Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Grimsö Wildlife Research Station

Moose foraging patterns: Implications for the use of browsing indices

Sara Lindqvist

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Sara Lindqvist

Supervisor:	Johan Månsson, Department of Ecology, SLU. Grimsö Wildlife Research Station, 730 91 Riddarhyttan, Email: Johan.Mansson@slu.se
Assistant supervisor:	Jean-Michel Roberge, Department of Wildlife, Fish and Environmental Studies, SLU. Inst. för vilt, fisk och miljö, Skogsmarksgränd, 901 83 UMEÅ Email: jean-michel.roberge@slu.se
Examiner:	Gunnar Jansson, Department of Ecology, SLU. Grimsö Wildlife Research Station, 730 91 Riddarhyttan E-mail: gunnar.jansson@slu.se

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Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Grimsö Wildlife Research Station
730 91 Riddarhyttan
SWEDEN

ABSTRACT

Moose (*Alces alces*) foraging on young Scots pine (*Pinus sylvestris*) might reduce economical profit in forestry due to deteriorated log quality and biomass loss. Different indices are used to quantitatively estimate browsing effect on this tree species. I wanted to compare the relationship between two commonly applied survey methods for assessing browsing: the Moose Damage and the Browsing Pressure surveys. Furthermore a variety of factors influencing browsing intensity have been identified, yet moose selectivity for apical or lateral shoots of Scots pine has never been tested. Data on damage and browsing pressure was collected in young Scots pine stands (n=60 stands) within the southern boreal zone in Sweden. Logistic models were fitted to test the relationship between the indices and other factors possibly influencing the relation: pine density and mean stand height. Moose browsed the same relative proportions of apical and lateral shoots in relation to availability and there was no significant difference in selectivity towards either of the shoot categories, suggesting that moose forage shoots proportionally to what is available. The relationship between the two browsing indices was significant but the fit was not statistically perfect. Damage and browsing pressure most often coincided but browsing pressure did not always equate to stem damage. The Moose Damage survey could be used in favor of Browsing Pressure survey although both pine density and mean stand height also significantly affected the relationship between the methods. Hence using stem damage to predict browsing pressure (and vice versa) should be done with caution.

Key words: *Alces alces*, selectivity, Scots pine, browsing pressure, stem damage

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INTRODUCTION

Moose and forest interaction occupies a central position in Scandinavian forestry (Hörnberg 2001; Lavsund et al. 2003). Effects of moose browsing on the economically valuable tree species Scots pine have been observed and documented in Sweden since the early 20^{th} century (Swedish Governmental Official Report; 1932:26). Due to changes in moose harvest strategies (Lavsund et al. 2003), silvicultural and agricultural practices combined with low predator densities, the Swedish moose population has increased in numbers compared to the levels observed during the first half of the last century (Kalén 2005). After the population peak in the 1980's (Lavsund et al. 2003) concerns considering moose affection for young Scots pine stands have been highlighted (Hörnberg 2001).

Browsing pressure at different scales

Forage availability (Bergström et al. 1995; Hörnberg 2001; Månsson et al. 2007a; Månsson et al. 2007b) and moose density (Bergqvist et al. 2001; Persson et al. 2005) are two identified factors influencing moose browsing intensity across different spatial and temporal scales. Browsing intensity is also affected by other factors such as tree height (Bergqvist et al. 2001), forage species composition (Edenius 1991; Månsson 2009), site productivity and snow depth (Hörnberg 2001). Forest practices such as regeneration strategies are also influential (Kalén 2005).

Moose is not only selective at the scales of landscapes, forest stands and individual trees but also at the within – tree scale. Hence, palatability (Gill 1992), as well as morphological and bromatological characteristics influence moose selectivity (Palo et al. 1992). At the within – tree level, moose has been suggested to select for 1) shoots with a slim diameter (Danell et al. 1991), 2) shoots that provide a high energy intake relative to the occurrence of substances like isoprenoids and phenols; i.e. chemical defense substances accumulate in apical shoots during wintertime (Palo 1984). Therefore a difference might be expected in the selection of lateral and apical shoots in moose diet.

