Spatial Behaviour of Wild Boar

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Abstract

The spatial behaviour of an animal is influenced by decisions relating to foraging, movement, avoidance, resting, territorial activity, mating and rearing young. Many of these behaviours can be explained by the optimal foraging theory, exceptions being reproductive behaviours and predator avoidance. Predation risk and associated avoidance behaviors varies across the landscape, resulting in a divergence from patterns predicted by optimal foraging theory, instead optimizing fitness. Such risk effects can be large and affect both individuals and population demography. This thesis focus on external factors affecting movements and habitat selection of wild boar females (N=15-17 depending on the question) using data from GPS collared individuals (N>100.000 data points analyzed) over 4 years in the southern part of Sweden.

My results show that habitat selection is affected by season and by risk effects, such as traffic and hunting. Intense traffic diverts wild boar from crossing roads, and reduce the number of traffic accidents when traffic intensity is high. Intense hunting results in fleeing while less intense hunting results in hiding. Hunts that results in flights affects habitat selection until wild boar returned to their homer range. Wild boar perceive crop fields as risky but rewarding habitats, and while using crop fields they prefer to be close to cover such as edges, hedges and ditches. Further, wild boar movement is affected by seasonal and temporal aspects and weather conditions. The most common reaction to stressful factors such as traffic, hunting and aversive weather was to reduce movement. The only exception was when wild boar were chased in drive hunts and fled.

These results are important for understanding how weather conditions affect optimal foraging strategies and how the animals' perception of risk affects movement patterns and habitat selection. From a management perspective, my results can be used to reduce crop damages and traffic accidents caused by wild boar. These findings are also useful in understanding how hunting as a management tool affects the space use of wild boar, and consequently can aid managers to select hunting methods that may reduce damages to crops.

Keywords: behaviour, movement, habitat selection, risk, landscape of fear, GPS, ungulate, management.

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Dedication

To myself, for *not* fleeing or hiding, despite stress *and* adverse environmental conditions....…

I learned long ago, never to wrestle with a pig, you get dirty; and besides, the pig likes it.

George Bernard Shaw.

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Thurfjell H, Ball JP, Åhlén PA, Kornacher P, Dettki H, Sjöberh K. (2009). Habitat use and spatial patterns of wild boar *Sus scrofa*, (L.): agricultural fields and edges. *European Journal of Wildlife Research* 55(5), 517-523.

II Thurfjell H, Spong G, Ericsson G Factors affecting wildlife-vehicle collisions (manuscript)

III Thurfjell H, Spong G, Ericsson G Effects of hunting on wild boar behaviour. (manuscript)

IV Thurfjell H, Spong G, Ericsson G. Effects of weather, season and daylight on wild boar movement (manuscript)

Paper I is reproduced with the kind permission of the publisher.

The contribution of Henrik Thurfjell to the papers included in this thesis was as follows:

I Some fieldwork, all analyses except that of rooting damage, most writing.

II Some fieldwork, all analyses and most writing.

III Some fieldwork, all analyses and most writing.

IV Some fieldwork, all analyses and most writing.

Abbreviations

AIC	Akaike´s Information Criterion
DOP	Dilution of precision
GPS	Global Positioning System
GSM	Groupe Spéciale Mobile or Global System for Mobile Communication
MCP	Minimum Convex Polygon
SMHI	Swedish Meteorological and Hydrological Institute
SMS	Short Message Service
RSF	Resource Selection Function
3D	3 Dimensional
Λ	Lambda

Introduction

Why does an animal choose to be in a certain place at a certain time? Why does it decide to leave one place and move to another, and why at that point in time? These questions on spatial behavior of individuals include many aspects and are dealt with in this thesis. My model organism is the wild boar (*Sus scrofa*, L.). I examine direct reactions to disturbance by humans such as avoidance or flight, but also habitat selection and effects of weather. The wild boar is a relevant model species since it is a large ungulate, both appreciated as game but also many times considered as a pest, with a rapid population growth, having a potentially large ecological and economic impact (Schley *et al.*, 2008).

The wild boar

Wild boar is the wild ancestor of the domestic pig (Fang *et al.*, 2009). The male is called boar, the female sow, and the subadult piglet or yearling. Wild boar are omnivorous ungulates native to Europe, Asia and northern Africa (Melis *et al.*, 2006). However, feral pigs and in some cases wild boar have been introduced in many parts of the world, and are now present on all continents except Antarctica (Dzieciolowski *et al.*, 1990; Engeman *et al.*, 2001; Simberloff *et al.*, 2003; Mitchell *et al.*, 2007). The historical northern limit for wild boar in Europe before the spread of agriculture was the northern limit of the broadleaved forest (Rosvold *et al.*, 2010). Wild boar is an adaptable species that also can be found in urban areas (Jansen *et al.*, 2007) utilizing both natural forage and human waste.

Wild boar live in social groups with adult females and their offspring, while adult males are solitary. The social groups may consist of related females, but this is not always the case as groups split and merge over time (Iacolina *et al.*, 2009). Females usually become sexually mature at a weight of around 30kg, (Sabrina *et al.*, 2009), and can reach sexual maturity as early as four months (Cellina, 2008). Males become sexually mature and leave the social group at 10 months of age (Truve & Lemel, 2003).

In central Europe, the "natural" diet of wild boar consist mainly of mast, grasses and leaves, roots, invertebrates (Groot Bruinderink & Hazelbroek, 1994) and cadavers (Melis *et al.*, 2006). In the agricultural landscape ripe crops dominate in the diet of the wild boar (Mackin, 1970; Lemel *et al.*, 2003; Herrero *et al.*, 2006; Schley *et al.*, 2008), and has done so since humans started cultivation (Rosvold *et al.*, 2010). Supplemental food is often provided by hunters to facilitate hunting and to dissuade wild boar from crops. Food provided by humans is less preferred than mast and crops (Geisser & Reyer, 2004; Cellina, 2008; Schley *et al.*, 2008).

