Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

Katedra myslivosti a lesnické zoologie

Vývoj a použití hybridní GPS-Biologging technologie pro studium volně žijících zvířat

Disertační práce

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ZADÁNÍ DISERTAČNÍ PRÁCE

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Lesní inženýrství
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Název práce

Vývoj a použití hybridní GPS-Biologging technologie pro studium volně žijících zvířat

Název anglicky

Development and usage of hybrid GPS-Biologging technology for research on wild animals

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Cíle práce

Cílem disertační práce je vyvinout a otestovat spojení GPS a biologging technologie pro studium detailního pohybu a chování zvířat. Pomocí dat zaznamenaných touto hybridní technologií klasifikovat a vyhodnotit různé typy chování zvířat a prostorovou aktivitu v rámci dílčích studií.

- Propojit biologging technologii s GPS telemetrií a otestovat vhodnost použití vyvinuté technologie a validovat získávaná akcelerometrická a magnetometrická vysokofrekvenční data pro studium detailního pohybu a chování sledovaných zvířat.

- Sestavit behaviorální model využívající akcelerometrická data pro popis jednotlivých typů chování.

- Otestovat vliv vyvinutého zařízení na sledované jedince z hlediska fyziologie pohybu a jeho změn vlivem neseného zařízení

- Klasifikovat detailní charakteristiky pohybu sledovaných zvířat a kvantifikovat pohybové strategie v závislosti na energetické náročnosti

- Využít akcelerometrická data a GPS pozice pro studium spánkové aktivity prasete divokého (Sus scrofa) v závislosti na klimatických podmínkách a lidské aktivitě.

- Otestovat návratové strategie a schopnost homingu u jelena evropského (Cervus elaphus).

- Definovat energetické potřeby jelení zvěře při managementu populací v přezimovacích obůrkách a mimo ně.

Metodika

Metodika disertační práce bude postavena na datech získaných z nově vyvinuté a ověřené hybridní GPS--Biologging technologie, která bude kontinuálně zaznamenávat poziční, akcelerometrická a magnetometrická data ve vysokofrekvenčním rozlišení. Pomocí této technologie budou označeny vybrané druhy zvířat

pro získání vhodných dat využitelných pro následující analýzy zaměřené na studium prostorového chování, navigace, detailního pohybu a jednotlivých typů chování sledovaných zvířat s ohledem na ostatní faktory prostředí.

1) Sestavení hybridní sledovací technologie

2) Rekonstrukce detailního pohybu a spotřeby energie

3) Behaviorální reakce zvířat na lidskou aktivitu a klimatické změny

4) Efekt řízené translokace a navigace jelení zvěře

5) Management přezimovacích obůrek pro jelení zvěř v závislosti na distribuci energetických potřeb

Veškerá manipulace se volně žijící zvěří bude prováděna na základě schváleného projektu pokusů s kvalifikací a odbornou způsobilostí na úseku pokusných zvířat dle §15d odstavce 2 písmeno a) zákona č. 246/1992 Sb., na ochranu zvířat proti týrání, v platném znění.

Harmonogram:

Říjen 2018 – Prosinec 2018 Technické propojení GPS telemetrie a biologging technologie

Leden 2018 – Únor 2018 Testování nových senzorů a primární zpracovávání nových dat

Únor 2018 – Duben 2018 Imobilizace jelení zvěře a označení jedinců pomocí GPS obojků s biologgery.

Duben 2018 – Duben 2019 Kontinuální sledování označených jedinců, zpracovávání dat za každý měsíc pozorování.

Únor 2019 – Duben 2019 Imobilizace již sledovaných jedinců a následná translokace do nových lokalit.

Duben 2019 – Duben 2020 Kontinuální sledování označených jedinců translokovaných do nových lokalit.

Květen 2020 – Květen 2021 Sledování jedinců, případné přemístění dalších jedinců do nových lokalit, analýzy a zpracovávání výsledků.

Duben 2020-Březen 2022 Analýza dat a publikování výsledků

Doporučený rozsah práce

60 – 120 stran

Klíčová slova

Bio-logging, GPS, chování zvířat, homing, navigace

Doporučené zdroje informací

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Děkan

V Praze dne 17. 10. 2024

"Prohlašuji, že jsem disertační práci na téma „Vývoj a použití hybridní GPS-Biologging technologie pro studium volně žijících zvířat“ vypracoval samostatně s použitím uvedené literatury a na základě konzultací a doporučení školitele. Souhlasím se zveřejněním disertační práce dle zákona č. 111/1998 Sb. o vysokých školách v platném znění, a to bez ohledu na výsledek její obhajoby."

V Praze dne 28. 9. 2024 Ing. Václav Silovský

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Abstrakt

Sledování a pozorování volně žijících zvířat pro získávání dat o místě, čase, pohybu a orientaci, nebo typu chování a aktivitě jsou stále více se rozvíjejícím trendem v ekologii mnoha živočišných druhů. Cílem studií je získávání komplexních poznatků vhodných pro rozšíření znalostí o biologii a ekologii daného druhu nebo pro jeho management a ochranu. Významným technologickým pokrokem je používání multi-senzorové biologging technologie v kombinaci se standartním GPS telemetrickým systémem ve formě obojkového systémů. V rámci našeho projektu jsme vyvinuli hybridní zařízení vybavené vysoko frekvenčním akcelerometrem a magnetometrem s tříosým záznamem dat na frekvenci 10 Hz a GPS modulem s frekvencí záznamu pozic v intervalu 30 minut. Vyvinuté zařízení bylo testováno pro dlouhodobé pořizování záznamu (více než 1 rok) u jedinců jelena evropského (*Cervus elaphus)* a prasete divokého (*Sus scrofa)*. Hybridní technologie byla testována vzhledem k hmotnosti celého systému vůči tělesné hmotnosti sledovaných zvířat. Výsledky prokázaly vhodnost použití vyvinutého zařízení, a to bez vlivu na změny v chování a pohyb sledovaných zvířat. Technologie splňuje doporučený 3% váhový limit hmotnosti zařízení z tělesné hmotnosti zvířete. Rekonstrukce detailního pohybu označených zvířat pomocí biologging technologie prokázala využívaní nižší rychlosti pohybu při vyšší směrové diferenciaci, ve srovnání s výrazně rychlejším přímým pohybem. Další výsledky práce pocházející z biologging dat byly zaměřené na spánkové rytmy prasete divokého (*Sus scrofa)*. Data prokázala negativní vliv extrémních klimatických faktorů na kvalitu a frekvenci spánkových cyklů sledovaných jedinců. U jelení zvěře byla pozitivně testována schopnost navigace (tzv. homingu) do původních domovských okrsků po řízené translokaci mimo ně. Směrová orientace vůči domovskému okrsku byla významná u GPS pozic, které byly ve vzdálenosti do 100 m a do 5000 m od místa vypuštění. Výsledky zdůrazňuji značnou fidelitu jelení zvěře k domovským okrskům. Stejně významný poznatkem je testovaná vhodnost použití přezimovacích obůrek pro jelení zvěř v zimním a jarním období s cílem redukce pohybu a energetických výdajů, potažmo snížení tlaku na lesní porosty. Jelení zvěř prokázala snížení pohybové aktivity po dobu strávenou uvnitř obůrky a značně vyšší aktivitu pohybu před samotným vypuštěním do volnosti. Publikované výsledky lze využít pro pochopení ekologie a chování několika druhů zvířat, případně ve spojení s ochranou a managementem přírody a procesů v ní probíhajících.

Klíčová slova: chování zvířat, akcelerometr, magnetometr, detailní pohyb, navigace

Abstract

Monitoring and observing wild animals to collect data on location, time, movement and orientation, or types of behavior and activity is an increasingly developing trend in the ecology of many animal species. The goal of these studies is to gain comprehensive insights suitable for expanding knowledge about the biology and ecology of a given species or for its management and conservation. A significant technological advancement is the use of multi-sensor biologging technology combined with standard GPS telemetry systems in the form of collar systems. As part of our project, we developed a hybrid device equipped with a high-frequency accelerometer and a magnetometer that records data in three axes at a frequency of 10 Hz, alongside a GPS module that records positions at intervals of 30 minutes. The developed device was tested for long-term data acquisition (over 1 year) on individuals of the European deer (Cervus elaphus) and wild boar (Sus scrofa). The hybrid technology was evaluated regarding the weight of the entire system relative to the body weight of the monitored animals. The results demonstrated the suitability of using the developed device without influencing changes in the behavior and movement of the monitored animals. The technology meets the recommended 3% weight limit of the device relative to the animal's body weight. The reconstruction of detailed movement of tagged animals using biologging technology showed a tendency for lower movement speeds with greater directional differentiation, compared to significantly faster direct movements. Other results derived from biologging data focused on the sleep rhythms of wild boars (Sus scrofa). The data indicated a negative impact of extreme climatic factors on the quality and frequency of sleep cycles of the monitored individuals. For deer, the ability to navigate (known as homing) back to their original home ranges after managed translocation was positively tested. Directional orientation towards the home range was significant for GPS positions within distances of up to 100 m and up to 5000 m from the release point. The results highlight a strong fidelity of deer to their home ranges. Another significant finding is the tested suitability of using winter enclosures for deer during the winter and spring periods to reduce movement and energy expenditure, thereby decreasing pressure on forest vegetation. The deer demonstrated reduced movement activity while inside the enclosure and significantly higher movement activity prior to their release into the wild. The published results can be utilized to understand the ecology and behavior of several animal species, as well as in connection with nature conservation and the processes occurring within it.

Keywords: animal behavior, accelerometer, magnetometer, detailed movement, navigation

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1. Úvod

Používání kontaktních senzorů a sledovacích zařízení umístěných na těle zvířat mění naše chápání ekologie a chování divokých zvířat (Brown et al., 2013a; Kays et al., 2015). Zařízení obsahující různé typy senzorů a systémy určující polohu byly použity napříč časem a prostorem již u mnoha živočišných druhů s cílem získání nejrůznějších poznatků, a to například od detailního popisu lovecké strategie šelem až po rozsáhlá srovnávání jednotlivých typů chování napříč taxony nebo jejich prostorové využití napříč všemi oceány (Block et al., 2011; Brown et al., 2013a; A. M. Wilson et al., 2013a). Integrace technologie GPS s akcelerometrickými a magnetometrickými daty dále zvyšuje přesnost a hloubku získávaných prostorových informací pro studie založené na vzdáleném sledování zvířat, což se odráží ve velmi rozšířeném používání GPS technologie napříč mnoha studiemi za poslední tři desetiletí (Kays et al., 2015). Kromě standartního použití GPS technologie pro získání časoprostorové informace je v současnosti využívána pro zpřesnění informace o pohybu funkce tzv. dead-reckoningu, která vytváří detailní rekonstrukci ušlé trasy sledovaného zvířete pomocí synchronizace vektorů z akcelerometru a magnetometru (Gunner et al., 2021). Inženýring multi-senzorových obojků (např. GPS, akcelerometr, magnetometr) schopných kontinuálně a dlouhodobě zaznamenávat detailní a velkoobjemová data o pohybu zvířat je stále výzvou pro vývoj a implementaci (Cook et al., 2017; Holton et al., 2021a; Kenward, 2000). V současné době je technologickou výzvou především vývoj zařízení s dlouhou dobou sledování.

Pohyb je základním principem živočišné říše, zvířata se pohybují různou rychlostí v jimi zvolených směrech tak, aby využívala prostor v průběhu času definovaným způsobem, o kterém předpokládají, že zlepšuje jejich přežití nebo reprodukční úspěch (B. K. Williams et al., 2002). Pohyb vyžaduje energii, která se liší podle velikosti zvířete (Dickinson et al., 2000). Rychlost, kterou zvíře volí pro pohyb, a tedy i spotřeba energie, která je mu určena v průběhu času, závisí na účelu pohybu, protože samotný pohyb může být méně důležitý než behaviorální role lokomoce (R. S. Wilson et al., 2015), která může vznikat v závislosti na čase nebo reprodukčním úspěchu (Shepard et al., 2009a).

Navigace zvířat, prostorová orientace a kognitivní paměť jsou základní schopnosti, které zvířatům umožňují dosáhnout konkrétních cílů, jako jsou zdroje potravy, lokality pro páření a odpočinek, a díky tomu tak efektivně využívat prostorově seskupené zdroje (Alerstam & Bäckman, 2018a; Kashetsky et al., 2021a). Mnoho živočišných druhů vykazuje věrnost dané

lokalitě - fidelitu, to znamená, že se každou sezónu vracejí do konkrétních míst nebo zůstávají ve stejné oblasti nebo kolem ní v průběhu celého roku (Milner-Gulland et al., 2011). Zvířata, která vykazují silnou fidelitu k domovským okrskům, se obvykle po jakémkoliv způsobu přemístění mimo jejich domovský areál, vracejí na své původní místo - lokalitu odchytu (Falcón-Cortés et al., 2021; Papi, 2012a). Důvody pro upřednostňování určitých „domovských oblastí“ mohou být různé, ale často jsou spojeny s teritoriálním chováním, anebo místy k páření (Crump, 1986; Lohmann et al., 2017), případně z důvodu vytváření domovského okrsku na základě paměti a prostorového vnímaní okolí (Merkle et al., 2014; Van Moorter et al., 2009). Studium prostorové aktivity a navigačních schopností velkých savců bylo podrobeno mnohem menšímu počtu přímo řízených experimentů, pravděpodobně kvůli praktickým problémům s jejich přemístěním. Studie na mnoha druzích naznačují, že existují druhově specifické limity translokačních vzdáleností, po jejichž překročení již zvířata nejsou schopna navigovat zpět (Rogers, 1984; Sinsch & Kirst, 2016). Tato omezení mohou být spojena s navigačními podněty používanými pro navádění, což může vyžadovat znalost prostředí. Schopnosti navádění mimo dříve navštívenou (tj. „známou“) oblast se často nazývají „pravá navigace“, což znamená, že zvířata mají schopnost extrapolovat navigační podněty mimo svůj domovský okrsek. Nicméně stále není známo, jaké druhy smyslových mechanismů používají velcí suchozemští savci pro svoji navigační schopnost. U menších savců se však ukázalo, že k orientaci lze použít čichové (Fischler-Ruiz et al., 2021), vizuální (Barry Jr & Francq, 1982) a magnetické podněty (Phillips et al., 2013). Větší savci, jako je jelen evropský *(Cervus elaphus)*, mohou v zásadě používat všechny tyto parametry, pokud jsou při navigaci k dispozici. Zatím však doposud nebyly provedeny žádné přímé testy příslušných navigačních funkcí. Pochopení naváděcích schopností větších savců je důležité při řízení populací, ať už pro ochranu ohrožených zvířat nebo pro management zvěře.

Důležitou součástí chování je spánek. Ten je pozorován prakticky u všech zvířat (Anafi et al., 2019), je nezbytný pro zdraví, kognitivní funkce a vývoj jedince, posiluje základní imunitní odpovědi na infekce (Besedovsky et al., 2019), podporuje produkci hormonů a metabolickou regulaci (Manzar et al., 2015; Medic et al., 2017), a také nervové spojení a vývoj mozku (Klinzing et al., 2019; Xie et al., 2013). Není proto divu, že krátká doba spánku a ztráta spánku jsou doprovázeny četnými škodlivými účinky na zdraví a kognitivní funkce v krátkodobém i dlouhodobém horizontu (Johnsson et al., 2022; Sabia et al., 2022; C. J. Wild et al., 2018). U zvířat v laboratorních podmínkách jsou často následovány delším spánkem, který pravděpodobně zmírňuje tyto následky (Kushida, 2004). Zatímco doposud byl spánek brán jako

aktivita, přinášející zejména benefity, tak je nutné připomenout, že v průběhu spánku se zvířata nemohou zapojit do reprodukce, rozvíjet sociální vztahy a shánět potravu. Velmi důležitý je také fakt, že v průběhu spánku jsou zvířata vystavena vyššímu riziku predace (Capellini et al., 2010a). Vzhledem k omezené plasticitě spánku nelze jeho účinky dlouhodobě opomíjet navzdory rizikům, která mohou nastat v jeho průběhu (S. S. Campbell & Tobler, 1984). Vnitrodruhové spánkové nároky jsou téměř totožné, jelikož se odvíjejí od neurofyziologických procesů daného druhu (Capellini et al., 2008).

2. Cíle

Cíle disertační práce jsou rozděleny do třech tematických částí a jejich pořadí na sebe metodicky navazuje. Prvním cílem práce bylo vyvinutí nové hybridní technologie pro vzdálené sledování volně žijících živočichů bez lidského ovlivnění, včetně testování vlivu zařízení na jejich prostorovou aktivitu a přirozené typy chování. Vyvinuté zařízení by mělo splňovat vhodné podmínky pro kontinuální sběr dat z označeného jedince a nemělo by negativně ovlivnit wellfare a wellbeing daného zvířete. Cílem je vyvinout technologii, která vznikne kombinací GPS obojku pro dlouhodobé sledování velkých suchozemských savců a biologging senzoru obsahujícího akcelerometr a magnetometr pro záznam vysokofrekvenčních dat. Vyvinuté zařízení bude schopné snímat kontinuální data z prostorové aktivity ve volné přírodě (GPS pozice), a také detailní data o akceleraci těla a prostorové orientaci jedince.

Na základě implementace nově vyvinuté hybridní technologie bylo cílem ověřit funkčnost technologie pro získávaných dat včetně možnosti jejich využití pro studium jednotlivých typů chování sledovaných druhů zvěře. Sběru dat byl prováděn u jelení a černé zvěře s cílem klasifikace chování na základně vysokofrekvenčních biologging dat a prostorové orientace. Posledním cílem disertační práce byla realizace řízeného experimentu s využitím GSP technologie pro stanovení návratových mechanismů volně žijící zvěře do původních domovských okrsků a otestování vhodnosti managementu jelení zvěře v přezimovacích obůrkách vzhledem na spotřebu energie na základě parametru VeDBA.

3. Rozbor problematiky

3.1. Vývoj, testování a použití hybridních technologií

V posledních desetiletích byly vyvinuty senzory, které jsou určené k aplikaci na zvířata s cílem získávání dat o fyziologických procesech, chování, pohybu a parametrů okolního prostředí. Způsobily revoluci ve studiu ekologie živočichů u různých taxonů (Ropert-Coudert & Wilson, n.d.; Rutz & Hays, 2009; Wilmers et al., 2015a), Tento posun ve vývoji byl umožněn díky pokrokům v technologii senzorů, evidenci a správě dat, a také díky analytických technikách, které nyní podporují teoretický i aplikovaný výzkum divokých zvířat (A. Cooke et al., 2012; Rattenborg et al., 2016; Wilmers et al., 2015b). Nutno však upozornit, že s příchodem nových biologických technik je vyžadován i multidisciplinární přístup, který se velmi často zaměřuje na různé odborné znalosti v oblastech mimo ekologii volně žijících živočichů (Kays et al., 2022; Portugal & White, 2018a; Tuia et al., 2022; T. A. Wild et al., 2023).

3.1.1. Multi-senzorová biologging technologie

Management a ochrana volně žijících populací zvířat potřebuje informace o tom, kde se vyskytují a kde by se mohly případně vyskytovat (Aarts et al., 2008). Z toho důvodu je monitoring populačních trendů a vzorců chování klíčovým aspektem v managementu volně žijící divoké zvěře (Buckland et al., 1996). Hlavními faktory, které ovlivňují výběr životního prostředí zvěře, jsou: potravní nabídka, bezpečí a klid. Nicméně každému typu biotopu chybí obvykle ideální kombinace těchto faktorů (Godvik et al., 2009). Telemetrická GPS data nám tak mohou poskytovat velmi dobrý základ pro posuzování habitatových preferencí a využití stanoviště (Gavrilov et al., 2015). Kombinace technologie GPS telemetrie s dalšími vybranými funkcemi je široce používána k analýzám habitatových preferencí sledovaných zvířat. Zmíněná kombinace díky své rychlosti a kvalitě posouzení struktury rozsáhlého zájmového území nabízí možnosti k překonání požadavků studií týkajících se výběru habitatů o malém rozsahu a velikosti (Ewald et al., 2014).

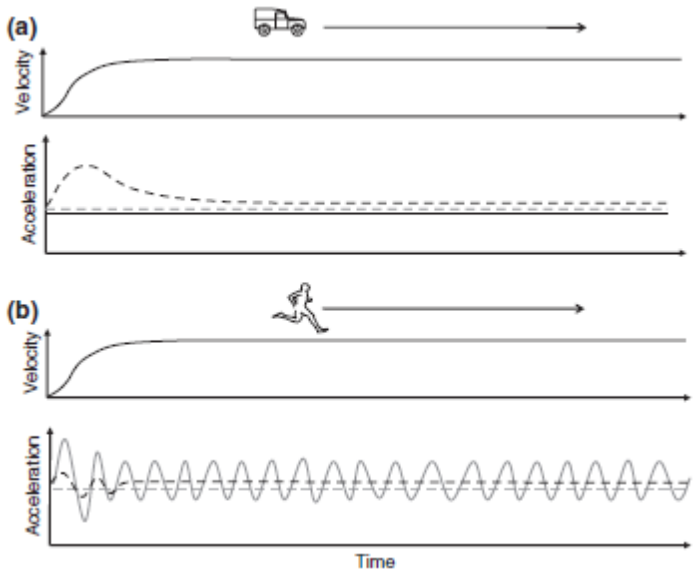
Zvířata se chovají takovým způsobem, kterým si podle svého behaviorálního repertoáru vybírají z podmínek vnějšího a vnitřního prostředí, čímž se snaží o zlepšení a jejich celoživotního fitness (Nathan et al., 2008). Techniky používané ke studiu a kvantifikaci chování

zvířat jdou nad rámec přímého pozorování jedinců. Dochází tak k nárůstu používání různých typů zařízení pro sledování (např. GPS moduly nebo "light-level logger“, což je zařízení vnímající teplotu a intenzitu světla (Cagnacci et al., 2010; Ropert-Coudert & Wilson, 2005). Zejména v posledním desetiletí došlo k rozsáhlému rozšíření použití akcelerometrů ke kvantifikaci metrik týkajících se chování (S. Watanabe et al., 2005; Yoda et al., 2001). Je tomu tak proto, že většina chování je definována pohyby a / nebo posturálními vzorci, které lze kvantifikovat pomocí akcelerometrů (Nathan et al., 2012; Shepard, Wilson, Quintana, et al., 2008a). Konkrétně ortogonálně orientované tříosé akcelerometry mohou poskytovat data vysokého rozlišení definující orientaci biologgeru s ohledem na gravitaci (pokud nepůsobí jiné síly), a proto rozpoznají držení těla („statická“ akcelerační složka; (Shepard, Wilson, Halsey, et al., 2008a; Shepard, Wilson, Liebsch, et al., 2008b), stejně jako rozsah pohybu způsobený dynamickou složkou - zrychlením (Shepard, Wilson, Liebsch, et al., 2008b; Yoda et al., 2001). Výsledkem je, že se akcelerometry běžně používají a umisťují různými způsoby na zvířata. V současnosti jsou uznávány jako extrémně výkonná součást metodologie pro objasnění chování zvířat (Nathan et al., 2012).

V rámci disertační práce bude použita kombinace GPS telemetrie s kombinací biologging technologie. Termín "biologging" znamená sledování jedince za použití miniaturního senzoru přiloženého na tělo zvířete pro přenos údajů o pohybech, chování a fyziologii zvířete, avšak senzor může zaznamenávat i informace o okolním prostředí. Biologging technologie podstatně rozšiřuje naši schopnost sledovat a provádět měření volně žijících živočichů bez vlivu přítomnosti člověka, který je v případě přímého pozorovaní téměř vždy zásadní. Poskytuje nám širší záběr pro posun základního i aplikovaného biologického výzkumu (Rutz et al., 2009). Kromě toho se ukázalo, že dynamický akcelerometr je také výkonný jako tzv. „proxy“ hodnota pro výpočet energetických výdajů založených na pohybu jedince (T. D. Clark et al., 2010; Gleiss et al., 2011; Halsey et al., 2011; R. P. Wilson et al., 2006). Dále poskytuje i další velmi cenné informace vedoucí k pochopení behaviorálních procesů (H. J. Williams et al., 2017).

Avšak ne všechny typy chování jsou možné a popsatelné pomocí akcelerometru. A co je nejdůležitější, samotný akcelerometr není schopný rozpoznat a zaznamenat orientaci (alignment) označeného zvířete. Interpretace pohybu na základě akcelerometru může být také zmatena např. silami, které samotné zvíře nevytváří, takový může být například pohyb vln pro vodní ptactvo sedící na vodní hladině (Halsey et al., 2011) nebo vibrace způsobené prouděním vzduchu okolo akcelerometru, což vede ke zvýšení poměru signál – šum v zaznamenaných

datech (Ropert-Coudert & Wilson, 2005). Navíc zvláštní problém nastává v případě, když je rychlost sledovaného zvířete konstantní a je indukováno jen malé nebo vůbec žádné zrychlení zvíře, ke kterému dochází zejména u mořských živočichů a u ptáků, kteří používají tzv. klouzavý let, při kterém využívají vzdušné proudění (H. J. Williams et al., 2015). Tento jev může vzniknout i při velmi pomalém pohybu různých částí těla za konstantní rychlosti. Ačkoliv jsou data spojená s postojem zvířete důležitou součástí pomáhající definovat chování (Shepard, Wilson, Halsey, et al., 2008a; Shepard, Wilson, Liebsch, et al., 2008c), lze je obecně odvodit použitím elektronického filtru „High-pass filter“ tzv. HPF nebo pomocí funkce vyhlazení akceleračních dat např. po rychlém otočení geparda v pohybu nebo při ostrém ponoru zvířete (C. J. Clark, 2009; A. M. Wilson et al., 2013b; J. W. Wilson et al., 2013).



Obrázek 1 - Schématický graf popisující rozdílnost jednotlivých typů akceleračních pohybů v porovnání s rychlostí u automobilu (a) a běžce (b). Černá čárkovaná čára charakterizuje prudké zrychlení při nárůstu rychlosti nikoliv při stabilní rychlosti pohybu. Na druhou stranu běžec při cyklu chůze navyšuje a snižuje svoji akceleraci i v průběhu stabilního rychlosti. To je způsobeno pohybem pohybu těla nahoru a dolů. ((Gleiss et al., 2011)).

Mnoho z těchto problémů lze však vyřešit pomocí dalších tříosých senzorů měřících úhlovou rotaci. Jsou to zejména gyroskopy nebo magnetometry (Martin Lopez et al., 2016), které jsou často kombinovány s akcelerometry a zaznamenávají údaje souběžně s akcelerometrem na jednom měřícím zařízení (Noda et al., 2014; R. P. Wilson et al., 2013). Gyroskopy měří úhlovou rychlost a jsou velmi citlivé na úhlovou rotaci, přestože jsou podmětem driftu za jednotku času (Fong et al., 2008). Magnetometry nejsou posouvány a můžou být použity k odvození zarovnání (alignmentu) jedince (obecně v asociaci

s akcelerometrem), ale produkují signály, které budou komplexní a složité pro interpretaci, protože výstupy se liší podle umístění na zemi (Bidder et al., 2015a).

Magnetometry nejsou citlivé na zrychlení jakéhokoli druhu (gravitační nebo dynamické), a proto je lze tedy použít společně s akcelerometry a zlepšit tak získávání metrických údajů užitečných pro kvantifikaci chování zvířat (Martin Lopez et al., 2016; Noda et al., 2014; R. P. Wilson et al., 2008). Současné použití těchto dvou typů senzorů umožňuje kvantifikovat zarovnání (alignment) zvířat v průběhu sledování, což poskytuje řešení pro sestavení přesné trajektorie zvířat (rekonstrukce jejich pohybu v prostoru), a to za předpokladu, pokud jsou údaje propojeny s vhodným časovým rozlišením a je možné použít tzv. dead-reckoning (Bidder et al., 2015a; Bidder, Soresina, et al., 2012). Magnetometry reagují na orientaci a intenzitu magnetického pole analogickým způsobem, jako fungují akcelerometry pro detekci pohybu. Proto je zde také potenciál používat magnetometry jako senzory pohybu, i když jejich reakce a charakteristiky se zásadně liší od vlastností akcelerometrů (H. J. Williams et al., 2017).

Magnetometry byly vyvinuty z relativně necitlivých, jednoosých senzorů, které měří vzdálenost k magnetu (ta je založena na síle lokálního magnetického pole) a z triaxiálních senzorů, které jsou schopné zaznamenávat orientaci ve vztahu k zemskému magnetickému poli (tyto senzory se nazývají „TriMag“). V počátku byly mono-axiální magnetometry použity k dokumentaci obecné aktivity karety obecné (*Caretta caretta)*, a to pomocí zaznamenávání pozice silného magnetu bez použití kompasu (Hochscheid & Wilson, 1999). Následně byly používány mono-axiální magnetometry primárně k měření vzdálenosti mezi senzorem umístěným na zvířeti a magnetem, který byl umístěn na jiné, pohybující se části těla zvířete (R. Wilson & Liebsch, 2003; R. P. Wilson, 2002). Tento přístup byl použit například pro kvantifikaci pohybu končetin u vodních živočichů (R. Wilson & Liebsch, 2003), a také pro kvantifikaci pohybu čelistí při přijímaní potravy a dýchání u volně žijících zvířat (Ropert-Coudert et al., 2002; R. P. Wilson, 2002). Každopádně, extrémní citlivost moderních magnetometrů nyní umožňuje snímání intenzity magnetického pole Země ve všech třech prostorových dimenzích, a proto dokáže rozpoznat úhlové zarovnání (alignment) označeného jedince s přesností 1–2° (Mitani et al., 2003; R. P. Wilson et al., 2007a).

Vzhledem k této vysoké citlivosti senzorů vzniká tak nový potenciál pro využití těchto systému k objasnění chování zvířat, které je založeno na úhlové rotaci. Současný trend směřuje zejména k dlouhodobějšímu označení volně žijících živočichů pomocí tříosých magnetometrů, které zaznamenávají údaje o osách každou sekundu. Tato přesnost velmi značně navyšuje přesnost hodnoty kvantifikující úhlové zarovnání. Ačkoli k dnešnímu dni byly magnetometry

velmi zřídka používané pro studium chování, je velmi pozoruhodné sledovat stále častější zmínky o tomto typu senzorů v odborné literatuře, zejména informace o použití magnetometrů ve spojení a akcelerometry nebo gyroskopy. Tato kombinace je zmiňována zejména jako nejlepší nástroj pro sběr dat použitelných pro funkci „dead-reconing“ (Johnson & Tyack, 2003; Matsumura et al., 2011; Mitani et al., 2003; Shiomi et al., 2010).

Jelikož magnetometry a akcelerometry poskytují velmi odlišné druhy informací o pohybu kvůli jejich rozdílnosti zaznamenávaných dat, budoucnost bychom měli zaměřit na synchronizované používání obou senzorů. V tomto případě totiž senzory vytvářejí výkonný nástroj pro přesnou kvantifikaci různých aspektů pohybu (H. J. Williams et al., 2017). Indexy odvozené z akcelerometrů, které se vztahují k energetice pohybu, jakým je např. VeDBA, (Qasem et al., 2012) by bylo možné použít k posílení relevantních ekvivalentů magnetometru (např. úhlová rychlost) (R. P. Wilson et al., 2013)

3.1.2. VeDBA

Dynamické zrychlení těla (Dynamic body acceleration (*DBA*)) bývá používáno jako parametr uvádějící energetické výdaje zvířat, které jsou opatřené biologgerem. Souhrnně bývá vědci používáno celkové zrychlení ODBA (overall dynamic body acceleration). Vektor dynamického zrychlení těla (VeDBA) může být lepším parametrem, z tohoto důvodu je níže popsáno porovnání ODBA a VeDBA jakožto parametrů pro rychlost spotřeby kyslíku u lidí a dalších 6 druhů. V uvedené studii bylo testováno 21 lidí na běžeckém pásu, kteří běhali různými rychlostmi. Po celou dobu běhu nosili na svém těle dva biologgery – první byl umístěn v přímé orientaci, druhý byl umístěn v šikmé orientaci. Po celou dobu běhu byla zaznamenávána spotřeba kyslíku (VO_2). Podobné údaje byly získávány i od zvířat, která byla opatřena pouze jedním biologgerem, a to v přímém směru. U testovaných lidí byla jak ODBA tak VeDBA dobrými parametry s hodnotami r^2 vyššími než 0,88. Nicméně ODBA představovala mírně, avšak signifikantně více variací ve VO_2 než VeDBA ($p < 0.03$). V této studii nebyly zjištěny žádné významné rozdíly zaznamenaného VO_2 mezi ODBA a VeDBA, a to i v případech, kdy bylo porovnáváno umístění biologgeru v přímém a šikmém směru. V části studie zaměřené na zvířata byly ODBA a VeDBA dobrými parametry vznikající z validních vstupních hodnot porovnávaných vůči naměřenému VO_2. Nicméně opět ODBA představovala mírnou, avšak signifikantně větší variabilitu v porovnání s VO_2 než VeDBA. Simultánní svalové kontrakce

pro zajištění stability končetin mohou částečně vést ke spotřebě kyslíku, což alespoň částečně odpovídá součtu složek pro odvození DBA (dynamic body acceleration – dynamická akcelerace těla). Nelze tedy předpokládat, že vektorový součet pro odvození DBA bude „správným“ výpočtem. Nicméně ačkoliv v rámci omezení této jednoduché studie se ODBA zdá jako nejvhodnější parametry pro stanovené spotřeby VO_2. V neobvyklé situaci, kdy výzkumníci nejsou schopni zaručit alespoň přiměřeně konzistentní a stabilní orientaci loggeru, by mělo být používáno parametru VeDBA pro spojování s hodnotami VO_2. V uvedené studii byla surová akcelerometrická data převedena do DBA zaprvé pomocí vyhlazení (smoothnig) každého záznamového kanálu s cílem vedoucím k odvození statické akcelerace (Qasem et al., 2012) (za použití klouzavého průměru) (Shepard, Wilson, Quintana, et al., 2008a). Následně se tato statická akcelerace odečetla ze surových dat (Gleiss et al., 2011). Tyto hodnoty pro DBA byly posléze sečteny, aby poskytky ODBA (R. P. Wilson et al., 2006).

$$ODBA = |A_x| + |A_y| + |A_z|$$

ODBA, kde Ay, Ax, AZ jsou odvozeny z dynamické akcelerace v jakémkoliv bodě v čase korespondujícím s tříosým ortogonálním akcelerometrem nebo s jejich vektorovým součtem (VeDBA) vycházejícím ze vztahu (Qasem et al., 2012).

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)}$$

3.1.3. Dead reckoning

Význam slova dead reckoning lze přeložit jako proces výpočtu pozice, zejména na moři, na základě odhadu směru a překonané vzdálenosti namísto použití orientačních bodů nebo astronomických pozorování. Díky rozšířené nabídce senzorů v chytrých telefonech lze vestavěné akcelerometry použít jako krokoměr a vestavěný magnetometr pro směrování kompasu. Použití dead reckoningu pro suchozemské pohyby (Pedestrian Dead Reckoning - PDR) lze použít k doplnění jiných metod navigace podobným způsobem jako automobilové navigace nebo k rozšíření navigace do oblastí, kde nejsou dostupné jiné navigační systémy. V jednoduché implementaci uživatel drží svůj telefon před sebou a každý krok způsobí, že se pozice posune vpřed o pevnou vzdálenost ve směru měřeném kompasem. Přesnost je omezena přesností senzoru, magnetickými poruchami uvnitř zařízení a neznámými proměnnými, jako je poloha přenášení a délka kroku. Další výzvou je odlišit chůzi od běhu a rozpoznat pohyby, jako

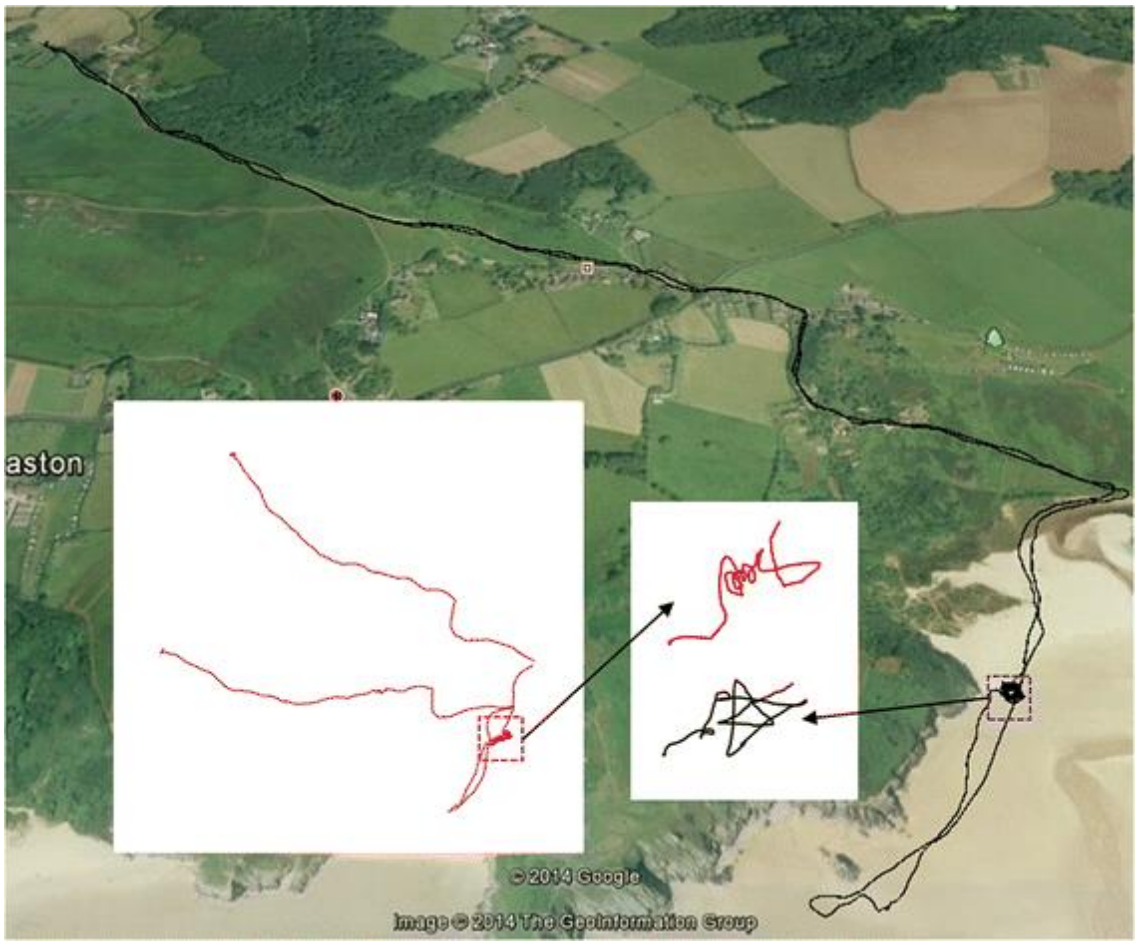
je jízda na kole, chůze po schodech nebo jízda výtahem. Před existencí telefonních systémů existovalo mnoho vlastních systémů PDR. Zatímco krokoměr lze použít pouze k měření lineární ušlé vzdálenosti, systémy PDR mají zabudovaný magnetometr pro měření směru. Vlastní systémy PDR mohou mít mnoho podob, včetně speciálních bot, opasků a hodinek, kde byla variabilita nosné polohy minimalizována, aby bylo možné lépe využít směr magnetometru. Reálný výpočet PDR je poměrně složitý, protože je důležité nejen minimalizovat základní drift, ale také zvládnout různé scénáře a pohyby při přenášení, jakož i hardwarové rozdíly mezi modely telefonů (Wikipedia).

Výzkum ekologie volně žijících zvířat stále více využívá technologii GPS telemetrie k určení polohy zvířat. Systémy GPS však zaznamenávají polohu sledovaného jedince přerušovaně a neposkytují žádné informace o pozicích mimo stanovenou dobu zaměření a o turtuozitě cesty mezi dvěma pozicemi. Vysokofrekvenční GPS mají vysoké požadavky na energii, což vyžaduje použití velkokapacitních baterií, které nelze použít při sledování malých živočichů, a u velkých savců dochází ke zkrácení doby sledování. Použití dead-reckoningu je alternativní přístup, který skýtá určitý potenciál, jak vyplnit mezery při telemetrickém sledování živočichů a dodat nám informaci o detailní poloze zvířete bez vysokých nároků na spotřebovanou energii. Přestože bývá metoda dead-reckoningu používána především ve vodním prostředí, nebyla doposud předložena žádná explicitní metoda použití pro pozemské druhy (Bidder et al., 2015a)

Pohyb zvířat zajímá biology, protože mimo jiné určuje úspěch jednotlivců v získávání potravních zdrojů, vyhýbání se před predací, maximalizaci předávání vlastní fitness a řízení zisku energie z okolí (Baird, 1994; Stephens & Krebs, 1986; Swingland & Greenwood, 1983). Úspěch jednotlivců modeluje populace a řídí vývoj a rozmanitost života (Nathan et al., 2008). Pro pochopení pohybu zvířat existuje také řada praktických výhod, jako je předpovídání dopadů změn ve využívání půdy, kontrola invazivních druhů a druhů škůdců, ochrana ohrožených druhů a předvídání šíření zoonóz (Dale et al., 2000; Kot et al., 1996; Patz et al., 2004; Stinner et al., 1983). Získání požadovaných informací o pohybu zvířat však zdaleka není zcela triviální, protože mnoho živočišných druhů žije v prostředích, která je brání před tím, být sledováni (L. S. Davis et al., 1996; Roper et al., 2001). Mnoho biotelemetrických studií se tímto zabývá, protože vylučují potřebu vizuálního kontaktu biolog-studovaný živočich (S. J. Cooke et al., 2004). Dvě metody, které se nejčastěji používají v terestrickém prostředí pro získávání údajů o poloze zvířat, jsou VHF a GPS telemetrie (Rodgers, 2001; White & Garrott, 2012). Obě metody však mají svá omezení (Recio et al., 2011). VHF je zavedená metoda, která ovšem vyžaduje

značné vynaložení energie v terénu pro implementaci výsledků (Fancy et al., 1988), zatímco GPS telemetrie se považuje za „přesnou“ metodu (Hulbert & French, 2001), ale náchylnou ke zkreslení podle podmínek prostředí (Dussault et al., 1999; Frair et al., 2004), zejména vlivem vegetace (Gamo et al., 2000) nebo topografie krajiny (D’Eon et al., 2002). Analýza dat získaných oběma metodami předpokládá přímý pohyb mezi zaměřenými polohami (Witte & Wilson, 2004), přesto je logické, že přirozený pohyb volně žijících zvířat je velmi různorodý a všesměrný (Kramer & McLaughlin, 2001). Je tedy zřejmé, že jsou zapotřebí údaje o pohybu zvířat v daleko přesnějším měřítku v prostoru i čase, aby modely o pohybu zvířat mohly lépe odrážet skutečnou povahu pohybu zvířat v prostoru a čase (Morales et al., 2010). Ve skutečnosti je jedinou biotelemetrickou metodou, jejímž cílem je produkovat údaje o pohybu suchozemských zvířat v malém měřítku (tj.> 1 Hz), metoda dead reckoning (Bramanti et al., 1988; R. P. Wilson et al., 1991; R. P. Wilson & Wilson, 1988), která dokáže rekonstruovat pohyb jedince tak přesně, že jej lze dokonce použít k odvození chování (R. P. Wilson et al., 2007a).

