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Experience shapes wild boar spatial response to drive hunts

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Human-induced disturbances of the environment are rapid and often unpredictable in space and time, exposing wildlife to strong selection pressure favouring plasticity in specific traits. Measuring wildlife behavioural plasticity in response to human-induced disturbances such as hunting pressures is crucial in understanding population expansion in the highly plastic wild boar species. We collected GPS-based movement data from 55 wild boars during drive hunts over three hunting seasons (2019–2022) in the Czech Republic and Sweden to identify behavioural plasticity in space use and movement strategies over a range of experienced hunting disturbances. Daily distance, daily range, and daily range overlap with hunting area were not affected by hunting intensity but were clearly related to wild boar hunting experience. On average, the post-hunt flight distance was 1.80 km, and the flight duration lasted 25.8 h until they returned to their previous ranging area. We detected no relationship in flight behaviour to hunting intensity or wild boar experience. Wild boar monitored in our study showed two behavioural responses to drive hunts, “remain” or “leave”. Wild boars tended to “leave” more often with increasing hunting experience. Overall, this study highlights the behavioural plasticity of wild boar in response to drive hunts.

Keywords Human disturbance, GPS tracking, Spatial behaviour, *Sus scrofa*

INTRODUCTION

One of the adaptations evolved to deal with environmental variability is phenotypic plasticity^{1,2}, which is the ability of a single genotype to produce alternative phenotypes in a changing environment³. In contrast to other adaptation mechanisms, such as individual variation in personalities⁴, phenotypic plasticity develops quickly within an animal's life cycle^{5,6}. In the Anthropocene, animals are increasingly facing novel environmental challenges due to human-induced rapid environmental changes (HIREC)⁷, such as deforestation⁸, urbanisation⁹, climate change¹⁰, introductions of novel predators or parasites¹¹, habitat fragmentation^{12,13}, or harvest¹⁴ including game hunting^{15,16}. These HIRECs create less predictable spatial and temporal environments than natural ones. Animals can cope with such varying conditions through behavioural plasticity^{1,6}. Behavioural plasticity involves the interaction between innate behavioural response and learning, which is the behavioural adjustment to a novel environment^{17,18}.

Behavioural plasticity is particularly important when animals need to make decisions in an environment which poses a risk of predation¹⁹, i.e. in the landscape of fear²⁰. Based on previous experience, animals can adjust their behavioural patterns to the perceived risk of predation or even develop new anti-predatory responses²¹ to increase the probability of survival^{18,22}. Besides behavioural plasticity, different personality traits in animals contribute to the success of survival in prey^{23,24}. Shy individuals are more likely to be hunted by ambush predators whereas bold individuals express higher mortality rate with active predators²³. As natural predators are absent from many human-dominated areas, hunting by humans has become the most important mortality factor for many species^{25,26}. Hunting can exert selection on morphological^{27,28} and behavioural traits^{29–31}. In addition, different hunting methods, varying in intensity of disturbance, can cause various behavioural reactions in hunted species³². Drive hunts, involving multiple hunters, beaters and dogs at a time, are a particularly efficient hunting method and can cause strong disturbance in a local population and influence the anti-predatory behaviour of surviving individuals involved in the hunt^{33,34}. Dogs are used during drive hunts to flush out hunted game species. The increased vigilance in sika deer scared by dogs in Japan resulted in a lower hunting efficiency in the following year. Conversely, hunting efficiency remained equal over the years for hunted animals in traps as no

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flee response was triggered³⁵. Thurfjell et al.¹⁸ showed the importance of behavioural plasticity in rifle and bow hunting events over the lifetime of a prey species. For example, female elk improve the probability of survival through learned behavioural changes in movement during the hunt¹⁸. Spatial changes in landscape use may also be accompanied by temporal changes in landscape use to avoid potential contact with hunters³⁶. For example, white-tailed deer were more active at night after a hunt than during the day in the vicinity of feeding sites³⁷. When animals are exposed to a hunting threat, two different behavioural responses are generally observed: (i) animals temporarily or permanently flee from the hunted area or (ii) hide and remain in the hunting area^{15,38}.

While hunting can be an efficient tool for population control of wildlife^{39,40}, some species seem to expand despite a high hunting bag. The success of those species has been attributed to species-specific features such as plasticity in the diet, selection of breeding sites, habitats, and behaviour in human proximity⁴¹. The wild boar (*Sus scrofa*) is one of the few mammal species that fulfil those plastic features^{42–44}, and its successful population expansion worldwide may be partially attributed to their plasticity^{45,46}. In response to drive hunts, wild boar adjusts their spatial behaviour to varying degrees of hunting pressure¹⁵, shift the area of their resting range⁴⁷, temporarily or permanently escape from the hunted area⁴⁸, and increase nocturnal activity⁴⁹. Wild boar remain in low-quality “refuge” areas during the hunting season due to higher perceived risk of being killed in relation to the benefits of obtaining quality food⁵⁰. Hunting is the main management tool to control populations of wild boar³² and seems to be the most effective compared to other management practices, e.g. supplementary feeding or fencing⁵¹. Due to high levels of population control through hunting, wild boar are an excellent species for studying behavioural plasticity to the risk of hunting.

This study analyses the behavioural response of GPS-collared wild boar exposed to drive hunts. We hypothesised that (i) the behavioural response to drive hunts would reflect avoidance behaviour towards disturbance and would be related to hunting intensity (HI), and that (ii) the spatial response to drive hunts would change with increasing experience, i.e., the number of hunts a wild boar experienced (WBE) throughout the season. We expected to observe (i) an increase in daily travel distance and range size following hunting, reduced daily overlap with the hunted area, and magnitude of flight behaviour proportional to hunting intensity (HI), and (ii) the proportion of “flee” and “remain” strategies shifting with accumulated experience throughout the hunting season, reflecting behavioural plasticity of individuals.

