Worse sleep and increased energy expenditure yet no movement changes in sub-urban wild boar experiencing an influx of human visitors (anthropulse) during the COVID-19 pandemic

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ABSTRACT

Expansion of urban areas, landscape transformation and increasing human outdoor activities strongly affect wildlife behaviour. The outbreak of the COVID-19 pandemic in particular led to drastic changes in human behaviour, exposing wildlife around the world to either reduced or increased human presence, potentially altering animal behaviour. Here, we investigate behavioural responses of wild boar (*Sus scrofa*) to changing numbers of human visitors to a suburban forest near Prague, Czech Republic, during the first 2.5 years of the COVID-19 epidemic (April 2019 - November 2021). We used bio-logging and movement data of 63 GPS-collared wild boar and human visitation data based on an automatic counter installed in the field. We hypothesised that higher levels of human leisure activity will have a disturbing effect on wild boar behaviour manifested in increased movements and ranging, energy spent, and disrupted sleep patterns. Interestingly, whilst the number of people visiting the forest varied by two orders of magnitude (from 36 to 3431 people weekly), even high levels of human presence (> 2000 visitors per week) did not affect weekly distance travelled, home range size, and maximum displacement of wild boar. Instead, individuals spent 41% more energy at high levels of human presence (> 2000 visitors per week), with more erratic sleep patterns, characterised by shorter and more frequent sleeping bouts. Our results highlight multifaceted effects of increased human activities (‘anthropulses’), such as those related to COVID-19 countermeasures, on animal behaviour. High human pressure may not affect animal movements or habitat use, especially in highly adaptable species such as wild boar, but may disrupt animal activity rhythms, with potentially detrimental fitness consequences. Such subtle behavioural responses can be overlooked if using only standard tracking technology.

KEYWORDS

Human impact, bio-logging, COVID-19 lockdown, disturbance, *sus scrofa*

1. Introduction

Anthropogenic pressure is growing worldwide, forcing wildlife to adapt to new environmental conditions and human presence (Vitousek et al., 1997, Tuomainen&Candolin 2011; Gunn et al. 2022). Expansion of urban areas (Gaynor et al., 2018), habitat fragmentation and landscape transformation (Bruinderink&Hazebroek, 1996; Said et al., 2016; Shi et al., 2018), as well as increasing human outdoor activities (Scholten et al., 2018; Sibbald et al., 2011) affect many aspects of wildlife behaviour. Behavioural responses can include shifts in habitat use and daily activity (Gaynor et al., 2018), overall reduction of movements (Tucker et al. 2018) or diel movements between safe and risky places (Courbin et al. 2022). Wildlife exposed to higher human activity tend to have smaller home ranges and higher rates of social associations at almost all times of the year (Gillich et al., 2021; Grund et al., 2002; Seip et al., 2007). Furthermore, wildlife adjusts its bedding and foraging behaviour in national parks by avoiding hiking or cycling trails during the weekend days with high human visitation rates (Jiang et al., 2007; Scholten et al., 2018; Sibbald et al., 2011), preferring areas that are difficult for humans to reach (Gaynor et al., 2018).

The outbreak of the worldwide COVID-19 pandemic at the end of 2019 added yet another dimension to human-wildlife interactions. Epidemic countermeasures, such as restrictions of activity and mobility, led to drastic changes in human behaviour, and with that reduction of disturbance, noise, and other pollution (Bar, 2021). The sudden confinement of roughly two-thirds of the global human population (peak lockdown on April 5, 2020) caused an immediate change in wildlife behaviour (Bates et al., 2020). Shortly after the first implementation of strict lockdowns, social media and online news reported sightings of naturally shy wildlife species in human-occupied landscapes, e.g., pumas in downtown Santiago, Chile or dolphins in the harbour of Trieste, Italy (Max-Planck-Gesellschaft, 2021). Those observations were supported by scientific studies which reported short-term effects of the sudden absence of human pressure, such as an increase of habitat use (Behera et al., 2022), a shift towards diurnal activity (Behera et al., 2022; Manenti et al., 2020; Zukerman et al., 2021), and less roadkill especially of amphibians and reptiles (Driessen, 2021; LeClair et al., 2021; Łopucki et al., 2021; Manenti et al., 2020). On the negative side, an increase in poaching caused by the partial stop of conservation actions was also observed during COVID-19 lockdowns actions (A. E. Bates et al., 2021; Koju et al., 2021; Lindsey et al., 2020; Rahman et al., 2021).

Human confinement during the initial COVID-19 lockdowns, termed "anthropause" by Rutz et al. 2020, provided the opportunity to investigate positive and negative effects of human presence and mobility on ecosystems and animal behaviour (Bates et al., 2020). The first COVID-19 lockdowns were followed by a series of periods with relaxed or stringent restrictions depending on the country-specific epidemiological situation. Human mobility fluctuated in accordance with the level of restrictions leading to a series of pulses and pauses of anthropogenic pressure (Rutz, 2022). These COVID-19-related pulses in human activity provide a unique experimental opportunity to test their impacts, yet studies taking such an approach are missing. Government responses to the pandemic varied greatly across the geopolitical spectrum and elicited different responses from the society. Thus, using periods of COVID-19 lockdowns as a simple covariate explaining environmental changes without underlying data on human activity may be insufficient, if not misleading. For example, most reports consider a reduction of human activity during COVID-19 lockdowns, but increased interest in outdoor recreational activities in response to the at-home-confinement was observed in some areas (Hockenhull et al., 2021; Kleinschroth&Kowarik, 2020; Weed, 2020). Nature parks in particular, where human entry was not restricted, experienced sudden increases in the number of visitors and pressure on the ecosystem. Higher numbers of visitors were observed during lockdown periods (Cukor et al., 2021; Derks et al., 2020; Venter et al., 2020) or shortly after the ease of some restrictions (Day, 2020; McGinlay et al., 2020). For example, in a forest located northeast of the city Zlín in the Czech Republic, the visitation rate of humans in the forest areas increased over five-fold from 200 people per day in April 2019 to 1100 people per day in April 2020 (recorded by 14 randomly placed camera traps), resulting in increased disturbance of wildlife species (Cukor et al., 2021).

