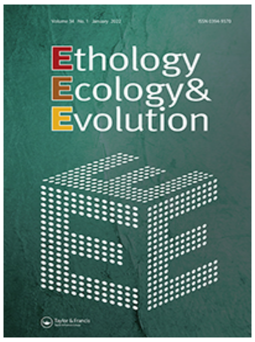

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Effect of supplemental feeding on habitat and crop selection by wild boar in Sweden

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The wild boar population has increased rapidly during the last 2 decades in Southern and Central Sweden. This rise in population size has caused severe damages to agricultural fields through their foraging behavior. Given the hierarchical nature of habitat and resource selection, wildlife management needs to understand the selection on both levels to better understand the ecology of nuisance species and mitigate the damages they infer. Thus, there is an urgent need for more knowledge on the factors that influence habitat selection as a tool in the evidence-based management of wild boar to reduce the losses they cause in the agricultural sector. This study aims to evaluate a common management action (feeding stations) influencing wild boar selection of (1) habitats and (2) resources i.e., crop types, in South-Central Sweden during summer. Eleven wild boars were fitted with GPS/GSM-collars to record movement among different habitats and crops. Wild boar shows a high preference for clear-cuts, agricultural fields, and deciduous forests. The animals showed a high preference for crop fields with oat, spring wheat, and mixed crops. A binary logistic model revealed both a positive and negative significant influence of distance to feeding stations on the selection of different habitats and crop fields. In general, feeding stations influenced the selection of different habitats and crops negatively i.e., the closer a habitat or crop field is to a feeding station, the higher the likelihood of its selection. The study recommends adjustments to wild boar management and cropping systems to reduce damages on highly selected crop fields.

KEY WORDS: wild boar, habitat selection, crop selection, feeding stations.

INTRODUCTION

The wild boar (*Sus scrofa*) is one of the most widely distributed ungulates in the world due to its high reproductive rate, adaptability, and opportunistic feeding (Ballari

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& Barrios-García 2014). Wild boar can adapt to varying climatic conditions and occupies an extremely wide range of ecosystems, from semi-arid environments to alpine grasslands (Massei et al. 2011). In the boreal forest, they also extend their range into mixed deciduous forests as well as pure Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) stands (Wilcox & van Vuren 2009; Olofsson 2015).

In terms of their diet, wild boar is an omnivorous species with a high preference for crops like corn (*Zea mays*), potato (*Solanum tuberosum*), bean (*Phaseolus* spp.), pea (*Pisum* spp.) and sugar beet (*Beta* spp.) (Herrero et al. 2006; Giménez-Anaya et al. 2008; Oja 2017). They also feed on some invertebrates, small mammals and scavenge on dead animals (Barrios-Garcia & Ballari 2012). In Sweden, it has been established that wild boar majorly feed on different types of cereals such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), oats (*Avena sativa*) as well as maize when available (Gentle et al. 2015).

Wild boar can extensively cause crop losses in agriculture, primarily due to their feeding and trampling but also through their rooting behaviors (Apollonio et al. 2010; Ballari & Barrios-García 2014). A drastic increase in wild boar (*Sus scrofa*) population size in Europe over the last few decades has led to intensified farm raids, leading to big economic losses in the agricultural sector (Thurfjell et al. 2009). In Sweden, the wild boar population was extinct at the beginning of the 1700s; but in the 1970s, the population increased after escapes from enclosures (Massei et al. 2015; Cozzi et al. 2019). A study by Massei et al. (2015) estimated the population of wild boar in Sweden to be 200,000–300,000 and a projected annual increase of 25–30%. This rise in population size has caused severe damages to agricultural fields through their foraging behavior.

Currently, Swedish farmers are incurring extensive losses due to crop-raiding. A survey by the Swedish Board of Agriculture (SBA) estimated the costs of wild boar damages on crops to be 60–70 million US dollars per year (Andersson et al. 2018; Engelman et al. 2018). According to Swedish legislation, wild boar is not a protected species and thus farmers and landowners are not compensated for the losses (Schön 2013). In this case and from a management perspective, improved knowledge on how to reduce the damages is urgently required.

Habitat and resource selection are central concepts in wildlife research (Horne et al. 2008; Crowell et al. 2016). Resources that an individual requires to survive and reproduce typically occur in limited quantity i.e., as food and shelter. Currently, animal-borne global positioning system (GPS) units can be used to determine the selection or avoidance of habitat through measuring the use of resources and comparing it to its availability (Cagnacci et al. 2010). Habitat selection occurs at multiple spatial scales where the home range usually represents the broadest level of selection of interest for an individual's performance or fitness (Gaillard et al. 2010). Within the home range, some locations or resources are used more frequently than others. For example, herbivores may choose to feed in different habitats, and within a habitat, they may select specific crops or plant species, individual plants, and particular parts of the plants such as leaves, stems, seeds (Boyce et al. 2003). Given the hierarchal nature of such choices, wildlife management needs to understand habitat and resource selection on multiple levels for many reasons, not the least to better understand the ecology and preventing damages of nuisance or pest species.

Environmental factors have previously been described to influence habitat selection by wild boar (including agricultural activities) (Thurfjell et al. 2009). Despite the forgoing, wild boar habitat use has been found to vary across time and space (Schley et al. 2008; Amici et al. 2012). For instance, water sources such as marshlands, bogs, and wetlands are preferred habitats in some ecosystems and during certain conditions (Paolini et al. 2018).

