

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.

Copyright: © 2014 Lone et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

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 (Mysterud 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 *R*² 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 (1–2 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 (Arneimo 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).

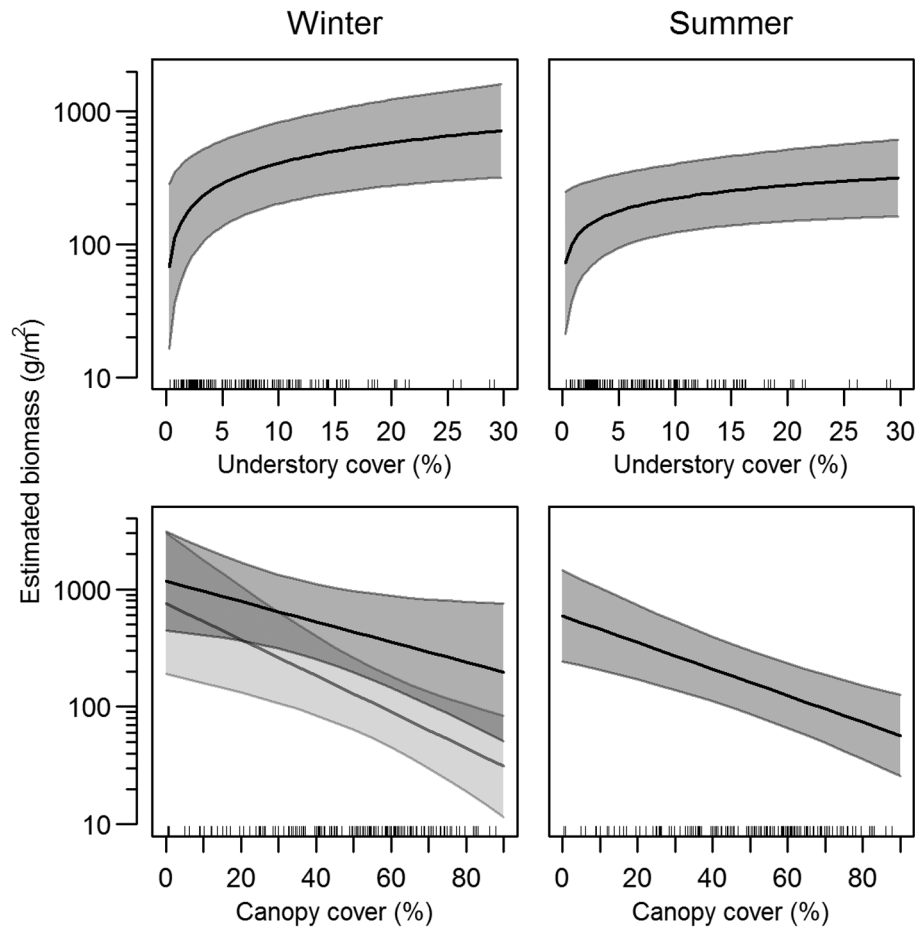


Fig. 1. Predicted effects of airborne laser scanning variables on amount of available forage, from the best models for total biomass in winter and summer (shown for deciduous stands of development class 2 with high productivity). Shaded regions are 95% confidence intervals. For total winter biomass, 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

