Wild boar habitat selection in south-central Sweden's forested habitats

- effects of season and time

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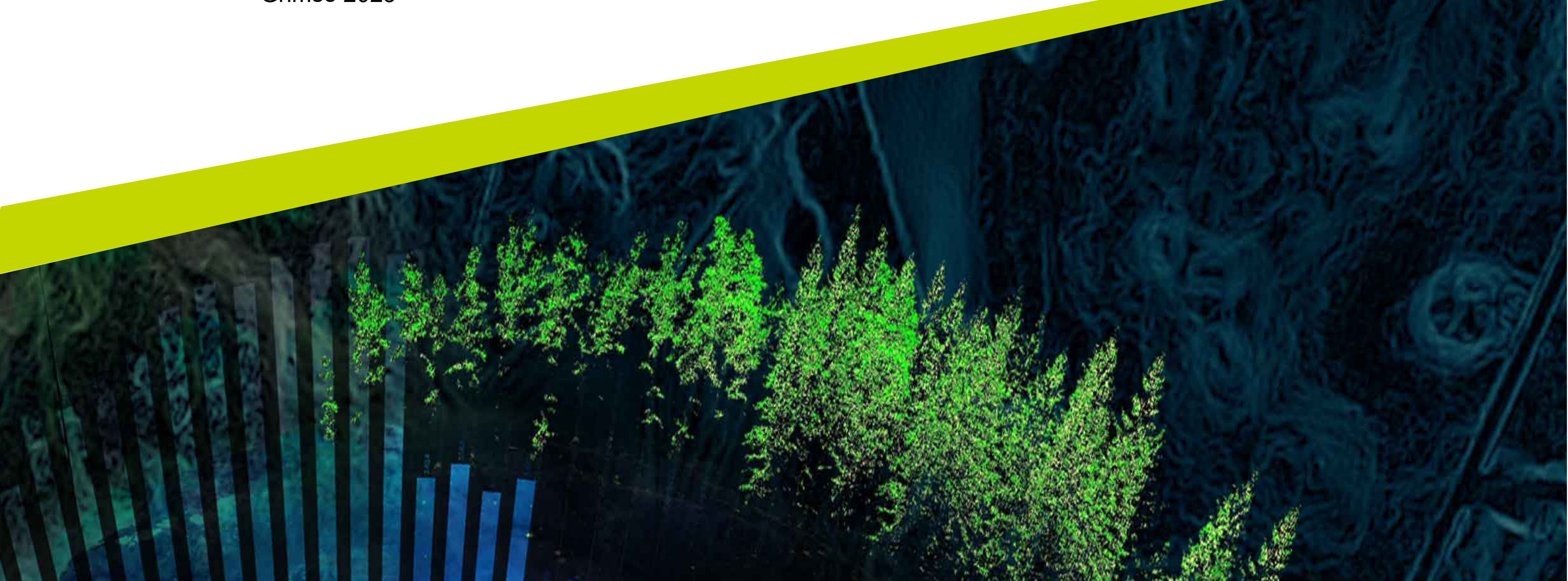

Wild boar habitat selection in south-central Sweden's forested habitats - effects of season and time

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Abstract

How wild boar utilize space, interact, and affect its surroundings is critical for understanding their ecology. Wild boar populations have increased rapidly in Sweden and continue to expand its distributional range further north. Little is known about how wild boar utilize the forest habitat in the boreal and hemi-boreal zone and increased knowledge is needed to ensure informed management decisions. Thus, this study aims to investigate wild boar habitat selection in forest habitats, depending on season and time of day. The study was conducted in six different study areas in south-central Sweden representing contrasting environmental conditions. Locations from 76 wild boar fitted with GPS-collars between 2018 - 2022 provided data on wild boar movements between habitats. Habitats were analysed using Generalized Linear Mixed Models, controlling for several different environmental covariates. Mature deciduous forests and young regenerated forests (approx. 3 - 7 m high) were the most preferred forest habitats by wild boar. Seasonal variation in habitat selection could primarily be attributed to natural variation of the respective habitat's ability to provide food and shelter. Differences in selection during daytime or night-time revealed that young forests were significantly more preferred by wild boar during daytime. During the night wild boar left young forests presumably to search for food in non-forested habitats as preference for such habitats increased. The effect of the environmental variables: tree height, soil moisture, slope, ruggedness and slope aspect, was unclear. However, when the environmental variables were included the general patterns of habitat selection remained, indicating that the habitat as a whole is the main determinant for selection.

Keywords: Wild boar, habitat selection, GLMM, Sweden

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Abbreviations

AIC	Akaike Information Criterion
DEM	Digital Elevation Model
GLMM	Generalized Linear Mixed Model
GIS	Geographical Information System
GPS	Global Positioning System
GSM	Global System for Mobile telecommunications
LiDAR	Light and Detection Ranging
NLD	National Landcover Data
SEPA	Swedish Environmental Protection Agency
SFA	Swedish Forest Agency
SMS	Short Messaging Service
SLU	Swedish University of Agricultural Sciences
VHF	Very High Frequency

1. Introduction

1.1 Habitat choice and resource selection

How species utilize space, affect and interact with its surroundings is critical for understanding a species ecology (Barnard 2004). Habitat choice and resource selection are two core concepts commonly used in the science of space use. They are both based on the assumption that available and utilized resources (e.g. food, shelter or nesting sites) are often limited and unevenly distributed in space and thus requiring animals to make deliberate choices and movements within its home range to optimize survival and reproduction (ibid.). Typically, choices are based on areas providing better than average conditions for physiological and behavioural demands, such as temperature, water, high food abundance and protection from predation (Johnson 1980). To be able to investigate and derive useful conclusions about resource selection, used resources must be compared to unused resources, corrected for its availability (ibid.).

Habitat choice can be defined as any behaviour causing an individual to spend more time in a certain habitat type compared to its availability i.e., compared to what would be expected from a random choice of habitat (Fox et al. 2001). Animals occur and select home ranges on the scale of a landscape, whereas individual habitat selection in sedentary species occurs within a limited home range and selection of a feeding or nesting site occurs within the habitat (Manly et al. 2007). However, not only is spatial scale of importance, the temporal scale is also an important consideration as variations in selection may occur depending on time of the day, season, or between years (Boyce 2006). As habitat selection occur over multiple scales, both spatially and temporally there are no correct answers to which scale that is the most appropriate and instead scale must be chosen based on the research question (Boyce et al. 2003). The fact that selection occur over multiple scales also implies that resource selection must be understood over several levels to fully understand the ecology of a species.

1.2 Wild boar habitat utilization

Wild boar (*Sus scrofa*) is a highly adaptable ungulate and widely spread all around the globe (Markov et al. 2022). Wild boar is an omnivorous animal with a highly varied diet depending on the environmental conditions (Genov 1981; Baubet et al. 2003a; Wilcox & van Vuren 2009). Agricultural crops are known to be highly preferred by wild boar, but most of the crops are only present during certain periods of the year (Schley & Roper 2003; Herrero et al. 2006). During other seasons of the year it has to resort to other food sources, with oak acorns (*Quercus* sp.) and beech nuts (*Fagus* sp.) being some of the most important food items provided naturally (Schley & Roper 2003; Zeman et al. 2016; Mikulka et al. 2018). Acorns is clearly so important that wild boar actively select oak stands (Kim et al. 2019) and adapt home range size during mast years (Singer et al. 1981).

Wild boar habitat selection within the boreal or hemi-boreal zone, dominated by coniferous forested habitats is poorly investigated, especially in a Nordic setting. In general, wild boar habitats consists of different types of forests, marshes, shrublands and river valleys and are often found in mixed landscapes dominated by agriculture (Corlatti & Zachos 2022). Meriggi & Sacchi (2001) found differences in habitat selection by wild boar in the Apennines depending both on differences found on macro, and micro-habitat scales. The study showed that wooded habitats were of great importance for both food and shelter and changes in habitat selection depended on seasonal changes in habitat specific characteristics providing food and shelter. Other studies on wild boar habitat selection has made the same conclusions, that the selection makes sense in regards to availability of food and shelter (Fonseca 2008; Thurfjell et al. 2009; Kim et al. 2019). Morelle & Lejeune (2015) found that the seasonal distribution of wild boar in agricultural landscapes is mostly influenced by the search for cover and food provided, alternatively by forest or agricultural crops. This indicates that there most likely also are seasonal variations in habitat selection within the forest as the availability of resources in the landscape changes. Furthermore, habitats may also be selected for seasonally due to differences between the habitats capability to provide thermoregulatory functions, where wetlands may be especially important (Paolini et al. 2018; Amendolia et al. 2019).

Wild boar are generally found to be nocturnal, with activity bouts normally starting around sunset (Boitani et al. 1994; Caley 1997; Lemel et al. 2003). However, Podgórski et al. (2013) found that high human presence pushes wild boar into nocturnal activity. In areas with low human presence, wild boar activity was spread out evenly throughout the day but with the same duration of daily activity. Lemel et al. (2003) found that wild boar adjusted the duration of activity bouts and movement distances depending on season, temperature and snow cover, which is supported by the findings of Thurfjell et al. (2014).

Hunting as a specific form of human presence affect wild boar activity rhythm in the same way, with increased activity during day in areas with low hunting pressure and vice versa (Keuling et al. 2008; Johann et al. 2020). Hunting may also have direct effects on wild boar habitat selection when disturbed in habitats they normally seek cover in, by forcing them away from habitats normally utilized (Saïd et al. 2012). Considering such demonstrated changes in movement patterns, it is likely that disturbance may have important consequences for wild boar selection of habitats.

1.3 Wild boar in Sweden and potential implications to forestry

Wild boar is native to Sweden although it has been eradicated several times through history (Jägareförbundet 2017). The most recent reintroduction to Swedish fauna was caused through escapes from enclosures (ibid.). In 1987 it was deemed domestic to Sweden in a legal sense and has since rapidly expanded and are commonly found throughout southern Sweden (ibid.). The increasing population of wild boar has led to large damages in agriculture with large economic losses as a consequence, and it is often in this context the species has been studied. Economic losses due to wild boar in Swedish agriculture has been estimated to cost farmers 120 million euro in 2015 (Andersson et al. 2016), however the economic impact on forestry is poorly understood.

