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Spatiotemporal competition patterns of Swedish roe deer and wild boar during the fawning season

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Photo: Torsten Berg

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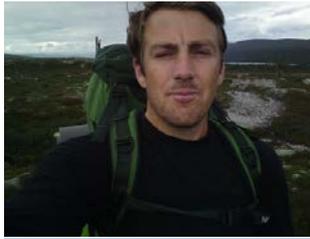


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Abstract

This study was performed on Bogesund research area, Sweden, in order to determine whether wild boar (*Sus scrofa*) predated on fawns of roe deer (*Capreolus capreolus*) and if the spatial and temporal patterns of roe deer are related to wild boar activity. A behavioural response is beneficial for many organisms when they are exposed to interspecific competition. A spatial and temporal avoidance towards their antagonist may be essential for survival in times of great competition. Little information is available about roe deer's behavioural response to wild boars competitive abilities. I performed spatial and temporal measurements to wild boar activity from my roe deer data in order to test my predictions of a roe deer avoidance towards wild boar. Data was collected from radio-marked roe deer fawns, pellet group counts and photographs from a wildlife camera survey. I was not able to demonstrate any wild boar predation on fawns. However, fawns display a non-random movement pattern towards wild boar rootings and the distance is longer to heavy wild boar activity. Roe deer adults are more present at cameras with lower wild boar presence and the both species display different diurnal activity patterns. I discuss the implications of these results in terms of roe deer fecundity and growth of populations.

Key words: Sus scrofa, Capreolus capreolus, interspecific competition, predation, spatiotemporal displacement.



Staffan Melberg tog/tar sin filosofie magisterexamen i biologi vid SLU (Sveriges lantbruksuniversitet) under 2012. Denna sammanfattning bygger på hans examensarbete i biologi, vilket skrevs vid Grimsö forskningsstation SLU.Handledare var Jonas Nordström, forskare vid institutionen för ekologi, Grimsö.

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Populärvetenskaplig sammanfattning:

Rådjur undviker platser med hög vildsvinsaktivitet

Rådjur tenderar att under kidsäsongen undvika platser med hög vildsvinsaktivitet enligt ett examensarbete vid Grimsö forskningsstation SLU. Den Svenska rådjursstammen har det senaste årtiondet decimerats, främst på grund av ökande populationer av varg och lo, men en minskning har även konstaterats utanför områden med stora rovdjur. Om rådjur är missgynnade av vildsvinaktivitet kan det vara möjligt att vildsvin delvis orsakat rådjursstammens nedgång i områden där stora rovdjur inte finns.

Konkurrens om föda och habitat uppstår där likartade organismer delar livsmiljö, enligt Darwins evolutionsteori. Vildsvin har visat sig vara en stark konkurrent gentemot andra arter. Främst på grund av deras behov av mat och habitat, men också genom ren predation. Till exempel återkommer det i jägarpress uppgifter om lamm och kalvar som påträffats dödade, eventuellt av vildsvin. Vildsvinsdödade lamm och kalvar av både vilda djur och tamdjur har dessutom observerats i USA och Australien. Med detta i åtanke ligger det nära till hands att vildsvin också äter rådjurskid. Rådjur som undviker områden med hög vildsvinsaktivitet minimerar risken att stöta på vildsvin, detta bör således vara särdeles viktigt för kidförande getter.

Samspelet mellan rådjur - vildsvin är dock hitintills dåligt studerat och med anledning av Sveriges växande vildsvinsstam växer också behovet av kunskap gällande vildsvins påverkan på andra djurarter. Svensk viltforskning har därför fått anslag för att studera rådjur - vildsvinskonkurrens - i syfte att anpassa viltförvaltningen på bästa sätt. Detta examensarbete kan ses som en del av detta arbete.

Inga sändarförsedda kid blev dödade av vildsvin i studien på Bogesund. Studien utesluter ändå inte helt predation med anledning av den lilla provstorleken (12 kid). Sändarmärkta kid visade dock ett icke slumpmässigt rörelsemönster i förhållande till vissa typer av vildsvinsaktivitet. Till exempel höll de sig långt från platser där vildsvin samlas för dagliga ritualer (t ex bök och pälsvård). Generellt sett visade även vuxna rådjur en preferens för områden med lägre vildsvinsaktivitet. Exempelvis minskade antalet rådjur med hela 40 % vid platser med ett högt antal vildsvin, baserat på fotografier från viltkameror. Aktivitetsmönstret var även skilt från vildsvinens. Rådjur och vildsvin fanns inte på bild på samma plats samtidigt.. Det verkade också som om bökstorleken (som är en indikation på gruppstorlek eller tid spenderad på platsen) tenderar att påverka avståndet till rådjursposition, i det här fallet ökar avståndet till rådjursposition med ökande bökstorlek.

Resultaten tyder på att rådjur undviker vildsvin. Osäkert är dock hur rådjuren påverkas av detta. Forskning kring, till exempel, rådjurens habitatutnyttjande före och efter vildsvinsetablering är ett värdefullt komplement till mina resultat. Kunskaper om lokala vildsvinspopulationer bör hursomhelst prioriteras av viltförvaltare när det årliga jaktliga uttaget av rådjursstammen planeras.

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Introduction

Study species

Wild boar (*sus scrofa*) is a species in *Suidae* family, originating from Eurasia. It is the most widespread of all *Suidae* species and are highly adaptable to all kinds of habitats up to 65°N (Leaper *et al.* 1999). Wild boar is an omnivore that feed opportunistically on plants and animals. It is predominantly herbivorous with plant material forming 80-90 % of their diet (Massei & Genov 2004). Underground food items such as roots, bulbs and soil invertebrates form a conspicuous part of the wild boar diet. Animal matter occurs, however, in 94 % of stomachs analysed (Genov 1981).

Wild boar is historically belonging to the Swedish fauna, but during medieval times, people in rural Sweden considered wild boar a pest. Hence, in the late 17th century wild boar went extinct due to extensive hunting and assimilation with domestic pigs, and so was the standoff for more than 200 years. However, in the 1970's wild boar escape from ranches in Södermanland county resulted in a re-entry into the Swedish fauna. After re-establishment, wild boar was by a parliament act in 1988 given domiciliary right and is thereby not treated as an invasive species (Truvé 2004; SJF 2009). The wild boar population has increased and colonized old territories since the 1970's (south of Sweden up to the north of Dalarna county), most possibly due to a combination of factors such as further escapes, lack of predators, climatic changes, and supplementary feeding (Massei & Genov 2004; SJF 2009).

The current Swedish wild boar population consists probably of more than 150 000 individuals. However, population size is, without a well functioning management, assumed to redouble within 3-5 years (SJF 2009). The yearly harvest has increased from low numbers (1990) to 50 000 (SJF 2008) and will most probably continue to increase (SJF 2009).

The European roe deer (*Capreolus capreolus*) is a small cervid, native to the Swedish fauna. Distributed from the Atlantic coast in the west to the Ural Mountains in the east (Linnell 1998). Amongst European ungulates, roe deer is the most widespread and

found in a variety of habitats. It is a generalist herbivore, preferring herbs and deciduous browse. The roe deer is described as a seasonal breeder with approximately 80 % of populations births synchronized within 20-30 days (Linell 1998). The roe deer is a typical hider species, hiding fawns in vegetation until the fawns reach an age of approximately 8 weeks. Hiding behaviour in fawns is a strategy against detection by eventual predators adapted for living in dense habitats (Lent 1974).

Hunting roe deer was in historical times only permitted to the noble of Sweden. A former king ended that legislation 1789 to the benefit of taxable property-owners. The new legislation resulted in depleted deer populations next to extinction. By 1850, the Swedish roe deer population consisted only of a couple of hundred individuals on protected properties in Övedsklosters countryseat (SJF 2012). However, concurrent extermination of large predators and removal of livestock from forest grazing resulted in a following population growth and dispersal. The population increased even more in the 1980's and 90's and peaked in 1993 when the hunting bag was 390 000 animals (SJF 2008). Possible explanations for the population increase are several mild winters and the outbreak of sarcoptic mange that reduced the red fox population, as red fox (*Vulpes vulpes*) is a severe predator on roe deer fawns (Lindström *et al.* 1994; Kjellander & Nordström 2003; Jarnemo & Liberg 2004). From the 1993 peak a major decline has been observed and today's hunting bag is about 100 000 animals (SJF 2008). Winter starvation, red fox and European lynx (*Lynx lynx*) predation, is the major mortality causes for roe deer in Sweden (Aguirre *et al.* 1999; Jarnemo 2004; Nordström 2010).