Thurfjell et al. (2009) reported marked seasonal changes in habitat selection in Southern Sweden. The study established that different habitats such as agricultural lands and deciduous forests were selected by wild boar during summers whereas open areas were the most selected habitat in fall, winter, and spring. This is because they offer large amounts of high-quality food (Schley & Roper 2003; Cellina 2008; Keuling et al. 2009). However, the extent to which these habitats (deciduous forest, coniferous forest, and open areas) are selected considering potential additive effects of an attractant as supplementary feeding on habitat selection is rarely investigated. Feeding stations are used either for diversionary feeding purposes, to divert or distract animals from agricultural fields, as supplementary feeding, to provide additional food for wild boar, or used for baiting in traps or to facilitate hunting (Calenge et al. 2004; Geisser & Reyer 2004; Massei et al. 2011; Miloš et al. 2016).

Moreover, the presence of a feeding station along with agricultural fields and near forest edges likely influences habitat use (Ficetola et al. 2014). For instance, the Maxent model results (Lee et al. 2018) indicated that the extent of damage on farmland by wild boar is closely related to the distance to preferred habitat and food resources.

Further, density and location of feeding stations seem to be important factors affecting the efficiency of artificial feeding for diversionary purposes (Novosel et al. 2012). Still, supplementary feeding is controversial in many areas and irrespective of the purpose, it might have unintended impacts on spatial movements that in turn may be associated with increased damages and also increased population growth rates (Geisser & Reyer 2004; Novosel et al. 2012). This justifies the need for further studies on the effectiveness of feeding stations in reducing wild boar damages in agriculture and natural ecosystems (Milner et al. 2014).

Therefore, this study contributes to fill that gap by evaluating the effect of feeding stations on wild boar habitat and crop selection as a step towards developing future appropriate prevention measures. We hypothesized that feeding stations have a significant influence on both habitat and crop selection by wild boars during summer. This hypothesis was tested through: (1) investigating the general habitat selection of wild boar during the vegetative season, where agricultural land is considered as one among many habitats. We then focused on the specific selection of the crop types among the agricultural fields since most of the management conflicts appear in that habitat. (2) We also evaluated how an anthropogenic factor such as the distance to feeding stations influences the selection of (a) the different habitats and (b) specific crops during vegetative seasons, in Southern Sweden.

MATERIALS AND METHODS

Study areas

The study was conducted in four different sites in three Counties of Sweden (Fig. 1). Koberg estate (58°02′13.42″N, 12°48′32.65″E) in Västergötland County covers approximately 100 km^2 and receives an average annual precipitation of 682 mm and has an average annual temperature of approximately 8.2 °C. The landscape is mostly covered with different types of forest (79%), mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with some mixed deciduous stands. The remaining area consists of arable land and pastures (16%), mires and marshes (2%), lakes, ponds, and gardens around houses (3%). Mörkö Island (65°42′96″N, 16° 06′90″E) in Stockholm County is approximately 59 km^2 and receives an average annual precipitation of about 500 mm and has an annual temperature of between 5–6 °C. The period of vegetative growth – days with an average temperature above 5 °C is about 200 days. The undulating landscape consists of approximately 25% agricultural land, 60% coniferous forest consisting mainly of Norway spruce and Scots pine, and 5% lakes and rivers while the remaining area is covered by deciduous forests. Boo castle site (59°16′26.83″N, 15°12′23.76″E) in Örebro County receives an annual average precipitation of about 555 mm and has an annual average temperature of between 5–6 °C. The main economic activities include active forestry and farming, as well as hunting and fishing. The forests cover approximately 116 km^2 of productive woodland and the arable land consists of about 7 km^2. Grimsö Wildlife Research Area (GWRA) (59°43′45.0″N, 15° 28′20.6″E) in Örebro County is about 130 km^2 and receives an average precipitation of about 555 mm and has an annual temperature of 4.7 °C. The area is covered mainly by mixed coniferous forests (74%), bogs, and mires (18%). About 85% of the area is managed by conventional forest practices. Farmland constitutes 3%, while lakes and rivers constitute 5% of the area. The landscape is relatively flat.

Capturing and radio-collaring of wild boar

To obtain wild boar positional data, wild boars were captured and radio-collared between March and May 2019. They were first immobilized with a tranquilizer gun from a four-wheeled vehicle or on foot alongside baiting traps. The darts had a standard mixture of 10 mg

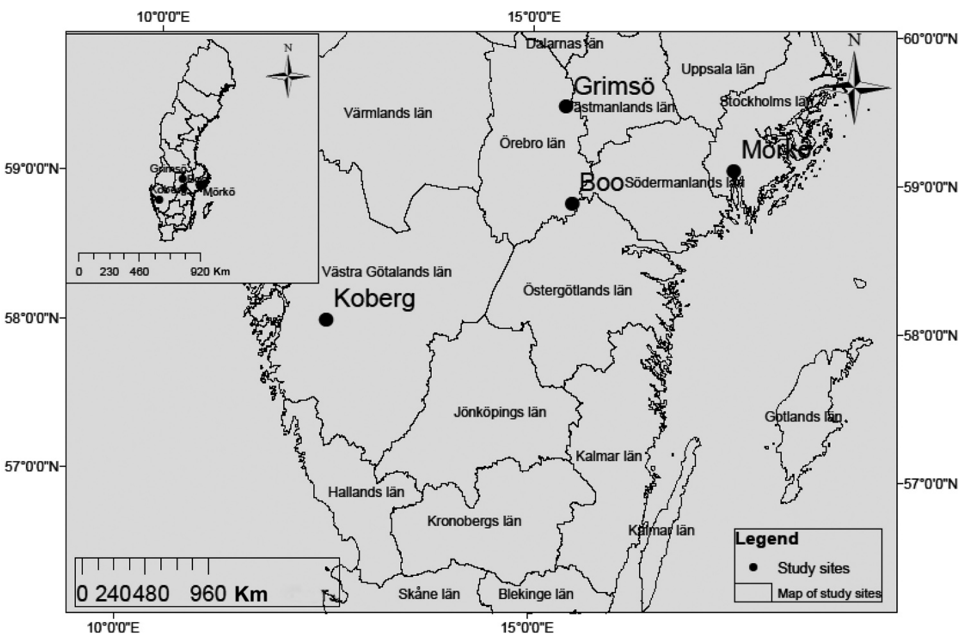

Fig. 1. — Map of the four study areas located in Southern Sweden, Koberg, Grimsö, Boo, and Mörkö.

