

Diet Selection, Forage Quality, and Forage Availability: Could Forage Limit Moose
Populations in Northern Idaho?

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Authorization to Submit Thesis

This thesis of Thomas V. Schrempp, submitted for the degree of Master of Science with a Major in Natural Resources and titled “Diet Selection, Forage Quality, and Forage Availability: Could Forage Limit Moose Populations in Northern Idaho?,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Several populations of Shiras moose (*Alces alces shirasi*) in northern Idaho have declined in recent decades for unknown reasons. Limitations in quality or quantity of forage have been proposed to drive or contribute to these declines, but relatively few data are available to assess this hypothesis. To fill this information gap, we evaluated diet selection, analyzed forage shrubs for nutritional quality, conducted field sampling to model forage availability, and looked for evidence of forage limitations. Moose in northern Idaho exhibited greater selection for forage species that are of moderate to high quality and highly available on the landscape. Variation in predicted forage quantity among GMUs was correlated with variation in indices of population performance. Results suggest that forage is an underlying factor in moose population performance trends observed across northern Idaho. This information can be used to shape forest management strategies and harvest recommendations, and to direct future research into proximate factors influencing Shiras moose throughout their range.

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Dedication

I dedicate this work to my late friend Lavon Bradley (L.B.) Ellis. A true lover of nature, the time and thoughtful conversation we shared over many summer days at Mystic Meadow taught me to see and appreciate beauty in all things.

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Diet selection, forage quality, and forage availability: could forage limit moose populations in northern Idaho?

Introduction

Forested lands in the western USA have undergone marked shifts in management and condition over the past century with broad implications for wildlife habitat and forest ungulates. Timber harvest has a long history on national forests, and indeed, the Organic Act of 1897 specifically includes direction to “furnish a continuous supply of timber”. Timber harvest typically increases forage for ungulates by increasing the availability of light, water, and nutrients for understory vegetation (Riegel et al. 1992). Passage of The Multiple Use-Sustained Yield Act of 1960 signaled growing recognition of non-utilitarian and social values of national forests (Koch and Kennedy 1991) and a general decline in timber harvest in western states (Cook et al. 2016, McIver et al. 2014, McIver et al. 2013, Simmons et al. 2016). Research on ungulates has shown that forest management practices can alter forage quantity (Edenius et al 2013, Milner et al. 2013, Long et al. 2008a), quality (Wam et al. 2016, Burney and Jacobs 2011, Long et al. 2008a), and habitat use (Heinze et al. 2011, Long et al. 2008b).

In addition to timber harvest practices, policies regarding management of forest fires also affect wildlife habitat. Fire suppression in the northern Rocky Mountains became effective in the 1930s, reducing the extent of forest fires on national forests, even within large wilderness areas (Brown et al. 1994). Fire is an important ecosystem process that increases early-seral vegetation (Leege and Hickey 1971, Merrill et al. 1982, Arno et al. 1985) that provides forage for ungulates such as moose (*Alces alces*, Peak 1974), mule deer (*Odocoileus hemionus*, Long et al. 2008a, Hobbs and Spowart 1984), and elk (*Cervus*

elaphus, Long et al. 2008a, Sachro et al 2005). Changes in forest management practices, including fire suppression and reduction of timber harvest, have the potential to reduce forage quality and quantity, and thereby impose nutritional limitations on wildlife that forage on early-seral stage plants.

Nutrition affects many components of individual fitness and ultimately population dynamics for numerous ungulate species. Evidence of inadequate nutrition limiting adult or juvenile mass gain has been reported for caribou (*Rangifer tarandus*; Crete and Huot 1993), elk (Cook et al. 2004), roe deer (*Capreolus caperolus*; Gaillard et al. 1996), mule deer (Tollefson et al. 2010), and moose (Bo and Hjeljord 1991, Saether and Heim 1993, Milner et al 2013). Pregnancy rates also have been linked to nutrition and body condition for mule deer (Tollefson et al. 2010), elk (Cook et al. 2001), caribou (Cameron et al 1993), and moose (Ruprecht et al. 2016). In addition, body mass and body condition of neonates, juveniles, and adults have been correlated with survival for caribou (Cameron et al. 1993), bighorn sheep (Festa-Bianchet et al. 1997), elk (Cook et al. 2004, Bender et al. 2008), and moose (Solberg et al. 2004, Hand et al. 2012).

Adequate nutrition is a key factor influencing population dynamics, and there is growing evidence that summer nutrition is especially important for ungulates. The role of summer nutrition in regulating reproduction and survival has been documented for elk (Bender et al. 2004, Cook et al. 2004, Cook et al. 2001), mule deer (Tollefson et al. 2010), and caribou (Crete and Huot 1993), and the same trend has been observed for moose through twinning rates (Franzmann and Schwartz 1985), recruitment (Monteith et al. 2015), and survival (Sand et al. 2012). High spring temperatures and hot and dry summers were correlated with more rapid forage phenological development, decreased forage quality, and

reduced weight gain of moose calves and adults in Norway (Bo and Hjeljord 1991, Solberg et al. 2004). Likewise, recruitment of moose in Wyoming, Utah, and Colorado was reduced by increased spring-summer temperatures, increased rates of green-up, decreased spring-summer precipitation, and shortened springs, presumably due to shortened periods of availability and reduced quality of forage (Monteith et al. 2015). If summer nutrition is inadequate, females can exhibit delayed age at first reproduction and reproductive pauses (Albright and Keith 1987). In addition to needing adequate nutrition for pregnancy and lactation, females also must recoup body mass lost over the previous winter in preparation for the coming winter (Schwartz and Renecker 1997). Failure to recover sufficient fat reserves can predispose individuals to mortality from diverse proximate causes, such as predation (Sand et al. 2012) or parasites (Lankester 2010, Joly and Messier 2004).

Population trends for Shiras moose (*A. a. shirasi*), which occur in the Pacific Northwestern USA and Canada, have been highly variable in recent decades. Populations in Washington and some parts of Idaho have increased (IDFG unpublished data, Muir 2006, Harris 2015), while populations in many states including some in Idaho (IDFG unpublished data), Montana (DeCesare 2014), and Wyoming (Oates et al. 2016) have experienced marked declines. A number of population drivers have been examined nationwide, including forage quality (McArt et al. 2009), predation (Mech and Fieberg 2014, Dussault et al. 2005), parasites and disease (Lankester and Samuel 2007), physiological tolerance to temperature (Lenarz et al. 2009), and indirect effects of climate change on plant phenology (Monteith et al. 2015). However, the mechanisms driving these processes and how they affect survival and reproduction, and ultimately population growth or decline, are not well understood for Shiras moose.

Declines in forage availability and quality could be contributing to declining population trends for some Shiras moose populations in Idaho. Changing forest management practices and continued fire suppression has resulted in advancing forest succession, which could alter forage quality and quantity, especially on national forest lands. However, information on moose diet selection and forage quality and availability necessary for a rigorous test of this hypothesis is limited. Objectives of this study were to fill this information gap for moose populations in northern Idaho by 1) evaluating diet composition and selection, 2) assessing forage quality parameters, 3) estimating forage quantity and quality across the landscape, 4) estimating changes in forage quantity and quality across 30 years, and 5) interpreting results in the context of population indices to evaluate the degree to which forage could be limiting declining populations. We predicted that individuals would select forage species that were both highly available and high in quality because moose are large-bodied, selective browsers that likely need to balance selection for quality with attaining adequate quantity. We also predicted that indices of population trend and productivity would be positively correlated with the current amount of quality forage and the change over time in the amount of quality forage. This information will provide a foundation for evaluating whether forage limitations could be affecting moose population dynamics in northern Idaho. Such knowledge can be used to shape forest management strategies and harvest recommendations, and to direct future research into proximate factors influencing Shiras moose throughout their range.

Methods

Study Area

We conducted this research in northern Idaho, USA (Figure 1), encompassing 21 game management units (GMUs), which define population management regions based on similarities in landscape features such as elevation, vegetation communities, and land use. Moose habitat in this region is generally mountainous and dominated by coniferous forests with limited riparian areas. Annual precipitation was highest in the northeastern part of the study area, whereas average summer temperatures were higher in the southwestern portion (Table 1). Landownership was mixed, consisting predominately of national forests but also including Idaho state endowment lands, corporate timber lands, and private property. The following trees and shrubs occur across the study region in northern Idaho: western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), western red cedar (*Thuja plicata*), western white pine (*Pinus monticola*), western large (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), rocky mountain maple (*Acer glabrum*), scouler willow (*Salix scouleriana*), redstem ceanothus (*Ceanothus sanguineus*), evergreen ceanothus (*Ceanothus velutinus*), rusty menziesia (*Menziesia ferruginea*), huckleberry species (*Vaccinium spp.*), cherry species (*Prunus spp.*), western thimbleberry (*Rubus parviflorus*), common snowberry (*Symphoricarpos albus*), alder species (*Alnus spp.*), mallow ninebark (*Physocarpus malvaceus*), and oceanspray (*Holodiscus discolor*).

Field sampling

An overview of the data collection and processing steps used to accomplish objectives is presented in Figure 2. We focused field sampling for forage parameters and diet

analyses in 3 GMUs that spanned the range of forest types, successional stages, land uses, and population trends representative of the broader study area (GMU3, GMU10, and GMU15; Figure 1). Early seral shrub communities in GMU10 were largely created by historical wildfires, whereas timber harvest created the majority of early seral shrub vegetation in GMU3, and a mixture of both shaped shrub communities in GMU15. Indices of population trend suggest that moose numbers in GMU15 have declined sharply since the 1980s, while populations appear to have increased in GMU3, and remained relatively stable or slightly declined in GMU10 (IDFG unpublished data).

We collected data to estimate forage quantity for the 3 selected GMUs during the summers (July to September) of 2015 and 2016. Field sampling was conducted in 2 stages; first, we employed a design-based sampling methodology to assess general trends in species composition and preferred growing conditions. Second, we adapted our sampling to target moose forage species in a spatially balanced manner to predict forage availability under a model-based design. Stage 1 was accomplished in 2015 using a stratified random sampling design with allocation proportional to stratum area. We used potential natural vegetation, grouped by the dominant tree species present at climax, and LANDFIRE (LF 2014) canopy cover data (binned into intervals of 0 to < 30%, 30 to < 60%, and \geq 60%) to create the sampling strata. Potential natural vegetation represents the relatively stable end-product of succession that is in equilibrium with its environment, and thus is a biologically useful index of factors that influence plant ecology (Cooper et al. 1991).

The cumulative amount of solar radiation a site receives regulates plant photosynthesis and influences soil moisture levels, therefore, we distributed sampling locations across the range of solar radiation present within each GMU. The cumulative

amount of solar radiation from May 1 to August 31 was calculated per pixel using the ‘area solar radiation’ tool in ArcMap 10.3 (ArcGIS 10, ESRI, Redlands, CA). Solar radiation values within each stratum were grouped into high, medium, and low bins, and sampling locations were equally allocated among bins. Sampling consisted of line transects ($n = 235$) that were 180 m in length with random starting points and directions. We occasionally made adjustments in the field due to terrain features (e.g., cliffs) or when a transect extended beyond a stratum boundary.