Interspecific relationship

Species interactions alter as environmental factors change, for example, introduced species integrating with native fauna (e.g., American mink (*Mustela vison*)), and recolonization of species that have been absent (e.g., Wolf (*Canis lupus*)). In ecosystems where wild boar is treated as an invasive species, managers and ecologists have questioned its competitive and predatory role in native systems (Taylor & Hellgren 1997). Wild boar may, according to studies made on ecologically equivalent feral hogs and introduced European wild boars in North America, be capable of competing with small to large-sized ungulates and feed on small vertebrates and invertebrates (Taylor & Hellgren 1997).

Further, studies report that ungulates habituated to a predator-free environment lack a proper behavioural response when encountering potential predators (Blumstein & Daniel 2005; Sand *et al.* 2006). Because wild boar were extinct from mainland Sweden for 200 years, it is possible that roe deer display a “naive” behaviour against wild boar when sharing habitat. Yet, even though wild boar is regarded as a part of native fauna, the importance of its impact on other ungulates is poorly understood (Taylor 1997). Most documented wild boar impacts in northern European ecosystems only cover disruption of vegetation succession and damage of resource-product industries (e.g., forestry and agriculture; Welander 2000).

Competition

Coexistence between wild boar and roe deer was part of a natural state (since the end of the last ice age), before the extinction in the 17th century (SJF 2012). As species share habitat and at the same time has a large population size, they evolve certain interspecific relationships (facilitation, mutualism, predation, competition, etc.) (Gause 1934; Crombie 1947). Studies from the African savannah (Odadi *et al.* 2011) report that ungulate interactions can sometimes be more facilitative than competitive. Nevertheless, the level of competition is depending on the availability of food or habitat and to what extent the species share those resources (Stewart & Levin 1973; Pianka 1983; Ilse & Hellgren 1995). Thus, the capability to coexist within a particular area is dependent of the species ability to partition resources, spatially or temporally.

Schoener (1983) describes that competitive interactions can be expressed as direct (interference interaction), when a resource is actively disputed over due to dominance by one species, or indirect (exploitative competition). Interference interaction over available resources will affect the less competitive species' fecundity, survivorship or growth (Connell 1983).

Because of wild boar having a larger body mass, displaying grouping behaviour, and opportunistic food habits (Nyman 2002), they are assumed to be a competitive superior to small and medium sized ungulates (Taylor 1997). Amarasekare (2002) stated that a “*species that is dominant at both resource exploitation and interference could exclude another species regardless of whether interference is costly or beneficial*”.

Body mass has been suggested as an important factor in interference competition, larger species usually being the superior one (Connell 1983; Schoener 1983). Barret (1982) saw that interference competition between ecologically similar white tailed deer (*Odocoileus virginianus*) and feral hogs increased with higher densities of pigs (deer withdraw in confrontations with pigs). Further, Pellerini (1993) reported that roe deer avoid wild boar feeding areas, and according to Latham (1999) roe deer is relatively susceptible to competition from other ungulates. For instance, they abandon feeding spots when groups of the larger fallow deer show a dominant behaviour (Ferretti 2008).

Predation

For long it was supposed that chimpanzees (*Pan troglodytes*) were an omnivorous herbivore. Nonetheless, ethological studies reported that the opportunistic primate predated on smaller monkeys (Teleki 1973). Similarly, diet studies of feral hogs in North America reports that they eat small on and underground-living vertebrates, invertebrates, and most likely white tailed deer fawns and livestock new-borns (Hellgren 1993; Asahi 1999). There is however very little research investigating wild boar predation on wild life juveniles. Nevertheless, birthing-grounds of sheep (*Ovis aries*) attract feral hogs where they eat new-born lambs and fetal tissue. Feral hog predation was reported to 32% of all new-born lambs in a year, the predation rate was also density dependent, thus more lambs were killed in areas with high pig density (Choquenot *et al.* 1996). Furthermore, a rare study targeting European wild boar predation showed that they could be a major predator on eggs and chicks of ground nesting birds (Calderon 1977).

Wild boar and feral hogs is according to studies (e. g. Calderon 1977; Hellgren 1993; Choquenot *et al.* 1996 & Asahi 1999) most likely to be opportunistic, feeding on animals when opportunity occurs. Hidden roe deer fawns might face the risk of getting detected by travelling groups of wild boar if they use the same areas. Hiding of fawns is an anti-predatory strategy to avoid predation by predators that first observe and then attack their prey (Lent 1974). Hidden fawns without a protecting mother in the immediate vicinity are susceptible to predation when discovered by a predator.

Roe deer serves as an economically important game species in Sweden and the economical importance is linked to the abundance. The major population decline in the last twenty years is most probably caused by the re-entry of lynx, which acts as a new major

predator on roe deer neonates (Nordström 2010) as well as all other age classes (Aanes *et al.*, 1998). But as the decline has also occurred in areas where lynx are not yet present, there must be some other factor negatively affecting the roe deer population.

I assumed that abundance of roe deer might decrease if wild boar acts as a strong competitor and possible predator. That would be a concern for landowners, sportsmen and ecologists that have shared interests in roe deer populations in areas that inhabits wild boar too. The roe deer project on Bogesund was initiated in 1988 with the intentions of enhancing the ecological knowledge of roe deer dynamics. The scientifically based knowledge acts as a foundation for future conservation and management actions. Present wild boar occurrence has forced the scientific community to improve the understanding of the coexistence between the two species. In this study I have received data from a 3-year wild life camera survey in order to evaluate interspecific competition between roe deer and wild boar. No former study has specifically quantified the possible competition between wild boar and other ungulates, although Singer *et al.* (1981) and Massei *et al.* (1996) mentioned that competition between wild boar and various mammals is likely to occur.

Objective

Based on the fact that the roe deer population has decreased in parts of Sweden without re-colonizing lynx I hypothesised that the predatory and competitive behaviour of wild boar can be related to the decline. Specifically, in order to test the hypothesis I predicted that: 1) Wild boar should kill roe deer fawns, 2) Roe deer fawns should show a non-random movement pattern in relation to wild boar activity, 3) Fawns home ranges should be situated further away from areas with high wild boar activity compared to low activity areas, 4) Roe deer adults should avoid areas with wild boar and the avoiding distance should be related to wild boar activity, 5) There should be a temporal separation between roe deer and wild boars utilization of the same habitat.

Study Area

The study was performed at Bogesund, a 1 300 ha peninsula within the hemiboreal zone, located (59 24`N, 18 12`E) about 20 km north of Stockholm (Fig. 1). Landscape consists of forest (65%), farmland (25%), and bogs and bedrock (10%). Dominating trees are conifers like Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). But deciduous stands of willow (*salix sp.*), aspen (*populus tremula*), oak (*quercus robur*), ash (*Fraxinus excelsior*) and birch (*Betula spp.*) are also present within the area. Farming cultivates wheat (*triticum sp.*), oats (*Avena sativa*), rape (*Brassica napus*), clover (*trifolium sp.*) and hay. Some farmland is used as pastures for mainly horses and some sheep (Jarnemo 2004).

The wild boar population on Bogesund consists of animals from adjacent areas that have immigrated in recent years. The population was by 2010 estimated to vary between 100-150 animals (Anon 2010).

The roe deer population on Bogesund consists of a couple of hundred individuals according to pellet group counts (Kjellander & Nordström unpubl.). Roe deer are generally living solitary or in small groups of two or three individuals composed of an adult female with her fawns, possibly accompanied by an adult male, although larger groups may aggregate next to feeding stations in winter. The roe deer population on Bogesund is well studied by the Swedish roe deer project, which has provided plentiful of valuable ecological knowledge to wildlife management since 1988. Both wild boar and roe deer is treated as game species and a hunting division linked to the Swedish hunters association runs the wildlife management on Bogesund. At wintertime wild boar and roe deer are supplementary fed at several feeding stations randomly distributed within the study area.

