



Density-dependent dinner: Wild boar overuse agricultural land at high densities

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Abstract

The Swedish wild boar (*Sus scrofa*) population has increased rapidly over the last decades, resulting in conflicts with human activities. Particularly, the increase has been challenging for agriculture as wild boar cause damage on crops and grasslands. To predict under what conditions to expect damage and where to prioritize management actions, basic knowledge about wild boar habitat and space use is needed. In this study, we used data from 99 wild boar equipped with GPS-collars, collected over a large temporal scale and throughout their distributional range in southern Sweden. We investigated wild boar home range size and habitat use across gradients of habitat availability and population density. Functional response in habitat use was assessed by estimating the use and availability of agricultural land on individual level and then, on population-level evaluating how use changed with changing availability. Finally, a potential response in habitat use was evaluated in relation to population density, i.e., the interaction between availability and population density. Home range size was negatively related to population density for both male and female wild boar. Wild boar used agricultural land more intensively with increasing population density and when other habitat types were less available. Our findings show that wild boar spatial behavior is highly context dependent and may vary considerably due to landscape characteristics and local conditions. Wild boars tend to overuse agricultural land at high densities which has strong implications for wildlife management. It is therefore important to consider local conditions when predicting space and habitat use by wild boar. Overall, this study provided a better understanding of the drivers of wild boar distribution and space use in agro-forested mosaic landscapes and how this knowledge can improve management practices.

Keywords Spatial behavior · Habitat use · Population density · Wild boar · *Sus scrofa*

Introduction

From being extirpated in the eighteenth century, the Swedish wild boar (*Sus scrofa*) population has increased rapidly since the 1970s, when some individuals escaped from enclosures in which they were held for recreational hunting and meat production (Truvé and Lemel 2003). Today, the population has re-established in the main parts of southern and central Sweden. The current population size is estimated to be over 300,000 animals and the reported annual hunting bag was more than 112,000 animals in 2023 (Swedish Association for Hunting and Wildlife Management). Wild boar can demonstrate high reproductive rates, adaptability, and opportunistic feeding habits (Massei et al. 1996; Schley and Roper 2003; Fonseca et al. 2011; Malmsten 2017). In Sweden, and other parts of Europe, this has led to a rapid range expansion and population increase as well as conflicts with human activities

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due to crop damage, vehicle collisions and disease transmission (Thurfjell et al. 2015; Gren et al. 2020; Stenberg et al. 2021). Agricultural fields are known to be a preferred habitat for wild boar (Thurfjell et al. 2009; Muthoka et al. 2022) and are used at a higher extent during summer than during the rest of the year (Sweden: Lemel et al. 2003, Thurfjell et al. 2009; Germany: Keuling et al. 2009). The challenge to agriculture has been of particular interest due to crop damage and severe economic losses for farmers. The modern agricultural landscape, providing a high abundance of nutritious feed over large areas, represents an interface for conflict between humans and wildlife. Farmers' economic losses are expected to grow as both intensification of agricultural activities and wild boar abundance increase (Gren et al. 2020). Moreover, the risk of disease transmission between wild boar and pig farms have been accentuated due to the first case of *Salmonella enterica* subsp. *enterica*, serovar Choleraesuis in more than 40 years (Ernholm et al. 2022), and the recent outbreak of African swine fever (ASF) in the Swedish wild boar population (SVA 2023). Due to such conflicts, the management of wild boar has, as in other parts of the world, become an issue of national concern in Sweden, and an increased understanding of the wild boar distribution in agro-forested mosaic landscapes is crucial.

A common contemporary approach to monitor and map animal movements is the tagging of animals with GPS telemetry collars. By spatially locating individuals with high precision at a given time, this technique allows to investigate distributional variation in relation to landscape characteristics and local conditions (Cagnacci et al. 2010). A well-established and frequently used method of describing animal distribution is to estimate home range sizes. Animal spatial behavior is shaped by both social and environmental factors; forage availability and competition level are well known to effect space use (e.g., Tufto et al. 1996; van Beest et al. 2016). Home range size is by theory predicted to decrease with increasing food abundance (Ford 1983), and generally, higher-quality habitats are associated with smaller home ranges. Adjustment of home range size to resource levels has been demonstrated in a wide range of mammalian species (Ims 1987; Boitani et al. 1994; Lucherini and Lovari 1996; McLoughlin and Ferguson 2000; Schradin et al. 2010; Bjørneraas et al. 2012) and wild boar home range has shown to be negatively correlated to increasing resources as in years with tree seed mast (Bisi et al. 2018) and around baiting areas (Keuling et al. 2008b). The “density-dependent hypothesis” predicts that changes in home-range size are inversely related to population density (Massei et al. 1997). Increased local animal density increases the competition (Focardi et al. 2006), why competition is considered a main mechanism promoting density dependence. A reduction of home range size at high density has been confirmed in several species (roe deer: Kjellander et al. 2004; wild boar: Massei et al. 1997;

moose: van Beest et al. 2016). In wild boar, inter-sexual differences in spatial behavior patterns are related to differences in reproductive strategies between males and females (Kurz and Marchinton 1972; Singer et al. 1981; Boitani et al. 1994; Cavazza et al. 2023; Miettinen et al. 2023). Females form family groups that can include several generations of adults and offspring, while adult males live isolated from the herd outside the rut period (Podgorski 2013). Although the territorial behavior in wild boar is poorly understood, male wild boar are reported to be less territorial than females, interacting more frequently with individuals of both sexes and with larger home ranges that overlap both sexes (Kay et al. 2017; Schlichting et al. 2022). Furthermore, due to their greater body size and advantageous physical characteristics (Spitz et al. 1998), males could be expected to be more resilient to interference competition.

