

Effects of Stand Age on Species Composition and Browse Density in Northeastern Minnesota



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Summary

Large ruminant herbivores like moose spend most of their time foraging and ruminating to acquire and process enough plant biomass to meet energy and nutrient requirements. In northeastern Minnesota, moose forage in a mosaic of forest stands with ages shaped by harvest and other disturbances. Distribution and abundance of browse species varies across the landscape and each browse species has unique growth patterns and a patchy distribution within and among different stand types. We measured browse availability and use along foraging paths of GPS radio-collared moose and within randomly selected regenerating stands in northeastern Minnesota. We measured all sites using traditional methods and a method that simulates moose foraging behavior by measuring large feeding stations. At each site we measured available species composition and available browse density. We tested three hypotheses: (1) the proportion of available browse species common in the diet along foraging paths would be greater than within randomly selected regenerating stands, (2) the density of available browse species would be greater along foraging paths than within randomly selected regenerating stands, and (3) the density of available twigs would be highest in young stands and decrease with stand age. Paper birch, willow, and quaking aspen were common in young stands while hazel, mountain maple, and balsam fir (winter) or juneberry (summer) were common in older stands. Browse density also changed with stand age, but the changes in species composition and browse density were similar along foraging paths and within randomly selected regenerating stands indicating that moose habitat restoration projects can effectively create forage for moose. In areas with and without collared moose the simulated browsing method was an effective tool for measuring browse availability and use.

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Introduction

Moose (*Alces alces*) spend large portions of their day foraging. During this time they are making decisions on which stands and feeding stations to visit (Senft et al. 1987). Moose choose where they will forage based on the spatial distribution of forage resources. At the landscape level moose will choose among younger stands that can provide large quantities of high quality browse and older stands that have grown out of reach of moose and provide less browse (Schwartz 1992, Peek 1997). At the stand level moose choose which feeding stations to visit based on the available browse species and tree and shrub ages at different feeding stations (Senft et al. 1987, Danell et al. 1991, Pastor and Danell 2003).

Repeated browsing on plants causes hedging which will keep browse within reach of moose and indicates that moose have used the same stands in consecutive years. A spatial memory would make it possible for moose to return to the same stands over multiple years. These stands could be more appealing for foraging because of browse availability, browse quality, browse species composition, predator avoidance, or canopy cover choices. Because repeated browsing can have negative consequences on the quality and quantity of future browse (Pastor and Danell 2003, De Jager et al. 2009, Pastor and De Jager 2013) it is beneficial to compare qualities of foraging sites and non-foraging sites to identify which factors may be influencing moose visitation and foraging.

Many moose populations occur in boreal forests which historically had large disturbances caused by forest fires, wind throw, insect infestations, and plant diseases (Peek 1997). Moose populations tend to increase following large disturbances presumably because they are using young stands for foraging (Aldous and Krefting 1946, Hatter 1949, Cowan et al. 1950, Spencer and Chatelain 1953). Since the arrival of Europeans in Minnesota timber harvest has become an increasingly important cause of forest disturbance. Between 1940 and 1995 forest harvest became the most common disturbance in northeastern Minnesota (White and Host 2008).

Post-disturbance stands offer abundant regenerating twigs of deciduous trees and shrubs which constitute most of the moose diet (Courtois et al. 2002). The range of years post-disturbance that offer moose the greatest browse availability varies in the published literature. In Alaska peak browse

availability varied between five and 20 years (Spencer and Hakala 1965), 11-30 years (Kelsall et al. 1977), and 20-30 years post-disturbance (Weixelman et al. 1998). In Newfoundland 7-10 years post-disturbance offered the greatest density of twigs (Parker and Morton 1978). This indicates that although moose populations may increase within a few years of disturbances, peak browse availability may not occur until years later. In northeastern Minnesota there has been a decline in forest harvest activity over the past decade (Wilson and Ek 2013) which may be affecting the availability of young habitat with moose forage. However, since we do not know which stand ages provide the most browse for moose in Minnesota it is difficult to interpret what effects a decline in forest harvest may have on moose populations in the region.

Browse density is often measured in square quadrats or along straight transects (Parker and Morton 1978, Cumming 1987, Weixelman et al. 1998, Pastor et al. 1998). These methods are simple to implement and can be standardized across studies. However, they measure the potential distribution of browse availability and can have empty plots or miss evidence of browsing. Other methods that have been used followed moose tracks or collared moose and counted twigs along the foraging paths (Risenhoover 1987, Hjeljord et al. 1990, Shipley et al. 1998). Following moose requires tracks in the snow and is therefore not a viable option in summer, or it requires collared moose, which can be cost prohibitive or unavailable.

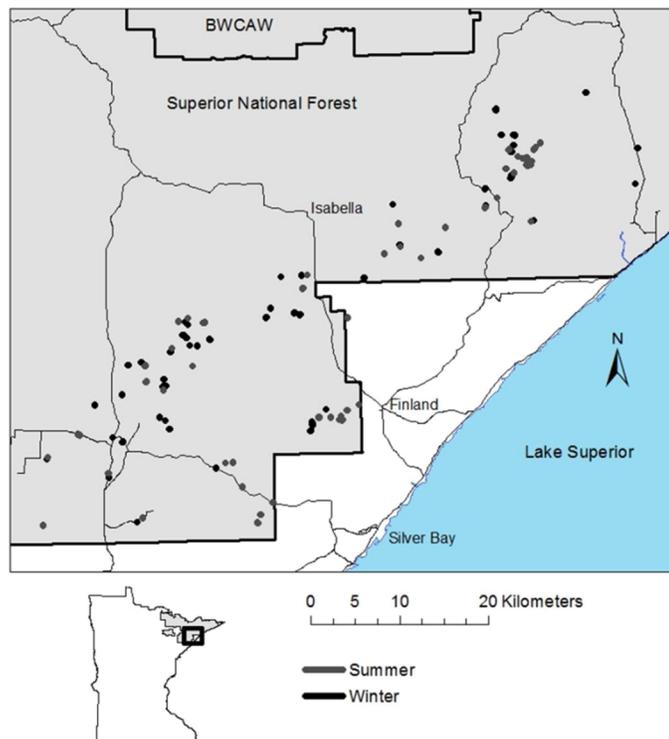
We found the large feeding station method measured browse availability and use along a foraging path and also measured browse density at higher quantities than a transect sampling method (Ward 2014). Therefore, we wanted to test if this feeding station method (Ward 2014) could be used to measure browse availability within randomly selected regenerating stands without foraging paths. If successful, it would enable measurement of browse availability from the perspective of a foraging moose without the need for collared animals. The hypotheses we tested were: (1) the proportion of available browse species common in the diet along foraging paths would be greater than within randomly selected regenerating stands, (2) the density of available browse species would be greater along foraging paths than within randomly

selected regenerating stands, and (3) the density of available twigs would be highest in young stands and decrease with stand age. We also tested for differences in species composition between three age classes.