Exposure to browsing may induce both chemical and morphological responses that transform the physical characteristics of the individual tree (Gill 1992). Depending on the extent, browsing of shoots might suppress future growth (Gill 1992; Edenius et al. 1993) and detriments to the stem may influence the shape of the tree (Gill 1992).

Browsing of Scots pine by moose mainly occurs in wintertime and can be subdivided in two categories, 1) browsing of apical shoots and/or other mechanical effects on the stem caused by bark stripping and stem breakage and 2) browsing of lateral shoots (Gill 1992; Bergqvist et al. 2001).

Assessments of browsing impacts

In forest industry the effects of browsing are frequently considered and equated to undesired conditions and damage (Putman 1996; Reimoser et al. 1999; Kalén 2005). The browsing impact on Scots pine is assumed to cause extensive economical loss from a forestry perspective due to reduced log quality (Bergqvist et al. 2001) and biomass loss (Putman 1996). Several methods have been developed to survey the effects of browsing (Bergström et al. 1995; Holm 2001; Morellet et al. 2001; Kalén et al. 2009). The definition of damage varies with spatial and temporal scale and is connected to the goals of the silvicultural practices.

In Sweden two methods are commonly used to estimate moose browsing effects on Scots pine trees: 1) the Browsing Pressure (BP) survey (Bergström et al. 1995; Hörnberg 2001; Månsson et al. 2007a) and 2) the Moose Damage (MD) survey (Bergqvist et al. 2001; Kalén et al. 2009). The two methods focus on slightly different aspects that may affect forest production negatively.

The BP survey focuses on quantitative measures of the percentage of available shoots (apical and lateral shoots) consumed. The method has mainly been used to increase the knowledge, and evaluate moose feeding behavior and biomass utilization in relation to forage availability under different conditions (Edenius 1991; Bergström et al. 1995; Hörnberg 2001; Månsson et al. 2007a; Månsson et al. 2007b).

MD is a method intended to register qualitative browsing effects on the main stem caused by apical shoot browsing, bark stripping and stem breakage. The method is utilized to estimate the proportion of stems negatively affected by moose browsing on a landscape level (Holm, 2001; Kalén et al. 2009; Rolander et al. 2011) and focuses primarily on Scots pine (Holm, 2001, Rolander et al. 2011). The method is mainly applied in commercial forestry as an attempt to assess and predict future economical losses due to a perceived reduction in quality of the tree stems caused by browsing.

Study objective

Knowledge about any relationship between the BP method and the MD survey is deficient. But apical shoot browsing is included in both survey methods; although in BP, shoots of different categories are not distinguished (Bergström et al., 1995). The aim of this study is to examine if and to what extent the two methods are comparable and whether one of the methods/indices can be used to predict the other. Knowledge about the extent to which the methods are related is interesting from a management perspective since the indices can be adjusted and improved to strengthen their field of application. Furthermore, if the relationship is strong the least expensive and time consuming method can be used as a substitute for the other.

A relationship between the indices is expected since browsing pressure and effects on the stem previously have revealed a positive relationship (Bergqvist et al. 2001). However, browsing pressure does not automatically equate with negative effects to the stem. The relationship may be affected if moose display selectivity between apical or lateral shoots. Based on moose foraging behavior, the proportion of browsed apical shoots in the diet is expected to be lower than the consumption of lateral shoots (Danell et al. 1991; Palo et al. 1992). At low level of browsing pressure, selectivity for lateral shoots would increase the number of occasions (compared to no selectivity or selectivity for apical shoots) where one would find browsing but no damage because the apical shoots are avoided. At higher level of browsing pressure such occasions would become increasingly rare.

The objective of this study was to examine 1) if there is any selectivity in moose utilization of apical versus lateral shoots in relation to availability, 2) to what extent the two survey methods are related and 3) to evaluate if additional variables affect the potential relationship between the two indices. Here the factors previously proven to influence browsing (tree density and stand height) were tested.

