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Estimating integrated measures of forage quality for herbivores by fusing optical and structural remote sensing data

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Abstract
Northern herbivore ranges are expanding in response to a warming climate. Forage quality also influences herbivore distributions, but less is known about the effects of climate change on plant biochemical properties. Remote sensing could enable landscape-scale estimations of forage quality, which is of interest to wildlife managers. Despite the importance of integrated forage quality metrics like digestible protein (DP) and digestible dry matter (DDM), few studies investigate remote sensing approaches to estimate these characteristics. We evaluated how well DP and DDM could be estimated using hyperspectral remote sensing and assessed whether incorporating shrub structural metrics affected by browsing would improve our ability to predict DP and DDM. We collected canopy-level spectra, destructive-vegetation samples, and flew unoccupied aerial vehicles (UAVs) in willow (Salix spp.) dominated areas in north central Alaska in July 2019. We derived vegetation canopy structural metrics from 3D point cloud data obtained from UAV imagery using structure-from-motion photogrammetry. The best performing model for DP included a spectral vegetation index (SVI) that used a red-edge and shortwave infrared band, and shrub height variability (hvar; Nagelkerke $R^2 = 0.81$, root mean square error RMSE = 1.42%, cross validation $\rho = 0.88$). DDM's best model included a SVI with a blue and a red band, the normalized difference red-edge index, and hvar (adjusted $R^2 = 0.73$, RMSE = 4.16%, cross validation $\rho = 0.80$). Results from our study demonstrate that integrated forage quality metrics may be successfully quantified using hyperspectral remote sensing data, and that models based on those data may be improved by incorporating additional shrub structural metrics such as height variability. Modern airborne sensor platforms such as Goddard’s LiDAR, Hyperspectral & Thermal Imager provide opportunities to fuse data streams from both structural and optical data, which may enhance our ability to estimate and scale important foliar properties.

1. Introduction
The ranges of some northern herbivores are expanding in response to increased forage biomass resulting from a warming climate (Tape et al 2016, Zhou et al 2017, 2020). Herbivore range expansions may impact nutrient cycling (Doiron et al 2014, Zamin et al 2017, Schmitz et al 2018). For example, high levels of herbivory may accelerate the successional transition of palatable forage species such as willow (Salix spp.) to unpalatable species such as alder (Alnus spp.) or conifers (Pastor et al 1988, Kielland and Bryant 1998, Christie et al 2015). Such transitions in species composition can alter ecosystem carbon and nitrogen dynamics (Schmitz et al 2018). For instance, nutrient turnover rates may decrease cellulose, and defensive chemicals are higher in less palatable species (Pastor et al 1993). In addition to forage biomass, herbivore distributions have also been linked to variation in forage quality (Ball et al 2000, Wu et al 2019).

Forage quality is influenced by the concentration of chemical constituents and has important
bottom-up effects on herbivore life-history traits such as maternal body condition, pregnancy rates, and survival (Parker et al 2009). Characterizing forage quality for herbivores is complex. Fiber, crude protein, and defensive chemical concentrations all play a role in defining forage quality (Mirik et al 2005, McArt et al 2009, DeGabriel et al 2014). Despite the importance of these individual chemical constituents, previous studies have called for increased attention to integrated measures of forage quality such as digestible protein (DP) and digestible dry matter (DDM; Foley and Moore 2005, McArt et al 2009), because simpler metrics of forage quality such as crude protein do not capture the full range of characteristics that can influence palatability and fitness.

Integrated forage quality metrics such as DP are strongly influenced by the presence of tannins (Robbins et al 1987a, 1987b, Hanley et al 1992), an important class of plant secondary compounds that significantly reduce protein digestion for herbivores by binding to plant proteins (Spalinger et al 2010). DP is particularly important in northern landscapes because plant available nitrogen is often limited (Sponseller et al 2016), which in turn limits nitrogen available to herbivores (White 1993, McArt et al 2009). Because DP estimates reflect a chemical relationship between the protein precipitating capacity of tannins and the total concentration of protein it can be used as a metric of forage quality for numerous herbivore species. However, DP does not account for the overall digestibility of forage, which varies according to herbivore species.

Body size exerts a strong influence on the digestive capabilities of herbivores (van Soest 1996, Barboza and Bowyer 2000). Smaller body size facilitates selective feeding choices, whereas larger body size increases the overall fraction of digestible forage retained by herbivores (Jarman 1974, Senft et al 1987, van Soest 1996). For instance, moose (Alces alces) are large-bodied ruminants whose large size enables even very poor-quality forage to be digested. DDM is an important integrated forage quality metric that quantifies the portion of plant matter that is digestible by an herbivore. DDM estimates vary depending on the herbivore in question and can be estimated in two ways. First, in vitro DDM can be estimated directly with fistulated animals, which provide an opening to the animal’s stomach. DDM can also be estimated mathematically for ruminants using developed equations that account for the concentrations of DP and fiber present in plant samples (Robbins et al 1987a, Hanley et al 1992). Estimates of forage quality have classically relied on laboratory analyses, or on direct assessments from fistulated animals. However, in the past two decades remote sensing has emerged as a viable method for assessing forage quality across broad geographic extents (Mirik et al 2005, Skidmore et al 2010, Knox et al 2011, Youngentob et al 2012).

Remote sensing enables landscape-scale monitoring of forage quality, which is of great interest to wildlife managers (Walton et al 2013, Vance et al 2016). Optical remote sensing approaches use reflected light from the visible (400–700 nm) to the short-wave infrared (SWIR; 1400–2500 nm) region and have been used to detect variation in foliar chemistry. To date, much of the optical remote sensing research has focused on detecting individual components of forage quality such as crude protein, fiber, or defense chemicals like condensed tannins (Mirik et al 2005, Ferwerda et al 2006, Skidmore et al 2010, Thulin et al 2012, Jennewein et al 2020). However, Youngentob et al’s (2012) pioneering work showed that DP and DDM could be successfully estimated across the landscape in Eucalyptus trees using hyperspectral remote sensing, which samples reflected light in very narrow (3–10 nm), contiguous spectral bands (Goetz 2009). More recent work demonstrated that DDM can also be estimated in grassland and pasture ecosystems using multispectral imagery obtained from unoccupied aerial vehicles (UAV) (Insua et al 2019, Michez et al 2020). Similarly, Wu et al (2019) provided the first example of successful DP estimation using the multispectral WorldView-3 satellite, which contains much broader spectral bands (30–180 nm) compared to hyperspectral data. Despite the importance of integrated forage quality metrics like DP and DDM, few studies apply remote sensing approaches to map these characteristics across the landscape and to our knowledge no studies have assessed them in Arctic-boreal regions that are undergoing rapid changes due to warming (Serreze et al 2000, Verbyla 2008, Wolken et al 2011).