Study Area

This study was conducted in northeastern Minnesota where moose had been previously collared for a VHF telemetry study (Figure 1) (Lenarz et al. 2010). Our locations spanned from Langley River Road in the southwest to the Sawbill Trail in the northeast. The study was in the Laurentian Great Lakes Forests which transition between the Canadian boreal forests and the northern hardwood forests and experience a continental climate with short warm summers and severe winters (Heinselman 1996). Forest harvest became common in the study area around 1940 and became the predominant disturbance after 1970 (White and Host 2008). Most of the land ownership was in the Superior National Forest. The remaining land in the study area was in state, county, tribal, or industrial ownership (Moen et al. 2011, Lenarz et al. 2010). Details on the study area and location in relation to the other Minnesota moose projects can be found in the Minnesota Moose Research and Management Plan (MNDNR 2011).

Figure 1. The study area and locations of foraging paths and regenerating stands in the Superior National Forest in northeastern Minnesota. The locations spanned from Langley River Road in the southwest up to Sawbill Trail in the northeast. Each black dot represents one measured foraging path or regenerating stand measured in winter and a dark gray dot represents a summer foraging path or regenerating stand.



Methods

Foraging Paths

We used GPS collar locations to identify and reach areas with moose foraging (Ward 2014). We measured 29 foraging paths in winter 2013 and 41 foraging paths from summers 2012 and 2013. The age of each stand in which the foraging paths occurred was determined in ArcMap 10.0 using aerial photographs and several coverage layers from which stand age could be obtained (Rack et al. 2007, Stueve et al. 2011, Joyce et al. 2014, MNDNR Data Deli 2012). At all foraging paths we measured browse availability and use within a site following the method outlined in Ward (2014) that measures a foraging path with a large feeding station path, a random feeding station path, a random plot path, and a straight transect.

We defined a large feeding station as a feeding station that appeared to have ≥ 10 bites that a moose could have consumed when standing in one location. A random plot was a plot completed at predetermined random distances along the foraging path. A random feeding station was identified based on the random plots and had to have ≥ 1 bite. If a bite was present in the random plot it was also a random feeding station. If no bites were taken in the random plot we followed the foraging path to the nearest browsed twig and this was the location of the random feeding station. Straight transect plots were plots completed along a straight transect through the area encompassing the foraging path (Figure 2). Plots in all path types were a half circle with a radius of 99.1 cm (39 inches). We counted all browsed and unbrowsed twigs of each browse species in the plot between 0.5 and 3 m above the ground (Shipley et al. 1998).

Regenerating Stands

We identified all the stands regenerating from forest harvest in the study area between 1 and 32 years old and placed them in one of three age classes: 1-11 years, 12-21 years, or 22-32 years post-disturbance. We randomly selected six stands in the youngest class and 12 stands in each of the older classes to sample. In summer we identified four regenerating stands between 1 and 11 years post-

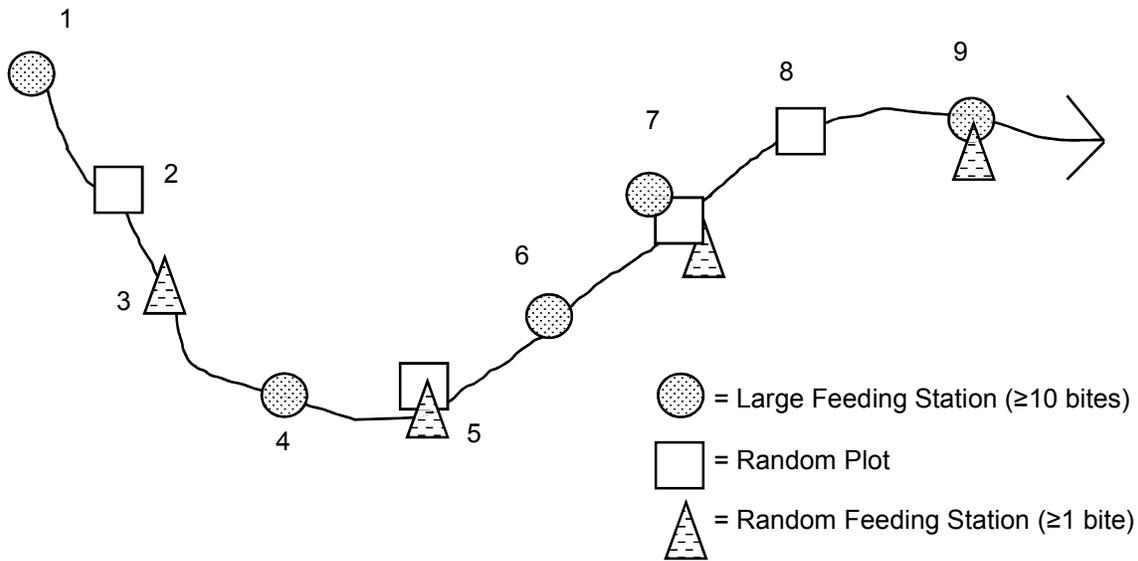


Figure 2. A diagram of how we measured a foraging path with three path types. Plot 1 is a large feeding station (≥ 10 bites). Plot 2 is a random plot. Because Plot 2 does not have any bites taken we stop at the next bite which becomes Plot 3, a random feeding station. Plot 4 is the second large feeding station. Plot 5 is the second random plot with 1-9 bites, so it is also the second random feeding station. Plot 6 is the third large feeding station. Plot 7 is the third random plot that has ≥ 10 bites, so it is also the third random feeding station and the fourth large feeding station. Plot 8 is the fourth random plot. Plot 9 is the fourth random feeding station and has ≥ 10 bites, so it is also the fifth large feeding station. We would continue until we measured 10 plots of each path type.

disturbance by driving along roads in the study area and stopping to measure recent cuts. In total, 30 regenerating stands were measured in winter and 27 regenerating stands were measured in summer.

