Moose (*Alces alces)* and red deer (*Cervus elaphus)* at winter feeding stations: interspecific avoidance in space and time?

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Contents

Abstract

A recent increase in the red deer (*Cervus elaphus*) population in Eastern Norway has raised concern among hunters and landowners that the red deer may outcompete and suppress the economically important moose (*Alces alces)*. Moose has been fed supplementary in winter time in Eastern Norway for many years, and in the recent years red deer has been observed more and more on the feeding stations. In this study, I have tested if these two species show a mutual spatiotemporal avoidance at winter feeding stations. I have used both pellet count data from feeding stations and GPS data from animals that use feeding stations. Moose and red deer tracks were documented at all of the 12 feeding stations visited during the pellet count. There was a significant negative relation between the density of moose pellet groups and the density of red deer pellet groups at the feeding station on a weekly basis ($p<0.001$). On a day-to-day basis, density of red deer pellet groups on feeding stations was related to volume of silage bale and feeding station region, while none of the factors seemed related with the density of moose pellet groups. There was no difference between the two species in proportion of time spent <100m from the feeding station (moose 25.1 % ± 2.4 %, red deer 22.4 % ± 3.4 %). Feeding station use occurred mostly during night hours for both species, but the red deer had a more distinct pattern for feeding station use than the moose: Red deer changed more abrupt from high-use to low-use periods. Feeding bouts for both species were longest if they entered the feeding station in the afternoon, but there was no significant difference in length of feeding bouts between the species. After having left the feeding station, red deer moved quicker away and stayed at slightly longer distances from the closest feeding station during daytime than moose did.

Key words: winter feeding stations, moose, red deer, pellet count, GPS positions, spatial and temporal avoidance, feeding bouts.

Sammendrag

De siste års økning i hjortepopulasjonen (*Cervus elaphus*) på Østlandet i Norge uroer mange jegere og grunneiere. De er bekymret for at hjorten kommer til å utkonkurrere og presse elgen (*Alces alces)* ut av sitt leveområde. Elgen har blitt fôret ekstra på vinterstid på Østlandet i mange år, og i den senere tiden har hjorten også blitt observert mer og mer på fôringsstasjonene. I dette studiet har jeg testet om elg og hjort unngår hverandre i tid og rom på fôringsstasjonene vinterstid. Jeg har brukt data både fra møkktaksering rundt fôringsplasser og GPS-posisjoner fra fôringsplassbrukere. Det ble dokumentert spor etter elg og hjort på alle de 12 fôringsstasjonene det ble gjort møkktakseringer på. Det var en signifikant sammenheng mellom tettheten av elg og tettheten av hjort rundt den samme fôrballen på en ukentlig basis ($p<0.001$). På en dag-til-dag basis hadde volumet av fôrballen og fôringsstasjonsområde en effekt på tettheten av hjort på fôringen, mens for elgen hadde ingen av faktorene noen effekt. Jeg fant ingen forskjell mellom elg og hjort på andel tid brukt <100m fra fôringsstasjonen (elg 25.1 % ± 2.4 %, hjort 22.4 % ± 3.4 %). Bruken av fôringsstasjonene skjedde mest på nattestid for begge arter, mens hjorten hadde et mer tydelig mønster for bruken av fôringsstasjonene enn elgen hadde, hvor hjorten skifter mye fortere fra perioder med mye bruk til perioder med lite bruk. Fôringsperiodene for begge arter er lengst når de ankommer fôringsstasjonene på ettermiddagen, men det var ingen signifikant forskjell i lengden på fôringsperiodene mellom artene. Etter å ha forlatt fôringsstasjonen beveget hjorten seg raskt bort fra fôringen, og den holdt seg så vidt lengre unna den nærmeste fôringsstasjonen på dagtid enn det elgen gjorde.

Nøkkelord: vinterfôringsstasjon, elg, hjort, møkktaksering, GPS-posisjoner, unngå hverandre i tid og rom, fôringsperioder.

Introduction

Supplementary winter feeding of large herbivores is a widespread practice in Northern Europe and parts of North America (Putman & Staines, 2004). In Austria, Germany and Hungary, the countries with continental Europe's highest red deer densities, supplemental winter feeding is even an obligation (Peek, Schmidt, Dorrance, & Smith, 2002). The reasons for supplementary feeding are several: reduce damages to crops and forest stands, maintain large populations, maximize size, body weight and antler size, control animal movement, or substitute the loss of winter habitats (Milner, Storaas, van Beest, & Lien, 2012; Peek et al., 2002; Storaas, Nicolaisen, Gundersen, & Zimmermann, 2005). But there are not only positive aspects of supplementary feeding (Gundersen, Andreassen, & Storaas, 2004; Smith, 2001; van Beest, Gundersen, Mathisen, Milner, & Skarpe, 2010a; van Beest, Loe, Mysterud, & Milner, 2010b). Putman and Staines (2004) have summarized a variety of the possible negative aspects associated with supplementary winter feeding. They especially pointed out that the uneven distribution of food may lead to intra- and interspecific competition among herbivores attracted to these places of forage concentrations.

The optimal foraging theory predicts that the benefits of foraging has to exceed the costs in order to increase survival and reproduction rates of an individual (Krebs & Davies, 1993). The central place foraging theory (Orians & Pearson, 1979) is a case of the optimal foraging theory where the individuals are dependent on returning to a certain place like a nest or a den, or another key resource place like a supplementary winter feeding station. The distance to this key point determines the forage decisions (van Beest, 2010). As a foraging central place the feeding stations will cause accumulations of individuals of both moose and red deer, and interference competition may occur (Miller, 2002). Interference competition is defined as "Competition in which access to a resource is limited by the presence of a competitor" (Smith & Smith, 2009). The essential for the presence of interference competition is if the individuals have different temporal niches (e. g. if the two potential competitors moose (*Alces alces*) and red deer (*Cervus elaphus*) use the feeding stations at different times of day) or not (e. g. red deer prevent the food access for moose) (Mysterud, 2010). Another example of central place foraging is waterholes in dry areas that many species and individuals are dependent on. In Hwange National Park in Zimbabwe they found that smaller species that interacted with larger and more dominant species changed their temporal niche around the waterholes in drier years to avoid high temporal overlap (Valeix, Chamaillé-Jammes, & Fritz, 2007).

