A NOVEL METHOD OF PERFORMING MOOSE BROWSE SURVEYS

Rachel L.W. Portinga[1,2,3] and Ron A. Moen[1,2]

[1]Biology Department, University of Minnesota Duluth, 1049 University Drive, Duluth, MN 55812;
[2]University of Minnesota Duluth Natural Resources Research Institute, 5013 Miller Trunk Hwy, Duluth, MN, 55811

ABSTRACT: We measured browse availability and use along foraging paths of GPS radio-collared moose (*Alces alces*) in northeastern Minnesota to estimate diet composition and browse species preference. On foraging paths during summer and winter we counted twigs via traditional methods for comparison with a novel method that attempted to better simulate moose foraging behavior. Twigs were collected and used to develop diameter at point of browsing – biomass regressions for each browse species. These regressions, different under open and closed canopy, were used to estimate biomass consumption on foraging paths and to compare 4 approaches. The average diets were similar to previously measured regional diets, and importantly, our data identified variance among individual seasonal diets. Our field method allowed us to better quantify and compare diet composition and browse selection of individual free-ranging moose directly on foraging paths.

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Key words: bite size, browse availability method, browse selection, diameter-biomass regressions, diet composition, Minnesota

Large herbivores like moose (*Alces alces*) view their food resources at the landscape, patch, and feeding station levels (Senft et al. 1987). At the landscape level moose choose which patches to visit based on the spatial distribution of browse density and forage availability within each patch. At the patch level, moose must choose where to forage based on the available browse species, and tree and shrub heights at different feeding stations. Younger patches can provide large quantities of high quality browse while older patches that have grown out of reach provide less browse (Schwartz 1992). Within a feeding station, bite size is based on the tradeoff between cropping and processing (Spalinger and Hobbs 1992).

Moose need to consume about 130 g dry mass/kg body weight$^{0.75}$ daily in summer and about 40 g dry mass/kg body weight$^{0.75}$ daily in winter (Renecker and Hudson 1985). Using an average bite size of 1.02 g/bite (Renecker and Hudson 1986), this equates to at least 13,000 bites in summer and 4,000 bites in winter for a 454 kg (1000 lb) moose. Winter consumption may be up to 50% higher depending on browse availability and species composition (Hjeljord et al. 1994). This large demand for forage forces moose to move between patches and feeding stations in order to consume enough biomass.

Browse availability and bite size have been measured by following moose or moose tracks in snow and counting the number of available twigs per species, the number of bites per species, and measuring diameter at point of browsing, dry mass, and twig length (Risenhoover 1987, Shipley et al. 1998). Locations of moose were found via radio telemetry (Risenhoover 1987, Hjeljord et al. 1990) or finding a track crossing a road (Shipley et al. 1998). These methods were largely opportunistic and data collection was either clumped (location

[3]Present Address: Hibbing Community College, 1515 25th St E, Hibbing, MN 55746

every hour for 2 days) or spread temporally (1–2 tracks weekly).

Another typical method is to measure browse availability in plots along randomly placed straight transects instead of following moose foraging paths. This provides an estimate of absolute browse density in a patch, rather than an estimate of browse availability encountered by moose. We measured intensively used feeding patches with 3 different protocols and a randomly placed straight transect in northeastern Minnesota. Our new protocol (the large feeding station method) attempted to simulate how a moose browses, which we contrasted with measurements along the foraging path and with absolute browse density.

STUDY AREA

This study was conducted in northeastern Minnesota where moose were previously collared for a VHF telemetry study (Fig. 1) (Lenarz et al. 2011). These forests transition between the Canadian boreal and northern hardwood forests and experience a continental climate with short warm summers and severe winters (Heinselman 1996). Most was part of the Superior National Forest with the remaining either state, county, tribal, or industrial forest land

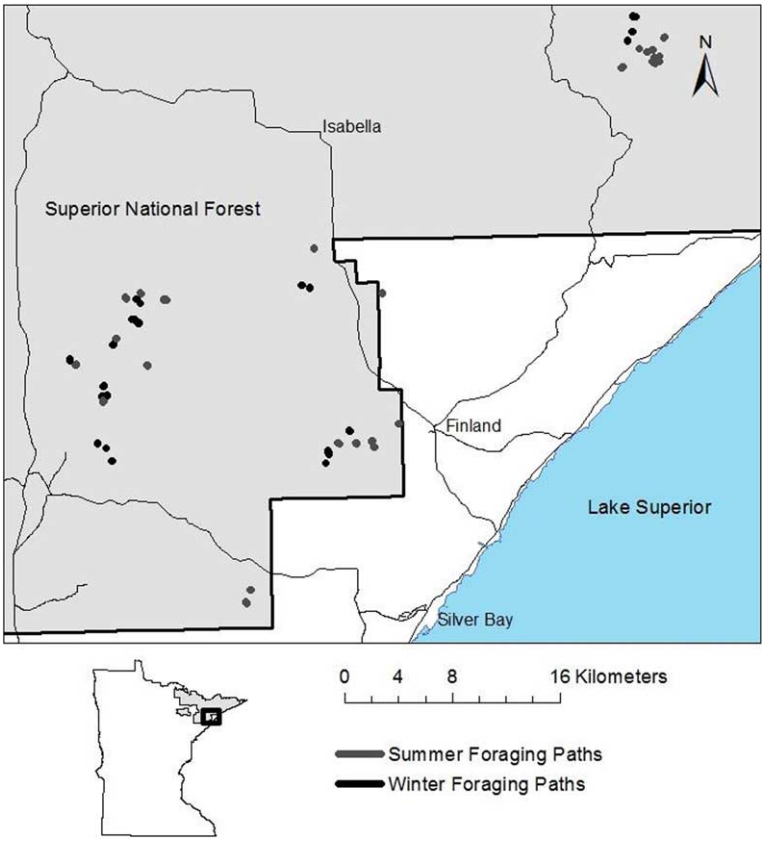

Fig. 1. The study area was within the Superior National Forest in northeastern Minnesota. Each black dot represents one measured foraging path in winter and a dark gray dot represents a summer foraging path.