Animals are known to adapt their spatial utilization according to perceived risk, often referred to as the “landscape of fear” (Gaynor et al. 2019). This suggests that animal movement patterns are influenced by predation risk. Although agricultural fields provide high energetic gain, it could also be a dangerous environment for wild boar considering that 20% of the annual hunting bag in Sweden is shot in crop fields (Swedish Association for Hunting and Wildlife Management 2017). However, the avoidance of risky areas (e.g., hunting areas) by wild boar is a debated issue, and is likely to vary at the local and individual scale (Tolon et al. 2009; Said et al. 2012; Brogi et al. 2020, 2022). Hence, context-dependency of animal spatial behavior is complex and behavioral decisions animals make often result in trade-offs between opposing needs, such as forage and safety (Brown et al. 1999).

While home range models may serve an important descriptive purpose, these models describe space use based solely on spatial location, and it is of ecological interest also to understand the causal processes of animal movement and distribution patterns. Analyzing a species' distribution across habitats, i.e., habitat use, links individual animals to their environment by connecting behavior to resource availability (Johnson 1980) and habitat use is most commonly studied by comparing the use of a given habitat in relation to the availability of that habitat in the surrounding landscape (Boyce and McDonald 1999; Manly et al. 2002; Johnson et al. 2006). Although the availability of suitable habitats and resource abundance are proven central determinants for habitat use patterns (Mysterud and Ims 1998; Pellerin et al. 2010; Boyce et al. 2016; Holbrook et al. 2019), the use-available relationship is often more complex. Individuals may change their preference of a particular habitat as a function of its availability. Hence, the use of a given habitat may be conditional on the availability of that habitat (Holbrook et al. 2019). This phenomenon was first termed “functional response” by Mysterud and Ims (1998) and its

importance has been demonstrated widely since (Godvik et al. 2009; Bjørneraas et al. 2012; Holbrook et al. 2017; Avgar et al. 2020; Oeser et al. 2023). In addition to adjustment in habitat use due to habitat availability, adaptive shifts in distribution may also be due to site-specific conditions in different populations (e.g., William et al. 2018). Avgar et al. (2020) showed that density dependence may provide a mechanistic explanation for the context-dependent outcomes often reported in habitat use analysis and empirical support for density-dependent habitat selection is growing (Mobæk et al. 2009; van Beest et al. 2014, 2016).

Functional responses have most commonly been studied by assessing how the use of a given habitat changes with its availability (Holbrook et al. 2019), but the number of studies linking variation in functional response to site-specific conditions is growing. Due to an expected increase in Swedish wild boar densities in areas recently recolonized, it is important to understand also how the species adjusts their space use under different population levels. Knowledge on the spatial behavior of wildlife is also crucial in order to predict, prevent, and manage diseases at the wild-domestic interface (Pascual-rico et al. 2022, Podgorski and Smietanka 2018). Management practices aiming to mitigate human-wildlife conflicts in agricultural landscapes require science-oriented and ecologically reliable information to be effective. However, such essential information is still not very well examined, and the knowledge of context dependencies and plasticity in wild boar space use is very limited.

Aims

In this study, we used wild boar telemetry data collected between 2004 and 2021 and throughout the species' distributional range in southern Sweden, allowing us to investigate two aspects of wild boar spatial behavior across gradients of habitat availability and population density. The aim was twofold: (1) investigate the influence of population density and availability of agricultural land on wild boar home range size, and (2) investigate the influence of population density and availability of agricultural land on wild boar use of agricultural land.

Based on the literature, we predict that wild boar home range size will (P1a) decrease at high population density (Massei et al. 1997), (P1b) the decrease in home range size due to population density will be more pronounced in females (Spitz et al. 1998; Kay et al. 2017; Schlichting et al. 2022), (P2a) home range size will decrease at high availability of agricultural land (Ford 1983), and (P2b) the decrease in home range size due to availability of agricultural land will be more pronounced in females (Podgorski 2013). In the context of landscape of fear, and the relatively high mortality risk associated with agricultural land, we predict that (P3)

wild boar use of agricultural land (in relation to availability) will increase at high population density.

Material and methods

Study area

We conducted this study within the main distributional range of wild boar in Sweden (55°–60° N, 12°–18° E, Fig. 1). The landscape composition varies across the study area, with the boreal forest being the dominating habitat in the north and farmland in the south. The duration of the growing season (days with average temperature > 5 °C) varies from 190 to 220 days. Average annual precipitation varies from 500 to 1100 mm and average snow cover is between 25 and 100 days per year (SMHI 2022). There tends to be a longer period of snow-covered ground and a shorter duration of the growing season in the northern sites compared to the southern sites. Supplemental feeding is common throughout the study area, although of unknown quantities.

