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Methodological advances in identifying foraging strategies in cooperative and solitary canids

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Abstract

Modern animal-attached sensors allow high resolution measurement of animal movement on physiological as well as geographical scales. Measuring fine-scale movements of animals in this way, i.e., biologging, can unlock behavioural insights which would otherwise not be possible. However, analysis of the large, complex datasets gathered from such sensors can propose significant challenges. Here I outline methods for refining study design, data collection and analysis of movement datasets, while maintaining and quantifying animal welfare. This thesis begins with a review of how advances in biologging can improve our understanding of predation energetics, including outlining key future directions and knowledge gaps. One key recommendation revolves around a combined approach working on captive and wild datasets. As such, I then describe insights obtained from two systems, captive African wild dogs (*Lycaon pictus*) and wild red foxes (*Vulpes vulpes*). Tri-axial accelerometer and magnetometer data collected on captive African wild dogs were used to assess anaesthesia recovery, quantify activity patterns in relation to food received and reveal fine-scale space use through dead-reckoning. Moving to a wild system, I outline the difficulties encountered and refinements made in capturing and collaring wild red foxes. GPS, accelerometer and magnetometer data were then analysed to reveal the movement dynamics of urban foxes in Dublin, Ireland and behaviour classification rules are provided. A case study shows the promise of linking behaviour classification and the dead-reckoning path reconstruction method to further contextualise fox behaviour in the landscape. I conclude with a discussion on future directions following the work presented here and lessons for working on biologging datasets. Continued and larger-scale application of the methods presented here can provide important ecological insights into the foraging ecology of social and solitary canids under global change.

Chapter List

Detailed Table of Contents

Statement of original authorship

I hereby certify that the submitted work is my own work, was completed while registered as a candidate for the degree stated on the Title Page, and I have not obtained a degree elsewhere on the basis of the research presented in this submitted work.

Holly English

Statement of contributions

Chapter 1, the Introduction, and Chapter 6, the Discussion, were written by Holly English and reviewed by Simone Ciuti. Contributions for each core chapter are outlined below. Chapters 2 and 3 have been published in peer-reviewed journals, while chapters 4 and 5 are currently being prepared for submission.

Chapter 2

Holly M. English	% Contribution: 65 % Brief outline of contribution: Conceptualisation – lead, Figures – lead, Writing – original draft and editing.
Luca Börger	% Contribution: 10 % Brief outline of contribution: Supervision, Conceptualisation, Writing – reviewing.
Adam Kane	% Contribution: 10 % Brief outline of contribution: Conceptualisation, Writing – reviewing, Figures.
Simone Ciuti	% Contribution: 15 % Brief outline of contribution: Supervision – lead, Writing – reviewing.

Chapter 3

Holly M. English	% Contribution: 65 % Brief outline of contribution: Conceptualisation, Methodology, Data collection, Data analysis, Figures, Writing – original draft and editing.
Luke Harvey	% Contribution: 5 % Brief outline of contribution: Methodology, Data collection.
Rory P. Wilson	% Contribution: 5 % Brief outline of contribution: Conceptualisation, Writing – reviewing.
Richard M. Gunner	% Contribution: 5 % Brief outline of contribution: Methodology, Data analysis.
Mark D. Holton	% Contribution: 5 % Brief outline of contribution: Methodology.
Rosie Woodroffe	% Contribution: 5 % Brief outline of contribution: Conceptualisation, Methodology.
Luca Börger	% Contribution: 10 % Brief outline of contribution: Supervision, Conceptualisation, Methodology, Data analysis, Writing – reviewing.

Chapter 4

Holly M. English	% Contribution: 65 % Brief outline of contribution: Conceptualisation, Methodology, Data collection, Data analysis, Figures, Writing – original draft and editing.
Lorraine Bull	% Contribution: 5 % Brief outline of contribution: Conceptualisation, Methodology.
Barry Nolan	% Contribution: 5 % Brief outline of contribution: Data collection.
Paolo Bongi	% Contribution: 5 % Brief outline of contribution: Data collection.
Patricia Romero Marco	% Contribution: 5 % Brief outline of contribution: Methodology, Data collection, Veterinary care.
Vilhelmiina Huuskonen	% Contribution: 5 % Brief outline of contribution: Conceptualisation, Methodology.
Simone Ciuti	% Contribution: 10 % Brief outline of contribution: Supervision, Conceptualisation, Methodology, Data collection, Data analysis, Writing – reviewing.

Chapter 5

Holly M. English	% Contribution: 70 % Brief outline of contribution: Conceptualisation, Methodology, Data collection, Data analysis, Figures, Writing – original draft and editing.
Luca Börger	% Contribution: 10 % Brief outline of contribution: Supervision.
Simone Ciuti	% Contribution: 20 % Brief outline of contribution: Supervision – lead, Conceptualisation, Methodology, Data collection, Data analysis, Writing – reviewing.

List of publications

The following is a list of all papers published during the PhD timeframe, including those arising from external collaborations.

First author papers:

2024	**English HM,** Börger L, Kane A, Ciuti S. Advances in biologging can identify nuanced energetic costs and gains in predators. *Movement Ecology*.
2023	**English HM**, Harvey L, Wilson RP, Gunner RM, Holton MD, Woodroffe R, Börger L. Multi-sensor biologgers and innovative training allow data collection with high conservation and welfare value in zoos. *Journal of Zoo and Aquarium Research*.
2020	**English HM** & Caravaggi A. Where's wallaby? Using public records and media reports to describe the status of red-necked wallabies in Britain. *Ecology and Evolution*.

Co-authored papers:

2024	Conteddu K, **English HM**, Byrne AW, Amin B, Griffin LL, Kaur P, Morera Pujol V, Murphy KJ, Salter-Townshend M, Smith AF, Ciuti S. A scoping review on bovine tuberculosis highlights the need for novel data streams and analytical approaches to curb zoonotic diseases. *Veterinary Research*.

Mortlock E, **English HM**, Fitzsimmons J, Börger L, Jennings DJ, Capellini I. Early-life sleep in free-living fallow deer (*Dama dama*): the role of ontogeny, environment and individual differences. *Animal Behaviour*.

Raulo AMV, Buerkner P, Dale J, **English HM**, Finerty G, Lamberth C, Firth J, Coulson T, Knowles SCL. Social and environmental transmission spread different sets of gut microbes in wild mice. *Nature Ecology & Evolution*.

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2021 Caravaggi A, Amado TF, Brook RK, Ciuti S, Darimont CT, Drouilly M, **English HM**, Field KA, Iossa G, Martin JE, McElligott AG, Mohammadi A, Nayeri D, O'Neill HMK, Paquet PC, Périquet S, Proulx G, Rabaiotti D, Recio MR, Soulsbury CD, Tadich T, Wynn-Grant R. On the need for rigorous welfare and methodological reporting for the live capture of large carnivores: A response to de Araujo et al. *Methods in Ecology and Evolution*.

Gunner RM, Holton MD, Scantlebury MD, Hopkins P, Shepard ELC, Fell AJ, Garde B, Quintana F, Gómez-Laich A, Yoda K, Yamamoto T, **English HM**, Ferreira S, Govender D, Viljoen P, Bruns A, van Schalkwyk OL, Cole NC, Tatayah V, Börger L, Redcliffe J, Bell SH, Marks NJ, Bennett NC, Tonini MH, Williams HJ, Duarte CM, van Rooyen MC, Bertelsen MF, Tambling CJ, Wilson

RP. How often should dead-reckoned animal movement paths be corrected for drift? *Animal Biotelemetry*.

Gunner RM, Holton MD, Scantlebury MD, van Schalkwyk OL, **English HM**, Williams HJ, Hopkins P, Quintana F, Gómez-Laich A, Börger L, Redcliffe J, Yoda K, Yamamoto T, Ferreira S, Govender D, Viljoen P, Bruns A, Bell SH, Marks N, Bennett NC, Tonini MH, Duarte CM, van Rooyen MC, Bertelsen MF, Tambling CJ, Wilson RP. Dead-reckoning animal movements in R – a reappraisal using Gundog.Tracks. *Animal Biotelemetry*.

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‘"All right," said Deep Thought. "The Answer to the Great Question..."

"Yes..!"

"Of Life, the Universe and Everything..." said Deep Thought.

"Yes...!"

"Is..." said Deep Thought, and paused.

"Yes...!"

"Is..."

"Yes...!!!...?"

"Forty-two," said Deep Thought, with infinite majesty and calm. "’

— Douglas Adams, The Hitchhiker’s Guide to the Galaxy

* * *

‘Dentition: Most canids have forty-two teeth.’

— José R. Castelló, Canids of the World: Wolves, Wild Dogs, Foxes, Jackals, Coyotes and their Relatives

* * *

Perhaps the right question is what takes place between a canid’s teeth, and how it gets there?

Chapter 1 Introduction

The 21st century ethologist

The 1973 Nobel Prize for Medicine or Physiology was jointly awarded to Niko Tinbergen, Konrad Lorenz and Karl von Frisch, who went on to be known as the founding fathers of ethology, or animal behaviour (Burkhardt, 2005). Tinbergen shed new light on courtship and mating behaviour through his study of gulls (Tinbergen, 1960), Lorenz characterised imprinting in geese (Lorenz, 1935) and von Frisch described the waggle dance whereby bees direct fellow hive members to food patches (von Frisch, 1950). This was a significant milestone in zoology, which had been primarily concerned with cataloguing what animals there were, where they lived and how they might be related to each other. Now zoology could become a dynamic field that considered how animals interact with their environment and each other through time (Burkhardt, 2005).

The seventies also gave rise to the first Earth Day, considered a significant event in the birth of the modern environmental movement (Gallagher, 1997). This coincided with a NASA-led project using satellite collars on wild animals for the first time (Craighead et al., 1971). The use of wildlife tracking technologies soon proliferated. It was now possible to track animal movements across large scales and begin to understand dynamic interactions between wildlife and habitat at scales not possible through observation alone (Cagnacci et al., 2010; Kays et al., 2015). The use of animal-attached sensors, i.e., biologging, has grown exponentially since, allowing detailed insights into animal behaviour and physiology, even when animals are out of sight (Williams et al., 2020; Wilson et al., 2018). The most commonly used of these sensors are locational, e.g., Global Positioning Systems (GPS) and Very High Frequency (VHF) radio transmission units, but accelerometers and other Inertial Measurement Unit (IMU) sensors have also seen significant increases in use (Kays et al., 2015). Accelerometers collect data on animal posture and energetics at infra-second frequencies and are often used to assess activity patterns or classify discrete behaviours (Brown et al., 2013). Such techniques can be used to compute detailed activity budgets or study specific behaviours of interest. For example, accelerometry has been used to compare activity patterns between hot and cool days in multiple antelope species (Berry et al., 2023) and detect caching behaviour in Arctic foxes (*Vulpes lagopus*; Clermont et al., 2021). Magnetometers also have a growing role to play in classifying discrete behaviours, and can be used to detect rotations in animal heading (Williams et al., 2017). Magnetometers have been found to have comparable behaviour classification accuracies to accelerometers and may, at least in some cases, be more robust in handling inter-individual variability (Chakravarty et al., 2019). Accelerometers, however, are more effective for estimating posture (Chakravarty et al., 2019) and as such combined units featuring both sensors are beneficial to deploy (Wilson et al., 2008). Combined accelerometer and magnetometer units also facilitate fine-scale path reconstruction through dead-reckoning, which captures the tortuosity of animal movement paths missed by the straight line distance estimates between consecutive positions captured when using locational sensors alone (Bidder et al., 2015; Gunner et al., 2021a). Thus, the use of animal-attached sensors allows insights into animal behaviour which were previously impossible.

Behaviour classification methods remain diverse with little consensus as to which, if any, should be preferred (though note Patterson et al., 2019; Sur et al., 2023). Machine learning is often used to process biologging data due to the large datasets collected (Pichler and Hartig, 2023). While machine learning methods can be implemented with relative ease, there are often drawbacks in terms of interpretability (and therefore generalisability) of outputs, the amount of input data required and processing time (Pichler and Hartig, 2023). Another approach to behaviour classification is using a Boolean search method, whereby user-inputted algorithms are used to isolate specific data signatures (Wilson et al., 2018). Classifying behaviours in this way produces algorithms which are easier to interpret and adapt, have no minimum data input requirements and process large datasets quickly and efficiently. Defining these behavioural search algorithms requires highly specialist input, however, detailing specific features in specific data channels (Wilson et al., 2018). As such, maximising the insights gained from animal-attached loggers typically requires some element of behavioural observation of tagged animals, so that distinct behaviours can be matched to their corresponding logger traces (Brown et al., 2013; Wilson et al., 2018; Yu et al., 2021).

Observations of tagged animals can be difficult to obtain where particular species or behaviours are difficult to observe in the wild (Brown et al., 2013; Wang et al., 2015). Captive systems provide valuable settings in which to develop and validate sensor technologies and analysis workflows (Pagano et al., 2017; Rast et al., 2020). Behaviour classification rules can be developed in zoos, where the focal individuals can be more readily observed. These classification rules can then be used to classify behaviours on wild tagged conspecifics, and in some cases related species, which are difficult or impossible to observe (Rast et al., 2020; Wang et al., 2015). Captive data collection can also be used to refine tag design and attachment methods (Skubel et al., 2020) and refine other analysis pipelines such as those used in dead-reckoning (Bidder et al., 2012). Dead-reckoned paths require some verified animal locations to correctly place the generated path in space and correct for drift (Gunner et al., 2021a). The amount of verified locations required to prevent drift can vary between species (Gunner et al., 2021b), hence captive trials are also valuable in refining dead-reckoning analysis pipelines.

The Canidae in context

The focal species of this thesis are the African wild dog (*Lycaon pictus*) and the red fox (*Vulpes vulpes*), both members of the canid family, or Canidae. The Canidae are an adaptable family of mammalian carnivores found across every continent except Antarctica (Sillero-Zubiri et al., 2004). Canids forage individually or in groups to exploit a wide variety of foods – meat, insects and even fruit (Macdonald and Sillero-Zubiri, 2004). The canids are skilled hunters and scavenging is also common, although not universal (Wirsing and Newsome, 2021). All species within this family display at least low levels of social association, though some strictly forage alone even if they live in social groups, while others are obligate cooperative hunters (Macdonald et al., 2019; Macdonald and Sillero-Zubiri, 2004).

Behavioural flexibility is key to the canid success story, in terms of the family's collective range, dietary diversity, the densities at which they can thrive in favourable conditions and their tolerance to human-dominated landscapes and activities (Castelló, 2018; Padilla and Hilton, 2015). Understanding the behaviour of members of the canid family is important to conservation management and trophic ecology due to their near global distribution, the important roles they perform in ecosystems and the fact that lethal control of their populations in conflict scenarios is often ineffective (Bengsen, 2014; Fox, 2006; Nattrass et al., 2020). Managing these species and mitigating human-canid conflict scenarios requires specific scientific evaluation and often, creative and informed management solutions (Fox, 2006; Moreira-Arce et al., 2018).

Thesis aims and chapter summary

The overarching theme of this thesis is consideration and refinement of various steps in the process of conducting a movement ecology study. I reflect on key areas identified as benefitting from advancement. These pertain to conceptual considerations in study design and methodological refinements in how data are collected and interpreted. By considering the obligately social, pack-hunting African wild dog and the solitarily foraging red fox specialised in ambush hunting and scavenging, the flexibility of the canid family is captured even in just these two species. Generalisable methodological refinements to biologging studies are presented; highlighting the benefits of applying such technology in captive settings, refining capture and tagging methods in captive and wild settings and exploring fine-scale space use and behaviour in the wild.

The introduction provided here is brief, as **Chapter 2** is an extended review on the use of biologging to better understand predator energetics, providing context for the subsequent chapters. This includes an extensive review on the development of many animal-attached sensors and specific consideration of how inter-individual variability and sociality affect predation. Further, this chapter concludes with key recommendations for improving our understanding of predation energetics.

Chapter 3 follows one of the key recommendations made in **Chapter 2**, to capitalise on studies in captive settings to improve the interpretation of accelerometer and magnetometer datasets (Figure 1). It also highlights how such studies can have specific benefits in captive systems by considering activity levels in relation to the type of food received on a given day. Enclosure use in response to both food received and captive management activities is revealed through dead-reckoning. We also assess activity levels during sedation recovery and describe an innovative approach to collaring captive carnivores without sedation through crate-training.

Figure 1. An African wild dog wearing a tri-axial accelerometer and magnetometer-equipped collar in London Zoo. Photograph by Holly English.

Next, I present two chapters on another canid species with different social and foraging strategies, the red fox (*Vulpes vulpes*). **Chapter 4** outlines how we refined our capturing and collaring protocols for foxes following initial difficulties deploying collars on this trap-shy species (Figure 2). Specific details on refining animal capture success rates, collar programming and optimised data retrieval efforts are often not reported. I intend this chapter to serve as a guide to researchers facing issues with animal capture and data recovery, having discussed such issues with many researchers at conferences and other settings throughout the period for which this project has been ongoing.

Chapter 5 presents insights into space use and behaviour of urban foxes in Dublin through the collection of GPS, accelerometer and magnetometer data. GPS data reveals restricted space use though with considerable variation between individuals. While limited behavioural observations were possible here, behaviour classification procedures were adapted and benefitted considerably from the knowledge previously gained on captive African wild dogs. A case study is presented on how dead-reckoning can be used to map feeding and predominant movement gait in the landscape. How the role of intentional feeding of urban foxes by residents may be shaping these patterns is discussed.

Figure 2. An urban red fox undergoing recovery following capture and collar-fitting. This was the first fox collared in Dublin, following an unsuccessful capture season the previous year. Photograph by Holly English.

Finally, **Chapter 6** provides a brief discussion of the broad conclusions of this thesis. I summarise the knowledge gained from the studies presented here and how they may inform future studies involving the collection of animal movement data. I reflect upon general principles in inferring animal behaviour from biologging data, including when it is beneficial to compare biologging datasets, while also identifying where caution is warranted in making interspecific comparisons. I also discuss animal welfare considerations, including collaring methods and sedation, emphasising where insights here may inform other studies.

The information we receive from animal-attached tags is invaluable. Quantitative data on animal activity patterns, movement and behaviour are provided at previously unprecedented scales. A major caveat of research involving the restraint and tagging of animals is its potential for negative animal welfare outcomes, however. Throughout this thesis I will outline how such research methods can be streamlined to minimise potential impacts on study animal welfare. This is particularly relevant to **Chapters 3** and **4**. In **Chapter 3**, we show how collar data collected on captive animals can be used to assess animal welfare, which directly informed management strategies and future interventions in the relevant zoos. Welfare considerations are central to the wild animal capture protocols outlined in **Chapter 4**.

In short, this thesis is a record of the considerations and experiences which I believe have made me a better behavioural and movement ecologist since embarking on this PhD programme in 2019. I hope the lessons learned here can act as a springboard for others with the same goal.

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Chapter 2

Advances in biologging can identify nuanced energetic costs and gains in predators

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Abstract

Foraging is a key driver of animal movement patterns, with specific challenges for predators which must search for mobile prey. These patterns are increasingly impacted by global changes, principally in land use and climate. Understanding the degree of flexibility in predator foraging and social strategies is pertinent to wildlife conservation under global change, including potential top-down effects on wider ecosystems. Here we propose key future research directions to better understand foraging strategies and social flexibility in predators. In particular, rapid continued advances in biologging technology are helping to record and understand dynamic behavioural and movement responses of animals to environmental changes, and their energetic consequences. Data collection can be optimised by calibrating behavioural interpretation methods in captive settings and strategic tagging decisions within and between social groups. Importantly, many species' social systems are increasingly being found to be more flexible than originally described in the literature, which may be more readily detectable through biologging approaches than behavioural observation. Integrating the effects of the physical landscape and biotic interactions will be key to explaining and predicting animal movements and energetic balance in a changing world.

Keywords: predation, energetics, foraging, movement ecology, biologging, GPS, accelerometer, social system.

Introduction

Box 1. Key outstanding questions in predation energetics

Predation is an ecologically critical behaviour, dictating predator energy budgets with cascading effects for prey. Predation can be difficult to observe and study in the wild however, and there remain knowledge gaps which are further complicated by variation between individuals and social systems. Some key outstanding questions may be filled using developments in animal-attached technology.

- How do environmental factors and within- and between-species interactions affect how prey are located, selected and captured, in both stable and changing habitats?
- How can we refine detection and quantification of complex, variable predation behaviours, such as those involved in handling prey and feeding?
- Are key predation dynamics incompletely captured by commonly used data collection strategies? For example, are intra-group interactions and hunting roles missed when few animals within a social group are tagged?
- How do hunting dynamics change if predators and their prey are unequally affected by climate change and habitat modification?

Animals adapt their behaviour to optimise gains and minimise losses in an environment, with energetic, ecological and evolutionary consequences (Studd et al., 2020). Foraging is a sequence of continuous behavioural decisions made to maximise energetic gains while minimising costs in the search for food and its handling (Pyke, 2019, 1984). Animals are faced with multiple foraging decisions, for example whether to target one prey species over another (MacArthur and Pianka, 1966) or whether to forage cooperatively with conspecifics (Packer and Ruttan, 1988). The costs associated with foraging are especially pertinent in predatory animals which must invest energy in the pursuit and handling of prey, often with risk of injury to themselves (Brown and Kotler, 2004). Foraging costs for predators are determined by the potential profitability of each prey item, encounter rate and handling time (Emlen, 1966). Whether the predator is social or solitary and the number of individuals in a cooperatively foraging group also affect individual prey selection and energy gain (Mittelbach, 1984).

Foraging strategies are shaped by external factors, such as resource availability and environmental conditions (Lewis et al., 2006; Segev et al., 2021), leading to considerable variation in foraging strategies within and between individuals, social groups, populations, species and taxa (Abrams, 2010; Aplin et al., 2014; Gulka and Davoren, 2019; Miller et al., 2009; Montevecchi et al., 2009). Flexibility in foraging strategy can occur in each of these levels. Individuals may display multiple foraging strategies (i.e., switching between multiple food types which require different handling) in complex or variable environments (Trapanese et al., 2019), including dynamic switches regarding the tolerance of satellites by territory owners (Davies and Houston, 1981). Distinct strategies may be associated with particular populations or habitats across temporal scales (Nisi et al., 2022). For example, bluegill sunfish (*Lepomis macrochirus*) modify their foraging search speed between open-water and vegetated habitats (Ehlinger, 1989), and foraging trip duration and rate of chick provisioning can vary between colonies of wedge-tailed shearwaters (*Puffinus pacificus*; Peck and Congdon, 2005). This variation across contexts, the difficulties associated with observing predation events, and the stochasticity inherent in food encounter rates (the role of 'luck' in finding food; Wilson et al., 2018), leave many open questions in our understanding of predator energetics (Box 1).

Predation is costly

Predation typically incurs high energetic costs, either through pursuing and subduing prey, for example in large mammalian predators such as African wild dogs (*Lycaon pictus*; Hubel et al., 2016a) and lions (*Panthera leo*; Williams and Yeates, 2004), or through shorter ambushes which require sudden bursts of energy, seen in diverse taxa including mantis shrimp (deVries et al., 2012) and snakes (Bury, 2021). Hunting success is a central consideration in predation energetics. Predators must intake enough energy to account for the hunt which has just taken place, but also unsuccessful hunts since the last meal, competition e.g., through kleptoparasitism (Gorman et al., 1998; Scantlebury et al., 2014), their basal metabolic rate, and other behaviours required for survival, growth and reproduction (Figure 1). Meeting these diverse demands may promote flexibility in foraging behaviour, with species implementing more diverse suites of predation strategies than can easily be observed and studied using standard methods (Andersen et al., 2020; Scantlebury et al., 2014). This can increasingly be rectified with the use of animal-attached technology to reveal out-of-sight animal behaviours across multiple species (Fehlmann et al., 2017; Tatler et al., 2018). Such insights into predator energetics are valuable given the increased demands of predation compared to other foraging methods, related to locating, restraining and handling prey, which we review in full here.

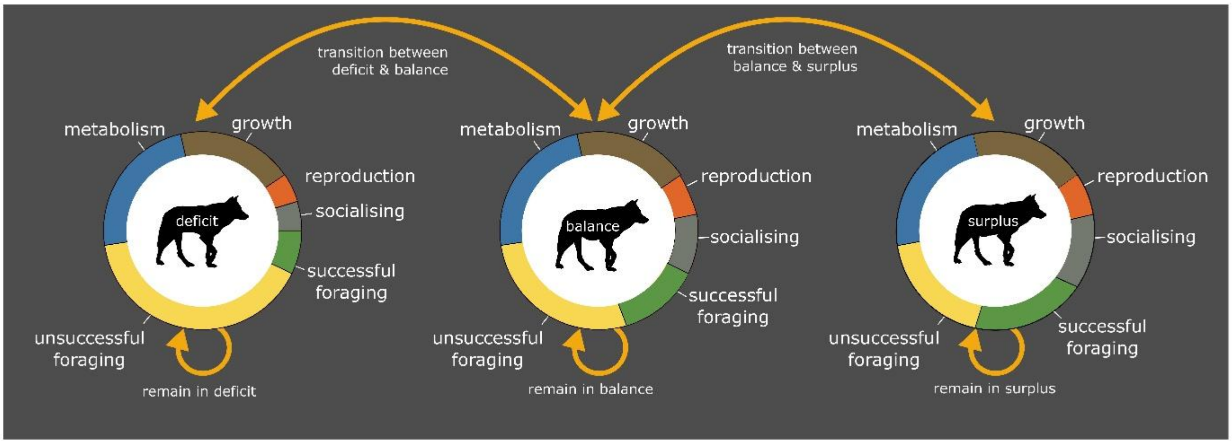

Figure 1. Animals can be in energy deficit, energy balance or energy surplus. The arrows here indicate that animals may remain in or transition between these states, mediated by foraging success. Animals in energy deficit incur costs which affect body condition and eventually breeding failure and death will occur if animals cannot regain energy balance. Energy balance allows normal daily functioning, while surplus energy allows investment in growth, reproduction and social behaviours.

Climate and land use change may cause shifts in predator-prey dynamics

Environmental conditions can add further energetic costs to foraging (Williams et al., 2020), for example, rising temperatures may subject predators to heat stress during pursuit (Rabaiotti and Woodroffe, 2019). Prey species are subject to this pressure as well, but for many predator-prey pairs, it is unclear whether the species are equally (un)affected or whether temperature changes could shift the balance in favour of one species or the other. From the predator perspective, this could shift prey preference, with cascading ecosystem effects (Evans and Moustakas, 2018). For marine predators, endotherms seem to have a competitive advantage over ectotherms at lower water temperatures, with consequences for species distributions (Grady et al., 2019). In terrestrial systems, cursorial predators (which chase prey) are more likely to be adversely affected than stalk and ambush predators, due to the additional energetic costs associated with pursuing prey over large distances (Rasmussen et al., 2008). Though disparities in prey *versus* predator responses to rising temperatures may also work in favour of the predator, if prey become more easily exhausted under heat stress. These concepts are understudied at present, especially given the precedence of indirect climate change impacts on ecosystems. Where studies have been carried out, there is disagreement on predator-prey dynamics under rising temperatures, for example in the case of the African wild dog, where there have been contrasting findings on whether the wild dogs themselves or their prey are more impacted by heat stress associated with rising temperatures (Creel et al., 2016; Woodroffe et al., 2017). These discrepancies may be partially explained by differences in prey preference across populations (Rabaiotti and Woodroffe, 2019). Assessing the energetics associated with different hunting and evasion strategies across populations is therefore a key consideration for understanding shifting predator-prey dynamics under climate change.

Land use represents another key form of global change with consequences for predator-prey dynamics, often working in tandem with climate change impacts (Labadie et al., 2023). In some cases, land use change can benefit predators by improving search efficiency as vegetation is thinned or removed (Boucher et al., 2022; Labadie et al., 2023). These dynamics can be complex, however, and vary significantly between land use types. For example, pumas (*Puma concolor*) were found to have higher body condition scores in areas of marginal anthropogenic development than in both wilderness and highly developed areas (Coon et al., 2019). Socio-ecological phenomena must be considered as habitats are modified; land use change increases human-wildlife conflict, particularly when predators of degraded habitats target livestock (Davie et al., 2014). Within increasingly human-dominated landscapes, some prey take advantage of carnivore avoidance of areas of high human activity, a phenomenon known as the human shield (Berger, 2007; Muhly et al., 2011), while others show stronger avoidance of human activity than their natural predators (Ciuti et al., 2012). Understanding these complex dynamics is a priority under ongoing habitat modification and degradation, particularly given the disparity in observed species' responses across both predators and prey.

Energetic landscapes reveal foraging costs

Climate and land use change may cause animal populations to shift in distribution (Pörtner et al., 2021) with consequences for how hunting animals locate, select and subdue their prey. Shifting population distributions lead to potential re-arrangement of prey preference and cascading ecosystem effects (Muhly et al., 2011). These dynamics may be better understood by mapping predation both in the physical landscape and the so-called landscapes of fear, food, disgust and energetics (Duparc et al., 2020; Nickel et al., 2021; Weinstein et al., 2018). The landscape of fear is the spatial and temporal variation seen in prey movements in response to their perceived risk of predation, typically visualised as peaks and valleys, similarly to terrain maps (Laundre et al., 2010). For example, in Yellowstone, landscape of fear maps computed for elk were strongly affected by the crepuscular activity patterns of wolves (*Canis lupus*; Kohl et al., 2018). Similarly, complex changes in diel activity patterns for roe deer across European landscapes were found in response to the threat of both lynx and humans (Bonnot et al., 2020). These dynamics become more complicated in multi-predator systems where prey must contend with predators using different hunting strategies, resulting in complex landscapes of fear with varying levels of risk (Lone et al., 2014). The concept of foodscapes, though developed for herbivores navigating immobile foraging resources (Duparc et al., 2020; Searle et al., 2007), can also be extended further up the food chain, as prey resource selection will shape the movements and selected hunting strategies of their predators (Owens and Keeley, 2022). The landscape of disgust arises from parasite avoidance behaviour, with further consequences for predator-prey interactions and scavenging decisions (Moleón et al., 2017; Weinstein et al., 2018).

Energetic landscapes, as revealed through accelerometry (i.e., using on-board accelerometer sensors measuring the rate of change of velocity), represent efforts to put animal behaviour and physiology in the context of wider ecosystems and environments (Gallagher et al., 2017). This concept was introduced by Wilson et al. (2011) assessing varying movement costs associated with foraging in a heterogeneous environment (Wilson et al., 2011). Specifically, Wilson et al. (2011) compared the foraging dives of imperial cormorants (*Phalacrocorax atriceps*) and the travel costs between the foraging area and the breeding site to a model where individuals were evenly spaced. Complexity was added to the energy landscape definition through *1)* cost functions and maps visualising areas of different energetic costs, *2)* adding speed and tortuosity of animal movement paths and *3)* environmental factors such as wind conditions for aerial travel (Shepard et al., 2013). More recent considerations have assumed broader energy requirements, to account for thermoregulation and maintenance of body condition, with quantification of individual foraging strategies highlighted as a future direction in using energetic landscapes for population ecology and global change inferences, considering predator performance (Amélineau et al., 2018). Integrating the landscapes of fear and energetics has been discussed elsewhere (Gallagher et al., 2017), but there is still little consideration of how species' social systems factor into this picture.

Social interactions influence predation strategies and may be more flexible than originally described

Research into how sociality affects animal spatial behaviour and general ecology has grown significantly in recent years, as the social landscape, including the distribution and density of conspecifics, can strongly affect the movements and behavioural decisions of individuals (Cozzi et al., 2018; see also: the social resistance hypothesis discussed by Armansin et al., 2020). Social network analysis in particular is becoming a dominant approach within behavioural ecology (Farine and Whitehead, 2015; Psorakis et al., 2015; Webber and Vander Wal, 2019; Wild et al., 2021). As well as looking at interactions within groups, social networks can be used to represent inter-group interactions such as territorial intrusions related to resource abundance (Webber et al., 2022) and social dynamics of semi-social conspecifics (Raulo et al., 2021). Investigating the role of species' social systems, and intraspecific variation in these systems, as a factor influencing energetics requires attention. Conspecifics can affect an individual's foraging behaviour (Firth et al., 2015). For example, information transfer pertaining to foraging sites can occur in colonially-breeding species, such as gannets (*Morus bassanus*; Wakefield et al., 2013). Social eavesdropping has been reported in vultures, as individuals obtain information about thermals from conspecifics, helping them choose energetically efficient foraging search paths (Williams et al., 2018). Social information transmission can influence every stage of predation, encompassing encounter, detection, identification, approach, subjugation and consumption of prey (Hämäläinen et al., 2022).

Whether an animal is social has profound implications for foraging ecology, particularly if social group members cooperate to obtain food, further compounded by dynamic group size responses by prey (Markham et al., 2015). Collective hunting allows the takedown of large prey which individual predators could not manage alone (Hayward and Kerley, 2005; MacNulty et al., 2014). Other species, such as the Ethiopian wolf (*Canis simensis*), target smaller prey individually, even though these predators live in a social group (Tallents et al., 2012). Some species that typically forage alone or in pairs can opportunistically adapt to cooperative hunting, such as the black backed-jackal (*Canis mesomelas*; Nattrass et al., 2020). Increasingly, there are reports of cooperative hunting in species thought to only forage alone, including harbour porpoises (*Phocoena phocoena*; Torres Ortiz et al., 2021), goshawks (*Accipiter gentilis*; Kusal and Kajtoch, 2020) and yellow-throated martens (*Martes flavigula*; Twining and Mills, 2021). Where cooperative hunting occurs opportunistically, this may be an attempt by individuals to achieve the benefits of cooperative hunting while minimising the costs which can arise through social foraging. Effort expended during cooperative hunting is not necessarily equal between individuals (MacNulty et al., 2012) and how food is shared within a group is influenced by intra-group competition, dominance hierarchies and kleptoparasitism (Macdonald, 1983; Malcolm and Marten, 1982). This opens research avenues focusing on dynamic behavioural decision-making, investigating spontaneous decisions on whether to cooperate to find food, mediated by internal state and animal personality, as well as environmental conditions (Sih et al., 2015; Wolf and Weissing, 2012).