(Lenarz et al. 2010, Moen et al. 2011). More specific details are provided in the Minnesota Moose Research and Management Plan (MNDNR 2011).

METHODS

Regressions and Estimating Bite Mass

Summer leaves were collected between July and September 2012, and winter twigs between January and April 2012 and 2013; twigs from both years were combined in the regression analyses. We clipped (standard garden clippers) browsed (~3 cm below the browse point) and unbrowsed twigs of all browse species (Table 1). Samples were bagged and labeled with the location, date, and species. All browsed and unbrowsed twigs and leaves were stored at 2–3 °C prior to measurements. These twigs were used to develop diameter-biomass regressions for each season (Telfer 1969). In summer we collected stripped twigs of each species which we clipped directly above the first unbrowsed petiole. A winter bite was equal to the twig biomass and a summer bite the leaf biomass from one twig, both with current annual growth >5 cm.

On browsed twigs we measured (nearest 0.01 mm) the diameter at point of browsing and on unbrowsed twigs the simulated diameter at point of browsing. In summer, the simulated point of browsing was the diameter underneath the last stripped petiole. The wet weight of winter twigs and stripped summer leaves was weighed to the nearest 0.01 g. After weighing the wet mass of leaves, they were placed in the same bag with the corresponding twig. All unbrowsed

Table 1. The common and scientific names for each potential browse species in northeastern Minnesota and seasons in which each species is consumed. "Rare" species make up <1% of the diet at large feeding station paths. "Not Browsed" species were not consumed along the foraging paths.

Common Name	Scientific Name	Winter	Summer
Balsam fir	*Abies balsamea*	Common	Not Browsed
Red maple	*Acer rubrum*	Common	Common
Mountain maple	*Acer spicatum*	Common	Common
Alder	*Alnus rugosa*	Rare	Rare
Juneberry	*Amelanchier* spp.	Common	Common
Paper birch	*Betula papyrifera*	Common	Common
Bog birch	*Betula pumila*	Not Browsed	Rare
Red-osier dogwood	*Cornus stolonifera*	Common	Rare
Hazel	*Corylus cornuta*	Common	Rare
Black ash	*Fraxinus niger*	Not Browsed	Rare
White pine	*Pinus strobus*	Rare	Rare
Balsam poplar	*Populus balsamifera*	Rare	Rare
Quaking aspen	*Populus tremuloides*	Common	Common
Pin cherry	*Prunus pennsylvanicus*	Common	Common
Choke cherry	*Prunus virginianus*	Common	Common
Oak	*Quercus* spp.	Not Browsed	Rare
Willow	*Salix* spp.	Common	Common
Elderberry	*Sambucus pubens*	Not Browsed	Rare
Mountain ash	*Sorbus decora*	Rare	Common

twigs in both seasons were stored in labeled bags.

All unbrowsed summer and winter twigs were dried at 60 °C for 48 h in a drying oven. Dried twigs in winter and dried leaves in summer were stored at room temperature before being weighed to the nearest 0.01 g. Most winter twigs (74%) and summer leaves (90%) were measured within 5 days of removal from the drying oven; the remainder was measured 6–9 days later.

GPS Collars

We captured adult moose in February and early March 2011 by darting them from helicopters. GPS radio-collars (Sirtrack Ltd. and Lotek Wireless) fitted to each moose were programmed to transmit a location every 20 min. Animal capture and handling protocols met the guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011) and were approved by University of Minnesota and National Park Service Animal Care and Use committees (#0912A75532).

Measuring Browse Availability

Summer browse availability was measured between 25 July and 14 September 2012, and winter browse availability between 3 January and 22 March 2013. Browse availability was measured at the patch scale which we identified from the GPS locations – patches had a concentrated number of moose locations. We used a handheld Garmin GPS to reach our pre-identified patches and then searched for a feeding station to identify a foraging path. A feeding station was defined as a plant or clump of plants with browsed twigs that were accessible when the forefeet of a moose are stationary (Goddard 1968, Novellie 1978, Senft et al. 1987).

A foraging path was defined as a trail of feeding stations within a patch. Summer foraging paths were measured 1 to 15 days after the moose departed, and winter foraging paths were measured 3 to 17 days after departure. Patches were considered accessible if they were on public land and we could access them by walking <2 km on a trail and/or <550 m from a trail. We measured winter patches containing 29 foraging paths from 8 moose (6F, 2M), and summer patches containing 31 foraging paths from 7 moose (5F, 2M).

We defined a large feeding station as a location that appeared to have ≥10 bites. At all sites we measured browse under 4 different protocols to produce 4 foraging path types: 1) large feeding stations along the foraging path, 2) random plots along the foraging path, 3) random feeding stations along the foraging path, and 4) plots along a straight transect through the area containing the foraging path. Each path type consisted of 10 measurement plots.

