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# Title: Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale

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## ABSTRACT

Supplementary feeding of wildlife is a common management practice, increasingly used to reduce or divert herbivore impact from sensitive habitats, forestry or agriculture. The landscape-scale spatial distribution of herbivory in relation to supplementary or diversionary feeding stations is of particular relevance to wildlife and land management, yet has never been quantified. We considered multiple hypotheses, based on central-place foraging theory, to investigate how landscape-scale browsing impact changed as a function of distance from feeding stations and thereby test the effectiveness of diversionary feeding. We assessed the landscape-scale browsing impact of moose by quantifying browsing patterns and moose density in commercially-valuable young Scots pine stands in an area of south-east Norway with a long history of winter feeding. We also used positions from GPS-collared female moose to investigate the spatial distribution of individuals across the landscape. Moose density and browsing impact at a fine spatial scale (<1km) followed an exponential decrease with distance from diversionary feeding stations. However, at a landscape scale (1-10 km), browsing impact did not show any relationship with distance to feeding stations. Leader stem browsing on Scots pine trees was high at both the local (< 1 km; 68 ± 12 %) and landscape (1-10 km; 56 ± 7 %) scales. In addition, browsing on commercially valuable Norway spruce, which is normally avoided by moose, was locally high around feeding stations. As currently practiced, long-term diversionary feeding of moose was ineffective in diverting browsing impact from young pine stands at the landscape scale. Browsing on commercially-important tree species was sufficiently high that economic consequences could be expected. To avoid further conflict, we suggest a combination of reducing the moose density and increasing the availability of natural or more attractive supplementary forage.



**Key-words**: *Alces alces*, browsing impact, central-place foraging, *Pinus sylvestris*, supplemental feeding, diversionary feeding,

## 1. Introduction

Supplementary feeding of wild large herbivores is often implemented as a management tool to increase wildlife productivity (Putman and Staines, 2004; Brown and Cooper, 2006), increase carrying capacity (Smith, 2001), or mitigate human-wildlife conflicts (Andreassen *et al.*, 2005; Barrio *et al.*, 2010; Kowalczyk *et al.*, 2011). In terms of mitigation, the provision of supplementary feed may either change animals' habitat use, diverting them away from sensitive habitats or attracting them to sacrifice areas or refuges (i.e. diversionary feeding), or alternatively, it may increase the overall availability of forage and so reduce consumption of sensitive natural vegetation, commercial forest or agricultural crops (Peek *et al.*, 2002; Putman and Staines, 2004; Brown and Cooper, 2006). Diversionary feeding has been used to reduce grazing in agricultural fields by free ranging European bison (*Bison bonasus*) (Kowalczyk *et al.*, 2011), to mitigate against traffic accidents and browsing on commercially valuable young forest by moose (*Alces alces*) in Scandinavia (Gundersen *et al.*, 2004; Andreassen *et al.*, 2005; van Beest *et al.*, 2010a), and to reduce browsing in vineyards by rabbits (*Oryctolagus cuniculus*) (Barrio *et al.*, 2010). However, many studies have shown that supplementary-fed animals continue to feed on natural vegetation in the proximity of feeding stations (Doenier *et al.*, 1997; Smith, 2001; Gundersen *et al.*, 2004; Cooper *et al.*, 2006). Most of these studies have been carried out at a fine spatial scale, whereas management of forest and wildlife often takes place at a landscape scale.

Supplementary feeding stations can be seen as spatially concentrated key resources within an animal's home range, comparable to mineral licks, salt pools or water holes (Bailey *et al.*, 1996; Laurian *et al.*, 2008). Such point sources of essential resources in the landscape may create radial patterns of habitat use such as the disturbance zones (piospheres) around water sources in dry rangelands (Graetz and Ludwig, 1976; Andrew, 1988; Jeltsch *et al.*, 1997). Central-place foraging theory, an application of the wider optimal foraging theory, describes space-use and foraging patterns by animals that frequently return to a focal place such as a den or a nest (Orians and Pearson, 1979). It has also been used as an effective tool to describe radial pattern of habitat use in a wide range of herbivores (Gallant *et al.*, 2004; Bakker *et al.*, 2005; Raffel *et al.*, 2009; Shrader *et al.*, 2012). Central-place foraging theory predicts a decline in space use and an increase in selectivity with increasing distance from the central place (Orians and Pearson, 1979; Rosenberg and McKelvey, 1999). Although feeding stations differ from dens or water points in offering a concentrated food resource, it has been

shown that fine-scale movements and browsing around feeding stations create space-use patterns and foraging decisions in accordance with the predictions of central-place foraging theory (van Beest *et al.*, 2010a; van Beest *et al.*, 2010b).

Numbers of large herbivores have increased across Europe and North America during recent decades (McShea *et al.*, 1997; Côté *et al.*, 2004), exacerbating human-wildlife conflicts (Austin *et al.*, 2010; Kuijper, 2011; Putman *et al.*, 2011). In Fennoscandia, moose numbers increased dramatically between 1950 and 1980, and have since stabilized at relatively high densities, often in the order of one moose per $km^2$ (Lavsund *et al.*, 2003). Moose depend primarily on birch (*Betula pubescens* and *B. pendula*) and Scots pine (*Pinus sylvestris*) as winter forage. As the latter species is an economically valuable timber species, moose browsing can lead to conflicts with commercial forestry (Hornberg, 2001). In Norway, diversionary feeding is practised in areas with high moose density to reduce browsing in young Scots pine stands. However, supplementary fed moose continue to browse on natural vegetation (Gundersen *et al.*, 2004), and to select for young Scots pine stands (van Beest *et al.*, 2010b). At a feeding station, browsing impact can be locally high, questioning the efficacy of diversionary feeding in reducing browsing in young Scots pine stands (van Beest *et al.*, 2010a). The effectiveness of diversionary feeding depends on the ability of feeding stations to attract animals and so reduce browsing further away. The length and shape of the resource use gradient from a central-place, like a feeding station, varies with the resource utilised, animal population size, and the period of use (Jeltsch *et al.*, 1997). This has not been quantified before in the context of supplementary feeding. If browsing impact in relation to distance from a feeding station can be predicted by central place foraging theory, it would be useful for evaluating the efficacy and placement of diversionary feeding stations.