Results

Space-use and movement pattern

We compared movement and space use on “the day before the hunt”, “the day of the hunt”, and “the day after the hunt” for all individuals with a daily range, which overlapped the hunting area ($n_{\text{ind.}} = 37$) (Fig. S2). The daily distance and the daily range were significantly greater on “the day of the hunt” (mean daily distance 7.99 km; Confidence Interval (CI) 95% 5.93–10.06, mean daily range 2.4 km²; CI 95% 1.95–2.84, respectively), compared to “the day before” (mean daily distance 5.02 km; CI 95% 3.51–6.53, mean daily range 0.99 km²; CI 95% 0.72–1.26, respectively; pairwise-Wilcoxon tests p value < 0.001 for both metrics; Fig. S1). The values on “the day of the hunt” were also greater when compared to the day “after the hunt” (mean daily distance 5.30 km; CI 95% 4.64–5.97, mean daily range 1.82 km²; CI 95% 1.26–2.38, respectively) in the daily distance (pairwise-Wilcoxon tests, p value = 0.006) and the daily range (pairwise-Wilcoxon tests, p value = 0.012) (Fig. S2). The daily range overlap to the hunting area decreased significantly on “the day of the hunt” compared to the “day before the hunt” (pairwise-Wilcoxon tests, p value < 0.001) and did not differ between “the day of the hunt” and “the day after the hunt” (pairwise-Wilcoxon tests, p value = 0.987). We compared the movement and space use of wild boars that were GPS-collared in the area close to the hunt but with daily ranges non-overlapping with the hunting area (i.e. the control group). The control group did not display differences in daily range between the three experimental days (Kruskal–Wallis chi-squared = 5.8995, $df = 2$, p value > 0.05) (Fig. S2). There was no difference in the daily distance (pairwise-Wilcoxon tests, p value = 0.569) and daily range (pairwise-Wilcoxon tests, p value = 0.076) on “the day before the hunt” between the wild boar from the overlap and no-overlap (control) group.

We found that WBE significantly affected each response variable in all three models built for daily distance, range and overlap with the hunting area (Table 1, Fig. 1). The daily distance increased by 0.59 km, and the daily range increased by 0.31 km² per hunting event experienced by an individual. The daily range overlap with the hunting area decreased by 2.5% per WBE. In contrast, HI and the HI interacting with WBE did not affect any of the three response variables (Table 1).

Post-hunting flight response, average, and maximum flight distance and flight duration was not influenced by HI nor by WBE (Table 2). The average flight distance was 1.80 km (CI 95% 1.40–2.20), the average maximum flight distance was 2.2 km (CI 95% 1.70–2.60), and the average flight duration was 25.8 h (CI 95% 10.0–41.53) (Fig. 2).

Behavioural variation

In the cluster analysis, we detected two different categories of spatial responses among wild boars involved in the hunts ($n_{\text{wb ind.}} = 30$): “Remain” or “Flee” (Fig. 3). Each strategy differed in the four-movement and space use parameters used for the cluster analysis. In the “Flee” cluster, the average values “day of the hunt” increased in daily distance (by 0.624 km), range size (by 0.575 km²), and centroid distance (by 0.331 km) while the overlap of daily range size and hunting area decreased (by –0.5%) as compared to the day “before the hunt”. In the “Remain” cluster, the average values “day of the hunt” decreased in the daily distance (–0.912 km), range size (–0.840 km²), and centroid distance (–0.484 km) while the overlap of daily range size and hunting area increased (0.73%). Our binomial model indicated that wild boars are more likely to adopt the “Remain” strategy during their first hunting experience (“Remain” $n_{\text{ind.}} = 18$; “Flight” $n_{\text{ind.}} = 12$), but gradually switched strategy to “Flee” as their experience increased (Predictors Odds Ratios: WBE 1.60; CI 95% 0.94–2.70; p value = 0.081). After the first hunting

Coefficient	(A) Daily distance difference			(B) Daily MCP difference			(C) Daily overlap distance		
	Estimates	<i>p</i> value	CI 95%	Estimates	<i>p</i> value	CI 95%	Estimates	<i>p</i> value s	CI 95%
(Intercept)	0.40	0.006	0.12–0.68	0.26	0.002	0.09–0.43	–0.01	0.370	–0.03–0.01
HI	0.07	0.509	–0.13–0.27	0.12	0.123	–0.03–0.26	0.01	0.296	–0.00–0.02
WB Experience	0.62	<0.001	0.41–0.84	0.29	0.001	0.12–0.46	–0.02	<0.001	–0.03 to –0.01
HI*WB Experience	–0.14	0.200	–0.36–0.08	–0.11	0.195	–0.28–0.06	0.00	0.813	–0.01–0.01
Random effects									
σ^2	7.09			4.35			0.02		
$\tau_{00_{\text{AnimalID:Area}}}$	0.53			0.09			0.00		
$\tau_{00_{\text{Area}}}$	0.00			0.00			0.00		
ICC	0.07			0.02			0.02		
N_{AnimalID}	53			53			53		
N_{Area}	4			4			4		
Observations	980			980			980		
Marginal R2/ Conditional R2	0.034/0.102			0.016/0.037			0.024/0.043		

Table 1. Effect of wild boar experience (WBE) and hunting intensity (HI) on three estimated spatial response variables in four hunting areas in the Czech Republic and Sweden: (A) Difference in the daily distance of the “day before the hunt” and “day of the hunt” in km (B) Difference in daily range size of the day “before the hunt” and “day of the hunt” in km² (C) Difference of the daily range size overlapping with the hunting area of the day “before the hunt” and “day of the hunt”. Estimates and ninety-five per cent confidence interval (CI 95%) are the values for the three response variables according to linear mixed models (LMM). Bold values indicate a significant test ($p < 0.05$).