Capture, collars, and positional data

In this study, we used multiple telemetry datasets (e.g., Thurfjell et al. 2009; Muthoka et al. 2022) collected between 2004 and 2021, from 99 wild boar (16 males and 83 females) equipped with GPS-collars. The animals were immobilized with a tranquiliser gun (Dan-inject model JM, Dan-inject, Kolding, Denmark) from a vehicle on agricultural fields or close to feeding stations, or a blowpipe (Dan-inject model Blow 125) after being captured in coral traps. Wild boars were immobilized using one of the following anaesthetizing combinations and adjusted for their body size: 10 mg medetomidine + 20 mg butorphanol + 500 mg ketamine (Kreeger and Arnemo 2007; Thurfjell et al. 2009); 15–30 mg romifidine + 300 mg zolazepam-tiletamine; or 5–6 mg medetomidine + 300–400 mg zolazepam-tiletamine. After immobilization, wild boars were equipped with one of the following GPS/GSM collars: Vertex Plus 2D or 3D; Vertex Lite 2D; or GPS Pro Light 3D (Vectronic Aerospace GmbH). Telemetry data was collected or subsampled to one location every 1 h and for a maximum of 365 days to obtain homogeneity among individuals.

Population density and space use

We obtained hunting bag for each hunting district and hunting year between 2004 and 2021 from the Swedish Association for Hunting and Wildlife Management, game monitoring. Hunting bag statistics are commonly used as a proxy for assessing the relative abundance of animals in several species (Apollonio et al. 2010; Putman et al. 2011). However,

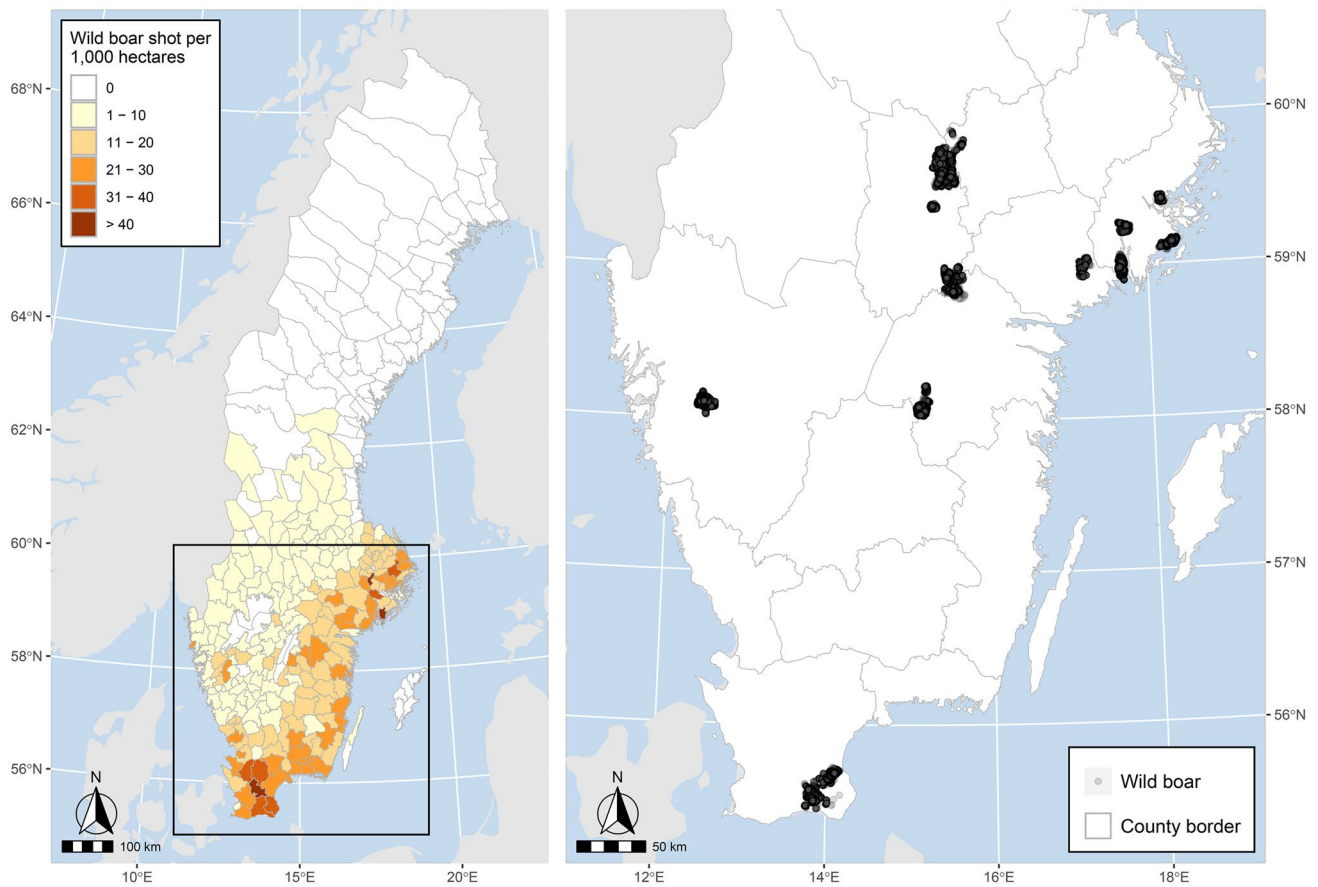


Fig. 1 Hunting bag estimates for each hunting district in the study area for hunting year 2020/2021 (left), illustrating the large density variation across the study area. A hunting bag was used as a proxy for population density and assigned to each individual wild boar accord-

