



Wild boar and Roe Deer in Conflict?

- An analysis of interspecific interactions under different wild boar densities

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Wild boar and Roe Deer in Conflict? An analysis of interspecific interactions under different wild boar densities.

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Keywords: Feeding Displacement, Generalized Additive Models, Interference Competition, Wild Boar, Roe Deer.

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Abstract

Roe deer and wild boar are both highly successful species of cervid found across much of Europe, and while similarities exist between them, to what extent do wild boar impact the daily activity pattern of roe deer at feeding sites? While a few studies explore interspecific interactions between ungulate species in Sweden, only a little research has been done on how wild boar and roe deer interact. This study aims to minimize the gap in knowledge surrounding these two species and the way they interact. I used GPS collars fitted onto wild boar and roe deer from 2012 – 2023 to study how roe deer spatially interact within their homeranges with wild boar, and to further study whether an increasing density of wild boar has altered the daily activity pattern of roe deer at supplementary feeding sites inside the Grimsö Wildlife Research Area. Roe deer were found to show avoidance towards wild boar. Furthermore, the study showed that roe deer changed their activity pattern at supplementary feeding sites by visiting closer to midday than sunset, when the density of wild boar increased in the study area. These results suggest that there is a level of interference competition occurring between these two species, but further research would be needed to fully explore this in the future.

Keywords: Feeding Displacement, Generalized Additive Models, Interference Competition, Wild Boar, Roe Deer.

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Abbreviations

| | |
|------|---|
| AIC | Akaike Information Criterion |
| GIS | Geographical Information System |
| GPS | Global Positioning System |
| GSM | Global System for Mobile telecommunications |
| GWRA | Grimsö Wildlife Research Area |
| MCP | Minimum Convex Polygon |
| SLU | Swedish University of Agricultural Sciences |
| VHF | Very High Frequency |

1. Introduction

1.1 Interspecific interactions

In the natural world, species interactions shape the way in which different organisms interact with one another. Processes such as competition, mutualism, commensalism and predation all play a role in the behavioural interactions between species (Latham 1999). The most common of these processes, competition, occurs between one or more species which require the same limiting resources (Lang & Benbow 2013). Which can have consequences not only on a day to day basis, but on an evolutionary scale. Competition drives the success or failure of a species, through the evolution of favourable traits, ultimately leading to genetic adaptation and niche separation, both contributing to species formation (Rautiainen et al. 2021).

Competition can occur between members of the same species (intraspecific) or between members of different species (interspecific), and will almost always have a negative impact on the weaker or submissive competitor (Lang & Benbow 2013). The two most common forms of competition are exploitation competition and interference competition. Exploitation competition refers to an indirect interaction, where one species denies another species of a limited resource, while interference competition refers to a direct interaction between two species, where one species dominates and thus reduces access to a limited resource for the second submissive species (Gilad 2008).

1.2 Study Species

1.2.1 Roe deer

The European roe deer (*Capreolus capreolus* L.) is one of the most abundant cervid species found throughout Europe. Historically, it was hunted almost to extinction and only in the early 20th century did it begin to re-colonize much of its historical distribution within Sweden. The recolonization reached its peak in 1993, with bag

statistics showing 382,000 individuals shot in Sweden, a record since almost facing extinction 80 years before. A sharp decline in hunting occurred from 1993 to 2010, and only in the last 12 years have numbers begun to rise again (*Viltdata* 2023). Being habitat opportunists, roe deer are found in most habitats, excluding mountainous areas of high elevation, particularly northern Scandinavia where their European distribution does not reach (Apollonio et al. 2010). As a species it is strongly associated with forests and woodlands, both coniferous and deciduous. However, they are also found in many other habitat types, including; open meadows, marshlands, moors and shrublands. Given their tolerance of humans, roe deer have also been successful in occupying many human-dominated habitats, such as forestry plantations, farmland and even gardens and more urbanized areas (Latham 1999). Although they exhibit some tolerance to human presence, one of their main habitat requirements is shelter from predators and humans (Tufto et al. 1996).

Roe deer are a solitary species that occasionally come together to feed in larger groups (~10 individuals). During the breeding season March – August, adult males become territorial, with fawns remaining close to their mothers before young males disperse, typically further afield than young females (Hewison et al. 2021). As a solitary species, the daily activity pattern of roe deer is dependent on many factors, both endogenous and exogenous (Aschoff 1954). Their normal activity follows a crepuscular rhythm, with activity peaks at dawn and dusk (Pagon et al. 2013), making these the periods of the day when food consumption is highest. Roe deer activity also varies seasonally due to changing circadian rhythm, where the length of day and night varies across the year (Stache et al. 2013). Another factor which may effect a roe deer's activity pattern, is weather, particularly snow depth during the winter months (Turner 1979).

As roe deer activity peaks during dawn and dusk, these are the periods when food consumption is highest but also predation risk is increased. A daily trade off occurs, known from the 'optimal foraging theory', which states that a foraging individual should balance gaining maximal energetic requirements while minimizing the amount of time spent acquiring said energy (MacArthur & Pianka 1966; Pyke et al. 1977). As resources providing the maximum energy are often associated with higher risk and increased predation potential (Fraser & Huntingford 1986), a roe deer must employ behavioural tactics to reduce predation probability. One example is vigilance, which allows prey species to use high energy resources whilst minimising predation risk (Lima & Bednekoff 1999). Given that roe deer are solitary species for the majority of the year and one of the smallest ungulates found in Sweden (adults weigh 10-25kg), their ability to detect predators is essential for their survival, especially because they are important prey for most of the large

carnivores found in Sweden (Arbieu 2012, Elofsson & Häggmark 2021). Additionally, roe deer are regarded a valued resource to humans, who actively hunt them, both to manage populations and for sport (Nordström 2010).

