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RESEARCH ARTICLE

# Frequent flight responses, but low escape distance of wild boar to nonlethal human disturbance

**Elodie Wielgus**[1] | **Maik Henrich**[1,2] | **Christian Fiderer**[1,2] | **Ariana Töws**[3] | **Jan-Niklas Michel**[2] | **Franz Kronthaler**[4] | **Marco Heurich**[1,2,5]

[1]Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Grafenau, Germany

[2]Chair of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

[3]Institute of Biology and Environmental Sciences, Faculty V-School of Mathematics and Science, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany

[4]Bavarian Health and Food Safety Authority, Oberschleißheim, Germany

[5]Institute of Forestry and Wildlife Management, Inland Norway University of Applied Science, Koppang, Norway

**Correspondence**
Marco Heurich
Email: marco.heurich@wildlife.uni-freiburg.de

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## Abstract

1. Human activities can affect the behaviour and fitness of wildlife. However, the response of animals to nonlethal human activities has not been well-studied in wild boar, *Sus scrofa*, even though it is a widespread species in Europe and has become of increasing concern because of crop damages and its vector capacity for diseases.
2. We study the behavioural responses of GPS-collared wild boar to nonlethal experimental human approaches in the Bohemian Forest Ecosystem along the border between Germany and the Czech Republic. We describe and quantify the flight responses of the animals and assess whether they vary with the distance to recreational paths and the occurrence of hunting in the area.
3. We show that wild boar were disturbed and displaced by human approaches on foot in 69% of the trials, but the average flight initiation and escape distances were relatively small (93 and 256 m, respectively). The probability of a flight response decreased with distance from the paths and increased with the ruggedness of the terrain. In the non-hunting zone, the flight initiation distances and flight durations were shorter than in the hunting zone.
4. Our results suggest a weak effect of nonlethal human disturbances on the movement of wild boar, although the animals were sensitive to the perceived risk in relation to recreation infrastructure and hunting.
5. For the management of diseases such as African swine fever, it can be concluded that nonlethal disturbances are unlikely to accelerate the spread of the disease due to far-distance movements. Guidelines for restrictions in case of an outbreak might be adjusted accordingly.

KEYWORDS
changepoint, flight response, GPS, human disturbance, recreation, ungulate, wild boar

# 1 | INTRODUCTION

A central topic in wildlife conservation and management is how human activities affect the behaviour and consequently the fitness of wild animals and at which spatial and temporal scales these effects occur (Steidl & Powell, 2006). Outdoor recreation and nature-based tourism have become increasingly popular in recent years, particularly in previously undisturbed landscapes such as protected areas (Balmford et al., 2009). Although first described as an essential conservation tool (Gössling, 1999), such recreational activities can have negative consequences for wildlife (Green & Higginbottom, 2001; Steven & Castley, 2013). Humans have not only direct impacts on ecological communities by structurally altering the landscape through the construction of infrastructure such as hiking and bicycling trails, and soil sealing (Scholten et al., 2018), but also through their general presence in natural areas, and these two types of pressure can have distinct effects (Nickel et al., 2020).

Many wildlife species experience predation and/or hunting and perceive human disturbance as a form of predation risk, even if the disturbance is not lethal (Frid & Dill, 2002). This generates a landscape of human-induced fear and shapes wildlife behaviour and habitat use (Frid & Dill, 2002; Lodberg-Holm et al., 2019). In the medium and long term, animals may alter their movement patterns to avoid areas most frequented by humans, such as roads and paths (spatial avoidance, Lewis et al., 2021; Muntifering et al., 2019; Plante et al., 2018), shift their activity to days or times of day when humans are less active (Pelletier, 2006; temporal avoidance, Gaynor et al., 2018; Lewis et al., 2021) and/or increase their vigilance rates when close to human infrastructure (behavioural avoidance, Jayakody et al., 2008; Worku et al., 2021). In the short term, wild animals can react to human activities, including hunting, with two main strategies: either fleeing or staying and hiding (Padié et al., 2015; Stankowich, 2008). The decision to flee is the result of a trade-off between the benefits of fleeing, that is, reducing the perceived risk of being predated, and the costs of fleeing, that is, increased energy expenditure and loss of time for foraging (Cooper & Frederick, 2007). The response often depends on the environmental context and can vary both spatially (with differences in vegetation openness, topography, and levels of human activity; Reimers et al., 2010; Taraborelli et al., 2014) and temporally (with seasonal differences in vulnerability; Meisingset et al., 2022). Other factors, such as the animal's characteristics (e.g. sex and age, Moen et al., 2012), its reproductive status (Andersen & Aars, 2007), its personality and previous experience (Found, 2021; Hansen & Aanes, 2014), or the kind of human behaviour and activity (e.g. on foot, off-track, Westekemper et al., 2018) can affect the animal's response (review in Stankowich, 2008). Although the impacts of outdoor recreation on wildlife are often unintended, humans can disrupt feeding and breeding activities, with negative consequences on the fitness of wild animals (Smith et al., 2017). Furthermore, wildlife reactions to human recreational activities can result in new conflicts with other forms of human land use. For example, fleeing animals can spread diseases across the landscape, or relocate to less disturbed areas, where they can damage crops or tree regeneration (Coppes et al., 2017; Guberti et al., 2022). Understanding the effects of outdoor recreation on wildlife is crucial for wildlife management, as human impacts on terrestrial wildlife continue to increase (Tucker et al., 2018).

