DOCTOR OF PHILOSOPHY

Assessing landscape-scale patterns of activity and habitat-use by fallow deer (Dama dama) in the Elwy Valley region of North Wales, UK

Barton, Owain

Award date:
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Assessing landscape-scale patterns of activity and habitat-use by fallow deer (*Dama dama*) in the Elwy Valley region of North Wales, UK

A thesis submitted to Bangor University by

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In candidature for the degree of

Doctor of Philosophy

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Lee Oliver, The Game and Wildlife Conservation Trust

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Dr Brian Gerber, The University of Rhode Island

Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

I confirm that I am submitting this work with the agreement of my Supervisor(s).

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy. Rwy'n cadarnhau fy mod yn cyflwyno'r gwaith hwn gyda chytundeb fy Ngoruchwyliwr (Goruchwylwyr)

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Abstract

Large herbivores are essential ecosystem components in the temperate northern hemisphere. They play critical roles in ecosystem functioning by influencing seed dispersal and nutrient cycling as well as shaping the structure and distribution of habitat for other species. In recent history, large herbivore populations have severely declined as a result of human activities, such as hunting, urban development and habitat modification. Some ungulate species are exceptions to this trend, and are now widespread in developed regions, such as Europe and North America. The expansion of ungulates alongside the growth and development of human populations has led to a diverse range of beneficial and detrimental interactions. Studies of their behaviour in human-dominated landscapes can provide important insights into the ecological processes that enable coexistence. This thesis focussed on the case study of fallow deer (*Dama dama*) in the UK, which is an excellent example of a large herbivore successfully inhabiting a complex landscape of human activities and land-use. The aim was to explore how humans influence the spatiotemporal behaviour of deer and provide evidence to support sustainable population management.

Existing evidence for the effects of population management on deer and other UK ungulate species was systematically mapped to identify key knowledge gaps and provide recommendations for future research and policy-making. The results revealed that the current extent of evidence is limited and unevenly distributed across species, interventions and outcomes. Empirical studies were conducted to address some of the knowledge gaps identified for fallow deer. An array of 29 motion-activated camera-traps were deployed in woodland sites to monitor deer in the Elwy Valley region of North Wales, UK. The local population in this area is largely isolated and provides a valuable opportunity to study the behaviour of deer at a tractable landscape scale. Data from the camera-trap survey were used to examine the influence of temporal, environmental and anthropogenic factors on patterns of daily activity and woodland habitat-use. Deer exhibited clear, non-random patterns of activity across the diel cycle and habitat-use was mostly driven by environmental landscape features (tree cover and slope). The results revealed different and interacting effects of lethal (hunting) and non-lethal (recreation and woodland management) human disturbance and show how deer resolve trade-offs between risk avoidance and resource acquisition in human-

dominated landscapes. These studies also demonstrate the utility of camera-trap surveys in expanding the range of data collected on ungulate populations to support an adaptive approach to management. Simulations were used to assess the optimisation of camera-trap surveys, with a focus on the use of covariates in occupancy models. The results offer guidance to practitioners to improve the robustness and efficiency of camera-trap studies and population monitoring programmes.

As human populations continue to grow and the demands for natural resources intensify, the potential for conflict with large herbivores increases. This thesis provides robust scientific evidence that may be used to develop strategies for coexistence, which conserve the important ecosystem-level benefits of large herbivores while mitigating their impacts on human interests.

Acknowledgements

I'd like to begin by thanking my lead supervisor, Dr Graeme Shannon, for the enormous contribution he made to this thesis and the tireless support he provided over the course of my studies. Graeme consistently went above and beyond the call of duty in offering feedback, replying to emails and developing ideas. Indeed, on many occasions he has helped me to 'see the wood for the trees' and recognise the value of my work. Perhaps most impressive of all is his selfless work ethic and the genuine enthusiasm he has for the successes of students under his supervision. I feel privileged to have worked with him these past few years and, as we both move on to new challenges, I sincerely hope we remain in contact as collaborators and friends.

Thanks must also go to Graeme's wife and my co-supervisor, Dr Line Cordes - together they make a formidable supervisory team. Line has operated as our resident statistics guru and sanity-check when plans occasionally drifted off-piste. I've never met anyone quite so passionate about 'ggplot' and it's fair to say that all of the prettiest figures in this thesis have benefitted for her substantial input. She has offered excellent technical advice, as well as many kind words of encouragement and guidance, for which I am very grateful.

I'm also hugely appreciative of the efforts of Prof John Healey, who acted as a co-supervisor alongside Line and made a similarly large contribution to this thesis. John has a potent intellect and a remarkable ability to make the connection from individual results to big-picture topics. I'm not quite sure how he manages to dedicate so much time and effort to supporting his students whilst performing his many other roles within the University, but I'm certainly thankful of it.

Regrettably, too many people have helped me and contributed towards this thesis to name them all here. Hopefully, they know who they are and how grateful I am of their support and involvement. There are, however, a few individuals whose input I would like to recognise. Firstly, Lee Oliver (The Game and Wildlife Trust) provided a huge amount of support with fieldwork and offered a practical perspective on the issues of population management. His predecessor at the Deer Initiative, Steve Griffiths, was also instrumental in acquiring the funding for the project and laying the groundwork for all of the deer management in the Elwy

Valley. Alastair Ward and David Jam (both formerly Deer Initiative) provided further advice on the application of this research and the challenges faced by management practitioners in the UK.

Fellow students: Amy Gresham, Will Justus and James Owens, made the whole PhD experience much more enjoyable and collectively put in an impressive shift to help me process the colossal volume of camera data. Brian Gerber (University of Rhode Island) offered invaluable advice on the simulation analyses and showed the utmost patience as I flooded his inbox with questions. Norman Dandy provided similarly useful advice on the questionnaire surveys used to assess human activity, which became a core component of the thesis. Lastly, I'd like to thank everyone who worked in the KESS programme (namely, Penny Dowdney and Brian Murcutt) for facilitating my research and ensuring I had everything I needed to complete it. To everyone listed and many more – thank you.

Finally, I will risk descending into a full Oscar-award-winning narrative by thanking my friends and family. It may well be cliché, but it also true that they have played the most important role of all in providing the unquestionable love and support that keeps me going, always. How you have all tolerated me being in school this long, I will never know.

To Mum, Dad, Ross, Laura and my beautiful partner, Beth – Thank you!

I love you all.

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Chapter 1

General Introduction

Understanding the effects of humans on wildlife is essential for species conservation and sustainable ecosystem management (Carroll et al., 2015; Johnson et al., 2017). Global biodiversity has declined at an unprecedented rate in recent history. Human population growth and increased consumption by developed nations has led to warming of the global climate as well as rapid and widespread changes in land-use, habitat destruction and overexploitation (Dirzo et al., 2014; Parmesan et al., 2003; Sandom et al., 2014a; Winkler et al., 2021). Studies of species occupying human-dominated landscapes provide critical insights into the effects of human activities on wildlife, which are essential for developing landscape-scale strategies of coexistence (Linnell et al., 2020).

Terrestrial mammalian herbivores are often the focus of research because of their effects on important ecological patterns and processes (Foster et al., 2014; Hobbs, 1996; Johnson, 2009). The trampling and consumption of plants by herbivores has direct effects on vegetation structure, primary production and plant community composition (Danell et al., 2006; Ripple et al., 2015; Sandom et al., 2014b). Indeed, large-bodied herbivores are highly mobile, and their behaviour can ultimately influence the diversity, structure and spatial distribution of terrestrial habitats at the ecosystem scale (Alexandre et al., 2018; Asner et al., 2009; Huntly, 1991). Consumption of plant material also plays a critical role in seed dispersal and the acceleration of carbon and nutrient cycling (Jara-Guerrero et al., 2018; Kristensen et al., 2022; O'Farrill et al., 2013; van der Waal et al., 2011). Additionally, herbivores are a vital source of food, especially for large-bodied obligate carnivores, such as wolves (*Canis lupis*), lions (*Panthera leo*) and tigers (*Panthera tigris*), which have high energetic demands (Ripple et al., 2014, 2015). Global population sizes vary considerably among herbivore species and range from fewer than a hundred individuals (e.g., Sumatran Rhinoceros, *Dicerorhinus sumatrensis*) to over a million (e.g., Springbok, *Antidorcas marsupialis*, IUCN, 2022). Developed regions (e.g., Europe, North America) are mostly populated by high numbers of relatively few, habitat generalist species (Bar-On et al., 2018; Ripple et al., 2015). Whereas in developing regions (e.g., Southeast Asia, Africa) there is a greater diversity of species, although many (e.g., Zebra duiker, *Cephalophus zebra* IUCN, 2022) have very specific habitat requirements that make them more sensitive to perturbation (Bar-On et al., 2018; Ripple et al., 2015; Sandom et al., 2014a). Understanding the relationship between human activities and geographic trends in terrestrial herbivore populations is critical for conserving species and maintaining healthy, functioning ecosystems.

Humans can induce fear in animals that mimics the effects of a natural predator (Ciuti, Northrup, et al., 2012; Colter Chitwood et al., 2022; Laundré et al., 2010). Often, individual animals shift their patterns of temporal activity and/or habitat-use to avoid encounters with humans, which can incur fitness costs by reducing access to resources (Colter Chitwood et al., 2022; Laundré et al., 2010; Wilson et al., 2020; Zbyryt et al., 2018). Learning to respond appropriately to humans is cognitively demanding, as the risk associated with encounters varies greatly from being lethal (e.g., hunting), to non-lethal (e.g., recreation) or even beneficial (e.g., feeding, Goumas et al., 2022). Reliably assessing risk is particularly challenging in complex human-dominated landscapes, where different types of disturbance cooccur and vary temporally (Goumas et al., 2022; Wevers et al., 2020). Previous studies have examined how species resolve the trade-off between resource-use and risk avoidance (e.g., Eldegard et al., 2012; Maren et al., 2009; Wevers et al., 2020). However, the results vary across studies and are only available for a narrow range of species and geographic regions (Mols et al., 2022; Paton et al., 2017). Wider investigations into the ecological mechanism of coexistence between ungulates and humans are needed to provide important insights for species conservation, especially in developing countries, and sustainable wildlife management, predominantly in developed regions.

Ungulates (*Artiodactyla*) are an order of species that have thrived in developed regions (e.g., Europe, North America) over the past few decades (Apollonio et al., 2010; Krausman & Bleich, 2013; Linnell et al., 2020). Indeed, their geographic ranges in Europe extend to approximately 90% of the total land area (Linnell et al., 2020). Population expansions have most likely occurred because of several human-related factors. Defaunation through over hunting has reduced competition for resources as well as reducing the abundance and diversity of natural predators that would have contributed to limiting population sizes (Carpio et al., 2021; Dirzo et al., 2014). Humans have also played an active role in increasing numbers via introductions and translocations to provide better hunting opportunities.

Increased tree planting and agricultural intensification has likely further contributed by offering shelter and a year-round source of food (Acevedo et al., 2011; Acevedo & Cassinello, 2009; Apollonio et al., 2010; Carpio et al., 2021). Although the factors outlined above go some way to explaining large-scale, historical trends in ungulate populations, there are considerable knowledge gaps relating to the ecological processes that enable their persistence in human-dominated landscapes. Addressing these gaps is critical for informing current and future management of populations as well as other natural resources.

Large ungulate populations provide opportunities for eco-tourism and hunting, which are economically valuable and culturally significant (Apollonio et al., 2010; Linnell et al., 2020). However, high densities have also been associated with a variety of unfavourable effects on woodland habitats and farmland (Carpio et al., 2021; Putman, Apollonio, et al., 2011; Valente et al., 2020). Excessive browsing and damaging behaviours (e.g., trampling, antler rubbing, bark stripping etc.) can severely impede the successful establishment, growth and proliferation of plant species, which alters habitat structure and composition (Eichhorn et al., 2017; Gill & Fuller, 2007; Martin & Baltzinger, 2002; White, 2012). This can have negative consequences for human interests of biodiversity conservation, forestry and agricultural production (Katona et al., 2013; Perea et al., 2014; Seward et al., 2004; Ward et al., 2004). Ungulate species also act as vectors and reservoirs of diseases, such as foot and mouth, bluetongue, bovine tuberculosis and chronic wasting disease, that can be transmitted to humans and domestic livestock. (Böhm et al., 2007; Dhollander et al., 2016; Gortázar et al., 2008; Martin et al., 2011). Furthermore, it is estimated that they are involved in around half a million road traffic collisions per year in Europe, which is a major concern for human health and well-being (Langbein et al., 2011; Linnell et al., 2020)

A range of interventions, including shooting, fencing, administering contraceptives, poisoning and repellents/deterrents are used to manage ungulate populations (Barton et al., 2022; Bengsen et al., 2014; Valente et al., 2020). Members of the scientific community have strongly advocated an adaptive approach to management, based on a continuous process of trial-and-error (Apollonio et al., 2017; Carpio et al., 2021; Lancia et al., 1996). Within the adaptive management framework, outcomes of interventions are assessed by monitoring indicators of ecological change (IECs) that are related to the focal population (e.g., population size, distribution, body condition etc.) and environment (e.g., plant species richness, crop yields, invertebrate abundance etc., Apollonio et al., 2017; Lancia et al., 1996; Morellet et al., 2007). Diligent population and environmental monitoring is key to evaluating interventions, developing effective practices and ensuring that management strategies are based on robust scientific evidence (Apollonio et al., 2017; Barton et al., 2022; Sutherland et al., 2004).

Monitoring large-bodied herbivores is challenging because they are often wide-ranging and highly mobile. Traditional methods, such as dung surveys or direct counts can be expensive and logistically demanding when conducted at the appropriate landscape scale of the population (Festa-Bianchet et al., 2017; Lindenmayer & Likens, 2010; Putman, Watson, et al., 2011). Advances in technologies such as Global Positioning Systems (GPS) devices, unmanned aerial vehicles and motion-activated digital cameras have made it easier for scientists to monitor wildlife species across the wider landscape (Pimm et al., 2015). In recent years, these technologies have also become less expensive and equipped with better features, which has promoted their widespread use in research (Burton et al., 2015; Delisle et al., 2021). Indeed, camera-traps are now a standard tool in scientific studies and population monitoring programmes (O'Connell et al., 2011; Trolliet et al., 2014). When deployed according to an effective study design, camera-trap surveys can support the adaptive management process by providing valuable data on populations and estimating changes in key characteristics, such as spatial distributions, abundance, habitat preferences, activity and species interactions (Burton et al., 2015; Frey et al., 2017; O'Connell et al., 2011; Trolliet et al., 2014).

Camera-traps are used in this thesis to monitor the behaviour of fallow deer (*Dama dama*) in the Elwy Valley region of North Wales, UK. Fallow deer in the UK provide an excellent example of an ungulate species that has been able to thrive in human-dominated landscapes. Fallow deer are one of six deer (Cervidae) species in the UK, all of which have expanded their numbers and geographic ranges in the past few decades (Croft et al., 2019; Putman, Apollonio, et al., 2011; Ward, 2005). Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are native, while sika deer (*Cervus nippon*), Chinese water deer (*Hydropotes inermis*) and Chinese muntjac (*Muntiacus reevesi*) are non-native species Apollonio et al., 2010). Fallow deer are considered naturalised as they were present during the last interglacial period but were reintroduced by the Romans and later by the Normans (Apollonio et al., 2010; Ward, 2005).

High densities of deer in the UK have been associated with a range of unfavourable effects on native flora and fauna (e.g., Dolman et al., 2010; Gill & Beardall, 2001; Gill & Fuller, 2007;

Gill & Morgan, 2010; Spake et al., 2020; Ward et al., 2008). Of particular concern for managers is the impact of deer on the regeneration and creation of woodland, which is a major component of national strategies to mitigate global climate change (Climate Change Committee, 2020). The Elwy Valley study area is a good example of a typical countryside landscape in the UK and is characterised by a mosaic of small parcels of land under independent ownership that are used for a range of purposes (e.g., agriculture, forestry, conservation, urban development). To be effective, population management must be coordinated across multiple landowner boundaries and satisfy the needs of a range of stakeholders, including conservationists, foresters, farmers and countryside visitors (Fattorini et al., 2020; Putman, Apollonio, et al., 2011; Wäber et al., 2013). The division of land in the UK also creates a complex landscape of risk for deer, as individuals may be exposed to a variety of co-occurring human disturbances (e.g., hunting, recreation etc.) within their home range area (Borkowski & Pudełko, 2007; Davini et al., 2004). The fallow deer population in the Elwy Valley study area descend from a captive herd and remain relatively isolated. This provides an ideal opportunity to study patterns of habitat-use and responses to human disturbance in a wild ungulate population at a tractable landscape scale.

Thesis structure

The aim of this thesis was to provide evidence to fill identified gaps in our understanding of ungulate ecology in human-dominated environments and to support the monitoring and management of populations at the landscape scale. The specific objectives were to (1) review the evidence currently available to support population management, (2) assess the effects of human disturbance and other landscape features on patterns of spatiotemporal behaviour and (3) investigate approaches to optimise camera-trap survey design.

Chapter two collates evidence on the effects of population management on the nine wild ungulate species in the UK. These include the six deer species and wild pigs (*Sus Scrofa*), feral goats (*Capra aegagrus hircus*) and feral sheep (*Ovis aries*). The purpose of the review was not to critically evaluate the literature, but rather to estimate its extent and distribution across species, interventions and outcomes (Barton et al., 2022).

Chapter three provides details of the Elwy Valley study area and a brief history of the local fallow deer population. It also describes the data collection process for chapters four and five.

Both are empirical chapters that utilise data from an array of 29 motion-activated camera-traps deployed at woodland sites for two years between January 2019 and December 2020. The aim of these chapters was to investigate the effects of human activities and other environmental features on the use of woodland habitat by deer.

Chapter four assesses temporal patterns of habitat-use and explores the effects of lethal (hunting) and non-lethal (recreation and woodland management) human disturbance on daily deer activity. Chapter five builds on this work to assess spatial patterns in behaviour. Statistical models are used to evaluate the relative importance of environmental and anthropogenic covariates on the probability (occupancy) and frequency of habitat-use.

Occupancy modelling utilised in chapter five is a widely used framework for analysing data obtained from camera-trap surveys (Burton et al., 2015; O'Connell et al., 2011). Chapter six uses a simulation approach to examine the effects of covariates on the precision and accuracy (i.e., error) of occupancy models in relation to camera-trap survey effort.

Chapter seven syntheses the main results and draws broad conclusions across the four key chapters. The findings are discussed in the contexts of animal ecology as well as biodiversity conservation and ungulate management.

Author's contributions

Owain Barton (OB) was the lead author for all chapters and Dr Graeme Shannon (GS) acted as lead supervisor. Prof John Healey (JH) and Dr Line Cordes (LC) were co-supervisors who assisted and guided OB on all aspects of the thesis. Studies were designed initially by OB and GS with later input from JH and LC. All data collection and analyses were performed by OB under the supervision of GS. LC co-developed several figures with OB. Amy Gresham (AG), Dr Norman Dandy (ND) and Dr Brian Gerber (BG) acted as key collaborators. ND and BG assisted in developing the landowner surveys (Chapter 3) and optimisation analyses (Chapter 6), respectively. AG contributed towards the screening of articles for the literature review (Chapter 2). Lee Oliver (LO) facilitated site access. GS, LC and JH read and approved the final manuscript.

Chapter 2

The effects of population management on wild ungulates: a systematic map of evidence for UK species

Owain Barton[1], Amy Gresham[1], John R. Healey[1], Line S. Cordes[2] and Graeme Shannon[1]

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Authors' contributions

OB acted as lead reviewer and conceived the study jointly with GS. GS and AG were second and third reviewers, respectively, and assisted in the screening of articles for eligibility. OB and GS jointly developed the strategy for data extraction and map presentation. OB coordinated the review and the analysis and presentation of results. OB, GS, and AG participated in the review of full text articles. OB wrote the review with input from GS, JH and LC. OB co-developed the figures in the review with LC. All authors read and approved the final manuscript.

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Introduction

Wild ungulates are integral to the functioning of grassland and forest ecosystems (Fornara & Du Toit, 2008; Manier & Hobbs, 2007; Murray et al., 2013a; Ohashi & Hoshino, 2014). As highly mobile and wide-ranging herbivore species, they have the capacity to influence ecological processes at multiple spatial scales (Côté et al., 2004; Dolman & Wäber, 2008; Hobbs, 1996). In recent decades, the abundance and geographic ranges of many ungulate species have rapidly increased across Europe (Apollonio et al., 2010; Linnell et al., 2020). Population growth has been attributed to translocations, the removal of natural predators, climate change and widespread alterations in land use (Putman, Apollonio, et al., 2011). These include the increased planting of trees to meet conservation targets, which has formed suitable habitat for a range of ungulates and agricultural intensification that provides a consistently available food-source throughout the year (Acevedo et al., 2011; Lewis et al., 2017; Putman et al., 1996). As their densities increase, a variety of interacting ecological and social factors must be considered in order to manage ungulate populations sustainably and satisfy the objectives of a range of stakeholders, including foresters, conservationists, farmers, landowners, recreational hunters and countryside visitors (Apollonio et al., 2017; Carpio et al., 2021; Putman, Apollonio, et al., 2011).

The effects of wild ungulates on ecosystems are species- and context-specific. Low-level herbivory by deer (Cervidae) and feral goats (*Capra spp.*) has been shown to suppress the growth of competitively dominant plant species and accelerate nitrogen and carbon cycling (Côté et al., 2004; Osawa et al., 2016). However, more intense browsing pressure has been linked to declines in biodiversity (Katona et al., 2013), reductions in forest understorey foliage (Eichhorn et al., 2017) and damage to agriculture (Bleier et al., 2012). In wetlands, rooting by wild pigs (*Sus scrofa*) can enhance microhabitat diversity and plant species richness (Arrington & Beach, 1999), whereas the same behaviour in forests has been associated with decreased plant diversity (Siemann et al., 2009) and the destruction of habitat for small mammals (Singer et al., 1984).

In human transformed landscapes, ungulates pose a threat to human health and well-being as a result of road traffic accidents (Langbein et al., 2011; Seiler, 2004). A recent assessment of the frequency of ungulate-vehicle collisions (UVCs) in Europe estimated that 30,000 incidents occur each year (Groot & Hazebroek, 1996). Additionally, ungulates are known to act as reservoirs of diseases, such as bovine tuberculosis (Martín-Hernando et al., 2007) and salmonella (Sato et al., 2000), as well as vectors of diseases, such as Lyme disease (Gilbert et al., 2012), that are transmissible to humans and domestic livestock (Barrios-Garcia & Ballari, 2012; Böhm et al., 2007). In the past two decades, the need to better understand the role of ungulates as ecosystem engineers and to mitigate their negative ecological and socio-economic impacts has been increasingly recognised by scientists, wildlife managers and conservationists (Apollonio et al., 2010, 2017).

Methods to mitigate ungulate impacts include control interventions, such as shooting, administering contraception, non-lethal deterrents and supplementary feeding (Bengsen et al., 2014; Putman, Apollonio, et al., 2011; Putman & Langbein, 2003). Typically, the efficacy of each practice is measured by observing how key environmental variables respond or monitoring changes in the prevalence of disease (Apollonio et al., 2010; Putman, Apollonio, et al., 2011). For example, in the UK the effectiveness of shooting deer is often estimated by observing the relationship between shooting effort and browsing damage to sensitive woodlands (Apollonio et al., 2010; Fattorini et al., 2020; Putman, Apollonio, et al., 2011). Monitoring environmental indicators of ecological change (IECs) is relatively inexpensive and provides convenient metrics for managers to compare the efficacy of different management strategies (Apollonio et al., 2010; Carpio et al., 2021; Putman, Langbein, et al., 2011). However, target species may respond to an intervention in a variety of ways that if not appropriately considered could lead to management strategies being ineffective or even counter-productive. For example, in the case of red deer (*Cervus elaphus*), shooting has been shown to reduce population densities and effectively mitigate the environmental impact of browsing (Tanentzap et al., 2009). However, there is evidence that shooting also has long-term effects on the morphology of red deer (Rivrud et al., 2013) and that the disturbance of shooting causes shifts in their home ranges, which may promote the spread of diseases (Jarnemo & Wikenros, 2014). Localised shooting of deer can lead to the development of source-sink dynamics in the population that neutralise efforts to reduce numbers at the scale of the landscape or region (Fattorini et al., 2020; Wäber et al., 2013). Additionally, responses of target species may be taxon-specific, which is particularly important in scenarios where a single intervention is applied to manage multiple species. For instance, supplementary feeding can reduce levels of bark damage by red deer (Rajský et al., 2008) but this intervention has also been shown to promote the population growth of wild pigs, leading to an increase in their disturbance on the environment (Bieber & Ruf, 2005).

A recent review (Apollonio et al., 2017) emphasised the importance of developing strategies for adaptive population management informed by robust empirical evidence. A total of ten measures were proposed to ensure the viability and long-term persistence of ungulate populations. These included long-term monitoring of habitat performance indicators (e.g., species richness), analysis of the indirect and unintended effects of supplementary feeding and a recognition for the impacts of hunting beyond reducing population densities (Apollonio et al., 2017). Accurate assessment of the responses of ungulate species to interventions typically requires intensive sampling (e.g., Simard et al., 2013) and specialist equipment, such as motion-activated cameras or global-positioning system (GPS) collars (e.g., Chynoweth et al., 2015). These approaches are typically unfeasible for most practitioners and formal studies are usually constrained to observations of a narrow range of responses for a single species or intervention. Consequently, individual studies may be of limited benefit to decision-makers faced with the challenge of developing strategies to manage multiple species simultaneously in order to meet a range of objectives (e.g., environmental impact mitigation, sustainable exploitation, reducing disease transmission). Therefore, syntheses of the literature, that provide information on the quantity and quality of the available evidence are needed to provide appropriate support for wildlife and land managers as well as policymakers. However, systematic assessments of the available evidence are lacking. This is of particular importance for wild ungulate management because the strength of the evidence-base supporting practices is unclear.

In this review, evidence for the effects of control interventions on the wild ungulate species resident in the UK was systematically mapped. The purpose of the systematic map was to collate, catalogue and describe the extent and distribution of evidence in relation to key variables (e.g., species, intervention type, response etc., Haddaway et al., 2016). Additionally, the map was used to identify important topics for primary research and serves as a valuable resource for scholars to more easily locate relevant articles for further systematic review or meta-analyses. The aim of the study was to support the development of more efficient and effective management strategies by collecting and characterising the evidence for species responses to commonly-adopted practices.

Scope of study

The primary objective of this systematic map was to collate existing research on the effects of management practices on the nine wild ungulate (Artiodactyla) species resident in the UK. Searches were restricted to these species to provide an appropriate focus and to ensure that the volume of literature screened for eligibility would be manageable. The species included represent a range of body sizes and ecological characteristics (e.g., feeding behaviour, reproduction rates, average lifespan etc.). Several (notably wild pigs, red deer and roe deer) are also abundant across Europe and are globally important for wildlife management (Apollonio et al., 2010; Tilman et al., 2017). Worldwide searches were conducted for peer-reviewed research articles but searches for ‘grey’ literature were restricted to UK-based sources only. It was beyond the scope of this review to critically appraise the evidence collected for each species. Instead, the synthesis provides a species-specific summary of the available evidence to identify important knowledge gaps and prioritise topics for future research and/or evidence synthesis. A protocol for this systematic map was not preregistered. In all other respects the procedure followed guidelines established by the Collaboration for Environmental Evidence (Pullin et al., 2018) and complies with PRISMA and ROSES reporting standards (Haddaway et al., 2018; Moher et al., 2009, S1 and S2).

Primary question

What evidence is available on the effects of control interventions, such as fencing, shooting, administering contraception, supplementary feeding and non-lethal deterrents, on the wild ungulate species that are resident in the UK?

Methods

Eligibility criteria

Eligible articles included any primary research study that collected data by way of an experiment or quasi-experiment (control-intervention and/or before-after) to examine the effects of an intervention on one or several features of ungulate biology. Articles originating from any country were considered for inclusion. No explicit date restrictions were applied but the date of the earliest available records varied between literature sources. Articles were required to meet the eligibility criteria for the elements of the primary question described in the following sections.

Population

All wild ungulate (Artiodactyla) species and subspecies currently resident in the UK, as described by Apollonio, Andersen and Putman (2010) including:

Chinese muntjac	*Muntiacus reevesi*
Chinese water deer	*Hydropotes inermis*
Fallow deer	*Dama dama*
Feral goats	*Capra aegagrus hircus*
Feral sheep	*Ovis aries*
Red deer (accepted sub-species common name: Scottish red deer)	*Cervus elaphus* (accepted sub-species: *elaphus* or *scoticus*)
Roe deer	*Capreolus capreolus*
Sika deer	*Cervus nippon*
Wild pigs*	*Sus scrofa*

* Following the advice of Keiter et al. (2016), the term 'wild pigs' was used as the common name for *Sus scrofa*, which may be described in articles by a range of common names including wild boar, feral pigs and feral hogs.

NOTE: If the population was a sub-species described by a scientific or common name that is not resident in the UK (e.g., *Sus scrofa sibiricus* or elk), the article was excluded. If no sub-species was named and no common name was used, (e.g., *Sus scrofa* or *Cervus elaphus*) the article was included.

Interventions

Deliberate human practices intended to mitigate the environmental and socio-economic impacts of wild ungulates by manipulating one or more features of their biology. Included in the review are interventions that directly influence target species such as shooting, administering contraception, supplementary feeding and non-lethal deterrents, as well as actions that have indirect effects, such as fencing and landscape modification. All practices considered are hereafter referred to as 'interventions'.

Comparator

No intervention. May be a (1) separate control site or population in a control/intervention (CI) study design, (2) time period of no intervention in a before/after (BA) study design, (3) combination of both 1 and 2 in a before/after/control/intervention study design (BACI)) or (4) an alternative level of intervention intensity. For example, the effect of shooting may be inferred by comparing sites, populations or time periods that experienced different levels of shooting effort in an observational (Obs) study.

Outcomes

Any responses of the target species to interventions were reported as they were stated in the relevant articles. Any effects on the biology of the target species were considered, including influences on population size and viability, morphology, physiology, movement behaviour, life history traits and habitat selection. The only outcomes included were effects on the target species and not secondary effects on other species, disease prevalence, plant and animal communities or habitat ecosystem components (e.g., evidence of the influence of an intervention on habitat selection by individuals of the target species from GPS location data or pellet counts was included as an outcome, but not inference from variation in tree growth or local species richness).

Searching for articles

An initial scoping search was conducted to identify suitable search terms, estimate the volume of relevant literature and validate the search methodology. Details of the search terms, number of hits and comments on the general quality of identified articles were recorded (S3). Terms describing the populations of interest were linked to intervention terms to form the following search string that was used to query Internet search engines and online bibliographic databases:

Population: ts = (muntjac OR "muntiacus reevesi" OR "chinese water deer" OR "hydropotes inermis" OR "roe deer" OR "capreolus capreolus" OR "red deer" OR "cervus elaphus" OR "sika deer" OR "cervus nippon" OR "fallow deer" OR "dama dama" OR "feral goat*" OR "capra aegagrus hircus " OR "wild goat*" OR "feral pig" OR "sus scrofa" OR "feral pigs" OR "feral hog*" OR "feral swine" OR "wild pig" OR "wild pigs" OR "wild hog*" OR "wild boar" OR "feral sheep")

AND

Intervention: ts = ("population control" OR "lethal control" OR hunt* OR cull* OR shoot* OR harvest* OR stalk* OR bait* OR poison* OR trapping OR (inhibit* AND reproduc*) OR immunocontracept* OR contracept* OR "fertility control" OR repel* OR deterrent* OR "diversionary feed*" OR (supplement* AND feed*) OR (supplement* AND food) OR "feed* station$" OR "forest management" OR "landscape structure" OR (manipulat* AND landscape) OR (manipulat* AND habitat) OR fenc*)

Sources of publications

A range of online sources were searched including four bibliographic databases (Clarivate Analytics Web of Science Core Collection and BIOSIS Citation Index, CAB Direct, Open Grey (www.opengrey.eu) and EThOS (www.ethos.bl.uk)), nine organisational websites and Google Scholar (S3). Where possible, search histories were saved in order to re-run the search if necessary. For each literature source, data were collected on: date accessed, search terms used, number of hits and a qualitative estimate of the relevance of identified articles (S3). Resource limitations constrained this study to an assessment of articles published in the English language.

Article screening and data coding

Articles identified by the search string were screened for eligibility using the online open-source platform of CADIMA (www.cadima.info/index.php). The CADIMA platform compiles records into a single reference library, automatically removes duplicates and facilitates the screening of articles at three levels; (1) Title, (2) Abstract and (3) Full text. The number of results from each literature source was recorded. A team of three reviewers screened articles for eligibility and reviewer consistency was checked at each stage. The lead reviewer (OB) applied the inclusion criteria at the title level to all potentially relevant articles. To check consistency, second (AG) and third (GS) reviewers also assessed a random subset of 200 articles each at the title and abstract level. The level of agreement between reviewers was estimated by calculating Cohen's kappa coefficient. A value of 0.49 was achieved indicating moderate agreement (Landis & Koch, 1977). Articles that passed the title stage, were screened for eligibility by the lead reviewer at the abstract level. The lead reviewer evaluated relevant studies that passed the title and abstract level stages by studying their full text. At this stage, a random subset of 20 articles were assessed by the third reviewer (GS) to check consistency. Articles that were considered ambiguous by one or more reviewers at any stage were marked as equivocal and retained for full text assessment. Equivocal articles were analysed by all reviewers to reach a consensus and the eligibility criteria was modified where necessary. Any reviewer who was the author of a study did not decide on the inclusion of that study and, in cases of uncertainty, the reviewer tended towards inclusion. Data were extracted for all articles that met the inclusion criteria and coded in an Excel spreadsheet to record the following information:

- Author(s)
- Study date
- Title
- Publication title
- Publication type (Journal article, report, thesis etc.)
- Country/countries of origin
- Total study area (km^2)
- Study duration (years)
- Study species
- Species status (native or non-native)
- Intervention(s)
- Outcome(s)
- Response data type
- Study design (BA, CI, BACI or Obs)

Species status (native or non-native) was based on the species ranges described by the IUCN Red List of Threatened Species (www.iucnredlist.org) and CABI Invasive Species Compendium (www.cabi.org/ISC). As escaped domestic animals, feral sheep and feral goats were considered to be non-native irrespective of country.

Results

Number and types of articles

A total of 13,659 articles were retrieved from bibliographic databases and Google Scholar, of which 5,560 were identified as duplicates and automatically removed by the CADIMA software. Very few articles (n=17) were obtained from 'grey' literature sources. Only 3% of articles (n=297) were retained after screening at the title and abstract level. The list of articles was further reduced following full-text assessment to a subset of 123 articles that were used for data extraction. Of the articles excluded at the full-text assessment stage (n=174), 52% were excluded because they did not meet the eligibility criteria (n=90) and the remaining 48% were either not accessible (n=7), not in the English language (n=26), could not be located (n=22) or were identified as duplicates (n=29, S4). Figure 1 illustrates the results of the literature searches and stages of article screening.

The duration of data-collection reported in articles ranged from less than 1 year to 27 years, excluding three studies that used multiple datasets (Putman et al., 2019; Rivrud et al., 2013; Servanty et al., 2011). The median duration of data collection was 3 years. Around 16% of articles used data collected over 10 or more years (n=20). The earliest article included in the systematic map was published in 1980 (Figure 2a). A noticeable increase in the number of articles published in the past decade (2010 to 2020, n=71) was found, compared with the previous three decades (1980 to 2009, n=52; Figure 2a). Studies designed to examine causal effects before and after an intervention were the most common and comprised 46% of the articles assessed (n=57). Observational studies that quantified effects by observing sites or time periods exposed to different levels of intervention intensity accounted for around 28% of articles (n=35). Approximately 15% of studies used designated control (non-treatment) and intervention (treatment) groups or sites (n=19) and around 10% used a combined before-after-control-intervention study design (n=12).

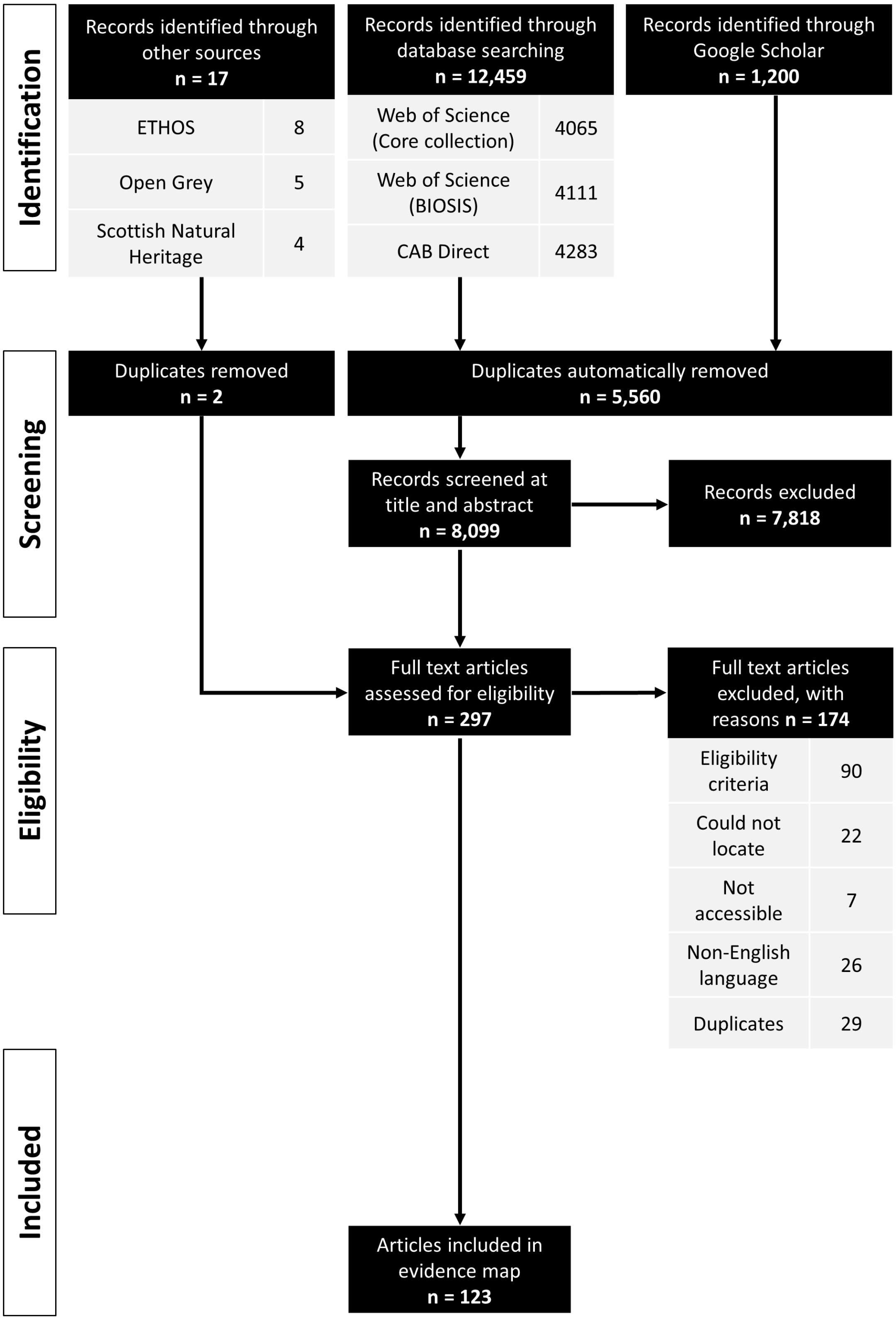


Figure 1. Flow diagram illustrating the number of articles gathered from each literature source, articles removed at each stage of screening and articles included in the evidence synthesis (diagram stages adapted from PRISMA guidance, Moher et al., 2009).

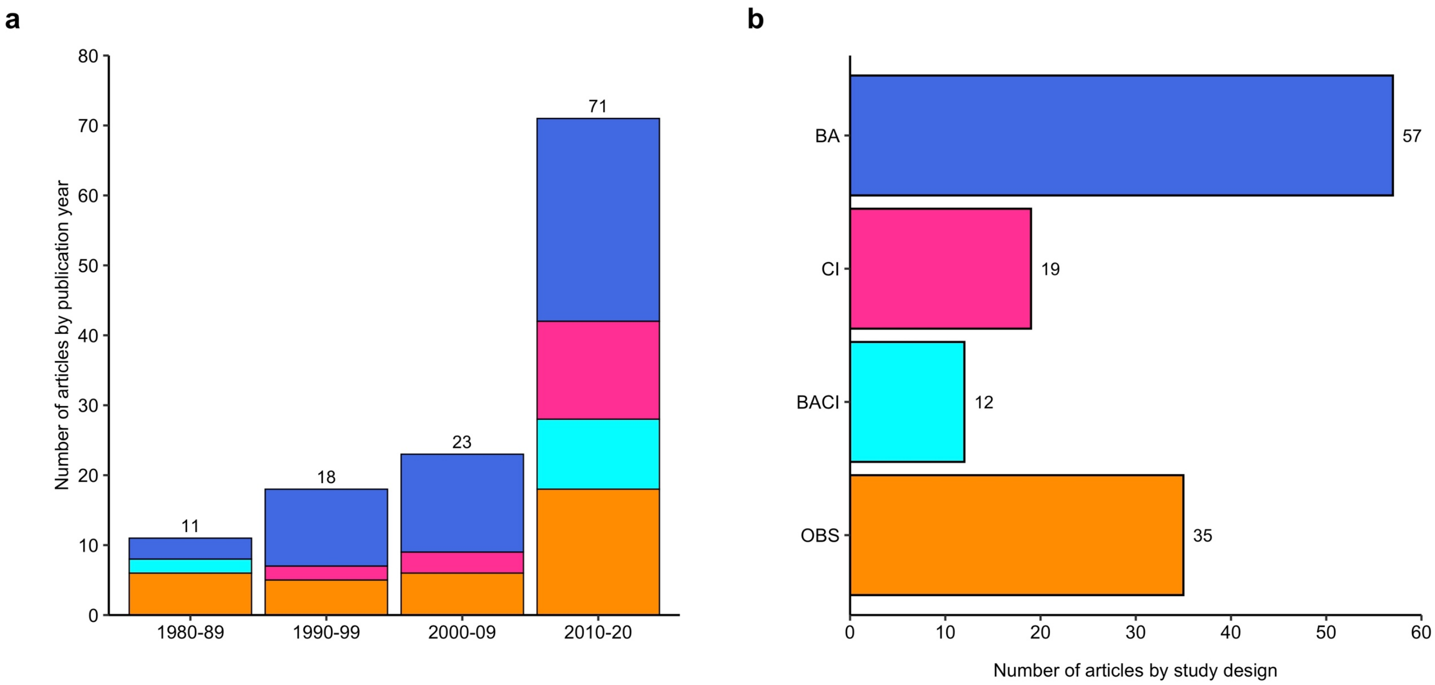


Figure 2. Number of articles by (**a**) publication year and (**b**) study design (BA = before-after, CI = control-intervention, BACI = before-after-control-intervention, and Obs = observation only). Totals are indicated by numerical values.

