

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

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

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Preface

The present paper constitutes a concise and original research study intended for publication in the journal Movement Ecology, published by Springer. It focuses on investigating Wild boars' movement and habitat use in Tofte Skov, Denmark. The data foundation for the project consisted of GPS and accelerometer data from GPS collars, however due to time constraints and for simplicity we opted not to use the accelerometer data and instead focused on the GPS collar data. The data spans from February 2019 to January 2021 and was collected from a total of 25 individual wild boar.

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12 **Abstract**

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

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

24 **Results:** We found significant differences in habitat use by wild boars in Tofte
25 Skov. Forests had the highest habitat use frequency, followed by other natural
26 habitats such as wet nature and dry nature. Artificial areas, streams, non-paved
27 roads, and lakes had the lowest use frequency. Habitat selection coefficients
28 revealed that forests, wet forests, streams, non-paved roads, artificial areas, and
29 extensive agriculture were preferred habitats. Wet nature (raised bog) had a
30 significantly lower habitat selection coefficient. The movement behavior of wild

31 boars varied during the day, with faster and more straight movements during the
32 day and slower and more turning movements during the night.

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

40 **Keywords:** Wild Boar, Habitat Selection, Movement Behaviour, GPS, Ecology

41 Background

42 In 2020, as part of the European Green Deal aimed at combatting the global loss of
43 biodiversity, the European Commission adopted a new strategy for the restoration and
44 conservation of biodiversity. One of the key goals of this strategy is to achieve 30%
45 protected nature areas on land and sea by 2030[3]. However, in Denmark, the Danish
46 Biodiversity Council estimates that the current extent of protected areas on land is
47 below 2.3%[4]. Therefore, there is an urgent need to establish more protected nature
48 areas in Denmark.

49 Large mammals, such as wild boars (*Sus scrofa*), can play a significant role in
50 increasing biodiversity within the future Nature-Nationalparks. They have been shown
51 to positively impact ecological processes[4]. However, the presence of wild boars in
52 European nature has been a subject of extensive discussion. Farmers are concerned
53 about substantial economic losses due to crop damage and the transmission of diseases
54 (especially African Swine Fever, ASF) to domesticated pigs. Furthermore, the invasive
55 capabilities of wild boars raise concerns among some conservation-/restoration-ists and
56 managers, as they can cause significant damage to native biodiversity and potentially
57 drive certain species to extinction[5, 6]. Although concerns about the invasive nature
58 of wild boar are valid by themselves, wild boars should be considered native in

59 Denmark under any conceivable definition of "native" considering that they have a
60 deep evolutionary history in Europe, which was only ended locally in Denmark in
61 1801 by intensive hunting[7, 8]. Today wild boar are common in most of their natural
62 range including Europe, Asia, and Northern Africa and have been introduced to novel
63 ecosystems in Australia, New Zealand, North and South America[9].

64 Simultaneously, wild boars is broadly considered as a keystone ecosystem engineers
65 by ecologists. They provide essential disturbances to habitats that have lost their natural
66 disturbance regimes, which were previously provided by extinct megafauna[4, 10]. The
67 unique rooting behavior of wild boars has been associated with increased biodiversity[11–
68 13], enhanced habitat heterogeneity[14, 15], and act as vectors for seed and fungi
69 dispersal[16, 17]. Therefore, the impact of wild boars on natural ecosystems is complex
70 and requires a deeper understanding. Gaining insights into the behavior and habitat
71 use of wild boars is crucial for comprehending the circumstances in which they can be
72 utilized as a tool for nature restoration, as well as recognizing situations in which they
73 may cause habitat damage. Studies of the historical-natural habitat use of wild boars in
74 Europe have found that wild boar mostly inhabit old deciduous forests containing some
75 wet areas and open meadows[18]. However, in the modern European landscape, wild
76 boars have benefited immensely from the expansion of agriculture and have adapted
77 to exist in human dominated areas close to human settlement[1, 2, 19].

78 One reason for concern arises from wild boars' ability to adapt to a wide range of
79 habitats in which it is introduced. Consequently, they have established populations in
80 almost all habitats they have been introduced to[20]. Furthermore, wild boars can also
81 feed on a wide array of food sources and can be classified as opportunistic omnivores
82 with a large geographical range.[9, 20] Furthermore, The boar's feeding habits are highly
83 determined by the season and available food in a given area, and they can adapt their
84 feeding methods to grazing, browsing, foraging, rooting, and even predation[20, 21].
85 Their rooting behavior is especially important for creating habitat heterogeneity by

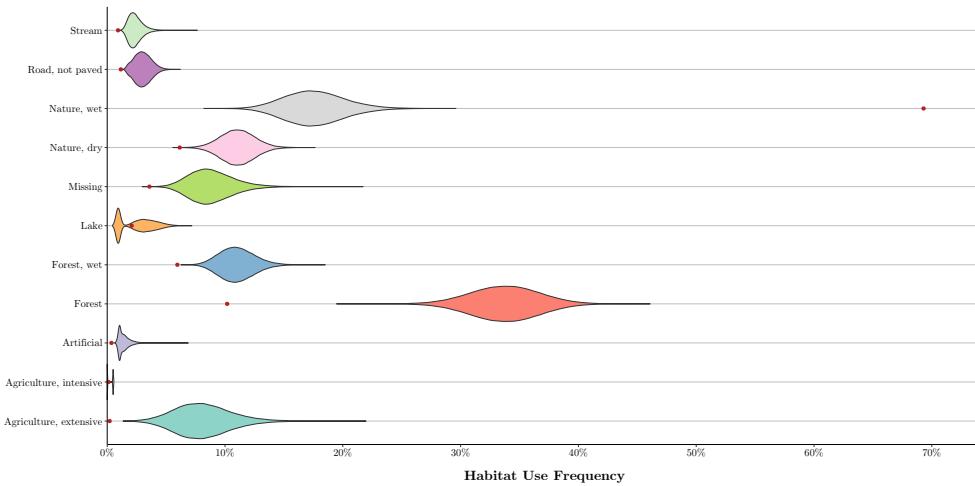


Fig. 1 Bootstrap distributions of *S. scrofa* habitat use frequencies in Tofte Skov.

removing monocultures of dominating plants and creating disturbed sites in the soil opening up areas for disturbance adapted species[22–25]. 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

102 Denmark, have opted to include wild boar populations in enclosed nature areas. This
103 makes it possible to investigate the behavior of wild boar in semi-natural conditions.
104 Deepening our understanding of wild boar behavior and habitat use is detrimental to
105 ensure optimal management of wild boar, if they are to be used as a tool for nature
106 restoration in the future.

107 This study aims to further the understanding of how wild boar utilizes different
108 habitats, and discuss how this could be used to improve management practices. We
109 investigate wild boar habitat-use by utilizing GPS-collar data, along with land use
110 maps, to describe the differences in behaviour and usage of different habitats in the
111 fenced nature area Tofte Skov in North-Eastern Jutland. Because wild boars naturally
112 prefer forests and semi-open areas[18, 29], we hypothesize that the wild boars core
113 area will be closed deciduous forest. We predict that there will be higher habitat-use
114 frequency and higher selection coefficients for forest habitats compared to the other
115 habitat types. Furthermore, we hypothesize that in open areas, where the wild boars are
116 more exposed, wild boars will perform shorter and faster excursions compared to times
117 of lower exposure. We predict that the step length in open areas compared to closed
118 areas will be longer, and that the turning index will be closer to zero. Furthermore, we
119 predict, that wild boars will have longer step lengths and higher turn indexes during
120 the day, as they are more exposed.

121 Methods

122 Software

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

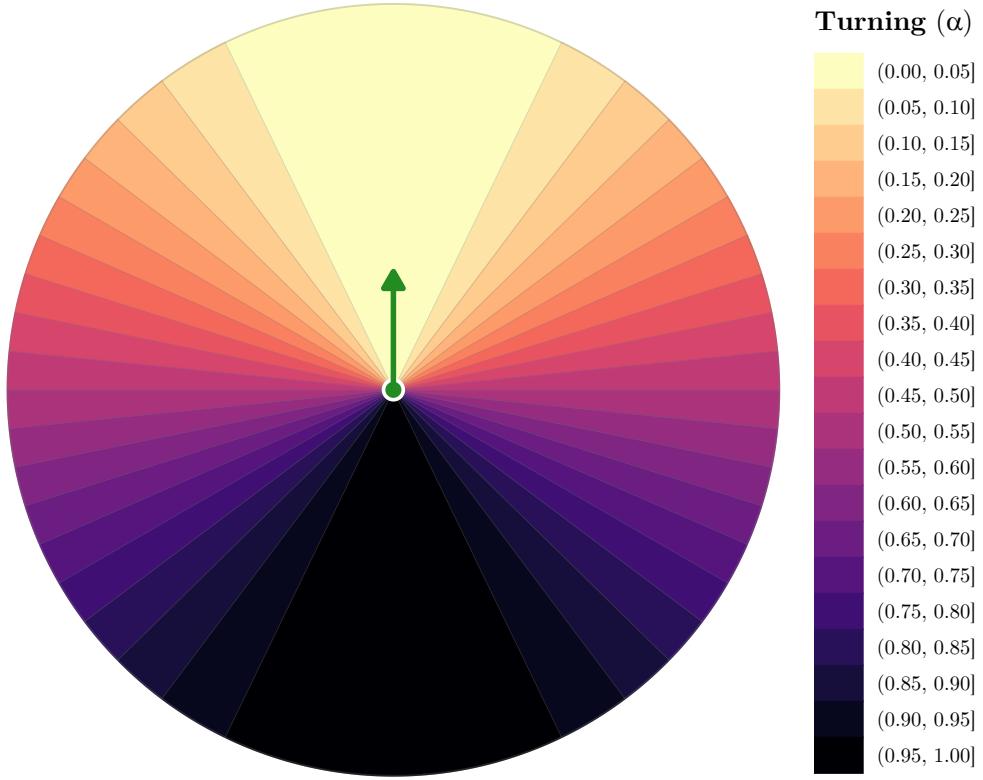


Fig. 2 Visualization of the values of the turning behaviour trait α given a preceding line-segment following the direction of the green arrow, and a following line-segment in the direction of the circle periphery joined at the center of the circle (green dot). Grey lines are equally spaced (0.05) α -contours.

¹²⁷ Study area

¹²⁸ Tofte Skov is a 27km² fenced area in the southern part of Lille Vildmose in eastern
¹²⁹ Himmerland, Denmark. It was fenced in 1907 as part of the preservation of the area.
¹³⁰ Tofte Skov lies within the Natura 2000 area number 17, which includes the entire Lille
¹³¹ Vildmose and Høstemark Skov. The area consists of numerous plains separated by
¹³² different kinds of deciduous forests including beech, oak, birch and alder. Common
¹³³ spruce and sitka spruce have previously been planted and widespread in the area, but
¹³⁴ as part of the preservation of the area these species are now being removed in favor of
¹³⁵ the native deciduous species. Tofte Skov is also characterized by having large areas of

¹³⁶ raised bog and different populations of wildlife including 150 wild boars, wisents and
¹³⁷ red deer[36, 37].

¹³⁸ Collection of data

¹³⁹ During a 2-year study conducted from February 2019 to January 2021, a total of 25
¹⁴⁰ wild boars were collared. The collaring process was divided into three rounds: the first
¹⁴¹ round occurred in February and March 2019, the second round took place in November
¹⁴² 2019, and the final round was conducted in November 2020. To facilitate the collaring
¹⁴³ process, the wild boars, which were accustomed to supplementary feeding, were enticed
by driving vehicles and distributing feed.

Procedure 1 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.

```
1: for each Individual-nested temporal block do
2:   Pre-calculate habitat frequencies
3: end for
4: for  $i \in \{1 \dots 100\,000\}$  do
5:   Bootstrap individuals ( $n = 25$ )
6:   for each individual do
7:     Bootstrap temporal blocks
8:   end for
9:   for each  $i \in \text{habitat}$  do
10:     $\text{HUF}_i = \text{Average use frequency}$ 
11:     $\text{HSC}_i = \frac{\text{HUF}_i}{E(\text{HUF}_i)}$ 
12:   end for
13:   for each  $\{i, j\} \in \text{habitats}$  do
14:      $\Delta_{i,j} = \frac{\text{HSC}_i}{\text{HSC}_j}$                                  $\triangleright$  Pairwise differences in HSC
15:   end for
16: end for
17: Summarize mean, median, lower and upper quantiles and empirical p-values
18: Adjust p-values for multiple hypothesis testing
```

¹⁴⁴

¹⁴⁵ The collaring procedure involved anesthetizing the wild boars using a CO₂ rifle.
¹⁴⁶ The anesthesia induction was accomplished by darting, and the animals remained

¹⁴⁷ under anesthesia for a few minutes, during which they were collared and ear tagged to
¹⁴⁸ facilitate individual identification. Proper ventilation of the anesthetized animals was
¹⁴⁹ ensured during the process. During the initial collaring rounds, the population of wild
¹⁵⁰ boars exceeded expectations, resulting in significant weight losses due to insufficient
¹⁵¹ food supply. Consequently, several collars did not fit properly and were not adequately
¹⁵² secured, leading to their subsequent detachment. Additionally, interactions between
¹⁵³ the boars also caused some collars to fall off. As a response to the suboptimal feeding
¹⁵⁴ conditions, a significant portion of the boar population was euthanized and excluded
¹⁵⁵ from the study in early 2020. Following this intervention, the remaining population
¹⁵⁶ experienced weight gain, resulting in better collar retention. Towards the end of the
¹⁵⁷ study, the last five collars were manually removed ahead of schedule due to concerns that
¹⁵⁸ they might be too tight. It should be noted that the wild boars received supplementary
¹⁵⁹ feed in late 2019, but not in the subsequent year.

¹⁶⁰ Information regarding the data collection was obtained from Lars Haugaard
¹⁶¹ (personal communication).

¹⁶² **Habitat types**

¹⁶³ To analyze habitat use, we used the land use classification Basemap04 produced by
¹⁶⁴ The institute for Environmental science in Aarhus University[38]. Basemap04 is a
¹⁶⁵ combination of remote sensing land cover classification maps and land cover census
¹⁶⁶ data. The map defines 34 land use / land cover categories. As many of the categories
¹⁶⁷ were redundant for our analysis, we joined all building categories, unused agriculture
¹⁶⁸ categories and other artificial land use as a single category called "Artificial". We
¹⁶⁹ kept the non-nature categories: "Road, not paved", "Agriculture, extensive" and
¹⁷⁰ "Agriculture, intensive". We included all the nature categories to differentiate land use
¹⁷¹ across different nature types.

