Czech University of Life Sciences

Faculty of Forestry and Wood Sciences
Department of Game Management and Wildlife Biology

Effects of wildlife management and human disturbance on movements and activity of mammalian wildlife

Ph.D. Thesis

Author: MSc. Astrid Olejarz
Supervisor: Dr. hab. Tomasz Podgórski
Consultant: Ing. Miloš Ježek, Ph.D.

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Abstract

Humans exert various impacts on wildlife by modifying their habitats and interactions with wildlife through agricultural, industrial, and management activities. Consequently, wildlife responds to these pressures by modifying behaviour, habitat use and vital rates. This doctoral thesis aims to analyse the impact of various anthropogenic activities on terrestrial mammals through spatial and temporal analysis of their behaviour. For this purpose, I i) measured the effect of human recreational activity during the COVID-19 pandemic in a suburban forest in the Czech Republic on GPS-collared wild boar *(Sus scrofa)* movement and sleep behaviour, ii) analysed spatial behavioural plasticity of wild boar in response to drive hunts in the Czech Republic and Sweden, and iii) analysed, based on existing literature, the impact of supplementary feeding on the home range size of terrestrial mammals. I showed that wild boar was moderately vulnerable to high human presence resulting from COVID-19 lockdown related increased recreational activity in the forest. While movement and space use metrics of wild boar did not change in response to high human activity, they displayed higher energy expenditure and disrupted sleep patterns, which may have potentially detrimental fitness consequences. Similarly, wild boar movements showed resilience to increasing intensity of drive hunts. However, drive hunts generated a shift in wild boar behavioural response. With an increasing number of experienced hunts, wild boar showed predominantly flight behaviour rather than hiding during drive hunts. Frequent drive hunts repeated over the same area can thus lead to population dispersion with potentially negative impacts on crop damage and disease transmission. Using quantitative meta-analysis of the existing literature, I detected an overall tendency of reduced home range in response to supplementary feeding in terrestrial mammals. However, the effect was inconsistent with strength and directions of the trends depending on species biology, feeding regime and methods of data collection and analysis. These results suggest that complex mechanisms of home range behaviour can make it insensitive to manipulation with supplementary feeding as a universal tool in wildlife management. More comprehensive research and transparent policy in wildlife management are needed to better understand the anthropogenic impact on wildlife. Spatial analyses of animal behaviour are a crucial and future-orientated tool for detecting human-caused changes in wildlife and should be used for science-based wildlife management.

Keywords

Anthropogenic pressure, behavioural plasticity, COVID-19 lockdown, drive hunts, home range, movement ecology, supplementary feeding, *Sus scrofa,* wildlife management

Author's Declaration

I hereby declare that this Doctoral Thesis (Detection of anthropogenic impact on terrestrial mammals through spatial analysis) is my own work and quoted only according to the references listed within. Neither any part of this thesis has been submitted as fulfilment to award a degree to any other institution. The thesis was written under the guidance of Dr. hab. Tomasz Podgórski.

I agree to the publication of the thesis according to Act No. 111/1998 Coll. on universities as amended, regardless of the outcome of its defence.

Prague, 2024

Signature……………………………

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1. Introduction

Humans, like other organisms, modify their environment. With human growth expansion and improved technology, however, the level of environmental modification has increased drastically since the Industrial Revolution into a “human-dominated landscape” (Kroll-Smith & Leon-Corwin, 2023; Vitousek et al., 1997). The environmental modifications are of fundamental changes, such as agricultural fields, pastures, conversion of forest or urban landscapes, altering more than 75% of Earth's ice-free land (Ellis & Ramankutty, 2008; Vitousek et al., 1997). The consequences of landscape modification are increased food, timber, and housing production, which enhances human economic and social life (Foley et al., 2005; Shah et al., 2019). The significant human or “anthropogenic” modifications on the earth's climate and ecosystem (Ellis & Ramankutty, 2008) created a new geological term for the Earth's present history, the “Anthropocene” (Crutzen & Stoermer, 2013; Lewis & Maslin, 2015).

Despite the human benefits in the Anthropocene, for most wildlife, it implies progressively disturbed and fragmented habitats (Brearley et al., 2013). Only a few intact natural habitats and fragments remain (Saunders et al., 1991), resulting in reduced biodiversity (Brooks et al., 2002; Foley et al., 2005). Mammals in highly fragmented habitats are at greater risk of extinction (Crooks et al., 2017). Especially large mammals with specialised resource requirements, wide-ranging and low density, are particularly vulnerable to the processes of habitat loss and fragmentation (Crooks, 2002; Noss et al., 1996; S. P. D. Riley et al., 2003). Also, extensive deforestation makes other animal classes, such as birds, highly vulnerable to extinction (Sodhi et al., 2010), and amphibian species richness decreases continuously with the land-use modification gradient (Wanger et al., 2010). In summary, the reduction in biodiversity leads to a declining genetic divergence among populations (Gibbs, 2001) and displaying less adaptation to changing environments (Hohenlohe et al., 2021), such as global warming (Höglund et al., 2021). In addition, evidence is growing that with the modifications in land use, the probability of animal-human interactions is rising and thus; disease transmission (Johnson et al., 2020) and human-wildlife conflicts (Magle et al., 2014; Poessel et al., 2017). Anthropogenic activities may affect the behavioural patterns of wildlife population through changes in the composition of the landscape and the availability of resources (Tucker et al., 2018). Dense transportation networks alter the movement behaviour of wildlife (Jerina, 2012; Saint-Andrieux et al., 2020; Trombulak & Frissell, 2000). Anthropogenic activities during the daytime shift the temporal dynamics of wildlife towards night (Gaynor et al., 2018; Podgórski et al., 2013). Species with high fragmented habitats have smaller ranges and a lower proportion of high-suitability habitats within their range (Crooks et al., 2017). For example, various deer species exposed to high anthropogenic pressure had a small home range size (Gillich et al., 2021; Grund et al., 2002; Seip et al., 2007). Preserved natural areas are facing an increased use of human recreational activities. To avoid human contact, the wildlife alters their movement, bedding, and foraging behaviour (Jiang et al., 2007). Red deer (*Cervus elaphus*) in the Highlands of Scotland are farther away from hiking trails on weekends than during the week (Sibbald et al., 2011). In Norway, mountain biking led red deer to avoid bike paths more than regular hiking trails (Scholten et al., 2018). Interestingly, some species seem to profit from the anthropogenic modifications on the landscape and to expand even in population size (Podgórski et al., 2013; Stillfried et al., 2017). For example, racoon (*Procyon lotor*) or black tailed prairie dog (*Cynomys ludovicianus*) densities are much greater in peri-urban and urban areas than in other habitats (Magle et al., 2007; S. Riley et al., 2011). 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 proximity (Slabbekoorn, 2013). As urban areas were created to produce human resources, they also increasingly did so for certain wildlife species (Chace & Walsh, 2006). Also, the wild boar (*Sus scrofa*) is one of the few mammal species with those plastic features (Bevins et al., 2014; Gamelon et al., 2013). With an increasing population, the wild boar is one of the most widespread mammals in the world (Apollonio et al., 2010; Russo et al., 1997). Some wild boar populations expanded from the natural environment by intruding into human-dominated landscapes such as peri-urban and urban areas (Cahill et al., 2012; Castillo-Contreras et al., 2018). Anthropogenic food, such as garbage as fallback food, is used as a new food resource (Stillfried et al., 2017). As a result, urban wild boar display a larger body size and better body condition than rural wild boar (Castillo-Contreras et al., 2021). In addition, the home ranges of wild boar in urban areas are significantly smaller than those of wild boar in natural habitats (Csókás et al., 2020). Under high human presence, wild boar display a higher nocturnal activity and rest under dense shrubby areas during the daytime (Boitani et al., 1994). The overabundance of wild boar in certain areas is raising substantial economic and ecologic conflicts, with the species being labelled as "invasive" or "pest" (Mayer, 2017). For example, wild boar species in Argentina are invasive, causing multiple threats (Ballari & Barrios-García, 2014). Damages on agricultural areas (Rutten et al., 2019; Schley et al., 2008), forest ecosystems (Bratton, 1975), vehicle collision (Kruuse et al., 2016), and disease transmission to domestic livestock (Bevins et al., 2014) are increasing, forcing the need for wild boar population control and reduction (Killian et al., 2006).

2. Objectives

This dissertation aims to test mammalian wildlife's behavioural responses to anthropogenic pressures related to human activity and wildlife management. Therefore, high-frequent and accurate GPS positions and bio-logger data from collared wild boar have been collected over multiple years and locations. Furthermore, the results of wildlife's behavioural responses towards anthropogenic pressure are supplemented with meta-analyses of existing scientific literature. The main target species of the dissertation is the wild boar (*Sus scrofa*), whose growing population in central Europe and current disease outbreaks show the complex interaction with humans and its need for wildlife management. The dissertation also gives general conclusions for terrestrial mammals in relation to anthropogenic pressures.

The study will focus on the following three specific objectives:

1) To what extent does the COVID-19 lockdown influence the spatial and sleep behaviour of wild boar?
2) Which behavioural adjustments does the wild boar develop when subjected to drive hunt pressure?
3) To what extent does supplementary feeding affect the home range behaviour of terrestrial mammals?

3. Literature review

Anthropogenic impacts on wildlife are complex, multifaceted and can be both positive and negative (Bhatia et al., 2020; Frank, 2016). Various research studies have tried to understand the anthropogenic impact by characterising their nature and examining the challenges of living with wildlife (Bhatia et al., 2020). In this dissertation I will focus on three different anthropogenic impacts and their known effects on wildlife. In the two case studies of chapter 3.1 and 3.2 I concentrate mainly on the anthropogenic impact on the wild boar (*Sus scrofa*), as this species provides ideal conditions for studying human effects on the behaviour of wild animals. In chapter 3.3 I provide with a literature search a general understanding of the effect of an anthropogenic impact on all mammalian wildlife.

The European wild boar ranks among the world's most widespread large mammal species (Apollonio et al., 2010). Its geographical range expanded drastically in the late 20th century to all continents apart from Antarctica (Markov et al., 2022). As global warming progresses, it is expected that the local population density and spread of wild boar to the north and northeast will continue (Melis et al., 2006). However, not all areas contain a naturally established wild boar population (Markov et al., 2022), but also intentionally released by humans. Those invasive wild boar populations are causing threat to native species and the physical environment (Olson, 2006). In Argentina, for example, where the wild boar is an invasive species, seed dispersal of native shrubs, such as tortuous mesquite (*Prosopis flexuosa)* and trees monkey puzzle tree (*Araucaria Araucana)* is negatively affected (Sanguinetti & Kitzberger, 2010). The speed at which a wild boar population can spread depends heavily on exogenous factors (Gethöffer et al., 2007). Central Europe display currently an optimal environmental habitat for wild boar population growth (Gethöffer et al., 2007), with moderate winters and sufficient rainfall. Interestingly, the predation by wolves has only minor impact on the abundance of wild boar population across the Eurasian range (Melis et al., 2006).

In the scientific literature, wild boar preferred habitat displays woody habitats with a high proportion of mature broad-leaved trees. Those mix forests provide the wild boar sufficient resting places and adequate food (Meriggi & Sacchi, 2001). As an opportunistic omnivore, the preferred wild boar diet is energy-rich plant seedlings such as acorns. However, vegetables and small animals, such as insects and earthworms, are also part of the diet (Schley & Roper, 2003). In times of limited food resources and close urban settlements, wild boar also consumes anthropogenic food such as garbage (Stillfried et al., 2017). With increasing urbanisation, the number of wild boar in the cities is rising, and anthropogenic food is becoming part of their main diet. Consequently, urban wild boar possess a larger body size and better body condition than rural wild boar (Castillo-Contreras et al., 2021).

Compared to other ungulates in Europe, the wild boar has a very high reproductive capacity, showing traits from both K -and r-strategists (Frauendorf et al., 2016). Generally, a female adult wild boar gives birth to one litter per year. However, under optimal environmental conditions, the litter size can increase to up to two litters per year (Kozdrowski & Dubiel, 2004). The proportion of breeding females depends strongly on the weight of the female wild boar (Rosell et al., 2012). Female wild boar stay in small groups, up to four adults with their young offspring (Maselli et al., 2014). The social structure in a group is matrilineal, based on several generations of female adults and their offspring (Poteaux et al., 2009). In contrast, male wild boar stay solitary for a lifetime (Maselli et al., 2014).

The wild boar ranging, and activity behaviour are highly adjusted to human presence. Adapted to human activity patterns over the daytime, wild boar are mainly active at night, after sunset until sunrise (Russo et al., 1997). During the daytime, wild boar rest in forests and dense shrubbery areas (Boitani et al., 1994). Activity behaviour is also closely linked to weather conditions. Extreme weather events such as heavy snowfall, extreme heat, or cold conditions decrease the activity ratio of wild boar (Thurfjell et al., 2014). For example, in Spain, wild boar are active mainly over the winter season, expressing moderate weather conditions with wet soil conditions (Cahill et al., 2003).

The home range size of wild boar varies within season (Geisser & Reyer, 2005), displaying the largest size in autumn, which is the mating season. Especially male wild boar are roaming widely, undertaking often mating excursions outside of their home range in search of receptive females (Singer et al., 1981). High home range overlaps have been measured between female wild boar but not for male wild boar (Boitani et al., 1994). Besides seasonal factors, environmental conditions also shape the wild boar home range size (Johann, 2020). With increasing temperatures, elevation, and altitude, wild boar home ranges increase in their size. In contrast, rainfall decreases wild boar home range size (Schlichting et al., 2016). Furthermore, urban areas are significantly smaller than those of wild boar that live in natural habitats (Csókás et al., 2020)

3.1 Recreational and COVID-19 related human activity and wild boar behaviour

A global network of protected areas has been established to prevent the continuous depletion of biodiversity (Laurance et al., 2012; Watson et al., 2014) and to protect wildlife populations and habitats (Joppa et al., 2008). Those protected areas prevent strong landscape conversions (Bruner et al., 2001; Joppa & Pfaff, 2010), such as curtailing deforestation in developing countries (Naughton-Treves et al., 2005), and increase wildlife population trends (Barnes et al., 2016). However, the anthropogenic value of protected areas has also been recognised through recreational activities (Nilsson et al., 2011; O'Brien & Snowdon, 2007), and the number of visitors is rising (Balmford et al., 2009). Nature-based tourism has become a crucial economic source for the protected areas (Watson et al., 2014). For example, in the Afromontane forests, protected areas for the critically endangered mountain gorillas (*Gorilla beringei beringei*) (Robbins et al., 2018) are financially supported mainly due to international tourism (Maekawa et al., 2013). However, increasing outdoor recreational activities in protected areas can negatively impact the recreation of wildlife and habitats (Marzano & Dandy, 2012). Adverse consequences are changes in wildlife behaviour leading to the spread of pests and pathogens (Jiang et al., 2007; Scholten et al., 2018; Sibbald et al., 2011).