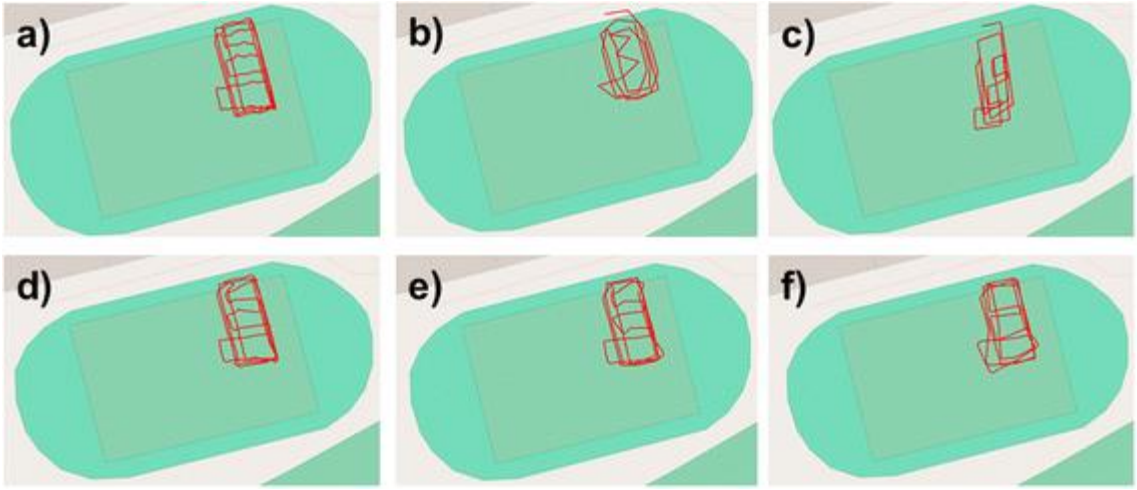
Funkce dead reckoning vypočítá vektor cesty pro daný časový interval pomocí informací o směru, rychlosti a změně ve svislé ose (R. P. Wilson, 2002). Jakmile je tohoto dosaženo, lze trojrozměrnou cestu pohybu rekonstruovat integrací všech vektorů v dané sekvenci (Johnson & Tyack, 2003; Mitani et al., 2003; Shiomi et al., 2008). Protože data jsou zaznamenávána senzory umístěnými na samotném bio-loggeru, jeho účinnost není ovlivněna permisivitou prostředí (Dussault et al., 1999; Frair et al., 2004), což je důležité pro získání přesných a nezaujatých dat (Bradshaw et al., 2004; Sims et al., 2005). Funkce dead reckoningu byla použita pro výpočet pohybu vodních druhů (R. W. Davis et al., 2001; Sato et al., 2003; Shepard, Wilson, Liebsch, et al., 2008b; Ware et al., 2011; R. P. Wilson, 2002; R. P. Wilson et al., 1991), ale nyní bude použito pro výpočet pohybu suchozemských živočichů. Použití dead reckoningu pro pohyb suchozemských živočichů je trochu složitější, a to z důvodu obtížného určení rychlosti pohybu suchozemských zvířat (Shepard et al., 2009b). To je proces, který je jednodušší pod vodou, kde lze použít mechanické metody kvůli stabilní hustotě a viskozitě vody (Eckert, 2002; Hassrick et al., 2007; Ponganis et al., 1990; Ropert-Coudert et al., 2006; Sato et al., 2003; Shepard, Wilson, Liebsch, et al., 2008b; R. P. Wilson et al., 1993; Yoda et al., 1999, 2001). Schopnost spolehlivě odhadnout rychlost u



Obrázek 2 – Pohyby člověkem vedeného koně, které začal a ukončil svou cestu v levém horním rohu obrázku. Černá trasa = sledovánní pomocí vysokofrekvenční GPS (1 Hz) a červená trasa určená pomocí Dead-Reckoningu (20Hz) bez pouzití GPS korekce. Trasa dead reckoningu nemá měřítko, protože vdálenost pohybu je odvozena od rychlosti a je zde předpoklad, že je v lineárním vztahu s hodnotou VeDBA. Co dokazuje potřebu korekce pomocí GPS technologie. Ve čtvercích je znázorněn časový úsek, kdy byl kůň vedený k pohybu v těsných kruzích. Podle GPS byla celková dráha koně dlouhá 10,127 km.

suchozemských zvířat by však ve skutečnosti měla umožnit přímočaré určení dead reckonignu přímočařejším než u vodních živočichů a u ptáků (R. P. Wilson et al., 2008), protože pozemský pohyb nepodléhá posunům způsobených vlivem vzdušného proudění (Dall'Antonia et al., 1995) nebo oceánských proudů. (Shiomi et al., 2008). Primárním problémem pro pozemský dead reckoning tedy může být jednoduše měření rychlosti zvířete, to by mělo být zajištěno, jelikož tento přístup by měl poskytnout prostředek ke stanovení detailních poloh zvířat mezi méně častými lokalizačními údaji získanými pomocí jiných prostředků telemetrie (R. P. Wilson et al., 2008)

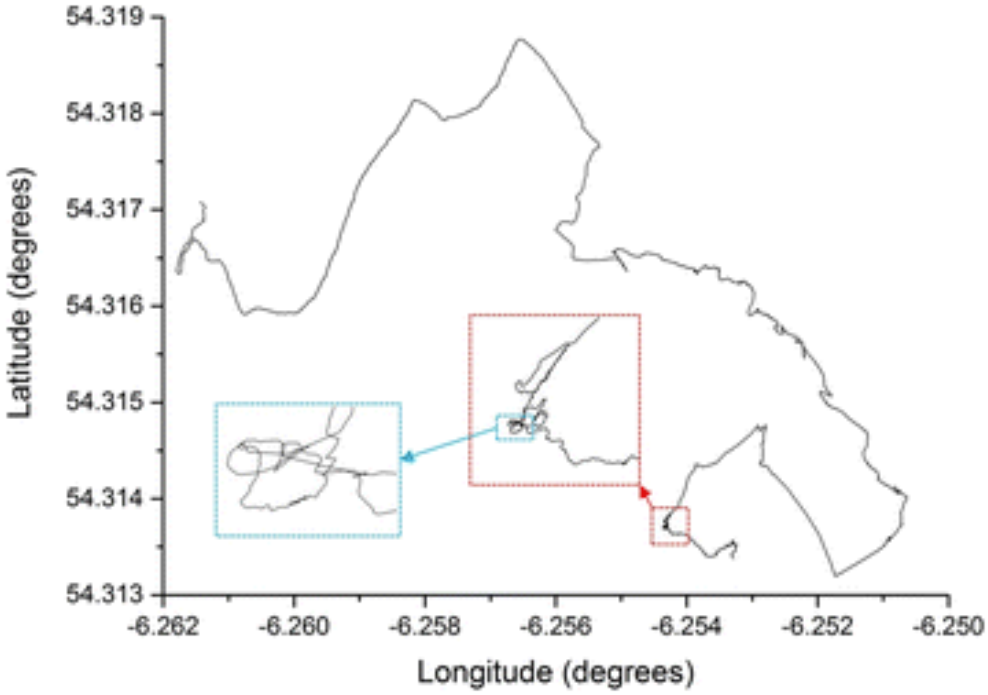
Dynamické zrychlení měřené pomocí inerciálních senzorů umístěných na zvířatech poskytuje vhodné údaje pro odhad rychlosti jedince (Bidder, Qasem, et al., 2012). Ačkoliv vztah mezi dynamickým zrychlením a rychlostí může být narušen různými změnami (sklon, terén) (Bidder, Soresina, et al., 2012), možné kumulativní odchylky, jaké byly zmíněny (R. P. Wilson et al., 2007b, 2008), mohou být odstraněny nebo opraveny pomocí informací získaných ze simultánní GPS telemetrie, která bude ve stejné době zaznamenávat pozice označeného jedince. Ve skutečnosti je tento způsob nejfunkčnějším teoretickým řešením pro suchozemský výpočet dead reckoningu. Další výhodou je použití akcelerometrických dat k definování určitých typů chování, které mohou být následně analyzovány (Brown et al., 2013b; H. A. Campbell et al., 2013; Shepard, Wilson, Halsey, et al., 2008a; Shepard, Wilson, Liebsch, et al., 2008b; Shepard, Wilson, Quintana, et al., 2008b). Metoda pozemského dead reckoningu a postup pro korekci ušlých tras na ověřené GPS polohy však dosud nebyly detailně popsány (Bidder et al., 2015a). Ten samý autor ve své nové studii popisuje postup pro využití dead reckoningu pro suchozemské živočichy pomocí nové korekce, která



Obrázek 3 - 2D cesty pohybu sledovaného člověka pomocí a) video záznamu, b) GPS, c) Dead-Reckoning bez korekce, d) Dead-Reckoning s korekcí každé 2 sec, e) Dead-Reckoning s korekcí každých 5 sec, f) Dead-Reckoning s korekcí každých 10 sec (Bidder et al., 2015)

spojuje data z akcelerometru, magnetometru s periodickými daty z GPS telemetrie. Počítání dead reckoningu má potenciál pro zaznamenávání pohybu suchozemských zvířat ve velmi detailním měřítku. Pro získání stejné úrovně podrobnosti pouze z GPS telemetrie by tato telemetrická zařízení vyžadovala velké množství energie a mohla by vyvolat v takto malém měřítku velké nepřesnosti v zaměření. Přestože se metoda dead reckoningu využívá pro mořské a sladkovodní druhy, četné metodické překážky omezily použití této fuknce na datech od suchozemských živočichů. Z počátku byl odhad rychlosti pro integraci s výpočtem dead

rekoningu pro suchozemská zvířata problematický, ale tento problém byl do zančné míry vyřešen použitím akcelerometrů a novou koreční metodou, která používá sekundarně zaměření pozice. Tato technika má potenciál rozvíjet naše chápání ekologie pohybu zvířat a informovat o modelech pohybu, které lépe odrážejí skutečnou povahu vzorců zvířecích pohybů (Bidder et al., 2015a).



Obrázek 4 - Korekce trasy dead reckoning pomocí GPS bodů zaznamenávaných v intervalu 30 minut. 670 metrů dlouhá trasa sledovaného jezevce lesního (Meles meles) po dobu přes 200 minut.Čtverce ukazují detailní pohyby zaznamenané pomocí dead reckoningu.

3.2. Analýza vysokofrekvenčních dat pro studium chování

3.2.1. Klasifikátor typů chování

Pro kvantifikaci chování zvířat se ukázalo, jako velmi účinné, použití akcelerometrů umístěných v biologgerech. Tato zařízení byla použita i pro stanovení jednotlivých typů chování u primátů - paviánů čakma (*Papio ursinus),* přestože se tento druh velmi intenzivně studuje přímým pozorováním v terénu. V této studii bylo provedeno označení volně žijících paviánu pomocí obojků, které nesly zařízení obsahující akcelerometr. Celkem bylo označeno deset jedinců. Označení jedinci byli natáčeni pomocí videokamery s cílem zachytit veškeré typy

přirozeného chování. Důležitou součástí byla následná synchronizace dat z akcelerometru a z videa z hlediska časové stopy. Na základě jednotlivých typů chování zachycených na videu byly následně popsány úseky akcelerometrických dat. K sestavení modelu chování a následné aplikaci tohoto modelu na zbylá zaznamenaná data bylo použito funkce zvané „machine learning“, která slouží k automatickému rozpoznávání nastavených a definovaných typů chování. Ve studii zaměřené na paviány se podařilo identifikovat celkem 6 typů chování, které následně rozeznal automaticky i počítač. Těchto šest typů chování pokrývalo celkem 93,3 % z celkového času pozorovaných paviánů. Odpočinek, chůze, běh a hledání potravy byly identifikovány s vysokou přesností automatického rozpoznávání chování a představující první klasifikaci více typů chování z dat akcelerometru umístěného na volně žijícím primátovi (Fehlmann et al., 2017).

Z akcelerometrických dat vycházel i Painter et al., 2016, který používal tento typ dat pro popis třech druhů chování u lišky obecné (*Vulpes vulpes).* Ve studii byl vyvinut klasifikátor typů chování a při aplikaci na získaných datech od jedné lišky pracoval s přesností 95,7 %. Tato přesnost se vztahovala k úsekům dat, které byly nejdříve manuálně roztříděny na základě pořízených videozáznamů chování označených jedinců. Metodika primární analýzy dat byla de-facto totožná s metodikou v práce Fehlmanna et al., (2017). V případě použití tzv. zobecnění klasifikátoru na druhého jedince lišky obecné (*Vulpes vulpes)* byla přesnost klasifikátoru 66,7 %, což umožňuje použití klasifikátoru na více označených jedincích a od nich získaných dat (Painter et al., 2016). Další klasifikátor chování byl vyvinut u ryb, konktrétně na druhu ryb (*Epinephelus akaara)* z čeledi kanicovitých. Data byla získávána opět z tříosého akcelerometru od biologgerem označených ryb. Ty byly natáčeny na videozáznam v akváriu se zaměřením zejména na chování při krmení potravou. Studie odlišuje tři druhy přijímání potravy vycházející z typu překládaného krmiva, a tím bylo pojídání krevet, ryb a krabů. Klasifikátor dokázal rozlišit tyto typy chování s přesností 77%, 73% a 71% (Horie et al., 2017). Akcelerometrická data definující druhy chování jsou zaznamenávána i u hospodářských zvířat. Například studie z Velké Británie od (Vázquez Diosdado et al., 2015) byla zaměřena na stanovení jednotlivých typů chování a vytvoření modelu určujícího tyto typy u mléčného skotu. Navržený model pracoval již pouze s jednou osou dat vycházejících z akcelerometru a s daty vyvozenými z tzv. VeDBA hodnoty. Metodika určení typů chování vycházela z kontinuálního sledování všech šesti označených jedinců a záznamu tohoto chování. Celkem bylo zaznamenáno 36 hodin záznamu. Ten byl použit k vyhodnocení typů chování. Výsledky porovnávající přesnost modelu vůči realitě byly následující. Pro typ ležení 98,63%, 55% pro stání, 93,10% pro krmení

(Vázquez Diosdado et al., 2015). Stejná metodika stanovení chování byla použita i u lachtanů z rodu *Arctocephalus*, kteří byli opatřeni akcelerometry a byli v průběhu této doby označení natáčeni na videokamery. Studie probíhala na území Austrálie v uzavřených akváriích. Zároveň tato studie porovnává jednotlivé typy modelů používaných pro automatické rozpoznávání typů chování na základě akcelerometrických dat. Na základě výsledků porovnání doporučuje metodu SVM („Support vector machines“) (Ladds et al., 2016). Podobná metodika byla použita i při sledování ovcí (*Dohne merino*) a nosorožců (*Ceratotherium simus, Diceros bicornis*) v jižní africe. Přesnost modelu, který zpracovával data pouze z časového úseku třech dnů u ovcí a jednoho týdne u nosorožců, byla 83,4% pro ovce a 96,1% pro nosorožce (Le Roux et al., 2017).

3.2.2. Ekologie spánkového chování

Spánek je pozorován prakticky u všech zvířat (Anafi et al., 2019) a je nezbytnou součástí života pro jeho zdraví, kognitivní výkon a vývoj. Dále posiluje základní imunitní hladinu a imunitní odpověď na případnou infekci organismu(Besedovsky et al., 2019), podporuje produkci hormonů a jejich metabolickou regulaci (Manzar et al., 2015; Medic et al., 2017), a podporuje udržování nervů, vývoj mozku a kognitivní funkce (Klinzing et al., 2019; Xie et al., 2013). Není pochyb o tom, že průměrná krátká doba spánku a ztráta spánku jsou doprovázeny četnými škodlivými účinky na zdraví a kognitivní funkce v krátkodobém i dlouhodobém horizontu (Johnsson et al., 2022; C. J. Wild et al., 2018). Zatímco množství důkazů prokazuje jeho zásadní přínosy, spánek s sebou nese také náklady na obětované příležitosti v jeho průběhu, jelikož spící zvířata se nemohou zapojit do chování zvyšujícího kondici, jakými je například potravy nebo partnerů, a také jsou v průběhu spánku vystavena většímu predačnímu riziku(Capellini et al., 2010b). Předpokládá se však, že spánek vykazuje pouze omezenou plasticitu, protože na výhody, které daným organismům fyziologicky poskytuje, nelze dlouhodobě opomíjet (S. S. Campbell & Tobler, 1984). Mezi obecný úzus patří, že jedinci stejného druhu budou mít podobnou dobu a vzorec spánkového chování, protože jejich spánek je regulován stejnými neurofyziologickými procesy (S. S. Campbell & Tobler, 1984). Zda má spánek omezené variace v rámci jednotlivců i mezi nimi, je však nejasné, protože tento jev byl studován především v laboratorním prostředí, kde chybí omezení doby spánku a přínosy pro zkrácení doby spánku. Laboratorní studie a několik existujících studií spánku ve volné přírodě jsou navíc velmi často omezeny malou velikostí vzorků nebo krátkou dobou záznamu a berou v úvahu pouze omezený rozsah podmínek prostředí. Z tohoto důvodu nedokážou odhadnout, jak se spánek mění uvnitř a mezi jednotlivci. Máme-li odhalit přínos spánku pro zdraví a vývoj

zvířat a kvantifikovat, jak se poměr přínosů a nákladů spánku liší mezi jednotlivci, kteří kontinuálně zažívají měnící se podmínky prostředí, musíme studovat spánek ve volné přírodě po dlouhou dobu (Mortlock et al., 2024).

3.3. Použití nových technologií pro studium pohybu a orientace

3.3.1. Prostorová kognice

Většina zvířat směřuje jejich pohybovou aktivitu do jimi známých oblastí, které následně tvoří domovské okrsky. Ačkoliv porozumění tvorby a změn velikosti domovských okrsků je velmi důležité pro základní výzkum a ochranu přírody, objasnění všech faktorů utvářejících dynamiku, velikost a tvorbu domovských okrsků je dosud nedostatečně zodpovězena. Obecně se má za to, že domovské okrsky jsou významně ovlivňovány základním tvarem krajiny, ve které se dané zvíře nachází (Bevanda et al., 2015). Psychometrické studie odhalují variabilitu, která se pohybuje mezi 30 a 75 % pro různé kognitivní procesy, a to jak u lidí, tak u zvířat. U dančí zvěře žijící v různě velkých societách byla kognitivní výkonnost skupiny ovlivněna faktorem tzv. kolektivní inteligence, odvozeným prostřednictvím proměnných popisujících hierarchickou strukturu studované populace, který však neovlivňuje individuální inteligenční kvocient členů skupiny. Současné studie prováděné na zvířatech k identifikaci individuálních rozdílů v kognitivních dovednostech jsou stále daleko od těch, které se používají u lidí (Pastrana et al., 2022).

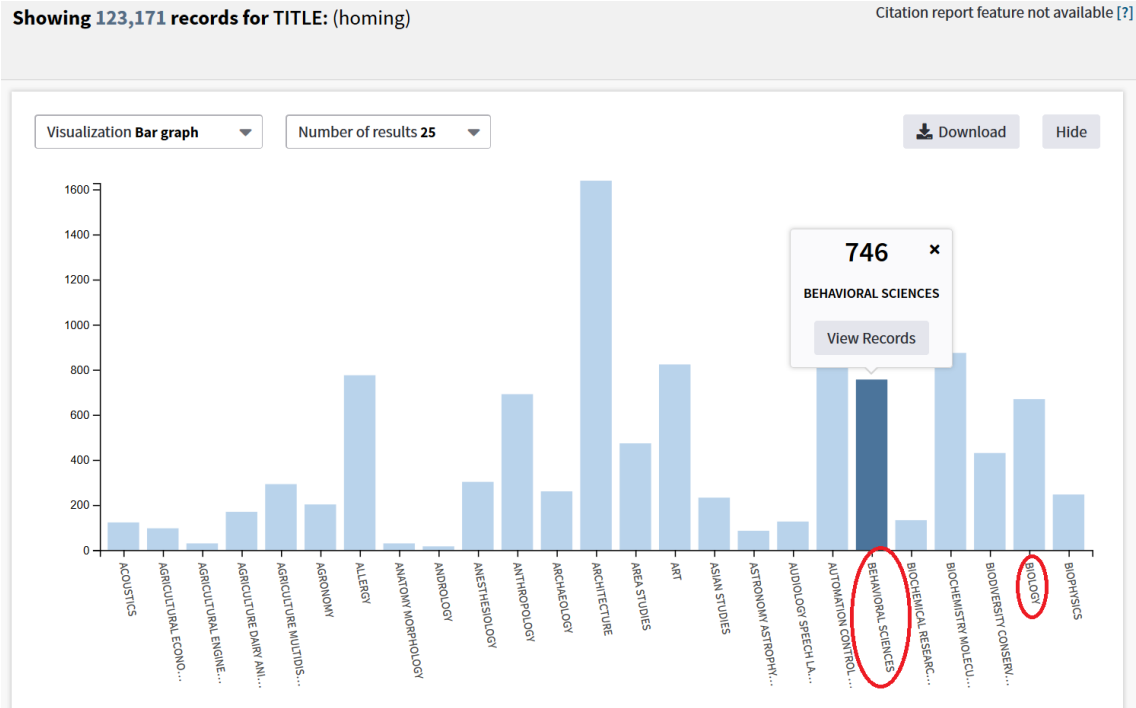
Je předpokládáno, že při nízké populační hustotě si jednotlivci volí stanoviště dle jejich vlastních preferencí a nároků, avšak s narůstající početností populace, která snižuje dostupnost zdrojů na preferovaném stanovišti, vede ke vzniku konkurence a nutí některé jedince využívat jimi méně preferované habitaty. Pro regulaci populací, složení společenstev a řízení vlivů na biodiverzitu ekosystému je velmi klíčové pochopit a porozumět, jak se mění výběr stanovišť v závislosti na populační hustotě (Pérez-Barbería et al., 2013). Narušení volně se pasoucích býložravců lidskou rekreační aktivitou může mít vliv na výživu zejména kvůli kompromisu, který vzniká ustoupením zvěře z potravně preferovaných stanovišť. K ústupu dochází z důvodu zvěří vnímaného predačního rizika (Jayakody et al., 2011).

3.3.2. Návratové strategie

Homing je schopnost zvířat najít cestů domů (Cabridge Dictionary). Homing může být také popisován jako inherentní schopnost zvířete navigovat k původnímu místu přes neznámé oblasti. Toto místo může být buď domovským okrskem, nebo místem, kde dochází k rozmnožování (Wikipedia).

Při zadání slova homing do vědecké databáze odborných publikací – Web of knowledge bylo nalezeno celkem 123 171 vědeckých publikací obsahujících slovo homing. Jelikož je termín homing používán ve více významech, které nemusí být přímo spjaty s výše uvedenou definicí týkající se našeho zájmu, je nutné se zaměřit pouze na biologická odvětví. Zde bylo nalezeno celkem 746 záznamů slova homing, a to pouze v odborné literatuře zabývající se studiem chování živočichů. Další zajímavostí byl výsledek 659 záznamů slova homing ve vědeckých publikacích umístěných v sekci biologie.

Vyvinutí účinného homingu, čímž je návrat na dříve známé místo, je zásadní pro přežití jakéhokoliv zvířete, které je uzpůsobeno k pohybu. Zvířata provádějí homing napříč různě velikými prostředími a jakýmkoliv typem krajiny, a to za použití různých typů mechanismů senzomotorických systémů, které byly formovány evolucí a ekologickými podmínkami.



Obrázek 5 - Grafické znázornění výsledků vyhledávání ve vědecké databázi slova homing v publikovaných článcích. Červeně zvýrazněné jsou oblasti zájmu této práce – vědy o chování a biologie. (zdroj – Web of knowledge)

Navigace zvířat, prostorová orientace a paměť jsou základní schopnosti, které zvířatům umožňují dosáhnout konkrétních cílů, jako jsou zdroje potravy, místa k páření a hnízdiště, a efektivně využívat prostorově seskupené zdroje (Alerstam & Bäckman, 2018b; Kashetsky et al., 2021b). Mnoho živočišných druhů vykazuje věrnost vůči nějaké lokalitě, což znamená, že se každou sezónu vracejí na určité místo nebo se celý rok zdržují v okolí této oblasti (Milner-Gulland et al., 2011). Obvykle se tato zvířata, která vykazují vysokou fidelitu vůči dané lokalitě, vracejí na místo odchytu ihned po translokaci nebo velmi blízko místu typickému pro jejich stávaniště (Falcón-Cortés et al., 2021; Papi, 2012a). Existují různé důvody pro takové upřednostňování určitých částí domovských okrsků, ale velmi často jsou spojeny s teritoriálním chováním, s místy páření (Crump, 1986; Lohmann et al., 2017), nebo prostorovou pamětí a vytvářením domovského okrsku na základě kognice (Merkle et al., 2014; Van Moorter et al., 2009).

Znalost podnětů, které zvířata používají při homingu, je jednou z hlavních výzev v tomto studijním oboru, a to zejména proto, že mnoho z těchto podnětů nejsou pro člověka rozpoznatelnými. Přes mezidruhové rozdíly, lze většinu mechanismů homingu vysvětlit pomocí některých obecných mechanismů (Mandal, 2018; Mandal et al., 2017). S naším současným chápáním však můžeme poukázat na tři zjevné podněty homingu. Těmi jsou podněty - genetické (neboli vrozené), smyslové a podněty závislé na paměti (Jander, 1975). Tyto zdroje informací lze také rozdělit na podněty vnější neboli alothetické podněty, které zvířata získávají z prostředí prostřednictvím smyslového vnímání (Mittelstardt & Mittelstardt, 1973), a vnitřní podněty, které zahrnují vrozené preference, vzpomínky z paměti a idiothetické podněty jakými je propriocepce (Mandal, 2018).

Ze všech alothetických podnětů je světlo vnímané jako vidění obvykle nejdůležitějším podnětem pro zvířata se zrakem (Cronin & Bok, 2016). Navzdory rozdílům ve vnímání vizuálních podnětů u zvířat získávají všechna „vidoucí“ zvířata mnohem spolehlivější prostorové informace prostřednictvím zraku, který jim umožňuje získávat informaci jak z astronomických podnětů, tak i z okolní krajiny (Mandal, 2018).

Již v roce 1911 Santschi demonstroval, že mravenci mohou používat polohu nebeských těles k výběru a udržení určitého směru pohybu (Santschi, 1911). Nyní je dobře známo, že zvířata používají různé nebeské podněty a tělesa pro orientaci a navigaci, v závislosti na době jejich činnosti a dostupnosti vybraných podnětů. Vše vždy vychází ze základní biologie

konkrétního druhu, zatímco noční hmyz se podstatně spoléhá na velká nebeská těla, jako je Měsíc nebo Mléčná dráha (Dacke et al., 2013; el Jundi et al., 2015; Warrant & Dacke, 2011, 2016); denní hmyz jako například pouštní mravenci se spoléhají spíše na polarizované sluneční světlo než na polohu slunce (Marshall & Cronin, 2011; v. Frisch, 1950; Wehner, 1984; Wehner & Müller, 2006). Když se mořské želvy vylíhnou v noci, dostanou se nejrychleji do moře pohybem směrem k „nejméně tmavému" horizontu (Lohmann & Lohmann, 1996), který moře obvykle poskytuje v noci. Pokud je ale pláž uměle osvětlená, což je docela běžné na plážích ovlivněných světelným znečištěním, namísto toho mláďata putují opačným (pro ně špatným) směrem do vnitrozemí.

Zvířata ale také odvozují podněty homingu z pevně stanovených bodů v terénu s odlišnými vlastnostmi (tvar, velikost a barva). Tyto body se nazývají orientační body – tzv. landmarks. Tyto orientační body se mohou vyskytovat podél známých cest, v okolí cíle nebo na poměrně vzdálených místech (např. pohoří). Zvířata se často orientují podle známých orientačních bodů, tyto body jsou pro ně ukazatelé směru cesty do požadovaného cíle. Zvířata si často stanoví směrové vedení od orientačních bodů, tyto orientační body pak fungují jako ukazatele. Namísto stanovení směru k orientačnímu bodu zvířata občas použijí tento bod jako počátek cesty, a poté si stanoví směr k dalšímu referenčnímu bodu směrem od bodu orientačního. Tento referenční bod je v tomto případě nazýván majákem (Mandal, 2018). Hmyz velmi často používá prominentní předměty (orientační body) v okolí svého domova nebo majáky v místě sběru potravy (Graham et al., 2003). Hmyz používá známé orientační body alespoň pro čtyři základní navigační účely: rozpoznávání okolí, k páření, pro směrování k majákům (např. místům s potravou) a pro rozpoznání daného místa (T. S. Collett, 1996). I vzdálené vizuální podněty mohou sloužit pro zvířata jako majáky (Gould & Gould, 2012), například mravenci (Nicholson et al., 1999) a včely medonosné (Apis melifera) (Anderson, 1977; Frisch, 1967) jsou známé z používání těchto vzdáleně umístěných majáků. Zvířata mohou také získat prostorový odkaz na cíl z vizuálního panoramatu okolní krajiny, který může být tvořen blízkými nebo vzdálenými orientačními body, a panoramatem oblohy (obrazový profil generovaný pozemskými objekty kontrastujícími proti obloze) (Graham & Cheng, 2009).

Olfakce je jednou z prvních smyslových modalit, která se objevila v průběhu evoluce a je rozhodně jednou z nejdůležitějších smyslových modalit, kterou zvířata používají pro orientaci a navigaci (Jacobs, 2012; D. A. Wilson & Stevenson, 2006). Zatímco mnoho zvířat používá čichové podněty produkované jimi samotnými nebo jinými zvířaty za tímto účelem, několik zvířat může používat gradienty pachů z prostředí (odvozených například z atmosférických

stopových plynů (Wallraff & Andreae, 2000). A také mnoho dalších, jako jsou můry (Cardé & Willis, 2008), korýši (Weissburg & Zimmer-Faust, 1994) a ptáci (Wallraff, 2015), používají pachy z okolního prostředí, které jsou distribuovány nepravidelně ve formě pachových chomáčků (Vickers, 2000) nebo čichových landmarků (Steck, 2012). Takové zápachy prostředí jsou pro zvířata čichovou krajinou (Atema, 1996).

Pohyb v prostoru způsobený čichovými podněty je dobře známý také u sociálního hmyzu – mravenci (Steck, 2012), včely (Frisch, 1967; Reinhard & Srinivasan, 2009). Mnoho druhů mravenců pokládá na zem tyto feromonové stezky v průběhu návratu od zdroje potravy, po kterých se další členové ze stejné kolonie mohou později vypravit k potravě, a poté zase vrátit zpět do svého hnízda (Cardé et al., 1995; Hölldobler & Wilson, 1990). Tento proces je aplikován každým jedincem po vyzvednutí potravy, což vede k navrstvení feromonu na cestu a zpět do svého hnízda, čímž se posíluje intenzita podnětu na dané cestě. Jakmile je ovšem zdroj potravy vyčerpán, přestane být pokládán feromon na cestu, a čichové podněty tak postupně vymizí. Je také známo, že mravenci (Sturgis et al., 2011), včely (Saleh et al., 2007) a vosy (Jandt et al., 2005) označují svůj vstup do hnízda nebo okolí svého hnízda chemikáliemi vylučovanými z těla a příslušící dané kolonii. Tento zápach, jim pomáhá určit jejich vchod do hnízda a odlišit ho od ostatních. Jako pachové orientační body se také používají pachy z okolního přírodního prostředí (Buehlmann et al., 2015; Menzel & Greggers, 2013). Zajímavé je, že při vystavení daného jedince pachu spojeného s některým známým místem může vyvolat navigaci na toto místo. Tento jev byl popsán zejména u včel (Balbuena et al., 2012; Reinhard et al., 2004). V současnosti je velmi detailně popsána olfakce u hmyzu, zejména již zmiňované stopovací feromony apod. Avšak u savců nebo ptáků je tento jev vztažený k prostorové orientaci popsán velmi málo.

Mnoho stěhovavých ryb (lososovité ryby (Phillips, 1986; Putman et al., 2013), mořská želva (Lohmann et al., 2008), ptáci a savci (Walker et al., 2002; Wiltschko & Wiltschko, 2005) a hmyz (Dreyer et al., 2018), a plus některá nemigrující zvířata (holuby (Mora et al., 2004), humr (Boles & Lohmann, 2003), včetně sociálního hmyzu (Wajnberg et al., 2010), využívají magnetické pole Země jako důležitý podnět orientace pomocí jejich biologického geomagnetického kompasu. Mravenci (Banks & Srygley, 2003; Buehlmann et al., 2012) a včely (Frier et al., 1996; Walker & Bitterman, 1989) jsou citliví na lokální anomálie v intenzitě geomagnetického pole a mohou takovéto anomálie používat jako orientační body pro navigaci v prostoru. Tyto anomálie mění orientaci železitých granulek nalezených v trofocytech, které obklopují abdomen těla hmyzu; to zase mění cytoskeletální strukturu těchto buněk a vytváří

neurální „magnetosignály“ (Hsu et al., 2007). Nedávná studie ukazuje, že geomagnetické pole poskytuje nezbytný a dostatečný referenční systém pro orientaci kompasu u mravenců (Fleischmann et al., 2018). Na magnetorecepci se pravděpodobně podílí více orgánů a tělesných mechanismů, které obecně fungují v kombinaci s jinými smyslovými podněty (Gould, 2008), jakými je například světlo (Muheim et al., 2016; Phillips et al., 2010).

Zvířata se někdy pohybují a udržují stabilní postavení těla vzhledem k podnětu. Například poštovní holubi a mnoho stěhovavých ptáků používá magnetické pole Země jako referenční bod, nicméně však samotný pohyb není vždy ve směru od severu na jih, ale používají různé azimuty (Leask, 1977). Orientují se částečně směrem vůči relativnímu podnětu, ale ne přímo ku nebo od daného podnětu. Přes své velmi časté používání není termín orientace pokaždé používán správně (Jander, 1975; Schone, 2014). Často může být odkazováno na orientaci jednotlivých částí těla vůči sobě navzájem, nebo na orientaci celého těla v prostoru vzhledem na působení vnější a vnitřních stimulů, stejně tak jako orientaci kompasu (Hansson & Åkesson, 2014). Orientace může být definována jako mechanismus, kterým zvířata posuzují svoji aktuální polohu v prostoru vzhledem ke stanovenému cíli (Able, 2001), což může zahrnovat chování, které aktivně kontroluje jejich umístění v prostoru (Jander, 1963), nebo to může být použito jako obecnější termín zahrnující také navigaci (Mandal, 2018).

Pro prostorovou orientaci se mohou zvířata spolehnout na svůj systém biologického kompasu (např. geomagnetický, nebeský nebo panoramatický kompas). Vektorová navigace a/nebo informace získaná konspecifika (komunikace tancem hmuzu nebo pomocí feromonů). Aby se sociální skupiny hmyzu správně orientovaly pomocí jejich allothetického kompasu, musí mít tzv. prostorovou znalost (Mandal et al., 2017; Pahl et al., 2011; Wystrach et al., 2012; Wystrach & Graham, 2012). Aby se sociální blanokřídlí hmyz stal obeznámeným s obklopujícím okolním prostředím, provádějí tzv. průzkumné pohyby kolem svých hnízd. Tyto pohyby se nazývají orientace a patří mezi ně např. průzkumné lety, které předcházejí pohybům spojeným s vyhledáváním a přinášením potravy. Díky těmto pohybům si vytvářejí a zapamatovávají orientační body v okolích svých hnízd a stávanišť (Fleischmann et al., 2016, 2017; Wystrach & Graham, 2012). Je velmi zajímavé, že ve struktuře orientačních letů/pochůzek apod., byla pozorována nápadná podobnost napříč různými taxony jakými, jsou např. hmyz, ptáci a savci (Capaldi et al., 1999).

Kognitivní mapa je mentální reprezentací prostoru, ve kterém si zvířata pamatují prostorové (a pravděpodobně i geometrické) vztahy napříč lokalitami s odkazem na relativní směry a vzdálenosti mezi nimi (O’Keefe, 1978; Tolman, 1948). V takové mentální reprezentaci mohou

známé alothetické podněty (orientační body) konstruovat komplexní rámec prostorových referencí (M. Collett et al., 2013; Fagan et al., 2013). Ačkoliv aximatická definice kognitivní mapy je stále předmětem debaty (Cheeseman et al., 2014; Cheung et al., 2014; Jacobs, 2003), tak kognitinví mapa zahrnuje obojí informaci – topologickou, která udává celkové prostorové uspořádání orientačních bodů, a metrickou informaci, která poskytuje údaje o lineárních a úhlových vzdálenostech mezi orientačními body (Poucet, 1993). Přítomnost takovýchto kognitivní map je naznačována u různých taxonů – korýši (Vannini & Cannicci, 1995), savci (Tsoar et al., 2011) a včely (Gould, 1986; Menzel et al., 2005).

Podobný model, ve kterém se zvířata navigují pomocí směru kompasu a prostorových vztahů mezi krajinnými prvky a relativní polohou cíle, bývá nazývána mozaikovou mapou (Wallraff, 1974). Zvířata mohou získat mozaikovou mapu svého domovského okrsku pomocí pravidelných návštěv příslušných lokalit, a mohou ji také rozšiřovat pomocí průzkumu nových oblastí (Gould, 2004). Mnoho zvířat se také může naučit tzv alinghment, a hodnotit tak rychlost změny jednoho nebo více gradientů v prostředí takovým způsobem, který jim umožní reprezentovat prostor jako mapu dvou souřadnicového systému (zeměpisnou šířkou a délkou) (Putman et al., 2011), často nazývána jako mapa gradientů nebo mřížková mapa. Zjišťováním polohy na dvou souřadnicích (např. porovnáním hodnot souřadnic neparalelních gradientů od aktuálního umístění a „domova“) mohou zvířata určovat svou polohu v dvourozměrném prostoru, což umožňuje i přemístěným zvířatům najít domov z neznámých míst. Například je známo, že zvířata hodnotí gradient olfakce a gradient magnetického pole Země (Buehlmann et al., 2012; Lohmann et al., 2007) ve známém prostoru a mimo známou oblast tyto hodnoty extrapolují (Gould, 2014; Phillips et al., 2006). Navigace s prostorovou referencí na kognitivní, mozaikové nebo gradientní/rastrové mapy je souhrnně označována jako mapami podložená navigace (Able, 2001; Papi, 2012b).

3.3.3. Translokace označených jedinců

Pravá navigace a navigace pomocí mapových podkladů během většiny cest při homingu má velmi zřídka přístup k domovským orientačním bodům, které jsou umístěné v oblasti cílového bodu. Zejména zvířata, která jsou pasivně přemístěna, mohou také potřebovat přímou cestu k domovu, kterou nikdy předtím neabsolvovala. Tyto zvířata často potřebují navigovat a spoléhat se pouze na informace, které mají k dispozici na velmi vzdálených místech. Je

předpokládáno, že mnoho zvířat použitím alothetických podnětů vytváří komplexní prostorové zobrazení, které jim umožňuje určit jejich relativní polohu vzhledem k cíli nebo jinému známému i neznámému místu, a to i z nových míst (Gould, 2014). Navigace pomocí takové prostorové reprezentace bývá označována jako tzv. pravá (skutečná) navigace (Able, 2001; Boles & Lohmann, 2003; Gould & Gould, 2012).

K homingu savců bylo publikováno již několik vědeckých článků. Například tendence translokovaných jedinců medvěda baribala (*Ursus americanus*) k navracení se na velké vzdálenosti z nového prostředí do svého původního areálu vedla k velmi intenzivnímu studiu homingu u tohoto druhu. Velmi často se tak autoři zabývali homingem u medvěda baribala (*Ursus americanus*) na americkém kontinentu viz (Harger, 1970); (McCollum, 1974); (Alt, 1977); (McLaughlin et al., 1981); (Rogers, 1986). Pozitivní vztah tohoto velkého savce poskytl některé velmi poučné informace o orientaci savců (Rogers, 1988).

Hawkins & Montgomery, (1969) provedl pokus na 28 jedincích jelence běloocasého (*Odocoileus virginianus*), které přemístil na vzdálenosti 25, 36 a 6 mil vzdušnou čarou do třech nových lokalit. Tyto jedinci byli po přemístění sledováni pomocí radiotelemetrie. Dva jedinci z celkového počtu 28 označených kusů projevili homing strategii. Dospělá laň se vrátila do původní lokality po 169 dnech od přemístění na vzdálenost 25 vzdušných mil. Dále se po 23 dnech od přemístění na vzdálenost 6 vzdušných mil vrátila jednoletá laň do své původní lokality.

Fernando et al., (2012) provedl ve své studii translokaci 12 jedinců slona indického (*Elaphas maximus*). Z celkového počtu projevili pozitivní homing chování tři jedinci, kteří se vraceli do původní lokality, a přitom překonávali vzdálenosti od 46 do 116 kilometrů. Jeden jedinec byl celkově třikrát přemístěn do nové lokality a po každé se vrátil do původního areálu. V této studii bylo použito GPS telemetrie, což je plánováno i v tomto grantu.

