ORIGINAL PAPER

Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges

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Abstract Rapidly increasing populations of wild boar in Sweden and Europe cause much damage to crops, and there is a critical need for more knowledge about their habitat utilization, especially of agricultural fields. In our study, we first assess the spatial pattern of damage in relation to the edges of agricultural fields. Next, with the aid of global positioning system collars, we studied the pattern of movement of wild boar on agricultural fields. Finally, in order to understand the role of agricultural fields, we studied how habitat selection may vary throughout the year. We found edge effects on damage patterns in agricultural fields. During winter and spring, we found wild boar not only to follow edges, but also to move along narrow landscape elements within agricultural fields. In our habitat analysis, we found strong avoidance of exposed agricultural fields throughout the year, but significantly less when crops are ripe.

Keywords GIS · Edge effect · Damage · Sweden

Introduction

Wild boar (*Sus scrofa*, L.) were hunted to extinction in Sweden in the seventeenth century, and reintroduced and hunted to extinction again in the 1940s. In the 1970s, wild

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boar escaped from enclosures where they were held for hunting and meat production. The population has grown rapidly in the southern and central parts of Sweden and wild boar are once again considered a part of the Swedish fauna (Truvé and Lemel 2003). Currently, farmers are suffering crop damage, and hunters feed the wild boar to increase their numbers and provide hunting opportunities. This has lead to a conflict of interests—a common problem in many areas of Europe (e.g., Wenum et al. 2003; Calenge et al. 2004; Geisser and Reyer 2004; Herrero et al. 2006). From a management perspective, it is important to evaluate and estimate the activity patterns of wild boar (Pettersson 2007).

In this study, we have both mapped the damage on agricultural fields to investigate their spatial pattern, and we have followed 17 large sows equipped with global positioning system (GPS) collars. Our aims were to determine the spatial patterns of damage to agricultural fields, to evaluate the spatial patterns of wild boar movements on the agricultural fields, and to analyze the habitat selection of wild boar in order to examine how this (especially their use of agricultural fields) may change over time.

Damage and forest edges

Previous studies have suggested that damage caused by wild boar is not located randomly with respect to forest edges (e.g., Briedermann 1990; Geisser 1998; Lemel 1999). If fields are located close to a forest edge, damage levels are often very high (Lemel 1999) and a relationship among the fragmentation of the landscape, the length of the forest-field edge and damage intensity have been suggested (Drozd 1988). In the scientific literature, there are few quantitative studies on how wild boar forages with respect to edges (e.g., Geisser 1998; Meriggi and Sacchi 2001) although it has been suggested that wild boar feeds close to edges in

order to be able to escape into the forest. Thus, our first aim is to quantitatively evaluate how wild boar forages with respect to distance from forest edges. We do this by testing the hypothesis that wild boar prefer to feed close to a forest edge by determining if the distance from wild boar damage to the nearest forest edge (i.e., cover) is indeed less than expected by chance.

Moving along edges and narrow landscape elements

In addition to the possible edge effects discussed above, many hunters claim that wild boar follows lines in the landscape such as hedges, ditches, stone walls, rows of trees or bushes, or streams, something that has not been evaluated in the published literature. This type of edge effect with narrow (i.e. 1 to 11 m) landscape elements is now possible to study with the aid of GPS technology and the highly detailed maps we use here. Thus, a second aim of this study is to evaluate if wild boar use these narrow landscape elements to move through their home ranges.

Seasonal variation in habitat selection

Finally, it is also of interest to show which habitats are utilized by wild boar during the night when they are active (Sodeikat and Pohlmeyer 2003; Keuling et al. 2008a), as this is the time of day when damage occurs. Wild boar usually rest in dense vegetation during daytime (Gerard et al. 1991; Lemel et al. 2003; Keuling et al. 2008a, 2009). More importantly, from a management perspective, we need to know to what extent the pattern of habitat selection may change when the crops are ripe, as suggested by Lemel (1999). Thus, our third and final aim is to evaluate how the pattern of nighttime habitat selection may change throughout the year, and to test the hypothesis that wild boar will particularly use agricultural fields during summer (July and August), when the crops are ripe in southern Sweden.