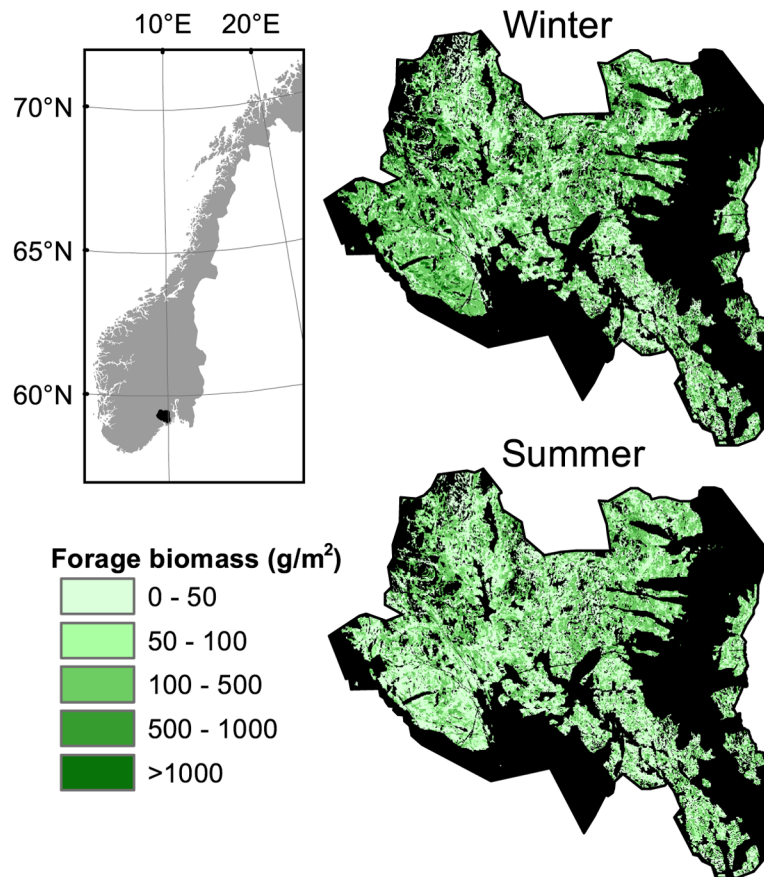


Fig. 2. Maps of predicted browse availability in the study area in southern Norway. Areas with no forest inventory data are shaded black, and include both non-forested land and forests under different ownership.

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 h_{90} is a good overall measure of vegetation height (Næsset and Bjercknes 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