V tuzemské a zahraniční literatuře bylo provedeno ve většině případů studium homingu velkých savců, které se zakládalo pouze na odchycení jedince v jedné lokalitě a následně přemístění do různě vzdálené nové lokality. Poté se sledovalo, zdali se podaří tohoto jedince znovu odchytit v první lokalitě, ze které byl přemístěn. Jen několik studií použilo pro sledování přemístěných jedinců telemetrické sledování, viz (Hawkins & Montgomery, (1969) u jelence běloocasého (*Odocoileus virginianus*), a dále Fernando et al., 2012) u slonů indických (*Elephas maximus*). V tuzemské literatuře nejsou o studiu homingu u velkých savců téměř žádná informace. Pokud se zaměříme na samotné druhy prasete divokého *(Sus scrofa*) a jelena

evropského (*Cervus elaphus*), tak nebyl nalezen žádný článek týkající se sledování těchto druhů pomocí GPS a biologging technologie a přemísťování do nových lokalit.

4. Metodika

Disertační práce je sestavena z celkem šesti vědeckých publikací, které byly tematicky zařazeny do tří hlavních okruhů. V první části byla metodika směřována na vývoj hybridního zařízení, které bude možné používat pro prostorovou orientaci a chování volně žijících druhů spárkaté zvěře. Prvotním krokem bylo využití dosavadního typu GPS obojku, který se standartně využívá pro sledování různých druhé živočichů, a v průběhu životnosti, která je u zařízení pro savce cca 700 dnů, se pokusit implementovat zařízení pro kontinuální záznam detailních parametrů zaměřených na akceleraci a magnetickou orientaci senzoru, potažmo označeného jedince. Pro testování vývoje hybridní technologie, která se skládala z GPS jednotky a multi-senzorového zařízení zvané „bio-logger“, bylo vybráno prase divoké (*Sus scrofa)* jako vzorový druh zvěře pro ověření funkčnosti zařízení, validaci dat a odolnosti hardware technologie. Následně byla použita data získaná z hybridního GPS-Biologging obojku i od jelení zvěře a dalších živočišných druhů uvedený v publikaci *„Animal lifestyle affects acceptable mass limits for attached tags“* (R. P. Wilson, Rose, Gunner, et al., 2021a).

4.1. Vývoj a testování hybridní GPS-Biologging technologie

Pro vývoj nového hybridního zařízení bylo použito několik dílčí kroků vedoucích k sestavení prototypu GPS obojku nesoucího tzv. biologger. Při vývoji probíhalo testování na celkem šesti jedincích prasete divokého (*Sus scrofa),* kteří byli uspaní a označeni 2 typy obojků nesoucí odlišně umístěné zařízení pro sběr dat. Tito jedinci byli označeni v aklimatizační obůrce o rozměrech 38 x 46 metrů a byli kontinuálně sledování pomocí kamerového systému.

Celkem byly použity dva tzv. multisenzorové obojky nesoucí zařízení v následujícím složení: GPS modul typu Vertex Plus od výrobce Vectronic Aerospace, GmbH včetně baterie a tzv. biologger typu „Thumb Daily Diary“. Tento typ biologgeru byl vybaven tříosým akcelerometrem, tříosým magnetometrem a naprogramován pro kontinuální záznam dat ve všech osách o frekvenci 10 Hz s úložištěm na kartu typu MicroSD. Multisenzorové obojky nesoucí výše zmiňované senzory byly vybaveny funkcí „Drop-off“, která umožňovala rozepnutí obojku pomocí vzdáleného ovládání a příkazu. V tomto případě tedy nebyla nutná imobilizace zvířete pro sundání obojku. GPS modul byl nastavený pro záznam pozičních dat

GPS o frekvenci 30 minut a zasílání zaměřených pozic pomocí dálkového spojení přes mobilní síť se serverem pro příjem GPS pozic každých 8 hodin. Celý systém byl napájen jednou baterií umístěnou ve spodní části obojku s odhadovanou dobou životnosti 730 dnů. Vyvinutý hybridní systém byl sestaven o celkové hmotnosti 716 g. V rámci studie byly použity i tzv. „Single-tag“ obojky, které obsahovaly pouze senzory typu „Square Daily Diary“ zaznamenávající akcelerometrická a magnetometrická data v tříosém systému na frekvenci 10 Hz na zařízení MicroSD bez dalšího záznamu GPS pozic a drop-off systému obojku. Získaná akcelerometrická a magnetometrická data byla použita zároveň i v analýzách spolu s daty získanými z hybridního obojku.

Celkem bylo v rámci výzkumu označeno 71 dospělých jedinců (starších dvou let nebo vážících více než 40 kg) prasete divokého (51 samic, 18 samců, 1 nevyhodnocený). Veškerá získaná data zahrnovala více než 6000 sledovacích dnů obsahujících validní data. Na základě dat získaných od šesti jedinců v aklimatizační obůrce byly vyvinut a následně na datech od volně žijících zvířat testován behaviorální model pro několik typů chování. Behaviorální model byl vyvinut na základě akcelerometrický dat, která byla vhodná pro odlišení těchto typů chování černé zvěře – chůze, běh, krmení, stání, odpočinek a ostatní). Na základě videozáznamů chování označených jedinců v aklimatizační obůrce byla synchronizována akcelerometrická data v software DDMT a tato informace byla použita pro tzv. „Machine learning“, který slouží k vytvoření automatické detekce stejných proměnných v záznamu akcelerometrických datech, což umožňuje následnou automatizace v rozpoznávání jednotlivých typů chování a jejich kvantifikaci v pořízených datech.

Vhodnost použití biologging senzorů obsahující akcelerometr a magnetometr v kombinaci s obojkovou GPS technologií, s váhovým limitem celého systému do 3% tělesné váhy zvířete, byla testována na několika dalších druzích, jakými byly jedinci od jelena evropského (*Cervus elaphus),* koaly medvídkovité *(Phascolarctos cinereus),* vačice horské *(Trichosurus cunninghami),* paviána anubi *(Papio Anubis)* a přímorožce arabského *(Oryx leucoryx).*

4.2. Použití nové technologie pro studium detailního pohybu a spánkových režimů zvířat

Pro studium detailního pohybu zvířat pomocí akcelerometrů a magnetometrů bylo vybráno celkem pět druhů volně žijících zvířat – prase divoké (*Sus scrofa*), lev africký (*Panthera leo*), kamzík horský (*Rupicapra rupicapra*), kozorožec horský (*Capra ibex*), ovce kruhorohá (*Ovis orientalis*) a koza bezoárová (*Capra aegagrus*). Označení jedinci byli sledování v rozmezí 15 – 250 dnů a po celou dobu byla zaznamenána akcelerometrická a magnetometrická data o frekvencích 10 – 40 Hz. Získaná data byla použita pro určení pohybových charakteristik pomocí funkce dead-reckoningu, která byla následně upravována pomocí periodicky získávaných GPS pozici. Z těchto dat bylo následně extrahováno cca 24-50 hodin dat s drobnými odchylkami tak, aby se zajistilo, že se jedná o pohybová data. Na exportovaném datasetu byla vyhodnocena hodnota VeDBA, která byla použita jako proxy hodnota pro rychlost, a také pro úhlovou rychlost. Celkem bylo vyhodnoceno přes 20 000 záznamů úhlové rychlosti založené na parametru VeDBA od téměř všech sledovaných druhů zvířat.

Pro klasifikaci a kvantifikaci spánkových režimů prasete divokého (*Sus scrofa)* ve volné přírodě v závislosti na lidské aktivitě v povětrnostních podmínkách v dané lokalitě bylo sledováno celkem 28 jedinců prasete divokého (4 samci, 24 samic) ve dvou oblastech České republiky – Doupovské hory a Kostelec nad Černými lesy (Lesy ČZU). Pomocí hybridní GPS-Biologging technologie byli sledovaní jedinci označeni po dobu v rozmezí 10 – 363 dnů. Klasifikace spánku na akcelerometrických datech byly vyhodnocena pomocí již dříve získaných akcelerometrických dat a s nimi synchronizovaných videozáznamů z aklimatizační obůrky (viz. Kapitola 4.1.). Pro stanovení spánku byla použita kombinace záznamu všech tří os z akcelerometru a parametr VeDBA. Dále byly použity meteorologické záznamy o teplotě a srážkách ze stanic v daných lokalitách, a také data o návštěvnosti lokalit lidmi v průběhu sledování. V lokalitě Doupov byla návštěvnost rovna nule, jelikož je prostor omezen pro vstup veřejnosti. V lokalitě Kostelec nad Černými lesy (Lesy ČZU) byla použita data z automatických přístrojů pro záznam návštěvnosti u turistických tras.

4.3. Navigační schopnosti sledovaných jedinců jelena evropského a distribuce energie v závislosti na managementu populace

Řízený experiment translokace celkem 23 jedinců jelena evropského (*Cervus elaphus*) byl realizován u dvou populací na území České republiky v lokalitách Kladská a Doupovské hory. Celkem bylo realizováno 35 řízených translokací od 23 jedinců jelena evropského, kteří byli označeni pomocí GPS a biologging technologie. Získaná GPS data v 30minutových intervalech byla použita pro výpočet relativního azimutu mezi bodem vypuštění a jádrem domovského okrsku. Data byla vyhodnocena pomocí testu MANOVA, a to pro všechny relativní azimuty z GPS pozic ve vzdálenosti 100 m, 500 m, 1 000 m a 5 000 m od lokality vypuštění směrem k lokalitě centra domovského okrsku.

Pro studium vhodnosti používání přezimovacích obůrek, jako nástroje pro management jelení zvěře v lesních oblastech s cílem eliminace škod na lesních porostech, z hlediska wellfare a wellbeingu byla analyzována akcelerometrická data od 11 samic jelena evropského (*Cervus elaphus).* Získaná akcelerometrická data od jelení zvěře v oblasti Doupovských hor byla vyhodnocena pro roky 2019 a 2020, kdy byli označení jedinci sledovaní paralelně uvnitř i vně přezimovací obůrky v dané zimní sezóně. Získaná akcelerometrická data poskytla hodnoty pro získání parametru VeDBA a jeho následné testování pro intra-druhové variance v závislosti na typy prostorového managementu. Hodnoty VeDBA byly využity jako proxy pro stanovení spotřeby energetické energie označených zvířat v průběhu zimního období. GPS data určila nebo vyvrátila využívání přezimovací obůrky a prostorovou aktivitu sledované zvěře.

Veškerá manipulace s volně žijící zvěří na území ČR byla prováděna na základě schváleného projektu pokusů s kvalifikací a odbornou způsobilostí na úseku pokusných zvířat dle §15d odstavce 2 písmeno a) zákona č. 246/1992 Sb., na ochranu zvířat proti týrání, v platném znění.

5. Syntéza výsledků

Disertační práce je složena z pěti publikovaných vědeckých publikací a jednoho submitovaného manuskriptu. Pořadí autora disertační práce v uvedených publikacích je následující: třikrát prvoautor (jeden článek je ve formě sdíleného prvoautorství z důvodu stejně významných rolí prvních dvou autorů), jedenkrát druhoautor a dvakrát člen kolektivu autorů. Celkový počet pět ze šesti vědeckých publikací byly přijaty a publikovány ve vědeckých časopisech uvedených na Web of Science. Jedna publikace má statut in review. Výsledky disertační práce jsou rozděleny do třech základních okruhů, které jsou tematicky propojeny a vedou ke splnění cílů uvedených v zadání disertační práce. První okruh výsledků – 5.1. (Vývoj a testování GPS-Biologging technologie), je zaměřen na vývoj a testování nového hybridního zařízení obsahující GPS telemetrii a biologging technologii. V rámci této části výsledků bylo testována funkčnost a vhodnost vyvinutého zařízení a reliabilita zařízením poskytovaných dat. Druhá část výsledků – Výsledky 5.2. (Analýza biologging dat pro studium chování a pohybu zvířat) obsahuje publikace zaměřené na použití vyvinuté technologie pro popis a studium pohybu a chování označených jedinců pomocí biologging technologie. Výsledky daných studií vycházení z použití hybridní technologie a zaměření se na primárně na biologging data. Poslední, třetí část výsledků disertační práce – Výsledky 5.3. (Prostorová orientace a fidelita zvěře) obsahují poznatky získané z analýzy dat získaných pomocí GPS technologie a zaměřených na prostorové chování, fidelitu velkých savců a využití energie.

5.1. Vývoj a testování GPS-Biologging technologie

5.1.1. Publikace č. 1 - Development of a multi-sensor biologging collar and analytical techniques to describe high-resolution spatial behavior in free ranging terrestrial mammals

První publikace – *„Development of a multi-sensor biologging collar and analytical techniques to describe high-resolution spatial behavior in free ranging terrestrial mammals*.“ je zaměřena na vývoj hybridní technologie, které obsahuje možnost kombinace a simultánního sběru dat z GPS technologie a Bio-logging technologie. V rámci studie bylo vyvinuto vlastní zařízení kombinující obě zmiňované technologie. Pro vývoj a testování hybridního systému bylo označeno a sledováno celkem 71 volně žijících jedinců prasete divokého (Sus scrofa), kteří poskytli validní data pro ověření pořízených dat a sestavení behaviorálního modelu pro šest základních typů chování sledovaného druhu. Od sledovaných jedinců se podařilo získat téměř 94 % zaznamenaných dat. Behaviorální model vytvořený na všech získaných biologging datech dosáhnul přesnosti 85 % ve všech šesti typech chování. Přesnost vyvinutého modelu byla ověřena pomocí reálných záznamů chování, které byly klasifikovány pomocí video záznamů všech uvedených druhů chování. Vyvinutý systém je vhodný pro sledování suchozemských druhů zvířat.

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Development of a multisensor biologging collar and analytical techniques to describe high-resolution spatial behavior in free-ranging terrestrial mammals

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Abstract

Biologging has proven to be a powerful approach to investigate diverse questions related to movement ecology across a range of spatiotemporal scales and increasingly relies on multidisciplinary expertise. However, the variety of animal-borne equipment, coupled with little consensus regarding analytical approaches to interpret large, complex data sets presents challenges and makes comparison between studies and study species difficult. Here, we present a combined hardware and analytical approach for standardizing the collection, analysis, and interpretation of multisensor biologging data. Here, we present (i) a custom-designed integrated multisensor collar (IMSC), which was field tested on 71 free-ranging wild boar (*Sus scrofa*) over 2 years; (ii) a machine learning behavioral classifier capable of identifying six behaviors in free-roaming boar, validated across individuals equipped with differing collar designs; and (iii) laboratory and field-based calibration and accuracy assessments of animal magnetic heading measurements derived from raw magnetometer data. The IMSC capacity and durability exceeded expectations, with a 94% collar recovery rate and a 75% cumulative data recording success rate, with a maximum logging duration of 421 days. The behavioral classifier had an overall accuracy of 85% in identifying the six behavioral classes when tested on multiple collar designs and improved to 90% when tested on data exclusively from the IMSC. Both laboratory and field tests of magnetic compass headings were in precise agreement with expectations, with overall median magnetic headings deviating from ground truth observations by 1.7° and 0°, respectively. Although multisensor equipment and sophisticated analyses are now commonplace in biologging studies, the IMSC hardware and analytical framework presented here provide a valuable tool for biologging researchers and will facilitate standardization of biologging data across studies. In addition, we highlight the potential of additional

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analyses available using this framework that can be adapted for use in future studies on terrestrial mammals.

KEYWORDS
accelerometer, behavioral classification, biologging, dead-reckoning, GPS, machine learning, magnetic compass heading, magnetometer

JEL CLASSIFICATION
Spatial ecology

1 | INTRODUCTION

In recent decades, animal-borne sensors designed to monitor physiology, behavior, movement, and environmental conditions have revolutionized studies of animal ecology in diverse taxa across a range of spatiotemporal scales (Ropert-Coudert & Wilson, 2005; Rutz & Hays, 2009; Williams et al., 2020; Wilmers et al., 2015). This has been made possible due to advances in sensor technology, data management, and analytical techniques, which now underpin both theoretical and applied research on wild animals (Cooke et al., 2012; Rattenborg et al., 2016; Vyssotski et al., 2006; Wilmers et al., 2015). However, the emergence of novel biologging techniques requires a multidisciplinary approach, often relying on diverse expertise in areas beyond wildlife ecology (Jolles, 2021; Kays et al., 2022; Portugal & White, 2018; Tuia et al., 2022; Wild et al., 2023). Furthermore, animal-borne electronics and data sets are increasingly tailored to a particular study or research group, making access to, and comparison between, biologging studies challenging.

Triaxial accelerometers and magnetometers form the bedrock of biologging studies and are capable of providing high-resolution data on animal movement and orientation (Shepard et al., 2008; Williams et al., 2017; Wilson et al., 2008; Yoda et al., 1999). However, transforming and interpreting the often large and complex data sets generated from biologgers into behaviorally and ecologically relevant information requires expertise from disciplines beyond ethology. For example, recent studies have applied various machine learning techniques to identify behaviors from raw accelerometer and/or magnetometer profiles (Balasso et al., 2023; Bidder et al., 2014; Chang et al., 2022; Dentinger et al., 2022; Painter et al., 2016; Studd et al., 2019; Wang, 2019; Yu et al., 2021), in addition to alternative approaches, such as template matching (Walker et al., 2015) and user-defined algorithms for behavior (Wilson et al., 2018). The performance of such models varies due to factors such as the frequency at which data are recorded and the degree of behavioral variation *within* and *between* the behavioral classes attempting to be identified. To date, no consensus has been reached on a single behavioral classification technique across biologging studies, further hindering comparison between studies and species (Wang, 2019; Wilson et al., 2018; Yu et al., 2021).

Magnetometer data, used in conjunction with accelerometers, can enhance machine learning performance by providing additional information regarding animal body or limb orientation (Alex Shorter et al., 2017; Brewster et al., 2021; Dickinson et al., 2021; Sakai et al., 2019; Williams et al., 2020). In some contexts, triaxial magnetometer data alone have been used to successfully identify behavior in free-roaming animals (Chakravarty et al., 2019; Williams et al., 2017). In addition, triaxial magnetometers are well suited to provide magnetic heading orientation (Matsumura et al., 2011), although extracting compass headings from raw data is not trivial and depends on sensor calibrations and accelerometer-based tilt-compensation corrections (Bidder et al., 2015). Unsurprisingly, calibration techniques are now commonplace in studies that report magnetic heading measurements derived from raw magnetometer data (Fannjiang et al., 2019; Gutzler & Watson III, 2022; Logan et al., 2023; Martín López et al., 2016; Noda et al., 2014); however, few (Wilson et al., 2007) have provided ground truth validation of magnetic compass accuracy and reliability across ecologically realistic movement dynamics or behaviors.

Integration of GPS technology with accelerometer and magnetometer data has further enhanced the accuracy and depth of spatial information in animal tracking studies and is reflected in the widespread deployment of GPS technology across a range of animal studies over the past three decades (Hebblewhite & Haydon, 2010; Katzner & Arlettaz, 2020; Kays et al., 2015). Beyond its utility in providing reliable positional fixes, GPS is now used to improve the performance (e.g., mitigate drift and heading error) of dead-reckoning path reconstruction that relies on vector integration obtained from synchronized accelerometer and magnetometer data (Gunner et al., 2021) and further underscores the importance of assessing the accuracy of magnetic heading measurements obtained from raw data. Engineering multisensor collars (e.g., GPS, accelerometers, magnetometers) capable of recording and storing large volumes of data over months or years that comply with animal welfare standards remains an additional challenge in biologging research (Cook et al., 2017; Holton et al., 2021; Kenward, 2000; Wilson et al., 1986, 2021).

Here we present the development of a multisensor biologging collar equipped with GPS and triaxial accelerometer and magnetometer sensors that has been extensively tested in free-ranging wild boar (*Sus scrofa*). In tandem, we have developed a method for classifying ecologically relevant behaviors from raw accelerometer data in wild boar using machine learning techniques and provide a detailed assessment of magnetic compass performance based on raw magnetometer data across a range of behavioral contexts. Our findings

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suggest that both the collars and analytical techniques are robust, adaptable, and suitable for long-term studies with terrestrial mammals, and we discuss the broader applications of this work for future wildlife research.

2 | METHODS

2.1 | Study site and subjects

Field testing of the integrated multisensor collars (IMSCs) was carried out in unrestricted, natural habitats throughout the Czech Republic. Boar were captured in corral traps, sedated using methods described below (see also Appendix S1), and fitted with the IMSC, then released into the surrounding environment. All data used to develop the behavioral classifier and evaluate magnetic compass performance were collected at a wildlife reserve (49°57′52.7″N 14°50′14.7″E) owned by the Czech University of Life Sciences. Inside the reserve, a semi-natural enclosure (~38 m × ~46 m), made from nonmagnetic wood fencing was used to collect ground truth behavioral data (hereafter "behavioral enclosure") from six adult wild boars between October 2017 and December 2018 (Figure S1). Boar were captured opportunistically using dart tranquilizer methods (see Appendix S1), then were transported inside the behavioral enclosure and fitted with one of the two biologging collar designs (see below). Four infrared game cameras (UOVision UM 565) were installed within the enclosure (Figure S1) to record ground truth data used for behavioral classifier and magnetic heading analyses (see below).

Trapping, handling, and collaring protocols were performed in accordance with the Ethics Committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361 and following ARRIVE guidelines (Percie du Sert et al., 2020). See Appendix S1 for additional study site information.

2.2 | Biologging collar development

Two collar systems were designed in this study: "IMSCs" and "single-tag collars" (STCs), both fitted with Wildbyte Technologies Daily Diary data loggers (http://www.wildbytetechnologies.com/). Loggers were equipped with triaxial accelerometers and triaxial magnetometers (LSM303DLHC, ST Microelectronics) programmed to record continuously at a sample rate of 10 Hz across all six sensors aligned along three orthogonal axes corresponding to the major axes of the boars' bodies (Figure 1).

2.3 | Integrated multi-sensor collar (IMSC)

The IMSCs included a "Thumb" Daily Diary tag (18 × 14 × 5 mm) with triaxial accelerometer and magnetometer sensors (LSM9DS1,

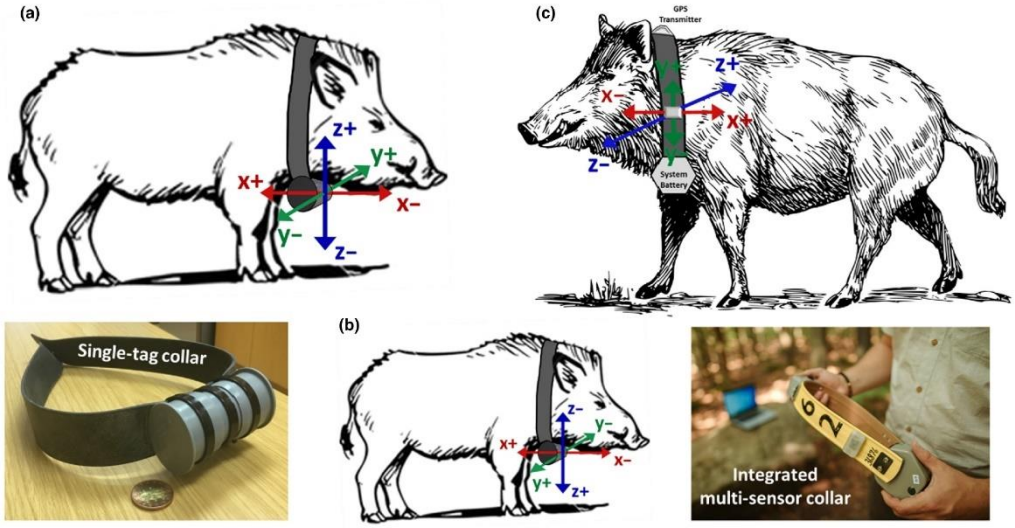

FIGURE 1 Biologging collars used throughout the study. Accelerometer axes orientation is superimposed on the logger and axis polarity indicates the acceleration value as the axis is pointed toward gravity. Note the different axis alignments between STC designs (a, b). Both the logger position and logger orientation used in all IMSCs (c) differ from the STC logger position and orientations. Photographs of both collar designs are shown below their respective schematics. IMSC, integrated multisensor collars; STC, single-tag collars.

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ST Microelectronics), as well as a Vertex Plus GPS collar, scheduled to record GPS fixes at 30-min intervals. All accelerometer and magnetometer data was recorded and stored on a removable 32 GB MicroSD card. Collars were equipped with an integrated "drop-off mechanism" and VHF beacon to enable collar recovery from the field. All collar electronics were powered from a single battery pack (4-D cell) and the total deployment weight was 716 g. The Daily Diary tag was protected by a custom-designed polyurethane housing (40 mm × 25 mm × 12 mm) positioned on the outside of the plastic collar belt. The orientation of the tag relative to the collar, as well as the orientation of collar relative to the animal, remained fixed for all IMSC deployments (Figure 1, Table 1).

2.4 | Single-tag collars (STCs)

All STCs were equipped with the "Square" Daily Diary tag (27 × 26 × 10 mm) and recorded data to a removable 32 GB MicroSD card. The logger was powered with a single cell 3.6 V lithium battery (SAFT, LS17500CNR) and was oriented and leveled within a 12 cm × 4.8 cm dia PVC-U cylindrical tube housing secured to a plastic collar belt. Total STC weight was 250 g. All STC housings were positioned ventrally at the base of the animal's neck (Figure 1a,b). However, logger orientation was rotated in one STC deployment (Figure 1b) to test the positional robustness of the behavioral classifier (see below).

See Appendix S1 for additional information regarding collar specifications and deployments.

2.5 | Data collection

Field testing of the IMSC involved 71 collar deployments over a 2-year period on adult (>12 months, >40 kg) free-roaming wild boar (52 females, 18 males, 1 unidentified). Collars were evaluated for robustness, capacity, and functionality over 6001 tracking days, cumulatively across all deployments.

Behavioral classifier and magnetic compass performance data were collected from six free-roaming individuals inside the behavioral enclosure. Before collaring, calibration data used for hard- and soft-iron magnetometer corrections (Gunner et al., 2021; Williams et al., 2017) were collected by rotating the collars through three-dimensional space for 5 min within the immediate area of the behavioral enclosure. The resulting accelerometer "calibration signature" was also used to time-sync biologging data with ground truth recordings from each game camera. Upon data retrieval, raw data files were uploaded to DDMT software (Wildbyte Technologies – Swansea University, Singleton Park, Swansea, UK, SA2 8PP), for further processing, including magnetometer calibrations. A summary of data collection and performance evaluations for each collar design is provided in Table 1.

2.6 | Behavioral classifier development

2.6.1 | Training data set construction

Triaxial (*x*, *y*, *z*) accelerometer data from three individuals fitted with STCs were used to develop the behavioral classifier (Table 1). Six broad behavioral classes ("Continuous Walk," "Foraging," "Resting," "Running," "Standing," and "Other") were established using the criteria listed in the Appendix S1. Behavioral classes were determined based on a collective knowledge of *Sus scrofa* behavioral repertoires within the Czech Republic are consistent with those reported in other Suidae behavioral classification studies (Dentinger et al., 2022; Erdtmann & Keuling, 2020; Zhang et al., 2022). Behaviors were identified using video records, and corresponding accelerometer profiles were located by matching video timestamps with synced timestamps in the DDMT software. Profiles were then extracted to create behavioral ethograms composed solely of triaxial accelerometer data falling into one of the six behavioral classes. To facilitate future refinement of the classifier, "Foraging," "Running," and "Standing" classes were further subdivided to produce three additional, "higher resolution" behavioral categories: "Rooting," "Trotting," and "Vigilance," respectively, resulting in a total of nine behavioral

TABLE 1 Collar design and data collection. Overview of collar design, biologger position and orientation, and data type collected (i.e., behavioral classifier training, testing, magnetic heading evaluation), per individual.

Collar design and data collection						
Boar ID	**Collar design**	**Tag position**	**Tag orientation**	**Classifier training**	**Classifier testing**	**Magnetometer testing**
B3	STC	1	A	Yes	No	No
B4	STC	1	B	No	Yes	No
B5	STC	1	A	Yes	No	No
B6	STC	1	A	Yes	No	Yes
B7	STC	1	A	No	Yes	Yes
B30	IMSC	2	C	No	Yes	Yes

Note: Numbers and letters listed for Tag Position and Orientation are arbitrary and indicate similarities and differences between collar designs.
Abbreviations: IMSC, integrated multisensor collar; STC, single-tag collar.

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TABLE 2 Summary of behavioral data used for classifier training. For each behavioral class, the total duration (seconds) and total observations (i.e., 4-s training windows) are shown, as well as the class proportion (%). A total of 14.96 h of training data were used for classifier development and proportions reflect those of the test set. The expanded suite of "higher resolution" behavioral classes are italicized and nested within the respective parent class (i.e., 669 of the "Forage" observations were subclassified as "Root," representing 5% of all training observations).

Classifier training: behavioral class summary			
Behavioral class	Total duration (s)	Total observations	%
Rest	25,380	6345	47.1
Forage	10,404	2601	19.3
Root	*(2676)*	*(669)*	*(5.0)*
Walk	5780	1445	10.7
Stand	6672	1668	12.4
Vigilance	*(472)*	*(118)*	*(0.9)*
Run	4168	1042	7.7
Trot	*(2556)*	*(639)*	*(4.8)*
Other	1440	360	2.7
Total	53,844	13,461	100.0

classes. The higher-resolution behavioral classes were collapsed into their parent classes for initial classifier evaluation.

Each marked behavioral epoch was subdivided into 4-s non-overlapping windows to generate baseline observations for classifier training (i.e., entities to be classified following feature extraction). The 4-s observation window was chosen in consideration of two factors: the shortest-duration behavior desirable to detect and the minimum acceptable detection latency. In total, there were 13,461 training observations (14.96 hours of marked data), with the following breakdown of observations and training percentage for the six "core" behavioral classes: "Continuous Walk" (1445, 11%), "Foraging" (2601, 19%), "Resting" (6345, 47%), "Running" (1042, 8%), "Standing" (1668, 12%), and "Other" (360, 3%) (Table 2, Table S1). Training data for the "higher resolution" behavioral subclasses are provided in Table 2, Table S1. The proportions of observations used to train the behavioral classifier were selected a priori to reflect the frequencies of these behavioral classes thought to occur in natural contexts (VS, MJ personal observations). The training data set was constructed from three individuals (B3, B6 male; B5, female), all fitted with STCs with identical tag orientations (Figure 1a, Table 1).

2.6.2 | Feature extraction

Eighteen features were extracted from each 4-s raw-data observation window. These features were the estimated "signal power" in each of four frequency bands (0–2.5 Hz, 2.5–5 Hz, 5–7.5 Hz, and 7.5–10 Hz; four features), the signal median (one feature), and the signal variance (one feature), for each of the three accelerometer axes. The power features were derived from the Welch method of power spectral density estimation (2 s windows with 1 s overlap, 64-point Discrete Fourier Transforms), by integrating the output in the designated frequency ranges. All features guaranteed to be nonnegative (i.e., all except the median features) were log-transformed to a decibel-proportional scale prior to further processing. Finally, features were *z*-scored and principal component analysis was performed, retaining a number of components required to preserve 95% of the total data variance (eight components). The resultant 13,461 × 8 matrix served as the training data for a 5-nearest neighbor classifier with cityblock distance as the metric (Hastie et al., 2009). A k-NN classifier was chosen for its ability to represent highly nonlinear decision boundaries, based on the demonstrated success of similar methods in prior biologging studies (Bidder et al., 2014; Painter et al., 2016; Sur et al., 2017). The number of neighbors and distance metric were chosen by grid-search optimization on a small holdout data set (Hastie et al., 2009).

2.6.3 | Behavioral classifier evaluation

Performance of the behavioral classifier was evaluated using continuous accelerometer recordings collected from three individuals (B4, B7, and B30) not used in classifier training (Table 1). Prior to evaluation, behaviors were verified using ground truth video recordings and corresponding accelerometer profiles were identified as described above. Because the tag orientation was not identical across training and test boar (Figure 1, Table 1), test data *x*, *y*, and *z* acceleration vectors at every time step were multiplied by the 3D rotation matrix required to map them to the coordinate frame used for training data. After 18-dimensional feature extraction, test data observations were transformed using the training data mean and standard deviation vectors before being projected onto the 8-dimensional principal component space of the training data for classification. Initial test data classifications were made at every possible time step using a 4-s symmetric, noncausal sliding window.

2.6.4 | Postprocessing

Initial classifications were smoothed with a nonlinear filter; specifically, the class at each time step was replaced with the modal class of a 1-s forward-looking window. This filtering step resulted in a set of candidate's behavioral events, each delimited by a starting and ending time, which were then subject to two predetermined heuristic criteria to yield the final set of classifications. The first was that each candidate behavioral event was required to be of a minimum duration: "Foraging" (5 s; "Rooting" 3 s), "Resting" (120 s), "Running" (3 s; "Trotting" 3 s), "Standing" (2 s; "Vigilance" 2 s), and "Other" (1 s). Any candidate event not meeting its minimum duration, which was used only in postprocessing, was reassigned to the next most likely class

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for which the duration criterion could be met. Class likelihoods were determined using the relative class proportions among the five nearest training set-neighbors corresponding to each time step in the candidate event. Class proportions were summed across time steps and sorted to produce a rank-ordered likelihood for the classes. Candidate events for which this procedure failed to yield a valid alternate class assignment were merged with the subsequent event.[1]

The second heuristic was that any candidate "Standing" event flanked by "Resting" activity was reassigned to the "Resting" class. Specifically, this reassignment was made if the majority of a 120 s window on either side of the candidate "Standing" event was classified as "Resting."

2.7 | Magnetometer data

To assess magnetic compass heading accuracy and reliability, magnetometer data were collected from four collars under two conditions: a controlled laboratory environment (hereafter, "lab evaluation") designed to test the precision of the magnetometer and from three free-roaming boar inside the behavioral enclosure (hereafter, "field test") (Table 1).

During the lab evaluation, the tag was leveled and centered inside an electromagnetic enclosure containing four Helmholtz's coils used to manipulate the strength and alignment of an experimentally generated magnetic field. Two orthogonally aligned coils were used to cancel the residual horizontal component of the Earth's magnetic field (+/− 0.1%) and to adjust the vertical component of the magnetic field to match that of an Earth strength vertical field (~45,000 nT). Two inner orthogonally aligned coils were used to generate Earth-strength magnetic fields (total strength ~50,000 nT) that could be rotated into alignment into one of four cardinal compass alignments corresponding to topographic North, South, East, and West (Kirschvink, 1992). The tag was oriented such that one end of the *x*-axis was aligned toward topographic North which was then defined as the "heading direction" in DDMT for analysis. Tag orientation remained static, whereas the horizontal component of the magnetic field was rotated by 90° increments into alignment with each of the four cardinal compass directions for a period of 10 s in each alignment. Magnetic heading measurements calculated by DDMT were plotted relative to the four expected cardinal compass directions using the gghistogram function in the R package ggpubr (Kassambara, 2020).

Field tests of magnetometer performance were carried out concurrently with data collected for the behavioral classifier within the behavioral enclosure on three free-roaming individuals (Table 1). Video recordings were used to estimate ground truth magnetic headings and a spatial array of "magnetic landmarks" were installed within the camera's field of view to provide known magnetic references to better estimate magnetic headings of focal subjects. Magnetic landmarks were either nonmagnetic cables tethered between trees or the nonmagnetic fence-line forming the behavioral enclosure (Figure S1). A total of 45 independent behavioral epochs from all core behavioral classes (excluding "other"), totaling 5:27 (min:s), were selected to test the precision of the magnetic heading data. Heading predictions were made by two investigators not involved in data collection and blind to all raw magnetometer data. Using only video records, investigators predicted boar magnetic heading using the available magnetic landmarks described above. For each prediction, the average magnetic heading was estimated over the duration of the behavioral segment identified. When investigator predictions differed by less than 20° ($n = 40$), they were averaged to establish the final magnetic heading, whereas when predictions differed by more than 20° ($n = 5$), investigators determined a final prediction after reevaluating the recording together. A third investigator blind to the magnetic predictions extracted the magnetic heading data from DDMT which was later compared to investigator predictions.

3 | RESULTS

3.1 | IMSC field performance: Durability, capacity, and lifetime

Between 2019 and 2022, 67 of the 71 total collars (~94%) deployed on free-ranging boar were recovered and data recording durations ranged from 9 to 421 days. The remaining four collars (~6%) experienced an unknown GPS malfunction and remain unrecovered. Of the 67 collars retrieved, 51 (76%) were fully functional and no appreciable damage was noted, whereas 11 (16%) exhibited mechanical damage likely due to physical stresses associated with boar behavior, and the remaining 5 collars (7%) failed prematurely due to an unexpected electrical fault. Of the fully functional subset, 35 (69%) collars recorded data until retrieval, whereas 9 collars (18%) recorded data for >50% of the deployment period and the remaining 7 collars (14%) recorded data for <50% of deployment period. Overall, free-ranging boar equipped with IMSCs were tracked for 6001 days and a total of 4547 days of biologging data were recorded, corresponding to 75% of the cumulative deployment duration.

3.2 | Behavioral classifier

Classifier performance was evaluated using accelerometer data from 2100 independent ground truth behavioral epochs (i.e., independent behaviors falling into one of the six behavioral classes) across three individuals, totaling 08:28:15 (HH:mm:ss) of data (Table 3, Table S1). Classifier performance was evaluated on an event-by-event basis (i.e., per 0.1 s sample). Overall behavioral classifier performance was 85.1% across all behaviors from all three individuals (Table 4) and includes data from the STC and IMSC designs with different tag positions and orientations. Of the five behavioral classes of interest (i.e., excluding "Other" which was composed of heterogeneous behaviors only identified by the classifier when a behavior did not fall into any of the five core behavioral categories), the likelihood

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that any given prediction matched the ground truth class label (i.e., precision), ranged from 77.1% ("Walking" and "Standing") to 96.5% ("Resting") (Table 4). Classifier recall, that is, the proportion of behavioral epochs correctly identified by the classifier, ranged from 74.7% ("Running") to 91.8% ("Resting") (Table 4). Classifier performance was consistent between the three deployments, ranging from 83.5% (B4) to 89.9% (B30), and surprisingly, the collar with the highest performance (B30, IMSC) was least similar in design (i.e., tag position and orientation) to those used to train the classifier (Table 5). All possible pairs of the eight principal components used to identify the six behavioral classes are plotted, along with histograms corresponding to each component in isolation, to illustrate the collective and relative contribution of the principal components toward class separability (Figure 2). Precision and recall metrics were substantially lower when tested on the three expanded behavioral classes, reflecting their similar acceleration profiles relative to their respective parent classes. However, overall classifier performance remained robust, with an accuracy of 78.4%, although there was larger variation in performance between collar designs when tested on the expanded classes (Table 6).

TABLE 3 Classifier testing data. Summary of accelerometer data used to test behavioral classifier performance in three individuals not used for classifier training. The total duration (s) and total number of independent behaviors per class (Epochs) as well as their proportions (%) in classifier testing are listed. The expanded suite of "higher resolution" behavioral classes are italicized and nested within their respective parent class, as in Table 2.

Behavioral classifier testing data				
	Duration		Epochs	
Behavioral Class	Sum (s)	%	Total	%
Rest	11,008	36.1	67	3.2
Forage	7436	24.4	343	16.3
Rooting	*(1562)*	*(5.1)*	*(98)*	*(4.7)*
Walk	4129	13.5	459	21.9
Stand	4590	15.1	685	32.6
Vigilance	*(439)*	*(1.4)*	*(106)*	*(5.0)*
Run	1827	6.0	157	7.5
Trot	*(647)*	*(2.1)*	*(106)*	*(5.0)*
Other	1505	4.9	389	18.5
Total	30,495	100	2100	100

3.3 | Magnetic heading: Lab evaluation

Following the calibration procedures described above, the median magnetic heading measurements calculated by DDMT were in agreement with each of the experimentally generated magnetic field alignments: N = 2.99°, S = 179.16°, East = 88.21°, W = 268.66° (Figure 3), with an overall median heading error of 1.7° relative to expected.

3.4 | Magnetic heading: Field test

Across all 45 magnetic heading samples, the median discrepancy between DDMT magnetic compass heading measurements and ground truth predictions was 0° (CI: −3.1° and 6.9°) (Figure 4b). Median bootstrapped 95% confidence intervals relative to predictions were calculated using the function boot from the boot package (Canty & Ripley, 2020). Discrepancy between DDMT heading and corresponding ground truth prediction ranged from −30° to 21° (Figure 4b). As shown in Figure 4a, the distribution of compass headings obtained was evenly distributed across all possible magnetic heading alignments, and the error in the DDMT magnetic compass heading measurements compared to predictions was uniform

TABLE 4 Behavioral classifier performance. Confusion matrix showing behavioral classifier accuracy tested on three individuals across six behavioral classes. Classifier predictions are listed on the left column and ground truth classes are listed across the second-to-last row. Values within the matrix represent the total number of events for each predicted class (rows) and for each ground truth observation (columns), where an event corresponds to one acceleration data point recorded by the logger. Light green-shaded cells inside the matrix represent classifier predictions that match ground truth observations. The likelihood that the classifier prediction matches that of the ground truth observation for each behavior class is represented by the Precision column shown on the right. The proportion of events in each class identified by the classifier is represented by Recall shown across the bottom row. Lighter to darker shades of green in Precision and Recall cells indicate lower to higher classification performance, respectively.

Prediction	Behavioral classifier confusion matrix						Precision (%)
Walk	36,851	2883	0	5514	472	2064	77.1
Other	2758	9863	15	5606	1580	3881	41.6
Rest	39	253	101,077	0	0	3379	96.5
Forage	962	1090	0	62,545	2361	995	92.0
Run	167	788	0	35	13,649	173	92.1
Stand	508	174	8987	656	209	35,409	77.1
Truth	Walk	Other	Rest	Forage	Run	Stand	
Recall (%)	89.3	65.5	91.8	84.1	74.7	77.1	

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TABLE 5 Behavioral classifier performance summary. Precision and recall percentages are shown for all six behavioral classes, partitioned by individual, as well as overall classifier accuracy (%) per individual.