Wild boar interactions with, and habitat selection in wooded habitats is poorly investigated but of growing interest to commercial forestry in Sweden. In Swedish counties where wild boar are present, ≥ 70% of the total land area constitute of forests (SCB 2020) and wild boar continues to expand northward into even more forested counties (Jägareförbundet 2017). The total financial turnover in commercial forestry exceeded 250 billion SEK in 2020 and constitute 9 - 12% of Sweden’s GDP (Skogsindustrierna 2022). There is therefore also an interest from the forest sector to better understand how wild boar utilize the forested landscape. Most of the forests in Sweden are intensively managed for timber production through clear-cutting, with stand cycle rotation time of 50 - 80 years (depending on local conditions and tree species), resulting in a constantly changing and fragmented landscape of forest habitats (KSLA 2015), likely affecting wild boar spatial behaviour. Due to the potentially high environmental impact of wild boar, mainly through rooting, (Massei & Genov 2004) it is also important to investigate how they might affect the landscape around them to understand if the impact is positive or negative.

There are some concerns regarding wild boar damage in the managed forests. Damages have been reported in forest plantations, where wild boar pull up seedlings with the root causing economic losses as landowners must replant clearcuts (Jansson & Månsson 2009). The main concern however is connected to their rooting behaviour in spruce stands, as it may induce root-rot into stands caused by *Heterobasidon sp.* fungi with reduced timber quality, loss of stand-stability, reduction of growth and requirements of extra management actions as consequences. Root-rot is already today the forest disease causing the largest economic losses in Swedish forestry and because the fungi is essentially impossible to eradicate from a stand where it has been established it is of great importance to reduce potential points of introduction if the disease is to be controlled (Berglund et al. 2017). Destruction of forest roads and ditches is also something that has been reported, although not directly damaging the forest but still cause economic loss to forestry (Jansson & Månsson 2009). In contrast, wild boar may also have positive effects in the forest, facilitating regeneration of trees and other plants by creating suitable micro-sites trough their rooting (Welander 2000a) which could potentially be of interest for specific forest management goals. An improved understanding about wild boar use of the forest habitat is highly requested, particularly among foresters and Swedish wildlife management, to make informed management decisions.

The aim of this study is to investigate wild boar habitat selection in forest habitats. In particular, spatial effects on selection of local environmental conditions as dominating tree species, tree height, soil moisture, slope, ruggedness, and slope aspect are investigated as well as temporal effects of, season and time of the day (day or night). This was done in six different and environmentally contrasting areas, in southern Sweden, where in total 76 animals of both sexes were supplied with GPS-collars, during 2018 - 2022.

2. Material and methods

2.1 Description of study areas

The study was conducted in six different study areas in southern Sweden (Fig 1.; Table 1.). The areas represent different types of landscapes found in southern Sweden with varied proportions of forest and agriculture. For most of the areas the main economic interest is forestry alongside agriculture. As most of the forest in the study sites are managed for conventional production purposes, the forests consist mainly of pure stands with either Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*). In Koberg, Boo, Hörningsholm and Boxholm commercial hunting is conducted. In Koberg it should be noted that all commercial cash crops are fenced off from wildlife and most of the grasslands are managed as game fields to provide food for wildlife. Bornsjön is a water protection area for one of Stockholm's water reservoirs with management to fit this purpose. All agriculture is managed for organic production, and the forest is managed with greater care of the soil, with some areas completely protected from logging. The proximity to the cities of Stockholm and Södertälje also makes the area frequently used as a recreational area for locals.

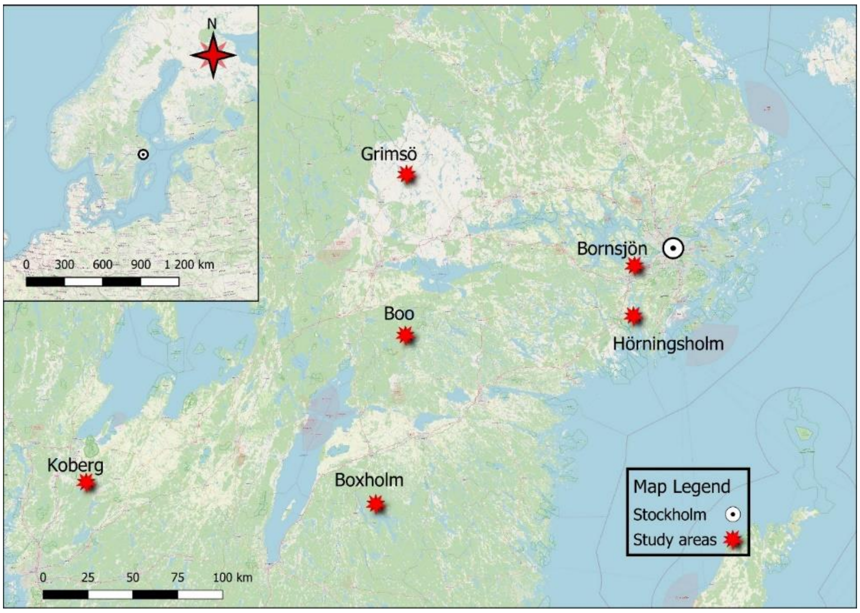


Figure 1. Map of the six study area's location in northern Europe (top left), and zoomed in for south-central Sweden (main panel) (OpenStreetMap ©, openstreetmap.org. (CC BY-SA 2.0).*)*

Table 1. Locations of the six study areas with descriptive metrics over local climatic conditions, presence of large carnivores and number of wild boars shot per square kilometre as a proxy for population density.

	Grimsö	**Koberg**	**Boo**	**Boxholm**	**Hörningsholm**	**Bornsjön**
Coordinates (WGS84)	59°43′45.0”N, 15°28′20.6”E	58°163’63.0”N, 12°412’05.3”E,	58°925’01.0”N, 15°514’54.7”E	58°097’04.1”N, 15°143’93.1”E	58°992’69.9N, 17°660’38.2E	59°241’26.7N, 17°736’18.0E
County	Örebro (northern)	Västra Götaland	Örebro (southern)	Östergötland	Stockholm	Stockholm
Area (hectare)	13 000	10 000	16 400	30 000	5000	5 500
Precipitation (mm/year)	600 - 800	800 - 1000	600 - 800	600 - 800	400 - 600	400 - 600
Average annual temperature (℃)	5 - 6	7 - 8	6 - 7	6 - 7	6 - 7	6 - 7
% Forest	78	79	70	95	70	60
% Agriculture	3	16	7	3	25	28
No of days with snow	100-125	50-75	100	75	75	75
Length of summer (days)	120	130-140	130	130-140	130	130
Large carnivore presence	Wolf and lynx	Lynx and occasional wolf	Lynx and occasional wolf	Lynx	Occasional lynx	None
No wild boar shot/km2	0.14	1.6	1.1	1.2	2.5	1.1

2.2 Data collection and processing

2.2.1 Capture and marking

The positional data were obtained by capturing and marking wild boar with GPS (Global Positioning System)/GSM (Global System for Mobile telecommunications)-collars with a total life span of approximately 56 weeks. A total of 76 individuals (65 females and 11 males) were marked in the six study areas, (19 at Grimsö, 24 at Koberg, 14 at Boo, 11 at Boxholm, 5 at Hörningsholm and 3 at Bornsjön), between 2018 - 2022. A full list of all marked individuals, sex, time of data collection and number of locations is provided in appendix 1. To be able to collar the animals they were first immobilized with a tranquilizer gun, either from a hide, vehicle, by foot or when trapped in approved wild boar traps. Only adult wild boar (≥60kg) were marked to avoid young animals outgrowing the GPS-collar. The method of marking from a car proved more effective in study areas with high densities of wild boar and where they exposed themselves more on fields in a calm enough manner to ensure safe shots with the tranquilizer gun. In more forested study areas with lower densities trapping showed to be more time effective. To ensure only capturing suitable animals, the traps were equipped with live-stream cameras and remote SMS (Short Message Service)-triggered devices, ensuring short waiting times for the animals in the trap before sedation and handling. The immobilization darts contained a mixture of 30 mg romifidine + 300 mg zolazepam-tiletamine or 5 mg medetomidine + 400 mg zolazepam-tiletamine. During immobilization the wild boar were measured, weighed, approximately aged based on tooth eruption, tooth wear and body size, earmarked and equipped with GPS/GSM collars (manufactured by Vectronic Aerospace Gmbh (N = 74) or Followit AB (N = 2) with a weight of approx. 750 g. During the marking process, body temperature and blood oxygen levels were continuously monitored to ensure the animals well-being during the process. After approx. 30 minutes, when marking and handling was completed, an antidote (Antisedan, 5 ml) was administered, and the animal released.

Ethical approval:

Approval to capture and mark free-ranging wild boar were given by the Ethical Committee in Animal research, Uppsala Sweden (permit C 5.2.18-2830/16 and 5.2.18-08758/2021).

2.2.2 GPS-data

Initially, during a 14-day period after marking, the collar recorded two locations per hour to enable better individual monitoring following the immobilization procedure. After that period the collar recorded 1 position per hour. Depending on GSM-network access collars upload seven hours of accumulated locations to a main server located at Grimsö. The battery lasts 13 months with this setup, meaning that no individual was monitored longer than 13 months. Some individuals have been marked during two separate periods. This was done to ensure a large enough collection of data if the population of wild boar an area was low. Such occurrences have still been treated as one individual in the analysis. To ensure that animals drop their collar when battery is depleted, a drop-off device releases the collar when battery level is low. The drop-off can, if necessary, be manually triggered to ensure that animals do not keep the collars for longer time periods than necessary. However, not all animals have been monitored for 13 months. Some has been accidentally shot, killed by cars, simply lost the collar, or because of collar malfunctions.

To ensure that collars can be retrieved and refurbished they are fitted with a VHF-transmitter that is active between 12.00 - 15.00 hrs. every day. To recognize that a collar has dropped off (or that an animal has died) each collar is fitted with an activity sensor registering if the animal is moving or not. If the collar is completely still for 24 hours a mortality message is sent via GSM. This enables field personnel to go out and find the collar and determine the fate of the animal.

For further analysis, one GPS position per hour was used. The GPS-data was cleaned to exclude faulty positions. First, all positions following a confirmed mortality message were removed. Secondly, all positions in the first 10 days after marking were removed as lower levels of activity and mobility can be expected because of the immobilization and sedation (Brogi et al. 2019). Thirdly, positions indicated to be of low precision by (< 4 satellites involved) were also removed to only include 3D validated positions as well as positions in extreme longitude or latitudes. Fourthly, all positions with unrealistic altitude were removed. Finally, the positions were visually examined in Q-GIS to remove apparent outliers.

2.3 Remote sensing data

2.3.1 National Landcover Data

The main data source used to determine different habitats used by the wild boar was the National Landcover Data (NLD) provided by the Swedish Environmental Protection Agency (SEPA), (NLD, 10 x 10m, 2020, basskikt v2.2). Data was provided as a rasterized map in 10 x 10m pixels. The map was then reclassified into 10 different habitat classes deemed to be of biological interest to wild boar. Non forested habitats were pooled into one habitat class ("Other") as they were of little interest for the research question (Table 2). To avoid inclusion of very small habitat patches the map was filtered using the sieve function in Q-GIS to only keep habitat patches containing a minimum of 5 pixels.