We estimated shrub crown volume as an index to the biomass of current annual growth (CAG) of shrubs (Peek 1970, Bonham 1989). To evaluate this relationship in our study system, we collected and oven-dried CAG for 34 willow shrubs, and despite including shrubs collected throughout our study region, crown volume was strongly correlated with biomass of CAG ($R^2 = 0.74$, $n = 34$). Each transect included 4 circular plots with a 2-m radius (12.56 m^2) placed every 60 m, within which we took 3 measurements of each shrub to estimate crown volume: height, longest canopy diameter, and canopy diameter perpendicular to the longest diameter. Measurements were to the nearest centimeter and when the density of a shrub species was high (≥ 20 shrubs per plot), the average crown volume of a representative subsample of shrubs ($n = 5 - 14$) was multiplied by the total count. We also recorded canopy cover directly over each plot using a densiometer and qualitatively assessed the browsing intensity of CAG for each shrub as none, low, moderate, or high.

The second stage of field sampling was accomplished in 2016, when we adapted our sampling design to target forage species based on preliminary analyses of fecal pellets (see ‘Diet composition and selection’ below) and shrub data collected during 2015. To improve sampling efficiency, we shortened transect length to 90 m and placed plots at 30 m intervals.

In addition, we only recorded the shrub diameter that was perpendicular to the longest diameter because this single measurement was strongly correlated with shrub volume across all forage species (mean $R^2 = 0.92$, range 0.86 to 0.98).

Because most forage species were associated with open-canopy forests, we identified potential sampling locations by converting a LANDFIRE canopy cover raster to polygons after reclassifying it to only include open-canopy forests (< 50% closure). Open-forest sampling polygons were attributed with environmental data including percent shrub cover, fire history (i.e., burned or not since 1985), elevation, potential natural vegetation, and aspect. We used ArcGIS 10.3 to create spatially balanced starting points with random transect bearings. We chose a spatially balanced design because these designs increase the information yielded per sampling unit by maximizing spatial independence among samples and distributing sampling effort across the population (Theobald et al. 2007). We compared histograms of environmental covariates for the selected sampling polygons to histograms for all polygons within the GMU to verify that we were sampling from the entire range of each covariate. A total 386 transects were completed in 2016 for a combined 2015-2016 total of 621 transects.

Diet composition and selection

To identify forage species we collected fresh fecal samples for microhistological analyses to estimate summer diet composition. We collected fecal samples opportunistically during vegetation surveys between late July and late September. Because vegetation surveys were distributed across the study regions in a spatially balanced manner, fecal samples were collected from across the GMUs. We only collected samples from adults based on pellet size, and we avoided collecting multiple samples from the same transect or area to avoid

repeat samples from the same individuals. Sex for each sample was unknown, but we assumed that diets did not differ markedly between sexes (Dungan and Wright 2005). Samples were analyzed by the Micro Composition Laboratory in Boulder, Colorado. Each sample was viewed 60 times (20 views per slide) and identification was made to the species level when possible. Minor forage species that comprised < 3% of the diet were excluded from analyses as these shrubs were typically low quality, had high availability, and were likely consumed casually without strong selection or avoidance. In addition, *Prunus* spp. were not differentiated in the samples, however, we assumed all *Prunus* species in the samples were bittercherry, as the only other *Prunus* spp. within the study area (chokecherry, *P. virginiana*) was very rare.

Relative selection for each forage species was evaluated using Ivlev's electivity index (Ivlev 1961) to compare use and availability. We estimated the proportion of each forage species within the diets from microhistological analyses (corrected for indigestibility). We defined availability of forage shrubs as the proportion of a circular buffer (500-m radius) surrounding the location where the fecal sample was collected in which a shrub species was predicted to occur. The buffer size was estimated as the area used by moose during the time between forage ingestion and defecation. Rumen turn-over times for moose were estimated to be 12.4 hours and 19.3 hours (Renecker and Hudson 1990). Location data from radio-collared moose in GMU10 (IDFG unpublished data) indicated that moose used areas of approximately 0.75 km² (approx. 500 m in radius) over a 24-hour period in summer. Ivlev's electivity index (E) was calculated for each diet sample according to equation 3;

$$E_i = \frac{(r_i - n_i)}{(r_i + n_i)} \quad (3)$$

Where E_i is the electivity index value for forage species i , r_i is the proportion of forage species i in the diet, and n_i is the proportion of forage species i within the availability buffer. Electivity values range from -1.0 to 1.0 with negative values indicating relative avoidance, and positive values indicating relative selection. Shrubs were categorized as selected, used, or avoided if bootstrapped confidence intervals at the GMU level for mean electivity values were > 0 , overlapped 0, or < 0 , respectively.

Forage quality

Forage species were ranked based on their relative digestible energy (DE) and digestible protein (DP) values. We collected 220 samples of CAG during the 2015-16 field seasons, and stored them at -20° C until they were freeze-dried and ground in a cyclone mill with 1.0-mm screen. We separated leaves and stems for analyses because nutritional parameters can differ between plant parts. Ground samples were composited by species, plant part, and GMU, thoroughly mixed, and stored in airtight containers at room temperature. To estimate DE (kJ/g) and DP (g per 100 g of forage) of browse samples, we first measured cell wall constituents (%) using sequential fiber analyses (Van Soest 1967) and crude protein (%) using combustion (AOAC 2005) at commercial lab (Dairy One, Ithaca, NY). Fiber analyses were modified for tanniferous browse by including sodium sulfite (Hanley et al. 1992). Tannin protein-precipitating capacity (mg/mg forage dry matter, Martin and Martin 1982) was assessed at the Wildlife Habitat and Nutrition Lab (Washington State University, Pullman, WA). Digestible protein (DP) and digestible dry matter (DDM) for each forage species were estimated with equations 1 and 2, respectively, from Hanley et al. (1992);

$$Z = -3.87 + 0.9283X - 11.82Y, \quad (1)$$

where Z = digestible protein, X = crude protein content ($6.25 \times$ total N) as a percent of dry matter, and Y = tannin protein-precipitating capacity;

$$D = [(0.9231 e^{-0.0451 A}) (NDF)] + [(-16.03 + 1.02 NDS) - 2.8 P], \quad (2)$$

where D = digestible dry matter (g per 100 g of forage), A = lignin plus cutin content as a percentage of neutral detergent fiber, NDF = natural detergent fiber in percent, NDS = neutral detergent soluble ($1 - NDF$), and P = reduction in protein digestion ($11.82 \times Y$ term in Eq. 1). We used published gross energy (GE, kJ/g) values from Golley (1961) to calculate digestible energy ($DE = GE \times DDM$) because GE for leaf and stem material vary little among species.

We categorized shrub species as high, moderate, or low energy based on their estimated DE relative to daily energetic costs for a non-lactating, non-pregnant female moose in summer. Energetic costs for non-lactating and non-pregnant moose were used because all forage species fall short of DE costs for lactating and pregnant females based on reported mean intake values. Grouping shrubs based on energetic costs was used only to develop a relative ranking of the forage species, and we acknowledge that reproductive females can respond to negative energy budgets by increasing intake and undergoing physiological changes to improve digestive efficiency (Barboza and Bowyer 2000). A daily energetic cost of $820 \text{ kJ/kg BW}^{0.75}$ was approximated for July through October based on free-ranging females in Alberta, Canada (Renecker and Hudson 1988). Estimated dry matter forage intake during summer for moose ranges from 116 to $142 \text{ g/kg BW}^{0.75}$ per day (Renecker and Hudson 1985, Schwartz and Renecker 1997). We used the mean value of dry matter intake ($129 \text{ g/kg BW}^{0.75}$) to calculate the mean DE in kJ/g needed to meet daily energetic costs. We estimated that 10.88 kJ/g of DE are needed to meet daily energetic costs after correcting for

energy lost to urine and methane (18% loss; Robbins 1993) and an efficiency coefficient of 71% (Hubbert 1987). Shrubs were then ranked as high, moderate, or low energy if their composited leaf DE was greater than 11.30, between 10.45 and 11.30, or less than 10.45, respectively.

Shrubs were categorized by digestible protein (DP) based on estimated protein intake needed to offset daily metabolic fecal nitrogen (MFN) and endogenous urine nitrogen (EUN) losses for a female moose in summer. We assumed an average body mass of 350 kg (Houston 1969) and summer dry matter daily intake of 129 g/kg BW^{0.75} (Renecker and Hudson 1985, Schwartz and Renecker 1997). Metabolic fecal nitrogen was estimated to be 5.06 g N/kg dry matter intake (Schwartz et al. 1987, Robbins et al. 1987) and EUN was estimated to be 56 mg N/kg^{0.75} per day (Schwartz et al. 1987). The DP needed to offset the loss was calculated to be 4.30 g/100g (4.3%) dry matter including an efficiency coefficient of 0.80 (Robbins 1993). If the DP value of a shrub was insufficient to offset N loss (i.e., < 4.3%) it was categorized as low in protein. A shrub was categorized as moderate or high in protein if the DP value was between 4.3 and 6.5%, or > 6.5%, respectively.

Shrub models for forage quantity

We constructed models for predicting shrub presence and volume across the landscape by first creating 10-m diameter buffers around each transect and attributed the covariates listed in Table 2. Lasso regression (Tibshirani 1996) was implemented using the R package ‘glmnet’ (Friedman et al. 2010) to model shrub species presence and the package ‘gamlr’ (Taddy 2015) was used to fit gamma models for shrub species volume. K-fold cross-validation (K = 10) was used to maximize the area under the curve (AUC) of the receiver-operating characteristic (ROC) curve for presence models and to minimize mean square error

(MSE) for volume models. We re-fit each model 30 times to assess stability of model fit statistics. The R package ‘PresenceAbsence’ (Freeman and Moisen 2008) was used to optimize presence-absence thresholds and estimate predictive accuracy and Cohen’s Kappa (Cohen 1960). Thresholds for each forage species were selected so that specificity equaled sensitivity in an effort to neither under- nor over-estimate the presence of moose forage.

To apply our models to GMUs, Ecognition software (Trimble Inc., Westminster, CO) was used to divide each GMU into polygons based on similarities in spectral signatures between pixels for 1-m aerial imagery (NAIP 2015). Polygons were attributed with covariate data (Table 2) using the ‘zonal statistics’ tool in ArcMap, and shrub presence and volume were predicted for each forage species using the ‘glmnet’ (Friedman et al. 2010) and ‘gamlr’ packages (Taddy 2015) in Program R.

Changes in forage quantity

We estimated current forage quantity across all GMUs in northern Idaho in 2016 and compared current values to estimates based on forest conditions in 1984. In addition, we identified areas of recent disturbance from 2011 to 2016 1) to correct estimates of current forage due to the delay in establishment of shrubs following recent disturbance; and 2) to estimate the forage trajectory (i.e., increasing, stable, or decreasing) for each GMU. For example, if a large proportion of a GMU burned in recent years, then forage quantity is likely to increase over time, however, current forage quantity would be overestimated by shrub models in the short term. In contrast, if little recent disturbance has occurred, then stable or declining amounts of forage would be expected in the near future. Many of the covariates used to predict shrub presence and volume would not change, or were nearly constant, through time (e.g., elevation, aspect, soil conditions, and temperature and precipitation 30-

year normals); however, tree canopy cover was likely to change over time due to forest succession or disturbance. We used image differencing and thresholding to detect changes in tree canopy (Nelson 1983) via changes in reflectance from 1984 to 2011 and from 2011 to 2016. Erdas Imagine image analysis software (Hexagon Geospatial, Norcross, GA) was used to convert 1984 and 2011 (Landsat 5 TM), and 2016 (Landsat 8 OLI), imagery to exo-atmospheric reflectance to account for differences in the earth-sun distance, sun angle, and the amount of solar irradiation between the image acquisition dates. Relative atmospheric correction (Hall et al. 1991) was conducted prior to calculating differences in reflectance.