It is particularly important to understand how recreational activities affect wild boar (*Sus scrofa*) populations, as the increase in wild boar populations over the past few decades has caused concern in several respects. Specifically, the wild boar acts as a vector for diseases that can affect livestock, such as African swine fever (ASF), which has recently spread across Europe. Infections of wild boar and domestic pigs (*Sus scrofa domesticus*) by highly virulent variants of the virus result in lethality rates close to 100% (Blome et al., 2012). Restricted zones must be established when ASF is focally introduced into a wild boar population, in which disturbance of wild boar must be minimized, for example, by limiting recreational activities (Dixon et al., 2020; European Commission [EC], 2018; Guberti et al., 2022). In addition, wild boar use cultivated farmland as feeding areas or resting sites (Schley et al., 2008), acting as crop destroyers. Despite the global distribution of wild boar, research on the effects of recreational activities on their behaviour is lacking (but see Marini et al., 2008 for a night-time study), while alterations in their behaviour due to disturbances could exacerbate existing conflicts with humans.

In this study, we investigated the behavioural responses of GPS-collared wild boar to experimental human approaches in the Bohemian Forest along the border between Germany and the Czech Republic. The aim of this study was twofold: (1) to describe and quantify the response of wild boar to immediate nonlethal human disturbance and (2) to assess whether wild boar behavioural responses vary according to the general level of human disturbance in an area. We used high-resolution GPS data from wild boar to calculate different metrics describing the behavioural responses and used the distance to linear infrastructure (forest roads and trails) and the local hunting regime (hunting or non-hunting zone) as proxies for human disturbance. Based on previous studies on ungulates, we hypothesized that the general level of human disturbance would increase the probability, initiation distance and intensity of flight responses (Muposhi et al., 2016; Stankowich, 2008). This knowledge can help managers to incorporate the effect of recreational activities on free-living wild boar in their considerations, for example, with regard to restrictions in the event of an ASF outbreak.

# 2 | MATERIALS AND METHODS

## 2.1 | Study site

The study was conducted along the German–Czech border in the Bavarian Forest National Park in southeastern Germany (245 km$^2$, 49°12′N, 12°58′E) and in the adjacent Šumava National Park (684 km$^2$, 49°12′N, 13°30′E) as well as its surroundings (Figure 1). Elevation ranges between 570 and 1453 m. Vegetation is mainly divided into mixed coniferous forests (Abies, Picea) in the lower

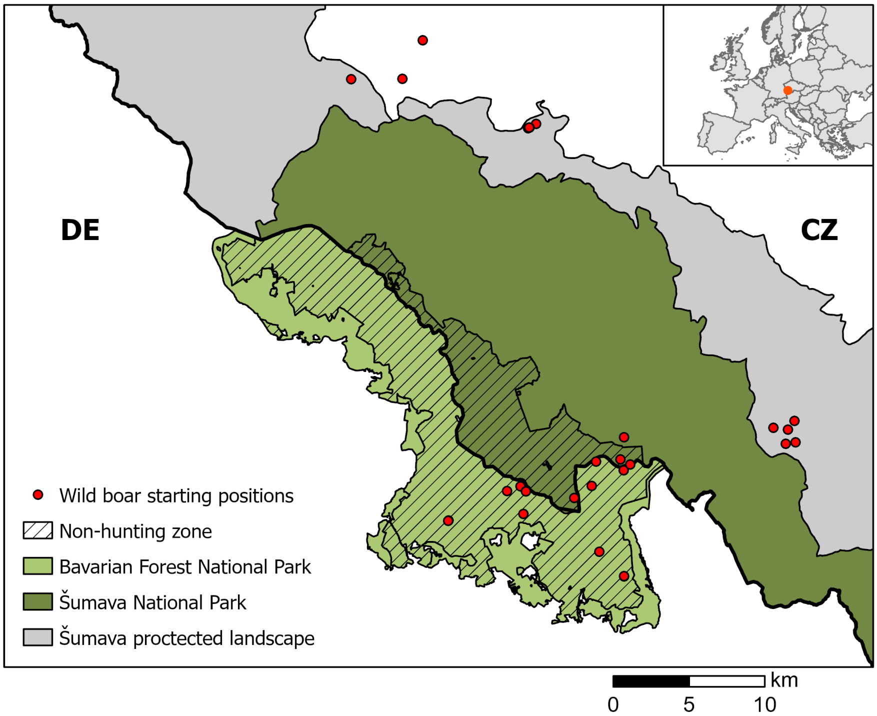


**FIGURE 1** Map of the study area with the location of the starting positions of the wild boar during the approach trials along the German (DE)–Czech (CZ) border.

regions and the valleys, mixed mountain forests at the mountain slopes (common beech *Fagus sylvatica*, silver fir *Abies alba*, Norway spruce *Picea abies*) and subalpine spruce forests mixed with a low proportion of mountain ash (*Sorbus aucuparia*) and common beech on peaks and high plateaus (Cailleret et al., 2014). The human population density within the study area varies between 2 inhabitants/km$^2$ inside the national parks and 30–70 inhabitants/km$^2$ in the nearby regions (Heurich et al., 2015).

