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Original article

Effects of hunting on wild boar *Sus scrofa* behaviour

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Predation risk may affect space use and foraging patterns of prey animals, with strong down-stream effects on diet composition and ecological interactions. Wild boar *Sus scrofa* is a notorious crop raider but also a popular game species, yet little is known about how risk perception of human hunting affects wild boar space use. We studied the effects of human hunting on the movement of GPS-collared female wild boar. We found that the hunting method affected whether the wild boar fled or hid. After fleeing into refuge ranges, wild boar moved less and preferred habitats that provided cover and forage such as mast or crops. This suggests that the wild boar tried to reduce the risk of being detected, and possibly also that they avoided competition with resident wild boar in the refuge by using forage that could not be monopolised. The type of hunting thus strongly affected the type of avoidance behaviour displayed by wild boar, with implications for their movement and space use. This suggests that adjusting hunting method to season could be an important management tool for minimising crop losses.

Key words: escape, GPS, hunting, movement, Sus scrofa, wild boar

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Animals often change their behaviour in relation to predation risk (Lima & Dill 1990); for example by selecting areas with lower food quality or quantity in return for decreased predation risk (Sih 1980). Risk can also be reduced by increased vigilance, which reduces foraging efficiency (Lima & Dill 1990). Predator presence may hence lead to consistent and large-scale avoidance behaviours in herbivores (Creel et al. 2007). This may lead to heterogeneities in browsing pressure across the landscape, where plants in safer foraging patches may be highly utilised and plants in risky foraging areas less affected by herbivory (Brown et al. 1999). Such trophic cascades occur both in marine and terrestrial systems and typically have major effects on the ecosystem's function and form (Terborgh & Estes 2007).

Human hunting is likely to be perceived as a risk by many animals and has accordingly been shown to affect habitat use (e.g. Kilgo et al. 1998, Benhaiem et al. 2008, Sunde et al. 2009, Kamei et al. 2010). The response to the perceived risk has also been shown to depend on hunting methods (Keuling et al. 2008b), where numerous factors play a role, e.g. the intensity of the hunt, detectability of hunters and the chance of animals learning from hunting experience. Reactions to hunting also depend on the prey's natural predators to which it has had evolutionary time to adapt. For example, dogs used for moose *Alces alces* hunting are behaviourally similar to wolves *Canis lupus*, and provoke similar reactions in the moose (Sand et al. 2005).

Farmers strive to minimise the loss of crops to wildlife. This may be accomplished by population control, fencing, dissuasive feeding (Geisser & Reyer 2004), deterring wildlife by scaring them (Beringer et al. 2003), or by using repellents such as odour (Baker et al. 2008). While maintaining a small population size by intensive hunting is perhaps the most efficient way of reducing crop damage (Geisser & Reyer 2004), this strategy may be at odds with management strategies aimed at improving hunting value or conservation of biodiversity. From a management perspective there is often a conflict of interest between stakeholders wanting to maintain a high population density of game species and stakeholders interested in minimising crop damage (Conover 1997, Brown et al. 2000, Riley et al. 2002, Gordon et al. 2004, Lischka et al. 2008). Thus the potential of inducing behavioural strategies that lead to avoidance of crop fields and preference of alternative habitats is an appealing management strategy as the use of crop fields could be assumed to be related to crop damages. However, we know relatively little about how hunting affects animal space use in agricultural regions, and in particular how hunting affects the behaviour of the wild boar *Sus scrofa*, which is now recolonising large areas of Europe (Thurfjell et al. 2009).

Wild boar can cause significant damage to crops (Genov 1981, Feichtner 1998, Bieber & Ruf 2005, Schley et al. 2008) and is also one of the more popular game species for recreational hunting (Geisser & Reyer 2004). Hunters commonly feed wild boar to facilitate hunting and sometimes also in an effort to reduce crop damage (Geisser & Reyer 2004). Wild boar hunting by humans has been studied previously (Feichtner 1998, Sodeikat & Pohlmeyer 2003, Geisser & Reyer 2004, Keuling et al. 2008b, Tolon et al. 2009), but few studies on wild boar and hunting have provided data on the whereabouts of animals through radio telemetry (Sodeikat & Pohlmeyer 2003, Keuling et al. 2008b, Tolon et al. 2009). Previous research has suggested that the wild boar has two main reactions to disturbance from hunting: hiding or running away (Sodeikat & Pohlmeyer 2003). Escape distances of wild boar after drive hunts, where hunters and dogs flush and chase wild boar towards other hunters, can be up to 6 km (Sodeikat & Pohlmeyer 2003). They usually show site fidelity (Graves 1984, Keuling et al. 2008a) and typically return to their home range a few weeks after being disturbed by a drive hunt (Sodeikat & Pohlmeyer 2003, Keuling et al. 2008b).