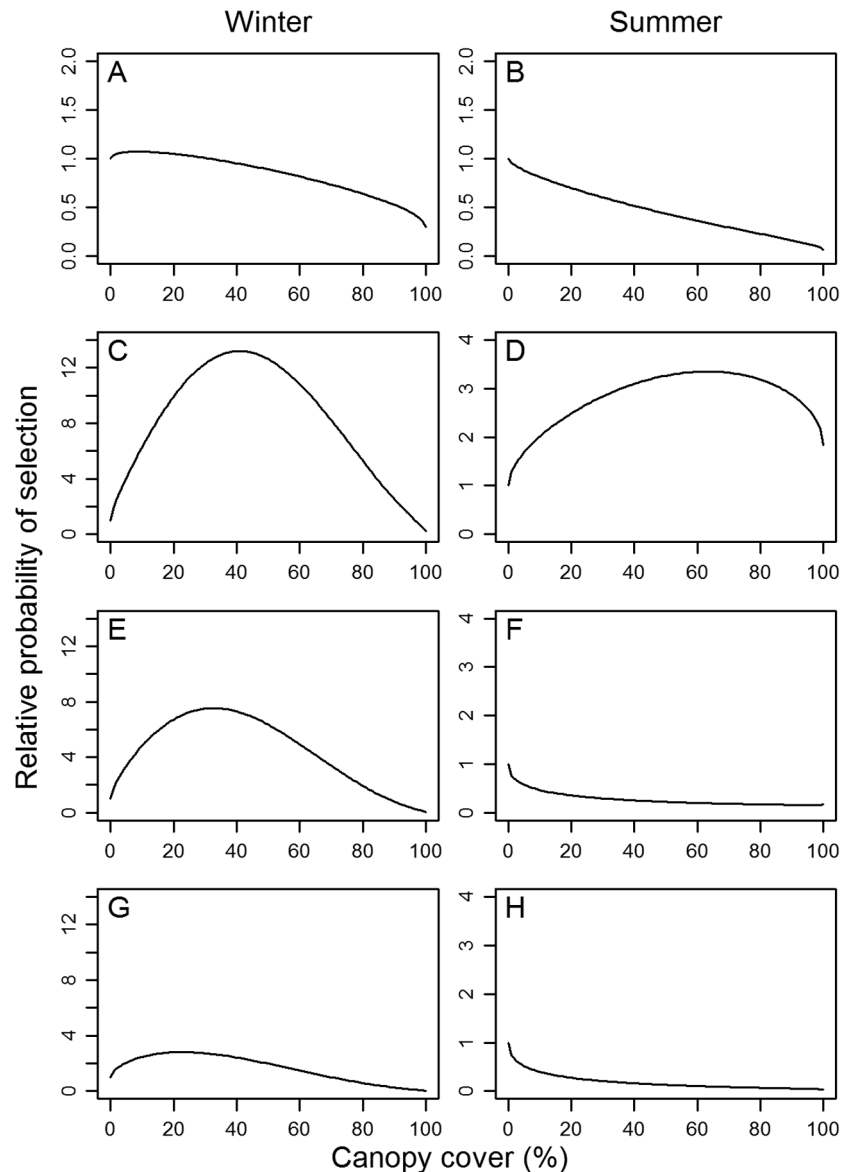


Fig. 3. Relative probability of selection of canopy cover by moose in southern Norway by season, scale and light condition. Panels show landscape scale (A, B) and home range scale during daylight (C, D), twilight (E, F) and darkness (G, H). Note that y -axis values (relative probability of selection) 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 (Mysterud 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.

LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Angelstam, P., and T. Kuuluvainen. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a European perspective. *Ecological Bulletins* 51:117–136.
- Arnemo, J. M., T. J. Kreeger, and T. Soveri. 2003. Chemical immobilization of free-ranging moose. *Alces* 39:243–253.
- Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology* 82:96–106.
- Axelsson, P. 2000. DEM generation from laser scanner data using adaptive TIN models. *International Archives of Photogrammetry and Remote Sensing* 33:111–118.
- Ball, J. P., C. Nordengren, and K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology* 7:39–47.
- Bates, D., M. Maechler, and B. Bolker. 2012. lme4: linear mixed-effects models using Eigen and S4 classes. R package version 0.999999-0. R Foundation for Statistical Computing, Vienna, Austria.
- Blix, A. W., A. Mysterud, L. E. Loe, and G. Austrheim. 2014. Temporal scales of density-dependent habitat selection in a large grazing herbivore. *Oikos* 123:933–942.
- Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, and N. Owen-Smith. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.
- Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife Research* 59:185–193.
- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421–431.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Brandtberg, T. 2007. Classifying individual tree species under leaf-off and leaf-on conditions using airborne lidar. *ISPRS Journal of Photogrammetry and Remote Sensing* 61:325–340.
- Camp, M., J. Rachlow, B. Woods, T. Johnson, and L. Shipley. 2013. Examining functional components of cover: the relationship between concealment and visibility in shrub-steppe habitat. *Ecosphere* 4:art19.
- Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69:1634–1638.
- Ciuti, S., T. B. Muhly, D. G. Paton, A. D. McDevitt, M. Musiani, and M. S. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B* 279:4407–4416.
- Coops, N. C., J. Duffe, and C. Koot. 2010. Assessing the utility of lidar remote sensing technology to identify mule deer winter habitat. *Canadian Journal of Remote Sensing* 36:81–88.
- Crosmary, W. G., M. Valeix, H. Fritz, H. Madzikanda, and S. D. Cote. 2012. African ungulates and their

