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Use and competition at artificial feeding sites

- the roe deer and fallow deer case

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Bachelor thesis
Grimsö 2012



Independent project/Degree project / SLU, Department of Ecology 2012:11

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Credits: 15 ECTS
Level: Bachelor, G2E
Course title: Independent Project in Biology
Course code: EX0688

Place of publishing: Grimsö
Year of publication: 2012
Title of series: Independent project/Degree project / SLU, Department of Ecology
Part no: 2012:11
Online publication: <http://stud.epsilon.slu.se>

Key words: Competition, roe deer, fallow deer, artificial feeding sites

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Abstract

Fallow deer is an exotic species in Sweden; it was brought here in the 1570s and has now established viable, wild populations in the southern parts of Sweden. Roe deer is native in Sweden and there is a concern that it is displaced by fallow deer in areas where both species exists, as reported from other countries. The aim of this study was to investigate if there is an effect of competition at artificial feeding sites by fallow deer on roe deer, more specific, to measure the use of feeding sites at different month and type of winters. In addition, by divide individuals into age classes and sex, also get a more precise measure of feeding site use. The data for this study consisted of GPS-positions from 31 roe deer and 50 fallow deer during six winter seasons (2006-2012). An individual within 50m of the feeding station was counted as utilizing the feeding site. Both roe deer and fallow deer increased feeding site use during a hard winter and decreased their use in a mild winter. Fallow deer males used feeding sites more than roe deer and fallow deer females. The two species did use the feeding sites differently each month. Fallow deer used feeding sites more than roe deer in all months except for February and March. However, the high use by roe deer in February and March were driven by 6 females and 1 male. The feeding site use was not different among different age classes in roe deer. There was a trend that older fallow deer males use feeding sites more than younger males. Fallow deer females always used feeding sites less than fallow deer males. Fallow deer males had three feeding activity peaks during a day and a long pause between each. Fallow deer females on the other hand, did have a daily pattern that is more similar to the roe deer. This study conclude that fallow deer used feeding sites more than roe deer, but it did not detect any clear evidence of competition between the two species. However, the low use by fallow deer females could be an indication of intra-specific competition.

Table of Contents

1 Introduction	1
2 Method	3
2.1 <i>Study area</i>	3
2.2 <i>Data collection</i>	5
2.3 <i>Data compilation & data analysis</i>	5
3 Results	6
3.1 <i>Winter type</i>	7
3.2 <i>Monthly use</i>	7
3.3 <i>Monthly use by age class</i>	8
3.4 <i>Circadian rhythm</i>	9
4 Discussion	11
4.1 <i>Winter type</i>	11
4.2 <i>Monthly use</i>	12
4.3 <i>Monthly use by age class</i>	12
4.4 <i>Circadian rhythm</i>	13
5 Conclusions	13
6 References	15
Appendix	

1 Introduction

Many studies have been conducted to investigate the effect and type of interactions between introduced exotic and native species (Dolman & Wäber 2008). Four types of interactions are typically identified between species: mutualism, facilitation, competition and predation. The two first are considered to generate positive effects and the two latter negative effects for the receiving individual (Ricklefs 2008). The effect of a successfully established non-native species can be huge and most often it has a negative effect on the native species (Dolman & Wäber 2008). Reintroduction of old but lost game species as well as introduction of new exotic species for hunting purposes have been common around the world for a long time (Moriarty 2004, Dolman & Wäber 2008). Fallow deer (*Dama dama*) in Sweden is an example of such an exotic introduction and it was brought to Sweden in the 1570s as a new game species (Carlström & Nyman 2005).

On the other hand, Roe deer (*Capreolus capreolus*) is native in Sweden since after the last ice age 10 000 – 15 000 years ago (Cederlund & Liberg 1995). The roe deer population almost went extinct in Sweden in the 1830s due to extensive hunting. However, the population recovered quickly after. The protection in the 19th century started with one estate and the last known remaining population in the 1840s by Count Corfitz Beck-Friis in southern Sweden (Cederlund & Liberg 1995). Today roe deer is found throughout most parts of Sweden with an annual reported harvest of approximately 100 000 animals (Jägareförbundet 2012).

Since the late 1900s, the fallow deer population has increased substantially in Sweden. In areas where fallow deer exists in higher densities today, people have expressed a concern that the roe deer population is decreasing. While there are ample of evidence for the sensitivity in roe deer ecology related to intra-specific competition (Kjellander 2000) is the sensitivity to inter-specific competition between roe deer and other ungulates less well investigated. Only three previous studies from Italy have previously reported an effect of competition between native roe deer and introduced fallow deer (Focardi 2006, Feretti et al. 2010, Feretti et al. 2011). However, roe deer is reported to be negatively affected not only by fallow deer, but also by red deer (*Cervus elaphus*) and muntjac (*Muntiacus reevesi*) (Hemami et al. 2005; Emmanuelle et al. 2010).

Fallow deer is, in contrast to roe deer, usually described as a gregarious and slow disperser that has a high tolerance for high animal densities (Carlström & Nyman 2005). The species are of the intermediate feeding type (Hofmann 1989). Intermediate feeders are opportunistic and eat what is abundant (Alm et al. 2002) as long as it doesn't contain too much fiber (Hofmann 1989).

