shot : After vs. Before	-0.62	0.22				
Male	Canopy cover ^a	(Intercept)	-0.11	0.15	0.02	0.39	0.58	0.81
		After vs. Before	0.21	0.11				
Male	G+H ^a	(Intercept)	-0.08	0.15	0.01	0.36	0.56	0.83
		After vs. Before	0.16	0.11				
Male	G+H+B	(Intercept)	-0.11	0.17	0.04	0.19	0.36	0.93
		Survive vs. Shot	0.28	0.24				
		After vs. Before	0.28	0.18				
		Survive vs. shot : After vs. Before	-0.69	0.25				
Male	Bilberry	(Intercept)	0.13	0.19	0.07	0.31	0.47	0.86
		Survive vs. Shot	0.08	0.27				
		After vs. Before	-0.03	0.16				
		Survive vs. shot : After vs. Before	-0.59	0.23				
Female	Sighting distance ^a	(Intercept)	-0.21	0.20	0.000	0.38	0.57	0.81
		Survive vs. Shot	0.40	0.28				
Female	Canopy cover ^a	(Intercept)	-0.19	0.18	0.000	0.32	0.51	0.85
		Survive vs. Shot	0.39	0.26				

Notes: Response variables were arcsine transformed (except sighting distance, which was log-transformed) and standardized for each analysis. In cases where null models (intercept only) were selected as the best model, parameter estimates are not shown (female forage models).

^a Best models with only limited support as they were within 2 AIC units of the null model

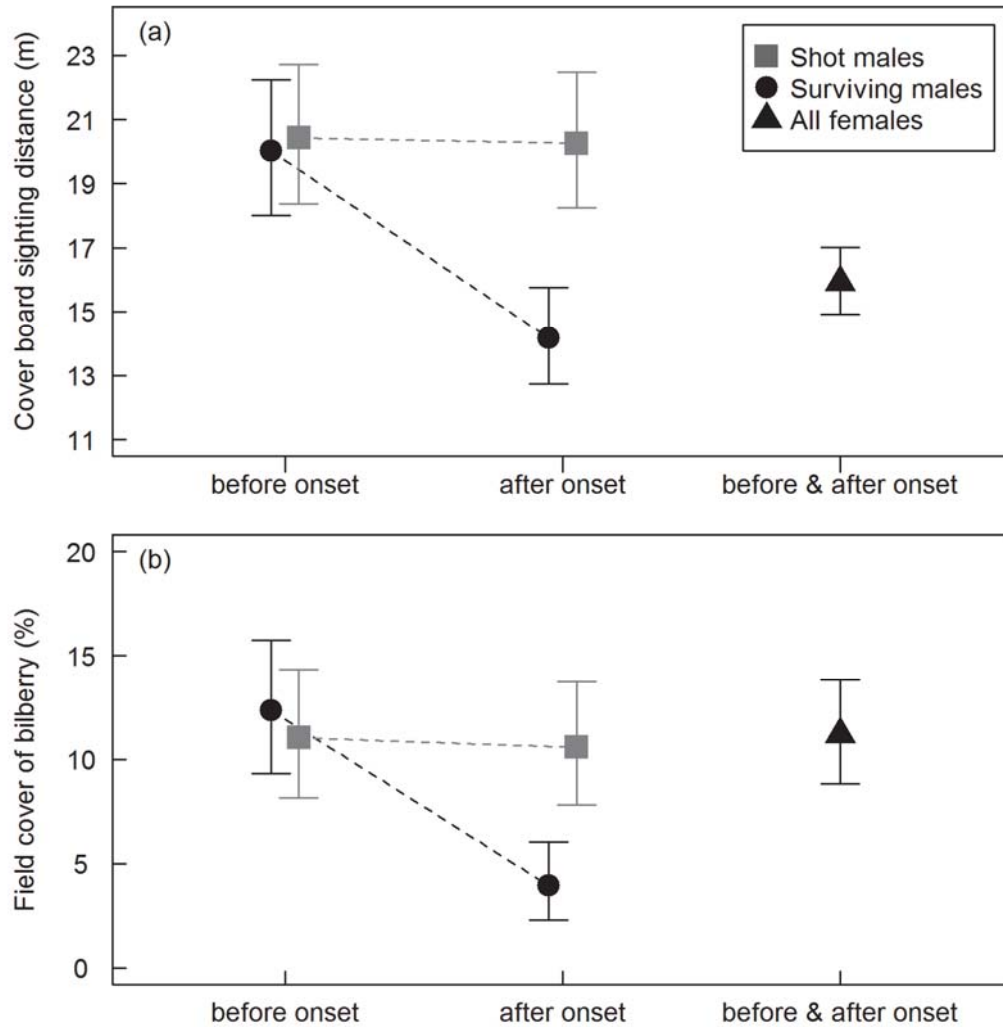


Figure 2: Red deer use of (a) cover and (b) forage habitat depending on sex, individual fate at the end of the hunting season (shot vs. surviving) and time (immediately before and/or after the onset of the hunting season). Fitted estimates of cover-board sighting distance (\pm SE) and field-layer cover of bilberry (\pm SE) from the best models for males and females as identified by AIC.

There was no support for the hypotheses that females responded to the onset of hunting or that differences among individual females influenced their survival (H1–4) relative to the null hypothesis (H0, Table 1, Table 2). Indeed, the degree of habitat cover was similar in shot and surviving females and was not affected by onset of hunting (Table 2). Note that females used habitat with 21% shorter sighting distance (more cover) than males before the onset of the hunting season (linear mixed model: $t_{38} = 2.05$, $P = 0.047$; Fig A2). There was no

correlation between bilberry availability and survival that could indicate a similar trade-off in females as seen in males (Table 2).

Overall, at the plot level, horizontal and vertical measures of cover were themselves only weakly correlated (canopy cover: range 0–96%; sighting distance: range 6–144 m; Pearson correlation coefficient $\rho = -0.28$). Second-order linear models relating forage availability with measures of cover revealed only weak correlations, the strongest being a humped relationship between bilberry cover (range 0–73%) and canopy cover, which nevertheless explained only 9% of the variation in bilberry cover (other correlation statistics are reported in Appendix 2).

There was no support for using Julian date in addition to or instead of the onset of hunting as a predictor variable for either sex. In the best models, replacing the time period contrast with the linear effect of Julian date always resulted in $\Delta AIC > 2$. Including the Julian date did not alter the parameter estimates of the other predictor variables. Thus, the data support the notion that the changes at the onset of the hunting season are abrupt rather than gradual.

DISCUSSION

Hunting is the main cause of mortality in many managed ungulate populations (Langvatn & Loison, 1999). Deer should therefore avoid humans in space and time, in line with general predator-prey theory. Previous studies have shown that individual deer using open habitat have a higher risk of mortality from hunting (Ciuti et al., 2012). But our study is the first to show that deer that survived and those that were shot during the hunting season differed in their immediate response to the onset of hunting, and that this survival strategy involved a trade-off with access to a key forage plant species. Our results show that managed ungulate populations in human-dominated landscapes, such as red deer in Norway, potentially

experience strong selection pressure for the ability respond to the risk of mortality associated with human presence in space and time.

We have linked a plastic response in behaviour at the onset of the hunting season to reduced hunting mortality in wild red deer. Surviving males shifted from using habitat with longer sight lines to habitat with 29% shorter sight lines within days of the start of the hunting season. Because it was a dynamic response to the hunting season we identify it as a deliberately employed spatial strategy in response to hunting, and from the differences between surviving and shot individuals, we infer that it successfully managed risk. That such an immediate response correlated with overall hunting-season survival suggests that we measured a general response that is sustained by the individuals in question throughout the hunting season.

There are several plausible mechanisms for how the red deer in our study were able to perceive the onset of hunting season. Deer likely assess predation risk using a variety of sensory cues, and presumably detect people and dogs using a combination of auditory, visual and olfactory inputs (Kluever, Howery, Breck, & Bergman, 2009; Kuijper et al., 2014; Lynch et al., 2014). Deer could be alerted by the heightened off-track human activity and the first gunshots. Ravens, *Corvus corax*, are known to react to gunshots (White, 2005), showing the potential for animals to react to such cues. The time of year could also play a role, as the timing of the hunt has been relatively fixed for several decades. The behavioural plasticity of responding to cues about hunting by adopting safer behaviour is central to explaining the pattern we documented in males. Whereas the deer's use of more open forests does not necessarily mean they are more likely to be shot in a forest, it does mean they are more likely to be shot in general (indeed most individuals were shot on agricultural pasture in our study). This dynamic spatial response to the onset of hunting could correlate with other risk-management behaviours such as increased vigilance (Bonnot et al., 2014) or the tendency to

hide rather than run when encountering humans (Ciuti et al., 2012). In contrast to our study, Ciuti et al. (2012) found that individual differences in behaviour existed before the hunting season started, and highlighted that this reflected personality traits. Personality traits have been found to be moderately heritable (Wolf & Weissing, 2012). Behavioural plasticity can also have a hereditary basis (Snell-Rood, 2013). The behavioural shift by males at the start of the hunting season appears to be adaptive, indicating that selection for risk-avoidance behaviour probably also operates in our system.

Linking individual survival with field-measured sighting distance corroborates earlier findings relating habitat selection to habitat visibility in coarse GIS-based land-use classes (Ciuti et al., 2012; Godvik et al., 2009), and extends them to fine-scale variability in horizontal visibility within a forested environment. Our results contrast with those of Kuijper et al. (2014) who found no link between risk-reducing behaviour by either deer or wild boar, *Sus scrofa*, and fine scale horizontal visibility. They attributed the lack of response to visibility being relatively homogenous in a dense forest, and a poor indicator of predation risk by wolves in that environment. Moreover, their study area had other predators, with deer being subjected also to predation by lynx, an ambush predator that hunts most efficiently in dense cover (Lone et al., 2014). Visibility is more variable in our study area, and the risk is undoubtedly biased towards open areas (Rivrud et al., in press) because humans are the only significant predator (Langvatn & Loison, 1999). Indeed, horizontal visibility and other characteristics of the habitats used by our deer differed substantially within and between individuals (Fig. A2), a typical feature of such small-scale habitat measures. Nevertheless, the mixed modelling framework allowed us to account for these inter- and intra-individual differences and extract the maximum information possible on the overall differences between shot and surviving deer, thereby providing clear support for some of our hypotheses about the associations between habitat use and survival.

The decreased use by survivors of habitats with substantial bilberry cover is indirect evidence of a cost associated with a successful spatial strategy for avoiding risk. Bilberry is probably the most important forage species during autumn. Herbs and grasses are higher quality and preferred forage during summer, but their crude protein content decreases exponentially through summer (outside of agricultural fields), and deer switch to bilberry from the end of July onwards (Albon & Langvatn, 1992). Surviving males that decreased their use of bilberry-dominated sites were consequently trading off higher survival against the use of the best forage resources. It is not clear if the associated cost comes from moving into denser vegetation, as the correlation between sighting distance and bilberry cover was weak at our measurement scale, or is incurred due to another underlying spatial strategy, (e.g. avoiding bilberry-dominated communities because hunters prefer such sites). The magnitude of the cost to the surviving animals of using less profitable habitats is also not clear, nor the degree to which they can compensate by increasing foraging time or being more selective in these other vegetation communities. Nonetheless, finding the same pattern of decline in forage quality and sighting distance (Fig. 2) strengthens the overall conclusion that some males survive because they respond dynamically to hunting cues, even at the expense of foraging opportunities.