Because changes in reflectance in the green band were negatively correlated with the amount of tree cover, we used changes in reflectance in the green band as an index to changes in tree canopy cover. We back-calculated tree canopy cover for 1984 by either adding to, or subtracting from, tree canopy cover values from the 2011 National Land Cover Database (NLCD 2011) based on the magnitude and direction of change in the green band. If little change was observed, no correction was made, but if moderate or large change occurred, canopy cover was either increased or decreased (depending on the direction of change) by 35% (moderate change) or 75% (large change). Selection of the 35% and 75% values were based on the rate at which conifer encroachment typically occurs. For example, based on field data, a 30-year old disturbance (e.g., logging clearcut) has typically regenerated into a fairly closed canopy forest, hence a correction factor of 75% for pixels that changed markedly in reflectance. Threshold values of change in the green band corresponding to none, moderate, or large change were determined by adjusting each threshold and visually comparing estimated tree canopy cover to the 1984 imagery. The resulting tree canopy cover layer matched with visual estimates of tree cover (Figure 3). To

correct canopy cover values for 2016 forest conditions, a similar process was used to update the 2011 NLCD tree canopy cover by assigning “0” values for recently disturbed areas; however, no attempts were made to account for forest succession due to the relatively short time period (2011 to 2016). The covariate, time since fire, also was corrected for conditions in 1984 and 2016 before shrub presence and volume models were re-fit using the same procedures described previously. Finally, 2016 estimates of forage quantity were corrected for recent disturbance by subtracting the estimated increase in forage from 2011 to 2016.

Population trend and productivity

The Idaho Department of Fish and Game has monitored moose populations in northern Idaho using several sources of data (including harvest statistics, aerial counts, and field observations; Toweill and Vecellio 2004) to index population growth and decline. We summarized these data by GMU to estimate population trends across northern Idaho from 1984 to 2016. The number of harvest permits offered for moose in northern Idaho in 1984 was relatively low (97 permits) and gradually increased, peaking in 2007 at 602 permits before declining to 431 in 2017. We created a qualitative population trend index by assigning integer values to each GMU based on changes through time in harvest success, the number of days hunted, and the number of permits offered (Table 3). Declining harvest success, increasing number of days hunted, and declining permit numbers suggest population declines in Idaho (IDFG unpublished data) and Montana (DeCesare et al. 2014). Assigned values were summed across data sources for each GMU for an overall population trend index value, which ranged from -5 to 5, with strongly negative values suggestive of population declines, whereas values near 0 suggest relative stability, and strongly positive values suggest an increasing population trend. Current population productivity was indexed for each GMU

as the number of moose harvested from 2011 to 2016 per km² multiplied by a rescaling factor of 1,000. We evaluated correlations between each population performance index and forage quantity metrics to test for significant relationships.

Results

Diet composition and selection

We collected 43 fecal samples (27 in GMU3 and 16 in GMU15) for diet composition and selection analyses. Proportions of grasses and forbs, shrubs, and conifers that occurred in fecal samples differed between the GMUs. GMU15 had substantially more grasses and forbs, less shrubs, and less conifers than GMU3. Within the shrub component of the diet, however, composition and proportions within diets were not significantly different based on bootstrapped 95% confidence intervals.

Moose consumed a variety of forage shrub species ($n = 20$), however, the number of shrubs that occurred frequently in the samples, and that were consumed in relatively high amounts in the diet, were relatively few. A total of 11 shrub species occurred in at least 14% of all fecal samples. The mean dietary proportion among these shrubs was 15%, and the most dominant shrub species consumed, based on occurrence and mean dietary proportion, were willow spp., bittercherry, mallow ninebark, ceanothus spp., and alder-birch spp. Of these, 3 shrubs (willow spp., bittercherry, and mallow ninebark) occurred in > 60% of the diets (Figure 4). Although ceanothus spp. were documented in only 1/3 of the samples, it comprised 24% of those diets on average. Similarly, Pacific yew occurred in only 12% of the samples, but it comprised 21% of those diets on average. Western red cedar and western hemlock were found in 9% and 7% of the samples, respectively and were the only conifer species with a dietary proportion > 3%. Other shrubs that occurred infrequently and had a

dietary proportion < 3% included Labrador tea (*Ledum groenlandicum*), Rocky Mountain maple, oceanspray, serviceberry, Oregon grape (*Mahonia repens*), and black hawthorn (*Crataegus douglasii*). Browsing intensity of shrubs varied, with redstem ceanothus receiving the heaviest use (> 70% of sampled shrubs were browsed), and thimbleberry received the least browsing (< 15% of shrubs sampled). Evergreen ceanothus was browsed substantially less than redstem ceanothus where 30% versus 70% of shrubs showed evidence of browsing.

Relative selection for shrubs varied among forage species based on predicted availability within a 500-m buffer around collection sites for fecal samples. Although confidence intervals for mean electivity values overlapped zero for about half of the shrub species (Figure 4), alder-birch spp. was significantly selected, and bittercherry, snowberry, and Pacific yew were significantly avoided. Other common forage species were consumed in proportion to their availability; however, electivity values for ceanothus spp., redosier dogwood, honeysuckle, and willow spp. were > 0, and values for mallow ninebark and thimbleberry were < 0. Selection or avoidance of forage shrubs typically was not correlated with the mean dietary proportion. For example, although alder-birch spp. were significantly selected, mean dietary proportion for this category was roughly equal to the mean dietary proportion across all shrubs consumed. Only snowberry was both significantly avoided and consumed significantly less than other shrubs (Figure 4).

Diet quality

Forage species consumed by moose in northern Idaho varied in leaf DE, and only half of forage species had the DE required to meet estimated energetic costs during summer based on a mean summer intake rate. The overall mean DE values for leaves (10.94 kJ/g dry

matter, range = 9.62 – 12.89 kJ/g) was about 50% higher than for stems (7.04 kJ/g dry matter, range = 5.06 – 9.50 kJ/g). Because the summer diets of moose consist primarily of leaves, we evaluated diet quality relative to summer energetic costs based on DE for leaves. Fifty percent of forage species were below the estimated DE threshold of 10.88 kJ/g dry matter needed to meet daily energetic costs during summer (Table 4). Species consumed by moose that were categorized as high-energy forage ($DE > 11.30$ kJ/g) were redosier dogwood, pacific yew, evergreen ceanothus, and redstem ceanothus. Moderate-energy forage (11.30 kJ/g $> DE > 10.45$ kJ/g) were bittercherry, mallow ninebark, and thimbleberry. Forage species categorized as low energy ($DE < 10.45$ kJ/g) were alder-birch spp., willow spp., honeysuckle, common snowberry, and huckleberry spp.

Like DE, DP content differed among forage species consumed by moose in our study area, and DP of stems was lower than leaves. Mean DP of leaves (5.49%, range = 1.73 – 7.90%) was about 300% higher than stems (1.35%, range = 0 – 3.72%) on a dry matter basis (Table 4). The DP content of leaf material for 37% of forage species failed to offset estimated daily MFN and EUN losses (4.3% DP). Species that were categorized as high-protein forage were ceanothus spp., bittercherry, and alder-birch spp., and moderate-protein species were redosier dogwood, willow spp., thimbleberry and snowberry. Mallow ninebark, honeysuckle, huckleberry, and Pacific yew were categorized as low-protein forage. Forage species with high DP were bittercherry, alder-birch spp., and ceanothus spp. The relative ranking of forage shrubs based on DP differed slightly from DE in that alder-birch spp. and willow spp. were ranked higher based on protein content. Ceanothus spp. were the only forage shrub ranked as high quality under both energy and protein criteria.

Predicted current and past forage quantity

Environmental parameters successfully predicted presence of forage shrubs across the landscape, however, models predicting shrub volume performed poorly based on model fit statistics. The number of polygons generated by Ecognition software for the northern Idaho study area was approximately 12.3 million, with mean area of 2,980 m² (SD = 5,300 m²). Forage presence models ($n = 12$) constructed from field sampling transects ($n = 621$) had a mean percent predicted correct (PCC) of 75.3% (range = 70.1% - 80.5%), whereas AUC values ranged from 0.672 to 0.853 with a mean value of 0.774 and kappa values ranged from 0.130 – 0.532 with a mean of 0.340 (Table 5). Although covariates (Table 2) were informative in predicting shrub presence across the landscape, they did not explain variation in shrub volume, resulting in intercept-only models being selected by the lasso cross-validation. Therefore, we used the mean volume for each forage shrub species (Table 5) along with predicted presence to estimate forage quantity across the landscape. Within each GMU, the total area (m²) of all polygons in which a forage species was predicted to occur was multiplied by the mean volume (cm³) of that shrub to estimate the total volume within occupied polygons. This value was divided by the total area of the GMU to estimate the average volume per meter squared across the GMU.

The predicted abundance of forage species varied markedly among GMUs (Figure 5), and those populations estimated to be increasing and more productive (Figure 6) were generally associated with higher levels of forage quantity. Northern GMUs associated with western red cedar PNV (GMUs 2, 3, 5, 6, 8, 8A, 10, and 10A) had greater predicted abundance of forage ($\bar{x} \approx 3.1 \times 10^5 \text{ cm}^3/\text{m}^2$, range = $2.6 \times 10^5 - 3.9 \times 10^5 \text{ cm}^3/\text{m}^2$), whereas southern GMUs dominated by grand fir or subalpine fir PNV (GMUs 12, 14, 15, 16A, 17, 19,

and 20) tended to have less forage ($\bar{x} \approx 2.4 \times 10^5 \text{ cm}^3/\text{m}^2$, range = $1.3 \times 10^5 - 2.7 \times 10^5 \text{ cm}^3/\text{m}^2$).

The quantity of moose forage was estimated to have declined over the past 30 years in about half of the GMUs, with the greatest decreases predicted for estimates of high-energy forage species (Figure 7). Total forage declined in 12 of 21 GMUs with an average decrease of 9% (range = 2 - 18%). Within these GMUs, the mean decrease in high-energy species was 15% (range = 10 - 26%). Increases in total and high-energy forage ranged from 2 to 16% and 4 to 21%, respectively. The largest predicted increases in forage occurred in GMUs 17, 19, and 20 due to recent forest fires that occurred in the 2000s.

Correlations between population performance indices and forage parameters

Population performance indices were correlated with forage parameters, and GMUs estimated to be increasing or more productive were generally associated with higher levels of forage quantity (Figure 8). GMUs that declined in forage quantity tended to have declining population trends and lower productivity than GMUs with predicted increases in available forage (Figure 8).

Estimates of population trend and productivity index values varied among GMUs across northern Idaho (Figure 6). Most populations in the northern half of the study area were estimated to be increasing (GMUs 1, 2, 3, 4, 5, 6, 7, 8, 8A, 9), whereas the strongest declines were estimated in southern portion of the study area (GMUs 12, 15, 16, 16A, 17, 19, 20). Only 2 GMUs (GMUs 4A and 10A) were estimated to have stable populations. Population productivity also varied among GMUs and somewhat tracked the population trend index (Figure 6). Northern GMUs generally had higher estimated productivity values than southern GMUs. We excluded GMUs 17, 19, and 20 from analyses because forage

estimates in these GMUs were driven by recent large forest fires, and the population trend and productivity indices prior to 2013 would not be sensitive to such recent disturbances. In addition, these GMUs were closed to hunting in 2013, precluding incorporation of recent harvest data.