Wild boar are close to capital breeders on a scale, which means that the energy status before piglets are born is important for the reproductive success (Sabrina *et al.*, 2009). They have a high potential reproductive rate for their size, and can reproduce throughout the year, but most piglets are born in late March and to some extent in September (Bieber & Ruf, 2005; Fernandez-Llario & Mateos-Quesada, 2005; Geisser & Reyer, 2005; Gethoffer *et al.*, 2007; Sabrina *et al.*, 2009; Bywater *et al.*, 2010). Since the seventies, the wild boar population has increased in continental Europe (Bieber & Ruf, 2005; Geisser & Reyer, 2005). In Scandinavia, the species was hunted to extinction in the seventeenth century, but has been reintroduced through escapes from hunting enclosures in the nineteen seventies, and the population has since then grown rapidly (Truve & Lemel, 2003).

The challenge in wildlife management is keeping all stakeholders satisfied (Riley *et al.*, 2002), and hunters generally seek higher population densities than farmers (Geisser & Reyer, 2004). Wild boar is a popular game species for many European hunters (Genov *et al.*, 1994; Feichtner, 1998; Geisser & Reyer, 2004; Braga *et al.*, 2010; Keuling *et al.*, 2010), and they have been hunted by humans in Europe since the stone-age (Magnell, 2005; Fornander *et al.*, 2008; Rosvold *et al.*, 2010). Wild boar cause damage to crops and meadows (Mackin, 1970; Drozd, 1988; Geisser & Reyer, 2004; Schley *et al.*, 2008). Many methods have been tried to reduce crop damage caused by wild boar such as dissuasive feeding, fencing, hunting in fields, and population reduction (Bruinderink *et al.*, 2000; Calenge *et al.*, 2004; Geisser & Reyer, 2005; Gethoffer *et al.*, 2007; Cellina, 2008). Dissuasive feeding may be counterproductive in reducing wild boar damage on crop fields as wild boar prefer crops over provided food, and provided food can support wild boar through harsh times when supplied during all seasons (Geisser &

Reyer, 2004; Geisser & Reyer, 2005; Gethoffer *et al.*, 2007; Schley *et al.*, 2008). Problems with preventive measures are that fences are expensive (Geisser & Reyer, 2004), and population reduction, even though considered most efficient, is not always popular among hunters (Geisser & Reyer, 2004).

Spatial behaviour

Spatial behaviour of an animal have a wide meaning such as movement, habitat selection, home range, core area, territoriality, migration, etcetera. Here, I will focus on two main aspects, namely movement and habitat selection. Movement and habitat selection of animals is often related to energetic demands (Ford, 1983; Tufto *et al.*, 1996). Animals balance their choice of habitat and need of movement for energy intake, as per the optimal foraging theory (MacArthur & Pianka, 1966). Generally less movement is required in more productive areas and during more productive seasons (Ford, 1983; Kie *et al.*, 2002; Borger *et al.*, 2006). The optimal choice of actions or habitats is not static but depends on the energetic state and the present conditions (Grubb & Greenwald, 1982). Exceptions from the optimal foraging theory are related to other fitness enhancing activities such as mating and breeding or avoiding predation (McNamara & Houston, 1986; Lind & Cresswell, 2005). Animals show avoidance behaviours when there is a risk of being predated upon, and they thereby reduce their foraging efficiency by increasing vigilance, and shift the balance of movement and habitat selection towards actions and habitats involving less risk, but possibly also less reward (Brown *et al.*, 1999; Lind & Cresswell, 2005).

There is a large range of behaviours included in avoidance. Habitat selection under risk is rather widely studied, and animals ranging from insects (Sih, 1980) to elk (*Cervus elaphus*, L.)(Ripple & Beschta, 2003), can balance the conflicting demands of predation risk and foraging opportunities in habitats of different quality. Changing the daily activity pattern to safe night-times generally reduce the risk of being eaten since many predators depend heavily on eyesight when hunting. Since night-time mostly means dark hours, a prey may escape a predator depending on eyesight by becoming nocturnal (Keuling *et al.*, 2008b), or a predator may be more efficient during the night since they are harder to detect for prey relying heavily on eyesight (Fischhoff *et al.*, 2007). When animals perceive the risk of predation as high, increased vigilance can reduce the risk with costs that the animal will spend less time foraging, or forage less efficiently (Brown *et* *al.*, 1999; Lind & Cresswell, 2005; Benhaiem *et al.*, 2008). Certain actions shown by wild boar can be closely related to risks, i.e., crossing roads (Dodd *et al.*, 2007) and giving birth in risky environments (Creel & Christianson, 2008). Risky actions should change habitat selection and shift activity patterns towards safer habitats and times.

When an animal is discovered, it must decide whether to fight or flee (Cannon, 1929). Fighting can be an efficient final response by some species (Lingle *et al.*, 2008), but many species, wild boar included, mostly flee. After an encounter with a predator or a hunter, the animal may alter the perception of risk and associate the habitat, the hunter presence, or the location of the encounter, as risky events (Lima & Dill, 1990) and thus change their landscape of fear (Brown, 1999).

Objectives

The main objectives of this thesis are to study the spatial behavior of wild boar and get a better understanding of factors affecting this behavior. As a wildlife species wild boar are greatly influenced by interactions with humans, and stakeholders have much interest in the species both as an asset (game) and as a cost (destroying crops). Successful management of wild boar benefit from good knowledge of the species and individual behaviours. In general this thesis is dealing with questions about risk assessment at different temporal scales, in particular this thesis deals with;

1 What are the spatial movement patterns of wild boar using crop fields?
2 What factors affect the rate of road crossing and timing of accidents with cars?
3 How does hunting of wild boar affect their movement and space use ?
4 How do ambient weather conditions affect wild boar movement?

Materials and Methods

Study area

Scania is the southernmost county of Sweden with an area of 10,939 square kilometers and located in the nemoral vegetation zone (Ahti *et al.*, 1968). The southern plains have extremely fertile soil, and are mainly agricultural areas and the forest is mainly beech or planted Norwegian spruce, although the north-eastern parts hold more coniferous forests.

