HETEROGENEITY AND POWER TO DETECT TRENDS IN MOOSE BROWSE UTILIZATION OF WILLOW COMMUNITIES

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ABSTRACT: Monitoring of browse utilization of plant communities is consistently recommended as an important component of monitoring moose (*Alces alces*) populations across regions. We monitored winter browse utilization by moose within a willow (*Salix* spp.) -dominated winter range of Montana in 2008–2010. We sought to improve our understanding of: 1) spatiotemporal heterogeneity of intensity of moose browsing across the winter range, 2) species-specific selection of willow by moose during winter, and 3) appropriate sample sizes, placement, and stratification of monitoring sites for estimating browse utilization. During 3 consecutive winters we monitored 108–111 transect segments, each 50 m in length, in a systematic distribution across willow communities and assessed the effects of covariates potentially predictive of variation in browsing. Mean annual estimated browse utilization across all segments was 11.5% of sampled twigs in 2008 (95% CI = 9.4 – 13.7%), 8.0% in 2009 (95% CI = 6.2 – 9.8%), and 8.3% in 2010 (95% CI = 6.5 – 10.1%). Modeling of variation in browse utilization revealed positive relationships with the proportion of preferred species ($\beta = 0.44$, $P = 0.05$) and previously browsed willow plants ($\beta = 3.13$, $P < 0.001$), and a negative relationship with willow patch width ($\beta = -0.002$, $P < 0.001$). We found that planeleaf (*Salix planifolia*), Wolf's (*S. wolfii*), and Booth's willow (*S. boothii*) were the most consistently preferred species, whereas Drummond's (*S. drummondiana*) and Geyer willow (*S. geyeriana*) willow were moderately preferred; Lemmon's willow (*S. lemmonii*) was used less than expected. Power analyses indicated that detecting a 10% increase in browse utilization with 95% confidence in consecutive years required measuring 38–41, 50-m segments. Because systems with low and heterogeneous browse utilization of willow present challenges for efficient monitoring, we encourage power analyses as a means of evaluating sampling protocols, in addition to consideration of covariates predictive of spatiotemporal heterogeneity.

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The dynamics of herbivores are inherently tied to those of the plant communities in which they forage (White 1983, Sinclair et al. 1985, Crête 1989). Large herbivores such as moose (*Alces alces*) are affected by the quantity, quality, and diversity of forage available to them, as evidenced by effects upon movement patterns, digestible intake, fecundity, population growth rates, and population density (Sæther and Andersen 1990, Vucetich and Peterson 2004, Boertje et al. 2007). Relative density of ungulate herbivores, in turn, affects dynamics of plant communities, with further implications across trophic levels (Berger et al. 2001, Pedersen et al. 2007). Thus, monitoring browse utilization of plant

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communities is recommended as an important component of monitoring moose populations across regions (Crête 1989, Keigley and Fager 2006, Seaton et al. 2011).

Moose are typically browsers, eating the current annual growth of shrubs and trees when foraging, though they occasionally consume forbs and grasses. In North America moose forage upon 221 different plant species and/or genera (Renecker and Schwartz 2007, Shipley 2010). However, individual moose browse predominantly on a few species, suggesting a degree of local specialization (Gillingham and Parker 2008, Portinga and Moen 2015). For the Shiras moose (*A. a. shirasi*) of the Rocky Mountains and other populations worldwide, willow (*Salix* spp.) species are both highly preferred and abundant, sometimes representing >90% of winter browse consumed (Dorn 1970, Shipley 2010).

Peek (1974) described 3 common types of Shiras moose winter range: conifer, riparian, and floodplain riparian. All 3 types of winter range are utilized by moose in Montana (Dorn 1970, Stevens 1970, Matchett 1985), with floodplain riparian systems supporting substantial populations and hunter opportunity in the southwest portion of the state (e.g., Big Hole Valley, Centennial Valley; DeCesare et al. 2014). Floodplain riparian systems yield expansive willow communities on low gradient streams that often provide the majority of winter browse consumption and may support year-round moose populations. In this study, we focus on monitoring browse utilization during winter within a willow-dominated, floodplain riparian winter range in Montana. Moose in our study population averaged >75% of their winter space-use within floodplain vegetation types (Burkholder 2012).

Moose browsing of willows during winter has been well-studied across all winter range types. Factors potentially influencing browse selection of willows include: 1) the species of willow, with potential differences in nutritional content and preference by moose (Risenhoover 1989, Stolter et al. 2005, McArt et al. 2009); 2) prior browsing history, with increased preference for previously browsed plants or branches (Bowyer and Bowyer 1997, Stolter 2008); 3) plant density (Shipley and Spalinger 1995, Palo et al. 2015); 4) browse biomass (Bowyer et al. 2001); 5) snow depth (Lundmark and Ball 2008); and 6) distance to conifer edge (Dussault et al. 2006). Lastly, and related to the above, habitat use and consumption of browse are generally heterogeneous and concentrated in local patches (Månsson 2009, Palo et al. 2015).