The body size differences and level of sexual dimorphism differs greatly between fallow deer and roe deer. The large and dimorphic adult male fallow deer are twice the size of females (Carlström & Nyman 2005) while male and female roe deer is again only half the size of a female fallow deer and more or less monomorphic (Cederlund & Liberg 1995; Carlström &

Nyman 2005). The similar body size and rumen in female and male roe deer means that their energy requirements are about the same (Hofmann 1989).

The fallow deer rut is usually described as a lek, and peak in Sweden in the shift of October and November (Carlström & Nyman 2005). During the rut adult males (4+ years) almost completely stops eating, while subadult males slightly decrease their feeding activity (Apollonio & Vittorio 2003). This means that adult males are very deprived of energy when the winter begins. Roe deer, on the other hand, have the rut in the summer (July/August) and males are usually fully recovered in time for the winter season (Cederlund & Liberg 1995).

Supplementary feeding has been conducted for some time in Sweden, at least since the 1950s (Hermanson et al. 1974). In Sweden, the roe deer population is limited mainly by hunting, food resources, predation by fox on fawns and harsh snow rich winters (Cederlund & Liberg 1995). The roe deer is poorly adapted to snow rich conditions and the mortality is high, even during moderate snow conditions (Cederlund & Liberg 1995). Supplementary feeding may therefore reduce the limiting factor of snow for the roe deer population (Cederlund & Liberg 1995). It has been shown that in an area without fallow deer, the roe deer utilize supplementary food to a high extent (Kjellander et al. 2006). Supplementary feeding during winter clearly directs also the fallow deer's feeding habits (Carlström & Nyman 2005). The fallow deer as an opportunist will utilize the feeding sites to optimize energy intake (Alm et al. 2002). Land owners who conduct supplementary feeding usually do so because they either want to redirect game from feeding on crops or forest and/or to increase the carrying capacity of the area (Putman & Staines 2004). Increasing the carrying capacity may result in a larger harvest for the land owner as the game densities can be increased. However, fallow deer is known to show antagonistic behavior towards other species at feeding sites (Feretti et al 2010). Also in Sweden it has been reported that roe deer avoid feeding sites if fallow deer approaches, especially if there are a group of fallow deer (Carlström & Nyman 2005). Thus, based on the level of sexual dimorphism in fallow deer and the previously reported effects of inter-specific competition between the two species it is obviously a high potential for both within and between species conflicts in areas with artificial winter feeding were both species occur. However, a study on effects of rank at feeding sites between individual roe deer failed to document effects of age as it was more important with closeness to summer territory for males and early visits at the feeding sites for females (Geiger & Krämer 1974).

In this study I analyzed GPS-positions from collared roe deer and fallow deer in order to investigate the two species use of artificial feeding sites, and possible competition effects within and between species. Based on previous studies I have identified six predictions:

1. Both species will use feeding sites more during a hard winter than during a mild winter.
2. Both sexes of fallow deer will have a higher use of feeding sites than roe deer.
3. No sex difference in use of feeding sites in roe deer.
4. There will be no age difference among roe deer in use of feeding sites.
5. Male fallow deer will spend more time at the feeding sites than fallow deer females.

6. Male fallow deer in their prime (4+ years) will spend more time at the feeding sites than other age classes.

2 Method

2.1 Study area

This study was conducted at the Koberg estate in south western Sweden. The estate is located in the county of Västra Götaland and constitute of 9000ha of which the study area cover ~8100ha. Koberg is divided in two separate management areas since 2004; a southern part and a northern part (Fig. 1); (Agnerud 2011). The division into two areas is due to a wildlife fenced road intersecting the estate. This road fence acts as a manmade barrier for animal dispersal (Agnerud 2011).

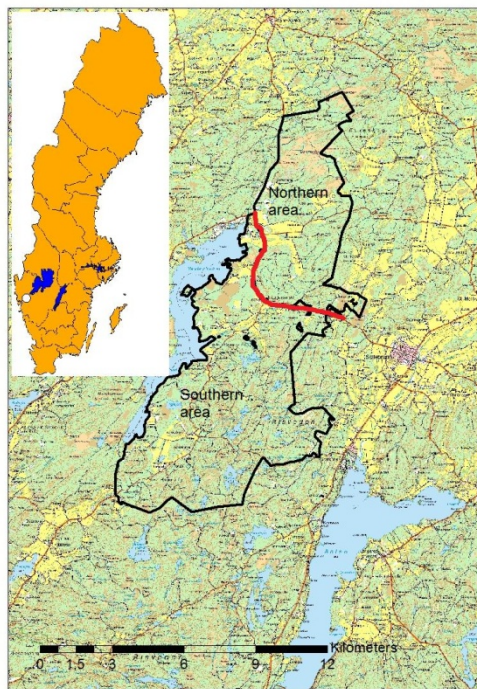


Figure 1. The location of Koberg estate in Sweden indicated with a white dot. The study area (black line) is divided by a wildlife fenced road (red line) in a Northern and a Southern part.

The region is in the boreonemoral zone consisting of mixed coniferous and deciduous forests. In Koberg the dominating habitat type is forest, (~80%) and approximately agricultural land (15%; Svartholm 2010). A large part of the agricultural land is used to grow crops for game species.