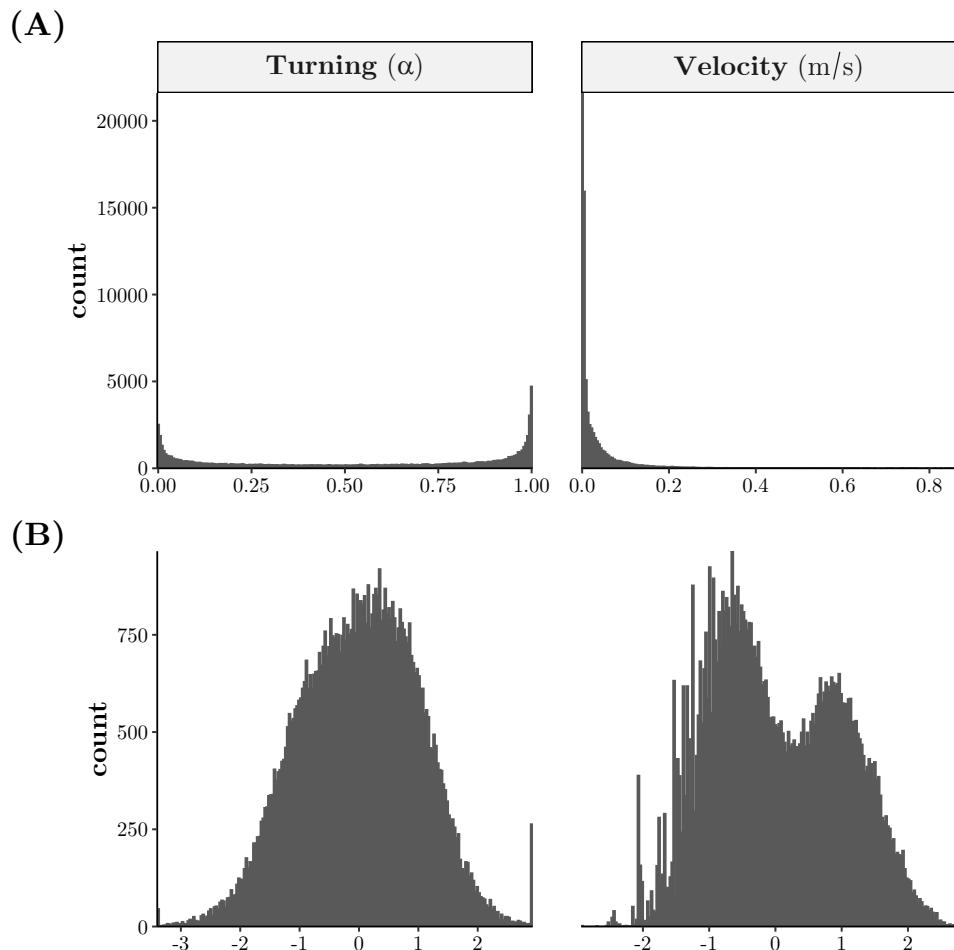


Fig. 3 Histograms of the behaviour traits (turning and velocity) on the raw data scale (first row, (A)) and transformed (second row, (B)). Velocity is simply log-transformed and scaled, while turning degree is transformed using a quantile-transformation between a fitted beta-distribution and a scaled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

172 Habitat Selection

The **Habitat Selection Coefficient** (abbreviated as HSC throughout this report), is an index which calculates the proportion between observed and expected habitat use frequency:

$$\text{HSC}_H = \frac{O(F_H)}{E(F_H)}, \quad F_H = \frac{n_H}{\sum n_i}$$

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

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

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

186 Behaviour traits

187 We wanted to investigate whether we could detect any differences in behaviour between
188 the different habitats. To do so we chose to investigate to parameters of behaviour
189 which are quantifiable, at least to some degree, from our GPS-data; (1) turning angle
190 and (2) mean velocity between fixes, both under the simplifying assumption that
191 individuals are walking in straight lines between the fixes. The latter assumption is
192 almost with complete certainty wrong, however it is not obvious that it would be
193 biased in either of the quantifiable behaviour traits across any kinds of stratifications
194 in our dataset. We have therefore limited our analysis to one of relative differences

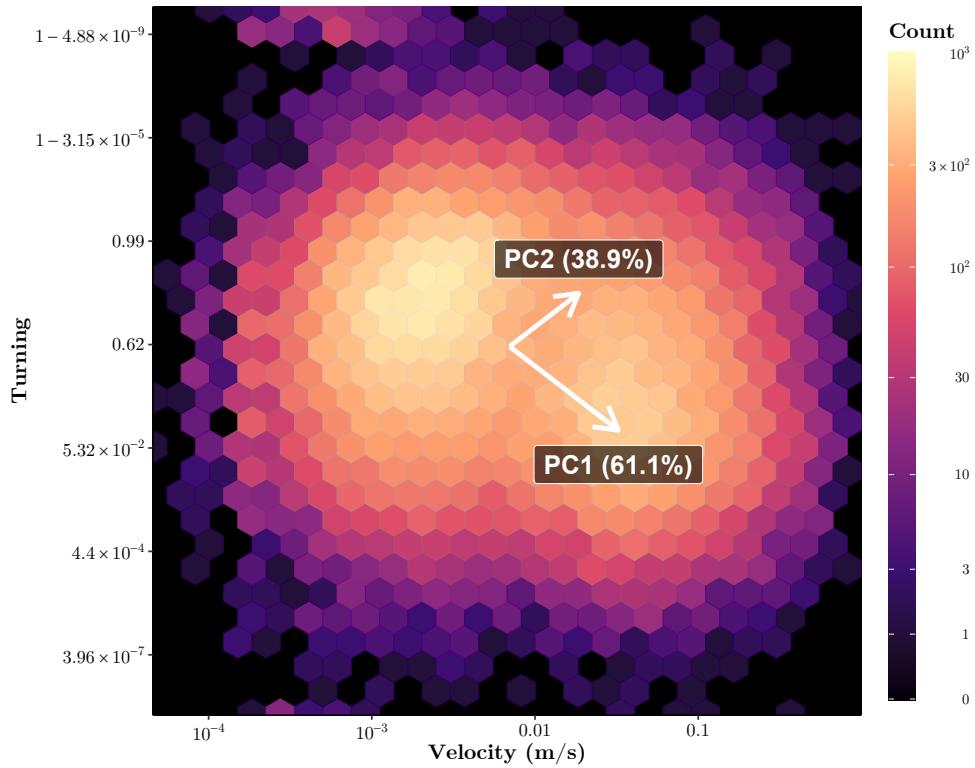


Fig. 4 Biplot of PCA analysis of behaviour traits overlayed on top of a heatmap of the observed trait values on the appropriate transformed scales (explaining the awkward axis breaks on the turning-axis in particular). The percentages next to the principal component labels are the percentage of variance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

195 between different types of habitats and times of day. The turning behaviour trait will
 196 be quantified using $\alpha = 1 - \frac{\cos(\theta)+1}{2}$ such that 0 corresponds to straight movement
 197 while 1 corresponds to turning around, while velocity is simply calculated by dividing
 198 the distance between two consecutive points in space by their distance in time¹. The
 199 cosine is used for quantifying turning, since it the cosine is equivalent to the lateral
 200 component of the direction vector, i.e. if the cosine is 0.4 then if the animal moves

¹we use SI-units for velocity; m/s .

201 1km then it moves 400 meters either left or right of where it would have been, if it had
202 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-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 data follows a multivariate normal distribution²[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-normalization"[41, 42]:

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

203 This procedure produces an extremely appropriate transformation of α as can be seen
204 in the second row (**B**) of [Figure 3](#). After these preprocessing steps it was possible to
205 conduct an appropriate PCA analysis ([Figure 4](#)) with the first principal component,

²For simplicity I only focus on the marginal distributions.

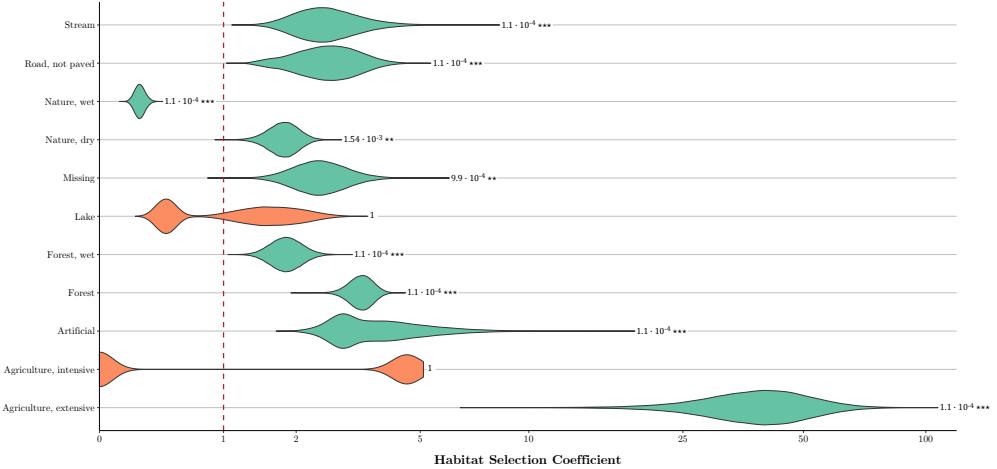


Fig. 5 Bootstrap distributions of *S. scrofa* habitat use anomalies in Tofte Skov. Anomalies are calculated as the difference between the observed habitat use frequency (see [Figure 1](#)) and the habitat frequencies in Tofte Skov.

[206](#) **PC1**, explaining $\sim 61.1\%$ of the variance going from (positive) fast and straight
[207](#) to (negative) slow and turning behaviour. We have chosen to refer to this principal
[208](#) component as *Spurtiness*.

[209](#) Results

[210](#) Habitat Selection

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

[215](#) We found a significantly higher than expected habitat selection coefficient (HSC) for
[216](#) the habitats “Stream”, “Road, not paved”, “Nature, dry”, “Missing”, “Forest” and “Forest,
[217](#) wet”, “Artificial” and “Agriculture, extensive” (former landing-strip, with feeding station
[218](#) and animal-release point), while “Nature, wet” (mostly raised bog) was the only habitat
[219](#) type with a significantly lower than expected HSC ([Figure 5](#)). Furthermore, we found

220 that after Bonferroni correction for multiple testing "Agriculture, extensive" had a
 221 significantly higher HSC than all other habitat types, while "Forest" had a significantly
 222 higher HSC than all other natural habitats, both open and closed, and unsurprisingly
 223 "Nature, wet" also had a significantly lower HSC than all other habitats. The only other
 224 habitat with a significantly different HSC from any other than the before mentioned is
 225 "Artifical" which had a very marginal higher HSC than "Nature, dry" ([Table 1](#)).

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} **

Time of Day	μ_{PC1}	μ_{Δ}	$Q_{50\%}(\Delta)$	$Q_{5\%}(\Delta)$	$Q_{95\%}(\Delta)$	P-value
[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

Fig. 6 Bootstrap results ($n = 100\,000$) of differences in sputtness behaviour between open and closed habitats across different times of day. All values except μ_{PC1} are differences calculated $\Delta = \text{Sputtness}_{\text{Open}} - \text{Sputtness}_{\text{Closed}}$, such that positive values indicate more sparty (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.

226 Habitat Behaviour

227 We then proceeded with an equivalent analysis of movement behaviour as we did
 228 with habitat selection (nested temporally blocked bootstrapping) stratified across
 229 four intervals of time of day ([00-06), [06-12), [12-18) and [18-24) and two habitat
 230 types "Open" and "Closed", where we chose to classify "Forest" and "Forest, wet" as
 231 "Closed" while the remaining habitats were classified as "Open". We found no significant
 232 differences between open and closed habitats at any time of day (Table 1). However,
 233 the movement behaviour of the wild boars differed during the day with faster and more
 234 straight movements during the day, especially between 12-18, and slower and more
 235 turning movements during the night between 00-06.

236 Conclusion

237 Habitat selection and preference

238 As hypothesized, our findings revealed that the wild boars showed a clear preference
 239 for the areas with closed deciduous forests. Both when comparing frequencies and
 240 when taking the size of the different habitats into account, by investigating habitat
 241 selection coefficients. The forest habitats in Tofte Skov create preferable conditions
 242 for the wild boars of the area, as they provide some of the key conditions and food
 243 sources for ideal wild boar habitats as outlined in a scientific review of the European

244 wild boar population by[18]. Amongst these conditions, forests provide: heavy brush
245 for predator protection, roots, fruits, nuts, bark, shoots, leaves and other food items.
246 The aversion of wet nature likely arises, as this habitat exclusively consists of nutrient
247 poor marshlands with low quality food availability, high exposure and possibly difficult
248 movement conditions caused by the deep sphagnum layer. Furthermore, investigating
249 [Figure B1 in Appendix B](#) it is evident that the wild boars primarily use the wet nature
250 habitat between the forest and the lake, and the wet nature closest to the forest edge.
251 This indicates that wild boars only use the wet nature habitat, when they are traveling
252 to and from the lake, likely to drink water, and will otherwise avoid walking in this
253 habitat.

254 Furthermore, the extensive agriculture habitat had a significantly larger selection
255 coefficient than the other habitats regardless of being an open area. This can be
256 explained by this area being the place in which they are fed. Furthermore, the holding
257 pen in which the wild boars are released from and caught for check-ups is close to
258 the extensive agriculture (personal observations and communication with Thomas
259 Holst Christensen). These interactions are generally positive for the wild boar, as they
260 include feeding. An explanation for the preference for this area could therefore be that
261 the wild boars associate this area with an abundant source of high quality food, and
262 are thus not encouraged to search for food in other habitats. This is comparable to
263 how European wild boar populations have adapted to prefer forest habitats close to
264 agricultural fields containing high value food, that makes the benefit of the area higher
265 than the potential cost[18, 20]. This is not surprising, as wild boars have a high degree
266 of behavioral plasticity[2]. Furthermore, the predation pressure in Tofte Skov is very
267 low. At the time of the data collection there were no top predators in the area. So
268 the only predatory risk the population is exposed to is hunting from humans. The
269 supplementary feeding changes the natural behavior of how the wild boars use the
270 different habitats, making it harder to broaden the results of this study to wild boars

²⁷¹ in non-managed unfenced nature areas. Future studies should include areas with no
²⁷² supplementary feeding to evaluate how the wild boars root in natural settings compared
²⁷³ to areas with supplementary feeding, such as Tofte Skov.

²⁷⁴ **Amount of turning/movement/habitat behavior**

²⁷⁵ Our results showed that there were no significant differences in movement behaviour
²⁷⁶ between open and closed habitats (table 2). Hence the wild boars do not move short
²⁷⁷ and fast in open areas, as hypothesized. They do not seem to be “scared” of the open
²⁷⁸ areas as predicted. As mentioned above this is likely because they have learned to
²⁷⁹ associate some of the open areas with feeding. Furthermore, the hunting pressure in
²⁸⁰ Tofte Skov at the time were almost non-existing. Today there is a wolf inside the fenced
²⁸¹ area, that could potentially predate on wild boar, though since first registration of
²⁸² the wolf in 2021 the employees have not registered any killings of wild boar (personal
²⁸³ communication with Thomas Holst Christensen). Future studies of GPS collar data
²⁸⁴ from Tofte Skov, could include comparison of the wild boars habitat use before and
²⁸⁵ after the wolf entered the area. Even though it does not seem like the wolf preys on
²⁸⁶ the wild boars, it could still have an effect on how the wild boars move around and
²⁸⁷ use the different habitats. Across all habitats the movement behaviour follows a clear
²⁸⁸ tendency with the boars having a higher amount of spurtiness during the day and less
²⁸⁹ during the night (PC1, movement table). Spurtiness is characterised by being fast and
²⁹⁰ straight movements with a low amount of turning, which would indicate that the boars
²⁹¹ use the daytime to move around between different areas or habitats. Conversely, the
²⁹² movements during the night are characterised by being slower and with more turning,
²⁹³ which could indicate rooting or other kind of foraging behaviour. This is consistent
²⁹⁴ with the boars being nocturnal animals that forage during the night[43].