Table 2. Classification of habitats based on NLD landcover classes.

Code in NLD	**Landcover class in NLD**	**Habitat**
2	Open wetland	Other
3	Agriculture	Other
41	Open land without vegetation	Other
42	Open land with vegetation	Other
51	Exploited land, buildings	Other
52	Exploited land, not buildings or roads/railways	Other
53	Exploited land, roads, or railways	Other
61	Lakes and watercourses	Other
111	Pine forest outside wetland (>70% crown coverage)	Pine
112	Spruce forest outside wetland (>70% crown coverage)	Spruce
113	Mixed coniferous forest (>70% crown coverage of spruce and pine)	Conifer
114	Deciduous mixed forest (Neither conifer nor deciduous trees >70% crown coverage)	Mixed forest
115	Deciduous forest (> 70% crown coverage of deciduous trees)	Deciduous
116	Temperate deciduous forest (> 70% crown coverage of deciduous trees, >50% crown coverage of temperate deciduous tree species)	Deciduous
117	Mixed deciduous forest with temperate deciduous tree elements (>70% deciduous trees with 20-50% temperate deciduous tree species)	Deciduous
118	Temporally not forest (Tree height <5m in 2018)	Young forest
121	Pine forest on wetland*	Pine
122	Spruce forest on wetland*	Spruce
123	Mixed coniferous forest on wetland*	Conifer
124	Deciduous mixed forest on wetland*	Mixed forest
125	Trivial deciduous forest on wetland*	Deciduous
126	Noble deciduous forest on wetland*	Deciduous
127	Trivial deciduous forest with noble deciduous tree elements on wetland*	Deciduous
128	Temporally not forest on wetland (Tree height <5m in 2018)	Young forest

*= Same rules regarding crown coverage applies on the forest types on wetland i.e., >70% crown coverage for dominating tree species/tree species group.

2.3.2 Forest basal data

To increase the resolution of the different forest habitat data over tree height was included. The data was provided by the Swedish Forest Agency (SFA) as a rasterized map containing tree heights in 12.5 x 12.5 m pixels (HGV, 12.5 x 12.5 m, 2022, Skogsstyrelsens skogliga grunddata,www.skogsstyrelsen.se, downloaded 2022-11-12). Tree height is derived from LiDAR (Light and Detection Ranging) scans of the forest and reference plots from the Swedish National Forest Inventory and provides measurements of equal quality as manual measurements. Tree height is weighted against the basal area meaning that trees contributing more to the basal area are given greater weight in the estimated average tree height and thus a measurement of overstory tree height. The map provides tree heights >3m as the crown closure of stands below 3m is generally too sparse to generate accurate estimates. Another known problem with tree height maps derived from LiDAR data is measurement-quality in steep terrain (Skogliga grunddata 2022). However, the data can be assumed to be the best for large scale descriptions of forest height and is commonly used for forest management inventories in forestry (Kangas et al. 2018). Data used for each study area are based on the most recent available LiDAR-scans (Boo 2011, Bornsjön 2020, Hörningsholm 2020, Grimsö 2021, Boxholm 2022 and Koberg 2022).

SLU (Swedish University of Agricultural Sciences) provided classified soil moisture maps as a raster with the pixel size of 2 x 2m. The soil moisture was defined in four classes, 1: Dry-Fresh, 2: Fresh-Moist, 3: Moist-Wet, 4: Open water. The map classifies soil moisture based on LiDAR scans trained on inventory plots from the Swedish National Forest Inventory (SLU 2020). The four soil moisture classes are defined by the depth to the ground water table. Dry-Mesic means that the ground water table is > 1m below ground, Mesic-Moist < 1m below ground, and on Moist-Wet soils the groundwater is visible on the ground surface. Data for soil moisture were added to the analysis as we suspected that soil moisture would affect wild boar habitat selection during certain environmental conditions. For example, it is expected that wild boar avoids wet areas especially during winter and spring, with high groundwater tables and selected for high moisture during summer draughts (Paolini et al. 2018; Amendolia et al. 2019). Soil moisture has also been found to affect rooting behaviour of wild boar (Welander 2000b) and thus potentially also habitat selection.

2.3.3 Clearcut data

As most of Swedish forests are intensely managed through clearcutting and replanting, information about when specific clearcuts had been made, were included. Thus, it was possible to distinguish between a recent clearcut and a replanted clearcut where trees had reached a height of ≥ 3m. This procedure also made it possible to update the NLD-map from 2018 with the most recent clearcuts. SFA provided maps where clearcuts had been identified on satellite imagery (Completed fellings SFA 2022). The date the clearcut had been identified was used to define if a wild boar position had been on a clearcut or not. A wild boar location after 2018 was thus considered to be in the habitat class Clearcut if the date was after the SFA-registered date of that stand. On clearcuts older than 10 years positions were considered to be in the habitat provided by the NLD.

2.3.4 Digital elevation model

To test for which degree ground surface structure affected wild boar habitat choice, data generated from a Digital Elevation Model (DEM) was included. DEM-data was provided by the Swedish National Land Survey as rasterized maps in two resolutions 2 x 2m and 50 x 50m (Lantmäteriet 2022). The data was later processed in Q-GIS to derive slope degree (50 x 50m), slope aspect (50 x 50m) and a ruggedness index (2 x 2m). The two variables (slope degree and aspect) were included to investigate how they interact with other environmental variables and ultimately affect wild boar habitat choice. The ruggedness index were constructed as described by Riley et al. (1999).

2.4 Data analysis

To analyse the GPS-data, Q-GIS (v. 3.28.1) and R Studio (v. 2022.07.2 576+) were used. All pre-processing of spatial data was done in Q-GIS while the cleaned wild boar location dataset was imported into R Studio. To assess habitat selection, randomized points in a 1:1 ratio were generated within each of the individual wild boar home ranges. Home ranges were defined using a minimum convex polygon (MCP). Randomized positions were used as a control to actual positions and expected to reflect random movements between habitats, i.e., no selection for any given habitat. Finally, all positions were defined into three different seasons: spring (March – May), summer (June – September) and winter (October – February). The definition of seasons was based on general wild boar ecological traits and climatic factors (Corlatti & Zachos 2022). The definition of spring season was based on the months were the majority of the sows in the study farrowed (peak in the shift between March and April) and the peak of adult female reproduction (Malmsten et al. 2017). Summer was defined as June-September and clearly related to the main vegetation season, mobile piglets, high temperatures and the period where agricultural crops are present. October was defined as the start of the winter with harsher weather conditions, fading vegetation, start of the main mating season as well as the start of the main hunting season for wild boar. All positions were also divided into day or night positions based on the time of dawn and dusk the given day. The hour the sun sets were defined as the start of the night as that is the time the activity bouts generally start (Lemel et al. 2003).

A General linear mixed model (GLMM) using binary logistic regression in R studio (v. 2022.07.2 576+) was used to evaluate habitat selection. The response variable indicated whether a location was a true wild boar location "1" or a random location in the available area "0". The explanatory variables were; habitat, season, day or night, tree height, soil moisture, slope, ruggedness, and slope aspect. The independent continuous variables were checked for autocorrelations using a correlation matrix. A potential correlation problem between slope and ruggedness was detected with a value of 0.507 (Appendix 2). Model selection was based on Akaike Information Criterion (AIC). The model with the lowest AIC compared to the simplest model was then selected as the best model to explain how the explanatory variables affect selection (Appendix 3). Models were also tested using confusion matrixes to assess model accuracy of prediction. Animal ID and study-area were used as random factors in the model. To handle the large number of variables the analysis was conducted in two steps. In the first step a simpler model containing only habitat, season and time as explanatory variables was used to test if season influenced habitat selection. In the second step, data was divided based on season and the full model was performed for each of the seasons to test the effects of all environmental variables.

3. Results

In this section the results from the first step of the analysis are presented. The second step of the analysis where the environmental variables were included is presented in the appendix section (Appendix 5, 6 and 7) as the results were inconclusive.

3.1 Home range sizes

Mean home range size for all 76 individuals in the study were 30 km² (±29.8 km²). Home range sizes varied between a maximum of 144.7 km² to a minimum of 1.5 km². Wild boar at Grimsö demonstrated the largest average home ranges of 47.1 km² (n = 19) while wild boar at Bornsjön demonstrated the smallest home ranges on average at 16.1 km² (n = 3). Males had a mean home range size of 46.4 km² (±35.6 km², n = 11) and females 26.8 km² (±27.3 km², n = 65).

Table 3. Mean, maximum and minimum home range sizes in km² with standard deviation from mean derived using MCP grouped on study area. All animals are included irrespective of the length of the period they were observed. Data from 6 different study areas in south central Sweden, 2018 - 2023.

Area	Mean	Min	Max	Standard Deviation
Boo	27.9	9.3	92.3	21
Hörningsholm	14.3	1.5	20.5	7.2
Koberg	26.7	3.7	144.7	35.6
Grimsö	47.1	13.6	139.5	31.3
Boxholm	24.3	3.1	77.5	20.9
Bornsjön	16.1	9.3	28.7	8.9
Total	30.02	1.5	144.7	29.8

3.2 Habitat selection independent of season and time of the day

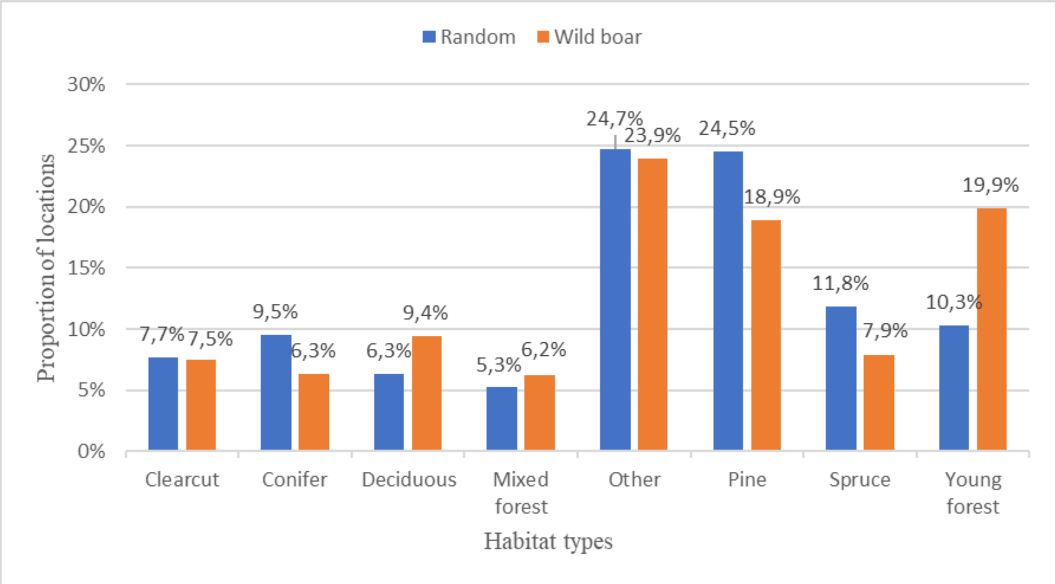


Figure 2. The proportion of all wild boar locations within a habitat compared to the proportion of random locations. A higher proportion of wild boar locations compared to random locations indicates selection for the habitat. Based on 76 GPS marked animals in six different study areas, south-central Sweden, 2018 - 2023.