Whilst many wildlife species are declining due to overexploitation, habitat loss, and traffic mortality. wild boar *(Sus scrofa)* numbers are increasing steadily over the last decades (Massei et al., 2015; Scandura et al., 2021). Studies show that the demographic success of the wild boar is in part due to their high adaptability to a wide range of environmental conditions and tolerance to humans (Fernández-Aguilar et al., 2018). This plasticity enables colonisation of habitats with high human pressure, such as agricultural areas (Morelle et al., 2016), and urban areas (Castillo-Contreras et al., 2018). For example, wild boar shift to nocturnal activity when human presence is high (Boitani et al., 1994; Ikeda et al., 2019; Podgórski et al., 2013; Russo et al., 2010). In response to hunting, wild boar increased movements in search for refuge habitats in dense woodlands to minimise the risk of being detected (Thurfjell et al., 2013). Furthermore, hunting is known to influence the resting behaviour of wild boars. In the period of hunts, the resting areas of the wild boar were clearly larger and more distant from each other (Scillitani et al., 2009; Sodeikat&Pohlmeyer, 2007). Resting areas fulfil an important fitness function for animals, including defence against predators, thermoregulation, rearing of offspring (Lutermann et al., 2010) and sleep. Despite the importance of resting areas, little is known about how increased human presence and activity affects the sleeping behaviour of wild boar.

The aim of our study was to describe the effects of changing human presence induced by the countermeasures to COVID-19 pandemic on the movements and space use, activity and sleep, and energy expenditure of wild boar. We hypothesised that higher levels of human leisure activity will have a disturbing effect on wild boar behaviour manifested in increased movements, ranging and energy spent, as well as disrupted sleep patterns. Specifically, we expected to see a positive relationship between weekly number of visitors to the forest and 1) weekly distance travelled, 2) proportion of distance travelled during nighttime (i.e. shift to nocturnality), 3) weekly range size, 4) spatial extent of movements, and 5) energy spent by wild boar. Additionally, we predicted that 1) sleep patterns will become more erratic (shorter and more frequent sleeping bouts) in response to disturbance by high human recreational activity, whereas 2) the total sleep time may remain the same, assuming that recreational activity of people is limited in space (trails) and time (daylight) and thus allow individuals to recover the lost sleep.

2. Material and methods

2.1. Study area

The study site is located within the municipality "Kostelec nad Černými Lesy", district Prague-East of the Czech Republic (N 49.93`- 49.99`,E 14.72 - 14.88, Figure A.1). The municipality area is covered by 43% of forest, 47% agricultural land, 9% other land-cover types, and 1% water surfaces (Ježek et al., 2016). Our study was conducted in the forested part of the municipality - a 2900 ha woodland administered by the Czech University of Life Sciences Forest Establishment in Kostelec nad Cernymi lesy. The altitude of the study site is 430 m a.s.l., with a mean annual precipitation of 600mm, and mean annual temperature of 7.5°C (Podrázský et al., 2009). The study area, which offers natural forest landscape and high plant and animal biodiversity, is an attractive place for recreational activities of local and Prague residents (Jarský et al., 2022).

2.2.Wild boar capture and tracking

Wild boars were trapped inside wooden traps using corn as bait. The immobilisation was done by airguns with a mixture of Ketamine, Xylasine and Zoletil inside the darts (Fenati et al., 2008). We followed the protocol of vets and checked the oxygen respiration during the immobilisation of the individuals. The wild boar trapping procedures were in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic, number MZP/2019/630/361. Captured animals were equipped with hybrid bio-logging collars comprising a GPS unit (Vectronic Aerospace GmBH) and a Daily Diary tag (Wildbyte Technologies Ltd). We recorded biologging data (3–axial accelerometer and 3–axial magnetometer data at 10 Hz frequency) and stored them on the microSD card inside the housing of the Daily Diary. The GPS fixes were collected every 30 minutes and sent by SMS to an online server. We used GPS data of 63 individuals (47 females, 16 males) collected from April 2019 to November 2021. For the analysis, we used only GPS fixes with a dilution of precision (DOP) (>= 1 and <=7) downloaded from the GPS Plus X software, and selected weeks (temporal unit of our study) with at least 5 days of telemetry data with a daily average of at least

40 GPS locations. According to these criteria,135 individual weeks were used for the analyses. Bio-logging data did not cover the study period uniformly and we therefore only used the six most and five least visited weeks for direct comparison. Bio-logging data originated from 13 individuals (2 males and 11 females). All GPS data were visualised and analysed using the coordinate reference system EPSG:32633-WGS 84/UTM zone 33N within the R software 4.1.0 (R Core Team, 2021).

2.3.Human visitation data

Human presence in the suburban forest was recorded hourly by an automatic counter (eco-counter.com, 2022) at the entrance of the main forest road in Jevany counter (Jarský et al., 2022). We aggregated the human count data into weekly periods, which was the basic temporal unit in our analyses (mean 1126.55 people weekly, 95% confidence interval (CI): 1089.6 – 1163.51). There were two COVID-19 lockdown periods during the study period (Figure 1). The lockdowns were defined by the "state of emergency" declared by the government of the Czech Republic (vlada.cz, 2020). The first COVID- 19 lockdown in the Czech Republic started on 24.03.2020 and ended on 24.04.2020. The second COVID-19 lockdown started on 22.10.2020 and ended on 11.04.2021. Furthermore, we divided the study period into seasons: Spring (Mar-May), Summer (Jun-Aug), Autumn (Sep-Nov), and Winter (Dec-Feb) and used season as a covariate.

2.4.Analysis of wild boar movement and space use

Using GPS-telemetry data we calculated the following movement and space use parameters: 1) weekly distance travelled as a sum of all distances between consecutive 30-minute relocations (i.e., step lengths) per week. In addition, we divided the weekly distance into distance travelled at daytime and distance travelled at night time. Daytime was defined from sunrise to sunset and night from sunset to sunrise, 2) weekly home range as 95% kernel utilisation distribution (UD) isopleths using the "reference bandwidth" method from the package "adehabitatHR" (Calenge, 2006), 3) maximum displacement as the maximum distance between GPS locations within a week. To examine the effect of human presence on wild boar movement and space use, we used generalised mixed-effects models with the package "lme4" (Bates et al., 2014). In total, we used 935 data points (i.e., individual weeks) to fit models to movement and space use data obtained from 63 collared wild boars. For each of the five response variables we fitted a model with fixed effects of weekly human counts (continuous predictor) and season (categorical predictor) as well as animal ID as a random effect. Residuals of all fitted models were normally distributed as evidenced by visual inspection of the quantile plots and histograms of the residuals. The home range and maximum displacement were log-transformed prior to modelling to reduce skewness and improve normality of the residuals. Using the package "ggeffect"(Lüdecke, 2018), we generated predictions of the effects of seasons and human activity on wild boar space use and movements in all five models.