Therefore, our first hypothesis (H1) was that integrated forage quality metrics—DP and DDM—in palatable willow shrubs can be predicted using hyperspectral remote sensing. We used hyperspectral remote sensing (as opposed to multispectral) because high spectral resolution data can enable direct linkage to absorption and scattering features of foliar properties known to influence forage quality (Curran 1989, Elvidge 1990, Kokaly et al 2009). Additionally, we used hyperspectral remote sensing as previous work indicates that common multispectral vegetation indices—such as the normalized difference vegetation index (NDVI)—can have mixed results when predicting forage quality metrics (Johnson et al 2018). We focused on willow species because they are the preferred forage resource for many vertebrate herbivores in Alaska. We predicted that red-edge (680–730 nm) spectral bands would be important for both DP and DDM predictions as red-edge indices are sensitive to plant chlorophyll and nitrogen content (Eitel et al 2007, Ramoelo et al 2012, Wang et al 2012). Additionally, we predicted that the SWIR region would be important for DDM predictions as its longer spectral wavelengths are sensitive to plant fibers (Kokaly et al 2009, Jennewein et al 2020).
Additionally, browsing intensity can drastically alter plant canopy architecture (Christie et al. 2014) and the concentrations of foliar chemical properties that influence forage quality (Bryant 1981, Bryant and Chapin 1986). For instance, moderate browsing stimulates compensatory growth, which in turn creates ‘bushier’ shrubs that are frequently re-browsed (Stouter 2008). In contrast, heavy browsing stunts growth, decreases shrub height, and increases canopy openness (Kielland and Bryant 1998, Christie et al. 2014). Although plant canopy architecture can be strongly influenced by browsing intensity, ground-based assessments traditionally use only three categories to classify browsing history—unbrowsed, browsed, and broomed (figure 1). Yet variation in broomed architecture can be pronounced (figures 1(A) and (D)) and may indicate distinct functional differences such as added nitrogen from herbivore excreta (Kielland and Bryant 1998, Butler and Kielland 2008).

Recently, remote sensing technologies such as lidar have shown utility in assessing vegetation structure for wildlife applications (e.g. Vierling et al. 2008, Lone et al. 2014, Melin et al. 2016). For example, studies in Europe’s boreal forests have demonstrated that metrics derived from aerial lidar can successfully detect insect defoliation (Solberg et al. 2006, Vastaranta et al. 2013) and heavy moose browsing (Melin et al. 2016) on young Scots pine (Pinus sylvestris) stands. There is also great potential for fusing lidar with optical remote sensing to improve the characterization of ecosystems (Asner et al. 2012, Torabzadeh et al. 2014, Luo et al. 2017). However, the collection of aerial lidar data may be cost-prohibitive, and ‘structure from motion’ (SfM) data acquired from UAVs are considered a viable alternative to aerial lidar (Wallace et al. 2016).

Figure 1. Photographs depicting examples of broomed (A and D), browsed (B), and unbrowsed (C) willow shrubs in northcentral Alaska. Plants that show signs of browsing on >50% of current annual growth (CAG) are considered ‘broomed’, while plants with <50% of CAG are classified as ‘browsed’, and plants with no sign of browsing are considered ‘unbrowsed’. (Photo credit: Jyoti Jennewein).

Our second hypothesis (H2) was that statistical models for estimating DP and DDM using hyperspectral data would be improved when shrub structural metrics obtained from UAV SfM point clouds were incorporated because herbivores can drastically alter canopy structure (figure 1; Christie et al. 2014). Additionally, because sunlit and shaded leaves in Alaska often differ in their concentrations of important foliar chemicals such as fiber (Molvar et al. 1993) and tannins (Bryant and Chapin 1986, Klein 1990, Thompson and Barboza 2014) that influence the palatability of forage species, we also hypothesized that including the cumulative irradiance (W m⁻²) incident on a shrub in a growing season would improve models (H3). We predicted that as cumulative irradiance declined, DP and DDM would increase because nitrogen concentrations increase and fiber decreases in shaded plants (Molvar et al. 1993, Lenart et al. 2002). Similarly, topographic attributes such as aspect and slope influence the amount of solar radiation received by plants. Additionally, elevational gradients influence plant phenology, where higher-elevation plants often have a delayed onset of budburst, which in turn influences migrant herbivore behaviors as they move to ‘surf the green wave’ (Bischof et al. 2012, Mysterud et al. 2017). Thus, our fourth hypothesis (H4) was that including topographic attributes would improve our ability to remotely monitor forage quality because previous work demonstrates that combining hyperspectral data with topographic features such as aspect, slope, and elevation can improve model predictions of forage quality (Knox et al. 2012, Pullanagari et al. 2018). Despite the importance of integrated forage quality metrics like DP and DDM, few studies to date investigated remote sensing approaches to estimate these characteristics, and none have occurred in Arctic-boreal landscapes. Thus, the overarching objective of this study was to assess the suitability of optical and structural remote sensing data to estimate DP and DDM in north central Alaska. Assessing remotely sensed measures of DP and DDM is an important first step toward mapping nutritional landscapes in high northern latitude regions subject to ongoing environmental change.
2. Methods and materials

2.1. Study area

The upper Koyukuk River drainage in north central Alaska (figure 2) contains a wide range of terrain and vegetation types, including boreal forest dominated by black spruce (*Picea mariana*), alpine tundra and shrubs such as alders, willows, and dwarf birch (*Betula glandulosa*), and muskegs and other riparian vegetation such as white spruce (*Picea glauca*) and poplar (*Populus spp.*). Located in the southern end of the Brooks Range, topography is rugged and varies from 80 to 2250 m. The region experiences continental climate patterns. In winter, the average temperature ranges from $-40^\circ C$ to $-22^\circ C$, with snow depths exceeding 60 cm most winters. In summer, the average temperature ranges from $3^\circ C$ to $16^\circ C$, but can also reach $>30^\circ C$.

2.2. Field-based forage-quality assessment study

We collected vegetation spectra and destructive vegetation samples from willow shrubs along a latitudinal transect in the Koyukuk River drainage ($n = 45$ in July 2019; figure 2). We stratified sites across soil types, elevation, and burn history. We used targeted sampling instead of a random sample because we were limited in our ability to select shrub locations *a priori* as no land cover product in this region accurately differentiates between preferred forage shrubs (e.g. willows) and other shrub species (e.g. alder and dwarf birch). Additionally, we purposefully selected willows that represented the three classes of browsing intensity (i.e. unbrowsed, browsed, and broomed; figure 1) to ensure we captured a full range of possible digestibility as herbivores influence plant biochemical properties and structure (Kielland and Bryant 1998, Stouter 2008, Christie et al 2014).

We collected spectral information using a FieldSpec Pro Full Range Spectroradiometer (Analytical Spectral Devices, Incorporated), which ranged from 350 to 2500 nm. This instrument has a full-width half-max spectral resolution of 3 nm in the visible and near infrared (NIR) range (i.e. 350–1050 nm), and 10–12 nm in both the NIR and short-wave infrared (SWIR) regions of the electromagnetic spectrum (i.e. 1050–2500 nm). We collected canopy-level spectra under low-cloud (<20%) conditions to minimize atmospheric interference and between 11:00
and 15:00 local time to mitigate confounding effects of viewing geometry.

Canopy-level spectra were collected on sun-exposed leaves in each of the four cardinal directions and averaged into a single representative spectral collection to eliminate canopy-level variation in nutrient distribution. Prior to sampling in each direction, white reference measures were obtained using a white reference panel (Spectralon Labsphere, Inc., North Sutton, New Hampshire, United States). Dark current—systematic noise from the instrument—was also recorded prior to collection. We then calculated spectral vegetation indices (SVIs) using all possible band combinations in the simple ratio-type vegetation index (Band A/Band B) and normalized difference-type vegetation index (Band A − Band B)/(Band A + Band B) formats and related them to calculated DP and DDM (H1).

We collected destructive vegetation samples, which we dried at 30°C to 40°C for 12 h. Each sample was then analyzed for percent: (a) crude protein, (b) neutral detergent fiber, (c) acid detergent fiber, (d) acid detergent lignin, (e) acid insoluble ash, and (f) tannins using the CBB-BSA (2000) methodology. Integrated measures of forage quality were calculated using the Robbins et al. (1987a, 1987b) equations for DP and DDM. Estimates of DDM and DP were quantified on a percent dry matter basis.