Behavioral classifier performance summary						
	B4		B7		B30	
Behavioral class	Precision (%)	Recall (%)	Precision (%)	Recall (%)	Precision (%)	Recall (%)
Walk	77.8	86.4	74.2	91.2	87.1	85.6
Other	34.1	58.0	53.7	72.3	4.3	17.4
Rest	93.5	85.6	98.3	95.0	98.6	100.0
Forage	96.1	88.6	62.9	39.1	94.6	96.2
Run	92.3	78.4	94.1	75.2	75.0	60.2
Stand	58.7	72.4	85.9	83.0	95.3	67.3
Overall accuracy (%)	83.5		**84.2**		**89.9**	

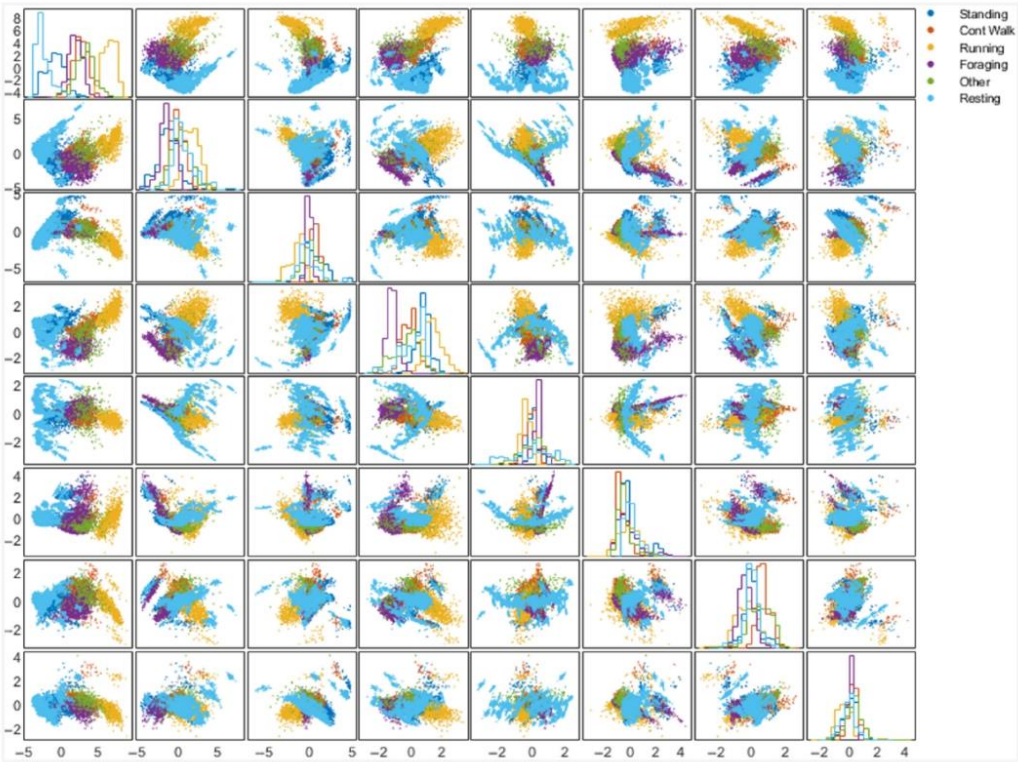

FIGURE 2 Matrix showing plots of all possible pairs of the 8 principal components (PCs) that were used in behavioral classification. Points correspond to training observations ($n = 13{,}461$ in each plot) and are colored according to behavioral class. Numbering columns and rows each from 1 to 8, respectively, beginning at the top left corner of the matrix, the column number corresponds to the PC plotted on the horizontal axis and the row number to the PC plotted on the vertical axis. For example, the plot in row 3, column 2 has the second PC plotted on the horizontal axis and the third PC plotted on the vertical axis. The plots along the diagonal are histograms, colored by class, for each of the 8 PCs. (Plots mirrored across the diagonal show the same two PCs with the axes swapped.)

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TABLE 6 Expanded classifier performance. Confusion matrix showing behavioral classifier accuracy tested on three individuals across the expanded suite of nine behavioral classes. Table format is identical to that shown in Table 4.

Prediction	Behavioral classifier confusion matrix									Precision (%)
Walk	36,851	2883	0	4643	871	172	300	1885	179	77.1
Other	2758	9863	15	3959	1647	601	979	3334	547	41.6
Rest	39	253	101,077	0	0	0	0	3330	49	96.5
Forage	170	587	0	42,458	4415	1	0	457	478	87.4
Root	792	503	0	7061	8611	2360	0	55	5	44.4
Run	0	129	0	35	0	7164	109	15	0	96.1
Trott	167	659	0	0	0	1306	5070	119	39	68.9
Stand	434	117	8372	585	64	203	2	27,766	2980	68.5
Vigilance	74	57	615	7	0	0	4	4547	116	2.1
Truth	Walk	Other	Rest	Forage	Root	Run	Trot	Stand	Vigilance	
Recall (%)	89.3	65.5	91.8	72.3	55.2	60.7	78.4	66.9	2.6	

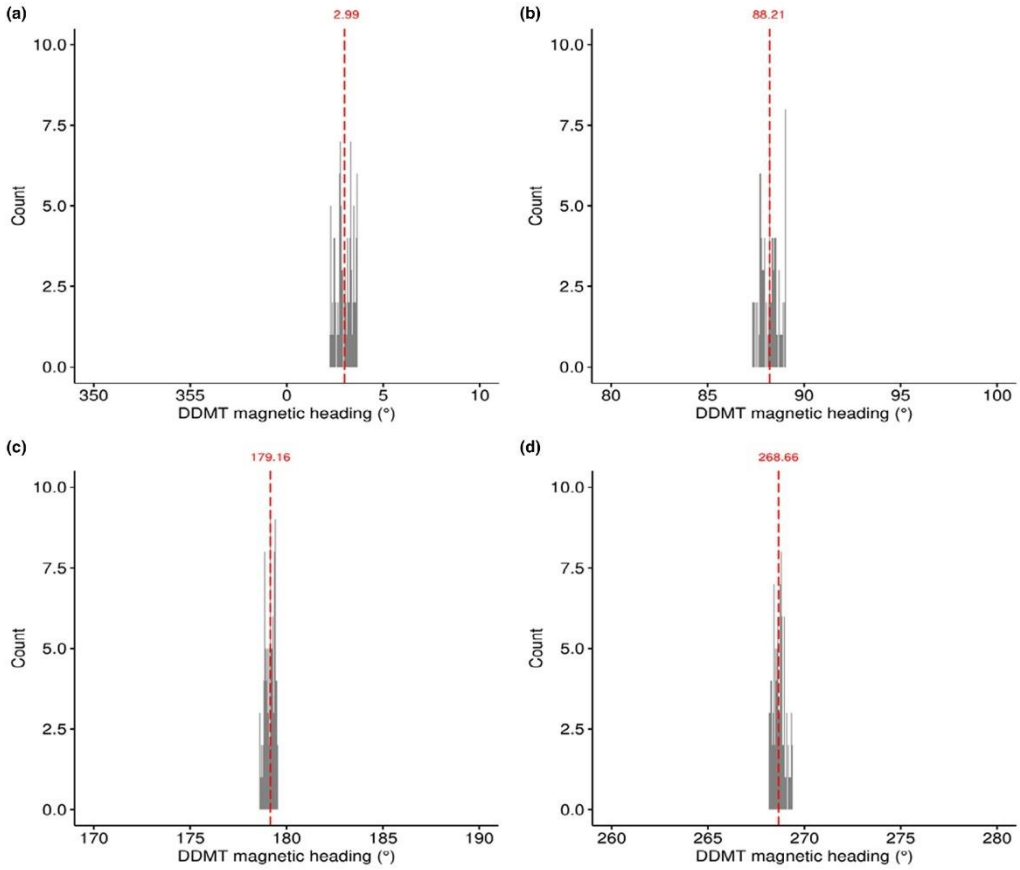

FIGURE 3 Lab test of triaxial magnetometer data used to calculate magnetic heading measurements after calibration in DDMT software. Histograms plot the total count of 100 samples (10 Hz × 10 s) recorded in each magnetic field alignment (i.e., mN = topoN, E, S, W), relative to magnetic heading bearings calculated in DDMT after performing magnetometer calibration procedures. Plots (a–d) correspond to experimentally generated Earth-strength magnetic fields aligned at North (0°), East (90°), South (180°), West (270°), respectively. Median values for each magnetic field alignment are shown in red.

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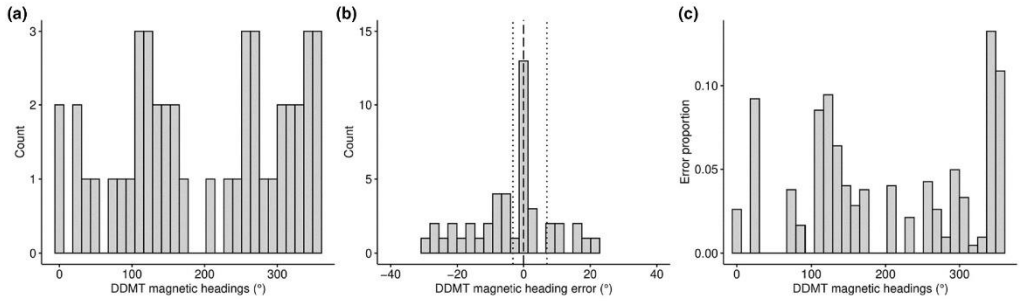

FIGURE 4 Results from the magnetometer field test collected from free-roaming individuals equipped with STC and IMSC designs. A total of 45 samples were evaluated and compared to ground-truth predictions of magnetic heading. (a) Histogram of the overall distribution of magnetic compass measurements produced by DDMT shows that samples were obtained from the range of possible compass directions. (b) The discrepancy between DDMT magnetic compass measurements and ground-truth recordings, that is, DDMT magnetic heading output error (median error = 0°, black dashed line; bootstrapped 95% CI: −3.1° and 6.9°). (c) The error produced by DDMT was uniform across the range of possible magnetic compass headings. IMSC, integrated multisensor collars; STC, single-tag collars.

TABLE 7 Magnetic heading field test. Summary and results of ground truth magnetic compass headings. The proportion of time (% Duration) and the proportion of epochs from each behavioral class (% Epochs) used to ground truth the magnetic headings are listed, partitioned by individual. Combined data from all individuals tested, per behavioral class, are shown. Median magnetic heading measurements calculated by DDMT, relative to ground truth predications are shown per behavioral class and partitioned by individual. In cases with a negative (−) median value, the corresponding magnetic compass heading is shown in parentheses.

	B6		B7		B30		Combined		
Behavioral class	% duration	% epochs	% duration	% epochs	% duration	% epochs	Total % duration	Total % epochs	Median heading Rel GT prediction
Rest	0	0	0	0	1	2	1	2	**−8° (352°)**
Forage	30	22	10	9	16	11	55	42	**−6° (354°)**
Walk	1	2	6	9	3	7	10	18	**0°**
Stand	5	7	17	13	11	16	33	36	**−0.5 (359.5°)**
Run	0	0	1	2	0	0	1	2	**9°**
Total	35	31	34	33	31	36	100	100	**n/a**
Median Heading Rel GT Prediction	**−0.5° (359.5°)**		**0°**		**−6° (354°)**				**0°**

(i.e., error was unbiased across the range of magnetic directions) as indicated by the manova model previously described in Landler et al. (2022) (model results: intercept: approx. $F = 0.65$, $p = .53$, error proportion: approx. $F = 0.79$, $p = .46$) (Figure 4c). The "error proportion" was calculated as the angular deviation between the DDMT measurement and the ground truth prediction divided by the total angular deviation. The cosine and sine of the magnetic heading in radians were used as the response variables and the error proportion as a linear covariate. The intercept of this model was used to test for a significant departure from uniformity (Landler et al., 2022). Importantly, the accuracy of magnetic compass headings was consistent across all three individuals evaluated (Table 7), fitted with different collar designs, biologger positions, and orientations (Figure 1, Table 1), as well as across all behavioral classes, including behaviors characterized by large acceleration amplitudes and variation (e.g., "Foraging," "Walking," "Running").

4 | DISCUSSION

Animal-borne telemetry systems have emerged as a powerful tool to further characterize animal movement, behavior, and ecology. The availability of reliable collar systems equipped with a range of sensor technologies adaptable across multiple studies and species is valuable for several reasons, including that it eliminates the need to develop and test novel equipment, and that data sets collected from a standardized system may catalyze additional collaboration, data sharing, and advance progress in analytical techniques.[2] The IMSC developed here, equipped with triaxial accelerometer and magnetometer sensors, GPS technology, as well as a variety of additional sensors not used in the current study, has proven to be highly reliable under the harsh demands imposed by wild boar under natural contexts. Across the 71 IMSC deployments, 94% of the collars were recovered resulting in biologging data recorded across 75% of

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the cumulative deployment duration. While the maximum recording duration was an impressive 421 days for one deployment, the majority of IMSCs (72%) were terminated prematurely due to hunting or automobile collisions, which does not reflect collar capacity. In a separate study, 36 IMSCs identical to those described above were deployed on free-ranging red deer (*Cervus elaphus*) and had an average and maximum data recording duration of 203 and 529 days, respectively. Given the standardization, durability, and functionality of the IMSC, these collars are well suited for long-term studies in terrestrial mammals, and we hope they will be adopted for use in future biologging studies.

Concurrent with the IMSC development, we have built a behavioral classifier capable of identifying ecologically relevant behaviors from six behavioral classes in wild boar. The classifier had an overall performance of 85% and, of the five core classes (i.e., excluding "Other"), "Resting" was identified with the highest precision, and "Standing" had the lowest precision, most often misclassified as "Resting", likely due to the similar acceleration profiles between resting and standing behaviors. Classification recall performance was highest in "Resting" and lowest in "Running." The majority of undetected "Runs" were misclassified as "Forage," a class that includes "Rooting" characterized by large and variable *x*-axis acceleration amplitudes, like those associated with "Running" accelerometer profiles. Importantly, the test data set for core and expanded behavioral classes reflected the proportions of behaviors used in classifier training, which in turn, approximated the overall behavioral repertoire of wild boar in natural contexts. This proportionality helps to mitigate performance biases caused by over- or underrepresented behaviors and better reflects true overall classification performance. The decision to use a k-NN classifier was based on classification performance reported in previous biologging literature (Bidder et al., 2014; Painter et al., 2016; Sur et al., 2017), coupled with the nonlinearity of its decision boundaries (Hastie et al., 2009), however, further optimization across classifiers and of hyperparameters could potentially yield performance improvements that can be empirically characterized in future studies.

The classifier exhibited the best overall performance (89.9% accuracy) when tested with data collected from the IMSC, despite being trained on data exclusively from STCs, suggesting that the classifier has an inherent plasticity and is capable of classifying behaviors from biologging tags attached in various orientations and positions. As expected, classifier performance on the expanded suite of behavioral classes was not as robust, largely due to the similarities between the parent class and higher resolution classes. To explore this further, we build upon the framework detailed in Wilson et al. (2018) using DDMT's *Behavior Builder* and *Time Series* functions in an attempt to distinguish between behavioral classes with similar acceleration profiles, such as "Standing" and "Vigilance" behaviors. Applying these postclassification techniques to a subset of our current dataset drastically improved "Vigilance" resulting in >50% precision and recall metrics (see Figure S1). Although encouraging, a more detailed investigation using larger data sets across multiple behaviors will be needed. Furthermore, we expect that a similar improvement in classification performance could also be achieved in the preprocessing stages of classifier development by creating new features that capture subtle differences in accelerometer signatures between similar classes, like those identified between "Standing" and "Vigilance" behaviors.

The classifier was trained and tested solely from triaxial accelerometer data, an important a priori consideration. Because spatial features of the behavioral enclosure remained consistent throughout the study (e.g., location of water source and feeding area, shaded areas used as bedding sites), including locations and viewing angles of the cameras used to collect ground truth videos, it was important to exclude magnetometer data from classifier training and testing, as behaviors under these circumstances cannot be assumed to be randomly oriented. For example, in our study, "Resting" alignment was biased due to limited shaded areas in the enclosure. Had magnetometer data been included in the behavioral analysis, the classifier would likely identify "Resting" using biased magnetometer data that have no relevance beyond the confines of the behavioral enclosure and would result in false positive classifications that artificially inflate precision and recall metrics. We acknowledge that magnetometer data can be valuable for behavioral identification under certain contexts (Chakravarty et al., 2019; Williams et al., 2017); however, it remains unclear if studies that incorporate magnetometer data into machine learning analyses could be predisposed to such biases, as the relative contribution of magnetometer data used for behavioral identification is rarely provided.

Nonetheless, triaxial magnetometer data can provide a wealth of opportunities for exploring movement ecology in greater detail, such as dead-reckoning analyses (Gunner et al., 2020) and studies of magnetic alignment (Begall et al., 2013; Červený et al., 2017). Given the salience of magnetometer data in biologging research, it is surprising that few studies have validated the precision of magnetic compass headings calculated from raw triaxial magnetometer data (but see Wilson et al., 2007). Therefore, we provide a detailed characterization of magnetic heading measurements under laboratory and natural contexts with magnetometer sensors mounted in different positions and orientations. Magnetic headings calculated by DDMT were consistent with ground truth predictions, with an overall median deviation from expected of 1.7° and 0° in the laboratory and field test, respectively. These data confirm that the magnetometer calibrations (i.e., soft- and hard-iron corrections) and tilt-compensation algorithms applied in DDMT are well suited for extracting high-frequency magnetic compass bearings from raw magnetometer data.

Importantly, the field test carried out on free-roaming boar included magnetic measurements that were obtained from the core behavioral classes. "Running" had the largest average deviation relative to expected (9°) and may be due to the large variation in acceleration amplitudes that introduce "noise" into accelerometer-dependent tilt-compensation calculations and/or the (in)ability of observers to accurately predict magnetic alignment from more spatially erratic behavioral classes, such as "Running." Unintuitively, however, magnetic headings obtained from "Resting" behavior, characterized by little-to-no variation in acceleration profile, also had a relatively high deviation from

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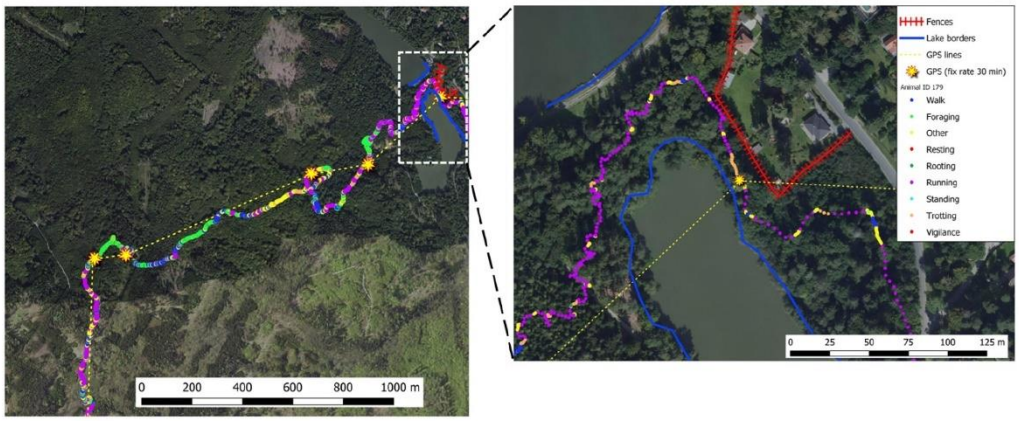

FIGURE 5 Example of dead-reckoning path reconstruction in a free-ranging wild boar equipped with the IMSC. Behaviors were first identified from continuous accelerometer data using the behavioral classifier and were then uploaded to DDMT. User-defined speed coefficients were assigned to each behavioral class which was then integrated with time-synced magnetic heading data to reconstruct movement traces between GPS fixes, which anchored the tack to the landscape. Right inset shows a detailed track segment that avoids obvious environemental boundaries and physical barriers, highlighting the added value of dead-reckoning analyses compared to using GPS data alone and lends further credibility to the precision of the dead-reckoning methodology used in this study.

expected (8°) and was likely due to an obstructed view of the animal's head alignment caused by a dense canopy covering the bedding area where boar would exclusively rest. It is noteworthy that magnetic compass performance remained accurate across all core behaviors (excluding "Other", which was not assessed), and compass performance was evaluated across a representative range of all possible magnetic directions (i.e., 0°–359°). This is the first study to our knowledge that has provided a detailed characterization of magnetic compass performance in free-roaming animals using ground truth data.

Of particular interest is the implementation of dead-reckoning to reconstruct high-resolution movement traces in free-roaming mammals. As a proof-of-concept, we take advantage of three important elements made possible by the IMSC presented in the current study: (i) the behavioral classifier capable of identifying ecologically relevant behaviors in free-roaming boar, (ii) a reliable stream of magnetic heading data recorded at subsecond intervals, and (iii) GPS fixes recorded at 30-min intervals. Dead-reckoning relies on vector integration, where vectors depend on speed (or distance traveled) and heading estimates derived from raw biologging data (for details, see Bidder et al., 2015; Gunner et al., 2021). Deriving speed from biologging data is notoriously difficult (Cade et al., 2018), and previous work has assigned speed coefficients to manually labeled behavioral classes to estimate vector lengths for dead-reckoning path reconstruction (Bidder et al., 2015). We build upon this approach by using machine learning to identify behavioral classes from large volumes of continuous biologging data, which were then assigned speed coefficients based on ground truth observations. Coupling our behavioral classification techniques with the accuracy of our verified magnetic heading data yielded high-resolution track reconstruction that was further refined by "anchoring" tracks to the landscape using time-synced GPS fixes (Figure 5). The tortuosity of the reconstructed track in Figure 5 that explicitly avoids environmental boundaries and physical obstacles highlights the precision of these methods compared to using GPS data alone and offers a powerful approach to investigate movement ecology over multiple spatiotemporal scales.

Although the emergence of biologging techniques has revolutionized studies of animal ecology, a growing set of challenges accompanies these technologies, requiring multidisciplinary expertise. The IMSCs developed here, coupled with a robust behavioral classifier and a detailed verification of magnetic heading performance, provide a commercially available system that can be adopted and adapted for future studies on terrestrial mammals.

AUTHOR CONTRIBUTIONS

Michael S. Painter: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); project administration (equal); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Václav Silovský:** Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (lead); project administration (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Justin Blanco:** Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); software (equal); validation (lead); writing – original draft (supporting); writing – review and editing (equal). **Mark Holton:** Methodology (equal); software (equal); visualization (equal); writing – review and editing (equal). **Monika Faltusová:** Formal analysis (supporting); methodology (supporting); writing – review and editing (supporting). **Rory**

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Wilson: Conceptualization (supporting); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Luca Börger:** Conceptualization (supporting); methodology (supporting); writing – review and editing (equal). **Liza Psotta:** Conceptualization (supporting); data curation (equal); formal analysis (supporting); methodology (supporting); validation (supporting); writing – review and editing (equal). **Fabian Ramos-Almodovar:** Formal analysis (supporting); methodology (supporting); software (supporting); validation (supporting); writing – review and editing (supporting). **Luis Estrada:** Data curation (supporting); methodology (supporting); software (supporting); writing – review and editing (supporting). **Lukas Landler:** Conceptualization (supporting); data curation (supporting); formal analysis (equal); methodology (supporting); validation (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal). **Pascal Malkemper:** Conceptualization (supporting); funding acquisition (supporting); methodology (supporting); writing – review and editing (supporting). **Vlastimil Hart:** Conceptualization (equal); data curation (equal); formal analysis (supporting); methodology (equal); project administration (equal); validation (equal); writing – review and editing (supporting). **Miloš Ježek:** Conceptualization (equal); data curation (equal); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All raw triaxial accelerometer and magnetometer data used for behavioral classifier development and tests of magnetic heading performance are available on Dryad at: https://datadryad.org/stash/share/4UhVGcozs_QpPViXRuwXSMTYllzqX3RXpHPWPZA6m1M.

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ENDNOTES

[1] If no subsequent event was available – only possible at the end of a file – the candidate event was discarded as unclassifiable. A small number of time steps at the beginning of each file were similarly discarded, since a fixed amount of time must accumulate before the classifier can make its first decision. Such edge-effects have negligible impact on classifier evaluation.

[2] We do not imply that the field of animal-borne telemetry and biologging is not collaborative, and indeed, would argue the opposite. However, we suggest that increased overlap between methodologies may encourage further collaboration and promote the growth of this emerging discipline.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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5.1.2. Publikace č. 2 - Animal lifestyle affects acceptable mass limits for attached tags.

Druhým článkem tohoto okruhů výsledků je publikace – *„Animal lifestyle affects acceptable mass limits for attached tags,“*, která je zaměřená na biologging data zaznamenaná pomocí senzorů na standartních obojcích pro sledování obratlovců. Studie se zaměřila na poznatek, že zařízení umístěná na zvířat pro různé typy výzkumů a sledování by neměla přesáhnout 3% hmotnosti sledovaného jedince. Z pořízených biologging napříč deseti druhy obratlovců vyplývá, že tato hodnota by měla být snížena v závislosti na atletice zvířena na hodnoty 1.6% - 2.98% hmotnosti neseného zařízení. Testovaná zařízení, která splňovala základní parametr 3% váhy tělesné hmotnosti se při pohybu sledovaného jedince projevovala vahou, která dosahovala hodnoty 4-19% tělesné hmotnosti jedince. V extrémních případě bylo zaznamenáno ovlivnění jedince hodnotou zařízení na úrovni 54% tělesné hmotnosti. Tyto poznatky mění pohled na dosavadní přístup k používání sledovacích zařízení pro studium chování a pohybu obratlovců.

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Animal lifestyle affects acceptable mass limits for attached tags

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Animal-attached devices have transformed our understanding of vertebrate ecology. To minimize any associated harm, researchers have long advocated that tag masses should not exceed 3% of carrier body mass. However, this ignores tag forces resulting from animal movement. Using data from collar-attached accelerometers on 10 diverse free-ranging terrestrial species from koalas to cheetahs, we detail a tag-based acceleration method to clarify acceptable tag mass limits. We quantify animal athleticism in terms of fractions of animal movement time devoted to different collar-recorded accelerations and convert those accelerations to forces (acceleration × tag mass) to allow derivation of any defined force limits for specified fractions of any animal's active time. Specifying that tags should exert forces that are less than 3% of the gravitational force exerted on the animal's body for 95% of the time led to corrected tag masses that should constitute between 1.6% and 2.98% of carrier mass, depending on athleticism. Strikingly, in four carnivore species encompassing two orders of magnitude in mass (*ca* 2–200 kg), forces exerted by '3%' tags were equivalent to 4–19% of carrier body mass during moving, with a maximum of 54% in a hunting cheetah. This fundamentally changes how acceptable tag mass limits should be determined by ethics bodies, irrespective of the force and time limits specified.

1. Introduction

The use of animal-attached devices is transforming our understanding of wild animal ecology and behaviour [1,2]. Indeed, tags containing multiple sensors

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and position-determining systems have been used across scales of time and space to measure everything from the extraordinary details of high performance hunts in cheetahs [3], to vast cross-taxon comparisons of animal behaviour and space-use over whole oceans (e.g. [1,4]). A critical proviso is, however, that such devices do affect survival or change the behaviour of their carriers, for both animal welfare issues as well as for scientific rigor [5]. Defining acceptable device loads for animals is critical because even diminishingly small tags can cause detriment. For example, Saraux *et al.* [6] showed that the addition of flipper rings to penguins can affect their populations, with adults having a survival rate 16% lower than untagged conspecifics and producing 39% fewer chicks, presumed to be because of the tags increasing the drag force in these fast-swimming birds. Performance is relevant in this case because drag-dependent energy expenditure to swim increases with the cube of the speed [7].

Although consideration of the physics of drag has been shown to be a powerful framework with which to understand tag detriment in aquatic animals (e.g. [8,9]), drag is negligible in terrestrial (though not aerial) systems even though tag detriment in terrestrial animals has been widely reported and is multi-facetted [10]. Reported issues range from minor behavioural changes [11] through skin-, subcutaneous- and muscle damage with ulceration [12,13] to reduced movement speed [14] and dramatically increased mortality [15]. As with drag, we advocate that a force-based framework is necessary to help understand such detriment. Indeed, force is implicit in ethics-based recommendations for acceptable tag loads because, for example, a central tenet is that animal tag mass should never exceed 3% or 5% of the animal-carrier body mass [16], this being based on early observations that tags weighing less than 5% of animal body masses apparently caused no change in behaviour [17]. Importantly though, there are now numerous studies that have reported highly variable impacts of animals carrying tags of masses less than the 3–5% limit [18–21] for reasons that are not always clear [20–22]. Implicit in this limit is that consequences, most particularly the physical forces experienced by animals owing to tags, are similarly limited. This cannot be true because Newton showed that mass, force and acceleration are linked via $F = ma$, so animal performance, specifically their acceleration, will affect the tag forces applied to the carriers. Tag forces on the animal carrier can therefore be assessed by measuring acceleration experienced by the tag as the animal moves. Specifically, reference to Newton's force/mass acceleration formulation shows that any time the tag acceleration exceeds 1 *g* (corresponding to Earth's gravity), the carrier animal will be subject to correspondingly higher tag-derived forces. We note here though, that this necessitates gathering on-animal data because simple consideration of acceleration from rigid-non-living bodies is inappropriate for living systems composed of multiple interacting segments [23].

Here, we examine the forces exerted by collar-mounted tags on moving animals. We investigate four species within the order Carnivora in detail; lions *Panthera leo*, European badgers *Meles meles*, pine martens *Martes martes* and a cheetah *Acinonyx jubatus* (with body masses roughly spanning 2–200 kg) equipped with accelerometers undertaking their normal activities in the wild for 1–21 days. In particular, because gait is known to affect acceleration in body-mounted tags [24] we examined how walking, trotting and bounding affected the forces imposed on the animals by the tags. We also equipped six other species of mammal from diverse animal families (a cercopithecid, a phascolarctid, a phalagerid, a bovid, a cervid and a suid) with different lifestyles with accelerometers *in situ* for periods between 7 and 168 days to examine the general patterns of forces they exhibited and compared them to the carnivores.

Because the act of travelling is known to produce particularly high forces [25], we also carried out controlled trials with 12 domestic dogs *Canis familiaris* (2–45 kg) equipped with the same tags moving at defined speeds to investigate how movement speed, body mass and tag mass interact to affect tag forces.

We document how the forces imposed by the collars changed with activity across all these species and conditions. Based on this, we propose a method based on acceleration data that allows researchers to define the breadth of forces exerted by tags on animals and their relative frequency of occurrence. We show how this information can then be used to derive appropriately force-based acceptable limits for tag masses, recognizing the effect of animal lifestyle and athleticism.

2. Material and methods

(a) Tag deployments on free-ranging species

We selected four species of free-living carnivores for detailed analysis, exemplifying about two orders of magnitude of mass; 10 lions *Panthera leo* (mean mass *ca* 152 kg), one cheetah *Acinonyx jubatus* (mass *ca* 41 kg), 10 badgers *Meles meles* (mean mass *ca* 9.1 kg) and five pine martens *Martes martes* (mean mass 1.9 kg), and fitted them with collar-mounted tri-axial accelerometers ('Daily Diaries—Wildbyte Technologies (http://www.wildbyte-technologies.com/); measurement range 0–16 *g* (resolution 0.49 m*g*), recording frequency 40 Hz), all of which constituted less than 3% of the mass of the animal carriers (electronic supplementary material, table S1). Owing to the weighting of the loggers, and more particularly their associated batteries, the units and sensors were positioned on the underside of the collar although during movement the collars could rotate, which could occasionally, temporarily bring the measuring system off the ventral position. After being equipped, the animals roamed freely, behaving normally, for periods ranging between 3 and 21 days before the devices were recovered.

In addition to these, we also deployed collar-mounted accelerometers constituting less than 3% of the carrier mass (electronic supplementary material, table S1) on six select free-ranging animal species. We chose these species by capitalizing on available data from animals equipped with high temporal resolution acceleration tags on collars from different mammal families with varying lifestyles for comparison with the carnivores. The species and lifestyles were: a savannah-dwelling monkey—the olive baboon *Papio Anubis* (mean mass 15 kg, $n = 5$); an arboreal herbivorous marsupial—the koala *Phascolarctos cinereus* (mean mass 10.3 kg, $n = 5$); a nocturnal, semi-arboreal, herbivorous marsupial—the mountain brushtail possum *Trichosurus cunninghami* (mean mass 3.2 kg, $n = 5$); a grass-eating, desert-dwelling bovid—the Arabian oryx *Oryx leucoryx* (mean mass 74 kg, $n = 5$); a grass-eating, wood- and moor-dwelling cervid—the red deer *Cervus elaphus* (mean mass 135 kg, $n = 5$); and a forest-dwelling, omnivorous pig—the wild boar *Sus scrofa* (mean mass 67 kg, $n = 5$). Extensive details on species-specific tagging procedures are included in the electronic supplementary material.

(b) Trials with domestic dogs

Twelve domestic dogs (*Canis lupus domesticus*) of seven different breed combinations and three main body types (small, racers and northern breeds), ranging 2–45 kg in body mass (electronic

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supplementary material, table S2), were volunteered by their owners and the Royal Society for the Prevention of Cruelty to Animals (RSPCA) Llys Nini Wildlife Centre (Penllergaer, Wales) to take part in this study. Dog body masses were obtained from the most recent measurements taken by a veterinarian, or the RSPCA, and we measured body length, forelimb length and hindlimb length to the nearest cm. Two leather dog collars (short and long) of the same width were used to cover the range in dog neck size. Combinations of pre-prepared lead plates (up to 10 cm in length) and varying in mass (25, 35, 45, 50, 100, 150 and 175 g) were fashioned into collar loads equivalent to 1, 2 and 3% of each carrier dog's body mass. The lead plates were stacked, the longest of them (for the greatest masses) being bent to replicate a 10 cm section of the collar circumference and attached securely to the ventral collar along their full-length using Tesa® tape. A tri-axial accelerometer and its supporting battery (3.2 V lithium ion) were taped securely to the load. The tag and battery combined weighed 11.9 g and, in the absence of any additional load, were considered negligible in mass and used as a control (0% carrier body mass). All trials were approved by the Swansea University Animal Welfare Ethical Review Body (ethical approval number IP-1617-21D).

Each dog was encouraged to traverse along a 25 m stretch of level, short-cut grass at slow (walk/amble), moderate (pace/trot) and fast (canter/gallop) speeds (because gait affects acceleration signatures substantially [24]) wearing collar-tags equivalent to 0, 1, 2 and 3% of their body mass (12 gait and tag mass combinations) and trial order was randomized. Posts were spaced every 5 m along the track. A stopwatch was used to record the time taken (to the nearest s) for a dog to travel 20 m in order to calculate an average speed of travel (m s^{-1}).

(c) Data processing

In all cases of animals equipped with accelerometers, the three channels of raw acceleration data were converted to a single metric by calculating the vectorial sum of the acceleration following Vect sum $= \sqrt{(a_x^2 + a_y^2 + a_z^2)}$, where a is the instantaneous acceleration and the subscripts denote the different (orthogonally placed) acceleration axes. We chose to use the Vect sum rather than dynamic body acceleration (DBA) metrics [26] because DBA values do not represent peak accelerations owing to the gravity-based component being removed [27]. The specifics of the surge, heave and sway accelerations were not considered separately owing to some collar roll. In the case of the free-living carnivores, we examined how travel gait affected the Vect sum by plotting the cumulative frequency distribution from each species during periods of walking, trotting and bounding.

For the domestic dogs, we selected the maximum four peak accelerations in the Vect sum from the gait waveforms using the peak analysis tool in OriginLab (2020) to examine them as a function of average speed, gait, body mass and tag mass as a percentage of carrier body mass. We standardized the use of four peaks because at the highest speeds some dogs only had four full waveforms during the test stretch. The relative forces (% body mass) exerted by the tags on their animal carriers were calculated using $F = ma$, where m is the mass of the tag plus collar as a percentage of carrier mass and a is the acceleration (g).

(d) Tag-based acceleration method

Finally, in a full cross-species comparison of the free-living animals, we plotted the cumulative frequency distribution of the Vect sum from each species during periods when they were active (by excluding periods where the acceleration signals were constant) to define the vector sum of the acceleration at species-specific 95% and 99% limits.

(e) Statistical analyses

Linear mixed-effects models were conducted in R (v. 4.0.3, [28]) within the 'lme4' package (v. 1.1-26) in order to investigate how the period between acceleration peaks, gait and body mass influenced peak accelerations across four species of wild carnivores, and separately in domestic dogs. Additionally, we investigated how travel speed (covariate), body mass (covariate), collar mass as a percentage of carrier body mass (fixed factor with four levels) and gait (fixed factor with three levels for slow, moderate and fast gaits) influenced peak accelerations and consequent forces exerted by the tags. Dog identity was included as a random factor in all models to account for repeated measures. All potential interaction effects were first investigated and a step-wise back-deletion of non-significant interaction terms was conducted. Standard model diagnostics were conducted in order to ensure that model assumptions were met (examining quantile-quantile plots and plotting the residuals against fitted values) and data transformations were conducted in order to meet assumptions where appropriate. The F statistic and marginal and conditional R^2 were determined using the 'car (3.0-5)' and 'MuMIn (1.46.6)' packages, respectively. Coefficients for best-fit lines in the figures were extracted from the final outputs of the models.

3. Results

(a) Changing acceleration according to activity in carnivores

Accelerometer data for periods when our carnivores travelled, displayed clear peaks in the waveforms with measurable frequency and, summarized as a frequency distribution of the vectorial sum of the three orthogonal axes, showed tri-modal distributions except for the pine martens which were mono-modal. Following [29] and examination of videos of the study animals engaged in travelling using different gaits with measurable step frequency, we could ascertain that these corresponded to walking, trotting and bounding (e.g. figure 1, which also tallied with our direct and filmed observations of the domestic dogs below); these were further exemplified by variation in the amplitude in this acceleration metric (figure 2). Cumulative frequencies of all acceleration values showed increasing acceleration from walking through trotting to bounding and typically had a roughly logarithmic-type curve for all gaits and animals (figure 1). The percentage time during which the tags carried by the carnivores had acceleration exceeding 1 g during specified activity, varied between a mean minimum of 31% for walking badgers to 88% for bounding cheetahs (electronic supplementary material, table S3). Furthermore, while differences in species acceleration distributions were not readily apparent for their walking gaits, the percentage time during which acceleration was in excess of 1 g was greatest during bounding, with cheetahs showing the highest values in this category (green line with circles in figure 1). Mean peak accelerations per stride across species varied between 1.37 g (s.d. 0.05) and 6.25 g (s.d. 0.79) for walking and bounding cheetahs, respectively (electronic supplementary material, table S4). The maximum recorded value was 18.1 g in a cheetah assumed to be chasing prey.

Across the four species, gait was the main factor dictating peak acceleration (figure 2) and there were no significant effects of body mass, nor period between peaks (linear mixed-effects model: log period: $F_{1,210} = 0.01$, $p = 0.908$; gait:

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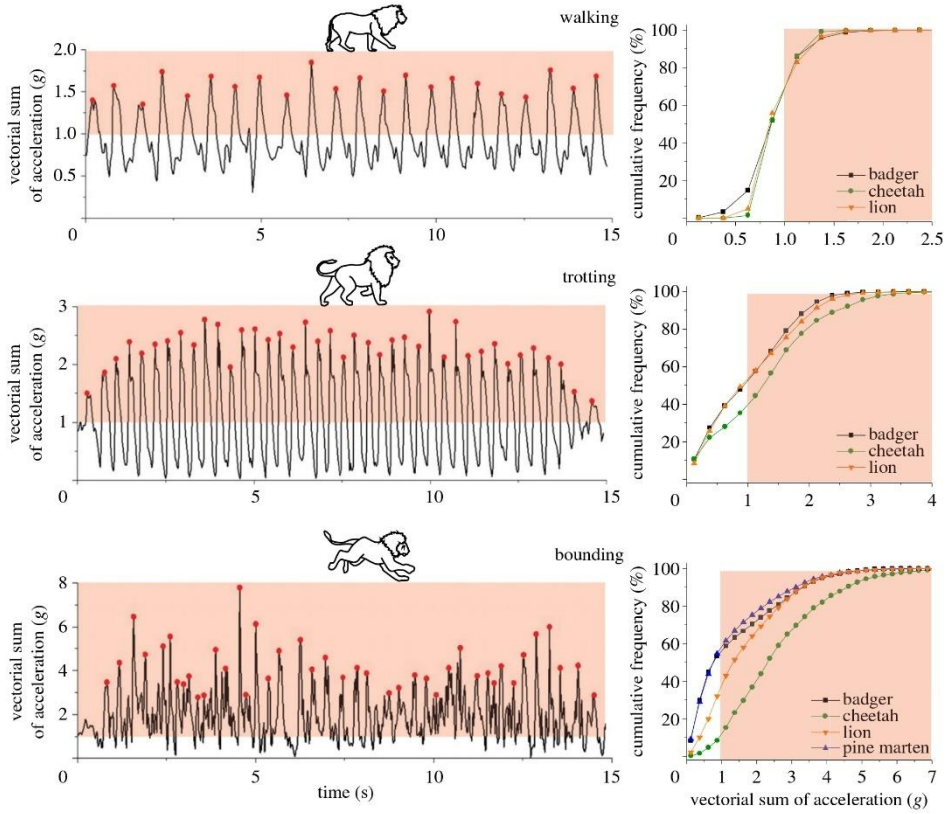

Figure 1. Acceleration signatures vary according to gait and lifestyle. Left-hand panels: acceleration signatures recorded by collar-mounted tags on a lion according to activity. The red areas show when the acceleration exceeded that of gravity (note the changing scales with gait). Right-hand panels: cumulative frequency of all acceleration values for four free-living carnivores according to gait. Note that the pine martens never walked or trotted. (Online version in colour.)