In the eastern part of Scania is Österlen, with the three estates Högestad, Christinehof and Kronovall covering a total of 16,000 hectares. The area is dominated by farmland (65%), which in turn is more dominating in the southern part of the estates. Wheat (*Triticum aestivum* L.), rye (*Secale cereale* L.), and oats (*Avena sativa* L.) are the main crops. A very minor but important part is the planted willow "forests" (*Salix sp.* L.), grown for energy production. Other open areas such as pastures, meadows and reed beds (*Phragmites australis*, Cav.) cover about 12% of the study area. Forest covers about 19% of the area, with 12% coniferous dominated forest, mostly planted stands of Norwegian spruce. Deciduous forest covers about 7% of the area, and is dominated by beech (*Fagus sylvatica*, L.) and oak (*Quercus robur*, L.). Only 2% of the area is covered by open water. The lakes in the area are shallow, usually surrounded by reed beds, and the waterline change a lot throughout the year. The study area is intersected by two Swedish national roads.

The wild boar hunting in the study area is mostly drive hunts which are well documented by the game keepers, and takes place from October through January. Other forms of hunting such as pheasant hunts, duck hunts, still hunts and small game hunts were also carefully recorded. The density of the wild boar population is high, even though no official census is carried out; the average harvest in Österlen is about 1 wild boar per km^2.

On the estates the hunting bag was lower, 0.4 wild boar per km^2 while on smaller farms in the surroundings the hunting bag varied extremely. The predation on wild boar in the study area is assumed to be insignificant as there are no large predators present.

Immobilization and fitting of collars (Paper I-IV)

Wild boar were darted and immobilized with a standard mixture of 10 mg medetomidine, 20 mg butorphanol, and 500 mg ketamine as described by Kreeger and Arnemo (2007), and were usually found within 200–300 m of the darting place, about 2–3 minutes after darting. To be able to dart the wild boar, we searched crop fields after harvest from a car, using a spotlight to localize groups of wild boar. We drove up to them and sedated them with a tranquilizer gun. Wild boar were also darted from blinds close to feeding stations. To ensure animals were not lost after darting, we used a transmitter–dart system (Pneu-dart, Williamsport, PA, USA). We equipped a total of 20 wild boar within the study area, 19 adult females and one male with GPS/GSM Plus 4D collar from Vectronics Aerospace GmbH (Fielitz, 2003). For the later data analysis, only functioning collars retained on females were used which means 17 sows in paper I where only habitat selection was analyzed and there were no need for consecutive successful positions. In the other papers (II-IV), 15 sows were used for the analyses where movement was studied. The collars were programmed to attempt to acquire a position every half hour, and to transmit accumulated positions to a computer using the 'Short Message Service' (SMS) on the local global system for mobile communication (GSM) cell phone network, which has excellent coverage in the study area.

Positions with a dilution of precision (DOP), i.e., the geometrical contribution to the uncertainty of a GPS position of less than 5, and a 3D position (calculated with at least four satellites) were used in our analysis, a common procedure when handling GPS data (Moen *et al.*, 1996). As it is harder for the GPS to successfully acquire a position under a dense canopy (Moen *et al.*, 1996; Cain *et al.*, 2005; DeCesare *et al.*, 2005), this will yield a somewhat biased sample where coniferous forest, such as very dense plantations of Norway spruce, are underrepresented.

An average of 28% of the attempts to acquire a position failed during the night (i.e., when the wild boar were active). To get a better estimate we omitted three collars which were only working sporadically, probably due to hardware failure, or that the collar might have turned around on the animal with the result that the GPS was on the bottom reducing signal strength. These problems were not related to GPS-performance or habitat, and thus expected to be random from a habitat selection perspective. By omitting those collars the failure rate went down to 19% during the night, and 25% during the day, which is regarded as acceptable (Zweifel-Schielly & Suter, 2007). It is likely that the lower average percentage of valid positions during daytime is due to the boar's habit of selecting daily rests in dense vegetation (Spitz & Janeau, 1990) and the fact mentioned before that the GPS units have more difficulty in obtaining a good position under dense canopies (DeCesare *et al.*, 2005; Zweifel-Schielly & Suter, 2007).

Maps

Different maps were used for different analyses. The most utilized map was the Swedish terrain map, which was the base for all habitat selection studies (Papers I-III). A hand-made map of linear objects in fields and other open areas was used to test if wild boar were following those objects when they were in open fields.

The Swedish Terrain Map is a detailed vector map of the study area in Österlen, based on aerial black and white photographs. The map over the study area was updated in 2002 by Lantmäteriet (2008). The accuracy, or average error in the database is about 10 meters.

The hand-made map of linear objects was done with the aid of rectified digital aerial black and white photographs taken in 2004. Objects such as hedges, rows of trees, low stone walls, etc. were digitized in ArcGIS 9.1 (ESRI 2005) on agricultural fields and other open areas from the Swedish terrain map.

Inventory of damages (Paper I)

To evaluate the spatial pattern of damage, we located wild boar rooting on pastures and meadows in the study area. The survey was carried out during six weeks in 2003 after agricultural fields (e.g. wheat, oats) had been harvested.

Data on traffic and accidents (Paper II)

Traffic intensity data for the two national roads intersecting the estates were obtained from the Swedish road administration. Temporal data on wildlife-vehicle collisions for 2008 in the county of Scania were obtained from the police database Hobit (Sävberger, 2010). We assume that temporal patterns of accidents are constant, which seems to be valid when looking at monthly data (Sävberger, 2010).

Data on hunting (Paper III)

Dates of hunts and types of hunts were acquired from the game managers journals. All wild boar were considered to be affected by hunts during the day of the hunt and the following night.

Data on weather conditions (Paper IV)

Daily weather data was acquired from the Swedish Meteorological and Hydrological Institute, SMHI, from a station located on the edge of the study area. At the station daily measures of temperature, precipitation and snow depth were measured.

Statistical analysis

Speed, or movement, was calculated by simply dividing the Euclidean distance between consecutive positions with the time separating them, using only consecutive successful locations.

Data for wild boar positions were divided into night, day and season; summer when crops are ripe (July and August in our study area); fall, after the harvest when mast can be available, (September-December), winter, when there is little mast and sometimes snow, (January-March), and spring, which is the period when the growing season has started but the crops are not consumed by the wild boar (April-June) (Paper I). Positions were also divided into connected and not connected with road crossings (Paper III).

