Spatial and behavioural impacts of disturbance on red deer, Cervus elaphus, in the Scottish uplands

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SMITH, EILIDH,MARGARET,WALKER (2025) *Spatial and behavioural impacts of disturbance on red deer, Cervus elaphus, in the Scottish uplands*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/16041/

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Eilidh Margaret Walker Smith

Abstract

Human activity in wildlife habitat has increased significantly in recent decades, causing widespread changes in animal movement and behaviour. These changes can lead to cascading environmental, welfare, and economic effects. Deer, *Cervids*, are of particular environmental and economic importance. This is especially true of red deer in Scotland, where contrasting management imperatives and land uses, including outdoor recreation, often lead to conflict. I investigated the effects of hillwalking on red deer within a focal estate in Scotland.

I found that red deer responded to hillwalker disturbances by substantially avoiding paths and altering their behaviour. Higher numbers of hillwalkers led to a more concentrated deer distribution, potentially causing significant ecological consequences from overgrazing and trampling. All measures of disturbance studied showed some response to hillwalker disturbances, though the extent varied depending on spatial and temporal contexts. Deer respond to disturbance in multiple ways, necessitating diverse approaches to accurately assess these responses. This complexity was highlighted by reviewing existing research on deer responses to recreation and hunting. Disturbance responses occurred over varying spatial and temporal scales, which must be considered when quantifying these behaviours. Cover is a critical modulator of deer disturbance responses; while topography can provide some protection, vegetation is more effective at reducing disturbance impacts. The study suggests that in open areas with high human disturbance, providing woodland cover and refuge zones can mitigate impacts on wildlife. Current tree planting initiatives in Scotland could be directed more effectively for this purpose. Additionally, the Scottish Outdoor Access Code should be updated to inform the public about the specific effects of hillwalking on deer, emphasising the importance of staying on established paths in sensitive areas to minimise wildlife impacts.

The results of this thesis underscore the value of tracking individual deer to understand the full extent of disturbance responses and their ecological and economic consequences, despite the challenges in obtaining such data. This research highlights the complexity of wildlife responses to human activities and emphasises the importance of tailored management strategies to mitigate these impacts for the benefit of both wildlife and human interests.

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By

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2024

Thesis submitted for the degree of Doctor of Philosophy

Acknowledgements

I would like to thank all the people that made this project possible. This was not always an easy task. Firstly, I would like to thank my supervisors, Phil Stephens and Sean Twiss, for their input from start to finish. Phil, in particular, has been saddled with much of the paperwork that comes with making a project like this happen, so thank you for your patience as well as your support and guidance in the last few years. I would also like to thank project partners Solène Marion, Urška Demšar, Scott Newey, Jed Long, and Althea Davies for your advice along the way. Special thanks to Solène for your input from the beginning.

Secondly, I would not have been able to complete this work without the support of North Chesthill estate. Thank you Alastair and Joe for all the time, effort, and logistical support you put in to make this project happen. Not to mention all the hours spent talking about deer. Thank you as well to Nick for use of the cabin in the woods that provided everything a soggy field researcher could need.

The collaring aspect of this project would not have been possible without the dedication and veterinary expertise of Neil Anderson. Thank you very much, and I hope the winters of your future are warmer. Thank you as well to Gidona Goodman for your advice throughout the licensing and training process. I would also like to thank all the volunteers who came out in their free time to provide their veterinary expertise.

Finally, thank you to all the family and friends that have supported me throughout this PhD, and taken the time to give thoughtful feedback on sections of the thesis.

Chapter 1. General introduction

1.1 Human-Wildlife Interactions in the Anthropocene: human impact on wildlife

The Anthropocene has been accompanied by a dramatic increase in human impact on natural environments, characterised by substantial encroachment into wildlife habitats. This increase is driven by trends in changing land use patterns, development, and recreation, with wider consequences for biodiversity and climate stability. Human-wildlife interactions in this context manifest in a number of forms, exerting various pressures on wildlife populations and ecosystems.

Infrastructure development, including residential buildings and energy projects such as mining and wind farms, fragments habitats and disrupts wildlife movement. Roads and traffic not only create physical barriers to animal migration (Passoni *et al.*, 2021) but also increase mortality rates due to vehicle collisions (Wakeling, Najar and O'Dell, 2007). Agricultural activities alter land use patterns, often resulting in habitat destruction and increased competition for resources between wildlife and livestock (Lemly, Kingsford and Thompson, 2000; Butt and Turner, 2012; Stears and Shrader, 2020; Yadav, Sachan and Dwivedi, 2024). Intensive farming creates monocultures that reduce landscape heterogeneity and resilience to habitat fragmentation, while extensive farming practices reduce the amount of land dedicated to nature (Gordon, 2018; Priyadarshana *et al.*, 2024). Intensive hunting directly reduces wildlife populations through increased mortality and indirectly affects behaviour and habitat use (Ikeda and Koizumi, 2024). Motorised recreation activities, such as all-terrain vehicle (ATV) riding and snowmobiling, cause significant disturbance through noise pollution and habitat degradation (Freddy, Bronaugh and Fowler, 1986; Trip and Wiersma, 2015; Wisdom *et al.*, 2018a). Non-motorised recreational activities like hiking, biking, horse riding, and skiing also lead to disturbances that affect wildlife behaviour and habitat use (Reimers, Sindre and Colman, 2003; Naidoo and Burton, 2020).

Wildlife responses to these disturbances are diverse but terrestrial species have generally been observed to exhibit greater responses to disturbance (Tablado and Jenni, 2017). Spatial avoidance is a common response in which animals temporarily or permanently move away from disturbed areas (Végvári *et al.*, 2011; Bateman and Fleming, 2017; Smith *et al.*, 2022a). Wildlife may also display substantial shifts in activity patterns (Martin *et al.*, 2010; Lewis *et al.*, 2021) or reduce activity overall (Nix *et al.*, 2018). Other behavioural responses include increased vigilance (Worku *et al.*, 2021) and changes in habitat use (Ngoprasert, Lynam and Gale, 2007), while decreased survival rates can also occur (Lamb *et al.*, 2020). Furthermore, chronically-elevated stress hormone levels indicate physiological stress, which can have long-term health consequences (Cañadas Santiago *et al.*, 2020).

Wildlife may exhibit coping mechanisms such as habituation, where animals become accustomed to human presence and show reduced behavioural responses over time (Bejder *et al.*, 2009; Wheat and Wilmers, 2016). This can also have negative consequences when wildlife cause damage to property or become dangerous (Herrero and Higgins, 2003; Ndava and Nyika, 2019) and may not represent a true cessation of disturbance response (Beale and Monaghan, 2004). Conversely, sensitisation can occur, leading to heightened responses to human activities if disturbances are perceived as increasingly threatening (Bejder *et al.*, 2009).

Understanding the complex dynamics of human-wildlife interactions in the Anthropocene is crucial for developing effective conservation and management strategies. By comprehensively studying these interactions, we can help mitigate the negative impacts of human activities on wildlife and promote coexistence in shared landscapes.

1.2 Land use conflicts, the environment, and wildlife

Land use conflicts are prevalent across the globe, varying to some degree by region but with common themes. Human activity has substantially altered landscapes, worldwide, through infrastructure development and expanding urban areas, timber harvesting, and intensive agriculture (de Jong *et al.*, 2021). Continued demand for land to meet human needs of food production, fuel, housing, industry, and recreation causes conflict between different land users, and places strain on the environment.

In many parts of Africa, conservation and wildlife tourism clash with local communities' needs for land for subsistence farming, access to hunting, firewood and water (Bob, 2011). In turn, wildlife tourism and trophy hunting come into conflict around ethical debates on trophy hunting (Mbaiwa and Hambira, 2023). Historical, and ongoing, conflicts between indigenous land uses and commercial interests in Africa are reflected in North America. Native American land use practices played a significant part in forming the ecology of much of the continent (Anderson and Moratto, 1996). However, the extirpation of the indigenous people from their native homelands has led to ongoing conflict over ownership as well as changes in the environment associated with the shift in landscape management (Anderson and Moratto, 1996; Keeley, 2002).

National parks and natural areas in North America are often characterised by high levels of tourism and recreation. Tourism and conservation goals for land use come into conflict when high levels of tourism facilitate the expansion of infrastructure and environmental degradation (Ingram and Smart, 2018). Impacts of recreation on conservation-based land use goals are similar to those of tourism, with greater emphasis on wildlife disturbance and path erosion (Salesa and Cerdà, 2020; Visscher *et al.*, 2023). National park nature-based objectives can also come into conflict with neighbouring land when predators leave the parks, threatening and killing both livestock and people (Bangs and Shivik, 2001; Linnell and Alleau, 2016).

Predator densities are generally lower in Europe than in North America, but relatively recent expansions of wolf, *Canis lupus*, populations have caused similar conflicts around livestock depredation (Rigg *et al.*, 2011). Parallel conflicts also exist in relation to the impact of tourism and recreation on the environment (Young *et al.*, 2005). Additional constraints occur in tourist and recreation mountain hotspots where the associated infrastructure development competes with traditional pastoral ways of life in the valley bottoms, where land availability is limited (Garcia-Ruiz and Lasanta-Martinez, 1993).

Despite environmental, economic, and social differences between regions, globally, patterns of land use conflict have common threads. Thus, research in one region can often reveal fundamental principles and strategies that are applicable in other contexts.

1.3 Red deer and the Scottish context

Red deer, *Cervus elaphus*, in Scotland are of significant environmental, economic, and cultural importance. Environmentally, they play a key role in shaping vegetation communities and influencing ecosystem dynamics via grazing, browsing, and trampling (Schütz *et al.*, 2003). Economically, red deer are a valuable resource for sport hunting and as a tourist attraction (Macmillan and Phillip, 2008). Culturally, they are an iconic species, integral in Scottish natural heritage and traditions (Edwards and Kenyon, 2013). In mainland Europe, red deer are closely associated with forest and woodland habitat but, in Scotland, they have also adapted to open hills due to the absence of extensive forests (Mitchell, Staines and Welch, 1977).

The open hills of the Scottish uplands are often associated with sporting estates or ‘deer forests’: land on which red deer stalking (hunting) is the primary use. These have been a significant part of land use in the Scottish uplands since the 19th century (Wightman and Higgins, 2000). Historically, red deer have been a source of land use conflict in Scotland where land for sport hunting was favoured over the livelihoods of tenant farmers, exacerbating existing socio-economic inequalities (Morgan-Davies, Wilson and Waterhouse, 2015). In modern Scotland, deer stalking and hill farming coexist as land uses across the Scottish uplands. Increasingly, land managed for ecological restoration (‘rewilding’) is replacing more traditional land uses. This change is largely driven by the growing popularity of rewilding, and carbon credit schemes that allow corporations to offset their carbon emissions by actions such as afforestation and peatland restoration (Brown, 2020; Martin *et al.*, 2021). Land is also owned by non-governmental organisations (NGOs) and managed for conservation.

These land uses are closely integrated with land ownership. However, due to Scottish access laws the public hold ‘right to responsible access’ to land across Scotland according to the *Land Reform (Scotland) Act 2003*. This provides widespread access for the public to pursue activities in the Scottish uplands such as hillwalking, rock climbing, mountain biking, cross-country skiing, and camping. Outdoor recreation represents a significant part of the Scottish economy and has been growing in popularity in recent decades (Higgins, 2000; Morgan-Davies, Wilson and Waterhouse, 2015). However, outdoor recreation is also a source of contention amongst other land users, and has the potential to negatively impact wildlife and the environment.

Access conflicts in Scotland include: soil erosion around paths, caused by large numbers of hillwalkers; gates left open, allowing livestock to escape; attacks on livestock by dogs; and disturbance of deer, affecting commercial stalking and deer management activities (MacMillan and Leitch, 2008; MacKay and Prager, 2021; Hunter, 2024). Cause and effect in most of these conflicts is clear and, whilst they remain difficult to solve, that is not a result of poor understanding of the system. In contrast, conflict surrounding the impacts of deer disturbance on commercial stalking and deer management is complex, with little agreement regarding even the scale of the problem. As a result, the situation is likely to benefit from research quantifying the extent to which outdoor recreation affects red deer distribution and behaviour.

The population of red deer in Scotland has more than doubled since the mid-20th century, causing widespread concern over the potential for environmental degradation (Pepper, Barbour and Glass, 2020). These concerns remain, despite more recent suggestions that population growth has declined (Pepper, Barbour and Glass, 2020) and that herbivore densities in Scotland may be generally lower than those observed elsewhere globally (Fløjgaard *et al.*, 2022). The current deer management model is based on deer management groups (DMGs), which are organised around population units to promote cohesive management strategies, largely operating on a voluntary basis (Edwards and Kenyon, 2013). The responsibility of population control is associated with the landowner, but voluntary agreements may be entered into with NatureScot (Scotland’s governmental nature agency) when current deer management is failing to prevent significant environmental damage (Pepper, Barbour and Glass, 2020). These agreements introduce strict cull targets for landowners. If they are not met by the landowners, Nature Scot can intervene to achieve the target and charge the landowner for doing so.

Given the responsibility of landowners and the importance associated with deer management, concerns over the impact of outdoor recreation on deer management require careful consideration. Recreational activities can affect deer distribution across the landscape (Vistnes *et al.*, 2008; Sibbald *et al.*, 2011), with potential to displace deer from important stalking grounds and concentrate deer in smaller areas causing vegetation damage. Larger group sizes that form due to disturbances (Skogland and Grøvan, 1988), and increased vigilance (Reimers *et al.*, 2010; Tsunoda, 2021) can further complicate stalking efforts. These disruptions can also negatively impact deer body condition and welfare, especially during calving and breeding (rut) seasons (Phillips and Alldredge, 2000; Lovari *et al.*, 2007). Therefore, balancing recreational use with effective deer management and conservation is essential to maintaining deer welfare and management efficacy.

1.4 Red deer biology

Red deer, *Cervus elaphus*, are taxonomically located within the *Cervidae* family. Historically, there has been considerable taxonomic debate as to whether *C. elaphus* populations in Europe and North America form part of a single *C. elaphus* complex, or two distinct species (Polziehn and Strobeck, 1998). In recent decades it has become more widely accepted to consider the two populations as separate species, with the North American population of elk (or wapiti) commonly referred to as *Cervus canadensis* (Ludt *et al.*, 2004).

Red deer naturally occur widely throughout Europe (Zachos and Hartl, 2011). Red deer are sexually dimorphic, with adult males (stags) weighing on average 25-30% (Mitchell, Staines and Welch, 1977), and as much as 50% (Pemberton, Kruuk and Clutton-Brock, 2022), more than adult females (hinds). Average weight of adult hinds is approximately 80-90 kg and stags 120 kg, but these weights vary depending on time of year, reproductive status, and population (Mitchell, Staines and Welch, 1977). Stags grow antlers annually but the hinds do not have antlers (Mitchell, Staines and Welch, 1977). Antlers are shed each spring and are full grown again by the end of summer. Antler size and form relate to genetics and body condition, with larger antlers representing greater fitness and fecundity (Kruuk *et al.*, 2002). Long-term research on the Isle of Rum in Scotland recorded a maximum age of 16 years for a stag and 24 years for a hind (Pemberton, Kruuk and Clutton-Brock, 2022).

1.4.1 Breeding

The breeding season (rut) occurs in late September to late October (Mitchell, Staines and Welch, 1977). During this period, stags compete for hinds and defend harems (Carranza, Alvarez and Redondo, 1990). Calving occurs in late May and June (Clutton-Brock and Guinness, 1975), with hinds typically separating from the herd to give birth and rejoining once the calves are old enough to keep up. During this time, nursery groups may form. Young calves display hiding behaviour as an anti-predator strategy, concealing themselves among vegetation and rocks while their mothers forage away from the area (Clutton-Brock and Guinness, 1975). Mothers return to feed their calves, moving them to a new location every few hours.

1.4.2 Early life

Calves remain with their mothers beyond weaning, with young stags joining or forming bachelor groups at 2 - 3 years of age (Pemberton, Kruuk and Clutton-Brock, 2022). Hinds usually remain associated with close relatives. While stags reach sexual maturity before 5 years of age, they are unlikely to breed successfully until then due to competition with older males. In the wild, females typically have their first calf at 3 - 4 years of age (Pemberton, Kruuk and Clutton-Brock, 2022).

1.4.3 Feeding

Red deer are ruminants, and daily activity patterns are characterised by foraging and rumination cycles. Interruptions to these cycles can reduce digestive efficiency with consequences for body condition (Mitchell, Staines and Welch, 1977). Red deer are mixed feeders, feeding on a wide variety of grasses, sedges and woody species (Gebert and Verheyden-Tixier, 2001). Hinds are more selective than stags, reflecting the general trend for larger animals to bulk-feed (Clutton-Brock, Iason and Guinness, 1987).

1.4.4 Mortality

In Scotland, red deer have no natural predators, but calves may be vulnerable to golden eagles, sea eagles, and foxes (Mitchell, Staines and Welch, 1977; Clutton-Brock, Guinness and Albon, 1982). Natural mortality in adults is largely associated with environmental conditions, while non-natural mortality is associated with hunting by humans and vehicle collisions (Mitchell, Staines and Welch, 1977; Kirkland *et al.*, 2021).

1.4.5 Distribution

Red deer exhibit sexual segregation throughout most of the year, except during the rut (Alves *et al.*, 2013). This segregation is attributed to differences in sensitivity to weather, nutritional requirements, and social and habitat preferences (Conradt, Clutton-Brock and Guinness, 2000; Alves *et al.*, 2013). Stags typically have larger home ranges and travel further than hinds, and variation in home range occurs in relation to habitat variables, season, and calving (Jarnemo, Nilsson and Wikenros, 2023). GPS collared female red deer at one site in Scotland were found to move, on average, less than 3 km from winter ranges, whereas collared males travelled further, around 3-21 km (Sibbald and R. Hooper, The Macauley Institute, Aberdeen, unpublished data *cited in* Pérez-Espona *et al.*, 2008). Red deer distribution is influenced by forage availability, cover availability, landscape features, and shelter-seeking behaviour (Mitchell, Staines and Welch, 1977; Pérez-Espona *et al.*, 2008; Jarnemo, Nilsson and Wikenros, 2023), in addition to human disturbance (Theuerkauf and Rouys, 2008; Bobrowski, Gillich and Stolter, 2020).

1.4.6 Population and management

The current red deer population in Scotland is estimated between 360,000 – 400,000, but there have been no updates of this figure since 2007 (Pepper, Barbour and Glass, 2020). The majority of Scotland's red deer population are found in the uplands of the geographical Highlands, in contrast with red deer elsewhere in Europe that predominantly occupy woodland habitat (Mitchell, Staines and Welch, 1977). The red deer population is widely considered to be unsustainable at its current levels (Edwards and Kenyon, 2013; Pepper, Barbour and Glass, 2020). The reasons for this primarily relate to the impact that deer have on vegetation. However, deer are also implicated in the spread of ticks and, consequently, Lyme disease due to their contribution to larger tick populations(Gilbert *et al.*, 2012; Gandy *et al.*, 2021), and vehicle collisions and damage to crops are an ongoing concern (Edwards and Kenyon, 2013).

Deer are predominantly managed by voluntary collaboration within population units by deer management groups (DMGs) (Phillip *et al.*, 2009; Edwards and Kenyon, 2013). Upland deer management typically carries out stag culls from the end of August to the end of October. The hind season immediately follows the stag season and continues until mid-February. The national cull has increased in recent years to approximately 79,568, but this is likely to be an underestimation (Pepper, Barbour and Glass, 2020). Fences are also used to confine deer to the uplands to reduce vehicle collisions and prevent damage to conservation or commercial forestry and agricultural interests.

Despite increasing efforts surrounding deer management, conflicts frequently arise between stakeholders with varying management objectives regarding target deer populations (Kirkland *et al.*, 2021). Against this backdrop, increasing our understanding of drivers of red deer movement and behaviour in sensitive environments is crucial. This is particularly important regarding changing and increasing human disturbance across the Scottish uplands.

1.5 Current knowledge of red deer responses to recreation disturbance

There have been few studies on the impacts of outdoor recreation on red deer in Scotland, and those that exist have varying results. Red deer stags on an upland estate in the geographical Highlands reported avoidance of hillwalker paths of 200 m (Sibbald *et al.*, 2011). Another study carried out in a similar area indicated displacement distances greater than 150 m, but were unable to specify further (Marion *et al.*, 2021). Furthermore, Sibbald *et al.,* (2011) found no sign of compensatory use of areas near the path in their study site overnight, whereas findings by Marion *et al*., (2021) showed that avoidance of the path was stronger during the day. Vigilance is often used to measure disturbance in deer because it reflects predation responses (Frid and Dill, 2002). Vigilance studies have been carried out in Scotland on the island of Ulva (O'Neill, 2017), and in the geographical Highlands (Jayakody *et al.*, 2008; Marion *et al.*, 2022a). Two of these studies suggested evidence for habituation processes in red deer (O'Neill, 2017; Marion *et al.*, 2022a), while the third found that red deer were significantly more vigilant in a disturbed site compared to an undisturbed site (Jayakody *et al.,* 2008). Few studies have been carried out elsewhere in Europe on vigilance responses of red deer to recreation disturbance, but spatial avoidance appears to be generally lower in Europe when compared to results in Scotland (Coppes *et al.*, 2017; Scholten, Moe and Hegland, 2018). Further measures of disturbance such as flight behaviour, group structure responses, and activity levels have been studied in other species, disturbance contexts, and countries (Westekemper *et al.*, 2018), but not in Scotland. Quantitative uncertainty therefore remains regarding how deer respond to recreational disturbance in Scotland, and what the underlying mechanisms of variation in responses might be.

1.6 Thesis outline

In this thesis, I explore the effects of hillwalkers on red deer spatial and behavioural patterns on a focal estate in the Scottish uplands (chapters 3 and 4). I examine important context-dependent factors, such as the timing and intensity of hillwalker activity, and landscape features. By quantifying the impact that hillwalkers have on red deer space use and behaviour I aim to identify management implications that can help mitigate conflicts and promote coexistence between land users and wildlife. Additionally, I review the variability in disturbance responses among deer, highlighting how different species and populations react to human activities (chapter 2). Finally, I assess challenges and benefits associated with individual-based, and fine-scale tracking methods (chapter 5). Thereby, I aim to provide a broader context for understanding the specific responses of red deer in Scotland to hillwalkers.

The focus of this thesis is the effect of hillwalkers on red deer. While hunting (stalking) provides important context for the responses of red deer to hillwalkers (Stankowich 2008) there is not sufficient overlap of the recreation season and the stalking season in the study to directly compare the responses. Furthermore, the beginning of the stalking season in September, coincides with changes in behaviour that may also be associated with the breeding season, the rut (Pemberton, Kruuk and Clutton-Brock, 2022). As a result, the scope of this thesis is limited to the consideration of responses of red deer to hillwalkers.

Overall, through this thesis, I seek to contribute to management of red deer in Scotland that balances the needs of wildlife, recreational access, landowner interests, and management imperatives. By understanding and addressing the complexities of human-wildlife interactions, I aim to inform the discussion surrounding land use conflict in Scotland and support the long-term coexistence of red deer and human activities in the Scottish uplands. This research adds to a growing body of literature that studies human impact on wildlife and the environment, providing valuable insights for managing human-wildlife interactions and land use conflicts in the wider global context.

Chapter 2. Responses to human disturbance of deer: do we know enough to generalise?

2.1 Abstract

Predicting wildlife responses to disturbance based on general principles is beneficial to developing conservation and management strategies across multiple contexts. However, wildlife responses to disturbance vary considerably, even within species. Focusing on taxonomic groups may facilitate the identification of generalisations and patterns in disturbance responses by wildlife. Here, I synthesise existing literature on deer, *Cervids*, to evaluate what, if any, generalisations can be made across species, the ways in which deer respond to disturbance, and types of disturbance. Specifically, I focus on non-motorised recreation and hunting. Responses to disturbance varied widely. Despite this, certain trends emerged: body size and sociality have some predictable effects, hunting is generally more disruptive than recreation, and louder activities have a greater impact than quieter ones. High levels of recreation can lead to habituation, but this is less likely if it exists alongside hunting. Cover was an important modulator in all responses, affecting both the magnitude and direction of responses. Importantly, multiple measures of impact are necessary to accurately assess disturbance responses due to trade-offs between different metrics. This review highlights the complex ways in which animals interact with their environment and suggests future research should be driven by specific management problems to maximise its applicability.

2.2 Introduction

Human encroachment into wildlife habitats is becoming increasingly common, with significant implications for wildlife and wildlife management (Balmford *et al.*, 2009). Wildlife often perceive humans as predators, responding to human presence and activities with behaviours typically associated with predator encounters, even when these activities are non-lethal (Frid and Dill, 2002). This has the potential to cause widespread changes in distribution and behaviour patterns, with consequences for important ecosystem processes and biodiversity (Mysterud, 2006; Western and Mose, 2023)

Science seeks to generalise because generalisations allow for the development of broad principles and, crucially, prediction (Peters, 1991). In the context of wildlife science, predictive models based on general principles can inform management and conservation strategies across multiple contexts. However, wildlife responses to disturbance are enormously variable, presenting significant challenges to the goal of generalisation. The types and magnitudes of wildlife responses to disturbance are not uniform, varying both between and within species, as well as across different spatial and temporal contexts and disturbance types (Stankowich, 2008; Tablado and Jenni, 2017). Although this finding is well-supported across studies of a wide range of species, responses within taxonomic groups may be more consistent, enabling the development of guidelines for land and wildlife managers.

Deer, *Cervids*, play an important role in environmental processes as well as being of economic and cultural significance (Rooney and Waller, 2003; Côté *et al.*, 2004; Macmillan and Phillip, 2008; Mcshea, 2012). Behavioural changes in deer are therefore of widespread concern. These changes can affect ecosystem health by altering vegetation patterns, influencing plant community dynamics, and impacting other wildlife species (Waller and Alverson, 1997). Economically, deer contribute to industries such as hunting and wildlife tourism, while holding cultural significance around the world (King, 2002; Macmillan and Phillip, 2008; Peterson *et al.*, 2016). Consequently, disruptions in deer behaviour due to human disturbances, such as recreational activities and hunting, can lead to broader ecological imbalances and economic losses. Understanding and predicting deer responses to disturbance is increasingly important to deer managers due to the critical role deer play in the environment and the economy, and as these disturbances increase. Despite a large body of literature about deer responses to disturbance, an attempt to synthesise that literature and apply it to management priorities is lacking.

In this review, I evaluate disturbance responses across deer species to identify what, if any, generalisations can be made across species, the ways in which deer respond to disturbance, and types of disturbance. I discuss these findings in relation to modulating, context-specific factors that may affect the disturbance responses of deer and I consider the implications for future research and deer management. In particular, I address the following questions:

1. What variation occurs in deer responses to disturbance and what are the sources of variation?
2. Are there common themes in disturbance responses of deer, and can generalisations be made?
3. What are the implications for management and the future direction of research?

2.3 Literature search

2.3.1 Methods

I conducted a systematic literature search and selection process (Figure 2.1). The literature search was carried out in Web of Science with no time limits imposed. The initial search term was "Deer Disturbance Response" in the Web of Science core collection. The first term was designed to cast a wide net from which to identify more specific, relevant search terms. Papers from the search were initially retained based on title and reviewed again for relevance from the abstract before collating the metadata in a database. The initial search results included many human disturbance types which were subsequently narrowed down to non-motorised recreation and hunting due to the low number of studies on other disturbance types.

Keywords were identified from papers in the initial search to refine the second term. In this way, the final search term was an expansion of the original term. The term relating to 'deer' was expanded to include key species/family names, plus 'cervid'. Disturbance specified the types of disturbance of interest and associated synonyms, for example recreation and hiking, and hunting and stalking. Response terms expanded on the description of human-wildlife interactions, without confining the search to significant responses.

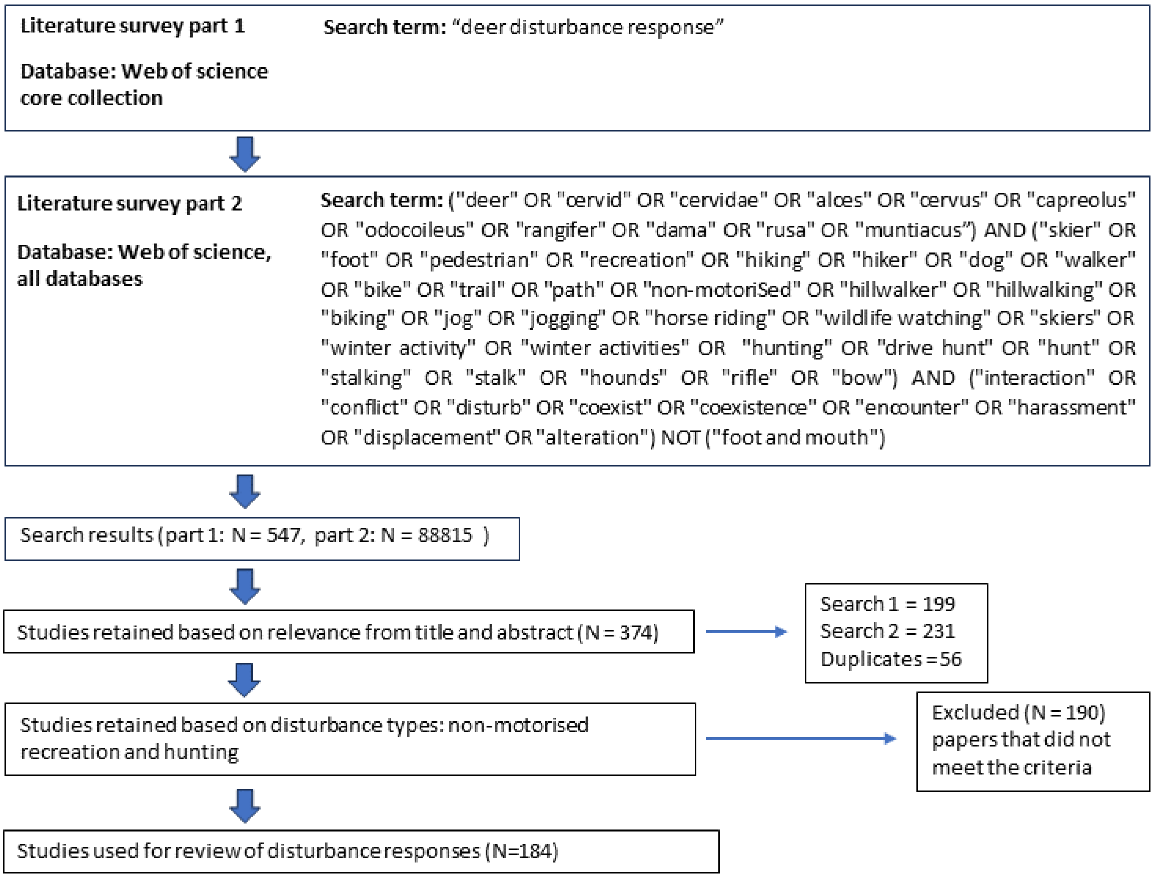

Figure 2.1. Flow diagram of literature search and selection process.

2.3.2 Results

The systematic literature search yielded 184 relevant papers focusing on 21 different deer species (Table 2.1). The most commonly occurring species was elk (*Cervus canadensis,* n = 35). The majority of studies were carried out in Europe or North America, representing 82% of the papers.

Table 2.1. Table of species included in the review and the associated common names, continents on which they were studied, and number of papers.

Latin binomial	Common name	Distribution	Papers
Alces alces	Moose	North America, Europe	12
Capreolus capreolus	Roe deer	Europe	17
Capreolus pygarus	Siberian roe deer	Asia	1
Cervus canadensis	Elk	North America	35
Cervus elaphus	Red deer	Europe, India	32
Cervus nippon	Sika deer	Asia, Europe	7
Dama dama	Fallow deer	Europe	5

Elaphodus cephalophus	Tufted deer	Asia	2
Elaphurus davidianus	Pere David's deer	Asia	1
Mazama americana	Red brocket	South America	3
Mazama chunyi	Dwarf brocket	South America	1
Mazama nemorivaga	Brown brocket	South America	1
Mazama gouazoubira	Gray brocket	South America	1
Muntiacus muntjak	Barking deer	Asia	1
Muntiacus reevesi	Muntjac	Asia, Europe	2
Odocoileus hemionus	Black tailed deer, mule deer	North America	18
Odocoileus virginianus	White-tailed deer	North America	22
Rangifer tarandus	Caribou, reindeer	North America, Europe	21
Rusa unicolor	Sambar deer	Asia	1

Despite methods such as ground survey and behavioural observation being well established (Ferguson and Keith, 1982; Freddy, Bronaugh and Fowler, 1986), studies were dominated by newer, technological methodologies. The most commonly used methodology occurring in the literature search was telemetry, using either GPS or VHF collars to track individual movements (Figure 2.2). Camera traps were also widely utilised. Telemetry papers were recorded from 1987, with the first GPS collar paper appearing in 2005. The first camera trap paper was published in 2006.

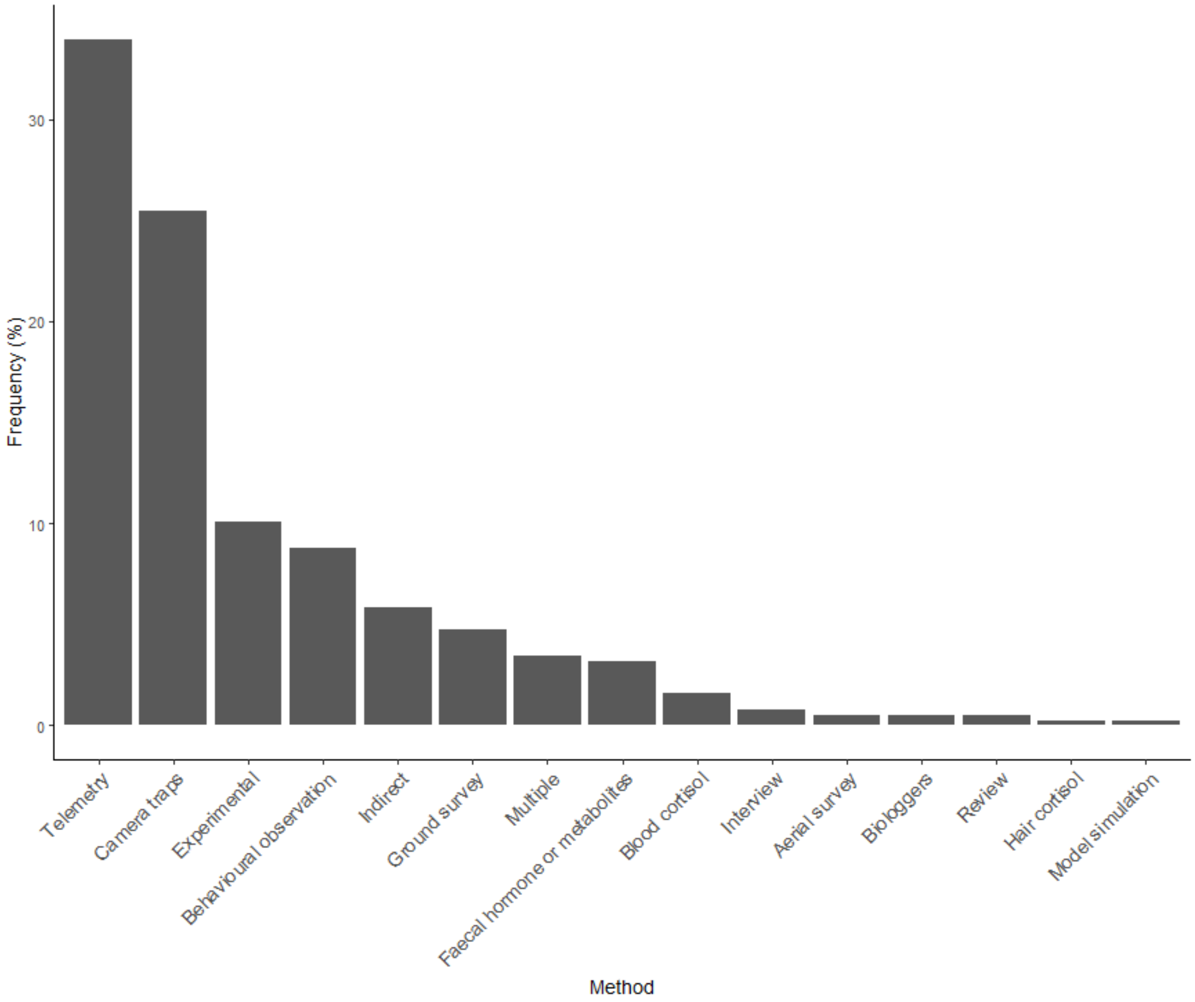

Figure 2.2. The proportion of studies using each data collection method.

2.4 Extracting information from the literature

Disturbance responses of wildlife are suggested to vary between species and disturbance types (Stankowich, 2008; Tablado and Jenni, 2017). Deer may also use different strategies to respond to disturbance; therefore, the detection of disturbance responses may depend on the measure of disturbance being used by the study. To explore the influences of, and nuances within these factors, I first categorised papers according to species, disturbance type, and measure of disturbance (Table 2.2). The combination of these factors leads to many sources of variation when studying responses to disturbance, as illustrated in Figure 2.3.

Table 2.2. Category values and definitions of control variables, disturbance type and disturbance measure, used to compare disturbance responses between studies.

	Definition
Disturbance type	
General recreation	Undefined recreation disturbances or papers in which the effects of different types of recreation were not separated.
Humans on foot	Recreation disturbances specified as humans on foot or where the majority of recreation was on foot, e.g. hiking and winter sports.
Biking	Non-motorised bikes.
Horse riding	Horse riding, pony trekking
Hunting	Rifle hunting on foot.
Hunting with dogs	Drive hunts with dogs.
Bow hunting	Hunting using a bow, archery
Measure of disturbance	
Vigilance	Deer vigilance as head raised or actively alert to indicate level of disturbance.
Habitat use	Habitat use or selection as response to disturbance.
Distribution change	Location in the landscape of individuals or populations, either static (e.g. annual survey) or dynamic (e.g. GPS collar locations) in relation to spatial responses to disturbances.
Migration	Effects of disturbance on migration routes, patterns, or rates.
Stress	Stress hormone levels in relation to disturbance.
Fecundity	Effects of disturbance on population recruitment (conception to offspring survival).
Activity pattern	Daily fluctuations in activity in relation to disturbance, e.g. increased nocturnality.
Flight behaviour	Presence/absence of flight behaviour, flight initiation distance and distance/duration of flights. Defined by immediate response, without making assumptions on longer-term distribution or return times.
Movement	Movement rates either directly measured or inferred by home range size (i.e. larger home ranges suggest greater movement).