In a first step, not considering season or time of the day, a considerable proportion (63%) of the wild boar locations are found within the habitats Other and Young forest and Pine. Wild boar spends more time in Deciduous and Young forest than expected irrespective of season and time (Fig 2). In Conifer, Pine and Spruce habitat classes wild boar spent less time than expected (Fig 2). Wild boar spent approximately the same amount of time in habitat classes Clearcut, Mixed forest, and Other as expected (Fig 2).

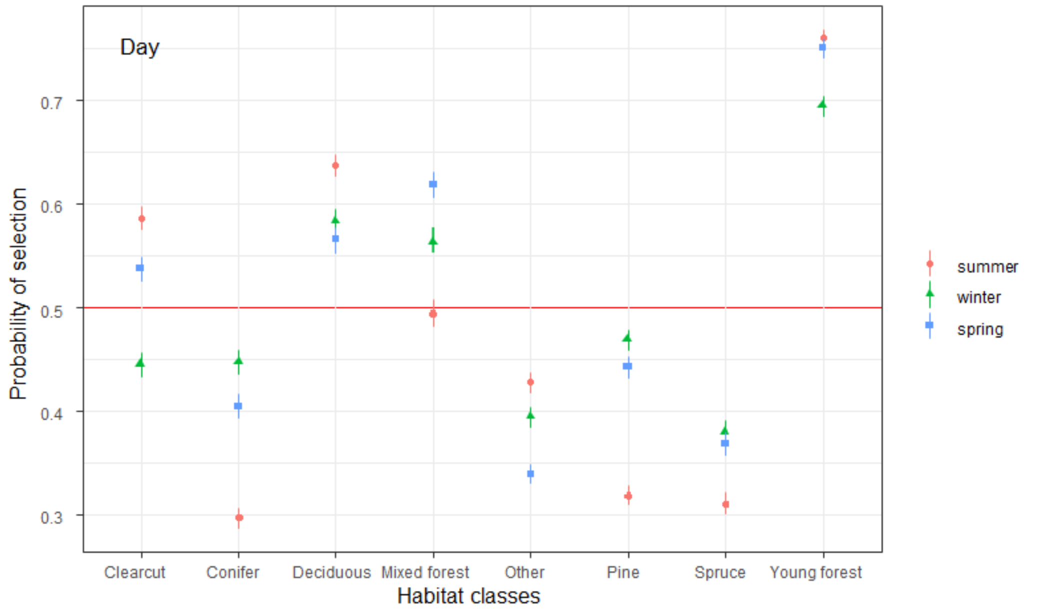
3.3 Habitat selection depending on season

The main effects of season on habitat selection were found between winter and summer seasons. Selection of Clearcut and Deciduous habitats increased significantly during summer and Clearcut is selected during both day and night during summer (Day = 0.59, Night = 0.53; Fig 3). Deciduous is selected for during all seasons but has the highest selection values during summer (summer = 0.63, spring = 0.56, winter = 0.58; Fig 3) with no significant differences between day or night.

The habitat classes Conifer, Pine and Spruce all have the highest selection values during winter and the lowest during summer, however the selection values are always below 0.5 indicating a general avoidance of those habitats (Fig 3). Pine is considerably less avoided during winter (0.48) compared to summer (0.33). Conifer is also considerably less avoided during winter (0.44) compared to summer (0.29). For both habitat Pine and Conifer, there were no significant differences for selection between day and night. Spruce was also less avoided by wild boar during winter (Day = 0.33, Night=0.44) compared to summer (Day = 0.31, Night = 0.37; Fig 3.). Although Conifer, Pine and Spruce are less selected compared to the habitat's availability, wild boar still spend a considerable amount of time in those habitats. Pine being the clearest example with 18.9% of all wild boar positions being in that habitat compared to 9.4% in Deciduous habitats (Fig 2.). Mixed forest is the only habitat that wild boar selected most for during spring (Day = 0.61, Night = 0.58) when compared to the other seasons. Mixed forest was also selected for during winter (Day = 0.56, Night = 0.52) but were used in relation to availability or slightly avoided during summer (Day = 0.49, Night = 0.45; Fig 3).

A detailed table containing predicted probabilities of selection for each habitat at a given season and time of day along standard errors can be found in Appendix 4.

a)



b)

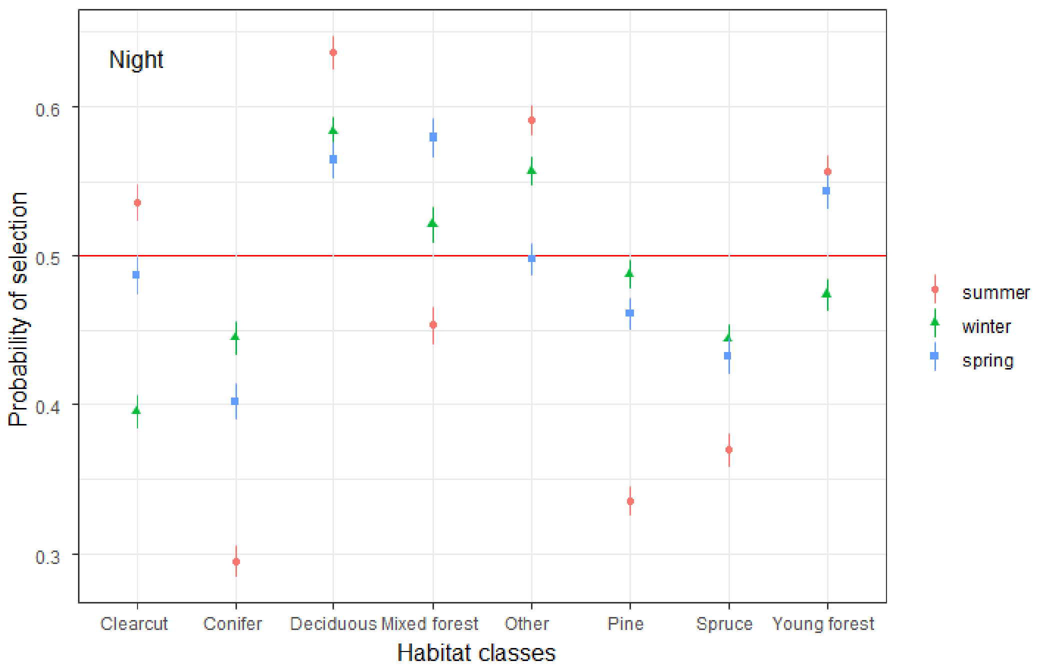


Figure 3. Wild boar selection of the different habitat classes divided between the three seasons. The upper table (a) depicts selection during daytime and the lower table (b) depicts selection during the night. A probability above 0.5 (red line) indicates a preference for the habitat while a probability below indicates avoidance. Each point represents selection during the respective seasons with 95% confidence interval.

3.4 Habitat selection depending on time of the day

Young forest is heavily selected for during daytime by wild boar during all three seasons and demonstrates the highest selection value of all habitats (spring = 0.76, summer = 0.76, winter = 0.69; Fig 3a). During nighttime wild boar selects less for Young forest compared to daytime, although the selection values still indicate selection for the habitat with exception during winter (spring = 0.53, summer = 0.55, winter = 0.47; Fig 3b). Habitats within the class Other (i.e. non-forested habitats) are selected for during nighttime during summer and winter by wild boar (summer = 0.59, winter = 0.55). During nighttime at spring wild boar shows neither preference nor avoidance for Other (0.5; Fig 3b). During daytime wild boar avoid the habitat (spring = 0.34, summer = 0.43, winter = 0.39). The Spruce habitat is avoided to a higher degree during day (spring = 0.37, summer = 0.31, winter = 0.38; Fig 3a) compared to night (spring = 0.43, summer = 0.37, winter = 0.44; Fig 3b).

3.5 Binary logistic regression model results on habitat selection

Selection was significantly determined at the level of habitat composition with strong effects of season and time of the day. Furthermore, all interactions between habitats and season were significant. All interactions between habitats and time were also significant except for Mixed forest and night (Table 4.).

*Table 4. Output from a binary logistic, general linear mixed model analysis analysing the influence of season and time on habitat selection. Model=habitat*season + habitat*time + (ID random factor) + (area random factor). Data based on 76 GPS marked wildboar in 6 different study areas in southcentral Sweden, 2018 – 2023.*

Predictors	Estimate	SE	p-value
Clearcut (Intercept)	0.15	0.024	<0.001
Conifer	-0.54	0.022	<0.001
Deciduous	0.11	0.022	<0.001
Mixed forest	0.33	0.02	<0.001
Other	-0.82	0.023	<0.001
Pine	-0.38	0.018	<0.001
Spruce	-0.69	0.021	<0.001
Young forest	0.95	0.019	<0.001
time (Night)	-0.21	0.014	<0.001
Season (Summer)	0.19	0.018	<0.001
Season (Winter)	-0.37	0.018	<0.001
Conifer × Night	0.19	0.02	<0.001
Deciduous × Night	0.2	0.02	<0.001
Mixed forest × Night	0.03	0.022	0.078
Other × Night	0.86	0.016	<0.001
Pine × Night	0.28	0.016	<0.001
Spruce × Night	0.47	0.019	<0.001
Young forest × Night	-0.72	0.018	<0.001
Conifer × Summer	-0.62	0.028	<0.001
Deciduous × Summer	0.1	0.027	<0.001
Mixed forest × Summer	-0.7	0.029	<0.001
Other × Summer	0.18	0.022	<0.001
Pine × Summer	-0.72	0.022	<0.001
Spruce × Summer	-0.46	0.026	<0.001
Young forest × Summer	-0.14	0.024	<0.001
Conifer × Winter	0.55	0.025	<0.001
Deciduous × Winter	0.45	0.026	<0.001
Mixed forest × Winter	0.13	0.027	<0.001
Other × Winter	0.61	0.021	<0.001
Pine × Winter	0.48	0.021	<0.001
Spruce × Winter	0.41	0.024	<0.001
Young forest × Winter	0.09	0.023	<0.001