2.3. Landscape and shrub structural variables
We collected UAV data prior to destructive vegetation sampling using a DJI Phantom 4 Pro (Los Angeles, California, USA). Flight elevation ranged from 20 to 25 m above ground level with a frontal and side overlap of 80% resulting in a spatial resolution of 1 cm. To minimize atmospheric interference and minimize the effects of viewing geometry, flights occurred on sunny days between 11:00 and 15:00. Three-dimensional (3D) structural information was obtained from UAV imagery using SfM photogrammetry implemented in the Pix4Dmapper software package (figure 3; Pix4D 2016). Using CloudCompare (CloudCompare 2020) open-source software we manually cropped the point cloud to the footprint of sampled shrub crowns and interpolated fine-scale (1 cm) digital surface models (DSMs) that were then processed to obtain information on canopy structural characteristics using the ‘rLiDAR’ package (Silva et al. 2017) and the ‘lidR’ package (Roussel et al. 2020; table 1). We focused on these UAV-based plant structural metrics with the aim of capturing the effect of browsing on willow canopies (H2; table 1), because plant canopy architecture may be drastically altered by herbivores thereby altering branching structure and increasing canopy openness (Kielland and Bryant 1998, Christie et al. 2014), which in turn can influence palatability (Bryant 1981, Bryant and Chapin 1986).

We also interpolated DSMs (10 cm resolution) for the plots from our UAV SfM point clouds, which were used to model the light environment of the outer portion of sampled willow canopies (H3) using the
2.4. Data analyses

All data analyses were conducted in R statistical software (R Core Team 2020). The best performing SVIs were identified using Akaike information criterion for small sample sizes (AICc; Cavanaugh 1997). We also assessed the role of known spectral indices for detecting plant structure and function such as water content (the normalized difference water index (NDWI; Gao 1996)), plant pigments (chlorophyll carotenoid index (CCI) (Springer et al 2017)), red-edge indices (Eitel et al 2007, Ramoelo et al 2012) and biomass (NDVI (Shippert et al 1995, Jia et al 2003) appendix A). Analysis of semivariograms for both DDM and DP indicated the potential for spatial autocorrelation in one or both of those response variables (figure B1). Accordingly, we used generalized least squares (GLSs) regression in the ‘nlme’ package in R (Pinheiro et al 2017) to determine (a) whether accounting for spatial autocorrelation improved model fit, and (b) if so, which spatial correlation structure was optimal for our data (table 2). We evaluated competing models using (a) AICc, (b) root mean square error (RMSE), and (c) either adjusted $R^2$ (for linear models) or two pseudo $R^2$ values, the McFadden and Nagelkerke (for GLS models). McFadden $R^2$ is often used to compare nested models (McFadden and Zarembka 1974), but values are less comparable to adjusted $R^2$ from linear regression (i.e. values from 0.2 to 0.4 indicate excellent fit; Hensher and Stopher 1979). Nagelkerke $R^2$ values can range from 0 to 1, making that metric similar to $R^2$ from linear regression as an indicator of overall model predictive strength (Field et al 2012).

Next, we assessed the benefit of adding shrub structure, topographic attributes, and irradiance to models by sequentially adding one metric at a time.

We also calculated AIC weights, which sum to one with values ranging from 0 to 1 and may be interpreted as the probability that a given model is the best model (Symonds and Moussalli 2011) in the set of candidate models for both DP and DDM. Additionally, we conducted leave-one-out cross validation (LOOCV) by sequentially leaving out one willow at a time and using the remaining observations to predict the excluded one. We compared LOOCV slopes (observed values plotted against predicted values) to assess bias and Spearman rank coefficients ($\rho$) to quantify predictive ability of these models. The residuals of the models met regression assumptions (i.e. homogeneity of variance, normality of residuals). Finally, we included all predictors that improved model fit (decreases in AICc > 2) into a single model for both DP and DDM. Predictors were only combined in the same model if collinearity between them was <0.70 (Dormann et al 2013).

3. Results

DP ranged from 1.57% to 13.37% of dry matter, while DDM ranged from 22.73% to 61.76% of dry matter. Most models under predicted DP and DDM (LOOCV slopes < 1; tables 3 and 4). However, we found that hyperspectral SVIs successfully predicted DP (adjusted $R^2 = 0.75$, RMSE = 1.42%, AICc = 166.27; appendix C) and DDM (adjusted $R^2 = 0.65$, RMSE = 5.11%, AICc = 330.97; appendix C), which supported our first hypothesis. The best performing SVI for DP included a red-edge and a SWIR band in the normalized difference format ($(\text{R}_{703\text{nm}} - \text{R}_{1719\text{nm}})/(\text{R}_{703\text{nm}} + \text{R}_{1719\text{nm}}))$. The best performing SVI for DDM included a blue and a red band in the simple ratio format (R$_{483\text{nm}}$/R$_{657\text{nm}}$). Many viable simple ratio SVIs were found for both DP and DDM (figure 4). Of the irradiance options

| Model                      | DP      | DDM    |
|----------------------------|---------|--------|
| Simple linear              | 163.17  | 259.10 |
| Spherical                  | 160.33  | 264.31 |
| Linear                     | Did not converge | 264.31 |
| Rational quadratic         | 160.65  | 264.31 |
| Gaussian                   | 159.24  | 264.31 |
| Exponential                | 158.87  | 264.31 |

Table 2. Results comparing spatial autocorrelation structures for GLSs regressions predicting DDM and DP. Model fit was assessed using AICc, where lower values are considered better.
Table 3. Results from DP GLS models included a Gaussian correlation structure. The SVI was regressed against percent DP. Shrub structural and landscape metrics included: median canopy height (hmed), mean canopy height (hmean), 90th (h90p) and 99th (h99p) height percentiles, coefficient of variation of height (hcv), variance of heights (hvar), kurtosis (hkur) and skew (hskew) of height distributions, median canopy height × canopy fractional cover (can_med_frac), fractional cover 1–3 m (can_fcov_1_3) and >3 (can_fcov_>3) height range, TWI, TRASP, slope, elevation, and total irradiance the week before sample harvest and were sequentially added to models and evaluated based on two pseudo $R^2$s: McFadden and Nagelkerke. RMSE quantified error. We used AICc to assess model fit and AICc weights to assess the probability of a given model being the best model. We used slopes and Spearman Rank correlation coefficients ($\rho$) from LOOCV to assess bias and predictive ability of models. The best model for DP was bolded for easy visualization.

| Models             | McFadden $R^2$ | Nagelkerke $R^2$ | RMSE  | AICc  | AICc weights | LOOCV slope | LOOCV $\rho$ |
|--------------------|----------------|------------------|-------|-------|--------------|--------------|--------------|
| SVI                | 0.33           | 0.81             | 1.42% | 159.11| 0.03         | 0.76         | 0.88         |
| SVI + hmed         | 0.36           | 0.84             | 1.40% | 154.30| 0.26         | 0.75         | 0.88         |
| SVI + hmean        | 0.35           | 0.83             | 1.42% | 154.91| 0.19         | 0.72         | 0.87         |
| SVI + h90p         | 0.34           | 0.83             | 1.47% | 155.72| 0.13         | 0.71         | 0.85         |
| SVI + h99p         | 0.33           | 0.81             | 1.42% | 161.45| 0.01         | 0.76         | 0.88         |
| SVI + hcv          | 0.36           | 0.84             | 1.37% | 162.96| 0            | 0.77         | 0.87         |
| SVI + hvar         | **0.34**       | **0.82**         | **1.46%** | **153.92** | **0.32** | **0.72** | **0.85** |
| SVI + hkur         | 0.33           | 0.82             | 1.41% | 166.07| 0            | 0.76         | 0.87         |
| SVI + hskew        | 0.34           | 0.83             | 1.40% | 159.19| 0.02         | 0.76         | 0.87         |
| SVI + can_med_frac | 0.36           | 0.84             | 1.41% | 163.11| 0            | 0.75         | 0.88         |
| SVI + can_fcov_1_3 | 0.33           | 0.82             | 1.42% | 167.42| 0            | 0.75         | 0.87         |
| SVI + can_fcov_>3  | 0.35           | 0.83             | 1.42% | 159.29| 0.02         | 0.76         | 0.88         |
| SVI + TWI          | 0.33           | 0.81             | 1.41% | 162.11| 0.01         | 0.75         | 0.88         |
| SVI + TRASP        | 0.33           | 0.81             | 1.42% | 171.94| 0            | 0.76         | 0.87         |
| SVI + slope        | 0.33           | 0.81             | 1.42% | 164.29| 0            | 0.75         | 0.88         |
| SVI + elevation    | 0.34           | 0.83             | 1.36% | 167.51| 0            | 0.80         | 0.89         |
| SVI + irradiance (1 week) | 0.33 | 0.81 | 1.41% | 190.92| 0 | 0.76 | 0.88 |
modeled—total irradiance experienced by a shrub one week, two weeks, and one month prior to harvest—the one-week cumulative irradiance before sample harvest produced the best model fit (not shown). Thus, we only present results from this model.