In this paper, we study the effects of different types of hunting activities on movement of female wild boar equipped with Global Positioning System (GPS) collars in southern Sweden. We also quantify movement and habitat utilisation after wild boar had fled to a refuge home range.

We predict that running away and changing home range occur when hunting is perceived as intense and in close proximity, resulting in an increase in movement. Conversely hiding should be the strategy to be used when hunting is not perceived as an immediate danger, i.e. less intense or further away, resulting in a reduction of movement. When leaving their home range, wild boar should move less and use habitats providing cover more than habitats providing forage compared to the period before the hunt in their home range, since the perceived risk should be higher after they have been chased.

Material and methods

Study area

Our 16,000 ha study area is located in southern Sweden, in the county of Scania (N 55°28'-55°43', E 13°44'- 14°12'; WGS84) within the Nemoral vegetation zone (Ahti et al. 1968). The area comprises three large estates and several smaller land owners, and it is a mosaic of open and closed habitats. Agricultural land covers most of the area (65%) with wheat, rye and oats being the main crops. Open pastures and other open land cover 12%. The deciduous forest covers 7%, and is dominated by beech *Fagus sylvatica* and oak *Quercus robur*. About 12% of the area is classified as mixed deciduous and coniferous forest, mainly Norway spruce *Picea abies*. Other habitats such as water and urban areas make up the remaining 4% of the area.

Hunting

All hunting activities on the estates were recorded by professional game managers. The main types of hunts were drive hunts, pheasant *Phasianus colchicus* hunts, duck *Anas platyrhynchos* hunts, small-game hunts and still hunts, during which hunters try to remain unnoticed by game through hiding (Table 1).

The wild boar population

The density of wild boar in the area is high (> 2 wild boar/km^2), partly due to supplementary feeding, mostly with sugar beet, but everything from maize to candy and bread were supplied at feeding stations surrounding the estates. The net supplementary feeding amounted to 100-200 kg/ha and year according to the game managers, which would be a large amount compared to amounts used in other countries in Europe (e.g. Keuling et al. 2008a). The hunting bag in the region was about 1 wild boar/km^2, but it was smaller on the estates (0.4 wild boar/km^2; A. Jonsson, pers. comm.).

Wild boar capture and fitting of GPS/GSM collars

To fit radio-collars, wild boar were anaesthetised

Table 1. Intensity of hunting pressure.

Type of hunting	Intensity	Dogs	Time of day, season, hunts/year	Target	Habitat
Still	Low, hunters wait for game	No	Morning or evening, August-January, 3/year	Ungulates	All, usually where animals feed
Duck	High, ducks are shot by hiding hunters, > 100 shots fired/ hunt	Yes, retrieving	Daytime, August-October, 5/year	Ducks	By water
Drive	High, game is chased towards a shooting line	Yes, chasing	Daytime, September-January, 11/year	Ungulates	Daytime resting areas
Pheasant	High, game is chased towards a shooting line, often > 100 shots fired.	Yes, retrieving	Daytime, October-December, 6/year	Pheasants	Open areas and brush
Small-game	Low-medium	Yes, searching	Daytime, August-January, 2/year	Small-game	Open areas and brush
Unknown	Not known, probably different, the category is added as a few times hunting was conducted and the method was not noted by the game keepers.				

using drugs administered via a tranquilliser gun. This was done either from a car or by still hunting close to feeding stations. We used a standard dose consisting of 10 mg Medetomidine, 20 mg Butorphanol and 500 mg Ketamine, as described in Kreeger & Arnemo (2007). Darted wild boar were usually anaesthetised within 2-3 minutes, or at a distance of about 200-300 m from where they were darted. To ensure that darted animals could be relocated, darts were fitted with a VHF transmitter. Each wild boar was equipped with a GPS/GSM Plus 2D collar from Vectronic Aerospace GmbH. A total of 15 females were collared. The collars obtained a position every half hour and transmitted accumulated positions to a computer using 'Short Message Service' (SMS) on the cell-phone network. Our study was approved by the Animal Care Committee for Northern Sweden, Umeå (Dnr A18-04).