Within the national parks, hunting restrictions have been imposed by nature conservation authorities to reduce animal disturbance and protect the resulting ecosystem processes. Wild boar hunting occurs in ~25% and 90% of the Bavarian Forest National Park and the Šumava National Park, respectively, to protect neighbouring private property from damage. Wild boar can be shot all year round, except females with piglets during spring. These regulations have led to different levels of hunting pressure within our study area. Tourism activities, for example, hiking and mushroom picking, occur in both hunting and non-hunting zones.

## 2.2 | Captures and collaring

Twelve wild boar (5 females, 7 males, 35 to 80 kg) were captured between October 2021 and March 2022 and equipped with a Vertex Plus GPS collar (Vectronic Aerospace GmbH, Berlin, Germany). Wild boar were captured at different locations in the Bavarian Forest National Park, each close to the non-hunting zone, using wood-clad corral traps of ~30 m$^2$ equipped with live monitoring cameras and gates that close after the animals move a counterweight. We separated a caught wild boar in an attached metal cage and drove it into a net tunnel. Two or three people held it on the ground, with its eyes covered with a cloth (Linderoth et al., 2020). The entire procedure took ~5 min per animal, after which the wild boar was released at the capture site. The handling procedure was approved by the ethics committee of the Upper Bavaria government and met animal welfare requirements (permit number ROB-55.2-2532.Vet-02-20-149).

## 2.3 | Experimental approach trials

The experimental human approaches were conducted from May to August 2022. We allowed a minimum of 14 days between consecutive trials on the same individuals to avoid habituation. We conducted the experiments by adapting the protocol developed by Eriksen et al. (2022) on wolves based on high-resolution GPS data. For this purpose, the collars were remotely reprogrammed to send positions at higher frequencies at three different periods on the day of an approach trial (Table 1) to identify the most recent location of the wild boar and thus define the experimental approach route, and capture the full response of the animal. To ensure that any movement of the animal was a response to the experimental disturbance, the approach trials were only conducted when the animals were stationary at a resting site, determined based on the last GPS positions before the trial started. Based on wild boar circadian activity patterns (Fradin & Chamaillé-Jammes, 2023; Johann et al., 2020; Keuling et al., 2008), we scheduled the approach period to begin at noon local time (10:00 UTC) to maximize the likelihood of the animal being at a day bed (Table 1).

The approach route was defined as follows: Observers started approaching the wild boar at a minimal distance of 1000 m from the wild boar position (last GPS position received prior to the trial), crossed over to a passing position 50 m from the wild boar position and

| Name | Time frame | Description |
|---|---|---|
| Preparation period | 07:00–10:00 UTC | 10-min GPS fixes to determine the latest boar's location and consider possible approach routes |
| Approach period | 10:00–13:00 UTC | 5-min GPS fixes to define the final approach route, provide fine-scale data for the initial flight response |
| Post-disturbance period | 13:00–16:00 UTC | 10-min GPS fixes to capture the entire flight and identify resettling |

TABLE 1 Classification of positioning intervals into three periods on the day of an approach trial.

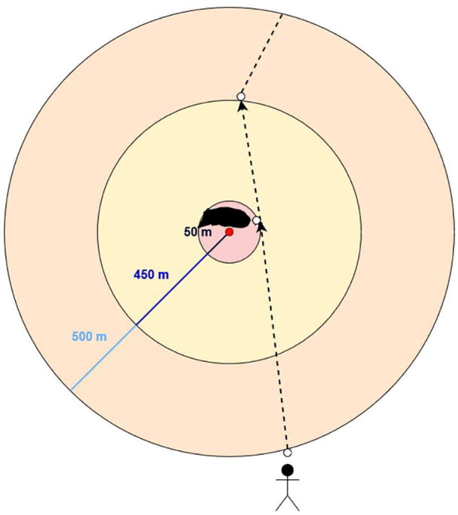


FIGURE 2 Schematic representation of an approach trial (as adapted from Eriksen et al., 2022). The observers approach the passing point in a 50 m distance to the resting position of the collared wild boar from a distance of 1 km in a route that follows a straight line as closely as possible. The walking direction is kept for 500 m more before the observers return at a larger distance from the animal.

continued walking for at least 500 m (Figure 2). The approach route was kept as straight as possible and did not follow roads or paths. Note that the final passing distance may not have been 50 m due to GPS errors and small movements of the wild boar after receiving the latest GPS position. During the approach, the observers (usually 2) recorded their trajectory with a handheld GPS device with one position per second to facilitate further comparison with the simultaneous positions of the wild boar. For the trials to represent relevant and realistic scenarios of human activities, observers conversed casually without making an effort to be quiet when approaching the animal.

