Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

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Behaviorální reakce prasat divokých na lidskou aktivitu a na opatření proti šíření afrického moru prasat

Disertační práce

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ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE

Fakulta lesnická a dřevařská

ZADÁNÍ DISERTAČNÍ PRÁCE

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Lesní inženýrství
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Název práce

Behaviorální reakce prasat divokých na lidskou aktivitu a na opatření proti šíření afrického moru prasat

Název anglicky

Behavioral Responses of Wild Boar to Human Activity and Measures Against the Spreading of African Swine Fever

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Cíle práce

Hlavním cílem disertační práce je vyhodnotit efekt různých managementových opatření na chování volně žijících prasat divokých. Práce se zaměří především na testování opatření související s pohybem lidí a jejich volnočasovými a hospodářskými aktivitami v prostoru výskytu prasat divokých a také na vliv aktivních technických opatření (afinita prasat divokých ke kadáverům; opatření proti omezení migrace prasat divokých).
Dílčí cíle disertační práce jsou:
1) Vyhodnotit dopad lidských disturbancí na chování prasat divokých a šíření AMP.
2) Prozkoumat fyziologické dopady zvýšené lidské aktivity na zdraví a stres prasat divokých během kritických období.
3) Posoudit účinnost omezení pohybu lidí při kontrole ohnisek AMP.
4) Vyhodnotit účinnost pachových ohradníků a prozkoumat alternativní strategie zvládání AMP.
5) Analyzovat změny chování u prasat divokých kolem kadáverů za účelem posouzení rizik přenosu AMP.
6) Stanovit možné managementové opatření při ochraně lesa vztažené k užití rušivých elementů jako nástroje možného ovlivnit prostorovou aktivitu kopytníkůprasat divokých.

Metodika

Disertační práce bude využívat kombinaci biologging technologie, GPS a fotopastí, aby prozkoumala chování prasat divokých v reakci na lidské disturbance v jejich přirozených podmínkách, vliv kadáverů prasat divokých na jejich aktivitu a důsledky pro přenos afrického moru prasat (AMP). Metodika je navržena tak, aby sbírala komplexní data napříč různými zalesněnými lokalitami v České republice.

Sběr dat bude prováděn s použitím multi-senzorových obojků (GPS, akcelerometr, magnetometr), GPS fix je 30 minut. Tyto obojky budou monitorovat pohyb a vzorce chování v jemném měřítku. Biologgery budou poskytovat nepřetržité údaje o aktivitě divočáků, což umožní podrobnou analýzu jejich reakcí na různé typy disturbancí. Pro stanovení behaviorálních modelů bude použit software DDMT, který byl vyvinut na Swansea University a je přímo určený pro zpracovávání dat z biologging senzorů. Získaná data budou následně zpracována pomocí dead-reckoningu právě v DDMT softwaru.

Kadávery prasat divokých budou umístěny náhodně v lesním komplexu a fotopasti budou monitorovat jak místa s kadávery, tak kontrolní oblasti. Tyto pasti budou zaznamenávat čas a datum. Následně budou v přípravě dat pro analýzy přidány další faktory jako frekvence návštěv a charakteristiky zvířat, jako je věk, pohlaví a chování. Místa kadáverů budou vybrána tak, aby odpovídala kontrolním místům z hlediska podmínek prostředí a zajistila srovnatelnost.

Vyhodnocení dat shromážděných z GPS, biologgerů a fotopastí bude provedeno pomocí softwaru R a GIS software bude aplikován pro vizualizaci dat.

Doporučený rozsah práce

60 – 120 stran

Klíčová slova

prase divoké, lidské rušení, chování, prostorová orientace, pachové ohradníky, AMP, kadávery

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Děkan

V Praze dne 17. 10. 2024

Prohlášení

Prohlašuji, že jsem disertační práci na téma: Behaviorální reakce prasat divokých na lidskou aktivitu a na opatření proti šíření afrického moru prasat vypracovala samostatně a citovala jsem všechny informační zdroje, které jsem v práci použila, a které jsem rovněž uvedla na konci práce v seznamu použitých informačních zdrojů.

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Svým podpisem rovněž prohlašuji, že elektronická verze práce je totožná s verzi tištěnou a že s údaji uvedenými v práci bylo nakládáno v souvislosti s GDPR.

V Praze dne 15.10.2024 ______________________________

Poděkování

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Disertační práce byla vypracována v rámci řešení projektů:
NAZV č. QK1910462 „Behaviorální reakce prasat divokých na opatření proti šíření afrického moru prasat.“
č.: 82/2021 „Lockdown period in the Czech Republic: Effect of human activity on animals’ spatial behavior and energy expenditure“ realizovaného v rámci projektu č. CZ.02.2.69/0.0/0.0/19_073/0016944, Zvyšování kvality interního grantového schématu na ČZU
FLD IGA č. A_20_27 „Vliv lidských aktivit na prasata divoká v Kostelci nad černými lesy a Doupovských horách vyhodnocený pomocí nové technologie dead-reckoning na základě dat získaných z biologgerů umístěných v obojcích zvířat“
FLD IGA č. A_25_22 „The impact of human activities on deer and wild boar spatiotemporal behavior by using dead-reckoning technology based on data obtained from biologgers located in animal's collars“

Behaviorální reakce prasat divokých na lidskou aktivitu a na opatření proti šíření afrického moru prasat

Abstrakt

Cílem disertační práce bylo posoudit, jak lidské aktivity ovlivňují chování prasat divokých a jak účinná jsou opatření zaměřená na omezení šíření afrického moru prasat (AMP). Dílčí cíle zahrnovaly detailní analýzu reakcí prasat na různé typy lidských disturbancí (turistika, motorová vozidla, přítomnost psů atd.) a zhodnocení efektivity technických opatření proti šíření AMP (pachové ohradníky a odstranění kadáverů infikovaných zvířat). Zvláštní pozornost byla věnována tomu, jak lze tato opatření zlepšit a jak optimalizovat přístup k regulaci populace prasat divokých v souvislosti s šířením AMP.

AMP představuje globální hrozbu pro populace divokých a domácích prasat. Virus má vysokou mortalitu, často dosahující až 100 %, a jeho dopady jsou závažné nejen z hlediska ekonomiky, ale i ochrany životního prostředí. Prasata divoká jsou klíčovým vektorem šíření nemoci. Výzkum probíhal v několika lokalitách v České republice, kde byla populace prasat sledována pomocí moderních technologií, jako je GPS telemetrie, biologging a fotopasti, což umožnilo podrobnou analýzu jejich pohybových vzorců a reakcí na rušivé faktory.

Metodický postup zahrnoval kombinaci terénních pozorování a pokročilých technologií pro sledování pohybu zvířat. Telemetrická zařízení byla využita k získání dat o prostorové orientaci, chování a fyziologickém stavu prasat divokých. GPS obojky a akcelerometry poskytly podrobná data o jejich denních aktivitách a reakcích na přítomnost lidí. Součástí výzkumu bylo testování účinnosti pachových ohradníků, které měly sloužit jako bariéra pro omezování pohybu prasat divokých, a analýza atraktivity kadáverů pro další jedince, což má přímý vliv na riziko šíření viru. Statistické analýzy zahrnovaly porovnání pohybových vzorců před a po aplikaci opatření, stejně jako hodnocení energetického výdeje a spánkových vzorců zvířat v oblastech s vysokou i nízkou mírou lidské aktivity.

Hlavní výsledky ukázaly, že prasata divoká jsou překvapivě tolerantní vůči lidským disturbancím. I když jejich pohybové vzorce zůstaly relativně stabilní, přítomnost lidí vedla k výraznému nárůstu energetického výdeje a k narušení spánkového cyklu. Tato zvířata vykazovala zvýšenou ostražitost a reakce na lidskou přítomnost, což může mít dlouhodobé důsledky na jejich fyziologický stav a reprodukční schopnosti. V rámci hodnocení technických opatření se ukázalo, že pachové ohradníky nejsou efektivní bariérou pro omezení pohybu prasat. Zvířata často pachové ohradníky ignorovala nebo rychle přizpůsobila své chování, čímž se jejich účinnost snížila na minimum. Na druhou stranu byla zjištěna výrazná afinita prasat ke kadáverům infikovaných jedinců, což znamená, že kadávery představují vysoké riziko pro další šíření viru mezi populacemi prasat. Včasné a důsledné odstranění kadáverů se ukazuje jako klíčový faktor v prevenci šíření AMP.

Přínos tohoto výzkumu spočívá především v detailní analýze vztahů mezi lidskými aktivitami, chováním prasat divokých a účinností opatření proti AMP. Výsledky ukazují, že současná opatření, jako jsou pachové ohradníky, nejsou dostatečně účinná, a naznačují, že by měly být hledány nové, efektivnější strategie. Zvláštní důraz je kladen na nutnost lepšího managementu populace prasat divokých, včetně kontroly jejich pohybu a důsledného odstraňování kadáverů, které jsou zásadním zdrojem přenosu viru. Výsledky výzkumu mohou

sloužit jako základ pro návrh efektivnějších strategií boje proti AMP a mohou významně přispět k udržitelné ochraně divokých zvířat a omezení šíření této nebezpečné nákazy.

Celkově tento výzkum poskytuje nové poznatky o adaptivních schopnostech prasat divokých v prostředí ovlivněném lidskou činností a ukazuje na slabiny některých současných opatření proti AMP. Je zřejmé, že kombinace technologií pro monitorování zvířat a účinných kontrolních opatření je nezbytná pro dlouhodobou kontrolu šíření afrického moru prasat.

Klíčová slova: prase divoké, lidské rušení, chování, prostorová orientace, pachové ohradníky, AMP, kadávery

Behavioral Responses of Wild Boar to Human Activity and Measures Against the Spreading of African Swine Fever

Abstract

The doctoral thesis aimed to assess how human activities affect the behavior of wild boar and the effectiveness of measures intended to limit the spread of African swine fever (ASF). The specific objectives included a detailed analysis of wild boar responses to various types of human disturbances (tourism, motor vehicles, the presence of dogs etc.), and an evaluation of the effectiveness of technical measures against ASF (odor fences and the removal of infected animal carcasses). Special attention was given to how these measures could be improved and how to optimize approaches to regulating wild boar populations in relation to ASF spread.

ASF represents a global threat to wild and domestic pig populations. The virus has a high mortality rate, often reaching up to 100%, and its impacts are severe, not only economically but also in terms of environmental conservation. Wild boars are a key vector in spreading the disease. This research was conducted at several locations in the Czech Republic, where wild boar populations were monitored using modern technologies such as GPS telemetry, biologging, and camera traps. These tools enabled a detailed analysis of their movement patterns and responses to disruptive factors.

The methodological procedure involved a combination of field observations and advanced technologies for tracking animal movements. Telemetry equipment was used to gather data on wild boars' spatial orientation, behavior, and physiological condition. GPS collars and accelerometers provided detailed data on their daily activities and reactions to human presence. The research also tested the effectiveness of odor fences, intended to serve as barriers to limit wild boar movement. Additionally, it analyzed the attractiveness of carcasses to other individuals, which directly impacts the risk of virus transmission. Statistical analyses compared movement patterns before and after the implementation of measures and evaluated energy expenditure and sleep patterns of animals in areas with high and low human activity.

The main results showed that wild boars are surprisingly tolerant to human disturbances. While their movement patterns remained relatively stable, the presence of humans led to a significant increase in energy expenditure and disruption of sleep cycles. These animals displayed heightened vigilance and reactions to human presence, which could have long-term effects on their physiological condition and reproductive capabilities. Regarding the evaluation of technical measures, odor fences proved ineffective in limiting wild boar movement. The animals often ignored the fences or quickly adapted their behavior, reducing the effectiveness to a minimum. On the other hand, wild boar exhibited a marked affinity for carcasses of infected individuals, meaning that carcasses pose a high risk for further virus spread among boar populations. Timely and thorough carcass removal appears to be a key factor in preventing ASF spread.

The contribution of this research lies mainly in the detailed analysis of the relationships between human activities, wild boar behavior, and the effectiveness of ASF control measures. The results show that current measures, such as odor fences, are not sufficiently effective, indicating that new, more efficient strategies are needed. Particular emphasis is placed on improved wild boar population management, including controlling their movement and ensuring consistent carcass removal, a critical source of virus transmission. The findings can serve as a basis for designing more effective strategies to combat ASF and significantly contribute to the sustainable protection of wildlife and the containment of this dangerous disease.

Overall, this research provides new insights into the adaptive capabilities of wild boar in environments influenced by human activity and highlights the weaknesses of some current ASF control measures. It is clear that a combination of animal monitoring technologies and effective control measures is essential for the long-term management of the spread of African swine fever.

Keywords: wild boar, human disturbances, behavior, spatial orientation, odor fences, ASF, carcasses

Obsah

1 Úvod

Africký mor prasat (AMP) představuje jednu z nejvýznamnějších hrozeb pro populace prasat a prasatovitých na celém světě, s dopady nejen ekonomickými, ale také ekologickými a sociálními. Virus, který je původcem této nemoci, patří do čeledi *Asfarviridae* a je charakterizován vysokou mortalitou, jež může dosahovat až 100 % u citlivých populací domácích i divokých prasat (Dixon et al., 2019). AMP poprvé vypukl v Africe na počátku 20. století, odkud se postupně rozšířil do Evropy a Asie (Beltrán-Alcrudo et al., 2017; Costard et al., 2013; Gallardo et al., 2019). V posledních několika desetiletích AMP postihl populace prasat v jihozápadní Evropě a zejména na Pyrenejském poloostrově, kromě toho způsobil ojedinělá ohniska v jiných evropských zemích. V roce 1995 byl AMP z Pyrenejského poloostrova eradikován, stále však zůstal endemický na Sardinii. V roce 2007 byl AMP znovu zaveden do Evropy přes Gruzii, pravděpodobně v důsledku nárůstu AMP v Africe, ve spojení s globalizací, ekonomickou krizí a používáním kontaminovaných odpadků a masných výrobků z mezinárodních lodí, což vedlo k rychlému rozšíření po východní Evropě a sousedních regionech (Sánchez-Vizcaíno et al., 2013). V Evropské unii byl genotyp II poprvé zjištěn v roce 2014 v Polsku a pobaltských státech (Ståhl et al., 2024). V celé Evropě i Asii nadále způsobuje vážné ekonomické ztráty a narušuje fungování ekosystémů (Beltrán-Alcrudo et al., 2017; Costard et al., 2013; Gallardo et al., 2019). AMP se primárně šíří přímým kontaktem mezi infikovanými a zdravými prasaty, včetně prasat divokých. Avšak AMP se neomezuje pouze na přímý přenos mezi jedince, ale významnou roli v něm hrají i další faktory, jako je lidská činnost a přenos prostřednictvím kontaminovaného prostředí a materiálů, jako je krmivo, vozidla a vybavení. Podstatnou úlohu v šíření viru hraje také nesprávná likvidace kontaminovaných kadáverům a vepřových produktů (Bellini et al., 2021; Sánchez-Vizcaíno et al., 2013). Dosavadní výzkum ukazuje, že jedním z hlavních vektorů šíření AMP v přírodních populacích jsou právě prasata divoká (*Sus scrofa*), která mají široké geografické rozšíření a vysokou populační hustotu (Keuling et al., 2018a). Díky své schopnosti překonávat velké vzdálenosti a přizpůsobovat se různým typům prostředí představují klíčový prvek v dynamice přenosu viru mezi různými lokalitami (Pepin et al., 2020). Nicméně přesné chování prasat divokých v kontextu AMP není zcela známo, což komplikuje implementaci efektivních kontrolních opatření. I když bylo provedeno několik studií zaměřených na behaviorální reakce prasat divokých na různé druhy bariér a lidské aktivity, stále existují mezery v poznání, zejména pokud jde o detailní analýzu jejich pohybových vzorců a reakce na specifická opatření, jako jsou pachové ohradníky nebo odstraňování kadáverů (Cukor et al., 2021).

Kontrola AMP je obtížná kvůli absenci účinné vakcíny a schopnosti viru přežívat dlouhodobě ve vnějším prostředí. Virus může přežívat měsíce až roky v kontaminovaném mase, krvi a tkáních, což z něj činí obtížně eliminovatelnou hrozbu (Probst et al., 2017). Klíčovým prvkem šíření viru jsou kadávery infikovaných prasat, které mohou sloužit jako významný zdroj infekce pro další jedince. Prasata divoká vykazují silnou afinitu k těmto kadáverům, což zvyšuje riziko přenosu AMP prostřednictvím přímého kontaktu, kanibalismu nebo skrze kontaminované prostředí (Bellini et al., 2021). Tento fenomén činí včasné a efektivní odstranění kadáverů zásadním opatřením v boji proti šíření AMP. Přesto zůstává otázkou, jak nejlépe monitorovat a minimalizovat riziko spojené s přítomností kadáverů v přírodním prostředí.

Dalším důležitým aspektem v boji proti AMP je vliv lidských aktivit na šíření této nemoci. Intenzivní lesnické a zemědělské aktivity, turistika a další formy rekreace mohou mít vliv na pohyb a chování prasat divokých, a tím i na šíření viru AMP (Cukor et al., 2021; Podgórski et al., 2013). V posledních letech došlo také k nárůstu studií zabývajících se vlivem omezení pohybu lidí a karanténních opatření během pandemie COVID-19 na chování volně žijících zvířat, včetně prasat divokých (Rutz et al., 2020). Výsledky naznačují, že snížení lidské aktivity během pandemie vedlo ke změnám v pohybových vzorcích zvířat a ke zvýšení jejich aktivity v dříve rušených oblastech. Tyto změny mohou mít důsledky pro dynamiku šíření AMP a naznačují potřebu zvážit dopady lidské činnosti při plánování kontrolních opatření (Soto et al., 2021).

Jedním z aktuálních přístupů ke kontrole pohybu prasat divokých je použití různých technologií pro sledování a řízení populací. Moderní technologie, jako jsou GPS telemetrické obojky, akcelerometry a fotopasti, umožňují detailní sledování pohybů a chování prasat divokých v reálném čase (Foley & Sillero-Zubiri, 2020; Laguna et al., 2021). Tyto metody umožňují získat cenné informace o prostorové orientaci, využívání stanovišť a reakci na různé typy rušení, což je nezbytné pro efektivní plánování managementových opatření. Přesto je jejich implementace v praxi často omezena technickými a finančními nároky, což brzdí širší aplikaci těchto metod při kontrole AMP (Palencia et al., 2023).

Současná opatření pro kontrolu AMP často zahrnují intenzivní lov s cílem snížit početnost populace prasat divokých v zasažených oblastech a fyzické bariéry, jako jsou elektrické ploty ke snížení pohybu jedinců (Gürtler et al., 2017; Honda, 2022; Mysterud & Rolandsen, 2019). Tyto metody však narážejí na omezení kvůli adaptivnímu chování prasat divokých, která mohou rychle měnit své pohybové vzorce a stanoviště v reakci na narušení a opatření proti AMP (Podgórski et al., 2013). Kromě toho je účinnost pachových ohradníků často sporná, protože prasata divoká mohou ignorovat nebo překonávat tyto bariéry, zejména pokud jsou v prostředí dlouhodobě přítomna (Schlageter & Haag-Wackernagel, 2012).

Dosavadní výzkumy se zaměřovaly především na obecné pohybové vzorce a reakce prasat divokých na základní opatření, jako jsou fyzické bariéry a depopulace. Avšak detailní zkoumání vlivu specifických faktorů, jako je přítomnost kadáverů nebo změny v lidských aktivitách, na behaviorální odpovědi prasat divokých a následný vliv na šíření AMP, je stále nedostatečné (Beltrán-Alcrudo et al., 2017; Pepin et al., 2020). Chybí komplexní přístup, který by integroval různé metody sledování a hodnocení efektivity opatření v reálném čase. Takový přístup by mohl poskytnout hlubší vhled do dynamiky šíření AMP a umožnit vyvinutí cílenějších a efektivnějších strategií pro kontrolu této nebezpečné nákazy.

2 Cíle práce

Disertační práce se skládá z pěti vědeckých článků rozdělených do tří tematických okruhů. Čtyři z těchto článků byly publikovány v časopisech v databázi Web of Science a jeden je momentálně v recenzním řízení.

Hlavním cílem disertační práce je vyhodnotit efekt různých managementových opatření na chování volně žijících prasat divokých. Práce se zaměří především na testování opatření související s pohybem lidí a jejich volnočasovými a hospodářskými aktivitami v prostoru výskytu prasat divokých a také na vliv aktivních technických opatření (afinita prasat divokých ke kadáverům; opatření proti omezení migrace prasat divokých).

Dílčí cíle disertační práce jsou:

1) Vyhodnotit dopad lidských disturbancí na chování prasat divokých a šíření AMP.
2) Prozkoumat fyziologické dopady zvýšené lidské aktivity na zdraví a stres prasat divokých během kritických období.
3) Posoudit účinnost omezení pohybu lidí při kontrole ohnisek AMP.
4) Vyhodnotit účinnost pachových ohradníků a prozkoumat alternativní strategie zvládání AMP.
5) Analyzovat změny chování u prasat divokých kolem kadáverů za účelem posouzení rizik přenosu AMP.
6) Stanovit možné managementové opatření při ochraně lesa vztažené k užití rušivých elementů jako nástroje možného ovlivnit prostorovou aktivitu prasat divokých.

3 Rozbor problematiky

3.1 Globální polohovací systém

Revoluci ve studiu ekologie zvířat za pomoci telemetrických sledovacích systémů přineslo zavedení globálního polohovacího systému (GPS), který od devadesátých let 20. století umožňuje sledovat pohyby volně žijících zvířat s vysokou přesností a v reálném čase (Clark et al., 2006). Rozvoj GPS technologie umožnil vědcům sledovat i kryptická a těžko dostupná zvířata v rozmanitých prostředích. Pokroky v satelitních systémech a miniaturizaci zařízení rovněž otevřely možnosti sledování širší škály druhů, včetně menších zvířat (Bidder et al., 2015).

GPS zařízení, často ve formě obojků, zaznamenávají polohu zvířat a umožňují sledování jejich pohybu v různých časových intervalech (Reynolds & Riley, 2002). Navzdory tomu, že GPS technologie poskytuje cenné informace, je její přesnost ovlivněna prostředím, ve kterém se zvíře nachází, což může vést k chybám v lokalizaci (Frair et al., 2010). Tato technologie je nyní standardem při studiu pohybu volně žijících živočichů (Foley & Sillero-Zubiri, 2020).

3.2 Biologging technologie

Biologgery jsou záznamová zařízení připevňovaná na volně žijící zvířata, která umožňují sledování různých proměnných jako je pohyb, chování nebo fyziologické stavy zvířat. Tyto technologie umožňují sbírat obrovské množství dat, aniž by přítomnost člověka v terénu ovlivnila chování sledovaných jedinců (Ropert-Coudert & Wilson, 2005). Biologgery se stávají nezbytnou součástí moderní ekologie pohybu, protože poskytují podrobné a kontinuální záznamy o aktivitách sledovaných jedinců (Wilson et al., 2008).

Biologging technologie zahrnuje různé typy senzorů, z nichž nejběžnější jsou akcelerometry a magnetometry. Akcelerometry měří dynamiku a orientaci těla zvířat (Shepard et al., 2008). Magnetometry zase umožňují určit směr pohybu zvířete ve vztahu k magnetickému poli Země, což doplňuje data z GPS a akcelerometrů (Williams et al., 2017). Tato kombinace senzorů poskytuje přesně vyřešené trajektorie pohybu zvířat a může být využita k popisu jemných aspektů jejich chování, jako je využití stanovišť nebo vliv prostředí na jejich pohybové vzorce (Bidder et al., 2015). Například metoda tzv. dead reckoning (DR), která využívá kombinaci akcelerometrů a magnetometrů, umožňuje přesně rekonstruovat pohybovou trasu zvířat a získat podrobné informace o jejich pohybových vzorcích v přirozeném prostředí (Walker et al., 2015). Tyto technologie se ukázaly jako velmi užitečné při studiu vlivu lidské činnosti na chování volně žijících zvířat, včetně prasat divokých, která reagují na různé druhy narušení, jako jsou turisté, psi nebo motorová vozidla (Faltusová et al., 2024a). Pokrok v biologgingu výrazně přispívá k detailnímu porozumění způsobu, jakým zvířata využívají své prostředí, což je klíčové pro jejich ochranu a management (Wilmers et al., 2015).

3.3 Fotopasti

Používání fotopastí pro výzkum divokých zvířat prudce stouplo od roku 2000 (Burton et al., 2015). Fotopasti se využívají ve výzkumu suchozemských obratlovců pro širokou škálu účelů, včetně kontroly druhů (Tobler et al., 2008), odhadů početnosti a hustoty (Gilbert et al, 2021) a studií pohybu a chování (Caravaggi et al., 2017; Niedballa et al., 2019). Fotopasti se staly nezbytným nástrojem ve výzkumu volně žijících živočichů, zejména díky nízkým nákladům (s výjimkou prvotního nákupu), jejich nenápadnému charakteru a schopnosti zaznamenávat pohyb a chování zvířat v jejich přirozeném prostředí bez přímého vlivu lidské přítomnosti (Rovero et al, 2013). Jedním z hlavních přínosů je možnost dlouhodobého monitoringu v rozsáhlých oblastech, což umožňuje přesnější studium etologických vzorců a usnadňuje porozumění ekologickým interakcím (Moore et al., 2021; Rowcliffe et al., 2014).

Použití fotopastí v terénu přináší řadu výzev. Technické specifikace fotopastí, zejména rychlost spouště a detekční zóna představují důležitý faktor. Výzkumy ukázaly, že některé druhy zvířat mohou vykazovat různou míru reakce na přítomnost fotopastí, což může vést k odlišné míře detekce v závislosti na druhu (Séquin et al., 2003). Například predátoři, jako jsou vlci a rysi, mohou fotopasti záměrně ignorovat nebo se jim vyhýbat (Caravaggi et al., 2020), zatímco jiní živočichové, jako jsou šimpanzi nebo medvědi, mohou vykazovat vyšší míru zvědavosti a zkoumat kameru (Kalan et al., 2019).

3.4 Prostorová orientace zvířat

Orientace zvířat v prostoru je nezbytným procesem, který jim umožňuje interakci s prostředím a hraje klíčovou roli v jejich přežití. Vzhledem k tomu, že pohyb je základní složkou chování, orientace a chování zvířat spolu neoddělitelně souvisejí. Každé chování zvířete zahrnuje určitou prostorovou složku, což znamená, že zvíře vždy reaguje na prostorové vlastnosti svého prostředí (Gautestad & Mysterud, 2010; Nathan et al., 2008; Schone, 2014). Výzkumy ukazují, že zvířata se většinou nepohybují v krajině náhodně, ale jejich pohyby jsou často ovlivněny známými oblastmi, které obsahují klíčové zdroje, jako je potrava, voda nebo úkryt (Fronhofer et al., 2013).

Prostorová orientace zvířat je často závislá na směru, který určují různé vnější podněty. Zvířata mohou k navigaci používat sluneční světlo, vzory polarizovaného světla, nebo vzdálené orientační body, jako jsou hory nebo stromy (Cheng & Newcombe, 2005; Dacke et al., 2013; el Jundi et al., 2015; Mandal, 2018). Kromě vizuálních podnětů hraje významnou roli v orientaci i čich, což je jeden z nejstarších smyslů vyvinutých v průběhu evoluce. Mnoho druhů zvířat, včetně prasat divokých, používá čichové podněty pro orientaci a navigaci v prostředí, přičemž některé druhy využívají například gradienty pachu v prostředí (Wallraff, 2015). Pachy mohou hrát důležitou roli při orientaci zejména u druhů, které žijí v hustých lesních nebo podzemních prostředích, kde je vizuální orientace omezená (Steck, 2012). Kromě toho řada druhů využívá geomagnetické pole Země jako kompas, který jim umožňuje navigaci na velké vzdálenosti bez závislosti na vizuálních nebo čichových podnětech (Mora et al., 2004; Putman et al., 2014).

Navzdory technologickému pokroku je stále výzvou pochopit, jak zvířata vytvářejí kognitivní mapy svého prostředí a jak tyto mapy ovlivňují jejich chování. Existují důkazy, že zvířata využívají více redundantních podnětů, což jim umožňuje přizpůsobit se různým prostorovým požadavkům (Mandal, 2018; Schone, 2014). Kognitivní mapy poskytují zvířatům flexibilitu v jejich prostorové orientaci, což je klíčové pro přežití v dynamických a neustále se měnících prostředích. Vytváření těchto map umožňuje zvířatům reagovat na podněty, které nejsou okamžitě přítomné, a překlenují informační mezery o prostředí, což zvyšuje jejich šanci na přežití (Poucet, 1993). Tento aspekt je klíčový pro chápání prostorového chování zvířat a jeho role v jejich adaptivním chování.