Large feeding station plots — The first large feeding station encountered was the first plot of the site and marked as a waypoint on the handheld GPS. The plot or feeding station to be measured was a half circle with radius of 99.1 cm (39 in), with the center of the back side (straight line diameter) held at the approximate place where the moose stood. Tracks in winter, other sign in either season, or placement of bites relative to open space were also used to determine where the moose stood and the direction it faced. At each large feeding station we counted the unbrowsed and browsed twigs of each browse species between 0.5 and 3 m above the ground (Table 1; Shipley et al. 1998). Each cut-off twig was considered a bite. Although an occasional large feeding station had <10 bites, we included it as a large feeding station because the observer estimated it had at least 10 bites. This only occurred at 10 of 290 (3%) large feeding stations in winter and 36 of 297 (12%) in summer.

We established the foraging path type from the first large feeding station by following tracks and browsing sign to the next large feeding station, marked it as the second waypoint on the GPS, and repeated the measurements (Fig. 2). Plots could not overlap and this process continued until 10 large feeding stations had been measured on the foraging path.

Random plots on the foraging path — We created the random plot path type by stopping along the foraging path and repeating our browse measurements in random plots. A list of random distances between 5 and 14 m was generated using Microsoft Excel, and in the field we established the random plots using these distances in the GPS "find" feature (Fig. 2).

Random feeding stations — If a random plot had been browsed (evident bites), then that random plot was also defined as a random feeding station. If no browsed bites were in the random plot, we followed the foraging path to the next browsed twig (even if only one bite) and this became the location of the next random feeding station (Fig. 2), eventually creating the random feeding path type.

Straight transect plots — After completing the large feeding station, random plot, and random feeding station measurements, we established a straight line transect that returned to the first plot. Along this transect we stopped at random distances between 5 and 14 m until 10 plots were measured. If we reached the first large feeding station plot before completing 10 plots, we lengthened the transect. If, however, the cover type changed past the first plot and <10 plots were measured, we established a new transect in a random direction within the same cover type; 10 of 29 straight transects were angled in winter and 15 of 31 in summer.

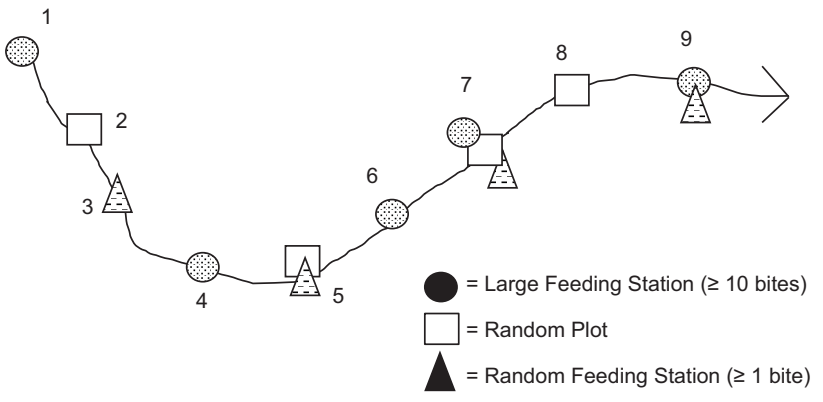

Fig. 2. A diagram of how we measured a foraging path. Plot 1 is a large feeding station plot with ≥10 bites. Plot 2 is a random plot. Because Plot 2 did not have any bites taken we stop at the next bite which becomes Plot 3, a random feeding station plot. Plot 4 is the second large feeding station plot. Plot 5 is the second random plot with 1–9 bites, so it is also the second random feeding station plot. Plot 6 is the third large feeding station plot. Plot 7 is the third random plot that had ≥10 bites, so it is also the third random feeding station plot and the fourth large feeding station plot. Plot 8 is the fourth random plot. Plot 9 is the fourth random feeding station that had ≥10 bites, so it is also the fifth large feeding station plot. We continued until there were 10 plots of each type.

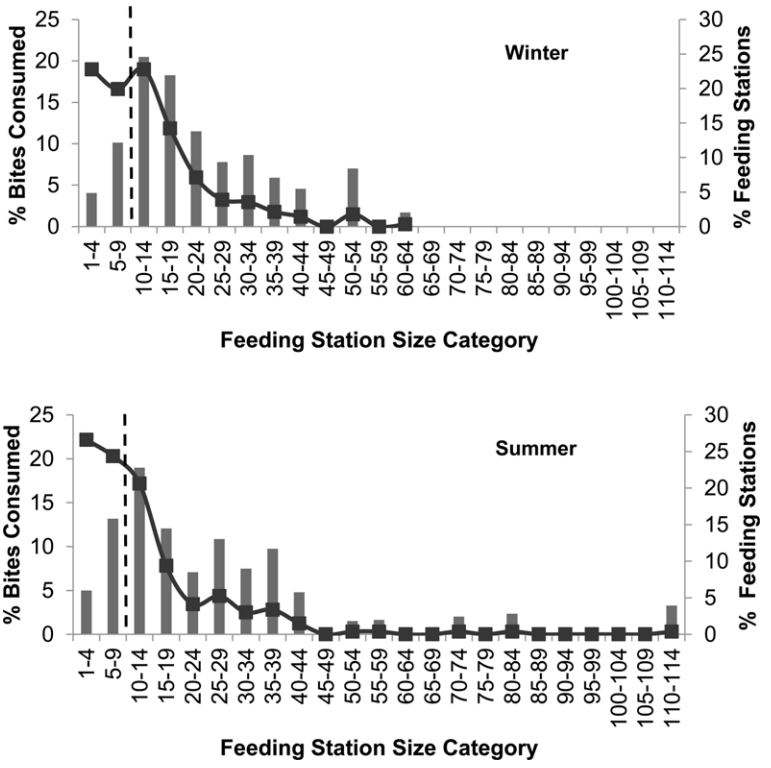

Fig. 3. The percent of random feeding stations measured in each size category (line) and the percent of bites consumed at all feeding stations of a given size category (bar) in winter and summer. The dashed line separates the small feeding stations (≤9 bites) from the large feeding stations. In winter, 57% of the random feeding stations were considered large but they accounted for 86% of the consumed bites. In summer, 49% of the random feeding stations were considered large but they accounted for 82% of the consumed bites.