A type III resource selection function (RSF) where the minimum convex polygon (MCP) is considered available to each single animal, was used to calculate habitat selection (Manly *et al.*, 2002). Selection ratios and Bonferroni adjusted confidence intervals were calculated as per Chapter 4 in "Resource selection by Animals" (Manly *et al.*, 2002).

5000 random positions were added to agricultural fields within the MCPs for each wild boar, and the distance from the random positions to the narrow landscape elements were compared to the same distances for the actual positions. Differences were tested with a binary logistic regression per season as suggested by Manly et al. (2002). This created one RSF per season and individual concerning distance to edge, and all RSF´s were tested in a sign rank test (Siegel & Castellan, 1988).

The distribution of wild boar rooting damage, regardless the size of the damage, was compared with an equal number of random points (Marcum and Loftsgaarden 1980) (Paper I).

Data on wild boar movement, road crossings and habitat selection before or after drive hunts was modeled using generalised linear mixed effects models with individual wild boar as a random variable with a random intercept using R (R Development Core Team, 2009). Depending on the paper, movement was either Box-cox transformed ($\lambda = 0.06$, paper IV) or belonging to a gamma distribution (Paper III). The model of accidents (binomially distributed per hour) did not include a random effect, and instead the average movement of all wild boar for each hour was used as a predictor. Road crossings and habitat selection were binomially distributed. The models accounted for seasonality including the factor month of year and the models with movement as a response also day or night as a predicting factor. When converging, I modeled all two way interactions but not interactions between vectors as they may be uninterpretable. To find the most parsimonious model I used the Akaike Information Criterion (AIC) (Akaike, 1974).

Results

What are the spatial patterns of wild boar using crop fields? (Paper I)

As expected from previous studies, rooting damage was closer to forest edge than expected by chance alone (damages *54* m from forest edges vs. random points *127* m N=171, $\chi 2 = 39$, $p = < .0001$). Wild boar positions at night were closer to linear objects such as hedges and ditches, during winter (p=.032) and spring (p=.0098). Seasonal variation in selection of night habitats (Fig. 1) shows that female wild boar avoid crop fields during all seasons, but less so during summer. During fall, winter and spring, open areas and coniferous- and deciduous forests were preferred, but during summer coniferous forest was avoided while deciduous forest and open areas were still preferred. Water bodies (shallow lakes in the study area) were a preferred habitat during all seasons except spring.

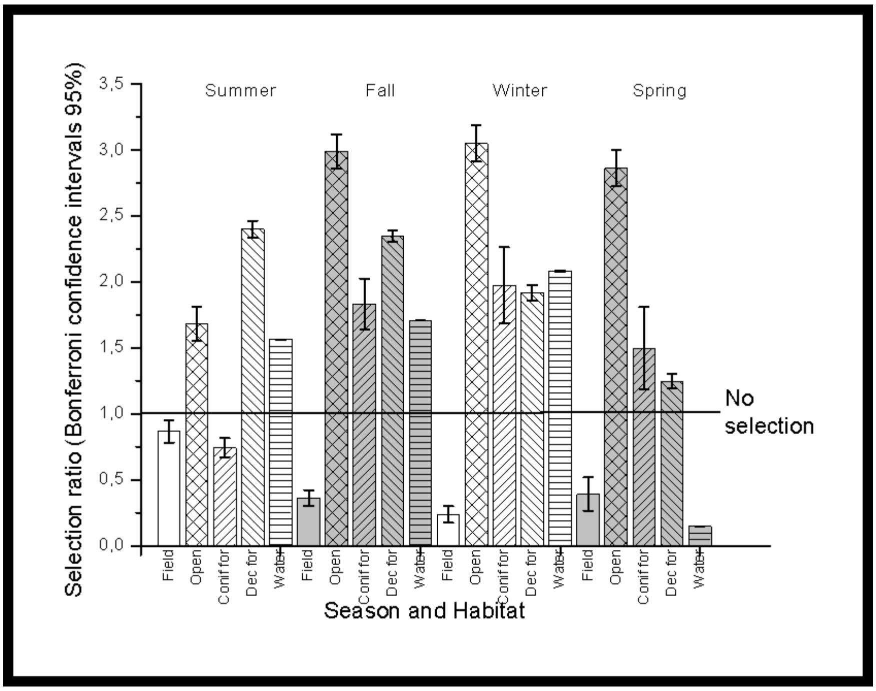

Figure 1. Seasonal selection for or against different habitat types by female wild boar (N=17) in Sweden. A bar above the "zero selection" line means preference, one below means avoidance. Habitats are Field Agricultural fields, Open Open areas, Conif for Coniferous forest, Dec for Deciduous forest, and Water.

What factors affect the rate of road crossing and timing of accidents with cars? (Paper II)

Road crossing by female wild boar is depending on seasonal effects (Fig. 2), with most road crossings occurring during summer months. Road crossings are negatively correlated with traffic intensity. Another factor affecting road crossings is which habitat they are in with the highest chances of in crop fields and lowest in coniferous forest (Fig. 3), (all $p < .001$).