Geographical representativeness and coverage of articles

The geographic location of the studies reported in the-articles included six regions (Figure 3). Europe was the most well-studied region with 69 articles. Oceania, North America and Asia were moderately well-studied with 25, 15 and 10 articles, respectively, while South America and Africa were the least-well studied regions with five articles between them. (Figure 3). The dataset used in the systematic map included articles from 28 countries (Figure 4). The most well-studied countries were Australia (n=20), the UK (n=16), USA (n=13), France (n=11) and Japan (n=10, Figure 4). Study areas that covered more than one country were reported for five articles. The total area of land covered in each study ranged from less than 1 km^2 to 175,000 km^2. Articles most commonly covered study areas that were either 0-50 km^2 or >600 km^2 (Figure 5).

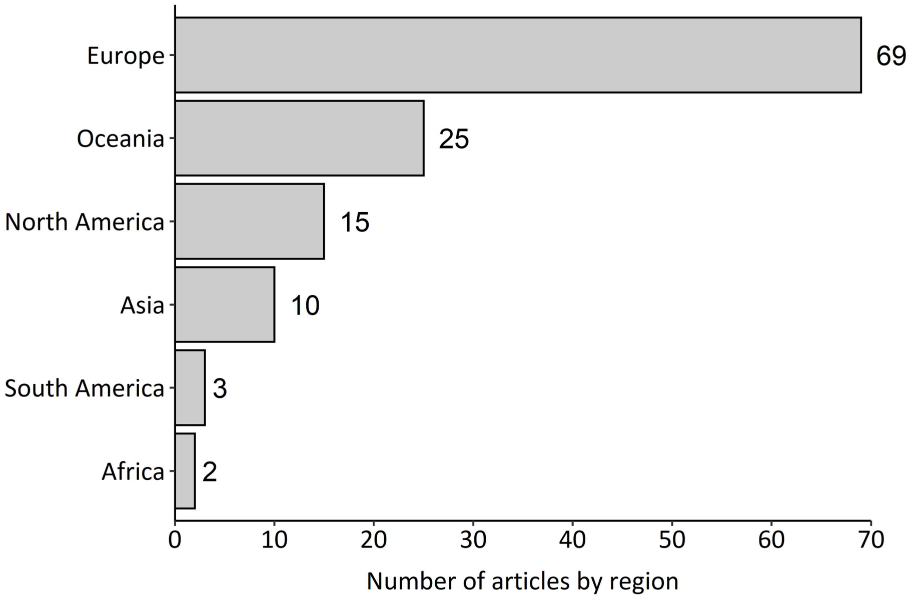


Figure 3. Number of articles by geographic region. Totals are indicated by numerical values.

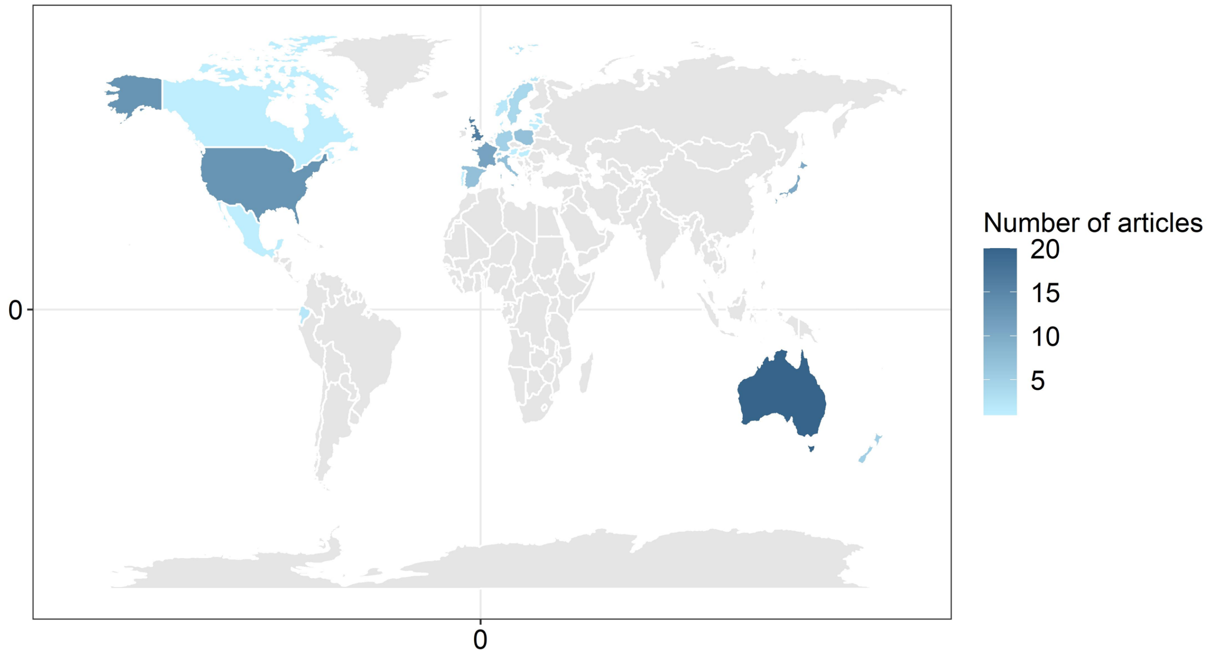


Figure 4. Geographical distribution of articles by country. Colours indicate the frequency of article occurrences. The map was developed using the 'ggplot2' and 'maps' packages in R (www.R-project.org), which utilise public domain data from Natural Earth (www.naturalearthdata.com).

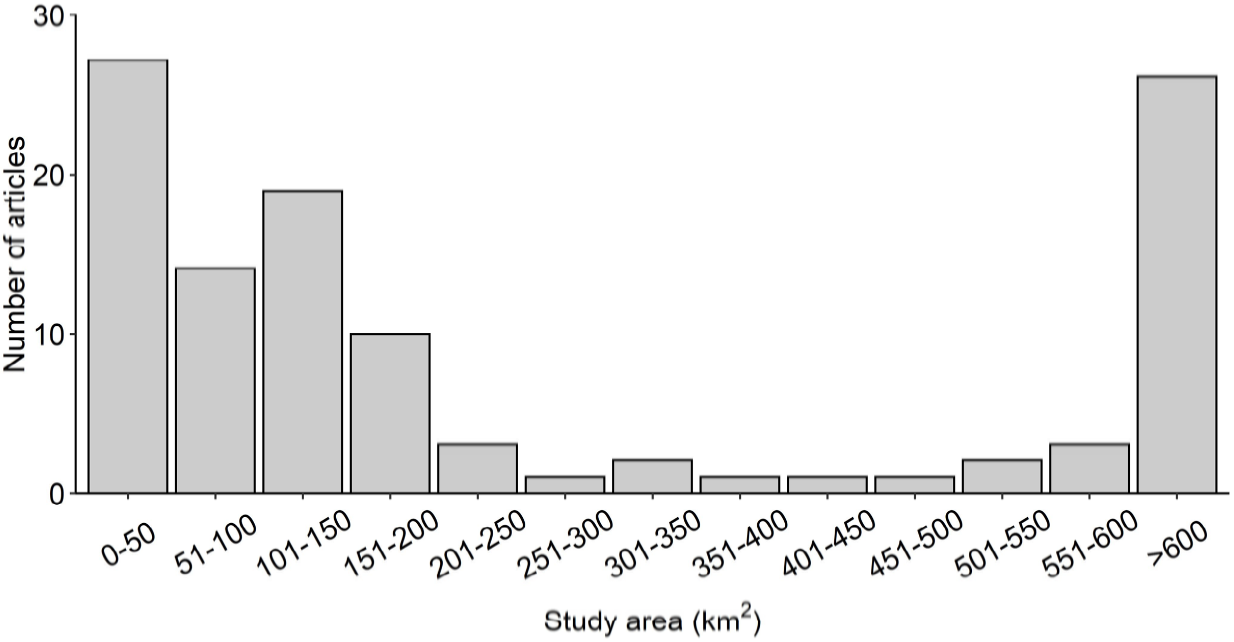


Figure 5. Number of articles by total study area (km^2).

Species representativeness

The number of articles included in the systematic map for each of the ungulate species resident in the UK is presented (Figure 6, no relevant articles were identified for Chinese water deer). Multiple species were reported in 13 articles. Species were studied inside their native ranges in approximately 59% (n=73) of articles and outside their native ranges in approximately 37% (n=46) of articles. Around 3% (n=4) of articles reported on multiple species, of which some were inside their native range and others were outside their native range. Wild pigs were the most well-studied species (n=58), followed by red deer (n=28) and roe deer (n=23), whereas few studies reported on sika deer (n=11), feral goats (n=10), fallow deer (n=5), feral sheep (n=2) or Chinese muntjac (n=2, Figure 6). Roughly equal numbers of articles reported on wild pigs inside (47%, n=27) and outside (53%, n=31) their native range. Articles that reported on roe deer (n=23) and most of the articles that reported on red deer (93%, n=26) and sika deer (91%, n=10) were conducted inside their native ranges, while articles that reported on feral goats (n=10), feral sheep (n=2) and Chinese muntjac (n=2), as well as the majority of articles for fallow deer (80%, n=4), were conducted outside their native ranges.

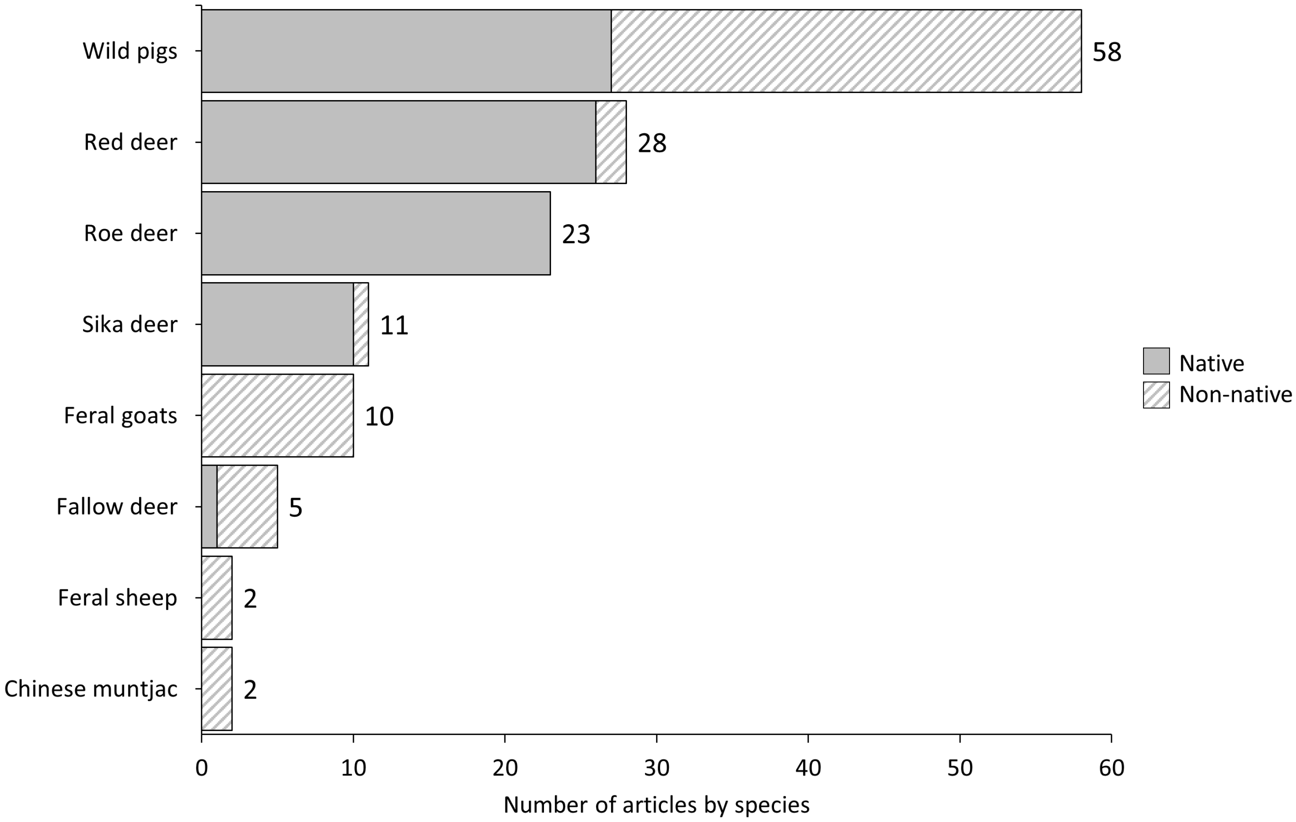


Figure 6. Number of articles for each of the ungulate species resident in the UK. Totals are indicated by numerical values. Patterns indicate the status of species studied in each article (native or non-native in relation to the geographic location of the study).

Types of interventions

Interventions were categorised and grouped into seven broader classes (Table 1). Multiple interventions were reported in 34 of the 123 included articles. Figure 7a presents the extent and distribution of articles in each intervention class. Shooting was the most well-studied intervention class and was examined in 78% of included articles (n=96). The top three most frequently documented intervention classes (shooting, capture and poisoning) involved lethal interventions (Figure 7a). Supplementary feeding was the most well-studied non-lethal intervention class but was examined in less than 10% of articles (n=12). The distribution of articles for native versus non-native species was roughly equal for shooting, supplementary feeding and contraception (Figure 7a). Articles that reported on the effects of poisoning (n=13) and the majority of articles that reported on the effects of capture (88%, n=14), focussed on non-native species. Whereas articles that reported on the effects of deterrents (n=5) and most of the articles that reported on the effects of barriers (80%, n=4), examined native species. The most frequently documented interventions were ground-based shooting (n=65), shooting with the assistance of dogs or human drivers (battues, n=40), trapping (n=16), shooting from an aerial vehicle (n=13) and poisoning (n=13, Figure 7b). The seven interventions that comprise the classes of barriers, contraception and deterrents (Table 1) were each reported in fewer than five articles (Figure 7b).

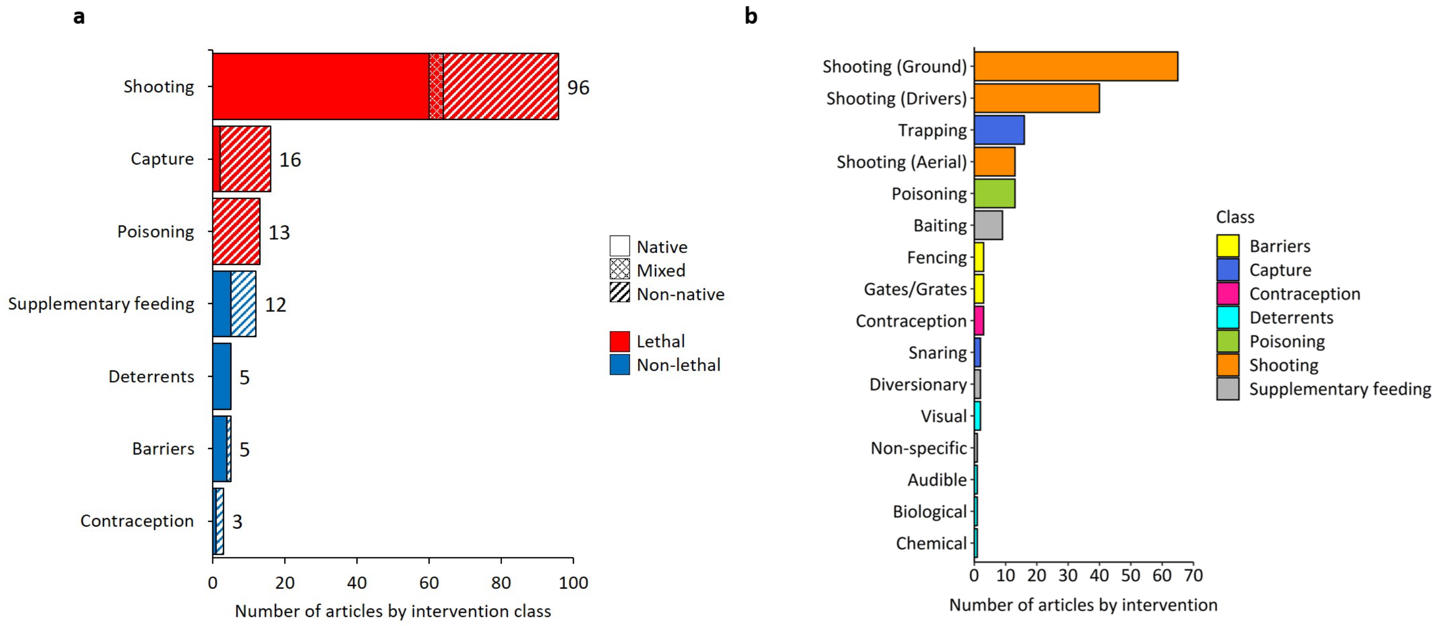


Figure 7. Number of articles by (**a**) intervention class and (**b**) intervention category. Totals are indicated by numerical values. Patterns indicate the status of species studied in each article (native, non-native or a mixture of native and non-native species), in relation to the geographic location of the study.

Table 1. Types of interventions used in the articles included in the systematic map. Interventions are categorised and assigned to a broad intervention class

Class	Category	Description
Barriers	Fencing	Man-made continuous barriers
	Gates/Grates	Man-made barriers for entrance/exit points
Capture	Trapping	Whole-animal capture
	Snaring	Part-animal capture
Contraception	Contraception	Administering contraception
Shooting	Shooting (Ground)	Shooting with a gun only
	Shooting (Aerial)	Shooting from an aerial vehicle
	Shooting (Drivers)	Shooting with the assistance of dogs or human drivers (battues), includes mustering
Deterrents	Audible	e.g., playback devices or bird-scarers
	Biological	e.g., grazing livestock
	Chemical	e.g., predator scents
	Visual	e.g., reflectors or lights
Poisoning	Poisoning	Use of lethal poison
Supplementary feeding	Baiting	Provision of food to assist shooting, capture or poisoning
	Diversionary	Provision of food to divert animals away from a site or vulnerable site component (e.g., crop trees)
	Non-specific	Provision of food without explicit reasoning of purpose other than to support population management*

*Studies that examined the effects of supplementary feeding used to increase survival or population growth to support recreational hunting were not included in the systematic map.

Types of outcome

The outcomes of interventions were categorised and grouped into five broad classes (Table 2). Multiple outcomes were reported in 39 of the 123 included articles. Figure 8a presents the number of articles for each outcome class. Demography and behaviour were the most well-studied outcome classes and were examined in 60% (n=74) and 40% (n=49) of included articles, respectively. Health, morphology and physiology were each reported in fewer than 5% of articles (Figure 8a). The most frequently documented outcomes were effects on population size (n=49), spatial behaviour (n=31), movement behaviour (n=13), survival or mortality (n=12) and habitat selection (n=11, Figure 8b).

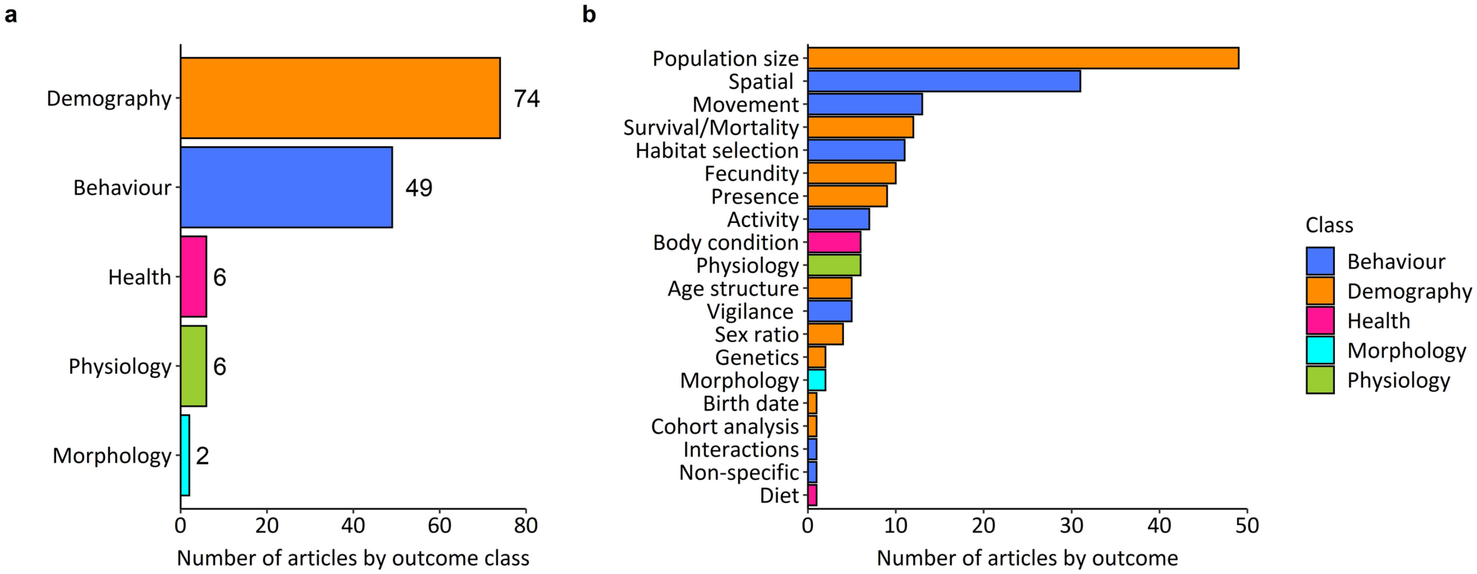


Figure 8. Number of articles by (**a**) outcome class and (**b**) outcome category. Totals are indicated by numerical values.

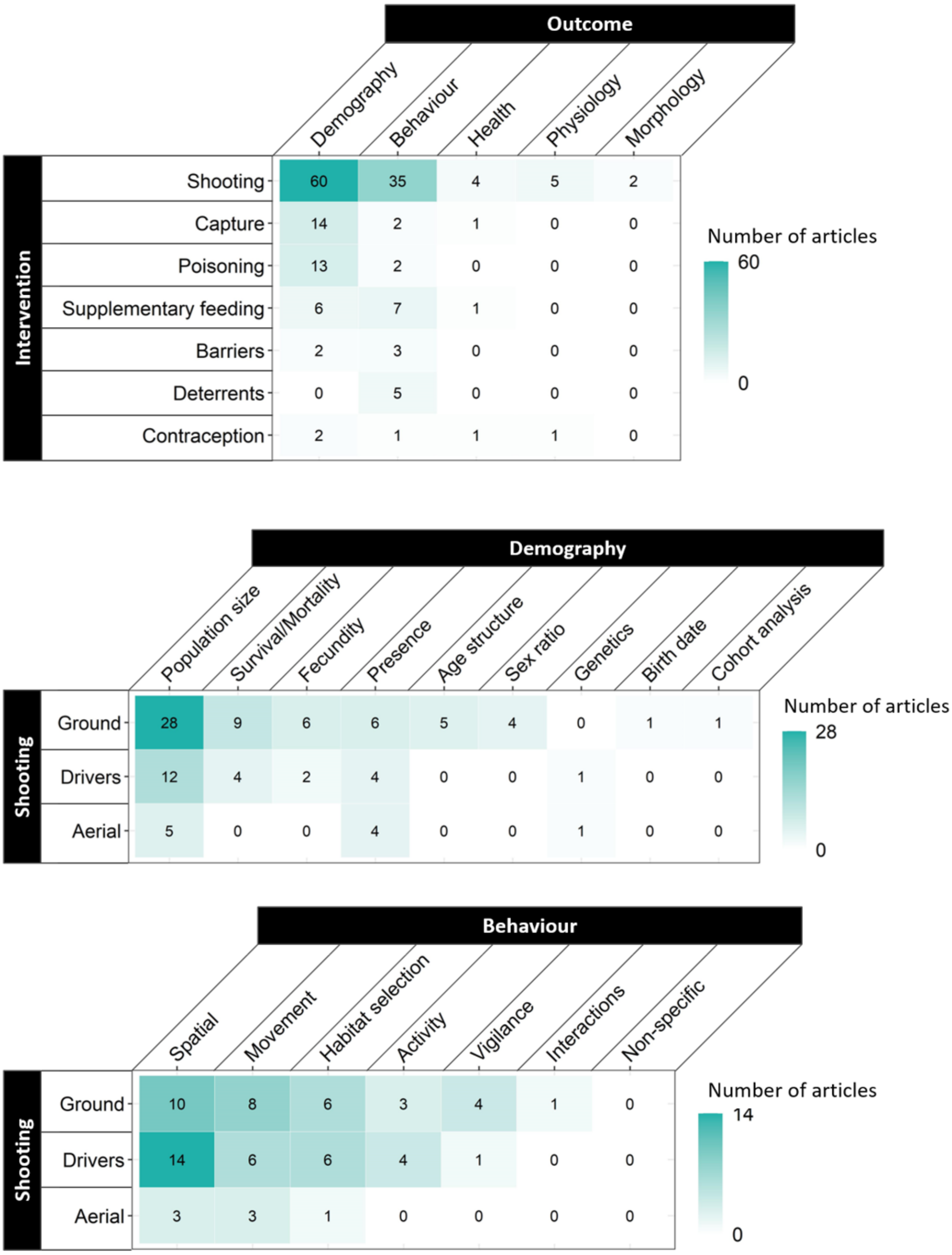
Table 2. Types of outcomes reported in the articles included in the systematic map. Outcomes are categorised and assigned to a broad outcome class.

Class	Category	Description
Behaviour	Activity	Activity patterns over time (not spatially-explicit)
	Habitat selection	Space-use with explicit selection of sites or habitat types
	Interactions	Intra- or inter-specific interactions
	Movement	Movement distances, speeds and rates
	Non-specific	E.g., mating, grazing and sitting
	Spatial	Space-use (includes home range sizes, migrations, seasonal movements, distributions etc.)
	Vigilance	E.g., head-up movements
Demography	Age structure	Proportions of individuals per age class
	Birth date	Timing/date of birth
	Cohort analysis	Proportion of individuals of each sex in age classes
	Fecundity	Reproductive output or potential (includes litter size, number of corpora lutea, reproductive success, proportion of pregnant females etc.)
	Genetics	Population genetics
	Population size	Density or abundance
	Presence	Presence or absence
	Sex ratio	Proportions of each sex
	Survival/mortality	Proportion of population or sub-population surviving or dying between time periods
Health	Body condition	Weight, body fat levels, general condition
	Diet	Food types or species consumed
Morphology	Morphology	E.g., shape and size of antlers
Physiology	Physiology	E.g., level of stress hormones

Linkages between interventions and outcomes

Figure 9a displays the number of articles linking the interventions and outcomes (both grouped by class, Tables 1 and 2) identified in the systematic map. Well-studied linkages may be suitable areas of focus for more in-depth review and critical evaluation. Poorly studied linkages that are relevant to population management or policy and decision-making may be promising areas for further research or investigation by practitioners. Of the 35 possible linkages between interventions and outcomes, 15 were not identified in any article and a further 16 were reported in fewer than ten articles (Figure 9a). The most well-studied linkages were those of shooting and demography (n=60), shooting and behaviour (n=35), capture and demography (n=14), and poisoning and demography (n=13). The distribution of articles within each intervention and outcome class is presented for linkages between shooting and demography (Figure 9b) and shooting and behaviour (Figure 9c). Within the demography class the most frequently reported linkages were between population size and ground-based shooting (n=28) or shooting with the assistance of drivers (n=12, Figure 9b). No studies linking ground-based shooting with population genetics were identified. Within the behaviour class there was a more even distribution of articles amongst linkages (Figure 9c). The most frequently reported linkages were between spatial behaviour and ground-based shooting (n=10) or shooting with the assistance of drivers (n=14). The linkages between these interventions and habitat selection and movement were reported in 6 to 8 articles each (Figure 9c).

Figure 10 maps the intersection of invention classes and outcome classes for each species. Shooting was the only intervention to be investigated across all eight reported species (Figure 10). Articles that examined species responses to contraception were identified for wild pigs, feral goats and fallow deer only. Evidence for the effects of deterrents was limited to studies of wild pigs, roe deer and sika deer, and the effects of poisoning were restricted to wild pigs and feral goats. For red deer and roe deer evidence was almost exclusively related to shooting. Wild pigs were the only species for which evidence was available on their responses to all seven of the intervention classes. Most of the articles found for sika deer examined behavioural responses. For feral goats, feral sheep and Chinese muntjac evidence was limited to the effects of interventions on demography only (Figure 10).



Intervention	Demography	Behaviour	Health	Physiology	Morphology
Shooting	60	35	4	5	2
Capture	14	2	1	0	0
Poisoning	13	2	0	0	0
Supplementary feeding	6	7	1	0	0
Barriers	2	3	0	0	0
Deterrents	0	5	0	0	0
Contraception	2	1	1	1	0

Shooting	Population size	Survival/Mortality	Fecundity	Presence	Age structure	Sex ratio	Genetics	Birth date	Cohort analysis
Ground	28	9	6	6	5	4	0	1	1
Drivers	12	4	2	4	0	0	1	0	0
Aerial	5	0	0	4	0	0	1	0	0

Shooting	Spatial	Movement	Habitat selection	Activity	Vigilance	Interactions	Non-specific
Ground	10	8	6	3	4	1	0
Drivers	14	6	6	4	1	0	0
Aerial	3	3	1	0	0	0	0

Figure 9. Structural matrices of the distribution and frequency of occurrence of studies reporting on the linkages between (**a**) intervention classes and outcome classes (**b**) shooting intervention categories and demography outcome categories and (**c**) shooting intervention categories and behaviour outcome categories for ungulate species resident in the UK. Matrix structure is adapted from McKinnon et al. (2016).

Wild pigs

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	27	15	1	0	0
Capture	12	1	1	0	0
Poisoning	12	2	0	0	0
Supplementary feeding	6	4	1	0	0
Barriers	1	1	0	0	0
Deterrents	0	3	0	0	0
Contraception	0	1	0	1	0

Red deer

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	14	7	2	4	1
Capture	0	0	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	2	0	0	0
Barriers	1	1	0	0	0
Deterrents	0	0	0	0	0
Contraception	0	0	0	0	0

Roe deer

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	9	9	1	2	1
Capture	0	0	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	0	0	0	0
Barriers	1	0	0	0	0
Deterrents	0	1	0	0	0
Contraception	0	0	0	0	0

Sika deer

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	4	3	0	0	0
Capture	0	1	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	1	0	0	0
Barriers	0	2	0	0	0
Deterrents	0	2	0	0	0
Contraception	0	0	0	0	0

Feral goats

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	8	0	0	0	0
Capture	1	0	0	0	0
Poisoning	1	0	0	0	0
Supplementary feeding	0	0	0	0	0
Barriers	1	0	0	0	0
Deterrents	0	0	0	0	0
Contraception	1	0	0	0	0

Fallow deer

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	1	3	0	2	0
Capture	0	0	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	0	0	0	0
Barriers	0	0	0	0	0
Deterrents	0	0	0	0	0
Contraception	1	0	1	0	0

Feral sheep

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	2	0	0	0	0
Capture	0	0	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	0	0	0	0
Barriers	0	0	0	0	0
Deterrents	0	0	0	0	0
Contraception	0	0	0	0	0

Chinese muntjac

	Demography	Behaviour	Health	Physiology	Morphology
Shooting	2	0	0	0	0
Capture	0	0	0	0	0
Poisoning	0	0	0	0	0
Supplementary feeding	0	0	0	0	0
Barriers	0	0	0	0	0
Deterrents	0	0	0	0	0
Contraception	0	0	0	0	0

Figure 10. Structural matrices illustrating the distribution and frequency of articles on linkages between intervention classes and outcome classes for each ungulate species resident in the UK.

Discussion

This review involved systematically mapping the existing worldwide research on the effects of population management interventions on the nine wild ungulate species that are resident in the UK. Peer-reviewed literature from 20 countries, supplemented by 'grey' literature from UK-based sources was collated to provide a species-specific summary of the evidence for commonly used interventions. The resulting map (S5) provides a resource for scholars, practitioners and decision-makers to more easily locate relevant articles, identify knowledge gaps and critically assess the state of the field.

The results describe important characteristics of the evidence-base and reveal significant unevenness in the distribution of research across species, interventions and the types of outcomes examined. The literature search identified 123 relevant articles after screening for eligibility. There was an upward trend in papers published over time. More articles have been published in the last decade (2010 to 2020, n=71) than in the preceding three decades (1980 to 2009, n=52). Overall, the robustness of the evidence-base was low and dominated by comparatively short-term studies that collected data for a median duration of three years. Long-term studies using data collected over 10 or more years were rare and accounted for only 16% of articles (n=20). The majority of studies were conducted over large areas > 50 km^2 (n=96), 27% of these involved areas > 600 km^2. Most of the articles originated from Europe, Oceania and North America, which is consistent with the geographic ranges of the species examined (Acevedo et al., 2019; Croft et al., 2019; Linnell et al., 2020).

Evidence extent

The relatively small number of articles included in the map (n=123) most likely reflects a general trend towards studies evaluating the efficacy of management using only environmental-based indicators of ecological change (IEC, Carpio et al., 2021; Morellet et al., 2007). A species is typically managed when its populations are negatively affecting human wellbeing, other species or ecosystem function (Carpio et al., 2021). Consequently, the outcomes reported by research are often environmental indicators, such as the frequency of ungulate-vehicle collisions, parasite loads and the growth rate/recruitment of plant species, and as such it often does not report metrics of the population of the wild ungulate species targeted by the intervention (Apollonio et al., 2017; Morellet et al., 2007). Additionally, efforts to quantify ungulate species responses are constrained by limited human and financial resources. The notable scarcity of robust, long-term studies was likely due to the expense and logistical challenges associated with monitoring ungulate populations at the appropriate scale of the landscape or region (Festa-Bianchet et al., 2017; Putman, Watson, et al., 2011). Technical advances and the decreasing cost of remote sensing technologies, such as motion-activated cameras and unmanned aerial vehicles, provide new opportunities for ungulate population monitoring, which can be used to overcome this deficit in the current evidence-base (Chapters three to six, Grignolio et al., 2020; Prosekov et al., 2020).

Evidence distribution: Species

The top three most-studied species in the map, wild pigs, red deer and roe deer, are the most widely distributed ungulate species in Europe (Linnell et al., 2020). Wild pigs are invasive alien species throughout much of their range, which covers every continent except Antarctica (Barrios-Garcia & Ballari, 2012; Massei & Genov, 2004). This was reflected in the results, which show that more than half (53%, n=31) of the studies on wild pigs were conducted outside of their native range. They are generalist feeders that reproduce prolifically and are widely regarded as being one of the most destructive invasive species globally (Barrios-Garcia & Ballari, 2012; Doherty et al., 2016; McClure et al., 2018). In contrast, almost all of the studies on red and roe deer were conducted within their native ranges (93% and 100% for red and roe deer, respectively). Both species are highly valued for recreational hunting and tourism (Apollonio et al., 2010), while overabundant populations can have a negative impact on woodland ecosystems, commercial forestry and agriculture, which makes them priority species for management (Apollonio et al., 2010; Linnell et al., 2020).

The top five countries with the highest frequency of articles were Australia, UK, USA, France and Japan. Feral goats and wild pigs are invasive alien species in Australia and USA and constitute a major threat to native biodiversity (Hone, 2020; Seward et al., 2004). Consequently, there is considerable interest in improving methods of population control and eradication (Heriot et al., 2019; Masters et al., 2018; McIlroy, 1995). With the exception of Chinese muntjac, all of the ungulate species resident in the UK are also present in France, so it was unsurprising that both countries make a large contribution to the existing evidence-base (Croft et al., 2019; Linnell et al., 2020). The high frequency of studies in Japan was likely driven by the declining popularity of hunting in recent years, which has created a need to explore alternative interventions such as fencing and non-lethal deterrents (Honda, 2019; Honda et al., 2020; Kaji et al., 2010).

Evidence distribution: Interventions

The distribution of evidence across different types of interventions was likely to be influenced by the effectiveness of the intervention, its availability and accessibility to practitioners as well as the range of legal restrictions and cultural views associated with its application. The results show that a large majority of studies focus on various methods of shooting (78%), including shooting from the ground, from an aerial vehicle and shooting with the assistance of drivers (dogs or human battues). Shooting is popular for a variety of reasons. There is evidence supporting its effectiveness as a tool to mitigate ecological impacts (e.g., Giménez-Anaya et al., 2016; Hothorn & Müller, 2010; Quirós-Fernández et al., 2017), it is relatively inexpensive (Gentle & Pople, 2013) and hunting has an important significance in many cultures worldwide (Alves et al., 2018). A key advantage of shooting is its specificity, which enables practitioners to target individuals or cohorts within the population (such as senescents, females or diseased individuals), that disproportionally contribute to ecological impacts or may be important for maintaining population health (Gordon et al., 2004; Putman, Apollonio, et al., 2011). In contrast, poisoning and capture (trapping and snaring) are less discriminate and so are typically only legally permitted for use on non-native invasive species. The results show that poisoning and capture were studied for non-native species in 100% (n=13) and 88% (n=14) of articles, respectively.

The low proportion (20%) of articles that reported on non-lethal interventions was most likely due to the limited theoretical support for their effectiveness in mitigating ecological impacts. Although the precise relationship between impacts and ungulate population density is complex and context-specific, theoretically there exists a threshold above which species begin to put unsustainable pressure on the environment (Fattorini et al., 2020; Putman, Langbein, et al., 2011; Spake et al., 2020). Most non-lethal interventions (barriers, diversionary feeding, repellents and deterrents) do not affect population density or reproductive performance and so are more likely to displace the environmental pressure caused by ungulates to other geographic areas, rather than bring about an overall reduction (Geisser & Reyer, 2004; Valente et al., 2020). Immunocontraception may be a viable alternative to lethal interventions and has been successfully developed for more than 85 different wildlife species (Kirkpatrick et al., 2011). However, most of the research on wildlife contraception has focussed on captive populations. There are several factors that currently inhibit the wider use of immunocontraceptive vaccines in free-ranging populations, including the variability of efficacy across species, limited long-term safety testing, the lack of effective delivery systems for elusive and mobile animals and concerns over the potential side-effects on behaviour (Kirkpatrick et al., 2011). Further research is needed to overcome these challenges and achieve general acceptance of immunocontraception as a management tool.

Evidence distribution: Outcomes

The results show that most studies focused on population size and space-use outcomes. This was likely because there are established links between these responses and ecological impacts. For example, the relationship between wild ungulate population densities and indices of ecological impact (e.g., forest regeneration) has been investigated in several studies (e.g., Bleier et al., 2012; Nuttle et al., 2014; Spake et al., 2020) and variation in space-use has been linked to the distribution of damage (e.g., Thurfjell et al., 2013) as well as the spread of diseases (e.g., Magle et al., 2015) and parasites (Mysterud et al., 2016). The types of biological responses examined may also be influenced by data availability. Demographic responses, such as variations in population size, are likely to be observable over much shorter timeframes than changes in physiology or morphology, which require longer periods of population monitoring (Festa-Bianchet et al., 2017). Estimating population sizes is relatively straightforward and can be achieved using a range of techniques such as track counts, distance sampling and dung surveys, which require minimal resources. Cull records may also be utilised and are often the only source of population data regularly collected over long timeframes and at regional or national scales (Engeman et al., 2013; Putman, Watson, et al., 2011). Data on individual health, physiology and morphology are more challenging to collect. Considerable effort is needed to obtain the blood, tissue or whole-organism samples typically required for analyses. Furthermore, accurately measuring indicators of responses, such as stress hormone levels, body condition and the size and shape of anatomical features often requires expertise and specialist equipment that are unavailable to most practitioners (Festa-Bianchet et al., 2017).

Recommendations for policy and management

Members of the international scientific community recently advocated for the implementation of an adaptive approach to management of wild ungulate species based on a continuous and systematic process of trial-and-error (Apollonio et al., 2017). They highlight the importance of evaluating the outcomes of management interventions using a set of environmental (e.g., browsing index, vegetation composition, ungulate-vehicle collisions) and population (e.g., body mass, antler quality, reproductive performance) indices. The results show that, to date, very few studies have utilised population-based metrics beyond estimates of population-size. Therefore, the existing call (Apollonio et al., 2017) for practitioners to record key information on the health, reproduction and genetic integrity of ungulate populations is strongly supported. Furthermore, a participatory approach to research, in which managers carrying out adaptive management, become integrated participants in the wider research programme is encouraged.

As the financial and human resources available to managers are typically limited, it may be sensible firstly to exploit opportunities for broadening the types of data collected from sources already utilised by existing monitoring programmes. For example, cull records could include information on indicators of health, such as body mass, jaw length and antler quality (Ramanzin & Sturaro, 2014). Blood and tissue samples used for the monitoring of diseases, could also be made available for studies on population genetics and physiology (Martin et al., 2011; Réveillaud et al., 2018). Data-sharing through collaborative projects, such as the EuroBoar (www.euroboar.org) and EuroDeer (www.eurodeer.org) networks, should be encouraged to facilitate comparative studies of populations under different socio-ecological conditions (Festa-Bianchet et al., 2017). The results of alternative strategies are particularly valuable in finding novel solutions to management challenges. For example, a study by (Cromsigt et al., 2013) proposed shooting in a way that creates a 'landscape of fear' to mimic the effects of a natural predator. Critically assessing approaches such as this would facilitate the refinement of existing practices and policies.

Recommendations for primary research

Researchers should focus on addressing knowledge gaps by conducting studies based on robust experimental designs (such as before-after-control-intervention) that account for different types of bias (Christie et al., 2019; Smokorowski & Randall, 2017). Resources should be invested in long-term studies that collect data for 10 or more years, which would provide valuable knowledge on the long-term effects of management and species responses to environmental variation, such as climate and land-use changes (Festa-Bianchet et al., 2017). Based on our results, the following three questions are suggested as research priorities: (1) how do ungulate species respond to non-lethal interventions (supplementary feeding, barriers, deterrents and administering contraception)? (2) what are the side-effects of shooting on ungulate (i) morphology, (ii) population genetics, (iii) physiology and (iv) species interactions? and (3) what are the effects of management interventions on sika deer and Chinese muntjac?

Non-lethal interventions provide important alternative methods of mitigating the impacts of ungulates in contexts where lethal interventions are not legally or socially acceptable to use (e.g., urban areas). Understanding species responses to non-lethal interventions is critical for developing more effective techniques and ensuring their long-term safety (e.g., exploring possible side-effects of contraceptives). More research on non-lethal interventions would also assist in identifying the combination of techniques that are most effective at the population-level scale of the landscape or region.

Identifying the side-effects of shooting is important for several reasons. Firstly, shooting is often a non-random process and individuals with certain morphological traits (e.g., large body mass or large antlers) may be preferentially targeted (Mysterud & Bischof, 2010; Rivrud et al., 2013). This can place selection pressures on populations that can cause undesirable life-history changes over shorter time-periods than would be expected from natural selection (Carroll et al., 2007; Rivrud et al., 2013). Secondly, the relatively slow rate of reproduction exhibited by ungulates puts them at risk of overexploitation (de Jong et al., 2020; Ripple et al., 2015). Extensive shooting and anthropogenic barriers (e.g., roads, buildings, fences etc.) can isolate populations, which may increase the rate of inbreeding (i.e., mating among closely related individuals), leading to inbreeding depression (i.e., the decreased fitness of inbred individuals, de Jong et al., 2020; Ralls et al., 2018). Finally, shooting can affect the rate of contact between individuals, which may influence the spread of diseases (Miguel et al., 2020; Prentice et al., 2019). There is also evidence to suggest that the social stress of culling activities causes immunosuppression, leading to greater disease expression (Riordan et al., 2011). There is a need to better understand the full range of side-effects associated with shooting to ensure the long-term viability of ungulate populations and improve management efficiency.