Whereas individual male survival depended on the strength of a dynamic response to the risk of predation through habitat use, females did not show the same response, nor did their survival depend on persistent individual differences in habitat use. The sex difference in response to the onset of hunting that we observed could be explained by females with calves already being more cautious prior to the start of the hunting season. Indeed, females used denser cover than males. Previous studies have shown that female red deer with offspring segregate from males, and also use denser habitat prior to the hunting season (Bonenfant et al., 2004), a common phenomenon in ungulates (Ruckstuhl & Neuhaus, 2005). That females

apparently use persistent risk avoidance in a setting in which risk varies temporally suggests that it could be a strategy adapted to past patterns of predation rather than current human hunting ones. In the adult female red deer of our study population there is a strong tendency to reproduce every year (Langvatn et al., 2004). Their response to the onset of hunting might be small because the reproductive females have already exhausted much of their potential to shift habitats earlier in the summer.

Conclusions and Perspectives

We have found that survival of male red deer was related to responding dynamically to the risk of predation by shifting habitats at the onset of the hunting season, showing that hunters can influence wildlife behaviour directly in ecological processes. These results also highlight the hunters' potential role in selecting for risk-avoidance behaviour. Other recent research has also shed light on how harvesting can unintentionally target 'bold' over 'shy' individuals (Ciuti et al., 2012; Madden & Whiteside, 2014). Nevertheless, even important fitness components such as adult survival might not always relate well to overall fitness (Lind & Cresswell, 2005). For example, are more risky adult males gaining access to more females during the coming rutting season, thus enhancing their reproduction? A priority for the future should be to relate behaviour with measures of overall fitness. Such an integrative endeavour could provide a better understanding of the ecological and evolutionary mechanisms of risk avoidance interacting with other aspects of animal ecology.

ACKNOWLEDGMENTS

Marking of the animals was funded by game funds of Møre & Romsdal and Sør-Trøndelag county administrations, the wildlife boards in Aure, Sunndal, Surnadal and Tingvoll municipalities, the Norwegian Institute for Agricultural and Environmental Research

and the University of Oslo, and grants by the Research Council of Norway (Project Nos. 179370 and 203786). We are grateful to everyone that assisted in the marking of animals. Thanks to Øystein Brekkum and Marius Bless for their assistance in the field, to Richard Bischof for statistical advice and to Peter Frost for language editing. We are also grateful for the feedback of four anonymous reviewers that greatly strengthened the paper.

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Appendix 1: *Further details on the selection of shot and surviving animals*

For the sake of analysis, we chose to have a balanced number of individuals and observations per individual. We selected 10 surviving and 10 shot deer of each sex, disregarding three shot males and seven surviving females that we could have potentially surveyed. Which of the candidate deer to leave out at this stage were chosen so as to have as even as possible geographical spread between categories. Where there were several candidate deer in one municipality, of which we were to retain one or two, these were chosen randomly. We always used data from the first year of monitoring, except in six cases in which deer were monitored for two years and shot in the second year. These three female and three male deer were thus classified as ‘shot’ and we used the GPS data from the year in which they were shot, rather than classifying them as ‘surviving’ and using data from the first year. This could influence the results by reducing differences between shot and surviving deer, but excluding these animals did not notably alter parameter estimates.

Table A1: Distribution of the data from the study animals across years

Year	Males		Females	
	Shot	Surviving	Shot	Surviving
2007	0	4	1	1
2008	4	0	4	1
2009	2	3	2	2
2010	3	1	2	3
2011	1	1	1	3
2012	0	1	0	0

Appendix 2: *Correlations between horizontal and vertical cover and forage measures*

Table A2: First- and second-order relationships between forage availability (cover of grasses (G), herbs (H), and/or bilberry (B)), and horizontal and vertical measures of cover.

	Estimate	SE	t-val	P-val	Adjusted R ²	Variation explained (%)
Bilberry						
Intercept	-0.45	0.31	-1.44	0.151	0.009	0.9
Sighting distance	0.51	0.20	2.49	0.013		
Sighting distance²	-0.08	0.03	-2.48	0.014		
G+H						
Intercept	1.03	0.29	3.54	0.000	0.002	0.2
Sighting distance	-0.33	0.19	-1.74	0.083		
Sighting distance ²	0.05	0.03	1.75	0.081		
G+H+B						
Intercept	0.74	0.27	2.74	0.006	-0.004	-0.4
Sighting distance	-0.01	0.17	-0.05	0.960		
Sighting distance ²	0.00	0.03	0.01	0.991		
Bilberry						
Intercept	0.13	0.04	3.24	0.001	0.091	9.1
Canopy cover	0.84	0.13	6.64	0.000		
Canopy cover²	-0.64	0.09	-6.90	0.000		
G+H						
Intercept	0.61	0.04	15.79	0.000	0.009	0.9
Canopy cover	-0.30	0.12	-2.44	0.015		
Canopy cover²	0.21	0.09	2.40	0.017		
G+H+B						
Intercept	0.65	0.04	18.19	0.000	0.011	1.1
Canopy cover	0.29	0.11	2.55	0.011		
Canopy cover²	-0.22	0.08	-2.67	0.008		

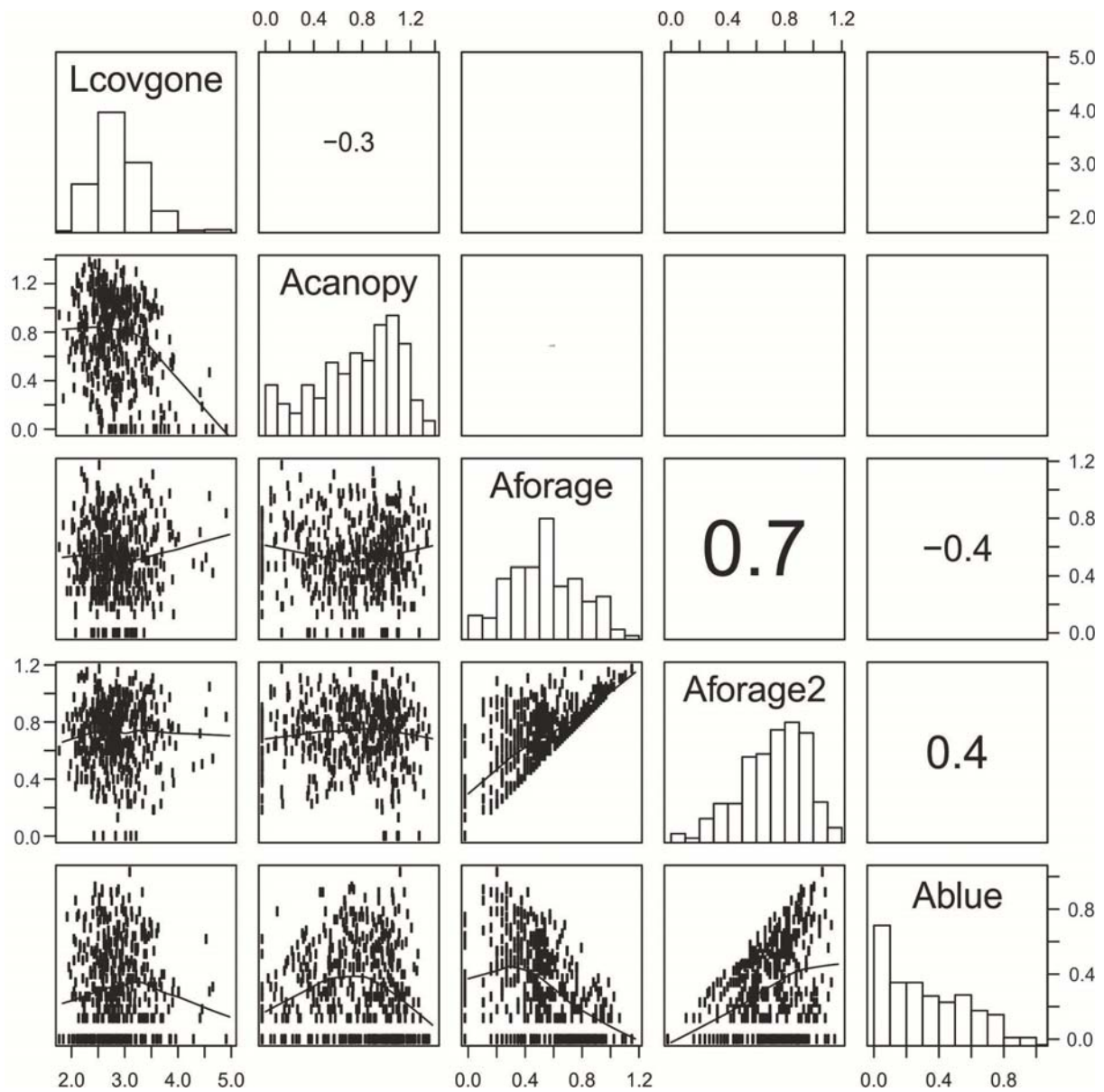


Figure A1: Correlations (only first order linear effects considered) between measures of sighting distance (Lcovgone), canopy cover (Acanopy) and forage measures (Aforage=grasses and herbs, Aforage2=grasses, herbs and bilberry, Ablue=bilberry).

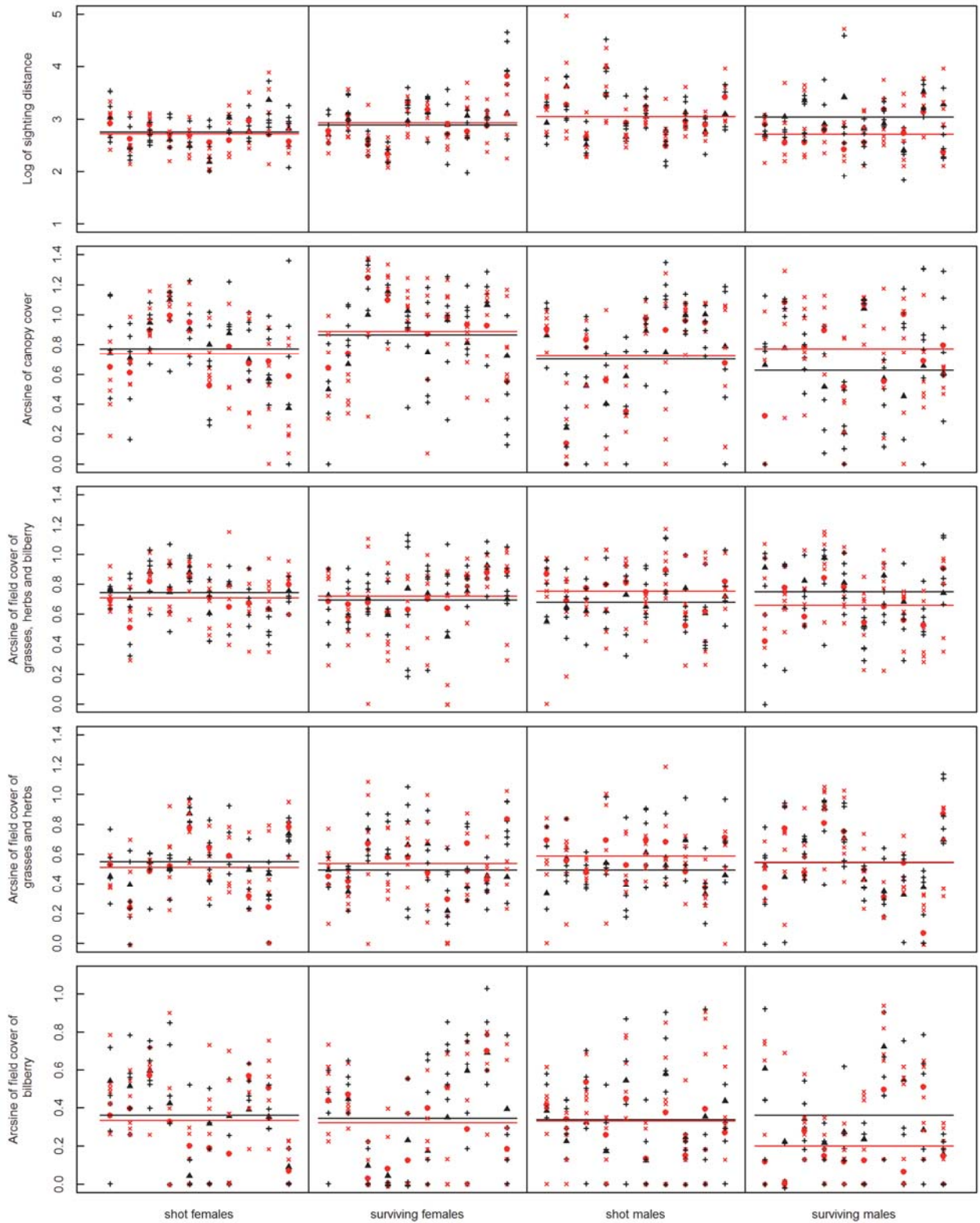


Figure A2: Raw data showing intra- and interindividual variation and group differences in habitat characteristics. Vertical scatterplots ($n=10-12$) represent each individual deer ($n=40$, balanced across each combination of sex and fate). Locations visited before the onset of the hunting season (+), their mean for each individual (filled triangle) and the mean of the individual means for each combination of sex and fate (line) are shown in black. Locations visited after the onset of hunting (\times), their mean for each individual (filled circle) and overall

mean of individual means (line) are shown in red. Original data were in m (sighting distance) and proportions.

