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Wild Boar, *Sus scrofa*, habitat use in the Danish fenced nature area Tofte Skov

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Abstract

Background Wild boars (*Sus scrofa*) are potential contributors to increasing biodiversity and are considered keystone ecosystem engineers. However, concerns exist regarding their invasive nature and potential damage to native biodiversity. Understanding the behavior and habitat use of wild boars is crucial for effective management and their potential role in nature restoration.

Methods The study was conducted in the fenced nature area Tofte Skov in North-Eastern Jutland, Denmark. GPS-collar data from 25 wild boars were collected over a two-year period. Land use maps were used to analyze habitat selection, and a nested temporally blocked bootstrap analysis was employed to estimate habitat selection coefficients. Behavior traits, including turning angle and mean velocity between fixes, were also examined.

Results We found significant differences in habitat use by wild boars in Tofte Skov. Forests had the highest habitat use frequency, followed by other natural habitats such as wet nature and dry nature. Artificial areas, streams, non-paved roads, and lakes had the lowest use frequency. Habitat selection coefficients revealed that forests, wet forests, streams, non-paved roads, artificial areas, and extensive agriculture were preferred habitats. Wet nature (raised bog) had a significantly lower habitat selection coefficient. The movement behavior of wild boars varied during the day, with faster and more straight movements during the day and slower and more turning movements during the night.

Conclusions We conclude that wild boars in Tofte Skov prefer closed deciduous forests as their main habitat and forage at night while traveling between habitats during the day. They can adapt to open habitats if these areas provide high-quality food. Wild boars could be included in fenced national parks, and improving food availability in forests may reduce their reliance on agricultural fields. Future research should explore wild boar behaviour when there is no supplementary feeding and if there are predators, like wolves, present.

Keywords Wild Boar, Habitat Selection, Movement Behaviour, GPS, Ecology

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Background

In 2020, as part of the European Green Deal aimed at combatting the global loss of biodiversity, the European Commission adopted a new strategy for the restoration and conservation of biodiversity. One of the key goals of this strategy is to achieve 30% protected nature areas on land and sea by 2030[1]. However, in Denmark, the Danish Biodiversity Council estimates that the current extent of protected areas on land is below 2.3%[2]. Therefore, there is an urgent need to establish more protected nature areas in Denmark.

Large mammals, such as wild boars (*Sus scrofa*), can play a significant role in increasing biodiversity within the future Nature-Nationalparks. They have been shown to positively impact ecological processes[2]. However, the presence of wild boars in European nature has been a subject of extensive discussion. Farmers are concerned about substantial economic losses due to crop damage and the transmission of diseases, especially African Swine Fever (ASF), to domesticated pigs. Furthermore, the invasive capabilities of wild boars raise concerns among some conservation-/restoration-ists and managers, as they can cause significant damage to native biodiversity and potentially drive certain species to extinction[3, 4]. Although concerns about the invasive nature of wild boar are valid by themselves, wild boars should be considered native in Denmark under any conceivable definition of "native" considering that they have a deep evolutionary history in Europe, which was only ended locally in Denmark in 1801 by intensive hunting[5, 6]. Today wild boar are common in most of their natural range including Europe, Asia, and Northern Africa and have been introduced to novel ecosystems in Australia, New Zealand, North and South America[7].

Simultaneously, wild boars is broadly considered as a keystone ecosystem engineers by ecologists. They provide essential disturbances to habitats that have lost their natural disturbance regimes, which were previously provided by extinct megafauna[2, 8]. The unique rooting behaviour of wild boars has been associated with increased biodiversity[9, 10, 11], enhanced habitat heterogeneity[12, 13], and act as vectors for seed and fungi dispersal.[14, 15] Therefore, the impact of wild boars on natural ecosystems is complex and requires a deeper understanding. Gaining insights into the behaviour and habitat use of wild boars is crucial for comprehending the circumstances in which they can be utilized as a tool for nature restoration, as well as recognizing situations in which they may cause habitat damage. Studies of the historical-natural habitat use of wild boars in Europe have found that wild boar mostly inhabit old deciduous forests containing some wet areas and open meadows[16]. However, in the modern European landscape, wild boars have benefited immensely from the expansion of agriculture and have adapted to exist in human dominated areas close to human settlement[17, 18, 19].