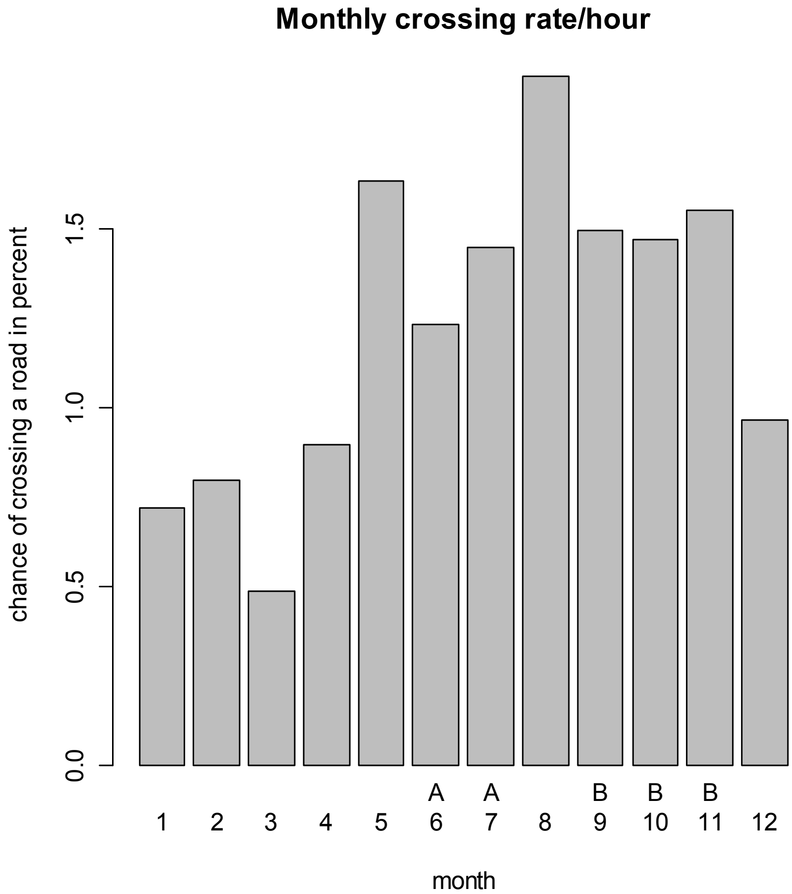

Figure 2. Added chance of female wild boar (N=15) crossing a road during different months. Months connected by the same letter could be combined (p>.05) based on a Likelihood ratio test, only consecutive months were tested.

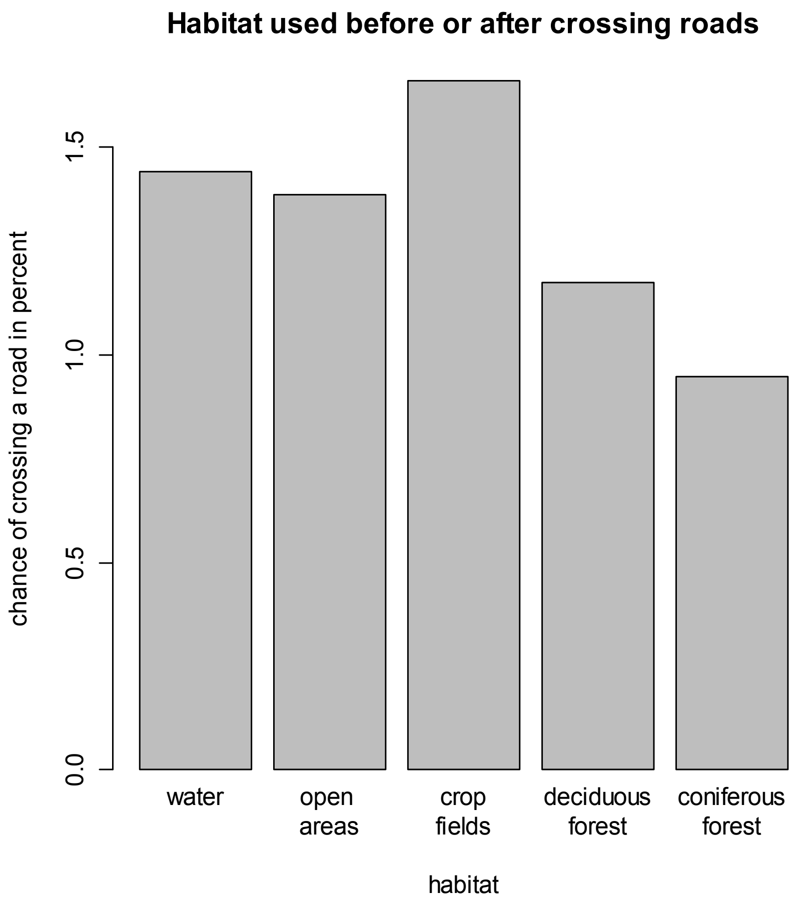

Figure 3. Added chance of female wild boar (N=15) crossing a road before or after being located in a habitat. Habitats were combined one by one, and the models tested in a Log likelihood test to see if they differed from each other. All habitats differed from all others ($p<0.05$) except water (shallow lakes) and open areas ($p=0.9$).

Wild boar are involved in traffic accidents when they are active and at intermediate traffic intensity levels, mostly during winter months (Fig. 4, all $p <.001$).

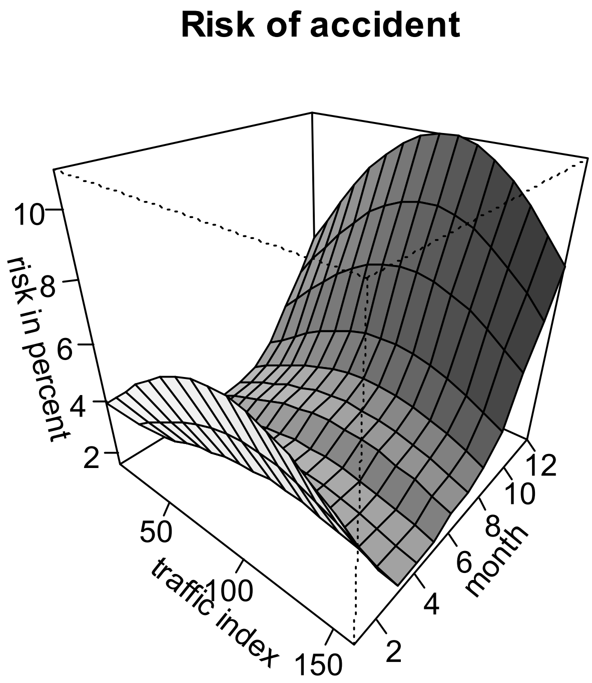

Figure 4. Added risk of an accident due to traffic intensity and month of year, per hour in Scania. The traffic index ranges from no traffic to rush hour traffic.

How does hunting of wild boar affect their movement and space use? (Paper III)

Hunting had an effect on the movement of female wild boar. During the day of a drive or pheasant hunt, wild boar movement increased. During the days when duck-, still- and unspecified hunting occurred wild boar movement decreased. The night after a pheasant or drive hunt, movement was reduced (Fig. 5). Six wild boar left their home range as an effect of a drive hunt, they ran between 2 and 20 km and stayed in the refuge area between 6 and 29 days.