The outbreak of the COVID-19 pandemic created drastic changes in human activity (Bar, 2021). Some areas were exposed to decreased human activity following reduced disturbance, noise, and pollution (Bar, 2021). As a result, wildlife increased their habitat use (Behera et al., 2022) or shifted towards diurnal activity (Behera et al., 2022; Manenti et al., 2020; Zukerman et al., 2021). Other areas such as natural parks near urban areas became targets for daily tourism (Cukor et al., 2021; Derks et al., 2020; Venter et al., 2020). The interest in outdoor recreational activities in certain areas increased up to 5-fold more human visitations to previous years (Cukor et al., 2021; Hockenhull et al., 2021; Kleinschroth & Kowarik, 2020; Weed, 2020). The influx of human recreational confinement to natural parks during the initial COVID-19 lockdowns provided the opportunity to investigate their impact on animal behaviour (Bates et al., 2020).

3.2 Hunting activity and wild boar behaviour

Wildlife does not restrict their living habitats to protected areas only, potentially creating human-wildlife conflicts, by such activities as damaging agricultural fields (Cozzi et al., 2019; Fattebert et al., 2017; Geisser & Reyer, 2004) and reducing forest regeneration through high browsing pressure on young trees in the forest (Akashi, 2009; Boulanger et al., 2015; Horsley et al., 2003). Crop damage by small and large wildlife often leads to significant economic losses (Linkie et al., 2007). For example, wildlife was responsible for 85% of crop loss in the Kibale National Park of Uganda (Naughton-Treves, 2008). To reduce the economic damage, local authorities compensate for wildlife damages. However, rising costs for compensation pose problems for local authorities (Cozzi et al., 2019).

Appropriate wildlife management is needed to mitigate conflicts and create solutions for a coexistence between wildlife and humans (Frank, 2016; Messmer, 2009). Several management strategies exist to maintain ecological and economical wildlife in human-dominated areas (Kamler & Drimaj, 2021; Vajas et al., 2020). One of the most efficient and frequently applied strategies in wildlife management is mortality control, specifically hunting (Kamler & Drimaj, 2021; Vajas et al., 2020). Different hunting types vary in their impact on wildlife (Kamler & Drimaj, 2021). While single hunts are carried out at a single place and hunter, drive hunts involve several hunters, dogs and beaters over a larger area (Scillitani et al., 2009). The central task of the beaters and dogs is to flush the wildlife out of their hiding places in the direction of the hunters (Vajas et al., 2020). The main season for drive hunts is between autumn and winter (Geisser & Reyer, 2004), with the main target to hunt large ungulates, such as deer and wild boar (Soliño et al., 2016).

Drive hunts are considered as an effective management tool, forcing wildlife such as the wild boar to leave their resting sites (Sodeikat & Pohlmeyer, 2003) and reducing the target game's population (Sweitzer et al., 2000). A lower wild boar density in Switzerland entails a reduction in crop damage (Geisser & Reyer, 2004). In addition, large carnivore species such as wolves (*Canis lupus*) and brown bears (*Ursus arctos*) in Europe might gain further acceptance from the public if the population is kept at an acceptable level through hunting (Kaltenborn et al., 2013). However, negative consequences from drive hunts also emerge when hunting mainly large adult individuals, creating selection on morphological traits (Coltman et al., 2003). In rams, the body weight and horn size have declined significantly over time due to hunting activity (Coltman et al., 2003). In addition, the lack of adult-dominant wildlife destabilised the population structure (Braga et al., 2010). Moreover, hunting may cause loss of social knowledge, sexually selected infanticide, habitat changes among reproductive females, and changes in offspring sex ratio (Milner et al., 2007; Sæther et al., 2004). For example, in Norway, 70% of the male moose (*Alces alces*) population is harvested by age three affecting the offspring sex ratio (Solberg et al., 1999, 2000). Furthermore, more vehicle collisions with red deer (*Cervus elaphus*) have been documented after hunting events (Saint-Andrieux et al., 2020) and increased bark browsing (Rajský et al., 2008), creating another human-wildlife effect. Hunting can exert selection on morphological traits such as a decline in body weight and horn size in rams (*Ovis canadensis*) (Coltman et al., 2003; Douhard et al., 2016). Twenty percent of harvested organisms declined in size-related traits and nearly 25% in life history traits (Darimont et al., 2009). Those phenotypic changes are much more rapid than in other non-harvest-related systems (Darimont et al., 2009). However, the impact of human hunting can also shape behavioural traits (Ciuti et al., 2012). Few studies have examined the impact of hunts on behavioural traits. For example, hunted elk (*Cervus elaphus*) showed bolder behaviour and increased movement than surviving elks (Ciuti et al., 2012). Bolder brown bears (*Ursus arctos*) were more likely to be hunted, as they were using habitats near roads (Leclerc et al., 2019). The consequences of drive hunts on the spatial behaviour of wildlife are hunt- and species-dependent. Different spatial responses have been reported in the case of the wild boar species (Keuling et al., 2008, 2010; Thurfjell et al., 2013). Furthermore, the ability of wildlife to learn and adapt to frequently occurring drive hunts shifts spatial responses to improve their survival rate (Sommer-Trembo et al., 2016; Thurfjell et al., 2017).

3.3 Supplementary feeding of wildlife

Food is a crucial resource for the population's survival, equally true for humans and wildlife. Most of the land conversion by humans aims to increase and ensure human food production. Human-wildlife conflicts arise when wildlife compete for food resources in human-dominated landscapes, often referred to as agricultural damages (Barrios-Garcia & Ballari, 2012; Murray et al., 2016) or browsing pressure (van Beest et al., 2010; Zamora et al., 2001). As a solution, the current wildlife management implication relies on either reducing the wildlife population or feeding it alternative food.

Supplementary feeding is defined as placing food into the environment to augment regular food sources (Sorensen et al., 2014) or attracting animals (Griffin & Ciuti, 2023). The extent, intensity, and form of wildlife feeding vary widely depending on its intended purpose. In game management, supplementary feeding has an intentional target to keep agricultural damages low (Barrios-Garcia & Ballari, 2012; Murray et al., 2016) and wildlife population stable (Bartoskewitz et al., 2003; Bruinderink et al., 1994; Milner et al., 2014). However, there are numerous examples where those management goals were not achieved using supplementary feeding (Peterson & Messmer, 2007; Van Beest et al., 2010). The anthropogenic impact on wildlife through supplementary feeding is tremendous: 2.8 trillion tons of bait are used annually in the USA (Oro et al., 2013), and 42 million USD worth of feed was provided to wildlife in

Sweden in 2013 (Felton et al., 2017). Eighty-three percent of European national parks manage ungulate by supplementary feeding (van Beeck Calkoen et al., 2020). In most central European countries (e.g., Poland and the Czech Republic), supplementary feeding of game in adverse climatic conditions is compulsory by law (Ježek et al., 2016; Mikulka et al., 2018). An increasing amount of wildlife receives supplementary food (Tryjanowski et al., 2017). For example, 83,367 ungulate feeding sites were reported in 2004 outside of national parks in the Czech Republic (Bartos et al., 2010). In conservation practice, subsidiary food can help recover and sustain threatened species (Thierry et al., 2020). Supplementary feeding has become ubiquitous in human-wildlife coexistence, not only through professional management but also by recreational nature enthusiasts. Backyard bird feeding has become very popular with millions of households, providing half a million tonnes of birdseed annually in the USA and UK (Robb et al., 2008). Baiting with food to facilitate wildlife observations has also become common in ecotourism and nature photography (Orams, 2002). In Japan, millions of tourists travel to Nara yearly to feed more than 1000 sika deer (*Cervus nippon*), which are designated as "natural monuments" in the city park (Torii & Tatsuzawa, 2009). In addition, up to 40% of all food products on Earth are wasted (Oro et al., 2013). Many human food waste products unintentionally serve as food resources to wildlife, such as leftovers from fish catches, hunted game offal, and municipal waste (Murray et al., 2016; Oro et al., 2013). Annually, tonnes of big game carrion in Europe and the USA serve as food for most vertebrate scavengers (Mateo-Tomás et al., 2015; Oro et al., 2013; Vicente et al., 2011). Human food waste has always attracted wildlife, and commensalism is postulated to play a major role in the domestication of dogs and pigs (Axelsson et al., 2013; Larson & Fuller, 2014).

Regardless of the motives to provide wild animals with food, supplementary feeding has wide-ranging consequences (Oro et al., 2013). Anthropogenic food is shaping micro-evolutionary changes in wildlife (Grant & Grant, 2008) and can result in greater body size (Castillo-Contreras et al., 2018; Peterson & Messmer, 2007), higher reproductive rates (Ballesteros et al., 2013) and reduced mortality (Apollonio et al., 2010; Putman & Staines, 2004). For example, winter supplementary-fed mule deer (*Odocoileus hemionus*) had a higher live body condition, lower mortality, and produced more fawns (Peterson & Messmer, 2007). Besides life-history traits, feeding-induced artificial selection of animal behavioural traits has been observed, reducing human fear and potentially augmenting human-wildlife conflicts (Griffin et al., 2022; Woodroffe et al., 2005). Feeding stations can act as pathogen transmission hotspots where higher risk is associated with aggregation of individuals and accumulation of pathogens (Becker

& Hall, 2014; Murray et al., 2016; Oja et al., 2017). Supplementary feeding can also have multiple indirect effects on ecosystems through modification of foraging patterns and habitat use, with impacts on plant species richness and composition (Oro et al., 2013; Smith, 2001), survival of ground-nesting birds (Oja et al., 2015; Selva et al., 2014), and habitat structure (Marie, 2011). For example, browsing damage by white-tailed deer (*Odocoileus virginianus*) was the highest around feeding stations in South Texas, USA (Cooper et al., 2006).

4. Material and Methods

The dissertation's methodology includes different analytical approaches to measure wildlife movement data and the anthropogenic impact on wildlife behaviour. In particular, I focused on studying the spatial behaviour of the wild boar (*Sus scrofa*) equipped with hybrid GPS and bio-logger collars.

GPS tracking is a well-established method for studying animal movements and behaviour (Wittemyer et al., 2019). Recently, the miniaturisation of tracking devices, their higher accuracy, and advances in analytical approaches created new opportunities for research directions beyond simple movement analysis (Cagnacci et al., 2010; Joo et al., 2020; Spiegel et al., 2017). In the Czech Republic wild boar were equipped with modern hybrid bio-logging collars comprising a GPS unit from Vectronic Aerospace GmBH and a Daily Diary tag from Wildbyte Technolgies Ltd. Collected data from collars were either stored on a microSD card inside the housing of the Daily Diary or sent by SMS to an online server. Calculating animal`s home ranges is one of the most common methods of obtaining information about the wildlife population (Schlichting et al., 2016). However, the calculation of home ranges is not uniform, as home ranges differ over time, depending on the animal species and individual (R. A. Powell & Mitchell, 2012). For example, an animal`s home range size can be affected by supplementary feeding sites, which increase the frequency of GPS points to a certain location (Olejarz & Podgórski, 2024) or by the length of GPS data collected for a certain analysis (Olejarz et al., 2024). To reflect an animal home range as accurately as possible, various methods have been developed. One standard method is the Minimum Convex Polygon (MCP) for calculating animal home ranges (Hayne, 1949). As the name implies, home ranges are calculated from convex polygons around the GPS point of the animal (Boyle et al., 2009) with interior angles smaller than 180 degrees. The advantage of MCP is that it is a relatively easy approach and has a high level of accuracy when only a few GPS points are available. Consequently, I calculated daily range size for drive hunt events with the MCP method (Olejarz et al., 2024). However, MCP often overestimates the actual home range area, including areas the animal has not originally used. Another widespread method to calculate home ranges is the so-called Kernel Density distribution (KDE). In 1989, Worton developed a method of nonparametric analysis of home ranges. KDE uses utilisation distribution to describe the probability of the animals´ location (Worton, 1989). KDEs are relatively unbiased regarding outliers and account for centres of activity (Börger et al., 2006; R. Powell, 2000). The KDE methods are better suited to study the effects of resource distribution on space use (Olejarz & Podgórski, 2024). Due to

KDE's complexity in calculation, it is relatively sensitive to the number of GPS points. The fewer GPS points available, the more inaccurate the KDE home range calculation (Laver & Kelly, 2008). Therefore, I applied the KDE method to detect seasonal variation in wild boar`s home range size (Olejarz et al., 2023). The possibility of collecting GPS data in a specific and regular time interval enables further analysis besides space use (Calenge et al., 2009), such as changes in behaviour (Bonnot et al., 2013). In drive hunt events, I discovered in spatial data that wild boar displayed behavioural plasticity depending on how much drive hunt experience they have gained within a season.

Detailed spatial data collection and analysis methodologies are explained in the original research articles included in this PhD dissertation. Here I briefly describe the main methodological approaches used in the presented research articles:

4.1 An empirical study for behavioural responses of wild boar to pulses of human leisure activity

To determine the effects of changing human presence induced by the COVID-19 pandemic on the wild boar, I tracked 63 wild boars with hybrid bio-logging collars comprising a GPS unit and a Daily Diary tag within the municipality "Kostelec nad Černými Lesy", district Prague-East of the Czech Republic throughout the period from April 2019 to November 2021. Using GPS-telemetry data, I calculated weekly distance travelled as a sum of all distances between consecutive 30-minute relocations (i.e., step lengths) per week. Furthermore, I calculated the weekly home range as 95% kernel utilisation distribution (UD) isopleths using the "reference bandwidth" method and the 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, I used generalised mixed-effects models. In addition, I used the vectorial sum of dynamic body acceleration (VeDBA) from the daily diaries to calculate the weekly energy expenditure. I identified periods of sleep in the daily diary data (Mortlock et al., 2024). Finally, I run linear mixed models to examine the differences in the energy expenditure and sleeping behaviour in relation to human visitation.