One reason for concern arises from wild boars' ability to adapt to a wide range of habitats in which it is introduced. Consequently, they have established populations in almost all habitats they have been introduced to[20]. Furthermore, wild boars exhibit opportunistic omnivorous feeding habits and can adapt their feeding methods to grazing, browsing, foraging, rooting, and even predation[20, 21]. Their rooting behaviour is especially important for creating habitat heterogeneity by removing monocultures of dominating plants and creating disturbed sites in the soil opening up areas for disturbance adapted species[22, 23, 24, 25]. Even though wild boars are able to access many different sources of food, wild boars will, to the farmers' dismay, feed almost exclusively on crops if possible. A review study on the wild boars diet[20] revealed that crops can make up 90% of their stomach contents, which contributes to the large conflict between farmers and wild boars. Additionally, authorities and farmers fear the transmission of African swine fever (ASF) from wild boars to domestic pigs[26], which would have detrimental consequences for the export of pork. Controlling the spread of ASF is strictly regulated for most countries in Europe with wild boar populations and is on the political agenda on an EU-level[27]. Some extreme measures implemented by countries like Denmark is to completely exterminate all wild boars in the country, to prevent transmission of ASF[28]. To conclude, the role of the wild boar in European nature is widely conflicted by, on one hand, being an effective tool for nature restoration in unnaturally undisturbed European ecosystems and on the other hand being an expensive pest for agricultural interests. To utilize these wild boars in nature restoration while reducing conflicts with human interests, some countries like Denmark, have opted to include wild boar populations in enclosed nature areas. This makes it possible to investigate the behaviour of wild boar in semi-natural conditions. Deepening our understanding of wild boar behaviour and habitat use is detrimental to ensure optimal management of wild boar, if they are to be used as a tool for nature restoration in the future.

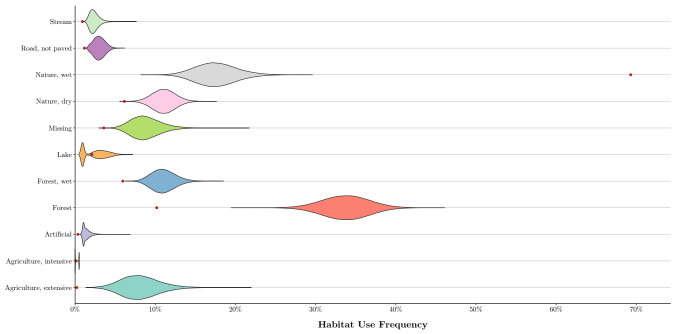

Fig. 1 Bootstrap distributions of *S. scrofa* habitat use frequencies in Tofte Skov.

This study aims to further the understanding of how wild boar utilizes different habitats, and discuss how this could be used to improve management practices. We investigate wild boar habitat-use by utilizing GPS-collar data, along with land use maps, to describe the differences in behaviour and usage of different habitats in the fenced nature area Tofte Skov in North-Eastern Jutland. Because wild boars naturally prefer forests and semi-open areas[16, 29], we hypothesize that the wild boars core area will be closed deciduous forest. We predict that there will be higher habitat-use frequency and higher selection coefficients for forest habitats compared to the other habitat types. Furthermore, we hypothesize that in open areas, where the wild boars are more exposed, wild boars will perform shorter and faster excursions compared to times of lower exposure. We predict that the step length in open areas compared to closed areas will be longer, and that the turning index will be closer to zero. Furthermore, we predict, that wild boars will have longer step lengths and higher turn indexes during the day, as they are more exposed.

Methods & Materials

Software

All data analysis was done in the `R` programming language[30]. General data wrangling was done using the `tidyverse` packages[31], using the `sf` package[32] for simple spatial features and the `stars` package[33] for spatial arrays. Figures were produced using the `ggplot2` package[34] and `metR` package[35] for contour plots.

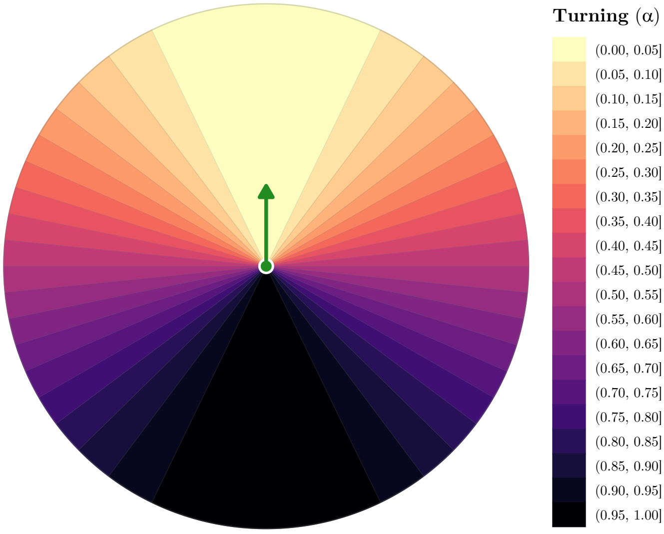

Fig. 2 Visualization of the values of the turning behaviour trait α given a preceding line-segment following the direction of the green arrow, and a following line-segment in the direction of the circle periphery joined at the center of the circle (green dot). Grey lines are equally spaced (0.05) α-contours.

Study area

Tofte Skov is a 27km^2 fenced area in the southern part of Lille Vildmose in eastern Himmerland, Denmark. It was fenced in 1907 as part of the preservation of the area. Tofte Skov lies within the Natura 2000 area number 17, which includes the entire Lille Vildmose and Høstemark Skov. The area consists of numerous plains separated by different kinds of deciduous forests including beech, oak, birch and alder. Common spruce and sitka spruce have previously been planted and widespread in the area, but as part of the preservation of the area these species are now being removed in favour of the native deciduous species. Tofte Skov is also characterized by having large areas of raised bog and different populations of wildlife including 150 wild boars, wisents and red deer[36, 37].