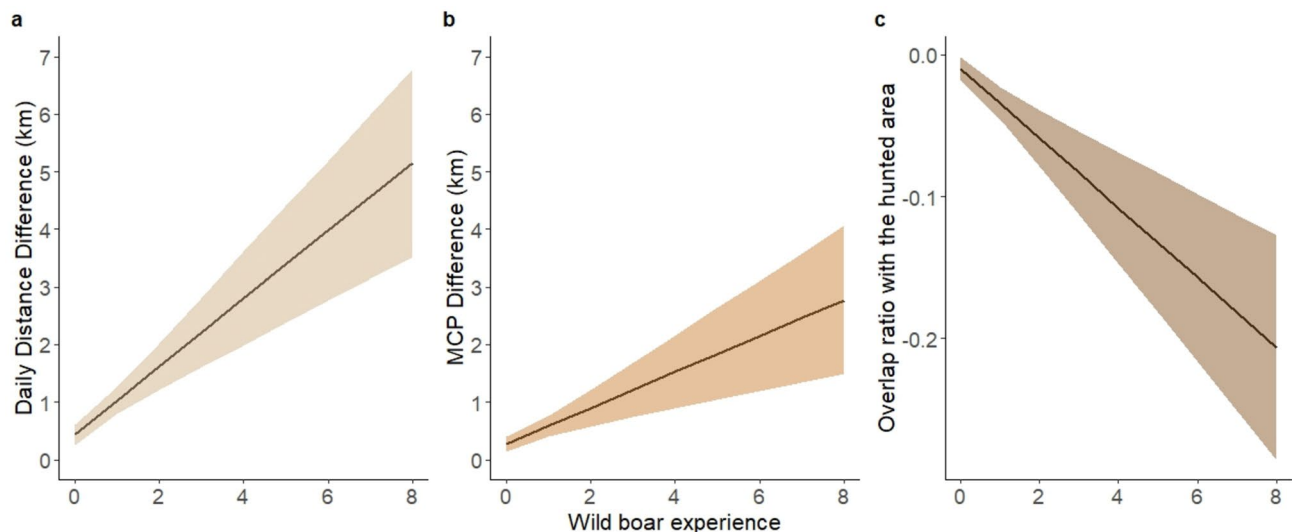


Fig. 1. Movement and space use response of wild boar ($n = 53$) in four hunting areas in the Czech Republic and Sweden to drive hunts as a function of wild boar experience (WBE) as predicted by the linear mixed model (LMM). Ninety-five per cent confidence intervals are shown as shaded areas: (A) Difference in the daily distance of the day “before the hunt” and “day of the hunt” in km (B) Difference in daily range size of the day “before the hunt” and “day of the hunt” in km² (C) Difference of the daily range size overlapping with the hunting area of the day “before the hunt” and “day of the hunt”.

experience, the probability of switching the strategy for a wild boar is estimated to be around 12%. Twenty-two individuals (73%) maintained their initial strategy throughout the hunting season while seven individuals (23%) switched the strategy from “Remain” to “Flee” with accumulated experience and one individual (3%) from “Flee” to “Remain” strategy. Wild boar with high levels of experience (> 4 hunts) were represented in both clusters. However, 75% of the wild boars that had more than 4 hunting experiences showed a change in strategy.

Coefficient	(A) Flight distance mean (km)			(B) Flight distance max. (km)			(C) Flight duration (h)		
	Estimates	<i>p</i> value	CI 95%	Estimates	<i>p</i> value	CI 95%	Estimates	<i>p</i> value	CI 95%
(Intercept)	3193.53	< 0.001	1729.89–5895.53	3834.55	< 0.001	2155.27–6822.27	80.23	< 0.001	12.18–528.42
HI	0.87	0.346	0.64–1.17	0.83	0.355	0.56–1.23	1.87	0.295	0.58–6.00
WB Experience	1.01	0.726	0.95–1.07	0.98	0.597	0.91–1.06	0.88	0.207	0.71–1.08
HI*WB Experience	1.04	0.517	0.93–1.15	1.05	0.519	0.91–1.21	1.85	0.468	0.56–1.31
Random effects									
σ^2	0.08			0.13			0.99		
$\tau_{00_{\text{AnimalID:Area}}}$	0.03			0.03			0.16		
$\tau_{00_{\text{Area}}}$	0.32			0.24			3.08		
ICC	0.81			0.67			0.77		
N_{AnimalID}	24			24			24		
N_{Area}	4			4			4		
Observations	68			68			68		
Marginal R2/ Conditional R2	0.008/0.815			0.020/0.677			0.024/0.829		

Table 2. Effect of wild boar experience (WBE) and hunting intensity (HI) on three estimated flight response variables in four hunting areas in the Czech Republic and Sweden: (A) Average flight distance in km (B) Maximum flight distance in km (C) Flight duration in hours (h). Estimates and ninety-five per cent confidence interval (CI 95%) are the values for the three response variables according to generalised linear mixed models (GLMM). Bold values indicate a significant test ($p < 0.05$).