ing to the location (hunting district) and time stamp (hunting year) of its first GPS location. The study area in southern Sweden with GPS-locations from 99 collared wild boar between 2004 and 2021 (right)

since this approach has formerly been criticized for not being fully reliable (Focardi et al. 2020), we collected wild boar-vehicle collision data for each county and hunting year represented among wild boar location data and conducted a complementary calibration study. Collisions data was compiled to match hunting year (July 1 to June 30). Motivated by the strong correlation between wild boar collisions data (wild boar-vehicle collisions/km²) and hunting bag (shot wild boar/km²) ($r=0.89$, $df=100$, $p<0.0001$; Fig. S1), also demonstrated by Massei et al. (2015) and Neumann et al. (2020), hunting bag (shot wild boar/km²) was assumed to be a reliable proxy for wild boar abundance and will hereon be referred to as “population density.” We assigned hunting bag to each individual animal according to the location (hunting district) and time stamp (hunting year) of its first GPS-location. For individuals with more than one monitoring period, we used the hunting bag for the first period.

To determine wild boar habitat use, we used CORINE land cover (CLC) data with 100 m spatial resolution, which

has 44 categorized land cover and land use classes in total (European Union 2000, 2006, 2012, 2018). We reclassified the CLC classes into two habitat groups: agricultural land and others. Agricultural land was defined as all subclasses of the CLC category agricultural area (Kosztra et al. 2017): areas principally occupied by agriculture, arable land, fruit and berry plantations, pastures, meadows, and other permanent grasslands under agricultural use. All remaining land cover classes were grouped as others. We assigned land cover data to each individual according to the year for its first GPS-location and the closest corresponding year of the CLC data.

Both day and night location data from 83 female and 16 male collared wild boar (mean locations per individual = 4081, range = 304–8697) were used to compute an alpha-concave hull with a concave distance of 3 km in order to estimate home range used by each wild boar (Asaeedi et al. 2017). We estimated the use of agricultural land by calculating the proportion of true locations

in agricultural land divided by the total number of true locations. We assessed available resources by generating an equal number of random locations to true locations, i.e., a ratio of 1:1, within the individual home range. This design ensured that availability was measured in the area known and in reach to each animal, and thus representing a type III analysis (Manly et al. 2002). Availability was calculated as the proportion of random locations in agricultural land divided by the total number of random locations. Seven individuals were omitted from the dataset before estimating habitat use due to a complete absence of agricultural land in their home range. The range of variables used in the statistical analysis is provided in Table 1. We used a two-stage approach (Fieberg et al. 2010): first, estimating the use of agricultural land and availability of agricultural land per individual and season; and second, on population-level assessing how the sample of use changed with the sample of availability (Holbrook et al. 2019).

As the hour of sunset is known to trigger the onset of activity (Boitani et al. 1994; Lemel et al. 2003; Thurfjell et al. 2014), each used location was assigned a daylight value (day = 1, night = 0) according to its sunrise and sunset (Schlyter 2021). We used night-time data from 76 female and 16 male collared wild boar (mean locations per individual = 1979, range = 110–4201) to analyze habitat use as wild boar are predominantly nocturnal (Boitani et al. 1994; Lemel et al. 2003; Keuling et al. 2008a; Podgorski et al. 2013; Thurfjell et al. 2014; Brivio et al. 2017).

We defined three different seasons related to the ecology of wild boar in Scandinavia: spring–early summer (reproductive season; March–June), summer–autumn (crop season; July–October), and winter (November–February; Mauget 1982; Thurfjell et al. 2014; Malmsten et al. 2017). To account for differences in habitat use across different seasons, all random locations were assigned a random season at an equal number to true locations for each season. This allowed us to test for the change in use while holding availability constant. Individuals with fewer than 10 days of data or 100 recorded locations per season were removed from the dataset before estimating habitat use.

Statistical analysis

We investigated variables influencing wild boar home range size (\log_{10}) by using a generalized linear mixed model with a Gaussian error term in the R package *glmmTMB* (Brooks et al. 2017). We investigated the effects of population density (shot wild boar/km²), availability (proportion of random locations in agricultural land), and sex (females coded as 0 and used as reference value, males coded as 1), including the interactions “population density * sex” and “availability * sex,” while controlling for monitoring days (\log_{10}).

We investigated variables influencing wild boar use of agricultural land by using a generalized linear mixed model with a Gaussian error term in the R package *glmmTMB*. We investigated the effects of population density and availability of agricultural land, including the interaction “population density * availability,” while controlling for season. Intersexual differences were excluded from the analysis due to the limited sample size of males. Animal ID was treated as a random factor to account for the dependency of repeated seasons within individuals (Zuur et al. 2010). For both analyses, we used Akaike information criterion, corrected for small sample sizes (AIC_C), to compare the relative strength of candidate models by calculating the ΔAIC_C (Akaike 1974), and performed AIC_C model selection on candidate models (Tables 2 and 4). To assess model quality and to further ensure that models fulfilled assumptions, models were screened using the package *performance* (Lüdtke et al. 2021). Figures were produced using the package *ggplot2* (Wickham 2016). For data analysis, we used R version 4.2.2 (R Core Team 2022).