The fallow deer was introduced to this area in the 1920s (Agnerud 2011) and since then the population has grown. Culling reports in the Koberg area show that from the mid 1980s until

1993 the bag statistics was less than 200 fallow deer / year (Agnerud 2011). From the mid 90s until 2000 the culling increased but remained below 400 fallow deer / year (Agnerud 2011). Since 2005, the fallow deer bag has increased profoundly and today the yearly cull is ~ 1000 individuals/year (Agnerud 2011). The roe deer population was approximately 20 individuals per 1000 ha during 2006 - 2012 (Kjellander unpubl.). The density of roe deer is low compared to similar areas within this region of Sweden. In 1993, the density in other areas within the same region was about 75-150 roe deer/1000ha (Cederlund & Liberg 1995). The fallow deer population was approximately 330 individuals per 1000 ha during the same period (Kjellander unpubl.) This is considered a dense to very dense population (Carlström & Nyman 2005).

Within the estate there are artificial feeding sites that were in use during the winter season. A total of 61 supplementary feeding sites were used during the study period between November 2006 and April 2012. The feeding stations are distributed over the entire study area. 55 feeding sites were used yearly. Approximately 500 – 1000 tonnes of supplementary food have been provided each winter season. The amount of food changed between years and months depending on how harsh the winter was. The food typically consists of oat silage, grass silage, sugar beets, potatoes, carrots, cabbage and since 2011 automatic corn spreaders have been used. The type of artificial food that was provided changed due to current market prices; the cheapest was most commonly used (Kjellander unpubl.).

In 2009/2010 the snow depth was more than 20 cm during 80 days of the 6 months (44%). In 2010/2011, 19% of the 181 winter days had a snow cover >20cm. 2006/2007, 2007/2008 and 2008/2009 winter did not have a single day of >20cm snow depth. Winter 2007/2008 and 2008/2009 had a top note of 12cm snow depth for one day each, winter 2006/2007 never even reached a snow depth of 10cm. See table 1.

Table 1. Mean daily precipitation (mm), temperature (°C) and snow depth (cm) during each winter 2006-2012 at Gendalen weather station a few km east of the study area. No data is available for the winter 2011-2012, however it is well documented that it was a mild almost snow free winter.

Winter	Precipitation (daily, mm)	Temperature (daily, °C)	Snow depth (daily, cm)
2006/07	2.6	3.8	0.75
2007/08	2.5	3.8	0.75
	1.3	1.9	0.8
2008/09			
2009/10	1.3	-1.1	18
2010/11	1.2	0.6	8.5
2011/12	No data	Mild but no quantitative data	Very little but no quantitative data
Mean 2006-2009	2.1	3.1	0.8
Mean 2009-2011	1.25	-0.25	13.25

2.2 Data collection

In this study 50 GPS-collared fallow deer ($n_{\text{female}}=22$, $n_{\text{male}}=28$) and 31 roe deer ($n_{\text{female}}=17$, $n_{\text{male}}=14$) were included (See appendix 1). Only 8 of the 31 collared roe deer had all of their positions in the southern area, consequently the remaining 24 roe deer all of their positions in the northern area of the collared fallow deer, 15 had all of their positions in the northern part while 35 fallow deer lived in the southern area. Although this barrier exists I treated all data as if there was no barrier.

Roe deer were caught in baited traps during the winter, while the fallow deer were sedated with anesthetic filled darts. The individuals were sex determined, their age was estimated, and they were marked with ear tags and collared with a GPS-transmitter. One can look at tooth wear and body size to roughly estimate the age, but tooth wear can reflect other things than age e.g. diet.

The GPS-transmitter can be located with a portable antenna since the transmitter also contains a VHF (Very High Frequency) component. The type of transmitter used is Vectronic GPS PRO Light. The GPS-transmitter also contains a GPS and a mobile phone. The mobile phone sends a text message with the current position to an e-mail. The computer that receives this message transforms it to X and Y-coordinates. All of the positions used in this study came from the GPS-transmitter type. The GPS-transmitter can hold up to 20 000 positions for fallow deer and 10 000 for roe deer. The difference is due to battery size. The battery needs to be smaller for roe deer than for fallow deer, because roe deer are smaller than fallow deer. The transmitters can be set to send coordinates at different time intervals. Directly after marking, the collars took positions with a 30 minute interval, while the standard programming was every 4th hour, starting at midnight.

2.3 Data compilation & data analysis

The GPS-coordinates was compiled in Microsoft Office Excel 2007. I only used validated positions (positions confirmed by at least 4 satellites) and positions from the 1st November until the 30th April. During this period supplementary food was provided. I used all positions regardless of the GPS position interval, which means that even though a transmitter take a position every 30 minutes or every 4th hour I used all positions, from the winter seasons of: 2006/2007, 2007/2008, 2008/2009, 2009/2010, 2010/2011 and 2011/2012. I included all positions directly after marking.

After the data management in Excel the coordinates were plotted in ESRI ArcGIS 9.3.1. By using GPS coordinates, 53 supplementary feeding sites were also plotted in ArcGIS. Since the summer of 2010, 2 feeding places have been removed, 10 have been added and 5 have been moved. These changes were recorded and added in ArcGIS. All in all there have been 61 artificial feeding stations in use continuously during the study period. A buffer zone with a

radius of 50 meters was created, around the artificial feeding sites. The size of the buffer was used to correct for errors in the exact location of the food placement, transmitter and GPS-receiver. Animal positions within this buffer were counted and treated as a visit to the feeding site. I used all available positions for each individual for the entire battery life of the GPS collar or until the death of the animal, during the November-April period, and categorized each position through excel in ArcGIS as inside or outside the 50m buffer around each feeding site. Depending on the sampling unit, winter, month or hour (circadian rhythm), I estimated the ratio between the number of locations inside the buffer and the total number of locations for the specific time period at an individual level. The ratio is then assumed to reflect the proportion of time (%), spent at the feeding station.