MATERIAL AND METHODS

Study area

The study was conducted in the southern boreal zone in an area (418 km^2) covering the Grimsö Wildlife Research Area (59˚44'N, 015˚28'E) (Figure 1). The vegetative growth period is 170 days per year (daily mean temperature > 5˚C). The annual precipitation averages from 600 – 800 mm, out of which roughly 30 % fall as snow. The snow covers the ground approximately 150 days from December to March and the depth generally varies between 20 – 30 cm. During the winter, 2011 – 2012, the number of days covered by snow was less than normal mean value (Swedish Meteorological and Hydrological Institute, 2012). The area is dominated by managed, coniferous forests (75 %), mires and bogs (12 %), rivers and lakes (7 %) and other land use (6 %). The dominating tree species in the forest matrix are Scots pine and Norway spruce (*Picea abies*) mixed with deciduous trees of silver (*Betula pendula*) and downy birch (*Betula pubescens*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and sallow species (*Salix* sp.) with sparse occurrence of lodgepole pine (*Pinus contorta*), juniper (*Juniperus communis*) and Siberian larch (*Larix sibirica*). Heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), and lichens (*Cladonia* sp.) mainly covers the field layer (Rönnegård et al. 2008).

Winter moose density was estimated, by aerial counts 2006, to 8 moose per 1000 ha (Rönnegård et al. 2008). Pellet group counts, conducted annually in spring within the Grimsö Wildlife Research Area, estimated population densities to 12.5 ± 1.54 for moose, and 9.87 ± 1.48 roe deer (*Capreolus capreolus*) per 1000 ha, in 2011, according to Jansson (pers. comm. May 2012). Red deer (*Cervus elaphus*) occurs in small numbers, mountain hare (*Lepus timidus*), European hare (*Lepus europaeus*) and wild boar (*Sus scrofa*) are also present within the study area.

Sampling design

The field work was carried out in April to early May 2012. Forest stands (n=60) (Figure 1) were randomly selected among stands that fulfilled the following criteria: 1) ≥ 50 % Scots pine, 2) age interval 3 – 15 years, 3) distance between stands ≥ 1 km and 4) height interval 0.3 – 3 m (Bergström et al. 1995; Månsson et al. 2007a; Rolander et al. 2011). The landowner's (state owned forest enterprise Sveaskog) stand database (GIS based) was used for the selection. If the stand did not meet the criteria when visited in field the next stand in order was selected. In every stand, 10 survey plots were systematically distributed within stands with a random starting point along the longest side of each stand (Figure 1), using a hand-held GPS device. Hence the distance between the sampling plots within the stands was dependent of stand size and ranged between 15 m and 60 m.

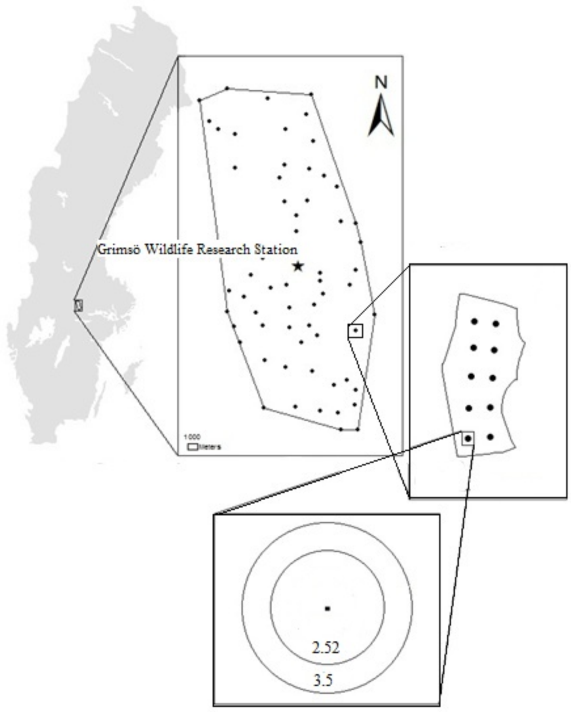

Figure 1. The location of the study area in and surrounding the Grimsö Wildlife Research Area in south central Sweden. The dots depict the surveyed stands. In each stand, 10 circular plots were systematically distributed in two parallel transects along the stand length. Each plot had two radii for collecting data: 2.52 m (for BP and MD), and 3.5 m (for MD).

Furthermore the distance criteria for the plots were ≥ 20 m from the edge of the surveyed stand with ≥ 50 m equidistant transects. If the plot did not contain any Scots pine tree or consisted of impediment e.g. water, bogs and rock, the plot was moved 10 additional meters along the transect until the criteria was fulfilled. Each plot was subdivided in two radii for collecting data (Figure 1).