Some cover types had little available browse making the foraging path difficult to follow in summer when 10 of 30 foraging paths had <10 plots in all path types. If no bites were found within 20 m of the previous feeding station when moving forward, we assumed the moose stopped foraging. Effectively this meant that there were <10 large feeding stations, random feeding stations, and/or random plots in that foraging path. Snow tracking in winter allowed us to more easily identify the foraging path; thus, 10 plots in all path types were measured in 28 of 30 foraging paths.

Canopy cover was measured 3 times with a densiometer (every 8th plot) to produce an average value in each patch. Twigs collected from sites with 0–50% canopy closure were considered grown in open canopy, and twigs from sites with 70–100% canopy closure were considered grown in closed canopy. Twigs from sites with 51–69% canopy cover were not used in the regressions or bite size summary statistics.

Statistical Analyses

Biomass-diameter at point of browsing regressions, ANOVAs on browse density,

Kruskal-Wallis comparisons of diet, Pearson χ^2 Goodness of Fit tests, and Bonferroni Z-tests were all performed in Jmp 10.0. Significance level was set at $P = 0.05$.

Regressions — Simulated diameters at point of browsing and dry masses of twigs from the unbrowsed winter twigs were $\log_{10}$ transformed and used to make 2 separate diameter-biomass regressions for each of the main browse species. The first regression used twigs grown in open canopy (0–50% shaded) and the second twigs from closed canopy (70–100% shaded). Similarly, 2 summer regressions were made using leaf dry mass of each browse species. The raw data are found in Ward (2014) and only results are presented here.

Statistics on bite size diameter and bite mass were calculated for each species. A t-test was used to test for statistical differences between the average diameter at point of browsing in open and closed canopy in both seasons for each species.

Available browse density — Browse density was estimated as twig counts and as biomass. To obtain the total number of available twigs per path, we added the number of available twigs and the number of browsed bites. We estimated the total biomass originally available (browsed or unbrowsed) along a foraging path by multiplying the number of twigs of a given species by the average biomass of one bite of that species. For foraging paths in 0–50% shade, we used the average biomass values from open canopy regressions. Likewise, we used the average biomass values from closed canopy regressions for foraging paths in 51–100% shade. Although the closed canopy regressions were developed with twigs grown in 70–100% shaded areas, we felt the foraging paths in 51–69% shade were better classified as closed canopy than open canopy. Balsam fir was not included in summer browse density estimates because it is not typically part of the summer diet.

Available and consumed browse density along each of the 4 path types were estimated using twig counts and biomass in both seasons. The length of each path was calculated by measuring the length of a line passing through all of the plots of each path type. The area of the foraging path was considered twice this distance to represent the ability of moose to browse either side of the foraging path. To calculate browse density we divided the twig count (available or consumed) by the area of the foraging path. These same calculations were made using biomass and twig counts. The browse density on large feeding station paths was compared with those on the random feeding, random, and straight transect paths using an ANOVA of the log transformed data.

Diet composition — Diet composition was calculated for each moose on the 4 path types in both seasons. We made a weighted average of those diet compositions to estimate diet composition for all moose on each path type in winter and summer. Species were considered rare when they made up <1% of the average diet (Shipley et al. 1998) at large feeding station paths. The percentage of the diet consisting of rare species is reported in the tables (but not text) to illustrate how a few individual moose consumed many bites of rare species.

Each individual diet had at least one browse species not identified on the foraging paths. Because these data were not normally distributed and no transformation could correct this skewedness, we used a Kruskal-Wallis test to test for significant differences between diet composition on the 4 path types. A Kruskal-Wallis test was also used to test for differences between each individual diet.

Browse species selection — We also determined the selection for each browse species from a combined average of all moose and for each individual using the

data from large feeding station paths. A Pearson χ^2 Goodness of Fit test and a Bonferroni Z-test were performed on the availability and use of all browse species for all moose combined and each individual moose (Neu et al. 1974). A species was considered "positively selected", "negatively selected", or neither if there was a significantly larger, smaller, or equal proportion of browsed versus available twigs.

RESULTS

Regressions

All of the twig diameter – biomass regressions had slopes significantly different from zero. The slopes ranged from 0.58–2.80 in winter and 0.45–2.07 in summer. In winter, 75% of the regressions had an R^2 >0.60, and in summer 43% had an R^2 >0.60. There was no consistent pattern between the open canopy or closed canopy regression slopes being larger or smaller (Ward 2014).

Bite Size

Across all species in winter, the mean diameter at point of browsing was 3.0 ± 0.02 mm in open canopy (range = 0.5–9.0 mm) and 3.1 ± 0.1 mm in closed canopy (range = 0.2–8.4 mm) (Table 2). In summer, the mean across species was 2.3 ± 0.02 mm in open canopy (range = 0.02–11.1 mm) and 2.4 ± 0.04 mm in closed canopy (range = 0.2–6.1 mm) (Table 3).