Due to the two types of winters appearing during this study, the winters of 2006/2007, 2007/2008, 2008/2009 and 2011/2012 were considered to be mild winters with little snow cover while winters of 2009/2010 and 2010/2011 were considered as harsh winters with a thick snow and long lasting snow cover (see table.1).

All analysis was performed in StatView 5.0.1 (SAS Institute Inc.). I used ANOVAs to test for differences in use of feeding sites between species, sex and age. I tested these variables monthly and in relation to winter type (harsh and mild). I also tested for interaction effects between species, sex and winter type. When I divided the age classes, I put all females in one class. I used this method because estimating age properly in the field is difficult

Circadian rhythm was only investigated descriptively, since the potential and deleterious effect of pseudo replication was obvious in the available database. Unfortunately I had no time to correct for that within the time frame of this study. To minimize the effect of gradually changing times of dawn and dusk I limited the analysis of circadian rhythm to one month. I analyzed February because it contained the highest number of individuals for the whole study period.

The month of September was used as a control (a period without artificial feeding), to test for positions not related to a true and directed visit to the feeding station, but rather resulting from spatial movements of an animal that through its movement pattern “visits” a feeding station. I choose September because it is long before the feeding stations are in action; it is well after the calving season for both species (Cederlund & Liberg 1995, Carlström & Nyman 2005), well after the rut for roe deer (Cederlund & Liberg 1995) and before the rut for fallow deer (Carlström & Nyman 2005) and should therefore not affect the species movement patterns. However, this kind of random “visits” during the control month did not affect the results (see appendix 4)

3 Results

In total 158 469 and 53 903 locations were used from fallow deer and roe deer respectively. Irrespective of age, sex, month and type of winter did fallow deer spend 8.5% and roe deer 6.2% of their time at the feeding stations.

3.1 Winter type

Both species used feeding sites more during harsh winters than in mild winters ($P < 0.001$; $F_{1, 111} = 15.34$; Fig. 2). Both species, regardless of sex, increased feeding site use during the hard winter and decreased their use during mild winters (winter*sex; $P = 0.5$; $F_{1, 111} = 0.39$) and there were no differences between species (winter*species; $P = 0.9$; $F_{1, 111} = 0.019$). There was a significant interaction effect between species and sex ($P = 0.03$; $F_{1, 111} = 4.97$). However, this is driven by the high use by fallow deer males since roe deer did not demonstrate any significant differences in feeding site use between the sexes (during mild or hard winters). The interaction between species, winter and sex was not significant ($P = 0.14$; $F_{1, 111} = 2.25$).

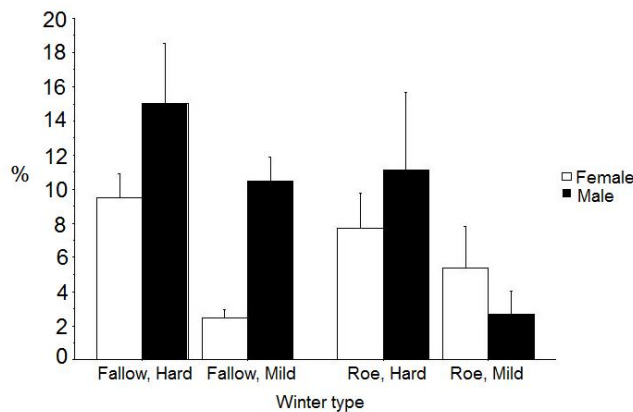


Figure. 2. Mean feeding site activity for fallow deer and roe deer during the six winter seasons at the study area. Error bars indicate the standard error. (For sample sizes see Appendix.2).

3.2 Monthly use

There was a significant difference to what extent feeding sites were used in different months ($P < 0.001$; $F_{5, 396} = 9.97$; Fig. 3). There was also a significant difference how the two species used the feeding stations each month ($P = 0.002$; $F_{6, 396} = 9.73$). However, the interaction between month and species was not significant ($P = 0.15$; $F_{5, 396} = 1.63$).

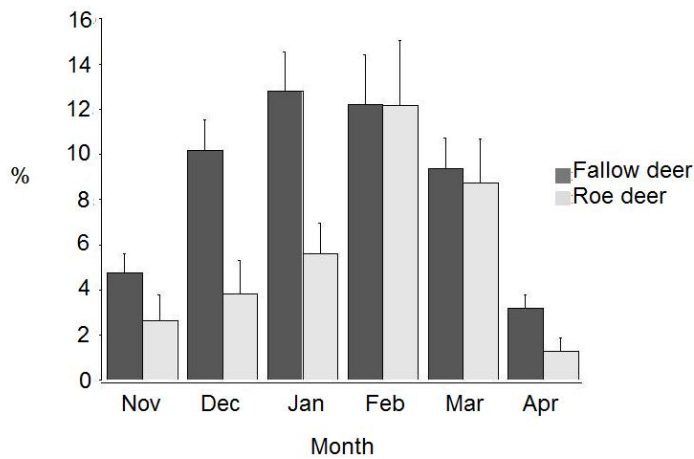


Figure 3. Mean use of feeding sites in fallow deer and roe deer during six winter months at Koberg in southwestern Sweden during 2006-2012. Error bars indicate the standard error. (For sample sizes see Appendix.3).

