
Winter feeding site choice of ungulates in relation to food quality

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Picture: Philipp I Otto



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Hjortdjurens val av vinterutfodringsplats i relation till fodrets kvalitet

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Keywords: Supplementary feeding, Salix, silage, moose, roe deer, fallow deer, red deer, wild boar, competition, Öster Malma

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Abstract

Supplementary feeding is a widespread practice in Sweden. In most cases, this is done in order to increase ungulate densities for hunting purposes. Forest regimes can also provide a high amount of natural food which influences densities. But high densities are not unproblematic and can cause several problems, e.g. increases in traffic accidents or browsing damages. In order to offset some of the problems while maintaining a high population, diversionary feeding has been proposed. In this study, I test the hypothesis that the type of supplementary feed influences the animals choices and degree of utilization, assuming that concentrate selectors (moose (*Alces alces*) and roe deer (*Capreolus capreolus*)) utilize willow to a greater extent than the intermediate feeders (red- and fallow deer (*Cervus elaphus* and *Dama dama*, respectively)) and wild boar (*Sus scrofa*), which mostly utilize the silage. A second focus of this study is to provide more information on when and where animals in the study area feed on supplementary fodder and why they choose a certain location over another. Öster Malma, the study area, has populations of five different ungulate species. The hypotheses here are that the habitat type surrounding a feeding site influences its attractiveness and the amount of natural browse in the vicinity plays a role. Based on my findings in this study, willow is not an applicable feed item for diversionary feeding. Silage was utilized much more – especially by fallow deer. Furthermore, a difference in diurnal activity was found between roe deer and the other species: roe deer was less nocturnal than the other four ungulate species. I also found some evidence that moose prefer feeding sites with forest cover. I hypothesize that competition for the resources between the species occurs and that fallow deer is a strong competitor.

Introduction

Most forests in Sweden are managed for wood production and forests are usually harvested by clear-cuts (Hansson 1994). Forest edges and border zones have decreased (Ihse 1995). Despite that, clear-cutting forestry creates a large amount of browse for concentrate selectors due to the abundance of early successional stages. Moose (and roe deer), have a pronounced preference for clear-cuts (Hansson 1994). Thus, the high density of wild browsers is presently acting in concert with forest management, both directly and indirectly, to create a spruce dominance in the Swedish hemiboreal zone (Nilsson 1997). Directly, because moose and roe deer browse heavily on everything except for spruce, relatively promoting this tree. Indirectly, because foresters react to the losses and plant more browse-resistant spruce than other trees. The large-scale use of clear-cutting forestry in Sweden has resulted in high ungulate densities, further promoted by a relatively low hunting pressure and the previous elimination of large carnivores in most of Sweden (Nilsson 1997). Problems arise here: high densities promote road accidents and browsing damages, while spruce monocultures lead to biodiversity issues (Felton et al. 2010), among other things.

To offset these problems while maintaining high populations for hunting purposes, diversionary feeding has been proposed as a measure. Winter feeding of game is already a widespread practice in Sweden. The assumed benefit is that the provision of fodder in one area can divert ungulates from other more vulnerable areas (young forest stands, agricultural fields, roads etc.). When it comes to moose, some studies suggest that this is a promising concept (Andreassen et al. 2005; Gundersen et al. 2004). But in order to be effective the offered fodder needs to be appealing and nutritionally satisfying (Annika Felton, unpublished data). Silage is a winter feed that is widely used for supplementary feeding. But it is questionable, if it is equally suitable for all wild ungulate species. According to the concept introduced by Hofmann and Stewart (1972) and Hofman (1989), moose (and roe deer) belong to a category termed “browser” or “concentrate selector”. They specialize in feeding on or digestion of plants and plant parts that are easy to digest. They are comparably “picky” and select for high-quality diets and their stomach has a high fermentation rate as well as fast absorption and turnover. On the other end of the scale are the “grazers” who are very well adapted to eat and process cellulose-rich, exceedingly fibrous food. Grasses (monocots) are very rich in fiber with less soluble cell contents and less protein than dicots and are thus considered low-quality food. Grazers have long feeding periods followed up by long rumination periods, which increases retention time in the guts and therefore a better fermentation. In between are the “intermediate feeders”. These animals very often rely on a change in feeding habits (together with seasonal anatomical changes of their digestive tract) depending on availability of high-quality food. Fallow deer and red deer can be found in this group. Wild boar does not belong to any of these groups since they are no ruminants. Their microbial digestion takes place in their intestine – they are hindgut-fermenters. There have also been a number of re-analyses of the data which show that there is little substantive evidence for differences in morphology and physiology between the feeding categories, once differences in body mass and phylogenetic relationships have been taken into account (Gordon 2003). Nevertheless, differences in nutritional requirements exist and there is probably a mismatch between provided feed and what an ungulate needs. The extent of this mismatch depends on the digestive physiology and body mass of the ungulate. Willow might be a food item that satisfies the requirements for moose since it is part of its natural diet and the nutritional composition of willow is

close to the nutritional target of the moose (Annika Felton, unpublished data).

To my knowledge, no study has been published on supplementary feeding of five different ungulate species (fallow deer, red deer, roe deer, moose and wild boar). It can be assumed that these species utilize the feed differently and maybe influence each other, as well, but to what extent? All five ungulate species differ in their dietary needs and feeding ecology: Moose – a concentrate selector (Hofmann 1989) – are specialized to live on woody species and herbs. Twigs and bark of trees and shrubs are eaten in winter; leaves of trees and shrubs, aquatic plants, herbs and grass during seasons without snow. For this reason, moose seem to have a preference for burnt forests, forest clearings or clear-cuts (cf. Baskin and Danell 2003:95/96, table 6.2) and sapling stages. Moose are particularly sensitive in terms of digestion and correct diet – a trait that sets them apart from virtually all other ungulates, which do much better on artificial diets provided by humans. Shochat et al. (1997) report that it is difficult to keep moose healthy in captivity: most die at a very young age due to diseases associated with their diet. Several reasons have been proposed; one hypothesis is that moose have difficulties digesting fresh grasses and legumes (Shochat et al. 1997). Butler et al. (2008) hypothesis that moose are particularly prone to grain overload since they have the longest retention time for digestion of all cervids. Shipley et al. (1999) found a bite size for moose on *Salix caprea* of 4.05 ± 0.12 . The roe deer is a concentrate selector (Hofmann 1989), too. Major sources of food are dicotyledonous herbs, trees and shrubs and – to a lesser extent – monocotyledonous species. The dominant plant parts taken include the leaves of small dicotyledonous herbs, and the leaves and young shoots of trees and shrubs, which may account for between 51 and 58 % of the total diet, rising to about 90 % during the growing season. The fallow deer has been widely introduced all over the world, but originally comes from the Near-East and some areas in Southern Europe and Turkey (Dolman and Wäber 2008). They belong to the intermediate feeding types and are probably the best equipped of the five species to digest grass and silage (cf. Hofmann 1989). But they seem to be a very competitive species in areas where they are present (Dolman and Wäber 2008) and are apparently spreading very slowly in relation to other (introduced) cervids (Nugent 1994), which might be because of a high intra-specific tolerance (Langbein et al. 2003). Red deer have a rather broad feeding niche (intermediate feeder). They use a wide variety of plant species and parts and even mushrooms and they are known to feed on spruce (*Picea schrenkiana*) in Kazakhstan (Baskin and Danell 2003). Red deer are often regarded as particularly shy. This might have to do with a selection process caused by the modern way of hunting (Ciuti et al. 2012). Wild boars are omnivorous, but in some areas they feed only on a few plant species. When feeding in soil 60 % of wild boar diet consists of invertebrates, but generally animal food makes up only 1.5-8.0 % of the diet. But when animal food is abundant, it may comprise 100% of the diet (Baskin and Danell 2003). The more food they find especially during autumn (oak and beech mast years) the better they are able to survive even more severe winters with cold temperatures and high amounts of snow.

