Česká zemědělská univerzita v Praze

Fakulta lesnická a dřevařská

Katedra myslivosti a lesnické zoologie

Studijní program: Lesní inženýrství, obor Ochrana lesů a myslivost

Prostorová orientace loveckých psů

Spatial orientation of hunting dogs

Disertační práce

Autor: Ing. Kateřina Benediktová

Školitel: prof. RNDr. Hynek Burda, CSc.

Praha 2021

ČESKÁ ZEMĚDĚLSKÁ UNIVERZITA V PRAZE

Fakulta lesnická a dřevařská

ZADÁNÍ DISERTAČNÍ PRÁCE

Ing. Kateřina Benediktová

Lesní inženýrství
Ochrana lesů a myslivost

Název práce

Prostorová orientace loveckých psů

Název anglicky

Spatial orientation of hunting dogs

Cíle práce

Cílem práce je pomocí řízených experimentů s GPS obojky získat nové poznatky o způsobu prostorové orientace loveckých psů v terénu a o možném propojení těchto schopností s magnetorecepcí.
Dalším cílem je vyhodnocení vlivu magnetického pole na poziční chování psů a popsání možných vlivů, které ovlivňují přirozené chování

Metodika

Sběr dat bude probíhat formou individuálních vycházek v rovinatých lesních terénech. Na začátku trasy bude sledovanému psovi nasazen GPS obojek, který bude zaznamenávat jeho trasu. Pes bude vypuštěn na volno a poslán vyhledávat zvěř. V momentě zahájení pronásledování zvěře se pes nechá pracovat samostatně a bez dalších povelů se bude čekat na jeho návrat.

Každá trasa bude následně pomocí speciálního softwaru rozdělena na úseky, které budou představovat jednotlivé útěky psa za zvěří. Analýzou těchto dílčích tras budou získány údaje pro další statistické zpracování (časy, vzdálenosti, azimuty apod.) s cílem provést hlubší analýzy všech proměnných, které mohou do procesu prostorové orientace a magnetorecepce vstupovat.

Bude použit základní soubor dat z diplomové práce studentky, který bude dále kvantitativně i kvalitativně rozšiřován.

Výsledky a závěry disertační práce budou publikovány formou odborného článku ve vědeckém časopise s impakt faktorem.

Harmonogram řešení:

2015 – 2017 – Sběr dat, průběžné zpracovávání, výběr vhodných statistických metod

2016 – 2019 – Statistické vyhodnocení a publikace dat

Doporučený rozsah práce

100-150 stran

Klíčová slova

prostorová orientace, magnetorecepce, poziční chování, kynologie

---

Doporučené zdroje informací

BARRY, C.; BURGESS, N. 2014: Neural mechanisms of self-location. Current Biology, 24 (8). 330–339. DOI: 10.1016/j.cub.2014.02.049.

BEGALL, S.; CERVENY, J.; NEEF, J.; VOJTECH, O.; BURDA, H. 2008: Magnetic alignment in grazing and resting cattle and deer. Proceedings of the National Academy of Sciences of the United States of America, 105 (36): 13451–13455. DOI: 10.1073/ pnas.0803650105.

BEGALL, S.; MALKEMPER, E. P.; CERVENY, J.; NEMEC, P.; BURDA, H. 2013: Magnetic alignment in mammals and other animals. Mammalian Biology – Zeitschrift für Säugetierkunde, 78 (1): 10-20. ISSN 1616–5047. DOI: 10.1016/j.mambio.2012.05.005.

HAFTING, T.; FYHN, M.; MOLDEN, S.; MOSER. M. B.; MOSER, E. I. 2005: Microstructure of a spatial map in the entorhinal cortex. Nature, 436 (7052): 801–806. DOI: 10.1038/ nature03721.

HART, V.; NOVÁKOVÁ, P.; MALKEMPER, E. P.; BEGALL, S.; HANZAL, V.; JEŽEK, M.; KUŠTA, T.; NĚMCOVÁ, V.; ADÁMKOVÁ, J.; BENEDIKTOVÁ, K.; ČERVENÝ, J.; BURDA, H. 2013B: Dogs are sensitive to small variations of the Earth’s magnetic field. Frontiers in Zoology, 10: 80. DOI: 10.1186/1742-9994-10-80.

O´KEEFE, J.; NADEL, L. 1979: The hippocampus as a cognitive map. Behavioral and Brain Sciences, 2 (4): 478-494. DOI: 10.1017/S0140525X00063949.

O’KEEFE, J.; DOSTROVSKY, J. 1971: The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely moving rat. Brain Research, 34 (1): 171-175. DOI: 10.1016/0006-8993(71)90358-1.

SOLSTAD, T.; BOCCARA, C. N.; KROPFF, E.; MOSER, M. B.; MOSER, E. I. 2008: Representation of geometric borders in the entorhinal cortex. Science, 322 (5909): 1865–1868. DOI: 10.2307/20177082.

SPENCER, W. D. 2012: Home ranges and the value of spatial information. Journal of Mammalogy, 93 (4): 929-947. DOI: 10.1644/12-MAMM-S-061.1.

WILTSCHKO, R.; WILTSCHKO, W. 1995: Magnetic orientation in animals. Journal of Navigation, 49 (03): 453-454. DOI: 10.1017/S0373463300013692.

Předběžný termín

2018/19 ZS – FLD – SDZ

Vedoucí práce

prof. RNDr. Hynek Burda, CSc.

Garantující pracoviště

Katedra myslivosti a lesnické zoologie

Elektronicky schváleno dne 30. 10. 2015

doc. Ing. Vlastimil Hart, Ph.D.

Vedoucí katedry

Elektronicky schváleno dne 13. 1. 2021

prof. Ing. Marek Turčáni, PhD.

Předseda oborové rady

Elektronicky schváleno dne 3. 6. 2021

prof. Ing. Róbert Marušák, PhD.

Děkan

V Praze dne 10. 06. 2021

Anotace

Práce se zabývá způsoby prostorové orientace loveckých psů v jejich přirozeném prostředí se zaměřením na propojení navigačních schopností s magnetorecepcí. Hodnotí vliv magnetického pole na poziční chování a popisuje další vlivy, které ovlivňují přirozené chování psů. Popisuje možnosti sledování loveckých psů v terénu a následné zpracování velkoobjemových dat.

The dissertation thesis is focused on the spatial orientation of hunting dogs in their natural environment and the involvement of magnetoreception in navigation abilities. The thesis evaluates the influence of magnetic field on alignment behaviour and the impact of other factors on the behaviour of dogs. In addition, describes the possibility of observing hunting dogs in the terrain and subsequent processing of long-lasting data.

Klíčová slova:

prostorová orientace, homing, magnetorecepce, poziční chování, kynologie

spatial orientation, homing, magnetoreception, alignment, cynology

Čestné prohlášení

Prohlašuji, že jsem disertační práci na téma „Prostorová orientace loveckých psů“ vypracovala 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 7. 6. 2021

Podpis autora Benediktová

„Biologie je nevytěžený zlatý důl, člověk zakopává o hroudy zlata.“

Pavel Jungwirth, 2016[1]

Jezevčík Puňťa sleduje jezevčíka Plyšáka užívajícího si bahenní koupele
(foto pořízeno u zaparkovaného auta během přípravy psů na sběr dat)

Lovecký pes v „plné zbroji“
(jezevčík Vendulka vracející se z útěku a natěšený jezevčík Puňťa při příjezdu na lokalitu sběru dat)

Poděkování

Ráda bych touto cestou poděkovala nejdříve své rodině, která mě bezvýhradně podporovala na cestě za mým snem. Rodičům za ochotu hodiny a hodiny hlídat a pečovat o mé zvířecí miláčky v době, kdy jsme trávili celé dny v terénu. Bratrovi, že mě propustil ze služby, byť se zatnutými zuby. Strejdovi, který vždy držel palce, ze zkoušek byl nervóznější než já a podporoval mě nejen morálně. Bez jejich obětavosti bych nikdy nedošla až sem.

Za skvělé pracovní zázemí, možnost učit se a přebírat cenné zkušenosti děkuji třem úžasným lidem, které mi osud přivedl do cesty v ten pravý okamžik. Vlasta Hart, Hynek Burda a Luděk Bartoš byli ti, kteří nahodili vědeckou udičku a pak společnými silami tahali a už nepustili. Každý svým osobitým a jedinečným způsobem.

Věda a výzkum je dvojice náročná na čas i nervovou soustavu. Moc děkuji mých kolegům Janě Adámkové, Honzovi Svobodovi a Mílovi Zikmundovi za společně strávené chvíle, za jejich nemalý podíl na výsledcích této práce a za neustálý příval morální podpory. Míše Másílkové za pečlivou kontrolu všeho, co jsem napsala a za důležitou radu, kterou si nechám pro sebe. Dále děkuji všem dalším kolegům a kamarádům z Katedry myslivost a lesnické zoologie za jejich pomoc s výzkumem a za cenné rady týkající se všech aspektů života na universitě. Nesmím zapomenout ani na samotnou Fakultu lesnickou a dřevařskou ČZU, která svou atmosférou a prostředím skutečně motivuje a popohání vpřed.

Děkuji rovněž kolegům z jezevčičího světa, našim studentům a jmenovitě Hedvice a Vaškovi Fuksovým za poskytnutí svých chlupatých kamarádů, bez kterých by naše výsledky byly jen poloviční.

Výzkum v rámci této disertační práce byl podpořen Interní grantovou agenturou FLD ČZU IGA B07/16 „Homing a magnetorecepce vybraných druhů obratlovců“, Celouniverzitní interní grantovou agenturou ČZU CIGA 20174319 „Prostorová orientace loveckých plemen psů: interakce mezi senzorickou percepcí a faktory ovlivňujícími schopnost orientace“ a projektem EVA4.0 z Operačního programu Výzkum, vývoj a vzdělávání MŠMT, podprogram SP1 „Vliv elektromagnetických polí (EMF) na biologii, ekologii a životní pohodu organismů“.

Obsah

1 Úvod 11

2 Cíle práce 13

3 Literární přehled 14
- **3.1 Orientace suchozemských savců 14**
  - 3.1.1 Funkce prostorové orientace 17
    - 3.1.1.1 Pátrací chování 17
    - 3.1.1.2 Migrace 17
    - 3.1.1.3 Homing 17
  - 3.1.2 Mechanismy prostorové orientace a informační zdroje 18
    - 3.1.2.1 Integrace cesty (Path integration) 18
    - 3.1.2.2 Pilotování (Piloting) 19
    - 3.1.2.3 Sledování stopy (Tracking) 20
    - 3.1.2.4 Mapování (Mapping) 21
    - 3.1.2.5 Kompasová orientace (Compass orientation) 22
    - 3.1.2.6 Navigace (Navigation) 24
  - 3.1.3 Smysly využívané při prostorové orientaci psů 25
    - 3.1.3.1 Čich 25
    - 3.1.3.2 Sluch 27
    - 3.1.3.3 Zrak 27
    - 3.1.3.4 Magnetorecepce 29
    - 3.1.3.5 Magnetorecepce psovitých šelem se zaměřením na psa domácího ... 31
- **3.2 Prostorová orientace a moderní technologie 35**
  - 3.2.1 Možnosti sledování zvířat 35
  - 3.2.2 Možnosti zpracování velkoobjemových dat 35

4 Metodika 37
- **4.1 Prostorová orientace loveckých psů v terénu 37**
  - 4.1.1 Charakteristika sledovaných psů 37
  - 4.1.2 Sledovací zařízení 37
  - 4.1.3 Sběr dat 38
  - 4.1.4 Zpracování dat 38
  - 4.1.5 Identifikace azimutů 40
  - 4.1.6 Statistická analýza dat 40
- **4.2 Vliv magnetického pole na poziční chování psů 40**
  - 4.2.1 Metodika terénních experimentů 40

4.2.1.1 Sběr dat ... 40
4.2.1.2 Zpracování a vyhodnocení dat ... 41
4.2.2 Metodika experimentu v magnetické cívce ... 42

5 Výsledky – seznam vědeckých článků ... 43
5.1 Prostorová orientace loveckých psů ... 43
5.1.1 Magnetic alignment enhances homing efficiency of hunting dogs ... 43
5.1.2 Processing Methods of Camera Record of Animal Movement ... 44
5.1.3 Automatic Analysis of Long-Lasting Video Sequences of Animal Movements ... 45
5.1.4 Hunting dogs bark differently when they encounter different animal species ... 45
5.2 Vliv magnetického pole na poziční chování psů ... 46
5.2.1 Dogs are sensitive to small variations of the Earth’s magnetic field ... 46
5.2.2 Directional preference in dogs: Laterality and “pull of the north.” ... 47
5.2.3 Turning preference in dogs: north attracts while south repels ... 48
5.3 Separáty vědeckých článků ... 48

6 Diskuse ... 165

7 Závěr a doporučení pro další rozvoj vědního oboru ... 173

8 Seznam citované literatury ... 175

1 Úvod

V roce 2014 byla udělena Nobelova cena za fyziologii a lékařství trojici vědců, kteří identifikovali v mozku savců buňky umožňující orientaci v prostoru. Nově objevené buňky jsou odpovědné za „vnitřní GPS“ zvířat (Hafting et al., 2005). Objev „navigačního systému“ v mozku tak představuje další posun v porozumění principům prostorové orientace (Solstad et al., 2008).

Orientace (prostorová či časová) je klíčová kognitivní funkce pro všechny pohybující se živočichy. Umožňuje jedincům cílený a efektivní pohyb v prostředí. V posledních desetiletích se v souvislosti s orientací hovoří o schopnosti zvířat získávat informace potřebné pro navigaci z magnetického pole Země.

Sdělovací prostředky přinesou občas informaci o neuvěřitelných navigačních schopnostech psů, kteří se vrátili zpět domů ze vzdálenosti mnoha desítek či stovek kilometrů. Asi nejznámějším příkladem je putování kolie Lassie. Ačkoli je tento příběh smyšlený, dobře demonstruje reálné navigační schopnosti psů. Během 1. světové války byli psi využíváni jako tzv. „messenger dogs“, kteří měli za úkol doručovat citlivé zprávy napříč bojištěm. Psi museli často běžet mnoho kilometrů neznámým terénem, za tmy, mlhy i deště, a přesto byla jejich úspěšnost vysoká. Plukovník Richardson, který tyto psy trénoval, poukázal na zajímavou skutečnost. Dle jeho názoru nelze tyto mimořádné homingové schopnosti psů vysvětlit jen použitím běžných smyslů a zmiňoval v této souvislosti termín „homing instinct“ (Richardson, 1920). Nemohla by se za neuvěřitelnými navigačními schopnostmi psů „ukrývat“ magnetorecepce?

Magnetorecepce, tj. schopnost vnímat magnetické pole Země, byla popsána u mnoha živočišných druhů. Od bezobratlých až po velké savce, od zvířat migrujících tisíce kilometrů až po zvířata pohybující se na prostoru velikosti tenisového hřiště. Mnoho migrujících zvířat využívá magnetické pole Země k navigaci. Otázkou ovšem zůstává, jaký biologický význam by mohla mít magnetorecepce pro nemigrující živočichy. Desítky let zaměřovali vědci svou pozornost především na ptáky, ryby a mořské želvy, zatímco savci zůstávali poněkud stranou.

Propojení těchto dvou fenoménů, homingu a magnetorecepce, se přímo nabízí. Je proto s podivem, že systematické studie charakterizující navigační strategie a zapojení senzorických mechanismů u nemigrujících savců v jejich přirozeném prostředí jsou velmi vzácné. Ideální zvířecí model pro studium homingu i magnetorecepce by mohl představovat pes domácí (*Canis familiaris*). Psi jsou snadno dostupní, ochotní spolupracovat s člověkem a zvyklí na jeho životní prostředí. Přesto si stále zachovávají své kognitivní dovednosti společné s divokými předky. To platí zvláště pro lovecké psy.

Existuje konkrétní skupina plemen loveckých psů (honiči a dále plemena schopná pracovat jako honiči), kteří jsou po generace šlechtěni k tomu, aby našli stopu zvěře, hlasitě ji sledovali a následně, po ukončení sledování, se spontánně vrátili zpět ke svému majiteli. Zvěř mohou sledovat i několik kilometrů terénem, kde nikdy předtím nebyli. Dostávají se tak do podobné situace, jako psí kurýři během války. Náhle se ocitnou relativně daleko od majitele, v neznámém terénu a v situaci, kdy využití běžných orientačních vodítek je velmi ztížené či přímo nemožné. A přesto nemají tito psi problém, aniž by je majitel musel přivolával, ho v nepřehledném lesním terénu opět najít.

Od majitelů loveckých psů i z vlastní zkušenosti víme, že se psi umějí vracet po své vlastní stopě, ale mnoho majitelů popisuje situace, kdy se psi prokazatelně po vlastní stopě nevraceli, ale přišli z úplně opačné strany. Případně se vrátili rovnou domů nebo čekali u auta. Jaké tajemství před námi psi ještě skrývají?

2 Cíle práce

Předložená disertační práce je komentovaným souborem sedmi vědeckých článků, které byly publikovány nebo odeslány do redakce.

Disertační práce volně navazuje na základní výsledky získané v rámci bakalářské a diplomové práce. Je zaměřena na kvantitativní i kvalitativní rozšíření a prohloubení poznatků o prostorové orientaci loveckých psů, dále zkoumá možný vliv magnetického pole Země jak na orientaci, tak i na přirozené chování psů. Hlavními cíli disertační práce byly:

1. Pomocí řízených experimentů s GPS obojky získat nové poznatky o způsobu prostorové orientace loveckých psů v terénu a o možném propojení těchto schopností s magnetorecepcí.
2. Vyhodnocení vlivu magnetického pole na poziční chování psů a popsání možných vlivů, které ovlivňují přirozené chování.

3 Literární přehled

Detailní náhled do studované problematiky je podrobně popsán v jednotlivých publikovaných článcích. V následujících kapitolách jsou představeny pouze základní informace v kontextu celé studované problematiky se zaměřením na čeleď psovitých (Canidae), s důrazem na psa domácího (*Canis familiaris*), a dále informace vysvětlující z jakého důvodu byly jednotlivé výzkumy prováděny (mezery v současném stavu poznání, vylepšení a vývoj nových postupů apod.).

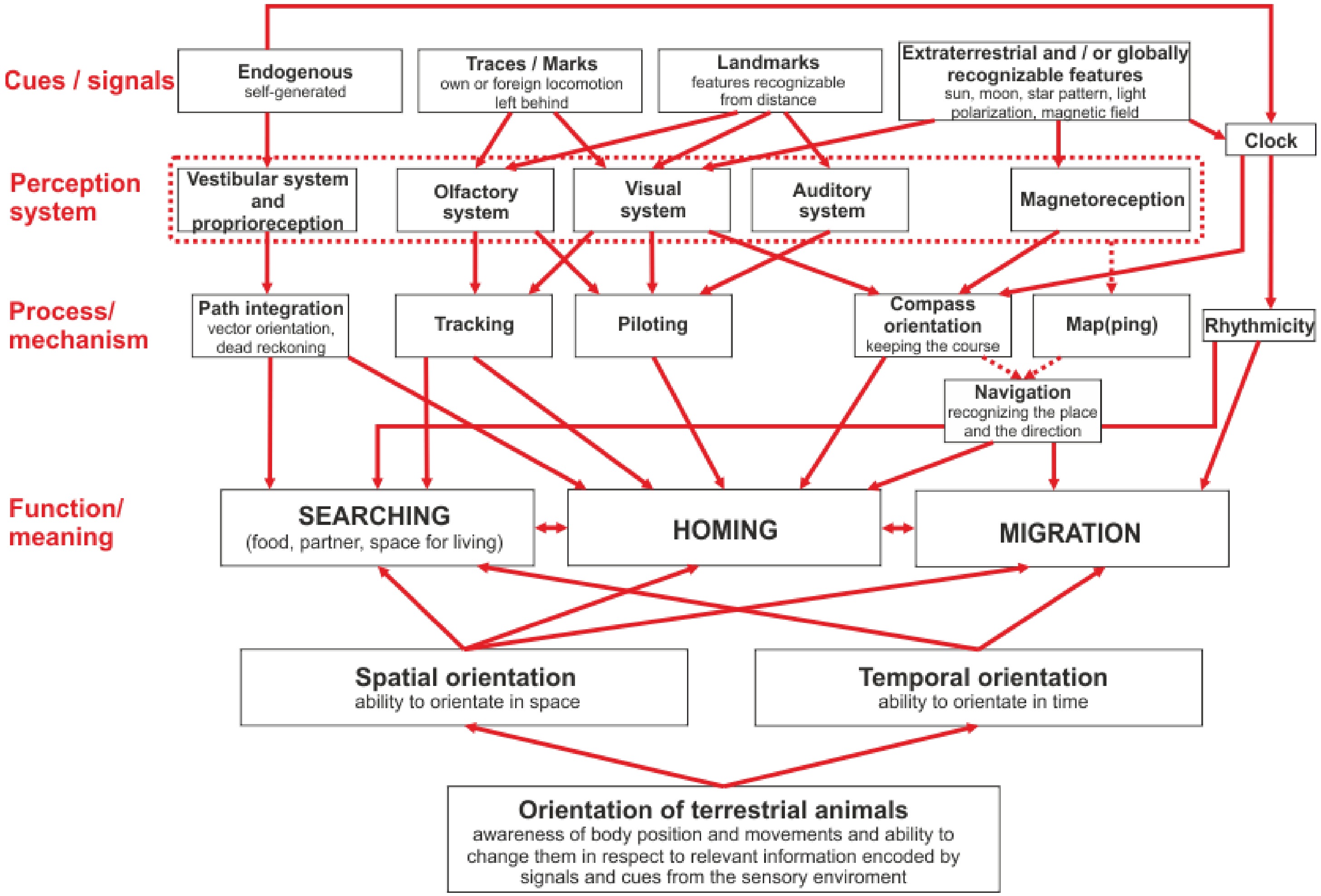
3.1 Orientace suchozemských savců

Orientaci můžeme definovat jako schopnost uvědomit si pozici a pohyb těla (nebo jeho části) a změnit je na základě relevantních informací získaných prostřednictvím kódovaných signálů přicházejících z prostředí, ve kterém se zvíře pohybuje. Orientaci můžeme rozdělit na *prostorovou orientaci* (schopnost orientovat se v prostoru) a *časovou orientaci* (schopnost orientovat se v čase). Přičemž oba typy jsou vzájemně propojeny a integrovány v jeden funkční celek (Poulter et al., 2018; Shiomi et al., 2019).

V odborné literatuře, zaměřené na prostorovou orientaci, se termíny orientace a navigace používají poměrně „promiskuitně“, kdy se výraz *navigace* často používá jako synonymum pro *orientaci*. Většina zvířat se pohybuje orientovaným způsobem, ale navigace znamená něco více (Gould, 2004). Jedná se o orientační procesy, které umožňují s využitím externích referencí stanovit směr ke konkrétnímu cíli nacházejícímu se mimo dosah smyslových orgánů (Wiltschko & Wiltschko, 1995). Navigace vyžaduje užití mapy (určení koordinátu místa, kde se jedinec nachází a místa, kam směřuje) a kompasu, který určí směr z daného místa do cíle (Griffin, 1952). V tomto smyslu jsou oba výrazy používány i v této práci.

Fungující prostorová orientace zvířat závisí na efektivní percepci, integraci a interpretaci informací získaných z okolního prostředí zvířete (allocentrická orientace a allothetické informace) nebo na základě zkušenosti a informací o vlastním pohybu a poloze (egocentrická orientace a idiothetické informace) (Poulter et al., 2018; Spiegel & Crofoot, 2016). Zahrnuje jak pohyb v prostoru domovského okrsku zvířete, tak i pohyb do vzdálených sezónních oblastí (shrnuto v Frost & Mouritsen, 2006). Podle funkce můžeme tedy prostorovou orientaci rozdělit na *pátrací chování*, *homing* a *migraci*. Mechanismy, které může zvíře použít v rámci těchto tří modalit zahrnují *integraci cesty*, *sledování stopy*, *pilotování*, *kompasovou orientaci* a *použití mapy*. Pokud má zvíře k dispozici „mapu“ (ukazuje zvířeti jeho polohu vzhledem k cíli) a „kompas“ (ukazuje zvířeti příslušný směr), je schopno použít ještě jeden mechanismus a to *navigaci*. V rámci prostorové orientace dochází více či méně k propojení a vzájemným interakcím všech zdrojů (informace a signály – percepční systém – mechanismy a procesy – funkce a význam) (grafické znázornění viz Obr. 1) (Fagan et al., 2013; Gauthreaux, 1980; Gould, 2004, 2014; Gould & Gould, 2012; Mouritsen, 2018; Nahm, 2015; Poulter et al., 2018; Schöne, 1984). Zvířata jsou často schopna vnímat a flexibilně využívat více informačních zdrojů, než kolik jich pro daný navigační úkol potřebují. To může komplikovat studium orientačních schopností zvířat a vést ke zdánlivě protichůdným zjištěním (Frost & Mouritsen, 2006).

Podrobnější vysvětlení jednotlivých komponent účastnících se procesů spojených s prostorovou orientací lze najít níže v kapitolách 3.1.1 až 3.1.3.



Obrázek 1: Schématické zobrazení vzájemných interakcí a propojení všech komponent orientace: informace a signály – percepční systém – mechanismy a procesy – funkce a význam (schéma s pomocí školitele sestaveno autorkou na základě většiny zdrojů citovaných v této práci).

3.1.1 Funkce prostorové orientace

V závislosti na ekologii daného druhu využívají zvířata prostorovou orientaci v rámci pátracího chování, migrace a homingu.

3.1.1.1 Pátrací chování

Pátrací chování je reprezentováno průzkumnými výlety zvířete do okolního prostředí. Je zvířetem využíváno při pátrání po zdrojích potravy, za účelem hledání partnera nebo nového habitatu v situaci, kdy informace o potenciálních cílech jsou omezené nebo zcela chybějí. Přičemž odchozí trasy jsou během pátracího chování delší, klikatější a přerušované zastávkami a skenováním okolí, příchozí trasy jsou přímější a rychlejší (Mueller & Fagan, 2008; shrnuto v Thompson et al., 2018). Jedinec se při něm může, ale také nemusí vracet zpět do svého domovského okrsku, často ho i natrvalo opouští (Bell & Bell, 1990).

3.1.1.2 Migrace

Migrace je obecně charakterizována jako pravidelný (sezónní) pohyb na dlouhou vzdálenost mezi prostorově nesouvisejícími habitaty (Fagan et al., 2013; Gauthreaux, 1980), tj. například mezi místem sloužícím k rozmnožování a zimovištěm (Kölzsch et al., 2020). Migrace je běžná populační strategie napříč různými taxony (Mueller & Fagan, 2008; O´Keefe & Nadel, 1978). Důležitou součástí poslední fáze migrace může být i homing, ale pouze u migrantů, kteří nemigrují poprvé (bez znalosti cíle nelze homing zapojit) (shrnuto v Thorup & Holland, 2009).

3.1.1.3 Homing

Homing lze definovat jako schopnost vrátit se (po přemístění) zpět do známé cílové lokality (Papi, 1992; Schmidt-Koenig & Keeton, 1978). Byl popsán u mnoha taxonomicky odlišných druhů obratlovců a závisí na celé řadě informačních zdrojů, podle kterých se může zvíře orientovat – vizuální, olfaktorické, akustické, nebeské, magnetické a idiothetické (Chernetsov, 2017; Cullen & Taube, 2017; Mouritsen, 2018; Papi, 1992; Schmidt-Koenig & Keeton, 1978; Wiltschko & Wiltschko, 1995). Nicméně systematických studií zaměřených na navigační strategie a zapojení konkrétních smyslů během homingu u nemigrujících zvířat bylo provedeno pouze několik (např.: August et al., 1989; Tsoar et al., 2011; Walton et al., 2001) a naše znalosti tak zůstávají neúplné (Poulter et al., 2018; Wolbers & Wiener, 2014).

Je známo mnoho anekdotických zpráv o neuvěřitelných homingových schopnostech psů, nicméně tyto schopnosti mohou být nadhodnocené (Miklósi, 2018). Možná nejlépe popsaným příkladem je využívání již zmiňovaných „messenger dogs“ během 1. světové války (Richardson, 1920). Později, v polovině minulého století, bylo provedeno několik dalších systematických studií dokazující homingové schopnosti psů (podrobnější popis viz kapitola 3.1.2.6), ale vzhledem k omezeným technickým možnostem té doby chybí mnoho detailů o konkrétním chování psů během navigace (shrnuto v Nahm, 2015). Od té doby (téměř 60 let) nebyly další systematické homingové studie se psy provedeny, příp. nebyly publikovány.

3.1.2 Mechanismy prostorové orientace a informační zdroje

Mechanismy prostorové orientace představují konkrétní prostředek, jakým zvíře dosáhne svého cíle. Jedná se o tyto strategie: integrace cesty, pilotování, sledování stopy, kompasová orientace, mapování, navigace. Informační zdroje již představují konkrétní orientační body, značky a signály, podle kterých se může zvíře orientovat.

3.1.2.1 Integrace cesty (Path integration)

Integrace cesty (Path integration neboli Dead reckoning) je proces, při kterém zvíře (ale i člověk) na základě informací o svém vlastním pohybu odhaduje směr a vzdálenost z výchozího bodu (integrace vlastního lineárního a úhlového pohybu), což může zpětně přispět k odhadu aktuální polohy zvířete a návratu do výchozího místa nejkratší možnou cestou. Zvíře aktualizuje svoji polohu na základě kumulativního odhadu směru a vzdálenosti, kterou urazilo (Etienne et al., 1996; Etienne & Jeffery, 2004; McNaughton et al., 2006; Poulter et al., 2018). Integrace cesty byla studována převážně v rámci homingu, po ukončení exploračního chování (Etienne & Jeffery, 2004). Nicméně během procesů spojených s integrací cesty se rychle hromadí chyby (Benhamou, 2014; Hartley et al., 2014), obzvláště v situacích, kdy nejsou k dispozici externí orientační body (Etienne et al., 1996). U psů bylo popsáno, že na vzdálenostech od 20 do 30 metrů se chyby v odhadu vzdálenosti pohybují mezi 3 až 8 % (průměr 6 %) a chyby v odhadu směru mezi 1 až 14 % (průměr 9 %) (Séguinot et al., 1998). Harootonian et al. (2020) uvádějí, že dobrovolníci měli tendenci přeceňovat úhel (směr pohybu) a podceňovat vzdálenost, přičemž s rostoucí vzdáleností docházelo k větší chybovosti s odchylkou rostoucí exponenciálně.

Bylo matematicky dokázáno, že integraci cesty lze použít pouze na krátkou vzdálenost a pokud chce zvíře cestovat dále, musí zapojit externí směrové reference (Cheung et al., 2008). Např. pouštní mravenec je schopen se vrátit zpět do hnízda ze vzdálenosti až 100 m. Pokud ovšem spočítáme délku kroku a směrovou chybu kolem 2° / krok, vyjde maximální možná vzdálenost 20 m, po kterou mravenec dokáže udržet přímý směr (Cheung et al., 2007). Integrace cesty, bez rekalibrace pomocí externích směrových odkazů (vizuální nebo olfaktorická vodítka či kompas, např. magnetický), je nepoužitelná na dlouhé vzdálenosti, neboť pohybová trajektorie by se začala přibližovat logaritmické spirále (Cheung et al., 2008).

3.1.2.2 Pilotování (Piloting)

Pilotování je založeno na vizuálních, akustických nebo olfaktorických vjemech (allothetické informace) (Whishaw et al., 2001). Jedná se o identifikaci polohy v prostoru s ohledem na vzdálenost a směr známých orientačních či referenční bodů (landmarks či beacons; termín *landmark* charakterizuje orientační bod, který leží poblíž cíle a neidentifikuje tak cíl přímo, zatímco *beacon* cíl identifikuje přímo (Shettleworth, 2010)) a o navigování směrem k těmto bodům (Gallistel, 1990). Při pilotování má navigace různé úrovně obtížnosti (Whishaw et al., 2001). V případě přímo viditelného/slyšitelného/cítitelného cíle se jedná o nejjednodušší formu navigace. Trochu složitější mechanismus zahrnuje navigaci k cíli, který není přímo viditelný, ale který se nachází v krátké vzdálenosti od orientačního bodu či bodů (např. ukrytý vchod do nory). Od zvířete to vyžaduje, mimo rozpoznání vlastního cíle, i rozpoznání blízkých orientačních bodů a zapamatování si prostorových vztahů mezi nimi a cílem (Tommasi et al., 2012). Při pilotování není zvíře závislé na informacích o svém vlastním pohybu (idiothetické informace) (Whishaw et al., 2001). Např. kaloni egyptští (*Rousettus aegyptiacus*) jsou schopni využít prostorové uspořádání vzdálených viditelných orientačních bodů (např. budovy) a pomocí triangulace určit směr požadovaného letu a pravděpodobně i vzdálenost k cíli (Harten et al., 2020). Fiset (2007) prokázal schopnost psů využívat informace o prostorových vztazích blízkých orientačních bodů. Při posunu bodů v jednom směru psi posunuli i své hledání. K posunu však nedošlo ve stejném rozsahu, v jakém byly posunuty body, což naznačuje využívání i jiných prostorových informací. To bylo potvrzeno i v navazujícím výzkumu, který potvrdil schopnost psů pracovat s průměrnými vzdálenostmi od jednotlivých orientačních bodů (Fiset, 2009).

Ačkoli je pravděpodobnější, že pro pilotování zvíře využije spíše allothetické informace, zatímco idiothetické informace použije spíše pro integraci cesty, zdroje informací mohou být komplementární a využity pro oba typy navigace (Whishaw et al., 2001).

3.1.2.3 Sledování stopy (Tracking)

Problematika sledování stopy (i své vlastní) v rámci homingu savců nebyla zatím příliš podrobně studována. Schopnost návratu po vlastní stopě je u loveckých psů všeobecně známa, ale systematické studie chybí. Většina vědeckých studií byla zaměřena spíše na sledování pachové stopy jiného subjektu, nejčastěji lidské pachové stopy.

Sledování stopy psy je založeno na jejich přirozené schopnosti sledovat pachovou stopu, kterou sledovaný subjekt zanechává (Miklósi, 2014). Bräuer & Blasi (2021) testovali, jakým způsobem psi sledují stopu svého majitele. Výsledky potvrdily schopnost psů rozpoznat individuální pach majitele. Pokud na konci stopy našli jinou osobu, projevovali rozrušení. Mezi psy se však vyskytovaly velké inter-individuální rozdíly v ochotě sledovat stopu, které nebyly závislé na olfaktorických zkušenostech. Navíc bylo zjištěno, že efektivita hledání souvisela s teplotou prostředí. Psi byli úspěšnější při nižších teplotách. Při sledování stopy je důležité správně určit její směr. Z 22 policejních psů sledovaných ve studii Wells & Hepper (2003) jich jen 36 % dokázalo identifikovat správný směr položené pachové stopy, úspěšnější byli psi-samci a mladší jedinci. Při sledování stopy bez ohledu na směr byli úspěšní všichni testovaní psi. Pro určení správného směru psi potřebovali v průměru 5 kroků, což odpovídá přibližně 2 sekundám (Hepper & Wells, 2005). Při řešení problému založeném na použití čichu se netrénovaní psi spoléhali spíše na vizuální informace než na dostupné čichové podněty (Polgár et al., 2015). Podobné chování bylo popsáno i u koček, kde při konfliktu vizuálních a olfaktorických informací většina koček preferovala vizuální informaci (Mayes et al., 2015).

3.1.2.4 Mapování (Mapping)

Dřívější laboratorní studie přinesly poznatky o tom, že zvířata jsou schopna si během pohybu v prostoru vytvářet mapy (nazvané kognitivní mapy), což jim umožňuje flexibilně využívat získané poznatky např. pro generování nových zkratek, pokud jsou známé cesty nedostupné (Tolman, 1948). Tolmanova teorie kognitivních map byla rozšířena a zdokonalena po objevu neurálních korelátů mapové reprezentace, konkrétně buněk místa (*place cell*) nalezených v hipokampu (O´Keefe & Nadel, 1978). Nejnovější definice popisují kognitivní mapu jako neurální model vnějšího světa, který představuje prostorové vztahy mezi vzdálenostmi a směry mezi místy. Umožňuje generování nových cest, jako jsou objížďky nebo zkratky, které nikdy předtím nebyly použity (Poulter et al., 2018). Použití zkratky, tj. navigování mezi známými body novou a přímější cestou, je považováno za důkaz použití mapy (O´Keefe & Nadel, 1978; Tolman, 1948). Mapové informace mohou být založeny na velkém množství dříve zjištěných orientačních bodů (vizuální, olfaktorické, sluchové, ale i magnetické). Nicméně to, které z nich nakonec zvíře použije, se může lišit jak mezi jednotlivými druhy, tak i dle dané situace a individualitě jedince (Frost & Mouritsen, 2006). Nicméně při pozorování divokých zvířat nelze spolehlivě určit, zda zvíře použilo zkratku na základě využití kognitivní mapy a nebo jiné navigační strategie, pokud neznáme historii jeho předchozího pohybu (Harten et al., 2020).

Peters & Mech (1975) a Peters (1978) popisují v rámci loveckého chování vlků používání zkratek a generování efektivnějších tras při návratech na konkrétní místa, která představují předpokládaný výskyt kořisti, místo ulovení nebo návrat zpět k doupěti. Použití zkratek bylo pomocí GPS technologie velmi dobře popsáno u netopýrů, kteří se při dlouhých letech za potravou byli schopni vracet novými a přímějšími trasami zcela neznámým prostředím. Autoři považují použití pilotování a integraci cesty za nepravděpodobné vzhledem k pohybu neznámým terénem na dlouhé vzdálenosti (Harten et al., 2020; Toledo et al., 2020; Tsoar et al., 2011).

Jedním ze zdrojů, který může poskytovat informace potřebné pro tvorbu kognitivních map, je i magnetické pole Země. Podle směru magnetických siločar lze získat referenční směr pro magnetický kompas, lokální síla magnetického pole a / nebo sklon siločar (inklinace) by mohly poskytnout informace o poloze pro využití v mapách (shrnuto v

Freake et al., 2006 a Frost & Mouritsen, 2006). Ačkoli je známo, že některá zvířata magnetické mapy používají, o jejich organizaci či případných omezeních se mnoho neví. K magnetické mapě je nutno přistupovat jako k jedné části integrované sady mechanismů zapojených do navigace, jejichž použití či nepoužití závisí na okolnostech a navigačních potřebách jednotlivce (Lohmann et al., 2007).

Psi se při značkování teritoria statisticky signifikantně zarovnávají podél severojižní magnetické osy v případě, že je magnetické pole Země klidné. Pokud by psi používali mapu k usnadnění orientace v prostoru, mohli by mít potřebu ji kalibrovat (centrovat) s ohledem na známé orientační body, ať už vizuální či magnetické. Zarovnání mapy by mohlo usnadňovat její čtení, nicméně kalibrace má smysl pouze tehdy, pokud jsou referenční body stabilní (Hart et al., 2013).

3.1.2.5 Kompasová orientace (Compass orientation)

Poté, co zvíře pomocí mapy určí svoji polohu vzhledem k vzdálenému cíli, potřebuje určit a následně udržet správný směr k tomuto cíli. K tomu může využít tzv. kompasovou orientaci neboli kompas (Frost & Mouritsen, 2006). Z hlediska prostorové orientace je termín kompas používán k označení jakéhokoliv mechanismu, který určuje absolutní geografický směr nezávisle na poloze (Guilford & Taylor, 2014). Jsou známy tři kompasové systémy – sluneční kompas, hvězdný kompas a magnetický kompas (shrnuto v Chernetsov, 2017). Bylo navrženo, že kompasové systémy jsou nezbytné pro každé zvíře pohybující se v komplexním prostředí, bez ohledu na prostorové měřítko (Finkelstein et al., 2016). Použití a funkce kompasových systémů byla zatím nejvíce studována u ptáků, hlavně u migrujících druhů (Wiltschko & Wiltschko, 2005).

Sluneční kompas může hrát klíčovou roli při určení směru u denních zvířat (např. Samson & Manser, 2016). Vzhledem k pohybu Slunce po obloze, i když se jedná o pohyb pravidelný a předvídatelný, disponují zvířata kompenzačními mechanismy zohledňujícími sluneční posun (shrnuto v Guilford & Taylor, 2014).

Naproti tomu *hvězdný kompas* je využíván spíše nočními migranty (např. Able & Able, 1990), i když informace ze slunečního kompasu může ovlivňovat i orientaci nočních zvířat (Cochran et al., 2004), stejně tak jako polarizované světlo (Greif et al., 2014;

Muheim et al., 2006). Podmínkou využití slunečního i hvězdného kompasu je nezatažená obloha (Chernetsov, 2017).

V současné době je nejvíce pozornosti věnováno *magnetickému kompasu* (Chernetsov, 2017), při jehož použití je směrová informace získávána s využitím magnetického pole Země (Wiltschko & Wiltschko, 2005). Ze savců je jeho použití nejpodrobněji popsáno u hlodavců v rámci tzv. „nest-building assay“ (určení směru pro stavbu hnízd). Zvířata preferovala stavbu hnízd podél severojižní magnetické osy, v případě experimentů v magnetických cívkách reagovala na posun magnetického pole posunem směru, ve kterém hnízda stavěla (např.: Burda et al., 1990; Malewski, Begall, & Burda, 2018; Malewski, Begall, Schleich, et al., 2018; Malkemper et al., 2015; Oliveriusová et al., 2014; Phillips et al., 2013).

Bylo navrženo, že magnetický kompas by mohl sloužit nejen jako zdroj směrových informací, ale i jako sférický souřadnicový systém propojující vzdálenost, směr a polohu v prostoru (Phillips et al., 2010). Například lišky pravděpodobně využívají magnetické pole Země jako zaměřovací systém při lovu kořisti a tím dosahují zvýšení své lovecké úspěšnosti (74 % úspěšných útoků byla vedeno v severovýchodním směru). V domovské oblasti lišek (jakožto nemigrujícího druhu) je sklon a intenzita magnetického pole Země v podstatě konstantní a sklon pole tak lze využít k odvození relativní vodorovné vzdálenosti (Červený et al., 2011). Detailněji je magnetorecepce psovitých šelem popsána v kapitole 3.1.3.5.

Nicméně stále není jasné, zda jsou tyto různé zdroje směrových informací používány společně a integrovány do výsledného vektoru, či zda převažuje ten nejdostupnější (Frost & Mouritsen, 2006). Rovněž zůstává otázkou, nakolik by magnetický kompas (jakožto vždy dostupný zdroj informací) mohl vstupovat i do ostatních navigačních mechanismů. Bylo např. prokázáno, že magnetické pole Země ovlivňuje směrovou složku integrace cesty u podzemních hlodavců v případě, kdy se zvíře pohybuje po relativně dlouhé a klikaté trase. S rostoucí vzdáleností se zvyšovalo i zapojení magnetického kompasu (Kimchi et al., 2004).

3.1.2.6 Navigace (Navigation)

Navigace, někdy se též používá výraz „pravá navigace“ (true navigation), je schopnost zvířat pohybovat se neznámým prostředím směrem k cíli (hnízdo, domovské území, zdroj potravy apod.) bez potřeby známých orientačních bodů. K tomu je potřeba mít mapu ukazující zvířeti jeho polohu vzhledem k cíli a dále kompas k nasměrování podél příslušného vektoru (shrnuto v Frost & Mouritsen, 2006; Gould & Gould, 2012; Wiltschko & Wiltschko, 2003). Těchto dvou kroků, které byly podrobněji popsány v předchozích dvou kapitolách, je dosaženo za pomoci podnětů z prostředí zvířete, které jsou detekovány prostřednictvím smyslů (Holland, 2018). Ačkoliv se předpokládá, že „pravou navigací“ disponuje mnoho druhů zvířat (obzvláště při pohybu na velké vzdálenosti), experimentálně byla prokázána pouze v několika málo případech. Potvrzení této schopnosti vyžaduje přemístění zvířete do neznámého prostředí bez přístupu k orientačním bodům během přesunu (tzv. „displacement experiment“). Pokud je zvíře schopno se po přesunu vrátit zpět domů, pravděpodobně můžeme uvažovat o schopnosti použít pravou navigaci (Thorup & Holland, 2009). Translokační experimenty byly prováděny převážně s ptáky (Åkesson, 2003), nejlépe je tato schopnost popsána u holubů (Wallraff, 1978; Wiltschko & Wiltschko, 1985).

Další evidence pochází od migrujících druhů (souhrn viz Thorup and Holland, 2009), z nemigrujících druhů savců např. od králíků (Lawes et al., 2012) a psů, se kterými bylo provedeno několik translokačních experimentů. První „pokusy“ se psy jsou známy z období před a během 1. světové války, kdy byli psi trénováni jako tzv. „messenger dogs“. Jejich úkolem bylo přenášet důležité zprávy skrz bojiště a i když se nejednalo o vědecké experimenty v pravém slova smyslu, lze v této souvislosti hovořit o pravé navigaci (Richardson, 1920). Nahm (2015) popisuje ve svém souhrnu další dvě méně známé práce zaměřené na navigační schopnosti psů: první systematické experimenty prováděné Bastienem Schmidtem ve 30. a 40. letech minulého století, který přemisťoval psy do 4–5 km vzdálených neznámých lokalit a sledoval pomocí terénních pozorovatelů způsob jejich návratu zpět domů. Schmidt poukazuje na zajímavou skutečnost, že psi během úspěšných návratů pravděpodobně nepoužívali k orientaci čich. Druhá práce, zaměřená na navigační schopnosti psů, probíhala mezi lety 1953 a 1962. Podobně jako Schmidt i Bernhard Müller přemisťoval psy na neznámá místa, ale pracoval s mnohem většími vzdálenostmi a větším množstvím psů. Experimenty prováděl za každého počasí, ve dne i v noci a popsal podobné chování psů jako Bastien Schmidt. Oba pak shodně konstatovali, že schopnost psů vrátit se po přemístění zpět domů nelze vysvětlit pouze použitím běžných smyslů.

Způsob, jakým zvířata dokáží určovat svoji polohu, není stále dostatečně objasněný. Jedním z důvodů je i množství informačních zdrojů a jejich vzájemné vztahy. Zůstává nejasné, jak jsou tyto zdroje zvířetem vzájemně kombinovány, upřednostňovány či potlačovány, obzvláště v situaci, kdy se zvíře nachází v pro ně neznámém prostředí (Holland, 2018). Zvířata mohou během navigování využívat allothetické informace, idiothetické informace, jejich kombinaci nebo mezi nimi flexibilně přepínat. Při plánování experimentů je nutno navrhnout takový design experimentu, který umožní používání informačních zdrojů cíleně kontrolovat (Whishaw et al., 2001). Navíc je potřeba vzít v úvahu další faktory ovlivňující orientační a navigační schopnosti – paměť, získané zkušenosti, vrozené vzorce chování nebo společenské vztahy (Fagan et al., 2013), protože např. Müller (1965) zmiňuje, že úspěšnost homingu u psů závisela na sociálním postavení, kdy dominantní jedinci měli téměř 100% návratovou úspěšnost, zatímco ze submisivních jedinců se nevrátil ani jeden (citováno v Nahm, 2015).

3.1.3 Smysly využívané při prostorové orientaci psů

Vnímání neboli percepce patří mezi základní mechanismy orientace. Je to soubor jevů působících v určitém okamžiku na smyslové orgány (receptory), které v následném kognitivním procesu organizují a interpretují informace z jednotlivých smyslů (Johnsen, 2017). Získané informace o prostředí ovlivňují pohyb zvířat, a naopak, pohyb zase ovlivňuje informace, které získávají o svém stanovišti (Spiegel & Crofoot, 2016). Jedná se o aktivní procesy kontrolované centrálním nervovým systémem (Miklósi, 2014). V této kapitole jsou popsány pouze smysly, které hrají roli při distanční prostorové orientaci psů – čich, sluch, zrak a magnetorecepce.

3.1.3.1 Čich

Psi jsou obecně považováni za makrosmatická zvířata (s vynikající čichovou schopností). Anatomická struktura nosní dutiny psa je přizpůsobena pro efektivní intranazální transport odorantu během čichání. Během aktivního čichání získává každá nozdra prostorově oddělené vzorky odorantu pro dvoustranné srovnání intenzity a lokalizace odorantu. Tato schopnost psa je v přímém kontrastu s nosním prouděním vzduchu u člověka (Craven et al., 2010). S ohledem na další morfologické rozdíly mezi člověkem a psem (u psa větší velikost a složitost olfaktorického epitelu, vyšší počet receptorů, větší velikost čichové oblasti v mozku) může dojít k podcenění významu čichových podnětů v okolí psa (Miklósi, 2014). Některé výsledky však naznačují, že navzdory schopnosti úspěšně řešit úkoly pomocí čichu, domestikovaní psi často upřednostňují před čichem jiné kognitivní strategie (Polgár et al., 2015).

Pro lidmi často zmiňovanou představu, že psi žijí ve „světě pachů“, existuje jen malé množství srovnávacích studií zaměřených na diskriminaci zdrojů pachů. Při výzkumech, ve kterých mohou hrát roli olfaktorické schopnosti psa, je rovněž nutné vzít v úvahu i zvolené plemeno psa. Jednotlivá plemena byla šlechtěna pro specifické využití a mohou se v čichových schopnostech diametrálně lišit. Rovněž je potřeba sledovat ostatní faktory, jako je např. individuální zkušenost, trénink nebo i vrozené vlastnosti (Miklósi, 2014). Samuel et al. (2020) testovali reakce psů na pach potenciálních predátorů (medvěd a rys). U psů docházelo při kontaktu s pachem predátora k fyziologickým změnám i ke změnám v chování. Nebyly však nalezeny rozdíly mezi zkušenými psy loveckých plemen a ostatními psy. Což naznačuje, že anti-predační chování by mohlo být u psů vrozené. Při volbě mezi čichovými zdroji informací a vizuálními zdroji se psi rozhodovali podle okolností (tzn. nespoléhali se striktně na čich). V případě rozporuplných podnětů využili i vizuální komunikační signály od člověka, pokud měli k dispozici pouze olfaktorické informace. Naopak, pokud měli k dispozici i vizuální informace, více spoléhali sami na sebe (Szetei et al., 2003). Podobně u koček, v případě konfliktu vizuální a olfaktorické informace, docházelo k preferenci vizuální informace. Rovněž byla pozorována velká individuální variabilita mezi jedinci (Mayes et al., 2015).

To vše dohromady může ovlivňovat přirozené chování během olfakce a částečně by mohlo pomoci pochopit rozdíly ve vnímání okolí prostřednictvím čichu mezi makrosmatickým psem a mikrosmatickým člověkem (Craven et al., 2010). Na druhou stranu jsou často podceňovány ostatní smysly psa, a naopak přeceňován význam čichu v kontextu celého smyslového vnímání (Miklósi, 2014).

3.1.3.2 Sluch

Dalším významným smyslem psa je sluch. Sluchový systém psovitých šelem se vyvinul, mimo jiné, k optimalizaci predačního chování – lokalizace zvuků vydávaných potenciální kořistí. To zahrnuje schopnost natáčet ušní boltec ve směru přicházejících zvuků a směrovat zvukové vlny do zvukovodu (Miklósi, 2014). Anatomie a fyziologie psího ucha byla velmi dobře popsána (Cole, 2009).

Frekvenční rozsah sluchu psa se od lidského liší jen částečně. Podobnost se ukazuje u nižších frekvencí, zatímco u vyšších frekvencí jsou rozdíly již výrazné. Frekvenční rozsah psa se pohybuje mezi 41 až 44000 Hz, zatímco u člověka mezi 31 až 17600 Hz. Rozdíly mezi jednotlivými plemeny nalezeny nebyly (Heffner, 1983). Sluch psa je velmi podobný sluchu lišky či kočky s tím rozdílem, že kočka má vyšší frekvenční rozsah (kolem 70000 Hz) (Malkemper et al., 2020).

Zdá se, že na sluchové schopnosti psů nemá vliv poměrně velká variabilita ve velikosti a tvaru ušních boltců různých plemen psů. Bylo potvrzeno, že pozice a tvar ušního boltce neovlivňuje schopnost vnímat vysokofrekvenční zvuky (Heffner, 1983). Liška, blízká příbuzná domácího psa, sdílí se psem anatomicky podobné struktury středního a vnitřního ucha a rovněž audiogramy obou druhů mají velmi podobný tvar. Naopak, sluch by mohly ovlivňovat některé vlastnosti sluchového systému, jako jsou specializace vláskových buněk či sluchové dráhy a nervová centra (Malkemper et al., 2020).

3.1.3.3 Zrak

Psa domácího lze považovat za zrakového generalistu schopného efektivně fungovat v širokém spektru světelných podmínek (Miller & Murphy, 1995). Hlavní funkcí zraku je kooperace při lovu a sociální interakce jak s člověkem, tak s ostatními příslušníky druhu (Miklósi, 2014). Psi disponují stereoskopickým viděním (frontální umístění očí), což jim umožňuje, stejně jako ostatním šelmám, prostorové (binokulární) vidění zlepšující odhad vzdálenosti (Miller & Murphy, 1995; Veselovský, 2008). Při výzkumu chování je nezbytné brát v potaz rozdílné zrakové vnímání psů v porovnání s člověkem (Miklósi, 2014; Pongrácz et al., 2017; Veselovský, 2008).

Znalosti o schopnosti psů rozlišovat barvy zůstávají i přes značný pokrok nekompletní. Psi mají odlišné barevné vidění než člověk: člověk vidí trichromaticky (disponuje třemi typy čípků), zatímco pes má vidění dichromatické (dva typy čípků). Měření pomocí elektroretinografie odhalilo citlivost čípků k vlnové délce 430 nm, resp. 555 nm. Z toho bylo odvozeno, že psi disponují tzv. „blue–yellow“ systémem a pravděpodobně vidí fialovou a modrofialovou barvu jako namodralou, zelenožlutou a červenožlutou jako nažloutlou a ostatní barvy ležící mezi těmito dvěma spektry vidí jako bílou nebo světle šedou. Bylo pozorováno, že psi mají problém odlišit zelenožlutou, žlutou, oranžovou a červenou barvu mezi sebou a zelenomodrou od šedé (Jacobs et al., 1993; Miller & Murphy, 1995; Neitz et al., 2001). Nicméně, některé výzkumy naznačují, že to nemusí být až tak jednoznačné, a že by psi mohli být schopni vidět více barev či dokonce rozlišovat červenou od zelené na základě jejich jasu (shrnuto v Byosiere et al., 2018). Například Byosiere et al. (2019) zjistili, že psi byli schopni rozlišovat mezi červenou a zelenou a mezi modrou a žlutou. V následných testech pracovali se třemi různými sytostmi barev a zde již výsledky nebyly tak jednoznačné. S rostoucím jasem se rozlišování barev stávalo pro psy obtížnější. Důvodem by mohlo být naladění vizuálního systému psa na tlumené světlo. Zdá se, že psi vykazují podobné barevné vidění jako barvoslepí lidé (lidská zeleno-červená slepota, tzv. daltonismus) (Siniscalchi et al., 2017).

Rozdíly mezi psem a člověkem lze najít i ve velikosti zorného pole. Psi, v závislosti na plemeni, mají zorné pole až o 70° širší než člověk. Mají však menší rozsah binokulárního vidění, dle plemene 30° až 60° oproti zhruba 140° u člověka (shrnuto v Byosiere et al., 2018; Miller & Murphy, 1995).

Psí vizuální systém je adaptován na zhoršené světelné podmínky, přesto funguje dobře i za denního světla. Psi mají sice větší podíl tyčinek (fotoreceptory citlivé na světlo) než člověk, ale fotopigment rhodopsin reaguje nejlépe na světlo vlnové délky mezi 506 a 510 nm, což je hodnota velmi podobná člověku (496 nm). Za výrazně lepší schopností psa vidět za tlumeného světla je zodpovědná struktura zvaná „tapetum lucidum“, kterou člověk nedisponuje (Byosiere et al., 2018; Miller & Murphy, 1995). Tapetum lucidum je vrstva mezi sítnicí a cévnatkou umožňující odrážení světla. Tato vrstva se vyskytuje u většiny nočních a soumračných savců. Umožňuje zpětný odraz světla zpět ke světločivným buňkám, čímž je dosaženo zlepšené viditelnosti při minimálním množství světla. Zároveň způsobuje známé „světélkování“ očí ve tmě (Jacobs et al., 1993; Yamaue et al., 2015).

Z dalších rozdílů je třeba zmínit vyšší citlivost psa při vnímání pohybu (pravděpodobně vidí „rychleji“ než člověk) (Byosiere et al., 2018). Naopak mají oproti člověku horší schopnost rozpoznávat detaily (Lind et al., 2017), nejsou schopni zaostřit na velmi blízké objekty (Miller & Murphy, 1995), rozlišování jasu je u psů asi 2x horší než u člověka (hůře rozpoznávají odstíny šedé) (Pretterer et al., 2004).

3.1.3.4 Magnetorecepce

V posledních pěti dekádách probíhá ve vědeckých kruzích diskuze o existenci dalšího smyslu, smyslu pro vnímání magnetického pole Země, tzv. magnetorecepce. V porovnání s ptáky byla magnetorecepce savců velmi málo studována. Typy experimentů použitých při studiu magnetorecepce u savců zahrnují zejména směrový test stavby hnízd, magnetický alignment, pokusy v bludištích, testy výběru směru, (telemetrické) sledování homingu (Burda et al., 2020).

Zemské magnetické pole může poskytovat jak směrové informace (magnetický kompas) (Able & Able, 1990; Wiltschko & Wiltschko, 2005), tak i poziční informace (magnetická mapa) (Freake et al., 2006; Lohmann et al., 2007). Bylo prokázáno, že celá škála živočišných druhů má schopnost tyto informace využívat pro prostorovou orientaci a navigaci (shrnuto např. v Begall et al., 2014; Weir, 2020; Wiltschko & Wiltschko, 1995; Wiltschko & Wiltschko, 2005) a magnetorecepce tak představuje důležitou součást celého komplexu smyslového vnímání (Johnsen & Lohmann, 2008).

V souvislosti se suchozemskými savci jsou zmiňovány dva možné mechanismy magnetorecepce – teorie radikálových párů a magnetitová teorie (shrnuto v Begall et al., 2014; Burda et al., 2020; Kobylkov, 2020).

Hlavním principem teorie radikálových párů je existence molekuly citlivé na světlo, která změní svůj oxidační stav na základě absorpce světla. Dochází k reakci, při které jedna molekula předává elektron druhé molekule a tvoří s ní radikálový pár (Ritz et al., 2010). Předpokládá se, že retinální protein kryptochrom (Cry1a), absorbující modré světlo, je zapojen do biochemické reakce, která vede k tvorbě radikálových párů citlivých na magnetické podněty u ptáků (Hore & Mouritsen, 2016). Nießner et al. (2016) hledali shodný typ kryptochromu (nazvaný Cry1) u 90 druhů savců. Ačkoli mezi zkoumanými savci byl Cry1 detekován pouze u několika druhů, přesto byl konzistentně přítomen u psovitých šelem, tj. u čeledi, kde byla reakce na magnetické pole opakovaně prokázána (Červený et al., 2011; Hart et al., 2013; Martini et al., 2018; Yosef et al., 2020). Stále však není známo, jaký druh mechanismu je např. u psů základem jejich reakcí na magnetické pole Země (Nießner et al., 2016). Zda mají smysl pro magnetický kompas a / nebo magnetickou mapu, a jaké je zapojení magnetorecepčního smyslu do procesů spojených s orientací v prostoru.

Ještě složitější situace je spojena s magnetitovou teorií. Předpokládá se zapojení feromagnetických částic tvořících v buňkách řetízky, fungující jako střelka kompasu. Magnetický „signál“ by pak mohl být přenášen např. otevíráním a zavíráním mechanicky citlivých iontových kanálů (Němec & Vácha, 2007). Nicméně, homeostáza železa je nezbytná pro správnou funkci organismu a oxidy železa lze najít v mnoha tkáních. Ačkoli existuje nespočet behaviorálních důkazů o magnetorecepčním mechanismu založeném na magnetitových částicích, identifikace magnetoreceptorové buňky je kvůli všudypřítomným strukturám obsahující železo velmi komplikovaná (shrnuto v Burda et al., 2020; Kobylkov, 2020; Mouritsen, 2018). V nedávné době byla navržena hypotéza, že by symbiotické magnetotaktické bakterie mohly pro hostitele zprostředkovávat vnímání geomagnetického pole. Jako potenciální místo, kde by bakterie mohly sídlit, byly navrženy slzné žlázy (Natan & Vortman, 2017). Tato hypotéza je zatím přijímána poměrně kontroverzně, neexistuje pro ni přesvědčivá podpora (Natan et al., 2020).

Nutno dodat, že je zmiňován ještě jeden mechanismus magnetorecepce, a to elektromagnetická indukce (Mouritsen, 2018). Elektromagnetická indukce nebyla považována za relevantní u suchozemských živočichů, protože pro tento způsob vnímání je zapotřebí přítomnost média s vysokou vodivostí a tuto podmínku splňuje pouze slaná mořská voda (Johnsen & Lohmann, 2008). Ritz et al. (2010) dále uvádějí, že jsou zapotřebí i konkrétní elektro-sensitivní struktury, tzv. Lorenziniho ampule, které nebyly nalezeny u suchozemských živočichů. Vzhledem k fyzikálním faktorům elektromagnetické indukce a potřebné citlivosti elektroreceptorů se o tomto mechanismu magnetorecepce uvažovalo pouze u velkých a rychlých mořských zvířat (Němec & Vácha, 2007). V roce 2019 však byla představena práce, poukazující na možné zapojení elektromagnetické indukce pro detekci magnetického pole u domácích holubů. Magnetické podněty vedly k neurální aktivitě ve vestibulárním aparátu vnitřního ucha holubů, kde byl rovněž identifikován molekulární aparát potřebný pro detekci elektrického pole. Sami autoři nicméně uvádějí, že pro prezentované výsledky existuje i alternativní vysvětlení popírající navrženou teorii a že další experimenty jsou nezbytné (Nimpf et al., 2019).

Živočichové (obratlovci, ale i bezobratlí) využívají informace získané z magnetického pole Země nejenom k orientaci na delší vzdálenosti během migrace, ale i pro prostorovou orientaci v menším měřítku v rámci homingu a pátracího chování (Burda et al., 2020). Jedním z projevů magnetorecepce, který byl popsán mnoha laboratorními i terénními studiemi, je spontánní poziční chování neboli „magnetic alignment“. Magnetický alignment představuje zarovnání osy těla ve směru magnetických siločar v případě, že na zvíře nepůsobí žádné jiné důležitější faktory (Begall et al., 2013). Magnetický alignment byl popsán v rozličných kontextech chování: při pastvě nebo odpočinku skotu, srnčí a jelení zvěře nebo divokých prasat (Begall et al., 2008, 2011; Červený et al., 2017; Slaby et al., 2013), při lovu drobné kořisti u lišek (Červený et al., 2011), při útěkových reakcích srnčí zvěře (Obleser et al., 2016), při stavbě hnízd hlodavců (Burda et al., 1990), jako indikátor směru hrabání tunelů u podzemních hlodavců (Malewski, Begall, Schleich, et al., 2018). V roce 2013 byl magnetický smysl poprvé prokázán i u domácích psů (Hart et al., 2013), což bylo následně potvrzeno dvěma dalšími studiemi (Martini et al., 2018; Yosef et al., 2020).

Ačkoli je adaptivní význam magnetického alignmentu vzhledem k jeho mnohostrannosti stále nejasný, Burda et al. (2020) diskutují možnost, že by mohl poskytovat globální referenční rámec („zakotvení“) mapovým neuronům v případech, kdy nemají k dispozici jiná allothetická (např. vizuální) vodítka.