Aims

Here we show how biologging technology can be used to provide new insights in predation energetics. First, we review the development of methods for estimating animal energetics and discuss how more recent technological and conceptual advances facilitate finer-scale, multifaceted insights, primarily through approximation of energy expenditure using accelerometry. Next, we briefly outline the importance of accounting for inter-individual variability. In the subsequent section, we discuss the energetics underlying predation in social and solitary contexts, as hunting alone versus with a team has significant implications for both the intake and output of energy, particularly under changing climate and land use scenarios. We conclude with a section on Future Directions, which suggests methods for optimised experimental design, data collection and analysis, aimed at addressing the questions raised at the beginning of this work (Box 1). Specifically, we posit that growing consideration of energetic landscapes and social networks can be combined. Energetic landscapes effectively capture the influence of abiotic factors on individual movement, behaviour and survival, while social networks often lack due consideration of temporal and spatial scales. We recommend calibrating sensors within captive settings prior to setting up experiments in the wild, which will improve our understanding of shifting animal movement patterns and energetics in the Anthropocene. Further suggestions are made outlining which animals to tag, the study design and which variables to include in statistical models.

Quantifying Predation Energetics

First investigations of animal energetics: from lab to field

Due to the difficulties associated with studying energetics in wild systems, initial investigations into animal energetics were lab-based. Treadmills were, and continue to be, valuable tools in estimating the energetic costs associated with moving at different gaits across multiple species. The use of treadmills to quantify energetics associated with animal locomotion dates back to the 19th Century (Zuntz, 1897) and has expanded to include multiple species across diverse taxa including mammals (Taylor et al., 1970), reptiles (Hertz et al., 1988) and birds (Ellerby et al., 2005). In controlled settings (including laboratories and zoos), treadmills combined with oxygen chambers allow measurement of animal speed and oxygen consumption, allowing energy expenditure to be calculated for many species performing multiple gaits. However, this experimental set-up is not possible with free-ranging wild animals; new developments were required.

The doubly-labelled water method, developed in the 1950s, allows estimation of an animal’s energy expenditure during the window between two blood samples by using isotopically-labelled water to assess carbon dioxide production (Lifson et al., 1955; Speakman, 1997). With this, research on animal energetics in the wild could commence. It was first used outside the laboratory to assess energy expenditure during rest and flight for homing pigeons (*Columba livia domestica*; LeFebvre, 1964) and has since been used extensively across diverse wild species (Acquarone et al., 2006; Masman et al., 1988; Peterson et al., 1998; Shaffer, 2011). While facilitating inferences across diverse systems, the major limitation of this method is the requirement to recapture animals within a rigid timeframe, as the second blood sample must be taken before the isotopes have been eliminated from the body (Butler et al., 2004). Additionally, this method provides energetic estimates from the study period as a whole and extensive behavioural observations are required to estimate the costs associated with specific behaviours (Butler et al., 2004; Flint and Nagy, 1984).

The development of animal-borne sensors

Time depth recorders, designed to record the diving depths of marine mammals, represented the first use of archival animal-attached sensors (Kooyman, 1965; Scholander, 1940). The development of VHF (Very High Frequency) telemetry allowed triangulation of animal location using an antenna to detect pulsed radio signals emitted from an animal-attached transmitter (Cochran et al., 1965; Cochran and Lord, 1963; LeMunyan et al., 1959). This allowed studies on movements, home ranges and mortality of wild animals to proliferate, and detection of both predator foraging and prey mortality through VHF telemetry continues to provide important insights into predation (Hebblewhite and Merrill, 2007; Laundré, 2008; Mech, 1980). Satellite collars were first developed in the early seventies (Craighead et al., 1971; Craighead et al., 1972), allowing location data to be collected and stored at regular intervals *via* satellite communication. Continued developments expanded options for collecting location information (Figure 2), and the wide adoption of GPS and Argos satellite telemetry has resulted in large, fine-scale datasets of animal movements across space (Cagnacci et al., 2010; Tomkiewicz et al., 2010). Beyond movement trajectories, these data provide detailed insights into behavioural states, including foraging (Merrill et al., 2010; Morales et al., 2004). More recent developments have expanded the range of animal-attached sensors and associated insights, known as biologging (Figure 2; Holton et al., 2021; Rutz and Hays, 2009; Williams et al., 2020; Wilmers et al., 2015).

Additional sensors for finer-scale locations and behaviours

Biologging devices incorporating Inertial Measurement Units (IMUs) such as accelerometers (measuring the rate of change of velocity), magnetometers (measuring Earth's magnetic field, which can be used to give compass-like orientation) and gyroscopes (measuring orientation through angular velocity), allow quantification of fine-scale movement patterns and the relationship between animal behaviour and energetics (Bidder et al., 2015; Halsey et al., 2009; Wilson et al., 2013). This is possible as biologging devices allow animal movement to be considered on physiological and biomechanical scales, measuring the individual movements and conditions of the body (Goossens et al., 2020). As such, these additional sensors provide data distinct from those obtained using even high-resolution locational units (such as those collecting data at the scale of seconds or minutes as opposed to hours).

Using IMUs in tandem with locational units such as GPS allows fine-scale animal behaviour to be mapped in space. This leads to greater insights than achievable with locational sensors alone. Such multi-sensor techniques can advance our understanding of animal energetics with field-based, sub-second-scale measures of movement costs using dynamic body acceleration metrics derived from tri-axial accelerometer data (Wilson et al., 2020). Deriving energetic landscapes through mapping energy expenditure in space can be used to test optimal foraging theory, by assessing whether animals maximise energy gain while minimising costs as they navigate their environment (Wilson et al., 2011). Further, precise animal movement paths can be reconstructed in space through dead-reckoning (Gunner et al., 2021). Dead-reckoning is a path reconstruction method where location data are combined with heading and speed data derived from IMUs (Bidder et al., 2015; Gunner et al., 2021; Wilson and Wilson, 1988). The result is a tortuous, high-resolution path which captures the changes in direction and variable speed of travel undertaken by an animal between subsequent locations. Such highly resolved paths allow more detailed investigations of the precise paths taken by animals and how the costs of moving across different habitat features may shape these.

High resolution GPS and IMU sensors offer different yet complementary information. The behaviour of the species under study and the environment in which it lives dictate the most appropriate sensor choice and sampling regime (Gunner et al., 2022). Dead-reckoning can be particularly valuable in environments where high frequency GPS sampling is prone to errors or high rates of missed fixes due to habitat composition and/or animal behaviour and posture (Gunner et al., 2022). High frequency data have been found to provide additional insights into animal behaviour where coarser datasets may result in inaccurate or incomplete interpretations. Some examples include contrasting exploratory movements between bold and shy individuals and detecting multi-animal interactions with consequences for disease transmission (Nathan et al., 2022).

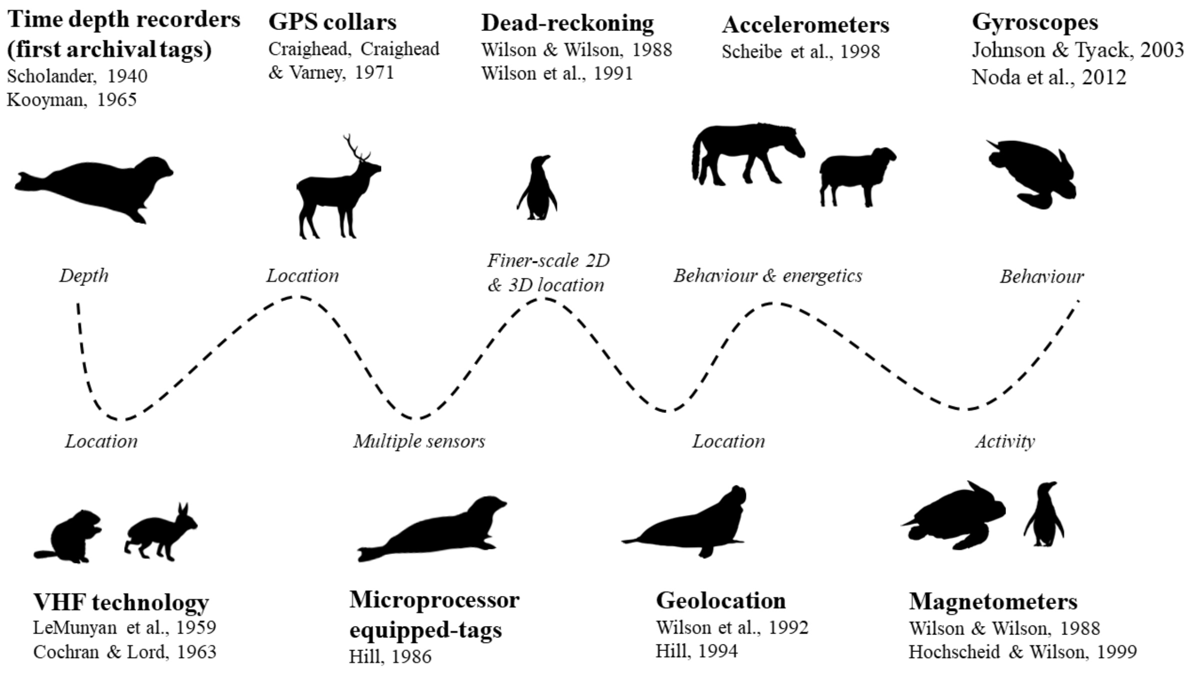

Figure 2. A timeline of key developments facilitating insights into animal energetics. Note all references refer to studies of animal ecology, rather than use of these tools in other fields (e.g., engineering, physics, robotics).

Detecting foraging behaviour

Information about the type and amount of food ingested by animals can answer fundamental ecological questions relating to how animals manage their energy budgets in the wild (Krebs and Davies, 2009). Inter-mandibular angle sensors (IMASEN), placed on animal jaws, have been used to reliably determine prey ingestion (Liebsch et al., 2007). More commonly, fine-scale movement data are used to reconstruct predation events. Clusters of GPS locations may indicate kill sites, often with field visits for verification (Merrill et al., 2010; Webb et al., 2008). It should be noted that this method is biased towards large predators hunting large prey, with kill sites of small prey typically classified at lower accuracies (Webb et al., 2008). Hidden Markov models (HMMs) allow movement data to be categorised into discrete states (Langrock et al., 2012). Although these states are typically not verified behaviours, kill sites can also be used to confirm HMM-defined predation occurrences (Franke et al., 2006).

Foraging strategies vary depending on the food items targeted, habitat type and whether foraging is cooperative or solitary (Lührs and Dammhahn, 2010; Suryan et al., 2000; Twining and Mills, 2021; Woodroffe et al., 2007). As different hunting strategies involve different body postures and energetic signatures, it should be possible to extract these separate hunting strategies from biologging data (Table 1). For example, combined tri-axial accelerometer and GPS data have shown promise in elucidating the energetics underlying prey capture by large predators like African leopards (*Panthera pardus*; Wilmers et al., 2017) and high frequency acceleration data have been used to classify behaviours related to foraging in smaller predators such as the Arctic fox (*Vulpes lagopus*; Clermont et al., 2021). As speed estimates can be derived from both GPS and acceleration data, and magnetometers can capture the tortuosity of animal movement paths (Potts et al., 2018), these technologies present opportunities to look at speed, pursuit and evasion in hunting predators and fleeing prey (Figure 3; Wilson et al., 2015).

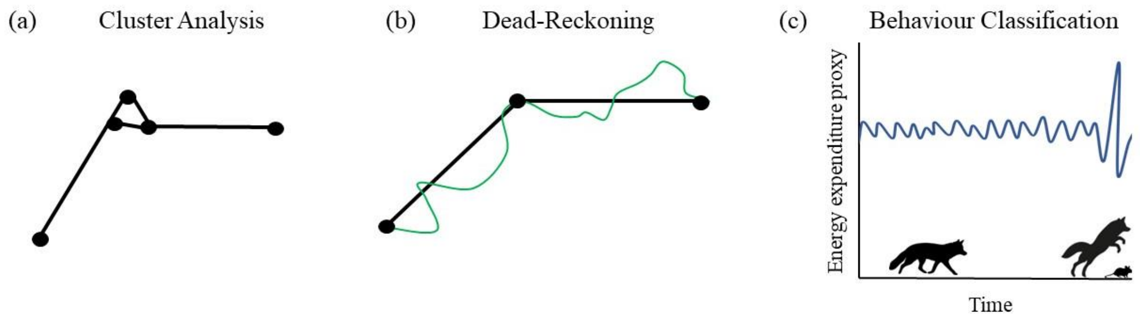

Figure 3. Examples of analysis methods for GPS and Inertial Measurement Unit data with relevance to predation energetics. (a) Cluster analysis of GPS data allows detection of kill sites by detecting spatially and temporally clustered locations, indicated by the dots here (e.g., Anderson and Lindzey, 2003; Webb et al., 2008). (b) Dead-reckoning animal movement paths using GPS, accelerometer and magnetometer data allow the tortuosity of movement paths to be captured and can be used to reconstruct paths of hunting predators (Gunner et al., 2021). Here the black line represents the straight-line distances between subsequent GPS points, while the green line represents a dead-reckoned path. (c) Behaviour classification of data from IMU sensors such as accelerometers can be used to distinguish predation from other behaviours (e.g., Studd et al., 2021). Note that the proxy for energy expenditure here can take the form of raw sensor data such as individual acceleration axes or metrics such as VeDBA or ODBA.

Table 1. A list of key sensors linked to behavioural interpretations relevant to predation energetics.

Sensor	**Behavioural Inferences**	**Examples**
GPS units	Identify locations visited during foraging trips	(Jones et al., 2018)
	Calculate distances travelled	(Dickie et al., 2017)
	Identify kill site clusters	(Anderson and Lindzey, 2003)
Accelerometers	Identify postures and movements related to pursuing prey	(McGowan et al., 2022; Viviant et al., 2010)
	Quantify predation success rate	(Viviant et al., 2010)
	Turns taken during foraging trips	(Wilson et al., 2015)
Magnetometers	Identify postures related to foraging	(Chakravarty et al., 2019)
	Turns taken during foraging trips	(Williams et al., 2017)
	Dead-reckoning	(Gunner et al., 2021)
Proximity sensors	Social interactions	(Ossi et al., 2016)
	Social foraging	(Ripperger and Carter, 2021)
Intermandibular Angle Sensor (IMASEN)	Opening/closing mandible during foraging	(Wilson et al., 2002)
Camera	Direct footage of all predation-related behaviours	(Andersen et al., 2020)
Microphone	Recordings of prey cries	(Stidsholt et al., 2019)
	Recordings of chewing sounds	(Greif and Yovel, 2019)
	Detection of calls associated with foraging	(Greif and Yovel, 2019)

Linking predation theory and biomechanics to sensors

Certain aspects of hunting behaviour should be kept in mind when quantifying predation energetics through biologging given the physiological and biomechanical insights available through such sensors. For example, prey may undertake complex escape manoeuvres as they choose where to flee and predators follow this route. As such, turning dynamics of coursing predators during a chase have been shown to vary with prey species and the mass of both predator and prey (Wilson et al., 2015). Combining movement data with high resolution habitat data, i.e., those collected using remote sensing and LiDAR methodologies (e.g., Ciuti et al., 2018), represents the highest accuracy framework for assessing turning dynamics in predator-prey chases (see Future Directions). Both pursuit and evasion have important energetic consequences, which ultimately determine hunt outcomes (Bryce et al., 2017; Wilson et al., 2015).

The energetic costs of predation can be split into costs of *1)* locating prey, *2)* pursuit or ambush and *3)* restraining and killing the prey, respectively. More time spent on any of these aspects results in higher energy expenditure, but the costs of each step are unequal and vary between predator-prey dyads. The energy required for separate stages of predation can be estimated through the collection of biologging data (Figure 4). For example, locating prey is less costly than the pursuit per unit time, where terrestrial predators switch from walking or trotting search gaits to running pursuit gaits (Creel and Creel, 1995). Behaviour classification of movement modes can identify and assign approximate costs to such behaviours. Longer search times could involve finding easier prey with shorter pursuit and restraint times (Griffiths, 1980). Therefore, time and energy are separate costs, but time spent on a given activity is critical to the total energetic cost of the hunt. Costs incurred by previous unsuccessful hunts and the sum of other behaviours performed by the animal should also be taken into consideration. Failed hunts, scavenging and foraging for smaller food items may also be accounted for through data from accelerometers and other IMU sensors as behaviour classification methods continue to advance (Clermont et al., 2021; Studd et al., 2021). Developing classification methods for these complex behaviours may be assisted considerably by the increasing use of animal-attached cameras and microphones, allowing further verification of IMU sensor outputs (Stidsholt et al., 2019; Watanabe and Takahashi, 2013). Proximity sensors can be used to detect cooperative foraging in predators (Ripperger and Carter, 2021), as well as encounters between predators and prey (Valerio et al., 2018).

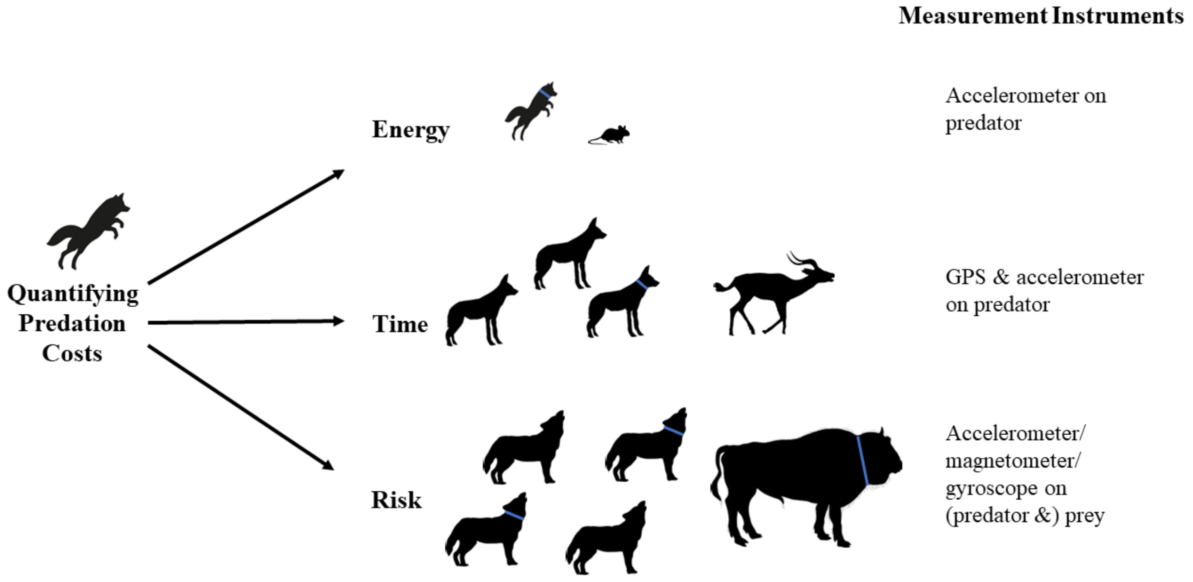

Figure 4. Predation requires investment of energy and time, while involving significant risks associated with attacking and subduing prey. Example predator-prey pairs are shown here, with predation costs linked to sensors which can be used to quantify them. Tagged animals are indicated with blue collars on the relevant silhouettes. Accelerometers allow the calculation of Dynamic Body Acceleration proxies which provide estimates of energy expenditure which can be matched to distinct behavioural states. GPS and accelerometer data allow the start and end points of predation to be identified so that time spent hunting can be quantified. Inertial

Measurement Units can be used to assess animal posture, to detect defensive or aggressive behaviours exhibited by prey and alert postures to be detected in predators. Predator retreat may also be identifiable from dead-reckoned movement paths.

As well as facilitating fine-scale, behavioural insights, animal-attached technology can also provide important information on broader ecological scales. Understanding the energetics of predation can provide information on trophic cascades and predator-prey dynamics with consequences for whole ecosystems (Ripple et al., 2016). Integrating biologging data into Dynamic Energy Budget-Individual Population Models (DEB-IPMs) has been identified as a powerful emerging method to link individual level behavioural energetic trade-offs and metabolic processes to population dynamics including survival and reproduction, with due consideration to environmental change (Chimienti et al., 2020). As such, despite the fine-scale nature of biologging data and often short deployment periods, these data can provide important, broader-scale inferences for population ecology (Morales et al., 2010; Urbano et al., 2021).

Inter-Individual Variability

There has been relatively little consideration of how consistent inter-individual differences (i.e., animal temperament or animal personality) might affect hunting prowess. Individual variation may lead to specialisation in solitary hunters like octopuses (Mather et al., 2012) or distinct roles in cooperative hunters, as seen in harbour porpoises (Torres Ortiz et al., 2021). Further, predator and prey personalities may interact in feedback loops (Sih et al., 2015), with some empirical evidence suggesting both predator and prey personality may interact with consequences for predation attempt outcomes (Chang et al., 2017).

If individuals adopt flexible foraging strategies such as exhibiting prey preference based on prey size and availability, as well as the broader ecological context, then it is reasonable to assume that differences in strategy will arise between individuals. Some differences may be linked to factors such as age and sex (Lewis et al., 2006), though further variation may be attributed to consistent intra-individual variability. This can be measured by considering the repeatability and predictability of behaviours. Protocols for extracting measures of personality from biologging data have recently been developed and are growing in popularity (Hertel et al., 2020). To date, these methods have largely focused on using parameters extracted from GPS data, including distance moved and activity patterns (Hertel et al., 2021) though there is considerable scope for IMU sensors to yield additional insights into individual variation in activity level and space use as influenced by foraging (Cecere et al., 2020; English et al., 2023). Individual variation in activity rhythms and how prey are approached and hunted may affect predation strategies and the roles performed by cooperative hunters, with potential energetic implications. These patterns can be better understood by using movement metrics such as daily travel distances and the amount and timing of activity to detect consistent behavioural differences between individuals (for full review, see Hertel et al., 2020). Despite the growing attention given to understanding animal personality in ecology and evolution (Wolf and Weissing, 2012), the role of personality in driving predator behaviour is still far from understood.

Social Predators

An animal's social environment can affect both the costs and benefits associated with finding food, warranting specific considerations for social predators. Social foraging can decrease the time and energy an individual invests in locating and consuming prey (Carbone et al., 2007;

Jones et al., 2018) and enable access to prey which cannot be obtained by a single predator (MacNulty et al., 2014; Yip et al., 2008). Unequal effort invested in securing prey and gained through how food is shared can present new challenges, however (Macdonald, 1983; Packer and Ruttan, 1988). Whether a predator hunts alone or with a team therefore has implications for how animal-attached sensor data should be interpreted and which wider conclusions on predation energetics can be drawn. In this section, we provide a brief overview of challenges and considerations for studies on social predators.

Often when studying social species, tags are deployed on one or a few members of multiple social groups, to gain insights into the larger population, though with consequences for our understanding of social group interactions (He et al., 2022). One of the primary difficulties in interpreting tag data from social foragers is that both the energy expended in acquiring a meal and the energy intake from successful predation may be unequal between group members. This is particularly true where group members perform different roles during a hunt (Boesch, 2002; Stander, 1992). This makes it difficult to extrapolate energy intake and output from tagged individuals to other group members, and indeed conspecifics more generally. This is particularly complex where social group sizes are unknown or fission-fusion dynamics are at play, leading to variable numbers of predators present at each predation event. The percentage of a social group or population which has been tagged affects how readily social interactions can be detected. Detection of interactions between members of the social group is further influenced by sampling frequency, which must also be taken into consideration when studying group dynamics (He et al., 2022). The strengths of within-group and between-group social interactions may also vary depending on ecological conditions, e.g., in lions (Mbizah et al., 2020). Thus, an additional complication is estimating the distribution of conspecifics across the landscape. Additional data, such as sightings, combined with tag data, may be used to build a social landscape providing the likely density of conspecifics from different groups (Cozzi et al., 2018). This will likely require intensive sampling and surveying across potentially large areas. Further analysis considerations are required for behaviour classification of IMU sensor data. For example, when some but not all members of a social group have made a kill and an untagged individual does not participate in the hunt but feeds on said kill, it may not be possible to decipher whether this feeding instance represents active predation by the group or opportunistic carcass scavenging.

Studies of predation energetics should consider the range of prey species taken by a social predator, as the degree of cooperation may vary with prey size and relative risk to the predator. This is particularly relevant to generalist predators with wide distributions, the range of which may encompass different habitat types and prey species compositions. This is not static, for example larger wolf packs are more cooperative during a hunt when hunting more dangerous prey (MacNulty et al., 2014). Where possible, simultaneous tagging of predators and their prey can improve our knowledge of interactions between groups of predators and dangerous prey (Figure 4).

It is important to note that other factors affect the size of animal social groups, including defending vulnerable young and territories. This may explain why social groups are often larger than identified optimum group sizes for cooperative hunting (Baird and Dill, 1996; Packer et al., 1990) and why some species, like the Ethiopian wolf, occupy shared territories and breed cooperatively but forage alone (Tallents et al., 2012). Even when the hunt itself is cooperative, feeding may still be competitive when groups contain more individuals than are necessary for optimised cooperative hunting (Macdonald, 1983; Malcolm and Marten, 1982). Dominant individuals may limit food access to more subordinate group members (Hamilton and Busse, 1982), though other factors beyond social hierarchies can also affect the roles social group members perform in hunts and the related energy intake and output from a kill. Further studies involving tagging all or most individuals within a social group can shed light on these cooperative hunting dynamics. While this is not practical in all cases, even studies on a single social group can help address these knowledge gaps and aid data interpretation where few or sole individuals in a group have been tagged (Hubel et al., 2016b).

Future Directions

In this review, we have summarised key theory in the predation energetics literature, outlined the development of biologging tools for measuring animal energetics and highlighted key considerations which must be accounted for when investigating intra-individual variability or working with social predators. We conclude by proposing future directions in predation energetics research, which will be key in identifying different energetic costs and gains experienced by predators in a changing world.

1. *Integrating energetic landscapes and social networks*. Animals navigate a spatial landscape and other animals, including predators and prey, affect movement and energetics in a similar fashion to abiotic landscape factors. These biotic factors have unequal avoidance and attraction effects with consequences for how animals navigate their environment (Couzin et al., 2002). Attraction to or avoidance of conspecifics and/or heterospecifics may result in suboptimal use of the physical landscape (e.g., expending more energy to traverse through rough terrain to search for prey or avoid competition). Conversely, an animal may choose the least costly path to navigate the local terrain, which then affects its biotic interactions. Studying such interactions within ecological communities is increasingly feasible due to large-scale tracking initiatives such as ICARUS (Jetz et al., 2022) and data-sharing platforms such as Movebank (which also contributes a data standardisation philosophy; Kranstauber et al., 2011). Energetic landscapes, which consider the costs of navigating the physical landscape,

and social networks, which define the relative strength of social interactions, can be unified to consider the abiotic and biotic factors shaping animal movement patterns in tandem. For example, integrating these methods could be used across predator and prey communities to investigate how the physical environment influences prey selection. Further, thermal shelters are likely to become more important to many species under climate change (González-del-Pliego et al., 2020; Melin et al., 2014), which may have knock-on effects for prey detection and predator avoidance strategies.

Social network analysis (in both intra- and inter-specific systems) offers an analytical means of assessing the role of social interactions in species ecology (Webber and Vander Wal, 2019). Social networks are typically visualised as nodes clustered by interaction frequency, but can be overlaid onto maps to better assess the role of spatial proximity and environmental variables in determining association strength (e.g., Raulo et al., 2021). This process can be taken a step further by overlaying social networks onto mapped energy landscapes, where individuals have been tagged with locational units and accelerometers (Figure 5). Beyond visualisation, the recently developed R package *aniSNA* can be used to resolve autocorrelation issues encountered in the computation of social network metrics using GPS data (Kaur et al., 2023). The most robust social network metrics for a given dataset, determined with due consideration to sampling regime and sociality, can then be modelled with measures of energy expenditure derived from mechanistically modelled energetic landscapes, integrating data on species interactions and energy expenditure. This unleashes new opportunities to test specific hypotheses on how social-energetic landscapes vary as a function of, for instance, prey availability or environmental conditions such as temperature, or how individuals modify the strength of their interactions with different prey species across habitats which are more or less costly to traverse. Energetic landscapes under global change scenarios (e.g., Amélineau et al., 2018) can be adapted to include shifting predator and prey interaction patterns, represented through social network centrality metrics such as mean network strength, to quantify altered ecosystem dynamics. Considering energetic landscapes in conjunction with within- and between-species interactions may expand proposed spatial-social data concepts (Webber et al., 2023) to provide new insights on how other animals affect how an individual navigates its environment.

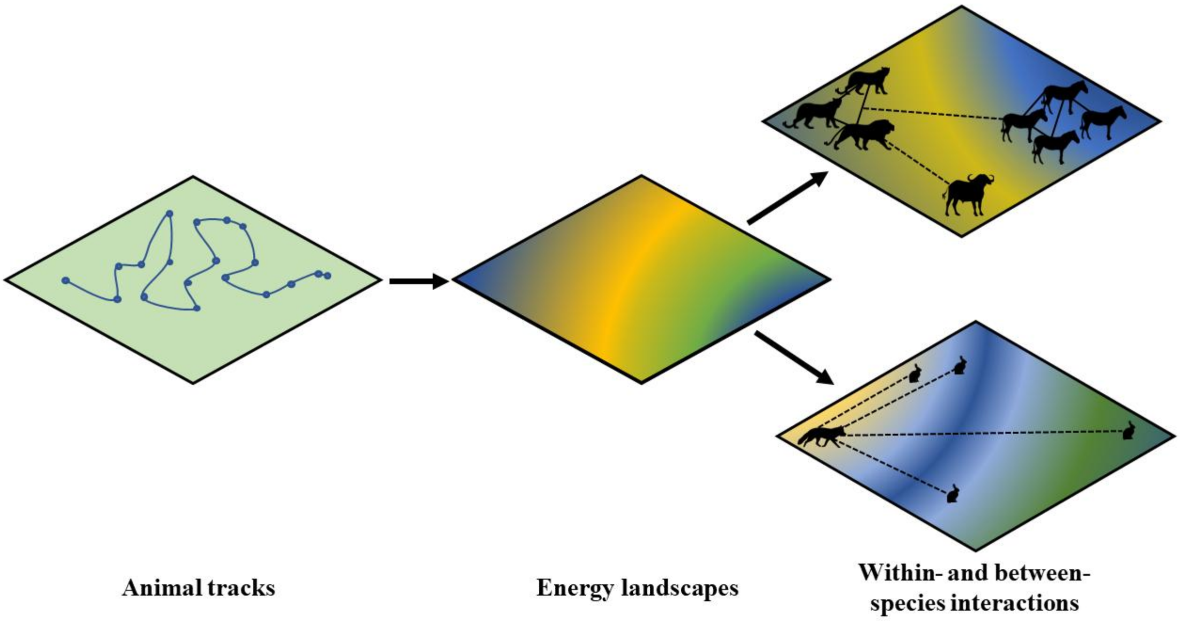

Figure 5. Infographic contrasting the energetic costs and gains between a social group of cooperative hunters and a solitary predator, incorporating energetic landscape and social network concepts. Sensor data on animal location and energetics can be computed into energy landscapes, which can in turn influence prey selection and encounter rates. The colour gradients here represent hypothetical energetic landscapes, where movement costs vary across the habitat in question. Solid black lines indicate interactions between social conspecifics, while dashed lines indicate directions of interest to predators due to prey presence.

2. *Refining data collection and analysis procedures using captive and domestic animals*. Pilot studies on captive and domestic animals allow refinements before wild tag deployments. Zoos provide settings where sensor data can easily be verified for improved data analysis procedures ahead of wild deployments (English et al., 2023). Captive studies can also have welfare benefits by piloting device attachment and deployment methods. Such studies can also detect potential species-specific considerations required ahead of long-term field deployments, e.g., maned wolves (*Chrysocyon brachyurus*; English et al., unpublished data). While there are limitations to using surrogates (Dickinson et al., 2021), with careful interpretation, data from captive and domestic animals can improve behaviour classification procedures for biologging data (Rast et al., 2020). This can be particularly useful when investigating complex postures and motions such as those associated with feeding.

3. *Tagging multiple or all individuals in a social group*. Simultaneously tagging multiple or all individuals in a single social group is rarely done for multiple reasons. Most studies typically have limited numbers of tags and aim to spread them across multiple social units so that broader population insights can be gained (He et al., 2022). Deploying tags in discrete social groups can also address statistical assumptions of independence of data points, depending on the analysis methods used. These constraints are valid, but currently limit our fine-scale knowledge of within-group interactions, including distinct roles which may be performed during coordinated hunting behaviour. Studies which target an entire social group can reveal whether a hunt is truly cooperative and quantify the influence of habitat on pursuit predation, with important considerations for how focal species may adapt in changing land-use and climate scenarios (Hubel et al., 2016a). While tackling entire social groups is easier where

groups are small, it is becoming increasingly feasible and common to also tag larger social groups (e.g., Papageorgiou and Farine, 2020). While tagging multiple or all members of a social group will lead to advances in our understanding of animal societies, tag burden should be kept in mind and research questions should be well formulated to ensure maximum information gain from studies with potential higher overall tag burden. Researchers can also implement non-invasive technologies to collect empirical data on group size, such as camera traps and drones, for example in scenarios where tagging all members of a social group is not feasible due to economic or logistical constraints, or to verify social bonds where these cannot easily be ascertained by an observer. For example, camera traps have been used to detect high contact rates between red foxes (*Vulpes vulpes*), which are considered solitary foragers, where food availability is high (Dorning and Harris, 2019).