Heterogeneity in browse utilization patterns creates a challenge to effectively monitor browse utilization as an index of moose population dynamics. Despite underlying changes in moose density, certain local patches or even individual plants may be chronically browsed, whereas other patches or plants remain unbrowsed (Bowyer and Bowyer 1997, Stolter 2008). Monitoring programs founded on estimation of browse utilization require careful attention to sampling in terms of distribution and quantity of measurements necessary to accurately capture trends in browsing and health of plant communities.

We evaluated patterns of browse utilization across multiple species of willows within southwestern Montana, and paid special attention to the drivers of heterogeneity in browse utilization and the ramifications of such heterogeneity on statistical power to detect trends. Specifically, we sought to improve our understanding of: 1) levels and drivers of heterogeneity of browsing across the winter range, 2) species-specific selection of willow during winter, and 3) appropriate sample sizes of sites for monitoring browse utilization of willows.

STUDY AREA

We studied winter browse utilization by moose during 2008–2010 in a 50 km^2 study area within the Mount Haggin Wildlife Management Area (MHWMA; 45° 57’ N, 113° 4’ W), a portion of the Upper Big Hole River Valley in southwestern Montana. The MHWMA straddles the Continental Divide, with streams that flow into the Big Hole and Clark Fork River drainages. Elevations ranged from 1750 to 2250 m and the topography varied from rolling hills and flats with meandering streams to steeper slopes at the bases of high mountains (>3200 m). Mean daily average temperature at nearby Wise River, Montana during 1981–2010 was –8 °C in January and 14 °C in July. Average annual precipitation during 1980–2010 was 48 cm (Calvert Creek SNOTEL site, 1965 m a.s.l), and mean February snow depth during 2004–2011 was 68 cm.

Willow communities are the primary cover type used by moose during winter, given that an average of 69% of winter telemetry locations occurred there (Burkholder 2012). Mixed willow communities included 6 primary species (Keigley and Fager 2006): Geyer willow (*Salix geyeriana*), Lemmon’s willow (*S. lemmonii*), Booth’s willow (*S. boothii*), Drummond’s willow (*S. drumondiana*), planeleaf willow (*S. planifolia*), and Wolf’s willow (*S. wolfii*). Bebb (*S. bebbiana*) and sandbar willow (*S. exigua*), and red-osier dogwood (*Cornus sericea*) were more sparsely distributed and occurred at lower elevations; snowberry (*Symphoricarpos albus*) and bog birch (*Betula pumila*) also occurred in riparian communities. Lodgepole pine (*Pinus contorta*) dominated the forests at lower elevations, with patches of quaking aspen (*Populus tremuloides*), and occasional Douglas fir (*Psuedotsuga menziesii*) and Engelmann spruce (*Picea engelmannii*) stands in mesic areas. Scouler’s willow (*Salix scouleriana*) and thinleaf alder (*Alnus incana*) were present in limited quantity within these lower elevation forest communities. Stands of whitebark pine (*Pinus albicaulis*), Engelmann spruce, and subalpine fir (*Abies lasiocarpa*) were dominant at higher elevations.

Moose were the only ungulate species wintering on the study area (January to mid-May; Keigley et al. 2003, Burkholder 2012). Other ungulate species present during summer and fall included pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), and mule (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*). Cattle (*Bos taurus*) were also in the study area during summer (15 June–10 Oct) under a strictly managed, rest-rotation grazing schedule and stocking rate. Predators included wolves (*Canis lupus*) and black bears (*Ursus americanus*).

Aerial surveys conducted mid-winter in the study area yielded an average minimum count of 51 moose per year in 1983–2014; the trend was generally stable, though with low precision (DeCesare et al. 2016). The number of annual moose hunting licenses declined from an average of 19 (11 antlered, 8 antlerless) in 2002–2009 to 6 antlered licenses in 2012.

METHODS

Browse utilization

We established browse transects in a systematic distribution across willow communities (Fig. 1). Transects 50 to 500 m in length were placed perpendicular to streams at 1 km intervals. Transects were divided into 50 m segments that were treated as the unit of analysis; no segments were <50 m. In total, we established 40 transects (5.55 km in total length) comprised of 111 segments.

Browse utilization was measured during early May which allowed easy identification of the previous winter’s browsing and