$F_{2,208} = 1083.07$, $p < 0.0001$; body mass: $F_{1,19} = 3.00$; $p = 0.100$; electronic supplementary material, table S5). The period between acceleration peaks was greater for larger species during slower gaits, but not for bounding (a linear mixed-effects model demonstrated a significant interaction effect between body mass and gait: $F_{2,209} = 3.00$, $p < 0.0001$; electronic supplementary material, table S5).

There was also appreciable variation in the vectorial sum of the acceleration within gaits and between sexes, as exemplified by prey chases by lions. Here, mean peak acceleration per stride across females and males increased from about 3 *g* at the outset to a maximum of about 3.8 *g* before decreasing again (figure 3). However, female peak acceleration was approximately 1 *g* higher than males for the duration of the chase (figure 3). Given that females and males were wearing tags that amounted to 0.72% and 1.02% of their mean body masses, respectively (electronic supplementary material, table S1), this translates to tag-dependent forces corresponding to greater than 2% and greater than 4% of the gravitational force exerted on the animal's body masses, respectively (figure 3). In the case of the cheetah, which showed the highest peak vectorial acceleration sum of our study animals, a 3% tag would impose forces equivalent to 54% of the gravitational force exerted on the animal's body at this time.

In dogs, stride peak accelerations increased linearly with travel speed (electronic supplementary material, figure S2), but at greater rates with increasing relative tag mass (there was a significant interaction effect between travel speed and tag per cent body mass: $F_{3,500.77} = 4.34$, $p = 0.004$; electronic supplementary material, table S6). There was also a significant interaction effect between gait and tag per cent body mass on stride peak accelerations ($F_{6,498.57} = 4.34$, $p = 0.0002$; electronic supplementary material, table S6). Peak tag accelerations ranged from 4 to 18 *g* during fast category (canter/gallop) trials in dogs wearing collar tags equivalent to 3% of their body mass (electronic supplementary material, figure S3). In this scenario, movement of the tag relative to the body (flapping/swinging) was exacerbated and, as a consequence, the force exerted by the tags ranged from 20–50% of the gravitational force exerted on the carrier animal's body mass (electronic supplementary material, figure S4).

Stride peak accelerations were largely invariant with body mass ($F_{1,10.12} = 3.51$, $p = 0.090$; electronic supplementary material, table S6) across dog breeds for any given gait (electronic supplementary material, figure S3). Consequently, the peak forces exerted by the tags were directly proportional to tag mass and body mass. Accordingly, relative tag forces (percentage of the gravitational force exerted on the carrier animal's body mass) were independent of carrier body

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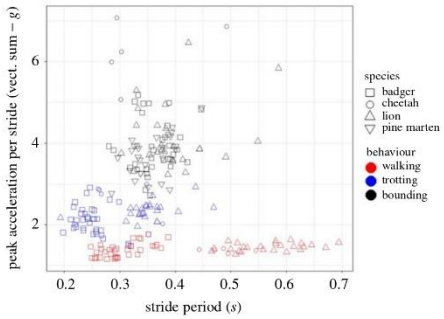

Figure 2. Body mass and stride period do not dictate peak tag acceleration. Distributions of peak amplitudes of (the vectorial sum of) accelerations and stride periods for four free-living carnivores (see symbols, with mean masses of *ca.* 2 kg, 9 kg, 41 kg and 152 kg for the pine martens, badgers, cheetah and lions, respectively) travelling using different assumed gaits (colours). Each individual point shows a mean from a duration of activity greater than 5 s from a single individual. See also the electronic supplementary material, figure S1 for similar data from domestic dogs. (Online version in colour.)

mass (electronic supplementary material, table S6 and figure S4).

(b) Using accelerometry to derive an over-arching tag-force rule

Although travelling is a major component across species, animal activity across all behaviours contributes to the acceleration, and therefore the tag force profiles, that animals experience. We produced cumulative frequency curves of the vectorial sum of the acceleration (cf. figure 1) for all 10 study species for periods when animals were considered active and these all showed a characteristic sigmoid pattern (figure 4*a*). These relationships were displaced further to the right as higher acceleration activities accounted for an increasing proportion of any animal's time (figure 4*a*). In order to have a scientifically robust acceptable threshold to limit the forces produced by a tag on an animal carrier, we suggest a tag-based acceleration method; that researchers should derive a similar cumulative acceleration profile for their study species and use a minimum of the 95% limits on the plot (although higher limits may be more appropriate). Assuming, in the case of our study animals, that these limits were intended to cater for a tag that should exert forces that are less than 3% of the gravitational force exerted on the animal's body, this limit would lead to corrected tag masses constituting between 1.6% and 2.98% of our study animals' masses (figure 4*b*). We note, however, that even these corrected tag masses would effectively exceed the 3% rule conditions for one-twentieth of the animals' active periods: the difference between the 95% and 99% thresholds for our study species indicates the extent of the force development for this period with some, such as the koalas, showing virtually no difference, whereas badgers, baboons and martens exhibited substantial differences (figure 4*b*). Importantly though, this method would allow researchers to define any tag force thresholds, not just 3%, and the times these were exceeded by the animal, not just 95%.

4. Discussion

The subject of detriment caused by tags on animals is complex because the general term 'detriment' has many facets [20], not least because the tag itself may cause the animal to move in an atypical manner, which may change how a device would affect an animal that did not respond to the device. One direct aspect that exemplifies this is, for example, measurable physical harm to the animal, such as pressure sores [12], the severity of which might be expected to depend on movement patterns. However, physical harm can also effectively occur if tagged animals or their offspring cannot balance energy budgets owing to compromised foraging stemming from tag interference [6,30,31]. Often, this is simply a result of higher movement costs or reduced performance in tagged animals as they travel [18]. This also means though, that precise limb kinematics may be different in travelling tagged animals, and this will affect acceleration signals recorded by animal-attached tags, which is relevant to a study such as ours. So, measurement affects performance [32] and we must bear this caveat in mind when we advocate that our tag data represent the norm of untagged animals. Against this, however, we can and should use proper physical frameworks to assess tag detriment because this is precisely what our tagged animals experience, whether their movement is 'normal' or not, because we have specifically equipped them with the source of detriment. Indeed, this is the fundamental premise behind our work although the issue of what untagged animals may experience remains problematic [5].

A rigid vehicle accelerating in a straight-line only experiences acceleration in the longitudinal axis. By contrast, the multiple limb-propelled motion of an animal with a flexible body produces complex three-dimensional trunk accelerations owing to the changing limb accelerations [23] caused by multiple muscle groups that ultimately transfer mechanical energy and affect shock absorption [33], and the mechanical work conducted within each stride [34]. Ultimately, the magnitude of trunk accelerations depends on the combined acceleration of the limbs, and the masses of those limbs (cf. [23]). Thus, animals engaging in high performance activities are expected to produce high body accelerations, and have physiological and anatomical adaptations to enhance performance, such as fast twitch muscles [35], and tendons designed for greater storage and release [36], which will increase this. Through all these complexities, tags mounted on the trunk of an animal result in greater forces being imposed that scale linearly with the acceleration of the tag and its mass. Consideration of animal lifestyle then, can already inform prospective tag users of the likely scale-up of the tag forces beyond the 1 *g* normally considered for tag detriment because force = mass × acceleration, the repercussions of which are discussed below in terms of potential detriment. Consequently, the 3–5% mass limits for slow-moving animals, such as sloths (Bradipodidae) or koalas (Phascolarctidae) (figure 4), seem most appropriate, though this does not mean that tags will not affect the animals. Against this, the 3–5% mass limits may be less appropriate for pursuit predators, such as wild dogs (*Lycaon pictus*), regularly jumping animals like kangaroos (Macropodidae) or martens (Mustelidae) (figure 4) and rutting ungulates (Ungulata). Beyond that, in our small sample of carnivores at least, which nonetheless covers about two orders of magnitude in

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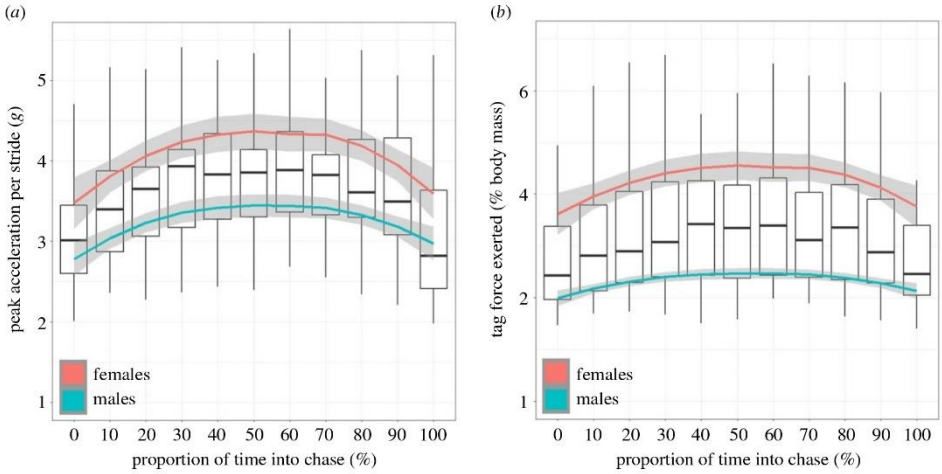

Figure 3. Hunting lions experience maximum tag forces mid-chase and show substantial inter-sex differences. Box and whisker plots (bold horizontal bars show means, boxes inter-quartile ranges (IQR) and whiskers 1.5 × IQR) of the: (*a*) vectorial sum of the acceleration peaks per bound (cf. figure 1), and (*b*) the tag-based forces exerted as a percentage of the gravitational force exerted on the animal's body (because our tag constituted 1.02% and 0.72% of the female and male body weights, respectively, see the electronic supplementary material, table S1) for lions chasing prey as a function of the percentage progression into the chase (considered to have started when bounding began). Red (upper) and blue (lower) lines show grand means for five females and five males, respectively. The maximum acceleration was 15.1 *g*, which would equate to a 3% tag exerting a force equivalent to 45.3% of the gravitational force exerted on the animal's body. (Online version in colour.)

mass, it seems that peak acceleration associated with gait varies little with mass, although larger animals have longer stride periods (figure 2, cf. [37]). If these animals were to carry tags constituting 3% of their normal body mass, mean peak forces imposed by the tags would constitute *ca* 4.5%, 6% and 12% of the gravitational forces exerted on the animals' bodies for walking, trotting and bounding gaits at frequencies of between 1.6 and 4 times per second (for walking lions and trotting badgers, respectively; figure 2; electronic supplementary material, table S4). We also note how minor differences in sex-dependent tag masses coupled with differences in performance affect the forces imposed by the tags, as exemplified by the lions (figure 3) and how, were the tags in this study to constitute 3% of the animals' masses, the tag-based forces would scale up accordingly. Against all this, we recognize two important trends: (i) that as animals get larger, deployed tags on them are likely to be a smaller fraction of their mass anyway; but that (ii) despite miniaturization advances in tag technology, researchers continue to deploy systems that are around the 3–5% mass limit on smaller animals [21].

Importantly, tag attachment is relevant in translating the acceleration experienced by the animal's trunk into tag-dependent forces acting on the animal, with collars predicted to be particularly problematic. A tag that couples tightly with its carrier's trunk, such as one attached with tape to a bird [38] or glue to a marine mammal [39], experiences acceleration that closely matches that of its substrate, so it exerts forces at a site where most of the animal's mass lies. By contrast, a device on a looser-fitting collar of a moving tetrapod not only exerts forces on the (less massive) head and neck areas, rather than the animal's trunk, but the tag also oscillates between essentially two states: one is analogous to 'freefall', which occurs between pulses of animal trunk acceleration in the stride cycle which project the collar in a particular direction owing to its inertia and lack of a tight couple with the neck. The collar is therefore subject to peaks in acceleration when it interacts with the animal's neck, causing greater collar acceleration than would be the case if it were tightly attached to the animal's body (cf. peaks in figure 1). This explains why Dickinson *et al*. [40] reported that acceleration signatures from collar-mounted tags deployed on (speed-controlled) goats *Capra aegagrus* became increasingly variable with increasing collar looseness, and is analogous to the concerns related to injuries sustained by people in vehicles depending on seatbelt tightness [41]. Partial answers to minimizing such problems may involve having padded collars that should reduce acceleration peaks, making sure that the tags themselves project minimally beyond the outer surface of the collar and having wider collars to reduce the pressure.

Having identified how animal movement changes the 3% tag rule, it is more problematic to understand how the identified forces translate into detriment. Within a general tag detriment framework, heavier tags require that animals perform more work (J) during movement because work done = force × distance, which helps clarify why the additional forces from a tag, on top of the animal weight, should relate to energy expenditure (cf. [42]). However, with respect to load carrying, how various tri-axial acceleration metrics such as DBA [26] relate to force and energy needs further research [43]. A prime effect of vectorially summed acceleration is that higher associated forces (because mass is constant) and smaller contact areas will lead to higher pressure at the tag-animal interface because pressure = force/area. This can affect anything from fur/feather wear [44] to changing the underlying tissue [45] and, as would be predicted, is notably prominent in species wearing thin collars

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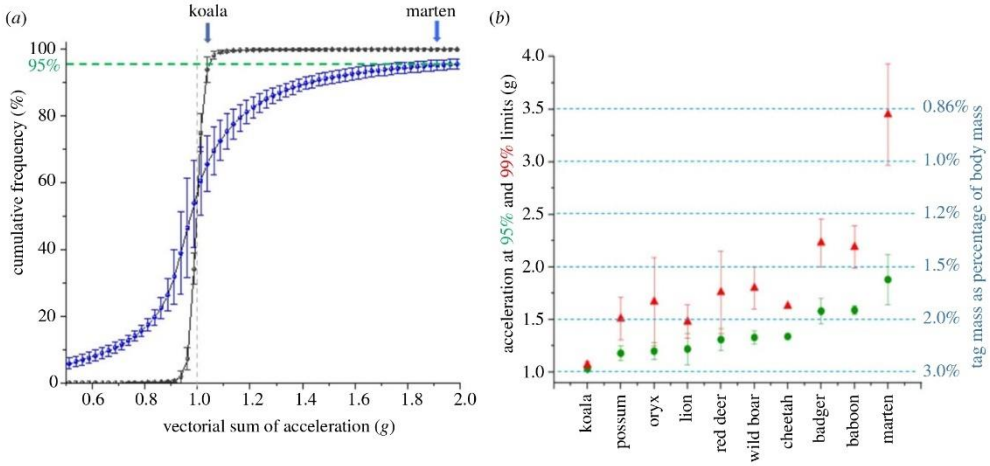

Figure 4. Defining tag mass limits based on cumulative time spent experiencing tag forces. Panel (*a*) shows the mean cumulative frequency (bars = s.d.) of the vectorial sum of the acceleration for two arboreal animals with very different athleticisms: five koalas (black line concentrated around 1 *g*) and five pine martens (blue line with much greater spread around 1 *g*). The 95% limit is shown by the dashed (green) line. Panel (*b*) shows these two species points (and the 99% limits in red triangles) adjacent to a broader species list highlighting variation in lifestyles. Assuming that a tag should only exert a force amounting to 3% of the gravitational force exerted on the carrier animal's body, the translation of these species-specific acceleration limits can be used to correct tag masses to be an appropriate percentage of the carrier animal mass (blue axis on the right). (Online version in colour.)

(e.g. howler monkeys *Alouatta palliatai*, where 31% of animals wearing ball-chain radio-collars constituting just 1.2% of their mass sustained severe damage extending into the subcutaneous neck tissue and muscle [12]). However, pressure-dependent detriment will also depend on the proportion and length of time to which an animal is exposed to excessive forces, with animals that spend large proportions of their time travelling, such as wild dogs, being particularly susceptible [46].

Perhaps more esoteric, is the extent to which the inertia of a variable force-exerting tag 'distracts' its wearer, aside from the physical issues of load-bearing by animals, and in this context, peak forces per stride are liable to be critical. The tag mass as a percentage of carrier mass did not affect the gait-specific speeds selected by the domestic dogs in this study. However, it remains to be seen the extent to which a typical 30 kg cheetah wearing a collar that is 3% of its body mass, and therefore experiencing an additional force equivalent to up to 16 kg during every bound of a prey pursuit, might have its hunting capacity compromised. We note that the survival of such animals is believed to be especially sensitive to the proportion of successful hunts (cf. [47]), which calls for critical evaluation of performance between tag-wearing and unequipped animals, or animals equipped with tags of different masses (cf. [32]).

In the meantime, our suggested approach of setting tag mass limits based on the overall (corrected) forces being less than 3% of the gravitational force exerted on the animal's body for 95% of the active time should go some way to getting a more realistic assessment of the potential for detriment. Where researchers adopting this approach do not have appropriate acceleration data for their study animal, they could use a surrogate species, perhaps from an online database. Such a resource should define the length of time that study animals were equipped to derive the acceleration frequency distribution because animal activities (and therefore the acceleration signals associated with them) occur variously over time. For this, longer periods are obviously better, but a pragmatic approach might be to plot cumulative frequencies of the vectorial sum of the acceleration as a function of recording time to see how they change or tend towards a stable value as the monitoring period increases. In this, we note that seasonal variation in animal behaviours, such as occurs in rutting ungulates, have potential to affect the distribution substantially, emphasizing the importance of considering the context under which the data were gathered.

Importantly, we do not advocate the 3% rule as such, but recognize that it has been widely adopted and could serve as a useful starting point with which to consider tag detriment if calculated as we have suggested here. In this, cognizance should also be given to the extent of tag forces for periods above the 95% threshold because, where these are excessive, it may be appropriate to use a 99% threshold or higher to derive appropriate tag masses. Notably though, even 99% limits do not highlight the high tag forces developed during prey pursuits exhibited by the cheetah. We suggest that the solution to this lies in more detailed consideration of the animal's lifestyle; in particular, identifying survival-critical behaviours with exceptionally high accelerations. Such periods may persuade ethics bodies to raise their thresholds still further. Underpinning this will be ongoing miniaturization, where tags benefit from the sensor revolution in human wearables, which will undoubtedly percolate through to animal applications: advanced smart phones have greater than 10 sensors, along with significant memory and data transmission capabilities, and typically weigh 150–200 g or about 0.2% of average human body mass, although human wearables benefit from regular contact with charging systems while many wildlife tag applications are projected for long-term deployments (e.g. [48]) that either necessitate correspondingly large batteries or autonomous charging systems, both of which increase the mass of tags [49].

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Finally, consideration of the acceleration-based forces generated by animal-attached tags does not cover all forms of detriment because other forces are at play, such as greater drag in swimming- and flying species (cf. [6]), and more esoteric elements, such as device colour, that affect animal behaviour [50]. However, our framework should take the current 'one-size-fits-all' basic 3% rule into an arena where quantitative assessment of acceleration can be compared to the myriad of tag-influenced behaviours recognized by the community to link animal lifestyle to putative detriment. Most importantly, these considerations should give ethics bodies a more useful rule of thumb than is currently the case and enable us to develop systems that minimize force-based tag effects, to the benefit of both animals and the science that their studies underpin.

Ethics. All trials with domestic dogs were approved by the Swansea University Animal Welfare Ethical Review Body (ethical approval number IP-1617-21D). Live trapping and collar deployment with badgers and pine martens was conducted at two sites under UK Home Office License and Northern Ireland Environment Agency, License 2228 between August and November 2019. For work with lions, all procedures followed recommendations of SANPark's Standard Operating Procedures for the Capture, Transportation and Maintenance in Holding Facilities of Wildlife. Conditions, permits and approvals for fieldwork on lions were granted from South African National Parks (permit number SCAM 1550), from Swansea University College of Science Ethics Committee (SU) (SU-Ethics-Student-260919/1229), the Animal Welfare Ethical Review Committee at Queens University Belfast (QUB-BS-AREC-18-006) and the University of Pretoria (NAS061-19). For work with olive baboons, research activities described in this paper were approved by the Republic of Kenya's National Council for Science and Technology (permit no. NCTS/RCD/12B/012/26B), Kenya Wildlife Services (KWS/BRM/5001) and the Smithsonian Tropical Research Institute's Animal Care and Use Committee (IACUC no. 2012.0601.2015). For koala work, methods were approved by the Deakin University Animal Ethics Committee (A312010) and conducted under permit (10005379) by the Victorian Department of Sustainability and Environment. For mountain brushtail possum work, methods were approved by the Deakin University Animal Ethics Committee (A45-2011, B33-2012) and conducted under permit by the Victorian Department of Sustainability and Environment. For red deer, all handling, anaesthesia and collaring procedures were approved by the ethics committee of the Ministry of the Environment (number MZP/2018/630/694). For wild boar, all handling, anaesthesia and collaring procedures were approved by ethics committee of the Ministry of the Environment (number MZP/2019/630/361).

Data accessibility. Data pertaining to this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rjdfn2zbm [51].

Authors' contributions. R.P.W.: conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing; K.A.R.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing; R.G.: formal analysis, methodology, visualization, writing—review and editing; M.D.H.: software, visualization, writing—review and editing; N.J.M.: funding acquisition, investigation, writing—review and editing; N.C.B.: investigation, writing—review and editing; S.H.B.: investigation, writing—review and editing; J.P.T.: investigation; J.H.: data curation, investigation, writing—review and editing; C.M.D.: investigation, writing—review and editing; N.B.: investigation, writing—review and editing; M.J.: investigation, writing—review and editing; M.P.: investigation, writing—review and editing; V.S.: investigation, writing—review and editing; R.H.: investigation, writing—review and editing; M.C.C.: investigation, writing—review and editing; J.P.Y.A.: investigation, writing—review and editing; B.M.A.: investigation, writing—review and editing; D.A.W.: investigation, writing—review and editing; A.A.: investigation, writing—review and editing; D.M.S.: investigation, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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5.2. Analýza biologging dat pro studium chování a pohybu zvířat

5.2.1. Publikace č. 3 - Sleep in the wild: the importance of individual effects and environmental conditions on sleep behaviour in wild boar

Tato oblast výsledků je zaměřena na poznatky vycházející z data, která byla pořízena pomocí biologging technologie a vycházejí z akcelerometrických a magnetometrických dat. Informace prohlubují poznatky o detailním chování a pohybu volně žijících zvířat. První publikace – *„Sleep in the wild: the importance of individual effects and environmental conditions on sleep behaviour in wild boar.“* popisuje pomocí získaných akcelerometrických dat z biologgingu změny spánkového režimu u prasat divokých (*Sus scrofa)* na území České republiky. Výsledky prokázaly snížení doby spánky v průběhu teplých dnů, a naopak lepší a dlouhodobější spánek v průběhu dnů s vyšší vzdušnou vlhkostí, vyššími srážkami a sněhovou pokrývkou. Takto dlouhodobá a podrobná studie spánku divokých zvířat poskytuje cenné informace o inter a intra-individuální rozmanitosti spánku. Vzhledem k hlavní roli spánku pro zdraví jedinců jsou výsledky cennou informací a naznačují, že klimatické výkyvy a změny mohou negativně ovlivnit spánek a potažmo i zdraví divokých zvířat, které jsou aktivní v průběhu noci.

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Sleep in the wild: the importance of individual effects and environmental conditions on sleep behaviour in wild boar

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Sleep serves vital physiological functions, yet how sleep in wild animals is influenced by environmental conditions is poorly understood. Here we use high-resolution biologgers to investigate sleep in wild animals over ecologically relevant time scales and quantify variability between individuals under changing conditions. We developed a robust classification for accelerometer data and measured multiple dimensions of sleep in the wild boar (*Sus scrofa*) over an annual cycle. In support of the hypothesis that environmental conditions determine thermoregulatory challenges, which regulate sleep, we show that sleep quantity, efficiency and quality are reduced on warmer days, sleep is less fragmented in longer and more humid days, while greater snow cover and rainfall promote sleep quality. Importantly, this longest and most detailed analysis of sleep in wild animals to date reveals large inter- and intra-individual variation. Specifically, short-sleepers sleep up to 46% less than long-sleepers but do not compensate for their short sleep through greater plasticity or quality, suggesting they may pay higher costs of sleep deprivation. Given the major role of sleep in health, our results suggest that global warming and the associated increase in extreme climatic events are likely to negatively impact sleep, and consequently health, in wildlife, particularly in nocturnal animals.

1. Introduction

Sleep is observed in virtually all animals [1]; it is essential for health, cognitive performance and development, boosting baseline immune levels and immune response to infection [2], promoting hormone production and metabolic regulation [3,4], and supporting neural maintenance, brain development and cognitive functions [5,6]. It is, therefore, not surprising that average short sleep times and sleep loss are accompanied by numerous detrimental effects on health and cognition in the short and long term [7–9], and, in the laboratory, are often followed by longer sleep which likely mitigates these costs [10]. While a wealth of evidence demonstrates its vital benefits, sleep also entails opportunity costs because sleeping animals cannot engage in fitness enhancing behaviours, like foraging or finding mates, and are exposed to greater predation risk [11]. However, sleep is believed to exhibit limited plasticity because the benefits it provides cannot be forgone for long [12]. Likewise, members of the same species are expected to have similar sleep times and patterns as

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their sleep is regulated by the same neurophysiological processes [12]. Whether sleep has limited variation within and between individuals is, however, unclear since it has been studied primarily in the laboratory where constraints on sleep time and benefits for reducing sleep time are absent. Furthermore, laboratory studies and the few existing sleep studies in the wild are often constrained by small sample sizes or short recording durations and consider a limited range of environmental conditions; therefore, they cannot estimate how sleep varies within and between individuals. If we are to unravel the contributions that sleep brings to the health and development of animals and quantify how the sleep benefits–costs balance differs among individuals experiencing changing conditions, we need to study sleep in the wild for long time periods. Using cutting-edge, minimally invasive biologgers, we investigated how environmental conditions influenced the quantity, efficiency, and quality of sleep within and between individuals in a wild population of wild boars (*Sus scrofa*) over the annual cycle.

Sleep time and patterns differ remarkably among species as a result of natural selection [11,13,14], but little is known about intraspecific variation in sleep and its causes and implications. While there is ample evidence that individuals within a species differ consistently and predictably in many behaviours [15], individual differences in sleep behaviour have not yet been investigated in wild animals. In humans, inter-individual differences in sleep time and patterns are well known to exist, but the magnitude of these differences is rarely quantified [16] and, importantly, it is unclear whether they reflect cultural and societal differences or natural variation [17]. Nonetheless, individuals that sleep less than average develop neurological disorders later in life, suggesting chronic short sleep durations entail long-term costs [8,9]. Similarly, whether individuals can adjust their sleep to changing conditions is poorly understood. While there is evidence of sleep loss in a handful of species, such as during large scale movement, or reproduction [18–20], previous studies are typically limited to short recording periods involving few individuals. This is problematic because wild populations experience a range of changing environmental conditions over the daily and annual cycle, and investigating these effects on sleep will permit us to quantify its plasticity over time.

In the laboratory, ambient temperature is a major driver of sleep quantity and quality [21]. As the first stage of deep sleep in mammals is characterized by low, constant body temperature, a cool ambient temperature promotes its onset, efficiency (reduced fragmentation into multiple sleep bouts), quality (longer sleep bouts) and overall daily duration [21]. Conversely, the thermoregulatory challenge presented by high temperature reduces sleep time, increases sleep fragmentation and compromises sleep quality in favour of behaviours that help thermoregulation [21,22]. As a result, ambient temperature is finely controlled in laboratory studies in humans and animals [21]. Altogether, this suggests that daily and seasonal changes in temperature should impact sleep in wild animals; accordingly, the few studies conducted under natural conditions find that cooler temperatures promote sleep [22–25]. Nevertheless, because these studies were conducted for few days/weeks, the subjects experienced only a narrow range of temperatures.

In the wild, animals are exposed to many other environmental conditions, such as humidity, rain, snow and light, that change throughout the day and across the year. These can mitigate or exacerbate the influence of temperature, but to date have been mostly neglected. For example, humidity makes thermoregulation more difficult by reducing the efficiency of evaporative cooling [26]. Thus, high humidity could compound the effects of higher temperatures on sleep, reducing duration and increasing fragmentation [21,26]. Conversely, rainfall and snow may promote sleep, by providing evaporative cooling or increasing the thermal value of bedding sites respectively.

Finally, light regulates the circadian rhythm in most mammals; hence day length controls when and how long to sleep [27]. For example, longer day lengths reduce, while shorter day lengths increase, sleep duration in humans [28]. Other light sources such as moonlight may also interfere with sleep regulation. Consistently, greater illumination from moonlight increases sleep duration in gibbons (*Hylobates* sp.) and humans, although not in baboons (*Papio anubis*) [24,25,29]. In the wild, sleep timing and duration should thus fluctuate with changing day lengths and moonlight, where longer days reduce sleep in diurnal species and increase sleep in nocturnal species. In addition, circadian type may influence the duration of sleep; for example, nocturnally active primate species sleep longer than diurnally active ones [30]. However, whether plasticity in circadian type affects sleep quantity, efficiency and quality is currently unknown. Furthermore, sleep in wild animals may be affected by human disturbance [31], particularly in nocturnally active species and by predation risk [13,32].

In this study, we investigate how changing environmental conditions influence sleep behaviour over the annual cycle in wild boar (*Sus scrofa*). Wild boar are a generalist species that exhibits considerable behavioural plasticity [33]; thus, it is a good model for investigating the plasticity of sleep under natural conditions. Studying sleep in wild animals has been difficult because of its elusive nature, and lack of reliable and minimally invasive recording equipment; thus some studies have used invasive recording equipment requiring surgery and capture–recapture methods. This approach is likely to be stressful for most wild animals and likely leads to inaccurate estimates because stress affects sleep [10,34]. Recent advances in minimally invasive biologging technology and analytical methods offer a promising solution to these problems: they allow accurate recording of behaviours and without direct observations over long time periods [35,36]. Importantly, laboratory studies with electroencephalogram on sleep in pigs, the domesticated relatives of wild boar, provide detailed information on which to base the classification of sleep with biologgers in this species [37–40].

Using multi-sensor biologgers that allow discrimination of complex behaviour in wild animals [36], we estimated total daily sleep time (TST, hours), which is an appropriate ecological estimate of sleep quantity in animals [11,13]. Moreover, unlike most previous studies in wild animals, we also considered sleep efficiency and quality to gain an ecologically meaningful and comprehensive assessment of sleep. The number of bouts over which TST occurs (sleep fragmentation/consolidation) reflects efficiency, since individuals that frequently wake up spend more time in transitional stages and less time in restorative deep sleep [11,41]. Like sleep deprivation, greater fragmentation is associated with negative effects on physiology and cognition [41,42]. Finally, the duration of the longest sleep bout in a 24 h period indicates sleep quality as deep sleep always follows lighter sleep stages in any mammal species thus far studied; hence the duration of the longest bout represents the best opportunity for an individual to accrue the benefits of deep sleep [11,41]. Consistent with this, sleep bouts following sleep deprivation are longer and deeper [10].

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We also investigated to what extent individuals differ in sleep quantity, efficiency and quality and in their plasticity over time, and how these three aspects of sleep covary. We therefore asked whether individuals sleeping less exhibit greater variance (i.e. plasticity) in TST, higher sleep quality or lower sleep fragmentation that could help them mitigate the detrimental effects of an average shorter sleep time and sleep deprivation. We tested the predictions that TST is reduced, the number of sleep bouts is higher, and the duration of the longest sleep bout is shorter when ambient temperature and humidity are higher. Conversely, we expected that greater rainfall and snow depth increase TST, reduce the number of sleep bouts, and increase the duration of the longest bout. Finally, we predicted that, in a mostly nocturnally active species like wild boar, longer day length increases TST, reduces the number of sleep bouts, and increases the duration of the longest bout, while greater moonlight should increase the number of sleep bouts, reduce TST and the duration of the longest bout. Because activity period can be plastic [43] especially in generalist species [33], and nocturnally active species sleep longer [30], we account for timing of sleep within the 24 h on all three sleep measures. Wild boars are active primarily during darkness [44,45] and therefore we expect them to concentrate their sleep during daylight. Because boar also adjust their activity levels with changing environmental conditions [45,46] we predict that individuals concentrating sleep during light hours sleep longer than those that acquire some of their sleep during darkness. Lastly, we predict that TST and the duration of the longest bout decrease, while fragmentation increases, with disturbance by more human visitors [31] and the presence of wolves.

2. Methods

(a) Study sites and animals

Data collection took place between 5 May 2019 and 1 December 2021 (941 days) in two areas, Kostelec (49.96 N, 14.78 E) and Doupov (50.24 N, 13.12 E), in the Czech Republic (electronic supplementary material, figure S1). Kostelec is a forested suburban area near Prague open to the public, while Doupov is characterized by mixed forest and hills, closed to the public with military and forestry access only. Wolves established a pack at Doupov in December 2020 while Kostelec has no wolves.

We employed traps to capture, immobilize, and fit 28 wild boars with customized Vertex Plus collars (Vectronic Aerospace GmbH, Berlin, Germany), carrying Daily Diaries (DD; Wildbyte Technologies Inc, Swansea, UK). Of this sample, 4 were male and 24 were female, all in reproductive age. While we have clear evidence of successful reproduction during the study period for some of these females, it is very likely that most, if not all, females reproduced since 95% of female boars older than seven months in the Czech population are reproducing [47]. The duration of recording time differed among individuals from 10 to 363 days (mean 89 days, total of 2424 days; electronic supplementary material, figure S3).

Under the same ethics permit, a captive wild boar was fitted with an identical biologging collar to those used in the wild individuals for two months. Video recordings of behaviour were collected so that the data derived from the biologger could be validated against observed behaviours. This animal was housed in a wildlife enclosure (approx 1 km^2) covered by mixed forest in Bohumile (Czech Republic), owned and managed by the CZU.

(b) Classification of sleep

The Daily Diary (DD) [36] is an inertial measurement unit (IMU) containing multiple sensors, including tri-axial accelerometers that capture acceleration data quantified in units of 'g' ($1g = 9.81\ m\ s^{-2}$) across a range of $\pm 16g$ and varying in frequency from low (10 Hz) to high (100 Hz), as set by the user (here set to 20 Hz). This allows DDs to detect a range of movement and behaviour, from subtle to vigorous, as acceleration is measured in three dimensions [48]. When the device is at rest, such as when an animal is asleep, the total force exerted on all three axes sums to approximately $1g$ (the effect of gravity), thus allowing the inference of posture based on the known, calibrated orientation of the device. While accelerometers and other biologging sensors are growing more popular generally [35], and can be used to study sleep in the wild [49], a naive application of metrics derived from biologgers risks conflating wakeful rest and sleep. Thus, we built a robust classification of sleep with DD based on laboratory studies in domestic pigs that provide a detailed description of sleep postures and sleep estimates quantified with electroencephalogram.

During sleep individuals enter a state of quiescence in a species-specific posture and require a stronger stimulus to elicit a response compared to awake individuals [1] but, unlike torpor and hibernation, return rapidly to a waking state [1]. Pigs sleep in either lateral or sternal recumbency with the head on the ground [38–40], accompanied by rapid loss of muscle tone at sleep onset [38]. Posture was derived from raw acceleration by calculating static acceleration; this isolates the gravitational component from dynamic acceleration (acceleration resulting from movement alone). Static acceleration was estimated using a 2 s running mean filter [50] applied to the raw 20 Hz data. Body pitch and roll angles were then derived from static acceleration using the arcsine of the surge (forward–backward) and sway (left–right) axis [48]. Sternal recumbency with head-down was defined as ($pitch < 0°$) and ($roll > -15°$ and $<+15°$), while lateral recumbency was defined as ($roll < -15°$ and $>+15°$). Sustained lack of movement, the other key behavioural cue for sleep, was identified using the dynamic acceleration (i.e. produced by movement only). This was calculated by subtracting static acceleration from raw acceleration on each axis (Ax, Ay, Az). We used a metric combining dynamic acceleration on all three axes, vectorial dynamic body acceleration (VeDBA), calculated as

$$\mathrm{VeDBA} = \sqrt{A_x^2 + A_y^2 + A_z^2},$$

where A_x^2, A_y^2, A_z^2 are the dynamic components of each of the three axes of acceleration [51]. Smoothed VeDBA was then calculated over a 2 s smoothing window of raw VeDBA (20 Hz). Employing VeDBA allowed us to distinguish between the animal's active and inactive states at a high resolution. We set a threshold for movement in sleep postures to 0.2 VeDBA such that sleep bouts ended if this threshold was crossed but allowed for minor movements, such as those due to postural adjustment during sleep. Finally, given that domestic pigs in recumbent posture require 4–5 min to transition from wakefulness to sleep [37,38], we discarded the initial 5 min of each sleep bout. Our classification thus distinguishes sleep from wakeful rest using behavioural markers for sleep (figure 1; electronic supplementary material, figure S4).

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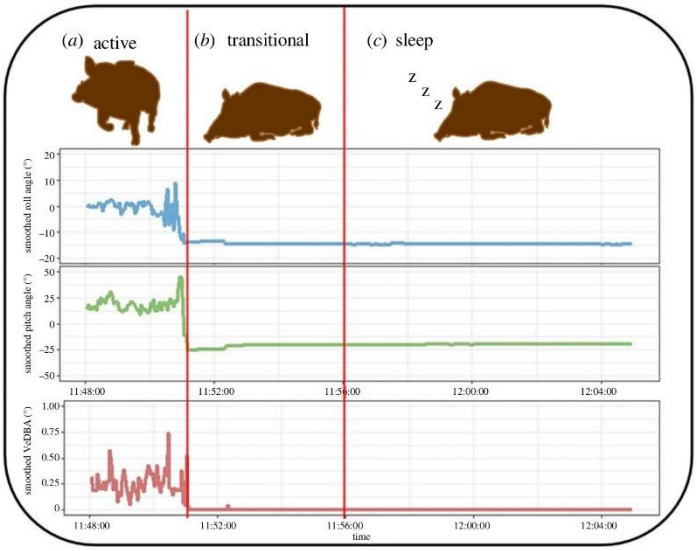

Figure 1. Example of DD data showing changes in smoothed roll, pitch and VeDBA values, corresponding to relevant behavioural types (separated by vertical red lines), to identify the onset of sleep. (*a*) General active behaviours such as movement and foraging; (*b*) sternal recumbency for the period of drowsiness/transitional stage; and (*c*) an individual is classified as asleep if it remains in sternal recumbency for longer than 5 min with little to no movement.

To assess the accuracy of our posture classification, behavioural observations of the captive boar were collected opportunistically with a handheld camera (Sony HDR-CX625). Footage of the individual in lateral and sternal recumbency was time-matched to the acceleration data. As our criteria for identification of sleep bouts filtered out any periods shorter than 5 min, we adjusted the time threshold to the duration of the shortest bout of recumbency in these videos (i.e. 31 s), allowing shorter periods to be included in accuracy testing. In total, 38.8 min of video were used, of which 11.4 min of recumbent postures and 27.4 min of other behaviours. Accuracy metrics were scored at 1 s resolution. Our classification distinguished lateral and sternal recumbency with an accuracy of 98% and specificity of 97% (electronic supplementary material, table S1).

From the biologger data we estimated the following sleep parameters for every 24 h: TST (hours); number of sleep bouts; duration of the longest sleep bout (minutes). In addition, following a commonly used approach to categorize diurnality, nocturnality and cathemerality in animal behaviour [43], we calculated the distribution of sleep (DS) as percentage of time slept between sunrise and sunset out of total daily sleep time. We discarded the first and last day of recording for each animal as these were incomplete 24 h periods.

(c) Environmental data

Hourly weather data were taken from the Jevany (Kostelec, 49.96 N, 14.80 E) and Kyelska Spa (Doupov, 50.26 N, 13.02 E) weather stations (www.visualcrossing.com). Daily means were computed for ambient temperature (°C); snow depth (cm); and relative humidity (the amount of water vapour present in the air compared to the maximum amount possible for a given temperature, as a percentage, %). Precipitation (mm) was quantified as the total daily rainfall. Day length (hours) was estimated as hours of light from sunrise to sunset. Moon phase was coded as a continuous variable ranging from new moon (dark; 0) to full moon (bright; 1). Based on [44], we adjusted the values for moon phase to account for cloud cover that reduces night brightness. We thus calculated a 'cloud-adjusted moon phase' by computing the percentage cloud cover as a percentage of the moon phase, and subtracting this from moon phase value. Electronic supplementary material, table S2, reports the range of environmental conditions recorded over the study period. We controlled for the potential impact of wolves on sleep with a binary predictor. We coded as 'wolf presence' at Doupov from December 2020 onwards, and coded Doupov prior to this date and Kostolec as 'wolf absence'. We controlled for the possible influence of human presence on sleep [31] by including as a fixed effect the total daily number of visitors recorded with an automated counter (Mobile multi, Eco-Compteur) [52] at Kostelec. The number of visitors at Doupov was coded 0, as this area is closed to the public.

(d) Statistical analysis

We used double-hierarchical generalized linear mixed-effects models (DHGLMs) to assess how wild boar altered their sleep in relation to changing environmental conditions [53]. Specifically, we modelled the changes in the mean of the three sleep measures (TST, number of sleep bouts, duration of the longest sleep bout) and their variance (sigma (σ) component) in a Bayesian framework with the R package 'brms' [54,55], and the Stan open source modelling platform [56]. Unlike standard linear mixed-effects models, DHGLMs can handle non-heterogeneous residual errors, allowing a more accurate assessment of fixed effects when the duration of recording time differs between individuals, as in our study (electronic supplementary material, figure S2) [57].

Prior to analyses, the duration of the longest sleep bout was log-transformed and all fixed effects were centred and scaled to improve model fitting. We assigned Gaussian distributions to response variables. Our data were hierarchically structured, thereby measures of sleep were nested inside individual ID. Therefore, we included ID as a random effect for both the mean and variance (sigma) component of each model to determine inter- and intra-individual variation in the three sleep measures, i.e. differences between individuals in sleep

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characteristics and in their plasticity, respectively. Thus, for each sleep parameter this model structure allows us to quantify the population mean and variance over the study period through the intercept (mean) and variance (sigma) fixed effects, and to quantify inter-individual differences in mean and variance (i.e. individual plasticity) through the intercept and variance (sigma) of the ID random effects respectively. We also estimated the correlation between the mean and variance of the random effect ID to investigate whether individuals with higher mean value of the sleep parameters also exhibited greater or lower variance (i.e. plasticity) in that sleep parameter. Finally, we included an autoregression term of order 1, applied to each individual, to control for temporal autocorrelation.