2.5. Analysis of wild boar energy expenditure

We used the vectorial sum of dynamic body acceleration (VeDBA) as a proxy for energy expenditure (Wilson et al. 2020). The VeDBA was calculated using the tri-axial acceleration measured by the daily diary tags on the collars. Dynamic body acceleration is a good indicator of oxygen consumption and movement-based power in both humans and animals (Miwa et al., 2017; Qasem et al., 2012; Wilson et al., 2020). We used available biologging data from 12 collared wild boars (1 male and 11 female). Using the DDMT software (Wildbyte Technologies Ltd, 2022), we set the smoothing of the VeDBA to 20 records (i.e., 2 seconds) and created 30 minute bookmarks. We then exported the sum of the smoothed VeDBA per half an hour for the whole period of available data. However, due to discontinuous data coverage of the study period we selected the top six of the most visited weeks (>2000 visitors) and bottom five weeks of the least visited weeks (<300 visitors; Figure 3), for which data provided by 12 individuals was available. All six weeks that had more than > 2000 visitors per week occurred during the first lockdown. Five weeks with less than < 300 visitors per week occurred during the non-lockdown and the second lockdown. We summarised the smoothed VeDBA for each week using the "collap" package (Krantz et al., 2022) within the R software. This data was obtained from twelve individuals. To examine the differences in VeDBA between the two extreme categories of human visitation, we run a linear mixed model, with the log-transformed VeDBA, human high or low visitation as a fixed effect, and Animal ID as a random effect.

2.6. Analysis of wild boar sleeping behaviour

We used a new method to identify periods of sleep in the daily diary data, developed by modifying existing published laboratory procedures and studies, based on actigraph recordings of sleep in domestic pigs, to use it on accelerometer data collected on wild boar in the wild (Mortlock et al., 2022). Specifically, behavioural sleeping bouts were classified using body pitch and roll angles, identifying the stereotypical sleep postures of either lateral or sternal recumbency, combined with immobility (defined as a VeDBA threshold < 0.2). Furthermore, based on existing physiological measures of sleep in domestic pigs, a transitional period of five minutes was discarded at the start of each bout. After removing the transitional time, the sleep time was calculated. The end of a sleeping bout was identified once the animal started moving, exceeding a smoothed VeDBA threshold of 0.2, which allowed for minor movement during sleep. Using this data, we calculated the average duration of sleep (hours) per animal and day during the specific weeks of high and low human visitation respectively, as well as the number and duration of sleeping bouts as an indicator of sleep continuity within the R software. To examine the differences in the sleeping behaviour between the two extreme categories of human visitation, we run three linear mixed models, with the log-transformed total duration of sleep per week as well as with the number and duration of sleeping bouts as a response variable, human visitation rate (high or low) as a fixed effect, and Animal ID as a random effect.

3. Results

3.1. Human visitation patterns

We compared human visitation rate obtained from the counter during the two lockdown periods and the non-lockdown period (Kruskal-Wallis chi-squared = 246.09, df = 2, p-value < 0.001). The number of human visitors during the first lockdown (median of 2066 visitors) was significantly higher compared to the second lockdown (902 visitors) and non-lockdown periods (1066 visitors) (pairwise-Wilcox tests, p-value < 0.001). The second lockdown showed no significant difference in the number of visitors compared to the non-lockdown (pairwise-Wilcox test, p = 0.75). Given those results, we believe that the actual visitation rate measured in the field provides better representation of human response to COVID-19 countermeasures than just using the dates of the officially imposed lockdowns. Thus, we used the weekly sum of visitors as a continuous predictor explaining wild boar movements, space use, activity and sleep instead of categorical lockdown and non-lockdown periods.

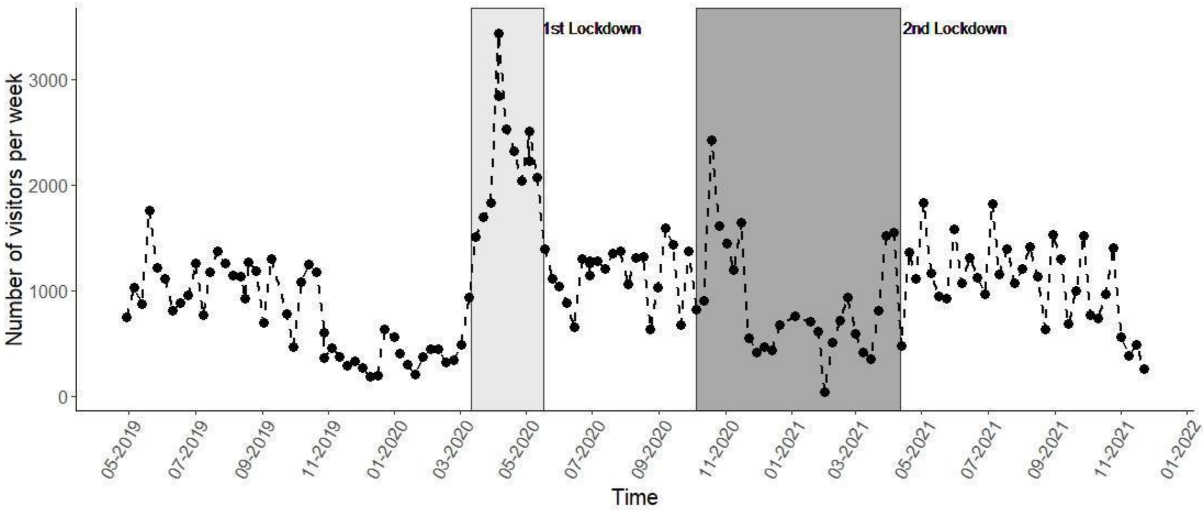

Figure 1: Count of human visitation per week in the forest area near the capital city Prague and the two official COVID-19 lockdowns as defined by the "state of emergency" declared by the government of the Czech Republic.

3.2. Space-use and movement patterns

We found that the number of visitors in the forest did not affect wild boar spatial behaviour as none of the five movement parameters was influenced by the weekly human count (Table 1, Figure A.2). The total weekly distance travelled by wild boar decreased marginally by 145 m per increase of 400 people visiting the forest and ranged between 34.43 km at 400 visitors and 33.26 km at 3600 visitors (3.4% decrease). The distance travelled during nighttime tended to decrease while distance travelled during daytime tended to increase when more people visited the forest (Figure A.2), yet these relationships were statistically insignificant (Table 1). Weekly home range size was positively, yet insignificantly, related to the number of visitors, showing a slight increase by 0.26 % per unit of 400 more people visiting the forest. Maximum displacement was increasing only by 0.06 % per unit of 400 people visiting the forest. Instead, in contrast to the number of visitors, all five movement and space use parameters varied significantly across seasons (Table 1).