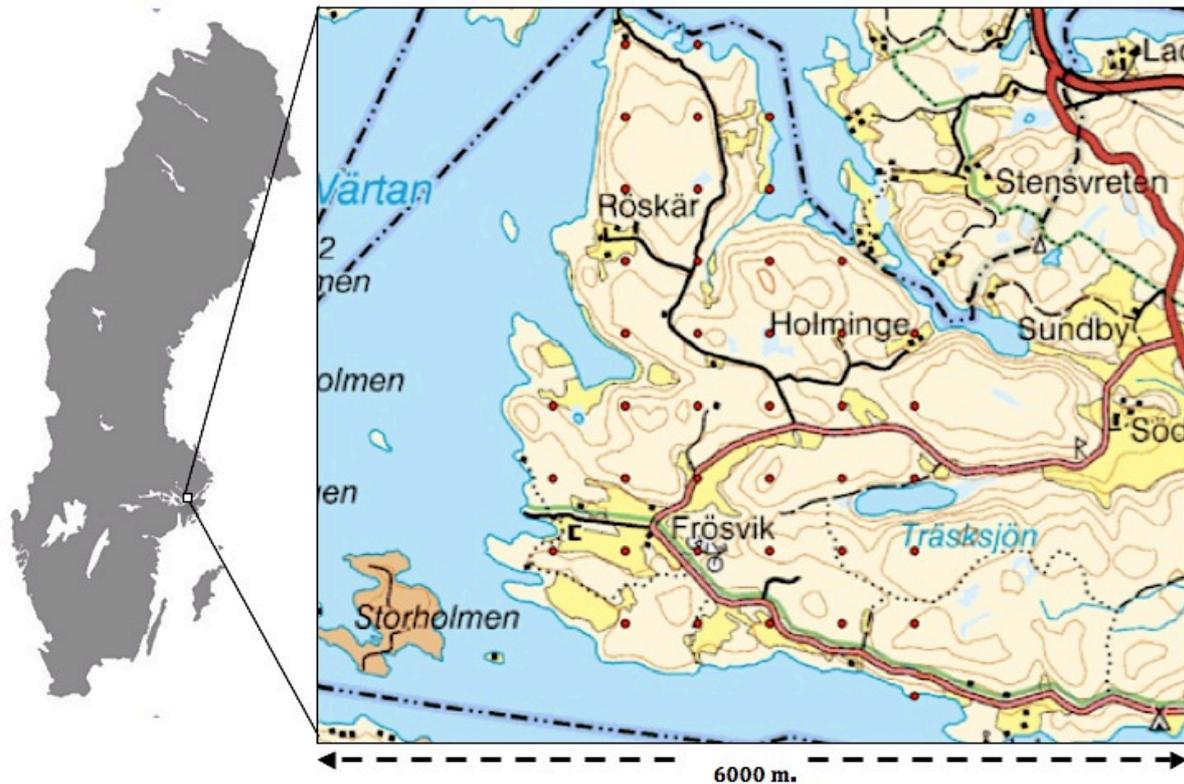


Fig. 1. Enlargement shows my study area at Bogesund, Sweden. Red dots represent wildlife camera distribution over the study area.

Methods

Roe deer fawn mortality

Data for this part of the study was collected on Bogesund during June and July 2011 mostly by driving in cars or waiting in places where does previously had been observed. Bogesund and its surroundings are during great parts of the year used for recreation activities. Roe deer may therefore show some tolerance to cars and human activities, which may have facilitated our car stalking when catching fawns. Working hours was linked to roe deer activity (e.g. 04.00-07.00 and 19.00-22.00). Roe deer fawns were captured by hand, mostly after observing does.

Observed does' status of pregnancy was determined. Does' udders and bellies were categorized into classes 0-3 by estimating the size in order to predict the chances of a

doe having partitioned. For example, a female with a thin belly (0) and an enlarged udder (3) was the best candidate for having a hidden fawn nearby.

After spotting a doe that was suspected to have fawns, the nearby surroundings were carefully searched for hidden fawns. Alternatively, does were watched until they visited fawns for suckling which occurs 2-7 times a day, where after fawns were approached and marked in their bed-site. Fawns were caught by hand and the sex, length of metatarsus and body mass was determined. The outer part of the ear was cut for further molecular research to determine kinship amongst individuals. The corresponding ear was equipped with an 5 mm numbered ear clip for future visual identification if the fawn gets killed or caught in a box trap later in life. Fawns were also equipped with radio transmitters attached to an expandable collar (VHF transmitters; Followit, Lindesberg Sweden THX-2). The collars weighed 65-70 gram and had a signal range of up to 1,5 km and a battery life of approximately 6-18 months depending on model year. Collars were designed to drop off within 1-2 years. All transmitters had a mortality function (motion sensitive). The signal per minute rate increased from 40 to 80 if no motion was registered for five hours.

We monitored fawns using a RX 98 receiver (Followit, Lindesberg Sweden) and a handheld 4-element Y-4FL antenna (Followit, Lindesberg Sweden). The fawn's location was determined by triangulation from three separate points along a trail or road easy to pinpoint on map. If an animal's location was difficult to determine by triangulation we were content with cross-tracking. Date, time, roe deer ID, radio collar frequency and compass bearing were recorded. The set position was plotted to a paper map along with time etc. If a marked fawn were spotted during tracking we ignored tracking and used the visual position. In case of getting a mortality signal during tracking we searched for the transmitter and analysed the site for tracks or scats from a predator. We looked for bite marks and other signs of possible predation on the transmitter collar. In case we found a dead fawn on the kill site, we necropsied it to be able to determine cause of death.

Wildlife Camera Study

In order to provide data on roe deer and wild boar habitat use and activity patterns we used wildlife cameras (Scoutgard, SG550V). About 40 wildlife cameras were set through 12 trap nights in June from 2009-2011. The cameras were passive infrared cameras equipped with a 2 GB memory card to guarantee a high number of photo captures. The cameras function independently of each other and measure motion and temperature in a targeted area via a heat and motion sensor. When an animal passes in front of the camera, the sensor detects motion and temperature changes and the camera is triggered to take a series of three photographs, then pause for one minute before taking an additional series of photographs if an animal still moved in front of it. Cameras take colour photographs by day and infrared by night.

Cameras were set up at a height of approximately 25-40 cm and were programmed to run continuously for 24 hours. 50% of cameras were rigged on trees opposite to artificial rubbing trees, i.e. a tree with applied tar at correspondent height as camera. Wallowing and rubbing is a daily ritual for wild boar, which helps them to reduce parasites and ticks attached to their skin.

Cameras were placed systematically in a grid with approximately 500 meters between cameras within the western part of Bogesund (Fig. 1). A photo series is from now on referred to as one capture. Both time and date was visualized in the lower corner on each picture. As my aim was to investigate temporal activity and habitat use, every roe deer capture was treated as one individual observation in the analyses. Same capture treatment was likewise used for wild boar captures.

Pellet group count and wild boar rooting survey

I was provided data from a roe deer faecal pellet-group count census including a rooting census because I wanted to estimate in which areas wild boar and roe deer were active (Kjellander & Nordström unpubl.). The pellet group count at Bogesund had been executed adjacent to snowmelt in early spring 2009-2011 and according to a protocol by Cederlund & Liberg (1995). Approximately 600 coordinates determining the centre of 10 m² circular plots were searched in order to count pellets of roe deer, hare and moose. The plots are positioned along 12 transects with an equal (400 m) distance between

them. During walking along transects, position, number, and length of wild boar rooting's in an 10 m wide transect was also documented. The roe deer pellets and wild boar rooting locations were recorded (<10 m accuracy) in RT90 coordinates with hand-held Global Positioning System (GPS) units (Garmin). These positions were later transferred into ArcView (Geographical Information System (GIS; ArcView 9. 3, Environmental Systems Research Institute, Inc., Redlands, CA) for further analysis.