Collection of data

During a two-year study conducted from February 2019 to January 2021, a total of 25 wild boars were collared. The collaring process was divided into three rounds: the first round occurred in February and March 2019, the second round took place in November 2019, and the final round was conducted in November 2020. To facilitate the collaring process, the wild boars, which were accustomed to supplementary feeding, were enticed by driving vehicles and distributing feed.

The collaring procedure involved anesthetizing the wild boars using a CO2 rifle. The anesthesia induction was accomplished by darting, and the animals remained under anesthesia for a few minutes, during which they were collared and ear tagged to facilitate individual identification. Proper ventilation of the anesthetized animals was ensured during the process. During the initial collaring rounds, the population of wild boars exceeded expectations, resulting in significant weight losses due to insufficient food supply. Consequently, several collars did not fit properly and were not adequately secured, leading to their subsequent detachment. Additionally, interactions between the boars also caused some collars to fall off. As a response to the suboptimal feeding conditions, a significant portion of the boar population was euthanized and excluded from the study in early 2020. Following this intervention, the remaining population experienced weight gain, resulting in better collar retention. Towards the end of the study, the last five collars were manually removed ahead of schedule due to concerns that they might be too tight. It should be noted that the wild boars received supplementary feed in late 2019, but not in the subsequent year.

Information regarding the data collection was obtained from Lars Haugaard (personal communication).

Procedure Statistical procedure for nested temporally blocked bootstrapping.

Data: Dataset of GPS-fixes annotated with habitat, time of recording and individual ID
Result: Nested temporally blocked bootstrap results with mean, quantiles, and p-values.

foreach *Individual-nested temporal block* **do**
  Pre-calculate habitat frequencies;
for $i \in \{1 \ldots 100\ 000\}$ **do**
  Bootstrap individuals ($n = 25$);
  foreach *individual* **do**
    Bootstrap temporal blocks;
  foreach $i \in$ *habitat* **do**
    $\mathrm{HUF_i}$ = Average use frequency;
    $\mathrm{HSC_i} = \frac{\mathrm{HUF_i}}{\mathrm{E(HUF_i)}}$;
  foreach $\{i, j\} \in$ *habitats* **do**
    $\Delta_{i,j} = \frac{\mathrm{HSC}_i}{\mathrm{HSC}_j}$;
  `// Pairwise differences in HSC`
Summarize mean, median, lower and upper quantiles and empirical p-values;
Adjust p-values for multiple hypothesis testing;

Habitat types

To analyze habitat use, we used the land use classification `Basemap04` produced by The institute for Environmental science in Aarhus University[38]. `Basemap04` is a combination of remote sensing land cover classification maps and land cover census data. The map defines 34 land use / land cover categories. As many of the categories were redundant for our analysis, we joined all building categories, unused agriculture categories and other artificial land use as a single category called "Artificial". We kept the non-nature categories: "Road, not paved", "Agriculture, extensive" and "Agriculture, intensive". We included all the nature categories to differentiate land use across different nature types.

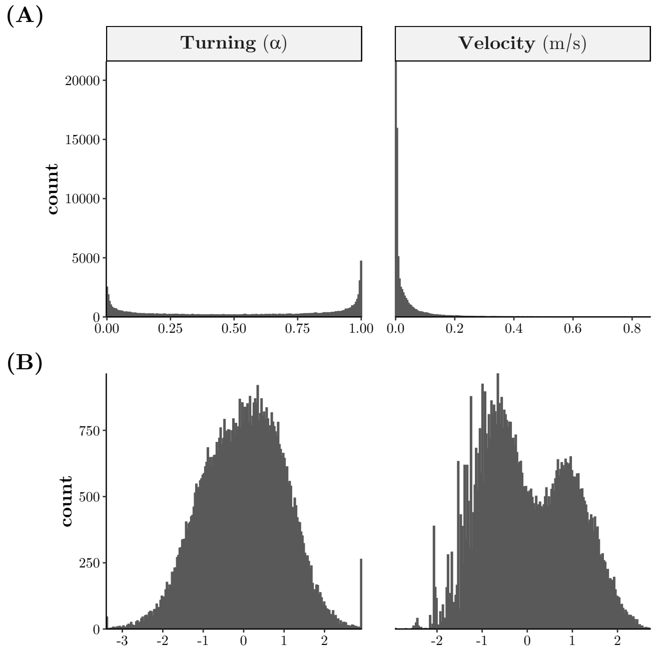

Fig. 3 Histograms of the behaviour traits (turning and velocity) on the raw data scale (first row, (A)) and transformed (second row, (B)). Velocity is simply log-transformed and scaled, while turning degree is transformed using a quantile-transformation between a fitted beta-distribution and a scaled normal distribution.