The study at hand is based on the hypothesis that

- a) the type of supplementary feed influences the animals choices and degree of utilization, assuming that concentrate selectors (moose and roe deer) utilize willow to a greater extent than the intermediate feeders (red- and fallow deer) and wild boar which mostly utilize the silage.

A second focus of this study is to provide more information on when and where animals in

the study area feed on supplementary fodder and why they choose a certain location over another. The hypotheses here are that

- b) the habitat type surrounding a feeding site influences its attractiveness and
- c) the amount of natural browse in the vicinity plays a role.

Material and methods

Study area and period

The study was carried out in the area around Öster Malma (N 58°57' - E 17°09'), north of Nyköping and south of Gnesta in Sweden. The study period comprised six consecutive weeks (28th of January until 10th of March). The area has a high ungulate density and features five species: fallow deer, red deer, roe deer, moose and wild boar. The landscape consists mainly of managed forests (spruce and pine of various ages), some agricultural fields and lakes. Winter feeding is carried out extensively with silage of different origins and compositions, as well as corn via an electronically timed feeder. All animals are therefore used to provision of winter feed. Dung-counts were available for the same area from another study (L. Edenius, unpublished data).

The study originally comprised nine sites, each with a randomly assigned *Salix* (willow), silage and a control plot, which makes 27 plots in total. This random assignment was only done as long as the respective game manager didn't object. In total, five different game managers were involved. All feeding was conducted in places that were previously established as feeding sites. The sites were at least 800 m away from each other and the plots within a site were always closer to each other than to the closest plot of the next site (Figure 1). The landscape variation within a site was minimized (e.g. all plots on a field, all plots at a forest road etc.). Each plot had 16 sampling plots associated with it (480 sampling plots in total for all sites). The sampling plots were placed along four 300-meter-transects that are placed in the four wind directions away from each plot. Four of them were on each transect; at 20, 100, 200, and 300 m away from the feeding station (

Figure 2). Each sampling plot had a 2 m radius ($\approx 12.5 \text{ m}^2$).

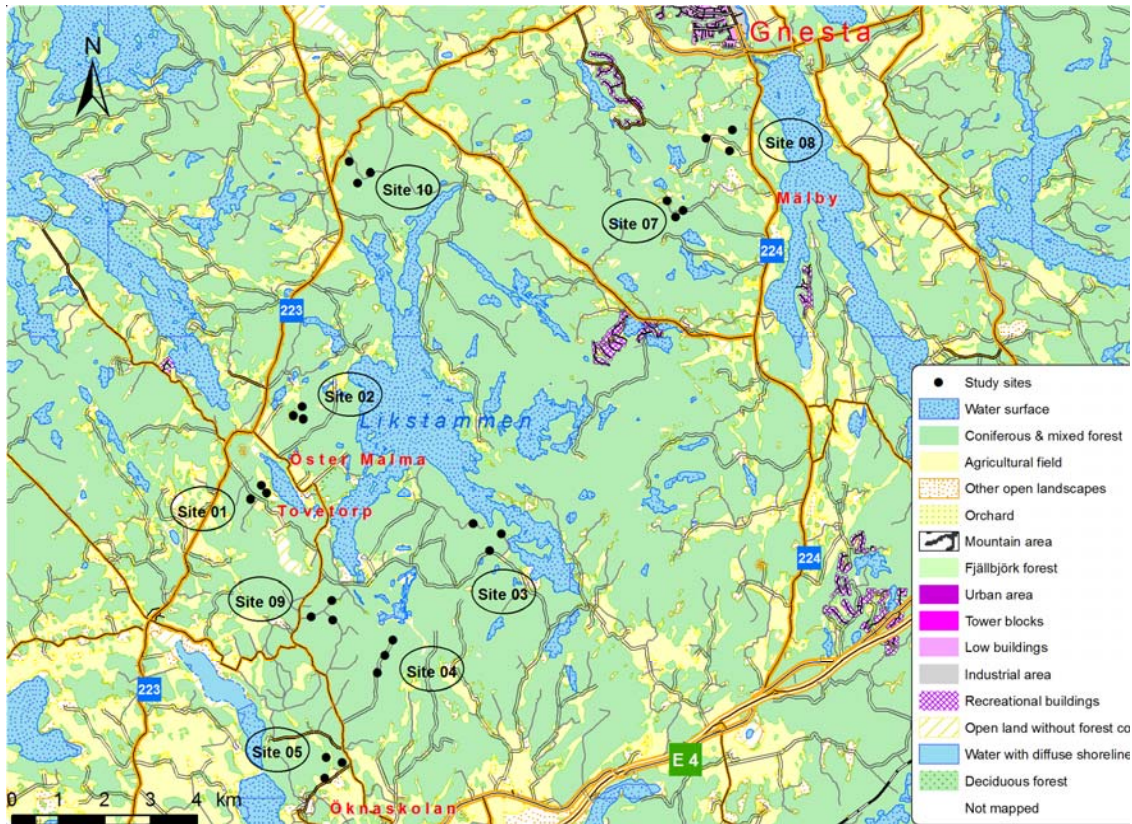


Figure 1: Map of the study area

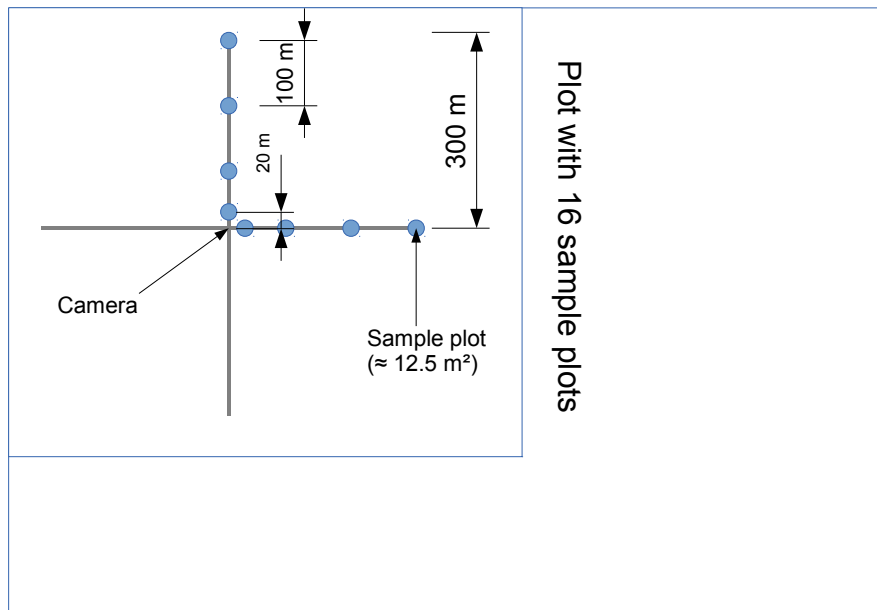


Figure 2: Outline of the sites

Feed

The silage in the experiment was not changed from what the respective game managers usually fed. The quality of the silages ranged from diverse lay mixtures specially designed for game to grass mixtures designed for cattle (crude protein content 9-15% of dry matter, fiber content (neutral detergent fiber) 41-64%, crude mineral content (ash) 7-14%, digestibility 54-85%; Annika Felton, unpublished data). Two types of willow were used in the experiment, both one year old shoots from short rotation coppices: Due to the animals ignoring the first clone, a different clone was ordered from a different supplier and presented in another way. The clones were exchanged after ~2.5 weeks. For both clones, the entire bark and shoots up to a diameter of around 4 mm were considered edible (Shipley et al. 1999). The first type was the clone *Inger* (*Salix triandra* x *S. viminalis*). The shoots (2.5 m long) were harvested at Billeberga (N 55°52'59 – E 12°59'59) one or two days before being delivered on a Euro-pallet encased with cardboard (Figure 3). For feeding, the cardboard was removed but a wooden structure was left to keep the shoots on top of the pallet. The second type was the clone *Klara* (((*Salix burjatica* x *S. viminalis*) x *S. burjatica*) x (*S. viminalis* x (*S. schwerinii* x *S. viminalis*))) (Stig Larsson, pers. comm.)). It was harvested at Gärsta Täby near Örebro (N 59°11'38 – E 15°05'45) and was delivered in bunches of shorter (1.5 m) shoots. They were harvested about a month before being delivered, but kept in cold storage. For feeding, a tripod was erected (made of hazel (*Corylus avellana*) or alder (*Alnus glutinosa*) branches) and the shoots were leaned to it. This was thought to better resemble natural browse than laying shoots in a box-like structure.