## 2.4 | Wild boar response

We used GPS data from observers and wild boar to determine whether the individual fled and, if this was the case, to identify the flight initiation and resettling positions and describe flight behaviour. To identify flight initiation, we conducted a change point analysis to detect significant changes in the mean and variance of the wild boar's speed between consecutive positions. The speed of an animal was calculated from GPS locations at a resolution of 5 min, as flight could only have been initiated during the approach period (Table 1). Since an exactly zero speed is nearly impossible due to the measurement error of the GPS, we adjusted the wild boar speed to a gamma distribution by changing the values from 0 to 0.01 m/min. We ran the changepoint analysis using the R package *changepoint* with a pruned exact linear time (PELT) algorithm and an Akaike information criterion (AIC) penalty on the 95% confidence interval of the speed (Killick et al., 2012, 2022; Killick & Eckley, 2014). The PELT algorithm efficiently identifies multiple changepoints in the mean and variance of the data by considering all possible partitioning options. The AIC penalty helps to select the optimal number and locations of changepoints by balancing the goodness-of-fit with the model complexity for each data partition. Flight initiation was defined as the first change point after the observers started the approach trial. We visually checked the consistency between the detected flight initiation position and the observers' positions, meaning that the observers had to be close enough that the flight could have occurred in response to their presence. When the boar fled, we identified the resettling position using change point analysis as described for flight initiation (i.e. changes in both mean and variance of speed), but using GPS data acquired every 10 min (subsampled from 5-min data of the approach period and 10-min data of the post-disturbance period). When no change points were detected, but visual inspection suggested that the animal was fleeing, we visually identified the flight initiation and resettling points. The change point analyses successfully detected 85% of flight initiation positions and 75% of resettling positions. We then classified the wild boar response as (i) 'flight' when flight initiation was identified, or (ii) 'no flight' when no flight initiation was identified and the boar remained stationary. When the individuals fled, we described the flight behaviour by calculating (1) the flight initiation distance (FID), that is, the Euclidean distance between the observer and wild boar positions at flight initiation, (2) the escape distance, as the Euclidian distance between flight initiation and resettling positions, and (3) the flight duration, that is, the time elapsed between flight initiation

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and resettling. When two collared wild boar were together during the same approach trial, we retained a single interaction, as the behaviour of the two wild boar may not be independent of each other. If a flight response was detected, we retained the individual that fled first; if not, we selected the individual that was closest to the observer (Versluijs et al., 2022).

## 2.5 | Data analyses

We investigated how the wild boar response to human approaches was influenced by the intensity of human disturbance, while accounting for landscape heterogeneity (Frid, 2003; Taraborelli et al., 2014). We used OpenStreetMap with Geofabrik (2018) to obtain data on walkable paths, such as minor roads and hiking trails (layer = roads and fclass = cycleway, footway, path, pedestrian, service, track, and track_grade1-5; from hereon called 'path'). The national parks provided the polygons of the non-hunting zone. We derived a measure of terrain ruggedness from the Copernicus Digital Elevation Model (EU-DEM v1.1) as a measure of topographic heterogeneity. We calculated the terrain ruggedness index at a 25-m resolution with the 'terrain' function of the 'raster' package in R, as the sum change in elevation between a grid cell and its eight neighbour grid cells. When an animal did not flee, we extracted the terrain ruggedness index, the distance to the nearest path and whether the animal was in a hunting zone or not for the position of the wild boar at which the distance to the observer was minimal. In case of a flight response, we extracted the values for both flight initiation and resettling positions.

We used a binomial generalized linear mixed model (GLMM) with a logit link function to assess the relationships between the covariates and the probability of wild boar flight. The binary response variable was whether the individual fled (scored 1) or not (scored 0), and the explanatory variables included distance to the nearest path, hunting zonation and ruggedness. We then fitted linear mixed models (LMM) with distance to the nearest path and hunting zonation as explanatory variables, and the different flight metrics (e.g. FID) as response variables. In the LMMs, the flight metrics were logarithmically transformed to ensure that model residuals adhered to a normal distribution. Due to sample size limitations (only flight events) and since we mainly focus on the effect of human activities on flight behaviour of wild boar, we did not include terrain ruggedness in these models. Wild boar identity was included in all models as a random effect due to repeated observations of the same individuals and different numbers of trials per individual. Given our small sample size, we did not include any interactions between the explanatory variables. Continuous predictors were mean-centered and scaled. Finally, when the animal fled, we tested whether and how the environment differed at the initiation and resettling position of the flight using Wilcoxon signed rank tests (for paired data). We tested for terrain ruggedness and distance to the nearest path. All the wild boar remained in the same type of management zone (i.e. hunting or non-hunting) before and after the flight, so we were unable to explore the effect of this variable.

All analyses were performed in the statistical R computing environment (R Core Team, 2020). We used the R package *glmmTMB* (Brooks et al., 2017) to estimate the (G)LMM parameters and all significance levels were established at 5%.