Habitat Selection

The **H**abitat **S**election **C**oefficient (abbreviated as HSC throughout this report), is an index which calculates the proportion between observed and expected habitat use frequency:

$$\mathrm{HSC_H} = \frac{\mathrm{O(F_H)}}{\mathrm{E(F_H)}}, \quad \mathrm{F_H} = \frac{n_\mathrm{H}}{\sum n_\mathrm{i}}$$

Then we compare the HSC between habitats by division not subtraction:

$$\delta_\mathrm{HSC}(i,j) = \frac{\mathrm{HSC_i}}{\mathrm{HSC_j}} = \frac{\mathrm{O(F_i)}}{\mathrm{O(F_j)}} \cdot \frac{\mathrm{E(F_i)}}{\mathrm{E(F_j)}}$$

In order to conduct a statistically sound analysis of habitat selection, we chose a nested temporally blocked bootstrap analysis in which the habitat selection coefficient is calculated in one week blocks stratified by individual. To estimate the habitat selection coefficients and the pairwise differences in habitat selection coefficients, δ_HSC, we estimated the empirical distribution of habitat selection by bootstrapping the stratified blocks 100 000 times. This procedure is meant to provide an unbiased estimate for habitat selection coefficients and pairwise factor differences, while taking into account temporal autocorrelation and individual effects. By temporally blocking in one week intervals, we eliminate most of the temporal autocorrelation as we expect GPS-fixes to be almost independent after one week. The nested bootstrapping then provides an assumption-free way of estimating the empirical distribution of habitat selection coefficients, and allows for differences in variance and non-unimodal over time, between habitats and individuals.

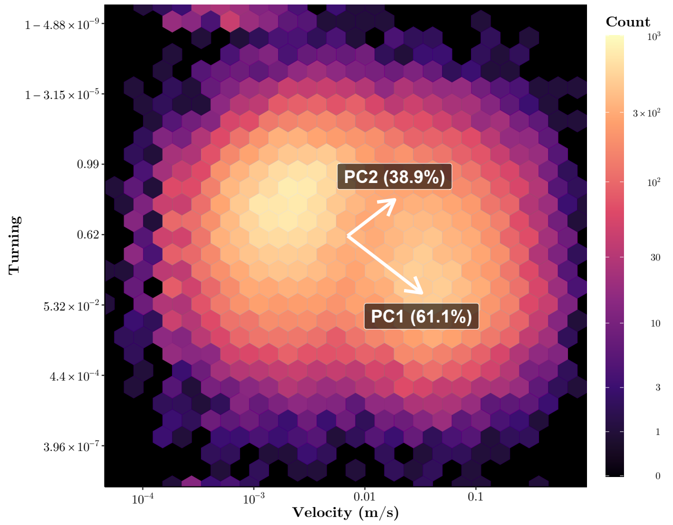

Fig. 4 Biplot of PCA analysis of behaviour traits overlayed on top of a heatmap of the observed trait values on the appropriate transformed scales (explaining the awkward axis breaks on the turning-axis in particular). The percentages next to the principal component labels are the percentage of variance explained by each principal component.

Behaviour traits

We wanted to investigate whether we could detect any differences in behaviour between the different habitats. To do so we chose to investigate to parameters of behaviour which are quantifiable, at least to some degree, from our GPS-data; (1) turning angle and (2) mean velocity between fixes, both under the simplifying assumption that individuals are walking in straight lines between the fixes. The latter assumption is almost with complete certainty wrong, however it is not obvious that it would be biased in either of the quantifiable behaviour traits across any kinds of stratifications in our dataset. We have therefore limited our analysis to one of relative differences between different types of habitats and times of day. The turning behaviour trait will be quantified using $\alpha = 1 - \frac{\cos(\theta)+1}{2}$ such that 0 corresponds to straight movement while 1 corresponds to turning around, while velocity is simply calculated by dividing the distance between two consecutive points in space by their distance in time[1]. The cosine is used for quantifying turning, since it the cosine is equivalent to the lateral component of the direction vector, i.e. if the cosine is 0.4 then if the animal moves 1km then it moves 400 meters either left or right of where it would have been, if it had continued straight for the same amount of time with the same velocity.

Given that turning, α, is an attribute of an angle or the mid-point of three consecutive points, while velocity is an attribute of a line-segment or two consecutive points, for this analysis velocity refers to the velocity leading up to a GPS-

[1]we use SI-units for velocity; m/s.