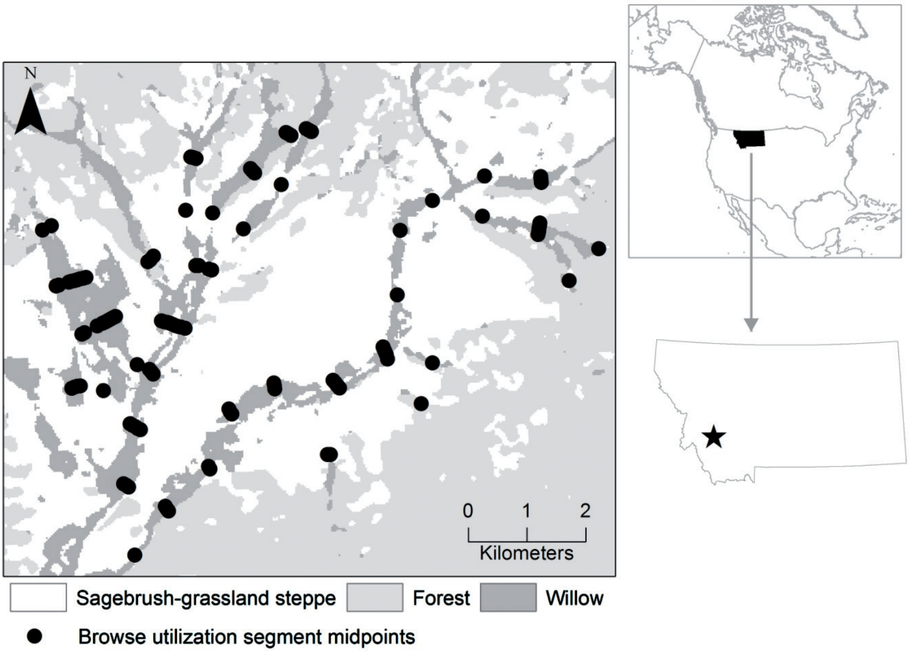

Fig. 1. Study area and sampling locations for measuring browse utilization surveys on the Mount Haggin Wildlife Management Area in southwestern Montana, 2008–2010.

preceded the arrival of other ungulates and spring green-up (Keigley et al. 2003, Seaton et al. 2011). All 111 segments were surveyed in 2009 and 2010, and 108 in 2008. We adapted a branch/twig sampling method developed by Stickney (1966) to estimate the percent of twigs browsed across a large sample of willow plants. To maximize the extent of sampling, we did not estimate biomass consumption.

The willow community was systematically sampled at 20 points on each 50-m segment, starting at the origin and at every 2.5 m thereafter. At each point, we used a graduated 2.5 m pole to locate the nearest willow plant, regardless of species; the sample point was skipped if no plant was within 2.5 m. The number of browsed twigs was counted on each plant from the 5 most distal twigs on each of 4 sampled branches. Branches were sampled following a key that prioritized branches nearest to the transect that were within a 0.75–2.0 m browse zone. We defined a twig as an unbranched portion of branch where apical or lateral growth is occurring, often consisting of the current and previous year's growth. Five twigs from each branch were selected according to those twigs for which the base of the current-year-growth of the twig was the closest to the leader, or tallest point of the branch. A detailed key for selecting plants, twigs, and branches is available in Burkholder (2012; pp. 240–243).

We marked sampled branches with aluminum tags to facilitate measuring the same willows and twigs across years. For each of 20 twigs sampled per willow, we noted them as either unbrowsed, browsed (only previous year's growth removed by browsing), or heavily browsed (more than previous year's growth removed by browsing). We excluded willows for which 4 branches with 5 twigs were not available for browsing (4.4% of sampled plants). We only counted browsing from the previous winter, as determined by the color, weathering, and new growth on the browsed twig. Each 50-m segment resulted in a maximum number of 400 twig examinations, if suitable plants were found at all sample points.

We adjusted the traditional estimator of browse utilization as the proportion of twigs browsed per segment (Jensen and Scotter 1977) to include increased weight for heavily browsed twigs with multiple years of growth removal. Field observations suggested that the average heavily browsed twig included the consumption of 3 previous year's growth based on comparison with unbrowsed twigs on the same plants. Thus, we multiplied the count of heavily browsed twigs by 3 to account for the influence of heavy browsing on the counts of twigs browsed and sampled, such that:

$$B_{adj} = \frac{N_b + (N_{hb} \times 3)}{N_{ub} + N_b + (N_{hb} \times 3)} \quad \text{(Equation 1)}$$

where B_{adj} was the intensity-adjusted browse utilization (i.e., proportion of twigs browsed) per segment, and N_{ub}, N_b, and N_{hb} were the counts of unbrowsed, browsed, and heavily browsed twigs, respectively. Estimates of B_{adj} ranged between 0 and 1 and reflected the proportion of twigs browsed, while accounting for the added effects of heavy browsing.

Hypothesized covariates to browse utilization

To explain patterns in browse utilization, we collected data on potentially influential covariates both in the field and using remotely sensed data. We documented willow species, growth form (see below) per plant, and patch width per transect. Sampled willows were revisited and identified to species in July 2008 to estimate species composition within each segment. Species were initially classified by vegetative separations (i.e., differences in branch and leaf structure as opposed to floral or catkin characteristics) based on the work of Dorn (1970). We sought additional guidance to distinctly identifying *Salix geyeriana* and *S. lemmonii* (Brunsfeld and Johnson 1985, Heinze 1994, Fertig and Markow 2001, Hoag 2005), and in June 2009 we examined pistillate catkins from a subsample of willows under a light microscope or hand lens to confirm prior classifications.

The proportion of preferred willow species along each segment was estimated by calculating the proportion of 3 willow species (planeleaf, Booth's, and Drummond's). Species preference was ascertained from palatability studies with moose and other ungulates in western North America (Dorn 1970, Stevens 1970, Tyers 2003). Growth forms of willow classified in this study were uninterrupted, released, arrested, and retrogressed (Keigley et al. 2003, Burkholder 2012: 244–245). The proportions of heavily browsed willows along each segment were estimated from growth form data according to the amount of arrested and retrogressed types. Height of the sampled willows was measured in July 2008 to establish an average height within each segment. The estimated width of each willow patch was used as a proxy for the general abundance of browse plants within a given area.