Figure 3: Presenting of the first (left) and second (right) delivery of willow

Cameras

In order to quantify ungulate visitation, camera traps have been used. For the monochrome nighttime-pictures the camera uses an array of Lo-Glow™ semi-covert infrared emitters that are barely visible to the human eye. The daytime-pictures are in color. The trigger works with a passive infrared motion detector precisely aligned with the lens. Detection range and trigger probability are dependent on body temperature in relation to ambient air temperature (Data taken from the RECONYX™ website and manual).

One camera was placed in every plot – resulting in a total of 27 cameras – and set to take a picture when triggered followed by a minute delay where triggering was not possible. I.e., cameras could take a maximum of 60x24 pictures per 24 hours. The cameras were exclusively mounted on trees at a height of approximately 1.5 m angling slightly downwards and about 5 m away from the offered feed; the existing feeding site was moved

closer to the edge of the forest, if needed.

Field measurements

In order to assess the natural food availability in a 300 m radius around each camera, all trees with shoots in a maximal height of 300 cm have been counted within each sampling plot. Tree species (or categories) were: aspen (*Populus tremula*), pine (*Pinus sylvestris*), rowan (*Sorbus aucuparia*), silver birch (*Betula pendula*), downy birch (*Betula pubescens*), willow (*Salix spec.*), oak (*Quercus spec.*), spruce (*Picea abies*) and other. Furthermore, all sample plots were categorized into habitat types; because of time constraints only the category “forest” was included in the analysis. “Forest” comprised of stands of all ages and all tree species. Due to time constraints in the field, a visual assessment of habitat types was conducted, without the aid of measurements.

In my study, I used dung-count data that was collected as part of the national thematic research program Wildlife & Forestry and the Environmental monitoring program Foma, as well (L. Edenius, unpublished data). For the dung-count methods, refer to Edenius (2012, in Swedish).

Picture scan-sampling

The original amount of pictures throughout the study period was about 100,000. To be able to fit the data analysis into the time limitations of a master’s thesis, not all pictures have been sampled. Instead, I prolonged the lag-phase between two possible pictures from 1 to 10 minutes. This resulted in a maximum possible number of pictures of 144 per day. Furthermore, some cameras have only been sampled every third day. The resulting amount of pictures processed and included is about 11,000. On every picture, the number of individuals of every species was noted – as long as a distinction between species was deemed possible. In uncertain cases these individuals were ignored. Every animal present was recorded, regardless of behavior. In situations where many individuals stood close together during nighttime, the number of animals was estimated. All sampling has been carried out by me. See (Table 2) for an overview. Only silage cameras are shown, but the same sampling has been done accordingly for the other cameras.

Statistical analysis

Two cameras malfunctioned and were not included into the analysis. To maintain my experimental design I excluded the complete sites in which these cameras were present. Hence, I ended up analyzing the data for a total of seven sites, and 21 plots.

Data analysis and statistical computing was carried out using LibreOffice Calc (Version 3.6; The Document Foundation) and R (Version 3.0; The R Foundation for Statistical Computing), both open source programs. I estimated visitation rate for each ungulate species as proportional daily occupancy of a site which I estimated as the number of photos per day with at least one individual of a species divided by the maximum amount of pictures possible per day (144). To control for repeated measures I averaged all daily occupancy values per site and used the 7 sites as my replicates. Inherent here is a “weighing” of species: By omitting the number of individuals on the pictures, the fact that fallow deer was mostly present in big groups, doesn’t distort the analysis. For all calculations a distinction between the five species was made.

To analyze differences in preference of treatment (silage, *Salix*, control), I used Generalized

Linear Models (GLMs) with the assumption of a binomial distributed response variable for proportion data.

A set of data on dung-counts obtained by Lars Edenius' group (L. Edenius, unpublished data) was used in ArcMap™ (Version 10.1; ESRI). The dung count sampling plots did not spatially overlap with the supplementary feeding sites I used in this study, so counts were extrapolated using the “Kriging” tool. Only silage plots were included. The values that were calculated by the “Kriging” tool were read out from ArcMap from the position of my plot and then used to create relative abundances for every species (Equation 1). All animals on all photos were considered; no distinction between individuals was made. The resulting selection indices were checked for correlation using Spearman's rank test.

$$S_{sp,si} = \frac{\left(\frac{p_{sp,si}}{d_{sp,si}}\right)}{\left(\frac{p_{ref}}{d_{ref}}\right)}$$

Equation 1

S = selection index
 sp = species
 si = site (only silage cameras were included)
 p = amount of animals on photo
 d = dung-counts (one unit here equals one pellet group)

I calculated a proportional occupancy for the daylight hours and nighttime for each day during the study period where daylight was defined as the hours from apparent sunrise to apparent sunset) using the NOAA Solar Calculator (Cornwall 2013). Subsequently, I calculated the average total number of possible daytime and nighttime pictures (out of 144 possible pictures, on an average 48 were daytime and 96 were nighttime pictures). I used these averages to estimate daily occupancy for daytime and nighttime. For analyzing differences in preference for day or night for feeding activities, I used Generalized Linear Models (GLMs) with the assumption of a binomial distributed response variable for proportion data. Only silage plots were included for this analysis.

In order to check whether environmental variables influence occupancy, I once again used Generalized Linear Models (GLMs) with the assumption of a binomial distributed response variable for proportion data. I tested for an effect of proportion of sample plots defined as forest-habitat in this model. Only silage plots were included for this analysis.

Results

Treatment

The inclusion of interactions between species and treatment didn't bring about an improvement of fit (determined by the p-values) and was therefore dropped; the variable was nevertheless left in the model. The preference for a certain feed type did not differ among species (species:treatment interaction, $p > 0.05$) (Figure 4). The standard error on some columns in Figure 4 is large, since the occupancy was varying greatly from site to site. On the *Salix* plots fallow deer's occupancy is slightly above 0.01 ($\sigma = 0.011$), whereas for all other species the occupancy is well below 0.01 or even zero. On the control plot pictures, moose, red and roe deer haven't been present on a single picture while occupancy

for fallow deer and wild boar is below 0.002

The average daily occupancy rate of fallow deer on the silage plots (Figure 5) was ~0.25 ($\sigma = 0.082$). That means on an average day fallow deer are present on 25 % of the possible pictures per day. The next frequent visitor is roe deer with roughly 0.05 ($\sigma = 0.025$) occupancy rate. Moose is the least frequent occupant with an occupancy rate of not even 0.01 ($\sigma = 0.004$).