3.1.3.5 *Magnetorecepce psovitých šelem se zaměřením na psa domácího*

Ačkoli jsou psovité šelmy poměrně hojně studovány, z hlediska výzkumu magnetorecepce stále stojí poněkud stranou. Důvodů je více, pozornost byla zaměřována převážně na laboratorní zvířata (Jacobs & Menzel, 2014) a dále na migrující druhy (shrnuto v Wiltschko & Wiltschko, 1995; Wiltschko & Wiltschko, 2005). Nicméně se ukazuje, že magnetorecepce může být zapojena také v kontextu každodenního života i u nemigrujících druhů (Burda et al., 2020). Další komplikací při studiu magnetorecepce u divokých druhů psovitých šelem může být i skutečnost, že většina žije skrytým životem, jejich pozorování ve volné přírodě je obtížné a „přenos“ experimentů do laboratoře velmi komplikovaný, ne-li nemožný, z důvodu jejich velikosti a mnohdy nesnadné manipulovatelnosti. Navíc „vytržení“ zvířat z jejich přirozeného prostředí může zcela změnit jejich chování (Jacobs & Menzel, 2014; Thorup & Holland, 2009). Existuje však zástupce psovitých šelem, který je nejen dobře chovatelný a manipulovatelný, ale i běžně dostupný, ochotný spolupracovat a zvyklý na životní prostředí člověka. Tím zástupcem je pes domácí (*Canis familiaris*) (Miklósi, 2014; Serpel, 2017). Cooper et al. (2003) zmiňuje tři hlavní důvody, proč lze psa domácího považovat za vhodný behaviorální model: (1) má společného předka s vlkem obecným (*Canis lupus*), sociálními zvířaty, které charakterizují rozvinuté kognitivní schopnosti a kooperativní chování; (2) během domestikace byli pravděpodobně upřednostňováni jedinci s dobrou schopností plnit roli v lidské společnosti (ochrana, lov apod.); (3) domácí psi žijí v lidském světě, velmi dobře vnímají a rozumí lidským gestům a postojům, ale stále si zachovávají své mentální dovednosti společné s divokými předky.

Mezi mnoha plemeny psů existuje navíc jedna skupina, která byla po generace chována a šlechtěna k nalezení a sledování stopy zvěře. Tito lovečtí psi ze skupiny honičů (a ostatní lovečtí psi pracující jako honiči) jsou schopni pracovat samostatně na velké vzdálenosti od majitelů (stovky až tisíce metrů) a po ukončení práce se spontánně vracet zpět k čekajícímu majiteli, aniž by museli být přivoláváni či jinak aktivně naváděni k cíli. Otázkou však stále zůstává, jak tito psi určují polohu místa, kam se musí vrátit, tj. polohu čekajícího majitele. Lovečtí psi by tudíž mohli představovat vhodný behaviorální model pro translokační experimenty.

To vše, v kombinaci s novými metodami studia volně žijících či volně se pohybujících zvířat, podporované rychlým technickým rozvojem směřujícím hlavně k miniaturizaci (Moll et al., 2007; dále viz kap. 3.2), umožňuje zaměřit se i na dříve obtížně proveditelný výzkum (Davidson et al., 2020; Gerencsér et al., 2013; Kays et al., 2015; Lush et al., 2016; Painter et al., 2016).

První, velmi nepřímé zmínky o možném využití magnetického pole Země psy pocházejí již z minulého století. Jedna z doby před sto lety, kdy byli psi používáni jako kurýři (Richardson, 1920). Nahm (2015) pak cituje dvě neznámé práce z druhé poloviny minulého století, které byly zaměřeny na homing psů ve spojení s jejich pasivním přemístěním (detaily viz kap. 3.1.2.6). Ve všech případech psi prokázali mimořádné homingové schopnosti, navíc všichni tři původní autoři poukazují na skutečnost, že vzhledem k okolnostem (neznámý terén, tma, mlha, déšť, velké vzdálenosti) nelze tyto schopnosti vysvětlit jen použitím běžných smyslů (zrak, čich, sluch) a zmiňují termíny jako „*Homing instinct*“ (Richardson, 1920), „*Absolute sense of orientation*“ (Schmidt, 1932 citováno v Nahm, 2015) nebo „*Polarized sense of direction*“ (Müller, 1965 citováno v Nahm, 2015). I když autoři nezmiňovali doslovně magnetorecepci, která v té době nebyla známá, resp. její výzkum byl v počátcích, mohla by se teoreticky za tímto „neznámým smyslem“ ukrývat.

Výzkum magnetorecepce se na psy domácí zaměřil poprvé v roce 2013. Psi byli sledováni během jejich každodenního rutinního chování, značkování teritoria. Byl potvrzen magnetický alignment, statisticky významná axiální preference pro zarovnání osy těla podél severojižní magnetické osy, ale pouze v případě klidného magnetického pole (0% relativní změna v deklinaci). S rostoucími změnami deklinace se zarovnání stávalo více náhodné a při změně větší než 2 % již bylo zcela náhodné. Na směrovou preferenci neměla vliv denní doba, roční období, poloha slunce ani pohlaví jedince (zanedbatelná odchylka byla způsobena rozdílným chováním psů a fen během urinace). Navíc výsledky naznačily, že psi nejenže preferovali zarovnání podél severojižní osy, ale zároveň se vyhýbali zarovnání podél východozápadní osy. Skutečnost, že změny magnetických podmínek vedou ke změně chování, by se dala vysvětlit buď rušením, či dokonce přímo „vypnutím“ magnetického smyslu (Hart et al., 2013).

O dva roky dříve, v roce 2011, byl magnetický alignment potvrzen u jiné psovité šelmy, u lišky obecné (*Vulpes vulpes*) v kontextu predačního chování. Liška lokalizuje svou kořist (obvykle malé hlodavce) akusticky a po pomalém přiblížení provede vysoký skok a zaútočí shora. Toto chování je známé pod pojmem „myškování“. Sledováním bylo zjištěno, že směr skoků není náhodný, lišky preferují skoky vedené v severovýchodním směru. Navíc, pokud se jednalo o skoky ve vysokém krytu (vysoká vegetace či sněhová pokrývka), byl lovecký úspěch výrazně vyšší pro skoky vedené v severním či jižním směru (72,5 % resp. 60 %) oproti skokům v jiných směrech (méně než 18 %). Zdá se, že chování spojené s myškováním lze považovat za další projev magnetického alignmentu (Červený et al., 2011). Walton et al. (2018) sledovali chování lišek během jejich disperze na velké vzdálenosti (kumulativní vzdálenost 132 až 1036 km). Zajímavé bylo, že většina lišek se pohybovala v severním až severozápadním směru. Dvě lišky navíc prokázaly mimořádné homingové schopnosti při návratu do míst, které navštívily již dříve a kde se nakonec usadily. Návratové trasy měřily 114 km a 256 km, přičemž se lišky vracely zcela jinou trasou, než po které přišly.

Pět let po prvním důkazu o přítomnosti magnetorecepce u psů byly publikovány výsledky pokusu zaměřeného přímo na magnetický smysl psa – hledání magnetu. Pomocí operantního podmiňování byli psi trénováni na hledání ukrytého magnetu za kontrolovaných podmínek. Úspěšnost byla průměrně 61 % (53 % až 73 %), což vysoce překračovalo 33,3% hranici náhody. Pohlaví psů, věk ani velikost těla neměly vliv. V kontrolním testu s potravou se úspěšnost pohybovala kolem 33 % a nebyla tak signifikantně odlišná od náhody. Psi byli schopni najít magnet, ale ne potravu, což vyloučilo použití čichu. Možné ovlivnění ze strany experimentátora bylo vyloučeno, studie byla dvojitě zaslepena (Martini et al., 2018).

Poslední výzkum zaměřený na magnetorecepci psů se zabýval vlivem tyčového magnetu na směrovou preferenci psů. Na třech lokalitách v Izraeli byla sledována směrová preference psů během exkrece. Podobně jako ve studii Hart et al. (2013), i izraelští psi vykazovali zarovnání podél severojižní magnetické osy v případě, že magnetické pole Země nebylo rušeno. Pokud však bylo magnetické pole rušeno tyčovým magnetem zahrabaným v zemi, docházelo k výraznému narušení pozičního chování psů (Yosef et al., 2020).

Všechny tyto výsledky (včetně potvrzené existence kryptochromu Cry1 v sítnici oka psa (Nießner et al., 2016)) naznačují, že psa domácího lze přidat na seznam druhů, u kterých byla potvrzena spontánní nebo naučená reakce na magnetické pole (Martini et al., 2018). Nicméně, finální důkaz lze získat buď experimentální manipulací s magnetickým polem, resp. ovlivněním předpokládaného mechanismu magnetorecepce (Burda et al., 2020), nebo použitím translokačních experimentů (Thorup & Holland, 2009) se zaměřením na detailní sledování a analýzu chování během návratové fáze.

3.2 Prostorová orientace a moderní technologie

3.2.1 Možnosti sledování zvířat

Plné porozumění navigačním schopnostem zvířat a celkovému chování v jejich přirozeném prostředí vyžaduje detailní informace o jejich smyslovém vnímání a kognitivních schopnostech (Kays et al., 2015). Zatímco průkopníci etologie zabývající se sledováním volně žijících zvířat se museli spokojit pouze s přímým pozorováním (např. Schmid 1932, 1936; Müller 1965 citováno v Nahm, 2015), současná věda se může spolehnout na nové technologie (telemetrie, GPS, bio-loggery) umožňující získat mnohem relevantnější a detailnější informace (Batsleer et al., 2020; Davidson et al., 2020; Gerencsér et al., 2013; Kays et al., 2015; Lush et al., 2016; Painter et al., 2016; Pašukonis et al., 2018; Walton et al., 2018; Yoda, 2019). Nicméně i přes značný technologický pokrok mají i tyto systémy své limity. Například stacionární foto a videopasti mohou zachytit chování zvířat pouze tehdy, pokud je zvíře v jejich dosahu (Kovács et al., 2017); použití dronů může zvířata vyrušovat nebo je nemožné kvůli husté vegetaci; použití telemetrie, GPS obojků nebo bio-loggerů nemusí poskytnout detailní informace o konkrétním chování, pokud je zvíře mimo dosah pozorovatele (shrnuto v Davidson et al., 2020; Yoda, 2019). Tyto nevýhody částečně odstraňuje použití videokamer umístěných přímo na sledovaném zvířeti (Andersen et al., 2020; Moll et al., 2007; Rutz et al., 2007). U volně žijících zvířat je použití limitováno krátkou výdrží baterií, paměťových médií a potížím spojeným s opětovným chycením zvířete za účelem sundání kamery. Na druhé straně, použití tohoto systému na krotkém zvířeti a zejména na domácích zvířatech, která mají možnost se volně pohybovat (kočky, psi, skot apod.), přináší nové příležitosti ve výzkumu behaviorální a senzorické ekologie (Bombara et al., 2017; Coughlin & van Heezik, 2014; Huck & Watson, 2019; Seymour et al., 2020). Jako ideální se jeví kombinace více systémů dohromady (Rosa, 2019).

3.2.2 Možnosti zpracování velkoobjemových dat

Etologický výzkum vyžaduje hodiny a hodiny pozorování zvířat a následné zpracování pozorovaných dat. Moderní technologie zkrátily čas potřebný k pozorování zvířat, na druhou stranu obrovské soubory pozičních dat a dlouhé audio-video záznamy mnohonásobně prodloužily čas potřebný pro zpracování a vyhodnocení dat (viz předchozí kapitola 3.2.1). Ruční vyhodnocení takových dat zabere neúměrné množství času a v mnoha případech je v podstatě nereálné. Vznikla tak poptávka po možnosti automatizovaného vyhodnocení velkoobjemových dat. V současné době je možnost zpracovávat data jak komerčními programy (Juszczak & Miller, 2016; Napolitano et al., 2015; Young et al., 2019), tak i volně dostupným softwarem (Rutz et al., 2007). Pokud charakter dat neumožňuje použití ani jednoho z výše uvedených systémů, je možno použít na zakázku připravený software (Christiansen et al., 2014; Dielenberg et al., 2006; Geldenhuys et al., 2015; Inayat et al., 2020; Ramazani et al., 2007; Samson et al., 2015; Zhang et al., 2020). Některé z těchto programů jsou poskytnuty široké vědecké obci k volnému použití a případným dalším úpravám, aby se daly programy přizpůsobit charakteru konkrétních zpracovávaných dat (např. Samson et al., 2015; Zhang et al., 2020).

4 Metodika

Podrobné metodické postupy vedoucí k naplnění cílů této disertační práce jsou popsány v jednotlivých publikacích. V této kapitole jsou shrnuty pouze základní informace a postupy rozdělené podle hlavních cílů disertační práce.

4.1 Prostorová orientace loveckých psů v terénu

4.1.1 Charakteristika sledovaných psů

Bylo využito vrozených vlastností určitých skupin plemen loveckých psů, konkrétně skupiny honičů a dále loveckých psů schopných pracovat jako honiči – převážně jezevčíci a teriéři. Tato plemena disponují vrozenou schopností aktivně pátrat po zvěři, hlasitě sledovat její stopu a po ukončení práce se spontánně vracet zpět k majiteli, aniž by museli být přivoláváni. Během této činnosti se mohou vzdálit od majitele i několik kilometrů. Všichni sledovaní jedinci náleželi k čistokrevným plemenům s průkazem původu, byli ve výborném zdravotním stavu.

Vybírána byla převážně malá a střední plemena psů, která nejsou schopna dohnat mnohem větší a rychlejší zvěř. Byla tak zajištěna vysoká míra bezpečnosti jak pro psa, tak i pro zvěř.

Vrozené schopnosti loveckých psů oznamovat štěkotem zvěř bylo využito rovněž v experimentu zaměřeném na rozdíly ve vokalizaci podle druhu sledované zvěře.

4.1.2 Sledovací zařízení

Psi byli vybaveni GPS obojky Garmin T5 mini, T5, resp. DC50 (starší typ používaný během sběru dat pro diplomovou práci) (Garmin Ltd., USA), které byly nastaveny na interval ukládání GPS polohy každé 2 sec. Majitel psa byl vybaven přijímačem Alpha 100, resp. Astro 320, který trasu psa zaznamenával a na displeji zobrazoval jeho aktuální polohu. V případě hrozícího nebezpečí (pokud se pes ztratil, dostal do blízkosti komunikací apod.) tak bylo možno včas zasáhnout, pokus přerušit a psa vyzvednout.

Část sledovaných psů byla v pozdější fázi sběru dat vybavena i kamerou Garmin Virb Elite (Garmin Ltd., USA) umístěnou v nemagnetickém nerezovém ochranném pouzdře. Pouzdro bylo přichyceno na vestu, kterou měl pes na sobě. Kamera byla umístěna tak, aby zachycovala podobný obraz, jaký vidí pes. Poskytovala tak informace o prostředí, kterým se pes pohyboval, příp. i o zvěři, kterou pes našel a sledoval. Navíc částečně zabírala i hlavu psa. Bylo tak možno sledovat jeho chování a pohybovou aktivitu. Vestavěný mikrofon zaznamenával, mimo jiné, i příp. akustické projevy psa. Konkrétně hlášení na stopě zvěře, které indikuje vizuální kontakt psa s kořistí.

Vesta byla vyrobena pro každého psa na míru, aby byla zajištěna plná mobilita.

4.1.3 Sběr dat

Sběr dat probíhal výhradně v lesních honitbách. Chodilo se s každým psem individuálně v různých denních dobách i ročních obdobích, v pro psa známém i neznámém terénu. Po příjezdu na danou lokalitu, nasazení GPS obojku a příp. kamery, se pes vypustil na volno a s majitelem procházel lesem. Majitel neovlivňoval psa žádnými povely a nechal ho volně pátrat po stopách zvěře, což je vrozené chování pro plemena psů použitých v této práci. V okamžiku, kdy pes našel stopu a vyrazil za zvěří, majitel zastavil, uložil GPS polohu (místo začátku útěku) a v úkrytu vyčkával na návrat psa. Ukrytí majitele minimalizovalo možnost vizuálního pilotování v poslední fázi návratu. Během samostatné práce psa, tj. v době, kdy byl pes mimo dosah majitele, nebyl pes nijak ovlivňován povely a majitel setrvával v naprostém tichu, aby ho vracející se pes nemohl lokalizovat ani sluchem. Po návratu byl pes krátce pochválen a dál pokračoval s majitelem v procházení lesa a v pátrání po dalších stopách. Aby se předešlo ovlivnění délky útěku případnou únavou psa, trvala každá „procházka“ maximálně 90 minut (obvykle kolem 60 min.). Pokud pes utekl na několika desítek minut a vrátil se evidentně unavený, byl pokus ukončen. V místě začátku útěku majitel zaznamenal teplotu, směr a rychlost větru, druh sledované zvěře (pokud byla identifikace možná), zda pes na stopě zvěře hlásil, příp. další okolnosti, které mohly mít vliv na chování psa.

4.1.4 Zpracování dat

Termínem „útěk“ či „trasa útěku“ je definována ta část trasy psa, ve které se pes vzdálil od majitele, pracoval samostatně mimo jeho dosah a zase se k majiteli vrátil. Začíná v místě začátku útěku psa (GPS pozice uložená majitelem v lese = start útěku) a končí okamžikem, kdy se pes dostal do opětovného kontaktu s ukrytým majitelem (= cíl útěku).

Všechny zaznamenané trasy (tj. trasa psa včetně všech útěků i trasa majitele) byly zpracovány programem Garmin BaseCamp 4.6.2 (Garmin Ltd., USA). Program umožňuje trasy editovat, dále obsahuje pomůcky pro měření vzdáleností, směrů a rychlostí. Z celé trasy psa byly jednotlivé útěky vystřiženy a dále s nimi bylo pracováno jako se samostatnými soubory. V několika málo případech se pes k majiteli nevrátil, tyto útěky byly z dalších analýz vyřazeny.

Trasa útěku byla rozdělena na tři části: 1) odchozí trajektorie – část mezi startem útěku a místem, kde pes ukončil sledování stopy a rozhodl se pro návrat; 2) otáčecí trajektorie – část trasy útěku, ve které se pes rozhodl pro návrat, zahrnuje i tzv. „bod návratu“, což je přesné určení GPS pozice, ve které se pes začal vracet; 3) příchozí trajektorie – část trasy útěku, kdy se pes vracel k majiteli.

Bylo předpokládáno, že otáčecí trajektorie (a speciálně bod návratu) bude charakterizována výrazným poklesem rychlosti, či přímo zastavením, sloužícím k zorientování psa. Proto byla celá trasa útěku rozdělena na 10 stejně dlouhých úseků, pro každý úsek byla spočítána průměrná rychlost a úsek s nejnižší průměrnou rychlostí byl považován za otáčecí trajektorii. Pokud se umístění tohoto úseku zdálo nepravděpodobné (např. příliš blízko ke startu/cíli, dlouhotrvající se pohybování na jednom místě apod.), byla situace zkontrolována na videu (pokud bylo k dispozici) k vyloučení možnosti, že zpomalení či zastavení bylo způsobeno např. pitím či koupáním v kaluži, čucháním nebo překonáváním obtížného terénu. Pokud to tak bylo nebo nebylo k dispozici video, byl jako otáčecí trajektorie určen druhý nejpomalejší úsek (<5 % ze všech případů). V případě, že i druhý nejpomalejší úsek byl nepravděpodobný, byl za otáčecí trajektorii považován úsek, který se vzdušnou čarou nacházel v nejvzdálenější části trasy útěku (z hlediska polohy majitele) (8,5 %). V rámci otáčecí trajektorie byl následně určen bod návratu, který je charakterizován nejpomalejší rychlostí. Bod návratu představuje konkrétní místo, kde pes zahájil svůj návrat k majiteli.

4.1.5 Identifikace azimutů

Pro vyhodnocení směrových preferencí psů byly měřeny magnetické azimuty v definovaných částech trasy útěku: 1) azimut začátku útěku – průměrný směr, kterým se pes pohyboval v prvních 5 sec. útěku neboli směr, kterým pes vybíhal od majitele; 2) azimut k majiteli – směr mezi bodem návratu a startem/cílem útěku, tj. směr, kterým se nacházel ukrytý majitel v okamžiku, kdy se pes rozhodl pro návrat; 3) azimut iniciační fáze návratu – směr, kterým pes vybíhal z bodu návratu. Byl měřen jako azimut mezi bodem návratu a bodem, ve kterém došlo k výrazné změně směru jeho pohybu.

4.1.6 Statistická analýza dat

Kruhové statistické analýzy byly vyhodnoceny programem Oriana 4.02 (Kovach Computing Services). Na základě předběžných výsledků z diplomové práce a podle charakteru směrových dat bylo použito buď angulární vyhodnocení nebo axiální (v případě silné bimodální distribuce dat).

Pro ostatní statistické analýzy byl použit program SAS 9.4 (SAS Institute Inc., USA) a zobecněné lineární smíšené modely (GLMM, PROC MIXED a GLIMMIX).

4.2 Vliv magnetického pole na poziční chování psů

Do experimentů byli zapojeni psi různých plemen a jejich kříženců, různého věku, pohlaví a velikosti, ve vlastnictví zaměstnanců a studentů České zemědělské univerzity a Univerzity Duisburg-Essen v Německu a dále od spolupracujících dobrovolníků. Psi se během experimentů pohybovali na volno, tj. nebyli připnuti na vodítku. Byla sledována jejich směrová preference při běžných činnostech – značkování teritoria a výběru mezi dvěma miskami s potravou.

4.2.1 Metodika terénních experimentů

4.2.1.1 Sběr dat

Sběr dat probíhal na volném prostoru (louky, pole, řídký les) na různých místech v České republice a v Německu, v různou denní a roční dobu. Na lokalitách sběru dat se nevyskytovaly žádné lineární struktury (zdi, ploty apod.), silnice, cesty, budovy, vedení vysoké napětí a lokality byly daleko od nápadných ocelových konstrukcí a výrazných orientačních bodů.

Zarovnání osy těla v linii hrudní páteře ve směru k hlavě bylo měřeno ručním kompasem. Bylo zaznamenáváno plemeno psa, pohlaví, věk, velikost, kondice (včetně příp. zdravotních problémů), datum, čas, lokalita a další okolnosti, které by mohly mít vliv na chování psů.

Pro experiment zaměřený na směrovou preferenci při značkování teritoria byly sbírány záznamy o zarovnání osy těla během urinace a defekace. Majitel se psem se volně pohybovali v dané lokalitě a jakmile pes začal značkovat, byl změřen směr osy těla a v případě psů-samců navíc zaznamenáno, kterou končetinu při urinaci zvedl.

Ve dvouvýběrovém testu směrové preference si pes volil mezi dvěma miskami s potravou umístěnými napravo a nalevo od psa, vždy ve dvou sousedních magnetických směrech (kombinace misek na sever vs. východ, východ vs. jih, jih vs. západ, západ vs. sever). Misky byly umístěny ve vzdálenosti 2–6 m od psa (dle velikosti psa) v úhlu 45° od místa vypouštění psa, tj. misky svíraly úhel 90°. Bylo zaznamenáváno, kterou misku si pes vybral jako první a dále přesný směr, ve kterém k misce přišel. Obě misky obsahovaly stejný druh a množství potravy. Před zahájením testu byl pes s touto skutečností seznámen, stejně jako s průběhem celého experimentu. Seznámení probíhalo tak, že se obě misky umístily cca 1 m před psa, v úhlu menším než 60°. Pes mohl potravu sežrat vždy v obou miskách. Postupně byly misky od psa oddalovány a byl zvětšován úhel mezi nimi až do dosažení konečného umístění misek. V této fázi seznamování byly misky z hlediska magnetických směrů umisťovány zcela náhodně.

4.2.1.2 Zpracování a vyhodnocení dat

Data pro experiment zaměřený na značkování teritoria byla rozdělena podle geomagnetických podmínek převládajících v době sběru dat. Hodnoty o stavu magnetického pole byly získávány z Geomagnetické observatoře Fürstenfeldbruck.

Ze zaznamenaných voleb misek při dvouvýběrovém testu byla spočítána preference pro levou nebo pravou stranu pro všechny testované kombinace a z toho následně spočítán index laterality pro každého testovaného psa.

Pomocí cirkulární statistiky v programu Oriana 4.02 (Kovach Computing Services) byly vypočteny směrové preference jednotlivých psů a průměrné vektory s ohledem na plemeno, velikost těla, pohlaví, věk a lateralitu.

4.2.2 Metodika experimentu v magnetické cívce

Metodika experimentu v magnetické cívce (výběr psů, sběr dat a jejich zpracování) je založená na výše popsaném dvouvýběrovém testu směrové preference mezi dvěma miskami s potravou. Celý experiment byl proveden v prostředí magnetické cívky, která se nachází v areálu šlechtitelské stanice Truba v Kostelci nad Černými lesy. Cívka má rozměry 4x4x4 m, je odstíněná a vybavená technikou pro záznam obrazu a zvuku. Cívka je ovládána z kontrolní místnosti, která je stavebně i prostorově oddělena.

Psi byli testováni ve dvou odlišných nastaveních magnetické cívky – za kontrolních podmínek s magnetickým severem nastaveným na topografický sever a s magnetickým severem nastaveným na topografický východ (tj. magnetické pole bylo otočeno o 90° směrem na východ).

Pro vyhodnocení dat byla použita kruhová statistika opět v programu Oriana 4.02, a dále zobecněné lineární smíšené modely v programu SAS 9.4.

5 Výsledky – seznam vědeckých článků

Předkládaná disertační práce je souborem čtyř uveřejněných vědeckých článků, dvou odeslaných a jednoho konferenčního příspěvku. Všechny publikované články vyšly v renomovaných vědeckých časopisech s IF.

Souhrnný přehled publikací je tematicky rozdělen podle dvou hlavních cílů disertační práce. Je však nutno poznamenat, že některé publikace nelze striktně zařadit, neboť výsledky mají přesah do obou cílů práce. Každý článek je doplněn krátkým vysvětlujícím komentářem a stručnou anotací.

5.1 Prostorová orientace loveckých psů

5.1.1 Magnetic alignment enhances homing efficiency of hunting dogs

Benediktová, K., Adámková, J., Svoboda, J., Painter, M. S., Bartoš, L., Nováková, P., Vynikalová, L., Hart, V., Phillips, J., Burda, H.

eLife, 2020, IF 7,08 https://doi.org/10.7554/eLife.55080

Výsledky diplomové práce přinesly první informace o způsobech prostorové orientace loveckých psů a naznačily, že do procesů spojených s navigací by mohly být prostřednictvím magnetorecepce zapojeny i informace z magnetického pole Země. Základní soubor dat byl proto v rámci disertační práce kvantitativně i kvalitativně rozšířen. Zvýšil se počet sledovaných psů ze 4 na 27 celkem 10 plemen, ke sběru dat bylo použito modernější GPS sledovací zařízení a postupně byly zapojeny i minikamery umístěné přímo na psech.

Navzdory anekdotickým zprávám o výjimečných homingových schopnostech psů, nejsou dosud jejich navigační schopnosti plně pochopeny. Dvacet sedm loveckých psů bylo vybaveno GPS obojky a mini-kamerami a analyzovány jejich homingové strategie. Vyhodnocením 622 návratů bylo zjištěno, že psi používají dva hlavní způsoby návratu: 1. návrat po vlastní stopě (tzv. „tracking“); 2. návrat zcela novou trasou (tzv. „scouting“). Porovnáním těchto dvou způsobů návratu bylo zjištěno, že zatímco během trackingu psi nevykazovali žádné zvláštní chování, zcela opačná situace nastala při použití scoutingu.

Bylo objeveno dříve nepopsané chování, které bylo pojmenováno „kompasový běh“ (compass run). Konkrétně, psi vracející se scoutingem začínali ve většině případů svůj návrat krátkým během podél severojižní magnetické osy, tedy jakýmsi „během podle kompasu“. Ukázalo se, že toto chování není samoúčelné, ale přináší psům zásadní výhodu. Při použití kompasového běhu se výrazně zvyšovala efektivita návratu (až o 30 %). Psi byli schopni se k majitelům vracet kratší cestou, oproti psům, kteří kompasový běh nepoužili. Kompasový běh pravděpodobně pomáhá se zarovnáním mentální mapy prostředí podle magnetického kompasu a tím k nastavení správného směru k majiteli.

V této práci byla poprvé potvrzena souvislost mezi dynamickým magnetickým alignmentem a navigací psů.

5.1.2 Processing Methods of Camera Record of Animal Movement

Kutilek, P., **Benediktova, K.**, Svoboda, J., Volf, P., Adamkova, J., Krivanek, V., Hejda, J., Kutilkova, E., de Brito, A. C. D. M.

Proceedings of the 18th International Conference on Mechatronics - Mechatronika 2018, Brno, ISBN 978-80-214-5542-9

S přibývajícím množstvím dlouhých audiovizuálních záznamů získaných v rámci sběru dat pro prostorovou orientaci loveckých psů se jejich ruční zpracování stávalo stále náročnější. Vyvstala tak potřeba automatického zpracování a vyhodnocení těchto velkoobjemových dat. Byla navázána spolupráce s Fakultou biomedicínského inženýrství ČVUT Praha, jejímž výsledkem je možnost automatického zpracování výše uvedených dat. Postup řešení byl vědecké komunitě poprvé představen v Brně na konferenci Mechatronika 2018 formou konferenčního příspěvku.

Publikace představila automatické metody pro zpracování záznamů z digitálních kamer. Byly použity dva typy nahrávek (video ze stacionární kamery a audio-video záznam z kamery připevněné přímo na tělo psa během jeho pohybu v terénu), pro které byly vyvinuty dvě metody zpracování. První metoda umožňuje určit polohu zvířete v prostoru a identifikovat intenzitu pohybu. Druhá metoda analyzuje pohybovou aktivitu, tj. identifikuje pasivní a aktivní fázi pohybu psa v době, kdy je mimo dohled majitele.

Systém pro zpracování dat byl vyvinut v prostředí MatLab® (MatLab R2010b, Mathworks, Inc., Natick, MA, USA).

5.1.3 Automatic Analysis of Long-Lasting Video Sequences of Animal Movements

Volf, P., **Benediktová, K.,** Adámková, J., Kutílek, P., Hejda, J., Svoboda, J., Křivánek, V.

Submitováno do Behavior Research Methods, IF 4,425

Automatický systém pro zpracování dat, představený v kap. 5.1.2, byl postupně rozšiřován a doplňován o nové funkce, které dále zrychlovaly celý proces zpracování dat a zvýšily úroveň zaslepenosti celého výzkumu.

Publikace představuje automatickou analýzu dlouhých obrazových a zvukových záznamů propojených s informacemi z globálního pozičního systému (GPS), což významně redukuje (o více než 80 %) nutnost fyzické přítomnosti uživatele v procesu zpracování dat. Systém byl vyvinut v prostředí MatLab® (MatLab R2010b, Mathworks, Inc., Natick, MA, USA). Vyvinutá metoda kombinuje analýzu pohybové aktivity psa s pozičními daty a synchronizuje tak pasivní a aktivní fáze pohybu s pohybovou trajektorií. V následném kroku měří předem definované parametry trasy, jako jsou azimuty v konkrétních místech pohybové trajektorie a vzdálenostní a časové hodnoty. V poslední fázi zpracování vypočítává a identifikuje bod návratu.

Metody matematického zpracování pohybových dat představené v této publikaci lze v širším měřítku použít pro rozpoznávání určitých vzorců chování v rámci výzkumu chování zvířat. Veškeré postupy (konkrétní skripty) použité pro zpracování dat byly poskytnuty vědecké komunitě k volnému využití.

5.1.4 Hunting dogs bark differently when they encounter different animal species

Policht, R., Matějka, O., **Benediktová, K.**, Adámková, J., Hart, V.

Submitováno do Scientific Reports, IF 3,998

Během sběru dat pro prostorovou orientaci byly zaznamenány rozdíly ve vokalizaci psů podle druhu sledované zvěře. Pro používaná plemena loveckých psů je typické tzv.

„hlášení“ na stopě zvěře. To znamená, že pes při kontaktu s teplou (čerstvou) stopou zvěře začne specificky štěkat, čímž informuje majitele o přítomnosti kořisti. Majitelé psů si všimli, že hlášení má jinou podobu v případě kontaktu např. s divokým prasetem v porovnání se zajícem. Protože tyto rozdíly v hlasovém projevu psa nebyly nikdy dříve popsány, provedli jsme experiment zaměřený na otestování této skutečnosti.

Předchozí výzkumy ukázaly, že vokalizace psů může poskytovat informace směrem k jejich lidským společníkům. Zatímco v posledním desetiletí byly akustické signály psů intenzivně studovány, štěkání během loveckých aktivit zůstává prakticky neprobádané. Cílem studie bylo otestovat na čtyřech druzích potencionální kořisti psů (divoké prase, liška, králík a slepice) rozdíly v hlášení (štěkání). Výsledky diskriminační analýzy ukázaly, že je možné kategorizovat, na který druh psi (konkrétně jezevčíci a teriéři) štěkali. Nejvýraznější štěkání bylo zjištěno při kontaktu s nejnebezpečnějším z těchto zvířat, s divokým prasetem. Naopak, štěkání při setkání s liškou bylo klasifikováno podobně jako štěkání při kontaktu s králíkem či slepicí, tj. druhy, které nepředstavují pro loveckého psa žádnou hrozbu. Dále bylo zjištěno, že při kontaktu s divočákem vykazuje štěkání nižší frekvenci a delší trvání v porovnání s ostatnímu druhy. Zdá se, že variabilita štěkání je spíše projevem vnitřního stavu psa než funkčně referenčními informacemi.

5.2 Vliv magnetického pole na poziční chování psů

5.2.1 Dogs are sensitive to small variations of the Earth’s magnetic field

Hart, V., Nováková, P., Malkemper, E., Begall, S., Hanzal, V., Ježek, M., Kušta, T., Němcová, V., Adámková, J., **Benediktová, K.**, Červený, J., Burda, H.

Frontiers in Zoology, 2013, IF 2,304 https://doi.org/10.1186/1742-9994-10-80

Jedná se o první práci, která potvrdila existenci magnetického smyslu u domácích psů. Část dat pro tento článek byla sbírána v rámci bakalářské práce. Výsledky této publikace podnítily vznik myšlenky o možném zapojení magnetorecepce při prostorové orientaci loveckých psů a vedly ke vzniku jak diplomové práce, tak následně i této disertační práce.

Spontánní zarovnávání osy těla (magnetický alignment) byl popsán u několika druhů savců v různých kontextech chování. Studium tohoto chování se ukázalo jako vhodné paradigma pro sledování výskytu magnetosensitivity u různých druhů zvířat. S ohledem na tuto skutečnost bylo pátráno po známkách magnetického alignmentu u domácích psů v kontextu jejich každodenního chování – značkování teritoria. Bylo měřeno zarovnání osy těla během defekace a urinace u 70 psů 37 plemen. Analýzou více než 7000 pozorování bylo zjištěno, že psi preferovali zarovnání osy těla podél severojižní magnetické osy, ale pouze v případě klidného magnetického pole Země. V případě nestabilního magnetického pole se zarovnávání stávalo více náhodné a nevykazovalo žádnou směrovou preferenci. Zjištění, že již malé fluktuace zemského magnetického pole vyvolávají behaviorální reakce je velmi významné a mělo by být bráno v potaz u dalších experimentů.

5.2.2 Directional preference in dogs: Laterality and "pull of the north."

Adámková, J., Svoboda, J., **Benediktová, K.**, Martini, S., Nováková, P., Tůma, D., Kučerová, M., Divišová, M., Begall, S., Hart, V., Burda, H.

Plos One, 2017, IF 2,766 https://doi.org/10.1371/journal.pone.0185243

Pro potvrzení výsledků předchozího článku o schopnosti psů vnímat magnetické pole Země a pro zjištění vlivu magnetického pole na přirozené chování psů byl připraven jednoduchý experiment založený na dvouvýběrovém testu během přirozeného chování psů, které představovalo krmení ve venkovním prostoru. Výsledky potvrdily závěry předchozího článku o magnetosensitivě psů, a navíc poukázaly na nový fenomén, který je nutno vzít v potaz při behaviorálních experimentech se zvířaty.

Lateralita je u domácích psů dlouhodobě sledována a dobře popsána. Zatím však nebylo nikdy uvažováno o možném vlivu laterality na magnetický alignment zvířat a opačně. Byly testovány preference psů při výběru mezi dvěma miskami s potravou umístěné vždy nalevo a napravo od psa v kombinaci dvou sousedních kompasových směrů (sever a východ, východ a jih, jih a západ, západ a sever). Část z 25 testovaných psů se ukázala být pravotočivými, část levotočivými a část neměla vyhraněnou lateralitu. V kombinaci misek umístěných na sever a východ se ukázala preference pro severně umístěné misky, tzv. tah severu, bez ohledu na lateralitu psa. Lateralita a „tah severu“ jsou tedy jevy, které by měly být brány v úvahu nejen při behaviorálních testech, ale i při experimentech zaměřených na prostorovou orientaci a navigaci.

5.2.3 Turning preference in dogs: north attracts while south repels

Adámková, J., **Benediktová, K.**, Svoboda, J., Bartoš, L., Vynikalová, L., Nováková, P., Hart, V., Painter, M. S., Burda, H.

Plos One, 2021, IF 2,74 *https://doi.org/10.1371/journal.pone.0245940*

Zjištění, že individuálně konzistentní preference (nebo ne-preference) pro určitý směr je narušována „tahem severu“, vedlo k opakování experimentu v magnetické cívce, kde bylo možno odfiltrovat vnější podněty a manipulovat s magnetickým polem.

Psi byli opět sledováni při dvouvýběrovém testu, jak v přirozeném magnetickém poli, tak i v magnetickém poli posunutém o 90°. Ukázalo se, že tah severu se projevil i v experimentálním prostředí. Psy přitahoval nikoli topografický, ale magnetický sever. Podrobné analýzy navíc odhalily, že tento jev zahrnuje také „odpuzování jihem“. Na základě těchto skutečností se dá usuzovat, že preference otáčení by mohla být vedena dominantním okem. Za předpokladu, že magnetorecepce psů je založena na mechanismu radikálových párů, lze očekávat konflikt v situaci, kdy je dominantní oko odvráceno od severu, zatímco kontralaterální oko „přitažlivý“ sever vidí. U psa by mohla vzniknout „potřeba“ nasměrovat dominantní oko k severu, což by mohlo vyvolat zarovnání těla podél severojižní osy.

5.3 Separáty vědeckých článků

Magnetic alignment enhances homing efficiency of hunting dogs

Kateřina Benediktová[1]*, Jana Adámková[1], Jan Svoboda[1], Michael Scott Painter[1,2], Luděk Bartoš[3,4], Petra Nováková[1], Lucie Vynikalová[5], Vlastimil Hart[1], John Phillips[6], Hynek Burda[1]*

[1]Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Praha, Czech Republic; [2]Biology Department, Barry University, Miami, United States; [3]Department of Ethology, Institute of Animal Science, Praha, Czech Republic; [4]Department of Ethology and Companion Animal Science, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences, Praha, Czech Republic; [5]Department of Zoology and Fisheries, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences, Praha, Czech Republic; [6]Department of Biological Sciences, Virginia Tech, Blacksburg, United States

Abstract Despite anecdotal reports of the astonishing homing abilities in dogs, their homing strategies are not fully understood. We equipped 27 hunting dogs with GPS collars and action cams, let them freely roam in forested areas, and analyzed components of homing in over 600 trials. When returning to the owner (homewards), dogs either followed their outbound track ('tracking') or used a novel route ('scouting'). The inbound track during scouting started mostly with a short (about 20 m) run along the north-south geomagnetic axis, irrespective of the actual direction homewards. Performing such a 'compass run' significantly increased homing efficiency. We propose that this run is instrumental for bringing the mental map into register with the magnetic compass and to establish the heading of the animal.

Introduction

Homing, broadly defined as the ability to return to a known goal location (e.g. breeding grounds, shelter sites) after displacement (***Schmidt-Koenig and Keeton, 1978***; ***Papi, 1992***; ***Wiltschko and Wiltschko, 1995***), has been shown in a taxonomically diverse range of vertebrates that rely on a multitude of cues, for example visual, olfactory, acoustic, celestial, magnetic, and idiothetic (***Schmidt-Koenig and Keeton, 1978***; ***Papi, 1992***; ***Wiltschko and Wiltschko, 1995***; ***Cullen and Taube, 2017***; ***Lohmann, 2018***; ***Mouritsen, 2018***). However, designing systematic studies to characterize the navigational strategies and underlying sensory mechanisms mediating homing behaviour in non-migratory species, particularly in free-ranging mammals, have proven difficult, and our understanding of large-scale navigation and homing remains incomplete (***Poulter et al., 2018***; ***Tsoar et al., 2011***; ***Wolbers and Wiener, 2014***).

Anecdotal accounts of the impressive navigation abilities of dogs have been commonplace, maybe best exemplified in World War I when 'messenger dogs' were used as couriers to deliver sensitive information across battlegrounds (***Richardson, 1920***). Nearly a century ago, the first studies designed to examine navigational abilities in dogs were performed, revealing homing success even if displaced to unfamiliar sites (Schmid 1932, 1936 cited in ***Nahm, 2015***). Decades later, a more comprehensive study observed consistent homing success in a total of 26 dogs displaced without exposure to visual cues in various geographic directions. Dogs often homed using novel routes and/or shortcuts, ruling out route reversal strategies, and making olfactory tracking and visual piloting

***For correspondence:**
benediktovak@fld.czu.cz (KB);
burda@fld.czu.cz (HB)

Competing interests: The authors declare that no competing interests exist.

Funding: See page 17

Received: 11 January 2020
Accepted: 27 May 2020
Published: 16 June 2020

Reviewing editor: Mihaela D Iordanova, Concordia University, Canada

unlikely. Indeed, as previous authors have suggested, shedding light on the mystery of mammalian homing may require unconventional research approaches that focus on 'unusual' senses (***Nahm, 2015***).

Hunting dogs, particularly the so-called scent hounds, have been selected over generations to detect and pursue tracks of game animals and, if not followed by the hunter, to return to the place where the pursuit started, often over distances of hundreds or thousands of meters. How dogs pinpoint the owner's location using novel routes of return in highly variable densely forested habitats remains perplexing.

We expect that either dogs can find their way to the owner following their own scent trail back (a strategy called 'tracking') or they can perform true navigation, the ability to home over large distances without relying on route-based landmarks or information acquired during the displacement, a strategy we termed 'scouting', searching for a new way. While tracking may be safe, it is lengthy. Scouting enables taking shortcuts and might be faster but requires navigation capability and, because of possible errors, is risky.

Using GPS data complemented by video recordings by action cams, we analyzed orientation of free-roaming scent hounds. We expected to find evidence for either tracking or scouting, to test the predictions about the route length and duration, and to see indications for the type of decision made at the turning point. Furthermore, we expected that should visual piloting (orientation towards landmarks) take place there would be an effect of the height of the dog as higher (taller) dogs should have better overview (farther horizon) than lower dogs.

Altogether, 27 hunting dogs from ten breeds were equipped with a GPS collar and in several cases also with an action camera capturing a portion of the dog's head, thus providing information about its movement, behaviour, and the landscape in front of and around the dog (***Figure 1***, ***Video 1***). In total, 622 trials (excursions) were performed at 62 locations during diurnal walks in forested hunting grounds in the Czech Republic from September 2014 to December 2017. Based on the records, we determined turning points, dividing the whole excursion into the outbound and inbound tracks, and we measured azimuths at particular points, length and speed of particular tracks (***Figure 2A***).

Results

Return strategy

In 399 cases (59.4 %), dogs homed by following their outbound track (tracking strategy), and in 223 cases (33.2 %), dogs homed using novel route (scouting strategy). In 50 cases (8.0 %), dogs combined both strategies during a single return (***Figure 2B–C***). In this study, we focus only on 'scouting'.

Speed and track length

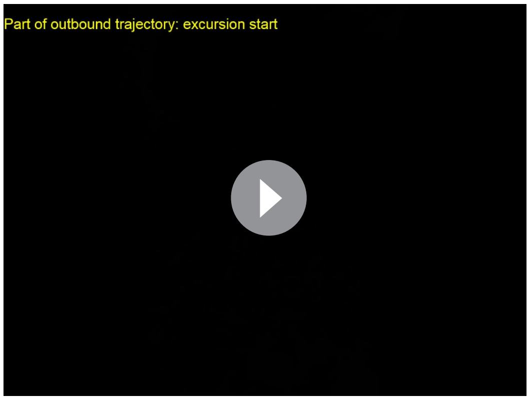
Scouting dogs were faster than tracking ones (***Figure 3***). As expected, taller dogs ran faster than smaller ones, but the shoulder height did not affect length of the inbound track (***Figure 4***) and the average speed of the inbound trajectory was faster when a portion of the return followed forest paths (***Figure 5***). Inbound track length was significantly longer when forest paths were used (***Figure 5***). Shoulder height did not affect inbound track length (***Supplementary file 1B***- Table 2). As expected, there was a positive correlation between direct ('beeline') distance between the turning point and the owner and the average inbound track length (***Figure 4***, ***Supplementary file 1B***- Table 2).

Azimuths and the 'compass run'

The compass directions in which dogs started the excursions (***Figure 2A***, azimuth A) and at the turning point relative to the excursion start, and thus to the goal (***Figure 2A***, azimuth B) were random, irrespective whether dogs were later tracking or scouting (***Figure 6***, ***Supplementary file 1E***- Table 5). The direction in which the dogs started to return (***Figure 2A***, azimuth C) was random in tracking dogs, but significantly aligned along the ~north-south magnetic axis in scouting dogs (***Figure 7***, ***Supplementary file 1E***- Table 5). Specifically, dogs homing by scouting started their return with a short (average length 18.1 m, ***Supplementary file 1D***- Table 4), 'compass run' aligned along the ~north-south geomagnetic axis (***Supplementary file 1E-F***- Tables 5-6, ***Video 2***).

Figure 1. Still shots of a fox terrier (left column) and a miniature dachshund (right column) used in this study showing the tracking equipment and habitat. Above: The GPS transmitter and antenna are fixed to a collar and fitted around the animal's neck (note that for safety and comfort of the animal, the collar is free to rotate). The black fabric harness is secured around the torso and chest and is used to attach the protective camera case containing the camera and battery. Below: A typical field of view captured by the video camera that includes the dog's head/neck, and provides a detailed view of the surrounding terrain. An on-board microphone (not visible) is used to record audio.

To determine if the position of the owner influenced the orientation of the compass run, we partitioned the data into four distributions (north, south, east, or west, + / - 45˚), according to the location of the owner relative to the turning point. In all four distributions, the compass run was significantly orientated along the ~north south geomagnetic axis, suggesting that its orientation was independent of the direction to the owner (***Figure 8***, ***Supplementary file 1F***- Table 6).



Video 1. Example of all three phases of an excursion. Labels of the left side of the video indicate the segment of the excursion. The video begins with the excursion start (i.e. the beginning of the outbound trajectory) when the dog becomes separated by >100 m from the owner, at which point the owner remains stationary in the forest. Shortly after, the dog detects and follows the olfactory track of a wild game animal, indicated by barking behaviour. After the outbound trajectory, the dog begins the turning trajectory phase of the excursion (see Materials and methods) and the turning point is shown when the dog briefly pauses. This location marks the beginning of the compass run (=alignment run, azimuth C, initial inbound segment). Lastly, the inbound trajectory is shown representing the phase when the dog is homing back to the location of the excursion start/owner.
https://elifesciences.org/articles/55080#video1

There were no significant differences in axial preference of the compass run between sexes (Watson's U^2 test, U = 0.027, p>0.5) or between familiar and unfamiliar areas (Watson's U^2 test, U = 0.036, p>0.5).

The probability of exhibiting a scouting strategy after compass run was aligned along the north-south axis was almost four times higher than the probability of exhibiting tracking (odds ratio = 3.60, p<0.0001) (***Figure 7E***, ***Supplementary file 1B***- Table 2). No other factors appeared influential.

Importantly, when the compass run was aligned along the ~north-south axis, homing was more efficient, i.e., the ratio between the length of the inbound track and the shortest distance between the turning point and the goal was significantly reduced compared to the ~east-west compass runs (F = 6.47, p=0.01) (***Figure 9 Supplementary file 1B***- Table 2).

Effect of sex, breed and study site familiarity

We partitioned the data by sex for all individuals and used a Rayleigh test to determine if sex influence the orientation of the 'compass run' (***Figure 2***, azimuth C) during scouting returns. There was no significant difference between the two resulting distributions (Watson's U2 test, U = 0.027, p>0.5), and therefore, no sex differences in the orientation of the compass run.

Sex and breed did not influence the probability of return strategy used during homing (GLMM, p>0.05). Furthermore, we tested whether study site familiarity influenced the orientation of the compass run. We grouped azimuth C into two groups, according to whether the dog had visited the study at least one time prior to the excursion or if the dog was experiencing the study site for the first time. No differences between the two distributions (familiar vs unfamiliar) were found (Watson's U2 test, U = 0.036, p>0.5).

Effect of sun

To test for an effect of sun and/or polarized light on the orientation of the compass run during scouting returns, the sun position was determined by estimating the sun's azimuth during the 15th day of each month, therefore accounting for seasonal variation in azimuth position (sun position data was taken from a central location in the Czech Republic, central to the locations of all test sites). Next, the sun azimuth direction was recorded for each hour during the 15th day of each month, for all available daylight hours. Thus, we created an average sun azimuth direction for each month of the year, with one-hour resolution. For circular analyses, we pooled the orientation of azimuth C relative to the sun position for each excursion, using the nearest hour of sun position according to each excursion time. A Rayleigh test was used to determine if the distribution of azimuth C was non-random when plotted relative to sun position. The position of sun, and thus polarization pattern, did not significantly influence the orientation of azimuth C during scouting returns at the individual level (n = 251, μ = 69°/249°, r = 0.04, p=0.673) or at the group level (n = 27, μ = 146°/326°, r = 0.021, p=0.989).

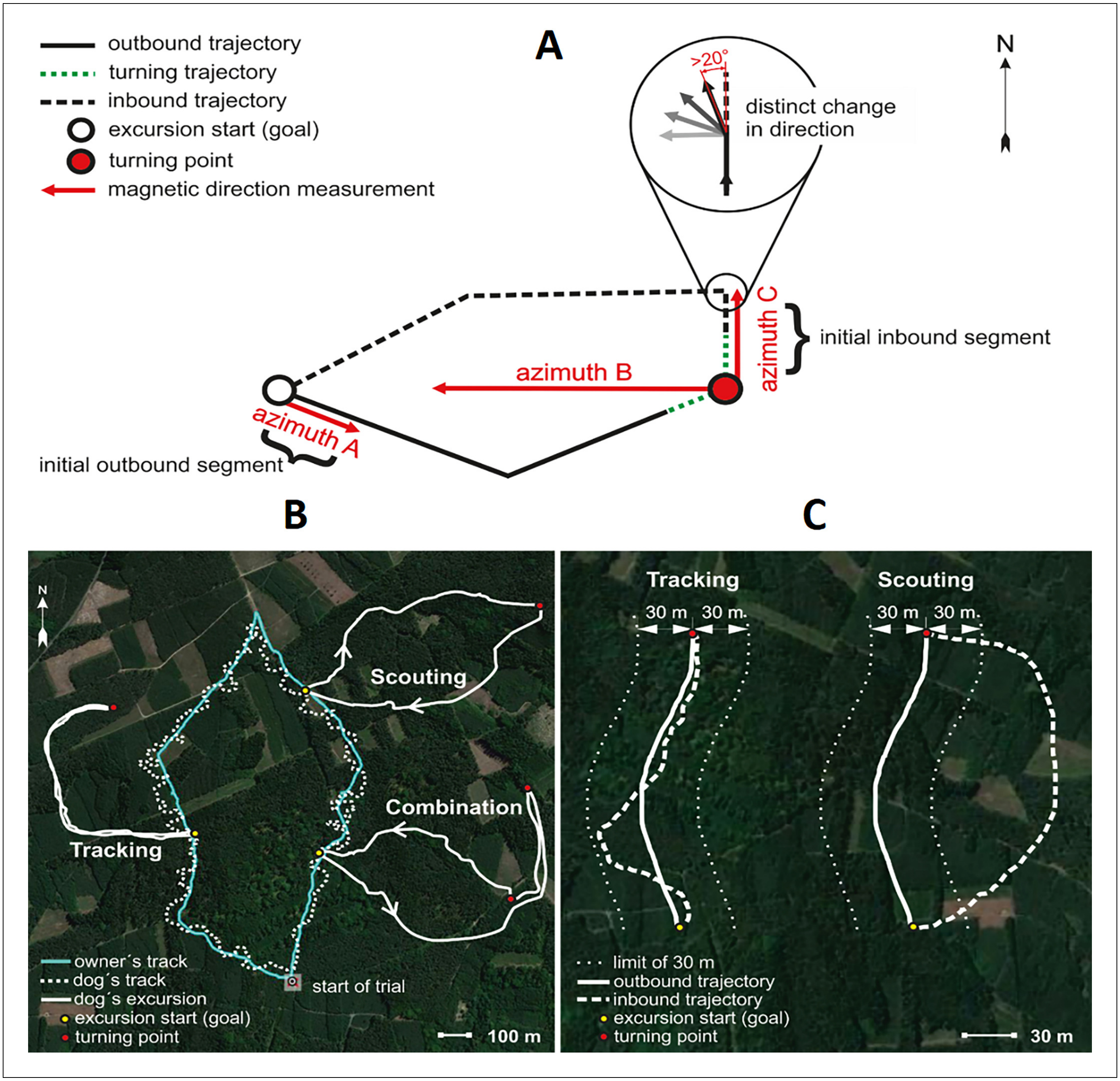


Figure 2. Spatial features and return strategies derived from GPS data used in analyses. (**A**) Schematic illustration of total excursion track. Excursion start marks location of owner when the dog is more than 100 m away, indicating that the dog is pursuing a game animal. Excursion start also marks the approximate location where the owner remains hidden until the dog returns. Turning point represents the location where the dog initiated its return to the owner. Azimuth A represents the magnetic direction of the initial outbound segment, calculated between the excursion start and the GPS point recorded 5 s after the excursion start. Azimuth B represents the magnetic direction of the owner relative to the dog at the turning point. Azimuth C represents the magnetic direction of the initial inbound segment, the 'compass run', calculated by measuring the direction between the turning point and the point where the dog exhibits a distinct (>20°) deflection in track direction (magnified inset). See Materials and methods for additional details. (**B**) GPS tracks showing examples of Tracking and Scouting strategies or combination of strategies. Solid white tracks show excursions. The turquoise line shows the owner's track and the white dotted line shows the dog's track during non-excursion portions of the trial. (**C**) Examples of Tracking and Scouting return strategies: Tracking: inbound return track falls within a ± 30 m corridor limit (shown by small white dots flanking each side of the track) of the outbound track. Scouting: the inbound return track is separated from the outbound trajectory by at least 30 m.

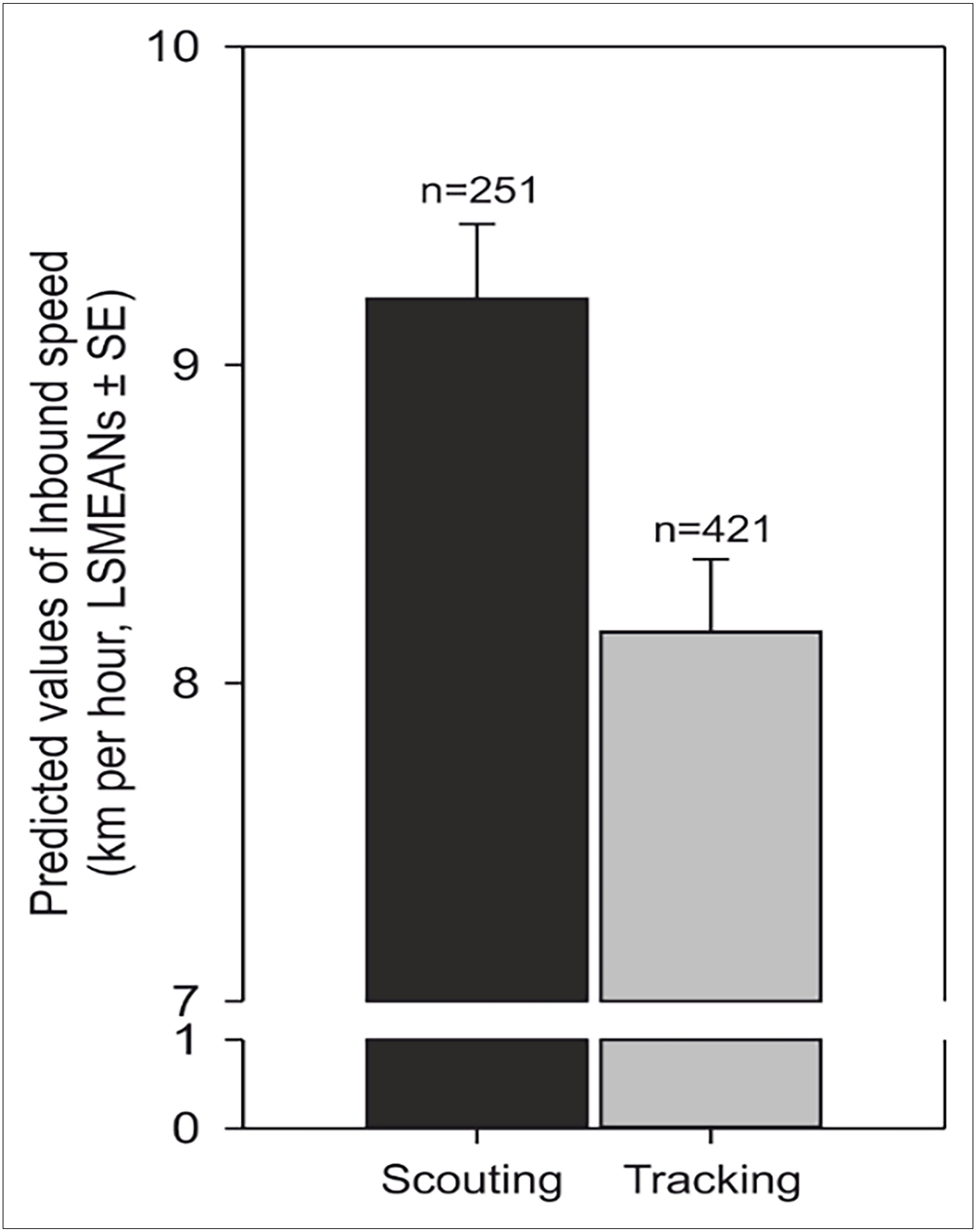


Figure 3. Average speed increases in scouting compared to tracking. Predicted values of inbound speed (km/hour, LSMEANs ± SE) according to return strategy and independent of the direction of the compass run (azimuth C).

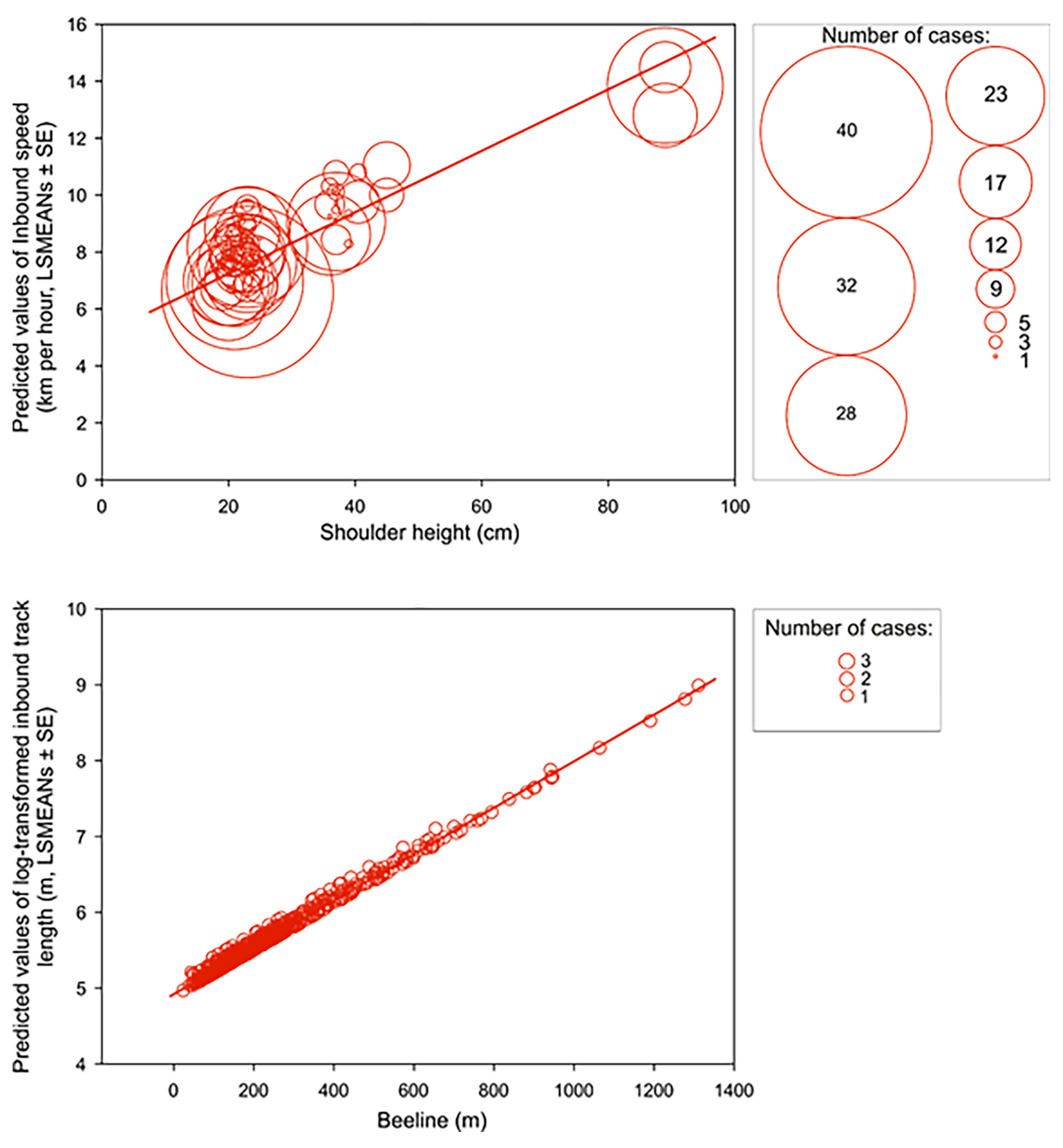


Figure 4. Inbound speed and track length positively correlate with shoulder height and beeline excursion distance, respectively. Upper row: A bubble-plot of predicted values of inbound speed (km per hour, LSMEANs ± SE) plotted relative to shoulder height (cm). The center of each bubble represents the predictive value and bubble size represents the number of cases for that value. Size class scale is shown on the right. Bottom row: A bubble-plot of predicted values of log-transformed total inbound track length (m, LSMEANs ± SE) as a function of direct ('beeline') distance between the turning point and the owner. The center of each bubble indicates the predictive value and bubble size is equivalent to the number of cases, as shown in the box on the right.

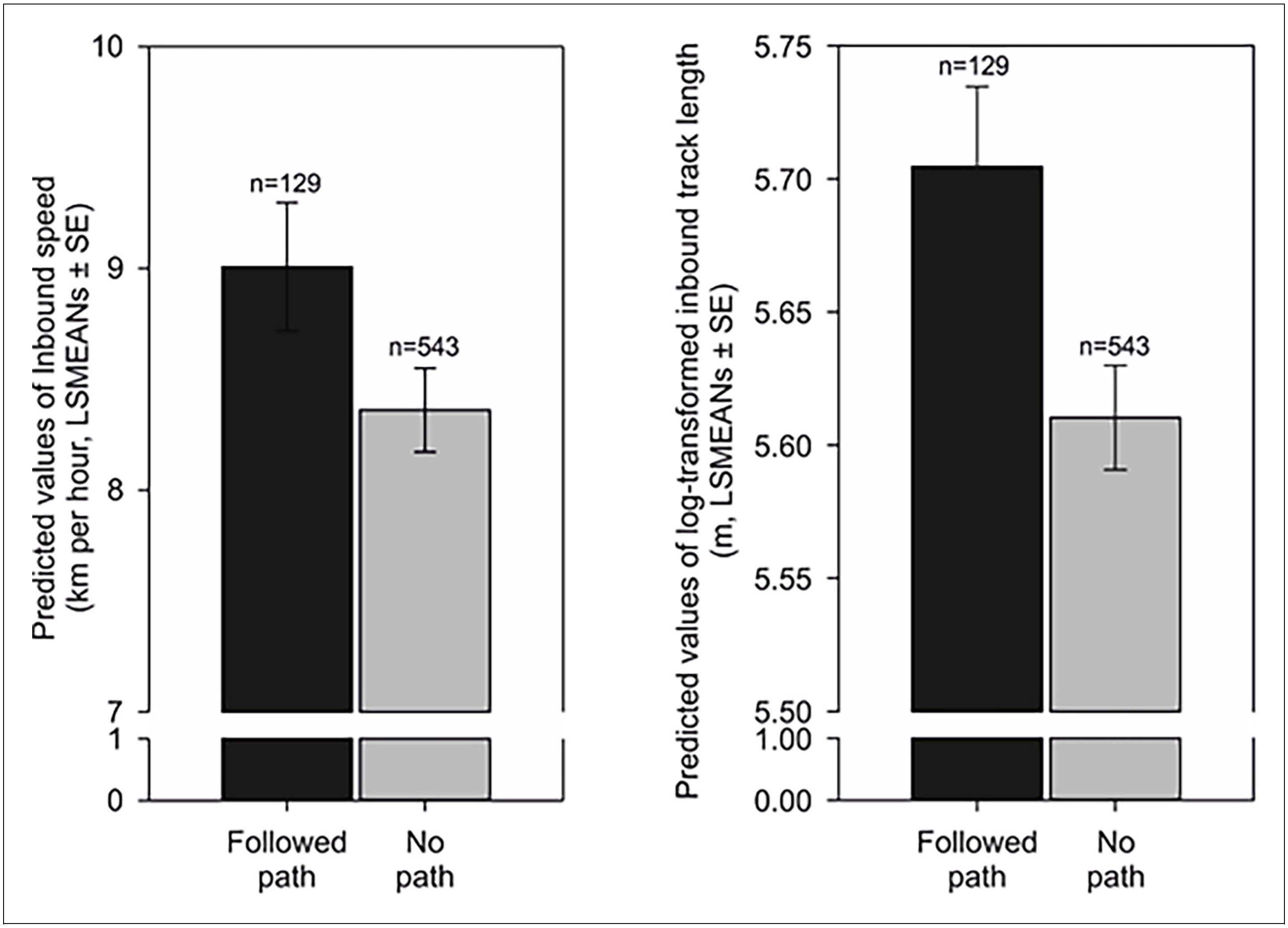


Figure 5. Inbound speed (length) and inbound track length (right) influenced by forest paths during the homing return. Left: Predicted values of inbound speed (km per hour, LSMEANs ± SE) grouped according to whether a portion of the inbound trajectory followed a forest path ('Followed path'), or if the return was completed without the use of a forest path ('No path'). Right: Predicted values of log-transformed total inbound track length (m, LSMEANs ± SE) between returns when at least a portion of the inbound track followed a forest path compared to returns when no forest paths were used.