Østerdalen in Hedmark county, Norway, is a wintering area for moose, where moose migrates from higher elevations with more snow to the valley bottoms where the snow conditions are not that hard in the winter (Gundersen et al., 2004). This seasonal migration causes higher densities then in the rest of the year in some areas. In Østerdalen, landowner association started with supplementary winter feeding for moose in 1989 (Milner et al., 2012) mainly for limiting the migratory movement across heavily trafficated roads and railway, but at the same time increase winter survival, and keep moose away from young pine stands (Gundersen et al., 2004). The moose has existed in Norway for centuries, but the population went through a bottleneck in the start of the 1800's, and only e few individuals existed, mainly in Hedmark county (Solberg, 2009). Hunting regulations and changes in forestry practices caused a strong population increase, and the population in Eastern Norway is today one of the world's most heavily harvested population (Lavsund, Nygrén, & Solberg, 2003), with almost 8000 moose harvested in Hedmark in 2011/2012 (Statistics Norway, 2012a). Red deer on the other hand is a relatively new and unknown species in the area. Exactly when red deer established in the eastern part of Norway is not well documented, but it is initially after the 1950's the red deer started to expand from the west coast, both demographically and spatially (Haanes, Røed, Flagstad, & Rosef, 2010). The red deer population in the East of Norway has most likely dispersed from Møre og Romsdal County, through northern parts of Gudbrandsdalen (Haanes et al., 2010). Over the past few years red deer has also started to use the winter feeding stations in Østerdalen, and according to the hunting statistics the density of red deer has increased rapidly (Figure 2). Many landowners have reported an increase in red deer sightings at feeding stations. This rapid increase of the red deer density may trace back to the large supply of winter forage in the area in terms of silage bales (Hegland, Solheim, Aarhus, & Røyrvik, 2011). Both moose and red deer are highly valued game and trophy animals for hunters in Norway. In the East of Norway moose has a high economic value for landowners, in addition to the recreational value. A big concern for some hunters and landowners is the idea that red deer will outcompete and suppress the moose from the area.

Little is known about interactions between moose and red deer in Norway (Mysterud, 2000) and how they behave when they encounter each other. This study is based on observations at supplementary winter feeding stations. If competition for feeding stations occurs between the two species, I would expect them to show patterns of avoidance in space and/or time. I predict to find:

P1) Exclusive use of feeding stations. Stations are predominantly used by either red deer or moose.

P2) The intensity of feeding station use (density of pellet groups) by one species affects the intensity of use by the other species on a day-to-day basis.

P3) The time spent at the feeding stations (percent positions <100 m from feeding station) is shorter for one and longer for the other (dominant) species.

P4) Moose and red deer visit feeding stations at different times of the day.

P5) Feeding bouts (time spent continuously at the feeding station) for one species are shorter than for the other (dominant) species.

P6) While not feeding at the feeding stations, one species keeps further away from the feeding station then the other (dominant) species.

For predictions P1) and P2), I visited feeding stations in Østerdalen throughout a winter and recorded moose and red deer tracks and pellet group densities. For prediction P3)-P6), I analyzed hourly GPS-positioning data of red deer and moose that had been collared by two different research projects with partly overlapping study areas and study periods (Milner et al., 2012; Zimmermann, 2012).

Material and methods

Study area

The study area is located in the four municipalities Rendalen, Stor-Elvdal, Elverum and Stange, in Hedmark county, southeast in Norway (Figure 1). The study area is in the boreal forest zone with forest stands dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and to a lesser extent mixed stands of deciduous trees. Rendalen, Stor-Elvdal and Elverum municipalities are located in the valley Østerdalen, with the river Glomma running trough. The valley bottom is at about 200-400 m.a.s.l., and is surrounded with mountains up to around 1200 m.a.s.l. Stange municipality has widespread arable lands, and it lies next to the big lake Mjøsa. Mjøsa is at about 150 m.a.s.l., while the feeding places in Stange are situated in the hill sides around 300 m.a.s.l. The density of moose in Hedmark in the winter has been quite stable around 1,3 moose per km^2 the last 15 years (Milner et al., 2012). There are no density estimates available for red deer, but densities seem to increase according to the hunting statistics (Statistics Norway, 2012b, 2012c)(Figure 2). Large predators are present in Hedmark, but hunting is the most important cause of death for red deer and moose (Lavsund et al., 2003). The mean winter temperature (1. January – 31. March) during the last 10 years at Haugedalen weather station (Åmot municipality), at 240 m.a.s.l., is -6°C, and the mean snow depth in the same period is 58 cm. For the same 10 year period, there was an average of 130 days of snow cover per year (Haugedalen weather station: Meterologisk institutt, 2012).

The supplementary feeding is initiated by landowners in Østerdalen, and by the managers in a public area in Stange. The supplemental food consists of silage bales, and the feeding stations are usually located close to gravel roads. On the most heavily used feeding stations they have fed up to 150 bales a year, but the average is around 25 bales per year per feeding station. One silage bale consists of around 800 kg (fresh weight) of food. The number of tons fed each year has increased linearly since they first got it quantified in 1998, from around 200 tons to around 2000 tons in 2010 (Milner et al., 2012).

