

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).

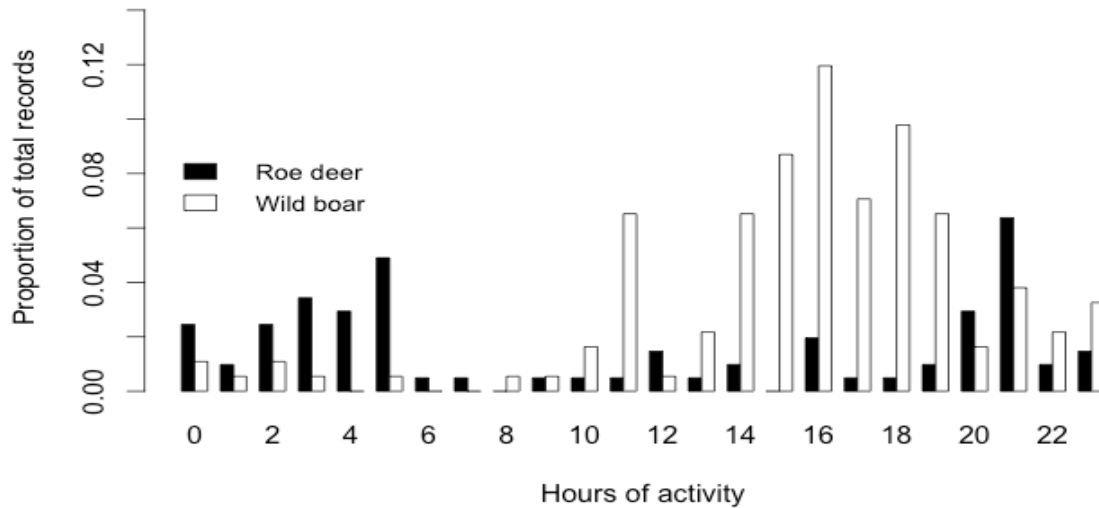


Figure 4. Activity patterns of roe deer and wild boar in spring at Bogesund 2009-2011. Shown as proportion of total captures for each species

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.

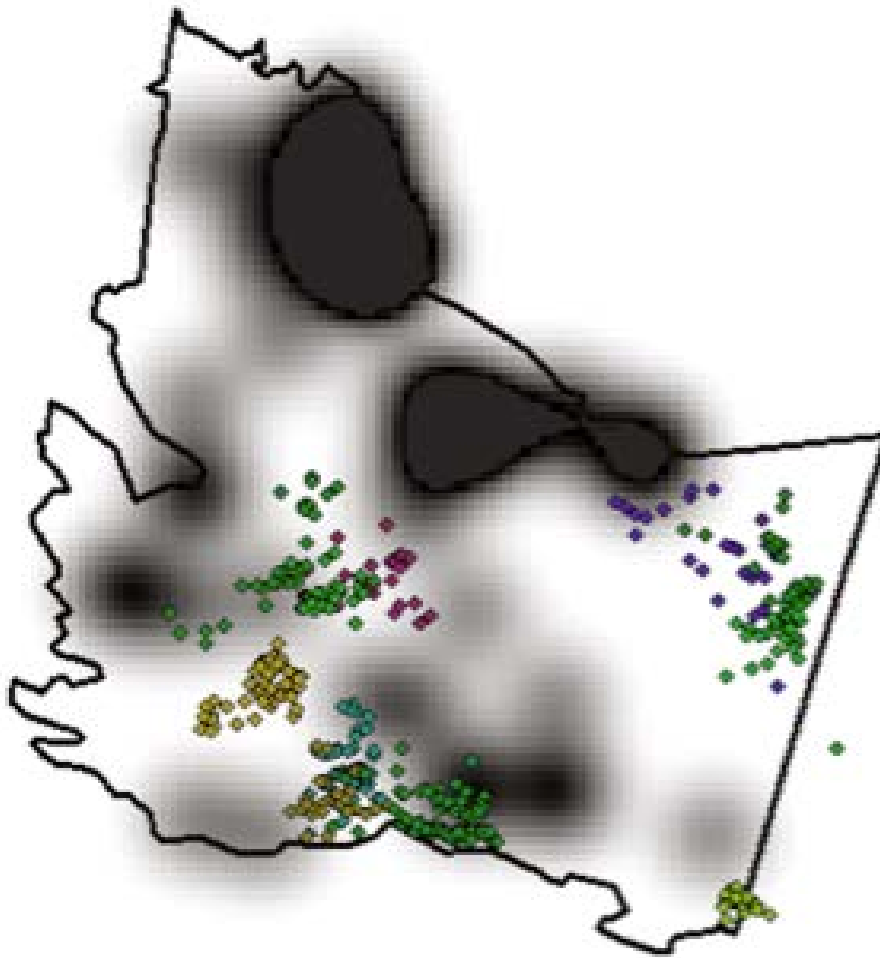


Figure. A. Contour on map of Bogesund displaying areas of high wild boar activity (black clouds) including both areas with rootings and photo captures. High frequency of photo captures as well as long distance rooted appears darker in colour. Coloured diamonds are VHF-positions of twelve marked fawns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