Chinese muntjac and sika deer, are among the worst invasive non-native species in Europe in terms of risk of causing environmental impacts (Nentwig et al., 2018; Volery et al., 2021). In the UK, high densities of Chinese muntjac have been associated with a range of impacts on native species of flora (Cooke, 1997), birds (Gill & Fuller, 2007) and invertebrates (Pollard & Cooke, 1994). Sika deer present an additional threat to native ungulate species through hybridisation with native red deer populations (e.g., Biedrzycka et al., 2012; McFarlane et al., 2020; Smith et al., 2018). Reliably predicting the responses of Chinese muntjac and sika deer to management interventions is critical in developing effective strategies to reduce population spread. It is recommended that researchers initially focus on outcomes relating to population growth (e.g., population size, fecundity, survival etc.) and space-use (e.g., distributions, dispersal, movement rates), as they are likely to be the most important factors driving population expansion.

Recommendations for systematic reviews and meta-analyses

Scholars may look to expand this review by including a broader range of species. Widening the scope of the review to include North American species such as elk, moose (*Alces alces*) and white-tailed deer is likely to yield a much greater volume of literature that may provide a more comprehensive overview of the evidence-base. Reviews that include a critical appraisal of the literature should prioritise estimating the relationship between outcomes and environmental factors (e.g., climate or land-use, analysed as 'effect modifiers' if the data permit a meta-analysis to be carried out). Systematic reviews or meta-analyses are needed to assess the validity of transposing results from one geographic region or ecological context to another. Future reviewers may categorise studies by ecological context and critically evaluate the results to estimate the effects of environmental conditions on species responses.

The map shows that shooting is the only intervention for which a sufficient volume of evidence currently exists to permit a meaningful systematic review or meta-analysis. Systematic reviews would provide insights on the quality of the literature as well as determining the magnitude, directionality and heterogeneity of effects between different species and ecological contexts (i.e., 'effect modifiers'). Systematic reviews and meta-analyses assessing the relationship between outcomes and variation in shooting practices (e.g., intensity, spatial scale, timing, selectivity) would be particularly valuable for understanding the mechanisms of how shooting works, and what modifiers affect species responses (Apollonio et al., 2010, 2017).

Limitations of the search strategy

It is important to consider the limitations of the search strategy when interpreting the results. Although the searches were comprehensive, finite time and resources prohibited actions, such as combing review papers, forward and backward screening of articles and searching additional databases, which may have yielded a greater number of relevant studies. The searches were also restricted to articles presented in the English language and 'grey' literature was obtained from UK-based sources only. It is unclear to what extent this limited the number of articles evaluated. However, it is likely that a greater volume of undiscovered articles exists for species, such as sika deer and Chinese muntjac, that have their native ranges in predominantly non-English speaking regions (e.g., East Asia). Efforts to build on this map should focus on expanding the geographic scope of the review by searching for studies from a wider range of sources, ideally through collaborations between multiple reviewers, which provide different institutional accesses and the option of screening articles in a broader range of languages. It is also expected that a number of studies exist based on environmental IEC containing information on species responses to management that are not reported in the title or abstract. Such articles would have been excluded at the screening stages of the search strategy in its current form. It is recommended that researchers consistently report population-based metrics and, where appropriate, include these details in their title, abstract or keyword list, which will enable future reviewers to more easily access this information.

Additionally, there are more general caveats associated with interpreting the outputs of systematic maps (for further details see CEE guidelines, www.environmentalevidence.org). Firstly, data were extracted to broadly characterise the evidence of linkages between interventions, outcomes and species. The synthesis did not extend to exploring the directionality of effects or estimating average effect sizes, as is typical of systematic reviews or meta-analyses. Secondly, the set of species responses covered in the study was derived from a synthesis of the included articles and is not exhaustive. Assessments of the literature related to other wild ungulate species may identify linkages between interventions and a wider range of outcomes than those reported by the studies in the map. Finally, although study designs give an indication of the robustness of evidence, the map does not provide a critical appraisal of the included articles. A detailed evaluation of how studies mitigate biases and account for heterogeneous effects is needed to more accurately assess the quality of the literature.

In conclusion, the management of wild ungulate populations should be informed by regular monitoring of both environmental and population-based indicators of ecological change (Apollonio et al., 2017; Carpio et al., 2021). The map reveals that the extent of the literature reporting on population-based responses to management is limited. The current lack of primary research constrains our ability to reliably predict the full range of effects an intervention will have on target species, which is critical for developing sustainable, effective and efficient strategies. Researchers and practitioners are encouraged to monitor a wider range of responses to interventions as an essential part of adaptive population management. New research and the articles identified in this review should be synthesized and, if reliable, utilized as the evidence-base for public policy and management practice decision-making. Although the results suggest that research effort in this field is increasing, the considerable gaps and biases in the current evidence-base need to be addressed before this knowledge can be transferred to real-world applications.

Chapter 3

Study area and data collection

Chapters four and five use the same dataset collected from an array of 29 motion-activated cameras deployed in the Elwy Valley study area between January 2019 and December 2020. Provided here is a description of the study area, a brief history of the fallow deer population and their management, as well as details of the data collection process.

Study area

Data were collected from an original study area of 218 km^2 in the Elwy Valley region of North Wales, UK (Figures 1 and 2). The boundary was defined by the Deer Initiative Ltd. (www.thedeerinitiative.co.uk) based on the presumed range of the fallow deer population from expert opinion, and for convenience is delineated by major roads. This boundary was later revised to a smaller area of 105 km^2 (Figure 2, for further details see the 'Site selection' section). There is a busy dual carriageway (A55) in the northern part of the study area, which runs in an east/west direction. The largest human settlements are Abergele (northwest), Bodelwyddan (north, centre) and St. Asaph (northeast). However, most of the land area has been modified for agriculture and artificial surfaces and constructions constitute only 2.5% of the total study area (Figure 3, Sentinel 2 Global Land Cover data, Malinowski et al., 2020). The dominant land cover type is herbaceous vegetation (61.7%; includes pastoral, semi-natural and improved grassland) followed by woodland (18.9%, of which 17% and 1.9% is classified as deciduous broadleaved and coniferous, respectively). Typical of UK countryside, the landscape is a mosaic of patches under different ownership. Within the area there is one site designated as a Site of Special Scientific Interest (SSSIs) and Special Area of Conservation (SAC, Figure 4) as well as 7.8 km^2 of ancient woodland. A large section of the River Elwy (21 km), together with its tributary the Afon Aled (8 km), traverses the study area, while the eastern boundary is defined by the River Clwyd (5 km). Elevation ranges from

2 m to 389 m above sea level. The gradient of the terrain around the River Clwyd is relatively shallow, whereas both sides of the River Elwy and River Aled are steeply sloped.

Figure 1. Location of the Elwy Valley study area within mainland UK

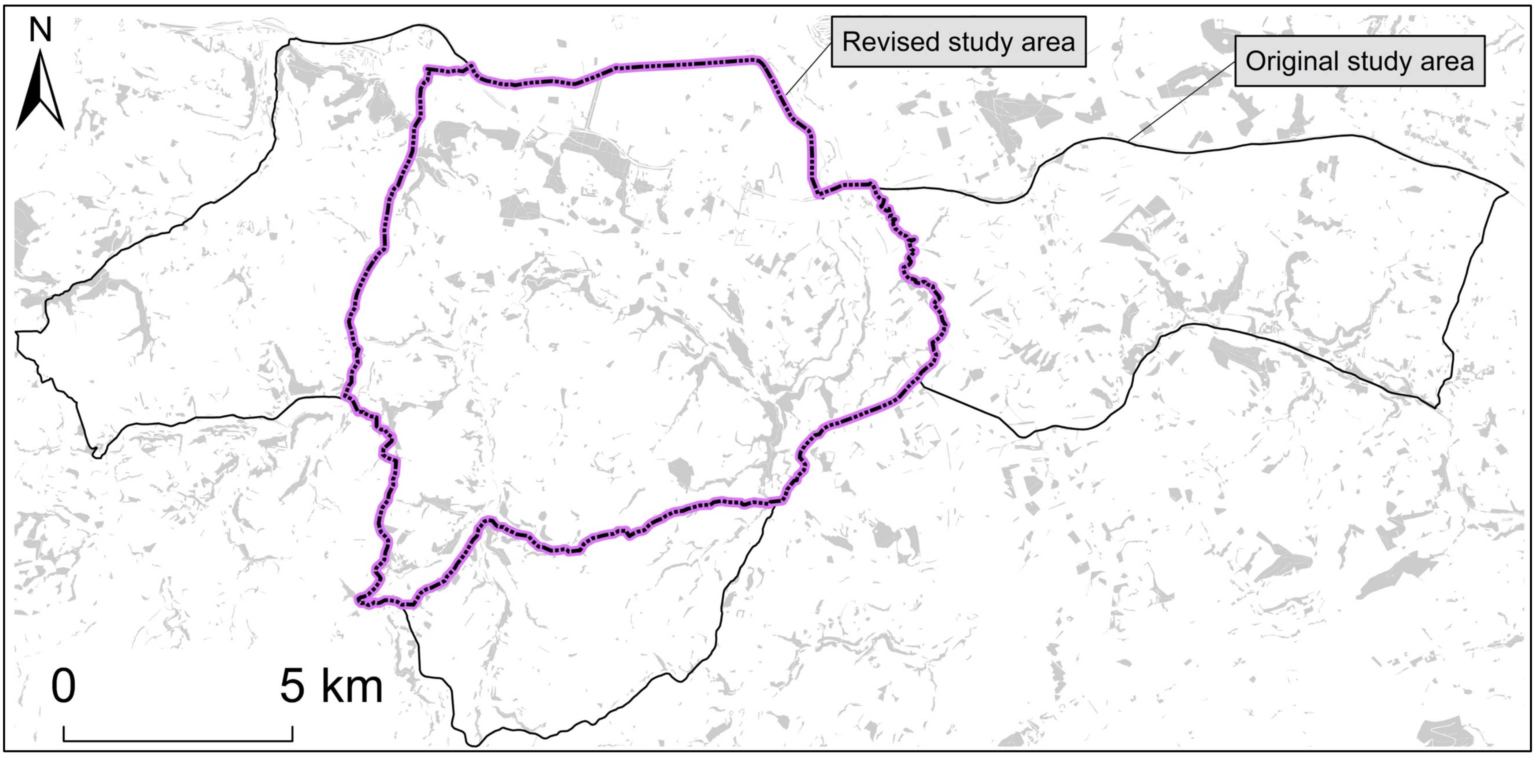


Figure 2. Boundaries of the original (218 km^2) and revised (105 km^2) Elwy Valley study areas. Grey shaded areas indicate woodland.

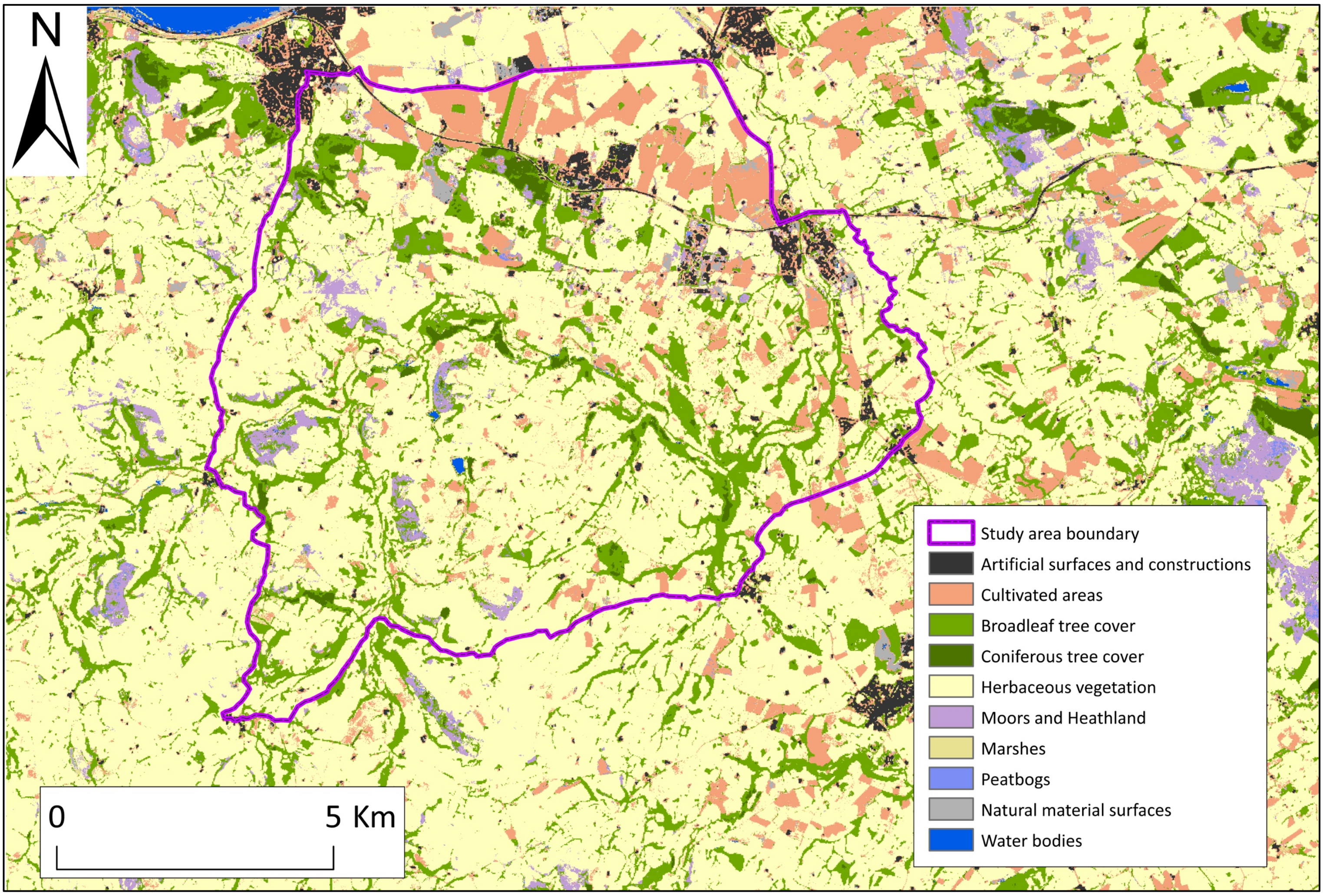


Figure 3. Land cover (Sentinel 2 Global Land Cover data, Malinowski et al., 2020) and Elwy Valley study area (105 km^2) boundary.

History of the Elwy Valley fallow deer population

The fallow deer population currently occupying the Elwy Valley region is thought to descend from captive herds, located at Kinmel Estate and Bodelwyddan Castle (Figure 4). Around the time of WW1, troops were stationed at these estates for training (Deer Initiative (DI), pers. comms). During their stay, fences were either removed or damaged and the fallow deer escaped into the surrounding countryside. Since then, the population has expanded its geographic range and numbers are thought to be around 1,500 individuals based on culling data, although no precise abundance estimates are available (DI, pers. comms.). In 2008, the Deer Initiative (DI) began working in the region to coordinate amongst landowners and stalkers and provide advice on landscape-scale deer management. The DI was established in 1995 and is a charitable partnership of statutory, voluntary and private interests dedicated to ensuring the sustainable management of deer in England and Wales. Much of their work focussed on the monitoring of deer activity and impacts on woodlands, which in several areas were showing signs of over browsing. A particular emphasis was placed on monitoring the SAC in the southeast of the study area. The DI promoted a collaborative approach to deer management, which is largely conducted by recreational stalkers as well as a few professional stalkers on the larger estates. Typical of many regions in the UK, stalking effort is highly variable across the landscape, with many landowners and land managers choosing not to implement any form of deer management. In 2020, the DI ceased to be operational and work in the area was taken over by the Game and Wildlife Conservation Trust (GWCT) – a charity whose purpose is to conduct research that will enhance the British countryside for public benefit (www.gwct.org.uk).

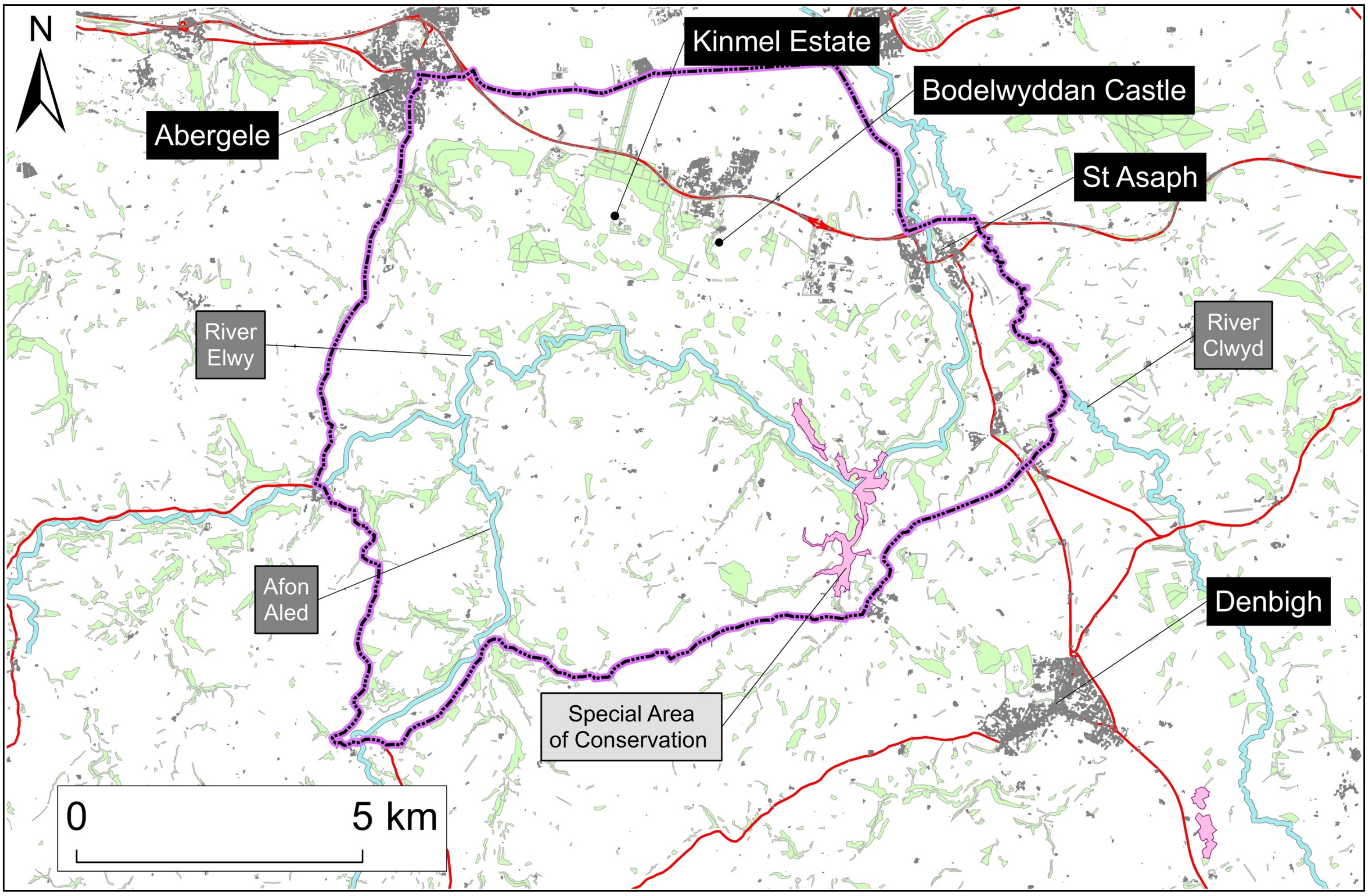


Figure 4. The revised Elwy Valley study area (105 km^2, purple line) in North Wales, UK. The original fallow deer population was located at Kinmel Estate and Bodelwyddan Castle prior to release around the time of WW1. Shaded patches indicate the following land cover types: green = woodland, grey = artificial surfaces and constructions, pink = Special Area of Conservation (SAC). Red lines indicate major roads. White areas indicate other land cover types not specified (mostly improved grassland).

Camera-trap survey

A total of 44 motion-activated cameras were deployed in 41 woodland sites within the original (218 km^2) study area. Woodland was chosen as the focal habitat for the empirical chapters (four and five) of this thesis for several reasons. Firstly, woodlands are critical ecosystem components that provide important sources of food and habitat for a wide range of other species. Secondly, deer are known to influence a variety of woodland characteristics including their structure, composition, health and natural regeneration (Cukor et al., 2019; Laurent et al., 2017; VanderMolen & Webster, 2021; Vuorinen et al., 2020). The creation and conservation of woodland is a key part of national and global-scale strategies to mitigate the effects of forecast global climate change and is often a motivation for deer population management (Bastin et al., 2019; Cook-Patton et al., 2020). Finally, local densities of deer were expected to be higher in woodlands than other habitat-types (e.g., grassland), where groups of individuals typically distribute themselves over larger geographic areas. Positioning cameras within woodlands was therefore likely to improve the probability of detecting individuals and provide more useful data for investigating the factors affecting their activity and habitat-use (Chapters four and five).

A single camera was deployed at each site and at three sites cameras were replaced due to malfunction. Six camera models were used: Reconyx HC500 Hyperfire (17), Browning Spec Ops Advantage (11), Bushnell Trophy Cam Essential HD (10), Bushnell Trophy Cam Aggressor HD (3), Uway VH400HD (2) and Ltl. Acorn 5210A (1). All cameras operated via a passive infra-red movement sensor and shared the following specifications: 8-megapixel minimum image resolution, detection range up 30 m and the capacity to take images at night with no-flash technology. Each camera was programmed to take three images when triggered with no interval between images and a maximum interval of 1 s between triggers. Cameras were set to record information on the date and time of image capture (Universal Coordinated Time (UTC) time zone), which was stored within the image metadata.

Cameras were placed along game trails that showed signs of deer activity (footprints, dung, browsed vegetation etc.), to maximise the probability of detection Each camera was mounted on a tree trunk at a height of 0.5-1.2 m. If no signs of activity were present, cameras were placed in accessible areas of the woodland at game trail intersections or likely entrance/exit points. Where possible, public footpaths or trails that showed signs of frequent use by humans were avoided. The location of cameras was recorded using a handheld Global

Positioning System (GPS) device. Cameras were monitored every 50 to 90 days to replace the batteries and Secure Digital (SD) cards. Typically, the cameras remained in-situ for most of the study duration (2019 and 2020). However, it was occasionally necessary to remove the cameras during periods of national holidays to minimise the risk of theft. If removed, cameras were redeployed at the exact same location (located via GPS and tree markings). A record of camera monitoring was kept, which included details of the operational status of each camera and tracked periods of removal and redeployment.

Images from the cameras were assigned a metadata tag to indicate species presence/absence using the open-source software, digiKam (www.digikam.org). The metadata from tagged images was then extracted and converted to a spreadsheet format in R (www.r-project.org) using the camtrapR package (Niedballa et al., 2016). Consecutive images of deer within a period of 10 minutes were considered non-independent and only data from the first image were used in analyses.

Survey seasons

The camera-trap data were filtered to retain records collected during three 90-day time periods each year. These time periods are hereafter referred to as 'biological seasons' and were defined based on the fallow deer reproductive cycle: rut (September-November), post-rut (January-March) and birthing (May-June, Chaplin & White, 1972). Biological seasons were each separated by a period of approximately 30 days. There are two main reasons for filtering the data based on biological seasons. Firstly, it reduced the proportion of time the cameras were inactive due to removal, as some of the time periods between seasons coincided with public holidays. Secondly, it provided a meaningful definition of a survey season for occupancy modelling. One of the key assumptions of occupancy modelling is that the occupancy status of a unit either (i) does not change during a survey season (i.e., occupancy is assumed to be closed) or (ii) changes in occupancy during a survey season are random (i.e., a relaxation of the closure assumption). As fallow deer are a highly mobile and wide-ranging species, the closure assumption was not reasonable given the size of the study area (for further details see Chapter five). However, changes in occupancy at each site were expected to be non-random throughout the year as there may be variable demand for resources at different stages of the reproductive cycle (e.g., woodlands may be favoured during the birthing period to shelter neonates, Kjellander et al., 2012). Years were therefore divided into biological seasons to better satisfy the assumption of random changes in occupancy during a survey season. In total, data were collected during six temporally independent sampling seasons (two years (2019-2020), three biological seasons per year).

Site selection

Woodland units

Sites for camera deployments were selected using a stratified sampling strategy based on woodland area. Land cover information was downloaded from Digimap (www.digimap.ac.uk) in the form of the Ordnance Survey (OS) Open Map – Local (Ordnance Survey, 2017). OS data were used for consistency with physical OS Explorer maps used in the field. The OS Open Map includes vector files for landscape features such as roads, rivers and woodlands. Features are derived from the OS MasterMap® Topography layer, which is accurate to approximately 4 m (Ordnance Survey, 2017). Geometries of features in the woodlands vector are defined by physical (e.g., fences) and non-physical (i.e., political/administrative) boundaries. Consequently, the woodlands vector was converted to a 10 m raster grid and then back-converted to a vector to aggregate closely neighbouring features using ArcGIS, ESRI ArcMap Version 10.6.1. Features of the aggregated woodlands vector are hereafter referred to as woodland units. Woodland units with an area < 0.01 km^2 were removed (n=2887). Woodland area was log-transformed as the distribution was highly positively skewed (Figure 5), and each unit was assigned one of the following scores: lower quartile = 1, interquartile range = 2 and upper quartile = 3 (Figures 5 and 6).

Original sampling strategy

A total of 40 cameras were distributed according to the proportion of total woodland area (19.68 km^2) represented by woodlands (n = 325) assigned each area score (Table 1) within the original study area (218 km^2, Figure 6). A minimum distance of 250 m between cameras (range: 255 m – 2314 m, mean = 715 m) was used to ensure some level of spatial independence in environmental covariates (land cover and slope) at the site and local scale (for more information on the spatial scale of environmental covariates and methods used to account for spatial autocorrelation between sites see Chapter five). The realised distribution of sampled units differed from the ideal sampling strategy due to access restrictions to private woodlands (Table 1). One camera was stolen during the study period and a replacement camera was deployed in the same woodland unit at the beginning of the next survey season, approximately 100 m from the location of the original. As the location had changed, this new deployment was treated as an independent site (i.e., site number 41).

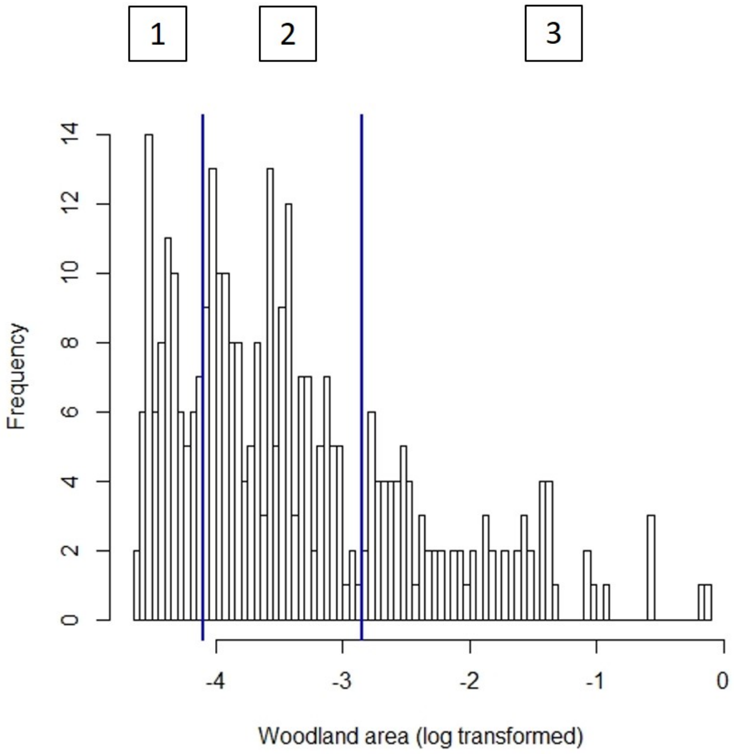


Figure 5. Distribution of areas of woodland units (log transformed) in the original Elwy Valley study area (218 km^2, n= 325). Blue lines denote the bounds of the interquartile range. Numbers in boxes represent woodland unit scores

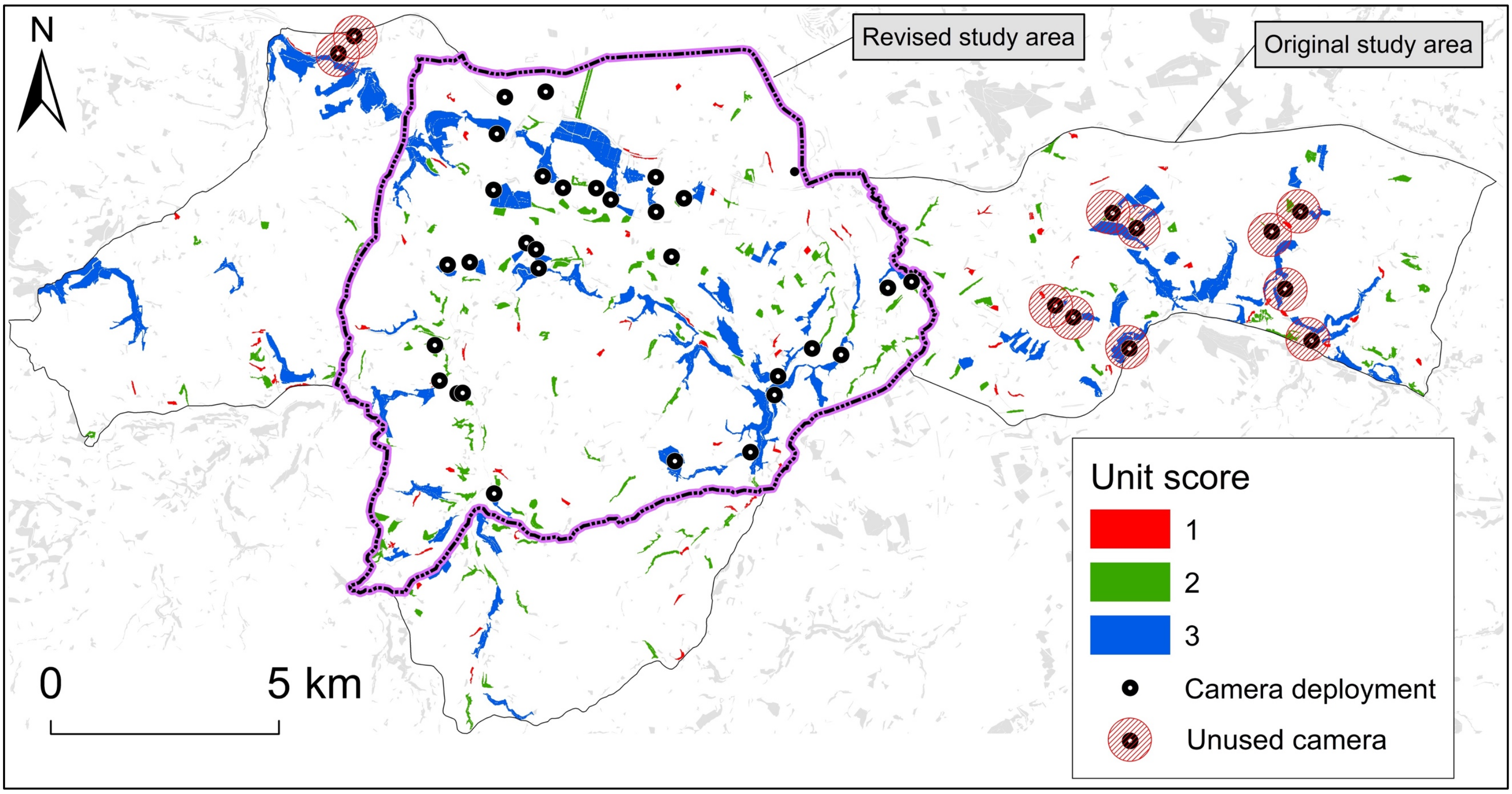


Figure 6. Boundaries of the original (218 km^2) and revised (105 km^2) study areas. Woodland units are coloured according to scores based on area. Dots indicate the location of camera deployments (n=41), of which 11 (surrounded by red shading) were not used for analyses.

Table 1. Stratified sampling of 40 woodland units in the original Elwy Valley study area (218 km^2) based on proportion of total woodland area.

Unit score	*n* units	Area km^2	Proportion of total area (19.68 km^2)	Ideal strategy *n* sampled units	Realised *n* sampled units
1	81	1.03	0.05	2	3
2	162	4.69	0.24	10	16
3	82	13.89	0.71	28	21

Revised sampling strategy

As data from the cameras began to be analysed, it became apparent that the number of detections at some sites was extremely low and, in several cases, cameras had failed to detect the species at least once throughout the entire study duration. When the total number of detections per site was visualised on a map it became clear there was a spatial pattern in the data. Eight of the nine cameras positioned east of the River Clwyd and both cameras located west of Abergele (i.e., away from the centre of the study area, Figure 6), failed to record a single detection. There was no evidence to suggest this pattern was linked to site-level environmental conditions. Instead, it was assumed more likely to be a driven by landscape features inhibiting the dispersal of individuals from the population source (Kinmel Estate and Bodelwyddan Castle, Figure 4). To reach the easternmost sites, individuals must traverse two major rivers and a main road, whereas the westernmost sites lie on the opposite side of Abergele, which is the largest human settlement in the area (Figure 4). Based on anecdotal evidence, these results were not wholly unexpected, and it was hoped that even if few detections were recorded by these cameras, they may still be valuable in exploring factors influencing landscape connectivity. However, as several cameras recorded no detections at all, such analyses were not possible. Ultimately, data from these sites (n=11) were not included in any analyses as they offered no information on deer activity or woodland-use.

The geometry of the study area was therefore revised (105 km^2), based on the distribution of the cameras that contributed data for analyses (Figure 7). The procedure for scoring woodland units (described above) was performed for units within the revised study area (Table 2 and Figure 7). A total of 29 cameras were deployed in woodland units at 30 independent sites (one camera was repositioned).

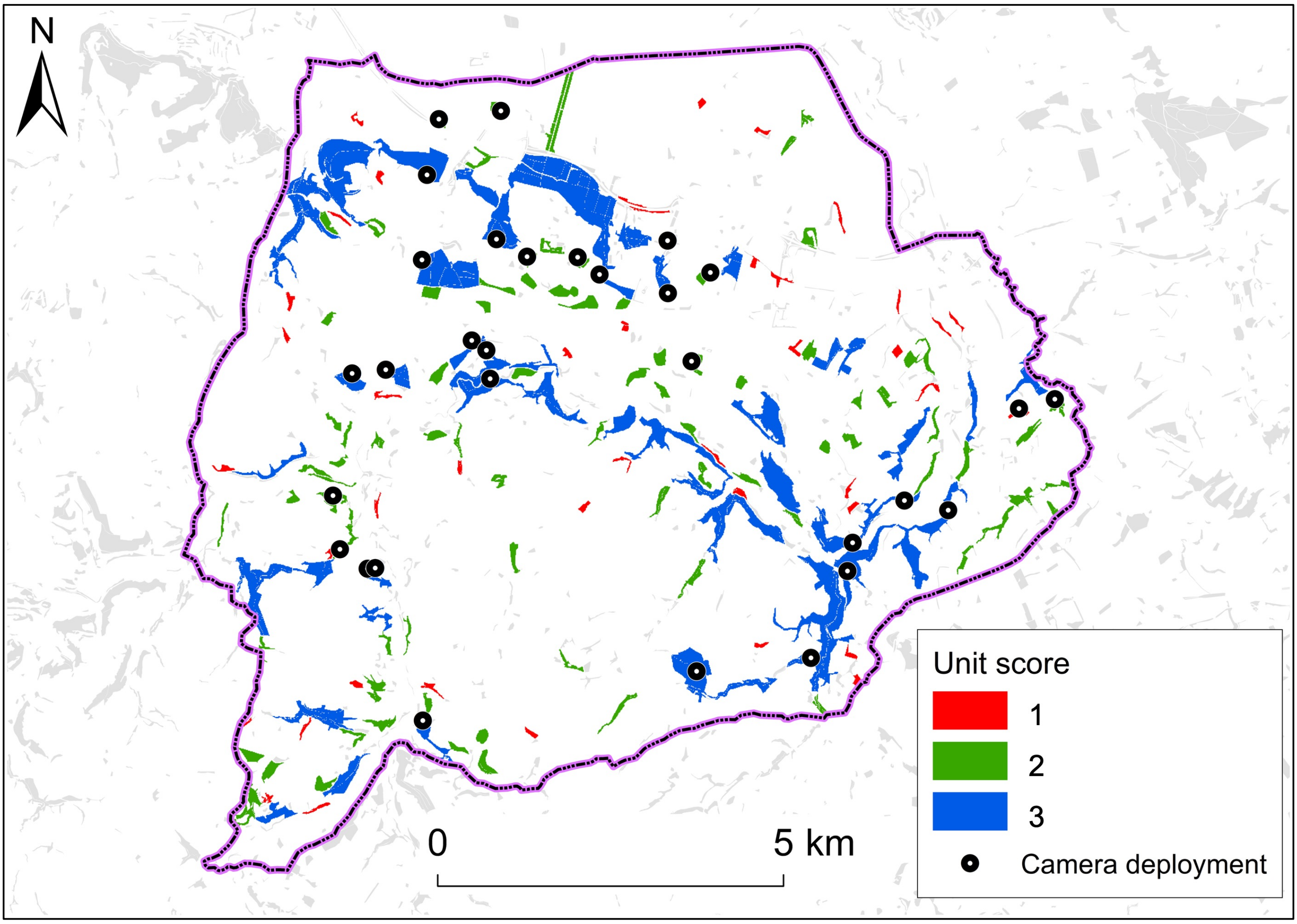


Figure 7. Locations of camera deployments (n=30) within the revised Elwy Valley study area. Woodland units are coloured according to scores based on area.

Table 2. Stratified sampling of 29 woodland units in the revised Elwy Valley study area (105 km^2) based on proportion of total woodland area.

Unit score	*n* units	Area km^2	Proportion of total area (10.61 km^2)	Ideal strategy *n* sampled units	Realised *n* sampled units
1	44	0.59	0.06	2	2
2	87	2.56	0.24	7	9
3	44	7.46	0.70	20	18

Human activity data

A questionnaire was given to landowners and land managers of woodland units (n = 15) where cameras were deployed to provide a qualitative estimate of the level of human activity (S6 and S7). The questionnaire consisted of seven questions of which the responses to three, related to (1) stalking, (2) recreation and (3) woodland management, were used in analyses. Respondents were interviewed at the end of each survey year and asked to assign a score from 0 to 3 based on the level of disturbances (e.g., the frequency of recreation or extent of woodland management) in each of the three biological seasons (rut, post-rut, birthing, S6). Scores were later reduced to binary (0 or 1) values to avoid model overparameterization and improve the reliability of the data (White et al., 2005). For recreation and woodland management, initial scores of 0 or 1 were reassigned a value of 0 and scores of 2 or 3 were given a value of 1. In contrast, for stalking, initial scores of 0 were retained as 0 and any greater than 0 were assigned a value of 1. Covariate scores were treated differently as the respondents generally reported that distinguishing between lower levels of non-lethal disturbances (e.g., no recreation at all = 0 versus recreation occurring at an average rate of less than once per week = 1) was more challenging than estimating stalking activities (e.g., stalked versus not-stalked). Note that ‘stalking’ is hereafter referred to as ‘hunting’, which will be a more familiar term for most readers. For more information on the distribution of cameras in relation to land ownership and human activity see S9-S13.

Environmental data

Land cover data were obtained from the Sentinel-2 Global Land Cover (S2GLC) project (Malinowski et al., 2020). The S2GLC data are available as a 10 m x 10 m resolution raster layer with 13 thematic land cover classes. Two classes: **herbaceous vegetation**, and an aggregation of two tree-related classes: broadleaf tree cover and coniferous tree cover (‘**tree cover**’, hereafter), were used in the analyses. A 5 m-resolution OS digital terrain map of surface elevation (Ordnance Survey, 2017) was resampled to a 10-m resolution to be consistent with the land cover data. The **slope** of each raster cell was calculated as the maximum rate of change in value from the cell to its immediate neighbours using the ‘Slope’ tool in ArcGIS. Units of slope are given as a percentage (rise/run*100).

Chapter 4

Lethal and non-lethal human activities influence the daily activity patterns of fallow deer (*Dama dama*) in woodlands within a human-dominated landscape

Introduction

The distribution of activity over time is a fundamental characteristic of animal ecology (Hutchinson, 1957; Macarthur & Levins, 1967). The timing of activities to access food and other resources while minimising the risk of encounters with predators, parasites and competitors is an important component of animal fitness (Anderson & Wiens, 2017; Kronfeld-Schor et al., 2017). Within species, individuals are typically consistent in their activity patterns across the 24-hour diel cycle (Ikeda et al., 2015; Kamler et al., 2007; Zanni et al., 2021). Differences in the temporal partitioning of activity between species is an important behavioural factor in determining the composition and structure of ecological communities (Anderson & Wiens, 2017; Valeix et al., 2007). While spatial components of habitat are widely recognised as being important for wildlife management and conservation, the temporal dimension of the ecological niche is often overlooked (Gallo et al., 2022; Gaston, 2019).

Humans can affect the temporal component of wildlife behaviour through activities, such as hunting (Santo Domingo et al., 2021), land-use change (Ramesh & Downs, 2013), recreation (Lewis et al., 2021), predator control (Brook et al., 2012) and the introduction of non-native invasive species (Frey et al., 2017; Zapata-Ríos & Branch, 2016). Human presence can induce fear in wildlife species, causing similar impacts to the non-consumptive effects of natural predators (Frid & Dill, 2002; Gaynor et al., 2018; Zanette & Clinchy, 2020). Animals may respond to fear through reactive responses, such as fleeing (Blumstein, 2016) or via proactive behaviours, such as spatiotemporal partitioning of activity (Gaynor et al., 2022;

Lamb et al., 2020; Marchand et al., 2014; Pęksa & Ciach, 2018). For example, prey species typically concentrate their activity at periods of low light (dawn, dusk and night) to avoid contact with predators whilst utilising the same space and habitat (Anderson & Wiens, 2017). Human presence is often perceived to be a threat analogous to that of natural predators (Smith et al., 2017; Suraci et al., 2019). Wildlife species usually respond to human presence by becoming more active at night, when human activity is generally low (Gallo et al., 2022; Gaynor et al., 2018). Although potentially beneficial, antipredator behaviours also incur fitness costs. Fear-induced shifts in activity may reduce access to mates and foraging opportunities as well as leading to greater exposure to other predators (Frid & Dill, 2002; Goumas et al., 2022). Through this pathway, human presence can strongly influence individual performance, which may have cascading effects on population dynamics (Smith et al., 2021; Zanette & Clinchy, 2020) and trophic interactions (Gaynor et al., 2019; Smith et al., 2015; Suraci et al., 2019).