Browsing Pressure

Browsing pressure was estimated; i.e. proportion of browsed shoots, in compliance with previous studies applying the methodology used to investigate browse utilization of moose (Edenius 1991; Bergström et al. 1995; Hörnberg 2001; Månsson 2009; Edenius et al. 2012), within a plot size of 20 m^2 (radius 2.52 m) and the height interval 0.3 – 3 m. This plot size has been used in previous studies and is generally accepted for browsing pressure estimation (Bergström et al. 1995; Hörnberg 2001; Månsson et al. 2007b). In the plots the browsing pressure was estimated by counting the number of available and freshly browsed shoots; ≥ 1 cm in length, originating from the previous vegetative period. Fresh browsing was assessed by the color of the wood, presence of new resin at the bite and/or the color of the cambium beneath the bark (regarded as fresh if green). Distinguishing bites from moose and roe deer is difficult. Nonetheless, all Scots pines in this study was presumed to be browsed by moose only, based on previous knowledge regarding food choice (Cederlund et al. 1980) and intake of fresh biomass for moose, approximately 10.2 kg (Hjeljord et al. 1982; Baskin and Danell, 2003), and roe deer, approximately 0.9 kg (Drozdz 1979; Baskin and Danell, 2003).

Moose Damage Survey

Moose damage survey (MD) was accomplished in conformity with applied methods in Swedish forestry and research (Kalén et al. 2009; Rolander et al. 2011; Edenius et al. 2012) by recording occurrence of fresh stem injuries; hereafter damage, caused by moose (Rolander et al. 2011) on Scots pine. The size of the sample plots was 38.48 m^2 (radius 3.5 m) and trees were considered as inside the plot if the stem was within the plot at ground level. Trees with a height equal to or greater than, half of the average height of the two highest coniferous trees were surveyed (Rolander et al. 2011). Trees that diverged extensively from the height level of the stand were not considered i.e. saved seed trees. Damage to the main stem was divided into three categories 1) bark stripping (gnawing or peeling of bark), 2) stem breakage (a broken stem beneath the top circuit of lateral shoots), 3) apical shoot browsing (browsing of the top – shoot i.e. above the top circuit of lateral shoots). If more than one type of damage occurred on the same tree it was registered separately.

In addition to the standardized MD sampling radius of 3.5 m (Rolander et al. 2011), the sampling radius of 2.52 m was also used, as a precaution to account for differences of the sampling radii effects between the two survey techniques.

Data analysis

The proportion (based on BP) of browsed apical and lateral shoots was determined, in relation to their availability, for the two shoot categories and tested for independence using a χ^2 test (Neu et al. 1974).

The means of BP and MD were estimated for the stands (n=60), expressed as proportions (of browsed shoots for BP and of damaged trees for MD), based on data collected in the sampling plots of each stand.

Generalized linear models (GLMs) (Nelder and Wedderburn 1972) with binomial errors and a logit link were fitted to test the relationship linkage of BP and MD at both sampling radii.

The same model procedure was used to explore whether other explanatory variables influence the relationship between the two indices (i.e. BP and MD) (Gill 2001; Berrington de González and Cox 2007). These additional variables were mean stand height (based on half the average height of the two highest coniferous trees), and pine density (number of Scots pine trees in each plot). Stand height may potentially affect the moose selectivity for apical or lateral shoots due to differing concentrations of chemical defense substances in the two shoot categories (Palo et al. 1992). Pine density might also influence the relative availability of lateral and apical shoots, since the morphology of Scots pines growing in dense stands differs from trees growing in more sparse stands (Edenius et al. 2002).

These predictors were tested using Pearson's correlation, to avoid interdependence ($r \geq 0.5$) (Edge et al. 1987) with MD, BP or each other. Collinearity was not regarded as a problem since all variables fell within the approved range.

To select the most parsimonious model, the corrected Akaike information criterion, (AICc), was estimated (Murtagh 2009) in a stepwise AIC model selection procedure. The model presenting the smallest AICc value was selected. All other plausible models had a ΔAICc > 2 excluding them as potential candidates, according to standard procedures (Burnham and Anderson 2004).