At regenerating stands we used the same method to measure browse availability as along foraging paths. However, we simulated a foraging path by moving from one large feeding station of available twigs of common browse species to the next closest large feeding station until we completed 10 plots each of the large feeding station path, the random feeding station path, and the random plot path. Then we completed a straight transect with ten plots. At regenerating stands we moved at least 10 meters into a stand to avoid being on the edge. If browsed bites fell within a plot at the regenerating stands they were recorded as browsed. We then continued along the simulated path towards the area with the highest density of currently available twigs. In contrast to the methods used in Ward (2014), we did not explicitly

follow foraging paths if one existed in regenerating stands. Fifteen of 30 regenerating stands in winter and seven of 27 regenerating stands in summer had signs of moose browsing.

Field Measurements

Summer browse availability at all regenerating stands and 30 of 41 foraging paths was measured between 25 July 2012 and 14 September 2012. The remaining 11 summer foraging paths were measured between 3 July 2013 and 23 July 2013. Winter browse availability at all foraging paths and all regenerating stands was measured between 3 January 2013 and 22 March 2013. At all foraging paths and regenerating stands canopy cover was measured after the eighth, sixteenth, and twenty-fourth plots using a densiometer and the three densiometer readings were averaged. In 17% of stands there were more than 32 plots measured, but we still measured canopy cover after the eighth, sixteenth, and twenty-fourth plots.

Common browse species were those making up >1% of the diet in either the winter or summer and included mountain maple (*Acer spicatum*), red maple (*Acer rubrum*), juneberry (*Amelanchier* spp.), paper birch (*Betula papyrifera*), red-osier dogwood (*Cornus stolonifera*), pin cherry (*Prunus pennsylvanicus*), quaking aspen (*Populus tremuloides*), and willow (*Salix* spp.) in both summer and winter. Beaked hazel (*Corylus cornuta*) and balsam fir (*Abies balsamea*) were common browse species in winter but not in summer and mountain ash (*Sorbus decora*) was a common browse species in summer but not in winter (Peek et al. 1976, Ward 2014).

In summer the rarely available species were alder (*Alnus rugosa*), bog birch (*Betula pumila*), black ash (*Fraxinus niger*), balsam poplar (*Populus balsamifera*), choke cherry (*Prunus virginianus*), elderberry (*Sambucus pubens*), oak (*Quercus* spp.) and *Viburnum* spp. In winter the rarely available species also included mountain ash (*Sorbus decora*).

Two browse species, balsam fir and beaked hazel, required special consideration in summer. Balsam fir was not consumed in summer and although beaked hazel is abundant it was only 0.3 percent of the diet in summer in Minnesota and therefore we did not count balsam fir or beaked hazel as available species in summer. If we had treated hazel as a potential common summer species, it would have constituted most of the available species composition. This would not realistically reflect what moose are

searching for and eating. Therefore, in summer the 10 required available twigs that defined a large feeding station could not be hazel. For the same reasons, random feeding stations had to have ≥ 1 available twig of a common summer browse species that was not hazel. However, if a large feeding station or random feeding station had the necessary number of twigs of common browse species, then any hazel also inside that plot was also counted as available.

As in Ward (2014), if a straight transect was going to leave the cover type by continuing in a straight line, we angled the transect to stay in the same cover type. In winter 12 of 30 straight transects at regenerating stands were angled a mean of 74 ± 10 degrees to remain in the same cover type. In summer 14 of 29 straight transects at regenerating stands were angled a mean of 70 ± 8 degrees to remain in the same cover type.

Statistical Analyses

The distance of each path was calculated in ArcMap 10.0 by measuring the line connecting all plots of a certain path type from first to last. This distance was multiplied by two to represent the ability of the moose to browse on either side of the foraging path. We calculated the browse density in each regenerating stand at all four path types by dividing the number of available twigs (or biomass) in a path by the area of that path type. Biomass values were calculated using regressions for the study area (Ward 2014). We compared the browse density at regenerating stands to the browse density at foraging paths measured during the same seasonal time periods.

We also calculated the available browse species composition for each regenerating stand at all four path types in both winter and summer and compared it to the available browse species composition at foraging paths. Available species composition was measured by twig counts. We also compared browse density and available species composition among three age classes (1-11, 12-21, and 22-32 years post-disturbance).

Differences in available browse density at foraging paths and regenerating stands were calculated for each path type with a *t*-test in RStudio (v 0.98.501, RStudio Inc. 2013). Differences between the densities of the three age classes and differences between densities measured by the four path types were

tested by an ANOVA in Jmp 10.0. Differences in available species composition among foraging paths and regenerating stands and the differences between the species composition at the different age classes were calculated with a Kruskal-Wallis comparison test in Jmp 10.0. Significance level was set at 0.05.

Results

Available Browse Density

The mean distance required to complete ten large feeding stations along foraging paths and within regenerating stands was less in winter (28 ± 2 m and 24 ± 3 m, respectively) than in summer (40 ± 4 m and 51 ± 5 m, respectively; Figure 3). The mean distance needed to complete ten random feeding stations, ten random plots, and ten straight transect plots was very similar at both foraging paths and regenerating stands in winter and summer (Range: 82 ± 5 to 93 ± 3 m).

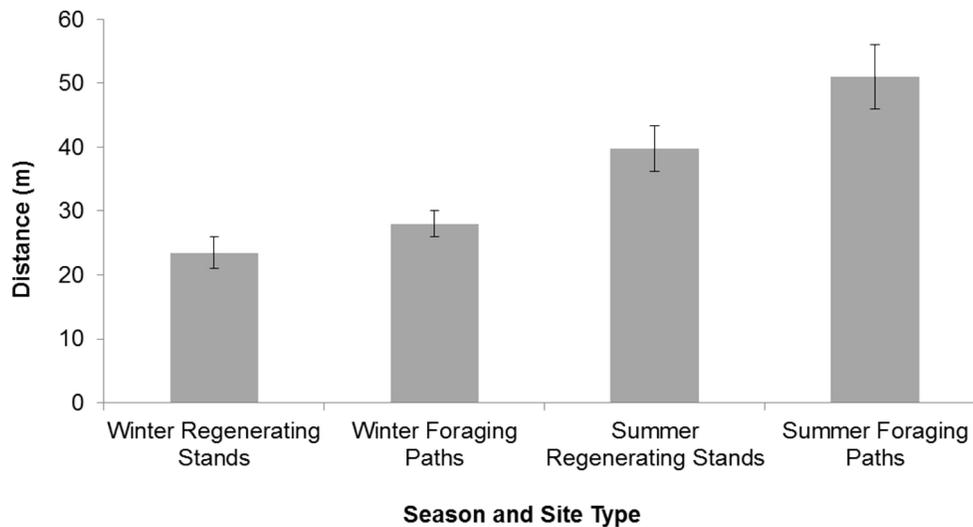


Figure 3. The mean distance (m) moved to complete ten large feeding stations at regenerating stands and foraging paths in winter and summer.