Population performance indices were positively associated with both the current (i.e., 2016) amount of forage and the change in forage since 1984. The percent change in moderate-energy forage was most correlated with population trend ($r = 0.60$), but current total and moderate-energy forage also were significantly correlated (Table 6, Figure 8). The current amounts of moderate and low-protein forage also were significantly correlated with population trend, however, the percent change in protein-based forage quantities were not. In contrast to the population trend index, the population productivity index was significantly correlated with current predicted abundance of high-protein forage ($r = 0.65$). Population productivity values also were significantly correlated with current total forage, however, the highest correlation was observed for the percent change in high-energy forage ($r = 0.68$). Significant correlations also were documented for the percent change in high and moderate-protein forage.

Forage trajectory based on recent disturbance

Overall forage quantity is expected to increase or remain stable for most of northern Idaho due to recent disturbances, however, the magnitude of change for each forage measure varied substantially among GMUs (Figure 9). Estimated changes in forage quantity between 2011 and 2016 were in response to recent disturbances that reduced tree canopy cover between those years. The largest increases are predicted for high quality forage. GMUs that

might have declining forage trajectories depending on rates of succession were those with small predicted increases (e.g., GMUs 4, 4A, 7, 8, 9, and 16).

Discussion

We employed a novel approach to estimate moose forage quantity across a large spatial extent (21,450 km²), and we documented that variation in abundance of quality forage was correlated with population performance trends, suggesting that forage might be limiting moose populations in northern Idaho. Traditional methods for estimating biomass of CAG, such as double sampling techniques (Bonham 1989) were impractical for implementation at this scale because they are time and labor intensive (Lyon 1968). By adapting established field sampling methods for implementation at large spatial scales and integrating those data with recent advancements in remote sensing analyses, we created a spatially explicit prediction of current and past quantity of forage shrubs across northern Idaho (Figure 2).

Our approach predicted that advancing forest succession across the study area over 3 decades reduced availability of important summer forage shrubs for moose. Closing forest canopies reduced the quantity of forage, especially forage with the highest nutritional value. Trends in indices of moose population change and productivity across northern Idaho were correlated with predicted quantity of forage shrubs and change in forage over the past 30 years, supporting the contention that forage might be affecting population dynamics. These results suggest that nutrition and habitat conditions unique to each GMU should be considered in evaluating strategies for understanding and mitigating factors causing population declines.

Diet selection and quality

Although both forage quality and availability influenced summer diets of moose in northern Idaho, the lack of strong selection or avoidance suggests that moose feed on the

most available forage species that also are of moderate or high quality. The only forage shrub with significant positive selection in our analyses was alder-birch spp., which had relatively high DP, but low DE values. Although Pacific yew was significantly avoided, the DE content was the highest among the forage shrubs we evaluated, which might explain its above-average dietary proportion in the 12% of diets in which it was detected (Figure 4). Significant avoidance of Pacific yew might be due in part to taxine alkaloids, which can be toxic to some animals (Wilson et al. 2001). Snowberry was significantly avoided as well as consumed in amounts less than average, in addition to having low occurrence in samples, and low DE. Bittercherry also was significantly avoided, however, it was consumed in amounts near the mean proportion, in addition to frequent occurrence in the diet, moderate DE content, and high DP content. Two types of currency can be considered with respects to wildlife nutrition, energy and protein, and whereas energy is critical for survival, energy and protein are needed for reproduction (Parker et al. 2009). In addition to high-protein demands during juvenile growth (Schwartz and Renecker 1997), protein is important for fetal growth of ungulates in late winter (Robbins 1993). Moose reproductive success in Norway varied in response to supplemented winter feed, perhaps due to changes in reproductive allocation of nutritional resources (Milner et al. 2013).

Several other shrubs were important in the summer diets of moose in our area, although significant selection was not detected. For example, ceanothus spp., which had high levels of both protein and energy, were some of the more commonly consumed forages, but confidence intervals for electivity overlapped zero (Figure 4). Similarly, other shrub species that comprised some of the largest portions of the diets, like willow spp. and mallow ninebark, also were not selected, however, these species were highly available and

consequently, even relatively high use did not result in a strong signal of selection. Both of these species exhibited moderate values for one of the quality parameters and low values for the other (Table 4). Ungulates that are browsers typically select higher quality forage, have a higher feeding frequency, and more rapid passage of digesta than grazers (Hofman 1985). Moose are the largest browser, and therefore, they require a greater absolute volume of forage compared to smaller browsers such as mule deer. Consequently, moose likely face a tradeoff between selecting the highest quality forage and maximizing intake. A review of the foraging ecology of moose by Shipley (2010) showed that moose tend to balance forage quality with increased quantity in order to maximize DE intake. Therefore, quantity, even of moderate quality species, might influence foraging behavior of moose in northern Idaho. Moose in our study area might be selecting feeding areas based on overall forage quantity, and subsequently, selecting relatively higher quality species available within the feeding area. Similar patterns of selection have been documented for moose in other studies (Van Beest et al. 2010). Bite size also is important, with moose typically selecting large bites (Shipley 2010), therefore, forage species that offer small bites such as common snowberry, huckleberry, grasses, and forbs are likely to be selected less when shrubs that allow more efficient foraging are available.

Forage selection by moose during summer also might reflect thermal constraints in habitat use that result in greater consumption of shade-tolerant species or lower quality shrubs. Our study area is near the southern portion of the distribution of moose in North America, and there is growing evidence of warm temperatures influencing habitat selection during summer (Street et al. 2015, Milner et al. 2013, McCann et al. 2013, Muir 2006, Dussault et al. 2004). *Ceanothus* spp. were high in both protein and energy, and although

consumed by moose, they were not strongly selected. However, based on field observations and our change detection analysis, it also is one of the least shade-tolerant forage shrubs that we detected in the diets of moose in our study area. Therefore, if moose are selecting areas of thermal refuge, typically associated with closed-canopy forests (Milner et al. 2013, Muir 2006), such shrubs might not be available. This might also explain the higher degree of selection documented for alder-birch spp., which are more shade tolerant than ceanothus spp. and prefer areas with moist growing conditions that might be used for thermal refuge. Although the two species of ceanothus were not differentiated by the diet analyses, both had similar DE and DP values. Redstem ceanothus received more summer browsing than evergreen ceanothus (70% versus 30% of shrubs showed evidence of browsing). Evergreen ceanothus appeared to be browsed more heavily in winter, and given that it is an evergreen shrub with relatively high protein and energy content, it might be an important source of energy and protein for moose during winter when thermal constraints would not limit use of open-canopy habitats. Less browsing of evergreen ceanothus in summer might be due to terpenes (Countryman 1982), which inhibit browsing by some herbivores (Vourc'h et al. 2000).

Forage estimates and trends across the landscape:

Our aim of modeling forage quantity for moose across a broad spatial extent (21,450 km²) necessitated an approach that maximized predictive accuracy and could easily be applied to the 12.3 million polygons that comprise the study area. We chose lasso regularized regression in part because of its ability to perform variable selection by constraining the sum of the absolute value of the coefficients to being less than some constant. This was advantageous because we had many possible covariates in relation to our

sample size. We also chose lasso because our primary objective was to maximize predictive accuracy to compare relative forage quantity among GMUs, and the lasso approach has been shown to improve predictive accuracy over ordinary least squares by sacrificing some bias (Tibshirani 1996). The R package “glmnet” was used to fit models that minimized prediction error via cross-validation and to predict shrub presence for the 12.3 million polygons that comprise the study area. Although shrub volume models were not predictive, shrub presence models performed reasonably well based on fit statistics. Shrub presence models had fairly high predictive accuracy ($\bar{x} = 75.3\%$, range 70.1% - 80.7%; Table 4) and the kappa statistic varied from slight to moderate accuracy ($\bar{x} = 0.340$, range 0.130 – 0.532), where values from 0.00 to 0.20, 0.21 to 0.40, and 0.41 to 0.60 confer slight, fair, and moderate accuracy after accounting for the probability of chance agreement (Landis and Koch 1977). The AUC values ($\bar{x} = 0.774$, range 0.672 – 0.853) indicated moderate to high confidence in results (Swets 1988).

Predicted 2016 forage quantity varied considerably among GMUs (Figure 5) and was generally higher for northern GMUs of western red cedar and western hemlock PNV series. These series are associated with high levels of soil moisture and are the 2 most productive series in northern Idaho for timber (Cooper et al. 1991). Growing conditions that contribute to high timber productivity likely also contribute to shrub productivity, as suggested by these results. GMUs predicted to have lower amounts of forage were associated with grand fir or subalpine fir PNV series. The grand fir series occurs at drier sites where the more moisture dependent western red cedar and western hemlock series cannot, and it can significantly overlap the subalpine fir series, where the latter is more shade tolerant and associated with colder, less productive sites (Cooper et al. 1991). The relationship between shrub

productivity and PNV might persist beyond northern Idaho where similar PNV series occur, such as western Montana.

Predicted changes in forage since 1984 also varied considerably among GMUs (Figure 7) with declines in forage predicted across the study area. Over 80% of GMUs (10 of 12) predicted to have lost forage consisted predominately of national forest land. GMUs where forage was predicted to have declined the most (GMUs 3, 4, 4A, 10, 10A) were associated with western red cedar and western hemlock PNV series, which could be due to the high productivity of these habitat types advancing forest succession at a relatively faster rate.

We made several simplifying assumptions in modeling forage quantity across the landscape. First, because we could not address potential variation in size of shrubs across the study area, we assumed mean size of forage shrubs together with predictions of shrub presence for estimating volume of potential forage. Inclusion of variation in shrub size would likely improve estimates of forage volume and contribute to greater variation in forage quantity estimates among GMUs, however, such variation is probably a minor factor in comparison to accurately predicting occurrence of shrub species at this spatial scale. Nonetheless, estimated differences among GMUs are likely to be conservative. Second, predicted forage values for all 21 GMUs were derived from shrub presence models constructed with field data from 3 GMUs. The 3 sampled GMUs were selected to represent the range of environmental variation across the broader northern Idaho study area, however, increased uncertainty is unavoidable when predicting beyond the sampled populations. Finally, although we conducted cross-validation to assess model fit, we did not collect additional field data to validate model predictions. We recognize this limitation and interpret

our forage predictions with caution. Nonetheless, predicted forage quantity and change in forage over time were strongly correlated with population performance metrics. Our results suggest that at a coarse resolution, forage quantity varies across the region in a predictable way and that availability of forage is associated with variation in performance of moose populations in northern Idaho.

Correlations between population performance indices and forage parameters

Correlations between forage parameters and the population trend index differed from correlations with the productivity index (Table 6). Significant correlations suggested that population trend was most strongly influenced by the percent change in moderate-energy forage from 1984 to 2016, in addition to the current (i.e., 2016) amount of moderate-energy and moderate-protein forage shrubs. We predicted that population trend would be positively associated with the percent change in high-energy forage, however, only the correlation with the percent change in moderate-energy forage was significant. We also predicted that population trend would be positively associated with the current amount of high-energy forage, but once again, the current amount of moderate-energy forage exhibited the stronger relationship. Additionally, the current amount of moderate and low-protein forage, but not high-protein forage, was significantly correlated with population trend. These results suggest that availability of moderate-energy and moderate-protein forage was associated with relative differences in population trends among GMUs. This pattern might indicate that a large amount of moderate-energy and moderate-protein forage buffers populations against declines. In addition, the percent change in moderate-energy forage had the highest correlation, highlighting the importance of maintaining availability of these forage shrubs

through time. Finally, because moose likely need to balance forage quantity with quality, highly available shrubs of moderate quality are likely to influence population trends.