PAPER IV

Improving broad scale forage mapping and habitat selection analyses with airborne laser scanning: the case of moose

KAREN LONE,^{1,†} FLORIS M. VAN BEEST,² ATLE MYSTERUD,³ TERJE GOBAKKEN,¹ JOS M. MILNER,^{4,5}
HANS-PETTER RUUD,¹ AND LEIF EGIL LOE¹

¹Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Aas, Norway

²Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark

³Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway

⁴Hedmark University College, Department of Forestry and Wildlife Management, Campus Evenstad, NO-2480 Koppang, Norway

Citation: 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(11):144. <http://dx.doi.org/10.1890/ES14-00156.1>

Abstract. Determining the spatial distribution of large herbivores is a key challenge in ecology and management. However, our ability to accurately predict this is often hampered by inadequate data on available forage and structural cover. Airborne laser scanning (ALS) can give direct and detailed measurements of vegetation structure. We assessed the effectiveness of ALS data to predict (1) the distribution of browse forage resources and (2) moose (*Alces alces*) habitat selection in southern Norway. Using ground reference data from 153 sampled forest stands, we predicted available browse biomass with predictor variables from ALS and/or forest inventory. Browse models based on both ALS and forest inventory variables performed better than either alone. Dominant tree species and development class of the forest stand remained important predictor variables and were not replaced by the ALS variables. The increased explanatory power from including ALS came from detection of canopy cover (negatively correlated with forage biomass) and understory density (positively correlated with forage biomass). Improved forage estimates resulted in improved predictive ability of moose resource selection functions (RSFs) at the landscape scale, but not at the home range scale. However, when also including ALS cover variables (understory cover density and canopy cover density) directly into the RSFs, we obtained the highest predictive ability, at both the landscape and home range scales. Generally, moose selected for high browse biomass, low amount of understory vegetation and for low or intermediate canopy cover depending on the time of day, season and scale of analyses. The auxiliary information on vegetation structure from ALS improved the prediction of browse moderately, but greatly improved the analysis of habitat selection, as it captured important functional gradients in the habitat apart from forage. We conclude that ALS is an effective and valuable tool for wildlife managers and ecologists to estimate the distribution of large herbivores.

Key words: Airborne laser scanning (ALS); *Alces alces*; cover; ecological indicators; habitat mapping; integration of forest and wildlife management; LiDAR; Norway; population monitoring; remote sensing; Resource Selection Functions (RSFs); ungulate management.

Received 30 May 2014; revised 23 August 2014; accepted 27 August 2014; final version received 18 September 2014; **published** 24 November 2014. Corresponding Editor: R. R. Parmenter.

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⁵ Present address: School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ United Kingdom.

† **E-mail:** karen.lone@nmbu.no

INTRODUCTION

Among ungulates, density-dependent food limitation is a main limiting factor in population dynamics (Bonenfant et al. 2009). Forage quality and quantity are therefore important determinants of foraging and habitat selection patterns of large herbivores (Fryxell 1991, Hanley 1997). Despite the strong influence of food resources on both habitat selection and population dynamics, quantification of food availability at large spatial scales remains challenging. Most studies rely on environmental proxies of forage availability and cover, such as NDVI (Mueller et al. 2008), land cover classes (Uzal et al. 2013), or forest stand characteristics like productivity (Godvik et al. 2009), dominant tree species (Dussault et al. 2005a) and age class (Mabille et al. 2012). Often, such proxies are used without quantifying levels of food and cover, though exceptions occur (van Beest et al. 2010b, Avgar et al. 2013, Blix et al. 2014). It is well known that the physical structure of the habitat is also important for habitat selection as cover is used for concealment and thermal shelter (Myserud and Østbye 1999, DePerno et al. 2003).

Scale matters greatly in the study of ecological phenomena (Wiens 1989). Habitat selection patterns often differ between scales, reflecting processes and behavioral decisions operating at different scales (Boyce et al. 2003, DeCesare et al. 2012). The scale of the study should reflect the question at hand. The concept of scale involves both extent of the study area, the resolution of the data, and in some cases, the range over which the environmental context is considered (De Knecht et al. 2011). In wildlife management, important questions on a broad scale include identifying a population's seasonal range use or what landscape elements are important within an animal's home range. GPS tracking collars for wildlife have enabled researchers to collect large quantities of precise location data covering large areas. On the other hand, environmental data covering the same broad scales often have low resolution and precision (such as GIS-based land use classes). This discrepancy frequently results in poor predictive ability of habitat selection models (Loe et al. 2012). New methods for monitoring forage resources and physical habitat structure with fine resolution at broad scales are therefore

of considerable interest for both basic and applied ecological research.

Airborne laser scanning (ALS) is a promising remote sensing technique for obtaining habitat information across large spatial scales. Besides providing detailed elevation models, these data hold three-dimensional information on the distribution of vegetation biomass. Forest parameters such as timber volume and stem density can be estimated with high precision, and these procedures have been operational in the Scandinavian countries for more than ten years (Holmgren 2004, Næsset 2004). ALS data are also increasingly applied in large-scale ecosystem studies (Lefsky et al. 2002), to estimate carbon storage (Stephens et al. 2007), biodiversity (Müller and Vierling 2014), to map standing dead wood (Pesonen et al. 2008) and to model habitat for various wildlife species (Hill et al. 2014), including birds (Hinsley et al. 2002) and ungulates (Coops et al. 2010, Melin et al. 2013, Lone et al. 2014). In these studies, laser data have been used directly to interpret the physical structure of the habitat relevant to each species or species assemblages. Despite the fundamental importance of forage and cover in understanding animal ecology, there has been no formal analysis linking structural information of habitat to forage resources, and few relating ALS derived cover variables to habitat selection (Graf et al. 2009, Melin et al. 2014).

The aim of this study was twofold: (1) to evaluate the use of ALS data in quantifying and predicting biomass of browse species common in the diet of Norwegian moose (*Alces alces*), and (2) to determine whether ALS-derived measures of forage and physical habitat structure (cover) are effective in predicting habitat selection of moose at multiple spatial and temporal scales. Moose in Scandinavia are partially migratory and typically migrate from high elevation summer habitats to low elevation winter habitats that have high availability of browse (commonly young pine stands) and more favorable snow conditions (Ball et al. 2001, Nikula et al. 2004). Moose habitat selection is related to forage availability and cover, both at the landscape and home-range scales (Dussault et al. 2005b, Månsson et al. 2007, Herfindal et al. 2009, van Beest et al. 2010b). At a landscape scale, moose select home ranges with large volumes of biomass, while they tend to

select for forage quality within home ranges (van Beest et al. 2010b). The moose represents an ideal model species to test the applicability of ALS because its food (mainly browse) is found in the bush and tree strata (Mysterud 2000), which can potentially be quantified with ALS data. Here, we build upon the study by van Beest et al. (2010b), in which forage distribution was modeled using forest stand-based inventory and terrain data. Using that dataset in combination with existing ALS data, we tested whether the predictive forage models were improved by including ALS-derived variables, and whether ALS data could predict browse biomass well on its own. Finally, we evaluated the usefulness of the spatial predictions of browse biomass and selected ALS variables in resource selection functions (RSFs) for GPS-marked moose in southern Norway.

METHODS

Study area and the study species

The study was conducted in an 1100-km² area within Telemark and Vestfold counties in southern Norway (Appendix: Fig. A1). The area is within the southern boreal to boreonemoral zones. Land cover is dominated by commercially managed forests of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Some mixed deciduous stands of birch species (*Betula pubescens* and *B. pendula*), rowan (*Sorbus aucuparia*), willow (*Salix* spp.) and aspen (*Populus tremula*) occur throughout the area. The mean monthly temperatures in June and January are 15 and -5°C, respectively (Siljan weather station at 100 m above sea level [asl], The Norwegian Meteorological Institute; <http://www.met.no>). Snow depths (mean ± SD) at a 430 m asl location during January–April 2007 and 2008 were 42 ± 29 cm and 73 ± 21 cm (Mykle weather station, The Norwegian Meteorological Institute). Moose densities in the area were estimated at 1.3 individuals/km² (Milner et al. 2012), but per capita available browse is low relative to its peak in the 1960s (Milner et al. 2013).

Field measured browse biomass

Field estimates of browse forage biomass were made for six tree species: pine, silver birch, downy birch, rowan, aspen, and goat willow

(*Salix caprea*). These species represent the most preferred species and, together with the ericaceous shrub bilberry (*Vaccinium myrtillus*), the bulk of what moose feed on in both summer and winter. In the original field-study 189 forest stands were sampled using a random stratified sampling design (van Beest et al. 2010b). Because the ALS data did not cover the entire original study area, data from only 153 forest stands were used here, but these were well spread among the originally chosen strata: development class (5 class factor: 1 = forest under regeneration, 2 = regenerated areas and young forest, 3 = young thinning stands, 4 = advanced thinning stands, and 5 = mature forest), dominant tree species (3 class factor: Scots pine, Norway spruce and mixed deciduous), and aspect (4 class factor: north, east, south and west). Each forest stand was sampled with five 50-m² circular subplots, and the center coordinates of the central subplot were recorded with a handheld GPS obtaining an average location over 10 min or more. Based on experience from GPS measurements of almost 1000 plots in similar forest areas we expect a mean location error from the true position of less than 3.5 m with a standard deviation of less than 3 m (O. M. Bollandsås, E. Næsset, and T. Gobakken, *unpublished data*). The four remaining subplots were placed 25 m away from the center subplot in each of the four cardinal directions, and were at least 15 m from the edge of the forest stand. Within each subplot, the canopy volume and stem diameter of individual trees of the target species were measured in order to predict the leaf (summer) or twig (winter) biomass accessible to moose (<3.0 m height, and accounting for snow cover in winter) using allometric models. The R² of the allometric models of available browse ranged from 0.63 to 0.92 (see van Beest et al. 2010b for more details on the allometric models). Rowan, aspen and willows are high quality but relatively less common browse species that were considered together as one category of browse (abbreviated as RAW). Total forage biomass in winter (twigs) included all six browse species while summer forage biomass (leaves) included all species except pine as moose do not forage on it during summer. The average biomass of the five 50-m² subplots was considered as the ground reference biomass for 2500-m² circular plots that encompassed the

Table 1. Summary statistics for the response variable browse biomass (g/m^2) at the 2500-m^2 plot level and the mean standard deviation (SD) of the five subplots.