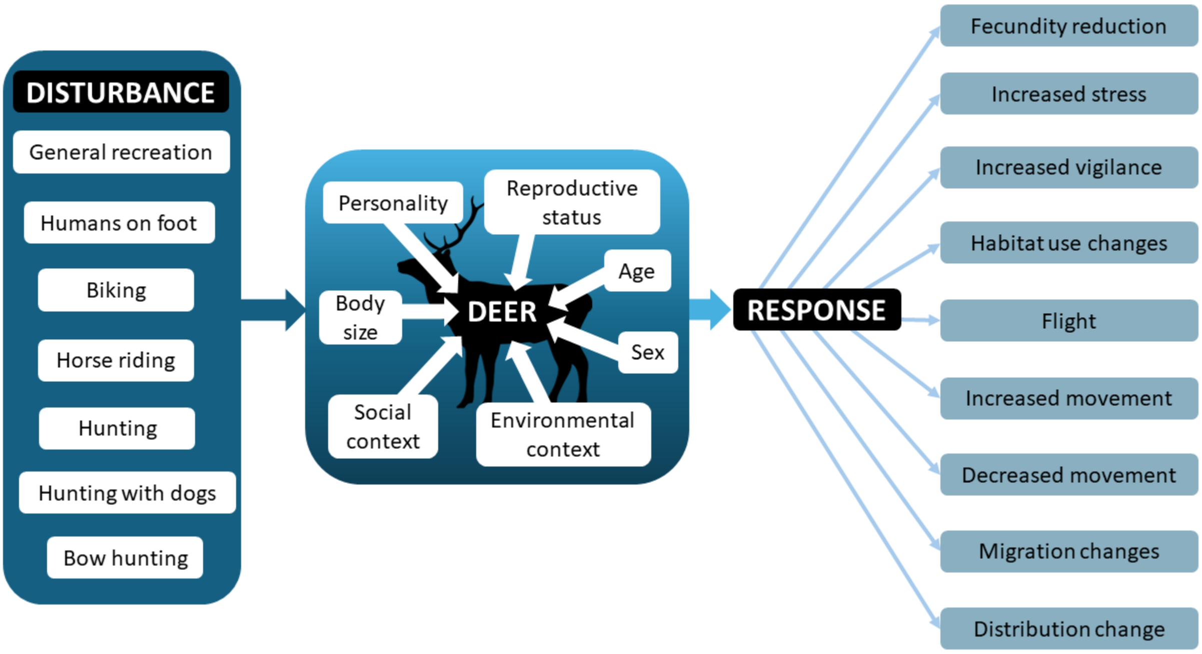

Figure 2.3. The flow of effects on deer response to disturbance, beginning with the disturbance type, then factors relating to individual deer and populations of deer, and finishing with the potential behaviours that occur in response to disturbance, dependent on the previous factors.

To demonstrate the range of variability, I used a vote counting system. Vote counting is limited in its application as a statistical method due to the lack of nuance it provides in relation to the magnitude of responses (Gurevitch *et al.*, 2018). However, due to the very wide range of study designs included in this review, as well as the variety of reporting methods, it was not possible to extract comparable quantitative results. This review aims to illustrate the range of variation in deer responses to disturbances, focusing on the diversity of observed behaviours rather than making quantitative assumptions about their significance. Thus, I used vote counting as a qualitative, visual representation of the range of variability that can occur among species, disturbance types, and disturbance measures.

Votes were organised according to whether the results of the study indicated a response to the disturbance or were reported as no significant response. Votes associated with significant responses to disturbance were further split into two groups (Figure 2.4). The first of these consisted of results that were associated with an increase in disturbance response as disturbances increased, hereafter referred to as ‘sensitive’. For example, sensitive outcomes would be observed where larger disturbance responses, such as greater displacement distance or increased vigilance, are associated with periods of greater disturbance at the same site, or between sites where one site has more disturbance than the other. The second group consisted of results in which disturbance responses were lower when disturbances increased or continued, hereafter referred to as ‘acclimated’. Non-significant results are referred to as indifferent.

In this framing, acclimated results may indicate habituation but are not referred to as such. The classification of habituation is complicated, requiring long-term, repeated measurements; habituation is often dependent on interactions between multiple variables (Bejder *et al.*, 2009). Furthermore, habituation assessment based on behavioural responses may not necessarily indicate a reduction in impact on wildlife from human disturbance (Beale and Monaghan, 2004). Behavioural responses may apparently decline, while stress responses remain, with important implications for welfare and fitness. Despite this, examples where disturbance responses seem to decrease with increasing disturbance levels appear distinct from sensitive responses and may indicate habituation. Sensitisation, distinct from sensitive responses described above, refers to the disproportionate escalation of disturbance responses (Bejder *et al.*, 2009). Sensitisation was only observed in one study, as the result of repeated experimental approaches over the course of a day (Freddy, Bronaugh and Fowler, 1986).

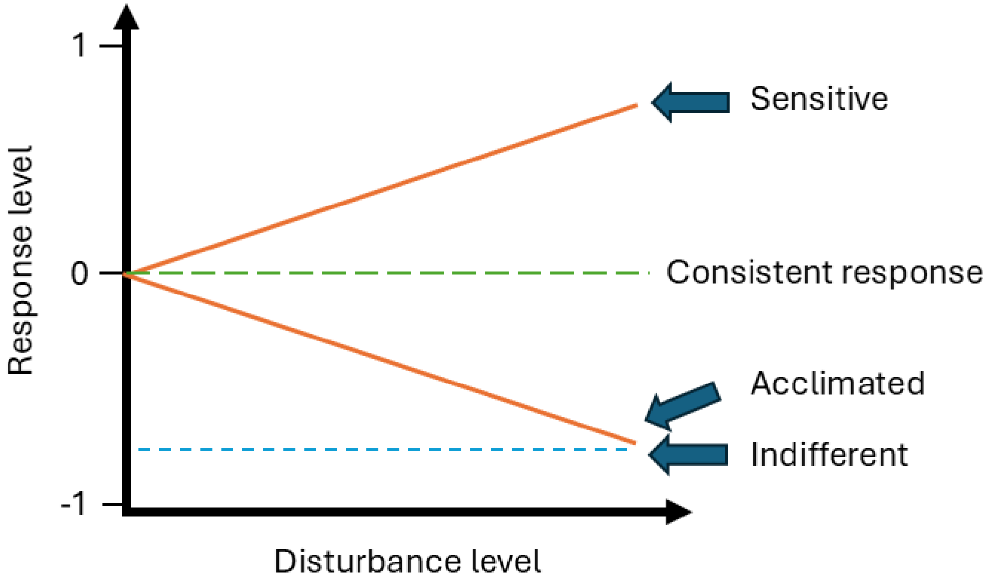

Figure 2.4. The relationship between the classifications of disturbance responses used in the vote counting system and the level of response observed.

Votes were assigned to studies but, for several reasons, individual studies could be represented by multiple votes. This occurred in a number of scenarios, including:

1) The study was conducted on multiple species, multiple populations, or multiple within-species or population factors such as sex, age class, or individual, irrespective of other factors (personality).

2) Multiple disturbance types were reported separately.

3) Multiple types of response, such as both habitat use and movement rates, were reported.

I extracted 265 datapoints from 167 papers. Deer were found to respond to disturbances from recreation and hunting by increasing disturbance response behaviours 72% of the time (Figure 2.5) and by decreasing disturbance response behaviours 6% of the time. Indifferent responses were reported 22% of the time. A higher percentage of responses to hunting (74%) were associated with an increase in disturbance responses than recreation (68%).

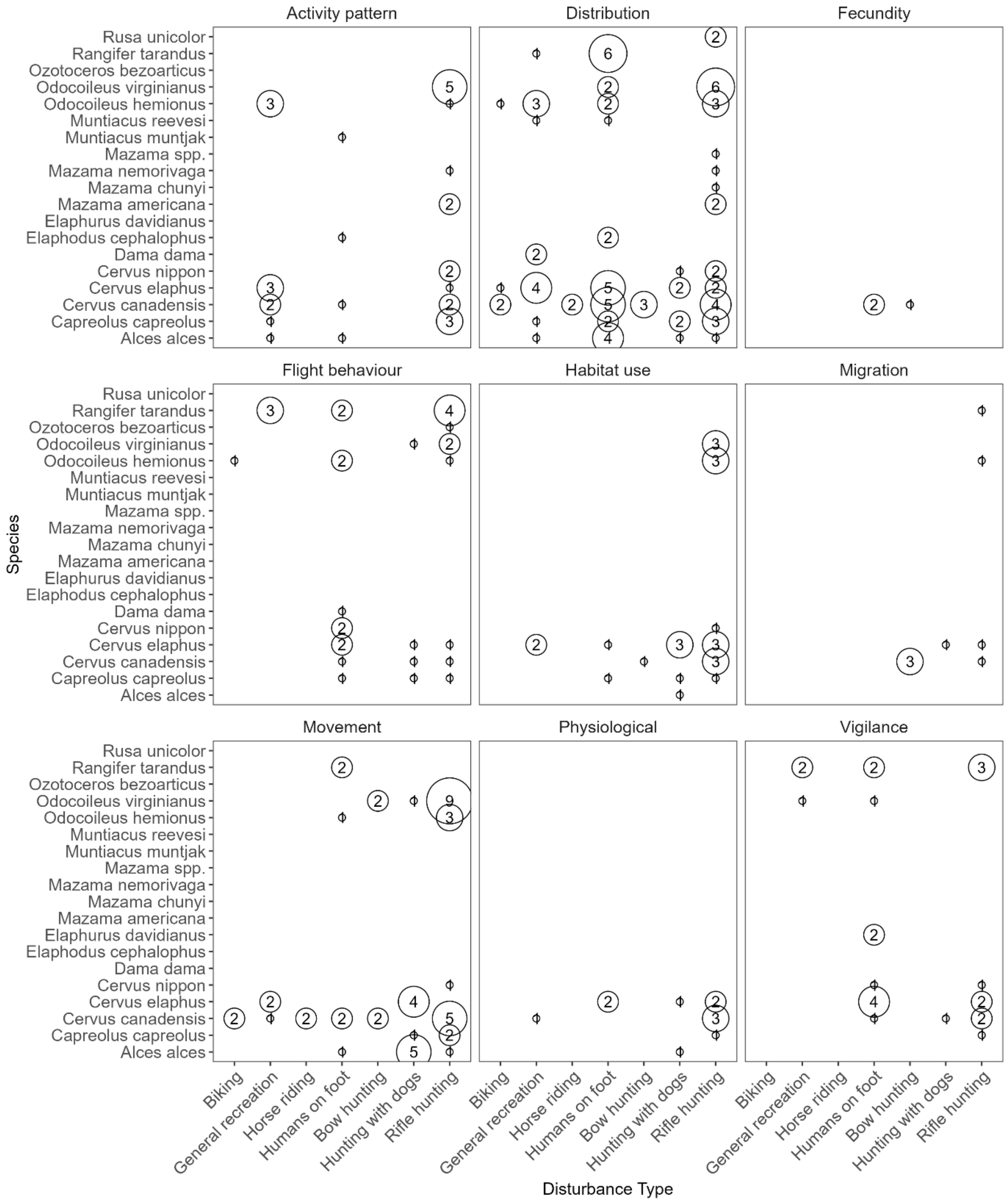

Figure 2.5. The number of results indicating sensitive responses to disturbance by species, disturbance type, and activity pattern indicated by the number and area inside the circle.

2.5 Question 1. What variation occurs in deer responses to disturbance and what are the sources of variation?

2.5.1 Variation between disturbance types

Rifle hunting was by far the most studied disturbance (Figure 2.6) and, overall, hunting was studied more than recreation. The lowest number of examples of acclimated disturbance responses were associated with hunting disturbances, but both recreation and hunting disturbances resulted in approximately 25% of indifferent responses.

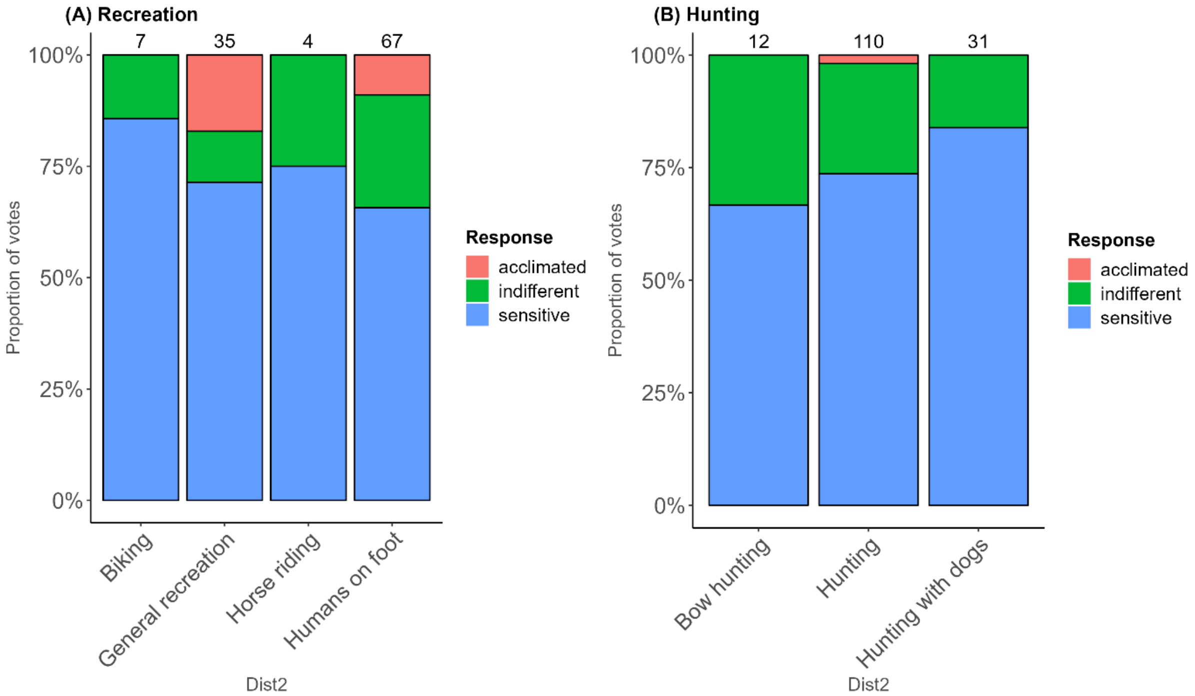

Figure 2.6. The variation in sensitive, acclimated, and indifferent responses to A) recreation and B) hunting disturbances between disturbance types.

More overt disturbances typically led to more pronounced responses. This may relate to increased probability of detection (Tablado and Jenni, 2017), or the perceived threat level (Stankowich, 2008). For example, rifle hunting, which involves loud gunshots, led to greater responses than bow hunting, which is quieter (Cleveland *et al.*, 2012; Smith *et al.*, 2022b). Hunting with dogs, involves noise from dogs barking, as well as gunshots and greater olfactory cues from multiple dogs and people. This might explain why it caused the largest response in the hunting category (Bateson and Bradshaw, 1997; Gentsch, Kjellander and Röken, 2018), even when the studied species was not the target of the hunting (Grignolio *et al.*, 2011).

Studies of both recreation and hunting mostly suggested that hunting caused more disturbance (Jeppesen, 1987; Jayakody *et al.*, 2008; Ciuti, Northrup, *et al.*, 2012). Within the recreation category, mountain biking was found to cause greater disturbance responses than humans on foot and horse riders (Naylor, Wisdom, Michael and Anthony, Robert, 2009; Preisler, Ager and Wisdom, 2013; Wisdom *et al.*, 2018b; Naidoo and Burton, 2020). This might be attributed to the combination of size and speed of the disturbance (Tablado and Jenni, 2017), but may still depend on factors such as cover availability (Scholten, Moe and Hegland, 2018). Though not a focus of this review, motorised recreation (off-road vehicles) typically causes greater responses than non-motorised recreational activities (Naylor, Wisdom and Anthony, 2009; Ciuti, Northrup, *et al.*, 2012). Motorised activities are generally louder and faster than non-motorised recreation, supporting the interpretation that more overt disturbances lead to greater responses.

2.5.2 Variation between and within species

Most species were found to respond to disturbances from recreation or hunting in some way (Figure 2.7). With the exception of some species with very small sample sizes (*Muntiacus muntjak, Mazama spp.*, and *Rusa unicolor*), all species were found to respond in multiple ways. Excluding species with sample sizes of less than ten, reindeer and caribou, *Rangifer tarandus*, had the lowest proportion of responses associated with an increase in disturbance (sensitive) and were the species that had the highest proportion of acclimated results. The *Cervus* species - elk, red deer, and sika deer - had similar proportions of sensitive responses (84%, 80%, 82% respectively). The two *Odocoileus* species, white-tailed deer and mule deer, also had similarly sensitive response rates overall. Moose (72%) and roe deer (70%) had comparatively lower rates of sensitive disturbance responses.

A relatively small number of studies included multiple species but, in these, responses between species varied in magnitude or direction more often than they were significantly consistent. Varying responses between species may relate to factors such as body size (Costa, Benchimol and Peres, 2021), social organisation (Aastrup, 2000; Reimers *et al.*, 2006), and diet (Costa, Benchimol and Peres, 2021). Smaller animals have higher metabolic requirements, resulting in a higher cost of disturbance responses (Preisser and Orrock, 2012). Small groups are less conspicuous to predators (Jackson *et al.*, 2005), and browsers are more likely to be associated with habitat that provides cover (Mysterud and Ostbye, 1999). Red deer are a large-bodied species and were found to be more responsive to disturbance than the smaller, roe deer (Theuerkauf and Rouys, 2008; Bobrowski, Gillich and Stolter, 2020) and fallow deer (Bullock *et al.*, 1993). Roe deer and tufted deer were more responsive than muntjac (Zhou *et al.*, 2013; Zini *et al.*, 2021), and moose and elk were more responsive than mule deer

(Naidoo and Burton, 2020; Green *et al.*, 2023). There were, however, exceptions to the principle that smaller bodied deer responded less to disturbance. Elk were more responsive than the larger-bodied moose (Green *et al.*, 2023), although this could be attributed to social differences between the species. Elk are often in large groups (Hebblewhite and Pletscher, 2002), whereas moose are typically solitary (Månsson *et al.*, 2017). In addition, moose are a browsing species (Månsson *et al.*, 2007), alongside roe deer and mule deer which also exhibited lower disturbances responses than red deer and elk, which are more likely to graze (Sandoval *et al.*, 2005; Storms *et al.*, 2008). While these principles appear sound, they can be influenced by context. In one study, both principles were undermined when relatively small and solitary roe deer were found to be more responsive than relatively large and gregarious fallow deer. The authors attributed this to the hunting pressure on roe deer, contrasting with the lack of hunting pressure on fallow deer (De Boer *et al.*, 2004).

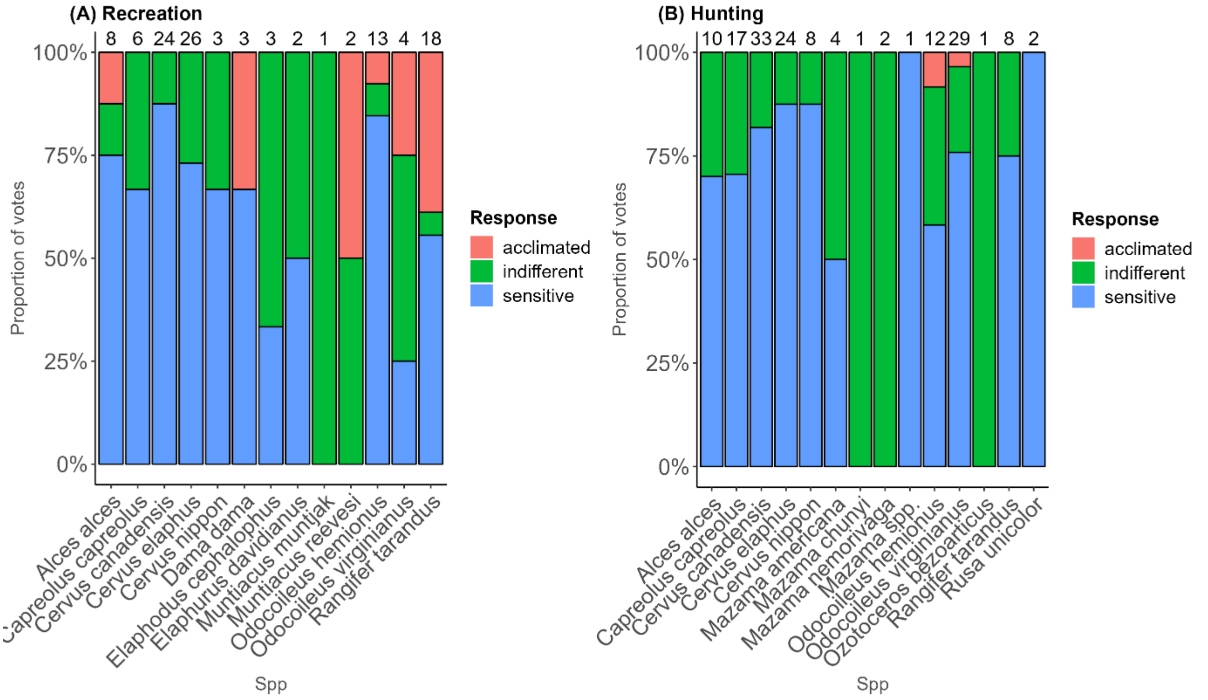

Figure 2.7. Variation in sensitive, acclimated, and indifferent responses to A) recreation and B) hunting disturbances between species.

Within-species variation in the results of individual studies was attributed to factors relating to sex (e.g. Root, Fritzell and Giessman, 1988), age (Thurfjell, Ciuti and Boyce, 2017), and body condition (Skogland and Grøvan, 1988). Females were more responsive to disturbance than males in the majority of those studies. Where males were more responsive to disturbance than females, the finding was typically attributed to males but not females being hunted (Rodgers *et al.*, 2021; Gaynor, McInturff and

Brashares, 2022). Females are often found to be more cautious than males because their smaller body size makes them more vulnerable to predation, and because of their association with vulnerable young (Clutton-Brock, Guinness and Albon, 1982; Pecorella *et al.*, 2019). Conversely, in some systems, proximity to human disturbance can be beneficial to females with young, due to the 'human shield' effect; this results in wildlife associating with areas of human activity to avoid predators that are more sensitive to disturbance (Berger, 2007). At one site, female caribou with calves selected areas closer to trails, while lone females avoided trails (Lesmerises, Johnson and St-Laurent, 2017).

Variations in personality traits may influence the responses of individual deer to disturbance (Bonnot *et al.*, 2018). Individual variation in risk avoidance appears to have contributed to differing disturbance responses. For example, unmarked black-tailed deer avoided bait stations, whereas marked deer did not (Le Saout *et al.*, 2014). This suggested that an association with individual predisposition for risk avoidance contributed to both probability of capture and use of bait stations. Personality traits affecting disturbance responses may also lead to fitness consequences for individuals (Ciuti, Muhly, *et al.*, 2012). Baskin, Ball and Danell (2004) found that moose that did not immediately run away from humans were more likely to be shot, and suggested that this could result in selection for particular behavioural traits in hunted deer. Similar results were observed for male red deer (Lone *et al.*, 2015).

Variation in disturbance responses occurred based on external factors relating to habitat and cover availability. This variation occurred between individuals (Root, Fritzell and Giessman, 1988; Chassagneux *et al.*, 2019), within populations (Naugle *et al.*, 1997), and between populations (Conner, White and Freddy, 2017). Different individuals showed increased likelihood of distribution responses when they had prior experience of refuge areas (areas not subject to disturbance) (Root, Fritzell and Giessman, 1988) and individuals were less likely to flee from disturbance if cover was available (Jarnemo and Wikenros, 2014; Chassagneux *et al.*, 2019). Deer also fled from experimentally approaching humans at larger distances in open habitat than closed habitats (De Boer *et al.*, 2004). The same population of white-tailed deer was observed before and after a large flood drastically reduced cover availability across their range (Naugle *et al.*, 1997). Following the reduction in cover, the deer adjusted their activity patterns to be less diurnal at the onset of hunting season, where previously there had been no effect on activity pattern. Variation in topographic features, habitat, and cover availability were attributed to differences in migration behaviour between two populations of elk (Conner, White and Freddy, 2017). These findings highlight the significant role that habitat and cover availability play in shaping deer responses to disturbances, influencing behaviour both within and between populations.

2.5.3 Variation between response types

With the exception of fecundity, which was assessed in very few studies, all measures of disturbance showed some variation in responses to disturbance (Figure 2.8). In most studies documenting changes in habitat use in response to disturbance, the cause of disturbance was hunting; only four studies showed changes in habitat use as a response to recreation (albeit that no studies showed no change in habitat use in response to recreation). Overall, habitat use represented the highest proportion of sensitive responses (92%), with just 8% of results indifferent and no examples of acclimated habitat use related responses. The lowest proportion of sensitive disturbance responses overall occurred in relation to vigilance measures, mainly due to high variation in recreation results.

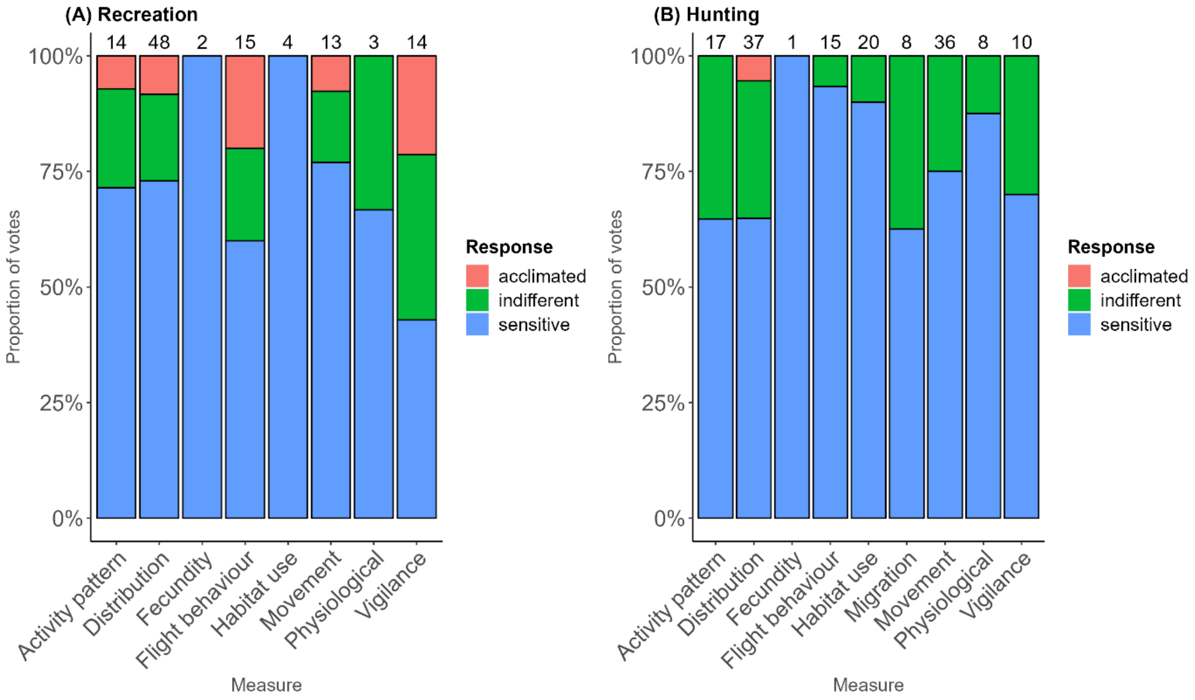

Figure 2.8. The variation in votes (instances of disturbance) associated with sensitive, acclimated, and indifferent responses to A) recreation and B) hunting disturbances between disturbance measures.

Detection of disturbance responses clearly depended on the disturbance measure used in the study. Multiple studies reported sensitive results based on one measure, but indifferent results by another measure. Distribution responses, in which deer avoided disturbance by changing their location in the landscape, appeared to be particularly at odds with other disturbance responses. Some studies that included multiple measures of disturbance reported effects on distribution in the absence of other responses (Parsons *et al.*, 2016, 2022; Lesmerises, Johnson and St-Laurent, 2017; Sytsma *et al.*, 2022). More frequently, the converse was true: there was no impact on distribution, even though other measures of disturbance were found (Root, Fritzell and Giessman, 1988; Naugle *et al.*, 1997; George and Crooks, 2006; Grignolio *et al.*, 2011; Padié *et al.*, 2015; Agetsuma *et al.*, 2016; Coppes *et al.*, 2017; Gaynor, McInturff and Brashares, 2022). The mismatch between inferences from studying spatial distribution or other responses was observed whether distribution was assessed as short-term displacements (Sytsma *et al.*, 2022) or longer-term patterns of space use (Parsons *et al.*, 2022). Shifts in distribution come at the cost of energy expended for movement (Frid and Dill, 2002), as well as loss of forage if deer move from high quality habitat to low quality habitat. Thus, in some cases, deer may select alternative behavioural adjustments in response to disturbance. These trade-offs can lead to situations in which the response switches in response to ongoing disturbance. For example, Colman *et al.*, (2012) observed that reindeer reduced their daytime feeding by up to 7.5% as numbers of skiers per day increased, representing a behavioural response only in the short-term. At 105 skiers, reindeer sought refuge away from trails and resumed normal foraging rates, representing a spatial response only in the longer-term. This example highlights why different measures of response might yield different inferences at different times, or different intensities of disturbance.

Even when only a specific type of response to disturbance was considered, responses could differ in both magnitude and direction. Differences in magnitude can be seen in studies of vigilance responses to disturbance. For example, Proudman *et al.,* (2021) found that red deer vigilance was 11% higher in the hunting season than the non-hunting season. In contrast, Jayakody *et al.,* (2008) found that vigilance increased by almost 50% in response to hunting. These results may be context dependent: the first study took place in forested habitat, while the second was mainly in open habitat. The presence of cover, where available, reduced vigilance levels (Jayakody *et al.*, 2008). Differences may also have been exaggerated by the timescale of measurements (daytime-only, Jayakody *et al.,* 2008; or 24 h, Proudman *et al.* 2021), or by definition of vigilance Jayakody *et al*., (2008) included vigilance whilst lying and walking; Proudman et al. 2021 did not). A third study that measured vigilance at a study site similar to that of Jayakody *et al.,* (2008) found non-significant effects of recreation on vigilance of red deer (Marion *et al.*, 2022a), contrasting sharply with a 30% increase in vigilance during periods of recreation (Jayakody *et al.,* 2008). Again, this difference might well be explained by methods of data collection and definitions of vigilance.

Not only the magnitude, but even the direction of a measured response can vary between studies. For example, movement could either increase or decrease in response to disturbances. Increases in movement rates following disturbance were associated with either short-term spatial avoidance or flight behaviour (Ericsson and Wallin, 1996; D'Angelo *et al.*, 2003; Sunde *et al.*, 2009; Neumann, Ericsson and Dettki, 2011; Ciuti, Northrup, *et al.*, 2012; Jarnemo and Wikenros, 2014; Chassagneux *et al.*, 2019; Brown *et al.*, 2020), or with increases in home range size (Grignolio *et al.*, 2011; Hygnstrom *et al.*, 2011; Amor *et al.*, 2019). Decreased movement rates in response to disturbance were attributed to restricting movements to areas that were familiar and safer (Little *et al.*, 2016; Gaynor, McInturff and Brashares, 2022), and to avoiding detection (Chassagneux *et al.*, 2019). The variation that occurred within these disturbance responses likely depended on the availability of suitable habitat and cover.

Activity patterns most often shifted from diurnal to nocturnal (Naugle *et al.*, 1997; George and Crooks, 2006; Di Bitetti *et al.*, 2008; Ensing *et al.*, 2014; Little *et al.*, 2016; Visscher *et al.*, 2017; Spitz *et al.*, 2019; Bonnot *et al.*, 2020; Lewis *et al.*, 2021; Gaynor, McInturff and Brashares, 2022; Jasińska *et al.*, 2022), in response to daytime disturbances. However, depending on the species' normal patterns of activity in relation to the timing of disturbances, diurnal to crepuscular (Agetsuma *et al.*, 2016), and crepuscular to nocturnal (Ikeda *et al.*, 2019) shifts also occurred. Activity pattern changes were also subtle shifts of as little as one hour to reduce overlap with human activity (Barrueto, Ford and Clevenger, 2014).

2.5.4 Red deer as a case study on the magnitude of responses to disturbance

The magnitude of deer responses to disturbance has important implications for management decisions. Demographic scale is important here, with population level responses having greater implications for management than individual deer responses. Magnitude can be considered as the level or duration of changes in behaviour in response to disturbance. Due to the varied methods and analyses in the literature, extracting these data quantitatively is challenging. Therefore, I mainly used a qualitative approach to investigate the magnitude of responses to disturbance indicated by the authors. Red deer have significant environmental and economic importance in Europe (Milner *et al.*, 2006), are a particular source of controversy within the UK (MacMillan and Phillip, 2010), and are also one of the most frequently studied species in the context of disturbance. Consequently, I chose to focus on red deer, specifically.

Generally, authors did not give more subjective opinions on the magnitude of responses unless they were notably low or nonsignificant. Of the 32 papers examined, only two emphasised low levels of a statistically significant disturbance response. One studied a public park with very high levels of disturbance (Langbein and Putman, 1992), whilst the other was dependent on disturbance being restricted to trails (Westekemper *et al.*, 2018). A third paper suggested that low levels of response indicated habituation (Marion *et al.*, 2022a). By contrast, most studies that observed significant disturbance responses noted the importance of findings and their potentially serious implications, and suggested management approaches to mitigate the effects of disturbance. Studies that noted particularly pronounced impacts included those of vigilance in response to hunting (Proudman *et al.*, 2021), and physiological responses to hunting with dogs (Bateson and Bradshaw, 1997). Two studies suggested that hunting by humans had a greater effect on red deer than hunting by wolves (Theuerkauf and Rouys, 2008; Proudman *et al.*, 2021).

In spite of the strength of language employed in some studies of disturbance impacts, no study strongly suggested that their findings currently indicated serious demographic or population-level effects, such as reduced survival of young or population decline. This might be taken to suggest that human disturbance does not have severe consequences for red deer populations, but it is likely that such consequences could only be uncovered with long-term studies. The downstream impact of disturbance on deer welfare, or the environment, more generally, was not well studied. Two of the papers focused on deer impact on vegetation (Lovari *et al.*, 2007; Bobrowski, Gillich and Stolter, 2020), but neither linked disturbance behaviour to vegetation impacts. In the case of Lovari *et al.,* (2007) this may have been due to the apparently limited impacts of human disturbance.

Although I was mostly restricted to considering qualitative interpretations of the severity of effects, it is possible to make comparisons between some studies that presented comparable quantitative data. Three of these, relating to red deer vigilance, were mentioned earlier. In addition, two studies reported the distance at which red deer avoided trails. Red deer avoided hiking trails by 200 metres (Sibbald *et al.*, 2011) and mountain bike trails by 40 metres (Scholten, Moe and Hegland, 2018). Scholten et al., (2018) attributed this discrepancy to the availability of cover next to the mountain bike trails. The distance travelled by deer immediately following a disturbance was reported as flight distance. In response to hunting with dogs, females were reported to have mean flight distances of 2.5 km and males 5.1 km (Jarnemo and Wikenros, 2014). Another study found that females had flight distances of 4 km (Sunde *et al*., 2009). A mean flight distance of 19 km was also reported in response to hunting with dogs, but since these deer were specifically targeted and pursued until death, this figure is not comparable with the other studies (Bateson and Bradshaw, 1997). In contrast, recreation elicited much shorter flight distances, both off trails (median = 610 m, 95% quartiles 66-1866 m) and on trails (median = 39 m 95% quartiles 9-321).

2.6 Question 2. Are there common themes in disturbance responses of deer, and can generalisations be made?

Most deer responses to disturbance can be broadly categorised as ‘flight’ or ‘hide’ (Stankowich, 2008), though ‘fight’ responses may also occur (Ericsson, Neumann and Dettki, 2015). Across seven different deer species, I found that all studies reporting changes in habitat use referred to increased use of cover. Moreover, cover availability was implicated in whether deer exhibited flight versus hide strategies (Naugle *et al.*, 1997; Chassagneux *et al.*, 2020). Cover availability is therefore likely to be an important predictor in determining deer responses to disturbance. While cover may hinder the detection of a disturbance (Stankowich, 2008), it also increases the effectiveness of the hide response strategy (Meisingset *et al.*, 2022). This is relevant when considering the findings suggesting that body size and social habits of different species affect disturbance responses because smaller deer, in smaller groups, are less detectable by predators (Jackson *et al.*, 2005; Preisser and Orrock, 2012).

The current and historical context of different populations can have predictable effects on disturbance responses. For example, animals that are hunted by humans may exhibit stronger responses to disturbance than those that are not hunted due to the increased risk associated with human activity (Kays *et al.*, 2017). A few studies compared populations with differing levels of hunting exposure. In these, responses to disturbance were lower in populations that were not subjected to hunting (Behrend and Lubeck, 1968; Aastrup, 2000; De Boer *et al.*, 2004; Reimers, Lund and Ergon, 2011). Even within the same site, hunted portions of a deer population typically showed greater disturbance responses (De Boer *et al.*, 2004; Rodgers *et al.*, 2021; Gaynor, McInturff and Brashares, 2022). When studying multiple populations of reindeer exposed to different degrees of recreation and hunting pressure, Reimers *et al.,* (2011) found that the combination of low recreation and even low levels of hunting resulted in greater disturbance responses than high levels of recreation alone. Furthermore, populations of reindeer with greater levels of domestic ancestry exhibited lower responses to disturbance than populations more closely related to wild reindeer (Reimers, Røed and Colman, 2012). The history of domestication in reindeer may further affect their propensity to habituate compared with other deer species. In the short term, reindeer were observed to reduce their level of response to multiple experimental approaches by humans (Reimers *et al.*, 2009). These examples demonstrate that the past and present experiences of populations and species can play a crucial role in shaping their disturbance responses.

In some situations, responses by deer to specific patterns of disturbance may be predictable. Deer commonly avoided recreation trails (Helle *et al.*, 2012; Zhou *et al.*, 2013; Westekemper *et al.*, 2018; Gundersen *et al.*, 2020; Naidoo and Burton, 2020). Increases in disturbance responses were also associated with increasing distance from trails or regular human activity (S. Miller, Knight and Miller, 2001; Taylor and Knight, 2003; Becker *et al.*, 2012; Price, Strombom and Blumstein, 2014; Westekemper *et al.*, 2018). However, the magnitude of these responses may still vary. Predictability of disturbances such as those associated with recreation trails, were considered important in determining magnitude of disturbance responses (Recarte, Vincent and Hewison, 1998; Taylor and Knight, 2003; Helle *et al.*, 2012; Westekemper *et al.*, 2018). These findings suggest that while disturbance responses to particular patterns of disturbance may be broadly general, variation remains regarding the degree to which these responses are observed.