Results

Home range size

The mean estimated alpha-concave hull home range size for individuals monitored for a minimum of 14 days was for males 49.6 km² (95% CI 24–75) and for females 17.3 km² (95% CI 14–20). The best predictive model explaining home

Table 1 Mean value and range for the variables used in the analyses

Variable	Unit	Mean	Range
Population density	Shot wild boar/km ²	1.42	0.0045–3.23
Availability	Proportion of random locations in agricultural land	0.24	0–0.95
Monitoring days	Days	242	14–365
Sex	Female = 0, male = 1		
Season	Spring–early summer: March–June Summer–autumn: July–October Winter: November–February		

Table 2 Competitive models on the effects of population density, availability, sex, and monitoring days on wild boar home range size (\log_{10})

Response	Corresponding predictions	Formula ^a	df	AIC _C	Δ AIC _C
Home range size	P1a, P1b, P2a, P2b	Population density * Sex + Availability * Sex + Monitoring days	8	26.5	0.0
	P1a, P1b	Population density * Sex + Monitoring days	6	26.9	0.38
	P1a, P2a, P2b	Availability * Sex + Population density + Monitoring days	7	27.2	0.61
	P1a, P2a, P1b	Population density * Sex + Availability + Monitoring days	7	27.9	1.38
	P1a	Population density + Sex + Monitoring days	5	30.9	4.39
	P1a, P1b, P2a	Availability + Population density + Sex + Monitoring days	6	32.3	5.74
	P2a, P2b	Availability * Sex + Monitoring days	6	59.8	33.26
	0	Sex + Monitoring days	4	65.0	38.44
	P2a	Availability + Monitoring days + Sex	5	67.1	40.61

^aInteractions include both main effects and interactions

range size included the predictors availability of agricultural land, population density and sex, and the interaction between availability of agricultural land and sex, and the interaction between population density and sex (Table 2). We found a strong negative effect of population density but a weaker effect of availability of agricultural land on home range size (Fig. 2, Table 3). Male home ranges were in general larger than female home ranges. Both females and males

showed an overall decrease in home range size with increasing population density. The effect of population density was more pronounced in male home range size than female home range size (Fig. 2). Males showed a decrease in home range size with increasing availability of agricultural land, while female home ranges increased with increasing availability of agricultural land, although the effect of availability of agricultural land was not as strong (Table 3).

Fig. 2 Home range size for male and female wild boar in relation to population density index (shot wild boar/km²). Points represent individual observed values for males (dark gray) and females (light gray). Lines show predicted values with 95% confidence limits (shaded areas) for males (solid line) and females (dashed line). Data was collected from GPS-locations of collared wild boars ($N=99$) in southern Sweden, 2004–2021

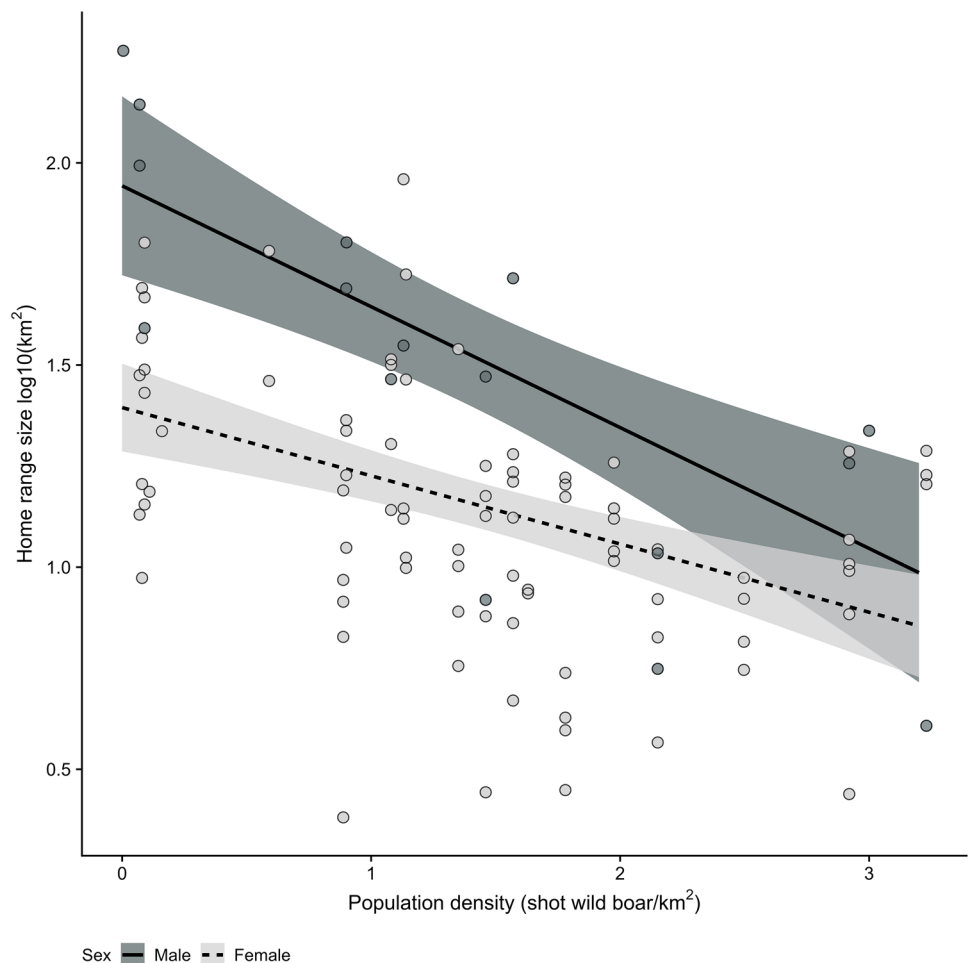


Table 3 Summary of model coefficients predicting wild boar home range size (log₁₀) for the highest ranked model based on AIC_C