Data collection

We only used positions with a dilution of precision (DOP) of < 5, and 3D positions calculated based on at least four satellites. Our study area was relatively flat with an altitudinal range of 100 m over 25 km; hence space use is unlikely to be affected by topological features of the landscape (Moen et al. 1996, Cain et al. 2005, DeCesare et al. 2005). On average, 81% of the attempts to localise a position were successful at night and 75% during the daytime for all collared wild boar, except for two individuals with malfunctioning collars. Because of the high success rate, we made no corrections for unsuccessful location attempts (Zweifel-Schielly & Suter 2007). In total, we retrieved > 100,000 successful locations from the 15 individuals. We analysed the data in ArcGIS 9.1 with Hawth's Analysis Tools for ArcGIS extension and in R 2.10.

Analyses of the effect of hunting on movement of wild boar

We tested the effects on movement of all collared wild boar during the same day and the following night for the different types of hunts. We used a generalised linear mixed-effects model with movement as the response variable (Gamma distributed with an inverse link function; Venables & Ripley 2002). The explanatory variables chosen were sun up or down, month of year and type of hunt (drive hunt, small-game hunt, pheasant hunt, duck hunt, no hunting or hunting with an unknown method; see Table 1) and the interaction between sun up or down and type of hunt. The variables were chosen to explore the effects of hunting and to account for major factors affecting wild boar movement such as seasonality and daily activity patterns. We used identity contrasts to distinguish the effects of the different types of hunting from no hunting, day from night and the interaction between day and night and type of hunt.

Analyses of the effect of movement and habitat use by wild boar leaving their home range

To analyse effects on movement of drive hunts when female wild boar escaped, we used data from wild boar that escaped known drive hunts and left their previous home ranges. For wild boar that moved into refuge ranges for at least a week (seven nights), we calculated the distance between the centroid point of the initial home range and the first daily rest in the refuge range. We used a period before the drive hunt of the same duration as the time the wild boar stayed in the refuge range as a basis for comparison. We constructed generalised linear mixed effects of models for different response variables; one with movement (Gamma distributed with an inverse link function) and four with habitat (Binomially distributed with a logit link function) as response variables. To correct for repeated measurements from the same individual, we fitted individual wild boar as a random variable. Hunting (before the hunt, during the hunt or after the hunt), month and sun up or down were fitted as fixed variables. Day or night and month were added to account for seasonal and daily differences in movement patterns.

Results

Type of hunt had an effect on movement of female collared wild boar. The effect of type of hunt was different during the day of the hunt compared to the night following the hunt (the interaction between sun up or down and hunting type), which means one type of hunting may increase movement of wild boar during the day of the hunt, but decrease movement during the following night. During the day of pheasant and drive hunting wild boar movement increased ($P < 0.001$), whereas duck hunting ($P < 0.05$), still hunting ($P < 0.01$) and unspecified hunting ($P < 0.001$) reduced their movement (Fig. 1). This suggests that unspecified hunting usually was a type of hunting that was noticed by wild boar, but was not targeting wild boar specifically. During the night after the hunt, pheasant hunting ($P < 0.001$) and still hunting ($P < 0.01$) reduced movement, whereas no effects were found from other the types of hunting. Factors other than hunting that were important for movement were month of the year and sun up or down (all Ps < 0.001). Identity contrasts applied to month of the year showed that all months except March and April differed from January (all Ps $<$ 0.001).

Six wild boar left their home range as an effect of a drive hunt; they moved between two and 20 km and stayed in the refuge area between six and 29 days. Hunting events that resulted in flights showed that boar movement was affected by drive hunts (Fig. 2). Female wild boar moved more when moving between the home range and the refuge range than before drive hunts, and less in the refuge range (both Ps < 0.001). The drive hunts that resulted in flight ($N = 6$) had an effect on the use of all four tested habitats either during relocation or in the refuge range (Fig. 3). Coniferous and deciduous forest was utilised more during relocation whereas open areas were less utilised. After relocation crop fields and forests were utilised more, whereas open areas were utilised less (all Ps < 0.001).