4. *Taking social groups as individual units to compare inter-group communication and interactions.* Complementary to studies of within-group interactions, there is scope for further consideration of between-group interactions, where territoriality may (at least occasionally) be weaker than first described, as has been found in black-backed jackals (Nattrass et al., 2020). This also applies to solitary species which may interact socially with conspecifics in neighbouring territories more readily than previously thought (e.g., maned wolves; Ferreira et al., 2021). These interactions may be aggressive or affiliative and include communication through scent-marking and vocalisations. These forms of communication also shape how an animal perceives and therefore navigates its environment, with consequences for territoriality and therefore the resources available to the territory holder. Such interactions are more difficult to visualise and frame in a social-energetic landscape context, but mapping instances of scent-marking behaviour

classified through IMU sensor data (Bidder et al., 2020) and continued advancements in acoustic recording research (Kershenbaum et al., 2016) may improve our understanding of these non-visual communication channels in shaping how animals move through their environment.

5. *Simultaneous tagging of predators and their prey.* As well as investigating the within- and between-group interactions of predators, further studies with simultaneous tagging of both predators and their prey are required. Studies where members of a predator and prey species within the same study area are tagged with location sensors can provide valuable information on predator and prey activity rhythms, their degree of spatial overlap and how these may interact with landscapes of fear and energetics (Eriksen et al., 2011; Smith et al., 2019). Where possible, tagging predators and prey simultaneously with IMU sensors may provide detailed data on individual hunt dynamics. Such data can be used to characterise chase paths, turning dynamics and evasive movements (Bryce et al., 2017). While the likelihood of a tagged predator hunting tagged prey is still quite small in most systems, any instances where this is recorded is likely to have profound insights into how the pursuit and restraint techniques of the predator and the escape strategies of the prey interact with one another. As well as these tagging approaches, continued advancements in tracking animal locations and postures through drone-collected aerial imagery (Koger et al., 2023) may hold significant potential in capturing pursuit and evasion dynamics of predators and prey.

6. *Account for factors such as hunting success rate and relative prey energy value in statistical model structures*. Fine-scale biologging data and related behaviour classification can also contribute additional variables to include in models of predation energetics. For example, where hunting can be defined, the approximate energetic costs of distinct prey species and their energy value when obtained (either estimated from time spent feeding if clear from IMU sensor traces or through a proxy derived from prey body size or estimated caloric value) can be included in model structures. Models explaining the likelihood of successful predation of a given prey would benefit from including the approximate energy value of the prey, encounter rate, handling time and individuality. Conversely, failed predation attempts can be an important consideration when considering a more general model of a predator's energetic balance.

7. *Increasing the diversity of species tagged and included in such studies*. One of the limitations of animal-attached sensors is that tag size and weight can limit the potential for the use of such technology on smaller animals. Considerable advancements have been and continue to be made, however, such as biologger sensor networks developed for tracking bats (Ripperger et al., 2020). Though the development of smaller tags facilitates deployments on smaller species, these developments should also aim to facilitate the use of reduced mass tags on individuals to minimise potential deleterious effects (Portugal and White, 2018). Biologging studies are also biased towards mammals, and to a lesser extent fish and birds (Joo et al., 2022); efforts should be made to increase the diversity of species represented in such studies.

8. *Sampling designs tackling the influence of climate and habitat modification on foraging behaviour*. Predator-prey interactions are key to trophic ecology and it is therefore important to assess energy balance in these relationships in a changing world. Further, robust understanding of energy intake and output is required to understand species responses to climate and habitat change. These questions can be tackled, for example, by comparing energetics across populations with different weather patterns to approximate species responses to climatic shifts (Woodroffe et al., 2017). Studies on wildlife in human-dominated landscapes such as urban areas or agricultural land can yield insights for areas undergoing current land-use change.

The future directions presented here offer a roadmap to further expand our knowledge of predation energetics using animal-attached sensors, accounting for sociality, individual variation and global change. Advances in animal-attached tagging technology have rapidly expanded the ecologist's toolkit for understanding animal energetics. The tools presented here, coupled with thoughtful study designs and integrated analysis concepts, can facilitate substantial advances in our understanding of predation energetics in a changing world.

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Chapter 3

Multi-sensor biologgers and innovative training allow data collection with high conservation and welfare value in zoos

This chapter is reformatted here from the following published version in the Journal of Zoo and Aquarium Research:

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The data presented in the following chapter were collected during my Master of Research degree from Swansea University (awarded 2018). A subset of the dataset collected during that time was repurposed here due to the Covid-19 pandemic delaying new data collection and in line with best practices on the reuse of animal tag data to maximise information gain from animals used in research (see Williams et al., 2020). Please note that an earlier version of dead-reckoning was included in English (2018), which has been updated and expanded here in line with Gunner et al. (2021).

Abstract

Zoos are valuable resources for research, providing scientists with access to rare and elusive species in an easy to observe environment. Animal-attached loggers (i.e., biologgers) offer profound insight into animal behaviour. Their use in zoos has high yet largely untapped potential to collect data relevant for wild animal research and conservation but also welfare and enrichment monitoring of the zoo animals themselves. However, affixing biologgers to study animals can be problematic in captive settings, limiting the accessibility of this technology for use on zoo species which ordinarily need to be sedated for the fitting of such devices, including large carnivores. Here we show that biologging collars and crate-training allow collection of novel datasets on captive animals with high welfare and conservation value, using endangered African wild dogs (*Lycaon pictus*) tagged with tri-axial accelerometer and tri-axial magnetometer loggers, as a case study. These methods are used to describe immediate recovery from anaesthesia (where used), investigate whether activity levels are higher on days with carcass feeds as opposed to feeds of meat pieces given using tongs, and explore refinements to the dead-reckoning analysis procedure through studying animals in a known, enclosed area. Two yearling female wild dogs were fitted with biologging collars while sedated in preparation for translocation from London to Whipsnade Zoo, with data collected for 10-26 hours until collar detachment. Two adult male wild dogs at London Zoo were trained to accept collars in a modified crate in exchange for a food reward, which allowed fitting and detaching the collars without sedation, with data collected for 28 days. First, we show how accelerometer and magnetometer data allow detection of fine-scale individual differences in the recovery from sedation as well as within- and between-individual variation in activity patterns in relation to the type of food received (tong-feeding meat pieces *vs* rabbit and pony carcasses). Using the vectorial dynamic body acceleration metric (VeDBA), a proxy for movement-related energy expenditure, further shows that daily energy expenditure was higher on days with partial pony carcass feeds compared to rabbit feeds but varied considerably between days where flesh pieces were fed with tongs. Using the dead-reckoning method allowed reconstruction of fine-scale (1 Hz locations) movement paths within enclosures, indoors and outdoors, allowing visualisation and quantification of fine-scale movement and space use differences between individuals and over time, for example in response to different enrichment methods. Using multi-sensor biologgers, combined with training captive animals to accept collars without the use of anaesthetic, can enable flexible, experimental approaches to data collection with minimal impact on study animals, providing novel understanding of relevance for both zoo and wild animals.

Keywords: biologging, captivity, daily diary, behaviour, welfare, enrichment, space use, dead-reckoning.

Introduction

Biologging, i.e., data collection of multiple variables using animal-attached tags, has seen considerable technological advancement in recent years (Ropert-Coudert and Wilson, 2005; Wilmers et al., 2015; Williams et al., 2020). Modern biologgers, such as Daily Diaries (hereafter DD; Wildbytes Ltd., Swansea University, UK), can collect fine-scale data at sub-second intervals, recording acceleration and compass data, as well as ambient temperature, pressure and light levels (Wilson et al., 2008; Williams et al., 2020). This level of detail allows detailed insight into animal activity and behaviour patterns, movements and space use, and individual state from the logger outputs (Wilson et al., 2018). Indeed, loggers such as the DD are typically used to investigate the behaviour of wild animals that cannot easily be observed (Brown et al., 2013) but also hold considerable potential in improving livestock management practices (Barker et al., 2018; Vázquez Diosdado et al., 2018) and optimising animal welfare in captive environments (Alex-Shorter et al., 2017). Understanding the behaviour of animals in human care can ensure effective welfare measures are in place under the 3Rs of reduction, refinement, and replacement framework (Russell and Burch, 1959; Flecknell, 2002), particularly regarding refinement. Note that while the 3Rs framework was initially developed for laboratory animal experiments, the framework is increasingly being applied to other contexts and there are mounting calls to consider this framework for wildlife, particularly in studies which manipulate animals such as those involving trapping and tagging (Field et al., 2019; Caravaggi et al., 2021). Logging data from captive animals can also aid behavioural interpretation of data from wild animals (Williams et al., 2014; English, 2018; Ladds et al., 2018; Studd et al., 2019; Rast et al., 2020), allowing refinements to data collection and analysis methods before deployment on wild animals.

Zoos can benefit from logged data collected on their animals to examine behaviour and improve enclosure design, enrichment activities, and feeding schedules to create more stimulating environments for zoo animals (Bassett and Buchanan-Smith, 2007; Mason et al., 2007). In particular, space use is an important potential indicator of enclosure appropriateness affecting captive animal welfare (Hunter et al., 2014). Providing sufficient space for captive animals has knock-on effects for social interactions and stress experienced in shared enclosures (Greggor et al., 2018), as enclosures with more usable space facilitate exploratory movement and social companion choice (Browning and Maple, 2019). This also affects reproductive success, which is particularly important in the captive management of endangered species (Carlstead and Shepherdson, 1994; Morgan and Tromborg, 2007). As accelerometers and magnetometers record the necessary information to derive estimates for both heading (Han and Wang, 2011) and speed (Bidder et al., 2012), the movement path of an animal fitted with these sensors can be reconstructed at a very fine scale, both indoors and outdoors, through dead-reckoning (Wilson and Wilson, 1988; Wilson et al., 1991; Bidder et al., 2015; Gunner et al., 2021a). This can provide specific, useful data with which to evaluate enclosure use and housing conditions of zoo animals, for example by detecting pacing, a common food anticipatory activity in captive carnivores (Bassett and Buchanan-Smith, 2007).

Although behavioural information can be collected unobtrusively in zoos with relative ease by simple observation, this approach is generally limited to zoo opening hours. This largely precludes the collection of nocturnal behaviour, as well as failing to collect data without the presence of a human observer. Closed-Circuit Television (hereafter, CCTV) recordings can be used to fill in some of these knowledge gaps (Ferguson and Turner, 2013; Walsh, 2017), but these also have limitations, including missing data when the study animals are out of sight of the cameras and the extent to which environmental factors (such as snow and rain) may affect film quality (Hall and Roshier, 2016).

Some of the advantages of biologgers in a zoo environment are, however, seemingly negated by problems, both ethical and technical (Hawkins, 2004; Minteer and Collins, 2013), of the animal capture and sedation process. Against this, biologging data, e.g., from accelerometers and magnetometers, has the potential to reveal and quantify even fine-scale individual differences in the recovery from sedation. However, capture and sedation is not always necessary because crate-training allows zoo-keepers to interact safely with zoo-housed animals without the use of sedation (Phillips et al., 1998; Rodden et al., 2012). Crate-training has successfully been used to collect blood samples from nyala (*Tragelaphus angasii;* Grandin et al., 1995), treat wounds and collect milk from bongo (*Tragelaphus eurycerus*; Phillips et al., 1998) and transport Marabou storks (*Leptoptilos crumenifer*; Miller and King, 2013). It is standard practice for large canids to be familiarised with crates prior to translocation (Rodden et al., 2012) and crate-training has been used to detect pregnancy in maned wolves (*Chrysocyon brachyurus*; Aitken-Palmer et al., 2017). As well as being key to captive animal transportation (Linhart et al., 2008) and veterinary interventions (Phillips et al., 1998), training exercises can also provide additional opportunities for behavioural stimulation and enrichment (Savastano et al., 2003; Szokalski et al., 2012; Westlund, 2014). Crate-training may therefore provide a safe method for deploying collars with loggers on carnivores while ensuring zoo-keeper safety, avoiding unnecessary sedation of animals, and providing a source of enrichment.

Here, we provide a methodological case study to showcase the opportunities and potential for zoos by combining innovative training and the use of multi-sensor biologgers for data collection with high conservation as well as animal welfare value. To do so, we report data from fitting DD-equipped collars (cf. Wilson et al., 2008) to four captive African wild dogs (*Lycaon pictus*) in London and Whipsnade zoos. African wild dogs are the second-most endangered canid species in Africa, with an estimated wild population of 6,600 individuals (Woodroffe and Sillero-Zubiri, 2012). Having experienced a range contraction of 93% (Wolf and Ripple, 2017), captive studies have a potentially significant role to play in the conservation of this species. Previous attempts to assess the efficacy of wild dog enrichments have focused on zoo-keeper surveys rather than quantitatively assessing variation in activity between days with and without enrichment, and on days with different enrichment types (Cloutier and Packard, 2014). DDs can effectively quantify changes in activity levels and prevalence of stereotypic behaviours (such as pacing) resulting from enrichment and allow assessment of enclosure use. Fitting captive members of a species with loggers also facilitates the construction of preliminary logger-based ethograms (Williams et al., 2014; Rast et al., 2020). This can inform studies deploying this technology in the wild, allowing more accurate behavioural interpretation, even when observations are not possible, thus benefitting conservation research.

Here we outline how captive African wild dogs were successfully trained for collar deployment and retrieval, while providing example applications of biologging collars in zoos. Using the wild dog data from these two zoos, we; (i) compare procedures for collar fitting with and without sedation, outlining for the latter a process for collaring captive African wild dogs through crate-training, (ii) assess post-sedation recovery, and enclosure use and activity patterns in relation to feeding regimes, and (iii) determine fine-scale movements and space use within enclosures through dead-reckoning. These analyses were chosen due to zoo staff interest in sedation recovery and activity in response to feeding and the value of the zoo context for refining dead-reckoning analysis procedures in known, enclosed areas. We provide a descriptive overview of sedation recovery in two individuals for adaptation in other contexts with larger datasets, investigate whether activity levels are higher on days with pony or rabbit carcass feeds due to prolonged interaction with food items and show how dead-reckoning can be used to generate highly resolved movement paths.

Materials and Methods

Ethics statement

The data presented here were collected prior to the commencement of this PhD programme. As such, ethical approval was obtained for this study from Swansea University under the approval codes STU_BIOL_29066_280817112012_2 and SU-Ethics-Student-180917/2, and the AWERB (Animal Welfare and Ethical Review Body) approval code IP-1617-8. The Zoological Society of London approved the work under the reference code ZDZ78.

Collar fitting strategies: sedation and crate-training

Captive African wild dog collar deployments began following a series of initial trials on domestic dogs (*Canis lupus familiaris*), conducted to test and improve collar design and formulate biologging data analysis procedures. On the 27th of March 2017, two collars equipped with a Daily Diary multi-sensor biologging tag (details below) and an automated drop-off mechanism, designed and constructed in Swansea University, were deployed on two female African wild dogs being moved from London to Whipsnade Zoo. These individuals were part of a pack of five female litter-mate yearlings, weighing 29 and 30 kg respectively. Following this, two adult males were trained to receive collars in a protected training crate in London Zoo. These individuals were the oldest, from a pack of eight, and responded better to training than the other pack members, who were litter-mate yearlings. Both males weighed >30 kg. All pack members were born in captivity. A modified crate was made in London Zoo, featuring a weighing platform as its base and an end slat with a hole where the head could fit through to rest on a wooden platform, surrounded by a wire mesh. First, the chosen individuals were familiarised with the crate, located in the indoor section of the enclosure. It was left in this position to allow free entry for wild dogs at any time they had indoor access. A food reward (i.e., meat pieces, typically horse meat) was given when a wild dog touched a metal rod used in contact training. This reward was dispensed *via* metal tongs to ensure the zoo-keeper was not at risk of being bitten. A leather strap of the same material used to make the collars was hooked over the top of the hole and screwed into the sides of the platform. This allowed each wild dog space to fit their head through, while familiarising them with the feeling of the leather strap. Further training took place using rope to familiarise the wild dogs with neck contact, as this was a familiar and durable material. This was swapped for a noose when the wild dogs repeatedly took the rope into the enclosure. The noose facilitated approximate measurements of neck circumference per individual with a tape measure and collar deployment.

The London Zoo enclosure consisted of two paddocks, affording a combined space of 1853 m^2. The larger paddock measured 998.75 m in length and had a width of 14.5 m while the smaller paddock was 28.5 m long and 14.5 m wide. These paddocks could be separated when necessary (e.g., males and females were separated prior to the translocation of the female wild dogs to Whipsnade), but remained connected for the duration of London Zoo collar data collection. The indoor section of the enclosure featured three dens, measuring 4.6 x 3.3 m each. All individuals in the pack had access to the full enclosure throughout the study period, including at night. 7 CCTV cameras (HandyKam, UK) were set up in the London Zoo enclosure for the duration of the collar deployment (see English (2018) for further detail). Due to the unique coat patterns of the wild dogs, it was possible to distinguish individuals consistently from the video footage. Times were recorded to the second by the CCTV system and noted during behavioural observations. All times, for cameras, behavioural observations and collar calibrations were standardised using the website time.is. Behavioural observations were then matched to collar outputs using the visualisation and analysis software DDMT (Daily Diary Multiple Trace, Wildbyte technologies – http://www.wildbytetechnologies.com/).

Throughout the study period, the wild dogs were fed according to their normal feeding schedule, with daily feeds consisting of either a partial pony carcass (twice a week), whole rabbit carcasses (once a week) or 1 kg of meat pieces administered by tongs (four times a week). The study period for the two London Zoo wild dogs consisted of 14 days during which wild dogs received meat pieces *via* tongs (typically horse, 1 kg per individual), 8 days where a partial pony carcass was shared amongst the pack, and 4 days where each wild dog received a rabbit carcass. Crate training continued during the period collars were worn and collars were removed while the wild dogs were in the crate receiving their food reward through use of the collar's quick-release buckle.

Collar design

For the Whipsnade Zoo deployment, standard leather dog collars were cut and sewn back together with nylon string. They featured a DD, with tri-axial accelerometers and magnetometers and environmental sensors (Wilson et al., 2008), and a drop-off mechanism governed by the DD turning on a separate battery connected to a burn resistor and double nylon line (60 kg resistance), and a battery for each component. The DD was powered by two 2/3 A Lithium batteries and the burn resistor was powered by a 100 mAh 3.7 V Lipo rechargeable battery. The DD was programmed to trigger the drop-off at a set time by passing high current through the resistor, which then became hot, causing the nylon line used to sew the collar to melt and sever, allowing the collar to drop. All components were contained in a robust 3D-printed nylon housing attached to a leather strap. This was adjusted to a suitable circumference, as determined by zoo veterinary staff, closed with a standard clasp and excess material was cut.

The London Zoo collars were made using leather belt blanks with a thickness of 4 mm and width of 28 mm. A quick release clasp with a breaking load of 200 kg (Pets Bits Online, UK) was chosen so that collars could be snapped on, and later released, in one swift motion. The collars were not adjustable, due to concerns that a pack mate might manipulate a looped collar, making it too tight on the neck. Conversely, if a collar was pulled loose, there was potential risk of a forelimb getting caught. The collars were initially riveted on one side only, so that adjustments could be made to get the best fit for both individuals. After zoo-keepers had adjusted the other side appropriately to fit the neck of the animals, collars were sent back to Swansea University to complete riveting and attach the logger housing. The housing was attached to sit at the ventral side of the neck so that the collar was bottom-weighted to reduce the incidence of collar roll, which affects accelerometer and magnetometer data. A supplementary training collar was provided while final adjustments were made. This allowed zoo-keepers to maintain regular training as the collars were completed. Training took place four days a week, from Tuesday to Friday inclusive, over a four-month training period. The training collar had a housing attached, containing two batteries and a DD, so that the weight would match that of the collars for deployment. The final weight of the collars, including all parts was 258 g, approximately 0.86% of the wild dogs' body mass and thus well below the 3% rule in accordance with standard welfare guidelines (Kenward, 2000) and with collar size and weight conforming with recommendations for high quality biologging data (Dickinson et al., 2020).

Housing units were designed in Swansea University, with space for two A batteries and a DD. Data were stored on 2 GB microSD cards within the DDs. Two SAFT (Levallois-Perret, France) 2/3A Lithium batteries connected by diodes were used to power the DD. These housings and loggers were used for both the Whipsnade and London deployments. However, as the drop-off mechanism was not robust enough to withstand wear by wild dogs (see Results), the collars for use in London Zoo did not feature a drop-off mechanism. The protective nylon housing for the DD and batteries was attached with countersunk screws and taped over with

Tesa© tape to ensure no irritation to the neck. The DD was set to record acceleration at 40 Hz, magnetometry at 16 Hz and environmental data at 4 Hz for one individual in London Zoo; data from the other three wild dogs were recorded at 20 Hz, 8 Hz and 2 Hz by the respective sensors. This decision was taken following consideration of the advantages and disadvantages of sampling rate on data value and information content, in relation to power requirements and battery size (discussed in English, 2018). DD start time was noted to the second using the website time.is to, later, define a start time in the logged data. Upon collar switch on, collars were then immediately calibrated using a series of distinct motions. These set motions were easily distinguishable in the logged data and the start and end points of each motion were noted to the second, confirming that timing was accurate. Behavioural observations and video footage were also timed using time.is for consistency.

Data interpretation

Upon collar retrieval, DD data were inspected using the complementary data visualisation software Daily Diary Multiple Trace (DDMT; Wildbyte Technologies Ltd., UK; available from https://github.com/DDMT-Software/DDMT). The data were calibrated to perform soft and hard iron corrections to the magnetometry channels (Bidder et al., 2015; Gunner et al., 2021a), accounting for any interference in magnetic data caused by metal on the collars themselves. 3D *m-sphere* visualisations (Williams et al., 2017) were used to inspect the data before and after corrections to confirm that magnetometry data had been corrected adequately to account for potential interference from metal enclosure fences.

Data were time-matched to concurrent behavioural observations for interpretation. Traces from the sedation recovery period for the two wild dogs moved to Whipsnade Zoo were visually inspected in DDMT. We considered the time periods from wild dogs being placed in their transport crates (i.e., the time point at which all manipulation including placement in crates had finished) until they were fully alert. Longer consideration of micro-movements once alert was not possible here due to subsequent transport to Whipsnade Zoo. As well as graphing raw sensor data, DDMT computes a range of metrics calculated from acceleration and magnetometry data, including Vectorial Dynamic Body Acceleration (VeDBA; Wilson et al., 2008; Wilson et al., 2020). VeDBA is a reliable proxy for movement-related energy expenditure (Wilson et al., 2020) and speed (Bidder et al., 2012); it was used to examine activity patterns and space use *via* dead-reckoning (see below) over 12-hour active periods, from approximately 6am – 6pm, for the London Zoo data. This period was chosen to correspond with the daily active period of the wild dogs, as determined from visual inspection of biologging traces in DDMT and CCTV footage. For the Whipsnade Zoo data, tracks were reconstructed over approximately two-hour periods, for both wild dogs upon arrival in a small outdoor enclosure and indoor house, and for the initial exploration of the main outdoor enclosure for one individual the following day.

Statistical analyses

The R Environment for Statistical Computing was used for statistical analyses (version 4.0.0; R Core Team, 2020). Logger data were first visualised and the relevant sections extracted using DDMT. All figures were plotted using *ggplot2* (Wickham, 2016) and dead-reckoned tracks were mapped using *ggmap* (Kahle and Wickham, 2013). Segmented regression was used to determine the start and end points of rapid awakening from sedation using the *segmented* R package. Total daily activity levels in response to food received were tested for significance through non-parametric permutation testing for linear models with the *lmPerm* package (Wheeler and Torchiano, 2016). Permutation testing with the *lmPerm* package ran for 5000 iterations. Tukey's HSD (Honest Significance Testing) was used to calculate adjusted p-values for multiple comparisons. Significance asterisks were plotted (Figure 5) with the R package *ggsignif* (Ahlmann-Eltze & Patil, 2021).

VeDBA, derived from the acceleration data, and heading values, derived from the acceleration and magnetometry data, were used to reconstruct fine-scale animal movement paths, in a process termed dead-reckoning (Wilson and Wilson, 1988; Bidder et al., 2015). Accumulation of errors along successive dead-reckoned location estimates can cause dead-reckoned paths to drift from true positions unless corrected using ground-truthed location data collected at a coarser temporal scale (Bidder et al., 2015). To correct for this, location data were obtained by searching through CCTV footage and finding the longitude and latitude coordinates of known enclosure landmarks with Google Earth©. These verified locations were used to correct the dead-reckoned tracks (cf. Gunner et al., 2021b). As dead-reckoning allows path reconstruction with location data supplied at flexible, irregular time intervals, the time periods between coordinates were not equal. VeDBA and heading data were smoothed to 1 Hz to minimise accumulated error in dead-reckoned tracks and reduce computational power requirements, then exported from DDMT to compute dead-reckoned tracks in R, including location-based error correction, following methods outlined in Gunner et al. (2021a). Briefly, location-based error correction involves providing time-stamped verified locations for the dead-reckoned path to pass through, to prevent the path drifting as errors are accumulated over time (typically verified locations may come from additional sensors such as GPS units, but here the camera-extracted locations performed the same role). Walking, trotting and running behaviours were identified in DDMT using a Boolean time series approach (English, 2018; cf. Wilson et al., 2018). Data from a two-hour observation session at Whipsnade Zoo were used to match behavioural observations to Daily Diary outputs. Separate CSV files were created whereby each file represented repeated bouts of a single gait. These files were used in classification tree analyses in R, using the packages *rpart* (Therneau et al., 2015) and *tree* (Ripley, 2005) to determine which sensor outputs were most appropriate for classifying movement gaits through binary recursive partitioning. Specifically, classification trees were constructed with input data from each raw and smoothed acceleration and magnetometry axis as well as several Dynamic Body Acceleration (DBA) metrics. The DBA metrics included were ODBA (Overall Body Dynamic Acceleration), VeDBA (Vectorial Dynamic Body Acceleration) and VeSBA (Vectorial Static Body Acceleration). Classification tree outputs provided approximate value ranges for these metrics corresponding to discrete behaviours. These were used as guidelines to assist manual development of rules for the DDMT Behaviour Builder, aided by further visual inspection in DDMT so that all occurrences of individual behaviours could be classified. Following this procedure, only data associated with walking, trotting and running bouts were exported for the calculation of dead-reckoned tracks. This allowed avoidance of the path being affected by non-movement behaviours, as initial inspection indicated that frequent lifting and lowering of the head while resting could affect the path if not excluded. Instances of collar roll were rare but easily detected through visual inspection in DDMT due to changes in axes positions, and also removed from the subset of data exported to create dead-reckoned tracks. For Whipsnade Zoo, dead-reckoned tracks were reconstructed following the arrival of the wild dogs in their new enclosure to capture initial exploratory behaviour. For the London Zoo wild dogs, dead-reckoned tracks were created over 12-hour time periods, from approximately 6am – 6pm, corresponding with days where different food types were provided in London Zoo. As with the VeDBA data extraction, these times were chosen to correspond with the activity patterns of the wild dogs, and the sleeping den was the start and end location for all tracks.

Results

Collar deployment via sedation versus crate-training

The resistor-powered drop-off mechanism was not robust enough to withstand the high activity levels and social manipulation of collars exhibited by African wild dogs, with the first collar having dropped off after 10 hours (1,749,880 acceleration events collected at 20Hz) and the second after 26 hours (2,307,400 events at 20Hz) - significantly shorter than the planned three weeks of data collection. The non-drop-off collars with a quick-release clasp deployed in London Zoo collected data for the full planned four-week collar deployment period and were both deployed and retrieved without complications. These collars were deployed on the 13th of July 2017 and recorded until the 9th of August, providing approximately 1,344 hours of data, 672 h per individual (93,246,120 acceleration events at 40 Hz and 46,908,828 at 20 Hz respectively).

Awakening after sedation showed similar VeDBA traces for both sedated wild dogs. The acceleration and VeDBA traces for the first minute after waking up for each individual show distinctive waveforms, shallow and repetitive, suggesting that both individuals were raising and lowering their heads repeatedly upon awakening, though without otherwise changing posture. The magnetometer traces highlight individual differences in the recovery between the two individuals, with one showing non-overlapping traces (Figure 1a) while the second shows a periodic, repeated crossing of magnetometer channels (Figure 1b), with the latter indicating changes in head orientation. Plots of VeDBA over a ten-minute interval from the moment each sedated individual had been placed in the transport crate and left to recover (Figure 2) show that both individuals ‘woke’ from sedation approximately five minutes after being placed in their crates. The rapid wake-up phases lasted 28.8 seconds for one individual and 50.5 seconds for the other. VeDBA traces stabilised 3 and 3.4 minutes after wake-up respectively for the two wild dogs (Figure 4).

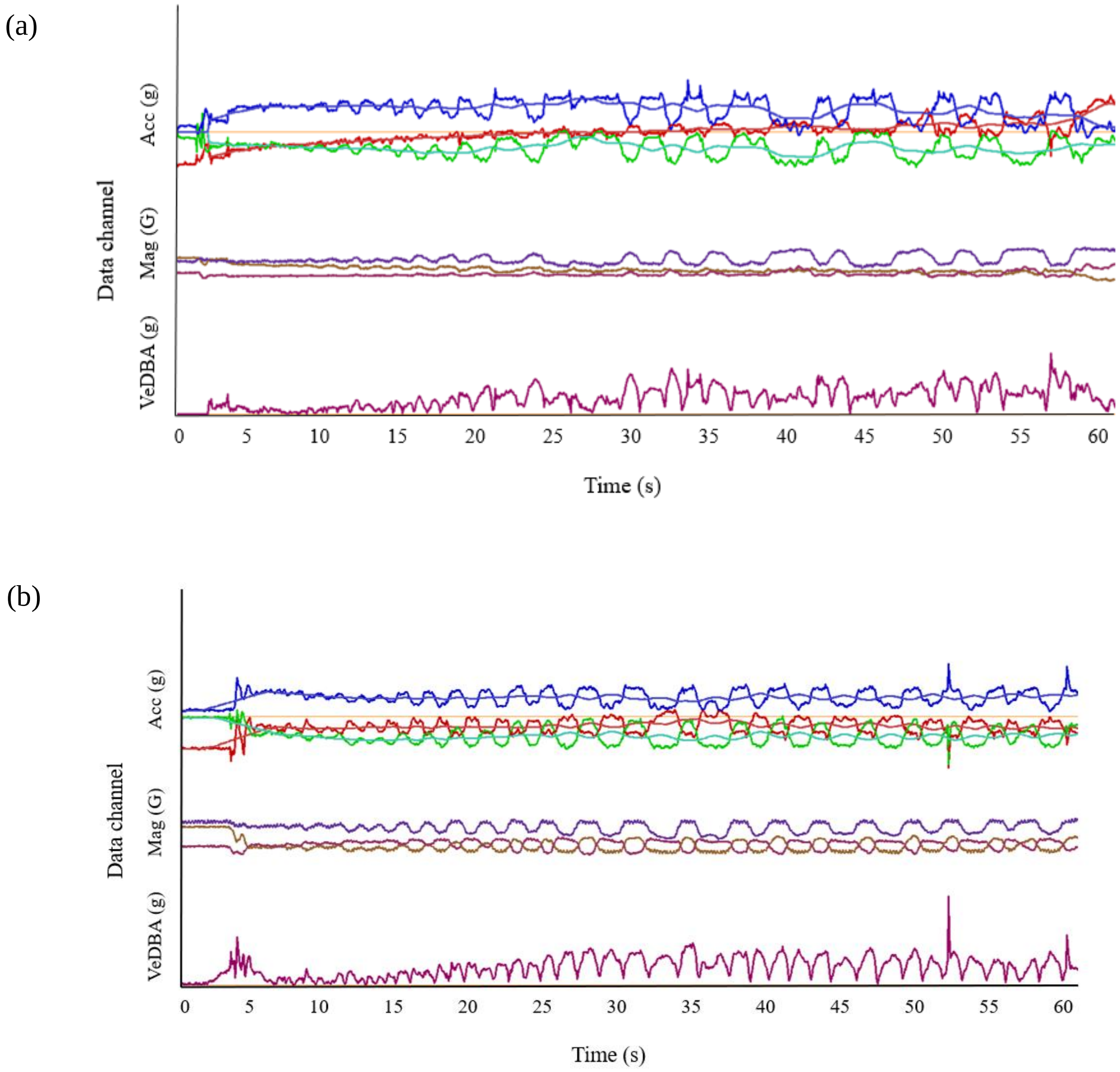

Figure 1. Acceleration, magnetometry and raw VeDBA traces from the first minute after waking up from sedation for the two wild dogs moved to Whipsnade Zoo (a) Brandy, (b) BeeBee, respectively. Tri-axial acceleration data were recorded at 20Hz (blue = heave, red = surge, green = sway). Raw acceleration depicts movement, while the smoothed line running through each acceleration axis indicates a lack of postural change. Acceleration data were smoothed at the default rate of 80 events in DDMT.