Model performance for predicting DP did not improve when well-known existing spectral indices for detecting plant characteristics (e.g. NDVI) were included (appendix A). The exponential correlation structure had the lowest AICc for DP (AICc = 158.87; table 2) but LOOCV models did not converge using this structure. Thus, we used the Gaussian correlation structure (AICc = 159.24). According to the DP semivariogram (appendix B), spatial correlation for DP content continued to show spatial autocorrelation throughout the range of distances present in our sample (i.e. ~2 km). The best performing SVI showed very strong predictive power (LOOCV $\rho = 0.88$, slope = 0.76) and a low error estimate (RMSE = 1.42%; table 3) without the inclusion of any structural metrics (H1). Model fit improved when some structural metrics (H2)—hmed (AICc = 154.30), hmean (AICc = 154.91), h90p (AICc = 155.72), hvar (AICc = 153.92)—were added to the base model (table 3). However, these metrics were all highly correlated ($r > 0.7$) and thus could not be considered in a single model. Thus, we identified hvar and SVI model as the best performing model (AIC weight = 0.32; figure 5). However, this model also demonstrated a slight decrease in predictive power when compared to the base model using only the SVI ($\Delta$LOOCV $\rho = -3\%$).

DMD model performance improved when NDVI and NDRE were included in addition to the SVI (appendix A). However, NDVI and NDRE were highly correlated ($r > 0.7$) and therefore only NDRE was included as it had the lowest AICc value. No correlation structures improved model fit for DDM (table 2). Thus, we used the simple linear model (AICc = 259.10). According to DDM semivariogram (appendix B), no spatial autocorrelation was present in our samples. Using only the SVI and NDRE, the model showed good predictive power (LOOCV $\rho = 0.77$, slope = 0.67) with a low error estimate (RMSE = 4.60%; table 4) without the inclusion of any structural metrics (H1). Model fit improved when some structural metrics (H2)—hmed (AICc = 271.62), hmean (AICc = 269.02), h90p (AICc = 268.04), h99p (AICc = 270.42), hcv (AICc = 271.36), hvar (AICc = 267.61), hskekew (AICc = 272.35), can_med_frac (AICc = 271.63) and can_fcov_1_3 (AICc = 269.81)—were added to the base model (table 4). The best performing combined model for DDM included SVI, NDRE, and hvar (table 4; figure 4; adjusted $R^2 = 0.73$, AIC weight = 0.25, LOOCV $\rho = 0.80$). Increased error estimates in DDM compared to DP may be related to the relative range of values associated with these estimates, 1.57%–13.37% for DP and 22.73%–61.76% for DDM. We observed limited evidence that including the light environment (H3) nor topographic attributes (H4) produced model improvements.

4. Discussion

We assessed how well integrated measures of forage quality—DP and DDM—could be predicted using a fusion of hyperspectral SVIs, shrub structural metrics, topographic attributes, and the light environment. Results from our study demonstrated that DP and DDM could be successfully estimated using hyperspectral remote sensing (supporting our H1). Remotely-sensed estimates of DP showed a strong correlation with observed estimates and low correlation with observed estimates and low
error (LOOCV $\rho = 0.88$, RMSE = 1.42%). DDM estimates also were highly correlated with measured values but with higher error (LOOCV $\rho = 0.77$, RMSE = 4.61%). These findings were consistent with previous work in Australian Eucalyptus forests where DP ($R^2 = 0.64$) and DDM ($R^2 = 0.78$) were estimated with high accuracy using hyperspectral remote sensing approaches (Youngentob et al 2012), though our results suggested DP in northern willows is more easily predicted than DDM.

Although wavelengths used in the SVIs in this study did not correspond exactly to existing absorption features previously identified for tannins, protein, or fibers (Curran 1989, Elvidge 1990, Ferwerda et al 2006), they were within 25 nm. The SVI for DP contained one wavelength (703 nm) in the red-edge portion of the spectrum, which is known to be sensitive to chlorophyll and has been used as a proxy for nitrogen content (Eitel et al 2007, Ramoelo et al 2012, Wang et al 2012). The second wavelength (1719 nm) used in the SVI for DP was directly adjacent to a known absorption feature of hemicellulose at 1720 nm (Elvidge 1990), though numerous tannin absorption features can be found in the SWIR region (Ferwerda et al 2006). In contrast to DP, the wavelengths in DDM’s SVI were both in the visible portion of the spectrum (483 and 657 nm) and near known spectral absorption features of chlorophyll pigments (Curran 1994, Ben-Dor et al 1997), which are often related to plant nitrogen concentrations. This was somewhat surprising because DDM estimates incorporated fiber concentrations that usually have absorption in the SWIR region (Curran 1989, Elvidge 1990). For instance, the SWIR region was shown to be sensitive to both DP and DDM in Australian Eucalyptus trees (Youngentob et al 2012). In our case, we found several viable vegetation indices for DP and DDM (figure 4), many of which also included SWIR wavelengths.

We also observed some improvement in model fit by incorporating shrub structural metrics such as hvar (H2). Model fit and AIC weights indicated that the best model for DP included hvar in addition to the SVI ($\Delta AICc = 5.19$; AIC weight = 0.32; table 3), although this addition slightly reduced predictive power ($\Delta LOOCV = -3\%$). The best model for DDM included hvar and NDRE, which somewhat enhanced predictive power ($\Delta LOOCV = +3\%$, AIC weight = 0.25; table 4). Herbivores strongly influence plant canopy architecture of palatable species such as willow. Previous work showed browsing influenced shrub height, canopy openness, and branching structure (Kielland and Bryant 1998, Christie et al 2014, 2015), which in turn can affect the palatability of forage species. To our knowledge, this study was the first to incorporate remotely-sensed shrub structural metrics as a proxy for browsing history in models to predict forage quality. Our results indicated that incorporating shrub structure may be an important, and often unconsidered, aspect of remotely sensed forage quality metrics.