Using the regressions found in Ward (2014), we calculated the average biomass consumed per bite for each browse species (Tables 2 and 3). In winter, pin cherry had the largest bite size (2.3 ± 1.4 g) under closed canopy and the smallest bite size under open canopy (0.4 ± 0.1 g). Mountain maple had the smallest bite size under closed canopy (0.4 ± 0.2 g). Mountain ash had the largest (1.7 ± 1.4 g) and quaking aspen the smallest bite size (0.3 ± 0.2 g) under closed canopy in summer.

Bite Density at Feeding Stations

One purpose of establishing the random feeding station plots was to estimate the frequency of feeding stations of different sizes occurring along foraging paths. In winter 57% of random feeding station plots (n = 281) had ≥10 or more bites, and in summer 49% (n = 267). In both seasons at least 80% of twig consumption on the foraging path was from feeding stations with ≥10 bites, although moose occasionally consumed <10 bites at a station.

Browse Density

Total available browse density was measured at 29 patches in winter and 30 patches in summer. It was significantly different among the 4 path types in both seasons using either method (winter twigs: $F_{3,\ 112}$= 62.7, summer twigs: $F_{3,\ 118}$ = 32.5, winter biomass: $F_{3,\ 112}$ = 84.3, summer biomass: $F_{3,\ 120}$ = 16.8, P_{all} < 0.0001). Likewise, density of consumed browse was also significantly different in winter and summer among the 4 path types (winter twigs: $F_{3,\ 112}$ = 63.4, summer twigs: $F_{3,\ 120}$ = 31.2, winter biomass: $F_{3,\ 112}$ = 70.9, summer biomass: $F_{3,\ 119}$ = 5.0, P_{all} < 0.0025). As expected, both available and consumed browse densities were highest at large feeding station paths, followed by random feeding station, random plot, and straight transect paths (Table 4).

The average available browse density estimated by biomass at large feeding stations was 53% higher in summer (15.2 ± 1.7 g/m^2) than winter (9.9 ± 1.0 g/m^2). Conversely, density estimated by twig counts was ~2.5x larger in winter (15.2 ± 1.6 twigs/m^2) than in summer (5.9 ± 0.6 twigs/m^2). Large feeding station paths had ~60% more available twigs (727 ± 3)

Table 2. Summary statistics on browsed twigs in winter for all browse species. Open canopy indicates twigs grown in locations shaded 0–50% and closed canopy indicates twigs grown in locations shaded 70–100%. *P*-values indicate *t*-test results between the diameter at point of browsing (DPB) of each species in open and closed canopy. We did not find enough individual twigs of juneberry, paper birch, pin cherry, or willow in closed canopy to calculate reliable averages for those categories.

		Diameter at Point of Browsing (mm)					
Species	Canopy	Average ± SE	Minimum	Maximum	Average Bite ± SE (g)	n	*P*
Balsam fir**	Open	2.7 ± 0.1	0.9	6.5	1.6 ± 0.3	82	*0.002*
	Closed	2.2 ± 0.1	1.0	4.0	1.2 ± 0.2	50	
Red maple**	Open	3.5 ± 0.1	1.3	7.4	0.7 ± 0.3	125	*0.009*
	Closed	4.1 ± 0.1	2.7	6.9	1.4 ± 0.5	27	
Mountain maple*	Open	2.8 ± 0.3	1.5	4.6	0.6 ± 0.3	47	*0.019*
	Closed	2.4 ± 0.3	0.4	4.9	0.4 ± 0.2	56	
Juneberry	Open	2.4 ± 0.1	0.9	4.5	0.5 ± 0.1	161	*0.583*
	Closed	NA	NA	NA	NA	8	
Paper birch	Open	2.7 ± 0.1	0.6	4.8	0.8 ± 0.1	188	*NA*
	Closed	NA	NA	NA	NA	7	
Hazel	Open	2.7 ± 0.1	1.1	5.3	0.6 ± 0.1	301	*0.104*
	Closed	2.8 ± 0.1	1.1	4.5	0.6 ± 0.1	132	
Red-osier dogwood***	Open	3.5 ± 0.1	1.5	6.1	1.1 ± 0.1	332	*<0.0001*
	Closed	4.3 ± 0.2	2.0	6.6	1.4 ± 0.4	40	
Quaking aspen	Open	3.5 ± 0.1	0.9	6.8	0.9 ± 0.1	209	*0.155*
	Closed	3.2 ± 0.1	1.0	5.7	0.7 ± 0.4	32	
Pin cherry	Open	2.4 ± 0.1	0.6	4.9	0.4 ± 0.1	216	*NA*
	Closed	NA	NA	NA	NA	6	
Choke cherry	Open	3.0 ± 0.3	1.5	4.8	0.7 ± 0.1	53	*0.120*
	Closed	2.6 ± 0.4	0.2	4.1	0.4 ± 0.1	20	
Willow	Open	3.1 ± 0.1	0.5	6.4	0.9 ± 0.1	501	*NA*
	Closed[1]	NA	NA	NA	NA	0	
Mountain ash*	Open	4.3 ± 0.1	1.6	6.8	1.3 ± 0.3	43	*0.045*
	Closed	3.7 ± 0.1	1.2	8.4	0.7 ± 0.5	53	
Combined	Open	3.0 ± 0.02	0.5	9.0	NA	2388	
	Closed	3.1 ± 0.1	0.2	8.4	NA	454	

in winter than in summer (460 ± 37), whereas the available biomass was ~2.5x larger in summer (1166 ± 88 g) than winter (471 ± 26 g). The same seasonal differences existed for consumed twigs and biomass. The distance walked in winter to complete the large feeding station paths (27.6 ± 2.0 m, n = 29) was about half that in summer (50.5 ± 4.9 m, n = 31).