295 Management implications

296 As discussed, the preference of wild boars to use feeding stations in the extensive
297 agriculture areas can be compared to the well documented preference of wild boars,
298 to forage on agricultural fields[20]. Wild boars are likely to have the same preference
299 in Denmark, considering the large availability of crops. Introducing wild boars into
300 Danish nature would therefore likely increase human-wildlife conflict with farmers, as
301 they could damage crops, and increase fear of transmission of African Swine Fever. It is
302 important to highlight that infection of AFS from wild boars to domestic pigs is most
303 likely in areas with many free range pigs such as Caucasus and Russia. Furthermore,
304 whilst wild boars can infect domestic pigs, AFS does not persist in populations of wild
305 boars, without continuous infection from other sources, such as areas with infected
306 domesticated pigs[44]. It is possible that proper fencing to avoid contact between wild
307 boars and domesticated pigs, would diminish infection risk. However, whilst the risk of
308 AFS spread from wild boars to domestic pigs, is contested, it is still, in the current
309 political landscape, unlikely that wild boars will be a tool for nature management in
310 unfenced nature areas. However, the issues relating to wild boar contact with domestic
311 pig production would be avoided, if wild boars were kept in large fenced nature areas
312 such as the proposed nature national parks in Denmark. This would allow the wild
313 boars to act as ecosystem engineers[10], creating much needed disturbances[4] whilst
314 minimizing human-wildlife conflict.

315 Concluding remarks/perspective

316 Our results provide valuable insights for the management of wild boar populations.
317 This study provides empirical evidence supporting the hypothesis that wild boars
318 prefer closed deciduous forests as their core habitat. We did not find any significant
319 differences in movement behavior across different habitat types. We did however find
320 that wild boars move further and more straight during the day compared to during

³²¹ the night. This suggests that they forage during the night and walk between habitats
³²² during the day. Furthermore, our results show that the wild boars in Tofte Skov can
³²³ adapt a significant preference for open habitats, if they are associated with positive
³²⁴ effects such as the provision of high quality food. This also indicates that if wild boars
³²⁵ were to be set free in Danish nature, they would forage on fields. To avoid escalating the
³²⁶ human-wildlife conflict, wild boars could be included in fenced nature national parks
³²⁷ where they could forage naturally and create needed disturbances in the landscape.
³²⁸ Furthermore, one could try to improve the natural food availability in areas with
³²⁹ closed deciduous forest of high quality in terms of food for the wild boars. This could
³³⁰ potentially decrease the wild boar's tendency to forage in agricultural fields. Further
³³¹ studies should include investigations on whether the wolf, which at the moment is the
³³² only potential predator in Denmark, can have a positive effect on avoiding wild boars
³³³ going into agricultural fields to forage.

³³⁴ **Supplementary information.** All code and data is available on <https://github.com/asgersvenning/Vildsvinene>.

³³⁶ **Appendix A Movement Ecology Guidelines for**
³³⁷ **Authors**



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Research

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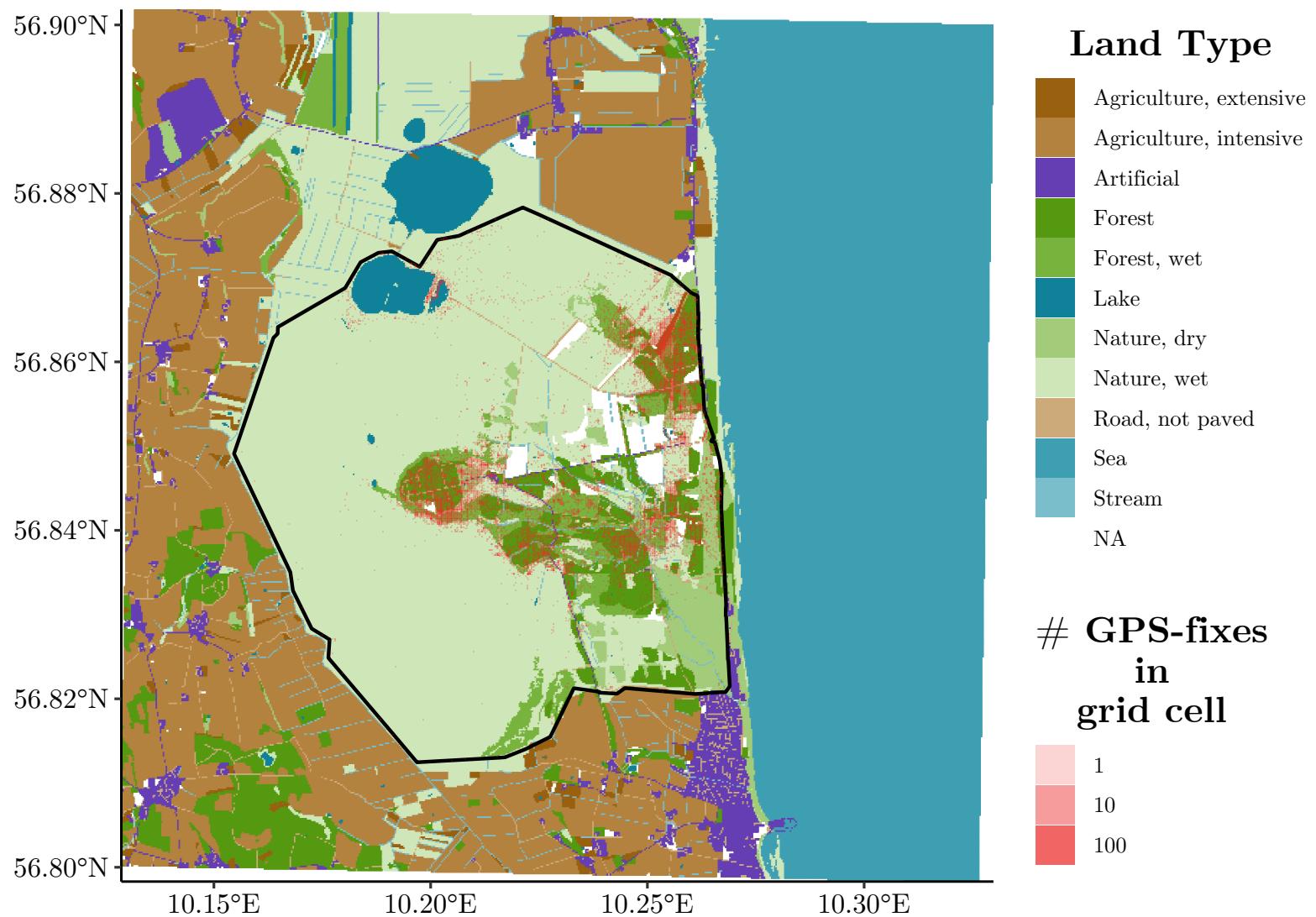
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Fig. B1 Supplementary map of habitat types and density of wild boar GPS-fixes in Tofte Skov

352 Appendix B Supplementary map



³⁵³ Appendix C Included articles

Article

Effect of Wild Boar (*Sus scrofa* L.) on Forests, Agricultural Lands and Population Management in Lithuania

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Abstract: The wild boar (*Sus scrofa* L., 1758) is one of the most common and widespread game species not only in the Baltic Sea region but also throughout its entire range. However, quantitative population management is required due to the danger of contagious diseases; the census is imprecise, and integrated management and monitoring are still missing in Lithuania. This study focused on the current condition of the wild boar population at the country level, species activity in forests and adjacent agricultural lands, the problem of damage to agriculture and forestry caused by wild boar, and methods for the management of the wild boar population. A methodology for the assessment of the effect of wild boar will help in reducing their impact. For the successful management of wild boar, an increase in the carrying capacity in conformity with animal density should be accomplished.

Keywords: wild boar; habitats; effect; damage; assessment; management



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1. Introduction

The wild boar (*Sus scrofa* L. 1758) is one of the most common and widespread game species not only in the Baltic Sea region but also throughout its entire range. It is native to forests ranging from Western and Northern Europe and North Africa to India, the Andaman Islands, and China and has been introduced to New Zealand and the United States [1,2]. Wild boars are an important and inherent component of the forest ecosystem in Lithuania.

The Lithuanian wild boar belongs to the central European subspecies *Sus scrofa*. In Lithuania, the spread of wild boars occurred no later than at the end of the early Holocene (i.e., 8–6 millennium B.C.), especially in the third to second millennium B.C [3]. The species was not rare: its bones make up 20–50% of ungulates' bones found at archaeological sites. In the period after World War II, the number of wild boars decreased because of an abundant population of predators (e.g., the wolf, *Canis lupus* L.), poaching, and other human disturbances (e.g., landscape conversion, forest operations, hunting, recreation, etc.). Historical sources indicate that [3] severe winters in the past negatively affected the annual increment of the population and caused the loss of at least a quarter of adults. Nevertheless, abundant supplementary feeding in winter, protection from poaching, a reduction in the predator numbers, and the improvement of habitat conditions (e.g., agricultural land mosaic; increase in the area under oak stands, and other measures to provide food and shelter) were suitable measures that allowed the species to recover and further increase in number. The behavioural plasticity of wild boars has allowed them to adapt to the feeding conditions of the anthropogenic landscape [4–6]. Consequently, the animals have gathered in the most suitable localities [4,6], causing a clumped distribution and inducing changes in their territorial and feeding behaviour while also becoming a prime risk factor for the spread of contagious diseases in a short time [7–16]. The distribution, movement, grouping, and abundance of wild boars depend on several key drivers, such as the available food supply, safety, and assurance of reproduction. When the animals' needs are unsatisfied [5,17–19], their adaptation to changes in their environment is disordered, and feeding requirements prevail [5,19,20]. Simultaneously, the damage caused to agricultural crops and forestry

increases [19–31]. Despite their omnivorous and highly opportunistic diet, wild boars mostly consume vegetative food, and a better food supply is found in deciduous and mixed forests [19,31,32]. Although wild boars are inseparable from forests, their effect on forests is not exceedingly significant, and their rooted area comprises only 0.9–2.9%, regardless of the high density of wild boar (e.g., density ranges from 15 to 82 individuals per 1000 ha) [33]. Wild boar rooting facilitates the sprouting and growth of tree seeds; moreover, the animals consume insects and rodents [32–35] and stimulate the decomposition of organic matter and the mobilization of soil nutrients [35]. Therefore, they have an important function in assisting nutrient transfer in native forest habitats [36–38]. Although wild boar rooting in forests reduces carbon (C) stocks in the forest soil, they have a negligible effect on large-scale emissions [37,38]. Wild boar mainly roots in older forests, and their rooting has little effect on the germination of seeds via the scarification of the topsoil layer [39]. One study found that rooting occurred in <1% of the area and caused negligible damage to the roots of trees with commercial value [39]. However, other authors have emphasized the considerable risk of damage to seedlings, especially during the first week after planting, with most damage occurring during the first four weeks [40,41]. Wild boars can be described as ecosystem engineers because they mechanically change their environment [42]. It has been found that the most damaged tree species are pine (*Pinus* spp.) or spruce (*Picea* spp.) [39–41] and hardwood species [41–46]. The damage caused by wild boar to seedlings in young forest plantations is site dependent and likely influenced by a combination of food availability, seedling accessibility, animal density, land cover, hunting pressure, and soil moisture [43]. Wild boar can also negatively affect forest litter (losses reaching 80–95%) [32]. Moreover, they contribute to the disappearance of rare plant species and damage tree roots, which cause slope erosion [44,45].

Wild boars cause hundreds of thousands of euros worth of damage [47–53] to almost all agricultural crops [20,21,28,45–47,54,55]. In Luxembourg, the damage caused by wild boar increased by 1600% from 1971 to 2004 [22]. The damage to crops differs in both space and time and is dependent on specific plant growth stages [22,47,48,54,56]. Wild boars spend less time in cultivated fields in March, April, and May than in the summer [48]. In mixed agricultural–forest landscapes, wild boars mostly use fields adjacent to forests [48,49,54]. Many authors have emphasized the severity of crop damage not only due to consumption but also due to trampling (e.g., [22,28,47]). Conflicts among landowners, hunters, and other stakeholders regarding wild boar have also increased. Damage assessment is one of the foremost objectives when addressing human/wildlife conflicts [25,46,50,53,57–60]. A methodology for the assessment of damage to agricultural crops, livestock, and forests caused by game animals, including wild boar, was approved in Lithuania in 2002, and a consolidated version has been valid since 20 October 2018 [59]. This methodology helps to mitigate the above-mentioned conflicts. It regulates the calculation of the monetary expression of the damage caused by wildlife to agricultural crops, livestock, forests, and hydraulic equipment for the owners, users, and managers of agricultural and forest lands and water bodies and lays out measures to protect crops against damage. Wild boar management techniques have been suggested in many countries, including the USA and Australia [61,62]. Problems caused by wild boar and the need for an assessment methodology and compensation have also been emphasized in different countries [40,59,63,64]. In eastern Germany, the needs of stakeholders were identified, and an integrated framework that leverages the individual strengths of previously isolated methodologies was proposed [65]. To assess the damage to agricultural crops caused by wild boar, unmanned aerial systems (drones) [66–68] are commonly used, or the assessments are based on surveys and questionnaires [40,69].

The overabundance of wild boar is a global issue of growing interest. To manage their numbers properly, knowledge of the density of local populations and any changes is needed. Density is an important indicator of animal living conditions and can be used as a tool for their monitoring, risk assessment, and management [19,28,54,70–78]. Various methods and models have been used to estimate density [70,71], including snow tracking, hunting-bag

data, drive hunts, pellet group counts, camera trapping, etc. A common practice with a long history is the counting of wild boar tracks in snow. Briefly, straight-line transects are located using a random or systematic sampling design and the location of each track or trail that crosses a transect is recorded [28,79–81]. However, snow tracking is available only for a short time, and snow conditions are often unsuitable for tracking [19,28,70,79]. Moreover, climate warming and drastic fluctuations in wild boar numbers due to contagious diseases [8–11] have encouraged the utilization of proper methods to estimate the density of wild boar populations. For example, in Lithuania, the wild boar population declined by 2–2.5 times from 1967 to 1990 due to outbreaks of classic swine fever (CSF) [82]; however, it recovered rapidly. The permissible quotas of wild boar densities were approved in 1995 [83] on the grounds of damage caused to agricultural crops and forests and the susceptibility of wild boar to contagious viral diseases. However, the quotas were cancelled in 2005 by the Ministry of Environment [84]. This shows that attention to wild boar management was abated in the absence of the direct emergency associated with zoonotic diseases. The abundance of wild boar has again exceeded permissible levels, and their environmental impact and the spread of contagious diseases [19,82,85] have become a challenge at the global level.

This situation causes great concern and questions about the further management of local populations of wild boar. Although the damage to landowners caused by wild boar is less visible today, the current situation encouraged us to present a long-term study on the effect of wild boar on agricultural crops and forests. We aimed to determine the occurrence of wild boar and assess the damage caused to forests and agricultural crops in different natural regions.

2. Materials and Methods

The study was conducted from 2010 to 2020 in different natural regions, including the model territory (MMMPV), with a total area of 5646 ha in the north-western part of Lithuania (Figure 1).

We employed an integrated method to assess the effect of wild boar on agricultural crops and forests as well as to determine animal distribution and habitat preferences. We estimate densities from indirect signs combining indirect snow-track surveys in the winter (in the presence of snow cover, considering the number of the ingoing and outgoing tracks both ways from the transect line within the grid of six parallel transects; the grid covered all forest stand) and counts of faeces taken within belt transects [31,70] in the early spring that was performed during the count of ungulates (belt transect unit 100 m × 2 m; each transect crosses all habitats and is established in parallel with the forest compartment line; habitat is characterized every 100 m) by pellet group counting (PGC + FGP) [6,28,31,85–90]. All counts were performed during the daytime. The density was calculated using the standard population density formula $D_p = N/A$, where N is the total number of individuals and A is the land area unit (1000 ha), considering the average defecation rate of the wild boar 4.95 for Lithuania [6]. The total number of counters was 7–12. The number of wild boars in the entire area of Lithuania was obtained from each hunting ground unit (HGU) ($n = 911$). Considering the delineation of territory for game animals [6,19,85,91], forests were divided into four categories as follows: (1) pure pine forests, including the maritime zone (western and southern Lithuania; other species comprise less than 10%; the study area 2736 ha and 5519 ha, respectively); (2) pine/spruce mixed forests (eastern and central Lithuania; deciduous species comprise 11–25%; the study area, 7505 ha); (3) mixed spruce/deciduous forests (deciduous species comprise 11–50%; the study area 3234 ha); and (4) deciduous forests with a mixture of spruce species (coniferous species comprise less than 10%; the study area 1043 ha), which were distributed in almost all natural regions. The data collected from the field studies and official statistics sets were stored in a database.