Effect of wind

Wind direction was recorded at the study site for each excursion by the owner. To test for an effect of wind direction, particularly in conditions when wind was blowing from the owner to the direction of the dog at the turning point, we used a Rayleigh test to determine if the wind direction was non-random across excursions when dogs used a scouting return strategy. In 55 cases (22 % of all scouting excursions), no wind was detected and therefore these excursions could not be included in the analyses. For the remainder of excursions (n = 196), Azimuth B (i.e. direction between the turning point and owner) (***Figure 2***) was plotted relative to the wind direction.

Partitioning the circular data into eight equal bin sizes (each bin ±22.5˚ and centered on the 45's, i.e. 0˚, 45˚, 90˚, 135˚, etc.), we found that the wind conditions in only 24 scouting returns (<10 % of scouting returns) were suitable for olfactory piloting to the owner (i.e. <10 % of scouting returns had wind conditions where the wind was blowing in the direction (±22.5˚) from the owner to the dog at the point of return/start of azimuth C.

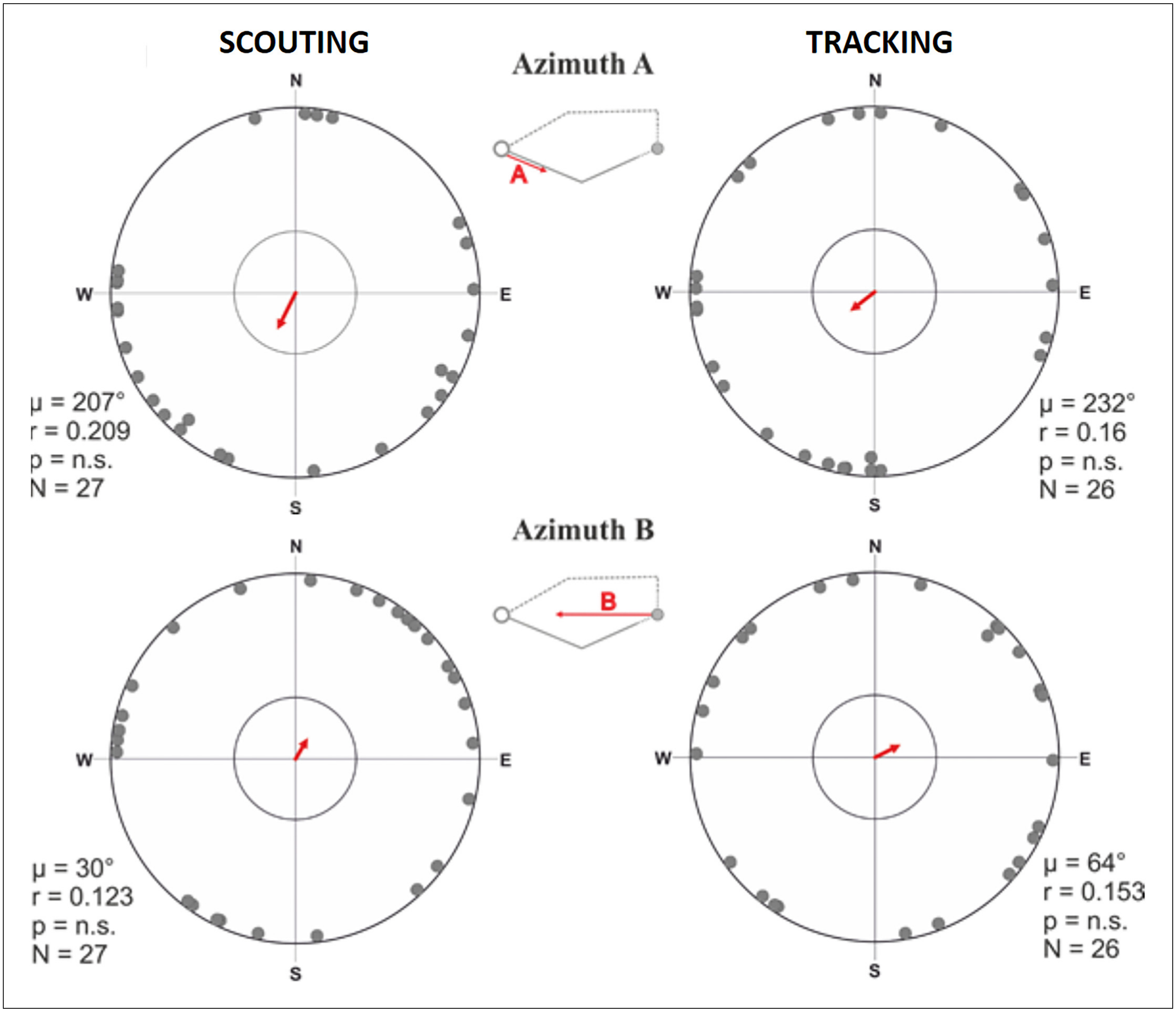


Figure 6. Circular distributions for azimuth A and azimuth B means grouped by return strategy. Circular distributions of magnetic orientation of the direction of the turning point relative to the excursion start/owner (azimuth B) and the initial outbound segment (azimuth A) for scouting (left column) and tracking (right column). The small schematics centered between each plot show the vector corresponding to the data in each distribution. The red arrow indicates the angular vector (μ) calculated over all angular means. The length of the mean vector (r) corresponds to the degree of clustering in the distribution on a scale of 0.0–1.0, where the circular plot radius = 1.0. The inner circle marks the 0.05 level of significance limit computed using the Rayleigh test.

Discussion

We found that dogs returning in a forest either follow back their outbound trajectory, a strategy called *tracking* or chose a completely new route, a strategy called *scouting*. In this study, we analyzed only scouting events and found a conspicuous phenomenon. In most cases, dogs start their return with a short (about 20 m long) run, called here *compass run*, mostly performed along the north-south axis irrespective of the actual homeward direction.

It is unlikely that the direct involvement of visual, olfactory or celestial cues can explain the highly stereotyped and consistent ~north south alignment of the compass run. For example, the forested habitat and dense vegetation of the study sites make visual piloting unreliable and, in many cases,

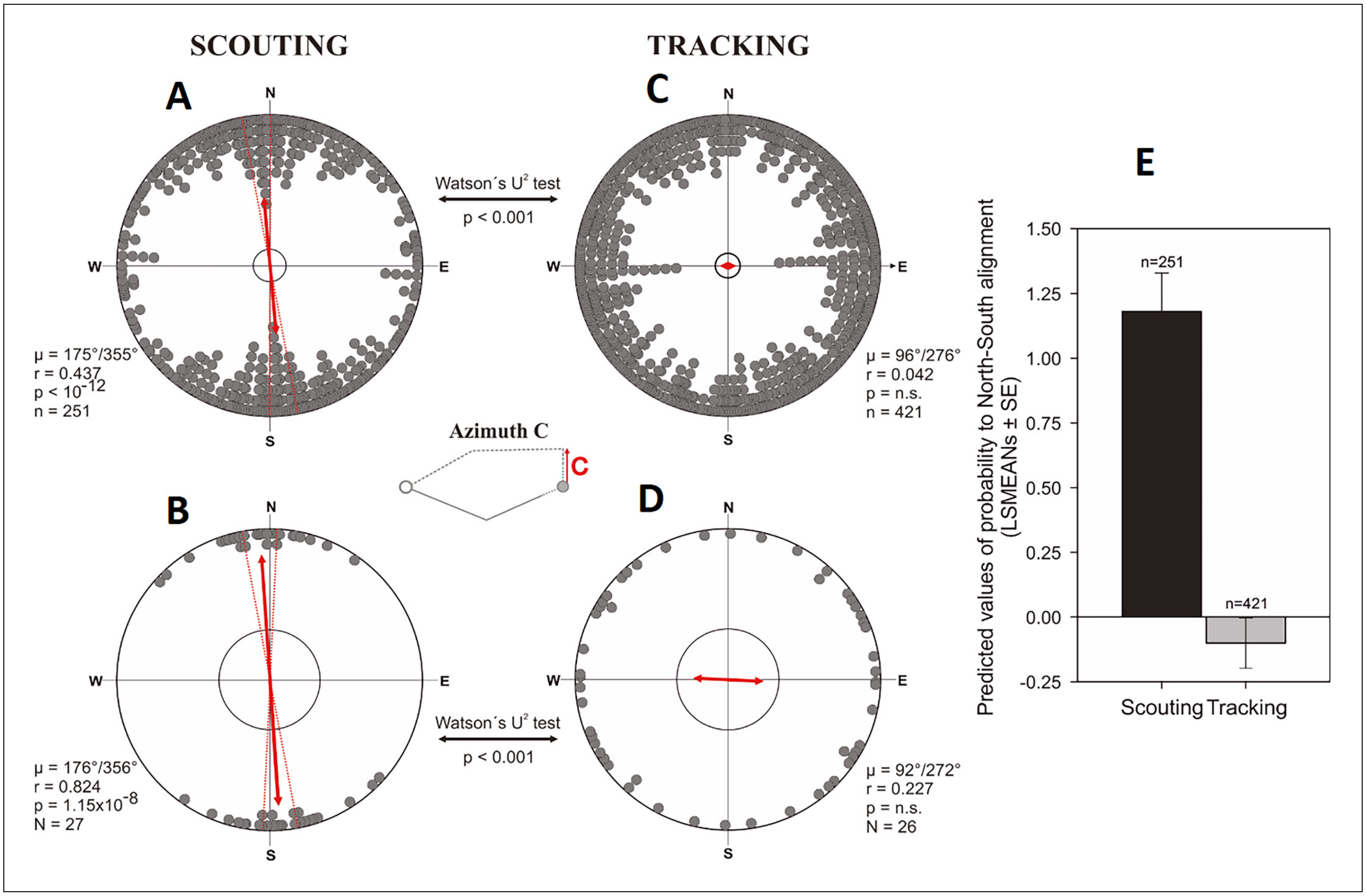
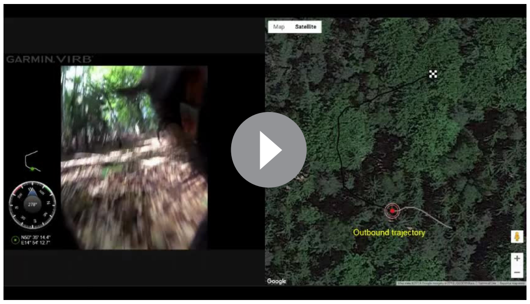


Figure 7. Alignment responses during the initial inbound return (= 'compass run') in free-roaming dogs. (**A–D**) Circular distributions showing geomagnetic alignment responses during the initial inbound segment (azimuth C, 'compass run'), when distributions are partitioned into Scouting (**A, B**) and Tracking (**C, D**) return strategies. Grey bearings plotted on the periphery of the distributions represent the axial orientation of compass runs for each excursion (**A, C**), each bearing treated as an independent data point, or (**B, D**) the axial orientation of compass runs when the mean orientation was first calculated for each dog. All data are plotted relative to magnetic north, indicated at the top of each plot, and the red double-headed arrow indicates the mean axial vector (μ) for each distribution. The length of the mean vector (r) corresponds to the degree of clustering around the mean and ranges from 0.0 to 1.0, with the radius of each plot = 1.0. Dashed red lines represent the 95% confidence intervals and the inner grey circle marks the p=0.05 level of significance limit computed using the Rayleigh test. Results from Watson's U^2 tests are shown between distributions, revealing significant differences in the compass run orientation between tracking a scouting return strategies. The small schematic centered between the plots shows azimuth C and the axial direction of the red vector corresponds to the orientation data plotted in each distribution. (**E**) Predicted values of the probability that dogs will exhibit a compass run along the ~north south geomagnetic axis (±45˚) during the initial inbound segment (LSMEANs ± SE) according to return strategy.

not possible. Furthermore, there was no effect of the body height (and thus the degree to which the dog's field of view of its surroundings was limited) on the probability of north-south alignment when compared to east-west alignment, a fact which is not consistent with a visual piloting hypothesis. Highly variable wind conditions, coupled with turbulence in the forest understory, rule out the use of olfactory piloting during scouting. In many cases, the Sun's disk was fully obstructed by cloud cover and/or overhead vegetation, making it challenging to use a sun or polarized light compass. And, although polarized light has been shown to calibrate the magnetic compass in bats (***Greif et al., 2014***), detection of skylight polarization is not thought to be widespread in mammals (***Horváth and Varjú, 2004***; ***Marshall and Cronin, 2011***). More generally, it is difficult to reconcile what advantage a north-south orientation response would provide for any of the sensory modaities discussed above.

In contrast, the Earth's magnetic field provides a stable, omnipresent cue, regardless of daily or seasonal temporal variation, visual cue availability or weather conditions. The north-south alignment of the compass run in dogs is consistent with a wealth of studies providing support for spontaneous



Video 2. Example video showing the compass run behaviour during a scouting strategy return. The GPS track is shown on the right half of the video with the red 'bulls-eye' tracker synced with the video shown on the left. The bulls-eye tracker moves across the track corresponding to the position of the dog in the video. The checkerboard square represents the location where the video ends, but does not represent any relevant features/landmarks used for analyses. Compass and GPS measurements are shown on the left and are synced to the video and bulls-eye tracker. Yellow labels appear superimposed on the right side of the screen to indicate relevant features of the excursion. Before reaching the turning point, the dog is travelling in a ~ west northwest direction. As shown, the compass run (=alignment run, azimuth C) starts at the turning point and the dog begins its initial inbound segment in the ~north direction. The compass run is terminated at 0:22 when the dog changes magnetic direction by >20˚ (see Materials and methods) and the inbound trajectory continues as the dog navigates back to the owner (not shown).
https://elifesciences.org/articles/55080#video2

magnetic alignment along the north-south magnetic axis in a range of vertebrates in the field (reviewed in ***Begall et al., 2013***; ***Malkemper et al., 2016***) as well as in the laboratory under controlled conditions (e.g. ***Burda et al., 1990***; ***Phillips et al., 2002***; ***Muheim et al., 2006***; ***Malkemper et al., 2015***; ***Painter et al., 2018***).

While the functional significance of magnetic alignment is not fully understood, magnetic alignment may help to organize and structure many aspects of spatial behaviour (***Begall et al., 2013***). This may help to explain the compass run at the beginning of homing in scouting dogs. Indeed, several recent studies have shown that dogs are sensitive to magnetic cues (***Hart et al., 2013***; ***Adámková et al., 2017***; ***Martini et al., 2018***), and behavioural studies show that Earth-strength magnetic fields play a direct role in homing responses also in the blind mole-rat, a subterranean mammal (***Kimchi et al., 2004***). Taken together, we propose that the compass run is mediated by magnetic cues, and it helps to increase the accuracy and reduce the complexity of long-distance navigation across unfamiliar and/or highly variable environments.

Noteworthy, scouting dogs in unfamiliar locations cannot use visual landmarks to recalibrate a path integration system. Therefore, in the absence of familiar landmarks, the compass run may serve to recalibrate a path integration system relative to Earth's magnetic field, so that errors accumulated during the outbound trajectory are not incorporated into the estimate of the homing direction. Importantly, dogs in our study were not passively displaced as is usual in most homing experiments (***Tsoar et al., 2011***; ***Ostfeld and Manson, 1996***), and therefore, the involvement of path integration seems plausible, and may be one of several reasons why the compass run has not been identified in previous studies.

Our findings clearly show the importance of further research on the role and involvement of magnetic cues in canine (and more generally mammalian) navigation. More specifically, the research suggests that the magnetic field may provide dogs (and mammals generally) with a 'universal' reference frame, which is essential for long-distance navigation and arguably the most important component that is 'missing' from our current understanding of mammalian spatial behaviour and cognition.

Materials and methods

Study subjects

A total of 27 hunting dogs (10 M, 17 F) from ten breeds were used in the study (***Supplementary file 1A***- Table 1). All dogs come from breeds with pedigrees in hunting and animal tracking and were regularly assessed by veterinarians throughout the study. These dogs innately detect and pursue the olfactory tracks of game, and in rare cases, dogs were able to spot game animals from a distance (i.e. >20 m) through the forest. However, the small breeds used in this study are unable to keep pace with the much larger and faster game animals. Therefore, dogs were almost immediately left to rely on olfactory tracking and never posed any physical threat to wild animals.

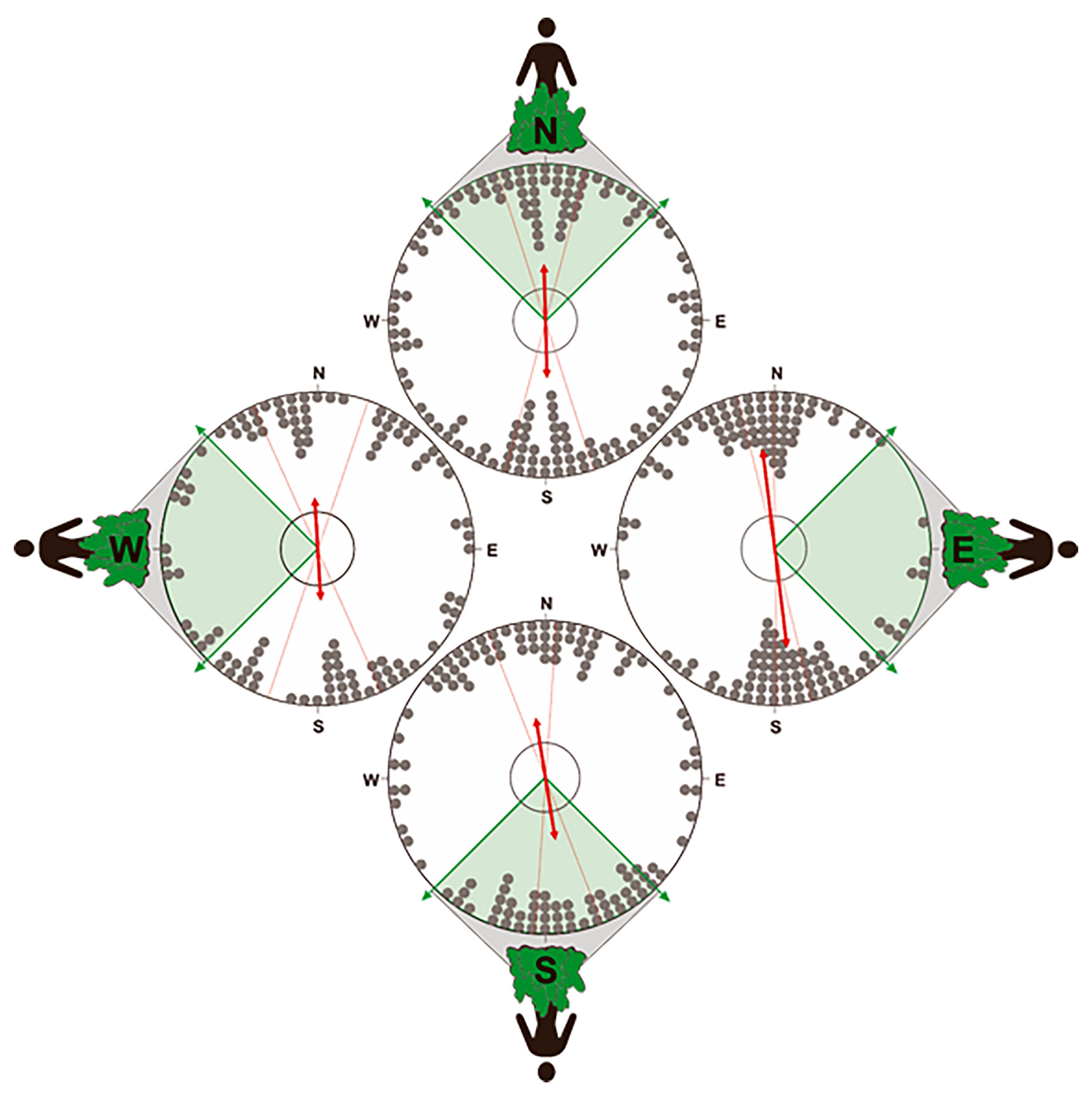


Figure 8. Orientation of the compass run plotted relative to the position of owner. To test for an influence of the owner on the orientation of the compass run (azimuth C) during scouting, the data was partitioned into four distributions corresponding to when the owner was located at one of the four cardinal compass directions (±45˚) relative to the turning point. Therefore, the distributions above show the orientation of azimuth C when the owner is positioned at magnetic ~north (316˚–45˚),~east (46˚–135˚),~south (136˚–225˚), or ~west (226˚–315˚) relative to the turning point (i.e. relative to the start of the compass run). If the N-S orientation of the compass run is a direct response to the owner (i.e. olfactory or visual piloting towards the owner), then in situations when the owner is located along the ~east west axis relative to the turning point, the orientation of the compass run should also align along the ~east-west axis. Alternatively, if the compass run is independent of the owner, then there should be no statistical difference in the orientation of azimuth C when the owner is position in different magnetic directions. Each distribution plots the axial bearings recorded from each excursion. The position of the owner relative to azimuth C is shown on the outside of each distribution and the shaded section of each plot bounded with green arrows shows the range of possible positions of the owner in each distribution (45˚ range centered on each cardinal compass direction). All other symbols are identical to those in ***Figure 6***. Note that the axial bearings have been rounded to the nearest 5˚ only to facilitate the graphical representation of the responses and all statistics were calculated using data values measured to 1˚ resolution.

Tracking equipment

Dogs were equipped with a Garmin T5 mini (or DC50) GPS collar (Garmin Ltd., USA) fitted around the neck and programed to record GPS positions at 2.5 or 5.0 s intervals (GPS accuracy ±4.2 m based on ground-truth measurements collected at study site locations). A portion of the trials (31 %) were carried out using a Garmin Virb Elite action camera (Garmin Ltd., USA) housed inside a non-magnetic stainless steel mount fixed to the side of a custom-fitted fabric harness (**Figure 1**). The camera captured a similar field of view to that of each dog (**Figure 1**), and thus provided information about the dog's visual surroundings, including habitat characteristics. In addition, a portion of the dog's head was also captured, providing information about the dog's behaviour and movement (e.g. activity, head scanning, head orientation) and an on-board microphone detected barking behaviour, an indicator that the dog was in pursuit of a game track (**Video 1**). The customized harness was designed to minimize discomfort and allowed full mobility for all dogs. Dog owners were equipped with a handheld Garmin Alpha 100 or Astro 320 receiver (Garmin Ltd., USA) used to monitor and record GPS tracks.

Experimental procedure

A total of 622 trials were performed in forested hunting grounds at 62 independent locations in the Czech Republic from September 2014 to December 2017. All trials were performed with a single dog (i.e. trials were not carried out with groups of dogs), in areas free from high voltage power lines, paved roads or buildings, and at different times of day (daylight hours only) and different times of year. Dogs were transported to each site by a car and were given a 10 min rest and acclimation period in the close surroundings of the car (<20 m radius). Dogs were then equipped with the GPS collar, and in some cases, the harness-camera setup, and walked off-leash alongside the owner into the surrounding forest. Dogs could freely roam and explore the area to search for wild game tracks using olfactory cues, as is an innate behaviour in this context for the breeds used in this study. The following game animals are common in the study region: fallow deer (*Dama dama*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), European hare (*Lepus europaeus*), and red fox (*Vulpes vulpes*). During the search period, owners did not provide visual or acoustic commands to instruct the dog. The handheld GPS device was programmed to indicate when the dog had travelled $\geq$100 m from the position of the owner. At this moment (designated as 'excursion start') the owners stopped walking and marked their location on the handheld GPS. Owners then hid behind trees or dense vegetation within a 10 m radius from the 'excursion start' to minimize the possibility of visual piloting by dogs in final stages of their inbound return (see below). The owners remained at this place until the dog returned. The location of each trial, the dog's familiarity with the location, and weather conditions (wind speed, wind direction, and temperature) were recorded. Locations visited for the first time were considered to be unfamiliar, whereas dogs who had visited the location at least once previously were considered familiar with the area. The entire trial, including excursions (see below), lasted between 30 and 90 min.

Analysis of excursions

Identifying excursion features

'Excursions' are defined as the track recorded between the excursion start (see above) and the point when the dog started its return to the owner, staying at, or within 10 m from the excursion start (**Figure 2**). All excursions were analyzed using Garmin BaseCamp 4.6.2 software (Garmin Ltd., USA). In very rare cases when dogs did not return to the owner, they were found via GPS position and excluded from further analysis (n = 16, 2.4 % of all excursions).

Based on preliminary analyses of GPS tracks used to standardize the study protocol, excursions were divided into three distinct phases: 1) *outbound trajectory*: from the excursion start to the point where the dog terminates its pursuit of the game track; 2) *turning trajectory*: the part where the dog initiates its return to the excursion start/owner; within this part, we narrowed the *turning point*; 3) *inbound trajectory*: the return track to the owner (**Figure 2A**). We expected that turning trajectory (and specifically turning point) would be characterized by slowing down, perhaps even short stop as the dog orientates.

The whole excursion length (=100 %) was divided into ten equidistant segments (i.e. each segment encompassing 10 % of the total excursion length). The average speed over each segment was

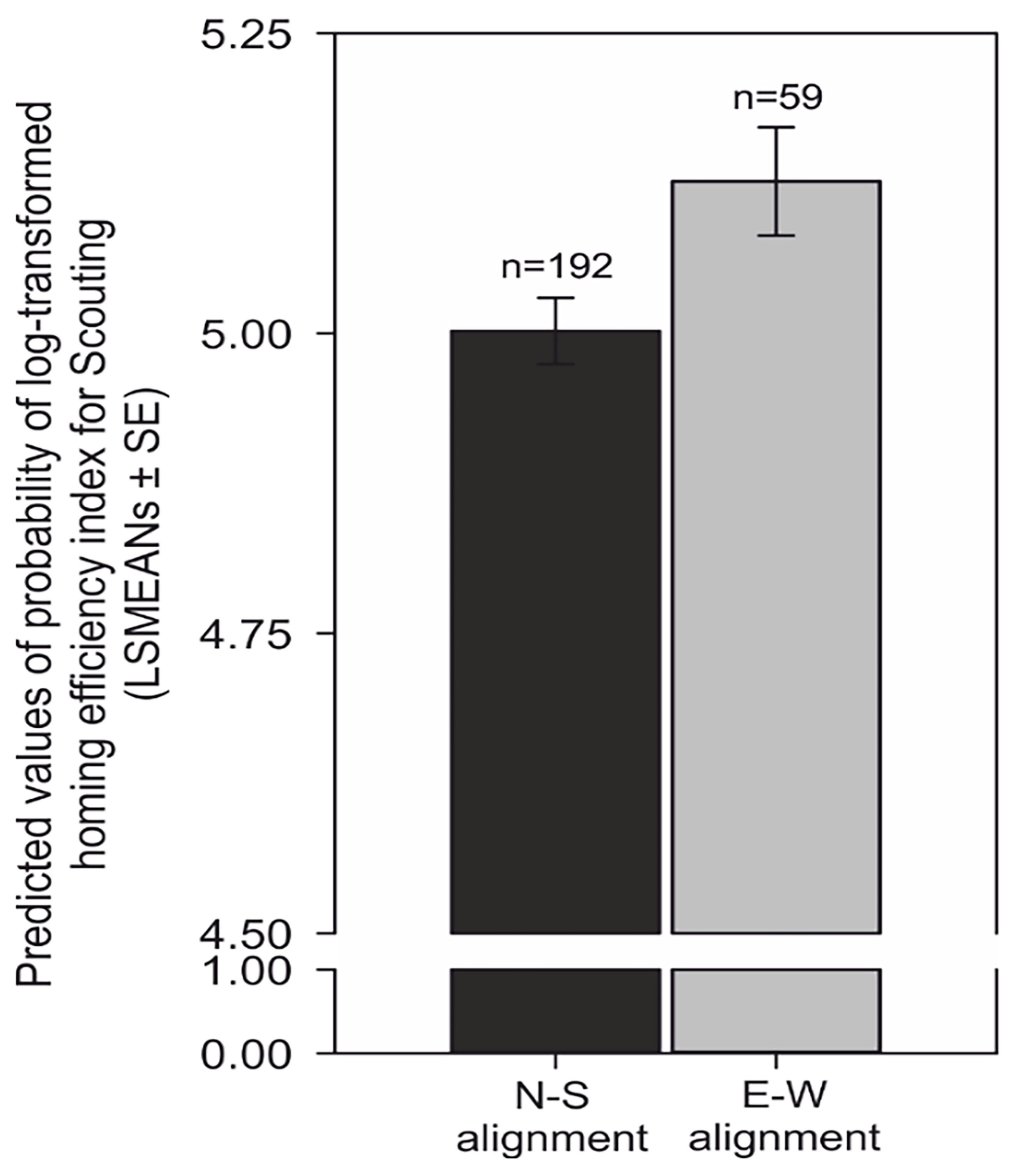


Figure 9. Compass run improves homing performance during scouting. Comparison of predicted values of the probability of log-transformed homing efficiency index (LSMEANs ± SE) between dogs exhibiting a compass run oriented along the ~north south (±45˚) compared to orientation along the east-west (±45˚) axis during scouting return strategies. The efficiency of homing is expressed as the ratio (%) between the length of the dog's inbound trajectory and the direct (beeline) distance between the turning point and the excursion start/owner. Titles and legends to supplementary videos.

calculated and the segment with the slowest speed was labelled as the *turning trajectory*. If the so determined place seems to be improbable (either too close to the start/goal or the dog pauses relatively long at one point) we checked the situation at video to exclude the possibility that the dog stopped to drink, bath, sniff at some interesting place or encountered difficult terrain. If this was the case or video was not available, the second slowest segment was identified as the turning trajectory (n = 26,<5 % of all excursions). If this segment was also located near the excursion start/owner, the respective situation was again checked at the video if available, and/or the slower segment with the farthest straight-line distance from the excursion start was labelled as the turning trajectory (n = 53, 8.5 % of all excursions).

Within the turning trajectory, the average speed was calculated between each successive GPS point. The point-to-point path within the turning trajectory with the slowest speed was identified and marked as the *turning point*, representing the specific location where the dog initiated its return to the owner (***Figure 2A***, ***Video 2***).

The focus of the current study was to evaluate long-distance navigation in free-roaming dogs, and therefore, excursions shorter than 200 m were excluded from the analyses.

Identifying azimuths

All magnetic measurements used in the analyses were made using measurement tools in Garmin BaseCamp 4.6.2 software and magnetic declination was taken into account. The magnetic direction between the point of the excursion start and the GPS point recorded five seconds after the excursion start was measured (i.e. the initial outbound segment) and is defined here as azimuth A (***Figure 2A***). Azimuth B represents the magnetic direction of the owner relative to the dog at the turning point (***Figure 2A***). The magnetic direction of the initial inbound segment, azimuth C (denoted here as *compass run*), was determined by measuring the direction between the turning point and the point where the dog exhibited a > 20˚ deflection in track direction without an immediate return to its preceding track heading (***Figure 2A***). These criteria helped to omit short-lived track deviations often caused by obstacles (e.g. fallen trees, dense clusters of vegetation) and were applied to all tracks. A criterion for classifying the compass run as either north-south or east-west, was established by grouping runs into one of four sectors corresponding to a sector of ±45˚ of the cardinal compass axes, i.e. ~north (316˚–45˚),~east (46˚–135˚),~south (136˚–225˚), or ~west (226˚–315˚).

Return strategies

Based on preliminary evaluations from a subset of excursions, each inbound return was categorized into two distinct return strategies:

1. Tracking: The inbound return trajectory followed the outbound trajectory, i.e. the dog 'simply' followed its outbound track back to the owner (***Figure 2***). Here, the inbound return track is no more than 30 m from the outbound track at any point along the return path (***Figure 2***).
2. Scouting: A novel route of return was taken to the owner (i.e. dog was not following its outbound trajectory) (***Figure 2***). Here, the inbound and outbound trajectories were separated by more than 30 m (***Figure 2***).

In some cases, dogs exhibited a combination of return strategies, e.g. dogs began the inbound return trajectory using a tracking strategy and later changed to a scouting strategy, or vice versa (***Figure 2***). In these relatively rare situations (n = 50, 8.4 % of all excursions), strategies were divided into two separate tracks and the initial inbound segments (azimuth C) were measured for each strategy.

Importantly, the personnel responsible for identifying the spatial features of excursions (i.e. excursion start, outbound, turning and inbound trajectory, turning point and owner position, see Identifying excursion features) as well as partitioning tracks into return strategy type were unaware of the directional data (azimuths A, B, C). Conversely, personnel responsible for measuring directional data were unaware to which segments and strategies each measurement belonged. Therefore, the analysis of all directional data was carried out using a double-blind protocol.

Statistical analysis

Circular statistical analyses were carried out with Oriana 4.02 (Kovach Computing Services). Before evaluation, all directional responses were grouped by return strategy. Magnetic headings for azimuth A and azimuth B were treated as angular data. However, preliminary results for azimuth C revealed a strong bimodal response within individuals, and therefore, azimuth C was treated as axial data (**Batschelet, 1981**). The Rayleigh test was used for circular statistics to determine if distributions were indistinguishable from random at the $p<0.05$ significance level. To test for non-random orientation, all responses were evaluated at the individual level (i.e. measurements from excursion treated as an independent bearing) and at the group level by calculating mean directional response from each dog then calculating a grand mean vector. A Watson's U2 test was used to test for differences between distributions (**Batschelet, 1981**).

Non-circular data were analyzed using SAS System (version 9.4). Associations between inbound speed and return strategy, as well as homing efficiency and geomagnetic alignment (N-S or E-W) were tested using a multivariate General Linear Mixed Model (GLMM, PROC MIXED), with inbound speed or homing efficiency as a dependent variable. A homing efficiency index was expressed by calculating the ratio (in %) between the track length of the inbound trajectory (i.e. track length of dog between turning point and excursion start) and the direct distance (i.e. beeline) between the turning point and excursion start. Additional analyses (i.e. alignment or return strategies as dependent variables) were performed using a GLMM with PROC GLIMMIX for binary distributions. Link function was logit and the distribution of error terms was binomial in the GLMM. Since models with PROC GLIMMIX did not converge due to an effect with considerably larger classes (dog ID and/or breed), we applied the procedure with Method = Laplace (**Kiernan et al., 2012**).

Models were constructed by entering the predicted effects, i.e. return strategy for dependent variables, inbound speed and alignment (modelling the probability that geomagnetic alignment = N s); and dependent variable for homing efficiency index. Each model was checked with additional factors that could affect the model predictions (see **Supplementary file 1C**- Table 3 for list of factors). Factors which did not contribute (i.e. factor significance $p>0.05$) were dropped from the model. Interaction terms were tested and all tests were treated as two-tailed distributions.

The effects used in the analyses were continuous variables and classes are listed in **Supplementary file 1. C** - Table 3. Where appropriate, variables were log-transformed to improve normality of residuals and to reduce skewness. All fitted models included the dog's identity as a random effect to account for the use of repeated measures across the same individuals.

Least-squares means (LSMEAN) were computed for each class and differences between classes were tested using a t-test. Associations between the dependent variable and time were estimated by fitting a random coefficient model using PROC MIXED (**Tao and Littell, 2002**). Predicted values of the dependent variable were calculated and plotted against the fixed effect with predicted regressions for each group. Where more than one value was plotted in the same position, a bubble plot was generated to represent the data.

To compare the probability of an event between two groups, an odds ratio was calculated (**Stokes et al., 2012**). Odds ratios greater than one imply that the event is more likely to occur in the first group, while an odds ratio less than one implies that the event is more likely to occur in the second group.

Acknowledgements

We thank the following students, colleagues and collaborators for helping to collect the field data: Tereza Březinová, Václav Fuks, Hedvika Fuksová, Mirka Jakšlová, Barbora Kletečková, Hana Kneřová, Alena Mottlová, Richard Policht, Jaroslav Spal, Hana Spalová, and Miloslav Zikmund. We thank Richard Holland, Diethard Tautz, and two anonymous reviewers for their constructive comments on the manuscript.

Additional information

Funding

Funder	Grant reference number	Author
European Social Fund	Operational Programme Research, Development and Education, EVA 4.0	Hynek Burda
European Social Fund	Operational Programme Research, Development and Education, CZ.02.1.01/0.0/0.0/16_019/0000803	Hynek Burda
Ministry of Agriculture of the Czech Republic	MZE-RO0718	Luděk Bartoš
Czech University of Life Sciences Prague	CIGA CZU (Project No. 20174319)	Hynek Burda
Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague	IGA (Project No. B07/16)	Hynek Burda
Grant Agency of the Czech Republic	No. 15-21840S	Hynek Burda
European Regional Development Fund	Operational Programme Research, Development and Education, EVA 4.0	Hynek Burda
European Regional Development Fund	Operational Programme Research, Development and Education, CZ.02.1.01/0.0/0.0/16_019/0000803	Hynek Burda

The funders had no role in study design, data collection and interpretation, or the decision to submit the work for publication.

Author contributions

Kateřina Benediktová, Conceptualization, Resources, Data curation, Formal analysis, Investigation, Visualization, Methodology, Writing - original draft; Jana Adámková, Investigation, Visualization, Methodology, Project administration; Jan Svoboda, Petra Nováková, Investigation; Michael Scott Painter, Formal analysis, Methodology, Writing - original draft, Writing - review and editing; Luděk Bartoš, Formal analysis, Visualization, Writing - original draft, Writing - review and editing; Lucie Vynikalová, Formal analysis, Visualization; Vlastimil Hart, Conceptualization, Supervision, Funding acquisition, Methodology, Writing - original draft, Project administration; John Phillips, Formal analysis, Writing - original draft, Writing - review and editing; Hynek Burda, Conceptualization, Formal analysis, Supervision, Funding acquisition, Validation, Visualization, Methodology, Writing - original draft, Project administration, Writing - review and editing

Author ORCIDs

Kateřina Benediktová https://orcid.org/0000-0003-0130-4770
Vlastimil Hart http://orcid.org/0000-0003-4901-3817
Hynek Burda https://orcid.org/0000-0003-2618-818X

Ethics

Animal experimentation: Permission from landowners and local game managers were obtained prior to entering each location, and searching and tracking methods were in accordance with the Czech national law and regulations for game management (§ 14 and § 15, Decree No. 244/2002, Ministry of Agriculture, Statue No. 449/2001, Game Management). The Professional Ethics Commission of the Czech University of Life Sciences in Prague has decided that according to the law and national and international rules, this study has not a character of an animal experiment and does not require a special permit.

Decision letter and Author response

Decision letter https://doi.org/10.7554/eLife.55080.sa1
Author response https://doi.org/10.7554/eLife.55080.sa2

Additional files

Supplementary files

- Source data 1. Basic raw data used in calculations.
- Supplementary file 1. Information on subjects studied, parameters included in the analyses, and results of circular statistics. (A) Table 1 Information about dogs used in the study. Owner = initials of owner accompanying dog during walks, Age = age or age-range during the study period, N_{OUT} = number of outbound trajectories, N_{IN} = total number of inbound trajectories, N_T = number of inbound returns using a tracking strategy, N_S = number of returns using a scouting strategy. (B) Table 2 Factors in the final GLMMs for the dependent variables (in bold). a) probability for N-S alignment (±45˚) during the initial inbound segment (i.e. 'compass run'); b) probability for scouting strategy; c) efficiency of return; d) speed of inbound trajectory; e) inbound track length. (C) Table 3 Effects used in General Linear Mixed Models. (D) Table 4 Length parameters during different phases of the excursion (data from combined strategies are excluded). (E) Table 5 Circular analyses of individual ('raw') and grouped means for azimuth A, B and C during scouting and tracking strategies, and when a scouting strategy was used as the second return strategy (tracking used as a second return strategy not shown). Means were calculated by averaging directional headings for each dog, then calculating a grand mean from all individuals. Raw data were calculated by treating each azimuth as an independent bearing. Note that due to the bimodal preference found within individual dogs for azimuth C, these bearings were treated as axial data. See ***Figures 6–8***. (F) Table 6 Axial analyses of azimuth C (=orientation of the compass run) partitioned into four groups to test for an influence of the owner on the orientation of the compass run during scouting strategy returns. Each analysis corresponds to the orientation of the compass run when the owner was located in one of four cardinal compass directions (±45˚) relative to the turning point. Therefore, owner positions relative to the turning point are: owner = magnetic ~ north (316˚–45˚),~east (46˚–135˚),~south (136˚–225˚), or ~west (226˚–315˚). All data are treated as independent bearings. (See ***Figure 8***).
- Transparent reporting form

Data availability

The raw source data are provided as Source Data 1.

References

Adámková J, Svoboda J, Benediktová K, Martini S, Nováková P, Tůma D, Kučerová M, Divišová M, Begall S, Hart V, Burda H. 2017. Directional preference in dogs: laterality and "pull of the north". *PLOS ONE* **12**:e0185243. DOI: https://doi.org/10.1371/journal.pone.0185243, PMID: 28945773

Batschelet E. 1981. *Circular Statistics in Biology*. London: Academic Press.

Begall S, Malkemper EP, Červený J, Němec P, Burda H. 2013. Magnetic alignment in mammals and other animals. *Mammalian Biology* **78**:10–20. DOI: https://doi.org/10.1016/j.mambio.2012.05.005

Burda H, Marhold S, Westenberger T, Wiltschko R, Wiltschko W. 1990. Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus (Bathyergidae)*. *Experientia* **46**:528–530. DOI: https://doi.org/10.1007/BF01954256, PMID: 2347407

Cullen KE, Taube JS. 2017. Our sense of direction: progress, controversies and challenges. *Nature Neuroscience* **20**:1465–1473. DOI: https://doi.org/10.1038/nn.4658, PMID: 29073639

Greif S, Borissov I, Yovel Y, Holland RA. 2014. A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. *Nature Communications* **5**:4488. DOI: https://doi.org/10.1038/ncomms5488, PMID: 25050897

Hart V, Nováková P, Malkemper EP, Begall S, Hanzal V, Ježek M, Kušta T, Němcová V, Adámková J, Benediktová K, Červený J, Burda H. 2013. Dogs are sensitive to small variations of the earth's magnetic field. *Frontiers in Zoology* **10**:80. DOI: https://doi.org/10.1186/1742-9994-10-80, PMID: 24370002

Horváth G, Varjú D. 2004. *Polarized Light in Animal Vision*. Berlin, Heidelberg: Springer. DOI: https://doi.org/10.1007/978-3-662-09387-0

Kiernan K, Tao J, Gibbs P. 2012. *Tips and Strategies for Mixed Modeling with SAS/STAT Procedures*. SAS Global Forum.

Kimchi T, Etienne AS, Terkel J. 2004. A subterranean mammal uses the magnetic compass for path integration. *PNAS* **101**:1105–1109. DOI: https://doi.org/10.1073/pnas.0307560100, PMID: 14732687

Lohmann KJ. 2018. Animal migration research takes wing. *Current Biology* **28**:R952–R955. DOI: https://doi.org/10.1016/j.cub.2018.08.016, PMID: 30205070

Malkemper EP, Eder SHK, Begall S, Phillips JB, Winklhofer M, Hart V, Burda H. 2015. Magnetoreception in the wood mouse (*Apodemus sylvaticus*): influence of weak frequency-modulated radio frequency fields. *Scientific Reports* **5**:9917. DOI: https://doi.org/10.1038/srep09917

Malkemper EP, Painter MS, Landler L. 2016. Shifted magnetic alignment in vertebrates: evidence for neural lateralization? *Journal of Theoretical Biology* **399**:141–147. DOI: https://doi.org/10.1016/j.jtbi.2016.03.040, PMID: 27059891

Marshall J, Cronin TW. 2011. Polarisation vision. *Current Biology* **21**:R101–R105. DOI: https://doi.org/10.1016/j.cub.2010.12.012, PMID: 21300269

Martini S, Begall S, Findeklee T, Schmitt M, Malkemper EP, Burda H. 2018. Dogs can be trained to find a bar magnet. *PeerJ* **6**:e6117. DOI: https://doi.org/10.7717/peerj.6117, PMID: 30588405

Mouritsen H. 2018. Long-distance navigation and magnetoreception in migratory animals. *Nature* **558**:50–59. DOI: https://doi.org/10.1038/s41586-018-0176-1, PMID: 29875486

Muheim R, Edgar NM, Sloan KA, Phillips JB. 2006. Magnetic compass orientation in C57BL/6J mice. *Learning & Behavior* **34**:366–373. DOI: https://doi.org/10.3758/BF03193201, PMID: 17330527

Nahm M. 2015. Mysterious ways : the riddle of the homing ability. *J. Soc. Psych. Res* **79**:140–155.

Ostfeld RS, Manson RH. 1996. Long-Distance homing in Meadow Voles, *Microtus pennsylvanicus*. *Journal of Mammalogy* **77**:870–873. DOI: https://doi.org/10.2307/1382692

Painter MS, Davis M, Ganesh S, Rak E, Brumet K, Bayne H, Malkemper EP, Phillips JB. 2018. Evidence for plasticity in magnetic nest-building orientation in laboratory mice. *Animal Behaviour* **138**:93–100. DOI: https://doi.org/10.1016/j.anbehav.2018.02.006

Papi F. 1992. *Animal Homing*. Berlin, Heidelberg: Springer. DOI: https://doi.org/10.1007/978-94-011-1588-9

Phillips JB, Freake MJ, Fischer JH, Borland CS. 2002. Behavioral titration of a magnetic map coordinate. *Journal of Comparative Physiology A* **188**:157–160. DOI: https://doi.org/10.1007/s00359-002-0286-x

Poulter S, Hartley T, Lever C. 2018. The neurobiology of mammalian navigation. *Current Biology* **28**:R1023–R1042. DOI: https://doi.org/10.1016/j.cub.2018.05.050, PMID: 30205053

Richardson EH. 1920. *Dogs Bwar Their Training and Psychology*. London: Skeffington & Son Ltd.

Schmidt-Koenig K, Keeton WT. 1978. *Animal Migration, Navigation, and Homing*. Berlin, Heidelberg: Springer. DOI: https://doi.org/10.1007/978-3-662-11147-5

Stokes ME, Davis CS, Koch GG. 2012. *Categorical Data Analysis Using SAS*. SAS Institute Inc.

Tao J, Littell R. 2002. *Mixed Models Analyses Using the SAS System: Course Notes*. SAS Institute Inc.

Tsoar A, Nathan R, Bartan Y, Vyssotski A, Dell'Omo G, Ulanovsky N. 2011. Large-scale navigational map in a mammal. *PNAS* **108**:E718–E724. DOI: https://doi.org/10.1073/pnas.1107365108, PMID: 21844350

Wiltschko R, Wiltschko W. 1995. *Magnetic Orientation in Animals*. Berlin, Heidelberg: Springer. DOI: https://doi.org/10.1007/978-3-642-79749-1

Wolbers T, Wiener JM. 2014. Challenges for identifying the neural mechanisms that support spatial navigation: the impact of spatial scale. *Frontiers in Human Neuroscience* **8**:1–12. DOI: https://doi.org/10.3389/fnhum.2014.00571, PMID: 25140139

Processing Methods of Camera Record of Animal Movement

Patrik Kutilek
Faculty of Biomedical Engineering
Czech Technical University in Prague
Kladno, Czech Republic
kutilek@fbmi.cvut.cz

Petr Volf
Faculty of Biomedical Engineering
Czech Technical University in Prague
Kladno, Czech Republic
petr.volf@fbmi.cvut.cz

Jan Hejda
Faculty of Biomedical Engineering
Czech Technical University in Prague
Kladno, Czech Republic
jan.hejda@fbmi.cvut.cz

Katerina Benediktova
Faculty of Forestry and Wood Sciences
Czech University of Life Sciences
Prague, Czech Republic
benediktovak@fld.czu.cz

Jana Adamkova
Faculty of Forestry and Wood Sciences
Czech University of Life Sciences
Prague, Czech Republic
adamkovaj@fld.czu.cz

Eva Kutilkova
Faculty of Biomedical Engineering
Czech Technical University in Prague
Kladno, Czech Republic
kutilkova@fbmi.cvut.cz

Jan Svoboda
Faculty of Forestry and Wood Sciences
Czech University of Life Sciences
Prague, Czech Republic
svoboda@oikt.czu.cz

Vaclav Krivanek
Faculty of Military Technology
University of Defence
Brno, Czech Republic
vaclav.krivanek@unob.cz

Ana Carolina D'Angeles M. de Brito
Faculty of Biomedical Engineering
Czech Technical University in Prague
Kladno, Czech Republic
ana-carolina.dangeles-mendes-de-brito@fbmi.cvut.cz

***Abstract*—The aim of this paper is to introduce in detail methods for processing of visible-light digital camera records of animals in their natural environment to study animal movements. Two types of recordings have been used – videos from a stationary camera and videos from wearable camera on animal body. For this reason, two different data processing procedures are introduced. The first method allows determine the position of the animal in the space using a stationary camera. The second method allows determine the intensity of the animal's movement using wearable camera. The methods have been tested. The movement of cattle and dogs was recorded by cameras. A software has been designed in MatLab® to process videos and preprocess motion data for further study. A part of the work's results is thus a presentation of a method for monitoring and preprocessing animal's movements. The described methods and procedures have been developed according to the specific requirements for recording of animal movements. The assumption for the future is the application of methods and movement parameters for studying the function of the nervous system.**

Keywords—camera, visible-light, recording, animals, kinematics, movement

I. INTRODUCTION

Past studies have already introduced the uniform methods of processing the visible-light camera records of the animal movement. The methods rely on the evaluation of videos from a stationary visible-light digital camera and videos from wearable visible-light digital camera. First measurements were carried out by stationary camera placed above the subject and recording the movement of animals. The method is based on an already established animal movement measurement methodology, see Table I. The method assumes a random or specific stationary location of the camera in front of the monitored subjects. These studies of the movement of animals in their natural environment usually serve to develop pharmacology or study the function of the nervous system [11]. In general, however, it is problematic to automatically process the video recordings captured by visible-light digital camera. Based on this, most of the recordings made with a visible-light digital camera are evaluated manually, see Tab. I. Usually, motion recording is performed in artificial environments using specialized camera-based motion capture (MoCap) systems in which, for accurate recording, active or passive markers are placed on the anatomical points of the animal's body segments [12]. These systems typically require a complex calibration before use and the specific placement of the cameras in space, i.e. environment. However, these specialized systems can't usually be used in the natural animal's environment. Also, such MoCap systems typically require the use of multiple cameras and are therefore extremely costly [13]. Other limitations of such systems are their specificity in. application offering limited versatility for measuring different species of animals [14].

In order to make animal movement measurements by visible-light digital camera more flexible, processing methods have been developed with MatLab software (MatLab R2010b, Mathworks, Inc., Natick, MA, USA) in which the body movement is recorded using common

TABLE I. TABLE OF VISIBLE-LIGHT DIGITAL CAMERA APPLICATIONS AND PROCESSING METHODS

Type of recording	*Camera placement*	*Method of processing*	*Studied animal*	*Reference*
stationary camera	random	manual	Raven	[1]
stationary camera	random	manual	Flamingo	[2]
stationary camera	above	manual	Wood mouse	[3]
stationary camera	above	manual	Carp	[4]
stationary camera	above	manual	Pheasant	[5]
stationary camera	above	manual	Hamster	[6, 7]
stationary camera	above	manual	Mole-rat	[8]
satellite camera	above	manual	Cattle, Deer	[9, 10]

This work was done in the framework of research project SGS17/108/OHK4/1T/17 sponsored by Czech Technical University in Prague. The work presented in this article has also been supported by the Czech Republic Ministry of Defence (University of Defence development program "Research of sensor and control systems to achieve battlefield information superiority").

visible-light digital camera. These methods allow the evaluation of body movement as a whole on small or big size animals. The method, designed in accordance with the requirements made by Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, shall be described in this article. To describe and test the methods, different animal species has been chosen since it is a representative sample of subjects for future research.

II. METHODS

A. *Movement Recording by Stationary Digital Camera*

For the study of the animal movement, it is best to use a "open field" test, as in [15], ideal for the animal to move freely. And for the observation of the movement in the vertical and horizontal plane, it is advisable to scan the planes separately. Of course, the entire scene of motion in both vertical and horizontal plane can be observed with one static camera. However, in this case, is necessary to transform the image which is, in the natural environment of the animal, a quite impossible task to achieve and thus, to accurately calculate the position of the animal. Therefore, the number of monitored motion parameters is also reduced.

B. *Movement Recording by Wearable Digital Camera*

For the study of the movement activity of animals by wearable camera placed on the animal body, it is necessary to place the camera on the body segment whose motion activity we want to evaluate. This placement must be done in such a way that the camera is able to record the movement of the surroundings in relation to the body segment of the animal. If we want to observe the movement in the vertical and horizontal plane, it is necessary to place the camera and its optical axes firmly on the body segment in accordance with the vertical and horizontal axis of the ground. However, for recording only general movement activity of a body segment, it is not necessary to meet this requirement. If you want to evaluate the physical activity of the whole body, it is necessary to place a wearable camera close to the center of gravity of the body, i.e. in case of a dog on the dog's trunk. To simplify the calculation, we can consider the trunk as a rigid object and neglect movements in the trunk.

C. *Processing of Records Captured by Stationary Digital Camera*

MatLab software can be used for image processing, which contains many useful functions and algorithms for image motion detection as well as image transformation, which is necessary if we want to convert animal position into specific defined planes using a single camera record. After the video is loaded, it is convenient to convert images to gray-scale images for further processing, which is done with the "rgb2gray" function. If we are interested in an animal movement only in the specific area of the picture, we can use the function of "roipoly" to specify polygonal region of interest (ROI). Select the region of interest using "roipoly" (similar to "imcrop", but ROI is a polygon) can be region in which the movement can be monitored. After that, ROIs of images recorded at time t_n and t_{n+1} are loaded using VideoReader and ReadFrame functions.

For the motion detection in the image, the most commonly used method is the differential method where the individual images are subtracted from each other, i.e. difference by simply subtracting the ROIs of the frames recorded at time t_n and t_{n+1} is calculated. Due to time and computational limitations, we set the reading of the pictures to 2 Hz. The difference obtained by simply subtracting the ROIs is then converted to the opposite brightness value, [16]. The differential method of motion detection is inherently inapplicable; it must be combined with other methods, such as the method of thresholding, as also described in [17]. That's why thresholds in the algorithm must be applied.

Among the image processing techniques, we also suggest the remotion of the noise and an overall adjustment of the difference obtained. The difference obtained is converted to a white area of detected difference in image using the "im2bw" function. The "rgb2gray" function is used to convert the image into grayscale image while the thresholding of the converted image is made by "im2bw". The "im2bw" function requires setting a threshold value that we have experimentally determined as 0.03 for our applications.

The MatLab software provides various features that determine the rate of erosion and dilation, resulting in sharper edges in the image obtained after the threshold. We suggested using the "imopen", "strel", "imerode" and / or "imdilate" MatLab morphological functions that covers both these image adjustments. Both of these modifications provide the "imopen" function, the input of which is the white area of detected difference and the variable with the "strel" function. The "strel" function determines the rate of erosion and image dilation to remove the noise and simplify the shape of the image of difference.

Another step is to define the center of the pixel clusters that represent the acquired difference in the animal position. The "regionprops" function was used for the calculation of the center of the pixel cluster of white area of detected difference. The position of this center is different at each reading, so we get the center coordinates of the x and y axes. Coordinates represent a change in the position of a point representing a moving of a subject over time.

Differential method has the disadvantage that if the animal stops moving, we lose information about its position in image. This problem has been resolved using the "isempty" function and matrix, which contains the unknown coordinates when the subject was not detected. Then, these coordinates were set to the last detected values of coordinates. The output is the coordinate matrix of animal position.

If we are interested in whether the animal is moving or not moving and at what movement intensity, we can again use the MatLab SW tools. If the change in position is not identified, i.e. no movement is detected, and we know that the animal is in the area of interest (according to the latest detected body position coordinates), we assume the animal does not move. This way, it can distinguish the resting and movement phases. In the case of movement, it can determine the intensity of movement. In the case of motion, it can determine the intensity of movement that is given by the difference in the position of the body (i.e., coordinates) in consecutive frames. If we do not know the real dimensions of the space in which the animal is moving, the intensity of the movement is determined by the distance of the coordinates (in pixels) in consecutive frames.

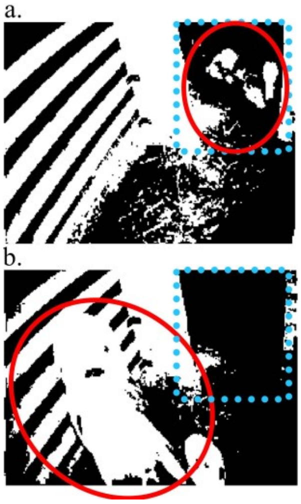


Fig. 1. Example of processing of records captured by stationary digital camera for measuring movement of animal; a) Animal under shetler in predefined bounding polygon (rectangle), b) Animal outside the shetler, i.e. outside the predefined bounding polygon.

The animal movement can also be monitored not only in the whole picture, but also in its parts. By using the digital cut of a certain area of pixels in the image, we can determine the movement of the animal in the defined areas (i.e. bounding polygons) in each picture by the above methods. For easier analysis, each bounding polygon can be resized and crop and analyzed separately.

D. Processing of Records Captured by Wearable Digital Camera

As in the case of processing of records captured by stationary digital camera, we can select the region of interest by using the Imcrop MatLab sw function. The selection of ROI is according to the part of the image that records the movements of the surroundings around the animal's body. After that, ROIs of images recorded at time t_n and t_{n+1} are loaded using VideoReader and ReadFrame functions. Due to time and computational limitations and the presumed accuracy of physical activity identification, we set the time step to 0.1 s. Next, we calculate the difference by simply subtracting the ROIs of the frames recorded at time t_n and t_{n+1}. Then, the low pass filter function is used to obtain the resulting difference vector of ROIs (smooth function, in MatLab SW, parameter set to 50). With respect to the evaluation of motion activity during locomotion, normalization of the resulting vector Y to the range of measured values can be applied:

$$Y_{\text{norm}} = \frac{Y - [\min(Y)]}{\max(Y) - \min(Y)}. \tag{1}$$

After normalization, it is possible to use a fixed threshold or any adaptive threshold to a normalized motion vector Y_{norm} to distinguish locomotion phases (rest, movement, etc.). For example, zero values in the vector of movement activity can be used after application of threshold to distinguish low movement activities, which correspond to rest locomotion phases.

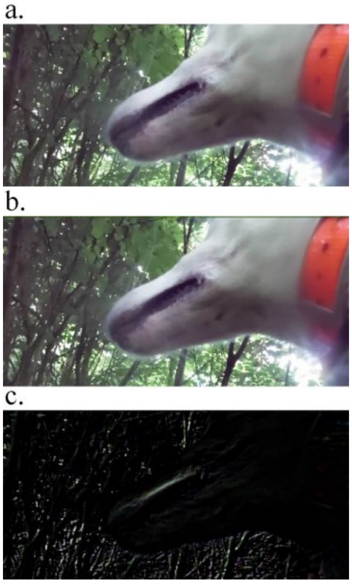


Fig. 2. Example of processing of records captured by wearable digital camera for measuring movement of animal; a) Frame recorded at time t_n of animal, b) Frame recorded at time t_{n+1} of animal, c) Result of subtracting the frames recorded at time t_n and t_{n+1} (differences are in white color).

E. Evaluation Methods of Data Captured by Stationary Digital Camera

After the image processing is completed, the x and y coordinates of the animal's positions in the image over time are obtained. If animal is monitored in its natural environment by a single camera and it is not possible to transform the animal position into individual planes (e.g. the Earth or animal body coordinate system) it is possible to determine the intensity of the animal's movement. Mathematical operations implemented in MatLab software can also be used to determine the time spent resting or moving. Also is possible to find out the moments the animal was in predefined areas in the image.

In order to determine the time spent at rest, zero values in the vector of changes of animal position in the image are used. Durations of the zero values in vector is assumed for other statistical analysis. In order to further statistically process the results, it is necessary to normalize the data, so that the calculated times (i.e. duration of the rest or movement) are divided by the total duration of the record.

F. Evaluation Methods of Data Captured by Wearable Digital Camera

After the image processing is completed, as well as the stationary cameras, the normalized motion vector informs about the intensity of movement of the relevant body segment. Mathematical operations implemented in MatLab software can be used to determine the time spent in rest or movement, or to find out the time the animal was in predefined areas in the image.

To determine the time spent at rest, zero values in the vector of movement activity of animal are used. Durations of the zero values in vector is assumed for other statistical analysis. In order to further statistically process the results, we can apply same methods as in the case of the evaluation of data captured by stationary camera.

III. EXPERIMENTS

A. *Selection of Subjects*

In accordance with the requirements of Faculty of Forestry and Wood Sciences Czech University of Life Sciences, the cow movements were monitored with a stationary digital camera. The aim of the technical proposal was to monitor the position of the cow, i.e. where the cow is located in the enclosure area.

In case of the movement recording by wearable digital camera, dogs with camera placed on the trunk were monitored. The aim of the technical proposal was to monitor the intensity of the animal's movement using wearable camera and identify stops and movement sections during locomotion.

B. *Application of Stationary Digital Camera*

The cows were placed in hutch and video recordings were captured by visible-light digital camera. The purpose of the study was to monitor whether the cow is under shelter or not and whether it is moving or not. One camera recorded pictures of space outside and inside the shelter, see Fig.1. Each picture of camera recording was digitally (by MatLab SW) divided in two areas. One area corresponded to the space inside the shelter and the other to the outside of the shelter. Areas are predefined by bounding polygons (rectangles). After that, a threshold was applied to see clearly the cow, see Fig.1. After, we used the above-described methods applied in the MatLab environment to identify the position and movement of animals.

C. *Application of Wearable Digital Camera*

The wearable camera was placed on trunk of the animal's body behind head of a dog. The camera allows you to monitor the environment in which the dog moves. The goal of this study was not to precisely track the movement in the horizontal and vertical axis, thus, the optical axis of the camera does not follow the exact directions. Each picture of camera recording was digitally processed by MatLab SW. We used the above-described methods applied in the MatLab environment to identify the intensity of animal movement, see Fig. 2.

IV. RESULTS

In accordance with the aim of this paper, the output from the custom written software created in MatLab environment is the information on all mentioned parameters to quantitatively describe the movement activity of animals. Considering the application of stationary digital camera, the Fig. 3 shows an example of diagrams of measuring animal activity. The graphs show passive and active phases of animal behavior, and location of animal (i.e. animal is inside or outside the shelter). From the Fig. 3 it is obvious the both graphs are corresponding to each other. This is because under the shelter the animal usually rests and sleeps, but the animal less often rests outside the shelter. However in some cases artifacts appear as in case of 395 s (Fig. 3a). These artifacts may be caused by movements of other animals, such as flies, near the camera or by the movement of specific parts of the cattle, for example tail. Diagrams (i.e. vectors of movement activities and location) were used to determine the ratio of the time of occurrence of the animal inside and outside the shelter, and the ratio of the time of rest and the time of the animal's movement.