The available and consumed browse density for each browse species was largest at large feeding station paths followed by random feeding station, random plot, and straight transect paths. The one exception (based on twig count) was that the highest browse density of hazel was found on the straight transect path in summer (when hazel is rarely consumed).

Table 3. Summary statistics on browsed twigs of all species in summer. Open canopy indicates twigs grown in locations shaded 0–50% and closed canopy indicates twigs grown in locations shaded 70–100%. P-values indicate t-test results between the diameter at point of browsing (DPB) of each species in open and closed canopy. We did not find enough individual twigs of red maple in open canopy or pin cherry, willow, or mountain ash in closed canopy to calculate reliable averages for those categories.

		Diameter at Point of Browsing (mm)					
Species	Canopy	Mean ± SE	Minimum	Maximum	Mean Bite ± SE (g)	n	*P*
Red maple	Open	NA	NA	NA	NA	14	*0.349*
	Closed	2.8 ± 0.2	1.3	6.0	1.4 ± 0.3	27	
Mountain maple***	Open	2.3 ± 0.03	0.5	4.7	0.7 ± 0.1	675	*<0.0001*
	Closed	3.0 ± 0.1	0.5	4.9	1.0 ± 0.1	264	
Juneberry	Open	1.6 ± 0.04	0.1	3.2	0.5 ± 0.04	149	*0.145*
	Closed	2.1 ± 0.3	0.2	4.2	1.0 ± 0.4	20	
Paper birch**	Open	2.3 ± 0.1	0.02	5.1	0.8 ± 0.1	316	*0.003*
	Closed	2.0 ± 0.1	0.6	3.8	0.5 ± 0.1	84	
Hazel	Open	1.6 ± 0.1	0.5	3.5	0.7 ± 0.04	105	*0.739*
	Closed	1.6 ± 0.1	0.6	2.5	0.6 ± 0.1	48	
Red-osier dogwood***	Open	2.9 ± 0.1	1.5	5.7	1.3 ± 0.1	41	*0.001*
	Closed	2.1 ± 0.2	0.5	4.4	0.7 ± 0.1	26	
Quaking aspen***	Open	3.1 ± 0.2	0.5	11.1	1.4 ± 0.2	169	*<0.0001*
	Closed	1.6 ± 0.1	0.3	4.3	0.3 ± 0.2	53	
Pin cherry	Open	2.2 ± 0.1	0.6	4.2	0.8 ± 0.1	53	*NA*
	Closed	NA	NA	NA	NA	0	
Choke cherry	Open	2.2 ± 0.1	1.0	4.1	0.8 ± 0.1	44	*0.085*
	Closed	2.0 ± 0.1	0.8	3.9	0.8 ± 0.1	80	
Willow***	Open	2.3 ± 0.1	0.5	5.5	0.9 ± 0.1	242	*<0.0001*
	Closed	NA	NA	NA	NA	14	
Mountain ash	Open	4.0 ± 0.1	2.0	7.0	1.1 ± 0.1	72	*0.802*
	Closed	NA	NA	NA	NA	7	
All Species	Open	2.3 ± 0.02	0.02	11.1	NA	2071	*NA*
	Closed	2.4 ± 0.04	0.2	6.1	NA	627	

Consumption Rate

The pattern of consumption rate was similar to that of consumed browse density. The proportion of consumed twigs was highest on the large feeding station paths and declined progressively to the random feeding station, random plot, and straight transect paths. Consumption was 45% in summer and 35% in winter on the large feeding station paths. Overall, it was 23–45% on all paths except the straight transects where rates were 13% in winter and 9% in summer.

Diet Composition

Season — At least 70% of all bites (all moose) consumed in winter along the 4 path types consisted of hazel, paper birch, willow, and quaking aspen. The remaining 30% consisted of balsam fir, juneberry, mountain maple, red maple, red-osier dogwood, pin

Table 4. Available browse density and consumed browse density along four path types in summer and winter measured by twigs/m^2 ± SE and biomass (g)/m^2 ± SE. W = winter, S = summer.

	Method	Season	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Available	# Twigs	W	15.4 ± 1.6	2.3 ± 0.2	2.0 ± 0.2	1.4 ± 0.2
		S	5.9 ± 0.6	2.0 ± 0.2	1.8 ± 0.3	1.1 ± 0.1
	Biomass	W	9.9 ± 1.0	1.7 ± 0.1	1.5 ± 0.1	1.0 ± 0.1
		S	15.2 ± 1.7	6.8 ± 1.9	4.5 ± 0.8	2.9 ± 0.4
Consumed	# Twigs	W	5.3 ± 0.6	2.1 ± 0.1	0.5 ± 0.1	0.2 ± 0.03
		S	2.7 ± 0.3	1.0 ± 0.3	0.4 ± 0.1	0.1 ± 0.03
	Biomass	W	4.0 ± 0.4	0.5 ± 0.04	0.4 ± 0.04	0.2 ± 0.02
		S	6.7 ± 0.7	2.4 ± 0.4	1.0 ± 0.2	0.3 ± 0.04

cherry, and choke cherry. Rare species were alder, mountain ash, balsam poplar, and white pine (Table 5).

In summer 70% of bites consisted of mountain maple, willow, and paper birch on large feeding station, random feeding station, and random plot paths. The remaining 30% was juneberry, red maple, pin cherry, choke cherry, quaking aspen, and mountain ash. Rare species were hazel, balsam poplar, red-osier dogwood, balsam fir, alder, bog birch, black ash, oak, elderberry, and white pine. On straight transects at least 70% of consumed twigs were mountain maple, willow, quaking aspen, and species considered rare (Table 5).