4.2 A cross-sectional study on wild boar behavioural plasticity to drive hunts

The behavioural plasticity in wild boar to hunting disturbances was evaluated based on collected movement data of 55 GPS-collared wild boar in four hunting estates in Sweden and the Czech Republic over three hunting seasons from 2019 to 2022. For each drive, I collected the exact hunting area, date, time and duration of the drive, numbers of shooters, beaters and dogs, and, if available, the number of wild boar killed. From the GPS data, I calculated daily ranges, daily distance, centroid distance and overlapping area of the home range with the hunting area for each wild boar. In addition, wild boar flight duration and distance were identified based on the net square displacement (NSD) estimate. A linear mixed model determined the relationship between drive hunts and wild boar space use and movement. A cluster analysis was performed on the four different movement and space use metrics to identify two groups of individuals, “flee” or “hide”, during drive hunts. I built a generalised linear mixed model with binomial distribution to detect a shift in wild boar strategy during drive hunts with accumulated experience.

4.3 A quantitative review analysis on supplementary feeding

I conducted a quantitative review analysis of the impact of supplementary feeding on the home range size of terrestrial mammals. On 21 March 2022, I searched publications that reported home range sizes with and without supplementary feeding, in Web of Science (WoS) and Scopus, two publisher-independent global citation databases. After the final screening, 28 scientific studies were approved to fit the analysis's scope. I extracted home range size, standard deviation (SD), and sample size from each publication for the experimental animals with supplementary feeding and the control group without supplementary feeding. In addition, for each home range comparison, I compiled information about the species, its taxonomic group (rodent, carnivore, and ungulate), individual's sex, supplementary food amount (limited or ad libitum) and feeding duration, spatial confinement (free-ranging or enclosure), source of spatial data (telemetry or capture-mark-recapture), and home range estimator (kernel density estimation (KDE) or minimum convex polygon (MCP)). I added body mass for each species from the panTHERIA database (Jones et al., 2009) to the collected dataset. Moreover, I divided the publications into intentional and unintentional feeding studies. To measure the change of the home range size from no-feeding to feeding treatment, I used the Hedges'g estimator of the effect size. Meta-analytic mixed-effects models, fitted with the function rma.rm of the metafor package, were used to examine the effects of supplementary feeding on home range size.

5. Results

The thesis` objectives were addressed through three original studies published in scientific journals with impact factor (IF). The publications focus on various detections of anthropogenic impact on terrestrial mammals through spatial analysis.

The first study analysed the influence of the COVID-19 lockdown on wild boars' spatial and sleep behaviour.

5.1 Olejarz A, Faltusová M, Börger L, Güldenpfennig J, Jarský V, Ježek M, Mortlock E, Silovský V, Podgórski T (2023) 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. Science of The Total Environment 879:163106 http://dx.doi.org/10.1016/j.scitotenv.2023.163106

The second study analysed the behavioural plasticity of wild boar when subjected to high drive hunt pressure.

5.2 Olejarz, A., Augustsson, E., Kjellander, P., Ježek, M., & Podgórski, T. (2024). Experience shapes wild boar spatial response to drive hunts. Scientific Reports, 14(1), 19930. https://doi.org/10.1038/s41598-024-71098-8

The third study analysed the effect of supplementary feeding on the home range size of terrestrial mammals.

5.3 Olejarz, A., & Podgórski, T. (2024). No evidence for the consistent effect of supplementary feeding on home range size in terrestrial mammals. Proceedings of the Royal Society B: Biological Sciences, 291(2024), 20232889. https://doi.org/10.1098/rspb.2023.2889

5.1 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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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

Astrid Olejarz [a,*], Monika Faltusová [a], Luca Börger [b], Justine Güldenpfennig [a], Vilém Jarský [c], Miloš Ježek [a], Euan Mortlock [d], Václav Silovský [a], Tomasz Podgórski [a,e]

[a] *Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences,Czech University of Life Sciences, Kamýcká 129, Prague 6-Suchdol, 165 00, Czech Republic*
[b] *Department of Biosciences, Swansea University, Singleton Park, Swansea SA2 8PP, Wales, UK*
[c] *Department of Forestry and Wood Economics, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, Prague 6-Suchdol, 165 00, Czech Republic*
[d] *School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast BT95DL, Northern Ireland, UK*
[e] *Mammal Research Institute, Polish Academy of Sciences, Stoczek 1, 17-230 Białowieża, Poland*

HIGHLIGHTS

- COVID-19 countermeasures can cause pulses of human activity in the environment.
- We studied impacts of those anthropulses on the behaviour of wild boar.
- Wild boar spent more energy when human activity was high (e. g. COVID-19 lockdown).
- Wild boar had more fragmented sleep patterns when human activity was high.
- Movements (e.g. travel distance and home range) were not affected by human activity.

GRAPHICAL ABSTRACT

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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

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[*] Corresponding author.
E-mail address: olejarz@fld.czu.cz (A. Olejarz).

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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.

1. Introduction

Anthropogenic pressure is growing worldwide, forcing wildlife to adapt to new environmental conditions and human presence (Vitousek et al., 1997; Tuomainen and Candolin, 2011; Gunn et al., 2022). Expansion of urban areas (Gaynor et al., 2018), habitat fragmentation and landscape transformation (Bruinderink and 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 (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 and 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 and 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, Fig. 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 600 mm, 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 min 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 33 N 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 (Fig. 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 s) and created 30 min 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; Fig. 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

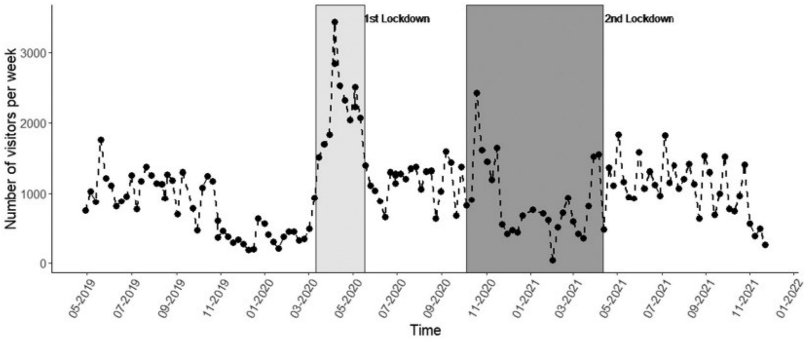

Fig. 1. Count of human visitation per week in the forest area near the capital city Prague and the two official COVID-19 lockdowns as defined by the "state of emergency" declared by the government of the Czech Republic.

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 5 min 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.

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, Fig. 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 whilst distance travelled during daytime tended to increase when more people visited the forest (Fig. 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).

Total Weekly distance travelled was highest in autumn (34.17 km on average; CI: 32.11–36.22; Fig. 2) and lowest in winter (25.40 km on average; CI:24.48–28.02; Fig. 2). Distance travelled at nighttime showed a similar pattern with a peak of 27.61 km (CI: 25.91–29.32) in autumn, whilst 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 3.36 km (CI: 3.01–3.76), respectively (Fig. 2).

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

Coefficient	Weekly daytime distance		Weekly nighttime distance		Weekly home range		Total weekly distance		Maximum displacement	
	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 to −9.33	**−0.72*****	−0.94 to −0.50	**−8.11*****	−9.95 to −6.26	**−0.44*****	−0.54 to −0.34
Summer	**3.89*****	3.33–4.44	**−8.61*****	−9.84 to −7.39	**−0.50*****	−0.66 to −0.33	**−4.66*****	−6.06 to −3.35	**−0.29*****	−0.37 to −0.22
Winter	**−1.41****	−2.26 to −0.57	**−7.44*****	−9.31 to −5.58	**−0.56*****	−0.81 to −0.30	**−8.77*****	−10.92 to −6.62	**−0.28*****	−0.40 to −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	

o σ2 = The random effect variance, σ2i, represents the mean random effect variance of the model.
o τ00 = Indicates how much groups or subjects differ from each other.
o ICC = (Intraclass-correlation coefficient) Is used in mixed models to give a sense of how much variance is explained by a random effect.
o N = Number of Animals.
o Observations = Total Number of Data.
o Marginal R2 = provides the variance explained only by fixed effects.

** p < 0.01.

*** p < 0.001.

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

Total weekly sleep time did not differ much between weeks with high (mean = 90.53 h per week, CI: 88.08–92.97, n = 212) and low human visitor numbers (mean = 91.41, CI: 87.9–94.93, n = 51; Fig. 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; Fig. 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; Fig. 4, Table 2).

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).

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 9 pm and 6 am. 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

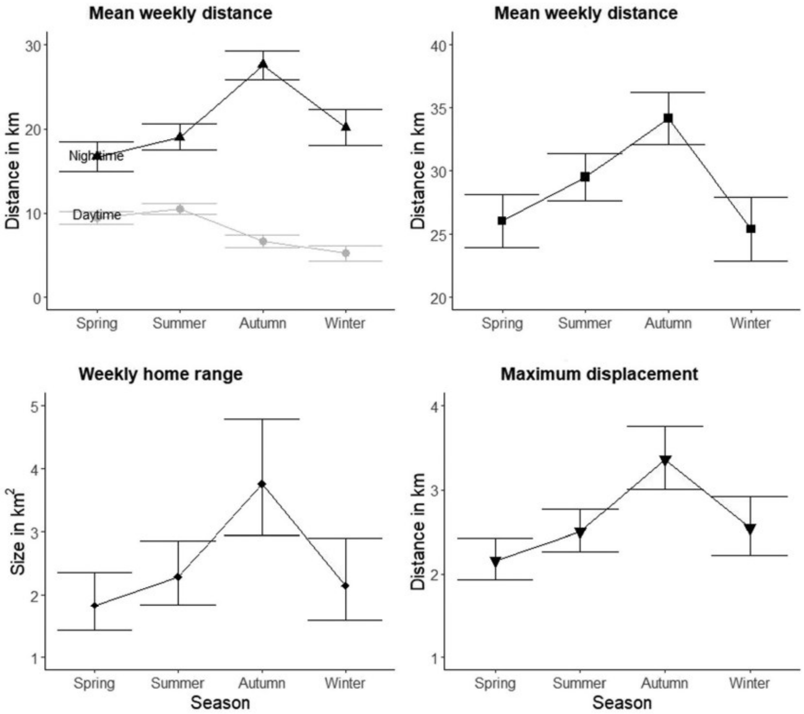

Fig. 2. Seasonal changes in the movement of wild boar: A) Mean weekly distance at nighttime and daytime B) Mean weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week).

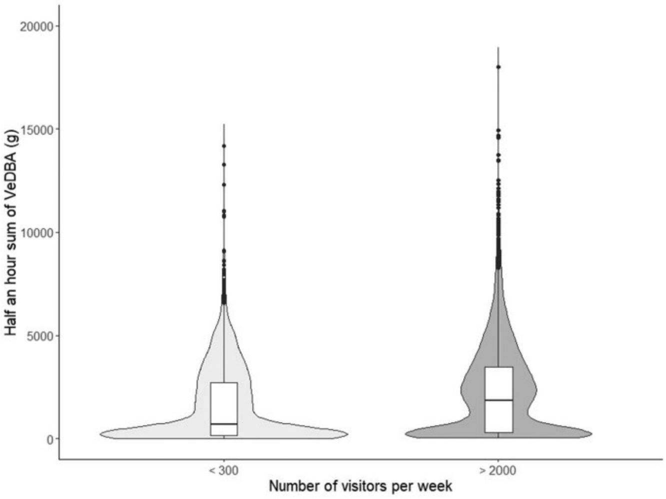

Fig. 3. Energy expenditure at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) number of human visitors.

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 and Massei, 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 and 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 Fattebert 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 (Fattebert 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

Table 2

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

Coefficient	Number weekly sleep bouts		Duration weekly sleep bouts		Total weekly sleep time		Weekly energy expenditure	
	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 to −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 to −0.04	−0.01	−0.09–0.07	**626.31***	83.59–1169.03
Random effects								
σ2	0.05		0.04		0.03		4,338,347.31	
τ00	0.17_{AnimalID}		0.11_{AnimalID}		0.02_{AnimalID}		$213{,}393.27_{\text{AnimalID}}$	
ICC	0.77		0.76		0.40		213,393.27	
N	13_{AnimalID}		13_{AnimalID}		13_{AnimalID}		12_{AnimalID}	
Observations	287		287		287		11,663	
Marginal R2/conditional R2	0.009/0.772		0.019/0.762		0.000/0.401		0.014/0.060	

o σ2 = The random effect variance, σ2i, represents the mean random effect variance of the model.

o τ00 = Indicates how much groups or subjects differ from each other.

o ICC = (Intraclass-correlation coefficient) Is used in mixed models to give a sense of how much variance is explained by a random effect.

o N = Number of Animals.

o Observations = Total Number of Data.

o Marginal R2 = provides the variance explained only by fixed effects.

o Conditional R2 = provides the variance explained by the entire model.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

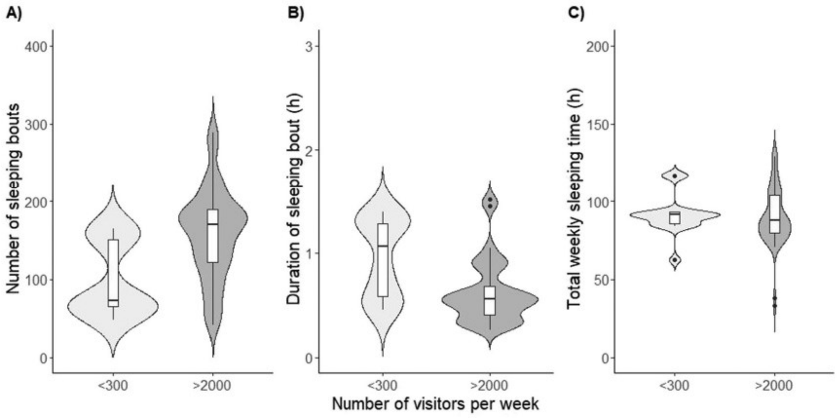

Fig. 4. Sleeping behaviour at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) numbers of human visitors: A) number of sleeping bouts per week B) duration of sleeping bouts C) total sleeping time per week.

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 and 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 particularly affected 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 winter snow 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 was 41% higher in the weeks where >2000 visitors were counted in the forest than in the weeks with <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) (Gunner et al., 2021).

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 2 h being enough (Gravett et al., 2017). In contrast, the total daily sleep duration of a sloth is between 9 and 10 h (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., 1997) 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 (Bonnet and Arand, 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 and 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.

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.

CRediT 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.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Milos Jezek reports financial support was provided by Ministry of Agriculture of the Czech Republic. Milos Jezek, Vaclav Silovsky reports financial support was provided by Ministry of Agriculture of the Czech Republic.