All analysis was performed using Microsoft Excel (2007) and the open – source statistical software R; version 2.15.1 (The R Development Core Team, 2005), using the packages Hmisc (Harrell 2012) and MASS (Venables and Ripley 2002).

RESULTS

Browsing proportions and moose selectivity

The total number of surveyed Scots pines across the stands was 4725 (radius 2.52 m) and 7706 (radius 3.5 m) individual trees. Browsing of the apical shoot was the main category of damage followed by stem breakage and bark stripping (Figure 2). This held true for both plot sizes. The mean proportion of Scots pine trees, across stands, exhibiting damage caused by moose (i.e. MD), averaged 0.042 ± 0.135 (± SD) (2.52 m plot radius) and 0.039 ± 0.117 (± SD) (3.5 m plot radius).

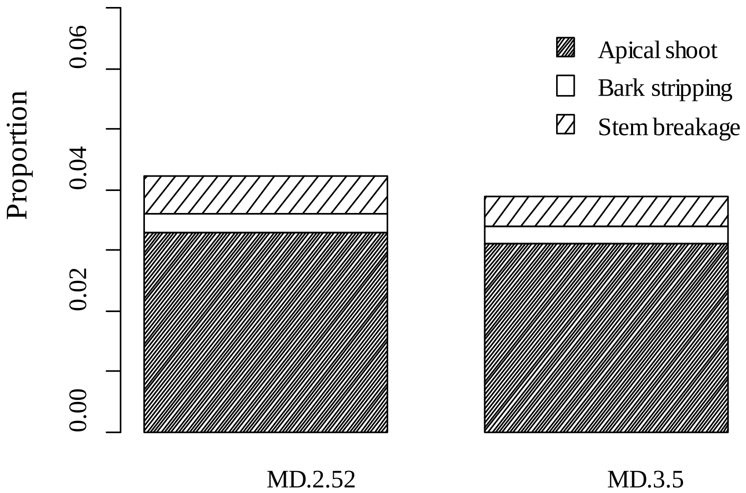

Figure 2: Distribution and proportion of the different types of stem damage in the total sample (n=60 stands) for MD 2.52 and MD 3.5 radii (m).

The total number of surveyed shoots was 295 892 out of which 6682, i.e. 0.023 were apical shoots. The browsing pressure; i.e. mean proportion of browsed available shoots (i.e. BP), averaged 0.042 ± 0.111 (± SD) across stands.

The proportions of browsed apical and lateral shoots did not differ and there was no significant selectivity for moose towards any shoot category (χ^2 = 0.060, p-value = 0.806).

Relationship between MD and BP

Logistic models (Table 1) fitting mean MD against mean BP in the stands demonstrate a highly significant ($p < 0.001$) and positive relationship between the two indices (Table 1 and Figure 3). The model parameters were very similar for the two MD survey radii (Table 1). Hence, further analyses were only conducted for the radius 3.5 m; i.e. the radius currently used for MD survey in Sweden.

Table 1: Logistic models at both radii with moose damage (MD) as the response and browsing pressure (BP) as the explanatory variable.

Model	Variable	estimate	std. error	z value	p value
MD ~ BP	Intercept	-4.19	0.12	-35.04	<0.001
(2.52 m)	BP	10.18	0.77	13.18	<0.001
MD ~ BP	Intercept	-4.32	0.10	-43.63	<0.001
(3.5 m)	BP	10.72	0.66	16.2	<0.001