Materials and methods

Study area

The study area is located in the Nemoral vegetation zone (Ahti et al. 1968) in the county of Scania in southern Sweden (N 55°27′–55°27′ E 13°45′–14°09′ 2002, WGS84). The area is covered by five main habitat types; agricultural land (65%) where wheat (*Triticum aestivum* L.), rye (*Secale cereale* L.), and oats (*Avena sativa* L.) are the main crops, but there are also some planted willow "forests" (*Salix* sp. L.), grown for energy production. Open areas, like pastures, meadows, and areas close to water dominated by common reed (*Phragmites australis* Cav.) covers about 12% of the

study area. The deciduous forest (7%) is dominated by beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.). The mixed coniferous forest consists mainly of planted stands of Norwegian spruce (*Picea abies* L.; 12%). Less than 2% of the area is covered by water, usually shallow lakes with a large variation in area throughout the year due to changing water levels. Housing estates cover only a very small fraction of the area. The main study area is located on three different estates, Högestad, Christinehof, and Kronovall. The three estates cover around 16,000 ha in total.

Hunting is carefully recorded in all of these three large estates by professional game keepers, but in the surrounding areas hunting is not well documented as there are many landowners and no coordination among hunters. There is a high density of wild boar due to extensive supplementary feeding and baiting, mostly with sugar beet (*Beta vulgaris* L.). A variety of other items including maize to surplus material from producers of candy and bread are used by hunters and landowners at feeding stations surrounding the study area. The net supplementary feeding is about 100–200 kg ha^{-1} year^{-1} according to the game keepers. The hunting bag in the study area is about 0.4 wild boar km^{-2} while on smaller surrounding farms, the hunting bag could be up to a hundredfold higher (e.g., up to 400 wild boar km^{-2}) with a large variation (Jonsson 2006, pers. comm.).

Damage inventory

First, to evaluate the spatial pattern of damage with respect to forest edges, we studied wild boar rooting damage on pastures and meadows of the study area. The time of this survey was deliberately chosen to be after agricultural fields (e.g., wheat, oats) had been harvested because it is difficult to precisely quantify the area damaged in such fields (Mackin 1970). To test if forest edges are important, we wished to avoid the potentially confounding effects of ripe crops for this first study.

The damage inventory was carried out during 6 weeks in autumn 2003 and all damage was located using a Garmin hand-held GPS device. All farmed fields within the study area were inspected, and if damage was found, the center of each was located using the GPS and the size of the damaged area was measured. The damage inventory was done by one person to ensure consistent data.

Capture, collars, and positional data

To gather positional data of animals (rather than the damage they caused) we equipped 17 wild boar with GPS collars. We immobilized wild boars with a tranquilizer gun from a four-wheeled vehicle out on the fields after the crops were harvested, or from stands close to the feeding stations. Wild boar were 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 min later. To guard against the loss of animals after darting, we used a transmitter–dart system (Pneu-dart, Williamsport, PA, USA).

After immobilization, we equipped 17 large sows from different groups with a GPS/GSM Plus 2D collar from Vectronics Aerospace GmbH (Fielitz 2003). The collars were programmed to acquire a position every half hour and 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.

All 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). This may yield a somewhat biased sample of all positions, since it is more difficult for the GPS unit below a dense canopy to localize satellites (Moen et al. 1996; Cain et al. 2005; DeCesare et al. 2005). Testing our preliminary data, we found that an average of 28% of the attempts failed during the night (i.e., when the wild boar were active). We therefore deleted three collars from our test that functioned only intermittently due to hardware failure, and which contributed to this bias. This brought down the average of failed attempts to just 19% during the night, which is regarded as acceptable (Zweifel-Schielly and Suter 2007) and 25% during the day. 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 (Lemel et al. 2003) and the fact that the GPS units have more difficulty in obtaining a good position under dense canopies (DeCesare et al. 2005; Zweifel-Schielly and Suter 2007).