medetomidine, 20 mg butorphanol, and 500 mg ketamine as described by (Kreeger & Arnemo 2007; Thurfjell et al. 2009). Wild boars were usually found within 100 m of the darting place. After immobilization, 11 wild boars (Grimsö: 2 males and 4 females, Mörkö: 1 male and 1 female, Boo: 2 females, and Koberg: 1 female) were aged, weighed, measured, earmarked, and equipped with GPS/GSM plus 3-D collars from Vectronic Aerospace GmbH, administered with antidotes, and released. The collars were programmed to acquire one position every hour and accumulated positions were transmitted to a server at Grimsö. The movement pattern for the 11 tracked wild boar were monitored during Summer season.

Data collection

To determine wild boar habitat use, we obtained detailed maps of the land use from the Swedish Environmental Protection Agency (SEPA), (Nationella marktäckedata basskikt 2018) and classified them into six habitat types; (1) "open wetlands" (open water for a large part of the year), (2) "agricultural lands" (arable land for cultivation), (3) "other open lands" (vegetated and non-vegetated open lands, areas with artificial surfaces around buildings, roads, and railways as parks and lawns), (4) "mixed coniferous forests" (forests consisting > 70% spruce or pine > 5 m high); (5) "mixed deciduous forests", [forests consisting > 50% broadleaved deciduous forest – mainly birch (*Betula pendula, B. pubescence*), aspen (*Populus tremula*), oak (*Quercus robur*), beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), linden (*Tilia cordata*) and maple (*Acer platanoides*) with trees > 5 m high], and (6) "clear-cuts" (open and re-growing clear-felled, storm-felled or burnt areas with trees < 5 m high). We obtained data on crop type from the Swedish Board of Agriculture (2019). Crop fields were reclassified into six main crop types; "spring barley", "winter wheat", "spring wheat", "oats", "mixed crops" (spring rapeseed, winter triticale, other cereals), and "grasslands".

To determine the effect of feeding stations on wild boar habitat selection, we collected data on 132 feeding stations from farmers and hunters. Automatic feeders with timers provided cereals, peas or mays twice or 4 times a day (3–6 kg in total per 24 hr) depending on the density of wild boars. GPS coordinates for the feeding stations were recorded and coded in Quantum Geographic Information System (QGIS) for analysis.

Data analysis

For the data analysis, we used Quantum GIS version 3.10.0 (QGIS Development Team 2015), and R studio 3.6.2 (R Core Team 2018). Wild boar GPS locations were georeferenced with the QGIS for further spatial analysis. In QGIS, concave hull (alpha shapes) tool was used to draw polygons to generate equal random points to the wild boar locations. Further, used point sampling tool to sample both wild boar location and random locations to create layer in the habitat map. The distance to the feeding sites was computed by getting the distance to the nearest wild boar location and random location using distance to the nearest points tool in QGIS.

A total of 26,911 (mean per individual = 2711, Min-Max = 1374–2912) locations from the 11 wild boar were used to create minimum convex polygons (MCP) in QGIS to estimate home ranges and to generate an equal number of random locations in relation to the actual wild boar locations, i.e., the ratio of 1:1 within the individual home range.

We used logistic regression to estimate habitat selection (Chetkiewicz & Boyce 2009). Habitat selection relies on a use-availability design, wherein locations used by the animal (hereafter "actual wild boar location", coded as "1") are compared to the available surrounding landscape (Boyce & McDonald 1999; Johnson et al. 2006; Manly et al. 2007). For availability data, random locations were generated within each minimum convex polygons (MCP) to represent available locations (hereafter "random location", coded as "0"; Boyce et al. 2003). To analyse the selection of crop fields, we used a subset of 3,904 actual wild boar locations in agricultural fields and generated an equal number of random locations.

The random and actual wild boar locations (1 location per hour) were used to analyze the probability of wild boar selection of different habitats and crop fields as the actual number of locations indicated the time wild boar spent in that habitat. Thus, if the number of actual wild boar locations is higher than the number of random locations in that habitat, then wild boar preferred that habitat. This corresponds to a coefficient significantly higher than 0 in logistic regression.

We used generalized linear mixed models (GLMM) to implement a binary logistic regression (package "lme4"; Bates et al. 2015) where we modeled the probability of selection in R 3.6 (R Core Team 2018) We first tested general habitat selection and in a second step we investigated the possible effects of the distance to feeding stations within the different habitat categories. After that we tested the selection for crop fields within agricultural land and the possible effects of the distance to feeding stations within the different crop fields. Thus, we did not perform any model selection and only tested the four specific models described above. The fixed explanatory variables for habitat selection were: "Different types of habitats" (six habitat categories) and "Distance to feeding stations ($\log_{10}$-transformed)" while for crop selection, the fixed explanatory variables were "Crop fields" (six crop types) and "Distance to feeding station ($\log_{10}$-transformed)". Individual animals were treated as random factors in both models.

The within habitat effects were calculated as the coefficient for the reference habitat plus the habitat coefficient that was relative to the reference. We used the same method to estimate the effect of distance to feeding station in different habitat categories; i.e. the slope of the reference habitat plus the habitat slope relative to the reference.

RESULTS

Habitat selection

Approximately 42.5% of all wild boar locations were found in "clear cuts" while only 6.6% of the random locations were found in that habitat (Fig. 2). Only 24.6% of the wild boar locations were found in "mixed coniferous forests", compared to 58.0% of the random locations (Fig. 2).