Figure 1. Location of Lithuania on a map of Europe (dark green colour) ($55^{\circ}10'24.96''$ N; $23^{\circ}53'41.29''$ E) and the model territory ($56^{\circ}01'54.9''$ N $21^{\circ}53'20.4''$ E (MMMPV) (red—borders of model territory and HGU names).

To estimate the number and age/sex structure of the local wild boar populations, we have used direct counting at baiting points reported during stand hunting, and camera traps, in the model territory. The camera traps were placed at the baiting points ($n = 10$). This method was combined with the tracking of wild boar herds, which stay outside of the attractive zone, using thermal imaging monoculars. To assess the age/sex structure of local wild boar populations, we distinguished three animal categories: (a) males older than 1 year; (b) females older than 1 year; and (c) juveniles aged up to 1 year. The total number of detected wild boar herds was 211. The herd index was defined on the grounds of the annual mean long-term recruitment, which reached 60%, considering species-specific susceptibility to diseases and mortality, differences in the age-related reproduction of females, and long-term observations [19,31]. To calculate herd indices for practical use, the summation of all observed animals in herds is divided by the number of herd observations in a certain territory.

The occurrence of wild boar and the damage caused to agricultural crops depending on animal density were studied during the summer–autumn period within a radius of 1 km from the forest edge. Belt transects were established every 100 metres from the forest edge for the whole agricultural crop area. The size of each belt transect unit was 0.1 ha ($100\text{ m} \times 10\text{ m}$). The number of transects depended on the length of the area. The total length of the transects was 920 km of the total area (921 ha). The intensity of the damage (i.e., “trampled”, “consumed”, etc.) to agricultural crops in the belt transects was estimated visually using a five-point scale as follows [85,92]:

- 0—no damage (intact);
- 1—sporadic damage, 5%;
- 2—less than half of all areas damaged, 30%;
- 3—more than half of all areas damaged, 75%;
- 4—all areas damaged, 100%.

The abundance of each agricultural crop (A) in their rotation was calculated using the formula below:

$$A = n \times 100/N\%$$

where n is the number of sample belt transects where each crop was found, and N is the total number of sample belt transects in all agricultural crops.

The average intensity (I) of the damage to each agricultural crop was calculated using the following formula:

$$I = i/N\%,$$

where i is the sum of the percentage of damage to each agricultural crop, and N is the total number of sample belt transects where each agricultural crop was found.

The index of the consumption (i.e., direct effects to plant tissues including mechanical damage) of each agricultural crop (trampled, eaten up, etc.) was calculated using the formula below:

$$C = A \times I\%,$$

The share of each agricultural crop consumed by animals was calculated using the following formula:

$$S = C \times 100/\Sigma c$$

where C is the consumption index of each agricultural crop in % and Σc is the sum of the percentage of the consumption indices of all agricultural crops.

The percentage (i.e., 5%, 30%, or 75%) of differently damaged agricultural crop area (D) was calculated using the following formula:

$$D = n \times 100/N\%,$$

where n is the number of belt transects, where the damage was 5%, 30%, or 75%, and N is the total number of sample belt transects.

The differently damaged (i.e., 5%, 30%, or 75%) agricultural crop area in hectares was calculated using the formula below:

$$D_{ha} = D_t \times D/100\%,$$

where D_t refers to the total area of each agricultural crop in hectares and D is the area of each agricultural crop differently damaged (5%, 30%, or 75%) by animals in hectares.

To study the wild boar diet, we analysed the stomach contents of 200 harvested wild boars. We collected 500 mL samples from the stomach and stored them in 5% formalin. The contents were washed with water in 1.7 mm and 5 mm mesh sieves. The food content of the samples was analysed using the standard volumetric method. We calculated and recorded the percentage by volume of each food item by displacing water in a volumetric beaker [91–93].

We assessed the effect of wild boar on the yield of different agricultural crops using a plot sampling method. The size of each sample plot unit was 1 m². The sample plots were established directly within the belt transects where crops were differently damaged (i.e., 5%, 30%, 75%, or 100%). Simultaneously, the control plots were established in areas with undamaged agricultural crops. The difference between the cereal mass of the control and sample plots allowed us to calculate the amount of trampled and consumed yield separately. This method enabled us to correctly ascertain the extent of the losses and predict certain preventive and precautionary means for the restoration and maintenance of the balance between animal numbers and the carrying capacity of their habitats.

Research outputs are the ground for population management. The quantitative method for the management of wild boar populations is based on the loss of agricultural

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crops, population size, and annual recruitment. The ratio of population use is calculated using the following formula [47,60,85,94]:

$$N = IN + (RN - PN)/y,$$

where N refers to the ratio of use; IN is the wild boar annual recruitment in animal units; RN is the actual number of animals in the territory; PN is the permissible number of animals in the territory (the number of animals approved for the territory based on the category of the forests and their corresponding carrying capacity); and y is the number of years needed to recover the balance between the animal number and carrying capacity of the territory.

Data Analysis

All of the analyses were performed using MS Excel spreadsheets and the Statistica 8.0 software packages [95]. The relationships between variables (damage—density of wild boar, density—herd index, etc.) were determined using linear regression analysis. The significant differences between the means were determined using one-way ANOVA. The significance of the difference between the means of the obtained data was evaluated using Student's t -test, where $p < 0.05$ was considered significant.

3. Results

3.1. Wild Boar Distribution and Foraging in the Different Habitats

The distribution of wild boar depends on food availability; human disturbances, e.g., hunting intensity; and seasonal changes ([11], et al.). Wild boars are most abundant in areas with high soil fertility [6,19] in the northern, southwestern, and northern central parts of the territory of Lithuania.

Although wild boars are omnivorous animals, plant fodder predominates their diet, comprising almost 97%. In forest rooting sites, the ratio of plant food to animal food was 3:1, showing the dominance of plant food. The average shares of the rooting sites (% of the total study area) and foraging supply of different origins (plant or animal) for the different categories of forests are shown in Table 1. The total share of forest food was only 4% while agricultural crops were available. The analysis of the rooting sites showed that the rooting character depended on the forest stand parameters and forest sites ($r = 0.589$, $p \leq 0.05$).

Table 1. Average seasonal food supply of different origin (plant or animal) and the share of rooting sites in different forest categories in Lithuania.

Forest		Spring			Summer			Winter	
Category	Rooting	Food Supply		Rooting	Food Supply		Rooting	Food Supply	
	Site	g/1 m ²		Site	g/1 m ²		Site	g/1 m ²	
	%	Plant	Animal	%	Plant	Animal	%	Plant	Animal
Pure pine	0.1	0.1	27	0.3	0.2	2.3	0.003	2	2.8
Pine with spruce	2.1	144	7	0.8	22	15.2	0.01	237	0.4
Mixed spruce									
deciduous	0.5	144	14	0.3	155	15.6	0.09	303	0.3
Deciduous with									
spruce	1.0	320	31	1.3	204	28.5	0.09	299	-
Natural meadow	3.6	475	37	x	x	x	0.2	128	0.5

In pure pine forests, there was a low food supply, except for *Alnetum filipendulosum* black alder stands, where earthworm stores of up to 100 g per 1 square meter could be found. In spring, the rooted sites most often occurred in *Betuletum vaccinio-myrtillousum*, *Tremuletum vaccinio-myrtillousum*, and *Alnetum filipendulosum* birch and aspen stands in territories belonging to the pure pine forest category, while the area of rooted sites was the largest in the forest sites containing *Pinetum vacciniosum* and *Pinetum vaccinio-myrtillousum*.

In summer, when mushrooms start growing, the rooted sites were predominant in *Pinetum vacciniosum* and *Pinetum cladoniosum* pine stands. These were the largest rooted sites. In winter, the largest rooting area was found in *Alnetum filipendulosum* black alder stands, where food consumption fluctuated from 65% to 100% (Table 1).

The stands belonging to the pine with spruce forest category provided more plant food for the wild boar. The plant forage store amounted to 500–700 g per 1 m² of the rooted sites in *Pinetum myrtillo-oxalidosum* and *Piceetum myrtillo-oxalidosum* pine and spruce stands and in *Alnetum urticosum* and *Alnetum caricosum* black alder stands. Food consumption ranged from 57% to 100%. (Table 1). In spring, the greatest rooting was observed in *Alnetum caricosum* and *Alnetum urticosum* black alder stands and *Pinetum vaccinio-oxalidosum* and *Pinetum oxalidosum* pine stands, while the largest rooted sites occurred in *Pinetum oxalidosum*, *Pinetum vaccinio-myrtillousum*, and *Pinetum myrtillo-oxalidosum* pine stands and *Piceetum oxalidosum*, *Piceetum myrtillo-oxalidosum*, and *Piceetum vaccinio-myrtillousum* spruce stands. In summer, the most rooting occurred in *Alnetum urticosum*, *Piceetum oxalidosum*, and *Pinetum oxalidosum* black alder, spruce, and pine stands, whereas the largest rooted sites were found in *Pinetum oxalidosum* and *Piceetum oxalidosum* pine and spruce stands. In winter, more rooted sites occurred in the *Alnetum caricosum* black alder stands of pine with spruce forests, whilst the largest rooted sites were found in the *Alnetum caricosum*, *Pinetum myrtillousum*, *Pinetum myrtillo-oxalidosum*, *Piceetum myrtillousum*, and *Piceetum myrtillo-oxalidosum* black alder, pine, and spruce stands of the pine with spruce forests.

In the stands of mixed spruce/deciduous forests, the food supply was similar to that of the stands of the pine with spruce forest category, with the exception of *Myrtillo-oxalidosa*, *Urticosa*, and *Caricosa* forest sites with deciduous stands, where the foraging supply ranged from 230 to 930 g/m². Food consumption reached 32–100% (Table 1). In spring, the rooted sites were mostly found in *Alnetum caricosum* black alder stands and *Piceetum oxalidosum* spruce stands, and natural meadows. The largest rooting areas were found in *Piceetum oxalidosum* spruce stands and *Aegopodiosa* and *Oxalidosa* forest sites with deciduous stands. In summer, the wild boars mostly rooted in *Piceetum oxalidosum* spruce and *Alnetum urticosum* black alder stands, while the largest rooting area occurred in *Piceetum oxalidosum* spruce and deciduous stands. In winter, rooting was observed mostly in the natural meadows and in *Oxalidosa-myrtillosa* and *Oxalidosa nemorosa* forest sites with deciduous stands. The largest rooting areas were found in *Piceetum aegopodiosum* spruce stands, natural meadows, and *Myrtillo-oxalidosa* and *Caricosa* forest sites with deciduous stands.

In the deciduous spruce forests, the food supply was the greatest (Table 1), and food consumption comprised 50–90% [3,28]. In spring, the most rooting occurred in natural meadows, *Carico-nemorosa* forest sites with deciduous stands, and *Alnetum urticosum* and *Alnetum filipendulosum* black alder stands, while the largest rooted sites were found in *Carico-mixtoherbosa* forest sites with deciduous and mixed stands. In summer, rooting mostly occurred in *Alnetum urticosum* and *Alnetum filipendulosum* black alder stands and in *Carico-mixtoherbosa* forest sites with deciduous spruce stands, while the largest rooted sites were found in *Carico-mixtoherbosa* forest sites with deciduous stands, *Alnetum urticosum* and *Alnetum filipendulosum* black alder stands, and *Piceetum carico-mixtoherbosum* spruce stands. In winter, wild boar mostly rooted in *Alnetum urticosum* black alder stands, while the largest rooting areas were found in *Alnetum urticosum* black alder stands and *Piceetum nemorosa-oxalidosum* spruce stands.

Agricultural crops comprised a major part of the plant food consumed by wild boar (ca. 81%). The largest shares of agricultural crops were consumed in the summer (ca. 90%) and autumn (83%). The available residues of crops in fields were found to attract animals and still prevailed in their diet during the winter (ca. 79%) and winter–spring (ca. 66%) periods. Natural plant fodder comprised, on average, 17% of the animals' diet. This food was important in the spring–summer period, but its importance decreased in winter and autumn [2,6,96]. Above-ground food predominated in the animals' diet, comprising ca. 57% of their diet, and was particularly prevalent in the summer (more than two-thirds). The share of the underground food reached 40%. Cereal comprised 47% and potatoes 53%

of their annual diet. The third most preferable food after cereal and potatoes was beets (ca. 12%). Beets were rarely found in the stomach samples from the summer period, but their importance as supplemental fodder increased during autumn and winter. Green plants were found in 85% of wild boar stomachs; however, the share of this food was only found to be nearly 6% of the diet. A frequently observed food was different roots and bulbs, the share of which was 5%, while the frequency of occurrence was approximately 77%. Wild boar preferred the roots of plants such as *Pteridium aquilinum*, *Urtica dioica*, *Asarum europaeum*, *Oxalis acetosella*, *Anemone nemorosa*, *Ficaria verna*, *Caltha* sp., *Phragmites* sp., *Typha* sp., *Ranunculus* sp., and small shrubs, among others. Berries and fruits accounted for 1.5–2% of their annual diet. Another important food was acorns. This kind of food comprised 10–40% of their diet during the productive time of year and about 1.5% of their annual diet. Needles, leaves, and moss were observed less frequently. These types of food comprised 2.5% of the animals' diet in the winter and up to 0.2–0.4% during other seasons. Other plant foods, such as the roots and shoots of trees and shrubs and mushrooms, were rarer in the wild boar diet (0.4–0.7%). Foods of animal origin comprised only 3–4% of their diet; this share was negligibly more during the winter (5%), when small rodents and different carrion predominated than in the spring–summer period (3%). Earthworms were the main contributor to foods of animal origin. Different insects, including the larvae of the cockchafer (*Melolontha hippocastani* L.), flea-beetles (Elateridae), the chrysalides of sawflies (*Lyda nemoralis* Thoms., *Diprion pini* L., *Neodiprion sertifer* Geoffr., *Gilpinia polytoma*), and others, comprised a lower share of the wild boar diet. In spring and autumn, the share of food of animal origin was similar (ca. 2%).

As mentioned above, wild boars inhabit all forests; however, coniferous forests and spruce stands were found to be preferred in this study. Deciduous forests are more important during the summer, not only for foraging but also for bathing—there are a number of suitable bathing points in these forests. Coniferous forests protect wild boar against precipitation (i.e., snow and rain). Many wild boar dens were found under older spruces. Dens were rarely established in the undergrowth of spruce, under pine, or in the pine plantations, while several dens were found in the cuttings and under the roots of fallen trees. The dens were usually found in the southern, southeastern, or southwestern parts of trees (41%) and were exceedingly rare in the western part of trees (6.3%) because of the predominating western winds. In winter, most dens (60%) were covered by spruce twigs or sometimes by juniper, pine, and moss (14.5%) or herbs (1.4%). The dens without any bedding were considered temporary (ca. 23% of cases) [3]. During the warmer weather, the dens had no bedding except those of the females with sucking piglets.