Strong responses to human presence may also be sub-optimal as, unlike natural predators, humans often usually do not present a lethal threat to wildlife species (Goumas et al., 2022). Indeed, humans may ignore animals or actively encourage their presence through feeding. Increased tolerance of human presence can be advantageous, as it reduces costly antipredator behaviours and human-populated areas may offer a refuge from disturbance-sensitive predators (Gallo et al., 2022; Lesmerises et al., 2017; Shannon, Cordes, et al., 2014). Animals may increase their tolerance of human presence through habituation, which is a process that leads to decreased responsiveness following repeated exposure to a non-threatening stimulus (Blumstein, 2016). For habituation to occur, animals must be repeatedly exposed to non-lethal human encounters (Blumstein, 2016; Frid & Dill, 2002; Geffroy et al., 2015).

Distinguishing between lethal and non-lethal human behaviour is cognitively demanding, especially in contexts where multiple sources of risk and disturbance co-occur (Ciuti, Muhly, et al., 2012; Courbin et al., 2022; Tablado & Jenni, 2017). There have been relatively few examinations of the interacting effects of lethal and non-lethal disturbance on wildlife species (e.g., Courbin et al., 2022; Mols et al., 2022; Paton et al., 2017). The findings from these studies suggest that animals are generally unable to differentiate between different human activities, which can have positive and negative consequences for individual fitness. For example, elk avoid roads more strongly in areas where they are hunted, which reduces their risk of mortality from road traffic collisions (Paton et al., 2017). In contrast, habituation to recreation (hiking and skiing) by chamois (*Rupicapra rupicapra rupicapra*) decreases their avoidance of hunters and makes them more vulnerable to being shot (Courbin et al., 2022). However, knowledge gaps exist for a wide range of taxa and further research is needed to better understand how temporal behavioural patterns of wildlife species are influenced by complex landscapes of human disturbance.

Understanding the impacts of human disturbance on wild ungulate species, such as deer (Cervidae), is of wider importance because of the key role they play in the functioning of forest and grassland ecosystems (Fornara & du Toit, 2008; Manier & Hobbs, 2007; Murray et al., 2013b; Ohashi & Hoshino, 2014). Temporal variation in their behaviour has community-level effects on social interactions (Palmer et al., 2021), nutrient cycling (Chollet et al., 2021; Ramirez, 2021) and the transmission of disease (Kjær et al., 2008). In many areas, such as Europe, North America and Japan, deer and human populations have grown simultaneously, which has created a complex scenario of coexistence and competition for shared resources (Carpio et al., 2021; Hernández et al., 2018; Saito et al., 2016; Ward, 2005).

Research has shown that deer avoid hunters by being more active at night and less active in the day (e.g., Bonnot et al., 2013; Ikeda et al., 2019; Kamei et al., 2010; van Doormaal et al., 2015). However, evidence is lacking for some species that have a major ecosystem impact, such as fallow deer and Chinese muntjac (Barton et al., 2022). Literature on the effects of non-lethal disturbance on deer activity patterns is also scarce and variable in its findings. For example, a study by Lewis et al. (2021) showed that mule deer (*Odocoileus hemionus*) alter their activity patterns near recreation trails to be more active at night, whereas a similar study by Ota et al. (2019) found no effect on the activity patterns of barking deer (*Muntiacus muntjak*). Furthermore, very little research has focussed on the effects of co-occurring lethal and non-lethal disturbance (but see Mols et al., 2022; Paton et al., 2017). Results from the few available studies suggest that behavioural responses to multiple stimuli are context-dependent and vary between individuals (Mols et al., 2022; Paton et al., 2017). To adequately support decision-making in conservation and wildlife management, it is therefore necessary to address knowledge gaps that exist for specific species, ecological contexts and real-world scenarios where species are simultaneously exposed to multiple sources of disturbance.

This study aims to examine the effects of human disturbance on the daily activity patterns of fallow deer in woodlands within the Elwy Valley region of North Wales, UK. Typical of countryside landscapes in the UK, the region is extensively human-transformed and is a mosaic of small parcels of land under multiple ownerships and management. Activity was monitored via an array of motion-activated camera-traps deployed in woodlands for a period of two years. Camera data were used to assess the relationship between daily activity patterns and different types of lethal (hunting) and non-lethal (recreation and woodland management) human disturbance. Based on existing research, it was hypothesised that (1) the distribution of activity across the diel cycle would be non-random (i.e., there would be consistent peaks and troughs of activity), (2) hunting would increase crepuscular and nocturnal activity (3) recreation and woodland management would increase diurnal (i.e., daytime) activity and (4) cooccurring lethal and non-lethal disturbance would more strongly increase crepuscular and nocturnal activity than lethal disturbance alone (i.e., there would be an additive effect).

Methods

Camera-trap data

Data collection

Data were collected from an array of 29 motion-activated camera-traps deployed in woodlands within the Elwy Valley study area. Cameras were deployed for two years from January 2019 to December 2020. Data were obtained from three 90-day sampling periods each year, which corresponded to key stages of the fallow deer reproductive cycle (‘biological seasons’ hereafter): rut (September-November), post-rut (January-March) and birthing (May-July). Camera images taken at least 10 minutes apart were considered independent detections (Crawford et al., 2021; Ridout & Linkie, 2009). Information on human activity at sample sites was obtained via questionnaire surveys given to landowners and land managers. For full details on the study area, deployment of cameras and data collection process see Chapter 3.

Data management

Daily activity patterns of animals are governed by endogenous circadian rhythms that are primarily entrained by light (Kronfeld-Schor & Dayan, 2003; Mistlberger & Skene, 2004). In the study area, the timing of sunrise and sunset varies seasonally by approximately 3.5 hours and 4.5 hours, respectively. To account for this variation, observations were standardised by transforming the clock-recorded time of each detection to a relative sun time corresponding to the actual sunrise and sunset (Bu et al., 2016; Nouvellet et al., 2011). Data were pooled from all cameras for the entire study duration to describe overall population-level activity patterns. To investigate sources of variation in activity patterns, subsets of the camera data were created based on temporal (year and biological season) and anthropogenic (recreation *Rec*, woodland management *WM* and hunting) covariates (Table 1, for more information on human activity data see Chapter 3, S6 and S7). Primary data subsets were based on a single covariate category (e.g., *Rec* (*High)*, Table 1). These were then further divided into secondary data subsets based on an additional covariate (e.g., *Rec* (*High) Hunted* /*Not-hunte*d). Primary and secondary data subsets were analysed using the techniques described below. For information on the survey effort (number of camera-trap days) for data subsets and distribution of cameras in relation to anthropogenic covariates, see S8-S13).

Table 1. Covariates and categories used to subset the camera data for daily activity pattern analyses of fallow deer in the Elwy Valley study area. For more information on human activity data see Chapter 3, S6 and S7)

Covariate	Category
Year	2019 2020
Bioseason	Rut Post-rut Birthing
Hunting	Hunted Not-hunted
Recreation (Rec)	High Low
Woodland management (WM)	High Low

Data analysis

Diel temporal overlap

The similarity of activity patterns between data subsets was evaluated in R (R Core Development Team, 2019) using the Overlap package (Meredith & Ridout, 2021). The Overlap package fits kernel density functions to estimate the probability of detecting the species at times throughout the diel cycle (Meredith & Ridout, 2021; Ridout & Linkie, 2009). A default smoothing parameter of 1.0 was used following the authors' recommendations (Ridout & Linkie, 2009). Similarity is described by the coefficient of overlap, which ranges from 0 (no overlap) to 1 (complete overlap; Ridout & Linkie, 2009). For each group comparison, 10,000 bootstrapped simulations were used to estimate 95% confidence intervals. The bootstrapping method assumes that the original sample (observed distribution of activity) is representative of the population and generates new samples by randomly resampling observations with replacement from the original (Ridout & Linkie, 2009). Activity patterns were considered to be different from each other if the upper bound of the 95% confidence limits of the coefficient of overlap was <0.9 (Lewis et al., 2021).

Time period selectivity

The 24-hour diel cycle was classified into three time periods: diurnal = from one hour after sunrise to one hour before sunset, nocturnal = from one hour after sunset to one hour before sunrise, and crepuscular = one hour before and after sunrise and sunset (Bu et al., 2016; Gerber et al., 2012). A Pearson chi-squared test was used to determine if activity was distributed non-randomly between the three periods for the data as a whole and each data subset:

Equation 1.

$$X^2 = \sum_{i=3}^{n} \frac{(O_i - E_i)^2}{E_i}$$

Where O_i is the observed number of detections in period i and E_i is the expected number of detections based on the total number of detections and the relative availability of the period (i.e., the length of period i in camera days as a proportion of the length of all periods). The relative strength of selection for each period was also quantified by calculating the selection ratio following Manly et al. (2002):

Equation 2.

$$w_i = o_i/\hat{\pi}_i$$

Where w_i is the selection ratio for the period i, o_i is the proportion of detections in period i and $\hat{\pi}_i$ is the length of period i as a proportion of the length of all periods. $w_i = 1$ indicates no selection or avoidance (i.e., use of the time period is proportional to its availability). Whereas $w_i > 1$ and $w_i < 1$ indicate selection and avoidance, respectively (Bu et al., 2016; Gerber et al., 2012). Shifts in selectivity of time periods were estimated by observing the difference in selection ratios between data subsets (i.e., $w_{i \cdot SubsetA} - w_{i \cdot SubsetB}$). Positive values indicate that selection for time period i is strongest for $Subset_A$ (i.e., activity patterns were more diurnal, crepuscular or nocturnal).

Results

A total of 8,409 independent detections of fallow deer were recorded from the 29 cameras deployed in the Elwy Valley study area between January 2019 and December 2020. Total survey effort was 13,478 camera days (Table 2) and the minimum survey effort for a data subset used in the analyses was 1,682 camera days (S8). Survey effort ranged from 4,271 to 4,697 camera days for the three biological seasons and was marginally greater for sites that were hunted (7,022 camera days) and sites where recreation and woodland management were low (8,203 and 8,626 camera days, respectively, Table 2). Detection rate (number of detections per camera day) was lower during the post-rut (0.28) than the rut (0.71) and birthing (0.87) seasons and was also lower at hunted sites (0.47) than at not-hunted sites (0.79, Table 2). Only minor differences in detection rate were observed between high and low recreation groups (0.61 and 0.64, respectively) as well as between high and low woodland management groups (0.53 and 0.68, respectively).

Table 2. Survey effort (number of cameras multiplied by the number of days of operational deployment), detections and detection rate (detections per camera day) for each primary (one covariate) subset of the camera data used in daily activity pattern analyses of fallow deer in the Elwy Valley study area (for details on two-covariate subsets see S8).

Data subset	Survey effort (Camera days)	Detections (n)	Detection rate (Detections per camera day)
All	13478	8409	0.62
Year (2019)	6589	3653	0.55
Year (2020)	6889	4756	0.69
Rut	4697	3312	0.71
Post-rut	4271	1180	0.28
Birthing	4510	3917	0.87
Hunted	7022	3335	0.47
Not-hunted	6456	5074	0.79
Recreation (High)	5275	3195	0.61
Recreation (Low)	8203	5214	0.64
Woodland management (High)	4852	2579	0.53
Woodland management (Low)	8626	5830	0.68

Time period selectivity

All data subsets exhibited non-random distribution of activity across the three diel time periods (crepuscular, diurnal and nocturnal, $P < 0.001$, Table 3 and S14). For the whole dataset (Table 3, Data subset 'All') the number of detections recorded was disproportionately higher ($w > 1$) during the crepuscular period ($w = 1.62$) and lower ($w < 1$) during the nocturnal period ($w = 0.57$). The number of detections during the diurnal period was approximately proportional ($w \sim 1$) to its availability ($w = 1.16$).

Table 3. Number of detections (n) across the three diel time periods: crepuscular, diurnal and nocturnal within each primary (one covariate) subset of the camera data used in daily activity pattern analyses of fallow deer in the Elwy Valley study area. Selection ratios (w) indicate the relative use of each period (i.e., proportion of detections) given their availability (i.e., proportion of the total length of data collection). The results of the Pearson chi-squared test (X^2) of the randomness of activity distribution across the three diel time periods are also included (for details on secondary data subsets, see S14).

Data subset	**n (w) in time periods**			**Pearson chi-squared test (X^2, df=2)**
	Crepuscular	**Diurnal**	**Nocturnal**	
All	2269 (1.62)	4203 (1.16)	1937 (0.57)	1235.45 ($P < 0.001$)
Year (2019)	999 (1.64)	1769 (1.12)	885 (0.60)	503.94 ($P < 0.001$)
Year (2020)	1270 (1.60)	2434 (1.18)	1052 (0.55)	736.93 ($P < 0.001$)
Rut	952 (1.72)	1228 (1.03)	1132 (0.72)	409.48 ($P < 0.001$)
Post-rut	375 (1.91)	426 (1.09)	379 (0.64)	240.48 ($P < 0.001$)
Birthing	942 (1.44)	2549 (1.08)	426 (0.47)	402.27 ($P < 0.001$)
Hunted	996 (1.79)	1380 (0.97)	959 (0.71)	467.08 ($P < 0.001$)
Not-hunted	1273 (1.51)	2823 (1.27)	978 (0.49)	895.75 ($P < 0.001$)
Recreation (High)	755 (1.42)	1872 (1.34)	568 (0.45)	631.37 ($P < 0.001$)
Recreation (Low)	1514 (1.74)	2331 (1.04)	1369 (0.65)	744.07 ($P < 0.001$)
Woodland management (High)	645 (1.50)	1501 (1.35)	433 (0.42)	600.22 ($P < 0.001$)
Woodland management (Low)	1624 (1.67)	2702 (1.07)	1504 (0.65)	742.49 ($P < 0.001$)

Diel temporal overlap

Year and Biological season

Daily activity patterns overlapped considerably between the two years (Overlap = 0.97, Table 4 and Figure 2b), but varied between biological seasons. Temporal overlap was high between the rut and post-rut (Overlap = 0.92, Table 4 and Figure 2c), whereas activity during each of these two seasons differed substantially from the birthing season (Rut: Overlap = 0.77, Post-rut: Overlap = 0.80, Table 4 and Figures 2d and 2e). Fallow deer shifted their activity to be more crepuscular and nocturnal during the rut (crepuscular: Δw = 0.28, nocturnal: Δw = 0.26) and post-rut (crepuscular: Δw = 0.46, nocturnal: Δw = 0.17) than they were in the birthing season.

Hunting

Activity patterns differed between hunted and not-hunted sites (Overlap = 0.86, Table 4 and Figure 2f). At hunted sites, the shift in selection was positive for the crepuscular (Δw = 0.29) and nocturnal (Δw = 0.22) periods and negative for the diurnal (Δw = -0.30) period (Table 4 and Figure 2f). Activity patterns only differed between hunted and not-hunted sites when recreation was high (Overlap = 0.77) or when woodland management was high (Overlap = 0.79, Table 5, Figure 1 and Figure 3a-3d). Only marginal differences in activity were observed in relation to hunting when either covariate was low.

Recreation and woodland management

The effects of recreation on daily activity patterns were similar to those observed for woodland management. For both covariates, activity patterns differed between high and low sites (recreation: Overlap = 0.85, woodland management: Overlap = 0.87, Table 4 and Figures 2g and 2h). The direction of the effects of recreation and woodland management was opposite to that observed for hunting. For sites where recreation or woodland management was high, the shift in selection was negative for the crepuscular and nocturnal periods (recreation Δw: crepuscular = -0.32, nocturnal = -0.20, woodland management Δw: crepuscular = -0.17, nocturnal = -0.23) and positive for the diurnal period (recreation Δw = 0.29, woodland management Δw = 0.28, Table 4 and Figures 2g and 2h). However, the effects of recreation and woodland management were only observed for not-hunted sites. At hunted sites, there were only marginal differences in activity patterns in relation to either covariate (Table 5, Figure 1 and Figure 3e-3h), which suggests that the effects of lethal (i.e., hunting) and non-lethal (i.e., recreation and woodland management) disturbance are not additive.

Table 4. Shifts in selectivity (i.e., difference in selection ratios, w) for each of the three diel time periods (i): crepuscular, diurnal and nocturnal for primary subsets (see Methods section for a description of data subsets) of the camera data used in daily activity pattern analyses of fallow deer in the Elwy Valley study area ($w_{i\cdot SubsetA} - w_{i\cdot SubsetB}$). Overlap estimate = estimated activity pattern overlap with associated 95% confidence intervals including lower and upper bounds (95% CI, Upper CI = * < 0.9, ** ≤ 0.8). Shading represents a positive (green) or negative (red) shift in selectivity from subset A to subset B > ± 0.1. Bold indicates non-overlapping activity patterns (Overlap Upper CI < 0.9).

	Data subset		**Shift in selectivity (Δw)**			**Overlap estimate**	**95% CI**		
Covariate	**A**	**B**	**Crepuscular**	**Diurnal**	**Nocturnal**		**Lower**	**Upper**	
Year	2019	2020	0.04	-0.06	0.05	0.97	0.95	0.98	
Bioseason	Rut	Post-rut	-0.18	-0.06	0.08	0.92	0.89	0.95	
	Post-rut	**Birthing**	**0.46**	**0.00**	**0.17**	**0.77**	**0.74**	**0.80**	**
	Birthing	**Rut**	**-0.28**	**0.06**	**-0.26**	**0.75**	**0.73**	**0.77**	**
Hunting	**Hunted**	**Not-hunted**	**0.29**	**-0.30**	**0.22**	**0.86**	**0.84**	**0.87**	*
Recreation	**High**	**Low**	**-0.32**	**0.29**	**-0.20**	**0.85**	**0.83**	**0.87**	*
WM	**High**	**Low**	**-0.17**	**0.28**	**-0.23**	**0.87**	**0.85**	**0.89**	*

Table 5. Shifts in selectivity (i.e., difference in selection ratios, w) for each of the three diel time periods (i): crepuscular, diurnal and nocturnal for secondary subsets (see Methods section for a description of data subsets) of the camera data used in daily activity pattern analyses of fallow deer in the Elwy Valley study area ($w_{i\cdot SubsetA} - w_{i\cdot SubsetB}$). Overlap estimate = estimated activity pattern overlap with associated 95% confidence intervals including lower and upper bounds (95% CI, Upper CI = * < 0.9, ** ≤ 0.8). Shading represents a positive (green) or negative (red) shift in selectivity from subset A to subset B > ± 0.1. Bold indicates non-overlapping activity patterns (Overlap Upper CI < 0.9). Rec = recreation. WM = Woodland management.

Primary subset	**Secondary subset**		**Shift in selectivity (Δw)**			**Overlap estimate**	**95% CI**		
	A	**B**	**Crepuscular**	**Diurnal**	**Nocturnal**		**Lower**	**Upper**	
Hunting									
Rec (High)	**Hunted**	**Not-hunted**	**0.37**	**-0.50**	**0.43**	**0.77**	**0.73**	**0.81**	*
Rec (Low)	Hunted	Not-hunted	0.15	-0.12	0.07	0.92	0.90	0.94	
WM (High)	**Hunted**	**Not-hunted**	**0.54**	**-0.53**	**0.33**	**0.79**	**0.75**	**0.83**	*
WM (Low)	Hunted	Not-hunted	0.17	-0.17	0.13	0.88	0.86	0.90	
Recreation									
Hunted	High	Low	-0.11	-0.05	0.10	0.86	0.83	0.90	
Not-hunted	**High**	**Low**	**-0.33**	**0.32**	**-0.25**	**0.83**	**0.81**	**0.86**	*
Woodland management									
Hunted	High	Low	0.11	0.02	-0.08	0.90	0.87	0.93	
Not hunted	**High**	**Low**	**-0.27**	**0.39**	**-0.28**	**0.85**	**0.82**	**0.87**	*

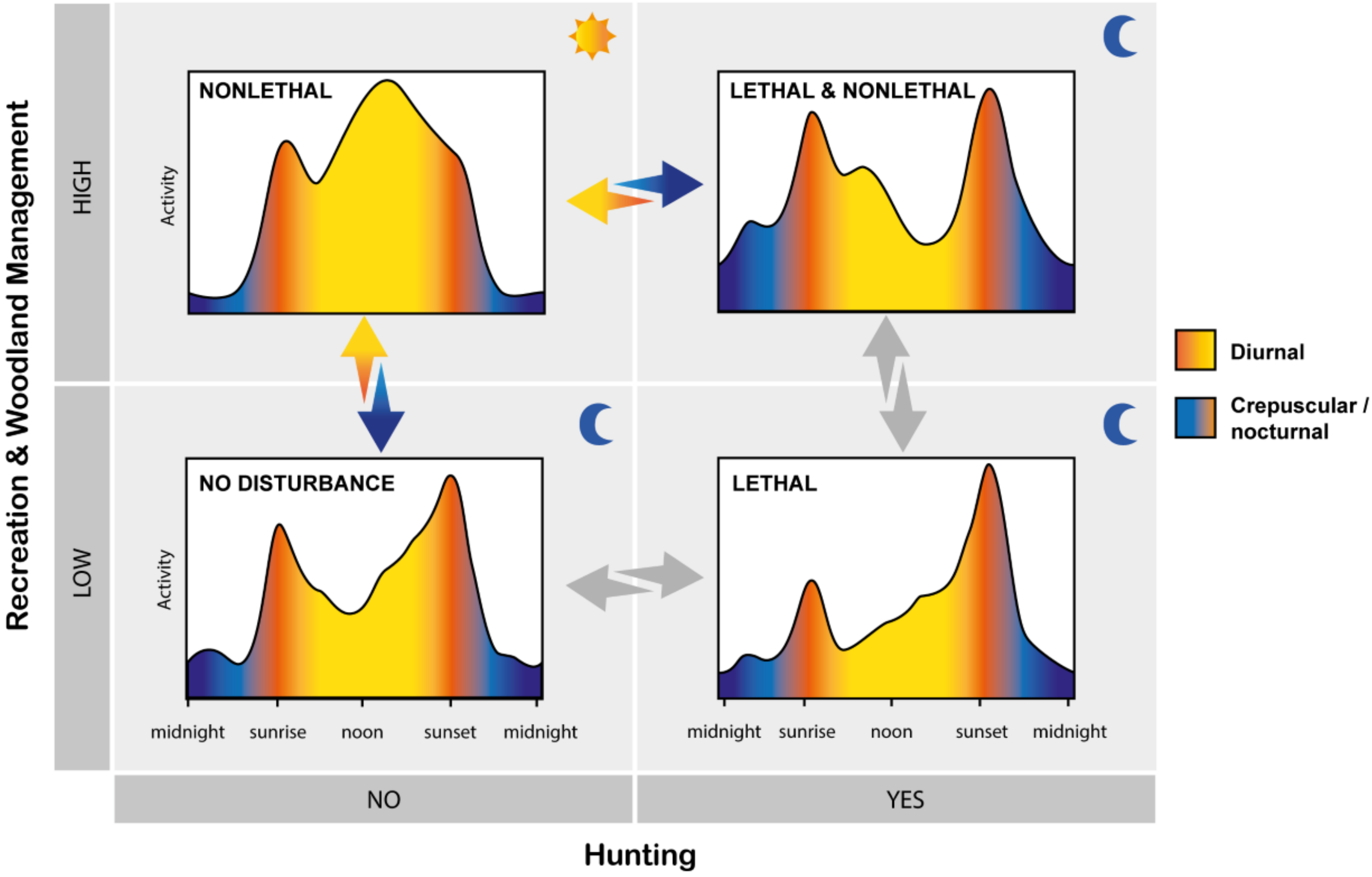


Figure 1. Illustration of the shifts in selectivity for three diel time periods: crepuscular, diurnal and nocturnal by fallow deer in the Elwy Valley study area in relation to lethal (hunting) and non-lethal (recreation and woodland management) human disturbance. Coloured arrows and grey arrows indicate non-overlapping (Overlap Upper 95% CI < 0.9) and overlapping (Overlap Upper 95% CI ≥ 0.9) activity patterns between data subsets (See Table 5 for details).

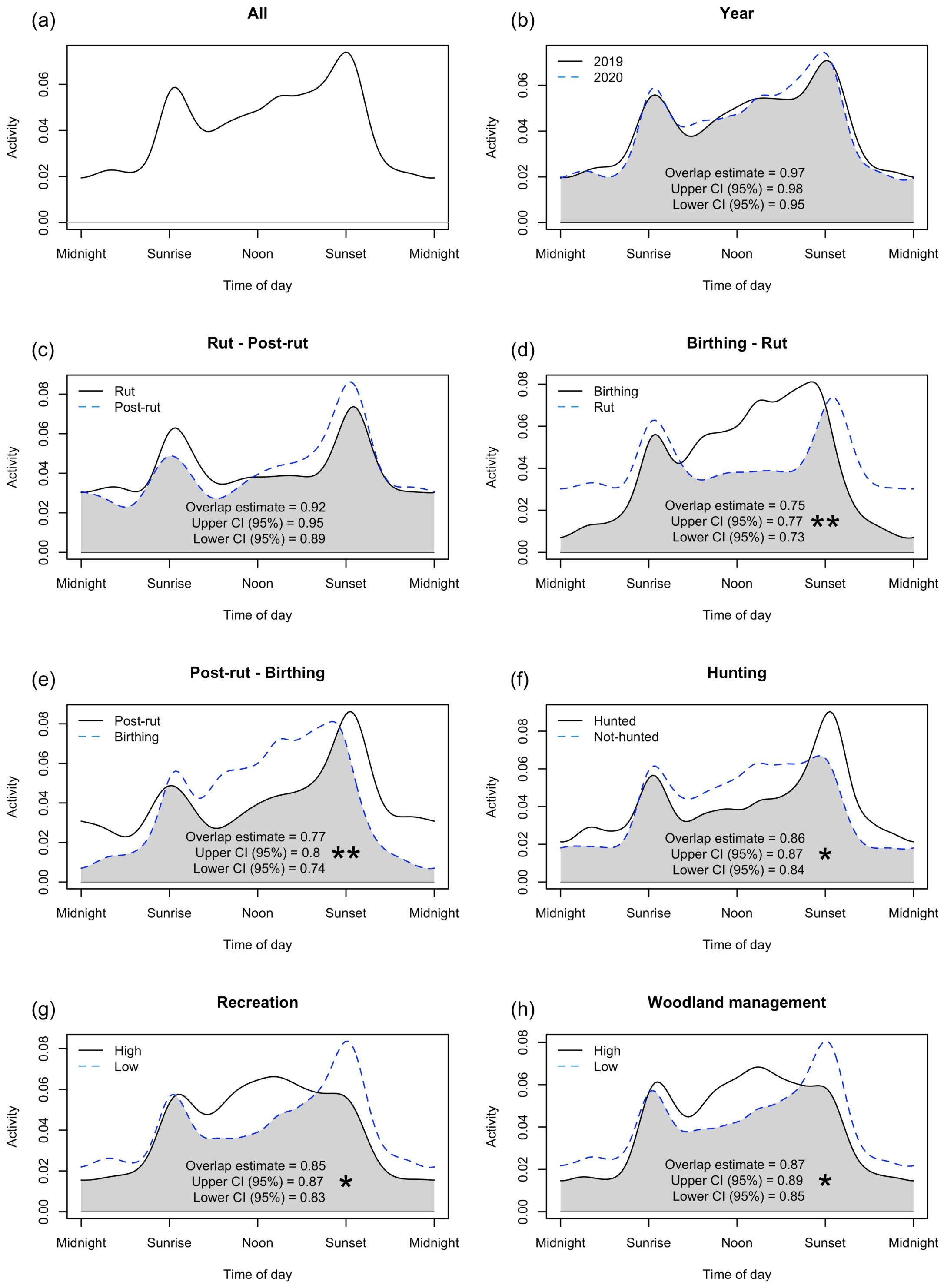


Figure 2. Variation in daily activity patterns of fallow deer in the Elwy Valley study area (a) with all data pooled (no covariates considered), (b) between primary data subsets (see Methods section for definition of data subsets): year (2019 and 2020), (c-e) biological season (rut, post-rut and birthing), (f) hunting (hunted, not-hunted), (g) recreation (high, low) and (h) woodland management (high, low). Upper 95% CI = * < 0.9, ** ≤ 0.8. Grey shading indicates overlap of activity.

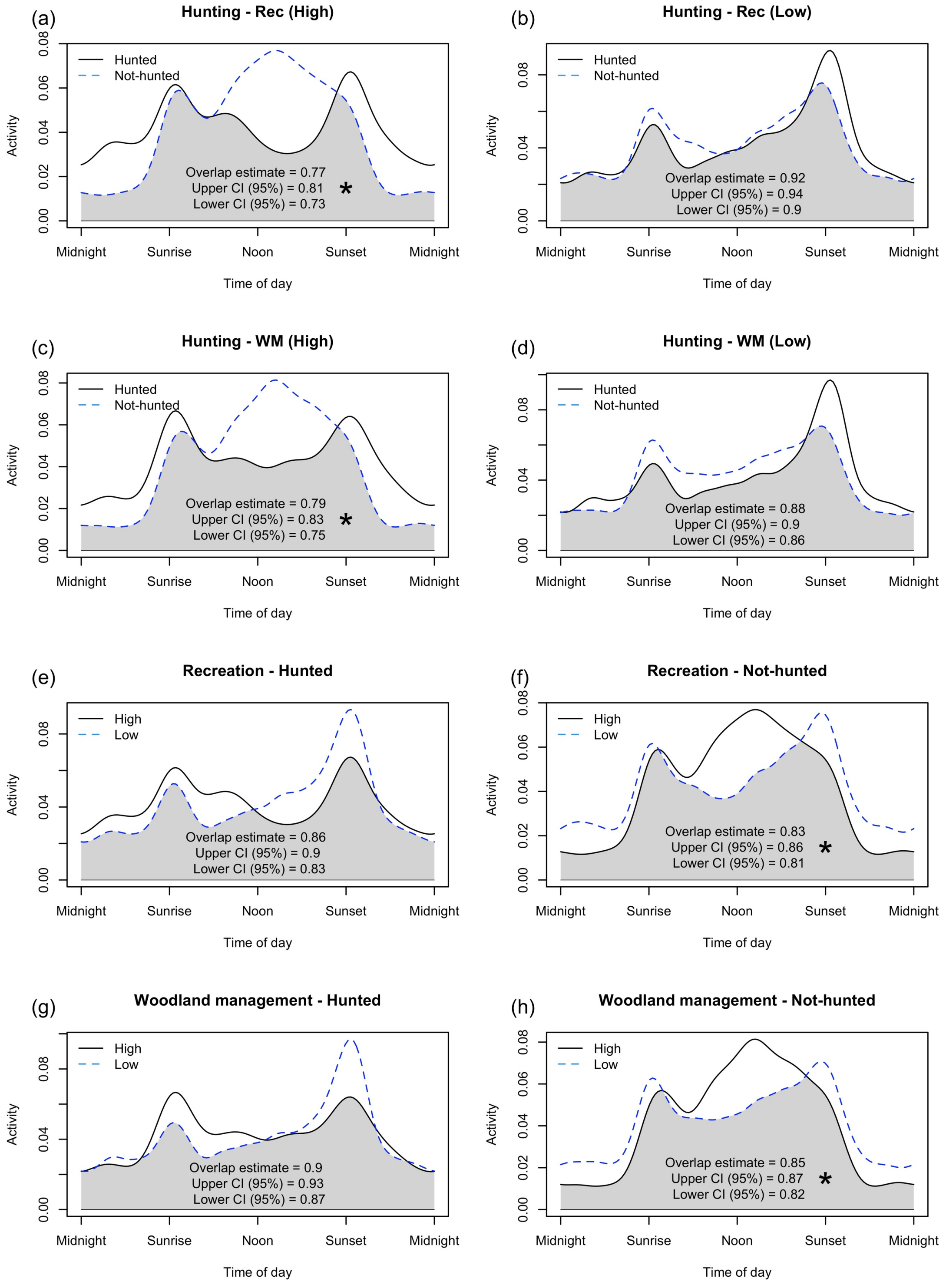


Figure 3. Variation in daily activity patterns of fallow deer in the Elwy Valley study area (a-b) between secondary data subsets (see Methods section for definition of data subsets): hunting in high and low recreation sites, (c-d) hunting in high and low woodland management sites, (e-f) recreation in hunted and not-hunted sites and (g-h) woodland management in hunted and not-hunted sites. Upper 95% CI = * < 0.9, ** ≤ 0.8. Rec = recreation; WM = woodland management. Grey shading indicates overlap of activity.

Discussion

In this study, the effects of lethal (hunting) and non-lethal (recreation and woodland management) human disturbance on the daily activity patterns of fallow deer in a human-transformed landscape were assessed. Results showed clear patterns of temporal partitioning of fallow deer activity across the diel cycle. Different sources of disturbance had contrasting and interacting effects on daily activity patterns, which also varied seasonally. The results from this study provide an insight into the learning capacity of ungulate species and the effects of different sources of co-occurring human disturbance on wildlife activity.

The results provided strong support for the hypothesis that daily activity patterns are non-random. Fallow deer tended to concentrate their activity at the crepuscular periods of dawn and dusk. Crepuscular activity has been observed in fallow deer (Torretta et al., 2017) and many other deer species, such as sika deer (Ikeda et al., 2015), red deer (Ensing et al., 2014) and roe deer (Stache et al., 2013). However, previous studies of fallow deer have found contradictory results of either predominantly diurnal (Caravaggi et al., 2018) or nocturnal behaviour (Zanni et al., 2021). There is also some uncertainty regarding seasonal variation in activity patterns. In this study, detection rate was noticeably lower post-rut (January-March) than during the rut (September-November) and birthing (May-July). Additionally, deer were more crepuscular and nocturnal in the rut and post-rut than during birthing. These results are consistent with a study by Caravaggi et al. (2018) of fallow deer in Northern Ireland but differ from another by Zanni et al. (2021), based on data from Italy, which found no seasonal effects. Variation amongst the results of the present study and the existing literature preclude a broad characterisation of the activity patterns of fallow deer and instead support evidence that activity is influenced by a range of context-specific factors such as ambient temperature, resource availability and interspecific interactions (Brivio et al., 2017; Kohl et al., 2018; Monterroso et al., 2013; Pagon et al., 2013)

Support was found for the hypothesis that hunting would increase crepuscular and nocturnal activity. An increase in nocturnality in response to hunting is a pattern that has been observed for a wide range of species (e.g., Gallo et al., 2022; Gaynor et al., 2018; Shamoon et al., 2018) and is evidence that human presence can trigger similar behavioural responses as natural predators (Smith et al., 2017; Suraci et al., 2019). The results also supported the hypothesis that non-lethal disturbance (recreation *Rec* and woodland management *WM*) would have the opposite effect to hunting and increase diurnal (i.e., daytime) activity. Deer were more active in the day at sites where the intensity of *Rec*/*WM* was high. The shift towards increased diurnality suggests that deer habituate to human presence in areas of high non-lethal disturbance, which has been observed in other ungulate species, such as chamois (Courbin et al., 2022), reindeer (*Rangifer tarandus*, Hansen & Aanes, 2015) and red deer (Marion et al., 2022). Greater tolerance of human presence may be advantageous, where it allows deer to exploit foraging opportunities over a larger proportion of the diel cycle due to human presence reducing the perceived risk of predation (Frid & Dill, 2002; Tablado & Jenni, 2017).

The results did not support the hypothesis that cooccurring lethal and non-lethal disturbance would more strongly increase crepuscular and nocturnal activity than lethal disturbance alone (i.e., there was no evidence of an additive effect). Rather, the findings showed that deer only adjust their activity patterns at sites where there is non-lethal disturbance alone (i.e., high *Rec*/*WM* and not-hunted). In these areas deer are repeatedly exposed to consistently non-harmful human encounters, which facilitates learning and the accurate assessment of there being a low mortality risk (Blumstein, 2016; Hansen & Aanes, 2015; Rankin et al., 2009; Ueda et al., 2021). Where deer are not regularly exposed to any human presence (i.e., low *Rec*/*WM* and not-hunted), they maintain a strictly crepuscular mode of activity that is only marginally shifted towards increased nocturnality by hunting. The results are largely consistent with those from a study of diel migrations by chamois (Courbin et al., 2022), and provide further evidence that hunting inhibits habituation to non-lethal disturbance (Goumas et al., 2022; Smith et al., 2021).

Results from this study have several implications for conservation and wildlife management. The efficiency and efficacy of hunting as a method of population management may be reduced by temporal behavioural adaptation and its interaction with other site factors. Hunters may encounter individuals of target species less often as they learn when and where they are most likely to be shot (Bonnot et al., 2013; Drimaj et al., 2021; Martin et al., 2018). Furthermore, areas used by humans for recreation, where hunting is not permitted, are particularly problematic as they may act as spatiotemporal refuges (Lesmerises et al., 2017; Lewis et al., 2021; Shannon, Cordes, et al., 2014). Indeed, inconsistency in local-scale hunting can create and maintain source-sink population dynamics that reduce its long-term efficacy at the scale of the landscape or region (Putman, Watson, et al., 2011; Wäber et al., 2013). High densities of deer in refuges are more likely to place unsustainable levels of pressure on local environments, which is a major challenge for biodiversity conversation and the protection of sensitive woodland habitats (Amici et al., 2012; Dolman et al., 2010).

It is widely recognised that management of ungulate species should be adaptive and based on a continuous process of monitoring species and environmental responses to interventions (Apollonio et al., 2017; Carpio et al., 2021; Putman, Apollonio, et al., 2011). An understanding of temporal behavioural patterns may help to refine hunting practices. Adaptations to human presence are strongly dependent on the predictability of the outcomes of human encounters (Blumstein, 2016; Gaynor et al., 2019). The more predictable a source of disturbance is in space and time, the more likely that species will develop behaviours of tolerance or avoidance (Ueda et al., 2021). Therefore, practitioners should consider the effects of randomness when evaluating options for management interventions. For example, hunting at night or periodically hunting in novel areas may decrease the predictability of hunting risk and limit the emergence of avoidance behaviour (Gaynor et al., 2021; van Doormaal et al., 2015). Monitoring temporal behavioural responses to interventions should be considered an integral component of the adaptive management process that may be used to optimise strategies and inform decision-making. It is also worth noting that inconsistency in activity patterns could affect the precision and reliability of population monitoring. For example, census techniques such as point counts or distance sampling are often conducted at times of assumed activity peaks (e.g., surveying deer at dawn and dusk), which may yield misleading results if activity levels in these periods are not representative of other periods within the diel cycle (McCullough et al., 1994)

When interpreting the results from this study it is important to acknowledge the context of the study area and design, and potential sources of variation that were not accounted for. All of the cameras that captured images of fallow deer were deployed in woodlands, and so the results of the study are limited to this habitat type. Variation in the frequency of camera-trap detections is likely to be influenced by temporal patterns of habitat selection. For example, a low number of detections may be recorded during a period of the diel cycle due to inactivity (i.e., because individuals are stationary) or because a different habitat-type was being utilised (e.g., regularly-timed movements to open fields for grazing). The results may also have been influenced by human disturbance near to woodland sites that was not accounted for (e.g., farming activity). Future studies may look to build upon this research by observing behaviour and human activity in a wider range of habitat types and ecological contexts. Studies that utilise Global Positioning Systems (GPS) tracking technology would be particularly valuable and provide information on spatial behavioural responses and the use of alternative habitats. Furthermore, in the present study there was some evidence of biases in the positioning of cameras relative to anthropogenic covariates (see Chapter 3 for details of camera deployment, S9-S13). Hunted sites were more closely-located to other hunted sites and generally less evenly-distributed in relation to land ownership than recreation and woodland management (S9, S12 and S13). Additionally, the proportion of cameras positioned in high-recreation, hunted sites (0.19) was lower than low-recreation, hunted sites (0.33, S10) and a lower proportion of cameras were positioned in high-woodland management, not-hunted sites (0.14) than low-woodland management, not-hunted sites (0.34, S11). Sample sizes were generally large (minimum survey effort for a data subset was 1,682 camera days) and the bootstrapping method accounted for uneven sample sizes in the calculation of confidence limits for the activity overlap estimates (Ridout & Linkie, 2009). However, it is important these biases are recognised when interpreting the results for interactions between disturbance types. Closely-located cameras may yield data on the behaviour of site-faithful individuals or groups of individuals that is inconsistent with the entire population. Future studies should, therefore, ideally aim to position cameras evenly across covariate categories where logistically possible.

The characterisation of human activity in binary terms of hunted/not-hunted and high/low used in this study omitted considerable detail that may explain some of the variation in the results. For example, hunting can vary in frequency (number of site visits), timing, intensity (number of hunters), effort (time spent hunting) and mode (stationary, mobile, with or without dogs or human battues etc.), which is likely to modify the effect it has on wildlife activity (Bengsen et al., 2020; Ikeda et al., 2019; Smith et al., 2022). Researchers may look to collect more precise human activity data that will enable these effects to be formally assessed. Additionally, it would be useful to evaluate the consistency of results between sexes and different age groups. Independently assessing the activity patterns of males and females as well as different cohorts of individuals (e.g., juveniles or senescents), would reveal the magnitude of intraspecific variation in activity patterns and provide further insight into the mechanism of disturbance effects. Lastly, future studies may look to expand the scope of investigation to components of individual fitness, population viability or effects on the environment and other species. Research in this area would improve our understanding of the wider effects of human disturbance on species longevity, community composition and ecosystem functioning.

In conclusion, fallow deer exhibit clear patterns of activity distribution across the diel cycle, which are affected by lethal and non-lethal sources of human disturbance. Ungulate species drive critical ecological processes across large spatial scales. Human-induced alterations to their behaviour could have a range of trophic-mediated effects on the community and ecosystem as a whole (Frid & Dill, 2002; Wilson et al., 2020; Zanette & Clinchy, 2020). Predictable landscapes of risk are likely to promote adaptation to humans, which may facilitate coexistence with ungulate species, but potentially jeopardise efforts to mitigate their impacts on sensitive habitats (Gaynor et al., 2019; Smith et al., 2021). This study provides further evidence of anthropogenic influence on animal behaviour and demonstrates the importance of time as a fundamental component of the ecological niche. As human populations continue to Impact ecosystems more strongly a comprehensive understanding of the indirect effects of anthropogenic pressure on wildlife species is needed for effective conservation planning and the sustainable use of shared resources.

Chapter 5

Environmental, anthropogenic and temporal factors drive woodland habitat-use by fallow deer (*Dama dama*) in a human-dominated landscape

Introduction

Large herbivores play an important role in the functioning of terrestrial ecosystems, with their movement, foraging and trampling behaviour driving habitat structure (Li et al., 2022; van der Waal et al., 2011), nutrient cycling (Mohr et al., 2005; Riesch et al., 2022) and the dispersal of plant propagules (Pellerin et al., 2016; Picard et al., 2015). As these species are often highly mobile and wide-ranging, they can influence ecological processes across large spatial scales (Owen-Smith, 2014). Identifying factors that affect how large herbivores utilize space and resources over time is therefore critical to biodiversity conservation and natural resource management (Apollonio et al., 2017; Carpio et al., 2021; Tucker et al., 2018). Research on this topic has tended to focus on trends in species distributions and demography at the national or regional scale (e.g., Acevedo et al., 2010; Croft et al., 2019; Linnell et al., 2020; Morelle & Lejeune, 2015). Studies at the population level are less common and often conducted in designated zones such as individually owned estates, protected areas or national parks (e.g., Grignolio et al., 2011; Kamler et al., 2007; Zanni et al., 2021), where land-use and land ownership are relatively homogenous. Considerable knowledge gaps exist concerning the spatiotemporal behaviour of large herbivore species in fragmented human-dominated landscapes, where land is used for a range of purposes, such as agriculture, forestry, hunting, recreation and human infrastructure. Information on the mechanisms of large herbivore coexistence with humans in multi-use landscapes is needed to better inform conservation planning and wildlife management.