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Appendix A Appendices A

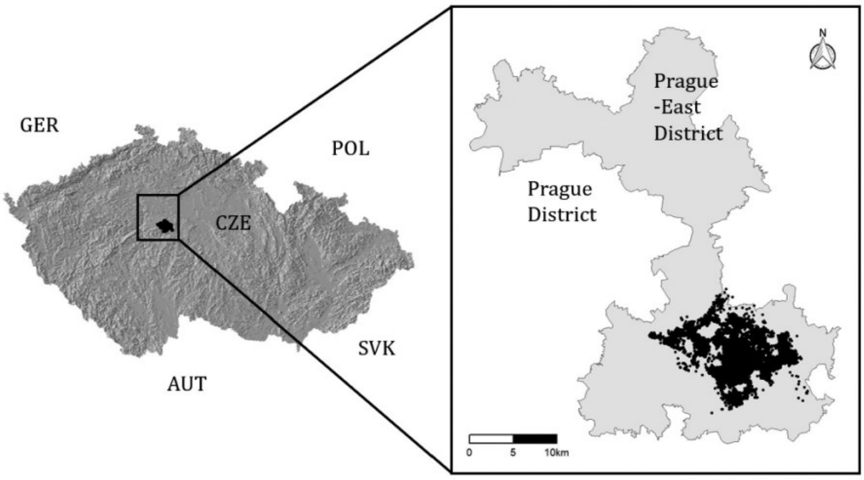

Fig. A.1. Location of the study area Prague-East in the Czech Republic (CZE) with GPS positions of the collared wild boars (black points).

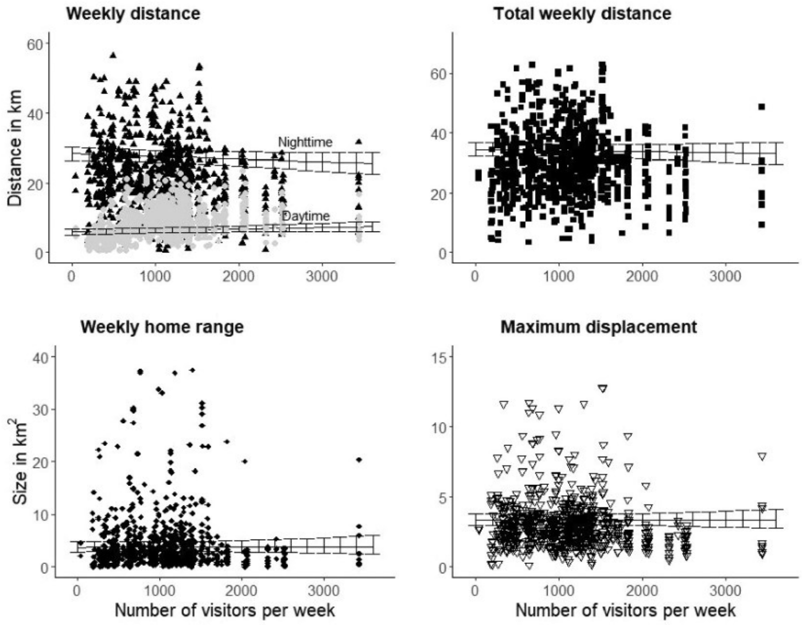

Fig. A.2. Changes in the movement of wild boar in relation to numbers of visitors per week: A) total weekly distance at nighttime and daytime B) total weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week).

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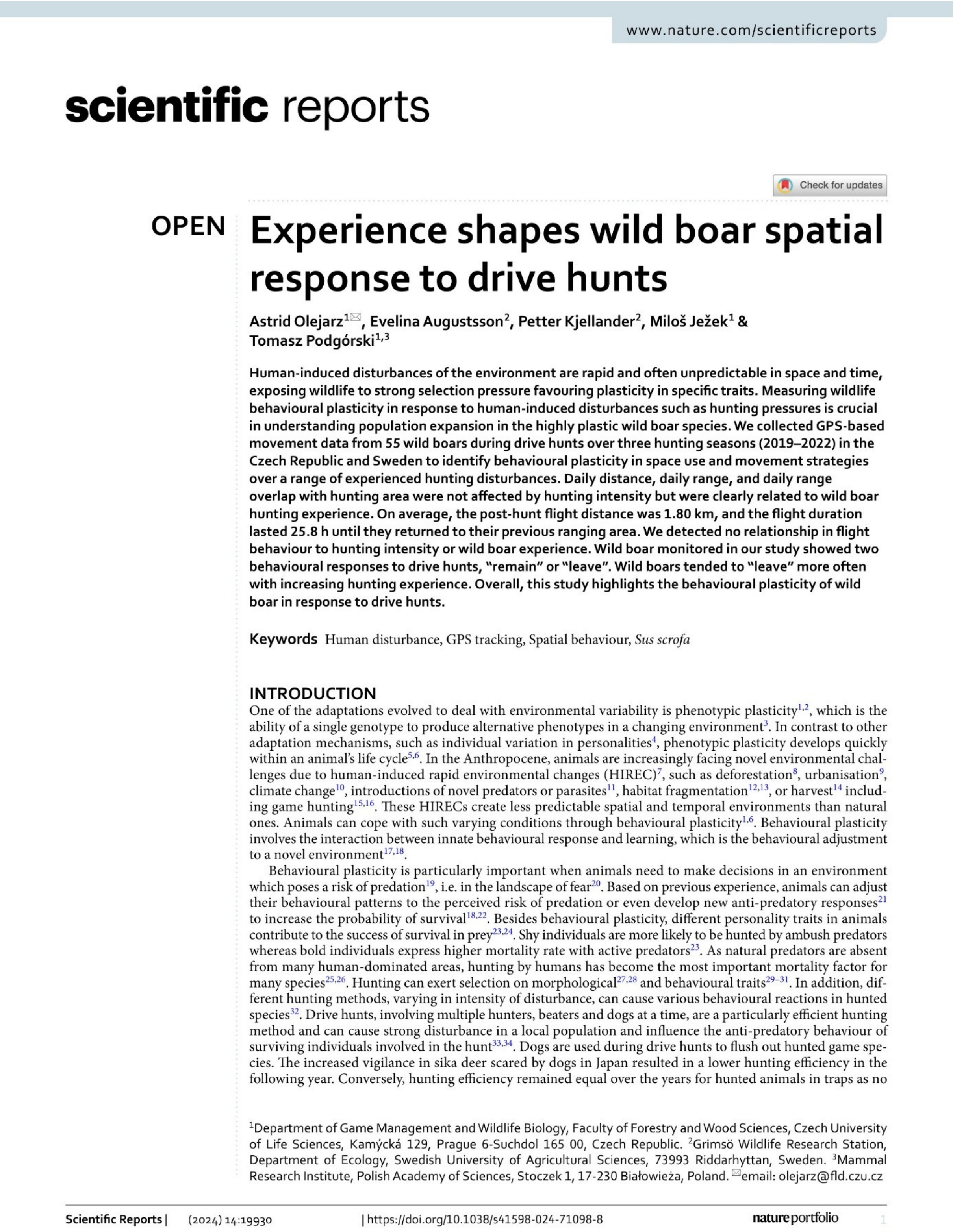
5.2 Experience shapes wild boar response to driven hunts



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Experience shapes wild boar spatial response to drive hunts

Astrid Olejarz[1]✉, Evelina Augustsson[2], Petter Kjellander[2], Miloš Ježek[1] &
Tomasz Podgórski[1,3]

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 environment[3]. In contrast to other adaptation mechanisms, such as individual variation in personalities[4], 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 deforestation[8], urbanisation[9], climate change[10], introductions of novel predators or parasites[11], habitat fragmentation[12,13], or harvest[14] 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 predation[19], i.e. in the landscape of fear[20]. Based on previous experience, animals can adjust their behavioural patterns to the perceived risk of predation or even develop new anti-predatory responses[21] 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 predators[23]. 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 species[32]. 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

[1]Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, Prague 6-Suchdol 165 00, Czech Republic. [2]Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, 73993 Riddarhyttan, Sweden. [3]Mammal Research Institute, Polish Academy of Sciences, Stoczek 1, 17-230 Białowieża, Poland. ✉email: olejarz@fld.czu.cz

flee response was triggered[35]. 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 hunt[18]. Spatial changes in landscape use may also be accompanied by temporal changes in landscape use to avoid potential contact with hunters[36]. For example, white-tailed deer were more active at night after a hunt than during the day in the vicinity of feeding sites[37]. 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 proximity[41]. 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 pressure[15], shift the area of their resting range[47], temporarily or permanently escape from the hunted area[48], and increase nocturnal activity[49]. 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 food[50]. Hunting is the main management tool to control populations of wild boar[32] and seems to be the most effective compared to other management practices, e.g. supplementary feeding or fencing[51]. 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 ($n_{ind.} = 37$) (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 km^2; 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 km^2; CI 95% 0.72–1.26, respectively; pairwise-Wilcox 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 km^2; CI 95% 1.26–2.38, respectively) in the daily distance (pairwise-Wilcox tests, p value = 0.006) and the daily range (pairwise-Wilcox 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-Wilcox tests, p value < 0.001) and did not differ between "the day of the hunt" and "the day after the hunt" (pairwise-Wilcox 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-Wilcox tests, p value = 0.569) and daily range (pairwise-Wilcox 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 km^2 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 ($n_{wb\ ind} = 30$): "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 km^2), 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 km^2), 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" $n_{ind.} = 18$; "Flight" $n_{ind.} = 12$), 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

	(A) Daily distance difference			(B) Daily MCP difference			(C) Daily overlap distance		
Coefficient	**Estimates**	***p* value**	**CI 95%**	**Estimates**	***p* value**	**CI 95%**	**Estimates**	***p* 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									
σ2	7.09			4.35			0.02		
$\tau00_{AnimalID:Area}$	0.53			0.09			0.00		
$\tau00_{Area}$	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 km^2 (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 ($p < 0.05$).

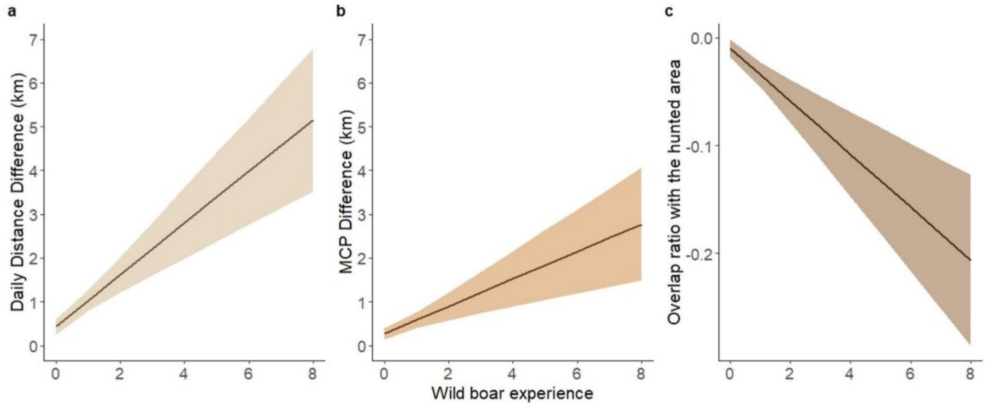

Fig. 1. Movement and space use response of wild boar (n = 53) in four hunting areas in the Czech Republic and Sweden to drive hunts as a function of wild boar experience (WBE) as predicted by the linear mixed model (LMM). Ninety-five per cent confidence intervals are shown as shaded areas: (**A**) Difference 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 km^2 (**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	***p* value**	**CI 95%**	**Estimates**	***p* value**	**CI 95%**	**Estimates**	***p* 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									
σ2	0.08			0.13			0.99		
$\tau00_{AnimalID:Area}$	0.03			0.03			0.16		
$\tau00_{Area}$	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 ($p < 0.05$).

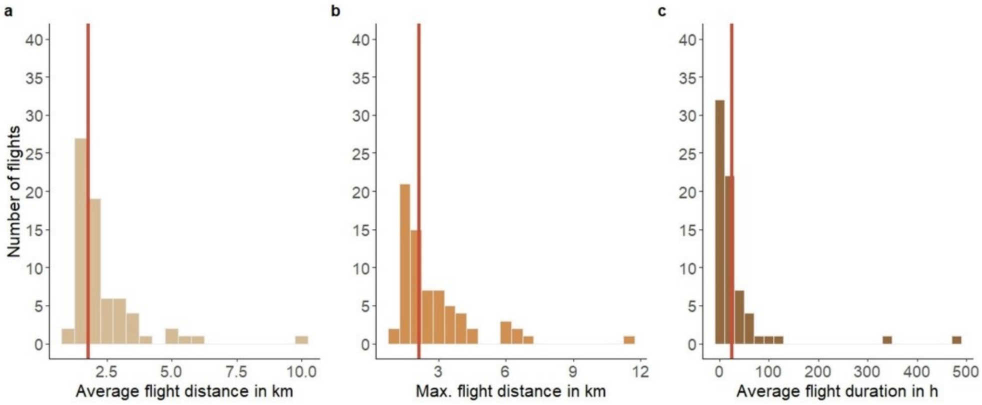

Fig. 2. Hunting-induced flight behaviour of wild boar in four hunting areas in the Czech Republic and Sweden. The red vertical line indicates the average value: (**A**) Average flight distance in km, (**B**) Maximum flight distance in km, and (**C**) Average flight distance in hour.