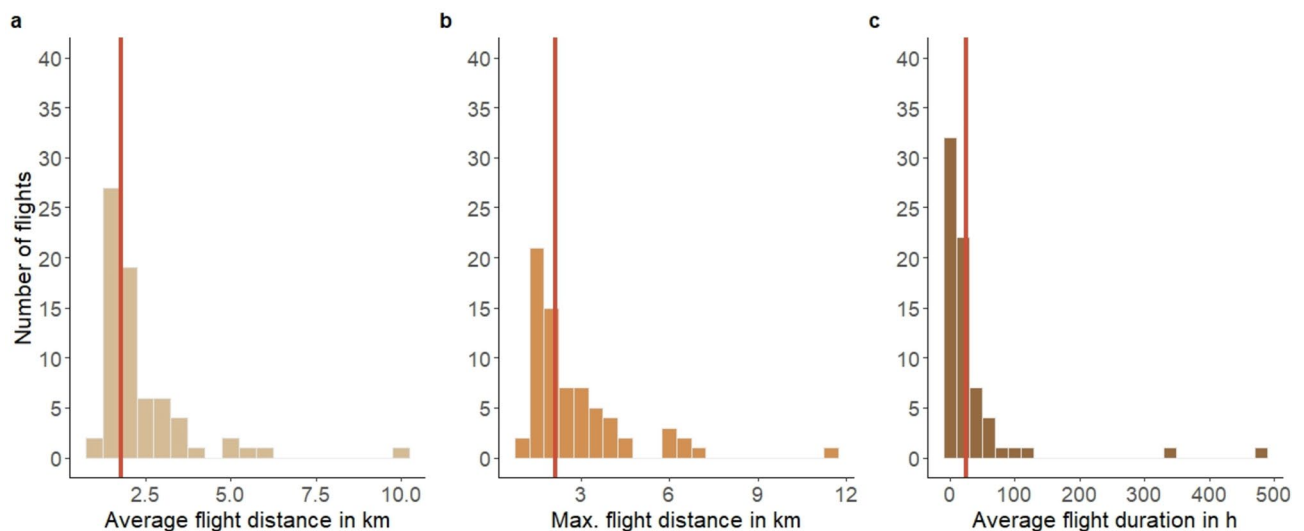


Fig. 2. Hunting-induced flight behaviour of wild boar in four hunting areas in the Czech Republic and Sweden. The red vertical line indicates the average value: (A) Average flight distance in km, (B) Maximum flight distance in km, and (C) Average flight duration in hour.

Discussion

Space-use and movement patterns

Our study indicates that drive hunts affect the spatial behaviour of wild boar. However, only those animals directly involved in the drive hunts showed a change in spatial behaviour. Compared to wild boar not involved in the hunts (control group), animals located within the drive hunt increased daily range size by 59% and daily distance by 41%. The effect of drive hunts on the spatial behaviour of wild boar has been analysed in several studies, but the results were inconsistent. In Germany, no changes in the home range size were observed^{48,52}. In contrast, in France and Sweden, an increase in home range size and movement was observed during drive hunts^{15,53}. However, the core area of the home range always remained the same, with no effect on the distribution of individuals⁵³. Drive hunts in Italy caused instability in space use, reflected in larger ranges and greater dispersion of resting sites⁵⁴. Resting ranges were larger and more interspersed in wild boar groups exposed to