- drinking problems: hunting and predation risks constrain access to water. *Animal Behaviour* 83:145–153.
- DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, and L. E. Morgantini. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications* 22:1068–1083.
- De Knegt, H. J., F. Van Langevelde, A. K. Skidmore, A. Delsink, R. Slotow, S. Henley, G. Bucini, W. F. De Boer, M. B. Coughenour, and C. C. Grant. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology* 80:270–281.
- DePerno, C. S., J. A. Jenks, and S. L. Griffin. 2003. Multidimensional cover characteristics: is variation in habitat selection related to white-tailed deer sexual segregation? *Journal of Mammalogy* 84:1316–1329.
- Dussault, C., R. Courtois, J.-P. Ouellet, and I. Girard. 2005a. Space use of moose in relation to food availability. *Canadian Journal of Zoology* 83:1431–1437.
- Dussault, C., and J. Ouellet. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 11:321–328.
- Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005b. Linking moose habitat selection to limiting factors. *Ecography* 28:619–628.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478–498.
- Gartlan, J., D. M. Newbery, D. Thomas, and P. Waterman. 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroun. *Vegetatio* 65:131–148.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Gobakken, T., and E. Næsset. 2009. Assessing effects of positioning errors and sample plot size on biophysical stand properties derived from airborne laser scanner data. *Canadian Journal of Forest Research* 39:1036–1052.
- Godvik, I. M. R., L. E. Loe, J. O. Vik, V. Veiberg, R. Langvatn, and A. Myrsterud. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* 90:699–710.
- Graf, R. F., L. Mathys, and K. Bollmann. 2009. Habitat assessment for forest dwelling species using LiDAR remote sensing: Capercaillie in the Alps. *Forest Ecology and Management* 257:160–167.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos* 79:209–218.
- Heithaus, M. R., A. J. Wirsing, D. Burkholder, J. Thomson, and L. M. Dill. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78:556–562.
- Herfindal, L., J. P. Tremblay, B. B. Hansen, E. J. Solberg, M. Heim, and B. E. Sæther. 2009. Scale dependency and functional response in moose habitat selection. *Ecography* 32:849–859.
- Hill, R. A., S. A. Hinsley, and R. K. Broughton. 2014. Assessing habitats and organism-habitat relationships by airborne laser scanning. Pages 335–356 *in* M. Maltamo, E. Næsset, and J. Vauhkonen, editors. *Forestry applications of airborne laser scanning: concepts and case studies*. Springer, Dordrecht, The Netherlands.
- Hinsley, S., R. Hill, D. L. Gaveau, and P. E. Bellamy. 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Functional Ecology* 16:851–857.
- Holmgren, J. 2004. Prediction of tree height, basal area and stem volume in forest stands using airborne laser scanning. *Scandinavian Journal of Forest Research* 19:543–553.
- Holmgren, J., Å. Persson, and U. Söderman. 2008. Species identification of individual trees by combining high resolution LiDAR data with multi-spectral images. *International Journal of Remote Sensing* 29:1537–1552.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kuuluvainen, T., and T. Aakala. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica* 45:823–841.
- Lefsky, M. A., W. B. Cohen, G. G. Parker, and D. J. Harding. 2002. Lidar remote sensing for ecosystem studies. *BioScience* 52:19–30.
- Loe, L. E., C. Bonenfant, E. L. Meisingset, and A. Myrsterud. 2012. Effects of spatial scale and sample size in GPS-based species distribution models: are the best models trivial for red deer management? *European Journal of Wildlife Research* 58:195–203.
- Lone, K., L. E. Loe, T. Gobakken, J. D. Linnell, J. Odden, J. Remmen, and A. Myrsterud. 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.
- Mabille, G., C. Dussault, J.-P. Ouellet, and C. Laurian. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose