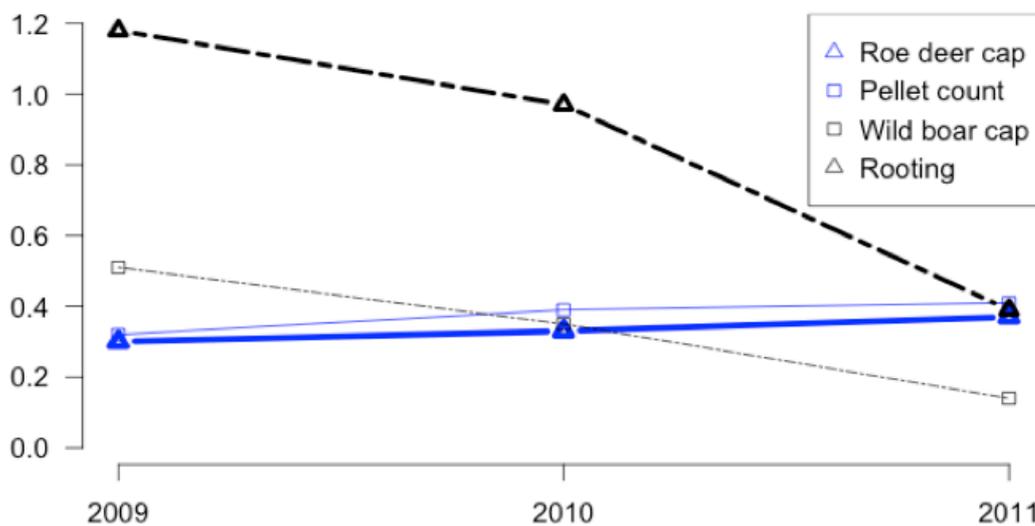


Figure 2. Annual local abundance of wild boar (black lines) and roe deer (blue lines) 2009-2011 based on roe deer pellets, wild boar rootings and camera captures of both species.

Number of roe deer pellets from pellet group count was divided with the number of squares to get an index of roe deer population (Kjellander 2000), and the number of wild boar observations (captures) was for each year divided with the mean length of same years wild boar rootings to get the rooting index for wild boar. Captures of roe deer and wild boar was divided with the total amount of captures to get two additional index of the species.

Analyses

VHF Study

Radio tracking positions for each fawn were exported to ArcView. When using kernel density estimator in Hawth's tools (Beyer 2004) it was possible to create home ranges on the 95% level for each fawn. The 95% fixed kernel method of home range analysis was used because it is less affected by outliers and sample size, and gives a more illustrative description of home range use and area. However, it can be difficult selecting a proper smoothing factor, because size of the home range increases significantly with an increase of the smoothing factor (Row & Blouin-Demers 2006).

There are several described methods of how to calculate smoothing and scaling factor. I choose to use minimum convex polygon (Hawth's tools) as the area of the home range and thereafter adjust the smoothing factor until the area of the 95% kernel equalled the area of the MCP (Row & Blouin-Demers 2006).

To obtain distance measurements I calculated the centroid position of each fawn home range (N=12). Home range centroid points were used to measure distances between fawn home ranges to wild boar rootings, wild boar camera captures and feeding stations. Because a control group was necessary I created corresponding artificial centroid points (N=12). With the tool generate random points (ArcView; Hawth's tools) 12 points were randomly distributed over the research area. To avoid the risk of the random centroids getting clumped, the minimum distance between them was set to be no smaller than the smallest distance between observed home range centroids. The purpose of this was to mimic observed conditions as far as I could.

From each centroid point I measured (Hawth's tools; Distance between points) distance to the closest wild boar rooting, wild boar photo capture, and feeding station. In the statistical analysis I used students t-test to evaluate eventual differences in distance to areas of wild boar activity between random and observed home range centroid points. Before analysis, distance data were checked for normality using Shapiro test. Because unequal variance was rare in data, transformations did not improve the outcome, so I used untransformed data for analyses. Simple linear regressions were used to analyse if size of wild boar rootings or frequency of wild boar captures affected the distance to fawn home range centroid points.

Camera Study

Activity pattern

Photo captures were analysed in line with my prediction that roe deer and wild boar activity patterns differ. I started the analysis creating a 24-hour pattern for the two species. However, problems may occur when analysing circular data. In a normally distributed curve are hour 0 and 24 placed in opposite ends, which will result in analytical problems. A circular distribution where hour 0 and 24 is next to each other is more representative in analysis. To avoid analytical problems I converted time of photo captures into 24-hour circular data for further analysis. In order to detect eventual circular

distributional differences between the two species I performed a Rayleigh's test. Rayleigh's test is a test for uniformity that trial H_0 : a uniform distribution around a circle, thus, a unimodal distribution with unknown mean direction and unknown mean resultant.

Wild boar and roe deer photo captures were treated as effective working hours and classified into hour intervals based on the time printed on each photograph, night [22:00-03:59]; dawn [04:00-09:59]; day [10:00-15:59]; dusk [16:00-21:59] (Tab.1). The relationship between number of captures and activity patterns were tested for independence performing a chi square test.

Spatial patterns

I started the spatial analysis by investigating if the frequency of photo captures were different between cameras at tar trees and cameras at control sites. The analysis was computed by taking the classified intervals of camera captures, for each species separately, and looking for differences between sites by using a chi square test. To investigate if roe deer avoid sites with signs of increased wild boar presence, I measured the distance from each roe deer capture to the closest wild boar rooting and wild boar capture. The effects of wild boar rooting size and camera capture frequency on distance to roe deer captures and positions of plots with roe deer pellet was analysed using simple linear regressions. I checked for normality and homogeneity of the data by looking at plots of residuals against fitted values and performed a Shapiro test. Throughout the paper, I present P -values that are considered significant at the $\alpha = 0.05$ level.

All data in this study were analysed using R (R Development Core Team, 2009) with package *circular* (Lund & Agostinelli, 2011)

Results

VHF Study

Fawn tracking survey totalled 636 hours. The number of fawns marked was 14, whereof 12 equipped with radio transmitters. I collected an average of 37.5 locations (range 25-58 points) for each fawn (N = 12) (Appendix I. Fig. A). The average size for fawn home ranges during the radio tracking period was calculated to $0.207 \pm \text{SD } 0.08 \text{ km}^2$ (range 0.06-0.35 km^2). No roe deer fawn could be confirmed as killed by wild boar, but fawn mortality was 33% (4 of 12 marked fawns). Red fox (most possibly) killed 2 fawns during the time when fawns are most susceptible to predation (< 8 weeks of age). Two fawns were found dead or killed after 8 weeks of age through lynx predation and hunting during the hunting season in the autumn.

Frequency of wild boar records was greater (Chi square test; $\chi^2 = 22.3$, $P = < 0.001$) at rubbing trees (142) than on control sites (42) (Tab.1) implying the expected high preference for rubbing trees by the boar. However, the distance between the closest rubbing tree and the observed fawn home range centroid points were not significantly longer ($1030 \pm 353 \text{ m}$) (mean+ s.d) than from artificial centroid points ($814 \pm 265 \text{ m}$) ($t = -1.82$, $df = 24.12$, $P = 0.08$) (Fig. 3). Mean distance to the closest control camera from observed fawn home range centroid points was shorter (226 m) but not significantly different between the two groups (Fig.3) ($t = 0.23$, $df = 25.91$, $P = 0.81$).

Further, mean distance to closest wild boar rooting was significantly greater from observed home range centroids ($657 \pm 248 \text{ m}$) ($t = -2.37$, $df = 25.1$, $P = 0.02$), than from artificial centroids ($457 \pm 201 \text{ m}$). The distance to closest wild boar feeding station was not significantly different between observed and artificial home range centroid points ($t = 0.72$, $df = 25.90$, $P = 0.47$). I used simple regressions in order to discover if wild boar frequency (measured as nr of wild boar captures per camera) affected distance to fawn home range centroids. The linear regression showed no relationship ($R^2 = 0.03$, $df = 12$, $P = 0.24$) between number of wild boar captures and the location of observed home range centroids. Further, the size of wild boar rooting did not seem to have any impact on fawn location ($R^2 = 0.08$, $df = 12$, $P = 0.16$).