The average elevation (m) of each segment was calculated using a digital elevation model from the National Elevation Dataset (Gesch et al. 2002). Elevation was used as a potential proxy for snow depth since deeper snows were expected at higher elevations as is typical in the Rocky Mountains (Brennan et al. 2013). Distance (m) to the nearest willow and coniferous forest cover types was measured for each segment as the distance from the segment centroid to the nearest edge of each cover type using ArcGIS Desktop 9.3 (Environmental Systems Research Institute, Redlands, California) and Montana Landcover Map data (MTNHP 2010).

Statistical analyses

Investigation of dependence. — Our sampling design of consecutive 50-m segments along the same transect created high potential for autocorrelation or a lack of independence among sample units (segments). We used a suite of plots and statistical tests to examine the effects of this potential autocorrelation problem. First, we created linked-segment profile plots to display how patterns of browse utilization (the response) varied from segment to segment across transects (Ramsey and Schafer 2012). Linked-segment profile plots display the utilization of browse (0-100%) at each segment across the entire transect and allow for an examination of notable drifts from the mean of a transect. Serial and spatial correlation detection techniques were then employed to quantify correlation. A partial autocorrelation function (PACF) was applied to the longest transects in the study (9-10 segments) to examine 1-dimensional serial correlation (Ramsey and Schafer 2012). Lastly, we examined spatial correlation (2-dimensional) by constructing correlograms of browse utilization per segment across the study area. All analyses were completed in R 2.13.1with the spatial package (Ripley 2011, R Core Team 2014).

Modeling variation in browse utilization. — We used model selection approaches to evaluate whether measured covariates explained patterns in browse utilization across our study area. Browse utilization data fit a binomial distribution with repeated Bernoulli trials resulting in unbrowsed (0) and browsed (1) responses. Data contained additional nuances of being overdispersed (i.e., containing more variation than expected within a binomial distribution) and containing correlation due to repeated measures of the same segments across years.

We used generalized estimating equations (GEE) to simultaneously model all 3 years of data while accounting for the correlations due to repeated visits. This approach accounted for clustering of repeated data within segments, while also accounting for overdispersion because no distribution is assumed. GEE also offered population-level, or marginal coefficient results rather than individual- or segment-level inferences, such as would be achieved with a generalized liner mixed-effects models (GLMM) approach (Koper and Manseau 2009). The quasi-likelihood under the independence model criterion (QIC) developed by Pan (2001) was used to facilitate model selection in an information criteria framework. Analyses were completed in R 2.13.1 with additional packages APE, bbmle, MuMIn, and geepack (Paradis et al. 2004, Bolker 2010, Barton 2011, Yan et al. 2011).

All possible candidate models were evaluated including main effects for 7 candidate variables: proportionate preferred species, proportionate previously browsed plants, willow patch width (m), elevation (m), distance to willow (m), distance to conifer (m), and study year. No covariates had correlations >0.6 nor variation inflation factors >5, thus multicollinearity was not considered further. We estimated QIC_c model weights for each model and considered top models as those with ΔQIC_c scores <4. Nested models with uninformative parameters were removed from the model set by evaluating ΔQIC_c, coefficient estimates, and standard errors (Arnold 2010). Using model weights, coefficients of covariates in remaining top models were averaged to weight individual estimates and calculate adjusted standard errors (Burnham and Anderson 2002).

We conducted additional post-hoc analyses that included 1 additional variable (willow height), quadratic forms of each covariate, and various interactions between year and each covariate. There was some statistical support for certain more complex models, but here we focus on those representing a priori hypotheses (for complex models see Burkholder 2012).

Selection of willow species. — Selection ratios (w_i) were estimated by comparing the proportionate counts of browsed and total twigs sampled for each of 6 species (*i*) of willows. The same multiplier as in Equation 1 was used to inflate counts of heavily browsed twigs within the sums of both browsed and total twigs sampled. We analysed both for each year and with data pooled across all 3 years using methods of Manly et al. (2002) in Program R with the package adehabitat (Calenge 2006). Selection results per species from our study area were compared with those used in our *a priori* classification of preferred species within our modeling of factors influencing browse utilization. Our top browse utilization model with a *post-hoc* recategorization of the proportionate preferred species covariate (according to these results) was run again to assess the importance of species-specific preferences within our particular study area.

Power analysis of sampling effort. — Accurately quantifying trends in ungulate browse utilization or willow community health may require increased sample sizes when faced with a large amount of heterogeneity in browse utilization. A power analysis was conducted using our browse utilization data to estimate the range of sample sizes that would be required to detect trends under future monitoring scenarios; additional covariates were not used in this analysis. We assessed the sample sizes necessary to detect increases of 5–25% in browse utilization over a given monitoring period with either 90 or 95% confidence. For example, an increase of 10% in browse utilization (e.g., from 10 to 20%) was identified as a target level for effective monitoring (Dobkin et al. 2002).