Table 1: Results of the mixed model regression for five estimated movement and space use parameters.

	Weekly daytime distance		**Weekly nighttime distance**		**Weekly home range**		**Total weekly distance**		**Maximum displacement**	
Coefficient	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*
Autumn (Intercept)	**6.18 *****	5.34 – 7.02	**28.48 *****	26.54 – 30.42	**1.32 *****	1.04 – 1.59	**34.57 *****	32.26 – 36.88	**1.21 *****	1.09 – 1.34
Human Count	0.00	-0.00 – 0.00	-0.00	-0.00 – 0.00	0.00	-0.00 – 0.00	-0.00	-0.00 – 0.00	-0.00	-0.00 – 0.00
Spring	**2.77*****	2.04 – 3.49	**-10.94 *****	-12.55 – -9.33	**-0.72 *****	-0.94 – -0.50	**-8.11 *****	-9.95 – -6.26	**-0.44 *****	-0.54 – -0.34
Summer	**3.89 *****	3.33 – 4.44	**-8.61 *****	-9.84 – -7.39	**-0.50 *****	-0.66 – -0.33	**-4.66 *****	-6.06 – -3.35	**-0.29 *****	-0.37 – -0.22
Winter	**-1.41 ****	-2.26 – -0.57	**-7.44 *****	-9.31 – -5.58	**-0.56 *****	-0.81 – -0.30	**-8.77 *****	-10.92 – -6.62	**-0.28 *****	-0.40 – -0.17
Random Effects										
σ2	9.35		45.54		0.84		59.61		0.17	
τ00	4.69 $_{AnimalID}$		27.42 $_{AnimalID}$		0.58 $_{AnimalID}$		42.17 $_{AnimalID}$		0.12 $_{AnimalID}$	
ICC	0.33		0.38		0.41		0.41		0.42	
N	63 $_{AnimalID}$		63 $_{AnimalID}$		63 $_{AnimalID}$		63 $_{AnimalID}$		63 $_{AnimalID}$	
Observations	935		935		935		935		934	
Marginal R2 / Conditional R2	0.237 / 0.492		0.201 / 0.501		0.046 / 0.434		0.093 / 0.469		0.078 / 0.461	

*** p<0.05 ** p<0.01 *** p<0.001**

Total Weekly distance travelled was highest in autumn (34.17 km on average; CI: 32.11 – 36.22; Figure 2) and lowest in winter (25.40 km on average; CI:24.48 – 28.02; Figure 2). Distance travelled at nighttime showed a similar pattern with a peak of 27.61 km (CI: 25.91 – 29.32) in autumn, while the weekly daytime distance peaked in summer at 10.53 km (CI: 9.87

– 11.19) and decreased towards winter. Both weekly home range and the maximum displacement showed similar seasonal patterns with the largest mean values during autumn: 3.76 km^2 (CI: 2.96 – 4.8) and 3.36km (CI: 3.01 –3.76), respectively (Figure 2).

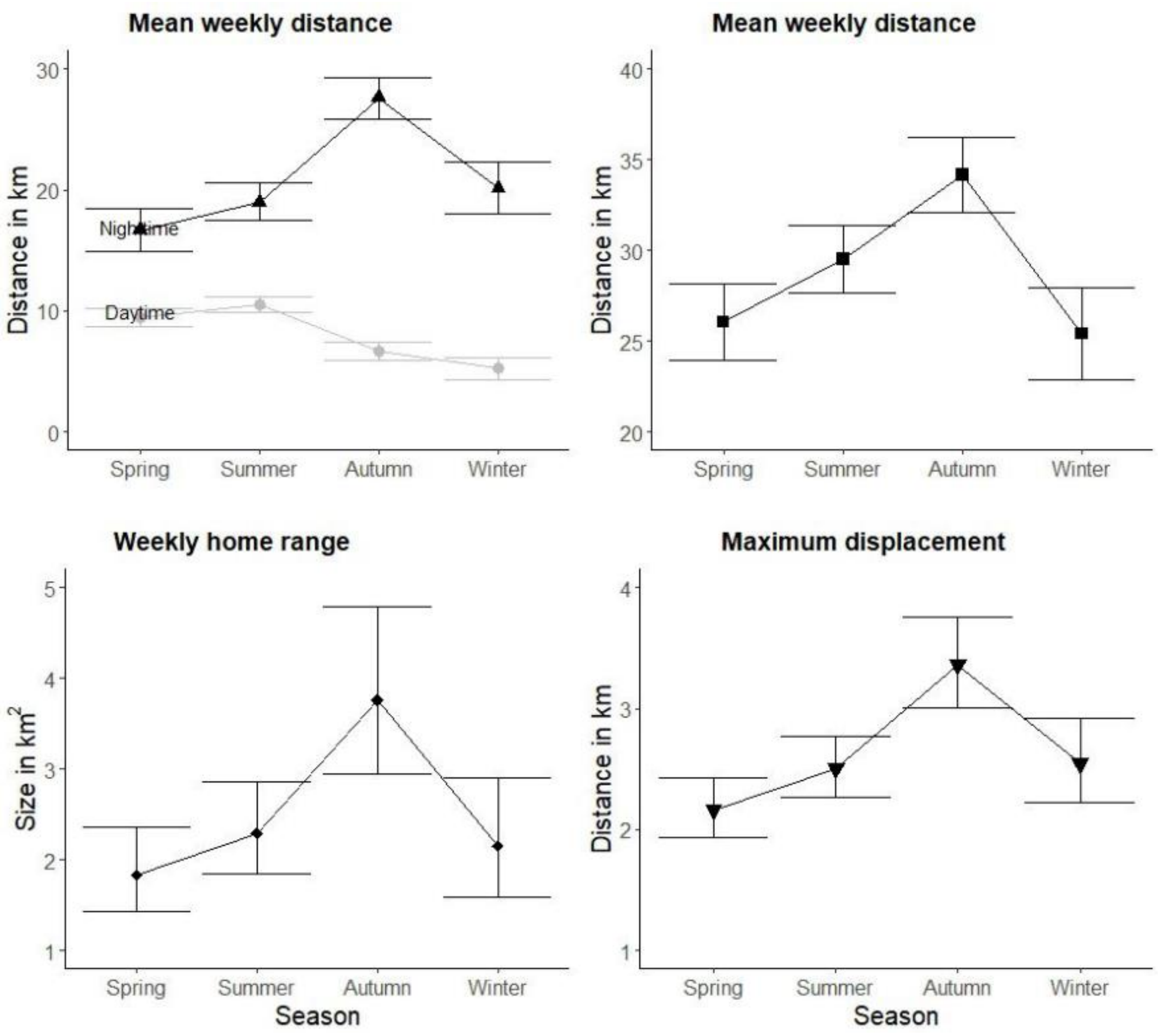

Figure2: Seasonal changes in the movement of wild boar: A) Mean weekly distance at nighttime and daytime B) Mean weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week)

3.3. Energy expenditure and sleeping behaviour

The analyses of the wild boar energy expenditure (half an hour sum of VeDBA) showed a 41% increase in the energy spent between the weeks with the lowest visitation (mean = 1602.24, CI:

1529.19 – 1675.3, n = 2448; Figure 3) and the weeks with the highest visitation rates (mean = 2260.54, CI: 2216.2 –2304.7, n = 9215; Figure 3, Table 2).