In this study we quantified the landscape-scale spatial pattern of moose distribution and browsing up to 10 km from feeding stations, with a focus on the diversionary aspect of supplementary feeding. This enabled us to firstly characterise the spatial pattern of resource use as a function of distance from feeding stations, using hypotheses based on central-place foraging theory, and thereby assess whether diversionary feeding was an effective tool to reduce moose browsing on commercially valuable forests at the landscape scale. We tested three alternative hypotheses for the shape of the decline in resource use with increasing distance from the central place (feeding station) and compared them with a null-hypothesis.

$H_0$: Browsing intensity is unaffected by distance from feeding stations.

$H_1$: Browsing intensity decreases linearly with increasing distance from feeding stations (linear model; Rosenberg and McKelvey (1999)).

$H_2$: Browsing intensity is high up to a threshold distance from feeding stations, and then drops to a lower level following the sigmoid response curve (sigmoid model) described for piospheres (Andrew, 1988; Thrash, 2000).

$H_3$: Browsing intensity decreases rapidly with increasing distance from feeding stations (exponential decrease model) until a low background level is reached at the landscape-scale (Thrash and Derry, 1999; Nemeth *et al.*, 2005).

If browsing impact can be predicted by either hypothesis 1-3, they may be used to recommend where to establish diversionary feeding stations in relation to distance from young forest stands. If browsing levels are too high to sustain timber production within a certain distance to feeding stations, this may be considered a sacrifice area.

## 2 Material and methods

### *2.1 Study area*

The study was carried out in Stor-Elvdal, Åmot and Rendalen municipalities in south-east Norway (~61$^{o}$N, 11$^{o}$E), situated between 250 and 1100 m.a.s.l. The vegetation was primarily boreal forest (Moen *et al.*, 1999) below the commercial timberline at 700 m. It consisted of managed stands of pure or mixed Scots pine, Norway spruce (*Picea abies*), downy birch (*Betula pubescens)* and silver birch *(Betula pendula*), interspersed with grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and willows (*Salix* spp.). The field layer vegetation was dominated by dwarf shrubs such as *Vaccinium* spp. Weather data from the valley bottom showed a 30 year mean summer (May-September) and winter (October – April) temperature of 10.6 $^{o}$C and -5.8 $^{o}$C, respectively. The 30 year mean annual precipitation was 628 mm and the mean snow depth (October- April) was 39 cm (NMI, 2008).

Moose were the dominant large herbivore in the area, with a population density ranging locally between 1.1 and 3.4 moose per km$^2$ (Gundersen *et al.*, 2004; Storaas *et al.*, 2005; Milner *et al.*, 2012a). Moose hunting is an important driver of the regional economy (Storaas

*et al.*, 2001). Simultaneously, the area is one of the most important regions for Scots pine forestry in Norway. There is therefore a conflict of interest between moose hunters and foresters. In the winter, the moose population concentrates in the lower valleys, leading to browsing damage to young pine stands. Landowners have been feeding moose with grass silage during winter since 1990, initially to divert moose away from the main road and railway but currently an estimated 60% of the moose population's winter food comes from supplementary feeding (Gundersen *et al.*, 2004; van Beest *et al.*, 2010a; Milner *et al.*, 2012a). Supplementary feed is provided *ad libitum* at fixed sites throughout the winter period (November-March). The amount supplied has increased from a few hundred kg in 1990 to around 200 tons in 1998 and almost 2000 tons in 2010, whilst the moose density has remained relatively constant (Milner *et al.*, 2012a). During the same period the number of feeding stations has increased to about 100, and the radius of the area with heavy browsing impact around feeding stations has expanded from 0.2 km in 1998 to 1 km in 2008 as browse depletion has occurred locally at feeding stations (van Beest *et al.*, 2010a).

### *2.2 Field procedures*

We plotted 1 km interval zones around all feeding stations currently in use within the study area, up to a distance of 10 km, by creating buffers using ArcGIS software (2012). The zones were overlaid on satellite maps of forest stands from the Norwegian Forest and Landscape Institute (Gjertsen, 2007), allowing us to identify young stands of pure and mixed Scots pine. We intended to sample a similar number of forest stands from each zone over 1 km from feeding stations but as 95% of the forested area was within 7 km of an active feeding station, fewer stands were sampled at distances ≥ 7 km (Table 1). All stands were visited to confirm that they had a dominance of Scots pine and the desired height of 0.5-8 m trees with live branches within moose browsing range ≤ 3 m; (Danell *et al.*, 1985). The resulting sample consisted of 69 stands. The zone 0-1 km from feeding stations had been investigated in an earlier local-scale study (van Beest *et al.*, 2010a), while the main focus of the current study was to evaluate landscape-scale effects. However, from a management perspective, we considered it more appropriate to evaluate both scales together, so we also included all young Scots pine stands from the previous survey in the present study.