The mean available browse density measured by all four path types at foraging paths in winter was not significantly different from regenerating stands (t -test, $t_{57} < 0.70$, $P > 0.07$; Table 1). When measured by biomass, the mean available browse density measured by large feeding station paths at foraging paths (9.9 ± 1.0 g/m²) was not significantly different from regenerating stands (14.0 ± 1.7 g/m²;

t-test, $t_{57} = 1.81$, $P = 0.08$; Table 1). However, there was a significant difference between the browse density at foraging paths compared to regenerating stands measured by biomass/m² in winter at the random feeding station paths, random plot paths, and straight transects (*t*-test, $t_{57} > 2.27$, $P < 0.01$, Table 1).

In summer the mean available browse density measured by twigs/m² by all four path types along foraging paths was not significantly different from the browse density within regenerating stands (*t*-test, $t_{70} < 0.88$, $P > 0.38$; Table 1). There was again not a significant difference between the browse density at foraging paths compared to regenerating stands measured by biomass/m² in winter at the four path types (*t*-test, $t_{70} < 1.15$, $P > 0.25$, Table 1).

Table 1. The available density of twigs and biomass along foraging paths and within regenerating stands in winter and summer. *P* values are from *t*-tests comparing twig density (or biomass density) in foraging paths to twig density (or biomass density) in regenerating stands. All comparisons of browse density among path types in each site were significantly different (ANOVA, Foraging Paths Winter $F_{3,112} > 66.1$; Regenerating Stands Winter $F_{3,116} > 40.9$; Foraging Paths Summer $F_{3,164} > 14.8$, Regenerating Stands Summer $F_{3,116} > 36.3$; all $p < 0.0001$). FS = Feeding Station, W = winter, S = summer.

| Season | Path Type | Mean Available Density | | | | | |
|--------|-------------------|------------------------|---------------------|----------|------------------------|---------------------|----------|
| | | Twigs/m ² | | | Biomass/m ² | | |
| | | Foraging Paths | Regenerating Stands | <i>P</i> | Foraging Paths | Regenerating Stands | <i>P</i> |
| W | Large FS | 15.4 ± 1.6 | 17.8 ± 2.3 | 0.51 | 9.9 ± 1.0 | 14.0 ± 1.7 | 0.08 |
| | Random FS | 2.6 ± 0.1 | 2.9 ± 0.2 | 0.44 | 1.7 ± 0.1 | 2.4 ± 0.2 | 0.01 |
| | Random Plot | 2.3 ± 0.2 | 2.6 ± 0.2 | 0.27 | 1.5 ± 0.1 | 2.2 ± 0.2 | 0.003 |
| | Straight Transect | 1.7 ± 0.2 | 2.2 ± 0.2 | 0.07 | 1.0 ± 0.1 | 1.9 ± 0.2 | 0.001 |
| | | | | | | | |
| S | Large FS | 7.2 ± 1.2 | 7.0 ± 0.9 | 0.91 | 18.1 ± 3.2 | 16.7 ± 1.9 | 0.75 |
| | Random FS | 2.2 ± 0.2 | 2.0 ± 0.2 | 0.42 | 6.7 ± 1.4 | 4.8 ± 0.4 | 0.25 |
| | Random Plot | 2.0 ± 0.3 | 1.7 ± 0.2 | 0.38 | 4.7 ± 0.6 | 4.0 ± 0.4 | 0.44 |
| | Straight Transect | 1.3 ± 0.1 | 1.2 ± 0.1 | 0.72 | 3.1 ± 0.3 | 2.9 ± 0.3 | 0.57 |
| | | | | | | | |

Browse density varied significantly among path types at foraging paths and regenerating stands in winter and summer (ANOVA, Foraging Paths Winter $F_{3,112} > 66.1$; Regenerating Stands Winter $F_{3,116} > 40.9$; Foraging Paths Summer $F_{3,164} > 14.8$, Regenerating Stands Summer $F_{3,116} > 36.3$; all comparisons $P < 0.0001$; Table 1). Regardless of density unit (twigs/m² or biomass/m²) large feeding station paths always had the highest density, followed by random feeding station paths, random plot paths, and straight transects. The density measured by large feeding station paths in winter and summer was approximately five times greater than the density measured using the other three path types.

In winter browse density increased with stand age, but the relationship was weak ($R^2 < 0.10$; Figure 4). When winter browse density at regenerating stands was averaged in three age classes (1-11, 12-