4. Discussion

4.1 Influence of season on habitat selection

This study found significant differences in wild boar habitat selection between seasons. In general, the largest differences in selection were found between summer and winter. Clear-cuts were preferred during summer and avoided during winter. A higher selection for clear-cuts during summer can be explained by re-growth on the clear-cut of herbs, grass, and shrubs. The re-growth might not only provide food for wild boar, but also attracts rodents that could be a food source for wild boar (Massei & Genov 2004). The regrowth also provides cover for wild boar which would only be present seasonally, explaining the increased preference during summer. Vigorous regrowth of wild raspberry (*Rubus idaeus*) and common bracken (*Pteridium aquilinum*) are commonly found on Swedish clear-cuts and potentially provide excellent cover for wildboar. Heavy regrowth of woody vegetation such as sprouts of downy birch (*Betula pubescens*), silver birch (*Betula pendula*) and aspen (*Populus tremula*) are also common and would provide better cover during the summer when the leaves are present on the saplings. Cover can probably also be found among voluntary set-asides for nature conservation consideration. Eom et al. (2019) found an increased presence by wild boar in clear-cuts of Japanese larch with a retained understory, supporting this explanation. The avoidance of clear-cuts during winter can be explained by a reduction of both food and cover as the vegetation is wilted during the progress of winter and early spring. During winter the regenerated trees not yet large enough to close the canopy and cannot provide sufficient cover from the harsher weather conditions or predators and thus other habitats might be more preferred for day bedding sites. Additionally, the lack of tall mature trees increases snow depth making food on the ground harder to access as well making the habitat costly to access. Wild boar has short legs and moving through deep snow requires a lot of energy and is known to limit their movements (Lemel et al. 2003). However, since this study does not control for the effects of snow depth nothing can be said of the true effects on habitat selection although it is possible snow has an impact on wild boar habitat selection.

While deciduous forests were preferred by wild boar during all seasons, the habitat was preferred most during summer. The high preference during summer can probably be explained by the food that the habitat provides. The forest floor provides a lot of food in the form of different herbs and grasses as well as the mast that certain tree species provide. The litter from deciduous trees also attracts several kinds of decomposers such as earth worms and other invertebrates that could serve as food for wild boar (Baubet et al. 2003b). Dense deciduous forests also provide good cover, especially if the understory is well developed and while the leaves remain on the trees. During winter the habitat provide less food, and this could be an explanation for the reduction in preference. Many studies on wild boar highlights about the importance of forest mast, perhaps especially the importance of oak acorns (Wilcox & van Vuren 2009; Zeman et al. 2016) that could have a large influence especially during the winter. However, oaks are not found within all types of deciduous forests in Sweden and rarely dominate stands. This imply that while oak trees may be important locally, presence of oak alone do not explain the general pattern of preference for deciduous forests irrespective of season in this study. Even when the above ground parts of the ground vegetation has died off, roots, rhizomes and tubers remain below ground which is excellent food for wild boar (Howe & Bratton 1976) and would explain why the habitat is preferred throughout the whole year. Wild boar has been found to root more extensively in deciduous forests compared to other habitats supporting that there probably is a lot of food to be found in the ground (Welander 2000b). The finding is also in line with Muthoka et al. (2022) and partly with Thurfjell et al. (2009). Contrasting to this study Thurfjell et al. (2009) found that while deciduous forest was a preferred habitat during all seasons, coniferous forest was more preferred than deciduous forest during spring. Furthermore, deciduous forests are often located in connection to agricultural lands in Sweden with increased human presence meaning the reduced preference could be explained by a risk adverse behaviour balancing risk and reward. When food in the surrounding agricultural fields disappears during winter and spring the risk of being killed near open fields is simply too high and the preference of such habitats is thus reduced. Such behaviour was observed by (Johann et al. 2020) who found that wild boar were more active during night with increasing hunting pressure and chose resting sites further from hiking trails with high activity.

All different types of coniferous forests (Conifer, Pine, and Spruce) were avoided irrespective of season. However, the degree of avoidance was different between the seasons. Mixed coniferous forests, pine forests and spruce forests were all avoided the most during summer. A reasonable explanation for this is that wild boar during summer trade the use of coniferous forest types for better habitats such as agricultural fields and deciduous forests providing better conditions, compared to the other seasons. The observed reduced avoidance of coniferous forests during winter is probably for the same reason. Reduced food in other habitats force wild boar to utilize coniferous forests to a greater extent during winter even though the habitats do not contain very much food or shelter. Stands of Norway spruce, Scots pine and mixes of the two under strict management for timber production (which is the most commonly found forest types in Sweden) are routinely cleaned throughout the rotation leaving little understory for wild boar to find shelter in. Pure mid-rotational spruce stands with dense, closed canopies allow very little light down to the ground, creating a forest floor with very sparse ground vegetation and thus providing less food for wild boar (Felton et al. 2020). However, a dense canopy provides shade on warm summer days that may explain why spruce forests are less avoided during that season compared to pine and mixed coniferous forests. The high temperatures during summer would increase a demand for habitats providing thermoregulatory functions as has been found important for wild boar (Amendolia et al. 2019). In stands where Scots pine dominates, more light reaches the ground and more ground vegetation can be found creating more food for wild boar, explaining a higher preference during winter and spring. Haaverstad et al. (2014) found that wild boar rooted more in pine forests of low fertility during winter, which may explain why pine forests are the least avoided of the coniferous forest habitats during winter. Still, a simpler explanation could be supplementary feeding. Hunters are recommended to provide supplementary food is in forests far away from agriculture (Jägareförbundet 2019) and may explain why wild boar spend more time in coniferous forests during this period of the year, when most of the feeding sites are in operation and would matter the most to the wild boar. This interpretation is supported by Muthoka et al. (2022) that found selection of coniferous forest to increase with reduced distance to feeding sites, indicating that supplementary feeding might have a strong effect on selection of coniferous forest during winter, in this study.

It is unclear why mixed forests are the only habitat wild boar prefers most during spring compared to the rest of the year. The mix of coniferous and deciduous trees may provide a good mix of both elements during a short period of the year and thus a possible difference in food availability compared to deciduous or agricultural habitats is not as apparent. However, Mixed forests are generally preferred during day for all seasons indicating that the habitat is primarily used for cover and not for food, as wild boar primarily bed during daytime (Lemel et al. 2003). As mixed forests in Sweden generally are a product of older, not managed forests (often containing an understory or multi-storeyed) or a result of a deliberate management to increase vertical variation in the forest structure, it is reasonable that such forest types provide better cover for wild boar.

4.2 Influence of time of the day on habitat selection

Changes in wild boar habitat preference between day and night is most pronounced in the use of young forests and habitat types found in the habitat class Other i.e., non-forested habitats. However, as Other is a mix of different habitat types such as water one should be cautious when interpreting the results on selection of this group of merged miscellaneous habitats. Young forests were a strongly preferred habitat in daytime during all seasons indicating that the habitat is primarily used for cover during the period of the day when wild boar are generally inactive (Lemel et al. 2003). Young forests in the conventional Swedish production forest are almost exclusively regenerated with plantations of either Norway spruce or Scots pine at a density of ca 1500 - 3000 plants per hectare, depending on site productivity (Skogskunskap 2023). Spontaneously regenerated sprouts of deciduous trees create dense thickets of an additional several thousands of plants per hectare, providing excellent cover against harsh weather and protection from being discovered by predators and humans. Young forests are likely less visited by humans for recreational purposes making the habitat ideal to avoid human presence. While young forests are less selected for during night-time the habitat is still preferred by wild boar in all seasons, except during winter. Likely because wild boar still utilizes the habitat for cover for at least in parts of the night as the duration of the activity bouts does not cover the entire duration of the night (Lemel et al. 2003). Another possible explanation is that some of the individuals may have a more diurnal activity rhythm, experiencing less disturbance from humans and hunting as suggested by Podgórski et al. (2013) and Keuling et al. (2008).

Wild boar reduce their preference for young forests during winter. (Lemel et al. 2003) found that the duration of activity bouts was the longest during winter implicating that wild boar spend more time searching for food, thus reducing their time spent in habitats providing cover and bed sites. The influence of hunting on habitat preference during this time of the year cannot be discarded. The period defined as winter in this study coincides with the main hunting season in Sweden and the use of hunting dogs. Especially female wild boar has been found to change selection for different habitats as a response to hunting, and leave frequently used resting habitats in favour of other habitats (Sodeikat & Pohlmeyer 2007; Saïd et al. 2012). As dogs are used to flush wild boar out of young forests where they normally are not hunted during other periods of the year, it is possible that an increased disturbance from hunting make wild boar seek shelter in other habitats. The reduced avoidance of spruce forests during night is unclear and could be an effect of an increased activity during night-time and since the habitat is highly abundant, animals might simply be forced to pass through spruce stands when traveling to more preferred habitats used for foraging.

There are opposite trends in habitat selection between non forested habitats (habitat class Other) during night versus young forests during day, indicating that wild boar leaves young forests during night-time for the benefit of non-forested habitats. The increased preference of non-forested habitats during night-time is probably because wild boar search for food on agricultural land included in the habitat class Other. Agricultural land is well known to be preferred by wild boar at least when crops are present (Thurfjell et al. 2009; Muthoka et al. 2022). Visiting agricultural areas (and human settlements/ other open areas also included in the habitat class) during daytime is probably connected with too much risk to be worth it. Wild boar are known to cause damage to such areas and are thus actively being hunted or chased away to reduce damage. During night-time when human activity decreases and lack of light makes hunting more difficult, the risk is reduced enough that wild boar dares to venture into open areas. As previously mentioned, hunting and human disturbance increases nocturnal activity and influences habitat selection. (Amici et al. 2012) found increased damages on agricultural crops in areas where hunting was banned. Presumably would wild boar utilize such areas much more and also during times of the day if the risk of being hunted is reduced.

4.3 Influence of environmental variables on habitat selection

The habitat selection analyses using separate seasons with all environmental variables included, were inconclusive. Still, the best model explaining habitat selection included all environmental variables and was supported by a lowered AIC. Soil moisture was the single environmental variable that improved AIC the most, but also introduced considerably increased variance (S.E.) in the predicted probabilities of selection for individual habitats. Why this is the case is unclear. One possible explanation can be that the data used to describe soil moisture is flawed in some way or at least of too low resolution to capture the variation of importance for wild boar. Still, wild boar has been found to respond to weather effects (Thurfjell et al. 2014b; Olczak et al. 2015) and speculatively could the high variance in selection be due to randomly occurring weather effects on the suitability of habitats. For example, a bed site on moist soil might be highly preferred during days with high temperature or periods of drought while being avoided when there is a lot of heavy rains. While this study is incapable of capturing such effects, it still raises interesting questions for future research.