Forest stands were surveyed for browsing, tree density and density of moose faecal pellet groups (a proxy for moose density) using similar methods in June-July 2008 (0-1 km) and 2010 (1-10 km). However, the sampling layout differed between the two studies. At the local scale (0-1 km), two transects were established radiating out from each feeding station in randomly chosen directions, a minimum of $25^{o}$ apart. Circular plots of 50 $m^2$ were surveyed along the transects at 12.5, 25, 50, 100, 200, 500 and 1000 m from feeding stations. A subset of 152 plots from 52 feeding stations were located in young Scots pine forest and these were used in the present study. At the landscape scale (1-10 km), four circular plots of 50 $m^2$ were surveyed within each stand. The plots were placed 20 m from the centre point of each stand, in each cardinal direction (N, S, E, and W). In all plots at both scales, moose pellet groups from the previous winter were counted (Månsson *et al.*, 2007a). Within each plot at the landscape scale, all trees taller than 0.5 m were counted and measured, but in the local scale study, one tree with an average height and canopy diameter per plot was measured.

For each measured tree, browsing by moose on the leading shoot during the last 4 winters was recorded (browsed/non-browsed), and hereafter called leader stem browsing. The total number of moose browsed and unbrowsed twigs (> 1cm long) from the last growing season occurring within a 0.5-3m height range were recorded. Browsing pressure was calculated per tree as % browsed twigs of total number of twigs available. We also recorded whether the leader stem was broken, and if there was visible bark browsing on the stem by moose. Diameters of three bites (if present) were measured on each tree and the average was used for further analysis. An accumulated browsing score (Skarpe *et al.*, 2007) was given to each tree, to estimate cumulative effect of previous years' browsing (i.e. excluding the most recent winter). The scores were as follows: 0 = no previous browsing, 1 = previous browsing visible but the growth form of the tree was unchanged, 2 = previous browsing had visibly changed the growth form of the tree (such as crooked stem, increased branching), 3 = previous browsing had strongly changed the growth form of the tree (i.e. multiple leader stems, bushy form). A tree was considered damaged for forestry purposes if it fell in any of the following categories: 1) $\geq$ 60% of twigs were browsed (Solbraa, 2002), 2) an accumulated browsing score of 2 or 3, 3) stem breakage, 4) bark browsing or 5) leader stem browsing.

*2.3 Moose distribution and movements*

Twenty adult female moose were captured in the study area in January 2010 as part of a wider project (Milner *et al.*, 2012b). Each was fitted with a GPS collar (Tellus Remote GSM, Followit AB, Lindesberg, Sweden) programmed with a 1-hour relocation schedule (van Beest *et al.*, 2010c; van Beest *et al.*, 2011). Due to the long-term and extensive nature of the feeding programme, all but 5 individuals spent at least 10% of their time between January and end of March within 100 m of feeding stations. As the spatial behaviour of these 5 individuals was not related to feeding stations, we considered them separately (non-users, n=5) from the other individuals (feeding station users, n=15). Feeding station users spent 71.7% of their time within 1 km of feeding stations and a median of 3.8 h per day (range 2.5 – 9.5 h) within 100 m of feeding stations, whereas non-users spent only 6.6% of their time within 1 km.

*2.4 Statistics*

The effect of distance from feeding stations on browsing levels was analysed for the three most common tree species; Scots pine, Norway spruce and downy birch, of which spruce is generally avoided by moose (Månsson *et al.*, 2007b). Other less abundant tree species did not have an adequate sample size to evaluate the effect of distance from feeding stations on browsing impact (Table 3). Pine and spruce are both commercially important species, and pine and downy birch are important winter browse for moose. To explore possible nonlinear effects of distance from feeding stations ($H_2$ and $H_3$), we used generalised additive mixed models (GAMM (Wood, 2006)) from the library 'mgcv' in the program R 2.15 (R Development Core Team, 2012). Moose pellet group counts were analysed with a Poisson error distribution and a log-link function, while proportions of shoots browsed and leader stem browsing were analysed with a binomial error distribution and a logit link function. To account for dependency of measurements from the same locality, locality/stand ID/plot ID (landscape scale) or feeding station ID (local scale) were fitted as nested random intercepts where appropriate. Distance from the nearest active feeding station was fitted as a smoothing term. We used thin plate regression splines, with the optimal smooth curve estimated by the generalised cross-validation procedure (Wood, 2006). The output from a GAMM gives the effective degrees of freedom for a smoother, where a value >1 indicates non-linearity (Zuur *et al.*, 2009). This method allowed us to explore the shape of the function describing moose use

in relation to distance from feeding stations, and we could use the amount of smoothing to separate the linear hypothesis ($H_1$) from the non-linear hypotheses ($H_2$ and $H_3$). We used $p<0.001$ to indicate significance, according to Zuur *et al.* (2009). As preliminary GAMMs showed that most significant effects showed exponential decreases with distance from feeding stations, an exponential decrease model ($H_3$) was fitted using non-linear least-squares regression. Analyses were carried out separately for the local scale and the landscape scale because the difference in sample sizes gave rise to spurious non-linear effects at 1 km from feeding stations, where the scales changed. We assessed whether browsing impact differed between the two scales using t-tests assuming unequal variances to compare tree densities, while linear and generalized linear models were used to compare browsing intensity between the two scales.

The proportion of moose GPS locations occurring within 500 m intervals from feeding stations were determined separately for feeding station users and non-users and divided by the availability of forest habitat within each interval (Table 1) to relate time use to the available area. The frequency distribution of locations was analysed using the procedure described above for pellet group counts.

## 3. Results

### *3.1 Moose spatial distribution in a landscape with feeding stations*

Moose pellet group density showed a significant exponential decrease ($y = 58.48\ e^{-18.22x}$; $H_3$) with distance (m) from feeding stations at the local scale (0-1 km), but no significant pattern ($H_0$) at the landscape scale (1-10 km; Table 2, Figure 1a). The GPS collared moose that used feeding stations also showed an exponential decrease ($y = 408.7\ e^{-2.36x}$) in time spent (hrs) at locations with increasing distance from feeding stations, while the distribution of those individuals not using feeding stations appeared to be bimodal (Table 2; Figure 1b). Feeding station users made more long daily movements than non-users, on average 45 ± 3.4 movements >500 m per individual during the winter season, compared with 15 ± 3.5 by non-users ($F_{1,18} = 23.5$; $p<0.001$). Mean daily distance moved by users was 1862 ± 63.6 m, which was approximately twice the distance moved by non-users (980 ± 113 m; $F_{1,18} = 47.57$; $p<0.001$).