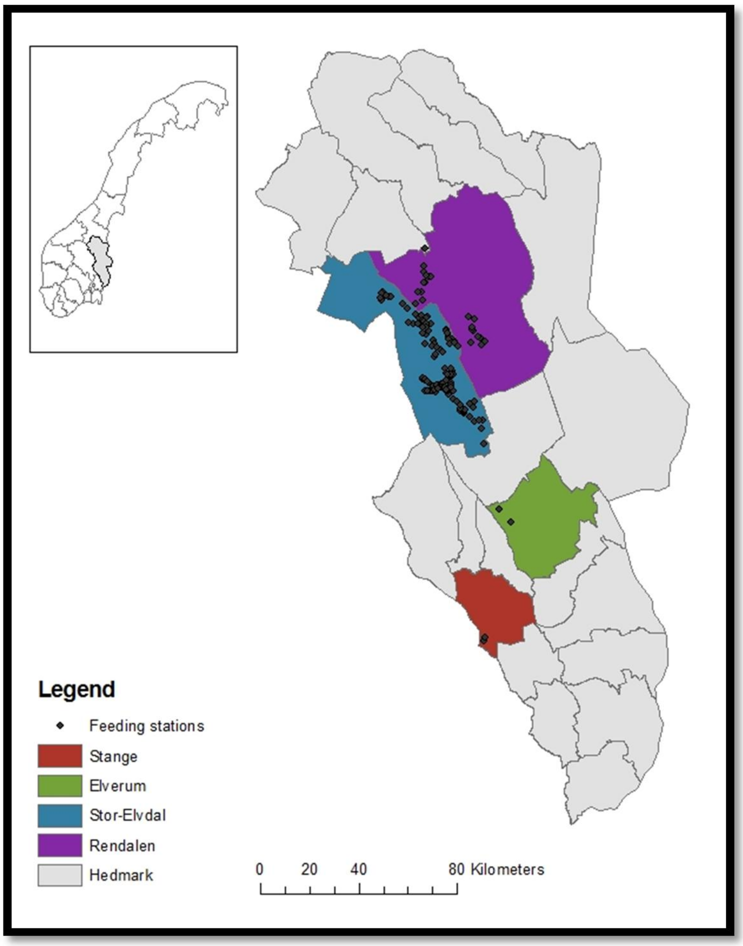

Figure 1. Study area. The study area included four municipalities of Hedmark county in Eastern Norway. Black dots are feeding stations for moose in the respective municipalities.

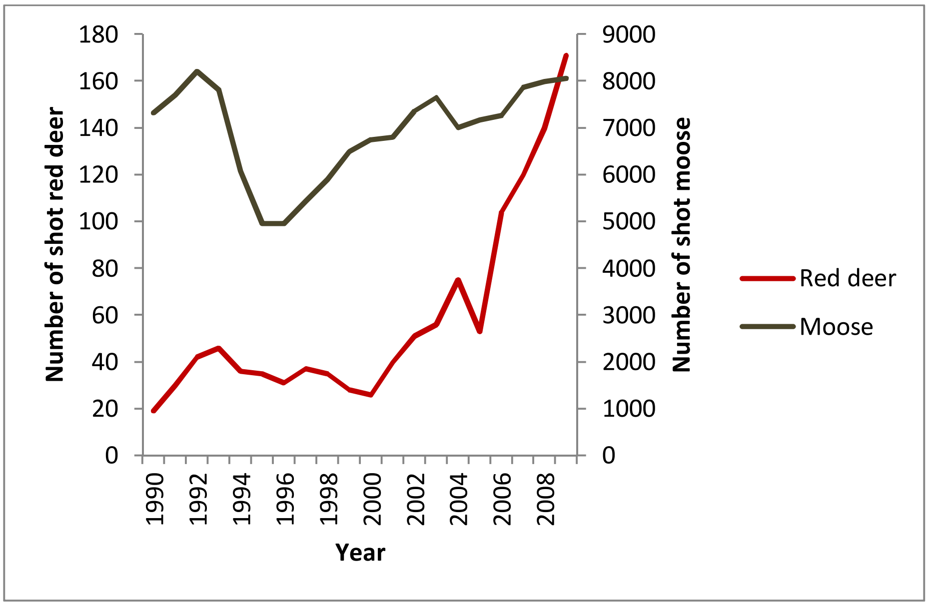

Figure 2. Hunting statistics of red deer and moose from Hedmark County.

Data collection

Pellet group count

Only feeding stations in the main valley in Stor-Elvdal and Rendalen counties were used in this field study (Figure 3). The reason for that was that I had information from the project "Improving moose forage with benefits for the hunting, forestry and farming sectors" that the side valleys were not visited much by red deer, which was important for this study. The field work was conducted from 22nd February – 17th March 2011. Because of early snow melting I had to end the fieldwork earlier than planned. The fieldwork was done in 6 different regions in Stor-Elvdal and Rendalen counties (Strand, Opphus, Grindfossberget, Skytebanevegen, Birkebeinervegen and Hanestad). One feeding station may consist of several bales, these single bales are from now on referred to as "bale sites". There was a total of 12 feeding stations and 18 bale site in this study.

Figure 3. Feeding stations used in pellet count method in Stor-Elvdal and Rendalen counties.

The feeding stations were visited 5, sometimes 4, subsequent days during a week. For one feeding station, we collected data during two weeks, one in the start and one in the end of the study period. On Monday we removed all the faecal pellet groups in a 10 meter buffer radius around the silage bale. On each subsequent day of the week, we counted the number of moose and red deer pellet groups inside a 10 meter radius around the silage bale, and then removed the pellet groups again. We also measured the height and width in two directions of the bale to be able to calculate the volume of the bale that was left. Lastly we noted if there were moose and red deer tracks present, and we measured snow depth, sinking depth of the observer and of a moose if possible, and if the 10 meter radius overlapped with a road. Feeding stations with road present is typically feeding stations where the silage bale is dropped beside the road at a casual place, while feeding stations with road absent are feeding stations that are prepared. If two bales were so close that the 10 meter buffer overlapped, we measured the overlap, and calculated the dissolved buffer area as one joint observation for those bales. The size of the area examined around the bale varied with the size of the bale, since it was measured from the edge of the bale, and not from the center.

GPS-data

The GPS-data were from the two projects “Improving moose forage with benefits for the hunting, forestry and farming sectors” (Milner et al., 2012) and “Red deer in Hedmark” (Zimmermann, 2012).

Female moose with calves were immobilized with a dart gun (Arnemo, Kreeger, & Soveri, 2003) from a helicopter in January 2009 and 2010. The moose cows (N=30) were collared with GPS-collars (Tellus Remote GSM, Followit AB, Lindesberg, Sweden) programmed to take positions hourly.

Red deer females were immobilized with a dart gun at feeding stations in Rendalen, Stor-Elvdal, Elverum and Stange municipalities, in February to April from 2002-2011. The red deer were darted from cars or small cabins maximum 15 meters from the silage bale. Most adults, and some juveniles (one and a half year) (N=12), were captured and collared with GPS-collars (Simplex, Tellus basic and Tellus GSM, Followit AB, Lindesberg, Sweden). The GPS-collars were programmed to take positions hourly.