Although high-quality forage was not as strongly correlated with population trend as predicted, it was strongly associated with estimated population productivity. Population productivity index values were most strongly related to change in high-energy forage, and in contrast to population trend, productivity also was correlated with the current quantity of high-protein forage (Table 6). Total forage quantity also was highly significant in addition to the percent change in all forage parameters except the percent change in low-protein forage. These results align with predictions and suggest that current productivity was influenced by both current forage quantity, particularly the quantity of high and moderate-energy and high-protein forage, in addition to the percent change in forage, particularly the change in high-energy and high-protein forage.

These results suggest differences in the relationships between population performance indices and forage parameters. High-protein and high-energy forage was more strongly associated with population productivity, whereas high-protein based forage parameters were not strongly associated with population trend. Adequate amounts of energy are needed to meet the challenges of survival, however, energy and protein are both important for reproduction, which could explain why protein was not more strongly associated with population trend, whereas energy and protein were both strongly associated with productivity. Nonetheless, because harvest data can be insensitive to short-term changes in population performance, results of correlations between forage metrics and population performance indices should be considered qualitative assessments of the relative influence of forage metrics on population trend and productivity.

Although results provide compelling evidence that forage could be limiting moose in northern Idaho, behaviorally mediated effects also might be influencing performance. Behavioral tradeoffs between time spent in foraging areas and thermal cover could occur during times of heat stress. Moose are large bodied and have low sweating capability (Schwartz and Renecker 1997), and therefore must resort to energetically expensive panting and behavioral responses for thermoregulation (Schwab and Pitt 1991). Behavioral responses, such as seeking shade, or foraging only at night might not fully negate such a tradeoff due to limitations in rumen capacity and passage rates. Moose also might avoid quality foraging areas if those areas have high predation risk (Dussault et al. 2005) or high human activity (Lykkja et al. 2009).

Predicted forage levels based on disturbances that occurred between 2011 and 2016 were used to correct 2016 estimates of forage quantity as well as to suggest increasing, stable, or declining forage levels for comparison among GMUs (Figure 8). The change detection analysis between 2011 and 2016 was only used to account for recent disturbances (e.g., timber harvest or forest fires), and we did not attempt to account for forest succession given the short time period. Because most forage shrubs are associated with relatively open tree canopy, forage was predicted to increase. Due to the delay in recruitment and growth of shrubs following disturbance, results should be interpreted as the potential forage trajectory; however, the trajectory for a GMU depends on both the areal extent and rate of disturbance (indexed here), and the areal extent and rate of succession during the same time period (not quantified in this study). The response of high-energy forage species to changes in tree canopy cover was more elastic than medium or low-quality species in most GMUs (Figures 6

and 9), which supports previous findings that maintenance of early seral shrub communities are needed to retain high-quality forage species (Fischer and Bradley 1987, Arno et al. 1985).

Results from this study can be used to prioritize GMUs for habitat management with the goal of improving forage conditions for moose in northern Idaho. Results suggest that the quantity of moderate and high-energy forage are important in maintaining productive and stable populations. Ceanothus species were high in both DE and DP and were the most sensitive to increases in canopy cover, and therefore, reoccurring disturbance is needed to maintain these species. Redstem ceanothus regeneration is largely dependent on fire (Mitchell 1983, Orme and Leege 1976). Both species of ceanothus seeds require heat treatment from fire in order to germinate properly or they will remain dormant (Gratkowski 1973, Gratkowski 1962). Redstem ceanothus remains abundant when burned every 10 – 15 years, but vigor and abundance degenerates quickly without periodic fires (Kathleen 2000). Ceanothus spp. also are nitrogen fixers (Johnson 2000, Anderson 2001) and consequently are important in maintaining soil fertility.

Other forage species of moderate-energy likely to be important based on occurrence and mean dietary proportion include mallow ninebark and bittercherry. Bittercherry sprouts vigorously following fire (Laursen 1984) and is benefitted by high-severity fires (Morgan and Neuenschwander 1988). Although highly available, bittercherry can quickly grow beyond browsing reach after several years (Esser 1995). Mallow ninebark also sprouts vigorously following fire (Habeck 1992) and remains a predominate shrub in late-seral vegetation communities (Steele and Geier-Hayes 1989). Willow spp. (predominately Scouler's willow) although low in DE, were the most commonly consumed species in the diets, and moose exhibited greater selection for them than bittercherry or mallow ninebark.

Willow spp. also were less available than bittercherry and mallow ninebark, which could be due in part to fire suppression, as Scouler's willow has higher recruitment and survival on heavily burned sites (Zasada et al. 1983). High severity fires that kill live foliage result in vigorous sprouting from the root crown (Bedunah et al. 1999), however, willows also can colonize disturbed areas via windborne seeds (Guell et al. 1982). Willow growth postfire can be rapid, especially at moist sites, reaching peak height and cover within 8 years (Stickney 1986). Finally, alder-birch spp. also might be important based on their mean electivity and dietary proportion. These spp. are frequently found in moist riparian areas such as along streams and wet meadows or seeps and can generally persist into late successional or even climax vegetation communities (Uchytíl 1989, Fryer 2011, Gucker 2012, Tollefson 2007). These species generally respond well to fire in addition to logging activities (Uchytíl 1989, Fryer 2011, Gucker 2012, Tollefson 2007). In summary, most summer moose forage species in northern Idaho are fire adapted and shade intolerant.

Conclusions

Our results indicated that availability of forage for moose varied in both quantity and quality across northern Idaho, and this variability was associated with indices of population trend and productivity. These correlations suggest that nutrition might be limiting moose populations or contributing to population declines. Research linking forage with nutrition and fitness of individuals is needed to quantify how forage might be influencing populations. We recommend that future research in moose population performance include consideration of the foraging landscape and its potential interaction with other population drivers. Not doing so could result in misidentification of proximate population drivers as ultimate. Consequently, management actions might not have the expected effects. In addition, the

relative influence of population drivers, including forage limitations, is likely to change over time and space, highlighting the need for data collected across large spatial scales and long timeframes. For example, past levels of nutrition that supported moose populations in northern Idaho might not be adequate given current environmental conditions that could include increased predation pressure (Fritts et al. 1997), heat stress (Lenarz et al. 2009), and parasite levels (Musante et al. 2007). It also is important to note that moose range and density in the recent past (i.e., 1990s), from which observed populations have declined, are unrepresentative of historical norms. Few recorded observations of moose in northern Idaho exist prior to 1900, and early explorers to the area in the 1800s did not observe moose (Toweill and Vecelio 2004). The expansion of moose populations in northern Idaho beginning in the 1950s was likely due to increasing timber harvest and large forest fires. For example, forest fires burned over 60% of the study area between 1910 and 1960 (Gibson 2005). In contrast, only about 12% of the study area burned between 1961 and 2000. Moose are colonizers of early seral habitat, and there are many examples where fire and logging were associated with range expansion (Darimont et al. 2005, Reeves and McCabe 1998) and population increases (Peek et al. 1976, Rempel et al. 1997, Milner et al. 2013). Without continued maintenance and creation of early seral vegetation communities, moose populations are likely to decline over long time periods.

Forage species browsed by moose in northern Idaho during summer are generally fire adapted and shade intolerant. Fire not only enhances recruitment and growth of these forage species, but also is a requirement for some, such as high-energy and high-protein *Ceanothus* spp. Timber harvest activities that exclude fire treatments are not likely to be as effective for establishing and regenerating these forage species. With reduced timber harvest on national

forests, and less frequent fires, maintenance of existing shrub communities in the short term might stabilize populations at current levels, while long-term objectives and strategies are established to create more early-seral habitat in the future. Maintenance using prescribed fire is likely most cost effective, especially at large spatial scales, with the added benefit of reducing fuel loads and future fire suppression costs; however, prescribed fire has some inherent public safety risks, and it can be controversial (Hesseln 2000). Mechanical disturbances using heavy equipment when terrain allows, or chainsaw crews when terrain is too rugged, are less risky options when conditions are unfavorable for prescribed burns. Both timber resources and moose forage can benefit from cutting of decadent shrubs when existing conifers are retained, so called 'conifer release' (Newton et al. 1989). Application of glyphosates in vegetation management, (reviewed by Sullivan and Sullivan 2003) for conifer release increased browse availability and moose use of treated areas 7 to 11 years post treatment compared to experimental controls; however, reductions in available forage were observed in the first few years after treatment. Habitat managers also should consider the innate productivity of sites. GMUs predicted to have a greater abundance of these shrub species tended to be those associated with western red cedar and western hemlock PNV, which have high relative timber productivity; therefore, they might require more frequent disturbance to maintain open canopy foraging areas than less productive PNV types.

Our results have important implications for management of moose habitat in northern Idaho and elsewhere. Changes in forest management over the past 50+ years have resulted in advancing forest succession that resulted in reduced abundance of quality forage available to moose in some parts of northern Idaho. GMUs managed primarily for timber production tended to have greater amounts of forage shrubs, whereas GMUs composed predominately of

national forests that are managed for multiple uses tended to have less. Land management practices, however, are not the only consideration for moose habitat management; the forage productivity potential of a GMU also warrants consideration. In addition, other population drivers that might impose higher level constraints, such as thermoregulation or predation risk, should be considered. This study highlights the importance of assessing how broad changes in land management across long time periods affect wildlife habitat and the species that depend on that habitat. This type of information is not only useful for moose management, but also can inform discussions about how best to manage limited natural resources for multiple uses and multiple objectives, including wildlife conservation.

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Tables

Table 1. Biophysical characteristics of Game Management Units (GMUs) included in analyses of forage for moose in northern Idaho, USA (excludes areas of non-moose habitat, e.g., urban areas and agriculture).

GMU	Dominant Potential Natural Vegetation (PNV) types ^a	Area (km ²)	Mean min./max. temp. (°C) ^b	Mean annual precip. (cm) ³	Elevation range (m)	Percent area with canopy cover 0 - 33%	Percent area with canopy cover 34 - 66%	Percent area with canopy cover 67 - 100%	Percent National Forest
1	TSHE/ABLA	5,200	-10 / 28	1,030	530 to 2,345	16%	32%	52%	59%
2	THPL	1,000	-7 / 28	840	625 to 1,550	35%	37%	28%	10%
3	TSHE/ABGR	1,110	-7 / 29	995	650 to 1,725	16%	27%	57%	63%
4	TSHE	3,075	-8 / 28	1,150	650 to 2,065	11%	26%	63%	70%
4A	TSHE/ABGR	400	-7 / 28	940	630 to 1,940	9%	25%	66%	87%
5	TSHE/THPL	900	-6 / 29	805	650 to 1,500	44%	37%	18%	1%
6	TSHE/THPL	2,630	-9 / 29	1,160	650 to 2,075	27%	27%	45%	42%
7	THPL/TSME	1,420	-10 / 28	1,240	755 to 2,300	14%	41%	45%	88%
8	THPL	295	-6 / 29	830	780 to 1,510	40%	37%	23%	3%
8A	THPL	1480	-7 / 31	930	395 to 1,690	29%	25%	46%	33%
9	THPL/TSME	510	-9 / 28	1,260	695 to 2,125	12%	35%	53%	79%
10	THPL/TSME/ABLA	2,980	-11 / 30	1,395	490 to 2,300	18%	39%	43%	98%
10A	THPL	3,665	-8 / 32	1,070	300 to 1,930	26%	26%	48%	25%
12	ABLA/ABGR	2,830	-12 / 31	1,230	435 to 2,580	20%	40%	40%	94%
14	ABGR/ABLA	940	-12 / 32	905	520 to 2,445	27%	45%	28%	83%
15	ABGR/ABLA	2,120	-12 / 31	865	470 to 2,435	10%	32%	58%	92%
16	THPL	850	-10 / 32	975	390 to 2,245	14%	26%	60%	89%
16A	ABGR/ABLA	690	-12 / 31	990	525 to 2,315	16%	41%	42%	100%
17	ABGR/ABLA/PSME	3,400	-13 / 31	1,050	530 to 2,845	37%	42%	21%	100%
19	ABGR/ABLA	400	-12 / 29	850	875 to 2,570	42%	47%	11%	100%
20	ABGR/ABLA	915	-13 / 29	940	980 to 2,680	32%	46%	22%	100%

^aABGR-grand fir; ABLA-subalpine fir; THPL-western red cedar; TSHE-western hemlock; TSME-mountain hemlock.