3.4.1 Antropogenní disturbance

Lidská činnost má zásadní vliv na prostorové chování zvířat, zejména v oblastech s vysokou mírou lidského zásahu. Zvířata, která žijí v blízkosti lidských sídel nebo v oblastech intenzivně využívaných k rekreačním účelům, vykazují změny ve svém chování, zejména v pohybových vzorcích a míře ostražitosti (Ohashi et al., 2013; Scheijen et al., 2021). Například prase divoké vykazuje vysokou toleranci k lidské činnosti. Prasata divoká jsou schopna rychle se adaptovat na přítomnost lidí a jejich chování se mění pouze v případech, kdy je lidská aktivita v jejich bezprostřední blízkosti (Faltusová et al., 2024a). To dokazuje, že zvířata jsou schopna se přizpůsobit opakovaným lidským zásahům, což může mít významné důsledky pro jejich prostorové chování. Tato schopnost přizpůsobení se liší podle druhu a typu narušení, což bylo prokázáno ve výzkumech zkoumajících vliv lidské činnosti na pohybové vzorce a prostorové chování různých druhů zvířat (Scheijen et al., 2021). V jiných případech mohou lidské aktivity u volně žijících zvířat vyvolat behaviorální a stresové reakce, což může mít dopad na celé populace (Pecorella et al., 2016).

Sílící lidské nároky na přírodu vedou i k rostoucímu množství silnic, které rozdělují a narušují přirozený habitat volně žijících zvířat. Výzkumy ukazují, že zvířata jsou ovlivněna nejen množstvím lidí, ale také typem lidské činnosti (Pecorella et al., 2016). Některé aktivity, jako je lov nebo motorizovaná rekreace, mají na zvířata silnější negativní dopad než například turistika (Naylor et al., 2009; Stankowich, 2008). Lov je často vnímán jako nástroj pro zmírnění škod způsobených volně žijícími zvířaty, avšak jeho účinnost je často sporná. Mnoho studií ukázalo, že snížení populace zvířat lovem má jen malý vliv na škody způsobené na plodinách (Honda et al., 2018). Ve světě, kde dominuje člověk, antropogenní vliv často překonává přirozené faktory, jako je predace nebo přirozený habitat. Chování zvířat je často více formováno lidským rušením než přírodními predátory, což je patrné v oblastech s intenzivní lidskou činností (Ciuti et al., 2012). Tento trend je dobře zdokumentován například u jelenů, kteří vykazují výrazné změny v pohybových vzorcích během lovecké sezóny, přičemž riziko predace zůstává vysoké i v dnech, kdy se lov nekoná (Proffitt et al., 2009).

Při přítomnosti člověka nebo jiných antropogenních faktorů mohou zvířata vykazovat zvýšenou ostražitost, což je energeticky náročné a může ovlivnit vyhledávání úkrytu a jejich schopnost efektivně hledat potravu, což může vést k nižšímu příjmu potravy a sníženému reprodukčnímu úspěchu (Ciuti et al., 2012; Padié et al., 2015). Přirozený výběr zvýhodňuje jedince, kteří dokážou vyvážit energetické náklady spojené se snížením rizika a přínosy, které toto chování přináší, a to zejména v případě, kdy je rušení člověkem předvídatelné a méně nebezpečné než přirozené predátorské hrozby (Creel et al., 2005). Tento princip je často popsán ve studiích zaměřených na vliv predátorů, avšak podobné mechanismy platí i pro lidské rušení (Proffitt et al., 2009).

Zvyšující se přítomnost lidí v přírodních oblastech však neovlivňuje pouze oblasti přímo využívané lidmi, ale také širší okolí. Například racek západní (*Larus accidentalis*) reaguje na lidskou činnost i ve vzdálenosti 2 000 metrů od turistických destinací (Webb & Blumstein, 2005). To vede ke konceptu „behaviorální stopy antropogenních dopadů“, který popisuje, jak daleko mohou sahat vlivy lidských aktivit na chování volně žijících zvířat. Tento prostorový rozsah dopadů je klíčový pro řízení ochrany zvířat a jejich habitatu. Studie zaměřené na měření této „behaviorální stopy“ ukazují, že lidé mají schopnost ovlivňovat chování volně žijících zvířat i na vzdálenost mnoha kilometrů (Blumstein, 2014).

3.4.2 Odstrašující prostředky

Odstrašující prostředky proti prasatům divokým byly zkoumány zejména z důvodu jejich přemnožení a s tím spojených rizik pro zemědělství a šíření nemocí, jako je africký mor prasat. Různé metody odstrašování prasat divokých se zaměřují na fyzické bariéry, akustické a chemické metody, a na moderní technologie jakožto inteligentní systémy odstrašování (Denzin et al., 2020; Palencia et al., 2023).

Akustické metody, jako je použití hlasitých zvuků nebo ultrazvukových frekvencí, byly testovány a prokázaly určitou účinnost při odrazování prasat divokých. Navíc jsou tyto metody ekologicky šetrné. Nicméně, jak uvádí Vercauteren et al. (2006), prasata divoká mohou po určité době na opakované zvuky ztratit citlivost. Singh et al. (2024) uvedli, že ultrazvukové přístroje využívající zvukové vlny s frekvencí nad 35 000 Hz jsou pro prasata divoká silně nepříjemné, což zajišťuje, že tato zařízení účinně odstrašují bez nutnosti chemických látek nebo fyzických bariér. Tento přístup minimalizuje potřebu chemikálií a snižuje rušení lidí, protože zvukové vlny jsou neslyšitelné pro člověka. Cappa et al. (2021) zmiňují, že tyto technologie mají také výhodu dlouhodobé udržitelnosti a lze je snadno nasadit na různých typech zemědělských pozemků. Když se ultrazvuková technologie kombinuje s pohybovými senzory, jak uvádí Singh et al. (2024), zvyšuje se její účinnost, protože systém se aktivuje pouze tehdy, když je zaznamenán pohyb prasat divokých.

Důležitým opatřením proti poškozování ekosystémů způsobeným zvířaty je fyzické oplocení, které se ukázalo být velmi účinné, pokud je správně navrženo a udržováno (Vercauteren et al., 2006). Fyzické bariéry omezují pohyb zvířat a chrání citlivé oblasti, avšak jejich účinnost může být snížena v místech, kde je neproveditelné vybudovat kontinuální oplocení, jako jsou řeky nebo silnice (Peterson et al., 2003). Fyzické bariéry jsou jednou z nejběžnějších metod ochrany proti prasatům divokým, zejména elektrické ploty, které poskytují mírný elektrický šok při kontaktu. Geisser & Reyer (2010) zjistili, že ploty mohou být účinné, avšak prasata divoká mají tendenci se adaptovat, například podhrabáváním pod plotem. Vercauteren et al. (2006) také zkoumali různé návrhy elektrických plotů a jejich účinnost a zjistili, že ploty s vyššími napěťovými impulsy mohou zlepšit ochranu proti prasatům divokým. Je nezbytné zmínit, že tyto bariéry mohou být v dlouhodobém horizontu neudržitelné z důvodu vysokých nákladů na údržbu a potřebu neustálých úprav v terénu (Singh et al., 2024).

Alternativou k fyzickým bariérám jsou chemické repelenty. Účinnost repelentů však bývá nižší než u fyzických bariér, zejména v případech, kdy jsou repelenty aplikovány na velké plochy (Wagner & Nolte, 2001). Denzin et al. (2020) testovali kombinace fyzických a chemických metod, jako jsou LED blinkry a chemické repelenty (např. Hukinol™ a Wildschwein-Stopp™). Výsledky ukázaly, že zatímco některé z těchto metod snižovaly kontakt prasat divokých s pastvami a uhynulými zvířaty, efektivita se lišila podle podmínek prostředí. K dalším chemickým metodám patří použití vonných repelentů nebo látek jako Wildschwein-

Stopp™, které napodobují pach predátorů. Studie ukazují že i tyto metody nejsou vždy dostatečně spolehlivé (Cappa et al., 2021; Faltusová et al., 2024b).

Inteligentní systémy odstrašování, které využívají deep learning a detekci pohybu, přinášejí další inovace v oblasti ochrany proti prasatům divokým. Tyto systémy mohou přesně identifikovat, zda se jedná o prase divoké, což umožňuje cílené odstrašovací akce. Díky těmto pokrokům je možné minimalizovat falešné poplachy a zajistit, že odstrašující prostředky budou aktivovány pouze tehdy, když jsou detekována prasata divoká (Khoei et al., 2023; Sarker, 2021; Xiao et al., 2020).

3.4.3 Africký mor prasat

Africký mor prasat je jednou z nejzávažnějších virových nákaz postihujících domácí i prasata divoká, která v posledních desetiletích způsobuje rozsáhlé ekonomické ztráty a představuje vážnou hrozbu pro zdraví prasat na celosvětové úrovni. Tento virus má schopnost způsobit velmi vysokou mortalitu v infikovaných populacích, která může dosahovat až 90 % a více v průběhu 7 až 14 dní od nákazy (Chenais et al., 2019; Cwynar et al., 2019).

První ohnisko AMP bylo zaznamenáno v roce 1957 v Portugalsku, odkud se virus postupně šířil po Evropě, přičemž jeho dopady se staly patrnými nejen ve střední, ale i západní Evropě (Cukor et al., 2020a; Cwynar et al., 2019; Mur et al., 2016). AMP se rozšířil zejména v posledních letech, přičemž klíčová ohniska byla zaznamenána v Maďarsku, Slovensku, České republice, Německu, Belgii a Itálii (Jarynowski et al., 2019; Linden et al., 2019; Sauter-Louis et al., 2021; Szymańska & Dziwulaki, 2022). Každá z postižených zemí přijala různá opatření v závislosti na míře infekce a specifických podmínkách.

Eradikace AMP byla úspěšně provedena v České republice a Belgii po prvotních zavlečeních viru, následovaných izolovanými ohnisky (Sauter-Louis et al., 2021). Přestože v těchto zemích došlo k úspěšné eradikaci, AMP se do České republiky vrátil v prosinci 2022, což vyvolalo nové vlny preventivních opatření (Juszkiewicz et al., 2023). Mezi nejčastější opatření v boji proti AMP patří masová depopulace prasat divokých v infikovaných oblastech, důsledné odstraňování uhynulých těl prasat a omezení lidských aktivit, jako je turistika nebo lesnictví, které mohou přenos viru zhoršit (Cukor et al., 2020b; Morelle et al., 2019; Sauter-Louis et al., 2021).

Důležitou roli v boji proti šíření AMP hrají také ploty, které byly úspěšně použity v několika evropských zemích, včetně České republiky a Belgie, s cílem omezit pohyb infikovaných zvířat. Tato opatření se ukázala jako efektivní při omezení šíření viru a kontrole populací prasat divokých (Cukor et al., 2021; Dellicour et al., 2020; Sauter-Louis et al., 2021). K podobným opatřením přistoupily také Německo a Francie, kde byla použita vícevrstvá oplocení (Jori et al., 2021; Sauter-Louis et al., 2021). Oproti tomu jedním z často diskutovaných prostředků jsou pachové bariéry. Testování pachových plotů odhalilo, že prasata divoká nepřikládají pachovým podnětům významnou váhu a často je ignorují (Faltusová et al., 2024b).

Jedním z klíčových faktorů šíření AMP je přirozený pohyb prasat divokých. Pohybové vzorce prasat výrazně přispívají k rychlosti přenosu viru, což činí eradikaci nákazy náročnou. Modelové studie provedené například v Polsku ukázaly, že AMP se šíří rychlostí přibližně 1,5 km za měsíc (Podgórski & Śmietanka, 2018). Podobné výsledky byly zaznamenány v Itálii, kde rychlost šíření viru činila mezi 33 a 90 metrů za den (Gervasi et al., 2023). Tyto údaje podtrhují význam monitorování pohybu prasat divokých a implementace opatření omezujících jejich pohyb ve snaze omezit šíření viru.

Lidské aktivity, jako je lesnictví, turistika a další rekreační činnosti, mohou mít dopad na přenos AMP, protože narušují přirozené prostředí prasat divokých a zvyšují jejich pohyblivost, což zvyšuje pravděpodobnost přenosu viru (Cukor et al., 2021). Reakce prasat divokých na lidské narušení jsou nejvýraznější do vzdálenosti 250 metrů od zdroje rušivých činností, což vede k jejich rychlejšímu pohybu od zdroje narušení (Faltusová et al., 2024a). Pokud jsou však lidské aktivity omezeny na lesní cesty, vliv na chování prasat divokých je minimální (Cukor et al., 2021; Skarin & Åhman, 2014). Například pandemie COVID-19 měla pozitivní vliv na omezení šíření AMP, protože omezující opatření, jako lockdown a snížení lidské mobility, vedla ke snížení počtu lidí v přírodních oblastech, což snížilo stres prasat divokých a omezilo jejich pohyb (Cukor et al., 2021).

K šíření viru dochází jak přímým kontaktem mezi nakaženými a zdravými prasaty, tak prostřednictvím kontaminovaného prostředí a kadáverů infikovaných jedinců, kde virus zůstává dlouhodobě životaschopný (Morelle et al., 2019). Kadávery prasat divokých hrají zásadní roli v šíření viru, protože virus AMP může přežít v tělech uhynulých prasat i několik měsíců či let, zejména při nižších teplotách (Cwynar et al., 2019; Probst et al., 2017). V případě, že infikovaná těla nejsou včas odstraněna, mohou přilákat další prasata divoká, která jsou vystavena přímému kontaktu s virem prostřednictvím kanibalismu, čichání a dotyků, což je jeden z hlavních způsobů přenosu AMP mezi volně žijícími prasaty (Cukor et al., 2020b). V oblastech, kde byly zaznamenány ohniska AMP, se ukázalo, že včasné odstranění nakažených těl může významně přispět k zpomalení šíření viru a jeho eradikaci (Morelle et al., 2019). Z těchto zjištění vyplývá, že hlavní opatření by měla být zaměřena na odstraňování kadáverů, omezení přístupu prasat divokých k nim a kontrolu jejich populace. Zatímco rozsáhlé uzávěry oblastí pro veřejnost mohou mít jen omezený efekt, efektivní řízení populace prasat divokých a biosecurity opatření mohou být klíčové pro dlouhodobou kontrolu a prevenci šíření AMP (Cukor et al., 2021; Morelle et al., 2019).

4 Metodika

Tato kapitola se zaměřuje na popis studijních oblastí, experimentálního uspořádání a metod používaných pro statistické analýzy v pěti publikacích, které tvoří základ této disertační práce. Metodika je rozdělena podle tematických okruhů zpracovaných v rámci disertační práce. První část se věnuje vlivu lidských aktivit na chování a pohyb prasat divokých. Druhá část se zaměřuje na vliv umístění plotů na pohyb těchto zvířat. Třetí část se zabývá vlivem kadáverů na chování a pohyb prasat divokých.

4.1 Vliv lidských aktivit na chování a pohyb prasat divokých

4.1.1 Kvantitativní analýza reakcí chování prasat divokých na simulované lidské rušení pomocí telemetrie a údajů z akcelerometru

Studie byla provedena v Kostelci nad Černými lesy, zalesněné oblasti 30 km východně od Prahy v České republice, spravované Českou zemědělskou univerzitou v Praze. Tento les o rozloze 2 900 ha, navštěvovaný návštěvníky z okolních obcí a Prahy, byl místem sběru dat od února 2020 do července 2021.

Divočáci byli odchyceni pomocí pastí s návnadou vybavených kamerovým monitoringem. Po odchytu byla zvířata anestetizována ketaminem a xylazinem, opatřena ušními známkami a telemetrickými obojky o hmotnosti 750 g a monitorována pod veterinárním dohledem. Telemetrické obojky kombinovaly biologgery GPS a Daily Diary, které zaznamenávaly data z akcelerometru a magnetometru s vysokým rozlišením při 10 Hz, což zajistilo přesný sběr dat. Celkem bylo označeno 15 divočáků. Rušení bylo simulováno auty, pohybujícími se turisty, volně pobíhajícími psy a zvuky motorové pily. Trasy rušení byly zaznamenány pomocí ručního GPS, přičemž bylo analyzováno 72 případů.

DR byl použit k rekonstrukci tras pohybu zvířat kombinací dat GPS s údaji z akcelerometru a magnetometru. Dráhy DR byly vypočteny pomocí softwaru DDMT, přičemž data GPS sloužila jako korekční faktory. Body GPS byly zaznamenávány každých 30 minut, zároveň byla použita pouze data s přijatelnou přesností (DOP >1 a <7). Zlepšení DR založená na chování byla implementována pomocí předem definovaného behaviorálního modelu, který klasifikoval aktivity divočáků do šesti typů: chůze, odpočinek, stání, běh, klus a ostražitost.

Statistické analýzy se zaměřily na chování divočáků v okruhu 1 km od lidských aktivit. Pro celkové a jednotlivé scénáře narušení byly vytvořeny grafy hustoty typů chování. Rozdíly ve vzdálenostech mezi prasaty divokými a lidmi byly hodnoceny pomocí Kruskal-Wallisova testu s vícenásobným srovnáním a výsledky byly vizualizovány ve sloupcových grafech indikujících statistickou homogenitu.

4.1.2 Empirická studie o účincích zvýšené návštěvnosti lidí během pandemie COVID-19 na spánek, energetický výdej a pohybové vzorce prasat divokých

Výzkum probíhal v zalesněné oblasti Kostelec nad Černými Lesy, Praha-východ, Česká republika, pokrývající 2900 ha lesů spravovaných Českou zemědělskou univerzitou. Tato oblast je oblíbená pro rekreační aktivity díky blízkosti Prahy.

Divočáci byli odchyceni pomocí dřevěných pastí s návnadou a znehybněni kombinací ketaminu, xylazinu a zoletilu. Po odchytu byla zvířata vybavena biologgerovými obojky vybavenými GPS modulem a Daily Diary pro záznam údajů z akcelerometru a magnetometru s vysokým rozlišením. Byla analyzována data od 63 prasat divokých, shromážděných od dubna 2019 do listopadu 2021, se zaměřením na GPS fixy s přijatelnou přesností a vybrané týdny s dostatečnými telemetrickými daty.

Přítomnost člověka v lese byla sledována každou hodinu pomocí automatického počítadla a data byla agregována do týdenních období. Období studie zahrnovalo dvě období lockdown pandemie COVID-19 a data byla analyzována podle ročního období, aby se prozkoumaly variace v návštěvnosti lidmi. Údaje o pohybu divočáků, využití prostoru, výdeji energie a spánku byly shromážděny a následně analyzovány. Pohyb prasat divokých a využití prostoru byly hodnoceny pomocí telemetrických dat GPS, výpočtu týdenní ušlé vzdálenosti, velikosti domovských okrsku a maximálního přemístění (maximální vzdálenost mezi polohami GPS za týden). K vyhodnocení dopadu lidské přítomnosti a ročního období na tyto parametry byly použity zobecněné modely se smíšenými efekty.

Výdej energie byl odhadnut pomocí vektorového součtu dynamické tělesné akcelerace (VeDBA) z údajů akcelerometru se zaměřením na týdny s vysokou a nízkou návštěvností člověkem. Rozdíly ve VeDBA byly analyzovány pomocí lineárních smíšených modelů. Kromě toho bylo chování při spánku divočáků analyzováno pomocí modifikované metody aktigrafie k identifikaci spánkových záchvatů na základě údajů z akcelerometru. Lineární smíšené modely zkoumaly trvání a kontinuitu spánku ve vztahu k míře návštěvnosti lidí.

4.1.3 Pozorovací studie hodnotící lidskou aktivitu a její dopad na chování volně žijících živočichů během vypuknutí AMP a pandemie COVID-19

Studie se zaměřila na lesní oblasti severovýchodně od Zlína, Česká republika, oblast silně zasaženou ohniskem afrického moru prasat od června 2017 do března 2019. Region se rozkládá na přibližně 5430,6 ha, přičemž 71,6 % půdy je využíváno pro zemědělství, 26,6 % pro komerčně obhospodařované lesy a minimální plochy pro sídla a vodní plochy. Cílem studie bylo pozorovat lidskou aktivitu, přítomnost divoké zvěře a potenciální dopad lidských návštěv na chování zvířat, se zvláštním zaměřením na prasata divoká a další běžné druhy.

Fotopasti byly umístěny do prostředí ke sledování návštěvnost lidí a aktivity zvěře v lesích větších než 50 ha. Čtrnáct kamer UO Vision UV 595 HD bylo strategicky situováno alespoň 100 m od okrajů lesa a cest napříč studovanou oblastí. Monitorování trvalo od 1. května do 30. června po dobu tří let (2018–2020) a zachycovalo data o přítomnosti lidí a volně žijících živočichů pomocí videozáznamů spouštěných pohybem. Kamery byly kontrolovány každé tři týdny, aby byla zachována jejich funkčnost a sběr dat.

Studie také zvažovala změny v důsledku omezení africkým morem prasat v roce 2018 a pandemií COVID-19 v roce 2020, která ovlivnila pohyb lidí a přístup do lesů. Během vypuknutí afrického moru prasat v letech 2017 až 2018 byl přístup veřejnosti do zasažených lesů omezen, s výjimkou oprávněných myslivců a jednotlivců s povolením místních úřadů. Po vymýcení ohniska se lesy v roce 2019 vrátily k běžnému užívání v souladu s ustanoveními zákona České republiky.

V roce 2020 přinesla pandemie COVID-19 další omezení, včetně nouzového stavu a omezení pohybu. Zatímco některé venkovní aktivity byly zpočátku omezeny, zákaz pohybu v přírodě byl po čase zrušen, což umožnilo přístup veřejnosti do lesů a parků. Uvolnění lockdownových opatření poskytlo příležitost porovnat lidskou činnost během pandemie s předchozími roky.

Analýza se zaměřila na vzorce návštěvnosti lidí, kategorizované podle věku a pohlaví, a jejich vliv na aktivitu divokých zvířat, která byla klasifikovány podle druhů. Statistické metody zahrnovaly lineární regresi, testy chí-kvadrát a logistickou regresi, přičemž data byla analyzována pomocí softwaru R. Vliv lidské přítomnosti na volně žijící zvířata, zejména na prasata divoká, byl hodnocen porovnáním aktivity zvířat v období ovlivněném přítomností člověka s obdobími bez ovlivnění.

4.2 Vliv umístění plotů na pohyb prasat divokých

4.2.1 Praktický výzkum založený na telemetrii hodnotící účinnost pachových ohradníků na pohyb a velikost domovského okrsku prasat divokých

V letech 2019 až 2021 byla prostorová aktivita divočáků sledována na dvou odlišných lokalitách: honitba Bohumile v okrese Praha-východ a honitba Hradiště v okrese Karlovy Vary. Lokalita Bohumile, charakteristická smíšenými lesy a vysokou lidskou rekreační aktivitou, ostře kontrastuje s lokalitou Hradiště, vojenským výcvikovým prostorem s omezeným přístupem veřejnosti.

Během studie bylo pro sledování 62 divočákům vybaveno GPS obojky. Vzorek tvořilo 21 jedinců z Hradiště a 41 z Bohumile, z toho 45 samic, 16 samců a 1 neurčený, s věkem určeným prořezáním zubů a rozdělenými na subadults (12-24 měsíců) a dospělé (nad 24 měsíců). GPS data byla sbírána každých 30 minut a byly použity pouze přesné polohy (DOP $\geq$ 1 a $\leq$ 7). Pro analýzu bylo vybráno 18 prasat divokých na základě jejich trajektorií pohybu překračujících plánované linie pachových ohradníků alespoň pětkrát během 30minutového intervalu před instalací pachových zábran. Ostatní jedinci (44) byli vyloučeni z důvodu brzkého odlovu nebo přesunů mimo studovanou oblast.

Pro testování účinnosti pachových ohradníků byl realizován řízený experimentální návrh. Každé monitorovací období trvalo šest týdnů, rozděleno na tři týdny bez pachové bariéry a tři týdny s pachovou bariérou. Pachový ohradník HAGOPUR Wildschwein-Stopp určený k odstrašování zvěře byl aplikován v pěnové formě na větve a kůru stromů podél veřejných a lesních cest. Linie pachového ohradníku, které se pohybovaly od 1 400 do 3 600 metrů, byly umístěny na základě údajů o pohybu divočáků a upraveny tak, aby protínaly oblasti s vysokou aktivitou. Od dubna do září bylo zřízeno 12 sekcí pachového ohradníku.

Prostorová data byla analyzována pomocí softwaru QGIS 3.36 a R 4.2.2. Hodnotili jsme změny v počtu překročení linií, velikosti domovského okrsku a překrytí domovského okrsku před a po instalaci pachového ohradníku pomocí lineárních modelů se smíšenými efekty. Kovarianty zahrnovaly pohlaví a věk, s umístěním jako náhodným efektem. Statistická významnost byla stanovena při $\alpha = 0{,}05$, přičemž modelová rezidua byla zkontrolována na normalitu pomocí Shapiro-Wilkových testů a Q-Q grafů.

4.3 Vliv kadáverů na chování a pohyb prasat divokých

4.3.1 Terénní studie hodnotící afinitu prasat divokých ke kadáverů ve vztahu k rizikům přenosu AMP

Studie byla provedena na sedmi lokalitách v České republice. Na základě předchozí studie o nálezu kadáverům (Cukor et al., 2020b), byla v těchto lokalitách vybrána místa pro založení experimentu. Do míst s největší pravděpodobností nálezu kadáveru (mladé lesní porosty v blízkosti vody) byla položena těla prasat divokých. Usmrcená prasata divoká byla umístěna na každé místo ve všech čtyřech ročních obdobích, přičemž kontrolní místa byla nastavena ve vzdálenosti 200 metrů, aby odpovídala podmínkám prostředí. Tato místa byla monitorována od ledna 2019 do února 2020. Kadávery pocházející z legálně ulovených divočáků byly monitorovány pomocí kamerových pastí UOVision UV 595 HD umístěných 4 až 8 metrů od každého mršiny. Kamery zaznamenávaly video data s časovými razítky a byly kontrolovány jednou za dva týdny vždy, dokud nebyl kadáver zcela zkonzumován nebo odtažen.

Analýza dat z fotopastí zahrnovala vyhodnocení přítomnosti a aktivity divočáků na experimentálních i kontrolních místech. Fotopasti zachycovaly počet, pohlaví a přibližný věk divočáků spolu s délkou expozice mršiny a načasováním vzhledem k východu a západu slunce. Časy východu a západu slunce byly získány z online databáze. Analýza se zaměřila na čtyři hlavní aspekty: počet záznamů divočáků, poměr pohlaví a věku, časy detekce vzhledem k východu/západu slunce a časové rozpětí do prvního kontaktu divočáka s kadáverem.

Statistická analýza zahrnovala souhrnné statistiky a srovnání Wilcoxonova dvouvýběrového párového testu kvůli nenormálním distribucím dat, jak potvrdil Shapiro-Wilkův test normality. Chí-kvadrát testy hodnotily závislosti mezi kategoriemi pohlaví a věku a mírou detekce. Údaje o čase detekce byly analyzovány pomocí kruhové statistiky s použitím Rayleighova testu pro uniformitu a Watson-Williamsova testu pro rozdíly mezi experimentálními a kontrolními místy. Doba od umístění mršin a umístění kamery do první aktivity divočáka byla porovnána pomocí Wilcoxonova dvouvýběrového párového testu. Všechny analýzy byly provedeny pomocí softwaru R s hladinou významnosti a = 0,05.

5 Přehled publikovaných prací

Disertační práce se skládá ze tří tematických okruhů. První část hodnotí vliv lidských aktivit na chování a pohyb prasat divokých. Tato část je sestavena ze tří rukopisů s impakt faktorem. Druhá část zkoumá vliv umístění plotů na pohyb prasat divokých ve vztahu k AMP, práce zahrnuje jeden rukopis v časopise s impakt faktorem. Třetí část je zaměřena na vliv kadáverů na chování a pohyb prasat divokých ve vztahu k AMP. Tato část obsahuje jeden článek v recenzentním řízení v časopise s impakt faktorem. Přehled publikovaných prací je složen z pěti rukopisů, ve dvou případech je student prvním autorem, u dvou prací je druhým autorem, a v případě dalších dvou rukopisů je u jedné čtvrtým a u druhé pátým autem.