Detailed maps of the study area were created from the digital Swedish terrain map, in turn based on aerial photographs from 1993 (taken from an altitude of 9,200 m) with ground-truthing fieldwork performed in 1994 and updated in 2002 by Lantmäteriet (2008). With the help of rectified aerial black and white photographs taken in 2004, we digitalized linear objects such as hedges, rows of trees, low stone walls, etc. to enhance the map in order to be able to find what the boar might perceive as cover and safe corridors. The resulting maps with these narrow landscape elements were of very fine resolution: as far as we have been able to determine, it is presently the highest resolution yet used in studies of wild boar habitat selection and/or movement. Unlike previous studies, this high resolution allows us to test if these narrow landscape elements may be important to wild boar.

Data analyses

Analyses of wild boar positions were done in ArcGIS 9.1 (ESRI 2005), JMP (SAS 2007), SAS (SAS 2001), Access (Microsoft 2003a), and Excel (Microsoft 2003b). Wild boar positions were taken between August 2004 and November 2007.

Damage and forest edges

For the analysis of the spatial pattern of damage per se, we used a simple conservative approach to examine the damage pattern found in the study area. The distribution of wild boar damage, regardless the size of the damage, was compared with an equal number of random points created in a GIS program (Marcum and Loftsgaarden 1980). If wild boar select foraging areas on meadows and pastures without regard to distance from edges, there will be no statistically significant difference between the distance of the damage or the random points to the nearest forest edge. The random points were located on the same open areas of the survey area that were damaged by wild boar. The use of random points is thus a simple and powerful tool to test our first hypothesis that wild boar prefers to feed close to a forest edge.

Moving along edges and narrow landscape elements

Our second aim was to test if the wild boar follows narrow landscape elements. Aerial photographs allowed us to easily detect and add linear features as narrow as 1 m to the maps, so it seems very likely that we detected most of the habitat features important to wild boar. The wild boar positions were divided into night and day and into seasons that were considered biologically relevant (Keuling et al. 2008a, 2009) with seasons starting 1.5 months later, and with shorter summer and longer fall to fit climate in Sweden (Lemel 1999) rather than north-eastern Germany. The seasons considered were (a) the summer when crops are ripe (July and August in our study area), (b) fall, after the harvest when mast can be available, (September–December), (c) winter, when there is little mast and sometimes snow, (January–March), and finally (d) spring, which is the period when the growing season has started but the crops are not consumed by the boar (April–June).

All positions for each wild boar were used to create minimum convex polygons (MCP) for each animal in order to be able to estimate the home range used by each boar (Mohr 1947). The agricultural fields that were covered by the MCPs for each boar were sampled with 5,000 random positions per boar. The distance from the random positions to the narrow landscape elements were compared to the same distances for the actual positions. The study was thus

a design III (Manly et al. 1993, 2002) which means that what was considered available to each wild boar depended on what was actually available to each separate animal (within its MCP home range in this case), thus avoiding an arbitrary definition of the boundaries of the study area, or what was "available" to the animals to select from. Using the 100% MCP ensured that our random points were taken from the area actually available to each wild boar.

Differences in distance to narrow landscape elements between the actual positions and the random points for each wild boar were tested with a binary logistic regression per season as suggested by Manly et al. (1993, 2002). We used the nighttime data to analyze selection as wild boar are mainly nocturnal and we were not interested in habitat selection of daytime resting sites (Sodeikat and Pohlmeyer 2002; Keuling et al. 2008a). This created several resource selection functions (RSFs), one per season and individual. The function of distance to edge was then tested in a sign rank test (Siegel and Castellan 1988).