*3.2 Moose browsing at the landscape scale*

3.2.1. Tree species composition

Only 30% of all Scots pine trees were undamaged by moose browsing, and the density of undamaged Scots pine was low compared to that of Norway spruce at a landscape scale (Table 3). At the local scale, ≤ 1km from feeding stations, Scots pine density (damaged and undamaged trees) was 68 % lower than at the landscape scale ($t=5.41$, $dF= 93$, $p<0.001$, Table 3), and Norway spruce and downy birch were the most common species (Table 3).

3.2.2. Scots pine

The proportion of Scots pine leader stems browsed did not change significantly with distance from feeding stations at either spatial scale ($H_0$; Table 2, Figure 2b) or differ between scales (local: 68 ± 12 %, landscape: 56 ± 8%, $\chi^2=1.16$, $p=0.282$, Table 3). At the local scale browsing pressure on Scots pine showed a humped relationship peaking at 500 m, but at the landscape scale it did not show any relationship with distance from feeding stations (Table 2, Figure 2a). Average browsing pressure on Scots pine was lower at the local (18 ± 9 %) than at the landscape scale (33 ± 7 %, $F_{1,119}=7.37$, $p=0.008$). However, the average bite diameter was larger at the local scale (local: 4.6 ± 0.7 mm, landscape: 3.9 ± 0.2 mm $F_{1,72}=8.42$, $p=0.005$), reflecting the lower local availability of pine. Accumulated browsing on pine showed no significant difference between local and landscape scale (local: 1.59 ± 0.25, landscape: 1.35 ± 0.19, $F_{1, 142} = 2.24$, $p= 0.137$). Only 1.8 ± 1.8 % of the pines showed signs of bark browsing at landscape scale and 1.7 ± 2.5 % at local scale. Stem breakage of pine was also low (local scale 2.1 ± 2.7%, landscape scale: 0.6 ± 0.6 %).

3.2.3. Norway spruce

Leader stem browsing on Norway spruce did not change significantly with distance from feeding stations at the local scale (Table 2, Figure 2d), while at the landscape scale, it showed a tendency to increase with increasing distance (Table 2, Figure 2d). However, the effect was marginal and probably caused by large variation and a small sample size at distances > 8km from feeding stations. Leader stem browsing was higher at the local than at the landscape

scale (local: 30 ± 10 %, landscape: 6 ± 4 %, $\chi^2$ =13.46, p<0.001). Browsing pressure showed an exponential decrease with increasing distance ($y = 0.10\ e^{-0.003x}$) at the local scale, but no significant effect at the landscape scale (Table 2, Figure 2c) and was higher at the local than at the landscape scale (local: 6.6 ± 3.2%, landscape: 0.5 ± 0.4%, $F_{1,183} = 6.39$, p=0.012). Accumulated browsing on spruce was also higher at the local than the landscape scale (local: 0.88 ± 0.16%, landscape: 0.08 ± 0.04%, $F_{1,193}$=42.42, p<0.001).

3.2.4. Downy birch

Browsing pressure on downy birch, the most common deciduous species (Table 3), showed an exponential decrease ($y = 0.28\ e^{-0.003x}$) with increasing distance from feeding stations at a local scale, but no significant distance effect at the landscape scale (Table 2, Figure 2e). Browsing pressure on downy birch showed a tendency to be lower at the local than at the landscape scale (local: 19.4 ± 5.4%, landscape: 27 ± 6 %, $F_{1,169}$ =2.97, p=0.087). The number of twigs available per tree was also lower at the local than at the landscape scale (local: 25 ± 6, landscape: 77 ± 30, F=31.33, p<0.001), and bite diameters were larger at the local than at the landscape scale (local: 2.71 ± 0.25 mm, landscape: 1.98 ± 0.12 mm, $F_{1,107}$ = 25.85, p<0.001).

## 4. Discussion

*4.1 Browsing impact and distance to the central place*

While moose density indices and browsing on some species decreased with distance from feeding stations at a local scale (0-1 km), as predicted by central-place foraging theory (Rosenberg and McKelvey, 1999), we found no effects of distance to feeding stations on browsing impact at a landscape-scale (1-10 km) after 20 years of diversionary feeding. Of the three proposed central-place foraging models, the exponential decrease model $H_{3;}$ (Thrash and Derry, 1999; Nemeth *et al.*, 2005) best characterised moose spatial distribution and browsing on Norway spruce and downy birch at the local scale. However, for Scots pine and, to a lesser extent, downy birch, both important winter forage species, there was a resource depletion zone observed within 200 m of feeding stations (van Beest *et al.*, 2010a) and no evidence of the expected landscape-scale decline in browsing pressure with increasing distance from

feeding stations. This confirms concerns about range degradation close to feeding sites (Cooper *et al.*, 2006) and corresponds with reports of resource depletion common around central places (Fryxell, 1992; Thrash and Derry, 1999; Elliott *et al.*, 2009; Shrader *et al.*, 2012). Furthermore, it suggests that diversionary feeding has been ineffective in reducing landscape-level browsing on pine.