Variable	Mean	Min	Max	SD	Within-plot SD
RAW (winter)	39.0	0	419	71.8	33.9
RAW (summer)	83.6	0	1021	152	62.1
Pine (winter)	157	0	2710	383	168
Total biomass (winter)	331	0	3286	524	311
Total biomass (summer)	158	0	1165	215	104

Note: RAW denotes a group of high quality browse species: rowan, aspen and goat willow.

subplots (Table 1). We chose to model biomass at this scale (2500 m^2) because it gave the best spatial match between the ground reference data and the ALS data, given the georeferencing inaccuracies of the field data material. There was considerable variability in the response variables between subplots within each plot, and although the between-plot variability was greater, the subsampling procedure likely introduced some noise in the response variable on the 2500-m^2 plot (Table 1).

Forest inventory data

We had access to the stand-based forest inventory for operational forest management for a large (40–80%) and fairly contiguous portion of the forested area in the municipalities we considered. Maps were available in Geographic Information System software and included information on stand delineations (polygons) and associated stand-level attributes: dominant tree species (deciduous, spruce, pine), development class (1–5) and h40 site index (SI) of productivity (defined in Tveite 1977). Productivity was reclassified as a two-level factor: “high” where $\text{SI} > 14$ and “low” where $\text{SI} \leq 14$. Field assessment confirmed that the accuracy of the maps was high (van Beest et al. 2010a).

ALS data

Laser scanning systems developed for airborne platforms are used to survey large areas in great detail. A laser beam with a small footprint is directed towards the ground in pulses, and scanned across the landscape perpendicular to the flight direction. Each flight line thus covers a strip of land, and the flight pattern can be

planned so each strip overlaps with the next to give continuous cover over the entire study area, as in this study. For each laser pulse, the ALS instrument registers one or more peaks in the return signal. From the position of the aircraft, the speed of light and the reflection time of each registered peak in the return signal, the system calculates the location where the beam was reflected from (see Wehr and Lohr 1999 for a technically detailed description). This yields a data set of ‘echoes’ from ground, vegetation or man-made structures with accurate X, Y, and Z coordinates, out of which the ground echoes are classified by standard algorithms (Axelsson 2000). Commercial providers of laser data would normally process the data to this stage where they are accessible to researchers in a specialized GIS environment, but do not require expertise in geomatics.

The laser data were collected for other purposes and as four separate projects in the period 2008–2010 (Appendix: Table A1). Project parameters were similar for the three projects with relatively low pulse density ($1\text{--}2\text{ m}^{-2}$), while the fourth had a higher pulse density (12 m^{-2}) due to a lower flying altitude, smaller scan angle, and higher pulse frequency than the other three projects. As the higher quality data in one region could potentially have affected results, we tested this possibility in the final models and found that none were significantly improved by including interactions between the ALS variables and region/laser project. Each project was delivered from the contractor as a point cloud with UTM coordinates and ellipsoidal height, with ground echoes classified. A triangular irregular network (TIN) representing the ground surface was made from the ground echoes and subtracted from the Z coordinates of the point cloud, to give height above ground (dz) for each echo. From the ground surface TIN, we derived a digital terrain model (DTM) with a 10-m cell size, and used it to calculate slope, aspect and hill shade. For each field plot, the corresponding ALS echoes were extracted from circular plots of 2500 m^2 centered on the ground reference field plots, thus encompassing the five subplots. Variables describing the vertical distribution of the echoes were calculated for each plot. These were summary statistics of the height values: the 10th, 20th, 30th, ..., 90th percentiles, mean, max, standard

deviation and coefficient of variation of the height of echoes with $dz > 0.5$ m. Additionally, the proportion of echoes within the height intervals corresponding to ground, understory and canopy: 0–0.5 m, 0.5–3.0 m, above 3.0 m (thus a measure of canopy cover), and, lastly, the ratio of understory echoes ($0.5 \text{ m} < dz \leq 2.0 \text{ m}$) to understory and ground echoes ($dz \leq 2.0 \text{ m}$) (a measure of understory cover). Wing et al. (2012) also utilized echo intensity to distinguish ground and vegetation echoes, but as we lacked calibrated intensity measures our definition of understory cover relied solely on echo height. Many of the ALS variables are correlated, and to aid model interpretation, we pre-screened them to avoid cross-correlation ($r > 0.5$), retaining the functionally most meaningful variables: canopy cover, understory cover, 90th percentile of height (h90) and coefficient of variation of height (hcv). A single pulse can give several echoes, and we used all echoes in the calculation of the variables in order to use all the information and because initial analyses showed better results than splitting into first and last echoes. Terrain variables were extracted from the cell that each plot center fell in.

Browse biomass models

We developed models for summer and winter biomass of RAW, winter biomass of pine, and total summer biomass and total winter biomass separately. To fulfill the assumption of homogeneity of the variance, we used log-linear regressions to model the available forage biomass. We used three sets of predictor variables, inventory variables alone, inventory and ALS variables together, and ALS variables alone. Terrain variables (elevation, slope, aspect and hill shade) were always included as topography influences growing conditions (Gartlan et al. 1986). We allowed for an interaction between h90 and canopy cover. Understory cover was log-transformed. For each of the three sets of candidate predictor variables, we identified the best model by backwards selection using F -tests with cutoff $p = 0.05$ (Murtaugh 2009). We assessed predictive performance using K -fold cross-validation with five folds, fitting the model to 80% of the data and using it to predict observations for the remaining 20%. From this, we determined the variation explained by the model using squared

Pearson's correlation coefficient between log-transformed responses and predictions on log scale. We assessed prediction accuracy by calculating the root-mean-square prediction error (RMSPE) for predictions, both on the log scale and back-transformed. We extrapolated our results to map total available moose forage in winter and summer across the study area. A grid with $50 \text{ m} \times 50 \text{ m}$ cells was superimposed on the ALS point cloud and for each cell we calculated the variables describing the vertical distribution of echoes using the same definitions as for the field plots. The resulting ALS raster maps were used together with the rasterized forest inventory variables to predict, cell by cell, the available browse biomass according to the final models for total winter biomass and total summer biomass. We applied the bias-correction factor of Snowdon (1991) to all predictions: after back-transformation from the log scale, they were multiplied by the ratio of the average value of response variables on the original scale to the average value of the predicted values after back-transformation. All analyses were done in R 2.14.1 (R Development Core Team 2011).

Moose data

In total 34 adult female moose were tranquilized by dart gun from a helicopter, using established techniques (Arnemo et al. 2003), and fitted with GPS collars (Tellus Remote GSM, Followit AB, Lindesberg, Sweden) programmed with a 1 hour relocation schedule. All animal handling was carried out with permission from the national management authority, the Directorate for Nature Management (protocol number: FOTS ID 1428), and evaluated and approved in accordance with the ethical guidelines and legal requirements set by the Norwegian Institute for Nature Research. Collar data were collected from January to November 2007 ($n = 16$) and 2008 ($n = 18$) but the sample size was reduced to 31 individuals during winter and to 20 individuals during summer due to collar malfunctions and exclusion of individuals with seasonal space use outside the area of ALS coverage. All GPS locations collected within 24 h of marking were excluded. Winter length was defined based on snow conditions (period with ≥ 30 cm snow depth). In 2007 winter stretched from 21 January until 8 April and in 2008 from 4

Table 2. The candidate moose RSF models compared within each combination of season and scale and the interpretation of specific inter-model comparisons.

Model no.	Data origin	Focal predictor variables	Evaluation and interpretation
1	Forest inventory maps	development class, dominant species	If best model, ALS information doesn't contribute anything new to moose selection models and forest stand classes capture moose selection better than simple functional gradients of total forage biomass or total amount of cover
2	Forage maps (inventory)	total forage biomass	If best model, ALS information doesn't contribute anything new to moose selection models and total forage biomass is the main driver of selection patterns
3	Forage maps (ALS)	total forage biomass	If nearly as good as model 2, ALS-only forage maps capture the wildlife-relevant variation in forage as well as other forage maps
4	Forage maps (inventory & ALS)	total forage biomass	If better than model 2, ALS-improved forage maps lead to improved predictions of moose space use
5	ALS variables	canopy cover, understory cover	If best model, ALS vegetation structure variables capture important habitat variation better than the forage estimates or the inventory categories, by capturing the same and/or additional information
6	Forage maps (inventory) and ALS variables	total forage biomass, canopy cover, understory cover	If better than model 4, ALS holds information relevant to moose habitat selection beyond how it relates to forage

January until 30 April. We defined summer as 1 June until 15 September for both years, and excluded spring and autumn positions altogether. The average GPS-collar fix rate was 96% (range 87–99%) during winter and 90% (range 83–97%) during summer. To correct for possible bias in GPS fix success prior to analyzing habitat selection, we simulated the missing GPS positions weighting by the terrain-specific probability of obtaining a fix (Frair et al. 2004, van Beest et al. 2010b).

Moose habitat selection analysis

To evaluate how effectively the forage maps and ALS information quantified habitat selection of moose, we used RSFs and followed procedures in van Beest et al. (2010b) as closely as possible. RSFs are defined as any function proportional to the probability of use of a resource unit by an animal (Manly et al. 2002). We computed RSFs for both summer and winter seasons and for two spatial scales commonly investigated in basic and applied ecology: where in the landscape seasonal home ranges are located and where within seasonal home ranges the animals spend time, i.e., second and third selection order of Johnson (1980). As such, habitat availability at the within home range scale was estimated by drawing a random sample of point locations from within each individual's wintering and summer home

range (delineated by a 95% minimum convex polygon). Available points were selected in equal number to the used points for each individual. At the landscape scale, habitat availability was defined as a random sample of point locations from within the study area boundaries and we considered availability at the within home range scale as used points (Aebischer et al. 1993). For each spatiotemporal scale, we compared six candidate RSFs (Table 2) that had forest inventory data, predicted forage availability, ALS estimates of canopy and understory cover, or some combination of these as predictor variables. The resource (predictor variable) value at a used or available point location was extracted from the 2500-m² cell of the resource map that the point fell within. A preliminary analysis showed a non-linear relationship with selection so we included a second order effect of canopy cover. At the home range scale we included interactions between all focal predictor variables and light condition (dark, daylight, twilight) as moose activity level depended on light conditions (highest activity levels during twilight; F. M. van Beest and J. M. Milner, *unpublished data*) and this may be related to resource use. Candidate models were selected a priori to assess whether the ALS variables improved the predictive ability of the RSFs, either directly by quantifying cover, or through better forage estimates.

Table 3. Predictive ability of the best browse biomass models using inventory (inv), airborne laser scanning (ALS), or inventory and ALS data; explained variation (R^2), cross-validated explained variation (Pearson r^2), root mean square prediction error normalized to the mean value of the response (RMSPE %), and number of estimated parameters (k).

Data type	R^2	Cross-validation† Pearson r^2	Cross-validation† RMSPE (%)	Cross-validation‡ RMSPE (%)	k
RAW (winter)					
inv	0.32	0.26	65.8	158	7
inv + ALS	0.37	0.29	64.7	151	10
ALS	0.18	0.15	70.5	175	4
RAW (summer)					
inv	0.33	0.28	52.9	159	7
inv + ALS	0.36	0.29	52.6	158	11
ALS	0.10	0.09	59.2	176	1
Pine (winter)					
inv	0.56	0.50	68.7	217	7
inv + ALS	0.58	0.50	68.3	209	8
ALS	0.23	0.18	87.6	248	4
Total biomass (winter)					
inv	0.45	0.38	33.5	145 (145)	8
inv + ALS	0.52	0.45	31.5	151 (144)	11
ALS	0.30	0.24	37.0	176 (178)	5
Total biomass (summer)					
inv	0.30	0.22	32.3	121	8
inv + ALS	0.35	0.28	30.9	117	9
ALS	0.18	0.13	33.8	134	5

Notes: RAW = rowan, aspen and goat willow. For total biomass winter the RMSPE of the back-transformed predictions with one influential point removed is shown in parentheses.

† Calculated with log-transformed responses and predictions on log scale.