# 3 | RESULTS

We conducted 29 experimental human approaches and each wild boar was approached on average 2.42 times (range: 1–4). The wild boar fled in 20 out of 29 interactions, which resulted in a probability of flight of 0.69. The probability of flight varied significantly with terrain ruggedness and distance to the nearest path (Table 2a): individuals were more likely to flee when the terrain was more rugged

**TABLE 2** (a) Effects of terrain ruggedness, distance to the nearest path, and hunting zonation on the probability of flight, and (b) effects of distance to the nearest path and hunting zonation on the flight initiation distance (FID), flight distance and flight duration of 14 tracked wild boar in the Bohemian Forest Ecosystem in 2022.

| Explanatory variables | $\beta$ | SE | Statistic | $p$ |
|---|---|---|---|---|
| **(a) Probability of flight ($n = 29$)** | | | | |
| (Intercept) | 2.51 | 1.30 | 1.93 | 0.054 |
| Terrain ruggedness | 2.05 | 1.02 | 2.01 | 0.045* |
| Distance to the nearest path | −1.39 | 0.68 | −2.04 | 0.041* |
| Zonation [non-hunting] | −1.51 | 1.36 | −1.11 | 0.267 |
| **(b) Flight behaviour** | | | | |
| FID ($n = 20$) | | | | |
| (Intercept) | 4.65 | 0.20 | 23.41 | <0.001*** |
| Distance to the nearest path | 0.08 | 0.14 | 0.59 | 0.555 |
| Zonation [non-hunting] | −0.61 | 0.27 | −2.28 | 0.023* |
| Escape distance ($n = 20$) | | | | |
| (Intercept) | 3.85 | 0.60 | 6.39 | <0.001*** |
| Distance to the nearest path | −0.43 | 0.32 | −1.34 | 0.179 |
| Zonation [non-hunting] | 0.99 | 0.75 | 1.31 | 0.190 |
| Flight duration ($n = 20$) | | | | |
| (Intercept) | 4.27 | 0.14 | 30.67 | <0.001*** |
| Distance to the nearest path | −0.04 | 0.10 | −0.45 | 0.655 |
| Zonation [non-hunting] | −0.37 | 0.19 | −1.98 | 0.047* |

*Note*: All continuous predictors are mean-centered and scaled by 1 standard deviation.

*$p < 0.05$.

**$p < 0.01$.

***$p < 0.001$.

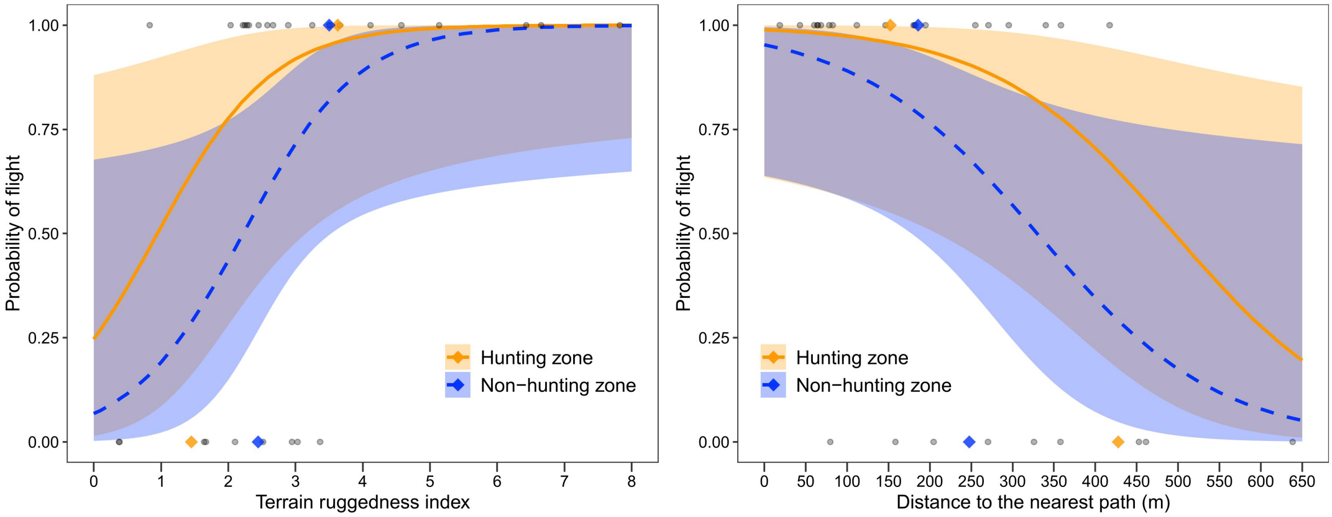


FIGURE 3 Predicted probability of flight in relation to the terrain ruggedness and the distance from the nearest path. The shaded areas represent 95% confidence intervals. Mean distance to path for ruggedness prediction = 219 m; mean ruggedness = 3.15. The terrain ruggedness index and distance to the nearest path at the observed locations are plotted by tick marks, with the marks at the bottom corresponding to the non-flight events and the marks at the top to the flight events. The coloured dots show the mean terrain ruggedness index and distance to the nearest path in the hunting and non-hunting zones.