For the analysis I have only used positions from the 1st of January to the 31st of March, because this is the period with most snow and therefore most heavy use of the feeding stations. Animals that have >10 % of the positions <100 meters from the bale were considered as feeding station users (Milner et al., 2012), and only these were included in the analysis. Positions that were <100 meters from the bale was defined as "using the feeding station" (Milner et al., 2012; Sahlsten et al., 2010; van Beest et al., 2010b). Because the animals were collared at different dates, and because the GPS success was not 100 %, the animals have different number of positions (Appendix). The time zone used throughout this paper is one hour ahead Greenwich Mean Time (GMT + 1).

Data analysis

Pellet count data

I analyzed the pellet count data with a generalized linear mixed model (GLMM) with the function lmer in the lme4 package (Bates & Maechler, 2009). To test if moose and red deer densities were negatively correlated at the feeding stations, I summarized the data for each bale and week (N=19 bale site weeks). The sum of moose piles per bale and week was set as the response with a poisson distribution. The explanatory variable was average pellet group density of red deer. I also included the number of days per bale and week as an offset variable to correct the response for varying study lengths. I included the feeding station region as a random variable, because the number of feeding stations and bales differed among areas. To test if there were additional factors that affected the moose pellet group density, I ran the same model again, but added two more explanatory factors and their interactions: Presence/absence of roads and snow depth.

To see what determines to what extent moose and red deer use feeding stations on a day-to-day basis, I ran two linear mixed effect models (lmer) with a poisson distribution, with respectively number of deer piles and number of moose piles as response variables. The offset variable was the log-transformed size of buffer area examined, and explanatory factors were feeding region, the pile density of the other species, snow depth and the volume of the silage bale. The feeding station was entered as a random factor, because there were different numbers of silage bales on each feeding station. For this analysis the statistical unit was the daily observation per bale site (N=71 bale site days), as opposed to the entire week in the previously analysis.

GPS data

I applied a spatial join in ArcMap to calculate the distance from the GPS-positions to the silage bales. I firstly tested the overall time, i. e. the proportion of GPS-positions at feeding stations differed between moose and red deer with a two sample t-test.

In a second step, I tested if the daily pattern of feeding station use was different for the two species, in order to detect any temporal avoidance. I analyzed the GPS data with generalized additive modelling (GAM) with the function gam in the mgcv package (Wood, 2010). To examine how the feeding stations were utilized during the day, I used presence absence of red deer and moose on the feeding station as a response variable with a binomial distribution. The variable time of day was set as the smoothing function, split up in moose and red deer. At the end I added month and species as explanatory variables. To examine their activity in the 24 positions after have been at the feeding station, I ran the same model one more time, but changed the response variable to distance from the bale, with a Gaussian distribution. For these analyses I used only GPS-positions >100 meters from feeding station, and excluded positions >24 positions since they have been on the feeding station (N=21471). To examine for how long they stayed at the feeding station at different times of day I ran the same analysis again, but changed the response variable to length of feeding bout, with a Gaussian distribution. For this analysis I only used positions <100 meters from the feeding station (N=2309).

If not written otherwise, the analysis is done in R (R Development Core Team, 2011). All the models are selected by backwards selection where all the non-significant (p>0,05) variables were removed.

Results

Spatial avoidance

Moose- and red deer tracks were documented at all of the 12 feeding stations and all of the 18 bale sites, but only on a weekly basis. As predicted in P1, there was a negative relation between the density of pellet groups of moose and the density of pellet groups of red deer at the same bale site week (<0.001): high densities of moose pellet groups were only recorded at bale sites with low density of red deer pellet groups, and high densities of red deer pellet groups were only recorded at bale sites with low density of moose pellet groups (Figure 4, Table 1). I could not find bale sites with high densities of both moose and red deer pellet groups. When I included presence of road in the model, the negative relation between density of moose and red deer was only evident at bale sites without roads close by (Table 1). There were generally more piles at feeding stations with absence of road. There was no correlation between the density of moose pellet groups and snow depth ($p>0.05$).

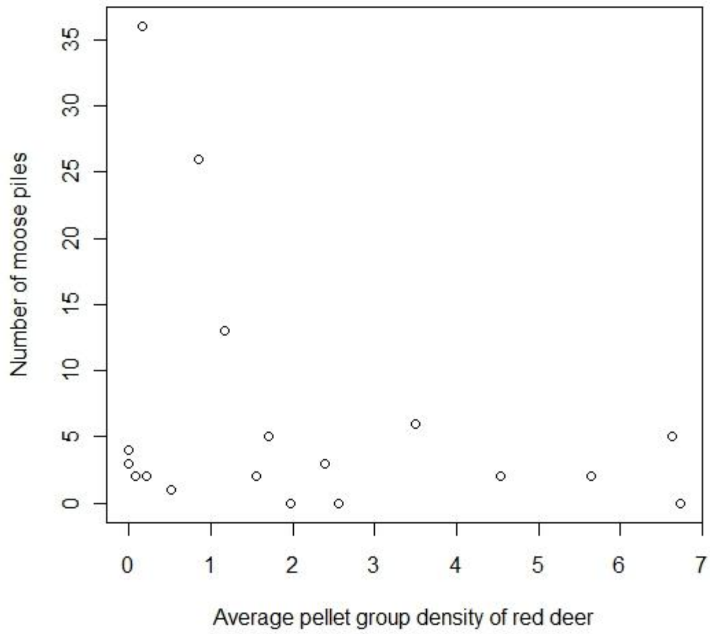

Figure 4. Number of moose pellet groups related to average pellet group density of red deer (piles per 100 m^2). N=19 bale site weeks.

Table 1. Parameter estimates of fixed effects from mixed Poisson regression models, with number of days as an offset and feeding area as a random factor, predicting avoidance between the two species, and if other factors affect it.