‡ Calculated with untransformed responses and back-transformed predictions.

Coefficients of the exponential RSFs were estimated from use–availability data in a mixed-effects logistic regression (design III data; Thomas and Taylor 2006) with moose ID as a random intercept (Gillies et al. 2006). Mixed-effect logistic regressions were fitted using the library ‘lme4’ (Bates et al. 2012) implemented in R (R Development Core Team 2011). For each spatiotemporal scale, we compared the fit (using AIC) and predictive performance (with K -fold validation; Boyce et al. 2002) of the six pre-defined candidate RSFs. For the K -fold cross-validation procedure, the model was repeatedly trained withholding 20% of the used locations every time. The points withheld for validation were then predicted using that model and their RSF scores were binned into ten bins that each represented an equal area, as calculated from the available locations. We calculated the Spearman-rank correlation (r_s) between the number of predicted used points in each bin and the bin rank from low to high RSF score (Boyce et al. 2002). This procedure was repeated 100 times to determine whether the r_s was significantly different from random.

RESULTS

Estimating biomass of browse forage

The explanatory power (R^2) of the best forage models for each browse category ranged from 0.35 to 0.58, while the K -fold cross-validated Pearson r^2 ranged from 0.28 to 0.50 (Table 3). All models tended to over-predict at low biomass and under-predict at higher biomass, so the estimated quantity is better interpreted as a relative rather than an absolute measure of forage biomass (Appendix: Fig. A2). Models including ALS variables typically had more predictor variables. To ensure that the improvement was not only due to the increased complexity of the model, we made our comparison on the basis of the cross-validation Pearson r^2 and RMSPE. The models including both ALS and inventory variables predicted as well or better than the inventory-only models. By including ALS variables, we could explain 7 percentage points and 6 percentage points more of the variation in total biomass for winter and summer, respectively, bringing the explained variation up to 45% and 28% (Table 3). The prediction

Table 4. The best models for predicting available forage biomass by browse category.

Predictor variable	RAW				Pine		Total biomass			
	Winter		Summer		Winter		Winter		Summer	
	β	SE	β	SE	β	SE	β	SE	β	SE
(Intercept)	3.30	0.97	3.80	1.1	3.09	0.60	6.32	0.94	6.76	0.65
Dominant tree species†										
Pine	-1.85	0.34	-2.42	0.40	1.93	0.40	0.31	0.35	-1.27	0.32
Spruce	-0.96	0.33	-0.69	0.36	-1.25	0.37	-1.28	0.32	-1.11	0.29
Development class‡										
2	-0.60	0.37	-0.35	0.41	0.43	0.43	0.85	0.36	0.24	0.33
3	-0.78	0.39	-0.65	0.43	-0.98	0.43	-0.40	0.38	-0.52	0.33
4	0.06	0.39	0.57	0.43	-1.25	0.45	-0.05	0.38	0.26	0.34
5	-0.87	0.39	-0.63	0.43	-1.74	0.46	-1.15	0.38	-1.10	0.34
Productivity§										
Low	0.71	0.37	1.24	0.36	0.83	0.33	0.91	0.27
h90	0.18	0.08	0.15	0.083	0.070	0.073
Canopy cover	4.82	1.92	2.88	2.3	-2.06	0.83	0.88	2.0	-2.61	0.65
h90:canopy cover	-0.40	0.13	-0.31	0.15	-0.26	0.13
log(understory cover)	0.53	0.19	0.43	0.21	0.51	0.18	0.32	0.15

Note: RAW = rowan, aspen and goat willow.

† Reference level = mixed deciduous stands.

‡ Reference level = development class 1.

§ Reference level = high productivity.

of biomass was not improved for pine, while it was slightly improved for the RAW species. Models that only used ALS variables had consistently poorer predictive abilities than either of the models including inventory variables (Table 3).

ALS variables were generally included in addition to the other variables, rather than outperforming them. In particular, ALS variables never replaced the inventory variables dominant tree species and development class, which were kept in nearly all relevant top models (Table 4). The important ALS variables were canopy cover, h90 in interaction with canopy cover, and understory cover. For total biomass in winter and summer, increasing ALS measured canopy cover was negatively correlated with forage availability (Fig. 1). For total biomass in winter, the steepness of this slope depended on the general height of the trees (h90), where taller trees meant a steeper decline in forage availability with canopy cover. An increase in understory cover was related to an increase in available forage biomass (Fig. 1). This was the case for all models where understory cover was included (Table 4).

The final product of browse modeling was summer and winter forage maps, based on ALS and/or inventory data. Fig. 2 shows maps based on the best models using inventory and ALS data.

Habitat selection of moose

Overall, the best performing RSF models were those containing ALS variables (models 5 and 6), both in terms of AIC rank and K-fold validation (Table 5). Although the RSFs based on the forest inventory maps only (model 1) often had relatively low AIC values, the K-fold validation showed that these models had low predictive power. The RSFs based on forage maps predicted only by means of ALS (model 3) were never ranked as the top-model. Moose selected for a low or intermediate amount of canopy cover depending on the time of day, season and spatial scale of analyses, and typically against (and never for) understory cover (Fig. 3; Tables A2–A5). At the landscape scale, moose selected for low canopy cover both during summer and winter (Fig. 3A, B). At the home range scale, moose selected for an intermediate optimum of canopy cover during daytime (Fig. 3C, D). At twilight and night, moose selected sites with lower canopy cover as low canopy cover was monotonically selected (summer: Fig. 3F, H) or the optimum was shifted to lower canopy cover relative to the daytime optimum (winter: Fig. 3E, G). Moose selected for sites with increased forage biomass in all seasons and times of day at both the landscape scale and the within home range scale (all $\beta > 0$, all $p < 0.05$; Appendix: Tables A2–A5).

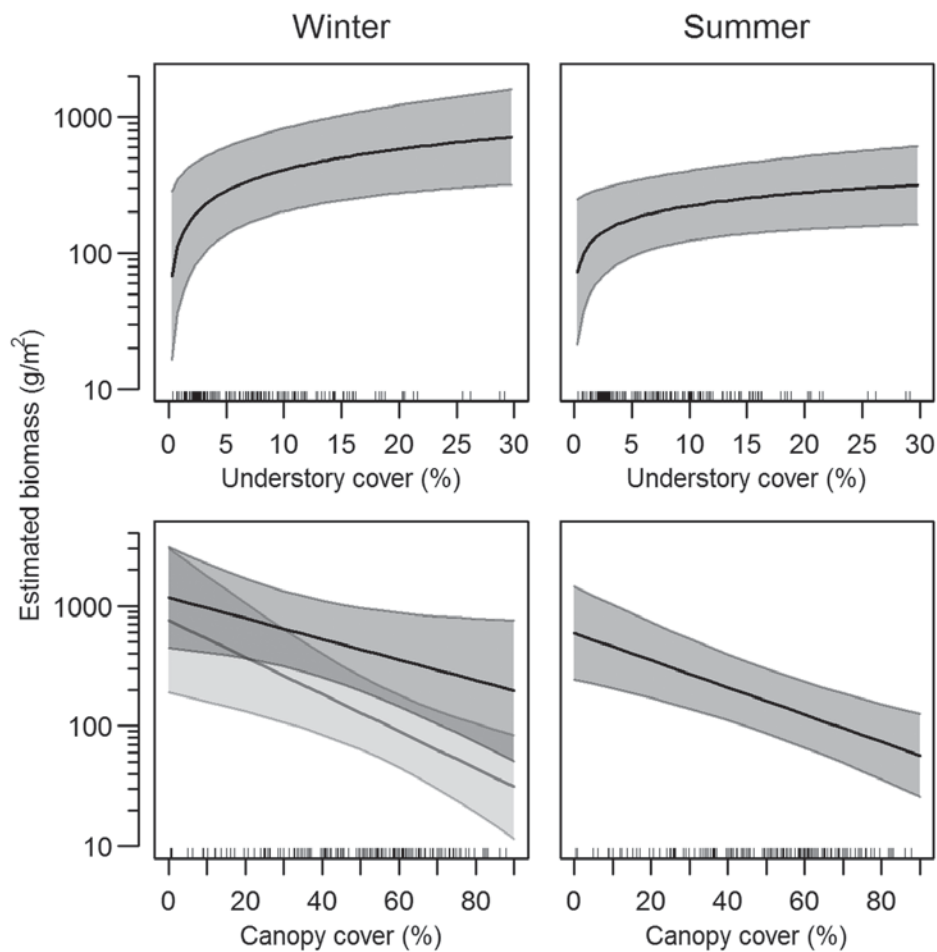


Fig. 1. Predicted effects of airborne laser scanning variables on amount of available forage, from the best models for total biomass in winter and summer (shown for deciduous stands of development class 2 with high productivity). Shaded regions are 95% confidence intervals. For total winter biomass, effect of canopy cover is shown for two values of 90th percentile echo height (h_{90}) to show the interaction of the two variables. In that panel, black is for $h_{90} = 11$ m, grey is for $h_{90} = 17$ m, this corresponds to the 20th and 80th percentiles of h_{90} in the entire dataset. Rugplots along the x -axis show the distribution of the data.

DISCUSSION

The lack of broad scale information on forage and cover availability has often hampered studies of spatial distribution of large herbivores, as field-based inventories of forage at large spatial and temporal scales are extremely costly and rarely available. Remote sensing techniques have great potential to fill this void as they can extract detailed information on biotic or abiotic environmental conditions relevant to ecological studies (Pettorelli et al. 2014). Here, we presented a novel use of ALS data to model browse

availability at the landscape scale in a managed boreal forest. Incorporating ALS data moderately improved models predicting browse biomass compared to models only using inventory map information. A significant challenge in our study was to fully exploit the potential of ALS information to estimate forage due to limitations in matching laser data to field data. This resulted in only conservative improvements in predictive ability. Nonetheless, ALS is a promising tool for quantifying forage for large browsers such as moose. Our study further showed that the ALS-based structural information on cover increased

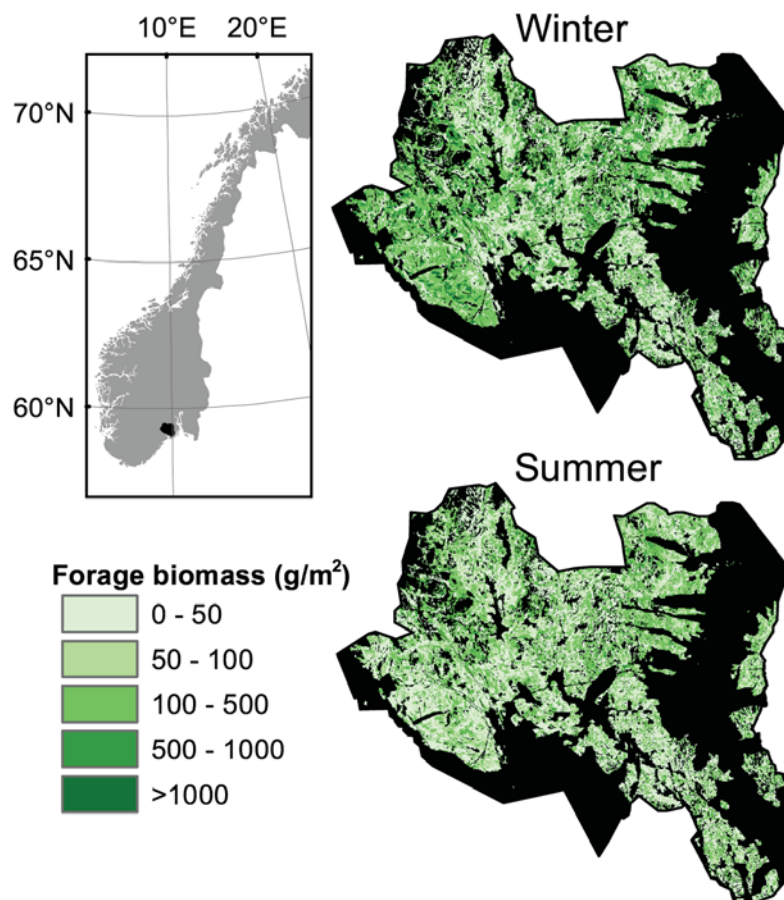


Fig. 2. Maps of predicted browse availability in the study area in southern Norway. Areas with no forest inventory data are shaded black, and include both non-forested land and forests under different ownership.

the predictive performance of moose habitat selection models. The possibility to obtain detailed and continuous maps of “new” environmental descriptors from ALS data offers great opportunities across a range of research disciplines in ecology, natural resource management and conservation (Graf et al. 2009, Martinuzzi et al. 2009, Wing et al. 2012).