Some disturbance types and intensities also affected responses in a predictable way. Low intensity disturbances and shorter duration disturbances tended to have lower responses. At the other end of the spectrum, high levels of recreation were more likely to lead to habituation (Schuttler *et al.*, 2017), although the level of disturbance required for this is unclear. Deer were less likely to tolerate hunting disturbances than recreation, but low levels of disturbance responses also occurred when hunting pressure was low (Reimers, Lund and Ergon, 2011; Osterhaus and Jensen, 2019). Typically, disturbance responses increased with increasing hunting pressure (Grau and Grau, 1980; Aastrup, 2000; Baskin and Hjälten, 2001).

While some common themes have emerged from the literature review, no generalisation appears to be absolute, with examples of exceptions in each case.

2.6.1 Difficulty in making generalisations

Identifying general rules for the disturbance responses of deer presents several challenges. An individual's response to disturbance depends on the species exposed to the disturbance, the individual's sex, age and reproductive status, individual personality traits, and current group dynamics. In addition, context-specific external factors, such as cover availability, forage, disturbance type, and intensity, drive further variation in response. These sources of variation may have varying degrees of influence, and interactions between them may be complex and non-linear (Tablado and Jenni 2017). With this in mind, the cumulative variation makes population level inferences and species generalisations highly complicated.

Studies differ in their scale, methods, and measurement units, complicating direct comparisons and affecting the probability of detecting responses. Findings depended on the scale at which the data were analysed (Reimers *et al.*, 2009; Naidoo and Burton, 2020). Furthermore, lack of data resolution at broader scales of analysis were suggested as reasons for observing low impacts of disturbance (Fullman, Joly and Ackerman, 2017; Diao *et al.*, 2021). The duration of studies varied widely. In many cases, it was not possible to determine how long effects following disturbance lasted, or if those effects were restricted to the duration of the disturbance. This is important, because even minor changes in behaviour could have large consequences if they are persistent.

Interpreting disturbance intensity is challenging due to inconsistencies in how it is quantified and reported. For example, studies between populations in different areas reported only relative intensities for each area as 'low', 'medium', and 'high' (Reimers, Lund and Ergon, 2011). Others used relative frequency of human activity at specific sites (Anderwald, Campell Andri and Palme, 2021; Procko *et al.*, 2022; Green *et al.*, 2023), but without covering all trails or access points this provides only a minimum value. This value is relevant for the study in question but cannot be compared to other studies. There seem to be thresholds in disturbance intensities that, when exceeded, trigger disturbance responses (Colman *et al.*, 2012; Gundersen *et al.*, 2020), but these remain difficult to identify. Cumulative effects of multiple disturbance types can further exacerbate disturbance responses (Ciuti, Northrup, *et al.*, 2012) in additive or multiplicative ways making responses less predictable.

Further limitations in our ability to make generalisations about deer disturbance responses occur at the point of publication. There may be publication bias towards studies reporting disturbance responses, as papers with null, or indifferent, results could be less likely to be published (Nakagawa *et al.*, 2022). Even where studies demonstrating no apparent impact of disturbance are published, these could be overlooked during literature searches, especially if 'human activity' was merely a parameter in models designed to answer different questions. This bias may over-represent the impacts of disturbance on deer. Together, these factors require careful consideration before using existing literature to make inferences regarding specific species and systems.

2.7 Question 3. What are the implications for management and the future direction of research?

This review has highlighted the extensive sources of biological and methodological variation in deer disturbance responses, and demonstrated how these variations hinder our ability to derive generalities. In light of this, there remain significant limitations in using existing literature to inform management decisions. Recognising that most studies of disturbance are motivated by a desire to identify and mitigate for problematic impacts of disturbance, it is important to consider what constitutes ‘problematic’. That, itself, might vary in different contexts. Generally, however, it is likely to be embodied in one or more of three goals: identifying and preventing population declines caused by disturbance; promoting welfare by identifying and avoiding acute stress (beyond that expected among populations in the absence of human disturbance); and identifying and mitigating for habitat impacts that arise from altered space use and aggregation. These goals lend themselves to different types of study, which might address, respectively: survival, recruitment and population change; differences in endocrine indicators of stress between populations in disturbed and undisturbed environments; and studies of habitat condition, ideally in comparable areas with and without disturbance.

Regardless of the focus of studies, several insights arising from this review should be considered when designing a new study. The first is that endeavours towards cross-species generality appear liable to fail. Body size, sociality, habitat preferences and innate propensities for habituation all hinder likely conformity across species. Second, many species appear capable of habituating to recreational disturbance, without deleterious impacts on population trajectory. That suggests that recreation, alone, is unlikely to have long-term negative impacts at the population level. Where recreation is combined with hunting, however, this may not be the case. Third, the availability of cover plays a large role in determining the magnitude and direction of responses, so comparisons (between areas with and without disturbance) must focus on areas with comparable terrain and vegetation. Fourth, different behavioural measures of response to disturbance trade-off against each other, so an absence of effect determined by one measure does not mean that the animals are not disturbed. Where behaviour is studied, multiple metrics are likely to be needed to provide a comprehensive picture of whether disturbance is causing large changes.

An even more general observation is that replication is often low in studies of the impacts of disturbance. Replication of studies is an essential part of scientific research to provide robust conclusions but is often difficult to achieve. This is particularly true in ecology, where high variability in field conditions presents unique challenges. I suggest that replication is essential for achieving research outcomes that enable generalisations about deer disturbance responses. However, funding and publication biases against replication in science exist, favouring novel research (Filazzola and Cahill, 2021). Given widely occurring limitations to funding, alternative approaches to solving management problems should be considered. Studies in this review highlighted the potential for welfare and environmental problems stemming from disturbance responses by deer; thus, we should measure these directly in relation to disturbance responses. For example, if changes in spatial distribution restrict forage availability for deer, we need to assess the impact on welfare via body condition and fitness measures, and on the environment by habitat impact assessment. Alternatively, need for further studies on disturbance responses of deer at specific sites could be determined based on specific management requirements. For instance, in areas where disturbance levels are high or liable to increase, monitoring body condition of deer and vegetation could establish if impacts are occurring. If impacts to welfare or vegetation become apparent, then steps can be taken to mitigate these impacts directly or undertake further research to determine site-specific deer disturbance responses. Lastly, research could develop methods widely applicable by land managers but adjustable to local contexts. These methods would assess the extent to which deer are affected by disturbances and determine if management intervention is required based on specific management concerns. In conclusion, I suggest that further research is required to answer key management questions. To maximise the efficiency of this research, studies should focus on specific management problems and adopt site-specific approaches.

Chapter 3. Spatial responses of red deer to hillwalker activity in Glen Lyon, Scotland

3.1 Abstract

Outdoor recreation is increasing globally and has the potential to substantially impact wildlife distribution and behaviour. In turn, changes in wildlife activity can have significant environmental, economic, and welfare implications that can also cause conflicts between different land uses. The impacts of human activity are exacerbated in sensitive upland environments where outdoor recreation is most appealing. I monitored red deer, *Cervus elaphus*, distribution over space and time alongside hillwalker numbers during three summers in an area with a popular hillwalking path. I found that deer exhibited avoidance of the hillwalker path, maintaining greater distance on days with high hillwalker numbers. When hillwalker numbers were higher, deer distribution was more concentrated within the study site, which could lead to significant ecological consequences from overgrazing and trampling by deer. Presence of topographic cover appeared to modulate deer spatial responses to disturbance. The results of this study suggest the potential for significant reduction in habitat that deer appear willing to use as a result of hillwalker disturbance, but further research is needed to identify any compensatory behaviour such as overnight feeding in areas close to the path. These results further emphasise the importance for recreationists to minimise their impact on wildlife by remaining on established paths in sensitive areas.

3.2 Introduction

Human incursions into natural environments are increasing globally. This issue is particularly prevalent in outdoor recreation, which has grown in popularity over recent decades (Cordell, Betz and Green, 2008; Balmford *et al.*, 2009; Naidoo and Burton, 2020). Human disturbance can affect wildlife fitness and fecundity (Shively *et al.* 2005; Leblond *et al.* 2013), short-term and long-term behaviour (Manor and Saltz 2003; Benhaiem *et al* 2008; Vistnes and Nellmen 2008; Gaynor *et al* 2018), and spatial distribution in the landscape (Vistnes and Nellmen 2008; Sawyer *et al* 2017). Human encroachment into nature affects wildlife distribution when animals seek to avoid disturbance or are displaced by human activity. This is particularly important because when animals alter their spatial distribution, it can affect the wider ecosystem. These changes can have cascading effects on species interactions, resource availability, and habitat use, leading to both negative consequences for the environment and economy (Jayakody *et al.*, 2011; Arnett and Southwick, 2015). Collectively, these observations highlight why understanding the impact of disturbance on wildlife distribution is integral to developing effective conservation and management strategies, and ensuring the health and sustainability of ecosystems.

Spatial avoidance by wildlife refers to the alteration of movement patterns and home ranges to minimise interactions with disturbances such as human activity (Marion *et al.*, 2021). Spatial avoidance may result in long-term displacement, where animals leave an area indefinitely (Sawyer *et al.*, 2017), or temporary avoidance associated with the duration of the disturbance (Sibbald *et al.*, 2011). Temporal spatial avoidance can occur when wildlife respond to daily patterns in disturbance, such as increasing distance from human activity while it occurs during the day and reducing distance at night (Marion *et al.*, 2021). Temporal avoidance also occurs as changes in activity patterns, whereby wildlife reduce diurnal activity to avoid disturbances (Gaynor *et al.*, 2018). This adaptive behaviour can have significant implications for how wildlife interact with their environments.

Among the various wildlife species affected, ungulates provide a particularly relevant and informative example due to their significant roles in ecosystem dynamics (Ferraro, Schmitz and McCary, 2022). Disturbance responses by ungulates are influenced by a number of spatial and temporal factors including habitat, topography, and time of year as it relates to breeding and body condition. Cover availability has been linked to the reduction in movement responses to disturbance (Jayakody *et al.*, 2008; Zong *et al.*, 2023). Variable topography can reduce disturbance responses by providing physical barriers between ungulates and the disturbance (Chassagneux *et al.*, 2019), but in some instances displacement distances may increase in rugged terrain (Hansen and Aanes, 2015). These areas may also provide suitable cover for bed sites during periods of reduced activity (Millspaugh *et al.*, 1998). Females with younger offspring have been shown to display greater disturbance responses

(Stankowich, 2008; Hansen and Aanes, 2015), while poor body condition may reduce disturbance responses due to constraints imposed by nutritional requirements (Beale and Monaghan, 2004; Crosmary *et al.*, 2012). Disturbance responses may also change over time if effects such as habituation or sensitisation occur. These could be spatially dependent (Hansen and Aanes, 2015) or seasonal (Haskell and Ballard, 2008), and short-term sensitisation effects have been observed following weekend peaks in human disturbance (Moscatelli *et al.*, 2023).

Ungulates can, in turn, have a significant influence on their environments as ecosystem engineers (Sinclair, 2003; Ramirez *et al.*, 2021), and they are often economically important as hunting quarry (Arnett and Southwick, 2015), tourism attractions (Arbieu *et al.*, 2018), and reservoirs of disease that might affect domestic populations (Böhm *et al.*, 2007). Spread of disease is also important to public health (Gilbert *et al.*, 2012), and negative human-wildlife interactions such as crop raiding by deer and vehicle collisions have both economic and public health relevance (MacMillan and Phillip, 2010; Pepper, Barbour and Glass, 2020). Adaptive responses such as habituation can exacerbate these issues and bring ungulates into closer contact with humans and livestock (Kloppers *et al.* 2005). Meanwhile, continued avoidance or sensitisation by ungulates can increase stress and affect long-term fitness and survival (Shively *et al.* 2005; Leblond *et al.* 2013; Dixon *et al.* 2021). Spatial responses such as avoidance or displacement are common responses to disturbance exhibited by ungulates (Stankowich 2008; Chitwood *et al* 2021).

In Scotland, red deer (*Cervus elaphus*) represent the largest free-roaming wild ungulate, and their population has more than doubled since the mid-20th century (Pepper *et al.*, 2019). Numbers have stabilised more recently (Pepper, Barbour and Glass, 2020), but are still considered by many to have unsustainable impacts (Edwards and Kenyon, 2013). This may be exacerbated the loss of ecosystem resilience in a deforested and degraded landscape (Davies, 2008; Fløjgaard *et al.*, 2022). Red deer can be key to maintaining certain habitats, and aiding seed dispersal and germination microclimate, but negative environmental impacts of deer are exacerbated by high population densities (Gill and Beardall, 2001; Shaw *et al.*, 2010; Edwards and Kenyon, 2013). Red deer in Scotland have long been recognised as harmful to tree regeneration, which can have a detrimental effect on forestation goals for conservation and commercial forestry (Miller *et al.* 1982; Putman and Moore 1998). More recently, potential red deer impact on peatland has come into the spotlight due to increasing global concerns about climate change and the Scottish Government's climate change mitigation goals (NatureScot, 2020). Deer impacts on peatland include loss of biodiversity through overgrazing, and increase of peat erosion and exposure due to trampling (Pellerin, Huot and Côté, 2006; Cummins *et al.*, 2011). Exposure of peat increases its susceptibility to water erosion (Pellerin, Huot and Côté, 2006) and the associated degradation releases carbon into the atmosphere with important implications for climate change (Turetsky *et al.*, 2002).

Red deer are also the most economically important wild ungulate in Scotland (MacMillan and Phillip 2010). As a charismatic species, the red deer is attractive to tourists and photographers (Macmillan and Phillip 2008). The stalking industry is important for rural employment, and for bringing income to rural areas and associated industries such as hospitality and vehicle maintenance (Edwards and Kenyon, 2013). Commercial stalking also helps to fund deer management activities in many places that would otherwise operate at a loss (Edwards and Kenyon, 2013).

The confluence of the ecological and economic importance of red deer in Scotland, plus the rise in popularity of hillwalking, create the potential for conflict amongst those who seek to manage deer populations for economic gain or conservation imperatives, and those who seek to use the landscape for recreation and aesthetic enjoyment. This is set in a context of an open countryside access policy which protects the public's 'right to responsible access' but which can also present management challenges. Changes in deer distribution caused by hillwalkers could lead to increased use of some areas by deer and reduce the land available to the deer (Sawyer *et al* 2008; Johnson *et al* 2020), with implications for environmental impact. Furthermore, deer might be pushed off important hunting grounds, affecting commercial stalking opportunities and population control, leading to conflict between land managers and outdoor recreationists.

Despite debate surrounding red deer management and recreation (Morgan-Davies, Wilson and Waterhouse, 2015), relatively little is known about the extent of red deer spatial responses to hillwalkers in Scotland. In this study, I aimed to quantify these responses by measuring the changes in deer distribution in relation to numbers of hillwalkers on a focal estate, chosen for its inclusion of a popular hillwalking path and because it is a particular focus of conflict between land-users. To do this, I used observational methods to collect an extensive dataset of deer locations and accompanying demographic and environmental variables from the summer recreation seasons in 2020, 2021, and 2022. I hypothesised that:

1. Deer would be located further away from the hillwalker path when hillwalker numbers were highest on the estate.
2. Given that ungulate responses to disturbance are often context-dependent (Stankowich 2008), I expected that greater topographic variation (slope and ruggedness) would provide cover or 'safety' (Mysterud and Ostbye, 1999), encouraging deer to remain or concentrate in these areas following disturbance, and mitigating the effect of hillwalkers.

3. Habituation, represented by a reduction in spatial response of deer to hillwalkers (seasonally and over the study period), will not be evident due to the presence of lethal disturbance (hunting) (De Boer *et al.*, 2004; Stankowich, 2008) and the relatively low density of non-lethal disturbances (hillwalkers) (Shuttler *et al* 2016; Marion *et al* 2022a; Sibbald *et al* 2011).

3.3 Study site

The study site was located in Glen Lyon in Perthshire, Scotland and is largely made up of the 2364 ha North Chesthill estate (56°37’04.5”N 4°10’50.7”W) (Figure 2.1). There are four mountains in the site classed as Munros (mountains in Scotland greater than 3000 ft / 914 m) which form part of the Grampian Mountain Range in the southern part of the geographical highlands of Scotland. The Glen Lyon Horseshoe path encircles the centre portion of the North Chesthill estate, allowing hillwalkers to summit each mountain in a 17 km loop. Munro ‘bagging’ is a widespread activity in Scotland where people aim to summit as many of Scotland’s 282 Munros as possible; this makes the Glen Lyon Horseshoe, with its four Munros, a popular walk.

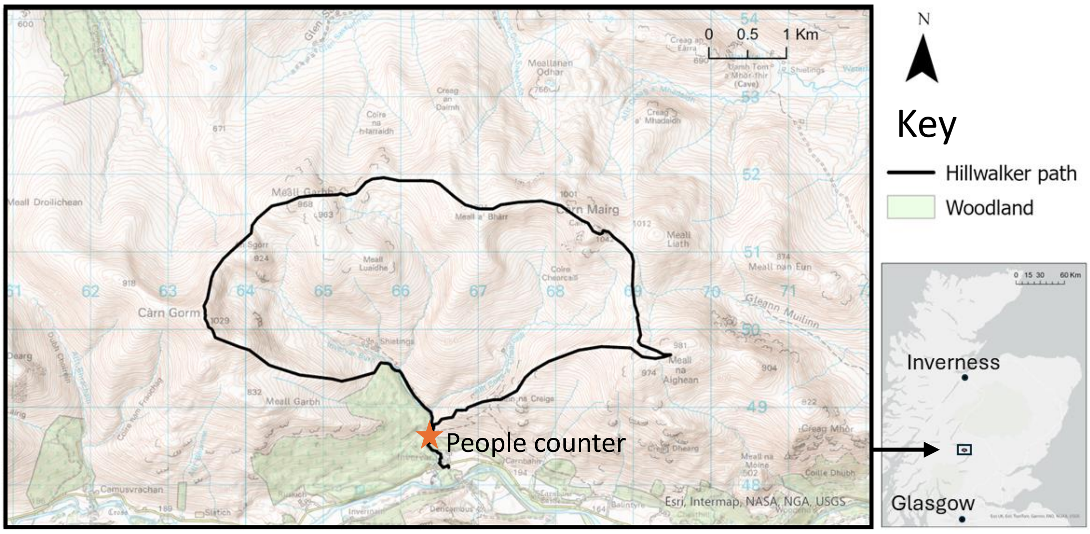

Figure 3.1. The study site and its location in Scotland.

The vegetation profile of the site consists of heather, grassland, and peat, with lower elevation areas containing some commercial and semi-natural forestry, including *Picea sitchensis, Pinus silvestris*, *Betula spp.* and *Sorbus aucuparia*. In the highest elevation areas of the site, arctic-alpine plant communities, snowbed, and montane heath historically made the area a Site of Special Scientific Interest (Nature Scot 2010).

North Chesthill Estate is managed for sheep grazing and deer stalking. Between 2020 and 2022, summer sheep densities averaged 30-34 sheep per km² (Estate management, *pers. com.*). The deer population was estimated as 21-25 deer per km² in the 2021 and 2023 counts, up from 10-14 deer per km² in 2019 (Breadalbane Deer Management Group). The estate is not fenced, so large fluctuations in deer numbers may reflect the locations of large groups of deer either within or outside the estate's boundary on census days. The majority of deer across the counts were in hind groups (adult females, calves, juveniles and sub-adults). The remainder were in stag groups (adult males), which were largely confined to the east and west peripheries of the site, except during the rut (breeding season) which occurs in late October into November (Pemberton, Kruuk and Clutton-Brock, 2022).

3.4 Methods

3.4.1 Hillwalker data

Hillwalker numbers were collected using a laser people counter (Chambers RadioBeam People Counter RBX_EB) placed at the beginning of the hillwalker path. The counter recorded number of people per hour to pass through by counting the times the laser between two points across the path was broken. Since the hillwalkers both arrive at and exit the study site via the people counter, the total number recorded per day was divided by 2 to account for each hillwalker passing through the counter twice. This provided the daily total number of hillwalkers. Number of hillwalkers on the path per hour of the day was calculated by progressively adding the hourly number of hillwalkers until the daily total number of hillwalkers was reached (Marion *et al.*, 2021). Once the daily total was reached, the hourly numbers were progressively subtracted from hourly totals until reaching 0. For example, if the daily total was reached between 12pm and 1pm, the number of hillwalkers to pass through the people counter between 1pm and 2pm would be subtracted from the daily total. The number of hillwalkers to pass through the counter between 2pm and 3pm would then be subtracted from the number of hillwalkers that remained on the hill at 2pm, and so on. Typically, hillwalkers have no reason to pass through the counter more than twice, so the counter was assumed to provide a good index of relative hillwalker activity and numbers across the season. The area between the points of the people counter was kept clear of vegetation to avoid false triggers.

To assess the timescale of hillwalker impacts on deer – i.e., whether impacts were acute and specific to a particular day, or chronic, accumulating over time – I defined a variety of indices of hillwalker activity. Specifically, I assessed the explanatory power of variants, including maximum number of hillwalkers on the day of observation, maximum number of hillwalkers on day of observation plus previous 1, 2, 4, 6, 13, or 27 days, cumulative number of hillwalkers from 01 May, and maximum number of hillwalkers from previous day.

To account for the implausibility of large numbers of hillwalkers reaching distant parts of the hillwalker path during the early part of the day, I created two new variables that represented hillwalker numbers at different points on the path. These were informed by the fact that the hillwalkers almost always progress clockwise around the path (Marion *et al.*, 2022b), by direct observations of their speed and typical times of arrival, and by accounting for the relative difficulty of terrain at different stages of the path.

In the first variable, hwtime, I split the path into two sections (red line in Figure 3.2). Observations outside the red line that occurred before 10am were assumed to be affected by only 10% of that day's hillwalker numbers. This was based on arrival times taken from the people counter and the time it takes to complete the first section of the path. An average of only 10% of hillwalkers were likely to reach later sections of the path by 10am. The 10% also accounts for any individuals choosing to complete the hillwalker circuit anti-clockwise. By contrast, observations within the red line that occurred before 10am were assumed to be affected by 100% of that day's hillwalker numbers. After 10am, all observations in the whole region were assumed to be affected by 100% of that day's hillwalker numbers. The second variable was more nuanced and included three sections (red line and blue line in Figure 2.2). In this variable, observations in the second section were assumed to be affected by 10% of that day's hillwalker numbers before 10am, and 100% after 10am. In the third, remaining section, observations were assumed to be affected by 10% of the day's hillwalker numbers until 12pm, and 100% after 12pm. Again, this was based on average arrival times of hillwalkers and the time it takes to progress through each section. Thus, these variables represent a step towards a more fine-scale descriptor of hillwalker disturbance, despite the difficulty in accurately tracking all individual progression along the hillwalker path

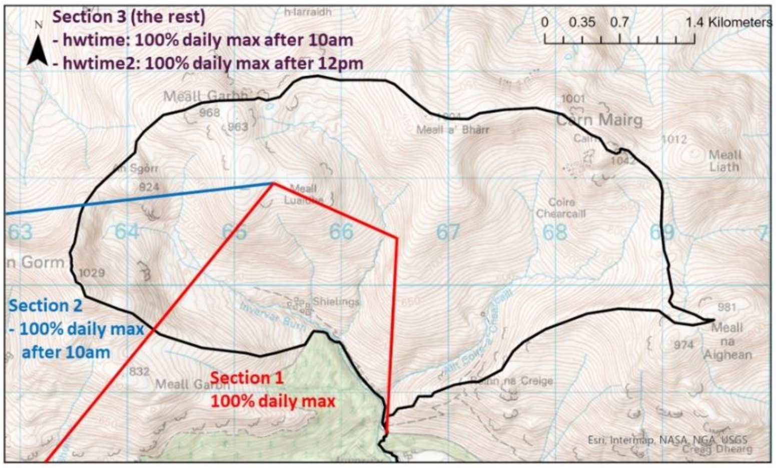

Figure 3.2. Map indicating the sections of the path used for estimating hillwalker numbers based on clockwise progress along the hillwalker path. Observations occurring in Section 1 were assigned 100%

of the daily hillwalker maximum regardless of time of day, on the basis that hillwalkers arrived there earliest. Section 2 was assigned 100% of the daily hillwalker maximum after 10am in the first adaptation of the daily hillwalker number value (hwtime). Section 3 was assigned 100% of the daily hillwalker maximum after 10am in hwtime, and after 12pm in hwtime2.

3.4.2 Deer data collection

Deer data collection occurred during the summer recreation seasons in 2020, 2021 and 2022. Data were collected in 2-3 week blocks 4 times in the season from early June to late September (2021 and 2022) or early October (2020) with approximately the same number of sample days each year.

Deer group data

The spatial distribution of red deer across the study site was quantified by spotting deer with binoculars (10x42) and recording the location of deer. The location was recorded using a mapping application on a mobile phone (Viewranger Jun 2020 – Aug 2021, Outdoor Active Sep 2021, Backcountry Navigator 2022) with OS 1:50,000 and 1:25,000 scale maps. Coordinates of deer were recorded as Latitude and Longitude. The locations of the deer were selected visually on the map, and accuracy was maximised using topographic detail from the map and landmarks such as prominent rocks, fence posts, and cairns, that had ground-truthed locations in the app. Date, time, and total number of deer were also recorded. Total number of deer counted in the group included calves, when seen. Counts were repeated until a consensus was reached to improve accuracy. Groups were defined as an aggregation of deer entirely isolated from other deer by at least 100 m (Childress and Lung, 2003; Proffitt *et al.*, 2009; Ciuti, Northrup, *et al.*, 2012). Two aggregations were counted as one group if individuals were dispersed in between, at intervals of < 100 m. Demographic composition of groups was recorded because male and female deer have been found to respond differently to disturbance (Stankowich and Coss 2006). However, because red deer females and males exhibit sexual segregation for most of the year (Clutton-Brock *et al* 1987; Alves *et al* 2013), and because of low numbers of stags in the study area, this variable was not analysed.

Data were collected on systematic and opportunistic bases. The hillwalker path was used as a transect four times per data collection round for systematic recording to ensure coverage of the whole site. The hillwalker path followed the ridges between mountain summits and provided vantage to observe deer at a range of distances from the path, across the study site. Half of the transects each round of data collection were carried out on ‘busy’ hillwalker days (weekends) and half on ‘quiet’ days (weekdays). Mondays and Fridays were avoided because hillwalker numbers on these days were more likely to be affected by people taking long weekends. During the transects, all visible areas along the path were checked systematically so that timings between transect days were as consistent as possible. Some deviations were made from the hillwalker path to maximise visibility, but these were repeated systematically, each time the transect was conducted. Some areas were visible from multiple sections of the hillwalker path, so data could be recorded from those areas at different times of day. On non-transect days, data were collected opportunistically during all other field activities.

To account for uneven sampling effort across the study site created by the data collection method, the study site was divided into observation areas defined according to their visibility from regular points. The number of times each observation area was searched for deer provided a record of sample effort. Deer group data were associated with specific areas, and when no deer were observable in these areas, an absence record was made. Absence records included all the same temporal data associated with deer group. An absence record was only made if the observation area was fully visible. The distinctions between observation areas were based on either topography (e.g., an area might be bounded by ridges) or distance (e.g., areas might be distinguished as a clear foreground [one area] and a background that was less likely to be visible in poorer conditions [another area]).

Environmental variables

Additional environmental factors were recorded to provide context and account for their effect on distribution and observability. Weather affects deer behaviour and movement; for example, bad weather may cause deer to seek cover (Mysterud and Østbye 1999) or avoid exposed areas (Conradt *et al* 2000). Additionally, hot weather may cause deer to seek ways to keep cool, such as shade or wallows (Alston *et al* 2020). These behavioural responses could affect deer distribution, as well as influencing the conspicuousness and visibility of the deer to the observer and the conspicuousness and visibility of the hillwalkers to the deer. Weather data were collected from a weather station approximately 5 km to the South, at a similar elevation. The weather station recorded data at 15-minute intervals as the average of the previous 15 minutes. Due to the distance between the weather station and the study site, three versions of each weather variable were calculated: the value nearest to the time of the observation; the average of the value nearest to the time of the observation and the following value; and the average of the value nearest to the time of the observation and both the following and preceding values. These variable versions were selected based on the prevailing wind (weather was expected to travel from the weather station to the study site the majority of the time) and the estimated timeframes for weather to reach the study site. These values were also compared to incomplete, direct observations from the field to ensure the weather station provided appropriate measures. Rainfall, temperature, windspeed, and cloud cover in the field were also recorded at time of each observation on a four-point scale, where 1 represented the lowest value and 4 the highest. However, this method of collecting weather data was considered less accurate than the weather station records due to lower consistency in data collection and the subjectivity of the method.

Corresponding weather variables from the weather station were summed rain, average air temperature, average windspeed, and summed sunlight.

Habitat was broadly categorised as grass, heather, peat, and woodland. The majority of deer were observed in grass or heather, these being the dominant vegetation types across the study site. Deer were almost never observed in woodland due to the limited amount of this habitat available in the site and the difficulty of seeing deer among the trees.

3.4.3 Detection

Variables thought to affect deer detection, in addition to weather, included habitat and distance from observer. Detection variables might help to explain numbers of deer observed, if they help to elucidate the probability of individuals being missed in deer counts. Among habitats, I initially considered heather to be more likely to obscure deer given its darker background and greater height compared to grass.

As distance between observer and deer increases, probability of detection often declines (Sunde and Jessen, 2013) . Observer location was recorded at time of deer presence and absence records with a mean precision of 8m. Distance to the deer location calculated in ArcMap 10.5 as Euclidean distance. Due to inconsistent collection in 2020, observer distance was only available for 74% of the dataset and so was omitted from the global model. To assess the significance of observer distance on deer density, the final model was repeated with the subset of the data for which observer distance was available.

Weather variables relating to sun hours, rainfall, and wind were included in the model selection process to control for their potential effect on deer detection. Brightness was thought to affect visibility if deer were easier to spot when the sun was on them compared to a dull, cloudy day. Rain and wind were also thought to reduce detection of deer by obscuring the deer and making it harder to focus binoculars.

3.4.4 GIS desktop variables

Topographic variables were derived using a geographical information system (ArcMap 10.5 and ArcGIS Pro 8) and Ordnance Survey Maps. Deer have been shown to have preference for different elevations (Stewart *et al.* 2002), particularly when disturbed (Cassirer, Freddy and Ables, 1992; Stankowich and Coss, 2006), and elevation can drive deer movement in relation to seasonal changes in vegetation (Debeljak *et al.* 2001; Zhang *et al.* 2022). Elevation values were determined from the nearest contour line (at 5m intervals).

Variation in topography can affect deer distribution if it impedes movement, for example rocky cliffs or energetically expensive steep slopes, or provides few foraging opportunities (Kie, Ager and Bowyer, 2005). Greater topographic variation has also been associated with reduced disturbance response (Chassagneux *et al.*, 2019; Meisingset *et al.*, 2022). Topographic variation was derived by calculating the total length of contour lines within buffers up to 250 m and 500 m away from the deer. Higher values corresponded with greater topographic variation because both an increase in steepness and increase in roughness of the terrain (contour line undulations) increase the overall length (Beasom *et al* 1983; Mukherjee *et al.* 2022). The topographic variation variable was highly influenced by gradient, whereby higher values were associated with steep slopes that could be either smooth or rugged. To isolate the effect of ruggedness, the Vector Ruggedness Measure (VRM) was also used (Sappington *et al* 2005). The vector ruggedness measure tool in ArcPro was used with a 50 x 50 m digital elevation map to generate outputs summarising terrain variation over a 150 x 150 m, 450 x 450 m area and 650 x 650 m area. An area of 90 x 90 m based on a 30 x 30 m digital elevation map was used by Sappington *et al.,* (2005) and was considered to be ecologically relevant for bighorn sheep, *Ovis canadensis nelsoni*. However, given the differences in species, ecological system, and resolution of elevation maps, two further area sizes were considered to identify the most relevant scale for this study.

The effect of topographic variables can be associated with visibility (Eisenberg *et al.*, 2014; Chassagneux *et al.*, 2019). To test the effect of visibility more explicitly, I used viewshed analyses to score each deer location or absence in terms of 1) visibility from the path and 2) general visibility across the study site. The viewshed analysis produces a map with 50 x 50 m cells, showing the number of 'observers' that can see each cell. The ‘observers’ in the visibility from the path variable were represented by points along the hillwalker path. The ‘observers’ in the general visibility variable were represented by points on a 100 x 100 m grid across the entire study site, providing a measure of relative visibility between deer locations.

3.4.5 Estimating relative landscape usefrom deer counts

Absences of deer from the observation areas were recorded to indicate frequency of presence of deer and to distinguish from instances when an area was simply not observed. Absence records were considerably more frequent than deer group counts. This method resulted in an imbalance of presence vs absence data since, in an area, an absence was only ever represented by one datapoint, whereas presences could be represented by multiple datapoints. To balance the dataset, while preserving the variation between multiple, concurrent deer groups within an area, I generated pseudoabsences for each time an observation area was sampled. This ensured an equal number of datapoints for each time an observation area was searched for deer. Pseudoabsences were randomly selected from within the bounding range of all deer locations in that observation area. This ensured that the relevant comparison of deer numbers was made, since there were parts of some observation areas where deer were never observed, irrespective of the breadth of conditions recorded. The number of total datapoints assigned to each observation area was determined by the maximum number of deer groups observed in that area at one time. Using this method, an index of area use, hereafter referred to as 'area use' was calculated.

3.4.6 Data analysis

Statistical analysis

I used a generalised linear mixed effects (GLMM) model to assess the relationship betwe Key use and hillwalker numbers, distance to the hillwalker path, topography, visibility, and time of year. Other variables included were sun hours, rainfall, average windspeed, average temperature, time of day as it related to midday, and year. Observation areas were simplified to create a region variable for analysis (Figure 3.3). Region was included as a random effect to account for unmeasured differences across the study site that may have affected deer distribution; for example, established home ranges, forage quality, and quality and availability of neighbouring areas. All continuous variables were standardised to have a mean of zero and a standard deviation of one to facilitate comparison of coefficients and improve numerical stability in models.

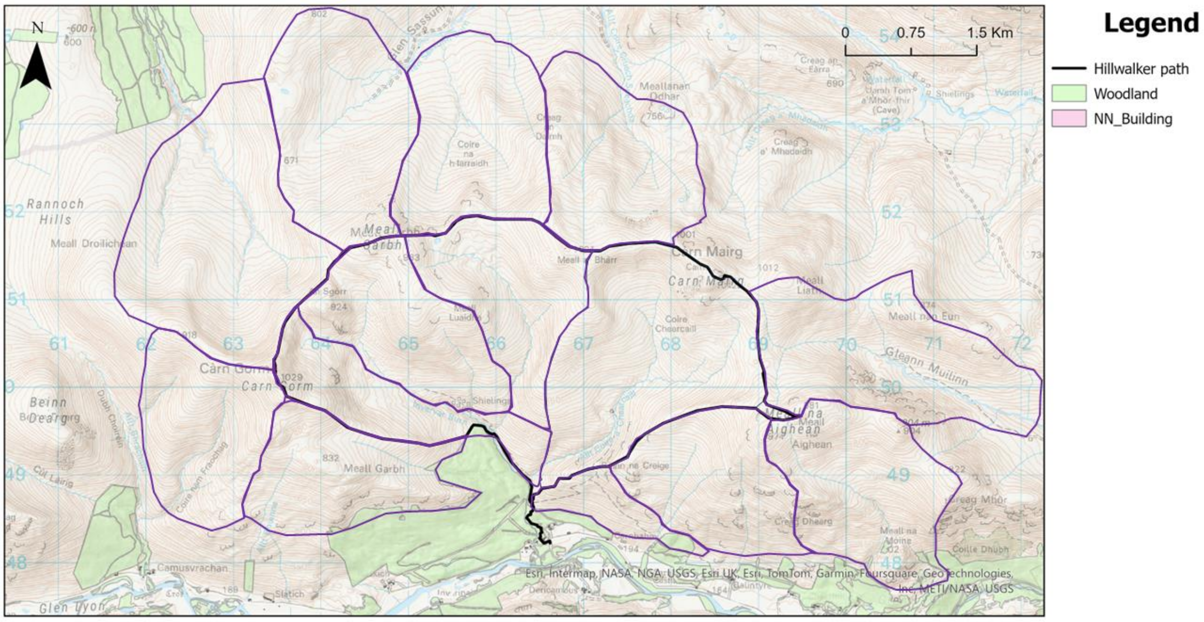

Figure 3.3. Defined regions of the study site, outlined in purple, included in the analysis as a random factor (region).

Interactions were included in the global model, where appropriate. The effect of hillwalker numbers may be greater with closer proximity to the path, particularly during times of the day when hillwalker numbers were greatest. Hillwalker numbers or proximity to the path may affect selection of topographic features, while topographic features may in turn exacerbate or mitigate the effect of hillwalkers (Sibbald *et al.*, 2011; Eisenberg *et al.*, 2014; Mols *et al.*, 2022). Finally, if progressive habituation effects were to be observed, then the effect of hillwalkers on deer distribution would interact with day of year and the year of study. Consequently, interactions between hillwalker numbers and distance to path, and hillwalker numbers/distance to path and each of topographic variation, ruggedness, visibility, day of year, and year were included.

A negative binomial distribution was used to account for the excessive number of 0 values created by the presence/absence data balancing process (White and Bennetts 1996; O'Hara and Kotze 2010; Stoklosa *et al.* 2022). I used the "dredge" function in the R package "MuMIn" to carry out model selection based on Akaike Information Criterion (AIC) (Bartoń, 2023). To manage the limitations on parameter numbers (Pollock *et al.*, 2019), I compared candidate models in two stages (Table 3.1). In the first stage, I defined two global models: one associated with temporal and weather variables, the other with topography and visibility variables. Each global model contained the disturbance variables and all plausible interactions. Those models suggested the most informative variables of each type. In the second stage, therefore, I combined the variables determined in stage 1 to create a new global model from which to assess all candidate models. Model assumptions were evaluated using residual diagnostics, variance inflation factors (VIFs), and model fit indices, confirming that the model met the necessary criteria for valid inference.

Table 3.1. Variables included at each stage of the model selection process, with Area as a random factor.

Model selection stage	Model selection input
Stage 1: temporal and weather variables	~ hillwalkers x day of year x distance to path x year + time of day x distance to path x hillwalkers + temperature + (1 | region)
Stage 1: topographic and visibility variables	~ distance to path x general visibility + hillwalkers x distance to path x topographic variation + hillwalkers x ruggedness + elevation + (1 | region)
Stage 2: final global model	~ distance to path x general visibility + hillwalkers x distance to path x topographic variation + hillwalkers x ruggedness + elevation + day of year x distance to path + time of day x distance to path + temperature + (1 | region)

All analyses were completed using R version 4.3.2 (R Core Team 2020). The GLMM models were carried out using the "MASS" (Venebles and Ripley, 2002) and "lme4" packages (Bates *et al*., 2015).