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 individuals[53]. Drive hunts in Italy caused instability in space use, reflected in larger ranges and greater dispersion of resting sites[54]. Resting ranges were larger and more interspersed in wild boar groups exposed to

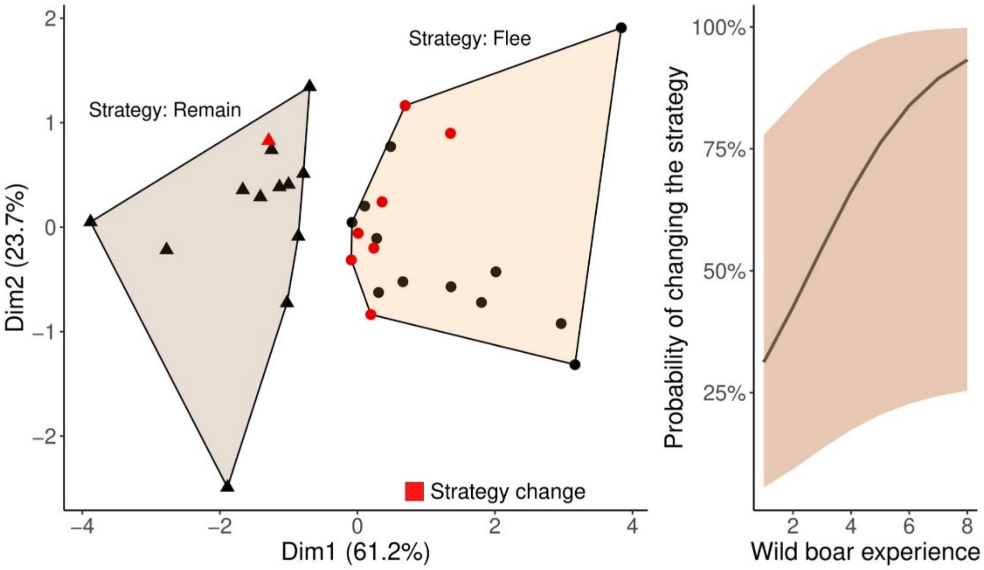

Fig. 3. Clustering of movement and space use similarities of wild boar in responses to drive hunts in four hunting areas in the Czech Republic and Sweden. Circles and triangles represent individuals and red-filled objects are individuals which changed their strategy with an increasing number of experienced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

frequent drive hunts[54]. 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 hunt[32]. 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 experience[55]. White-tailed deer, which experience greater hunting pressure on weekends, decreased their movement rate, net displacement and activity on Sunday after encountering hunters multiple times[56]. After experiencing foxes as predators, tammar wallabies showed an anti-predator response by increasing movement rates in the presence of foxes followed by a prolonged increase in vigilance[57]. 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 cover[33], 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 dogs[33]. 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 reaction[59]. Besides external factors, internal factors such as differences in personality, cause animals to use different habitats with unequal predation risk[23]. 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 supply[23]. 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 predators[60]. 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 Sweden[15], 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 Germany[15]. Short flight distance observed in Germany could be linked with habituation to frequent drive hunts[61]. 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 ranges[62]. Red deer, for example, fled outside their established home range to "refuge" areas during a hunting event and returned within a few days[63]. 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 common[15]. 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 Norweigan 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 individuals[64] because different personalities lead to contrasting strategies when faced with risky situations[22], such as drive hunts. However, with increasing predator exposure and learning through experience, individuals can modify spatial behaviour towards one consistent strategy[64]. 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 hunters[18]. Similarly, white-tailed deer adapted behavioural strategies during rifle deer hunting season by minimising movement[65]. 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 risk[66]. Increased experience with predation risk amplifies risk perception[67] 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 risk[69]. Bow hunting causes a more pronounced anti-predator response than rifle hunting[18]. 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 events[72]. 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 areas[75]. 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 composition[42]. 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 Republic[76] and is composed of large shrub patches, beech and ash forests, dry grasslands, and wetlands[77]. 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 areas[78] and is exposed to high human leisure activity[79]. 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.

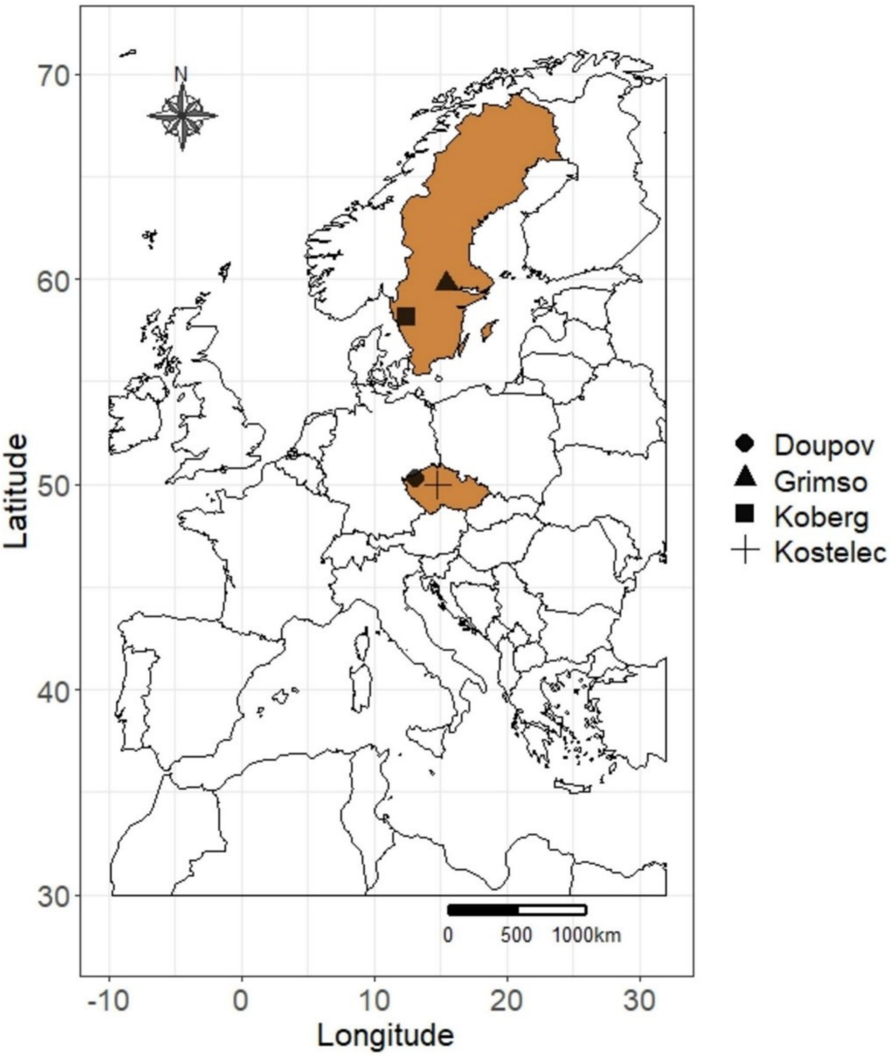

Fig. 4. Map of Europe, highlighting the Czech Republic and Sweden in colour. Analysed drive hunt areas are labelled with different symbols and assigned by name on the side. This figure was drawn using the R package rwoldmap[80].

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 software[81] 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 3.14[82] and R 4.2.2[83]. The study was carried out in compliance with the recommendations of ARRIVE guidelines[84].

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 (km^2) of the hunting area with the "amt" package in the R environment[85]. On average, the size of the hunting area for Grimsö was 2.70 km^2; (Confidence Interval (CI) 95% 2.46–2.93), in Koberg 2.21 km^2; (CI 95% 2.10–2.33), in Kostelec 2.17 km^2; (CI 95% 2.03–2.32), and in Doupov 1.65 km^2; (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./km^2; (CI 95% 4.62–2.99), Grimsö 0.03 ind./km^2; (CI 95% 0.04–0.01), Koberg 1.48 ind./km^2; (CI 95% 1.72–1.24), and Kostelec 4.76 ind./km^2; (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/km^2; (CI 95% 29.11–34.45), Grimsö 3.54 person/km^2; (CI 95% 3.14–3.94), Koberg 23.82 person/km^2; (CI 95% 22.13–25.51), and Kostelec 37.44 person/km^2; (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 km^2; (CI 95% 1.88–2.68), in Koberg 1.14 km^2; (CI 95% 0.94–1.33), in Kostelec 1.34 km^2; (CI 95% 1.17–1.50), and in Doupov 0.68 km^2; (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 glmmTMB[86]. 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 R[87], and no collinearity issues were detected. Additionally, we ran a visual model diagnostic with the DHARMa package[88] 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" package[90]. 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 R[91]. The optimal number of clusters (n = 2, corresponding to the "flight" and "remain" strategy) was determined using the average silhouette method and theory-led-decision[92]. 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.

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The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to A.O.

5.3 No evidence for the consistent effect of supplementary feeding on home range size in terrestrial mammals

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Author for correspondence:
Astrid Olejarz
e-mail: olejarz@fld.czu.cz

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No evidence for the consistent effect of supplementary feeding on home range size in terrestrial mammals

Astrid Olejarz[1] and Tomasz Podgórski[1,2]

[1]Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, Prague 6-Suchdol 165 00, Czech Republic
[2]Mammal Research Institute, Polish Academy of Sciences, Stoczek 1, 17-230 Białowieża, Poland

AO, 0000-0002-5543-7416

Food availability and distribution are key drivers of animal space use. Supplemental food provided by humans can be more abundant and predictable than natural resources. It is thus believed that supplementary feeding modifies the spatial behaviour of wildlife. Yet, such effects have not been tested quantitatively across species. Here, we analysed changes in home range size owing to supplementary feeding in 23 species of terrestrial mammals using a meta-analysis of 28 studies. Additionally, we investigated the moderating effect of factors related to (i) species biology (sex, body mass and taxonomic group), (ii) feeding regimen (duration, amount and purpose), and (iii) methods of data collection and analysis (source of data, estimator and spatial confinement). We found no consistent effect of supplementary feeding on changes in home range size. While an overall tendency of reduced home range was observed, moderators varied in the direction and strength of the trends. Our results suggest that multiple drivers and complex mechanisms of home range behaviour can make it insensitive to manipulation with supplementary feeding. The small number of available studies stands in contrast with the ubiquity and magnitude of supplementary feeding worldwide, highlighting a knowledge gap in our understanding of the effects of supplementary feeding on ranging behaviour.

1. Introduction

Spatial and temporal heterogeneity in the abundance of food resources is one of the key challenges animals face when navigating the environment. This variation shapes foraging decisions and space use of animals, which try to balance the energetic costs and benefits of acquiring food. Optimal foraging theory (OFT) posits that the most successful foraging strategy will minimize foraging costs to the benefit of increased fitness [1]. Resource-rich habitats offer high nutritional gains with a low-energetic cost of travel. Thus, animals' home ranges are predicted to be smaller when resources are abundant [2]. Many species experience food provisioning through wildlife management practices [3], eco-tourism [4], recreational feeding [5,6], food waste mismanagement [7,8] and conservation efforts [9], potentially inducing changes in movement [10] and space use patterns [11]. In contrast to the general assumption that supplementary feeding leads to a reduction in the home range size, the literature provides ambiguous evidence, with some studies reporting a decrease [12–15], no change [16,17] or an increase [18,19]. The previous reviews on supplementary feeding [13,20,21] have qualitatively summarized various effects on wildlife but have not quantitatively addressed spatial behaviour.

While food resources are one of the key determinants of ranging behaviour, other factors like species biology also contribute to home range size. Home range size is positively related to body mass in mammals owing to the higher metabolic requirements of larger species [22–24]. Food is limited in space and time and, to fulfil metabolic requirements, larger animals have to increase foraging and travel costs. Supplemental food helps satisfy metabolic needs at lower foraging and travel costs and can thus be expected to cause a decrease in the home range size, potentially flattening out of the relationship between body size and home range size. Inter-specific differences in predator avoidance strategies [25], territorial behaviour [26,27] and social structure [23] can further modify the relationship between food availability and home range size across taxonomic groups. Energetic requirements differ between sexes and in many species, males have larger home ranges than females [28–31]. Female home ranges are further reduced during the rearing of offspring [32,33] owing to limited offspring mobility, protection from infanticide [34] and from predators [35]. Predictable and abundant food resources from supplementary feeding, particularly for females with offspring, could further enhance site fidelity. Males, on the other hand, can expand or maintain large home ranges to improve their reproductive success [36–39]. Those reproductive needs may outweigh the energy savings offered by supplementary feeding in shaping the home range [33]. Thus, we can expect a stronger spatial response to supplemental feeding in females.

Anthropogenic food resources are often more predictable, abundant and energy rich than natural resources [8] and they may provide a strong spatial signal inducing fidelity to resource-rich areas and, consequently, decline of home range [40]. However, those food resources should be consistently available for a long period of time to induce behavioural change. OFT assumes that, owing to their cognitive abilities, animals own complete knowledge of the spatio-temporal distribution of resources [41]. Yet, mammals continuously update their cognitive map to decide where to forage [42]. Only rich food patches leave a strong cognitive imprint on the spatial map of resources and can thus influence the decisions of where to move [31,43]. We can distinguish two different anthropogenic food resources: intentional and unintentional supplementary feeding. Intentional (subsidiary and artificial) feeding can be defined as placing natural or non-natural food into the environment to augment regular food sources [44] or attract animals [6]. The extent, intensity and form of wildlife feeding vary widely depending on its intended purpose. In game management, supplementary feeding is a deliberate tool to keep the target population stable or improve its performance, especially when natural food resources are scarce [20,21,45,46], or to mitigate damage to agricultural crops [47] and tree regeneration [48,49]. Thus, this type of feeding is often seasonal to address specific aims. The scale of game feeding is enormous: 2.8 trillion tons of bait are used annually in the USA [7] and 42 million USD worth of feed was provided to wildlife in Sweden in 2013 [50]. Unintentional feeding offers anthropogenic food sources (e.g. landfills, municipal and agricultural waste, and hunted game offal) but is not specifically targeted at feeding wildlife, and thus without pre-defined target species or a timeframe of feeding. This form of feeding is also very prevalent [7,51]. Up to 40% of all food products on Earth are wasted [7] and become a potential food resource for wildlife. Annually, tonnes of big game carrion in Europe and the USA serve as food for the large majority of vertebrate scavengers [7,47,52]. We can expect longer-lasting and more consistent unintentional feeding to produce a stronger habituation effect and thus have a stronger decreasing effect on the home range size. Food availability plays a crucial role in the spatial behaviour of animals and supplemental food can be expected to alter natural space use patterns. For example, the home range size of wood mouse in a low-quality habitat with supplementary feeding was smaller than without, and similar to high-quality deciduous woodland [36]. We can thus expect a stronger decrease in home range size when supplemental food is more abundant.

Home range is a fundamental outcome of animal movement [2], reflecting its ecology and spatial behaviour [42] and is one of the most commonly used metrics of space use [42]. Owing to the constant development of tracking technologies, analytical approaches and home range concepts [53–55], different methods exist to analyse home range data [56]. One common method is the geometric estimator, such as minimum convex polygon (MCP), which builds home range polygons by using the locations of an observed animal. Alternatively, probabilistic estimators, such as the kernel density estimator, calculate home range based on the frequency distribution of animal locations [57]. If animals preferentially use supplementary feeding sites and their surroundings, the kernel estimator should perform better in capturing this effect than the MCP, which does not account for the utilization distribution. Many species, particularly game, are kept temporarily in enclosures for ecological and economic reasons [58,59]. The enclosures can alter natural conditions by excluding predators and/or maintaining high population density and, consequently, high levels of intra-specific competition. Both of these factors may lead to smaller home ranges in terrestrial mammals [31,60,61]. We can expect that supplementary feeding in enclosures will lead to a stronger decrease in home range compared with free-ranging populations where additional variables (e.g. distribution of other vital resources, location of supplementary feeding sites and disturbances) may counterbalance the effect of feeding.