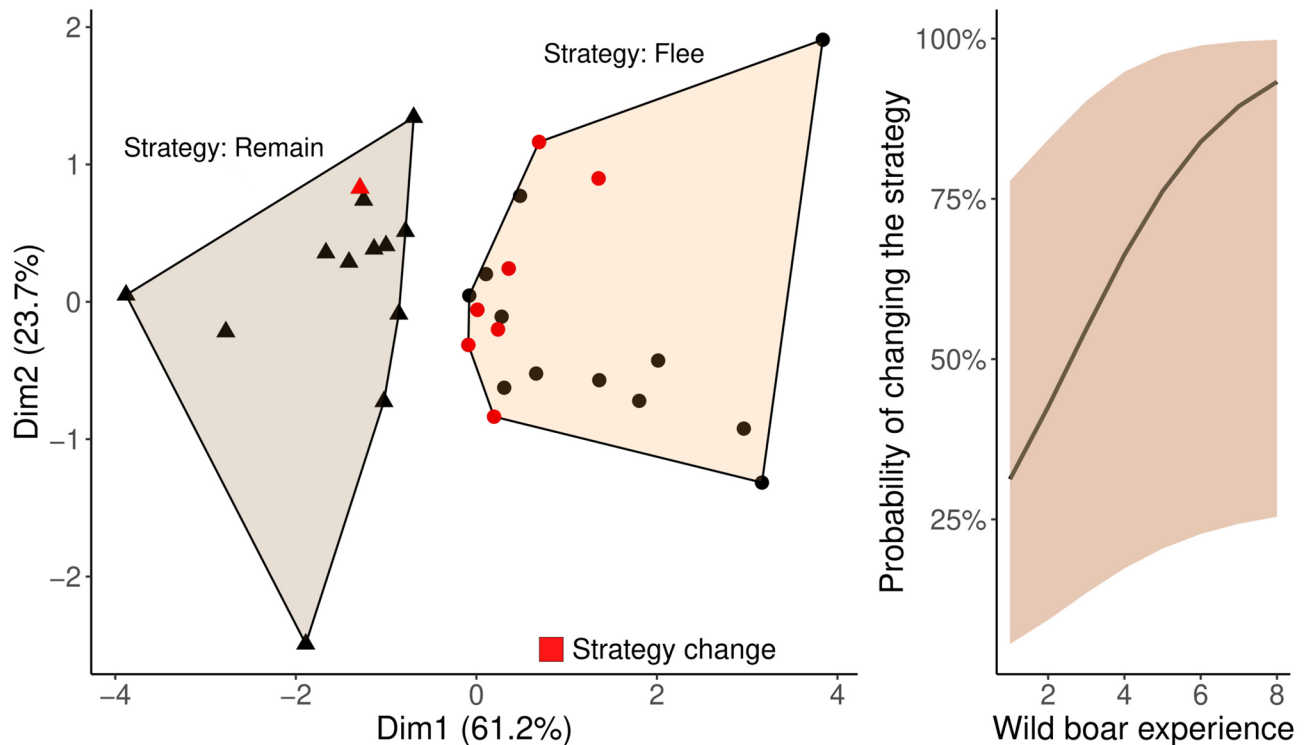


Fig. 3. Clustering of movement and space use similarities of wild boar in responses to drive hunts in four hunting areas in the Czech Republic and Sweden. Circles and triangles represent individuals and red-filled objects are individuals which changed their strategy with an increasing number of experienced hunts.

frequent drive hunts⁵⁴. However, similar to our study, Scillitani et al.⁵⁴ observed that only individuals directly involved in the hunts tended to change their spatial behaviour to hunting disturbance.

Levels of disturbance induced by different types of hunts are important when measuring changes in spatial behaviour. Likewise, variations in frequency and intensity occur within a type of hunt³². Our analyses showed that wild boar did not express different spatial responses during drive hunts of varying intensity (i.e., number of hunters and beaters combined) ranging from 0.68 to 148.28 people per square kilometre. It is possible that hunting disturbance in the immediate vicinity of the focal individual triggers behavioural response and thus makes the total size of the drive irrelevant. However, it seems that the frequency of drive hunts within the study area can change the spatial response of wild boar. With an increasing number of experienced hunts during a hunting season, wild boars showed an increase in daily range size, daily distance, and decreased range overlap with the hunted area. These spatial responses can be collectively described as an anti-predator response based on experience⁵⁵. White-tailed deer, which experience greater hunting pressure on weekends, decreased their movement rate, net displacement and activity on Sunday after encountering hunters multiple times⁵⁶. After experiencing foxes as predators, tamar wallabies showed an anti-predator response by increasing movement rates in the presence of foxes followed by a prolonged increase in vigilance⁵⁷. We must emphasise, however, that the wild boar in our study might have gained experience with hunting events before being GPS-collared, i.e. in the previous hunting season. Pre-experiences might have impacted the direction of the anti-predator response.

Behavioural variation

The type of behavioural response to drive hunts can depend on various external factors, such as the vegetation cover³³, the intensity of drive hunts, or prey group size. Wildlife primarily displays a remain rather than a flee strategy in dense habitats with reduced visibility during drive hunts, mitigating the detection probability by beaters and dogs³³. A flee strategy is favoured in open habitats, where beaters more easily detect game species and shelter is limited^{33,58}. We detected the occurrence of both “remain” and “flee” strategy in wild boar. While we could not test for the effect of habitat structure, we found that the effect of HI for the change of strategy was not decisive. The group size of prey might affect behavioural response to hunting events. For example, large groups of zebras and Thomson’s gazelles showed a stronger anti-predator response towards humans by increasing the distance from human observers than small groups. Similarly, smaller wild boar groups might be less prone to “remain” in the hunting areas and display a stronger flight reaction⁵⁹. Besides external factors, internal factors such as differences in personality, cause animals to use different habitats with unequal predation risk²³. For example, bold animals spend more time in risky areas with energetically advantageous rich food patches while shy animals prefer to stay in safe habitats with shelter but with lower food supply²³. Therefore, the strategy adopted during a drive hunt should also vary with individual personalities. Largespring mosquitofishes with active and exploratory personalities had a greater ability to escape from novel predators⁶⁰. While we were not focusing explicitly on individual personalities in our study, we found considerable variation in behavioural responses to

drive hunts regardless of hunting experience. Eleven individuals displayed a “flee” strategy consistently throughout the hunting season and eleven individuals showed a consistent “remain” strategy. Twenty-seven per cent of wild boar did not possess a fixed strategy and changed mainly into a “flee” strategy with increasing experience.

In our study, 60% of wild boar showed a limited flight response to hunting with a short average flight distance and duration (1.8 km and 25.8 h, respectively). Sodeikat et al.⁴⁸, reported the flight distance of wild boar after drive hunts in Germany to be up to 6 km and a return time of 4–6 weeks. In a study in Sweden¹⁵, 40% of wild boar responses to drive hunts resulted in flight. Wild boar’s flight distance and duration in Sweden after a drive hunt were greater than in Germany¹⁵. Short flight distance observed in Germany could be linked with habituation to frequent drive hunts⁶¹. In contrast to our findings, Scillitani et al.⁵⁴ argued that intensively hunted wild boar groups have higher flight distances than occasionally hunted wild boar groups. Higher flight distance may be linked with the availability of distance to “refuge” areas with no hunting risk outside of their home ranges⁶². Red deer, for example, fled outside their established home range to “refuge” areas during a hunting event and returned within a few days⁶³. However, the “refuge” areas were not clearly distinguishable in our study areas. Furthermore, different sizes of dogs can cause individual variation in the flight reaction of game species. In central Europe, dogs of rather small size < 15 kg are used in drive hunts, whereas in northern Europe, medium-sized dogs of 20–40 kg are common¹⁵. Larger dogs can follow game species for a longer period, increasing the flight distance of the prey. However, we found no difference in flight distance between our study areas in Sweden and the Czech Republic. Smaller hunting dog breeds were favoured in the Czech Republic, such as hunt terriers, Dachshunds, and Slovakian hounds. In Sweden larger hunting dog breeds such as “moose-hunting dogs” i.e. Jämthund and Norwegian elk hound or Small Münsterländer and Alpine Dachsbracke were preferred. However, these are only tendencies and both small and large hounds can be encountered in all four study areas.