1.2.2 Wild boar

Much like roe deer, wild boar (*Sus scrofa*) historically faced extreme hunting pressure to the point where they became extinct in Sweden during the 16th century (Burton et al. 2018). In recent decades, reintroductions through escapes from enclosures (Truvé & Lemel 2003) has led to a recovery and huge increase in numbers throughout Sweden. Furthermore, wild boar are omnivorous opportunistic feeders, which benefit from the ever expanding agriculture throughout much of Europe and Sweden, making it one of most widely distributed mammals worldwide today (Markov et al. 2022). Specific characteristics have aided in their rapid distribution and population expansion, such as a high reproductive rate, a flexible diet, and an ability to quickly adapt to new environments (Barrios-Garcia & Ballari 2012). Anthropogenic factors like supplementary feeding, reduced hunting effort and intentional releases have also proved significant in the continued recolonization of Sweden by wild boar (Aschim & Brook 2019). Low predator densities within their native range also contribute to the fast expansion rate (Massei & Genov 2004). The main threat to wild boar is from humans. In 2020 over 160,000 wild boar were shot by humans (*Viltdata* 2023) meaning that other than large carnivores, no other animal species has an impact on the spatiotemporal behaviour of wild boar, in the same way that humans do (Keuling et al. 2017).

Conflict mainly arises between wild boar and humans due to the rooting behaviour exhibited by wild boar, where they overturn areas of soil to find plants parts, fungi and small invertebrates to feed on (Baubet et al. 2003). For Swedish farmers, a large economic loss comes every year from wild boar not only from rooting behaviour but also from damage to machinery and reduced quality of hay and silage. Further economic loss occurs due to prevention methods used to discourage wild boar from entering agricultural land, such as fencing fields, scaring and trapping methods or use of supplementary feeding to entice them away from crops (Gren et al. 2020). Supplementary feeding for wild boar and other ungulates in Sweden has become a more popular method for reducing crop damage, aiming primarily to distract wild boar from causing damage to crops, but also employed by hunters who wish to entice wild boar to a particular place, so called diversionary feeding (Lemel et al. 2003). Not only do the supplementary feeding sites provide an alternate food source, they may also become a wild boar or roe deers only food source during winter months when food is scarce due to high snow cover. However, supplementary and diversionary feeding are relatively new methods, so the true impact of these deterrent methods is unknown, and further research is needed.

1.3 A multi-ungulate system

Sweden, like many European countries, is home to numerous wild herbivores, including cervidae such as roe deer, red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and moose (*Alces alces*), bovidae including muskox (*Ovibos moschatus*) and mouflon (*Ovis aries musimon*) and the only member of the suidae family, wild boar. Each species inhabits its own specialised ecological niche, which is essential for coexistence (Putman 1996). For example, moose, roe deer, red deer, fallow deer and wild boar can often be observed in similar habitats, such as forests, open fields and wetlands. These similarities can lead to interference competition between species, for shared resources such as food and shelter, particularly due to adverse environmental conditions during the breeding season and winter (Ferretti & Fattorini 2021). Such competitive conditions may have a significant impact on the fecundity, reproductive success and growth of a species (Boer & Prins 1990). Although they exhibit forage partitioning, along a scale from grazing to browsing (Spitzer et al. 2020), there is still a crossover between the different species, and interference competition is at play. A study by Ferretti et al (2012) explored the relationship between native roe deer and non-native fallow deer in a Mediterranean coastal area, and found that displacement of roe deer by fallow deer was not dependent on the habitat in which they met, but rather by the habitat used most frequently by the subordinate species (roe deer). Furthermore, they observed that the dominant species (fallow deer) induced interference interactions between the two species, with particular correlation to the seasonal use of habitats. Although interference competition is more prevalent between species who show resource overlap, as in the case of roe deer and fallow deer, there is also evidence of the presence of wild boar causing roe deer to be displaced (Ferretti et al. 2011).

Current studies on interspecific interactions between wild boar and other ungulates in Sweden is lacking. Research focusing on wild boar in Sweden mainly covers topics including crop damage, habitat selection, transmission of disease (Barasona et al. 2014, Muthoka et al. 2022, Thurffjell et al. 2009) and its increasing distributional range. Given that wild boar and roe deer have a lot in common, including a similar history regarding human induced population changes, and both have a large and increasing population density and distribution within Sweden, how will the continued increase of wild boar in Sweden impact the solitary behaviour of roe deer and their daily activity pattern?

1.4 Aims and study questions

The aim of this study was i) to compare the use of supplementary feeding sites by roe deer under two different wild boar population densities, and ii) through use of GPS data monitor the spatiotemporal response in roe deer within their home ranges, towards wild boar. Thus, hypothesising that roe deer and wild boar will engage in interspecific interactions, and one species will be dominant over the other. By investigating the interaction occurring between these two species, more comprehensive conclusions can be made on their interactions and how the increase in wild boar is potentially affecting the behaviour of roe deer but also the wider Swedish ungulate community. With the aim to explore the spatiotemporal interactions occurring between roe deer and wild boar, the research questions of this project were:

2. Material and Method

2.1 Study area

The study was conducted in the Grimsö Wildlife Research Area (13,000 ha; Örebro County, south-central Sweden; 59.7286 N, 15.4724), a scientific research area primarily focusing on natural resource and wildlife management. Comprised of mainly cultivated mixed forest, the study area holds two nature reserves (~900 and 450 ha each) and is easily accessible by roads throughout. The area consists mainly of forest (ca. 70 %), with the majority being coniferous plantations, but also other habitats including wetlands, bogs, mires, agricultural land, lakes and small human settlements (Angelstam et al. 1982). The elevation ranges between 100 m and 150 m, the mean annual temperature is 6 °C, and there is approx. 700 mm of rain per year. Snow coverage lasts for approx. 110 days per year, with highest cumulative snow fall occurring between late November – March (Nygren & Frid 2017). This study will focus on the winter season, with the study using data from December – March.