^bTemperature and precipitation data from downscaled PRISM 30-year normals (see Table 2).

Table 2. Environmental covariates used to model shrub presence and volume to estimate forage availability for moose in northern Idaho, USA.

Covariate	Description	Source
Elevation	Digital elevation model	InsideIdaho.org
Topographic wetness index	Steady-state wetness index	InsideIdaho.org
Topographic position index	Describes elevation of cell relative to elevation of specified neighborhood	Calculated from DEM using ArcGIS extension from Jennessent.com
Solar radiation	Estimated solar radiation of cell	ESRI's solar radiation tool
Sine and cosine of aspect	Decomposes aspect into north-south and east-west components	InsideIdaho.org
Heat load index	Estimates direct radiation from latitude, slope, and aspect	Calculated using ArcGIS following McCune and Keon (2002)
Available water supply	Soil water storage capacity ^a	Nrcs.usda.gov
Soil percent clay	Soil percent clay ^a	Nrcs.usda.gov
Soil percent sand	Soil percent sand ^a	Nrcs.usda.gov
Soil percent silt	Soil percent silt ^a	Nrcs.usda.gov
Soil organic matter	Soil organic matter ^a	Nrcs.usda.gov
Soil cation-exchange capacity	Soil cation-exchange capacity (measure of nutrient content) ^a	Nrcs.usda.gov
Soil depth to restrictive layer	Soil depth to any restrictive layer (cm)	Nrcs.usda.gov
Soil pH	Soil pH ^a	Nrcs.usda.gov
30-year average min precip	Downscaled from 30-year normals (1981 to 2010) from PRISM Climate Group	Prism.oregonstate.edu
30-year average max precip	Downscaled from 30-year normals (1981 to 2010) from PRISM Climate Group	Prism.oregonstate.edu
30-year average annual	Downscaled from 30-year normals (1981 to 2010) from PRISM Climate Group	Prism.oregonstate.edu
30-year average min temp	Downscaled from 30-year normals (1981 to 2010) from PRISM Climate Group	Prism.oregonstate.edu
30-year average max temp	Downscaled from 30-year normals (1981 to 2010) from PRISM Climate Group	Prism.oregonstate.edu
Percent tree cover	Percent tree cover	Nlcd.gov
Time since fire	Number of years since last fire	USFS fire history 1889 to 2015

^aSoil parameters measured in the 0-25 cm depth layer.

Table 3. Criteria used to assign trend index values for moose populations in northern Idaho, USA, based on harvest data from 1984 to 2016 for each game management unit (GMU). An overall population trend index was calculated by summing the assigned values for each data source.

Data source	Criteria				
Harvest success rate	Sustained between 80 and 100%	Increased by 20 to 39 percentage points	Increased or decreased by < 20 percentage points	Declined by 20 to 39 percentage points	Declined by \geq 40 percentage points
Assigned value	2	1	0	-1	-2
No. of permits offered	Increased \geq 300%	Increased \geq 100% but < 300%	Increased or decreased by < 100%	Increased and then declined to within 25% of historical lows	Declined below historical levels by > 25% or harvest season closed
Assigned value	2	1	0	-1	-2
No. of days hunted	Decreasing trend	Stable trend	Increasing trend or harvest season closed		
Assigned value	1	0	-1		

Table 4. Mean digestible energy and digestible protein on a dry matter basis for leaves and stems of shrubs consumed by moose in northern Idaho, USA. Gray shading indicates high-energy and high-protein forage species.

	Digestible energy (kJ/g) leaf (stem)	Digestible protein (%) leaf (stem)
Willow spp.	9.62 (7.66)	5.44 (0.39)
Mallow ninebark	10.50 (5.98)	1.73 (0.29)
Bittercherry	10.92 (6.65)	7.39 (0.58)
Alder-birch spp.	10.00 (9.50)	7.37 (3.72)
Redstem ceanothus	11.55 (6.40)	7.90 (1.08)
Evergreen ceanothus	11.63 (8.16)	6.69 (1.78)
Honeysuckle	10.25 (5.06)	4.21 (0.96)
Redosier dogwood	12.13 (8.49)	5.79 (1.35)
Common snowberry	10.41 (5.23)	5.65 (0.77)
Huckleberry spp.	10.33 (7.53)	4.02 (3.62)
Thimbleberry	11.05 (6.78)	6.37 (-0.18)
Pacific yew ^a	12.89 (NA)	2.23 (NA)

^aLeaves and stems were analyzed together

Table 5. Mean (\bar{x}) and standard deviation (SD) for the model fit statistics area under the curve (AUC) of the receiver operating characteristic, Cohen's Kappa (Kappa), and percent predicted correct (PCC) generated by iterating cross-validated lasso regression for each shrub presence model 30 times. Also reported is the mean shrub volume (cm^3/m^2) for each forage shrub.

Shrub	AUC	Kappa	PCC	Shrub Volume
	\bar{x} (SD)	\bar{x} (SD)	\bar{x} (SD)	\bar{x}
Willow spp.	0.726 (0.022)	0.348 (0.037)	0.703 (0.018)	265,145
Mallow ninebark	0.853 (0.021)	0.492 (0.045)	0.790 (0.019)	201,345
Bittercherry	0.821 (0.021)	0.398 (0.039)	0.766 (0.017)	122,097
Alder-birch spp.	0.774 (0.036)	0.200 (0.043)	0.702 (0.022)	273,675
Redstem ceanothus	0.826 (0.026)	0.335 (0.039)	0.766 (0.017)	119,574
Evergreen ceanothus	0.758 (0.026)	0.251 (0.036)	0.701 (0.018)	127,663
Honeysuckle	0.672 (0.041)	0.256 (0.046)	0.753 (0.021)	7,144
Redosier dogwood	0.776 (0.054)	0.193 (0.048)	0.807 (0.015)	111,425
Common snowberry	0.797 (0.024)	0.476 (0.043)	0.747 (0.021)	18,900
Huckleberry spp.	0.825 (0.019)	0.532 (0.034)	0.767 (0.017)	26,976
Thimbleberry	0.755 (0.020)	0.467 (0.035)	0.736 (0.018)	46,965
Pacific yew	0.703 (0.064)	0.130 (0.038)	0.798 (0.016)	20,542

Table 6. Relationships (Pearson correlation, r) between indices of moose population performance and forage volume estimates for 18 game management units (GMUs) in northern Idaho, USA. Forage volume estimates (cm^3/m^2) represent current estimates for 2016. Change estimates represent percent change in volume from 1984-2016.

Independent variable	Population trend index		Population productivity index	
	r		r	
Total forage	0.54	**	0.65	**
High-energy forage	0.43	*	0.54	**
Moderate-energy forage	0.52	**	0.55	**
Low-energy forage	0.07		0.16	
High-protein forage	0.29		0.65	**
Moderate-protein forage	0.56	**	0.32	
Low-protein forage	0.48	**	0.53	**
% Change in total forage	0.35		0.60	**
% Change in high-energy forage	0.35		0.68	**
% Change in moderate-energy forage	0.60	**	0.46	*
% Change in low-energy forage	0.14		0.57	**
% Change in high-protein forage	0.30		0.58	**
% Change in moderate-protein forage	0.10		0.54	**
% Change in low-protein forage	-0.01		-0.33	

** $P < 0.05$, * $P < 0.10$

Figures

Figure 1. Location of the study area and field sampling Game Management Units (GMUs) in northern Idaho, USA.

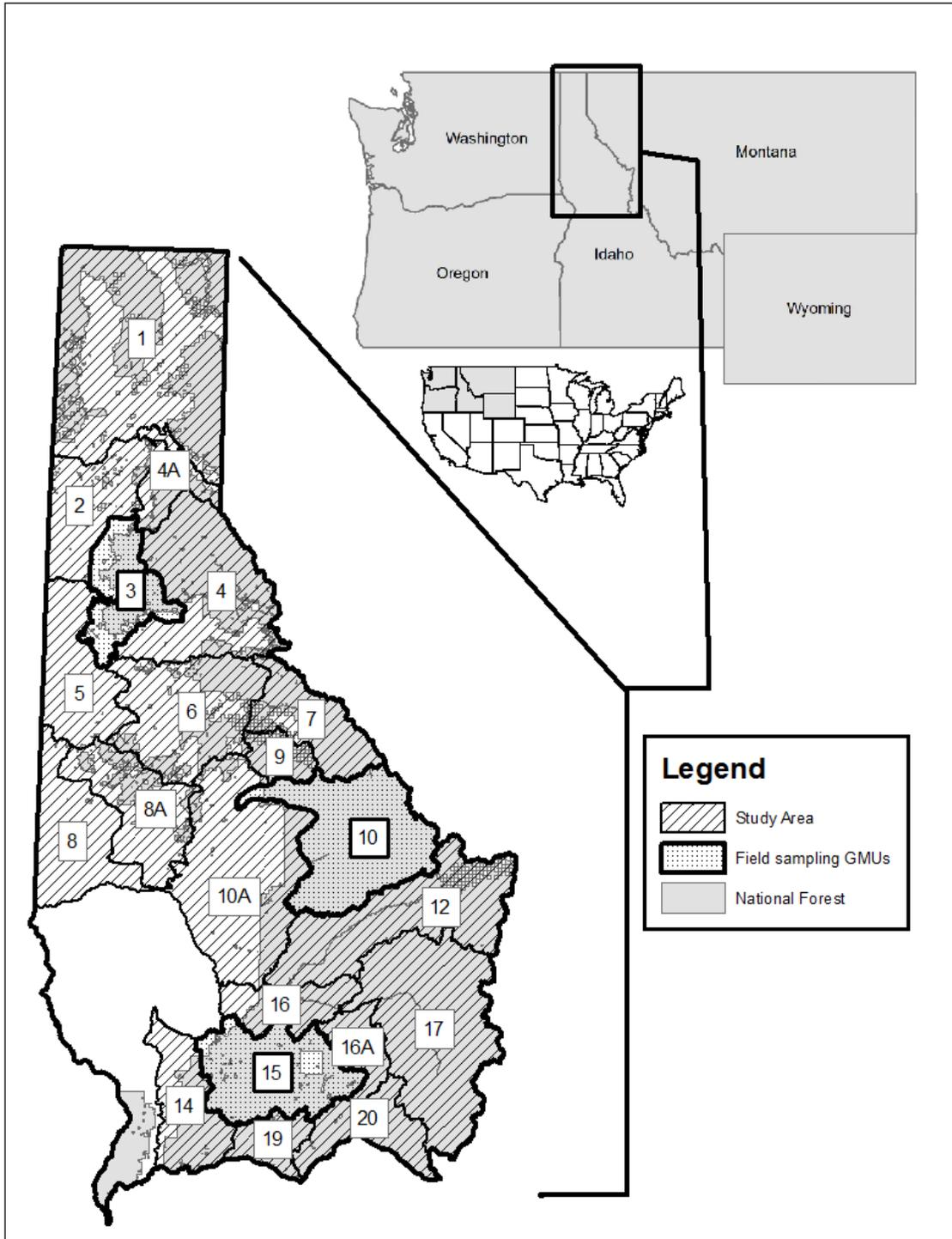


Figure 2. Data generation and processing steps for accomplishing study objectives evaluating moose forage and nutrition in northern Idaho, USA.