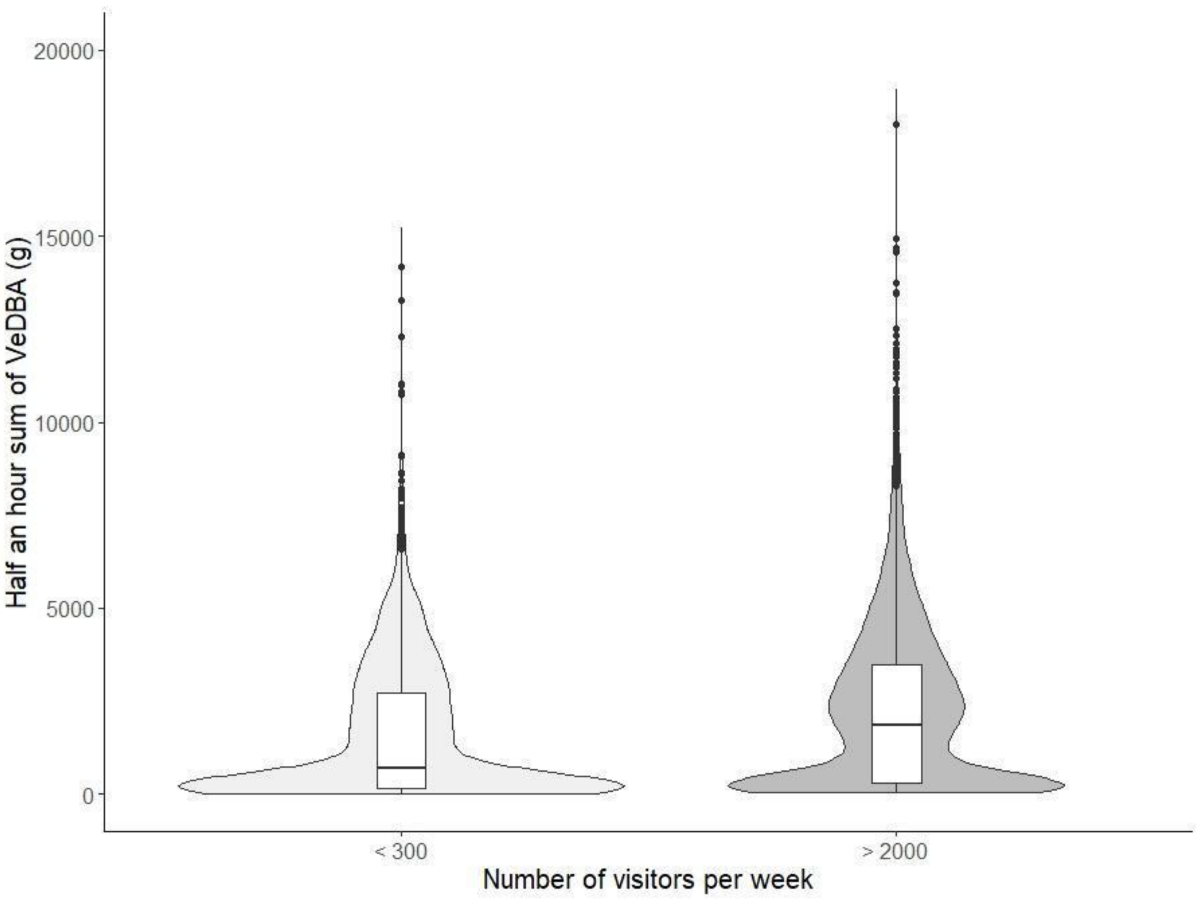

Figure 3: Energy expenditure at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) number of human visitors.

Total weekly sleep time did not differ much between weeks with high (mean = 90.53 hours per week, CI: 88.08 – 92.97, n = 212) and low human visitor numbers (mean = 91.41, CI: 87.9 – 94.93, n = 51; Figure 4, Table 2). However, we observed significantly more sleeping bouts during weeks with high human visitation (mean = 161.63, CI: 154.19 –169.07, n = 212) than in weeks with few visits (mean = 102.4, CI: 89.52 – 115.26, n = 51; Figure 4; Table 2). Accordingly, the average duration of a sleeping bout was shorter with high human visitation (mean = 0.64 h, CI: 0.602 – 0.684, n = 212) than in weeks with few visits in the forest (mean = 0.98 h, CI = 0.874 – 1.09, n = 51; Figure 4, Table 2).