Behavioural plasticity

Our study highlights wild boar adaptability towards hunting pressure. The proportion of response strategies shifted from predominantly ‘remain’ towards predominantly “flee” with more experience throughout the drive hunting season. The innate behavioural response can vary within individuals⁶⁴ because different personalities lead to contrasting strategies when faced with risky situations²², such as drive hunts. However, with increasing predator exposure and learning through experience, individuals can modify spatial behaviour towards one consistent strategy⁶⁴. With age, female elk reduce movement rates and increase the use of forests; this shift in behaviour, led to a successful avoidance of rifle and bow hunters¹⁸. Similarly, white-tailed deer adapted behavioural strategies during rifle deer hunting season by minimising movement⁶⁵. The behavioural change in wild boar strategy from “remain” to “flee”, seems to stand in opposition to the deer studies^{18,65}. A flight response may be favoured in our wild boar study as drive hunts differ to bow and rifle hunting. Flight is advantageous when there is a low predator search speed, a low cost to escape from the predation risk, and a large advantage to the prey in initiating chases rather than waiting and reacting to the predation risk⁶⁶. Increased experience with predation risk amplifies risk perception⁶⁷ and can cause changes in individual spatial responses. The magnitude of the spatial response is proportional to the alleged perceived risk^{18,68}, as some studies have proven. For example, elk movement was positively related to predation risk. The spatial response to human predation was stronger than to wolf predation risk⁶⁹. Bow hunting causes a more pronounced anti-predator response than rifle hunting¹⁸. Recreational human activities also affect spatial behaviour in wildlife^{70,71}. However, nonlethal human disturbance created a shorter flight response in wild boar than hunting events⁷². Adjustment in spatial behaviour through learning provided a higher survival rate in female elks^{18,29}. However, we could not test if the detected change in strategy increased the survival of the collared wild boar. Therefore, further research is needed to compare behavioural adjustment with survival rates. Changes in animal behaviour are considered as the most rapid form of adaptive response to disturbance^{73,74}, such as hunting pressure or any other form of “human-induced rapid environmental change” (HIREC)⁷ and might be partially responsible for the wild boar’s successful population expansion.

Material and methods

Study area

Our study areas were located in two different countries, Sweden and the Czech Republic. Each country provided two hunting districts. “Grimsö” hunting district is located in south-central Sweden (N 59.67’–59.76’, E 15.42–15.58) approximately 190 km northwest of Stockholm (Fig. 4). The relatively flat area, with an average elevation of 100 m a.s.l., contains forest, water, agricultural, and marsh areas⁷⁵. The “Koberg” hunting district is located in southwestern Sweden (N 58.07’–58.17’, E 12.34–12.47), 400 km southwest of Stockholm. Changing forests and farmland dominate the landscape composition⁴². The “Doupov” hunting district is located in the western part of the Czech Republic (N 50.18’–50.33’, E 13.04–13.22), at an average altitude of 558 m a.s.l. The hunting district is maintained by the state-owned company Military Forests and Estates of the Czech Republic⁷⁶ and is composed of large shrub patches, beech and ash forests, dry grasslands, and wetlands⁷⁷. The “Kostelec” hunting district is located in the centre of the Czech Republic (N 49.93’–49.99’, E 14.72–14.88), 50 km east of the capital, Prague. The area, with an average altitude of 430 m a.s.l., comprises forest, agricultural land, water, and building areas⁷⁸ and is exposed to high human leisure activity⁷⁹. Most drive hunts occurred in the nature reserve and forested part called “Voděradské bučiny”.

Wild boar capture and tracking

The capturing and handling of wild boar was approved by the Ethical Committee in Animal Research, Uppsala, Sweden (permit C 5.2.18-2830/16) and the ethics committee of the Ministry of the Environment of the Czech Republic, number MZP/2019/630/361. In Sweden, wild boar were immobilised with a tranquiliser gun from a vehicle on agricultural fields or close to feeding stations or with a blowpipe after being captured in coral traps.