5.1 Vliv lidských aktivit na chování a pohyb prasat divokých

5.1.1 Wild boar proves high tolerance to human-caused disruptions: management implications in African swine fever outbreaks

Faltusová, M., Cukor, J., Linda, R., Silovský, V., Kušta, T., Ježek, M. (2024). Wild Boar Proves High Tolerance to Human-Caused Dsruptions: Management Implications in african Swine Fever Outbreaks. *Animals*, *14*(18), 2710, DOI: https://doi.org/10.3390/ani14182710.

Článek byl zaměřen na dílčí cíl 1. Práce zkoumá, jak různé typy lidského rušení – jako jsou zvuky aut, přítomnost psů, zvuky motorové pily a turistika – ovlivňují chování divočáků, zejména v oblastech postižených africkým morem prasat. Pomocí pokročilé biologické technologie a metody DR výzkum sleduje pohyby divočáků, aby vyhodnotil změny chování v reakci na blízkost člověka. Zjištění naznačují, že prasata divoká vykazují pouze malé změny chování, jako je zvýšená ostražitost nebo změněné vzorce pohybu, v závislosti na vzdálenosti rušení. Celkový dopad těchto disturbací je však omezený, přičemž nejběžnějším pozorovaným chováním je odpočinek. Výsledky naznačují, že přísná omezení pohybu při nakládání s AMP mohou být zbytečná, pokud je lidská činnost omezena na konkrétní oblasti, jako jsou lesní cesty.

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Wild Boar Proves High Tolerance to Human-Caused Disruptions: Management Implications in African Swine Fever Outbreaks

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Simple Summary: Wildlife in human-dominated landscapes often faces a range of disturbances that can alter their natural behaviors. Wild boar (*Sus scrofa*) populations are increasing across Europe, raising concerns about ecological impacts and the spread of diseases such as African swine fever (ASF). This research focuses on the behavioral adaptations of wild boars in response to specific human disturbances. Utilizing advanced biologging technologies, specifically accelerometer and magnetometer combined with dead reckoning methods, fifteen wild boars in a suburban forest near Prague were monitored over a period from February 2020 to July 2021. This study provides insights into the wild boar's resilience, revealing that while the animals are inclined to flee when near disturbances, they predominantly remain in a resting state otherwise. Their most common reaction was to continue resting. These observations underscore the potential role of disturbance management in controlling the spread of zoonotic diseases such as African swine fever (ASF) within wild boar populations.

Abstract: Currently, African swine fever (ASF), a highly fatal disease has become pervasive, with outbreaks recorded across European countries, leading to preventative measures to restrict wild boar (*Sus scrofa* L.) movement, and, therefore, keep ASF from spreading. This study aims to detail how specific human activities—defined as "car", "dog", "chainsaw", and "tourism"—affect wild boar behavior, considering the disturbance proximity, and evaluate possible implications for wild boar management in ASF-affected areas. Wild boar behavior was studied using advanced biologging technology. This study tracks and analyzes wild boar movements and behavioral responses to human disturbances. This study utilizes the dead reckoning method to precisely reconstruct the animal movements and evaluate behavioral changes based on proximity to disturbances. The sound of specific human activities was reproduced for telemetered animals from forest roads from different distances. Statistical analyses show that wild boars exhibit increased vigilance and altered movement patterns in response to closer human activity, but only in a small number of cases and with no significantly longer time scale. The relative representation of behaviors after disruption confirmed a high instance of resting behavior (83%). Running was the least observed reaction in only 0.9% of all cases. The remaining reactions were identified as foraging (5.1%), walking (5.0%), standing (2.2%), and other (3.8%). The findings suggest that while human presence and activities do influence wild boar behavior, adherence to movement restrictions and careful management of human activity in ASF-infected areas is not a necessary measure if human movement is limited to forest roads.

Keywords: biologging; wild boar; behavior; movement; anthropogenic disturbances

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1. Introduction

Wild boar is an opportunistic animal whose population density is increasing throughout the European continent [1–3]. The unprecedented population increase is caused by several factors, including the high availability of suitable food sources represented by high-energy crops and supplementary feeding, low hunting efficiency, reforestation or climate change [4,5]. Warmer winters are an example of climate change. Milder winters lead to increased juvenile survival [6], while warmer springs boost pollination, resulting in higher seeding rates for oaks and beeches in the autumn [7–9]. The high population density is typical of Central European countries, where it ranges from 1.15 to 5.31 ind./100 ha [10], and the numbers of wild boar locally reach overpopulation, even with the emergence of human–wildlife conflicts [11]. On the other hand, the overpopulation of wildlife species is often suppressed by diseases, which is also the case with wild boar in Europe, where African swine fever (ASF) is a fatal disease with a high morbidity and mortality rate that can reach 90% or more [10,12].

The first ASF outbreak in Europe was reported in Portugal in 1957, with subsequent outbreaks over most of Western Europe [10,13,14]. Moreover, in recent years, the virus also reached Central Europe, including Hungary, Slovakia, the Czech Republic, and Germany [15,16], as well as Western European countries, e.g., Belgium, or Italy [17,18]. Every state reacted differently to the infection, and the management measures had evolved from the initial outbreak. The eradication of ASF was successful in the Czech Republic and Belgium after a single introduction event with subsequent isolated outbreaks [15]. However, the Czech Republic was infected repeatedly in December 2022 [19]. The most frequently implemented measures consist of massive depopulation in the affected areas and the removal of wild boar carcasses [14,15,20]. Additionally, the infected areas are fenced with iron or scent fences as in the Czech Republic and Belgium [15,21,22] but also in other countries, such as France or Germany, which also included layered fences [1,15]. At the same time, restrictions were implemented, consisting of entrance bans to areas infected by ASF.

The evidence of how wild boar ecology, including movement and behavior, is influenced by human disruption is still limited. Stressors such as noise, light, habitat destruction, hunting, and pollution can lead to short- and long-term physiological, behavioral, psychological, and demographic changes [23]. Human activity has profoundly changed the activity patterns of many wildlife species. Animals commonly exhibit behavioral changes, including altered movement patterns and increased alertness, often accompanied by the secretion of stress-related hormones [24,25]. This is true for a wide range of human activities in nature, including recreation. The development of nature tourism and recreation in forests is related to increased interest in outdoor sports activities such as hiking, skiing, horseback riding, biking, berry and mushroom collecting, short-term camping, walking, and dog walking [24,26–30], which leads to a decrease in biological diversity [29].

The reactions of various wildlife species differ significantly according to animal species and disturbance type [31]. Animals modify their behavior to minimize the effects of human activities, with sensitization and habituation being key processes [29]. Habituation or sensitization are common responses to repeated human presence. They change their tolerance to disturbance, which occurs over time and can affect animal behavior and movement [24]. Habituation, considered favorable for tourism and research, allows for closer interactions with observed or studied animals [30]. However, it can also have the opposite effect on animals. Differences in tolerance do not always indicate habituation and are often misunderstood [32].

A crucial parameter for observing animals is their behavior, influenced by their living conditions, both the environment and the individual's physiological state. Unfortunately, that was the limitation of previously realized telemetry studies, which offered only limited movement data of tracked animals [33]. Nowadays, accelerometric sensors are increasingly used as a tool to obtain detailed information [34–36]. As accelerometers measure animal orientation and movement dynamics, these sensors attached to animals can provide data on a wide range of their behaviors [34]. Magnetometers are other sensors that respond to the orientation and intensity of the Earth's magnetic field [35]. The new dead reckoning method uses an accelerometer and a magnetometer for its calculations. It is a unique tool for describing animal movements at a fine scale [37] and, therefore, seems to be a new and promising method for the exact tracking.

Since existing studies on the influence of human activities were limited by technological procedures, we decided to use the new biologging technology to describe in detail the reactions of animals to various anthropogenic disturbance phenomena, which was not possible with wild individuals until now. Therefore, the aims of this study are to evaluate (i) how the different human activities/disturbances defined as "car", "dog", "chainsaw", and "tourism" can affect wild boar behavior reactions; (ii) how the wild boar behavior is impacted by the distance from the source of the disturbance; and (iii) how the investigated results can be implemented into ASF management strategies.

2. Materials and Methods

2.1. Study Area

The study area was Kostelec nad Černými lesy (49.9959631 N, 14.8633939 E), located 30 km east of the capital city of Prague, the Czech Republic. This study was performed in a wooded part of the town—2900 ha of forest managed by the Czech University of Life Sciences Prague (Lesy ČZU). These suburban forests are widely sought after as a location for leisure activities. They are, therefore, characterized by high attendance due to the number of surrounding villages and their location in the vicinity of the capital city of Prague, which has ca. 1.3 million inhabitants. Data collection in the study location occurred from February 2020 to July 2021.

2.2. Data Acquisition

For the evaluation of wild boar behavior, the animals were caught and then tagged with telemetry transmitters. The wild boars were lured with bait into a wooden trapping cage with a trapdoor lowered when the wild boar consumed the bait (mostly corn seeds). The wild boars in the trapping cage were monitored by camera traps UOVision Compact LTE (UOVision, Cvikov, Czech Republic) with a resolution of 5 megapixels and a trigger speed of 0.4 sec. The camera traps were installed at a height of 1.5 to 2 m to accommodate the inner surfaces of the cage and warn by sending a picture via email of the presence of wild boar inside the trap. After capture, the animals were anesthetized with a mixture of ketamine and xylazine (3 mL per 100 kg of body weight). Under anesthesia, the wild boars were marked with an ear tag and a telemetry collar. The total weight of the collar was 750 g, which is <3% of the animal's body weight and is considered acceptable according to welfare rules for wildlife telemetry [38]. During immobilization, the individuals were under the supervision of veterinarians and other experts.

Data were collected using multi-sensor collars consisting of a Global Positioning System (GPS Vectronic Aerospace GmBH, Berlin, Germany) and Daily Diary biologgers (Wildbyte Technologies Ltd., Swansea, United Kingdom). Daily Diary consisted of a 3-axial high-resolution accelerometer and a 3-axial magnetometer at a frequency of 10 Hz. Because all of the data are recorded by sensors inside the loggers, its efficiency is not affected by the environment, which is crucial for obtaining accurate and unbiased data. A total of 15 wild boar were collared this way. For an overview of trapped wild boar, see the Supplementary Table S1.

The exposure of collared individuals to various types of human disturbances was carried out. Specifically, four types were selected: a recording of a car driving, a moving tourist, a domestic dog running freely, and the sound of a chainsaw was played to simulate forest work. The disturbance phenomena paths were recorded with a hand-held GPS Garmin eTrex 22x. GPS positions for every second were available in the case of human disturbance. All of the disruptive influences listed were randomly tested. A total of 72 cases of disturbances were analyzed.

2.3. Dead Reckoning Procedure

The dead reckoning (DR) method was used to obtain the exact path of the animals, which is a unique tool that allows reconstructing the precise track of animal movement on a fine scale, which was not possible in the past. DR is based on the fact that the position of the animal at any time "t" can be derived from the position of the animal at the previous time "t-1", the distance and heading between two time intervals [39]. The DR paths were calculated using the Daily Diary Multiple Trace Graphing Tool, 2024 (13/Jan/2024), developed at Swansea University, and directly intended to process data from biologging sensors.

In this study, DR recorded the path between two GPS fixes using an accelerometer and a magnetometer. GPS points were used as ground truth. Ground truth in the DR method served as a correction factor. The frequency of GPS fixes was set to a 30-min interval. GPS data were utilized only if the dilution of precision (DOP) >1 and <7, otherwise, the data were deleted for low precision. QGIS 3.8 software was used to visualize and check the validity of the data and their location in space.

Behavior based on accelerometric data were included to improve the DR calculation (Figure 1). The applied behavioral model was previously defined by colleagues, primarily from the Czech University of Life Sciences Prague [40]. A total of nine types of behavior were defined in the model: walking, foraging, other, resting, rooting, running, standing, trotting, and vigilance. A threshold was calculated for each type of behavior, which refined the DR track. Thresholds were calculated based on the actual speeds of wild boar for each behavioral category. To increase the accuracy of the behavioral model, the following behaviors of foraging and rooting, standing and vigilance, and running and trotting were combined. In the end, nine types of behavior combined into six were used for behavior analysis of the two hours after the disturbance. The other, foraging, and rooting categories were not used for the reaction analysis. Foraging and rooting were not thought to be a response to human disturbance, and no more specific behavior is known for the "other" category.

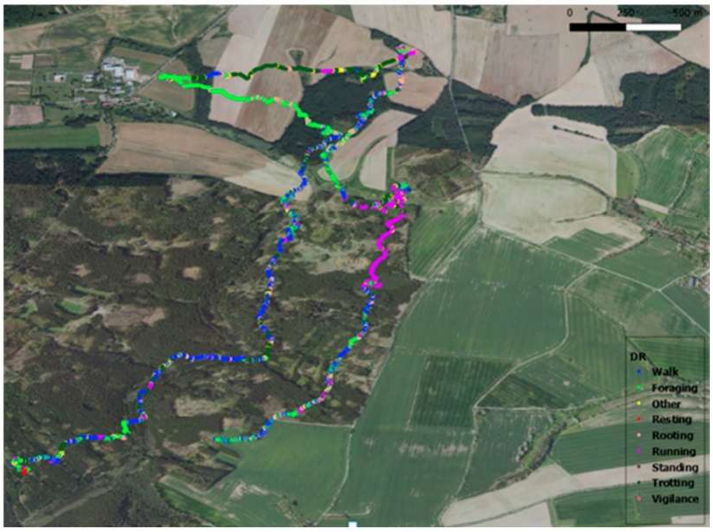

Figure 1. Map of dead reckoning for one day, including color separation of behavior.

2.4. Statistic Analyses

For all analyses, only wild boar occurrences within a radius of 1 km from humans were considered. As a first analysis, a density plot of behavior types based on the distance between humans and wild boar for all records was created for a general overview of a behavior data structure. An identical analysis was also created separately for each disturbance type ("car", "dog", "chainsaw", and "tourism").

The Kruskal–Wallis test with subsequent multiple comparisons was used for testing for differences in recorded distances between wild boars and humans for a selected wild boar behavior type. The results were presented in the form of a bar plot with indices of statistical homogeneity above each variant (Figure 2).

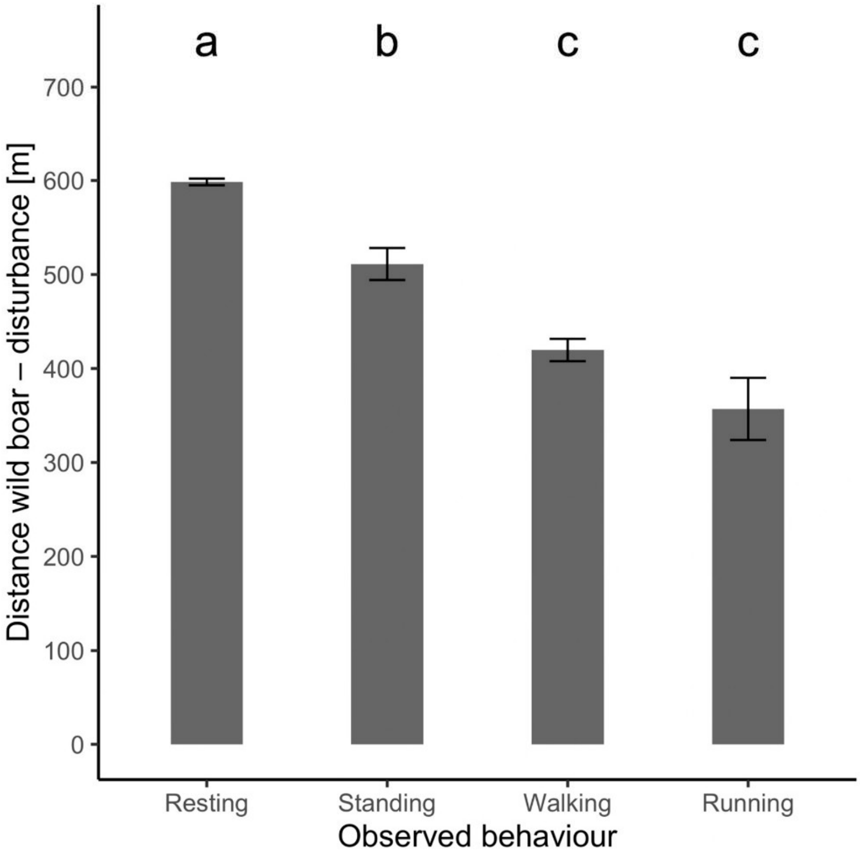

Figure 2. Mean observed distance between wild boar and humans for each type of wild boar behavior. Indices above each show statistical homogeneity between variants (different indices mean significant difference and vice versa).

To evaluate wild boar behavior immediately after the disruption, we added a plot of absolute values of observed animals in relation to the distance between humans and wild boar recorded in the first two hours after disturbance. The distances were grouped into four groups (0–100 m, 100–200 m, 200–500 m, and 500–1000 m).

Lastly, we analyzed wild boar behavior composition to show the relative proportion of each behavior type throughout the day. We compared recorded wild boar behavior during days with and without human disturbance to evaluate the impact. For statistical testing, the difference in the relative proportion of each behavior for each animal was computed for disturbance and non-disturbance periods, and its difference was statistically tested by *t*-test. The null hypothesis stated that there is no difference in behavior proportion during disturbance and non-disturbance periods. The proportions were also depicted by pie charts (Figure 3).

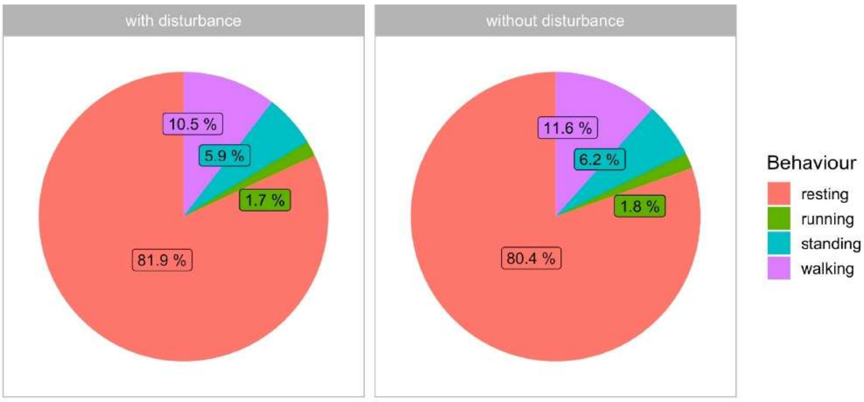

Figure 3. Two pie charts comparing animal behavior under conditions of disturbance and without disturbance.

3. Results

To assess human disturbances on wild boar behavior throughout the day, we have compared relative numbers of records with each of the presented wild boar behavior. For each animal, we analyzed relative differences, i.e., differences in a relative count for each behavior between the disturbance and non-disturbance period. The results show highly insignificant differences (*t*-test, $t < 0.001$, $df = 17$, $p > 0.99$), which suggest no differences in wild boar behavior structures between disturbance and non-disturbance periods. The results for all animals summarized are presented in the form of pie charts (Figure 3).

The density plot of all records was created for a broad overview of data (Figure 4). Only records where the distance between wild boar and humans was under 1000 m were considered. The results show a general trend—that running is most likely observed at shorter distances from humans (up to ca. 250 m), followed by walking, standing, and resting, which is most likely observed at distances of ca. 700 m or more. Wild boars exhibit a clear pattern of behavioral responses based on their distance from a disturbance. They tend to run when close to the disturbance, switch to standing and walking at moderate distances and only rest when they are far from the disruption. It is necessary to mention that not all behaviors entered into the analysis. The “other, foraging, and rooting” behaviors were not used in the after-disruption analysis, because they are not a reaction nor are they precisely specified. The relative representation of behaviors from the whole is as follows: foraging 5.1%, other 3.8%, running 0.9%, standing 2.2%, walking 5%, resting 83%.

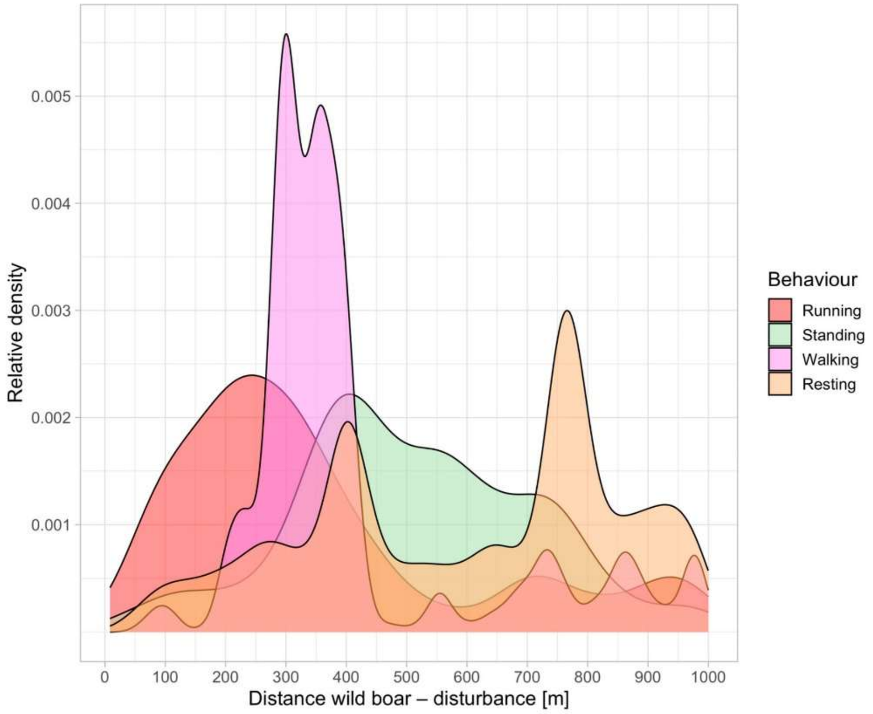

Figure 4. Density plot (relationship of the relative number of occurrences on the distance between wild boar and humans) of all records across all studied animals, disturbance periods, and disturbance types.

The composite graph (Figure 5) illustrates the relative density of wild boar behaviors (running, standing, walking, and resting) in response to various disturbances: car, chainsaw, dog, and tourism. Wild boars exhibit an immediate flight response within 0–300 m for chainsaw and tourism disturbances, with running peaking closer to these upsetting stimuli. For car and dog disturbances, running peaks at slightly greater distances. Between 300–600 m, standing and walking behaviors are more common across all disturbance types, indicating a cautious approach during these moderate distances. At greater distances, 600–1000 m, resting behavior becomes more prevalent, suggesting that wild boar feel safer and more relaxed farther from the disturbance.

The comparison between observed distances for each wild boar behavior type was conducted via the Kruskal–Wallis test with subsequent multiple comparisons. Overall, the Kruskal–Wallis test showed significant results (K-W chi-squared: 835.07, df = 3, $p < 0.001$). Other multiple comparisons revealed significant differences between all variants except for walking and running. For a graphical depiction of the results, see Figure 2. The bar graph illustrates the average distance of wild boar from disturbances for different observed behaviors: resting, standing, walking, and running. Resting behavior occurs at the greatest average distance from the disturbance, at 598.57 m, indicating that wild boars prefer to rest further away from disturbances where they feel safe. Standing behavior is observed at an average distance of 511.19 m, suggesting increased vigilance at a moderate distance. Walking behavior is seen at an average distance of 419.65 m, indicating a transition phase as the wild boar moves away. Running behavior occurs at the closest average distance to the disturbance, approximately 356.97 m, reflecting an immediate flight response. The letters above the bars (a, b, c) indicate statistically significant differences between the behaviors, with resting significantly different from the other behaviors, and standing, walking, and running forming distinct groups based on their average distances from the disturbance.

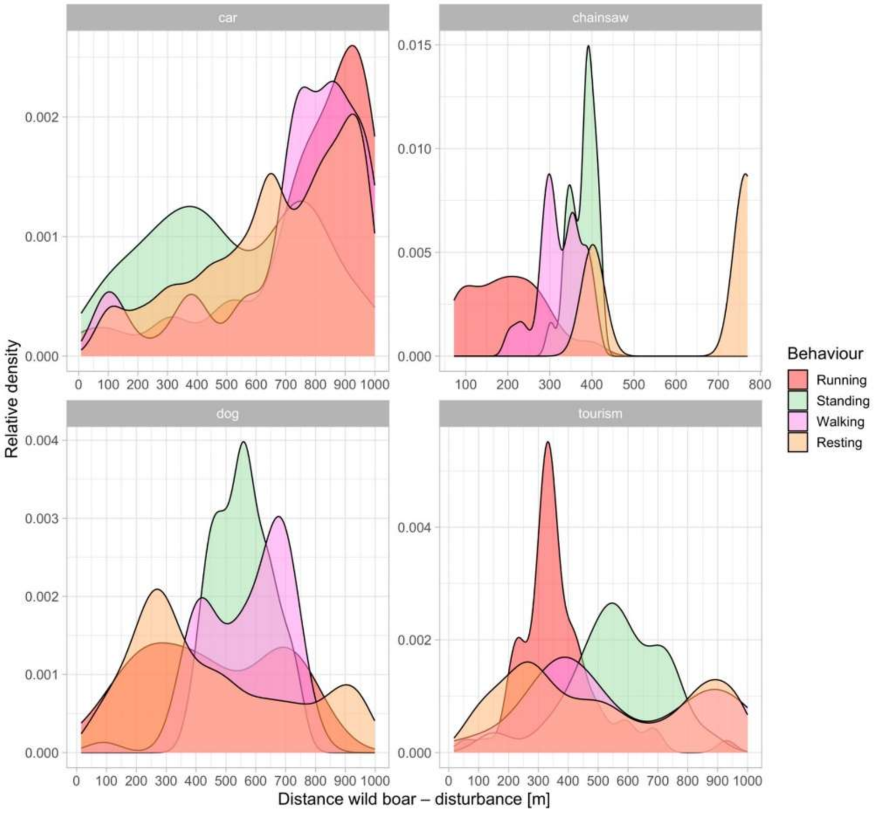

Figure 5. Density plot (relationship of the relative number of occurrences on the distance between wild boar and humans) of all records across all studied animals, disturbance periods, and different types of disturbances.

For graphical depiction of the relative number (in percent) of wild boar detected immediately (2 h) after disturbance at various distances from the stimulus, categorized into 0–100 m, 100–200 m, 200–500 m, and 500–1000 m, a bar plot for each behavior type is presented (Figure 6). Foraging behavior increases significantly at 500–1000 m (4.79%) compared to closer distances. The "Other" category peaks at 100–200 m (8.64%), then decreases. Resting remains relatively constant across all distances, maintaining approximately 86.5%. Running behavior shows a marked decrease as the distance increases, from 4.81% at 0–100 m to 0.38% at 500–1000 m. Standing is highest at 100–200 m (1.6%) and diminishes as the distance increases. Walking is most frequent at 200–500 m (3.22%). This analysis reveals distinct trends, such as increased foraging and decreased running at a greater distance from the disturbance, while resting remains stable regardless of proximity. From these numbers, resting is the most prevalent (average 86.5%), foraging is represented in 2.99%, and other in 5.15%. Proving that wild boars' reactions (running, standing, walking) to human disturbance are almost minuscule and represented in a small percentage of cases in 5.36%.

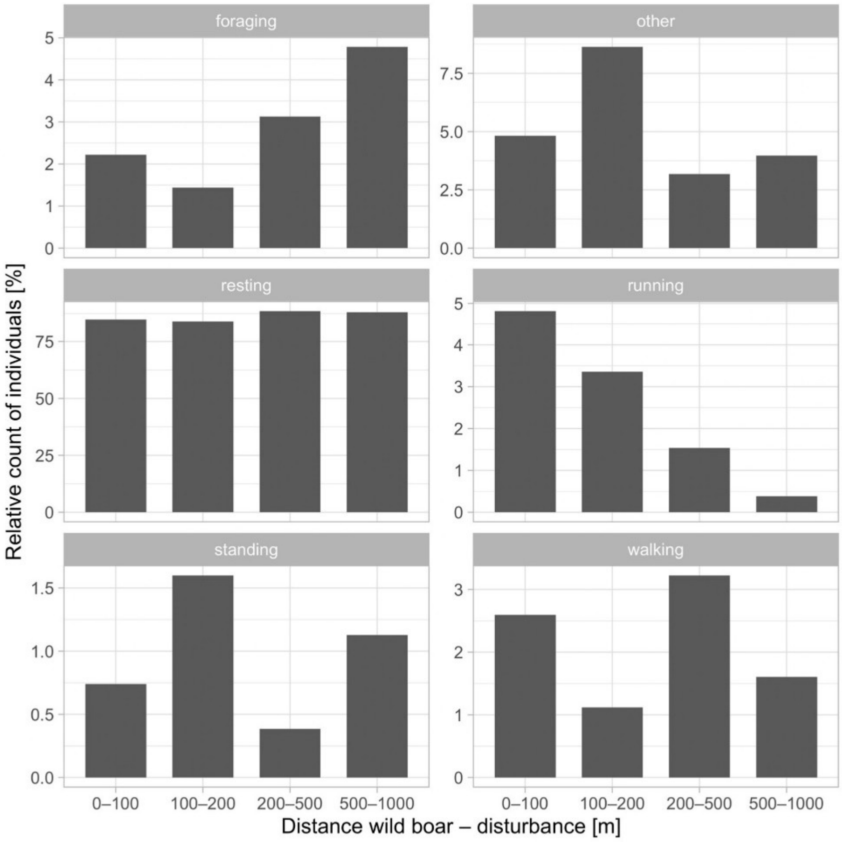

Figure 6. Relative number of wild boars detected in the immediate two hours after disturbance at different distances.