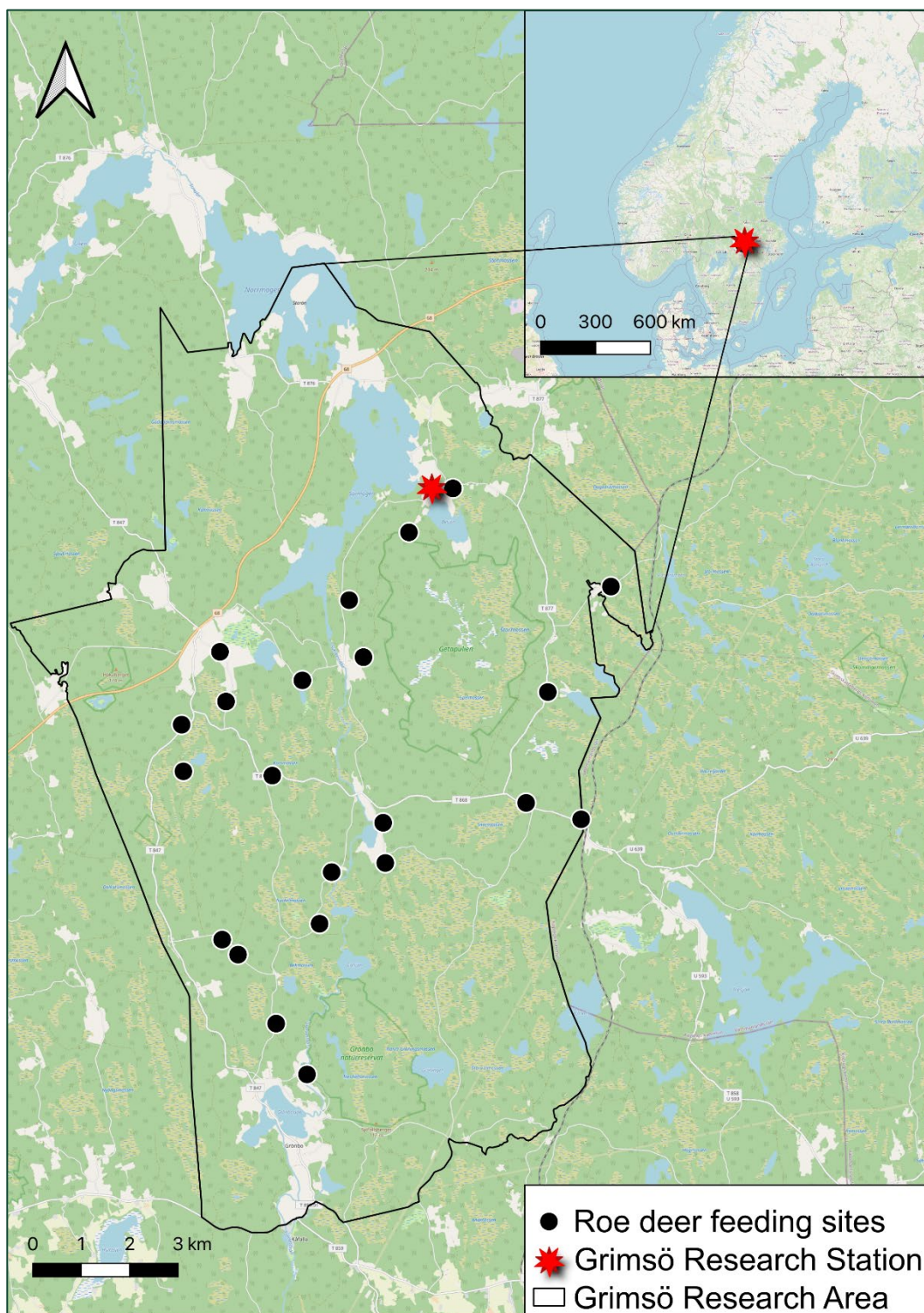


Figure 1. The GWRA boundary situated in south central Sweden (top right), with the research site highlighted (red) and the locations of the 20 roe deer feeding sites (black dots) all within the boundary (main panel). (OpenStreetMap[®], openstreetmap.org. (CC BY-SA 2.0).)

2.2 Study species

2.2.1 Roe deer

Between 2012 and 2023, 117 roe deer were captured using box traps and equipped with GPS (Global Positioning System) and/or VHF (Very High Frequency) radio collars. Capturing took place between November - April each year, as reduced food availability in this winter period attracts roe deer to the trap sites where supplementary food is available. Supplementary food is added to feeding sites between midday and sunset. Capturing ended in late March/early April each year to reduce damage to the newly growing antlers of male roe deer, and to reduce stress to females who may be pregnant. Ethical approval was granted yearly, before the start of each capturing season. There were 85 individual roe deer (32 males and 53 females) included in the data set after the pre-processing and cleaning procedure.

2.2.2 Wild boar

Between January 2019 and March 2023, 19 wild boar (3 males and 16 females) were captured within the study area using corral traps and equipped with GPS collars. Only animals weighing greater than 60 kg were fitted with a GPS collar. Wild boar were immobilised with a tranquiliser gun (Dan-inject model JM, Dan-inject, Kolding, Denmark) or a blowpipe (Dan-inject model Blow 125) after being captured in corral traps. Wild boars were immobilised using one of the following anaesthetising combinations: 30 mg romifidine + 300 mg zolazepam-tiletamine or 5 mg medetomidine + 400 mg zolazepam-tiletamine. After immobilisation, wild boars were equipped with one of the following GPS/GSM collars: Vertex Lite 2D or GPS Pro Light 3D (Vectronic Aerospace GmbH). The collars were programmed to attempt location fixes every hour for a maximum of 80 weeks. After data processing and cleaning the final sample size of wild boar included in this study was 15 (2 males and 13 females).