The other environmental variables besides soil moisture seemed to have negligible additive effects on the predicted probabilities of selection for the different habitats. The predicted probabilities differ somewhat compared to the results presented from the first stage of the analysis. The general pattern of habitat selection with effects of seasons and time of day remains, with some minor variation in estimates. This indicates that it is rather the habitat as a whole that is the main determinant of selection in wild boar. Previous studies agree that habitat selection by wild boar in large is determined by the availability of food and shelter (Meriggi & Sacchi 2001; Fonseca 2008; Thurfjell et al. 2009; Kim et al. 2019; Muthoka et al. 2022). To what degree a habitat can provide food and shelter is likely determined by characteristics inherent to the habitat as a whole such as vegetational composition. The environmental variables used in this study may have local effects or in interaction with randomly occurring events such as weather and would therefore not affect habitat selection on the larger spatial and temporal scales used in this study.

4.4 Potential implications for forestry

The general avoidance of spruce forests implies that wild boar has a limited potential to cause damage in the forest by spreading root-rot *Heterobasidon sp.* to spruce stands. Even though wild boar does spend time rooting in spruce forests, they do so primarily during winter when air temperatures are low enough to limit *Heterobasidon sp.* spore counts (Berglund et al. 2017). Furthermore could Haaverstad et al. (2014) establish that their rooting rarely damages the roots of spruce, thereby limiting potential entry points for the fungi. Clearcuts were selected for about to the same degree as is available when not taking season or time into account. Wild boar are known to cause damage to both coniferous and deciduous seedlings on clearcuts and can cause severe economic losses (Fern et al. 2020). In this study, clearcuts were more preferred during summer and spring which is the seasons when seedlings generally are planted and thus most sensitive. Because of that may wild boar potentially become a problem in Swedish forest plantations. However, more studies would be needed to be able to quantify the damages and to establish what ecological drivers causing wild boar to damage seedlings. The high preference for deciduous forests throughout the year could potentially lead to damages on ecological values within nature conservation areas. Extensive wild boar rooting can have detrimental effects on certain types of ground flora in Swedish temperate deciduous forests (Brunet et al. 2016). Since such forest types are quite rare in Sweden might a disproportionately high use of those habitats lead to damage on rare ecological values such as sensitive ground flora. Based on the results of this study we can only speculate what the actual impact of wild boar would be in such habitats and more research in the area is needed in both sensitive deciduous and coniferous forests.

4.5 Weaknesses with the study

In the analysis, study area was included as a random factor as the purpose was to investigate the general habitat selection in wild boar in south-central Sweden. Thus, this choice renders the study unable to capture differences in habitat selection between study areas. For example, would a deciduous habitat in Koberg be quite different from one found at Grimsö with both differences in tree species composition and site productivity. One might also suspect that areas with a higher proportion of agriculture and open fields causes wild boar to have a different dynamic between the use of forests and open fields. Paolini et al. (2018) found that the proportional coverage of different habitats had effects on the probability of selection by wild boar supporting this suggestion.

However, the largest differences between the study areas that potentially can be observed is likely not due to differences of the habitats but rather behavioural differences of wild boar in the respective subpopulations. At the study area Koberg, a large proportion of the wild boar is suspected to have diurnal activity patters. Given that 24 out of 76 marked animals is from Koberg may have detrimental effects on the results and especially on differences between day and night given the large representation within the data set.
The largest difference of habitat selection between day and night was of non-forested habitats while use of forested habitats was largely unaffected apart from young forests. While the focus of this study was the use of forested habitats, future studies should consider not pooling non-forested habitats together as there is an apparent high use of such areas by wild boar with interesting dynamics worth further investigation for mitigating damages on agriculture as an example.

Another problem with the study is the fact that no consideration was taken into how wild boar behaviour affects the results of selection. During the day most wild boar laid still in their bed sites which means that positions would accumulate in those habitats resulting in an overrepresentation of those habitats. Although we assume a primarily nocturnal activity of wild boar in this study it is of interest to be able to distinguish between different behaviours as it is of importance when assessing what effect wild boar may have in each habitat. Other types of habitat selection analyses able to distinguish between behaviours and movement patterns would be more suitable to make useful conclusions concerning such questions (Thurfjell et al. 2014a).

4.6 Conclusions

Wild boar clearly preferred deciduous forests, and young forests during all seasons. Clear-cuts, deciduous forests, young forests, and non-forested habitats were selected for more during summer. During winter, preference for those habitats was reduced while selection for coniferous habitats increased. Although mixed coniferous forests, pine forests and spruce forests were generally avoided habitats throughout the seasons, they were less avoided during winter. The variation in habitat selection between seasons is probably explained by the degree habitats may provide food and shelter. Thus, wild boar likely adjusts the use of habitats to optimize resource utilization within the home range due to seasonal changes in the availability of food and shelter.

In daytime wild boar preferred young forests during all three seasons and clearcuts during summer and spring. During night, preference for young forests was reduced while selection for non-forested habitats increased significantly. Avoidance of spruce forests declined during night but was still avoided. The selection of non-forested habitats during night-time when wild boar is known to be active suggests that those habitats are primarily used for foraging. The increased selection during night is probably a risk adverse behavioural response to avoid an increased risk to be killed or disturbed in those habitats during daylight. The inactive hours of the day are contrastingly spent in habitats providing ample shelter and reduced risk of predation and disturbance. Young forests are perfect for that purpose, both providing dense cover and little interference from human activities or large predators.

This study provides useful insights for management and future research on how wild boar utilize the landscape with special regard to the boreal and hemi-boreal forest ecosystem. Increased knowledge of how wild boar use the forest in a hemi-boreal setting fills a knowledge gap and might help to understand how wild boar might respond when expanding its distributional range further north. Finally, the results of this study may help to improve Swedish wildlife management strategies and understanding about how forest management impact and is impacted by wild boar.

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Populärvetenskaplig sammanfattning

Hur vildsvin utnyttjar och interagerar med, samt påverkar sin omgivning är av stor vikt för att förstå deras ekologi. I Sverige har vildsvinsstammarna ökat dramatiskt under de senaste decennierna och arten fortsätter att spridas norrut. Vildsvinet är en generalist både i sitt födoval och val av habitat och har en stor förmåga att anpassa sig till olika typer av levnadsmiljöer. Kunskapsläget kring hur vildsvinen utnyttjar våra nordliga barrträdsdominerade skogar är dålig och ett bättre kunskapsunderlag krävs för att kunna fatta faktabaserade beslut om hur djuren ska förvaltas. Det finns även en ökad oro för att vildsvinen skulle kunna orsaka skador för skogsbruket. Syftet med denna studie är därför att undersöka vildsvinens utnyttjande av de skogliga levnandsmiljöerna i norra Götaland och södra Svealand samt hur utnyttjandet påverkas av årstid samt tid på dygnet.

Vildsvinens utnyttjande av skogsmiljöerna studerades genom att följa 76 individer försedda med sändar-halsband i sex olika studieområden i Mellansverige mellan åren 2018 - 2022. Varje individs rörelse inom sitt hemområde och i de olika skogliga miljöer som fanns tillgängliga jämfördes med slumpmässiga rörelser för att kunna utvärdera vilken typ av skog som föredrogs eller undveks (habitatval). Studien tog också hänsyn till vilken grad olika andra miljö-faktorer så som lutning, småskaliga skillnader i topografi, lutningsrikting, trädhöjd och markfuktighet påverkar habitatvalet.

Vildsvinen föredrog att vistas i lövskogar under hela året. Generellt undveks olika typer av barrskog men vintertid så undveks barrskogarna mindre, sannolikt på grund av att födotillgången då sjunker i alla habitat. Kalhyggen och ej beskogade habitat utnyttjades i högre grad under sommaren. Sannolikt för att den vegetation som grönskar under vår och sommar erbjuder både mat och skydd åt vildsvinen. Resultaten visade att vildsvin under dagtid och alla årstider föredrog ungskogar som var ca 3 – 7m höga. Kalhygge och blandskog utnyttjades också mer under dagtid. Sannolikt kan den högre preferensen under dagtid av ungskog, kalhygge och blandskog förklaras av att det är områden som djuren gärna söker skydd i när dom oftast är inaktiva. Ej beskogade områden utnyttjades främst nattetid vilket indikerar att vildsvinen lämnar ungskogarna på natten för att söka föda ute på öppna ytor. Förmodligen undviks dessa områden dagtid då risken för att dö eller bli störd på grund av jakt eller andra mänskliga aktiviteter är för stor.

Sammanfattningsvis kan förändringen i vildsvinens habitatval mellan olika årstider förklaras av hur mycket mat och skydd det finns. Dagtid utnyttjas habitat som i huvudsak kan erbjuda skydd åt vildsvinen medan nattetid utnyttjas habitat som erbjuder gott om föda. Denna studies resultat fyller flera kunskapsluckor kring hur vildsvin utnyttjar våra nordiska skogar i södra Mellansverige under olika tider på året och bidrar till att förutse vilka miljöer de söker när de fortsätter sprida sig norrut. Slutligen kan resultaten av den här studien hjälpa till att förbättra den framtida viltförvaltningen och öka förståelsen för hur svenskt skogsbruk påverkar och påverkas av vildsvin.