Non-parametric bootstrapping was employed to simulate data because our measure of interest (i.e., browse utilization) failed to meet assumptions of normality for standard power methods (Cohen 1988, Manly 2006). Instead, we adapted a 1-sample method using techniques for testing sample means and sequential sample size testing (Bros and Cowell 1987, Manly 2006). We resampled data sets ranging in sample size from 4 to 100. For each set of simulations, 10,000 samples of responses of a set sample size were randomly drawn (with replacement) from our observed data. From this bootstrap *t*-distribution, we estimated an observed $t = \frac{\text{Specified difference in browse utilization}}{SD/\sqrt{n}}$. Estimates of *t* were compared to the 95% confidence interval created from the bootstrap-*t* distribution for each sample size to determine at which sample size the detection of an actual difference would become significant with either 90 or 95% confidence. We completed this analysis independently for each year's data to assess if annual distribution of browse utilization data affected results.

RESULTS

Assessing browse utilization

We sampled 35,320 twigs along 108, 50-m segments in 2008, 35,560 twigs along 111 segments in 2009, and 35,320 twigs along 111 segments in 2010. Mean annual estimated browse utilization across all segments was 11.5% in 2008 (95% CI = 9.4 – 13.7%, median = 8.9%, range = 0–54%), 8.0% in 2009 (95% CI = 6.2 – 9.8%, median = 4.6%, range = 0–48%), and 8.3% in 2010 (95% CI = 6.5 – 10.1%, median = 4.4%, range = 0–48%). The distributions of browse utilization per segment were heavily skewed each year (Fig. 2). Several segments had 0% use each year; 14 in 2008, 27 in 2009, and 23 in 2010. A total of 1826 individual willows were measured over the course of this study, 1766–1778 annually; slight annual variation was due to tag attrition, loss to beavers (*Castor canadensis*), and the absence of 3 segments in 2008. The number of plants classified to species (n = 1910) consisted of 700 Lemmon's, 459 Geyer, 348

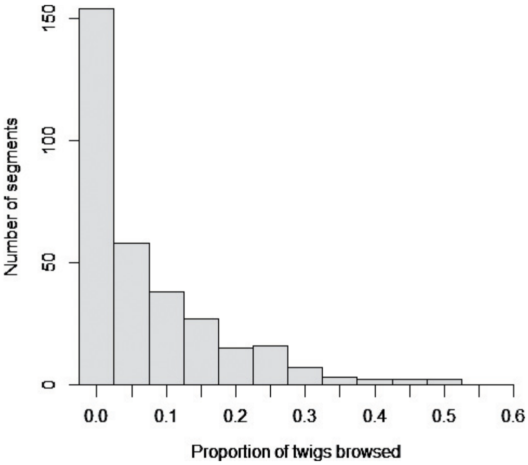

Fig. 2. Histogram of willow browse utilization per segment-year during 2008–2010 within Mount Haggin Wildlife Management Area, Montana.

Booth's, 340 Drummond's, 35 planeleaf, and 28 Wolf's willows.

Investigation of dependence

Analyses designed to assess dependence among segment data did not indicate significant levels of correlation among segments. We examined a total of 75 linked-segment profile plots for all transects with >1 segment (n = 25) and each of 3 years, and they generally indicated minimal possible serial correlation (plots available in Burkholder 2012, pp. 251–256). Applying a PACF to the 3 longest transects revealed virtually no correlation; the largest lag-1 serial correlation coefficient was <0.25 and most were <0 (Fig. 3; Ramsey and Shafer 2012). While PACF-based tests of significance were hampered by the small sample size, the lack of a consistent trend suggesting higher

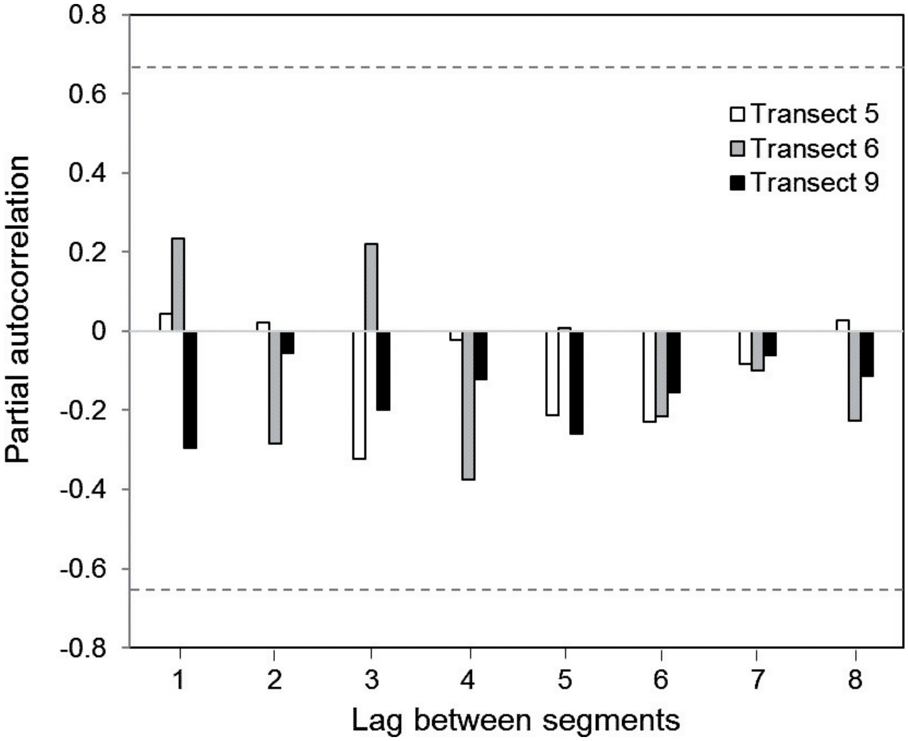

Fig. 3. Partial autocorrelations among browse utilization of willows per segment along the 3 longest transects (9–10 segments each), by lag, and 95% confidence bands (dashed lines) within the Mount Haggin Wildlife Management Area in southwestern Montana, 2008–2010.