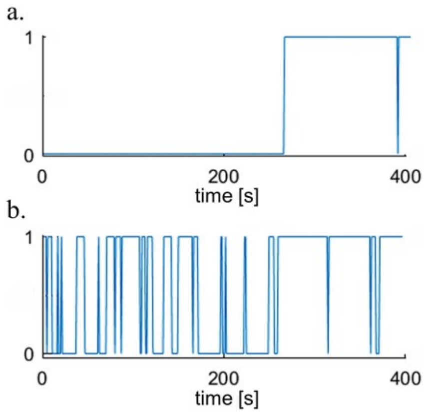


Fig. 3. Example of output from method for processing of stationary digital camera records; a. Identification of animal under shelter (1-animal inside the shelter, 0- animal outside the shelter), b. Identification of animal activity (1-animal is passive, 0- animal is active).

In the case of the application of wearable digital camera and the camera record processing described above, the Fig. 4 shows an example of diagrams of measuring animal activity. The graphs show passive and active phases of animal behavior, and normalized intensity of movement. Diagrams (i.e. vectors of normalized movement activities) were used to determine the ratio of ratio of the time of rest and the time of the animal's movement.

V. DISCUSSION

A special method for a movement activities of animals were designed, especially for quantitative evaluation of ratio of the time of rest and the time of the animal's movement by stationary digital camera and wearable digital camera in accordance with the requirements of Faculty of Forestry and Wood Sciences, Czech University of Life Sciences. Parameters of movement activity and animal location in space, which are outputs from the custom written software, are mentioned to further scientific research to develop pharmacology or study the function of the nervous system. Within the testing of the designed methods and procedures, movement of the body of cows and dogs was measured during daily activities of animals (movement for food, hunting, etc.). The proposed methods of the camera record processing enabled the desired indicators of movement activity to be determined. Moreover, we can use the output

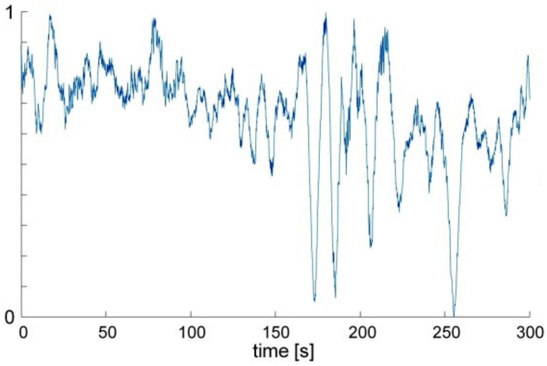


Fig. 4. Example of output from method for processing of wearable digital camera records (1 - maximum movement activity, 0 - minimum movement activity).

graphs and vectors of activity for calculation of other indicators. For example, in the case of the application of stationary digital camera, the calculations can use both graphs (Fig. 3) and we can calculate e.g. the ratio of rest and the time of the animal's movement outside the shelter.

If we compare the designed methods for processing of records captured by stationary digital camera with other methods, for example [2], the software we created enables the calculation of new parameters automatically without other software or specific type of camera (expensive cameras based on active or passive markers, etc. [18, 19]), which speeds up the processing of the record. If we compare the designed methods for processing of records captured by wearable digital camera with other methods, no designed software currently allows the determination of movement activity of animals automatically.

When comparing the camera applications with our proposed procedures with other MoCap systems, specifically accelerometers or GPS, stationary cameras, we get complete information about what specific activity the animals performed, and there is no need to use a complicated algorithm, e.g. to calculate the location. This algorithm must be used in an accelerometer system because of an integration in the calculations when this measurement is long. Another advantage is contactless motion sensing, such as accelerometer, GPS etc. do not allow [20].

Of course, the use of camera systems by our proposed procedures also has limitations, but these are mostly solved as camera systems are used in medicine for the longest time of all MoCap systems [21]. For example, in the case of low illumination the environment can be illuminated by an external source of light, or we can use infrared spectrum cameras that do not affect the animal [22]. Of course, it is possible to use different types of specific cameras, i.e. camera systems. The applicability of the proposed methods is not affected by the electromagnetic spectrum in which the subjects are recorded.

VI. CONCLUSION

The article presents methods of processing the visible-light camera records of animal movement. The methods allow the evaluation of videos from a stationary visible-light digital camera and videos from wearable visible-light digital camera. The methods are dedicated to measure movements of small animals within the scope of veterinary and scientific use and enables determination of pathological or unique states in attitude of the animal. Therefore, there is an assumption of future testing of the methods for movement evaluation of different animal species in the natural environment for veterinary and scientific use.

REFERENCES

[1] L.Pleskac, V. Hart, P. Nováková, MS. Painter 'Spatial orientation of foraging corvids consistent with spontaneous magnetic alignment responses observed in a variety of free-roaming vertebrates', Folia Zoologica, vol. 66, no. 2, pp. 87-94, 2017.

[2] P. Nováková, D. Kořanová, S. Begall, E.P. Malkemper, L. Pleskač, F. Čapek, J. Červený, V. Hart, V. Hartová, V. Husinec, H. Burda, "Direction indicator and magnetic compass-aided tracking of the sun by flamingos?" Folia Zoologica. 66 (2): 79–86, 2017.

[3] E.P. Malkemper, S.H.K. Eder, S. Begall, J.B. Phillips, M. Winklhofer, V. Hart, H. Burda, "Magnetoreception in the wood mouse (Apodemus sylvaticus): Influence of weak frequency-modulated radio frequency fields", Scientific Reports 4 : 9917, doi: 10.1038/srep09917, 2015.

[4] V. Hart, T. Kušta, P. Němec, V. Bláhová, M. Ježek, P. Nováková, S. Begall, J. Červený, V. Hanzal, E.P. Malkemper, K. Štípek, C.Vole, H. Burda, "Magnetic alignment in carps: Evidence from the Czech Christmas fish market", Plos One, PONE-D-12-23466R1, 2012.

[5] F. Čapek, J. Průcha, V. Socha, V. Hart, H. Burda, "Directional orientation of pheasant chicks at the drinking dish and its potential for research on avian magnetoreception" Folia Zoologica, 66(3):175-182, 2017.

[6] S. Malewski, S. Begall, H. Burda, "Learned and spontaneous magnetosensitive behaviour in the Roborovski hamster (Phodopus roborovskii)", Ethology. 124, 6, 423-431, ISSN: 0179-1613. June 2018.

[7] S. Malewski, S. Begall, H. Burda, "Light-independent magnetosensitive behaviour in the Djungarian hamster (Phodopus sungorus)", Mammalian Biology. July 2018.

[8] S. Malewski, E.P. Malkemper, F. Sedláček, R. Šumbera, K.R. Caspar, K. Burda, S. Begall, "Attracted by a magnet: Exploration behaviour of rodents in the presence of magnetic objects", Behavioural Processes, vol. 151, pp. 11-15, 2018.

[9] S. Begall, J. Cervený, J. Neef, O. Vojtěch, H. Burda, "Magnetic alignment in grazing and resting cattle and deer", Proceedings of the National Academy of Sciences of the United States of America, 105(36), 13451e13455, 2008.

[10] H. Burda, S. Begall, L. Cervený, J. Neef, P. Němec, "Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants", Proceedings of the National Academy of Sciences of the United States of America, 106, 5708e5713, 2008.

[11] T. Kolbabová, E.P. Malkemper, L. Barto, J. Vanderstraeten, M. Turčáni, H. Burda, "Effect of exposure to extremely low frequency magnetic fields on melatonin levels in calves is seasonally dependent", Scientific Reports, 2015.

[12] P. Kutilek, V. Socha, J. Schlenker, D. Skoda, J. Hybl, D. Frynta, E. Landova, T. Haskova, R. Cerny, and A. Kurali, "System for Measuring Movement Response of Small Animals to Changes in Their Orientation," in Proceeding of International Conference on Applied Electronics, Pilsen, Czech Rep., pp. 139-144, Sept. 2015.

[13] S. Roy, J.L. Bryant, Y. Cao, D.H. Heck, eCollection, "High-precision, three-dimensional tracking of mouse whisker movements with optical motion capture technology", Front Behav Neurosci. doi: 10.3389/fnbeh.2011.00027. Jun 2011.

[14] W.J. Geldenhuys, T.L. Guseman, I.S. Pienaar, D.E. Dluzen, J.W. Young, "A novel biomechanical analysis of gait changes in the MPTP mouse model of Parkinson's disease" Yuan T, ed. PeerJ. 2015.

[15] A. L. Samson, L. H. Ah Kim, S. R. Zhang, J. A. A. Lee, S. A. Sturgeon, S. M. Schoenwaelder, "MouseMove: an open source program for semi-automated analysis of movement and cognitive testing in rodents", Scientific Reports, 5, 2015.

[16] R.B. Ramazani, H.R. Krishnan, E.B. Susan, S. Nigel, J.N. Atkinson, Neurosci Method, Computer automated movement detection for the analysis of behavior, May 2007.

[17] R.A. Dielenberg, P. Halasz, T.A. Day, "A method for tracking rats in a complex and completely dark environment using computerized video analysis", Journal of Neuroscience Methods [online]. 2006.

[18] W.I. SellerI, E. Hirasaki E, Markerless 3D motion capture for animal locomotion studies. Biol Ope, vol. 3, pp. 656–668, 2014.

[19] L. Ren, M. Butler, C. Miller, H. Paxton, D. Schwerda, M. S. Fischer, J.R. Hutchinson, "The movements of limb segments and joints during locomotion in African and Asian elephants", Journal of Experimental Biology, vol. 211, pp. 2735-2751, 2008.

[20] P. Kutilek, J. Charfreitag, J. Hozman, "Comparison of Methods of Measurement of Head Position in Neurological Practice". In: Bamidis P.D., Pallikarakis N. (eds) XII Mediterranean Conference on Medical and Biological Engineering and Computing 2010. IFMBE Proceedings, vol. 29. Springer, Berlin, Heidelberg 2010.

[21] M.J. Gómez, C. Castejón, J.C. García-Prada, M. Ceccarelli, "Analysis and Comparison of Motion Capture Systems for Human Walking" Exp. Tech. 2016, Volume 40, Issue 2, pp. 875–883, 2016.

[22] P. Christiansen, K. Arild Steen, R.N. Jørgensen, H. Karstoft, Automated Detection and Recognition of Wildlife Using Thermal Cameras; Sensors (Basel), pp. 13778–13793, 2014.

Automatic Analysis of Long-Lasting Video Sequences of Animal Movements

Petr Volf[1], Kateřina Benediktová[2*], Jana Adámková[2], Patrik Kutílek[1,3], Jan Hejda[1], Jan Svoboda[2] and Václav Křivánek[3]

[1] Department of Natural Sciences, Faculty of Biomedical Engineering, Czech Technical University in Prague

[2] Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences

[3] Department of Air Defence Systems, Faculty of Military Technology, University of Defence in Brno

Author Note

Kateřina Benediktová ORCID iD https://orcid.org/0000-0003-0130-4770

Correspondence concerning this article should be addressed to Kateřina Benediktová, Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521 Praha 6, Czech Republic, email: benediktovak@fld.czu.cz, phone number: +420 603815473

Abstract

Analysis of long (covering many hours to months) video and audio recordings of animal behaviour require, even when employing commercial observational systems, the physical presence of the observer to scan the records, diagnose and code the behavioural patterns of interest. Here, we describe automatic methods for processing long video and audio recordings combined with global position system (GPS) information, making the physical presence of the observer in the scanning process unnecessary. We illustrate the solution on two study cases involving videos from a stationary camera and a wearable camera mounted on the animal's body. Accordingly, two different data processing procedures are presented. The first method allows determining the position of the animal within a defined space using a stationary camera. The second method allows determining the intensity of the animal's movement by the animal-borne camera. The software to process motion data was designed using MATLAB. The methods and procedures were developed under specific requirements related to the recording of animal movements yet can be used more broadly in behavioural research.

Keywords: audio-video recordings, MATLAB software, movement, animal-borne camera, automated behavioural analysis

Introduction

Ethological research is mainly based on the observation of animal behaviour and analysis of observational data. This analysis consists of a qualitative part (recognition of particular behavioural patterns and attribution to different behavioural categories) and a quantitative component (determining and comparing the distribution of behavioural patterns or categories in time and space). The ultimate aim of the ethological research is to make the research well-documented and thus reproducible, representative (i.e., to collect large data sets), and to make the analysis fast and objective (blind). Besides that, it may be important not to disturb or otherwise affect the animals by the very presence of the observer, or it is even technically impossible to observe the animals personally all the time. To fulfil these goals, visual and acoustic monitoring using cameras and recording devices (Bombara et al., 2017; Huck & Watson, 2019; Moll et al., 2007; Rutz et al., 2007), collecting data from GPS, diverse chips, and biologgers (Gerencsér et al., 2013; Painter et al., 2016; Walton et al., 2018; Yoda, 2019), by using satellite images (Begall et al., 2008; Burda et al., 2009; Slaby et al., 2013) are methods of choice. Still, visual monitoring by digital photographs, continuous filming, time-lapse photographing, or movement-induced phototrapping are the most common methods employed in behavioural research (Čapek et al., 2017; Hart et al., 2012; Malkemper et al., 2015a; Malkemper et al., 2015b; Nováková et al., 2017; Palencia et al., 2019; Pleskač et al., 2017). To evaluate (*nota bene* objectively) vast amounts of photos or video materials, several custom-made (Christiansen et al., 2014; Dielenberg et al., 2006; Geldenhuys et al., 2015; Ramazani et al., 2007), commercially available programs (Juszczak & Miller, 2016; Napolitano et al., 2015; Young et al., 2019), or free software (Rutz et al., 2007; Samson et al., 2015) have been used.

While the commercial systems have reached wide popularity and distribution in ethological and psychological labs, they have higher financial costs and certain limitations. We demonstrate these limitations on the example of two case studies from the Department of Game Management and Wildlife Biology (Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague), representing many other behavioural studies. Moreover, we show the solution to these problems. We describe the processing methods we have developed with MATLAB software (MatLab R2010b, Mathworks, Inc., Natick, MA, USA) to evaluate animal movement from video recordings. A common denominator of both studies was a tremendous amount of video material collected and to be surveyed and analysed. The scripts are free available for academic purposes (Supplementary Materials). The data processing was carried out on a computer with parameters: Intel(R) Core(TM) i5-8300H CPU @ 2.30GHz, 32 GB RAM, OS MS Windows 10.

Due to the challenges of monitoring animals, it seems inevitable to automate the processes that sort and analyse the data, reducing the overall time required to process the experiment's results.

Methods and Results

Case study Nr. 1: Study of calves - Movement recording by a stationary digital video camera

Starting situation

Altogether 16 calves have been housed for 35 days in individual boxes with enclosures under control and experimental conditions (Figure 1), and salivary melatonin concentration was analysed (Kolbabová et al., 2015). Besides that, all calves were continuously video-recorded to analyse (as a part of a separate follow-up study) whether the sleeping/activity distribution differed between the control and experimental groups and correlated with the melatonin profile. It means that 13,440 hours of video recordings have to be surveyed, and sleep/resting versus standing/moving behaviours have to be scored and coded into the data file to calculate the frequencies of those behaviours. This task requires to be somehow automated.

It is advisable to scan the planes separately for observing the movement in the vertical and horizontal planes. Although the entire scene of motion in both vertical and horizontal planes can be observed with one static camera, in this case, it is necessary to transform the image. The transformed image is needed for accurate calculation of the animal's position. The number of monitored motion parameters is reduced to achieve the highest possible accuracy.

One camera recorded pictures of the space outside and inside the shelter. Each picture of the camera recording was digitally divided (by MatLab software (SW)) into two areas. One area corresponded to the space inside the shelter and the other to the enclosure outside the shelter (Figures 2c and 2d). The areas were predefined by bounding polygons (rectangles) (Figures 2a and 2b). Following that, a threshold value was applied to see the cattle clearly. Finally, the below-described method for identifying the position and movement of animals was used in the MatLab environment.

Figure 1

Calf Houses in the Individual Wooden Box

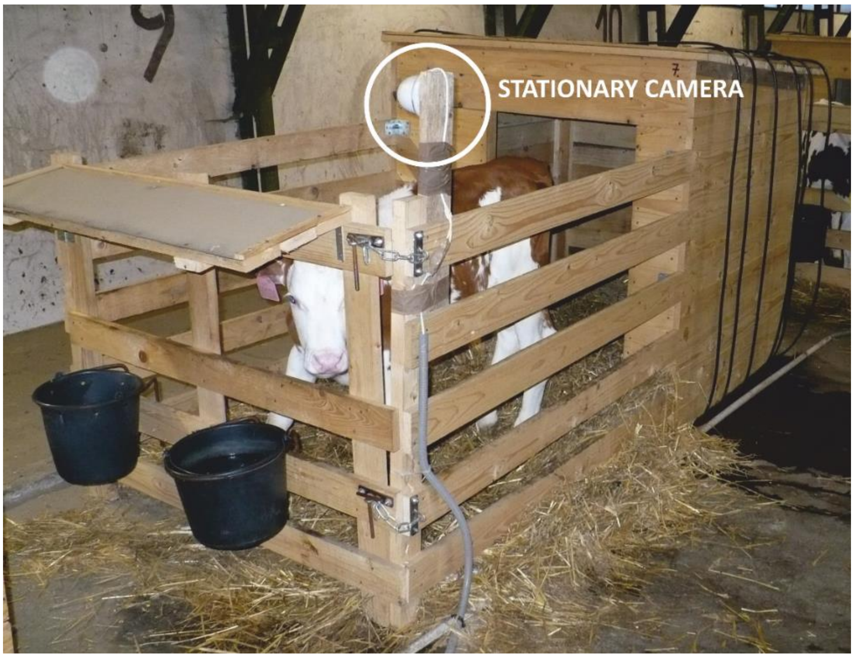
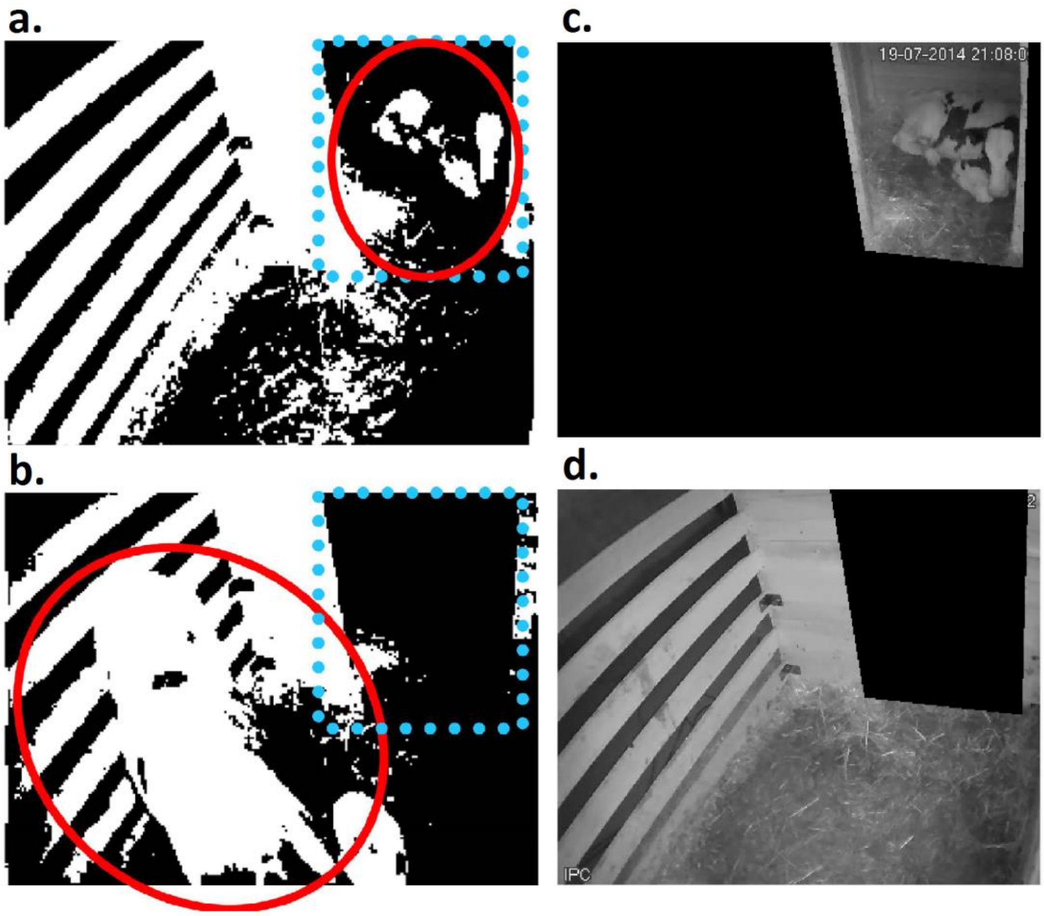


Figure 2

Examples of Processing Records Captured by a Stationary Digital Camera for Measuring the Animal's Movement



Note. (a) Animal resting in a shelter in the predefined bounding polygon (dotted rectangle), (b) Animal in the enclosure, i.e., outside the predefined bounding polygon (dotted rectangle). Recorded pictures of the space inside (c) and outside (d) the shelter.

Video data

The results of the image processing completion are the x and y coordinates determining the animal's positions in the image over time. Even if the animal is monitored in its natural environment by a single camera and its position cannot be transformed into individual planes (e.g., the Earth or animal body coordinate system), the intensity of the animal's movement can be determined. Mathematical operations implemented in MatLab SW can also determine the time the animal spent resting or moving. It is also possible to detect the animal's moments within predefined areas of the image.

Zero values in the vector of changes of an animal's position in the image demonstrate the time spent at rest. The period of zero values in the vector is assumed to be used in other statistical analyses. For further statistical processing, it is necessary to normalise the data so that the calculated times (i.e., the period of rest or movement) are divided by the overall duration of the record.

MatLab SW contains many useful functions and algorithms for image motion detection and transformation, which is necessary if the animal's position is to be converted into specifically defined planes using a single camera recording.

After the video is loaded, it is convenient to convert the images to grey-scale images for further processing. It is done with the" rgb2gray" function. If the researcher is interested only in the movement in a specific area of the picture, the function" roipoly" specifying the polygonal region of interest (ROI) can be applied. After the ROI has been selected by" roipoly" (similar to "imcrop", but ROI is a polygon), the movement can be monitored. Following this step, ROIs of images recorded at time t_n and t_{n+1} are loaded using VideoReader and ReadFrame functions (Kutilek et al., 2018).

To detect motion in a particular image, in most cases, the differential method has been used. When using this method, individual images are subtracted from each other, i.e., the difference is calculated by subtracting the ROIs of the frames recorded at time t_n and t_{n+1}. Due to time and computational limitations, the frame-capturing rate was set to 2 Hz. The difference obtained by subtracting the ROIs was then converted to the opposite brightness value (Ramazani et al., 2007). The differential method of motion detection is inherently inapplicable; it must be combined with other methods, such as thresholding (Dielenberg et al., 2006). It is the reason thresholds must also be applied in the algorithm.

When applying image processing techniques, it is recommended to reduce the noise and generally to adjust the difference obtained. The difference obtained is converted into a white area in the image using the" im2bw" function. The" rgb2gray" function is used to convert the image into the grayscale image, while the thresholding of the converted image is done by" im2bw". The" im2bw" function requires setting a threshold value that was experimental for the needs of the application used, set to 0.03 (Kutilek et al., 2018).

The MatLab SW offers various functions for morphological transformation, such as erosion (" imerode"), dilation (" imdilate"), morphological opening (" imopen") and closing (" imclose"). These functions were used for noise reduction. The property of the morphological transformation is determined by the structural elements generated by "strel" function.

The next step was to define the centre of pixel clusters representing the acquired difference in the animal's position. The "regionprops" function was used to calculate the centre of the pixel cluster in the white area of the detected difference. The position of this centre was different at each reading. The coordinates on the x and y-axes show a change in the position of a point representing the moving subject over time.

The differential method has a disadvantage: if the animal stops moving, information about its position in the image is lost. This problem has been resolved using the" empty" function and the matrix that contains the unknown coordinates when the subject is not detected. These coordinates were then set to the last detected values of coordinates. The output was a coordinate matrix of the animal's position (Kutilek et al., 2018).

The MatLab SW tools can also be used to recognise whether the animal is moving or not or the intensity with which it is moving. Suppose the change in position is not identified.

In that case, i.e., no movement is detected. It is known that the animal is in the area of interest (according to the latest detected body position coordinates); the researcher will assume that the animal does not move. In this way, resting and movement phases can be distinguished. If the animal is moving, the intensity of movement can be determined by the difference in the body position (i.e., coordinates) in consecutive frames. Suppose the real dimensions of the space where the animal is moving are unknown. In that case, the intensity of movement is determined by the distance of the coordinates (in pixels) in consecutive frames. The animal's movement can be monitored not only as a whole picture but also in its parts. By using the digital cut of a certain area of pixels in the image, it is possible to determine the animal's movement in the predefined areas (i.e., bounding polygons) in each picture by the above methods. For easier analysis, each bounding polygon can be resized, cropped, and analysed separately (Kutilek et al., 2018).

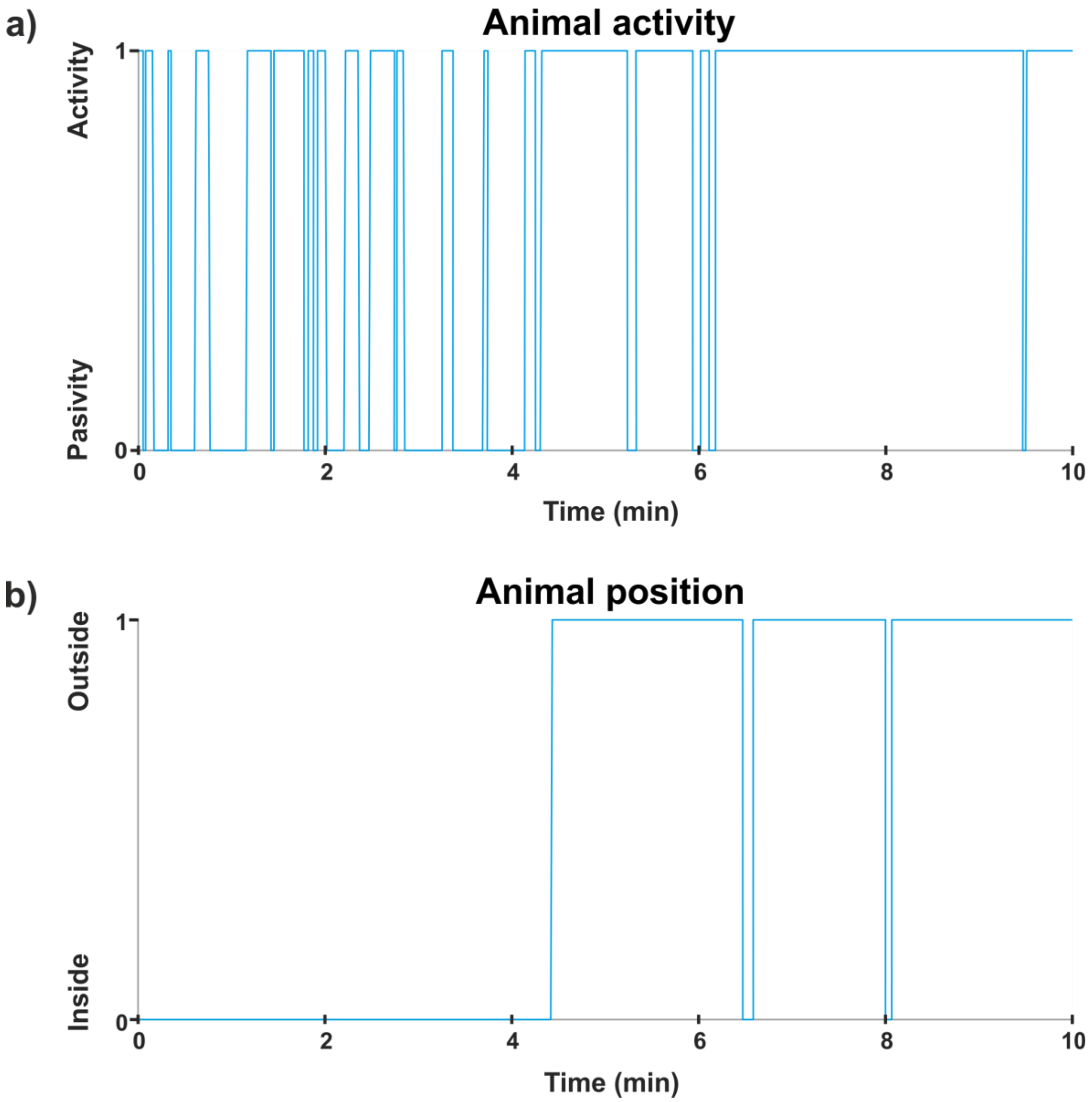
Output

The output from the customised software created in the MatLab environment provides information about all parameters that quantitatively describe animals' movement activity (the sample input video file and the script are available in Supplementary file 1 and 2 for testing).

Figure 3 shows the diagrams of the animal activity, i.e., passive and active phases of animal behaviour and position inside or outside the shelter. Both graphs correspond to each other. When the animals are under the shelter, they usually rest or sleep, while this only rarely happens outside a shelter. However, in several cases, some artefacts, which may have been caused by other animal's movement near the camera or the movement of a specific part of the body (tail), are also visible in the image. Diagrams (i.e., vectors of movement activity and location) were used to determine the ratio of an animal's time inside to the time spent outside the shelter, as well as the percentage of the time spent resting to the time spent moving. The graphic output represents the video file, where the passive and active phases are labelled (Supplementary file 3). It takes ~10 min to process 30 min long-lasting video record.

Figure 3

Graphs Representing the Output from the Method for Processing of Stationary Digital Camera Records



Note. (a) Identification of passive (value zero on the y-axis) and active (value one on the y-axis) phases of animal activity and (b) Identification of animal position in the shelter – inside (value zero on the y-axis) or outside (value one on the y-axis)

Case study Nr. 2: Study of homing dogs – Movement recordings from an action camera and GPS collar

Starting situation

In this study, 27 free-ranging hunting dogs were equipped with action cams and GPS collars (Figure 4), and their homing behaviour was analysed (Benediktová et al., 2020). In this way, 940 hours of audio-video recordings were sampled. One task, among others, was to find in the video of each dog’s excursion a moment when the dog stops for a while and then changes the direction to return home, the so-called *turning point*. It was also necessary to check the dog’s behaviour at that point and exclude the possibility that it stopped, e.g., due to drinking, bathing, and sniffing. While in the quoted study, the recordings were evaluated “manually”, our research continues and expands, requiring automation of video evaluation.

For movement evaluation, video data, audio data, and GPS data were sampled.

Video data

The Garmin Virb Elite action camera (Garmin Ltd., USA) was mounted by means of a custom-made harness on the side of the dog’s thorax. The camera focused on the side of the dog’s head and the environment in front of it (Figure 4). It was not the goal of this study to track the movement in the horizontal and vertical axes precisely. Therefore, the optical axis of the camera does not follow the exact direction. MatLab SW digitally processed each picture of the camera recording. Again, the below-described methods applied in the MatLab environment were used to identify the intensity of the animal’s movement (Figure 5).

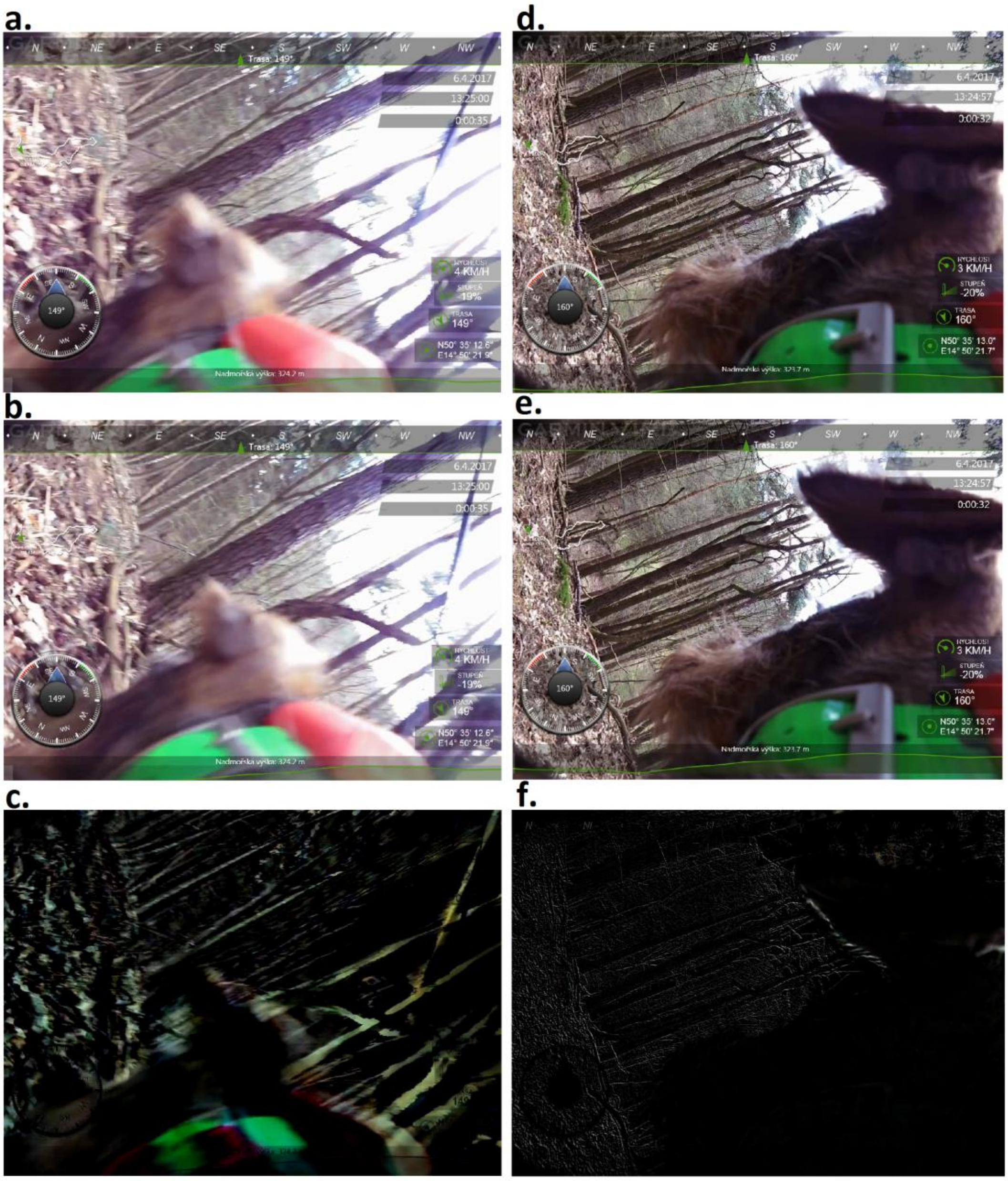
Figure 4

The Dog Equipped with the Wearable Camera and the GPS Collar

Note. The camera is inserted in a stainless-steel non-magnetic mount and mounted utilising a custom-made harness on the side of the dog’s thorax (left); the camera is focused on the side of the dog’s head and the environment in front of it (right).

Figure 5

Examples of Processing Records Captured by a Wearable Digital Camera for Measuring the Movement of an Animal



Note. (a) Frames recorded at time t_n of an animal with high activity, (b) Frame recorded at time t_{n+1} of an animal with high activity, (c) Result of subtracting the frames a) and b) recorded at time t_n and $t_{n+1;}$ (d) Frame recorded at time t_n of an animal with low activity, (e) Frame recorded at time t_{n+1} of an animal with low activity, (f) Result of subtracting the frames d) and e) recorded at time t_n and t_{n+1}.

Similarly to the processing records captured by the stationary digital camera, the region of interest can be selected by the *Imcrop* MatLab SW function. The ROI selection depends on which part of the image records the movements of the animal's surroundings. Subsequently, ROI images recorded at time t_n and t_{n+1} are loaded by *VideoReader* and *ReadFrame* functions. Due to time and computational limitations and the presumed identification of the accuracy of physical activity, the time step was set to 0.1 sec. Next, the difference was calculated by simply subtracting the ROIs of the frames recorded at time t_n and t_{n+1}. Following that, the low pass filter function was used to obtain the resulting difference vector of ROIs (MatLab function" smooth" – moving average with a span of 50). For the evaluation of movement activity in the phase of locomotion, it is possible to apply the normalisation of the resulting vector Y to the range of measured values:

$$Y_{norm} = \frac{Y - [\min(Y)]}{\max(Y) - \min(Y)}$$

In the next step, a fixed threshold or any adaptive threshold can be used to a normalised motion vector Y_{norm} to distinguish between locomotion phases (rest, movement, etc.). For example, zero values in the vector of movement activity can be used after applying a threshold to distinguish low movement activities corresponding with rest or calm locomotion phases (Kutilek et al., 2018).

Audio Data

Audio data for activity determination were used when the image data were not usable (i.e., poor light conditions at night or an unintentional shift of camera). In such a case, activity/movement was evaluated using the sound channel with a sampling frequency of 44100 Hz. Similarly to visible-light video data in previous cases, the sound data was normalised, and the Adaptive Threshold method was applied. The usability of audio data for the activity/movement determination was verified by Time-Frequency analysis and its function Spectrogram Hanning window with the length of 2000 samples and an overlap of 50% (1000 samples).

GPS data

GPS data stored in the gpx format was used to display the pauses in a dog's activity (non-activity) and identify his turning point when the dog started returning to his owner. To load the gpx format, the xmlread function and *getElementsByTagName* ("trkpt") function were applied. The baseline sampling frequency was set to 1 Hz, but a new position was stored after 2 seconds in some cases. The experimentally detected sampling frequency was approximately 0.933 Hz. Information about the time sample [s], longitude [°], latitude [°] and altitude [m] was used for further analysis. The altitude in the gpx format was marked by <ele> (elevation). To convert geodetic latitude, longitude, and altitude into a flat Earth position" lla2flat" function with WGS84 ellipsoid model was used. The distance between the two points was calculated using three-dimensional Euclidean space:

$$distance = \sqrt{(lon_{t_{n+1}} - lon_{t_n})^2 + (lat_{t_{n+1}} - lat_{t_n})^2 + (alt_{t_{n+1}} - alt_{t_n})^2}$$

Similarly to the image processing from stationary cameras, the normalised motion vector offers information about the intensity of movement of a relevant body segment. Mathematical operations implemented in MatLab SW can determine the time spent at rest or moving or identify the animal´s time in predefined image areas.

Zero values in the vector of movement activity of the animal determine the period spent at rest. The period of zero values in the vector is expected to be used in other statistical analyses. The same methods as evaluating data captured by a stationary camera can be applied to further statistically processing results.

The excursion was divided into ten equidistant segments to identify the turning point of the dog. The slowest segment (i.e., the segment which took the dog the longest time) was identified as the turning trajectory. The slowest point (the slowest average speed between two points) of that section was identified as the turning point (Figure 9).

Output

Figure 6 shows the diagrams of the animal’s activity measured by the wearable digital camera and visible-light camera data with the audio data processing described above. The graphs demonstrate the passive and active phases of the animal’s behaviour and the normalised intensity of movement. Diagrams (i.e., vectors of normalised movement activities) were used to determine the time spent resting against the time spent moving.

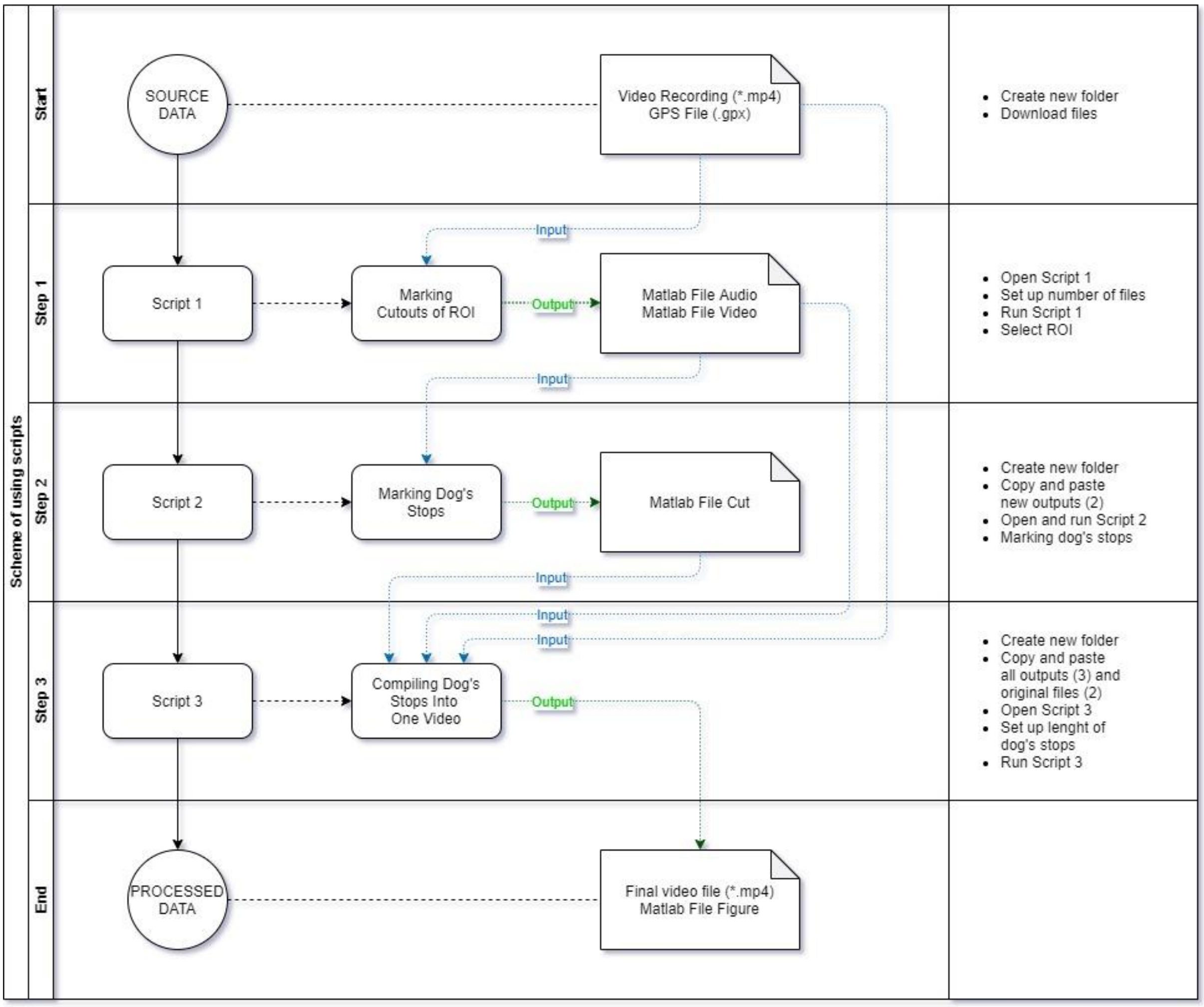
Time-Frequency analysis of audio data demonstrating individual stops from the wearable digital camera is shown in Figure 7. Figure 8 shows the Time-Frequency analysis for high activity (sprinting), medium activity (relaxed running), and barking activity.

Figure 9 shows the information about pauses in the movement (green point – the start of no activity; red point – the end of no activity), the turning trajectory (bold black line), and the turning point (pink star) in the Earth Coordinate System. Information about altitude is displayed in the appropriate colour. The video record analysis framework is described in Box 1.

The graphical output represents the video file containing the dog´s stops (the active movement´s phases are cut out) with the defined cutting length, i.e., the length of the record left before and after stopping. The user can specify the cutting size according to the duration of the dog´s stops (Supplementary file 4). It takes ~ 8 min to process a 6 min long-lasting video record. It is important to note that the portion of human work is only ~ 1 min, while the rest of the work appertains to Matlab SW, where the human presence is not necessary. In the case of 15 min record, the whole processing takes ~ 20 min with ~ 3 min of human work. Thus, the time saved by the user is more than 80% (for more details, see Table 1). The sample input files and scripts are available for testing (Supplementary files 2 and 5).

Box 1

The framework of video record analysis



Note. The schematic representation of the whole process of video record proceeding. The rows show particular steps and input and output files. The right column shows the user´s inputs.

Table 1

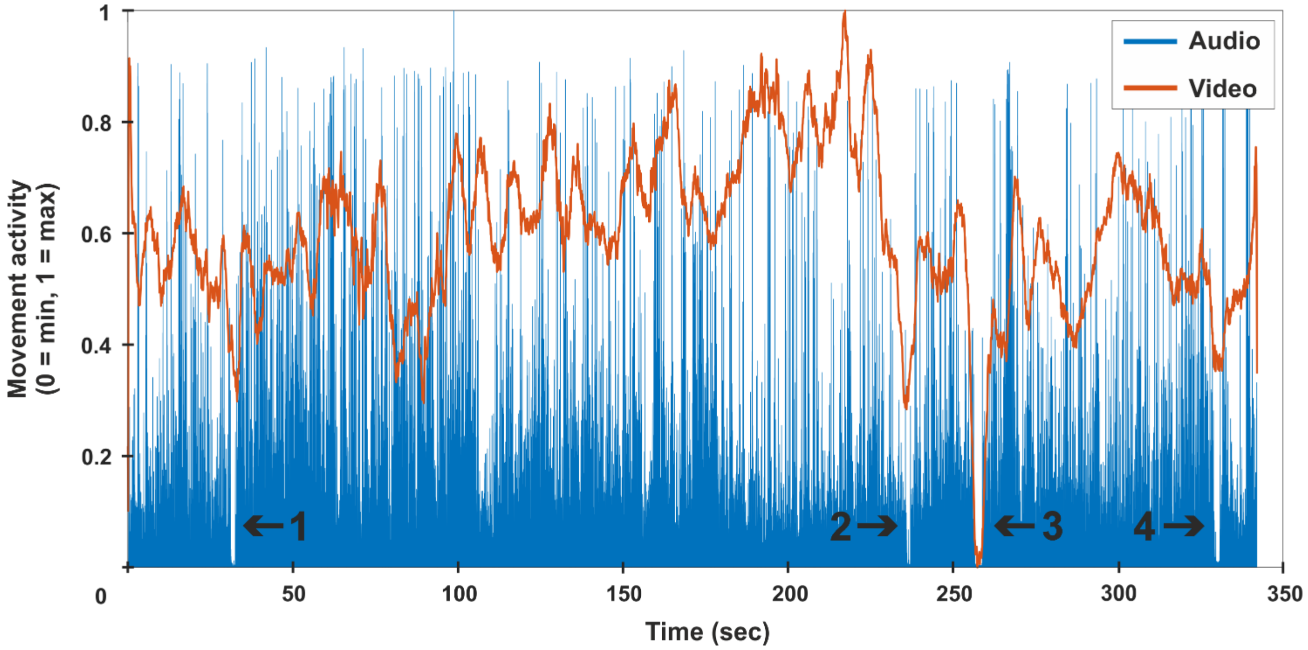
Comparing the time consumed manually processing and by Matlab SW for records of different duration

ID	Duration (min)	Manually processing (min)	Number of stops	Matlab processing Step 1 (min)		Matlab processing Step 2 (min)		Matlab processing Step 3 (min)		Time savings (min)
				PHW	PMW	PHW	PMW	PHW	PMW	
Gofi108	06:03	09:09	7	00:06	5:09	0:55	0:05	0:15	1:20	7:53 (86%)
Gofi70	15:05	31:40	28	00:06	13:00	2:25	0:05	0:15	3:47	28:54 (91%)

Note. PHW = portion of human work, PMW = portion of Matlab work (not necessary human presence). The table shows the example of two different excursions and their time-consuming processing and then compares the time need for every step divided into the portion of human work and Matlab SW work. The saving time of the user is presented in the last column.

Figure 6

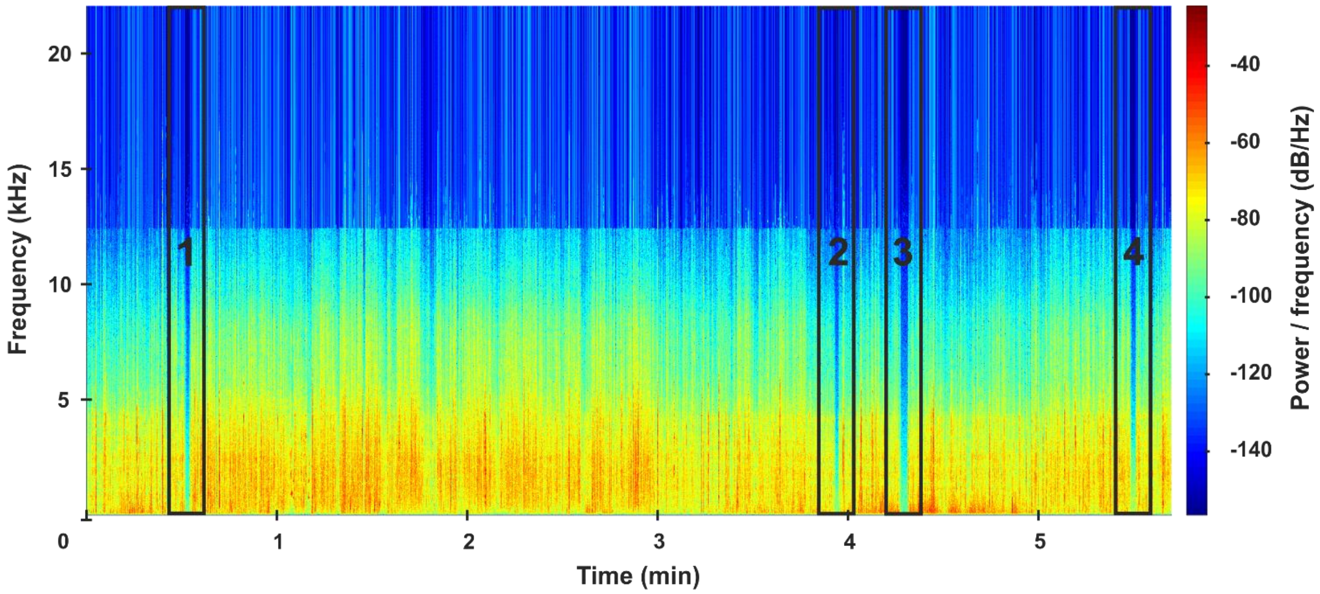
Graphs Representing the Output from the Method for Processing of Wearable Digital Camera Records



Note. 0 – minimum movement activity, 1 – maximum movement activity (y-axis). Black arrows (labelled by numbers 1 – 4) demonstrate pauses in movement (minimum activity).

Figure 7

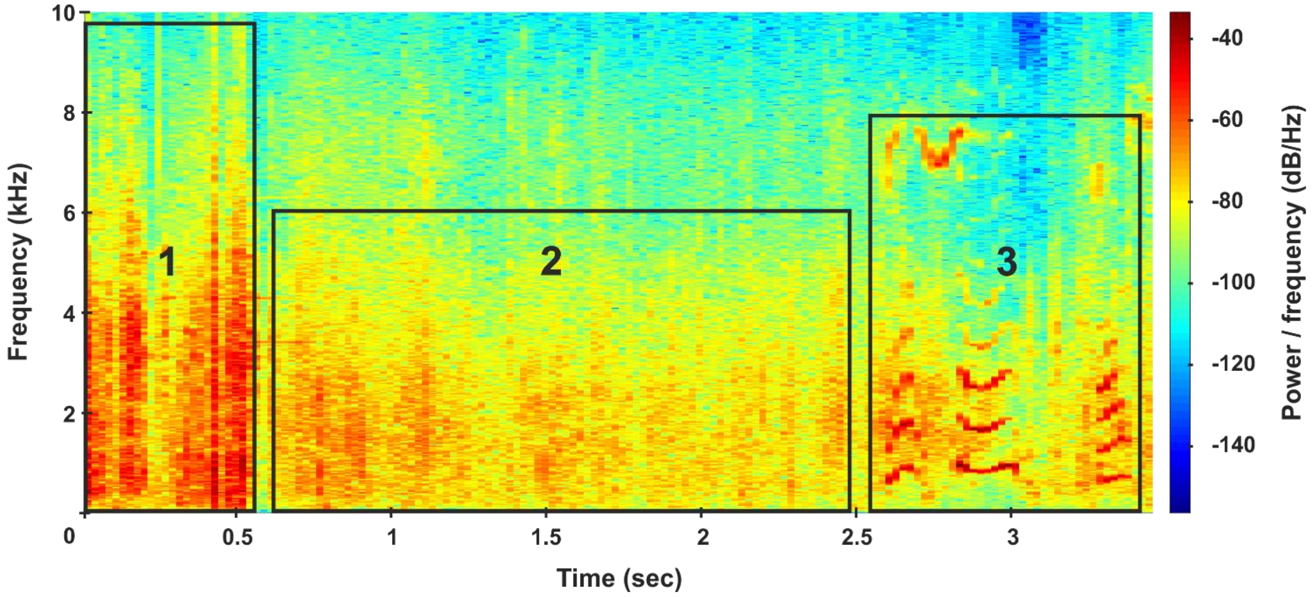
Time-Frequency Analysis of Audio Data Taken by the Wearable Digital Camera



Note. Numbers 1 – 4 demonstrate the pauses in movement (minimum activity).

Figure 8

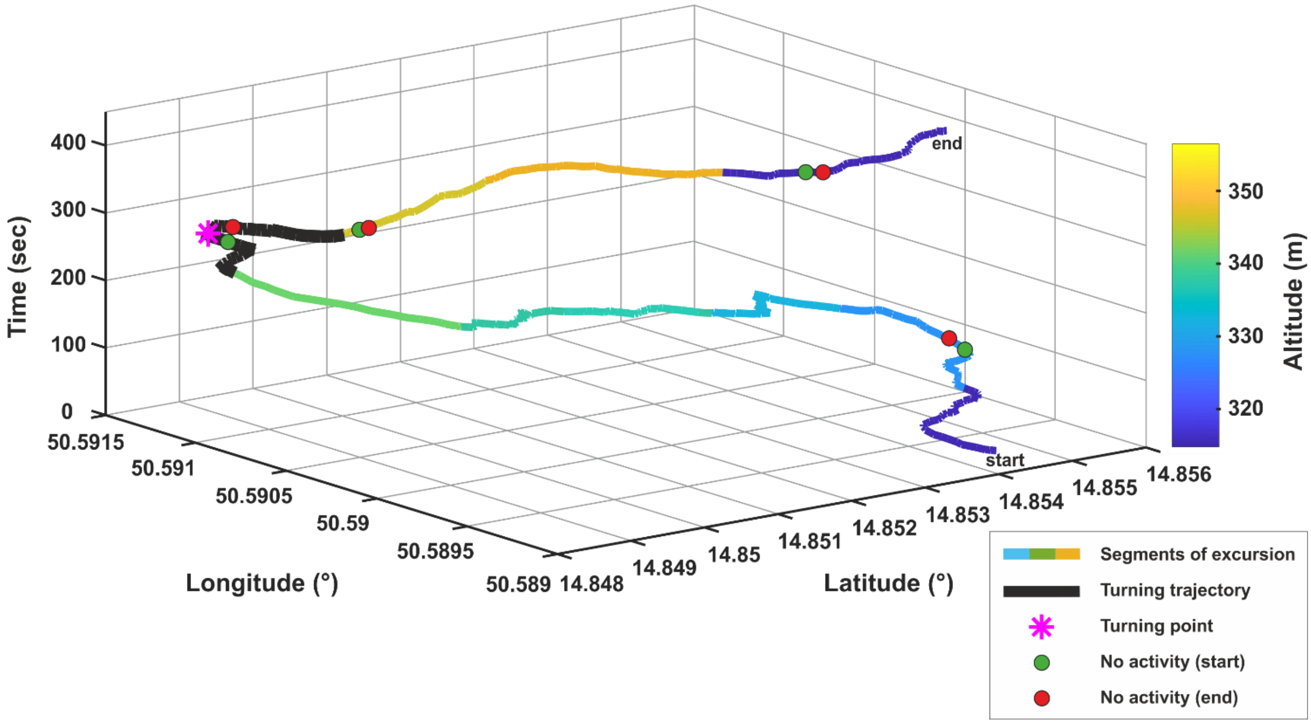
Time-Frequency Analysis of Audio Data taking the Wearable Digital Camera



Note. Every rectangle represents a specific animal activity. 1 – high movement activity, 2 – medium movement activity, 3 – medium barking activity.

Figure 9

GPS Data with Information about the Characteristics of Movement in the Earth Coordinate System



Note. The coloured line represents the excursion divided into ten equidistant segments. The bold black line is the turning trajectory (i.e., the segment with the slowest average speed). The turning point of the dog (the slowest average speed between two points) (pink star) is identified within this segment. The pauses in the movement are marked by green points (the start of no activity) and red points (the end of no activity). Information about altitude is displayed with the appropriate colour on the right side.

Statistical evaluation

Statistical evaluation is based on comparing data obtained from randomly selected camera recordings with the recordings evaluated by an expert. The method was designed to minimise errors when any other automated process which is not applicable for camera recording is used.

Study of calves

Since the animals have to be monitored and recorded during extended periods (weeks to months) to successfully evaluate the animals’ resting state, inter-frame analysis methods were employed. Due to the relatively undemanding computing performance required, the proposed method enables processing even longer data sets. The expert, however, examined and evaluated only a part of the data records, namely, ten records, each with a duration of one hour. The difference between the results obtained by the proposed method and the expert was registered. The difference, i.e., the method´s error rate in the number of recorded rest states, is about 2%–5% depending on the camera location, lighting conditions, and the type of environment. No difference was observed between the results obtained by the proposed method and the expert when evaluating the position outside and inside the shelter.

Study of homing dogs

Twenty records, each approximately 30 minutes long, were subjected to evaluation. The differences between the results obtained by the proposed method and the expert were registered. The method identifying the rest states both from video and acoustic records shows an error rate resulting from failing to detect a rest stop of about 2%–5% depending on the accuracy of the camera location, breed of dog, light conditions and type of environment (trees, grass, etc.). The falsely marked rest stops can then occur in about 1%–3% of cases (again depending on the conditions, for example, when the dog crawls under a fallen tree, when the brightness suddenly decreases, or when the camera moves and partly captures the animal’s coat, ear etc.).

Discussion

The long-time monitoring of animals in their natural environment by recording devices allows obtaining objective and valuable data not influenced by observers (Bombara et al., 2017; Huck & Watson, 2019; Loyd et al., 2013; Rutz et al., 2007). On the other hand, it is necessary to analyse vast amounts of data, which is almost impossible to evaluate manually (Moll et al., 2007). Using commercially available programs or free software helps to increase the efficiency of processing data, but there is always a significant portion of manual work inevitable (watching the video and marking specific behavioural patterns) (Napolitano et al., 2015; Rutz et al., 2007; Young et al., 2019). The proposed camera record processing method enables the determination of movement activity indicators without long-lasting watching of video records by scientists and speeds up the record´s processing.

The designed methods for the processing of records captured by a stationary digital camera (study of calves) enable the calculation of new parameters automatically, without any additional software or a specific type of camera recording (expensive equipment based on active or passive markers, etc.) (Ren et al., 2008; Sellers & Hirasaki, 2014). Moreover, the graphs and vectors displaying these activities can also be used to calculate other indicators. For example, in the case of stationary digital camera applications, calculations can be used for both graphs (Figure 4); thus, the ratio of time the animal spends resting and the time the animal spends moving outside the shelter can be calculated.

Comparing this camera application and the proposed procedures with other Motion Capture systems (e.g., accelerometer) reflects the complete, complex information about specific activities performed by animals. There is no need to use a complicated algorithm, e.g., for the calculation of locations. This algorithm needs to be used in an accelerometer system because the calculations have to be integrated when the measurement is too long.

Another advantage is contactless motion sensing, which is impossible when exploiting an accelerometer (Kutilek et al., 2010).

The different situation occurs when evaluating audio-video records obtained by the wearable digital camera system (study of homing dogs). Suppose the designed methods for processing records are compared with other methods. In that case, no currently designed software allows for the automatic evaluation of animals' movement activity and capturing particular behaviour while using the animal-borne camera.

In the study of homing dogs, we predicted that the change of behaviour would precede the activity change. This change of a level of activity can be observed in many cases - e.g., predation by cats (Huck & Watson, 2019; Loyd et al., 2013), social contact among free-roaming dogs (Bombara et al., 2017) or head movement of sea turtles (Okuyama et al., 2015). This situation can also be recognised using bio-loggers (Gerencsér et al., 2013; Painter et al., 2016). However, information about specific behaviour is lacking (e.g., kind of prey, type of obstacle, particular behaviour during a stop, etc.) when the animals are out of sight (reviewed in Yoda, 2019) or the recording of data is set up to long intervals (Bombara et al., 2017). In addition, a bio-logger was not always used during the study for different reasons (Loyd et al., 2013; Moll et al., 2007; Rutz et al., 2007).

Our customised software created in the MatLab environment allows automatic analysis of audio-video data for the purpose to identify specific behavioural patterns (passive and active phases and intensity of movement, pauses in motion, the ratio of time spent resting or moving, the activity of barking) in a few simple steps (see Box 1 and Figure 6 – Figure 9). In addition, the possibility to set up user´s parameters between particular steps and the graph preview of motion activity enables capturing unusual behaviour and modifies the output video (Box 1). In the case of using Matlab SW, human work is more or less constant regardless of the length of the record. Moreover, with increasing length, the time-saving is also growing. On the other hand, during manual processing (without Matlab SW), the total processing time grows significantly with increasing video length. Furthermore, the long-lasting video records put enormous demands on attention which could cause errors.

The parameters of movement activities and location animals in space and time as the outputs of Matlab SW could be used for follow-up scientific research. Moreover, this manner of analysis fulfils the significant aim of the ethological study. To make the research well-documented, reproducible, and to make subsequent analyses fast, comfortable, and objective (blindly). The error rate of 5% compared to manual evaluation can be considered, in long-term research, involving large datasets negligible.

Conclusion

This article presents methods used for automatically processing long-time records of animal movements captured by cameras. The MatLab environment´s mathematical methods enable identifying and recognising specific behavioural patterns automatically and evaluating long videos from a stationary digital camera or a wearable digital camera, sparing the time otherwise required for watching the videos and coding for behavioural patterns of interest manually.

Funding

This work was done in the framework of the research project SGS17/108/OHK4/1T/17 sponsored by the Czech Technical University in Prague. The work presented in this article has also been supported by the Czech Republic Ministry of Defence (University of Defence development program” Advanced Automated Command and Control System II – PASVR II”). The study was supported by the Grant Agency of the Czech University of Life Sciences in Prague, CIGA CZU (Project No. 20174319); the Grant Agency of the Czech Republic (Project. No. 15-21840S); the grant “EVA4.0”, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE.

Acknowledgements

We thank for the collecting of data to our students, colleagues, and friends: Tereza Březinová, Václav Fuks, Hedvika Fuksová, Mirka Jakšlová, Alena Mottlová, Petra Nováková, Hana Spalová, Jaroslav Spal, Miloslav Zikmund. We also thank to Tereza Kolbabová for providing video recordings of calves obtained within the framework of her study. And finally, we would like to thank Hynek Burda for constructive comments on the manuscript.

Author contributions

KB, JA, JS collected the data for study cases, KB prepared the data for processing procedures, PV, JH designed the algorithm in the MatLab environment, PV performed the statistical analysis, PV, KB, JS, PK, EK, VK wrote the manuscript and prepared the figures. All authors read and reviewed the final version of this manuscript.

Competing interests

The authors declare that no competing interests exist.

Open Practices Statement

The data and materials (including custom codes for the MATLAB scripts) reported here are available in Supplementary Material.