Based on these findings we suggest that future work should consider shrub structure when using remote sensing to study forage quality metrics. Variation in canopy structure increases the complexity of the three-dimensional space where photons interact (Asner 1998, Knyazikhin et al 2013); hence, SVIs calculated from reflectance spectroscopy are influenced by plant structural characteristics.
Table 4. Results from DDM linear models. The SVI and the NDRE was regressed against percent DDM. Shrub structural and landscape metrics included: median canopy height (hmed), mean canopy height (hmean), 90th (h90p) and 99th (h99p) height percentiles, coefficient of variation of height (hcv), variance of heights (hvar), kurtosis (hkur) and skew (hskew) of height distributions, median canopy height * canopy fractional cover (can_med_frac), fractional cover 1–3 m (can_fcov_1_3) and >3 (can_fcov_>3) height range, TWI, TRASP, slope, elevation, and total irradiance the week before sample harvest and were sequentially added to models and evaluated based adjusted $R^2$, RMSE, AICc, and AICc weights to assess the probability of a given model being the best model. We used slopes and Spearman Rank correlation coefficients ($\rho$) from LOOCV to assess bias and predictive ability of models. The best models for DDM were bolded for easy visualization.

| Models          | Adjusted $R^2$ | RMSE  | AICc  | AICc weights | LOOCV slope | LOOCV $\rho$ |
|-----------------|----------------|-------|-------|--------------|--------------|--------------|
| SVI + NDRE      | 0.68           | 4.60% | 274.18| 0.01         | 0.67         | 0.77         |
| SVI + NDRE + hmed| 0.70           | 4.35% | 271.62| 0.03         | 1.25         | 0.78         |
| SVI + NDRE + hmean| 0.72           | 4.22% | 269.02| 0.13         | 0.81         | 0.79         |
| SVI + NDRE + h90p| 0.73           | 4.18% | 268.04| 0.20         | 0.76         | 0.79         |
| SVI + NDRE + h99p| 0.71           | 4.30% | 270.42| 0.06         | 0.70         | 0.79         |
| SVI + NDRE + hcv | 0.71           | 4.34% | 271.36| 0.04         | 0.69         | 0.76         |
| **SVI + NDRE + hvar** | **0.73** | **4.16%** | **267.61** | **0.25** | **0.75** | **0.80** |
| SVI + NDRE + hkur| 0.69           | 4.49% | 274.37| 0.01         | 0.67         | 0.77         |
| SVI + NDRE + hskew| 0.70           | 4.39% | 272.35| 0.02         | 0.68         | 0.77         |
| SVI + NDRE + can_med_frac| 0.70 | 4.35% | 271.63| 0.03         | 1.27         | 0.77         |
| SVI + NDRE + can_fcov_1_3| 0.72 | 4.27% | 269.81| 0.08         | 0.71         | 0.80         |
| SVI + NDRE + can_fcov_>3| 0.67 | 4.60% | 276.51| 0   | 0.67         | 0.77         |
| SVI + NDRE + TWI | 0.68           | 4.60% | 275.79| 0   | 0.67         | 0.77         |
| SVI + NDRE + TRASP | 0.67           | 4.60% | 276.62| 0   | 0.66         | 0.78         |
| SVI + NDRE + slope| 0.68           | 4.54% | 275.46| 0.01         | 0.67         | 0.78         |
| SVI + NDRE + elevation| 0.67           | 4.60% | 276.65| 0   | 0.67         | 0.77         |
| SVI + NDRE + irradiance (1 week) | 0.69 | 4.49% | 274.35| 0.01         | 0.68         | 0.78         |
| SVI + hvar + hcv | 0.78           | 4.13% | 269.56| 0.10         | 0.78         | 0.80         |
(Chen and Cihlar 1996, Turner et al 1999, Eitel et al 2008). This, coupled with the impacts of browsing, suggests a growing need to incorporate structure into remotely sensed models of forage quality to better estimate and map these metrics across the landscape. Modern airborne sensor platforms such as Goddard’s LiDAR, Hyperspectral & Thermal Imager (G-LiHT; 1 m pixels, with 6 lidar pulses per m²), the Airborne Visible-Infrared Imaging Spectrometer - Next Generation (AVIRIS-NG; 0.3–4.0 m pixels) and the land, vegetation, and ice sensor (LVIS; 5–25 m spots) provide opportunities to fuse data streams from both structural and optical data, which may enhance our ability to estimate and scale important foliar properties such as DP and DDM.

Strategies for estimating spatiotemporal variation in forage quality metrics are needed because northern ecosystems are rapidly changing. The range of northern forage quality is less clear and will likely vary depending on region and species (Lenart et al 2002, Hansen et al 2006, Turunen et al 2009, Elmendorf et al 2012). Since forage quality strongly influences herbivore life-history traits like maternal body condition, pregnancy rates, and survival (Parker et al 2009), monitoring ‘nutritional landscapes’ (sensu Merems et al 2020) that include integrated metrics of forage quality—like DP and DDM—is urgently needed. In addition to the importance of forage quality on fitness, secondary effects related to changes in herbivore populations can have cascading effects on ecosystem structure and function.

We did not see any improvement in model fit or predictive power when we included the light environment (H3), which contrasted with previous work indicating that light conditions influenced fiber and nitrogen concentrations as well as DDM (Molvare et al 1993, Lenart et al 2002). This may in part be because the light modeling employed in this study did not account for cloud cover or variation in illumination throughout the canopy (i.e. we only modeled the surface foliage of the shrub canopy). Indeed, one study compared various techniques for quantifying the light environment of Salix pulchra and found that only lidar-based techniques captured photosynthetic partitioning of nitrogen and chlorophyll in canopies (Magney et al 2016).

Moreover, our findings may be related to the relatively coarse spatial scale of the atmospheric variables (with a spatial resolution of 32 km) included within the models of solar irradiance employed in this study. Future work may benefit from applying the approaches used in Magney et al (2016) or ground-based sensors that estimate the instantaneous irradiance at the location of shrubs to determine how solar energy influences DP and DDM. Similarly, including topographic attributes produced no model improvements (H4). This is surprising considering that elevation, slope and aspect have been shown to influence forage quality (Knox et al 2012, Pullanagari et al 2018).

One limitation of our study was that we did not quantify shrub biomass, because we did not have the resources locally to do so. Yet, the total energy acquired through browsing is a function of both forage quantity and quality, and thus both of these metrics are needed to truly map nutritional landscapes. Additionally, forage quality is normally the highest after budburst and then declines throughout the remainder of the growing season as fiber content increases and digestibility and nitrogen decrease (Klein 1990, McArt et al 2009, Shively et al 2019). Our study demonstrated that remote sensing of DP and DDM is possible during peak biomass. However, future work should consider the seasonal dynamics of these integrated metrics.

Finally, future work should investigate the possibility of scaling these plot-level assessments to airborne and satellite platforms. Although we advocate for future work to include both optical and structural data streams, we also observed strong relationships between hyperspectral SVIs and DP and DDM without additional shrub structural inputs (tables 3 and 4; appendix C; figure C1). Therefore, we anticipate that as new hyperspectral satellite platforms—such as the Environmental Mapping and Analysis Program (EnMAP; Guanter et al 2015) and PRRecursore IperSpettrale della Missione Applicativa (PRISMA; Loizzo et al 2018)—become more widely available, our ability to monitor integrated forage quality metrics seasonally and interannually at the landscape scale will be enhanced. We also suggest that future work that employs satellite data should couple with finer scale structural remotely sensed data that would help characterize the uncertainty in canopy structure attributes as the spatial resolution will be much coarser than our shrub-level assessments. Structural data may be sourced from aerial lidar transects, which can provide estimates of plant height variability (hvar) but would not provide wall-to-wall coverage. One alternative to aerial lidar in high latitude regions would be canopy height models estimated from the ArcticDEM (Meddins et al 2018) to estimate canopy hvar, which we found to be an important predictor of both DP and DDM. Assessments would be needed for aerial lidar (∼1 m grid cells), satellite imagery, and canopy height models (∼5 m grid cells) to determine if these data sources are sufficiently fine-scale to provide useful information for canopy hvar, as our UAV SFM point clouds were 1 cm spatial resolution.
5. Conclusion

Results from our study demonstrate that integrated forage quality metrics like DP and DDM can be successfully quantified using hyperspectral remote sensing data, and that models based on those data can be improved by incorporating shrub structural metrics. Mapping DP and DDM to create a spatially explicit representation of the nutritional landscape available to herbivores may assist in management decisions in the face of ongoing environmental change. Mapping nutritional landscapes will become a more important tool for understanding wildlife ecology in the rapidly changing Arctic.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Appendix A: Plant structure and function spectral index analysis

We conducted an additional analysis that targeted four spectral indices identified in the literature: (a) the NDWI (Gao 1996), (b) the CCI (Springer et al 2017), (c) the NDRE (Eitel et al 2007, Ramoelo et al 2012), and (d) the NDVI (Shippert et al 1995, Jia et al 2003). These four indices are relevant to assessing biochemical and structural properties of plants such as water content (NDWI), plant pigments (CCI and NDRE), and biomass (NDVI). To assess value added by including these spectral indices, we used the best-performing SVI for each of the two integrated forage quality metrics as a base model and added one additional spectral index and again assessed model performance.