fix and turning is based on the angle created by the prior and next point. In order to incorporate both of these behavioural characteristics into a single index of behaviour suitable for our analysis, we then conducted a PCA on the data matrix consisting of all points for which turning and velocity could be quantified. However for this to statistically sound, the behaviour traits must first be examined and if necessary transformed to approximately follow a scaled normal distribution as PCA assumes that the the data follows a multivariate normal distribution[2][39]. As can be clearly seen in the first row **(A)** of Figure 3 the behaviour traits are *not* normally distributed or scaled. However the velocity trait is easily transformed to an approximate scaled normal distribution by a log-transform followed by scaling by mean and standard deviation (see second row **(B)** of Figure 3). The turning trait is somewhat more complicated as it follows a bounded and bi-modal distribution ($\alpha \in [0, 1]$), however we have chosen to solve this problem by fitting a beta distribution on the calculated turning trait, α, values with the following parameters $a \approx 0.403$ and $b \approx 0.322$ using the `fitdistrplus` package.[40] By fitting a suitable distribution to the data, it is possible to do an invertible "quantile-normailzation"[41, 42]:

$$f^*(\alpha) = \phi_{\mathcal{N}}(\phi^{-1}_{\text{Beta}}(\alpha))$$

This procedure produces an extremely appropriate transformation of α as can be seen in the second row **(B)** of Figure 3. After these preprocessing steps it was possible to conduct an appropriate PCA analysis (Figure 4) with the first principal component, **PC1**, explaining $\sim$ 61.1% of the variance going from (positive) fast and straight to (negative) slow and turning behaviour. We have chosen to refer to this principal component as *Spurtiness*.

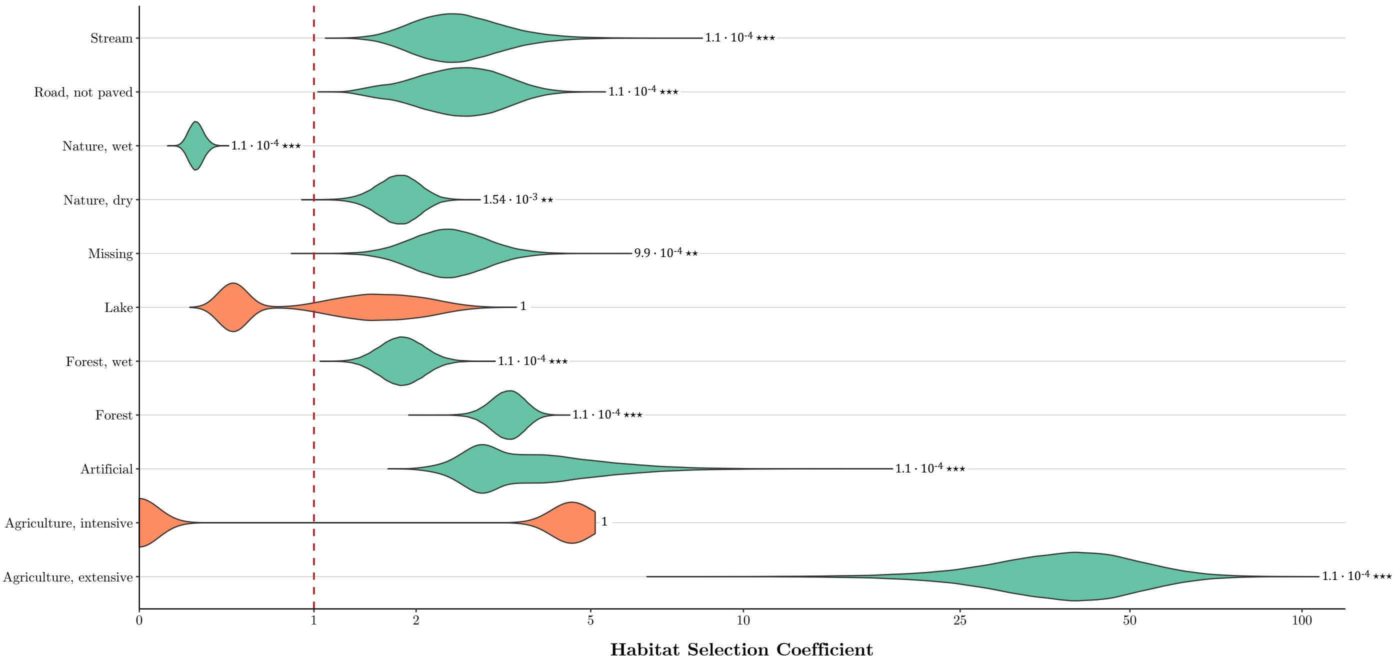

Fig. 5 Bootstrap distributions of *S. scrofa* habitat use anomalies in Tofte Skov. Anomalies are calculated as the difference between the observed habitat use frequency (see Figure 1) and the habitat frequencies in Tofte Skov.

Results

Habitat Selection

We found significant differences in habitat use by wild boars in Tofte Skov. The largest habitat use frequency of around 35% were, as expected, for "Forest". This is followed by other natural habitats such as wet nature, dry nature and wet forests. The areas of lowest use frequency are: artificial areas, streams, non-paved roads and lakes (Figure 1) .