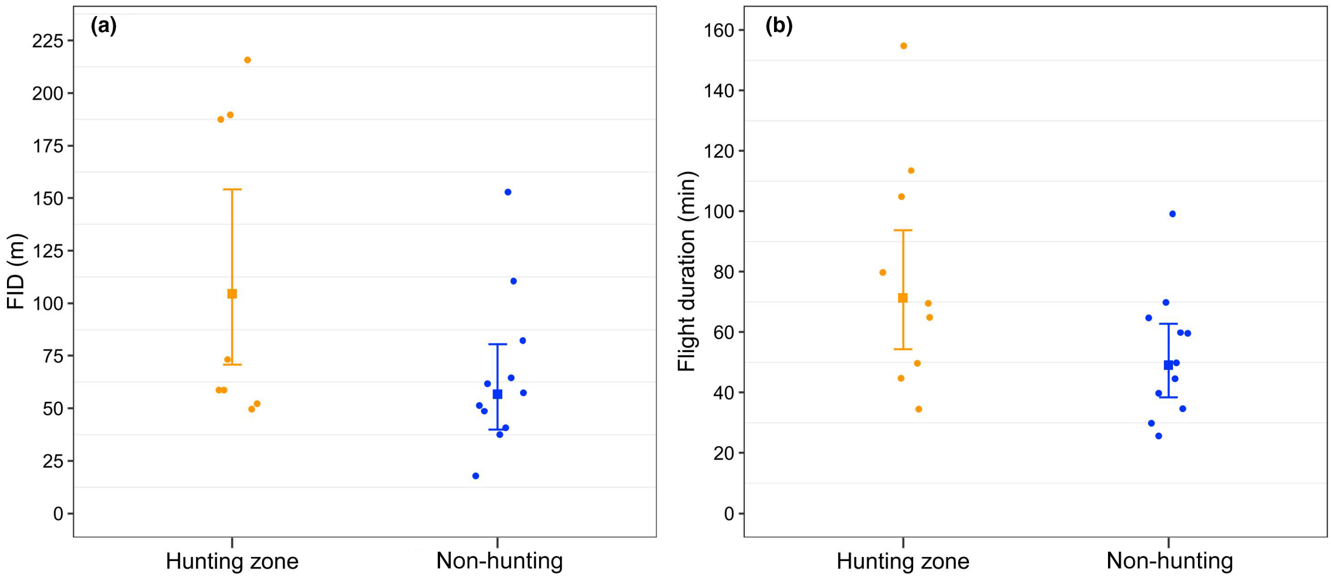


FIGURE 4 (a) Predicted flight initiation distance and (b) flight duration in the hunting and non-hunting zones. The error bars represent 95% confidence intervals around the model estimates. Mean distance from the path for the prediction = 170 m. The observed values are indicated by the circles.

and when they were closer to a path at the time of the approach (Figure 3).

Mean ± SD FID was 93.66 ± 69.03 m (range = 17.79–262.46 m, median = 60.21 m), mean ± SD escape distance was 256.41 ± 404.52 m (range = 1.84–1464.31 m, median = 119.15 m) and mean ± SD flight duration was 64.68 ± 32.48 min (range = 25.65–154.80 min, median = 59.72 min). While escape distance was not related to the distance to the nearest path and hunting zonation, FID and flight duration decreased significantly when the animal was in a non-hunting zone during the approach (Table 2b, Figure 4). This means that individuals fled later and for a shorter time in the non-hunting zone compared with the hunting zone.

Flight initiation and resettling positions differed significantly in terms of terrain ruggedness, with the resettling positions located in more rugged terrain than the flight initiation positions (Wilcoxon signed-rank test: $V = 36$, $p = 0.019$, $n = 20$, Figure 5a). No difference in the distance to the nearest path between flight initiation and resettling positions was detected (Wilcoxon signed-rank test: $V = 61$, $p = 0.105$, $n = 20$, Figure 5b).