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5. Appendix

5.1 Appendix 1: Collared wildboar in each study area

Area	ID	Sex	Observed period	Number of locations
Grimsö	15	M	16/2-2019 - 16/8-2019	4837
	16	F	16/3-2019 - 26/9-2020	13913
	14	F	25/4-2019 - 1/9-2019	5275
	17	M	10/5-2019 - 21/4-2020	9021
	18	F	5/7-2019 - 27/7-2020	9821
	19	F	5/7-2019 - 14/1-2021, (14/4-2021 - 8/6-2022)	13874
	135	F	21/11-2019 - 12/7-2020	5463
	171	F	7/2-2020 - 3/5-2020	13147
	125	F	8/3-2021 - 11/9-2021	4973
	148	F	9/3-2021 - 3/5-2022	10527
	126	F	15/6-2021 - 9/8-2022	10209
	198	M	1/7-2021 - 18/8-2021	1697
	159	F	9/7-2021 - 25/4-2022	3882
	240	F	5/8-2021 - 24/2-2022, (25/2-2022 - 31/12-2022)	11456
	110	F	5/4-2022 - 16/7-2022	2939
	242	F	21/6-2022 - 16/11-2022	4026
	153	F	30/3-2022 - 31/12-2022	7314
	1201	F	11/1-2022 - 31/12-2022	1248
	182	F	30/3-2022 - 31/12-2022	6032

Boo	1	F	22/8-2018 - 21/3-2019	5554
	3	M	23/8-2018 - 17/12-2018	3297
	2	F	23/8-2018 - 4/3-2020	13932
	6	F	19/9-2018 - 13/1-2020	12037
	105	F	24/8-2020 - 17/10-2021	10561
	175	F	24/8-2020 - 18/10-2021	10547
	174	M	27/8-2020 - 18/12-2020	3202
	143	F	28/8-2020 - 22/10-2021	10413
	141	F	9/9-2020 - 30/5-2021, (15/9-2021 - 8/11-2022)	17350
	197	F	24/8-2021 - 18/10-2022	8075
	161	F	25/8-2021 - 8/3-2022	4853
	111	F	15/9-2021 - 9/11-2022	10584
	112	F	24/8-2022 - 31/12-2022	3589
	1235	F	26/8-2022 -31/12-2022	3552
Bornsjön	140	M	22/4-2020 - 17/6-2021	10575
	106	F	2/7-2020 - 25/8-2021	10565
	195	F	26/10-2020 - 17/11-2021	9779
Boxholm	136	F	19/1-2019 - 26/11-2019	10541
	170	F	9/9-2019 - 12/9-2020	9253
	104	F	17/12-2019 - 2/8-2020	5955
	139	F	11/3-2020 - 2/6-2020	2480
	173	F	19/2-2020 - 28/5-2020	2798
	160	F	2/6-2020 - 23/5-2021	11057
	179	F	24/3-2021 - 26/4-2022	9986
	127	F	27/3-2021 - 18/4-2021	145
	196	F	23/3-2022 - 31/12-2022	8132
	180	M	11/5-2022 - 31/12-2022	7307
	152	F	11/5-2022 - 21/12-2022	5835
Hörningsholm	4	F	30/8-2018 - 13/1-2019	3749
	5	F	12/9-2018 - 25/3-2020	13925
	12	F	12/12-2018 - 5/1-2019	1080
	13	M	12/12-2018 - 24/6-2020	13880
	145	F	2/7-2021 - 16/8-2022	5513

Koberg	7	F	24/9-2018 - 1/4-2019	5036
	8	F	24/9-2018 - 6/4-2020	13911
	11	M	25/9-2018 - 15/11-2018	1718
	10	F	25/9-2018 - 20/10-2018	1191
	9	F	25/9-2018 - 30/1-2019	3545
	137	F	18/9-2019 - 11/11-2020	10576
	138	F	18/8-2019 - 31/3-2021, (28/9-2021 - 1/10-2022)	23217
	101	F	19/9-2019 - 12/11-2020	10532
	172	M	19/9-2019 - 5/10-2019	726
	102	F	22/9-2020 - 22/4-2022	12433
	146	F	23/9-2020 - 25/2-2021	4220
	186	F	24/9-2020 - 18/11-2021	10532
	107	F	25/9-2020 - 19/11-2021	10546
	177	F	27/9-2021 - 22/11-2022	10589
	149	F	27/9-2021 - 21/11-2022	10585
	419	F	27/9-2021 - 21/11-2022	10556
	109	F	28/9-2021 - 22/11-2022	10560
	178	M	28/9-2021 - 10/9-2022	7524
	150	F	19/9-2022 - 31/12-2022	2916
	1200	F	19/9-2022 - 13/10-2022	1058
	1234	F	20/9-2022 - 31/12-2022	2943
	1233	F	20/9-2022 - 31/12-2022	2962
	181	F	20/9-2022 - 31/12-2022	3171
	22	F	21/9-2022 - 31/12-2022	2767

5.2 Appendix 2: Multicollinearity test of the independent variables

	Tree height	**Ruggedness**	**Slope**
Tree height	1.0000000		
Ruggedness	0.2170912	1.0000000	
Slope	0.1953886	0.5070168	1.0000000

5.3 Appendix 3: Model selection

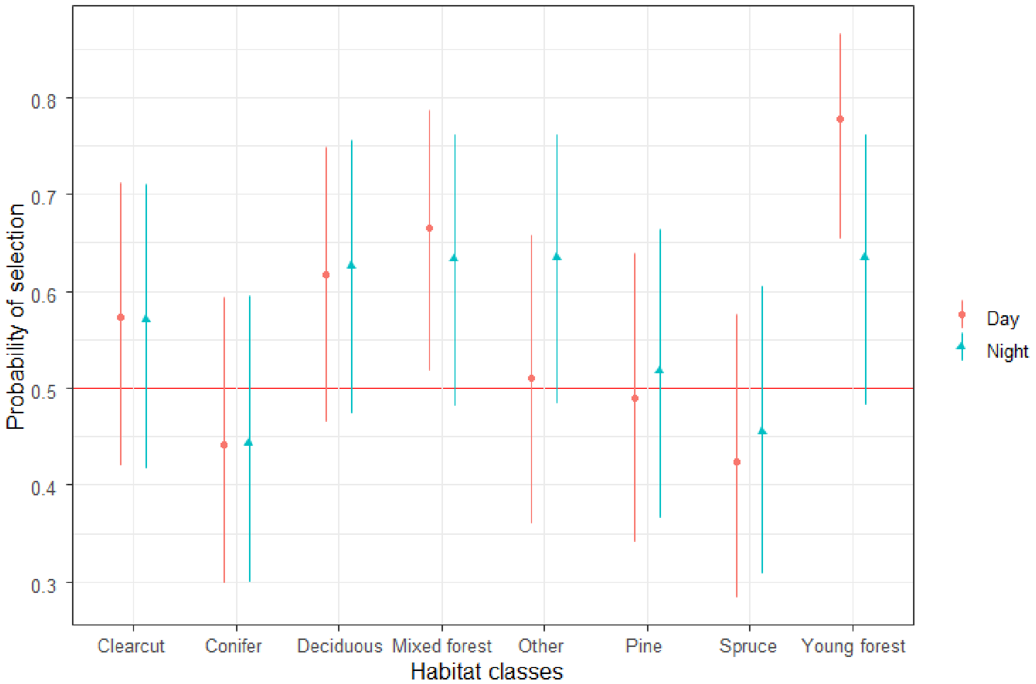
	Model	AIC	ΔAIC	Kappa	Sensitivity	Specificity	Accuracy
1	Habitat+(ID random factor)+ (area random factor)	1419316	59441	0.1496	0.6772	0.4724	0.5748
2	Habitat+season+(ID random factor) + (area random factor)	1419155	59280	0.1405	0.6782	0.4623	0.5703
3	Habitat+time+(ID random factor) + (area random factor)	1419004	59129	0.1512	0.6915	0.4597	0.5756
4	Habitat+season+time+(ID random factor) (area random factor)	1418933	59058	0.148	0.6770	0.4710	0.574
5	Habitat+season+time+habitat*time+(ID random factor) + (area random factor)	1403829	43954	0.1695	0.6324	0.5371	0.5847
6	Habitat+season+time+habitat*time+habitat*season+sex+ (ID random factor) + (area random factor)	1394210	34335	0.1838	0.6494	0.5344	0.5919
7	Habitat+season+time+habitat*time+habitat*season+(ID random factor)+ (area random factor)	1394208	34333	0.1838	0.6494	0.5344	0.5919
8	Habitat+season+time+habitat*time+habitat*season+soil moisture+(ID random factor)+ (area random factor)	1362835	2960	0.2233	0.6442	0.5792	0.6117
9	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+(ID random factor)+ (area random factor)	1362605	2730	0.2247	0.6391	0.5856	0.6124
10	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+ruggedness+(ID random factor)+ (area random factor)	1362594	2719	0.225	0.6394	0.5856	0.6125
11	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+slope+(ID random factor)+ (area random factor)	1361850	1975	0.2274	0.6375	0.5899	0.6137
12	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+ruggedness+slope+(ID random factor)+ (area random factor)	1361653	1778	0.2285	0.6367	0.5918	0.6142
13	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+ruggedness+aspect+(ID random factor)+ (area random factor)	1361096	1221	0.2238	0.6338	0.5900	0.6118
14	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+slope+aspect+(ID random factor)+ (area random factor)	1360432	557	0.2257	0.6320	0.5937	0.6128
15	Habitat+season+time+habitat*time+habitat*season+soil moisture+tree height+ruggedness+slope+aspect+(ID random factor)+ (area random factor)	1359875	0	0.2259	0.6303	0.5956	0.6129

5.4 Appendix 4: Full list of predicted selection values without environmental variables

*Table 5. Predicted selection values with standard errors for each habitat at a given season and time of day. Model=habitat*season + habitat*time + (ID random factor) + (area random factor).*

Habitat	Predicted value	SE	Season	Time
Clearcut	0.538	0.024	Spring	Day
Clearcut	0.487	0.025	Spring	Night
Clearcut	0.586	0.023	Summer	Day
Clearcut	0.536	0.024	Summer	Night
Clearcut	0.445	0.023	Winter	Day
Clearcut	0.395	0.023	Winter	Night
Conifer	0.405	0.025	Spring	Day
Conifer	0.402	0.025	Spring	Night
Conifer	0.297	0.025	Summer	Day
Conifer	0.295	0.025	Summer	Night
Conifer	0.447	0.023	Winter	Day
Conifer	0.445	0.022	Winter	Night
Deciduous	0.565	0.025	Spring	Day
Deciduous	0.564	0.025	Spring	Night
Deciduous	0.637	0.023	Summer	Day
Deciduous	0.636	0.024	Summer	Night
Deciduous	0.584	0.023	Winter	Day
Deciduous	0.583	0.022	Winter	Night
Mixed forest	0.619	0.026	Spring	Day
Mixed forest	0.579	0.026	Spring	Night
Mixed forest	0.495	0.025	Summer	Day
Mixed forest	0.453	0.026	Summer	Night
Mixed forest	0.562	0.024	Winter	Day
Mixed forest	0.521	0.023	Winter	Night
Other	0.339	0.021	Spring	Day
Other	0.498	0.021	Spring	Night
Other	0.428	0.020	Summer	Day
Other	0.591	0.020	Summer	Night
Other	0.394	0.020	Winter	Day
Other	0.557	0.020	Winter	Night
Pine	0.442	0.021	Spring	Day
Pine	0.461	0.021	Spring	Night
Pine	0.319	0.021	Summer	Day
Pine	0.335	0.021	Summer	Night
Pine	0.469	0.020	Winter	Day
Pine	0.488	0.020	Winter	Night
Spruce	0.369	0.024	Spring	Day
Spruce	0.433	0.024	Spring	Night
Spruce	0.311	0.024	Summer	Day
Spruce	0.370	0.024	Summer	Night
Spruce	0.380	0.022	Winter	Day
Spruce	0.444	0.021	Winter	Night
Young forest	0.751	0.022	Spring	Day
Young forest	0.543	0.023	Spring	Night
Young forest	0.760	0.021	Summer	Day
Young forest	0.556	0.022	Summer	Night
Young forest	0.695	0.021	Winter	Day
Young forest	0.474	0.021	Winter	Night