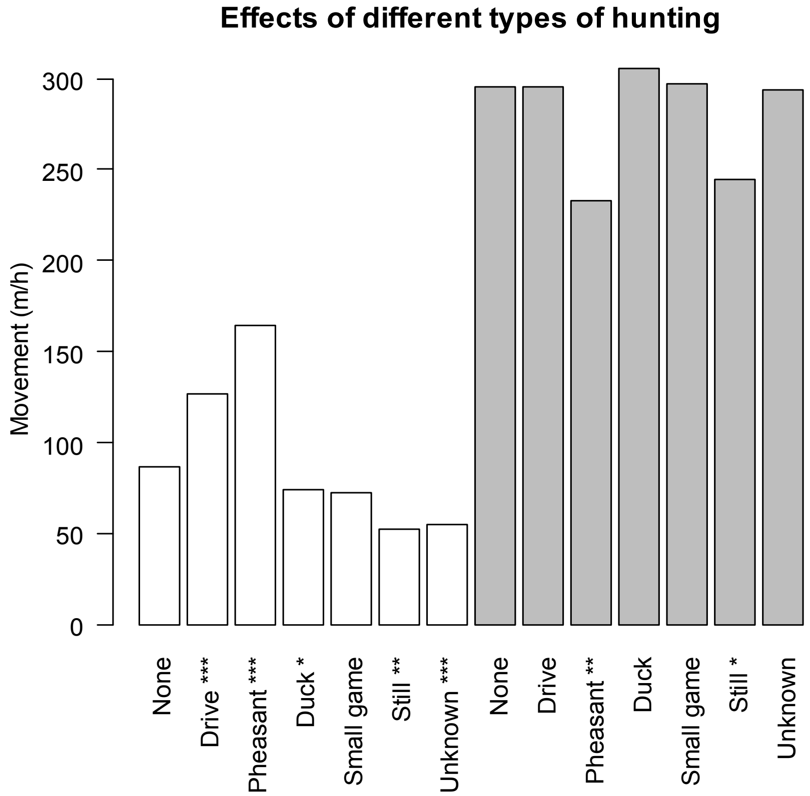

Figure 5. Effects of different types of hunting on movement of wild boar (N=15). White bars represent the day of the hunt and gray bars represent the following night. Asterixes indicate if there is a difference compared to when there is no hunting (*= $p<.05$, **=$p<.01$, ***=$p<.001$ based on identity contrasts). November is the month represented.

Hunting events that resulted in wild boar leaving their home range showed that movement was affected by drive hunts. Female wild boar moved more during relocation than before drive hunts and less in the refuge range ($p<.001$, based on identity contrasts). Habitat selection was also affected by drive hunts (Fig. 6). Coniferous and deciduous forest was used more during relocation while open areas were used less. After relocation crop fields and forests were used more, while open areas was used less (all $p<.001$).

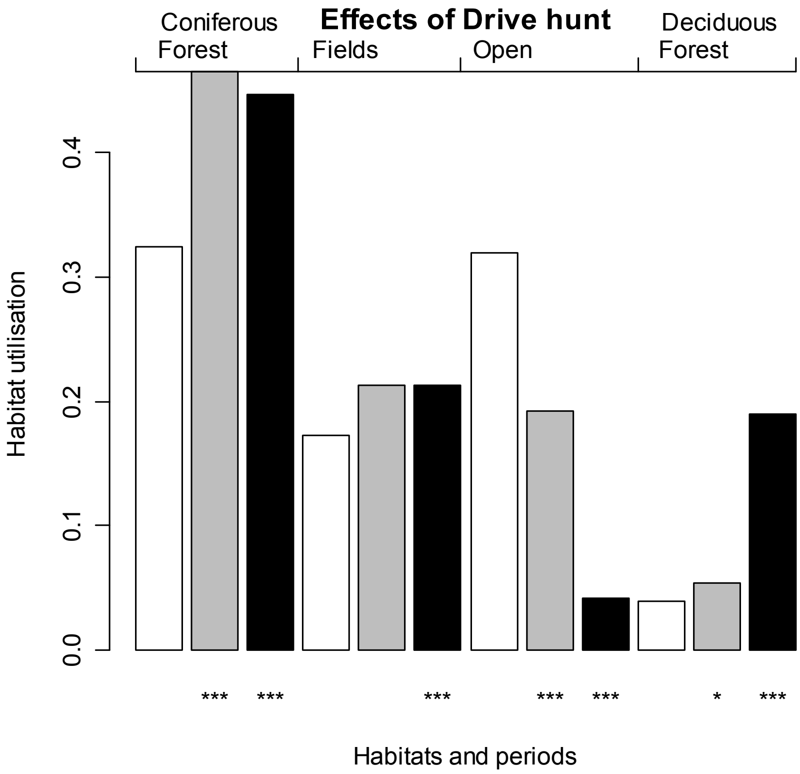

Figure 6. Effects of drive hunts on habitat selection of wild boar (N=6). The staples shows the effects of drive hunts on each model of habitat choice (probability), before drive hunts (white), during (gray) and after (black). Asterixes indicate if there is a difference compared to the period before the drive hunt (*= $p<.05$, **=$p<.01$, ***=$p<.001$ based on identity contrasts)

How does ambient weather conditions affect wild boar movement? (Paper IV)

Warm weather affected movement ($p < .001$) positively during nights from November till March ($p< .05$) and negatively during nights in May, July and September ($p< .05$, Fig. 7). Rain only affected movement positively during nights of July and November ($p<.05$) and negatively during nights of March ($p<.05$) (precipitation $p=.11$, precipitation*Day/Night $p=.15$, precipitation*month $p<.001$ and precipitation*Day/Night*month $p=.007$,

Fig. 7). Snow reduce movements during day and night (p <.001). During the night wild boar moved more than during the day (p<.05).