References

Begall, S., Cerveny, J., Neef, J., Vojtech, O., & Burda, H. (2008). Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Academy of Sciences, 105*(36), 13451–13455. https://doi.org/10.1073/pnas.0803650105

Benediktová, K., Adámková, J., Svoboda, J., Painter, M. S., Bartoš, L., Nováková, P., Vynikalová, L., Hart, V., Phillips, J., & Burda, H. (2020). Magnetic alignment enhances homing efficiency of hunting dogs. *ELife*, *9*. https://doi.org/10.7554/eLife.55080

Bombara, C. B., Dürr, S., Machovsky-Capuska, G. E., Jones, P. W., & Ward, M. P. (2017). A preliminary study to estimate contact rates between free-roaming domestic dogs using novel miniature cameras. *PLoS ONE*, *12*(7). https://doi.org/10.1371/journal.pone.0181859

Burda, H., Begall, S., Cerveny, J., Neef, J., & Nemec, P. (2009). Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants. *Proceedings of the National Academy of Sciences*, *106*(14), 5708–5713. https://doi.org/10.1073/pnas.0811194106

Čapek, F., Průcha, J., Socha, V., Hart, V., & Burda, H. (2017). Directional orientation of pheasant chicks at the drinking dish and its potential for research on avian magnetoreception. *Folia Zoologica*, *66*(3), 175–182. https://doi.org/10.25225/fozo.v66.i3.a5.2017

Christiansen, P., Steen, K., Jørgensen, R., & Karstoft, H. (2014). Automated Detection and Recognition of Wildlife Using Thermal Cameras. *Sensors*, *14*(8), 13778–13793. https://doi.org/10.3390/s140813778

Dielenberg, R. A., Halasz, P., & Day, T. A. (2006). A method for tracking rats in a complex and completely dark environment using computerized video analysis. *Journal of Neuroscience Methods*, *158*(2), 279–286. https://doi.org/10.1016/j.jneumeth.2006.05.024

Geldenhuys, W. J., Guseman, T. L., Pienaar, I. S., Dluzen, D. E., & Young, J. W. (2015). A novel biomechanical analysis of gait changes in the MPTP mouse model of Parkinson's disease. *PeerJ*, *3*(8), e1175. https://doi.org/10.7717/peerj.1175

Gerencsér, L., Vásárhelyi, G., Nagy, M., Vicsek, T., & Miklósi, A. (2013). Identification of Behaviour in Freely Moving Dogs (*Canis familiaris*) Using Inertial Sensors. *PLoS ONE*, *8*(10), e77814. https://doi.org/10.1371/journal.pone.0077814

Hart, V., Kušta, T., Němec, P., Bláhová, V., Ježek, M., Nováková, P., Begall, S., Červený, J., Hanzal, V., Malkemper, E. P., Štípek, K., Vole, C., & Burda, H. (2012). Magnetic Alignment in Carps: Evidence from the Czech Christmas Fish Market. *PLoS ONE, 7*(12), e51100. https://doi.org/10.1371/journal.pone.0051100

Huck, M., & Watson, S. (2019). The use of animal-borne cameras to video-track the behaviour of domestic cats. *Applied Animal Behaviour Science, 217*(February), 63–72. https://doi.org/10.1016/j.applanim.2019.04.016

Juszczak, G. R., & Miller, M. (2016). Detour Behavior of Mice Trained with Transparent, Semitransparent and Opaque Barriers. *PLOS ONE, 11*(9), e0162018. https://doi.org/10.1371/journal.pone.0162018

Kolbabová, T., Pascal Malkemper, E., Bartoš, L., Vanderstraeten, J., Turčáni, M., & Burda, H. (2015). Effect of exposure to extremely low frequency magnetic fields on melatonin levels in calves is seasonally dependent. *Scientific Reports*, *5*(1), 14206. https://doi.org/10.1038/srep14206

Kutilek, P., Charfreitag, J., & Hozman, J. (2010). Comparison of Methods of Measurement of Head Position in Neurological Practice. In *IFMBE Proceedings* (Vol. 29, pp. 455–458). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-13039-7_114

Kutilek, Patrik, Benediktova, K., Svoboda, J., Volf, P., Adamkova, J., Krivanek, V., Hejda, J., Kutilkova, E., & de Brito, A. C. D. M. (2018). Processing Methods of Camera Record of Animal Movement. *2018 18th International Conference on Mechatronics - Mechatronika (ME),* 1–5. https://doi.org/ISBN: 978-1-5386-4364-8

Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J., & Marshall, G. J. (2013). Quantifying free-roaming domestic cat predation using animal-borne video cameras.

Biological Conservation, 160, 183–189. https://doi.org/10.1016/j.biocon.2013.01.008

Malkemper, E. P., Eder, S. H. K., Begall, S., Phillips, J. B., Winklhofer, M., Hart, V., & Burda, H. (2015). Magnetoreception in the wood mouse (*Apodemus sylvaticus*): influence of weak frequency-modulated radio frequency fields. *Scientific Reports, 4*, 9917. https://doi.org/10.1038/srep09917

Malkemper, E. P., Topinka, V., & Burda, H. (2015). A behavioral audiogram of the red fox (*Vulpes vulpes*). *Hearing Research, 320*, 30–37. https://doi.org/10.1016/j.heares.2014.12.001

Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution, 22*(12), 660–668. https://doi.org/10.1016/j.tree.2007.09.007

Napolitano, F., De Rosa, G., Serrapica, M., & Braghieri, A. (2015). A continuous recording approach to qualitative behaviour assessment in dairy buffaloes (*Bubalus bubalis*). *Applied Animal Behaviour Science, 166*(1), 35–43. https://doi.org/10.1016/j.applanim.2015.01.017

Nováková, P., Kořanová, D., Begall, S., Malkemper, E. P., Pleskač, L., Čapek, F., Červený, J., Hart, V., Hartová, V., Husinec, V., & Burda, H. (2017). Direction indicator and magnetic compass-aided tracking of the sun by flamingos? *Folia Zoologica, 66*(2), 79–86. https://doi.org/10.25225/fozo.v66.i2.a2.2017

Okuyama, J., Nakajima, K., Matsui, K., Nakamura, Y., Kondo, K., Koizumi, T., & Arai, N. (2015). Application of a computer vision technique to animal-borne video data: extraction of head movement to understand sea turtles' visual assessment of surroundings. *Animal Biotelemetry, 3*(1), 35. https://doi.org/10.1186/s40317-015-0079-y

Painter, M. S., Blanco, J. A., Malkemper, E. P., Anderson, C., Sweeney, D. C., Hewgley, C.

W., Červený, J., Hart, V., Topinka, V., Belotti, E., Burda, H., & Phillips, J. B. (2016). Use of bio-loggers to characterize red fox behavior with implications for studies of magnetic alignment responses in free-roaming animals. *Animal Biotelemetry*, *4*(1), 20. https://doi.org/10.1186/s40317-016-0113-8

Palencia, P., Vicente, J., Barroso, P., Barasona, J., Soriguer, R. C., & Acevedo, P. (2019). Estimating day range from camera-trap data: the animals' behaviour as a key parameter. *Journal of Zoology*, *309*(3), 182–190. https://doi.org/10.1111/jzo.12710

Pleskač, L., Hart, V., Nováková, P., & Painter, M. S. (2017). Spatial orientation of foraging corvids consistent with spontaneous magnetic alignment responses observed in a variety of free-roaming vertebrates. *Folia Zoologica*, *66*(2), 87–94. https://doi.org/10.25225/fozo.v66.i2.a3.2017

Ramazani, R. B., Krishnan, H. R., Bergeson, S. E., & Atkinson, N. S. (2007). Computer automated movement detection for the analysis of behavior. *Journal of Neuroscience Methods*, *162*(1–2), 171–179. https://doi.org/10.1016/j.jneumeth.2007.01.005

Ren, L., Butler, M., Miller, C., Paxton, H., Schwerda, D., Fischer, M. S., & Hutchinson, J. R. (2008). The movements of limb segments and joints during locomotion in African and Asian elephants. *Journal of Experimental Biology*, *211*(17), 2735–2751. https://doi.org/10.1242/jeb.018820

Rutz, C., Bluff, L. A., Weir, A. A. S., & Kacelnik, A. (2007). Video Cameras on Wild Birds. *Science*, *318*(5851), 765–765. https://doi.org/10.1126/science.1146788

Samson, A. L., Ju, L., Kim, H. A., Zhang, S. R., Lee, J. A. A., Sturgeon, S. A., Sobey, C. G., Jackson, S. P., & Schoenwaelder, S. M. (2015). MouseMove: An open source program for semi-automated analysis of movement and cognitive testing in rodents. *Scientific Reports*, *5*(November). https://doi.org/10.1038/srep16171

Sellers, W. I., & Hirasaki, E. (2014). Markerless 3D motion capture for animal locomotion studies. *Biology Open*, *3*(7), 656–668. https://doi.org/10.1242/bio.20148086

Slaby, P., Tomanova, K., & Vacha, M. (2013). Cattle on pastures do align along the North-South axis, but the alignment depends on herd density. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *199*(8), 695–701. https://doi.org/10.1007/s00359-013-0827-5

Walton, Z., Samelius, G., Odden, M., & Willebrand, T. (2018). Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking. *European Journal of Wildlife Research*, *64*(6), 64. https://doi.org/10.1007/s10344-018-1223-9

Yoda, K. (2019). Advances in bio-logging techniques and their application to study navigation in wild seabirds. *Advanced Robotics*, *33*(3–4), 108–117. https://doi.org/10.1080/01691864.2018.1553686

Young, J. K., Touzot, L., & Brummer, S. P. (2019). Persistence and conspecific observations improve problem-solving abilities of coyotes. *PLOS ONE*, *14*(7), e0218778. https://doi.org/10.1371/journal.pone.0218778

Supplementary materials:

- Supplementary File 1: The Matlab script for processing the stationary video-recording; the study of calves (Comments inside the script describe the processing process).
- Supplementary File 2: Instructions for using the Matlab program for the study of calves and dogs
- Supplementary File 3: The preview of the output video file for the study of calves (30 min long-lasting sequence)
- Supplementary File 4: The output video file for the study of dogs
- Supplementary File 5: The Matlab script for processing the video-recording from the wearable camera; the study of dogs (Comments inside the script describe the processing process).

Hunting dogs bark differently when they encounter different animal species

Richard Policht*, Ondřej Matějka, Kateřina Benediktová, Jana Adámková, Vlastimil Hart

Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

* Corresponding author

E-mail: polichtr@yahoo.com (RP)

Abstract

Previous studies have shown that vocalizations of dogs can provide information to human companions. While acoustic signals of dogs have been intensively studied during the last decade, barking during hunting activities remains unstudied. Experiences of hunters indicate that owners can recognize what animal species has been found based on the bark of their dog. Such a phenomenon has never been tested before. We tested such an ability by comparing barks that were produced when dogs encountered four different animal species: wild boar, red fox, rabbit and fowl. Classification results of a discrimination analysis showed, that based on barks of dachshunds and terriers, it is possible to categorize towards which animal species barks were produced. The most distinctive barks were produced during encounters with the most dangerous of these animals, the wild boar. On the contrary, barks evoked by red fox encounters were classified similarly as those towards other smaller and non-dangerous animals like rabbits and fowl. Although the red fox represents a potentially dangerous species, the barking provoked was not classified with a much higher result than barking at animals that pose no threat. This might indicate that the key parameter could be the body size of the animal the dog meets. We further tested whether the degree of threat from the species of animal the dog encounters is reflected in the structure of the acoustic parameters based on the Morton's motivation-structural hypothesis. We found that barks produced in contact with a wild boar showed significantly lower frequency parameters and longest duration compared to other barks. We also found differences in the energy profile between the beginning and end parts of a signal duration. According to these results, it seems that the variability of barking depending on the species of animal a dog encounters is an expression of the dog's inner state rather than functionally reference information.

Keywords: Dogs; barking; acoustic communication; vocalization; domestication; Canis; hunting

Introduction

Relationships between people and dogs, which represent the earliest domesticated animals, attract the attention of researchers in many ways [1-3]. The genetic history of dogs extends into the Palaeolithic, when at least five major ancestral lineages had diversified [4]. The exact timing of the emergence of the dog lineage remains unknown [5]. Current genetic studies estimate a time of dog–wolf divergence between 25,000 and 40,000 years ago [4,6]. Domestication of dogs caused differences from wolves in several ways. Adaptations included alterations in sequences of ritualized behaviour, and changes in motivational context for certain behaviours including changes in response thresholds [7,8]. Dogs are better at cooperating with humans than wolves are. They are more able to recognize our facial expressions and our communication signals; therefore, they work better with humans than wolves do [9]. Dog puppies display more communicative signals to facilitate social interactions, in contrast to wolf pups [9,10]. Thus, dogs show a unique complex of skills acquired for communication with humans [11]. Dogs bark frequently and use them in a wider range of contexts than their close relatives the wolf [12,13] and coyote [12], and the barks seem to have evolved from the low-frequency barks of wolves, which are mainly produced during agonistic interactions [14]. Barks changed quantitatively and qualitatively during the domestication process [15]. The complexity of the dog's vocal repertoire has been extended by using mixed sounds in barking context. Various barking forms are generated via a mix of transitions and gradations of harmonics, intermediates and noisy subunits [3]. Some authors suggest that the original function of barks is mobbing (alerting other pack members and calling them in to defend the territory together) [17]. From this, hunting barks may have also be derived, as their function is to alert humans and lead them to the prey that the dog has found. Hunting-dog breeds were originally bred to fulfill some kind of hunting work. Humans artificially selected some breeds to bark frequently [14,19,20]. These facts indicate a strong selection force on barking performance in hunting dogs, which are also mentioned for several dog breed standards [14]. Additionally, sport-hunting breeds have been adapted to specific hunting work via an improved physiology, e.g. cardiac function, blood flow, and cognitive performance [21]. Some breeds have been bred for specific kinds of hunt, e.g. pointing breeds (pointers) were bred from dogs that were able to stand quietly and maintain its position in the face of the animal's scent until the human counterpart reaches the place where the animal is hiding. In contrast, other breeds were developed for multiple purposes or to be versatile and able to perform a number of tasks (e.g. hounds, retrievers, spaniels). Spaniels and retrievers will find and bring a shot animal to a hunter [22,23]. The dachshund is considered according to Fédération Cynologique Internationale one of the most versatile hunting breeds and not just for hunting below ground. Cooperative hunting dogs keep close contact with the hunter during the hunt (e.g. retrievers) whilst non-cooperative hunting dogs perform independent work, either chasing (e.g. beagles) or attacking (e.g. terriers) the animal [24]. Small terriers locate and hunt smaller mammals, while larger terriers are able hunt larger animals. Selected hunting breeds were bred to follow prey while barking, and some are even capable of specialised barking; on the other hand, other breeds have to stand silently and motionless near the found animal until the arrival of the hunter [22,25]. Specific forms of barking produced by some hunting dogs are even requested in the dog breed standards of international cynological organizations [14]. Recent studies have also shown that barks contain meaningful information based on context [19,26-29], individual identity [26,28,29], inner states [27], and emotionality [30,31].

We aimed to test whether hunting dogs produce barks differentially during encounters with different animal species. In order to test the barking of dogs at animals of different sizes, we needed to choose a universal dog breed. The choice of breeds for such a purpose was determined by the legislation of the Czech Republic. The Hunting Act distinguishes and defines four types of work performance. Dachshunds and terriers are the only groups of hunting dogs that can pass all four tests and be used for all types of hunting work in the Czech Republic. Although hounds are better suited to hunting wild boar, our law prohibits the use of dogs of a height of 55 cm or more for hunting ungulates. Dachshunds and terriers are no longer bred for earth-hunt work only, but are used for their independence and ability to adapt to surface work. For these reasons, dachshunds and terriers belong among the most common breeds for hunting all kinds of game in the Czech Republic. These breeds are considered to be independently working breeds that are able to work without visual contact with the hunter.

We used two different dog-breed groups: (A) dachshunds and (B) terriers. The hunting style of both breeds is as follows: looking for an animal, starting to bark, following in the footsteps of the animal, continuing to bark and chasing the animal to the hunter. In order to test potential bark differentiation, we recorded barks elicited by encounters with four different animal species. We selected animal models that would represent both (1) potentially dangerous animals (red fox, wild boar) and (2) non-dangerous animals (fowl, rabbit). Encounters with wild boars represent, for the small-bodied dog breeds used in our study, a real life-threatening situation.

We have postulated the following hypotheses:

(1) Barks produced during encounters with different animal species will have different acoustic structures. We can predict this based on previous robust literature showing that dog barks can be categorized based on various types of context [19,26]. Barks during hunting should vary with the demands of the situation, e.g. based on urgency or a common species-specific

animal response, such as running away in hares, flight in pheasants, active defence in wild boar, etc.

(2) Barks will show a different acoustic structure depending on the arousal of the caller. We predict that barks produced during the presence of non-dangerous species might differ from those produced in the presence of potentially dangerous species. We tested whether the degree of threat from the species of animal the dog encounters (e.g. wild boar versus rabbit) is reflected in the structure of the acoustic parameters based on the Morton hypothesis [32]. According to this hypothesis, signals containing high frequencies and tonality rather correlate with affiliative behaviours (e.g. appeasement, submission and care-solicitation), while signals with lower frequencies and noise components correlate with aggressive behaviours like dominance and threat. Motivation-structural rules may be explained by the underlying emotional state of the signaller during aggressive and friendly contexts [33]. Muscular tension and action of vocal apparatus accompanied by the specific emotional state of the caller can influence the acoustic parameters of a bark; this is done in such a way that we can predict how the acoustic parameters will change based on the arousal level or emotional state valence (positive/negative) generated during agonistic interactions, e.g. signals with low frequencies, longer durations, wider frequency ranges and little frequency modulations. On the contrary, signals produced during nonaggressive interactions show a structure with higher frequencies and modulations, shorter durations and less spectral noise ratio [33].

Results

Animal species context

We analyzed 1888 barks of 19 individual dogs belonging to two breeds – (1) dachsund and (2) terrier – which were produced in response to four different animal species (Fig. 1): wild boar, red fox, rabbit and fowl (Table 1). Figure 1 shows the bark spectrograms of the four types of barks (audio files: Additional Files 1–4).

To investigate whether acoustic parameters of barks differ in response to encountered animal species, we performed three separate stepwise discriminant function analyses (DFA) for three datasets (1) dachshunds only, (2) terriers only and (3) pooled data of both breeds.

The resulting models show a similar pattern for all three datasets independently (Table 2), including classification results (Table 3-4): the dachshund model (N = 9, n = 810, Wilks' lambda = 0. 495, $p < 0.001$) included 8 acoustic parameters, the terrier model (N = 10, n = 1078, Wilks' lambda = 0. 528, $p < 0.001$) included 10 parameters, and the pooled model (N = 19, n = 1888, Wilks' lambda = 0. 549, $p < 0.001$) included 12 variables (Table 5). DFA for all three datasets showed that barks of dachshunds and terriers are recognizable based on the animal encountered with a higher probability than would be classified by chance (Table 2). The randomization procedure confirmed that these results were significant (pDFA, $p < 0.001$) for all three DFA models. Barks evoked by wild boar were classified better than those evoked by other animals (dachshund model: 60.6%; terrier model: 80.5%; pooled model: 73.3%), which is much higher than classification by chance (22.2%; 19.5% and 20.7% respectively) (Table 3). The percentages of correctly classified barks evoked by the other three animals were similar in all three models: dachshund model (43.3–52.1%), terrier model (27.8–56.2%), pooled model (35.7–49.8%). Classification outputs were significantly higher in comparison to classification by chance (dachshund model: Chi-Square = 128.7, df = 3, $p < 0.001$; terrier model: Chi-Square = 232.9, df = 3, $p < 0.001$; pooled model: Chi-Square = 170.9, df = 3, $p < 0.001$).

Motivational-structural test

From the measured acoustic parameters we selected four frequency parameters: F5 and Q1F showing the proportion of the acoustic energy in low frequencies, and F 95 and Q3F showing signal components in higher frequencies. We also selected six temporal parameters: Duration, Center Time Rel, Time 5 Rel, Time 95 Rel, Q1T Rel and Q3T Rel. These parameters show how acoustic energy is spread across a signal's duration. We aimed to test in which part of the signal the information related to Motivational-structural role could be encoded.

Frequency parameters

Results from testing of frequency parameters were consistent with motivation-structural theory.

Barks in response to a wild boar showed significantly lower frequency parameters (Figure 2): F5 (GLM: $F_{3,18} = 8.3$, $p < 0.001$), F 95 (GLM: $F_{3,18} = 12.8$, $p < 0.001$), Q3F (GLM: $F_{3,18} = 6.99$, $p = 0.001$). Q1F multiple comparison also showed significantly lower frequencies for barks produced in the presence of a wild boar, although the overall model did not show a significant effect of animal species (GLM: $F_{3,18} = 1.52$, $p = 0.222$).

Temporal parameters

Temporal parameters revealed significantly the longest Duration (GLM: $F_{3,18} = 32.4$, $p < 0.001$), while the shortest Center Time Rel (GLM: $F_{3,18} = 5.6$, $p = 0.003$).

Barks produced in the presence of a wild boar showed non-significant difference at the beginning part of the signal (Time 5 Rel: GLM, $F_{3,18} = 1.54$, $p < 0.220$; Q1T Rel: GLM, $F_{3,18} = 0.97$, $p = 0.418$) and the significant difference at the end part of the signal (Q3T Rel: GLM, $F_{3,18} = 8.90$, $p < 0.001$; Time 95 Rel: GLM, $F_{3,18} = 9.80$, $p < 0.001$) could indicate the location of information at the end part of the signal, specifically around the section located 75–95% through the signal duration. These two significant parameters were the shortest in barks at wild boar.

Discussion

We aimed to test for potential differences in the barking of dogs when they encounter four different animal species – wild boar, red fox, rabbit and fowl – which represent models of various size and danger level for dogs. We used two groups of dogs – dachshunds and terriers. Classification results of a discrimination analysis showed that barks of dachshunds and terriers can be categorized based on the animal species they encountered with a higher probability than would be expected if classification was random. It was revealed that the most distinctive barks were made during encounters with the most dangerous animal, the wild boar. The same pattern was shown when we pooled both datasets together. On the contrary, barks evoked by red fox encounters were classified with a similar result to the other smaller and non-dangerous animals – here, the rabbit and fowl. Although the red fox represents a potentially dangerous species for small dog breeds, the provoked barks were not classified with a much higher success rate than barks at animals that pose no threat. This would indicate that the key parameter might be the body size of the animal the dog meets. When we compare the average success in the classification of barks at different animals with the classification results of different bark-classifying methods from different contexts we can see comparable results (see Table 4); however, different classification methods with different numbers of individuals and chance levels were used in these studies. When we take into account the resulting classification by chance level using weighting classification outputs by chance level, such a comparison may give us a general overview of the classification success generated by different classification methods.

The question is why hunting dogs bark differently at different animal species; is it because of a different inner state or it is a signal directed at their human companions? The barks investigated in previous studies were collected in different distinct social scenarios such as disturbance, isolation, play, presence of a stranger, fight training, begging, walk preparation, etc. [14,26], and the acoustic structure of barks presumably reflects the inner states of dogs [34] associated with these social contexts, which can be also recognized by humans [27,30,35]. Across these different contexts the emotional state of a dog may likely differ. We tested therefore whether the degree of threat from the species of animal the dog encounters (wild boar versus rabbit, red fox and fowl) can be reflected by the acoustic parameter structure according to the Morton's hypothesis, and we found that the acoustic structure of barks really follows these structural-acoustic rules. Barks produced during contact with a wild boar showed significantly lower frequency parameters and the longest duration. We also found evidence to suggest that the key information is located towards the end of the signal (close to the 95% quartile of bark duration). Within this part of the signal we found the biggest differences in temporal parameters of barks produced in the presence of the wild boar versus other animal species.

The motivational-structural rules theory has been previously documented in dog barking as an association of the motivational states accompanying mobbing behaviour [17]. In our case, it seems that the variability of barking, which depends on the species of animal the dog encounters, is an expression of a dog's inner state rather than functionally reference information. In addition, the expression of the inner state in barking appears to depend on the size of the potential threat. Barking in the case of a great threat (wild boar) is more specific than barking in the case of a smaller threat (red fox) or no threat (rabbit, fowl). This phenomenon then appears to be innate, as it has been reported in the case of naive dogs, without previous experience with wild boar.

Both dog owners and non-owners, including adults and young children, are able to categorize a dog's emotional state and barking context above the level of chance [19,26,27,30]. Domestic dogs bark frequently in comparison to feral dogs, which produce barks relatively rarely [36]. This fact could indicate that barking is at least in some way used for communication with humans [24]. Some authors have considered barks to be an exaggerated by-product of the domestication process that has no specific function [12]. Previous studies have shown that dog barks are able to express a wider range of emotions compared to those of wolves. Such a change in the acoustic communication of dogs has resulted from their association with humans [37]. Recognizing dog barks may be advantageous in inter-specific interactions since dog domestication occurred at least 30,000 years ago [38-40]. This process was initiated by European hunter-gatherers [39]. Mutualism between dog and hunter probably took place early after domestication [41] when dogs assisted in the hunting of prey [39]. The ability to draw attention to different animal species complements hitherto known communicative skills like human–dog communication via eye contact [42], changes in facial expressions of dogs affected by human attentional state [43], the ability of dogs to understand the communicative cues of humans [44] or communication using eye gaze [45,46] , and the widely known ability of dogs to understand human pointing gestures [44,47].

Hunting dogs were bred to follow the trail of an animal. Some of these breeds were probably selected for a specific type of barking [14]. Such specialization could lead to the forming of an additional ability in comparison to other breeds not selected for hunting abilities. The hearing system of canids has primarily evolved to optimize predation, especially to localize sounds produced by potential prey [48]. Recognition of animal species could be favoured in reciprocal cooperation during hunting, e.g. recognition of potentially dangerous vs. non-dangerous animals could be especially favoured. Understanding the regulation mechanisms of mutual communication between humans and animals is especially important for animals such as dogs living in close contact with their human partners, depending on them for food, care and health [49]. The hunting activity of dogs with humans is considered to be derived from the cooperative behavior of wolves [24]. In hunting dogs, we might suppose that animal-encounter-specific barking may significantly increase the effectiveness of hunting events.

Methods

Ethics statement

This is a statement to confirm that all experimental protocols were approved by a named institutional or licensing committee. The authors declare that the present study complies with the current laws of the Czech Republic. The research was carried out in accordance with recommendations in the Guide for Care and Use of Animals of the Czech University of Life Sciences, Prague. This study focused on the recording of sounds, which was not considered an invasive experimental technique by The Professional Ethics Commission of the Czech University of Life Sciences Prague (project no 14/19) and did not require a special permit.

Subjects

We recorded barks from 19 dogs (nine dachshunds – two males and seven females, eight fox terriers – four males and four females, one male Welsh terrier and one male jagdterrier) (Table 1) during December 2016 and March 2017. The age of both dachshunds and fox terriers ranged 1 to 11 years, the Welsh terrier was three years old and the jagdterrier two years old. Some dogs had previous experience with tested animal species and others were naive, with no previous experience (Table 1). The dog owners were coauthors of this study, their colleagues.

Experimental procedure

Recordings were conducted under semi-controlled conditions during outdoor experiments, not during huntig events. The experimental site was chosen in isolation from other objects and potential noise. No vegetation other than low grass was present during the winter and early spring. The experiments were performed in sunny weather without rainfall and almost no wind. Each dog was tested only once per day. The interval between experimental days was longer than fourteen days. Each of 19 dogs was randomly assigned to one of the four treatments (wild boar, red fox, rabbit and fowl). Recorded barks were elicited by encounters with four different animal species through the fence mesh. There was no direct contact between the tested animals. Only one individual dog was tested during the experiment. Each tested dog was brought to the fence, released and left alone for 5–15 minutes depending on the frequency of barking required. The recording microphone was placed at a distance of two metres from the fence. We used an Olympus Linear PCM LS-5 audio-recorder with a Sennheiser ME 67 microphone (frequency response 20 Hz–20 kHz) with a K6 powering module.

Acoustic analyses

We randomly selected a maximum of 30 barks per individual. These were chosen from a sample of barks of the best quality: non-overlapping barks with low background noise and a good signal-to-noise ratio. We did not obtain a full matrix as some dogs gave fewer than 30 barks. A total of 1888 barks were analyzed: 390 barks from the wild boar experiment, 508 barks from the red fox experiment, 510 barks from the rabbit experiment and 480 barks collected during the fowl experiment.We analyzed recordings using Raven Pro Sound Analysis Software (Cornell Lab of Ornithology, New York, USA) from which spectrograms were generated using the following parameters: Hann window type with a 1050 point window size, an overlap of 50%, a hop size of 11.9 ms, and grid spacing of 21 Hz. We measured 20 acousticaparameters (Table 5).

Statistical analyses

From the measured parameters we excluded those that were highly correlated, and the remaining variables were entered into the discriminant function analysis (DFA) (Table 3). We performed three types of analyses: (1) for dachshunds, (2) for terriers and (3) for both breeds together (pooled model). We performed a stepwise DFA in order to test whether dog barks can be classified based on the animal species that they were produced in response to. The procedure selected predictors using the Wilks' lambda criterion. We used F values as a criterion for entering or removing an acoustic parameter from a classification model (F to enter = 3.84; F to remove = 2.71). For external validation of this model we used leave-one-out cross-validation using IBM SPSS 20 (IBM Corp., Armonk, USA). The context of the bark (provoked by a particular animal species) was used as a group identifier and the acoustic variables were used as discriminant variables. We normalized measured variables using Z score transformation (by subtracting the mean and dividing by the variable's standard deviation), which avoids the false attribution of weights in relation to variables measured in different units (IBM Corp., Armonk, USA). We then performed a permuted DFA (pDFA) for nested designs, which serves as a randomization procedure for non-independent data [50]. We calculated pDFAs using a script written in software "R" (provided by Roger Mundry) using 100 random selections and 10,000 permutations. This procedure gave a p-value which was used to determine the significance of the correct classification rate of barks to the test factor (animal species), while controlling for a single nested factor (individual). N refers to number of individuals (dogs), n refers to number of calls (barks).

We used univariate general linear models (GLM) for the motivational-structural test to see if barks differ between the animal species they were produced in response to. Acoustic variables were used as dependent variables, animal species as a fixed factor, and individual dogs as a random factor. We used Bonferroni corrected post hoc multiple comparison.

Data Availability

The datasets generated during and analyzed during the current study are available from the corresponding author on request.

References

1 Yeomans, L., Martin, L. & Richter, T. Close companions: Early evidence for dogs in northeast Jordan and the potential impact of new hunting methods. *J. Anthropol. Archaeol.* **53**, 161-173, doi:https://doi.org/10.1016/j.jaa.2018.12.005 (2019).

2 Serpell, J. *The domestic dog: Its evolution, behavior and interactions with people. Second edition.* 2 edn, 875 (Cambridge University Press, 2016).

3 Jensen, P. *Behavioural biology of dogs*. 266 (CABI Publishing, 2007).

4 Bergström, A. *et al.* Origins and genetic legacy of prehistoric dogs. *Science* **370**, 557-564, doi:10.1126/science.aba9572 (2020).

5 Pavlidis, P. & Somel, M. Of dogs and men. *Science* **370**, 522-523, doi:10.1126/science.abe7823 (2020).

6 Botigué, L. R. *et al.* Ancient European dog genomes reveal continuity since the Early Neolithic. *Nat. Commun.* **8**, 16082, doi:10.1038/ncomms16082 (2017).

7 Bradshaw, J. W. S. & Lea, A. M. Dyadic interactions between domestic dogs. *Anthrozoös* **5**, 245-253, doi:10.2752/089279392787011287 (1992).

8 Fox, M. W. *Behaviour of wolves, dogs and related canids*. 220 (Harper & Row, 1971).

9 Gácsi, M. *et al.* Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. *Dev. Psychobiol.* **47**, 111-122, doi:10.1002/dev.20082 (2005).

10 Topál, J. *et al.* Attachment to humans: A comparative study on hand-reared wolves and differently socialized dog puppies. *Anim. Behav.* **70**, 1367-1375, doi:10.1016/j.anbehav.2005.03.025 (2005).

11 Hare, B., Brown, M., Williamson, C. & Tomasello, M. The domestication of social cognition in dogs. *Science (New York, N.Y.)* **298**, 1634-1636, doi:10.1126/science.1072702 (2002).

12 Cohen, J. A. & Fox, M. W. Vocalizations in wild canids and possible effects of domestication. *Behav. Process.* **1**, 77-92, doi:http://dx.doi.org/10.1016/0376-6357(76)90008-5 (1976).

13 Siniscalchi, M., d'Ingeo, S., Minunno, M. & Quaranta, A. Communication in dogs. *Animals (Basel)* **8**, doi:10.3390/ani8080131 (2018).

14 Pongrácz, P., Molnár, C. & Miklósi, Á. Barking in family dogs: An ethological approach. *Vet. J.* **183**, 141-147, doi:http://dx.doi.org/10.1016/j.tvjl.2008.12.010 (2010).

15 Pongrácz, P., Szabó, É., Kis, A., Péter, A. & Miklósi, Á. More than noise?—Field investigations of intraspecific acoustic communication in dogs (*Canis familiaris*). *Appl. Anim. Behav. Sci.* **159**, 62-68, doi:https://doi.org/10.1016/j.applanim.2014.08.003 (2014).

16 Boitani, L., Francisci, F., Ciucci, P. & Andreoli, G. in *The domestic dog: Its evolution, behaviour and interactions with people* (ed J. Serpell) 217-244 (Cambridge University Press, 1995).

17 Lord, K., Feinstein, M. & Coppinger, R. Barking and mobbing. *Behav. Process.* **81**, 358-368, doi:http://dx.doi.org/10.1016/j.beproc.2009.04.008 (2009).

18 Gácsi, M., McGreevy, P., Kara, E. & Miklosi, A. Effects of selection for cooperation and attention in dogs. *Behav. Brain. Funct.* **5**, 31, doi:10.1186/1744-9081-5-31 (2009).

19 Yin, S. A new perspective on barking in dogs (*Canis familaris*). *J. Comp. Psychol.* **116**, 189-193, doi:10.1037/0735-7036.116.2.189 (2002).

20 Yeon, S. C. The vocal communication of canines. *J. Vet. Behav.* **2**, 141-144, doi:http://dx.doi.org/10.1016/j.jveb.2007.07.006 (2007).

21 Kim, J. *et al.* Genetic selection of athletic success in sport-hunting dogs. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E7212, doi:10.1073/pnas.1800455115 (2018).

22 Lamb, V. *The ultimate hunting dog reference book: A comprehensive guide to more than 60 sporting breeds.* (Globe Pequot Press, 2006).

23 Jakovcevic, A., Elgier, A. M., Mustaca, A. & Bentosela, M. Breed differences in dogs' (Canis familiaris) gaze to the human face. *Behav. Process.* **84**, 602-607, doi:10.1016/j.beproc.2010.04.003 (2010).

24 Miklosi, A. *Dog behaviour, evolution, and cognition.* 274 (Oxford University Press, 2007).

25 Christiansen, F. O., Bakken, M. & Braastad, B. O. Behavioural differences between three breed groups of hunting dogs confronted

with domestic sheep. *Appl. Anim. Behav. Sci.* **72**, 115-129, doi:https://doi.org/10.1016/S0168-1591(00)00202-1 (2001).

26 Yin, S. & McCowan, B. Barking in domestic dogs: context specificity and individual identification. *Anim. Behav.* **68**, 343-355, doi:10.1016/j.anbehav.2003.07.016 (2004).

27 Pongracz, P., Molnar, C., Doka, A. & Miklosi, A. Do children understand man's best friend? Classification of dog barks by pre-adolescents and adults. *Appl. Anim. Behav. Sci.* **135**, 95-102, doi:10.1016/j.applanim.2011.09.005 (2011).

28 Molnár, C., Pongrácz, P., Faragó, T., Dóka, A. & Miklósi, Á. Dogs discriminate between barks: The effect of context and identity of the caller. *Behav. Process.* **82**, 198-201, doi:http://dx.doi.org/10.1016/j.beproc.2009.06.011 (2009).

29 Molnar, C. *et al.* Classification of dog barks: a machine learning approach. *Anim. Cogn.* **11**, 389-400, doi:10.1007/s10071-007-0129-9 (2008).

30 Pongrácz, P., Molnár, C., Miklósi, Á. & Csányi, V. Human listeners are able to classify dog (Canis familiaris) barks recorded in different situations. *J. Comp. Psychol.* **119**, 136-144, doi:10.1037/0735-7036.119.2.136 (2005).

31 Pongrácz, P., Molnár, C. & Miklósi, Á. Acoustic parameters of dog barks carry emotional information for humans. *Appl. Anim. Behav. Sci.* **100**, 228-240, doi:http://dx.doi.org/10.1016/j.applanim.2005.12.004 (2006).

32 Morton, E. S. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Am. Nat.* **111**, 855-869 (1977).

33 Briefer, E. F. Vocal expression of emotions in mammals: mechanisms of production and evidence. *J. Zool.* 288, 1-20 (2012).

34 Pongracz, P. Modeling evolutionary changes in information transfer: Effects of domestication on the vocal communication of dogs (*Canis familiaris*). *Eur. Psychol.* **22**, 219-232, doi:10.1027/1016-9040/a000300 (2017).

35 Molnar, C., Pongracz, P., Doka, A. & Miklosi, A. Can humans discriminate between dogs on the base of the acoustic parameters of barks? *Behav. Process.* **73**, 76-83, doi:10.1016/j.beproc.2006.03.014 (2006).

36 Boitani, L. & Ciucci, P. Comparative social ecology of feral dogs and wolves. *Ethol. Ecol. Evol.* **7**, 49-72 (1995).

37 Miklosi, A. in *Behavioural biology of dogs* (ed Per Jensen) 207-222 (CABI Publishing, 2007).

38 Grimm, D. Dogs may have been domesticated more than once. *Science* **352**, 1153-1154, doi:10.1126/science.352.6290.1153 (2016).

39 Thalmann, O. *et al.* Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science* **342**, 871-874, doi:10.1126/science.1243650 (2013).

40 Amici, F., Waterman, J., Kellermann, C. M., Karimullah, K. & Bräuer, J. The ability to recognize dog emotions depends on the cultural milieu in which we grow up. *Sci. Rep.* **9**, 16414, doi:10.1038/s41598-019-52938-4 (2019).

41 Clutton-Brock, J. *A natural history of domesticated animals*. (Cambridge University Press, Cambridge, UK, 1987).

42 Kaminski, J., Schulz, L. & Tomasello, M. How dogs know when communication is intended for them. *Dev. Sci.* **15**, 222-232, doi:10.1111/j.1467-7687.2011.01120.x (2012).

43 Kaminski, J., Hynds, J., Morris, P. & Waller, B. M. Human attention affects facial expressions in domestic dogs. *Sci. Rep.* **7**, 12914, doi:10.1038/s41598-017-12781-x (2017).

44 Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M. Making inferences about the location of hidden food: Social dog, causal ape. *J. Comp. Psychol.* **120**, 38-47, doi:10.1037/0735-7036.120.1.38 (2006).

45 Soproni, K., Miklosi, A., Topál, J. & Csányi, V. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J. Comp. Psychol.* **115**, 122-126, doi:10.1037/0735-7036.115.2.122 (2001).

46 Téglás, E., Gergely, A., Kupán, K., Miklosi, A. & Topál, J. Dogs' gaze following Is tuned to human communicative signals. *Curr. biol.* **22**, 209-212, doi:10.1016/j.cub.2011.12.018 (2012).

47 Miklosi, A. & Soproni, K. A comparative analysis of animals' understanding of the human pointing gesture. *Anim. Cogn.* **9**, 81-93, doi:10.1007/s10071-005-0008-1 (2006).

48 Bradshaw, J. & Rooney, N. in *The domestic dog: Its evolution, behavior and interactions with people. Second edition.* (ed James Serpell) (Cambridge University Press, 2016).

49 Ntalampiras, S. A. *et al.* Automatic classification of cat vocalizations emitted in different contexts. *Animals (Basel)* **9**, 543, doi:10.3390/ani9080543 (2019).

50 Mundry, R. & Sommer, C. Discriminant function analysis with nonindependent data: consequences and an alternative. *Anim. Behav.* **74**, 965-976, doi:10.1016/j.anbehav.2006.12.028 (2007).

51 Larranaga, A. *et al.* Comparing supervised learning methods for classifying sex, age, context and individual Mudi dogs from barking. *Anim. Cogn.* **18**, 405-421, doi:10.1007/s10071-014-0811-7 (2015).

Figure 1. Spectrograms showing barking responses to wild boar, red fox, rabbit and fowl. Barks in each panel were produced by the same individual: Dachshunds Pecka (a) and Vendula (b). Fox Terriers Hard (c) and Gam (d).

Figure 2. Univariate GLM comparison of acoustic parameters for testing of Motivation-structural theory.

Frequency parameters F5 and Q1F show the proportion of the acoustic energy in low frequencies (a-b), and F 95 and Q3F (c-d) show signal components in higher frequencies. Temporal parameters show how acoustic energy is spread across a signal's duration (e-j).

Acknowledgements

The study was funded by Internal Grants of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, reg. numbers B04_18 and A_19_13 and the European Social Fund (Operational Programme Research, Development and Education, EVA 4.0). We also thank František Šveda who was of great help during our experiments.

Author Contributions

R.P. and V.H. designed the study, R.P., K.B. and J.A. collected the data. R.P. and O.M. analyzed the data. R.P. wrote the paper. All the authors read and approved the final manuscript.

Competing Interests Statement

The authors declare no competing interests.

Breed	Subject	Sex	Weight	Age	Wild boar	Red fox	Rabbit	Fowl
Dachshund	Hurvinek	M	7	6	30	30*	30*	30*
Dachshund	Amalka	F	5	4	0	30	30*	30*
Dachshund	Terezka	F	6	2	30	0	0*	0*
Dachshund	Nikolka	F	4	11	0*	30*	30*	30*
Dachshund	Venda-Benda	F	5	1	0	0	30*	30*
Dachshund	Vendula	F	7	10	30	30*	30*	30*
Dachshund	Kacka	F	5	4	30	30	30*	30*
Dachshund	Pecka	F	4	1	30	0	30*	30*
Dachshund	Punta	M	5	2	30	30	0*	30*
Fox Terrier	Gofi	F	7	2	0*	30*	30*	30*
Fox Terrier	Hard	M	10	1	30*	30*	30*	30*
Fox Terrier	Gam	M	9	2	30	30*	30*	30*
Fox Terrier	Cita	F	8	11	30*	30*	30*	0*
Fox Terrier	Bessy	F	8	7	30*	28*	30*	30*
Fox Terrier	Cerbis	M	10	3	30	30*	30*	30*
Fox Terrier	Nerys	M	9	9	0	30*	30*	30*
Fox Terrier	Ypsa	F	8	5	0*	30*	30*	30*
Welsh Terrier	Cit	M	7	3	30*	30*	30*	30*
Jagdterrier	Ar	M	10	2	30*	30*	30*	30*

Table 1. Tested dogs and number of analyzed barks per context. (*) Previous experience with tested animal model. Dachshund Nikolka was castrated, everyone else was fertile.

Result model	**Classif Orig/Valid /a priori (%)**			**DF1 (correlation)**	**DF2 (correlation)**
Dachshund	53.2	51.9	25	Duration (r = -0.49)	Q3T Rel (r = -0.43)
Terrier	52.8	51.1	25	Duration (r = 0.78)	Time 5% Rel (r = 0.57)
Pooled	50.9	49.6	25	Duration (r = -0.69)	Q1F Rel (r = 0.58)

Table 2. The resulting discrimination function models. (Classif Orig/Valid /a priori) percentage of correct classification based on stepwise DFA, cross-validated DFA and a priori probability (classification by chance); (DF1, DF2) variable mostly correlated with the first and second discrimination function.

Result model	**Rabbit**	**Fowl**	**Red fox**	**Wild boar**	**Prior probability**
Dachshund					
Rabbit	**51.4**	32.9	2.9	12.9	25.9
Fowl	21.3	**52.1**	14.6	12.1	29.6
Red fox	10.6	33.9	**43.3**	12.2	22.2
Wild boar	13.9	23.9	1.7	**60.6**	22.2
Terrier					
Rabbit	**46.3**	19.3	27.3	7.0	27.9
Fowl	31.9	**27.8**	34.8	5.6	25.1
Red fox	23.6	14.8	**56.2**	5.4	27.6
Wild boar	10.5	1.4	7.6	**80.5**	19.5
Pooled					
Rabbit	**49.8**	24.9	16.3	9.0	27.0
Fowl	33.9	**35.7**	19.2	11.2	27.0
Red fox	21.0	23.9	**44.9**	10.3	25.3
Wild boar	9.0	11.0	6.7	**73.3**	20.7

Table 3. Confusion matrix for the animal species categorization task. Percentage of correct classification represents cross-validated results. A priori probability shows classification by chance (weighted by the number of analyzed barks). Bold numbers represent the percentage of correct classifications. Other values in rows show the percentages of incorrect classifications – that is, the percentage of barks wrongly classified as barks at another animal species.

Categ	No categ	Breed	N Dogs	Method	Classif	Chance	Differ	Reference
Animal	4	Dachshund	9	DFA valid	51.9	25.0	28.2	This study
Animal	4	Terriers	10	DFA valid	51.1	25.0	26.9	This study
Context	7	Mudi	8	k-nearest	55.5	14.3	41.2	[51]
Context	6	Mudi		humans listening	65-70	50	17.5	[35]
Context	6	Mudi	14	machine learning	43	18	25	[29]

Table 4. Classification results of bark subcategories in other studies. (Categ) classified categories, (No categ) number of classified categories, (Classif) correct classification percentage, (Chance) classification by chance, (Differ) difference between correct classification and classification by chance.

Abbreviation	Name	Description	Units	DFA model
Duration	**Duration.**	Signal duration	(s)	I,II,III
Time 5 Rel	**Time 5% relative.**	The point in time that divides the signal into two time intervals containing 5% and 95% of the energy	(Rel)	I,II,III
Time 95 Rel	**Time 95% relative.**	The point in time that divides the signal into two time intervals containing 95% and 5% of the energy	(Rel)	
Q1T Rel	**First quartile time relative.**	The point in time that divides the signal into two time intervals containing 25% and 75% of the energy	(Rel)	II
Q3T Rel	**Third quartile time relative.**	The point in time that divides the signal into two time intervals containing 75% and 25% of the energy	(s)	I,III
F5 Rel	**Frequency 5% relative.**	The frequency that divides the signal into two frequency intervals containing 5% and 95% of the energy relative to frequency range	(Rel)	I,II
F5	**Frequency 5%.**	The frequency that divides the signal into two frequency intervals containing 5% and 95% of the energy	(Hz)	II,III
F 95 Rel	**Frequency 95% relative.**	The frequency that divides the signal into two frequency intervals containing 95% and 5% of the energy relative to signal duration	(Rel)	II
F 95	**Frequency 95%.**	The frequency dividing the signal into two frequency intervals containing 95% and 5% of the energy	(Hz)	I
Q1F Rel	**First quartile frequency relative.**	The frequency that divides the signal into two frequency intervals containing 25% and 75% of the energy relative to frequency range	(Rel)	I,II,III
Q1F	**First quartile frequency.**	The frequency that divides the signal into two frequency intervals containing 25% and 75% of the energy	(Hz)	
Q3F	**Third quartile frequency.**	The frequency that divides the signal into two frequency intervals containing 75%	(Hz)	III

	and 25% of the energy		
CF	**Center frequency.** The frequency that divides the signal into two frequency intervals of equal energy.	(Hz)	II,III
CT Rel	**Center time relative.** The point in time that divides a signal into two time intervals of equal energy	(Rel)	
IQRBW	**Inter-quartile Range.** The difference between the 1st and 3rd Quartile Frequencies	(Hz)	III
BW90	**Bandwidth 90%.** The difference between the 5% and 95% frequencies.	(Hz)	III
Agg Entropy	**Aggregate Entropy.** The aggregate entropy measures the disorder in a sound by analyzing the energy. Higher values correspond to greater disorder in the signal whereas a pure tone have zero entropy. It corresponds to the overall disorder in the sound.	(Bits)	I,III
Avg Entropy	**Average Entropy.** The average entropy measures the average disorder in a sound. Describes the amount of disorder for a typical spectrum within the signal	(Bits)	II,III
Max Entropy	**Maximum Entropy.** This entropy is calculated by finding the entropy for each frame in the signal and then taking the maximum values	(Bits)	II,III
Min Entropy	**Minimum Entropy.** This entropy is calculated by finding the entropy for each frame and taking the minimum values	(Bits)	I

Table 5. Measured acousticparameters. Measurements based on the Raven Pro manual.

DFA model: (I) for dachshunds, (II) for terriers, and (III) pooled data of both breeds.

Hart *et al. Frontiers in Zoology* 2013, **10**:80
http://www.frontiersinzoology.com/content/10/1/80

FRONTIERS IN ZOOLOGY

RESEARCH Open Access

Dogs are sensitive to small variations of the Earth's magnetic field

Vlastimil Hart[1], Petra Nováková[1], Erich Pascal Malkemper[2†], Sabine Begall[2†], Vladimír Hanzal[1], Miloš Ježek[1], Tomáš Kušta[1], Veronika Němcová[1], Jana Adámková[1], Kateřina Benediktová[1], Jaroslav Červený[1] and Hynek Burda[1,2*]

Abstract

Introduction: Several mammalian species spontaneously align their body axis with respect to the Earth's magnetic field (MF) lines in diverse behavioral contexts. Magnetic alignment is a suitable paradigm to scan for the occurrence of magnetosensitivity across animal taxa with the heuristic potential to contribute to the understanding of the mechanism of magnetoreception and identify further functions of magnetosensation apart from navigation. With this in mind we searched for signs of magnetic alignment in dogs. We measured the direction of the body axis in 70 dogs of 37 breeds during defecation (1,893 observations) and urination (5,582 observations) over a two-year period. After complete sampling, we sorted the data according to the geomagnetic conditions prevailing during the respective sampling periods. Relative declination and intensity changes of the MF during the respective dog walks were calculated from daily magnetograms. Directional preferences of dogs under different MF conditions were analyzed and tested by means of circular statistics.

Results: Dogs preferred to excrete with the body being aligned along the North–South axis under calm MF conditions. This directional behavior was abolished under unstable MF. The best predictor of the behavioral switch was the rate of change in declination, i.e., polar orientation of the MF.

Conclusions: It is for the first time that (a) magnetic sensitivity was proved in dogs, (b) a measurable, predictable behavioral reaction upon natural MF fluctuations could be unambiguously proven in a mammal, and (c) high sensitivity to small changes in polarity, rather than in intensity, of MF was identified as biologically meaningful. Our findings open new horizons in magnetoreception research. Since the MF is calm in only about 20% of the daylight period, our findings might provide an explanation why many magnetoreception experiments were hardly replicable and why directional values of records in diverse observations are frequently compromised by scatter.

Keywords: Magnetoreception, Magnetosensitivity, Magnetic field, Magnetic storm, Magnetic alignment, Dog, Canid, Mammal

Introduction

Magnetic alignment, i.e., spontaneous alignment of the body with respect to the magnetic field lines, when other determinants (e.g. wind direction, sun position, curiosity) of the body position are negligible, has been demonstrated in several species of mammals in diverse behavioral contexts: in grazing and resting cattle, roe deer and red deer [1-4] and hunting red foxes [5] as well as in several other mammalian species (under preparation). Magnetic alignment proved to be a suitable paradigm to scan for the occurrence of magnetosensitivity across animal taxa with a heuristic potential to contribute to the understanding of the mechanism of magnetoreception and identify further functions of a magnetic sense apart from navigation [1-9]. With this in mind we decided to look for examples of expression of magnetic alignment in dogs. Expecting magnetoreception in dogs is reasonable given the extraordinary homing abilities of dogs [10] and closely related species like red foxes, coyotes and grey wolves [11-13]. Wolves, as the progenitors of domestic dogs, possess extraordinary large (about 150–200 km^2) home ranges

---

* Correspondence: hynek.burda@uni-due.de
†Equal contributors
[1] Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, 16521 Praha 6, Czech Republic
[2] Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, 45117 Essen, Germany

[14], suggesting superior orientation abilities. Furthermore, strong indications for magnetosensation in the red fox [5] add on to the growing evidence.

A discovery of magnetoreception in dogs would open totally new horizons for magnetobiological research: Dogs are widely available experimental subjects all over the world and can easily be trained to react on diverse sensory stimuli [15]. In addition, as dogs are still readily used as experimental animals in a wide array of biomedical applications [16], the discovery of a new sense would have far reaching consequences also in this sector.

Having been inspired by our hitherto observations in other animals [1-3,5-8,17], we monitored spontaneous alignment in dogs during diverse activities (resting, feeding and excreting) and eventually focused on excreting (defecation and urination incl. marking) as this activity appeared to be most promising with regard to obtaining large sets of data independent of time and space, and at the same time it seems to be least prone to be affected by the surroundings.

Results

Circular analysis of the distribution of all values of all dogs irrespective of the magnetic field conditions revealed significant but highly scattered axial orientation during defecation (Table 1). This orientation was, however, not confirmed by the grand mean vector (calculated over the dogs' mean values, Figure 1, Table 1). Since no significant differences between males and females and since no angular preferences during defecation were found (not shown here), we only present the axial analyses combined for both sexes here.

After the data were sorted according to the magnetic field conditions (specifically, Kp-index, relative changes of magnetic field intensity or of declination) at the time

Table 1 Analysis of body orientation during defecation (all records, i.e., no differentiation between different magnetic conditions)

	Defecation: all records			
Variable	**Pooled**	**Pooled**	**Means (n > 5)**	**Means (n > 5)**
Data type	angular	axial	angular	axial
Number of observations	1,893	1,893	49	49
Mean vector (μ)	133°	157°/337°	80°	148°/328°
Length of mean vector (r)	0.013	0.052	0.043	0.209
Circular standard deviation	169°	70°	144°	51°
95% Confidence interval (−/+) for μ	-	-	-	121°-174°
99% Confidence interval (−/+) for μ	-	-	-	112°-183°
Rayleigh test (Z)	0.307	5.203	0.091	2.143
Rayleigh test (p)	0.736	0.006	0.914	0.117

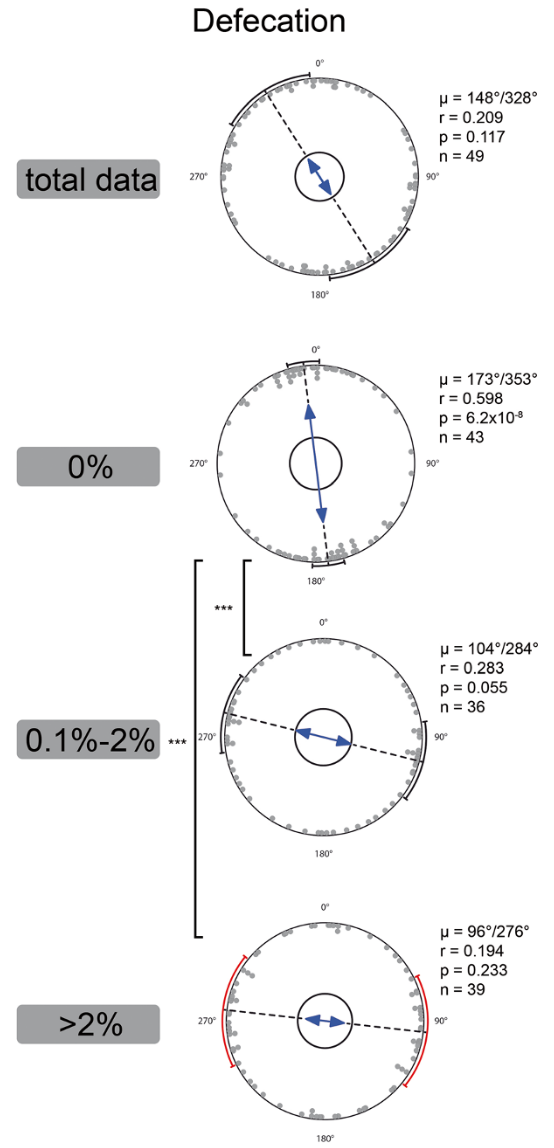


Figure 1 Analysis of dog body alignment during defecation. Axial analysis of mean vectors of dogs with more than 5 observations. Total data and observations from three different categories of relative changes of the declination of the Earth's magnetic field are shown from top to bottom (0%, 0.1-2%, >2%). Each pair of opposite dots indicates the axis of the mean vector of all observations of a single dog. The direction (μ) and length (r) of the (grand) mean vector and the p-value of the Rayleigh uniformity test as well as the sample size are given next to each diagram. μ and r are indicated by the direction and length of the blue arrows, respectively. Small inner circles indicate the 5%-significance level of the Rayleigh test. Circle segments at the outer circle represent the 95%-confidence intervals (red circle segments indicate intervals that could not be calculated with confidence due to large circular standard deviations). Statistically significant differences between the distributions according to the Mardia-Watson-Wheeler test are indicated by asterisks (*** = $p < 0.001$). A significant N-S axial orientation (i.e., 95%-confidence interval includes the N-S axis) can only be seen under conditions of zero declination change. See Tables 1–2 for further details on statistics.

Table 2 Axial analysis of alignment during defecation in all dogs (pooled data or mean vectors of particular dogs sorted into three categories according to the rate of changes of magnetic field declination)

	Pooled raw data			**Means per dog (n > 5)**		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	607	542	744	43	36	39
Mean vector (μ)	176°/356°	111°/291°	109°/289°	173°/353°	104°/184°	96°/276°
Length of mean vector (r)	0.216	0.106	0.03	0.598	0.283	0.194
Circular standard deviation	50°	61°	76°	29°	45°	52°
95% Confidence interval (−/+) for μ	168°-183°	-	-	164°-182°	81°-127°	-
99% Confidence interval (−/+) for μ	166°-185°	-	-	161°-185°	74°-134°	-
Rayleigh test (Z)	28.248	6.133	0.672	15.353	2.891	1.464
Rayleigh test (p)	$<10^{-12}$	0.002	0.511	$6.20 \cdot 10^{-8}$	0.055	0.233

of recording, a differentiated picture emerged. The relative declination change proved to be the best predictor of alignment, i.e.,. sorting the data according to this parameter provided the most significant results. Analysis of pooled recordings as well as of mean vectors of recordings in dogs sampled during calm magnetic field conditions (relative change in declination = 0%; minimum of 5 observations per dog) revealed a highly significant axial preference for North–South alignment during defecation (for 0% declination change: $\mu = 173^\circ/353^\circ \pm 9^\circ$ (mean vector orientation angle; 95% confidence interval), $r = 0.598$ (mean vector length), Rayleigh test: $n = 43$, $p = 6.2 \cdot 10^{-8}$, $Z = 15.353$; second order (weighted) statistics: weighted mean vector (WMV): 175°/355°, $r = 0.253$, Hotelling test: $n = 43$, $p = 1.02 \cdot 10^{-7}$, $F = 24.463$; Tables 2 and 3, Figures 1 and 2). With increasing relative declination changes the distribution of dogs' body orientations became more scattered and in the category "> 2%" the distribution was random, and no directional preference was apparent (Table 2, Figure 1). The distributions of dogs' body orientations in the intervals of relative declination change "0.1%-2%" as well as "> 2%" were significantly different from the distribution at 0%, both, when pooled raw data and when means per dog were analyzed (Mardia-Watson-Wheeler test, $p < 0.001$, Figure 1). The same dependence of the directional preference on the relative changes of the magnetic declination appeared when males and females were treated separately (not shown here).

Analysis of the alignment during defecation under conditions of stable magnetic declination (0% changes) revealed no significant effect of sex. There may be a slight effect of age: dogs in the age category 2.5-7 years showed a clearer preference than younger or elder dogs (not shown). The effect of the dog breed could not be tested because of small sample sizes.

Circular analysis of the distribution of the pooled raw data demonstrated a significant deviation from random distribution also in urinating dogs (Table 4). Analyzing

Table 3 Alignment during defecation in dogs (females and males) in two-hour periods

Variable	**All records 20:01–08:00**	**Quiet MF 20:01–08:00**	**All records 08:01–12:00**	**Quiet MF 08:01–12:00**	**All records 12:01–16:00**	**Quiet MF 12:01–16:00**	**All records 16:01–20:00**	**Quiet MF 16:01–20:00**
Number of observations	442	173	599	188	396	109	455	144
Mean vector (μ)	157°/337°	177°/357°	152°/332°	178°/358°	12°/192°	170°/350°	147°/327°	173°/353°
Length of mean vector (r)	0.042	0.239	0.073	0.2	0.074	0.26	0.088	0.176
Circular standard deviation	72°	48°	65°	51°	65°	47°	63°	53°
95% Confidence interval (−/+) for μ	112°-202°	165°-190°	130°-174°	163°-192°	345°-39°	155°-184°	126°-168°	155°-192°
99% Confidence interval (−/+) for μ	98°-217°	161°-193°	123°-181°	159°-106°	337°-48°	151°-189°	119°-175°	149°-198°
Rayleigh test (Z)	0.769	9.866	3.17	7.533	2.145	7.367	3.54	4.474
Rayleigh test (p)	0.463	0.000052	0.042	0.000535	0.117	0.000632	0.029	0.011

Columns denoted "quiet MF (magnetic field)" give statistic values based on analysis of those data from the respective column "all values" which were collected under conditions of stable declination (0% change). Due to small sample sizes for single dogs, the data of all observations done in the given period are pooled. Pooling is justified in this case because samples for respective dogs have comparable sizes and because males and females show comparable posture and alignment during defecation. The data were not sorted here according to months but the distribution of observations during respective months of the year is comparable, so that the distribution of the data (and resulting analysis) would not change if winter and summer observations were further separated. Note random circular distribution of the alignment when all data for respective time periods are analyzed, but highly significant preference for the North–South axis when only observations made under quiet magnetic field are considered.

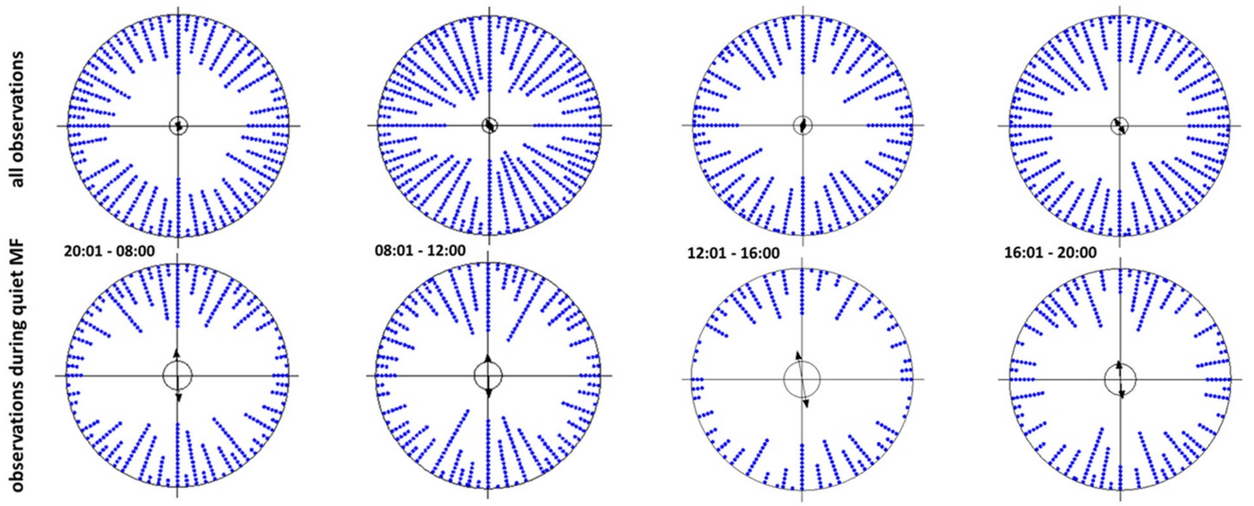


Figure 2 Alignment during defecation in dogs (females and males) in different day periods. Columns denoted "quiet MF (magnetic field)" give statistic values based on analysis of those data from the respective column "all values" which were collected under conditions of stable declination (0% change). Due to small sample sizes for single dogs, the data of all observations done in the given period are pooled. Pooling is justified in this case because samples for respective dogs have comparable sizes and because males and females show comparable posture and alignment during defecation. The data were not sorted here according to months but the distribution of observations during respective months of the year is comparable, so that the distribution of the data (and resulting analysis) would not change if winter and summer observations were further separated. Note random circular distribution of the alignment when all data for respective time periods are analyzed, but highly significant preference for the North–South axis when only observations made under quiet magnetic field are considered.

this data for males and females separately we found a slight difference in the patterns between sexes: Pooled data (without the dog M07) and mean values of all males with at least 5 observations revealed a significant angular preference for North-West heading during urination (Table 5). The male borzoi M07 contributed approximately one third of the urination data and was analyzed separately (Table 6); the results were similar to the pooled data of all other males. In contrast, females showed an axial preference for approximately the North–South axis during urination (Table 7). As in the case of defecation, sorting the data according to the relative changes of declination revealed a significant effect of this factor and a significant axial North–South alignment only under calm MF conditions (for 0% declination change: μ = 167°/347° ± 16°, r = 0.343, Rayleigh test: n = 49, p = 0.003, Z = 5.766; second order (weighted) statistics: WMV: 173°/353°, r = 0.165, Hotelling test: n = 49, $p = 5.08 \cdot 10^{-4}$, F = 8.952; Figure 3, Tables 5, 6, 7). The raw data distributions during changing declination were significantly different from the

Table 4 Angular and axial analysis of body orientation in dogs during urination

Data type	Urination: (all records)									
	Angular					Axial				
	Pooled			Means (n ≥ 5)		Pooled			Means (n ≥ 5)	
	Males	M07	Females	Males	Females	Males	M07	Females	Males	Females
Number of observations	1,402	2,478	1,702	24	35	1,402	2,478	1,702	24	35
Mean vector (μ)	312°	298°	13°	292°	331°	154°/334°	175°/355°	5°/185°	89°/269°	11°/191°
Length of mean vector (r)	0.048	0.105	0.03	0.213	0.213	0.037	0.196	0.132	0.101	0.292
Circular standard deviation	141°	122°	152°	101°	101°	74°	52°	58°	61°	45°
95% Confidence interval (−/+) for μ	268°-356°	283°-313°	309°-78°	217°-8°	269°-34°	125°-183°	171°-179°	358°-12°	9°-169°	348°-33°
99% Confidence interval (−/+) for μ	254°-10°	278°-318°	288°-98°	193°-31°	249°-53°	116°-192°	169°-180°	356°-15°	343°-194°	341°-40°
Rayleigh test (Z)	3.215	27.075	1.517	1.088	1.584	1.875	94.735	29.524	0.246	2.99
Rayleigh test (p)	0.04	$1.74 \cdot 10^{-12}$	0.219	0.341	0.206	0.153	$< 10^{-12}$	$< 10^{-12}$	0.786	0.049
Rao's spacing test (U)	307.618	354.479	339.271	140.383	131.675	325.078	357.094	346.675	134.75	145.847
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.1	>0.1	<0.01	<0.01	<0.01	>0.1	>0.1

Data for the male dog M07 are presented in a separate column due to large sample size.