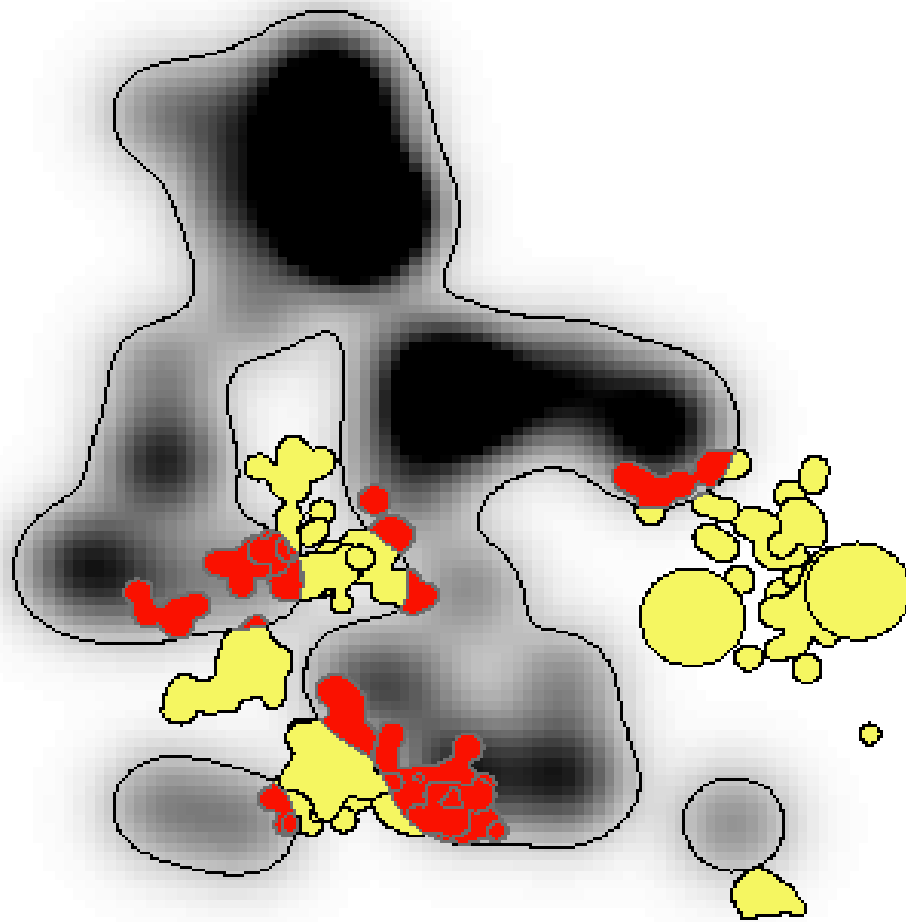


Figure. B. Fawn home ranges (yellow) overlapping (red) with wild boar activity (black). Overlap area was calculated to be 20 %, but differed not significantly from the artificial home ranges overlap (30 %). High frequency of wild boar photo captures as well as long distance rooted appears darker in colour.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

Appendix II.

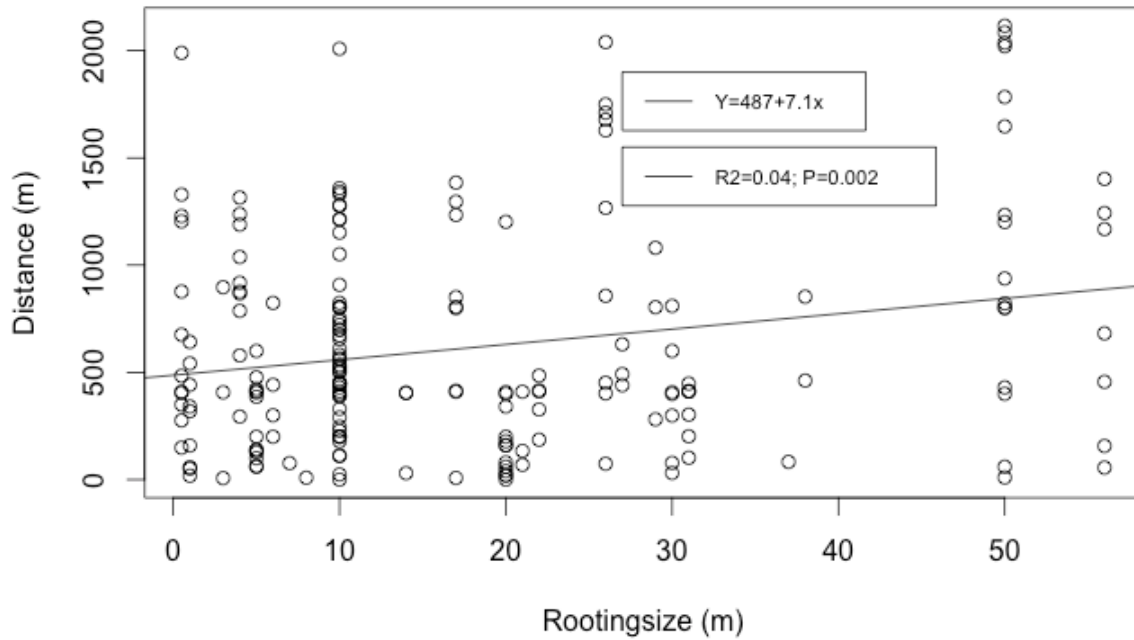


Figure. C. Relation between the response (i.e. distance to rooting from pellet group count plots with roe deer pellets) and rooting size. The legend shows the equation of regression line, its explanatory power and the model p-value.