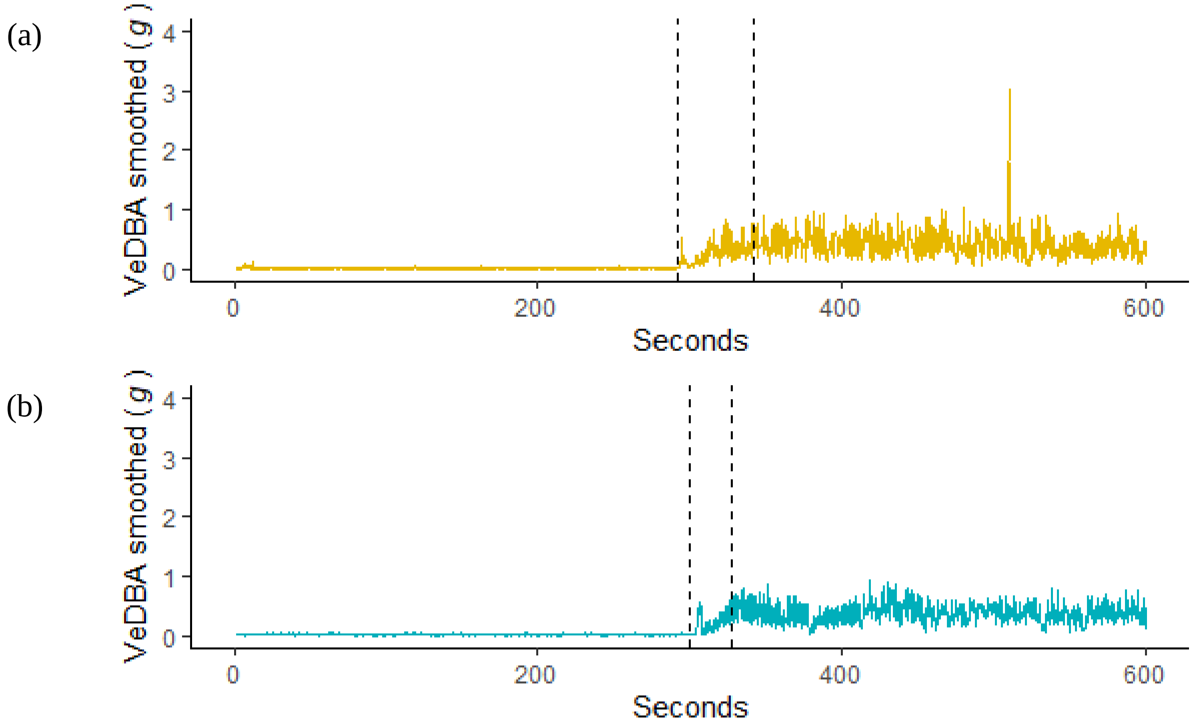

Figure 2. VeDBA over time for 600 seconds following two African wild dogs, (a) Brandy and (b) BeeBee, being placed into the transport crate following a veterinary check and collar fitting. Both individuals became fully alert after approximately 300 seconds. The dashed lines identify the breakpoints identified by segmented regression analysis, representing the start and end points of the rapid wake-up phase for each individual.

Activity patterns in relation to feeding regimes

Adjusted p-values were computed with post-hoc pairwise comparisons of food types, which found significant differences between pony carcass and rabbit feeds ($p = 0.039$), but not tong and pony carcass feeds ($p = 0.07$) or tong and rabbit feeds ($p = 0.666$). There were significant differences in daily activity levels, measured by total daily VeDBA, both between individuals ($p = 0.006$) and between days where different foods were provided ($p = 0.036$). Tong feeds of meat pieces showed the most variation in total daily VeDBA values, with both the lowest and highest activity days corresponding with tong feeding for both individuals (Figure 3). Carcass feeds were associated with higher daily total VeDBA values than rabbit feeds (Figure 3).

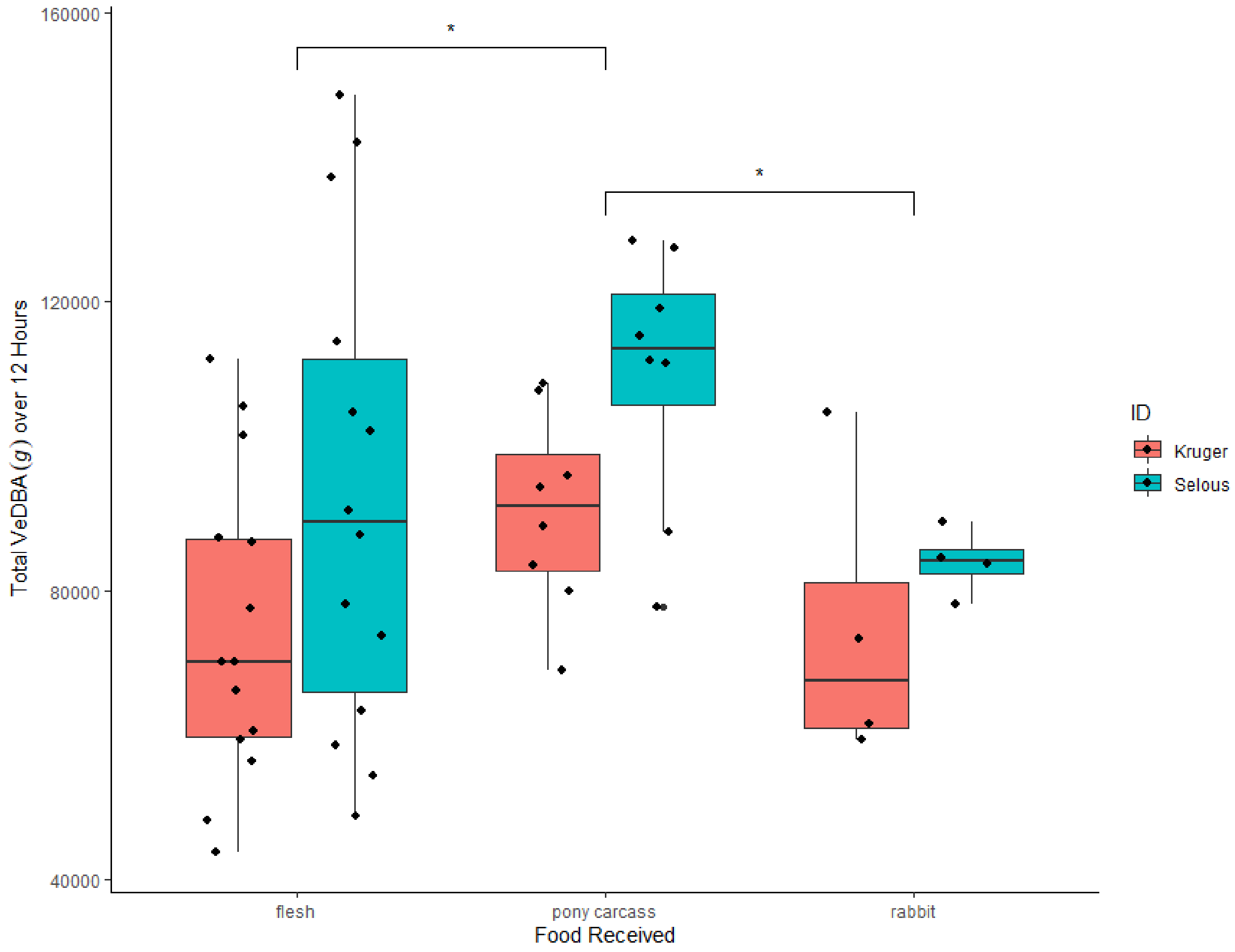

Figure 3. Total VeDBA values over a 12-hour period for two individuals in relation to food type received on a given day at 40Hz (Kruger, salmon shading) and 20Hz (Selous, blue shading). These data were collected in London Zoo on the individuals which did not undergo sedation and translocation.

Enclosure use via dead-reckoning

Paths were successfully reconstructed encompassing both indoor and outdoor areas of the enclosures and showed no indication of pacing behaviour in any of the study individuals (Figure 4). A dead-reckoned track representing the first exploration of the main outdoor enclosure area in Whipsnade the morning following translocation shows wide coverage of the new enclosure, traveling a cumulative distance of 1238 m (Figure 5). The dead-reckoning procedure was considered highly accurate as paths approach, but stay within, the confines of the enclosure boundaries.

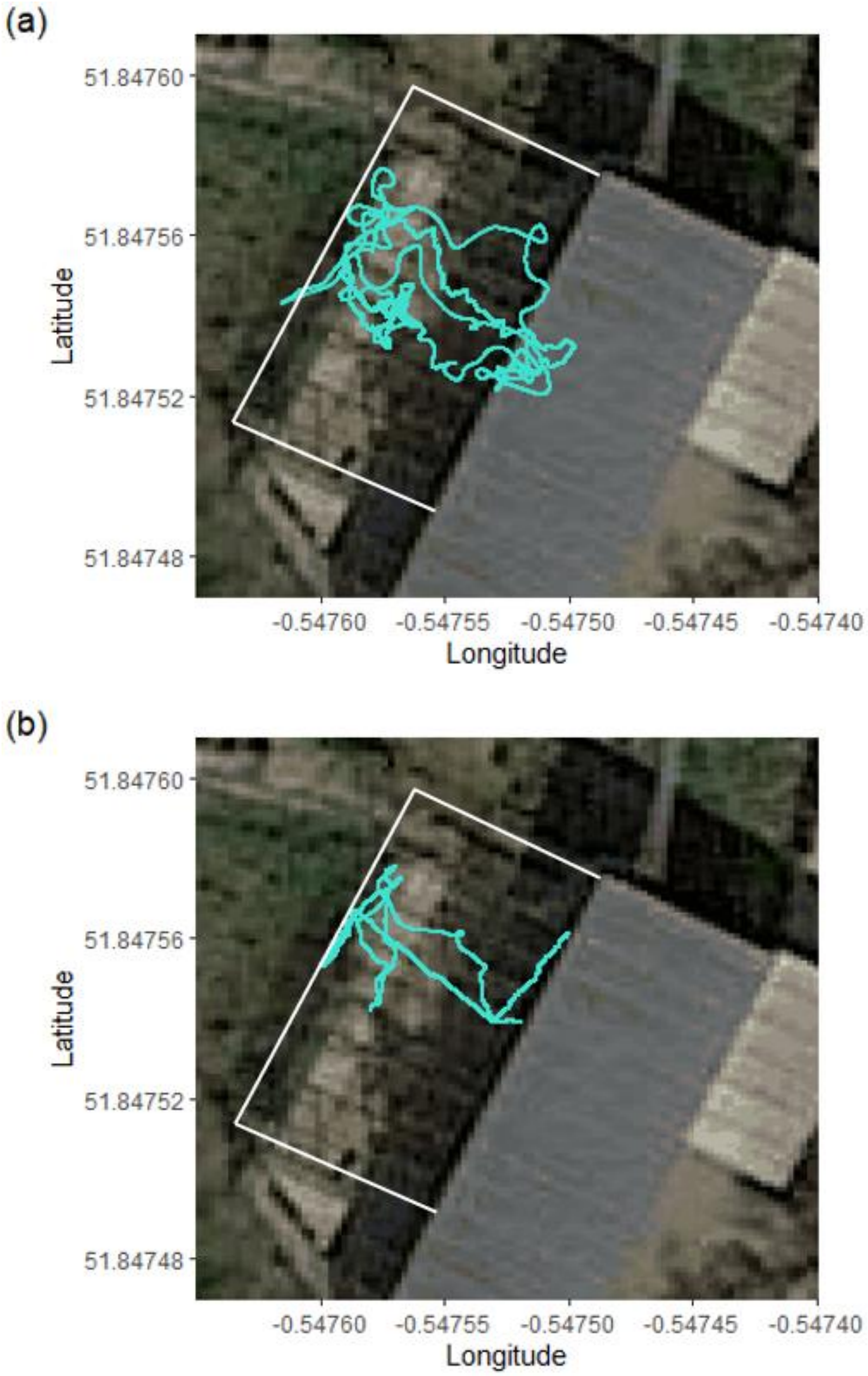

Figure 4. Moving in and out of the house to the small outdoor area on the night the wild dogs arrived in Whipsnade, (a) Brandy, (b) BeeBee. The tracks relate to the same two-hour period with 6 and 14 longitude and latitude coordinates for correction respectively, taken opportunistically based on confirmed individual presence at a landmark location. The white lines outline the outdoor portion of the enclosure which was accessible to the wild dogs on the day of arrival.

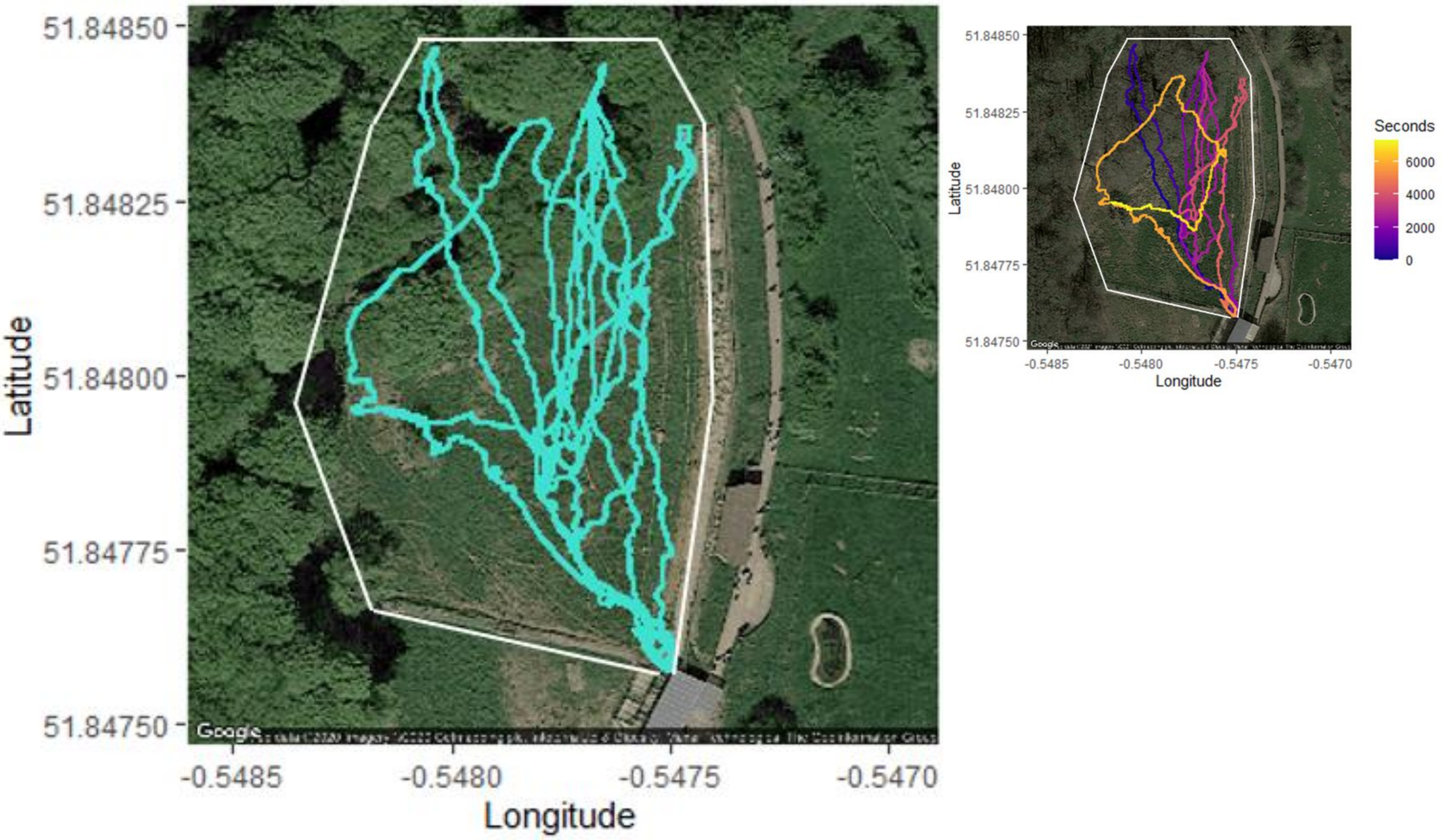

Figure 5. A 1 Hz dead-reckoned track obtained from 20Hz Daily Diary data representing the first exploration of a new outdoor enclosure at Whipsnade Zoo by a female African wild dog yearling (Brandy). 27 longitude and latitude coordinates were used in path correction over the two-hour period. The inset represents the same track coloured by time, moving from darker (blue) to lighter (yellow) colours. The boundaries of the outdoor paddock are marked in white.

The dead-reckoned tracks shown in Figure 6 were created using 24 longitude and latitude coordinates for location correction which had been extracted from CCTV camera footage. While the overall shape of these paths can be generated with fewer correction locations, this affects the cumulative distance estimates (Figure 7). Visual inspections of carcass feeds showed clustering at the carcass position, but rabbit and flesh chunk feeds did not have discernible effects on daily enclosure use (Figure 6). The cumulative distance moved of both individuals was highest for the rabbit feed days, at 466.1 m and 507.4 m respectively, compared to 332.3 m and 296.9 m for carcass feeds and 310.0 m and 249.7 m for tong feeds (Figure 7). The London Zoo dead-reckoned tracks show markedly more restricted movements than the initial enclosure exploration seen in Whipsnade Zoo, as not all areas of the enclosure were visited daily.

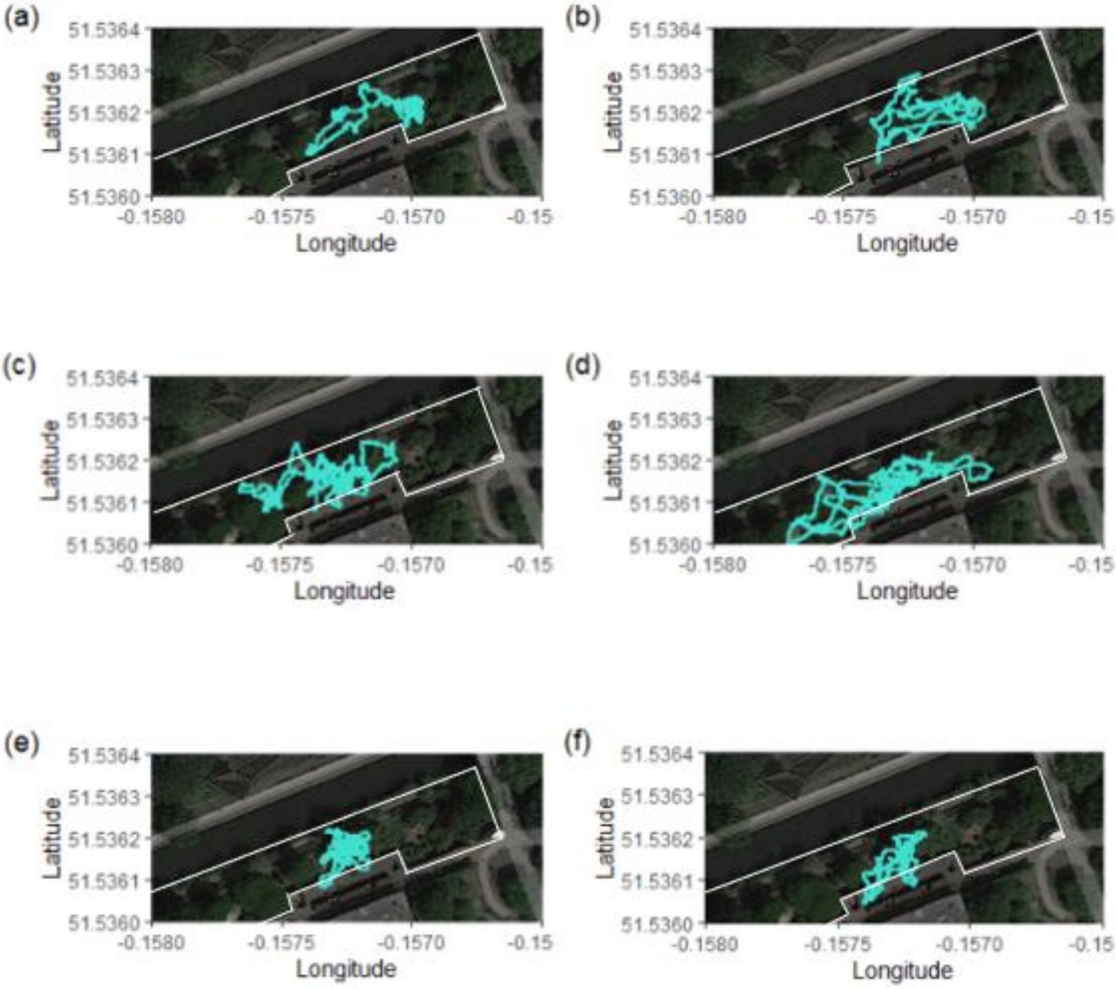

Figure 6. Three 12-hour dead-reckoned tracks for each of the two male African wild dogs which were collared in London Zoo, corresponding with different food days. The left column shows data from Selous (20Hz) and the right column shows data from Kruger (40Hz). The upper row shows tracks from a day where a partial pony carcass was fed (the 15th of July 2017), the middle row shows tracks when rabbits were fed (the 16th of July 2017) and the lower row shows tracks from a day where meat pieces were fed via tongs (the 19th of July). Carcass feeds appeared to bias wild dog space-use to where the carcass was deposited in the outdoor enclosure, whereas when meat pieces were tong fed, space-use was biased towards the middle of enclosure, close to the indoor access point, where these feeds took place. All dead-reckoned tracks were produced at 1 Hz. The white lines indicate outdoor enclosure boundaries, though access to underground indoor housing was available to the south.

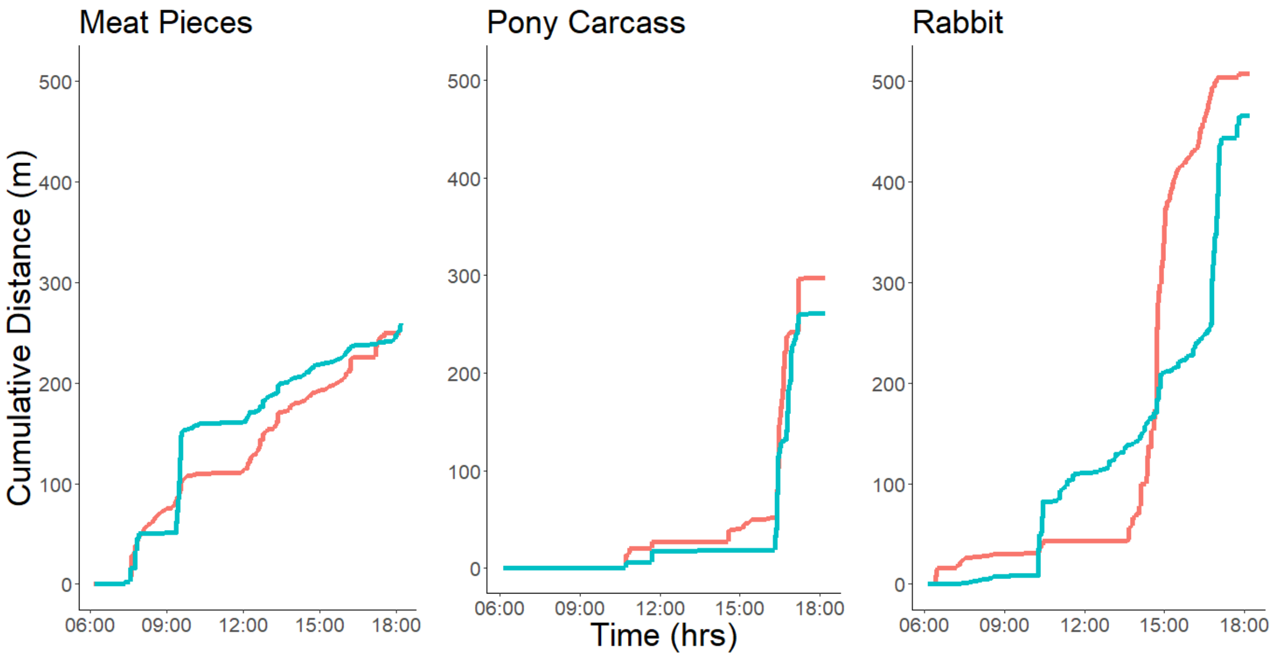

Figure 7. Cumulative distance moved per individual derived from the dead-reckoned data for three days with three different feeding schedules. The meat pieces and pony carcass feed days (which occurred on the 19th and 15th of July 2017 respectively) shown depict similar distances moved, while the rabbit feed day (16th of July 2017) shows larger distance covered. (Kruger data shown in salmon, Selous data shown in blue).

Discussion

We show the potential of biologging in zoo-based research, with positive implications for animal welfare, using biologging data collected on four wild dogs from two zoos. The resulting data can be used to quantify responses to sedation, activity levels and enclosure use, with potential benefits to captive welfare management decisions and trialling methods to inform studies on wild counterparts.

Though the available timeframe for sedation recovery analysis was short, before translocation affected the logger data through crate lifting and transport *via* truck, the data presented here indicate quick recovery times. However, where longer-term consideration is possible, VeDBA may be examined over several days post-sedation to assess impacts on activity (Wilson et al., 2019). Nonetheless, here, despite the short timeframe available, VeDBA was useful in examining immediate responses and activity following sedation recovery (Figures 1-2). The success of the crate-training and the second collar design that followed suggest that future translocations may implement similar training procedures and thus negate the need for sedation prior to transport. Conversely, future cases where sedation is still required for veterinary procedures without translocations would allow individual differences in sedation recovery to be examined over longer time frames. Sedating animals comes with many risks, such as hypothermia, respiratory depression, and even mortality in rare cases (Stegmann, 2000; Muir and Hubbell, 2014). Avoiding anaesthetic in the second deployment allowed collection of valuable data without these risks with the added advantage that training exercises in captive animals provide a source of enrichment (Melfi, 2013).

Increased activity levels are often associated with improved captive welfare, but not if the activity stems from stereotypic behaviours (Bashaw et al., 2003; Andrews and Ha, 2014): using dead-reckoned tracks we could investigate this in unprecedented detail (see below). Both individuals collared in London Zoo showed higher daily VeDBA values when a partial pony carcass had been fed compared to rabbits but days where flesh chunks had been fed showed greatest variability in VeDBA (Figure 3). This could be an artefact of sample size, as flesh chunk feed days were the most prevalent, occurring four times a week compared to twice a week (partial pony carcass) and once a week (rabbits). Variety in feeding times and spatial distribution of food items are widely reported to be effective enrichment techniques for captive carnivores (Shepherdson et al., 1993; Cummings et al., 2007; Kistler et al., 2009; Wagman et al., 2018). Feeding in London Zoo occurred at approximately the same time each day during the study period, but the different foods provided were given from different enclosure locations and required different handling behaviours from the wild dogs. Hence, food type variation may play a role in the absence of stereotypies detected from the logger data or CCTV footage. Food items which stimulate natural foraging and food handling behaviours, such as the partial pony carcasses and whole rabbits provided here, can positively stimulate captive carnivore behaviour for several days after being given and may account for the high variability in activity levels on days when flesh chunks were fed (Shepherdson et al., 1993; Wagman et al., 2018).

In Whipsnade Zoo, we quantified the exploratory behaviour of African wild dogs released into a new enclosure for the first time. Translocating animals between zoos is crucial for maintaining genetic integrity of species in captive breeding programmes (Lacy, 2013). Despite the importance and prevalence of this activity, there is relatively little consideration of the effects of between-zoo translocation in the literature. The preliminary data here depicting space use immediately following a translocation event highlight the use of logging devices as a promising method for understanding post-translocation behaviour of endangered captive species. Future work should consider prolonged logger deployment, with data collection also collected in the zoo occupied before translocation for comparative purposes where feasible.

‘Pacing’ is a locomotory stereotypy which typically involves pacing over and back along a fixed route, typically a straight line but sometimes in circles or figures of eight shapes (Clubb and Vickery, 2006). This distinctive movement behaviour should form clear patterns in dead-reckoned tracks where it occurs, but no evidence of stereotypic pacing was detected in the African wild dogs in this study. Stereotypies are thought to arise when captive animals cannot conduct their natural behaviours, especially those related to ranging and foraging (Clubb and Mason, 2003). While conditions in captivity can never match the large territory sizes of free-roaming African wild dogs, feeding enrichment is feasible and widely implemented (Packard et al., 2010; Price, 2010; Cloutier and Packard, 2014). Food-related enrichment is thought to be the most effective in reducing or eliminating African wild dog stereotypies

(Cloutier and Packard, 2014) but positive benefits have been found from adding even short training periods to the care schedules of pacing captive wild dogs (Shyne and Block, 2010). The rotation of food type given and incorporation of whole rabbits and partial pony carcass feeds may contribute to the absence of stereotypic pacing. The regular training exercises for collar fitting may also be considered as enrichment (Westlund, 2014; Fernandez et al., 2019).

The lower cumulative distance estimates for the London Zoo dead-reckoned tracks are in accordance with the advanced age of both adult males and, though cumulative distance estimates vary with the frequency of location corrections, this study highlights the value of this metric as a relative measure to compare between days. This has wider implications for other studies implementing dead-reckoning methods and may provide guidance for selecting sampling frequency in wild deployments where loggers are being used in conjunction with units collecting location data such as through GPS or Argos satellite telemetry. Performing behaviour classification to isolate movement from non-movement behaviours prior to reconstructing dead-reckoned paths was an important methodological step to ensure tracks stayed within enclosure boundaries. This too has wider implications, suggesting that at least preliminary behaviour classification is an important and under-utilised step of the dead-reckoning procedure. This study provides important evidence in response to pertinent questions regarding sampling frequencies and behaviour classification in track reconstruction procedures and warrants further study, particularly involving animals in enclosures.

Developing new training regimes such as the one outlined here facilitates the collection of useful activity data which can inform animal welfare in captive settings, which is broadly applicable to a range of species living in zoos. These training activities also have positive consequences for captive animal health. Continued training with the modified crate has facilitated regular collection of individual body mass data. A number of veterinary interventions have also been streamlined by continued crate training while avoiding anaesthesia, including administering eye drops to an individual that developed an ulcer and taking samples of facial lesions which broke out in multiple pack members with unknown cause (L. Harvey, pers. obs.). Where sedation is still required, crate training has also been used in London Zoo to calmly separate two wild dogs for procedures requiring general anaesthesia. Crate training is felt by staff to have increased the general training standard by increasing the trust between keeper and animal, with one individual having successfully undergone venepuncture without sedatives in another training area. As such, of the two different collaring approaches used, the quick-release collars and associated training procedures were more advantageous for the zoo environment than the drop-off collars.

There is a lack of consensus regarding whether tags on collars, or even collars themselves, have negative impacts on animal behavioural patterns and a resultant need for species-specific, and perhaps even individual-specific, assessments (Horback et al., 2012). Wide-ranging carnivores are particularly vulnerable to stereotypic behaviours (Clubb and Mason, 2003), and so training captive carnivores to accept collars for the collection of logging data could be beneficial to their welfare by offering detailed insight into behavioural patterns. However, social carnivores should be monitored to assess reactions from conspecifics to collars. Another important consideration for tagging animals in zoos is the reactions of visitors, as entrance fees are often an important source of funding for zoos. Here, both London and Whipsnade zoos used this study as an opportunity to educate the public about the research that these zoos support, with relevant signage added to wild dog enclosures.

Conclusion

Biologging studies conducted in captivity provide information on the space use and activity patterns of captive animals. As well as the implications for captive carnivore welfare, this study highlights the enormous research potential of zoos to contribute to biologging studies by providing opportunities to develop new collar designs and trial data interpretation methods in a setting where non-domesticated animals can be observed with ease. The training exercise outlined here showcases a creative mechanism for fitting collars on a captive carnivore, with benefits for captive animal welfare and veterinary care.

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Chapter 4

Refining capture and collaring protocols for red foxes

Abstract

Wildlife species are often captured in ecological studies to take morphometric measurements, collect biological samples and/or fit animal-attached tags to collect data on movement and behaviour. Capture can be more or less difficult depending on the target species, with implications for the effort required by field teams, overall capture success and study goals. Though routine practice, wildlife captures have important welfare implications which should be carefully considered prior to each study. Full details on capture protocols are rarely shared with the international community, often limited to short descriptions in the methods sections of papers. This is a major issue as information sharing can improve knowledge on methods that lead to increased or reduced capture success. This ultimately saves researcher time and resources and, most importantly, boosts animal welfare. Here we pursue all of the above aims; collect morphometric data, collect biological samples and fit sensor-equipped collars. We share detailed capture protocols to offer insights to other researchers, while aiming to optimise welfare protocols. Having faced challenges in initial captures for our trap-shy target species, we present methodological considerations and refinements undertaken to successfully trap urban red foxes (*Vulpes vulpes*) in Dublin, Ireland (n = 16 captures) and related efforts as part of a pilot study in rural Tuscany, Italy (n = 3 captures). We recommend setting multiple capture sites but caution against prolonged time spent in traps for foxes. Remote transmission camera traps and remote trap alert systems are highly recommended to remotely monitor multiple trapping sites at once with reduced disturbance and to facilitate quick arrival at capture sites. We discuss a cheap, lightweight collar drop-off solution to negate the need for a second capture for collar retrieval. In Dublin, we found the likelihood of capturing a fox was significantly affected by rainfall but not temperature. We conclude with an easy-to-consult checklist, providing advice on trap set, pre-baiting, collar drop-offs and weather conditions, to aid researchers embarking on the capture of foxes and other difficult to trap species, particularly in urban areas with high levels of human activity.

Keywords: wildlife welfare, red fox, *Vulpes vulpes*, urban wildlife, trapping, tagging, movement ecology.

Introduction

Many ecological studies involve the capture of wild animals, for example to collect morphometric data or fit transmitters. Morphometric data offer important insights into within- and between-population intraspecific variation in physical traits, such as body condition, with potential implications for survival and fecundity (Murray, 2002; Reading, 2007; Newey et al., 2010). Biological samples collected through animal capture can be used for myriad purposes including hormone analysis (Amin et al., 2021), assessment of the microbiome (Raulo et al., 2021) and disease screening (Hidalgo-Hermoso et al., 2021). Behaviour during the capture event or upon release can be used as measures of animal personality (Mella et al., 2016; Amin et al., 2021). Animal-attached sensors such as GPS units and accelerometers provide insights into many facets of animal movement and behaviour, including space use, habitat selection, and feeding patterns (Darnell et al., 2014; Hanscom et al., 2023; Kobryn et al., 2023). Wildlife captures therefore facilitate the collection of multiple important data types which can inform wildlife conservation and management, with long-term studies shedding light on animal adaptations to global change (Lindenmayer et al., 2012). The capture of wild animals is therefore a routine and important aspect of many ecological studies, but requires careful consideration to ensure the highest possible welfare standards are maintained for study animals (McCarthy et al., 2013).