4. Discussion

The African swine fever virus spreads in a free-ranging wild boar population influenced by a wide range of natural factors of which the social structure, density, hunting pressure, food sources availability, and especially, infected carcass availability in the environment are the most important [41–45]. Moreover, the movement of wild boar is also one of the natural factors that influence ASF transmission unless we consider the most important human-caused leaps over long distances in hundreds of kilometers as in the Czech Republic, Belgium, or Italy [15,46,47]. The ASF transmission speed was analyzed in 2014 and 2015 in Poland. During this two-year study, ASF spread gradually at a steady pace of 1.5 km/month, corresponding to the range of wild boar movements on a monthly scale [43]. The model of ASF's spreading speed was also produced in the Italian case, with a comparable spread of infection ranging from 33 to 90 m/day [48].

The movement patterns of wild boars and the speed at which ASF spreads are influenced by various factors, including human disturbances. It is essential to limit human disturbances to prevent the spread of ASF in the environment. However, it depends on the specific type of disturbance. Our study showed that forestry work and tourism, including driving a car, are not the case. Our study found that wild boars have low reaction rates to four different models of human disturbances in their natural environment. From the ASF spreading point of view, running was the most problematic reaction, and therefore, fast movement was observed in boar most frequently at shorter distances from humans (up to about 250 m; Figure 4). On the other hand, at distances farther than 700 m, the animals rested in most cases, so it is evident that the reactions decrease with increasing distance. Moreover, it is necessary to mention that resting was the most common behavior within two hours after the disturbance had happened in all tested distances from the disturbance source (0–1000 m).

The high wild boar tolerance to human disruptions is confirmed by several other studies that evaluated the wild boar behavior and home range sizes, which are significantly smaller in the vicinity of human settlements, including big cities [8,49,50]. The adaptation of wild boar populations to urban and periurban areas has led to increased human-wild boar interactions, resulting in more road traffic accidents, damage to urban infrastructure, and the spread of diseases with pets and humans. Additionally, wild boars can ransack rubbish bins, harm private gardens, and occasionally pose direct threats to people [51]. A high tolerance to common human activities was also proven by our study in a long-term period where no changes were found between behavior on days with disturbance vs. on days without disturbance. This demonstrates how wild boars can adapt to human disturbance. Therefore, their adaptation means a risk for humans, domestic and farm animals, and a threatened change in biodiversity. In addition, wild animals are affected not only by the common recreational activity (e.g., tourism vs. hunting; Ciuti et al., 2012 [52]). Changes in their behavior can also be caused by different stimuli. For example, previous studies suggested that specific hunting methods and motorized recreational activities have a more profound impact on animals than less disruptive stimuli [53–55]. Hunting disturbances, especially driven hunts, may induce escape movements, resulting in greater distances traveled and a larger range [8,53,56].

The regime and intensity of human activity in the wild boar natural environment is another factor that requires consideration. The trend of a rapid increase in human visitors outside forest roads has a significant impact on the behavior of animals [2], i.e., their movements in the landscape, which leads to the transmission of various types of diseases, including ASF. Regardless of the activity performed (tourism, forestry work, and others), strict respect for the trails is of primary importance [21]. Our study proves that if the rule of movement on forest roads is observed, the presence of people in the forest environment does not have a significant effect on changes in the behavior and movement of wild boar.

All of the above-mentioned findings can be easily incorporated into the measures that can be applied in the fight against African swine fever. Stopping or slowing the spread of ASF requires mitigation strategies that are effective and practical [57]. For this reason, many measures are used in combination, so it is difficult to prove which ones were effective and which were not. The intensive measures are adopted primarily in areas with isolated outbreaks, as were the cases in the Czech Republic and Belgium. Within the central core area of the outbreak, wild boar populations were left undisturbed during the ASF outbreak [46,58]. That means a strict hunting ban and free circulation in the forests for walking, hiking, and professional forestry activities [46]. However, as our results indicate, the effect of entrance bans on wild boar behavior in ASF-infected areas is, at the least, highly debatable. Moreover, as proven in a previously published study, the movement restrictions during ASF are not always adhered to by forest visitors [21]. Conversely, the long-term entrance ban to ASF-infected areas can have the opposite effect on residents who are used to spending time in nature, and therefore, it seems that managed entrance and human movement on forest roads can be an ideal solution.

5. Conclusions

Key findings reveal that wild boar reactions to human disturbances are generally minimal. The most significant behavioral response—running—is primarily observed at distances within 250 m of the disturbance while resting becomes the predominant behavior at distances exceeding 700 m. These reactions suggest that wild boars quickly habituate to human presence, displaying increased vigilance and altered movement patterns only in close proximity to the disruption. Over the long term, no substantial differences in behavior were found between disturbance and non-disturbance days, indicating high tolerance to regular human activities.

From an ASF management perspective, this study's findings suggest that strict adherence to movement restrictions for humans in ASF-affected areas may not be essential. The high tolerance of wild boar to human activities, as demonstrated by the negligible impact on their behavior in a natural environment, indicates that current measures involving entrance bans and activity restrictions might not significantly influence ASF transmission dynamics. Instead, focusing on other effective mitigation strategies, such as carcass removal and population control, could be more impactful in managing ASF outbreaks. On the whole, this research contributes valuable knowledge to wildlife management and disease control, highlighting the nuanced interactions between human activities and wildlife behavior. By understanding these dynamics, more efficient and targeted approaches can be developed for managing wild boar populations and controlling the spread of diseases like ASF.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ani14182710/s1, Table S1: Wild_boar_informations.

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5.1.2 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

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*, DOI: https://doi.org/10.1016/j.scitotenv.2023.163106.

Cílem studie bylo zjistit dopad zvýšené lidské aktivity v období pandemie COVID-19 na chování prasat divokých v příměstském lese nedaleko Prahy. Použili jsme biologgery a data GPS od 63 divočáků k analýze změn v pohybu, výdeji energie a spánku. Přes značné výkyvy v návštěvnosti lidí zůstaly pohybové vzorce divočáků z velké části nedotčeny. Zvýšená přítomnost člověka však vedla k 41% nárůstu energetického výdeje a fragmentovanějšímu spánku, což naznačuje, že zatímco divočáci snesou vysokou lidskou aktivitu, narušuje to jejich rytmus aktivity a potenciálně ovlivňuje jejich kondici. Existuje předpoklad, že rytmus aktivity může mít dopad i na vývoj AMP v krajině. V článku jsou shromážděné výsledky k dílčím cílům 2 a 3.

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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

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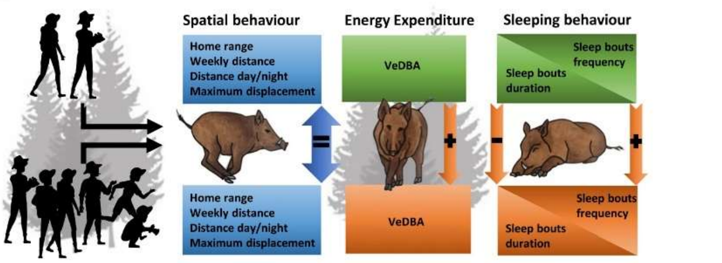
HIGHLIGHTS

- 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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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

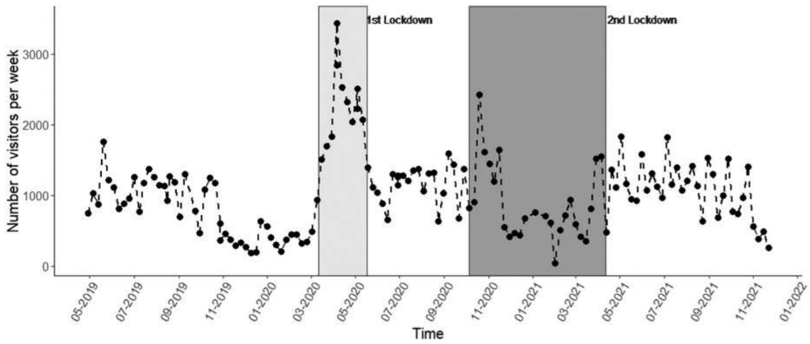

Fig. 1. Count of human visitation per week in the forest area near the capital city Prague and the two official COVID-19 lockdowns as defined by the "state of emergency" declared by the government of the Czech Republic.

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

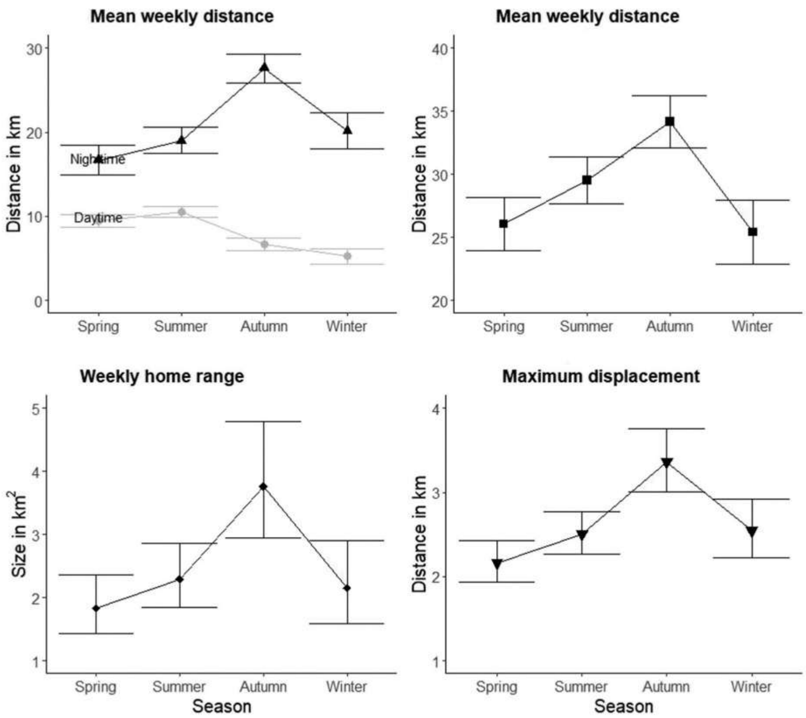

Fig. 2. Seasonal changes in the movement of wild boar: A) Mean weekly distance at nighttime and daytime B) Mean weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week).

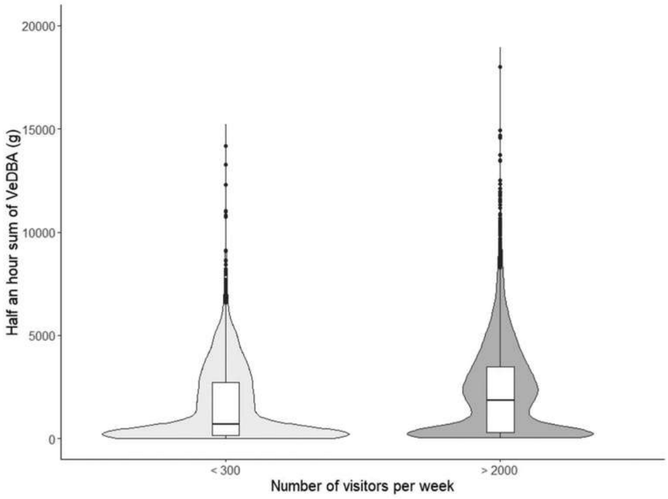

Fig. 3. Energy expenditure at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) number of human visitors.

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	$0.17_{AnimalID}$		$0.11_{AnimalID}$		$0.02_{AnimalID}$		$213{,}393.27_{AnimalID}$	
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.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

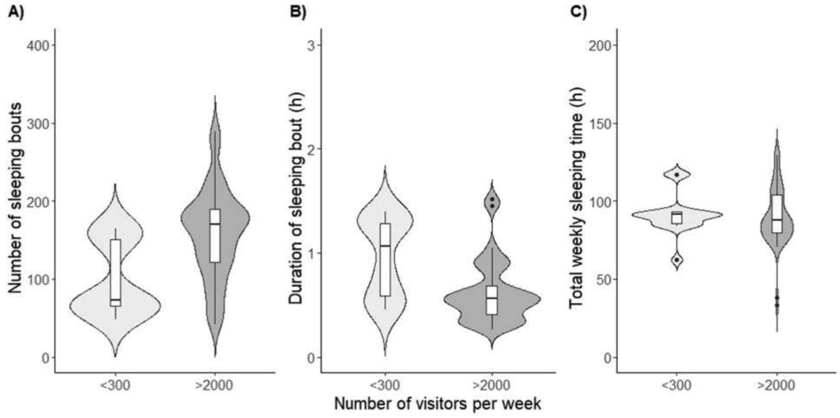

Fig. 4. Sleeping behaviour at the lowest (<300 per week, 5 weeks) and the highest (>2000 per week, 6 weeks) numbers of human visitors: A) number of sleeping bouts per week B) duration of sleeping bouts C) total sleeping time per week.

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

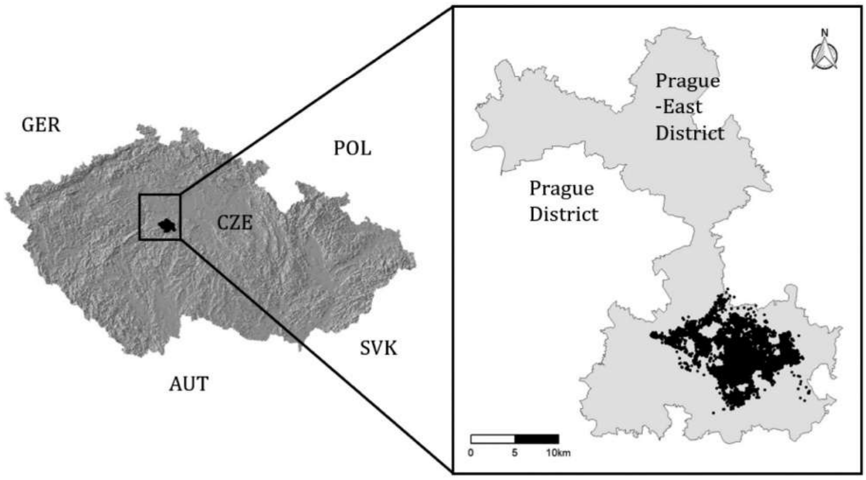

Fig. A.1. Location of the study area Prague-East in the Czech Republic (CZE) with GPS positions of the collared wild boars (black points).

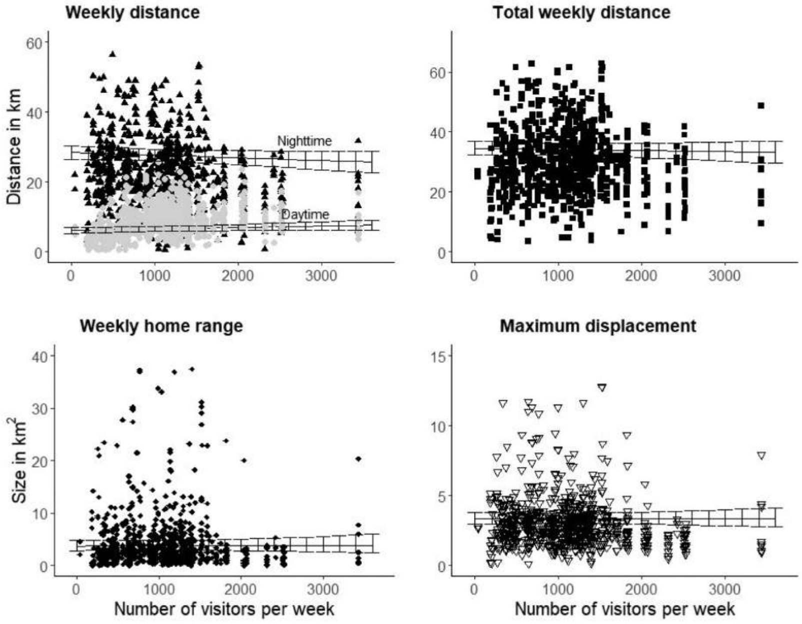

Fig. A.2. Changes in the movement of wild boar in relation to numbers of visitors per week: A) total weekly distance at nighttime and daytime B) total weekly distance C) weekly home range 95 % Kernel D) maximum displacement (maximum distance of GPS locations within a week).

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5.1.3 Different patterns of human activities in nature during Covid-19 pandemic and African swine fever outbreak confirm direct

Cukor, J., Linda, R., Mahlerová, K., Vacek, Z., **Faltusová, M.**, Marada, P., Havránek, F. & Hart, V. (2021). Different patterns of human activities in nature during Covid-19 pandemic and African swine fever outbreak confirm direct impact on wildlife disruption. *Scientific Reports*, *11*(1), 20791, DOI: https://doi.org/10.1038/s41598-021-99862-0.

Publikace se soustředí na dílčí cíl 3. Tato práce zkoumá dopad změn lidské činnosti během pandemie COVID-19 a vypuknutí afrického moru prasat na chování volně žijících zvířat v lesní oblasti v České republice. Hlavními cíli bylo vyhodnotit účinnost zákazu vstupu AMP, porovnat vzorce aktivity lidí a volně žijících živočichů za normálních podmínek a pandemie COVID-19 a určit vliv lidské přítomnosti na volně žijící zvířata. Zjistili jsme, že lidské aktivity výrazně narušují divokou přírodu a zvířata se vyhýbají oblastem navštěvovaným lidmi. Pandemie COVID-19 vedla k podstatnému nárůstu návštěvníků lesa, zatímco epidemie AMP zaznamenala pokles. Zjištění zdůrazňují potřebu lepšího řízení a vzdělávání ke zmírnění negativních dopadů na volně žijící zvířata, zejména v citlivých obdobích, jako jsou období rozmnožování.

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Different patterns of human activities in nature during Covid-19 pandemic and African swine fever outbreak confirm direct impact on wildlife disruption

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Implementation of various restrictions to eradicate viral diseases has globally affected human activity and subsequently nature. But how can the altered routines of human activity (restrictions, lockdowns) affect wildlife behaviour? This study compared the differences between human and wildlife occurrences in the study forest area with acreage of 5430.6 ha in 2018 (African swine fever outbreak, complete entrance ban), 2019 (standard pattern) and 2020 (COVID-19 restrictions) during the breeding season. The number of visitors was lower by 64% in 2018 (non-respecting of the entry ban by forest visitors) compared to standard 2019, while in 2020, the number of visitors increased to 151%. In the COVID-19 period, distinct peaks in the number of visitors were observed between 8–11 AM and 4–7 PM. The peaks of wildlife activity were recorded between 4–7 AM and 9–12 PM. Animals avoided the localities that were visited by humans during the people-influenced time (24 h after people visit), which confirmed the direct negative impact of human activities on wildlife.

Land-use changes, including urbanization, have led to severe habitat fragmentation, degradation, and loss, so therefore humans and wildlife live in closer proximity[1]. Human-wildlife interactions affect the behaviour and movement of both parties[2]. Outdoor recreational activities disturb wildlife in terms of the energy expenditure, impact on animal behaviour and physical fitness, and cause circumventing an otherwise suitable habitat, synergistically resulting in changes in wildlife activity, feeding time, reproduction, and survival[3–5]. Therefore, tourism and recreation are considered a major threat to wilderness ecosystems[5,6]. The negative impact of tourism and recreation has been known for almost a century[7]. The rising impact of recreational activities on the environment goes hand in hand with the growing numbers of outdoor recreationists[5,8], which is globally documented, especially in protected areas and urban forests[5,9,10].

The development of nature tourism and recreation in forests is related to increasing interest in outdoor sports activities such as hiking, skiing, horseback riding, biking, berry and mushroom foraging, short-term camping, walking, and dog walking[5,7,11]. Other factors are the adequate accessibility of nature areas with well-developed road networks[5,12]. The impact of recreation and tourism changes in relation to landscape characteristics where the long-term impact on wildlife might be particularly high in the urban framework and is related to the local population size[13,14]. The number of visitors in nature are related to various rules of protection, especially in national parks and protected areas [13,15,16]. Furthermore, political decisions such as different patterns of human activity in relation to the eradication of serious viral diseases that affect continents or are widespread globally, undoubtedly influenced the extent of nature tourism and recreation activities[17,18].

Currently, the COVID-19 pandemic is the greatest health and economic challenge in modern history, which threatens millions of human lives and has devastating consequences on social and economic life worldwide[19–21]. The virus spread globally within about 2 months from its origin in Wuhan, China[22], infecting people at an

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exponential rate, and leading to measures that are disrupting the global economy in an attempt to contain it [23,24]. The available methods to mitigate the spread of the epidemic are standard control measures, such as social distancing (mitigating contacts by home office), hand hygiene, face mask use, isolation of confirmed cases, contact tracing, and quarantine[25,26]. Moreover, many countries around the world went into lockdown to control the spread of the virus[27], with total shutdowns of whole large and small cities[28]. The reduction in human mobility on land and at sea including air transport is unprecedented in recent history[29,30]. Therefore, the general assumption is that the reduction of traffic and other human activities leads to improving the wildlife environment[31], and reduces the stress to wildlife[19]. First estimations and unofficial observations from the beginning of the COVID-19 pandemic has indicated that many animal species are enjoying the unforeseen peace and quiet reflected in significant changes in the environment and the natural habitats[27]. The recent field data confirmed the positive effects on wildlife conservation, such as reduced stress on sensitive animals, increased species richness in less disturbed habitats, higher breeding success of aerial insectivorous birds, and reduced wildlife collisions with traffic[32,33]. In the first months of pandemic, the positive effect of the COVID-19 on wildlife was observed principally in national parks and protected areas where the dramatic declines in the number of visitors is easily measured[33,34]. However, there is limited knowledge on the impact of the COVID-19 pandemic on wildlife on a local scale.

Another serious viral disease impacting human behaviour and causing considerable socio-economic losses is African swine fever (ASF)[35,36]. The current outbreaks of the epidemic have been reported from 17 European and 12 Asian countries[37]. The impact of the ASF outbreak in China led to the reduction of pig industry by 9–34% in global production, which leads to increasing pork prices by 17–85%[38]. The spread of African swine fever is exacerbated by several factors such as the natural movement of wild boars and direct contact between individuals[37,39]. Forestry and human leisure activities can also affect the disease transmission by the disruption and subsequent movement of infected wild boar[40]. Therefore, one of the most effective measures is to forbid entrance into the areas with local outbreaks, as was done in 2018 the Czech Republic (described in the Methods section).

The last 3 years gave us the unique opportunity to compare different levels of outdoor activities according to legislative regulations, which influence the human behaviour in relation to aforementioned viral diseases. The Czech Republic was affected by African swine fever in 2018, with movement restriction enforced in the outbreak area. In 2019, ASF was eradicated and human movement returned to the standard regimen without any restrictions. In 2020, the COVID-19 pandemic emerged, which brought several mitigation measures including the closing of schools, recommending working from home, and finally, a full lockdown. Nevertheless, walks in nature, staying in the sunlight and other outdoor activities were highly recommended due to improving health status and immunity[41–43]. However, the direct impact of these measures on wildlife, especially in the breeding season (spring months), was not considered. Therefore, the objectives of this study were to: (1) evaluate the efficiency of the ban on entering the forest during the ASF outbreak in 2018; (2) compare the prohibition regimen with normal forest visiting in 2019; (3) describe altered patterns of human visits and wildlife occurrences in forests in the normal situation (2019) and during the COVID-19 pandemic (2020); and (4) determine the effect of the frequency of human presence on wildlife, all in the forest ecosystems close to urban centers.

Results

In total, we have recorded 241 people via camera traps from the selected study area (30 people in 2018, 84 in 2019, and 127 in 2020). Men and women accounted for 60.2% and 39.8% of the total number of visitors, respectively (93.3% and 6.7% in 2018, 53.6% and 46.4% in 2019, 56.7% and 43.3% in 2019). The numbers of records were divided to subadults, adults and seniors, and further by gender, as depicted in Fig. 1.

The positive trend of recorded adults (male and female together) was tested via linear regression and was statistically significant ($p = 0.026$). Among all records, 6 people were apparently working in the forest, 5 in 2018 and 1 in 2019.

The most people were recorded on June 25, 2020 (Thursday, 12 people), followed by May 24, 2020 (Sunday, 10 people); in 2019, the most people were recorded on May 7 (Tuesday, a day before the public holiday), May 9 (Thursday, a day after the public holiday), and June 29 (Saturday); in 2018, on May 26 (Saturday) and June 13 (Wednesday).

Regarding the weekdays, the highest number of records was observed on Thursday (50 records, 20.7%), followed by Wednesday and Sunday, including public holidays (both 40 records, 16.6% each). Differing frequencies of human activities between the weekdays and weekends were observed. In 2018 we detected 107.1% of visits during the weekends compared to weekdays. In standard pattern (2019) was the difference most prominent during the weekends (125.0% of visitors compared to weekdays). In COVID-19 period (2020) was observed the opposite situation when during the weekends the camera traps recorded 80.7% of visitors compared to weekdays. The distribution of records during weekdays is depicted in Fig. 2.

The chi-square test for equality of probabilities for people detection on different weekdays showed significant differences between them (Chi-squared = 17.419, df = 6, $p = 0.008$). Thursday was found as the most frequent day in 2019 and 2020 (there are not enough records in 2018 to make a solid conclusion about the most frequent day), but there were significant differences found in the proportion of human records on different weekdays between 2019 and 2020 (Chi-squared = 19.301, df = 6, $p = 0.004$). The most prominent differences were observed in the case of Tuesday (which accounts for 17.9% in 2019, but only for 3.9% in 2020) and Saturday (16.7% in 2019, but only 7.1% in 2020).

The overall analysis of the daytime hours showed that most of the records appeared in the morning hours; 46.5% of all individuals were recorded between 7 and 12 AM. During the day hours (from 4 AM to 8 PM), 229 out of total 241 people (95.0%) were observed. Most were observed between 10 and 11 AM (28 records) and between 9 and 10 AM (25 records). Relatively high counts were also observed in the afternoon, e.g. 20 records between 4 and 5 PM and 19 records between 6 and 7 PM. An hour histogram of detected people is depicted in Fig. 3.

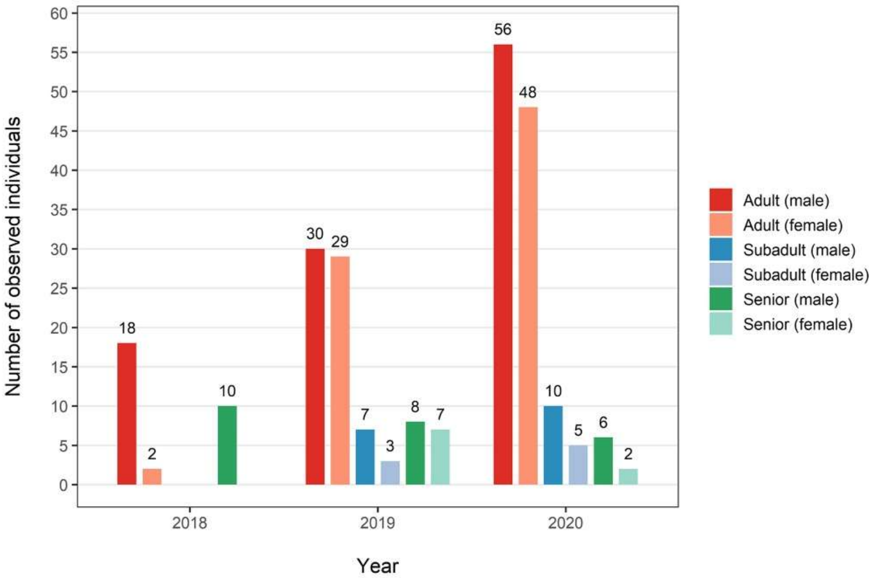

Figure 1. Numbers of records divided by age category and gender in studied months of selected years.