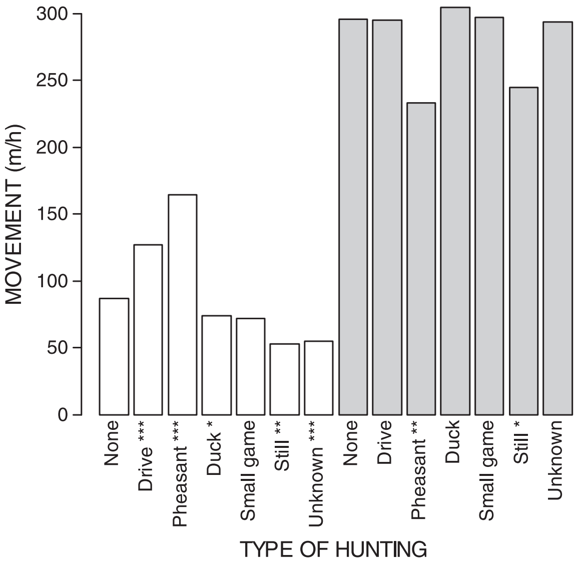

Figure 1. Effects of different types of hunting on the average movement speed of 15 female wild boar during November which is the month when most types of hunting commonly are performed. The white bars represent the day of the hunt and the grey bars represent the following night. Asterisks indicate significant differences compared to no hunting (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ based on identity contrasts).

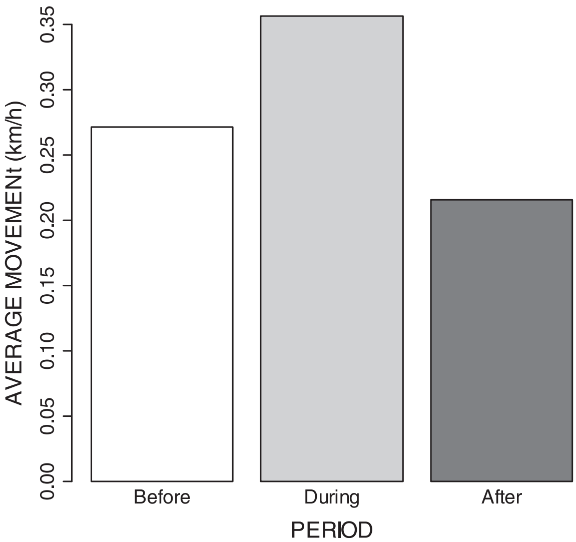

Figure 2. Effect of drive hunts that resulted in six wild boar leaving their home range. During the relocation wild boar moved more than before the hunt, and in the refuge range wild boar moved less ($P <$ 0.001 based on identity contrasts).

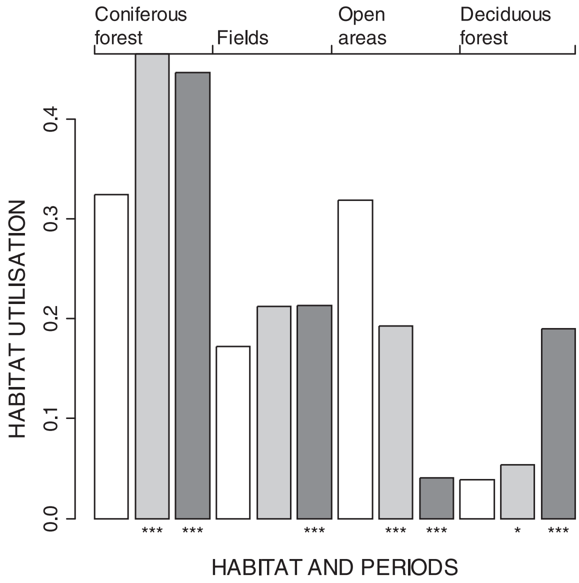

Figure 3. Effects of six drive hunts on habitat use. The bars show the effects of drive hunts on each model of habitat choice (probability), before drive hunts (□), during (■) and after (■). Asterisks indicate whether there is a difference compared to the period before the drive hunt (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ based on identity contrasts).