The results are summarized in the table below. Results show that model performance decreased when we included NDWI, CCI, NDRE, and NDVI in addition to the SVI for DP. Similarly, no model improvements were observed when we include NDWI and CCI in addition to digestible dry matter (DDM) SVI. In contrast, we observed model improvements when both NDRE and NDVI were included. As NDVI and NDRE are correlation (Pearson’s $r = 0.74$) only one could be included in the analysis presented in the paper. As the DDM model performed best when NDRE was included, we opted to include that as a predictor in the ‘base model’ within our paper.
Table A1. Results from plant structure and function spectral index analysis. Each spectral index was added to the best performing index identified in this study.

| Model                                                                 | Adjusted $R^2$ | RMSE     | AICc     |
|----------------------------------------------------------------------|---------------|----------|----------|
| DDM                                                                  |               |          |          |
| SVI ($R_{483nm}/R_{657nm}$)                                          | 0.61          | 5.11%    | 281.08   |
| SVI + NDWI                                                            | 0.61          | 5.05%    | 282.39   |
| SVI + CCI                                                             | 0.60          | 5.09%    | 283.19   |
| SVI + NDRE                                                            | 0.68          | 4.61%    | 274.18   |
| SVI + NDVI                                                            | 0.65          | 4.82%    | 278.20   |
| DP                                                                   |               |          |          |
| SVI (($R_{703nm} - R_{1719nm})/(R_{703nm} + R_{1719nm})$)             | 0.77          | 1.42%    | 165.85   |
| SVI + NDWI                                                            | 0.77          | 1.39%    | 166.61   |
| SVI + CCI                                                             | 0.76          | 1.41%    | 167.67   |
| SVI + NDRE                                                            | 0.76          | 1.41%    | 167.69   |
| SVI + NDVI                                                            | 0.76          | 1.42%    | 168.22   |
Appendix B: Semivariograms for DP and DDM

Figure B1. Semivariograms depicting spatial correlation present for DP and DDM in our samples. The magnitude of spatial correlation between pairs of points did not appear to attenuate with distance within the range of distances included in our analysis, evidenced by the lack of a clear sill in the semivariograms for DP. No spatial correlation was found in DDM models.
Appendix C: Best SVIs cross validation results

Figure C1. Observed vs predicted concentrations of DP (A) and DDM (B) of the best performing SVIs. The best performing SVI for DP included a red-edge and a SWIR band in the normalized difference format \( \left( \frac{R_{703\text{nm}} - R_{1719\text{nm}}}{R_{703\text{nm}} + R_{1719\text{nm}}} \right) \). The best performing SVI for DDM included a blue and a red band in the simple ratio format \( \left( \frac{R_{483\text{nm}}}{R_{657\text{nm}}} \right) \). All DDM models also included the NDRE, refer to table A1.
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References

Asner G P 1998 Biophysical and biochemical sources of variability in canopy reflectance Remote Sens. Environ. 64 234–53
Asner G P, Knapp D E, Boardman J, Green R O, Kennedy-Bowdoin T, Eastwood M, Martin R E, Anderson C and Field C B 2012 Carnegie airborne observatory-2: increasing science data dimensionality via high-fidelity multi-sensor fusion Remote Sens. Environ. 124 454–65
Ball J P, Danell K and Sunesson P 2000 Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest J. Appl. Ecol. 37 247–55
Barboza P S and Bowyer R T 2000 Sexual segregation in dimorphic deer: a new gastrocentric hypothesis J. Mammal. 81 475–89
Ben-Dor E, Inbar Y and Chen Y 1997 The reflectance spectra of organic matter in the visible near-infrared and short-wave infrared region (400–2500 nm) during a controlled decomposition process Remote Sens. Environ. 61 1–15
Bischof R, Loe L E, Meisingset E L, Zimmerman B, van Moorter B and Mysterud A 2012 A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? Am. Nat. 180 407–24
Bryant J P 1981 Physiochemical deterrence of Snowshoe Hare browsing by adventitious shoots of four Alaskan trees Science 213 890–90
Bryant J P and Chapin III F S 1986 Browsing-woody plant interactions during boreal forest plant succession Forest Ecosystems in the Alaskan Taiga ed K van Cleve and F S Chapin III (Berlin: Springer) pp 213–25
Butler L G and Kielland K 2008 Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems J. Ecol. 96 136–44
Cavanaugh J E 1997 Unifying the derivations for the Akaike and corrected Akaike information criteria Stat. Amp. Probab. Lett. 33 201–8
Chen J M and Cihlar J 1996 Retrieving leaf area index of boreal conifer forests using Landsat TM images Remote Sens. Environ. 55 153–62
Christie K S, Bryant J P, Gough L, Ravolainen V T, Ruesw R W and Tape K D 2013 The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis BioScience 63 1123–33
Christie K S, Ruesw R W, Lindberg M S and Mulder C P 2014 Herbivores influence the growth, reproduction, and morphology of a widespread arctic willow PluS One 12 1–9
CloudCompare 2020 GPL software (version 2.2) (available at: www.cloudcompare.org)
Corripio M J 2015 Package 'Insol'
Curran P J 1989 Remote sensing of foliar chemistry Remote Sens. Environ. 30 271–8
DeGabriel J L, Moore B D, Felton A M, Ganzhorn J U, Stoller C, Wallis I R, Johnson C N and Foley W J 2014 Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers OIKOS 123 298–308
Dodge S, Bohrer G, Woinzrill R, Davidson S, Kays R, Douglas D, Cruz S, Han J, Brandes D and Wäkeleki M 2013 The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data Mov. Ecol. 1
Doiron M, Gauthier G and Lévesque E 2014 Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore J. Ecol. 102 508–17
Dormann C F et al 2013 Collinearity: a review of methods to deal with it and a simulation study evaluating their performance Ecology 54 27–46
Eitel J U H, Long D S, Gessler P E and Hunt E R 2008 Combined spectral index to improve ground-based estimates of nitrogen status in dryland wheat Agron. J. 100 1694–702
Eitel J U H, Long D S, Gessler P E and Smith A M S 2007 Using in-situ measurements to evaluate the new RapidEye TM satellite series for prediction of wheat nitrogen status Int. J. Remote Sens. 28 4183–90
Elmendorf S C et al 2012 Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time Ecol. Lett. 15 164–75
Elvidge C D 1990 Visible and near-infrared reflectance characteristics of dry plant materials Int. J. Remote Sens. 11 1775–95
Ferwerda J G, Skidmore A K and Stein A 2006 A bootstrap procedure to select hyperspectral wavebands related to tannin content Int. J. Remote Sens. 27 1413–24
Field A, Miles J and Field Z 2012 Discovering Statistics Using R (London: Sage publications)
Foley W J and Moore B D 2005 Plant secondary metabolites and vertebrate herbivores—from physiological regulation to ecosystem function Curr. Opin. Plant Biol. 8 430–5
Gao B C 1996 NDWI—a normalized difference water index for remote sensing of vegetation liquid water from space Remote Sens. Environ. 58 257–66
Goetz A F H 2001 Three decades of hyperspectral remote sensing of the Earth: a personal view Remote Sens. Environ. 113 5–16
Guanter L et al 2015 The EnMAP spaceborne imaging spectroscopy mission for earth observation Remote Sens. 7 4830–51
Hanley T A, Robbins C T, Hagerman A E and McArthur C 1992 Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants Ecology 73 537–41
Hansen A H, Jonasson S, Michelsen A and Jalkunen-Titto R 2006 Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs Oecologia 147 1–11
Hensher D A and Stopher P R 1979 Behavioural Travel Modelling (London: Taylor & Francis)
Houborg R and McCabe M F 2018 Daily retrieval of NDVI and LAI at 3 m resolution via the fusion of CubeSat, Landsat, and MODIS data Remote Sens. 10 890
Insua J R, Utsumi S A and Basso B 2019 Estimation of spatial and temporal variability of pasture growth and digestibility in grazing rotations coupling unmanned aerial vehicle (UAV) with crop simulation models PluS One 14 e0212773
Jarman P 1974 The social organisation of antelope in relation to their ecology Behaviour 48 215–67
Jennewein J S, Eitel J U, Pinto J R and Vierling L A 2020 Toward mapping dietary fibers in northern ecosystems using hyperspectral and multispectral data Remote Sens. 12 2579
Jia G, Epstein H E and Walker D A 2003 Greening of Arctic Alaska, 1981–2001 Geophys. Res. Lett. 30 20
Johnson H E, Gustine D D, Adams L G, Parrett L S, Jarman P 1974 The social organisation of antelope in relation to their ecology Behaviour 48 215–67
Johnson H E, Gustine D D, Adams L G, Parrett L S, Lenart E A and Barboza P S 2018 NDVI exhibits mixed success in predicting spatiotemporal variation in caribou summer forage quality and quantity Ecosphere 9 e02461
Kielland K and Bryant J P 1998 Moose herbivory in Taiga: effects on biogeochemistry and vegetation dynamics in primary succession OIKOS 82 377–83
Klein D R 1990 Variation in quality of caribou and reindeer forage associated with season, plant part, and phenology Rangifer 10 123–30
Knoo N M et al 2011 Dry season mapping of savanna forage quality, using the hyperspectral Carnegie Airborne Observatory sensor. Remote Sens. Environ. 115 1478–88
Knox N M, Skidmore A K, Prins H H T, Heitkönig I M A, Slotow R, van der W C and de Boer W F 2012 Remote sensing of forage nutrients: combining ecological and spectral absorption feature data ISPRS J. Photogramm. Remote Sens. 72 27–35