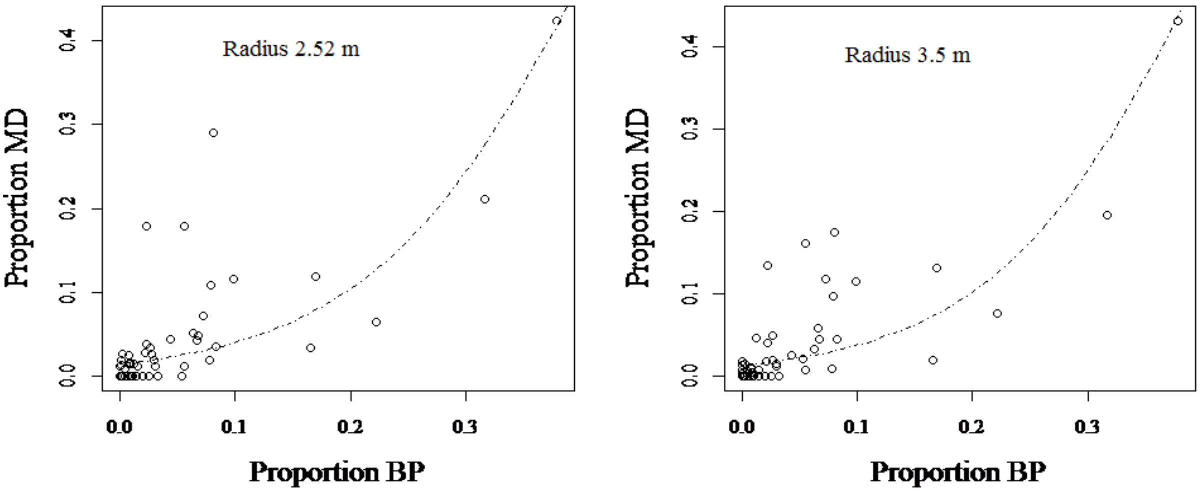

Figure 3. Relationship between moose damage (MD) at the radii 2.52 m and 3.5 m and browsing pressure (BP) at radius 2.52 m, based on the logistic models presented in Table 1 (n = 60 stands). The mean proportions of damaged Scots pines are used as the response variable and the mean proportions of browsing pressure as the explanatory variable.

Interaction model selection and exploration

According to the model selection procedure the most parsimonious model was significant (Table 2) and included, in addition to BP, mean number of Scots pine trees (Pine) in each plot, mean stand height (H), as well as the interactions between BP and Pine, as well as BP and H.

Both interactions showed a significant positive effect on the relationship between MD and BP (Table 2 and Figure 4). The slope of the relationship between MD and BP was steeper for stands with high density of pines (Figure 4A) and for stands with greater height (Figure 4B).

Table 2. Most parsimonious logistic model including AICc value, degrees of freedom and estimates. Standard errors, t- and p- values of each predictor are also shown.

Model	AICc	df	Variable	estimate	std. error	z value	p value
MDS ~ BP +	314.96	54	(Intercept)	-3.58	0.44	-8.15	<0.001
Pine + H +BP*			BP	-10.47	3.76	-2.79	0.01
Pine + BP*H			H	0.34	0.36	0.93	0.35
			Pine	-0.11	0.03	-4.27	<0.001
			BP*H	22.44	5.06	4.44	<0.001
			BP* Pine	0.81	0.17	4.74	<0.001

MD: Moose damage, BP: Browsing pressure, Pine: mean number of Scots pine trees in each plot (3.5 m), H: mean stand height