Over time, an outward expansion of the depletion zone affected by feeding stations has been observed (van Beest *et al.*, 2010a), similar to the expansion of piosphere zones around water holes (Jeltsch *et al.*, 1997; Thrash and Derry, 1999). Nonetheless, the highest moose impact was restricted to the area within 1 km of feeding stations, likely due to the constraints of daily movement distances. Herbivore daily travel distance is the most important factor affecting the extent of piosphere zones (Jeltsch *et al.*, 1997; Thrash and Derry, 1999). In moose, movements in winter are restricted by snow and low food quality and availability, with daily travel distances being about 1 km (Persson *et al.*, 2000). In our study, feeding station users moved more than non-users, but with average daily travel distances of 1.8 km, their effects on the vegetation would generally be restricted to an area around feeding stations with a radius of approximately half this distance. Deep snow is also known to restrict other deer species close to feeding grounds (Romme *et al.*, 1995; Doenier *et al.*, 1997; Rinella *et al.*, 2012).

Input of supplementary feed and moose use of feeding stations has increased over time in our study area (van Beest *et al.*, 2010a; Milner *et al.*, 2012a). Previous studies, after a shorter time period of supplementary feeding, showed a gradient in browsing impact with distance to feeding stations at a landscape scale (Gundersen *et al.*, 2004; Tange, 2007). The steep gradient in moose use within 1 km of feeding stations and the lack of any gradient at a landscape scale, may be due to a higher proportion of the moose population using feeding stations than earlier (Milner *et al.*, 2012a), indicating that the effect of feeding stations on browsing impact changes over time. Browsing in the wider landscape was primarily caused either by non-users, estimated to be around 26% of the population (Milner *et al.*, 2012a), or by feeding station users in the time period before or after they have migrated to the feeding stations. So even though a high proportion of the moose population used feeding stations, browsing levels at the landscape scale were still high.

*4.2. Food availability and forest damage at the landscape scale*

A decrease in browsing pressure with distance from feeding stations has previously been reported at landscape scales, at 5-10 years after feeding station establishment (Gundersen *et al.*, 2004; Tange, 2007). By contrast, and in line with our null model, browsing impact on leader stems of Scots pine was uniformly high across the landscape after 20 years of diversionary feeding. Scots pine top shoots are preferred by moose and leader stem browsing changes the architecture of the tree, which is then regarded as stem damage from a forestry perspective (Bergqvist *et al.*, 2001). Thus, while browsing on less preferred species such as spruce (Månsson *et al.*, 2007b) declined with distance from the feeding stations as expected from central-place foraging theory (Orians and Pearson, 1979), the more preferred Scots pine was heavily browsed at all distances. If moose prefer pine tops to silage, this may explain why the current supplementary feeding practice fails to reduce browsing impact on important forage species. Seasonal resource depletion of preferred species has been reported from other similar areas (van Beest *et al.*, 2010c). Furthermore, a study of moose diet at feeding stations in our study area, showed a seasonal decrease in the proportion of pine, and an increase in spruce in the moose diet during winter (Nanji, 2013), suggesting depletion of available pine browse. This is further supported by the large bite diameters of pine observed close to feeding stations. Other potentially more attractive forage supplements than silage should be evaluated, as well as measures to increase the production of natural forage.

The high accumulated browsing level on Scots pine at the landscape scale indicates a long period of high moose density relative to the natural forage availability in the area. This is consistent with general forestry patterns in Fennoscandia, whereby declines in logging and subsequent rejuvenation lead to less available natural browse for moose, whilst hunting interests keep the moose population high (Lavsund *et al.*, 2003; Milner *et al.*, 2013). Browsing on non-commercial species, including non-preferred species such as alder, was also high at a landscape scale, indicating low forage availability (Edenius, 1991). Although Scots pine was the dominant tree species in the young forest stands surveyed, the density of undamaged Scots pines was low because of the high browsing impact, while the density of undamaged Norway spruce was high. Consequently the dominance is shifting from Scots pine to Norway spruce due to current forestry trends (Nilsson *et al.*, 2012) and, possibly, to changing competitive hierarchies caused by browsing (Pastor and Naiman, 1992). This, in

turn, will further reduce natural moose forage availability over time, and exacerbate conflicts between forestry and hunting interests.

This study demonstrates that although winter feeding in an area with a high herbivore density relative to forage availability may be successful in attracting individuals to a sacrifice area close to feeding stations, it may still not have the desired diversionary effect in reducing browsing damage to valuable habitats and trees at the landscape-scale. Young pine stands and top shoots from pine constitute a preferred habitat and food source for moose that are heavily utilised, regardless of the presence of less preferred forage at feeding stations. Supplementary feeding may potentially reduce browsing impact in two ways: 1) by creating a spatial gradient in browsing impact (diversionary feeding) or 2) by replacing natural forage and reducing total browsing impact (supplementary feeding). At present, it would be impossible to sustain such a high moose population without supplementary feeding with the current level of natural forage availability. Thus, the provision of large amounts of supplementary forage has increased the carrying capacity for wintering moose (Peek *et al.*, 2002; Putman and Staines, 2004; Brown and Cooper, 2006; Mysterud, 2010) rather than reduced forest damage by replacing natural forage. To avoid further conflict between moose hunters and forest owners, we suggest a combination of reducing the moose density and increasing the availability of natural or more attractive supplementary forage.

## 5. Conclusions

As large herbivore numbers rise across the northern hemisphere, wildlife-forestry conflicts are expected to increase (Kuijper, 2011). Whilst supplementary feeding intuitively seems a promising tool to mitigate such conflicts, our results suggest that in the long term, site specific relationships between forage availability and herbivore population density may determine whether supplementary feeding has the desired diversionary effect. The application of feeding as a diversionary tool requires knowledge of preferences by the herbivore, and continuous monitoring of herbivore density, forage availability and damage to the resources to be protected (Morellet *et al.*, 2007). Our study also shows that the extent and effects of supplementary feeding systems may change over time, which highlights the need for long-term planning when feeding programs are initiated. In many situations a more integrated

management of renewable natural resources, including large herbivores, is necessary to secure the future economic and ecological sustainability of managed ecosystems.