We found a significantly higher than expected habitat selection coefficient (HSC) for the habitats "Stream", "Road, not paved", "Nature, dry", "Missing", "Forest" and "Forest, wet", "Artificial" and "Agriculture, extensive" (former landing-strip, with feeding station and animal-release point), while "Nature, wet" (mostly raised bog) was the only habitat type with a significantly lower than expected HSC (Figure 5). Furthermore, we found that after Bonferroni correction for multiple testing "Agriculture, extensive" had a significantly higher HSC than all other habitat types, while "Forest" had a significantly higher HSC than all other natural habitats, both open and closed, and unsurprisingly "Nature, wet" also had a significantly lower HSC than all other habitats. The only other habitat with a significantly different HSC from any other than the before mentioned is "Artifical" which had a very marginal higher HSC than "Nature, dry" (Table 1).

Habitat Behaviour

We then proceeded with an equivalent analysis of movement behaviour as we did with habitat selection (nested temporally

[2]For simplicity I only focus on the marginal distributions.

Table 1 Bootstrap estimates ($n = 100\,000$) of pairwise factor differences in habitat selection coefficients (HSC), only significant comparisons ($P \leq 0.05$) are included in the table. *P-values are Bonferroni adjusted ($n = 55$) and only one digit is displayed in the table. The full unrounded table can be found in the supplementary materials.

Habitat	Compared habitat	μ_Δ	$Q_{50\%}(\Delta)$	$Q_{5\%}(\Delta)$	$Q_{95\%}(\Delta)$	*P-value
Agriculture, extensive						
	Agriculture, intensive	∞	∞	5.2	∞	5.5×10^{-4} ⋆⋆
	Artificial	11.3	10.7	4.7	19.8	5.5×10^{-4} ⋆⋆
	Forest	12.2	11.8	6.1	19.7	5.5×10^{-4} ⋆⋆
	Forest, wet	22.0	21.1	11.0	36.0	5.5×10^{-4} ⋆⋆
	Lake	49.0	32.0	13.8	126.3	5.5×10^{-4} ⋆⋆
	Missing	16.9	15.9	8.0	29.3	5.5×10^{-4} ⋆⋆
	Nature, dry	22.5	21.7	11.4	36.6	5.5×10^{-4} ⋆⋆
	Nature, wet	159.5	151.6	85.2	260.7	5.5×10^{-4} ⋆⋆
	Road, not paved	16.4	15.1	7.2	30.2	5.5×10^{-4} ⋆⋆
	Stream	16.1	15.1	7.3	28.5	5.5×10^{-4} ⋆⋆
Artificial						
	Nature, dry	2.2	1.9	1.3	3.9	0.04 ⋆
	Nature, wet	15.6	14.0	8.8	27.6	5.5×10^{-4} ⋆⋆
Forest						
	Forest, wet	1.8	1.8	1.4	2.3	8.2×10^{-3} ⋆
	Nature, dry	1.9	1.8	1.5	2.4	2.7×10^{-3} ⋆⋆
	Nature, wet	13.4	13.1	9.3	18.5	5.5×10^{-4} ⋆⋆
Forest, wet						
	Nature, wet	7.5	7.3	5.0	10.8	5.5×10^{-4} ⋆⋆
Lake						
	Nature, wet	4.6	4.9	1.7	8.3	3.3×10^{-3} ⋆⋆
Missing						
	Nature, wet	10.0	9.6	6.1	15.2	5.5×10^{-4} ⋆⋆
Nature, dry						
	Nature, wet	7.3	7.2	4.9	9.9	5.5×10^{-4} ⋆⋆
Road, not paved						
	Nature, wet	9.6	10.2	5.8	16.7	5.5×10^{-4} ⋆⋆
Stream						
	Nature, wet	9.7	10.1	6.2	16.7	5.5×10^{-4} ⋆⋆

blocked bootstrapping) stratified across four intervals of time of day ([00–06), [06–12), [12–18) and [18–24) and two habitat types "Open" and "Closed", where we chose to classify "Forest" and "Forest, wet" as "Closed" while the remaining habitats were classified as "Open". We found no significant differences between open and closed habitats at any time of day (Table 2). However, the movement behaviour of the wild boars differed during the day with faster and more straight movements at daytime, especially between 12–18, and slower and more turning movements at night between 00–06.

Time of Day	μ_{PC1}	μ_Δ	$Q_{50\%}$	$Q_{5\%}$	$Q_{95\%}$	P
[00-06)	−0.42	−0.02	−0.11	−0.85	1.04	0.322
[06-12)	0.25	−0.08	−0.09	−1.43	1.20	0.429
[12-18)	0.59	−0.10	−0.08	−1.20	1.00	0.383
[18-24)	0.07	0.05	0.05	−0.95	1.11	0.407

Table 2 Bootstrap results ($n = 100\,000$)) of differences in spurtiness behaviour between open and closed habitats across different times of day. All values except μ_{PC1} are differences calculated $\Delta = \text{Spurtiness}_{\text{Open}} - \text{Spurtiness}_{\text{Closed}}$, such that positive values indicate more spurty (fast and straight) behaviour in open habitats. P-values are not corrected for multiple testing. μ_{PC1} is simply the mean of PC1 across both "Open" and "Closed" habitats in the given time of day interval.