Many ungulate (Artiodactyla) species have increased in numbers and expanded their geographic ranges, particularly across Europe and North America (Croft et al., 2019; Linnell et al., 2020; McClure et al., 2015). For some species, population growth may be considered a conservation success. For instance, roe deer populations in the UK have recovered from being hunted nearly to extirpation in the eighteenth century (Andersen et al., 1998). However, in some areas, high ungulate densities are having a wide range of detrimental impacts. For example, there is evidence that red deer reduce agricultural crop yields (Corgatelli et al., 2019) and damage trees through sapling browsing (Renaud et al., 2003) and bark stripping (Jarnemo et al., 2022). High ungulate numbers also present a threat to human health through the increased risk of road traffic collisions) and as vectors of diseases, such as foot and mouth, bluetongue and bovine tuberculosis (Böhm et al., 2007). Expansion of ungulate populations in the northern hemisphere has coincided with rapid growth in the human population and economy, which has led to widespread changes in land-use, proliferation of infrastructure and increased species persecution (Linnell et al., 2020; Tucker et al., 2018; Waters et al., 2016). It has also been suggested that wild ungulates have benefitted from the removal of natural predators by humans and the intensification of agriculture, which has provided a year-round source of food and shelter (Carpio et al., 2021; Putman, Apollonio, et al., 2011). However, there remain intriguing questions as to how ungulate species have been, and continue to be, successful in ecosystems characterised by high human disturbance.

Hunting and vehicle collisions are considered to be the main causes of mortality for ungulate species in Europe (Hothorn et al., 2015; Valente et al., 2020). Additionally, humans may affect wildlife species via habitat destruction and the introduction of non-native species (Dirzo et al., 2014; Johnson et al., 2017; Ripple et al., 2015). Humans also induce fear in wildlife species, which can strongly influence individual behaviour (Ciuti, Northrup, et al., 2012; Colter Chitwood et al., 2022; Suraci et al., 2019; Zanette & Clinchy, 2020). Indeed, the landscape of fear (i.e., the distribution of predation risk across space and time) is a major driver of movement and space-use (Gaynor et al., 2019; Leblond et al., 2010; Tucker et al., 2018). To maximise fitness (e.g., survival and reproductive performance), individuals must acquire resources while minimising predation risk (Colter Chitwood et al., 2022). In human-dominated landscapes the trade-off between fear and resource acquisition is particularly acute, as perceived predation risk may be exceedingly high and habitats that provide shelter (e.g., woodlands) are typically less abundant and more fragmented (Eldegard et al., 2012; Maren et al., 2009; Wevers et al., 2020). The non-consumptive influence of humans on wildlife species may equal or exceed that of natural predators (Ciuti, Northrup, et al., 2012) and can have cascading effects on community structure, nutrient cycling and ecosystem functioning (Laundré et al., 2010; Suraci et al., 2019; Wilson et al., 2020).

Ungulates often respond to human disturbance by adjusting their space-use and activity to access resources in safer areas at times of low risk (Gaynor et al., 2018, 2019). For example, high human pressure has been associated with a shift in space-use away from disturbed areas in a range of ungulate species, including wild boar (Sus scrofa, Stillfried et al., 2017), moose (McLoughlin et al., 2011) and red deer (Lone et al., 2015). It is also common amongst wildlife species that activity becomes more concentrated in crepuscular and nocturnal periods, which reduces encounters with humans, who are generally more active during the day (Chapter 4, Gaynor et al., 2018). Although several studies have examined the spatial and temporal responses of ungulates in relation to human disturbance, few have considered other landscape variables, such as food availability, terrain and habitat distribution, which may modify responses. A recent study by Wevers et al. (2020) investigated the effects of forest cover, hunting and recreation on space-use by wild boar and roe deer in an urban protected area. Forest cover was identified as the most important driver of space-use in both species. Hunting only influenced wild boar and there were no effects of recreation (Wevers et al., 2020). The study highlights the variation in responses to disturbance between species and the relative importance of food versus fear in shaping spatial behaviour. Observations across a variety of ecological contexts are needed to identify specific traits of ungulates, such as body size, sociality, home-range size and dietary physiology that influence how ungulates resolve the trade-off between resource acquisition and safety.

Fallow deer (*Dama dama*) in the UK provide a good example of an ungulate species that has thrived in a human-dominated landscape. Between 1972 and 2002, numbers of fallow deer increased at a compound annual rate of approximately 1.8% (Ward, 2005) and their current range is estimated at 35% of the total land area of the country (Croft et al., 2019). The expansion of deer in the UK is a concern for biodiversity conservation and a major threat to national-scale strategies aiming to restore and create new native woodland (Climate Change Committee, 2020; Gill & Beardall, 2001; Gill & Morgan, 2010). Approximately 71% of the UK land area is used for agriculture and the landscape is a mosaic of patches under different ownership (Defra, 2022). The geographic range of fallow deer populations typically extend across multiple landowner boundaries, which increases the difficulty of management, as there is a requirement to balance the needs of a range of stakeholders including farmers, foresters, conservationists and countryside visitors (Apollonio et al., 2017; Putman, Apollonio, et al., 2011). Understanding how human disturbance and other landscape features influence the spatial behaviour of fallow deer is critical to efficiently achieve multiple management objectives. Although studies have been conducted to estimate the population expansion and spatial extent of suitable habitat for fallow deer at a national scale (e.g., Acevedo et al., 2010; Croft et al., 2019; Ward, 2005), information is lacking on their use of space and resources at the landscape scale.

In this chapter, camera-trap data were used to assess patterns of woodland habitat-use by fallow deer in the Elwy Valley region (105 km2) of North Wales, UK. The fallow deer population in this area descend from a captive herd that escaped enclosure approximately one hundred years ago. The area provides a rare opportunity to study a largely isolated ungulate population at a tractable landscape scale. Cameras were deployed continuously for two years at woodland sites embedded in a matrix of mostly pastoral farmland, interspersed with small human settlements.

The aim of the study was to assess the effects of environmental landscape features (tree cover, herbaceous vegetation cover and slope) and human disturbance (hunting, recreation and woodland management) on the probability and frequency of woodland habitat-use. It was hypothesised that habitat-use would be (1) primarily driven by environmental features, (2) positively related to tree and herbaceous vegetation cover, as these habitat types provide important sources of food and (3) negatively related to slope and human disturbance, as humans may be perceived as a predatory threat, and steeper terrain increases the energetic costs of movement. It was also hypothesised that (4) habitat-use would vary seasonally.

Methods

Camera-trap data

Data were collected from an array of 29 motion-activated camera-traps deployed according to a stratified sampling strategy in woodlands within the Elwy Valley study area. Cameras were deployed for two years from January 2019 to December 2020. Data were obtained from three 90-day sampling periods each year (i.e., a total of six ‘survey seasons’), which corresponded to key stages of the fallow deer reproductive cycle (‘biological seasons’), hereafter: rut (September-November), post-rut (January-March) and birthing (May-July). Year (YEAR:

2019/2020) and biological season (BIOSEASON: rut/post-rut/birthing) were considered as temporal covariates in models. For purposes of independence, data were filtered to only include camera images taken at least 10 minutes apart (Meek et al., 2014). A minimum distance of 250 m between cameras was used to ensure sampling of an appropriate range of environmental conditions. Sites were not assumed to be spatially independent, as fallow deer are a highly mobile species and it is likely that individuals could move between multiple sites within a survey season. In this study, spatial independence between sites was not necessary, as the focus was on relative 'use' of habitat, rather than estimation of species presence/absence or abundance (Burton et al., 2015; MacKenzie et al., 2017). Additionally, 'sites' were assumed to be the detection zone directly in front of each camera, rather than some larger area defined by camera spacing (Efford & Dawson, 2012; Kays et al., 2020). For full details on the study area, deployment of cameras and data collection process see Chapter 3, S6 and S7.

Landscape covariates

Environmental data

Land cover data were obtained from the Sentinel-2 Global Land Cover (S2GLC) project at a spatial resolution of 10 m x 10 m (Malinowski et al., 2020). Two covariates, based on S2GLC thematic classes, were included in analyses: cover (proportion of total area, 0-1) of herbaceous vegetation (HERB) and trees (TREE). An additional covariate for land slope angle (SLOPE) was derived from an OS digital terrain map of surface elevation (Ordnance Survey, 2017). Slope was calculated at the same 10 m spatial resolution as the land cover data, as the maximum rate of change in elevation between neighbouring raster cells using the 'Slope' tool in ArcGIS. Units of slope were given as a percentage (rise/run*100). For more information on the collection and processing of environmental data see Chapter 3.

The observed responses of organisms to the environment may depend on the spatial scale at which landscape features are measured (Boscolo & Metzger, 2009; Nagy-Reis et al., 2017). To account for this, a multiscale approach was adopted. Three scales were defined by circular buffer regions of 100 m, 250 m and 500 m radii, centred on the camera sites. Buffer regions may be regarded as site (i.e., immediate vicinity), local (i.e., whole woodland or managed area) and landscape (i.e., multiple habitat patches) scales. The proportion of area represented by the two land cover covariates (HERB and TREE) as well as mean slope was calculated for each spatial scale (i.e., HERB_100, HERB_250 etc.). All environmental covariates were standardised using z-score scaling and no collinear covariates were used in the same model sets (S15-S18).

Anthropogenic data

Human activity data were obtained via questionnaire surveys given to landowners and land managers of woodland units where cameras were deployed. Information was gathered on three types of anthropogenic covariates: hunting (HUNT: hunted/not-hunted), recreation (REC: high/low) and woodland management (WM: high/low, see Chapter 3, S6 and S7). Hunting was a site-specific covariate (i.e., each site was either hunted or not-hunted). Recreation and woodland management were, however, site- and season-specific (i.e., values could vary between sites and survey seasons).

Probability of habitat-use (Occupancy)

The occupancy parameter of a multi-season occupancy model (Mackenzie et al., 2002; MacKenzie et al., 2017) was used to quantify probability of habitat-use by fallow deer. Camera-trap data were summarised as daily detection histories (detected/not-detected) for each site and survey season (site-season, hereafter). The technique uses logistic regression and maximum-likelihood estimation for occupancy (ψ), while accounting for imperfect detection (Mackenzie et al., 2002; MacKenzie et al., 2017). Occupancy models were developed using the 'RPresence' package, which implements the software PRESENCE (available from http://www.mbr-pwrc.usgs.gov/software/presence.shtml) in R (R Core Development Team, 2019). Colonisation and extinction rates were held constant (similar to Nagy-Reis et al., 2017), as variation in site-level presence of the species was assumed to be nominal over the study duration as there were no major changes in the rate of hunting activity. The purpose of the study was to investigate sources of variation in occupancy. Variation in detection probability (p) was not of central interest and preliminary analyses showed that it was poorly explained by any of the landscape covariates considered (S19). Therefore, for stages 1 and 2 (see 'Modelling habitat-use' section), detection probability was either held constant or allowed to vary by the same covariate(s) used to model occupancy. In stage 3, a general model (i.e., one that included as many covariates as possible) was used, so that any variance in the data due to heterogeneity in detection probability was accounted for as well as possible, and not erroneously attributed to variation in occupancy (MacKenzie et al., 2017, S19).

Frequency of habitat-use (Detection rate)

The frequency of habitat-use was defined by camera detection rate, which was calculated as the total count of independent detections of the species divided by the number of operational camera days (i.e., number of detections/day) for each site-season. Site-seasons that were not surveyed (n = 7) as well as data for sites where no detections were recorded over the study duration (n = 2) were removed. A total of 161 site-seasons were used for the detection rate analysis. Zero-inflated negative binomial regression models were fitted using the 'glmmTMB' package (Brooks et al., 2017, see S20 for details on selection of model structure) in R. The number of independent detections was used as the response variable and the natural log of the number of camera days was included as an offset term. To account for unmodeled variation in animal activity and local abundance between sites, site identification was also included as a random effect (1|SITE) and unique intercepts were estimated for each site (Hansen et al., 2020; Kays et al., 2020).

Modelling habitat-use

A three-stage approach to model development was used for the occupancy and detection rate analyses: (1) evaluate the importance of temporal covariates (YEAR and BIOSEASON), (2) assess the appropriate scale for each environmental covariate (HERB, TREE and SLOPE) and (3) identify the environmental and anthropogenic covariates (HUNT, REC and WM) that best explain variation in each response variable. Covariates were combined using additive terms (+) only. At all stages, models were compared and ranked using the corrected Akaike Information Criterion (AICc, Burnham & Anderson, 2004).

Stage 1 – Temporal covariates

Occupancy and detection rates were either held constant (i.e., no covariate was used) or were modelled using a single temporal covariate. The covariates that featured in the highest-ranked models were included in all models in the following stages.

Stage 2 – Spatial scale of responses

Separate model sets were constructed for each environmental covariate and response variable. Occupancy and detection rate were held constant or allowed to vary by the focal landscape covariate, measured at the various scales of the buffer regions (100 m, 250 m and 500 m) around each site. The covariates that featured in the highest-ranked model from each set for each response variable were used to build candidate models in stage 3.

Stage 3 – Covariate importance

A set of 42 *a priori* candidate models was constructed for each response variable. Each model represented a biologically plausible hypothesis regarding occupancy or detection rate and consisted of single-, two- and three-factor combinations of environmental and/or anthropogenic covariates in addition to the highest-ranked temporal covariate(s) from stage 1. The model sets were balanced (i.e., all covariates were present in the same number of models), and variable importance was determined by summing the Akaike weights (w_i) of models in which each covariate was present. The direction and magnitude of the effects of covariates was determined by observing the regression coefficients (β) and associated 95% confidence intervals (CIs) from the top-ranked model(s) (w_i > 0.05) within each model set (Burnham & Anderson, 2004).

Finally, model-averaging was used to predict the relationship between each response variable and landscape covariate from the top-ranked model(s), while accounting for model uncertainty. Predictions were made using the ‘RPresence’ and ‘MuMIn’ (Kamil Barton, 2022) packages in R for occupancy and detection rate, respectively. The approach estimates a weighted average for occupancy or detection rate from each model rather than by calculating model-averaged regression coefficients, which is considered preferable as it ensures consistent interpretation of the parameters being averaged across models (Allen et al., 2015; MacKenzie et al., 2017). Plotting model-averaged response variables against each covariate required specifying values for the other covariates that featured in the top-ranked model(s). Following (Allen et al., (2015), the median value and conditions of ‘not-hunted’ and ‘low recreation/woodland management’ were used for environmental and anthropogenic covariates, respectively. For detection rate, random effects were not included in model predictions, and it was assumed that site-seasons were surveyed for 90 days.

Assessing model fit

For the occupancy analyses, model fit was evaluated following the approach introduced by Mackenzie and Bailey (2004) using the 'RPresence' package in R. A global model was fitted to the observed data, which included the covariates featured in the highest-ranked models from stages 1 and 2 as well as the anthropogenic covariates for each parameter (occupancy and detection probability). The Pearson's chi squared statistic was calculated, which compared the number of observed sites with a given detection history to the expected number based on the fitted model (Mackenzie & Bailey, 2004). This procedure was repeated 10,000 times to estimate the probability of observing a test statistic from the bootstrapped data set that was ≥ the test statistic for the fitted model (values closer to 1 indicated better model fit). An overdispersion parameter $\hat{c}$ was also estimated by dividing the observed test statistic by the average of the test statistics obtained from the parametric bootstrap.

For the detection rate analyses, model fit was evaluated from a model built using covariates that featured in the top-ranked model from stage 3 for which 95% CIs did not overlap zero. Fit was assessed by visual inspection of model residuals as well as a check of dispersion using the 'DHARMa' package in R (Hartig, 2022, for results of model fit assessments see S21-S23).

Results

For information on sampling effort and the number of independent detections recorded in relation to model covariates see S8.

Modelling habitat-use

Stage 1 – Temporal covariates

For occupancy, none of the models featuring temporal covariates had greater support than a dot model (i.e., no covariate, AICc weight (w) = 0.60, Table 1), which suggests that the probability of habitat-use was constant throughout the study duration. In contrast, results from the detection rate models showed strong support for an effect of biological season ('bioseason', w=1.00, Table 1), and that covariate was therefore used in the following stages.

Stage 2 – Spatial scale of responses

The spatial scale of the strongest response for tree and herbaceous vegetation cover was larger for occupancy (tree cover = 500 m: w = 0.85, herbaceous vegetation cover = 500 m: w = 0.29) than for detection rate (tree cover = 100 m: w = 0.43, herbaceous vegetation cover = 250 m: w = 0.52, Table 1). However, both response variables responded most strongly to slope at the 250 m scale (occupancy: w = 0.46, detection rate: w = 0.46, Table 1).

Table 1. AICc weights (w) of the highest-ranked models for covariates from stages 1 and 2 of the occupancy (ψ) and detection rate (*DR*) analyses for fallow deer in the Elwy Valley study area. (.) = no covariate (see Methods section for details of analyses and covariate definitions). Bold numbers indicate covariates retained for model building in stage 3.

			w	
Covariate type	**Covariate**	**Buffer radii (m)**	ψ	***DR***
Temporal (Stage 1)	(.)	-	**0.60**	0.00
	Bioseason	-	0.19	**1.00**
	Year	-	0.21	0.00
Environmental (Stage 2)	Tree cover	100	0.00	**0.43**
		250	0.15	0.28
		500	**0.85**	0.29
	Herbaceous vegetation cover	250	0.18	**0.52**
		500	**0.29**	0.48
	Slope	100	0.07	0.15
		250	**0.46**	**0.46**
		500	0.31	0.39

Note: Herbaceous vegetation cover with a buffer radius of 100 m was removed due to collinearity, S15.

Stage 3 – Covariate importance

From the set of 42 *a priori* candidate models evaluated for each response variable the importance of covariates was estimated based on the sum of weights ($\sum w_i$) from models that included each covariate. The ranking of covariates by importance was consistent for occupancy (ψ) and detection rate (*DR*; Table 2). For both response variables, strong support was found for the importance of slope (Table 2). Recreation was identified as the most important anthropogenic covariate and there was considerably less evidence supporting the importance of hunting, herbaceous vegetation cover (and woodland management (Table2).

Two and four models accounted for 93% and 75% of model weights in the occupancy and detection rate model sets, respectively (Table 2). The highest-ranked models for occupancy (w=0.77) and detection rate (w=0.44) both included tree cover, slope and recreation (Table 3). Hunting also appeared in the top-ranked models for both response variables, whereas woodland management featured in the model for detection rate only (Table 3). Averaging of top-ranked models was used to predict the relationship between occupancy or detection rate and each covariate (Figures 1 and 2). Daily detection rate was predicted to be highest during birthing (0.96 $\pm$ 0.24 SE), intermediate in the rut (0.72 $\pm$ 0.17) and lowest in the post-rut period (0.31 $\pm$ 0.08, Figure 2a). Predicted occupancy and detection rate increased with tree cover (Table 3, Figures 1a and 2b) and decreased with slope (Table 3, Figures 1b and 2c). The direction of responses to recreation differed between response variables. Compared to low-recreation conditions, occupancy was predicted to be higher (high = 0.98 $\pm$ 0.01 SE, low = 0.92 $\pm$ 0.04) and detection rate was predicted to be lower when recreation was high (high = 0.71 $\pm$ 0.22, low = 0.96 $\pm$ 0.24, Table 3, Figures 1c and 2d). Relative to the size of effects, there was considerable uncertainty associated with predictions in relation to hunting and woodland management (Figures 1d and 2e-2f). Occupancy and detection rate were not predicted to be different between hunted and not-hunted sites (occupancy: hunted = 0.91 $\pm$ 0.04, not-hunted = 0.92 $\pm$ 0.04, detection rate: hunted = 0.89 $\pm$ 0.25, not-hunted = 0.96 $\pm$ 0.24, Figures 2d and 2e). Detection rate was also predicted to be similar between high and low woodland management sites (high = 0.95 $\pm$ 0.24, low = 0.96 $\pm$ 0.24, Figure 2f).

Table 2. Summed Akaike weights ($\sum w_i$) from the sets of 42 candidate models used in stage 3 of the analyses of occupancy (ψ) and detection rate (*DR*) for fallow deer in the Elwy Valley study area. *measured at the scale of strongest response (see 'Results, Stage 2 – Spatial scale of responses').

	$\sum w_i$	
Covariate	ψ	*DR*
Slope*	1.00	0.95
Tree cover*	1.00	0.81
Recreation	0.77	0.61
Hunting	0.16	0.17
Herbaceous cover*	0.02	0.11
Woodland management	0.01	0.10

Table 3. Top-ranked ($w_i > 0.05$) models from stage 3 of the occupancy (ψ) and detection rate (DR) analyses for fallow deer in the Elwy Valley study area, including regression coefficients ($\boldsymbol{\beta}$) in bold with upper/lower 95% confidence intervals (CI). Model = environmental and anthropogenic covariates used. ΔAICc = relative difference in Akaike Information Criterion. K = number of model parameters. w = AIC model weight (see 'Methods' section for details of analyses and covariate definitions).

				$\boldsymbol{\beta}$ (95% CI)				
Model	ΔAICc	K	w	Tree cover*	Slope*	Recreation	Hunting	Woodland management
Occupancy ($\boldsymbol{\psi}$)								
Tree cover* + Slope* + Recreation	0	13	0.77	**2.66** (1.51/3.81)	**-1.39** (-2.02/-0.75)	**1.79** (0.42/3.15)	-	-
Tree cover* + Slope* + Hunting	3.18	13	0.16	**2.30** (1.29/3.31)	**-1.00** (-1.57/-0.43)	-	**-1.31** (-2.52/-0.10)	-
Detection rate (*DR*)								
Tree cover* + Slope* + Recreation	0	9	0.44	**0.55** (0.17/0.92)	**-0.75** (-1.15/-0.35)	**-0.50** (-0.96/-0.05)	-	-
Tree cover* + Slope*	2.52	8	0.13	**0.56** (0.19/0.93)	**-0.75** (-1.14/-0.36)	-	-	-
Tree cover* + Slope* + Hunting	2.69	9	0.12	**0.58** (0.22/0.94)	**-0.77** (-1.15/-0.39)	-	**-0.48** (-1.12/0.17)	-
Tree cover* + Slope* + Woodland management	3.97	9	0.06	**0.55** (0.18/0.92)	**-0.74** (-1.13/-0.35)	-	-	**-0.16** (-0.53/0.20)

*measured at the scale of strongest response (see 'Results, Stage 2 – Spatial scale of responses').

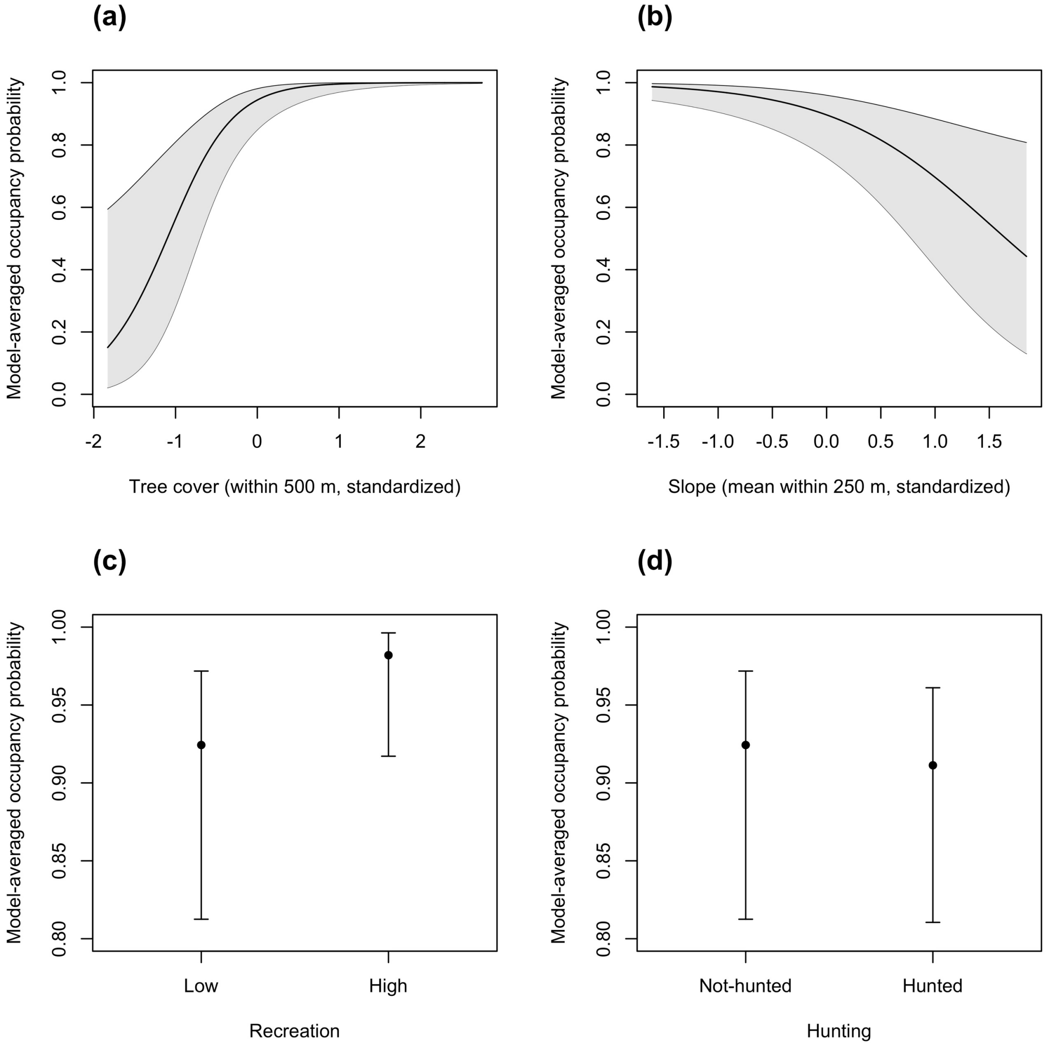


Figure 1. Model-averaged predictions of fallow deer occupancy at woodland sites in the Elwy Valley study area in relation to (a) tree cover within a 500 m radius, (b) slope within a 250 m radius, (c) recreation and (d) hunting. Shaded areas and error bars represent 95% confidence intervals.

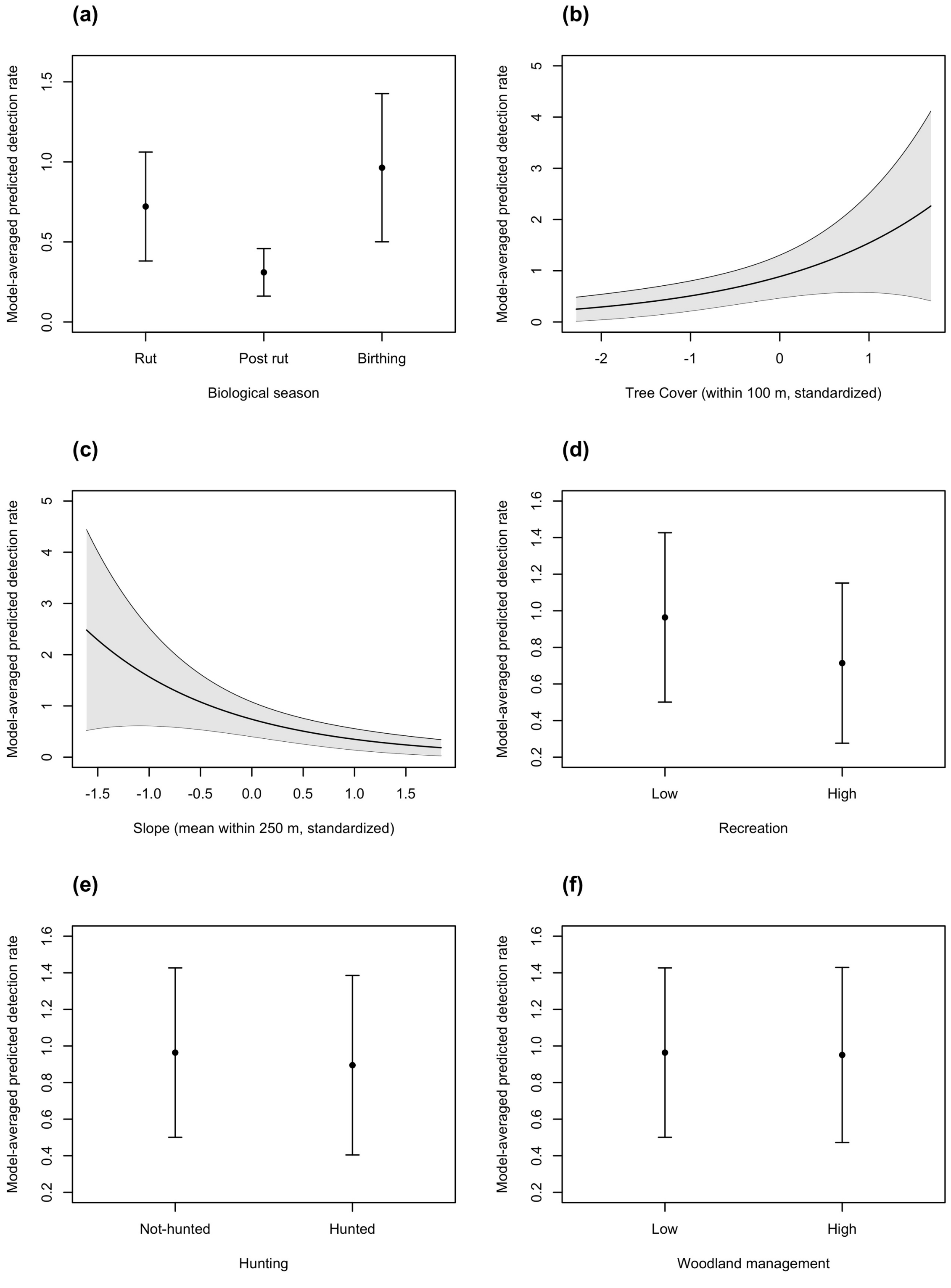


Figure 2. Model-averaged predictions of the daily detection rate of fallow deer at woodland sites in the Elwy Valley study area in relation to (a) biological season, (b) tree cover within a 100 m radius, (c) slope within a 250 m radius, (d) recreation, (e) hunting and (f) woodland management. Shaded areas and error bars represent 95% confidence intervals.

Discussion

This study examined the effects of landscape characteristics and human disturbance on habitat-use by a large, highly-mobile herbivore in a multi-use, rural landscape. The influence of temporal, environmental and anthropogenic covariates on patterns of woodland habitat-use by fallow deer was assessed using a large camera-trap data set collected in the Elwy Valley region of North Wales, UK. The results reveal how individuals of a wide-ranging ungulate species resolve trade-offs between resource acquisition and exposure to disturbance in a highly-transformed landscape.

The results strongly supported the hypothesis that environmental covariates (tree cover, herbaceous vegetation cover and slope) would have a stronger effect on the probability (occupancy) and frequency (detection rate) of habitat-use by fallow deer than anthropogenic covariates (recreation, hunting and woodland management). The findings suggest that habitat-use is primarily driven by selection for favourable environmental features, rather than avoidance of disturbance. Previous studies have yielded similar results for roe deer (Dupke et al., 2017; Wevers et al., 2020), wild boar (Stillfried et al., 2017) and elk (Rowland et al., 2018).

Tree cover and slope were identified as the most important drivers of habitat-use, followed by recreation. Consistent with our hypotheses, occupancy and detection rate increased with tree cover and decreased with slope. Woodlands are an important source of food for many deer species (Esattore et al., 2022; Spitzer et al., 2020) and they provide the additional benefit of shelter from predators and unfavourable weather conditions (Kjellander et al., 2012; Thirgood, 1995). Although hunting mostly occurs within woodlands, the perception of predation risk is likely to be lower where trees and understory vegetation provide cover (Borkowski et al., 2016; Jepsen & Topping, 2004). Furthermore, flatter terrain was most likely preferred as it reduces the energetic costs of movement (Monteith et al., 2018; Newmark & Rickart, 2012). The results showed that occupancy was temporally constant, which is consistent with previous studies that observed a high level of site-fidelity by fallow deer (e.g., Apollonio et al., 2003; Morse et al., 2009). Detection rate varied seasonally and was highest during birthing (May-July), intermediate in the rut (September-November) and lowest in the post-rut period (January-March). Seasonal patterns in detection rate are most likely due to variation in animal activity driven by the reproductive cycle, forage availability and weather conditions (Csányi et al., 2022; Krop-Benesch et al., 2013; Thurfjell et al., 2014). For example, group sizes typically increase during the rut, which may lead to a greater rate of detection (Apollonio, 1989; Parsons et al., 2017).

The hypothesis that human disturbance would negatively affect habitat-use was not supported by the results of this study. Indeed, a small positive effect was observed for occupancy where human recreation was higher. This result may be evidence of habituation to non-lethal human interactions (Blumstein, 2016; Rankin et al., 2009). Habituation to recreation has been observed in several ungulate species, including fallow deer (Recarte et al., 1998), red deer (Marion et al., 2022) and Svalbard reindeer (*R.t. platyrhynchus* Hansen & Aanes, 2015). It has been suggested that human-populated areas may be preferred because they offer shelter from disturbance-sensitive predators (Rebolo-Ifrán et al., 2017; Shannon, Cordes, et al., 2014). As there are no natural predators of fallow deer in the study area, recreation most likely acts by lowering the perceived risk of habitat-use, rather than decreasing actual predation. In contrast to occupancy, recreation had a weak negative effect on detection rate. However, there was a high level of uncertainty associated with predictions and the slight decrease observed may be confounded by density-dependent effects on movement rates (Broadley et al., 2019; Burton et al., 2015). This result may also be due to the positioning of cameras relative to pathways within the woodland. To avoid thefts, cameras were generally placed away from pathways that showed signs of being used by humans. Detection rate may be lower in these areas also prefer to use such pathways, perhaps because they offer less resistance to movement (Zeller et al., 2012).

Although hunting appeared in the top performing models for occupancy and detection rate, the overall weight of evidence supporting its importance was low. Model-averaged predictions showed that hunting had little effect on either response variable and the uncertainty associated with the predictions was high. Hunting can affect wildlife species directly, by removing individuals from the population and indirectly, by creating a ‘landscape of fear’ (Colter Chitwood et al., 2022; Cromsigt et al., 2013; Suraci et al., 2019). The lack of a strong response to hunting may be due to several factors associated with its application. Within the Elwy Valley study area, hunting effort was generally low and spatially uneven. Limited coordination of hunting at the landscape scale can create dynamics of population sources (not-hunted sites) and sinks (hunted sites), that mitigate its effect on abundance and habitat-use at the site scale (Carpio et al., 2021; Fattorini et al., 2020; Redick & Jacobs, 2020; Wäber et al., 2013). Additionally, hunting occurred on the ground without the assistance dogs, human battues or aerial vehicles, and may therefore not have provided a sufficiently strong stimulus to influence patterns of habitat-use by eliciting fear (Cromsigt et al., 2013; Gaynor et al., 2019). However, it is also important to note that the effects of hunting were assessed in this study only at the site scale, and it is unclear what effects, if any, hunting had on habitat-use at the landscape scale (i.e., the occupancy and detection rate for all sites).

The results of this study have important implications for biodiversity conservation and wildlife management. Large-scale tree planting has been widely implemented globally, with a recent further incentive of sequestering atmospheric carbon to mitigate the impacts of global climate change (Bastin et al., 2019; Cook-Patton et al., 2020). In the UK, it is estimated that trees need to be planted at a rate of 30,000 ha per year to contribute to the national commitment of net-zero carbon emissions by 2050 (Climate Change Committee, 2020). Herbivory and bark-stripping by deer can severely impede the successful establishment and growth of trees (Cukor et al., 2019; Laurent et al., 2017; VanderMolen & Webster, 2021; Vuorinen et al., 2020). The strong positive relationship observed between tree cover and fallow deer habitat-use in this study suggests that tree planting is likely to benefit deer populations in these kinds of mosaic landscapes and may exacerbate their impacts on sensitive woodlands. Indeed, a recent study by Spake et al. (2020) showed that deer impacts in the UK were positively correlated with tree cover, which was measured at the same spatial scale (500 m) used for the analysis of occupancy in this study. Therefore, it is strongly recommended that plans to significantly increase tree cover in a given landscape are accompanied by a greater investment in deer population management.

Hunting is the most widely used method to mitigate the negative impacts caused by ungulate species across the northern hemisphere (Apollonio et al., 2010; Valente et al., 2020). However, there is limited evidence supporting its efficacy or efficiency (Fattorini et al., 2020; Redick & Jacobs, 2020; Simard et al., 2013). In the landscape of this study, hunting was inconsistently executed, and the results showed that it was ineffective at reducing the use of woodland resources by deer at the site scale. It is important to note that, typical of many regions of the UK, hunting in the study area was almost exclusively performed by recreational hunters, rather than paid professionals. A recent review by Bengsen et al. (2020) reported that recreational hunters of mammals achieved their stated management targets in only 30% (n=19) of the cases they examined, compared with 72% (n=46) for government agency hunters or commercial contractors. When evaluating the efficacy of hunting as a management tool it is important to acknowledge that many factors may affect species responses, such as hunting effort, timing and mode of application (e.g., ground-based, aerial, driven etc., Barton et al., 2022; Bengsen et al., 2020; Iijima, 2017).

Population control can be challenging to implement, and it may take a long time to significantly reduce deer numbers at the scale of the landscape or region (Apollonio et al., 2017; Redick & Jacobs, 2020; Simard et al., 2013). Non-lethal interventions, such as fencing and deterrents, may provide more effective protection from deer-related impacts until populations are restricted to sustainable densities (Redick & Jacobs, 2020). At sites where human recreation is high, such as urban areas and public parks, hunting is often not permitted by law or local landowners. The positive relationship between recreation and deer occupancy (habitat-use) in this study suggest that woods with high recreation pressure may provide important refuges that are likely counter act measures used to control population growth. This result further emphasises the need to develop and evaluate non-lethal interventions that can support long-term landscape-scale strategies for impact mitigation.

When interpreting the results, it is important to highlight sources of variation in habitat-use that were not accounted for. In this study, the effects of site variables were assessed across the whole population of fallow deer. Future studies may expand on this research by exploring how habitat-use varies between sexes and age classes. Additionally, the focus of the study was restricted to woodland sites. Observing behaviour across a broader range of habitats would provide more comprehensive information on the habitat preferences of fallow deer and how they vary temporally. Movement data collected via global positioning systems (GPS) tracking could be utilised to explore the underlying behavioural mechanisms of responses to landscape variables across spatial scales as well as the effects of inter- and intra-specific interactions (Kays et al., 2015). An interesting avenue of research is the interaction between deer and domestic livestock. A study by Weiss et al. (2022) showed that red deer were displaced by sheep and goats, which suggests that livestock distribution and density may be additional factors to consider in future studies of deer habitat-use. Furthermore, quantifying the spatiotemporal overlap of space-use between wild deer populations and livestock would provide valuable information for estimating the transmission risk of infectious diseases, such as foot and mouth disease, bluetongue disease and bovine tuberculosis (Böhm et al., 2007; Lavelle et al., 2014; Proffitt et al., 2011).

Heterogeneity in detectability between survey sites can cause estimates derived from camera-trap surveys to be biased and inaccurate (Mackenzie et al., 2002; Nichols et al., 2008). Hence, it was accounted for in this study by using an occupancy model, which explicitly models a detectability parameter, and by including ‘site’ as a random effect in the detection rate models. However, although accounted for, detection probability itself was not well explained by any the landscape covariates considered. It is likely that detectability was influenced more by finer-scale features, such as woodland structure, understorey density, fencing and the position of cameras relative to man-made pathways (Allen et al., 2015; Wäber & Dolman, 2015). Formally identifying the drivers of detectability may improve the robustness of study designs for camera-trap surveys as well as census techniques, such as track and dung counts (Forsyth et al., 2022).

In conclusion, exceptional growth in the global human population and increased consumption of resources in developed regions over the past century has placed unprecedented pressure on ecosystems. Many ungulate species have exhibited a remarkable capacity to adjust their behaviour in response to rapid changes in land-use, community composition and anthropogenic development. Although population expansion of wild ungulate species may be considered a conservation success, it is also creating contributing to unsustainable demand for important natural resources (Linnell et al., 2020). In this study, patterns of habitat-use by fallow deer were analysed to assess the spatiotemporal trade-offs between food acquisition, energetic costs of movement and exposure to human disturbance. Results showed that habitat-use was primarily driven by tree cover, terrain steepness, human recreation and seasonality related to their reproductive cycle. The study provides important information to support the sustainable management of ungulate populations and offers insights into the ecological processes responsible for the success of many species in the Anthropocene.

Chapter 6

Covariates affect the efficiency of reliably estimating occupancy from camera-trap surveys

Introduction

Monitoring the location of species or groups within species and tracking their activity over time is a fundamental component of biodiversity conservation and ecological research (Burton et al., 2015; Kays et al., 2015). It provides essential information for assessing the local extinction risk of vulnerable species, understanding human-wildlife conflicts and forecasting the effects of global climate change on wildlife populations (Dirzo et al., 2014; Johnson et al., 2017). Collecting data on the behaviour and space-use of wide-ranging terrestrial animals can be logistically challenging, particularly for rare or cryptic species, and may require investment of sizeable financial and human resources (Festa-Bianchet et al., 2017; Lindenmayer & Likens, 2010). Motion-activated digital cameras are one of several technologies, including Global Positioning System (GPS) devices and satellite imagery, that have advanced rapidly in recent years and provided new opportunities for scientists to monitor populations remotely over large geographic areas (Pimm et al., 2015).

Camera-traps offer advantages over traditional monitoring techniques (e.g., direct counts, track surveys etc.) as the data collection process is largely non-invasive and requires minimal surveyor effort (Blount et al., 2021; Trolliet et al., 2014). Additionally, the widespread use of camera-traps for recreation (e.g., sport hunting and wildlife observation) has made them increasingly affordable and equipped with improved features (e.g., image resolution, battery life, storage capacity etc.), further promoting their use in wildlife research (Burton et al., 2015; Delisle et al., 2021). Camera-traps have been used to investigate a wide range of biological questions relating to population density (Parsons et al., 2017; Rowcliffe et al., 2008) and species interactions (Gorczynski et al., 2022), as well as temporal activity (Frey et al., 2017; Lazzeri et al., 2022) and population dynamics (Kasada et al., 2022; Trolliet et al., 2014). As is the case for other survey techniques, the reliability and utility of camera-trap surveys in wildlife research depends on robust and appropriate study design. It is critical that plans for analyses are considered in the initial study design to ensure surveys collect data of a sufficient type and quality to achieve study objectives (MacKenzie et al., 2017).