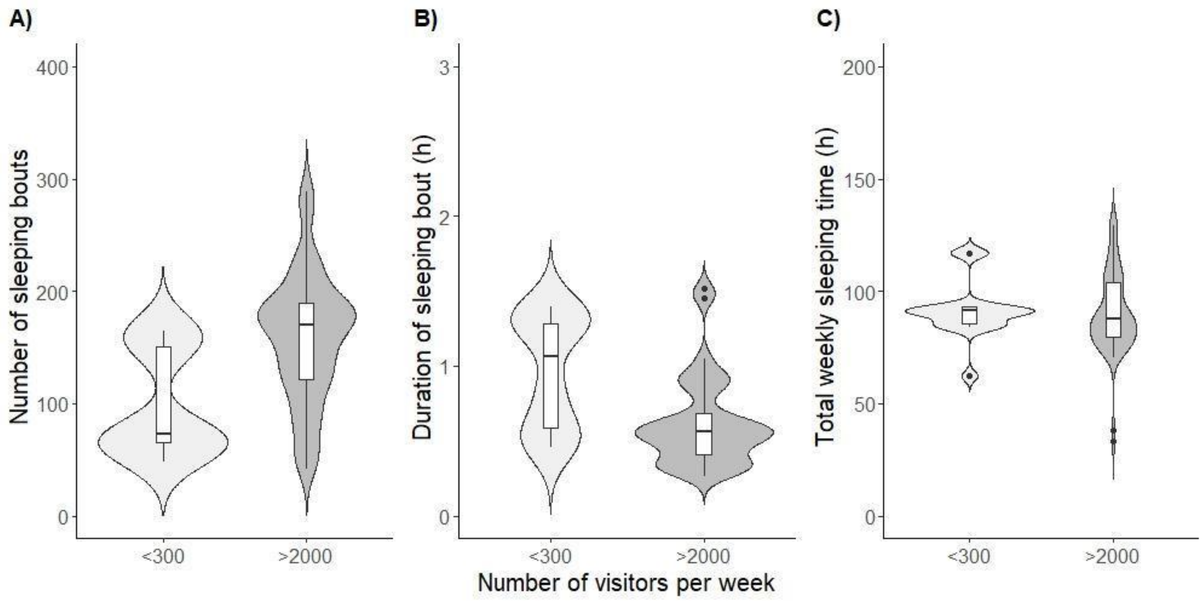

Figure 4: Sleeping behaviour at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) numbers of human visitors: A) number of sleeping bouts per week B) duration of sleeping bouts C) total sleeping time per week.

Except for the analysis of the total sleep time, linear mixed models of the weekly energy expenditure, number of sleeping bouts and duration of sleep bouts showed a significant difference between weeks with low and high human visitation (Table 2).

Table 2: Results of the mixed model regression for sleep metrics and energy expenditure.

	Number weekly sleep bouts		**Duration weekly sleep bouts**		**Total weekly sleep time**		**Weekly energy expenditure**	
Coefficient	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*	*Estimates*	*Conf. Int (95%)*
Visitation < 300 (Intercept)	**4.81*** **	4.58 – 5.05	**-0.44 *** **	-0.63 – -0.25	**4.49 *** **	4.39 – 4.59	**1579.79 *** **	1161.33 – 1998.25
Visitation > 2000	**0.11 ***	0.00 – 0.22	**-0.13 ****	-0.23 – -0.04	-0.01	-0.09 – 0.07	**626.31 ***	83.59 – 1169.03
Random Effects								
σ2	0.05		0.04		0.03		4338347.31	
τ00	0.17 AnimalID		0.11 AnimalID		0.02 AnimalID		213393.27 AnimalID	
ICC	0.77		0.76		0.40		213393.27	
N	13 AnimalID		13 AnimalID		13 AnimalID		12 AnimalID	
Observations	287		287		287		11663	
Marginal R2 / Conditional R2	**0.009 / 0.772**		**0.019 / 0.762**		**0.000 / 0.401**		**0.014 / 0.060**	

*** p<0.05 ** p<0.01 *** p<0.001**

4. Discussion

4.1. Human presence during COVID-19 lockdown

We showed that the numbers of human visitors to the suburban forest "Kostelec nad cernymi lesy" of Prague and hence the intensity of recreational use of the forest varied markedly between the two Covid-19 lockdowns. During the first COVID-19 lockdown, there was a strong increase in visitors to the study area which exceeded all levels recorded during the pre-lockdown period as well as those recorded in the following year. This effect can be explained by the type of restrictions imposed on school, work, and recreational facilities by the government during the "state of emergency" declared in the Czech Republic to deal with the Covid-19 pandemic. During this first lockdown, natural areas, parks, and forests were one of the few places freely accessible for visitors and they attracted people seeking relief from the at-home-confinement. Contrastingly, the number of visitors to the forest did not increase during the second lockdown. Although the "state of emergency" was declared in both lockdowns, the restrictions in the second lockdown were much more severe in addition to the restrictions on school, work and recreational facilities, further restrictions on travelling between municipalities (prohibited under a penalty of a fine) were implemented and a curfew was imposed between 9pm and 6am. Those additional restrictions likely discouraged people from extended travelling and made forest visits less likely. Patterns of fluctuating human pressure (i.e., anthropulses) observed in our study highlight the need of using the actual indices of human activity rather than crude administrative measures (i.e., timing of lockdowns or state of emergency declaration) because small changes in the details of each policy can have profound effects on human behaviour and potentially on wildlife.

4.2. Human disturbance and wild boar movement

During our study, human visitation rate in study area fluctuated greatly (varying by two orders of magnitude), yet we did not detect any significant difference in space use and movement patterns of wild boar resulting from these changes. This agrees with the high tolerance and habituation towards anthropogenic pressure recorded for wild boars in urban areas (Licoppe et al., 2013). Similarly, urban wild boars are characterised by a shorter flight distance and reuse of traps (Stillfried et al., 2017). We suspect that the suburban forest is exposed to a constant high pressure of human leisure activities, so that behavioural response of wild boar to human presence may already have occurred before the sharp increase in visitor numbers during the first lockdown. This is supported by our observation of larger distances travelled by wild boar at nighttime across seasons, in accordance with several studies reporting more nocturnal activity of wild boar in response to human disturbances (Gaynor et al., 2018; Johann, et al., 2020a; Podgórski et al., 2013). Hunting events, depending on location and type, can cause instability in wild boar spatio-temporal behaviour but the effects vary across studies (Keuling et al 2021). Some publications report an increase of home range size (Scillitani et al 2009), whilst others report a spatial shift of home range after hunts (Sodeikat&Pohlmeyer 2002, 2003) or did not observe any significant change in home range size (Keuling et al 2008b). Conversely, our results indicate that non-lethalhuman leisure activities, which are usually restricted to established roads and paths, may not be as disturbing as hunts, and thus do not lead to temporal displacement of animals. Our findings provide similar conclusions to Fatterbert et al (2017) who found that non-lethal human disturbances, measured by the proximity to infrastructures, in the Geneva Basin, Switzerland, had no effect on wild boar ranging patterns. In addition, whilst landscape configuration and topography can have a strong effect on the home range size of wild boar (Fatterbert et. al 2017), our study area was relatively homogenous in terms of forest configuration (continuous cover) and topography (minor differences in elevation), and we did not consider those variables a strong drivers of wild boar spatial behaviour.