Table 5 Angular analysis of alignment during urination in all males (pooled data without dog M07 and mean vectors of all males sorted into three categories according to the relative changes of magnetic field declination)

	Pooled raw data			**Means per dog (n ≥ 5)**		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	491	256	655	22	15	22
Mean vector (μ)	293°	12°	84°	291°	355°	195°
Length of mean vector (r)	0.129	0.08	0.006	0.367	0.349	0.07°
Circular standard deviation	116°	129°	182°	81°	83°	132°
95% Conf. interval (−/+) for μ	265°-321°	310°-74°	-	246°-335°	290°-61°	315°-76°
99% Conf. interval (−/+) for μ	256°-329°	290°-94°	-	232°-349°	270°-81°	239°-151°
Rayleigh test (Z)	8.17	1.619	0.028	2.959	1.828	0.109
Rayleigh test (p)	$2.83 \cdot 10^{-4}$	0.198	0.973	0.05	0.162	0.899
Rao's spacing test (U)	260.285	281.656	283.053	148.258	147.139	127.188
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.1	>0.1	>0.5

distribution under calm magnetic conditions (Mardia-Watson-Wheeler test, $p < 0.05$, Figure 3).

Discussion

Dogs rely much on their owner, and for many tasks they might anticipate the demanded behavior by reading their owner's facial expression and make use of unintentional experimenter-given cues [18-20]. This adds a bias-trap to any research relying on behavioral studies and particularly conditioning. However, this is certainly not a confounder in our study because the dogs do not have to fulfill a certain task, but perform everyday routine behavior.

The study was truly blind. Although the observers were acquainted with our previous studies on magnetic alignment in animals and could have consciously or unconsciously biased the results, no one, not even the coordinators of the study, hypothesized that expression of alignment could have been affected by the geomagnetic situation, and particularly by such subtle changes of the magnetic declination. The idea leading to the discovery of the correlation emerged after sampling was closed and the first statistical analyses (with rather negative results, cf. Figure 1) had been performed. Also, the acquisition of data on magnetic declination was carried out without knowledge of heading values on the respective time and date.

Table 6 Angular analysis of alignment during urination in male borzoi (M07)

Declination rate	**0-1.7%**	**1.8-3.3%**	**≥3.4%**
Number of observations	957	818	703
Mean vector (μ)	310°	285°	280°
Length of mean vector (r)	0.154	0.08	0.078
Circular standard deviation	111°	129°	130°
95% Confidence interval (−/+) for μ	294°-327°	250°-320°	241°-318°
99% Confidence interval (−/+) for μ	289°-332°	240°-331°	229°-331°
Rayleigh test (Z)	22.64	5.18	5.517
Rayleigh test (p)	$1.47 \cdot 10^{-10}$	0.006	0.015
Rao's spacing test (U)	345.705	344.156	341.565
Rao's spacing test (p)	< 0.01	< 0.01	< 0.01

Data are sorted into three categories according to the *relative changes* of magnetic field declination. Limits of the categories were chosen so that sample sizes are comparable.

We found no differences in alignment of females and males during defecation and of females during urination, which might be related to a similar posture the animals are adopting during defecation (in all dogs) and urination (in females). Urinating males have a slightly different preference to orient their body axis than urinating females (cf. Figure 3); this could be caused by leg lifting during urination in males. Indications of different directional tendencies depending on which leg (left or right) is lifted are currently under study. All recordings were made outside on open fields, and routes of walks were routinely changed to exclude or limit pseudoreplications which would arise when dogs are defecating or urinating at just a few places within their kennel or house yard.

Natural fluctuations of the Earth's magnetic field [21,22] have previously been suggested to disturb orientation in birds [23-25], bees [26] and whales [27]; and even to affect vegetative functions and behavior in humans [28,29], reviewed also in [22].

In this study, we provide the first clear and simply measurable evidence for influence of geomagnetic field variations on mammal behavior. Furthermore, it is the first demonstration of the effect of the shift of declination, which has to our knowledge never been investigated before. Previous studies of the effect focused mainly on the variations in field intensity. Although intensity and declination changes are mostly concomitant, declination change was a better predictor of dog alignment. Interestingly, the rate and direction of the changes disturb more effectively

Table 7 Axial analysis of alignment during urination in all females (pooled data and mean vectors of particular dogs sorted into three categories according to the relative changes of magnetic field declination)

	Pooled raw data			Means per dog ($n \geq 5$)		
Declination rate	**0%**	**0.1-2%**	**>2%**	**0%**	**0.1-2%**	**>2%**
Number of observations	603	396	703	27	20	29
Mean vector (μ)	5°/185°	2°/182°	11°/191°	0°/180°	7°/187°	23°/203°
Length of mean vector (r)	0.208	0.131	0.068	0.434	0.159	0.134
Circular standard deviation	51°	58°	66°	37°	55°	57°
95% Conf. interval (−/+) for μ	357°-12°	347°-17°	349°-33°	163°-196°	312°-63°	328°-78°
99% Conf. interval (−/+) for μ	354°-15°	342°-22°	342°-40°	157°-201°	294°-80°	311°-95°
Rayleigh test (Z)	26.146	6.839	3.251	5.085	0.503	0.52
Rayleigh test (p)	$4.41 \cdot 10^{-12}$	0.001	0.039	0.005	0.61	0.598
Rao's spacing test (U)	312.836	330	339.004	156.975	135.002	129.554
Rao's spacing test (p)	<0.01	<0.01	<0.01	>0.05	>0.1	>0.5

than absolute values. Here, for the first time the response can be attributed to the rate of magnetic field changes.

Typically, the daily declination comprises westward-shifts in the morning and eastward-shifts in the afternoon, while the magnetic field is rather stable at night [21,22]. This calls for necessity to test whether the dog alignment is not actually influenced primarily by time of the day and most probably by position of the sun on the sky. We can, however, exclude this alternative. First, days when the magnetic field parameters change erratically and unpredictably (i.e., magnetic storms) are quite frequent. These changes have been well studied by others and are described in the literature (cf. [21,22] for reviews). Second, the data collection was not biased to either morning or afternoon (Table 8). Third, periods of sampling under conditions of quiet magnetic field were rather evenly distributed in the course of the day. Fourth, and most importantly, alignment during excreting was apparent under conditions of quiet magnet field, irrespective of the time of day or month. Time of day per se was not a reliable predictor of expression of alignment (Figure 2, Tables 3, 9). Fifth, generally, there are on average 1,450 sunshine hours per year at maximum in the Czech Republic and in Germany, on localities where measurements were done. Even if we would assume that these sunshine hours were evenly distributed over the daylight period and the year (as our observations were), there would only be a probability of 33% that the

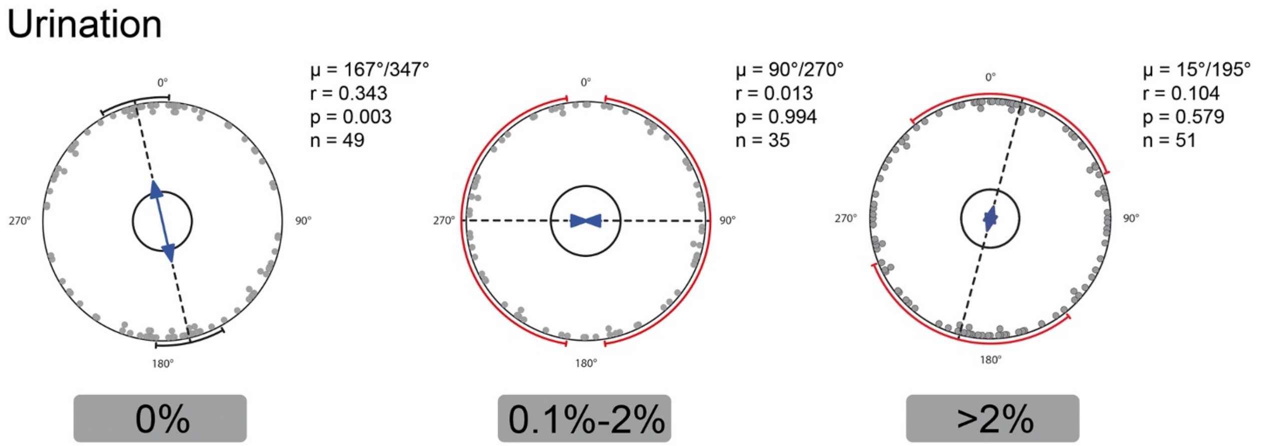


Figure 3 Analysis of dog body alignment during urination. Axial analysis of mean vectors of dogs of both sexes with at least five observations. Observations from three different categories of relative changes of the declination of the Earth's magnetic field are shown from left to right (0%, 0.1-2%, >2%). Each pair of opposite dots indicates the axis of the mean vector of all observations of a single dog. The direction (μ) and length (r) of the (grand) mean vector and the p-value of the Rayleigh uniformity test as well as the sample size are given next to each diagram. μ and r are indicated by the direction and length of the blue arrows, respectively. Small inner circles indicate the 5%-significance level of the Rayleigh test. Circle segments at the outer circle represent the 95%-confidence intervals (red circle segments indicate intervals that could not be calculated with confidence due to large circular standard deviations). A significant N-S axial orientation (i.e., 95%-confidence interval includes the N-S axis) can only be seen under conditions of zero declination change. See Tables for further details on statistics.

Table 8 Proportion of observations made under different conditions of the Earth's magnetic field expressed in rate of changes of declination during the sampling period

Declination changes (%)	Proportion of observations (%)
0	18
0.1-1.0	6
1.1-2.0	19
2.1-3.0	17
3.1-4.0	16
4.1-5.0	12
5.1-6	3
6.1-8.0	6
>8.1	3

observation was made when the sun was visible. Hence, with high probability (67%) most walks during the daylight period were made when it was cloudy.

Last but not least, the argument that the dogs might orient with regard to sun position so that they turn with their back to the sun in order to avoid dazzling by sunshine during such a sensitive and vulnerable act as excretion can be questioned. This argument is not plausible for urine marking, which is a brief act. We doubt that a dog that cares of not being attacked would always make sure to be turned away from the sun. The dog will likely look in that direction from where danger can most probably be expected - and this is for sure not always the direction away from the sun. In contrast to a human, the dog is relying also on its nose and its ears (in some breeds even more than on its eyes) when monitoring its surroundings - so we may expect that the dog heads with its nose and pinnae against the wind or in the direction of interest. Directing the pinnae and the nose may take priority over eyes. One can also often observe that dogs (especially during defecation) align in a certain direction, which is actually a different one from the direction of interest and they turn their head then in that other direction. Also we have to take into account that dogs are smaller than humans, they look at a different angle over the horizon and even in situations when we are dazzled, they might be not. Quite important: note also that the preference is axial - there are many cases when the dog actually looks southwards. There is no evidence for shift of the alignment axis during the day.

Table 9 Proportion of measurements of alignment sampled during 2 hrs-periods (and during the night) and proportion of measurements (from the total) sampled in respective periods under conditions of quiet magnetic field (i.e., with no changes in declination)

Period (time)	Proportion of all observations (%)	Proportion of observations under quiet MF (%)
05:01–07:00	2.2	1.6
07:01–09:00	9.9	12.2
09:01–11:00	26	18.5
11:01–13:00	16.8	6.3
13:01–15:00	11.5	12.8
15:01–17:00	13.6	20.8
17:01–19:00	10.3	5.8
19:01–21:00	7.9	18
21:01–23:00	1.3	2.8
23:01–05:00	0.5	1.2

It is still enigmatic why the dogs do align at all, whether they do it "consciously" (i.e., whether the magnetic field is sensorial perceived (the dogs "see", "hear" or "smell" the compass direction or perceive it as a haptic stimulus) or whether its reception is controlled on the vegetative level (they "feel better/more comfortable or worse/less comfortable" in a certain direction). Our analysis of the raw data (not shown here) indicates that dogs not only *prefer* N-S direction, but at the same time they also *avoid* E-W direction. The fact that larger and faster changes in magnetic conditions result in random distribution of body directions, i.e., a lowering of the preferences and ceasing of the avoidances, can be explained either through disturbing or conscious "shutdown" of the magnetoreception mechanism. From the two putative mechanisms that are discussed in birds and other vertebrates (radical-pairs and single-domain or superparamagnetic particles [30,31]) both might account for the observed alignment of the dogs and their sensitivity to declination changes.

An answer may lie in the biological meaning of the behavior: if dogs would use a visual (radical-pair based) magnetic map to aid general orientation in space as has been proposed for rodents [32], they might have the need to center/calibrate the map now and then with regard to landmarks or a magnetic reference. Aligning the map and the view towards North (or South) facilitates reading the map. Furthermore, calibration only makes sense when the reference is stable and reliable. We might think of this the same way as a human is stopping during a hike to read a map. When the map is blurred or the reference (perceived magnetic direction) is dispersed or moving due to magnetic disturbances, however, calibration is impossible. In the case of the dogs it thus would totally make sense to not pay attention to magnetic body alignment any more under conditions of a shifting magnetic field.

Conclusions

We demonstrate, for the first time (a) magnetic sensitivity in dogs, (b) a measurable, predictable behavioral reaction

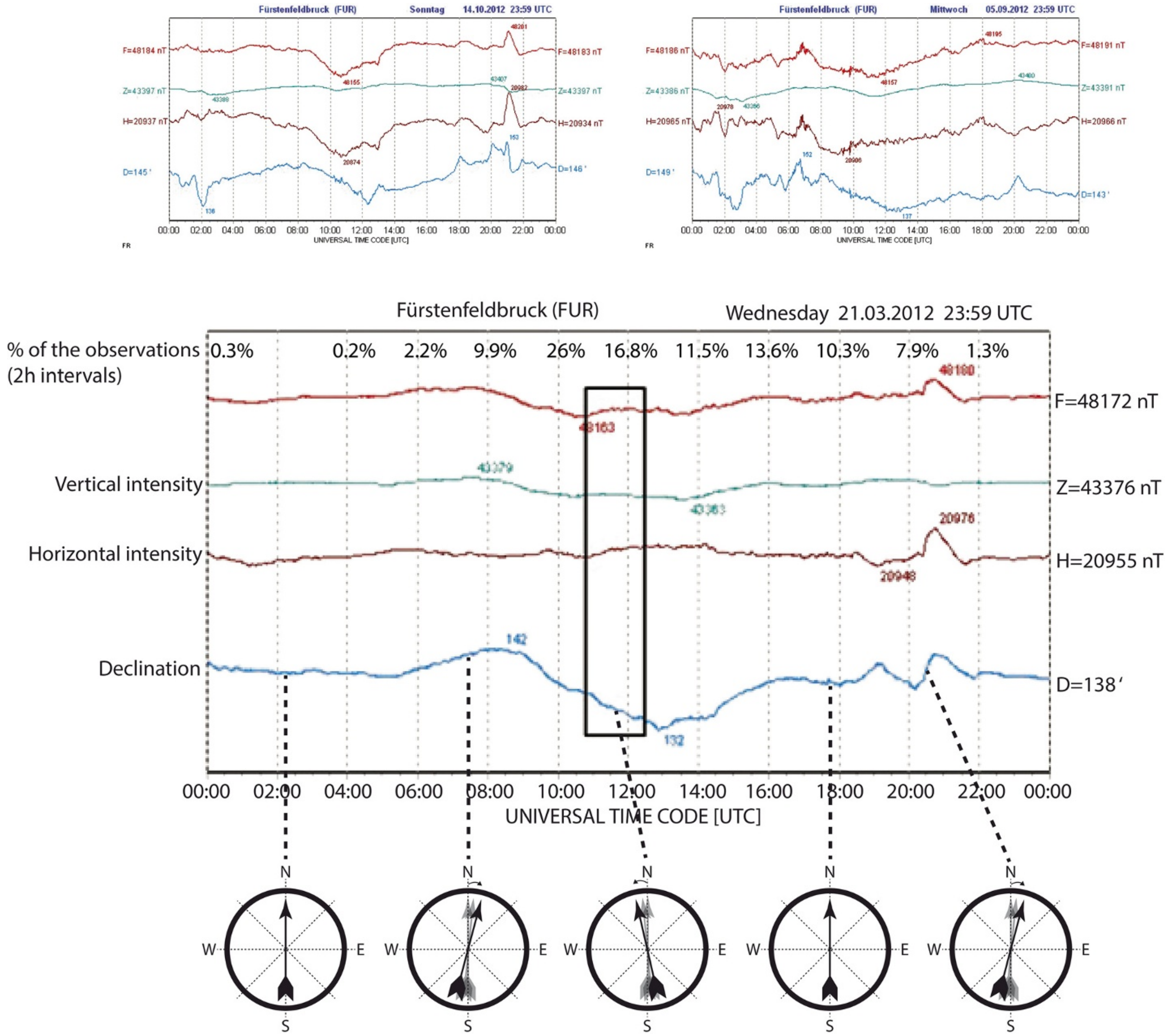


Figure 4 An example of three typical daily magnetograms obtained from the Geomagnetic Observatory Fürstenfeldbruck (Munich, Germany): http://www.geophysik.uni-muenchen.de/observatory/geomagnetism F = total intensity, Z = vertical intensity, H = horizontal intensity, D = declination of the Earth's magnetic field. In the given time period (marked by a rectangle in the lower graph), declination was changing westwards with the following rate: from 142 to 132 arch minutes in 240 time minutes = Difference of 10 arch minutes/240 min. = 4.2 %. The row of compasses illustrates the effect of the declination change in a highly exaggerated manner at different times of the day shown in the example. In reality, the changes in MF direction were much smaller. Note that even though the daily declination changes show some regularity (cf. ref. 22) they are not reliably predictable as illustrated by the frequent highly erratic changes, which are exemplarily shown in the two upper graphs.

upon natural magnetic field (MF) fluctuation in a mammal, and (c) high sensitivity to small changes in polarity, rather than in intensity, of the MF. Our findings open new horizons in magnetoreception research. The newly introduced animal model (dog), paradigm (alignment during excretion) and parameter (relative declination change) open new horizons for biomagnetic research. Particularly the findings that already small fluctuations in Earth's magnetic field elicit a behavioral response and the fact that "normal" magnetic conditions under which dogs express their orientation behavior occur only in about 30% of all cases call for caution. When extrapolated upon other animals and other experiments and observations on animal magnetoreception, this might explain the non-replicability of many findings and high scatter in others. Behavioral scientists need to revise their former experiments and observations and consider the phenomenon in their current and future experiments. The phenomenon challenges biophysicists to formulate testable hypotheses for mechanisms responsible for magnetoreception of inconsistencies

Table 10 List of recorded female dogs and respective numbers of records

	ID dog	Breed	Reporter (Abbrev.)	Age (years)	Weight (kg)	n defecation	n urination
1.	F22	Airedale Terrier	Hanz	4	25	39	14
2.	F06	Beagle	Nova	3	10	0	7
3.	F29	Beagle	Krej	7	10	92	52
4.	F01	Bearded Collie	Niets	11	25	102	30
5.	F23	Border Terrier	Hanz	13	7	15	2
6.	F69	Bouvier des Flandres	Elli	1	34	4	6
7.	F35	Dachshund	Hart	2.5	7	22	110
8.	F37	Dachshund	Faif	4	9	33	36
9.	F48	Dachshund	Bene	11	7	31	21
10.	F54	Dachshund	Bene	6	4	16	8
11.	F55	Dachshund	Bene	3.5	10	0	21
12.	F57	Dachshund	Bene	1	4	18	9
13.	F58	Dachshund	Bene	10	4	17	91
14.	F60	Dachshund	Bene	1	4	11	7
15.	F82	Dachshund	Bene	5.5	6.5	0	0
16.	F83	Dachshund	Bene	13	6	0	0
17.	F90	Dachshund	Dohm	2	4.5	5	42
18.	F40	Dalmatian	Kriv	14	20	64	153
19.	F21	English Springer Spaniel	Hanz	1	20	58	18
20.	F81	English Springer Spaniel	Zdar	7	21	0	0
21.	F77	Entlebucher Mountain Dog	Hron	4	18	0	34
22.	F41	Fox Terrier Smooth	Adam	12	8	37	75
23.	F42	Fox Terrier Smooth	Adam	2	6.5	33	39
24.	F43	Fox Terrier Smooth	Adam	6	8.5	20	65
25.	F44	Fox Terrier Smooth	Adam	2	10	16	16
26.	F36	German Spaniel	Faif	3	13	46	33
27.	F13	German Wirehaired Pointer	Cuko	4	30	5	0
28.	F14	German Wirehaired Pointer	Cuko	7	30	3	0
29.	F20	Golden Retriever	Hanz	10	30	29	16
30.	F39	Irish Terrier	Tres	1.5	15	15	16
31.	F24	Jack Russell Terrier	Jura	3	7	0	32
32.	F75	Mix	Hron	12	20	4	79
33.	F66	Mix: Lhasa Apso/Jack Russell Terrier	Rick	4	x	22	0
34.	F09	Rhodesian Ridgeback	Nova	5	30	0	59
35.	F71	Small Münsterländer	Pali	10	24	24	50
36.	F32	Standard Schnauzer	Posp	12	6	34	125
37.	F45	Tibetan Spaniel	Hegl	6	5	14	101
38.	F70	Transylvanian Hound	Zema	0.7	30	0	10
39.	F08	Weimaraner	Nova	6	30	2	71
40.	F10	West Highland White Terrier	Nova	3	7	0	42
41.	F34	West Highland White Terrier	Hart	8	7	56	212
42.	F11	Yorkshire Terrier	Garc	6.5	2	30	0
		records/dogs				*917*	*1702*

of the direction of the MF direction. Finally, it forces biologists and physicians to seriously reconsider effects magnetic storms might pose on organisms.

Methods

Alignment of the body (along the thoracic spine) in direction towards the head (heading) was measured in freely moving dogs (i.e., not on the leash) in “open field” (on meadows, fields, in the wood etc., i.e., unconstrained, and uninfluenced by linear structures, such as walls and fences) away from the road traffic, high voltage power lines, and conspicuous steel constructions during defecation and urination by a hand-held compass (Figure 4). Dog breed, sex, age, body mass, condition, dog-ID were protocolled as well as date, time, locality, and further circumstances of recordings (e.g. within the home range, in unfamiliar surroundings etc.). Thanks to the commitment of altogether 37 dog owners/reporters and the involvement of 70 dogs (28 males, 42 females) belonging to 37 breeds (Tables 10 and 11) we collected data on heading during defecation (n = 1,893 observations; 55 dogs) and urination (n = 5,582; 59 dogs) from December 2011 till July 2013. The samples were collected in the Czech Republic and in Germany.

After sampling and the first analysis (which yielded negative or at least ambiguous results) had been completed, we decided to sort the data according to the geomagnetic conditions predominating during the respective sampling times. Correlative values on Earth’s magnetic field strength and direction for all the particular times of recordings were obtained from the Geomagnetic Observatory Fürstenfeldbruck (Munich, Germany): http://www.geophysik.uni-muenchen.de/observatory/geomagnetism

Data on K and C values expressing the magnitude of disturbances in horizontal intensity of the Earth’s magnetic

Table 11 List of recorded male dogs and respective numbers of records

	ID dog	Breed	Reporter (Abbrev.)	Age (years)	weight (kg)	n defecation	n urination
1.	M27	Beagle	Krej	4	10	95	53
2.	M28	Beagle	Krej	2	10	92	53
3.	M33	Beagle	Posp	3	10	14	39
4.	M04	Bernese Mountain Dog	Leu	5	40	29	0
5.	M76	Border Terrier	Hron	7	8	0	37
6.	M07	Borzoi	Nova	4	40	96	2478
7.	M31	Coton de Tulear	Acke	4	4	11	106
8.	M05	Dachsbracke	Cerv	7	15	54	127
9.	M26	Dachshund	Komi	5	7	46	92
10.	M52	Dachshund	Bene	7	5	0	23
11.	M53	Dachshund	Bene	8	4	10	43
12.	M59	Dachshund	Bene	1	4	20	19
13.	M61	Dachshund	Bene	12	6	2	50
14.	M62	Dachshund	Bene	1	6	15	16
15.	M65	Dachshund	Faif	3	7	10	7
16.	M74	German Spitz	Hron	3.5	5	0	36
17.	M72	Hanoverian Hound	Krau	5.5	45	15	0
18.	M03	Irish Red Setter	Gros	3	30	47	0
19.	M80	Mix: German Shepherd x Schnauzer	Spor	10	35	71	85
20.	M63	Mix: Husky-Australian Shepherd	Rick	5	25	46	0
21.	M16	Norfolk Terrier	Kust	3	9	48	245
22.	M73	Norwich Terrier	Hron	3	8	0	36
23.	M46	Old English Sheepdog	Baum	4	45	38	122
24.	M19	Pug	Plac	3	9	66	60
25.	M25	Rhodesian Ridgeback	Jura	3	30	0	34
26.	M02	Schapendoes	Kour	1.5	25	86	84
27.	M30	Styrian Coarse-haired Hound	Kubi	7	15	45	19
28.	M38	Transylvanian Hound	Klem	0.5	30	20	16
		records/dogs				*976*	*3880*

Figure 5 Body orientation in dogs during defecation or urination was measured as a compass direction of the thoracic spine (between scapulae) towards the head. (We included the photo just to illustrate the measurement. Owing to the photographer's effort to shoot the photo with the sun from behind and to demonstrate the way of measurement, the dog on the photo looks away from the sun.) Photo Credits go to Jenny Ricken.

field were obtained from: ftp://ftp.ngdc.noaa.gov/stp/geomagnetic_data/indices/kp_ap/.

Relative declination and intensity changes during the respective dog walks were assorted into the categories according to the relative changes (in percent) calculated from graphs by dividing the difference between the initial and end (minimum/maximum) values by the duration (in minutes) of the respective period of changes (Figure 5).

Circular statistics were carried out with Oriana 4.02 (Kovach Computing). Both pooled individual data and means of particular dogs or walks were considered and analyzed. We performed angular and axial analysis on the measurements of each dog. Second order analysis was performed on the data which yielded the higher significance in the first order analysis (angular or axial). Only dogs with at least five measurements were analyzed. Statistically significant deviations from random distributions were investigated using the Rayleigh test of circular statistics. Differences between distributions were tested for significance with the Mardia-Watson-Wheeler test. Level of significance was set at 5%. Since about 44% data on urination under control conditions originated from one dog (M07, male borzoi) we also performed analyses for this particular dog separately.

Ethics statement

The study did not involve any disturbance of the animals under observation.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

Bur, Har, Nov conceived the study with significant input from Beg and Mal; All authors sampled data and/or coordinated sampling by assistants; Beg, Bur, Har, Mal, Nov carried out statistical analyses; Beg, Bur, Mal wrote the paper with input from Har and Nov; Bur discovered dependency of alignment upon Earth's magnetic conditions; All authors discussed the findings; Beg, Bur, Har, Mal, Nov interpreted the observations. All authors read and approved the final manuscript.

Acknowledgements

The study was supported by the Grant Agency of the Czech Republic (project. nr. 506/11/2121). We thank P. Němec for valuable comments on the manuscript. Usable (i.e., fully protocolled) data were provided by the co-authors and our students, colleagues and friends: Ackermannová, Baum, Cukor, Dohmen, Faifr, Garcia-Montero, Grosse, Heglas, Hronková, Juráčková, Klementová, Komín, Kouřimský, Kraus, Krejzková, Kubíček, Leu, Nietsche, Palivcová, Pospíchalová, Ricken, Sporka, Tresky, Zeman, Ždárská.

Received: 25 November 2013 Accepted: 23 December 2013
Published: 27 December 2013

References

1. Begall S, Červený J, Neef J, Vojtěch O, Burda H: **Magnetic alignment in grazing and resting cattle and deer.** *Proc Natl Acad Sci USA* 2008, **105:**13451–13455.

2. Burda H, Begall S, Červený J, Neef J, Němec P: **Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants.** *Proc Natl Acad Sci USA* 2009, **106:**5708–5713.
3. Begall S, Burda H, Červený J, Gerter O, Neef-Weisse J, Němec P: **Further support for the alignment of cattle along magnetic field lines.** *Reply to Hert et al. J Comp Physiol A* 2011, **197:**1127–1133.
4. Slabý P, Tomanová K, Vácha M: **Cattle on pastures do align along the North–South axis, but the alignment depends on herd density.** *J Comp Physiol A* 2013. DOI 10.1007/s00359-013-0827-5.
5. Červený J, Begall S, Koubek P, Nováková P, Burda H: **Directional preference may enhance hunting accuracy in foraging foxes.** *Biol Lett* 2011, **7:**355–357.
6. Begall S, Malkemper EP, Červený J, Němec P, Burda H: **Magnetic alignment in mammals and other animals.** *Mammal Biol* 2013, **78:**10–20.
7. Hart V, Kušta T, Němec P, Bláhová V, Ježek M, Nováková P, Begall S, Červený J, Hanzal V, Malkemper EP, Štípek K, Vole C, Burda H: **Magnetic alignment in carps: evidence from the Czech Christmas fish market.** *PLoS One* 2012, **7:**e51100.
8. Hart V, Malkemper EP, Kušta T, Begall S, Nováková P, Hanzal V, Pleskač L, Ježek M, Policht R, Husinec V, Červený J, Burda H: **Directional compass preference for landing in water birds.** *Frontiers Zool* 2013, **10:**38.
9. Vanderstraeten J, Burda H: **Does magnetoreception mediate biological effects of power-frequency magnetic fields?** *Sci. Total Environm (STOTEN)* 2012, **417–418:**299–304.
10. Harry W: **The homing of a dog.** *Science* 1922, **56:**339.
11. Phillips R, Mech L: **Homing behavior of a red fox.** *J Mammal* 1970, **51:**621.
12. Henshaw RE, Stephenson RO: **Homing in the gray wolf (*Canis lupus*).** *J Mammal* 1974, **55:**234–237.
13. Danner DA, Fisher AR: **Evidence of homing by a coyote (*Canis latrans*).** *J Mammal* 1977, **58:**244–245.
14. Kusak J, Skrbinšek AM, Huber D: **Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia.** *Europ J Wildlife Res* 2005, **51:**254–262.
15. Bensky MK, Gosling SD, Sinn DL: **The world from a dog's point of view: a review and synthesis of dog cognition research.** *Adv Study Anim Behav* 2013, **45:**209–406.
16. Bähr A, Wolf E: **Domestic animal models for biomedical research.** *Repr Domest Anim* 2012, **47:**59–71.
17. Burda H, Marhold S, Westenberger T, Wiltschko W, Wiltschko R: **Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae, Rodentia).** *Experientia* 1990, **46:**528–530.
18. Agnetta B, Hare B, Tomasello M: **Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use.** *Anim Cogn* 2000, **3:**107–112.
19. Miklósi Á, Polgárdi R, Topál J, Csányi V: **Use of experimenter-given cues in dogs.** *Anim Cogn* 1998, **1:**113–121.
20. Virányi Z, Topál J, Gácsi M, Miklósi Á, Csányi V: **Dogs respond appropriately to cues of humans' attentional focus.** *Behav Proc* 2004, **66:**161–172.
21. Courtillot V, Le Mouel JL: **Time variations of the Earth's magnetic field: from daily to secular.** *Ann Rev Earth Planet Sci* 1988, **16:**389–476.
22. Liboff AR: **Why are Living Things Sensitive to Weak Magnetic Fields?** *Electromagn Biol Med* 2013:1–5. doi:10.3109/15368378.2013.809579.
23. Southern WE: **Influence of disturbances in the earth's magnetic field on Ring-billed Gull orientation.** *Condor* 1972, **74:**102–105.
24. Keeton WT, Larkin TS, Windsor DM: **Normal fluctuations in the earth's magnetic field influence pigeon orientation.** *J Comp Physiol* 1974, **95:**95–103.
25. Moore FR: **Geomagnetic disturbance and the orientation of nocturnally migrating birds.** *Science* 1977, **196:**682–684.
26. Martin H, Lindauer M: **Der Einfluss des Erdmagnetfeldes auf die Schwereorientierung der Honigbiene (*Apis mellifera*).** *J Comp Physiol* 1977, **122:**145–187.
27. Vanselow KH, Ricklefs K: **Are solar activity and sperm whale *Physeter macrocephalus* strandings around the North Sea related?** *J Sea Res* 2005, **53:**319–327.
28. Dimitrova S, Stoilova I, Cholakov I: **Influence of local geomagnetic storms on arterial blood pressure.** *Bioelectromagnetics* 2004, **25:**408–414.
29. Berk M, Dodd S, Henry M: **Do ambient electromagnetic fields affect behaviour? A demonstration of the relationship between geomagnetic storm activity and suicide.** *Bioelectromagnetics* 2006, **27:**151–155.
30. Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W: **Resonance effects indicate a radical-pair mechanism for avian magnetic compass.** *Nature* 2004, **429:**177–180.
31. Winklhofer M, Kirschvink JL: **A quantitative assessment of torque-transducer models for magnetoreception.** *J Roy Soc Interface* 2010, **7:**273–289.
32. Phillips JB, Muheim R, Jorge PE: **A behavioral perspective on the biophysics of the light-dependent magnetic compass: a link between directional and spatial perception?** *J exp Biol* 2010, **213:**3247–3255.

doi:10.1186/1742-9994-10-80
Cite this article as: Hart *et al.*: Dogs are sensitive to small variations of the Earth's magnetic field. *Frontiers in Zoology* 2013 **10**:80.

PLOS | ONE

RESEARCH ARTICLE

Directional preference in dogs: Laterality and "pull of the north"

Jana Adámková[1], Jan Svoboda[1], Kateřina Benediktová[1], Sabine Martini[2], Petra Nováková[1], David Tůma[1], Michaela Kučerová[1], Michaela Divišová[1], Sabine Begall[2], Vlastimil Hart[1], Hynek Burda[1,2]*

1 Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 129, Praha 6, Czech Republic, **2** Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, Essen, Germany

* hynek.burda@uni-due.de

Citation: Adámková J, Svoboda J, Benediktová K, Martini S, Nováková P, Tůma D, et al. (2017) Directional preference in dogs: Laterality and "pull of the north" PLoS ONE 12(9): e0185243. https://doi.org/10.1371/journal.pone.0185243

Editor: Lesley Joy Rogers, University of New England, Australia, AUSTRALIA

Received: February 20, 2017

Accepted: September 9, 2017

Published: September 25, 2017

Data Availability Statement: The information supporting the conclusions of this article is included within the article. The table with raw data entering the analyses are included in the excel file attached as supporting material (S1 Table). Further information will be provided from the corresponding author upon reasonable request.

Funding: This study was supported by the Grant Agency of the Czech Republic (Project No. 15-21840S); the Grant Agency of the Czech University of Life Sciences in Prague, CIGA (Project No. 20174319), and the Internal Grant Agency of the

Abstract

Laterality is a well described phenomenon in domestic dogs. It was shown that dogs, under calm Earth's magnetic field conditions, when marking their home ranges, tend to head about north- or southwards and display thus magnetic alignment. The question arises whether magnetic alignment might be affected or even compromised by laterality and vice versa. We tested the preference of dogs to choose between two dishes with snacks that were placed left and right, in different compass directions (north and east, east and south, south and west or west and north) in front of them. Some dogs were right-lateral, some left-lateral but most of them were ambilateral. There was a preference for the dish placed north compared to the one placed east of the dog ("pull of the north"). This effect was highly significant in small and medium-sized breeds but not in larger breeds, highly significant in females, in older dogs, in lateralized dogs but less significant or not significant in males, younger dogs, or ambilateral dogs. Laterality and "pull of the north" are phenomena which should be considered in diverse tasks and behavioral tests with which dogs or other animals might be confronted. The interaction and possible conflict between lateralization and "pull of the north" might be also considered as a reason for shifted magnetic alignment observed in different animal species in different contexts.

Introduction

Laterality, i.e. the predictable, non-random preference for using one side of the body (limbs, brain hemisphere, sensory organs) spontaneously or if forced or restricted to choose between two sides has been intensively studied and is well described in humans but it seems to be also a widespread phenomenon among animals. Laterality may be inborn, imprinted or entrained and has to be taken into account in maze and behavioral two-choice animal experiments [1–5]. The laterality effect is often tested (and excluded) by counting the animals' choice for either side of a T- or Y-maze under control conditions (e.g. without a stimulus or reward) and/or under conditions where the stimulus or reward is randomly alternating between both arms of the maze. While such a behavioral test for laterality (and the exclusion of its effect) is a

Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, IGA (Project No. B07/16). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

standard in two-choice-experiments of this kind, potential preference for a certain (magnetic) compass direction remains usually unconsidered, and this in spite of the fact that magnetic compass preference (displayed in the so-called magnetic alignment) has been documented in a wide array of animal species in diverse behavioral contexts, reviewed in [6–10]. On the other hand, however, laterality effects should be considered also in studies dealing with compass orientation and navigation [9].

Recently, we have shown that dogs, under calm Earth's magnetic field conditions, when marking their home ranges tend to head about north- or south-wards and display thus magnetic alignment [10]. In that particular study, a test for laterality was not relevant and not necessary to exclude the existence and significance of magnetic alignment. Nevertheless, we cannot exclude that laterality played a role under some circumstances and could have influenced the angularity of the response—e.g. does a "left-handed" dog turn southwards if it comes from east but northwards if it comes from the west? Laterality in dogs was examined behaviorally in more than 20 studies e.g. [11–23]. The most commonly used motor test was the so-called "Kong test", in which the preference for a paw holding a Kong (a toy stuffed with food, KONG Company) is recorded. This laterality test is most probably not influenced by magnetoreception, cannot be masked by it but, at the same time, cannot be used to address the question whether laterality affects directional preference in the context of long-distance locomotor spatial orientation. However, there are also some other tests of lateralization—e.g. preference to approach food items placed either right or left of the dog [12] and studies of performance requiring movement in a prescribed direction [23] which can theoretically be affected or even be compromised by magnetic alignment.

Materials and methods

No permits were required for the described study, which complied with all relevant regulations. All the dog owners were informed about the study, consented with the set-up and use of their dog(s) and were present at trials.

Altogether 25 dogs (12 M, 13 F) of 14 breeds, aged on average 5.3 (SD 3.3, 1–12) years were tested in the Czech Republic (12 dogs) and in Germany (13 dogs) (Table 1, S1 Table). The 12 dogs in the Czech Republic were tested at altogether 23 localities (distinct cities and country districts, each dog in 36 test series at each locality), the dogs in Germany were tested at altogether eight localities, each dog in 20 test series at each locality. At each locality, the dogs were tested at at least two different sites. Test series were performed at different places at each site, at different days over several months, at different times of the day, so that tests with each dog evenly covered all daytimes. In all the cases, study sites were open fields, away from communications, buildings, high voltage power lines and conspicuous landmarks. Altogether 1,088 test series were performed.

Each test series involved 4 trials where the dog should make a choice between two identical dishes placed in front of it, at a distance of 2–6 m, according to the size of the dog, so that it could not look into the dishes from its starting point. The dishes were placed in an angle plus and minus 45° from the starting point, so that one dish was e.g. eastwards of the dog and the second one was placed southwards. Each test series involved four trials (test combinations): north versus east, east versus south, south versus west, and west versus north. The sequence of the tests was changed randomly. Both dishes contained identical dog snack. The dog could not see the preparation of the test, i.e. the placement of the dishes. The dog was brought to the starting point and waited to get permission to go to the dish (of its choice). Two experimenters were involved in this test. The first experimenter was setting up the test, while the dog owner (who was uninformed about the actual directions of the dishes and gave the voice command)

Table 1. Survey of the tested dogs and their factors.

breed	subject	country	size	sex	age	laterality	n test series	μ (1st locality)	μ (2nd locality)
borzoi	Hen	CZ	L	M	1	left	36 + 36	**225°**	**135°**
labrador retriever	Mon	CZ	L	M	12	ambi	36	**72°**	**x**
wirehaired pointer	Aja	CZ	L	F	4	ambi	36 + 36	**220°**	**305°**
beagle	Azi	CZ	M	M	4	right	36 + 36	**354°**	**45°**
cocker spaniel	Bar	CZ	M	F	2	left	36 + 36	**353°**	**18°**
cocker spaniel	Nel	CZ	M	F	8	ambi	36 + 36	**281°**	**278°**
foxterrier	Fre	CZ	M	F	1	left	36 + 36	**54°**	**333°**
foxterrier	Gof	CZ	M	F	1	left	36 + 36	**45°**	**62°**
foxterrier	Bes	CZ	M	F	6	right	36 + 36	**18°**	**349°**
dachshund	Ter	CZ	S	F	4	ambi	36 + 36	**270°**	**257°**
dachshund	Can	CZ	S	F	6	ambi	36 + 36	**323°**	**315°**
dachshund	Ven	CZ	S	F	9	right	36 + 36	**349°**	**333°**
border collie x münsterlander	Paa	GER	L	F	9	ambi	20	**146°**	**x**
bullterrier	Gis	GER	L	F	10	ambi	20	**135°**	**x**
flat-coated retriever	Fje	GER	L	M	2	ambi	20	**270°**	**x**
labrador retriever	Lor	GER	L	M	3	ambi	20	**180°**	**x**
labrador retriever x rottweiler	Jim	GER	L	M	3	ambi	20	**90°**	**x**
labrador retriever x rottweiler	Sam	GER	L	M	3	ambi	20	**135°**	**x**
labrador retriever	Pal	GER	L	M	5	ambi	20	**101°**	**x**
labrador retriever	Lot	GER	L	F	7	left	20	**54°**	**x**
jack russel terrier	Jac	GER	M	M	12	left	20	**31°**	**x**
chihuahua	Att	GER	S	M	3	right	20	**72°**	**x**
chihuahua	Ger	GER	S	M	4	right	20	**0°**	**x**
chihuahua	Hen	GER	S	M	5	ambi	20	**0°**	**x**
yorkshire terrier	Bri	GER	S	F	10	ambi	20	**31°**	**x**

Size: L = large, M = medium, S = small, Sex: F = female, M = male, Age is given in years, laterality: ambi-, left- or right-lateral, n = number of test series (in each test series 4 trials were performed), μ = mean vector in ° at the first locality and, if tested, at the second (distant) locality; at each of those distant localities 36 test series were performed., x = the dog was not tested at the second locality. The column "subject" refers to the first three letters of the respective dog's name. See the supporting information (S1 Table) for further detail.

https://doi.org/10.1371/journal.pone.0185243.t001

was either standing behind the dog, and had no eye contact with it, in the Czech Republic (Fig 1), or had dark sun glasses and stood on the opposing side of the dishes, facing the dog, in Germany.

All the dog owners were informed about the study, consented with the set-up and use of their dog(s) and were present at trials. The owners in the Czech Republic were coauthors of this study, their colleagues, and friends; the dog owners in Germany were approached via dog-training clubs.

Only the direction of the first choice was recorded. The dog was allowed to visit and take the snack also from the other dish. Apart from the chosen first direction in a given combination, the sequence of tested combinations within the trial, the dog's and owner's identities, locality, place, date, daytime, weather (sunny, cloudy, overcast, rainy), wind strength and direction were recorded. (However, no tests were performed on windy days.)

From the recorded choices, preferences for either left or right turn were calculated for all test combinations (N-E, E-S, S-W, W-N) within each trial, and the sum for all trials for each dog. Index of laterality was then calculated for each dog according to the formula (R–L) / (R + L) x

Fig 1. Photo illustrating the study setup.

https://doi.org/10.1371/journal.pone.0185243.g001

100, where R and L is the preference for using the right and left side, respectively [11]. Significance of lateralization was tested by chi-square test.

Independently, mean directional compass preference based on the frequency of first choices at a given locality in all pooled trials (at different day times, different days, different places within the locality) was calculated for each dog using circular statistics with Oriana 4.02 (Kovach Computing). Grand mean vectors were then calculated on the base of those mean dog/locality vectors for all the dogs, and subgroups with respect to laterality, breed, body size, sex, and age.

Results

Laterality

In dish-choice trials, altogether six dogs were identified as left-sided, five dogs as right-sided and 14 dogs were ambilateral based on the choices the respective dogs made in approaching one of the dishes placed left and right in front of them. There was no clear effect of breed and sex on laterality.

Compass preference

Testing the circular distribution of mean vectors of all dogs, as well as of dogs of a particular lateralization, body size, sex, and age revealed that there was an apparent preference for the north ("pull of the north") which was highly significant in small and medium-sized breeds but not in larger breeds, highly significant in females, in older dogs, in lateralized dogs but less significant or not significant in males, younger dogs, or ambilateral dogs (Table 2, Figs 2–5).

Table 2. Circular statistics for frequencies of choices of a dish placed in north or east or south or west in front of a dog in dual choice experiments where the dog chose between north or east, east or south, south or west, west or north.

Variable	all dogs	males	females	small- and medium-sized	large-sized	ambi-lateral	left-lateral	right-lateral	< 3 years	> 4 years
Number of observations	36	14	22	23	13	18	10	8	13	23
Mean vector (μ)	11˚	68˚	345˚	356˚	142˚	274˚	37˚	9˚	65˚	350˚
Length of mean vector (r)	0.328	0.362	0.457	0.686	0.405	0.128	0.578	0.862	0.322	0.432
Circular standard deviation	86˚	82˚	72˚	50˚	77˚	116˚	60˚	31˚	86˚	74˚
Rayleigh test (Z)	3.868	1.832	4.593	10.821	2.135	0.294	3.338	5.939	1.351	4.295
Rayleigh test (p)	0.017	0.161	0.009	4.8×10^{-6}	0.118	0.750	0.031	6.79×10^{-4}	0.264	0.012

Each compass direction was offered with the same frequency. The number of observations refers to the number of dogs and localities. Mean vectors in this table represent thus grand mean vectors.

https://doi.org/10.1371/journal.pone.0185243.t002

Testing the frequencies of compass preferences combining always two neighboring test combinations centered at one compass direction (e.g. triad W-N-E combined results of tests W-N and N-E, and frequency of choices 25–50–25% would be expected if there were no preferences and no laterality) revealed statistically significant difference from random distribution in tests involving North and East (W-N-E, N-E-S, chi-square p = 0.0001 and 0.0022, respectively) but not in both other combinations (E-S-W, p = 0.5011; S-W-N, p = 0.1446).

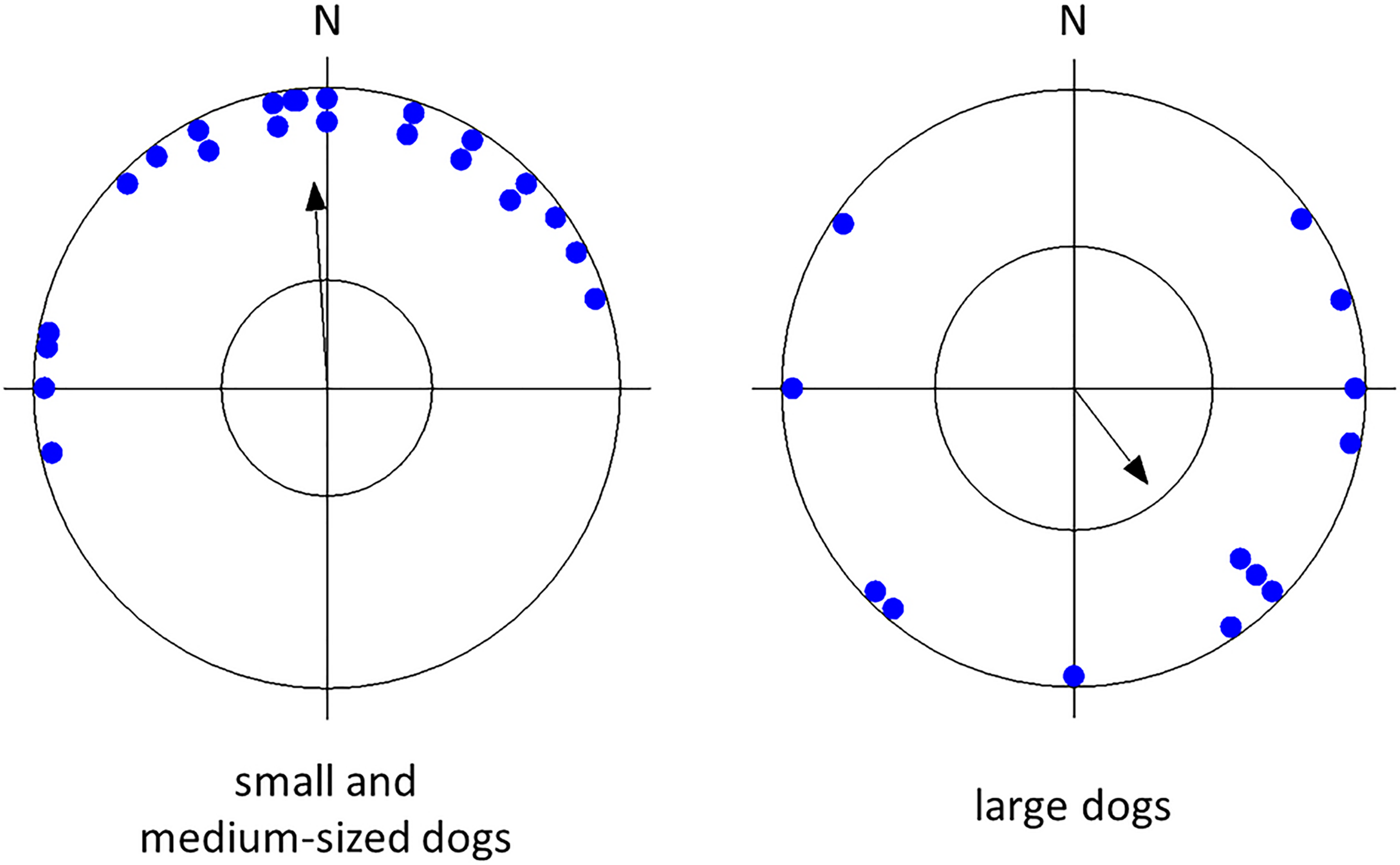


Fig 2. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of small, medium-sized, and large breeds. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

https://doi.org/10.1371/journal.pone.0185243.g002

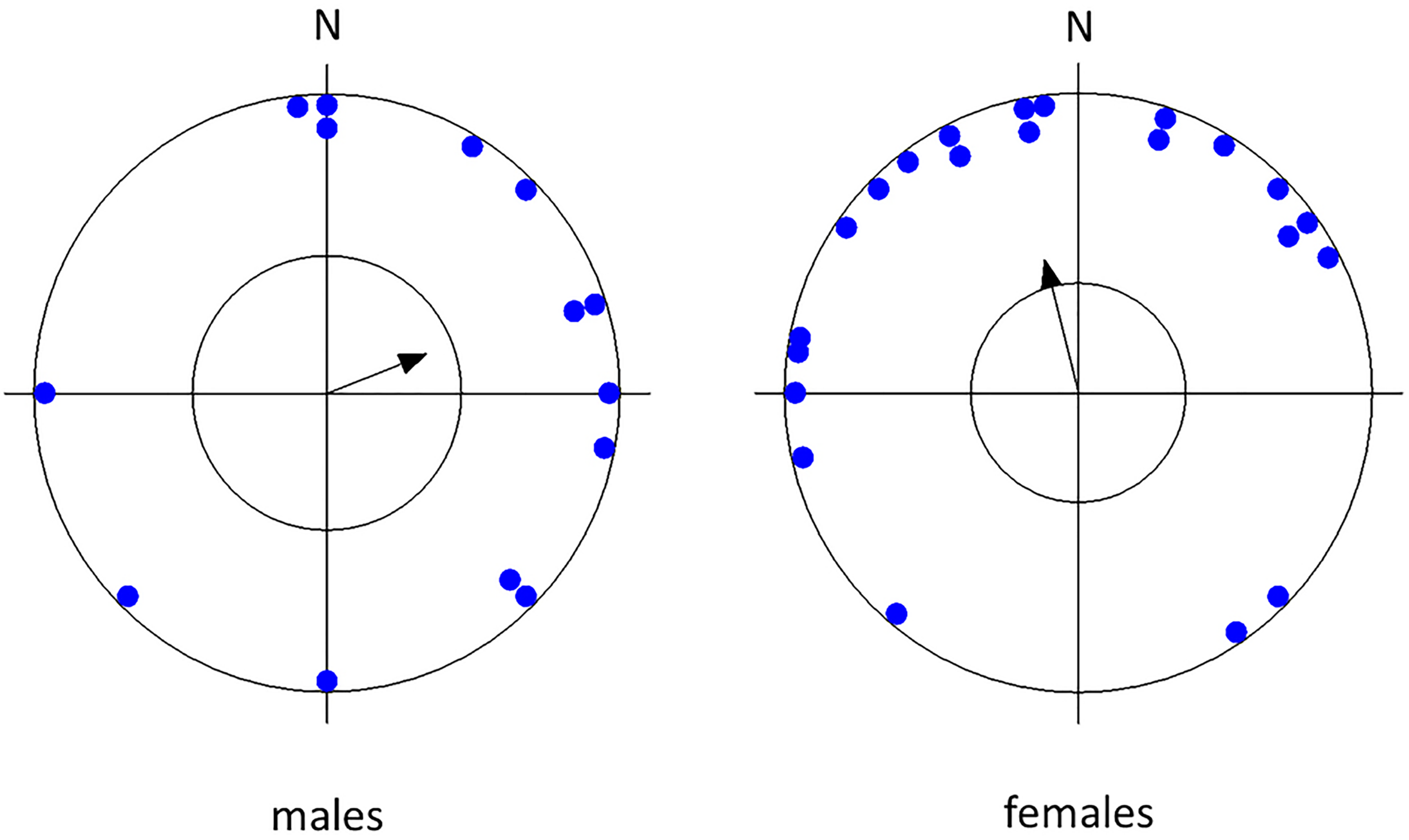


Fig 3. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over males and females separately. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

https://doi.org/10.1371/journal.pone.0185243.g003

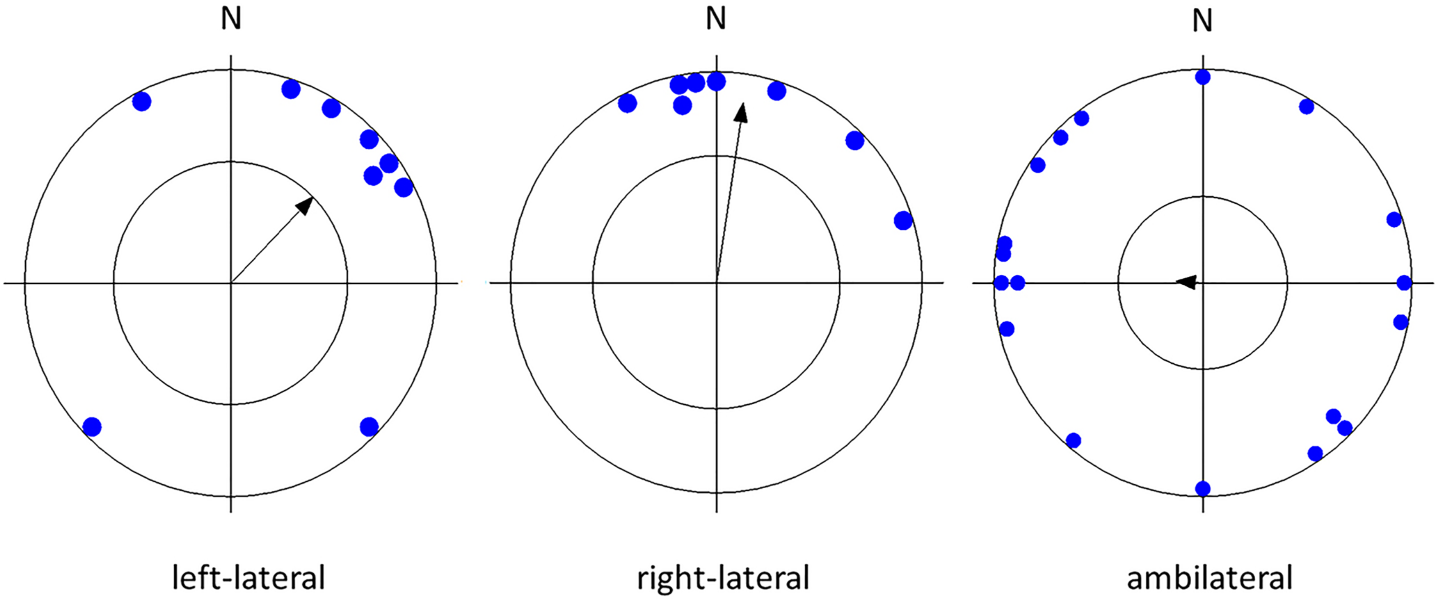


Fig 4. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of different lateralization types. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

https://doi.org/10.1371/journal.pone.0185243.g004

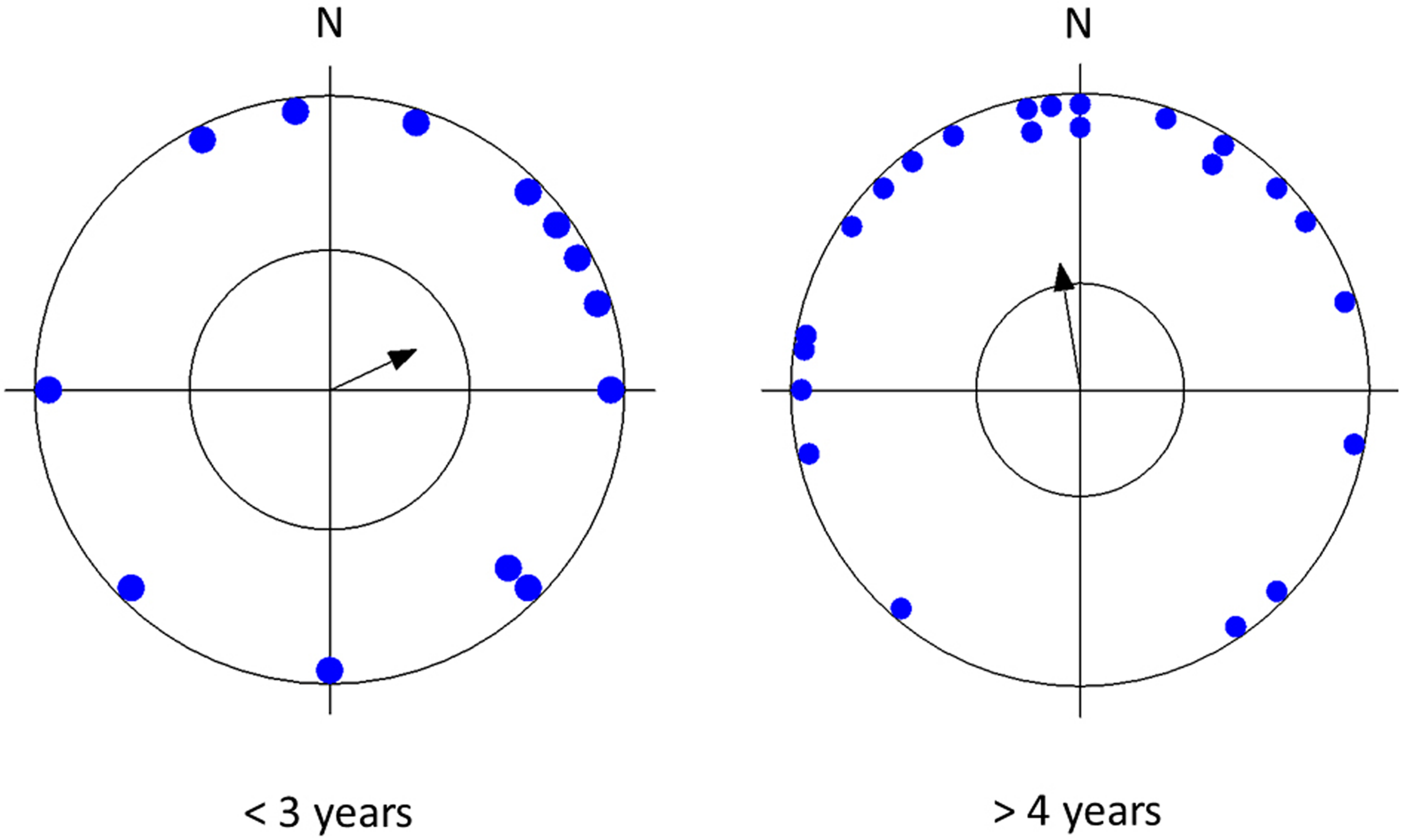


Fig 5. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs of different age categories. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

https://doi.org/10.1371/journal.pone.0185243.g005

Discussion

We tested the preference of dogs to choose between two dishes with snacks that were placed left and right, in different compass directions (north and east, east and south, south and west or west and north) in front of them. Some dogs were right-lateral, some left-lateral but most of them were ambilateral. There was a preference for the dish placed north compared to the one placed east of the dog ("pull of the north"). This effect was significant in small and medium-sized breeds but not in larger breeds, significant in females, in older dogs, in lateralized dogs but not significant in males, younger dogs, or ambilateral dogs. None of the extrinsic factors which might have influenced the directional choice, but the Earth's magnetic field, was stable in space and time. All other factors (possible hints from the owners, landmarks, sun position, weather, homing direction) were stochastically changing and could not have systematically influenced the observed "pull of the north".

His master's voice?

The test was performed by several different dog owners. We do not see any possibility how the dogs might have been systematically (i.e. in one common direction and only in a compass combination involving north and east) influenced in their decision by their owners. The dogs had no eye contact with their owners. In fact, every choice was rewarded, and the dogs were allowed to take also the reward from the second dish, so that effective learning, e.g. on some landmark in the surroundings, was not possible. Besides that, the next trial occurred at another place, or site or even at another locality, at another day, another day-time, and the sequence of tested compass direction pairs changed.

Effect of sun?

"Pull of the north" could be theoretically explained as avoidance of blinding sun. This explanation is rather anthropomorphic and does not consider the fact that dogs are lower than human and that the dishes were placed on the ground. Moreover, this argument would be valid only in the choice test "north x east" on sunny mornings in spring and autumn when sun is low. Analogously, however, preference for the north would be expected also in the choice test "north x west" in the evening on sunny days. Furthermore, dogs would be expected to avoid south during midday on sunny days. Larger (higher) dogs are expected to be more prone to blinding than smaller (lower) dogs. Apart from the fact that actually there was never a choice test "north x south" or "east x west" where sun avoidance could be actually realized, none of these possible explanations for the results was supported. Circular analysis of the tests performed in "lateral" dogs in the morning (grand mean vector $\mu = 42^\circ$, $r = 0.510$, SD = 66, Rayleigh test $p = 0.041$, $N = 12$) and in the afternoon (grand mean vector $\mu = 22^\circ$, $r = 0.650$, SD = 53, Rayleigh test $p = 0.0006$, $N = 16$) revealed no differences (99% confidence interval for μ a.m. 343°-100°, for p.m. 347°-57°). Also "ambilateral" dogs displayed no differences between morning and afternoon choices (morning: $\mu = 286^\circ$, $p = 0161$, $N = 12$; afternoon = 269°, $p = 0.488$, $N = 15$). There were no significant differences between whatever combination of directions (N x W, N x E, S x E, S x W) tested in the morning and in the afternoon, respectively.