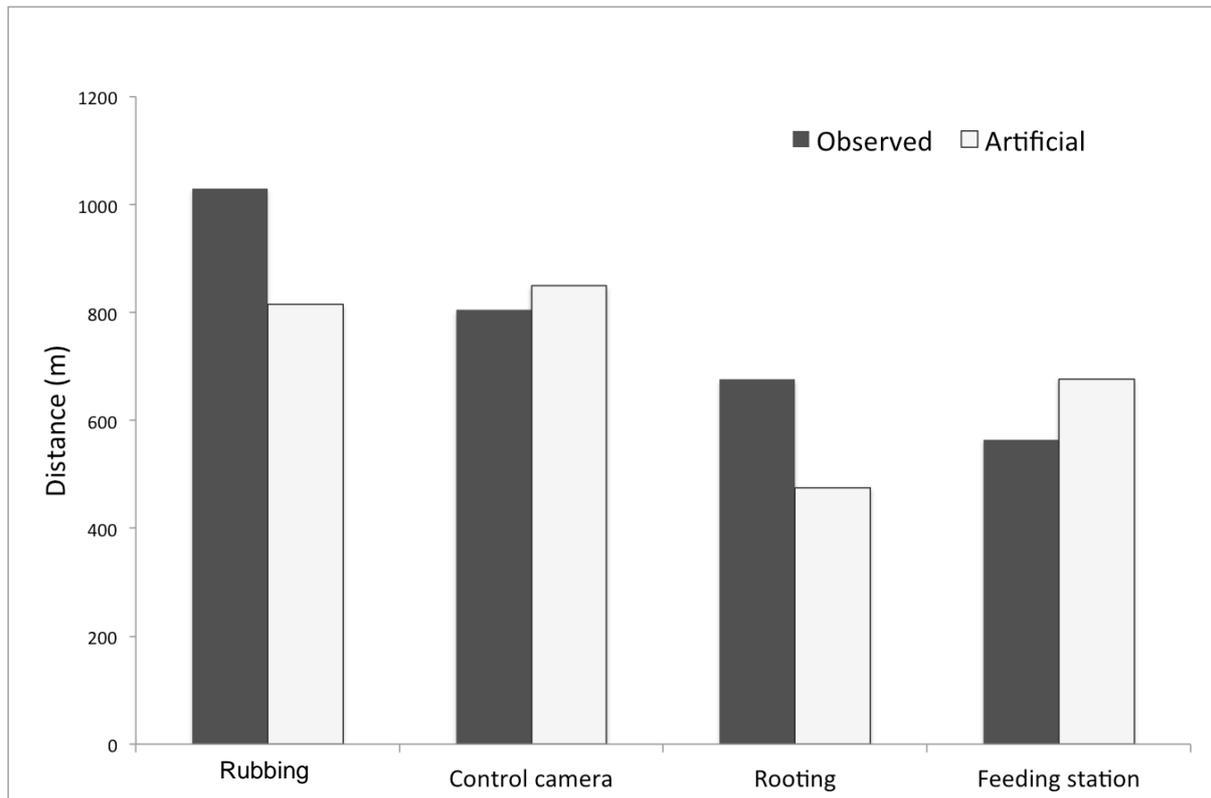


Figure 3. Mean distances to places of wild boar activity from observed and artificial home ranges of roe deer fawns on Bogesund, summer 2011.

Camera Study

The camera-trapping stations covered a minimum-convex polygon area of average 6,61 km² (varying size of camera grid because of varying number of cameras between years). The sampling effort of 1200 camera-trap-nights (39 traps in 2009, 29 traps in 2010 and 32 traps in 2011 all set up 12 days each year) resulted in a total of 188 photos capture of wild boar and 204 photos capture of roe deer (Tab. 1).

Table 1. Roe deer and wild boar temporal (classified intervals) and spatial (rubbing and control) distribution at a wild life camera study, Bogesund 2009-2011.

| Time of day | Roe deer Tar tree | Roe deer Control | Wild boar Tar tree | Wild boar Control |
|-------------|----------------------|---------------------|-----------------------|----------------------|
| Night | 24 | 39 | 16 | 10 |
| Dawn | 19 | 39 | 3 | 6 |
| Day | 8 | 15 | 48 | 15 |
| Dusk | 27 | 32 | 75 | 10 |

Spatial distribution

Roe deer photo capture frequency was significantly lower at rubbing trees than expected (Tab. 1) (Chi square test; $\chi^2 = 5.05$, $P = 0.02$). There were no indications that the frequency of wild boar from nearest capture affects the distance to photo captures of roe deer (Linear model; $R^2 = 0.0019$, $df = 200$, $P = 0.43$). Nor did the size of nearest wild boar rooting yield any significant effect on the distance to roe deer captures (Linear model; $R^2 = -0.003$, $df = 200$, $P = 0.55$). Further, size of wild boar rootings seemed to affect the distance between rootings and pellet group count plots with roe deer pellets but with a very low R squared value (Linear model; $R^2 = 0.04$, $df = 200$, $P = 0.002$) (Appendix II. Fig C).

Temporal distribution

Rayleigh's tests showed that wild boar have a rather uniform distribution over day ($P = 0.073$) while roe deer differed from the assumption of uniformity (unimodal distribution) ($P = < 0.001$), showing more of a bimodal distribution. Based on the result of Rayleigh's test, I tested the goodness of fit between records and periods of activity and found that they were statistically independent ($\chi^2 = 38.92$, $P = < 0.001$), indicating that the two species have different activity patterns. The two species concentrated most of their activity from dusk till dawn, but varied in their daily activity. The activity of wild boar had a peak in afternoon (Fig. 4, Tab. 1). While roe deer had two activity peaks, one in the morning and another at late evening (Fig. 4. Tab. 1).

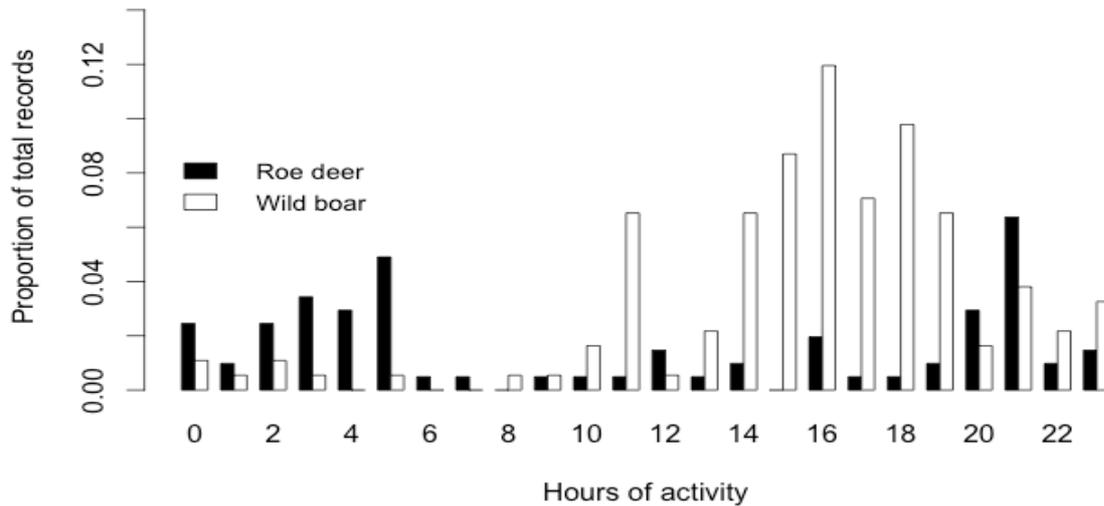


Figure 4. Activity patterns of roe deer and wild boar in spring at Bogesund 2009-2011. Shown as proportion of total captures for each species

Discussion

VHF Study

Predation

I was not able to support my prediction (1) regarding predation on roe deer fawns. Even though radio marking is an appropriate way to monitor mortality there are several explanations for this result. Primarily, a large sample size is a nice tool for absorbing rare events in a greater population (Raudys & Jain 1991). My sample size is most likely too small ($N = 12$) to detect mortality caused by wild boar predation, especially if this is a rare event. It is also possible that the focal year's low wild boar activity (Fig. 2) did not result in a demonstrable predation rate. Based on wild boar captures and rootings of 2011, the wild boar density is roughly estimated to be lower than previous years. Correlated predator density and consumptive impact have been shown in another study (Arditi & Ginzburg 1989). Additionally, Choquenot *et al.* (1997) reports that lamb loss in sheep increased with increased pig density above a threshold. His experiment showed that predation was non-existent when pig density was low (0.4 pig/km^2) but

Increased with higher densities (5.8 pig/km², predation rate 29%). The wild boar density on Bogesund was 7 - 7.6 individuals/km² (2009) based on a crude estimation of population size of a hundred individuals on Bogesund (Anon 2010) + (2009 camera survey).