Despite the prevalence and fundamental importance of trapping in ecological research, detailed capture protocols and related animal welfare considerations are frequently not included in published outputs (Wilson and McMahon, 2006; Iossa et al., 2007). Trapping protocols are often only briefly mentioned in the methods sections of scientific publications, with insufficient information provided to ensure replication by other researchers and ensure animal welfare standards are met (Caravaggi et al., 2021). This results in an inability for researchers to replicate trapping protocols without contacting the original researchers directly, which is not always possible and with the relevant insights remaining obscure to a broader audience (Haddaway and Verhoeven, 2015). It is therefore of fundamental importance to share methodological details and advances gained in developing trapping protocols so that (i) researchers can learn from others' mistakes and (ii) researchers can reduce time, effort and resources wasted in repeating protocols which have been previously trialled unsuccessfully but remained unreported (Jakob and Long, 2016). Sharing such information allows for more informed, reliable capture protocols with positive outcomes for animal welfare and conserved researcher effort.

The relative difficulty of capturing an animal can vary between individuals, populations and species (Tuyttens et al., 1999; Stokes, 2012). Inter-individual variation, or personality, may result in bolder, more explorative individuals being captured more often than shy, less explorative conspecifics (Biro and Dingemanse, 2009). At the population level, there may be differences in trappability driven by degree of familiarity with human activity or past interactions with humans, such as that experienced between urban and rural populations (Shivik et al., 2005; Stillfried et al., 2017). Urban wildlife are more familiar with human structures and activities, which may make novel objects such as traps appear less daunting (Shivik et al., 2005; Barrett et al., 2019; Jarjour et al., 2020). Conversely, urban wildlife can maintain high levels of neophobia to avoid negative interactions with humans (Feng and Himsworth, 2014; Mazza et al., 2021), leading to heightened caution around traps. The lack of consensus regarding neophobia *versus* neophilia in urban populations (Griffin, Netto and Peneaux, 2017) suggests that species-specific investigations are warranted, with these traits having consequences for trapping and monitoring efforts.

There is considerable variation in how easy or difficult it can be to capture a particular species, with consequences for fieldwork protocols, researcher effort and animal welfare considerations. The red fox (*Vulpes vulpes*) is known to be difficult to capture for ecological studies (Kay et al., 2000). This is despite being one of the most studied carnivore species globally (Brooke et al., 2014) and with the largest range of any extant member of the carnivore family (Sillero-Zubiri and Macdonald, 2004). Despite the considerable body of research already conducted on the red fox, this species is of continued research interest for many reasons. Foxes show variable behavioural traits across their large range (Cavallini, 1996; Sillero-Zubiri and Macdonald, 2004; Main et al., 2020), come into conflict with humans in rural and urban areas (Kimmig et al., 2020; Basak et al., 2022), are sometimes managed in response to conservation efforts for other species (Fletcher et al., 2010; Tobajas et al., 2020) and are controlled as an invasive species in parts of their range (Harding et al., 2001; Mahon, 2009). Due to this wealth of research, foxes may be considered as an important ecological model organism. The extensive research conducted to date on the red fox, its wide range, cosmopolitan distribution and common occurrence in human-dominated environments, make it a suitable candidate for long-term studies on adaptation to global change, human-wildlife conflict and tolerance, invasive species ecology, predator control and more.

It is important that efforts to boost capture success do not lead to sub-optimal welfare standards for captured animals. Many studies have reported higher capture success rates using capture devices which restrain a single leg (such as cable restraint devices or padded foot snares) than with box or cage traps, which contain an animal as a door is triggered to close upon stepping on a treadle (Shivik et al., 2005; Muñoz-Igualada et al., 2008; McCarthy et al., 2013). However, leg-restraining traps have also frequently been reported to have higher injury rates, particularly to juveniles or non-target species which may also be captured (Muñoz-Igualada et al., 2008; McCarthy et al., 2013). The frequency of trap checks is another important aspect of trapping with relevance to both capture success and animal welfare. Reducing the frequency of trap checks can reduce effort and improve capture rates of species wary of human scent and activity (Arthur, 1988; Benevides Jr. et al., 2008), but may risk captured animals spending longer periods in traps (McCarthy et al., 2013). Reported trap check times for red foxes vary, with different studies typically reporting checks every 12 hours (Kobryn et al., 2023) or every 24 hours (Muñoz-Igualada et al., 2008), and many studies not reporting the frequency of trap checks. Reducing time spent in traps, for example through remote trap monitoring systems, is recommended to improve welfare of captured animals (McCarthy et al., 2013; Keiter et al., 2022). Potential welfare refinements to trapping protocols are an important area of research, particularly for species such as foxes which are widely captured for research and management.

Here we present challenges encountered and subsequent methodological refinements in capturing red foxes as part of a collaborative project on movement ecology and wildlife anaesthesia protocols. Briefly, the movement ecology study aimed to investigate movement rates and behaviour in Dublin's urban fox population for the first time, the results of which are presented in the subsequent chapter. The anaesthesia study aimed to compare fox vital signs and behaviour upon recovery between two different anaesthetic drug protocols (Romero Marco et al., in prep.). Meeting the aims of these two studies involved the live capture, sedation, morphometric measurement recording, biological sampling and collar fitting of red foxes. We report on capture efforts on urban foxes in Dublin, Ireland taking place from 2022-2024, following a related pilot study on rural foxes in Tuscany, Italy in 2022. We present detailed considerations and refinements required to ensure capture success of a trap-shy species. We also explore trapping success in relation to weather conditions, specifically temperature and rainfall. The issues encountered and resolved here and the presented methods should aid other researchers working on this species to improve capture success and collect important data under the above topics and beyond, while maintaining high welfare standards.

Materials and Methods

Data were collected in two distinct environments representing distinct management goals. We collaborated with two management authorities – a city council in Dublin (Ireland) and a game management authority in Lunigiana (Tuscany, Italy). A summary of key considerations for successful fox trapping is presented in Figure 1.

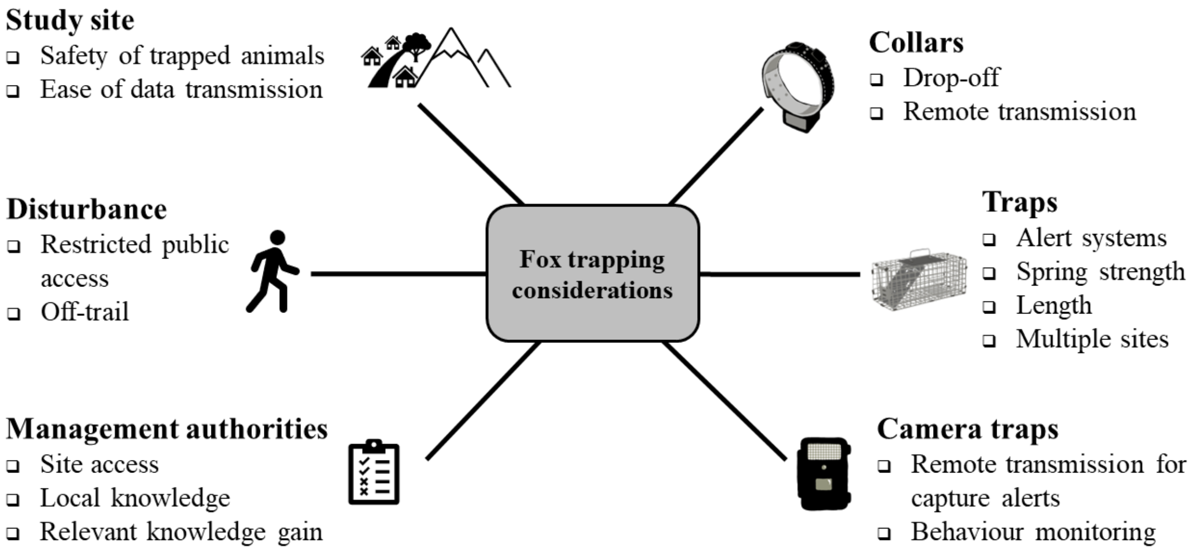

Figure 1. Infographic showing key considerations for refining capture protocols for both rural and urban foxes. Study sites should be chosen in safe locations which also optimise the likelihood of data transmission where possible. Disturbance to traps can be minimised by placing traps where there is restricted public access in areas of high human population density like towns and cities. Traps in rural areas should be placed so that they are offset from hiking trails. Collaborating with management authorities can assist with site access as well as providing important local knowledge and ensuring the outcomes of the research project are in line with management goals. Collars with drop-off mechanisms and remote transmission capabilities reduce the need for recaptures, which may not be feasible for trap-shy species, and

can boost data retrieval. Traps should be fitted with alert systems, such as trap alert tags and remote camera traps, notifying the field team of captures. Trap length, the strength of the spring in the trigger mechanism and the total number of traps and trapping sites used simultaneously can further improve capture success rates. Camera traps can provide important insights into animal behaviour around traps. When remote transmission cameras are used they can act as a secondary capture alert system and immediately confirm whether the target species or a bycatch species has been caught. GPS collar, trap and camera trap silhouettes created by Gabriela Palomo-Munoz.

Ethics statement

All fox captures and related activities were carried out with full ethical approval. In Dublin, the study was approved under AREC-E-23-22 by University College Dublin at the university level and AE18982/P216 by the Health Products Regulatory Authority (HPRA) at the national level. In Lunigiana, approval was granted under AREC-E-21-61 by University College Dublin and 2022AD000106 by Direzione Agricoltura e Sviluppo Rurale (Regione Toscana).

Selecting trapping locations

In Dublin, trapping sites were spread across the city so that different conditions within the urban environment were represented (Figure 2). Trapping locations were chosen through close consultation with Dublin City Council’s biodiversity office and park management staff. Traps were placed in secure locations to prevent disturbance or interference from members of the public. Five trapping sites were in gated park depot areas, one was in a pitch and putt golf course which was locked overnight, one was in a secured wildlife management area in an industrial estate and one was in the garden of a private, residential property.

In Lunigiana, traps were placed in rural sites which did not have restricted public access. To minimise disturbance in this setting, traps were placed in zones where human hunting activities were not allowed (which was also a requirement of the trapping permit). Care was taken to ensure traps were not visible from roads or hiking trails.

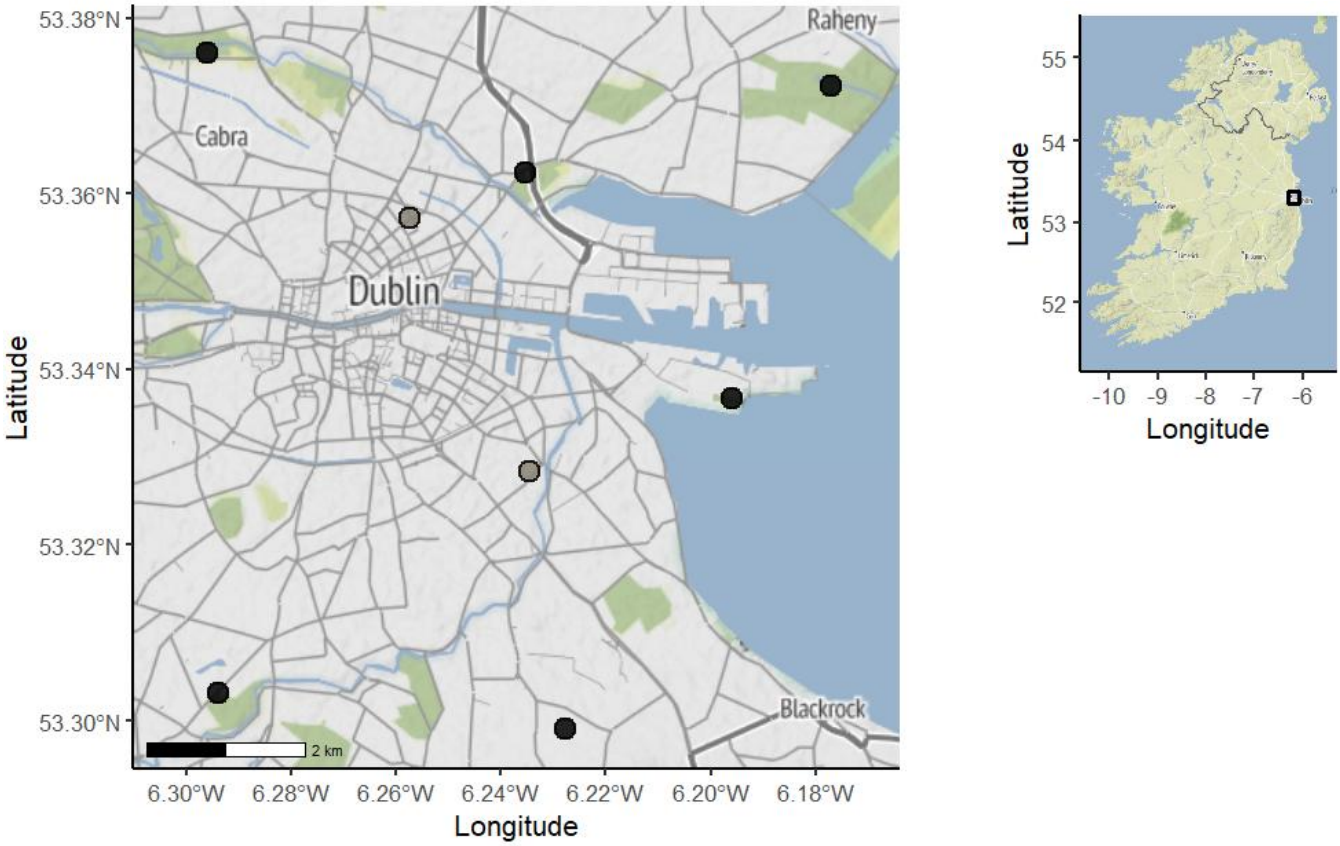

Figure 2. Trapping sites in (a) Dublin. Black circles indicate sites with capture success while grey circles show sites where trapping efforts were conducted but no foxes were captured. The inset shows the location of the study sites within Ireland.

Trapping protocols and trap specifications

In Dublin, trapping sites were pre-baited for several nights before trapping efforts began. The traps were left open and unarmed and baited daily to allow foxes to become familiar with the traps and associate them with food. A camera trap (Browning, USA or Victure, UK), which in this preliminary stage did not have remote transmission capabilities, was mounted nearby with the trap in view. This allowed us to determine when foxes were readily entering traps so that active trapping attempts could commence (Figure 3). Initial capture attempts took place in Autumn 2022, with one of two trapping sites, a private garden, being intensely monitored per night with hourly trap checks without disturbance from a window. The other site, a gated park depot, required a member of the field team to approach the trap for trap checks. Camera traps were deployed in both sites to inspect fox behaviour in between hourly visual trap checks.

Figure 3. These three camera trap video stills show stages of trap investigation during initial pre-baiting: (a) Inspecting the outside of the trap, including sniffing and circling. (b) Placing the head and forelegs inside the trap before retreating. (c) Full body inside the trap and bait taken.

Following poor success, with significant fox activity recorded at trapping sites but no successful captures, efforts were scaled up so that 3-4 trapping sites were active on a given night in Dublin, in collaboration with an independent wildlife management consultancy. Trap alert tags (Perdix, UK) and remote transmission camera traps (Perdix, UK) were deployed to minimise disturbance to the trapping site from manual trap checks, which were thought to contribute to the unsuccessful pilot Autumn capture season. This allowed us to reduce disturbance while continuing to minimise the amount of time captured foxes spent in traps. Sites with captures were prioritised and travelled to before sites with no captures and the remote cameras further provided immediate information about the length of time the fox had spent in the trap and its behavioural state (Figure 4). Further, remote monitoring conserved researcher effort and minimised fatigue, making trapping periods more sustainable and reducing the chance of tiredness-induced accidents in the field.

A variety of cage traps were used, which varied in measurement. The initial Autumn 2022 capture attempts in Dublin used Alive Predator Cage Traps (Tirlán Farm Life, Ireland). Traps measured 40 x 33 x 120 cm and featured a door on each end with a central treadle which triggered both doors to close when pressed. A two-door trap was used following anecdotal advice received concerning how foxes react as a trap triggers. Following unsuccessful trapping attempts, where foxes triggered the traps while evading capture, it was deemed that the length between the trap doors and central treadle was not long enough to fully enclose the fox if it stretched its body and left at least one paw outside the trap to reach the centrally placed bait. During the 2023 and 2024 Spring captures, traps measured 52 x 46 x 153 cm. These traps had one door and bait was placed at the opposite end. Additionally, these traps were reinforced with a strong spring, to prevent captured foxes from pushing the door up before it had fully shut upon the trap triggering, as had been witnessed from camera trap footage during the Autumn trial (Figure 4b).

In Lunigiana, cage traps were also used, each with two doors and measuring 38 x 38 x 116 cm. While the two-door traps trialled in Dublin had fixed doors which opened out horizontally and closed at an angle, the Lunigiana two-door traps were separate pieces which fit into vertical slats at trap entrances and fell vertically. The one-door traps used in Dublin for the subsequent capture seasons also had vertically closing doors.

A variety of baits were used and in high quantities to incentivise foxes to enter traps. Baits used in Dublin included chicken, whole pigeon carcasses, household food waste, venison and tinned sardines. In Lunigiana, chicken bones and liver, roe deer meat, hare scraps, dry dog food and wet cat food were used as bait. Small amounts of bait items were spread around the trap so that foxes could sample the foodstuffs before entering the trap, thought to further incentivise wild animals to enter traps.

Figure 4. Camera trap photos or video stills illustrating additional behavioural insights that were gained from camera trapping. (a) Camera traps confirmed whether foxes were visiting traps, which was important both before commencing the trapping attempt and choosing whether to continue using a particular trapping site during ongoing trapping efforts. (b) In two-door traps with weaker springs and shorter length, foxes were able to reach centrally placed bait by stretching and pushing back against closing trap doors, evading capture. (c) A second fox outside the trap containing a captured fox. Observing trapped individuals may have

educated other foxes in the area about the potential to become trapped. (d) Revisits by collared foxes indicated continued use of the trapping sites following capture, which may vary between individuals. Regular interspecific interactions were documented with camera trap videos frequently capturing foxes, visiting traps with (e) cats or (f) badgers present, without apparent direct aggression.

Animal handling

Captured foxes were anaesthetised by the vets authorised by the research permits in both study sites to reduce stress and risk of injury to both animals and handlers. As soon as researchers arrived at the trapping site, fox body mass was visually estimated to determine drug dosages and foxes were immobilised. Injecting foxes involved the use of a custom-made padded wall attached to a pole, which was used to restrain the fox to the end of the trap. When this was not effective, a snare loop was used to restrain the fox by the trap entrance to allow the vet to administer the drug. The fox was then left inside the trap as the anaesthetic took effect, with the research team waiting out of sight to reduce disturbance. Restraining foxes to administer anaesthetic lasted less than one minute.

In Dublin, one of two anaesthetic drug combinations were used, as part of a separate study on anaesthesia recovery in foxes, either 0.07 mg/kg medetomidine and 0.8 mg/kg midazolam or 3 mg/kg alfaxalone and 0.8 mg/kg midazolam. Anaesthesia was reversed with either atipamezole or flumazenil, respectively. In Lunigiana, foxes were anaesthetised using 4 mg/kg tiletamine-zolazepam and 0.08 mg/kg medetomidine, which does not require reversal. In all cases, the anaesthetic was administered intramuscularly in the hind-quarter by handheld injection. The vet assessed the sedated fox for visible signs of injury or ill health, based on overall appearance and including checking the teeth and gums. Sex and body mass were recorded for all individuals and females were palpated to check for pregnancy. Age category was simply recorded as adult or juvenile, as it is difficult to visually assess fox age after the first six months (Harding et al., 2001) and trapping efforts did not coincide with the cub season. In Dublin, pulse rate, respiratory rate, body temperature and blood pressure were additionally monitored during anaesthesia and blood samples were taken as part of the anaesthesia study. Blankets and/or bubble wrap were used to maintain body temperature as required. Foxes were placed back in traps after the anaesthetic reversal agent had been administered and released when they were alert and witnessed moving in the trap with no visible ataxia. Foxes were observed upon release until out of sight.

Collar deployment and retrieval

We used Axytrek collars (Technosmart, Italy) to collect GPS locations. UHF remote transmission and download was possible using an associated mobile base station. This is a small waterproof unit with a solar panel, which was placed in park depot capture sites or nearby gardens with known fox visitation for up to one week at a time. The base station recorded the number of data download sessions for each collar, but not the timestamps for when these occurred. Sampling rates were either 5, 10 or 20 minutes, with later deployments using less frequent sampling frequencies to extend the data collection period. Specifically, the initial trial in Lunigiana used a 5 minute GPS sampling frequency for the first capture, which was then increased to 10 minutes. The 5 minute sampling frequency was too demanding for this study site due to its landscape composition, with consequences for GPS battery life. GPS settings were further adjusted to shorten the period the collar would spend searching for satellites from 5 minutes for the initial capture (i.e., the full 5 minute period until the next location was due to be recorded) to 3 minutes (1 minute longer than the minimum recommended setting advised by the manufacturer). The 2023 Dublin deployments used a 10 minute sampling frequency and 2024 Dublin deployments used a 20 minute sampling frequency, with both using the 3 minute satellite search period adopted in Lunigiana. Additionally, the time intervals during which collars could connect to the remote GPS base station were shortened from 24 to 10 hours in 2024 and the GPS acquisition off time was extended from 30 to 40 minutes (though note that Technosmart loggers require this value to be specified in seconds, so this input value was changed from 1800 to 2400). In other words, once a collar could not obtain a GPS fix, it would not try to obtain the next fix for 30 minutes for collars deployed in 2023 and 40 minutes in 2024. These decisions were taken to reduce battery consumption while foxes were inside the den and improve battery life, while still allowing sporadic but critical diurnal movements to be recorded, which would have been lost if we imposed a strict monitoring schedule from dusk to dawn.

Technosmart Axytrek collars also featured a tri-axial accelerometer, which was activated for Lunigiana deployments but not those in Dublin. Acceleration data collected by Axytrek units had a sampling frequency of 25 Hz. In Dublin, thirteen collars were equipped with a Daily Diary biologger (hereafter DD; Wildbyte Technologies, UK; Wilson et al., 2008). The DD is an archival unit comprised of a tri-axial accelerometer and tri-axial magnetometer, recording at 20 Hz and 8 Hz respectively. Data were stored on a 16 GB Sandisk Ultra microSD card. The “thumb” DD model was used due to its small size (18 x 14 x 5 mm, 1.7 g). The use of the additional DD unit was preferred over the Axytrek in Dublin to extend the GPS data collection period, optimise GPS data transmission and to facilitate comparisons with other DD canid datasets. The DD’s tri-axial magnetometer also allowed computation of dead-reckoned tracks (details in the subsequent chapter). DD settings were the same for the 2023 and 2024 capture seasons, apart from changing the low battery monitor setting to cease data recording and shutdown (for the purposes of protecting recorded data) from 3 V in 2023 to 2.9 V in 2024, to see if this prolongs the data collection period. The DD and an AA cell Saft battery were in a separate compartment added to the base of the custom-made collars (Technosmart, Italy; Figure 5). Attaching the DD in this way kept the collar more streamlined and helped minimise the overall weight of the collar. A multi-step waterproofing process was conducted to minimise and protect against potential water ingress where the compartment was sealed. Both the DD and its battery were coated in Plastidip© rubber coating, with tape first secured over the microSD card slot to protect its contacts. Silicone gel was applied to the area where the DD compartment met the lid, and the lid was secured with Loctite© super glue. Gorilla© two-part epoxy resin was then applied around the seal. Collar mass was 90 g without the DD and associated battery, or 120 g including these.

All collars were further equipped with a light-weight VHF unit (Advanced Telemetry Systems, USA, in 2023, or Perdix, UK, in 2024) for monitoring and collar retrieval. The Perdix units, which were only used in 2024, emitted a stronger signal particularly needed to relocate the collar within densely inhabited areas, and were therefore used for the five collars containing the archival Daily Diary biologger units. VHF units were glued to the collar strap using epoxy resin and further secured with small cable ties, with the ends clipped and melted to ensure no sharp edges, and an outer layer of duct tape (Figure 5).

We made collars with degradable drop-off mechanisms to allow collar recovery and for welfare purposes, to ensure collars would not stay on foxes indefinitely. We considered two key potential consequences of automated, electronic drop-offs. The first is the risk that the mechanism would fail, which can commonly occur with species with underground dens, where the drop-off mechanism may become clogged with soil (Matthews et al., 2013). The second consideration is added weight to the collar, which is particularly important to consider for smaller animals (Matthews et al., 2013; Rafiq et al., 2019). This is significant when trying to stick to the standard rule of thumb of keeping tag weight < 3% of the tagged animal's overall body mass (Kenward, 2000). Collars were not to be deployed on any foxes weighing < 4 kg (i.e., in which case the collar would surpass 3% of body mass), however all captured foxes surpassed this minimum weight threshold.

To construct the degradable drop-off mechanisms, we cut the leather collar and added a weaker material section repurposed from rucksack strap webbing. The webbing section was added where the collar was fastened and so holes were added to facilitate collar fit with either a soldering iron or handheld hole punch tool. This section was further cut in two and sewn back together with surgical suture (Figure 5). Multiple suture types were used with varying rates of decay. Polyglactin 910 was used for most drop-off mechanisms but Polydioxanone and Poliglecaprone 25 were also used. Critically, all suture types were absorbable, meaning they degrade over time with exposure to moisture as well as wear. Approximate durations of collar wear before drop-off breakage were estimated for collars with known fates based on the collar data itself, camera trap footage, public sightings and VHF-confirmed movement. All collars were labelled with researcher and university names as well as contact information so that members of the public could report dropped collars. This was hand-written in 2023 while label-maker printed labels were used in 2024. Both labelling methods were covered with an epoxy resin layer to minimise weathering.

Figure 5. Collars were modified to include a suture-based drop-off mechanism. The leather collars were cut and sewn back together with webbing and absorbable surgical suture (see inset), which degrades over time with exposure to moisture. Note that the yellow tape on top of the collar is securing a magnet which is removed from the VHF unit prior to collar deployment. The collar shown here is the model including the Daily Diary compartment.

Capture success likelihood by weather conditions

Minimum and maximum daily temperature and rainfall data were obtained from the Phoenix Park weather station in Dublin for February and March 2023 and 2024 via Met Éireann, the Irish Meteorological Service (see https://www.met.ie/climate/available-data/historical-data and https://www.met.ie/climate/available-data/daily-data for 2023 and 2024, respectively). We used an asymptotic Wilcoxon-Mann-Whitney test from the *coin* package (Hothorn et al., 2006) in R 4.3.1 (R Core Team, 2023) to test if weather conditions on nights traps were armed affected the likelihood of capture success. This was carried out on the Dublin data only due to the low number of fox captures in Lunigiana.

Results

In Lunigiana, there were three fox captures between the 8th of February 2022 and the 9th of March 2022, with one of these being a recapture (Table 1). Both individuals captured were female. Trapping efforts continued without further success until the 20th of May, when traps were closed for the breeding season. Traps were reset for an Autumn capture season without any further captures. All fox captures occurred in a single trapping site, which was at the edge of a small village. This was unlike the six other trapping sites used, which were all positioned off hiking trails in forested areas. Camera traps positioned at each trapping site confirmed fox presence at each one. There was no consistency in bait type between these three capture events, with the traps containing a different main bait item each time. These were roe deer meat, dry dog food and meat scraps, respectively.

In Dublin, the initial capture season from the 26th of September to the 30th of November 2022 across two capture sites did not lead to any successful fox captures. Eight foxes (three females, five males) were trapped across five locations in Dublin between the 19th and 28th of February 2023 (Table 1). A sixth capture site did not have any successful captures. Capture efforts briefly continued from the 13th to the 16th of March with no further captures. Traps were set for 14 nights over this period with seven nights having successful captures (50% success rate). Seven additional foxes (four females, three males) were captured in Dublin between the 8th of February and 21st of March 2024 (Table 1). One individual was recaptured within this capture season and released without manipulation. Collars were otherwise deployed on all captured individuals. Traps were set for thirty-one nights over this capture season, with eight nights having fox captures (25.8% success rate). Traps were set across four sites with two having capture success. As in Lunigiana, fox presence was confirmed at each trapping site. Traps were closed and captures were halted in mid-March in both years to avoid capturing vixens who were heavily pregnant or lactating. Excluding recaptures, the sex ratio of captured foxes in Dublin from 2023 and 2024 combined was 1:1 (Table 1).

Table 1. Metadata of animals captured across all trapping locations, listed in order of date of capture. A capital R indicates recaptures.

Year	Fox ID	Sex	Region	Site
2022	Samantha	F	Lunigiana	Olivola
	Megan	F	Lunigiana	Olivola
	Samantha (R)	F	Lunigiana	Olivola
2023	Ruby	F	Dublin	Bushy Park
	Rocky	M	Dublin	Bushy Park
	Freddie	M	Dublin	Bushy Park
	Fantastic Mr	M	Dublin	St. Anne’s Park
	Merida	F	Dublin	Tolka Valley Park
	Eevee	F	Dublin	Bushy Park
	Tom	M	Dublin	Irishtown Nature Reserve
	Alfie	M	Dublin	Clonskeagh
2024	Kas	F	Dublin	Bushy Park
	Daría	F	Dublin	Fairview Park
	Ash	M	Dublin	Bushy Park
	Gráinne	F	Dublin	Fairview Park
	Freddie (R)	M	Dublin	Bushy Park
	Tobi	M	Dublin	Fairview Park
	Rua	F	Dublin	Fairview Park
	Ash (R)*	M	Dublin	Bushy Park

* Released without manipulation

Bycatch

Thirty individuals across seven species were caught as bycatch in Lunigiana; domestic cat (*Felis domesticus*, n=14), common buzzard (*Buteo buteo*, n=6), crested porcupine (*Hystrix cristata*, n=4), beech marten (*Martes foina*, n=3), European hedgehog (*Erinaceus europaeus*, n=1), European polecat (*Mustela putorius*, n=1) and European badger (*Meles meles*, n=1). Bycatch was less common in Dublin, though badgers and cats were captured on two occasions each. One domestic dog of the Labrador breed investigated, took bait and triggered the trap in the private garden location on multiple instances but was too large to be trapped and showed no adverse reaction to the motion of the trap door when triggered. No trap-related injuries were observed in Dublin or Lunigiana, in the target or bycatch species.

Suture drop-offs

Two of three deployed collars were recovered in Lunigiana but neither through drop-off breakage. In the first case, the fox was recaptured and in the second case the same individual had been shot by poachers. In both instances, the drop-off showed signs of visible wear. In Dublin, four of the eight deployed collars were retrieved from the 2023 capture season, as such the breakage of the drop-offs was confirmed for these cases (Table 2). Further, one fox had an identifiable scar over his eye and was seen on a camera trap 36 days after collar deployment without the collar (Table 2). As such, while the collar was not recovered, the drop-off also seems to have worked in this case. We received some reports from members of the public who had sighted collared foxes, but none later than July in 2023, supporting potential drops of unretrieved collars. All collars from the 2024 capture season are believed to still be deployed on foxes at the time of writing.

Table 2. Drop-off specifications and approximate duration of each suture drop-off per confirmed dropped collar with known attachment length. Tensile resistance and total absorption are according to manufacturer guidelines for the material's intended purpose to degrade inside the body following surgery. Tensile resistance is the timeframe after which the material loses its strength whereas total absorption is when the material has completely dissolved in the body cavity through hydrolysis. These timeframes are not expected to be accurate for collar-attached suture, but may provide a guideline when considering suture-based drop-off mechanisms.

Year	**Collar ID**	**Suture material**	**Tensile Resistance**	**Total absorption**	**Approx. drop-off duration**
2022	162	Polydioxanone	42 days	182-238 days	29 days*
	182				65 days**
2023	51	Polyglactin 910	32 days	56-70 days	154 days
	53				3 days
	54				211 days
	55				52 days
	59				36 days***

* Fox recaptured and collar swapped

** Fox shot and collar reported to local management agency

*** Collar not recovered but drop confirmed from camera trap

Of the five confirmed dropped collars in 2023, the first three collars to drop had been worn by males and dropped 3-52 days following deployment, as deduced from the collar data for the two males for which collars were retrieved and from camera trap footage for the third male for whom the collar was not relocated. Two collars worn by females dropped-off after an estimated 154 and 211 days respectively.

Capture success likelihood by weather conditions

Neither minimum (n = 44 trapping nights, Z = -1.16, p = 0.25) nor maximum (n = 44 trapping nights, Z = -0.01, p = 0.99) daily temperature affected capture success. Capture success had a significant relationship with precipitation (n = 44 trapping nights, Z = 2.18, p = 0.029), with more fox captures occurring on nights with lower rainfall (Figure 6).