In Lithuania, the largest herds of wild boar occurred in the spring. The average herd size was ca. six individuals; however, there could be up to twenty-two animals at the maximum. Generally, the females stayed with the juveniles, and separate herds sometimes joined. During summer and the beginning of autumn, the average herd size decreased to up to five animals. Simultaneously, more abundant herds of up to thirty-five individuals were also found. After the weather became cooler, the animals gathered into larger herds. The largest herds were observed in the winter, with up to twenty-seven animals, while their average size was 5.5 animals.

Although the wild boars were settled when the food supply was sufficient and the animals were not disturbed, they could move about 10–20 km per day because of human disturbances (e.g., four-wheel motor vehicles). Longer movements were characteristic of males. The average movement distance of wild boar is from 0.3 km to 10.5 km depending on the local conditions, such as the season, animal age, and sex [6,31,96,97]. The average herd of wild boar moves about 1–2 km in the wintertime and up to 10–12 km during the summer [96,97].

3.2. Effect of Wild Boar on Forests and Agricultural Crops and Management Issues

Wild boars visit the agricultural lands surrounded by forests depending on crop rotation and animal density. One individual can root 1 ha in the forest, ravage 0.3–0.4 ha

of crops from milky ripeness to harvest, and damage other crops yearly. The damage to agriculture caused by wild boar comprises 70–75% of total damage to agriculture; in comparison, damage by deer amounts to 25–30%. Wild boar trample, root, and consume winter and summer cereals, root crops, potatoes, damaged caraway, and other available species depending on their occurrence.

The total annual (excepting autumn) area of forest litter rooted by wild boar was, on average, 0.4% in pine forests, 2.9% in spruce/pine forests, 0.9% in mixed spruce/deciduous forests, and 2.4% in deciduous forests. The damage caused by wild boars was strongly and positively related to animal density ($r = 0.59$, $y = -0.140 + 0.120x$; $p < 0.001$), and stronger damage was observed in winter while less was found during summer ($r = 0.88$, $p < 0.05$).

The intensity of damage to rye and wheat was weakly but positively related to the distance from the forest. Animals are safer away from the forest in comparison to its edges because of possible disturbance factors (hunting, recreational activities, etc.). Wild boar can settle there for a long time. Similar but negative relationships were found between the damage caused by wild boar and potato and beet fields. The intensity of damage to oats was the greatest and was negatively related to the distance from the forest edge ($r = -0.80$, $p < 0.04$). The damage to potatoes and sugar beets was negatively related to the distance from the forest edge ($r = -0.48$ and $r = -0.41$, respectively; $p \leq 0.05$). The animals damaged more plants in smaller oat, potato, and beet fields. The principal factor of damage intensity was animal density (number of individuals per 1000 ha; $r = 0.59$; $p \leq 0.05$). The animals mostly trampled crops (ca. 80%), and less damage was due to the consumption of cereals and root crops (ca. 20%). Therefore, the damage caused by wild boar considerably changed the structure of the agricultural crops considered.

When the density of wild boar exceeds 100 animals per 1000 hectares (i.e., up to 115/1000 ha), the animals visit 23–52% of the agricultural crops within a radius of 1 km. At a density of 12 animals per 1000 ha, wild boars attend 6% of the agricultural crops, and when the density is only 6/1000 ha, this value is decreased to 3% [3,6,28].

4. Discussion

4.1. Effect of Wild Boar on Forests and Agricultural Crops

In Lithuania, foresters and game managers have long dealt with the problem of restraining and reducing the damage caused by wild boars, despite the considerable decline in the wild boar population since the first detection of African swine fever (ASF) in 2014. Today, ASF continues to expand its range in Lithuania, despite efforts to eradicate it and implement national disease control measures, including intensive hunting at the national level and in the model territory (MMMPV) (Figure 2).

Effective protection and a decrease in losses are possible if the reasons for wild boar damage and the factors necessary to improve methods for damage prediction and assessment are perfectly understood. Nevertheless, the assessment of the damage caused by wild boar and management strategies for practical application have not been sufficiently presented [40,50,51,59,63,64,98,99]. A methodology for the assessment of the damage caused by wild boar to agricultural crops and forests was included in the Wild Boar Management Programme, a legal act on the damage caused by wildlife to agricultural crops, facilities, and forests [19,100] in Lithuania, and is currently used to estimate crop losses.

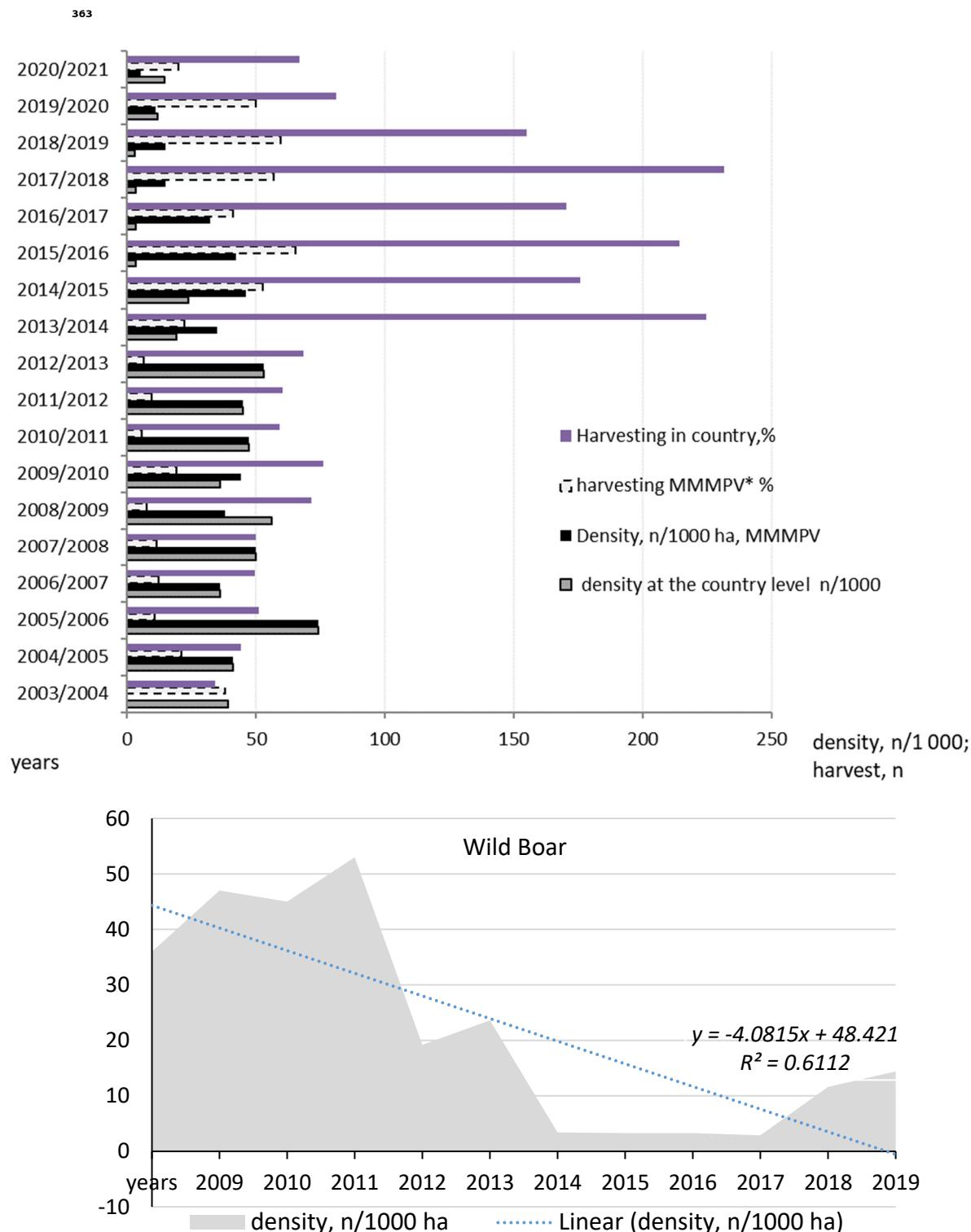


Figure 2. Changes in wild boar harvesting and density in the model territory and entire country.
Note: MMMPV is the abbreviation of the model area.

4.2. Management of the Wild Boar Population

The management of local wild boar populations depends on wild boar numbers and their effect on agriculture and forestry. There are different management plans for wild boar populations [101–112]. Wild boar populations are managed territorially, quantitatively, and qualitatively [6,19,28,85]. The essence of territorial management is harvest planning and the regulation of numbers in the local wild boar populations despite any administrative borders, such as a region, forest enterprise, or single forest. The local wild boar population

should be the object of management. This approach provides scientific ground for the use of the population when considering the carrying capacity of a certain territory and maintaining an optimal population density. Territorial management is performed in forest stand complexes with an area from 5 to 10 thousand hectares when considering the size of the home range and seasonal migration of wild boars [27,30,84].

Direct observations are important measures for the qualitative management of wild boar. This method is suitable when considering the age/sex structure of the population. The scientifically grounded count method is necessary for the successful management of wild boar populations. The combination of several count methods can be used, for example, the count of animals during drive hunting; at baiting points; by faecal group (FPG), which can be combined with the usual deer count by pellet groups at the beginning of the growing season; or via the camera trapping method [68,71,72,113]. To manage local populations properly, an increase in the carrying capacity of the habitat and its conformity to animal density should be accomplished. In this respect, three categories of wild boar densities were distinguished in Lithuania [28,31,85]:

- Minimum density, when animal distribution is random, forage consumption is low, and the negative impact on the habitat is intangible. At this density, infection by parasitic diseases is not intensive, and the population size increases; immigration is common, while emigration is negligible;
- Permissible density, when the distribution of wild boar is spaced, forage consumption does not exceed the permissible limits, and the negative impact is insignificant;
- Ecological density, when animal distribution is clumped in favourable habitats. Here, the forage demand conforms to forage resources.

The permissible quotas for wild boar and other ungulates in the different forests were already legally approved (Table 2)). The group of food supply is officially approved according to the forest category in Lithuania [114] (hunters pay taxes for the use of wildlife resources in each hunting ground unit HGU based on the group of food resources of their HGU).

Table 2. Permissible quotas for the local wild boar population density in the different forests [85,99,114].

Forest Category	Group of Food Supply	Density in All Forests		Wild Boar Density, n/1000 ha		
		Permissible	Ecological	Protective Forests	Managed, Recreational	Commercial Hunting
				Agroforests	Forests	Grounds
Pure pine (dominant forest sites: <i>Cladoniosa, Vacciniosa</i>)	IV	4–7	5–10	4	7	≥15
Pine with spruce (dominant forest sites: <i>Vacciniosa-myrtillosa, Myrtillosa</i>)-	III	6–11	10–15	6	11	≥20
Mixed spruce/deciduous (dominant forest sites: <i>Oxalidosa, Oxalido-myrtillosa</i>)	II	8–14	10–15	8	14	≥30
Deciduous with spruce (dominant forest sites: <i>Aegopodiosa, Carico-mixtoherbosa</i>)	I	10–15	15–20	10	15	≥30

Note: Variations in soil conditions were observed in *Piceetum myrtillo-sphagnosum*, *Piceetum oxalido-myrtillosum*, and *Piceetum asperulo-tiliosum* (+ = to).

The density quotas must correspond to the local conditions and consider the limiting ecological factors. In addition, the damage caused by wild boars to agricultural crops may not exceed 3–5%. The differences between the density of wild boar and harvesting in the model territory and the whole country are shown in Figure 2. The permissible density of wild boar should be kept in protected areas, forests used for recreational purposes, and agroforests. Ecological density would be suitable for commercial hunting ground units.

In these forests, wild boar density could exceed the ecological density depending on the foraging supply.

The qualitative management of the wild boar population is based on population structure, as shown in Table 3. The local wild boar population structure in Lithuania also depends on the feeding conditions during winter.

Table 3. Age and sex structure of the wild boar population in different forest stand categories.

Stand	Population Structure					
	Herd Index, av	Males Older than 1 Year, %	Females Older than 1 Year, %	Sex Ratio	Piglets below 1 Year of Age, %	Recruitment Coefficient
Pure pine	3.9	28.3 ± 3.8	27.6 ± 2.7	1:1.2	48.6 ± 4.1	0.9
Pine with spruce	4.9	18.7 ± 1.9	30.8 ± 1.2	1:1.6	50.5 ± 1.8	1.0
Mixed spruce/deciduous	5.5	16.4 ± 2.2	28.6 ± 1.9	1:1.7	55.0 ± 3.3	1.2
Deciduous with spruce	4.9	18.1 ± 1.3	33.7 ± 2.7	1:1.9	48.2 ± 3.1	0.9

If baiting during the winter was insufficient, the recruitment coefficient was only 0.9, while under the conditions of sufficient abundant feeding in the winter, it reached 1.7.

Until now, the herd index was not discussed in scientific publications, while it was emphasized several decades ago in Lithuania. However, its importance has emerged during the last decade in the context of the spread of ASF. As the herd index was not considered, the number of harvested animals exceeded 200–400%. A model of the relation between wild boar density and herd index can be expressed as follows: $y = -30.4 + 12.1x - 0.3x^2 - 0.03x^3$, where x is the herd index ($r = 0.89$, $t = 6.12$, $p \leq 0.05$). We recommend considering this useful parameter for wild boar management. The herd index for the different natural regions was determined as follows: 2–3 for pure pine forests in southern Lithuania and 3–4 for the same forests in western Lithuania; 3–4 for mixed coniferous forests in eastern Lithuania and 4–5 for the same forests in central Lithuania; 5–5.5 for mixed spruce/deciduous forests; and 5 for deciduous forests with spruce admixture, including a herd index of 4–5 for the same type of forests in northern Lithuania [19].

In pure pine forests, the herd index was 2–3, and the actual density of wild boar reached 27/1000 ha in 2013; however, because of ASF, it was reduced to 7/1000 ha in 2016, and long-term density stands at only 5/1000 ha.

In stands belonging to the pine with spruce forest category, the herd index was 3–4 in eastern Lithuania and 4–5 in the central part of the country.

In the stands of mixed spruce/deciduous forests, the herd index reached 5–5.5. Wild boar density was reduced to 14–22/1000 ha (2–4 times) because of the general measures against ASF. However, it should be less—around 8–12/1000 ha—considering the carrying capacity of these territories, the herd index, and the risk of ASF.

In the stands of deciduous forests with spruce, the average herd index was 5; however, it was less (4–5) in northern Lithuania.

To ascertain the carrying capacity of territories, game managers should consider the following criteria:

1. Forest species composition and forest habitats in the whole territory settled by local wild boar populations.
2. The distribution of the food supply.
3. The volume of losses to the agricultural crops and forests caused by wild boars.

The long-term annual recruitment of the local wild boar population in Lithuania is 50–60%, while the annual recruitment coefficient is 1.0–1.5. If animal foraging in winter is insufficient, a harvest volume of 80–100% is allowed. Following variable winters with severe and warm periods, harvesting should be reduced by up to 60–70%, which will allow the annual recruitment coefficient to decrease to 0.6–0.7 despite the high reproductive potential of wild boar [115]. To avoid sudden changes in animal numbers, the sex ratio of males to females should be 1.5:1.0. With respect to hunting, the share of juveniles below

1 year should be 70–80%, 15–20% for sub-adults, and 5–10% for adult animals. We must consider not only the high reproductive potential of wild boar but also their biological plasticity [116,117], sociality [4,118], and adaptability; damage to agriculture and forestry; habitat suitability; and other ecological features.