2.3 Avoidance behaviour

To assess the avoidance behaviour of roe deer to wild boar, the GPS locations of roe deer and wild boar, from January 2019 – March 2023 were used. During this time period, 36 roe deer (19 males and 17 females) had GPS data available, which overlapped with the wild boar data available in the same time period. In order to avoid pseudoreplication, data of each roe deer was used for one winter period only. Home ranges were defined using the minimum convex polygon (MCP) in Q-GIS. Within each roe deer home range, wild boar locations and randomized points were selected at a 1:1 ratio. In R studio, the distance between each roe deer location and

the closest wild boar location at the same hour was calculated. At the same hour of wild boar location, the closest distance between a roe deer location and a randomized point was calculated. A paired t.test was then performed to compare distance between roe deer and wild boar locations, and roe deer locations and randomized points, all within the roe deer's home range. All data was analysed using Q-GIS (3.22.5-Białowieża) or R Studio (Version 2023.03.0-daily+709).

2.4 Presence at feeding sites

2.4.1 Roe deer

Roe deer presence at the feeding sites was defined following Ossi et al. (2017) as an individual spending more than 10 % of its total time inside the buffer zone around feeding sites per hour, then assigned either present (1) or absent (0), here after refer red to as roe deer presence at feeding sites. In order to determine roe deer presence, I created a buffer around each feeding site (radius = 100 m (ibid.), area = 0.031 km²) using the sf package (Pebesma 2018).

2.4.2 Wild boar

The activity of wild boar at roe deer feeding sites followed the same methodology as for roe deer (2.4.1), for all parts excluding an individual spending 10 % of its total time inside the buffer zone around feeding sites per hour.

Field notes from every roe deer capture, provided data on when wild boar were caught as bi-catch in roe deer feeding sites. Based on the capture rate of wild boar at the roe deer feeding sites (table 1), I divided the study period into two intervals: *low-density* of wild boar (2012 - 2015) and *high-density* of wild boar (2021 - 2023). The years between the two time periods (2016 - 2020) were excluded to clearly distinguish between the *low* and *high density* periods. Here after, I refer to this variable as wild boar presence.

Table 1. Capture rate of wild boar at roe deer trap sites (2012-2023), used to define the low and high density periods of wild boar in the study area. Wild boar density is defined by two time periods, low (2012 – 2015) and high (2021 – 2023).

| YEAR | NUMBER OF WILD BOAR | WILD BOAR DENSITY |
|------|---------------------|-------------------|
| 2012 | 5 | Low |
| 2013 | 11 | Low |
| 2014 | 2 | Low |
| 2015 | 1 | Low |
| 2016 | 11 | Omitted |
| 2017 | 21 | Omitted |
| 2018 | 29 | Omitted |
| 2019 | 10 | Omitted |
| 2020 | 5 | Omitted |
| 2021 | 20 | High |
| 2022 | 24 | High |
| 2023 | 35 | High |

2.4.3 Day length standardization

As the study period is from 1st December to 31st March, the daylength varies significantly during that period. In early December there are approx. 6.2 hrs of daylight at the study site, compared to late March when there is 13 hrs of daylight. To account for this high variability in daylength, I used the sunTime function from the overlap package (Ridout & Linkie 2009) and the circ_rad function from the card package (Refinetti et al. 2007), on the GPS data of both the roe deer and wild boar data sets. All data was analysed using R Studio (Version 2023.03.0-daily+709).

2.5 Statistical analysis

2.5.1 Roe deer

Generalized Additive Models (GAMs) were used to model potential non-linear patterns of roe deer presence in relation to sex, time of the day, wild boar presence and animal id. I used Akaike Information Criterion (AIC) (Akaike 1974) to select the best model explaining variation in roe deer activity. All data was analysed using Q-GIS (3.22.5-Białowieża) or R Studio (Version 2023.03.0-daily+709). The GAMs were fit using the gam package (Hastie 2017) and mgcv package (Wood 2011) in R studio.

Table 2. Variables used for GAMs analysis

| | Variable | Unit & range |
|--------------------|------------------------|-------------------------|
| Roe deer presence | Response (discrete) | Present = 1, Absent = 0 |
| Sex | Predictor (discrete) | M or F |
| Time of the day | Predictor (continuous) | Hour (0-23) |
| Wild boar presence | Predictor (discrete) | Present = 1, Absent = 0 |

3. Results

3.1 Avoidance behaviour

The mean home range size for the 36 roe deer was 1.9 km². The largest home range was 5.814 km² and the smallest home range was 0.357 km². The distance between roe deer to the nearest wild boar or nearest random locations at the same hour was significantly different ($t = 3.5389$, $df = 251$, $p = <0.0005$). Roe deer were on average at 882 ± 465 m distance from wild boar while the mean distance to random locations was 759 ± 412 m (Appendix 1).