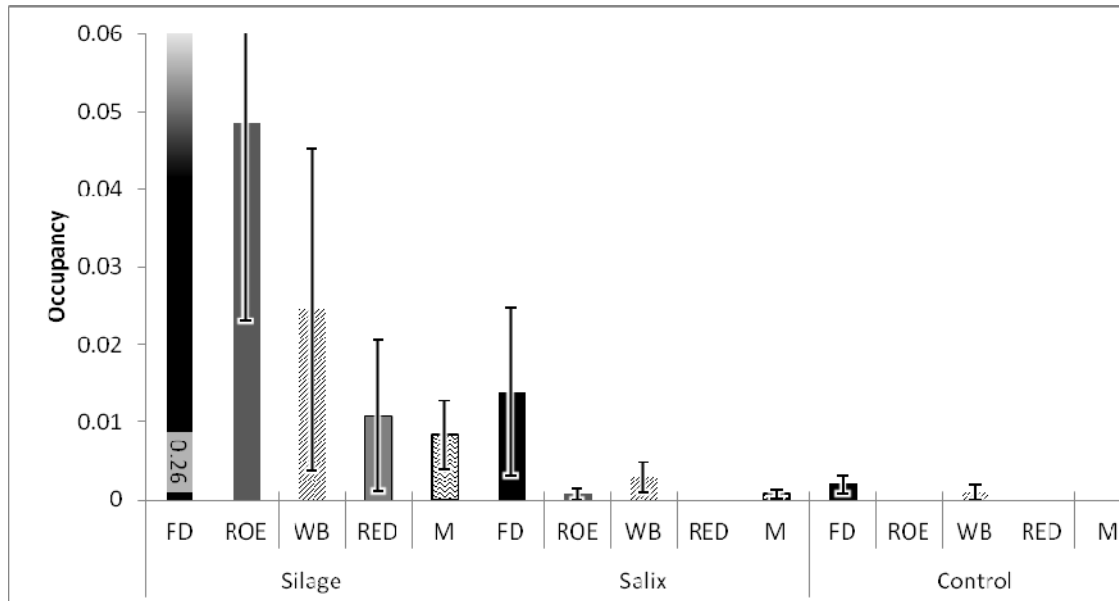


Figure 4: Occupancy of the different treatments; a gradient fill indicates that the bar stretches out beyond the graph, the actual value is shown in the column's base

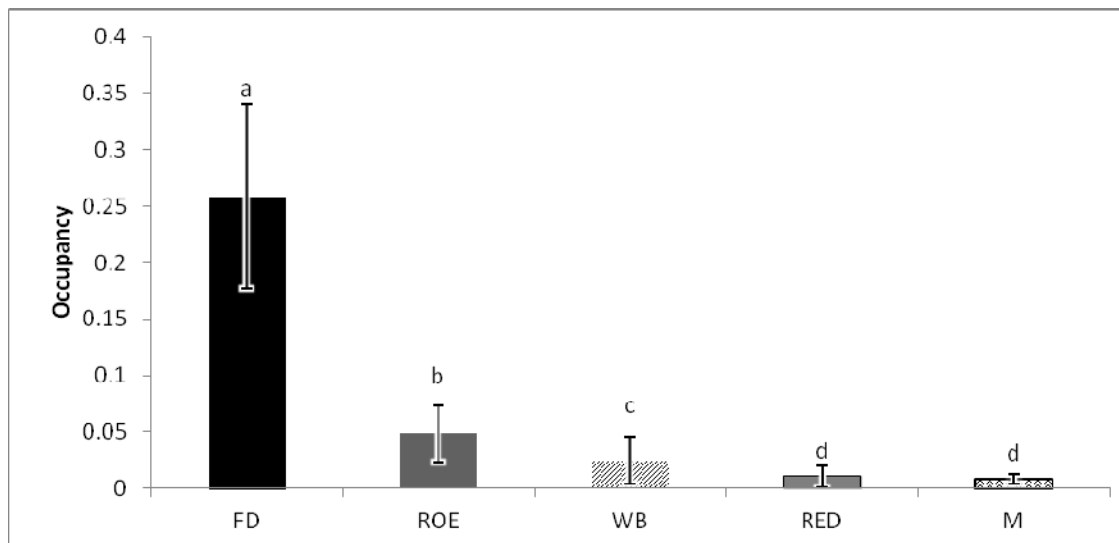


Figure 5: Occupancy for silage sites; small letters indicate significant differences among bars ($p < 0.05$)

In Figure 6 one can see that the difference between treatments was significant for each species.

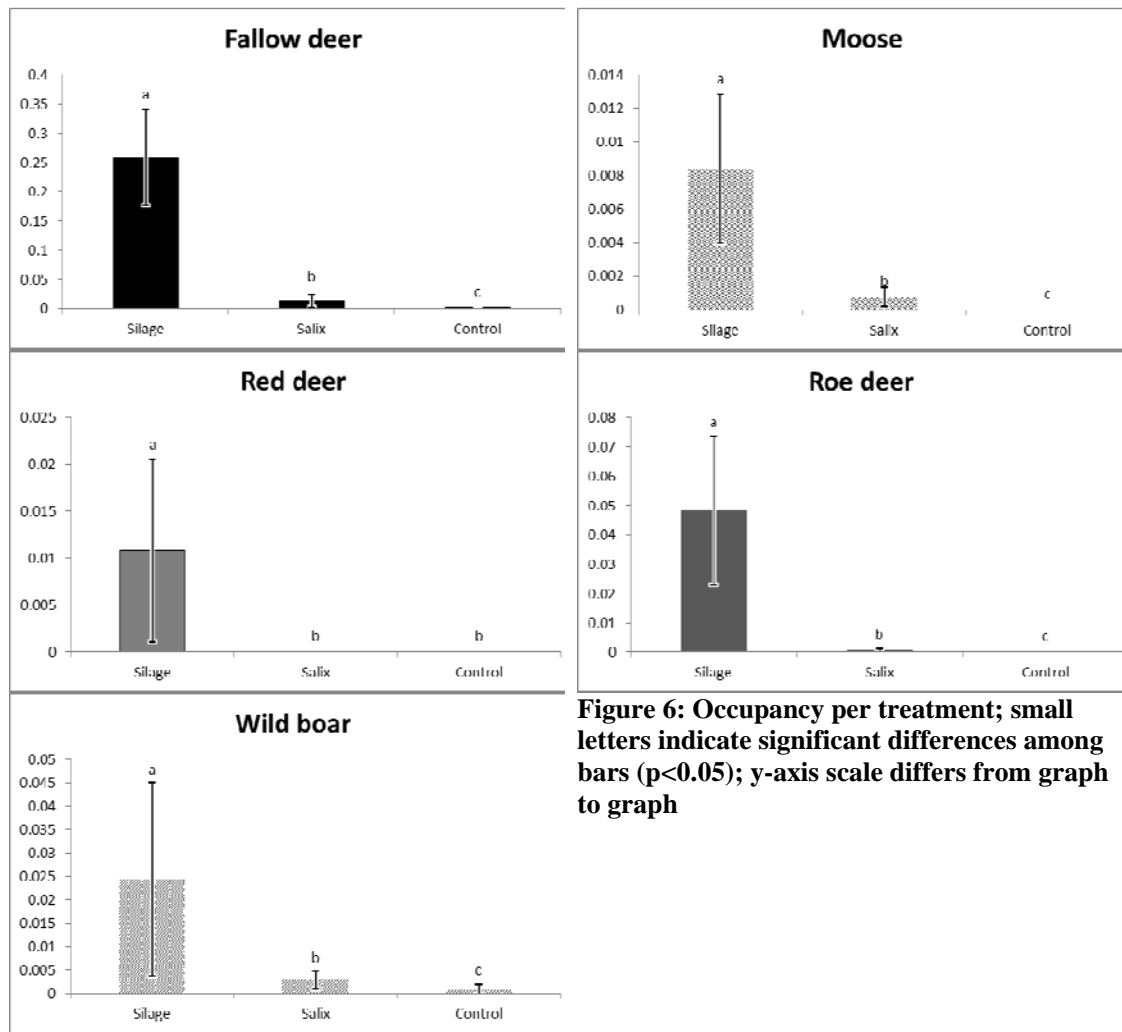


Figure 6: Occupancy per treatment; small letters indicate significant differences among bars ($p < 0.05$); y-axis scale differs from graph to graph

Figure 7 shows the large difference in occupancy between the different sites. In the model “Occupancy~Treatment+Species”, fallow deer’s occupancy was clearly the highest on silage plots ($p < 0.001$), followed by *Salix* and last the control. All other species had a lower occupancy on the silage plots than fallow deer.