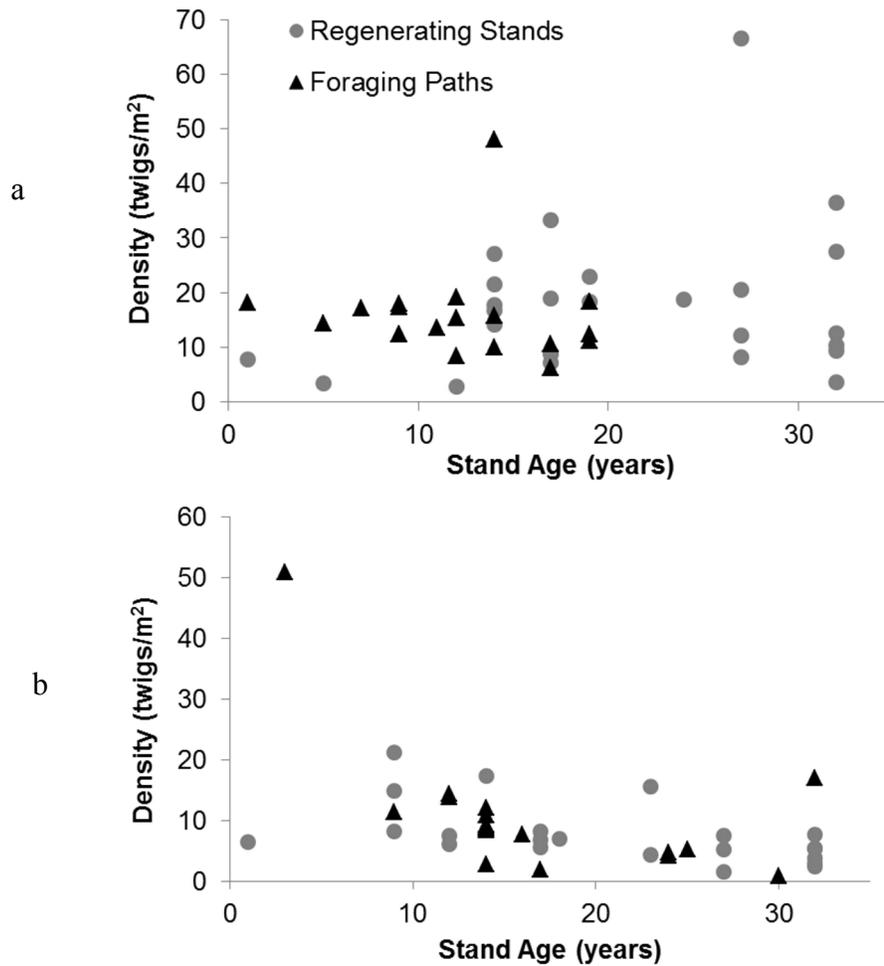


Figure 4. Relationship between browse density as stands mature after forest harvest in (a) winter and (b) summer.

21, and 22-32 years post-disturbance) the browse density was always largest 22-32 years post-disturbance regardless of path type (Table 2). In winter browse density at large feeding stations 1-11 years post-disturbance was 9.3 ± 2.6 twigs/m². The density nearly doubled to 18.4 ± 2.2 twigs/m² 12-21 years post-disturbance and then increased to 20.2 ± 5.04 twigs/m² 22-32 years post-disturbance (Table 2). The difference in density between the three age classes at large feeding station paths and random feeding station paths was not significantly different between the three age classes (ANOVA, $F_{2,27} < 3.2$, $P > 0.06$) while the differences at random plot paths and straight transects were significant (ANOVA, $F_{2,27} > 3.48$, $P < 0.045$).

In contrast to winter density, summer browse density decreased with stand age, although the relationship was again weak ($R^2 < 0.27$; Figure 4). When summer browse density was averaged in three age classes the browse density was always largest 1-11 years post-disturbance regardless of path type. Density at regenerating stands measured by large feeding stations was 12.7 ± 3.4 twigs/m². The density decreased to 7.1 ± 1.1 twigs/m² 12-21 years post-disturbance, and then decreased to 5.3 ± 1.2 twigs/m² 22-32 years post-disturbance (Table 2). The difference between age classes was significant when measured by large feeding station paths (ANOVA, $F_{2,25} = 4.5$, $P = 0.02$). However, the difference in

Table 2. Browse density \pm SE (twigs/m²) in regenerating stands of three age classes measured by four path types in winter and summer. FS = Feeding Station. In winter N was 6 in the 1-11 years class and 12 in the 12-21 and 22-32 years classes. In summer N was 4 in the 1-11 years class, 12 in the 12-32 years class, and 11 in the 22-32 years class.

| Season | Path Type | Stand Age (years) | | | <i>P</i> |
|--------|-------------------|-------------------|----------------|----------------|--------------|
| | | 1-11 | 12-21 | 22-32 | |
| Winter | Large FS | 9.3 ± 2.6 | 18.4 ± 2.2 | 20.2 ± 5.0 | <i>0.21</i> |
| | Random FS | 2.0 ± 0.4 | 3.0 ± 0.2 | 3.1 ± 0.3 | <i>0.06</i> |
| | Random Plot | 1.7 ± 0.4 | 2.8 ± 0.2 | 2.7 ± 0.2 | <i>0.03</i> |
| | Straight Transect | 1.2 ± 0.4 | 2.5 ± 0.3 | 2.3 ± 0.3 | <i>0.045</i> |
| Summer | Large FS | 12.7 ± 3.4 | 7.1 ± 1.1 | 5.3 ± 1.2 | <i>0.02</i> |
| | Random FS | 2.5 ± 0.2 | 2.3 ± 0.3 | 2.0 ± 0.4 | <i>0.051</i> |
| | Random Plot | 2.0 ± 0.3 | 1.8 ± 0.2 | 1.5 ± 0.2 | <i>0.16</i> |
| | Straight Transect | 1.7 ± 0.3 | 1.3 ± 0.3 | 1.0 ± 0.2 | <i>0.29</i> |

browse density among the three age classes was not significant when measured by random feeding station paths, random plot paths, and straight transects (ANOVA, $F_{2,25} < 3.4, P > 0.051$). Large feeding station paths again had the highest density, followed by random feeding station paths, random plot paths, and then straight transects in both winter and summer (Table 2).

Available Species Composition

Winter

In winter 75% of the available twigs along foraging paths were hazel, paper birch, willow, and balsam fir (Table 3). At these locations there was no significant difference in the available species composition measured by the four path types (Kruskal-Wallis test, $H_3 < 6.69, P > 0.08$). Similarly, within regenerating stands 75% of the available twigs were again hazel, paper birch, and balsam fir plus

Table 3. Mean available species composition (%) at all four path types along foraging paths (FP) and within regenerating stands (RS) in winter. Regenerating stands were chosen independently of moose foraging. Significant differences between foraging paths and regenerating stands at each path type are denoted by an asterisk. Sums do not add up to 100% because rare species are not shown. FS = Feeding Station.

| Species | Path Type | | | | | | | |
|-------------------|-----------|------|-----------|------|-------------|------|-------------------|-----|
| | Large FS | | Random FS | | Random Plot | | Straight Transect | |
| | FP | RS | FP | RS | FP | RS | FP | RS |
| Hazel | 34 | 32 | 32 | 34 | 34 | 34 | 39 | 30 |
| Paper birch | 20 | * 12 | 19 | * 13 | 17 | * 13 | 10 | 12 |
| Willow | 11 | 8 | 12 | 6 | 11 | 6 | 8 | 5 |
| Balsam fir | 10 | * 22 | 13 | * 26 | 15 | * 26 | 18 | 29 |
| Quaking aspen | 5 | * 4 | 7 | 3 | 7 | * 2 | 8 | * 4 |
| Juneberry | 5 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| Red maple | 4 | <1 | 2 | <1 | 2 | <1 | 1 | <1 |
| Red-osier dogwood | 3 | 3 | 2 | 2 | 2 | 2 | 3 | 2 |
| Mountain maple | 3 | * 11 | 3 | 9 | 3 | 9 | 4 | 9 |
| Pin cherry | 3 | 2 | 2 | 3 | 3 | 3 | 2 | 2 |
| Sum | 98 | 97 | 97 | 96 | 98 | 98 | 98 | 96 |

mountain maple and again, there was no significant difference in the available species composition measured by the four path types in winter at regenerating stands (Kruskal-Wallis test, $H_3 < 3.15$, $P > 0.37$; Table 3).