Table 3. Results of the paired t-test analysing distance between roe deer locations and wild boar/ randomized locations

| Conditions | Minimum distance | Maximum distance | Mean distance |
|-------------------------------|------------------|------------------|---------------|
| Roe deer to wild boar | 33 m | 2398 m | 882 m |
| Roe deer to randomized points | 25 m | 2219 m | 759 m |

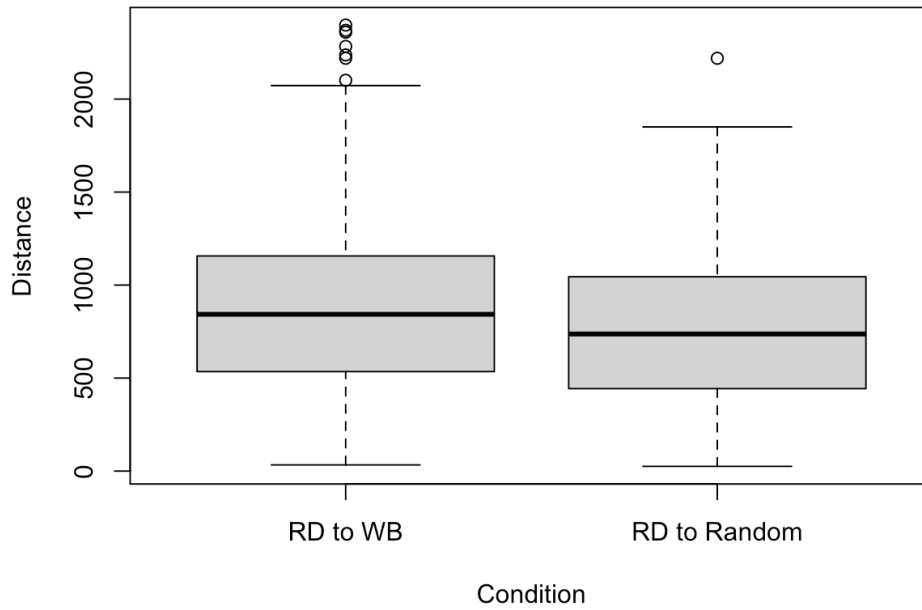


Figure 2. The results of the paired *t*-test of the distance between roe deer points to wild boar points, and roe deer to randomized locations at the same hour ($t = 3.5389$, $df = 251$, $p = <0.0005$). The mean of each category is shown by the thick black line. Data based on 36 roe deer and 15 WB collected at Grimsö Wildlife Research Area in Sweden, 2019 – 2023.

3.2 Daily activity patterns

3.2.1 Wild boar

The most likely time for a wild boar to be close to a feeding site is the hours surrounding sunset, for the rest of the day the probability remains low (Figure 3).

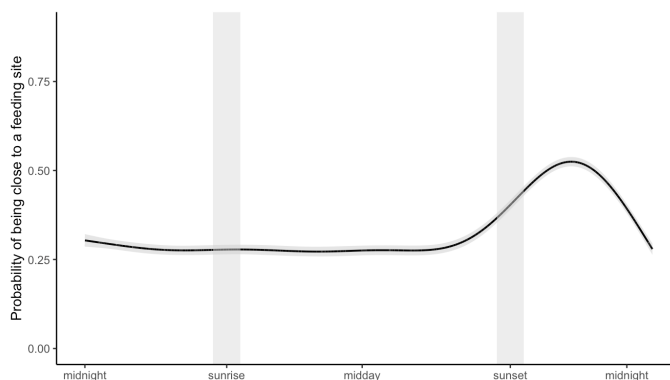


Figure 3. The probability of a wild boar to be close to a feeding site between December to march, using the sunTime function to standardize for sunrise and sunset times during our study period.

3.2.2 Roe deer

Several GAMs were performed on the probability of roe deer to be close to a feeding site (Table 4), and the best fitting model was Gam 5, as it has the lowest AIC value. In the best model, several variables had significant impacts on the response variable (Table 5). Firstly, the smoothed term of hour alone was significant. Further significant relationships were the interaction of hour with both periods of wild boar density. Additionally, animal_id is also significant (Table 5), meaning that the inter individual variation in the presence of roe deer at feeding sites was high.

Table 4. Model selection procedure to determine the best fitting model

| | Model * | AIC | Δ AIC |
|------|---|----------|--------------|
| Gam5 | rd_presence ~ s(suntime)+ sex + s(suntime, by = sex) + s(suntime, by = wb_presence) | 25515.36 | 0 |
| Gam4 | rd_presence ~ s(suntime)+ sex + s(suntime, by = sex) + wb_presence | 39097.74 | 13552.38 |
| Gam1 | rd_presence ~ s(suntime) | 56788.04 | 31272.68 |
| Gam2 | rd_presence ~ s(suntime)+ sex | 56788.05 | 31272.69 |
| Gam3 | rd_presence ~ s(suntime)+ sex + s(suntime, by = sex) | 79509.07 | 53993.71 |

*all models include animal id as a random effect (animal_id, bs = “re”)

Table 5. Smooth terms and their statistical significance, retained in the best model (gam 5). See text for further details.

| Term | EDF | Level of significance |
|-----------------------------|--------|-----------------------|
| s(suntime) | 8.0698 | < 2e-16 *** |
| s(suntime):female | 6.3561 | 0.000468 *** |
| s(suntime):male | 0.9305 | 0.8067 |
| s(suntime):wb-presence-high | 0.7907 | 7.79e-07 *** |
| s(suntime):wb-presence-low | 7.3478 | < 2e-16 *** |

The best model (gam5) shows varying temporal patterns during the different periods of wild boar density (Fig. 4). During low wild boar density, roe deer showed high probability of being at feeding sites during dawn and dusk, and that they have very little day time activity at the feeding sites. During the period of high wild boar density, the day time activity of roe deer at feeding sites changes, and roe deer visit the feeding sites from early afternoon to after sunset, after which the probability decreases again.