Predictor	Estimate (± SE)	z value	p value
Intercept (female)	0.518 (±0.171)	3.030	0.002
Population density	-0.169 (±0.033)	-5.142	<0.001
Availability	0.186 (±0.109)	1.707	0.088
Sex male	0.711 (±0.127)	5.613	<0.001
log10(monitoring days)	0.360 (±0.074)	4.897	<0.001
Population density * sex male	-0.130 (±0.075)	-1.740	0.082
Availability * sex male	-0.710 (±0.364)	-1.954	0.051

The reference category for “Sex” was “Female”

Use of agricultural land

The best predictive model explaining wild boar use of agricultural land included the predictors availability of agricultural land and population density as well as the interaction between these two variables (Table 4). We found that wild boar increased their use of agricultural land with increasing availability of agricultural land (Fig. 3, Table 5). Moreover, wild boar used agricultural land more intensively with increasing population density, and when the availability of agricultural land was high. We found an overuse of agricultural land at high wild boar densities, an underuse of agricultural land at low densities, and a proportional use of agricultural land (in relation to availability) at intermediate densities (Fig. 3). Additionally, wild boar showed a higher use of agricultural land during summer–autumn than in other seasons (Table 5).

Discussion

In this study, we show that high wild boar densities lead to an overuse of agricultural land. We found that wild boar home range size was negatively related to population density for both male and female wild boar, thus confirming our prediction that home range size will decrease at high population density (P1a). We found no support for that this negative relationship between home range size and population

density should be more pronounced for females (P1b). On the contrary, we found the effect of population density to be more pronounced in male home range size. Males showed a decrease in home range size with increasing availability of agricultural land, thus partially confirming our prediction that home range size will decrease at high availability of agricultural land (P2a). However, we found no support for this in female home range size, nor for our prediction that the negative relationship between home range size and availability of agricultural land should be more pronounced for females (P2b). Wild boar adjusted their use of agricultural land in relation to availability of agricultural land and population density, supporting our prediction that wild boar will increase their use of agricultural land (in relation to availability) at high population density (P3).

Home range size

Wild boar exhibited smaller home ranges at higher densities (Fig. 2). This is in support of our prediction and suggests that the level of intraspecific competition may influence home range size. It is also in line with previous literature on wild boar spatial behavior (Massei et al. 1997), as well as in other ungulate species (roe deer: Kjellander et al. 2004; moose: van Beest et al. 2016). This knowledge can be used to inform management policies, particularly for disease control where adaptive strategies can be applied according to wildlife ecology (Smith et al. 2022). Realistic home range sizes are crucial when assessing contaminated areas or potential rate of disease transmission. Contrary to our prediction, population density was more important for male home range size than for female home range size. Keuling and Massei (2021) concluded that recreational hunting caused changes in wild boar home range size. In this study, we used hunting bag as a proxy for population density. As hunting bag also reflects hunting pressure, the more pronounced effect in male home range size could be due to the higher hunting pressure on males. The observed behavior in males may also been affected by age. Cederlund and Sand (1994) showed that size of male moose home ranges was strongly dependent on age, in contrast to that of females. Due to unknown animal age

Table 4 Competitive models on the effects of population density, availability, sex, and season on the use of agricultural land by wild boar

Response	Corresponding predictions	Formula ^{a,b}	df	AIC _C	ΔAIC _C
Use of agricultural land	P3	Availability * Population density + Season	8	-212.6	0.00
	0	Availability + Season	6	-209.9	2.70
	P3	Availability + Population density + Season	7	-207.9	4.74