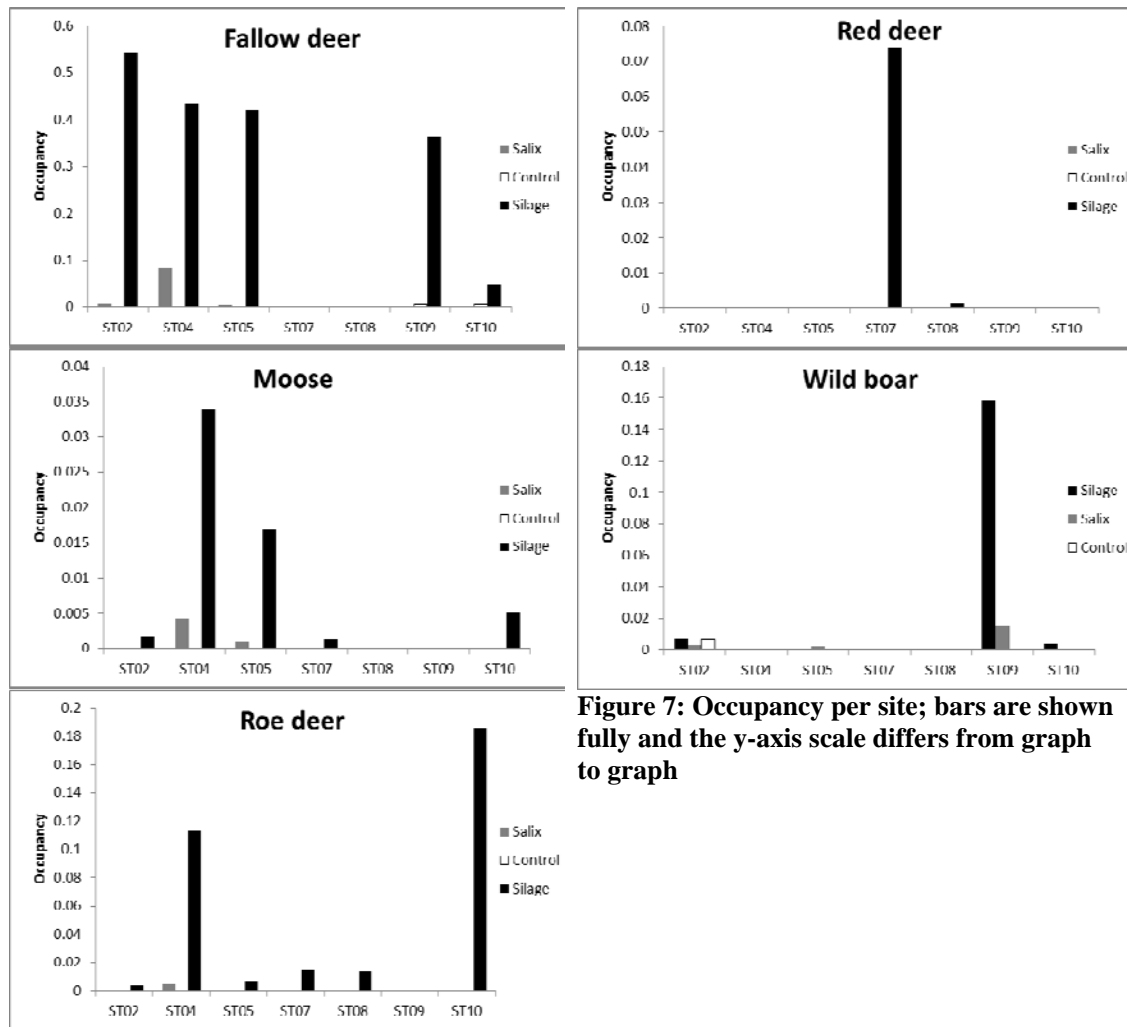


Figure 7: Occupancy per site; bars are shown fully and the y-axis scale differs from graph to graph

Selection

In Figure 8, a value around 1 means the species is present on silage plots in similar proportions as expected from the dung-counts, while >1 points at a clear selection for silage. Fallow deer selected quite strongly for silage, except for sites 7 & 8. On these sites, red deer was strongly selecting for silage. Roe deer was only selecting for silage on some plots. Wild boar and moose were not selecting for silage. The selection strength of fallow deer and roe deer as well as fallow deer and red deer seems to have a trend towards negative correlation ($p = 0.09$ and $p = 0.06$, respectively), whereas the selection strength of red deer and roe deer seems to have a trend towards positive correlation with each other (Table 1).

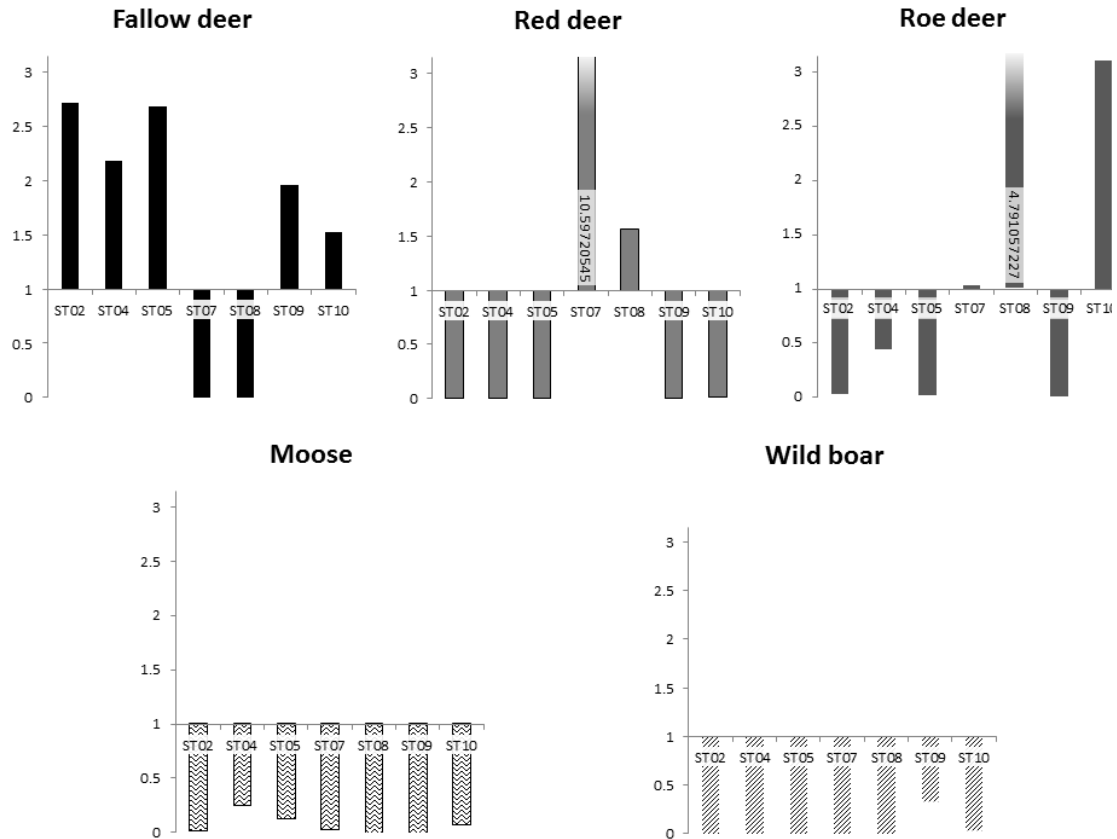


Figure 8: Selection indices; The values from the position of my plot were read out from ArcMap and then used to create relative abundances for every species (Equation 1) All animals on all photos were considered; no distinction between individuals. 1 reads as “is present on silage plots in relation to the other species as predicted by relative dung-counts”, while >1 points at a clear selection for silage.