Selecting variable versions

As above, some potential covariates of observed deer distribution were represented by different variants. These were weather variables over different time periods, topographic variation with different buffer sizes, different scales of vector ruggedness measure, visibility from the path at different distances, and different representations of hillwalker numbers. To establish which variants of these variables were most informative, I repeated all models with all variants, holding variables consistent except for the one being tested. I assessed the *P* values of the different variables, as well as the AIC values of the models in which they appeared. The only variable for which the lowest *P* value and lowest AIC values did not align was the hillwalker numbers variable. In this case, I selected the variable version that produced the highest marginal R^2 value. This version coincided with the lowest *P* value and the most significant interaction with distance to the path.

Visual representation

To present the variation in deer distribution between busy and quiet days of hillwalker activity, I used the Kernel Density estimation tool in ArcGIS Pro 8. I defined busy and quiet days as days above (busy) or below (quiet) the overall mean daily number of hillwalkers (n = 30), and calculated separate kernel densities for each. Deer numbers were standardised between the busy and quiet kernel densities according to sample effort per area and per busy or quiet subset of the data. I then subtracted spatially corresponding kernel density grid cell values to determine the areas where the biggest differences in density occurred between busy and quiet days. Positive and negative values indicated the direction of the difference, as either higher density on busy days or quiet days. The distance of the value from 0 indicated the magnitude of the difference. The final kernel density map was based on these values to indicate where deer were more likely to be on busy days, and where they were more likely to be on quiet days.

3.5 Results

3.5.1 Assessment of variables for inclusion in variable selection stage 1

Detection. Group size varied significantly between habitat classes: grass, heather, and grass + heather (Kruskal-wallis: x^2 = 139.97, df = 2, P <0.001). The largest groups were associated with the grass + heather habitat class. There was no difference in mean group size between habitat classes grass and heather (Wilcoxon signed rank: W = 61965, P = 0.256), suggesting habitat did not affect detectability.

Deer detectability was thought to be affected by distance between the observer and the deer, with detection capability declining with increasing distance. In a separate GLMM, observer distance was found to have a significant, negative effect on deer area use (Estimate = -0.341 ± 0.066 SE, $z = -5.151$, $P < 0.001$), but this did not affect inferences regarding other variables (Appendix 3.1).

3.5.2 Assessment of variables for inclusion in variable selection stage 2

I selected variables for inclusion in the final model in two stages. In the first stage, two global models provided the most informative variables for inclusion in the second stage (Table 3.1). All plausible interactions were included, and outcomes of complex interactions were interpreted by numerical prediction.

The final model included the most informative variables selected in stage 2 by AIC (Table 3.2). These included disturbance variables hillwalker numbers and distance to the path, topographic and visibility variables, temporal variables, and weather variables.

Table 3.2. List of variables included in the global model to evaluate deer area use.

Variable name/code	Description
Hillwalker numbers	Total number of hillwalkers on day of observation and previous 1 day
Distance to the path	Distance to hillwalker path
Topographic variation	Topographical variation within a 250 m radius buffer of deer observation
Ruggedness	Vector ruggedness value over 650 x 650 m
Visibility from the path	Degree of visibility from the path within 1500m
General visibility	General visibility of the deer location
Day of year	Ordinal day of year
Elevation	Elevation of deer or absence
Year	2020, 2021, 2023
Time of day	Relative decimal time as distance in time from midday
Temperature	Average temperature over 30 minutes at time of observation
Windspeed	Average windspeed over 15 minutes at time of observation
Rainfall	Total amount of rain in 15 minutes at time of observation
Sun hours	Total amount of sun in 30 minutes at time of observation

3.5.3 Hillwalker numbers

Hillwalker numbers during the study exceeded those recorded in the previous two years (2018 and 2019; Marion *et al.,* 2021) (Figure 3.4A). Average number of hillwalkers per day on days when deer data collection occurred was 35.6 (SD = 33.5) in 2020, 29.6 (SD = 20.1) in 2021, and 24.8 (SD = 16.3) in 2022 (*cf*. 8 in Marion *et al.,* 2021). Hillwalker numbers in 2020 and 2021 were affected by the Covid-19 pandemic and associated restrictions on movement and activity. In 2020, this was characterised by very low hillwalker numbers in June, followed by a drastic increase over the rest of the season. Hillwalker numbers remained high in June and July 2021 while some Covid-19 restrictions remained in place. On average, hillwalker numbers were ~2.5 times higher on weekend days (mean = 43.7 ± 40.2 SD per day, median = 36, IQR (interquartile range) 16-59) than on weekdays (mean = 15.9 ± 13.7 SD per day, median = 13, IQR 5-24). Numbers of hillwalkers on the path during the day peaked around midday and were lower towards dawn and dusk (Figure 3.4B).

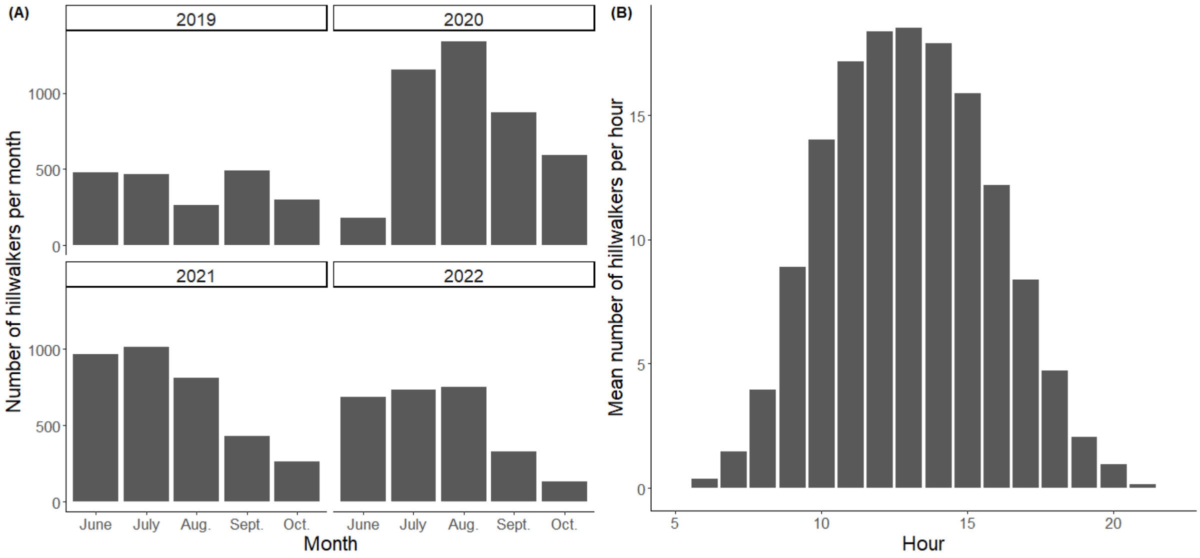

Figure 3.4. Hillwalker numbers in the study site as A) monthly hillwalker totals for the summer hillwalking season (June to October) for the three years of data collection and the previous one year, and B) maximum number of hillwalkers on the path per hour of the day, UTC.

3.5.4 Deer data

Over the data collection period, 3864 area observations resulted in the locations of 1726 groups of deer and 2138 area absences. Data were collected on a total of 113 days, that had a mean daily number of hillwalkers of 30 (max = 139, min = 0, median = 22).

Relative landscape use model output…………..

The most informative variables determining deer use of the landscape related to hillwalker numbers over two days, distance to the path, topographic variation, ruggedness, elevation, day of year, time of day and temperature (Table 3.3). The proportion of variance explained by the fixed effects was 0.146 (marginal R^2), and the total variance explained by the model, including the random effect, Area, was 0.272 (conditional R^2), leaving a large proportion of variance in the data unexplained. The interaction between hillwalker numbers and distance to the path was also influential.

Table 3.3. Coefficients (estimate and standard error), z-value and associated degree of significance of variables included in the top model selected by AIC to explain variation in deer area use.

Coefficients	Estimate	Std. Error	z value	*P* value	
(Intercept)	1.599	0.191	8.382	<0.001	***
Hillwalker numbers	-0.077	0.048	-1.602	0.109	
Distance to path	0.339	0.069	4.907	<0.001	***
Topographic variation	0.283	0.054	5.282	<0.001	***
Ruggedness	0.085	0.054	1.573	0.116	
Elevation	0.229	0.063	3.604	<0.001	***
Day of year	0.133	0.052	2.570	0.010	*
Time of day	0.069	0.056	1.247	0.212	
Temperature	0.239	0.050	4.732	<0.001	***
Hillwalker numbers x Distance to path	0.206	0.055	3.727	<0.001	***
Distance to path x Topographic variation	-0.136	0.055	-2.493	0.013	*
Hillwalker numbers x Topographic variation	-0.104	0.053	-1.942	0.052	.
Hillwalker numbers x Ruggedness	0.108	0.059	1.838	0.066	.
Distance to path x Day of year	0.131	0.057	2.316	0.021	*
Distance to path x Time of day	-0.254	0.053	-4.832	<0.001	***

Are deer further away from the path when hillwalker numbers are higher?

Deer were further away from the path when hillwalker numbers were higher (Figure 3.5A). Deer were also further away from the path closer to midday than dawn and dusk (Figure 3.5B), corresponding with being furthest away from the path when hillwalker numbers peaked during the day. Individual deer were, on average, 945 m from the path (SD = 401 m, interquartile range (IQR) = 684-1118 m, median 924 m). On days when hillwalker numbers were below the daily hillwalker mean, this distance decreased to 882 m (n = 28812, IQR = 625-1951 m, median = 875 m). On days when hillwalker numbers were equal to or above the daily hillwalker mean, the mean distance of deer from the path was 1032 m (n = 20684, IQR = 749-1288, median = 985 m).

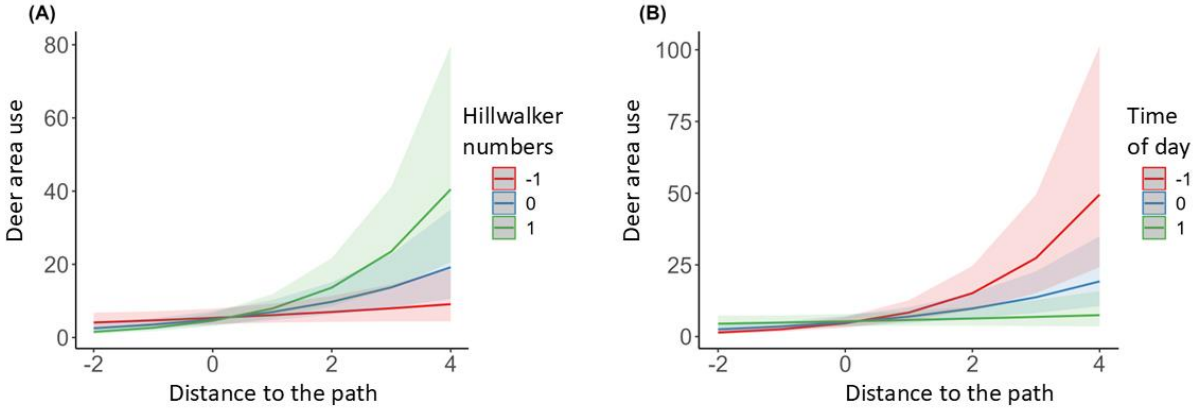

Figure 3.5. The effect of standardised distance to the path (0 m to 2430 m) on deer area use in relation to a) standardised hillwalker numbers where -1 = 0 hillwalkers and 1 = 100 hillwalkers, and b) standardised time of day, where -1 = midday, 1 = dawn/dusk.

The areas where the biggest differences in area use occurred between busy and quiet hillwalker days are indicated in (Figure 3.6). The distribution of blue shows where deer were more likely to be on quiet days, and the distribution of pale green to red shows where they were more likely to be on busy hillwalker days. Deer appear to have been more concentrated, and further from the path on busy hillwalker days.

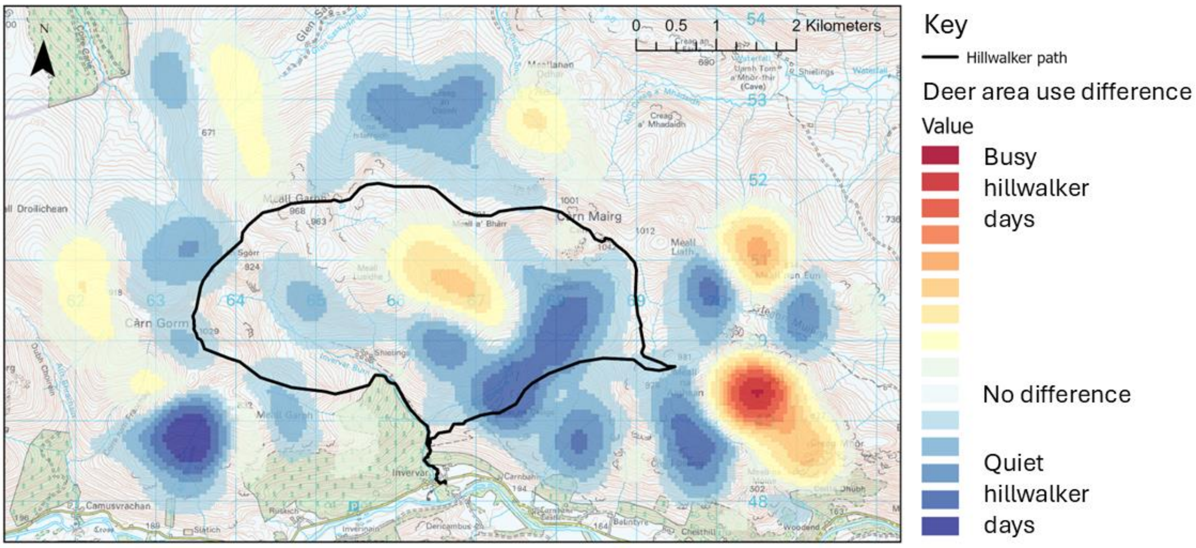

Figure 3.6. Map of the North Chesthill Estate and wider study area, showing the difference in distribution of deer on quiet days (< mean number of hillwalkers per day), and busy days (> mean number of hillwalkers per day). Areas where deer area use was higher on quiet days than on busy days are indicated in blue, and areas where deer area use was higher on busy days than quiet days are indicated from light green to red.

Does topography mitigate the spatial response of deer to hillwalkers?

The effect of distance to the path on deer area use was greater when deer were in areas with low topographic variation. Further away from the path, deer were more likely to be in places with low topographic variation and near to the path deer were more likely to be in areas with high topographic variation. (Figure 3.7A). Overall, deer were more likely to be in places with high topographic variation.

Deer area use was higher at greater elevations, but this was not significantly related to hillwalker numbers or distance to the path (Figure 3.7B).

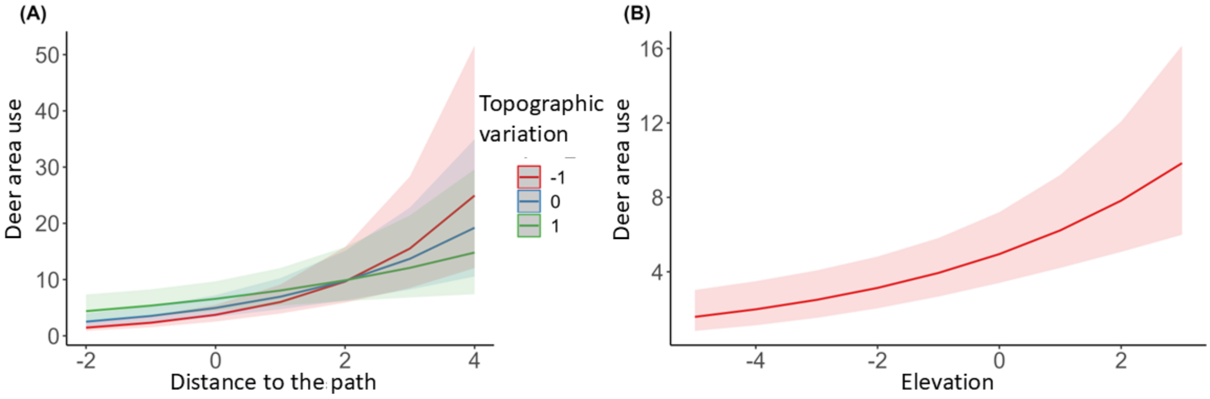

Figure 3.7. The relationship between a) distance to the path (0 m to 2430 m) on deer area use at different levels of topographic variation, and b) distance to the path and elevation (286 m to 2111 m) on deer area use.

Does the spatial response of deer to hillwalkers decrease later in the year, or across the study period?

Deer were further away from the path later in the season (Figure 3.8A), and overall area use in the study area increased as the season progressed (Figure 3.8B). Deer area use did not vary significantly between years and year did not significantly interact with hillwalker numbers or distance to the path.

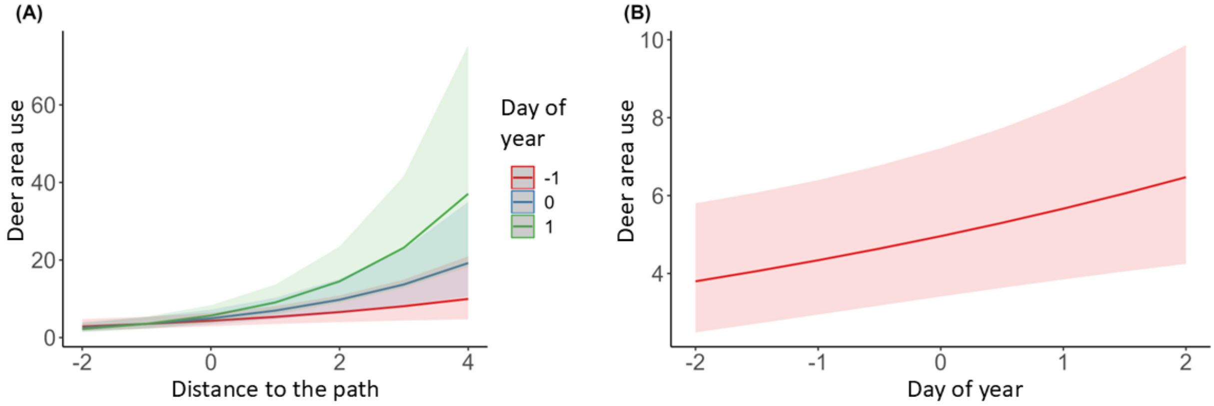

Figure 3.8. The effect of standardised day of year (01 June to 10 October) on deer area use a) in relation to standardised distance to the path (0 m to 2430 m), and b) overall across the study site.

3.6 Discussion

This study indicates spatial avoidance by red deer of a popular hillwalker path in Scotland. The magnitude of this response was sensitive to fluctuations in hillwalker numbers and affected by topographic variables. In accordance with hypothesis 1, deer were observed further from the path when hillwalker numbers were higher, including during times of the day when numbers of hillwalkers on the path were highest. The effect of hillwalkers varied significantly with topography, suggesting that topography mitigates against disturbance in accordance with hypothesis 2. Close to the path, deer area use was higher in places with higher topographic variation and the effect of distance to the path on area use was greater in places with lower topographic variation. I found no evidence that a seasonal or longer-term habituation process was occurring, supporting hypothesis 3. Habituation may still occur beyond the timeframe of this study, but no significant variation in spatial avoidance occurred between years. I discuss these findings with reference to the three questions posed in the Introduction, before considering potential improvements on the study approach. I conclude by discussing the management implications of my findings.

3.6.1 Are deer further away from the path when hillwalker numbers are higher?

Deer in this study area avoided human disturbance spatially and this avoidance was affected by the number of hillwalkers, consistent with similar studies (e.g. Sibbald *et al.,* 2011; Coppes *et al.,* 2017). The number of hillwalkers on the day of observation plus the previous day appeared to give the best explanation of deer distribution. This variable may more accurately reflect the hillwalker activity level of the period if a proportion of the observations each day occur before hillwalkers arrive at the specific location. This may be particularly relevant when considering weekly fluctuations in hillwalker numbers which peaked in the two days of the weekend but were also higher than average on Fridays and Mondays. The 'weekend effect' has been associated with short-term sensitisation of deer to disturbances, whereby responses to disturbances are greater on Sundays and Mondays (Moscatelli *et al.*, 2023).

Deer area use was generally higher further away from the hillwalker path, but this effect was more pronounced when hillwalker numbers were higher. Marion *et al.,* (2021) and Sibbald *et al.,* (2011) in the same and similar study sites, respectively, specified avoidance within 200 m from hillwalker paths when hillwalker numbers were higher. I showed that avoidance can occur at larger scales than this. On average, areas more likely to be occupied on busy hillwalker days were over half a kilometre further from the path than those more likely to be occupied on quiet days (Figure 3.6). At this scale, that represents a substantial shift in distribution and a significant potential reduction in habitat that deer are willing to use. The differences in the magnitude of the results in this study compared to others can be attributed to several factors. Marion *et al.,* (2021) were constrained by the use of camera traps deployed up to 150 m from the path, limiting the spatial scope of their observations. In contrast, I recorded deer locations up to 2.5 km away from the hillwalker path, providing a broader scope for assessing disturbance. Sibbald *et al.,* (2011) focused on only a small number of adult males (n = 8), which are often less sensitive to disturbance than females are (Stankowich, 2008). My findings support research highlighting the importance of spatial scale when evaluating the effects of disturbance (Vistnes and Nellemann, 2008).

3.6.2 Does topography mitigate the spatial response of deer to hillwalkers?

Topographic variation (ruggedness + slope) affected the spatial response of deer to hillwalkers in relation to the hillwalker path. In areas with low topographic variation, deer were more likely to be further away from the path. Deer area use was generally higher in places with higher topographic variation and elevation. In contrast, ruggedness did not significantly affect area use. This suggests that the effect of slope in the topographic variation variable was more important than ruggedness alone in mitigating the spatial response of deer to hillwalkers.

Landscape features can affect perceived risk in deer, resulting in varying patterns of space use across the landscape (Gaynor *et al.* 2019). For example, topographic obstacles can modulate prey response by either obscuring a threat or acting as a barrier to predators (Cassirer, Freddy and Ables, 1992; Chassagneux *et al.,* 2019). Deer were more likely to be in areas with high topographic variation closer to the hillwalker path which may be attributed to the screening effect provided by steep slopes (Montgomery, Roloff and Millspaugh, 2012). Slopes may also represent topographic obstacles better than ruggedness due to the greater discrepancy between surface distance and Euclidean (straight-line) distance associated with steep slopes. When steep slopes are between deer and the disturbance, the surface distance is longer than in flat terrain. This could be important if the ability of deer to maximise distance between themselves and the path is limited by the path acting as barrier to movement. This may occur because the path encircles a large portion of the study site, with low availability of distances greater than 1 km in that portion. In these areas, deer may make greater use of topographic features, such as slopes, to mitigate their spatial response. Finally, flatter areas may be preferred because they are associated with reduced energy expenditure (Ganskopp and Vavra, 1987; Kie, Ager and Bowyer, 2005). These areas may be more acceptable to deer at greater distances from the path where perceived risk is lower.

The use of landscape features by deer in response to disturbance is often related to visibility (Montgomery, Roloff and Millspaugh, 2012; Chassagneux *et al.*, 2019). However, visibility variables did not appear to affect deer area use in my study. I suggest that, in this case, the effects of topography on deer space use are more complicated than visibility alone. For example, deer were generally more likely to be associated with greater topographic variation and may also have selected these areas for reasons not relating to disturbance. In mountain environments, slopes may be particularly important to deer for shelter from the wind (Staines, 1976). This could be particularly relevant given that deer were also more likely to be in areas of high elevation. Red deer in the Scottish uplands are more likely to be at high elevations during the day (Mitchell, Staines and Welch, 1977), but slope and elevation may also represent areas associated with greater safety. Deer have been shown to flee uphill when disturbed (Cassirer, Freddy and Ables, 1992; Stankowich and Coss, 2006) and proximity to slopes may help facilitate this preferred response.

3.6.3 Does the spatial response of deer to hillwalkers decrease seasonally, or across the study period?

Deer can reduce their response to disturbance with increased exposure via habituation processes (Reimers *et al.*, 2010; Schuttler *et al.*, 2017). This can repeat annually, occurring over the course of a season (Haskell and Ballard, 2008), or can be a progressive response over many years (Helle *et al.*, 2012). From a deer management perspective, a reduction in spatial avoidance of hillwalkers by deer could be considered beneficial. This would occur because deer may be less likely to congregate and overgraze areas (Little *et al.*, 2016; Nix *et al.*, 2018), less likely to leave the estate during stalking seasons (Lesmerises, Johnson and St-Laurent, 2017), and be less likely to be hyperalert to stalkers (Reimers *et al.*, 2010). Deer area use far away from the hillwalker path increased as the season progressed, and overall area use in the study area increased over time. Given that the path is central to the study site, the combination of these factors suggests an increase in deer detected at the periphery of the study site later in the season. This could be due to deer groups from the surrounding area moving into the site, or increased detectability of the deer. Seasonal patterns in dispersal occur as small nursery groups join the main herd when calves get older, which would result in larger and more conspicuous groups on the landscape. Red deer can also occupy different areas depending on the breeding cycle (Jayakody *et al.,* 2008) and stags are drawn to areas with hinds in preparation for the rut from September (Lincoln, Guinness and Short, 1972). This result could also reflect increased spatial avoidance due to a sensitisation process. However, without a significant association with hillwalker numbers, and because deer use of areas closest to the path appeared consistent, this is unsubstantiated. These results seem to contrast with studies that show seasonal habituation processes, or temporary increases in tolerance, to outdoor recreation (Lovari *et al.*, 2007; Haskell and Ballard, 2008).

Despite a significant association between deer area use, hillwalker numbers and distance to the path, and an upward annual trend in hillwalker activity throughout the study period and the preceding two years (Marion *et al.*, 2022a), there was no apparent change in spatial response to hillwalker activity over this time. This suggests that long term habituation is not occurring or is ongoing but not measurable within the timeframe of this study. The timeframe for habituation by ungulates to recreation in the literature is varied. Morrison *et al.* (2018) reported partial acclimatisation by elk, *Cervus canadensis*, in the 4 years following ski resort development, Helle *et al.* (2012) found evidence for habituation over 10 years, and Ciach and Peksa (2018) showed a gradual habituation process in chamois, *Rupicapra rupicapra*, over 50 years. However, a study of mule deer, *Odocoileus hemionus*, response to energy development showed no evidence of habituation over a 17-year period (Sawyer *et al.*, 2017). A study of caribou, *Rangifer tarandus*, responses to 40 years of energy development also suggested weak or absent evidence of habituation (Johnson *et al.*, 2020). Long term habituation in this study may require more time, or may be inhibited by other factors (Stankowich, 2008; Bejder *et al.*, 2009).

Numbers of hillwalkers may play an important role in the occurrence of habituation, with deer that experience greater exposure to human recreation tolerating closer proximity to humans (Sutton and Heske, 2017), lower vigilance levels (Schuttler *et al.*, 2017), and lower levels of stress hormone (Dixon *et al.*, 2021). Comparisons to similar sites with apparently smaller spatial responses suggest that hillwalker numbers in this study are relatively low (Sibbald *et al.,* 2011). This response may be more apparent due to lack of natural predation. In areas where natural predation occurs in the absence of hunting by humans, elk have been observed to use human activity or infrastructure as a refuge from wolves, *Canis lupus* (Rogala *et al.*, 2011; Brook, 2015). The presence of hunting in this study site may further reduce probability of habituation (Baskin and Hjälten, 2001; Stankowich, 2008). Coppes *et al.* (2017) suggested that red deer in their study were unable to distinguish between recreationists and hunters, and Ikeda and Koizumi, (2024) found that deer in hunted areas showed year-round adaptations to hunting, even in non-hunted areas. Moreover, red deer on the isle of Rum in Scotland have habituated where hunting has been absent since 1972, despite low recreation levels (Pemberton, Kruuk and Clutton-Brock, 2022). Finally, hunting may select for a more sensitive population if those with lower responses to human activity, are more likely to be shot (Baskin, Ball and Danell, 2004; Ciuti, Muhly, *et al.*, 2012).

3.6.4 Model performance and potential improvements

Overall, the model explained only a small fraction of the variation in the data. Several factors may have contributed to this. Ecological data are often noisy due to the stochastic nature of the environment and inherent variability in wildlife behaviour. Wildlife behaviour in montane environments can be particularly difficult to predict due to small-scale spatial and temporal shifts in weather variables such as wind and temperature, depending on local topography. An on-site weather station would improve the accuracy of the weather variables. Lack of resolution in topographic variables might have also obscured finer-scale spatial patterns. These would be improved using higher resolution digital elevation maps, which are currently unavailable for the study area. Variation in deer detectability may have contributed to the model's limited explanatory power. Differences in number of deer observed based on habitat appeared to be driven by group size, since larger groups were more likely to span multiple habitats and larger groups were observed on heather, despite the expected decrease in detectability associated with this habitat. However, while greater observer-deer distances were associated with fewer deer being observed, this factor was ultimately excluded from the final model due to limited availability of that data. Overall, these results suggest the need for refined detection methods to improve model accuracy in future studies.Finally, while every effort was made to capture all potentially relevant factors, unmeasured variables may have contributed to additional variation in the data. For example, hillwalker clothing, group size, presence of dogs, behaviour, and presence on or off the path may have affected deer responses to the hillwalkers (Jayakody *et al.*, 2008; Stankowich, 2008; Westekemper *et al.*, 2018). Use of camera traps at the start of the path to capture some variation in hillwalkers would enable some quantification of these effects, since it is unlikely otherwise that all hillwalkers would be observed during the course of other data collection. Furthermore, forage is an important driver of movement and distribution in deer (Pettorelli *et al.*, 2005; Hebblewhite, 2008; Bjørneraas *et al.*, 2012), but forage quality was assumed to be uniform across the study site. Vegetation surveys to broadly classify habitat across the study site by forage quality and availability would help determine the relative importance of forage and disturbance responses in determining deer distribution.

3.6.5 Management implications

Deer distribution in this study site is affected by hillwalkers, and deer significantly avoid the hillwalker path, especially when hillwalker numbers are high. While deer appeared to use landscape features to mitigate spatial responses, the mechanisms for this are unclear. The hillwalker path encircles a substantial proportion of the study site and may inhibit movement of deer during the day. Deer can compensate for reduced foraging opportunities during the day by occupying areas frequented by hillwalkers at night instead (Coppes *et al.*, 2017). Due to the limitations of the methods of this study, it is unclear whether this is occurring. A similar study found no evidence for compensatory use of favoured habitat overnight by GPS-collared stags (Sibbald *et al.*, 2011). In the same site as this study, camera traps observed an increase in deer detections at nighttime, suggesting temporal avoidance (Marion *et al.,* 2021). However, this does not necessarily indicate time spent foraging near the path rather than using the undisturbed period to move between areas on either side of the path. Within 150 m from the path, deer were more likely to be travelling than foraging when observed at night (Marion *et al.,* 2022a), suggesting that compensatory foraging was not occurring. The hillwalker path acting as a barrier and restricting movement may have environmental consequences as concentrated deer are more likely to overgraze and trample areas they can access. This is particularly important when considering peatland erosion and climate change mitigation in a landscape that has already been degraded by human use (Davies, 2008). Future research should focus on providing more detailed information on deer spatial responses to disturbance over 24 hours. This would allow any compensatory behaviour to be identified and determine the duration of disturbance responses. To identify the duration of disturbance responses and compensatory behaviour, GPS tracking collars could be deployed. These would establish the displacement distance of individual deer, how long they stay away following high disturbance periods, and the true extent to which areas nearest the path are selected against. A more general indication of compensatory use of areas close to the path could be gained using camera traps placed across the full breadth of the spatial avoidance of the path in the site.

Deer concentrated in locally high densities are likely to result in larger group sizes (Borkowski, 2000; Hebblewhite and Pletscher, 2002) and deer have been shown to increase group size in response to disturbance (Baskin and Hjälten, 2001; Wilson and Wilmshurst, 2019). More deer reduces the availability of cover for approaching stalkers because, collectively, the deer have better visual coverage of the area. This can make both culling for essential deer management and commercial stalking more difficult. Furthermore, hillwalker activity has the potential to push deer off the estate, reducing stalking opportunities. This is particularly significant if it occurs at the onset of winter snows, which may inhibit return over the ridges (Mysterud *et al.*, 2011).

Spatial avoidance by deer may be exacerbated when responding to spatially and temporally predictable disturbances on the landscape, such as the hillwalker path (Laundre, Hernandez and Ripple, 2010; Visscher *et al.*, 2017; Sullivan *et al.*, 2018). However, deer have also been shown to be more tolerant to disturbance when disturbances are predictable, such as restricted to established paths (Westekemper *et al.*, 2018). Given that persistent spatial avoidance is likely to be inevitable, hillwalkers should be encouraged to stick to the path where possible to minimise the scale of avoidance and spatial impact (Helle *et al.*, 2012). This is particularly important during the stalking season and other critical times of year, such as the rut and calving. In this way, the potential for land use conflict can also be reduced, allowing the Scottish uplands to facilitate multiple land uses more successfully, while promoting better conditions for wildlife.

Chapter 4. Behavioural responses of deer to hillwalker activity in Glen Lyon, Scotland

4.1 Abstract

Human activity in wildlife habitat can be perceived by wildlife as predation risk. Behavioural responses to human disturbance can therefore represent trade-offs between maximising energy intake and minimising predation risk. In deer, behavioural responses to disturbance include increased vigilance, reduced activity, increases in costly alert and flight behaviour, and changes in group structure. I investigated these disturbance responses in red deer on a focal estate in Scotland with a popular hillwalking path. Red deer are important to the environment and economy in Scotland but are thought by some landowners to be disturbed by recreational activity. I observed behavioural changes in relation to fluctuations in hillwalker numbers and proximity to the hillwalker path across all measures investigated. However, the degree to which this occurred varied between measures and contexts. Vigilance was higher and activity levels were lower on days with more hillwalkers. Deer were more likely to exhibit acute disturbance behaviours near the path regardless of fluctuations in hillwalker numbers. The effect of hillwalker pressure on group structure was context dependent. Larger groups of deer were observed further from the path and increased aggregation occurred in areas with lower visibility when hillwalker numbers were higher. These results highlighted the variety of ways in which deer respond to disturbance and the importance of using multiple approaches when assessing wildlife behavioural responses to disturbance. While deer show considerable plasticity to a changing environment, no evidence of habituation was observed in this study which could have important implications for deer welfare. Disturbance responses such as reduced activity may not be obvious to hillwalkers as disturbed behaviours, thus education is required to make recreationists aware of their potential impact on wildlife.

4.2 Introduction

Popularity of outdoor recreation is rising globally, increasing exposure of wildlife to human activity (Balmford *et al.*, 2009; Larson *et al.*, 2016). In Scotland, land access laws allow the public the 'right to responsible access' to the countryside, and hillwalking is a popular pastime. However, land use conflict occurs when those who rely on deer for income perceive negative impacts on red deer, *Cervus elaphus*, caused by hillwalkers (MacMillan and Leitch, 2008; Reis and Higham, 2009).

Human activity can cause behavioural responses in wildlife similar to those elicited by predators (Frid and Dill, 2002). These behavioural responses can represent trade-offs between fitness and survival, with both individual and population consequences. Disturbance responses of deer to human activity may even exceed that of predation, particularly in hunted populations or areas in which human activity is pervasive (Ciuti, Northrup, *et al.*, 2012; Visscher *et al.*, 2023). In Scotland, red deer no longer have a natural predator, but an increase in popularity of hillwalking has the potential to impact red deer behaviour in similar ways (Jayakody *et al.*, 2008; Visscher *et al.*, 2023). This impact may be particularly significant if deer stalking (hunting) in the same areas inhibits adaptive behavioural modifications such as habituation or an increase in tolerance (Stankowich, 2008). An alternative response of sensitisation, whereby deer become more reactive in response to disturbance, could have additional welfare consequences and exacerbate environmental and economic impacts. For example, sensitisation to engine noises occurred in reindeer following capture from a helicopter (Reimers and Colman, 2009).

If deer are responding to disturbances, they are spending less time foraging and expending more energy in evasive behaviour, reducing their net energy intake (Chambers *et al.*, 2022). Increases in vigilance levels are often associated with disturbance responses in deer (Fortin *et al.*, 2004; Jayakody *et al.*, 2008; Ciuti, Muhly, *et al.*, 2012; Tsunoda, 2021; Bhardwaj *et al.*, 2022), but can also be related to breeding season (Lung and Childress, 2007). Vigilance and foraging are not entirely mutually exclusive but vigilance whilst foraging reduces bite rate, leading to a trade-off between energy intake and predator avoidance (Fortin *et al.*, 2004). Increased disturbance levels may also cause deer to reduce their movements to avoid detection (Little *et al.*, 2016) or increase their movements to avoid the disturbance (Smith *et al.*, 2022b). Both strategies have the potential to reduce foraging opportunities if deer do not move to find more forage, or if they travel more and spend less time foraging. Habitat selection may also change as a response to disturbance, with deer selecting areas deemed safer because they provide cover or are further from the disturbance, rather than due to forage quality (Filla *et al.*, 2017). Movement patterns and activity cycles can be affected as deer commonly avoid human activity spatially or by reducing temporal overlap with humans (e.g. Gaynor *et al.*, 2018; Scholten, Moe and Hegland, 2018; Naidoo and Burton, 2020). Reduction in net energy intake caused by disturbance responses can lead to reduced body condition (Putman, Nelli and Matthiopoulos, 2019). In turn, poor maternal condition has negative consequences for calf survival (Duquette *et al.*, 2014; Shallow *et al.*, 2015). Studies have also shown that disturbances in the first weeks after birth can have longer term survival implications for calves if they miss critical feeding opportunities (Phillips and Alldredge 2000). Consequently, disturbances can lower individual survival rates and fitness, which could lead to population-level effects (Sutherland, 1996; DeWitt *et al.*, 2019).

In addition to increased levels of vigilance, disturbed deer may be more likely to be found in larger groups (Skogland and Grøvan, 1988; Lingle, 2001). This combination of heightened vigilance and larger group sizes makes stalking more difficult, potentially impacting commercial activities and management. Deer stalking is important for rural income and employment, and helps to fund land management, including essential population control (Macmillan and Phillip 2008). In the absence of natural predators, red deer in Scotland are commonly considered over-abundant (Macmillan and Phillip, 2008; Edwards and Kenyon, 2013). Population control has been highlighted by government policy as a priority to counteract the detrimental effects of over-population relating to conservation, climate change mitigation, public health, and the economy (Pepper *et al.* 2019).