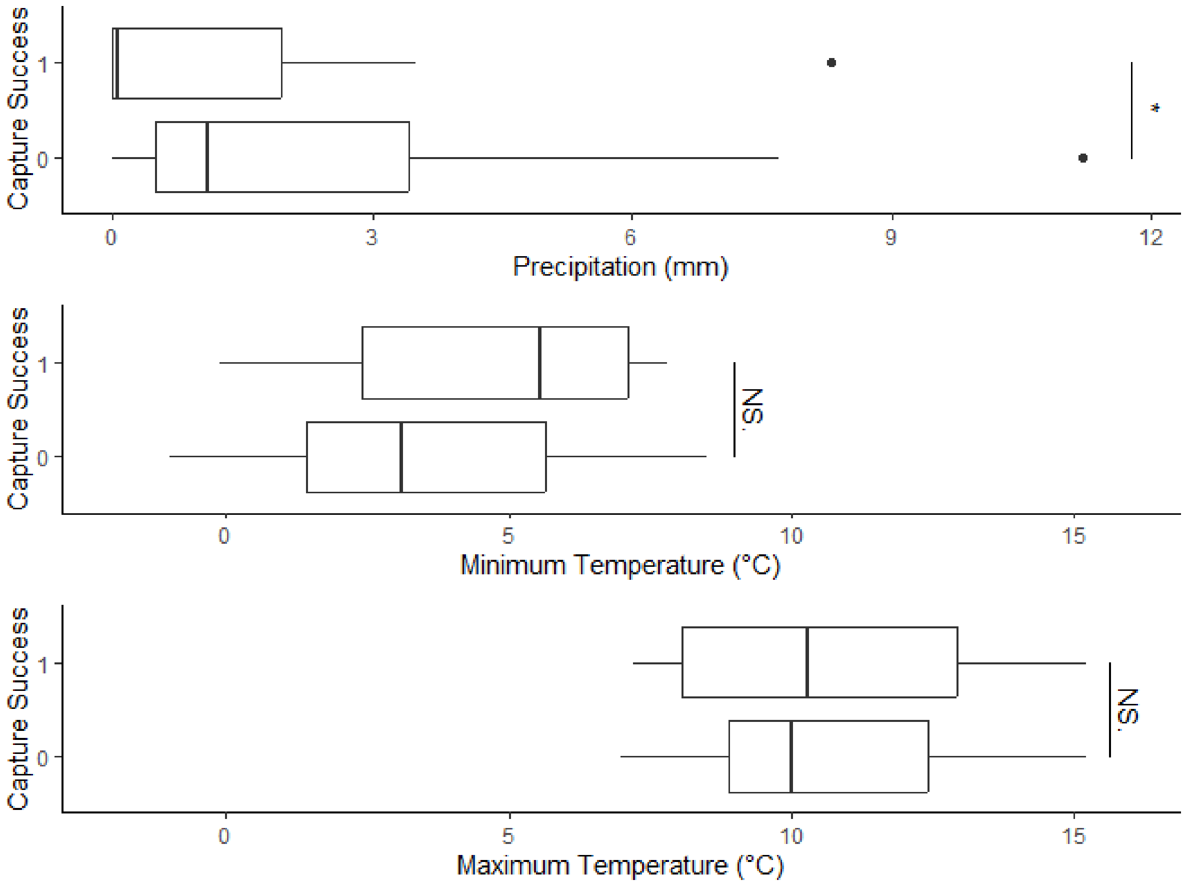

Figure 6. Capture success or failure in relation to (a) precipitation (b) minimum temperature recorded on day of trapping attempt and (c) maximum temperature recorded on day of trapping attempt.

Discussion

Here, we report our strategies to refine fox capture and data retrieval efforts over three years of trapping in two distinct settings. A full checklist of recommendations is provided in Box 1. Briefly, we found improved trapping success when using larger traps and operating multiple trapping sites simultaneously, with remote camera traps and trap alert tags being favoured over more frequent manual trap checks (Figure 1).

Capture success is often expressed as the number of fox captures per number of trapping nights. In Dublin, we had 16 fox captures over 45 trapping nights between the 2023 and 2024 seasons, giving a trapping efficiency of one fox per 2.8 trapping nights. This efficiency is quite high compared to other studies. For example, Kay et al. (2000) report a trapping efficiency of one fox per 147 trapping nights, Muñoz-Igualada et al. (2008) report 18 foxes per 1,000 trapping nights (i.e., one fox per 55 trapping nights) and Main (2020) reports four foxes in 96 trapping nights (i.e., one fox per 24 trapping nights). Notably, the most efficient of these, Main (2020), was also conducted on an urban rather than rural fox population. This may be because urban foxes have more frequent interaction with human scent, activity and novel objects than their rural counterparts. Accordingly, the capture efficiency for Lunigiana was lower than Dublin, but still favourable compared to previous studies with 3 captures in the initial capture season of an estimated 122 trapping nights, or one fox per 40.66 trapping nights. This was followed by subsequent capture efforts with no fox captures, however. While only females were captured in Lunigiana, this sample size is too low to make meaningful inferences about sex ratios of captured animals in the region. There was no significant difference between the number of male and female foxes caught in Dublin, with an equal number of unique males and females captured and two male recaptures. The sex ratio of trapped foxes seems to vary considerably with previous studies reporting no sex differences in trappability (Baker et al., 2001), bias towards male captures (Kay et al., 2000) and bias towards female captures (Henry et al., 2005), respectively. As such, this may be important to evaluate and document for each population.

Cage traps are commonly used for animal capture due to their low risk of significant injuries (Iossa et al., 2007; McCarthy et al., 2013). Foxes and other species can be reluctant to enter cage traps, however, which is likely why it was important here to arm multiple traps simultaneously to increase capture success. Trap length was also important to consider. While the traps used in the initial 2022 capture season in Dublin were advertised specifically as fox traps, they were found to be too short to ensure capture of foxes which entered these traps. This may be especially important when purchasing traps which are manufactured elsewhere and imported, as foxes range in body size across their geographic distribution (Cavallini, 1995). For this reason, we recommend checking trap measurements of advertised traps against trap measurements reported in successful capture studies of the target species instead of relying upon manufacturer guidelines. Potential differences in body size between the target study area and reference studies should also be considered.

A need to continuously evaluate and refine trapping methods has been identified (Iossa et al., 2007; Muñoz-Igualada et al., 2008; Caravaggi et al., 2021). Specifically, injury rates and trap selectivity (i.e., prevalence of bycatch) have been highlighted as requiring increased consideration and reporting (Iossa et al., 2007; White et al., 2021). The most frequently reported injuries associated with cage traps tend to be tooth damage, associated with animals chewing on the wire mesh of the trap, and skin abrasions, typically to the limbs or snout (Woodroffe et al., 2005; McCarthy et al., 2013; White et al., 2021). Here we had no instances of such injuries. While bycatch captures were released without the sedation and full veterinary assessment received by captured foxes, no visible injuries were observed in bycatch species. There was a high occurrence of non-target species bycatch in Lunigiana compared to Dublin. This is likely due to Lunigiana being a wilder, more biodiverse study site. High levels of bycatch associated with cage traps has been reported in other studies (Shivik et al., 2005; Muñoz-Igualada et al., 2008), though their low reported injury rates warrant continued use. One possible refinement to minimise bycatch may include testing for more target-species specific baits or lures (Shivik and Gruver, 2002; McCarthy et al., 2013). While live bait and the use of fox urine as a lure have been found to increase red fox capture efficiency, neither led to a reduction in bycatch (Díaz-Ruiz et al., 2016) and using live bait has separate welfare concerns for the animals being used as bait (Caravaggi et al., 2021). Lures may warrant further consideration, however, as canid-specific lures have shown promise in improving trapping selectivity elsewhere (Shivik and Gruver, 2002). In the current study, capture success varied considerably by trapping site (Table 1) and we suspect the scent of previously captured conspecifics may have acted as an attractant, as has been documented in other species (Pawlina and Proulx, 1999; Martin et al., 2014). As such, this may be worth exploring in future trapping efforts.

Of the seven trapping sites used in Lunigiana, only one had successful fox captures. Notably, this capture site was on the edge of a small village, unlike all the others which were in forested areas. We suspect that novel objects such as traps seem less daunting close to human settlements where the presence of novel human objects is high, compared with natural woodland areas. Based on our experience in Lunigiana, we expected that urban foxes would be less wary of traps due to familiarity with human activity and scent. Urban animals also encounter novel human-made objects frequently, but urban foxes were also wary around traps (Figure 3, Figure 4). Urban wildlife populations can show reduced neophobia and higher tolerance of novel objects to exploit feeding resources (Lefebvre, 1995; Lowry et al., 2013). However, urban wildlife can also be at increased risk of primary and secondary poisoning (Riley et al., 2014) and must navigate heavy human and vehicular traffic (Lowry et al., 2013). As such, urban wildlife can also exhibit high neophobia to avoid persecution, as has been documented in fox populations elsewhere (Padovani et al., 2021). Degree of neophobia may be object-specific, but with urban populations being faster to explore novel objects than rural counterparts (Greggor et al., 2016). This highlights the need for habituation periods for newly placed traps regardless of environment, although the habituation process will likely be faster in human-dominated environments.

Our ability to monitor multiple trapping sites without extending the amount of time captured foxes spent in traps was facilitated by the dual use of trap alert tags and remote transmission camera traps. Trap alert tags notified the capture team of any trap closures, while remote transmission camera traps allowed verification of capture as well as identifying the captured species. The use of these technologies in tandem also ensured there was a back-up if either system failed, which occurred once with the remote cameras in the 2024 capture season. Manual trap checks were continued once per day, which also served as an opportunity to top up bait as necessary, but these technological aids ensured faster, prioritised arrivals at traps where a capture had taken place. Remote monitoring of trapping sites also minimised disturbance, which may improve capture success of trap-shy species (Arthur, 1988; McCarthy et al., 2013). Remote transmission camera traps can also conserve research team effort and improve coordination (Campbell and Griffith, 2015; Keiter et al., 2022). False triggers or bycatch captures can be dealt with by one team member while full capture teams can immediately coordinate arrival for target species captures. While cellular signal can be inconsistent in some study areas (Keiter et al., 2022), these remote monitoring tools are valuable in urban areas with reliable coverage.

Camera traps contributed considerably to our understanding of fox behaviour around traps and potential reasons for unsuccessful trapping attempts. Traps were armed only when foxes were confirmed to be both visiting the trapping sites and entering traps (Figure 3), which conserved the researcher effort required in monitoring active traps. Arming traps after a habituation period also minimised the risk of unsuccessful trap triggers by wary foxes which may have deterred foxes from returning to traps. It was through camera trap footage that we realised our first traps were too short in length and had weak spring mechanisms that could be pushed up by foxes, despite being advertised as fox-specific traps (Figure 4). Foxes which visited traps with another fox already captured inside may have been educated about the possibility of capture and subsequently avoided traps (Figure 4). Fox capture rates have been found to decrease with successful captures in neighbouring traps for longer trapping periods (Ruette et al., 2003), which may indicate captured fox reluctance to re-enter traps but also potentially learned trap avoidance from conspecifics. Trap aversion has been shown in captive coyotes, for example, which socially learn trap avoidance behaviour from demonstrators (Young et al., 2022).

Collar failure rates can be high, significantly impacting sample sizes in movement ecology (Hebblewhite and Haydon, 2010). For example, (Hofman et al., 2019) reported that 48% of GPS collar deployments end prematurely and many studies report significant proportions of deployed collars undergoing technical failure and/or retrieval failure (Gau et al., 2004; Kaczensky et al., 2010; Matthews et al., 2013; Jung et al., 2018; Studd et al., 2021). This can be particularly detrimental when working with difficult-to-capture species. Here, we successfully recovered data from all retrieved units and recovered additional data from unretrieved collars through base station download. In other words, we recovered GPS data from two of three individuals in Lunigiana (66.66%) six of eight individuals collared in Dublin in 2023 (75%) and five of seven individuals to date in Dublin in 2024 (71.42%). Accelerometer data were also recovered from two of three individuals in Lunigiana (66.66%) as these were combined units. DD data was recovered from 50% of individuals in 2023 and are still deployed in 2024, so DD data recovery for this capture season cannot yet be confirmed. While only 50% of DDs were recovered, all had data extracted successfully so were not subject to the mechanical failures often experienced by these tags (Wang et al., 2015; Kay, 2021; Mortlock et al., 2024). This was likely aided by our waterproofing procedure, with water ingress being a common issue in custom tag set-ups (Redcliffe, 2021; Mortlock et al., 2024). We have reported the detailed collar specifications used here, including minor variations between deployments, to inform future studies in accordance with the recommendations set out in Hofman et al. (2019). Further, a need has been identified for metadata of all deployed tags to be reported, including accounting for those which fail or do not contribute to published datasets (Rutz, 2022). More detailed reporting of collar specifications and data recovery may be particularly important in urban areas, where data transmission capabilities are not as well understood as other environments (Adams et al., 2013).

Animal movement and activity patterns can be influenced by the capture event, with recent work indicating this period may be 4-7 days for mammals (Stiegler et al., 2022). This is especially pertinent to short data collection periods and often a concern when collecting biologging data in particular, with shorter logging durations associated with high-frequency data collection (Williams et al., 2020). Battery life optimisation and improved unit recovery are key to increase sample sizes in the future. Data from Lunigiana are not comparable to the data from Dublin due to the different environmental setting, small sample size and the fact both deployments ended before collars died. Whether changes to collar programming improved battery life in Dublin is currently difficult to assess as the 2024 monitoring season is ongoing. However, GPS data retrievals to date indicate ongoing data transmission to the base station at the time of writing (accurate as of the 13th of April 2024). As the last collar to stop recording in 2023 stopped on the 9th of April and the 2024 capture season began one week earlier, battery life for the 2024 deployments has already surpassed those obtained in 2023. As no collars have been confirmed to have dropped or been retrieved so far in the 2024 data collection season, it is not yet clear whether the only change in DD settings between the two years, adjusting the battery voltage level that triggers switch-off, has an effect on data collection duration.

Remote transmission through the base station significantly boosted data retrieval, with two of six GPS datasets recovered in 2023 being through the base station alone and all 2024 data collected to date obtained *via* the base station. This is despite the base station range being significantly more limited than expected, as ascertained from the base station failing to connect to collars within a few hundred metres with collared fox presence confirmed *via* VHF tracking. Limited base station range may have biased the collected data by failing to connect to the collars of wider ranging or dispersing foxes. Optimising remote transmission may be a challenge when working in urban environments. Another study on urban foxes collected data from five individuals, with four of these five only connecting to the base station once and the other three times (Kobryn et al., 2023). Collars which remotely transmit data *via* satellites or the Global System for Mobile communications (GSM) may resolve this issue in future, though come with increased costs (Pastorini et al., 2015). Long Range Wide Area Networks (LoRaWAN), which involve the use of a system of gateways, show considerable promise as a low-cost data transmission option (Gauld et al., 2023). More simply, base stations which record the times of data download may help to refine programmed remote download intervals in the future.

Suture drop-offs can act as a lightweight alternative to electronic drop-off systems. Suture may also be cost effective, particularly where expired suture not fit for surgical use can be repurposed, as was the case here. While Lunigiana collars were retrieved before drop-off breakage and there have been no suspected or confirmed dropped collars thus far in 2024, we report five estimated drop-off durations from the Dublin 2023 capture season (Table 2). Unrecovered collars may have dropped in inaccessible locations such as dens or been discarded by members of the public. Further, we suspect collar recovery was impacted by limited VHF unit range. For confirmed dropped collars, there was considerable variation in the duration each drop-off lasted, which may result from individual variation in force exerted on the collar. Of the five collars with drop-off estimates, the collars with the three shortest confirmed drop-off durations were worn by males and the two longest were worn by females (Table 2). This suggests a difference in force exerted upon collars between males and females, warranting future consideration with larger sample sizes. We also suggest researchers experiment with different types of suture with different tensile resistance and absorption specifications.

Animal responses to weather conditions can affect activity levels and therefore the likelihood of trap visitation and capture success (Cox and Hunt, 1992; Pawlina and Proulx, 1999). Minimum and maximum recorded temperatures on days where traps were set did not affect capture success. Precipitation did have a significant relationship with capture success, with capture likelihood decreasing with increased rainfall. This suggests that foxes in Dublin may be less active on nights with higher rainfall and therefore less likely to enter traps. This may explain why 2023 had a greater proportion of successful trapping nights than 2024. March 2023 and 2024 were two of the wettest on record in Ireland. While February 2024 also had high rainfall, February 2023 was dryer (Met Éireann, 2024; RTÉ News, 2024) and all 2023 captures occurred in February. Temperature may be more important in other seasons, particularly in regions experiencing both higher and lower temperature extremes than typical in Ireland’s mild climate. There are contrasting reports of which seasons are associated with higher trapping success for foxes (Baker et al., 2001; Valcarcel et al., 2020), indicating that this may vary with local climate conditions.

Box 1. Checklist of recommendations for capturing wild foxes.

1. *Choose safe capture locations where the risk of disturbance from members of the public is minimal*. Private property and areas that are locked at night such as park depots are useful urban trapping sites. In rural areas, care should be taken to ensure traps are hidden from view of roads and trails.

2. *Choose a time interval for trap checks which optimises the welfare of study animals while remaining mindful of practical considerations*. Trap checks should be frequent enough to minimise the amount of time the fox spends in the trap without disturbing the site so often that foxes are deterred from the area. Trap alert tags and camera traps with remote transmission capabilities considerably minimise the potential conflict between these two aims as frequent checks can be carried out with no disturbance to the capture location. Using both these systems in tandem also ensures continued monitoring even if one system fails.

3. *Decide how many traps to arm simultaneously and how many trapping sites to use*. The simplest way to improve the chances of capturing foxes is to set more traps in more locations simultaneously. This is feasible when using remote trap monitoring systems as outlined above. The number of trapping locations should be determined by picking a realistic maximum without drastically increasing the amount of time foxes spend in traps. This will be determined by the length of time required to process the animal upon capture and travel time between trapping sites. Ensure all traps are of adequate length to trap foxes. Some trapping sites may be closed and substituted for new locations if all foxes visiting the area are thought to have been captured, educated about the trap or otherwise unwilling to enter traps.

4. *Choose a pre-baiting timeframe that allows target animals to become familiar with traps*. Setting traps when foxes are freely entering them may reduce the chance of false triggers from cautious foxes and conserves research team effort. Novel traps may select for bolder individuals. Allowing the traps to become familiar removes novelty, which may increase the likelihood of capturing more trap-shy individuals.

5. *Include a drop-off mechanism to account for low recapture rates of collars.* Drop-off mechanisms are particularly valuable where recapture rates are low, promoting data recovery and ensuring animals are not left wearing collars indefinitely. The suture-based degradable drop-off used here is imprecise in terms of drop-off date but this can likely be manipulated by using sutures of different suture strengths and using multiple, independently-sewn strands. This provides a cheap, lightweight option without risk of mechanical failure.
6. *Evaluate whether local weather conditions are influencing trap visitation and therefore capture success*. This may inform which seasons to prioritise for trapping efforts and conserve researcher effort by pausing trapping during unfavourable weather periods.

Conclusion

Despite the prevalence of animal capture and tag deployment in ecology, many studies highlight an under-reporting of trapping protocols. Here we present in detail the considerations and refinements implemented during the capture and collaring of a species considered trap-shy, with the aim of informing future studies involving animal capture.

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Chapter 5

Fox in the City: movement and behaviour of the red fox in a human-dominated environment

Abstract

The red fox (*Vulpes vulpes*) thrives in diverse landscapes through adapting its foraging behaviour, which frequently implicates this species in human-wildlife conflict. Foxes can provoke extreme and disparate reactions in city-dwellers, with some people seeing fox presence as an opportunity to connect with nature while others consider them a pest. Using tri-axial accelerometers and magnetometers recording at infra-second frequencies (i.e., multiple data points per second) in conjunction with GPS tracking, we present detailed data on urban fox space use, activity patterns and behaviour in Dublin, Ireland, across a gradient of urbanisation. Minimum Convex Polygon home ranges were calculated across multiple thresholds to investigate space use in an urban setting. Generalised additive mixed-models were used to investigate the factors influencing GPS-derived movement speed and daily home range area estimates as a function of urbanisation levels. Behaviour classification rules for stationary, moving and feeding behaviours were adapted from procedures developed on other canid species and dead-reckoned tracks were computed to contextualise these behaviours in the landscape. Analysis of GPS data found that most foxes occupied small home ranges <0.4 km^2, though with two individuals ranging much more widely than the other collared foxes (2.78 km^2 and 15.96 km^2, respectively, based on 95% Minimum Convex Polygon estimates). Core home ranges show heavy use of residential rather than natural areas, with 56.99% of all locations occurring in residential areas (e.g., gardens). Movement speed was slower in residential areas than natural areas and during the day compared to at night. Daily home range area estimates were smaller in residential *versus* more natural areas. Activity was mostly nocturnal but foxes were also active during daylight hours. Six behaviours were classified using the acceleration and magnetometry data, namely stationary, resting, walking, trotting, running and feeding. A case study of how dead-reckoning can be used to compare behaviour and movement rates across habitats is also provided. Anthropogenic feeding of foxes may drive these trends, though further research is warranted. This study, however, demonstrates how foxes have adapted to live in highly urbanised areas. The techniques and methodological approaches defined here are those needed to disentangle foraging strategies and estimate the level of reliance on human-derived food sources *versus* natural prey within human-dominated landscapes.

Keywords: red fox, urban ecology, movement ecology, biologging, GPS, accelerometer, behaviour classification, dead-reckoning, foraging.

Introduction

As cities continue to grow and spread, wildlife in and surrounding urban centres are increasingly brought into contact with human activity and infrastructure (Sih et al., 2011). While some species are sensitive to human disturbance and cannot live in such areas, many wildlife species have adapted to thrive in urban environments (Sih et al., 2011). While bird species richness has been found to decrease with urbanisation (Strohbach et al., 2014), mammal assemblages in developed areas are now larger and more diverse than wild areas (Parsons et al., 2018). But even where species seemingly persist alongside humans quite well, the Anthropocene is causing shifts in animal behaviour, allowing these species to adapt to human-dominated landscapes by reducing their movements (Tucker et al., 2018) and becoming more nocturnal (Gaynor et al., 2018). Further, often the ecology of a species is well understood in natural areas, with a comparative dearth of information on how it moves, behaves and forages in urban areas (Méndez et al., 2020). This is despite widely documented differences in animal behaviour in natural *versus* urban areas (Breck et al., 2019; Lowry et al., 2013). Studies of urban wildlife are therefore of considerable and growing importance.

The prevalence of wildlife in urban areas, coupled with the increase in boldness commonly documented in urban wildlife (Breck et al., 2019; Morton et al., 2023; Samia et al., 2017), can lead to human-wildlife conflict. People in urban environments exhibit diverse responses to wildlife, which can be positive, negative or neutral in nature and with some species better tolerated than others (McCance et al., 2017; Puri et al., 2024). Tolerance of urban wildlife varies with taxonomic group, previous interactions with wildlife and beliefs held about particular species (Dickman, 2010; Puri et al., 2024; Schell et al., 2021). Perceptions of carnivores are often more negative than those of other species, but there is considerable variation in how carnivores are viewed in urban areas (Puri et al., 2024). Causes of conflict include human fear and anxiety, property damage and road collisions (Basak et al., 2022; Schell et al., 2021). Conversely, wildlife encounters can be viewed positively, stemming from interest in coexistence and wildlife watching opportunities as well as perceived beneficial ecosystem service provision such as pest control (Brand and Baldwin, 2020). However, even interactions arising from positive human sentiment can lead to conflict or other urban wildlife management issues. Food provisioning, for example, can be a considerable cause of human-wildlife conflict in urban settings, as animals that associate humans with food may approach humans (Schell et al., 2021). In this way, human viewpoints and behaviour surrounding wildlife can in turn influence the behaviour of the wildlife in question, with potential consequences including disease transmission or injury (Cox and Gaston, 2018; Schell et al., 2021). Understanding animal space use in cities is therefore important, for example through establishing where private property such as gardens are being heavily used by species which can be considered pests. Studies on animal behaviour can be used to reduce potential conflict, refine wildlife management strategies and offer practical, evidence-based guidance on interacting with urban wildlife to urban residents (Fehlmann et al., 2023; Wilkinson et al., 2023).

The red fox (*Vulpes vulpes*) is an adaptable mesocarnivore with the largest extant range of any carnivore species spanning virtually the entire northern hemisphere (Sillero-Zubiri and Macdonald, 2004). Foxes are habitat generalists with high tolerance of anthropogenic activity, leading to their proliferation in urban environments (Contesse et al., 2004; Duduś et al., 2014; Harris and Rayner, 1986). Foxes can provoke extreme and disparate reactions in city-dwellers, with some people seeing fox presence as an opportunity to connect with nature while others feel fearful (Cassidy and Mills, 2012). Citizen science initiatives have reported foxes adapting to even the most built-up inner city environments (Fung et al., 2024; Parsons et al., 2018). Increasing populations of urban foxes have been reported in the UK (Scott et al., 2018; Scott et al., 2014), and Switzerland (Gloor et al., 2001) and similar increases are likely occurring elsewhere.

As generalists, foxes thrive in both rural and urban landscapes by adapting their foraging behaviour, with associated variation in social and spatial dynamics in response to resource availability (Johnson et al., 2002; Lavin et al., 2003). Foxes readily exploit anthropogenic food sources, both through scavenging from bins, compost heaps and pet food as well as availing of food provided through intentional feeding (Bateman and Fleming, 2012; Contesse et al., 2004; Doncaster et al., 1990). As hunters, foxes frequently consume rodents, lagomorphs, birds and invertebrates and show strong seasonal variation in diet (Contesse et al., 2004; Doncaster et al., 1990). This includes species such as mice, rats and pigeons, which are commonly viewed as pests, and therefore highlights a potential ecosystem service that could be played by urban foxes in pest control. Scavenging carcasses of these species and others can also provide a valuable ecosystem role by removing carcasses, with implications for disease transmission (Inger et al., 2016). These potential ecosystem services are likely reduced by intentional feeding however, with greater food availability satiating foxes and directly supplementing the diets of rodents and other pests (Sorace, 2002).

Understanding the movements, activity patterns and behaviour of wild animals is difficult where such animals are difficult to observe, nocturnal or secretive (Brown et al., 2013). Further, some behaviours are easier to observe than others and the presence of a human observer can affect the behaviour of observed animals, introducing bias in resulting activity budgets (Christiansen et al., 2013). Animal-attached sensors can be used to collect continuous behavioural data without these biases (Brown et al., 2013). Collection of GPS data allows detailed insights into animal space use and activity rhythms, including analysis of home ranges, circadian rhythms and habitat selection (Cagnacci et al., 2010; Ensing et al., 2014; Kobryn et al., 2023). While GPS cluster analysis can be used to detect predation in some instances, issues remain in detecting kills of small-bodied prey which are consumed quickly (Merrill et al., 2010). This is particularly relevant when working on small and medium-sized predators such as foxes, which specialise in hunting small prey and scavenging. High-frequency biologging sensors such as accelerometers and magnetometers can be used to fill in some of these data gaps left by GPS data. Biologging methods are increasingly facilitating detection of quick, difficult-to-detect foraging behaviours such as nest predation and prey caching in Arctic foxes *Vulpes lagopus* (Clermont et al., 2021) and kill rates of hares by lynx (Studd et al., 2021). Combined deployments of GPS and biologging sensors are particularly powerful, allowing detailed insights into animal behaviour which are contextualised in space. For example, accelerometer, magnetometer and GPS data can be combined to create fine-scale movement paths on a second-by-second basis through dead-reckoning (Bidder et al., 2015; Gunner et al., 2021a). This can, in turn, be paired with behaviour classification, allowing fine-scale matching of behaviours to environmental variables such as habitat composition.

Currently, information on the behaviour and movement of foxes in Ireland is largely informed by studies from other European countries. Red foxes in Ireland have been found to be genetically distinct from other populations (Statham et al., 2018) however, and whether this results in behavioural differences in Irish foxes is unknown. Further, foxes exhibit such behavioural variation across their range that local studies are required for informed local management (Kobryn et al., 2023). Anthropogenic feeding of foxes is now thought to be a common occurrence in Dublin, with potential implications for fox behaviour and space use. This is based on anecdotal reports, with no quantitative research on fox behavioural and movement ecology occurring in Dublin to date.

Aims

Here we investigate urban fox space use and foraging behaviour across an urban habitat gradient through collection of GPS, accelerometer and magnetometer data. We aim to:

(i) quantify and examine within-population variation in home range size and overlap for foxes in Dublin;

(ii) assess whether fox GPS locations were predominantly associated with natural areas such as parks or residential areas such as gardens;

(iii) confirm whether foxes were also exhibiting diurnal activity, which may indicate reduced fear of humans and habituation;

(iv) create behaviour classification rules for movement, resting and foraging behaviours,

(v) provide a case study on how mapping behaviours to dead-reckoned tracks can identify place behaviours in context in the landscape.

These aims, particularly the latter two, will provide a methodological framework for future research aimed at disentangling foraging strategies and reliance on human food sources in urban environments.

Materials and Methods

Ethics statement

Fox capture, anaesthesia and collaring were carried out with full ethical approval. Ethical approval was granted by University College Dublin under the approval code AREC-E-23-22 and by the Health Products Regulatory Authority (HPRA) under AE18982/P216.

Data collection

Eight foxes were fit with multi-sensor tracking collars in February 2023 and a further seven individuals were collared in February-March 2024. One individual was collared in both 2023 and 2024, all other foxes were collared once. Foxes were collared at six trapping sites (Bushy Park, St. Anne’s Park, Tolka Valley Park, Fairview Park, Irishtown Nature Reserve, Clonskeagh suburb) across Dublin city (see Chapter 4, Figure 2). Multiple sites were chosen to capture an urban habitat gradient and maximise capture success. Full details regarding collar set up and fieldwork protocols are provided in the previous chapter. Briefly, collars comprised of Axytrek GPS units (Technosmart, Italy), Daily Diary biologgers (Wildbyte Technologies, UK) and a VHF unit (Advanced Telemetry Systems, USA in 2023 or Perdix, UK in 2024). The Axytrek unit was comprised of a remote transmission GPS unit collecting location data every 10 minutes in 2023 and every 20 minutes in 2024. GPS data were recorded throughout the day (i.e., no timed off periods) to assess whether Dublin’s urban foxes exhibit any diurnal activity. Where possible, the GPS data were downloaded using an associated base station. The Axytrek unit is also capable of recording acceleration data. This functionality was not used here, as when remote transmission is enabled, both GPS and accelerometer data are transmitted, and transmitting accelerometer data have considerable power demands and consequences for battery life (Wilson et al., 2008). The Daily Diary (DD) is a multi-sensor biologger which comprises a tri-axial accelerometer, tri-axial magnetometer, temperature and pressure sensors (Wilson et al., 2008). The DD is available in multiple models; here we used the “thumb” model, which measures 18 x 14 x 5 mm and weighs 1.7 g including a microSD card. The DD was stored in its own housing with an AA cell battery. Both the DD and the battery were painted with Plastidip to protect them from water ingress. The housing lid was sealed with silicone gel, superglue and epoxy resin to further minimise the risk of water ingress. DDs collected data at 20 Hz acceleration, 8 Hz magnetometry, 2 Hz pressure and 2 Hz temperature. This is an archival tag, as such these data were only available for animals for which collars were successfully retrieved. All DD data presented here are from the 2023 capture season.

Statistical analysis

All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2023). Once data were retrieved, GPS data were first cleaned to remove points recorded before or after the collar deployment and screened for duplicate records. Home ranges were calculated to examine fox space use. We first calculated 100%, 95% and 50% Minimum Convex Polygon (MCP) home ranges for each individual for the entire data collection period. 100% and 95% MCP home ranges were chosen for consistency with a recent meta-analysis on global variability in fox home range sizes (Main et al., 2020), while 50% MCP home ranges were also included to identify core home ranges. Home range size estimates were converted to km^2 for ease of interpretation. We examined home range overlap using data from the Bushy Park study site for 2023 and 2024, respectively, as there were multiple captures at this site in both years. Daily 100% MCP home range estimates were then calculated for each fox using 24-hour periods from noon to noon instead of midnight to midnight to more accurately represent the activity periods of foxes. Step lengths and the time difference between steps were calculated using vector calculations, which were then used to produce speed estimates between successive locations. Home range area and overlap estimates were calculated using the *amt* package in R (Signer et al., 2019) and all spatial data processing was conducted using the *sf* package (Pebesma, 2018). All figures including background maps were plotted using *ggmap* (Kahle and Wickham, 2023).

Daily 100% MCP home ranges and speed were used to model daily movement rates in relation to land use class. Spatial environmental data on land use class were obtained from

Open Street map (see https://download.geofabrik.de/europe/ireland-and-northern-ireland.html). Fox locations were matched to land use class using the *sf* R package. Land use classes were grouped into three categories: natural, residential and commercial. Locations in commercial areas were removed from subsequent analyses due to low occurrence (approximately 0.1% of the dataset). The fox with the smallest home range, for which GPS locations were only available for one day, was also removed from subsequent analyses. The proportion of locations occurring in residential areas was derived for each daily home range polygon. We used generalised additive mixed-effect models (GAMMs) with Gaussian error distributions, constructed using the *gam* function from the *mgcv* R package (Wood, 2023), to test the effects of sex, time of day (in hours), Julian day, year of data collection and proportion of time spent in residential areas on movement speed and daily home range area estimates, respectively, with fox ID as a random effect. Proportion of time spent in residential areas, time of day, Julian day and fox ID were fitted as smoothed terms. When computing the splines for time of day and Julian day, the default number of knots were used ($k = 9$) to allow for full flexibility in model fitting. Proportion of time spent in residential areas was fitted with $k = 3$ to avoid overfitting. Speed and home range area estimates were log-transformed to normalise model residuals. Model outputs were plotted using the *gratia* package (Simpson, 2024).

We further plotted actograms of fox activity over 24 hour periods to visualise peak activity times. Actograms were plotted for ten individuals (note one individual which was captured in both the 2023 and 2024 capture seasons is represented twice) by aggregating mean GPS speed per hour per deployment day. Fine-scale actograms were then computed from acceleration data for four individuals. Specifically, we used Vectorial Dynamic Body Acceleration (hereafter VeDBA), a metric for both speed and energy expenditure derived from the three raw acceleration axes (Bidder et al., 2012; Wilson et al., 2020). Mean VeDBA was aggregated for each hour of each day of data collection for these four individuals.