Further, hunters on Bogesund have found hooves of roe deer fawns in wild boar scats (Anon 2011), but difficulties appear when rejecting scavenging as an explanation.

During the study, one third (n = 4) of the radio-marked fawns were killed, whereof two fawns during the period when fawns are most exposed to predation by red fox (Jarnemo 2004). Causes for mortality was, fox, most probably lynx (a rare event at Bogesund which holds no resident lynx), hunting, and unknown (only transmitter found). In the latter occasion, the event occurred (25th of June) during the time when fawns are most exposed to predation by red fox, the location resembled that of a kill site, but without any remains of the body. Australian and Texas feral hog managers describes that hog predation can be hard to detect because hogs often eat the entire animal, leaving little or no evidence. A missing carcass is, however not uncommon in case of red fox predation either and after a molecular examination of remaining DNA on the collar could wild boar be ruled out as the cause of death while neither fox nor dog could be excluded (Åkesson & Hedmark unpubl.).

Furthermore, radio marked fawns was maybe to old being targeted as a potential prey for wild boar. The mean age of fawns at marking time was 11,5 days, based on their weight, and several of them were able to run before and after marking. Pavlov (1981) reported that lambs chased by pigs were never caught when the distance or duration of the chase exceeded 40 m or 10 sec, respectively. He concluded that the probability for a lamb evading capture was a function of the lambs size and strength. Wild boar is attracted to animal tissue and mainly predate on animals with less mobility (i.e. bird nests, small on and underground mammals, new-born live stock, and injured and sick individuals) (Hellgren 1999; Anon 2012). Hence, maybe I measured survival on fawns that had already evaded wild boar predation risk.

Practical problems then occur on how to radio mark fawns immediately after birth in order to identify wild boar predation before fawns grow too large. One way of doing so may be to monitor roe deer does equipped with GPS transmitters. When females shrink

down their home range in order to give birth, the time and place of fawning will be easily detected and make it possible to mark the fawn at an earlier age.

Moreover, it is possible that several factors (time of day, habitat type, distance to roads, and human activity) related to position of fawn affects fawn survival when wild boar is present. This can be supported by an Australian study (McGaw & Mitchell 1998), which reported that habitat type preferred by feral hogs is related to pig density, which in turn is related to predation rate as explained above. Alternatively the non-existent predation by wild boar in this study can simply be explained as a non-predatory behaviour by wild boar in general. Nevertheless, the question of wild boar predation is difficult to reject with knowledge of feral hog predation on lambs for example. No scientific studies regarding wild boar predation on small to large sized ungulates has been reported from places where the species belongs to the native fauna, but that does not necessarily mean that it does not exist, just that no one has studied the phenomenon.

Spatial use

Roe deer fawns tend to be spatially segregated in relation to wild boar activity (prediction 2). The non-random movement of fawns is related to wild boar rooting's (significant) and rubbing trees (nearly significant). Highly interestingly, I found that fawns displayed a random movement pattern in relation to the control cameras (42 wild boar captures). The mean distance was on average 200 m shorter to control cameras compared to rubbing trees, providing support to my third prediction that roe deer might be disturbed (interference) by increased wild boar activity. The greater distance between observed fawn home ranges and sites with wild boar activity as opposed to randomly distributed home ranges also imply seasonality in spatial segregation. The reason why does would avoid wild boar in the fawning season can be found in the U-shaped mortality pattern of ungulates in the absence of large carnivores (Coughley 1966). Being a fawn is simply a risky thing, why does would benefit hugely in lifetime reproductive success from avoiding areas of elevated risk for predation, interference and displacement during the fawning season (Appendix Fig. A, B). Seasonal spatial segregation is rarely described for ungulates, although, seasonal spatial segregation between two competitive species of small mammals is reported by Glass (1980) who saw that one species withdraw in the onset of reproductive season.

Roe deer females with offspring showing little mobility, will limit their home range size (Saïd 2005) and the trade-off between high quality forage and the risk for neonatal predation determines the size and location of the home range (Jarnemo 2004; Saïd 2005). Latham (1999) describes that roe deer in general is sensitive to interference interactions and Focardi *et al.* (2006) showed that roe deer is displaced into less favourable spots when sharing habitat with high densities of fallow deer. Predation risk might not be the only reason why a doe would avoid areas of intense wild boar activity as wild boar makes lots of noise during foraging and rooting, and the disturbance caused by this might render the doe less prone to discover stalking predators as lynx.

Surprisingly and contrary to my prediction 2, no significant non-random patterns of fawn locations was shown in relation to the closest supplementary feeding sites intended for wild boar. Possible explanations can be that feeding stations happens to be located at a particular distance from fawn positions that it is not fearful enough. Because managers determine the location of feeding stations, surroundings may not be associated with a general wild boar habitat use. Wild boars that travel between feeding stations may not use the surroundings for foraging because they have a sufficient amount of food at feeding stations. My analysis also showed that the observed fawns' home range centroids were situated closer to feeding stations compared with artificial centroids, implying that feeding stations may in fact attract roe deer. Roe deer has been seen to use feeding stations for wild boar especially in scarcity of food. However, other studies (Pellerin 1993; Feretti *et al.* 2008) have opposingly reported that roe deer avoid feeding stations when groups of wild boar and larger ungulates are present.

The relationship between wild boar frequency (number of wild boar captures and rooting size) and the distance to fawn hypothesized by me (prediction 3) could not be confirmed with the analysis I performed. Even though the longer distance to rubbing trees (Fig. 1) indicates that high wild boar activity areas is more avoided by fawns. Cameras with wild boar captures closest to fawns were all low wild boar activity areas (1-2 wild boar captures). This makes it virtually impossible to quantify the effect a gradient of wild boar frequencies would have on the distance between fawn home ranges and places with wild boar activities. It does however imply that roe deer does choose to give birth to their fawns at quite a distance from sites where wild boar often appear which supports my prediction (3).

Moreover, one reason for the fact that location of fawns is not directly affected by rooting size may be the timing by which these indices of wild boar activity were collected. Wild boar rootings are surveyed in spring but reflects wild boar activity throughout the winter, why many of the rootings reflects historic wild boar activity with little or no effect on roe deer does' assessment of risk in the fawning season. Photo captures on the other hand are collected in the fawning period and a site with high frequency of wild boar photos is more likely to be viewed as a high risk environment by does. I would maybe have received a more equitable result if only rootings made in the fawning season were surveyed.

My intention by radio marking fawns was to achieve a random distribution of marked fawns in the research area. I surveyed large parts of the study area, including interior forest trails and areas away from roads and open habitats, but found all fawns near roads (< 100 m) in open habitat or along edges between forest and field. This may have biased my sample towards fawns that predominantly use such habitat. Wild boar is treated as more or less forest dwelling based on that photo captures and rooting's were mainly recorded in forest habitats. Thus the risks for marked roe deer fawns in open habitats to be affected by wild boar activity might be less, as compared to forest-dwelling fawns supposedly closer to wild boar activity. However, all radio-marked fawns had home ranges covering both open and forested land so I considered them representative for the total fawn population with respect to possible predation risk by wild boar.

The risk for predation should also be equal between fawns because wild boar is covering large areas overlapping fawn home ranges in search for primary food. Moreover, wild boar is a forage generalist and predation by generalists do not occur through directed search for prey in prey-specific habitats, but through incidental encounters when generalists are engaged in search for primary food sources (Schmidt *et al.* 2001). I propose that marked and unmarked roe deer fawns are not separated by habitat preferences and thereby limit the risk for my sample being biased.