^aInteractions include both main effects and interactions

^bAnimal ID was included as a random effect in all models

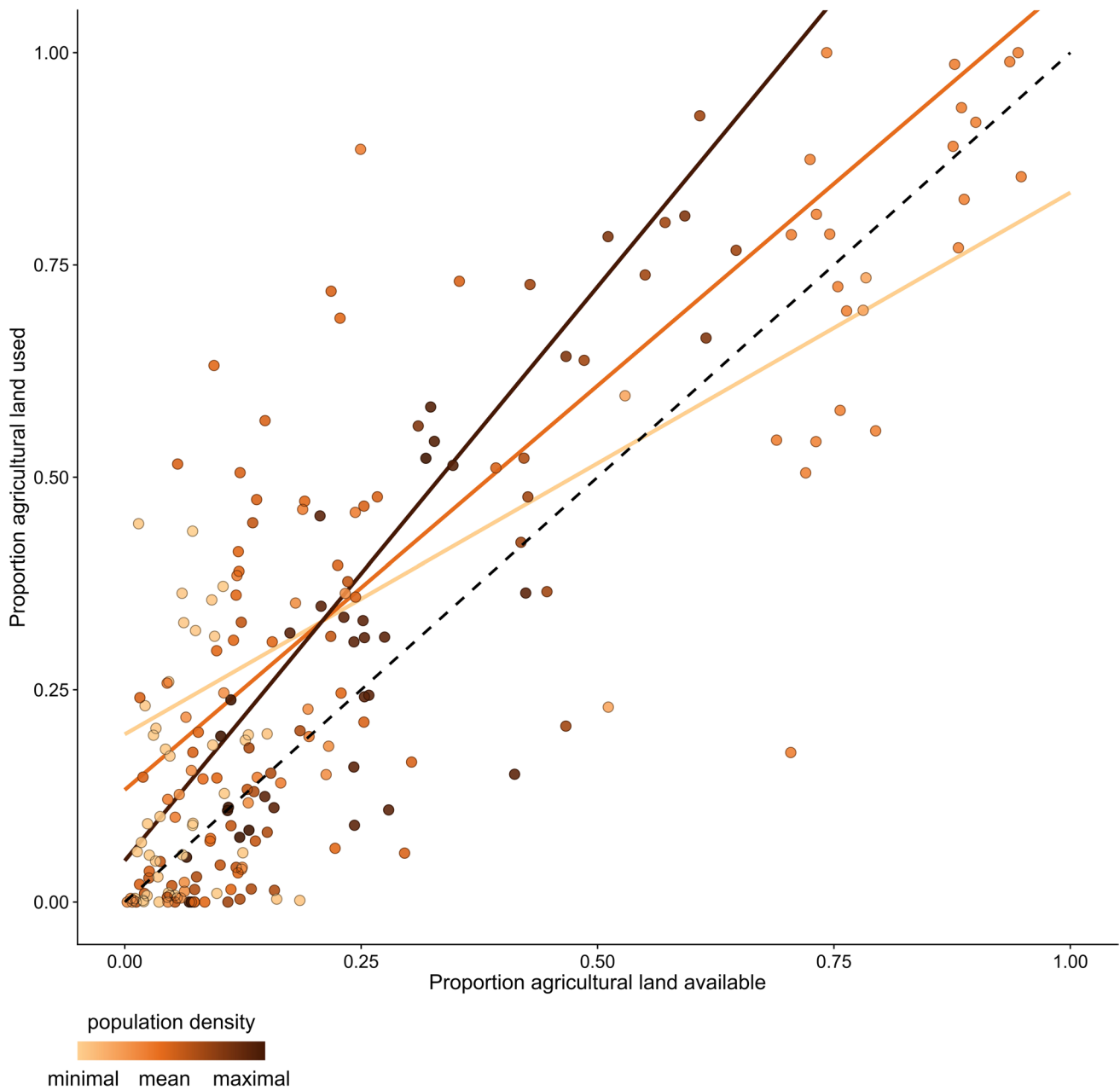


Fig. 3 Wild boar use of agricultural land in relation to availability of agricultural land and population density within the home range. Dashed line indicates proportional use as availability changes. Points represent observed values of each individual, repeated for several seasons ($N=211$). Lines show predicted values for different population

densities: min ($0.0045/\text{km}^2$; light yellow), mean ($1.42/\text{km}^2$; orange), and max ($3.23/\text{km}^2$; dark brown) for season summer-autumn. Shading of points indicates the individual population density within the home range. Data was collected from GPS-locations of collared wild boars ($N=92$) in southern Sweden, 2004–2021

in our sample, besides being adults, we could not correct for this in the analysis.

Theory on food exploitation suggests that when food supply decreases, home range size should increase due to increased activity, a relationship that has been demonstrated in the wild boar literature (Singer et al. 1981; Boitani et al. 1994; Massei et al. 1997; Bisi et al. 2018). Although the availability of agricultural land alone does not provide a

complete understanding of an area's food supply, agricultural crops are highly nutritious and could therefore be considered a high-quality resource. We found that male home range size was negatively affected by the availability of agricultural land. For females, however, this relationship was more complex, and it is possible that the effect of population density may mask or override the effect of availability of agricultural land. Moreover, animal spatial behavior is often

Table 5 Summary of model coefficients predicting wild boar use of agricultural land for the highest ranked model based on AIC_C

Predictor	Estimate (\pm SE)	z value	p value
Intercept (spring–early summer)	0.086 (\pm 0.032)	2.698	0.007
Population density	−0.046 (\pm 0.021)	−2.251	0.024
Availability	0.637 (\pm 0.112)	5.678	<0.001
Season summer–autumn	0.111 (\pm 0.022)	5.092	<0.001
Season winter	−0.006 (\pm 0.023)	−0.247	0.805
Population density * availability	0.221 (\pm 0.083)	2.670	0.008

The reference category for “Season” was “Spring–Early summer”

subjected to a food/cover trade-off (Mysterud and Ims 1998; Brown et al. 1999); thus, once the need for food is saturated, other factors, such as shelter, may become more important. In summary, our results suggest that home range size is context dependent and affected by a complex combination of multiple conditions, such as food availability, access to cover, and level of competition.

Our results support previous findings on that males of wild boar have larger home ranges than females (Kurz and Marchinton 1972; Singer et al. 1981; Boitani et al. 1994). This is a probable consequence of the wild boar social- and mating system through males trying to optimize mating opportunities by searching and visiting several spatially separated female groups for females in heat (Singer et al. 1981; Dardaillon 1988). In species where males compete for breeding females during the mating season and female movement is restricted by the limited physical capacity of their offspring during certain times of the year, this usually leads to larger home ranges in males (e.g., Kjellander et al. 2004).