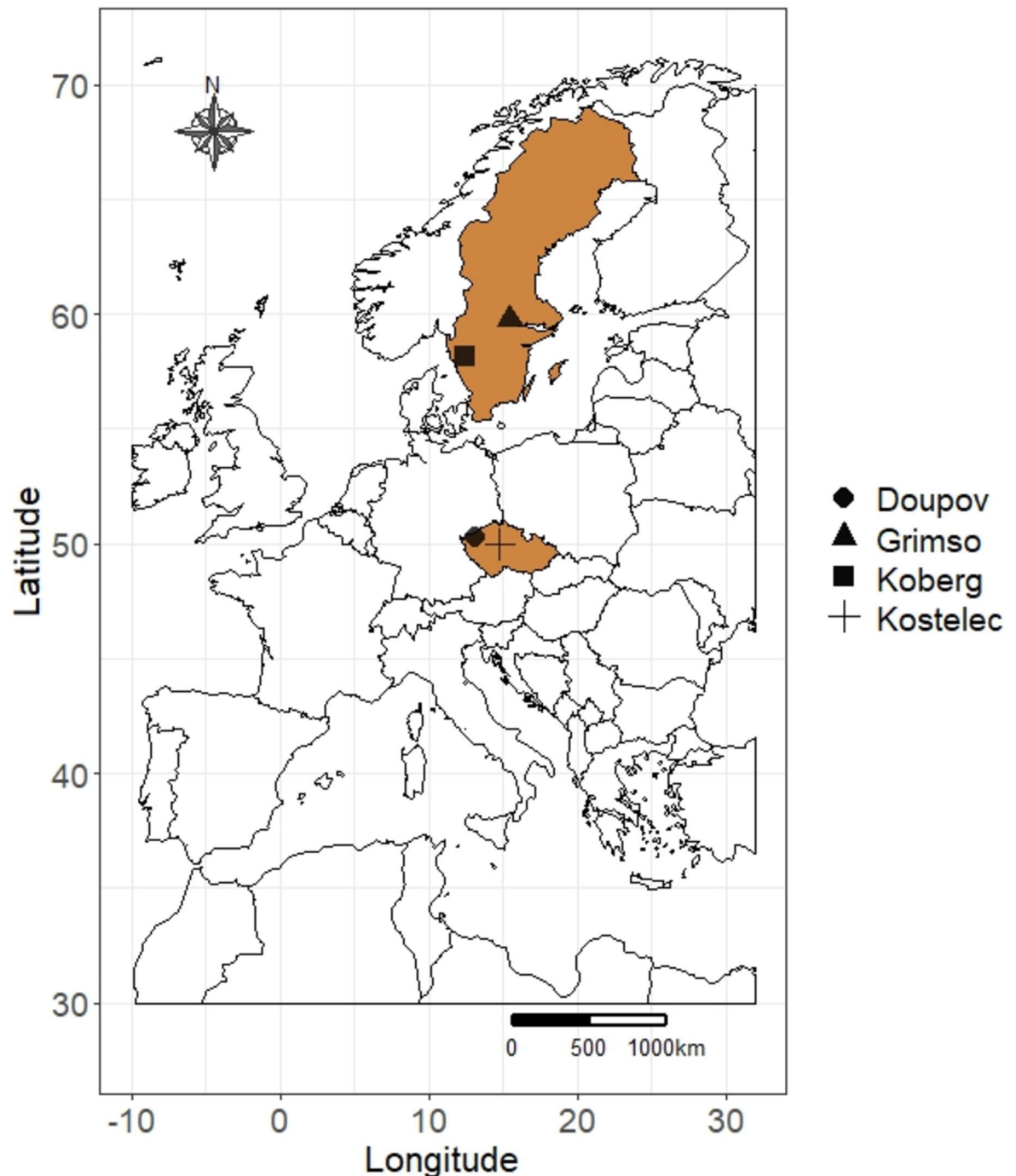


Fig. 4. Map of Europe, highlighting the Czech Republic and Sweden in colour. Analysed drive hunt areas are labelled with different symbols and assigned by name on the side. This figure was drawn using the R package `rworldmap`⁸⁰.

The wild boar was immobilised using anaesthetic drugs and equipped with GPS/GSM collars from Vectronic Aerospace GmbH. The collaring process of the wild boar in the Czech Republic was carried out inside wooden traps using corn as bait. All wild boars were immobilised using airguns with an anaesthetic dart. The trapping and handling of each wild boar was protocolled. Captured wild boar were equipped with a GPS collar from Vectronic Aerospace GmbH. For the analysis, we only used GPS fixes with a dilution of precision (DOP) (≥ 1 and ≤ 7) downloaded from the GPS Plus X software⁸¹ and GPS data with a correct elevation and a fixed rate between 30 and 60 min. In total, we collected GPS data of 55 collared individuals over three hunting seasons (2019–2022) (8 individuals, in Grimsö, 13 in Koberg, 27 in Kostelec, and 7 in Doupov). We used the coordinate reference system EPSG:32633-WGS 84/UTM zone 33N for all GPS positions. We analysed the data in QGIS 3.14⁸² and R 4.2.2⁸³. The study was carried out in compliance with the recommendations of ARRIVE guidelines⁸⁴.

Hunting data collection

We collected drive hunt data for each hunting area from three hunting seasons (2019–2022). The drive hunt season started in October and lasted until January (in Sweden) or February (in the Czech Republic) of the following year. For each drive, we collected the exact hunting area, date, time and duration of the drive, numbers of shooters, beaters and dogs, and, if available, the number of killed wild boar. We created polygons of the hunting areas with the QGIS software, based on the drawn hunting areas for each single drive hunt from paper maps received from the hunters and calculated the spatial extent (km²) of the hunting area with the “amt” package in the R environment⁸⁵. On average, the size of the hunting area for Grimsö was 2.70 km²; (Confidence Interval (CI) 95% 2.46–2.93), in Koberg 2.21 km²; (CI 95% 2.10–2.33), in Kostelec 2.17 km²; (CI 95% 2.03–2.32), and in Doupov 1.65 km²; (CI 95% 1.54–1.76). In total, we analysed 280 drive hunts (108 in Grimsö, 71 in Koberg, 48 in Kostelec, and 53 in Doupov). We calculated wild boar density for each study area across the three hunting seasons by dividing the number of killed wild boar by the size of the hunting polygon. On average, the wild boar density for Doupov was 3.81 ind./km²; (CI 95% 4.62–2.99), Grimsö 0.03 ind./km²; (CI 95% 0.04–0.01), Koberg 1.48 ind./km²; (CI 95% 1.72–1.24), and Kostelec 4.76 ind./km²; (CI 95% 5.24–4.28). Based on the hunting data, we also calculated the hunting intensity (HI) for each drive by dividing the cumulative number of hunters and beaters by the size of the hunting polygon. On average, the HI for Doupov was 31.78 person/km²; (CI 95% 29.11–34.45), Grimsö 3.54 person/km²; (CI 95% 3.14–3.94), Koberg 23.82 person/km²; (CI 95% 22.13–25.51), and Kostelec 37.44 person/km²; (CI 95% 33.85–41.04) (Fig. S1). Next, we calculated the number of hunts experienced by each individual wild boar per season, hereafter wild boar experience (WBE).