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Table 1: Area of forest occurring within 1 km distance intervals of supplementary feeding stations currently in use within the Stor-Elvdal study area, together with the number of young pine stands sampled

| **Buffer distance (km)** | **Area of forest ($km^2$)** | **Forest area (%)** | **Cumulative (%)** | **No. stands sampled** |
|---|---|---|---|---|
| 0-1 | 148 | 16 | 16 | 1 |
| 1-2 | 201 | 22 | 38 | 8 |
| 2-3 | 175 | 19 | 58 | 7 |
| 3-4 | 133 | 15 | 72 | 10 |
| 4-5 | 95 | 10 | 83 | 8 |
| 5-6 | 64 | 7 | 90 | 14 |
| 6-7 | 45 | 5 | 95 | 14 |
| 7-8 | 27 | 3 | 98 | 5 |
| 8-9 | 12 | 1 | 99 | 1 |
| 9-10 | 9 | 1 | 100 | 1 |

Table 2: Main effects of distance from feeding station for moose on pellet group density and browsing from analysis with generalized additive mixed models: approximate p-values for the effect of the smoothing term distance from the closest active feeding station and estimated degrees of freedom (edf)

| **Feeding station use** | **Response** | **Edf** | **F-value** | **p-value** | **$R^2$** |
|---|---|---|---|---|---|
| Feeding station users | Proportion of time | 8.31 | 31.27 | <0.001 | 0.935 |
| Non-users | | 4.92 | 2.692 | 0.059 | 0.445 |

| **Local scale ≤1km** | **Response** | **Edf** | **F-value** | **p-value** | **$R^2$** |
|---|---|---|---|---|---|
| Moose | Pellet groups | 3.66 | 1774 | <0.001 | 0.156 |
| Scots pine | Leader stem browsing | 1 | 0.004 | 0.951 | 0.018 |
| | Browsing pressure | 3.98 | 148.5 | <0.001 | 0.792 |
| Norway spruce | Leader stem browsing | 1 | 2.978 | 0.084 | 0.033 |
| | Browsing pressure | 3.9 | 424.4 | <0.001 | 0.282 |
| Downy birch | Browsing pressure | 2.61 | 45.38 | <0.001 | 0.114 |

| **Landscape scale 1-10 km** | **Response** | **Edf** | **F-value** | **p-value** | **$R^2$** |
|---|---|---|---|---|---|
| Moose | Pellet groups | 1 | 1.57 | 0.210 | 0.012 |
| Scots pine | Leader stem browsing | 1 | 0.277 | 0.599 | 0.015 |
| | Browsing pressure | 1 | 0.746 | 0.388 | 0.113 |
| Norway spruce | Leader stem browsing | 1 | 8.42 | 0.004 | 0.025 |
| | Browsing pressure | 1 | 7.69 | 0.006 | 0.007 |
| Downy birch | Browsing pressure | 1 | 0.73 | 0.394 | 0.320 |

Table 3 Browsing pressure and browse availability (means ± 2SE) across tree species sampled at a local (0-1 km from feeding stations (FS) for moose) and landscape (1-10 km) scale. "Plots" gives the number of plots and corresponding number of feeding stations that each species was present at from a total of 468 plots and 44 feeding stations surveyed along transects radiating out from feeding stations at the local scale. "Distance from FS" gives the mean distance from feeding stations for the plots where the species was present. "Stands" gives the number of stands where each species was present from a total of 69 young forest stands surveyed at the landscape scale.

| Local scale 0-1 km from FS | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **Plots /FS 0-1 km** | **Leader stem browsing (%)** | **Browsing pressure (%)** | **Accumulated browsing (0-3)** | **Bite diameter (mm)** | **Available twigs per tree** | **Tree density (trees ha$^{-1}$)** | **Distance from FS (m)** |
| Scots pine | 81 / 44 | 68 ± 12 | 17.7 ± 9.1 | 1.59 ± 0.25 | 4.59 ± 0.69 | 23 ± 25 | 737 ± 234 | 244 |
| Norway spruce | 139 / 42 | 30 ± 10 | 6.6 ± 3.2 | 0.88 ± 0.16 | 3.35 ± 0.47 | 276 ± 92 | 1492 ± 420 | 216 |
| Downy birch | 129 / 43 | 69 ± 9 | 19.4 ± 5.4 | 1.53 ± 0.16 | 2.71 ± 0.25 | 25 ± 6 | 1308 ± 301 | 189 |
| Silver birch | 28 / 12 | 63 ± 20 | 33.7 ± 14.5 | 1.85 ± 0.36 | 2.74 ± 0.27 | 26 ± 11 | 495 ± 370 | 81 |
| Rowan | 29 / 15 | 73 ± 18 | 37.6 ± 19.5 | 1.93 ± 0.34 | 2.44 ± 0.98 | 3 ± 2 | 117 ± 111 | 154 |
| Salix | 43 / 21 | 77 ± 14 | 25.1 ± 11.8 | 1.67 ± 0.34 | 2.55 ± 0.62 | 33 ± 29 | 426 ± 232 | 122 |
| Aspen | 10 / 7 | 57 ± 40 | 4.2 ± 8.3 | 0.78 ± 0.73 | 3.00 ± 0.00 | 7 ± 6 | 116 ± 134 | 86 |
| Juniper | 1 / 1 | 100 ± n.a. | n.a. | 2.00 ± n.a. | n.a. | 0 ± n.a. | 4 ± 8 | 200 |
| Alder | 8 / 5 | 60 ± 49 | 28.5 ± 28.7 | 1.38 ± 0.53 | 3.26 ± 0.41 | 18 ± 14 | 529 ± 537 | 16 |