Use of agricultural land

Wild boar use of agricultural land was influenced by the amount of agricultural land available (Fig. 3), confirming the importance of resource availability in habitat use patterns (Mysterud and Ims 1998; Pellerin et al. 2010; Boyce et al. 2016; Holbrook et al. 2019). Wild boar demonstrate an opportunistic feeding behavior, and its diet reflects local environmental conditions (Schley and Roper 2003), why we could expect the species to utilize resources in relation to availability and abundance. Population-density effects on spatial behavior are not well described in the wild boar literature, but have been demonstrated in several other ungulate species (e.g., moose: van Beest et al. 2014), and the importance of considering density-dependent changes in habitat selection in a theoretical framework was shown by Avgar et al. (2020). We found that the effect of population density on wild boar use of agricultural land was

conditional on the availability of agricultural land. Wild boar adjusted their use of agricultural land in relation to population density, with an underuse of agricultural land at low densities and an overuse at high densities, and with a stronger effect of density at high availability of agricultural land (Fig. 3). Theory on density-dependent habitat selection predicts that animals exhibit a specialized behavior when densities are low and a more generalized behavior during high densities to reduce competition for resources. In this perspective, an increased use of a habitat type due to increased competition would suggest that it is not the most preferred habitat. Although previous studies suggest that agricultural crops are highly attractive and are selected for by wild boar (Keuling et al. 2009; Thurfjell et al. 2009; Muthoka et al. 2022), the observed response may be explained by that animal behavior is also influenced by human predation risk. Trade-offs between access to high-quality resources and risk-taking may result in adjustments in habitat use (Valeix et al. 2009; Bonnot et al. 2013). Agricultural land is due to its openness, a relatively unsafe environment. Under low competitive conditions, wild boar should prefer to forage in more concealed habitats, if available. The quality of an otherwise poor area can be artificially increased by providing supplementary food (Muthoka et al. 2022) and wild boar are known to modify their spatial behavior around feeding sites (Keuling et al. 2008b). In the Swedish context, artificial feeding sites are often placed in areas of high cover, and thus, when available, provides easy access to high energetic gain under safe conditions. Such local food sources, however, are likely to be monopolized quickly and therefore lack the capacity to sustain dense populations. Agricultural areas are harder to monopolize due to its larger size. This provides a potential explanation for the observed overuse of agricultural land at high densities: strong competitive conditions push wild boar towards high-risk forage areas, i.e., agricultural fields. A similar behavior was shown by van Beest et al. (2016) who demonstrated an increased selection for riskier habitat in elk with increasing animal density. Furthermore, we found a stronger effect of population density when availability of agricultural land was high. In this study, we focus on the use and availability of a single habitat type: agricultural land. As the selection for a given habitat is conditional on other habitat types being available to the individual, an increase in the proportional availability of agricultural land indicates a decrease in the proportional availability of other, “safer,” habitat types, and consequently, an increased competition in these areas. Competition may act on different limited resources, where food may be one and safety another. It is likely that the observed functional responses in wild boar habitat use reflect the competitive conditions for cover rather than the competitive conditions for food, or possibly a combination of both resources.

We confirmed a seasonal variation in wild boar use of agricultural land, previously demonstrated by several studies (Lemel et al. 2003; Keuling et al. 2009; Thurfjell et al. 2009). Wild boar overused agricultural land during late summer and early autumn while demonstrating a proportional use in relation to its availability during other seasons. This seasonal variation is likely due to that agricultural land offers different food items throughout the year and is most attractive during periods when crops are ripe.

Conclusions

Wild boar spatial behavior is highly context dependent and may vary considerably due to landscape characteristics and local conditions. In this study, we show that we can expect adjustments in habitat use due to both habitat availability and population density. High wild boar densities are expected to lead to disproportionately high damage levels on agricultural fields which has strong implications for management. Realistic and achievable goals increase the chances of farmers and hunters agreeing on management practices and our results imply that, in many cases, it may in fact be enough to reduce wild boar density to moderate levels to reduce crop damage. We demonstrate the importance of identifying the level of plasticity in wild boar spatial behavior due to population-level characteristics. Applying static space use models not considering density may thus lead to inaccurate inferences with ecological and management consequences. Still, this observed plasticity in wild boar use of agricultural land and its consequences for crop damages requires further research to better assess the consistency in our observed overuse at high densities. This study provided a better understanding of the drivers of wild boar distribution and space use in agro-forested mosaic landscapes and showed that improved knowledge in wildlife spatial behavior can enhance management practices by directing actions to where they operate most usefully.

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Author contribution P. Kjellander, H. Thurfjell, S. Widgren, H. Kim, and E. Augustsson developed the study design. P. Kjellander, H. Thurfjell, S. Widgren, H. Kim, J. Malmsten, and J. Månsson provided data. Data were analyzed by E. Augustsson, H. Thurfjell, H. Kim, H. Andrén, and L. Graf. E. Augustsson led the writing of the manuscript and drafted the initial version. All authors revised the manuscript, contributed with supportive information, and gave final approval for publication.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All wild boar captures and handling were approved by the Ethical Committee in Animal Research, Umeå, Sweden (permit A 18-04), and Uppsala, Sweden (permit C 80/9, C 77/10, C 5.2.18-2830/16, and 5.8.18-00845/2017), and in compliance with Swedish laws and regulations.

Competing interests The authors declare no competing interests.

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