Traditional methods for wild boar hunting include drive hunting, excluding localities of ASF outbreaks, and stand hunting; stalking and chase are also popular, depending on the season. In Lithuania, before the detection of ASF in 2014, the hunting of males and second-year juveniles was allowed from 1 May to 1 March, and the hunting season for females was from 1 October to 1 March. The number of harvested animals was similar over 5 years (Figure 2). A total of 10.3 thousand animals were harvested in 1998/1999, while 10.84 thousand animals were harvested in the 2003 hunting season. However, this number reached 35.56 in the 2017/2018 season, representing an increase of 231.5%. It would be unrealistic to hunt more than 200 percent of the population. What is the reason for such an increase? All harvested animals and their number during the last hunting season must be reported until 5 April annually [114]. However, we recognized that hunters do not consider recruitment of the local population and the region-specific herd index. Since 2015, wild boar hunting has been allowed year-round. Maintaining the minimum permissible density depends on the category of the forest under consideration, i.e., pure pine, pine with spruce, mixed spruce/deciduous, or deciduous with spruce forests, and its functional purposes; its value can fluctuate from 4 to more than 30.

Wild boars are not welcome in agroforests of less than 300–500 ha. Near the forest edges, less preferable agricultural crops are sowed, and cultural pastures are established. In addition, in regions with the most damaged agricultural crops, hunter lookout towers have been established for hunting and frightening away wild boar. Moreover, electric fencing is also used to frighten away wild boar. These means are most notably used by landowners.

5. Conclusions

There is marked evidence of the importance of wild boar in Lithuanian game management, forestry, and agriculture. Considering the damage caused by wild boar, it is necessary to maintain the permissible density of the local wild boar population. This density depends on the local conditions of the forests and surrounding areas, in addition to the functional purposes of the land.

The wild boar population should be managed territorially, quantitatively, and qualitatively considering the density of the local population; the carrying capacity of the territory under consideration and the possibility of it increasing; the age-sex structure of the wild boar population; the annual recruitment of the population; and agricultural crop losses in the territory. In particular, we should seek to maintain the permissible density of the local population. Herd index could be a useful parameter to manage populations. The omission of this index causes incompatibility between the actual number of wild boars and the number of harvested animals (i.e., harvest can reach 120% or more, even reaching 400–550% in some localities). The herd index in the different natural regions was determined as follows: 2–3 for pure pine forests in southern Lithuania and 3–4 for the same forests in western Lithuania; 3–4 for mixed coniferous forests in eastern Lithuania and 4–5 for the same forests in central Lithuania; 5–5.5 for mixed spruce/deciduous forests; and 5 for deciduous forests with spruce admixture, including a herd index of 4–5 for the same type of forests in northern Lithuania.

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Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area

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The aim of this study was to examine the effects of sex and age of individuals, season, and human pressure (both human presence and habitat structure) on spatiotemporal behavior of wild boar (*Sus scrofa*). Specifically, we compared wild boar behavior under contrasting conditions of human pressure, within the primeval temperate forest of Białowieża (eastern Poland) and the metropolitan area of Cracow (Poland). It was predicted that, compared with the forest, wild boar within the urban area will have smaller home ranges due to restricted space, will show longer daily movements due to patchy resources, and will exhibit increased nocturnal activity and ranging behavior in an attempt to avoid human interference. We used radiotracking data from 35 wild boar. Animals inhabiting the urban area had smaller home ranges, yet covered almost twice as much distance on a daily basis than individuals inhabiting primeval forest. Daily duration of activity was similar in the 2 study areas. However, distribution of activity throughout the day differed considerably. In the urban area wild boar were almost exclusively nocturnal, whereas in the primeval forest wild boar activity was evenly distributed throughout the day. Additionally, in the urban area, activity was strongly associated with traveling speed, whereas in the primeval forest active wild boar moved about to little extent. Seasonal effects were stronger in the primeval forest and affected daily distance traveled, duration of activity, and level of diurnality. This study showed that wild boar can adjust their spatiotemporal behavior to local conditions and this may be one factor explaining recent rapid demographic expansion in Europe.

Key words: activity, daily distance, home range, Poland, space use, urban area

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The ranging behavior and spatiotemporal activity of mammals reflect interactions between individuals and their environment. Numerous factors have been shown to affect home range size: body size, sex, and age (McLoughlin and Ferguson 2000; McNab 1963; Mysterud et al. 2001), food abundance and distribution (Clutton-Brock and Harvey 1978; Taitt 1981), population density and social structure (Damuth 1981; Jetz et al. 2004), and risk of predation (Tufto et al. 1996). However, the importance of each factor depends on the scale of analysis, i.e., species, population, or individual level (McLoughlin and Ferguson 2000). Similarly, observed patterns of temporal activity are shaped by intrinsic and extrinsic factors. Internally controlled activity rhythms are influenced by a number of cyclic environmental factors, such as photoperiod, temperature fluctuations, regular feeding bouts (Daan and

Aschoff 1982), and temporal disturbances (e.g. predation, human interference—Keuling et al. 2008a; Kitchen et al. 2000).

In addition to these factors that, often interactively, shape spatiotemporal behavior of mammals, human activity modifies behavior and home ranges of animals. Human pressure (e.g., hunting, tourism) can directly affect behavior and may result in shifts toward nocturnal activity (Kitchen et al. 2000) or influence movements and space use patterns (Frank and Woodroffe 2001; Jeppesen 1987). In contrast, human activity may indirectly influence behavior because human-induced



habitat fragmentation has a profound effect on the spatial behavior of mammals due to the creation of patchy resource distribution and barriers that constrain animal movements (Campbell-Smith et al. 2011; Tolon et al. 2009; Vistnes et al. 2004).

Studies have highlighted considerable intraspecific variation in home range size of wild boar (*Sus scrofa*), but with no clear pattern with regard to sex and age-related differences, seasonal changes, and geographic location (Baber and Coblenz 1986; Boitani et al. 1994; Keuling et al. 2008b; Lemel et al. 2003; Massei et al. 1997; Russo et al. 1997; Singer et al. 1981). In mammals, it is predicted that changes in home range size are inversely related to population density ("density-dependent hypothesis"—Abramsky and Tracy 1980; Wood and Brenneman 1980) and food availability ("food-exploitation hypothesis"—Larter and Gates 1994). However, studies testing these hypotheses in wild boar populations reached conflicting conclusions (Bertolotto 2010; Massei et al. 1997).

Besides considerable variation in spatial behavior, temporal patterns can also be modified by several factors. Wild boars are active for approximately 12 h a day and their activity is mainly confined to dusk, dawn, and night (Boitani et al. 1994; Keuling et al. 2008a; Lemel et al. 2003; Massei et al. 1997; Russo et al. 1997; Singer et al. 1981). The duration and distribution of activity is affected by weather conditions (Lemel et al. 2003), habitat type (Boitani et al. 1994; Singer et al. 1981), and seasonality (daylight length, food availability; Keuling et al. 2008a). However, these studies were conducted in areas with high levels of human interference (e.g., hunting) and/or areas transformed by human activities, which may alter the natural behavior of the species. Information on wild boar ranging behavior and activity in undisturbed ecosystems is lacking.

In response to human activities, wild boar can adjust their spatiotemporal activity in an attempt to avoid human contact or to take advantage of the human-induced changes within the landscape. For example, wild boars have been shown to increase their nocturnal activity in response to increased hunting pressure and in proximity to human settlements (Keuling et al. 2008a). Furthermore, hunting pressure affects home range size (Maillard and Fournier 1995; Sodekat and Pohlmeyer 2001) and can cause temporary range shifts to ensure access to seasonal food resources offered by agricultural crops (Keuling et al. 2009).

In recent decades the wild boar numbers within Europe have increased significantly (Apollonio et al. 2010; Sáez-Royuela and Telleria 1986). This creates potential for serious conflicts between humans and wild boar in agricultural regions as well as densely populated rural and urban areas (Geisser and Reyer 2004). Several factors have been proposed that may have contributed to increase of wild boar densities, such as increasing global temperatures, more frequent mast fruiting events, as well as management practices that are ineffective in regulating population numbers (Bieber and Ruf 2005). However, the expansion of populations and their growth may be partially attributed to the behavioral plasticity of the species.

In this paper, we compared the activity and spatiotemporal behavior of wild boar populations in 2 contrasting environments differing in human pressure, namely one population inhabiting the primeval temperate forest of Białowieża (eastern Poland) and another inhabiting the metropolitan area of Cracow, the second largest city in Poland. These 2 areas differ in human pressure (both human presence and habitat structure), with high exposure in Cracow and low in primeval forest. This study is the first direct comparison between populations to investigate wild boar behavioral plasticity under contrasting conditions of human pressure and habitat structure. We hypothesized that, compared with primeval forest, wild boar within urban areas will have smaller home range sizes due to restricted space; show increased daily movement due to patchy resources; and exhibit increased nocturnal activity and ranging behavior to avoid human interference.

MATERIALS AND METHODS

Study area.—The study was conducted in 2 areas of Poland—Białowieża Primeval Forest in the eastern part of the country and a metropolitan area of Cracow in the south—characterized by profound differences in human pressure and habitat structure (Fig. 1). The Białowieża Primeval Forest (BPF)—located on the Polish–Belarusian border ($52^{\circ}47'N$, $23^{\circ}48'E$; $\sim 1,450 \text{ km}^2$)—is the last remnant of the European temperate lowland forest. Within Poland, BPF (600 km^2) is dominated by 3 main forest types, including a high proportion of old growth: pedunculate oak (*Quercus robur*), small-leaved lime (*Tilia cordata*), European hornbeam (*Carpinus betulus*) stands, mixed coniferous stands, and European ash (*Fraxinus excelsior*), black alder (*Alnus glutinosa*) stands.

The study area was located in the center of the Polish part of the BPF. The study area consisted of 92.6% forest, 7.2% open land (meadows, river valleys), and 0.2% anthropogenic areas (e.g., allotments)—Corine Land Cover database (European Environment Agency, <http://www.eea.europa.eu/>). Two-thirds of the study area was within the borders of the Białowieża National Park and its buffer zone, where hunting is prohibited, motorized traffic is allowed only under permission from the National Park, and forest managements are limited to sanitary cutting and fencing off regeneration areas. Tourists are restricted to day hikes on designated trails and overnight camping is prohibited. The remaining part of the study area is within the commercial part of the BPF, where limited logging and hunting occur. However, hunting from fixed locations is only permitted at a few designated sites. Motorized traffic in the commercial part of the BPF is allowed only for forestry service vehicles. Human density in the Polish part of the BPF is about 7 inhabitants/ km^2 and the density of roads accessible for 2-wheel-drive is about 1.2 km/km^2 in the commercial part of the forest (Theuerkauf et al. 2003). However, there was no human settlement in the close vicinity of the study area.

The density of the wild boar population is estimated to be 2.35 ind./ km^2 . In addition to wild boar, four other ungulate species occur in the forest, including red deer (*Cervus elaphus*),

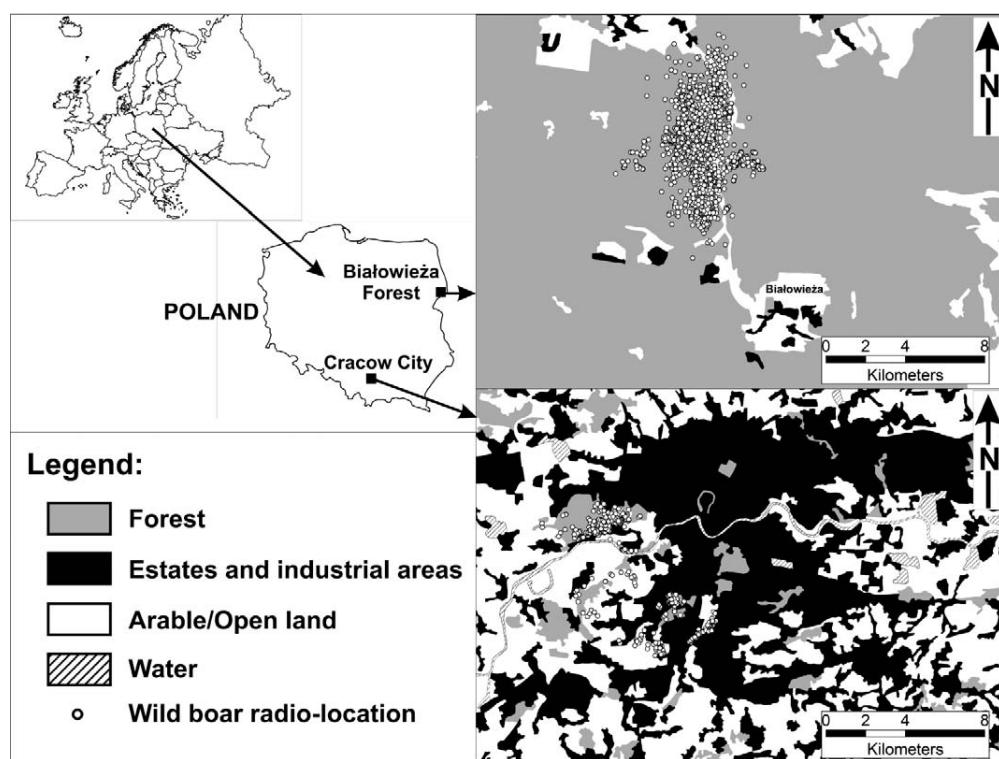


Fig 1.—Maps detailing location of the study areas in Poland and radiolocations of wild boars (*Sus scrofa*; all individuals) in the study areas. In Cracow City, areas occupied by radiotracked wild boar consisted of 18% forest, 43% arable/open land, and 39% estates and industrial areas, whereas in Białowieża Primeval Forest 92.6%, 7.2%, and 0.2%, respectively.

roe deer (*Capreolus capreolus*), moose (*Alces alces*), and the European bison (*Bison bonasus*). Two large carnivores, Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*), also occur in stable populations (Jędrzejewska and Jędrzejewski 1998). The climate is transitional between Atlantic and continental types, with stronger influence of the latter (Jędrzejewska and Jędrzejewski 1998). Mean January temperature is -4.1°C and the mean number of days with snow cover is 105 (Institute of Soil Science and Plant Cultivation, <http://www.zazi.iung.pulawy.pl/>). Annual precipitation ranges from 550 to 600 mm (Institute of Geography and Spatial Planning, Polish Academy of Sciences, <http://www.igipz.pan.pl/>).

The second study area, Cracow metropolitan area, is located in the south of Poland ($50^{\circ}1'N$, $19^{\circ}53'E$). Cracow is the second biggest city of the country, with an estimated human population of 750,000. Approximately one-third of the city area is covered with meadows, pastures, orchards, arable lands, parks, and woods. The wild boar population in this area is located in the peripheral part of the city and its habitat is a mosaic of woods, parks, open land (meadows, gardens, and agricultural fields), and anthropogenic areas (housing estates, warehouses, and industrial estates). Forests, covering 4% of the city, are mainly concentrated to the western part and largely consist of European beech (*Fagus sylvatica*) and pedunculate oak-dominated stands. Radiolocations were taken over a 40-km^2 area in the western part of the city and consisted of 18% forest, 43% open land, and 39% anthropogenic area (Corine

Land Cover database). Roe deer is the only other ungulate sympatric species within the city limits. Single-hunter hunts are permitted in the outskirts of the city and nearly one-half of the wild boar population is harvested annually. Wild boar population density is estimated to be 0.15 ind./km^2 within this area (unpublished data of the Institute for Nature Conservation, Polish Academy of Sciences, Cracow). Mean January temperature is -2.1°C and the mean number of days with snow cover is 62. Annual precipitation ranges from 650 to 700 mm (Institute of Climatology, Jagiellonian University, Cracow, <http://www.klimat.geo.uj.edu.pl/>).