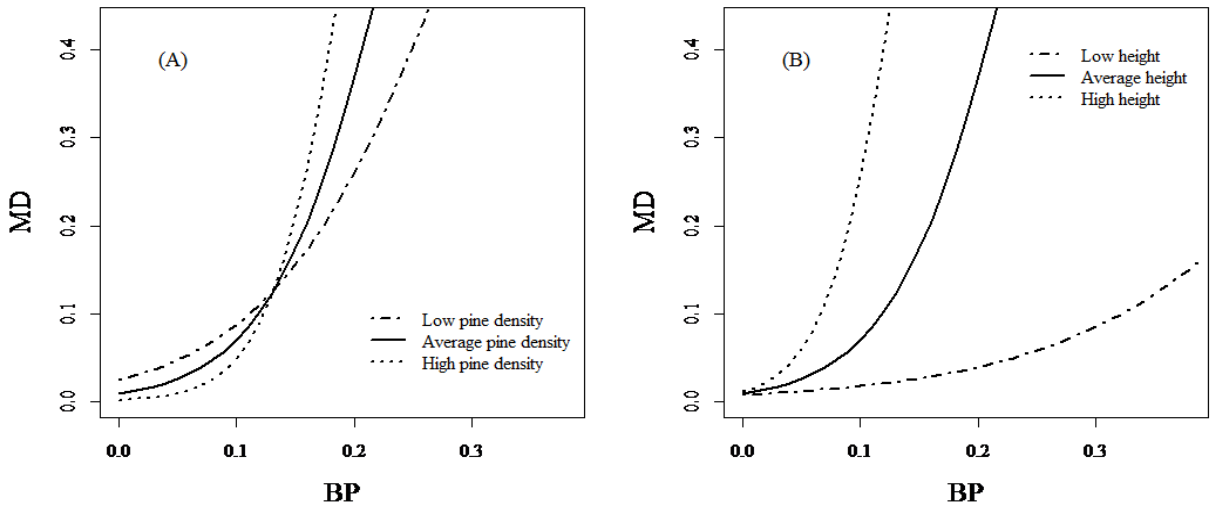

Figure 4. Graphical illustrations of the interactions between browsing pressure (BP) and (A) pine density (Pine) and (B) stand height (H) in a model predicting moose damage (MD). The factors were fixed at low, average and high levels corresponding to 3.5, 12.8 and 27.8 trees per plot for Pine and 0.74, 1.84 and 3.0 m for H, respectively.

DISCUSSION

Moose utilization of Scots pine shoots

There was no statistical significance in moose selectivity of apical versus lateral Scots pine shoots in my study. Earlier studies have suggested that moose should select for shoots with favorable palatable and morphological characteristics (Gill 1992; Bryant and Kuropat 1980). It has previously been shown that the concentration of secondary metabolites tend to increase in apical shoots during winter (Palo 1984). In addition, moose tend to forage on shoots with thin rather than thick shoot diameter (Danell et al. 1991). Hence lateral shoots were expected to be more selected than apical shoots. However my results suggest that moose forage on Scots pine shoots in accordance to what is available. An allocation of chemical defense substances may not have an apparent influence on moose foraging of Scots pine shoots, as Palo (1984) showed in his study on deciduous trees from a general herbivore perspective.

However the results from my study, addressing browsing over the whole winter, cannot discriminate whether a selective pattern applies throughout the season. In Scotland, apical shoot browsing by red deer and roe deer on sitka spruce (*Picea sitchensis*) was more frequent towards the end of winter than earlier in the season (Welch et al. 1989). Furthermore, an increase in bite diameter as winter progressed was shown on Scots pine in Norway (Histøl and Hjeljord 1993). To detect such a dynamic progress, browsing pattern would need to be surveyed repeatedly throughout the winter. In addition a non-selective foraging pattern might be derived from qualitative overlap between apical and lateral shoots; i.e. apical shoots of high quality might be selected above lateral shoots of low quality. Such a process would be difficult to capture with my methodology and requires further future investigation.

The relative availability of apical and lateral shoots is affected when apical shoots grow out of reach for moose (Bergström et al. 1995; Kalén 2005). This is not believed to strongly influence on the results of this study, since all surveyed trees and shoots were within browsing range (maximum stand height 3 m) and most were much lower than the upper limit for moose reach (mean stand height 1.84 m). Previous experiences report that most apical shoot browsing by moose occurs between 1.5 – 2 m average tree heights (Lyly and Saksa 1992), hence the conditions for detecting potential selectivity towards apical shoots should have been advantageous within the framework of this study.

Since availability of lateral shoots was much higher than apical shoots (44 times) in my study area, lateral shoots represents the bulk of moose winter diet, i.e. nonselective moose foraging behavior does not equate to equal biomass intake of the different shoot categories (Lyly and Saksa 1992).

Evaluating the relationship between MD and BP

The observed lack of selectivity for lateral or apical shoots has implications for the relationship between the two browsing indices. If apical shoots would have been selected the fitted curve would have had a steeper slope at low levels of browsing pressure compared to nonselective browsing or to selection for lateral shoots. The shape of the fitted logistic curve supports unselective pattern. However, interpretations only by looking at the curve should be made with caution, since the combination of the skewed distribution of availability of apical and lateral shoots as well as a restricted sample size (n=60) may also affect the shape of the curve. Indeed, a small sample size increases the probability to, by chance, find stands with some browsing pressure but without damage when the availability of shoot categories is strongly skewed.

The relation between the browsing indices was highly significant and did not differ between the two MD sampling radii, which implies that plot size might be of lesser importance for the relationship between the two indices.