3.3 Monthly use by age class

Roe deer

Roe deer show no significant difference in use of feeding sites between age classes ($P = 0.13$; $F_{3, 168} = 1.93$; Fig. 4), except that adult females use feeding sites more than 1-2 year old males ($P = 0.04$). There was no difference in the monthly use ($P = 0.07$; $F_{3, 110} = 2.43$), and there was no significant interaction effect between month and age class ($P = 0.32$; $F_{9, 116} = 1.16$). However, the analysis did show that adult females used feeding sites more than juveniles ($P = 0.03$). High use of feeding sites by in February and March by six roe deer females and one roe deer male (mean February = 37.3%) ranging between 18 to 65% and in March (mean March = 28.7%) ranging between 23 and 38%

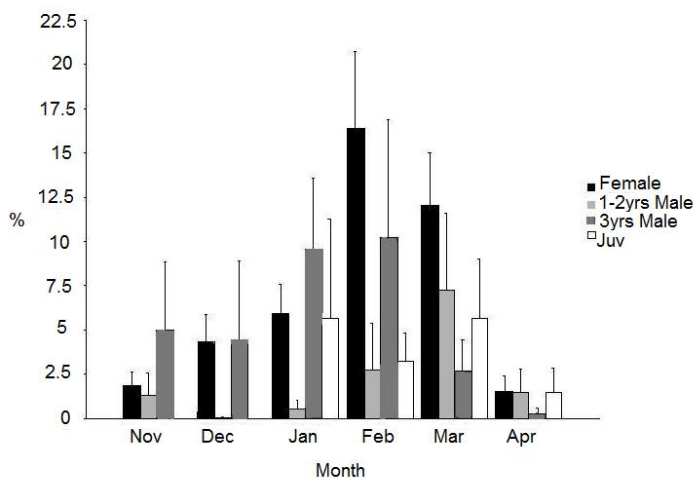


Figure 4. Roe deer feeding site use per month in divided different age classes. The female class contains all females 1+ year and the juvenile class contains both male and female younger than 1 year. Data missing from juveniles in November and December and from 1-2 year old males in December Error bars indicate the standard error. for sample sizes see appendix 1).

Fallow deer

Fallow deer feeding site use was age class dependent ($P < 0.001$; $F_{4, 249} = 8.13$; Fig. 5). However, this was driven of the low use by fallow deer females. Fallow deer females always used feeding sites to a lesser extent than 6+ yrs males ($P = 0.02$; $F_{5, 250} = 7.95$), 4-5 yrs males ($P < 0.001$ $F_{5, 250} = 7.95$), 3 yrs males ($P < 0.0014$; $F_{5, 250} = 7.95$) and 1-2 yrs males ($P < 0.001$; $F_{5, 250} = 7.95$). Feeding sites were used significantly different during the winter months ($P < 0.001$; $F_{5, 250} = 7.95$). April and November were almost always used to a lesser extent by all age classes. The interaction between age class and month was not significant ($P = 0.5$; $F_{20, 265} = 0.99$). A trend indicates that 6+ year old males increased their use of feeding sites until March, while 4-5 year old males seemed to increase their use in the first half of the winter, peak their use in January and February and decreased feeding site use after February.

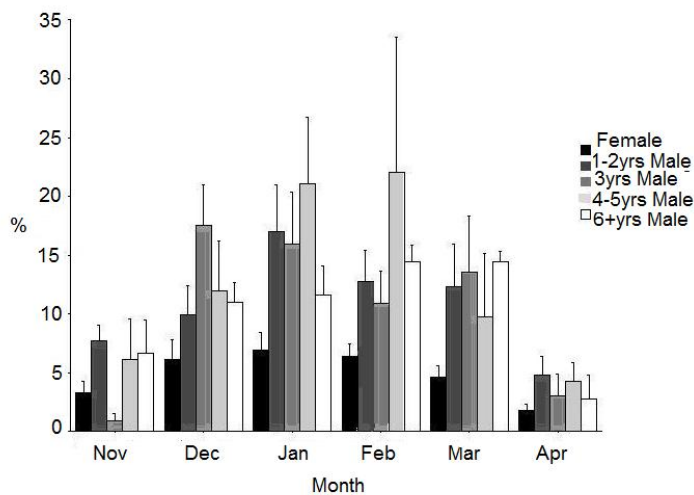


Figure 5. Fallow deer use of feeding sites during the study period divided in different age classes. The female class contains all females regardless of age Error bars indicate the standard error. (for sample size see appendix.1).

3.4 Circadian rhythm

The trend as interpreted from these graphs was that fallow deer males had three activity peaks during the 24 hour period and a long pause in feeding activity from 06.00 until 16.00 hrs. On the other hand, female fallow deer had several minor peaks. Both female and male roe deer showed similar patterns. The roe deer males did show a delayed peak compared to the

females. The roe deer pattern is quite similar to the female fallow deer pattern. While the circadian rhythm for fallow deer males and roe deer, the patterns were very distinctly different from each other.