In this study, I observed deer throughout the summer hillwalking season to determine how deer vigilance levels, activity levels, frequency of acute disturbance behaviour, and group structure are affected by hillwalker activity. I hypothesised that when hillwalkers were abundant and close to the deer, deer would:

1) increase vigilance levels as a response to increased perception of risk (vigilance hypothesis),
2) reduce activity to avoid hillwalkers (activity hypothesis),
3) be more likely to display acute disturbance behaviours due to increased likelihood of encountering hillwalkers (disturbance behaviour hypothesis),
4) be observed in larger and more closely aggregated groups to benefit from collective vigilance and as a direct disturbance response (group structure hypothesis).

4.3 Study site

The study site is located in Glen Lyon in Perthshire, Scotland and is largely made up of the North Chesthill estate (56°37’04.5”N 4°10’50.7”W) (Figure 3.1). The site includes four mountains classed as Munros (mountains in Scotland greater than 3000 ft / 914 m) which attract hillwalkers. The Glen Lyon Horseshoe path encircles the centre portion of the North Chesthill estate, allowing hillwalkers to summit each mountain in a 17 km loop.

4.4 Methods

4.4.1 Data collection period

Data collection occurred during the summer recreation seasons in 2020, 2021 and 2022. Data were collected 4 times between early June and either late September (2021 and 2022) or early October (2020), in 2-3 week blocks.

4.4.2 Field methods

Data on hillwalker numbers were collected using a people counter located at the beginning of the path. Full details of this are outlined in Chapter 3.

Locations for behavioural observations were selected with the aim of covering the east, centre, and west portions of the study site (Appendix 4.1). Timings of observation sessions were selected so that, at least twice per data collection round, observations took place both before and after midday, on busy (weekend) and quiet (week) days. A combination of repeating areas and opportunistic observations of deer in less frequented areas was used to allow temporal comparisons whilst also maximising spatial coverage.

Deer were observed using binoculars or a spotting scope, depending on the distance of the observation. Scans were recorded verbally, into a phone, and later transcribed. During a scan, behaviour for each deer in the group was classified as standing head up, standing head down, lying head up, lying head down, walking or running (Table 3.1). Scans were carried out at 3-minute intervals (Jayakody *et al.*, 2008), a frequency that allowed the entire group to be scanned while effectively capturing variation in short-duration behaviours like vigilance, which can change rapidly and benefit from high-frequency of observations..Any relevant notes on behaviour, disturbances, deer movement, and demographics were also recorded. If groups were too large to be scanned within the 3-minute timeframe, a subset was scanned instead. A subset was only used if it was deemed representative of the wider group in aggregation and current behaviour, and recognisable for repeated scans of the same individuals. The location of the subsets was as close to the centroid of the group as possible, or two subsets representing distinct distances from the hillwalker path were chosen. Where appropriate, the location of the scans was recorded for the specific subset observed, while the overall group size was that of the wider group. The effect of this was assessed by comparing the performance of models using the full dataset to those using only datapoints where at least 50% of the group was recorded during scans. This comparison was based on marginal R^2 value, with a higher R^2 value representing a better fit (R package: *modelsummary*, Arel-Bundock, 2022). Calves were reported separately where possible.

Table 4.1. Ethogram of recorded behaviours. Definition of vigilance is in accordance with Jayakody et al., (2008).

Behaviour	Description
Standing head up – **vigilant, inactive, stationary**	Deer on its feet, head raised above the shoulders, not travelling
Standing head down – **non-vigilant, active, stationary**	Deer on its feet, head below the shoulders, usually grazing, may be travelling slowly. Short behaviours such as scratching or grooming included.
Lying head up – **vigilant, inactive, stationary**	Deer lying down, head raised above shoulders, may be ruminating or resting, assumed to be vigilant given that it was not always possible to tell if the deer had its eyes open or closed.
Lying head down – **non-vigilant, inactive, stationary**	Deer lying down with head below the shoulders, usually sleeping or resting. Short behaviours whilst lying such as scratching, grooming, or rolling also included.
Walking – **vigilant, active, travelling**	Deer travelling at a walk, head raised above the shoulder
Running – **non-vigilant, active, travelling**	Deer either trotting or running, usually in response to disturbance but sometimes in response to flies, temperature, or to catch up with main group.

Snapshot data on deer groups were collected in accordance with methods outlined in Chapter 3, 3.4.2. This also included behaviour and aggregation of the group at time of observation. Behaviour was recorded as grazing, resting, moving, running, alert, other. Behaviours were recorded to represent the majority of the group and multiple behaviours were recorded if there was no significant majority. The 'other' behaviour category included less common behaviours such as 'catching a breeze (specifically in hot weather, standing head up, and ruminating)', and social interactions. For further analyses, recorded behaviours were used to derive 3 additional binomial variables: alert/running versus all other behaviours; settled (grazing and/or resting behaviour) versus unsettled (moving, alert, running); and resting versus all other behaviours. Alert and running are suggested as disturbance behaviours (Stankowich and Coss, 2006; Meisingset *et al.*, 2022). Alert behaviour was defined as standing, head up, ears upright and actively scanning or focused on a stimulus (Clutton-Brock and Guinness, 1975). Degree of aggregation can indicate disturbance (Jayakody *et. al.,* 2008). The aggregation of the groups was classified on a scale of 1 to 3, where: 1 represented a dispersed group; 2 represented a loosely aggregated group with deer on average greater than 2 deer-lengths apart (Jayakody *et al.,* 2008), or a concentrated nucleus of deer in the group <50% of the total group; and 3 represented a highly aggregated group with deer on average closer than 2 deer-lengths apart or a nucleus of >50%. Aggregations were also recorded as ‘multiple’ when there were 2 or more clearly defined groups <100 m apart or with individuals dispersed in between.

Weather, habitat, and topographic variables were calculated according to the methods outlined in Chapter 3. Observer distance was included in the analysis of the behavioural observation data to control for the potential effect of the observer on the behaviour of the deer. In addition, if the observer was evidently detected by the deer (deer looking in direction of observer and responding with increased alertness or running away), subsequent scans were removed from the analysis (n = 280).

4.4.3 Data analysis

The proportion of deer per scan performing behaviours that could be classed as vigilant (standing head up, lying head up, walking), and the proportion of deer per scan performing behaviours that were classed as active (standing head down, walking, running) were analysed separately. Solitary deer were included in the analysis, and group size was included as an explanatory variable. Proportion of deer travelling vs stationary was dropped as a dependent variable due to the low occurrence of travelling (1.13% of individuals scanned). Proportion values were arcsine square root transformed (Childress and Lung, 2003) and analysed per scan, and by averaging scans across 10 minutes (n = 3) and 30 minutes (n = 10). A linear mixed effects model (lmer) in R package “lme4” (Bates *et al*., 2015) was used to test for effects of the different explanatory variables, with group ID as a random effect to control for unmeasured aspects of context including, for example, the composition of individual personalities within a group (Bonnot *et al.*, 2015). Deer were not individually marked, so unknown repetitions of groups of deer within data collection periods may have occurred; however, the sampling protocol was focused specifically on a representative sample of deer based on location, time of day (am or pm), and level of hillwalker disturbance. Repetition of deer within these conditions was limited by using consistent group IDs. Region was also included as a random effect to account for any unmeasured differences between different areas within the study site. Probability of deer running or being alert was modelled using a binomial general linear model (GLM) in R package “lme4” (Bates *et al*., 2015). Degree of aggregation was modelled with an ordinal regression using 3 levels from 1, dispersed, to 3, most aggregated, using R package “MASS” (Venebles and Ripley, 2002). Group size of deer was modelled using a linear mixed effects model (lmer) in R package “lme4”, and region (Figure 3.3) was included as random effect. All analyses were completed using R version 4.3.2 (R Core Team 2020) and candidate models were compared using Akaike's information criterion (AIC) with R package "MuMIn" (Barton 2018) to determine input variables for the final model. The model with the lowest AIC was identified as the top model, and alternative models with a ΔAIC (delta AIC) value of ≤6 were considered plausible competitors (Richards, Whittingham and Stephens, 2011). The simplest of the models in this plausible set was selected, as the lower-ranking models, while within the acceptable ΔAIC range, included additional variables that did not substantially improve model performance. All continuous variables were standardised to have a mean of zero and a standard deviation of one to facilitate comparison of coefficients and improve numerical stability in models.

Interactions were included in the global model, where appropriate. The effect of hillwalker numbers on deer may be greater with closer proximity of deer to the path, particularly during times of the day when hillwalker numbers were greatest. Topographic features may exacerbate or mitigate the effect of hillwalkers (Sibbald *et al.*, 2011; Eisenberg *et al.*, 2014; Mols *et al.*, 2022). Finally, if developing habituation effects were to be observed, then the effect of hillwalkers on deer behaviour would interact with day of year (seasonal habituation occurring over the busy summer hillwalker period) and the year of study.

Multiple versions of some variables were calculated (Table 4.2). These were weather variables over different time periods, topographic variation with different buffer sizes, different scales of vector ruggedness measures, visibility from the path at different distances, and different organisation of hillwalker numbers. To decide which versions of the variables to include in the global model, I compared the different versions by repeating the model with all variables consistent except for the one being tested. I then used the *P* values to compare the significance levels between these versions and selected the variable version with the lowest associated *P* value (greatest significance).

Table 4.2. Description of the variables used to model behavioural responses of red deer to hillwalkers and the specific hypotheses they were applied to: Vigilance (Vig), Activity (Act), Disturbance behaviour (DiB), Group structure – size (GSS), aggregation (GSA). Descriptive names of each variable are indicated in bold.

Variable name	Description	Hypotheses
Hillwalker numbers		
Hw_daily	Maximum number of hillwalkers on day of observation	DiB

Hw_2days	Maximum number of hillwalkers on day of observation and previous 1 day	GSS
Hwtime2	Maximum number of hillwalkers on day on day of observation, accounting for clockwise progress around path in 3 sections	Vig, Act, GSA
Distance to path	Distance to the hillwalker path	All
Topographic variation		
Topographic variation250	Topographic variation within a 250 m radius buffer of deer observation	DiB, GSS, GSA
Topographic variation500	Topographic variation within a 500 m radius buffer of deer observation	Vig, Act
Ruggedness		
Ruggedness3	Vector ruggedness value with neighbourhood value 3 or 150 x 150 m area	Vig, Act, GSS
Ruggedness9	Vector ruggedness value with neighbourhood value 9 or 450 x 450 m area	DiB, GSA
Visibility from path		
Pathvis1000	Degree of visibility from the path within 1000m	GSS, GSA
Pathvis1500	Degree of visibility from the path within 1500m	Vig, Act, DiB
General visibility	General visibility of the deer location based on 100 x 100 grid	All
Day of year	Ordinal day of year	All
Elevation	Elevation of deer (m.a.s.l)	All
Year	2020, 2021, 2023	All
Time of day	Relative decimal time as distance in time from midday	All
nDeer	Number of deer in group, including calves	All
Temperature		
av_temp0	Average air temperature (°C) over 15 minutes at time of observation	DiB, GSA
av_temp1	Average air temperature (°C) over 30 minutes at time of observation	GSS
av_temp6	Average air temperature (°C) over 90 minutes at time of observation	Vig, Act
Windspeed		
av_wsp0	Average windspeed over 15 minutes at time of observation	DiB, GSS, GSA
av_wsp4	Average windspeed over 60 minutes at time of observation	Vig, Act

Sum rain		
sum_rain0	Total amount of rain in 15 minutes at time of observation	DiB, GSS
sum_rain1	Total amount of rain in 30 minutes at time of observation	GSA
sum_rain12	Total amount of rain in 3 hours at time of observation	Vig, Act
Sun hours		
sum_sun0	Total amount of sun in 15 minutes at time of observation	GSS
sum_sun1	Total amount of sun in 30 minutes at time of observation	DiB, GSA
sum_sun2	Total amount of sun in 45 minutes at time of observation	Vig, Act

4.5 Results

4.5.1 Hillwalker numbers

Hillwalker numbers during the study exceeded those recorded in the previous two years (Marion *et al.*, 2021). Average number of hillwalkers per day on days when deer data collection occurred was 35.6 in 2020, 29.6 in 2021, and 24.8 in 2022. Hillwalker numbers in 2022 were most consistent across the whole summer recreation season (mean = 19.0 SD ± 17.5, median = 16, IQR 11-30), though lower than in the previous 2 years (2020: mean = 27.4 SD ± 31.2, median = 21.5, IQR 13-34, 2021: mean = 23.0 SD ± 19.3, median = 16, IQR 11-30). Hillwalker numbers in 2020 and 2021 were affected by the COVID-19 pandemic and associated restrictions on movement and activity. In June 2020, in Scotland, movement for recreation purposes was limited to a 5-mile radius around homes, resulting in initially very low hillwalker numbers in the study site (Figure 4.1). Following the removal of these restrictions in July 2020, combined with the continued limits on social gatherings indoors, hillwalker numbers increased drastically. Hillwalker numbers remained high in June and July 2021 which may also have been related to COVID-19 restrictions. The region-based restriction system at the time could have led to accumulated demand and lack of alternative activities.

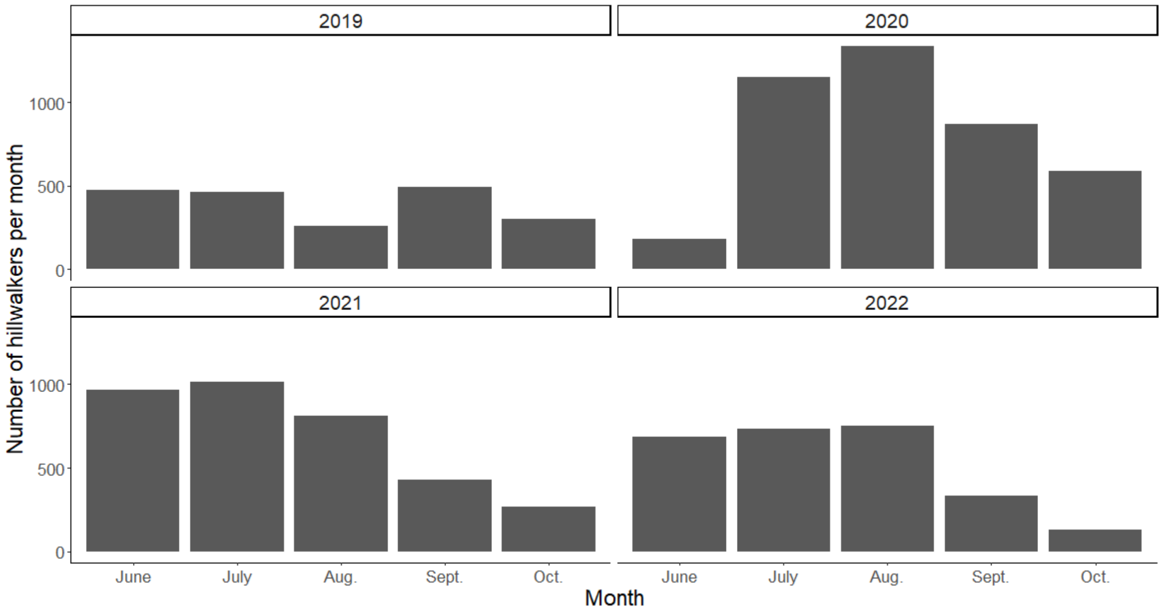

Figure 4.1. Monthly hillwalker totals for the summer hillwalking season (June to October) for the three years of data collection and the previous one year.

Hillwalker numbers were ~2.5 times higher on weekend days (mean = 43.7 ± 40.2 SD per day) than weekdays (mean = 15.9 ± 13.7 SD per day) (Figure 4.2). Numbers of hillwalkers on the path during the day peaked around midday and were lower towards dawn and dusk.

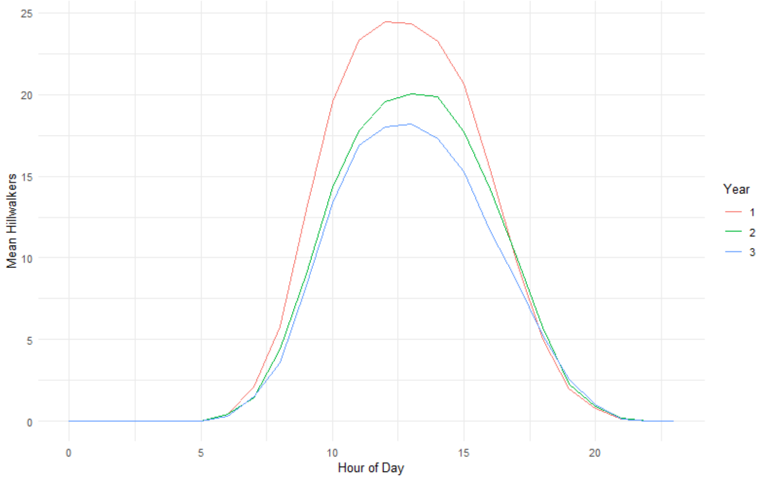

Figure 4.2. Maximum number of hillwalkers on the path per hour of the day, UTC.

4.5.2 Data collection

Cleaned scan sample data for analysis of vigilance and activity consisted of 7161 scans across 234 observations, totalling 358 hours. Average length of observations was approximately 30 scans, or 1.53 hours (max = 6.7 hrs, min = 0.05 hrs, SD = 0.96 hrs, median = 1.55 hrs). Data were analysed per scan for both vigilance and activity models. When scans were averaged over 30 minutes the resulting sample size was too small to test all potential effects. When the scan data were averaged over 10 minutes, the top models produced lower marginal R^2 values when compared to the non-averaged dataset, suggesting reduced performance.

A total of 1726 groups of deer were observed and used for the disturbance behaviour and group size analyses. Nearly 70% (n=1179) of these observations included both behaviour and aggregation data for analysis of group aggregations.

4.5.3 Vigilance: Do deer increase vigilance in response to increased perception of risk?

Deer were more vigilant when hillwalker numbers, version Hwtime2, were higher (Figure 4.3A), and when amount of sun was higher (Figure 4.3B) (Table 4.3). However, these variables explained only a small proportion of the variance in the data (marginal R^2 = 0.042), while the total proportion of the variance explained by the model, including the random effect group ID, was 0.326. Region was dropped as random effect due to lack of contribution to the explanatory power of the model. When the daily hillwalker numbers were below the average for days when behavioural observations occurred (n = 28), an average of 44.6% of deer per scan were vigilant. On days when the daily hillwalker number was equal to or above average, 51.6% of deer were vigilant.

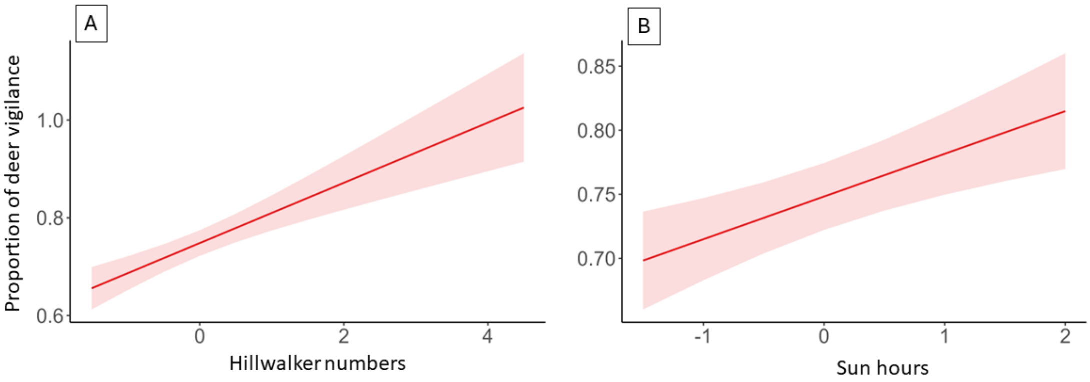

Figure 4.3. The effect of A) standardised number of hillwalkers (0 to 136 hillwalkers), and B) sun hours on the proportion of deer vigilant in a group.

Table 4.3. Coefficients (estimate and standard error), t-statistic and associated degree of significance of variables included in the top model selected by AIC to explain variation in deer vigilance

	Estimate	Std. Error	df	t value	P value
(Intercept)	0.749	0.013	210	56.248	< 0.001 ***
hwtime2	0.062	0.012	356	5.087	< 0.001 ***
Sun hours2	0.033	0.009	888	3.532	< 0.001 ***

4.5.4 Activity: Do deer reduce activity to avoid hillwalkers?

Deer were less active when hillwalker numbers, version Hwtime2, were higher (Figure 4.4A. This effect was stronger earlier in the season compared to later (Figure 4.4B).

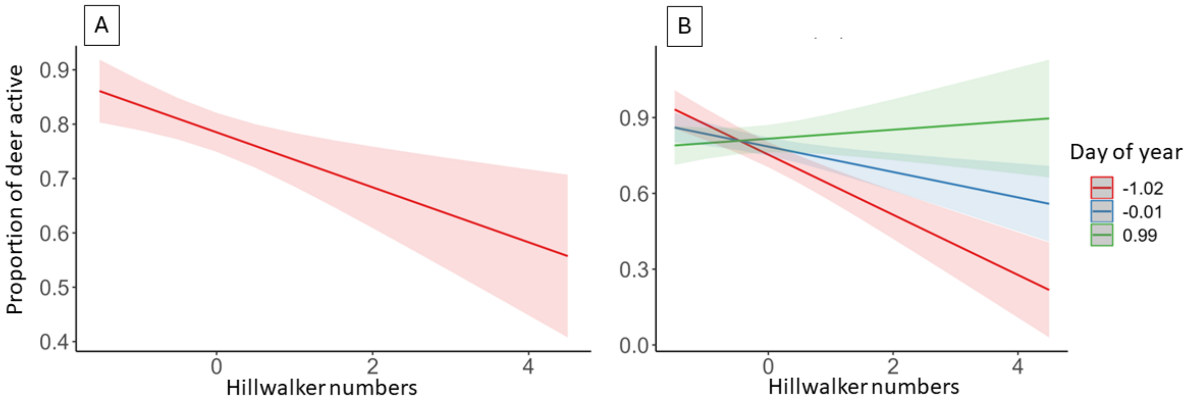

Figure 4.4. The effect of A) standardised number of hillwalkers (0 to 136 hillwalkers) on proportion of deer active in a group , and B) standardised hillwalker numbers on proportion of deer active in a group early in the season, -1, the middle of the season, 0, and the end of the season, 1.

The proportion of variance accounted for by fixed effects was 0.090 (marginal R^2) and the total variance explained by the fixed effects and the random effect, group ID, was 0.432 (conditional R^2). Region was dropped as a random effect due its lack of contribution to the explanatory power of the model. Proportion of deer active was also affected by sun hours (Figure 4.5), average windspeed, and proportion of calves in the group (Table 4.4, Appendix 4.2).

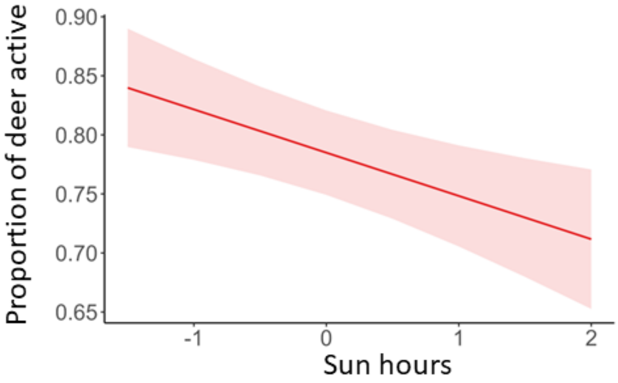

Figure 4.5. The effect of standardised sun hours (0 to 0.5 hours of sun) on the proportion of deer active in a group.

Table 4.4. Coefficients (estimate and standard error), t-statistic and associated degree of significance of variables included in the top model selected by AIC to explain variation in active versus inactive behaviour.

Coefficients	Estimate	Std. Error	df	t value	P value
(Intercept)	0.787	0.018	207	43.069	< 0.001 ***
hwtime2	-0.050	0.016	343	-3.051	0.003 **
Day of year	0.031	0.019	236	1.635	0.103
Sun hours2	-0.037	0.012	1207	-3.058	0.002 **
Windspeed	0.087	0.015	439	5.730	< 0.001 ***
Proportion of calves	0.041	0.008	6062	5.279	< 0.001 ***
hwtime2 x day of year	0.068	0.015	585	4.477	< 0.001 ***

4.5.5 Disturbance behaviour: Are deer more likely to display disturbance behaviours when likelihood of encountering hillwalkers is greater?

Probability of acute disturbance behaviour (alertness or running) was higher when closer to the hillwalker path (Figure 4.6) but was not affected by hillwalker numbers, version Hw_daily, singularly.

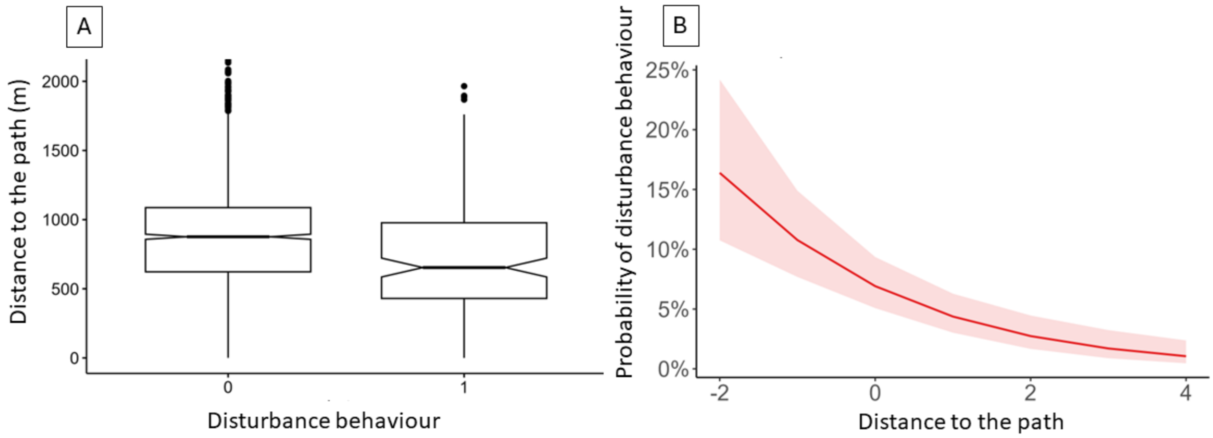

Figure 4.6. The effect of standardised distance to the path (90 m to 2470 m) and disturbance behaviours as A) difference in mean distance to the path for observations displaying disturbance behaviours (1) or not (0) and B) probability of disturbance behaviours with increasing standardised distance from the path.

A two-way interaction occurred between distance to the path and terrain ruggedness and the effect on disturbance behaviour probability (Table 4.5, Figure 4.7A, B). There was a slight increase in probability of disturbance behaviours in areas with higher terrain ruggedness when close to the path (Figure 4.7A). Overall, deer were most likely to show disturbance behaviours in 2022 and least likely in 2020 (Figure 4.7C). Probability of disturbance behaviours was also affected by elevation. Deer were more likely to show disturbance behaviours when elevation was lower (Appendix 4.3).

Table 4.5. Coefficients (estimate and standard error), z-value and associated degree of significance of variables included in the top model selected by AIC to explain variation in the probability of disturbance behaviour.

	Estimate	Std. Error	z value	P value
(Intercept)	-2.665	0.173	-15.426	< 0.001***
Number of deer	0.090	0.048	1.861	0.063 .
Distance to path	-0.490	0.096	-5.126	<0.001 ***
Ruggedness	0.184	0.073	2.508	0.012 *
Year2	0.125	0.224	0.557	0.578
Year3	0.600	0.213	2.813	0.005 **
Time of day	0.123	0.080	1.541	0.123
Elevation	-0.284	0.080	-3.545	< 0.001 ***
Distance to path x Ruggedness	0.193	0.082	2.348	0.019 *

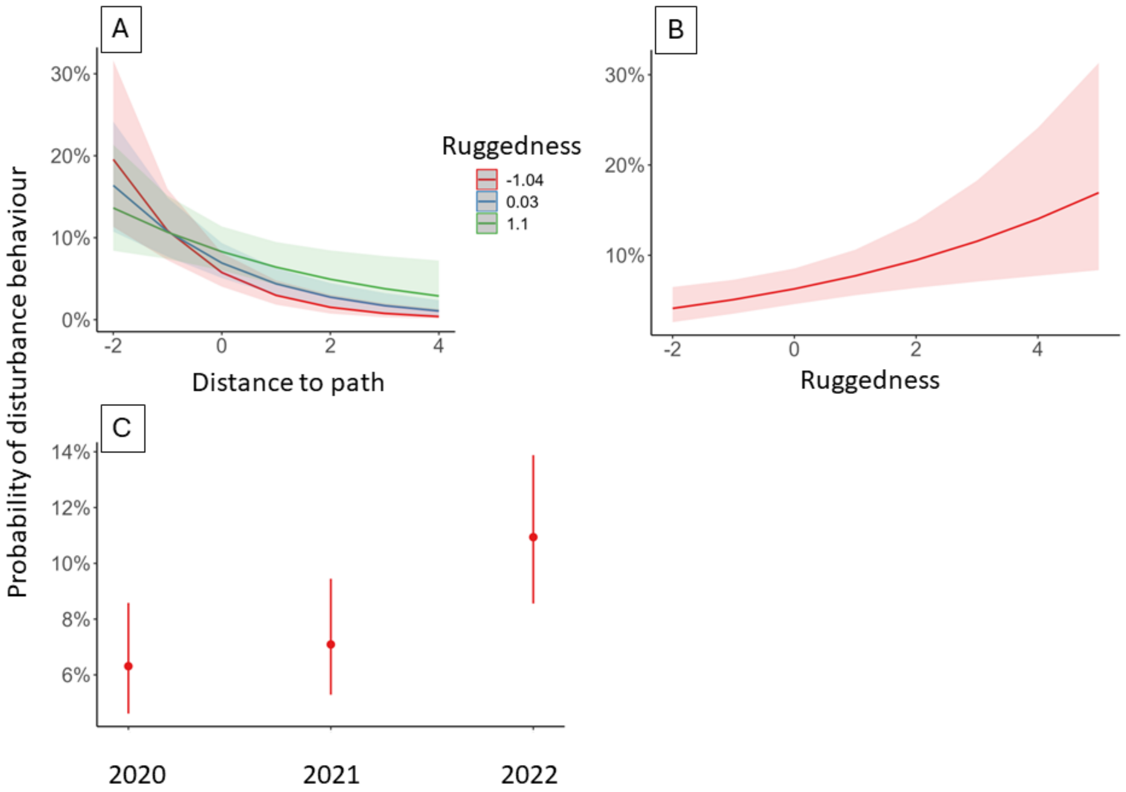

Figure 4.7. The effect on probability of disturbance behaviour of A) standardised distance to the path (90 m to 2470 m) and its association with standardised level of ruggedness where -1 represents low terrain ruggedness and 1 high terrain ruggedness (, B) standardised ruggedness, and D) year.

4.5.6 Group structure: Do deer respond to disturbance by forming larger, more closely aggregated groups?

4.5.6.1 Group size

Group size was affected by hillwalker numbers, version Hw_2days, and distance to the path (Table 4.6, Figure 4.8A), though the association with hillwalker numbers was limited to interactions with other variables. Deer formed larger groups further away from the path, particularly when there were more hillwalkers (Figure 4.8B), and when they were also in areas with low topographic variation (Figure 4.8C). Distance to the path was more strongly associated with group size in areas with low visibility compared to areas with high visibility (Figure 4.8D).

Table 4.6. Coefficients (estimate and standard error), t-statistic and associated degree of significance of variables included in the top model selected by AIC to explain variation in deer group size.

	Estimate	Std. Error	df	t value	P value
(Intercept)	2.390	0.119	16.7	20.174	<0.001 ***

hw_2days	0.014	0.032	1720	0.455	0.649
Distance to path	0.135	0.041	637	3.314	<0.001 ***
Topographic variation250	0.049	0.031	1730	1.572	0.116
Day of year	0.252	0.032	1720	7.829	<0.001 ***
General visibility	0.037	0.048	613	0.775	0.439
Ruggedness3	-0.079	0.033	1610	-2.357	0.019 *
Year2	0.008	0.076	1720	0.101	0.920
Year3	0.133	0.074	1710	1.787	0.074 .
Temperature1	0.138	0.032	1720	4.311	<0.001 ***
RDT2	-0.090	0.034	1670	-2.653	0.008 **
Elevation	0.146	0.037	560	3.972	<0.001 ***
hw_2days x distance to path	0.082	0.029	1720	2.815	0.005 **
hw_2days x Topographic variation250	-0.014	0.034	1710	-0.412	0.680
Distance to path x Topographic variation 250	-0.027	0.028	1690	-0.955	0.340
hw_2days x day of year	0.077	0.033	1720	2.357	0.019 *
Topographic variation250 x day of year	-0.064	0.027	1720	-2.347	0.019 *
Distance to path x General visibiltiy	-0.078	0.038	1680	-2.035	0.042*
hw_2days x pathdist x topo250_sum	-0.065	0.027	1720	-2.408	0.016 *

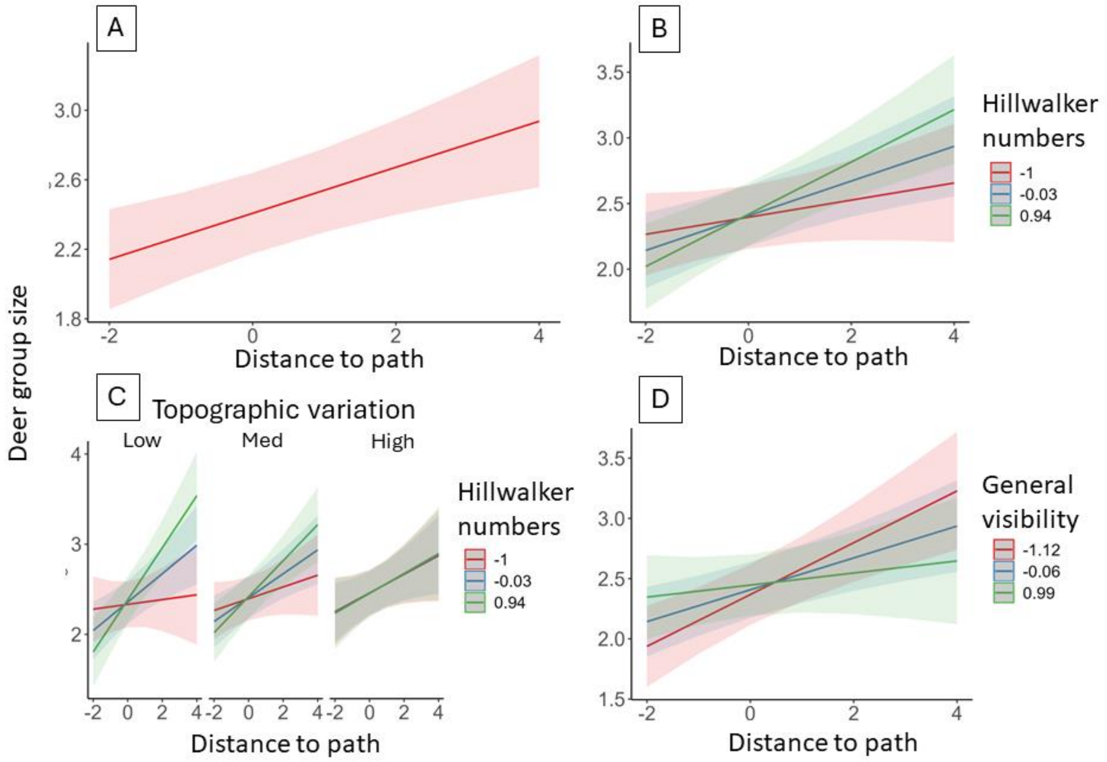

Figure 4.8. The effect on deer group size of A) standardised distance to the path (80 m to 1670 m), B) standardised number of hillwalkers where -1 represents 12 hillwalkers and 1 represents 98 hillwalkers and distance to the path, C) standardised number of hillwalkers, topographic variation, and distance

to the path, and D) standardised general visibility where -1 represents low visibility and 1 represents high visibility and distance to the path .

Hillwalker numbers were also associated with group size in relation to day of year. Group size was more likely to increase with increasing hillwalker numbers later in the season than early in the season (Figure 4.9A). Group size increased overall as the season progressed (Figure 4.9B).

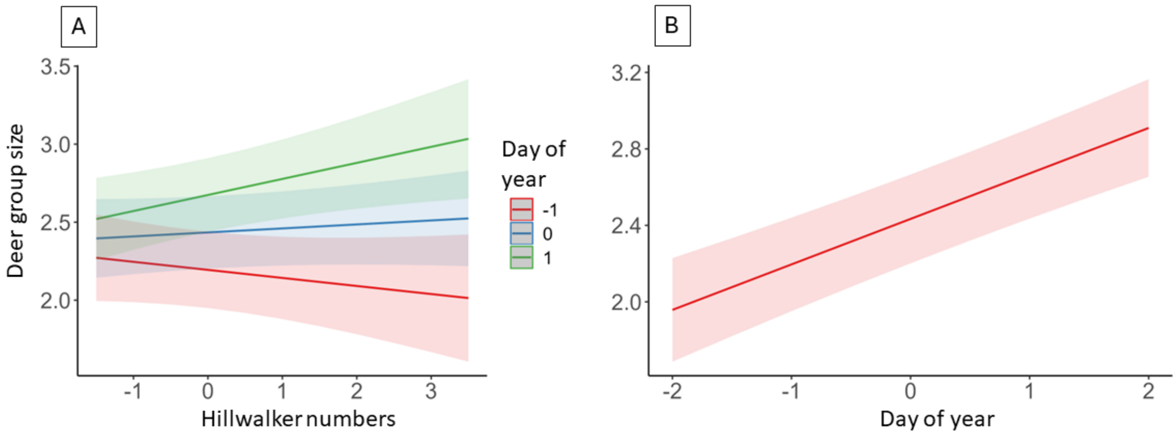

Figure 4.9. A) The interacting effect of standardised hillwalker numbers and day of year on deer group size where early season = -1 and late season = 1, , and B) the effect of day of year on deer group size where early season/24 May = -2 and late season/19 October = 2.

A number of variables besides those obviously relating to hillwalker pressure significantly influenced the size of deer groups (Table 4.6). These additional variables included ruggedness and elevation (Appendix 4.4, 4.5). Temperature, time of day, and the interaction between topographic variation and day of year were also significant. The proportion of variance explained by the fixed effects was 0.090 (marginal R^2), and the total variance explained by the model, including the random effect Area, was 0.203 (conditional R^2).