Note also that in Central Europe, Czech Rep. and Germany, where the experiments were done, the sun hours make on average only about 35% of the light hours—so, if the experiments are randomly and evenly distributed throughout the year and daytimes, the probability of being blinded by the sun (if one lifts the head or the sun is low and one looks into it), is 35%. The probability that one actually has problems to recognize where on the sky the sun stands is 65%. Note also that according to the hitherto knowledge dogs do not perceive polarized light.

Other possible effects?

The Earth's magnetic field parameters in both countries are comparable. The declination in Essen (Germany) is 1.5°, the declination in Prague (Czech Rep.) is 3.5°, and the difference is thus only 2°. The dogs had to decide, however, for one of the two directions which were 90° apart. Most importantly, directions in the field in both countries were measured by means of a compass which shows *always* a direction to the magnetic pole, i.e. not by means of a geographical map which would show direction to the geographic pole.

Although in Germany relatively more larger dogs were represented in the sample than in the Czech Republic, there was no apparent country bias if smaller versus larger, lateral versus ambilateral, etc. dogs in the two countries, were compared. In spite of the large dataset, the subgroups (breeds, age, sex, lateralization) were still rather small and heterogeneous and did not enable us to reliably test which of those facts was most decisive. We have also no idea why larger breeds "failed" in the compass test. It should be noticed that this category was composed mainly of (labrador) retrievers but it would be preliminary to claim that this breed is ambilateral and/or "magnet-blind". The fact that older dogs oriented more towards the north than younger dogs might correlate with their experience and established orientation strategies.

We have purposely performed the experiments outdoors because the magnetic field in buildings might be disturbed and because dogs tested indoors might orient with respect to geometry of rooms. Since it cannot be excluded that dogs might orient with respect to landmarks also outdoors, care was taken when selecting the testing place that its surroundings were free of any landmarks within the radius of at least 30 m, a condition which could not be complied with indoors.

Conclusions and prospects

The here presented two-dish choice test widens the range of tests reviewed in [12, 24] suitable for assessment of lateralization in dogs. At the same time it shows that laterality plays a role not only in intrinsic kinesthetic reactions but also in directional goal-oriented decisions. Moreover there is an apparent "pull of the north", which is particularly strong in the test combination "north—east". Laterality and "pull of the north" are thus phenomena which should be considered in diverse tasks (and behavioral tests) with which dogs or other animals might be confronted. On the other hand, the phenomenon of laterality should be likewise considered in studies of spatial orientation and navigation. The interaction and possible conflict between lateralization and "pull of the north" might be also considered as a reason for shifted magnetic alignment observed in different animal species in different contexts [9]. It might prove to be significant for understanding the putative (and thus far unknown) mechanism of magnetoreception that the field observations and laboratory experiments in diverse animal species consistently show a shift of directional preference from north or south to the east after a treatment with a strong magnetic pulse e.g. [25–26]. Moreover, roe deer were found to prefer to escape northwards but to avoid escaping eastwards [27]. These (and further own unpublished) observations indicate some sensory interaction between perceiving north and east directions.

Supporting information

S1 Table. Information on tested dogs, particulars of trials and their results. Age is given in years, the choice for a dish in the respective combination in compass degrees.
(XLSX)

Acknowledgments

This study was supported by the Grant Agency of the Czech Republic (Project No. 15-21840S); the Grant Agency of the Czech University of Life Sciences in Prague, CIGA (Project No. 20174319), and the Internal Grant Agency of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, IGA (Project No. B07/16).

Author Contributions

Conceptualization: Jana Adámková, Jan Svoboda, Sabine Martini, Petra Nováková, Vlastimil Hart, Hynek Burda.

Data curation: Jana Adámková, Jan Svoboda, Kateřina Benediktová, Sabine Martini, Hynek Burda.

Formal analysis: Jana Adámková, Kateřina Benediktová, Sabine Martini, Hynek Burda.

Funding acquisition: Jana Adámková, Kateřina Benediktová, Petra Nováková, Vlastimil Hart, Hynek Burda.

Investigation: Jana Adámková, Jan Svoboda, Kateřina Benediktová, Sabine Martini, Petra Nováková, David Tůma, Michaela Kučerová, Michaela Divišová, Sabine Begall.

Methodology: Jana Adámková, Kateřina Benediktová, Vlastimil Hart, Hynek Burda.

Project administration: Jana Adámková, Sabine Martini, Hynek Burda.

Supervision: Jana Adámková, Jan Svoboda, Kateřina Benediktová, Sabine Martini.

Writing – original draft: Jana Adámková, Sabine Martini, Petra Nováková, Sabine Begall, Vlastimil Hart, Hynek Burda.

Writing – review & editing: Jana Adámková, Sabine Martini, Sabine Begall, Hynek Burda.

References

1. Rogers LJ. Laterality in animals. Internat J Comp Psychol. 1989; 3:5–25.
2. Rogers LJ. Lateralization in vertebrates: its early evolution, general pattern, and development. Adv Study Behav. 2002; 31:107–161.
3. Rogers LJ, Vallortigara G, Andrew R.J. Divided brains. The Biology and Behaviour of Brain Asymmetries. 2013; Cambridge University Press, New York.
4. Schaafsma SM, Riedstra BJ, Pfannkuche KA, Bouma A, Groothuis TG. Epigenesis of behavioural lateralization in humans and other animals. Phil Trans Roy Soc B. 2009; 364:915–927.
5. Warren JM. Handedness and laterality in humans and other animals. Physiol. 1980; 8:351–359.
6. Begall S, Malkemper EP, Červený J, Němec P, Burda H. Magnetic alignment in mammals and other animals. Mammal Biol. 2013; 78:10–20.
7. Begall S, Malkemper EP, Burda H. Magnetoreception in mammals. Adv Study Behav. 2014; 46:45–88.
8. Wiltschko R, Wiltschko W. Magnetic orientation in animals. 1995; Springer, Berlin.
9. Malkemper EP, Painter MS, Landler L. Shifted magnetic alignment in vertebrates: Evidence for neural lateralization? J Theor Biol. 2016; 399:141–147. https://doi.org/10.1016/j.jtbi.2016.03.040 PMID: 27059891
10. Hart V, Nováková P, Begall S, Malkemper EP, Hanzal V, Ježek M, et al. Dogs are sensitive to small variations of the Earth's magnetic field. Front Zool. 2013; 10:80. https://doi.org/10.1186/1742-9994-10-80 PMID: 24370002
11. Batt L, Batt M, McGreevy P. Two tests for motor laterality in dogs. J Vet Behav. 2007; 2:47–51.
12. Berta C. Lateralized behavior in domesticated dogs. ESSAI. 2010; 8:9.
13. Branson NJ, Rogers LJ. Relationship between paw preference strength and noise phobia in *Canis familiaris*. J Comp Psychol. 2006; 120:176–183. https://doi.org/10.1037/0735-7036.120.3.176 PMID: 16893254
14. Nagasawa M, Kawai E, Mogi K, Kikusui T. Dogs show left facial lateralization upon reunion with their owners. Behav Proc. 2013; 98:112–116.
15. Plueckham TC, Schneider LA, Delfabbro PH. Assessing lateralization in domestic dogs: Performance by *Canis familiaris* on the Kong test. J Vet Behav. 2016; 15:25–30.
16. Schneider LA, Delfabbro PH, Burns NR. Temperament and lateralization in the domestic dog (*Canis familiaris*). J Vet Behav. 2013; 8:124–134.
17. Siniscalchi M, Sasso R, Pepe AM, Vallortigara G, Quaranta A. Dogs turn left to emotional stimuli. Behav Brain Res. 2010; 208:516–521. https://doi.org/10.1016/j.bbr.2009.12.042 PMID: 20060016
18. Siniscalchi M, Quaranta A, Rogers LJ. Hemispheric specialization in dogs for processing different acoustic stimuli. PLoS ONE. 2008; 3:e3349. https://doi.org/10.1371/journal.pone.0003349 PMID: 18843371
19. Siniscalchi M; Pergola G, Quaranta A. Detour behaviour in attack-trained dogs: Left-turners perform better than right-turners. Laterality. 2013; 18:282–293. https://doi.org/10.1080/1357650X.2012.662234 PMID: 22713109
20. Siniscalchi M.; d'Ingeo S.; Fornelli S.; Quaranta A. Relationship between visuospatial attention and paw preference in dogs. Sci Rep 2016, 6
21. Siniscalchi M, d'Ingeo S, Quaranta A. The dog nose "KNOWS" fear: Asymmetric nostril use during sniffing at canine and human emotional stimuli. Behav Brain Res. 2016; 304:34–41. https://doi.org/10.1016/j.bbr.2016.02.011 PMID: 26876141

22. Tomkins LM, Thomson PC, McGreevy PD. First-stepping Test as a measure of motor laterality in dogs (*Canis familiaris*). J Vet Behav. 2010; 5:247–255.

23. Tomkins LM, Williams KA, Thomson PC, McGreevy PD. Lateralization in the domestic dog (*Canis familiaris*): Relationships between structural, motor, and sensory laterality. J Vet Behav. 2012; 7:70–79.

24. Rogers L, Vallortigara G (Eds). Lateralized Brain Functions. Methods in Human and Non-Human Species. 2017; Springer, New York.

25. Wiltschko R, Wiltschko W. Magnetic orientation in animals. 1995; Springer, Heidelberg.

26. Marhold S, Burda H., Kreilos I, Wiltschko W. Magnetic orientation in common mole-rats from Zambia. In: Orientation and Navigation: Birds, Humans and Other Animals. 1997; Paper No 5. Royal Institute of Navigation, Oxford.

27. Obleser P, Hart V, Malkemper EP, Begall S, Holá M, Painter MS, et al. Compass-controlled escape behavior in roe deer. Behav Ecol Sociobiol. 2016; 70:1345–1355.

PLOS ONE

RESEARCH ARTICLE

Turning preference in dogs: North attracts while south repels

Jana Adámková[1], **Kateřina Benediktová**[1], **Jan Svoboda**[1], **Luděk Bartoš**[2,3], **Lucie Vynikalová**[4], **Petra Nováková**[1], **Vlastimil Hart**[1], **Michael S. Painter**[1], **Hynek Burda**[1]*

1 Faculty of Forestry and Wood Sciences, Department of Game Management and Wildlife Biology, Czech University of Life Sciences, Praha, Czech Republic, **2** Department of Ethology, Institute of Animal Science, Praha, Czech Republic, **3** Faculty of Agrobiology, Food and Natural Resources, Department of Ethology and Companion Animal Science, University of Life Sciences, Praha, Czech Republic, **4** Faculty of Agrobiology, Food and Natural Resources, Department of Zoology and Fisheries, Czech University of Life Sciences, Praha, Czech Republic

* burda@fld.czu.cz

Citation: Adámková J, Benediktová K, Svoboda J, Bartoš L, Vynikalová L, Nováková P, et al. (2021) Turning preference in dogs: North attracts while south repels. PLoS ONE 16(1): e0245940. https://doi.org/10.1371/journal.pone.0245940

Editor: Gregg Roman, University of Mississippi, UNITED STATES

Received: October 3, 2020

Accepted: January 8, 2021

Published: January 28, 2021

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0245940

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The grant "EVA4.0", No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE to JA,

Abstract

It was shown earlier that dogs, when selecting between two dishes with snacks placed in front of them, left and right, prefer to turn either clockwise or counterclockwise or randomly in either direction. This preference (or non-preference) is individually consistent in all trials but it is biased in favor of north if they choose between dishes positioned north and east or north and west, a phenomenon denoted as "pull of the north". Here, we replicated these experiments indoors, in magnetic coils, under natural magnetic field and under magnetic field shifted 90˚ clockwise. We demonstrate that "pull of the north" was present also in an environment without any outdoor cues and that the magnetic (and not topographic) north exerted the effect. The detailed analysis shows that the phenomenon involves also "repulsion of the south". The clockwise turning preference in the right-preferring dogs is more pronounced in the S-W combination, while the counterclockwise turning preference in the left-preferring dogs is pronounced in the S-E combination. In this way, south-placed dishes are less frequently chosen than would be expected, while the north-placed dishes are apparently more preferred. Turning preference did not correlate with the motoric paw laterality (Kong test). Given that the choice of a dish is visually guided, we postulate that the turning preference was determined by the dominant eye, so that a dominant right eye resulted in clockwise, and a dominant left eye in counterclockwise turning. Assuming further that magnetoreception in canines is based on the radical-pair mechanism, a "conflict of interests" may be expected, if the dominant eye guides turning away from north, yet the contralateral eye "sees the north", which generally acts attractive, provoking body alignment along the north-south axis.

Introduction

Dogs in two-choice experiments, when selecting between two dishes with snacks placed in front of them, 90˚ apart, left and right, prefer to turn either clockwise ("right-preferring") or

KB, HB, VH, MSP; the Grant Agency of the Czech University of Life Sciences in Prague, CIGA (Project No. 20174319) to JA, HB, KB, VH, PN, JS, LV; the grant of the Ministry of Agriculture of the Czech Republic MZE-RO0718 to LB.

Competing interests: No authors have competing interests.

counterclockwise ("left-preferring") or randomly in either direction ("irresolute"). This turning preference (or non-preference) is individually consistent in all trials but it is biased in favor of north if they choose between dishes positioned north and east or north and west, a phenomenon we denoted as "pull of the north" [1]. This phenomenon was particularly pronounced in older dogs, females, smaller and medium-sized breeds, dogs exhibiting a turning preference, and especially in the north-east choice. We suggested that "pull of the north" represents a further indication of magnetoreception in dogs, the other being non-random directional alignment during marking [2], which was, however, significantly changed when exposed to bar magnets [3], the ability to find a bar magnet [4], or the existence of the so-called "compass run" exhibited during homing [5].

We are, however, aware that for the ultimate evidence of magnetoreception, experiments in defined manipulated magnetic field and/or under conditions of disturbed magnetoreception are necessary. Moreover, the proximate reason for "pull of the north" remains unclear and should be at least hypothesized.

Laterality, i.e. a predictable, non-random preference for using one side of the body (limbs, brain hemisphere, sensory organs) spontaneously or if forced or restricted to choose between two sides, is a known phenomenon in humans and animals. Laterality may be inborn, imprinted, or entrained and has to be taken into account in maze and behavioral two-choice animal experiments [6–10].

Laterality in dogs has been intensively studied with regard to the motoric (efferent) aspect (paw laterality, Kong-test: [11–15]; sensory (afferent) aspect [16–18]; cognitive [19], and emotional aspects [20–22]. Interestingly, and contrary to studies in humans, turning (directional, rotational) preference has remained understudied.

Most people are right-handed, yet tend to instinctively veer to the left upon entering a new space [23]. Interestingly, the counterclockwise action goes also for most athletic tracks, horse and car races, and for baseball players running the bases [24]. There is even evidence that the chariot races at ancient Rome's Circus Maximus ran counterclockwise, too [25,26]. So, in sports, where competitors enter the field of play from the outside of a traced circle, a right-directional choice would lead to a counter-clockwise motion. But when entering the field of action from within the circle—walking out of your apartment to take the dog for a walk, and encountering intersections—right directional choices would tend towards tracing a clockwise path [23]. Interestingly, in the countries, where people drive on the left side of the road, retail shoppers tend to turn counterclockwise—when navigating store aisles, while in the countries, where people drive and keep on sidewalks right, veer clockwise [23]. Tendencies of people to turn either direction are known to architects who use them to design shopping galleries to funnel shoppers in the wished direction [23].

While the preference to turn in a certain direction can be explained by individual inborn laterality (handedness) and experience (facilitation), or–e.g. in the context of our experiment of choice between two dishes, which is a visually guided task, through visual laterality—the "pull of north" is expected to have a magnetoreceptive ground. Examination of this phenomenon has a heuristic potential in getting insight into the very seat and mechanism of magnetoreception, which still remain enigmatic [27].

Sensory laterality (or asymmetry) has been described also in the context of spatial orientation in general and magnetoreception in particular. It has been found that homing pigeons rely more on the right olfactory system in processing the olfactory information needed for the operation of the navigational map [28]. An earlier study [29] has shown that the magnetic compass of a migratory bird, the European robin (*Erithacus rubecula*), was lateralized in favour of the right eye/left brain hemisphere. However, it has been later demonstrated [30] that the described lateralization is not present from the beginning, but develops only as the birds grow older. In another study [31], it was shown that pigeons can perceive and process magnetic compass directions with the right eye and left brain hemisphere as well as the left eye and right brain hemisphere. However, while the right brain hemisphere tended to confuse the learned direction with its opposite (axial response), the left brain hemisphere specifically preferred the correct direction (angular response). The findings thus demonstrated bilateral processing of magnetic information, but also suggested qualitative differences in how the left and the right brain deal with magnetic cues.

Based on the hitherto knowledge and the above arguments,

1. We hypothesize that if "pull of the north" is due to magnetoreception (and indeed no other explanation is apparent), it should be demonstrated also in an artificial magnetic field shifted by magnetic coils, i.e. the artificially shifted magnetic North should exert the same effect as the natural geomagnetic North.
2. We expect that, consistently with results of the previous study [1] "pull of the north" is more pronounced in "lateralized" dogs and more in the North-East (N-E) combination than in the North-West (N-W) choice.

Furthermore, following questions can be raised (and should be tested) to get insight into the nature of the turning preference:

3. Does the directional preference for turning correlate with motoric laterality (such as paw-laterality, i.e. "handedness")?
4. Is pull of the north a) symmetrical (bilateral, i.e. of the same strength in the clockwise as in counterclockwise direction), or b) asymmetrical (unilateral, i.e. stronger in one particular direction)?

Material and methods

Ethics statement

The study did not involve any disturbance or discomfort to the study subjects. The Professional Ethics Commission of the Czech University of Life Sciences in Prague has decided that according to the law and national and international rules, this study has not a character of an animal experiment and does not require a special permit.

Subjects

Altogether, 23 domestic dogs *Canis familiaris* (11 M, 12 F) from six breeds with pedigree and an average age of 4.8 (± 2.8) years (Table 1) were used in this study. The dogs were pets living in households. All the dog owners were present with their dogs at trials.

Experimental equipment

The experiment took place in a magnetic coil at the field research station Truba, Kostelec nad Černými lesy, (N 50˚0.40480', E 14˚50.11145'), a detached workplace of the Faculty of Forestry and Wood Sciences, Czech University of Life Sciences in Prague, Czech Republic. The magnetic coil (a Merritt coil, built according Kirschvink [32]) was 4 x 4 x 4 m and was located in a separate special building. It was shielded from radiofrequency waves. It was controlled from a separate building next to the coil building. The magnetic field in coils was manipulated by a MagFieldG control software through a GMP4 RJ4.01 control unit and three current amplifiers, each for the Bx axis, the By axis and the Bz axis. The generation system for GMP4 3D coil

Table 1. List of the tested dogs and resulting indices of directional preference.

Dog	Owner	Breed	Sex	Age	Paw motorical laterality	Initial turning preference	Mean turning preference
Amalka	KB	Dachshund D	F	5	51	17	46
Arthur	ES	Dachshund N	M	2	n.m.	-32	-45
Azizi	JS	Beagle	M	6	6	-4	19
Barca	LS	Fox Terrier	F	12	0	67	42
Bertik	KB	Dachshund D	M	6	8	-29	-48
Bessy	JA	Fox Terrier	F	8	26	22	42
Figy	KB	Dachshund D	F	5	9	-4	8
Gofi	JA	Fox Terrier	F	3	-70	-95	-96
Hard	JA	Fox Terrier	M	2	-46	22	2
Hugo	KB	Dachshund D	M	3	n.m.	-25	-17
Hurvinek	KB	Dachshund D	M	7	51	-46	-45
Jimmy	ES	Dachshund N	M	2	n.m.	60	35
Kacka	KB	Dachshund D	F	5	25	-17	-18
Kuky	KB	Dachshund D	M	7	27	50	40
Naty	ES	Münsterländer	M	3	n.m.	-45	-62
Offi	JS	Beagle	F	9	-3	8	6
Pecka	KB	Dachshund D	F	2	-44	17	29
Plysak	KB	Dachshund D	F	2	10	-37	-60
Punta	KB	Dachshund D	M	3	-1	-8	-34
Roxxy	JS	Beagle	F	9	100	62	67
Shedy	ES	Weimaraner	M	5	n.m.	27	40
Sisi	KB	Dachshund D	F	3	n.m.	12	42
Zofka	KB	Dachshund D	F	2	-20	54	46

Paw motoric laterality = laterality index based on the Kong test; Initial turning preference Turning preference index in the first trials of each dog. Mean turning preference = = mean turning preference index over all trials of each dog. The value of the index can range from -100 to -25 (= left-turning dog) to 25–100 (= right-turning dog). Sex: F = female, M = male. Age is given in years. Dachshund N = normal-sized dachshund, Dachshund D = dwarf-sized dachshund, n.m. = not measured.

https://doi.org/10.1371/journal.pone.0245940.t001

system was used to create a defined direct and slowly changing magnetic field and it served to drive the coil system to create a defined magnetic field.

Magnetic induction values in the Cartesian coordinate system (axis Bx = -3225 nT; axis By = 17800 nT; axis Bz = 45448 nT) were set for the experiment, thereby rotating the magnetic field by 90° magnetic North was shifted to the topographic (= geomagnetic) East. The magnetic field strength and inclination were maintained as for geomagnetic values for local geographic conditions. The magnetic coil space was used also for the control experiment to test the dogs under local geomagnetic conditions, while other experimental conditions were preserved identic, i.e. shielding of radiofrequency waves, avoiding other influences (wind, sun, outside sounds). The coil room was equipped with cameras (AXIS P5624-E 50HZ—PTZ IP camera, TD / N, 18x zoom, HD 720p, IP66, PoE +) for video recording of the entire experimental space, network speaker with SIP, PoE support (AXIS C3003-E NETWORK HORN SPEAKER, Double—sided audio) and microphone (AXIS T8353A MICROPHONE 3.5MM) at the control station to secure communication of the leading experimenter in the control workplace with two experimenters in the coil.

Experimental procedure

Dogs were tested indoors, in a room housing the magnetic coils, and should make the choice between two identical dishes. The dishes were placed at a distance of 2.9 m from the point of release of the dog, always a plus and minus 30˚ from the starting point. Both dishes contained the same treats and dogs were always allowed to empty both. After placing the dishes, the dog was ready for the starting point and waited to obtain a permit to go to a dish. The dogs could not see the placement of the reward dishes. Three experimenters were involved in the experiment; two were present in the magnetic coil (the owner was guarding the dog and prohibited it from seeing the preparation procedure, and the other was preparing the placement of the rewarded dishes), the third experimenter was in the control room using a microphone and headsets to communicate with the two other colleagues, changed the experimental magnetic conditions (switching between control and experimental conditions) according to a randomized schedule and recorded the results (direction of dog first choice) (Fig 1). Note that this person was the only one who knew the actual position of the magnetic North inside the coil.

Each dog was tested in three to five test series under the control conditions with the magnetic North (mN) being 0˚, and in the same number of test series in an artificially shifted magnetic field with mN = 90˚ (where magnetic north was set on topographic east). The order of the test series (control first, shifted field second or shifted field first, control second) was taken into account. Tests series were performed at different days, at different daytimes, evenly distributed over the whole day.

Because a series included four trials in each dish combination alignment (i.e. N-E, E-S, S-W, and W-N), individual dogs experienced either 48 or 80 trials (in 12 or 20 complete series) in which their turning preference (first dish choice) was recorded under control conditions and the same number of records was gathered for experiments in the shifted magnetic field. The difference in the number of series and trials experienced by individual dogs was given by their availability for our study.

In addition, the dog's identity, date, time, sequence of trials combinations, and the order of the trials in the respective series were recorded.

Paw preferences

To determine paw preference (motoric laterality of dogs), a modified Kong test [e.g. 12,16,33] was used. In this test, it is recorded with which paw (left or right) the dog holds a Kong, a dog toy (KONG Company) when trying to get the food stuffed inside. A plastic yoghurt cup was used instead of Kong. The inner walls and bottom of the cup were covered with a dog's delicacy such as lard, cream cheese. Each dog was tested at home in an open area for 10 minutes while the dog played with the cup and tried to lick it out and the number of touches with either paw was recorded. Simultaneous touches with both paws were also recorded but were not included in the calculation of the index of laterality. The dogs who did not touch the cup during test of paw preference are excluded from the analysis of the Kong test.

Data analyses

From the recorded choices for each dog, in each trial, the left and right turning preferences were summed, for all four combinations (W-N; N-E; E-S; S-W) separately. For data analysis, the **turning preference index** was calculated in tests performed in the control and shifted magnetic field. The formula (R-L / R + L) x 100 was used, where the R = right and L = left sides are the total numbers of the first choice of left or right dishes. The **laterality index** for the paw preference (Kong test) was calculated using the same formula. The value of the index can range from -100 to -25 (= left-pawed dog) to 25–100 (= right-pawed dog). Dogs with index values between -24 and 24 were considered ambilateral. For the turning preference, altogether ten indices (LI) were calculated; one for each dish combination alignment (N-E, E-S, S-W, and W-N), i.e. four altogether in the control conditions and four altogether in the shifted magnetic

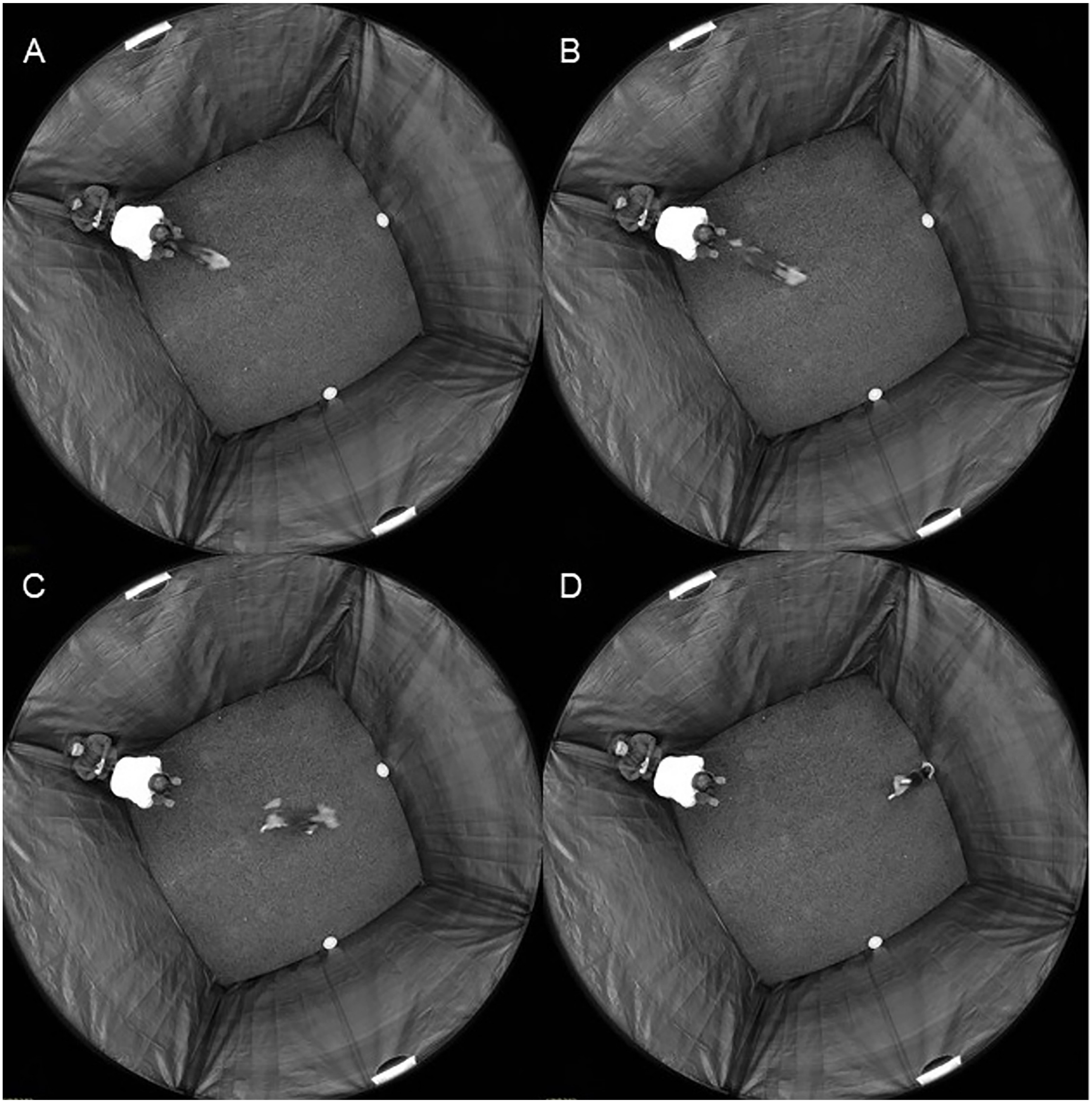


Fig 1. Experimental setup as monitored from above by a camera placed at the ceiling of the room, showing the sequence from release of the dog (A) to its choice of one of two dishes (D).

https://doi.org/10.1371/journal.pone.0245940.g001

field conditions. Furthermore, we calculated one mean index for control conditions and one mean index for shifted magnetic field (S1 Table). The dogs were divided in turning preference left-preferring, right-preferring or irresolute (ambilateral) preference according to [33] based on results of the first trials (Initial turning preference in Table 1). Generalized Linear Model (GLM) contained the interaction between Magnetic field and Turning preference classes.

From the recorded choices, preferences for either left or right turn were calculated for all test combinations (N-E, E-S, S-W, W-N) within each trial, and the sum of all trials of each dog. Index of directional preference was then calculated (according to the above formula) for each dog.

All data were analyzed using the SAS System (SAS, version 9.4). For calculating Spearman correlation coefficient we used PROC CORR. To analyze the factors affecting the directional preference index (dependent variable) we used a multivariate Generalized Linear Mixed Model (GLM, PROC MIXED). We constructed two GLMs. The models were applied as a fixed-effect models designed for the repeated measures, i.e., in SAS, with REPEATED = order of testing and the SUBJECT = Name of the dog with compound symmetric covariance structures for repeated measures (TYPE = cs). The first GLM was constructed with the predicted fixed factors Magnetic coil in an interaction with the Turning preference classes, and then we added other variables listed in S2 Table in case they could affect the directional preference index. None of these variables appeared significant and therefore we will not mention them in the text any more. Least squares means (LSMEANs) were calculated for the categorical fixed effects by computing the mean of each treatment and averaging the treatment means. These means of means were then used to compare the factors.

The second model was designed to estimate repeatability of the directional preference across experimental conditions. The GLM contained the only fixed factor Magnetic coil. We calculated repeatability as the intraclass correlation coefficient [34] by adding the RCORR option to the REPEATED.

Independently, mean directional compass preference based on the frequency of first choices in a given combination in all pooled trials was calculated for each dog using circular statistics with Oriana 4.02 (Kovach Computing). Grand mean vectors were then calculated on the base of those mean dog vectors for all the dogs, and subgroups with respect to turning preference, experimental condition, sex, and age.

Results

Paw preference (motoric laterality, Kong test)

Following the a priori set criterion, out of altogether 17 dogs tested, 3 dogs were classified as left-lateral, 6 as right-lateral, and 8 as irresolute (ambi-lateral) (Table 1). There was no apparent effect of sex, age, breed or owner on this type of laterality. The correlation between the Kong and overall turning preference tests was rather weak ($r_s = 0.317$, $P = 0.22$).

Turning preference under the control (mN = 0˚) and experimental (mN = 90˚) conditions

Following the a priori set criterion, out of altogether 23 dogs tested, 6 dogs were classified as clockwise-preferring (right-lateral), 7 dogs as counterclockwise-preferring (left-lateral), and 10 as irresolute (ambi-lateral) (Table 1). There was no significant difference in turning preferences of individual dogs between control conditions (mN = 0˚) and the shifted magnetic field conditions (mN = 90˚) (Fig 2). There was a variation in the turning preference index according to the magnetic north direction and Turning preference classes ($F_{(23,\ 131)} = 4.59$, $P<0.0001$, Figs 2 and 3). For the dogs with clockwise turning preference, there was a trend towards increasing the turning preference index from NE, SE, SW and NW. In other words, the clockwise turning dogs exhibited the lowest turning preference index in the combination North-

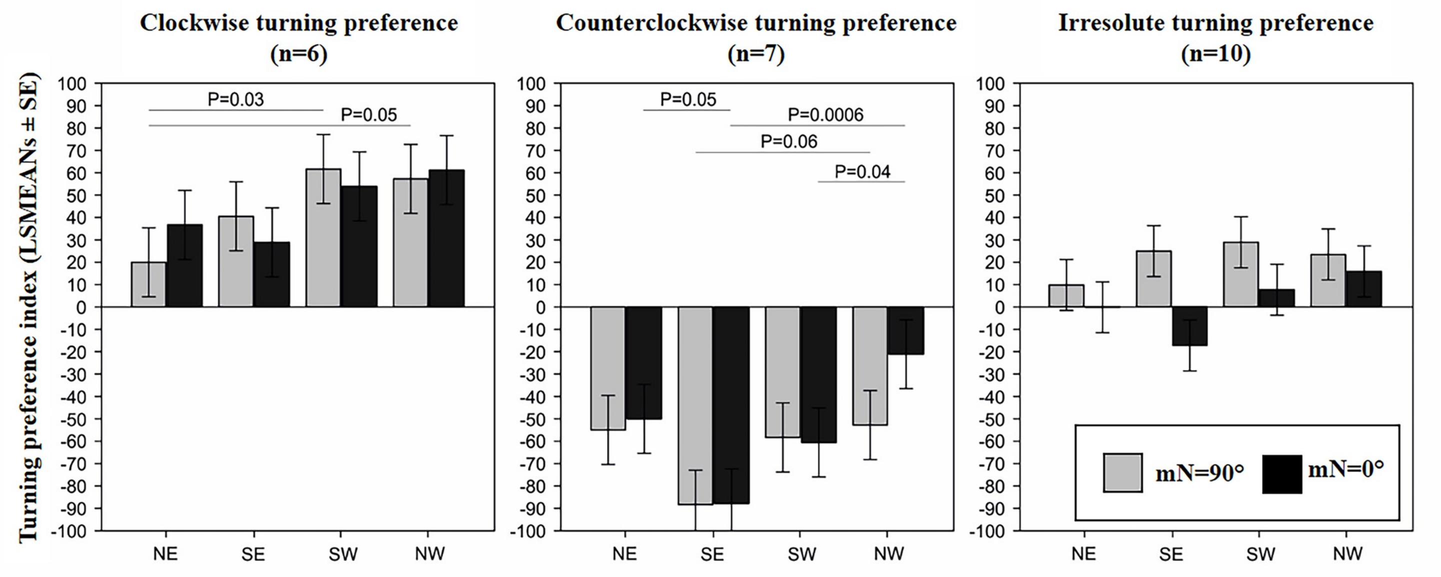


Fig 2. Turning preference index. (Least Square Means ± SE) for clockwise-preferring (left), counterclockwise-preferring (middle), and irresolute (right) dogs under the conditions of the magnetic North (mN) = 0˚ (control) and mN = 90˚ (shifted magnetic field) for the four particular combinations of the placement of dishes.

https://doi.org/10.1371/journal.pone.0245940.g002

East. However, only the difference between NE vs NW and between NE and SW, and only in the shifted magnetic field, reached the level of significance (P = 0.05) (Fig 2 left). For the dogs with counterclockwise turning preference, the most intensive counterclockwise preference was shown in SE orientation in comparison with NW and partly NE, while the weakest preference was in shown in the NW combination. Significant differences were achieved in the shifted magnetic field in SE vs NW, and under control conditions in NE vs SE, SE vs NW, SW vs NW (Fig 2, middle). No trend nor differences were detected for dogs showing irresolute turning preference (Fig 2, right).

There was significant bias from the overall turning preferences in the eastern hemisphere, expressed as the "pull of the north", in that a dish placed eastwards was more frequently chosen than a dish placed southwards and a dish placed northwards more frequently chosen than a dish placed eastwards, resulting in an average (theoretical) preference for NNE (Fig 4, Table 2). In a more differentiated view, this result was due to a dominant preference of females and/or clockwise preferring dogs for North (over East) and to an additional weaker pull of the East over South in males and/or counterclockwise preferring dogs. "Pull of the north" in irresolute dogs was indicated but not significant (Table 2, Figs 2 and 3).

Repeatability of turning preference. A single factor of Magnetic coil was not significant ($F_{1,\,22} = 1.16$, P = 0.86). On the other hand, Repeatability was high (r = 0.76).

Discussion

Turning preference did not correlate with the motoric paw laterality (Kong test). Apparently, both types of preferences are controlled by different proximate mechanisms / pathways. This conclusion is consistent with earlier findings [35] showing that visual (sensory) and paw (motoric) laterality in dogs are independent of each other. None of the dogs had any previous experience with emptying cups (i.e. Kong-type tests). None of the dogs used in this study had a history of being trained "Heel" to come and follow the master at her/his left (or right) side. Consequently, their turning preferences can be considered natural, spontaneous, inborne, and

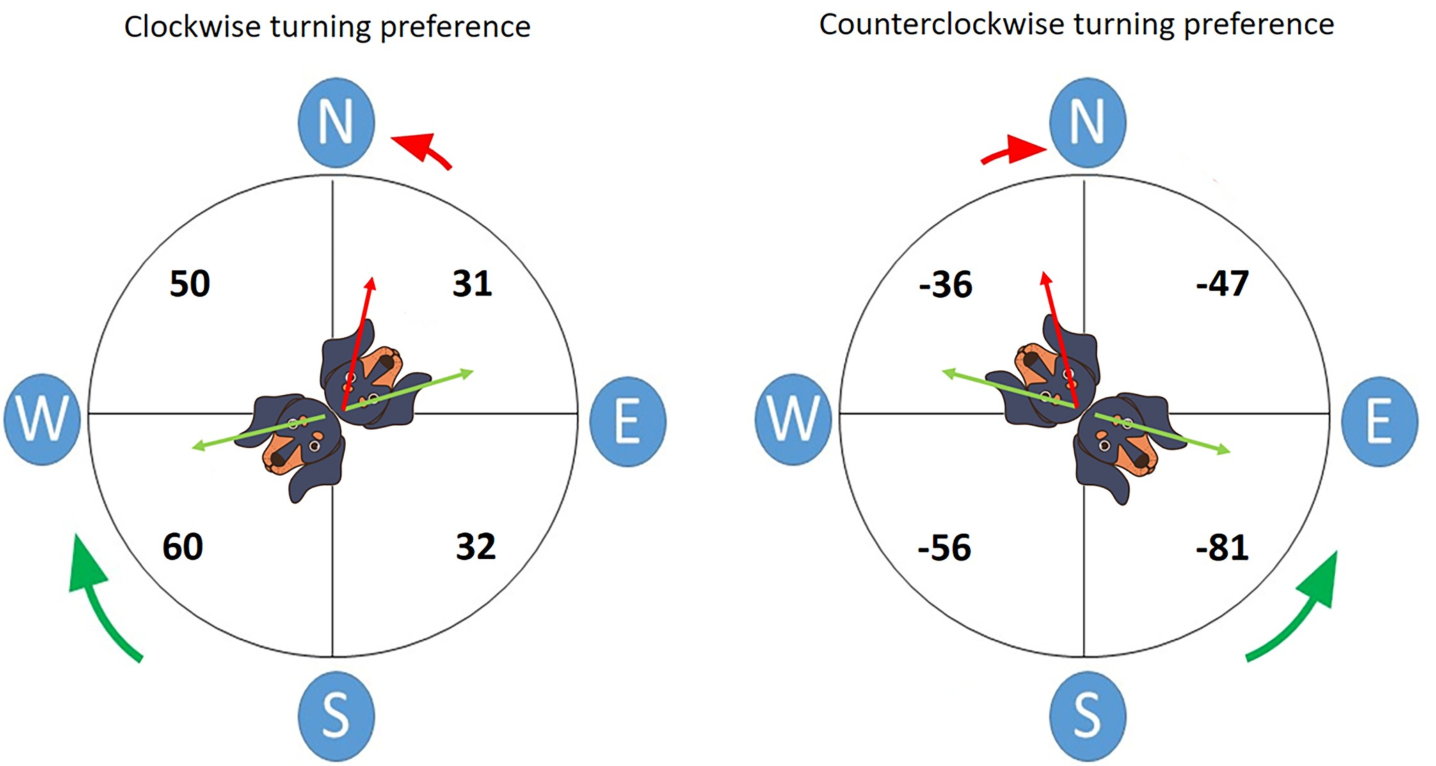


Fig 3. Numbers in each quadrant (in the respective four compass combinations: N-E, E-S, S-W, W-N) show mean values of turning preference indices calculated from individual dogs and pooled across all trials (both control and shifted magnetic field conditions). The value of the index can range from -100 to -25 (= left-turning dog) to 25–100 (= right-turning dog). Data were partitioned by turning preference (left figure shows clockwise turning preference, right figure shows counterclockwise turning preference; irresolute dogs were not calculated. The green arrow over the dog's head in the centre of the circle indicates the direction of view of the (supposedly) dominant eye which guides turning direction, while the red arrow shows the direction of view of the contralateral eye, supposed to exert "pull of the north" if heading northwards. Green arrow outside the circle designates the preferred direction of turning, the shorter red arrow designates "pull of the north".

https://doi.org/10.1371/journal.pone.0245940.g003

not entrained. Accordingly, there was no significant difference in the turning preference in particular dogs between the first and second experimental series and there was no effect of the respective owner. Interestingly, among the dogs who turned clockwise there were more females, while among the dogs turning counterclockwise there were more males. The sample was, however, too small to allow any general conclusion with regard to the effect of sex on turning preference. In fact, no clear effect of sex on turning preference was found in a previous study (with a different composition of the study sample) [1].

Consistently with results, of the previous study in open field [1], the turning preference was consistent for each particular dog for all combinations of placement of dishes also in an interior with uniform walls, no apparent landmarks, and no sun or wind cues. Concordantly with the results of the previous study, this preference was slightly, yet significantly disturbed (or pronounced) in that the north-placed dishes were more frequently chosen than would be expected according to the average turning preference of each particular dog. Most important in the context of the present study is the finding that, magnetic and not topographic, north affected the mentioned bias.

The detailed analysis shows, however, that the "pull of the north" is a more complex phenomenon, involving also "repulsion of the south". These effects are unilateral: the clockwise turning preference in the right-preferring dogs is more pronounced ("accelerated") in the S-W combination, while the counterclockwise turning preference in the left-preferring dogs is

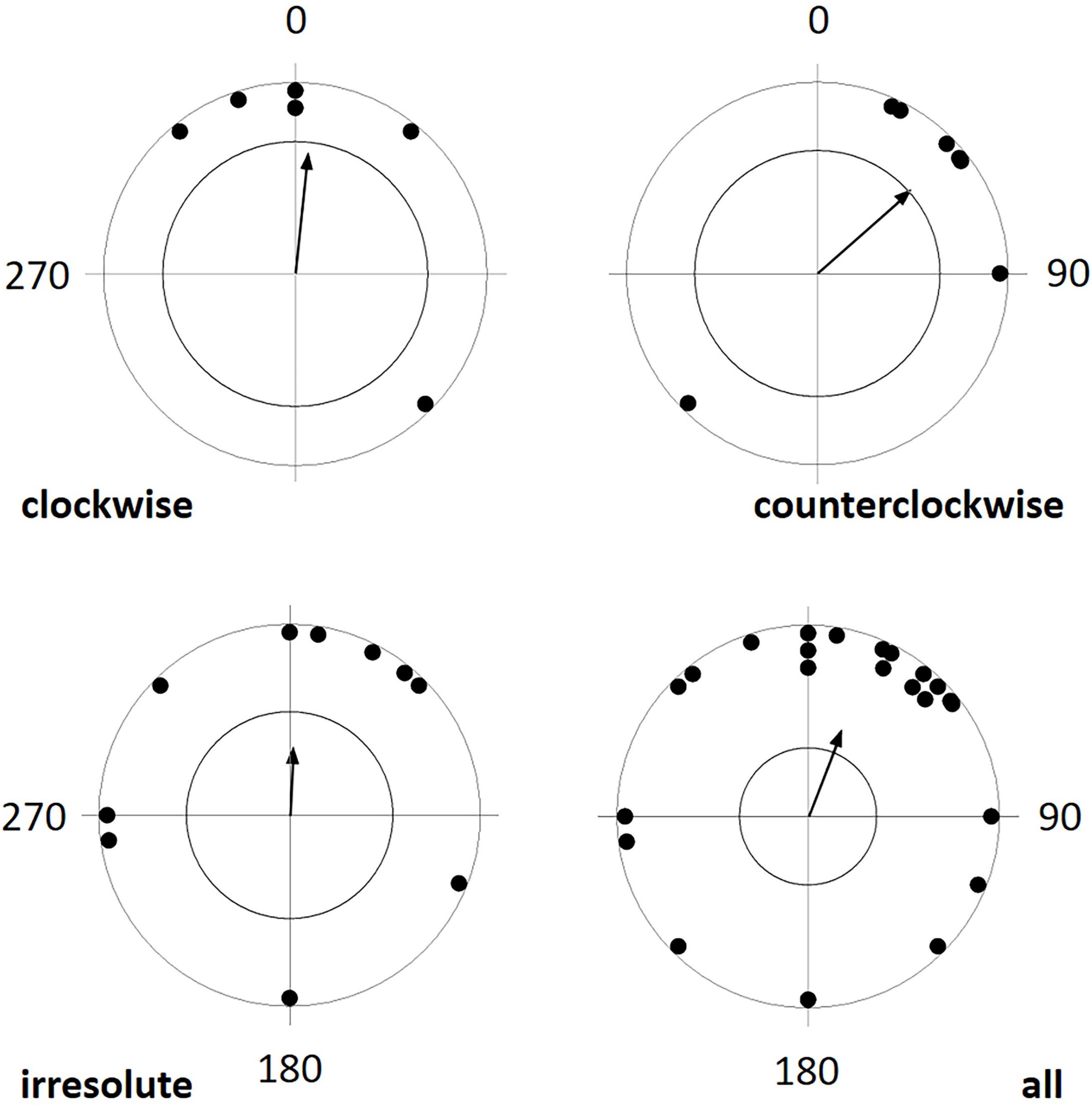


Fig 4. Mean preference for compass direction of a dish with snacks of the first choice. Angular means over dogs preferring to turn clockwise, those preferring to turn counterclockwise, dogs which were irresolute in their preference, and over all dogs. The arrow indicates the grand mean axial vector (μ) calculated over all angular means. The length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the mean vectors. The inner circle marks the 0.05 level of significance border of the Rayleigh test. See Table 2 for statistics.

https://doi.org/10.1371/journal.pone.0245940.g004

"accelerated" in the S-E combination. On the other hand, N-E combination decreases ("decelerates") clockwise turning preference in the right-preferring dogs, while in the N-W combination, the counterclockwise turning preference in the left-preferring dogs will be reduced. In

Table 2. Circular statistics for frequencies of choices of a dish placed in different cardinal compass directions in front of a dog in dual choice experiments, where the dog chose between north or east, east or south, south or west, west or north.

Variable	All trials	mN = 0°	mN = 90°	1st series	2nd series
Number of dogs tested	23	23	23	23	23
Mean vector (μ)	21°	43°	350°	22°	17°
Length of mean vector (r)	0.485	0.557	0.464	0.347	0.566
Circular standard deviation	69°	622°	71°	83°	61°
95% Confidence interval (-/+) for μ	349°-53°	16°-70°	316°-23°	335°-68°	351°-44°
99% Confidence interval (-/+) for μ	339°-63°	7°-78°	305°-34°	321°-82°	342°-52°
Rayleigh test (Z)	5.402	7.134	4.945	2.766	7.378
Rayleigh test (p)	0.004	4.92E-04	0.006	0.061	3.68E-04
Variable	males	females	clockwise preferring	counterclockwise preferring	irresolute
Number of dogs tested	11	12	6	7	10
Mean vector (μ)	44°	0°	6°	48°	3°
Length of mean vector (r)	0.517	0.529	0.637	0.655	0.356
Circular standard deviation	66°	65°	54°	53°	82°
95% Confidence interval (-/+) for μ	358°-90°	318°-42°	318°-53°	9°-90°	279°-87°
99% Confidence interval (-/+) for μ	344°-105°	304°-56°	303°-68°	354°-103°	252°-113°
Rayleigh test (Z)	2.939	3.357	2.431	3.005	1.268
Rayleigh test (p)	0.049	0.031	0.084	0.043	0.288

Each compass direction was offered with the same frequency. Mean vectors in this table represent thus grand mean vectors. Cf. Fig 4.

https://doi.org/10.1371/journal.pone.0245940.t002

this way, in the total, south-placed dishes are less frequently chosen than would be expected, while the north-placed dishes are apparently more preferred. Since "rotational deceleration" is stronger in N-E than the N-W combination, while the "acceleration" is stronger in the S-E than in the S-W combination, the resulting theoretical mean preference is for Northeast.

It may be of relevance and significance in this context that the analysis of published results on magnetic alignment behaviour in a variety of vertebrate species revealed that magnetic alignment typically coincides with the north-south magnetic axis, however, the mean directional preferences of an individual or group of organisms is often rotated clockwise from the north-south axis [36–38]. The deviation from the magnetic north-south axis could originate at different levels in the sensory hierarchy: it could be related either to asymmetries at the sensor level or to functional brain asymmetries, i.e. central processing.

Although the mode of the perception of the magnetic compass direction in animals remains enigmatic [27], findings from behavioral, histological, neuroanatomical, and electrophysiological studies have led to several physically viable theoretical models that might also apply to dogs. Two mechanisms are most widely discussed in the literature: the magnetite-based mechanism and the radical-pair mechanism.

Perhaps the most intuitively appealing mechanism to explain magnetosensitivity in animals is the idea of a small permanent magnet inside the animal that acts like a compass needle [39]. Magnetite-based sensors may be located anywhere in the body, they do not need to be concentrated in (paired) organs and they can be very tiny.

Another proposed mechanism for magnetoreception in animals is based on an effect of the magnetic field on the quantum spin states of a photo-excited chemical reaction that forms long-lived, spin correlated radical pair intermediates (radical pair mechanism; [40,41]. It is believed to occur in the specialized retinal cells [42,43]. It is assumed that the magnetic field may generate a “visual” pattern of varying light intensity, color, and/or contrast superimposed on the normal visual scene [40,44,45]. The model suggests that north or south “patterns” are more clearly recognizable and easier to be followed than east or west "patterns". Accordingly, and alternatively, the "pull of the north" could be also interpreted as a "deflection / repellence by the east or west".

Given that the choice of a dish in our experiment was visually guided, we may postulate that the turning preference was determined by the dominant eye, so that a dominant right eye resulted in clockwise, and a dominant left eye in counterclockwise turning. Assuming further that magnetoreception in canines is based on the radical-pair mechanism [46,47], a "conflict of interests" may be expected, if the dominant eye guides turning away from north, yet the contralateral eye "sees the north", which generally acts attractive, provoking body alignment along the north-south axis. To test this hypothesis, visual dominance (eyedness) in particular dogs should be studied in an independent test, e.g. sensory jump test [35].

Magnetic alignment might have an adaptive function in that it provides a global reference frame that helps to structure and organize spatial behavior and perception over many different spatial scales. For example, one possibility is that magnetic alignment helps to put the animal into register with a known orientation of a mental (cognitive) map, reducing the complexity of local and long-distance navigation, and reduces the demands on spatial memory [44]. This would be analogous to strategies used in human orientation; it is much simpler and intuitive to navigate when the navigators align themselves with a physical map (i.e. the users rotate their body direction to coincide with the alignment of the physical map), rather than to navigate by mentally rotating the physical map to align with the user's orientation. Therefore, we suggested that the mental map in animals is fixed in alignment with respect to the magnetic field [2,38]. Indeed, important component(s) of the cognitive map may be derived from the magnetic field (see below) and spontaneous magnetic alignment behavior may help to place the animal into register with this map. This relatively simple alignment strategy would help animals to reliably and accurately 'read' their cognitive map and/or extend the range of their maps when exploring unfamiliar environments. Accordingly, animals of different taxa were frequently reported to prefer to head about northwards when feeding (reviewed in [36–38]).

We suggest that the described simple turning test has a high heuristic potential and should be extended for tests of visual laterality and be performed under a wider array of experimental conditions to get more insight into the very mechanism, seat and function of magnetoreception.

Supporting information

S1 Table. Indices of laterality each tested dog. ITP = index of turning preference; W-N designates the combination in which the test dishes were placed west and north; N-E = designates the combination in which the test dishes were placed north and east; E-S designates the combination in which the test dishes were placed east and south; S-W = designates the combination in which the test dishes were placed south and west, mN = 0˚ designates a control experiment; mN = 90˚ designates an experimental condition with a shifted magnet field.
(DOCX)

S2 Table. Variables available for statistical analysis.
(DOCX)

S3 Table. Source data.
(XLSX)

Author Contributions

Conceptualization: Jana Adámková, Kateřina Benediktová, Vlastimil Hart, Hynek Burda.

Data curation: Jana Adámková, Kateřina Benediktová.

Formal analysis: Jana Adámková, Kateřina Benediktová, Luděk Bartoš, Hynek Burda.

Funding acquisition: Jana Adámková, Kateřina Benediktová, Jan Svoboda, Luděk Bartoš, Vlastimil Hart, Hynek Burda.

Investigation: Jana Adámková, Kateřina Benediktová, Jan Svoboda, Lucie Vynikalová, Petra Nováková, Michael S. Painter.

Methodology: Jana Adámková, Kateřina Benediktová, Vlastimil Hart, Michael S. Painter, Hynek Burda.

Project administration: Jana Adámková, Kateřina Benediktová, Vlastimil Hart, Hynek Burda.

Resources: Vlastimil Hart, Hynek Burda.

Supervision: Jana Adámková, Kateřina Benediktová, Vlastimil Hart, Hynek Burda.

Validation: Jana Adámková, Kateřina Benediktová, Hynek Burda.

Visualization: Jana Adámková, Luděk Bartoš, Hynek Burda.

Writing – original draft: Jana Adámková, Kateřina Benediktová, Luděk Bartoš, Michael S. Painter, Hynek Burda.

Writing – review & editing: Hynek Burda.

References

1. Adámková J, Svoboda J, Benediktová K, Martini S, Nováková P, Tůma D, et al. Directional preference in dogs: Laterality and "pull of the north". PLOS ONE. 2017; 12(9): e0185243. https://doi.org/10.1371/journal.pone.0185243 PMID: 28945773
2. Hart V, Nováková P, Begall S, Malkemper EP, Hanzal V, Ježek M, et al. Dogs are sensitive to small variations of the Earth's magnetic field. Front Zool. 2013; 10: 80. https://doi.org/10.1186/1742-9994-10-80 PMID: 24370002
3. Yosef R, Raz M, Ben-Baruch N, Shmueli L, Kosicki JZ, Fratczak M, et al, Directional preferences of dogs' changes in the presence of a bar magnet: Educational experiments in Israel. J Vet Behav. 2020; 35: 34e37. https://doi.org/10.1016/j.jveb.2019.10.003.
4. Martini S, Begall S, Findeklee T, Schmitt M, Malkemper EP, Burda H. Dogs can be trained to find a bar magnet. PeerJ. 2018; 6: e6117. https://doi.org/10.7717/peerj.6117 PMID: 30588405
5. Benediktová K, Adámková J, Svoboda J, Painter MS, Bartoš L, Nováková P, et al. Magnetic alignment enhances homing efficiency of hunting dogs. eLife. 2020 9: e55080. https://doi.org/10.7554/eLife.55080 PMID: 32539933
6. Rogers LJ. Laterality in animals. Internat J Comp Psychol. 1989; 3: 5–25. https://escholarship.org/content/qt9h15z1vr/qt9h15z1vr.pdf.
7. Rogers LJ. Lateralization in vertebrates: its early evolution, general pattern, and development. Adv Study Behav. 2002; 31: 107–161. 10.1016/S0065-3454(02)80007-9
8. Rogers LJ, Vallortigara G, Andrew R.J. Divided brains. The biology and behaviour of brain asymmetries. 2013; Cambridge University Press, New York. ISBN: 9781107005358.
9. Schaafsma SM, Riedstra BJ, Pfannkuche KA, Bouma A, Groothuis TG. Epigenesis of behavioural lateralization in humans and other animals. Phil Trans Roy Soc B. 2009; 364: 915–927. https://doi.org/10.1098/rstb.2008.0244 PMID: 19064352
10. Warren JM. Handedness and laterality in humans and other animals. Physiol. 1980; 8:351–359. https://doi.org/10.3758/BF03337470.
11. Batt L, Batt M, McGreevy P. Two tests for motor laterality in dogs. J Vet Behav. 2007; 2(2): 47–51. https://doi.org/10.1016/j.jveb.2007.01.002.
12. McGreevy PD, Brueckner A, Thomson PC, Branson NJ. Motor laterality in 4 breeds of dog, J Vet Behav. 2010; 5(6): 318323. https://doi.org/10.1016/j.jveb.2010.05.001.

13. Lee S, Konno A, Hasegawa T. Asymmetrical paw preference and personality. J Vet Behav. 2011; 6(1): 84–85. https://doi.org/10.1016/j.jveb.2010.09.002.

14. Plueckhahn TC, Schneider LA, Delfabbro PH. Assessing lateralization in domestic dogs: Performance by *Canis familiaris* on the Kong test. J Vet Behav. 2016; 15: 25–30. https://doi.org/10.1016/j.jveb.2016.08.004.

15. Ocklenburg S, Isparta S, Peterburs J, Papadatou-Pastou M. Paw preferences in cats and dogs: Meta-analysis. Laterality. 2019; 24(6): 647–677. https://doi.org/10.1080/1357650X.2019.1578228.

16. Siniscalchi M, d'Ingeo S, Formelli S, Quaranta A. Relationship between visuospatial attention and paw preference in dogs. Sci Reps. 2016; 6: 31682. https://doi.org/10.1038/srep31682 PMID: 27545695

17. Siniscalchi M, d'Ingeo S, Minunno M, Quaranta A. Communication in dogs. Animals. 2018; 8(8): 131. https://doi.org/10.3390/ani8080131 PMID: 30065156

18. Tomkins LM, Thomson PC, McGreevy PD. Associations between motor, sensory and structural lateralisation and guide dog success, Vet J. 2012; 192(3): 359–367. https://doi.org/10.1016/j.tvjl.2011.09.010 PMID: 22023850

19. Pongrácz P., Ujvári V, Faragó T, Miklósi À, Péter A. Do you see what I see? The difference between dog and human visual perception may affect the outcome of experiments, Behav Proc. 2017; 140: 53–60. https://doi.org/10.1016/j.beproc.2017.04.002.

20. Batt LS, Batt MS, Baguley JA, McGreevy PD. The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. J Vet Behav. 2009; 4(6), 216–222. https://doi.org/10.1016/j.jveb.2009.02.001.

21. Schneider LA, Delfabbro PH, Burns NR. Temperament and lateralization in the domestic dog (*Canis familiaris*). J Vet Behav. 2013; 8(3): 124–134. https://doi.org/10.1016/j.jveb.2012.06.004.

22. Siniscalchi M, d'Ingeo S, Formelli S, Quaranta A. Lateralized behavior and cardiac activity of dogs in response to human emotional vocalizations. Sci Reps, 2018; 8(1): 77. https://doi.org/10.1038/s41598-017-18417-4 PMID: 29311574

23. Sorensen H. Inside the mind of the shopper. 2nd ed. 2017; Pearson Education, Old Tappan, New Jersey. ISBN: 9780137013005.

24. Scharine AA, McBeath MK. Right-handers and Americans favor turning to the right. Human Factors. 2002; 44(2): 248–256. https://doi.org/10.1518/0018720024497916 PMID: 12452271

25. Eber A. Clandestine Curses: Hidden dangers to charioteers Roman spectacles and entertainment. 2010; Available at: https://www.brown.edu/academics/archaeology/sites/academics-archaeology/files/publication/document/Eber2010.pdf.

26. Tavakkoli MH, Jose TP. The reason why do athletes run around the track counter- clockwise? 2013; Internat Edu E-J. 2(4): 23–30. https://www.oiirj.org/ejournal/oct-nov-dec2013/phy-edu/04.pdf.

27. Nordmann GC, Hochstoeger T, Keays DA. Unsolved mysteries: Magnetoreception—A sense without a receptor. PLoS Biol. 2017; 15(10): 1–10. https://doi.org/10.1371/journal.pbio.2003234.

28. Gagliardo A, Flannino C, Ioalè P, Pecchia T, Wikleski M, Vallortigara G. Olfactory lateralization in homing pigeons: A GPS study on birds released with unilateral olfactory inputs', J Exp Biol. 2011; 214(4), 593–598. https://doi.org/10.1242/jeb.049510.

29. Wiltschko W, Traudt J, Güntürkün O, Prior H, Wiltschko R. Lateralization of magnetic compass orientation in a migratory bird. Nature. 2002; 419: 467–470. https://doi.org/10.1038/nature00958 PMID: 12368853

30. Gehring D, Wiltschko W, Güntürkün O, Denzau S, Wiltschko R. Development of lateralization of the magnetic compass in a migratory bird. Proc Roy Soc B. 2012; 279(1745), 4230–4235. https://doi.org/10.1098/rspb.2012.1654.

31. Wilzeck C., Wiltschko W, Güntürkün O, Buschmann J-U, Wiltschko R, Prior H. Learning of magnetic compass directions in pigeons. Anim Cogn. 2010; 13(3): 443–451. https://doi.org/10.1007/s10071-009-0294-0 PMID: 19937359

32. Kirschvink JK. Uniform Magnetic Fields and Double-Wrapped Coil Systems: Improved Techniques for the Design of Bioelectromagnetic Experiments. Biectromagnetix. 1992; 13: 401–411. https://doi.org/10.1002/bem.2250130507 PMID: 1445421

33. Tomkins LM, Thomson PC, McGreevy PD. First-stepping Test as a measure of motor laterality in dogs (*Canis familiaris*). J Vet Behav. 2010; 5(5): 247–255. https://doi.org/10.1016/j.jveb.2010.03.001.

34. Sokal RR, Rohlf FJ. Biometry. 1981; W. H. Freeman, San Francisco.

35. Tomkins LM, Williams KA, Thomson PC, McGreevy PD. Sensory Jump Test as a measure of sensory (visual) lateralization in dogs (*Canis familiaris*). J Vet Behav. 2010 5: 256–267.

36. Begall S, Malkemper EP, Červený J, Němec P, Burda H. Magnetic alignment in mammals and other animals. Mammal Biol. 2013; 78(1): 10–20. http://dx.doi.org/10.1016/j.mambio.2012.05.005.

37. Malkemper EP, Painter MS, Landler L. Shifted magnetic alignment in vertebrates: Evidence for neural lateralization? J Theor Biol. 2016; 399:141–147. https://doi.org/10.1016/j.jtbi.2016.03.040 PMID: 27059891

38. Burda H, Begall S, Hart V, Malkemper EP, Painter MS, Phillips JB, 2020. Magnetoreception in Mammals. In: Fritzsch B (ed.) and Bleckmann H (Volume ed.), The Senses: A Comprehensive Reference, vol. 7. Elsevier, Academic Press, pp. 421–444.

39. Yorke ED. A possible magnetic transducer in birds. J Theor Biol. 1979; 77(1): 101–105. https://doi.org/10.1016/0022-5193(79)90140-1 PMID: 449364

40. Ritz T, Adem S, Schulten K. A model for photoreceptor-based magnetoreception in birds. Biophys J. 2000; 78: 707–718. https://doi.org/10.1016/S0006-3495(00)76629-X PMID: 10653784

41. Hore PJ, Mouritsen H. The radical-pair mechanism of magnetoreception. Ann Rev Biophys. 2016; 45 (1): 299–344. https://doi.org/10.1146/annurev-biophys-032116-094545.