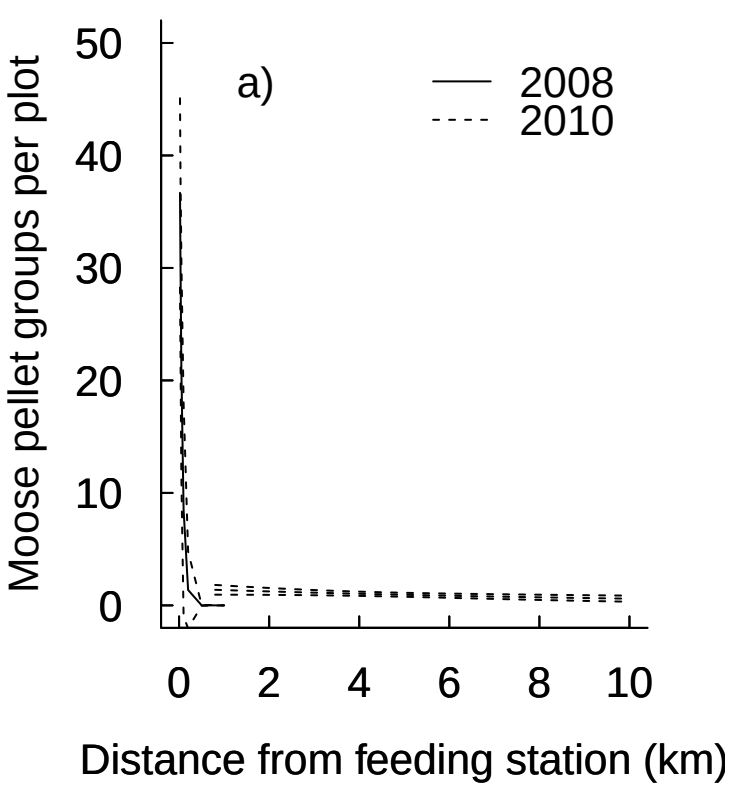
8

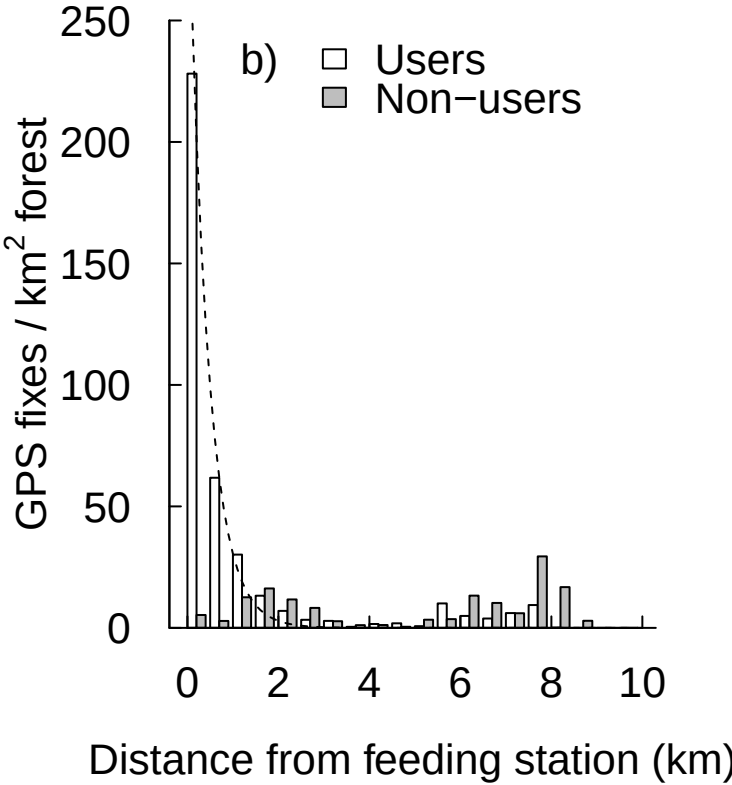
| Landscape scale 1-10 km from FS | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Species** | **Stands 1-10 km** | **Leader stem browsing (%)** | **Browsing pressure (%)** | **Accumulated browsing (0-3)** | **Bite diameter (mm)** | **Available twigs per tree** | **Tree density (trees ha$^{-1}$)** | **Trees undamaged by moose (ha$^{-1}$)** |
| Scots pine | 63 | 56 ± 8 | 33 ± 7 | 1.35 ± 0.19 | 3.87 ± 0.17 | 51 ± 18 | 2275 ± 518 | 696 ± 195 |
| Norway spruce | 58 | 6 ± 4 | 0.5 ± 0.4 | 0.08 ± 0.04 | 3.34 ± 0.34 | 1031 ± 519 | 1130 ± 424 | 1051 ± 401 |
| Downy birch | 52 | 66 ± 9 | 27 ± 6 | 1.57 ± 0.21 | 1.98 ± 0.12 | 77 ± 30 | 1503 ± 688 | 576 ± 322 |
| Silver birch | 34 | 77 ± 11 | 34 ± 9 | 1.68 ± 0.28 | 2.34 ± 0.26 | 56 ± 31 | 681 ± 402 | 153 ± 113 |
| Rowan | 29 | 88 ± 8 | 44 ± 9 | 1.96 ± 0.24 | 2.53 ± 0.33 | 7 ± 2 | 366 ± 228 | 18 ± 14 |
| Salix | 24 | 74 ± 14 | 42 ± 12 | 1.85 ± 0.43 | 2.53 ± 0.38 | 46 ± 40 | 213 ± 106 | 42 ± 34 |
| Aspen | 10 | 86 ± 20 | 44 ± 20 | 2.13 ± 0.54 | 2.69 ± 0.35 | 8 ± 4 | 213 ± 248 | 12 ± 14 |
| Juniper | 10 | 63 ± 26 | 11 ± 12 | 1.41 ± 0.65 | 2.40 ± 0.63 | 196 ± 90 | 79 ± 55 | 29 ± 26 |
| Alder | 4 | 50 ± 45 | 35 ± 45 | 0.90 ± 0.83 | 2.85 ± 0.61 | 44 ± 76 | 90 ± 106 | 58 ± 68 |