Damage most often coincided with some proportion of browsing pressure, in line with what previously has been proposed by Bergqvist et al. (2001). On the contrary browsing pressure also occurred frequently without presence of damage (Figure 3). This is plausibly related to moose being nonselective and also influenced by the skewed availability between apical and lateral shoots.

BP estimates the loss of biomass, regardless of the part of the tree, and does not distinguish between apical and lateral shoots (Bergström et al. 1995; Hörnberg, 2001). Hence by only applying the BP survey, browsing of apical shoots risks concealment and one may miss information about stem damage. On the other hand, MD measures stem damage (Holm 2001; Rolander et al. 2011) and risks missing information of biomass loss, which may affect tree growth negatively (Gill 1992). However, the fact that there is a significant relationship between the two indices suggests that rough predictions of the degree of stem damage can potentially be made based on BP, and vice versa.

My study area is probably representative for the southern boreal zone, consisting of a landscape dominated by forests and with non-migratory moose, a situation similar to large parts of Fennoscandia. Furthermore, browsing pressure on Scots pine found in this study was similar to previous estimates from other parts of Sweden (Andrén and Angelstam 1993;

Bergström et al. 1995; Hörnberg 2001). Moreover, stem damage proportions resemble those that Härkönen et al. (2008) showed for main stems of Scots pine in Finland as well as the distribution of damage types was equivalent to what previously has been shown at a Swedish national level (Bergqvist et al. 2001). However, for a more comprehensive understanding further investigations are desired across a national level due to possible regional differences such as landscape characteristics (e.g. silvicultural practices, forage composition, moose density), climate (e.g. snow conditions) as well as moose behavior (e.g. non migratory versus migratory) (Andrén and Angelstam, 1993; Hörnberg, 2001; Kalén, 2005; Persson et al. 2005; Härkönen et al. 2008; Månsson, 2009; Månsson et al. 2010).

Interpreting the interacting variables

Even though there was a significant relationship between the two browsing indices BP and MD, it was not a perfect fit between the two indices suggesting that also other factors may influence this relationship. The most parsimonious model showed that both the number of Scots pine trees per plot (i.e. pine density) and stand height had significant effects on the relationship between MD and BP.

The relationship between the indices was affected by pine density. With increasing pine density, the relative increase in the availability of apical shoots is hypothesized to be larger than the relative increase in availability of lateral shoots due to the early death of lower lateral branches in dense stands (Lanner 1985). Hence apical shoot browsing by moose was expected to increase, with an increase in pine density, which previously has been suggested by Vivås and Sæther (1987). Surprisingly, the relation between the indices was initially more affected at low and average pine densities and less evident at high densities, opposite to what was expected from the above studies. This might be due to that the stands in my study did not reach the densities where lateral twigs die, but also the fact that lateral shoots are still the more numerously abundant shoot category and might be more easily accessible for moose, which would explain the revealed relationship effect.

Different heights also affected the relationship between BP and MD. The increase in MD was higher for a given change in BP when stands are higher compared to average and low heights of stands. The risk of apical shoots being browsed might be affected by the concentration of secondary metabolites which is relatively higher within all shoots (but generally so in the apical shoot) in trees of low heights than for trees with higher heights (Palo et al. 1992). Hence to reduce consumption of defense substances moose might tend to select the shoots with the lower concentrations. This would result in lateral shoots being selected to a greater extent than apical shoots in trees with low height. In addition, stem breakage and bark stripping occur more frequently at higher than at lower heights (Bergqvist et al. 2001). Altogether these aspects contribute to the reflected pattern suggested for the relationship between the indices at different heights.

Implementation and recommendations for management

I suggest MD can be applied in favor of BP, even though they estimate slightly different effects of browsing (stem damage versus biomass loss). MD is less time consuming (i.e. counting stems versus counting shoots) and can be chosen without losing to much information about BP and biomass loss, and hence is the most economically viable alternative. However, depending on the aim of the survey, predictions of browsing pressure proportions, based on the relationship between MD and BP, should be made with caution since, as previously mentioned, the relation between these indices is far from showing a perfect fit and is significantly influenced by other variables (i.e. pine density and mean stand height).

BP could be improved with one small adjustment: by implementing the methodology applied in this study, that is, separating apical shoots from lateral shoots in the protocol. By incorporating this measurement into the BP method, browsing effects on stem quality would also be indicated.

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