Analysis of wild boar movement and space use

From the GPS data, we calculated daily ranges (100% Minimum Convex Polygon) and daily distance travelled for each individual wild boar for “the day before the hunt”, “the day of the hunt”, and “the day after the hunt”. On average, wild boar daily range size for Grimsö was 2.28 km²; (CI 95% 1.88–2.68), in Koberg 1.14 km²; (CI 95% 0.94–1.33), in Kostelec 1.34 km²; (CI 95% 1.17–1.50), and in Doupov 0.68 km²; (CI 95% 0.39–0.98). Next, we calculated the overlapping area as a ratio between the hunting polygon and daily ranges. The value “1” indicates the complete overlap of the daily range with the hunting polygon, and the value “0” indicates no overlap. Furthermore, we calculated the distance between the centroid of the daily range and the hunting polygon of “the day before the hunt”, “day of the hunt”, and “day after the hunt” with the “amt” package in R. We identified two spatial categories for wild boar in drive hunts. Daily range size, which overlapped with the hunting area and was affected by the drive hunt, was classified as “Overlap”. Daily range size, which did not overlap with the hunting area, was used as a control group and classified as “No-Overlap” (Fig. S1). In total, of all collared wild boar, we calculated 104 overlaps per day and 934 non-overlaps per day (control group) (Table S2). If two or more drive hunt events occurred on consecutive days, the days before and after the sequence of hunts were considered as contrasts. For all four movement and space use parameters, we calculated the difference between the day of the hunt and the day before. Daily distance, daily range size, and overlap difference were used as response variables in the models. Furthermore, we calculated the net square displacement (NSD) from the hunt day to identify the occurrence, duration, and mean and maximum distance of the hunt-induced flight. We only calculated NSD for those wild boars that overlapped their daily range on the day of the hunt with the actual hunting area. We defined flight as a travel distance greater than the squared distance of the two furthest GPS locations from the day before the hunt, hereafter flight threshold. For a more robust threshold, we used the average of all wild boar individuals per study area that overlapped their daily range on the day of the hunt (Fig. 2). The threshold value for Doupov was 1.90 km, Grimsö 2.95 km, Kostelec 1.40 km, and Koberg 1.15 km. Flight duration was calculated as the continuous time the wild boar moved at a greater rate than the defined flight threshold. The end of the flight response was defined by entering the daily range area, which is below the given flight threshold.

Modelling of movement, space use and flight

To analyse the effects of drive hunts on wild boar space use and movement, we created linear mixed models with the R package glmmTMB⁸⁶. We constructed a model for each of the three response variables: daily distance travelled, daily range, and range overlap with the hunted area, all expressed as the difference between the day before the hunt and the day of the hunt. In each model, we fitted the same set of explanatory variables: HI, WBE, and the interaction between HI and WBE. To correct for repeated measurements, we added a crossed random factor, including AnimalID, within each area. The fitted variables were checked for collinearity by inspecting the Variation Inflation Factor (VIF) with the “performance” package in R⁸⁷, and no collinearity issues were detected. Additionally, we ran a visual model diagnostic with the DHARMA package⁸⁸ to check the distribution and dispersion of the residuals and detected no deviation from model assumption. The results of the model were presented with the tab_model () function of the R package “sjPlot”⁸⁹ and the results were visualised in a diagnostic plot with the predict () function and the settings of the “ggplot2” package⁹⁰. To test the effect of drive hunt on flight behaviour, we fitted generalised linear mixed-effect models (gamma distributed with a log-link function) to three response variables (flight duration, mean, and maximum distance) with a set of explanatory and random variables identical to the previous models.

Cluster analysis

To identify groups of individuals with similar reactions to the drive hunt, a cluster analysis was performed on the four different movement and space use metrics (difference of the day before the hunt to the day of the hunt for daily distance, daily range, overlap and centroid distance) with the “cluster” package in R⁹¹. The optimal number of clusters (n = 2, corresponding to the “flight” and “remain” strategy) was determined using the average silhouette method and theory-led-decision⁹². The results were visualised with the “factoextra”⁹³ and “ggplot2” package via

a principal component analysis (PCA). The data points were plotted according to the first two principal components that explain the majority of the variance of the data set (Dimension 1: 61.7%; Dimension 2: 23.7%). To examine if wild boar shifted strategy towards drive hunts with accumulated experience, we built a generalised linear mixed model with binomial distribution and family (link = logit) with the cluster as the response variable and the growing WBE, i.e. the number of hunting events that an individual experienced, as the explanatory variable. As in other models, we applied the same crossed random factor, including AnimalID, within each area.

Ethical approval

The wild boar trapping was implemented in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361 and by the approval of the Ethical Committee in Animal Research, Uppsala Sweden (permit 5.2.18-2830/16).

Data availability

The datasets analysed during the current study are available from the corresponding author upon reasonable request.

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Author contributions

A. O.: Data collection, Conceptualisation, Methodology, Data processing and analysis, Writing. E. A.: Data collection, Writing. P. K.: Data Collection, Conceptualisation, Writing. M. J.: Data collection. T. P.: Conceptualisation, Supervision, Data analysis, Writing. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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