Conclusion

Habitat selection

As hypothesized, our findings revealed that the wild boars showed a clear preference for the areas with closed deciduous forests. Both when comparing frequencies and when taking the size of the different habitats into account, by investigating habitat selection coefficients. The forest habitats in Tofte Skov create preferable conditions for the wild boars of the area, as they provide some of the key conditions and food sources for ideal wild boar habitats as outlined in a scientific review of the European wild boar population[16]. Amongst these conditions, forests provide: heavy brush for predator protection, roots, fruits, nuts, bark, shoots, leaves and other food items.

The aversion of wet nature likely arises, as this habitat exclusively consists of nutrient poor marshlands with low quality food availability, high exposure and possibly difficult movement conditions caused by the deep sphagnum layer. Furthermore, investigating Figure A.1 in Appendix A it is evident that the wild boars primarily use the wet nature habitat between the forest and the lake, and the wet nature closest to the forest edge. This indicates that wild boars only use the wet nature habitat, when they are traveling to and from the lake, likely to drink water, and will otherwise avoid walking in this habitat.

Furthermore, the extensive agriculture habitat had a significantly larger selection coefficient than the other habitats regardless of being an open area. This can be explained by this area being the place in which they are fed. Furthermore, the holding pen in which the wild boars are released from and caught for check-ups is close to the extensive agriculture (personal observations and communication with Thomas Holst Christensen). These interactions are generally positive for the wild boar, as they include feeding. An explanation for the preference for this area could therefore be that the wild boars associate this area with an abundant source of high quality food, and are thus not encouraged to search for food in other habitats. This is comparable to how European wild boar populations have adapted to prefer forest habitats close to agricultural fields containing high value food, that makes the benefit of the area higher than the potential cost[16, 20]. This is not surprising, as wild boars have a high degree of behavioural plasticity[19]. Furthermore, the predation pressure in Tofte Skov is very low. At the time of the data collection there were no top predators in the area. So the only predatory risk the population is exposed to is hunting from humans. The supplementary feeding changes the natural behaviour of how the wild boars use the different habitats, making it harder to broaden the results of this study to wild boars in non-managed unfenced nature areas. Future studies should include areas with no supplementary feeding to evaluate how the wild boars root in natural settings compared to areas with supplementary feeding, such as Tofte Skov.

Behavioural differences between habitats

Our results showed that there were no significant differences in movement behaviour between open and closed habitats (Table 2). Hence the wild boars do not move short and fast in open areas, as hypothesized. They do not seem to be "scared" of the open areas as predicted. As mentioned above this is likely because they have learned to associate some of the open areas with feeding. Furthermore, the hunting pressure in Tofte Skov at the time were almost non-existing. Today there is a wolf inside the fenced area, that could potentially predate on wild boar, though since first registration of the wolf in 2021 the employees have not registered any killings of wild boar (personal communication with Thomas Holst Christensen). Future studies of GPS collar data from Tofte Skov, could include comparison of the wild boars habitat use before and after the wolf entered the area. Even though it does not seem like the wolf preys on the wild boars, it could still have an effect on how the wild boars move around and use the different habitats. Across all habitats the movement behaviour follows a clear tendency with the boars having a higher amount of spurtiness during the day and less during the night (Table 2). Spurtiness is characterised by being fast and straight movements with a low amount of turning, which would indicate that the boars use the daytime to move around between different areas or habitats. Conversely, the movements during the night are characterised by being slower and with more turning, which could indicate rooting or other kind of foraging behaviour. This is consistent with the boars being nocturnal animals that forage during the night[43].

Management implications

As discussed, the preference of wild boars to use feeding stations in the extensive agriculture area (the former landing strip) can be compared to the well documented preference of wild boars, to forage on agricultural fields[20]. Wild boars are likely to have the same preference in Denmark, considering the large availability of crops. Introducing wild boars into Danish nature would therefore likely increase human-wildlife conflict with farmers, as they could damage crops, and increase fear of transmission of African Swine Fever. It is important to highlight that infection of AFS from wild boars to domestic pigs is most likely in areas with many free range pigs such as Caucasus and Russia. Furthermore, whilst wild boars can infect domestic pigs, AFS does not persist in populations of wild boars, without continuous infection from other sources, such as areas with infected domesticated pigs[44]. It is possible that proper fencing to avoid contact between wild boars and domesticated pigs, would diminish infection risk. However, whilst the risk of AFS spread from wild boars to domestic pigs, is contested, it is still, in the current political landscape, unlikely that wild boars will be a tool for nature management in unfenced nature areas. However, the issues relating to wild boar contact with domestic pig production would be avoided, if wild boars were kept in large fenced nature areas such as the proposed nature national parks in Denmark. This would allow the wild boars to act as ecosystem engineers[8], creating much needed disturbances[2] whilst minimizing human-wildlife conflict.