Occupancy modelling is one of the most widely used frameworks for analysing camera-trap data (Burton et al., 2015; O'Connell et al., 2011). The method is based on the premise that the probability of capturing an image of the target species at a site is determined by two factors: (1) the occupancy status of the species (i.e., present/absent) and (2) the probability of detecting the species if it is present (Mackenzie et al., 2002; MacKenzie et al., 2017). Often, the probability of detection is less than one, which may bias occupancy estimates if not explicitly accounted for. Occupancy models address this issue by calculating detection probability from repeated surveys of multiple sites and including this information in the occupancy estimate (Mackenzie et al., 2002; MacKenzie et al., 2017).

One of the key benefits of the occupancy framework is the potential to model occupancy and detectability as a function of site-specific covariates (e.g., habitat type, patch size, forage quality, Bailey et al., 2007; Mackenzie et al., 2002). Incorporating covariate information will generally improve the biological realism of estimates as the assumption of equal occupancy and detectability across sites is unlikely to be reasonable (Lahoz-Monfort et al., 2014; MacKenzie et al., 2017). Furthermore, quantifying how the probabilities of occupancy and detectability vary in relation to site characteristics is often the primary focus of studies. For example, occupancy-covariate relationships have been investigated to explore predator-prey interactions (Widodo et al., 2022), habitat-use (Lamichhane et al., 2020, Chapter 5), anthropogenic disturbance (Li et al., 2022) and population viability (Farr et al., 2022). These studies provide useful information to support decision-making in conservation and wildlife management and enable practitioners to direct their efforts towards landscape features identified as being important to the species or suite of species of interest (Bailey et al., 2014; Noon et al., 2012).

Many assessments of the design of camera-trap surveys for occupancy studies have been conducted, including studies based on simulated (e.g., Bailey et al., 2007; Guillera-Arroita et al., 2010; Mackenzie & Royle, 2005; Pacifici et al., 2012) and real-world, empirical data (e.g., Chatterjee et al., 2021; Gálvez et al., 2016; Kays et al., 2020; O'Connor et al., 2017;

Reich, 2020; Shannon et al., 2014). A consistent finding across these evaluations is that increasing survey effort (i.e., number of camera sites and number of survey days) increases the accuracy and precision (i.e., reduces error) associated with occupancy estimates. However, the implementation of camera-trap surveys is often constrained by logistical issues, such as equipment costs, personnel requirements for camera maintenance, site access restrictions and data storage. Finite resources create trade-offs between efficiency and efficacy that need to be considered when designing studies in order to set objectives that are achievable within the constraints of available time and funding (Gálvez et al., 2016; Kays et al., 2020; Shannon, Lewis, et al., 2014).

Evaluations of the relative importance of survey design components on the reliability and inference of estimates are essential to inform fundamental decisions about how many cameras to use as well as where and when to deploy them. . Indeed, studies have shown that optimal survey strategies may depend on biological characteristics of the target species. For rare species that are easy to detect, error is most efficiently reduced by increasing the number of camera sites. For species that are difficult to detect but spatially common, however, error may be minimised more effectively by increasing the number of survey days (Chatterjee et al., 2021; Kays et al., 2020; Mackenzie & Royle, 2005; Shannon, Lewis, et al., 2014). Studies on survey optimisation provide practitioners, who may lack expertise in statistical modelling or study design, with useful guidance on the relative costs and benefits of different strategies of effort allocation (Gálvez et al., 2016; Kays et al., 2020; Shannon, Lewis, et al., 2014). However, the assessments to date have generally assumed that the probabilities of occupancy and detection are constant across sites (i.e., no covariates were used in the analyses). Therefore, there remains a lack of understanding of how covariates affect the relationship between survey effort and estimation error, despite their widespread use and importance as a fundamental component of the occupancy modelling framework.

A study by Kays et al. (2020) hypothesised that adding covariates would allow more precise occupancy estimates to be made with fewer cameras. An alternative hypothesis was suggested by Gálvez et al. (2016), that with the inclusion of covariates, more camera sites would be needed to provide a better representation of the landscape. Testing these hypotheses with empirical data is challenging, as there may be differences in a wide-ranging of conditions (e.g., habitat, weather, elevation etc.) between sites and their effects are likely to vary across taxa (Chatterjee et al., 2021; Kays et al., 2020; Mackenzie & Royle, 2005). Studies based on computer simulations may be better-suited to explore the effects of covariates on survey design trade-offs, as properties of the covariate (e.g., spatial extent) can be manipulated to facilitate the investigation (Lotterhos et al., 2022). Although simulation tools are available to explore study design (GENPRES: Bailey et al., 2007; SODA: Guillera-Arroita et al., 2010), the functionality of these programs is currently limited to comparisons of occupancy between predefined groups of sites (i.e., to investigate the effect of a categorical covariate only). Also, there is a need to expand the current range of study design assessments (e.g., Chatterjee et al., 2021; Kays et al., 2020; Shannon et al., 2014) to support practitioners, who may lack the statistical expertise to use and interpret results from existing tools.

The aim of this study was to examine the effects of covariates on the accuracy and precision (i.e., error) of occupancy models in relation to survey effort. Detection histories of a 'virtual' species were simulated as a function of a randomly generated, site-specific covariate that affected both occupancy and detectability. Occupancy models were then used to investigate how varying the number of survey days, number of camera sites, and proportion of sites that provide a sample of the covariate influences parameter error with and without the inclusion of covariate information. It was hypothesised that (1) for the same level of survey effort, less error would be associated with estimates based on models with covariates (i.e., covariate models), rather than without (i.e., dot models), (2) covariate models would require less survey effort to achieve a level of error below a target threshold and (3) including the covariate would reduce the sensitivity of estimates to variation in survey effort Additionally, it was expected that (4) increasing survey effort would decrease the error associated with slope parameters (beta estimates) describing the functional relationship between the covariate and occupancy.

Methods

The methods used in this study are an extension of the simulation approach introduced by Shannon et al. (2014). Simulations were parameterised to investigate 150 different scenarios that varied by number of cameras (sites: $N = 10, 30, 50, 70, 90$), number of survey days (occasions: $S = 20, 40, 60, 80, 100$) and proportion of cameras located in habitat patches ($Prop = 0, 0.2, 0.4, 0.6, 0.8, 1$). A covariate was simulated to mimic a patchily-distributed resource (e.g., woodland, water source, wetland etc.) surrounded by a matrix of other habitat types. *Prop* described the proportion of camera sites (*N*) located in these habitat patches and was used to represent real-world scenarios, where the observed heterogeneity in a covariate may be influenced by variation in its spatial extent and distribution or the strategy used for camera deployment (Figure 1). For example, uniform sampling across the extent of a study area is often used when the objective is to estimate habitat preferences (e.g., Estevo et al., 2017). Alternatively, non-uniform sampling may be used when the relationship between occupancy and some characteristic of the habitat patch (e.g., size, salinity, plant species richness) is the focus of the study (e.g., Hansen et al., 2020, Chapter 5), or there is a need to stratify sampling across habitat types (Bailey et al., 2007; Kays et al., 2020; MacKenzie et al., 2017).

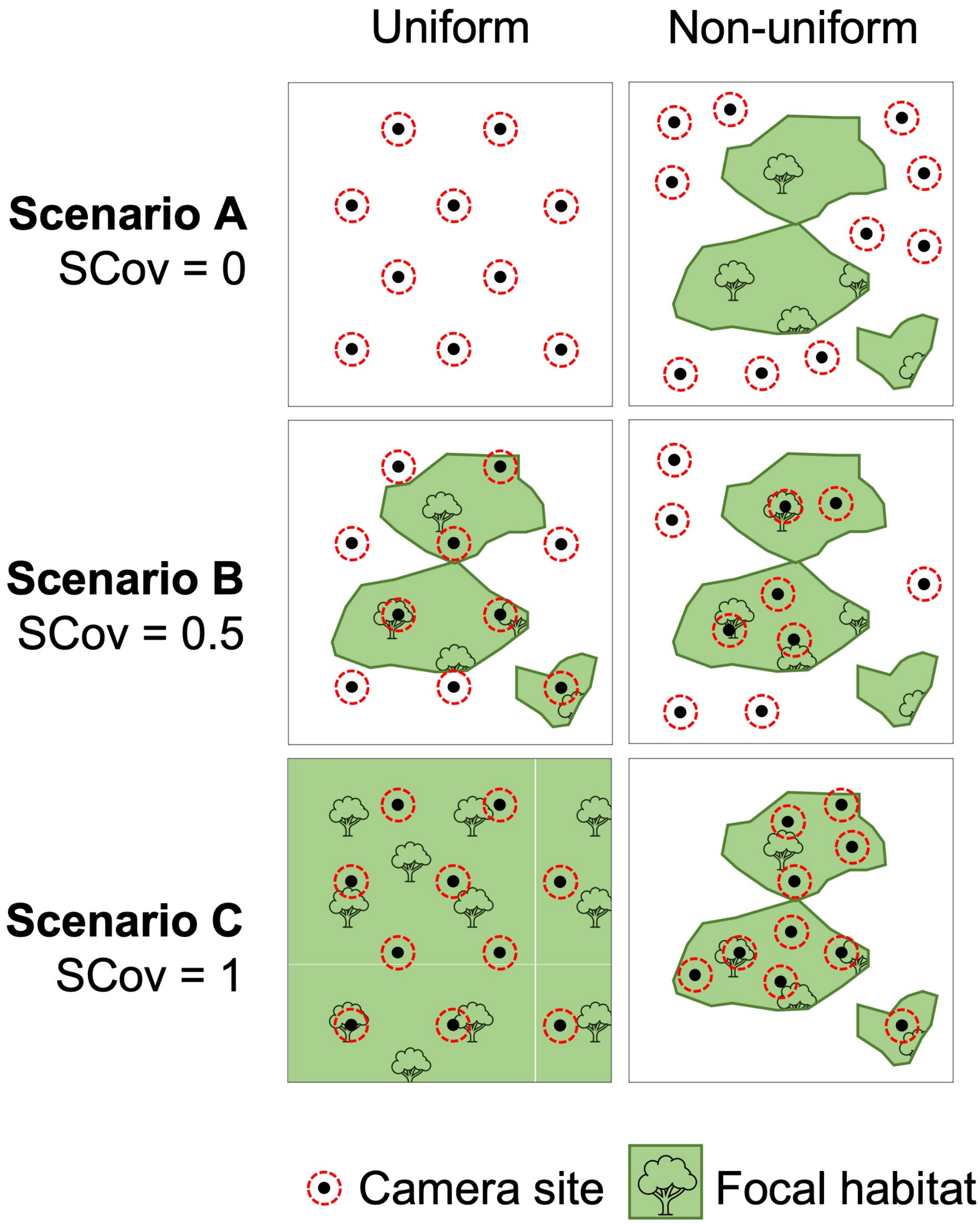


Figure 1. Camera data collection scenarios represented by varying the proportion of camera sites (N) located in patches of a given habitat type (*Prop*). Scenario A: the habitat type is either not present or deliberately not-sampled. Scenario B: 50% of cameras are located in patches of the habitat type, either by design or due to the spatial distribution of habitat. Scenario C: 100% of cameras are located in patches of the habitat type, either by design or because there is contiguous cover of the habitat type.

Simulated detection histories

A total of 500 sets of detection histories were created for each combination of N, S and $Prop$. Detection histories consisted of $N \times S$ events, where each camera site N_i was considered to be occupied or not following a Bernoulli process with probability ψ_i. At occupied sites, it was then determined if the species was detected or not for each occasion S_j following a Bernoulli process with probability p_i (Shannon, Lewis, et al., 2014).

Following a similar approach to Mackenzie & Bailey (2004), the parameters of occupancy (ψ) and detection probability (p) were modelled as a function of site-specific covariates. In each simulation, sites were either considered to be located in patches of the focal habitat (n = $N \times$ *Prop*) or the surrounding matrix (n = $N \times$ (1-*Prop*)). For each camera site in the habitat patches, a random value between 0 and 10 was generated from a uniform distribution to represent a characteristic of the patch (patch size, say). Camera sites in the matrix were assigned habitat values of 0. ψ_i was calculated using the logistic model (Eqn. 1) with slope and intercept terms of 0.40 and -0.41, respectively (Mackenzie et al., 2002):

Eqn. 1
$$\psi_i = \frac{\exp\,(-0.41+0.40*Hab)}{1+\exp\,(-0.41+0.40*Hab)}$$

where Hab is the habitat value (0-10) generated from the uniform distribution. ψ was therefore constant (0.4) at matrix sites and increased with increasing size of the habitat patch for the camera site it contains, representing a mechanism whereby a species uses a range of habitats but prefers larger patches of a given type (Figure 2). The central 95% of values for ψ were between 0.42 and 0.97. p was also modelled to be lower (0.05) at matrix sites than patch sites (0.30), which represents a scenario where the species is more detectable in habitat patches, possibly because activity is higher, or game trails are easier to identify. The slope and intercept terms for p were 2.10 and -2.94, respectively:

Eqn. 2
$$p_i = \frac{\exp\,(-2.94+2.10*HabType)}{1+\exp\,(-2.94+2.10*HabType)}$$

where $HabType$ equals 0 for matrix sites and 1 for patch sites. The occupancy and detection probabilities used to create detection histories of the virtual species in this chapter are representative of the range of values observed in empirical studies of terrestrial mammals

(Chatterjee et al., 2021; Kays et al., 2020; Shannon, Lewis, et al., 2014). The findings should therefore be applicable to a wide variety of taxa and applications where camera-traps are used to study patterns of site occupancy.

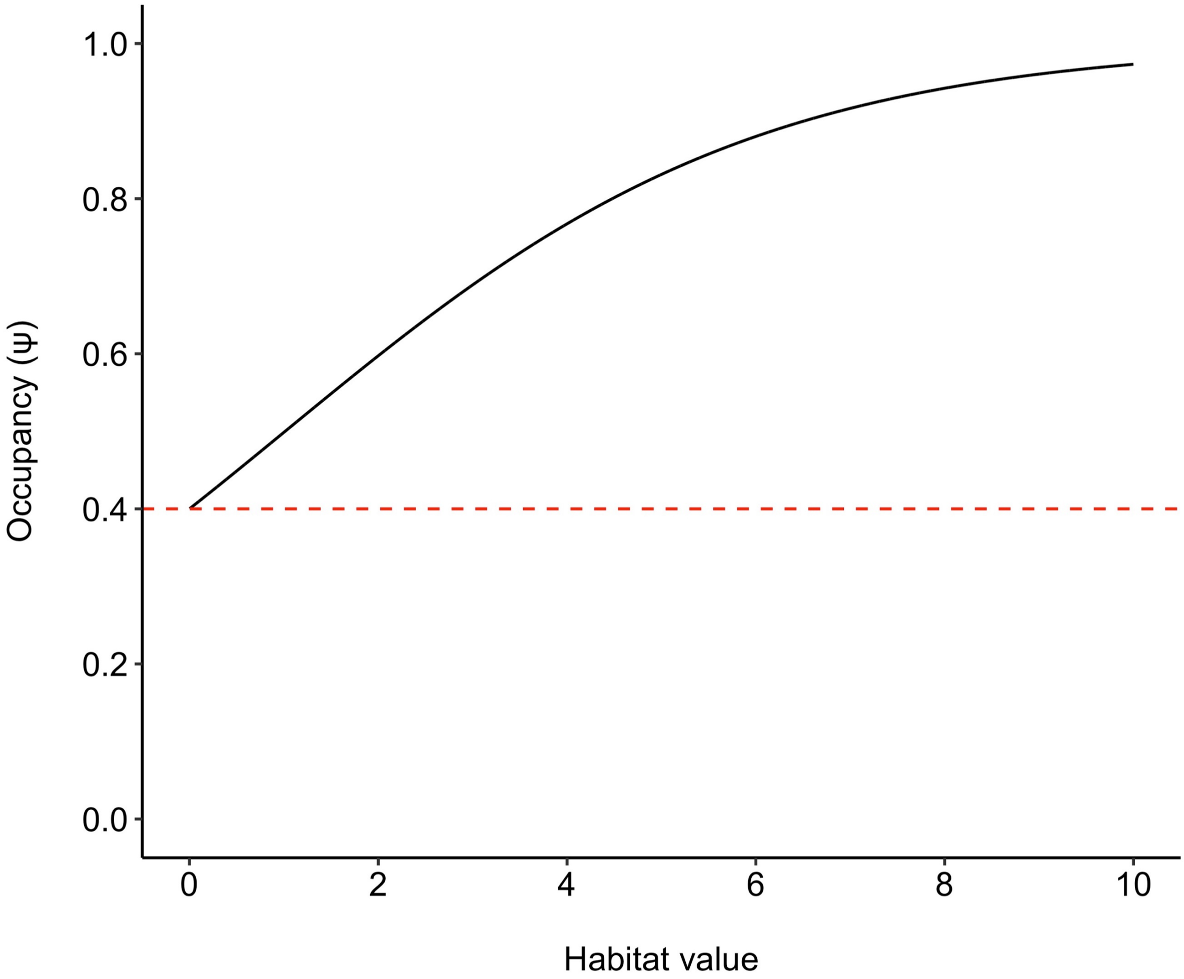


Figure 2. Relationship between habitat values randomly generated from the uniform distribution and occupancy (ψ) used to determine the species occupancy status (occupied/not occupied) at simulated sites. The red dashed line indicates ψ for matrix sites (0.4), which were assigned habitat values of 0.

Occupancy modelling and error estimation

Simulated detection histories were analysed using single-season single-species occupancy models (Mackenzie et al., 2002), developed using the 'RPresence' package, which implements the software PRESENCE (available from www.mbrpwrc.usgs.gov/software/presence.shtml) in R (R Core Development Team, 2019). It was assumed sites were (i) closed to changes in occupancy, (ii) detection of species and detection histories at each site were independent, and (iii) individuals were correctly identified (i.e., no false positives, MacKenzie et al., 2017). For each combination (j) of *N*, *S* and *Prop*, occupancy (ψ) and detectability (p) were either assumed to be constant (dot model) or allowed to vary in relation to the covariate (covariate model). Error was calculated using root mean squared error (RMSE), which is a measure of both accuracy and precision:

Eqn. 3
$$RMSE_j = \sqrt{\sum[\hat{\psi}_i - \psi_i)^2]}$$

where $\hat{\psi}$ and ψ are the model-estimated and simulated values for occupancy at site i, respectively. The same equation was used to calculate error for p. To assess the effect of the covariate on the optimal survey design, three different RMSE target values (0.15, 0.10 and 0.075) were selected to represent differing levels of error, consistent with the analyses conducted by Shannon et al. (2014). Number of occasions (S) and number of cameras (N) were weighted equally. The optimal survey design was estimated as the minimum survey effort $(N \times S)$ required to estimate occupancy to a desired level of error at each value of *Prop*.

Finally, beta coefficients (β), that described the relationship between each of the two parameters (ψ and p) and the covariate were estimated in simulations where *Prop* > 0. Equation 3 was adapted to calculate error for β estimates using RMSE as:

Eqn. 4
$$RMSE_j = \sqrt{\sum[\hat{\beta}_k - \beta)^2]}$$

where $\hat{\beta}_k$ is the model-estimated beta coefficient for detection history k. It should be noted that only outputs from valid models were included in the results. For a model to be valid it had to meet the following criteria: (1) converge to a minimum of 3 significant digits, (2) no variance-covariance (VC) warnings, (3) naive occupancy >0 and <1 and (4) β estimates <=

6.906755 and >= -6.906755, which represents a maximum of a 0.999 change in the estimate of a parameter (ψ or p) for a 1 standard deviation unit change in the covariate (applies to covariate models only, S).

Results

Root mean square error (RMSE) of occupancy (ψ) estimates was lower with covariate models than with dot models across nearly all simulated combinations of N (number of camera sites), S (number of survey days) and *Prop* (proportion of camera sites located in habitat patches (patch sites), Figure 3 and 4). Increasing total survey effort ($N \times S$) decreased RMSE for both dot and covariate models (Figure 3). For dot models, this effect was only observed when none of the cameras were located in habitat patches (i.e., *Prop* = 0, Figure 3). Covariate models were more sensitive to variation in survey effort but generally yielded estimates with less associated error (Figures 3 and 4). Variance in the results for covariate models is most likely due to the differing effects of N and S on error for the occupancy parameter (S25-S26). The difference in error between dot and covariate models (i.e., the performance advantage of covariate models) increased with an increasing number of cameras but was not affected by the number of survey days (Figure 4). Additionally, the difference in error between model types was largest at an intermediate proportion of patch sites (*Prop* = 0.6) and smallest at very low (*Prop* = 0.2) or high (*Prop* = 1) proportions (Figure 4). When the proportion of patch sites was > 0, dot models failed to achieve any of the pre-defined precision thresholds of error (RMSE = 0.15, 0.10, 0.075) even with the maximum possible survey effort (9,000 camera days, Table 1). For covariate models, the survey effort required to reduce error to the desired level ranged from 600 (RMSE: 0.15, *Prop*: 1) to 3,600 (RMSE: 0.075, *Prop*: 0.2) camera days and generally decreased as the proportion of patch sites increased (Table 1). The error associated with the β estimates from covariate models decreased with an increasing number of cameras or an increasing proportion of patch sites but was unaffected by number of survey days (Figure 5).

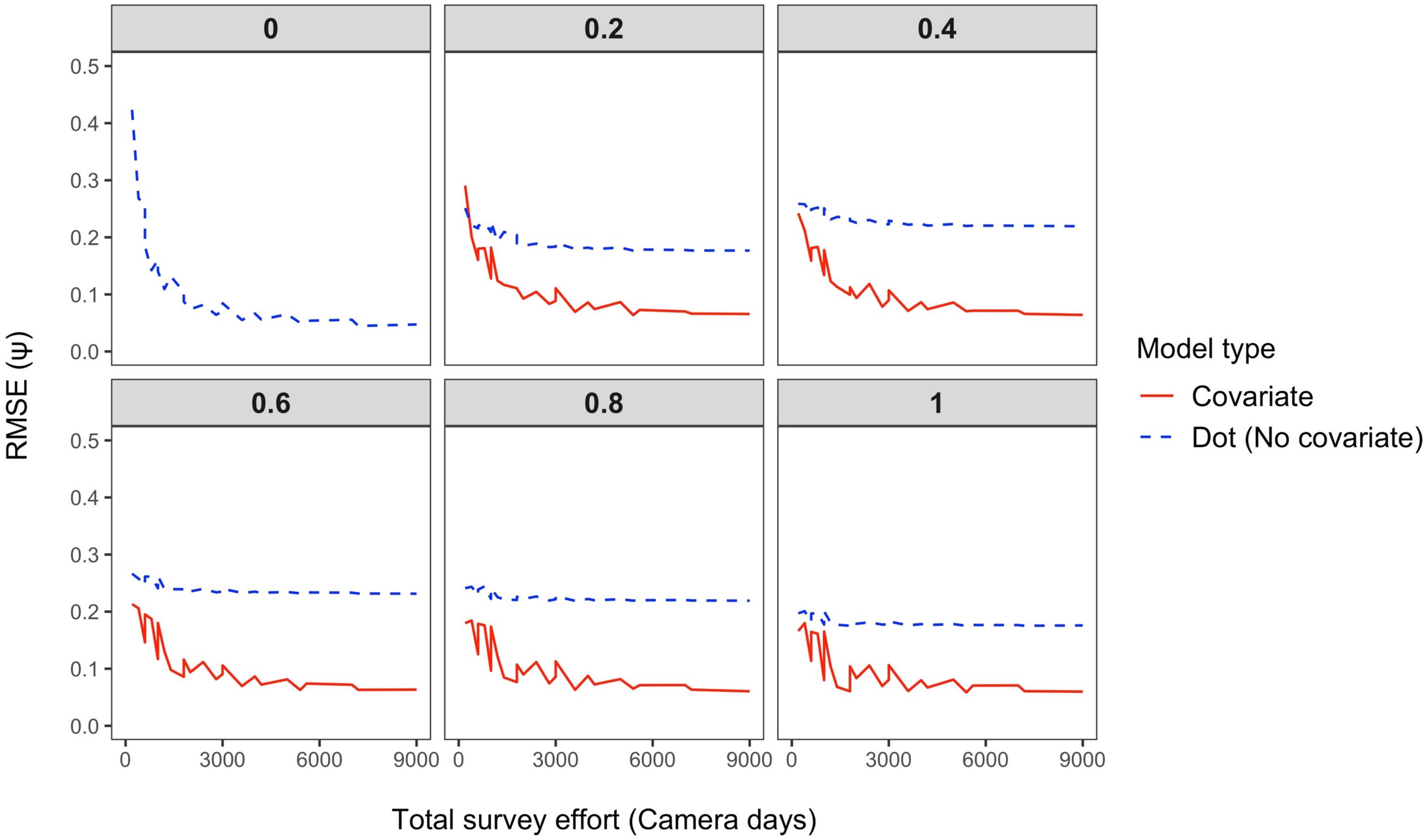


Figure 3. Root mean squared error (RMSE) for estimates of occupancy (ψ) in relation to total survey effort (Camera days: number of cameras × number of days of deployment) for dot (no covariate) and covariate models. Bold numbers above are the proportion of camera sites located in habitat patches (*Prop*). Covariate models were not applicable where *Prop* = 0.

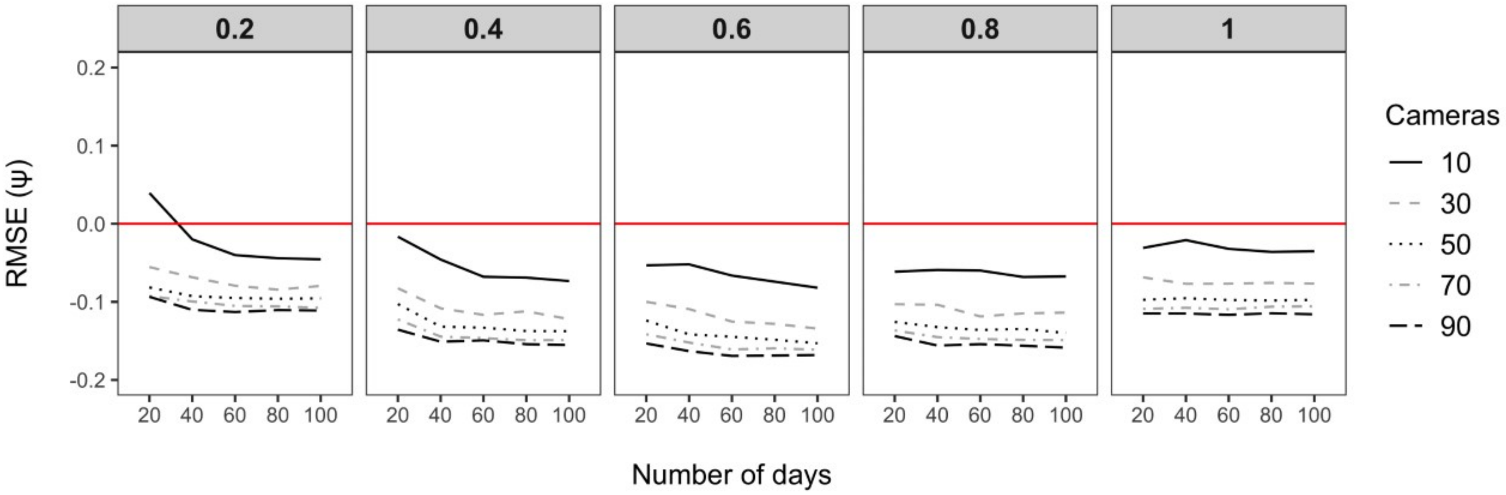


Figure 4. Difference in root mean squared error (RMSE) for estimates of occupancy (ψ) between dot (no covariate) and covariate models ($\text{RMSE}_{\text{covariate}}$ - RMSE_{dot}) in relation to the number of cameras and number of days of deployment. Bold numbers above are the proportion of camera sites located in habitat patches (*Prop*).

Table 1. The minimum total survey effort (Number of cameras x number of days of deployment) required to achieve a minimum level of precision (root mean squared error, RMSE) of 0.15, 0.10 and 0.075 for dot and covariate models. Dashes indicate failure to achieve the precision threshold with the maximum possible survey effort (9000 camera days). *Prop*: proportion of camera sites located in habitat patches.

Minimum precision threshold (RMSE)	***Prop***	**Total survey effort (Camera days)**	
		Dot model	**Covariate model**
0.15	0	800	
	0.2	-	1000
	0.4	-	1000
	0.6	-	600
	0.8	-	600
	1	-	600
0.10	0	1800	
	0.2	-	2000
	0.4	-	1800
	0.6	-	1400
	0.8	-	1000
	1	-	1000
0.075	0	2000	
	0.2	-	3600
	0.4	-	3600
	0.6	-	3600
	0.8	-	2800
	1	-	1400

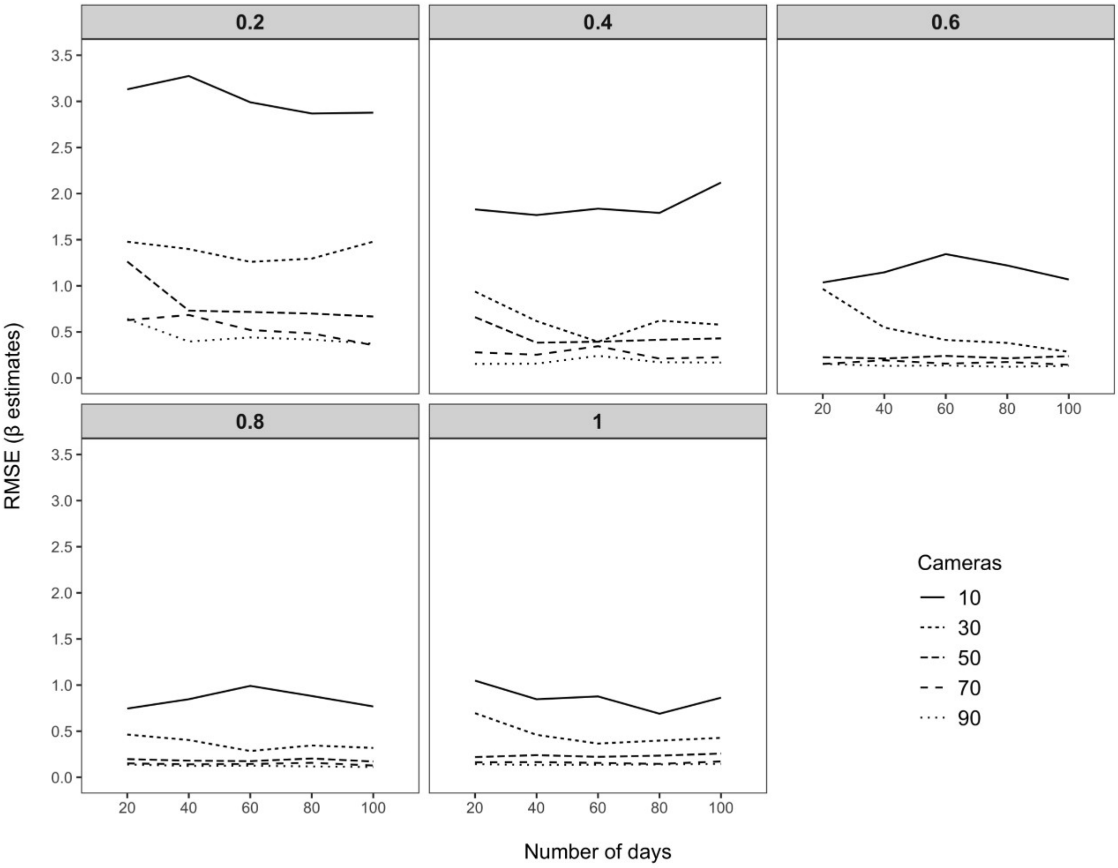


Figure 5. Root mean squared error (RMSE) of beta (β) estimates for the effects of the covariate on estimates of occupancy (ψ) in relation to the number of cameras and number of days of their deployment. Bold numbers above are the proportion of cameras located in habitat patches (*Prop*).

Discussion

In this chapter, a simulation approach was used to assess the effects of covariates on the precision and accuracy (i.e., error) of occupancy models in relation to camera-trap survey effort. Detection histories of a virtual species were simulated as a function of a site-specific covariate (habitat type) and used to evaluate model performance in a variety of survey scenarios. The results showed that including covariate information in models strongly influenced how efficiently a reliable occupancy estimate could be obtained. The findings can be used to inform the design of camera-trap surveys and optimise the allocation of human and financial resources in research studies and population monitoring programmes (Chatterjee et al., 2021; Kays et al., 2020; Shannon, Lewis, et al., 2014).

The results strongly supported the prediction that, for the same level of survey effort, covariate models would yield occupancy estimates with lower error than models without a covariate (i.e., dot models). Covariates are used in occupancy models to satisfy the assumption that heterogeneity in occupancy and detection probabilities across sites is accounted for in the modelling of each parameter (Mackenzie et al., 2002; MacKenzie et al., 2017). The results showed that with increasing heterogeneity in habitat type (patch vs. matrix, Figure 1) across camera sites, the benefit of including covariate information increased. When the proportion of camera sites located in habitat patches was very small, with most located in the matrix (*Prop* = 0.2), or very large, with all located in the habitat patches (*Prop* = 1) the difference in performance between the two model types was reduced. However, covariate models consistently produced estimates with lower associated error than for the dot models across most of the survey scenarios evaluated.

Strong support was also found for the hypothesis that use of covariate models would enable less total survey effort (camera days: number of cameras × number of survey days) being required to achieve error below a target value. Indeed, dot models failed to achieve errors below any of the specified thresholds (root mean squared error, RMSE = 0.15, 0.10, 0.075), even with the maximum possible survey effort of 9,000 camera days. It is well-understood that increasing survey effort decreases estimation error (Bailey et al., 2007; Chatterjee et al., 2021; Kays et al., 2020; Mackenzie & Royle, 2005; Shannon, Lewis, et al., 2014). However, the results reported in this chapter show that survey effort had no effect on error for dot models when habitat type varied between camera sites (i.e., *Prop* > 0). In contrast, covariate models did successfully achieve errors below the specified thresholds, though they were more sensitive to variation in survey effort. Variable performance can be explained by the estimates of the slope parameter (beta), which describes the functional relationship between habitat and occupancy. The error associated with the estimates of beta decreased with increasing number of camera sites (N) and proportion of sites located in habitat patches ($Prop$). The combination of these two survey components may be described more simply as the total number of patch sites (i.e., $N \times Prop$). Increasing the number of camera sites located in habitat patches improved model performance by expanding the range and number of habitat values (e.g., patch sizes) used to estimate the habitat-occupancy relationship (MacKenzie et al., 2017; Thompson & Seber, 1996).

Accounting for site-level heterogeneity is an essential component of designing camera-trap surveys (Mackenzie et al., 2002; MacKenzie et al., 2017). In scenarios where a non-dynamic, spatial covariate (e.g., variation in habitat type) is the source of heterogeneity, the number and selection of camera sites amongst different habitat types is of primary importance. Heterogeneity may be reduced by standardising site selection based on an influential covariate (e.g., by selecting all sites of the same habitat type). However, a dot model may still be inappropriate, as occupancy/detectability is typically influenced by a range of behavioural and ecological factors. Thus, including covariate information is likely to be beneficial in most cases (MacKenzie et al., 2017). Indeed, the results reported in this chapter showed that covariates improved the reliability of model outputs, even in scenarios where habitat heterogeneity was relatively low (i.e., $Prop = 0.2$). Furthermore, the number and range of covariate values (e.g., habitat types) sampled by camera sites determines how appropriate it is to generalise the results to the wider landscape and the efficacy of models to discriminate between competing hypotheses (e.g., to assess habitat preferences, Bailey et al., 2007; Guillera-Arroita & Lahoz-Monfort, 2012; MacKenzie et al., 2017).

A wide range of sampling strategies may be used as a basis for selecting camera sites, including systematic, random, stratified random and cluster sampling (for reviews see: Cochran, 1977; Thompson & Seber, 1996). Clearly defining objectives and identifying appropriate analytical methods at the earliest stages of study design is critical to implementing an effective survey that yields data of a sufficient type and quality (MacKenzie et al., 2017). Once a design has been established, the general principles for allocating survey effort (i.e., maximising number of camera sites for rare species and number of days for hard to detect species) will apply in most cases (Chatterjee et al., 2021; Kays et al., 2020; Shannon, Lewis, et al., 2014). However, the results from this chapter suggest that unless site-level heterogeneity is appropriately modelled using covariates, increasing survey effort is unlikely to provide any benefit for model performance. Collecting covariate data is therefore an efficient approach to obtaining a reliable occupancy estimate because it will reduce the additional number of cameras or survey days required to obtain a reliable occupancy estimate.

It is important to acknowledge potential sources of variation in the results of this chapter that were not assessed. The strength and direction of the relationship between the covariate and occupancy/detectability is likely to strongly affect the relative performance of dot and covariate models as well as the survey effort required to obtain reliable estimates. It is reasonable to assume that the stronger the effect of the covariate, the greater the impact that including covariate information will have on model performance (MacKenzie et al., 2017). Future research can build on this chapter by evaluating the effects of variation in covariate strength on the relationship between survey effort and estimation accuracy/precision using a similar simulation approach. It should, however, be noted that such analyses are likely to be computationally demanding. Researchers may also look to explore the effects of different types of covariates. In this chapter, simulations were based on a site-specific covariate, which was selected as being of primary interest to most occupancy studies (Bailey et al., 2014). However, the occupancy modelling framework also allows the inclusion of survey-specific covariates (e.g., temperature, visibility, etc.) to explain variation in detectability (Mackenzie et al., 2002; MacKenzie et al., 2017). Assessments of the effect of such survey-specific covariates on model performance would be beneficial, as they affect the importance of camera deployment duration (i.e., number of survey days) relative to other survey components (Guillera-Arroita & Lahoz-Monfort, 2012).

When calculating the minimum survey effort required to achieve error below a target value, the number of cameras and number of survey days were weighted equally in the present study. In real-world scenarios, each survey component may have different human and financial costs that need to be considered to find an efficient solution within the logistic constraints of a study. Actual costs have been included in previous assessments of camera-trap surveys (Gálvez et al., 2016; Guillera-Arroita et al., 2010; Shannon, Lewis, et al., 2014). Such assessments could be expanded to evaluate the cost of collecting covariate data, which may vary greatly between studies. For example, large-scale studies may use remotely-sensed environmental data, which have been collected for many countries worldwide and are free to access from sources such as the European Space Agency (https://worldcover2020.esa.int/)

and Copernicus Global Land Service (https://land.copernicus.eu/global/products/). Collecting data on finer-scale (e.g., habitat structure) or dynamic (e.g., prey availability) covariates may be more challenging and require greater investment of resources.

Finally, although simulation studies provide useful theoretical guidance for the planning of occupancy studies, it is important to validate the results with real-world empirical data. Modelling covariates adds a dimension of complexity that makes validation with empirical data very challenging. A wide range of factors may influence the observed relationship between covariates and occupancy/detectability, including spatial and temporal scale, ecological context, community composition and species abundance (Heino & Tolonen, 2018; Hofmeester et al., 2019; Morán-López et al., 2022; Steenweg et al., 2018). Results are also likely to vary between species that have different occupancy (i.e., rare or common) and detection (i.e., easy or difficult to detect) characteristics (Shannon, Lewis, et al., 2014; Si et al., 2014) . Confounding variables make it difficult to use empirical data to draw general conclusions about survey efficiency and the effects of covariates. Initiatives such as Wildlife Insights powered by Google (Thau et al., 2019) and the eMammal repository (McShea et al., 2016) have collated camera-trap data for a wide range of species from around the world. These large, centralised datasets may facilitate appropriately detailed analyses, from which the results may be transposed to a range of species, ecological contexts and survey scenarios.

In conclusion, motion-activated cameras have become a standard tool for monitoring terrestrial animal populations in conservation and wildlife research. Occupancy modelling is a powerful, versatile and widely used framework for analysing camera-trap data that provides valuable insight on species distributions, habitat-use and population dynamics (Mackenzie et al., 2002; MacKenzie et al., 2017). This chapter investigated the effects of including information on camera-site condition (as a covariate) on the accuracy and precision (i.e., error) of model estimates for scenarios of varying survey effort. The results showed that accounting for site condition greatly improved the efficiency of obtaining a reliable occupancy estimate. Furthermore, it was demonstrated that increasing survey effort without appropriate modelling of occupancy/detectability with covariates may provide no benefit to model performance and incur wasteful costs. This chapter builds on the existing research on camera-trap survey optimisation (e.g., Gálvez et al., 2016; Guillera-Arroita & Lahoz-Monfort, 2012; Kays et al., 2020; Shannon et al., 2014) and provides useful guidance to help practitioners design efficient studies.

Chapter 7

General discussion

This thesis addressed a range of research questions via a systematic literature review and studies that used both empirical and simulated data. Chapter two systematically mapped the evidence for the effects of management interventions (e.g., shooting, fencing and administering contraceptives) on UK ungulate (Artiodactyla) species to reveal its extent and distribution across species, interventions and outcomes. Chapters three to five used a camera-trap survey to explore how human disturbance and other landscape features influenced spatiotemporal patterns of habitat-use by fallow deer in the Elwy Valley region of North Wales, UK. Chapter six investigated the optimisation of camera-trap surveys with a focus on the use of covariates in occupancy studies. The findings advance existing knowledge of ungulate ecology in human-dominated landscapes and provide information to support monitoring and sustainable population management.

Managing deer (Cervidae) populations in the UK is challenging due to the extensive physical division of land and diversity of land-uses at comparatively small spatial scales (Fattorini et al., 2020; Putman, Apollonio, et al., 2011). There is no legal obligation to undertake management and interventions can only be applied at sites with permission from the landowner (Putman, Apollonio, et al., 2011). Site-level objectives vary greatly, and each small parcel of land may be used for a variety of purposes including farming, forestry, recreation, biodiversity conservation and urban development. Motivation for management can be limited, as high numbers of deer are not considered to be a concern for some of these objectives. Indeed, stakeholders may actively welcome large populations as they provide opportunities for wildlife encounters and eco-tourism (Carpio et al., 2021; Linnell et al., 2020). Additionally, landowners may be morally opposed to the use of some interventions (e.g., hunting) or unable to invest the time and financial resources required to implement them. This diversity of opinions and objectives at the site level makes it difficult to set management aims and coordinate actions at the appropriate landscape scale of deer populations (Fattorini et al., 2020; Pérez-Espona et al., 2009; Putman, Apollonio, et al., 2011). Robust scientific evidence is needed to make informed, objective management decisions and develop strategies that successfully balance the needs of a range of stakeholders.