Behaviour classification of biologging data

All behaviour classification rules were developed using the Behaviour Builder functionality in the open access Daily Diary Multiple Trace software (hereafter DDMT; available from https://github.com/DDMT-Software/DDMT). Behaviour classification in DDMT uses a Boolean search approach, whereby specific, user-defined algorithms are used to search for sections of data matching input values across the entire biologging dataset (Wilson et al., 2018). These algorithms include user-assigned flexibility thresholds to account for the innate variation in how a behaviour can be executed, for example the depth of steps varying with the substrate on which an animal is moving. Data matching the input criteria are flagged as "marked events", with a unique number assigned to each behaviour category. Here events refer to acceleration data points, i.e., the 20 Hz data here comprised of 20 events per second. Initial behavioural classification rules were developed by adapting rules previously used for African wild dogs (*Lycaon pictus*) and domestic dogs (*Canis lupus familiaris*; English, 2018). These were adjusted and verified using release videos and observations reported by a member of the public. VeDBA data were smoothed using the default DDMT smoothing rate. Behaviour classification rules for walking, trotting and running had the minimum and maximum VeDBA smoothed thresholds adjusted until they were visually discrete and matched the consistent waveforms with mean peak amplitude increasing between gaits, as seen in African wild dogs and domestic dogs. The time series function in DDMT's Behaviour Builder was used to set approximate minimum behaviour durations, i.e., a minimum number of events the behavioural search algorithm must be valid for in order to classify the behaviour. This improved behaviour classification results, by preventing brief high energy motions from being classified as running, for example. The time series functionality was also used to specify a higher minimum number of acceleration events for resting than stationary, to distinguish between brief pauses in activity and true resting bouts. Reports of one fox regularly exploiting food provided in a member of the public's garden were used to refine and verify the feeding rule, which was adapted from feeding rules defined for African wild dogs.

Dead-reckoning

Two dead-reckoned tracks are provided as a case study in how this fine-scale path reconstruction method can be used to contextualise behaviour in the landscape. Dead-reckoned tracks were produced to represent two 24 hour periods, one from a fox primarily active in residential areas and one from a fox primarily active in natural areas. To produce dead-reckoned tracks, GPS data were reformatted to be readable by DDMT. Specifically, date, time, latitude, longitude and altitude were kept and presented in that order while any remaining columns were removed. GPS and DD data were then simultaneously loaded into DDMT. Time and device orientation corrections were applied to the DD data, as well as hard and soft iron corrections using pre-deployment calibration data to counteract magnetometer drift (Bidder et al., 2015; Gunner et al., 2021b). Behaviour classification rules were applied so that only data labelled as one of the three movement behaviours, walking, trotting and running, were used to compute the dead-reckoned tracks, removing noise from other behaviours which can falsely expand the track (English et al., 2023; Gunner et al., 2021a). Where data were classified as one of these movement gaits, dead-reckoned tracks were computed on a second-by-second basis. GPS locations were used to correct dead-reckoned tracks, which can be subject to drift over time without verified positions (Gunner et al., 2021a, 2021b). The computed dead-reckoned tracks were then exported from DDMT and plotted in R with *ggmap* (Kahle and Wickham, 2023). Dead-reckoned tracks were colour-coded by movement gait and feeding events were time-matched and plotted on the dead-reckoned tracks to indicate where feeding occurred in the landscape. The *viridis* package in R was used to ensure colour-coded dead-reckoned tracks are colourblind-friendly (Garnier et al., 2024).

Results

GPS data from ten foxes (with data available from one of these individuals for both 2023 and 2024) and biologging data from four foxes have been recovered to date. As the GPS units used had remote capabilities and could connect to a base station, the GPS dataset comprises a greater number of foxes than the accelerometer and magnetometer biologging dataset. Note that these sample sizes are accurate at the time of writing (May 2024) but due to ongoing collar deployments and recovery efforts, the analyses here may be presented with a larger sample size in the near future.

Of the eight collars deployed in 2023, we retrieved GPS data from six and Daily Diary data from four. Failure to retrieve data was due to inability to connect to the collar with the base station and failure to recover these collars following drop-off. GPS data were recorded for 4-50 days (mean: 24.66 days) while daily diary data recorded for 4-44 days (mean: 20 days; Table 1). Daily Diaries stopped recording when the battery had been depleted with the exception of one unit, where the device remained switched on but ceased operating correctly by unknown cause after two weeks. Preliminary GPS data from the ongoing 2024 season comprise 1-55 days (mean: 24 days) of data collection from five individuals, recovered through the GPS base station (Table 1).

Table 1. Summary of retrieved sensor data with metadata of animals included in the study, listed in order of date of capture. A capital R in brackets indicates the recapture of one individual from the 2023 cohort in 2024. Data days are rounded to the nearest complete day. The boundary line mid-table separates 2023 and 2024 captures.

Fox ID	Sex	Location	GPS Sampling	GPS Data Days	DD Data Days
Ruby	F	Bushy Park	10 mins	50	44
Rocky	M	Bushy Park	10 mins	17	Not recovered
Freddie	M	Bushy Park	10 mins	4	4
Fantastic Mr	M	St. Anne’s	10 mins	29	14
Merida	F	Tolka	10 mins	40	18
Alfie	M	Clonskeagh	10 mins	8	Not recovered
Kas	F	Bushy Park	20 mins	55	Ongoing
Ash	M	Bushy Park	20 mins	24	Ongoing
Gráinne	F	Fairview Park	20 mins	1	Ongoing
Freddie (R)	M	Bushy Park	20 mins	31	Ongoing
Rua	F	Fairview Park	20 mins	9	Ongoing

Fox home range size estimates ranged from 0.006 to 15.958 km^2 (mean: 1.86 km^2), as calculated from the 95% MCP values (Figure 1, Figure 2, Table 2). Core home range size estimates, based on 50% MCPs, ranged from 0.001 to 4.39 km^2 (mean: 0.47 km^2; Table 2).

Table 2. 100%, 95% and 50% home range area estimates for each individual in the study. All estimates are provided in squared kilometres (km^2).

Year	Fox ID	Sex	100% MCP HR size (km^2)	95% MCP HR Size (km^2)	50% MCP HR Size (km^2)
2023	Ruby	F	0.85	0.126	0.017
	Rocky	M	0.314	0.089	0.016
	Freddie	M	0.194	0.133	0.029
	Fantastic Mr	M	0.533	0.298	0.073
	Merida	F	16.775	15.958	4.395
	Alfie	M	0.149	0.108	0.064
2024	Kas	F	0.435	0.342	0.142
	Ash	M	4.171	2.778	0.337
	Gráinne	F	0.078	0.006	0.001
	Freddie (R)	M	0.545	0.239	0.012
	Rua	F	0.415	0.347	0.126

The three foxes tagged in Bushy Park in 2023 all showed considerable home range overlap (Figure 1a, Table 3), with core home ranges falling entirely within a residential area rather than the neighbouring park (Figure 1b). In 2024, high home range overlap was seen between a resident male and female (Figure 1c, Table 3). The male maintained a core home range in the residential area and the female’s larger core home range covered both the residential area and the park (Figure 1d). A second male visited the area while maintaining a core home range in another neighbourhood (Figure 1c). This core home range also falls within a park-adjacent residential area (Figure 1d). Home ranges of foxes from other capture sites show individual variation in size and use of residential *versus* natural areas (Figure 2). The highest proportion of grouped fox locations were found in residential areas, with 56.99% of all locations occurring in areas classed as residential and 42.89% occurring in natural areas.

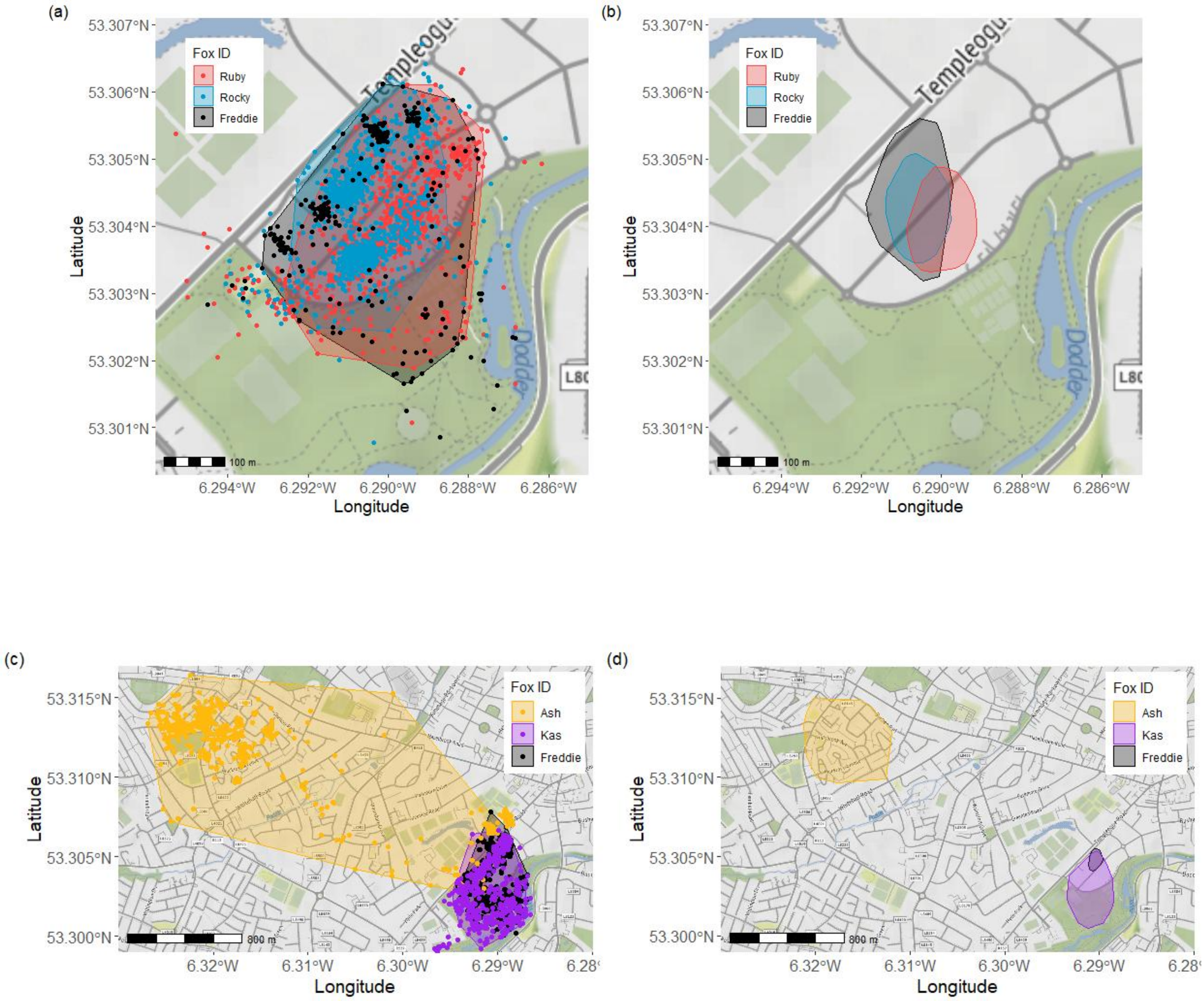
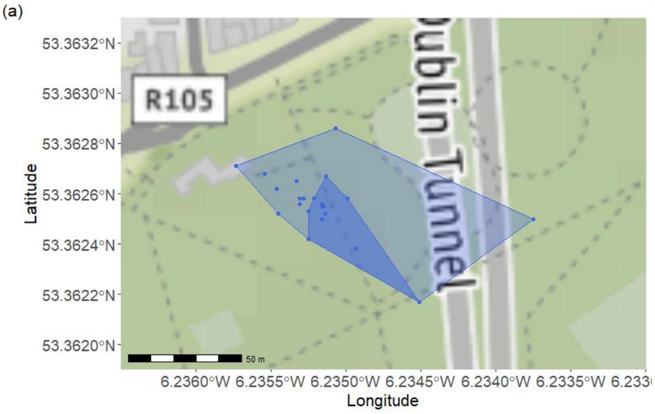
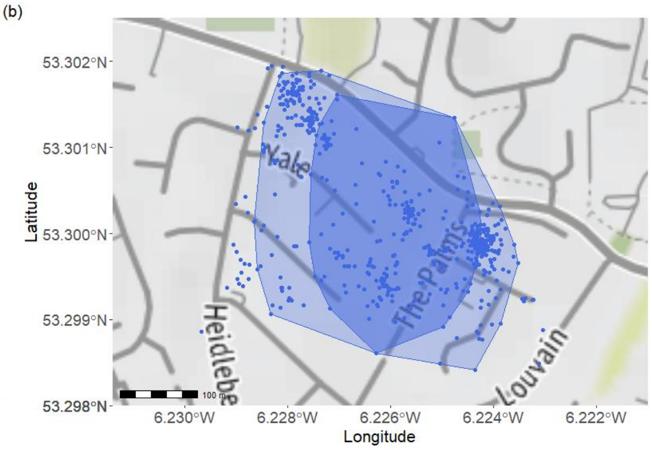


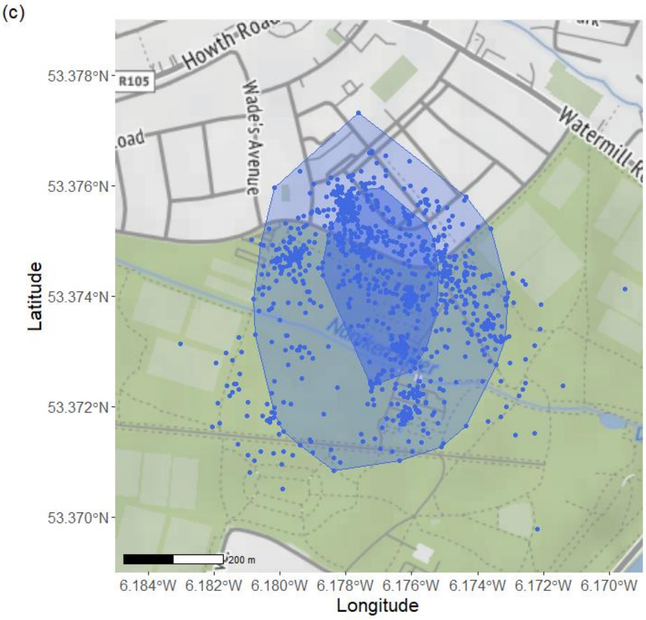
Figure 1. Multi-panel plot showing Bushy Park home ranges. (a) and (c) show 95% minimum convex polygon home range with GPS location points mapped on top for 2023 and 2024, respectively. (b) and (d) show 50% minimum convex polygon home range, for 2023 and 2024. 2023 home ranges show high overlap and all three foxes maintaining the entirety of their core home ranges in gardens instead of the neighbouring park. 2024 shows greater park usage by one of the two resident foxes. The third fox visits the area as part of a much larger home range, with a core home range which is also predominantly residential but park adjacent in another neighbourhood.

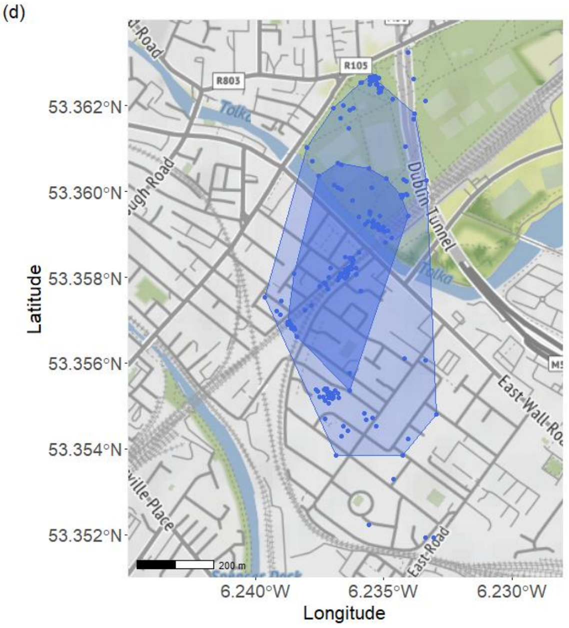
Table 3. Directional home range overlap values between foxes from the Bushy Park capture site area. Directional home range overlap was calculated based on 95% Minimum Convex Polygons (MCPs).

Year	ID1	ID2	Directional HR Overlap
2023	Ruby	Rocky	0.597
	Rocky	Ruby	0.948
	Ruby	Freddie	0.751
	Freddie	Ruby	0.977
	Rocky	Freddie	0.914
	Freddie	Rocky	0.749
2024	Freddie	Kas	0.912
	Kas	Freddie	0.633
	Freddie	Ash	0.286
	Ash	Freddie	0.0244
	Kas	Ash	0.239
	Ash	Kas	0.0294


(a)
53.3632°N
53.3630°N
53.3628°N
53.3626°N
53.3624°N
53.3622°N
53.3620°N
Latitude
R105
Dublin Tunnel
50 m
6.2360°W
6.2355°W
6.2350°W
6.2345°W
6.2340°W
6.2335°W
Longitude


(b)
53.302°N
53.301°N
53.300°N
53.299°N
53.298°N
Latitude
Yale
The Palms
Heidlebe
Louvain
100 m
6.230°W
6.228°W
6.226°W
6.224°W
6.222°W
Longitude


(c)
53.378°N
53.376°N
53.374°N
53.372°N
53.370°N
Latitude
Howth Road
R105
Wade's Avenue
Watermill R
200 m
6.184°W
6.182°W
6.180°W
6.178°W
6.176°W
6.174°W
6.172°W
6.170°W
Longitude


(d)
53.362°N
53.360°N
53.358°N
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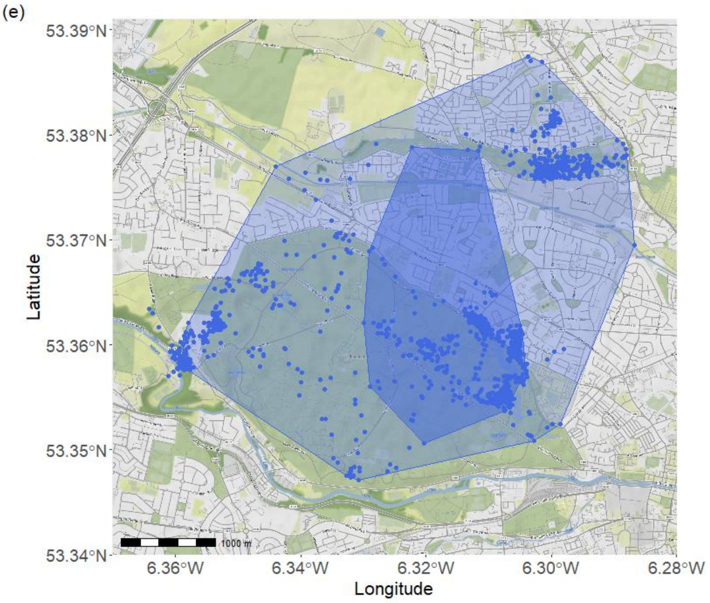
(e)
53.39°N
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Longitude

Figure 2. MCP home range polygons for foxes from all other capture sites, ordered by size. Larger, lighter polygons represent 95% MCP home ranges while smaller, darker polygons represent the 50% MCP core home ranges.

Our model of factors affecting movement speed explained 25.5% of deviance. Movement speeds were significantly slower during the day than at night (edf = 7.8, Ref.df = 8, F = 340.32, $p < 0.001$, $n = 11212$ locations from $n = 9$ foxes; Figure 3). Speed was also significantly reduced in residential compared to natural areas (Estimate = -0.382, SE = 0.026, $t = -14.878$, $p < 0.001$; Figure 3) and increased with Julian day (edf = 4.216, Ref.df = 9, F = 22.07, $p = 0.0141$; Figure 3). There was significant variation between individuals (edf = 6.8, Ref.df = 7, F = 25.15, $p < 0.001$, Figure 3). Speed did not vary significantly between males and females (Estimate = -0.033, SE = 0.156, $t = -0.213$, $p = 0.831$, Figure 3) or year of data collection (Estimate = -0.242, SE = 0.156, $t = -1.548$, $p = 0.122$, Figure 3).

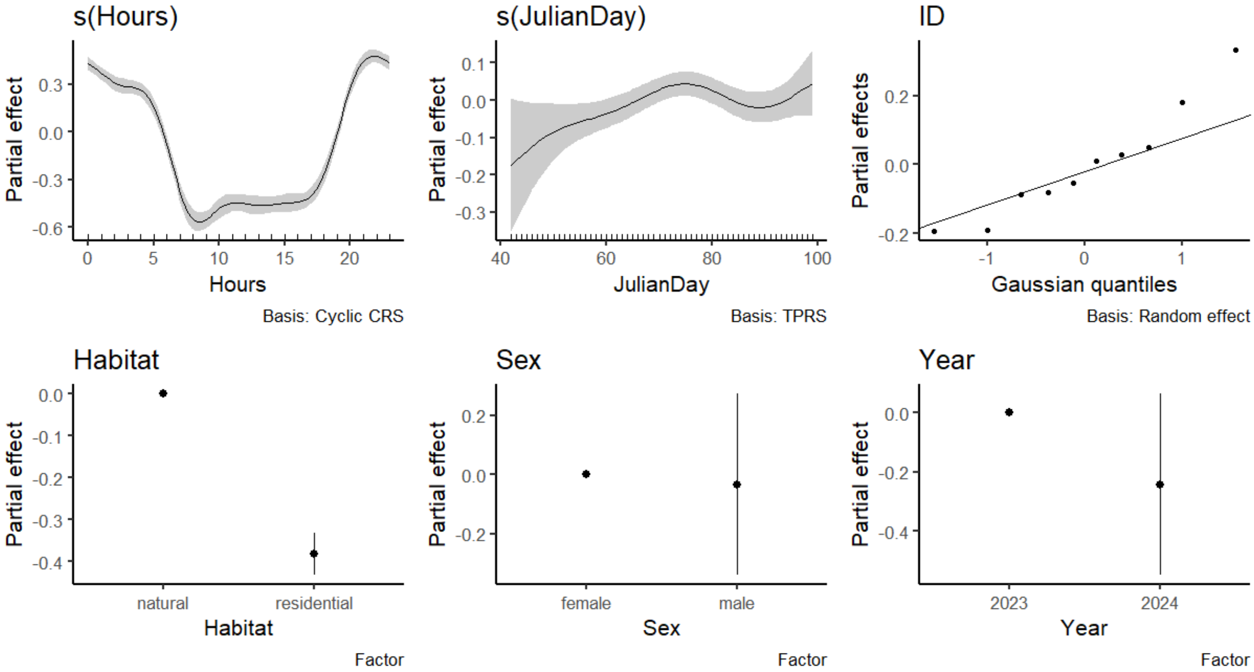

Figure 3. A panel plot showing the results from the first model. Movement speed showed a clear nocturnal pattern, with lower activity during the day and lower movement speeds in residential areas.

The model of factors affecting daily home range area estimates explained 49.5% of deviation. Daily home range area estimates were smallest when foxes were predominantly in residential areas (edf < 0.001, Ref.df = 2, F = 211.36, *p* = 0.001, *n* = 258 daily home range area estimates from *n* = 9 foxes; Figure 4). There was strong individual variation in daily home range area (edf < 0.001, Ref.df = 7, F = 18.46, *p* < 0.001). Julian day did not influence daily home range area estimates (edf < 0.001, Ref.df = 4, F = 0, *p* = 0.55). There was no significant difference in daily home range between males and females (Estimate = 0.0347, SE = 0.393, *t* = 0.088, *p* = 0.929) or between years of data collection (Estimate = 0.136, SE = 0.269, *t* = 0.505, *p* = 0.614).

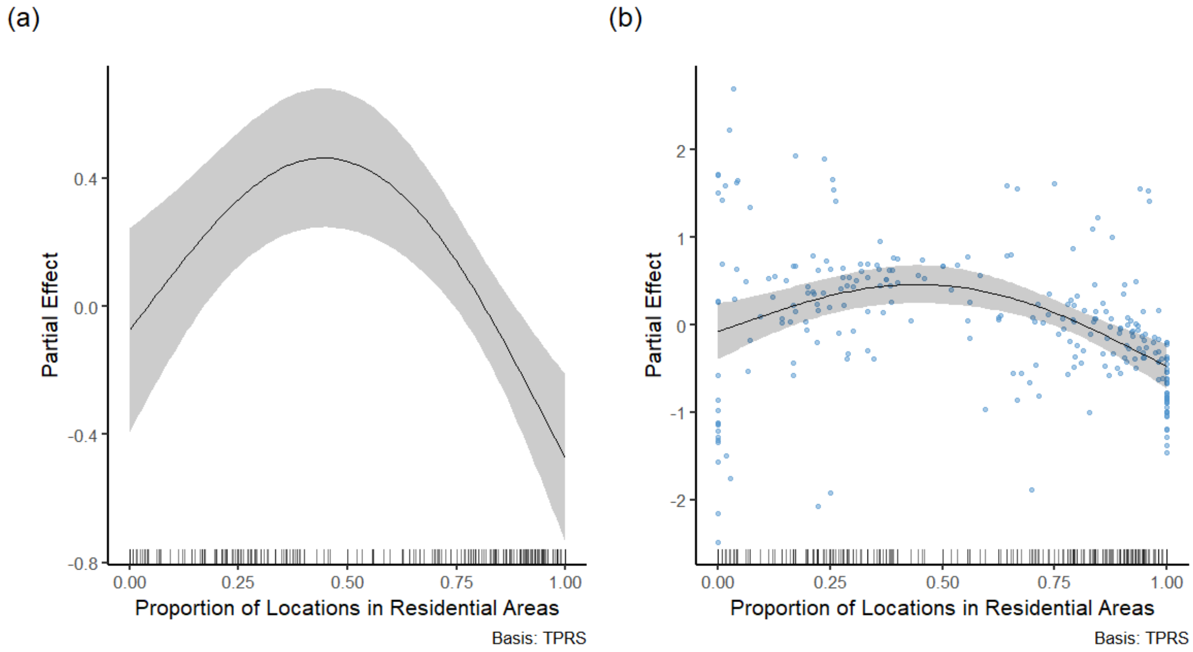

Figure 4. GAMM results showing the effect of the proportion of locations occurring in residential areas on daily home range size. Daily home range area estimates were smallest when foxes were primarily in residential areas and largest when a mix of residential and natural areas were used. Residuals are shown in (b) and indicate high variability.

Actograms allowed further visualisation of the considerable individual variation in movement rates (Figure 5). Activity was primarily nocturnal but with diurnal activity also present. Acceleration-based actograms show clearer nocturnal activity patterns for three of four individuals, with one individual showing less consolidated activity rhythms with more diurnal activity (Figure 6).

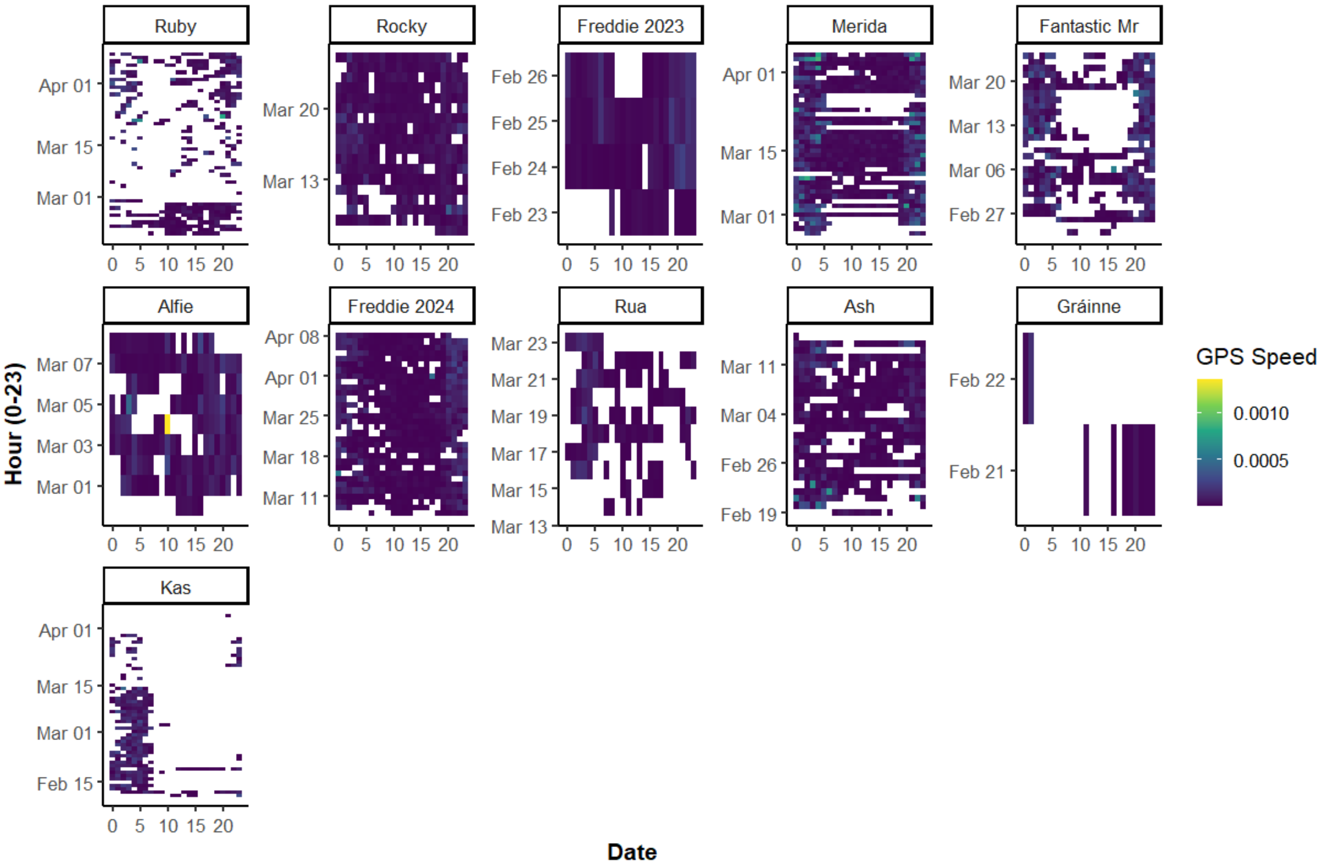

Figure 5. Actograms for ten foxes derived from GPS speed estimates. Mean speed was aggregated by hour for clearer visualisation of trends. Note that two separate plots are presented for Freddie, who was collared in both 2023 and 2024. White blocks represent hours without GPS fixes, which can approximate inactive periods.

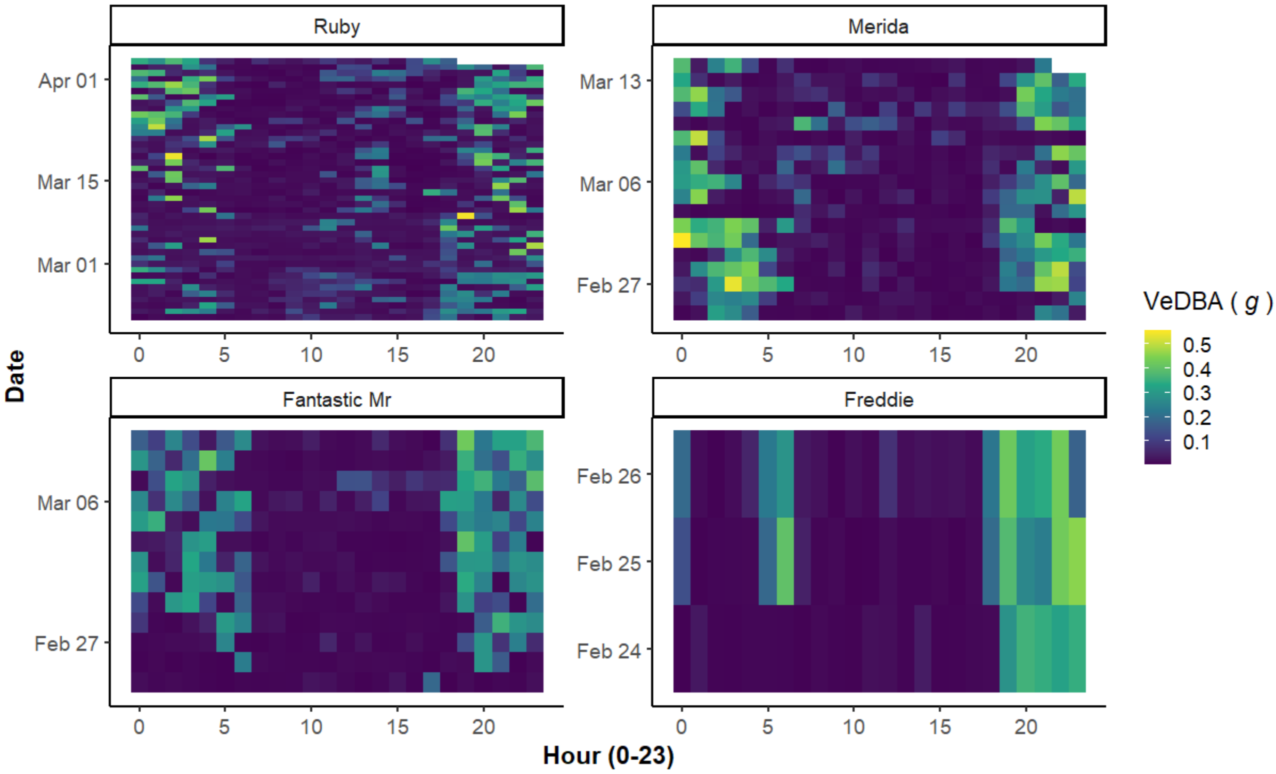

Figure 6. Actograms for four foxes showing mean Vectorial Dynamic Body Acceleration (VeDBA, *g*) aggregated hourly, derived from the accelerometer data. Sample size varies from 3-44 days and plots are shown in descending order of sample size.

Behaviour classification rules were developed for six behaviours (Table 4) pertaining to resting, movement, and feeding. Specifically, we provide rules for stationary, resting (prolonged stationary periods), walking, trotting, running and feeding. Classification rules for resting and movement gaits adapted from previous work (English, 2018) performed well with minimal adjustments to VeDBA thresholds. Instances of stationary, walking, trotting and running recorded in release videos were identified accurately by these behaviour classification rules. Feeding was classified using a combination of heave acceleration and VeDBA and was detected in line with reported observations (Figure 7). Heave acceleration was associated with feeding when it was +/- 3 *g* and its variance over 10 events was greater than 2 *g*, with VeDBA simultaneously greater than 3 *g*.