Concluding remarks & perspective

Our results provide valuable insights for the management of wild boar populations. This study provides empirical evidence supporting the hypothesis that wild boars prefer closed deciduous forests as their core habitat. We did not find any significant differences in movement behaviour across different habitat types. We did however find that wild boars move further and more straight during the day compared to during the night. This suggests that they forage during the night and walk between habitats during the day. Furthermore, our results show that the wild boars in Tofte Skov can adapt a significant preference for open habitats, if they are associated with positive effects such as the provision of high quality food. This also indicates that if wild boars were to be set free in Danish nature, they would forage on fields. To avoid escalating the human-wildlife conflict, wild boars could be included in fenced nature national parks where they could forage naturally and create needed disturbances in the landscape. Furthermore, one could try to improve the natural food availability in areas with closed deciduous forest of high quality in terms of food for the wild boars. This could potentially decrease the wild boar's tendency to forage in agricultural fields. Further studies should include investigations on whether the wolf, which at the moment is the only potential predator in Denmark, can have a positive effect on avoiding wild boars going into agricultural fields to forage.

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Appendix

A Supplementary map

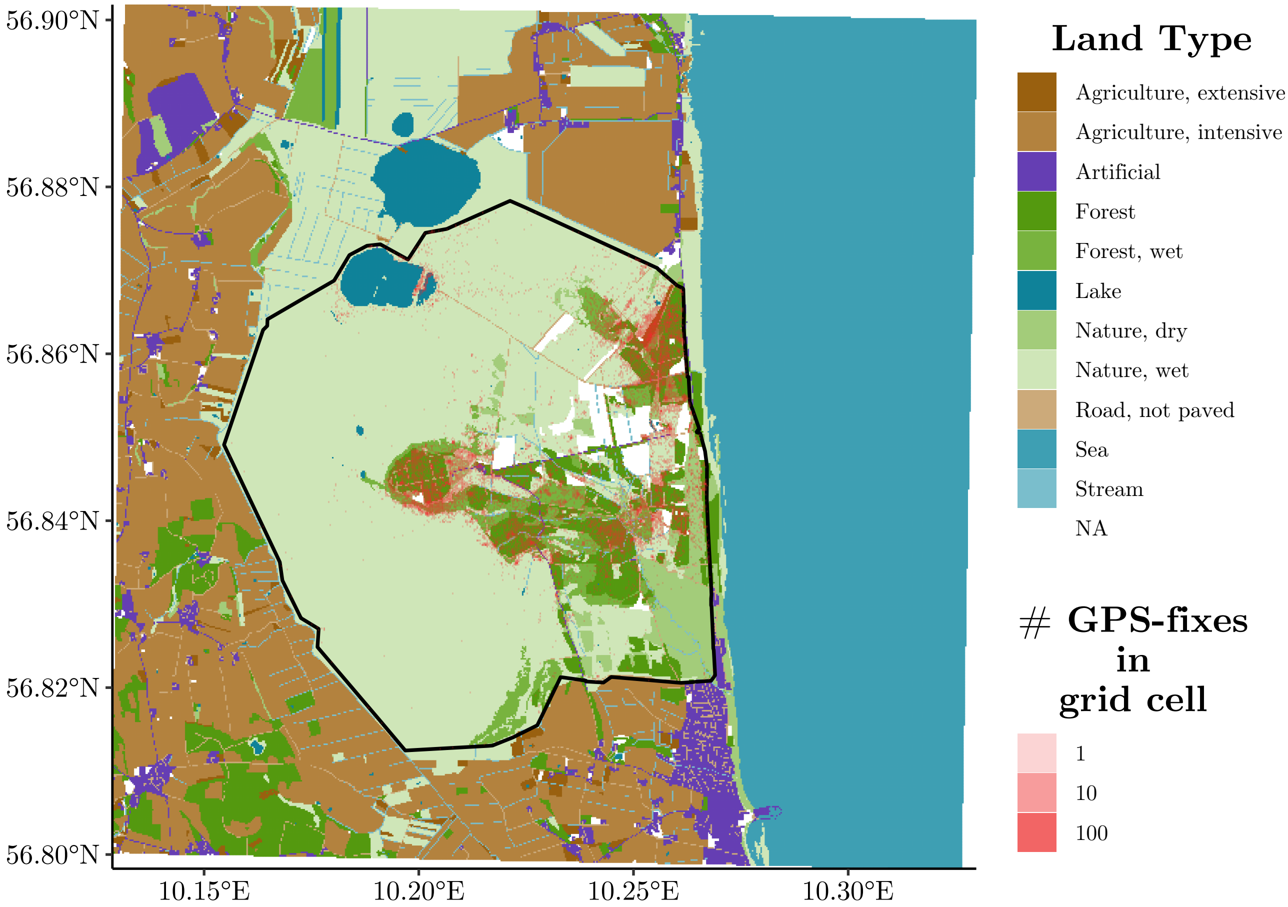

Fig. A.1 Supplementary map of habitat types and density of wild boar GPS-fixes in Tofte Skov.