Response variable	Fixed effects	Estimates	S.E	z-value	Pr(>|z|)
Sum moose piles	Intercept	-1.65763	0.34798	-4.764	<0.001
	Average red deer density	-0.2544	0.07193	-3.537	<0.001
Sum moose piles	Intercept	1.0213	0.8523	1.198	0.231
	Av. deer pile density	-1.1351	0.1826	-6.215	<0.001
	Presence of road	-3.8969	0.4492	-8.675	<0.001
	Av. deer pile density*road	1.3933	0.2138	6.518	<0.001

For prediction P2, I looked at factors that explained red deer and moose pellet group densities at bale sites on a day-to-day basis. With an increasing volume of silage bale the density of red deer pellet groups increased (Table 2). The lowest density of red deer pellet groups was in Birkebeinervegen, while the highest density was in Hanestad (Table 2), independent of the volume of the silage bale. None of the included parameters was correlated with the density of moose pellet groups at bale sites. None of the regions had significant higher or lower density of moose pellet groups than the others, and the bale volume had nothing to say for the moose to come to the bale site or not (p>0.05).

Table 2. Parameter estimates from mixed Poisson regression models, with size of area examined as an offset and feeding station as a random factor, predicting the intensity of use of feeding stations, for red deer and moose.

Response variable	Fixed effects	Estimate	S.E.	z-value	Pr(>|z|)
Red deer piles	Intercept	-6.6273	0.6533	-10.145	< 2e-16
	Moose pile density	0.6097	12.0882	0.05	0.959772
	Volume of bale	0.7092	0.2336	3.035	0.002403
	Region(G)	2.6792	0.804	3.332	<0.001
	Region(H)	3.6775	1.1486	3.202	0.001367
	Region(O)	0.1391	1.2879	0.108	0.914
	Region(S)	-1.1938	1.3575	-0.879	0.379197
	Region(Sk)	2.7044	1.1534	2.345	0.01904
Moose piles	Intercept	-5.5277	0.50763	-10.889	<0.001
	Volume of bale	-0.68501	0.56827	-1.205	0.228
	Region(G)	-0.53581	0.64195	-0.835	0.404
	Region(H)	0.03634	0.97111	0.037	0.97
	Region(O)	-1.25271	1.13659	-1.102	0.27
	Region(S)	1.18375	0.87663	1.35	0.177
	Region(Sk)	-1.70992	1.05889	-1.615	0.106

Species-specific movement behavior at feeding stations

There was no difference between red deer and moose regarding the proportion of time spent at the feeding stations (t = 1.678, p>0.05). Moose spent on average 25.1 % ± 2.4 %, and red deer 22.4 % ± 3.4 % of the time at distances <100 m from the closest bale site, during the whole study period.

Red deer and moose used feeding stations most intensively during February with an average of 29.3 % ± 3.5 % of positions <100 m from feeding stations for both species. Degree of use was significantly lower in January and no difference in March (Table 3). For both red deer and moose, use of feeding stations occurred mostly during night hours (Figure 5). Red deer showed a more distinct temporal pattern of feeding station use than moose with higher top-use and lower low-use periods, and changes from high to low use periods occurring at shorter time intervals (Figure 5). While the top-use period of red deer lasted from about 20:00 – 03:00 (GMT + 1), the top-use period for moose from 20:00 – 05:00 (GMT + 1) ended two hours later (Figure 5).

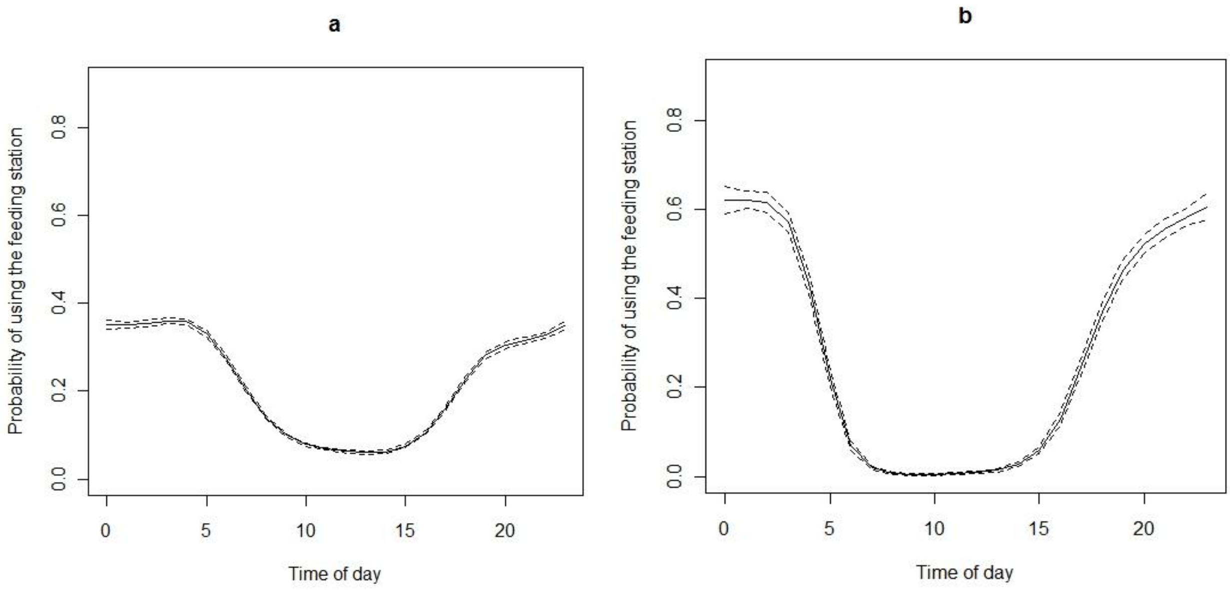

Figure 5. Probability of moose (a) and red deer (b) using the feeding station at different times of day (GMT + 1) (±SE). Model predictions are given for January and would be higher for February.

Feeding bouts for moose at feeding stations averaged 6.3 ± 0.1 hours, and of red deer 5.7 ± 0.3 hours, for the whole study period. The longest continuous time spent at a feeding station was 60 hours for moose and 18 hours for red deer. There were no significant differences on the length of feeding bouts during the whole study period between moose and red deer, nor between the months (Table 3). Feeding bouts for moose were longest when they entered the feeding station between 15:00 and 18:00 (GMT + 1), and for red deer between 15:00 and 19:00 (GMT + 1) (Figure 6). They were shortest for animals arriving during morning hours.