correlation at low lags also suggests a lack of relevant serial autocorrelation in the data. Spatial correlograms also indicated minimal spatial correlation for segments within the same transect (plots available in Burkholder 2012, pp. 251–256). Given these analyses, we concluded that segments were functionally independent, and proceeded with all subsequent analyses assuming that the segments were uncorrelated sample units.

Modeling variation in browse utilization

After screening models for uninformative parameters and ΔQIC_c scores <4, we found a single top GEE model to best explain the effects of covariates on browse utilization across the study area and time period (Table 1). The proportion of preferred species ($\beta = 0.44$, $z = 3.86$, $P = 0.05$) and the proportion of previously browsed willow ($\beta = 3.13$, $z = 80.3$, $P < 0.001$) were positively associated with browse utilization, whereas willow patch width ($\beta = -0.002$, $z = 26.5$, $P < 0.001$) had negative association with browse utilization (Fig. 4). An indicator variable for year was also included. Model selection results did not support associations between browse utilization and elevation, distance to forest edge, or distance to willow edge. Willow twigs within segments entirely consisting of preferred species were 1.6 × more likely to be browsed than those within segments with no preferred species. Additionally, twigs within a segment within which all plants were previously browsed were 23 × more likely to be browsed than those within segments composed entirely of unbrowsed plants. Twigs within a narrow, 50-m wide willow patch were approximately 3 × more likely to be browsed than those within a patch 500 m wide.

Table 1. Coefficient values (β_i) and 95% confidence intervals (in parentheses) for the best GEE binomial regression model explaining winter browse utilization of willow twigs by moose during 2008–2010, Montana.

Parameter	β	SE	*z*	*P*
Intercept	–2.63	0.18	214.1	<0.001
Year (2009)	–0.362	0.13	7.65	0.006
Year (2010)	–0.322	0.12	6.89	0.009
Proportionate preferred species	0.444	0.23	3.86	0.050
Proportionate previously browsed	3.13	0.35	80.3	<0.001
Willow patch width (m)	–0.002	0.0005	26.5	<0.001

Selection of willow species

Species-specific browse preferences were examined to identify "preferred species" within our modeling framework. Counts of used and available twigs per plant and the resulting selection ratios (w_i) differed significantly among species. Planeleaf, Wolf's, and Booth's willow were the most consistently preferred (selection ratio (w_i) >1.50), Drummond's and Geyer willow were moderately preferred ($1.50 > w_i > 1.00$), and Lemmon's willow was used substantially less than expected ($w_i < 0.50$) (Table 2). These patterns existed to varying degree in all years, although Drummond's and Geyer willow were used in proportion to their availability in 2010.

A post-hoc analysis of our browse utilization model was conducted due to the discrepancies between the a priori species preference classifications and our observed preferences. All species except Lemmon's willow were reclassified as preferred. This covariate was then used to replace the previous parameter within the top model which substantially improved the strength of this covariate ($\beta = 0.92$, $z = 13.6$, $P < 0.001$). The predicted effect of a willow segment consisting entirely of preferred species being browsed compared to a segment with no preferred species increased from 1.6 × more likely in the a priori model to 2.5 × more likely in this reformulated model.

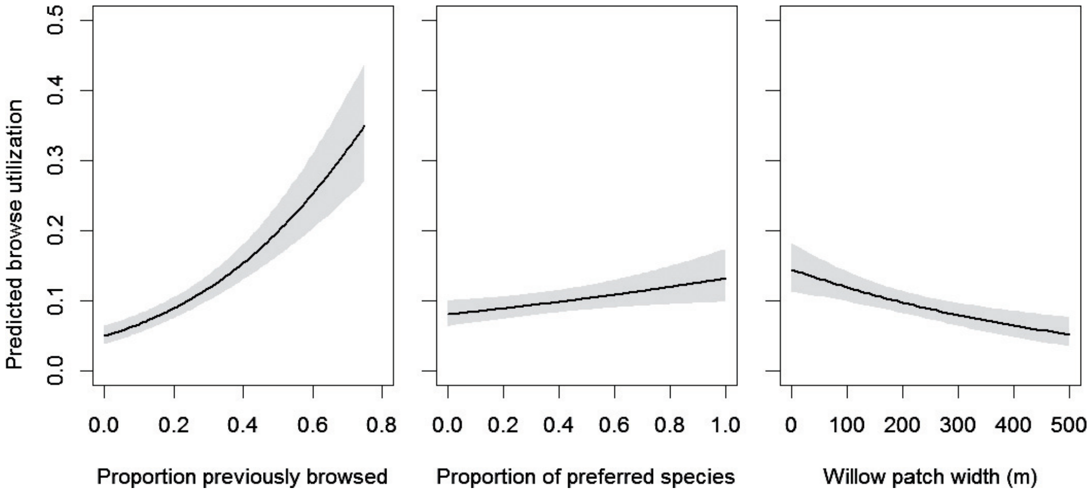

Fig. 4. Predicted values from GEE binomial regression models of the proportionate willow browse utilization by moose within a given transect segment as a function of proportion of willow plants previously browsed, proportion of preferred willow species, and willow patch width (m) during the 2008 winter season, Mount Haggin Wildlife Management Area, Montana.