Path type — Despite the general similarities in diet diversity, all browse species comprised different portions of the winter diet on the 4 path types (Kruskal-Wallis, $H_3 > 12.3$, $P < 0.007$) except paper birch and hazel (Kruskal-Wallis, $H_3 < 1.2$, $P > 0.60$; Table 6). In summer Juneberry, quaking aspen, and mountain ash comprised different portions of the diet on all 4 path types in summer (Kruskal-Wallis, $H_3 > 8.1$, $P < 0.045$; Table 5). No difference existed among the 4 path types for red maple, mountain maple, paper birch, cherry, and willow (Kruskal-Wallis, $H_3 < 5.7$, $P > 0.13$).

Individuals — Diets based on twigs consumed on large feeding station paths varied individually and from the pooled average (Tables 6 and 7). One winter example of this individual difference was female moose 31180 that consumed 26% red maple and 50% hazel (4 paths combined) compared to the group average of 5% red maple and 26% hazel (Table 6); red maple was more available in her foraging patches. An example in summer was male moose 31190 that consumed 10% mountain maple and 61% willow (4 paths combined) compared to the group average of 41% mountain maple and 21% willow (Table 7).

Browse Species Selection

The average diet in winter (all moose combined) was different from that available ($\chi^2_9 = 3122$, $P < 0.0001$). A Bonferroni Z-test on the combined data indicated that juneberry, red maple, mountain maple, paper birch, red-osier dogwood, and quaking aspen were eaten more than available in summer. Hazel was eaten less than available, and cherry and willow were used in proportion to availability (Table 8). Individual diets were also different from browse availability on their respective foraging paths (all moose: $\chi^2_{\leq 9} \geq 74.6$, $P < 0.0001$ for all moose).

The average summer diet (all moose combined) was also different from available ($\chi^2_8 = 840$, $P < 0.0001$), as were individual diets (all moose: $\chi^2_{\leq 8} \geq 43.9$, $P < 0.0001$).

Table 5. Diet composition (average percent of diet ± SE) measured on four path types. Averages and SE were weighted by moose. Rare includes species that made up <1% of the diet at large feeding station paths. 29 foraging paths were measured in winter 2013 and 31 were measured in summer 2012.

Species	Large Feeding Station	Random Feeding Station	Random Plot	Straight Transect
Winter				
Hazel	27 ± 7	26 ± 8	27 ± 9	28 ± 8
Paper birch	26 ± 7	26 ± 6	25 ± 6	18 ± 6
Willow	11 ± 5	14 ± 6	13 ± 6	11 ± 5
Quaking aspen	7 ± 3	8 ± 4	10 ± 5	13 ± 6
Juneberry	6 ± 2	5 ± 2	4 ± 1	4 ± 2
Red maple	5 ± 3	4 ± 2	5 ± 3	4 ± 4
Red-osier dogwood	5 ± 4	3 ± 3	3 ± 3	10 ± 11
Balsam fir	4 ± 2	6 ± 2	6 ± 3	2 ± 2
Mountain maple	4 ± 3	3 ± 1	2 ± 1	2 ± 1
Cherry	3 ± 1	2 ± 1	2 ± 1	2 ± 1
Rare	2 ± 2	2 ± 1	2 ± 1	5 ± 6
Summer				
Mountain maple	42 ± 11	45 ± 10	43 ± 11	25 ± 11
Willow	21 ± 8	21 ± 9	28 ± 11	23 ± 11
Paper birch	11 ± 3	9 ± 4	6 ± 4	6 ± 5
Cherry	9 ± 4	7 ± 4	6 ± 4	3 ± 5
Quaking aspen	8 ± 4	10 ± 3	8 ± 3	14 ± 7
Mountain ash	4 ± 2	3 ± 2	4 ± 4	0
Juneberry	2 ± 1	3 ± 2	2 ± 1	8 ± 5
Red maple	1 ± 1	0	0	7 ± 4
Rare	1 ± 0.3	1 ± 0.4	0.2 ± 0.1	10 ± 7

A Bonferroni Z-test on the combined summer data indicated that red maple, mountain maple, cherry, and mountain ash were eaten more than available in summer, willow less than available, and juneberry, paper birch, and quaking aspen proportional to availability (Table 8).

DISCUSSION

We initially chose to measure large feeding stations (≥10 bites) because field observations indicated that these sites were common and theory (Senft et al. 1987) supports the strategy of such foraging behavior. By contrasting browse density along a foraging path at large feeding stations with alternate routes, we demonstrated how moose increased effective browse density by selecting a specific foraging path. For example, moose took at least 80% of their bites at large feeding stations with ≥10 bites. The identification of large feeding stations provided a fast and efficient manner to measure browse availability and consumption along presumed foraging paths, and this method can also be used to evaluate the relative quality of browsed and unbrowsed patches (Ward 2014, Ward and Moen 2014)

This method avoids 2 potential complications associated with the straight transect

Table 6. Diet composition of individual moose in winter 2013 measured by twigs consumed at large feeding station paths. There are diets for eight collared moose. 31189 and 31190 are male, the rest are females. N is the number of foraging paths measured. Rare species made up <1% of the combined moose diet at large feeding stations.