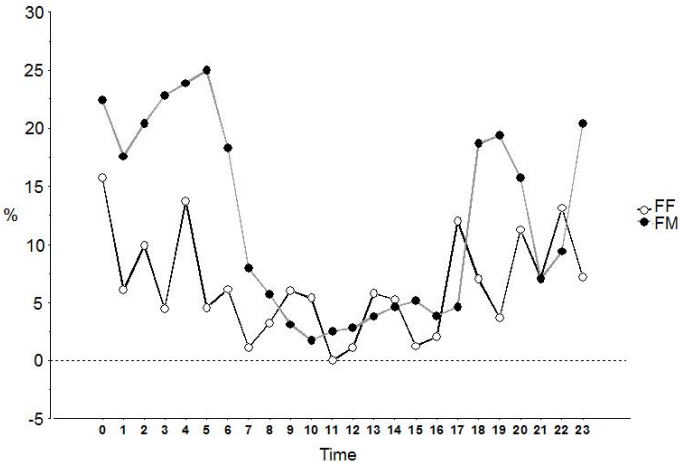


Figure 6. Proportion of time (%) at feeding sites in February during 24 hrs: Fallow deer. Data from Koberg, southwestern Sweden, 2006-2012.

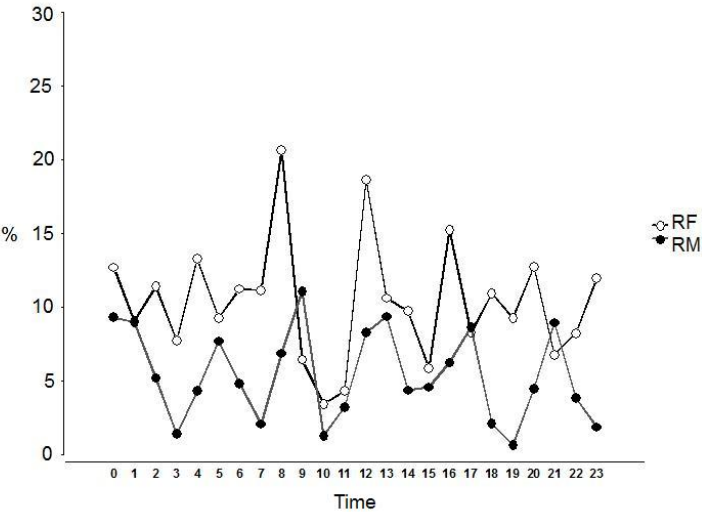


Figure 7. Proportion of time (%) at feeding sites in February during 24hrs: Roe deer.

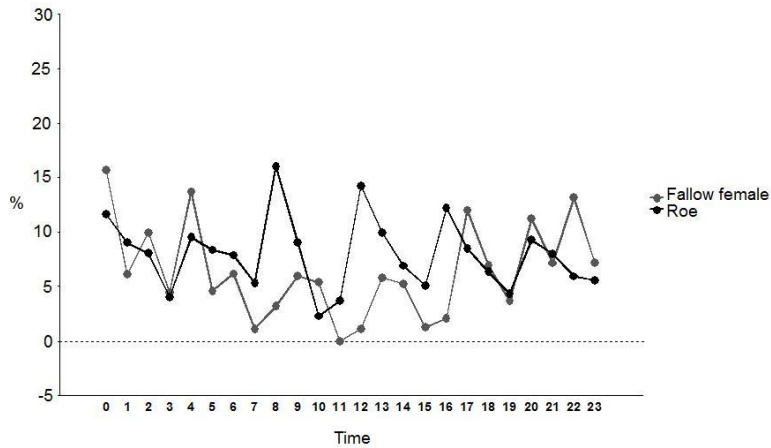


Figure 8. Proportion of time (%) at feeding sites in February during 24hrs: Fallow deer females vs. Roe deer.

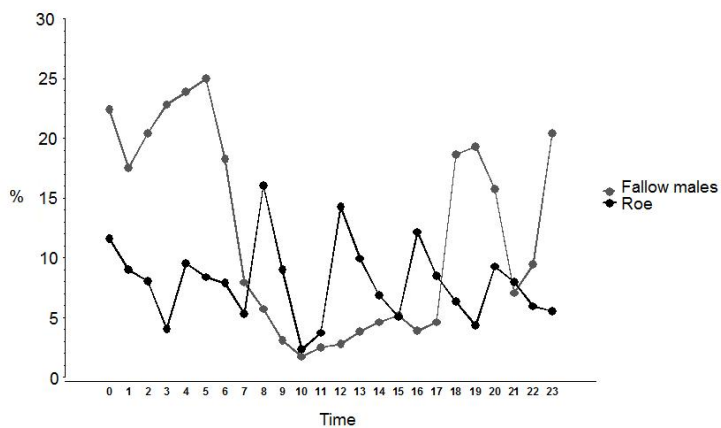


Figure 9. Proportion of time (%) at feeding sites in February during 24hrs: Fallow deer males vs. Roe deer.

4 Discussion

Both species used feeding sites more in a hard winter than in a mild winter. Fallow deer males used feeding sites more than all other categories. Both species used feeding sites different due to month and there was a difference in how the two species used feeding sites in the 6 months. Roe deer do not show an age dependent feeding site use. Older fallow deer males tend to use feeding sites more in all months than the younger males. Fallow deer females always use feeding sites to a lesser extent than males. The hourly feeding site use by fallow deer males clearly differs from both fallow deer females and roe deer. Below I will discuss the results more in detail.

4.1 Winter type

My first prediction (1) that both species would increase their use during hard winters and decrease use of feeding sites during mild winters was supported. This is most likely because food is harder to find in a thick snow cover. It also cost more energy for the deer to dig for food than to eat food that is already above the snow, as is the food at the feeding sites.