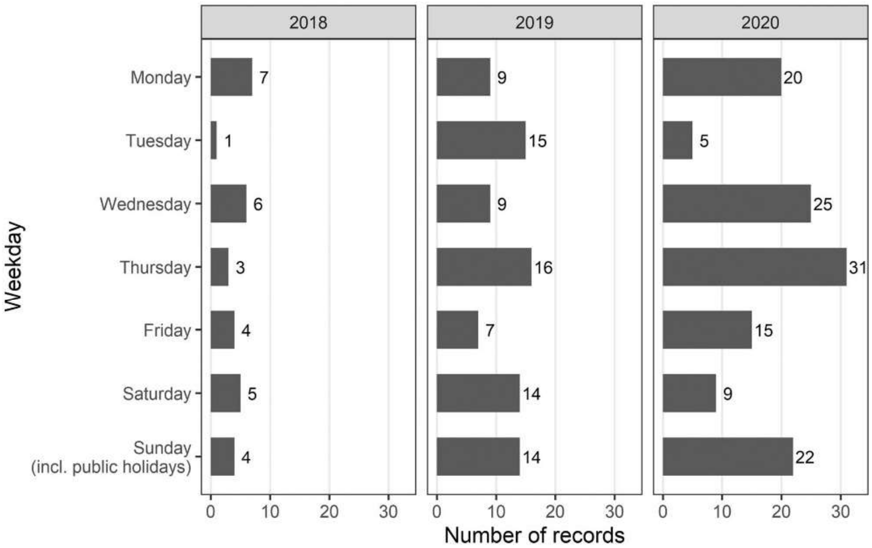

Figure 2. The distribution of human records on different weekdays.

We have found one revealing peak in the number of recorded people in 2018 (around 10 AM). The majority of the people in 2018 were observed between 7 AM and 3 PM (26 out of 30 records in 2018; 87%). Contrary to 2018, we found an "evening peak" in 2019 and in 2020. In 2019, we observed a relatively stable frequency between 7 AM and 8 PM with a few peaks around 9 AM, 1 PM and 6 PM, and one drop around lunchtime. In total, 79 out of 84 (94%) recorded people were observed between 7 AM and 8 PM in 2019. In 2020, we observed two main

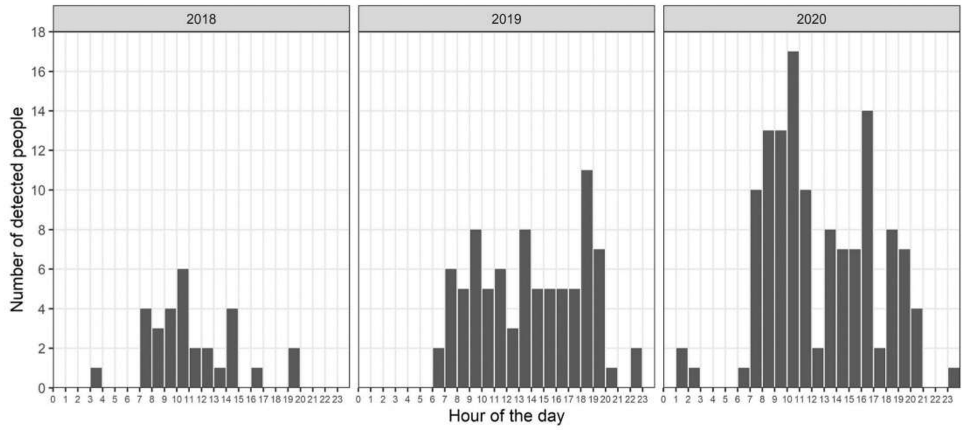

Figure 3. Hour histogram of people recorded on camera traps during the study period.

peaks in human records, at approximately 10 AM and 4 PM. In 2020, people were usually recorded between 7 AM and 9 PM (122 out of 127 cases, 96%).

Unlike people, animals were observed in the vast majority of cases during night hours or during sunrise or sunset. In the case of wild boar, 240 out of total 615 records (39.0%) appeared during the day (4 AM to 8 PM), which accounted for a statistically significant difference (Chi-squared = 29.634, df = 1, $p < 0.001$). Only 4 records of wild boar were recorded between 8 AM and 8 PM. The low number of wild boar records in 2018 is caused by previous ASF outbreak (in area was found 208 ASF positive wild boar carcasses[44]). However, the times of visits were in all 3 years comparable with morning and evening peeks regardless of population density. In the case of roe deer, 890 out of a total of 1589 records (56.0%) were detected during the day, although only 287 records of roe deer (18.1%) appeared between 8 AM and 7 PM. Other animal species (both martens, red fox, European badger or European hare) were detected during the day or night with similar frequency (203 records during the day from total of 400 records), although their activity was relatively low between 10 AM and 6 PM. Fallow deer were recorded during the whole day, with small peaks around 5 AM, 9 AM, 2 PM and 9 PM. The distribution of animal species records during the day is depicted in Fig. 4.

The testing for differences in frequency of animal visits between the people-influenced time (24 h after people visit) and the non-influenced time showed significant results (Wilcoxon paired-sample rank-sum test, V = 91, $p < 0.001$). The mean frequency of animal visits during the people-influenced time was 1.41 visits per day (95% CI 0.94–1.88), during the non-influenced time 3.76 visits per day (95% CI 2.79–4.73), which is ca. 160% higher.

The logistic regression model for predicting the presence of people on a particular camera trap record for each day, based on forest type and distance from roads and pathways, showed significant results for coniferous forests (pine/spruce), species-rich mixed forests and distances from roads and pathways. People were more likely to be recorded in pine/spruce forests (Effect coefficient = 1.9890), species-rich mixed forests (0.6703), and also far from roads (− 0.0025) and pathways (− 0.066). In all cases of statistically significant effects, very low p values ($p < 0.001$ in all cases) were observed. The results of the model are shown in Table1.

Discussion

An unexpected effect of the COVID-19 pandemic was a surprisingly dramatic change in nature visits after the first measures reducing human mobility were implemented[27,45]. In countries where strict lockdown restrictions were imposed, a reduction in visitor numbers was initially observed[45,46]. Similarly, the number of visitors increased rapidly as soon as these restrictions were eased[45,46]. This pattern was also observed in our study, as the camera traps registered an increase of visitors of 151% during the COVID-19 period in 2020 compared to the same time period (May and June) in the previous year. This unprecedented boom of human visitors after short-term measures to mitigate the COVID-19 pandemic during the spring and summer 2020 were also reported from Nature Protected Areas and peri-urban forests globally[12,45,46]. For instance, the increase of forest visitors in peri-urban forests south of the Cologne-Bonn agglomeration (Germany) had increased almost 140% compared to pre-COVID-19 pandemic [46]. A rapid increase was also observed in Oslo (Norway), where outdoor recreational activity increased by 291% during the 2020 lockdown dates relative to the 3-yr baseline average in previous years. In this case, the dramatic increase could be explained by easy availability of peri-urban forest around Oslo[47].

In our study, the number of forest visitors could not only be compared to the pre-COVID-19 time period in 2019, but also to 2018, when a strict ban on entering the monitored area was applied due to an ASF breakout. This total restriction of forest access was relatively respected by women (only 6.7%) compared to men (93.3%). However, men and women accounted for 53.6% and 46.4% of the total number of visitors in 2019, and 56.7% and 43.3% in 2020. The same gender share was found in the normal situation (excluding ASF and COVID-19)

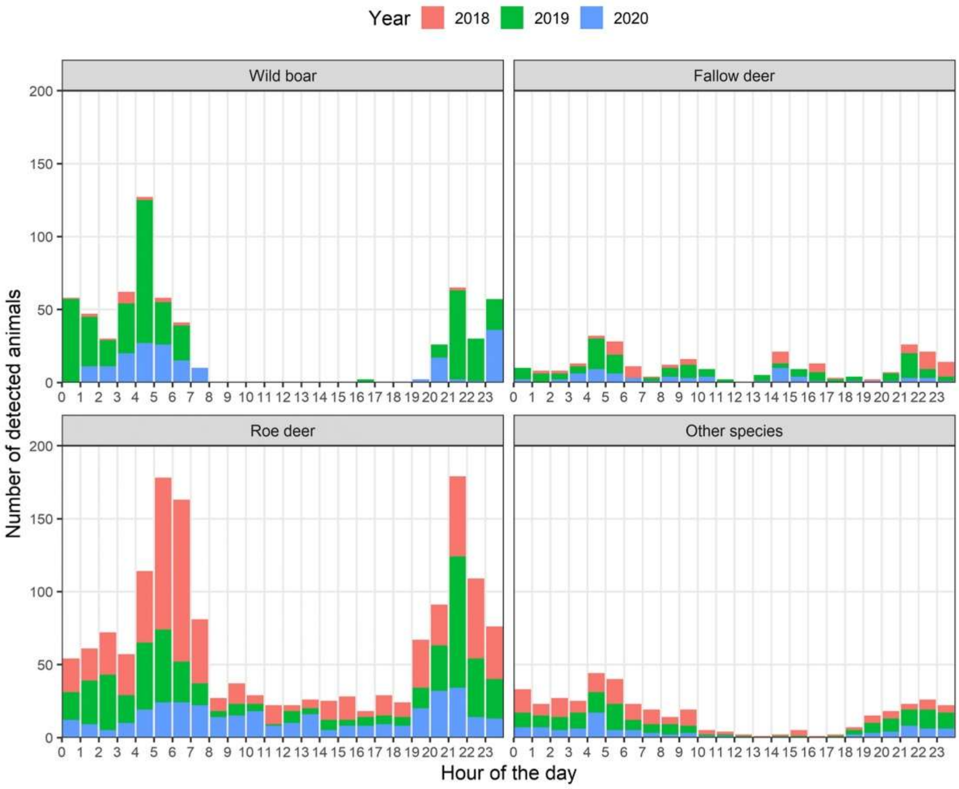

Figure 4. Hour histogram of all recorded animals in a day period.

		Coefficient	Test. statistics	*p* value
	Intercept	−3.2246	−8.367	<0.001
	Distance from roads	−0.0025	−3.525	**<0.001**
	Distance from pathways	−0.0066	−4.683	**<0.001**
Forest type	Pine/hornbeam	−0.2150	−0.413	0.68
	Pine/spruce	1.9890	3.842	**<0.001**
	Oak/hornbeam	0.7403	1.519	0.13
	Hornbeam	−0.4261	−0.522	0.60
	Spruce	0.2420	0.573	0.57
	Species-rich mixed forest	0.6703	1.625	**<0.001**

Table 1. Presence/absence probability of people on camera traps (daily data). The significant effects of measured parameters ($p < 0.05$) are marked in bold.

in 2016 in the urban forests of Hradec Králové (56.2% men and 43.8% women; [48]). In our study, the number of visitors during the period of forest entrance prohibition in 2018 was ca. 36% of the normal situation in 2019, and ca. 24% of the increased number of visitors in 2020. Therefore, the evaluation of entrance ban effectiveness in the ASF infected area is quite disputable. The complete standstill of any activities in the infected area was also prescribed e.g. in Belgium[49], however the effectiveness was not evaluated. All activities outside of the forestry trails are particularly disturbing to wild boars. Indeed, whatever the activity being performed, the strict respect of trails is of prime importance[40]. The ASF spreading is affected by several factors such as natural movement of wild boar, including both home-range movement and long-range dispersal[37,39]. Therefore, the prohibition of human leisure activities is recommended in the outbreak area[40].

In the normal situation, the number of daily visits is generally higher on weekends (up to 125%) compared to weekdays. This trend was confirmed e.g. in the peri-urban forest in the vicinity of Hradec Králové (CZ)[48]. In our study, we have also observed a relatively larger number of people on Saturdays, Sundays, and public holidays as expected, but surprisingly, the highest number of people were detected on Thursday, June 25, 2020. During the ongoing COVID-19 pandemic (2020), Thursdays were the days with the highest total number of recorded people, followed by Wednesdays and Sundays including public holidays. In 2019, 67% of visits were recorded during working days, increasing to 76% in 2020. This increase could be partly explained by the post-lockdown period, which increased the enthusiasm for going for a walk even on workdays. A comparable trend was described by Derks et al. (2020), where the clear difference between the number of visitors on weekdays and weekends substantially decreased after the lockdown measures were implemented, compared to the pre-COVID-19 times. In the COVID-19 period, people had more available time, more flexibility, more pressure at home, but also fewer alternative pastimes. In terms of the number of forest visitors, the tree species composition was an important predictor[48,50]. In our study, people preferred mixed coniferous forests (pine/spruce) and species-rich mixed forests, while conversely, attendance was the lowest in monospecific deciduous forests. Similarly, visitors to the Municipal forest in Ostrava (CZ) preferred more structured mixed forests, while spruce and pine were the most favorable tree species[51]. Italian responders preferred mixed forests (66%) over coniferous forests (28%) and deciduous forests (6%)[52], while another study from the Protected Landscape Area Žďárské vrchy (CZ) documented the visitor preference of coniferous forests[53].

The increase of outdoor recreational activities and nature tourism was indicated in a majority of published studies measured by Google mobility data, automatised visitor counters on forest roads, or by questionnaires [46,47,48]. Therefore, human movement in the forests, in the context of wildlife disruption (outside of the forest roads), was impossible to evaluate. Conversely, in our study, the animals were monitored together with humans. The threat risk predicts that animals will avoid human disruption and react as expected during an encounter with a predator[54], which was also confirmed in our study. The continuous monitoring showed that the presence of wildlife was significantly lower (more than 2.6 times) directly after human movement was recorded by camera traps—compared to the period without human presence. It is evident from these results, that on a short-time scale, the wildlife species avoided the areas visited by humans.

The impact of human activities can trigger behavioural and stress response in wild animals[55,56], with a significant impact on entire wildlife populations[54,57]. When animals face the risk of predation, many engage in behaviour that reduces that risk, but also generate an increased energy cost[58]. For instance, animals may be more vigilant in the vicinity of different types of anthropogenic disturbances[54], which results in a reduced immune response[59], increased susceptibility to diseases[60,61], reduced growth[62] and a decreased fitness[63]. Moreover, the short-term disturbance could compel the animals to utilize lower quality habitats, which leads to damage of forest ecosystems or agricultural crops. The direct effect of human disruption has been proven, e.g. the increase of browsing pressure by ungulates[64,65], which significantly affects the forest stability, wood production and sensitivity to fluctuation of climatic factors[66,67]. Another serious effect of human disturbance to wildlife is increased risk of wildlife-vehicle collisions in areas with higher human activity[68] or close to urban areas with growing rate of human disturbances[69].

However, the wildlife species that regularly encounter humans without negative consequences should get used to their presence[70,71]. The animals detected in our study area are mainly the common wild ungulates which are relatively accustomed to human disruption in the long-term, and able to occupy a highly modified cultural landscape. The tolerance is reflected e.g. by the dramatically increased population densities in Europe[72–74]. Conversely, the endangered animal species are much more sensitive to human disturbance than common species that successfully adapted to the recent land use changes. The most sensitive birds and mammal species decline or disappear from the highly disturbed sites, and the species composition shifts from "wild" species to cultural and human-associated species[5]. For instance, the study from northern Finland reveals that the proportion of ground-nesting birds is higher in forests than in tourist destinations[5]. Although open-cup nesters nesting on the ground showed a negative response to the number of visits on hiking trails, yet the species richness remained unaffected, as sensitive species were apparently replaced by generalist species[5,75]. However, the endangered species could successfully adapt to a regular and managed human presence in the vicinity of the areas of occurrence (e.g. human movement only of forest roads). A study from Germany (Lower Saxony) confirmed adaptation of black grouse (*Lyrurus tetrix*), critically endangered in Central Europe, to the human disruption. Differences in black grouse movement were monitored by GPS transmitters. Tagged individuals avoided the vicinity of public routes, and the contact distances were directly related to the intensity of human activity. Individuals used the vicinity of public trails at night and dawn but avoided these habitats during peak human activity around noon and afternoon[76].

To our knowledge, this is the first study which compares the unique situation of differences in human visits in forests outside of forest roads in relation to distinct movement patterns. We have confirmed the rapid increase of visitors in the forests during the COVID-19 pandemic in May and June 2020. Our study confirmed that forest ecosystems play an indispensable role during pandemics and related economic crises—in relation to recreation services that the forests offer. On the other hand, apart from improving physical and mental health of visitors, they may possibly contribute to spreading of diseases. Contrarily, we have observed the decrease of visitors in the same area during the African swine fever outbreak, during which the entrance into the forests of the affected areas was completely prohibited. However, our findings demonstrate that the restrictions during the ASF outbreak were not fully respected. The trends in the rapid increase of human visitors outside of forest roads has a significant impact on wildlife behaviour. The places visited by humans were then avoided by animals in a short-time period. The confirmed impact of human visitation on wildlife behaviour highlights the need for new measures that should mitigate the negative effects on wildlife disruption through visitor's education, especially during the breeding season. Our results suggest that management measures are highly important, particularly in the areas where the threatened animal species live because they are much more sensitive to human disruption. Essentially, the political authorities should improve the communication of the restrictions concerning the African swine fever outbreaks which are expanding into new territories in central Europe. The disregard of entrance prohibitions could have an immeasurable impact on the disease transmission outside of the affected areas. Therefore, comprehension of the direct effects of human behaviour on wildlife and natural processes in forest ecosystems is indisputably important.

Material and methods

Study area. The study of human visits to the forest areas was focused on a location northeast of the city of Zlín in eastern Czech Republic (N 49°15′, E 17°44′). Zlín is the eleventh largest city in the Czech Republic with 74,921 residents. The population density of the Zlín district is 187 inhabitants/km^2, while 72.5% inhabitants live in towns. The proportion of women to men is 51.5% to 48.5%, and the average age is 39.9 years (www.zlin.eu). The location was selected due to the African swine fever outbreak which began on June 21, 2017. The outbreak was officially eradicated—according to the European commission—on March 12, 2019.

The average annual temperature in the location reaches 13.2 °C, and the total sum of precipitation is 656 mm, while it is 20.5 °C and a monthly 73 mm in the studied months. The study area has a humid continental climate characterized by hot and humid summers and cold to severely cold winters (Cfb region) according to the worldwide[77] classification.

The acreage of the monitored area was about 5430.6 ha with the following land use composition: standard commercially managed forests—26.6% (1443.8 ha), human settlements—1.7% (92.5 ha), agricultural land—71.6% (3889.7 ha), and water bodies—0.1% (4.6 ha). Thirteen villages are located in the area of interest, with an average population of 863 inhabitants. The altitude ranges from 221 to 413 m a.s.l.

Study design and camera trap monitoring. The forest areas in the location of interest were sorted according to their acreage into categories of small forests (0–50 ha; marked by green), bigger forests (50.1–200 ha; yellow) and large forest complexes (˃200 ha; red). Human visits were monitored only in the forests larger than 50 ha (Fig. 5.). Human presence in the forest and the activity of common animal species was monitored by 14 randomly placed camera traps, i.e. 1 camera trap per 100 ha of forest area. The locations for camera traps were previously selected via random points tool in GIS software (ArcGIS 10.8). All camera traps were placed at least 100 m from the forest edge and forest road. The monitoring was implemented in three consecutive seasons (2018, 2019 and 2020) utilizing the same time period from 1st May to 30th June (61 monitoring days every year).

The UO Vision UV 595 HD cameras were used with the following parameters: invisible IR camera (resolution of 12 megapixels), utilizing a trigger speed of 0.65 s and HD video (1080P) recording (for more information see www.uovision.com). All cameras were installed on a tree at a height between 1 and 1.5 m. The date and time were recorded automatically at the beginning of each video. The sites were inspected every 3 weeks to check the cameras and download recorded videos. The camera traps triggered video recording automatically when motion was detected. Settings of the camera traps were set to 30-s videos with a 1-min window between each video sequence.

African swine fever pattern in 2018. Visiting the affected location was banned during the time of African swine fever to prevent possible transmission of the disease out of the outbreak area. These restrictions were valid from August 9, 2017, to November 26, 2018. Regulation forbade the entry into the suburbs of municipalities in the defined area, with the exception of gamekeepers exercising measures to prevent the spread of African swine fever, and with the exception of individuals permitted by the Mayor of the city of Zlín. The area was intensively monitored by police patrol, with the fines for infringement of the regulations reaching 20,000 CZK (approx. 770 EUR).

Standard situation in 2019. The movement of citizens in the forests of the Czech Republic is defined by the Article 19, Act No. 289/1995 Coll. In general, every individual is entitled to enter forest stands at their own risk. Visitors must not damage the forest, nor interfere with the forest environment. They are obliged to follow the instructions of the owner or tenant of the forest and their staff. Act No. 289/1995 also further defines restrictions for forest users.

COVID-19 pandemic in 2020. On March 12 at 2.00 PM, a state of emergency was declared pursuant to Articles 5 and 6 of the Constitution Act No. 110/1998 (on the Security of the Czech Republic) limiting certain rights and freedoms of citizens (Resolution No. 194/2020). On March 13, the security measures progressed further, as full-time education and organized indoor and outdoor events and activities of more than 30 people were banned, and facilities such as gyms, wellness centers and solariums were closed (Resolution No. 72/2020, Resolution No. 84/2020). With effect from March 14, 2020, the government banned all foreign entry into the territory of the Czech Republic from high-risk areas, with specified exceptions (Resolution No. 76/2020). From March 16, 0:00 AM, until March 24, 06:00 AM, the free movement of citizens was limited throughout the Czech Republic with several exceptions, such as visits to nature and parks. Furthermore, the government strongly recommended to all employers to implement and encourage home office in order to limit the movement and direct contact of citizens[78] (Resolution No. 85/2020). The state of emergency was further extended until May 17, which included most of the previously declared restrictions (Regulation No. 219/2020). However, the restrictions regarding free movement and outdoor activities were gradually lifted starting on April 7, when individual outdoor sports were permitted, and on April 24, free movement of the public was restored (in groups smaller than 10 people). On

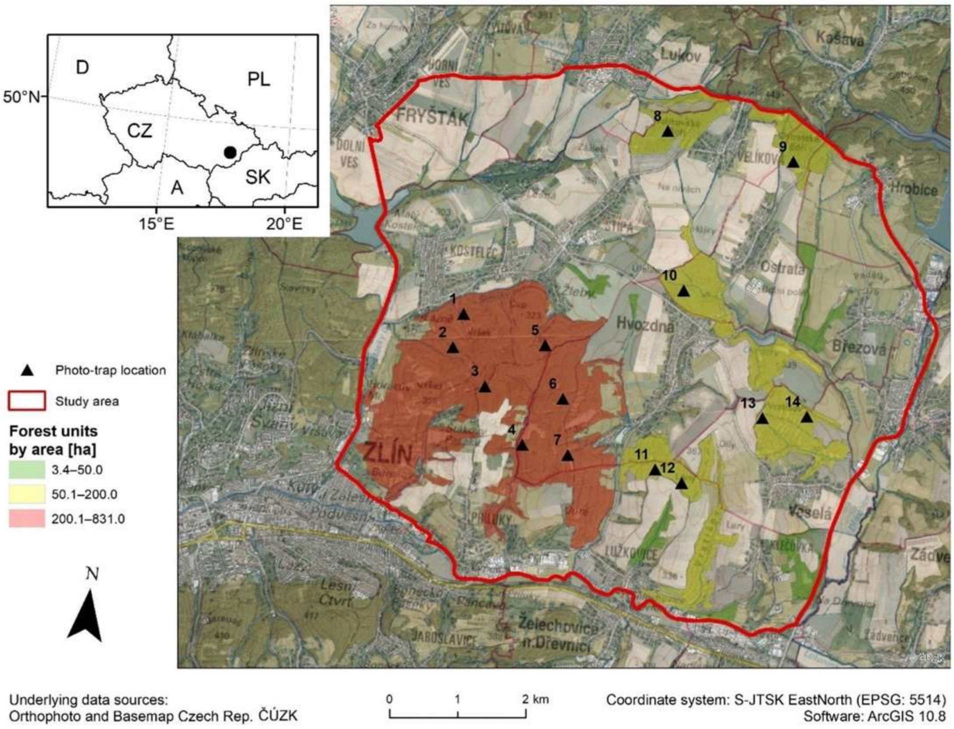

Figure 5. Distribution of forest areas and camera traps in the study area (▲). The study area (northeast from the city of Zlín) is marked by a black dot (●) for context of the Czech Republic and neighboring countries. This map was created in ESRI ArcMap 10.8 (https://desktop.arcgis.com/zh-cn/arcmap/).

May 11, full-time education was restored for the last year of primary schoo ls and the last year of secondary schools (Regulation No. 220/2020), all businesses including shops, shopping centers, and gyms were re opened on May 25, and on June 8, all pupils were allowed to return to schools[79].

Statistical analysis. All the videorecords were manually inspected. Records were sorted for statistical analysis and the database was created in MS Excel according to year, date, time of visit, wildlife species, and the visitors data. The visitors data set was divided according to age (subadults, adults and seniors) and gender (male and female). The possible duplicity records of visitors were not included in the analysis. The animal data set was divided according to wildlife species present in the monitored area to wild boar (*Sus scrofa* L.), fallow deer (*Dama dama* L.), roe deer (*Capreolus capreolus* L.), and a group of other animal species, including martens (pine marten [*Martes martes* L.] and stone marten [*Martes foina* L.]), red fox (*Vulpes vulpes* L.), European badger (*Meles meles* L.), and European hare (*Lepus europaeus* Pallas).

For a basic overview on the record of people visiting in different years, a simple histogram of human records divided into subadults, adults and seniors is presented. We have also presented basic statistics and comparisons of selected study years. The upward trend of human records between study years was confirmed by linear regression. For the description of most frequent weekdays, histograms for each study year were presented. We have tested for differences in human records on different weekdays together for all study years via chi-squared test. The testing for differences in proportion to visits on different weekdays in 2019 and 2020 were also tested via chi-squared test.

The times of human and animal visits are presented by an hour histogram of records for each study year. In the case of wild boar (the game species with the most prominent differences in the number of records during the day vs. the number of night records), the differences in proportion of day and night records were also tested by chi-square test (according to accurate sunrise and sunset in particular days; Central European Time).

We have tested for differences in animal visit frequency during "people-influenced" time (24 h after the time when people were detected on camera traps) and non-influenced time (opposite cases, e.g. more than 24 h from the last people detected). The intensity was calculated as a sum of detected animals (number of records) divided by the total "people-influenced" time, and vice versa for each camera trap in all study years combined.

A logistic regression model was used to test the dependency of people's presence, which were recorded by camera traps, at a distance from the roads and pathways, and the forest type involved—Scots pine (*Pinus sylvestris* L.) and European hornbeam (*Carpinus betulus* L.) forests, pine and Norway spruce [*Picea abies* (L.) Karst] forests, oak (*Quercus* spp.) and hornbeam forest, monospecific hornbeam forests, monospecific spruce forests, and species-rich mixed forests, which were represented in the data collection.

All computations were performed in R software on selected alpha level of 0.05. The plots were made in "ggplot2"package[80].

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Author contributions

Conceptualization, J.C., R.L. and F.H.; data curation, R.L. and; investigation, J.C., F.H. and R.L.; methodology, J.C., and R.L.; supervision, J.C., F.H., P.M., V.H.; writing—original draft, J.C., R.L., K.M., Z.V., M.F., F.H., P.M., V.H.

Competing interests

The authors declare no competing interests.

Additional information

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5.2 Vliv umístění plotů na pohyb prasat divokých

5.2.1 Odor fences have no effect on wild boar movement and home range size

Faltusová, M., Ježek, M., Ševčík, R., Silovský, V. & Cukor, J. (2024). Odor Fences Have No Effect on Wild Boar Movement and Home Range Size. *Animals*, *14*(17), 2556, DOI: https://doi.org/10.3390/ani14172556

Hlavním cílem studie bylo vyhodnotit účinnost pachových ohradníků jako bariéry pro pohyb divočáků, zejména ve vztahu ke zmírnění šíření afrického moru prasat a ochraně plodin před poškozením. Studie sledovala chování divočáků označených GPS před a po instalaci pachových ohradníků. Výsledky neukázaly žádný významný vliv pachových ohradníků na pohybové vzorce nebo velikost domovského okrsku divočáků. V důsledku toho studie dospěla k závěru, že pachové ohradníky nejsou účinnou metodou pro zabránění pohybu divočáků, snížení přenosu AMP nebo ochranu plodin. Publikace splnila dílčí cíl 4.