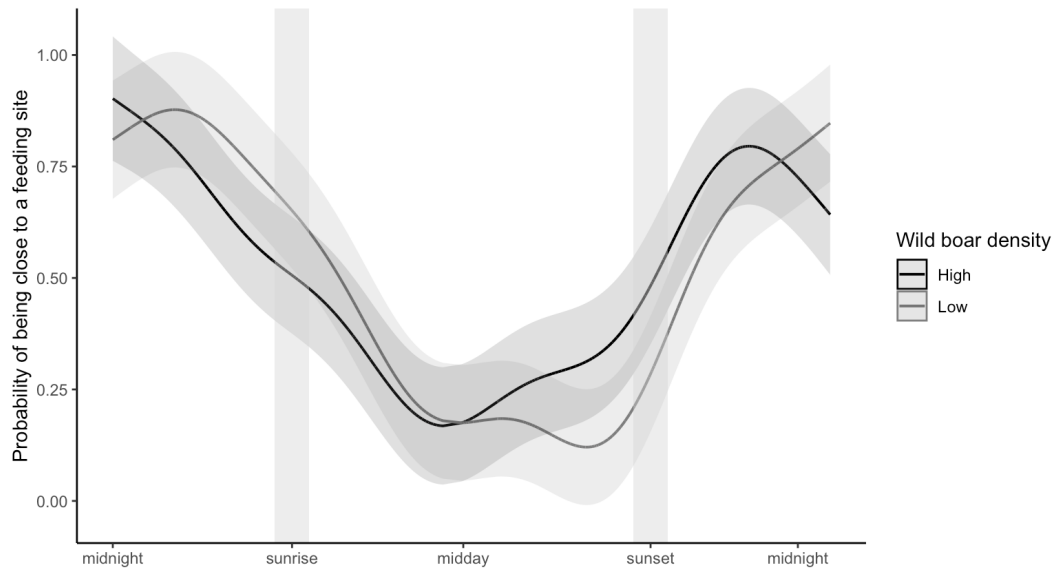


Figure 4. The probability of a roe deer to be inside the 100m buffer around feeding sites, during the periods of low (2012 – 2015) and high (2021 – 2023) wild boar density. The shaded area represents the 95 % confidence interval of the predictor variable - wild boar presence - in relation to the presence of roe deer at feeding sites.

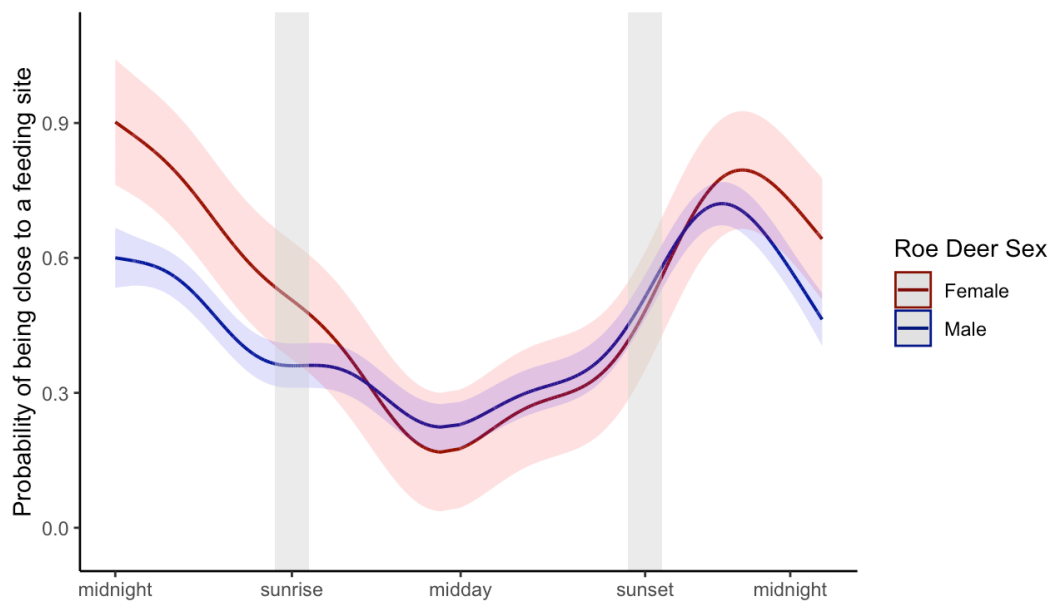


Figure 5. The probability of a roe deer to be inside the 100m buffer around feeding sites, during 2012 - 2023, divided by sex (male or female). The shaded area represents the 95 % confidence interval of the predictor variable – roe deer sex - in relation to the presence of roe deer at feeding sites.

4. Discussion

In this study I investigated whether different wild boar densities affected the spatiotemporal behaviour of roe deer within the Grimsö Wildlife Research Area. The main findings were that the use of feeding sites by roe deer changed when wild boar population density increased from low to high. In accordance with the hypothesis of the study, roe deer and wild boar engage in interspecific interactions, and wild boar showed dominance over roe deer within both the roe deer's home range and at feeding sites.

The findings of the avoidance behaviour analysis supported the hypothesis, indicating that roe deer showed a level of spatial avoidance behaviour towards wild boar, as on average they were closer to randomized locations than to a wild boar location within their home ranges. This is the expected result, given that roe deer are a solitary species and when compared to other ungulate species, they will often be the species which gets displaced by the other more dominant species (Ferretti et al. 2011). Ungulates such as wild boar and fallow deer have a high probability to cause displacement rather than being displaced themselves. Roe deer however, showed a much lower probability of displacing other species, and were often the submissive species when involved in this type of interaction (Ferretti & Mori 2020). Further support of my hypothesis was shown by the probability of roe deer presence at feeding sites changing depending on wild boar densities. The change in behaviour of roe deer at feeding sites (Fig. 4), shows that roe deer have changed their activity when the density of wild boar has increased. During the high wild boar density period, roe deer are visiting the feeding site after midday to a higher degree compared to during the low wild boar density period (Fig. 4), most likely so that they access the food which is left in feeding sites before wild boar enter the area. This behaviour indicates that a level of interference competition may be at work and roe deer are changing their behaviour to ensure they have access to the supplementary food left at feeding sites. Furthermore, at each feeding site there is a limited supply of food (4 - 8kg) meaning roe deer must visit the feeding sites earlier than wild boar to ensure there is food available to them. One final consideration relating to roe deer visiting the feeding sites after midday is that the food is left in the feeding sites between 8am and 12pm each day, so for the roe deer

to benefit from the food they must go before the wild boar as close to 12pm as possible, which they appear to do from the results obtained in this study (Figure 4). As the probability of wild boar being at the feeding sites are highest at dusk, roe deer must adapt their preferred feeding time, to ensure food is still available when they visit.