Monitoring the outcomes of interventions is a fundamental component of adaptive, evidence-based management (Apollonio et al., 2017; Lancia et al., 1996). In the UK, population monitoring of deer is conducted by a range of non-government (e.g., The Game and Wildlife Conservation Trust www.gwct.org.uk, British Deer Society www.bds.org.uk, and British Association of Shooting and Conservation www.basc.org.uk) and government organisations (e.g., Animal and Plant Health Agency www.apha.gov.uk). A variety of methods are used, most of which collect data in a non-systematic manner and/or observe species indirectly. For example, citizen science in the form of repeated questionnaire surveys has been used to estimate species distributions at the national level at a spatial resolution of 10 km^2 (Croft et al., 2019; Ward, 2005). While at the site level, indicators of deer activity (e.g., footprints, dung, trails etc.) and impact (e.g., seedling damage, bramble browsing, bark stripping etc.) have been monitored via field surveys (Putman, Watson, et al., 2011; Smar T et al., 2004). These techniques are relatively simple, inexpensive and provide a convenient method of qualitatively assessing management efficacy. However, the data they yield is generally coarse and only relevant for a narrow range of demographic metrics (e.g., presence/absence, relative abundance etc.), which constrains our ability to evaluate the full range of effects of interventions on target species.

The results from the review (Chapter 2) revealed that there is limited published literature on the effects of management to support policy and decision-making. Substantial knowledge gaps exist for important interventions (e.g., fencing, diversionary feeding, deterrents), outcomes (e.g., health, physiology, morphology) and species (e.g., Chinese muntjac, fallow deer, sika deer). Furthermore, the robustness of the evidence-base is generally low and dominated by short-term studies (Barton et al., 2022). Expanding the scope of population monitoring would improve our knowledge of species responses to interventions and help us to better understand the mechanisms of how they work to meet strategic objectives. For example, hunting is widely used in the UK to mitigate the effects of deer on sensitive woodland habitat (Fattorini et al., 2020; Putman, Apollonio, et al., 2011). The results from this thesis (Chapter 5) showed that hunting had no effect on the probability or frequency of woodland sites being used by deer, which brings into question the effectiveness of this intervention at a site-level. However, there were effects of hunting on daily activity patterns (Chapter 4), suggesting it may play an important role at the landscape level by preventing sites used by humans for recreation becoming temporal refuges. Insights such as these are useful to develop efficient strategies that most effectively utilise a combination of interventions within the socio-political constraints of the landscape (Carpio et al., 2021; Wäber et al., 2013; Walter et al., 2010). For instance, hunting may be used as a long-term strategy to regulate population sizes and maintain a landscape of fear that mimics the effects of a natural predator (Baskin, 2016; Cromsigt et al., 2013; Valente et al., 2020). Other interventions (e.g., fencing or deterrents) may provide better short-term protection for particularly high-value or vulnerable features (e.g., planted seedlings), and are often the only management option in areas where hunting is not permitted by law or local landowners (e.g., public parks, Geisser & Reyer, 2004; Putman & Langbein, 2003; Valente et al., 2020).

Motion-activated camera-traps are a useful tool for population monitoring that offer important advantages over traditional methods (e.g., dung counts, transect surveys etc., (Frey et al., 2017; Nichols, O'Connell, et al., 2011). Crucially, they provide precise records of target species in space and time, which minimises the possibility of misidentification and facilitates studies of a wider range of behaviours, such as habitat preferences, seasonal activity and species interactions (Burton et al., 2015; Trolliet et al., 2014). They are also relatively inexpensive and require minimal effort to collect data continually over long time periods. Additionally, machine learning methods have been developed to automate the processing of camera-trap data (i.e., applying metadata tags to images to identify species captured), which enable large datasets to be processed and analysed more quickly and with fewer human resources (Delisle et al., 2021; Norouzzadeh et al., 2018; Zaragozí et al., 2015).

The efficacy of camera-trap surveys depends on robust and detailed survey design (Kelly, 2008; Shannon, Lewis, et al., 2014). Camera-traps only directly survey the small area in front of each camera and several critical assumptions need to be met to extrapolate the results to the wider landscape (Burton et al., 2015; O'Connell et al., 2011). For example, occupancy modelling is widely used to analyse camera-trap data (Mackenzie et al., 2002; MacKenzie et al., 2017). One of the key assumptions of the occupancy modelling framework is that parameters (i.e., occupancy or detectability) are constant across sites or that differences are modelled using covariates (e.g., habitat type, MacKenzie et al., 2017). The results from the simulation study (Chapter 6) showed that violating this assumption by using a model without covariates (i.e., a dot model) strongly affected the accuracy and precision of the occupancy estimates. The findings also suggested that investing time and resources to increase survey effort (i.e., number of cameras and length of deployment) may be wasted if this assumption is not appropriately considered in the study design. It is possible that wildlife practitioners may not have the expertise in ecological modelling and statistics to design effective studies. Therefore, collaboration between researchers and practitioners is strongly encouraged to maximise the efficiency of monitoring programmes and ensure that they yield data of the appropriate type and quality to support decision-making (Burton et al., 2015; MacKenzie et al., 2017; Nichols, Karanth, et al., 2011). Wider and more systematic use of camera-traps by practitioners as well as data-sharing through collaborative projects, such as Snapshot Europe (https://app.wildlifeinsights.org/initiatives/2000166/Snapshot-Europe), would also provide researchers with valuable data to further refine techniques and address a range of fundamental questions in animal ecology.

Camera-traps were used in this thesis to explore the effects of human activities on the spatiotemporal behaviour of fallow deer. In human-dominated landscapes, there are trade-offs for wildlife species between resource acquisition and risk avoidance (Eldegard et al., 2012; Maren et al., 2009; Wevers et al., 2020). Chapters four and five examined how fallow deer resolve these trade-offs and respond to various sources of lethal (hunting) and non-lethal (recreation and woodland management) human disturbance. The results showed that recreation was the most important anthropogenic driver of behaviour. Deer preferred sites where recreation was high and were also more active during the day in these areas. Both findings are consistent with previous studies, which have suggested that areas of non-lethal human activity may be preferred because they offer shelter from perceived predation risk (Gallo et al., 2022; Lesmerises et al., 2017; Shannon, Cordes, et al., 2014).

Interestingly, hunting did not lead to avoidance of sites, as predicted (Chapter 5) and it had limited effects on daily activity (Chapter 4), which suggests that risk perception by deer is not entirely accurate. The lack of behavioural response to hunting in contrast to recreation, may be due to differences in the consistency between the two types of disturbance. The more predictable human activity is in space and time, the greater the likelihood that animals will learn to reliably assess the level of risk associated with encounters and respond appropriately (Blumstein, 2016; Rankin et al., 2009; Riotte-Lambert & Matthiopoulos, 2020; Ueda et al., 2021). Indeed, a study by Hansen and Aanes (2015) showed that Svalbard reindeer respond to humans less strongly (i.e., exhibit shorter escape movements) the closer they are to human settlements, where encounters occur more often. Recreation is likely to be less variable than hunting over the duration of a biological season (e.g., the rut period – approximately three months), with regular peaks of activity on certain days of the week (e.g., Saturday and Sunday) and more often occurring along trails or pathways. Therefore, it may provide a more consistent stimulus, which enables learning and the emergence of behavioural responses (Blumstein, 2016; Ueda et al., 2021).

The comparatively high tolerance of disturbance exhibited by some ungulate species is an important and often overlooked factor of their success and persistence in human-dominated landscapes. Ungulates are commonly perceived as being overabundant in developed regions, such as Europe and North America, because of the negative impacts populations can have on human interests (e.g., forestry, agricultural crops etc., Carpio et al., 2021; Krausman & Bleich, 2013; Linnell et al., 2020). However, such perceptions are subjective, and it is important to recognise the crucial benefits they also provide for the functioning and resilience of forest and grassland ecosystems. The diversity and total biomass of large herbivores in the northern hemisphere is substantially lower today than it was during the last inter-glacial period (132,000–110,000 y B.P., Ripple et al., 2015; Sandom et al., 2014a; Sandom et al., 2014b). Indeed, wild terrestrial mammals currently only account for 4% of the extant global mammalian biomass (Bar-On et al., 2018). Large herbivores play a key role in maintaining a high structural diversity of vegetation at the landscape scale that provides a range of habitat for other species (Foster et al., 2014; Hobbs, 1996; Huntly, 1991; van der Waal et al., 2011). The removal of species and disturbance of natural habitats by humans has led to the degradation of these important processes and resulted in large-scale losses in biodiversity (Dirzo et al., 2014; Ripple et al., 2015; Sandom et al., 2014a). It has also increased the vulnerability of ecosystems to the effects of forecast global climate change, which raises concerns over their capacity to continue to provide valuable services to humans (e.g., pollination, food production, pest control etc., Champagne et al., 2021; Stevens et al., 2022; Timpane-Padgham et al., 2017; Velamazán et al., 2020). The establishment of healthy and sustainable populations of large herbivores should, therefore, be considered a vital component of ecosystem restoration (Fløjgaard et al., 2022; Montoya et al., 2012; Ripple et al., 2015; Sandom et al., 2014b).

Conclusion

This thesis examined the daily activity patterns and habitat-use of fallow deer in a highly-transformed, human-dominated landscape. The results demonstrate how the behavioural flexibility of ungulate species helps them to resolve trade-offs between risk avoidance and resource acquisition. Monitoring populations of large herbivores at the appropriate landscape-scale is logistically challenging (Apollonio et al., 2017; Festa-Bianchet et al., 2017). Typical of studies of this kind, the scope of data collection in this thesis was constrained by limitations of time, financial resources and restrictions to site access. Future studies should look to build upon this research by conducting similar surveys that include a larger number of camera sites, which are ideally, distributed more evenly across a gradient of anthropogenic disturbance. Quantifying human activity and environmental covariates with greater precision would also improve the strength of inferences and permit assessments to be made of behaviour at finer spatial and temporal scales. Exploring variation in responses between individuals of different sexes and age classes is another interesting avenue for future research that would provide insights into the relationship between seasonal patterns in behaviour and stages of the reproductive cycle. Data-sharing and the collation of large camera-trap datasets in repositories such as Wildlife Insights powered by Google (Thau et al., 2019) and eMammal (McShea et al., 2016) are likely to become increasingly valuable for studying a wide range of species across a variety of ecological contexts. Continued research is essential to gain a better understanding of the factors determining the distribution of large herbivores and improving methods to monitor and model the dynamics and viability of populations. Scientific evidence will play a crucial role in enabling management to effectively maximise their benefits for ecosystem function and ensure that coexistence with humans is ecologically and economically sustainable.

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Appendices

Chapter 2: Supporting information

S1. ROSES checklist. Excel spreadsheet available online at

https://doi.org/10.1371/journal.pone.0267385.s001

S2. Preferred Reporting Items for Systematic reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-ScR) Checklist. Note: page numbers refer to the manuscript as it was submitted for publication. Also available online at https://doi.org/10.1371/journal.pone.0267385.s002

SECTION	ITEM	PRISMA-ScR CHECKLIST ITEM	REPORTED ON PAGE #
TITLE			
Title	1	Identify the report as a scoping review.	1
ABSTRACT			
Structured summary	2	Provide a structured summary that includes (as applicable): background, objectives, eligibility criteria, sources of evidence, charting methods, results, and conclusions that relate to the review questions and objectives.	2
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of what is already known. Explain why the review questions/objectives lend themselves to a scoping review approach.	3-6
Objectives	4	Provide an explicit statement of the questions and objectives being addressed with reference to their key elements (e.g., population or participants, concepts, and context) or other relevant key elements used to conceptualize the review questions and/or objectives.	7
METHODS			
Protocol and registration	5	Indicate whether a review protocol exists; state if and where it can be accessed (e.g., a Web address); and if available, provide	n/a

SECTION	ITEM	PRISMA-ScR CHECKLIST ITEM	REPORTED ON PAGE #
		registration information, including the registration number.	
Eligibility criteria	6	Specify characteristics of the sources of evidence used as eligibility criteria (e.g., years considered, language, and publication status), and provide a rationale.	8-10
Information sources*	7	Describe all information sources in the search (e.g., databases with dates of coverage and contact with authors to identify additional sources), as well as the date the most recent search was executed.	S3
Search	8	Present the full electronic search strategy for at least 1 database, including any limits used, such that it could be repeated.	10 and S3
Selection of sources of evidence†	9	State the process for selecting sources of evidence (i.e., screening and eligibility) included in the scoping review.	11-12 and S3
Data charting process‡	10	Describe the methods of charting data from the included sources of evidence (e.g., calibrated forms or forms that have been tested by the team before their use, and whether data charting was done independently or in duplicate) and any processes for obtaining and confirming data from investigators.	11-12
Data items	11	List and define all variables for which data were sought and any assumptions and simplifications made.	11-12
Critical appraisal of individual sources of evidence§	12	If done, provide a rationale for conducting a critical appraisal of included sources of evidence; describe the methods used and how this information was used in any data synthesis (if appropriate).	n/a
Synthesis of results	13	Describe the methods of handling and summarizing the data that were charted.	S3
RESULTS			
Selection of sources of evidence	14	Give numbers of sources of evidence screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally using a flow diagram.	14
Characteristics of sources of evidence	15	For each source of evidence, present characteristics for which data were charted and provide the citations.	S3-S5
Critical appraisal within sources of evidence	16	If done, present data on critical appraisal of included sources of evidence (see item 12).	n/a

SECTION	ITEM	PRISMA-ScR CHECKLIST ITEM	REPORTED ON PAGE #
Results of individual sources of evidence	17	For each included source of evidence, present the relevant data that were charted that relate to the review questions and objectives.	13-22
Synthesis of results	18	Summarize and/or present the charting results as they relate to the review questions and objectives.	13-22
DISCUSSION			
Summary of evidence	19	Summarize the main results (including an overview of concepts, themes, and types of evidence available), link to the review questions and objectives, and consider the relevance to key groups.	23-27
Limitations	20	Discuss the limitations of the scoping review process.	32-33
Conclusions	21	Provide a general interpretation of the results with respect to the review questions and objectives, as well as potential implications and/or next steps.	27-33
FUNDING			
Funding	22	Describe sources of funding for the included sources of evidence, as well as sources of funding for the scoping review. Describe the role of the funders of the scoping review.	Financial disclosure – Submission system

JBI = Joanna Briggs Institute; PRISMA-ScR = Preferred Reporting Items for Systematic reviews and Meta-Analyses extension for Scoping Reviews.

* Where *sources of evidence* (see second footnote) are compiled from, such as bibliographic databases, social media platforms, and Web sites.

† A more inclusive/heterogeneous term used to account for the different types of evidence or data sources (e.g., quantitative and/or qualitative research, expert opinion, and policy documents) that may be eligible in a scoping review as opposed to only studies. This is not to be confused with *information sources* (see first footnote).

‡ The frameworks by Arksey and O'Malley (6) and Levac and colleagues (7) and the JBI guidance (4, 5) refer to the process of data extraction in a scoping review as data charting.

§ The process of systematically examining research evidence to assess its validity, results, and relevance before using it to inform a decision. This term is used for items 12 and 19 instead of "risk of bias" (which is more applicable to systematic reviews of interventions) to include and acknowledge the various sources of evidence that may be used in a scoping review (e.g., quantitative and/or qualitative research, expert opinion, and policy document).

From: Tricco AC, Lillie E, Zarin W, O'Brien KK, Colquhoun H, Levac D, et al. PRISMA Extension for Scoping Reviews (PRISMAScR): Checklist and Explanation. Ann Intern Med. 2018;169:467–473. doi: 10.7326/M18-0850.

S3. Literature searches. Also available online at https://doi.org/10.1371/journal.pone.0267385.s003

Estimating the comprehensiveness of the search

Each of three reviewers was given the primary question, background, objectives and eligibility criteria for the review and asked to compile a list of 10 articles, including both published peer-reviewed and 'grey' literature that they considered suitable for inclusion following a full text analysis. The combined library of 30 articles was used as a test list to assess the efficacy of the search strategy. Only search strings that identified all 30 articles were used for the literature search.

Searching for articles

Search terms were tested for sensitivity and specificity in October 2019 using the Clarivate Analytics Web of Science (Core collection) database. Boolean search operators were employed where accepted by a database and wildcards (* and $) were used to detect multiple word endings, for example fenc* would pick up fence, fences, fencing, fenced, etc. and station$ would pick up station or stations. Literature sources that did not accept Boolean search operators were queried with a subset of these terms.

Publication sources [number of articles identified]

Clarivate Analytics Web of Science including: Web of Science Core Collection and BIOSIS Citation Index 02/03/20

Core [**4065**]

BIOSIS [**4111**]

(muntjac OR "muntiacus reevesi" OR "chinese water deer" OR "hydropotes inermis" OR "roe deer" OR "capreolus capreolus" OR "red deer" OR "cervus elaphus" OR "sika deer" OR "cervus nippon" OR "fallow deer" OR "dama dama" OR "feral goat*" OR "capra aegagrus hircus " OR "wild goat*" OR "feral pig" OR "sus scrofa" OR "feral pigs" OR "feral hog*" OR "feral swine" OR "wild pig" OR "wild pigs" OR "wild hog*" OR "wild boar" OR "feral sheep")

AND

("population control" OR "lethal control" OR hunt* OR cull* OR shoot* OR harvest* OR stalk* OR bait* OR poison* OR trapping OR (inhibit* AND reproduc*) OR immunocontracept* OR contracept* OR "fertility control" OR repel* OR deterrent* OR "diversionary feed*" OR (supplement* AND feed*) OR (supplement* AND food) OR "feed* station$" OR "forest management" OR "landscape structure" OR (manipulat* AND landscape) OR (manipulat* AND habitat) OR fenc*)

CAB Direct including CAB Abstracts and CABI full text (removed "Sus scrofa" term – too many hits for domestic pigs) 02/03/20

[**4283**]

(muntjac OR "muntiacus reevesi" OR "chinese water deer" OR "hydropotes inermis" OR "roe deer" OR "capreolus capreolus" OR "red deer" OR "cervus elaphus" OR "sika deer" OR "cervus nippon" OR "fallow deer" OR "dama dama" OR "feral goat*" OR "capra aegagrus hircus " OR "wild goat*" OR "feral pig" OR "feral pigs" OR "feral hog*" OR "feral swine" OR "wild pig" OR "wild pigs" OR "wild hog*" OR "wild boar" OR "feral sheep")

AND

("population control" OR "lethal control" OR hunt* OR cull* OR shoot* OR harvest* OR stalk* OR bait* OR poison* OR trapping OR (inhibit* AND reproduc*) OR immunocontracept* OR contracept* OR "fertility control" OR repel* OR deterrent* OR "diversionary feed*" OR (supplement* AND feed*) OR (supplement* AND food) OR "feed* station$" OR "forest management" OR "landscape structure" OR (manipulat* AND landscape) OR (manipulat* AND habitat) OR fenc*)

Google Scholar (First 100 hits from each intervention term ordered by relevance. Excluded citations and patents. 250-character limit) 10/03/20

"muntjac" OR "muntiacus reevesi" OR "chinese water deer" OR "roe deer" OR "red deer" OR "sika deer" OR "fallow deer" OR "feral goat*" OR "wild goat*" OR "feral sheep" OR "wild boar" OR "feral pigs" OR "wild pigs" OR "feral hog*"

[AND]

"population control" [**3570**]

hunting [**23200**]

stalking [**14700**]

culling [**14500**]

shooting [**16100**]

poisoning [**20200**]

contracept* [**2930**]

repellent [**6310**]

deterrent [**8250**]

"supplementary feeding" [**2770**]

trapping [**22600**]

fencing [**20700**]

Animal and Plant Health Agency (APHA) 17/03/20

https://www.gov.uk/government/organisations/animal-and-plant-health-agency

Research and statistics

[Research only/Statistics (published) only] search using the following terms

Deer [**7**/**0**] – 0 relevant

Goat [**18**/**6**] – 0 relevant

Boar [**5**/**0**] – 0 relevant

Wild Pig [**27**/**1**] – 0 relevant

Feral sheep [**21**/**6**] – 0 relevant

Department for Environment Food and Rural Affairs (Defra) 17/03/20

https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs

Research and statistics

[Research only/Statistics (published) only] search using the following terms

Deer [**2**/**1**] – 0 relevant

Goat [**3**/**3**] – 0 relevant

Boar [**7**/**0**] – 0 relevant

Wild Pig [**20**/**45**] – 0 relevant

Feral sheep [**6**/**45**] – 0 relevant

Forestry Commission 17/03/20

https://www.gov.uk/government/organisations/forestry-commission

Research and statistics

[Research only/Statistics (published) only] search using the following terms

Deer [**0**/**0**] – 0 relevant

Goat [**0**/**0**] – 0 relevant

Boar [**0**/**0**] – 0 relevant

Wild Pig [**0**/**0**] – 0 relevant

Feral sheep [**0**/**0**] – 0 relevant

Forest Research 17/03/20

https://www.forestresearch.gov.uk/

Publications and research

Deer [**40**] – 0 relevant

Goat [**4**] – 0 relevant

Boar [**17**] – 0 relevant

Pig [**2**] – 0 relevant (excluded 'wild' term – too many irrelevant hits)

Feral sheep [**7**] – 0 relevant

Natural England 17/03/20

https://www.gov.uk/government/organisations/natural-england

Research and statistics

[Research only/Statistics (published) only] search using the following terms

Deer [**0**/**0**] – 0 relevant

Goat [**0**/**0**] – 0 relevant

Boar [**0**/**0**] – 0 relevant

Wild Pig [**0**/**0**] – 0 relevant

Feral sheep [**0**/**0**] – 0 relevant

Natural Resources Wales 17/03/20

https://naturalresources.wales/evidence-and-data/research-and-reports/?lang=en

Research and Reports

Invasive non-native species reports [**6**] – 0 relevant

Species reports – [**81**] – 0 relevant

Scottish Natural Heritage 17/03/20

https://www.nature.scot/

Information Hub

Information Library

Search for: publications and statistics

Deer [**24**] – **4** relevant (including additional material)

Goat [**0**] – 0 relevant

Boar [**0**] – 0 relevant

Wild Pig [**23**] – 0 relevant

Feral sheep [**3**] – 0 relevant

Game and Wildlife Conservation Trust 17/03/20

https://www.gwct.org.uk/

Research

Scientific Publications

Deer [**34**] – **1** relevant (also captured from other sources)

Goat [**1**] – 0 relevant

Boar [**8**] – 0 relevant

Wild Pig [**0**] – 0 relevant

Feral sheep [**0**] – 0 relevant

Department of Agriculture, Environment and Rural Affairs (Northern Ireland) 17/03/20

Publications

Deer [**6**] – 0 relevant

Goat [**28**] – 0 relevant

Boar [**3**] – 0 relevant

Wild Pig [**74**] – 0 relevant

Feral sheep [**53**] – 0 relevant

Open Grey (www.opengrey.eu) 20/03/20

(muntjac OR "muntiacus reevesi" OR "chinese water deer" OR "hydropotes inermis" OR "roe deer" OR "capreolus capreolus" OR "red deer" OR "cervus elaphus" OR "sika deer" OR "cervus nippon" OR "fallow deer" OR "dama dama" OR "feral goat*" OR "capra aegagrus hircus " OR "wild goat*" OR "feral pig" OR "sus scrofa" OR "feral pigs" OR "feral hog*" OR "feral swine" OR "wild pig" OR "wild pigs" OR "wild hog*" OR "wild boar" OR "feral sheep")

AND

("population control" OR "lethal control" OR hunt* OR cull* OR shoot* OR harvest* OR stalk* OR bait* OR poison* OR trapping OR (inhibit* AND reproduc*) OR immunocontracept* OR contracept* OR "fertility control" OR repel* OR deterrent* OR "diversionary feed*" OR (supplement* AND feed*) OR (supplement* AND food) OR "feed* station$" OR "forest management" OR "landscape structure" OR (manipulat* AND landscape) OR (manipulat* AND habitat) OR fenc*)

Screened title and abstract before download as only individual downloads permitted – only immediately downloadable documents were included

Records: **30**

Relevant: **7 (2 available from ETHOS)**

EThOS (www.ethos.bl.uk) 06/04/20

Can only use single terms related by Boolean operators up to a maximum of 6 terms

Screened title and abstract before download as only individual downloads permitted – only immediately downloadable documents were included

[all records/**immediate download only**]

deer [287/**192**] – 6 relevant

wild boar [18/**10**] – 2 relevant

feral goat [5/**4**] – 1 relevant

feral sheep [0/0] – 0 relevant

Relevant: **8**

S4. Database of articles excluded at the full-text level. Excel spreadsheet available online at https://doi.org/10.1371/journal.pone.0267385.s004

S5. Systematic map database. Excel spreadsheet available online at https://doi.org/10.1371/journal.pone.0267385.s005

Chapter 3: Supporting information

S6. Study information form given to landowners or land managers to collect human activity data

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STUDY INFORMATION FORM

Study title: Identifying the drivers of fallow deer (*Dama dama*) distribution, resource use and movement

WHY IS THIS SURVEY NEEDED?

This survey is part of a larger study exploring the effects of the environment on the use of woodlands by fallow deer. Fallow deer influence woodlands in a variety of ways. Low-level deer activity may improve the cycling of nutrients and control the growth of dominant plant species. However, higher levels of activity can impact the natural regeneration of woodlands, leading to declines in biodiversity and a reduction of their economic value. Understanding why some woodlands are used more frequently by fallow deer than others can help us to manage populations and other natural resources more sustainably.

We are using camera-trap technology to identify important landscape features that influence woodland-use by deer. The images captured by the cameras will be used to develop a statistical model that relates deer activity to information about the environment. Data for some environmental features, such as roads and buildings, can be obtained from satellite imagery. This survey is designed to estimate human activity in woodlands, which is more difficult to assess remotely. We need this information so that we can answer important questions such as:

- Does recreational activity, such as dog walking or cycling affect woodland-use by deer?
- Does stalking affect deer activity in woodlands?
- How does woodland management, such as felling or planting, affect woodland-use by deer?

HOW WILL THE INFORMATION BE USED?

The information collected in this survey will be used for research purposes only. Participant details will not be disclosed in any published material or presentation. Survey data will not be displayed spatially (i.e. plotted on a map) with any identifiable features, such as place names or landmarks, in any published material or presentation. The data will be stored on the Bangor University network. Only personnel directly involved with the project (i.e. supervisors, collaborators, industry partners) will be granted access to the data.

WHAT IS INVOLVED IN THE SURVEY?

You will be asked a total of 7 questions relating to human activity in a woodland. The questions are broadly related to 3 types of disturbance: (1) **lethal or potentially lethal** (i.e. stalking), (2) **recreational** (i.e. hiking) and (3) **habitat** (i.e. woodland management). Answers to these questions will be assigned a score from 0 to 3 based on the criteria given in the variable scoring sheet. The majority of questions require a separate response for each of the three camera seasons described below.

HOW DO I RAISE A CONCERN?

If you have any complaints or concerns regarding the survey then please contact my supervisor, Dr Graeme Shannon. His contact details are as follows:

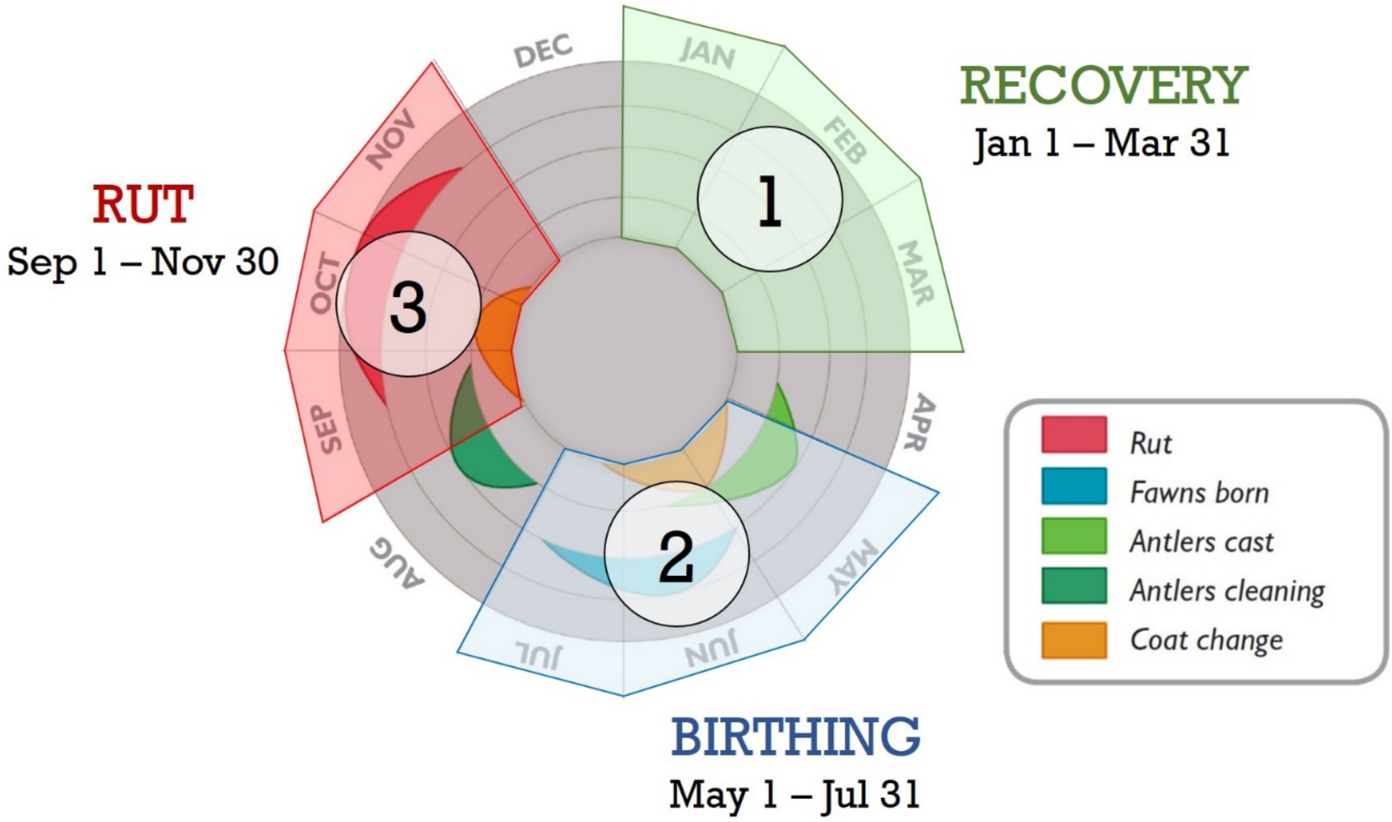
Dr Graeme Shannon
Lecturer
School of Natural Sciences
Bangor University
Bangor, Gwynedd
LL57 2UW

Email: g.shannon@bangor.ac.uk
Phone: 01248 382318

DEFINITION OF TERMS

Term	Definition
Stalking	Locating and following deer
High-seat use	Sitting in an elevated chair
Shooting	Discharging a firearm
Other recreational activity	Human activity that does not intentionally threaten the life of deer or modify habitat (e.g. walking, dog walking, running, cycling, bird watching etc.)
Woodland management	Human activity that intentionally changes the structure and/or composition of habitat (e.g. felling trees, planting trees, landscaping, strimming etc.)

CAMERA SEASONS



SCORE SHEET

UnitID:

	Survey season		
Variable	**1** (Jan 1 – Mar 31)	**2** (May 1 – Jul 31)	**3** (Sep 1 – Nov 30)
Stalking			
High-seat use			
Shooting			
Recreational activity			
Woodland management			
History of Stalking or High-seat use			

VARIABLE SCORING

Variable	Score	Description
Stalking	0	No stalking occurred
	1	Stalking occurred at an average rate of **less than one** day per week
	2	Stalking occurred at an average rate of **one to three** days per week
	3	Stalking occurred at an average rate of **more than three** days per week
High-seat use	0	No high-seat use occurred
	1	High-seat use occurred at an average rate of **less than one** day per week
	2	High-seat use occurred at an average rate of **one to three** days per week
	3	High-seat use occurred at an average rate of **more than three** days per week
Shooting	0	No discharge of a firearm occurred
	1	Firearm discharge occurred at an average rate of **less than one** day per week
	2	Firearm discharge occurred at an average rate of **one to three** days per week
	3	Firearm discharge occurred at an average rate of **more than three** days per week
Woodland management	0	No habitat modification occurred
	1	**Minimal** habitat modification occurred (no structural changes, low-level activity such as the collection of dead trees and plant material for firewood, no powered equipment)
	2	**Moderate** habitat modification occurred (minor structural changes including occasional tree felling/planting and/or regular activity including the use of personal powered equipment only, such as a chainsaw or strimmer)
	3	**Extensive** habitat modification occurred (major structural changes such as clear felling and/or very frequent activity including the use of large machinery such as harvesters or diggers)
Other recreational activity	0	No recreational activity occurred
	1	Recreational activity occurred at an average rate of **less than one** day per week
	2	Recreational activity occurred at an average rate of **one to three** days per week
	3	Recreational activity occurred at an average rate of **more than three** days per week
History of Stalking or High-seat use	0	No stalking or high-seat use has occurred for at least 5 years
	1	Stalking or high-seat use has been ongoing for **one year or less**
	2	Stalking or high-seat use has been ongoing for **more than one year but less than five years**
	3	Stalking or high-seat use has been ongoing for a **minimum of 5 years**

QUESTIONS

Question 1

During camera season [1/2/3] how often did stalking occur?

Question 2

During camera season [1/2/3] how often did high-seat use occur?

Question 3

During camera season [1/2/3] how often did shooting occur?

Question 4

During camera season [1/2/3] how often did other recreational activity occur?

Question 5

During camera season [1/2/3] what extent of habitat modification occurred?

Question 6 (note: 0 if Question 1 and 2 = 0)

For how long has stalking or high-seat use been ongoing?

Question 7

Do you have any other information relating to human activity that may be relevant?

OTHER INFORMATION

S7. Participant consent form given to landowners or land managers to collect human activity data

---

PARTICIPANT CONSENT FORM

Study title: Identifying the drivers of fallow deer (*Dama dama*) distribution, resource use and movement

Purpose of study: To better understand why some woodlands are used by fallow deer more than others, how woodland-use changes over time and what features of the landscape promote or limit population spread.

Please initial each box

1 I confirm that I have read and understand the information sheet for the above study. I have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. ☐

2 I understand that my participation is voluntary and that I am free to withdraw at any time, without giving any reason, and without any adverse consequences or penalty. ☐

3 I understand that withdrawal from this survey will not prevent me from being involved with any other elements of the above study now or in the future ☐

4 I understand that research data collected during the study may be looked at by authorised people outside the research team. I give permission for these individuals to access the data. ☐

5 I understand that this project has been reviewed by, and received ethics clearance through, the Bangor University Research Ethics Committee. ☐

6 I understand who will have access to personal data provided, how the data will be stored and what will happen to the data at the end of the project. ☐

7 I understand how this research will be written up and published. ☐

8 I understand how to raise a concern or make a complaint. ☐

9 I agree to take part in the above study ☐

____

UnitID

______________________ dd / mm / yy ______________________

Name of Participant Date Signature

______________________ dd / mm / yy ______________________

Name of person Date Signature
taking consent

Chapter 4: Supporting information

S8. Survey effort, number of detections and detection rate in camera days (number of cameras multiplied by the number of days of operational deployment) for each primary and secondary subsets of the camera data used in daily activity pattern analyses of fallow deer (*Dama dama*) in the Elwy Valley study area. Rec = recreation. WM = woodland management.

Subset type	Covariate 1 category	Covariate 2 category	Survey effort (Camera days)	Detections (n)	Detection rate (Detections per camera day)
Primary	All		13478	8409	0.62
	Year (2019)		6589	3653	0.55
	Year (2020)		6889	4756	0.69
	Rut		4697	3312	0.71
	Post rut		4271	1180	0.28
	Birthing		4510	3917	0.87
	Hunted		7022	3335	0.47
	Not-hunted		6456	5074	0.79
	Rec (High)		5275	3195	0.61
	Rec (Low)		8203	5214	0.64
	WM (High)		4852	2579	0.53
	WM (Low)		8626	5830	0.68
	BIOSEASON	**HUNTING**			
Secondary	Post rut	Hunted	2039	353	0.17
	Post rut	Not-hunted	2232	827	0.37
	Rut	Hunted	2135	1500	0.70
	Rut	Not-hunted	2562	1812	0.71
	Birthing	Hunted	2221	1444	0.65
	Birthing	Not-hunted	2289	2473	1.08
	BIOSEASON	**REC**			
Secondary	Post rut	Rec (High)	1589	506	0.32
	Post rut	Rec (Low)	2682	674	0.25
	Rut	Rec (High)	1804	1063	0.59
	Rut	Rec (Low)	2893	2249	0.78
	Birthing	Rec (High)	1882	1626	0.86

	Birthing	Rec (Low)	2628	2291	0.87
	BIOSEASON	**WM**			
Secondary	Post rut	WM (High)	1491	505	0.34
	Post rut	WM (Low)	2780	675	0.24
	Rut	WM (High)	1802	860	0.48
	Rut	WM (Low)	2895	2452	0.85
	Birthing	WM (High)	1559	1214	0.78
	Birthing	WM (Low)	2951	2703	0.92
	HUNTING	**Rec**			
Secondary	Hunted	Rec (High)	2420	711	0.29
	Hunted	Rec (Low)	4602	2624	0.57
	Not-hunted	Rec (High)	2855	2484	0.87
	Not-hunted	Rec (Low)	3601	2590	0.72
	HUNTING	**WM**			
Secondary	Hunted	WM (High)	3170	811	0.26
	Hunted	WM (Low)	3852	2524	0.66
	Not-hunted	WM (High)	1682	1768	1.05
	Not-hunted	WM (Low)	4774	3306	0.69

S9. Number of camera sites per landowner/land manager in the Elwy Valley study area in relation to human disturbance: Hunting (*Not-hunted/Hunted*), Recreation (*Rec, Low/High*) and Woodland management (*WM, Low/High*).

	n sites	Sites per landowner (n)				
		Min	Max	Median	Mean	SD
All	30	1	7	2	2	1.6
Not-hunted	15	1	3	1	1.5	0.7
Hunted	15	1	5	2	2.1	1.5
Rec (Low)	14	1	5	1	1.8	1.4
Rec (High)	16	1	2	1	1.5	0.5
WM (Low)	12	1	6	1	2	2
WM (High)	18	1	2	1.5	1.5	0.5

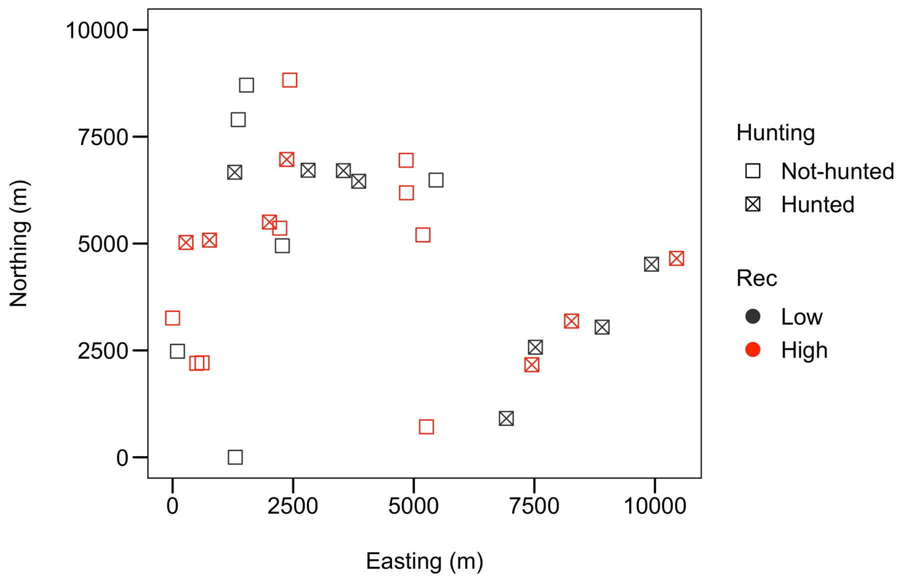
S10. Number of cameras deployed in each of the six survey seasons (2019-2020), grouped by two site-level covariates: hunting (hunted vs. not-hunted) and recreation (high vs. low). Mean proportion = Mean number of cameras from the six survey seasons divided by the total number of cameras (n=29).

			Hunted		Not-hunted	
Year	Survey season	Bioseason	Rec (High)	Rec (Low)	Rec (High)	Rec (Low)
2019	1	Post rut	6	9	6	8
	2	Birthing	6	9	7	7
	3	Rut	6	9	7	7
2020	4	Post rut	5	10	5	9
	5	Birthing	5	10	7	7
	6	Rut	5	10	6	8
		Mean Proportion	0.19	0.33	0.22	0.26

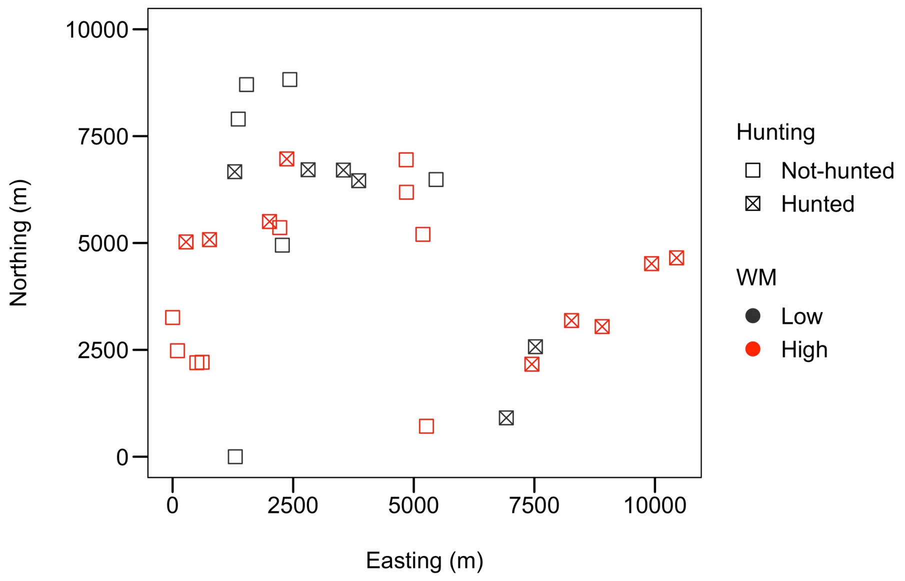
S11. Number of cameras (total n=29) deployed in each of the six survey seasons (2019-2020), grouped by two site-level covariates: hunting (hunted vs. not-hunted) and woodland management (high vs. low). Mean proportion = Mean number of cameras from the six survey seasons divided by the total number of cameras (n=29).