Table 1: Spearman's ranked correlation of the selection indices

| | FD-ROE | FD-RED | FD-WB | FD-M | RED-WB | RED-M | RED-ROE | ROE-WB | ROE-M | M-WB |
|-----|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| rho | -0.68471 | -0.72926 | 0.162169 | 0.336364 | -0.14825 | -0.33658 | 0.778312 | -0.46429 | -0.03604 | -0.25226 |
| p | 0.08967 | 0.06292 | 0.7283 | 0.4607 | 0.7511 | 0.4604 | 0.03928 | 0.3024 | 0.9389 | 0.5852 |

Day & Night

This time, the interaction improved the fit and was therefore kept in the model (“Occupancy~DN*Species”; determined by p-values). Day- and nighttime occupancy did differ among species (species:DN interaction, $p > 0.05$ for all but red deer).

Roe deer is significantly different in its circadian occupancy of silage plots from the other species ($p < 0.001$), except probably for red deer where there is not enough data. Its occupancy is higher during daytime (~ 0.08), whereas all other species prefer nighttime for feeding on silage (Figure 9). Fallow deer occupancy was ~ 0.34 during nighttime and ~ 0.12 during daytime.

Its daytime occupancy is also different to that of moose and wild boar ($p < 0.001$), but not different to fallow deer ($p > 0.1$). The occupancy of all species at silage plots is dependent on

daytime ($p < 0.001$). The data for red deer is scarce, therefore no significant tendencies. Roe deer's nighttime occupancy is not significantly different from that of wild boar.

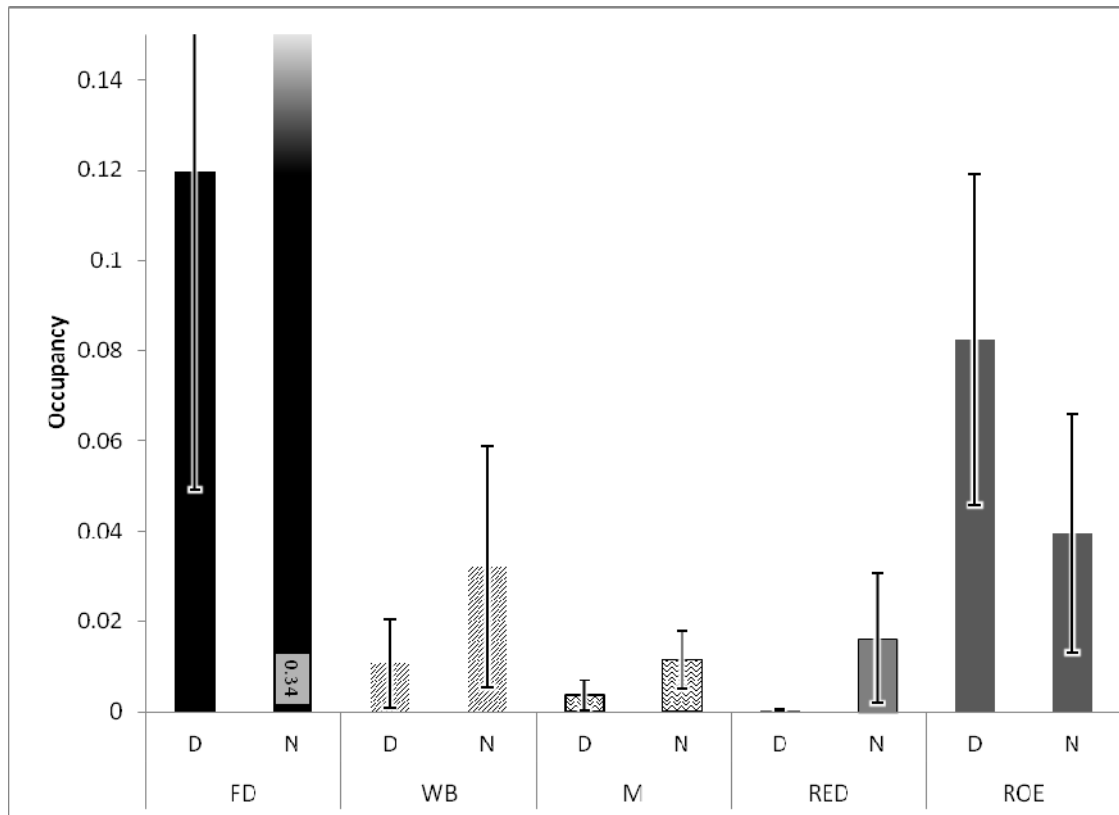


Figure 9: Occupancy for day- & nighttime; a gradient fill indicates that the bar stretches out beyond the graph, the actual value is shown in the column's base; cf. for the modeling results

Environment

Due to the small replication ($n = 7$), few relationships between habitat type and species relative occupancies can be discerned in this study (Figure 10). The relation of daily occupancy versus % of forest habitat is very weak for roe deer, red deer and wild boar ($R^2 < 0.1$), reasonable for fallow deer ($R^2 = 0.42$) and fairly strong for moose ($R^2 = 0.84$).