The results show that wild boar significantly selected clear-cuts, agricultural lands, mixed deciduous forests, and other open lands. Open wetlands and mixed coniferous forests were significantly avoided during summer (Table 1).

There was a negative significant influence of "distance to feeding station" on wild boar selection on the habitat types "agricultural land", "mixed coniferous forest", and "other open land", whereas the relationship was significantly positive in "open wetland" and not significant in "clear-cut" and "mixed deciduous forests" (Table 2, Fig. 3). The negative effect means the closer to a feeding station, the more likely the habitat was selected.

Crop selection

The results show a positive significant selection for "mixed crops", "oat", "spring wheat", and "spring barley" (Table 3). On the other hand, "winter wheat" and "grasslands" were significantly avoided by wild boar during summer with grasslands the most avoided crop type (Table 3).

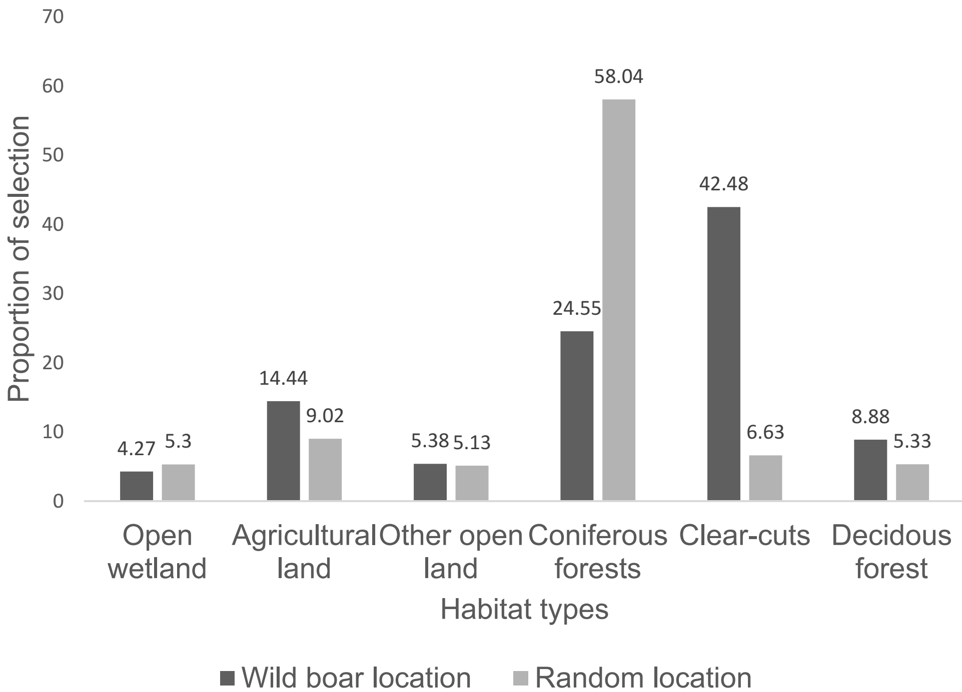

Fig. 2. — The proportion of wild boar locations in all habitats and the proportion of random locations in six different habitat classes.

Oat fields had the highest proportion of wild boar locations (16.8%) compared to the random locations (4.3%) (4 times higher). Furthermore, "grasslands" had the lowest proportion of wild boar locations (60.3%) compared to the random locations (79.7%) (Fig. 4).

Wild boar selection for different crop fields was significantly influenced by the "distance to the feeding station" (Table 4, Fig. 5). The closer to a feeding station the stronger selection for "grasslands", while the opposite effect was found for "mixed crops" i.e the closer to feeding stations the lower use of "mixed crops" (Table 4, Fig. 5).

DISCUSSION

General habitat selection

In this study, based on data from GPS-collared wild boar, by measuring wild boar use of habitats and crop types and comparing it to its availability, we found clear patterns of summer habitat and resource selection. The habitat "clear-cut", "mixed deciduous forest", "other open lands" and "agricultural land" were preferred over "wetlands" and "coniferous forests" during summer. In particular, "clear-cuts" was the most preferred habitat (Table 1, Fig. 2). A plausible explanation for this is that

Table 1.

Summary of model with location type (actual wild boar and random locations) as the dependent variable and habitat type as the explanatory variable, animal ID as a random factor, and open wetlands as the intercept ("reference"). Model = Habitat + (ID random factor).

			Within habitat effect	
Fixed factor	Coefficient ± SE	*P*-value	Coefficient ± SE	*P*-value
Open wetlands (intercept)	– 0.22 ± 0.05	0.0001	– 0.22 ± 0.05[a]	0.0001[b]
Agricultural lands	0.77 ± 0.05	< 0.0001	0.55 ± 0.05[c]	< 0.0001
Other open land	0.33 ± 0.06	< 0.0001	0.11 ± 0.05	0.046
Mixed Coniferous forests	– 0.60 ± 0.04	< 0.0001	– 0.83 ± 0.05	< 0.0001
Clear-cuts	1.27 ± 0.05	< 0.0001	1.05 ± 0.05	< 0.0001
Mixed deciduous forests	0.57 ± 0.05	< 0.0001	0.34 ± 0.05	< 0.0001

[a]Open wetland was the "reference habitat".
[b]The if the within habitat coefficients differ from 0, which indicates a significant difference from random habitat selection [log(odds) = 0 in logistic regression].
[c]The within habitat effects were estimated as "reference coefficient" + "habitat coefficient". For example, for "Agricultural land": 0.55 = – 0.22 + 0.77; SE = 0.05 = $\sqrt{(0.05^2 + 0.05^2)/2}$.

clear-cuts as an open re-growing and clear-felled land have been gradually regenerated for the last 1–5 years with abundant shrubs and dens sprouts providing good opportunities for shelter, day bedding as well as food for wild boar. Clear cuts could provide a fairly high abundance of food in terms of invertebrates, rodents, and re-growing vegetation with fresh grass that potentially can be attractive to wild boar during summer. Similarly, Eom et al. (2019) found that there was a positive selection for clear-cuts by wild boar due to an abundant understory.