- living in two nearby study areas. *Oecologia* 170:965–977.
- Maltamo, M., P. Packalén, E. Kallio, J. Kangas, J. Uuttera, and J. Heikkilä. 2011. Airborne laser scanning based stand level management inventory in Finland. Pages 1–10 in *Proceedings of SilviLaser 2011*, 11th International Conference on LiDAR Applications for Assessing Forest Ecosystems. Hobart, Australia, October 16–20, 2011. Conference Secretariat, Hobart, Australia.
- Manly, B., L. McDonald, D. Thomas, T. McDonald, and W. Erickson. 2002. *Resource selection by animals: statistical analysis and design for field studies*. Kluwer, Dordrecht, The Netherlands.
- Martinuzzi, S., L. A. Vierling, W. A. Gould, M. J. Falkowski, J. S. Evans, A. T. Hudak, and K. T. Vierling. 2009. Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sensing of Environment* 113:2533–2546.
- Melin, M., J. Matala, L. Mehtätalo, R. Tiilikainen, O. P. Tikkanen, M. Maltamo, J. Pusenius, and P. Packalén. 2014. Moose (*Alces alces*) reacts to high summer temperatures by utilising thermal shelters in boreal forests—an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology* 20:1115–1125.
- Melin, M., P. Packalén, J. Matala, L. Mehtätalo, and J. Pusenius. 2013. Assessing and modeling moose (*Alces alces*) habitats with airborne laser scanning data. *International Journal of Applied Earth Observation and Geoinformation* 23:389–396.
- Milner, J. M., T. Storaas, F. M. van Beest, and G. Lien. 2012. Sluttrapport for elgföringsprosjektet: Final report of the project Improving moose forage with benefits for the hunting, forestry and farming sectors. Commissioned report nr. 1-2012. Hedmark University College, Norway.
- Milner, J. M., F. M. van Beest, and T. Storaas. 2013. Boom and bust of a moose population: a call for integrated forest management. *European Journal of Forest Research* 132:959–967.
- Mueller, T., K. A. Olson, T. K. Fuller, G. B. Schaller, M. G. Murray, and P. Leimgruber. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology* 45:649–658.
- Müller, J., and K. Vierling. 2014. Assessing biodiversity by airborne laser scanning. Pages 357–374 in M. Maltamo, E. Næsset, and J. Vauhkonen, editors. *Forestry applications of airborne laser scanning: concepts and case studies*. Springer, Dordrecht, The Netherlands.
- Murtaugh, P. A. 2009. Performance of several variable-selection methods applied to real ecological data. *Ecology Letters* 12:1061–1068.
- Mysterud, A. 2000. Diet overlap among ruminants in Fennoscandia. *Oecologia* 124:130–137.
- Mysterud, A., and E. Østbye. 1999. Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography. *Wildlife Society Bulletin* 27:385–394.
- Månsson, J., H. Andrén, Å. Pehrson, and R. Bergström. 2007. Moose browsing and forage availability: a scale-dependent relationship? *Canadian Journal of Zoology* 85:372–380.
- Næsset, E. 2004. Practical large-scale forest stand inventory using a small-footprint airborne scanning laser. *Scandinavian Journal of Forest Research* 19:164–179.
- Næsset, E., and K.-O. Bjerknes. 2001. Estimating tree heights and number of stems in young forest stands using airborne laser scanner data. *Remote Sensing of Environment* 78:328–340.
- Nikula, A., S. Heikkinen, and E. Helle. 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildlife Biology* 10:121–135.
- Ørka, H. O., M. Dalponte, T. Gobakken, E. Næsset, and L. T. Ene. 2013. Characterizing forest species composition using multiple remote sensing data sources and inventory approaches. *Scandinavian Journal of Forest Research* 28:677–688.
- Pesonen, A., M. Maltamo, K. Eerikäinen, and P. Packalén. 2008. Airborne laser scanning-based prediction of coarse woody debris volumes in a conservation area. *Forest Ecology and Management* 255:3288–3296.
- Pettorelli, N., W. F. Laurance, T. G. O'Brien, M. Wegmann, H. Nagendra, and W. Turner. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. *Journal of Applied Ecology* 51:839–848.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Schooley, R. L., P. B. Sharpe, and B. VanHorne. 1996. Can shrub cover increase predation risk for a desert rodent? *Canadian Journal of Zoology* 74:157–163.
- Snowdon, P. 1991. A ratio estimator for bias correction in logarithmic regressions. *Canadian Journal of Forest Research* 21:720–724.
- Stephens, P., P. Watt, D. Loubser, A. Haywood, and M. Kimberley. 2007. Estimation of carbon stocks in New Zealand planted forests using airborne scanning LiDAR. Pages 389–394 in Rönholm, P., H. Hyyppä, and J. Hyyppä, editors. *Proceedings of the ISPRS Workshop 'Laser Scanning 2007 and SilviLaser 2007'*. Espoo, Finland, September 12–14, 2007. International Society for Photogrammetry and Remote Sensing, Istanbul, Turkey.
- Suratno, A., C. Seielstad, and L. Queen. 2009. Tree species identification in mixed coniferous forest

- using airborne laser scanning. *ISPRS Journal of Photogrammetry and Remote Sensing* 64:683–693.
- Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* 70:324–336.
- Tolon, V., J. Martin, S. Dray, A. Loison, C. Fischer, and E. Baubet. 2012. Predator-prey spatial game as a tool to understand the effects of protected areas on harvester-wildlife interactions. *Ecological Applications* 22:648–657.
- Tveite, B. 1977. Bonitetskurver for gran: Site-index curves for Norway spruce (*Picea abies* (L.) Karst.). Reports of the Norwegian Forest Research Institute, 33. Norwegian Forest Research Institute, Norway.
- Uzal, A., S. Walls, R. A. Stillman, and A. Diaz. 2013. Sika deer distribution and habitat selection: the influence of the availability and distribution of food, cover, and threats. *European Journal of Wildlife Research* 59:563–572.
- van Beest, F. M., L. E. Loe, A. Mysterud, and J. M. Milner. 2010a. Comparative space use and habitat selection of moose around feeding stations. *Journal of Wildlife Management* 74:219–227.
- van Beest, F. M., and J. M. Milner. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS one* 8:e65972.
- van Beest, F. M., A. Mysterud, L. E. Loe, and J. M. Milner. 2010b. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology* 79:910–922.
- van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84:723–735.
- Wehr, A., and U. Lohr. 1999. Airborne laser scanning—an introduction and overview. *ISPRS Journal of Photogrammetry and Remote Sensing* 54:68–82.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wing, B. M., M. W. Ritchie, K. Boston, W. B. Cohen, A. Gitelman, and M. J. Olsen. 2012. Prediction of understory vegetation cover with airborne lidar in an interior ponderosa pine forest. *Remote Sensing of Environment* 124:730–741.