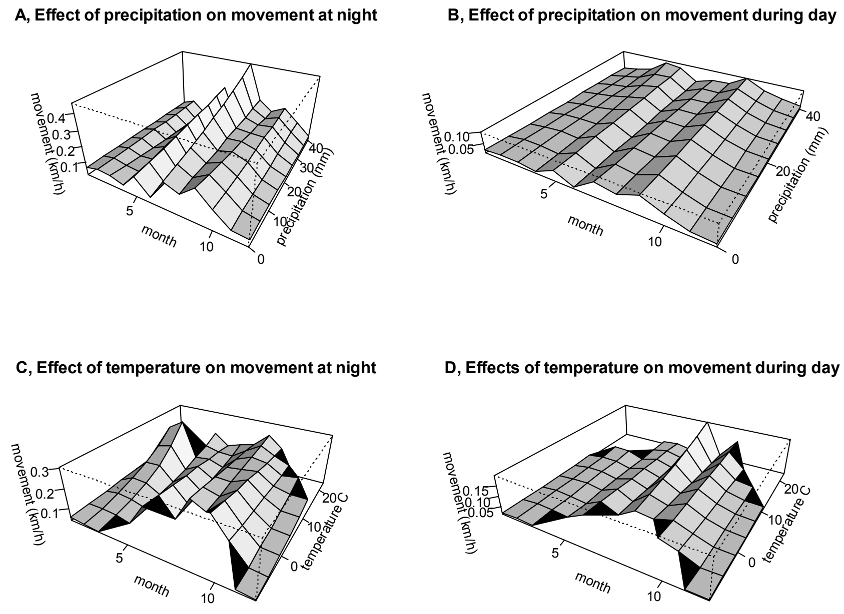

Figure 7. A, B, C, D showing the effects of precipitation, temperature and daylight on wild boar movement (N=15) throughout the year, all graphs are on the same scale. The figures show that wild boar moved more during night and summer. Figures A and B show that nightly movement increased with precipitation from April to August, decreased with precipitation during nights in March. Figure C shows an increase in movement with temperature during nights in winter, especially during February–March, and a decrease in movement with temperature during summer nights.

Discussion

This thesis combines accurate individual data with large enough sample size to draw conclusions about behavourial changes on the level of the wild boar population in the study area. Even if data are gained from wild boar, methods and some conclusions should be species independent, such as the avoidance of intense traffic, the increased use of safer habitats after being hunted etcetera. The use of GPS technology gives us good information of individual animals' geographical position most of the time. This is one of the earlier studies with GPS technology applied on enough wild boar to make conclusions on a population level, to my knowledge the first.

Wild boar movement and habitat selection differs depending on time of year and time of day (Papers I, II and IV). These differences are related to seasonal foraging and day length patterns (Keuling *et al.*, 2008a). In the absence of any disturbance, mating or giving birth, movement and habitat selection patterns should follow the optimal foraging theory (MacArthur & Pianka, 1966). Disturbance results in animals perceiving risk. Perceived risk over the landscape is called the "landscape of fear", with some areas perceived as high risk and some as low risk (Brown *et al.*, 1999; Lind & Cresswell, 2005). An animal should balance the need of energy intake with the risk involved (Brown *et al.*, 1999; Lind & Cresswell, 2005).

Wild boar do assess risks and change behaviour from optimal foraging behaviour accordingly (Papers I-III). This is expected as even insects have that capacity (Sih, 1980). Thus we expect to find a "landscape of fear" (Brown *et al.*, 1999) where wild boar change their behaviour from optimal foraging to account for the risk involved in certain actions or habitats (Papers I-III). It is hard to differentiate the effects of differences in forage quality and risk, especially a risk that the animal perceives throughout the year. The presence of such a risk perception is evident in paper I, where wild boar mostly use safer parts of crop fields with even quality.

The landscape of fear perceived by wild boar is not only spatial but also temporal, and perceived risk change with actual risk changes throughout the day, where previous studies have shown more diurnal patterns of activity when risk is lower (Keuling *et al.*, 2008b). I show that wild boar reduce the number of risky actions (road crossings) when the risk is high (high traffic intensity). This in turn has a positive effect on wild boar survival as the avoidance of road crossings reduces the number of accidents between vehicles and wild boar.

Certain actions or times can be perceived as more risky, such as crossing roads or rearing piglets (paper II, III). The landscape of fear should be stronger in association to those actions (Brown *et al.*, 1999). This should lead to differences in habitat selection during those times or in association to those actions. Evidence of this is found in reduction of risk when rearing young in relation to road crossings, and in the fact that roads are crossed mostly in relation to risky and rewarding habitats rather than safe habitats (Paper II) Safer habitats in this case have dense vegetation such as forest, while risky habitats are crop fields.

Certain actions may change the perception of risk and change the landscape of fear for a time. Wild boar that left their previous home range (calculated with Minimum convex polygon, MCP) as a response to drive hunts reduced movement and changed habitat selection when they were in the refuge home range (Paper III). The reasons for the changes are not completely clear as there may be due to higher perceived risk, but another possibility is an increased competition with resident wild boar groups. The increased use of forest and reduced use of open areas supports that the perceived risk is higher after drive hunts, while the increased use of crop fields supports that increased competition with resident wild boar groups has an effect (Paper III).

Different weather conditions affect which behaviour is optimal, as it makes movements more costly or is averse for the animal. When wild boar are not starving, the main reaction to aversive weather is to reduce movement (Paper IV). If wild boar are starving, wild boar may have a stronger motivation and search for forage in aversive weather (Lemel *et al.*, 2003).

These kinds of divergences from optimal foraging may in the long run lead to a decrease in body condition and even a lower birth rate in some species. This may present a problem for vulnerable species, but wild boar seems to be very adaptable, even able to live in urban areas (Jansen *et al.*, 2007), and the high reproductive rate suggests that wild boar as a species is well adapted to hunting and predation (Focardi *et al.*, 2008).

Even though avoidance, which is the result of disturbance, seem like a negative effect from the animals point of view, the mechanism behind avoidance is to increase the individual survival and relevant avoidance is beneficial for the animal (Brown *et al.*, 1999). Avoidance of non-lethal threats may be of no real value for the animal, and may decrease over time due to habituation (Lima & Dill, 1990).

Conclusions

Wild boar space use and movement is affected by season, weather and human activity. Wild boar reduce the negative effects of suboptimal weather by reducing activity.