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Article

Odor Fences Have No Effect on Wild Boar Movement and Home Range Size

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Simple Summary: The rapidly growing wild boar population has resulted in an increasing rate of human–wildlife conflicts, including economic damage to crops or spreading African swine fever (ASF), which affects the pork industry. This situation necessitates the adoption of various measures to prevent wild boar movement, mitigate spreading of diseases, and protect crops. We evaluated the impact of commonly used odor fences (Wildschwein Stopp) using GPS telemetry of tagged individuals. The telemetry of free-ranging wild boars demonstrated no effect on their crossing of the odor fence lines compared to before the installation. Moreover, no difference was found when comparing the home range size of monitored individuals during the 22 days before and after odor fence installation. Therefore, our findings do not support using odor fences to prevent wild boar movement as a mitigation measure of ASF transmission or line protection against the damage caused by wild boars to crops.

Abstract: Wild boars are an opportunistic wildlife species that has successfully colonized the human-modified landscape in Europe. However, the current population boom has negative consequences, which result in a rapid increase in human–wildlife conflicts and disease transmission, including African swine fever (ASF). The increasing frequency of conflicts requires adequate solutions for these issues through various measures. Application of deterrents is a common non-lethal measure whose effects have been insufficiently verified until recently. Thus, this study aims to evaluate the effectiveness of odor fences, often applied as a barrier against wild boar movement. For this purpose, 18 wild boars were marked with GPS collars. After 22 days of initial monitoring, 12 sections of odor fences were installed on their home ranges. The monitored wild boars crossed the area 20.5 ± 9.2 times during the pre-installation period and 19.9 ± 8.4 times after the odor fence installation. Moreover, the average home range varied between 377.9 ± 185.0 ha before and 378.1 ± 142.2 ha after the odor fence installation. Based on GPS telemetry results, we do not support using odor repellent lines for crop protection or for limiting wild boar movement to lessen ASF outbreaks.

Keywords: GPS telemetry; crop protection; African swine fever; deterrents

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1. Introduction

As a species, wild boars have adapted perfectly to a human-modified landscape [1]. Changes related to the intensification of agricultural management offered wild boars an ideal environment with enough shelter and food sources for most of the year [2]. This has led to a population boom in wild boars, primarily throughout Central Europe, as the increase in their physical condition, associated with faster sexual maturation of juveniles due to available food, affects the population dynamics through earlier reproduction than previously observed. It is reflected in the rising numbers of wild boar harvested annually in countries like Spain, Poland, France, Italy, and Germany. Although growth rates varied among countries, the overall trend shows consistent population growth, with occasional stabilization periods followed by further increases [3]. However, the population increase has several explanations in Europe, including hunting regulations and hunting philosophy and the decreasing number of active hunters [3,4], very high reproduction rates [5], lack of large predators [6], reforestation, habitat alterations due to humans [7], mild winters [8], mast seeding [9], and supplementary feeding [10].

The rapid increase in the wild boar population is also associated with negative impacts on human interaction, including an increased frequency of human–wildlife conflicts [2,11]. The cost of crop damage has reached extreme amounts in certain Central European countries [12]. Still, the fundamental impacts are related to the spread of viral diseases, such as African swine fever (ASF), which is now moving from Eastern Europe through Central Europe into Western European countries [13,14]. Despite the limited host range of ASF, the socioeconomic impact of the spread of the virus is enormous [15]. Moreover, ASF outbreaks have the potential to devastate the pork industry. ASF outbreaks in China have resulted in the culling of 1.2 million pigs, and the estimated economic impact of these outbreaks is 0.78% (111.2 billion USD) of China's gross domestic product in 2019 [16]. Similarly, ASF outbreaks in Europe caused significant declines in wild boar and domestic pig populations [17]. The assumption is that global pork prices will increase by 17–85% and the unsatisfied demand will lead to higher prices of other types of meat. For example, in 2019, beef and poultry prices rose worldwide by 1.5–6.0% and 1.6–6.7%, respectively. Of course, higher pork prices are one of the factors that reduce pork demand in all regions, with an average global per capita demand falling by 0.7–2.4 kg per year^{-1} (4–16%), with the largest consequences observed in Europe (7.9 kg per year^{-1}) [18].

The increased frequency of conflicts, followed by economic impacts, has led to the use of various measures with varying effects to solve these problems. One frequently used measure is odor fences, based on a scent that simulates danger or the presence of a predator or humans [19–21]. Smell is a sense that serves as an extended arm of the nervous system for remote sensing of stimuli in the environment [22]. The olfactory stimulus is often one of the first impulses that alert an individual to danger. This method is used in boar population management, most often to minimize damage to agricultural and forest stands [23] or to prevent wild animal collisions on roads [24]. The odors of a natural predator [25] or an odor imitating human presence [26] are the most often used scents.

However, the effectiveness of individual measures, including odor fences, is highly debatable. In crop protection, it was evaluated as ineffective for wild boars, e.g., by Schlageter and Haag-Wackernagel, Zamojska et al. [23,27], who noted that resistance to the tested odor repellents occurred relatively quickly or was simply ineffective. Similar results were reached by Elmeros et al. [28] in cervids in forest stands. Contrarily, some studies indicate that odor repellents can be effective against browsing for up to several weeks [29,30]. The same is true in the case of reducing the number of accidents involving wild animals. Although the results show a reduction in the number of accidents after applying the so-called odor barrier by 23% to 43% [31,32], the mechanism of functionality is still not explained. The primary premise of companies that manufacture odor barriers is that installing odor fences will reduce the number of road crossings. However, [26] compared the occurrence of roe deer near roads where odor fences were installed and found no differences in the frequency of occurrence. A change in the game's behavior rather than a reduction in the frequency of crossings is likely behind the reduced number of game collisions.

Despite the conflicting results of scientific studies, the supply of commercial preparations designed to repel wild animals from the installed fence areas is growing and is constantly finding new uses. For example, the installation of an odor barrier to prevent wild boar movement from and beyond the ASF-infected zone was utilized in the Czech Republic, Lithuania, Poland, Denmark, and India [17,33]. Because the virus did not spread from the infected area in the Czech Republic between 2017 and 2019 during the focal case [34], this method was believed to be effective. However, an exact evaluation of the reactions of the movement of wild boars to odor fences is still unexplored, and thus, it is not definitive if the odor fence was an effective measure as believed, or if the ASF virus was not spreading due to other implemented measures. As a practical matter, the only effective way to evaluate these protective measures is to use GPS-marked wild boar individuals in places with odor fences, which has not been conducted until now.

Therefore, the aims of the presented study are (i) to evaluate the effectiveness of the application of odor fences as a barrier against wild boar movement, (ii) to assess the possible impacts of odor fences on the home ranges of GPS-marked wild boar individuals, and (iii) to evaluate any differences in behavior according to the sex of the monitored individuals.

2. Materials and Methods

2.1. Study Area

In 2019–2021, the spatial activity of wild boars was monitored at two locations. The first was the Bohumile hunting ground, Prague-East district (49.9622 N, 14.7875 E), and the second was the Hradiště hunting ground, Karlovy Vary district (50.2483 N, 13.1907 E). The Bohumile hunting ground is located in a suburban area in the wider Prague agglomeration. The area has mixed forest complexes interwoven with intensively farmed agricultural land and rural municipalities. A high level of human leisure activity is typical in the area. Contrarily, the Hradiště hunting ground is situated on the territory of a military training area, where public access is prohibited, and only activities related to forest management and army training take place here.

2.2. Wild Boar Telemetry

During the monitoring period (2019–2023), 62 wild boars were marked with a GPS collar (locality: 21 Hradiště, 41 Bohumile; sex: 45 females, 16 males, 1 unknown). The wild boars' exact ages were determined by tooth eruption and then categorized into two groups: subadults (12–24 months) and adults (over 24 months). Wild boars were captured in trapping cages, immobilized, and fitted with a tracking collar [35]. The collar contained a GPS unit (Vectronic Aerospace GmbH; Berlin, Germany) and a Daily Diary biologger (Wildbyte Technologies Ltd.; Swansea, United Kingdom). We recorded data from the biologgers (3-axis accelerometer and 3-axis magnetometer with a frequency of 10 Hz). GPS positions were collected every 30 min using a GPS module and sent via SMS to an online server. We used only GPS positions with a variance of accuracy (DOP) ($\geq$1 and $\leq$7) for analysis. From all the captured wild boar individuals, we included 18 wild boars in the analyses for the evaluation of the number of crossings whose movement trajectory during a 30-min interval (before the installation of the foam) crossed the planned route of the installation of the odor barrier at least five times in the control period. Other wild boars were not included in the experiment because (a) they were hunted before odor fence line application or (b) their home range and daily movement were outside the planned odor fence lines at the time of evaluation.

2.3. Deterrent Application

To test the effectiveness of odor fences, we used a design based on control periods [24]. The monitored period always lasted six weeks and was divided into two sections. In the control section (three weeks), no odor barrier was installed. For the experimental section, we installed a linear odor fence along the road, which we left in place for three weeks, after which the odor barrier was removed. In this study, we used the odor fence HAGOPUR—Wildschwein stop (WS-Stopp). The manufacturer (HAGOPUR AG) states that this product was developed to reduce or prevent road accidents and to prevent crop and tree browsing. Then, using an applicator, a foam was used to create the odor fence. The dispersion is a carrier material that contains a natural odor concentrate that works for one week after application. After this time, it is necessary to add concentrate for roe deer or boar (in our case, WS-Stopp). Regularly reapplying the concentrate every two to three months ensures the optimal long-term effect. According to the instructions, we applied the foam, which held to the mat, in formations roughly the size of tennis balls on the forks of branches, tree bark, tree stumps, or hammered pins. We applied the foam balls five meters from each other, as recommended by the producer, and as was evaluated before in a study by Bíl et al. [36]. According to the instructions, we added the concentrate after a week.

We installed the sections with an odor barrier based on the movement of wild boars determined by data from GPS collars (Figure 1). It means that at first, the tracked wild boar movement was evaluated for 22 days during April or October 2019–2023. Then, the line of odor fence was applied to the detected home range size, and the GPS was carried out for 22 days after application. We always placed the line of the odor fence so that it approximately intersected the area of occurrence from the last three weeks. The lines were run along public and forest roads. The length of the lines always reached a minimum of 500 m of the marked territory. Line lengths ranged from 1400 m to 3600 m. The lines were installed from April to September, i.e., when the temperature was high enough to ensure the release of the smell. We installed a total of 12 lines of odor fences and used a total of 18 wild boar individuals in the analyses that passed through the lines. The others (44) were not near the installed odor fence lines, or they missed the experiment.

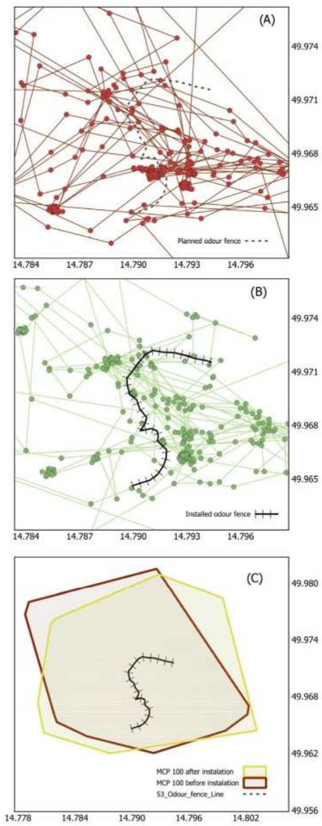

Figure 1. The movement of a wild boar during the tested period depicted as connections between individual GPS positions (30-min intervals) before the installation of the odor fence (**A**) and after its installation (**B**); overlap of the utilized area (MCP 100%) before and after the installation of the odor fence (**C**).

2.4. Statistic Evaluation

We vectorized the obtained lines in QGIS 3.36 [37]. At the same time, we exported the GPS positions of the marked wild boars and selected only those that spatially and temporally corresponded to the established odor fence lines. Subsequently, we crossed the lines of the odor fences with the movement trajectories of wild boars between individual points obtained using GPS collars (interval between points, 30 min). Furthermore, we calculated the territory over which the marked individuals moved before and after the odor fence (home range) installation, using the Minimum Convex Polygon method (MCP 100%). At the same time, we exported the polygons of the home precincts and, by using the intersection of both polygons, we calculated the overlap of paired polygons of individuals before and after. The data were evaluated, visualized in R 4.2.2 software [38], tested for normality, and subsequently, evaluated for statistical differences.

We used three linear mixed-effects models (LMM) to evaluate the differences in the number of transitions, home range size, and home range overlap of wild boars (dependent variables) between the period before (A) and after (B) the installation of odor fences (independent variable) using the lmer function (lme4 and lmerTest packages) [39,40]. We included the sex (female/male) and age (adult/subadult) as covariates and locations (Bohumile/Hradiště) as random effects in all three models. The significance level was set at $\alpha = 0.05$ for all statistical tests performed using the lmer function. The evaluation of differences between the periods of paired samples (identical animals monitored before and after the installation of odor fences) was also evaluated using 95% confidence intervals (CI). We checked for the normality of residuals for all models using the Shapiro–Wilk normality test and Q-Q plots.

3. Results

In total, we installed 12 lines of odor fences. On average, wild boars crossed the odor fence line 20.5 ± 9.2 times (mean ± SD) in the pre-installation period (A) and 19.9 ± 8.4 times when the odor fence was installed (B). The number of transitions decreased by 0.6 (95% CI, −6.0 to 4.8) after the installation of the odor barrier in the study areas. However, there is no statistical difference in the number of transitions between the two periods (Table 1, Figure 2).

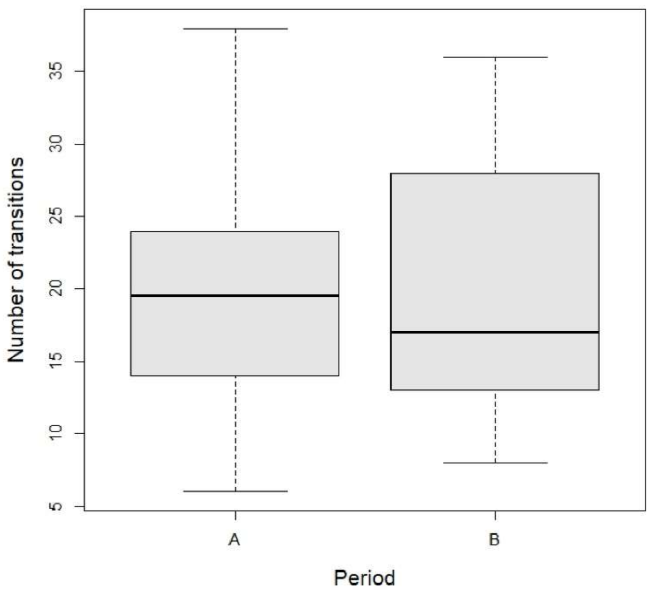

Figure 2. Number of wild boar transitions before (A) and after (B) installation of odor fences in the study area. Boxplots show the median values (middle bar in rectangles), upper and lower quartiles (length of rectangles), and maximum and minimum values (whiskers).

Table 1. Results of the linear mixed-effects model testing differences between the number of transitions (dependent variable) and periods (independent variable) in the study areas. Sex and age were included as covariates and locations as random effects. For each variable, we report the slope (estimate) and its standard error (SE), t-values, and *p*-values.

Variable	Estimate	SE	t-Value	*p*-Value
Intercept	23.6748	4.4175	5.359	0.0526
Period (B)	−0.6111	2.8010	−0.218	0.8287
Sex (M)	−1.0040	3.3941	−0.296	0.7693
Age (S)	−2.8906	3.0233	−0.956	0.3464

The evaluated home range size before the odor fences installation (home range for 22 days) was, on average, 377.9 ± 185 ha for animals located in the areas assigned for future installation of odor fences. When the odor fences were installed, the average size of the home area was 378.1 ± 142.2 ha for the same length of the evaluated period (22 days). The average home range size decreased by 0.2 ha (95% CI, −105.6 to 106.1) after the installation of odor fences. At the same time, there was no statistical difference in the size of home ranges between periods (Table 2, Figure 3).

At the same time, there was no change in the overlap of home ranges if we compared the period before the installation and during its implementation in the study area. Before installation, the average overlap was 0.62 ± 0.17 and after, it was 0.71 ± 0.18. The average difference in overlap was 0.09 (95% CI, −0.03 to 0.20). Again, no statistical difference was noted in the overlap of home ranges between the period before and after the installation of odor fences (Table 3, Figure 4).

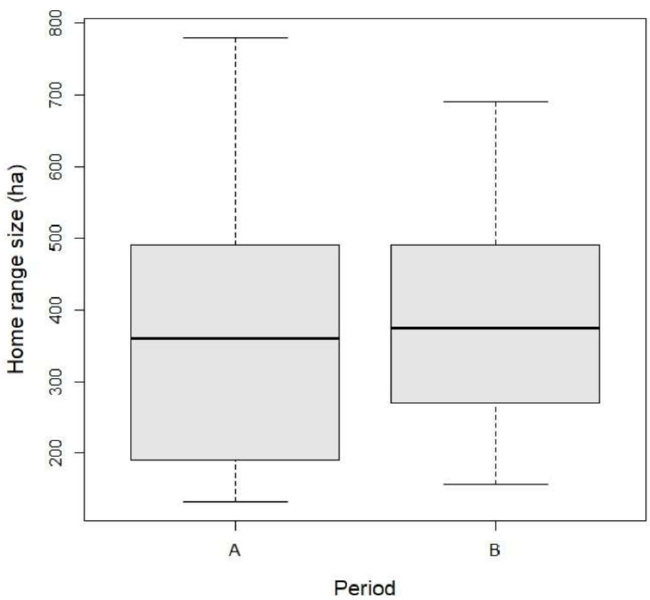

Figure 3. Average size of home range during two periods, before (A) and after (B) installation of odor fences in the study area. Boxplots show the median values (middle bar in rectangles), upper and lower quartiles (length of rectangles), and maximum and minimum values (whiskers).

Table 2. Results of the linear mixed-effects model testing differences between the home range size (dependent variable) and periods (independent variable) in the study areas. Sex and age were included as covariates and locations as random effects. For each variable, we report the slope (estimate) and its standard error (SE), t-values, and *p*-values.

Variable	Estimate	SE	t-Value	*p*-Value
Intercept	388.5824	57.0172	6.815	0.0083
Period (B)	0.2222	55.0948	0.004	0.9968
Sex (M)	−72.0198	66.5263	−1.083	0.2872
Age (S)	35.0190	59.4157	0.589	0.5599

Table 3. Results of the linear mixed-effects model testing the differences between home range overlap (dependent variable) and periods (independent variable) in the study areas. Sex and age were included as covariates and locations as random effects. For each variable, we report the slope (estimate) and its standard error (SE), t-values, and *p*-values.

Variable	Estimate	SE	t-Value	*p*-Value
Intercept	0.6528	0.0641	10.191	0.0033
Period (B)	0.0861	0.0601	1.433	0.1619
Sex (M)	−0.0048	0.0726	0.066	0.9478
Age (S)	−0.0442	0.0648	−0.682	0.5002

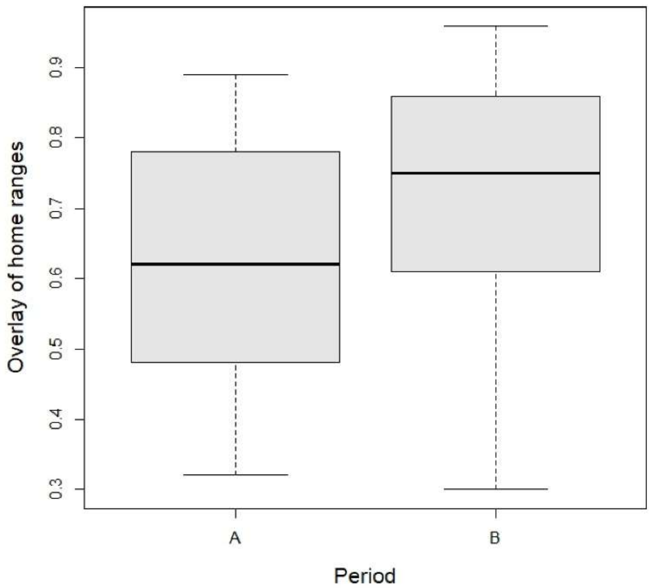

Figure 4. Overlay of home ranges before (A) and after installation (B) of odor fences in the study area. Boxplots show the median values (middle bar in rectangles), upper and lower quartiles (length of rectangles), and maximum and minimum values (whiskers).

4. Discussion

Wild boar populations have been increasing worldwide in recent decades, resulting in a rapid increase in human–wildlife conflicts, such as crop damage or traffic accidents. Currently, the most negative impact is related to the spreading of ASF worldwide with negative consequences for the pork industry [41]. Therefore, various methods are being tested to channel and limit wild boar presence and movement from ASF-infected zones or valuable agricultural fields for crop protection. For these purposes, various deterrent measures are being used with limited knowledge of their effectiveness, highlighted primarily by vendors or producers claiming that the preventative substances are effective as wild boar deterrents [23].

We tested the effect of odor fences on wild boar movement in areas where the wild boar individuals were tagged with GPS telemetry transmitters, which seemed the best way to evaluate the odor fence effect, using WS-Stopp odor barriers. However, we observed no significant effect of the odor fences on wild boar movement with the installed line prepared with foam balls five meters apart. In the period before application, the wild boar crossed the line 20.5 ± 9.2 times compared to 19.8 ± 8.4 times after the fence installation. This offers new insight into evaluating the odor repellent's effect on limiting wild boar movement in the landscape when used before to mitigate wild boar migration from ASF-affected areas or to protect attractive crops. Previously, the odor repellents were tested predominantly at baited luring sites in pairs designed where one luring site was protected and the second was the supplementary feeding site without any protection. The experiment by Schlageter and Haag-Wackernagel [23] recorded a minimal and non-significant deterrent effect of 0.4%, which means that both luring sites were visited at almost the same frequency, thus they concluded that the repellent is ineffective and not recommended for crop protection.

The monitoring of wild boar odor repellent efficiency also confirmed no effect on wild boar home range size, which was surprisingly the same for all individuals. On average, home ranges for the monitored period of 22 days were 377.9 ± 185.0 ha before and similar (378.1 ± 142.2 ha) for the period after the odor fence installation. This corresponds to monthly home range size, usually in the low hundreds of hectares [42–44]. For instance, in Tuscany along the Apennines, the average monthly home range size of wild boars was 187.1 ha [42], while in other Italian regions, it was 136 ha [43]. Moreover, we did not confirm significant differences in the home range sizes before and after the odor repellent installation based on the sex and age of monitored animals. This fact easily confirms that the odor fence was not respected by any age or sex group of wild boars. At the same time, no differences in the home range size of wild boar individuals according to sex classes in adult individuals are commensurate with previously published research [43,45].

There is little evidence to suggest that odor repellents effectively deter wild boar movement. Studies have shown that various types of deterrents are generally ineffective in protecting against wild boar. Benten et al. [46] revealed the ineffectiveness of wildlife warning lights in reducing wildlife–vehicle collisions on the roads. All the tested reflector models were unable to reduce the number of collisions during the experiment. Schlageter and Haag-Wackernagel [47] found LED flashers to be ineffective. In a pairing experiment, the luring sites with LED flashers were compared to those without protection. The data from 504 wild boar inspections of the luring sites indicated that solar blinkers reduced the probability of wild boar visits by 8.1% compared to the control sites. Still, the authors admit that the red light they used may have been inappropriate because wild boars seem unable to distinguish red from grey [48]. However, there are exceptions. Denzin et al. [49] reported that LED blinkers and aluminum strips performed surprisingly well in adults and juveniles, and deterrents appeared to be more effective on young wild boars.

If the application of odor fences was to reduce the spread of diseases (including ASF), it was assumed that odor fences could be one of the solutions. As described above, our study showed that the use of odor fences is insufficient in controlling the spread of ASF. Therefore, this study does not support their use, as was previously done in the Czech Republic and Poland [50]. It appears that permanent fencing is the only effective solution to prevent the spreading of ASF, hand in hand with other measures such as reducing wild boar population, and biosecurity, which were implemented in most European countries [51]. This is true, especially for hot spot fencing used to reduce transmission of diseases once endemic, but the construction of fences requires consideration, especially in the case of wild boars [52]. The iron fence was successfully used in Belgium, eradicating a separate outbreak of African swine fever, similar to the Czech Republic. According to Mysterud and Rolandsen [52], perimeter fencing minimizes the number of animal crossings, and thus, the probability of spreading diseases. However, a problem arises with this type of fencing because of its impact on nature conservation. Furthermore, it is crucial to highlight that ASF transmission is not only due to direct contact between animals, but also through human interaction. In this case, fencing does not prevent transmission. Moreover, human disruptions can be another source that increases wild boar movement, including home range movement and long-distance dispersal [46,53], and may influence the spread of ASF. Therefore, human visitation to the affected locations, including all recreational activities, was prohibited during the ASF to prevent possible disease transmission from the outbreak in the Czech Republic. This overall restriction of access to the forest was relatively adhered to by women (who constituted only 6.7% of trespassers) compared to men (93.3%). Men and women accounted for 53.6% and 46.4% of the total visitors, respectively. Therefore, the restriction during ASF was not fully observed; consequently, the evaluation of the effectiveness of the ban on entry into the infected area is debatable [54]. The successful control measures in the Czech Republic were most likely due to muffled shootings in the high-risk ASF-outbreak areas with minimal disturbance caused by standard game management. Moreover, ostensibly, leaving attractive crops unharvested provides sufficient cover and food sources and is an effective way to mitigate wild boar movement over longer distances [34]. However, removing the carcasses and disinfecting the habitat are crucial measures in addition to those mentioned above. Altogether, the mitigation of ASF spreading is a complicated discipline made up of individual measures that can only ensure success when in sync. Based on our findings, the installation of odor fences to prevent wild boar movement between zones is not as effective as previously thought [50].

5. Conclusions

Our study investigated the efficacy of odor fences as a barrier to limit wild boar movement, which are used to control the spread of ASF and provide protection against crop damage. Despite previous theoretical support, our analysis of positioning data from GPS telemetry of free-ranging wild boars did not confirm any significant effects on the movement of tagged individuals. Wild boars crossed the odor fence lines with the same frequency after the odor fence installation as before. Moreover, we found no significant changes in their home range sizes or overlaps after the odor fence installation. This suggests that odor fences are ineffective as a short or long-term deterrent for managing wild boar populations and mitigating the spread of ASF.

Our findings concur with the preponderance of other research questioning the effectiveness of various deterrents, such as wildlife warning lights and odor repellents, in reducing wildlife-related conflicts. Although some deterrents may show short-term effects for wild boars, the evidence for these exceptions was not based on GPS telemetry. Thus, patterns describing reasons for deterrent efficiency are still unclear and can be affected by wild boar individuality or previous experience. Given the significant socioeconomic impacts of ASF and the persistent human–wildlife conflicts, exploring alternative, more reliable methods is crucial. Permanent perimeter fencing, intensive surveillance, and strategic hunting practices appear more effective. However, these solutions also negatively affect wildlife, including non-targeted species, which needs to be considered before installation. Therefore, future efforts should focus on developing and testing new deterrent systems that consider the wild boar's natural behavior and movement patterns and effectively address this ongoing issue.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ani14172556/s1.

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5.3 Vliv kadáverů na chování a pohyb prasat divokých

5.3.1 Wild boar carcasses in the center of boar activity: Crucial risks of ASF transmission

Cukor, J., **Faltusová M.**, Vacek Z., Linda R., Skoták V., Václavek P., Ježek M., Šálek M., Havránek F.
* v recenzentním řízení

Primárním cílem této studie bylo zhodnotit atraktivitu kadáverů prasat divokých pro jedince stejného druhu, konkrétně ve srovnání s kontrolními místy, v různých ročních obdobích. Cílem výzkumu bylo pochopit důsledky tohoto chování na přenos afrického moru prasat mezi populacemi prasat divokých. Zjistili jsme, že kadávery prasat divokých jsou výrazně atraktivnější pro volně se krmící divočáky než kontrolní místa, přičemž v místech kadáverů byl zaznamenán mnohem vyšší počet návštěv. Tato vysoká úroveň afinity podtrhuje důležitost odstraňování kadáverů jako zásadního opatření pro kontrolu šíření AMP mezi populacemi prasat divokých. Článek objasňuje dílčí cíl 5.