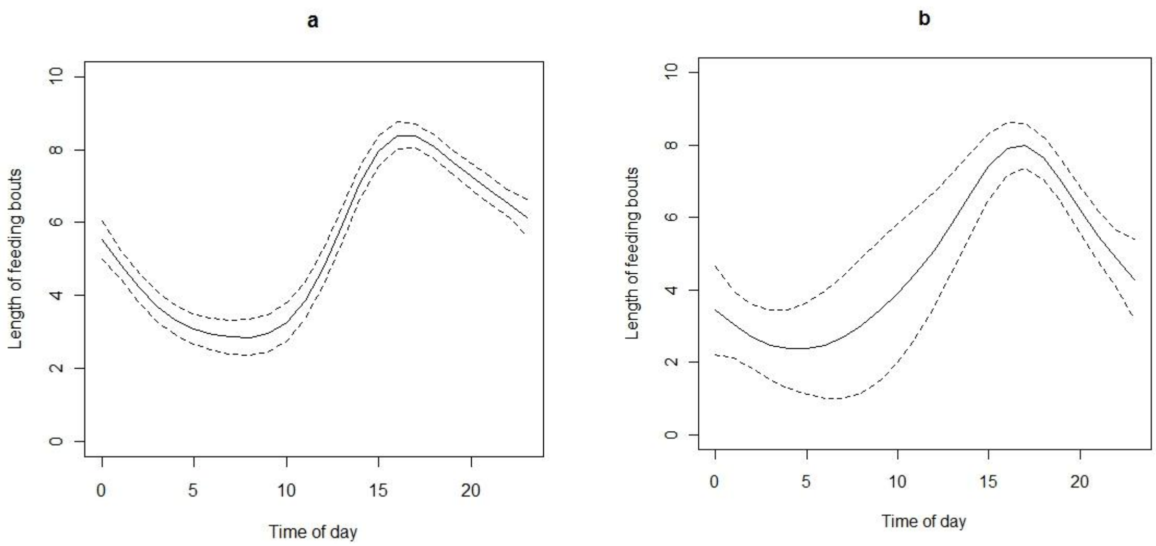

Figure 6. Length of the moose's (a) and the red deer's (b) feeding bouts divided on time of day (GMT + 1) (±SE). Model predicts are given for January.

Moose kept a generally longer distance to the feeding station than red deer during the 24 positions after having been at the feeding station. Both species kept longer distance from the feeding station in March than in February, and even longer distance in January than March (Table 3). Moose kept the longest distance from the feeding station between 14:00 - 20:00 (GMT + 1), and red deer between 10:00 - 16:00 (GMT + 1) (Figure 7). In the afternoon (between 14:00 – 16:00), moose kept an average distance to the feeding station at 602 m ± 12 m and red deer 645 m ± 15 m. The maximum distance kept from the feeding station during the 24 positions after have been on the feeding was for moose 11.2 km, and for red deer 2.9 km.

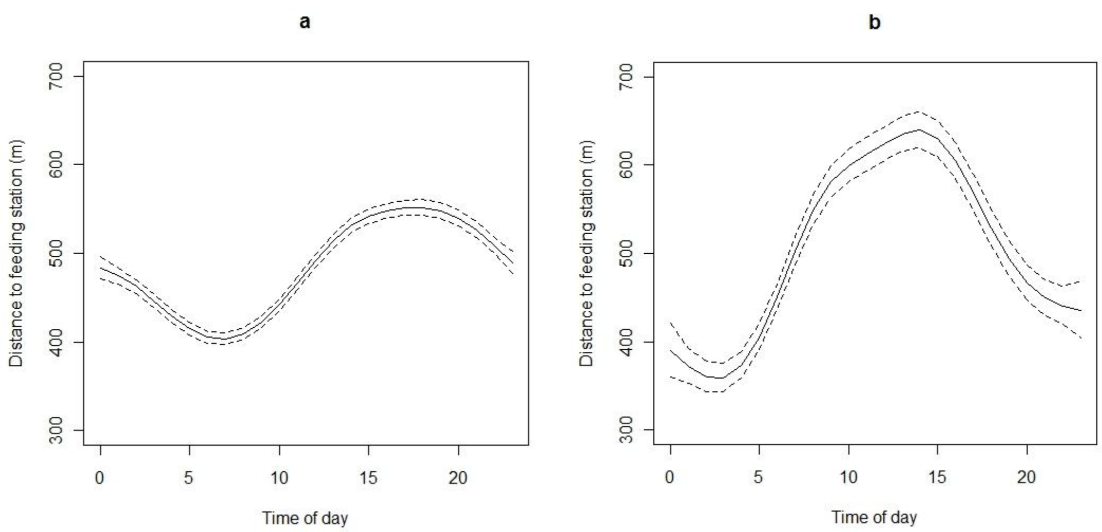

Figure 7. Distance to feeding station (meter) divided on time of day (GMT + 1), for moose (a) and red deer (b) (±SE). Model predicts are given for January and would be lower for March and lowest for February.

Table 3. Parameter estimates from GAM models, predicting presence/absence on feeding station, distance to bale and length of feedingbout, for moose and red deer.

Response variable	Parametric coefficients	Estiamte	S.E.	z-value	Pr(>|z|)
Presence/absence on feeding station	Intercept	-1.27627	0.26021	-4.905	<0.001
	Month(Feb)	0.33201	0.02741	12.113	<0.001
	Month(March)	0.02826	0.02752	1.027	0.304
	Smooth terms	edf	Ref.df	Chi.sq	p-value
	s(Time of day=moose)	8.68	8.969	3777	<0.001
	s(Time of day=red deer)	9.056	9.718	826	<0.001
Length of feedingbout	Intercept	2.0292	1.9178	1.058	0.29
	Month(Feb)	0.4034	0.3205	1.258	0.208
	Month(March)	-0.2122	0.3217	-0.66	0.51
	Specie(moose)	0.4499	1.3588	0.331	0.741
	Smooth terms	edf	Ref.df	F	p-value
	s(Time of day=moose)	6.602	7.743	30.833	<0.001
	s(Time of day=red deer)	4.622	5.466	6.868	<0.001
Distance to feeding station	Intercept	3.57831	0.13054	27.411	<0.001
	Month(Feb)	-0.20959	0.01349	-15.532	<0.001
	Month(March)	-0.09161	0.01298	-7.056	<0.001
	Specie(moose)	1.35903	0.07761	17.51	<0.001
	Smooth terms	edf	Ref.df	F	p-value
	s(Time of day=moose)	6.758	7.904	85.87	<0.001
	s(Time of day=red deer)	7.065	8.195	84.74	<0.001