			Hunted		Not-hunted	
Year	Survey season	Bioseason	WM (High)	WM (Low)	WM (High)	WM (Low)
2019	1	Post rut	7	8	6	8
	2	Birthing	8	7	3	11
	3	Rut	7	8	7	7
2020	4	Post rut	7	8	2	12
	5	Birthing	6	9	3	11
	6	Rut	6	9	3	11
		Mean proportion	0.24	0.28	0.14	0.34

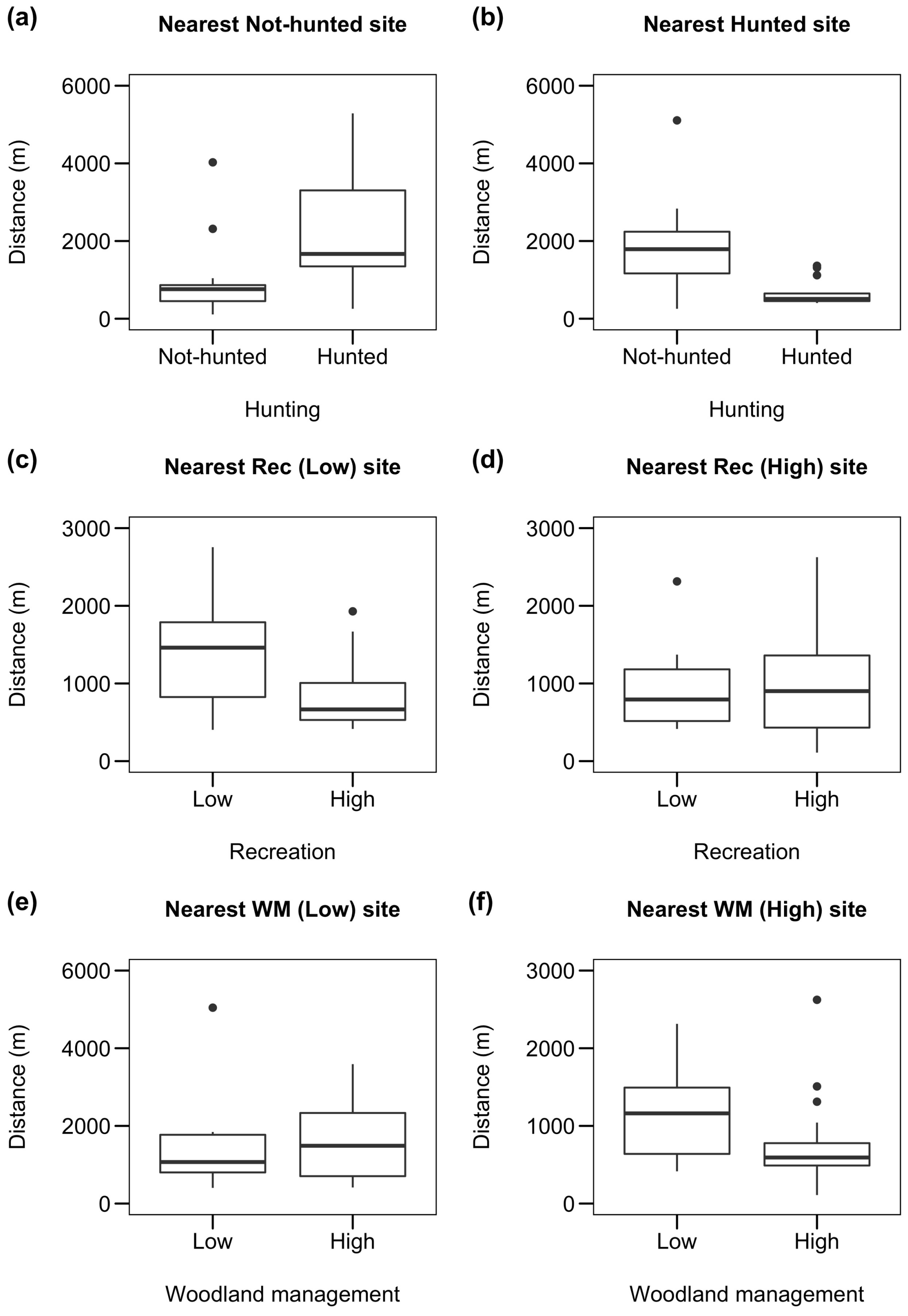
(a) Hunting and Recreation



(b) Hunting and Woodland management



S12. Distribution of camera sites in the Elwy Valley study area in relation to human disturbance: Hunting (Not-hunted/Hunted), Recreation (Rec, Low/High) and Woodland Management (WM, Low/High). Coordinates have been standardised to show the relative positioning of cameras for data protection reasons.



S13. Distance to nearest neighbouring camera site for cameras deployed in the Elwy Valley study area in relation to human disturbance: Hunting (Not-hunted/Hunted), Recreation (Rec, Low/High) and Woodland Management (WM, Low/High).

S14. Number of detections (n) across the three diel time periods: crepuscular, diurnal and nocturnal within each primary (one covariate) and secondary (two-covariate) subsets (rows) of the camera data used in daily activity pattern analyses of fallow deer in the Elwy Valley study area. Selection ratios (w) indicate the relative use of each period (i.e., proportion of detections) given their availability (i.e., proportion of the total length of data collection). The results of the Pearson chi-squared test (X^2) of the randomness of activity distribution across the three diel time periods are included.

Covariate 1 category	**Covariate 2 category**	**Crepuscular**		**Diurnal**		**Nocturnal**		**Pearson chi-squared test (X^2, df=2)**	
		n	w	**n**	w	**n**	w		
All		2269	1.62	4203	1.16	1937	0.57	1235.45	< 0.001
Year (2019)		999	1.64	1769	1.12	885	0.60	503.94	< 0.001
Year (2020)		1270	1.60	2434	1.18	1052	0.55	736.93	< 0.001
Rut		952	1.72	1228	1.03	1132	0.72	409.48	< 0.001
Post rut		375	1.91	426	1.09	379	0.64	240.48	< 0.001
Birthing		942	1.44	2549	1.08	426	0.47	402.27	< 0.001
Hunted		996	1.79	1380	0.97	959	0.71	467.08	< 0.001
Not-hunted		1273	1.51	2823	1.27	978	0.49	895.75	< 0.001
Rec (High)		755	1.42	1872	1.34	568	0.45	631.37	< 0.001
Rec (Low)		1514	1.74	2331	1.04	1369	0.65	744.07	< 0.001
WM (High)		645	1.50	1501	1.35	433	0.42	600.22	< 0.001
WM (Low)		1624	1.67	2702	1.07	1504	0.65	742.49	< 0.001
BIOSEASON	**HUNTING**								
Post rut	Hunted	114	1.94	73	0.62	166	0.94	68.91	< 0.001
Post rut	Not-hunted	261	1.89	353	1.28	213	0.52	228.01	< 0.001
Rut	Hunted	439	1.76	487	0.90	574	0.81	174.17	< 0.001
Rut	Not-hunted	513	1.70	741	1.13	558	0.65	259.93	< 0.001
Birthing	Hunted	436	1.81	816	0.94	192	0.57	223.63	< 0.001
Birthing	Not-hunted	506	1.23	1733	1.17	234	0.41	262.89	< 0.001
BIOSEASON	**REC**								
Post rut	Rec (High)	151	1.79	219	1.30	136	0.54	121.92	< 0.001
Post rut	Rec (Low)	224	1.99	207	0.92	243	0.72	138.83	< 0.001
Rut	Rec (High)	289	1.63	490	1.27	284	0.57	193.08	< 0.001
Rut	Rec (Low)	663	1.77	738	0.91	848	0.80	271.51	< 0.001
Birthing	Rec (High)	315	1.16	1163	1.19	148	0.39	181.82	< 0.001
Birthing	Rec (Low)	627	1.64	1386	1.01	278	0.52	279.65	< 0.001
BIOSEASON	**WM**								

Post rut	WM (High)	173	2.06	213	1.26	119	0.47	174.93	< 0.001
Post rut	WM (Low)	202	1.80	213	0.95	260	0.77	90.06	< 0.001
Rut	WM (High)	217	1.51	465	1.50	178	0.44	242.47	< 0.001
Rut	WM (Low)	735	1.80	763	0.86	954	0.82	313.36	< 0.001
Birthing	WM (High)	255	1.26	823	1.13	136	0.48	101.94	< 0.001
Birthing	WM (Low)	687	1.52	1726	1.06	290	0.46	312.34	< 0.001
HUNTING	**REC**								
Hunted	Rec (High)	202	1.70	283	0.93	226	0.78	73.85	< 0.001
Hunted	Rec (Low)	794	1.82	1097	0.98	733	0.68	397.60	< 0.001
Not-hunted	Rec (High)	553	1.34	1589	1.43	342	0.36	644.26	< 0.001
Not-hunted	Rec (Low)	720	1.67	1234	1.10	636	0.61	360.60	< 0.001
HUNTING	**WM**								
Hunted	WM (High)	253	1.87	348	0.99	210	0.64	143.81	< 0.001
Hunted	WM (Low)	743	1.77	1032	0.97	749	0.72	329.23	< 0.001
Not-hunted	WM (High)	392	1.33	1153	1.53	223	0.31	583.76	< 0.001
Not-hunted	WM (Low)	881	1.60	1670	1.14	755	0.59	446.47	< 0.001

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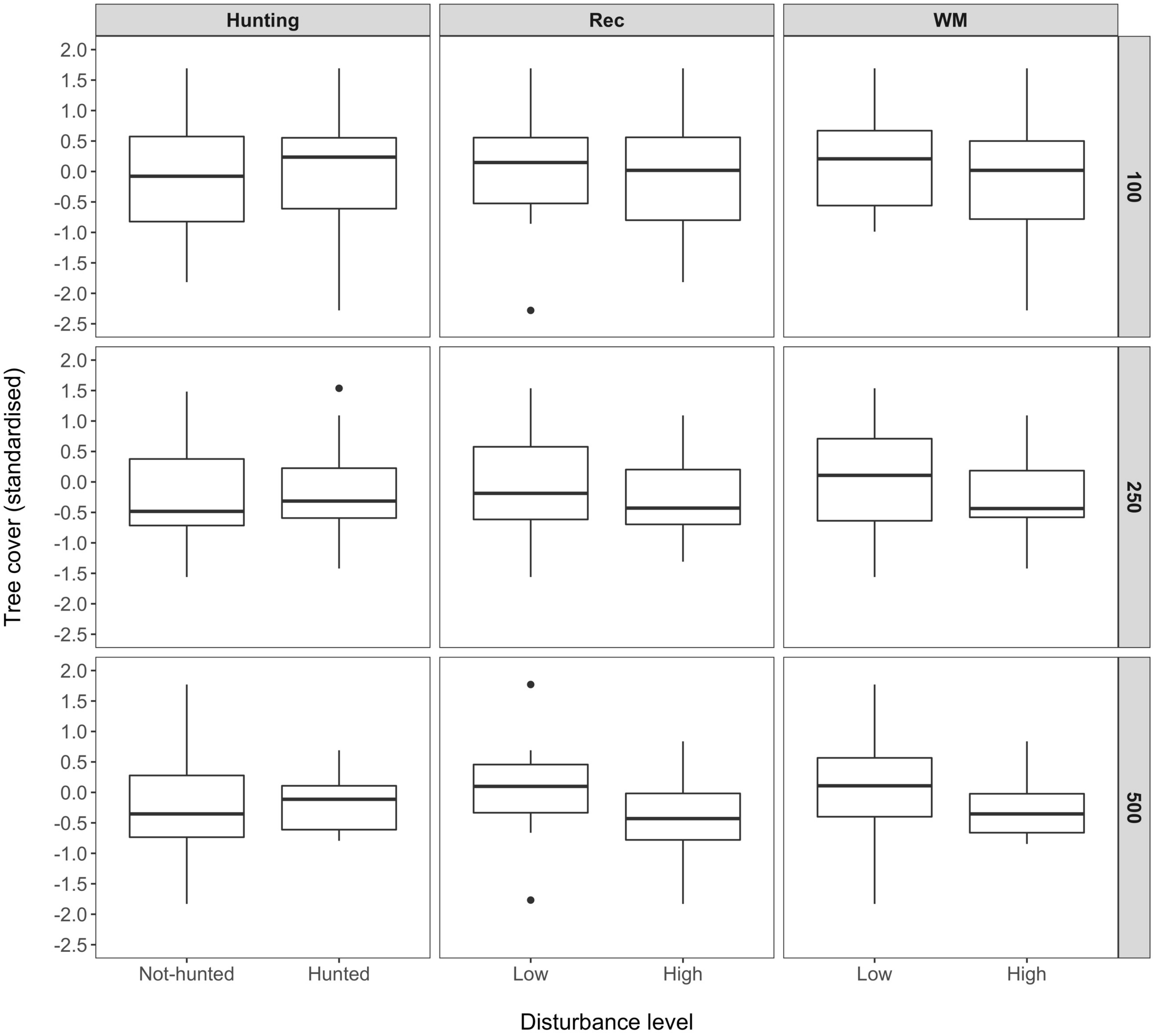
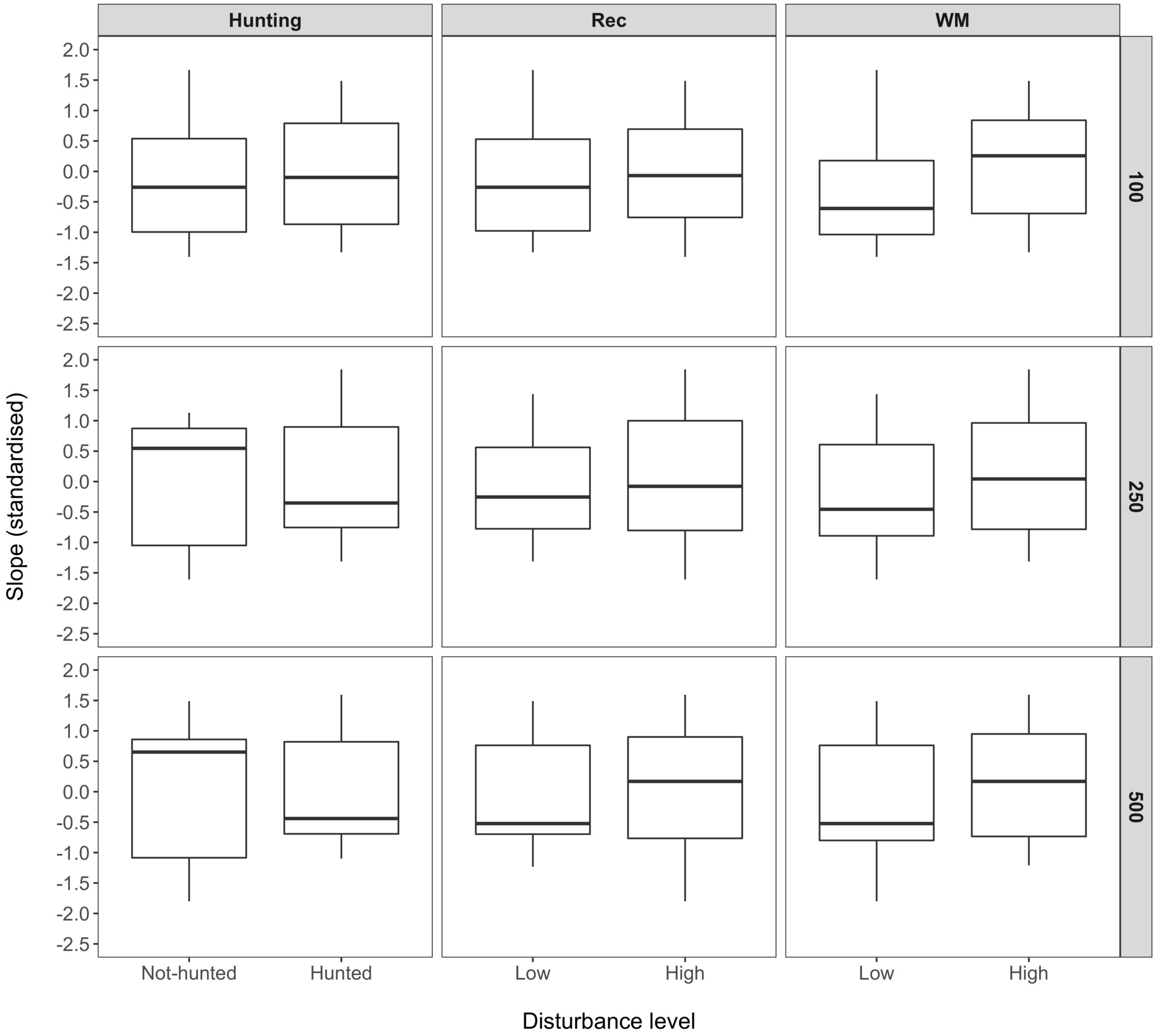
S15. Pearson correlation coefficients (r) used to estimate collinearity between environmental covariates used in the occupancy and detection rate analyses of fallow deer in the Elwy Valley region of North Wales, UK. Integers along the outermost row and column indicate the radius of the buffer region (in meters) around each of the cameras used to summarise the data (see Chapter 3 for details of the collection and processing of environmental data). HERB = herbaceous vegetation cover. TREE = tree cover. SLOPE = mean land slope angle. **Bold** numbers indicate collinear ($r > 0.7$) covariates. * indicates covariates that were removed from analyses.

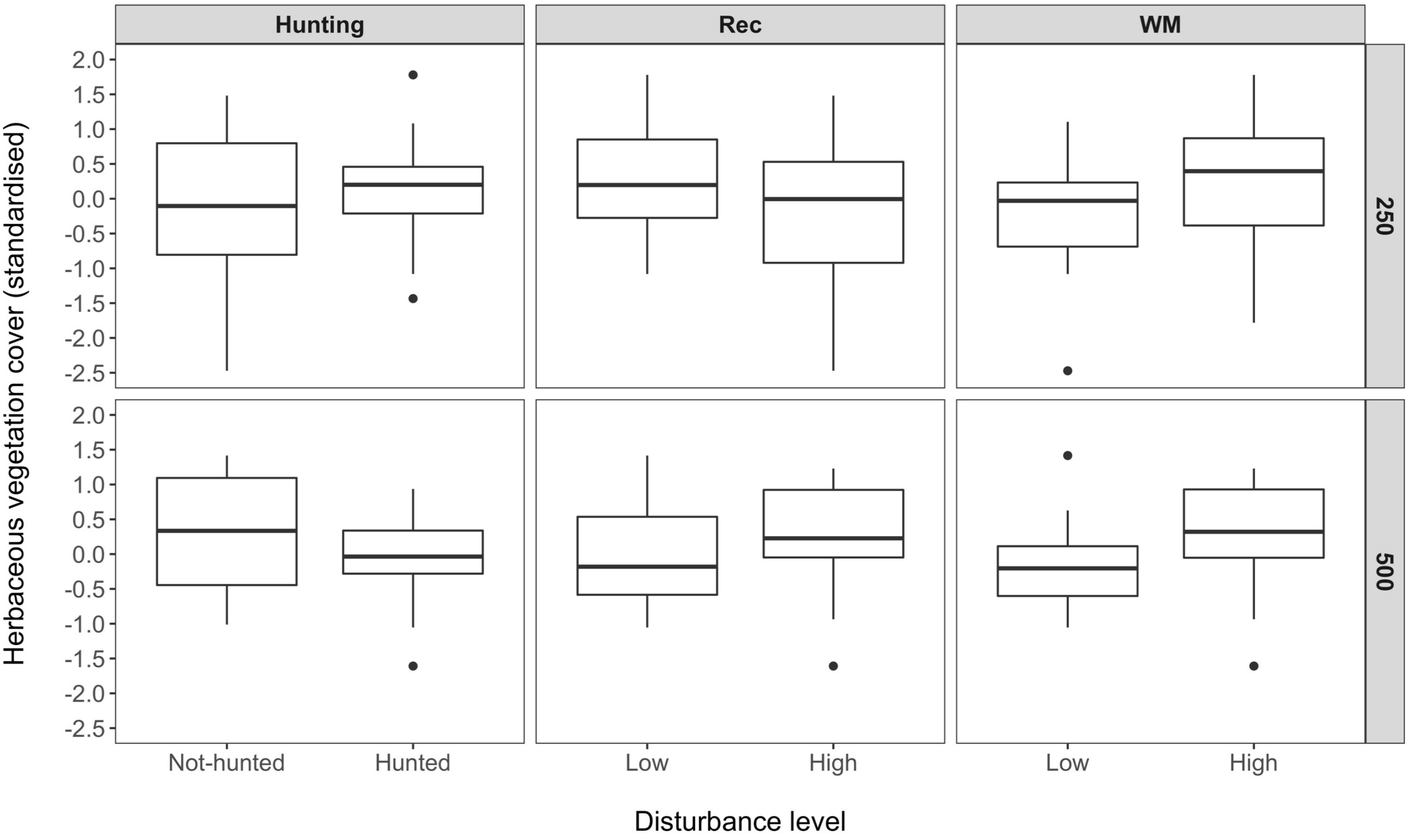
		100			250			500		
		HERB*	**TREE**	**SLOPE**	**HERB**	**TREE**	**SLOPE**	**HERB**	**TREE**	**SLOPE**
100	**HERB***	-	**-0.82**	-0.20	-	-	-	-	-	-
	TREE	**-0.82**	-	0.39	-	-	-	-	-	-
	SLOPE	-0.20	0.39	-	-	-	-	-	-	-
250	**HERB**	-	-	-	-	-0.50	-0.15	-	-	-
	TREE	-	-	-	-0.50	-	0.46	-	-	-
	SLOPE	-	-	-	-0.15	0.46	-	-	-	-
500	**HERB**	-	-	-	-	-	-	-	-0.22	0.13
	TREE	-	-	-	-	-	-	-0.22	-	0.47
	SLOPE	-	-	-	-	-	-	0.13	0.47	-



S16. Relationship between tree cover and human disturbance covariates (Hunting: *Not-hunted/Hunted*, Recreation: *Rec, Low/High* and Woodland Management: *WM, Low/High*) used in the occupancy and detection rate analyses of fallow deer in the Elwy Valley region of North Wales, UK. Integers along the right of each row indicate the radius of the buffer region (in meters) around each of the cameras used to summarise the data (see Chapter 3 for details of the collection and processing of environmental data).



S17. Relationship between slope and human disturbance covariates (Hunting: *Not-hunted/Hunted*, Recreation: *Rec, Low/High* and Woodland Management: *WM, Low/High*) used in the occupancy and detection rate analyses of fallow deer in the Elwy Valley region of North Wales, UK. Integers along the right of each row indicate the radius of the buffer region (in meters) around each of the cameras used to summarise the data (see Chapter 3 for details of the collection and processing of environmental data).



S18. Relationship between herbaceous vegetation cover and human disturbance covariates (Hunting: *Not-hunted/Hunted*, Recreation: *Rec, Low/High* and Woodland Management: *WM, Low/High*) used in the occupancy and detection rate analyses of fallow deer in the Elwy Valley region of North Wales, UK. Integers along the right of each row indicate the radius of the buffer region (in meters) around each of the cameras used to summarise the data (see Chapter 3 for details of the collection and processing of environmental data).

S19. Results from the occupancy analyses for fallow deer in the Elwy Valley region of North Wales, UK in which sources of variation in detection probability (p) were investigated. psi = occupancy. BIOSEASON = biological season, TREE = tree cover, SLOPE = mean land slope angle, WM = woodland management, REC = recreation, HUNT = hunting (for details on the covariates see Chapter 3). Numbers given after covariate names indicate the radius of the buffer region used to summarise the data. Information is provided on the structure of the global model used to assess overall model fit.

Model	**AICc**	**npar**	**ΔAICc**	**wgt**
psi(General)p(General)	13681.53	16	0.00	1
psi(General)p(BIOSEASON + TREE_100 + SLOPE_100 + WM)	13746.10	13	64.57	0
psi(General)p(BIOSEASON + TREE_100 + SLOPE_100 + HUNT)	13748.49	13	66.96	0
psi(General)p(BIOSEASON + TREE_100 + SLOPE_100)	13755.41	12	73.88	0
psi(General)p(BIOSEASON + SLOPE_100 + HUNT + WM)	14167.58	13	486.05	0
psi(General)p(BIOSEASON + SLOPE_100 + WM)	14174.89	12	493.36	0
psi(General)p(BIOSEASON + SLOPE_100 + HUNT)	14191.27	12	509.74	0
psi(General)p(BIOSEASON + SLOPE_100)	14201.61	11	520.08	0
psi(General)p(BIOSEASON + TREE_100 + HUNT + WM)	14223.35	13	541.82	0
psi(General)p(BIOSEASON + TREE_100 + HUNT)	14234.89	12	553.36	0
psi(General)p(BIOSEASON + TREE_100 + WM)	14239.18	12	557.65	0
psi(General)p(BIOSEASON + TREE_100)	14254.06	11	572.53	0
psi(General)p(BIOSEASON + HUNT + WM)	14371.13	12	689.60	0
psi(General)p(BIOSEASON + WM)	14383.69	11	702.16	0
psi(General)p(BIOSEASON + HUNT)	14392.40	11	710.87	0
psi(General)p(BIOSEASON)	14408.80	10	727.27	0

Note:

Global model = psi(General)p(General)

General psi = psi~TREE_500+HERB_500+SLOPE_250+HUNT+REC+WM

General p = p~BIOSEASON+TREE_100+HERB_250+SLOPE_100+HUNT+REC+WM

S20. Summary of the procedure used to determine the structure of the detection rate models used to estimate patterns of habitat-use by fallow deer in the Elwy Valley region of North Wales, UK.

The following procedure for model selection based on methods used in previous studies (Hansen et al., 2020; Kays et al., 2020)

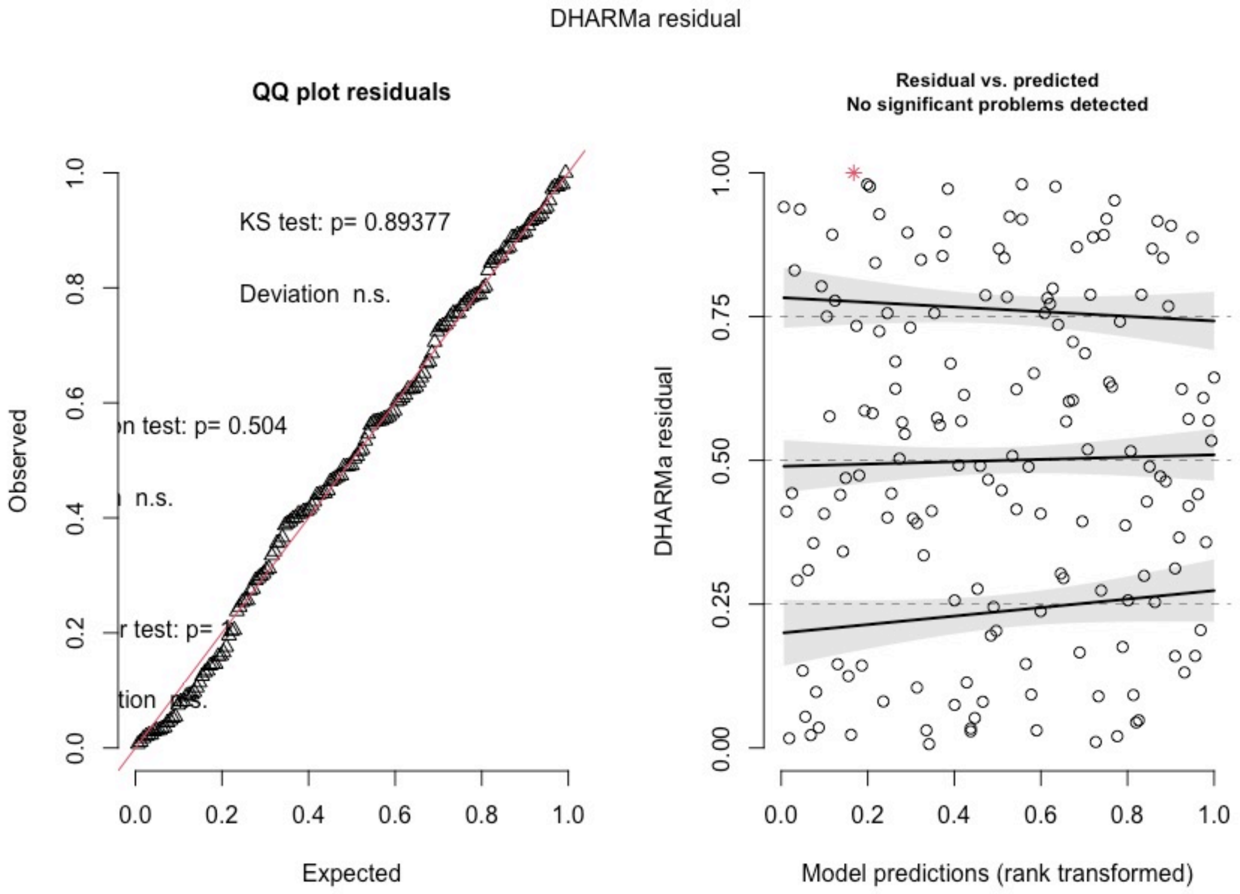
- Initially a poisson logistic regression model was fit with number of independent detections (separated by ≥ 10 mins) for each site-season (DETS, see Chapter 5 for definition of site-season) as the response and the natural log of the number of operational camera days per site-season (ln(CAMDAYS)) as an offset term. The maximum number of CAMDAYS was 90. Site-seasons that were not surveyed (i.e., CAMDAYS = 0, n = 7) were removed. Two sites (n = 12 site-seasons) failed to record a single detection over the study duration and were also removed. A total of 161 site-seasons were considered for the detection rate analysis.
- The performance of a fixed effects model was compared to a mixed effects model with a different intercept for each SITE (DETS ~ 1 vs. DETS ~ (1|SITE)), based on AICc values. The mixed effects model was considered to account for spatial autocorrelation and unmodelled heterogeneity in conditions between sites. The mixed effects model performed substantially better (AICc = 4779) than a fixed effects model (AICc = 11966) and was used for subsequent models
- Covariates from the global occupancy model (S19) were used to assess the fit of a global detection rate model (DETS ~ (1|SITE)+BIOSEASON+TREE_500+HERB_500+SLOPE_250+HUNT+REC+WM).
- The ‘DHARMa’ package was used, which utilises a simulation-based approach to estimate residuals from fitted mixed effects models
- The poisson model showed evidence of overdispersion and zero-inflation
- Three alternative models were developed (1) a zero-inflated poisson, (2) a negative binomial and (3) a zero-inflated negative binomial
- The zero-inflated poisson model showed evidence of overdispersion and the negative binomial model showed evidence of zero-inflation. The zero-inflated negative binomial showed no evidence of overdispersion or zero-inflation and the plotted

residuals indicated good model fit. A zero-inflated negative binomial model was therefore used for all staged of the detection rate analyses (Chapter 5).

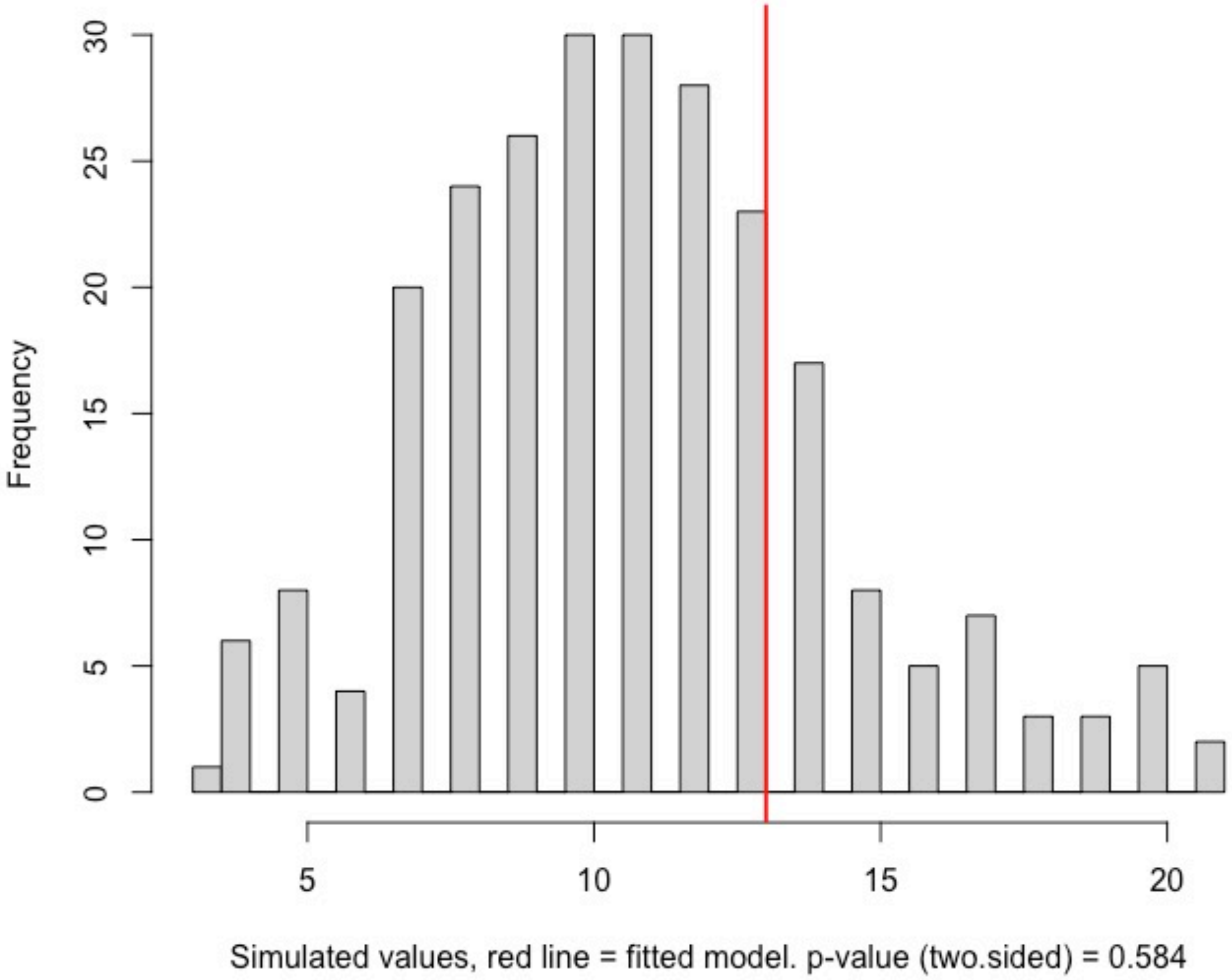
S21. Results from the assessment of model fit for the occupancy analyses of fallow deer in the Elwy Valley region of North Wales, UK.

- Pr = 0.98 (probability of observing a test statistic from the bootstrapped data set ≥ the test statistic for model fit – closer to 1 indicates better model fit, Mackenzie & Bailey, 2004)
- c-hat = 0.91 (measure of overdispersion – nearer to 1 indicates lower overdispersion)

S22. Residual plots from the DHARMa (Hartig, 2022) residual diagnostics tests of the top-ranked detection rate model (glmmTMB(DETS~(1|SITE)+BIOSEASON+TREE_100+SLOPE_250+REC, family="nbinom2", offset = CAMDAYS_ln, ziformula = ~1). For covariate details see Chapters 3 and 5.



S23. DHARMa (Hartig, 2022) zero-inflation test via comparison to expected zeros with simulation under H0 = fitted model, using the top-ranked detection rate model (glmmTMB(DETS~(1|SITE)+BIOSEASON+TREE_100+SLOPE_250+REC, family="nbinom2", offset = CAMDAYS_ln, ziformula = ~1). For covariate details see Chapters 3 and 5.



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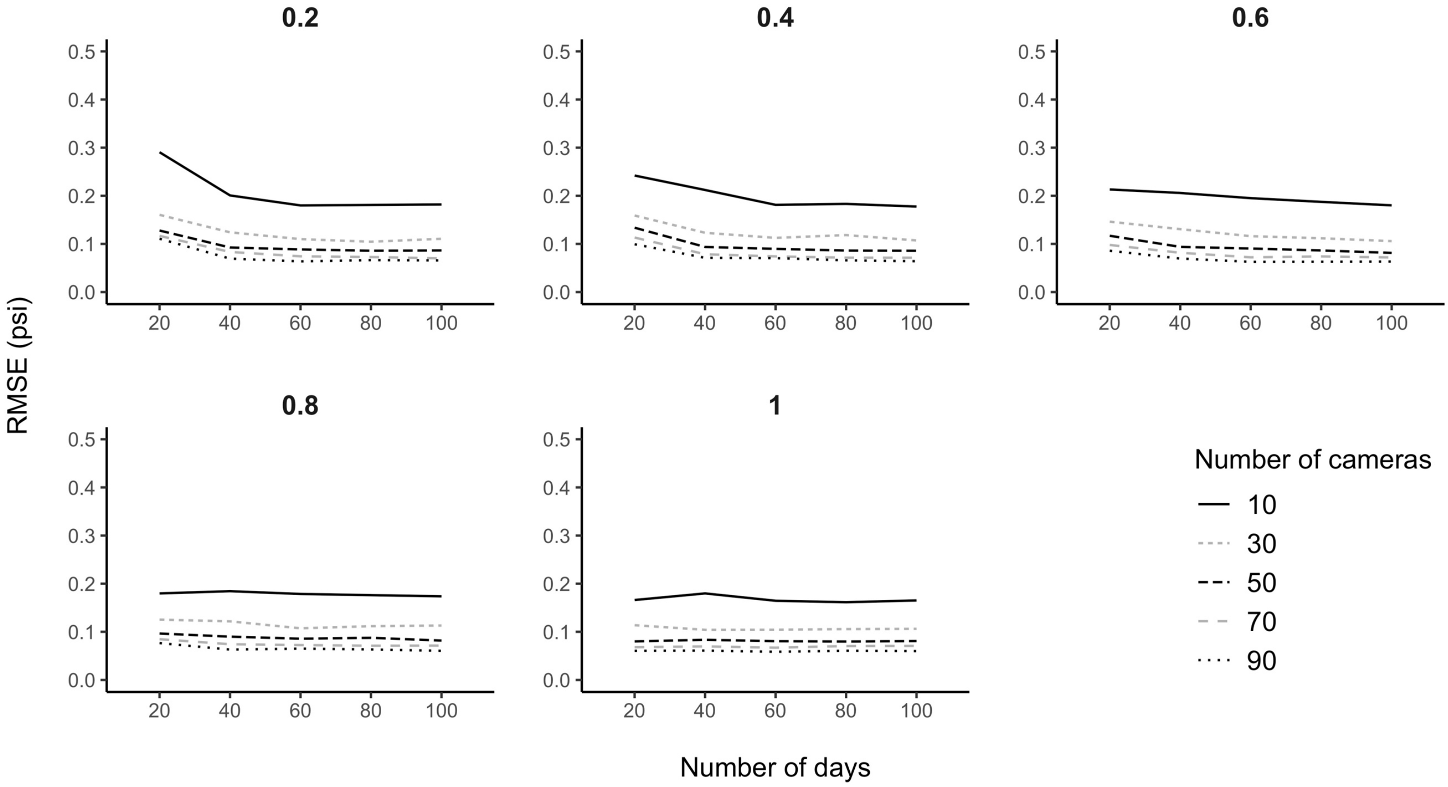
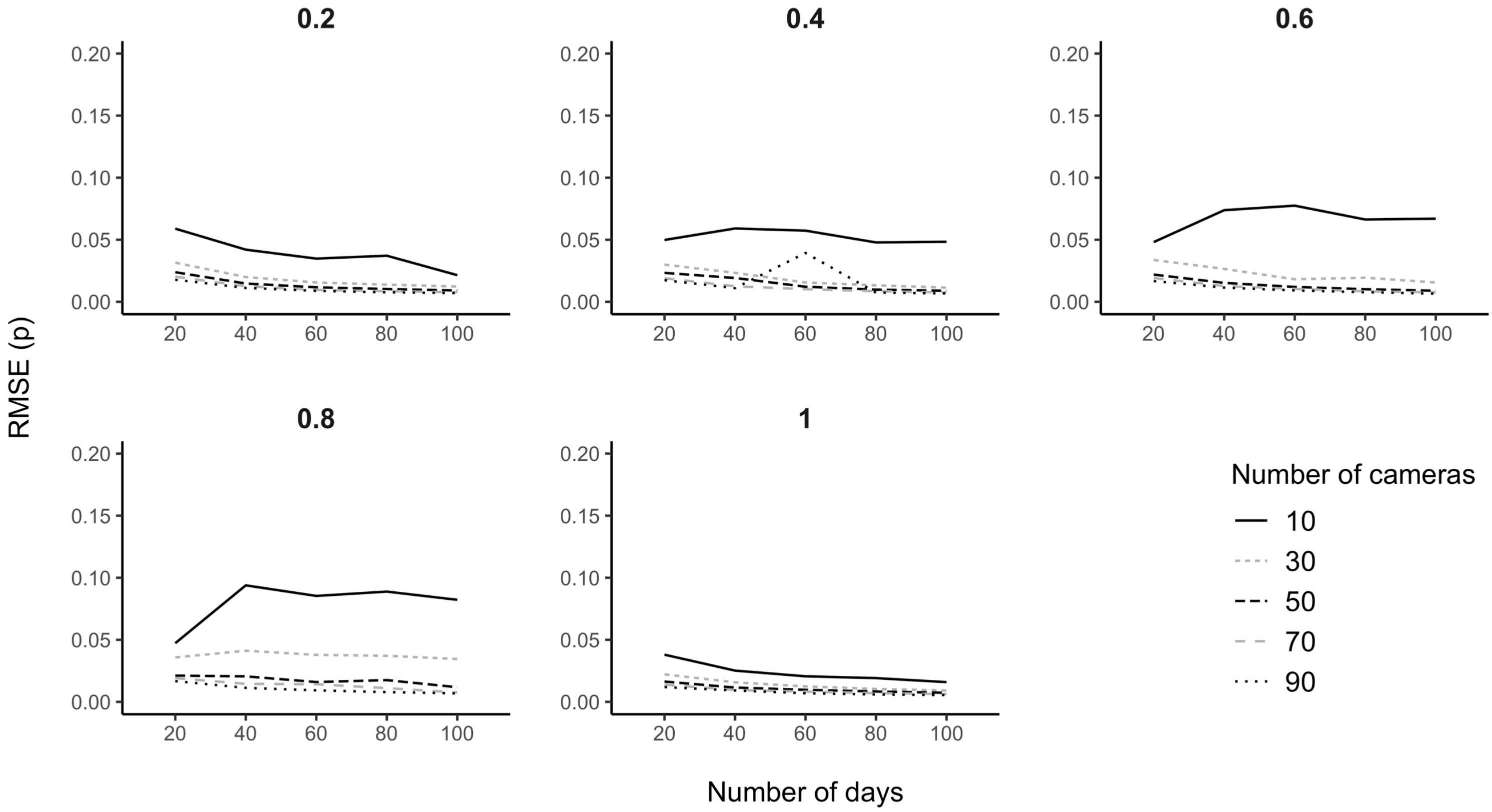
S24. Proportion of simulation sets (unique combinations of number of cameras, number of days and *Prop*, total n=150) with > 10% invalid models. For a model to be valid it had to meet the following criteria: (1) converge to a minimum of 3 significant digits, (2) no variance-covariance (VC) warnings, (3) naive occupancy >0 and <1 and (4) β estimates <= 6.906755 and >= -6.906755, which represents a maximum of a 0.999 change in the estimate of a parameter (ψ or p) for a 1 standard deviation unit change in the covariate.

	Proportion of simulation sets with >10% invalid models (n)	
Reason for invalidation	**Dot models**	**Covariate models**
Variance-covariance matrix	<0.01 (1)	0.09 (13)
Convergence	0	0.09 (13)
Invalid beta estimate (psi)	_	0.23 (34)
Invalid beta estimate (p)	_	0.03 (5)



S25. Root mean squared error (RMSE) for estimates of occupancy (psi) from covariate models in relation to the number of cameras and number of days of deployment. Bold numbers above are the proportion of camera sites located in habitat patches (*Prop*).



S26. Root mean squared error (RMSE) for estimates of detectability (p) from covariate models in relation to the number of cameras and number of days of deployment. Bold numbers above are the proportion of camera sites located in habitat patches (*Prop*).