Perceived risk changes movement and habitat selection of wild boar. Exposed but rewarding habitats such as crop fields are mostly used close to safe areas such as forests, ditches or hedges. When the perceived risk is high (traffic is intense), wild boar are less likely to expose themselves to risk (cross roads). Hunting either results in wild boar hiding or fleeing, depending on intensity of the hunting and the location in relation to the wild boar. After fleeing (drive hunts), wild boar reduce movement and use safer habitats (forest). Risky actions such as crossing roads takes place to use rewarding habitats (crop fields).

Management Implications

Avoidance behaviour related to human activity is one of the stronger tools managers can use, as they, by carrying out certain activities can control the behaviour of animals in desired ways. However, one needs to remember that both frequency and scale has to be considered before drawing conclusions on the effort needed to change the behavior of animals on a population level.

The long flights and the size of the home ranges of wild boar suggests that wild boar is an animal best managed in large management units, as the wild boar in my relatively large study area of ca. 16,000 hectares did not stay there at all times. Thus wild boar managed in one place will affects adjacent areas up to at least 20 kilometers away (Paper III). If stakeholders in different areas sharing wild boar have different goals for the management, none will be satisfied. Thus, stakeholders need to cooperate and agree on the goals for management to be successful (Riley *et al.*, 2002). The practice of feeding wild boar in the forest in order to get them out of the crop fields seems not to be working, as wild boar still use crop fields during the time when crops are ripe despite heavy feeding (Paper I). Hunting pressure at night in mature crop fields may be to low to have a serious disturbing effect and force wild boar into forests and feeding stations. The question is whether it is plausible to increase hunting pressure in crop fields enough to affect the habitat selection of wild boar. A weak effect has been found (Calenge *et al.*, 2004) in the French vineyards with a massive hunting effort. But most studies seem to suggest no effects of feeding in the forest and hunting in the crop fields (Geisser & Reyer, 2004; Geisser & Reyer, 2005; Cellina, 2008; Schley *et al.*, 2008), or even effects where damages increase with feeding in forests (Geisser & Reyer, 2004).

A possible solution in some areas is to grow desirable crops in fields with good cover as dissuasive fields, as they are more likely to draw the attention of wild boar than feeding stations since they have the same content as other fields, paired with a lower risk. Concerning traffic, populations should be kept low to limit accidents, and supplemental food and other sources of forage that can be manipulated should be kept as far from roads as possible. Relocating roads and agricultural fields may not be feasible, but fencing roads where there are a lot of fields where crops desirable to wild boar that mature late, are grown may be useful.

Future Perspectives

The importance of group size and composition is a subject that needs to be addressed in future work. Does age of the oldest individuals, number of adults, ratio between adults and juveniles etcetera change space use and activity patterns. Briedermann (1989) claimed that young wild boar without an old female used crops more for example. With smaller and cheaper GPS-units, possibly applicable by ear tag, or by reoccurring visual inspection of groups containing tagged individuals this issue could be easily addressed.

So far little is known on the effects of wild boar on other species and vice versa, as some suitable areas in Scandinavia are still unoccupied, there is an opportunity to make before and after studies addressing the effects of wild boar on the entire ecosystem and its interactions with other species.

Concerning the landscape of fear, this thesis focuses on man, and to some extent hunting dog induced effects on wild boar behaviour. If there is a different main predator, such as wolves, behaviour may differ. In some areas wolves are responsible for over 90% of piglet mortality (Jedrzejewski *et al.*, 2002). This should lead to behavourial adaptations among wild boar towards wolves rather than humans, i.e., wild boar change their behavior if wolf predation pressure is high and thus avoid areas where they are most vulnerable to predation. These areas could be fields and meadows since the wolves' higher agility may be more useful when the wild boar cannot protect its hinds, as P. Pavlov[1] noted when a similar predator, dingo (Canis lupus, L.), took feral pigs.

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[1] Peter Pavlov, oral presentation at the 6th international Wild Boar symposium in Kykkos, Cyprus, October 2006.

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Swedish Summary-Svensk sammanfattning

Rumsliga beteenden hos djur påverkas av en mängd faktorer som oftast är relaterade till födosök, rörelse, undvikande, vila, territoriellt beteende, parning eller att ta hand om avkomma. Många av dessa beteenden kan förklaras av optimering av födointaget förutom reproduktiva beteenden och undvikande av predatorer. Predationsrisk och undvikande varierar över landskapet och får djurets beteende att avvika från optimal födosök genom att säkrare habitat utnyttjas mer än riskabla. Den här typen av undvikande påverkar både individer och populationer. Den här avhandlingen tar upp externa faktorer som påverkar rörelse och habitatval hos vildsvinssuggor försedda med GPS halsband.

Mina resultat visar att vildsvin utnyttjar olika habitat beroende på vilken säsong det är men också beroende på vilken risk det innebär att befinna sig i habitatet. Exempel på risker är intensiv trafik eller jakt. Intensiv trafik får vildsvin att undvika att korsa vägar, vilket leder till färre olyckor när det är mycket trafik. Intensiv jakt leder till att vildsvin flyr istället för att gömma sig som de gör om jakten inte är lika intensiv. Habitatutnyttjandet hos vildsvin som flydde från sitt hemområde förändrades tills de återvände. Vildsvin uppfattar åkermark som riskfylld, men åtråvärd. Medan vildsvin befinner sig på åkrar föredrar de att vara nära skydd som skogskanter, diken eller häckar. Vildsvinens aktivitet påverkas av säsong, om solen är uppe eller nere och av väderleken. Den vanligaste reaktionen på stressfyllda förhållanden som trafik, jakt eller dåligt väder var att reducera rörelse, enda undantagen var drevjakter som fick vildsvinen att fly.

De här resultaten är viktiga för att förstå hur väder påverkar födosök och hur djurens uppfattning av risk påverkar rörelsemönster och habitatutnyttjande. Från ett förvaltningsperspektiv kan resultaten utnyttjas för att reducera skador på gröda och minska antalet trafikolyckor. Resultaten är också viktiga för att förstå hur jakt som förvaltningsredskap påverkar rumsliga beteenden, och vid samförvaltning över större områden kan detta användas för att reducera skador på gröda.