The effectiveness of ALS to quantify browse at broad scales

ALS increased explanatory power in the browse models by capturing variability in canopy cover and density of understory vegetation within and between forest stands of a given combination of development class and dominant tree species. Increasing canopy cover led to lower available forage biomass. This harmonizes with the general ecological and silvicultural under-

standing that canopy gaps alter understory conditions by increasing light levels (Canham 1988) in favor of early colonizing species, such as the forage species considered here. The interaction between h90 (the 90th percentile height of non-ground laser echoes) and canopy cover in some of the models may be an expression of “effective openness” that depends on both the height of the trees and canopy density. At the same percentage canopy cover, shorter trees will shade less than tall trees and therefore be associated with a greater effective openness. In contrast to canopy cover, the ALS measured understory cover also had a strong positive relationship with forage biomass. This is expected as understory cover consists of forage tree species within browsing range of the moose. Among remote sensing technologies, ALS is uniquely suited to obtain such information on

Table 5. Model fit according to AIC and model predictive performance according to K -fold cross-validation.

Scale	Season	Model no.	k	AIC	Δ AIC	AIC Wt	LL	K -fold r_s
Landscape	Winter	6	6	120887.8	0	1	-60437.88	0.83
		5	5	120935.5	47.7	0	-60462.75	0.79
		1	8	122320.7	1432.9	0	-61152.33	0.17
		2	3	122531.3	1643.5	0	-61262.65	0.67
		4	3	122648.8	1761.0	0	-61321.41	0.73
		3	3	122721.5	1833.7	0	-61357.77	0.09†
Landscape	Summer	6	6	71259.1	0	1	-35623.55	0.99
		5	5	71285.9	26.8	0	-35637.92	0.99
		1	8	71322.1	63.0	0	-35653.05	0.31
		3	3	72830.3	1571.2	0	-36412.14	0.80
		4	3	73091.4	1832.3	0	-36542.69	0.57
		2	3	73167.4	1908.3	0	-36580.68	0.50
Home range	Winter	6	16	124807.0	0	1	-62387.50	1.00
		1	22	125766.5	959.5	0	-62861.25	0.59
		5	13	126421.6	1614.6	0	-63197.81	1.00
		2	7	127510.9	2703.9	0	-63748.47	0.92
		4	7	128037.0	3230.0	0	-64011.52	0.78
		3	7	129598.6	4791.6	0	-64792.32	0.82
Home range	Summer	6	16	88182.2	0	1	-44075.11	0.97
		5	13	88423.8	241.4	0	-44198.87	0.98
		1	22	88814.0	631.8	0	-44385.01	0.59
		4	7	89395.5	1213.3	0	-44690.74	0.71
		2	7	89777.6	1595.2	0	-44881.80	0.81
		3	7	90279.4	2097.2	0	-45132.69	0.82

Note: The models with the best K -fold values within each spatiotemporal scale are shown in boldface.

† K -fold values that were not better than random (two-sample t -test, $p > 0.05$).

the amount of understory, as some of the narrow laser beams are able to penetrate through small gaps in the canopy, even when it is relatively dense.

Boreal forest ecosystems are dynamic landscapes with successional processes having a considerable impact on the physical structure and hence wildlife forage availability, including browse (Angelstam and Kuuluvainen 2004). Although natural processes such as fire and storms can open up forest canopies, Scandinavian forest dynamics are largely determined by silvicultural practices and clear-cutting (Kuuluvainen and Aakala 2011). Indeed, the inventory variables forest development class and tree species were never replaced by ALS variables in the best models, which likely reflected the importance of forestry practices in the dynamics of wildlife forage availability. Although h90 is a good overall measure of vegetation height (Næsset and Bjerknæs 2001), and thus the development from young to old forests, the categorical representation of stand age and structure as development class in the inventory maps performed better in the models. While ALS can identify vegetation in the understory range, distinguishing between preferred and non-preferred species or inedible material is more

difficult. Because of this, the improvement we found in tree species-specific models was marginal compared to the improvement on total browse biomass estimates. That none of the ALS variables could be interpreted in terms of tree species composition, was probably the main reason that the ALS-only model did not perform satisfactorily. As an alternative to using inventory data as we did here, information on tree species could be obtained using other remote sensing techniques. Although there are no readily available ALS proxy measures of species composition, it can be modeled by ALS data if one also considers echo intensity measures (Brandtberg 2007, Suratno et al. 2009, Ørka et al. 2013). Unfortunately, our ALS data did not have calibrated intensity measures. Combining ALS with multi- or hyperspectral images is another option for obtaining reliable species classification (Holmgren et al. 2008, Ørka et al. 2013). In the Scandinavian forest management context, development class, dominant tree species, site productivity and stand delineations are typically obtained from stereographic photo interpretation. As ALS forest inventories commonly rely on this information (Næsset 2004), development class and tree species would be readily available covariates if browse was estimated in conjunction

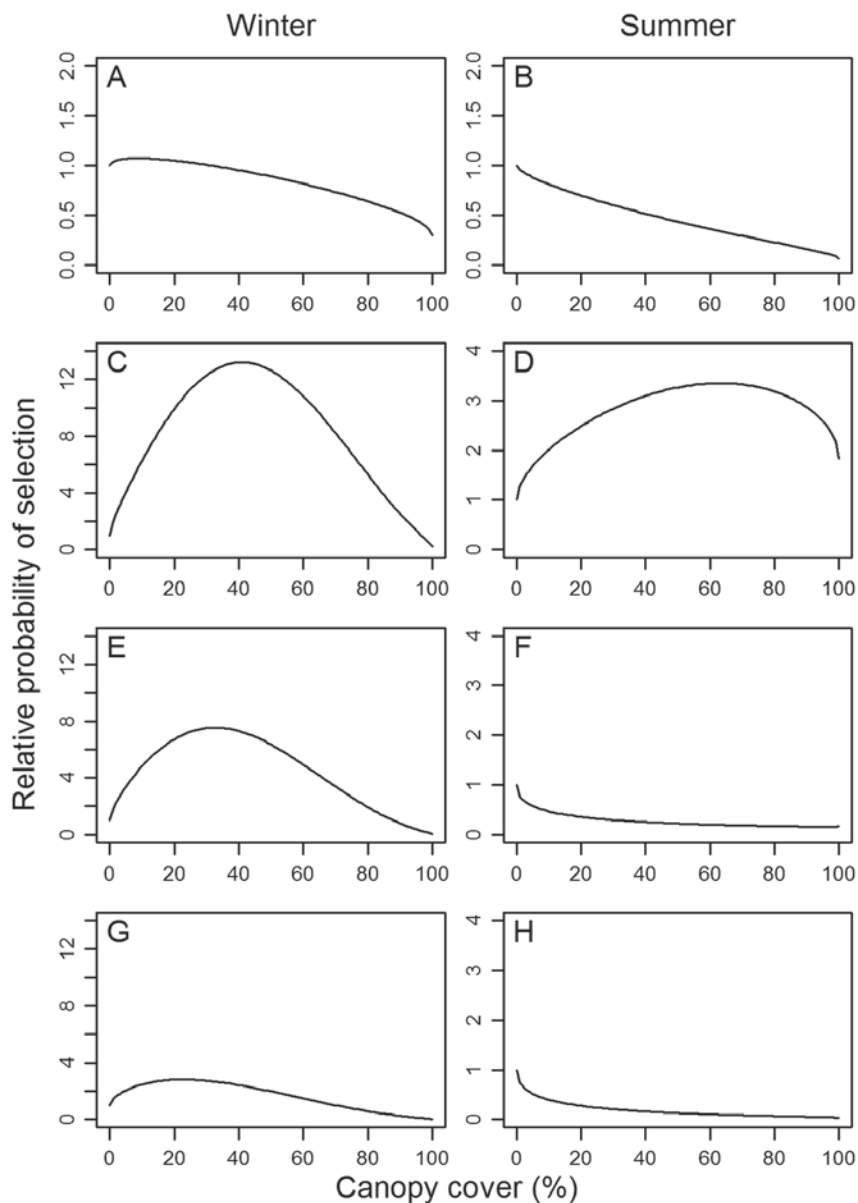


Fig. 3. Relative probability of selection of canopy cover by moose in southern Norway by season, scale and light condition. Panels show landscape scale (A, B) and home range scale during daylight (C, D), twilight (E, F) and darkness (G, H). Note that y -axis values (relative probability of selection) can be compared within, but not between models.

with this.

ALS can be a viable stand-alone alternative if it can predict browse availability without a substantial drop in performance relative to the inventory data. The predictive power of the models based on only ALS was too low to promote this as based on the current study, yet it should not be excluded until tested under

optimal field sampling design. Here we aimed to best exploit existing field data, with the drawback that survey grade GPS receivers were not used for plot positioning and only 10% of the ALS plot area was measured in the field. Furthermore, the four ALS projects were collected over a three year time span and were collected with different acquisition settings. Addressing

these issues in future studies would reduce the noise in the data (Gobakken and Næsset 2009) with the expected consequence that ALS variables would capture more of the variation and thus further improve predictions of browse compared to our findings.

ALS improves understanding of habitat selection

In addition to forage, we framed our habitat selection analyses specifically around the concept of cover, which is an important structural element of the habitat as it modifies interactions with conspecifics or predators due to reduced visual detection rates or hindrances in escaping (Schooley et al. 1996, Heithaus et al. 2009, Camp et al. 2013). Moreover, cover affects food availability and abiotic factors such as temperature, wind speed, humidity, snow depth and precipitation (Myserud and Østbye 1999). Our study shows that incorporating ALS data improved habitat selection models of moose. The main contribution towards this result was through quantification of cover, rather than the improvement in forage predictions. Direct inclusion of structural variables is a common approach to ALS based habitat studies (Graf et al. 2009, Coops et al. 2010, Melin et al. 2013), but the ecological links are not always obvious. Habitat selection studies that lack detailed field data on forage and cover availability typically characterize habitat as “open” or “dense” (Godvik et al. 2009, Ciuti et al. 2012, Tolon et al. 2012) and assume these are “forage” and “cover” habitat types respectively. There are clear drawbacks to this, as we can expect variation in selection within habitat types (Blix et al. 2014) linked to variation in one or multiple resources or characteristics within a habitat type. By using ALS instead of subjective habitat classes, we have decoupled the physical structure of the habitat from other resources, and moved towards a direct investigation of animals’ habitat selection on a functional gradient in cover that is fully quantitative. Moose in our study avoided stands with dense understory vegetation, implying that they avoid visual shelter at ground level and (at least weakly) high forage availability. Although the reason for this finding remains unclear it could be related to understory vegetation creating movement obstructions or reducing the overview of the surroundings (Camp et al.