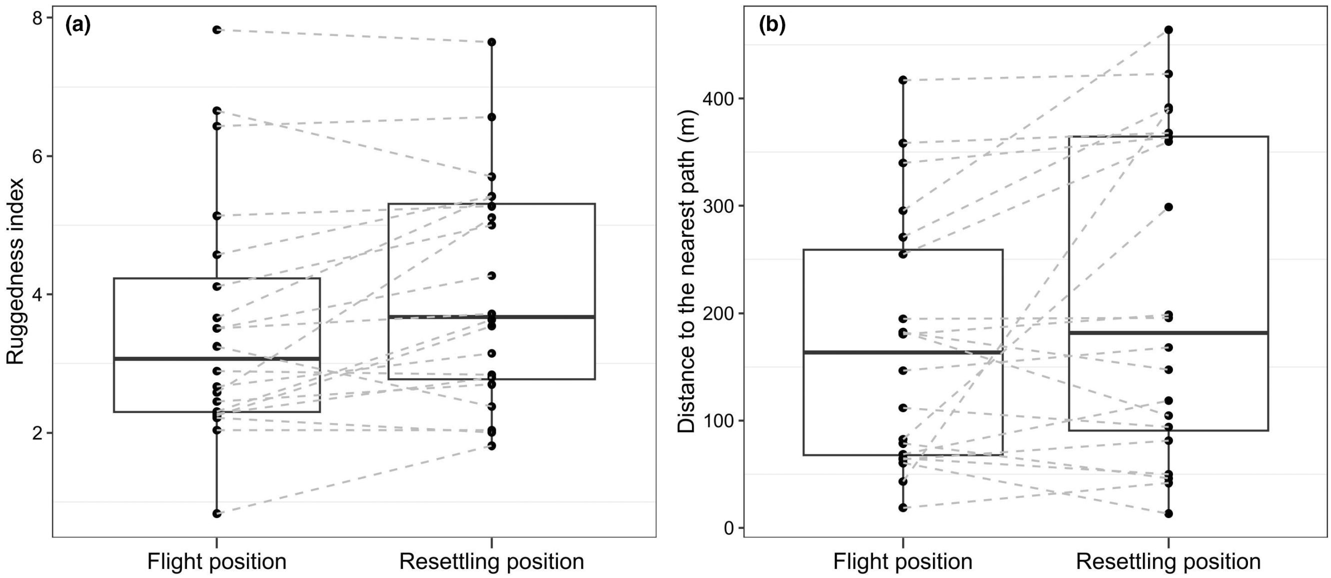


**FIGURE 5** (a) Terrain ruggedness index and (b) distance to the nearest path (in meters) at the flight initiation and resettling positions of wild boar. The grey dashed lines indicate paired observations.

## 4 | DISCUSSION

To our knowledge, we conducted the first experimental study to quantify and describe the behavioural response of wild boar to non-lethal human encounters using fine-scale GPS data. We showed that wild boar were disturbed and displaced by the approach of humans on foot, but FID and escape distances were relatively small, suggesting a low impact on their movement behaviour. As we hypothesized, wild boar adjusted their response to the perceived risk related to the general level of human disturbance in an area. Based on these results, we derive recommendations for wild boar management, in particular in the context of ASF.

Our results show that the probability of wild boar fleeing in response to the approach of humans on foot was high, indicating that the wild boar were disturbed. However, the flight initiation and escape distances were relatively small. These results are in agreement with those of Marini et al. (2008), who calculated a mean escape distance of 94 m in closed habitats (such as in our study area) and 138 m in open habitats. The difference from our study was that their experiments were carried out in a fenced-off reserve without access to the public and at night, probably contributing to a decrease in escape distances. As animals are more difficult to detect by humans at night, they may not feel the need to move as far after a disturbance. Fradin and Chamaillé-Jammes (2023) also showed that wild boar exhibit limited daytime movement, even in highly human-dominated landscapes, but when they do move, possibly due to human disturbance, their distances are typically short (<500 m), except when they are actively hunted. During our experimental approaches, we did not observe any aggressive reactions from wild boar towards the observers, who were only observed or heard on two occasions (out of 29 trials). This observation reinforces the tendency of wild boar to avoid humans. On a fine scale, wild boar may rely on vegetation for hiding or escape (Marini et al., 2008; Fradin & Chamaillé-Jammes, 2023; personal observation) and on a landscape scale, wild boar may avoid human structures during the day when human activity is the highest (Ohashi et al., 2013).

We predicted that wild boar in areas of high perceived risk, that is, in the hunting zone or near paths, would be more sensitive to human approaches than those in the non-hunting zone or further away from paths (Fradin & Chamaillé-Jammes, 2023; Keuling et al., 2008; Muntifering et al., 2019). Our results support this prediction partly, as the likelihood of wild boar fleeing from approaching humans was higher when they were closer to paths. We argue that the repeated and frequent occurrence of encounters with humans, on foot or in vehicles near paths is responsible for the low levels of tolerance to approaching humans. In addition, approaches by humans on foot are often associated with a risk of targeted harassment, such as hunting. Wild boar might be less sensitive or vigilant to humans when they appear far from paths because of the expected low frequency of encounters (notably fatal). We found no effect of the non-hunting zone on the probability of flight. One explanation could be that animals may already be choosing day beds with higher perceived safety, for example, due to dense vegetation, in the hunting compared with the non-hunting zone (Fradin & Chamaillé-Jammes, 2023). However, FID were shorter in the non-hunting zone than in the hunting zone, which is consistent with our prediction that a higher perceived risk would lead to an earlier flight response, as observed, for example, in red deer (Meisingset et al., 2022). Therefore, wild boar might be less tolerant of humans in high-risk habitats and respond more quickly with anti-predator strategies. Stankowich (2008) reviewed that, in general, ungulates in areas with hunting activity had greater flight responses, such as increased FID, than in non-hunting areas.

The flight response, once initiated, was also dependent on the perceived risk: wild boar approached in the hunting zone fled for longer than those in the non-hunting zone. When animals are disturbed by the presence of vehicles or humans or the noise of firearms, they normally move to safe areas where the perceived risk is low. In our study area, most of the approaches in the hunting zone were outside protected areas in the Czech Republic. At the time of the approaches, wild boar were often in small forest patches surrounded by agricultural or urban areas, which could limit their movement (Baguette et al., 2013), thus explaining their larger flight duration but not distance. Furthermore, the risks of hunting are spatially less predictable than those of linear infrastructure, which may favour a more tortuous path to increase the probability of escaping. Little (2011) found that male white-tailed deer (*Odocoileus virginianus*) increased the tortuosity of the movement path fivefold in areas of high hunting pressure. Moreover, in non-hunting zones, repeated encounters with humans in a non-threatening context might result in reduced flight responses. Our results point to an adaptation of wild boar flight behaviour to reduce perceived risks.