I found that there was a degree of individual variation in presence at feeding sites due to individual specific characteristics or traits. The first trait which we know has an impact is gender (Figure 5), female roe deer have a higher energy requirement during pregnancy (Rautiainen et al. 2021) and post partum when caring for offspring. Meaning if food is scarce they may seek out supplementary feeding sites to a higher degree than male roe deer. Additionally, roe deer and other deer species who carry more than one offspring require more energy and protein to survive (ibid.). This could also cause the trend we see in Figure 5, that females are visiting the sites more than males. This could be particularly prevalent in the later months of our study period when roe deer females are likely to already carry their offspring. A second factor relating to females visiting mostly during the crepuscular rhythm, could be as they have fawns with them, so they will try to avoid more risky time periods, such as daylight hours. Although, female roe deer are continuously considering their 'lifetime reproductive success', meaning all their actions also must be an investment in their own survival to maximise current and future reproductions (Nordström 2010, Stearns 1992).

The results of this study could also be interesting to consider in the future management of these two species in Sweden, and the wider Europe. This study shows preliminary evidence that roe deer may be locally and temporarily displaced by wild boar. This could be interesting to observe if wild boar numbers continue to increase, however roe deer and wild boar have largely coexisted so it is unclear as to whether there would be a hugely negative impact on roe deer if wild boar numbers increased.

Therefore, the continued control of wild boar populations could be important to avoid further interference to roe deer populations depending on the management goal. Both roe deer and wild boar are important game species in Sweden, for their meat, recreational hunting and other for other benefits in their role in ecosystem maintenance (Elofsson et al. 2017), so fully understanding the ways in which these two species coexist and interact could be very important to the Swedish economy.

4.1 Study limitations

There were a number of limitations to this study which possibly affected the final results. To determine the presence of wild boar at the feeding sites, only wild boar with GPS collars were used. However, it is almost certain that many other wild boar would be using these feeding sites, which could have altered the activity pattern of roe deer (Figure 3), and may have given us a clearer insight into the times of day when wild boar are most active. Following this, the feeding sites which were used in this study are not the main supplementary feeding sites present in the study area, therefore its highly likely that if our sites were the only sources of supplementary food, the effect of wild boar presence on the daily activity pattern of roe deer would have been more pronounced.

Other factors which may impact the presence of roe deer at sites could include weather, human presence, hunting intensity, season, size of wild boar group, presence of other large ungulates. When considering weather and season, winter periods vary every year. A year with higher snow fall and harsher weather, would reduce a deer access to natural food and potentially make them seek access to supplementary food more (Ossi et al. 2017), even when more dominant species are close by. Additionally, roe deer have been found to be very sensitive to low temperatures, as the increased energy needed for thermoregulation can be difficult to source during harsh winter months (Heurich et al. 2012). These factors all corroborate why a roe deer would increase their presence at feeding sites during the day, regardless of the increased risks associated with day time activity, and that sometimes the feeding sites provide food without which a roe deer would not survive. Whereas, warmer years with less snow fall may allow deer to use feeding sites to a much lower degree.

When considering wild boar density, the collared wild boar involved in this study likely only represent a small portion of the actual wild boar present in the research area. For example, figure 3 shows the probability of collared wild boar to be at the feeding sites. The pattern is not clearly defined, particularly during the earlier part of the day from midnight to midday. It is possible that if the study had a larger number of collared wild boar, we would see a stronger pattern of when wild boar are most present at the feeding sites. Furthermore, each collared individual wild boar tells us nothing about the size of group that the wild boar is travelling in. This would likely have a large impact on whether a roe deer is displaced. Considering that a roe deer relies heavily on vigilance to detect predators while also consuming high value resources, the amount of noise created by a solitary or large group of wild boar, would potentially have a high impact on a roe deer's behaviour and ability to detect other predators.

4.2 Future research

Due to time limitations, there were other areas of analysis which couldn't be fulfilled, such as including each of the roe deer feeding sites as an individual variable. This would have been very interesting to determine if certain sites are preferred by one or both species. Considering this, it could have also been interesting to explore if there is any preference to the type of habitat that the feeding sites are located in. As roe deer show preference for forested areas, maybe because they offer more protection from predators, the proximity of the feeding sites to forest vs open field or human settlements would be very interesting to explore, especially considering they also seek protection from predators close to human settlements. Additionally, looking at the proximity between these feeding sites and the larger wild boar feeding sites which are present around the study area. It would be interesting to see if higher activity of wild boar at the larger feeding sites would impact a roe deer's presence at nearby roe deer feeding sites. Finally, another variable to look at in the future could be snow depth, to further explore whether the effects of the "adverse weather conditions hypothesis" outweighs probability of displacement at feeding sites by wild boar, and also other ungulates and even predators.

5. Conclusions

In conclusion, the study explored the spatiotemporal behaviour of roe deer in response to different wild boar densities within the Grimsö Research Area. The study suggests that roe deer avoid being in the close vicinity to wild boar, however, more research is needed to look at the interactions occurring between these two species and the wider ungulate community present in Sweden. Continued research into how the recent re-colonization and increase in wild boar density is effecting nature in Sweden is also needed, particularly their ecological impact on vegetation communities, increased rooting behaviour, soil erosion and displacement of native species. The study also highlights the importance of winter supplementary feeding for roe deer, but the overall impacts of supplementary feeding were not explored in this study.