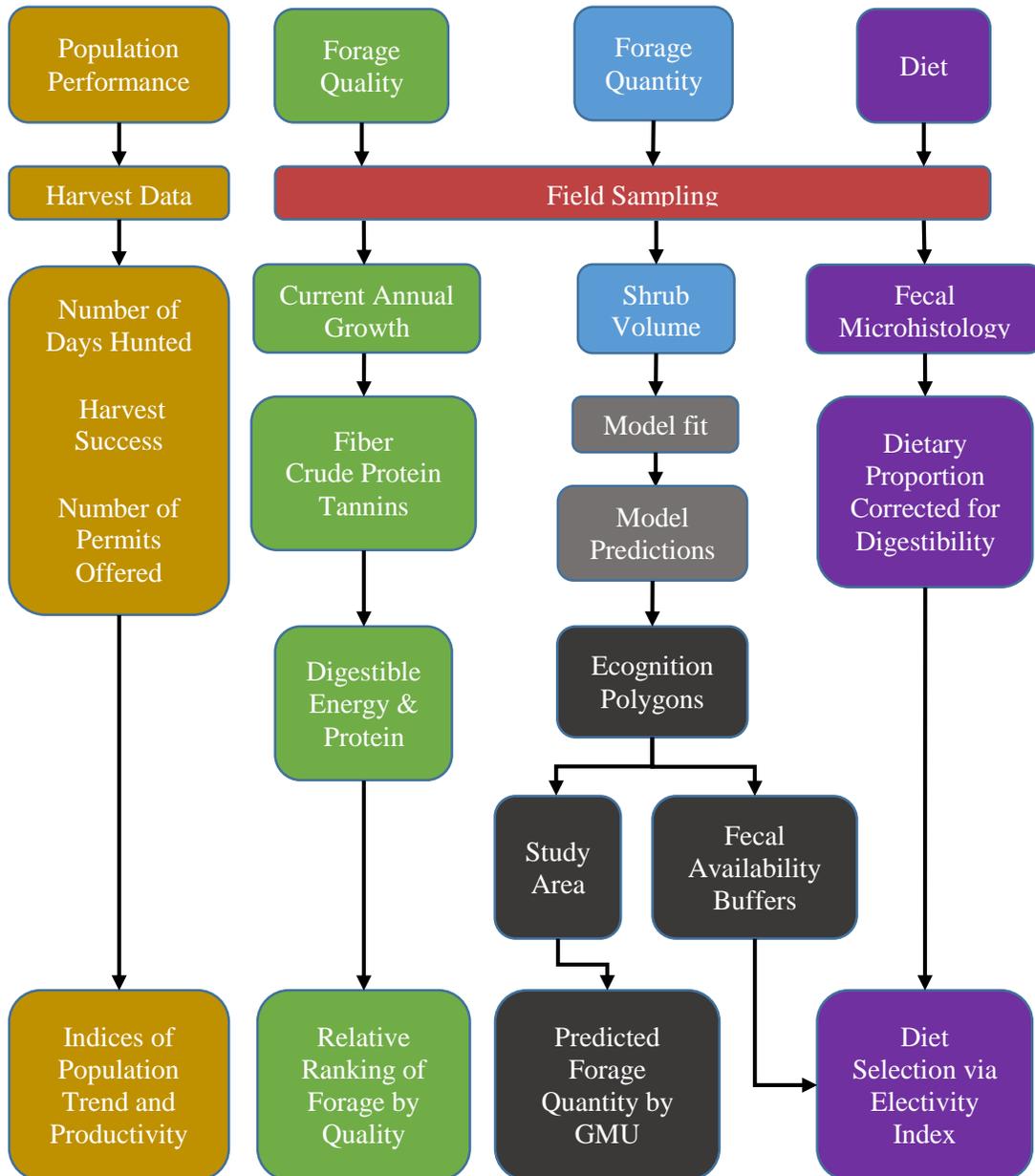


Figure 3. Visual comparison between a) 2011 Landsat 5 TM Imagery and b) 2011 tree canopy cover from the National Land Cover Database shows concordance between the data layers. Similar concordance is apparent between c) 1984 Landsat 5 TM Imagery and d) estimated 1984 tree canopy cover. Imagery scene is from GMU15 in northern Idaho, USA. Brighter pixels represent areas of decreased tree canopy.

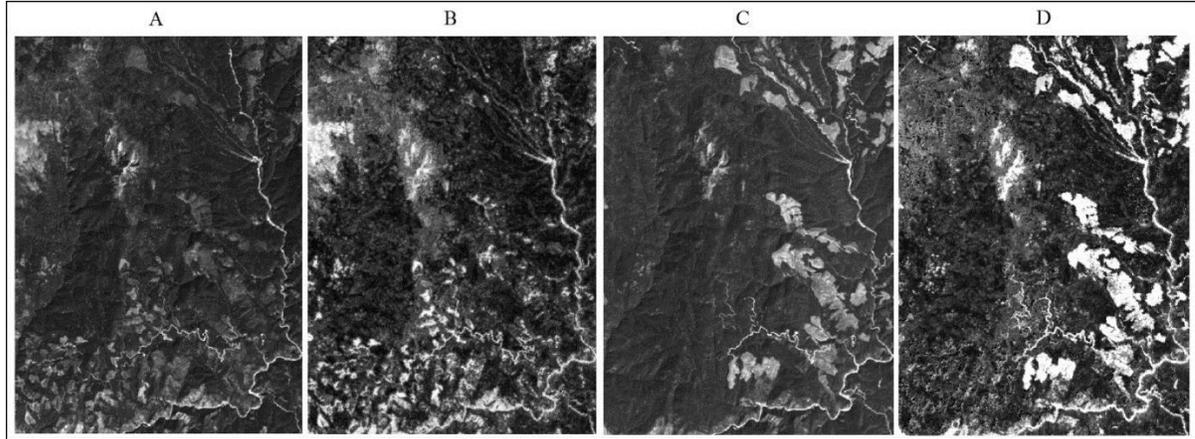


Figure 4. Mean dietary proportion and electivity with bootstrapped ($n = 1,000$) 95% confidence intervals for moose forage species identified via microhistological analyses of 43 fecal samples collected in northern Idaho, USA. Forage availability for electivity values was based on predicted forage in the 500-m buffer around sample collection sites. The vertical dashed line represents the mean dietary proportion across all shrubs and use proportional to availability (electivity = 0). Electivity index was not calculated for huckleberry spp. because predicted availability was zero for 5 of 7 diets in which it occurred.

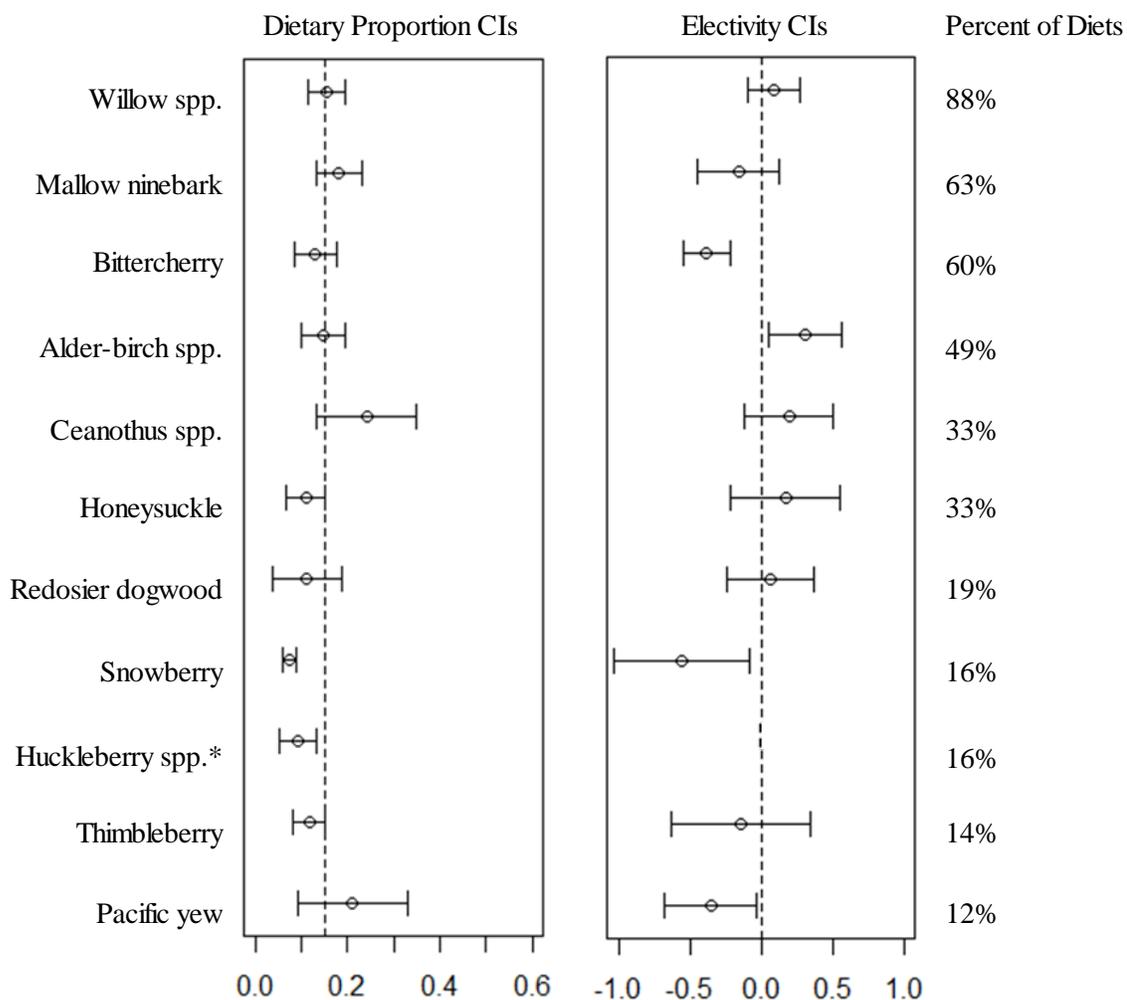


Figure 5. Estimated shrub volume (cm^3/m^2) for high, moderate, and low-energy forage shrubs in 21 Game Management Units (GMUs) in northern Idaho, USA, in

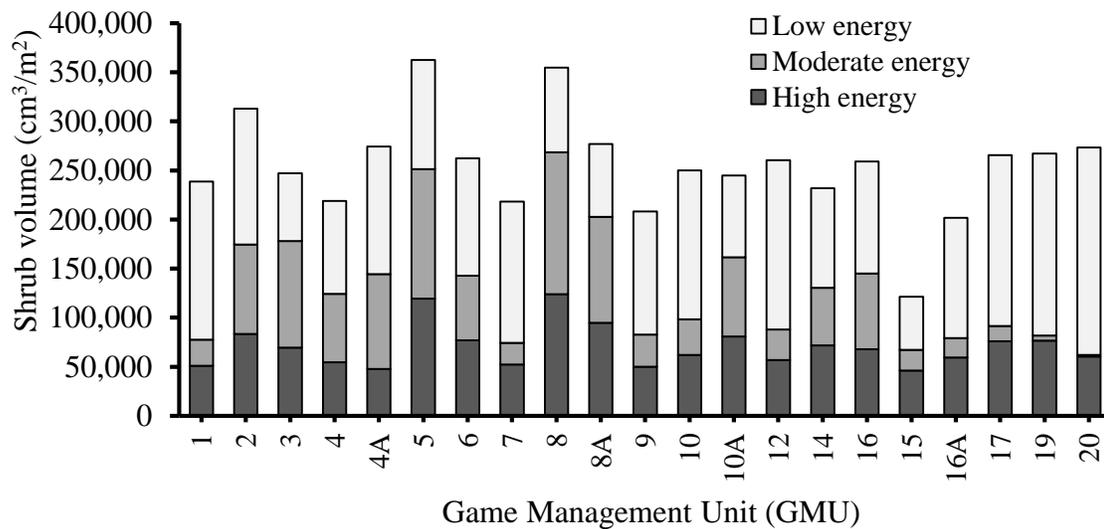


Figure 6. Spatial distribution of moose population trend and productivity index values estimated from harvest and management data since 1984 for 21 Game Management Units (GMU) in northern Idaho, USA.