Most (34 of 44) species composition comparisons between foraging paths and regenerating stands measured by each path type in winter were not significantly different (Kruskal-Wallis test, $H_3 < 3.65$, $P > 0.06$). However, there was a significant difference between the available proportion along foraging paths and within regenerating stands for balsam fir measured by large feeding station paths, mountain maple measured by large feeding stations paths, paper birch measured by large feeding station paths, random feeding station paths, and random plot paths, and quaking aspen measured by large feeding station paths, random plot paths and straight transects (Kruskal-Wallis test, $H_3 > 2.8$, $P < 0.05$; Table 3).

Summer

In summer 75% of the available twigs at foraging paths were mountain maple, willow, hazel, and quaking aspen (Table 4). There was no significant difference in the available species composition measured by the four path types at summer foraging paths (Kruskal-Wallis test, $H_3 < 6.75$, $P > 0.08$). At regenerating stands in summer 70% of the available twigs were again mountain maple, willow, and hazel with the addition of juneberry (Table 4). As in the foraging paths, within the regenerating stands in summer there was no significant difference in the available species composition measured by the four path types (Kruskal-Wallis test, $H_3 < 3.15$, $P > 0.37$). The one exception occurred in both foraging paths and regenerating stands when approximately 38% of available twigs were hazel along straight transects while 14% were hazel at large feeding stations (Kruskal-Wallis test, $H_3 > 9.69$, $P < 0.02$).

Most (36 of 44) species composition comparisons between foraging paths and regenerating stands by each path type in summer were not significantly different (Kruskal-Wallis test, $H_3 < 3.58$, $P > 0.06$). However, there was a significant difference between the available proportion at foraging paths and regenerating stands for juneberry measured by all path types, red-osier dogwood measured by random plot paths and straight transects, mountain ash measured by random feeding station paths and random plot

paths, and rarely available species measured by large feeding station paths, random feeding station paths, and random plot paths (Kruskal-Wallis test, $H_3 > 4.47$, $P < 0.03$; Table 4).

Table 4. Mean available species composition at all four path types along foraging paths (FP) and within regenerating stands (RS) in summer. Regenerating stands were chosen independently of moose foraging. Significant differences between foraging paths and regenerating stands at each path type are denoted by an asterisk. Sums do not add up to 100% because rare species are not shown. FS = Feeding Station.

| Species | Path Type | | | | | | | |
|--------------------------------|-----------|------|-----------|------|-------------|------|-------------------|-----|
| | Large FS | | Random FS | | Random Plot | | Straight Transect | |
| | FP | RS | FP | RS | FP | RS | FP | RS |
| Mountain maple | 38 | 22 | 36 | 23 | 29 | 22 | 17 | 15 |
| Willow | 16 | 16 | 13 | 10 | 14 | 10 | 12 | 10 |
| Hazel ¹ | 14 | 14 | 17 | 19 | 27 | 23 | 39 | 37 |
| Quaking aspen | 9 | 3 | 9 | 5 | 9 | 6 | 7 | 6 |
| Paper birch | 8 | 15 | 9 | 18 | 6 | 17 | 10 | 9 |
| Mountain ash | 3 | 1 | 4 | * 1 | 4 | * 0 | 2 | 1 |
| Juneberry | 3 | * 17 | 3 | * 13 | 3 | * 10 | 4 | * 7 |
| Pin cherry | 2 | 0 | 1 | 2 | 1 | 2 | 2 | 1 |
| Red maple | 1 | 6 | 1 | 5 | 1 | 5 | 2 | 6 |
| Red-osier dogwood ¹ | 1 | 4 | 1 | 4 | 0 | * 4 | 1 | * 4 |
| Sum | 94 | 94 | 94 | 95 | 98 | 98 | 98 | 96 |

¹ These species are rare in the diet in summer (Ward 2014)

Regenerating Stand Age

Species composition at the regenerating stands varied by age class. Most of the changes between age classes were true in winter and summer. Paper birch, quaking aspen and pin cherry were most abundant 1-11 years post-disturbance and became less available with increasing stand age in both seasons (Tables 5 and 6). Hazel, mountain maple, and juneberry were available in low proportions 1-11 years post-disturbance and became increasingly available with stand age in both seasons. Hazel and mountain maple became common enough to be two of the top four available species by 22 years post-disturbance. Balsam fir was only measured in winter, but it was also found in low proportions at young stands and became increasingly available 12 years post-disturbance. Red-osier dogwood and red maple consistently occurred at low proportions in all age classes in both seasons. Mountain ash was also available at

consistently low proportions in all age classes in summer and was included in the “rarely available” species in winter.

Table 5. Available species composition at regenerating stands of three different age classes measured by four path types in winter. “LF” = Large Feeding Station path, “RF” = Random Feeding Station path, “RP” = Random Plot path, “ST” = Straight Transect. Significant differences between age classes within one path type are denoted by an asterisk in the 1-11 years age class. There were no significant differences between the path types within an age class.