4.5.6.2 Aggregation

Deer groups were slightly more likely to be closely aggregated when hillwalker numbers, version Hwtime2, were higher, but only in areas where visibility was low (Figure 4.10A). This is converse to the overall tendency for greater aggregation to occur where general visibility was higher (Figure 4.10B).

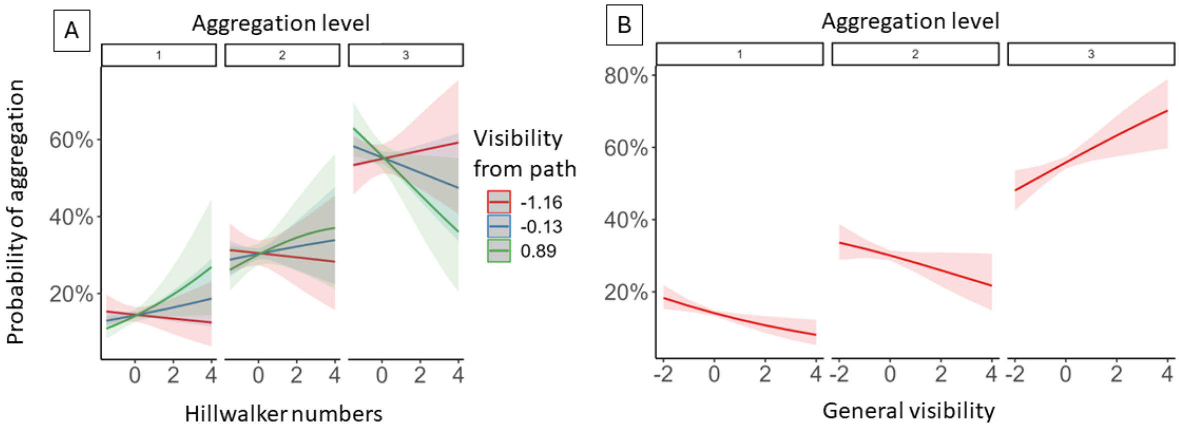

Figure 4.10. The interacting effects of A) standardised hillwalker numbers, where 0 = 30 hillwalkers and 4 = 136 hillwalkers, and visibility from the path where -1 represents low visibility and 1 represents high visibility, and B) standardised general visibility on the probability of deer being either dispersed (aggregation level 1) to highly aggregated (aggregation level 3).

Additional variables retained by the AIC model selection process, and found to be significant, were number of deer in the group, rainfall, sun hours, elevation, and state behaviours "settled" and "resting" (Table 4.7, Appendix 4.6, 4.7, 4.8). Visibility from the path within 1000 m and hillwalker numbers were only significant as interactions.

Table 4.7. Coefficients (estimate and standard error), t-statistic and associated degree of significance of variables included in the top model selected by AIC to explain variation in degree of aggregation.

Coefficients	Value	Std. Error	t value	P value
Number of deer	-0.09815	0.03129	-3.1364	< 0.01 **
General visibilty	0.15583	0.05697	2.7355	< 0.01 **
hwtime2	-0.09489	0.07414	-1.2799	> 0.05
Visibility from path1000	0.01426	0.06377	0.2236	> 0.05
Sum rain1	0.30258	0.10424	2.9027	< 0.01 **
Sun hours1	0.15472	0.05766	2.6835	< 0.01 **
Elevation	-0.202	0.06588	-3.066	< 0.01 **
Settled1	-0.84518	0.12425	-6.802	< 0.001 ***
Resting11	0.98914	0.23985	4.124	< 0.001 ***
hwtime2 x Visibility from path1000	-0.1191	0.05855	-2.0342	< 0.05 *
1|2	-1.8966	0.121	-15.6806	< 0.001 ***
2|3	-0.3236	0.1067	-3.0321	< 0.01 **

4.6 DISCUSSION

This study showed that red deer behaviour was significantly related to hillwalker activity in Glen Lyon, Scotland. I predicted that deer would respond to hillwalker pressure by increasing vigilance, reducing activity, displaying disturbance behaviours more frequently, and being found in larger, more aggregated groups. In accordance with these predictions, red deer in this study showed increased levels of vigilance and reduced activity when hillwalker numbers were higher. Deer were also more likely to show disturbance behaviours close to the hillwalker path. Group structure was affected by hillwalker pressure under certain conditions, though the effect on aggregation was less clearly aligned with the hypothesis. Behavioural responses of deer to stimuli are often context-dependent and the results of this study support that assertion. Here, I discuss the extent to which these findings support the initial predictions, and the additional factors that may have mitigated or exacerbated the observed responses of deer to disturbance. I finish the discussion with a brief overview of potential improvements for future studies and a short conclusion on the wider implications of these results.

4.6.1 Vigilance: Do deer increase vigilance in response to increased perception of risk?

Increased vigilance has frequently been shown as a response to disturbance (Benhaiem *et al.*, 2008; Jayakody *et al.*, 2008; Ciuti, Northrup, *et al.*, 2012; Proudman *et al.*, 2021). Red deer in this study were more vigilant when hillwalker numbers were higher, suggesting that deer may increase vigilance in response to increased perception of risk. Interestingly, vigilance responses were not associated with distance to the hillwalker path. This suggests that deer increase vigilance in response to disturbance when perceived, regardless of its proximity. Behavioural observations of deer in this study occurred up to 2100 m (mean = 888.5 m ± 383.4 m SD) from the hillwalker path. Other studies have also shown a lack of relationship between proximity to human activity and vigilance responses. At the same study site, Marion *et al.,* (2021) found only weak evidence for variation in behavioural responses of deer to hillwalkers based on camera trap images at varying distances from the hillwalker path. Similarly, Jayakody *et al.* (2008) found that deer were more vigilant in a disturbed area than an undisturbed area, but that vigilance within the disturbed area did not correspond with hillwalker numbers or distance to paths. Spatial scale may then be an important consideration when studying behaviour in deer (Vistnes and Nellemann, 2008; Perry *et al.*, 2020). Deer may also avoid the hillwalker path altogether or when hillwalker numbers are higher. Consequently, individuals that are more sensitive to disturbance are more likely to be further from the path, resulting in less sensitive deer being observed closest to the path (Bejder *et al.*, 2009; Sutton and Heske, 2017). This spatial organisation of deer by sensitivity could result in a smoothing effect along the gradient of distance from the path. Observing the same individuals at different distances from the path, facilitated by marked individuals, would help control for this.

The absence of differential vigilance responses by deer relative to the proximity of disturbances may have energetic consequences via loss of foraging opportunity (Underwood, 1982). However, studies have found that vigilance and foraging can frequently coincide, allowing for greater efficiency in both behaviours (Illius and Fitzgibbon 1994; Fortin *et al.* 2004). If foraging and vigilance are sufficiently integrated into the daily activity of the deer, deer may be more likely to increase vigilance even if far from the disturbance because the cost of the vigilance is low.

4.6.2 Activity: Do deer reduce activity to avoid hillwalkers?

Deer displayed lower activity during observation hours when hillwalker numbers were higher. Deer have widely been shown to reduce diurnal activity when human disturbance is high (e.g. Agetsuma *et al.*, 2016; Bonnot *et al.*, 2020; Proudman *et al.*, 2021). The benefit of reducing movement in the presence of disturbance has been attributed to detection avoidance (Little *et al.*, 2016). This is more likely in habitat that provides cover (Mysterud and Ostbye, 1999). Cover facilitates concealment from predators, and lower presence or density of cover has been reported as a key predictor of flight by red deer (Jarnemo and Wikenros, 2014; Chassagneux *et al.,* 2019). The majority of the study site is considered open habitat, with tree cover availability restricted to lower elevations. Deer may have compensated for lack of cover by lying down which makes them less conspicuous (Jayakody *et al.*, 2008), particularly in heather and amongst peat hags. Consequently, deer were less likely to be active to avoid detection by hillwalkers. Deer were only observed during the day, so it is unknown whether this reduction in activity was limited to the daytime or extended throughout the night as well.

Deer have also been shown to respond to human disturbance by increasing activity. Often this is associated with increased movement rates and spatial avoidance (Lovari *et al.*, 2007; Naylor, Wisdom and Anthony, 2009; Garcia *et al.*, 2023). Due to the hillwalker path encircling a substantial portion of the study site, movement of deer may be inhibited when hillwalker presence on the path is higher. Thus, reduced activity may be a consequence of the path acting as a barrier to movement as deer seek to avoid interaction with hillwalkers.

Hillwalker numbers were more strongly associated with activity levels early in the season compared to later in the season. This may coincide with age of calves. Female deer have been shown to reduce mobility post-partum (D’Angelo *et al.*, 2004), and be more sensitive to disturbance when their calves are younger (Stankowich, 2008). A reduction in disturbance response seasonally could also indicate seasonal habituation effect (Haskell and Ballard, 2008). Furthermore, energy strategies in deer change seasonally (Kie, 1999). For example, as calves get older and winter approaches, deer may prioritise energy intake over risk avoidance.

4.6.3 Disturbance behaviour: Are deer more likely to display disturbance behaviours when likelihood of encountering hillwalkers is greater?

Deer were more likely to exhibit acute disturbance behaviours closer to the hillwalker path, where likelihood of encountering hillwalkers was greatest. This effect was observed regardless of numbers of hillwalkers on the day. Hillwalkers in the study site typically remain on the path 90% of the time (Marion, 2021). Deer have been found to respond to spatially and temporally predictable threats in a landscape of fear (Laundre, Hernandez and Ripple, 2010). With this in mind, the path may represent a fixed anthropogenic feature that deer respond to by increasing their state of alertness, irrespective of fluctuations in hillwalker numbers. Similar behaviour has been observed in white-tailed deer, *Odocoileus virginianus*, approaching roads (Waring, Griffis and Vaughn, 1991).

Hillwalker patterns of activity may have exerted more of an influence on the significance of the path as a potential threat than fluctuations in hillwalker numbers. The highest probability of disturbance behaviours occurred in 2022, coinciding with a more consistent pattern of hillwalker activity recorded in this year despite lower numbers of hillwalkers generally. COVID-19 restrictions resulted in periods of very low hillwalker activity which may have reduced the association between the path and disturbance perceived by the deer. Thus, in 2020 and 2021 deer may have been less likely to be overtly alert when near or approaching the hillwalker path. High degrees of behavioural plasticity have been widely observed in deer (Pan *et al.*, 2011; Thurfjell, Ciuti and Boyce, 2017; Rickbeil *et al.*, 2019). These results suggest red deer show considerable behavioural flexibility in adjusting disturbance responses according to the prevailing level of perceived threat.

Fluctuations in hillwalker numbers may also be less important when considering acute disturbance responses if a disturbance threshold exists in relation to the number of hillwalkers (Colman *et al.*, 2012; Gundersen *et al.*, 2020; Sawyer, Lambert and Merkle, 2020). After this threshold is reached, the deer may choose alternative measures to avoid disturbance, such as displacement, and the absolute hillwalker number is irrelevant. Similarly, if displacement occurred early in the day, deer were less likely to be close to the path where these behaviours were more frequently observed. Consequently, more disturbances may then have occurred in 2022 due to the lower frequency of days with very high numbers of hillwalkers causing deer to displace. In this scenario deer remained closer to the path in 2022 where they were more likely to encounter hillwalkers. Acute disturbance behaviours can be energetically costly via time lost foraging and energy expended running (Chambers *et al.*, 2022), therefore spatial avoidance may be preferable.

4.6.4 Group structure: Do deer respond to disturbance by forming larger, more closely aggregated groups?

Increased group size and cohesion can have benefits related to collective detection of predators, the dilution effect (Childress and Lung 2003), and anti-predator related communication to conspecifics (Rands *et al.* 2014; Hoyle *et al.* 2021). At the same time, increased group size and cohesion may come at the cost of effective foraging (Focardi and Pecchioli 2005; Stutz *et al.* 2018), increased competition (Cherry *et al.* 2015), and reduced mobility (Pays *et al* 2012). Group size and cohesion can also reflect direct disturbance responses (Skogland and Grøvan, 1988; Lingle, 2001). I found that variation in group size and cohesion occurred in relation to multiple factors, reflecting the complex and varied mechanisms that determine group structure in deer.

Deer formed larger groups when hillwalker numbers were higher, but only in areas further away from the path. This may relate to spatial avoidance of the path when hillwalker numbers are higher (as indicated in chapter 3). This is supported by findings by White, Proffitt and Lemke, (2012) showing that when predation risk was higher, group sizes of elk, *Cervus canadensis*, increased in areas further away from the threat. I also found that group sizes were larger closer to the middle of the day, corresponding with peak numbers of hillwalkers on the path in the middle of the day. Furthermore, density has been shown to positively influence group size (Borkowski, 2000; Hebblewhite and Pletscher, 2002). Increased density of deer further from the path resulting from spatial avoidance may also have contributed to the general association between increased group size and distance from the path. In this case, group size can be considered an indirect consequence of displacement, rather than the direct consequence of flocking behaviour.

Degree of aggregation was less closely related to hillwalker disturbance. Hillwalker numbers only increased the probability of deer being closely aggregated in low-visibility areas. A less direct association between disturbance and aggregation may reflect the diversity of factors affecting group structure and social cohesion. For instance, social cohesion relates to forage availability whereby deer are more likely to disperse where resources are sparse (Focardi and Pecchioli, 2005). This is due to the negative effect on foraging opportunities that being central or rear to a group has. In larger groups the probability of being in these positions is greater, exacerbating the effect. State behaviour variables were also significantly related to degree of aggregation, with deer more likely to be closely aggregated when either resting or unsettled. Occurrence of these behaviours may itself be a direct response to disturbance, or incidental and reflective of inherent behavioural patterns. For example, deer were shown to be less active (resting) when hillwalker numbers were higher, and more aggregated when inactive. Thus, aggregation variation in this study may be a direct or indirect disturbance response, or indicative of natural behavioural variations.

4.6.5 Context-dependent findings

Behavioural responses of deer to disturbances are often highly context-dependent (Stankowich, 2008; Padié *et al.*, 2015; Wirsing *et al.*, 2021). This assertion is supported by findings in this study that included influence of landscape and environmental variables on disturbance responses.

Elevation

Deer may respond to disturbance by increasing elevation as well as, or instead of increasing distance (Cassirer, Freddy and Ables, 1992; Stankowich and Coss, 2006). Group sizes tended to be larger at higher elevations, and deer were more likely to be dispersed at higher elevations. This may be indicative of a secondary disturbance effect of deer displacing to, and then dispersing in, areas that appear safer. This is further supported by the finding that deer were less likely to show acute disturbance behaviours at higher elevations.

Topographic variation and ruggedness

I investigated the effects of topography on disturbance responses in deer using two measures. Topographic variation referred to slope gradient + ruggedness, whereas the ruggedness measure excluded the effect of slope gradient. Topography can provide cover from disturbance by visually separating the deer and the disturbance (Chassagneux *et al.*, 2019). However, topography could also increase some disturbance responses by preventing deer from detecting disturbances at longer distances (Eisenberg *et al.*, 2014). When the distance at which deer become alert to a threat is shorter, deer may be more likely to show stronger responses (Lingle and Wilson, 2001). Deer were more likely to show acute disturbance behaviours in more rugged terrain, which may reflect shorter detection distances. In contrast, in the areas closest to the path the reverse was observed. In this case it is possible that the increased probability of encountering hillwalkers interacted with the increased level of exposure or lack of cover (Chassagneux *et al.*, 2019). Furthermore, deer situated close to the path are likely to be aware of potential hillwalker presence. Deer adapt to predictable disturbances in their environment (Westekemper *et al.*, 2018), and have the capacity to learn disturbance-specific responses (Thurfjell, Ciuti and Boyce, 2017). Therefore, in areas closest to the path deer may select rugged areas that provide cover to reduce acute disturbance responses (Mysterud and Ostbye, 1999).

This study shows that slope gradient and ruggedness can exert subtly different effects on deer behaviour. Both topographic variation and ruggedness influenced group size. Group size decreased with increasing ruggedness but topographic variation as a singular effect was insignificant. In a 3-way interaction, hillwalker numbers and distance to the path exerted more influence on group size in low-gradient, flatter terrain. I suggest that similar mechanisms account for these findings. Smaller group sizes in more rugged areas reflect the forage limitations and physical obstacles to movement associated with this terrain (Fritz and Garine-Wichatitsky, 1996; Fortin *et al.*, 2009). Similarly, lower-gradient, flatter terrain may facilitate the larger group sizes that formed in the areas further away from the path when hillwalker numbers were higher (Clutton-Brock, Guinness and Albon, 1982).

Visibility

Much of the discourse around topographic effects on disturbance responses relates to visibility in the landscape (Eisenberg *et al.*, 2014; Chassagneux *et al.*, 2019). However, topographic effects are complex and multifaceted. I used viewshed analyses based on changes in elevation to explore the effect of visibility more explicitly. I considered visibility as it related to the hillwalker path, and more generally using relative visibility across a 100 x 100 m grid. I also suggest that the importance of the weather variable, sun hours, is related to improved visibility in brighter conditions due to its positive association with disturbance responses. Cloud cover, which represents lower light, has been linked to a decrease in the ability of white-tailed deer to perceive predators (Newman *et al.*, 2023). While this observation was specifically associated with twilight and an avoidance of riskier habitats, it does suggest that level of light (indicated by sun hours) could have an effect the ability of deer to detect predators.

Areas with high visibility can represent greater risk to deer and increase disturbance responses (Mols *et al.*, 2022). Reflecting this, deer were more likely to be closely aggregated in areas with higher general visibility. Conversely, probability of close aggregation decreased with increasing visibility from the path when hillwalker numbers were higher, but the mechanism for this is less clear. I suggest that high visibility from the path occurs due to a combination of optimal distance from the path and lack of visual impediments. For example, when the deer are on opposite slopes to the hillwalker path, visibility to the path is likely to be high. However, while the Euclidean distance is relatively short, the true distance overground is greater, potentially reducing the sense of threat to the deer. These results highlight the importance of considering multiple variables studying disturbance responses in deer (Montgomery, Roloff and Millspaugh, 2012).

The positive association between group size and distance to the path was stronger in areas with lower general visibility. Given that the effect of disturbance on group size was contingent on removal to areas further from the path, this may be a consequence of deer selecting areas perceived as less risky (Mols *et al.*, 2022).

4.6.6 Lessons for future studies of disturbance behaviour

The data were characterised by high levels of unexplained variation and, where applicable, random effects explained more variation than fixed effects. There are a number of likely reasons for this, associated with unmeasured variables as well limitations to the measured variables and study design.

Some factors could not be controlled for. Human behaviour, group sizes, and colour of clothing have all been shown to affect disturbance responses (Stankowich, 2008). Hillwalkers that talked loudly may have been particularly noticeable in the data. Audio stimuli have been found to produce longer lasting effects on behaviour than visual stimuli (Hodgetts, Waas and Matthews, 1998), which could make responses more likely to be detected using the scan interval method. Dogs commonly accompany hillwalkers in Scotland and their presence may be reminiscent to the deer of wolves, *Canis lupus* (Jayakody *et al.* 2008). While previous studies in the area indicated that the majority of hillwalkers remain on the path (Marion *et al.*, 2021), the effect of hillwalkers off the path was not measured. Off-trail recreation has been shown to increase disturbance responses of red deer (Westekemper *et al.*, 2018). Recording variation in hillwalker characteristics during observations may help to control for the variable effects hillwalkers, while providing further insight into factors that influence disturbance responses in deer.

The effect of wind direction and speed on olfactory detection was tested as a function of downwind distance to the path and windspeed, but was not found to be a useful variable. This may have been due to the high variation in wind direction in mountain terrain. The effect of wind direction could be partially accounted for by logging changes in wind direction against changes in deer behaviour, even if the direction of the wind at the deer's location is unknown.

It was not possible to track individual deer. Some variation may be explained by differences in tolerance between deer and the effect that has on conspecifics (Rands, Muir and Terry, 2014), and pre-existing spatial organisation of deer based on sensitivity to disturbance. In addition, deer may respond to hillwalker pressure by means other than those discussed here, such as spatial avoidance (as shown in chapter 3). Future studies should address these limitations using more precise data collection methods, such as GPS collars with activity sensors.

Limitations in measured variables may also have caused ambiguity. Behavioural observations were often necessarily carried out at distances which did not allow for the distinction between head-up: vigilant, and head-up: non-vigilant. This may have resulted in obscuring subtle changes in vigilance. The significant result that higher proportion of calves in a group was associated with increased activity is likely due to calves being more visible when active. Similarly, the significant association between rainfall and increased aggregation is likely due to the difficulty in observing single individuals on the periphery of a group through the rain, inflated by the tendency to avoid data collection in these circumstances. Lack of significant spatial effects in the vigilance and activity models compared to the models that used the deer count dataset may be the result of a relatively small range of locations. The magnitude of the impact disturbance by hillwalkers has on red deer may be better assessed using a comparison between sites of differing hillwalker pressures or conducting the study over a larger spatial scale (Jayakody *et al.,* 2008), rather than relying on potentially more subtle, temporal effects.

4.6.7 Conclusions

This study showed that deer respond to hillwalker activity by increasing vigilance, reducing activity, and being more likely to show acute disturbance responses when hillwalker pressure is higher. Group structure was potentially both directly and indirectly affected by hillwalker pressure. The responses of deer to hillwalkers were also closely integrated with environmental and landscape variables. More research is needed at both a fine-scale (e.g. habitat, terrain, weather) and a large-scale (e.g. comparisons over greater variations in hillwalker pressure) to tease apart these effects.

Without longer term datasets there is little evidence for adaptive behavioural responses, such as habituation or sensitisation. However, over the three years of the study, the largest disturbance behaviour and group size responses were seen in the final year (2022), despite higher numbers of hillwalkers in the previous two years. This suggests that long-term habituation is not occurring, or is not measurable over the current study period. Moreover, weak model performance may suggest that habituation has already occurred to some degree. Despite this, the more consistent presence of hillwalkers observed in 2022 may have caused an increase in responses which could indicate some degree of sensitisation. I suggest that red deer behavioural responses in this study site increase with increasing hillwalker pressure up to a threshold, after which further increases in numbers are less meaningful as deer have likely already removed themselves from the area. If this is true, the greater disturbance responses in 2022 could be a result of more days with moderate numbers of hillwalkers. Additionally, ungulates have been found to be more responsive to human disturbance in areas where hunting also occurs, which could inhibit long-term behavioural adaptations to recreation, such as habituation (Stankowich, 2008). This may be particularly relevant if recreation levels are not high enough to provide the reinforcement required for habituation. The numbers of hillwalkers in this site, though highly concentrated, appear to be relatively low when compared to similar studies in Scotland (Jayakody *et al.,* 2008; Sibbald *et al.* 2011).

While red deer evolved alongside predators such as wolves, responses to natural predators and human disturbance can differ (Proudman *et al.,* 2021), and human disturbances can have greater impacts than natural predators (Ciuti *et al.,* 2012; Visscher *et al.,* 2022). These effects may have welfare implications if sustained disturbance responses significantly reduce foraging opportunities and increase energy expenditure. With this in mind, deer managers in areas where outdoor recreation is significant should monitor deer body condition closely. Studies have shown that the impact of outdoor recreation can be greater away from established paths and trails (Recarte, Vincent and Hewison, 1998; Taylor and Knight, 2003; Helle *et al.*, 2012; Westekemper *et al.*, 2018). Encouraging hillwalkers to remain on the path, where possible, may reduce the real or perceived impact that recreation can have on deer, management, and economic activity, thus, reducing conflict between land users.

Chapter 5. Tracking individuals using visual marking and GPS collars in Scotland

Pib22 – hind calf, tagged 18th of June 2022 at 18:04

5.1 Abstract

The tracking of marked individuals in wildlife research is commonly used to answer key ecological and biological questions. GPS tracking of terrestrial mammals, such as deer, provides precise and continuous data on animal movements, enabling researchers to study movement behaviour and habitat use. Even without remote tracking, having identifiable individuals within a population can be beneficial to understanding movements and social dynamics. However, significant financial, legislative, and practical challenges associated with these methods can be challenges to achieving desired research outcomes. In the UK in particular, the tracking of marked deer is not widely employed. In this study, I describe methods trialled in a study site in Glen Lyon, Scotland, to evaluate the practicality, applicability, and efficacy of individual-based tracking of red deer in the Scottish uplands. I deployed one GPS tracking collar on an adult female, using a dart gun for remote injection of anaesthesia, and tagged 22 calves. Practical challenges in achieving substantial sample sizes of collared adults related to acquiring required licensing and training, getting within range of adult deer to dart them, and limitations in the equipment. Logistic challenges to calf capture limited the capacity of the calf tagging component of this study. Nevertheless, pilot data from this study yielded valuable insights into red deer movement and behaviour, whilst also providing substantial knowledge and experience on which to improve future studies.

5.2 Introduction

Tracking marked individuals is a key method for monitoring deer populations and understanding their behaviour. Having marked individuals in a population offers many advantages, including insights into displacement (Sunde *et al.*, 2009) or dispersal distances (Lutz, Diefenbach and Rosenberry, 2016), time to return following disturbances (Chassagneux *et al.*, 2020), individual variation in behaviour (Stache *et al.*, 2013), survival rates (Webb, Gee and Wang, 2010), and population estimation based on the rate of resights of marked individuals (Curtis *et al.*, 2009).

Different marking methods are associated with a range of advantages and disadvantages. One common option in deer studies is ear tagging neonates (e.g., Moyes *et al.*, 2006; McLaughlin *et al.*, 2022; Berg *et al.*, 2023). The advantages of tagging neonates relate to the low cost and simple procedure. While it is important to handle young animals with care, in most cases deer neonates display a freeze response on capture (Espmark and Langvatn, 1985). This allows researchers to take measurements and place the tag quickly, limiting the distress of the animal. Once placed, tags are lightweight and, as such, have minimal impacts on welfare. In addition, if tags become caught, for example in trees or fences, they are unlikely to cause more than superficial damage. If the study species is large enough, ear tags can be fitted with tracking devices to monitor movement and survival (e.g., elk, *Cervus canadensis*: Berg *et al.*, 2023). However, due to the tendency of deer species to conceal their young for long periods of time, tagging neonates can be difficult. One option for locating neonates is to observe lactating females, often for many hours, until the neonate emerges from hiding for feeding and travel to a new location. The new location must then be carefully noted and approached once the mother has moved away (Clutton-Brock, Guinness and Albon, 1982). A second option for locating neonates is to fit pregnant females with vaginal implant transmitters (VITs) that provide location and time of birth; however, this involves costly and often difficult capture, in addition to the cost of the VITs themselves (Bishop *et al.*, 2007). This method also relies on rapid location before the neonate is moved from the birth site. Regardless of the method used to locate the neonate, the method is not without risk. Some mothers have been known to reject their young following tagging due to the change in appearance or smell of the neonate, interruption of bonding and imprinting period, or capture related stress (Livezey, 1990). The presence of brightly coloured tags or distress calls by the neonate may also increase susceptibility to predation, causing ethical concerns and biases in the data.

A second frequently used marking method in deer studies is tracking collars (e.g. Skarin *et al.*, 2008; Mysterud *et al.*, 2012; Ensing *et al.*, 2014). Small animals cannot carry heavy devices, so the information gained from tagging neonates is limited by the weight associated with datalogging technology, its storage and battery capacity (Wilson *et al.*, 2021). Tracking collars provisioned with large battery packs provide extensive data and enable continuous monitoring without the disadvantages of alternative methods such as observer bias, human observation limitations such as daylight requirements, or the spatial range limitations of both humans and camera traps. Technological advances in recent years mean that, among other things, highly accurate GPS locations can be recorded and transmitted remotely (Hofman *et al.*, 2019), accelerometers or activity sensors allow fine-scale behaviour identification (Rautiainen *et al.*, 2022), mounted cameras provide rare, candid footage of behaviour and social interactions (Thompson *et al.*, 2012), and proximity loggers record contact rates between collared individuals (Tallian *et al.*, 2023). Animal-attached loggers facilitate comparisons between collared animals, offering insights into individual variation in behaviour and responses to environmental influences. However, the deployment of tracking collars poses its own set of challenges. These include the financial cost of purchase and maintenance, the time and cost of deployment, and the potential stress inflicted upon the animals being collared. Technical failures compound these challenges, and the associated risks (Hofman *et al.*, 2019).

Given the complexities and financial requirements of tracking studies, it is important to maximise the scientific and conservation benefits while working with often limited resources (Sequeira *et al.*, 2019; Shimada *et al.*, 2021). The question of appropriate sample sizes is important in terms of scientific output, animal welfare and associated licensing considerations, as well as resources available. Sample sizes need to be large enough to make population level inferences but without putting more animals than necessary under the stress of capture. In particular, projects involving wildlife capture should consider the ethical framework ‘the three Rs’: Replacement, Reduction, and Refinement (Tannenbaum and Bennett, 2015). Replacement refers to the question of alternatives, for example modelling approaches or indirect measures such as dung counts. Reduction refers to minimising the number of animals used to ensure only the number required to answer specific research questions are used. Lastly, refinement refers to adjusting the procedures being carried out on animals to minimise their impact on the individual. Appropriate sample sizes depend on a number of factors, including the goal of the study and the size of the population being studied. For example, a sample size of one may provide novel insights into species that are otherwise difficult to observe, but a larger sample is need to study individual variability, and larger again to make population level inferences (Sequeira *et al.*, 2019). The resolution of the data being collected per individual may also be taken into consideration. For example, a very high rate of location recording (fix rate) from one individual can provide information on physical and movement capabilities (Sequeira *et al.*, 2019) and improve fix success rate generally (Cain *et al.*, 2005).

In this chapter, I describe the trial of red deer neonate tagging and tracking collar methodologies carried out to determine their practicality, applicability and efficacy for deer movement and behavioural monitoring in Glen Lyon, Scotland. Owing to the COVID-19 pandemic, administration and fieldwork were subject to significant delays and disruptions. Nevertheless, the processes involved yielded considerable insight and learning. Here, therefore, I describe my approach and some of the insights gained in relation to common biological questions. By consolidating these aspects, I aim to contribute valuable knowledge and experience to inform future projects of deer monitoring in the United Kingdom. Specifically, I ask:

1. Can individual-based tracking and behavioural data be obtained in this testing environment?
2. In principle, can the data be used to address biological questions on:
    a. Calf survival and population recruitment rates
    b. Social interactions
    c. Home range sizes
    d. Activity pattern and activity budgets
    e. Disturbance frequency and vigilance

5.3 Methods

5.3.1 Calf tagging: obtaining data in Glen Lyon

Calf capture

Red deer calves were tagged within 2-3 days after birth, at locations across the study site. They were located by observing the behaviour of adult females and waiting for them to return to their calves for feeding (Clutton-Brock, Guinness and Albon, 1982). Once the calf had selected a new bedsite and the mother had moved out of the immediate area, the calf was approached. Data were collected on calf location, sex, estimated age and associated characteristics, identification information (tag type and colour), vegetation type and additional notes on behaviour and general welfare. Rejection by the mother is a risk when handling deer neonates (Clutton-Brock, Guinness and Albon, 1982) and, to reduce impact on the calf and surrounding area, only the essential information was recorded at the calf. Secondary information was completed immediately after leaving the calf and duration of capture was < 10 minutes (median = 3 minutes). Further measures to minimise the transfer of scent to the calf were use of medical gloves rubbed with moss and vegetation prior to handling. Tags were painted with water-soluble brown paint and positioned, initially, to avoid affecting the overall shape of the ear. This minimised the visual impact of marking to reduce the likelihood of rejection. On each calf, one of two types of tags was used: small, round button tags, and larger cow tags trimmed to reduce width and visual impact. Where possible, pick-up by the mother was observed to ensure reacceptance.

Age of calf was estimated using indicators including behavioural and movement characteristics, degree of wetness at capture (excepting the effect of rain) and hoof hardness. Older calves spend more time moving around than younger calves, and younger calf movement is characterised by a slower, creeping gait.

Calf resights

Calf resights were achieved during deer group observations, and on camera traps. Deer observations were carried out from late May to October in 2021 and 2022, and from June to mid-October in 2020. Camera traps (n=22) were deployed for the same period (Figure 5.1). Some visual observations occurred during winter 2021/22 during the course of fieldwork and on camera traps placed at three bait stations associated with collaring efforts during this time. Between November and April in the 2022/23 winter, four cameras were placed strategically across the study site with the aim of detecting tagged calves. Date, location and ID were recorded when tagged calves were observed, either during the course of deer observations or on camera traps.

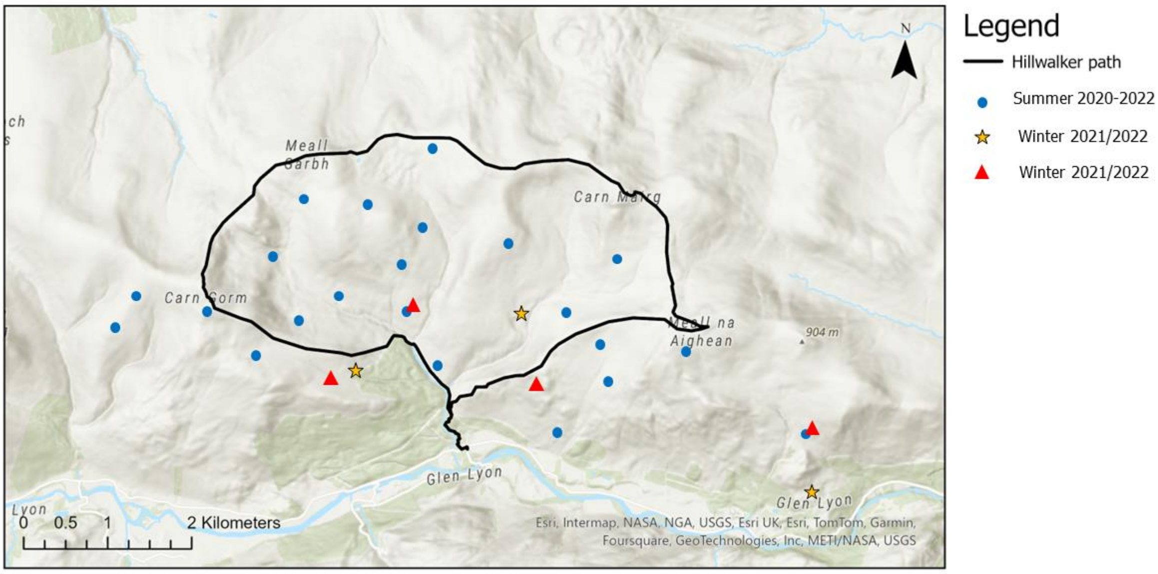

Figure 5.1. Camera trap locations for calf resights.

5.3.2 Calf tagging: addressing specific questions

Calf survival

Calf resights were used to confirm survival up until the last observation date. The focus was winter survival to establish recruitment rates (Loison and Langvatn, 1998; Berg *et al.*, 2023).

Calf movement and interactions

Calf resight data were used to establish maximum ranges per calf to indicate areas of use (use areas). This was achieved using a minimum convex hull polygon (MCP) calculated in ArcGIS Pro version 3.2. Use areas were calculated using MCP because numbers of locations for each calf were insufficient for more comprehensive, statistical measures of home range.

5.3.3 Collaring adults: obtaining data in Glen Lyon

Deer capture

Deer capture was carried out under Home Office License PP9637584, Personal License held by Eilidh Smith I00450783, and establishment license held by Durham University X78C87E61 and all procedures were designed under veterinary advisement and reviewed by Durham University Animal Welfare and Ethics board (AWERB). Home Office licensing is required to carry out regulated procedures on animals for science under the Animals (Scientific Procedures) Act 1986 (ASPA). A regulated procedure is one that may cause an animal a "level of pain, suffering, distress or lasting harm equivalent to, or higher than, that caused by inserting a hypodermic needle". Anaesthetising deer is considered a regulated procedure due to the duration of the procedures (anaesthesia and tracking device deployment). Three licenses are required under ASPA for carrying out research on animals using regulated procedures: an establishment license, a project license, and a personal license. The establishment license is granted to the organisation or institution that takes ultimate responsibility for the work carried out. The project license specifies the location of the research, the procedures carried out, and the justification for these procedures. The project license also names the personal license holders that will carry out the procedures. Personal licenses require an examination of theoretical principles regarding ethics, general procedures, and procedures specific to the project in question. To carry out procedures unsupervised, the project license holder must also be trained and assessed by qualified persons to do the procedures. Importantly, this must be on the species stated in the project license.

Capture was achieved in only one deer via remote anaesthesia applied using Dan Inject model JM Special dart gun. I used a combination of Zoletil (tiletamine + zolazepam, 200 mg/ml) and Domidine (detomidine, 10 mg/ml). Though capture procedures were of short duration, at least 45 minutes were allowed to elapse from administration of the anaesthetic to administration of the reversal drug. This was because the reversal drug, Antisedan (atipamazol, 5 mg / ml), was only effective on the Zoletil component of the anaesthetic. Allowing time for the detomidine to wear off naturally prevented the deer from regaining consciousness before the effects of the detomidine on limb control had reduced. In the intervening time the deer's vital signs (breathing rate, pulse, and temperature) were monitored closely. Due to the natural reduction in the anaesthetic effects, only a partial (3 ml) dose of the reversal drug was administered. Full protocols can be found in Appendix 5.1 and consideration of the Replacement, Reduction, and Refinement principals can be found in Appendix 5.2.

To get within range (~30 m) of deer for darting, I used a combination of stalking and baiting methods. Bait stations were stocked with kibbled maize which, unlike processed feed, does not disintegrate when wet; other baits used included turnips, hay, and rumevite (mineral) blocks. Hay was trialled in the first collaring season but was not eaten by the deer. Turnips were introduced in the second collaring season at all bait stations and were eaten by the deer at the more active stations. Measures to prevent sheep from accessing the feed included a raised trough (Figure 5.2A), hurdle gates high enough to prevent sheep from jumping over but low enough for deer to cross (Figure 5.2B), and hanging rumevite blocks on posts out of the reach of sheep (Figure 5.2C). The locations of bait stations were chosen to provide safe areas for darting deer, to promote frequent deer encounters, and for natural landscape features that provided cover for approach and waiting for deer. Steep areas were avoided for darting due to the risk of injuries caused by anaesthetised deer falling from height. Capture occurred during winter to minimise the impact on calves, and to reduce the risk of hyperthermia during capture. Darting in winter also maximises the effectiveness of the bait stations. The collar was fitted loose enough to prevent excessive rubbing and minimise risk of getting caught on fences and trees by leaving a gap between the collar and the neck of approximately 1.5 inches, based on advice from researchers with extensive experience collaring deer. One risk for deer fitted with collars is that they get a hind foot stuck in the collar whilst scratching. Consequently, collars were also fitted to be loose enough that, if that happened, the deer would easily be able to remove its foot.