Power analysis of sampling effort.

As expected, the required sample sizes increased as the level of change of interest decreased (e.g., from 20 to 5%) and as the desired level of confidence increased (e.g., from 90 to 95%; Fig. 5). For example, detecting an increase of 10% in browse utilization from one year to the next with 95% confidence required 38–41 segments (with up to 20 plants sampled in each) based on the distributions of data collected in 2008–2010; 32–35 sites would be required for 90% confidence. Results differed somewhat across years due to the among-year variation in the mean and variation of browse utilization. Slightly larger sample sizes were recommended to detect a given increase based on data from 2008 when the mean and variation of browse utilization was highest.

DISCUSSION

Browse utilization has been measured for decades to quantify the effects of ungulates on shrubs and trees (Stickney 1966, Jensen and Scotter 1977, Singer et al. 1994). Monitoring browse condition has been suggested as a potential tool for monitoring and managing the abundance and condition of wild ungulate populations, including moose (Keigley et al. 2002, Seaton et al. 2011). However, implementation of this tool would benefit from increased understanding of spatial drivers of variation in browse utilization and the amount of effort required to detect meaningful changes. Our results include the identification of several factors that were predictive of variation in browse use by moose, as well as a demonstration of power analysis to identify sample sizes necessary to monitor trends in our study area.

The annual winter browse utilization was low–moderate (~10%) on our study area, and willows increase new growth in specific response to winter browsing (Molvar et al. 1993, Guillet and Bergström 2006). This complicates our understanding of optimal browse utilization for the health of willow plants and ecological communities. For willows, browsing thresholds that define overutilization, sufficient to cause negative effects, range from 20% (Dobkin et al. 2002)

Table 2. Counts of used and available twigs and selection ratios (w_i) for different species of willow (*Salix* spp.) surveyed for winter browse utilization by moose across 3 years (2008–2010) of sampling, Montana. Selection ratios >1 indicate selection for a species, and selection ratios <1 indicate selection against that species, with * indicating values significantly different from 1.0 at α=0.05.

Species	2008			2009			2010			Pooled (2008–2010)		
	Used	Available	w_i	Used	Available	w_i	Used	Available	w_i	Used	Available	w_i
Planeleaf	171	540	2.61*	204	604	4.01*	288	596	5.70*	663	1,740	4.01*
Wolf's	41	182	1.86*	53	174	3.61*	39	172	2.67*	133	528	3.61*
Booth's	1267	7,376	1.42*	908	7,018	1.53*	951	7,072	1.59*	3,126	21,466	1.53*
Geyer	1360	9,038	1.24*	936	8,780	1.26*	750	8,368	1.06	3,046	26,186	1.26*
Drummond's	1,090	7,088	1.27*	665	6,912	1.14*	615	6,804	1.07	2,370	20,804	1.14*
Lemmon's	568	12,894	0.36*	347	13,432	0.31*	453	13,486	0.40*	1,368	39,812	0.31*

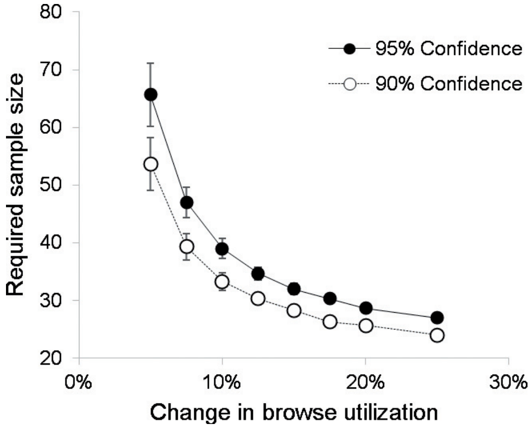

Fig. 5. Average required sample sizes and standard deviations (among years of data) for detecting changes in willow browse utilization with either 90% or 95% confidence according to power analyses based on the empirical distribution of browsing within the Mount Haggin Wildlife Management Area in southwestern Montana during 3 years of sampling, 2008–2010. Note: Changes for these purposes are additive rather than proportional, e.g., a 10% change would be from 10% to 20%, rather than from 10% to 11%.

to upwards of 50–75% (Wolff 1978). While browse utilization exceeded 40% at certain sites each year, we found no evidence, overall, that willows were overutilized. Further, we did not detect spatial autocorrelation in browsing among segments, which suggests a high degree of heterogeneity in browsing across fine and broad spatial scales. This heterogeneous consumption of browse is consistent with that observed in previous studies (e.g., Tyers 2003, Månsson 2009, Palo et al. 2015), and adds to the challenge of detecting meaningful differences from a given sample of measurements.