42. Liedvogel M, Mouritsen H. Cryptochromes—A potential magnetoreceptor: What do we know and what do we want to know? J Roy Soc Interface. 2010; 7: S147–S162. https://doi.org/10.1098/rsif.2009.0411.focus PMID: 19906675

43. Worster S, Kattnig DR, Hore PJ. Spin relaxation of radicals in cryptochrome and its role in avian magnetoreception. J Chem Phys. 2016; 145(3): 1–13. https://doi.org/10.1063/1.4958624 PMID: 27448908

44. Phillips JB, Jorge PE, Muheim R. Light-dependent magnetic compass orientation in amphibians and insects: Candidate receptors and candidate molecular mechanisms, J Roy Soc Interface. 2010; 7: S241–S256. https://doi.org/10.1098/rsif.2009.0459.focus.

45. Solov'yov IA, Mouritsen H, Schulten K. Acuity of a cryptochrome and vision-based magnetoreception system in birds, Biophys J. 2010; 99(1): 40–49. https://doi.org/10.1016/j.bpj.2010.03.053 PMID: 20655831

46. Červený J, Begall S, Koubek P, Nováková P, Burda H. Directional preference may enhance hunting accuracy in foraging foxes. Biol Letters. 2011; 7:355–357. https://doi.org/10.1098/rsbl.2010.1145 PMID: 21227977

47. Niessner C, Denzau S, Malkemper EP, Gross JC, Burda H, Winklhofer M, et al. Cryptochrome 1 in retinal cone photoreceptors suggests a novel functional role in mammals. Sci Reps. 2016; 6: 21848. https://doi.org/10.1038/srep21848 PMID: 26898837

6 Diskuse

Systematické studie zaměřené na navigační strategie a na zapojení konkrétních smyslů během homingu u nemigrujících zvířat (např. August et al., 1989; Tsoar et al., 2011), a zvláště u psovitých šelem (např. Walton et al., 2018), nejsou zatím příliš časté. Navigační schopnosti zvířat v jejich přirozeném prostředí jsou fascinující, ale paradoxně mají na svědomí obtíže spojené s jejich poznáváním. Plné porozumění vyžaduje získat detailní informace jak o smyslovém vnímání a projevech chování zvířat, tak i o prostředí, ve kterém se pohybují (Kays et al., 2015; Moll et al., 2007). Zatímco dříve byli vědci závislí pouze na poznatcích získaných přímým pozorováním (např. Schmid 1932, 1936; Müller 1965 citováno v Nahm, 2015), současný technologický rozvoj (telemetrie, GPS, bio-loggery, foto a video pasti), se souběžně probíhající miniaturizací, umožnuje získávat mnohem relevantnější a detailnější informace (Batsleer et al., 2020; Davidson et al., 2020; Gerencsér et al., 2013; Kays et al., 2015; Lush et al., 2016; Painter et al., 2016; Pašukonis et al., 2018; Walton et al., 2018; Yoda, 2019). I přesto stále narážíme na některé limity. Stacionární zařízení „nevidí“ zvíře mimo svůj dosah (Kovács et al., 2017), drony mohou vyrušovat nebo jsou omezeny hustou vegetací, GPS technologie a bio-loggery nemusí poskytnou dostatečně detailní informace o konkrétních projevech chování, pokud je zvíře mimo přímý dohled (Davidson et al., 2020). Řešením může být použití minikamer umístěných přímo na zvířeti (Andersen et al., 2020; Moll et al., 2007; Rutz et al., 2007). U volně žijících zvířat jsme stále limitováni malou výdrží baterie a datového úložiště, ale vhodnou alternativou by mohla být domestikovaná zvířata pod kontrolou člověka, která mají možnost se volně pohybovat (např. psi a kočky) (Bombara et al., 2017; Huck & Watson, 2019; Loyd et al., 2013).

Spojili jsme výhody výše uvedených metod a z běžně komerčně dostupných zařízení vyvinuli nositelný audio-video systém pro psy (wearable dog audio-video system – WDAVS) kombinovaný s GPS technologií (článek v přípravě). Kombinaci malé outdoorové kamery s integrovanou GPS, ochranného pouzdra a oblékatelné vesty jsme po otestování používali pro zkvalitnění sběru dat v rámci homingových experimentů se psy. Výhody kombinovaných systémů jsou nesporné. Umožňují systematicky spojovat data o pohybu a chování zvířat s údaji o okolním prostředím (Rosa, 2019). Náš systém (WDAVS) je navíc výrazně levnější a běžně dostupný oproti systémům vyráběným na zakázku. Ty jsou buď drahé nebo vyžadují rozsáhlé znalosti o výrobě a programování (Rosa, 2019). Na druhou stranu umožňují systém lépe přizpůsobit konkrétním požadavkům výzkumu s ohledem na např. velikost sledovaného druhu a tím minimalizovat případný vliv na přirozené chování zvířat (Yoda, 2019). WDAVS je sice o něco těžší než doporučované 3 % hmotnosti zvíře (3,2–6,4 % hmotnosti dle velikosti psa), ale existují i studie, kde hmotnost video systému tvořila až 9 % bez negativního vlivu na zvíře (shrnuto v Moll et al., 2007). Na druhou stranu, psi WDAVS nosili pouze po krátkou dobu (max. 90 min), ne dlouhodobě jako v jiných studiích, pro které byla hodnota počítána (např. Bombara et al., 2017; Loyd et al., 2013). Během testování nebyl prokázán žádný negativní vliv na pohybovou aktivitu a homingové chování psů. Do budoucna by bylo vhodné celý systém doplnit ještě o bio-logger, který by ve spojení s WDAVS mohl poskytnout detailnější informace o chování zvířat během homingu a ještě více urychlit a zkvalitnit následné zpracování dat (Kutilek et al., 2018; Painter et al., 2016).

Mnoho poznatků o prostorové orientaci zvířat bylo získáno behaviorálními pokusy v laboratořích, ale jak poukazují Jacobs & Menzel (2014), laboratorní prostředí je poněkud problematické, protože neposkytuje zvířatům dostatek přirozených podnětů pro rozvoj složitějších navigačních mechanismů. Navíc „vytržení“ zvířat z jejich přirozeného prostředí může výrazně ovlivnit jejich chování (Thorup & Holland, 2009). Další překážkou je skutečnost, že každý druh může používat způsob orientace uzpůsobený své životní strategii. Studium navigačních mechanismů u co nejširší škály druhů je proto nezbytné (Jacobs & Menzel, 2014). Zavedení nového modelového druhu, kterým by pes domácí mohl být (jakožto zástupce psovitých šelem) (Cooper et al., 2003) a jeho sledování v přirozeném prostředí (Adámková et al., 2017; Benediktová et al., 2020; Hart et al., 2013; Yosef et al., 2020), by mohlo posunout výzkum prostorové orientace savců novým směrem. Psi jsou dobře manipulovatelní, vyskytují se téměř po celém světě a jsou ochotní spolupracovat s člověkem (Miklósi, 2014; Serpel, 2017). Navíc, stále existuje skupina plemen psů, kteří mají blízko k přírodě a zachovali si dovednosti a schopnosti blízké divokým předkům. Tou skupinou jsou lovečtí psi používaní jako honiči, kteří jsou charakterističtí vrozenou ochotou vyhledávat zvěř, hlasitě sledovat její stopu a následně se vracet zpět ke svému majiteli. Přitom jsou dostatečně samostatní, aby se vzdalovali relativně daleko od majitele (i několik kilometrů), na druhou stranu mají s majitelem dostatečně blízký vztah, aby se ochotně vraceli zpět bez přivolávání (Bräuer & Blasi, 2021).

Využili jsme této vrozené vlastnosti loveckých psů, vybavili je GPS obojky a částečně kamerami a sledovali, jakým způsobem se psi (po ukončení sledování stopy) vraceli zpět k majiteli (Benediktová et al., 2020). Vracející se psi používali pro návrat dva rozdílné způsoby. Návrat po své vlastní stopě (pojmenovaný tracking) a návrat zcela novou trasou, často s využitím zkratek a lesních cest (pojmenovaný scouting).

Při použití scoutingu byli psi schopni se vracet rychleji, než když použili tracking. Jedním z důvodů může být, že se při scoutingu nezdržovali sledováním své vlastní stopy, kdy je klíčové určit její správný směr. To vyžaduje určitý čas a pro psy to představuje obtížnější úkol než samotné sledování stopy (Hepper & Wells, 2005). Je otázkou, zda se pes při trackingu spoléhá výhradně na čich. Z videozáznamů je patrné, že neběží s nosem u země, čehož si všimli i terénní pozorovatelé v původních homingových experimentech (Schmid, 1932 citován v Nahm, 2015). Mohlo by se tak jednat i o piloting založený na řadě orientačních bodů, který byl u psů potvrzen, byť pouze v laboratorních podmínkách (Fiset, 2007, 2009). Je však možné, a z našeho pohledu vysoce pravděpodobné, že využití olfaktorických a vizuálních informací je navzájem komplementární a pes obě smyslové modality kombinuje. Jak u psů, tak i u koček bylo potvrzeno, že i přes jejich vynikající čichové schopnosti preferují v určitých situacích vizuální vnímání (Mayes et al., 2015; Polgár et al., 2015). Další homingové experimenty by bylo možné provádět např. za tmy, kdy by bylo vizuální vnímání psů částečně limitováno.

Dalším důvodem pro rychlejší návrat při použití scoutingu může být využívání lesních cest a pěšin. Což samotnou příchozí trajektorii sice prodlužovalo, ale zároveň zrychlovalo. Pro psy malých a středních plemen je z hlediska šetření energie výhodnější pohybovat se po cestě či vyšlapané pěšině než se prodírat hustým lesním podrostem. Podobné chování bylo popsáno i u vlků, kteří tímto způsobem generovali efektivnější návratové trasy (Peters, 1978; Peters & Mech, 1975). Využívání cest ve známém terénu je v souladu s teorií o tvorbě kognitivních map u zvířat (Tolman, 1948). Pozorované používání zkratek (Poulter et al., 2018), by rovněž mohlo vysvětlovat rychlejší návrat při použití scoutingu. Není však jasné, jakým způsobem dokáží psi využívat cesty a zkratky v neznámém terénu. Všimli jsme si, že psi přesně vědí, kdy mají cestu opustit, aby si zbytečně nezaběhli. Stejně tak využívali jen cesty, které jim pomohly se přiblížit k cíli. Schopnost vracet se novými a přímějšími trasami zcela neznámým prostředím byla dobře popsána např. u netopýrů, u kterých bylo navrženo, že jedno z vodítek při navigaci neznámým terénem by mohlo poskytovat magnetické pole Země (Harten et al., 2020; Toledo et al., 2020; Tsoar et al., 2011).

Obecně se dá říci, že tracking je spolehlivá návratová strategie, ale delší. Scouting umožňuje používání zkratek a je rychlejší, vyžaduje však vyšší navigační schopnosti a kvůli možným chybám může být riskantní. Psi scouting používali o něco častěji ve známém prostředí než v neznámém, což je opět v souladu s teorií kognitivních map (O´Keefe & Nadel, 1978; Tolman, 1948).

Jak jsme předpokládali, psi vyšší kohoutkové výšky se v průměru pohybovali rychleji, nemělo to však překvapivě vliv na délku odchozí trajektorie. To znamená, že i malá plemena psů, jako jsou např. jezevčíci, jsou schopna a ochotna se vzdalovat od majitele stejně daleko jako větší plemena psů. Rozdíly mezi plemeny a často i mezi psy a fenami jsou při různých typech kognitivních úloh diskutovány. Například při testování olfaktorických schopností byly meziplemenné rozdíly potvrzeny (Miklósi, 2014), naopak nebyly potvrzeny v případě antipredačního chování (Samuel et al., 2020) ani v případě hledání ukrytého magnetu (Martini et al., 2018). V našem případě nebyly nalezeny rozdíly mezi plemeny ani mezi pohlavími jak u homingového chování psů (Benediktová et al., 2020), tak během značkování teritoria (Hart et al., 2013) či při dvouvýběrovém testu v magnetické cívce (Adámková et al., 2021). U dvouvýběrového testu v přirozeném prostředí (Adámková et al., 2017) se sice objevily rozdíly mezi velkými a menšími psy i mezi pohlavími, ale vzhledem k malým velikostem podskupin a jejich heterogenitě mohou být výsledky zkreslené. Bräuer & Blasi (2021) zmiňují, že větší rozdíly v chování psů lze najít spíše v inter-individuální rovině nežli v meziplemenné.

Detailnějším porovnáním návratových strategií tracking a scouting bylo odhaleno vysoce robustní a konsistentní chování v počáteční fázi návratu u psů vracejících se scoutingem. Konkrétně, v případě scoutingu psi začínali svůj návrat krátkým během podél severojižní magnetické osy, bez ohledu na aktuální polohu ukrytého majitele. Psi ve většině případů z bodu návratu nevyráželi rovnou směrem k majiteli, ale nejprve provedli zarovnaný dynamický alignment, nazvaný „kompasový běh“ a teprve poté se stáčeli směrem k majiteli. Naopak, v případě použití trackingu se toto vysoce statisticky signifikantní chování neprojevovalo a psi z bodu návratu vyráželi v náhodných směrech. Nejčastěji směrem, odkud přiběhli.

Použití návratové strategie scouting bylo u psů během homingu pozorováno již dříve. Jak u psů, kteří byli využíváni jako kurýři během 1. světové války (Richardson, 1920), tak ve dvou experimentech provedených ve 30. resp. 60. letech minulého století Bastianem Schmidtem a Bernhardem Müllerem (shrnuto v Nahm, 2015). Od té doby žádné další experimenty zaměřené na homing psů provedeny nebyly. Zajímavou poznámku lze najít v práci Bastiena Schmidta. Zmiňuje se o iniciační fázi orientace, teprve po ní následoval pohyb směrem k domovu. I když není známo nic o případném směru pohybu psa v této fázi, lze si představit možnou podobnost s kompasovým během loveckých psů vracejících se scoutingem.

Je nepravděpodobné, že by přímé zapojení vizuálních, olfaktorických nebo nebeských podnětů mohlo vysvětlovat vysoce stereotypní a konsistentní alignment kompasového běhu při scoutingu. Zalesněné prostředí a hustá podrostová vegetace spolu s malou výškou psů nedovoluje vizuální pilotování. Navíc se potvrdilo, že na kompasový běh nemá vliv kohoutková výška (a tedy úroveň omezení zorného pole), což je v rozporu s hypotézou vizuálního pilotingu. Rovněž lze vyloučit olfaktorické pilotování vzhledem k vysoké variabilitě povětrnostních podmínek během sběru dat doprovázené lokálními turbulencemi v podrostu. Ve 22 % případů bylo úplné bezvětří a pouze v méně než 10 % ze zbylých 78 % by pes mohl hypoteticky využít směr větru, který foukal od majitele k němu. To nevysvětluje vysoce signifikantní zarovnání kompasového běhu. Některé studie dokonce naznačují, že navzdory schopnosti úspěšně řešit úkoly pomocí čichu, domestikovaní psi často upřednostňují jiné kognitivní strategie (Polgár et al., 2015). Podobně lze vyloučit polarizované světlo. Slunečních dní je v České republice poměrně málo a vzhledem ke sběru dat v různých denních i ročních dobách, množství oblačnosti a husté vegetaci, pod kterou se psi pohybovali, se využití polarizovaného světla zdá nepravděpodobné. Obecně není u savců jeho detekce považována za příliš rozšířenou (Marshall & Cronin, 2011). Pes by při návratu mohl teoreticky použít proces integrace cesty (Etienne & Jeffery, 2004). Je ovšem známo, že tento proces rychle hromadí chyby lineárního i úhlového charakteru (Benhamou, 2014; Harootonian et al., 2020) a není tak použitelný při pohybu na delší vzdálenosti bez zapojení externích směrových informací

(Cheung et al., 2007, 2008). U psů bylo zjištěno, že chyby v odhadu vzdálenosti se pohybují kolem 6 % a chyby v odhadu směru dokonce 9 % při vzdálenosti pouhých 20 až 30 metrů (Séguinot et al., 1998). Naši psi se vraceli ze vzdálenosti často větší než 1000 m, v mnoha případech neznámým terénem, a přesto polohu ukrytého majitele lokalizovali velice přesně.

V několika málo případech lovečtí psi předvedli zajímavé chování. Po útěku se nevrátili k ukrytému majiteli ani k zaparkovanému autu, ale z bodu návratu zamířili rovnou na místo, kde byli před započetím sběru dat venčeni, kdy venčení trvalo cca 20 min. Vzdálenost mezi místem venčení a místem sběru dat byla obvykle půl kilometru. Vzhledem k tomu, že mezi těmito místy byli psi převáženi autem bez možnosti výhledu ven, použití integrace cesty lze v těchto případech vyloučit, neboť psům chybí klíčová informace o jejich vlastním pohybu (Etienne & Jeffery, 2004; McNaughton et al., 2006).

Teoreticky by mohlo být zarovnání kompasového běhu podél severojižní magnetické osy i reakcí na pozici ukrytého majitele. Pokud by se majitel nacházel často na sever nebo na jih od psa, nebo by pes častěji v některých směrech od majitele utíkal, logicky by se pes tímto směrem mohl začít vracet. Nicméně výsledky statistické analýzy nic takového nepotvrdily – pes vybíhal od majitele v náhodných směrech a také pozice ukrytého majitele vzhledem k vracejícímu se psovi byla náhodná. Na provedení kompasového běhu nemělo vliv plemeno psa, pohlaví, věk ani znalost prostředí. Navíc, pokud psi začali svůj návrat pomocí kompasového běhu, byla téměř čtyřikrát větší pravděpodobnost, že se budou vracet scoutingem než trackingem. Shrnuto dohromady, je obtížné si představit, že by některá z výše uvedených modalit měla zásadní vliv na provedení kompasového běhu v iniciační fázi návratu.

Naopak, zemské magnetické pole poskytuje stabilní, všude dostupný a vždy přítomný zdroj navigačních informací. Severojižní alignment kompasového běhu podporuje výsledky našich předchozích studií o schopnosti psů vnímat magnetické pole. Náš první výzkum zaměřený na magnetorecepci psů potvrdil preferenci pro zarovnání osy těla podél severojižní magnetické osy při značkování teritoria, ale jen v případech klidného magnetického pole (Hart et al., 2013). Další potvrzení magnetorecepčních schopností psů přinesly naše navazující práce. Terénní studie zaměřená na dvouvýběrový test preference misek s potravou potvrdila, že psi v kombinaci severní a východní strany upřednostňují severně umístěnou misku (Adámková et al., 2017). Studie stejného typu přenesená do magnetické cívky ukázala, že tzv. „tah severu“ byl přítomen jak v přirozeném magnetickém poli, tak i v magnetické poli otočeném o 90° (Adámková et al., 2021). U psů byla schopnost magnetorecepce potvrzena i dalšími nezávislými studiemi (Martini et al., 2018; Yosef et al., 2020). Přestože byl magnetický alignment potvrzen u mnoha druhů zvířat v rozličných kontextech chování (shrnuto v Begall et al., 2013; Burda et al., 2020), stále není zcela jasné, jaký adaptivní význam by mohl mít pro psy. Nicméně vzhledem k vysoce konsistentnímu chování v iniciační fázi návratu (kompasový běh) u psů, kteří se rozhodli pro návrat scoutingem, lze předpokládat signifikantní výhodu takového chování. Porovnáním poměru mezi délkou příchozí trajektorie a vzdušnou vzdáleností z bodu návratu k cíli (ukrytý majitel) bylo zjištěno, že kompasový běh zvyšoval efektivitu návratu. Psi byli schopni se k majiteli vracet přímější, a tudíž kratší cestou, než když kompasový běh na začátku scoutingu nepoužili. Rozdíl v účinnosti se pohyboval okolo 30 %.

Navrhujeme proto, že kompasový běh je příkladem použití magnetických informací. Mohl by pomáhat se zarovnáním mentální mapy prostředí podle magnetického kompasu a tím k nastavení správného směru k majiteli. Použití kompasového běhu zvyšuje přesnost navigace, což dokládá zvýšená efektivita homingu.

Kamery, které lovečtí psi nosili během homingových experimentů, přinesly mnoho doplňujících informací a detailů o konkrétním chování a o prostředí, ve kterém se psi pohybovali. Např. důvody nečekaného zpomalení či zastavení, druh sledované zvěře a její chování, natočily zloděje shozů apod. To vše viděno z perspektivy psa. Dále pomohly s objektivnějším určením bodu návratu, ale hlavně s identifikací chování, které zatím u psů, v souvislosti s prostorovou orientací, nebylo nikdy dříve popsáno. Psi během pohybu v terénu prováděli krátké zastávky. Tyto zastávky prokazatelně nesloužily k odpočinku, protože pes při nich zůstal stát se vztyčenou hlavou a zavřenou mordou, krátce se rozhlédl na jednu nebo na obě strany a velmi často vyběhl ze zastávky novým směrem. Toto chování je nápadně podobné tzv. „Head scanningu“ a chování „Vicarious trial and error“, které byly popsány během pátracího chování a orientace potkanů a jiných živočichů v souvislosti s rozhodovacími procesy (Dupret & Csicsvari, 2014; Monaco et al., 2014; Redish, 2016; Santos-Pata & Verschure, 2018; Tolman, 1948). Nicméně, u větších savců jsou záznamy z důvodu nedostatku systematických experimentů nekompletní (Kral, 2003). U ptáků byl head scanning pozorován při migračních experimentech, kde bylo navrženo, že skenování slouží k lokalizaci referenčního směru poskytovaného geomagnetickým polem (Mouritsen et al., 2004).

Proto uvažujeme o další možné funkci kompasového běhu. Psi pohybující se scoutingem v neznámém prostředí nemohou použít vizuální značky pro kalibraci integraci cesty. Zapojení magnetorecepce, zvláště v neznámém terénu (kde jiný než magnetický kompas není k dispozici), by se dalo předpokládat. Kompasový běh by tak mohl sloužit k rekalibraci procesů spojených s integrací cesty tím, že by poskytoval globální referenční směr ve vztahu k magnetickému poli Země. Což by zvýšilo dosah a přesnost integrace cesty (Cheung et al., 2007, 2008). Jak již bylo zmíněno výše, pokud psi během scoutingu provedli kompasový běh, jejich návratová trajektorie vedla přímější cestou k cíli, než když ho neprovedli. Zapojení magnetorecepce do procesů spojených s integrací cesty u podzemních hlodavců výrazně snižovalo akumulaci chyb, s rostoucí vzdáleností se navíc zvyšovalo její zapojení (Kimchi et al., 2004).

Otázkou zůstává funkce head scanningu během homingu loveckých psů. Na základě dostupných znalostí (např. Dupret & Csicsvari, 2014; Kral, 2003; Monaco et al., 2014; R. Peters, 1978; Redish, 2016; Santos-Pata & Verschure, 2018) je jeho propojení s magnetorecepcí pravděpodobné. Ať už ve spojení s integrací cesty (Cheung et al., 2007, 2008), detekcí směru (Mouritsen et al., 2004), či přímo s mechanismem vnímání magnetického pole Země (shrnuto v Kobylkov, 2020).

7 Závěr a doporučení pro další rozvoj vědního oboru

Navigační schopnosti zvířat udivují člověka od nepaměti. Zvláště, když nám je předvede domestikované zvíře, konkrétně pes domácí. Jak se psi orientují, když na rozdíl od člověka nemají v kapse mapu a kompas (v dnešní době spíš „GPSku“), zůstalo dlouho zahaleno tajemstvím. V souvislosti s orientací se v posledních desetiletích hovoří o schopnosti zvířat získávat potřebné navigační údaje z magnetického pole Země.

Předkládaná disertační práce představila možnosti studia zvířat v jejich přirozeném prostředí, včetně zapojení moderních sledovacích zařízení a následného zpracování velkoobjemových dat. Cílem bylo získat nové poznatky o prostorové orientaci loveckých psů v terénu a o možném zapojení magnetorecepce do procesů spojených s navigací. Dále byla zaměřena na vyhodnocení vlivu magnetického pole na poziční chování psů:

- Analýza pozičního chování psů při značkování domovských okrsků přinesla první důkaz o magnetosensitivě domácích psů a o vlivu přirozených fluktuací magnetického pole Země na jejich chování.
- Dvouvýběrové testy, jak v přirozeném prostředí, tak i v experimentálním prostředí magnetické cívky potvrdily výsledky předchozí studie o magnetorecepčních schopnostech domácích psů.
- Homingové experimenty potvrdily schopnost loveckých psů využívat magnetické pole Země i pro navigaci.
- Sledováním homingových strategií loveckých psů v jejich přirozeném prostředí bylo zjištěno, že psi jsou ochotni a schopni se vzdalovat od majitele i na několik kilometrů a vracet se spontánně buď po vlastní stopě (strategie pojmenovaná Tracking) nebo zcela novou trasou, často s využitím lesních cest a zkratek (strategie pojmenovaná Scouting).
- Na uběhnutou vzdálenost nemá vliv velikost psa.
- Při návratu scoutingem začínali lovečtí psi svůj návrat krátkým během podél severojižní magnetické osy, tj. provedli tzv. dynamický alignment nazvaný „kompasový běh“.
- Použití kompasového běhu při scoutingu zvýšilo efektivitu návratové trasy, psi byli schopni běžet rychleji a přímočařeji, než když kompasový běh nepoužili.

- Vyvinutý a do praxe zavedený WDAVS (nositelný audiovideo systém pro psy) umožnil kvalitativně i kvantitativně rozšířit sběr dat a jejich následné zpracování.
- Pomocí softwaru vyvinutého v prostředí Matlab® pro zpracování velkoobjemových dat bylo odhaleno dříve nepopsané chování psů (tzv. head scanning).

Výsledky disertační práce přinesly nové poznatky o způsobech prostorové orientace a navigace loveckých psů a potvrdili existenci magnetického smyslu a vliv magnetického pole Země na přirozené chování psů. Zavedení moderních technologií při sledování zvířat v jejich přirozeném prostředí rozšiřuje možnosti výzkumu behaviorální a senzorické ekologie.

Ačkoli stále přesně neznáme mechanismy, jakými psi i ostatní zvířata vnímají a zpracovávají poziční a směrové informace poskytované magnetickým polem Země, poznatky prezentované v této disertační práci by nás mohly posunout zase o kousek blíže k poznání tajemství magnetického smyslu zvířat.

Jak je u základního výzkumu časté, nakonec vyvstalo více otázek, než kolik jich bylo zodpovězeno:

1. Jaký vliv by měla na homingové schopnosti psů změna vnějších podmínek, např. sledování orientačních schopností za tmy nebo nasazení malých lokálních magnetů?
2. Mají psi magnetorecepci založenou na teorii radikálových párů a / nebo principu magnetitových částic? Docházelo by při nočním homingu nebo nasazení magnetů „jen“ ke změně poměru ve využití jednotlivých návratových strategií nebo by se psi i více ztráceli?
3. Využívají psi magnetický kompas (směrové informace) a / nebo magnetickou mapu (poziční informace)? Jak magnetorecepce interaguje s ostatními smysly?
4. Jaký funkční význam má pro psy head scanning a jaká je jeho role při orientaci a navigaci v prostoru?

8 Seznam citované literatury

Able, K. P., & Able, M. A. (1990). Calibration of the magnetic compass of a migratory bird by celestial rotation. *Nature*, *347*, 378–380.

Adámková, J., Benediktová, K., Svoboda, J., Bartoš, L., Vynikalová, L., Nováková, P., Hart, V., Painter, M. S., & Burda, H. (2021). Turning preference in dogs: North attracts while south repels. *PLOS ONE*, *16*(1), e0245940. https://doi.org/10.1371/journal.pone.0245940

Adámková, J., Svoboda, J., Benediktová, K., Martini, S., Nováková, P., Tůma, D., Kučerová, M., Divišová, M., Begall, S., Hart, V., & Burda, H. (2017). Directional preference in dogs: Laterality and "pull of the north." *PLOS ONE*, *12*(9), e0185243. https://doi.org/10.1371/journal.pone.0185243

Åkesson, S. (2003). Avian Long-Distance Navigation: Experiments with Migratory Birds. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 471–492). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-05957-9_33

Andersen, G. E., McGregor, H. W., Johnson, C. N., & Jones, M. E. (2020). Activity and social interactions in a wide-ranging specialist scavenger, the Tasmanian devil (*Sarcophilus harrisii*), revealed by animal-borne video collars. *PLOS ONE*, *15*(3), e0230216. https://doi.org/10.1371/journal.pone.0230216

August, P. V, Ayvazian, S. G., & Anderson, J. G. T. (1989). Magnetic orientation in a small mammal, *Peromyscus leucopus*. *Journal of Mammalogy*, *70*(1), 1–9. https://doi.org/10.2307/1381663

Batsleer, F., Bonte, D., Dekeukeleire, D., Goossens, S., Poelmans, W., Van der Cruyssen, E., Maes, D., & Vandegehuchte, M. L. (2020). The neglected impact of tracking devices on terrestrial arthropods. *Methods in Ecology and Evolution*, *11*(3), 350–361. https://doi.org/10.1111/2041-210X.13356

Begall, S., Burda, H., Červený, J., Gerter, O., Neef-Weisse, J., & Němec, P. (2011). Further support for the alignment of cattle along magnetic field lines: reply to Hert et al. *Journal of Comparative Physiology A, 197*(12), 1127–1133. https://doi.org/10.1007/s00359-011-0674-1

Begall, S., Burda, H., & Malkemper, E. P. (2014). Magnetoreception in Mammals. *Advances in the Study of Behavior*, *46*, 45–88. https://doi.org/10.1016/B978-0-12-800286-5.00002-X

Begall, S., Cerveny, J., Neef, J., Vojtech, O., & Burda, H. (2008). Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Academy of Sciences*, *105*(36), 13451–13455. https://doi.org/10.1073/pnas.0803650105

Begall, S., Malkemper, E. P., Červený, J., Němec, P., & Burda, H. (2013). Magnetic alignment in mammals and other animals. *Mammalian Biology*, *78*(1), 10–20. https://doi.org/10.1016/j.mambio.2012.05.005

Bell, W. J., & Bell, W. J. (1990). When to return to a resource patch. In *Searching Behaviour* (pp. 117–129). Springer Netherlands. https://doi.org/10.1007/978-94-011-3098-1_9

Benediktová, K., Adámková, J., Svoboda, J., Painter, M. S., Bartoš, L., Nováková, P., Vynikalová, L., Hart, V., Phillips, J., & Burda, H. (2020). Magnetic alignment enhances homing efficiency of hunting dogs. *ELife, 9*. https://doi.org/10.7554/eLife.55080

Benhamou, S. (2014). Path integration and coordinate systems. *Journal of Theoretical Biology, 349*, 163–166. https://doi.org/10.1016/j.jtbi.2014.02.012

Bombara, C. B., Dürr, S., Machovsky-Capuska, G. E., Jones, P. W., & Ward, M. P. (2017). A preliminary study to estimate contact rates between free-roaming domestic dogs using novel miniature cameras. *PLoS ONE, 12*(7). https://doi.org/10.1371/journal.pone.0181859

Bräuer, J., & Blasi, D. (2021). Dogs display owner-specific expectations based on olfaction. *Scientific Reports, 11*(1), 3291. https://doi.org/10.1038/s41598-021-82952-4

Burda, H., Begall, S., Hart, V., Malkemper, E. P., Painter, M. S., & Phillips, J. B. (2020). Magnetoreception in Mammals. In B. Fritzsch (Ed.), *The Senses: A Comprehensive*

Reference (II., pp. 421–444). Elsevier. https://doi.org/10.1016/b978-0-12-809324-5.24131-x

Burda, H., Marhold, S., Westenberger, T., Wiltschko, R., & Wiltschko, W. (1990). Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae). *Experientia*, *46*(5), 528–530. https://doi.org/10.1007/BF01954256

Byosiere, S. E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2018). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin and Review*, *25*(5), 1798–1813. https://doi.org/10.3758/s13423-017-1404-7

Byosiere, S. E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2019). The effects of physical luminance on colour discrimination in dogs: A cautionary tale. *Applied Animal Behaviour Science*, *212*(December 2018), 58–65. https://doi.org/10.1016/j.applanim.2019.01.004

Červený, J., Begall, S., Koubek, P., Nováková, P., & Burda, H. (2011). Directional preference may enhance hunting accuracy in foraging foxes. *Biology Letters*, *7*(3), 355–357. https://doi.org/10.1098/rsbl.2010.1145

Červený, J., Burda, H., Ježek, M., Kušta, T., Husinec, V., Nováková, P., Hart, V., Hartová, V., Begall, S., & Malkemper, E. P. (2017). Magnetic alignment in warthogs *Phacochoerus africanus* and wild boars *Sus scrofa*. *Mammal Review*, *47*(1), 1–5. https://doi.org/10.1111/mam.12077

Chernetsov, N. (2017). Compass systems. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *203*(6–7), 447–453. https://doi.org/10.1007/s00359-016-1140-x

Cheung, A., Zhang, S., Stricker, C., & Srinivasan, M. V. (2007). Animal navigation: The difficulty of moving in a straight line. *Biological Cybernetics*, *97*(1), 47–61. https://doi.org/10.1007/s00422-007-0158-0

Cheung, A., Zhang, S., Stricker, C., & Srinivasan, M. V. (2008). Animal navigation: General properties of directed walks. *Biological Cybernetics*, *99*(3), 197–217. https://doi.org/10.1007/s00422-008-0251-z

Christiansen, P., Steen, K., Jørgensen, R., & Karstoft, H. (2014). Automated Detection and Recognition of Wildlife Using Thermal Cameras. *Sensors*, *14*(8), 13778–13793. https://doi.org/10.3390/s140813778

Cochran, W. W., Mouritsen, H., & Wikelski, M. (2004). Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues. *Science*, *304*(5669), 405–408. https://doi.org/10.1126/science.1095844

Cole, L. K. (2009). Anatomy and physiology of the canine ear. *Veterinary Dermatology*, *20*(5–6), 412–421. https://doi.org/10.1111/j.1365-3164.2009.00849.x

Cooper, J. J., Ashton, C., Bishop, S., West, R., Mills, D. S., & Young, R. J. (2003). Clever hounds: Social cognition in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, *81*(3), 229–244. https://doi.org/10.1016/S0168-1591(02)00284-8

Coughlin, C. E., & van Heezik, Y. (2014). Weighed down by science: do collar-mounted devices affect domestic cat behaviour and movement? *Wildlife Research*, *41*(7), 606. https://doi.org/10.1071/WR14160

Craven, B. A., Paterson, E. G., & Settles, G. S. (2010). The fluid dynamics of canine olfaction: unique nasal airflow patterns as an explanation of macrosmia. *Journal of The Royal Society Interface*, *7*(47), 933–943. https://doi.org/10.1098/rsif.2009.0490

Cullen, K. E., & Taube, J. S. (2017). Our sense of direction: Progress, controversies and challenges. *Nature Neuroscience*, *20*(11), 1465–1473. https://doi.org/10.1038/nn.4658

Davidson, S. C., Bohrer, G., Gurarie, E., LaPoint, S., Mahoney, P. J., Boelman, N. T., Eitel, J. U. H., Prugh, L. R., Vierling, L. A., Jennewein, J., Grier, E., Couriot, O., Kelly, A. P., Meddens, A. J. H., Oliver, R. Y., Kays, R., Wikelski, M., Aarvak, T., Ackerman, J. T., … Hebblewhite, M. (2020). Ecological insights from three decades of animal movement tracking across a changing Arctic. *Science*, *370*(6517), 712–715. https://doi.org/10.1126/science.abb7080

Dielenberg, R. A., Halasz, P., & Day, T. A. (2006). A method for tracking rats in a complex and completely dark environment using computerized video analysis.

Journal of Neuroscience Methods, *158*(2), 279–286. https://doi.org/10.1016/j.jneumeth.2006.05.024

Dupret, D., & Csicsvari, J. (2014). Turning heads to remember places. *Nature Neuroscience*, *17*(5), 643–644. https://doi.org/10.1038/nn.3700

Etienne, A S, Maurer, R., Seguinot, V., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *J Exp Biol*, *199*(Pt 1), 201–209. https://doi.org/print

Etienne, Ariane S, & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus*, *14*(2), 180–192. https://doi.org/10.1002/hipo.10173

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*(10), 1316–1329. https://doi.org/10.1111/ele.12165

Finkelstein, A., Las, L., & Ulanovsky, N. (2016). 3-D Maps and Compasses in the Brain. *Annual Review of Neuroscience*, *39*(1), 171–196. https://doi.org/10.1146/annurev-neuro-070815-013831

Fiset, S. (2007). Landmark-based search memory in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology*, *121*(4), 345–353. https://doi.org/10.1037/0735-7036.121.4.345

Fiset, S. (2009). Evidence for averaging of distance from landmarks in the domestic dog. *Behavioural Processes*, *81*(3), 429–438. https://doi.org/10.1016/j.beproc.2009.03.016

Freake, M. J., Muheim, R., & Phillips, J. B. (2006). Magnetic Maps in Animals: A Theory Comes of Age? *The Quarterly Review of Biology*, *81*(4), 327–347. https://doi.org/10.1086/511528

Frost, B. J., & Mouritsen, H. (2006). The neural mechanisms of long distance animal navigation. *Current Opinion in Neurobiology*, *16*(4), 481–488. https://doi.org/10.1016/j.conb.2006.06.005

Gallistel, C. R. (1990). *The organization of learning. Learning, development, and conceptual change.* (Issue 1990). The MIT Press. https://psycnet.apa.org/record/1990-98569-000

Gauthreaux, S. A. J. (1980). *Animal Migration, Orientation, and Navigation: Vol. II* (J. Gauthreaux, Sidney A. (Ed.); II.). Academic Press, Inc.

Geldenhuys, W. J., Guseman, T. L., Pienaar, I. S., Dluzen, D. E., & Young, J. W. (2015). A novel biomechanical analysis of gait changes in the MPTP mouse model of Parkinson's disease. *PeerJ*, *3*(8), e1175. https://doi.org/10.7717/peerj.1175

Gerencsér, L., Vásárhelyi, G., Nagy, M., Vicsek, T., & Miklósi, A. (2013). Identification of Behaviour in Freely Moving Dogs (*Canis familiaris*) Using Inertial Sensors. *PLoS ONE*, *8*(10), e77814. https://doi.org/10.1371/journal.pone.0077814

Gould, J. L. (2004). Animal Navigation: A Novel Map Strategy. *Current Biology*, *27*(17), R833–R834. https://doi.org/10.1016/j.cub.2004.02.049

Gould, J. L. (2014). Animal navigation: A map for all seasons. *Current Biology*, *24*(4), R153–R155. https://doi.org/10.1016/j.cub.2014.01.030

Gould, J. L., & Gould, C. G. (2012). *Nature's Compass*. Princeton University Press. http://www.jstor.org/stable/j.ctt7sxp6

Greif, S., Borissov, I., Yovel, Y., & Holland, R. A. (2014). A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. *Nature Communications*, *5*(1), 4488. https://doi.org/10.1038/ncomms5488

Griffin, D. R. (1952). Bird navigation. *Biological Reviews*, *27*(4), 359–390. https://doi.org/10.1111/j.1469-185X.1952.tb01509.x

Guilford, T., & Taylor, G. K. (2014). The sun compass revisited. *Animal Behaviour*, *97*, 135–143. https://doi.org/10.1016/j.anbehav.2014.09.005

Hafting, T., Fyhn, M., Molden, S., Moser, M., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801–806. https://doi.org/10.1038/nature03721

Harootonian, S. K., Wilson, R. C., Hejtmánek, L., Ziskin, E. M., & Ekstrom, A. D. (2020).

Path integration in large-scale space and with novel geometries: Comparing vector addition and encoding-error models. *PLoS Computational Biology*, *16*(5), 1–27. https://doi.org/10.1371/journal.pcbi.1007489

Hart, V., Nováková, P., Malkemper, E., Begall, S., Hanzal, V., Ježek, M., Kušta, T., Němcová, V., Adámková, J., Benediktová, K., Červený, J., & Burda, H. (2013). Dogs are sensitive to small variations of the Earth's magnetic field. *Frontiers in Zoology*, *10*(1), 80. https://doi.org/10.1186/1742-9994-10-80

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, *369*(6500), 194–197. https://doi.org/10.1126/science.aay3354

Hartley, T., Lever, C., Burgess, N., & O'Keefe, J. (2014). Space in the brain: How the hippocampal formation supports spatial cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1635). https://doi.org/10.1098/rstb.2012.0510

Heffner, H. E. (1983). Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. *Behavioral Neuroscience*, *97*(2), 310–318. https://doi.org/10.1037/0735-7044.97.2.310

Hepper, P. G., & Wells, D. L. (2005). How Many Footsteps Do Dogs Need to Determine the Direction of an Odour Trail? *Chemical Senses*, *30*(4), 291–298. https://doi.org/10.1093/chemse/bji023

Holland, R. A. (2018). *Orientation, Navigation and Homing in Bats*. *6*, 84–89.

Hore, P. J., & Mouritsen, H. (2016). The Radical-Pair Mechanism of Magnetoreception. *Annual Review of Biophysics*, *45*(1), 299–344. https://doi.org/10.1146/annurev-biophys-032116-094545

Huck, M., & Watson, S. (2019). The use of animal-borne cameras to video-track the behaviour of domestic cats. *Applied Animal Behaviour Science*, *217*(February), 63–72. https://doi.org/10.1016/j.applanim.2019.04.016

Inayat, S., Singh, S., Ghasroddashti, A., Qandeel, Q., Egodage, P., Whishaw, I. Q., & Mohajerani, M. H. (2020). A Matlab-based toolbox for characterizing behavior of rodents engaged in string-pulling. *ELife*, *9*, 1–31. https://doi.org/10.7554/elife.54540

Jacobs, H. G., Deegan, F. J., Crognale, A. M., & Fenwick, A. J. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience*, *10*(1), 173–180. https://doi.org/10.1017/S0952523800003291

Jacobs, L. F., & Menzel, R. (2014). Navigation outside of the box: what the lab can learn from the field and what the field can learn from the lab. *Movement Ecology*, *2*(1), 3. https://doi.org/10.1186/2051-3933-2-3

Johnsen, S. (2017). Open Questions: We don't really know anything, do we? Open questions in sensory biology. *BMC Biology*, *15*(1), 43. https://doi.org/10.1186/s12915-017-0385-3

Johnsen, S., & Lohmann, K. J. (2008). Magnetoreception in animals. *Physics Today*, *61*(3), 29–35. https://doi.org/10.1063/1.2897947

Juszczak, G. R., & Miller, M. (2016). Detour Behavior of Mice Trained with Transparent, Semitransparent and Opaque Barriers. *PLOS ONE*, *11*(9), e0162018. https://doi.org/10.1371/journal.pone.0162018

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kimchi, T., Etienne, A. S., & Terkel, J. (2004). A subterranean mammal uses the magnetic compass for path integration. *Proceedings of the National Academy of Sciences*, *101*(4), 1105–1109. https://doi.org/10.1073/pnas.0307560100

Kobylkov, D. (2020). Transduction Mechanisms in Magnetoreception. In *The Senses: A Comprehensive Reference* (pp. 459–478). Elsevier. https://doi.org/10.1016/b978-0-12-805408-6.00004-x

Kölzsch, A., Flack, A., Müskens, G. J. D. M., Kruckenberg, H., Glazov, P., & Wikelski, M. (2020). Goose parents lead migration V. *Journal of Avian Biology*, *51*(3), jav.02392. https://doi.org/10.1111/jav.02392

Kovács, V., Újváry, D., & Szemethy, L. (2017). Availability of camera trapping for behavioural analysis: An example with wild boar (*Sus scrofa*). *Applied Animal Behaviour Science, 195* (May), 112–114. https://doi.org/10.1016/j.applanim.2017.05.019

Kral, K. (2003). Behavioural-analytical studies of the role of head movements in depth perception in insects, birds and mammals. *Behavioural Processes*, *64*(1), 1–12. https://doi.org/10.1016/S0376-6357(03)00054-8

Kutilek, P., Benediktova, K., Svoboda, J., Volf, P., Adamkova, J., Krivanek, V., Hejda, J., Kutilkova, E., & de Brito, A. C. D. M. (2018). Processing Methods of Camera Record of Animal Movement. *2018 18th International Conference on Mechatronics - Mechatronika (ME)*, 1–5. https://doi.org/ISBN: 978-1-5386-4364-8

Lawes, T. J., Anthony, R. G., Robinson, W. D., Forbes, J. T., & Lorton, G. A. (2012). Homing Behavior and Survival of Pygmy Rabbits After Experimental Translocation. *Western North American Naturalist*, *72*(4), 569–581. https://doi.org/10.3398/064.072.0418

Lind, O., Milton, I., Andersson, E., Jensen, P., & Roth, L. S. V. (2017). High visual acuity revealed in dogs. *PLoS ONE*, *12*(12), e0188557. https://doi.org/10.1371/journal.pone.0188557

Lohmann, K. J., Lohmann, C. M. F., & Putman, N. F. (2007). Magnetic maps in animals: nature’s GPS. *Journal of Experimental Biology*, *210*(Pt 21), 3697–3705. https://doi.org/10.1242/jeb.001313

Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J., & Marshall, G. J. (2013). Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation*, *160*, 183–189. https://doi.org/10.1016/j.biocon.2013.01.008

Lush, L., Ellwood, S., Markham, A., Ward, A. I., & Wheeler, P. (2016). Use of tri-axial accelerometers to assess terrestrial mammal behaviour in the wild. *Journal of Zoology*, *298*(4), 257–265. https://doi.org/10.1111/jzo.12308

Malewski, S., Begall, S., & Burda, H. (2018). Learned and spontaneous magnetosensitive behaviour in the Roborovski hamster (*Phodopus roborovskii*). *Ethology*, *124*(6), 423–431. https://doi.org/10.1111/eth.12744

Malewski, S., Begall, S., Schleich, E. C., Antenucci, C. D., & Burda, H. (2018). Do subterranean mammals use the Earth’s magnetic field as a heading indicator to dig straight tunnels? *PeerJ*, *6*, e5819. https://doi.org/10.7717/peerj.5819

Malkemper, E. P., Eder, S. H. K., Begall, S., Phillips, J. B., Winklhofer, M., Hart, V., & Burda, H. (2015). Magnetoreception in the wood mouse (*Apodemus sylvaticus*): influence of weak frequency-modulated radio frequency fields. *Scientific Reports*, *4*, 9917. https://doi.org/10.1038/srep09917

Malkemper, E. P., Mason, M. J., & Burda, H. (2020). Functional anatomy of the middle and inner ears of the red fox, in comparison to domestic dogs and cats. *Journal of Anatomy*, *January*, joa.13159. https://doi.org/10.1111/joa.13159

Marshall, J., & Cronin, T. W. (2011). Polarisation vision. *Current Biology*, *21*(3), R101–R105. https://doi.org/10.1016/j.cub.2010.12.012

Martini, S., Begall, S., Findeklee, T., Schmitt, M., Malkemper, E. P., & Burda, H. (2018). Dogs can be trained to find a bar magnet. *PeerJ*, *6*, e6117. https://doi.org/10.7717/peerj.6117

Mayes, E.-R. E., Wilkinson, A., Pike, T. W., & Mills, D. S. (2015). Individual differences in visual and olfactory cue preference and use by cats (*Felis catus*). *Applied Animal Behaviour Science*, *173*, 52–59. https://doi.org/10.1016/j.applanim.2015.01.003

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M.-B. (2006). Path integration and the neural basis of the “cognitive map.” *Nature Reviews Neuroscience*, *7*(8), 663–678. https://doi.org/10.1038/nrn1932

Miklósi, Á. (2014). Dog Behaviour, Evolution, and Cognition. In *Dog Behaviour, Evolution, and Cognition* (2.). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199646661.001.0001

Miklósi, Á. (2018). *The dog : a natural history*. Princeton University Press. https://press.princeton.edu/titles/11288.html

Miller, P. E., & Murphy, C. J. (1995). Vision in dogs. *Journal of the American Veterinary Medical Association*, *207*(12), 1623–1634.

Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology & Evolution*, *22*(12), 660–668. https://doi.org/10.1016/j.tree.2007.09.007

Monaco, J. D., Rao, G., Roth, E. D., & Knierim, J. J. (2014). Attentive scanning behavior drives one-trial potentiation of hippocampal place fields. *Nature Neuroscience*, *17*(5), 725–731. https://doi.org/10.1038/nn.3687

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature*, *558*(7708), 50–59. https://doi.org/10.1038/s41586-018-0176-1

Mouritsen, H., Feenders, G., Liedvogel, M., & Kropp, W. (2004). Migratory birds use head scans to detect the direction of the earth's magnetic field. *Current Biology*, *14*(21), 1946–1949. https://doi.org/10.1016/j.cub.2004.10.025

Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments - From individual behaviors to population distributions. *Oikos*, *117*(5), 654–664. https://doi.org/10.1111/j.0030-1299.2008.16291.x

Muheim, R., Phillips, J. B., & Akesson, S. (2006). Polarized light cues underlie compass calibration in migratory songbirds - Supporting Online Material. *Science*, *313*(5788), 837. https://doi.org/10.1126/science.1129709

Nahm, M. (2015). Mysterious Ways : the Riddle of the Homing Ability. *Journal of the Society for Psychical Research*, *79*(920), 140–155.

Napolitano, F., De Rosa, G., Serrapica, M., & Braghieri, A. (2015). A continuous recording approach to qualitative behaviour assessment in dairy buffaloes (*Bubalus bubalis*). *Applied Animal Behaviour Science*, *166*(1), 35–43. https://doi.org/10.1016/j.applanim.2015.01.017

Natan, E., Fitak, R. R., Werber, Y., & Vortman, Y. (2020). Symbiotic magnetic sensing: raising evidence and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1808), 20190595. https://doi.org/10.1098/rstb.2019.0595

Natan, E., & Vortman, Y. (2017). The symbiotic magnetic-sensing hypothesis: do Magnetotactic Bacteria underlie the magnetic sensing capability of animals? *Movement Ecology*, *5*(1), 22. https://doi.org/10.1186/s40462-017-0113-1

Neitz, J., Carroll, J., & Neitz, M. (2001). Color Vision: Almost Reason Enough for Having Eyes. *Optics and Photonics News*, *12*(1), 26. https://doi.org/10.1364/OPN.12.1.000026

Němec, P., & Vácha, M. (2007). Mechanismy magnetorecepce - Jak živočichové vnímají geomagnetické pole Země. *Vesmír*, 284–289. https://vesmir.cz/cz/casopis/archiv-casopisu/2007/cislo-5/mechanismy-magnetorecepce.html

Nießner, C., Denzau, S., Malkemper, E. P., Gross, J. C., Burda, H., Winklhofer, M., & Peichl, L. (2016). Cryptochrome 1 in Retinal Cone Photoreceptors Suggests a Novel Functional Role in Mammals. *Scientific Reports*, *6*(1), 21848. https://doi.org/10.1038/srep21848

Nimpf, S., Nordmann, G. C., Kagerbauer, D., Malkemper, E. P., Landler, L., Papadaki-Anastasopoulou, A., Ushakova, L., Wenninger-Weinzierl, A., Novatchkova, M., Vincent, P., Lendl, T., Colombini, M., Mason, M. J., & Keays, D. A. (2019). A Putative Mechanism for Magnetoreception by Electromagnetic Induction in the Pigeon Inner Ear. *Current Biology*, *29*(23), 4052-4059.e4. https://doi.org/10.1016/j.cub.2019.09.048

O´Keefe, J., & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford University Press. https://doi.org/10.5840/philstudies19802725

Oliveriusová, L., Němec, P., Pavelková, Z., & Sedláček, F. (2014). Spontaneous expression of magnetic compass orientation in an epigeic rodent: The bank vole, *Clethrionomys glareolus*. *Naturwissenschaften*, *101*(7), 557–563. https://doi.org/10.1007/s00114-014-1192-0

Painter, M. S., Blanco, J. A., Malkemper, E. P., Anderson, C., Sweeney, D. C., Hewgley, C. W., Červený, J., Hart, V., Topinka, V., Belotti, E., Burda, H., & Phillips, J. B. (2016). Use of bio-loggers to characterize red fox behavior with implications for studies of magnetic alignment responses in free-roaming animals. *Animal*

Biotelemetry, *4*(1), 20. https://doi.org/10.1186/s40317-016-0113-8

Papi, F. (1992). *Animal Homing*. Springer Netherlands.

Pašukonis, A., Loretto, M.-C., & Hödl, W. (2018). Map-like navigation from distances exceeding routine movements in the three-striped poison frog (*Ameerega trivittata*). *The Journal of Experimental Biology*, *221*(2), jeb169714. https://doi.org/10.1242/jeb.169714

Peters, R. (1978). Communication, Cognitive Mapping, and Strategy in Wolves and Hominids. In *Wolf and Man* (pp. 95–107). Elsevier. https://doi.org/10.1016/B978-0-12-319250-9.50013-X

Peters, R. P., & Mech, L. D. (1975). Behavioral and Intellectual Adaptations of Selected Mammalian Predators to the Problem of Hunting Large Animals. In *Socioecology and Psychology of Primates* (pp. 279–300). De Gruyter Mouton. https://doi.org/10.1515/9783110803839.279

Phillips, J. B., Muheim, R., & Jorge, P. E. (2010). A behavioral perspective on the biophysics of the light-dependent magnetic compass: a link between directional and spatial perception? *Journal of Experimental Biology*, *213*(19), 3247–3255. https://doi.org/10.1242/jeb.020792

Phillips, John B., Youmans, P. W., Muheim, R., Sloan, K. A., Landler, L., Painter, M. S., & Anderson, C. R. (2013). Rapid Learning of Magnetic Compass Direction by C57BL/6 Mice in a 4-Armed “Plus” Water Maze. *PLoS ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0073112

Polgár, Z., Miklósi, Á., & Gácsi, M. (2015). Strategies Used by Pet Dogs for Solving Olfaction-Based Problems at Various Distances. *PLOS ONE*, *10*(7), e0131610. https://doi.org/10.1371/journal.pone.0131610

Pongrácz, P., Ujvári, V., Faragó, T., Miklósi, Á., & Péter, A. (2017). Do you see what I see? The difference between dog and human visual perception may affect the outcome of experiments. *Behavioural Processes*, *140*(November 2016), 53–60. https://doi.org/10.1016/j.beproc.2017.04.002

Poulter, S., Hartley, T., & Lever, C. (2018). The Neurobiology of Mammalian

Navigation. *Current Biology*, *28*(17), R1023–R1042. https://doi.org/10.1016/j.cub.2018.05.050

Pretterer, G., Bubna-Littitz, H., Windischbauer, G., Gabler, C., & Griebel, U. (2004). Brightness discrimination in the dog. *Journal of Vision*, *4*(3), 10. https://doi.org/10.1167/4.3.10

Ramazani, R. B., Krishnan, H. R., Bergeson, S. E., & Atkinson, N. S. (2007). Computer automated movement detection for the analysis of behavior. *Journal of Neuroscience Methods*, *162*(1–2), 171–179. https://doi.org/10.1016/j.jneumeth.2007.01.005

Redish, A. D. (2016). Vicarious trial and error. *Nat Rev Neurosci*, *17*(3), 147–159. https://doi.org/10.1038/nrn.2015.30

Richardson, E. H. (1920). *British war dogs, their training and psychology, by Lt. Colonel E. H. Richardson ...* Skeffington & son, Ltd. https://doi.org/10.5962/bhl.title.26715

Ritz, T., Ahmad, M., Mouritsen, H., Wiltschko, R., & Wiltschko, W. (2010). Photoreceptor-based magnetoreception: optimal design of receptor molecules, cells, and neuronal processing. *Journal of The Royal Society Interface*, *7*(suppl_2). https://doi.org/10.1098/rsif.2009.0456.focus

Rosa, C. A. (2019). An inexpensive and open-source method to study large terrestrial animal diet and behaviour using time-lapse video and GPS. *Methods in Ecology and Evolution*, *10*(5), 615–625. https://doi.org/10.1111/2041-210X.13146

Rutz, C., Bluff, L. A., Weir, A. A. S., & Kacelnik, A. (2007). Video Cameras on Wild Birds. *Science*, *318*(5851), 765–765. https://doi.org/10.1126/science.1146788

Samson, A. L., Ju, L., Kim, H. A., Zhang, S. R., Lee, J. A. A., Sturgeon, S. A., Sobey, C. G., Jackson, S. P., & Schoenwaelder, S. M. (2015). MouseMove: An open source program for semi-automated analysis of movement and cognitive testing in rodents. *Scientific Reports*, *5*(November). https://doi.org/10.1038/srep16171

Samson, J., & Manser, M. B. (2016). Use of the sun as a heading indicator when caching and recovering in a wild rodent. *Scientific Reports*, *6*(1), 32570. https://doi.org/10.1038/srep32570

Samuel, L., Arnesen, C., Zedrosser, A., & Rosell, F. (2020). Fears from the past? The innate ability of dogs to detect predator scents. *Animal Cognition*, *23*(4), 721–729. https://doi.org/10.1007/s10071-020-01379-y

Santos-Pata, D., & Verschure, P. F. M. J. (2018). Human vicarious trial and error is predictive of spatial navigation performance. *Frontiers in Behavioral Neuroscience, 12*. https://doi.org/10.3389/fnbeh.2018.00237

Schmidt-Koenig, K., & Keeton, W. T. (Eds.). (1978). *Animal Migration, Navigation, and Homing*. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-11147-5

Schöne, H. (1984). Orientation: Its Meaning and Scope. In *Spatial Orientation: The Spatial Control of Behavior in Animals and Man* (pp. 3–16). Princeton University Press. https://doi.org/10.2307/j.ctt7zv25m.6

Séguinot, V., Cattet, J., & Benhamou, S. (1998). Path integration in dogs. *Animal Behaviour, 55*(4), 787–797. https://doi.org/10.1006/anbe.1997.0662

Serpel, J. (2017). the Domestic Dog. In *Cambridge University Press* (Vol. 31). https://doi.org/10.1017/9781139161800

Seymour, C. L., Simmons, R. E., Morling, F., George, S. T., Peters, K., & O'Riain, M. J. (2020). Caught on camera: The impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. *Global Ecology and Conservation, 23*, e01198. https://doi.org/10.1016/j.gecco.2020.e01198

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). Oxford University Press. https://books.google.cz/books/about/Cognition_Evolution_and_Behavior.html?id=-Qs1qGys0AwC&redir_esc=y

Shiomi, K., Sato, K., Katsumata, N., & Yoda, K. (2019). Temporal and spatial determinants of route selection in homing seabirds. *Behaviour, 156*(11), 1165–1183. https://doi.org/10.1163/1568539x-00003560

Siniscalchi, M., D'Ingeo, S., Fornelli, S., & Quaranta, A. (2017). Are dogs red–green colour blind? *Royal Society Open Science, 4*(11), 170869. https://doi.org/10.1098/rsos.170869

Slaby, P., Tomanova, K., & Vacha, M. (2013). Cattle on pastures do align along the North-South axis, but the alignment depends on herd density. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 199*(8), 695–701. https://doi.org/10.1007/s00359-013-0827-5

Solstad, T., Boccara, C. N., Kropff, E., Moser, M. B., & Moser, E. I. (2008). Representation of Geometric Borders in the Entorhinal Cortex. *Science*, *1109*(2005), 17–20. https://doi.org/10.1126/science.1166466

Spiegel, O., & Crofoot, M. C. (2016). The feedback between where we go and what we know — information shapes movement, but movement also impacts information acquisition. *Current Opinion in Behavioral Sciences*, *12*, 90–96. https://doi.org/10.1016/j.cobeha.2016.09.009

Szetei, V., Miklósi, Á., Topál, J., & Csányi, V. (2003). When dogs seem to lose their nose: An investigation on the use of visual and olfactory cues in communicative context between dog and owner. *Applied Animal Behaviour Science, 83*(2), 141–152. https://doi.org/10.1016/S0168-1591(03)00114-X

Thompson, S. M., Berkowitz, L. E., & Clark, B. J. (2018). Behavioral and neural subsystems of rodent exploration. *Learning and Motivation*, *61*(March 2017), 3–15. https://doi.org/10.1016/j.lmot.2017.03.009

Thorup, K., & Holland, R. A. (2009). The bird GPS - long-range navigation in migrants. *Journal of Experimental Biology*, *212*(22), 3597–3604. https://doi.org/10.1242/jeb.021238

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map-based navigation in wild bats revealed by a new high-throughput wildlife tracking system. *Science*, *193*(July), 188–193.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*(4), 189–208. https://doi.org/10.1037/h0061626

Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience & Biobehavioral Reviews*, *36*(2), 799–824. https://doi.org/10.1016/j.neubiorev.2011.12.007

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences, 108*(37), E718–E724. https://doi.org/10.1073/pnas.1107365108

Tsoar, Asaf, Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G., & Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proceedings of the National Academy of Sciences, 108*(37), E718–E724. https://doi.org/10.1073/pnas.1107365108

Veselovský, Z. (2008). *Etologie: Biologie chování zvířat* (2.). Academia.

Wallraff, H. G. (1978). Preferred compass directions in initial orientation of homing pigeons. In Schmidt-Koenig K. Keeton W.T. (Ed.), *Animal Migration, Navigation, and Homing. Proceedings in Life Sciences.* (pp. 171–183). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-11147-5_16

Walton, R. L., Cluff, H. D., Paquet, C. P., & Ramsay, A. M. (2001). Movement patterns of barren-ground wolves in the central canadian arctic. *Journal of Mammalogy, 82*(3), 867. https://doi.org/10.1644/1545-1542(2001)082<0867:MPOBGW>2.0.CO;2

Walton, Z., Samelius, G., Odden, M., & Willebrand, T. (2018). Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking. *European Journal of Wildlife Research, 64*(6), 64. https://doi.org/10.1007/s10344-018-1223-9

Weir, E. (2020). Animals and the Ability to Sense Magnetic Fields. *Journal of Agricultural and Food Information, 0*(0), 1–5. https://doi.org/10.1080/10496505.2020.1801125

Wells, D. L., & Hepper, P. G. (2003). Directional tracking in the domestic dog, *Canis familiaris*. *Applied Animal Behaviour Science, 84*(4), 297–305. https://doi.org/10.1016/j.applanim.2003.08.009

Whishaw, I. Q., Hines, D. J., & Wallace, D. G. (2001). Dead reckoning (path integration) requires the hippocampal formation: evidence from spontaneous exploration and spatial learning tasks in light (allothetic) and dark (idiothetic) tests. *Behavioural Brain Research, 127*(1–2), 49–69. https://doi.org/10.1016/S0166-4328(01)00359-X

Wiltschko, R., & Wiltschko, W. (1985). Pigeon homing: Does initial orientation include a “preferred compass direction”? *Journal of Comparative Physiology A*, *157*(4), 469–476. https://doi.org/10.1130/G33000.1

Wiltschko, R., & Wiltschko, W. (1995). Magnetic Orientation in Animals. In *Magnetic Orienation in Animals* (Vol. 33). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-79749-1

Wiltschko, R., & Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. *Animal Behaviour*, *65*(2), 257–272. https://doi.org/10.1006/anbe.2003.2054

Wiltschko, W., & Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 191*(8), 675–693. https://doi.org/10.1007/s00359-005-0627-7

Wolbers, T., & Wiener, J. M. (2014). Challenges for identifying the neural mechanisms that support spatial navigation: the impact of spatial scale. *Frontiers in Human Neuroscience*, *8*(August), 1–12. https://doi.org/10.3389/fnhum.2014.00571

Yamaue, Y., Hosaka, Y. Z., & Uehara, M. (2015). Spatial relationships among the cellular tapetum, visual streak and rod density in dogs. *Journal of Veterinary Medical Science*, *77*(2), 175–179. https://doi.org/10.1292/jvms.14-0447

Yoda, K. (2019). Advances in bio-logging techniques and their application to study navigation in wild seabirds. *Advanced Robotics*, *33*(3–4), 108–117. https://doi.org/10.1080/01691864.2018.1553686

Yosef, R., Raz, M., Ben-Baruch, N., Shmueli, L., Kosicki, J. Z., Fratczak, M., & Tryjanowski, P. (2020). Directional preferences of dogs’ changes in the presence of a bar magnet: Educational experiments in Israel. *Journal of Veterinary Behavior*, *35*, 34–37. https://doi.org/10.1016/j.jveb.2019.10.003

Young, J. K., Touzot, L., & Brummer, S. P. (2019). Persistence and conspecific observations improve problem-solving abilities of coyotes. *PLOS ONE*, *14*(7), e0218778. https://doi.org/10.1371/journal.pone.0218778

Zhang, C., Li, H., & Han, R. (2020). An open-source video tracking system for mouse locomotor activity analysis. *BMC Research Notes*, *13*(1), 48. https://doi.org/10.1186/s13104-020-4916-6