| Species | Stand Age (years) | | | | | | | | | | | |
|-------------------|-------------------|-----|-----|-----|-------|----|----|----|-------|----|----|----|
| | 1-11 | | | | 12-21 | | | | 22-32 | | | |
| | LF | RF | RP | ST | LF | RF | RP | ST | LF | RF | RP | ST |
| Paper birch | 43* | 40 | 41* | 43* | 6 | 9 | 9 | 7 | 1 | 4 | 4 | 2 |
| Willow | 26 | 22 | 20 | 20* | 7 | 2 | 1 | 2 | 1 | 3 | 3 | 1 |
| Quaking aspen | 18 | 10 | 10 | 18* | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 |
| Pin cherry | 8 | 8 | 7 | 1 | 1 | 3 | 3 | 5 | 1 | 1 | 1 | 0 |
| Balsam fir | 2* | 12 | 13 | 2* | 20 | 30 | 30 | 31 | 34 | 29 | 29 | 42 |
| Red-osier dogwood | 1 | 3 | 5 | 5 | 3 | 2 | 2 | 0 | 4 | 0 | 0 | 1 |
| Hazel | 0* | 4* | 4* | 6* | 45 | 39 | 39 | 38 | 35 | 44 | 44 | 34 |
| Mountain maple | 0* | 0* | 0* | 0* | 11 | 7 | 7 | 8 | 17 | 15 | 15 | 15 |
| Juneberry | 0 | 0 | 0 | 0 | 4 | 4 | 4 | 3 | 4 | 3 | 3 | 4 |
| Red maple | 0 | 0* | 0* | 0* | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 |
| Sum | 98 | 100 | 100 | 95 | 98 | 97 | 97 | 96 | 99 | 99 | 99 | 98 |
| N | 6 | | | | 12 | | | | 12 | | | |

Willow was the only species with different trends depending on the season. In winter, willow was most abundant 1-11 years post-disturbance and became less available in older stands (Table 5). In summer willow occurred at similar proportions in all three age classes (Table 6). However, the average amount of willow was skewed toward a higher estimate at the 12-21 year and 22-32 year post-disturbance regenerating stands because a few sites in each of these age classes had more than 50% willow while most of the sites in those age classes had 0% willow.

Many (22 of 44) species composition comparisons between age classes were not significantly different in winter (Kruskal-Wallis test, $H_3 < 5.43$, $P > 0.07$). However, there was a significant difference between the available proportion at the three age classes for hazel and mountain maple measured by all

Table 6. Available species composition at regenerating stands of three different age classes measured by four path types in summer. “LF” = Large Feeding Station path, “RF” = Random Feeding Station path, “RP” = Random Plot path, “ST” = Straight Transect. Significant differences between age classes within one path type are denoted by an asterisk in the 1-11 years age class. There were no significant differences between the path types within an age class.

| Species | Regenerating Stands (years) | | | | | | | | | | | |
|-------------------|-----------------------------|----|-----|-----|-------|----|----|----|-------|-----|-----|----|
| | 1-11 | | | | 12-21 | | | | 22-32 | | | |
| | LF | RF | RP | ST | LF | RF | RP | ST | LF | RF | RP | ST |
| Paper birch | 52* | 40 | 38* | 18 | 14 | 15 | 15 | 11 | 4 | 16 | 14 | 6 |
| Quaking aspen | 11* | 16 | 21 | 29* | 2 | 6 | 6 | 5 | 0 | 2 | 1 | 0 |
| Willow | 11 | 10 | 10 | 14 | 13 | 10 | 8 | 5 | 22 | 11 | 13 | 14 |
| Juneberry | 6 | 5 | 5 | 8 | 15 | 14 | 9 | 6 | 19 | 14 | 12 | 6 |
| Hazel | 6 | 14 | 15 | 18 | 18 | 20 | 24 | 38 | 12 | 19 | 24 | 43 |
| Red-osier dogwood | 5 | 1 | 1 | 1 | 3 | 4 | 5 | 7 | 5 | 5 | 4 | 2 |
| Red maple | 4 | 5* | 2* | 4 | 2 | 1 | 1 | 4 | 6 | 2 | 3 | 5 |
| Pin cherry | 2* | 4 | 4 | 5 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 1 |
| Mountain maple | 1 | 2 | 2 | 1 | 28 | 24 | 23 | 15 | 22 | 31 | 28 | 20 |
| Mountain ash | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| Sum | 100 | 99 | 99 | 97 | 96 | 97 | 95 | 92 | 91 | 100 | 100 | 99 |
| N | 4 | | | | 12 | | | | 11 | | | |

path types, paper birch measured by all paths except random feeding station paths, quaking aspen and willow measured by straight transects, balsam fir measured by large feeding station paths and straight transects, and red maple measured by all paths except large feeding station paths (Kruskal-Wallis test, $H_3 > 8.10$, $P < 0.04$; Table 5).

Most (37 of 44) species composition comparisons between age class in summer were not significantly different (Kruskal-Wallis test, $H_3 < 7.55$, $P > 0.06$). However, there was a significant difference between the available proportion at the three age classes for paper birch measured by large feeding station paths and random plot paths, quaking aspen measured by large feeding station paths and straight transects, pin cherry measured by large feeding station paths, red maple measured by random feeding station paths and random plot paths, and rarely available species measured by random feeding station paths (Kruskal-Wallis test, $H_3 > 8.10$, $P < 0.04$; Table 6).

Within each age class the proportions of each species measured by the four path types were never statistically different in winter (Kruskal-Wallis test, $H_3 < 4.56, P > 0.20$) or summer (Kruskal-Wallis test, $H_3 < 6.97, P > 0.07$).

Foraging Path Stand Age

In winter 8 of 29 foraging paths were in stands 1-11 years post-disturbance, 11 were in stands 12-21 years post-disturbance, none were in stands 22-32 years post-disturbance and the remaining 10 were in stands 33+ years post-disturbance. In summer 2 of 42 foraging paths were in regenerating stands 1-11 years post-disturbance, 10 were in stands 12-21 years post-disturbance, 3 were in stands 22-32 years post-disturbance and the remaining 27 were in stands 33+ years post-disturbance.

Because over two thirds of the foraging paths in summer were in stands 33+ years post-disturbance we averaged the available species composition at the foraging paths we measured in that age class. At these foraging paths 55% of the available twigs at large feeding stations were mountain maple, 15% were hazel, 8% were quaking aspen, and 7% were willow (Table 7).

Table 7. The percent of available twigs of each species at 27 foraging paths in the 33+ years post-disturbance age class in summer. FS = Feeding Station.

| Species | Path Type | | | |
|-------------------|-----------|-----------|-------------|-------------------|
| | Large FS | Random FS | Random Plot | Straight Transect |
| Willow | 7 | 12 | 13 | 8 |
| Hazel | 15 | 19 | 28 | 42 |
| Mountain maple | 55 | 43 | 34 | 15 |
| Paper birch | 5 | 5 | 3 | 11 |
| Juneberry | 1 | 2 | 2 | 5 |
| Mountain ash | 3 | 1 | 3 | 1 |
| Red-osier dogwood | 1 | 1 | 0 | 1 |
| Quaking aspen | 8 | 10 | 10 | 9 |
| Pin cherry | 0 | 0 | 0 | 2 |
| Red maple | 1 | 1 | 1 | 2 |
| Rare | 5 | 6 | 5 | 4 |

Discussion

Browse species composition was similar at foraging paths and regenerating stands. This led us to reject our first hypothesis that foraging paths would have more commonly browsed species available than the regenerating stands. It also indicates that some regenerating stands have a species composition that is similar to areas in which moose are choosing to forage. This provides evidence that moose habitat restoration projects which create regenerating forest by harvesting, shearing, or otherwise removing older plant growth can effectively provide the same browse species in similar proportions to current foraging locations.