Table 4. Behaviour classification rules developed for foxes. Events refer to acceleration data points, which occur at a rate of 20 times per second (20 Hz). Validity relates to the minimum duration of behaviours, with neighbouring detections then merged to capture the full duration of a given behaviour. Stationary detects brief periods when the fox is not moving while resting is used to detect longer periods of immobility suggesting true resting bouts. Walking, trotting and running represent distinct movement modes with increasing smoothed VeDBA thresholds. While the feeding rule specifies 1 event validity, this was placed in a time series with an additional range parameter to look for multiple occurrences of this characteristic feeding motion within fifteen seconds of each other. ABS is shorthand for absolute, i.e., the specified value for heave acceleration could be positive or negative. Note that VeDBA was not smoothed when detecting feeding as peaks in the raw VeDBA data were key to identifying this behaviour.

Behaviour	**Boolean Behaviour Classification Rule**	**Valid for (min. *n* events)**	**Valid % pass**
Stationary	If (VeDBA smoothed < 0.1) then Mark Events	60	90
Resting	If (VeDBA smoothed < 0.05) then Mark Events	200	90
Walking	If (VeDBA smoothed > 0.14 AND VeDBA smoothed < 0.35) then Mark Events	60	80
Trotting	If (VeDBA smoothed > 0.35 AND VeDBA smoothed < 0.85) then Mark Events	60	70
Running	If (VeDBA smoothed > 0.85) then Mark Events	60	70
Feeding	If VeDBA > 3 AND (ABS(Accel Z) > 3 AND Variance(Accel Z | 10)> 2) then Mark Events	1	100

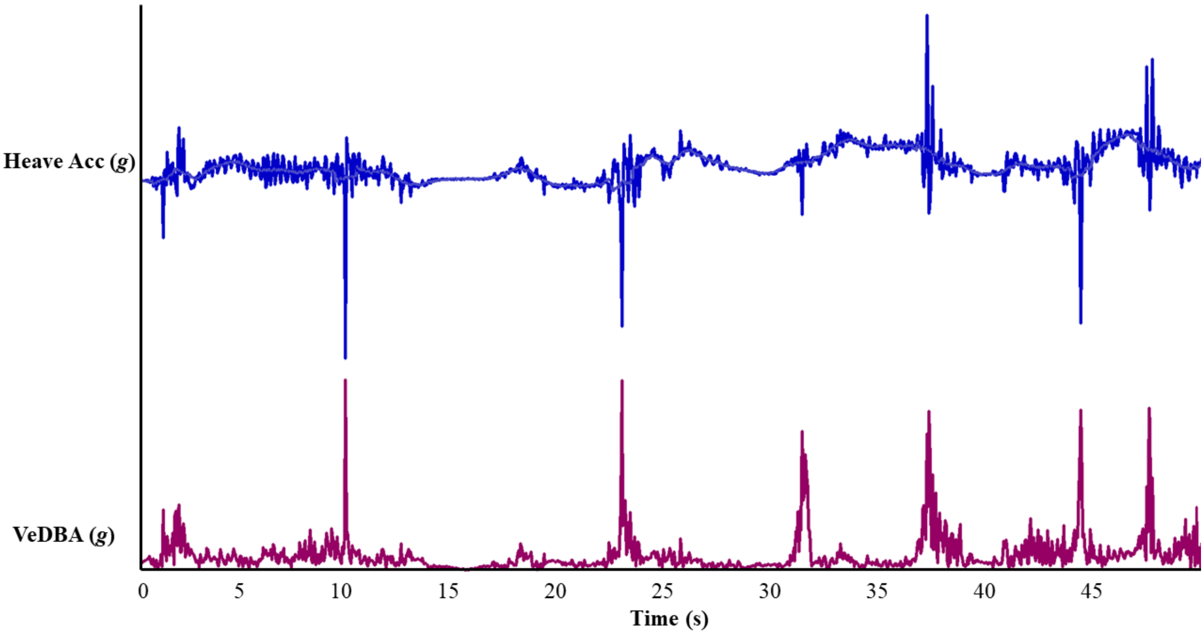

Figure 7. Fifty seconds of fox behaviour, with concurrent peaks in heave acceleration (shown in blue) and VeDBA (shown in purple) classified as feeding. The data shown are from a fox feeding from food scraps provided by a member of the public in their garden, with the feeding event subsequently reported to the research team.

Our case study visualising two representative days of data from (a) a fox primarily active in residential areas and (b) a fox primarily active in natural areas, showed considerable differences between these individuals. Faster locomotion is more obvious from the natural areas track (lighter colours; Figure 8a), while slower locomotion is clearer from the residential areas track (darker colours; Figure 8b). Additionally, despite the small home ranges exhibited in residential areas, initial dead-reckoning suggests that movement rates may still be high, through a highly tortuous, overlapping track. The majority of feeding events shown in Figure 8a occurred between 6pm and 11pm, while most feeding events in Figure 8b occurred between 12am and 3am.

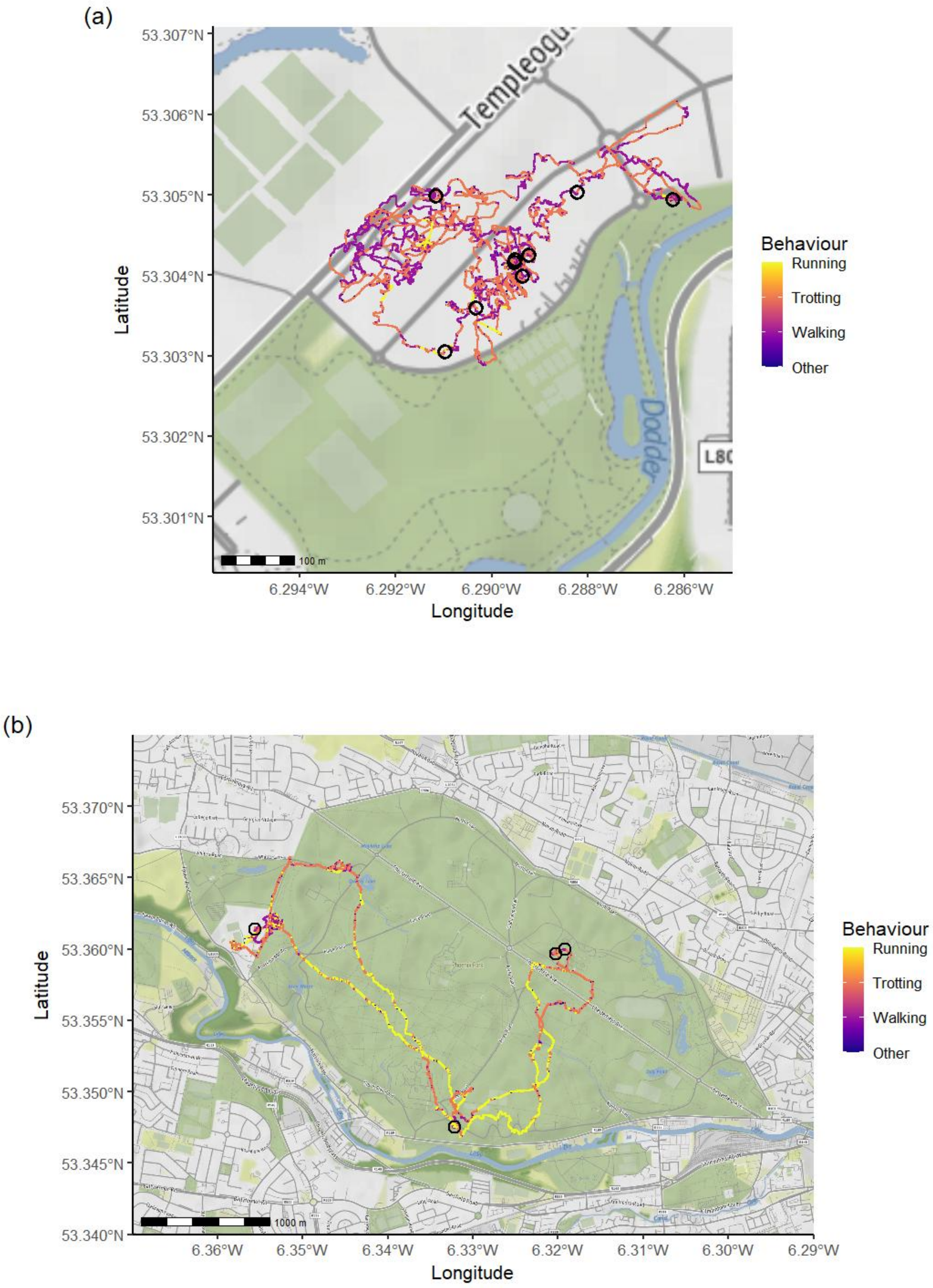

Figure 8. Two dead-reckoned tracks coloured by behaviour, each representing a 24 hour period. Black circles represent feeding events, with feeding events less than 30 minutes apart

grouped for clearer visualisation. (a) A fox primarily active in a residential area adjacent to the Bushy Park trapping site. The data shown include confirmed feeding observations reported by a member of the public and additional feeding events identified using the classification rule alone. (b) A fox active in natural areas, specifically Phoenix Park. No confirmed observations of feeding were available for this individual, but the feeding classification rule detected data using the same numeric value thresholds and producing visually similar data traces, i.e., the waveforms shown in Figure 7.

Discussion

Here we provide valuable insights into urban fox movement and behaviour, gained from GPS and biologging data. GPS data were used to characterise space use, including home range size and overlap estimation, and compare movement rates between individuals in relation to land use type, sex, time of day and Julian day. GPS and accelerometer data were used to visualise circadian rhythms. Accelerometer data were then used to classify six behaviours, before providing a case study on how behaviours can be mapped in the landscape for an urban mesopredator through dead-reckoning, using GPS, accelerometer and magnetometer data.

The abundance of resources available in cities and the ability of foxes to exploit these generally leads to urban foxes maintaining smaller home ranges than their rural counterparts (Main et al., 2020; Šálek et al., 2015). Specifically, home range sizes have been found to shrink with increasing Human Footprint Index (HFI) and human population density (Main et al., 2020). Here, home ranges at the 95% MCP level were <0.4 km^2 for eight of the ten foxes, agreeing with studies from other regions which report similar home range size estimates for urban foxes (Kobryn et al., 2023; Marks and Bloomfield, 2006; Mueller et al., 2018; O'Connor et al., 2021). However, our largest home range size estimate is larger than those reported in any of these studies, with the exception of one individual in Kobryn et al. (2023). Further, the largest home range presented here surpasses predicted home range sizes at even the lowest human population densities (Main et al., 2020). Kobryn et al. (2023) suggest that urban fox home range sizes may be underestimated due to significant numbers of “lost” individuals moving outside of VHF detection ranges. The variation in home range sizes found here supports this claim. We suspect most unrecovered collars were worn by individuals who dispersed or generally ranged more widely, resulting in cases where the VHF signal could not be detected. GSM (Global System for Mobile communications) or satellite GPS units, transmitting data directly to researchers online, can mitigate this widespread issue in future studies, though come with higher costs. Other technologies such as LoRaWAN (Long Range Wide Area Networks) should receive greater attention, as these may serve as a more cost effective solution (Gauld et al., 2023).

Foxes show flexibility in their social behaviour, being more social at higher population densities, such as those found in urban environments (Dorning and Harris, 2019). Where groups of foxes are reported to share territories, these are typically comprised of one male and multiple females (Macdonald, 1983; Sillero-Zubiri et al., 2004). This is thought to typically consist of a breeding pair and daughters from previous litters (Iossa et al., 2009; Lindström, 1986). Social groups of up to ten adults with equal proportions of males and females have been reported from a long-running study of a high-density urban fox population in Bristol, UK, however (Baker et al., 2004). This suggests that groups transition from female-biased to a more equal sex distribution as population density increases (Baker et al., 2004; Soulsbury et al., 2008). The home range overlap seen in the Bushy Park study site here is therefore interesting, particularly as the two males collared in 2023 showed higher home range overlap with each other than either did with the female. Despite the wealth of research conducted on red foxes to date, their social systems remain understudied (Dorning and Harris, 2019), making insights such as these valuable.

Behavioural flexibility is thought to be an important trait facilitating urban wildlife adaptation to human-dominated environments (Lowry et al., 2013). This flexibility may involve individual flexibility in response to a dynamic environment (Bateman and Fleming, 2012; Lowry et al., 2013) or flexibility on the population level with different individuals exhibiting different behavioural strategies (Wolf and Weissing, 2012). Kobryn et al. (2023) found foxes avoided residential areas and selected for parklands. Here, while there was strong individual variation in movement speed and daily home range area, we did not see this trend. Rather our results suggest urban foxes in Dublin employ different strategies. Foxes spending time in residential areas move more slowly with reduced space use, while travelling at higher speeds and with greater overall space use when using parks and other natural areas. Travel speed may necessarily be slower when navigating between gardens and across roads than in large open areas like parks, as suggested by preliminary behaviour-classified dead-reckoning efforts (Figure 8). We suspect anthropogenic food sources including deliberate feeding by members of the public also play a role. Conversations with residents living in or close to study areas revealed diverse foods are being provided to foxes, including dog and cat food, ham sandwiches, roast chicken and potatoes. Slices and rolls of bread were also detected being carried away from gardens on camera traps, which may indicate caching of these items.

Geographic landscape features such as roads can act as barriers to wildlife movement (Bischof et al., 2017; Shepard et al., 2008). Road fatalities are a significant cause of mortality for red foxes in both urban and rural populations (Bateman and Fleming, 2012). Roads are not thought to be driving the encamped daily home ranges in residential areas here, however. Foxes are primarily active at night when traffic is low and foxes were observed crossing roads at night in several of the study areas as well as in busy city centre locations (H.M. English, pers. obs.).

Foxes elsewhere have been found to track linear features like roads (Bischof et al., 2019) and roads were not found to predict fox home range size in a global meta-analysis (Main et al., 2020).

Foxes were largely nocturnal, though with some diurnal activity, particularly in the early evening (Figure 3). Actograms allowed detailed visualisation of individual fox activity patterns. Acceleration-based actograms offer more detailed insights on a subset of the data, while the GPS-based actograms provide a larger sample size, in terms of both number of individuals and recording durations per individual. The most diurnal activity was exhibited by Ruby, a fox confirmed to be pregnant at capture and later confirmed to be availing of intentional anthropogenic feeding. The energetic demands of pregnancy and cub-rearing may promote increased diurnal or crepuscular activity in foxes (Caravaggi et al., 2018; Phillips and Catling, 1991). Intentional feeding of foxes is widely reported in cities (Contesse et al., 2004), and activity may increase in the early evening before nightfall to coincide with food provisioning (Dorning and Harris, 2017). Future research should investigate whether early evening activity is associated with predominantly residential space use. Positive perceptions of urban foxes, which result in intentional feeding, may allow urban foxes to exhibit more diurnal activity patterns than their rural counterparts, which are often considered pests. Many urban residents may still view foxes as pests however and this discrepancy in human attitudes may drive human-wildlife conflict (Cassidy and Mills, 2012), with implications for management.

We present behaviour classification rules for six behaviours (stationary, resting, walking, trotting, running and feeding) using continuous acceleration data and a Boolean search approach. Previous work on fox behaviour classification used machine learning methods to identify six behaviours from burst acceleration data though with mixed classification success (Rast et al., 2020). Arctic fox data has been classified into four behaviours (motionless, walking, running and digging) from burst acceleration data (Clermont et al., 2021). While our available observations for verification of classified behaviours were limited, release videos confirmed that rules for movement gaits were correctly identifying stationary, walking, trotting and running. Resting could also be confirmed using footage of foxes recovering from anaesthesia prior to release and public reports of feeding indicate accurate detection of this behaviour. Classifying feeding behaviour is widely reported at lower accuracies than other behaviours and is acknowledged to be particularly difficult in smaller predators consuming small prey items (Clermont et al., 2021; Studd et al., 2021). We provide a rule for stationary as well as for resting, so that pauses during active periods can be detected. Such pauses are sometimes associated with searching behaviour during foraging bouts (Seymour et al., 2004) and can potentially be adapted into future multi-step behaviour classification rules.

Classifying behaviours through a Boolean search approach can provide behaviour algorithms which are easier to interpret and adapt across studies compared to many machine learning methods (Wilson et al., 2018). This is significant as improving generalisability of behaviour classification rules across systems is often difficult to achieve (Chakravarty et al., 2019). The use of VeDBA to determine stationary, resting and all movement behaviours, as well as its role as a component in feeding, point to the power of this metric in interpreting animal behaviour from acceleration data. Many other studies have similarly highlighted the value of this metric in behaviour classification (Clarke et al., 2021; Dunford et al., 2024; Fehlmann et al., 2017; Uenishi et al., 2021; Vázquez Diosdado et al., 2015). While further refinements are warranted, vertical, or heave, acceleration showed promise in identifying feeding. VeDBA and heave acceleration were also both found to be important in classifying cheetah behaviour (McGowan et al., 2022). Heave acceleration has also previously been used to classify grazing behaviour in goats (*Capra hircus*; Moreau et al., 2009) and multiple behaviours including walking, swimming, grooming and feeding in beavers (*Castor fiber*; Graf et al., 2015). Using heave acceleration for carnivore species which primarily handle smaller food items, where classification of feeding behaviour has traditionally been difficult to achieve (Studd et al., 2021), may therefore be a promising research direction.

Future work estimating food intake based on time spent feeding, e.g., by the number of peaks in heave acceleration, is worth consideration and has been recommended elsewhere (van Donk et al., 2019). Quantifying food intake in this way may allow greater understanding of fox diet and energy intake, though a complementary study with captive surrogates may be required to ensure accuracy of methods. This may be achievable by collaring foxes temporarily held in rescue centres where behavioural observations are easier to conduct. Alternatively, further cooperation with members of the public to gather more time-matched observations of feeding may also facilitate refined behaviour classification methods. Separating a general feeding rule into scavenging and predation respectively would allow greater understanding of how intentional feeding of foxes by members of the public may be influencing fox activity patterns in both spatial and temporal ways. For example, anecdotal reports suggest that regularly fed foxes return to gardens at set times where feeding times are regular (P. Rumley, pers. comm.). This could drive temporal activity patterns as well as driving selection for use of these gardens where food is offered.

Despite small home range sizes, dead-reckoning showed highly tortuous and overlapping movement tracks in a residential area. Future work will examine these trends across full datasets. Though preliminary, this shows the additional insights available through dead-reckoning, where GPS path analysis alone may accurately capture general space use patterns while underestimating movement rates where space use is restricted. Such information is important in better understanding the energy requirements of urban foxes. Overlapping, tortuous movement paths may be a result of frequent den visits due to cub-rearing. Foxes may also be navigating a temporally dynamic risk landscape, with some gardens containing real and perceived threats that must be navigated, including intermittent use by humans and pets. Foxes also readily engage in caching behaviour (Gadbois et al., 2015; Macdonald, 1976). Where anthropogenic feeding rates are high, caching behaviour is also likely to be high (Sillero-Zubiri et al., 2004), with foxes potentially making multiple visits to gardens with large amounts of food provided and creating multiple cache stores. This is significant as caching is thought to be a key potential conflict behaviour in Dublin (Fallon, 2019), as it is often considered a problematic behaviour by gardeners (Unwin, 2015). As well as conflict arising from caching behaviour, anthropogenic feeding can result in artificial selection for bolder begging behaviours, as is already being seen elsewhere with Dublin's wildlife (Griffin et al., 2022).

This is the first study to collect GPS or biologging data on foxes in Ireland. This Irish context is important as the Irish public have shown considerable interest in foxes, with frequent coverage in news media (e.g., Fallon, 2019; McCaughren, 2023; Moore, 2021). Due to the extirpation of large carnivores (Guilfoyle et al., 2023), the fox can currently be considered a top terrestrial predator in Ireland. Further, species can behave differently on islands (Brodin et al., 2013), with behavioural differences noted in some Irish species compared to their conspecifics elsewhere in Europe, e.g., badgers *(Meles meles*; Mullen et al., 2015). The Irish fox population has also been found to be genetically distinct (Statham et al., 2018).

Conclusion

This study provides insights into space use, activity patterns and behaviour of urban foxes in Dublin and indeed Ireland, for the first time. Future work should aim to apply behaviour classification and dead-reckoning methods across larger biologging datasets to elucidate urban fox behaviour budgets and space use in natural *versus* residential urban habitats.

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Chapter 6 Discussion

The development of increasingly sophisticated biologging technology is opening new research avenues, allowing us to understand where animals go and what they do while out of human sight (Brown et al., 2013). Biologging devices incorporating accelerometers and magnetometers allow state-of-the-art quantification of fine-scale movement patterns, activity rhythms and animal behaviour (Bidder et al., 2015; Chimienti et al., 2020; Gunner et al., 2021a; Williams et al., 2020). Collecting, analysing and interpreting such datasets remains complex, however, and methodological advancements remain a considerable research priority for movement ecologists. In this thesis, I present a review of how such methodological advances can be applied to better understand predator ecology, highlight the insights obtainable from captive systems, describe how wild animal capture protocols were refined for collar fitting and detail fine-scale space use, activity rhythms and behaviour classification in the wild. Applying these techniques to members of the canid family can improve our understanding of their space use and foraging behaviour, which is fundamental to their conservation and management, yet difficult to achieve (Bryce et al., 2017; López-Bao et al., 2017).

Summary of results

As techniques and tools in movement ecology continue to advance, it can be difficult for researchers entering the field to become familiar with the suite of available animal-attached sensors and use them effectively. **Chapter 2** reviews available sensors and outlines how these may be put to use, with specific focus on elucidating predation energetics. This is valuable in considering the energetic implications of global changes in land use and climate. Specific consideration is given to the roles of inter-individual variability and sociality in shaping predation dynamics. This chapter concludes with recommendations for future work, which pertain to study design, data collection and analysis. This includes considering the concepts of energetic landscapes and social networks in tandem, greater use of captive systems to inform biologging studies and tagging multiple individuals within a shared social group.

Chapter 3 shows the value of biologging studies in zoos, with insights for captive management practices as well as refining methods which may be later implemented in wild systems. Zoos provide valuable access to species of conservation concern, such as the African wild dogs (*Lycaon pictus*) in this study. Short-term recovery from sedation is examined and a novel and safe technique for deploying collars on captive carnivores without anaesthesia is described. Activity levels and space use are assessed in relation to food type received on a given day, with implications for feeding enrichment practices. A pipeline for producing dead-reckoned movement tracks is developed, with readily observed and filmed captive wild dogs providing a robust system to ensure accurate path reconstruction. Behaviour classification of movement behaviours (i.e., walking, trotting and running), and only advancing the path where these behaviours have been classified, is identified as an important and overlooked aspect of accurate dead-reckoning. This work also provided positive outcomes for animal welfare. No pacing or other stereotypic behaviours often seen in captive carnivores were detected during the study, and the crate-training used for data collection has since been more widely implemented, reducing the use of anaesthesia for veterinary procedures in London Zoo.

Animal-attached sensors cannot be effectively put to use if the target study animals cannot be captured without undue compromises to animal welfare standards. **Chapter 4** therefore details the considerations and steps taken here to ensure successful capture and collar deployment on red foxes (*Vulpes vulpes*), while also conserving researcher time and effort. Camera traps provided insights into fox behaviour around traps, which informed when trapping efforts could commence following a period of habituation. Remote transmission trap tags and camera traps were essential for monitoring multiple trapping sites simultaneously and ensuring swift arrival at traps with captured foxes. Cheap, lightweight drop-off mechanisms were added to collars and ensured no fox needed to be captured twice. Capture success was affected by high rainfall, but neither minimum nor maximum recorded temperatures for a given capture night. The checklist provided at the end of this chapter should serve as a succinct and generalisable guide to improving capture success of trap-shy species.

Quantifying animal space use, activity rhythms and behaviour in human-dominated environments is essential to understanding animal adaptation in the Anthropocene. **Chapter 5** provides insights into each of these parameters for an urban fox population. Home range estimation shows considerable overlap between foxes collared at the same trapping site. Home range sizes are generally restricted, but with two individuals showing much larger space use. Activity was largely nocturnal, as expected for this species, but with diurnal activity also occurring with significant variation between individuals. Behaviour classification rules for stationary, resting, walking, trotting, running and feeding are presented for red foxes. Behaviours are contextualised in the urban landscape through dead-reckoning, showing behavioural differences between residential and more natural areas. The use of dead-reckoning here also shows that movement rates may still be high where space use is restricted, highlighting the value of this method in urban environments.

The work presented here is continuing to develop beyond the scope of this thesis. Ongoing collaboration with Dublin City Council and an increased sample size of fox biologging data are anticipated over the coming months. Further, external international collaborations are refining and applying the methods developed on captive African wild dogs to wild populations of this species to compare behavioural activity budgets across populations experiencing different climatic conditions.

Canids: conserved and managed

Macdonald et al. (2019) describe the canid family as having three notable attributes: being remarkably similar, remarkably different and remarkably successful. This thesis has benefited from considering the African wild dog (*Lycaon pictus*) and the red fox (V*ulpes vulpes*), which in many ways can be considered both remarkably similar and remarkably different. While body size within the canid family shows variation spanning two orders of magnitude, most canids share a highly physiologically conserved body plan (Tangredi and Lawler, 2024), which can be beneficial for adapting behaviour classification procedures across species. Indeed, wild dogs and foxes share this typical lithe, long-limbed canid body design despite the size differences between the two species. In terms of conservation and population status, on the other hand, wild dogs and foxes certainly differ. The African wild dog is classified as endangered on the IUCN red list of threatened species (Woodroffe and Sillero-Zubiri, 2012; Woodroffe and Sillero-Zubiri, 2020), while the red fox is widespread and often actively managed as a predator of threatened species (Harding et al., 2001; Tobajas et al., 2020). As such, the remarkable similarities between these species allow valuable transfer of research methods, while their remarkable differences provide insights relevant to conservation and wildlife management, respectively. These in turn reflect cases where remarkable canid success constitutes simply surviving or actively thriving under human-driven change.

This thesis began with a reflection on how the study of animal behaviour and animal movement, respectively, grew to prominence over the preceding decades. In the present, both sub-fields are shaped by the urgent need to understand animal responses to global change. Habitat loss and direct persecution caused a dramatic decrease in African wild dog populations throughout the 20th century (Creel and Creel, 2002). More recently, wild dogs have been shown to be vulnerable to climate change, with reductions in both activity and pup recruitment associated with higher ambient temperatures (Woodroffe et al., 2017). The exact mechanisms driving this vulnerability remain uncertain. One leading hypothesis is that rising temperatures are affecting wild dog hunting success, resulting in more abandoned hunts due to heat stress and changes in the timing of hunting bouts (Abrahms et al., 2022; Rabaiotti and Woodroffe, 2019; Woodroffe et al., 2017). Increased nocturnal activity on days with higher maximum temperatures has been documented, though nocturnality remains limited during the pup-rearing period (Rabaiotti and Woodroffe, 2019). A better understanding of behavioural activity budgets for these nocturnal activity periods is required to assess the ability of wild dogs to compensate for reduced activity on hotter days. Behaviour classification of biologging data constitutes a promising approach, as low visibility at night often makes effective behavioural observations impossible (Brown et al., 2013) and following wide-ranging wild dog packs for sustained periods is often difficult to achieve (Woodroffe et al., 2007). The captive data presented here can, and indeed are, being adapted to wild systems, to further elucidate these potential behavioural adaptations in a warming world.

Conversely, the red fox is a clear example of success in the Anthropocene. With a distribution across the northern hemisphere and an introduced population in Australia, the red fox has the largest global range of any wild carnivore (Sillero-Zubiri et al., 2004). The key to the fox's success is its propensity to adapt, by exploiting a variety of food sources, thriving under a wide range of climatic and habitat variables and tolerating widespread human persecution (Sillero-Zubiri et al., 2004; Stubbe, 1980). The resulting variation in fox behaviour between populations, their frequent involvement in human-wildlife conflict and their role as a predator and competitor of species of conservation concern collectively ensure the continued relevance of research on foxes in wildlife management practices (Elmhagen et al., 2017; Liordos et al., 2020; Tobajas et al., 2020). Beyond conflict, the varied attitudes of people in areas of high population densities for both humans and foxes warrant continued investigation

(Brand and Baldwin, 2020; Puri et al., 2024). Here, combining fox behavioural datasets with sociological research on human perceptions is a valuable research direction.

Working with biologging data: methodological insights and recommendations

Bespoke visualisation software programmes can be hugely valuable in easily searching for patterns in large biologging datasets. Here, I use DDMT (Daily Diary Multiple Trace; https://github.com/DDMT-Software/DDMT) for this purpose. Deriving behaviour classification rules manually in software programmes such as DDMT requires expert user knowledge and can be a slow process involving a degree of trial and error. Despite these potential drawbacks, the resulting classification rules are likely easier to interpret, adapt and apply by other researchers and could contribute to an online library of defined behaviour algorithms, as recommended by Wilson et al. (2018). There is certainly potential for such a library to be established in conjunction with existing initiatives within the movement ecology community. MoveApps, which aims to make analytical tools accessible to broader audiences, may be a particularly good fit in this regard (see https://www.moveapps.org/; Kölzsch et al., 2022). Such integration may make behaviour classification methods more accessible outside of research as well as to other research teams (Kölzsch et al., 2022), for example to those working in zoos and management authorities, such as those partnered with throughout the work detailed here.

Despite the potential limitations in adopting behaviour classification rules across species (Dickinson et al., 2021), here we found behaviour classification rules could be generalised from captive to wild systems and between canid species. While the absolute values used in behaviour classification rules require some flexibility across settings, overall rule structures may be more transferable than often thought. For example, implementing VeDBA smoothed thresholds proved an effective method for classifying both African wild dog and red fox gaits. To continue refining behaviour classification procedures for biologging data, it is key to break complex behaviours down into the sum of their physiological components, or create sequences of postures and behaviours to represent more complex behavioural patterns. Easier-to-classify behaviours can be placed in temporal sequences which can be adapted to the specific behavioural strategies of the study species. For example, African wild dogs are expected to be running before feeding as they are pursuit predators. Foxes, which typically pounce on their prey, are expected to be walking or trotting as they search for food. Foxes, unlike wild dogs, are also frequent scavengers, which would also be proceeded by walking or trotting searching gaits. As such, by knowing the ecology of the target species, there is promise in classifying complex behaviours by reconstructing these in logical sequences, once a baseline of simpler behaviour "building blocks" have been defined.

The benefits of captive data collection in refining dead-reckoning procedures may be less obvious than those pertaining to behaviour classification. While dead-reckoning does not require behavioural observations for validation in the same way as behaviour classification methods, a major consideration in reconstructing fine-scale dead-reckoned movement tracks is accounting for drift. Drift occurs as dead-reckoned paths accumulate error over time (Gunner et al., 2021b). This is resolved by including verified locations at intervals, which may be obtained through locational sensors, video footage or direct observation (Gunner et al., 2021a, 2021b). It was determined while computing the dead-reckoned tracks for captive African wild dogs presented in Chapter 3 that including locations at approximately 30 minute intervals, i.e., 24 locations for 12 hour tracks, resulted in highly accurate path reconstruction. This is more readily ascertained in captivity than in wild settings, as enclosure boundaries provide clear indication of where the animal can and cannot access. Further, wild dog locations within enclosures could be verified by video footage. While drift can vary between species, this is largely determined by movement mode, i.e., whether an animal walks, swims, flies or climbs (Gunner et al., 2021b). The GPS sampling rate for the subsequent study on wild foxes was at a higher frequency than the effective sampling frequency used for captive African wild dogs. As wild dogs and foxes share the same movement modes (walking, trotting and running) and the highly conserved typical canid body plan (Tangredi and Lawler, 2024), the dead-reckoned tracks for foxes were therefore reconstructed with high confidence. Captive surrogates can therefore serve a useful role in refining dead-reckoning protocols and more widely implementing this valuable path reconstruction method in the future.

Animal welfare

Animal welfare was a central consideration throughout the work presented here. The crate-training used to collar captive African wild dogs shows a promising method which can be adapted for many captive animals which are difficult to handle, while maintaining animal and zoo-keeper safety. While it is impossible to remove all stress from capture and sedation of wild animals for collar fitting, remote alert systems ensured foxes did not spend extended periods in traps. Researchers should continuously strive to refine data collection methods to reduce potential harms and uphold the highest possible welfare standards, particularly when directly handling animals. To this aim, efforts are currently being made to explore non-invasive animal tagging procedures, whereby tags could be deployed without direct handling. To date, non-invasive tagging remains difficult to execute but positive advancements are being made in this area, for example by dropping bur-equipped tags from motion sensor operated gates when an animal walks underneath (Wilson et al., 2024). Such devices may be particularly useful for species such as foxes which follow known paths and frequently pass through gaps in hedges and fences. Initial trials have showed some promise in adopting this method in future (Figure

1). If successful, such tagging methods could have profound benefits in reducing handling-associated stress. While the welfare of animals in research is central in its own right, this also has important consequences for data quality, as minimising stress provides more reliable insights into natural behaviour (Jewell, 2013).

Figure 1. Camera trap still of a fox passing underneath a remote tagging system gate. Note that the gate was installed beside a trap as this area was already being baited and monitored. In this instance, the fox triggered the gate but the tag did not attach to its fur. Further refinements to bur-tags hold promise for boosting sample sizes of difficult-to-capture species in the future, while removing the stress of handling from tagging.

Conclusion

The development and now widespread use of animal-attached sensors has facilitated unprecedented insights into animal behaviour on the scale of seconds. The challenge is now, in many ways, on the researcher, to maximise the value that can be obtained from such detailed and comprehensive datasets. This involves every step of the research process, from thoughtful study design, to refined data collection and analysis, to considered interpretation. The lessons learned here are presented in the hope that they inform this discipline which keeps coming of age (Holton et al., 2021; Wilmers et al., 2015). Happily, there seems no end in sight to the questions we must answer about what animals do and where they go.

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