Environmental conditions, human visitation, wolf presence, DS, area, sex and year were treated as fixed effects, and we included month of the year to account for seasonal changes not captured by environmental predictors. We used a second-order polynomial term to capture possible nonlinear effects of high and low temperatures, and the distribution of sleep across 24 h, on sleep. Further, because the effect of 'month' is cyclical (e.g. where month 12 is more similar to month 1 than month 6), we used a second-order polynomial term applied both as a fixed effect and a random slope term in the model formula. Widely applicable information criterion (WAIC) confirmed that models fitted with the random slope for month provided a better fit to the data than an intercept-only model (ΔWAIC > 7 indicates a superior model fit).

We ran models using Markov chain Monte Carlo (MCMC) with weakly informative, normally distributed priors for the fixed effects with a mean of 0 and variance of 100. We assigned weakly informative, scaled *t*-distributed priors with 3 degrees of freedom to the random effects (individual-level variation) and error terms in both components of the models [58]. We ran chains of 15 000 iterations with a burn-in of 1000 iterations for the three models, sampling every 15th iteration. Visual inspection of the traces in the resulting posterior distributions showed adequate mixing and convergence. The Gelman–Rubin convergence statistic (Rhat) confirmed convergence as values were equal to 1 for all parameters [59]. Effective sample size (ESS) for all estimated parameters over 1000 confirmed that the posterior distributions had negligible levels of autocorrelation (electronic supplementary material, tables S2–S4). Models were run in triplicate and converged on similar solutions.

All fixed effects were first entered simultaneously in a starting maximal model. We reduced the maximal model by eliminating the least meaningful fixed effect, starting from quadratic terms if not meaningful, and re-ran the model, repeating the procedure until only meaningful predictors remained in a minimal statistically justifiable model (reduced model [50]). Fixed effects predictors and the correlation between mean and variance of the ID random effects were considered meaningful if the percentage of the posterior distribution crossing zero in the opposite direction of effect was less than 5 (percentage across-zero: P_x [49]). In the DHGLM, random effects estimates are constrained to be greater than zero as they are calculated on a log scale, making P_x unsuitable for assessment of effects. Therefore for random effects we considered a posterior distribution shifted away from zero, and the 95% CI not abutting zero, as evidence for a meaningful effect. Finally, we investigated whether, at the population and individual level, a greater TST also resulted in more sleep bouts per day and increased duration of the longest bout per day. To this end, we ran two mixed-effects models in the same Bayesian modelling framework, with TST as the response and number of bouts per day or duration of the longest bout per day as predictor, using normally distributed priors with a mean of zero and variance of 10 000. We included a random slope (ID slope) for the predictor with a random effect for individual (ID intercept), an intercept-only random effect for year, and an autocorrelation structure of order 1 applied at the individual level. The model also estimated correlations between individual random slope (ID slope) and individual intercept (ID intercept) at the population level, to investigate whether individuals with a higher or lower mean TST showed a bigger or smaller change in TST with bouts per day or duration of the longest bout per day.

3. Results

For each model, we report below the median and credible intervals of the posterior distributions of meaningful effects within brackets; results for the maximal and reduced models are in the electronic supplementary material, tables S3–S8; S10–S11.

(a) Sleep quantity: total sleep time (hours per day)

Boars slept primarily during daylight, although some individuals slept also during darkness (electronic supplementary material, figure S5), and there were no days of total sleep deprivation (electronic supplementary material, figure S5). From a maximal model with all predictors (electronic supplementary material, table S6), the reduced model found a quadratic effect for both temperature (temperature: −21.73 [−29.81, −19.67]; temperature^2: 8.17 [2.11, 14.31]; figure 2*a,j*; electronic supplementary material, table S3) and the distribution of sleep over 24 h (DS: −24.02 [−30.43, −17.04]; DS^2: −24.61 [−29.40, −19.67]; figure 2*a,g*; electronic supplementary material, table S3). Thus, TST was shorter when some sleep occurred during darkness and at higher temperatures (figure 2*g,j*). The model estimated that boars slept for 10.43 h per day across the year, ranging from an average of 10.14 h in summer (June–August) and an average of 12.22 h in winter (November–February). However, the random effects for between-individual variation revealed differences in their mean TST (2.39 [1.84, 3.29]; electronic supplementary material, table S3; figure 2*d*), as the model estimates varied from 6.81 h for the shortest sleeping individual to 14.94 h for the longest sleeping individual (electronic supplementary material, table S9). Individual boars also differed in the variance in TST (0.21 [0.15, 0.31]; electronic supplementary material, table S3; figure 2*d*), with estimates ranging from 1.09 to 3.20 h across individuals (electronic supplementary material, table S9). These values thus ranged across individuals from a minimum 12.86% to a maximum of 37.39% of TST (electronic supplementary material, table S9). There was no correlation between mean TST and variance in TST at the individual level (0.08 [−0.34, 0.47]; electronic supplementary material, table S3; figure 2*d*), indicating that short-sleepers did not exhibit greater or lower variance in TST than long-sleepers.

(b) Sleep efficiency: number of sleep bouts per day (sleep fragmentation/consolidation)

From a maximal model with all predictors (electronic supplementary material, table S7), the reduced model identified a curvilinear effect of the distribution of sleep over 24 h (DS: −20.49 [−36.21, −4.65]; DS^2: −47.98 [−60.45, −35.25]; figure 2*b,h*; electronic supplementary material, table S4). The model also indicated that the number of sleep bouts increased linearly with warmer

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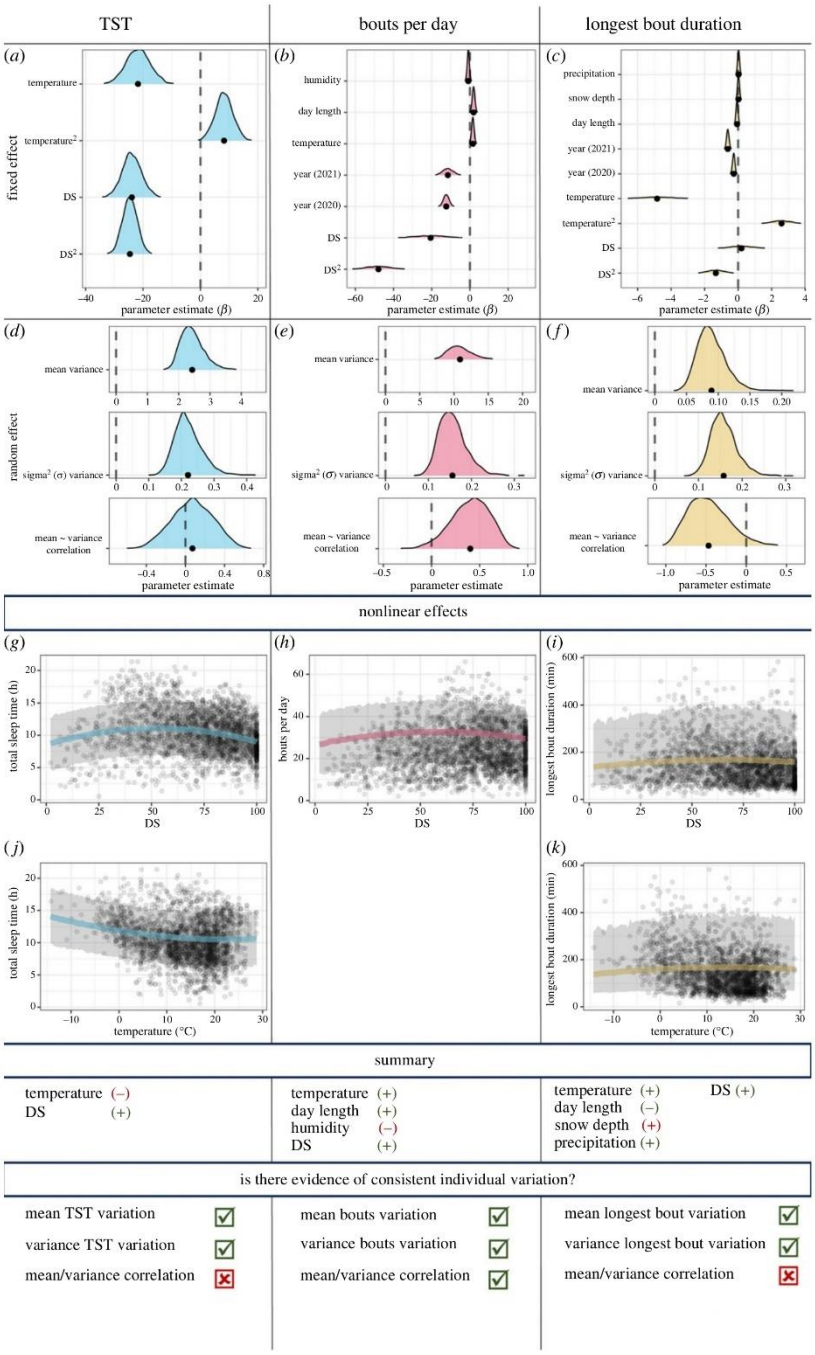

Figure 2. Reduced model results for total sleep time (TST, blue), number of bouts per day (red) and duration of the longest sleep bout per day (yellow). (*a–c*) The posterior distributions for the fixed effects, with dashed line denoting 0. (*d–f*) Posterior distributions of the random effects for inter-individual differences in the mean (ID intercept) and variance (ID sigma) of the sleep parameter and their correlation (ID intercept approx. ID sigma). (*g–k*) Nonlinear predicted effects of the distribution of sleep over 24 h (DS) and temperature. The summary reports the direction of effect for environmental variables and the general direction of effect for nonlinear DS (denoted with ±), and evidence of individual variation from the individual effects.

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temperature (1.54 [0.74, 2.38]) and longer days (1.92 [1.02, 2.79]), but decreased with greater humidity (−0.85 [−1.27, −0.41]; figure 2*b*; electronic supplementary material, table S4). Finally, sleep was less fragmented in 2020 (−12.40 [−15.08, −9.64]) and 2021 (−11.56 [−16.69, −6.52]; figure 2*b*; electronic supplementary material, table S4) compared to 2019.

The model estimated that, on average, boars slept in 24.44 bouts per day across the year, ranging from a minimum of 17.49 in winter to a maximum of 25.21 in summer. The random effects revealed that individuals differed in the mean number of sleep bouts (10.67 [7.97, 15.02]; electronic supplementary material, table S4; figure 2*e*), which ranged across individuals from a minimum of 13.58 bouts per day for the boar sleeping more efficiently to a maximum 35.27 bouts per day for the individual exhibiting the greatest sleep fragmentation. Model estimates for individual boar also differed in the variance in the number of sleep bouts (0.15 [0.10, 0.23]; electronic supplementary material, table S4; figure 2*e*), with model estimates varying from 4.56 to 13.91 bouts per day across individuals. There was a positive correlation between mean number of sleep bouts per day and variance in the number of sleep bouts per day at the individual level (0.42 [−0.01, 0.74]; electronic supplementary material, table S4; figure 2*e*), indicating that boar sleeping in more bouts also exhibited higher variance in the number of bouts.

(c) Sleep quality: duration of the longest sleep bout

From a maximal model with all predictors (electronic supplementary material, table S8), the reduced model for duration of the longest bout identified a weak curvilinear effects of temperature (temperature: −4.84 [−6.67, −3.03]; temperature^2: 2.59 [1.58, 3.59]; electronic supplementary material, table S5; figure 2*c*,*i*) and the distribution of sleep over 24 h (DS: 0.20 [−1.11, 1.49]; DS^2: −1.33 [−2.25, −0.41]; electronic supplementary material, table S5; figure 2*c*,*k*) such that the longest bout was shorter when some sleep occurred during darkness and lower temperatures. The model also found that the duration of the longest bout was shorter with longer day length (−0.06 [−0.10, −0.03]) but increased with greater snow depth (0.02 [0.00, 0.04]) and precipitation (0.03 [0.01, 0.04]; electronic supplementary material, table S5; figure 2*c*). Finally, the duration of the longest bout was shorter in 2020 (−0.26 [−0.35, −0.18]) and 2021 (−0.62 [−0.70, −0.51]) than 2019, and in 2021 compared to 2020 (electronic supplementary material, table S5; figure 2*c*).

The model estimated that, on average, the longest sleep bout lasted for 2.10 h across the year, ranging from a minimum of 1.99 in summer and a maximum of 2.83 in winter. The random effects of the model showed that individual boar differed in the estimated mean duration of the longest sleep bout (0.09 [0.05, 0.14]; electronic supplementary material, table S5; figure 2*f*) and in the variance of the longest bout duration (0.16 [0.11, 0.23]), with model estimates ranging from 1.36 to 1.81 h per day across individuals (electronic supplementary material, table S5; figure 2*f*). Finally, there was a positive correlation between mean duration and variance in the longest bout at individual level (−0.49 [−0.87, 0.09]; electronic supplementary material, table S5; figure 2*f*), indicating that boars with greater duration for the longest sleep bout exhibited higher variance in its duration.

(d) Relationships between sleep parameters

At the population level, TST and the number of bouts per day were unrelated (0.02 [−0.02, 0.05]; electronic supplementary material, table S10); thus, TST did not increase with more sleeping bouts but individuals varied in their slope between TST and the number of bouts per day (0.08 [0.05, 0.11]; electronic supplementary material, table S10). Furthermore, there was a negative correlation between the random intercept (ID intercept) and random slope (ID slope) for number of bouts per day, indicating that boars with greater TST were more likely to have a negative relationship between mean TST and number of bouts per day, while those with lower TST were more likely to show a positive relationship (−0.73 [−0.88, −0.44]; electronic supplementary material, table S10, figure S7*a*).

At the population level, greater TST was associated with increased duration of longest bout per day (0.68 [0.36, 1.03]; electronic supplementary material, table S11), hence when the duration of the longest bout increased so did total daily sleep time. Individuals varied in this relationship with some showing a greater slope for TST with duration of longest bout than others (0.67 [0.39, 1.03]; electronic supplementary material, table S11, figure S7*b*). There was also a strong negative correlation between mean TST and the slope between TST and the duration of the longest bout, indicating that individuals with a lower mean TST showed a stronger increase in TST as sleep quality increased (−0.77 [−0.91, −0.37]; electronic supplementary material, table S11).

4. Discussion

Sleep is vital, yet how it varies within and between individuals, and responds to changing environmental conditions over time remains an open question. Recent studies have started to use minimally invasive, accelerometer-based measurements of sleep in wild animals to improve understanding of the ecology of sleep [25]. Here, in the longest and most detailed analysis of sleep in wild animals to date, we show that boars slept on average for 10.43 h per day in 24.40 bouts, with the longest bout lasting on average 2.10 h, but, contrary to expectations [12] individual wild boars differed markedly in the mean sleep quantity (TST), efficiency (sleep fragmentation/consolidation as the number of sleep bouts per day), quality (duration of the longest bout per day), and in their variance, i.e. plasticity. Sleep responded plastically to changes in environmental conditions that influence thermoregulation. Specifically, total daily sleep time was approximately 17% shorter, more fragmented, and of poorer quality in hot, summer days, potentially leading to sleep deprivation. Conversely, rainfall and snow favoured higher sleep quality. Thus, contrary to the idea that sleep is inflexible and consistent between individuals [12], we demonstrate that sleep differs between individuals and responds plastically and predictably to changing environmental conditions. Since sleep is an essential self-maintenance process, these results suggest that individuals differ in the amount of benefit gained from sleeping, and in their ability to mitigate the costs associated with sleep deprivation.

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Our analytic approach reveals a complex diversity in sleep between and within individuals that has not been previously quantified in nonhuman animals and highlights the importance of considering multiple dimensions of sleep. We expected that individuals consistently sleeping less could try and mitigate the costs of their average shorter sleep through greater plasticity (i.e. variance) in TST, higher sleep quality (longest bout duration) and/or greater efficiency (fewer sleep bouts per day). We find that boars differ in sleep quantity (TST individual mean) and its plasticity (TST individual variance), with short sleepers sleeping up to 46% less per day than long sleepers. Contrary to our expectations, short-sleeping individuals do not show greater plasticity in sleep quantity relative to long-sleeping individuals, nor do they enjoy higher sleep quality given that sleep quantity and quality increase with one another. Therefore, short-sleeping individuals do not compensate for their short sleep by increased plasticity or quality. Boar also differ in sleep fragmentation; individuals sleeping less efficiently distribute sleep in over twice as many bouts as those sleeping more efficiently and show higher plasticity in fragmentation suggesting that they likely attempt to compensate their poorer sleep by increasing the number of bouts. However, sleeping in more bouts does not systematically lead to longer TST, as sleep quantity and fragmentation are unrelated. Specifically, we find that only few individuals can increase TST by sleeping in more bouts, others reduce TST with more bouts presumably by increasing sleep depth, while in most boar TST does not vary with the number of sleep bouts (electronic supplementary material, figure S7). Considering that wild baboons fail to exhibit compensatory sleep rebound after a poor night's sleep [25], altogether our results suggest that individuals sleeping consistently less, or less efficiently, are likely to gain fewer benefits of sleep and may pay higher costs when sleep deprived.

We propose that the plasticity of sleep may vary across species in relation to their ecology. Our findings show that sleep in wild boar aligns with the general behavioural flexibility and adaptability documented for this species [33,60,61]. We thus expect similar levels of sleep inter- and intra-individual variation in cathemeral species, longer-sleeping species such as in many predators [11], and those exhibiting greater behavioural plasticity. However, species that sleep little in the laboratory, such as artiodactyls and perissodactyls [13,38], are likely at the physiological minimum for sleep in mammals, and may show lower inter- and intra-individual differences, and plasticity. Quantifying sleep variation within and across species will help evaluate to what extent globally increasing environmental changes, such as land change use, climate change and other anthropogenic stressors, impact on the key benefits that wild animals accrue from sleeping. Estimating time spent in each of the two mammalian sleep stages, REM (rapid-eye-movement) and NREM (non-REM) sleep, will permit improved investigation of costs and benefits of each sleep stage [13,30]. However, distinguishing REM and NREM sleep is currently an intractable problem for long-term, minimally invasive monitoring of wildlife. High-resolution accelerometery represents a promising step towards this goal, as shown in this study, and future developments in sensor technology and analysis might help detect physiological parameters associated with sleep stages (e.g. body temperature, heart and breathing rate).

Ambient temperature and light affect sleep quantity, fragmentation and quality in the laboratory [27,62]; thus, they are considered important mediators of sleep behaviour. However, how multiple environmental conditions influence sleep in the wild has not been investigated. Weather and light levels are also known to influence activity patterns in wild boar; for example, higher temperatures during the night and low moonlight favour nocturnal activity [44,45,63]. Likewise, our study reveals that the broad range of environmental conditions that wild animals face over time also affects sleep in more complex ways than anticipated. Consistent with the hypothesis that higher temperatures impair sleep [21,26], we find that sleep is shorter, more fragmented and of lower quality at higher temperature. Unexpectedly, though, higher humidity leads to greater sleep consolidation into fewer bouts. Conversely, precipitation and snow which are expected to favour thermoregulation and sleep, increase sleep quality. Contrary to predictions that light promotes sleep in nocturnal species, sleep in wild boar is more fragmented and of lower quality during longer days, but unaffected by our cloud-adjusted measure of moon phase. Therefore, winter favours sleep since lower temperature and snow likely enhance the thermal value of bed sites [62,64], and snow increases the energetic cost of travelling [46]. Conversely, sleep is shorter, fragmented and of poorer quality in summer which is the reproductive season for temperate species. Since female mammals with dependent offspring trade off sleep for parental care in captivity [18,20], our results suggest that hot and humid summer days may exacerbate the detrimental effects of sleep loss in reproducing females. Reproduction and thermoregulation may also help explain why individuals that sleep more during the night sleep less overall. Because piglets sleep in short, frequent bouts [40] and are likely more challenged by high temperatures than adults [65], we suggest that lactating females might shift sleep during darkness in response to offspring needs. Consistent with this suggestion, sleeping patterns and circadian rhythm of neonates are still developing during early life [66], and during the farrowing season female boars increase diurnal activity leading to a polyphasic activity pattern [67]. Given the vital role of sleep for health [4], we propose that compromised sleep in reproducing individuals likely contributes to explaining some costs of reproduction, such as compromised immunity, lower survival and reduced future reproductive investment [68,69].

We did not detect any influence of the arrival of wolves and human visitation on sleep in wild boar. However, this is likely due to the fact that changes in sleep due to predation risk or human disturbance occur are brief and occur at very short temporal scales [31,32]. Thus, to assess whether predation risk affects sleep in wild animals, targeted studies with high resolution data at short temporal scales are needed, for example with data on where and when predators move relative to prey, and where and when predation events occur. Likewise, behavioural responses to short-lived changes in human activity are difficult to detect and are often context-dependent, thus only fine-scale approaches can reveal these effects [31,70].

Given the essential benefits of sleep [2], we propose that sleep can be viewed as a behaviour favouring self-maintenance and survival; furthermore, the variation among individuals may be explained by models such as the extended pace-of-life syndrome theory (ePOLS) [10,71]. According to ePOLS, individual differences in behavioural and physiological traits covary with life-history traits. Therefore, 'fast-living' individuals are expected to grow quickly, invest more in reproduction and less in self-maintenance, and ultimately die younger. At the opposite extreme, 'slow-living' individuals should grow slowly, invest more resources in self--maintenance than reproduction, and live longer. Thus, shorter sleep may represent a facet of the 'fast' living strategy where sleep is reduced in favour of behaviours that enhance reproductive investment. Consistent with this suggestion, individual differences

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in TST in fruit flies (*Drosophila melanogaster*) are genetically determined and shorter-sleeping flies die younger [72]. Given that sleep loss comes at substantial costs [10], we expect that individuals with shorter and more fragmented TST exhibit traits such as reduced immunocompetence, and may be particularly affected by sleep deprivation, for example impaired cognitive abilities like decision making (e.g. response time to approaching predators, navigation). We thus anticipate that short-sleeping individuals within species show correlated tendencies with traits such as growth rate and reproductive behaviour.

To conclude, our study further demonstrates that high-resolution biologgers can be used to investigate sleep in wild animals [49] over ecologically relevant time scales. This approach reveals meaningful and unpredicted inter- and intra-individual differences in daily sleep quantity and efficiency that likely have important implications for health, cognitive abilities, and response to natural and anthropogenic stressors in wildlife. In contrast to views that sleep has limited plasticity [11,73], our study demonstrates that sleep in the wild is shaped by changing environmental conditions that affect thermoregulation in more complex ways than anticipated. Importantly, sleep is shorter, more fragmented and of lower quality in warmer temperatures, leading to a reduction of sleep time by 17% in summer. Given the major role that sleep plays in health [2,41], global warming and the associated increase in extreme climatic events are likely to impact sleep, and consequently health, in wildlife, particularly in nocturnal animals in unpredictable ways. Such detrimental effects may be further exacerbated if wild animals are exposed to anthropogenic stressors that disrupt sleep.

Ethics. This work was carried out in accordance with the guidelines of the Ministry of the Environment of the Czech Republic. The trapping and handling protocol was approved by the ethics committee of the Ministry of the Environment of the Czech Republic and carried out in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361. A full description of trapping, immobilization, and handling procedures is available in the electronic supplementary material.

Data accessibility. Supplementary material is available online [74].

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

Authors' contributions. E.M.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; J.G.: data curation, writing—review and editing; M.F.: data curation, writing—review and editing; V.S.: data curation, project administration, writing—review and editing; A.O.: data curation, writing—review and editing; L.B.: conceptualization, investigation, supervision, writing—review and editing; M.J.: conceptualization, data curation, funding acquisition, project administration, writing—review and editing; D.J.J.: conceptualization, methodology, supervision, writing—original draft, writing—review and editing; I.C.: conceptualization, funding acquisition, methodology, project administration, supervision, writing—original draft, writing—review and editing.

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

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

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5.2.2. Publikace č. 4 - Path tortuosity changes the transport cost paradigm in terrestrial animals

Druhá publikace této části výsledků je zaměřena na studium pohybu šesti druhů suchozemských zvířat sledovaných pomocí biologging technologie. Analýza dat poskytla výsledky, které prokazují, že sledovaní jedinci obecně snížili jejich rychlost pohybu a zvýšili počet stranových změn pohybu v přesunu z jedné lokality na jinou, a to za účelem snížení celkové energie pohybu. Tyto výsledky jsou zcela protichůdné pro teorii, která popisuje zvýšenou rychlost suchozemských zvířat při přesunu mezi lokalitami za účelem úspory energie. Avšak výsledky poukazují na vysvětlení, proč jsou měřené rychlosti pohybu divokých savců odlišné od výsledků naměřených v laboratořích.

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Research

Path tortuosity changes the transport cost paradigm in terrestrial animals

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The time that animals spend travelling at various speeds and the tortuosity of their movement paths are two of the many things that affect space-use by animals. In this, high turn rates are predicted to be energetically costly, especially at high travel speeds, which implies that animals should modulate their speed according to path characteristics. When animals move so as to maximize distance and minimize metabolic energy expenditure, they travel most efficiently at the speed that gives them a minimum cost of transport (COT_{min}), a well-defined point for animals that move entirely in fluid media. Theoretical considerations show though, that land animals should travel at their maximum speed to minimize COT, which they do not, instead travelling at walking pace. So, to what extent does COT_{min} depend on speed and turn rate and how might this relate to movement paths? We measured oxygen consumption in humans walking along paths with varied tortuosity at defined speeds to demonstrate that the energetic costs of negotiating these paths increase disproportionately with both speed and angular velocity. This resulted in the COT_{min} occurring at very low speeds, and these COT_{min} speeds reduced with increased path tortuosity and angular velocity. Logged movement data from six free-ranging terrestrial species underpinned this because all individuals turned with greater angular velocity the slower their travel speeds across their full speed range. It seems, therefore, that land animals may strive to achieve minimum movement costs by reducing speed with increasing path variability, providing one of many possible explanations as to why speed is much lower than currently predicted based on lab measurements of mammalian locomotor performance.

Keywords: angular velocity, energy landscape, minimum cost of transport, movement paths, preferred walking speed, track tortuosity

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Introduction

Movement is a fundamental tenet of the animal kingdom, with animals moving at varying speeds in chosen directions to use space over time in defined ways that is presumed to enhance their survival and lifetime reproductive success (Williams et al. 2002). Movement requires energy, which varies according to the speed of the animal (Dickinson et al. 2000). The speed that an animal selects for movement, and therefore the energy designated to it over time, depends on the purpose of the movement because locomotor efficiency may be less important than the behavioural role of locomotion (Wilson et al. 2015) which may depend on a variety of currencies including time or reproductive success (Shepard et al. 2009). There are three primary reasons for this: 1) animals may move at any speed, including their maximum, to evade predators or capture prey (Williams et al. 2014), to maximize net rate of acquisition of food energy (Wilson et al. 2002) or to provide young with food at an appropriate rate for their growth (Shepard et al. 2009); 2) animals may move at a speed that minimizes power costs (a concept that is primarily applicable for flying animals) (Tucker 1973). In addition, 3) animals may move at a speed that minimizes the cost of transport (COT_{min} speed), maximizing the distance travelled per unit of energy (Tucker 1970, Watanabe et al. 2011). This last paradigm (Taylor et al. 1970) is particularly important because most travel is assumed to be under strong selection pressure for animals to maximize output while minimizing input, which occurs at COT_{min} (Langman et al. 2012, van der Hoop et al. 2014). The COT_{min} speed is well defined for any instance where power for movement increases with speed at a greater than linear rate, such as in aquatic and volant animals. Indeed, wild animals moving entirely in fluid media generally travel at these speeds (Pennycuick et al. 2013) although there are exceptions, for instance when birds are minimizing power alone or when saving time is a more important currency than saving energy (Hedenström and Alerstam 1996). However, most terrestrial animals have a linear relationship between power and speed (Taylor et al. 1970, 1982) and therefore, because COT is derived by dividing the power by the speed, COT in these animals will always decrease with increasing speed. In short, the lowest theoretical costs of transport in terrestrial animals should occur at their maximum speeds (but see Hoyt and Taylor 1981, Daley et al. 2016). Yet these are not the speeds at which animals normally travel as they move through their environment in natural contexts (Schooley et al. 1996). Although the probability of accident and injury increases at very high speeds (Wynn et al. 2015), which is a clear reason to avoid them unless there is a compelling motive to sprint (e.g. in cursorial predators and their prey (Wilson et al. 2018)), there is currently no energy-based explanation as to why land animals travel through their environments at their normal chosen speeds.

Based on recent studies that found that the costs associated with turning are substantial (Wilson et al. 2013, McNarry et al. 2017), we hypothesized that track tortuosity should therefore alter the speed of COT_{min} in terrestrial animals. To test this, we set up experiments to gain empirical data on how speed and angular velocity in humans relate to energy expenditure and thereby to the cost of transport. At the same time, we equipped six species of free-living animal with tags that allowed us to study animal speed in tandem with angular velocity to see how our physiological findings translated into patterns of movement in the natural environment.

Material and methods

Participants

Twenty able-bodied male participants (mean ± SD: age 30 ± 8 years; body mass 75.6 ± 11.2 kg; stature 1.78 ± 0.06 m; body mass index: 24.0 ± 3.2 kg m^{-2}) gave their written informed consent to volunteer for this study. Stature (Holtain, Crymych, UK) was measured to the nearest 0.01 m and body mass (Seca, Germany) to the nearest 0.01 kg.

Trials

Participants walked at four different speeds (0.69, 0.97, 1.25 and 1.53 m s^{-1}) and four turn angle extents (0, 90, 135 and 180°), giving a total of sixteen speed and angle combinations. Separate walking tracks were marked onto a flat-surfaced sports lab floor using tape for each angle of interest. Each track alternated between 5 m straight lines and turns with equal numbers of left and right turns (0°: a 25 m straight line with markers every 5 m; 90°: two squares sharing one 5 m straight; 135°: two eight-angled star polygons sharing a 5 m straight; 180°: a 5 m straight). Participants' average walking speed was controlled using a metronome at either 8, 12, 15 or 18 bpm. Participants walked barefooted, carried out only step-turns (not spin-turns), and reached a corner (or 5 m mark) on each metronome beat (i.e. travelled 5 m between beats). Walking conditions were block-randomized by turning angle: all speed trials for a given angle were conducted before moving on to the next angle, but average travel speed and the sequence in which the angle conditions were completed by each participant were randomized and counterbalanced. Each walking condition lasted 3 min to allow achievement of a metabolic steady state, and each condition was separated with 3-min of quiet seated rest.

Respirometry

A portable and wireless breath-by-breath respirometry system (MetaMax 3B-R2, Cortex, Biophysik, Leipzig, Germany) was used to measure rates of oxygen consumption (VO_2, l min^{-1} kg^{-1}, see the Supporting information for an example trace) and carbon dioxide production (VCO_2, l min^{-1} kg^{-1}). The system (1.4 kg) was attached to each participant using a harness with the weight of battery and sensors (infrared analyser and electrochemical cell for CO_2 and O_2 measurements, respectively) equally divided between the left and right sides

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of the chest. Volume of inspired/expired gas was measured using a bidirectional digital turbine fitted within a mask (Hans Rudolph 7450 Series V2) from which a sample of gas was extracted via a 60 cm sampling tube for gas analysis. Prior to each trial, reference gases were used to calibrate the O_2 and CO_2 analysers and the turbine volume transducer was calibrated using a 3 l syringe (Hans Rudolph, Kansas City, MO). VO_2 and VCO_2 were calculated using continuous measurements of F_IO_2 and F_ICO_2 and the Haldane transformation. Metasoft 3 software ver. 3.7.0 SR2 was used to monitor traces during trials and export data. Respiratory exchange ratios (VCO_2:VO_2) and their thermal equivalents taken from (Brody 1945) were used to convert VO_2 to metabolic power (P_{met}, W kg^{-1}). The cost of transport (J kg^{-1} m^{-1}) was calculated by dividing P_{met} by average travel speed (m s^{-1}).

Identifying angular velocity from turns

All participants were equipped with a lower back, mid-line mounted 'Daily Diary' tag (Wilson et al. 2008) recording tri-axial (orthogonal) acceleration and magnetic field intensity at 40 Hz. Post-experiment, all magnetic field data were plotted on a tri-axial spherical plot of magnetic field intensity (m-sphere; see Williams et al. 2017 for details). While participants walking in straight-lines led to little variation in tri-axial plotted position on the m-sphere, those that executed turns resulted in rapid movement of points across the m-sphere surface which clearly showed at which points turns began and ended so that turn duration could be derived. Maximum resolution for this was 1/40th second. The duration of turns was determined for five turns per individual per speed and turn angle combination.

Derivation of costs

Metabolic measurements for the 0° trials were corrected for the costs of 180° turns that were necessary at the end of every 25 m of straight-line walking. In order to calculate the cost of transport for straight line walking, a series of calculations were undertaken. Firstly, the time taken, t, to travel one length (either 5 m or 25 m) and execute one turn for any given track was calculated as distance travelled divided by speed, d/v. The total mass-specific cost of walking one length and executing one turn was then calculated as the time taken × P_{met} (tP_{met}). The total mass-specific cost of walking in a straight line for 20 m was then calculated by subtracting the mass-specific cost of walking 5 m + 1 turn in 180° trials from 25 m + 1 turn in the 0° trials; $T_{CoW} = tP_{met}|_{d=25} - tP_{met}|_{d=5}$. The total mass-specific cost of walking in a straight line for 20 m was then divided by 20 in order to derive the total mass-specific cost of transport (J kg^{-1} m^{-1}). Turn costs for any given speed and angle combination were calculated by subtracting 5 × the cost of transport for straight-line walking from the total mass-specific cost of walking 5 m and executing one turn. Each participant's turn costs were divided by their mean turn durations in order to calculate turn power (W kg^{-1}). Costs of transport were determined by dividing power by speed and the minima for the various speeds were derived from the best fit curves.

Animal tagging

Five wild mammal species (African lions *Pathera leo*, chamois *Rupicapra rupicapra*, ibex *Capra ibex*, mouflon *Ovis orientalis* and wild boar *Sus scrofa*) and one domestic mammal (domestic goat *Capra aegagrus*), which was allowed to range freely, were fitted with collar-mounted GPS-enabled 'Daily Diary' tags (Wilson et al. 2008) recording tri-axial magnetic field intensity and tri-axial acceleration at 10–40 Hz (see species-specific details in Table 1). Tags were left in place for between 15 and > 250 days before being retrieved. Downloaded data were treated to determine movement patterns using dead-reckoning as described in Bidder et al. (2015), correcting for drift using the periodic GPS positions (Bidder et al. 2015). From these data, a random period (24–50 h) was isolated from each individual, with some variation in durations to ensure that appreciable movement had taken place. For these periods, the vectorial dynamic body acceleration (VeDBA), a good proxy for speed (Bidder et al. 2012a, b), was calculated according to Qasem et al. (2012) as well as the angular velocity over one second at approximately 10 s intervals so as to give ca 20 000 angular velocity-VeDBA pairs per individual. Data from five individuals for all species were used in this manner except for the mouflon, where only four animals were used.

Statistical analyses

Linear mixed-effects models (lme4 package (ver. 1.1-26) in R Studio ver. 4.0.3) were conducted in order to investigate the relationship between angular velocity and average travel speed with differing angle extent; angular velocity with angle

Table 1. Details of tag deployments on free living animals.

Species	No.	Study area	Body mass (kg)	Tag weight (g)	Tag weight as % body weight	Deployment period	Deployment length (days)
Panthera leo	5	Kalahari, S. Africa	62–66.5	1240–1330	< 2	February 2019	18–21
Rupicapra rupicapra	5	Les Bauges, France	39.82	450	1.13	June 2017–May 2018	> 250
Capra ibex	5	Belledonne, France	28.8	450	0.64	April 2017–March 2018	> 250
Ovis gmelini	4	Caroux-Espinouse, France	50	450	0.90	May 2017–April 2018	> 250
Sus scrofa	5	Kostelec, Czech republic	6.15–10.63	850	0.8–1.3	May–Oct 2019	30–120
Capra aegagrus	5	Les Bauges, France	39.84	510	1.28	August–September 2017	29

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extent at different speeds, mass-specific metabolic parameters and speed with different angle extent; and mass-specific metabolic parameters with angular velocity at different speeds or angle extent. Participant identity was included in the models as a random factor. The F statistic and marginal and conditional R^2 were determined using the car (ver. 3.0-5) and 'MuMIn (ver. 1.43.6) packages, respectively.

Results

Empirical data from humans show how increasing track tortuosity reduces the minimum cost of transport speed to a slow walk

Our calculations of power-use by participants walking variously angled courses showed a significant interaction effect between walking speed and turn angle on total mass-specific metabolic power (speed^2 × angle category, $F = 101.81$, $p < 0.001$), with the rate of increase in power for a given increase in travel speed increasing disproportionately with turn angle (Fig. 1a, Table 2). Accordingly, there was a significant interaction effect between walking speed and turn angle on the total mass-specific cost of transport (speed^2 × angle category, $F = 59.13$, $p < 0.001$) (Fig. 1b, Table 2). The cost of transport curve showed distinct minima for paths incorporating turns, becoming more U-shaped, and with COT_{min} shifting to progressively lower walking speeds with increasing turn angle (Fig. 1b).

3-D plots of the interrelationship between metabolic power or the cost of transport with speed and angular velocity demonstrate how power increased disproportionately with increasing angular velocity, which resulted in clear COT_{min} that did not occur at the higher walking speeds. Rather,

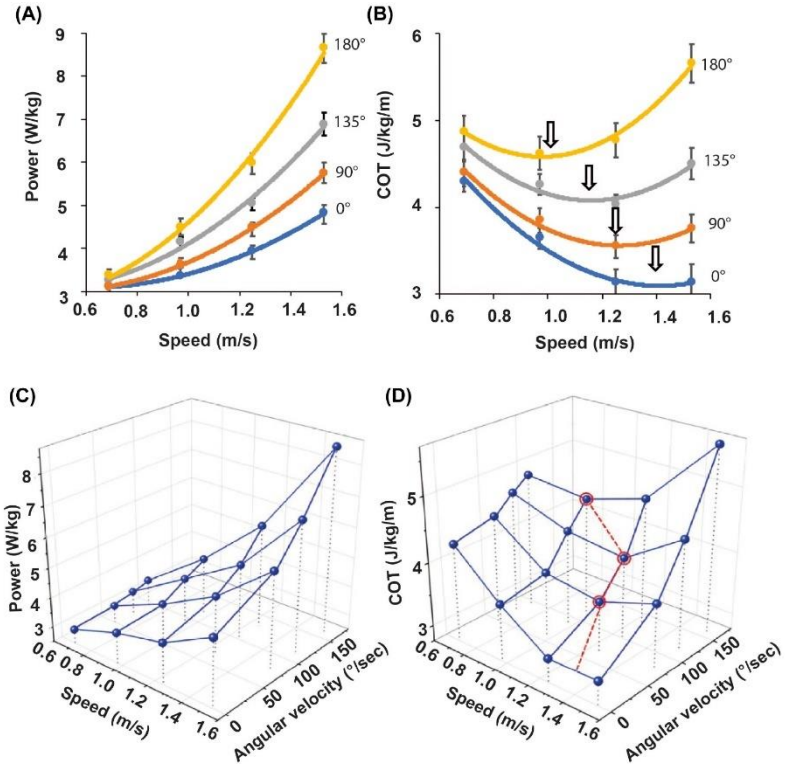

Figure 1. Metabolic measurements versus average travel speed or both travel speed and angular velocity for 20 human participants walking tracks with turns of varied extent. (A) Mean (± SE) total mass-specific power and (B) mean (± SE) total mass-specific cost of transport for straight movement (blue), 90° turns every 5 m (orange), 135° turns every 5 m (grey) and a 180° turns every 5 m (yellow). Quadratic curves were fitted using the coefficients of the outputs of linear mixed-effects models (Table 1). Arrows show COT_{min} speeds. (C) and (D) are 3D plots of the same data including angular velocity as a covariate. The accelerating power costs of higher angular velocities produce cost of transit minima (highlighted in red) where any turning occurs and these minima occur at lower speeds with higher angular velocities.

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Table 2. Summary of the outputs of linear mixed-effects models conducted to investigate the effects of speed and angle on angular velocity or metabolic parameters and the effects of speed and angular velocity on metabolic parameters.