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 |
| 3 | log(winter forage combined) \times Twilight | -0.034 | 0.022 | -1.59 | 0.112 |
| | log(winter forage als) | 0.327 | 0.011 | 30.61 | <0.001 |
| | Light condition§ | | | | |
| 2 | 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 |
| | log(winter forage inventory) | 0.356 | 0.008 | 44.51 | <0.001 |
| 1 | Light condition§ | | | | |
| | Daylight | 0.423 | 0.059 | 7.22 | <0.001 |
| | Twilight | 0.077 | 0.122 | 0.63 | 0.527 |
| | 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 | |
| 2 | log(summer forage als) × Twilight | 0.030 | 0.048 | 0.63 | 0.528 | |
| | log(summer forage inventory) | 0.502 | 0.023 | 22.00 | <0.001 | |
| | Light condition§ | | | | | |
| | Daylight | 1.919 | 0.123 | 15.62 | <0.001 | |
| 1 | Twilight | 0.525 | 0.188 | 2.80 | 0.005 | |
| | 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.

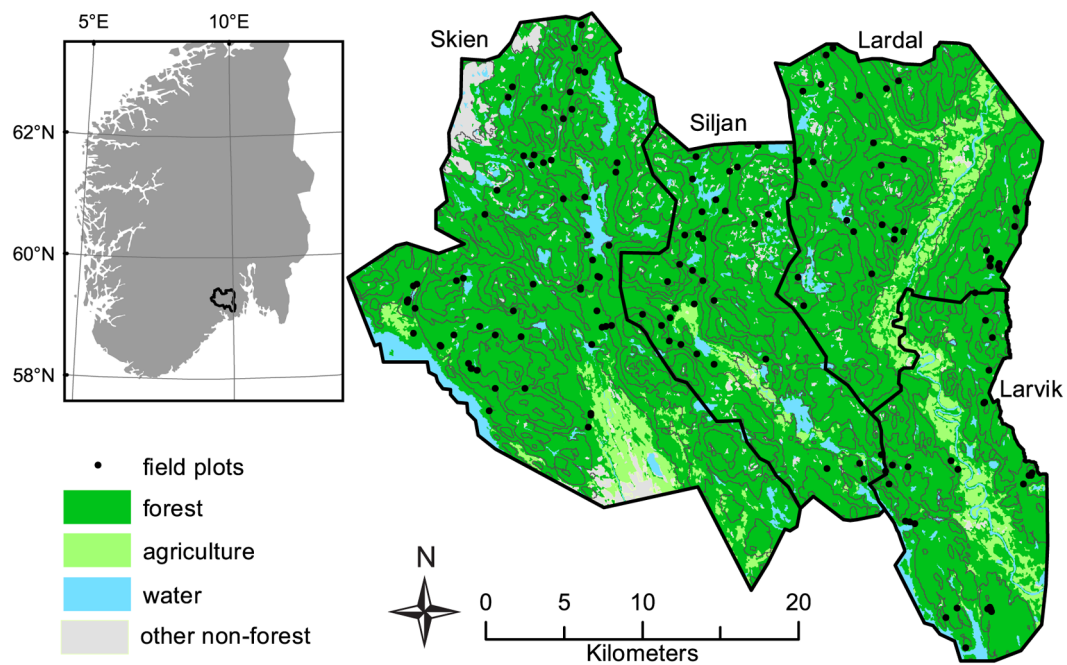


Fig. A1. Map of the study area in southern Norway, showing land use, topography and the ground reference field plots. The four ALS data projects that define the study area are outlined and named.