Seasonal variation in habitat selection

For our third aim, to test the habitat selection of wild boar among the seasons, we used the MCPs to find the composition of habitats available to each boar, thus again following a Type III design (Manly et al. 1993, 2002). The selection ratios were calculated separately for each season and only nighttime data was used (see above). Selection ratios and Bonferroni adjusted confidence intervals were calculated as per Chapter 4 in "Resource selection by Animals" (Manly et al. 1993, 2002).

Results

Damage and forest edges

Comparing the distance of damage to forest edge, our results clearly confirm that wild boar damage was located much closer to the forest edge than expected by chance alone (damages 54 m from forest edges vs. random points 127 m $N=171$, $\chi^2=38.6482$, $p<0.0001$).

Moving along edges and narrow landscape elements

The distance between the wild boar positions on the fields and the edges or linear objects compared to the same distances to random points tested in the logistic regression resulted in several different RSFs (Manly et al. 1993, 2002). When the distance to the edge from the RSFs was analyzed in the sign rank test (Siegel and Castellan 1988) per season, the results were significant during the nights of winter and spring indicating that, on average, wild boar were closer to edges than expected by random points ($p=0.0098$ for spring and $p=0.032$ for winter).

Seasonal variation in habitat selection

We found statistically significant results showing that the wild boar sows avoid agricultural fields during all seasons, but significantly less so during the summer when crops are ripe (Fig. 1). They also preferred the mixed coniferous forest during all seasons except summer; the same pattern can be seen for open areas, except that they are preferred

Fig. 1 Seasonal selection for or against different habitat types by wild boar (*Sus scrofa*) 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*
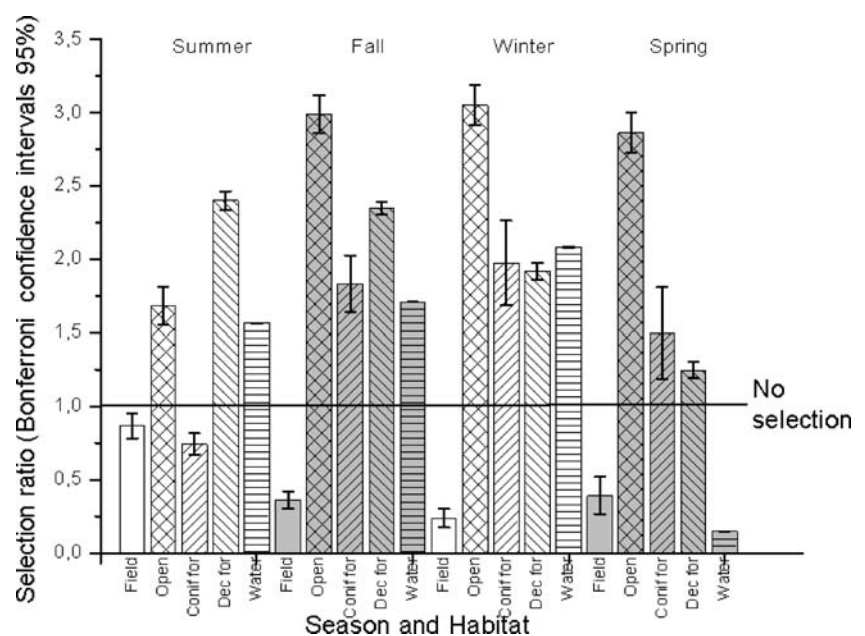
during all seasons but significantly less during the summer. Deciduous forest was preferred during all seasons but significantly less so during the spring. Water was a preferred habitat during all seasons except spring when it was avoided. Open areas were the most preferred habitat during all seasons but summer, when deciduous forest was most preferred. Deciduous forest was more preferred than coniferous forest during summer and fall, but no difference was seen during winter and spring.