Parameter	Term	F	df	p	R^2 Fixed factors	R^2 total model	Coefficients
Angular velocity (° s^{-1})	*U*	1037.87	1,289	< 0.001	0.979	0.983	0°: = 0*U* + 0
	angle [as factor]	5365.33	3,289	< 0.001			90°: = 31.94*U* + 28.07
	U: angle [as factor]	170.86	3,289	< 0.001			135°: = 46.60*U* + 43.28
							180°: = 73.5 *U* + 43.92
Angular velocity (° s^{-1})	angle	16001.97	1,289	< 0.001	0.979	0.982	0.69 m s^{-1}: = 0.54(angle) + 0.89
	U [as factor]	345.09	3,289	< 0.001			0.97 m s^{-1}: = 0.64(angle) + 0.38
	angle: *U* [as factor]	168.49	3,289	< 0.001			1.25 m s^{-1}: = 0.74(angle) + 0.86
							1.53 m s^{-1}: = 0.88(angle) − 1.10
P_{met} (W kg^{-1})	*U*	9.37	1,284	0.002	0.769	0.919	0°: = 1.99$(speed)^2$ − 2.39(speed) + 3.80
	U^2	65.29	1,284	< 0.001			90°: = 2.48$(speed)^2$ − 2.39(speed) + 3.59
	angle [as factor]	201.83	3,284	< 0.001			135°: = 2.97$(speed)^2$ − 2.39(speed) + 3.53
	U^2: angle [as factor]	101.81	3,284	< 0.001			180°: = 3.87$(speed)^2$ − 2.39(speed) + 3.13
CoT (J kg^{-1} m^{-1})	*U*	137.17	1,284	< 0.001	0.471	0.860	0°: = 2.38$(speed)^2$ − 6.71(speed) + 7.83
	U^2	122.52	1,284	< 0.001			90°: = 2.66$(speed)^2$ − 6.71(speed) + 7.80
	angle [as factor]	234.82	3,284	< 0.001			135°: = 2.90$(speed)^2$ − 6.71(speed) + 7.97
	U^2: angle [as factor]	59.13	3,284	< 0.001			180°: = 3.43$(speed)^2$ − 6.71(speed) + 7.86
Turn cost (J kg^{-1})	*U*	1.58	1,203	0.209	0.658	0.770	90°: = 3.46$(speed)^2$ − 4.66(speed) + 2.29
	U^2	9.73	1,203	0.002			135°: = 4.70$(speed)^2$ − 4.66(speed) + 2.99
	angle [as factor]	147.09	2,203	< 0.001			180°: = 7.34$(speed)^2$ − 4.66(speed) + 2.56
	U^2: angle [as factor]	37.98	2,203	< 0.001			
Turn P_{met} (W kg^{-1})	*U*	7.77	1,203	0.006	0.739	0.814	90°: = 4.73$(speed)^2$ − 7.79(speed) + 3.62
	U^2	26.60	1,203	< 0.001			135°: = 6.00$(speed)^2$ − 7.79(speed) + 3.71
	angle [as factor]	154.09	2,203	< 0.001			180°: = 8.62$(speed)^2$ − 7.79(speed) + 2.64
	U^2: angle [as factor]	66.87	2,203	< 0.001			
Turn cost (J kg^{-1})	*Angular velocity*	1.87	1,284	0.285	0.711	0.770	0.69 m s^{-1}: 0.0002$(angular\ velocity)^2$ + 0.0079(angular velocity) − 0.0686
	Angle [as factor]^2	13.67	1,282	< 0.001			0.97 m s^{-1}: 0.0003$(angular\ velocity)^2$ + 0.0079(angular velocity) − 0.2339
	U [as factor]	5.66	2,280	< 0.001			1.25 m s^{-1}: 0.0004$(angular\ velocity)^2$ + 0.0079(angular velocity) − 0.1453
	Angle [as factor]^2: *U* [as factor]	3.49	2,280	0.016			1.53 m s^{-1}: 0.0004$(angular\ velocity)^2$ + 0.0079(angular velocity) − 0.2471
Turn P_{met} (W kg^{-1})	*Angular velocity*	0.80	1,204	0.371	0.734	0.817	0.69 m s^{-1}: 0.0002$(angular\ velocity)^2$ + 0.0018(angular velocity) − 0.0334
	Angle [as factor]^2	46.83	1,204	< 0.001			0.97 m s^{-1}: 0.0002$(angular\ velocity)^2$ + 0.0018(angular velocity) − 0.1211
	U [as factor]	21.46	3,204	< 0.001			1.25 m s^{-1}: 0.0003$(angular\ velocity)^2$ + 0.0018(angular velocity) − 0.0595
	Angle [as factor]^2: *U* [as factor]	3.75	3,204	0.011			1.53 m s^{-1}: 0.0004$(angular\ velocity)^2$ + 0.0018(angular velocity) − 0.1199

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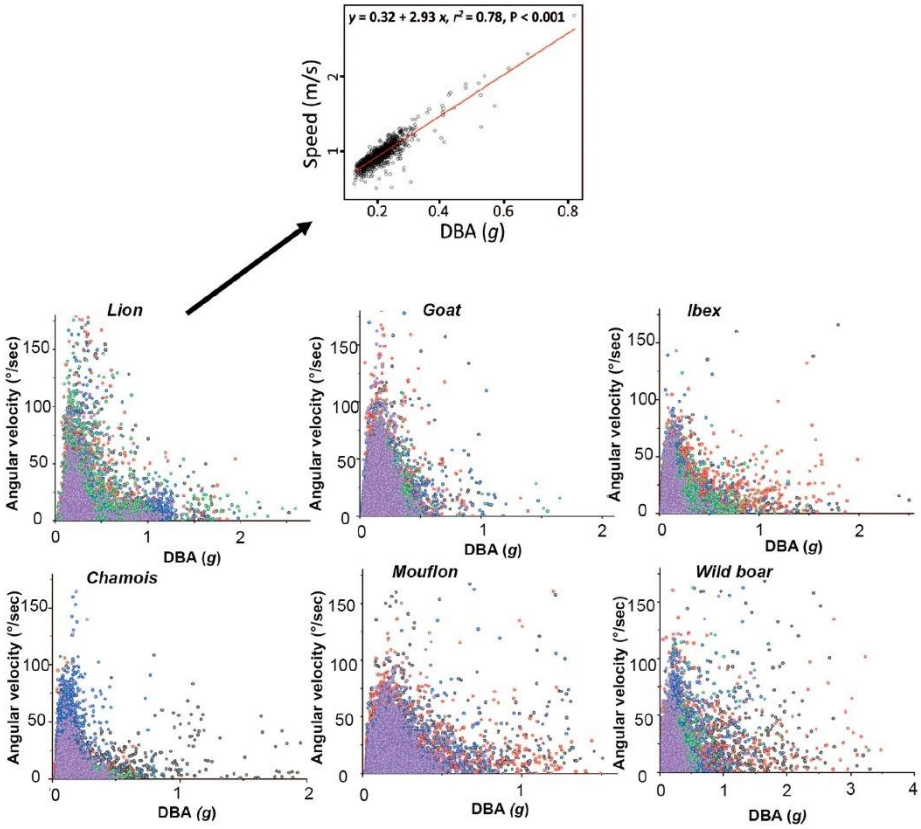

Figure 2. Incidence of angular velocity against dynamic body acceleration (DBA) – a linear proxy for travel speed – in six free-living terrestrial species. The lion data shows an inset that clarifies the relationship between DBA and speed for this species, these animals being equipped with GPS recording at 1 Hz. Each point shows a value taken at ca 10 s intervals over a length of time that corresponds to about 20 000 points for each individual (n = 5 per species except for the mouflon where n = 4, with individuals depicted by different colors – the predominance of purple simply reflects data from the last individual graphed by the package). Note how all distributions show decreasing angular velocities with increasing speed across all speed ranges, starting with the slowest.

minimum costs of transport occurred at lower walking speeds when angular velocities were high (Fig. 1c–d).

Similarly, significant effects of interaction terms were found for the quadratic relationships between speed and cost per turn (J kg^{-1}, speed^2 × angle category, $F = 37.98$, $p < 0.001$) and turn power (W kg^{-1}, speed^2 × angle category, $F = 66.87$, $p < 0.001$) with the rate of increase of power with speed becoming greater as angle increased (Table 2).

Wild animal data support the idea that preferred travel speed decreases with increasing angular velocity

In free-ranging wild mammal species (African lions *Pathera leo*, chamois *Capra rubicapra*, ibex *Capra ibex*, mouflon *Ovis orientalis*, wild boar *Sus scrofa*) and one domestic animal (the goat *Capra aegagrus*), all individuals tended to travel relatively slowly, but they predominantly engaged in the highest angular velocities at the lowest travel speeds (using dynamic body acceleration as a proxy for speed (Bidder et al. 2012b)) decreasing angular velocities in their turns as their travel speeds increased (Fig. 2). The incidence of turning behavior was apparent in examples of the free-living animal movement data when resolved at sub-second level, which showed intensive and extensive turning behavior, even when movement paths appeared directed at larger scales (Fig. 3).

Discussion

There have been extensive studies of the relationship between terrestrial animal speed and power, the vast majority of which have been conducted on a treadmill to show that power increases linearly with speed (Taylor et al. 1970).

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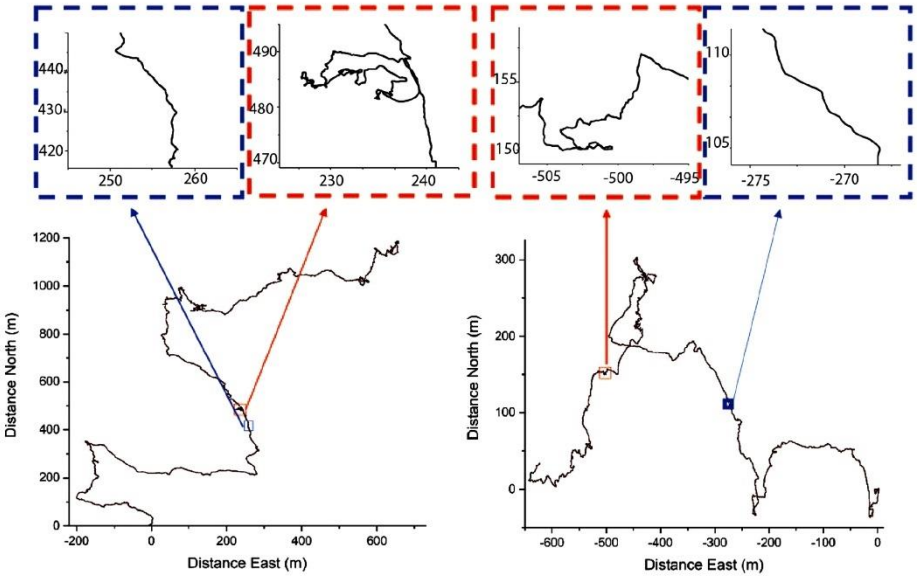

Figure 3. Examples of 20 h movement paths (at 4 Hz and elucidated by dead-reckoning) of two of the study animals. (A) a chamois and (B) an ibex, showing in the insets the scale over which turns are made (cf. our VO_2 study on humans). Note how even apparently straight-line paths (blue boxes) show clear turns, although angles are obtuse, while tortuous sections (red boxes) show both obtuse and acute turns.

While fundamental, this highly controlled scenario does not simulate the situation found in nature where variability in, for example, topography and surface penetrability of the environment will also affect power to travel (Shepard et al. 2013) and thereby the cost of transport. Interestingly, in a recent study of how scaling affects costs in animals moving on inclines, Halsey and White (2017) present data that show clear minima in costs of transport with slope (although the effect of speed is not detailed). This, therefore, already points to an important effect of how the environment is expected to structure selection of animal speed for energetically optimum movement. But beyond this, animals may turn to avoid energetically onerous landscape features such as inclines (Shepard et al. 2013) and, for this and for many other reasons, they turn frequently, as our Fig. 3 shows. Previous works have indicated that turns are energetically costly (Wilson et al. 2013, McNarry et al. 2017) but, due to their experimental protocol, these authors could not define how the costs of transport relate to angular velocity and speed, nor that angular velocity could have created clear minima in costs of transport at such low speeds. The extraordinary magnitude of the increase in power costs with increasing angular velocity and speed is, in part, explained by animals having to develop forces to counteract the centripetal force incurred in the turn, given by; $F = m \times v^2/r$, where m is the mass, v, the velocity and r the radius of the turn. Thus, some of the energy used for turning has to be used in developing lateral forces. However, acute turns will also require some forces opposing the drive force, manifesting as deceleration followed by corrective acceleration for straight-line travel after a turn. This will occur even at low speeds, which explains the sharp drop off in angular velocity in turns, even at low speeds in our wild animals (Fig. 2), and the minimum cost of transport occurring at such low walking speeds of humans during 180° turns (Fig. 1). Indeed, application of the COT_{min} travel speeds for straight line paths in humans to our scenario with 180° turns would incur a predicted increase of 13% in travel costs above the angle-specific COT_{min} (cf. Fig. 1b). We note that the specifics of the power- and COT values for humans, with their bipedal inverted pendulum locomotion (Kuo et al. 2005), are unlikely to translate directly to quadrupeds, particularly given the variation in locomotory morphologies within this group (Steudel 1990, Pontzer 2007) but the physical principles are the same so the general patterns observed for humans should be apparent in wild animals to a greater or lesser degree.

The high power associated with turns translates into well-defined minima in the costs of transport for defined speeds and angular velocities (Fig. 1d). This means that an overall optimum speed for a wild animal, moving to minimize transport costs, will depend on the frequency and extent of turns. These will depend on a large number of turn elicitors that confer benefit to the animal if it turns. These, in turn, will range from barriers, including localized ones such as trees/shrubs (Schooley et al. 1996), or navigating through differential energy landscapes (Shepard et al. 2013), through to acquisition strategies for food, such as area-restricted search

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(Walsh 1996), or mates (Bau and Carde 2015). Indeed, we suggest that the incidence of turning behavior in wild animals has been underestimated, not least because we have little capacity to resolve it at the scale necessary to be energetically meaningful, even using GPS technology (Hulbert and French 2001). A notable exception is with inertial/dead-reckoned data (Bidder et al. 2015), which show that animal paths can consist of extensive and intensive turning behavior (Fig. 3).

Variation in the environment or in animal behavior would also lead us to expect animals to vary travel speed accordingly, even intra-specifically, reflecting different motivations for speed selection (Wilson et al. 2015), which is consistent with the animal data we present here (Fig. 3). Clearly, although such data may not always agree with animals actually using COT_{min} for a number of reasons (Wilson et al. 2015), the interplay of speed and angular velocity, and the huge effect that they have on movement energetics, points to the importance of both in modulating trajectories according to function. Indeed, future treatises that attempt to link this with the multiple other factors that affect the energy costs of travel (e.g. the energy landscape (Shepard et al. 2013)) may find that we can explain animal speed- and turn velocity-selection more satisfactorily than we can at present.

Our treatment is simplistic for a number of reasons. Not least, we only consider power and COT metrics as bi-dimensional when they will be affected by multiple properties of the environment that modulate power use, such as slope and surface penetrability (Shepard et al. 2013). This will be further complicated by gait changes (Dawson and Taylor 1973, Maloiy et al. 2009, Nudds et al. 2011, Watson et al. 2011, Granatosky et al. 2018). This work nevertheless demonstrates the profound effect that turns have on cost of transport for terrestrial animals using humans as a model, although we expect the principle to be the same for flying and aquatic animals. If we are to progress with models purporting to help us understand animal trajectories through varying environmental space from an energetic, and ultimately behavioral, perspective though, we will have to accept that small things such as acute corners can sometimes make big differences in understanding the details and elicitors of movement trajectories (Schick et al. 2008).

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Author contributions

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Data availability statement

Data are available via the Figshare repository: <https://doi.org/10.6084/m9.figshare.16553787.v2> (Wilson et al. 2021).

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5.3. Prostorová orientace a fidelita zvěře

5.3.1. Publikace č. 5 – A GPS assisted translocation experiment to study the homing behaviour of red deer

Poslední část výsledků obsahuje poznatky o prostorové orientaci samic jelena evropského (*Cervus elaphus)* při řízené translokaci jedinců do nového prostředí a jejich následné chování. V rámci experimentu bylo provedeno celkem 35 řízených translokací v průběhu dvou let s výsledkem celkem 31 úspěšných návratů do původního domovského okrsku v časovém od 1.23-100 dní od vypuštění v nové lokalitě. Translokace byly prováděny na vzdálenost cca 11 km od místa imobilizace. Výsledky ukázaly tři fáze homing založený na délce a orientaci pohybu v závislosti na čase. Studie prokázala porovnatelné schopnosti homingu u jelení zvěře jako u ostatních drůhu zvířat, které byly pozorovány již v minulosti.

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A GPS assisted translocation experiment to study the homing behavior of red deer

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Many animals return to their home areas (i.e., 'homing') after translocation to sites further away. Such translocations have traditionally been used in behavioral ecology to understand the orientation and migration behavior of animals. The movement itself can then be followed by marking and recapturing animals or by tracking, for example, using GPS systems. Most detailed studies investigating this behavior have been conducted in smaller vertebrates (e.g., birds, amphibians, and mice), whereas information on larger mammals, such as red deer, is sparse. We conducted GPS-assisted translocation experiments with red deer at two sites in the Czech Republic. Individuals were translocated over a distance of approximately 11 km and their home journey was tracked. Circular statistics were used to test for significant homeward orientation at distances of 100, 500, 1000, and 5000 m from the release site. In addition, we applied Lavielle trajectory segmentation to identify the different phases of homing behavior. Thirty-one out of 35 translocations resulted in successful homing, with a median time of 4.75 days (range 1.23–100 days). Animals were significantly oriented towards home immediately after release and again when they came closer to home; however, they did not show a significant orientation at the distances in between. We were able to identify three homing phases, an initial 'exploratory phase', followed by a 'homing phase' which sometimes was again followed by an 'arrival phase'. The 'homing phase' was characterized by the straightest paths and fastest movements. However, the variation between translocation events was considerable. We showed good homing abilities of red deer after translocation. Our results demonstrate the feasibility of conducting experiments with environmental manipulations (e.g., to impede the use of sensory cues) close to the release site. The homing behavior of red deer is comparable to that of other species, and might represent general homing behavior patterns in animals. Follow-up studies should further dissect and investigate the drivers of the individual variations observed and try to identify the sensory cues used during homing.

Keywords Mammal navigation, Satellite tracking, *Cervus elaphus*, Czech Republic, Spatial orientation

Animal navigation, spatial cognition, and memory are essential abilities that allow animals to reach specific destinations, such as food resources, mating grounds, and nesting sites, and exploit spatially clustered resources efficiently[1,2]. Many species display site fidelity, that is, they return to specific locations every season or stay in the same general area year around[3]. Typically, animals that show site fidelity return to their approximate capture location after translocation to a site outside their typical residence[4,5]. The reason for such a preference for certain 'home areas' can be manifold, but is often associated with territorial behavior and/or mating sites (for example[6,7]) or spatial learning and memory-based home range formation[8,9]. The return behavior to such specific sites is called 'homing' and has been extensively studied in smaller terrestrial vertebrate species such as birds[10,11] and, to a lesser extent, amphibians[12], mice[13–15], rabbits[16,17], bats[18], and dogs[19]. Large terrestrial mammals also show

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good homing abilities[20], and some perform seasonal migrations (for example[21]). However, spatial movements of large non-migratory mammals have been subjected to far fewer experimental/manipulative investigations, probably due to practical issues with their translocation.

Studies across many species suggest that there are species-specific limits of translocation distances beyond which animals are no longer able to navigate back[20,22]. These limitations might be associated with the navigational cues used for homing, which might require familiarity with the environment. Homing abilities outside the previously visited (i.e. 'familiar') area are often termed 'true navigation', meaning that the animals can extrapolate the navigation cues beyond their home range. It is unknown what kinds of sensory mechanisms large terrestrial mammals use for their navigation performance. However, in smaller mammals it has been shown that olfactory[23], visual[24] and magnetic cues[25] can be used for orientation. In principle, larger mammals, such as the red deer (*Cervus elaphus*), can use all of these cues, if available. However, no direct tests of the cues involved have yet been performed.

Understanding the homing abilities of larger mammals is important when managing populations, either for the protection of endangered animals or for game management. For instance, bears are sometimes relocated to avoid conflict with human settlements, which is considered a better alternative to sacrificing animals[26]. However, such efforts are unsuccessful if individuals return to their home sites. Bears can find their way home from up to 100 km[26], which is likely an especially well-developed homing ability for large terrestrial mammals. For white-tailed deer (*Odocoileus virginianus*), studies on homing performance showed frequent settlement of the animals in an area approximately 30 km from the release site[20]. For instance, in a study in Illinois of 28 translocated individuals (distance 10–58 km), only two returned home[27]. Such studies usually rely on mark-recapture or radio telemetry, while advancements in remote sensing allow detailed movement monitoring of animals over long periods due to GPS-assisted tracking. Translocation studies with red deer are still missing, although they show high site fidelity for their home ranges, regardless of whether they show seasonal migration between home ranges or whether they remain resident in an area during the year[28,29]. High site fidelity could lead to issues when managing populations because translocations that may be intended to resettle animals can fail if they show homing. In contrast, well-developed homing abilities may provide us with a study system that can be used to investigate navigational cues in larger mammals. This might reveal similarities and differences in cue use and integration based on the scale of migration, for example, a few hundred meters for mice or a few kilometers for deer.

In the current study, we performed translocation experiments with GPS-monitored red deer, followed by detailed analyses of the homing performance and tracks. We show overall consistent and fast homing behavior, with most animals returning within days from a 10 km distance.

Methods

Study site and species

Translocation experiments with red deer (*Cervus elaphus*) were conducted on two different populations in 2019, 2020, and 2021 in the Czech Republic (Fig. 1) at two different locations in West Bohemia. The first was in the Doupov Mountains, a military training site that is closed to the public and used only for military training, game species hunting, and forestry. This area spans 331 km^2. The second location was Kladska, which is situated in the west and consists of a semi-natural coniferous forest. The total area is 140 km^2 and forest stands are used for timber production and recreation. Stable deer populations are present at both locations and both are managed by hunting. In total, we translocated 23 individuals at least once (15 animals in Doupov and eight animals in Kladska). Thirteen animals were translocated a second time and two animals were translocated a third time. Two animals were excluded from the analysis: one was killed by wolfs one day after translocation, and for another one the tracking device was malfunctioning. One animal was male, and the others were adult females. Translocations took place during early spring from February to April, which is the spring season without large-scale movements, while the rutting season starts in mid-September and continues until mid-October.

Translocation procedure

Animals were anesthetized using a mixture of Ketamine and Xylazine (3 ml per 100 kg of body mass). The concentrations of ketamine and xylazine were 50 mg/ml and 250 mg/ml, respectively. The animals were then secured in a wooden transport box on the trailer behind a pick-up truck and driven to the release sites (11.9 ± 1.8 km distance), which were either approximately towards the north ($n = 4 + 2$), south ($n = 15 + 7$), or west ($n = 8$) of the capture location and 12 km away. All individuals were transported in a wooden box developed for animal transport. The wooden box used for transport included ventilation holes in the lower part of the construction. The animals were unable to see the outside of the box during transport. The translocation time was less than 90 min. The animals were released from the box after translocation and visually checked by the veterinary staff. All individuals left the box without injury, and none needed an antidote.

GPS tracking

Red deer individuals were tracked using GPS Vertex Plus collars (Vectronic Aerospace GmbH) (Fig. 2). The total mass of the collars was 750 g, and their lifetime was approximately 1 year. The collar mass was < 3% of the animal's body mass [46]. GPS data were retrieved via GSM every 8 h and stored on servers. The frequency of GPS fixes was set to 30 min intervals and the collars included a VHF drop-off mechanism (Vectronic Aerospace GmbH) for non-invasive collar release after the end of the project or before the end of the battery lifetime.

Track analysis

For the aim of this study, we defined all animals that reached or crossed a circle of 1 km radius around their capture location within 180 days after translocation as "homed successfully" and animals that did not reach

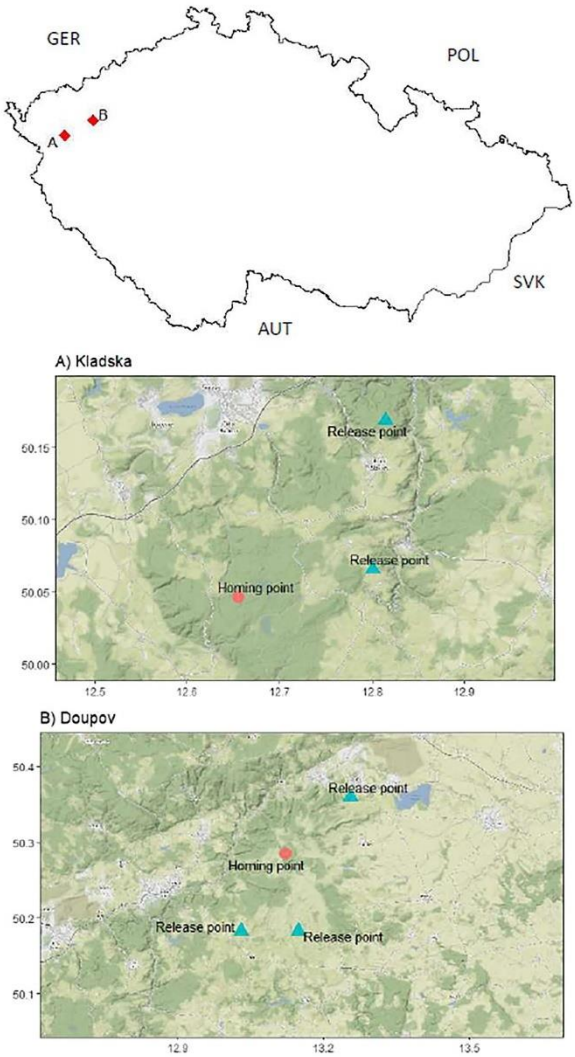

Figure 1. Map with all release sites and respective goals (homes) in Location Kladska (**A**) and Doupov (**B**)[45].

this criterion as "did not home". This does not necessarily mean that animals defined as "did not home" did not home at a later time point.

For all animals ("all together", "homed successfully" and "did not home") we calculated the homeward bearings at a distance of (at least) 100 m, 500 m, 1 km and 5 km from the release location. The bearings were calculated as the angle of the vector between the release location and the closest GPS fix after individuals crossed the respective distance mark. For this analysis, we used the recently described MANOVA approach[30]. We used the animals' ID as a random error term (intercept) in the mixed-effects MANOVA model to account for the repeated testing of individuals (we only applied this approach to distributions with at least five bearings). This approach was used to circumvent non-independence issues caused by animal retesting. Our aim was to test whether animals orient more strongly towards home with increasing distance from the release location. The idea behind this analysis was that a deer might, at first, disperse in a random direction when released after re-orienting itself

Figure 2. Translocated female red deer (Animal ID 105) were equipped with a GPS collar.

and then following a homeward direction. Circular plots were generated using the wrapper function presented in Pail et al.[31], which is based on the plot.circular function from the circular package in R[32].

To analyze the different homing segments for all deer that homed successfully, we used the approach described by Lavielle[33,34], using the function *lavielle.ltraj* from the R package adehabitatLT[35]. In this approach, a track is partitioned using a contrast function, in which we set the minimum length of a segment to four, used four as the maximum possible segments, and set the type of segmentation to "mean", following the suggestions by Calenge[36]. We then applied the *chooseseg* function to determine the optimum number of segments for individual tracks. In the final step, we applied the *findpath* function to divide the tracks into the suggested segments; this was only done if more than one segment was suggested from the *chooseseg* function. For each segment in each track we calculated the average speed, straightness (as the standardized vector length 'r') and proportion of entire track. We also correlated the number of days required for homing with the number of trajectory segments using the cor. test function.

Ethical approval

Red deer trapping was implemented in accordance with the decision of the Ethics Committee of the Ministry of the Environment of the Czech Republic (number MZP/2019/630/361). This study was conducted in compliance with the recommendations of the ARRIVE guidelines. The trapping and handling protocol was approved by the ethics committee of the Ministry of the Environment of the Czech Republic, and we confirm that the experiment was performed in accordance with the relevant guidelines and regulations.

Results

Of all deer translocations 89% (31 of 35) ended with successful homing, i.e., returned back to the capture location in a vicinity of a 1 km radius within 180 days (see Supplementary Information: Overview_Table_S1.pdf, tracks can be found in Tracks_All_animals.pdf and Tracks_homed.pdf supplementary files). Of the four translocations without homing, two were individuals that had been translocated the second time. Of all individuals, 19 homed at least once, and two did not.

The median homing time was 4.75 days (range 1.23–100 days) (Fig. 3).

The initial orientation (100 m) of deer that homed successfully was significantly directed towards the home direction (Fig. 4, MANOVA tables in Supplementary Information: MANOVA_results_tables.pdf). The subsequent orientations at distances of 500 m and 1 km from the release site were randomly oriented, whereas at a distance of 5 km, the animals were again oriented towards home. As only four releases were included in the analyses that did not include home, we did not perform a statistical analysis. However, the general patterns, especially for the initial homeward trend, appeared comparable to those of the animals that did home. When taken together, the orientation at a distance of 500 m showed a weakly significant homeward vector (Fig. 4B).

The segmentation algorithm resulted in 10 trajectories that were not split up (i.e., one segment for the entire track, herein assigned to segment 1), 10 trajectories were split into two segments (assigned to segments 1 and 2), and 11 were split into three segments (Fig. 5). None was split into four segments (the highest segmentation possible in our analysis). The general trend for the trajectories showed that the animals had lower average speed and straightness in segment 1 than in segment 2, and lower values in segment 3 (Fig. 5). In contrast, the relative proportion of segments (i.e., the relative proportion of each segment on the entire trajectory) showed the opposite trend (lower proportion in segment 2 than in segments 1 and 3). The two animals with directly opposite trends consisted of only two segments, suggesting that they might belong to segments 2 and 3 compared with the other animals (i.e., missing segment 1). Our results show a possible separation in three phases of homing, which could be classified as an initial exploration of the release site, a faster homing phase, and a (possible) exploration close to the home site, until our criteria of a 1 km radius around the release site were met. The number of days the animals needed home was significantly negatively correlated with the number of segments (Pearson's product-moment correlation: -0.45, $t = -2.7195$, $df = 29$, p-value $= 0.011$); that is, animals that needed longer were more likely to be classified into fewer segments using our segmentation algorithm.

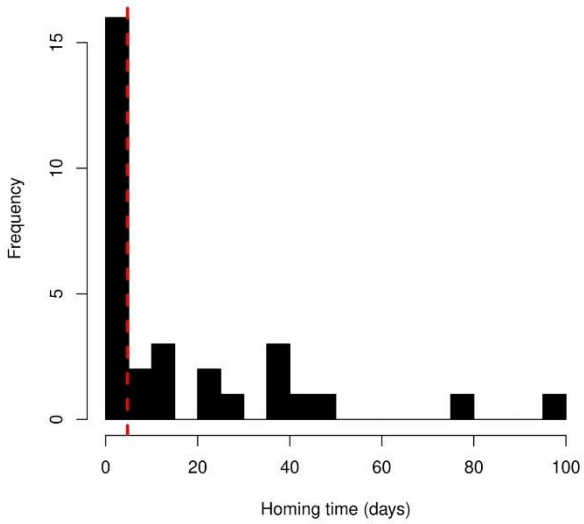

Figure 3. The frequency distribution of deer homing times (in days) is shown in a histogram. The median homing time (4.75 days) is indicated by a red dashed vertical line.

Discussion

Our study showed the excellent homing abilities of red deer when translocated by approximately 11 km. This is surprising, as the selected release sites may be beyond the home ranges of the investigated deer, suggesting that the individuals likely navigated homewards from a novel location. Interestingly, the initial orientation at the release sites was significantly oriented towards the animals' homes. This may suggest good navigational capabilities, potentially based on a global map cue, such as a magnetic or olfactory internal map[37,38]. Alternatively, deer may have a very large area of familiarity and used familiar landmarks (e.g., visual cues) to orient towards home or perceived some salient visual or olfactory cues directly from the home area. While we cannot exclude the possibility that deer path-integrated the way back to their home location, using the information they memorized during the translocation, this is highly unlikely. They were anesthetized during at least part of the translocation and could not see out of the transport box while being transported at higher speeds that they usually experience.

After this initial orientation, the animals appeared to explore their release areas before starting their journey home. This is again exemplified by the highly significant homeward orientation at a distance of 5 km from the release site. Overall, the homing abilities of red deer appear to be better than those of white-tailed deer, at least according to the available literature, where the latter species failed to return from comparable distances in many cases (c.f.[20]).

Despite considerable variation, homeward navigation contains repeatable features among some individuals. There often was a first 'exploratory phase' immediately after release which is recognizable by its more irregular and slower movement. The animals then started the 'homing phase', and these trajectories were characterized by straight and fast movements. Close to home, there often was a final 'arrival phase' where the animals are again moving slower and less straight. Typically, the homing phases are shorter than those of the other two (first and third segments). Two animals did not show the initial exploration phase and started immediately with the homing phase, and 10 animals did not show discrete phases according to our classification algorithm. The arrival phase appeared in 11 of the animals and might only be entered when the animals miss the goal or if they assume they have reached 'home'. The longer the animals needed to reach home, the fewer phases the classification algorithm detected. This is possibly because they never entered the homing phase and slowly wandered towards home, never transitioning into a fast and straight movement.

Interestingly, our results are comparable to pigeon homing analyses, which also showed an initial phase with an individual variable duration and a homing phase with steeply increased steadiness (i.e., straightness)[39]. This suggests a common mechanism underlying the navigational process, presumably related to the cues used for homing, as well as the individuals' motivational state. In pigeons, studies have shown the importance of the hippocampus in navigational tasks[40–42], a brain structure that is also important in mammal navigation[43]. It is very likely that further investigation would find comparable neuronal processes underlying these strikingly similar behavioral patterns.

It would be highly interesting to gain further insights into the specific behavior of the animals during the identified homing phases. Furthermore, exploring what happens when they do not home could provide insights into the navigation cues that deer use. For instance, electromagnetic anomalies, obscured sun (cloud cover), or

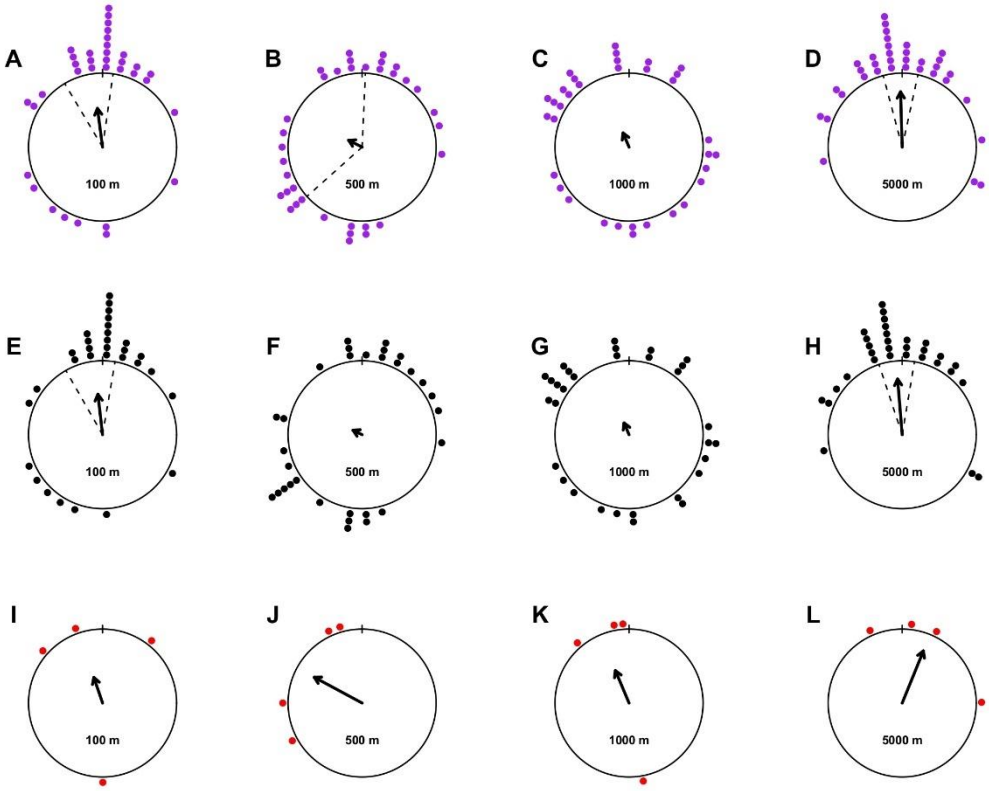

Figure 4. The bearings relative to the goal direction at a radius of 100 m (**A,E,I**), 500 m (**B,F,J**), 1000 m (**C,G,K**), and 5000 m (**D,H,L**) around the release location for all trials (purple dots, **A–D**), trials where animals homed successfully (black dots, **E–H**), and trials where they did not home (red dots, **I–L**). The mean vectors are shown as solid lines with arrowheads, whereas the length corresponds to the r-value of the mean vector. Bootstrap confidence intervals (dashed lines) around the means were calculated for significant distributions according to the MANOVA approach (for all distributions with a minimum sample size of five).

wind from directions other than home (lacking home odors) could interfere with homing abilities and either delay homing or impede homing during the time interval we considered homing. Manipulating the sensory environments of the release sites could be an option for discerning the sensory mechanisms used for homing (e.g., radio-frequency noise to disrupt the magnetic sense (c.f.[44])). This is possible because the initial orientation of the animals corresponded well with their direction towards home. In conclusion, we provide evidence for the excellent homing abilities of red deer, which fits well with the homing behavior found in other animals (e.g., well-studied pigeons). Further studies regarding sensory cues and behavioral switches along the route would be a fruitful endeavor for the future.

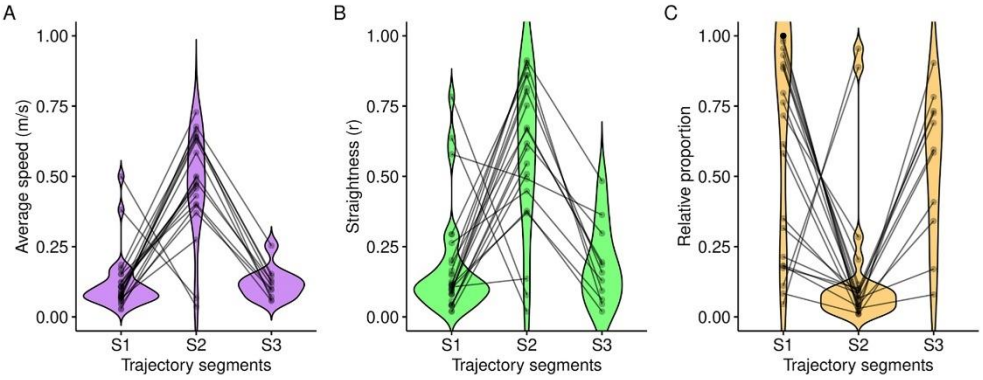

Figure 5. The trajectory segments based on the Lavielle segmentation (Segment 1 to Segment 3, labeled S1 to S3) compared the average speed (**A**), straightness of the tracks (using the standardized vector length r, **B**), and relative proportion of the segments in comparison to the overall trajectories (**C**).

Data availability

The datasets used and analyzed during the current study are available from the corresponding author upon reasonable request.

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Author contributions
V.S., L.L. and H.B. originated the idea. A.V. and M.J. did the animal handling and data collection. L.L., V.S., M.F. and M.S. wrote the manuscript and did data analyses with the contribution of L.B., and E.P.M., A.O., O.L. and M.H. contributed data and assisted with writing the final version of the manuscript.

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Competing interests
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Additional information
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5.3.2. Publikace č. 6 – Impact of winter enclosures on energy expenditure and movement acivity of european red deer

Poslední vědeckou publikací této disertační práce je studie zaměřená na vyhodnocení vhodnosti managementu přezimovacích obůrek pro jelení zvěř v oblastech střední Evropy. Výsledky pocházejí z biologging data získaných pomocí výše zmiňované hybridní technologie, kdy byla použita akcelerometrická data z obojku umístěných na jedincích jelena evropského (*Cervus elaphus)* v oblasti Doupovských hor. V průběhu dvou let došlo k zisku dat od označených jedinců, kteří alespoň část zimního a jarního období trávili uvnitř sezónní přezimovací obůrky. V porovnání s daty od jedinců mimo přezimovací obůrky v témže období došlo signifikantním změnám ve spotřebě energie, která byla definována pomocí parametru VeDBA (Vectoral Dynamic Body Acceleration). Poznatky studie přináší náhled na vhodnost managementu jelení zvěře v přezimovacích obůrkách v oblastech s možným rizikem vzniku škod na lesní hospodářských porostech.

Title

Impact of winter enclosures on energy expenditure and movement activity of european reed deer

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Abstract

The management of red deer enclosures, combined with supplementary feeding, can reduce the energy expenditure of confined animals. These enclosed individuals minimize their spatio-temporal movement and energy usage during their time inside the winter enclosure compared to those living in free range during the same period. The datasets used in this study were based on biologging technology. All measured animals (n=11) were equipped with GPS collars and Daily Dairy sensors to record Vectorial Dynamic Body Acceleration (VeDBA). The study revealed differences in the daily summary and daily mean of VeDBA parameters between enclosed and free-living animals in the study area. Energy expenditure was similar for both groups only at the moment of winter enclosure release. After the enclosure was opened, the released individuals increased their movement and energy expenditure. The use of winter enclosures for red deer management can reduce animal movement and minimize potential damage to young forest stands and seedlings. The opening of the winter enclosure

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must be synchronized with the availability of natural food resources in the locality. The management of winter enclosures should be carried out with a system of supplementary feeding inside.

Key words

winter enclosure, spatio-temporal activity, movement ecology, *Cervus elaphus,* red deer

Introduction

In recent decades, Europe has experienced an increase in both the abundance and geographical range of ungulate game populations (Carpio et al., 2021; Heurich et al., 2015; Valente et al., 2020; van Beeck Calkoen et al., 2023). This growth is attributed to climate and environmental changes, and the limited presence of large carnivores has left ungulate populations primarily regulated by food availability and hunting (Heurich et al., 2015; Kuijper et al., 2013; Martin et al., 2020). Hunting has become a major method for managing these populations, but its effectiveness varies based on effort, legislation, and hunting philosophies (Bischof et al., 2012; Heurich et al., 2015; Jarnemo & Wikenros, 2014; Linnell et al., 2020; Möst et al., 2015). The management of deer populations in European forests presents a complex challenge, balancing ecological integrity with conservation and human interests. This usually relates to the state of the environment and especially to the economic damages caused to forests. Their management then includes many activities, which usually relate to supplementary feeding or hunting. In connection with red deer, so-called winter enclosures are often used. In Europe, this is a common practice based on enclosing wild animals in fenced areas of relatively small size (units, max. lower tens of hectares), where the animals are dependent only on food provided by humans. Enclosures are usually closed from the beginning of January to the end of April, i.e., during the period of the most frequent forest damage. This activity likely significantly affects their spatial and behavioral ecology by determining resource allocation and movement barriers. In protected areas, they prevent forest damage and support biodiversity conservation during critical seasons (Riesch et al., 2019). In hunting areas, the management supports population productivity, winter survival, density, and trophy quality (Carpio et al., 2021; Putman et al., 2004). One key aspect of this challenge is understanding the energy requirements and spatial activity patterns of deer across different seasons (Apollonio et al., 2017).