Knyazikhin Y et al 2013 Hyperpectral remote sensing of foliar nitrogen content Proc. Natl Acad. Sci. USA 110 E183–E92

Kokaly R F, Aner G P, Ollinger S V, Martin M E and Wesson C A 2009 Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies Remote Sens. Environ. 113 78–91

Lenart E A, Bowyer R T, Ver Hoef J and Russ E W 2002 Climate change and caribou: effects of summer weather on forage Can. J. Zool. 80 604–78

Loizzo R, Guarini R, Longo S, Scopa T, Formaro R, Facchinetti C and Varacalli G 2018 PRISMA: the Italian hyperspectral mission IGARSS 2018–2018 IEEE Int. Geoscience and Remote Sensing Symp. (July) (IEEE) pp 175–8

Lone K, van Beest F M, Mysterud A, Gobakken T, Milner J M, Rudd H P and Loe E L 2014 Improving broad scale foraging and habitat selection analyses with airborne laser scanning: the case of moose Ecosphere 5 1–22

Luo S, Wang C, Xi X, Pan F, Peng D, Zou J, Nie S and Qin H 2017 Fusion of airborne LiDAR data and hyperspectral imagery for aboveground and belowground forest biomass estimation Ecol. Indic. 73 378–87

Magny T S et al 2016 LiDAR canopy radiation model reveals patterns of photosynthetic partitioning in an Arctic shrub Agric. For. Meteorol. 221 78–93

McArt S H, Spalding D E, Collins W B, Schoen E R, Stevenson T and Bucho M 2009 Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska Ecology 90 1400–1

McFadden D and Zarembska P 1974 Conditional logit analysis of qualitative choice behavior Frontiers in Econometrics ed P Zarembska (New York: Academic) pp 105–42

Meddens A J, Vierling I A, Eitel J U, Jennewein J S, White J C and Walder M A 2018 Developing 5 m resolution canopy height and digital terrain models from WorldView and ArcDefEM data Remote Sens. Environ. 218 174–88

Melin M, Matala J, Mehtitalo L, Savanto A and Packalen P 2016 Detecting moose (Alces alces) browsing damage in young boreal forests from airborne laser scanning data NRC Res. Press 46 10–9

Mereuas J L, Shipley I A, Levi T, Ruprecht J, Clark D A, Wisdom J M, Jackson N J, Stewart K M and Long R A 2020 Nutritional-landscape models link habitat use to condition of mule deer (Odocoileus hemionus) Front. Ecol. Evol. 8 1–13

Michalak F, Philippe L, David K, Sébastien D, Christian D and Binellde J 2020 Can low-cost unmanned aerial systems describe the forage quality heterogeneity? Insight from a Timothy Pasture case study in Southern Belgium Remote Sens. 12 1650

Mirk M, Norland J E, Crabtree R L and Biondini M E 2005 Hyperspectral one-meter-resolution remote sensing in Yellowstone National Park, Wyoming: Forage nutritional values Sec. Range Manage. 58 452–8

Molvær E M, Bowyer R T and van Ballenberghe V 1993 Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community Oecologia 94 472–9

Mysterud A, Vike B K, Meisingset E L and Rivrud IM 2017 The role of landscape characteristics for forage maturation and nutritional benefits of migration in red deer Ecol. Evol. 7 4448–55

Ogawa A, Shibata H, Suzuki K, Mitchell M J and Ikgamani Y 2006 Relationship of topography to surface water chemistry with particular focus on nitrogen and organic carbon solutes within a forested watershed in Hokkaido, Japan Hydrol. Process. 20 251–65

Parker K L, Barboza P S and Michael P 2009 Nutrition integrates environmental responses of ungulates Funct. Ecol. 23 57–69

Pastor J, Dewey B, Naiman R J, McInnes P F and Cohen Y 1993 Moose browsing and soil fertility in the boreal forests of Isle Royale National Park Ecology 74 467–80

Pastor J, Naiman R J, Dewey B, McInnes P, Forest B, Pastor J, Naiman R J, Dewey B and McInnes P 1988 Moose, microbes, and the boreal forest BioScience 38 770–7

Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, van Willigen B and Maintainer R 2017 Package ‘nlme.’ Linear and Nonlinear Mixed Effects Models, Version 3.1

Pix4D 2016 Pix4D—drone mapping software (available at: https://pix4d.com/)

Porter C et al 2018 ArcticDefEM. Harvard Dataverse (VI, 2018) (https://doi.org/10.7910/DVN/OHHUKH) (Accessed 10 January 2018)

Pullanagari R R, Kereszturi G and Yule I 2018 Integrating airborne hyperspectral, topographic, and soil data for estimating pasture quality using recursive feature elimination with random forest regression Remote Sens. 10 1–14

R Core Team 2020 R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing) (https://www.R-project.org/)