2013). The selection for open canopy at the landscape scale likely reflected selection for young forest stands, which is to be expected as moose select for forage quantity at this scale (van Beest et al. 2010b). At the within home range scale, we observed a diurnal shift in use of cover. In daytime, selection peaked at an intermediate level of canopy cover. At intermediate levels, animals limited their exposure to wind, sun, rain, and humans, while actively selecting for forage under these conditions. Moose selected forage with a similar strength at night, but at the same time were more willing to leave cover during the dark or twilight hours, as is a common response of ungulates subject to human disturbance and risk in daytime (Crosmarty et al. 2012, Bonnot et al. 2013). Thermoregulatory behavior could also explain some of the observed patterns and is increasingly being reported as an important driver of moose habitat selection across their distribution (Dussault and Ouellet 2004, Melin et al. 2014), including our study population (van Beest et al. 2012). In support, the use of greater canopy cover we observed in daytime may be related to more favorable abiotic conditions in the forest interior. The use of dense forest as thermal shelter in response to critically high temperatures, especially during summers, has been identified as a fine-scale habitat selection pattern in this population (van Beest et al. 2012), with likely consequences for individual fitness (van Beest and Milner 2013).

Conclusions

ALS data improved our ability to predict browse biomass when used in combination with traditional forest inventory information, such as site productivity index, dominant tree species and forest development class. In boreal forests, there is also variation in habitat quality within these habitat classes, and laser data captured some aspects of this variation. Using ALS techniques, we generated continuous measures of ecologically meaningful quantities such as understory cover density and canopy gaps, which are related to forage availability, thermal cover and hiding cover for wildlife. These are important environmental descriptors that are otherwise difficult to quantify in great detail and over large areas. ALS data unfortunately has a relatively large price tag: we estimate that the

data used in our study cost around US \$200 per km² to the initial collectors. But there are several options for accessing ALS data at lower cost. Existing data collected for other purposes may in many regions be cheaply available to researchers or managers. Costs could also be reduced by undertaking collaborative data collection for multiple purposes. In the Scandinavian countries, mapping of browse and cover could easily be implemented on a large scale (nearly countrywide) by incorporating it in the ongoing ALS based forest inventories, as most stand level forest inventories in Scandinavia now use this method (Maltamo et al. 2011). This provides a great opportunity to further integrate forest and wildlife management (Milner et al. 2013). We conclude that ALS characterizes functional habitat gradients important to wildlife and has the potential to bring us one step closer to effectively quantify the abundance and distribution of large herbivores at the spatial scale necessary for sound management and conservation.

ACKNOWLEDGMENTS

We thank forest companies Fritzøe Skoger & Løvenskiold-Fossum in Telemark County, Norway for their assistance in logistics and access to their property. Funding for the original moose vegetation biomass project in 2010 was provided by Norwegian Research Council (173868 / AREAL), Innovation Norway, Telemark County, Hedmark County and municipalities in Telemark, Vestfold and Hedmark. We are also grateful to two anonymous reviewers for their input. K. Lone was financially supported by the Norwegian University of Life Sciences.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Sensor and flight parameters for the four airborne laser scanning projects.

Parameter	Skien	Siljan	Larvik	Lardal
Instrument	Optech ALTM Gemini	Optech ALTM Gemini	Optech ALTM Gemini	Optech ALTM Gemini
Aircraft	fixed wing	fixed wing	fixed wing	fixed wing
Date of acquisition	5, 26–27 May 2008	2 June 2010	24 May 2010	21–25 May 2009
Average flying altitude	1400–1700 m a.g.l.	1600 m a.g.l.	1275 m a.g.l.	690 m a.g.l.
Flight speed	75 m s ⁻¹	75 m s ⁻¹	75 m s ⁻¹	80 m s ⁻¹
Pulse repetition frequency	70 kHz	70 kHz	100 kHz	125 kHz
Scan angle	23.0°	19.0°	20.0°	12.0°
Pulse density on ground				
Mean	1.0 m ⁻²	1.4 m ⁻²	2.2 m ⁻²	12.5 m ⁻²
Range	0.5–2.8 m ⁻²	0.7–2.6 m ⁻²	0.9–4.4 m ⁻²	7.9–22 m ⁻²

Table A2. Landscape scale winter exponential RSF coefficient estimates.

Model no.	Fixed effect	β	SE	z	p
6	log(winter forage inventory)	0.041	0.006	6.63	<0.001
	arcsin(sqrt(canopy cover))	0.468	0.140	3.33	<0.001
	arcsin(sqrt(canopy cover)) ²	-0.786	0.103	-7.60	<0.001
	arcsin(sqrt(understory cover))	-2.311	0.072	-32.16	<0.001
5	arcsin(sqrt(canopy cover))	0.580	0.140	4.15	<0.001
	arcsin(sqrt(canopy cover)) ²	-0.942	0.101	-9.33	<0.001
	arcsin(sqrt(understory cover))	-2.296	0.072	-31.98	<0.001
4	log(winter forage combined)	0.063	0.005	12.96	<0.001
3	log(winter forage als)	-0.062	0.006	-9.79	<0.001
2	log(winter forage inventory)	0.091	0.005	16.88	<0.001
1	Development class†				
	2	0.305	0.045	6.84	<0.001
	3	0.173	0.044	3.89	<0.001
	4	-0.133	0.048	-2.76	0.006
	5	0.230	0.046	5.04	<0.001
	Dominant tree species‡				
	Pine	0.342	0.045	7.57	<0.001
	Spruce	0.306	0.043	7.06	<0.001

† Reference level = development class 1.

‡ Reference level = mixed deciduous forest.

Table A3. Landscape scale summer exponential RSF coefficient estimates.

Model no.	Fixed effect	β	SE	z	p
6	log(summer forage inventory)	0.075	0.014	5.36	<0.001
	arcsin(sqrt(canopy cover))	-0.366	0.175	-2.09	0.037
	arcsin(sqrt(canopy cover)) ²	-0.878	0.131	-6.72	<0.001
	arcsin(sqrt(understory cover))	-2.062	0.098	-21.04	<0.001
5	arcsin(sqrt(canopy cover))	-0.423	0.175	-2.42	0.016
	arcsin(sqrt(canopy cover)) ²	-0.918	0.131	-7.03	<0.001
	arcsin(sqrt(understory cover))	-1.933	0.095	-20.38	<0.001
4	log(summer forage combined)	0.193	0.009	21.19	<0.001
3	log(summer forage als)	-0.352	0.013	-26.43	<0.001
2	log(summer forage inventory)	0.228	0.012	19.35	<0.001
1	Development class†				
	2	0.833	0.073	11.43	<0.001
	3	0.551	0.073	7.56	<0.001
	4	-0.074	0.079	-0.94	0.348
	5	1.267	0.074	17.18	<0.001
	Dominant tree species‡				
	Pine	0.349	0.076	4.61	<0.001
	Spruce	0.875	0.073	11.93	<0.001

Note: Symbols are as in Table A2.

Table A4. Home range winter exponential RSF coefficient estimates.

Model no.	Fixed effect	β	SE	z	p
6	log(winter forage inventory)	0.247	0.009	27.61	<0.001
	arcsin(sqrt(canopy cover))	4.174	0.232	17.97	<0.001
	arcsin(sqrt(canopy cover)) ²	-4.195	0.181	-23.12	<0.001
	arcsin(sqrt(understory cover))	-2.758	0.117	-23.64	<0.001
	Light condition§				
	Daylight	-1.857	0.143	-12.94	<0.001
	Twilight	-1.344	0.289	-4.64	<0.001

Table A4. Continued.

Model no.	Fixed effect	β	SE	z	p	
5	log(winter forage inventory) \times Daylight	0.002	0.013	0.18	0.860	
	log(winter forage inventory) \times Twilight	0.023	0.026	0.88	0.382	
	arcsin(sqrt(canopy cover)) \times Daylight	3.260	0.365	8.94	<0.001	
	arcsin(sqrt(canopy cover)) \times Twilight	2.469	0.732	3.38	<0.001	
	arcsin(sqrt(canopy cover)) ² \times Daylight	-1.154	0.273	-4.23	<0.001	
	arcsin(sqrt(canopy cover)) ² \times Twilight	-1.262	0.557	-2.27	0.023	
	arcsin(sqrt(understory cover)) \times Daylight	0.749	0.165	4.54	<0.001	
	arcsin(sqrt(understory cover)) \times Twilight	0.700	0.341	2.05	0.040	
	arcsin(sqrt(canopy cover))	4.888	0.230	21.30	<0.001	
	arcsin(sqrt(canopy cover)) ²	-5.235	0.177	-29.52	<0.001	
	arcsin(sqrt(understory cover))	-2.683	0.116	-23.16	<0.001	
	Light condition§					
	Daylight	-1.823	0.125	-14.61	<0.001	
	Twilight	-1.152	0.246	-4.68	<0.001	
	arcsin(sqrt(canopy cover)) \times Daylight	3.256	0.360	9.04	<0.001	
	arcsin(sqrt(canopy cover)) \times Twilight	2.339	0.722	3.24	0.001	
	arcsin(sqrt(canopy cover)) ² \times Daylight	-1.141	0.267	-4.28	<0.001	
arcsin(sqrt(canopy cover)) ² \times Twilight	-1.226	0.545	-2.25	0.025		
arcsin(sqrt(understory cover)) \times Daylight	0.651	0.164	3.98	<0.001		
arcsin(sqrt(understory cover)) \times Twilight	0.685	0.338	2.02	0.043		
4	log(winter forage combined)	0.323	0.008	43.13	<0.001	
	Light condition§					
	Daylight	0.568	0.055	10.41	<0.001	
	Twilight	0.161	0.113	1.43	0.152	
	log(winter forage combined) \times Daylight	-0.110	0.010	-10.46	<0.001	
	log(winter forage combined) \times Twilight	-0.034	0.022	-1.59	0.112	
	3	log(winter forage als)	0.327	0.011	30.61	<0.001
		Light condition§				
		Daylight	0.774	0.083	9.39	<0.001
		Twilight	0.184	0.170	1.08	0.279
log(winter forage als) \times Daylight		-0.138	0.015	-9.44	<0.001	
log(winter forage als) \times Twilight		-0.036	0.030	-1.21	0.228	
2	log(winter forage inventory)	0.356	0.008	44.51	<0.001	
	Light condition§					
	Daylight	0.423	0.059	7.22	<0.001	
	Twilight	0.077	0.122	0.63	0.527	
1	log(winter forage inventory) \times Daylight	-0.082	0.011	-7.28	<0.001	
	Development class†					
	2	0.761	0.066	11.57	<0.001	
	3	0.279	0.065	4.27	<0.001	
	4	0.384	0.073	5.23	<0.001	
	5	0.395	0.067	5.86	<0.001	
	Dominant tree species‡					
	Pine	0.639	0.070	9.17	<0.001	
	Spruce	-0.441	0.068	-6.44	<0.001	
	Light condition§					
	Daylight	-1.070	0.147	-7.31	<0.001	
	Twilight	-0.493	0.286	-1.72	0.085	
	Development class \times Light condition					
	2 \times Daylight	0.625	0.110	5.69	<0.001	
	3 \times Daylight	0.957	0.109	8.76	<0.001	
	4 \times Daylight	0.825	0.119	6.93	<0.001	
	5 \times Daylight	0.894	0.111	8.04	<0.001	
	2 \times Twilight	0.161	0.204	0.79	0.431	
	3 \times Twilight	0.331	0.203	1.63	0.103	
	4 \times Twilight	0.048	0.227	0.21	0.833	
5 \times Twilight	0.302	0.208	1.46	0.145		
Dominant tree species \times Light condition						
Pine \times Daylight	0.212	0.102	2.08	0.038		
Spruce \times Daylight	0.331	0.100	3.30	<0.001		
Pine \times Twilight	0.249	0.211	1.18	0.239		
Spruce \times Twilight	0.258	0.207	1.25	0.213		

† Reference level = development class 1.

‡ Reference level = mixed deciduous forest.

§ Reference level = darkness.

Table A5. Home range summer exponential RSF coefficient estimates.