"Mixed coniferous forests" were strongly avoided during summer. Most likely this was observed because of the generally low productivity and low food abundance and lack of shelter that this habitat provides in contrast to the preferred habitats ("deciduous forests", "clear-cuts", and "agricultural land"). "Deciduous forests" and "clear cuts" provide an abundance of day bed sites due to their dense cover of shrubs and dense plantations, unlike mature coniferous forests that generally are not as dense. This is supported by Thurfjell et al. (2009) and Zeman et al. (2016) findings that coniferous forests tend to be avoided by wild boar during summer in comparison to other forest types. Similarly, Massei and Genov (2004) found that wild boars searched for food to a higher extent in deciduous forests than in coniferous forests.

Influence of distance from the feeding station on habitat selection

Anthropogenic factors affect wild boar habitat use either directly or indirectly. Human influence like the provision of supplemental feeds attracts wild boar toward a given habitat more than habitats without. Thus, shorter distances to feeding stations increase the probability of wild boar feeding in that site (Kubasiewicz et al. 2016). In this study, we can confirm that general pattern, as we found that closeness to feeding stations increases the selection of "agricultural lands", "mixed coniferous forests", and

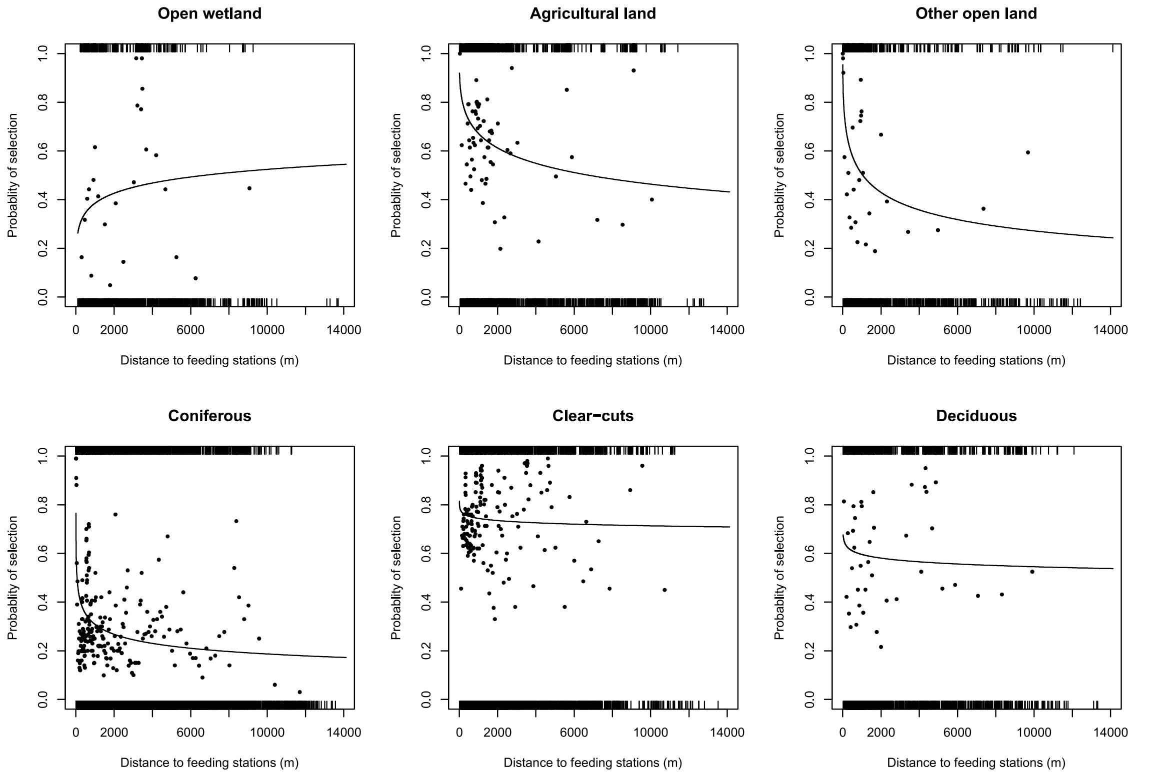

Fig. 3. — Model predictions of the probability of selection (odds from logistic regression) in the six habitat types in relation to the distance to feeding stations (Table 2). The dots are based on binning the actual wild boar locations/random locations (1 and 0) data into groups of 100 samples and estimating the proportion of actual wild boar locations and the mean distance to feeding stations in the binned group. The analyses were done using log10(x + 1)-transformation of distance to feeding stations. The figures show the results back-transformed. The jitter along the upper and lower axes represents the sample of actual wild boar locations and random locations, respectively.

Table 2.

Summary of the model accounting for the influence of distance to feeding stations on habitat selection by wild boar. Open wetlands are the intercept (reference category). Model = Habitat + Dist. feeds + Habitat*Dist. feeds + (ID random factor).