Browsing heterogeneity presents a problem for sampling efficiency, but variation in browse utilization provides some level of predictability, as indicated by our analysis. The complexity of plant species being foraged represents one axis of potential predictability. We sampled 6 species of willow in proportion to their availability, and found significant differences in browse utilization by species (Tables 1 and 2). In our case, focus on a subset of preferred species or stratification of effort according to species may allow more efficient sampling at the current density of animals and intensity of browsing. However, heterogeneity in browse utilization is likely to vary among and within plant species with changes in density, making sampling of less preferred species necessary (Connor et al. 2000, Speed et al. 2013). Identification of preferred species in new study areas or over time would also require multiple years of winter sampling and associated summer data before any form of species-based subsampling or stratification would be possible. To provide a robust depiction of browse utilization and willow community health across multiple levels of moose density, monitoring all species of potential relevance in a random or stratified-random manner may be the best option.

As evidenced by the Wald (z) statistic that was an order of magnitude greater than those for most other variables, previous browsing of willows was another axis of predictability and was highly predictive of current browsing (Table 1, Fig. 4). This tendency has been identified elsewhere, and the positive feedback loop related to specific browsing and preference history likely explains the overall spatial heterogeneity in browsing patterns (Bowyer and Bowyer 1997, Stolter 2008). For tea-leaved willow (*Salix phylicifolia*), Stolter (2008) found that new growth from previously browsed twigs was more palatable, and had lower concentrations of phenolics and higher biomass. Similarly, Bowyer and Bowyer (1997) found a significant increase in biomass of previously browsed grayleaf willow twigs (*S. glauca*) versus unbrowsed twigs.

Fidelity to previously browsed patches may facilitate stratified sampling as one means of improving the efficiency of sampling, assuming that previous browsing surveys can accurately identify and stratify the landscape of interest. At a broader scale, Seaton et al. (2011) used estimates of moose density or space use from aerial survey and telemetry data to stratify sites prior to browse sampling. The cross-scale spatial correlations between broad-scale patterns of animal density or space use and fine-scale browse selection is an area worthy of future research with application to vegetation-based monitoring of wildlife populations. Generally speaking, scale-dependent patterns of resource selection are common (DeCesare et al. 2012), which suggests that a high level of fine-scale heterogeneity may still exist within strata developed at broader scales. Preliminary analyses of our browse utilization data with sample units pooled to the level of the transect (averaging adjacent segments) resulted in a "washed-out" model with no covariates predictive of browsing (Burkholder 2012). Thus, in our case, detecting heterogeneity in browsing was sensitive to spatial scale.

We also found that browse utilization was negatively associated with willow patch width. That patch width is a proxy for forage abundance would, in part, contrast with previous findings that browse utilization correlates positively with biomass availability (Bowyer et al. 2001, Shipley 2010, Herfindal et al. 2015). Certainly browse utilization may correlate with plant abundance or density at different scales than those measured here (Herfindal et al. 2015). Patch width could be a proxy for an unmeasured, but important variable characterizing variation in willow communities or individual plants on our study area. An approach for future work might be to measure plant density or biomass within the sample unit; we could not make this comparison because width was a transect-level variable and did not vary among segments within each transect.

Moose exhibited different patterns of selection among willow species (Table 2). Notably, moose appeared to prefer Geyer willow over Lemmon's willow despite some debate as to these being distinct species (Brunsfeld and Johnson 1985, Heinze 1994, Hoag 2005). Selection for individual species also varied somewhat among years (Table 2); for example, moose appeared more selective during the milder winter of 2010 (Burkholder 2012). Because snow depth influences browse availability and foraging behavior, milder conditions may have facilitated more selective foraging (Schwab and Pitt 1991, Nordengren et al. 2003, Lundmark and Ball 2008). Our post-hoc analysis resulted in better model fit when compared to the a priori classification of preference based on available literature.

We recommend power analysis as an important component of any wildlife or wildlife habitat monitoring program (Tanke and Bonham 1985, Zielinski and Stauffer 1996). Our power analysis indicated that 32 segments were required to detect a 10% difference in browse utilization (with 90% confidence) on the study area. The projected sample size is specific to the distribution of browse utilization measured in this study; change in the abundance/availability of plant species composition would affect the statistical power to detect trends (Frerker et al. 2013). Our methods employed at a site with similar access would require ~1.5 person-hours per segment, or ~48 h of field time to measure 32 segments. In summer, an additional 0.5 h/segment may be needed for subsequent plant identification. Also, it may be more rigorous (and time-intensive) to enforce spatial independence of segments at the time of their establishment. In our case, having adjacent segments improved field efficiency and did not violate assumptions of independence.

Our technique of monitoring browse utilization may be impractical or cost prohibitive at the landscape level to monitor moose populations. However, it worked well within a modestly sized study area (50 km^2) that served as winter range for <100 moose. Considerably more resources would be required to employ this method across a broader scale or larger population, which makes it somewhat challenging to use with the numerous, low density moose populations in much of Montana. However, our approach could be applied in select situations, especially if overpopulation and detrimental impacts to a willow community were suspected. Because winter habitat use and browse consumption in willow communities are directly related to survival and productivity of many western moose populations, adequate assessment of willow communities is essential for effective moose management.

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