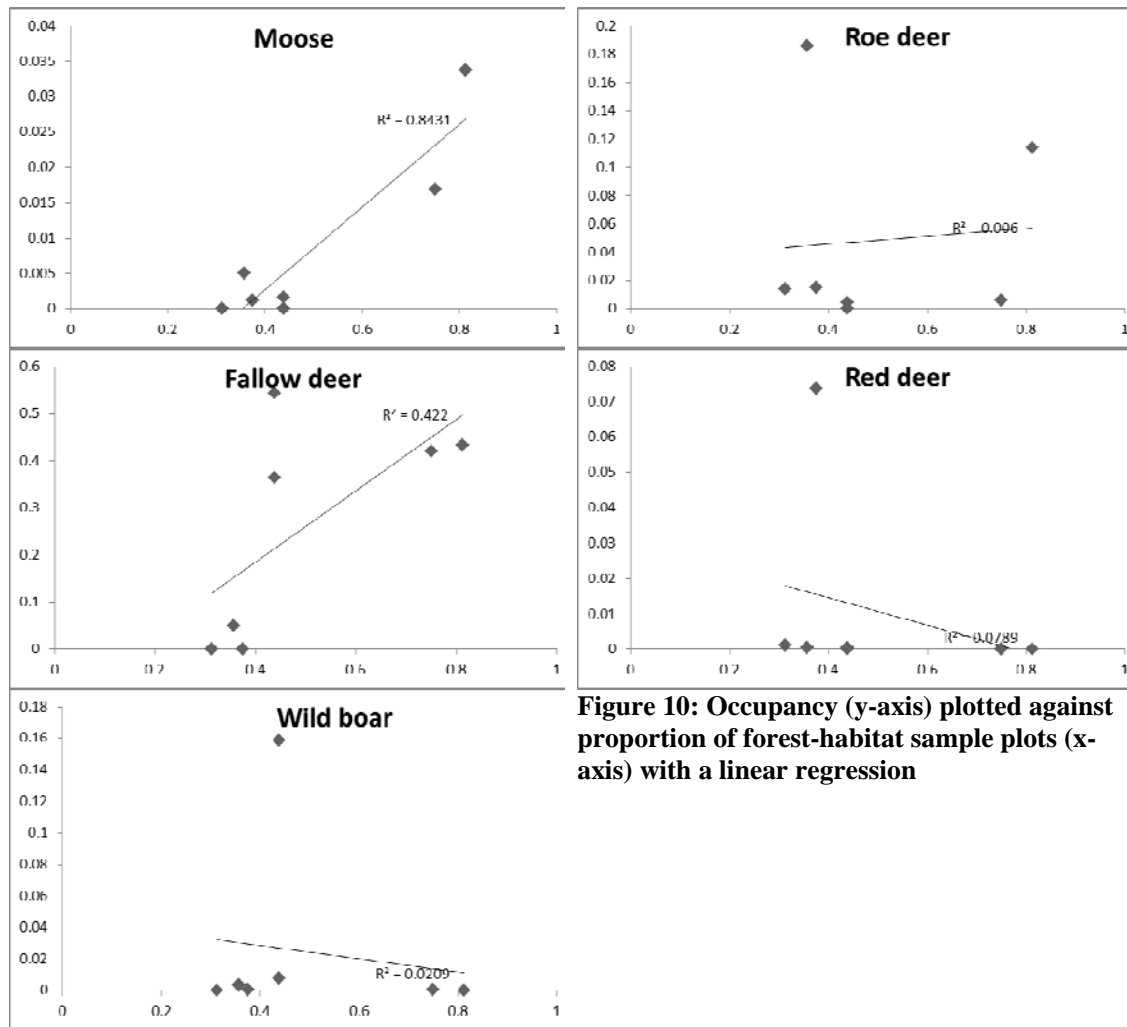


Figure 10: Occupancy (y-axis) plotted against proportion of forest-habitat sample plots (x-axis) with a linear regression

In the model “Occupancy~Forest*Species”, the dependence of fallow deer’s occupancy on forest habitat is significantly different from all species, except for moose, which is also exhibiting a quite strong positive correlation (Figure 10).

Discussion

Treatment & Selection

My hypothesis, that the type of the supplementary food would influence concentrate selectors and intermediate feeders differently did not gain support in this study; nor did the assumption that willow provided from short rotation forestry can be used as a diversion technique for moose (or any ungulate for that matter). Even though the daily occupation on the *Salix* plots was significantly higher than on the control plots, this is probably explained by the fact that all *Salix* plots were established on a former silage feeding site, while many control plots were created *de novo* for the study. The animals therefore passed by with a higher probability since it was a known feeding location to them. The willow shoots of both deliveries were in fact hardly touched at all (*personal observations*). On the contrary, enclosed moose and fallow deer (at Öster Malma and Tovetorp, respectively) were feeding on the shoots and stripping the bark of them (albeit a bit reluctantly), so these shoots were not completely unpalatable. There are two possible explanations:

1. *The ungulates were not used to this type of food.* The shoots might have been ruled out as “dead” right away because especially in the first delivery (on the Euro-palette) they looked clearly artificial and uprooted. The enclosed animals were used to be fed with “dead branches” alongside their pellet-based diet. So maybe there is a learning process involved. Anecdotal evidence suggests that moose are particularly “picky”. On the other hand, one would think that during a tough winter any food source would be used to avert starvation.
2. *The clones are less palatable than expected.* But at least *Klara* is known for being browsed by moose in the short rotation coppice (Sten Segerslätt & Anders Jönsson, pers.comm). Maybe the way they were handled, stored or transported led to a deterioration of their nutritional value which made them unattractive. It is probably relevant to note that these clones were developed with the aim to increase growth rate and frost- and fungus resistance compared to previous clones (Jordbruksverket 2012). They were not developed to resist browsing.

Silage plots were visited far more frequently. Since the occupancy measure is based on photos regardless of the number of individuals per photo, the fact that fallow deer was mostly present in big groups is accounted for (e.g. a picture with one moose weights as much as a picture with 30 fallow deer). With this in mind it becomes clear that fallow deer spend by far the most time at the silage plots and it can be safely deducted that they are consuming much more than any other species. The selection index shows the same. Moose are consuming the least amount of silage which is also reflected in their very low selection index. Only some individual moose showed up every now and again to feed at certain feeding sites. Taking their dietary needs into account this is probably not surprising and supports the hypothesis that the traditional supplementary feed is oftentimes not suitable for them.

Red deer and fallow deer have different distributions within the study area – fallow deer is almost absent in the area around sites 7 and 8, while red deer are utilizing the silage frequently there. This probably explains the trend towards a negative correlation of selection indices between these species (Table 1). Wild boar was present on many pictures, but they don't seem to select for silage that much, at least in relation to their abundance in the landscape. In addition, most individuals on the pictures were very young and were building nests in the silage instead of feeding on it (*personal observation*). Wild boar is in

fact fed with corn in the study area on a large scale, which might explain why they were utilizing silage for sleeping rather than food.

Day & Night

All species preferred to feed at night – except for roe deer: They preferred to feed on silage during daylight hours. Moreover, the site specific selection indices of fallow deer tend to be opposite those of roe deer in this study, which implies spatial avoidance. Ferretti et al. (2011a) suggests that roe deer avoid areas with high fallow deer densities and that “interspecific interference from the latter affects the density and distribution of the former both at a fine and at a large scale”. In another study, Ferretti et al. (2011b) show that fallow deer always dominates roe deer and distribution might even change in favor of fallow deer. Inverse population trends between roe deer and fallow deer have been reported from other areas, as well (Batcheler 1960; Focardi et al. 2006). Dolman and Wäber (2008) suggest that fallow deer might be a particularly effective competitor against other intermediate feeders and concentrate selectors, which might be explained by them evolving in the semi-arid, relatively poor habitats of Asia Minor (Ferretti et al. 2011b). I hypothesize that roe deer does not only avoid fallow deer spatially, but maybe temporally, as well. Since fallow deer show a strong preference for nighttime feeding, roe deer might evade them by switching to daytime feeding at the same sites.

Contrary to the above, Raesfeld and Neuhaus (2003) suggest that roe deer is naturally diurnal and might in this case simply exhibit its natural activity pattern. But fallow deer is also diurnal (Steinbach n. d.), and is undoubtedly more nocturnal than roe deer in this study. If one assumes that cervids become more nocturnal because of them being disturbed by hunting activities, this disturbance would apply to both species. More research is needed to test for this hypothesis.

Environment

The results here are rather weak because the replication is so small. Moose and fallow deer seem to prefer feeding sites with a higher forest cover in the vicinity, but only the R^2 -value of moose seems to be reasonably strong (>0.8).

Management implications

As a possible result of fallow deer being almost omnipresent at high densities, both moose and roe deer might be negatively affected. All three species can theoretically utilize silage, but fallow deer leaves the other two species behind in terms of digestion of roughage (cf. Hofmann 1989). So fallow deer is not only benefiting the most from silage from a nutritional view point, but might be competing for this resource with at least roe deer. Since fallow deer have a broad feeding niche they maybe continue to compete with both moose and roe deer for the emerging green in spring and might even outcompete them over the scarce resources in a landscape dominated by spruce (however, this assumption needs further research). If competition occurs – whether direct or indirect –, this could also explain why moose are in a comparably bad condition in the area with lower slaughter weight, lower reproduction and higher calf mortality than in other regions of Sweden (Henricson 2011).