Discussion

Spatial avoidance at feeding stations

Hostility between ruminants occurs rarely. This is probably due to evenly spread resources (Mysterud & Mysterud, 2000; Månsson, Bunnefeld, Andrén, & Ericsson, 2012). But at supplementary winter feeding stations, the resources are concentrated at small patches, which may lead to interference competition (Mysterud & Mysterud, 2000). One way to avoid interference competition is spatial avoidance (Boer, 2007; Mysterud, 2000). All the 18 bale sites had tracks of both moose and red deer on a weekly basis. I found no exclusive use by only one species at any bale sites on a weekly basis. However some bale sites were predominantly used by moose and some predominantly used by red deer. Those bale sites that were used about equally by red deer and moose, were used to only a small extent by the two species. None of the bale sites was used a lot by both species. This finding supports to a certain degree the prediction P1 of spatial avoidance between red deer and moose at feeding stations. I however saw that at low pellet group densities of both species, they can use the same bale site. This pattern of spatial avoidance was only present at feeding stations with absence of road, and there was also a greater density at these feeding stations. An explanation for this may be that there is less human disturbance at these feeding stations, and therefore they are more used by both species than the feeding stations with road present. This may be explained with the density dependence of interference competition, predicting that at higher densities of both species, there would be more competition (Mysterud & Mysterud, 2000).

The intensity of feeding station use by one species is not affected by the intensity of use by the other species on a day-to-day basis, and I have to reject prediction P2. On a day-to-day basis the different factors on the bale site can be more unstable than during a week as a whole. Factors that can change from day-to-day can be snow and weather conditions, and freshness and condition on the silage related to whether the food is recently put out or not. The available amount of silage on the bale site is decisive for the presence of red deer on a day-to-day basis. When the volume of the silage bale is greater, it is more likely that the silage is fresh and tastier as well. Hanestad, the region with the highest density of red deer pellet groups at the bale sites, is an area that is known for having winter populations of red deer for several years (Jensen, 2004), and some of the feeding stations have been put up especially for red deer. Birkebeinervegen, the region with the lowest red deer pellet group density in this study, is not known for having winter populations of red deer until lately. For moose, Gundersen et al. (2004) have found that animals need some time to locate and start using the feeding stations, and also get used to eat silage . This may also be true for red deer, and as the population increases and needs more food the differences among feeding station areas may fade. Neither volume of food available nor region affects the day-to-day utilization of bale sites by moose.

It seems like the moose feeds no matter how much food that is available, or at least comes there to look for it. It also uses all the areas equally much, probably because of the high density of moose present in the entire region and on the long history of feeding moose in these areas.

Species-specific movement behavior at feeding stations

Another way to avoid interference competition at feeding stations is temporal avoidance (Mysterud, 2000). There is on average a greater probability to meet a moose then a red deer at the feeding station. This is probably due to a higher density of moose than red deer in the area, since there are, according to my results, no difference between the two species in how much of their time they spend <100 m from the bale. Based on this I have to reject prediction P3. February is the month when feeding stations were used most heavily, both by moose and red deer. February is registered as the month with highest average snow depth, and low temperatures during the last 10 year (Haugedalen weather station: Meterologisk institutt, 2012). These climatic factors can affect the ability to find natural forage, and increase the needs for supplementary food (Gundersen, Andreassen, & Storaas, 1998). It was mostly during night hours that the feeding stations were used. This is probably due to the daily activity pattern of moose and red deer, and its influence by predators and humans. Because feeding stations most often are placed close to roads, it is also close to human activity. The animals may therefore keep away from the feeding station and-, rest in more dense vegetation-, during daytime, when the human activity is highest and the animals are easiest to spot. Also other studies report more movement and foraging activities for moose and red deer during evening-, night- and morning hours (Georgii & Schröder, 1983; Green & Bear, 1990; Meisingset, 2008; Risenhoover, 1986). According to my results the red deer showed a more distinct temporal pattern of feeding station use than moose. This may indicate that red deer is more influenced by disturbance around the feeding station than moose. Moose may not care so much about disturbance because of the long history of feeding stations in Østerdalen, and the absence of hunting at feeding stations. Both species started their top-use periods at the feeding station at the same time of day, but the moose ended two hours later in the morning than the red deer, which reflects the less distinctive temporal pattern of the moose. It does not seem to be any temporal avoidance between moose and red deer, and I have to reject prediction P4.

There was no difference in length of feeding bouts between moose and red deer, and I have to reject prediction P5. In normal winter conditions, with no supplementary feeding stations, moose has an average length of feeding bout of 68 minutes (Risenhoover, 1986), and the red deer has an average of 88.5 minutes (Clutton-Brock, Guinness, & Albon, 1982). This is considerable shorter than my results show for feeding station use. The longer bouts in my study may be explained with optimal foraging theory: it may be beneficial to stay at the feeding station, as a source of food concentration, for many hours continuously at the time. That way the animals will save energy, instead of going forth and back between the feeding station and the resting place repeatedly (Krebs & Davies, 1993). Feeding bouts were longest for both species if they entered the feeding station in the evening. This makes sense when compared with my results showing that feeding stations were mostly used during night hours. If the animals entered the feeding stations in the evening, they had the whole night to stay there, before they moved away in the morning to avoid humans and predators.

In the afternoons after having been on the feeding station, moose kept a significantly longer distance to the feeding station then red deer. This supports prediction P6. One reason for this may be that the red deer is a social animal and stays in small groups (Hall, 1983), while the moose has a low degree of sociability (Bubenik, 2007) and has to move further away from the feeding stations to be able to find a place by its own. Another reason may be that red deer is more affected by the snow conditions than moose (Lundmark & Ball, 2008; Mysterud et al., 2011) moving through snow may cost more energy for red deer, so they won't move as far away from the feeding station as moose does to avoid disturbance and find natural forage. Whereas moose is browsing predominantly on pine (Gundersen et al., 2004; van Beest et al., 2010a), red deer does not seem to be adapted to this natural, abundant forage. It may therefore depend more strongly on supplementary food and therefore remain closer to the silage bales.