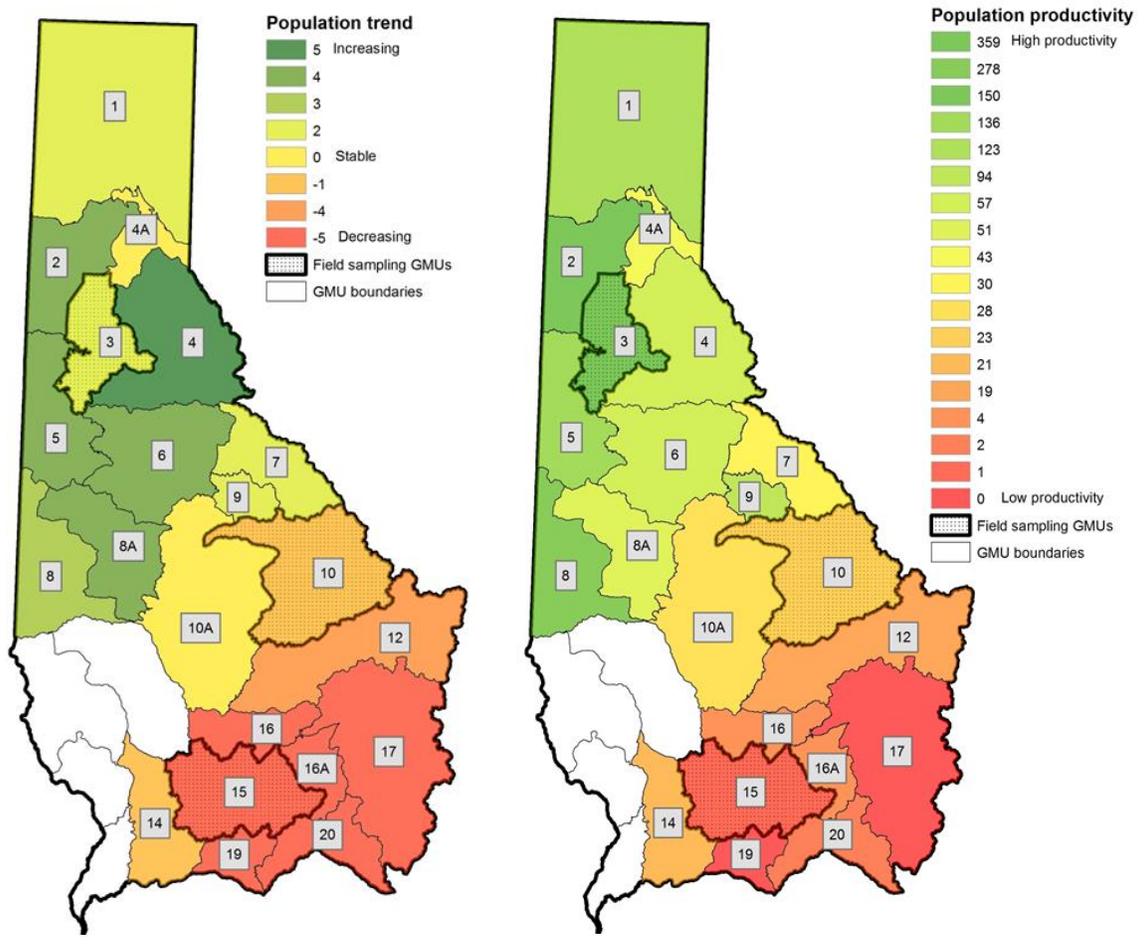


Figure 7. Percent change in estimated volume (cm^3/m^2) of total forage shrubs, and high-energy and moderate-energy shrubs consumed by moose in northern Idaho Game Management Units (GMUs) from 1984 to 2016. Low-energy forage is not included due to insignificant correlations with performance indices.

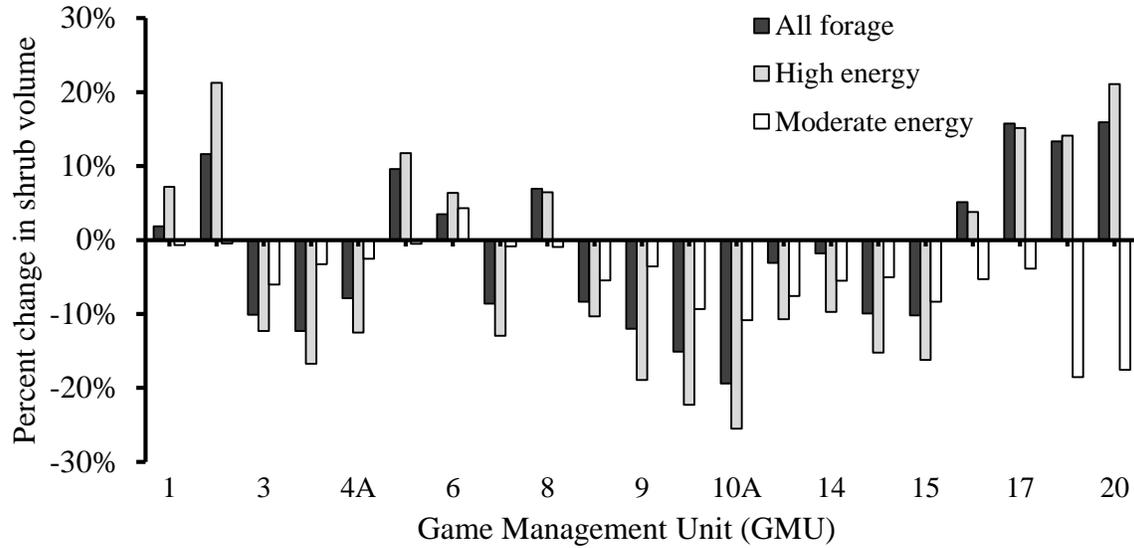


Figure 8. Relationships between indices of moose population performance and forage quantity and quality parameters for 18 Game Management Units in northern Idaho, USA.

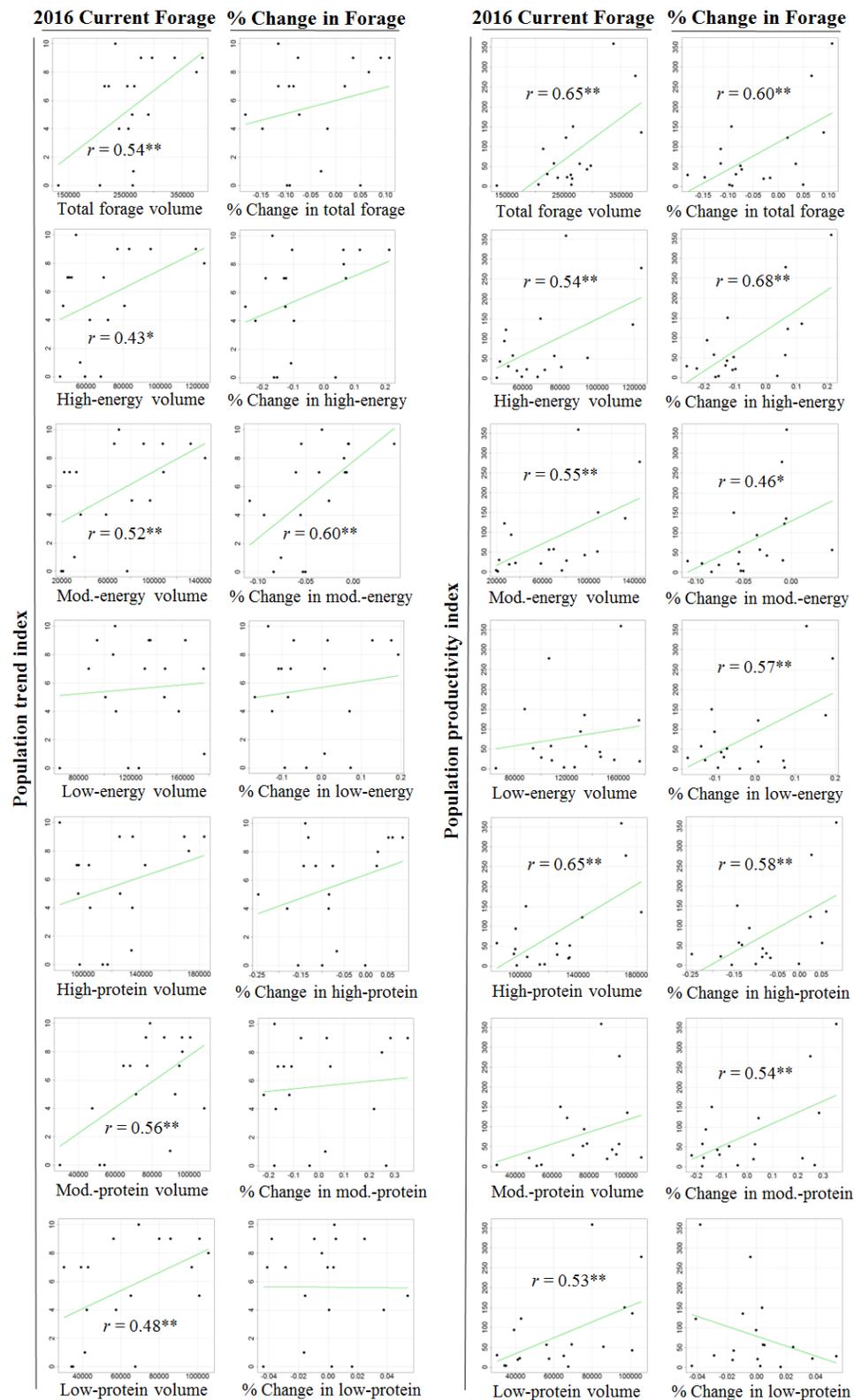


Figure 9. Percent change in estimated volume (cm^3/m^2) of total forage shrubs, and high-energy and moderate-energy shrubs for northern Idaho Game Management Units (GMUs) from 2011 to 2016. Low-energy forage was not included due to insignificant correlations with performance indices. Changes in forage are the result of recent disturbances, and therefore, represent the expected trend in forage levels due to the delay in shrub recruitment and growth post disturbance; however, the impact of forest succession on forage was not estimated here due to the short time period used to assess recent disturbance.