Ramoelo A, Skidmore A K, Cho M A, Schlerf M, Mathieu R and Heitkönig I M A 2012 Regional estimation of savanna grass nitrogen using the red-edge band of the spaceborne RapidEye sensor Int. J. Appl. Earth Obs. Geoinf. 19 373–81

Robbins C T, Hanley T A, Hagerman A E, Hjeljord O, Baker D L, Schwartz C C and Mautz W W 1987a Role of tannins in defending plants against tannin-feeding red deer: reduction in protein availability Ecology 68 98–107

Robbins C T, Mole S, Hagerman A E and Hanley T A 1987b Role of tannins in defending plants against tannin-feeding red deer: reduction in dry matter digestibility? Ecology 68 1606–15

Roberts D W and Cooper S V 1989 Land Classifications Based on Vegetation: Applications for Resource Management General Technical Report INT-257 United States Department of Agriculture: Forest Service

Roussel J, Auyt D, Coops N C, Tompalski P, Goodbody T R, Meador A S, Bourdon J, de Boissieu F and Achim A 2020 LiDAR: an R package for analysis of airborne laser scanning (ALS) data Remote Sens. Environ. 251 112261

Schmitz O J, Wilmers C C, Lewis B E 1995 Role of herbivory on forest patterns of photosynthetic partitioning in an Arctic shrub Ecol. Evol. 5 187–201

Senft R L, Coughenour M B, Bailey D W, Rittenhouse L, Sala O E and Swift D M 1987 Large herbivore foraging and ecological hierarchies BioScience 37 789–99

Serreze M C, Walsh J E, Chapin F S I, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel W C, Morison J, Zhang T and Barry R G 2000 Observational evidence of recent change in the northern high- latitude environment Clim. Change 46 159–207

Shippert M W, Walker D A, Auerbach N A and Lewis B E 1995 Biomass and leaf-area index maps derived from SPOT images for Toolik Lake and Imnavait Creek areas, Alaska Polar Rec. 31 147–54

Shively R D, Crousse J A, Thompson D P and Barboza P S 2019 Is survival food intake a limiting factor for boreal browsers? Diet, temperature, and reproduction as drivers of consumption in female moose PlaS One 14 1–18

Silva M C A 2017 Package ‘rLiDAR’ Computing

Skidmore A K, Ferwerda J G, Mutanga O, van Wieren S E, Peel M, Roussel J, Auty D, Coops N C, Tompalski P, Goodbody T R, Meador A S, Bourdon J, de Boissieu F and Achim A 2020 LiDAR: an R package for analysis of airborne laser scanning (ALS) data Remote Sens. Environ. 251 112261

Soldberg N, Nesset E, Holt K and Christiansen E 2006 Mapping defoliation during a severe insect attack on Scots pine using airborne laser scanning Remote Sens. Environ. 102 364–76

Spalding D E, Collins W B, Hanley T A, Cassara N E and Carnahan A M 2010 The impact of tannins on protein, dry

Environ. Res. Lett. 16 (2021) 075006

J S Jennwein et al
matter, and energy digestion in moose (Alces alces) Can. J. Zool. 88 977–87
Sponseller R A, Gundale M J, Futter M, Ring E, Nordin A, Nåsholm T and Laudon H 2016 Nitrogen dynamics in managed boreal forests: recent advances and future research directions Ambio 45 175–87
Springer K R, Wang R and Gannon J A 2017 Parallel seasonal patterns of photosynthesis, fluorescence, and reflectance indices in boreal trees Remote Sens. 9 691
Stouten C 2008 Intra-individual plant response to moose browsing: feedback loops and impacts on multiple consumers Ecol. Monogr. 78 167–83
Symonds M R E and Moussalli A 2011 A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion Behav. Ecol. Sociobiol. 65 13–21
Tape K D, Gustine D D, Ruess R W, Adams L G and Clark J A 2016 Range expansion of moose in Arctic Alaska linked to warming and increased shrub habitat PLoS One 11 1–12
Thompson D P and Barboza P S 2014 Nutritional implications of increased shrub cover for caribou (Rangifer tarandus) in the Arctic Can. J. Zool. 92 339–51
Thulín S, Hill M J, Held A, Jones S and Woodgate P 2012 Hyperspectral determination of feed quality constituents in temperate pastures: effect of processing methods on predictive relationships from partial least squares regression Int. J. Appl. Earth Obs. Geoinf. 19 322–34
Toorabzadeh H, Morsdorf F and Schaepman M E 2014 Fusion of imaging spectroscopy and airborne laser scanning data for characterization of forest ecosystems—a review ISPRS J. Photogramm. Remote Sens. 97 25–35
Turner D P, Cohen W B, Kennedy R E, Fassnacht K S and Briggs J M 1999 Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites Remote Sens. Environ. 70 52–68
Turunen M, Soppepa P, Kinnunen H, Sutinen M L and Martz F 2009 Does climate change influence the availability and quality of reindeer forage plants? Polar Biol. 32 813–32
Van Soest P J 1996 Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review Zoo Biology 15 455–79
Vance C K, Tolleson D R, Kinoshita K, Rodriguez J and Foley W J 2016 Near infrared spectroscopy in wildlife and biodiversity J. Near Infrared Spectrosc. 24 1–25
Vastaranta M, Kantola T, Lyytikäinen-Saarenmaa P, Holopainen M, Kankare V, Wulder M A, Hyvärä H and Hyvärä H 2013 Area-based mapping of defoliation of Scots pine stands using airborne scanning LiDAR Remote Sens. 5 1220–34
Verbyla D 2008 The greening and browning of Alaska based on 1982–2003 satellite data Glob. Ecol. Biogeogr. 17 547–55
Vierling K T, Vierling L A, Gould W A, Martinuzzi S and Clawges R M 2008 Lidar: shedding new light on habitat characterization and modeling Front. Ecol. Environ. 6 90–8
Wallace L, Luicer A, Malenovský Z, Turner D and Vopěnka P 2016 Assessment of forest structure using two UAV techniques: a comparison of airborne laser scanning and structure from motion (SfM) point clouds Forests 7 1–16
Walton K M, Spalinger D E, Harris N R, Collins W B and Willacker J J 2013 High spatial resolution vegetation mapping for assessment of wildlife habitat Wildl. Soc. Bull. 37 906–15
Wang W, Yao X, Yao X F, Tian Y C, Liu X J, Ni J, Cao W X and Zhu Y 2012 Estimating leaf nitrogen concentration with three-band vegetation indices in rice and wheat Field Crops Res. 129 90–8
White T C 1993 The Inadequate Environment: Nitrogen and the Abundance of Animals (Berlin: Springer)
Wollen J M et al 2011 Evidence and implications of recent and projected climate change in Alaska’s forest ecosystems Ecosphere 2 art124
Wu H, Levin N, Seabrook L, Moore B and McAlpine C 2019 Mapping foliar nutrition using WorldView-3 and WorldView-2 to assess Koala habitat suitability Remote Sens. 11 1–17
Yougentob K N, Renzullo L J, Held A A, Jia X, Lindenmayer D B and Foley W J 2012 Using imaging spectroscopy to estimate integrated measures of foliage nutritional quality Methods Ecol. Evol. 3 416–26
Zamin T J, Côté S D, Tremblay J P and Grogan P 2017 Experimental warming alters migratory caribou forage quality Ecol. Appl. 27 2061–73
Zhou J, Prugh L D, Tape K, Kofinas G and Kielland K 2017 The role of vegetation structure in controlling distributions of vertebrate herbivores in Arctic Alaska Arct. Antarct. Alp. Res. 49 291–304
Zhou J, Tape K D, Prugh L, Kofinas G, Carroll G and Kielland K 2020 Enhanced shrub growth in the Arctic increases habitat connectivity for browsing herbivores Glob. Change Biol. 1–12