Both species kept the longest distance from the feeding station in January, a bit shorter in March and shortest in February. The supplemental feeding starts when the moose starts migrating from the summer areas to the lower winter areas (Gundersen et al., 2004). Depending on snow and temperature, this happens most often sometimes during January. The animals may need some time before they find and start using feeding stations. Natural forage in the valley bottoms may still be more accessible in January before snow depth gets too high. Deep snow and cold temperature can most likely explain why they are closest to the feeding station in February. In the end of March the snow starts to melt, and it is easier to move around again, and easier to find natural forage. The moose kept the longest distance from the feeding station in the afternoon and evening. Then it probably has been feeding most of the night and all morning, and moves slowly away from the feeding station in the morning. The distance to feeding station kept by red deer matches very good with the probability of using the feeding station. They were furthest away from the feeding station at the same time as the probability of use was lowest. Red deer enters the feeding station relatively quickly in the evening, and moves away relatively quickly in the morning.

Methodological limitations

When deciding the size of the buffer radius around the silage bale to count piles inside, I tried different distances before I ended up with 10 m. 10 m was the distance which covered most of the piles close to the feeding station. If I wanted to include significantly more piles inside the buffer radius, I had to increase the radius a great deal. This buffer radius distance can of course have an impact on the result. Moose and red deer may exhibit different behavior when it comes to place and time of defecation. If one of the species is defecating close to and the other far from a food resource, or one is defecating while feeding whereas the other is not, the interpretation of my results may be affected.

To strengthen my results from the pellet group count method, I should have repeated the field study the next year, but time did not allow it.

A factor that can affect how popular a feeding station is, is the quality of the silage bales on the feeding station. It is clearly to see on some feeding stations that the animals prefer one silage bale over the other, when one bale is almost eaten up while the other one right next to it is hardly touched. So if there is only low quality forage on a feeding station it can influence if an animal comes back to that feeding station or not.

Only female individuals were collared and included in my movement analysis, and there can be differences between sexes that I am not able to document with this paper. However, Kamler, Jedrzejewska, and Jedrzejewski (2007) did not find any significant difference between red deer hinds and stags on daily activity pattern.

Conclusion

Looking at spatial and temporal avoidance at winter feeding stations, my results suggest that there is a certain spatial avoidance, but no particular temporal avoidance between moose and red deer. It seems that red deer has taken over and dominate some of the feeding stations originally established for moose. If the red deer population will continue to increase as it did the last years according to the hunting statistics, there is a chance that red deer will take over more feeding stations. This may weaken the originally planned effects of feeding stations for moose. Actually, the existence of feeding stations may be one of the reasons why red deer populations have increased the recent years in Hedmark county.

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Appendix

Table: Differences in number of positions and GPS success of all the individuals.

Specie	Id	Start date and time	Stop date and time	Number of positions	GPS success %
Red deer	311	27.03.2006 19:03	05.01.2007 13:01	185	88
Red deer	312	30.03.2006 20:00	05.01.2007 13:00	129	93
Red deer	332	21.03.2010 19:00	31.03.2010 22:00	241	99
Red deer	333	22.03.2010 19:04	31.03.2010 23:00	193	87
Red deer	338	05.03.2008 19:00	31.03.2008 23:00	621	99
Red deer	355	26.03.2010 19:12	31.03.2010 23:00	122	82
Red deer	358	22.02.2011 19:12	31.03.2011 23:00	879	98
Red deer	359	24.02.2011 18:23	31.03.2011 23:00	836	99
Red deer	360	25.02.2011 17:25	31.03.2011 23:00	808	98
Red deer	361	01.03.2011 17:00	31.03.2011 23:00	697	96
Red deer	362	12.03.2011 00:00	31.03.2011 23:00	430	90
Red deer	364	23.03.2011 19:53	31.03.2011 23:00	176	89
Moose	1010	18.01.2010 11:00	31.03.2010 23:00	1713	98
Moose	1310	17.01.2010 14:00	31.03.2010 23:00	1748	99
Moose	1409	09.01.2009 09:00	31.03.2009 23:00	1821	93
Moose	1410	12.01.2010 20:00	31.03.2010 23:00	1838	98
Moose	1709	08.01.2009 14:00	31.03.2009 23:00	1852	94
Moose	1710	13.01.2010 16:00	31.03.2010 23:00	1826	98
Moose	1809	12.01.2009 09:00	25.03.2009 06:00	1547	83
Moose	1810	17.01.2010 17:00	31.03.2010 23:00	1729	98
Moose	2109	10.01.2009 15:00	31.03.2009 23:00	1817	94
Moose	2110	15.01.2010 16:00	31.03.2010 22:00	1142	63
Moose	3009	11.01.2009 10:00	31.03.2009 23:00	1579	83
Moose	3210	15.01.2010 14:00	31.03.2010 23:00	1652	91
Moose	3309	09.01.2009 13:00	31.03.2009 23:00	1745	89
Moose	3310	16.01.2010 16:00	31.03.2010 23:00	1688	95
Moose	3909	11.01.2009 11:00	18.01.2010 12:00	1902	81
Moose	4009	09.01.2009 14:00	31.03.2009 23:00	1846	94
Moose	4010	13.01.2010 11:00	31.03.2010 23:00	1835	99
Moose	4109	27.03.2009 18:00	31.03.2009 23:00	102	100
Moose	4110	16.01.2010 15:00	22.01.2011 23:00	2307	99
Moose	4309	11.01.2009 15:00	31.03.2009 23:00	1770	92
Moose	4310	17.01.2010 12:00	31.03.2010 23:00	1734	97
Moose	4409	09.01.2009 11:00	31.03.2009 23:00	1774	90
Moose	4410	13.01.2010 13:00	31.03.2010 23:00	1803	96
Moose	5109	12.01.2009 10:00	31.03.2009 23:00	1766	94
Moose	5110	16.01.2010 12:00	31.03.2010 23:00	1781	99
Moose	5210	14.01.2010 16:00	31.03.2010 23:00	1808	99

Moose	5309	10.01.2009 10:00	31.03.2009 23:00	1814	94
Moose	5310	13.01.2010 15:00	31.03.2010 23:00	1850	100
Moose	5509	11.01.2009 13:00	12.01.2010 08:00	1976	90
Moose	5510	16.01.2010 17:00	31.03.2010 23:00	1768	99