5.5 Appendix 5: Results on habitat selection including environmental variables during spring.

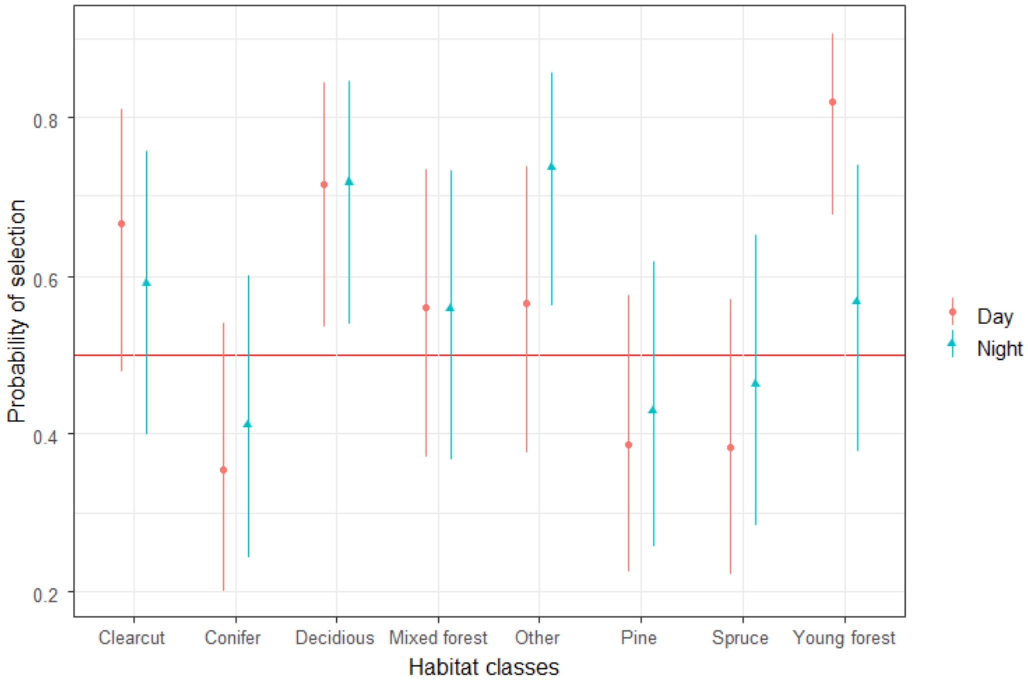


Wild boar selection of the different habitat classes during spring divided between daytime and night-time. A probability above 0,5 (red line) indicates a preference for the habitat while a probability below indicates avoidance.

*GLMM, binary logistic regression model for the influence of time and environmental variables on habitat selection during spring. Model=habitat+time+habitat*time+tree height+moisture+slope+ruggedness+aspect + (ID random factor) + (area random factor).*

Predictors	Estimate	SE	p-value
Clearcut (Intercept)	0.18	0,312	0,56
Conifer	-0.53	0.028	<0.001
Deciduous	0.18	0.028	<0.001
Mixed forest	0.39	0.028	<0.001
Other	-0.25	0.023	<0.001
Pine	-0.33	0.022	<0.001
Spruce	-0.59	0.026	<0.001
Young forest	0.96	0.023	<0.001
Time (Night)	-0.01	0.029	0.71
Tree height	0.008	0.0007	<0.001
Soil moisture (mesic-moist)	-0.16	0.01	<0.001
Soil moisture (moist-wet)	-1.04	0.02	<0.001
Soil moisture (open water)	-2.2	0.04	<0.001
Slope	0.01	0.002	<0,001
Ruggedness	-0.06	0.009	<0.001
Aspect (east)	0.19	0,012	<0.001
Aspect (south)	0.29	0.013	<0.001
Aspect (west)	0.25	0.012	<0.001
Conifer × Night	0.018	0.044	0.65
Deciduous × Night	0.05	0.042	0.26
Mixed forest × Night	-0.13	0.044	0.002
Other × Night	0.52	0.035	<0.001
Pine × Night	0.12	0.033	<0.001
Spruce × Night	0.13	0.04	0.001
Young forest × Night	-0.69	0.04	<0.001

5.6 Appendix 6: Results on habitat selection including environmental variables during summer.

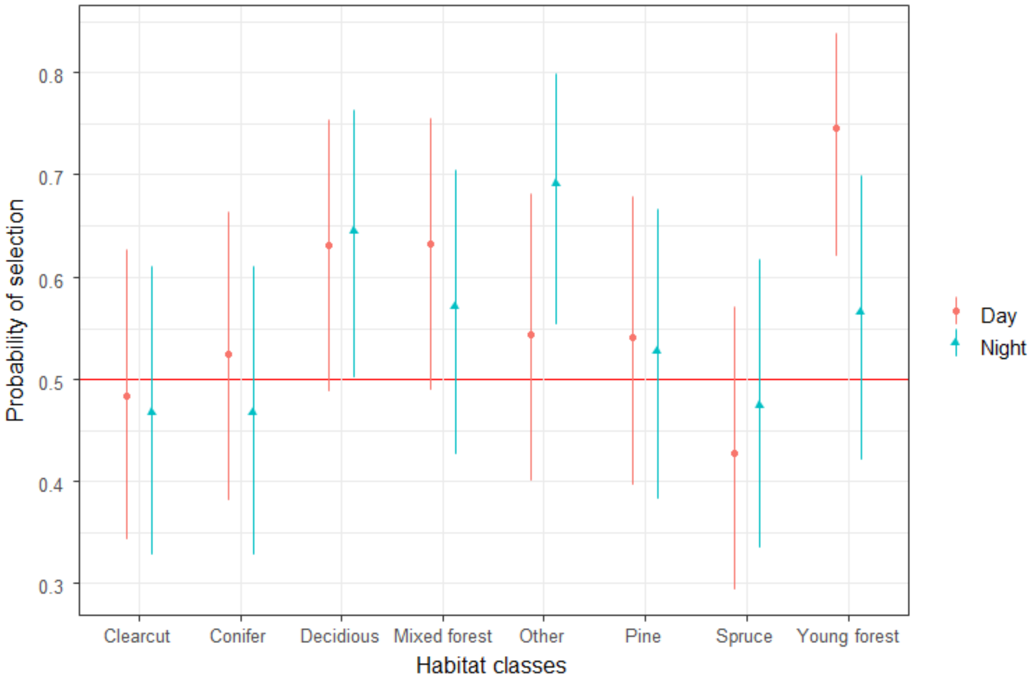


Wild boar selection of the different habitat classes during summer divided between daytime and night-time. A probability above 0,5 (red line) indicates a preference for the habitat while a probability below indicates avoidance.

*GLMM, binary logistic regression model for the influence of time and environmental variables on habitat selection during summer. Model=habitat+time+habitat*time+tree height+moisture+slope+ruggedness+aspect + (ID random factor) + (area random factor).*

Predictors	Estimate	SE	p-value
Clearcut (Intercept)	0.76	0.39	0.05
Conifer	-1.29	0.024	<0.001
Deciduous	0.23	0.022	<0.001
Mixed forest	-0.44	0.02	<0.001
Other	-0.42	0.019	<0.001
Pine	-1.14	0.019	<0.001
Spruce	-1.16	0.023	<0.001
Young forest	0.82	0.018	<0.001
Time (Night)	-0.32	0.027	<0.001
Tree height	-0.004	0.0006	<0.001
Soil moisture (mesic-moist)	0.22	0.009	<0.001
Soil moisture (moist-wet)	-0.49	0,021	<0.001
Soil moisture (open water)	-2.67	0.036	<0.001
Slope	0.03	0.002	<0.001
Ruggedness	-0.24	0.009	<0.001
Aspect (east)	0.09	0.011	<0.001
Aspect (south)	0.1	0.011	<0.001
Aspect (west)	0.13	0.011	<0.001
Conifer × Night	0.56	0.041	<0.001
Deciduous × Night	0.33	0.037	<0.001
Mixed forest × Night	0.31	0.041	<0.001
Other × Night	1.08	0.031	<0.001
Pine × Night	0.49	0.033	<0.001
Spruce × Night	0.65	0.038	<0.001
Young forest × Night	-0.91	0.034	<0.001

5.7 Appendix 7: Results on habitat selection including environmental variables during winter.



Wild boar selection of the different habitat classes during winter divided between daytime and night-time. A probability above 0,5 (red line) indicates a preference for the habitat while a probability below indicates avoidance.

*GLMM, binary logistic regression model for the influence of time and environmental variables on habitat selection during winter. Model=habitat+time+habitat*time+tree height+moisture+slope+ruggedness+aspect + (ID random factor) + (area random factor).*

Predictors	**Estimate**	**SE**	**p-value**
Clearcut (Intercept)	-0.29	0.29	0.325
Conifer	0.16	0.025	<0.001
Deciduous	0.60	0.027	<0.001
Mixed forest	0.6	0.028	<0.001
Other	0.24	0.023	<0.001
Pine	0.23	0.022	<0.001
Spruce	-0.23	0.024	<0.001
Young forest	1.13	0.023	<0.001
Time (Night)	-0.07	0.023	0.003
Tree height	0,009	0.005	<0.001
Soil moisture (mesic-moist)	-0.04	0.008	<0.001
Soil moisture (moist-wet)	-0.73	0.019	<0.001
Soil moisture (open water)	-2.11	0.026	<0.001
Slope	0.04	0.001	<0.001
Ruggedness	0.014	0.006	0.017
Aspect (east)	0.11	0.008	<0.001
Aspect (south)	0.17	0.009	<0.001
Aspect (west)	0.09	0.008	<0.001
Conifer × Night	-0.16	0.033	<0.001
Deciduous × Night	0.12	0.033	0.001
Mixed forest × Night	-0.19	0.034	<0.001
Other × Night	0.69	0.027	<0.001
Pine × Night	0.013	0.02	0.62
Spruce × Night	0.26	0.03	<0.001
Young forest × Night	-0.74	0.029	<0.001

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