Figure 5.2. Deer bait station set ups: A) shows a raised trough and a post with a salt block attached. The bait station was built and salt block placed at it in July 2021 to allow deer to become accustomed to the new infrastructure before the winter. B) shows a site where hurdles were used to prevent sheep accessing food that was left on the ground, and C) shows a rumevite block hanging from a post out of the reach of sheep.

Collar settings and data retrieval

The collar used was a Lotek Litetrack 420 Iridium, which was programmed with a 15-minute location sampling interval (fix rate) from May to November, and a 1-hour sampling interval for the remainder of the year. A tri-axial accelerometer recorded instantaneous acceleration every 90 seconds, the maximum rate for the collar's specifications. A drop-off device was programmed for collar removal at 50 weeks, and every sixth location was transmitted, four at a time, via Iridium satellite communication. Iridium transmission rates were limited due to the associated financial cost of transmitting data and to reduce battery consumption. Each transmitted location cost approximately £0.20 and battery consumption increased with the number of transmissions and the amount of data transmitted.

All GPS locations and activity data were retrieved from the collar when it dropped off the deer on schedule. Locations with dilution of precision (DOP) values less than 10 were discarded due to associated inaccuracy (Adrados *et al.*, 2003; Coppes *et al.*, 2017). All successful GPS locations had at least 3 satellites, however 2-D locations associated with locations from 3 satellites were also discarded because these have been shown to be less accurate (Adrados *et al.*, 2002; Cain *et al.*, 2005). Locations were visually assessed using ArcGIS Pro 3.2 to identify further outliers, conspicuous by being located several kilometres from the rest of the deer locations.

Acceleration summary statistics

Summary statistics derived from acceleration data for behavioural classification were calculated using methodology adapted from Fehlman *et al.* (2017). Of these, I used the summary statistics static X (stX) and Vectorial Dynamic Body Acceleration (VeDBA) to estimate head position and activity level. Tri-axial acceleration data measure the 'surge' (X axis), 'sway' (Y axis), and 'heave' (Z axis) of the deer's motion. The static components of each axis relate to the orientation of the accelerometer in the collar and help to infer the position of the collared animal (Fehlmann *et al.*, 2017). The dynamic components refer to movement and indicate activity level.

Dynamic Body Acceleration (DBA) was calculated as VeDBA from the dynamic component of the acceleration data, with higher values representing greater motion (e.g., running vs walking) (Walker *et al.*, 2015). Overall Dynamic Body Acceleration (ODBA) is also commonly used to measure activity; however, VeDBA is suggested to be less influenced by the angle of the tag (Qasem *et al.*, 2012), and was considered more appropriate given the potential for variation in position of the collar on the deer at different times of the year. Dynamic body acceleration was used to obtain daily activity patterns which were averaged by hour of the day over the summer and winter seasons.

Behavioural observation

Behavioural observations on the collared deer were carried out to provide calibration data from which to classify behaviour from the acceleration data. During observations deer behaviour was recorded broadly as lying, standing, walking, or running (Table 4.1). Head position was distinguished for lying and standing postures, with standing head down generally indicating foraging behaviour. Behaviour changes were recorded verbally, as they occurred, and subsequently transcribed. Time was kept using the android app ’24-Hour Time’ to ensure that behavioural observation data could be matched with acceleration data. Disturbances occurring when the deer was encountered were recorded.

Table 5.1. Ethogram of behaviours recorded during behavioural observations of the collared deer.

Behaviour	Description
Standing head up	Deer on its feet, head raised above the shoulders, not travelling
Standing head down	Deer on its feet, head below the shoulders, usually grazing, may be travelling slowly. Short behaviours such as scratching or grooming included.
Lying head up	Deer lying down, head raised above shoulders, may be ruminating or resting, assumed to be vigilant given that it was not always possible to tell if the deer had its eyes open or closed.
Lying head down	Deer lying down with head below the shoulders, usually sleeping or resting. Short behaviours whilst lying such as scratching, grooming, or rolling also included.
Walking	Deer travelling at a walk, head raised above the shoulder
Running	Deer either trotting or running, usually in response to disturbance but sometimes in response to flies, temperature, or to catch up with main group.

5.3.4 Collaring adults: addressing specific questions

Space use and effect of sampling rate

To investigate the effect of sampling effort on biological conclusions, I compared use areas calculated using locations collected at 15-minute and 60-minute frequencies. Home range analyses are often carried out using statistical methods that are robust but have minimum data requirements (Börger *et al.*, 2006; Seigle-Ferrand *et al.*, 2021). In contrast, MCP is a simple method that can provide valuable insight into movements and total area used by deer over short timeframes. I computed use areas on daily and five-daily bases using minimum convex hull polygons (MCP) (Northrup *et al.*, 2016). Daily or short-term MCPs can provide valuable information on fluctuations in activity and movement rates in animals (Russo, Massei and Genov, 1997; Nicholson *et al.*, 2019). I restricted the data to the summer period, during which 15-minute sampling frequency was available. The 15-minute interval data were filtered to provide sampling frequencies of one location per hour to compare to that obtained using four locations per hour. Specifically, size of use area over equivalent periods were compared. Use areas and step length (distance between locations) were calculated in R software version 4.3.2 (R Core Team 2023) using the sf package (Pebesma *et al.,* 2024). Distribution of collared deer locations were visualised by time of day (day and night) using the Kernel Density tool in ArcGIS Pro. This method highlighted spatial use patterns, avoiding the overlap and obscurity associated with plotting raw fixes. The kernel density estimation results were classified using the quantile classification method in ArcGIS Pro, dividing the deer locations into 20 equally sized classes for comparison of daytime and nighttime distributions.

Behaviour and acceleration data calibration from observations

Behavioural observation data and acceleration data were matched by timestamp to determine stX and VeDBA values associated with different behavioural states. Due to small sample sizes, this was done manually. Acceleration records occurred at 90 second intervals and these were assigned the behaviour in the observation at the time. For disturbance events, acceleration data were extracted with a wide buffer of 60 minutes (40 acceleration records) around observation times to visually assess patterns in the acceleration data and ensure all potential disturbance effects were considered.

Behaviour classification

Small sample sizes of behavioural observations combined with the 90 second sampling interval limited the scope of behavioural classification. Thus, machine learning methods widely applied to acceleration data (Brown *et al.*, 2013) were not attempted. I carried out simple exploration of patterns in acceleration data based on visual assessment of the calibrated dataset and prior knowledge of deer behaviour. These included attempts to identify disturbance events using spikes in DBA over varying periods of time, and in relation to distance travelled (step length).

To determine whether different behaviours could be recognised, I examined thresholds in stX and VeDBA. Head position can be inferred from values on the x axis of the accelerometer, with lower values indicating a head down position and higher values an upright position (Moreau *et al.*, 2009; Shepard *et al.*, 2010). Head up position could indicate vigilance in deer (Jayakody *et al.*, 2008). Ranges of stX indicating either head up or head down positions were extracted from calibrated data and applied to the wider dataset to investigate whether vigilance could be reasonably inferred from these data. I used k-means clustering (R package ClusterR: Mouslimis 2024) to determine whether reliable thresholds existed between state behaviours. For example, if DBA indicates stationary versus mobile behaviour, the behaviours resting and moving could be distinguished. Head position could then be used to distinguish between foraging behaviour and travelling.

Vigilance in relation to spatial and temporal factors

Statistical analyses were carried out in R version 4.3.2. Vigilance was identified for each acceleration record from head position, with ‘head-up’ (1) representing vigilant, and all other head positions (0) representing not vigilant. Variation in vigilance was investigated using a binomial General Linear Model (GLM) using the lme4 package (Machler *et al.,* 2015). Model selection used Akaike’s information criterion (AIC) to compare candidate models (R package MuMIn: Bartoń 2009). The selected model was associated with the lowest AIC value, whilst also representing the simplest version of the model (Chapter 3, 4). Potential temporal explanatory variables included were time period (day 08:00-16:00, night 20:00-03:00, and dawn/dusk 04:00-07:00 and 17:00-19:00); season, as Spring (April until June), Summer (June until September), Autumn (September until December) and Winter (December until April); Stalking season, as September to February; and individual month. Human activity fluctuates seasonally and is greater during the summer and during the day. Certain times of year are also influenced by seasonal activity such as lambing in April, and stalking season between September and February. Potential spatial explanatory variables were distance to buildings, distance to roads, and distance to woodland. Distance to buildings and roads were thought to have a bearing on vigilance due to associated disturbance from human activity, and distance to woodland in terms of distance to cover which provides relative safety (Jayakody *et al.*, 2008). Dynamic body acceleration (as VeDBA) was also included to account for natural fluctuations in activity and associated head position, and therefore isolate vigilance responses. Interactions between spatial variables and time of day variables were included because it was expected that vigilance would alter in relation to spatial variables depending on the time of day. For example, vigilance might only increase around buildings during the day when human activity is higher than at night. Spatial variables were calculated using the Near tool in ArcGIS Pro 3.2. Shapefiles for woodland cover, roads, and buildings were obtained from the OS datahub, OS OpenMap - Local (https://osdatahub.os.uk/downloads/open/OpenMapLocal).

5.4 Results

5.4.1 Calf tagging: obtaining data in Glen Lyon

Capture

Nineteen calves were tagged over the 3 capture seasons. Only one calf was tagged in 2020 due to COVID-19-related delays to fieldwork; nine calves were tagged in both 2021 and 2022. The locations of captures spanned the study site from east to west but were predominantly in the more accessible, southern portion of the site. During the course of the calf tagging period, three calves were approached without success due to flight responses. These calves were estimated at approximately two-four days old. One calf of similar age was captured but subsequently released without tagging due to excessive struggling and apparent distress.

Of the 19 calves captured, 11 were captured during late afternoon and early evening, with the latest capture occurring at 21:55. Due to the timings of captures, the return of the hind to the calf was only observed in seven cases. However, no evidence of abandonment following tagging was found via observation of the return of the hind or, later, by searching the area for the calf. Estimated ages of tagged calves ranged from three hours to 48 hours.

Habitat used by captured calves was predominantly grass. Four calves were also associated with cover from clumps of heather, and four with rushes. Three calves were captured in heather. One calf was captured in a prominent location on a well-used deer track, having appeared to ‘freeze’ on discovery rather than having selected the location.

Calf resights

During the course of summer fieldwork, 1823 deer group observations were recorded, with 593 in 2020, 635 in 2021, and 595 in 2022. Winter observations occurred on an ad-hoc basis and only calf resights were recorded. The 22 summer camera trap sites yielded 2683 camera trap days in 2020, 2996 in 2021, and 2479 2022. Winter camera trap days in the 2021/22 winter totalled 240 days and 510 days in the 2022/23 winter.

Direct visual observations accounted for 22 of the resights, while camera traps accounted for 32 resights. Three observations were from nocturnal camera trap images, from which individual ID was uncertain, owing to uncertainty regarding the colour of the tag. Two of these observations occurred approximately 2 hours apart in September 2021 at the same location, and the third occurred in November 2022.

The locations of all resights and captures (Figure 4.3) show that the maximum distance between capture location and any resight was 2.7 km (calf ID Gyc21).

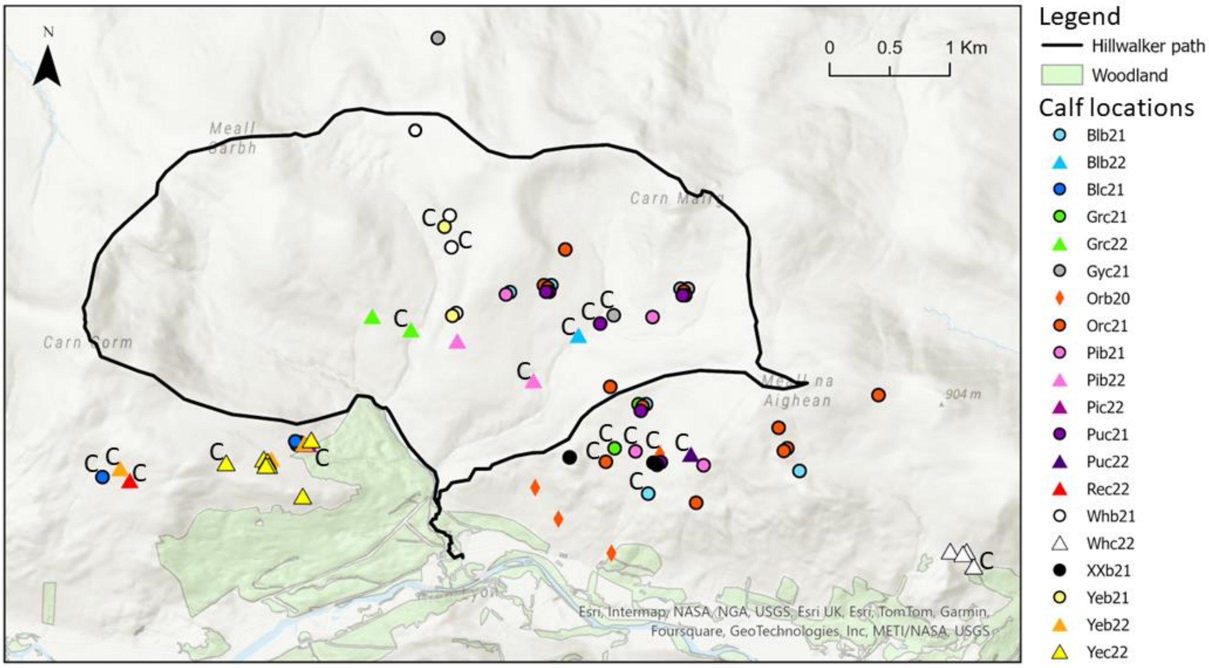

Figure 5.3. Calf locations including capture, with each calf individually identifiable. Shape of point indicates year of birth. 2020 calves = diamond, 2021 calves = circle, 2022 calves = triangle. Calf ID XXb21 refers to unknown nighttime observations at 2 camera trap locations. "C" indicates capture locations.

5.4.2 Calf tagging: addressing specific questions

5.4.2.1 *Calf survival*

Of the 19 tagged calves, 4 were not re-observed after capture (Table 5.2). Winter survival rate of the 2020 and 2021 calves was at least 60%, with 5 calves not seen after their first summer, and 4 observed during the following winter but not after. Data collection after September 2022 was limited, so the survival of the 2022 calves is unknown.

Table 5.2. Information on tagged calves, capture date and resight information.

Calf ID	Capture date	Last resight date	Winter survival	No. resights
Orb20	17/06/2020	20/09/2020	Unknown	3
Pib21	01/06/2021	07/05/2022	Yes	3
Blb21	03/06/2021	16/09/2022	Yes	4
Yeb21	07/06/2021	23/08/2022	Yes	1
Whb21	08/06/2021	23/08/2022	Yes	3
Orc21	09/06/2021	14/09/2022	Yes	12

Grc21	15/06/2021	16/08/2021	Unknown	1
Gyc21	16/06/2021	13/07/2021	Unknown	2
Puc21	16/06/2021	16/09/2022	Yes	5
Blc21	18/06/2021	12/01/2022	Unknown	3
Pic22	04/06/2022	NA	Unknown	0
Rec22	05/06/2022	NA	Unknown	0
Yec22	05/06/2022	26/11/2022	Unknown	7
Blb22	06/06/2022	NA	Unknown	0
Puc22	07/06/2022	NA	Unknown	0
Whc22	11/06/2022	01/01/2023-30/03/2023*	Unknown	4
Grc22	13/06/2022	29/07/2022	Unknown	1
Pib22	18/06/2022	11/09/2022	Unknown	1
Yeb22	20/06/2022	03/11/2022	Unknown	2

*No precise date due to camera trap malfunction

Calf movement and social interactions

Use-areas increased with increasing number of resights, Pearson's correlation test: t = 4.46, df = 13, *P* = 0.001 (Figure 5.4). The largest area occupied by any calf was Orc21 with 3.04 km², which was also the calf with the largest number of resights. In contrast, Yec22 was the most frequently observed calf after Orc21 with 7 re-sights but, despite this, occupied an area smaller than 9 other calves.

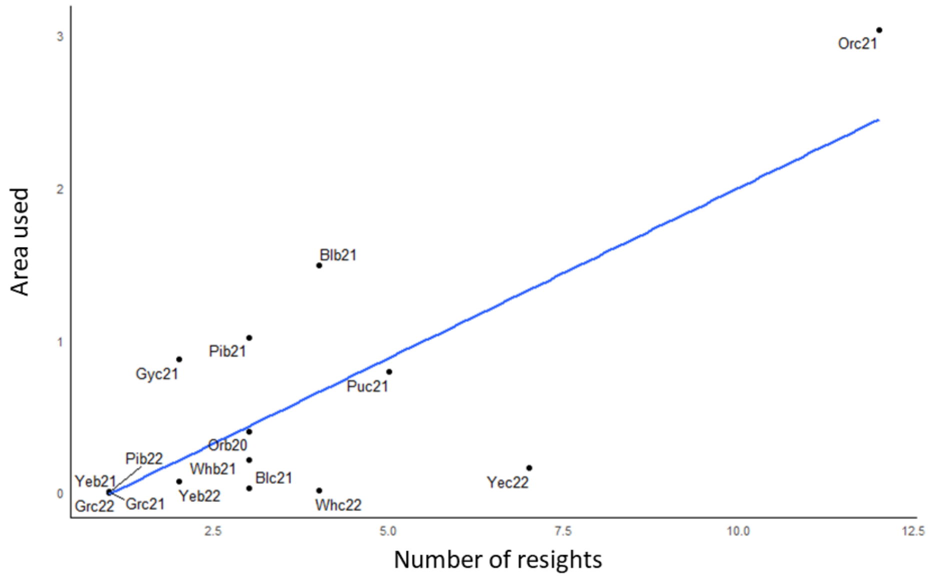

Figure 5.4. Number of resights and estimated area use for each tagged calf with at least one resight (n = 15).

Calf resights also provided information on interactions or social groupings between the deer. There were 5 observations in which calves were observed with other calves at the same time or within 20 minutes, and one observation at the same location within 1.5 hours (Table 5.3). One association occurred when two calves were tagged in the same place, at the same time.

Table 5.3. Table of calf associations.

Date	Calf ID 1	Calf ID 2
16/06/2021*	Gyc21	Puc21
06/07/2021	Blb21	Puc21
11/07/2021	Gyc21	Puc21
18/03/2022	Blb21	Pib21
23/03/2022	Whb21	Yeb21
16/09/2022	Blb21	Puc21

*Capture

5.4.3 Collaring adults: obtaining data

Deer capture

The deer was darted at 6am, the 30th of April 2022. The effects of the drugs were apparent almost immediately and the deer was fully recumbent within 10 minutes. The 3 ml dose size was reduced to 2 ml due to the dart malfunctioning. Initial vital signs showed elevated breathing and heart rate but, within minutes, this stabilised; body temperature was measured using a rectal thermometer and was within a safe range (38.5-39.5°C) throughout the capture. The deer was estimated to be three or four years old and pregnant. During the capture, the collar was fitted and both ears were tagged.

A partial dose of reversal drug was administered 43 minutes after darting. The blindfold was left on the deer until she showed signs of trying to get up, at which point it was removed and the area was cleared. The deer was observed from a distance for a further hour to ensure full recovery.

Data retrieval

The GPS collar was successfully retrieved from the field 50 weeks after deployment, as programmed. Over 300,000 acceleration records were downloaded. During the deployment period, a total of 21,807 fix (location) attempts were made; of these, 9.81% failed. A further 1.60% were removed due to estimated inaccuracy, indicated by a DOP (dilution of precision) value greater than or equal to 10 (Adrados *et al.*, 2002; Coppes *et al.*, 2017). Minimum number of satellites for successful fixes was 3. The minimum number of satellites required for a 3-D location is 4; however, 2-D fixes represented 5.28% of the remaining fixes (n = 1020). Mean distance travelled between fixes was substantially higher for 2-D fixes (138 m) than 3-D (36 m), suggesting reduced accuracy. As a result of this, 2-D fixes were removed from the dataset in accordance with Adrados *et al.* (2003). Four outlier fixes at implausible distances (> 4 km from preceding and following locations) from the site were also removed, despite not meeting prior criteria for removal.

Acceleration summary statistics

Dynamic body acceleration values were calculated using the vectorial dynamic body acceleration summary statistic. The deer showed a crepuscular activity pattern with more activity occurring at night than during the day, and lower activity in the winter months from November to May (Figure 5.5).

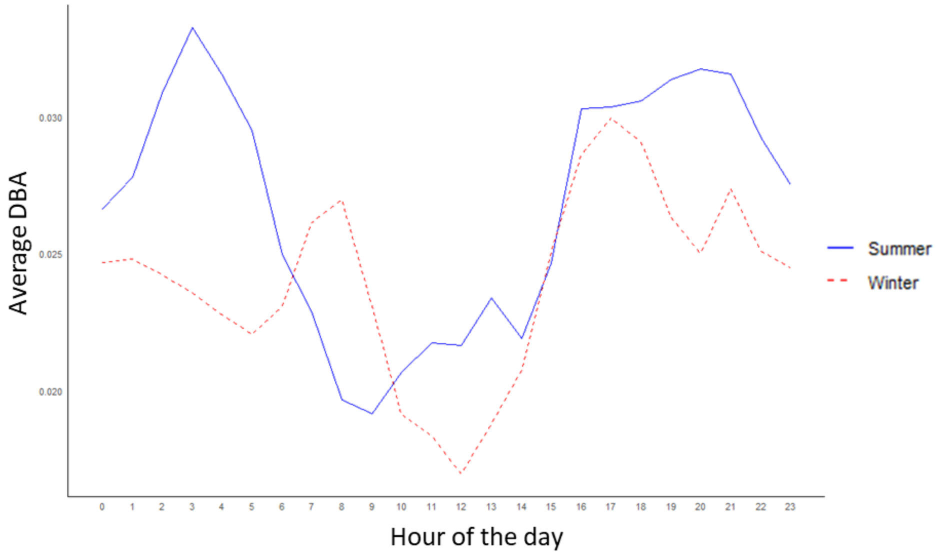

Figure 5.5. Activity levels over 24 hours in summer and winter based on dynamic body acceleration.

Behavioural observation

Behavioural observations were carried out to associate behaviour with acceleration data. Only one observation lasting 2.25 hours was achieved, including one disturbance. One further disturbance was recorded but the resulting observation was very short in duration and the disturbance was not discernible in the acceleration data. The longer behavioural observation provided just 55 data points from which to identify patterns and thresholds in acceleration data. Of those datapoints, 45 were of pre-disturbance behaviours: resting and grazing. Shortly after the disturbance occurred, the deer left the field of view and only one further datapoint was achieved after this. Only one acceleration record was associated with running behaviour.

5.4.4 Collaring adults: addressing specific questions

Space use and effect of sampling rate

The density of collared deer locations (Figure 5.6) showed 33.5% of locations in woodland, and a further 56% within 100 m of woodland. The deer was significantly further from roads (Mann-Whitney U: W = 186335936, p-value < 0.001) and buildings (Mann-Whitney U: W = 167089266, p-value = <0.001) during the day than at night. From May to November, GPS locations were recorded at a 15-minute interval which allowed use area to be compared between the 15-minute sampling rate and an hourly sampling rate. Daily use area size with an hourly sampling rate (mean = 0.15 km^2, SD = 0.16 km^2) was, on average, 33.4% smaller than the 15-minute sampling rate (mean = 0.23 km^2, SD = 0.20 km^2), representing a significant difference (Wilcox Signed Rank test: V = 13861, $p < 0.001$). However, the two datasets were highly correlated (Pearson's correlation test: t = 36.162, df = 184, $p < 0.001$). The scale of difference between the two sampling rates decreased when daily use area was increased to a 5-day use area (hourly sampling rate 29.6% smaller) but remained significantly different (Wilcox Signed Rank test: V = 703, $p = <0.001$).

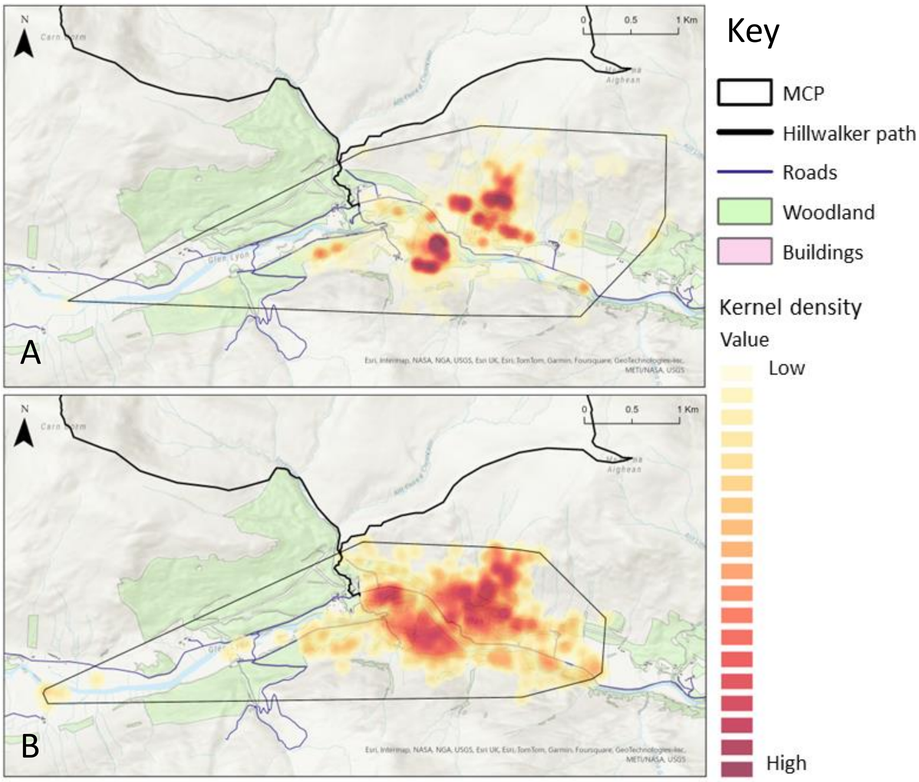

Figure 5.6. Kernel density estimates showing the distribution of collared deer locations during the day (A) and at night (B) and use areas for these periods indicated by minimum convex polygons (MCP).

Behaviour calibration

Acceleration data for the period during which the behavioural observation was carried out was labelled based on the behaviours observed. The labelled data was then visually assessed to identify characteristic patterns for different behavioural states (Figure 5.7). Variation between pre-disturbance and post-disturbance behaviour was evident from an increase in dynamic body acceleration associated with initial alertness (stX) followed by running away (DBA).

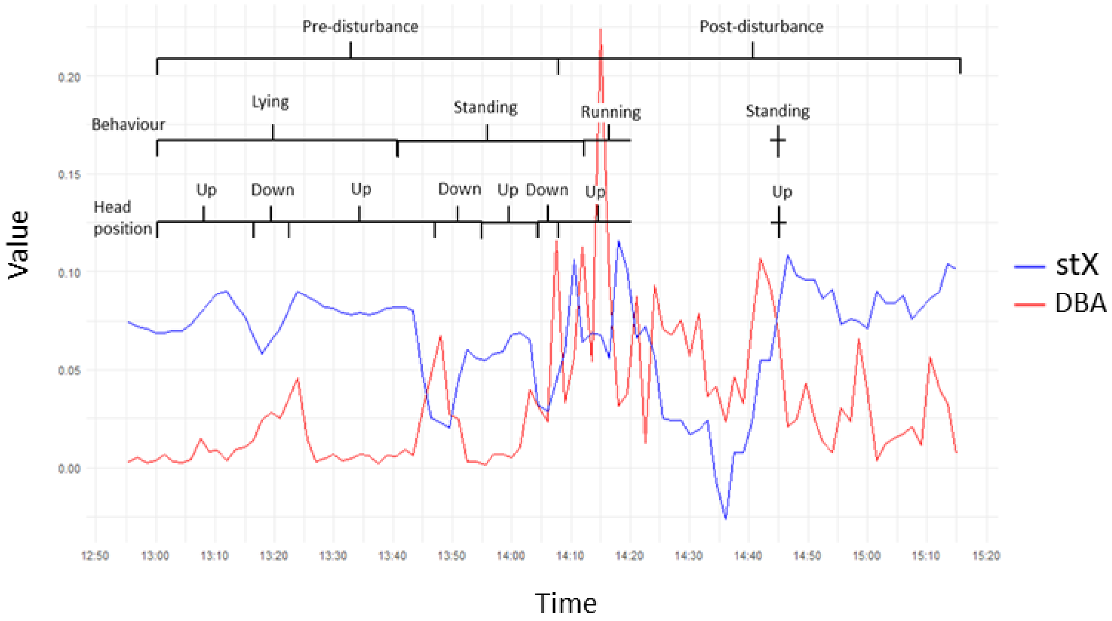

Figure 5.7. Assessing vigilance and disturbance behaviour from acceleration data summary variables static X (stX) and vectorial dynamic body acceleration (VeDBA) using a) thresholds in stX values and b) calibration with behavioural observation. The deer was out of view between 14:13:30 and 14:43:43 and after 14:45:36.

Behaviour classification of acceleration data

I explored the potential identifying state behaviours from acceleration data using possible thresholds suggesting in the labelled acceleration data (Figure 5.7), but this was unsuccessful. Very few periods of high activity indicating potential disturbance events were flagged overall, and a substantial portion of these occurred at night when human disturbance is unlikely to have been the cause. An association between DBA and step-length was thought to indicate flight behaviour because a deer running away would increase speed (DBA) and, thus, travel further (step-length). However, increased DBA did not appear to be reliably associated with increased step-length (Figure 5.8).

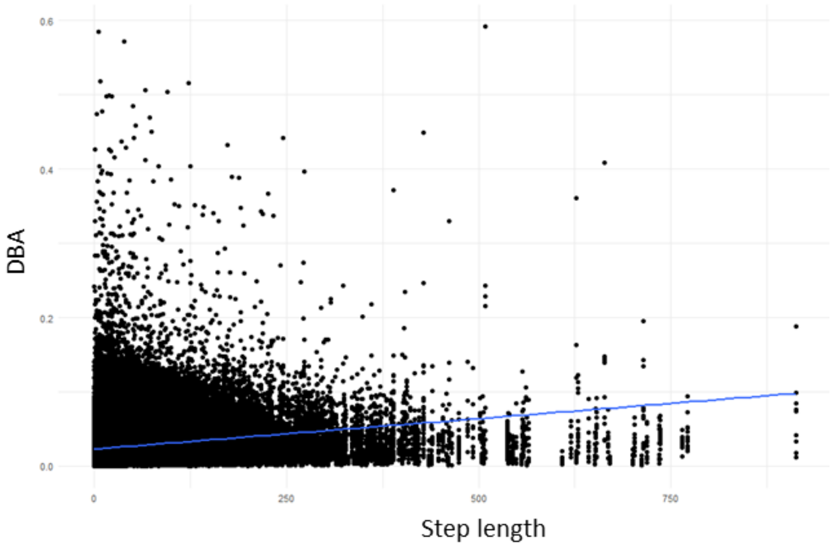

Figure 5.8. Association between DBA and step length/distance travelled between consecutive fixes, including the linear regression line indicating a positive association between DBA and step length.

Static acceleration on the x-axis of the acceleration data (stX) was used to determine head position to infer vigilance levels. I identified the values that most likely corresponded with the ‘head down’ and ‘head up’ positions based on the frequency of values (Figure 5.9). This was based on the assumption that the lower frequency of intermediate values was associated with the lower likelihood of the deer’s head position being level with its shoulders. Head position can indicate levels of vigilance, but cross-examination of stX values (Figure 5.9) and behavioural observations (Figure 5.7) suggested that active vigilance and alert behaviour were not distinguishable from a more relaxed head-up position, such as when ruminating. To investigate this, two versions of the vigilance variable, based on different thresholds of stX values, were evaluated. In each version, values above the threshold were taken to indicate head-up position. The first version (stxvig1) had a threshold of 0.05 which was the expected threshold, and the second (stxvig2) was 0.06 which was included as a more conservative option. The percentage of time spent ‘vigilant’ (stxvig1 or stxvig2) by the collared deer in summer was compared with scan sampling results from groups of deer observed on the open hill (Appendix 5.3) during the same daily and monthly time periods. The results of scan sampling suggested that deer were vigilant 47% of the time, during observable hours of the day (8am to 7pm). In comparison, stxvig1 suggested the collared deer was vigilant 45% of the time, and stxvig2 32% of the time. Finally, when comparing the results of models investigating the variation in vigilance, smaller margins of error were associated with the stxvig1 version.

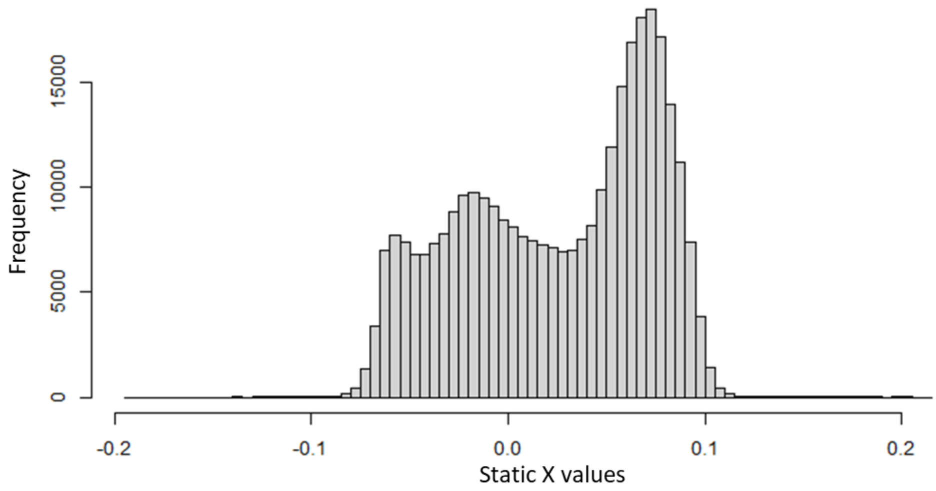

Figure 5.9. Frequency of static X values indicating two peaks in values related to frequency of head down (low value peak) and head up (high value peak).

Vigilance in relation to spatial and temporal factors

Behavioural observations and visual assessment of frequencies of static X (stX) values were used to identify head-up, or vigilance, and variation in probability of vigilance was investigated. Dynamic body acceleration (DBA), time period, month, distance to buildings, roads, and woodland, and the associated interactions with time period were retained as informative predictors of the probability of vigilance (Appendix 5.4). Due to high levels of collinearity, only the interaction with the largest effect on vigilance was included in the final model: time period x distance to buildings.

Dynamic body acceleration affected the vigilance of the collared deer negatively, suggesting that, as activity increased, probability of vigilance decreased. Month and time of day were the only temporal variables included in the top model. Vigilance spiked in April and October and decreased from November to February (Figure 5.10A). Due to the date of collaring (30/04/2022) and the removal of the collar after 50 weeks, April is represented by only 2 weeks of data. Vigilance was lowest in July. Daytime had the highest probability of vigilance and night-time the lowest probability of vigilance (Figure 5.10B). The dawn and dusk period showed an intermediate probability of vigilance.

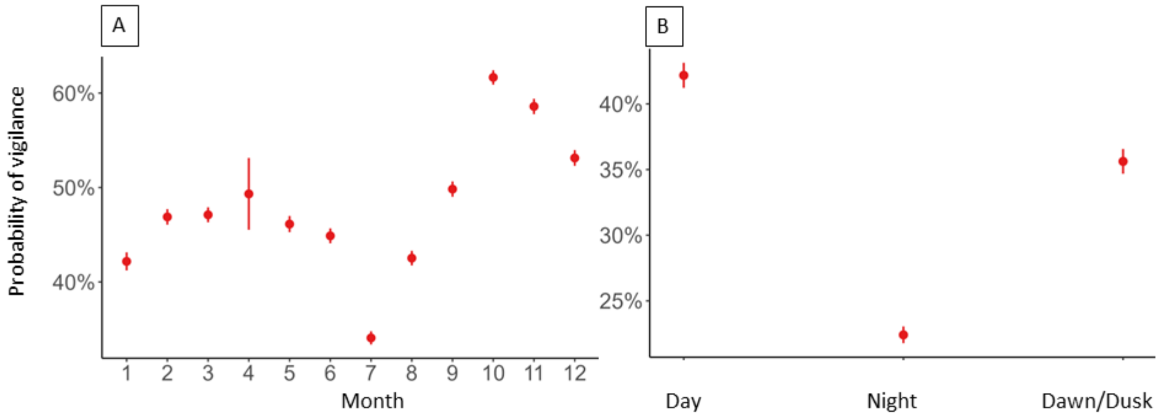

Figure 5.10. Probability of vigilance A) by month and B) by time of day as day, night, and dawn/dusk.

All spatial variables were significantly related to probability of vigilance. Vigilance declined with increasing distance from woodland (Figure 5.11A) but increased with increasing distance from roads (Figure 5.11B). Vigilance declined with increasing distance from buildings during the day, but the effect was less pronounced at dawn or dusk and at night vigilance increased slightly further away from buildings (Figure 5.11C).

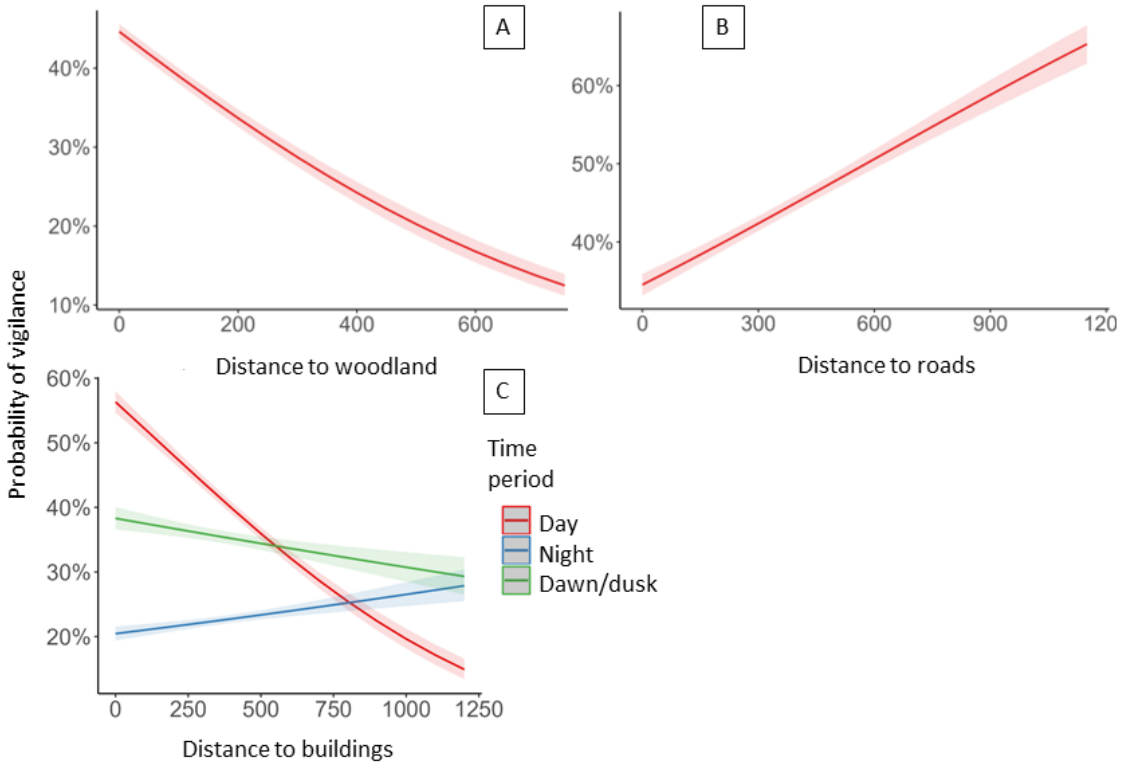

Figure 5.11. Model outputs for spatial variables A) distance to woodland, B) distance to buildings and C) and distance to roads x time of day.