I expected that fallow deer would use feeding sites significantly more than roe deer (Prediction 2). The fact that there was no significant difference between species is a bit surprising. Food is harder to find during a snow rich winter then during a winter with less snow, but also when resources are scarce animals experience greater competition (Ricklefs 2008). Contrary to this statement the competitive behavior by fallow deer on roe deer was not due to seasons of scarcity (Feretti et al 2010). Previous studies have shown that roe deer, in fallow deer free areas; actually spend a large amount of time close to feeding sites (7 hrs. a day (29% of 24hr) within 200m of the feeding site) if they have access to them (Kjellander et al. 2006). If there is competition by fallow deer on roe deer, roe deer should use feeding sites to a much lesser extent. Fallow deer have been seen to displace roe deer and even exert aggressive behavior such as chasing the roe deer (Focardi 2006, Feretti et.al 2010, Feretti et al 2011), this kind of behavior should increase at artificial feeding stations since the feeding station area is much smaller than non-artificial feeding sites such as fields. The gender/species difference in this study stem from the high use by fallow deer males. Fallow deer males are depleted of energy due to their rutting behavior and this is probably why they use the feeding sites to a larger extent (Apollonio & Vittorio 2003). The interactions, “winter*gender” and the “winter*gender*species” were not significant, since both females and males of both roe deer and fallow deer increase their use in harsh winters and decrease use in mild winters. Both species and sexes respond to winter conditions in the same way although not to the same extent.

4.2 Monthly use

As predicted (2) the fallow deer use feeding sites more than roe deer. During the first three winter months roe deer use feeding sites a lot less then fallow deer, half as much as fallow deer in November and about a third as much in December and January. The extraordinary high utilization of feeding sites by roe deer in February and March was a surprise. This high utilization was driven by 6 roe deer females and one male The roe deer do suffer from high mortality in winters due to energy depletion, especially young and old individuals (Cederlund & Liberg 1995) Three roe deer females were in their prime age and should not have suffered as much, but the winter of 2009/2010 was a hard winter with a lot of snow. One explanation for these three females’ high utilization in February and March might be that they were pregnant. It is during these months the fetus starts to grow a lot and they need more energy (Cederlund & Liberg 1995).

4.3 Monthly use by age class

Roe deer use feeding sites at the same rate regardless of age, thus confirming my prediction (3). Age is previously reported to not affect feeding site use in roe deer, since it has been

shown that the timing of the arrival, for females, (i.e. the more familiar an individual is with the feeding site), to the feeding site is more important (Geiger & Krämer 1974). The only factor that have been shown to be able to drive roe deer male rank at the feeding sites is its distance to summer territory (Geiger & Krämer 1974).

Roe deer females did use feeding sites to a larger extent than both juveniles and 1-2 year old roe deer males. This is most likely driven by the high use of the previously mentioned, six roe deer females in February and March.

As predicted (5), regardless of month, fallow deer females use feeding sites significantly less than fallow deer males. This might be an indication of intra-specific competition, but this conclusion should be made with caution because there may be other reasons why fallow deer females use feeding sites to a lesser extent than males. One reason may be the previously mentioned energy depletion in fallow deer males that increase their need for food. In November and April, feeding site activity is much lower compared to the other months, irrespective of age class. This is probably because other food resources are available during these two months. Contrary to my prediction (6) the use of feeding sites did not differ relative to age in the different months. Fallow deer feeding site activity is not age dependent. This is surprising since I expected older fallow deer males to be dominant at the feeding sites. Even if the result is not significant, two trends can be seen in the two older age classes. Fallow deer males (4-5 yrs) increase their use of feeding sites during the first half of the winter, peak in mid winter and decrease in late winter. Older fallow deer males (6+ yrs), increase their use during the whole winter and greatly decrease use of feeding sites in April.

4.4 *Circadian rhythm*

The fact that fallow deer males only have three activity peaks during the day (24hrs) and have a long pause from 06.00 until 16.00 hrs, compared to the more abundant activity peaks found in female fallow deer and both sexes of roe deer support Hofmann (1989) reporting on the relationship between body size and rumination/feeding bouts. Fallow deer males are about 2-3 times larger than a female, which was reflected in the circadian rhythm. Fallow deer males rather fill up their comparatively larger rumens at these three feeding bouts and then have long rumination bouts in between.

Therefore, female fallow deer, like the roe deer, have several minor peaks (9/24hrs and 6/24hrs respectively). Female fallow deer therefore need to eat more often in order to fill up the rumen.

Roe deer females are the smallest of these four categories and should show the most peaks (Hofmann 1989). However, roe deer females have the same amount of feeding site use peaks as fallow deer females (9/24hrs). The roe deer females have their three highest feeding activity peaks during the long pause of the fallow deer males. Again, this might be driven by the six females' extraordinary high use in February. On the other hand, it is possible that this is the only time the roe deer females actually get access to the food, when the fallow deer males leave the site, and thus avoid directed inter-specific competition from the large fallow males.