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European red deer (Cervus elaphus), especially in winter and spring, exhibit a variety of spatial activities and energy requirements due to changes in environmental conditions and resource availability (Berger et al., 2002; Luccarini et al., 2006; Náhlik et al., 2009). Winter represents a significant energy restriction as deer have to move in the snow, face low temperatures, and cope with reduced forage quality and accessibility. In contrast, spring increases deer activity as they exploit the abundance of new vegetation and improved weather conditions (Bobek et al., 2016; Mysterud et al., 2001). Forage availability and distribution influence home range sizes due to climate change (Bobek et al., 2016; Van Beest et al., 2011), predator presence, or hunting season (Jarnemo & Wikenros, 2014). Other factors affecting home range size include age, sex, migratory strategies, supplemental feeding, and human disturbance (Börger et al., 2006; Luccarini et al., 2006; Mysterud et al., 2001; Reinecke et al., 2014). Red deer show significant variation in home range sizes across Europe (Jan F. Kamler et al., 2008), up to over 5000 ha seasonally (Náhlik et al., 2009), and to over 7000 ha annually (Zlatanova et al., 2019) depending on body mass due to higher metabolic needs (Makarieva et al., 2005; McNab, 1963). Spatial movement tends to be lower in resource-rich habitats, where nutritional gains are high, and travel costs are low (Börger et al., 2008).

Therefore, supplementary feeding can modify red deer spatial behavior, leading to smaller home ranges and changes in foraging habits and migrations (Felton et al., 2022; Jerina, 2012; Putman et al., 2004). Moreover, intensive feeding strategies mainly cause deer to establish home ranges near feeding sites, an effect intensified when natural resources are limited. This local aggregation increases pathogen transmission risks (Sorensen et al., 2014).

High deer densities lead to over-browsing, negatively affecting forest regeneration and biodiversity (Carpio et al., 2021; Čermák et al., 2004; Linnell et al., 2020; Valente et al., 2020). The effect of deer on woodland vegetation has resulted in significant changes in forest stand structure, composition, and stability (Gill & Beardall, 2001). The most known impact of red deer damage is browsing on young trees, which changes the stand structure and species composition and affects woodland development (Čermák et al., 2004; Cukor et al., 2022; Felton et al., 2022). Additionally, bark stripping is another severe damage that directly impacts the radial growth and productivity of affected forest stands (Cukor et al., 2019; Vacek et al., 2020).

Current advances in biologging technology and analytical methods provide an optimal solution for the precise recording of animal behaviors in the wild. These tools allow for non-

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invasive, long-term monitoring without the need for direct observations (Wilson et al., 2014). Biologging devices, such as GPS collars with accelerometers and magnetometers, enable continuous monitoring of animal movement and behavior, providing high-resolution data on spatial use and activity levels (Kirchner et al., 2023; Nathan et al., 2012; Williams et al., 2020).

In this study, we employ such technology to monitor the movement and energy expenditure of red deer, with a specific focus on the VeDBA (Vectorial Dynamic Body Acceleration) parameter (Wilson et al., 2019). Calculation works with raw acceleration excluding the gravitational component; VeDBA = Ax2+Ay2+Az2

where Ax, Ay, Az are the dynamic components of each acceleration axis (Williams et al., 2020). This metric offers a detailed quantification of energy expenditure through the measurement of animal acceleration, providing a proxy for movement intensity and overall activity (Qasem et al., 2012; Wilson et al., 2014). Energy expenditure is a useful tool to measure the cost of specific activities that have a direct impact on fitness and natural selection, such as foraging, sleep, or movement (Gallagher et al., 2017; Qasem et al., 2012).

This study addresses a fundamental question: does the confinement of deer into seasonal enclosures reduce their movement and consequently their energy expenditure?

Material and methods

Study site and species

European red deer (*Cervus elaphus*), especially in winter and spring, exhibit a variety of spatial activities and energy requirements due to changes in environmental conditions and resource availability (Berger et al., 2002; Luccarini et al., 2006; Náhlik et al., 2009). Winter represents a significant energy restriction as deer have to move in the snow, face low temperatures and cope with reduced forage quality and accessibility. In opposition, spring increases deer activity as they exploit the abundance of new vegetation and improve weather conditions (Bobek et al., 2016; Mysterud et al., 2001). Forage availability and distribution influence home range sizes due to climate change (Bobek et al., 2016; Van Beest et al., 2011), predator presence, or hunting season (Jarnemo & Wikenros, 2014). Also, other factors affect home range size including age, sex, migratory strategies, supplemental feeding, and human disturbance (Börger et al., 2006; Luccarini et al., 2006; Mysterud et al., 2001; Reinecke et al., 2014). Red deer show significant variation in home range sizes across Europe (Jan F. Kamler

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This study addresses a fundamental question: does the confinement of deer into seasonal enclosures reduce their movement and consequently their energy expenditure?

Material and methods

Study site and species

The red deer (*Cervus elaphus*) enclosure management were conducted in the years 2019, 2020 and 2021 in the Czech Republic (Table 1). This study was realized in a state military training site which is closed for public and used only for military training, game species hunting and forestry. This location is situated at the Doupov and the area includes 331 km^2. The red deer populations are managed by hunting for decades and the populations is stable. We chose 11 individuals in two seasons during the years 2019 and 2020 for this experiment and collected the spatial and movement data about. We used the winter enclosure (area 20 hectares) for this experiment. The winter enclosure is fenced area including pasture, bushes, forest stands and supplementary feeding sites inside. The enclosure is usually closed and managed by supplementary feeding since beginning of January until the end of April. The red deer individuals are able to jump inside the enclosure based on their decision during the managed season thru the one-way-entrance, but they are not able to go out until the managed opening time.

Collaring

The immobilization for tagging were done by using the mixture of Ketamine and Xylazine then the individuals were tagged by GPS collar including the biologging sensor and battery. Animals handling was realized in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361 which approved the procedures.

Data recording and tracking

We observed the red deer individuals by using GPS Vertex Plus collars (Vectronic Aerospace GmbH). The total weight of the collar was 750g and the lifetime was app. 1 year. The collar mass was lower than 3% of the animal's body mass (Wilson 2021). The biologging data were

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recorded onboard SD cards with 16GB capacity. These data were downloaded after one year of observations when the animal was re-collared by the new GPS collar and new biologging tag. Once we had the collar back with one-year dataset we downloaded the biologging data. We also collected the GPS data in interval of 30 minutes during the observation period. The GPS data were updated remotely online on the server as a package of 8 hours-dataset.

Based on the GPS data we described the period when the individual was situated inside the winter enclosure and when the individual was released (direct management release) or escaped (not direct management release). We marked the time sequences inside the biologging data and used the information about spatial status as a factor for following analyses. In total we have data of 11 individuals and for 5 of them we were able to collect second season of tracking. The data of 8 individuals were recorded when the animals was inside the winter enclosure. The 3 individuals did not come inside the winter enclosure but were in close distance around. For all animals we have spatial and movement data from free range period. The 2 of 5 individuals were recorded two times inside the winter enclosure in the second year (Table 1). The winter enclosure was closed from 4/1/2019 until 29/4/2019 and from 28/1/2020 until 30/4/2020.

Table 1. Overview of collared red deer individuals

Animal ID	Time period	Data status	Sex	Year
107	01/04/2020 – 30/06/2020	Inside	F	2020
120	04/04/2020 – 30/06/2020	Inside	F	2020
117	12/03/2020 – 30/06/2020	Inside	F	2020
115	22/03/2020 – 07/04/2020	Outside	F	2020
108	28/03/2020 – 30/06/2020	Inside	F	2020
137	26/04/2020 – 30/06/2020	Inside	F	2020
135	20/03/2020 – 30/06/2020	Inside	F	2020
133	26/04/2020 – 30/06/2020	Inside	F	2020
104	21/04/2020 – 30/06/2020	Outside	F	2020
96	02/04/2020 – 30/06/2020	Outside	F	2020
151	30/03/2019 – 30/06/2019	Outside	F	2019
120	02/04/2019 – 30/06/2019	Outside	F	2019
117	27/03/2019 – 30/06/2019	Outside	F	2019
115	27/03/2019 – 30/06/2019	Outside	F	2019

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108	31/03/2019 – 30/06/2019	Inside	F	2019
107	28/03/2019 – 30/06/2019	Inside	F	2019

Data analyses

The biologging data were analyzed by daily summary of VeDBA values to evaluate the overall daily activity over 24 hours and by VeDBA sums in 60-minute intervals to assess activity in different parts of the day. The data were tested for normality, and differences were subsequently tested using one-way ANOVA followed by Tukey's post-hoc test to determine differences between individual groups. A t-test was used to evaluate differences between two groups where applicable. The data were processed using Statistica, MS Excel, and R Studio. The ggPlot package was used for data visualization. For data comparison, we used the control period method (Bíl et al., 2018), where the control period was the time after the animals were released from the winter enclosure. Additionally, animals permanently living outside the winter enclosure were used as a control group.

Results

Total Daily Energy Expenditure

When comparing the total daily sum of VeDBA between animals that lived inside the winter enclosure and those outside (Fig. 1), a statistically significant difference was found only in March (t=6.181; p=0.000). During this period, the activity of animals in the winter enclosure was significantly lower compared to those living in the wild. The average VeDBA value for animals outside the winter enclosure was 4,473 ± 496, while for those inside the enclosure it was 107,615 ± 11,807. In April, the activity of both groups of animals equalized, and there was no statistical difference between them. The average VeDBA sum for animals in the wild in April was 114,679 ± 20,075, while for those in the enclosure it was 108,101 ± 35,905. However, the data variability for animals in the winter enclosure was very high, both in March and especially in April. The daily maximum VeDBA values for both groups in April were similar (13,341 and 13,703, respectively), but the minimum values for animals in the winter enclosure (43,238) were significantly lower compared to those living in the wild (min=93,042). The higher variability in the total daily VeDBA values for animals in the enclosure is also confirmed by the quartiles, which are almost twice as high as those for animals living in the wild (see Fig. 1). After the release of individuals from the winter

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enclosure, the daily energy sums were almost identical, and there were no differences between the two groups, with average daily VeDBA sums ranging from 94,414 ± 15,104 to 97,763 ± 13,353. When comparing the total daily VeDBA sum across individual months, April was statistically significantly different (36.893; p=0.000) from other months for animals living in the wild throughout the observation period, unlike animals from the winter enclosure, where their total daily activity differed statistically each month, with the highest again in April (F=20.415; p=0.000).

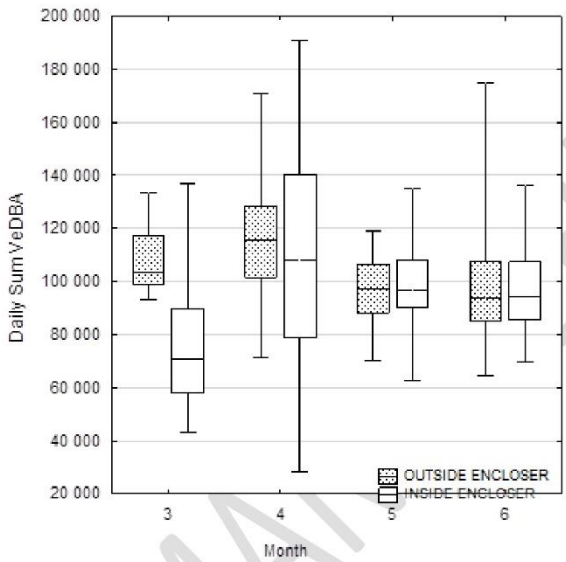

Fig.1**.** Daily sum of VeDBA for the animals which did not visit the winter encloser during March and April (OUTSIDE ENCLOSER) and for those who visited the encloser and were closed inside during March and April (INSIDE ENCLOSURE). Boxplots show the median values (middle bar in rectangles), upper and lower quartiles (length of rectangles), and maximum and minimum values (whiskers).

Some of the animals escaped from the winter enclosure during the period it was closed, and their activity significantly increased after leaving the enclosure, both in March and April (Fig. 2). This differs from the animals that remained inside and those that lived in the wild (March: F=44.415; p=0.000; April: F=4.897; p=0.007).

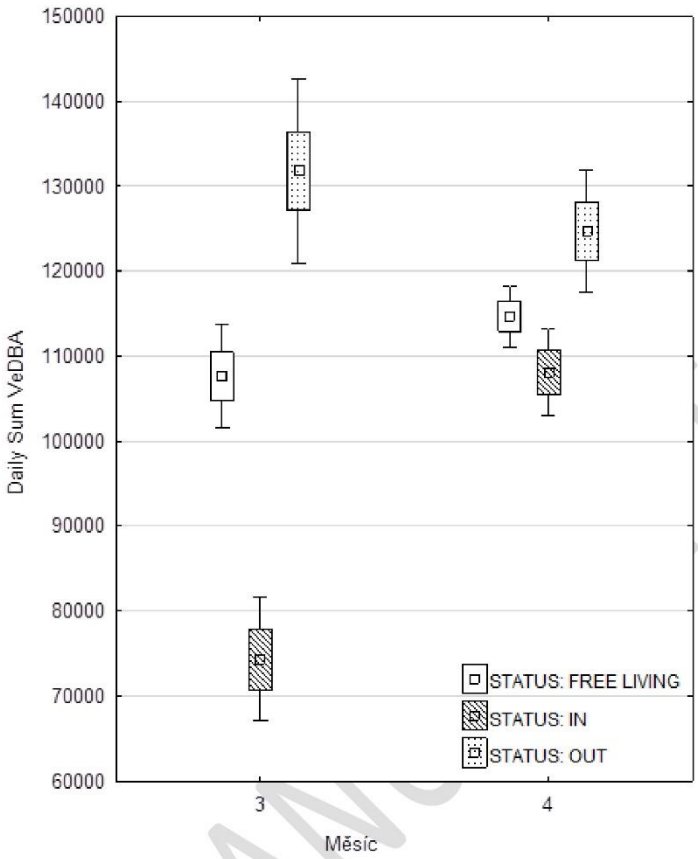

Fig.2**.** Daily sum of VeDBA for the animals which escaped from winter encloser during March and April (OUT); were closed inside (IN) and lived outside all the time). Boxplots show the mean values (middle bar in rectangles), standard error (length of rectangles), and 95% confidence intervals values (whiskers).

It appears that the period of release from the winter enclosure represents a significant moment for the animals. When evaluating the activity 15 days before and 15 days after the release, the activity 3 days before the release differed significantly from all other days (F=3.947; p=0.001). The VeDBA values increased significantly during these three days and returned to normal immediately after the release from the winter enclosure (Fig. 3).

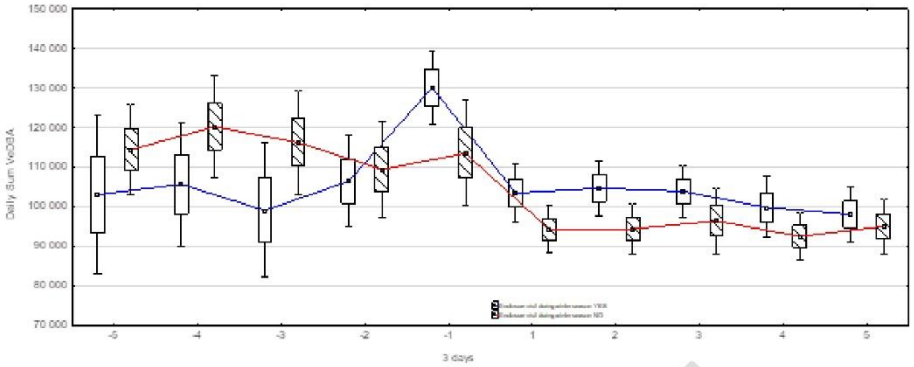

Fig. 3 Daily sum of VeDBA for the animals 15 days before (-5 to -1, 1 step= 3 days) and 15 days after releasing from encloser (1 to 5) - red line and control group which were the same period outside (blue line) . Boxplots show the mean values (middle bar in rectangles), standard error (length of rectangles), and 95% confidence intervals values (whiskers)

Daily Activity Pattern

The daily activity pattern of individuals in the winter enclosure shows no deviations from the daily activity pattern of deer living in the wild (Fig. 4). The peak activity occurs at sunrise and sunset. The lowest activity is shortly after midnight and then during the midday hours. Activity then gradually increases, reaching its peak during sunset. In March, it is evident that the highest activity is observed in individuals that left the winter enclosure, followed by those living in the wild, and the lowest activity is seen in individuals confined to the winter enclosure.

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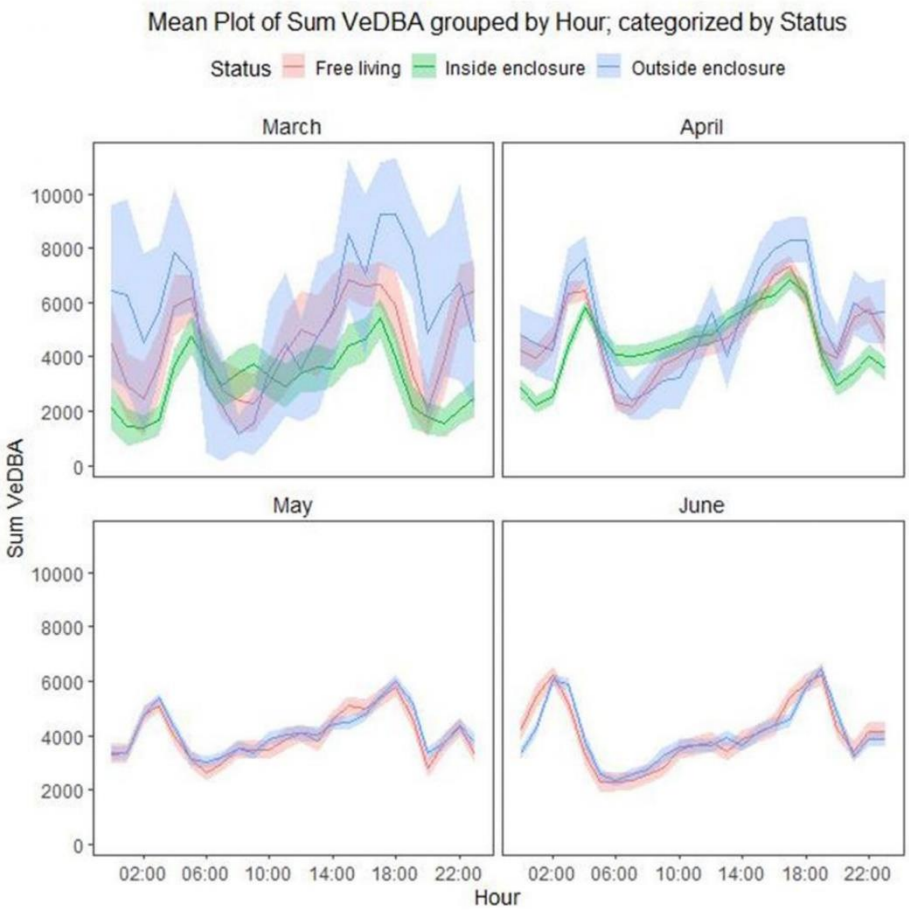

Fig. 4 Hourly Sum of VeDBA during the day (24 hours) in different months.

Discussion

The activity of red deer throughout the year (seasons) and also during the day (24-hour cycle) has most often been evaluated using movement data, specifically based on the distance traveled during individual time intervals (Pépin et al., 2009; Georgii, 1980; Copes et al., 2017; Náhlik et al., 2009; Papon et al., 2013), or using activity sensors that measure activity over longer periods (Ensing et al., 2014; Lottker et al., 2009; Sunde et al., 2009). In recent years, high-speed accelerometers have been increasingly used to estimate energy expenditure – the so-called VeDBA (Goncalves et al., 2024; Benoit et al., 2020; Mortlock et al., 2024). Estimating activity based on locomotion (i.e., distance traveled) is still the most common tool for evaluating activity. It is based on the assumption that locomotion causes a significant

increase in energy expenditure and is much more energetically demanding than other types of behavior (Hudson, 1985). Therefore, most studies based on GPS telemetry report activity as the distance traveled between two GPS points. In this context, we hypothesized that individuals confined to the winter enclosure would have significantly lower energy expenditure than those living in the wild, primarily due to their limited movement. This hypothesis was confirmed for March but not for April. This likely relates to the increasing temperatures, which cause increased activity in cervids (Kamler et al., 2007). This is also confirmed by the research of Pépin et al. (2006), which showed increasing activity during spring and summer in captive red deer hinds, and by Reimoser et al., who confirmed increased heart activity from April to July, likely related to pregnancy and care for offspring. This suggests that increased energy expenditure is indeed dependent on general seasonal changes in the environment, and the confinement of wild animals in the winter enclosure does not significantly affect these processes.

We also expected that the daily activity pattern of animals confined to the winter enclosure would change significantly. Red deer living in the wild most often exhibit a circadian rhythm of activity, which is usually caused by anthropogenic pressure (Ensing et al., 2014; Vazquez et al., 2019; Hazlerigg and Tyler, 2019). This is confirmed by a study from the Białowieża Forest, where anthropogenic disturbance is minimal, and deer exhibited this rhythm only in winter, unlike the rest of the year (Kamler et al., 2007). In our study, the daily rhythm of individuals confined to the winter enclosure did not change and was consistent with the daily rhythm of deer in the wild. It is therefore evident that deer confined to the winter enclosure retain their daily cycles observed in the wild, and that confinement does not significantly reduce their wariness – i.e., their activity remains minimal during the day. The fact that the daily rhythm and behavior do not change significantly after confinement could be evidence of high welfare, indicating that wild animals do not suffer from being confined to the winter enclosure.

We observed a change in behavior only shortly before the individuals were released back into the wild. There was a significant increase in activity and thus energy expenditure in the last three days before release. This increase in activity just before release could be an indicator of how to maintain high welfare and could serve as a tool for determining when to release the animals back into the wild. According to a series of interviews with workers who care for animals in winter enclosures, the timing of release back into the wild is variable, and they usually recognize when the confined animals “want to go out” by observing changes in behavior, such as running around the fence and being significantly more restless than before.

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It is therefore evident that their field observations and experience are based on real behavioral changes, which we confirmed. Therefore, long-term observation of individuals in winter enclosures is important for their welfare and maintaining natural rhythms as wild animals. The increase in activity could be one of the indicators of when it is necessary to release the animals.

Conclusion

Our study demonstrated that red deer within winter enclosures exhibited significantly lower energy expenditure and reduced movement compared to those in free range, particularly in March. The average VeDBA values for deer inside the enclosures were substantially lower than those for free-ranging deer, indicating reduced activity levels. This suggests that the confinement within enclosures, combined with supplementary feeding, effectively limits the deer's need to move extensively in search of food, thereby conserving their energy.

However, this difference in energy expenditure diminished in April as temperatures rose, suggesting that seasonal changes influence deer activity regardless of enclosure status. The increased temperatures likely lead to higher metabolic rates and greater activity as deer prepare for the more active spring and summer months.

Additionally, deer released from the enclosures showed a marked increase in activity and energy expenditure just before and after release. This spike in VeDBA values highlights the importance of timing the release to coincide with the availability of natural food resources. Proper timing ensures that the deer can transition smoothly back to free-ranging conditions without experiencing undue stress or energy deficits, which is crucial for their welfare and for minimizing potential damage to forest vegetation.

The use of winter enclosures, combined with supplementary feeding, effectively reduces deer movement and potential damage to young forest stands and seedlings during periods of low natural food availability. By concentrating deer in specific areas and providing consistent food sources, the enclosures help mitigate the negative impacts of over-browsing and bark stripping on forest regeneration.

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Synchronizing the opening of enclosures with the availability of natural food resources is crucial for maintaining deer welfare and minimizing their impact on the environment. This approach not only supports the health and well-being of the deer but also protects forest ecosystems from excessive damage during critical periods of growth and recovery.

Overall, our findings suggest that winter enclosure management, when properly timed and supplemented with adequate feeding, can be an effective strategy for balancing the needs of wildlife conservation and forest management. Future research should continue to explore the long-term impacts of such management practices on both deer populations and forest health to refine and optimize these strategies further.

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Figure 7. Female red deer with GPS collar.

Figure 8. Detail of the used GPS collar including biologging sensor.

Ethical approval:

The red deer tagging was realized in accordance with the decision of the ethics committee of the Ministry of the Environment of the Czech Republic number MZP/2019/630/361.

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V.S. and M.J. originated the idea. V.S., M.F. and M.J. realized the trapping. V.S., M.F. and A.P. wrote the manuscript with the contribution of M.J.

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There are no competing interests.

Additional information:

Supplementary information is available for this paper at **LINK**

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Figure legends:

Table 1. Overview of collared red deer individuals

Figure 1 – Box plot of Daily mean VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure

Figure 2 – Box plot of Daily Sum VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure

Figure 3 – Box plot of Daily sum VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure classified by months.

Figure 4 – Box plot of Daily mean VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure classified by months.

Figure 5 – Box plot of Sum VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure classified by hours.

Figure 6 – Box plot of Mean VeDBA values of all individuals inside = 1 and outside= 0 of the enclosure classified by hours.

Figure 7. Female red deer with GPS collar.

Figure 8. Detail of the used GPS collar

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6. Diskuse

6.1. Hybridní GPS-Biologging technologie

Biotelemetrické systémy pro studium pohybu a chování označených zvířat se ukázaly jako velmi výkonný nástroj pro detailní klasifikaci jednotlivých typů chování, rekonstrukci pohybu ve vysokém rozlišení a ekologii daných druhů. Získání technologie založené na systému obojku, která umožňuje vybavenost pomocí citlivých senzorů, a lze nastavit její použití pro několik živočišných druhů a pro různorodé studie, je cenné zjištění z několika důvodů, včetně toho, že není nutné vyvíjet druhově specifická zařízení a testovat jejich použitelnost a přesnost získaných dat pro každý typ studie. Vyvinuté hybridní zařízení obsahující GPS systému, tříosý akcelerometr a magnetometr slouží ke sběru standardizovaných dat a může být využito napříč širokou škálou živočichů a výzkum na nich prováděných (Bidder et al., 2015b). Vliv sledovacího zařízení na označeného jedince může mít několik podob. Ovlivněn může být přirozený pohyb zvířete vlivem atypického pohybu sledovacího zařízení, což může vést k chybě záznamu dat, které budou řádně zaznamenaná, ale z nestandartního pohybu jedince (Bodey et al., 2018). Jedním z přímých aspektů, který toto tvrzení dokládá, je například zvýšený krevní tlak u sledovaných jedinců. Další fyzická újma u označených zvířat může nastat, pokud jsou mezi označenými jedinci dospělí nebo potomci v přímé vazbě na rodiče, kteří musí vynaložit vyšší úsilí ke shánění potravy a vyrovnání energetických nároků pramenících z interference sledovacích zařízení (Pakanen et al., 2020; Saraux et al., 2011; R. P. Wilson et al., 2015). Toto je velmi často jednoduchým důvodem zaznamenaných zvýšených energetických nároků na pohyb nebo naopak sníženého výkonu označených zvířat (Gessaman & Nagy, 1988). Na základě publikovaných výsledků je doporučeno používání u pomalu se pohybujících živočichů, jakou jsou například lenochodi nebo koaly, sledovací zařízení o hmotnosti 3 – 5% tělesné hmotnosti jedince. Naproti tomu může být 3 – 5% hmotnostní limit pro sledovací zařízení méně vhodný pro různé typy predátorů z řádu šelem, skákavá zvířata jako jsou klokani popřípadě kuny nebo samci kopytníků v průběhu říje. Naproti těmto poznatků byly v rámci studie rozpoznány dva důležité trendy – s rostoucí velikostí zvířete je klesající trend v procentech poměru váhy zařízení a značeného jedincem, avšak druhým trendem je stále trvající označování malých živočichů pomocí zařízení, která jsou na hodnotě 3 – 5% jejich tělesné hmotnosti, navzdory tomu, že jsou možné technologie využití podstatně menších zařízení (Portugal & White, 2018b). Na základě stále se rozvíjející miniaturizace zařízení, která se vyvíjejí zejména v zařízeních určených pro nošení u lidí, dochází i k revoluci senzorů pro použití na zvířatech.

Například lidmi používané chytré telefony obsahují více než 10 různých senzorů schopných záznamů do interní paměti zařízení případně pomocí přímému přenosu dat na jiná úložiště, a zároveň dosahují svojí průměrnou vahou 150 – 200 g přibližně 0.2% hmotnosti lidského těla. Bohužel nevýhodou těchto lidmi používaných zařízení vyžadují velmi častý kontakt se zdrojem na dobití energie, zatímco u zvířat je tento krok řešený použitím baterií nebo nabíjecími systémy (Holton et al., 2021b; Pennisi, 2011).

6.2. Použití multi-senzorové technologie pro studium detailního pochybu a chování zvířat

Výsledky disertační práce potvrzují vhodnost použití biologging senzorů s vysokým rozlišením pro výzkum spánku u divokých zvířat v relevantní časové ose (Y. Y. Watanabe & Rutz, 2022). Tento způsob sledování odhaluje významné a nepředvídatelné inter a intra-individuální rozdíly v množství a kvalitě každodenního spánku, které pravděpodobně mají velké dopady na zdraví, kognitivní schopnosti a odezvu na přirozené a antropogenní stresové faktory ve volné přírodě. Na rozdíl od názorů, že spánek má omezenou plasticitu (Capellini et al., 2010b; Tobler, 1995), výsledky disertační práce založené na datech z bilogging senzorů ukazují, že spánek je tvořen měnícími se podmínkami prostředí, které ovlivňuji hlavně termoregulaci komplexnějšími způsoby, než se předpokládalo. Důležitým poznatkem disertační práce je, že spánek sledovaných zvířat je kratší, roztříštěnější a méně kvalitní při vyšších teplotách, což vedlo ke zkrácení spánku v letním období o 17 %. Vzhledem ke zmiňované důležité roli spánku v životě jedinců je pro jejich zdraví (Besedovsky et al., 2019; Kushida, 2004), globální oteplování a změna klimatu s nárustem extrémních výkyvů teplot pravděpodobně ovlivní spánek, potažmo zdraví volně žijících zvířat nepředvídatelným způsobem, a to zejména noční živočichy, jakým je v kulturně osídlené krajině střední Evropy i prase divoké (*Sus scrofa).* Tyto škodlivé účinky mohou být prohloubeny vlivem stresových faktorů způsobovaných lidskou aktivitou narušující spánek zvířat ve volné přírodě.

Zároveň tato technologie může být použita vhodně ke stanovení spotřebované energie a rychlosti pohybu. V minulosti byly provedeny rozsáhlé studie vztahu mezi rychlostí a spotřebou energie u suchozemských zvířat, z nichž velká většina byla provedena laboratorně na běžícím pásu, aby se ukázalo, že výkon roste lineárně s rychlostí (Taylor et al., 1970). Přestože je tento způsob měření velmi dobře kontrolovatelný, tak bohužel nesimuluje reálnou situaci ve volné

přírodě, kdy variabilita topografie povrchu a prostupnost terénem značně ovlivní sílu, a tudíž i samotný výkon pro pohyb (Shepard et al., 2013). Publikované výsledky v disertační práci prokazují značný vliv směrových obratů v pohybu – trajektorii suchozemských zvířat na vynaloženou energii. Na základě výsledků je predikováno podobné chování a výsledky u létajících a vodních živočichů. Pokud chceme dále vyvíjet modely, které nám mají pomoci porozumět trajektoriím zvířat v prostředí, kde se kontinuálně mění environmentální podmínky, a také energetické a behaviorální hodnoty, budeme si muset uvědomit, že detaily pohybu, jako jsou například otočky a drobné změny směru, mohou někdy způsobit velké rozdíly v pochopení pohybových vzorců zvířat (Schick et al., 2008).

6.3. Návratové strategie a habitatové preference

Publikované výsledky prokázaly vynikající navigační schopnosti jelena evropského (*Cervus elaphus)* při řízené translokaci (přibližně o 11 km mimo domovský okrsek). Vycházíme z toho, že vybraná místa vypuštění jsou mimo domovské okrsky zkoumaných jelenů, což naznačuje, že jedinci pravděpodobně navigovali domů z úplně nového místa. Je zajímavé, že počáteční směrová orientace v místech vypouštění, byla výrazně orientována směrem na domovské okrsky. To může naznačovat velmi dobré navigační schopnosti, založené potenciálně na globální mapové paměti, v kombinaci s magnetickou orientací nebo čichovou kognitivní mapou (Freake et al., 2006; Gagliardo, 2013). Je pozoruhodné, že výsledky disertační práce jsou srovnatelné s analýzami u homingu holubů, které také ukázaly počáteční fázi s individuálně proměnnou délkou trvání, a také další fázi navádění se strmě zvyšující ustáleností pohybu (přímočarostí homingu) (Schiffner et al., 2018). Toto poznání naznačuje výskyt podobného mechanismu, který je základem navigačního procesu, a pravděpodobně souvisí s podněty používanými pro navigaci, stejně jako motivační stav jednotlivců. U holubů studie prokázaly značnou důležitost hipokampu v navigačních úkonech (Bingman et al., 1988; Bingman & Mench, 1990; Gagliardo et al., 1996), což je mozková struktura, která je také důležitá při navigaci savců (Poulter et al., 2018). Je velmi pravděpodobné, že další výzkum by našel srovnatelné neurologické procesy, které jsou základem těchto významně podobných typů navigačního chování, potažmo homingu.

7. Závěr a doporučení pro praxi

Výzkum a studium prostorové aktivity, samotného pohybu a jednotlivých typů chování zvířat je založený na datech získaných ze standartně využívaných sledovacích zařízení různých podob. Tato zařízení dokážou parciálně zaznamenávat určitý typ hodnot, které slouží k dílčím analýzám buďto pohybu nebo chování. Hybridní GPS-Biologging technologie vyvinutá v rámci disertační práce (Painter et al., 2024) poskytuje unikátní řešení pro dlouhodobý sběr dat využitelných pro většinu typů studií suchozemských zvířat. Technologie poskytuje možnost záznamu vysokofrekvenčních dat ze dvou senzorů (akcelerometr a magnetometr) a následné přesné umístění v prostoru pomocí informace o poloze GPS. Hybridní technologie projevila vhodnost použití pro testované druhy zvěře, jakými byly jelen evropský (*Cervus elaphus)* a prase divoké (*Sus scrofa)*. Technologie byla testována a aplikována pro sledování více druhů zvířat, nicméně tyto dva výše zmíněné byly dále intenzivněji popisovány v disertační práci. Vyvinutý hybridní obojek splňuje váhové kritérium, kdy při použití na jelení a černé zvěři dosahuje se svojí hmotností včetně baterie 3% tělesné hmotnosti zvířete, což je obecně uznávaný limit pro sledovací zařízení umisťovaná na těla živočichu (R. P. Wilson, Rose, Gunner, et al., 2021b). Dodržení parametru 3% tělesné hmotnosti sledovaného zvířete prokazuje vhodnost a použitelnost hybridního zařízení pro studium detailních funkcí pohybu a chování, jelikož označení jedinci by měli prokazovat standartní chování a sledovací zařízení by pro ně nemělo být limitující. Samozřejmě není možné vyloučit vliv sledovací zařízení na fyziologické a behaviorální reakce zvířete, ale obecně by takto lehká zařízení neměla způsobovat signifikantní vliv. Pouze použití vhodných zařízení, která nenarušují a minimálně či nulově ovlivňují chování sledovaných zvířat, nám mohou poskytnout validní data pro studium a pochopení behaviorálních reakcí a prostorové aktivity zvířat.

Čas, který zvířata tráví pohybem při různých rychlostech a různorodé trajektorii pohybu, je jeden z dalších parametrů, které ovlivňují využití daného prostoru zvířaty a distribuci jejich energie (R. P. Wilson, Rose, Metcalfe, et al., 2021). Teoreticky se předpokládá, že vysoká rychlost otáčení bude energeticky nákladná, zejména při vysokých rychlostech pohybu. To znamená, že zvířata by měla upravovat svou rychlost podle charakteristiky dráhy pohybu. Když se zvířata pohybují tak, aby maximalizovala vzdálenost, kterou urazí a minimalizovala výdej metabolické energie, cestují nejúčinněji takovou rychlostí, která jim poskytuje minimální náklady na přesun, což je dobře definovaný bod pro zvířata, která se pohybují ale výhradně ve vodě. Teoretické úvahy však ukazují, že suchozemská zvířata by měla cestovat svou maximální

rychlostí, aby se minimalizovaly náklady na přesun, což nedělají, místo toho se přesouvají tempem běžné chůze. Výsledky práce ukazují, že suchozemská zvířata se mohou snažit dosáhnout minimálních nákladů na pohyb snižováním rychlosti se zvyšující se variabilitou dráhy, což poskytuje jedno z mnoha možných vysvětlení, proč je rychlost pohybu suchozemských zvířat mnohem nižší, než se v současnosti předpovídá na základě laboratorních měření lokomoční výkonnosti savců.

Dalším aspektem, který byl zaměřen na konkrétní typ chování, a přinesl významné poznatky o chování černé zvěře, je spánek. Výsledky studie vcházející z dat vysokofrekvenčního akcelerometru umístěného na černé zvěři prokázaly silnou interakci mezi spánkovými cykly (frekvencí, délkou) ve vztahu na teplotu vzduchu a lidskou aktivitu v blízkém okolí označených jedinců. Černá zvěř, která se vyskytuje na území střední Evropy ve značné populační hustotě se dokáže velmi dobře přizpůsobit zvýšené lidské aktivitě v jejím bezprostředním okolí a nebere lidskou aktivitu jako hrozbu. Zatímco spánková reakce černé zvěře na dny s vysokou teplotou vzduchu byla v rámci studie popsána za značně negativní, a to ve smyslu roztříštění spánkových cyklů a jejich zkrácení v průběhu těchto dnů. Lze tedy předpokládat, že s probíhající klimatickou změnou mohou nastat fyziologické změny u černé zvěře v důsledku nedostatku spánku vlivem teplého klimatu. Zřejmá je možnost adaptace na měníce se klima, nicméně dynamika změn klimatu je značně rychlejší, než mohou být změny fyziologických funkcí včetně spánku a jeho kvality.

Fidelita zvířat k danému územnímu celku je známa u spousty živočišných druhů. Tato vlastnost je velmi důležitou informací v případě, že daný živočišný druh je cílem jakéhokoliv typu lidského managementu (lesní hospodářství, zemědělství, krajino-tvorba, vodní hospodářství apod.) nebo jím může být přímo či nepřímo ovlivněn. Jelení zvěř na území České republiky se vyskytuje na významné část zejména lesní plochy, což přináší různé typy interakcí. Vlivem poznatků z výsledků disertační práce je prokázáno, že i po řízené translokaci jedinců jelena evropského na vzdálenosti kolem 11 km od jejich domovského okrsku se mohou tito jedinci vrátit do původního domovského okrsku. Tento poznatek přináší velmi důležitou informaci vzhledem k managementu populací jelení zvěře, která prokázala schopnosti homingu, návratu do původní domovského areálu, a tudíž i značnou fidelitu k prostředí a societě, ve které se nacházela před translokací. Jakékoliv zásahy do prostředí, ve kterém se jelení zvěř nachází by měli brát v potaz interakci, která může nastat vlivem toho, že se jelení zvěř z dané lokality nemusí stáhnout a vymizet, ale naopak ji může více preferovat. To však

může z pohledu lidského managementu v krajině přinášet negativní interakci z lidského pohledu na věc.

Výsledky disertační práce přinášejí novou a ověřenou sledovací technologii, kterou lze použít pro dlouhodobé sledování zejména suchozemských zvířat a studovat jejich prostorovou aktivitu, chování a ekologii. Dílčí výsledky práce vycházejí ze širšího použití vyvinuté hybridních technologie a zobrazují možnosti studií a výzkumů včetně jejich výsledků. Pouze validně zaznamenaná data z pohybu a chování zvířat nám mohou deklarovat odpovědi na stanovené hypotézy. Díky poznání standartního chování zvířat a jeho případných změn na různé podněty můžeme detailněji pochopit přírodní procesy a na základě tohoto pochopení pak stanovit pravidla vhodného typu lidského managementu, ať už pro samotné populace nebo pro enviromentální prostředí. Bez validně získaných a vyhodnocených dat, která pochází z nestresovaných a neovlivněných zvířat nejsme schopni adekvátně nastavit jakákoliv managementová opatření a vše provedené mohou být jen domněnky s vyšší pravděpodobností chybovosti.

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9. Seznam obrázků a grafů

Obrázek 1 - Schématický graf popisující rozdílnost jednotlivých typů akceleračních pohybů v porovnání s rychlostí u automobilu (a) a běžce (b). Černá čárkovaná čára charakterizuje prudké zrychlení při nárůstu rychlosti nikoliv při stabilní rychlosti pohybu. Na druhou stranu běžec při cyklu chůze navyšuje a snižuje svoji akceleraci i v průběhu stabilního rychlosti. To je způsobeno pohybem pohybu těla nahoru a dolů. ((Gleiss et al., 2011)).....17

Obrázek 2 – Pohyby člověkem vedeného koně, které začal a ukončil svou cestu v levém horním rohu obrázku. Černá trasa = sledovánní pomocí vysokofrekvenční GPS (1 Hz) a červená trasa určená pomocí Dead-Reckoningu (20Hz) bez pouzití GPS korekce. Trasa dead reckoningu nemá měřítko, protože vdálenost pohybu je odvozena od rychlosti a je zde předpoklad, že je v lineárním vztahu s hodnotou VeDBA. Co dokazuje potřebu korekce pomocí GPS technologie. Ve čtvercích je znázorněn časový úsek, kdy byl kůň vedený k pohybu v těsných kruzích. Podle GPS byla celková dráha koně dlouhá 10,127 km.....23

Obrázek 3 - 2D cesty pohybu sledovaného člověka pomocí a) video záznamu, b) GPS, c) Dead-Reckoning bez korekce, d) Dead-Reckoning s korekcí každé 2 sec, e) Dead-Reckoning s korekcí každých 5 sec, f) Dead-Reckoning s korekcí každých 10 sec (Bidder et al., 2015) 24

Obrázek 4 - Korekce trasy dead reckoning pomocí GPS bodů zaznamenávaných v intervalu 30 minut. 670 metrů dlouhá trasa sledovaného jezevce lesního (Meles meles) po dobu přes 200 minut.Čtverce ukazují detailní pohyby zaznamenané pomocí dead reckoningu. 25

Obrázek 5 - Grafické znázornění výsledků vyhledávání ve věděcké databázi slova homing v publikovaných článcích. Červeně zvýrazněné jsou oblasti zájmu této práce – vědy o chování a biologie. (zdroj – Web of knowledge) 29