Discussion

Damage and forest edges

Confirming our first hypothesis (that wild boar prefer to feed close to a forest edge), the analysis of the spatial pattern of wild boar damage revealed strong evidence that damage was located closer to the forest edge than expected by chance alone. The average damage was located 54 m from edges vs. random points 127 m from edges. This suggests that the distance to potential escape cover is indeed a major aspect that influences wild boar foraging behavior (Spitz and Janeau 1995). In areas with small fields, damage levels may be high everywhere because all areas of these small fields will be close to a forest edge. The reason that wild boar forage close to edges may be the result of an innate tendency (shaped by, for example, fear of wolves, see Jedrzejewski et al. (2002)) or hunting (causing the same effect). In either case, the centers of large agricultural fields may be spared from severe wild boar damage. An exception is when hunting pressure in the fields is lower than in the surrounding area, then centers of large fields apparently act as refuges for wild boar (Keuling et al. 2008b).

Moving along edges and narrow landscape elements

The second aim of the study, using high-resolution maps and GPS data to test the hypothesis that wild boar follow narrow landscape elements and edges while moving through the exposed crop fields yielded mixed results. When leaving foraging habitats, we might expect that the wild boar were unwilling to expose themselves and thus stayed close to cover (Lemel 1999; Calenge et al. 2004). Considered on a year-round basis, this did not seem to be the case on the population level.

Indeed, the prediction that wild boar will follow edges and narrow landscape elements was supported during the nights of winter and spring. We suggest that the non-significant results during summer were caused by ripe crops providing both cover and forage while hunting pressure was low. During the fall, when wild boar are hunted and

there is only a little leftover food on the fields, it is much more difficult to explain. Perhaps there is a learning curve involved which does not have an effect on behavior until late in the hunting season (winter). Still, the fact that the wild boar in our study did not have a significant preference for edges and narrow landscape elements during fall is a very interesting finding that requires further study and more detailed field work.

Seasonal variation in habitat selection

Our third hypothesis that wild boar will utilize open fields during summer (when crops are ripe) was supported. The results show that wild boar avoided the exposed agricultural fields and preferred the cover of the mixed coniferous forest during all seasons except summer, when they avoided the mixed coniferous forest and avoided the agricultural fields significantly less than during the rest of the year (Fig. 1). One interpretation of this might be that the agricultural fields are of great interest as a food source for the wild boar only during the season when crops are ripe, and that artificial feeding stations (in the mixed coniferous forest) are less attractive than ripe crops, and thus not utilized. This agrees with earlier studies in Sweden (Lemel et al. 2003) and Germany (Keuling et al. 2009).

Agricultural fields and mixed coniferous forest are perhaps the two most extreme habitats, one is very exposed, and one is very dense (usually consisting of very dense Norway spruce plantations). One might be surprised at how many wild boar preferred the class "open areas" as this category shows the same seasonal pattern as the coniferous forest (Fig. 1), except they did not avoid it during the summer, just preferred it significantly less during the rest of the year. Since this category often has small patches of trees and shrubs, and consists of some pastureland, it may provide good cover for wild boar with plenty of feeding opportunities. During summer, with the abundance of crops, this habitat becomes less attractive. It is interesting to see that the main patterns for open areas and mixed coniferous forest are the same; we speculate that perhaps these areas are used for the same purposes, mainly cover and to some extent access to feeding stations.

The deciduous forest is more preferred than the mixed coniferous forest, and it is only less preferred during spring, than other times of year. Here, we speculate that during spring, there is unlikely to be any mast left. This does not account for the higher preference of this habitat during summer, but it is possible that wallowing in muddy areas or eating some plants of the forest floor might be a possible explanation for the preference during this time of year. It is interesting to see that the wild boar seems not to prefer the deciduous forest over the coniferous forest during winter. The opposite pattern was shown in Poland (Fonseca 2008).