Discussion

Our study suggests that wild boar react to hunting by either fleeing or hiding, depending on the intensity of the hunt and the distance to the hunting activity. After a flight reaction, wild boar reduced their movement and used habitats with good cover (to reduce visibility), but they also increased their use of habitats containing natural forage, possibly to avoid competition with resident wild boar using supplemental food.

Drive and pheasant hunts flushed wild boar out of their daily rest (see also Sodeikat & Pohlmeyer 2003, Keuling et al. 2008b, Scillitani et al. 2010). Pheasant hunts also resulted in an overall reduction in movement during the night after the hunt. A possible explanation for the stronger reaction to pheasant hunting is that they may involve more people and that more shots are fired, thus creating a greater disturbance, leading to more cautious behaviour the night after the hunt. Duck and still hunting reduced boar movement during the same day, but only still hunting reduced their movement the following night. There may be different mechanisms behind these similar reactions. Duck hunting is probably perceived to be just as intense as pheasant hunting but limited to wetlands, which means that it is usually further away, resulting in hiding rather than fleeing. Still hunting is often carried out after sun down, and as the wild boar does not perceive still hunters as an immediate risk, they react to still hunters by reducing their activity to reduce risk of detection. Our data clearly show that hunters are noticed by wild boar when still hunting, but as animals are not flushed, they stay in hiding.

Drive hunts resulted in escapes where wild boar left their home range and ran longer in our study than in previous studies performed in Germany (Sodeikat & Pohlmeyer 2003, Keuling et al. 2008b). The reasons for these differences may be several. Difference in dog size used; terriers < 15 kg were used in Germany (O. Keuling, pers. comm.) and medium-sized dogs of 20-40 kg were used in our study. Harvest of wild boar is less intensive (1.1/km^2) in our study area than in the study area of Keuling et al. (2008b; 2.8-5.1 animals/km^2). The fragmentation and composition of the habitat seems to be similar on the European spatial pattern map (Vogt et al. 2007) although there are more forests in the German study areas than in ours (Sodeikat & Pohlmeyer 2003, Keuling et al. 2008b). Thus, fragmentation does not seem to be a main reason for the difference in the results.

After fleeing to and relocating in a refuge range, wild boar reduced movement and changed their habitat use. Habitat with better cover, e.g. forest, was used more and open areas were used less. This suggests that the perception of an increased risk by wild boar makes them more cautious and increases the effect of fear on habitat use (Brown et al. 1999) as predicted. However, the increased use of crop fields after relocation is not in accordance with our prediction that foraging habitats should be used less. Instead, the increased use of crop fields and deciduous forest may be due to competition with resident wild boar groups. Crop fields and deciduous forests contain food that may not be monopolised in the same way as food at feeding stations. This may mean that part of the reason to why they return to their original home range may be competition with resident wild boar groups.

Further studies of hunting at a lower density of wild boar and at the edges of their current distribution might reveal if the effects of drive hunts on their behaviour are partially due to competition with other groups of wild boar or not. Such studies might also shed light on the recorded differences in flight distances, although controlled experiments changing one parameter at a time would be preferable. Spatial data on hunters' and dogs' location during hunts would be preferable and would clarify the effects of distance and intensity of drive hunts on the reactions of wild boar. A spatial study including several areas with different hunting regimes (Keuling et al. 2008b) and with focus on damage to crops might be the most useful study from a management perspective.

Conclusions and management implications

Most types of hunting affect the behaviour of wild boar. But wild boar are not easily driven out of their home range by hunters and their dogs. However, when wild boar flee, pronounced changes in their movement and habitat use occur. These effects may arise from an increased perception of risk, but might also be due to increased competition with resident wild boar. The most important implication for crop damage is that female wild boar that have fled from drive hunts increase their use of crop fields. Thus, drive hunts should take place after the crops have been harvested.

Wild boar also show behavioural modifications during still hunting (even before any shot has been fired), suggesting that hunters have commonly been detected. Therefore, the strategies to stay unnoticed for hunters are to some extent inadequate and if improved, they might allow for an increased hunting success.

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