In this study, we collected the home range size of terrestrial mammals under supplementary feeding to examine its effect on space use. We created a meta-analysis of 28 studies from 23 species to test an overarching hypothesis of reduced home range size when supplementary feeding is present. Additionally, we investigated the modifying effect of three groups of factors related to (i) species biology (sex, body mass and taxonomic group), (ii) feeding regimen (duration, amount and purpose), and (iii) methods of data collection and analysis (source of spatial data, home range estimator and spatial confinement). The results are discussed in the context of wildlife conservation and game management.

2. Methods

(a) Article search

We used Web of Science (WoS) and Scopus, two publisher-independent global citation databases, to identify published articles that analysed the effect of supplementary feeding on home range size in terrestrial mammals. On 21 March 2022, we created a Boolean operator, consisting of (i) ((‘Supplement* feed*’ OR ‘Artificial feeding’ OR ‘Food supplementation’ OR ‘Winter feeding’ OR ‘Bait* sites’ OR ‘Waste’ OR ‘Trash’ OR ‘Garbage’ OR ‘Recreational feeding’ OR ‘Dumps’ OR ‘Landfill’ OR ‘Refuse*’ OR ‘Feeding site’ OR ‘Supplemented food’ OR ‘Anthropogenic Resources’), (ii) AND (‘Home range*’), and (iii) NOT (‘Bird’ OR ‘Amphibians’ OR ‘Fish’ OR ‘Reptiles’ OR ‘Radioactive’ OR ‘Human’)). In addition to the Boolean operator, we used an additional filter in the Scopus database by only allowing publications assigned to the subject area Agricultural and Biological Sciences and Environmental Sciences. We did not use platforms with grey literature for two reasons: (i) an advanced search with the help of the Boolean operator is only possible to a limited extent and (ii) platforms such as Open Grey and Google Scholar include unpublished and non-peer-reviewed research with results which could not be verified [62].

The search returned 191 hits in WoS and 162 hits in Scopus. To avoid duplications, the titles of both searches were compared in the package dplyr [63] in the R environment (v. 4.2.2 [64]), and duplications were removed from the Scopus table. In the end, this resulted in 259 scientific papers. In the next step, we conducted an abstract screening of all hits, excluding studies that did not focus on terrestrial mammals. After the abstract screening, 135 studies which were deemed potentially relevant underwent a second screening round of the full text. Only studies that reported home range sizes with and without supplementary feeding were selected, which provided a contrast of experimental treatment (supplementary feeding) and control group (no feeding). After the full-text screening, 24 scientific studies were selected, and we added four further publications that appeared in the reference lists of the 24 publications. In total, we used 28 publications for the meta-analysis (electronic supplementary material, figure S1).

(b) Data extraction

We extracted the home range size, its standard deviation (s.d.) and sample size from each publication for the experimental group of animals with supplementary feeding and the control group without. All home range sizes were converted into square kilometres. If s.d. was not given in the publication, we either calculated the s.d. from the raw data or converted it from standard error (s.e.) or confidence interval (CI) [65]. For each home range comparison, we compiled information about the species, its taxonomic group (rodent, carnivore and ungulate), individual’s sex, supplementary food amount (limited or ad libitum) and feeding duration, spatial confinement (free-ranging or enclosure), source of spatial data (telemetry or capture-mark-recapture) and home range estimator (kernel density estimation (KDE) or MCP). Moreover, we divided the publications into intentional and unintentional feeding studies. We defined intentional feeding as supplementary food provided to a target species with a fixed timeframe and defined aim. Unintentional feeding, in contrast, was classified as supplementary food available from anthropogenic sources (e.g. landfills and municipality waste) but not specifically targeted at feeding wildlife, and thus without pre-defined target species or a timeframe of feeding. Therefore, we only analysed feeding duration for intentional feeding studies. We added body mass for each species from the panTHERIA database [66] to the collected dataset.

(c) Statistical analysis

To measure the change of the home range size from no-feeding to feeding treatment, we used the Hedges’ g estimator of the effect size [67]. For each study, we calculated the Hedges’ g and its variance with the escalc() function of the metafor package in R [68]. Negative values of the Hedges’ g represent the decrease in the home range size owing to feeding. Some publications provided multiple home range comparisons across seasons, sex and areas which contributed to a final total of 64 effect sizes from 28 studies. The publication bias within the collected dataset was visually examined with a funnel plot [69] and tested with Egger’s regression [70]. Meta-analytic mixed-effects models, fitted with the function rma.rm of the metafor package, were used to examine the effects of supplementary feeding on home range size. An intercept-only model was used to determine the mean effect size across the entire dataset. The proportion of heterogeneity relative to sampling error was quantified with the I^2 statistic [71], from the intercept-only model. We created a random effect variable, ‘group within study’, which combined study identity and within-study grouping levels (e.g. areas, sex and seasons) in one unique identifier and thus accounted for between and within study variance. We then fitted nine separate meta-analytic mixed effects models to examine the effect of different moderators (i.e. sex, body mass, taxonomic group, food amount, feeding purpose, feeding duration, spatial confinement, source of spatial data and home range estimator) (electronic supplementary material, tables S1 and S2). We created a forest plot for all nine predictors using the modelplot function of the modelsummary package [72].

3. Results

In total, 28 studies originating from 24 countries and 23 species met our criteria for meta-analysis (table 1, figure 1). From those studies, we extracted 64 effects, which were symmetrically spread in the funnel plot (electronic

Table 1. Studies used in the meta-analysis examining changes in the home range size of terrestrial mammals in response to supplementary feeding.

references	class	species	data
Akbar & Gorman [36]	rodent	*Apodemus sylvaticus*	telemetry
Broughton & Dickman [73]	marsupial	*Isoodon obesulus*	mark-recapture
Campbell *et al*. [74]	ungulate	*Odocoileus virginianus*	telemetry
Cooper *et al*. [75]	ungulate	*Odocoileus virginianus*	telemetry
Desy *et al*. [25]	rodent	*Microtus ochrogaster*	telemetry
Dickmann [76]	rodent	*Antechinus stuartii*	mark-recapture
Festerer *et al*. [17]	carnivore	*Ursus americanus*	telemetry
Gilchrist & Otali [77]	carnivore	*Mungos mungo*	telemetry
Grenier *et al*. [78]	ungulate	*Odocoileus virginianus*	telemetry
Hall *et al*. 1998 [79]	rodent	*Peromyscus truei*	telemetry
Haspel & Morrison [80]	carnivore	*Felis catus*	observation
Hidalgo-Mihart *et al*. [81]	carnivore	*Canis latrans*	telemetry
Lacki *et al*. [82]	rodent	*Tamias striatus*	boundary strip
Lopez Bao *et al*. [83]	carnivore	*Lynx pardinus*	telemetry
McRae *et al*. [84]	ungulate	*Sus scrofa*	telemetry
Mondajem & Perrin [85]	rodent	*Mastomys natalensis*	mark-recapture
Morris *et al*. [86]	rodent	*Sigmodon hispidus*	telemetry
Mysterud *et al*. [87]	ungulate	*Cervus elaphus*	telemetry
Ranc *et al*. [88]	ungulate	*Capreolus capreolus*	telemetry
Reinecke *et al*. [89]	ungulate	*Cervus elaphus*	telemetry
Rotem *et al*. [90]	carnivore	*Canis aureus*	telemetry
Schoepf *et al*. [91]	rodent	*Rhabdomys pumilio*	telemetry
Sulok *et al*. [92]	rodent	*Sigmodon hispidus*	mark-recapture
Teferi & Millar [93]	rodent	*Peromyscus maniculatus*	mark-recapture
Todorov *et al*. [94]	carnivore	*Ursus arctos*	telemetry
Van Beest *et al*. 2010 [49]	ungulate	*Alces alces*	telemetry
Webb *et al*. [19]	ungulate	*Odocoileus virginianus*	telemetry
Young *et al*. [32]	carnivore	*Canis latrans*	telemetry

supplementary material, figure S2), indicating no publication bias in the dataset. This was confirmed by the insignificant result of the Egger's test (e = 0.541, p = 0.522). Across the studies, we found moderate heterogeneity (I^2 = 33.68%). The overall effect of supplementary feeding on the home range size was negligible (g = −0.297, 95% CI = −0.708 to 0.113, p = 0.1553, n = 64 effects; figure 2; electronic supplementary material, table S2).

(a) Species biology

We did not find consistent effects of biological moderators (sex, body mass or taxonomic group) on the relationship between supplementary feeding and home range size (figure 2). Opposite tendencies were observed between sexes. Females showed a relatively strong reduction in the home range size owing to supplementary feeding (g =–0.55, 95% CI = −1.2 to 0.1) while a slight increase (g = 0.13, 95% CI = −0.18 to 0.43) was observed in males. Species body mass showed no consistent effect on changes in home range in response to feeding, despite a 20 000-fold range of this parameter in the dataset (0.02–461.9 kg). Only species with a body mass below 1 kg (91% rodents and 9% marsupial) showed a strong tendency of reduced home range size (g = −0.63, 95% CI = −1.29 to 0.03). Heavier species showed the opposite trend of increased home range (figure 2). The taxonomic groups showed a mixed response to supplementary feeding, with home range size tending to decrease in rodents (g =–0.54, 95% CI = −1.57 to 0.5) and carnivores (g =–0.2, 95% CI = −1.0 to 0.6) while increasing in ungulates (g =0.25, 95% CI = −0.83 to 1.32).

(b) Feeding regimen

We did not find consistent effects of supplementary feeding on home range size in relation to food amount, feeding purpose and duration (figure 2). Animals with access to unlimited (ad libitum) food resources showed a relatively strong tendency to

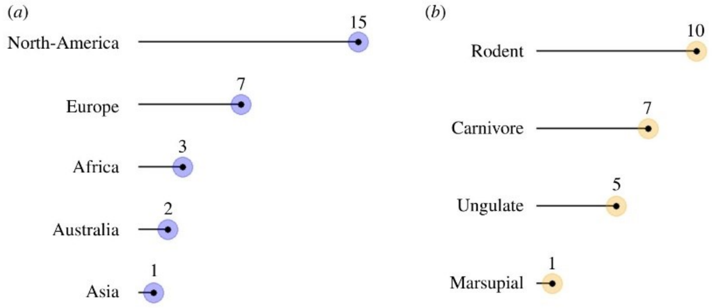

Figure 1. Distribution of studies across continents and species across taxonomic groups in the meta-analysis. (*a*) Number of studies per continent and (*b*) number of species per taxonomic group.

decrease in home range size (g =−0.48, 95% CI = −1.04 to 0.07), while those that received limited supplementary food tended to strongly increase the home range size (g =0.79, 95% CI = −0.12 to 1.69). Duration of intentional supplementary feeding averaged 16 months (min–max: 1–84). Despite the large time range, home range size showed little change in response to feeding duration. Feeding duration showed a consistently positive yet weak effect on the home range size, with g ranging from 0.1 to 0.36 for the feeding duration of >12 months and <6 months, respectively. The purpose of feeding did not affect the way animals responded to food provisioning but it modified the strength of the response. Both intentional and unintentional feeding induced a tendency of reduction in the home range size with a notably stronger effect of unintentional feeding. In fact, unintentional feeding had the strongest effect (g = −1.1, CI = −2.48 to 0.28) of all moderators tested (g < 0.8) (figure 2; electronic supplementary material, table S2).

(c) Methods of data collection and analysis

Contrasting trends were observed for the spatial confinement of the studied animals. Animals in enclosures tended to reduce home range size under supplementary feeding (g =−0.75, 95% CI = −1.61 to 0.11), whereas free-ranging ones tended to increase home range size (g =0.58, 95% CI = −0.4 to 1.56). Most of the studies (76%) were conducted on free-ranging animals and all enclosure studies were conducted on rodents. Methods of spatial data collection did not change the relationship between supplementary feeding and home range size, though a stronger signal for reduced home range was detected for telemetry-derived data (g =−0.42, 95% CI = −1.34 to 0.5) compared with mark-recapture data, which showed virtually no effect (g =−0.06, 95% CI = −0.86 to 0.74) (figure 2). Across home range estimators, only kernel 90 showed a negative tendency of reduced home range under feeding (g =−0.58, 95% CI = −1.43 to 60.28). All of the other estimators showed positive trends of varying strength, with the strongest signal for MCP 100 (g = 0.74, 95% CI = −0.32 to 1.81) (figure 2).

4. Discussion

Our literature search yielded 28 studies (64 effects) containing proper control of feeding experiments. This relatively small sample stands in glaring contrast with the ubiquity and magnitude of supplementary feeding worldwide and highlights the need for further research on the effects of supplementary feeding on movement and space use. Nevertheless, the results of this meta-analysis provided new and unexpected insights. Contrary to the assumption made by OFT, the effect of higher food availability offered by supplementary feeding on the reduction in the home range size was inconclusive. While a negative trend towards smaller home ranges under supplementary feeding was observed, our dataset provided weak evidence (p = 0.16) against the null hypothesis of no effect. It should be noted that home range behaviour is shaped not only by the availability of food but also by other resources, such as predation risk, population density and social interactions, which OFT does not account for. The predation strongly influences foraging behaviour as animals make foraging decisions in relation to predation risk to maximize biological fitness [95–98]. Trade-off between food and safety can force animals to forage over larger areas if the presence of predators compromises foraging opportunities [99]. Rearing of offspring can also strongly impact home range size. Around parturition, female white-tailed deer [100,101] and wild boar [102] reduce their movements and home range size. Food availability can interact with the distribution of other key resources to influence the home range size. In semi-arid environments, density of and proximity to waterholes has been shown to be inversely related to home range size in African elephants [103] and southern mule deer [104].