The distance moose traveled to complete ten large feeding stations along a foraging path (and the distance we traveled to complete ten simulated large feeding stations within regenerating stands) was half of the distance required to complete ten plots of the other three path types in summer and one quarter the distance in winter. This indicates that browsing moose would reduce travel time between feeding stations while gaining the greatest amount of browse.

Browse density along foraging paths and within regenerating stands was not significantly different in summer and in most comparisons in winter. The few that were statistically different in winter were not biologically different. For example, the density at foraging paths estimated by biomass along random feeding stations in winter ($1.7 \pm 0.1 \text{ g/m}^2$) was 0.7 g/m^2 smaller than at regenerating stands ($2.4 \pm 0.2 \text{ g/m}^2$). This led us to reject our second hypothesis that moose were foraging in areas with higher browse densities than recently disturbed areas that we selected at random. This also provides support for moose habitat restoration projects because regenerating stands provide a similar density of twigs as areas which moose are foraging in based on GPS collar locations.

We partially accepted our third hypothesis that browse density would be highest in young stands and decrease with age because we observed this trend in summer but not in winter. Browse density is widely accepted to decrease with stand age (Peek 1997) although the winter trend we measured was also observed in Alaska (Weixelman et al. 1998). Part of the winter browse density trend was due to counting balsam fir and hazel as available species in winter but not in summer. Balsam fir and hazel have growth

patterns that increase the number of these plants in a stand and the number of twigs per plant (Ward 2014). These characteristics allowed very high twig counts of hazel and balsam fir in short distances in winter. However, hazel and balsam fir did not become prevalent in the regenerating stands we measured until 12 years post-disturbance in winter, which is also when winter densities began to increase above 20 twigs/m² (Figure 4). By 22 years post-disturbance hazel and balsam fir made up >65% of the available twigs we measured. Therefore, because hazel and balsam fir had high twig counts when present, and they became more prevalent as stands aged, the overall browse density increased as stands aged in winter.

We were surprised that hazel was present in low proportions in stands 1-11 years post-disturbance in winter because it is one of the most constant species across the landscape and was abundant in summer stands we measured 1-11 years post-disturbance. One explanation for this discrepancy was that we only measured six stands in the youngest age class in winter. It is possible that increasing the number of plots sampled would modify the proportion of hazel in younger stands.

Browse density was significantly different among path types and large feeding stations always had higher densities of browse. Browse density from the perspective of a moose that forages from large feeding station to large feeding station is greater than browse density that is measured with a straight transect. Similarly, using the large feeding station method to measure available browse would result in measuring browse patches with high densities of twigs. Browse density measured at what we call large feeding stations will be greater than browse densities measured by straight transects or square quadrats. Additionally, browse species composition was similar regardless of the path type in both randomly selected regenerating stands and actual moose foraging paths. This provides additional evidence for the accuracy of the large feeding station method.

The foraging paths we measured occurred evenly in three of four age classes in winter (1-11, 12-21, and 33+ years post-disturbance), but in summer the foraging paths were mostly in the 12-21 and 33+ years post-disturbance age classes. We never measured a foraging path in the 22-32 year age class in winter and only three of the summer foraging paths were in this age class indicating that stands in the age class may have a characteristic that deters moose from foraging in them. It is also possible that when we

chose which foraging paths to measure these 22-32 year old stands were less accessible and therefore measured less often. However, since stands in this age class were harvested 22-32 years earlier, there are often roads or paths leading to them, which indicates that lack of access may not have been a factor. A more likely explanation is that moose are choosing to walk through these 22-32 year old stands instead of stopping to browse. The stands between 22 and 32 years post-disturbance in winter have >65% hazel and balsam fir, and in summer (when balsam fir was not counted) hazel was 12% of the available twigs at large feeding stations and 43% of the available twigs at straight transects. Additionally, because hazel and balsam fir are so common they are consumed, but classified as avoided, in summer and winter (Ward 2014). This indicates that stands between 22 and 32 years of age offer many twigs of two negatively selected species and small amounts of other species.

Although the browse density of summer twigs we measured was highest in the youngest age class, only two of the 42 foraging paths we measured were in the 1-11 year age class while two thirds of the foraging paths we measured were in stands 33+ years post-disturbance. One explanation for this is that our foraging paths were measured in mid to late summer when leaves in shaded areas are more nutritious and senesce later (Peek 1997, Augsburger and Bartlett 2003). Moose also appeared to prefer mature stands in late summer in Minnesota in the past (Peek et al. 1976). Moose could also be foraging in shaded areas because of other benefits such as cover from predators, cooler air temperatures, and closer proximity to thermal refugia.

Because our youngest age class had a small sample size and our study area was restricted to the southern edge of moose range in northeastern Minnesota we cannot make any statements about the best years post-disturbance for browse availability in northeastern Minnesota with confidence. However we can suggest trends based on our data that should be tested. First, the data suggests that although stands 22-32 years post-disturbance in winter offered the highest densities of common browse species, we did not observe moose foraging in these stands. Second, although the youngest stands offered the highest browse densities and high quantities of three of the most common browse species in summer, we had only two moose foraging paths in this age class. These trends suggest that factors other than browse density and

available browse species composition influence where moose forage. This data also indicates that moose use stands of different ages for foraging during late summer and winter. One possible future test would be to analyze the entire data set of locations for all GPS collared moose instead of focusing on only the foraging paths we visited (Ward 2014).

In efforts to restore moose habitat, maintaining a mosaic landscape of many different stand ages may help provide moose with different habitats and browse species. Future research should be completed across a larger area of moose range in Minnesota to determine which stand ages provide the best browse for moose in the region. Furthermore, measuring stands in the years following different disturbances such as fire, wind throw, and forest harvest could inform us about effects these various disturbances have on browse density and composition in Minnesota.

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