We consider it a likely explanation that hunters provide more food in Sweden (i.e. 100–200 kg ha^{-1} year^{-1} in our study area!), and mast therefore may be less important, thus enabling the wild boar to stay in the cover of the coniferous forest. It might be surprising that our wild boar showed a preference for water, but we suggest that this may be because the waterline will change over the year, thus containing the zone of common reed when water levels are below those shown on the maps (i.e., summer, fall, and winter). In this zone, mud-bathing, resting, and rooting are likely activities. During spring, our analysis revealed that the water habitat is avoided. We suggest that the high water levels in spring mean that the shoreline shown on our maps is too deeply flooded for wild boar to forage in at this time, and that they thus utilize the reed zone that is outside of the area classified as water on the map. In other words, wild boar do select habitats along the edge of water all year long, but seasonal variation in water levels are not detectable on our static maps.

Based on the results of our analysis, we suggest that the next step for researchers working with large amounts of high precision spatial data, such as GPS collar data, is to start thinking about the background material and scale. With more and more accurate GPS positions, detection of patterns related to small-scale landscape elements omitted from the maps is possible, and these are potentially important for many species, such as the wild boar. Therefore, there is a need for more accurate maps such as the ones constructed here.

Conclusions

The results of our study confirmed that the distance to forest edges, and distance to potential cover are major factors influencing the spatial pattern of damage caused by wild boar foraging. In areas with many small fields, little can be done except to reduce the population, but in areas where the fields are larger, it may be that hunting, especially in the fields (Keuling et al. 2008b), or an innate tendency of wild boar to forage close to forest edges, may help spare at least the center of large fields from severe damage.

Our second hypothesis that wild boar would tend to follow the edges and narrow landscape elements when they are on the agricultural fields, was supported during 6 months of the year. Thus, in addition to the size of fields, our analysis shows the importance of these narrow landscape elements during winter and spring. This has to be considered when planting crops that are sensitive to damage from wild boar.

Our third hypothesis, that wild boar will utilize agricultural fields during summer, was supported. The similarity in patterns of habitat use suggest their use as cover (open areas and coniferous forest) and the probable food-dependent shift from preference of deciduous forest (Fonseca 2008) to coniferous forest. This leads us to conclude that active damage prevention like hunting on agricultural fields should take place during this time of year.

Finally, in order to understand the spatial patterns of damages and movement, many factors have to be considered, and our results show that it may not be an easy task. Our results shed light on the patterns of damage and movement by wild boar, and on the spatial utilization of the narrow landscape elements found in the matrix of the crop fields. These narrow landscape elements have been largely overlooked, but our analysis suggest that they might be an important aspect of habitat selection by wild boar, and thus are an interesting feature worth further investigation.

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5:169–211

Briedermann L (1990) Schwarzwild. VEB, Berlin

Cain JW, Krausman PR, Jansen BD, Morgart JR (2005) Influence of topography and GPS fix interval on GPS collar performance. Wildl Soc Bull 33:926–934. doi:10.2193/0091-7648(2005)33[926:IOTAGF]2.0.CO;2

Calenge C, Maillard D, Fournier P, Fouque C (2004) Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. Eur J Wildl Res 50:112–120. doi:10.1007/s10344-004-0047-y

DeCesare NJ, Squires JR, Kolbe JA (2005) Effect of forest canopy on GPS-based movement data. Wildl Soc Bull 33:935–941

Drozd L (1988) Damage caused by wild-boars in the field culture in the macroregion of central-eastern Poland. Ann Univ Marie Curie-Sklodowska Lublin 29:224–253

ESRI (2005) ArcGIS. Redlands, CA, USA

Fielitz U (2003) Remote GPS-data transmission via mobile phone. http://www.environmental-studies.de/products/02/gps-gsm_collars.html. Accessed 26 sept 2008

Fonseca C (2008) Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. Eur J Wildl Res 54:361–366. doi:10.1007/s10344-007-0144-9

Geisser H (1998) The Wild Boar (*Sus scrofa*) in the Thurgau (Northeastern Switzerland): Population status, damages and the influence of supplementary feeding on damage frequency. Gibier Faune Sauvage. Game Wildl 15:547–554

Geisser H, Reyer HU (2004) Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J Wildl Manage 68:939–946. doi:10.2193/0022-541X(2004)068[0939:EOHFAF]2.0.CO;2