			Within habitat effects	
Fixed factor	Coefficient ± SE	*P*-value	Coefficient ± SE	*P*-value
Open wetland (intercept)	– 2.16 ± 0.37	< 0.001	– 2.16 ± 0.37[a]	< 0.001[b]
Agricultural land	5.47 ± 0.42	< 0.001	3.30 ± 0.39[c]	< 0.001
Other open land	5.20 ± 0.41	< 0.001	3.04 ± 0.39	< 0.001
Mixed coniferous forest	3.34 ± 0.37	< 0.001	1.18 ± 0.37	< 0.001
Clear cuts	3.69 ± 0.38	< 0.001	1.53 ± 0.38	< 0.001
Mixed deciduous forest	3.17 ± 0.42	< 0.001	1.01 ± 0.39	0.01
Slope:				
Log_{10}Dist. feed (reference; Open wetland)	0.56 ± 0.11	< 0.001	0.56 ± 0.11[a]	< 0.001[d]
Log_{10}Dist. feed: Agricultural land	– 1.43 ± 0.13	< 0.001	– 0.86 ± 0.12	< 0.001
Log_{10}Dist. feed: Other open land	– 1.57 ± 0.13	< 0.001	– 1.01 ± 0.12	< 0.001
Log_{10}Dist. feed: Mixed coniferous forests	– 1.23 ± 0.11	< 0.001	– 0.66 ± 0.11	< 0.001
Log_{10}Dist. feed: Clear cuts	– 0.72 ± 0.12	< 0.001	– 0.15 ± 0.11	0.17
Log_{10}Dist. feed: Mixed deciduous forests	– 0.77 ± 0.13	< 0.001	– 0.21 ± 0.12	0.08

[a]Open wetland was the “reference habitat”.
[b]Test if the within habitat coefficients differ from 0.
[c]The within habitat effects were estimated as “reference coefficient” + “habitat coefficient”. For example, for “Agricultural land”: 3.30 = – 2.16 + 5.47; SE = 0.39 = $\sqrt{(0.37^2 + 0.42^2)/2}$.
[d]Test if the slopes within the habitat differ from 0.

“other open lands”. The possible credible explanation is that the feeding sites are not randomly distributed but situated far from agricultural lands to divert wild boar from fields. Further, the feeding sites were situated in areas which had already been selected by wild boar.

Similarly to our results, studies on moose (*Alces alces*) and red deer (*Cervus elaphus*) found extensive damages in Scandinavian pine plantations occur within a distance of 1 km from the feeding stations (Gundersen et al. 2004; van Beest et al. 2010; Milner et al. 2014) while fallow deer (*Dama dama*) damages in the spruce forest are documented to cease at approximately 200 m from the feeding sites (Garrido et al. 2014). Further, Massé et al. (2014) study on how artificial feeding modifies brown bear habitat selection found that, fed bears strongly selected the area surrounding the feeding stations and in addition spent a significant proportion of their time close to the feeding station in summer and fall, with on average ≥ 50% of locations being < 1 km from the feeding site. On the contrary, a review by Kubasiewicz et al. (2016) found that diversionary feeding was mitigating and reducing damages by several species and they found a 15% improvement in respective measures of success across all studies, thus ungulates concentrated their forage intake at the feeding stations rather than feeding on the natural forage the specific habitats provide. Further, Arnold et al.

Table 3.

Summary of the model for crop selection by wild boars. Crop fields were the explanatory variable while the dependent variable was the location types (actual wild boar locations and random locations) and animal ID was the random effect. Spring barley as the intercept ("reference"). Model = Crop field + (ID random factor).

Fixed factor	Coefficient ± SE	*P*-value	Coefficient ± SE	*P*-value
Spring barley (intercept)	0.28 ± 0.12	0.016	0.28 ± 0.12[a]	0.016[b]
Oat	1.12 ± 0.14	< 0.001	1.40 ± 0.13[c]	< 0.001
Winter wheat	– 0.78 ± 0.14	< 0.001	– 0.50 ± 0.13	< 0.001
Spring wheat	0.74 ± 0.15	< 0.001	1.02 ± 0.14	< 0.001
Grasslands	– 0.62 ± 0.11	< 0.001	– 0.34 ± 0.11	0.002
Mixed crop	0.84 ± 0.20	< 0.001	1.12 ± 0.16	< 0.001

[a]Spring barley was the "reference habitat".
[b]Test if the within habitat coefficients differ from 0, which indicates a significant difference from random habitat selection [log(odds) = 0 in logistic regression].
[c]The within habitat effects were estimated as "reference coefficient" + "habitat coefficient". For example, for "Oat": 1.40 = 0.28 + 1.12; SE = 0.13 = $\sqrt{(0.12^2 + 0.14^2)}/2$.

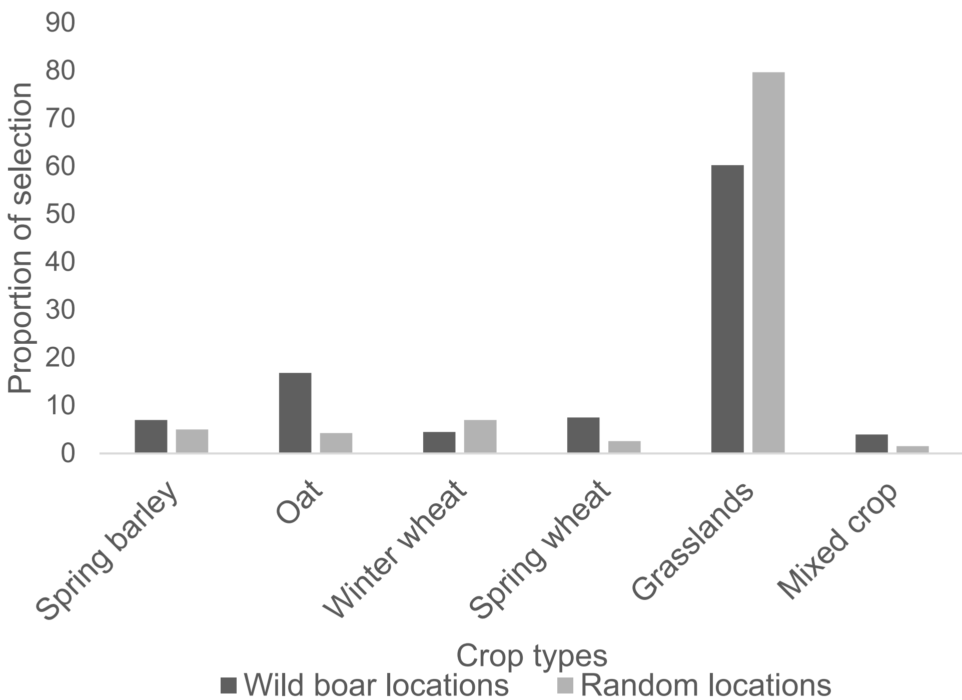

Fig. 4. — The proportion of wild boar locations and the proportion of random locations in six different crop fields.