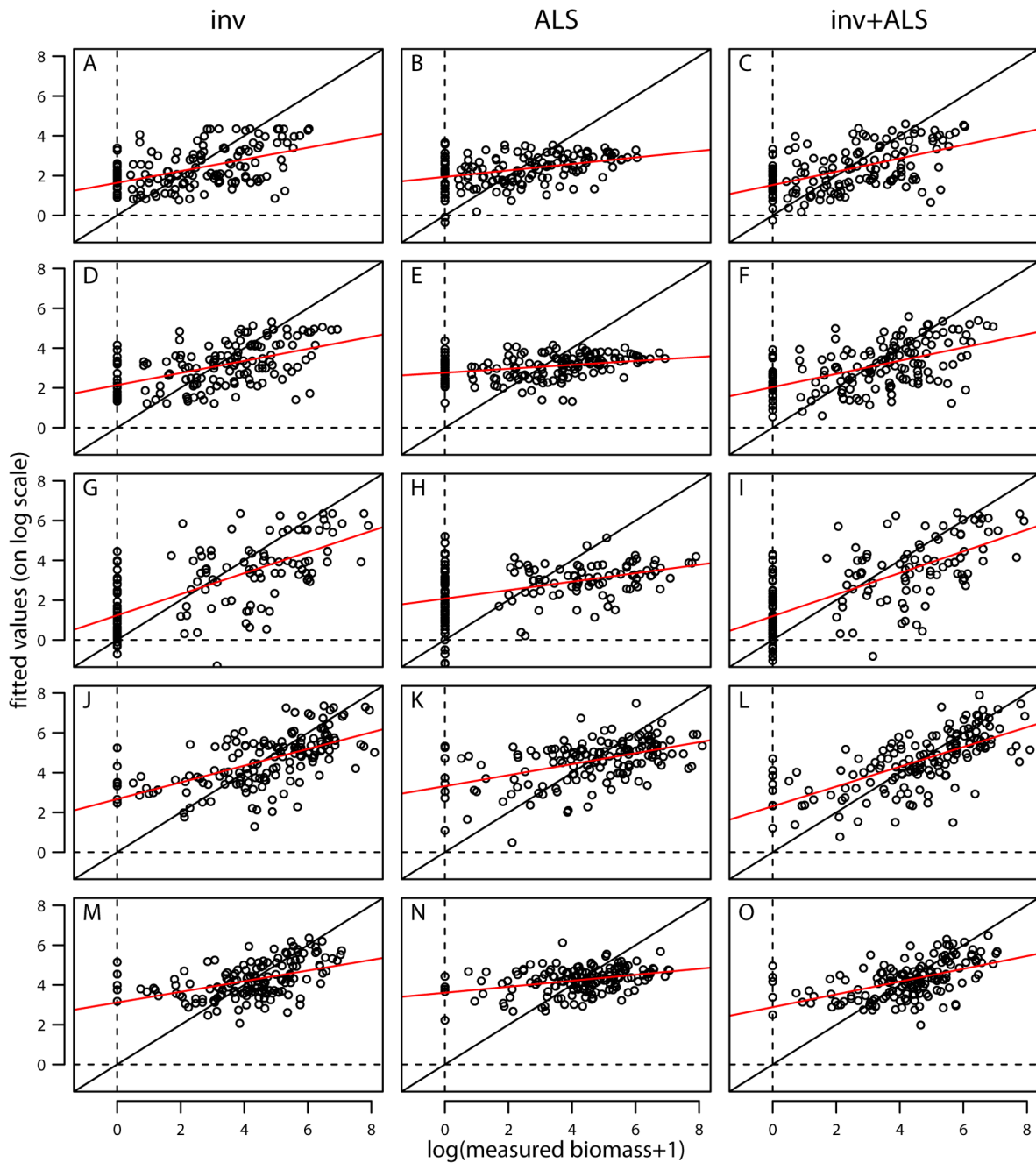


Fig. A2. K-fold ($k=5$) cross-validation plots for the best forage biomass models based on forest inventory data (inv), ALS data (ALS), or forest inventory and ALS data (inv+ALS). Modeled browse categories are (A, B, C) RAW winter, (D, E, F) RAW summer, (G, H, I) pine winter, (J, K, L) total biomass 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 .