Gerard JF, Cargnelutti B, Spitz F, Valet G, Sardin T (1991) Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriol (Warsz) 36:119–129

Herrero J, Garcia-Serrano A, Couto S, Ortuno VM, Garcia-Gonzalez R (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur J Wildl Res 52:245–250. doi:10.1007/s10344-006-0045-3

Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Selva N, Zub K, Szymura L (2002) Kill rates and predation by wolves on ungulate populations in Bialow ieza Primeval Forest (Poland). Ecology 83:1341–1356. doi:10.2307/3071948

Keuling O, Stier N, Roth M (2008a) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur J Wildl Res 54:403–412. doi:10.1007/s10344-007-0157-4

Keuling O, Stier N, Roth M (2008b) How does hunting influence and spatial usage in wild boar *Sus scrofa* L. Eur J Wildl Res 54:729–737. doi:10.1007/s10344-008-0204-9

Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mamm Biol-Z Für Saugetierkunde 74:145–152. doi:10.1016/j.mambio.2008.05.007

Kreeger TJ, Arnemo JM (2007) Handbook of wildlife chemical immobilization, 3rd edn. Wildlife Pharmaceuticals, Fort Collins, CO, USA

Lantmäteriet 2008 http://www.lantmateriet.se Accessed 8 okt 2008

Lemel J (1999) Populationstillväxt, dynamik och spridning hos vildsvinet, *Sus scrofa,* i mellersta Sverige. Svenska Jägareförbundet, Nyköping

Lemel J, Truvé J, Söderberg B (2003) Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. Wildl Biol 9:29–36

Mackin R (1970) Dynamics of damage caused by wild boar to different agricultural crops. Acta Theriol (Warsz) 15(27):447–458

Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman & Hall, London, Great Britain

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals, 2nd edn, vol. 1. Kluwer, Dordrect, The Netherlands

Marcum CL, Loftsgaarden DO (1980) A nonmappingtechnique for studying habitat preferences. J Wildl Manage 44:963–968. doi:10.2307/3808336

Meriggi A, Sacchi O (2001) Habitat requirements of wild boars in the northern Appennines (N Italy): a multi- level approach. Ital J Zool (Modena) 68:47–55. doi:10.1080/11250000109356382

Microsoft (2003a) Microsoft Access. Redmond, WA, USA

Microsoft (2003b) Microsoft Excel. Redmond, WA, USA

Moen R, Pastor J, Cohen Y, Schwartz C (1996) Effects of moose movement and habitat use on GPS collar performance. J Wildl Manage 60:659–668. doi:10.2307/3802085

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–249. doi:10.2307/2421652

Pettersson C (2007) Redovisning av regeringens uppdrag ifråga om förvaltning av vildsvin m.m. Swedish Environmental Protection Agency, Stockholm

SAS I. I. (2001) SAS. Cary, North Carolina, USA

SAS I. I. (2007) JMP. Cary, North Carolina, USA

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Sodeikat G, Pohlmeyer K (2002) Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). Z Jagdwiss 48:161–166. doi:10.1007/BF02192404

Sodeikat G, Pohlmeyer K (2003) Escape movements of family groups of wild boar *Sus scrofa* influenced by drive hunts in Lower Saxony, Germany. Wildl Biol 9:43–49

Spitz F, Janeau G (1995) Daily selection of habitat of wild boar. J Zool (Lond) 237:423–434

Truvé J, Lemel J (2003) Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. Wildl Biol 9:51–57

Wenum JHV, Wossink GAA, Renkema JA (2003) Location-specific modeling for optimizing wildlife managemant on crop farms. Ecol Econ 48:395–407

Zweifel-Schielly B, Suter W (2007) Performance of GPS telemetry collars for red deer *Cervus elaphus* in rugged Alpine terrain under controlled and free-living conditions. Wildl Biol 13:299–312. doi:10.2981/0909-6396(2007)13[299:POGTCF]2.0.CO;2