4.3.Seasonal effects on wild boar movement

Contrary to the effect of human presence, we found a strong seasonal effect on all our movement and space use parameters, suggesting that wild boar movements and space use are more strongly affected by the species annual life cycle or by resource distribution than by human leisure activities. Weekly distance travelled, weekly home range and maximum displacement showed a similar seasonal pattern with the highest values observed in autumn. As a capital breeder, gaining sufficient fat reserves before winter is crucial for wild boar survival and reproduction in the following year (Geisser&Reyer, 2005; Jędrzejewska et al., 1997). The autumn mast of oak acorn and beech nuts provides natural resources to achieve good body condition before winter but localising those resources may require extended movements and higher spatial activity. Additionally, during the mating season (October - December, Rosell et al., 2012), male wild boar roam widely and often undertakes mating excursions outside of their home range in search of receptive females (Singer et al., 1981), which could further explainthe increased home range sizes observed in autumn. In winter, home ranges can increase due to food shortage (Boitani et al., 1994) but not after a tree masting season (Keuling et al., 2008a). We did not observe any home range size increase during the winter period, possibly due to the supplementary feeding practised by managers in the study area. The smallest weekly home ranges were observed during spring which coincides with the peak of parturition and weaning of newborn piglets, whereas in early summer the increasing movement capacity of growing piglets, and high energy demands of sows still nursing the piglets result in larger home ranges compared to spring (Keuling et al., 2008b). As our dataset was female-biased and these seasonal changes in female behaviour may have particularlyaffected the seasonal space use patterns we observed. Finally, weather conditions can also strongly influence animal movement behaviourin addition to regular seasonal changes (Börger et al., 2006). The more extreme the weather is, the less wild boar move;in wintersnow depth and low temperature can reduce the movement activity of wild boar (Johann et al., 2020b; Thurfjell et al., 2014), as do high temperatures in summer (Johann, et al., 2020a).

4.4.Effect of human disturbance on wild boar energy expenditure and sleeping behaviour

Increased human presence on roads and trails in the suburban forest significantly affected the index of energy expenditure (VeDBA) of wild boar. It was41% higher in the weeks where more than 2000 visitors were counted in the forest than in the weeks with less than 300 visitors. Taken together, our results show that higher recreational human activity did not cause an increase in travel distances, as could be expected for a species habituated to human presence, but sufficiently disturbed the individuals to cause an increase in small-scale body movements and activity on site, as evidenced by higher energy expenditure values. Typically, at high human disturbance levels, wild boars spend their daytime resting in forests and dense shrubbery areas (Boitani et al., 1994). However, at extreme values of human presence (>2000 visitors), animals may have trouble finding sufficiently secluded resting sites and may need to increase their vigilance and thus energy expenditure. Small on-site movements (i.e. non-travel), not detectable by the 30-minute scale GPS data, may also have occurred, but importantly these did not lead to the individuals moving away from their sites (which would have been detected by the GPS data).

Our analyses of sleep patterns at high and low human visitation rate further support this prediction. Wild boar sleep was more fragmented (short and frequent sleeping bouts) when human presence on forest roads was high compared to weeks of low human presence, where sleep was more consolidated and thus of higher quality (longer but fewer bouts of sleep). Despite the differences in sleep pattern, total sleep time was similar at high and low human visitation rate. The total sleep time of wild boars may not be affected by human presence. Instead, environmental conditions, such as temperature, humidity, precipitation and snow cover can affect both sleep duration and structure in wild boar (Mortlock et al., 2022). Sleep quantity and quality also varies across and within individuals (Mortlock et al., 2022), which may help explain high variability in the weekly sleep measures observed in our study. Sleep, characterised by rest and reduced reactivity (Zaid et al., 2022), has fundamental functions for the immune (Rogers et al., 2001), neuronal (McDermott et al., 2003) and cognitive system (Roth et al., 2010) in all animals in which sleep has been recorded. Depending on the species, sleep quality differs in duration and number of sleeping bouts during the day (Capellini et al., 2008). Elephants, for example, need only a small amount of sleep, an average daily total sleep time of 2h being enough (Gravett et al., 2017). In contrast, the total daily sleep duration of a sloth is between 9 and 10 hours (Voirin et al., 2014). Sleep is so essential that lack of sleep can be fatal for the animal (Rechtschaffen and Bergmann, 2002). Although sleep fragmentation does not necessarily reduce the total sleep time, as in our study, it has an impact on the sleep quality (Martin et al., 2012) and may negatively impact metabolic stability or endocrine and autonomous systems (Baud et al., 2013). Fragmentation of sleep can cause increased sleepiness, decreased psychomotory performance such as reduced short-term memory, reaction time, or vigilance (Bonnot and Arand et al., 2003, Phillipson et al., 1980). Further, in humans sleep disturbance negatively affects cardiovascular health (Gangwisch et al., 2005). Social and ecological pressures, such as predation risk, food competition, and social relationships, can influence sleep homeostasis in animals (Loftus et al., 2022, Voirin et al., 2014). Within the context of sleep, our results provide new evidence that short-term increased leisure human activity can disrupt sleep quality in a natural setting even in a species with high tolerance to human presence like the wild boar. Our high-resolution approach to quantifying sleep allowed us to see that although wild boar sleep duration was unaffected, sleep quality was reduced by disturbance (being more fragmented), highlighting the need for ecologists to view sleep behaviour in multiple dimensions to capture all potential effects. Our findings are therefore important for the management of natural areas, in particular of eco-tourism and use of green areas by humans. If high numbers of humans visiting natural areas are maintained over prolonged periods, this may have a cumulative deleterious effect on animal physiology and survival. The consequences of sleep disturbance and deprivation in wild animals is a topic requiring further study, holding significance for management and conservation of wildlife populations in human-dominated landscapes.

4.5. Conclusions

Our results show that high levels of human recreational activity, mostly restricted to tourist trails and forest roads, did not affect wild boar space use and long-distance movements. However, we showed that increased human presence influenced *in situ* body movements and sleep behaviour. Disrupted sleeping behaviour, identified as increased sleep fragmentation, could lead to increased energy expenditure and elevated stress levels and disruptthe vital functions of sleep in maintaining natural immunity and neuronal and cognitive functions (Ferrara & De Gennaro, 2001; Rogers et al., 2001) with potentially serious consequences on fitness. We thus highlight the need for more detailed research on the effects of non-lethal human disturbance on animal behaviour to better manage human-wildlife coexistence.

Data availability

The dataset analysed during the current study is available on request to the corresponding authors.

CRedi'T authorship contribution statement

A. Olejarz: Conceptualisation, Methodology, Data processing and analysis, Writing. **M. Faltusová:** Conceptualization. **L. Börger:** Data processing and analysis, Writing **J. Güldenpfennig:** Methodology, Data analysis, Writing. **V Jarský:** Data collection.**M. Ježek:** Data collection. **E. Mortlock:** Data processing and analysis. **V. Silovský:** Data collection and processing, Writing. **T. Podgorski:** Conceptualisation, Supervision, Data analysis, Writing.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Ethical approval

The wild boar trapping was realised in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361.