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Popular science summary

In the natural world animal species are interacting with one another on a daily basis and these interactions can be both positive and negative. Competition is an example of a negative interaction, which can occur between members of the same or different species. Two species of wild ungulate in Sweden which may interact through competition are roe deer and wild boar, although there are currently few scientific studies which have examined this relationship.

Roe deer are naturally occurring in Sweden, and currently have a stable population, although historically were hunted almost to extinction. They are the smallest species of deer in Sweden, and typically weigh between 10 and 25kg. In comparison, wild boar is a larger and heavier species, with adult individuals weighing between 60 and 100kg. The wild boar was once extinct in Sweden, but accidental escapes from farms resulted in its population and distribution once again expanding. Both species live in similar habitats, such as in forests and on agricultural land, so they can interact to some extent every day. This study attempts to understand how roe deer are impacted by the increase in wild boar, by comparing the use of feeding sites by roe deer under two different wild boar densities (low, from 2012 – 2015 and high, from 2021 – 2023).

The study is located within the Grimsö Wildlife Research Area in south central Sweden. Using GPS/VHF data collected from roe deer which were collared between 2012 and 2023, and wild boar collared between 2019 and 2023. The study firstly examined if roe deer showed any avoidance behaviour inside their home ranges, towards wild boar and secondly, how the increase in wild boar density has changed the use of feeding sites by roe deer.

The results indicate that roe deer show an avoidance behaviour inside their home ranges, towards wild boar. When comparing the distance between roe deer to wild boar and roe deer to randomized points, roe deer were on average closer to randomized points than to wild boar. The second part of the analysis showed that roe deer changed their behaviour at feeding sites, between two different wild boar densities.

In conclusion, roe deer appear to avoid wild boar at feeding sites, which could be explained by roe deer being the smaller, more submissive species in the relationship. The study offers a first look at this type of interaction between these two species, but further research is needed to fully understand what interaction is occurring. Future consideration should be made in the management of these species, regarding the interactions taking place.

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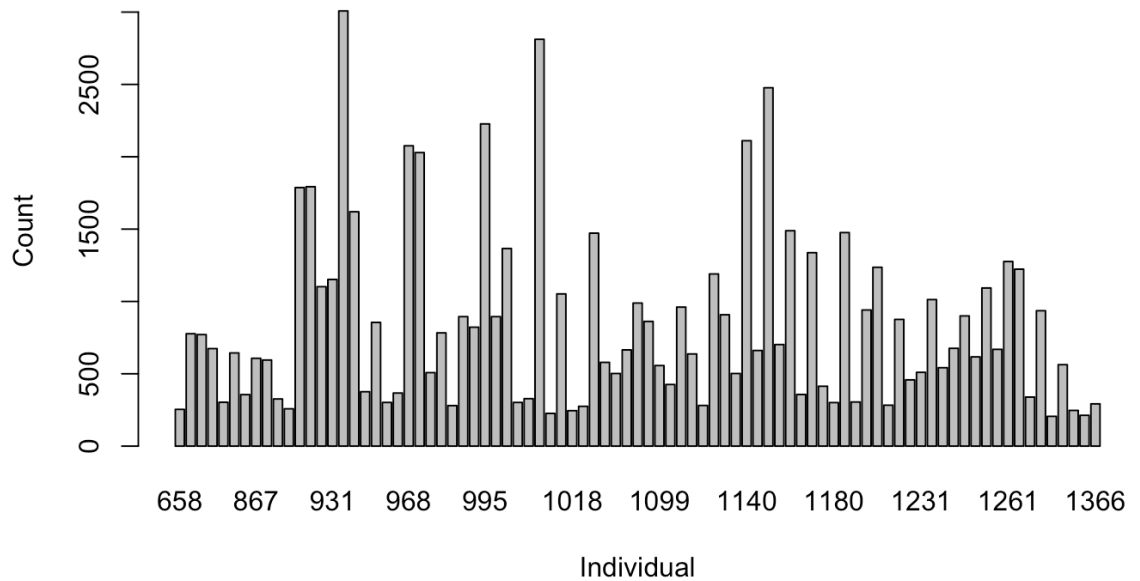
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6. Appendix

6.1 Appendix 1: The number of positions each roe deer had, only including roe deer with >199 positions, during the winter period of December – March from 2012 – 2023.



6.2 Appendix 2: The home range size for each roe deer collared within the grimso research area between December 2019- March 2023.

| Animal ID | Home range size (km ²) |
|-----------|------------------------------------|
| 1352 | 2.919 |
| 1332 | 1.597 |
| 1336 | 0.536 |
| 1366 | 3.470 |
| 1344 | 1.586 |
| 1337 | 0.357 |
| 1326 | 0.948 |
| 1316 | 1.451 |
| 1310 | 3.714 |
| 1268 | 2.470 |
| 1265 | 2.400 |
| 1261 | 1.481 |
| 1259 | 1.021 |
| 1253 | 0.994 |
| 1252 | 1.344 |
| 1238 | 2.211 |
| 1234 | 4.585 |
| 1229 | 1.265 |
| 1225 | 0.658 |
| 1216 | 3.329 |
| 1199 | 5.814 |
| 1197 | 3.041 |
| 1191 | 1.124 |
| 1181 | 0.778 |
| 1180 | 1.053 |
| 1174 | 1.781 |
| 1137 | 1.816 |
| 1144 | 1.728 |
| 1140 | 2.284 |
| 1143 | 0.626 |
| 1099 | 1.787 |
| 1151 | 1.346 |
| 1029 | 0.701 |
| 996 | 2.066 |
| 981 | 2.242 |

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