Trapping and radiotracking.—Data were collected between February 2006 and December 2008. The same method was used to capture wild boar in both study areas: cage and wooden traps ($1.5 \times 1 \times 2 \text{ m}$) and large drop-net traps (Jędrzejewski and Kamler 2004) baited with maize. A combination of Zoletil (tilotamide and zolazepam) and Domitor (medetomidine) mixture (1:0.025 ratio) was administered intramuscularly to immobilize captured wild boar. Atipemazole hydrochloride (Antisedan) was used as an antidote (Kreeger 1997). In some instances a combination of ketamine and xylazine was used (1:0.05 ratio). Animals weighing less than 30 kg were only immobilized with ketamine (0.2 ml/kg) and were handled without being fully anesthetized. Finally, captured animals were fitted with ear-tag radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota, and Wagener Telemetriealanlagen, Cologne, Germany). Procedures used for capture and

immobilization followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and our research and handling protocol was approved by the Local Ethical Commission for Experiments on Animals in Białystok and Cracow, Poland.

Upon capture, wild boars were classified as juveniles (<12 months old; hereinafter referred to as juv.), subadults (12–24 months; referred to as subad.), or adults (>24 months; referred to as ad.) dependent on tooth eruption (Matschke 1967). However, because trapping mainly took place during winter months, when some animals were about to enter the next age class, individuals were assigned to their respective age classes during the tracking period for analytical purposes (e.g., juveniles captured at age of 10 months and tracked for 7 months would be considered as subadults). A total of 35 wild boar was radiotagged (BPF: 9 ad. and 8 subad. females, 3 ad. and 9 subad. males; Cracow: 2 ad. and 1 subad. females; 2 ad. and 1 subad. males), 26 of which belonged to 7 marked social groups (BPF: 24 ind. in 6 groups; Cracow: 2 ind. in 1 group). The remaining 9 individuals (BPF: 5; Cracow: 4) were either solitary or members of unmarked groups.

Radiotagged individuals were located 2–4 times per week with equal intensity during the day and night (G-test: $G_1 = 0.48$, $P = 0.49$). Consecutive locations were separated by at least 12 h to ensure independence of observations (Swihart and Slade 1985). The locations of individuals were determined on foot by recording at least 3 bearings for each triangulation using a 3-element Yagi antenna (Titley Scientific, Lawnton, Australia) and Yaesu FT-817 transceiver (Yaesu Musen Co., Tokyo, Japan). A vehicle was used to move about the study areas. The location of an individual was calculated from a given set of bearings and using the maximum likelihood estimator method described by Lenth (1981). Only location estimates with error ellipse ≤ 2 ha were included for further analysis, and the program LOAS (Ecological Software Solutions) was used to calculate positions from triangulation. Accuracy of triangulation was determined in the field by locating transmitters in known location (Harris et al. 1990). Mean estimated error between the known transmitter location and those obtained from telemetry was 153 ± 107 m ($\bar{X} \pm SD$, $n = 120$).

Throughout the study tagged individuals were monitored during 24-h continuous tracking sessions, when both location and the activity of individuals were recorded at 30-min intervals. Animals were tracked by a single person (6-h shifts) taking bearings approximately every 10 min from forest roads (BPF) or streets and park trails (Cracow). Continuous tracking followed methodology used by Kamler et al. (2007a,b). Individual activity was determined by assessing irregularities in signal strength when each bearing was taken (Boitani et al. 1994; Kenward 1987; Keuling et al. 2008a; Massei et al. 1997). Researchers listened to the signal for 1 min and classified wild boar as active if the signal was alternating in strength, or inactive when the signal was constant. Direct observations of radiotagged individuals confirmed that changes in signal strength were attributed to both traveling and on-site activity

(e.g., foraging), whereas constant signals indicated a lack of movement (e.g., resting).

Data analysis.—Wild boars were followed for 9.7 ± 3.16 ($\pm SD$, $n = 34$, min = 6, max = 18) months (BPF: 9.5 ± 2.8 , $n = 29$; Cracow: 11.0 ± 5.1 , $n = 5$) and 86 ± 39.4 (min = 35, max = 177) locations were collected per individual (BPF: 74 ± 27.7 , Cracow: 153 ± 28.8). To avoid underestimation of home range size, only those individuals tracked for >3 months and that yielded >30 locations were used in analyses. Using this threshold value we found no effect of increased tracking time or number of locations on home range size (Spearman's $r = 0.06$, $n = 34$, $P = 0.74$ and $r = 0.04$, $P = 0.81$, respectively).

We estimated home range size using two methods: local-convex-hull (LoCoH—Getz and Wilmers 2004) and minimum convex polygon (MCP). The LoCoH method has an advantage over classical methods, e.g., MCP, because hard boundaries and inaccessible areas within the home range (e.g., rivers, highways, buildings) are identified (Getz et al. 2007; Huck et al. 2008). Thus, home ranges are constructed in such a way that only the areas truly utilized by animals were included, which is of great importance for accurate estimation of home ranges in fragmented habitats, e.g., urban or agricultural areas. However, we included results obtained with MCP to allow for comparison with other studies (Table 1). Specifically, the adaptive LoCoH method (a -LoCoH) was used, because it is remarkably robust to deviations from the optimal value of the parameter a , and, compared with other LoCoH methods, is considered to be the superior method of estimating home range size (Getz et al. 2007). Value of a parameter was set at the greatest distance between any 2 points in a set of an individual's locations, as suggested by Getz et al. (2007). Huck et al. (2008) showed that a -LoCoH estimates home range size reliably with number of locations comparable with our sample sizes. Ninety percent isopleths were used for home range estimation as it was recently demonstrated that using isopleths greater than 90% can result in unreliable area estimates biased by sample size and sensitive to outliers (Börger et al. 2006).

During the study, 26 wild boars were monitored 71 times during continuous, 24-h tracking sessions. The number of sessions was distributed evenly across sex and age classes (ad. M: 20; subad. M: 15; ad. F: 20; subad. F: 16). Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) to reflect changes in climate, vegetation, and life cycle of wild boar. Continuous tracking was conducted during every season (winter: 12 sessions; spring: 23; summer: 17; autumn: 17). Using data collected from 24-h tracking sessions, the following parameters of the daily behavior were calculated: daily range size: using a -LoCoH and MCP. All locations were used under the assumption that they would reflect the actual area utilized within the 24-h period; daily distance traveled: sum of distances between consecutive locations; duration of activity: sum of active readings recorded at 10-min intervals (assuming each active reading = 10 min) over the 24-h period; diurnality: proportion of active readings during daylight (time from

Table 1.—Mean values of home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) in Cracow City and Białowieża Forest study areas, Poland, during 2006–2008.

	Białowieża Primeval Forest			Cracow City			<i>P</i> -value ^a
	<i>n</i> ^b	$\bar{X} \pm SD$	Min–max	<i>n</i>	$\bar{X} \pm SD$	Min–max	
Home range size (km ²)							
α -LoCoH 90%	29	2.2 ± 0.94	0.8–4.6	5	1.0 ± 0.60	0.6–2.1	0.044
MCP 90%	29	4.2 ± 2.51	0.9–9.9	5	3.9 ± 3.16	1.0–8.7	—
Daily range size (km ²)							
α -LoCoH 100%	20 (35)	1.0 ± 0.73	0.1–3.6	6 (36)	0.9 ± 0.64	0.1–2.5	—
MCP 100%	20 (35)	1.3 ± 1.36	0.1–7.3	6 (36)	2.4 ± 2.19	0.1–8.8	—
Daily distance traveled (km)	20 (35)	6.8 ± 2.56	2.5–16.4	6 (36)	12.9 ± 6.51	3.1–26.7	0.002
Activity duration (h/day)	20 (35)	11.2 ± 5.23	3.3–22.8	6 (36)	11.4 ± 1.70	7.2–14.9	0.299
Diurnality ^c	20 (35)	0.52 ± 0.24	0.0–1.0	6 (36)	0.1 ± 0.08	0.0–0.3	<0.001

^a If shown, *P*-value refers to parameter Area in the most parsimonious model for the given response variable.

^b Number of animals, in parentheses: number of 24-h continuous tracking sessions.

^c Percent of active fixes during daylight hours.

sunrise to sunset) compared with the total number of active readings during each 24-h period. Data were controlled for seasonal changes in day length, daylight-saving time changes, and difference of sunrise and sunset time between the study areas. Finally, the distribution of activity and speed of movement throughout the day were investigated in both study areas. For such analysis, data were pooled into 2-h intervals before the percentage of active locations and cumulative distances traveled was calculated for each interval within both study areas. All spatial and home-range analyses were conducted using R version 2.13.1 software (R Development Core Team 2011) and visualized in Arc View GIS 9.1 (ESRI, Redlands, California).

Statistical analyses.—Linear mixed models (Pinheiro and Bates 2000) were used to analyze relationships between dependent variables (home range size, daily range size, daily distance traveled, and duration of activity) and explanatory variables (study area, season, sex, and age of individuals). Factor “study area” incorporated differences between study areas due to combined effect of human pressure (human presence and activity, habitat structure). Mixed models were used because of the nonindependent nature of the data. When fitting models to home range size data, group ID was treated as a random factor because some individuals belonged to the same social groups (see subsection “Trapping and radiotracking). Similarly, in models used to analyze variables derived from continuous tracking sessions, individual ID was treated as a random factor because numerous animals were sampled more than once (on average, 2.9 sessions/ind.). The distribution of model residuals was checked for normality using the Shapiro–Wilk test. Data on daily range size were log-transformed to improve normality and reduce skewness. Diurnality data (proportion of active fixes during daytime) were arcsin transformed. Interactions between explanatory variables were included in each model. Akaike information criterion (AIC), with a second-order correction for small sample size (AIC_c), was used to rank models dependent on their fit (Burnham and Anderson 2002). Models with the lowest AIC_c values were considered to be the best-fit models, and models within 2 AIC_c units were considered of similar

quality to the most parsimonious model. All statistical analyses were conducted using R version 2.13.1 software (R Development Core Team 2011).

RESULTS

Spatial behavior.—Home range size estimates obtained using α -LoCoH and MCP were highly correlated, both in total home range and daily range (Spearman’s *r* = 0.73, *n* = 34, *P* < 0.001 and *r* = 0.80, *n* = 71, *P* < 0.001, respectively). Therefore, we restricted further analysis only to α -LoCoH estimates because they reflect area actually used by wild boar.

In Cracow City, average home range was less than half the size of that in BPF (Table 1). Variation in home range size of wild boar was best explained by differences between the 2 study areas (Tables 2 and 3). The model including only study area as an explanatory variable explained the variation in home range size better than other models, and accounted for 41% of the model weight (Table 2).

On a daily basis wild boar utilized areas of similar size in each study area (Table 1). However, in Cracow City daily occupied range constituted 90% of the total home range, whereas in BPF the daily range only covered 45% of the total home range. None of the explanatory variables sufficiently explained variation in daily range size. Consequently, the intercept-only model provided the best fit (Tables 2 and 3).

In Cracow City, daily distance traveled by wild boar was almost twice that of wild boar within the BPF (Table 1). On average, subadult wild boar covered 65% longer distances on a daily basis compared with adults ($\bar{X} \pm SD$; 12.6 ± 6.51 km, 8.1 ± 4.52 km, respectively). In Cracow City distances covered daily were lower during the spring compared with other seasons, whereas in BPF, contrastingly, daily movement distance was consistent during all seasons (Fig. 2a). The best model explaining variation in daily distance traveled included study area, age, season, and an interaction between study area and season (Table 2). Although overall effect of season was insignificant in the best model (Table 3), different seasonal effects between the study areas were identified, as indicated by a significant interaction term (Table 3).

Table 2.—Confidence set of mixed linear models ($\Delta\text{AIC}_c < 2$) for variables explaining home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas, Poland studied in 2006–2008. Included in the table are corrected Akaike information criterion (AIC_c) values and the difference between each model and the best-fitting model (ΔAIC_c), number of model parameters (k), and model Akaike's weights (ω_i). The models were ranked dependent on the AIC_c value and in descending order (the most parsimonious models are on the top of each list).

Response variable	Variables included in a model	k	AIC_c	ΔAIC_c	ω_i
Home range size	Area	4	79.98	0	0.412
	Area + Age	5	81.23	1.25	0.220
	Area + Sex	5	81.56	1.58	0.187
	Area + Age + Sex	6	81.64	1.66	0.180
Daily range size	Intercept	3	69.80	0	0.355
	Age	4	70.69	0.89	0.227
	Sex	4	71.64	1.84	0.141
	Area + Season + Area \times Season	10	71.65	1.85	0.140
Daily distance	Area	4	71.70	1.90	0.137
	Area + Age + Season + Area \times Season	11	1,361.74	0	0.484
	Area + Age + Season	8	1,362.55	0.81	0.322
Activity duration	Area + Age + Season + Sex + Area \times Season	9	1,363.58	1.84	0.193
	Season + Area + Area \times Season	10	363.56	0	0.404
	Season + Area + Age + Area \times Season	11	364.87	1.31	0.210
	Season + Area + Sex + Area \times Season	11	364.97	1.42	0.199
Diurnality	Season	6	365.10	1.55	0.187
	Area + Season + Area \times Season	10	-383.54	0	0.342
	Area + Season + Age + Area \times Season	11	-383.40	0.13	0.320
	Area + Season + Sex + Area \times Season	11	-382.29	1.25	0.183
	Area + Season + Age + Sex + Area \times Season	12	-381.95	1.59	0.155

Table 3.—Parameters and their statistics included in the most parsimonious model from the confidential set of models ($\Delta\text{AIC}_c < 2$), and with home range size, daily range size, daily distance traveled, duration of activity, and diurnality of wild boar (*Sus scrofa*) as response variables. All explanatory variables were factors and estimates for factor levels are presented in relation to: area (Białowieża), season (winter), and age (adult).