5 Conclusions

Roe deer do use feeding sites less than fallow deer on a monthly basis, except in February and March. I cannot conclude that this is due to competition, however, roe deer in areas without fallow deer have been shown to use feeding sites to a much larger extent than in the Koberg area (Kjellander et al. 2006). The two species do not differ in their use of feeding sites in harsh or in mild winters. The fact that fallow deer males use feeding sites to a great extent is probably because of energy depletion after the rut (Apollonio & Vittorio 2004). Use of feeding sites is not age dependent, although a trend can be seen in older fallow deer males. However, the low use by fallow deer females could perhaps result from the high use by fallow deer males. The circadian rhythm shows different feeding activity patterns for fallow deer and roe deer and for fallow deer males and females. The three roe deer peaks in mid-day when the fallow deer males exhibit a long feeding activity pause may be an indication of competition, but such conclusions should be made with caution. To further develop this study, one can look at each individual feeding site in order to determine who (only one species or both) visits it and when. This would more clearly resolve potential competition effects (if there is one) because it would distinguish if roe deer at a feeding site used by fallow deer actually leaves it when fallow deer approaches.

Acknowledgements

Thanks to Fam. Silfverschiöld for being so forthcoming when using their land for collection of the data needed in this study. I also would like to show my appreciation to the field technicians (who marked and collared the animals used in this study) and the personnel at Koberg estate. Thanks to my examiner Johan Månsson and my supervisor Ulrika Bergvall. I would also like to thank my co-supervisor Petter Kjellander for great advice and support during this whole project.

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Appendix 1.

Age, sex and species specific sample sizes in fallow deer female (FF), male (FM) and roe deer female (RF) and male (RM).

Age	FF	FM	All F	RF	RM	All R
0	0	0	0	3	5	8
1	6	5	11	3	2	5
2	8	7	15	3	4	7
3	8	10	18	4	5	9
4	7	6	13	6	3	9
5	5	7	12	6	2	8
6	3	3	6	3	0	3
7	6	4	10	3	1	4
8	7	1	8	2	0	2
9	5	0	5	1	0	1
10	4	1	5	0	0	0
11	3	1	4	0	0	0
12	1	0	1	0	0	0
Total	63	45	108	34	22	56

Appendix 2.

Number of individuals divided by species, sex and type of winter.

Species	Sex	Winter type	Number of individuals
Fallow deer	M	Mild	21
Fallow deer	M	Hard	11
Fallow deer	F	Mild	21
Fallow deer	F	Hard	16
Roe deer	M	Mild	11
Roe deer	M	Hard	6
Roe deer	F	Mild	13
Roe deer	F	Hard	13

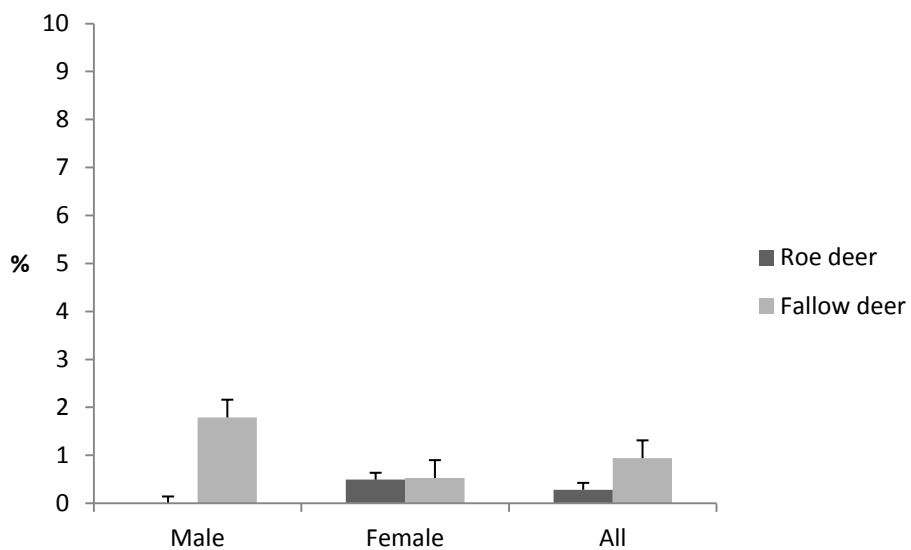
Appendix 3.

Number of individuals divided by month and sex.

Species	Sex	Month	Number of individuals	Species	Sex	Month	Number of individuals
Fallow deer	F	Nov	21	Roe deer	F	Nov	14
Fallow deer	F	Dec	20	Roe deer	F	Dec	16
Fallow deer	F	Jan	21	Roe deer	F	Jan	14
Fallow deer	F	Feb	22	Roe deer	F	Feb	16
Fallow deer	F	Mar	21	Roe deer	F	Mar	16
Fallow deer	F	Apr	20	Roe deer	F	Apr	15
Fallow deer	M	Nov	17	Roe deer	M	Nov	8
Fallow deer	M	Dec	22	Roe deer	M	Dec	8
Fallow deer	M	Jan	22	Roe deer	M	Jan	12
Fallow deer	M	Feb	23	Roe deer	M	Feb	13
Fallow deer	M	Mar	22	Roe deer	M	Mar	10
Fallow deer	M	Apr	23	Roe deer	M	Apr	10
Total M	M	All	28	Total M	M	All	14
Total F	F	All	22	Total F	F	All	17
Total All	M&F	All	50	Total All	M&F	All	31

Appendix 4.

Relative number (%) of positions within buffer zone during September.



Species	Sex	Number of individuals
Roe deer	M	9
Roe deer	F	12
Fallow deer	M	14
Fallow deer	F	18