Short rotation coppice willow doesn't seem to be a suitable winter feed for moose, at least not based on the findings of this study. As I have mentioned earlier, anecdotal evidence suggests moose to be quite picky and slow to accept new supplementary feed (however, no

scientific study has been published yet), so trying for a few more winters might eventually lead to them recognizing the provided willow as a food item. When used at a small scale, short rotation coppice willow is a relatively expensive winter feed, especially compared to silage. So taking its apparent inefficiency and high cost into account, it might not be economically feasible.

It could be shown that silage is not utilized by moose much and that the species utilizing current feeding practice the most is fallow deer. Depending on management goals, the feeding regime needs to be changed: If one would like to improve the body condition of roe deer and moose and increase their densities, it is probably crucial to decrease fallow deer density. In addition, feeding of silage might be further promoting fallow deer because roe deer probably suffers from competition and it doesn't target moose. So even if willow is not suitable it might still be necessary to find a more specific food item for moose (under the assumption that winter feeding in general is deemed necessary, that is).

Possible sources of error

Changing the treatment of the *Salix* plots (exchange of the clones) during the study period might have caused a distortion. E.g. moose had grown accustomed to the specific *Salix* clone if I wouldn't have exchanged the shoots before that happened. However, it is highly unlikely that a change in occupancy would have occurred without an exchange, so an influence on the data is improbable. There are some gaps in the camera data due to malfunctions and sampling method. This could have caused a distortion of the occupancy, especially if those missing pictures were showing a species other than fallow deer.

Further studies

The Öster Malma area is a very interesting area in terms of interspecific competition among all the ungulates present. A possible study would be to map as many silage feeding sites in the Öster Malma area as possible, note the date when the first bale is brought out to each site (and also when or whether feeding is discontinued). Then one would monitor the movement of the collared moose (SLU has a couple of collared moose in the Öster Malma area) in that area over the winter feeding period. The time they spend close or at the feeding sites would be of particular interest. To refine the scale of behavioral observation, one could also set up camera traps at the sites again – but this time recording short film sequences to visualize direct competition. The correlation of fallow deer & moose and fallow deer & roe deer density, as well as body condition, reproduction, slaughter weight etc. would also be an interesting addition. One could increase the annual fallow deer bag size and monitor if there is a change in the above mentioned traits over the following years.

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Appendix

Table 2: Pictures included in the study; only silage cameras are shown, but the other cameras' pictures were treated accordingly

| | Site 01 | Site 02 | Site 09 | Site 05 | Site 04 | Site 10 | Site 03 | Site 07 | Site 08 |
|------------|---------|---------|---------|---------|---------|---------|----------|---------|---------|
| Date | CAM01 | CAM06 | CAM07 | CAM11 | CAM16 | CAM17 | CAM18 | CAM23 | CAM25 |
| 2013-01-28 | | | | | | | NO FOOD | | |
| 2013-01-29 | | | | | x | | NO FOOD | | |
| 2013-01-30 | | | | | x | | NO FOOD | | |
| 2013-01-31 | | | | | x | | NO FOOD | | |
| 2013-02-01 | | | | | x | | NO FOOD | | |
| 2013-02-02 | | | | | x | | NO FOOD | | |
| 2013-02-03 | | | | | x | | NO FOOD | | |
| 2013-02-04 | | | | | x | | x | | |
| 2013-02-05 | | | | | | | NO FOOD | | |
| 2013-02-06 | | | | | | | NO FOOD | | |
| 2013-02-07 | x | | | | | | | | |
| 2013-02-08 | x | | | | | | | | x |
| 2013-02-09 | x | | | | | | | | |
| 2013-02-10 | x | | | | x | | | | |
| 2013-02-11 | x | | | | | | | | |
| 2013-02-12 | x | | | | | | | | |
| 2013-02-13 | x | | | | | | | | |
| 2013-02-14 | x | | | | | | | | |
| 2013-02-15 | x | | | | | | | | |
| 2013-02-16 | x | | | | | | | | |
| 2013-02-17 | x | | | | | | | | |
| 2013-02-18 | x | | | | | | | | |
| 2013-02-19 | x | | | | | | | | |
| 2013-02-20 | x | | | | | | | | |
| 2013-02-21 | x | | | | | | | | |
| 2013-02-22 | x | | | | | | | | |
| 2013-02-23 | x | | | | | | | | |
| 2013-02-24 | x | | | | | | | | |
| 2013-02-25 | x | | | | | | | | |
| 2013-02-26 | x | | | | | | | | |
| 2013-02-27 | x | x | | | | | LOW FOOD | | |
| 2013-02-28 | x | x | | | | | | | |
| 2013-03-01 | x | x | | | | | | | |
| 2013-03-02 | x | x | | | | | NO FOOD | | |
| 2013-03-03 | x | x | | | | | | | |
| 2013-03-04 | x | x | | | | | | | |
| 2013-03-05 | x | x | | | | | NO FOOD | | |
| 2013-03-06 | x | | | | | | | | |
| 2013-03-07 | x | | | | | | | | |
| 2013-03-08 | x | | | | | | NO FOOD | | |
| 2013-03-09 | x | | | | | | | | |
| 2013-03-10 | x | | | | | | x | | |

Legend

| | |
|---|--------------------------------------|
| x | : No pictures/presumably malfunction |
| | : Sampled |
| | : Excluded from analysis |
| | : Not sampled |

Table 3: Modeling results for day- and nighttime occupancy; Intercept: roe deer and daytime; DNN=nighttime, FD=fallow deer, M=moose, RED=red deer, WB=wild boar

```

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    -2.3979     0.1974  -12.148 < 2e-16 ***
DNN             -0.8148     0.2810   -2.899 0.003738 **
SpeciesFD        0.3964     0.2595    1.528 0.126607
SpeciesM       -3.4162     1.0208   -3.347 0.000818 ***
SpeciesRED     -17.1931    594.0236  -0.029 0.976910
SpeciesWB       -2.0209     0.5403   -3.740 0.000184 ***
DNN:SpeciesFD    2.1564     0.3376    6.388 1.69e-10 ***
DNN:SpeciesM     2.2101     1.0993    2.010 0.044383 *
DNN:SpeciesRED  16.3099    594.0237    0.027 0.978096
DNN:SpeciesWB    1.8477     0.6156    3.001 0.002687 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1315.81  on 69  degrees of freedom
Residual deviance:  646.33  on 60  degrees of freedom
AIC: 760.82

```

Table 4: Modeling results for day- and nighttime occupancy; Intercept: roe deer and nighttime; DND=daytime, FD=fallow deer, M=moose, RED=red deer, WB=wild boar

```

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    -3.2127     0.2000  -16.062 < 2e-16 ***
DND             0.8148     0.2810    2.899 0.00374 **
SpeciesFD       2.5529     0.2159   11.822 < 2e-16 ***
SpeciesM       -1.2061     0.4081   -2.956 0.00312 **
SpeciesRED     -0.8832     0.3639   -2.427 0.01523 *
SpeciesWB      -0.1732     0.2950   -0.587 0.55701
DND:SpeciesFD  -2.1564     0.3376   -6.388 1.69e-10 ***
DND:SpeciesM   -2.2101     1.0993   -2.010 0.04438 *
DND:SpeciesRED -16.3099    594.0237  -0.027 0.97810
DND:SpeciesWB  -1.8477     0.6156   -3.001 0.00269 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1315.81  on 69  degrees of freedom
Residual deviance:  646.33  on 60  degrees of freedom
AIC: 760.82

```

SENASTE UTGIVNA NUMMER

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