(2018) study on red deer established that, feeding stations did not affect red deer habitat selection during summer, although, red deer had strong selection of areas close to feeding stations during winter.

The significant positive effect of increased use of "open wetlands" with the increasing distance that was found is likely a result of that feeding sites are systematically located alongside forests while wetland habitats are intentionally avoided when managers select where to place a feeding site. Also, wild boar tends to avoid wetlands, especially during the vegetation season when there are abundant feeds in the farmlands.

Crop selection in agricultural land

Within the habitat "agricultural land", we examined the selection of all occurring crops in the home ranges and how this was affected by artificial feeding stations. Within "agricultural land", "oat", "spring barley", "spring wheat" and "mixed crops "were highly preferred, whereas "winter wheat" and "grasslands" were significantly avoided (Table 3) (Schley et al. 2008; Frackowiak et al. 2013; Ballari & Barrios-García 2014; Bobek et al. 2017). The high preference for these cereals found support in an inquiry among Swedish farmers (Clarin & Karlsson 2010) pointing out oat, wheat, and barley as particularly targeted by wild boar. A study in a Spanish riparian river area also supports the pattern that wheat fields seem to be selected over barley even if maize fields were the most preferred crop (Herrero et al. 2006).

A clear difference in preference was found between "spring wheat" and "winter wheat" as the latter was not actively selected at all. This difference in selection is probably explained by the difference in exposure time to damages of these two crop categories. Since "winter wheat" normally matures early in the summer and thus is harvested 2–4 weeks earlier than the "spring wheat", the wild boar simply has a shorter time to visit mature "winter wheat" fields compared to the more prolonged milky stage in "spring wheat".

"Grasslands" were significantly avoided during summer. Grasslands (pastures and leys) are grown throughout the year and thus provide food for wild boar in most of the seasons but perhaps less so during summer. Schley et al. (2008) and Amici et al. (2012) study found that grasslands were selected throughout the year but mostly during winter whereas cereals were selected during summer. Additionally, Caruso et al. (2018) found that wild boar use grasslands less during summer since other more productive habitats were available.

Influence of the distance from feeding station on crop selection

We found a significant effect of distance to feeding stations on the crop selection by wild boar. The use of "grasslands" increases the closer they are situated to a feeding station. Wild boar likely accumulate and roam around the feeding sites and when feeds are limited in the stations, they shift to feed in the nearby area. Hence, having feeding stations close to the crop fields increases the chances of wild boar selecting those fields (Table 4, Fig. 5). These results are in agreement with Schley and Roper (2003) and Geisser and Reyer's (2004) findings that the shorter the distance between crop and feeding stations, the higher the likelihood of damage to the crops. In