(a) Species biology

Factors related to species biology, feeding regime and methods of data collection and analysis had varying moderating effects, in size and direction, on the relationship between supplementary feeding and home range size. Space used

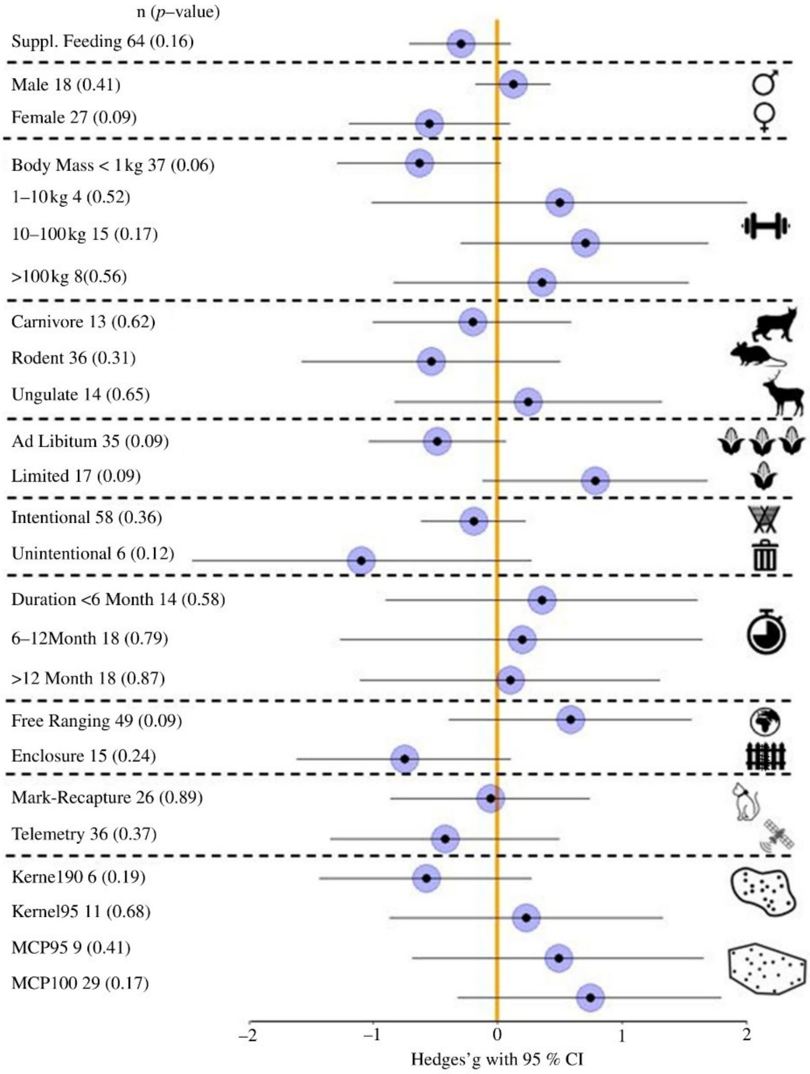

Figure 2. Response of home range size to supplementary feeding (sample size, *p*-value, Hedges' *g* estimate and its 95% CI) across all effects and for nine moderators: sex, body mass, taxonomic group, food availability, feeding purpose, feeding duration, presence of enclosure, source of spatial data and home range estimator. Positive values of Hedges' *g* indicate an increase in home range size during supplementary feeding and negative values indicate a decrease.

by animals is expected to increase with increasing body mass [22,105]. Our results did not show a consistent effect of body mass on the relationship between supplementary feeding and home range size across a wide range of body sizes considered (0.02–461.9 kg). Species with body mass below 1 kg (91% of which were rodents) tended to show a relatively strong negative response when supplementary food was provided. There was a 6% probability of our result arising by chance, assuming no effect in this weight class, which provided moderate evidence for the effect. Heavier species, on the other hand, showed positive trends with large uncertainty and weak support against null hypothesis of no effect (*p*-values from 0.17 to 0.56). Small mammals have higher energy expenditure relative to their body size than large mammals as they spend more energy regulating body temperature [24,106]. It is possible that energetic constraints of small mammals make them sensitive to manipulation of food resources and easier to induce spatial response. Larger and more energetically robust species, on the other hand, may require greater amounts and/or more nutritionally rich food for the spatial response to manifest. Besides the relationship between body mass and home range size, space use patterns are also influenced by sexual differences [107]. Consistent with our expectation, females showed a strong tendency to decreased home range size after supplementary feeding and a moderate concordance with the null hypothesis of no effect ($p = 0.09$), providing some support for the effect. Males contrasted with a negligible change in home range size. Differences in mating strategies can lead to contrasting space use patterns in males and females. According to the range size hypothesis [37], superior males in promiscuous or polygynous mating systems roam widely for multiple mates [36,38,39]. Our results indicate that male movement decisions can be driven by reproductive needs rather than energy savings offered by supplementary feeding. In contrast, predictable and abundant food resources offered by supplementary feeding can enhance further site fidelity in females, particularly those with offspring, which are already constrained by energetic requirements of gestation or lactation, immobility of offspring and the need to protect them from predation [34,35].

Response in home range size owing to supplementary food varied in three taxonomic groups. The marginal tendency of home range size decrease was identified for carnivores and rodents, while a weak trend of home range increase was observed in ungulates. However, those results were in high concordance with the null hypothesis of no effects of supplementary feeding on home range size across taxonomic groups (*p*-values from 0.31 to 0.65) and thus provided poor evidence for the actual differences. An adequate size of a home range in carnivores is not only determined by the available food resources but also by social organization [23]. Many carnivore species show pronounced territorial behaviour [26,27] and maintain their home range size in relation to population density [108,109]. This fairly rigid socio-spatial population structure can allow only limited changes in home range size in response to feeding [32]. Additionally, carnivores rely on mobile and patchily distributed food, which requires large home ranges [110,111]. Spatially predictable resources offered by supplementary food could partly relax the requirement of large home ranges. A declining trend in home range size was also observed in rodents but this pattern could be triggered by a different behavioural mechanism compared to carnivores. Rodents, which are prey species to many other animal groups, adopt the strategy of staying close to burrows and reducing their home range size when predation risk is high [25]. Supplemental feeding could potentially enhance movement restriction in the face of high predation risk, but we were not able to test this effect with our data. Ungulates, on the other hand, tended to increase home range size under supplementary feeding. It has been shown in white-tailed deer [19] and roe deer [88] that the location of feeding stations at the periphery of the core range can lead to home range shift and increase in range size. Although this effect is not necessarily specific to ungulates, it could be responsible for the increase in home range size observed in 5 out of 9 studies on ungulates that we analysed. In all considered taxonomic groups, the potential effects of supplemental food could have been balanced out by other drivers of home range behaviour, such as predation avoidance, social interactions and other resources.

(b) Feeding regimen

Unexpectedly, opposing trends in the direction of change in the home range size were observed between studies providing a limited and unlimited (ad libitum) amount of food. In experiments with limited feeding, food was delivered according to a specific protocol at fixed quantities and time intervals. However, we were not able to compile information on the exact amount of food provided in relation to species nutritional demands and quantify the degree of food limitation. In unlimited feeding experiments, in contrast, food was available all the time and topped up as depleted. Animals receiving unlimited food tended to decrease their home range size while the opposite trend was observed when the amount of supplemental food was limited. Both estimates had a 9% probability of being obtained by chance, assuming no differences in home range size depending on the amount of supplementary food, which provided some evidence for the effects. It is possible that food limitation provided a too-weak signal to induce changes in home range size. In free-ranging cats, for example, only continuous supplementary feeding can efficiently reduce home range size in an unproductive habitat [80].

When feeding intentionally, it is usually possible to track the duration of supplementary feeding, while the time at which wild animals start to use unintentional anthropogenic food sources is usually unknown. In our meta-analysis, unintentional feeding induced a much stronger negative response in home range size compared with intentional feeding. All studies with unintentional feeding reported a substantial reduction in the home range size when food was available [77,81,90,112], while studies with intentional feeding reported no consistent response in home range size change. The strong spatial response of wildlife after the closure of unintentional feeding spots can be attributed to the cognitive abilities of mammals [31,42,43]. For example, spotted hyenas preferentially used areas around human waste pits which constituted a primary food source. After closure of the pits, home range size of the spotted hyenas increased [112]. Golden jackals maintained smaller home ranges near villages compared with natural areas, supposedly in response to availability of anthropogenic food [90].

Most studies with unintentional feeding did not provide an exact timeframe of food provisioning and therefore only studies with intentional feeding were included in the analysis of the effect of feeding duration. Feeding durations covered a wide range of timespans (from 1 to 84 months), but we found a very weak trend of increasing home range size regardless of whether feeding was short (<6 months), medium (6–12 months) or long terms (>12 months). Additionally, this data provided no evidence against the null hypothesis of no effect of supplementary feeding depending on its duration (*p*-values from 0.58 to 0.87). Intentional feeding is often used to prevent damage to agricultural fields by abundant game species, such as deer and wild boar [113]. As feeding duration in this case is often limited to one season [114,115], the anticipated change of ranging behaviour through supplementary feeding might not occur, as demonstrated in our meta-analysis.

(c) Methods of data collection and analysis

Twenty-four per cent of the studies were conducted in enclosures, exclusively on rodents. The enclosures were usually large enough to not constrain movement (i.e. larger than home range size) but could exclude predators or sustain high individual densities and high levels of intra-specific competition. Free-ranging mammals showed a tendency to increase home range size with supplementary feeding, while the opposite trend was observed in enclosures. Free-ranging data provided some evidence for the observed difference (p = 0.09), while data from enclosures was concordant with the null hypothesis of no effect (p = 0.24). One possible explanation might be that, in the open settings, feeding sites were located on the periphery of an animal's home range, causing additional movement [19,32]. Supplementary feeding in enclosures tended to lead to smaller home ranges. If enclosures exclude predators, prey can become less vigilant [116] and feel less pressure to seek out and explore different habitats to hide from predators [117]. Besides removing predation risk, enclosures can also increase intra-specific competition, as there is no way to migrate out of the enclosure. High intra-specific competition for the habitat can force animals to keep the home range small and to increase it when intra-specific competitors are lacking [31,60,61].

Home range reflects an animal's ecology and behaviour in space [42] and estimations of home range area are widely applied in animal ecology [118]. While almost any type of animal location data can be used to calculate home range, higher temporal granularity and spatial accuracy will yield more precise and biologically relevant estimates. We have identified two major types of spatial data used in the studies we examined: capture-mark-recapture and telemetry (radio and GPS). The former is typically of much lower spatio-temporal resolution than the latter, which can result in less precise estimation of home range size. Yet, we found that the type of spatial data used to calculate home range size did not consistently affect its response to supplementary feeding. While home ranges based on capture-mark-recapture data showed no response to supplementary feeding, telemetry-based home ranges showed a decreasing trend in response to feeding. In our meta-analysis, we included two broad categories of home range estimators, historically older MCP and more modern KDE. Differences in assumptions, calculations and interpretations between the estimators may have led to different trends in our meta-analysis results. Home ranges computed with kernel 90 showed a relatively strong decline under supplementary feeding, whereas all the other estimators tended to show a positive effect, with the strongest for MCP 100. MCP is frequently used in animal studies because it is easy to compute and compare [119,120]. Yet, it is sensitive to outliers, sample size and spatial resolution, which can create estimates biased upwards and does not reflect intensity of use. Kernel estimators, on the other hand, are relatively unbiased and account for centres of activity [53]. Thus, kernel-based methods are better suited to study the effects of resource distribution on space use. In our meta-analysis, only isopleth 90 of the kernel, representing the innermost part of the home range of all estimators considered, showed a trend similar in strength and direction to the overall effect of supplementary feeding on home range size. Interestingly, Borger *et al*. [53] found kernel 90 to be less biased and more accurate than outer kernel isopleths and MCP estimators.

5. Conclusion

Contrary to the common belief and the prediction of OFT that supplementary feeding would reduce home range, we did not detect a consistent effect with our meta-analysis. While an overall tendency of reduced home range was observed, the effect was not consistent across the available studies and the uncertainty around the estimate indicated the possibility of no effect. Moreover, moderators varied in the direction and strength of the trends, highlighting inconsistencies in the effects of supplementary feeding on home range size depending on species biology, feeding management and home range estimation methods. We conclude that home range size is resistant to manipulation with supplementary feeding owing to a multitude of drivers and complex mechanisms of home range behaviour. Despite the widespread practice of wildlife feeding, our literature research shows that only a small amount of data exists that examines the effect of supplementary feeding on the spatial behaviour of terrestrial mammals. More comprehensive research and clear policies are needed to better understand and manage the effects of supplementary feeding on spatial behaviour. In wildlife management, it is recommended to weigh the economic, health and ecological risks before providing supplementary food. In the case of unintentional feeding through food waste, initial steps have been taken by the European Union (EU). In 2016, an EU Platform on Food Losses and Food Waste was created. Combining a group of EU institutions, experts and international organizations, the platform aims to prevent food waste and to share best practices. The European Commission has set the target of reducing food waste in food manufacture and processing by up to 10% and by up to 30% in households by 2030.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and R Scripts are available from the Dryad Digital Repository [121].

Electronic supplementary material is available online [122].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.O.: conceptualization, data collection, methodology, data processing and analysis, writing; T.P.: conceptualization, supervision, data analysis, writing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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6. Discussion

This dissertation aims to detect changes in the behavioural patterns of wildlife under different anthropogenic impacts using spatial tracking data. The following section discusses the key findings for each anthropogenic impact of the presented scientific articles.

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

My investigation showed that wild boar (*Sus scrofa*) space use and movement did not change during the increased recreational activity in the COVID-19 lockdown in the suburban forest. I assumed that human leisure activity is not uncommon in a suburban forest. As a result, wild boar might have created a behavioural response to human leisure activity already before the COVID-19 outbreak (Gaynor et al., 2018; Johann et al., 2020). Alternatively, human leisure activity is restricted to established roads and paths, which can be less disturbing and not lead to any temporal displacements of wildlife (Fattebert et al., 2017). Although the space use and movement of wild boars did not increase during the lockdown period, I detected an increased energy expenditure (VeDBA) from the bio-loggers in the collared wild boars. The energy expenditure was 41% higher in weeks with high human leisure activity. The increased energy expenditure can result from small-scale body movements and activity on site, which GPS positions sending location every 30 minutes cannot capture (Gunner et al., 2021). Further analysis of sleep patterns confirms an increased small-scale body movement of wild boar during high human leisure activity. Wild boar sleep was more fragmented (short and frequent sleeping bouts) under high human leisure activity 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 patterns, total sleep time was similar at high and low human visitation rates. The results of disrupted sleep patterns and increased energy expenditure might severely impact the health of the wild boar. Sleep has fundamental functions in the immune system (Rogers et al., 2001), neuronal (McDermott et al., 2003), and cognitive system (Roth et al., 2010). Lack of sleep quantity and quality can be fatal for wildlife, causing sleepiness and decreased psychomotor performance, such as reduced short-term memory, reaction time, or vigilance (Bonnet & Arand, 2003; Phillipson et al., 1980). Outdoor recreational activities are a rising topic in human-wildlife interaction as the intensity and space use of human outdoor activities have significantly increased over the last years (Balmford et al., 2009). Over the last two decades, 3.3 million km2 of global wilderness areas have been lost (Watson et al., 2016).