Model no.	Fixed effect	β	SE	z	p	
6	log(summer forage inventory)	0.196	0.028	7.12	<0.001	
	arcsin(sqrt(canopy cover))	-3.062	0.312	-9.81	<0.001	
	arcsin(sqrt(canopy cover)) ²	0.594	0.263	2.26	0.024	
	arcsin(sqrt(understory cover))	-1.128	0.210	-5.38	<0.001	
	Light condition§					
	Daylight	-2.846	0.189	-15.10	<0.001	
	Twilight	-0.519	0.284	-1.83	0.068	
	log(summer forage inventory) × Daylight	0.016	0.032	0.52	0.602	
	log(summer forage inventory) × Twilight	-0.022	0.048	-0.45	0.652	
	arcsin(sqrt(canopy cover)) × Daylight	5.695	0.367	15.50	<0.001	
	arcsin(sqrt(canopy cover)) × Twilight	0.380	0.551	0.69	0.490	
	arcsin(sqrt(canopy cover)) ² × Daylight	-2.026	0.300	-6.75	<0.001	
	arcsin(sqrt(canopy cover)) ² × Twilight	0.390	0.450	0.87	0.387	
	arcsin(sqrt(understory cover)) × Daylight	0.590	0.238	2.48	0.013	
	arcsin(sqrt(understory cover)) × Twilight	1.183	0.358	3.30	<0.001	
	5	arcsin(sqrt(canopy cover))	-3.106	0.316	-9.84	<0.001
		arcsin(sqrt(canopy cover)) ²	0.377	0.264	1.43	0.154
arcsin(sqrt(understory cover))		-0.715	0.202	-3.54	<0.001	
Light condition§						
Daylight		-2.723	0.112	-24.36	<0.001	
Twilight		-0.614	0.169	-3.64	<0.001	
arcsin(sqrt(canopy cover)) × Daylight		5.469	0.369	14.84	<0.001	
arcsin(sqrt(canopy cover)) × Twilight		0.343	0.555	0.62	0.537	
arcsin(sqrt(canopy cover)) ² × Daylight		-1.854	0.301	-6.17	<0.001	
arcsin(sqrt(canopy cover)) ² × Twilight		0.449	0.452	0.99	0.320	
arcsin(sqrt(understory cover)) × Daylight		0.652	0.228	2.86	0.004	
arcsin(sqrt(understory cover)) × Twilight		1.150	0.343	3.35	<0.001	
4		log(summer forage combined)	0.498	0.018	28.07	<0.001
		Light condition§				
		Daylight	2.332	0.096	24.27	<0.001
		Twilight	0.594	0.146	4.07	<0.001
		log(summer forage combined) × Daylight	-0.501	0.020	-24.80	<0.001
	log(summer forage combined) × Twilight	-0.123	0.031	-4.02	<0.001	
	3	log(summer forage als)	0.283	0.028	10.29	<0.001
		Light condition§				
		Daylight	1.426	0.149	9.54	<0.001
		Twilight	-0.154	0.231	-0.67	0.505
log(summer forage als) × Daylight		-0.305	0.031	-9.79	<0.001	
log(summer forage als) × Twilight		0.030	0.048	0.63	0.528	
2	log(summer forage inventory)	0.502	0.023	22.00	<0.001	
	Light condition§					
	Daylight	1.919	0.123	15.62	<0.001	
	Twilight	0.525	0.188	2.80	0.005	
1	log(summer forage inventory) × Daylight	-0.415	0.026	-15.86	<0.001	
	Development class†					
	2	-0.263	0.111	-2.37	0.018	
	3	-1.458	0.114	-12.76	<0.001	
	4	-0.831	0.130	-6.40	<0.001	
	5	-0.959	0.116	-8.30	<0.001	
	Dominant tree species‡					
	Pine	-0.762	0.202	-3.78	<0.001	
	Spruce	-0.122	0.195	-0.62	0.533	
	Light condition§					
	Daylight	-1.524	0.261	-5.85	<0.001	
	Twilight	-0.287	0.388	-0.74	0.459	
	Development class × Light condition					
	2 × Daylight	0.560	0.136	4.13	<0.001	
	3 × Daylight	1.775	0.139	12.81	<0.001	
	4 × Daylight	1.018	0.156	6.52	<0.001	
	5 × Daylight	1.429	0.140	10.21	<0.001	
	2 × Twilight	-0.097	0.212	-0.46	0.645	
	3 × Twilight	0.283	0.216	1.31	0.190	
	4 × Twilight	0.020	0.244	0.08	0.936	
	5 × Twilight	0.087	0.219	0.40	0.693	

Table A5. Continued.

Model no.	Fixed effect	β	SE	z	p
	Dominant tree species \times Light condition				
	Pine \times Daylight	0.678	0.231	2.93	0.003
	Spruce \times Daylight	0.442	0.225	1.97	0.049
	Pine \times Twilight	0.377	0.339	1.11	0.266
	Spruce \times Twilight	0.269	0.328	0.82	0.413

Note: Symbols are as in Table A4.

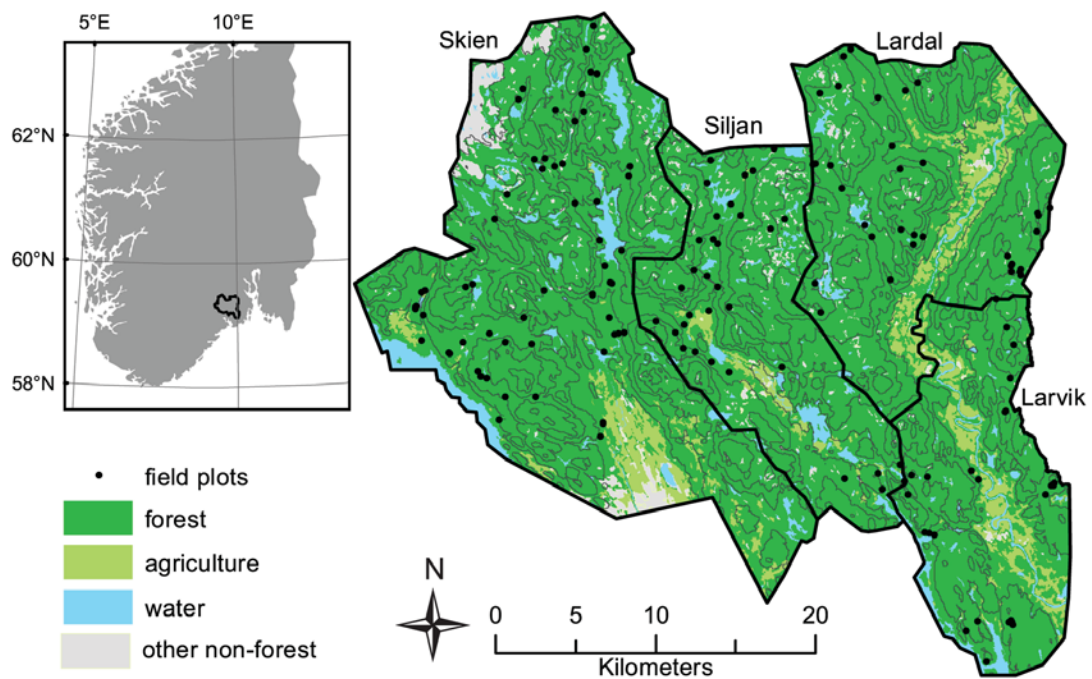


Fig. A1. Map of the study area in southern Norway, showing land use, topography and the ground reference field plots. The four ALS data projects that define the study area are outlined and named.

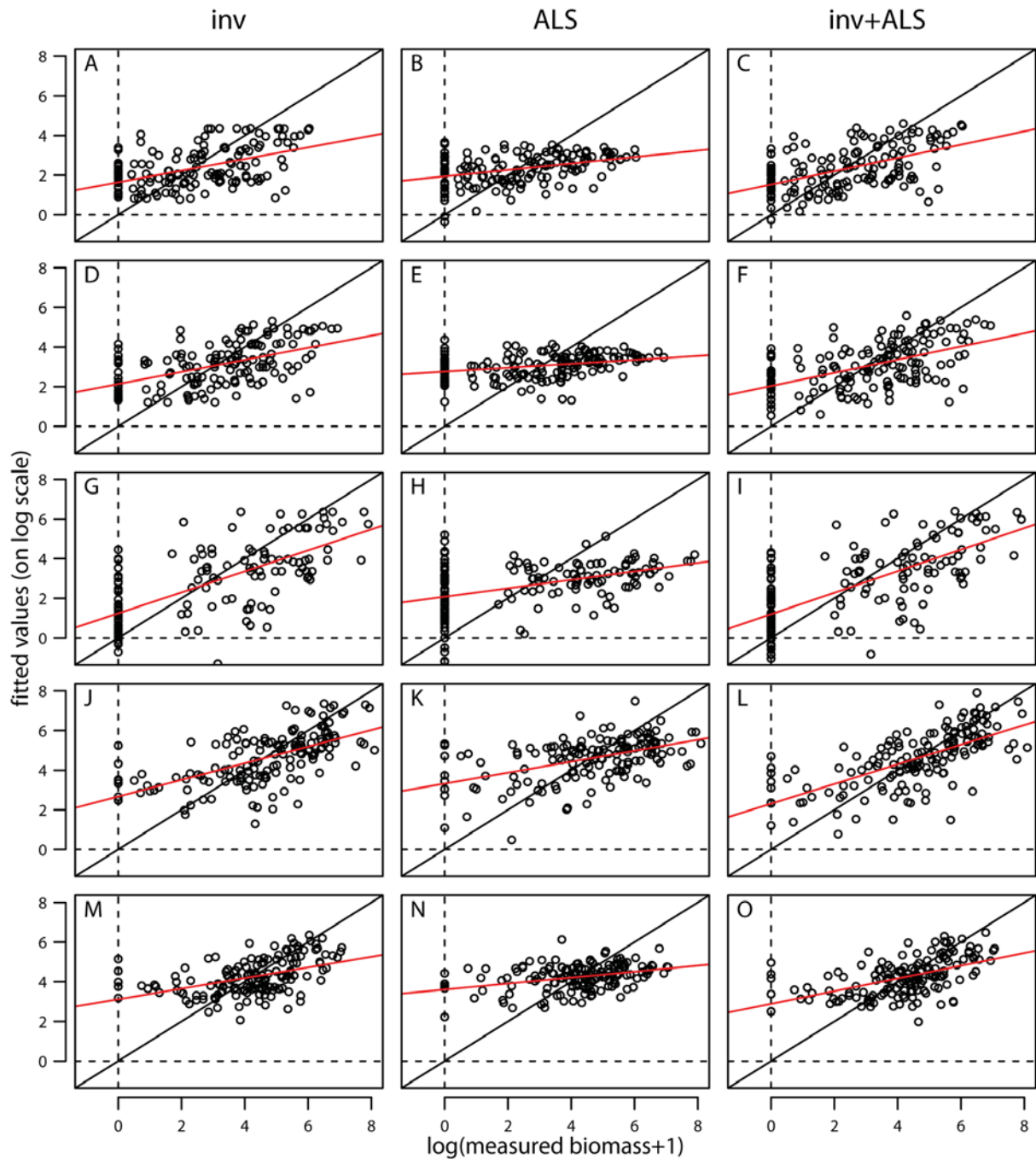
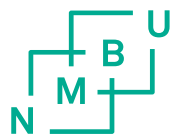


Fig. A2. K-fold ($k = 5$) cross-validation plots for the best forage biomass models based on forest inventory data (inv), ALS data (ALS), or forest inventory and ALS data (inv+ALS). Modeled browse categories are (A, B, C) RAW winter, (D, E, F) RAW summer, (G, H, I) pine winter, (J, K, L) total biomass winter, and (M, N, O) total biomass summer. Two trend lines are shown: the ideal 1:1 relationship (black) and the least-squares trend line (red) between predicted and field measured values. The original biomass data were in g/m^2 .

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



Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no