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Appendices

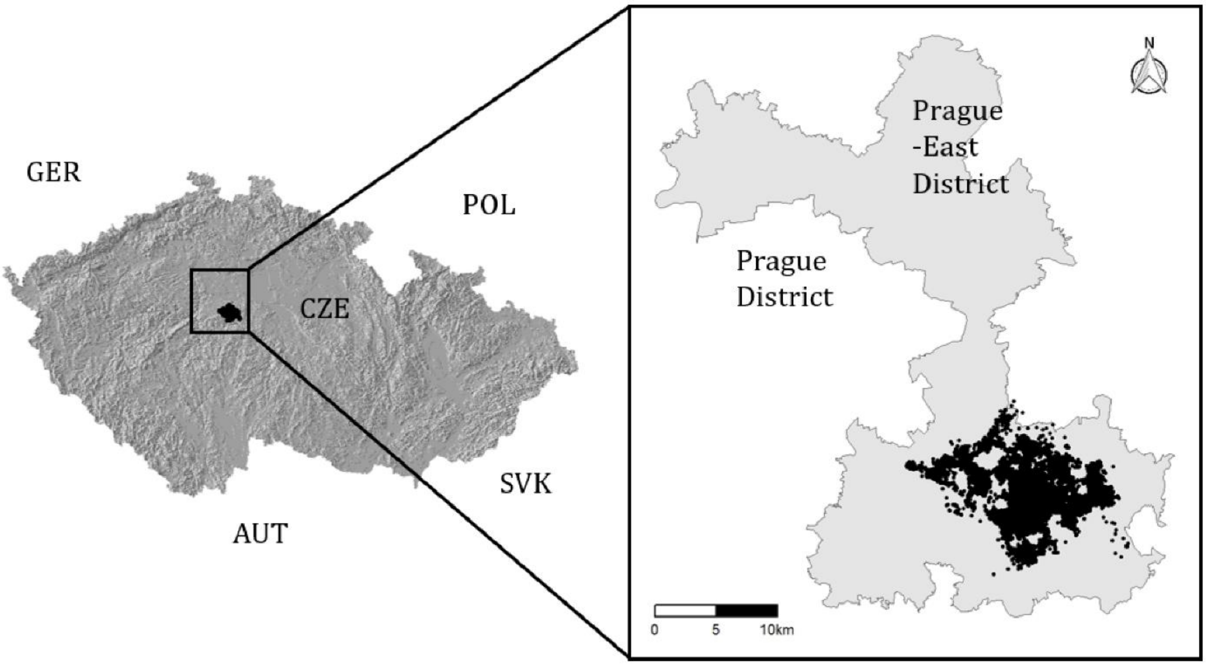

Figure A.1: Location of the study area Prague-East in the Czech Republic (CZE) with GPS positions of the collared wild boars (black points).

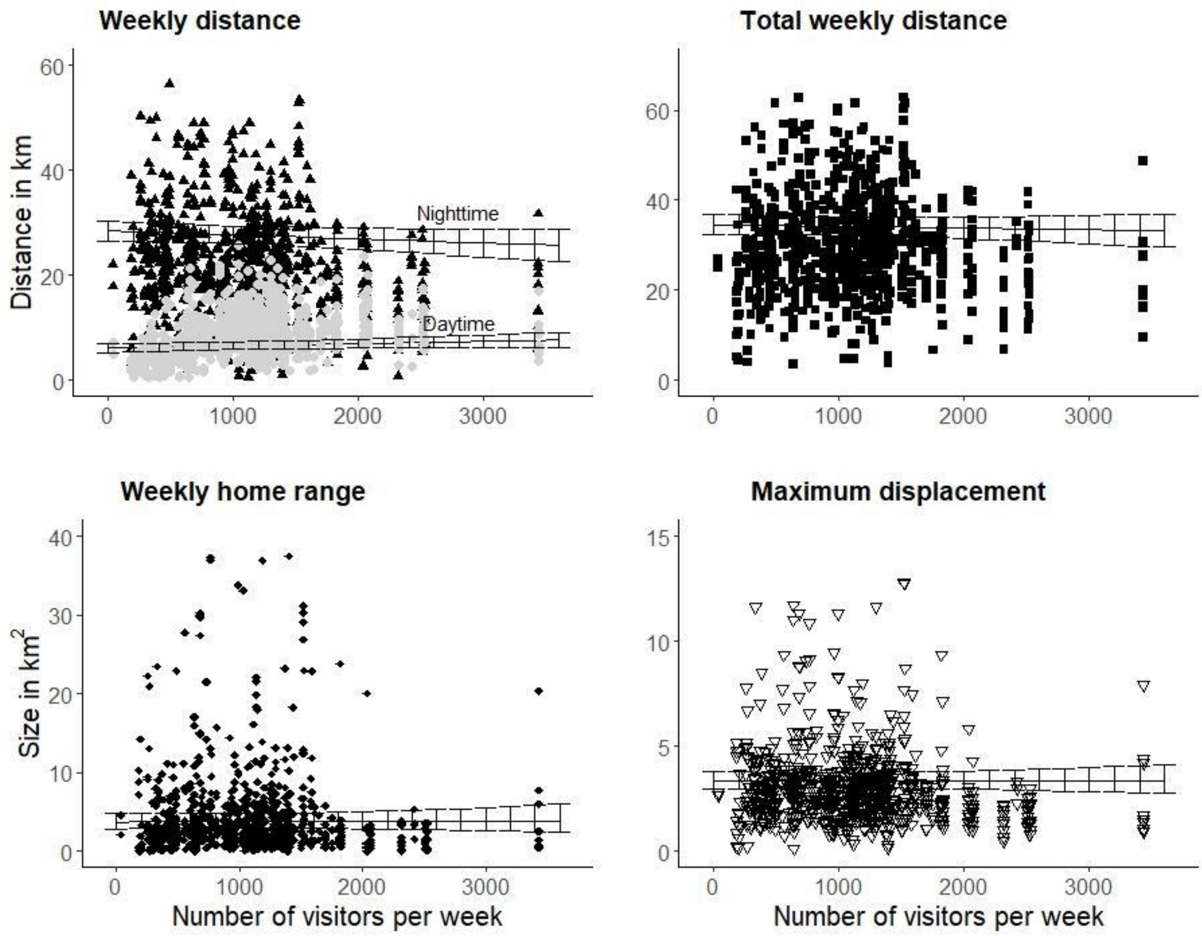

Figure A.2: Changes in the movement of wild boar in relation to numbers of visitors per week: A) total weekly distance at nighttime and daytime B) total weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week)