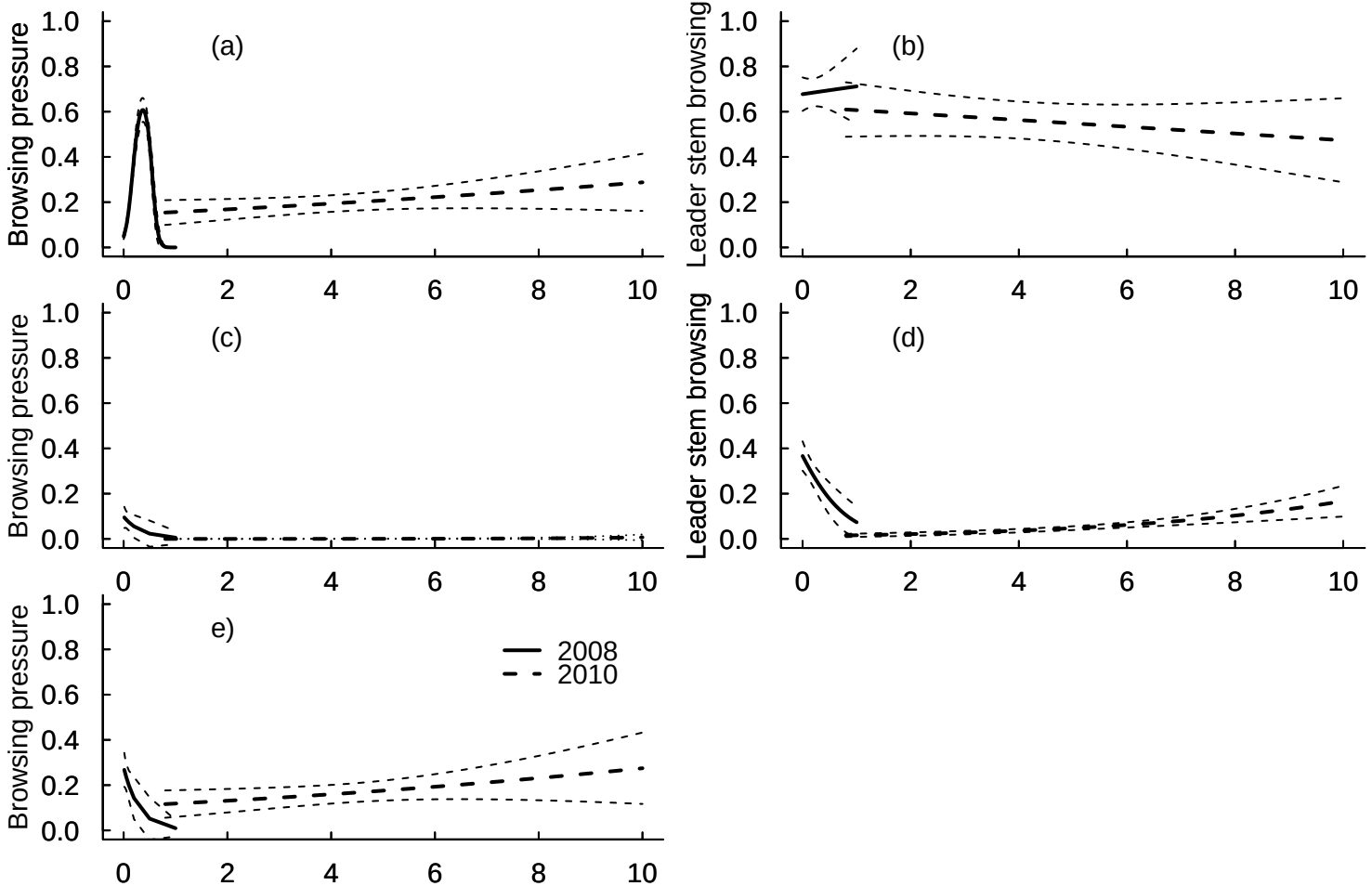
Figures

Figure 1 a) Moose winter pellet groups (per $50m^2$) in relation to distance from feeding stations. An exponential curve was fitted to the local scale (0-1 km from feeding stations, data from 2008), a curve from the GAMM with 95% CIs to the landscape scale (1-10 km, data from 2010). b) Proportion of time spent by GPS-marked moose (GPS fixes (1 per hr) per $km^2$ forest area) in relation to distance from feeding stations in the winter of 2010, for feeding station users (n=15) and non-users (n=5). An exponential decrease model (dotted line) was fitted to the feeding station user data.

Figure 2 The relationship between distance from moose feeding stations and browsing impact in young forest stands for a) and b) Scots pine, c) and d) Norway spruce and e) Downy birch. Leader stem browsing (right hand side) is the proportion of leading shoots browsed during the last 4 years. Browsing pressure (left hand side) is the proportion of browsed shoots of shoots available from the last winter. The fitted lines represent the effect of distance as a smoothing function from generalised additive models (GAMM) with 95% CIs, except figs. c and e, in which exponential curves are fitted to the local scale data with 95% CIs. Browsing was surveyed at 0-1 km from feeding stations in 2008, and at 1-10 km from feeding stations in 2010.


a)
2008
2010
Moose pellet groups per plot
0
10
20
30
40
50
0
2
4
6
8
10
Distance from feeding station (km)


b)
Users
Non−users
GPS fixes / km2 forest
0
50
100
150
200
250
0
2
4
6
8
10
Distance from feeding station (km)


(a)
(b)
(c)
(d)
e)
Browsing pressure
Leader stem browsing
2008
2010
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
Distance from feeding station (km)