Topographic heterogeneity appears to increase the perceived risk in wild boar, since the probability of flight was higher in rugged terrain than in flat terrain. In a steep environment, animals may expect fewer encounters with humans and may respond more strongly. Additionally, in such an environment, visibility is poor and the ability to detect a human is often limited (Frid, 2003; Meisingset et al., 2022; Taraborelli et al., 2014). Once the danger has been detected, for example, by noise, the animal has more difficulty locating it and may therefore be more likely to flee immediately to safety. On flat terrain, animals can assess the distance separating them from the danger more easily and can maintain a safe distance, relying on vegetation to hide and only fleeing when the danger is very close. We were unable to investigate the effect of the terrain ruggedness on the flight parameters together with the effects of paths and hunting zonation due to our small sample size, but our hypotheses could be tested in the future with more data. When disturbed, wild boar chose more rugged terrain than before they fled, suggesting that they felt safer in this type of environment (Oeser et al., 2023).

We acknowledge that due to the experimental approach, our sample size is relatively small and we were unable to test the effect of other variables. Our approaches were carried out in the same season, at the same time of day, and in relatively similar habitats (forest) by two observers. Individual characteristics, such as sex, age, reproductive status and group behaviour (solitary male vs. group), could explain the variation observed in flight responses (Stankowich, 2008), but our sample was unequally distributed to test this hypothesis, as 92.31% of the trials we carried out in the hunting zone were on four subadult males. The intensity of conversation by the observers was not standardized between approaches, but there was always some talking at the passing point (50 m from the wild boar position) in order to document environmental variables. We are therefore confident that the variability between approaches was too small to potentially cause a bias. Our GPS fix interval of 5 min could lead to an underestimation of the flight response because we could not determine the exact moment at which the boar fled and the FID could, in reality, be greater. In the future, we strongly recommend increasing the resolution of the locations during the approach period, which would avoid planned but unsuccessful trials because recent enough location data were not received and would result in a better chance of detecting flight initiation and resettling positions.

The way, in which animals move through a landscape, has a strong influence on how they interact with conspecifics, which in turn affects the dynamics of infectious diseases (Daversa et al., 2017). Beyond quantifying and describing the behavioural responses of wild boar to nonlethal human encounters, our results provide information for disease management, especially with regard to ASF. The virus is transmitted between wild boar mainly through direct contact with infected individuals or carcasses of animals that have succumbed to ASF, and the movement of newly infected individuals, even if it may be small, contributes to the spread of the disease (Guberti et al., 2022). We conclude that recreational activities, such as off-trail hiking, have a small impact on the travel distances of wild boar. As infected wild boar are infectious for only a few days and are less active than healthy wild boar (Morelle et al., 2023), we expect the potential acceleration of disease spread through nonlethal human disturbance to be negligible. Therefore, our results do not justify severe human activity restrictions in case of an ASF outbreak due to an effect on wild boar movement. However, it must be considered that humans themselves may act as a vector for the disease (e.g. by transporting the virus on footwear). The observed differences in flight behaviour due to hunting zonation suggest that a hunting break may reduce the impact of other human activities on wild boar displacement and therefore on the transmission of the virus in the long term. However, it may take several years before a noticeable behaviour change occurs, as a one-year break in hunting during COVID-19 did not significantly affect wild boar activity patterns in Argentina (Nicosia et al., 2023). Caution is warranted, and these processes need to be studied in detail before assessing the necessity of restrictions. We also expect that the intensive search for infected wild boar carcasses has only a minor impact on wild boar movements. The flight parameters from our study can be used in future in epidemiological models to simulate pathogen spread at the landscape scale.

Our results provide important insights into wild boar responses to nonlethal human activities in a central European low mountain range, but we encourage similar studies in other habitats to reveal potential differences and similarities in wild boar behaviour across different human disturbance gradients and activities (e.g. hiking with domestic dogs) and alternative wildlife management scenarios.

## AUTHOR CONTRIBUTIONS

Elodie Wielgus, Marco Heurich, Maik Henrich, Christian Fiderer and Franz Kronthaler conceived the ideas and designed the methodology. Christian Fiderer, Elodie Wielgus and Maik Henrich organized and did the wild boar captures, while Ariana Töws and Jan-Niklas Michel conducted most of the field trials, as part of their bachelor and master thesis, respectively. Elodie Wielgus, Maik Henrich, Ariana Töws and Jan-Niklas Michel analysed the data. Elodie Wielgus and Maik Henrich led the writing of the manuscript. All authors contributed to the final writing and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

The data sets analysed as part of this study are available from OSF repository https://doi.org/10.17605/OSF.IO/VT2NQ (Wielgus, 2024).

## ORCID

*Elodie Wielgus* https://orcid.org/0000-0001-8323-5128
*Maik Henrich* https://orcid.org/0000-0001-5942-1668
*Franz Kronthaler* https://orcid.org/0009-0004-8917-9752
*Marco Heurich* https://orcid.org/0000-0003-0051-2930

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