Wild boar carcasses in the center of boar activity: Crucial risks of ASF transmission

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Abstract
African swine fever (ASF) is a highly virulent disease rapidly spreading through Europe with fatal consequences for wild boar and domestic pigs. Understanding pathogen transmission among individuals and populations is crucial for disease control. However, the carcass attractiveness for free-ranging boars was surprisingly almost unstudied. Here, we evaluated if the wild boar carcasses are perceived as an attractant compared to the control sites throughout the year. For this purpose, 28 wild boar carcasses were placed in seven forest stands and continuously monitored in 2019–2020 by camera traps combined with control locations situated at least 200 m away in comparable habitats. Overall, we have recorded 3602 wild boar visits, from which 3017 (83.8%) were recorded in locations with placed carcasses and 585 (16.2%) in control locations. Most visits were recorded after sunset and before sunrise, corresponding to common peaks of wild boar activity. On average, the first visits were detected 4.7 days after carcass placement. Contrarily, it was 61.5 days for the control site. In conclusion, we have proven an enormous wild boar carcass attractiveness for free-ranging boars, which exhibits an entirely new aspect of wild boar behavior. Therefore, the carcass removal is crucial measure for controlling the spread of ASF.
Keywords
African swine fever, disease control, biosecurity, wild boar behavior, camera-trapping

Introduction

African swine fever (ASF) is a global viral disease affecting wild boar (*Sus scrofa* L.) and domestic pigs (*Sus scrofa domesticus* Erxleben) with a negative socioeconomic impact, especially on the pork industry [1–3]. From 2007, when ASF was detected in Eastern Europe, the virus had rapidly spread to numerous Central and Western European countries, including Germany, Slovakia, Poland, Czech Republic, and Italy [4–6]. Moreover, the ASF is also spreading throughout Asia, including China and other southeastern Asian countries, with a significant negative impact on pork meat production [7,8] Evaluation of ASF outbreak impacts in China assumes a reduction of the pork industry by 9–34% in global production which may lead to an increase in pork prices by 17–85% worldwide [9]. In the worst-case scenario, the global effects of ASF disease on food security can increase the number of humans at risk of hunger by 13–14 million, especially in India and Southeast Asia [10]. Therefore, controlling the spread of ASF in the wild boar population is one of the crucial topics worldwide, not only in Europe. The ASF has a fatal consequence for infected *Suidae* individuals. Infected animals usually die up to ten days after infection, and the mortality rate reaches 90% or even more [11,12]. In the acute-lethal course of ASF, most animals die within 7 to 14 days after infection [4]. However, previous evidence also suggests that some animals may survive longer or completely recover [13], which can lead to a higher risk of infection transmission. The spreading of the ASF virus differs according to conditions in the area of the virus occurrence. The sylvatic cycle, tick-pig cycle, and domestic cycle are described for the sub-Saharan Africa region [14]. However, the situation is unlike Europe, where most outbreaks were found in free-ranging wild boar populations [5,14]. Since 2007, ca. 50,000 cases of ASF have been reported in Europe, and the vast majority (86%) were confirmed in wild boar [15]. Based on differing European climates and environments in comparison to sub-Saharan Africa, the new epidemiologic cycle of wild boar habitat was defined. The wild boar habitat cycle is characterized by direct transmission between infected and susceptible wild boar and indirect transmission through carcasses and contaminated environment [16].

The possible ways of ASF transmission through infected carcasses were described by Probst et al. (2017). The risky behavior of wild boar to infected carcasses consisted of direct contacts especially by sniffing and poking on the carcass and much less by chewing bare bone once skeletonization of the carcasses was complete which was most frequently documented for piglets [17]. Moreover, wild boar cannibalism was initially detected in another study [18]. This behavior represents a very effective way of infection transmission. The risk of ASF transmission through carcasses is significant due to the relatively long-term virus stability. The long-term survival of the virus in the environment depends on several environmental and climatic factors, with temperature as one of the most important [19]. The ASF virus can survive over a year in the blood at 4 °C, several months in boned meat, and several years in frozen carcasses [20,21]. Moreover, ASF virus can persist in contaminated soils where the virus stability depends on the soil type, pH, organic material percentage, and to a lesser extent, the ambient temperature [22,23]. The low temperatures are crucial in the process of overwintering when the virus can persist in the carcass from the autumn through winter with the following risk of cannibalism of infected body mass in spring, which could result in the subsequent ASF outbreaks in the wild boar population [18].

Based on the abovementioned findings, it is evident that the infected carcasses play a critical role in ASF transmission in the wild boar population. Surprisingly, there is still insufficient evidence describing the attractiveness of the wild boar carcass for their fellow boar, which may be a crucial behavioral aspect for setting effective disease control strategies. Therefore, the main aims of this study were to (i) describe the attractiveness of wild boar carcass for free-ranging individuals; (ii) evaluate the sex and age structure of individuals in the location with a carcass and the control site; and (iii) evaluate the effect of daytime and season on visit intensity of the carcass compared to the control site on randomly chosen locations in comparable habitat, which has never been described until now.

Methods

Data acquisition

The research was conducted in seven forest stands in the Czech Republic, Central Europe. The selected sites were previously described by Cukor et al. [18], and this research builds on the data collected during that study by placing additional carcasses on sites in the subsequent seasons. The forests mainly consisted of Norway spruce (*Picea abies* [L.] Karst.) on young forest stands (39 years on average) in altitudes ranging from 358 to 626 m a.s.l. (see Table 1). The study sites have humid continental and oceanic climates, characterized by warm to hot summers and cold winters, and, respectively, by cool summers and mild winters with a relatively narrow annual temperature range [26]. The population density of wild boar is comparable among individual selected sites (Cukor, unpublished data). All of the study sites are located in the Czech Republic, that has one of the highest wild boar population densities (1.15 to 5.31 ind./100 ha) in Central Europe [27].

Table 1. Overview of carcasses and sites included into the study.

Site	GPS	Age class, gender, body weight	Date of exposure	End of monitoring	Forest stand type and altitude
Onomyšl (I)	N 49°55.34427' E 15°6.65680'	piglet ♂ 36 kg	11 JAN 2019	28 APR 2019	*Picea abies* and *Pinus sylvestris*, 30 years; 414 m a.s.l.
		yearling ♂ 48 kg	03 MAY 2019	05 AUG 2019	
		adult ♀ 73 kg	07 AUG 2019	07 NOV 2019	
		piglet ♂ 23 kg	02 NOV 2019	06 FEB 2020	
Kostelec nad Černými lesy (II)	N 49°56.92620' E 14°54.36413'	adult ♀ 74 kg	19 JAN 2019	21 MAY 2019	*Picea abies*, 40 years; 443 m a.s.l..
		adult ♀ 82 kg	03 MAY 2019	06 AUG 2019	
		yearling ♂ 63 kg	30 JUL 2019	08 SEP 2019	
		piglet ♀ 18 kg	13 NOV 2019	04 JAN 2020	
Slapy – Buš (III)	N 49°47.43740' E 14°24.28262'	adult ♂ 68 kg	22 JAN 2019	21 JUN 2019	*Betula pendula*, 20 years; 358 m a.s.l..
		yearling ♂46 kg	11 MAY 2019	13 JUL 2019	
		yearling ♀ 62 kg	6 AUG 2019	XXXXXXX	
		piglet ♀ 20 kg	4 NOV 2019	19 JAN 2020	
Drahany (IV)	N 49°27.01468' E 16°48.58247'	piglet ♂ 43 kg	15 JAN 2019	13 APR 2019	*Picea abies*, 40 years; 614 m a.s.l.
		yearling ♂ 52 kg	10 MAY 2019	05 AUG 2019	
		yearling ♀ 71 kg	02 AUG 2019	23 SEP 2019	
		piglet ♂ 20 kg	01 NOV 2019	18 NOV 2019	
Loket (V)	N 50°11.40495' E 12°46.78647'	piglet ♀ 38 kg	06 FEB 2019	23 MAR 2019	*Picea abies*, 100 years with natural regeneration; 626 m a.s.l.
		adult ♂103 kg	02 MAY 2019	10 AUG 2019	
		piglet ♀ 17 kg	01 AUG 2019	08 SEP 2019	
		piglet ♀ 22 kg	06 NOV 2019	14 DEC 2019	
Podveky (VI)	N 49°50.17067' E 14°59.70358'	piglet ♀ 38 kg	18 JAN 2019	26 MAY 2019	*Picea abies*, 15 years; 452 m a.s.l.
		yearling ♀ 55 kg	01 MAY 2019	01 AUG 2019	
		yearling ♂ 53 kg	29 JUL 2019	30 OCT 2019	
		piglet ♂ 19 kg	30 SEP 2019	30 DEC 2019	
Zalíbená (VII)	N 49°48.88495' E 14°58.77662'	piglet ♂ 45 kg	18 JAN 2019	02 MAY 2019	*Picea abies*, 30 years; 418 m a.s.l.
		yearling ♂ 57 kg	06 MAY 2019	09 JUN 2019	
		yearling ♀ 52 kg	01 JUL 2019	29 SEP 2019	
		yearling ♀ 56 kg	03 OCT 2019	28 DEC 2019	

Note: The camera trap was stolen in the case of location III. (Autumn season).

The individual studied forest stands were preselected before the study in the GIS environment according to the age of young forest stands where the infected carcasses were primarily found in the Czech outbreak in 2017. The young forest stands consisted mainly of coniferous tree species that were chosen according to previous research, which confirmed a significant preference for coniferous younger than 40 years as deathbed choices for ASF-infected animals [24]. Similar results were confirmed also by a recent study in Lithuania, where infected wild boars sought shelter in quiet areas [25]. Again, that corresponds to conditions of young coniferous stands, and therefore, this is very similar to the deathbed choice of ASF-infected individuals in the real outbreak. For the carcass attractiveness evaluation, seven wild boar carcasses were placed in seven preselected sites during every season (winter, spring, summer, and autumn) during the monitored study period from January 2019 to February 2020. The control location was randomly selected in the same forest stands and comparable environmental conditions (e.g., altitude, tree species composition, local and landscape habitat structure and vegetation cover) at 200 meters from the carcass, and were placed in the field at the same time as the cameras which monitored the carcasses. To ensure comparable, slower decomposition of the carcasses, all wild boar were hunted and killed by a single head shot following Czech legislative regulations. The carcass data, such as sex, age class, weight, and placement date, are listed in Table 1.

The wild boar presence and activity on study and control sites were monitored by camera traps UOVision UV 595 HD with a resolution of 12 megapixels, HD video (1080 P), and trigger speed of 0.65 (www.uovision.com). The game cameras were installed on a selected tree at a distance of 4 to 8 meters from the carcass. Cameras were set in video mode with automatic recording of the date and time of the wild boar visit. The video length was set to 30 seconds with a window of 1 minute between recordings. The carcasses and cameras were inspected every two weeks to check the carcass status and battery charge. The monitoring was completed when all edible biomass of the carcass was consumed or removed by scavengers or wild boar, and no evidence of the carcass was on the monitored plots. All video sequences with wild boar presence were analyzed from the aspect of number, sex, and approximate age of individuals (i.e., adult male, adult female, unspecified adult, subadult, and piglet). For each recording, we evaluated additional parameters such as duration of carcass setting (in days), and time duration from sunrise and sunset. Sunrise and sunset data were obtained from the web source Sunrise Sunset (https://api.sunrise-sunset.org/) for each location.

Statistical analyses

The analyses were separated into four parts: analysis of the number of wild boar recordings, sex-age proportion analysis, wild boar detection time analysis, and analysis of the time span before the first contact with the carcass.

Regarding the analysis of the number of wild boar recordings, basic summary statistics were computed to provide a general overview of collected data. Subsequently, analysis of detected individuals for each study location and season was conducted, and these data were statistically compared between locations where the carcass was placed in comparison to control locations using paired-sample Wilcoxon rank-sum test (non-parametric statistics were selected because the assumption of normality, tested by the Shapiro-Wilk test was violated).

To test the dependence of sex-age categories and numbers of detected wild boar in the location with the carcass and the control location, we used the chi-squared test separately for each season.

The times of wild boar detections were analyzed in relation to sunrise and sunset on the current day. For each recording, the time difference from sunrise/sunset was computed (depending on which was closer to the time of detection), and those values were compared between locations with carcass and control in every season. For such comparison, the Wilcoxon rank-sum test was used separately for each season (the assumption of data normality, tested by the Shapiro-Wilk test, was violated in some cases). We have also statistically tested for difference variance between locations with the carcass and control locations using the Levene test. The time of recording relating to sunrise/sunset was also analyzed via circular statistics. Besides the visual representation of the numbers of detected wild boar in the carcass and control locations, we have specifically tested for "uniformity" of observations via the Rayleigh Test and for the differences between the time of detection of individuals in relation to sunrise/sunset for the carcass and control locations via the Watson-Williams Test. We have divided time data into an hour scale for this analysis.

Lastly, the analysis of the time duration in days from carcass and photo-trap setting to the first recorded activity of wild boar was performed. Besides basic statistics and graphical representation of data, the paired-sample Wilcoxon rank-sum test was used for testing for differences between carcass and control locations.

All statistical procedures were performed using R software at a confidence level alpha = 0.05.

Results

The overall comparison of numbers of wild boar visits in the carcass and control locations showed significant results (data for each study area in each season were compared; paired-sample Wilcoxon rank-sum test, $V = 5.5$, $p < 0.001$; Fig. 1). In particular, the number of recordings of wild boar in locations with a carcass (3017 records) were 5.2 higher than on control locations (585 records), which suggest an extreme level of attractiveness of wild boar to the carcass. Similarly, we found significant differences for individual seasons (spring: 1248 vs. 247, summer: 642 vs. 96, autumn: 541 vs. 75, winter: 586 vs. 167 recordings for the location with a carcass and control location, respectively; see Fig. 1).

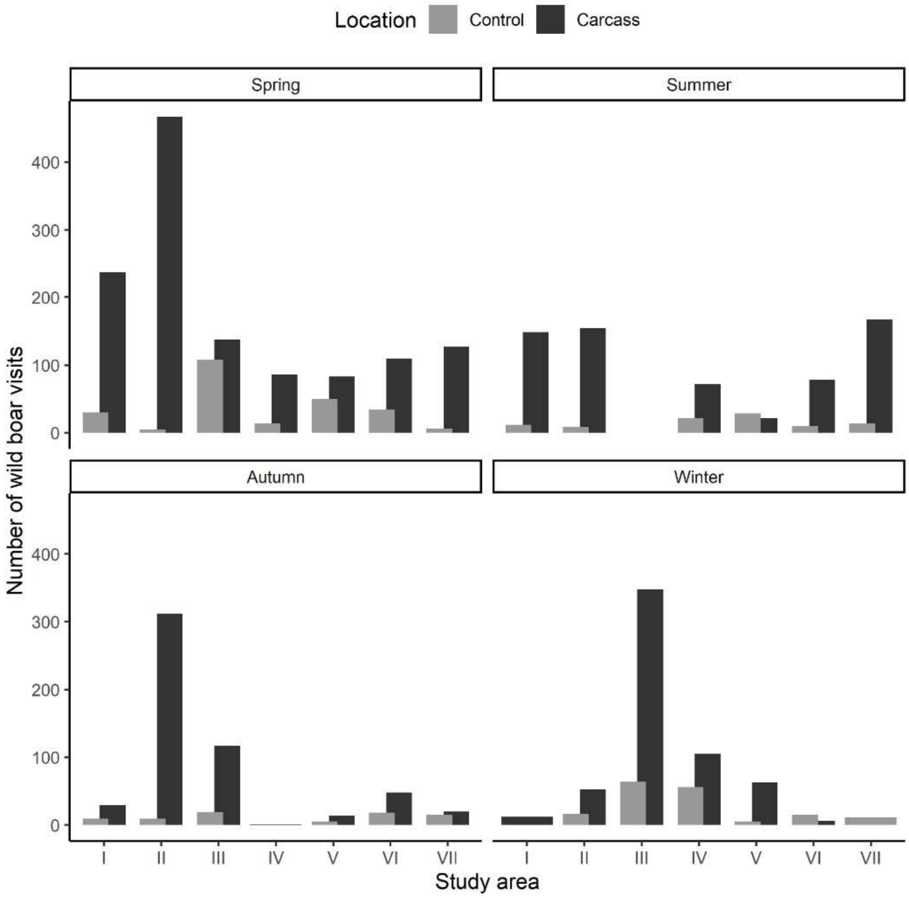

Fig. 1—Number of detected wild boar in particular study locations (I–VII) with a carcass and control sites in different seasons.

From the total of 3602 detected wild boar, we were able to determine the age of individuals in the case of adults, as well as the sex for 3437 individuals (95%). The other 165 individuals were recognized as adults without further sex specification (5%). The most frequent category was piglets, with 1817 recordings (50%), followed by subadults (942 recordings, 26%), adult females (509 individuals, 14%), and adult males (169 individuals, 5%). The chi-squared test used for testing independence between numbers of individuals in defined sex-age categories detected in the carcass and control locations was performed separately for each season. Except for autumn, we found ratio significant differences between the number of individuals observed in the location with the carcass and control location between sex-age categories for each season ($p < 0.001$).

In spring, only 8% (17 individuals) of all detected subadults were identified at the control location, and other individuals (203 individuals) were recorded close to the carcass. For additional sex-age categories, the difference was not as pronounced: adult females (31 individuals, i.e., 13% at the control location, 203 individuals at the location with a carcass), piglets (173 individuals, i.e., 19% at the control location, 730 individuals at the location with a carcass), and adult males (13 individuals, i.e., 24% at the control location, 41 individuals at the location with a carcass). The overall chi-squared test showed significant results (chi-squared = 20.87, df = 3, $p < 0.001$).

A similar trend was observed in the summer: only 5% of subadults were observed at the control locations (7 vs. 141 individuals at the location with a carcass), followed by adult females (11 vs. 106 individuals, 9%), piglets (66 vs. 362 individuals, 15%), and adult males (10 vs. 21 individuals, 32%) as in the previous example. The overall chi-squared test also showed significant results (chi-squared = 22.70, df = 3, $p < 0.001$).

No significant differences in ratios of detected individuals divided by sex-age categories and location of detection were found in the autumn. The numbers of individuals detected at control locations were as follows: 10% for subadults (21 vs. 217 individuals), 8% for adult females (7 vs. 77 individuals), 12% for adult males (5 vs. 36 individuals), and 15% for piglets (32 vs. 177 individuals). The overall chi-squared test showed insignificant results (chi-squared = 5.55, df = 3, p = 0.14).

In winter, the ratios of detected individuals at the control locations were higher than in other seasons. The lowest ratio was found for piglets (15%, 41 vs. 236 individuals), followed by subadults (26%, 86 vs. 250 individuals, adult females (32%, 24 vs. 50 individuals), and adult males (33%, 14 vs. 29 individuals). The overall chi-squared test showed significant results (chi-squared = 17.88, df = 3, $p < 0.001$).

For a graphical depiction of sex-age category composition in each season, see Fig. 2.

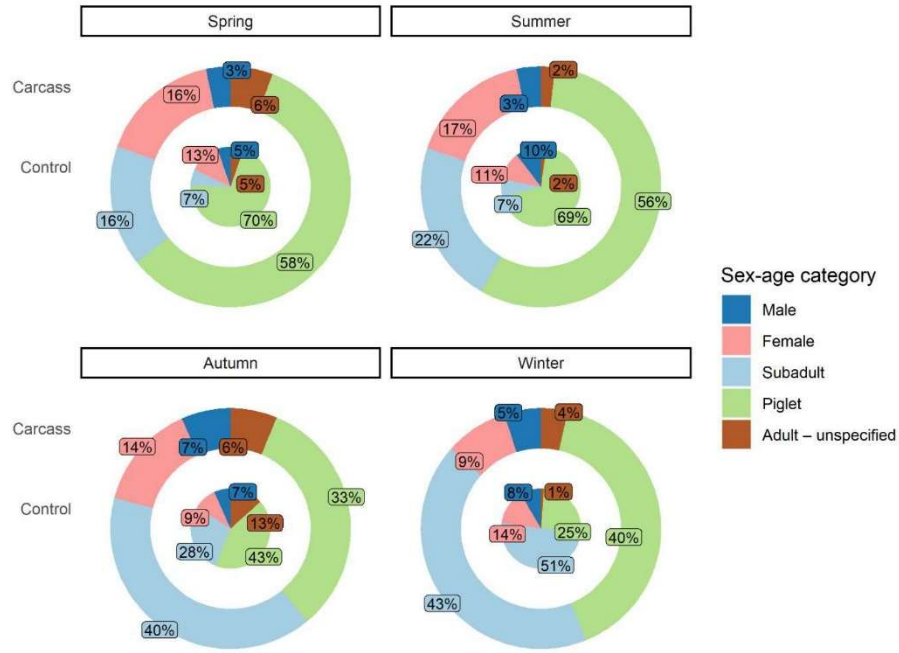

Fig. 2—The proportion of sex-age categories in locations with a carcass and control locations for different seasons. The outer circle shows the sex-age categories in a location with a carcass, and the inner circle represents the control location.

Regarding the time of wild boar recordings, we analyzed the recorded time difference to sunrise/sunset to eliminate the effect of the day length in different seasons.

For sunrise, the only season for which significant differences between the median time of recordings at the location with a carcass and control location was spring, where recordings at the carcass location were obtained sooner before sunrise (mean: 1.49 hours before sunrise for the carcass location and 0.88 hours before sunrise for the control location, p = 0.006). Comparisons for other seasons were not significant. Obtained p-values are as follows: summer—p = 0.61, autumn—p = 0.24, winter—p = 0.12. Mean difference values from sunrise in hours are negative in all cases, i.e., the majority of wild boar were recorded before sunrise. The mean hour differences for seasons with insignificant differences are as follows: summer—3.18 hours before sunrise for the location with a carcass, 2.67 hours before sunrise for control locations, autumn—4.60 and 4.18 hours, and winter—2.31 and 2.04 hours.

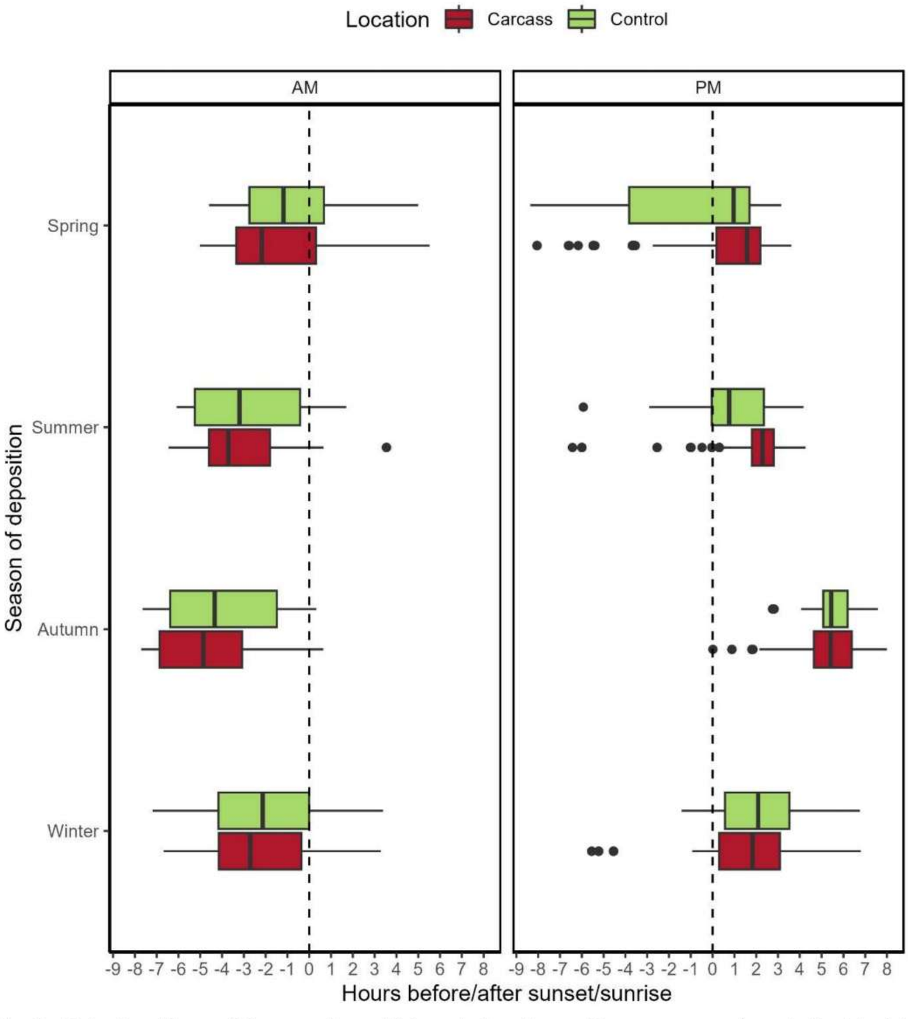

Fig. 3—Detection times of free-ranging wild boar in locations with a carcass and control related to sunset/sunrise. Sunset/sunrise is depicted by a dashed line in the plot. The plot is divided into two parts—AM, for sunrise, and PM, for sunset. The dots indicate outliers for respective variants. In the case of the time difference of recordings from sunset, significant differences were observed in spring

and summer ($p < 0.001$ in both cases, and the recordings for the location with the carcass were both observed later). The mean values of time difference to sunset for individual seasons are as follows: spring—0.85 hours after sunset for the location with a carcass and 1.10 hours before sunset for the control location, summer—1.98 and 0.90 hours after sunset, autumn—5.43 and 5.60 hours after sunset and winter—1.70 and 2.16 hours.

We have also tested variations between the wild boar recording to sunrise/sunset for the location with the carcass and control location. For the sunrise, significant differences were observed in all cases, except for spring—p-values: spring—$p = 0.74$, summer—$p < 0.001$, autumn—$p = 0.03$, and winter—$p = 0.005$. The variation was always higher at the control locations for significant results. For the sunset data, the results were the opposite, the only significant result was obtained for spring ($p < 0.001$, variation for the control location was again higher). Other p-values are as follows: summer—$p = 0.25$, autumn—$p = 0.24$, and winter—$p = 0.78$). For a graphical depiction of the results, see Fig. 3.

In addition, circular statistics analyses showed that the distribution of wild boar recording times is not uniform (see Fig. 4). Watson tests for the location with the carcass and control location separately for sunrise/sunset (for all seasons combined) showed significant differences in all cases ($p < 0.01$), similarly as a comparison of time difference between locations with a carcass and control locations for all seasons combined ($p < 0.001$ for both sunrise and sunset).

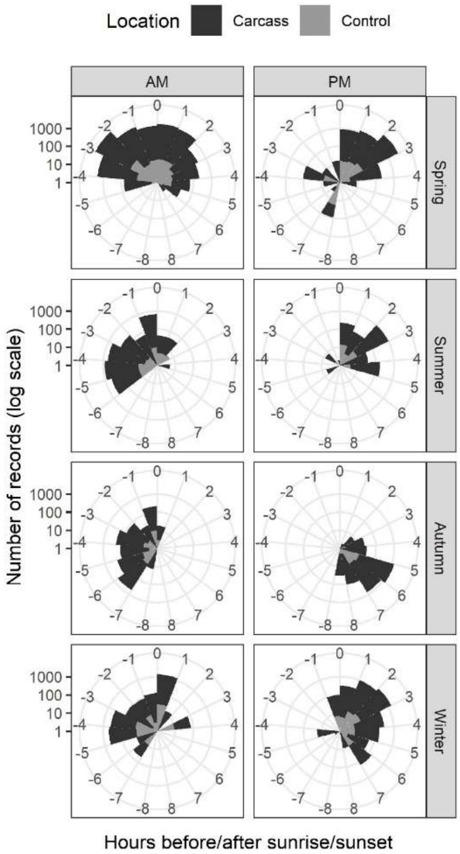

Fig. 4—Circular plots for the location with the carcass and control location. Y axis is represented on log-scale due to significant differences between the number of recordings for the location with the carcass and control location.

The analysis of the time of the first visit to the carcass showed that wild boar found the carcass in a relatively short time (Fig. 5). The average values were around 2 days in spring and summer, around 6 days in autumn, and 8 days in winter. Also, during spring and summer, the maximum recorded times to find the dead body were 7 and 5 days in particular locations. In autumn, the maximum days needed to find the dead body were 19 days, and in winter, up to 36 days. Nevertheless, in all seasons, some cases when wild boar were able to find the dead body on the same day it was placed were observed. The comparison of days between the date of carcass setting and the first recording of wild boar activity showed significant results (Wilcoxon paired-sample test, $p = 0.03$). On control locations, the first wild boar detection was found after a much longer period compared to locations with the carcass (spring—2.6 days on average for the carcass location vs. 61 days on average for control locations, summer—2 vs. 69 days, autumn—5.7 vs. 104 days, and winter—8.4 vs. 11.8 days), although very high variance was observed for all seasons. Minimum values for control locations were 0 days for winter and 4 days for spring, while maximal values were 36 days for winter, followed by 128 days for spring, 207 days for summer, and 275 days for autumn. The average values through the year were 4.7 days to the first visit to the carcass location and 61.5 for the control.