Response variable	Parameter	Coefficient	SE	t-value	P-value
Home range size	Intercept	2.29	0.27	8.44	<0.001
	Area (Cracow)	-1.20	0.54	-2.23	0.044
Daily range size	Intercept	-0.16	0.047	-3.52	<0.001
	Intercept	4,648.3	2,491.64	1.86	0.069
Daily distance	Area (Cracow)	9,775.4	2,856.52	3.42	0.002
	Age (Subadult)	2,978.5	1,092.78	2.72	0.009
	Area (Cracow \times spring)	-8,074.1	3,380.86	-2.39	0.022
	Area (Cracow \times summer)	-5,314.7	3,642.97	-1.46	0.153
	Area (Cracow \times autumn)	-3,708.0	3,587.29	-1.03	0.307
	Season (autumn)	3,075.6	3,024.32	1.02	0.315
	Season (summer)	1,465.4	2,757.31	0.53	0.598
	Season (spring)	460.8	2,761.82	0.17	0.868
	Intercept	9.61	1.80	5.33	<0.001
	Season (autumn)	6.14	2.04	3.01	0.004
	Area (Cracow \times autumn)	-6.73	2.30	-2.91	0.005
	Area (Cracow \times spring)	-3.55	2.09	-1.70	0.096
Activity duration	Area (Cracow \times summer)	-3.81	2.25	-1.69	0.098
	Season (spring)	2.82	1.78	1.58	0.121
	Area (Cracow)	2.58	2.42	1.07	0.299
	Season (summer)	0.78	1.81	0.43	0.666
	Intercept	0.058	0.0056	10.31	<0.001
	Area (Cracow)	-0.053	0.0071	-7.45	<0.001
	Season (summer)	0.054	0.0089	6.05	<0.001
	Season (spring)	0.044	0.0088	4.91	<0.001
	Area (Cracow \times summer)	-0.043	0.0117	-3.68	<0.001
	Area (Cracow \times autumn)	-0.039	0.0115	-3.39	0.002
Diurnality	Season (autumn)	0.030	0.0097	3.05	0.004
	Area (Cracow \times spring)	-0.026	0.0108	-2.42	0.021

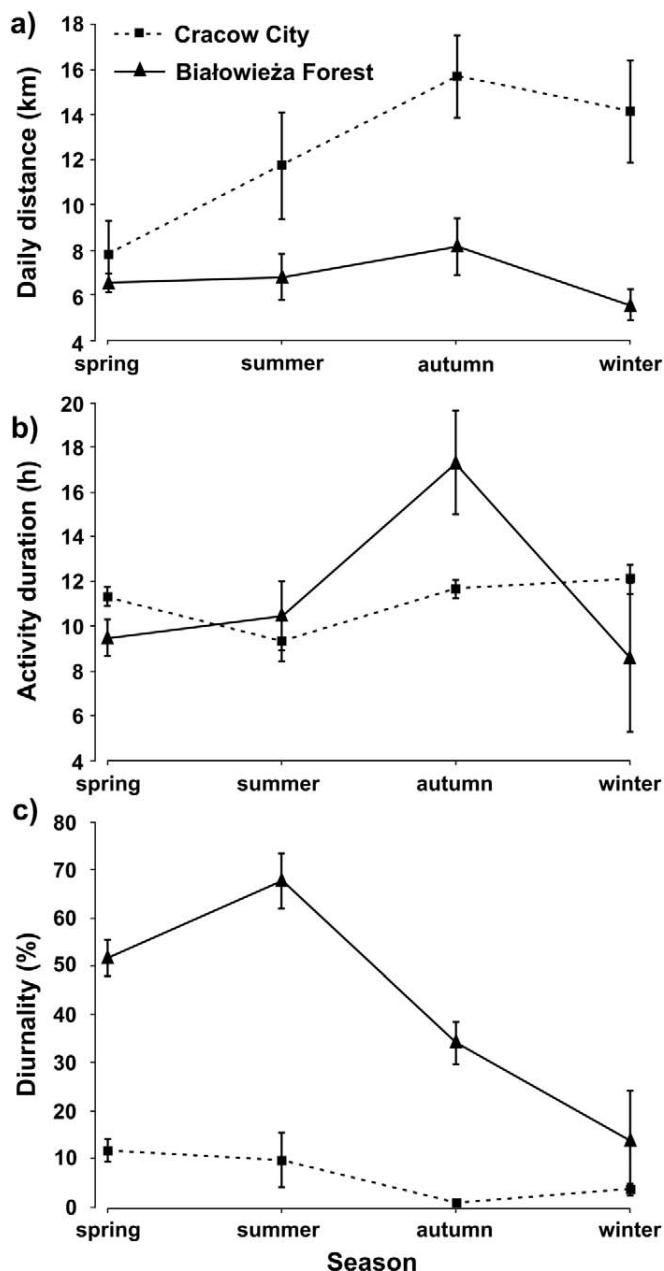


Fig 2.—Seasonal changes in mean values ($\pm SE$) of a) daily distance traveled, b) duration of activity, and c) diurnality (proportion of active fixes taken during daylight hours from total number of active fixes during 24-h period) of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas during 2006–2008.

Activity patterns.—Variation in duration of activity was largely driven by seasonal changes and the different effects of season in the 2 study areas (Tables 2 and 3). Specifically, seasonal variation in the duration of activity was a result of the wild boar in BPF being active for longer periods (by 5.7 h on average) in autumn compared with Cracow City (Fig. 2b, Table 3). During other seasons duration of activity was comparable between study areas (Fig. 2b, Table 3). Overall, differences

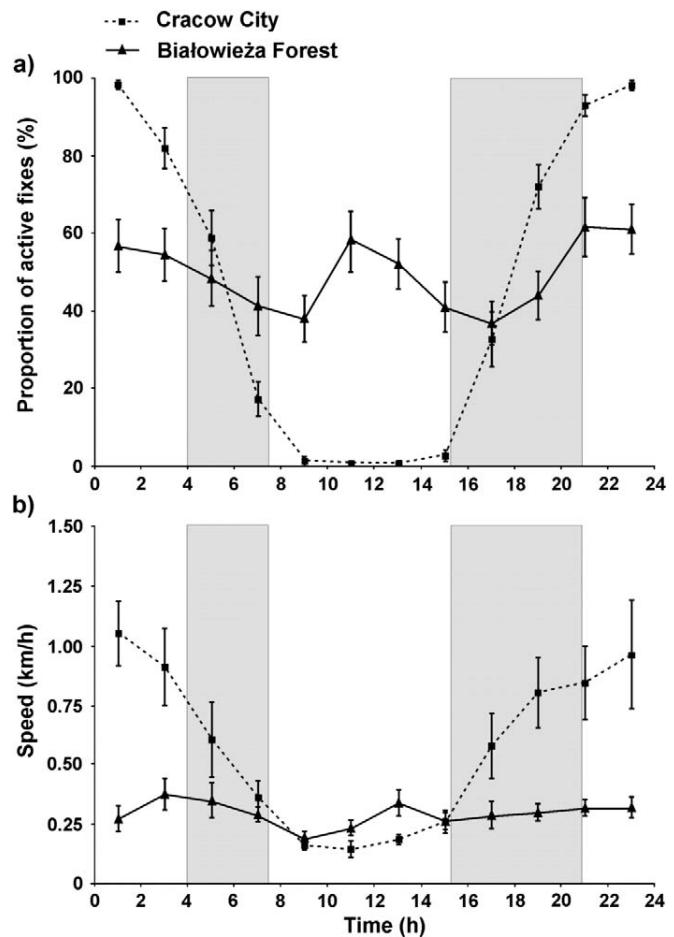


Fig 3.—Distribution of a) activity and b) speed of movement during 24-h period of wild boar (*Sus scrofa*) in Cracow City and Białowieża Primeval Forest study areas during 2006–2008. Mean ($\pm SE$) values are shown for 2-h time intervals. Shaded areas represent the shifting times for sunrise and sunset throughout the year.

between study areas did not contribute significantly to explained variation in activity duration (Tables 2 and 3).

Wild boars in BPF were more active during daylight compared with Cracow City, where they were virtually inactive during daylight (Fig. 3a, Table 1). Study area, season, and an interaction between study area and season were included in the best model describing variation in diurnality (Table 2). Furthermore, seasonal changes in diurnality contributed significantly to explained variation of this parameter (Fig. 2c, Table 3). Effect of season on daytime activity was particularly strong in BPF, with the lowest values observed during winter (Fig. 2c, Table 3).

In BPF, activity was evenly distributed throughout the 24-h period (Kruskal–Wallis $H_{11,409} = 18.16, P = 0.078$; Fig. 3a), whereas in Cracow City activity was concentrated to crepuscular and dark hours (Kruskal–Wallis $H_{11,421} = 375.98, P < 0.001$; Fig. 3a). A similar pattern was observed with regard to speed of movement. Movements were uniformly distributed throughout the day in BPF, but not in Cracow City (Kruskal–Wallis $H_{11,409} = 15.13, P = 0.18$; $H_{11,421} = 106.01, P$

< 0.001, respectively; Fig. 3b). Finally, the proportion of active fixes within 2-h intervals in Cracow City was correlated with the speed of movement (Spearman's $r = 0.97$, $P < 0.001$), whereas in BPF, activity was not significantly associated with movement (Spearman's $r = 0.44$, $P = 0.15$).

DISCUSSION

This study demonstrated high behavioral plasticity in wild boar living in 2 contrasting areas differing in human pressure, both direct human presence and indirect human-induced habitat changes. Wild boar inhabiting urban areas occupied smaller home ranges, were more mobile on a daily basis, and were more nocturnal when compared with the population inhabiting a primeval forest characterized by low levels of human pressure. In contrast, daily duration of activity and daily range size were comparable between both study areas. Some behavioral parameters (daily distance traveled, activity duration, and diurnality) were affected by seasonal changes, although the effects were different in the 2 study areas. Seasonal effects were stronger in the BPF compared with the urban area of Cracow City. However, because our study was based on a relative small number of individuals that were also unevenly distributed between the study areas, our results should be interpreted with caution.

Spatial behavior in areas with low and high human pressure.—In contrast to the continuous forest habitat of BPF, the urban area of Cracow City provides patchy habitat with dispersed resources (e.g., food, resting, and breeding sites). This difference in habitat structure most likely contributed to contrasting spatiotemporal patterns observed between both study areas. Within the urban environment wild boar had to cover distance almost twice as long as those in primeval forest to meet their daily energetic requirements, as well as to locate shelter for long periods of diurnal inactivity. Interestingly, wild boar showed similar seasonal patterns in both areas, except during spring when a reduction in daily distance traveled was observed in Cracow City. Spring is the breeding season for wild boar (Fernandez-Llario and Carranza 2000; Jędrzejewska and Jędrzejewski 1998) and restricted daily movement could be a result of parturition and weaning of offspring (females yielded 65% of data for this season), as detailed in Spitz and Janeau (1990).

Wild boar is a generalist omnivore with opportunistic feeding habits, and its diet reflects local environmental conditions (Herrero et al. 2006; Schley and Roper 2003). Consequently, wild boar can take advantage of a variety of food resources offered by urban environments (e.g., crop fields, metropolitan parks and forests, garbage dumps, and orchards). In contrast to BPF, where food abundance is seasonally variable (Jędrzejewska and Jędrzejewski 1998), urban environments provide relatively high and constant food resources, which could explain the smaller home ranges observed in Cracow City. Therefore, our result may support the “food-exploitation hypothesis,” which predicts an inverse relationship between food abundance and home range size (Larter and

Gates 1994). However, in this study we did not quantify food resource abundance. Besides food abundance, habitat fragmentation could also contribute to smaller home ranges observed in the urban area.

Wild boar in BPF occupied daily ranges that constituted less than half (45%) of their total home range, whereas in Cracow City almost the entire home range (90%) was covered on a daily basis. A potential explanation could be that wild boar in the BPF shift their ranges spatially according to spatiotemporal changes in food resources, which is similar to shifts described by Keuling et al. (2009) for wild boar in Germany.

No effect of study area, season, sex, or age on daily range size was detected in our study. Other studies have had similar findings, e.g., the lack of seasonal and sexual differences in daily range size were reported in a study from Italy (Russo et al. 1997). However, variation in daily range size may also be shaped by subtle site-specific factors (e.g., daily ambient temperature—Kamler et al. 2007a), which were not included in our group of robust explanatory variables.

Activity patterns in areas with low and high human pressure.—In both study areas wild boars were active for similar periods of time (~11 h/day), which suggests that individuals had to balance comparable energy budgets. However, there was a remarkable difference between the distributions of activity throughout the day among the 2 habitats. Wild boar in the urban area exhibited crepuscular and nocturnal activity, which could have been a strategy of avoiding interference with humans. This finding is consistent with other studies investigating urban mammal populations (wild boar in Barcelona, Spain—Cahill et al. 2003; red fox [*Vulpes vulpes*] in Oxford, United Kingdom—Doncaster and Macdonald 1997). Furthermore, activity was strongly associated with movement, which suggests that wild boar visited numerous food patches and spent relatively little time foraging on one patch before finding secluded sites for daytime resting. In contrast, activity of wild boar in the primeval forest was evenly distributed throughout the 24-h period and showed a polyphasic pattern characterized by alternating phases of activity and resting. Interestingly, similar patterns have been found in other ungulates inhabiting BPF (red deer—Kamler et al. 2007b; European bison—Caboń-Raczyńska et al. 1987). However, in those species the alternating peaks of activity and resting are attributed to the foraging habits of ruminants (food intake and regurgitation), which is not the case in wild boar. High level of diurnality observed in the BPF was possibly caused by very limited hunting pressure in this area, as it had been shown that high hunting pressure increased nocturnal activity of wild boar (Keuling et al. 2008a). Thus, observed activity patterns, as well as high activity during daylight hours, are likely a consequence of low levels of human activity. Wild boar in the BPF showed mainly on-site activity, as suggested by a nonsignificant relationship between activity and speed of movement, and this can be explained by uniformly distributed and readily available resources (food, water, and resting sites) that minimize the need for extensive movement.

Wild boars from BPF were active for exceptionally long periods during the autumn when compared with other seasons, as well as to Cracow City. Two interacting factors may be responsible for this pattern. First, the severity of winter has been shown to be a main factor affecting survival and reproduction of wild boar (Geisser and Reyer 2005; Jędrzejewska and Jędrzejewski 1998). Therefore, achieving good body condition and gaining fat reserves before winter is crucial for wild boar survival. Second, the acorn crop occurring in autumn is the most efficient way to obtain sufficient fat reserves within the BPF (Jędrzejewska and Jędrzejewski 1998), explaining the higher activity observed in autumn. In contrast, no seasonal effect was observed for this parameter in Cracow City, which may indicate that urban environments provide stable, season-independent food resources. Alternatively, the milder climate within the city may reduce the requirement for gaining crucial fat reserves.

In the BPF, wild boar co-occur with 2 natural predators, wolf and lynx. However, predation constitutes a relatively small portion of natural mortality of wild boar in the area, only 19% from wolf and 1% from lynx (Jędrzejewska and Jędrzejewski 1998). Predation risk affects spatiotemporal behavior at various scales and may lead to, e.g., reduced locomotory activity and range size, and changes in habitat use (Borkowski and Owadowska 2010; Valeix et al. 2009). However, literature on spatiotemporal response of wild boar to predation risk is lacking. In our study, we could not quantify the effect of predation and separate it from other factors (low human pressure, habitat structure). Season also had strong effects on the proportion of time wild boars were active during daylight hours (diurnality). This effect was particularly pronounced in the BPF. It was apparent that seasonal changes in levels of diurnality mirrored seasonal changes in day length. Diurnality, with regard to our calculations, was a relative measure giving proportion of the total amount of activity during a 24-h period allocated to daylight hours. Therefore, it is sensitive to varying day length, especially when duration of activity is constant throughout the year, which was found to be the case in our study (except for autumn in the BPF). Overall, levels of diurnal activity within the urban area were much lower than those in the primeval forest (usually below 10% of total daily activity time). Moreover, urban populations maintained nocturnal activity almost irrespective of season, whereas forest population followed natural changes in day length. This difference may demonstrate effect of human pressure on activity patterns of wild boar.

In summary, our study showed that wild boar can adjust their spatiotemporal behavior to local conditions. The spatial behavior and activity of wild boar population inhabiting primeval forest seemed to be mainly driven by seasonal changes in food availability and abiotic conditions, whereas human activity shaped spatiotemporal patterns of the urban population.

Densities of wild boar have been increasing over the last decades within Europe (Apollonio et al. 2010; Geisser and Reyer 2004; Sáez-Royuela and Telleria 1986). Additionally, this expansion is accompanied by invasion of new habitats densely

populated by humans (Cahill et al. 2003; Fisher et al. 2004), including urban areas that may offer new unexplored niches. Several factors have been proposed to explain demographic expansion of wild boar (Bieber and Ruf 2005). Until now, however, behavioral plasticity of the species has not drawn much attention, although it may play an important role in this process.

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