Research on the effects of recreational activities on capercaillie (*Tetrao urogallus*), such as ski tourism, shows a negative overall fitness and body condition (Thiel et al., 2008). Likewise, camping next to ospreys' (*Pandian haliaetus*) nests decreases reproductive success (Kerlinger et al., 1995; Swenson, 1979). Unconscious anthropogenic impacts, such as recreational activities and tourism, must be treated as seriously as conscious anthropogenic impacts, such as hunting activities (Bateman & Fleming, 2017), as wildlife perceive humans as a threat (Tablado & Jenni, 2017).

Recreational activity potentially negatively affects wildlife's sleep behaviour and, out of that, the overall physiology of wildlife (Bateman & Fleming, 2017). At the same time high interest in recreational activities provide political capital to keep the remaining wilderness areas (Buckley, 2009). To harmonise recreational activity and wildlife protection in wilderness areas a control system is needed. Managing a coexistence between humans and undisturbed wildlife will become increasingly important. Current management options for coexistence distinguish between the integration of "land sharing", where land is less intensively maintained for agricultural purposes to maintain some biodiversity (Green et al., 2005) and the separation of "land sparing", where conservation and production are independent (Fischer et al., 2014). "Land sparing" implementations are refuge areas where human access is restricted and used only by wildlife. Those refuge areas provide shelters for resting and breeding (Kerlinger et al., 1995). Another example of "land sparing" is when certain islands have been established as sanctuaries with limited human access to increase nesting success in Artic loon (*Gavia arctica*) (Götmark et al., 1989). "Land sharing" can be achieved when hiking in the forest is restricted to marked trails and trailless areas for wildlife (Taylor & Knight, 2003). On agricultural fields, shared land approaches combine coffee plants with canopy cover and lower strata vegetation to enable coexistence with small mammals (Caudill et al., 2015). However, the ideal conceptual framework for wildlife management is rarely given (Fischer et al., 2014). For example, the "land sparing" approach faces increasing challenges for large mammals which maintain huge home ranges and territories. Large areas only for wildlife use are scarce. Carnivores and people increasingly overlap (López-Bao et al., 2017) highlighting the need of constant evaluation and scientific debate on promising management approaches for human-wildlife coexistence.

Experience shapes wild boar response to drive hunts

As natural predators are absent from many human-dominated areas, hunting by humans has become crucial (Keuling et al., 2013; Sweitzer et al., 2000) to control the population of wild ungulates and to decrease the number of economic damages (Kamler & Drimaj, 2021; Vajas et al., 2020). The analysis showed that drive hunts affect the spatial behaviour of wild boar by increasing their daily range size by up to 59% and daily distance by up to 41% on the hunting day. Those results are consistent with the studies from France and Sweden (Maillard, 2002; Thurfjell et al., 2013). However, new findings show that effect on wild boar spatial behaviour is related to the number of experienced hunts of a wild boar (Olejarz et al., 2024). The daily range size and distance increased with the increasing wild boar hunting experience over the season, and the range overlap with the hunted area decreased. These spatial responses can be collectively described as an anti-predator response based on experience (Saxon-Mills et al., 2018). In this study, 60% of wild boar showed a flight response with a distance of 1.80 km and a flight duration of 25.8 h. In addition to the spatial response, individual wild boar responses can vary due to external and internal factors (Belgrad & Griffen, 2016; Sommer-Trembo et al., 2016). For example, largespring mosquitofishes (*Gambusia geiseri*) with active and exploratory personalities had a greater ability to escape predators (Blake & Gabor, 2014). During a drive hunt, I found considerable variation in wild boar to show a “remain” or “flee” behaviour during hunting events. In most cases, the individual variation in spatial response was consistent. However, twenty-seven per cent of wild boar had no fixed behavioural response. Wild boar with inconsistent strategy changed mainly into a “flee” strategy with increasing hunting experience over the season. Those results highlight wild boar's adaptability towards hunting pressure. With increasing hunting exposure and learning through experience, individuals can modify spatial behaviour towards one consistent strategy (Sommer-Trembo et al., 2016). For example, with age, female elks (*Cervus elaphus*) reduce movement rates and increase the use of forests (Thurfjell et al., 2017). The increased preference to display a “flee” strategy over the season in wild boars might be advantageous because of the low hunting speed and the low cost of escaping from the hunting risk (Broom & Ruxton, 2005). Animals' survival, reproductive success and distribution (Tuomainen & Candolin, 2011) might be positively linked to behavioural adaptability.

Behaviour plasticity has been mainly observed in species that display a generalist’s strategy rather than highly specialised species (Kitahara & Fujii, 1994). In butterfly communities, the diversity of butterfly species is negatively related to human disturbance as the number of specialist species decreased, but not the number of generalist species (Kitahara & Fujii, 1994). Although behavioural plasticity can buffer HIRECs, maladaptive behavioural scenarios, also known as “evolutionary traps”, are common (Robertson et al., 2013; Robertson & Chalfoun, 2016), especially when the animals have not encountered changing conditions during their evolutionary history (Ghalambor et al., 2007; Schlaepfer et al., 2002). Habitat loss and fragmentation force birds to use more anthropogenic edges for breeding. However, those habitats are more dangerous as they accumulate nest predators at higher densities (Weldon & Haddad, 2005). Similarly, an "evolutionary trap" has been identified in usually solitary foraging stingrays due to tourist feeding. Stingrays created novel grouping behaviour in areas where tourists provide quickly renewing food patches. However, stingrays (*Dasyatis americana*) displayed lower body conditions in those feeding spots and were more susceptible to ectodermal parasites (Semeniuk & Rothley, 2008). Another example of evolutionary trap is illustrated by non-native coyotes (*Canis latrans*) introduced into the southeastern USA and predating on white-tailed deer (*Odocoileus virginianus*). As an antipredator strategy, white-tailed deer hide neonates in greater plant cover, however neonates that moved less and were covered in denser areas were more likely to be depredated by coyotes (Chitwood et al., 2017).

Hunting is known to shape morphological and behavioural traits in wildlife (Ciuti et al., 2012; Leclerc et al., 2019; Lone et al., 2015). Some behavioural adaptations are beneficial for wildlife, ensuring the survival of a species (Thurfjell et al., 2017). In the case of drive hunts, I showed 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 (Olejarz et al., 2024). However, I could not confirm that the detected behavioural plasticity over the season in the study on drive hunts was beneficial or an "evolutionary trap" for the wild boar population (Olejarz et al., 2024). Hunting adult dominant male bears (*Ursus arctos*) potentially causes an ecological trap as locally socially stable structures get disrupted (Penteriani et al., 2018; Steyaert et al., 2016). New immigrating male bears increase the risk of sexually selected infanticide to bring females back into a reproductive stadium (Leclerc et al., 2017). Knowing if the drive hunts are shaping a positive or negative adaptation in plastic species is vital for managing the population. Therefore, further research on hunting activity is highly recommended for conscious wildlife management through hunting.

No evidence for the consistent effect of supplementary feeding on home range size in terrestrial mammals

Based on the literature search and meta-analysis, I found, contrary to the expectation, no consistent reduction in the home range size of terrestrial mammals when animals were provided with supplementary food. Resources for food are one of the critical factors for an animal to decide how to use space (Pyke et al., 1977). Often agriculture areas intended for human consumption are exposed to depletion by wildlife (Richard, 2021). To the detriment of forestry, forest areas are exposed to browsing pressure by deer, causing tree damage and reducing shrubs and herbaceous plant biomass (Gill, 1992). Creating supplementary feeding areas might shift wildlife away from conflicting human food resource areas. In addition, supplemental food provided by humans to wildlife can be more abundant and predictable for animals than natural resources and, consequently, potentially change their spatial behaviour (Griffin & Ciuti, 2023; Milner et al., 2014; Oro et al., 2013). However, ranging behaviour in wildlife is not only related to food. The availability of other resources, such as predation risk (Verdolin, 2006), and social interactions are crucial for an animal home range (Gehrt & Fritzell, 1998). By neglecting other functions of an animal home range, supplementary feeding might remain without any effect on the ranging behaviour. For example, grey squirrels (*Sciurus carolinensis*) trade off their energy intake rate against predation risk and consume immediate food when exposed to predation (Lima et al., 1985). Roe deer (*Capreolus capreolus*) decreased their use of high crops daily to avoid human disturbances (Bonnot et al., 2013).

Adding body mass into the meta-analysis, I figured out that only species with a body mass below 1 kg (91% rodents and 9% marsupials) strongly tended to reduce home range size. Using sex as an additional predictable variable, I observe contrasting effects. Males tend to increase and females to decrease range size due to supplementary feeding. Female home ranges, however, are reduced during the rearing of offspring (Van Beest et al., 2011; Young et al., 2008) due to limited mobility of the offspring, protection from infanticide (Dahle & Swenson, 2003), and predators (Grignoli et al., 2007). Predictable and abundant food resources from supplementary feeding, particularly for females with offspring, could further enhance site fidelity and sex-related differences in home range decline. Although some trends were visible, I did not see consistent changes in home range size due to supplementary food in three different taxonomic groups. Furthermore, the results showed opposing trends between studies providing limited and unlimited (ad libitum) amounts of food. Animals' complete knowledge of the spatiotemporal distribution of resources and changes in range size might be only efficient when ad libitum food is provided (Stephens & Krebs, 1986). The range size tends to decrease for intentionally and unintentionally supplementary feeding. However, the effect is stronger in unintentional feeding. For example, spotted hyenas (*Crocuta Crocuta*) preferentially used areas around human waste pits constitute a primary food source. After the closure of the pits, the home range size of the spotted hyenas increased significantly (Kolowski & Holekamp, 2008). Feeding durations were only available for intentional feeding and provided no evidence of an effect on range size due to supplementary feeding. Intentionally feeding is often limited to one season (Newey et al., 2010; Peterson & Messmer, 2007). Therefore, it is too short to trigger an effect.

Opposing tendencies, I found range size in response to supplementary feeding between free-ranging and enclosed animals. Free-ranging mammals tended to increase home range size with supplementary feeding, while the opposite trend was observed in enclosures. One possible explanation might be that feeding sites in the open settings were located on the periphery of an animal's home range, causing additional movement (Webb et al., 2008; Young et al., 2008). I found no consistent effect of the type of spatial data (telemetry, capture-mark-recapture) used to calculate home range size on the response to supplementary feeding. However, different home range estimators led to different trends in the meta-analysis. Home ranges computed with kernel 90 showed a relatively strong decline under supplementary feeding. In contrast, all the other estimators tended to show a positive effect, with the strongest for MCP 100. Kernel-based methods are better suited to study the effects of resource distribution on space use, as they are relatively unbiased and account for centres of activity (Börger et al., 2006).

The global expansion of the human population caused fragmentation and loss of existing habitats for wildlife (Richard, 2021). The remaining habitats are exposed to a strong resource competition between humans and wildlife (Richard, 2021). Practical wildlife management tools are urgently needed to reduce conflicts between humans and wildlife. Supplementary feeding may mitigate conflicts, such as depredating agricultural fields and browsing pressure in forests (Calenge et al., 2004; Van Beest et al., 2010). In addition, it can serve for conservation implications, e.g. to sustain endangered species (Milner et al., 2014; Thierry et al., 2020) or to reintroduce extinct populations (Ewen et al., 2015). However, besides the positive outcomes, many publications raise concerns about supplementary feeding to wildlife, highlighting potential negative impacts (Penteriani et al., 2021). Supplementary feeding can potentially negatively affect population size, structure and the behaviour of wildlife (Carranza et al., 1995; Pérez-González et al., 2010). The concentration of high densities of wildlife around supplementary feeding stations may increase the risk of infection (Putman & Staines, 2004; Sorensen et al., 2014). Contrary to the planned management output, supplementary feeding can even increase the browsing pressure of red deer (*Cervus elaphus hispanicus*) on shrubs. Red deer must raise the consumption of plant species whose nutritional composition complements the supplementary food (Miranda et al., 2015). Likewise, feeding programs in winter for deer are only successful for population recovery when providing pelleted grain mixed with wood sawdust instead of hay (Ouellet et al., 2001). Wildlife physiological requirements should be studied well before providing supplementary food (Miranda et al., 2015). Otherwise, management measures may not have the desired effect or contribute to an opposing effect. The meta-analysis shows no consistent evidence of spatial modification of wildlife to supplementary feeding and scarcity of studies on the topic despite worldwide ubiquity of supplementary feeding. (Olejarz & Podgórski, 2024). This highlights a knowledge gap in our understanding of the effects of supplementary feeding on ranging behaviour. More comprehensive research is needed to better understand supplementary feeding on wildlife before applying it as a management tool.

7. Conclusion

During the Anthropocene, wildlife must cope with various anthropogenic impacts. This applies especially to species closely interacting and sharing their natural habitats with humans, such as the wild boar (Fattebert et al., 2017). In this dissertation thesis I showed behavioural modifications and plasticity in wild boar under the impact of hunting (Olejarz et al., 2024) and recreational activities (Olejarz et al., 2023). I showed that wild boar was moderately vulnerable to high human presence resulting from COVID-19 lockdown related to increased recreational activity in the forest. While movement and space use metrics of wild boar did not change in response to high human activity, they displayed higher energy expenditure and disrupted sleep patterns, which may have potentially detrimental fitness consequences. Similarly, wild boar movements showed resilience to increasing intensity of drive hunts. However, drive hunts generated a shift in wild boar behavioural response. With an increasing number of experienced hunts, wild boar showed predominantly flight behaviour rather than hiding during drive hunts. Frequent drive hunts repeated over the same area can thus lead to population dispersion with potentially negative impacts on crop damage and disease transmission. Furthermore, I disproved the common belief of simple modifications of ranging behaviour due to supplementary feeding of terrestrial mammalian wildlife (Olejarz & Podgórski, 2024). While an overall tendency of reduced home range in response to supplementary feeding was observed, the effect was inconsistent with strength and directions of the trends depending on species biology, feeding regime and methods of data collection and analysis. These results suggest that complex mechanisms of home range behaviour can make it insensitive to manipulation with supplementary feeding as a universal tool in wildlife management.

This dissertation's findings provide insights into mammalian wildlife response to anthropogenic impacts. Those insights can facilitates effective, science-based, wildlife management (Apollonio et al., 2017). Further efforts for well-designed research and monitoring of wildlife are recommended, such as consistent long-term monitoring, systematically collected data, joint cross-country actions, and the engagement of various stakeholders, such as hunters, foresters, and farmers, for game research and field work (Apollonio et al., 2017; Linnell et al., 2020). In addition, using the newest technologies in remote tracking, such as GPS telemetry and biologging systems, can provide new insights into an animal's life history and behaviour (Wall et al., 2014). and improve current wildlife management practices (Wilson, 2008).

8. References

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