My findings partly support the prediction (2 & 3) that roe deer fawns may be disturbed or displaced by wild boar activity. During fawning season does possibly select habitats with less wild boar activity (Appendix Fig. B). Then the question arises whether this is a disadvantage for roe deer females or not. Are roe deer avoiding areas that otherwise

would have been beneficial for them? Jarnemo (2004) found a higher risk of predation by red fox in open habitat at high fox density. If roe deer does are relying more on open habitat for rearing their young after the return of the wild boar, then their fawns will be more susceptible to red fox predation when the red fox population density is high. Hence, displaced roe deer might experience a lower yearly reproductive success because of the increased risk of red fox predation. However, in this study red fox predation on roe deer fawns was relatively low and similar to predation-rates from earlier studies within the same area (Jarnemo 2004). This might be explained by the low fox index this year, calculated as number of foxes observed per manday in field during fawn catching. Red fox index during fawning period of 2011 was calculated to 0.13/manday and 33 % of the marked fawns was killed by red fox. Compared to Jarnemo (2004) who noticed during fawn catching period on Bogesund that 36 % of marked fawns was killed at a red fox density of 0.15 fox/manday in 1998. The roe deer recruitment in wild boar areas needs however to be further investigated. One way of doing this is investigating the reproductive success in a roe deer population before and after re-colonization of wild boar.

Camera study

Spatial patterns

I found a significantly lower roe deer occurrence at rubbing trees than on control sites (Tab. 1), suggesting that roe deer adults avoid sites of high wild boar activity (prediction 4), possibly because of disturbance. The greater roe deer abundance at control cameras may be explained by that roe deer wants to forage in areas without being disturbed by wild boar. Ferretti *et al.* (2010) showed that when roe deer foraged in food spots without fallow deer, the time spent foraging on that spot increased significantly, compared to spots where roe deer were frequently encountered by groups of fallow deer. He concluded that spatial avoidance was a way to increase the time spent on foraging. Roe deer is an income breeder, meaning that they maximize their foraging concurrently with breeding, without relying on stored reserves (Andersen *et al.* 2000). Reduced food consumption, depending on season, affects roe deer's reproductive success (Pettorelli *et al.* 2005). Continuous occasions of feeding displacement through interference interactions may decrease the total time that roe deer spend on foraging because roe deer are forced to abandon feeding grounds. Displacement to areas with lower wild boar

density might also result in decreased foraging because the intraspecific exploitative competition is bigger in areas with high roe deer densities (Kjellander 2000).

Unfortunately, when analysing my fourth prediction, I did not find any relationship between increased wild boar activity (number of captures and rooting size) and distance to roe deer camera capture positions. Negative results can be hard to explain because they might depend on different methodological procedures, which always can be improved. For example, the fact that roe deer was not individually identified at photo captures might increase the risk that the same animal is captured multiple times close to, or at same cameras with high wild boar activity. The risk of pseudo replication might mask the effects of a general roe deer spatial avoidance towards high wild boar frequency because of a few tolerant individuals. Secondly, it is also possible that a more fine-grained camera grid would detect evidence of roe deer spatial avoidance in a better way.

Finally, it is also possible that the data collected in different seasons (cameras in June and rooting survey covering the fall-spring boar activity) mask an eventual growing gradient of avoidance between roe deer captures and larger wild boar rootings. Moreover, a gradient of avoidance by roe deer against increased wild boar frequency may be masked because of the low level of exploitative competition (due to relatively small overlap in diets and the amount of available resources in summer). This supports the hypothesis that temporal or spatial displacement during fawning season is caused solely by direct interactions (interference interactions).

Although there was a significant effect of rooting size related to the position of roe deer pellets, it was linked with a low grade of explanation ($R^2= 0,04$) (Appendix Fig. C). Such result is difficult to interpret and the result must consider with caution. Nevertheless, the significant position of the Y-intercept (expected mean value of Y when all X=0) from the model indicates that roe deer pellets in general is placed 487 meters away from wild boar rootings. It is possible that rooting size affects the distance to positions of roe deer pellets because the data was here collected in the same season. But it seems equally likely that several additional factors not investigated in this study and not necessarily related to wild boar influence the distance. Nevertheless, results imply that roe deer may associate wild boar rooting areas with an increased risk of being disturbed. Hence, an area with rootings is linked with a general risk being encountered by wild boar and

not so much to the size of rooting. Suggesting that roe deer spatially avoids rooting areas irrespective of size.

Temporal patterns

I did find patterns of temporal avoidance between roe deer and wild boar (prediction 5). I suggest that avoidance is active rather than passive, because the two species use the same habitat and the camera period was limited, so thereby I can reject different habitat preferences and seasonality's in activity. The difference in daily activity patterns is not total, roe deer and wild boar are active during the same hours but with different frequency. This means that one species for unknown reasons choose to avoid the other because they are never captured on photos simultaneously. Roe deer used the same or nearby locations as wild boar regardless of the frequency, but avoided to be at the same place as wild boar at the same time.

It is hard to say whether avoidance was mutual or part of natural activity patterns, but it is likely that the smaller and less competitive roe deer avoid being at the same places at the same time as wild boar. My findings are supported by one study (Carothers & Jaksić 1984) showing that interference competition is much more likely to result in temporal partitioning. Carothers & Jaksić (1984) concludes that interference competition allows separated patterns of activity to become a dimension over which organisms may reduce the effects of aggressive interactions. Visual observations on the research area during field work indicate that roe deer is either leaving voluntarily or are in fact chased away when encountering wild boar (Melberg unpubl.).

Use of wild life cameras has in this study been proven to act as a suitable complement to telemetry as a method of studying social interactions. Camera trapping can strengthen the telemetry data on individual movement schedules by sampling through the spatiotemporal patterns of multiple individuals. The mechanisms that allow the two species to coexist needs however consequently to be further investigated. Temporal analyses of which species who is avoiding the other can in future studies be analysed by investigating differences in time lag between inter and intra-species photo captures. Interspecific competition can also be higher at different seasons with different ratios of available food. This is of course important in Scandinavia where roe deer lives on the border to its northern range, because of the food shortage in winter. Yarrow & Kroll

(1989) suggested that during years of low mast availability, white tailed deer populations might be seriously impacted by competition with feral hogs for scarce food and Connell (1983) stated that interference competition vary in time depending on available resources. Interference competition between Swedish roe deer and wild boar is thus likely to increase, especially in severe winters as both species rely heavily on supplementary feeding.

Conclusions

My main results based on my predictions revealed that:

1. No marked fawn was demonstrably killed by wild boar
2. Roe deer fawns tended to show a non-random movement pattern in relation to wild boar activity.
3. Location of fawns were not affected by increased wild boar frequency (nr of captures and size of rooting's)
4. Roe deer adults did avoid areas with increased wild boar activity but irrespective of capture frequency. Rooting size seemed to be related with a growing distance to positions of pellet group counts with roe deer pellets.
5. Roe deer and wild boars' utilization of shared habitat is temporally separated.

Competition between herbivores may depend on their behavioural characteristics, population densities, spatiotemporal distribution and resource availability (Pianka 1983; Arsenault & Owen-Smith 2002). Wild boar has made a strong comeback to Swedish fauna and occupied old territories but roe deer's behavioural response to that has been rather vague. My study is to my knowledge the first one specifically showing effects of wild boar and roe deer interactions in Europe. The main results from my field study is that roe deer to some extent spatially and temporally segregates from wild boar indicating a behavioural response to interspecific competition.

This study failed to demonstrate wild boar predation on roe deer fawns. However, overall effects of interactions may consequently affect the fecundity, survivorship or growth of roe deer, and this could, in turn, result in a roe deer population decline. Managers have to take this into account when calculating long-term goals regarding local roe deer

populations. A good monitoring of local wild boar populations may therefore be an important tool to predict the success of roe deer recruitment. To accomplish an adjustment of roe deer harvest to status of local wild boar populations, wildlife managers can make a wild boar index during spring by counting length and number of rootings to forecast status and re-plan harvest of the roe deer population.

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Appendix I.