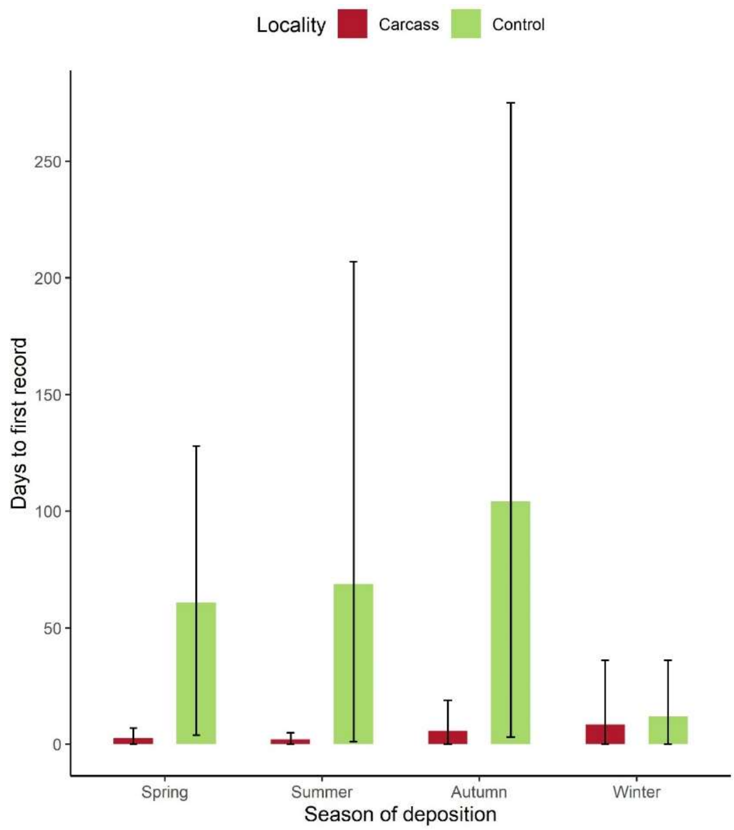

Fig. 5—Number of days to the first recording of wild boar activity on control locations and locations with the carcass. Bars stand for mean values, whiskers for min and max values for each season, and location type.

Discussion

African swine fever transmission is driven by several factors that are changing across the geographic conditions where the virus is present, both in wild boar and domestic pigs' populations [12]. In Europe, it seems that the infected carcasses play the most crucial role in transmission [24,28–30] besides the human factor, which transports the virus long distances, for hundreds of kilometers, mostly through pork products [31]. Therefore, it is necessary to understand all aspects of wild boar behavior toward the carcasses of its own species, about which we still have limited information. However, the data on carcass attractiveness can be compared only with general knowledge of wild boar activity within the home range because carcass attractiveness to live wild boars has not been studied until now. One of the main ways to compare and express carcass attractiveness is by comparing the number of wild boar visits to the control location in comparable conditions, which was over five times higher throughout the year. Based on those findings, it is apparent that the carcass is perceived by wild boar as an attractant. The highest difference in the number of visits was found in the spring and summer seasons. During the warmer period, the wild boar activity around the carcass was greater compared to the control location. This can be explained by the rapid carcass decomposition by scavenging insects, which is followed by a strong odor of decaying carcasses [32] and therefore, carcasses could be more easily detected.

In general, we have detected 3602 wild boar visits for carcass and control locations combined, from which the sex and age could be determined in 95% of the visits. Not surprisingly, piglets were detected in most of the cases, which corresponds to normal wild boar population structure and high litter size per adult female [33]. In our case, the proportion of piglet detection exceeded 50% of recordings in the spring and summer periods in the carcass location, with a decreasing tendency for autumn and winter. A similar trend was also found in the control locations. It can be explained by hunting pressure followed by decreasing piglet proportion through the season. Moreover, wild boar has enough fodder opportunities in a fragmented landscape of high-energy crops throughout most of the year [34,35], and therefore, the body mass and appearance soon resemble subadults more than piglets. From the ASF transmission point of view, it is important to highlight that there is an explicit assumption that the individuals, due to the fluctuating age distribution, are from different groups and simultaneously visited the same carcass. These facts allow us to observe how quickly ASF can spread during out-group interactions.

The time of detected wild boar activity was another aspect of behavior that was analyzed. In common circumstances, the diurnal activity usually involves movement between resting areas and feeding sites (Boitani et al., 1994). The highest proportion of wild boar active behavior occurs around midnight and morning hours (Johann et al., 2020; Cukor et al., 2021). In this study, the wild boar activity was recorded especially close to sunset/sunrise during most of the year. The earliest visits after sunset were found in spring, when the decomposition process is relatively fast, which is characterized by a strong odor (Probst et al. 2020;mentioned earlier).

The greatest differences between the location with the carcass compared to the control site were found at the time of the first wild boar recording on the camera trap. On average, the first wild boar was detected after 4.7 days in the carcass location and after 61.5 days in the control site, with the highest average difference found in autumn (5.7 vs. 104 days). The number of recordings between the carcass and control locations could be caused by variations in wild boar population density throughout locations and by the home range size changes. Wild boar shows remarkable intraspecific variations in home ranges across various habitats. Annual home range size varies between 400 ha to 6000 ha, with an average size of around 800 ha [39,40]. The larger home range sizes were confirmed in the autumn and winter periods [41], which is influenced by several factors, e.g., by the rut season where the wild boar has higher daily home range sizes compared to the rest of the year [42]. Another aspect can be the rebalance caused by the autumn hunting season, which also affects the home range size and the wild boar activity and space use [43]. Moreover, the habitat preference of free-ranging wild boar is driven by food source availability. In the late summer, the standard behavior patterns and habitat utilization of wild boar can be disrupted and changed by the crop harvest. In forested areas, the habitat preference is affected by oak species *Quercus* spp. and European beech *Fagus sylvatica* L., especially in the mast years of the aforementioned deciduous trees [33,34,44]. This means that if the wild boar's basic life needs are satisfied, it does not make much sense for them to move over greater distances. On the contrary, most of the carcass and control sites in our study were in Norway spruce forests without any natural food availability for wild boar, which may explain the later visits after sunset during autumn. It was previously proven that in poor nutritional conditions, wild boars move more in search of food and water, increasing their home range [42,45]. Moreover, wild boar behavior and the time of the carcass visits can be significantly affected by supplementary feeding provided by hunters. The space use is influenced by the location of feeding sites. The amount of supplemental food can be approximately 1000 kg per year per 100 ha in particular locations, and the feeding is targeted primarily in the autumn and winter periods [39].

Therefore, it appears that the high risk of ASF transmission through infected carcasses is prevalent throughout the year. The potential ASF transmission is affected by subsequent wild boar movement after contact with the infected carcass. The daily distances traveled by wild boar are usually between 10 to 20 km [40,46,47]. However, if the area lacks suitable food sources, the wild boar is forced to increase the distances traveled, which increases the risk of spreading ASF. On the other hand, if there is sufficient food, water, and shelter, most young wild boar (70–80%) do not disperse further than 5 km from their natal ranges [48,49]. Young animals, adult males, and adult females with offspring occasionally move long distances of 50–250 km in a straight line in rare situations [48,49], and in this example, wild boar can walk 30–40 km within 24 hours and 200–300 km in 10–15 days [47].

Conclusion

Thus far, it has not been determined whether the wild boar carcasses are visited purposefully or whether they are visited as part of the habitual movement of wild boar in the location. The answer to this question is made clear by the conclusions presented in this study, which confirmed the immense attractiveness of the carcass for the wild boar population across the seasons. The results described an entirely new aspect of wild boar behavior, which was unknown until now. Based on the visit differences between locations with the carcass and the control in a comparable habitat, it is evident how attractive the wild boar carcass is to their own species, which has confirmed a critical role in the ASF transmission. Our results confirm important implications for the understanding of ASF spreading among individuals of wild boar populations. We clearly demonstrated that carcasses of wild boars are highly attractive for free-ranging wild boars during the different seasons, which pose a high risk of ASF transmission throughout the year. Therefore, there is an urgent need for early detection and removal of infected carcasses from the environment, followed by microhabitat disinfection.

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6 Diskuse

Chování prasat divokých ve vztahu k lidem je v posledních letech předmětem intenzivního výzkumu, zejména kvůli rostoucímu zájmu o vliv člověka na přírodu a šíření chorob, jako je AMP. Zatímco populace prasat divokých v Evropě nadále roste, zvyšuje se riziko střetu s lidskými aktivitami, a to jak v zemědělských oblastech, tak v přírodních rezervacích a městských parcích (Cukor et al., 2021; Faltusová et al., 2024a; Olejarz et al., 2023). Jedním z hlavních problémů spojených s rostoucí populací prasat divokých je právě jejich vysoká adaptabilita na lidské prostředí (Keuling et al., 2008a; Podgórski et al., 2013; Rutz et al., 2020; Venter et al., 2020).

6.1 Vliv lidských aktivit na chování a pohyb prasat divokých

Naše studie poskytují pohled na vztahy mezi lidskými aktivitami a chováním prasat divokých, zejména v souvislosti s globálními událostmi, jako jsou pandemie COVID-19 a vypuknutí AMP. Výsledky ukazují, že přestože prasata divoká vykazují vysokou schopnost adaptace na různé formy lidského narušení, dopady lidské činnosti na jejich fyziologii a chování jsou vícevrstevné a komplexní (Cukor et al., 2021; Faltusová et al., 2024a; Olejarz et al., 2023). Tři sledované situace (zvýšená lidská aktivita během pandemie, standardní podmínky a restrikce během AMP) ukazují, že lidská přítomnost ovlivňuje různé aspekty chování divokých zvířat (Cukor et al., 2021). Přestože jsou divoká prasata schopna udržet své prostorové chování relativně stabilní i v prostředí s intenzivní lidskou aktivitou, toto přizpůsobení s sebou nese fyziologické náklady, jako je vyšší energetická spotřeba a narušení spánkových cyklů (Mortlock et al., 2024; Olejarz et al., 2023). Tyto výsledky jsou důležité zejména z hlediska dlouhodobé udržitelnosti populací prasat divokých a jejich vlivu na ekosystémy.

V průběhu pandemie COVID-19 došlo k výraznému zvýšení návštěvnosti lesů a jiných příměstských přírodních oblastí. Tento fenomén, známý jako „anthropulse“, představoval pro prasata divoká nový typ lidského tlaku, protože množství návštěvníků během období pandemických omezení dosáhlo v některých oblastech několikanásobného nárůstu ve srovnání s předchozími lety (Cukor et al., 2021; Rutz et al., 2020). Zvýšená návštěvnost lesů a parků, kdy lidé využívali přírodu jako jedinou formu rekreace, měla negativní vliv na zvířata, která se musela znovu přizpůsobit lidské přítomnosti (Coman et al., 2022). Naše studie ukazují, že prasata divoká vykazují vysokou toleranci k lidskému narušení (Faltusová et al., 2024a), a to i během období zvýšené lidské aktivity jako je pandemie COVID-19 (Olejarz et al., 2023), kdy nedošlo k výrazným změnám v pohybových vzorcích prasat, jako je velikost domovského okrsku, celkově ušlá vzdálenost či denní pohybové rytmy. Tyto výsledky jsou v souladu s předchozími studiemi, které naznačují, že prasata divoká jsou schopna přizpůsobit své chování tak, aby minimalizovala kontakt s lidmi, například tím, že se vyhýbají oblastem s vysokou návštěvností, nebo přesunem své aktivity do nočních hodin (Boitani et al., 2007; Morelle et al., 2013).

Navzdory této schopnosti zachovat své prostorové chování bylo v našich datech zaznamenáno významné zvýšení energetického výdeje prasat divokých během období intenzivní lidské přítomnosti, a to především kvůli častějšímu přerušování jejich odpočinku a spánku. Zvýšená energetická náročnost spojená s adaptací na lidskou přítomnost je důležitým faktorem, který může mít vážné důsledky pro populaci prasat divokých (Olejarz et al., 2023). Fragmentace spánku, která se projevila kratšími a více přerušovanými spánkovými epizodami, může mít negativní důsledky pro celkovou fyziologickou kondici zvířat, což může dále ovlivnit jejich reprodukční úspěšnost, schopnost vyhýbat se predátorům a odolnost vůči stresovým faktorům (Bieber & Ruf, 2005; Keuling et al., 2008b; Mortlock et al., 2024). Tyto změny, i když jemné a na první pohled nepatrné, mající kumulativní účinek, mohou vést k významným dopadům na dlouhodobé přežití populací v oblastech s vysokým stupněm lidského narušení, zejména pokud se jedná o příměstské a rekreačně využívané lesy (Olejarz et al., 2023).

Kromě fyziologických důsledků je třeba zohlednit i sezónní vlivy na chování prasat divokých. Naše analýzy odhalily sezónní variace v reakcích na lidské aktivity, přičemž například podzim vykazoval zvýšenou pohybovou aktivitu ve srovnání s ostatními ročními obdobími (Cukor et al., 2021). Toto zjištění je v souladu s dřívějšími studiemi, které ukázaly, že sezónní změny, jako jsou dostupnost potravy, teplotní podmínky a reprodukční cykly, mohou významně ovlivnit chování zvířat v přírodě (Bronson, 2009; Keuling et al., 2008a; Podgórski et al., 2013). Tyto sezónní variace jsou také důležité při plánování zásahů v oblastech postižených AMP, kde může být zvýšená pohybová aktivita spojená s vyšším rizikem šíření této vysoce nakažlivé nemoci. Narušení přirozených pohybových vzorců prasat divokých lidskou činností může vést k většímu šíření AMP, což dále zdůrazňuje důležitost správného řízení lidských aktivit v zasažených oblastech.

AMP je stále jedním z hlavních faktorů ovlivňujících populace prasat divokých v Evropě. Naše studie potvrzují, že lidská aktivita hraje roli v šíření této nemoci, zejména prostřednictvím narušení přirozených behaviorálních vzorců (Cukor et al., 2021; Faltusová et al., 2024a; Olejarz et al., 2023). V oblastech postižených AMP byla zaznamenána vysoká mortalita prasat divokých, přičemž lidské aktivity, jako jsou lesnické práce, turistika nebo volný pohyb psů, mohou přispívat k pohybu a šíření nakažených jedinců (Cukor et al., 2021; Faltusová et al., 2024a; Gervasi et al., 2022; Guberti et al., 2022). Opatření jako zákazy vstupu do zasažených oblastí, zavádění pachových nebo fyzických zábran a intenzivní odchyt zvířat se ukázaly jako efektivní strategie pro minimalizaci šíření AMP (Jori et al., 2021; More et al., 2018). Nicméně, naše studie naznačuje, že přísná omezení lidské aktivity nejsou vždy nezbytná, pokud jsou dodržována základní pravidla pro omezení na vyhrazené lesní cesty (Cukor et al., 2021), což potvrzuje dřívější výzkum o minimalizaci kontaktu mezi lidmi a divokými zvířaty (Griffin et al., 2022).

6.2 Vliv umístění plotů na pohyb prasat divokých

Jedním z navrhovaných řešení pro prevenci šíření AMP je zavedení pachových plotů, které by omezily pohyb prasat divokých přes infikované oblasti. Naše studie ukázala, že instalace pachových plotů neměla v testovaných oblastech žádný signifikantní vliv na pohyb či velikost jejich domovských okrsků. Prasata divoká přecházela přes linie pachových plotů stejně často před i po jejich instalaci. Tento výsledek zpochybňuje efektivitu pachových plotů jako krátkodobého či dlouhodobého opatření pro řízení populace prasat divokých nebo pro ochranu zemědělských plodin, což je v souladu s dalšími studiemi, které zpochybňují účinnost různých pachových odpuzovačů (Faltusová et al., 2024b). Podobné závěry o neefektivitě pachových odpuzovačů uvádí i Bíl, et al. (2018), kteří zjistili, že pachové ploty neměly žádný statisticky významný efekt na snížení počtu kolizí se zvěří na silnicích. Stejně tak Elmeros et al. (2011) ve své studii zaměřené na jelenovité zjistili, že pachové ploty měly jen velmi omezený účinek a nepřispěly ke snížení poškození plodin. Schlageter & Haag-Wackernagel (2012) zhodnotili použití pachových odpuzovačů k ochraně plodin a zjistili, že účinnost těchto opatření je omezená, protože prasata se na pachy rychle adaptují, a nakonec se naučí bariéry ignorovat nebo obcházet.

Zavádění pachových plotů, zejména v oblasti ochrany proti šíření AMP, se ukázalo jako nedostatečné (Faltusová et al., 2024b). Navzdory této omezené účinnosti pachových plotů existuje celá řada dalších opatření, která mohou být zavedena, aby se šíření AMP zabránilo. Ve většině evropských zemí zavedena opatření zahrnující aktivní snižování populace prasat divokých a zvýšenou biologickou bezpečnost (Palencia et al., 2023). Trvalé oplocení, jak bylo úspěšně použito v Belgii a České republice, bylo prokázáno jako účinné řešení pro zabránění šíření AMP (Mysterud & Rolandsen, 2019). Je však doporučováno, aby se více pozornosti věnovalo aktivnímu řízení populace prasat divokých a monitoringu jejich pohybu, což může přinést lepší výsledky než pouhé zavádění pasivních opatření (European Food Safety Authority, 2014; More et al., 2018).

6.3 Vliv kadáverů na chování a pohyb prasat divokých

(Probst et al., 2017) zjistili, že prasata divoká vykazují kanibalistické chování, což významně zvyšuje riziko šíření AMP. Kontakt s mrtvými těly infikovaných prasat představuje zásadní riziko, protože virus je schopen přežít v tělech uhynulých zvířat po mnoho měsíců, zejména v chladném prostředí. Chenais et al. (2019) a Liu et al. (2021) dodávají, že tento virus je schopen přežívat i ve velmi nepříznivých podmínkách, po mnoho měsíců, zejména při nízkých teplotách, což vytváří trvalé ohnisko infekce v zamořených oblastech a značně komplikuje snahy o jeho eradikaci. Z výsledků naší studie vyplývá, že kadávery prasat divokých opravdu hrají klíčovou roli v šíření AMP. Přítomnost uhynulých jedinců zvyšuje riziko šíření viru díky výrazné atraktivitě kadáverů pro živé jedince, kteří je opakovaně navštěvují (Cukor et al., v recenzentním řízení).

Blome et al. (2013) uvádějí, že AMP se šíří přímým kontaktem mezi infikovanými jedinci, ale i prostřednictvím kontaminovaných materiálů, včetně tělesných tekutin a uhynulých těl. Potvrzení o významné afinitě kadáverů přináší také studie Morelle et al. (2019), která zmiňuje, že nalezení uhynulých prasat nakažených AMP je zásadní pro kontrolu šíření infekce. Bylo prokázáno, že kadávery jsou pro prasata významným lákadlem, přičemž počet návštěv na lokalitách s kadávery byl několikanásobně vyšší než na kontrolních lokalitách (Cukor et al., v recenzentním řízení). Tento behaviorální rys zvyšuje riziko přenosu infekce v oblastech s vysokou hustotou prasat, zejména tam, kde je nedostatek potravy a prasata jsou nucena konzumovat ostatní uhynulé jedince (Probst et al., 2017).

Kanibalismus byl pozorován ve všech ročních obdobích, což potvrzuje konstantní riziko šíření AMP v průběhu celého roku. Nicméně naše data dále naznačují, že největší aktivita divočáků okolo kadáverů byla zaznamenána v jarním a letním období, kdy proces rozkladu kadáverů, zejména vlivem vysokých teplot a činnosti mrchožravců, generuje silné pachy (Cukor et al., v recenzentním řízení). Tento jev je v souladu se zjištěními Probst et al. (2017), kteří uvedli, že divočáci vykazují vysokou míru zájmu o kadávery díky silnému zápachu, zejména v teplejších měsících. Naopak během zimy se prasata divoká ke kadáverům dostávají později, což souvisí s pomalejším procesem rozkladu při nízkých teplotách.

Z praktického hlediska naše výsledky potvrzují, že včasná detekce a odstranění kadaverů představují důležité faktory v prevenci šíření AMP (Cukor et al., v recenzentním řízení). Je nutné ale dodat, že Blome et al. (2020) a Liu et al. (2021) zjistili, že virus může přežívat v kontaminovaných materiálech, jako je vegetace, půda a tělesné tekutiny, po několik měsíců. Tento fakt značně ztěžuje kontrolu šíření AMP, protože zamořené oblasti mohou představovat riziko nákazy i dlouho po odstranění infikovaných jedinců. Je tedy zřejmé, že pasivní opatření nejsou dostatečná a měla by být doplněna aktivními kroky, včetně monitoringu populace prasat divokých a managementu kadáverů. Tyto poznatky mohou sloužit jako základ pro formulaci efektivnějších strategií boje proti šíření AMP (Cukor et al., v recenzentním řízení). Zmíněné skutečnosti podtrhují potřebu komplexních preventivních opatření zaměřených na omezení pohybu prasat diokvých mezi infikovanými oblastmi.

7 Závěr

Bylo identifikováno několik klíčových faktorů, které přispívají k šíření AMP mezi divokými a domácími prasaty. Důraz by měl být kladen na zlepšení biologické bezpečnosti v oblastech, kde dochází ke kontaktu mezi domácími a divokými prasaty. Polaček et al. (2021) a Viltrop et al. (2022) upozorňují na neefektivní opatření v oblasti biologické bezpečnosti, což je významný rizikový faktor jak u divokých zvířat, tak na farmách. Nedostatečná biologická bezpečnost v těchto zónách zvyšuje riziko přenosu AMP. Proto je nutné zavést přísnější opatření v těchto oblastech. I přes přísné regulace Evropské unie se stále objevují mezery v aplikaci těchto opatření, zejména právě v oblastech, kde dochází ke kontaktu mezi divokými a domácími zvířaty.

Aktivní monitorování prasat divokých je zásadní nejen pro prevenci šíření AMP, ale také pro řízení populací prasat divokých, což se stává jednou z hlavních strategií v boji proti AMP. Bollen et al. (2021) doporučují využívání technologií, jako jsou fotopasti, které umožňují sledování pohybu prasat v rizikových oblastech. Tím se zvyšuje schopnost rychle reagovat na přítomnost viru a přijmout nezbytná opatření. Dále lze využít GPS sledování jako účinný nástroj pro lepší porozumění prostorovému chování prasat a identifikaci míst, kde může dojít k přenosu viru. V oblastech s vysokým výskytem AMP je zavedení systematického monitorování nezbytné, aby bylo možné rychle reagovat a zabránit dalšímu šíření nákazy.

Kromě lidských aktivit a preventivních opatření proti šíření afrického moru prasat je důležité zohlednit také vliv klimatických změn. Liu et al. (2021) poukazují na to, že mírnější zimy v důsledku globálního oteplování mohou prodloužit dobu přežití viru v prostředí, což zvyšuje riziko jeho šíření Guberti et al. (2022) dále zdůrazňují, že klimatické změny podporující růst populace prasat divokých zvyšují pravděpodobnost, že virus přetrvá v ekosystémech déle a bude se šířit mezi různými druhy prasat.

Dalším faktorem, který komplikuje kontrolu nad šířením AMP, je chování prasat divokých v blízkosti lidských sídel. Zde již nemluvíme o aktivním lidském přičinění, ale i pasivní lidská činnost má vliv na šíření AMP. Beasley et al. (2018) a Cahill et al. (2012) zjistili, že dostupnost potravy, včetně odpadu a nezabezpečeného jídla v blízkosti lidských sídel, vede ke zvyšování populace prasat divokých, čímž se zvyšuje riziko šíření virových infekcí. Probst et al. (2017) navíc zjistili, že prasata divoká se často pohybují v blízkosti cest a odpočívadel, kde mohou konzumovat antropogenní odpad, což zvyšuje riziko přenosu viru z kontaminovaných potravin. Podobné závěry uvádějí i Taylor et al. (2020), kteří identifikovali odpad v blízkosti lidských sídel jako významný faktor přispívající k šíření AMP. Z těchto důvodů je zásadní zavést přísnější kontrolu nad odpadem v oblastech, kde se pohybují prasata divoká, aby se snížilo riziko nákazy. Zjištění o šíření AMP a klíčových faktorech, které k tomuto šíření přispívají, mají úzkou souvislost s lidskými aktivitami a způsobem, jakým ovlivňují ekosystémy a divokou zvěř.

Zjištění prezentovaná v této studii mají dalekosáhlé důsledky nejen pro ochranu přírody a management populací prasat divokých, ale také pro řízení lidských aktivit v přírodním prostředí. Výsledky ukazují, že změny v lidském chování, ať už způsobené pandemickými omezeními nebo preventivními opatřeními proti přenosu chorob, mohou mít zásadní vliv na ekosystémy a volně žijící zvířata. Tato zjištění by měla být zohledněna v politice a strategiích ochrany přírody, které nejenže reflektují okamžité dopady lidských aktivit, ale také jejich dlouhodobý vliv na fyziologii a chování zvířat.

Dlouhodobé sledování chování prasat divokých za použití moderních technologií, jako jsou biologické senzory a GPS obojky, umožnilo podrobně zmapovat jejich reakce na různá lidská narušení. Tyto technologie odhalily jemné, ale významné změny v energetické rovnováze a spánkových vzorcích, které by tradiční metody mohly snadno přehlédnout. Tato data představují cenný příspěvek pro budoucí výzkum i praktické řízení populací, zejména v oblastech, kde se střetávají zájmy ochrany přírody a rekreačních aktivit.

Naše výzkumy ukazují, že lidské aktivity mají vliv na chování prasat divokých v různém rozsahu, a to od jejich prostorových strategií až po fyziologické reakce na stres. I když jsou prasata schopna se do určité míry přizpůsobit přítomnosti člověka, je důležité brát v úvahu dlouhodobé fyziologické důsledky, které mohou ovlivnit jejich kondici a reprodukční schopnosti. Tato zjištění jsou zásadní pro efektivní management volně žijících populací a kontrolu šíření chorob, jako je AMP, kde by mělo být minimalizováno narušení přirozeného prostředí a přímý kontakt s divokou zvěří.

Řízení šíření afrického moru prasat vyžaduje interdisciplinární přístup. Přizpůsobení prasat divokých lidské přítomnosti je stále málo zdokumentováno. Adaptace zahrnuje různé behaviorální mechanismy, jako je změna denní aktivity a migrace do méně přístupných oblastí. Tyto uzpůsobení, i když účinné v krátkodobém horizontu, vedou k vyšším energetickým nákladům a mohou negativně ovlivnit dlouhodobé reprodukční schopnosti zvířat. Virus AMP představuje zvlášť závažnou hrozbu, vzhledem k jeho schopnosti přetrvávat ve vnějším prostředí a kontaminovaných materiálech po dlouhou dobu. Efektivní kontrola tohoto onemocnění bude záviset na kombinaci technických, biologických a environmentálních opatření, včetně monitorování populace prasat a důsledného odstranění kontaminovaných materiálů.

Klíčovým faktorem je monitorování pohybu prasat divokých, zlepšení biologické bezpečnosti a omezení jejich přístupu k lidským zdrojům potravy. Mezinárodní spolupráce a zlepšení řízení rizik v zemědělských oblastech jsou také nezbytné pro účinné zvládnutí tohoto problému. Kombinace těchto přístupů umožní účinně čelit dynamicky se měnícím rizikům spojeným s lidskou činností a šířením nemocí.

Závěrem lze říci, že úspěšné zvládnutí problémů spojených s prasaty divokými a šířením afrického moru prasat bude vyžadovat kombinaci pokročilých monitorovacích technologií, efektivních opatření biologické bezpečnosti a důsledné kontroly přístupu prasat divokých do vysoce rizikových oblastí. Výzkumy také ukazují, že vývoj nových metod prevence, jako je zavedení účinnějších opatření ke kontrole pohybu prasat, je nezbytný pro úspěšné zvládnutí této hrozby. Klíčovou roli v prevenci bude hrát i dlouhodobé řízení rizik spojených s lidskými aktivitami a epidemiologickými hrozbami. Celkově tedy platí, že komplexní přístup k managementu prasat divokých je nezbytný pro řešení nejen šíření afrického moru, ale i pro minimalizaci konfliktů s lidskými aktivitami.

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9 Seznam použitých zkratek

AMP – africký mor prasat
COVID-19 – coronavirus disease 2019
DR – dead reckoning
GPS – Global Positioning System