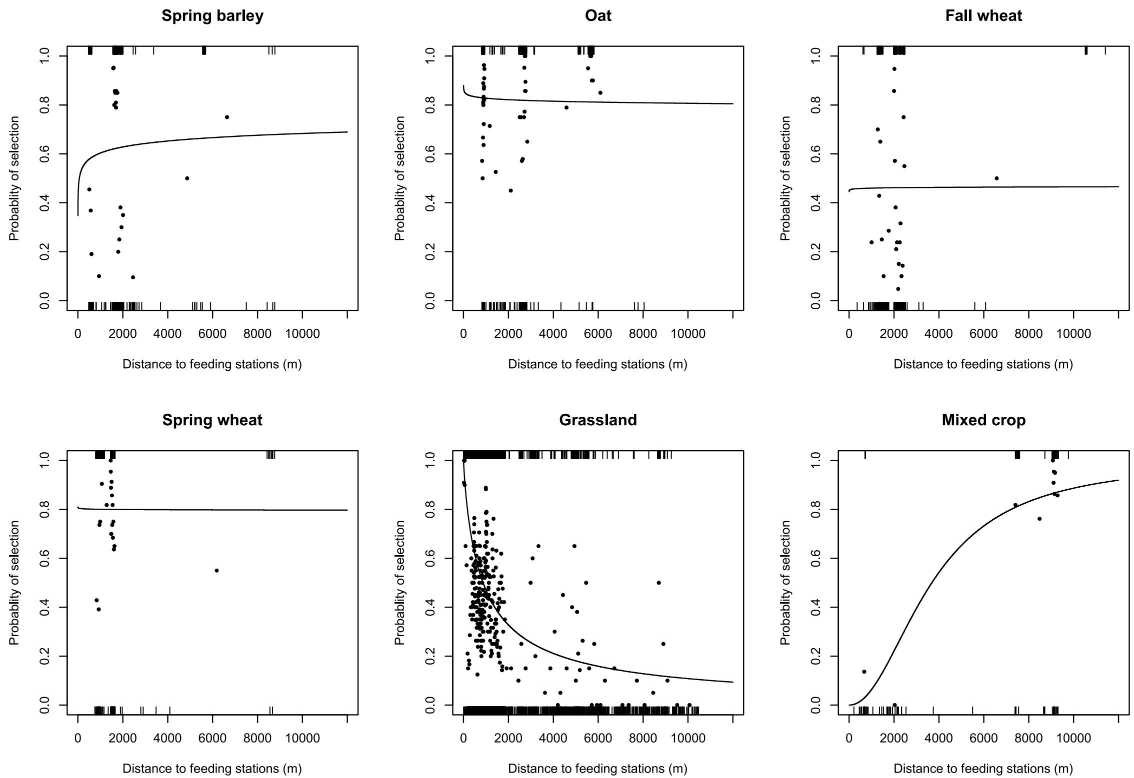

Fig. 5. — Model predictions of the probability of selection (odds from logistic regression) in the six crop types in relation to the distance to feeding stations (Table 4). The dots are based on binning the actual wild boar locations/random locations (1 and 0) data into groups of 20 samples and estimating the proportion of actual wild boar locations and the mean distance to feeding stations in the binned group. The analyses were done using log10(x + 1)-transformation of distance to feeding stations. The figures show the results back-transformed. The jitter along the upper and lower axes represents the sample of actual wild boar locations and random locations, respectively.

Table 4.

Summary of the model accounting for the effect of $\log_{10}$ distance to feeding station on crop selection by wild boar with Spring barley as the intercept ("reference"). Model = Crop field + Dist. feeds + Crop fields*Dist. feeds + (ID random factor).

			Within habitat effects	
Fixed factor	Coefficient ± SE	*P*-value	Coefficient ± SE	*P*-value
Spring barley (intercept)	– 0.64 ± 1.37	0.64	– 0.64 ± 1.37[a]	0.64[b]
Oat	2.63 ± 1.65	0.11	1.99 ± 1.51[c]	0.18
Winter wheat	0.42 ± 2.45	0.87	– 0.22 ± 1.99	0.91
Spring wheat	2.08 ± 2.58	0.42	1.45 ± 2.06	0.48
Grassland	6.48 ± 1.33	< 0.001	5.84 ± 1.35	< 0.001
Mixed crops	– 16.31 ± 3.39	< 0.002	– 16.9 ± 2.59	< 0.001
Log_{10}. Dist. feeds: Spring barley (references)	0.35 ± 0.42	0.41	0.35 ± 0.42	0.41[d]
Log_{10}. Dist. feeds: Oat	– 0.49 ± 0.51	0.34	– 0.14 ± 0.47	0.77
Log_{10}. Dist. feeds: Winter wheat	– 0.33 ± 0.75	0.66	0.02 ± 0.61	0.97
Log_{10}. Dist. feeds: Spring wheat	– 0.37 ± 0.82	0.65	– 0.02 ± 0.65	0.98
Log_{10}. Dist. feeds: Grasslands	– 2.34 ± 0.41	< 0.001	– 1.99 ± 0.42	< 0.001
Log_{10}. Dist. feeds: Mixed crops	4.40 ± 0.92	< 0.001	4.75 ± 0.71	< 0.001

[a]Spring barley was the "reference habitat".
[b]Test if the within habitat coefficients differ from 0.
[c]The within habitat effects were estimated as "reference coefficient" + "habitat coefficient". For example, for "Oat": 1.99 = – 0.64 + 2.63; SE = 1.51 = $\sqrt{(1.37^2 + 1.65^2)/2}$.
[d]Test if the slopes within the habitat differ from 0.

addition, Milner et al. (2014) study established that, the efficiency of diversionary feeding is related with the distance from the feeding stations and the vulnerable vegetations.

Conversely, the selection for "mixed crop" fields occurs when distance to feeding station increases. (Table 4, Fig. 5). This is in line with Calenge et al. (2004), Cellina (2008), and TryjanowskI et al. (2017), findings that feeding stations concentrate wild boar to those sites and thus reduces their feeding on nearby agricultural fields. Why this should be true for "mixed crop" fields only, is still unclear.

CONCLUSION

Wild boar prefers clear-cuts, mixed deciduous forests, other open lands, and agricultural lands during summer. Mixed coniferous forests and open wetlands are generally not selected, or are avoided probably because there is surplus food in the farmlands and deciduous forests. In the agricultural lands, fields containing spring barley, spring wheat, oats, and mixed crops, in particular, are the most attractive crop types.

Feeding stations aim to attract wild boar and reduce the damage they may cause to agricultural fields close by. In this study, we found that distance to feeding sites significantly influences the selection of different habitats, thus supporting the hypothesis of the study. For instance, shorter distances between feeding stations and agricultural land led to a higher probability of the field being selected. To protect sensitive fields from visits by wild boar, feeding sites should be situated far away from the field since the wild boar use of particular fields, and grasslands, increases the closer these fields are situated to a feeding station.

This study provides a first basis for further investigations of landscape factor's effects on the spatial and temporal variation in wild boar habitat selection in Sweden. Knowledge of wild boar seasonal variation in selection will be useful to improve future wildlife management strategies, e.g. to adjust cropping systems to reduce damages on more selected crop fields.

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No potential conflict of interest was reported by the authors.

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ETHICAL STANDARD

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Approval to capture and mark free-ranging wild boar was given by the Ethical Committee on Animal Research, Uppsala Sweden (permit C-5.2.18-2830/16).

AUTHOR CONTRIBUTION

P. Kjellander and H. Andren coordinated the study. P. Kjellander and E. Augustsson designed the field protocol for captures, marking, and GPS-location structure. Field data were collected by E. Augustsson and C.M. Muthoka. Data were analyzed by C.M. Muthoka and H. Andren. All authors contributed to the study design and data interpretation. C.M. Muthoka wrote the first draft with assistance from P. Kjellander and J.N. Nyaga All authors substantially revised it, read and approved the final version.

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