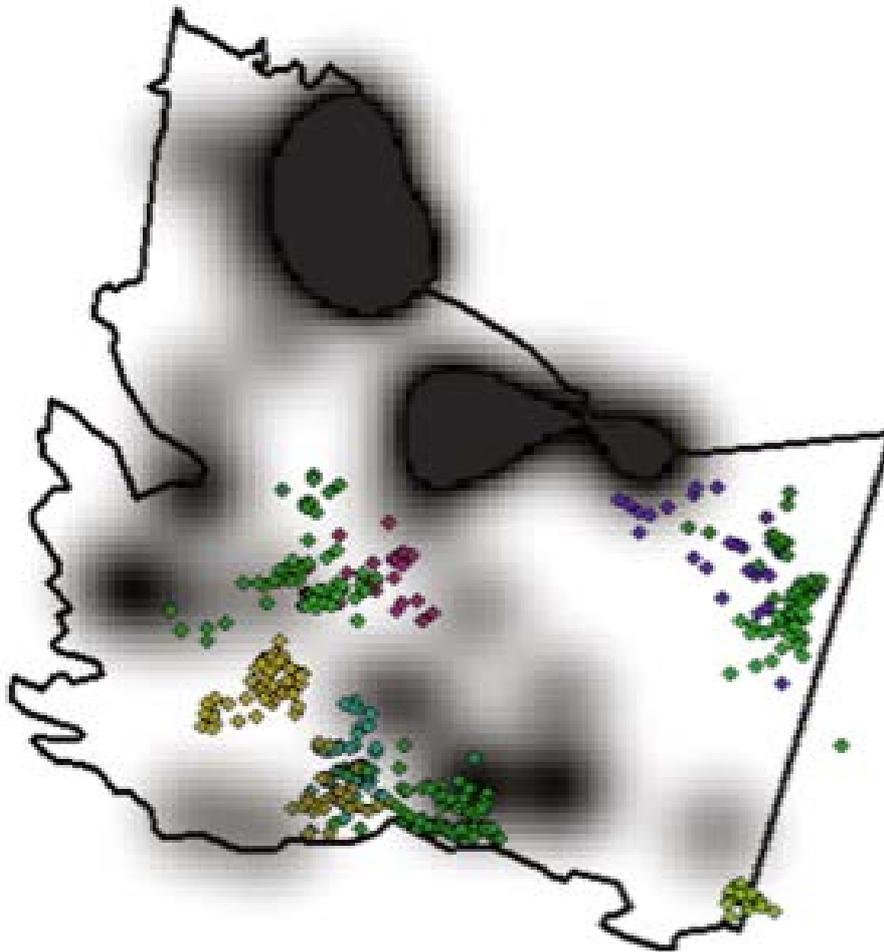


Figure. A. Contour on map of Bogesund displaying areas of high wild boar activity (black clouds) including both areas with rootings and photo captures. High frequency of photo captures as well as long distance rooted appears darker in colour. Coloured diamonds are VHF-positions of twelve marked fawns at Bogesund in summer 2011.

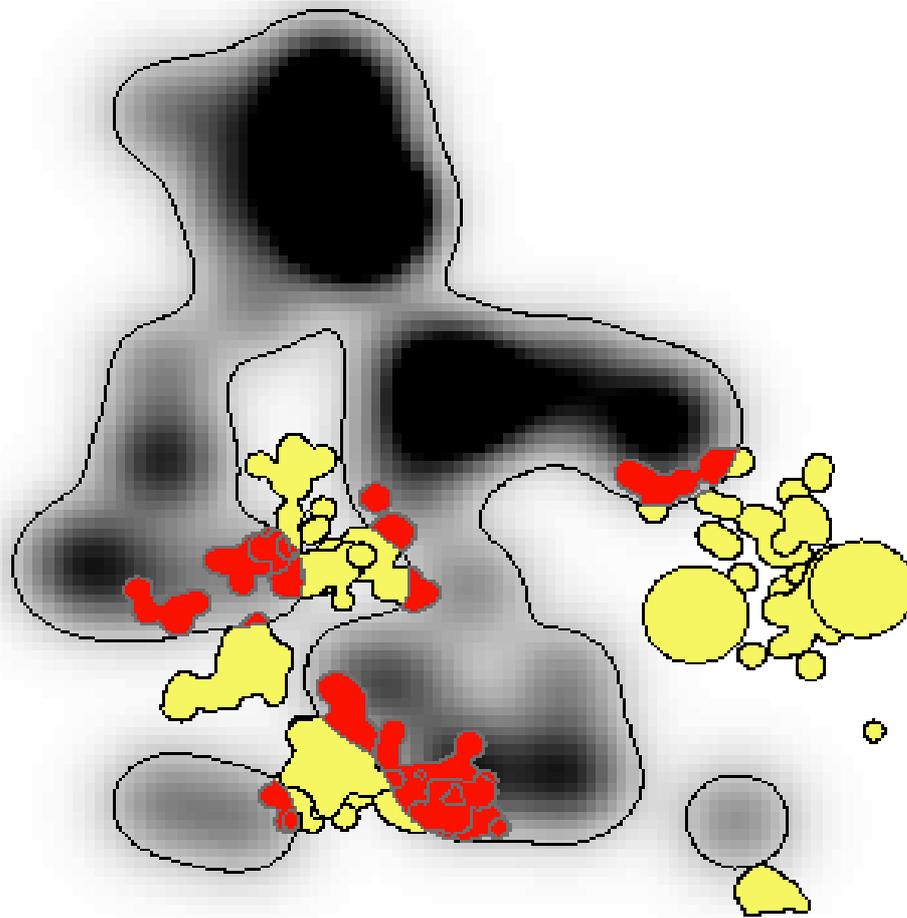


Figure. B. Fawn home ranges (yellow) overlapping (red) with wild boar activity (black). Overlap area was calculated to be 20 %, but differed not significantly from the artificial home ranges overlap (30 %). High frequency of wild boar photo captures as well as long distance rooted appears darker in colour. Both fawn home ranges and wild boar activity are created with the kernel fixed contour on the 95 % level.

Appendix II.

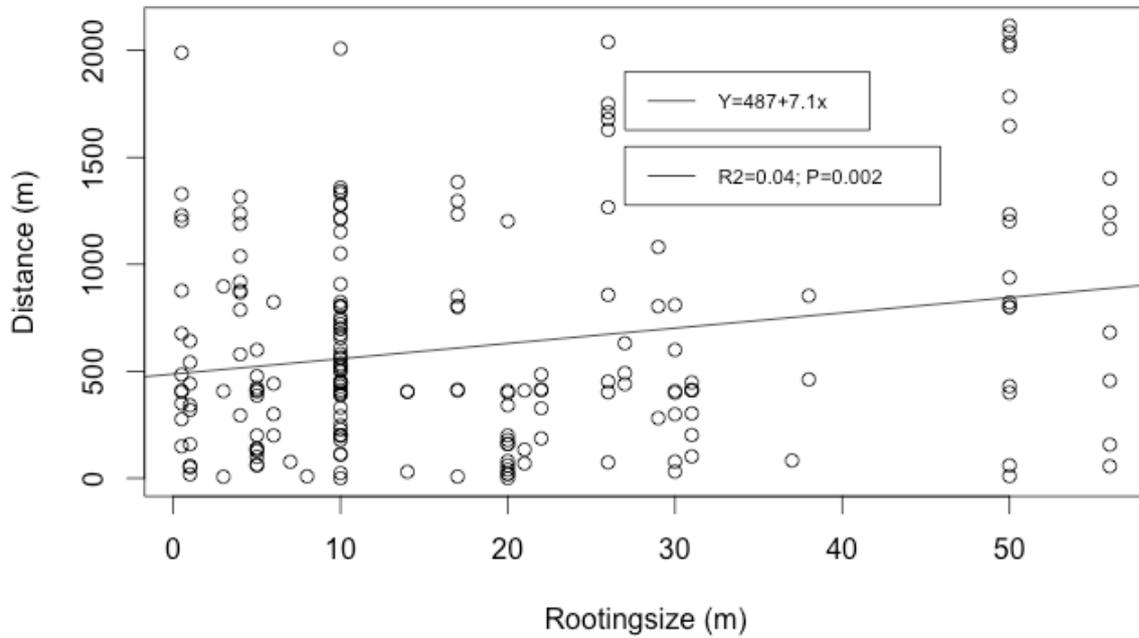


Figure. C. Relation between the response (i.e. distance to rooting from pellet group count plots with roe deer pellets) and rooting size. The legend shows the equation of regression line, its explanatory power and the model p-value.