		Moose Number							
Species	All Moose	31166	31174	31175	31178	31180	31182	31189	31190
Hazel	27	21	38	29	13	50	33	9	68
Paper birch	26	14	41	15	57	9	3	56	3
Willow	11	5		9	6	5	3		
Quaking aspen	7	28	16	12	<1	8	2		
Juneberry	6	18		1	8	9	1		
Red maple	5				26	9			
Red-osier dogwood	5		15	<1	38	4			
Balsam fir	4	2	4	15	1	14			
Mountain maple	4	16	1		1	25			
Cherry	3	11	1	5	6	<1	3	6	
Rare	1	2	5	1					
N	29	2	2	3	3	4	2	5	3

Table 7. Diet composition of individual moose in summer 2012 measured by twigs consumed at large feeding stations only. There are diets for seven collared moose. 31189 and 31190 are male, the rest are females. N is the number of sites measured. Rare species made up <1% of the combined moose diet at large feeding stations.

		Moose Number						
Species	All Moose	31166	31168	31175	31178	31180	31189	31190
Mountain maple	41	3	57	84	90	36	57	10
Willow	21	53	3	9		17		61
Paper birch	11	12			1	17	13	7
Cherry	9	8	5	3	2	24	1	3
Quaking aspen	8	4	36			1	23	2
Mountain ash	4	17			5	5		3
Juneberry	2						1	12
Red maple	1						5	
Rare	1			1	1			3
N	31	3	2	3	3	3	6	4

method: 1) measuring random locations, and 2) empty plots. The foraging path approach eliminates these concerns by ensuring plentiful data at actual foraging locations. Arguably, it also reflects the browse availability a moose would actually perceive. Randomly placed plots in straight transects are often empty, which would mean that many more plots would be required to accurately estimate the availability of patchy browse. Our method avoids empty plots, incorporates distance moved between feeding stations, and

Table 8. Browse species selection in both seasons when data from all moose was combined. If the moose were simply browsing at random, we would expect the 95% confidence interval of the percent browsed to contain the percent available at large feeding stations.

Season	Species	Percent Available at Large Feeding Stations	95% Confidence Interval of Percent Browsed at Large Feeding Stations	Selection
Winter	Juneberry	4.7	$5.1 \leq - \geq 6.8$	+
	Red maple	3.3	$3.8 \leq - \geq 5.3$	+
	Mountain maple	2.7	$4.0 \leq - \geq 5.5$	+
	Paper birch	19.3	$24.7 \leq - \geq 27.9$	+
	Red-osier dogwood	2.1	$3.3 \leq - \geq 4.8$	+
	Quaking aspen	5.6	$5.8 \leq - \geq 7.6$	+
	Cherry	3.0	$2.7 \leq - \geq 4.0$	0
	Willow	11.9	$11.2 \leq - \geq 13.5$	0
	Balsam fir	9.0	$2.8 \leq - \geq 4.1$	–
	Hazel	36.8	$26.3 \leq - \geq 29.5$	–
Summer	Red maple	0.5	$0.6 \leq - \geq 1.3$	+
	Mountain maple	27.6	$34.6 \leq - \geq 38.2$	+
	Cherry	7.2	$8.3 \leq - \geq 10.5$	+
	Mountain ash	4.2	$8.6 \leq - \geq 10.8$	+
	Juneberry	3.3	$2.2 \leq - \geq 3.4$	0
	Paper birch	10.4	$9.8 \leq - \geq 12.1$	0
	Quaking aspen	8.1	$6.1 \leq - \geq 8.1$	0
	Willow	28.6	$18.9 \leq - \geq 21.9$	–

provides an estimate of effective browse density. A challenge to simulating foraging decision rules when following a foraging path is that humans find large feeding stations by sight, but moose likely use other senses as well.

Diet composition was statistically different among seasons and path types. The average combined diet in both winter and summer was best categorized as generalist because one genus did not account for >60% of the diet (Shipley 2010). The two primary browsed species were hazel and paper birch in winter and mountain maple and willow in summer, hence, moose may forage in different areas in winter and summer. For example, available browse density estimated by twig counts was higher in winter than in summer, with hazel consumed commonly in winter but rarely in summer. Use of GPS locations may help distinguish seasonal differences in foraging locations and browse species availability.

The diet composition was similar to that measured >3 decades previously in the region (Peek et al. 1976). The top 5 summer species (percent of diet) were the same in both studies: mountain maple, willow, paper birch, cherry, and quaking aspen. Mountain maple was ranked first in our study and fifth by Peek et al. (1976), and quaking aspen had the opposite rankings. Hazel, willow, and quaking aspen were 3 of the top 5 winter species in both studies. One difference was that paper birch and juneberry were included in our top 5, whereas Peek et al. (1976) had balsam fir and red-osier dogwood. During both seasons the primary species consumed

were consistent regardless of path type. Because more twigs were counted on the large feeding station paths, they probably provided the better estimate of diet and species consumption rates.

This study was unique because we collected data from individual free-ranging moose by using their GPS locations to identify their foraging paths shortly after use. Presumably each moose selected browse based on availability within the patch they occupied. Individual consumption differences occurred in both winter and summer, and though previous studies have not provided for analysis and comparison of individual diet selection, individual differences in habitat selection by moose were documented in British Columbia (Gillingham and Parker 2010). Pooling the data from many foraging paths identified the generalized seasonal diets and the most important browse species in this region, and concurred with previous research. It also identified individual diet variation which suggests that moose adapt their diet based on the local composition and availability of browse species.

We were able to simulate how a moose browsed in a patch using the large feeding station method. There was some subjectivity in choosing which large feeding station was closest (consecutive) when establishing the foraging path; however, a moose would face the same choice. Contrasting browse measurements between simulated and actual foraging paths in the same patch would provide a good evaluation of our approach and potential differences. We offer that incorporating large feeding stations and the distance between adjacent large feeding stations is an efficient method to estimate browse availability at the patch level.

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