5.5 Discussion

Throughout this research, significant practical challenges arose that affected the sample sizes and subsequent applicability of the methods. Nevertheless, the results provide valuable insights and suggest the potential benefits to ecological understanding that could be gained if larger sample sizes were obtained. By tagging calves, I confirmed winter survival for some calves, but increased sample size and resight effort is required to reduce uncertainty when estimating recruitment rates. Calf resights suggested potential to answer questions relating to home ranges and social dynamics of groups. Location data from collared hinds underscored important considerations for assessing movement rates, showing that the sampling rate of locations subtly but significantly influenced the results. Behavioural inferences were substantially limited by sample size relative to the length of behavioural observations needed to classify acceleration data and the low sampling rate of the accelerometer. While classifying disturbance events or behavioural states such as resting, feeding, and traveling was not feasible, overall activity levels and vigilance levels were successfully determined. In this discussion, I review these results and highlight where the methods could be improved to both widen the applicability of the data and improve the overall effectiveness of tracking studies in Scotland.

5.5.1 Calf tagging

The sample size of tagged calves was small, comprising less than 5% of the estimated total deer population, or 15% of the estimated calf population. At its maximum, sample size was 22; however, at that point, the survival of four calves was unknown, so sample size may have been as low as 18. Capturing calves presented a number of challenges. Significant among these challenges was the size and relative inaccessibility of the area in which calf capture was carried out. Effective coverage of this area was limited by the distance I could travel in steep terrain in a day, on top of time spent observing deer. In some places it was possible to monitor large areas at a time, but areas where this was possible did not appear to be favoured by deer as calving sites. It is possible that the presence of hillwalkers influenced the probability of young calves being observed in visible areas and during the middle of the day. Deer may have avoided these areas while the hillwalker path was active. They could do this by either keeping their calves in areas with topographic cover from the path, or leaving them for longer periods throughout the day. In the area where the most calves were caught (Figure 5.3), deer were observed to return from adjacent areas screened from the path by topography, from approximately 5pm. On several occasions, deer turned back without reaching and feeding their calves. At the same time, hillwalkers were observed on the path. In these instances, observation periods suggest a minimum of seven hours between feed times for the calves. High frequencies of events reducing feeding opportunities for calves may have significant consequences for calf survival (Phillips and

Alldredge, 2000). The sample size of tagged calves could be increased with a larger capture team to cover more areas of the study site. Use of a vehicle to get onto the hill would substantially reduce travel times to access deer, allowing capture teams to utilise both the early morning and late afternoon active periods. Despite the limited sample size and challenges in inferring survival rates, tagged calf resights yielded interesting insights into deer movement patterns and group dynamics.

The movements of calf Orc21 is a good case study, with double the number of resights of any other calf. The reasons behind this are unclear, given that she was tagged in the same place as five calves that appeared rather less frequently. Tag characteristics, such as size and colour, may have influenced visibility. For instance, two calves in the same area were tagged with button tags, which could have been more challenging to spot during field observations due to their smaller size. The larger, green cow tag on one other calf might have been harder to detect than the orange tag of Orc21. Detection bias may also be a factor due to variations in personality and activity levels. Individual personality can affect the probability of calves approaching camera traps (Johnstone, McArthur and Banks, 2021) and activity levels may vary with body condition, with more active calves more conspicuous to an observer. Finally, deer movements were not confined to the study site, making individuals with more of their home range within the site more likely to be observed. Orc21 was observed in a greater variety of locations than the other calves. The larger sample of resights associated with Orc21 may explain this; however, it might also suggest that a substantial portion of the home range of Orc21's mother was within the study site. Consequently, there were more opportunities to observe Orc21. In comparison, other calves may have occupied areas both inside and outside the study area. This seems particularly likely in the cases of Whb21 and Gyc21 that were observed closer to the peripheries of the study site. Whc22 was exclusively observed on the eastern boundary of the study site but was also restricted to an area within a fence until at least 13/07/2022. Finally, large areas in the west of the study site, near where 3 calves were tagged, have lower visibility for observation and are less accessible, providing less opportunity for observation.

Calves born in the same area, even within the same year, were not necessarily observed together as part of the same social group, and calves that were born in different areas were observed in the same group. This has potential implications for the flexibility and fission/fusion of groups. Deer have been shown to associate with closely related individuals (Biosa *et al.*, 2015; Albon, Staines and Guinness, 2016), but factors such as population density, individual energy requirements (relating to age and size) and spatial features are also important (Conradt and Roper, 2000; Albon, Staines and Guinness, 2016; Le Goff *et al.*, 2024)

The use of camera traps proved invaluable in capturing additional resight data but imposed limitations in confirming associations within groups. Not all individuals were necessarily visible in the images and distinguishing between tags of the same shape in nighttime images was not possible. To enhance the effectiveness of future tagging efforts, the larger, more visible cow tags should be used exclusively and numbered to facilitate individual identification in camera trap images, particularly at night. This would also be valuable for visual resights. We have received no reports of tagged calves outside the study site, despite all relevant people being made aware of the project. Even the larger tags are sometimes difficult to make out at a distance, particularly if deer managers are focused on adults suitable for culling.

In summary, with larger sample sizes, a visually marked subset of the population could provide valuable insights into individual deer movement and social dynamics. Particular attention should be paid to potential biases relating to the visibility of different tags and individual home ranges. Some studies have also fixed tracking devices to tags (e.g. Berg *et al.*, 2023), including Licoppe, (2006) that tagged red deer neonates. Similarly, some studies also fit neonates with GPS or VHF collars which improves the capacity for data collection (e.g. Licoppe, 2006; Kjellander *et al.*, 2012). Ethical considerations in terms of the risk of rejection by the mother, and weight carried by the calf would need to be thoroughly assessed, however.

5.5.2 Collaring adults

There were obstacles to collaring adult deer at every stage of the proceedings, from licensing to anaesthetising. Much of the legislation and training surrounding Home Office licensing procedures under ASPA refer to laboratory-based animal testing. As a result, adapting existing guidance to research on wildlife was an extensive process requiring considerable extra communication with the licensing officer. Furthermore, difficulty in obtaining the required practical training on deer was responsible for substantially reducing darting opportunities until February 2022. This was in part due to the difficulty in accessing deer in the first place, in addition to the limited availability of veterinary supervision caused by the COVID-19 pandemic. The darting process itself presented multiple challenges. The first among these was getting to within range of the deer. Areas and conditions which facilitate very close approach of wild deer were not conducive to darting. For example, steep, rugged terrain provides cover for approach, but steep slopes are dangerous for anaesthetised deer. Weather is also a limiting factor. Wind reduces the ability of deer to detect people but is liable to cause darts to blow off course. Two of the bait stations were regularly used by deer but the deer appeared to show heightened vigilance around them. Despite this, multiple shots were taken at bait stations. At the point of darting, further complications related to the darting system. Large darts travel slowly, which in one case allowed a deer to avoid the dart by jumping forward. The darting system is based on specific levels of air pressure for specific darting distances. On multiple occasions darts bounced ineffectually out of deer, indicating high levels of sensitivity in this mechanism. This is a problem when setting up shots in close-range where the noise and movement associated with checking distance could disturb the deer. In addition, there appears to have been a consistent effect of incorrect pressure due to the longer barrel used in this project to improve longer-range accuracy. The longer barrel may require slightly lower pressure than levels instructed by the manufacturer, which are based on a shorter barrel. Darts were also observed to discharge only partially. The dart injection system is based on pressure that is released on impact, depressing the plunger. It appears that pressure may leak from darts slowly over a period of minutes or hours. This is a problem because even small noises associated with pressurising and loading darts within short distances of deer can be a source of disturbance. Therefore, darts should periodically be repressurised whilst waiting for deer or during long approaches.

The GPS fix success rate of 90% was comparable to those obtained in other studies (Hebblewhite, Percy and Merril, 2007; Takii *et al.*, 2012; Stewart *et al.*, 2022), despite potentially unfavourable conditions. Tree canopy cover and topography have been shown to reduce GPS fix rates of collared animals (Frair *et al.*, 2004; Cain *et al.*, 2005). The collared deer frequently occupied dense woodland that was in the low ground of an area bounded by steep mountains. However, a further 6% of fix attempts were removed due to potential inaccuracy associated with higher DOP value and lower quality, 2-D fixes. The proportion of time the deer spent in woodland may be underestimated if a disproportionately high number of fix attempts in dense woodland failed or were discarded due to inaccuracy (Hebblewhite, Percy and Merril, 2007; Coulon *et al.*, 2008).

Space use and effect of sampling rate

Use areas of the collared deer were calculated over different periods of time to investigate the effect of sample rate on biological conclusions. Inferred daily and five-day use area sizes depended on the sampling rate (15 minutes or 60 minutes), although use areas were strongly, positively correlated, regardless of the fix rate. In addition, the difference between use area sizes reduced as the period of time over which the use area was calculated over increased. The distinction between absolute size, for which accuracy initially increases with increasing sampling frequency, and relative size, is important depending on the research question. For example, if the research goal was to determine variation between individuals, then a relative value would be sufficient for comparison. Similarly, GPS sampling rate is important when considering distance travelled throughout the day, with longer sampling intervals potentially leading to an underestimation of distances because they assume a straight-line trajectory, while too frequent a sampling interval can artificially inflate distances due to location error (Poulin, Clermont and Berteaux, 2021). These results may be inflated by the relatively small size of the daily use areas, such that minor variations between the sampling rates cause large changes in percentage difference.

Behaviour from accelerometers

Acceleration data from tracking collars can provide important insights into wildlife behaviour (Brown *et al.*, 2013). Compared to other collar-mounted behavioural observation options, such as on-board cameras (Thompson *et al.*, 2015), accelerometers are lightweight and allow for more data to be collected and stored due to lower battery and data storage use. The downside is complicated processing and analysis of the data to classify records as specific behaviours (Collins *et al.*, 2015). Many methods, particularly when fine-scale behaviour classification is the goal, also require a labelled, training dataset obtained via observations of the collared animal (Fehlmann *et al.*, 2017; Studd *et al.*, 2019). I used a tri-axial accelerometer mounted to a collar with a sampling frequency of 90 seconds (the maximum possible with that collar model) to measure deer activity and classify behaviour in relation to human disturbance. The collared deer in this study spent a large proportion of her time both out of the study site and in wooded habitat, which severely reduced the opportunity for the behavioural observations needed to classify behaviours. This is a recognised problem with the requirements of this method. Some studies have tried to address this limitation by mounting accelerometers on captive animals of their study species (e.g., Mosser *et al.*, 2014; Wang *et al.*, 2015; Pagano *et al.*, 2017). However, this creates biases in the data if captive animals do not move the same way as their wild counterparts, or if the full range of behaviours exhibited by wild animals is not seen in captivity - for example, certain foraging, social or habitat specific behaviours. Furthermore, Dickinson *et al.* (2021) observed that variation between individuals was sufficient to reduce the effectiveness of classification models. Thus, it may be important to calibrate each device to the individual via observation. Visual examination of summarised acceleration data alongside existing knowledge of species' life histories has also been used to interpret movement patterns and identify behaviours. Figure 4.7 indicates a clear visual distinction between the pre-disturbance resting behaviour and the disturbance response; however, large intervals between records disrupt the continuity of the movement. Studies typically use sampling frequencies of 1-64Hz (Brown *et al.*, 2013). The 90 second sampling interval of acceleration data in this study limits the effectiveness of the descriptive statistics because it is illogical to consider the change in acceleration over such a large interval as a behaviour characteristic. As the sampling frequency was imposed by the model of collar, we recommend that researchers interested in identifying behaviours from accelerometry consider alternative models of collar that provide the additional accelerometer functionality.

It was not possible to distinguish disturbance events using data collected in this study. This is due to a combination of factors: lack of behavioural observation sample size to generate labelled datasets, the relatively short duration of many disturbance responses, and the long interval between records. A more extensive labelled dataset would provide statistical power to analyse more acceleration data summary statistics, representing a more detailed picture of the deer's movements (Fehlmann *et al.*, 2017), and would enable the use of more sophisticated analyses, such as machine learning approaches (Wang, 2019). The sampling frequency of the acceleration records also increases the required duration of observations, particularly to capture rarer behaviours such as running. Even with an extensive labelled dataset for training models, key short-duration behaviours may be missed if they fall between the 90 second sampling interval. For example, of the two observed disturbances, only one occurrence of 'running' was observed in the data. Despite the deer continuing to move away from the disturbance following the event, there was no further visual indication of disturbance in the data. This was reflected in the poor correlation I found between DBA and step length. When close to closed habitat such as woodland, deer may also make a very short flight to cover (safety) and stop there, although longer flight distances may be observed in areas without cover (Stankowich, 2008; Chassagneux *et al.*, 2019). Even if longer flight distances occur in open habitat, deer are likely to stop regularly to assess the situation rather carry out an extended flight. If flights are short or fragmented, the probability of bouts of running falling between intervals and being missed is greater. Given my findings, the accelerometer technology used in this study is unlikely to be suitable for research questions studying fine-scale behavioural variation. As demonstrated here, these include quantifying disturbance events, but diet studies assessing variation in foraging behaviour would also be challenging. A larger calibrated acceleration dataset could, however, enable broad-scale behavioural inferences to be made, particularly if combined with spatial context from location data. Such questions include how human disturbance levels affect time spent foraging. Foraging behaviour could be determined from head position and activity level and location data could provide spatial context in relation to sources of disturbance.

I determined head position using a small sample of calibrated acceleration data and assessing thresholds in the wider acceleration dataset. Using a head-up position to indicate vigilance, this measure was comparable to scan sampling observations carried out nearby on deer living in more open, and more easily observable, terrain. The slightly higher proportion of time spent vigilant according to scan sampling (47% versus 44%) may relate to discrepancies or limitations in the data collection methods. However, it may also reflect the habitat and nature of the deer being observed. The collared deer locations were entirely within 1km of woodland. Red deer have been shown to be less vigilant near or in closed habitat (Jayakody *et al.*, 2008), and exhibit larger disturbance responses in open habitat compared to closed (Jarnemo and Wikenros, 2014). The collared deer also lived in closer proximity to a wide range of benign human activity and, as such, may have had more opportunity to habituate to human disturbance than the deer on the open hill (Found *et al.*, 2018).

The results from modelling variation in vigilance for the collared deer generally corresponded with existing literature. Vigilance varied monthly, likely reflecting key events throughout the year such as increased human disturbance during lambing (April) (Jayakody *et al.*, 2008), or biological variation in behaviour during the rut (October) (Carranza, Alvarez and Redondo, 1990). However, very low vigilance levels in July in this particular case do not align with research showing an increase in vigilance following calving (Clutton-Brock and Guinness, 1975). Deer have been shown to reduce activity (Laguna *et al.*, 2021) and increase nocturnality (Gaynor *et al.*, 2018) in areas where human activity is high. Daylight hours when human activity is greatest elicited a stronger vigilance response from the deer, and activity levels were lower. The effects of proximity to buildings on vigilance were also stronger during the day but reflected the variation in disturbance responses by deer to different types of disturbance. Red deer have been shown to move less (Chassagneux *et al.*, 2019) and decrease vigilance when in or near cover and woodland habitat (Jayakody *et al.*, 2008). It was therefore expected that vigilance would increase further away from woodland. Contrary to this prediction, the collared deer was more likely to be vigilant in or closer to woodland, with only a slight significant variation between time periods. This may have occurred as a result of selection of woodland habitat or close proximity to woodland when disturbances were higher (Lovari *et al.*, 2007). Areas further away from woodland may also have been further from human disturbance. Finally, the deer spent 67% of her time in or within 50 m of woodland. Low vigilance levels further from woodland may have been driven by relatively few events that could have represented exceptionally low-disturbance periods. In these cases, times when disturbance was low resulted in low vigilance levels and a higher probability of venturing further from woodland. Overall, the data from a single collared deer yield biologically sensible results, suggesting that identifying vigilance from thresholds in static X is a viable method for interpreting acceleration data with limited calibration data and a low sampling frequency. Data from more deer could be used to support our understanding of the responses of deer to disturbance but collars with the potential for higher frequencies of accelerometer recording would be much more informative.

5.6 Conclusion

From the pilot data collected in this study, the value of marking and tracking even small numbers of individuals is clear, particularly in areas where individual level fine-scale movement and behaviour data are rare. Furthermore, this data highlights the limitations of the study in its current scope, as well as identifying potential pitfalls going forward, providing a useful guide for future research.

Scaling up these methods to include a larger sample size of marked individuals would contribute to current understanding of population-level movement patterns, social dynamics, and responses to environmental cues. This would enable a more robust, quantitative approach to analyses. Expanded datasets would be invaluable for informing land management objectives related to deer management and conservation, providing insight into how deer move through the anthropogenic landscape and the potential consequences of disturbance. Tracking marked individuals is particularly useful for understanding the relationship between disturbances and space use, such as whether deer congregate in specific areas following disturbances. This information can evaluate how disturbances affect deer and their distribution. Understanding these impacts is vital where conservation efforts, such as peat restoration or woodland regeneration, can be hindered by overgrazing, browsing, and trampling.

Chapter 6. General discussion

5.7 Summary of main findings

In this thesis, I have quantified spatial and behavioural responses of red deer to hillwalkers, evaluated the challenges and benefits associated with capturing and tracking individual red deer, and explored variation in disturbance responses of deer. In reviewing the literature on deer responses to disturbance, I established that there are many sources of variation in behavioural and physiological disturbance responses. Notably, deer show disturbance responses by one measure of disturbance, but not others, and individual and population variation in responses indicate high levels of behavioural plasticity in deer. The complexities involved in deer responses to disturbance were reflected in chapters 2 and 3, which focused on spatial and behavioural responses of red deer to disturbance by hillwalkers.

I found that red deer responded to hillwalker disturbance by substantial avoidance of the hillwalker path and by altering behaviour. Overall, the spatial avoidance was much greater than has been suggested by other studies in Scotland (Sibbald *et al.*, 2011; Marion *et al.*, 2021) and other European countries (Coppes *et al.*, 2017; Scholten, Moe and Hegland, 2018). Furthermore, comparison of the distribution of deer on quiet and busy hillwalker days showed that deer were considerably more concentrated on busy days. Deer increased vigilance, reduced activity, and were more likely to show acute disturbance behaviours when hillwalker pressure, as either distance to the path or hillwalker numbers, was higher. Group structure was also influenced, to some degree, by disturbance from hillwalkers. While all the measures that I investigated showed some response to hillwalker disturbance, the extent to which this occurred varied, depending on both spatial and temporal contexts. In keeping with my review of the literature on deer responses to disturbance, the findings of my field study highlight the importance of considering multiple measures of response when assessing the impact of human disturbance on wildlife; this is essential to accurately identify disturbance behaviour and its pervasiveness. The conclusions of these chapters emphasised the need for more fine-scale individual-based data to address remaining uncertainty in our understanding of deer disturbance responses. These uncertainties include the degree to which nocturnal foraging can compensate for habitat loss and reduced activity during the day, how fine-scale habitat use varies in response to hillwalkers, and the duration and magnitude of individual disturbance responses.

My final data chapter explored the practicalities and the value of tracking individual deer to provide those required further insights into fine-scale movement and behaviour, and individual variation in disturbance responses. This chapter highlighted substantial challenges associated with capturing both adult and neonate deer. Furthermore, I also pointed to limitations on and difficulties with monitoring tagged calves and extracting behavioural data from a GPS collared adult female. Nonetheless, even at the small scale piloted in this thesis, interesting insights were gained on individual-based movement, behaviour, and group dynamics. Improvements to capture methods and meaningful sample sizes would enable significant contributions to our understanding of deer disturbance responses. Methods for capturing calves could be improved by increasing search effort – for example, by using more people and cutting down on travel time to and from the deer. Adult capture could be improved by use of enclosures to bait and then trap deer, minimising loss of opportunities due to technical malfunctions and minimising drug wastage. Further advantages to this relate to capturing and holding deer when they go in at nighttime. Deer were more likely to access bait stations at night, or at dusk but cannot be darted in the dark.

In the remainder of this chapter, I will discuss these findings as a whole and how they contribute to the discussion surrounding responses of wildlife to human disturbance, land management, and land use conflict in Scotland. I will also discuss the limitations of this study in the context of alternative methods and the direction of future research.

5.8 Spatial and behavioural impacts of disturbance on deer

Hillwalker numbers over time

The temporal scale of variables indexing hillwalker numbers influenced whether hillwalker numbers appeared to affect deer behaviour, but this depended on the disturbance response being measured. Deer exhibited spatial responses to hillwalker numbers summed over longer time periods, whereas behavioural responses occurred in relation to shorter-term fluctuations in hillwalker numbers. Deer spatial responses were best explained by the total number of hillwalkers on the day of the observation and the previous day. By contrast, behavioural responses were better explained by temporal fluctuations in hillwalker numbers at the scale of less than a day. Specifically, the variable that considered clockwise hillwalker progress throughout the day best explained the effect of hillwalkers when investigating vigilance, activity, and aggregation disturbance responses. The exception was the effect of hillwalkers on deer group size. This was best explained by total hillwalker numbers over two days, likely reflecting the influence of spatial distribution on these results (Borkowski, 2000; Hebblewhite and Pletscher, 2002). No hillwalker number variable was significant in explaining variation in acute disturbance behaviours. I suggest that these observations assist with inferring the timing and persistence of different measures of disturbance behaviour. Changes in deer distributions as a response to disturbance often occur separately from short-term behavioural modifications (Naugle *et al.*, 1997; Grignolio *et al.*, 2011; Parsons *et al.*, 2016; Proudman *et al.*, 2021; Gaynor, McInturff and Brashares, 2022). This suggests that red deer in Glen Lyon may adjust their behaviour in the short-term based on fine-scale fluctuations in hillwalker numbers, before making energy costly movement decisions that affect distribution. The decision to increase distance from the hillwalker path may depend on hillwalker numbers exceeding a threshold (Colman *et al.*, 2012; Gundersen *et al.*, 2020). These results broadly reflect studies showing the effect of scale on prevalence of disturbance responses (Reimers *et al.*, 2009; Naidoo and Burton, 2020). For example, Naidoo and Burton (2020) observed disturbance responses for all 13 species studied at daily scales, but only two at weekly scales.

Spatial scale of disturbance responses

The spatial scale over which disturbance responses are measured may have important implications for research outcomes (Vistnes and Nellemann, 2008). Vigilance and activity levels were not affected by distance to the hillwalker path. There may be biological explanations for this, relating to low cost of vigilance to deer (Illius and Fitzgibbon, 1994; Fortin, Boyce and Merrill, 2004), or hillwalkers provoking specific anti-predator responses regardless of distance (Frid and Dill, 2002). The consequences of these effects on activity levels compared to vigilance are less clear, therefore sample limitations may also have resulted in a lack of spatial variation in the vigilance and activity dataset. This would occur if sample sizes at different distances from the path were not sufficient to detect spatial effects. Measurements may also have occurred over too small a spatial scale to detect a decline in vigilance and activity responses with increasing distance from the hillwalker path. Jayakody *et al.* (2008) failed to detect spatial variation in vigilance within a single site but did when comparing two sites with different levels of disturbance. Comparatively, vigilance levels in this study site were higher than in a similar site in Scotland (Jayakody *et al.*, 2008). This could suggest that vigilance levels were affected by disturbance at all distances from the path sampled in this study. Spatial scale also appears to have been an important factor when considering the magnitude of spatial avoidance of the hillwalker path. In the same study site, Marion *et al.* (2022a) were unable to detect strong evidence for spatial avoidance within 150 m using camera traps. These findings reflect those of Vistnes and Nellemann (2008) who showed variation in the significance of disturbance responses by reindeer depending on whether studies were carried out on a local or regional scale. Disturbance responses detected at a larger spatial scale are more likely to reflect long-term responses to disturbance (Vistnes and Nellemann, 2008). Consideration of both spatial and temporal scales in research are important. Research on disturbance responses of deer carried out at too small a scale could severely underestimate the magnitude of disturbance responses observed. The magnitude of spatial avoidance in this study has revealed substantial potential habitat loss, which could have serious implications for deer welfare or the vegetation in areas where deer concentrate to avoid disturbance.

Individual variation

The literature review highlighted the prevalence of variation in responses to disturbance within a population. Consideration of within-population variation in disturbance responses is important because variation in ability to tolerate disturbance can have population level implications (Merrick and Koprowski, 2017). Furthermore, these effects may make it more challenging to make empirical conclusions. Overall, red deer in the study site avoided the hillwalker path regardless of number of hillwalkers. However, distance increased when hillwalker numbers were higher, and behavioural responses increased closer to the path. This may suggest varying behavioural strategies and levels of tolerance between individuals, contributing to low explanatory power of both spatial and behavioural statistical models. A wide range of factors affect individual based variation in deer disturbance responses (body condition, Skogland and Grøvan, 1988; sex, Neumann, Ericsson and Dettki, 2011; personality traits, Le Saout *et al.*, 2014; reproductive status, Lesmerises, Johnson and St-Laurent, 2017; learned experience, Thurfjell, Ciuti and Boyce, 2017). In this study, individual based variation in disturbance responses may have affected research outcomes in relation to spatial partitioning of deer according to risk sensitivity, sex, and reproductive status. Effects of hillwalker numbers and distance to the path may have been modulated by spatial organisation of deer based on varying sensitivity to disturbance (Bejder *et al.*, 2009; Found and St. Clair, 2016). This would occur if deer more sensitive to disturbance were located further from the path but exhibited similar response levels to less sensitive deer located closer to the path. Male deer have been shown to exhibit lower disturbance responses than females (Clutton-Brock, Guinness and Albon, 1982; Neumann, Ericsson and Dettki, 2010; Pecorella *et al.*, 2019). The spatial distribution of male deer in the study site was typically towards the periphery of the study site, and further from the path. If the distribution of males is attributed to sexual segregation within the species (Clutton-Brock, Guinness and Albon, 1982), less responsive stags further from the path may have reduced the overall effect of distance to the path on disturbance responses. Finally, female deer have been shown to be more sensitive to disturbance when they have young calves (Aastrup, 2000; Hansen and Aanes, 2015). Hillwalker activity was a more important influence on activity levels early in the season than later in the season. This may have been a result of increased sensitivity or constraints on spatial means of avoiding hillwalkers due to the relative immobility of neonates. These findings demonstrate the ways in which within-population variation in disturbance responses could influence the results of ecological research. These effects could be magnified if studies are carried out over limited spatio-temporal scales or include sample sizes that are too small.

Landscape features and context dependency

Cover availability was shown by the literature review to be an important modulating factor in deer disturbance responses. In the absence of vegetative cover availability for deer, I investigated the use of landscape features as cover using several measures. Topographic and visibility variables affected deer responses to disturbance differently depending on the disturbance measure. The relative importance of these variables may reflect differences in the spatial and temporal responses to which they relate. Topographic variables were more important in the spatial model, which may therefore relate to habitat selection by deer following disturbances. Deer may seek cover when disturbed, which includes topographic cover (Mysterud and Ostbye, 1999; Chassagneux *et al.*, 2019). Group structure responses to disturbance represent more transient behavioural responses than spatial responses (Skogland and Grøvan, 1988; Lingle, 2001) and may therefore be more responsive to visibility variables. This is because visibility variables are susceptible to temporal variability based on weather conditions, orientation of the deer, and hillwalker conspicuousness. Therefore, group structure responses may fluctuate more frequently and rapidly in accordance with these changing visibility conditions, providing a more immediate indicator of disturbance levels. In contrast, acute disturbance behaviours interacted more closely with ruggedness than visibility variables despite acute disturbance behaviour also being a transient behavioural response. I suggest this is the result of a combination of factors exemplifying the complexities of deer behavioural interactions with their environment and humans. Deer display varying levels of tolerance to disturbance (Le Saout *et al.*, 2014), adapt to predictable disturbances in their environment (Westekemper *et al.*, 2018), and have the capacity to learn disturbance-specific responses (Thurfjell, Ciuti and Boyce, 2017). Acute disturbance responses are more likely to occur when deer encounter hillwalkers unexpectedly (Lingle and Wilson, 2001). Deer situated closest to the hillwalker path are therefore likely to be aware of potential hillwalker presence and, consequently, select areas in which they feel safer. These may include areas with greater topographic variation (Mysterud and Ostbye, 1999). This combination of factors mitigates the probability of acute disturbance behaviours. Therefore, the combination of habitat selection and visibility related to ruggedness serves as a more significant predictor of acute disturbance behaviour than visibility alone. In summary, the effect of landscape features on deer disturbance responses vary with both the type of response and the temporal dynamics of the landscape.

Cover plays an important role in deer disturbance responses (Naugle *et al.*, 1997; Meisingset *et al.*, 2022). However, though deer in the study site appear to use topography as cover, vegetative understory and canopy cover may be preferred to topographic cover (Mysterud and Ostbye, 1999). Deer in open areas display greater disturbance responses (Padié *et al.*, 2015; Chassagneux *et al.*, 2019). Vegetative cover is unavailable across the majority of the study site, which may result in greater disturbance responses by deer in this area relative to others (Jarnemo and Wikenros, 2014). Extensive deforestation in Scotland has severely reduced the availability of wooded habitat. Most woodland habitat occurs in the low ground and forestry plantations from which deer are largely excluded by fencing or culling. The variation in habitat quality used by deer in Scotland compared to mainland Europe has already been implicated in the small size of Scottish red deer compared to European red deer (Suttie and Hamilton, 1983). Energetic costs of excessive disturbance responses could continue to inflate this difference.

5.9 Management implications

Nature-based outdoor recreation is increasingly recognised as beneficial to people's physical and mental wellbeing (Bratman *et al.*, 2015). The opportunity to connect to nature also fosters an appreciation of the natural world and encourages engagement in environmental issues (Teisl and O'Brien, 2003). However, it also presents potential downsides to the environment and wildlife welfare (Simpson and Terry, 2000; Naidoo and Burton, 2020; Salesa and Cerdà, 2020). Here, I showed that red deer in Glen Lyon are undoubtedly affected by hillwalker activity, though the broader implications for the environment and wildlife welfare require further assessment.

Unmanaged outdoor recreation can have serious impacts on sensitive ecosystems via soil erosion on or off paths and effects on keystone species such as deer (Coppes and Braunisch, 2013; Salesa and Cerdà, 2020). Given the potential for reduced habitat deer are willing to use near the path, taking steps to minimise the spatial impact of hillwalking may be beneficial. These impacts can be exacerbated by unpredictable, off-path activity(Miller, Knight and Miller, 2001; Taylor and Knight, 2003; Helle *et al.*, 2012; Westekemper *et al.*, 2018). Minimising off-path recreation therefore may limiting the potential disruption to commercial stalking and deer management activities by making hillwalker activity more predictable to both deer and deer managers. By endeavouring to remain on the path, hillwalkers may reduce their impact on the environment and wildlife. Importantly, this could contribute to reducing conflict between land users where hillwalker impacts on deer are perceived to affect management and economic activity.

The study site in Glen Lyon may be particularly susceptible to hillwalker disturbance because the path encircles a large portion of the estate, thus influencing a greater proportion of the estate. In Scotland, more generally, disturbances by hillwalkers are most likely to occur in the uplands where hillwalking and red deer coincide. In these areas, lack of vegetative cover for deer likely exacerbates disturbance responses (Padié *et al.*, 2015; Scholten, Moe and Hegland, 2018). With this in mind, further management interventions should be considered. In areas with high levels of recreation in Germany, refuge zones have been shown to minimise the effects of disturbance on the distribution of red deer (Coppes *et al.*, 2017). Refuge zones are areas where recreation access is restricted either permanently or during specific times of the day or year. Refuge zones should be identified as areas that provide forage, shelter, and ideally, vegetative cover. In addition, land managers can identify areas currently used by deer, such as corries. Corries are bowls in the topography, often with steep sides that may provide cover. Furthermore, these areas are likely to be important calving areas (Birtles *et al.*, 1998).

Woodland habitat to provide vegetative cover in the Scottish uplands is limited, but availability could be improved in the short term by allowing deer access to mature growth areas while disturbances are high during the summer recreation season. In part of the Glen Lyon study site, such an area is used by deer year-round, but is not available to deer elsewhere in the site. In some places, access to these areas is currently restricted for deer by fencing. In the long term, new stands of woodland could be planted strategically to address these issues. While there is already a significant amount of tree planting occurring, it could be directed more effectively to mitigate disturbance impacts on deer and other wildlife. Vegetative impact on these areas is liable to be a concern and should be monitored closely. Impact on vegetation could be limited by increasing the number of refuge zones available. Implementing such targeted measures could significantly enhance the sustainability of outdoor recreation while preserving the ecological balance in sensitive areas. Allowing deer access to woodland may be controversial because of the damage they can cause (Côté *et al.*, 2004; Charco *et al.*, 2016), and the increased difficulty of managing deer in woodlands. However, by supplying more refuge areas in the long run, it is possible to strike a balance between the needs of wildlife and the interests of land users, promoting sustainable land use practices.

The Land Reform (Scotland) Act 2003 provides legal access rights to the public based on principles of responsible access. Guidelines on what this means for hillwalkers are outlined in the Scottish Outdoor Access Code (Outdoor_Access_Code, 2005). Advice regarding deer is limited to preventing dogs from chasing deer, and to the potential impact that the public can have on deer management activity. More generally, people are advised not to disturb wildlife and some examples are given, but these do not include deer. Recommendations for using paths are given in the context of near buildings, crop fields, and around livestock. Education is important when managing recreation in nature, because many recreationists are unaware of the extent of impact that their behaviour could have (Taylor and Knight, 2003). A straight-forward improvement to the access code could therefore be to emphasise this impact, with particular reference to deer in the uplands. Specific guidance regarding remaining on hillwalking paths would also improve public awareness. Special consideration should be made for calving season, in addition to during the rut which is already covered because it coincides with the core stalking season. More widely, public awareness could be raised via popular organisations such as Mountaineering Scotland, or on the hillwalking route website Walkhighlands.co.uk. Due to ongoing land use conflict, backing from sources that advocate for hillwalking directly could be more effective than signage from land managers. Increasing public awareness of their potential impact on deer is an easy, but potentially effective way to minimise hillwalker impact on wildlife (Taylor and Knight, 2003). The outdoor access code should be updated to include this advice. Site-specific information should be made available to hillwalkers to identify areas where hillwalking is likely to cause large impacts, highlighting refuge zones where all access is strongly discouraged.

Effective management of natural areas with high recreational use requires monitoring for welfare and ecological impacts. Land managers in areas with high levels of recreation should monitor vegetation for signs of over-grazing and loss of biodiversity (Côté *et al.*, 2004; Putman *et al.*, 2011). Declines in body condition in populations could indicate negative consequences of disturbance (Frid and Dill, 2002; Leblond, Dussault and Ouellet, 2013) and so should also be monitored closely. Historical records of larder (carcass) weights could be used to identify trends in body condition in relation to changes in the scale of human disturbances. By carefully tracking these indicators, land managers can better detect and mitigate the ecological consequences of recreational activities.

5.10. Future research

5.10.1. Addressing methodological limitations with technology

The data collection methods in this thesis (specifically, chapters 3 and 4) largely comprised direct observation methods. Direct observation provides valuable insights into the context of observed behaviours and spatial distributions. Despite advances in wildlife-monitoring technology, these methods continue to be important in ecology by connecting researchers to their subjects and improving understanding via first-hand demonstration of ecological theory (Hebblewhite and Haydon, 2010). Furthermore, field-based studies and the researchers who carry them out, may be viewed as more relatable and therefore more credible to key stakeholders such as gamekeepers (*pers.obs*). This is important in deer management, where uptake of scientific output is often slow and a source of conflict (MacMillan, 2004).

Despite their benefits, direct observation methods are restricted to times when a researcher is present and able to observe research subjects; thus, these times are limited by daylight and weather conditions. In this study, for example, it was not possible to determine whether deer compensated for daytime spatial avoidance with nighttime movements, or during periods of bad weather associated with low hillwalker numbers, and limited access to the hill. Accessing research subjects to observe them is an additional time cost, particularly in high-elevation areas with limited vehicle access. Human capacity limits are not only practical but may also relate to data integrity if observer presence affects animal behaviour, or observer bias and consistent inaccuracies occur (Burghardt *et al.*, 2012). In this regard, modern technology has substantial advantages due to its ability to monitor wildlife 24 hours a day, with minimal disturbance to research subjects. In addition, the data biases that occur as a result of technology-based monitoring, such as uneven GPS location failures across habitat types, are more predictable and therefore can be accounted for more easily.

Modern technology has allowed researchers to compensate for some of the limitations of more traditional field methods. Camera traps, for example, have been increasingly used in wildlife research due to their practicality and versatility (Burton *et al.*, 2015) but may also impose limitations on data collection (Newey *et al.*, 2015). In my study, camera traps provided more tagged calf resights than were obtained using direct observation. Wider use over winter and early spring may have increased the confirmed survival rate of calves, although winter use of camera traps can be limited by snow. Monitoring calf-survival by tagging individuals would also be substantially improved by using lightweight ear tags with VHF or GPS tracking technology (Berg *et al.*, 2023).

The use of GPS collars to track wildlife disturbance responses has also increased in recent decades (Marion *et al.*, 2020). GPS tracking of wildlife provides precise and continuous data on animal movements, enabling researchers to study movement behaviour and habitat use (Singh and Bais, 2018). Data from GPS collars and associated activity sensors provide detailed information on individuals, though studies using this technology are often limited in their capacity to make generalisations across populations. This is due to the small sample sizes often associated with these studies, and unknown degrees of influence of individual personality (Hebblewhite and Haydon, 2010; Latham *et al.*, 2015; Foley and Sillero-Zubiri, 2020).

In some cases, GPS tracking may be infeasible due to the difficulties associated with capture, and resultant small sample sizes. In this study, I attempted to anaesthetise red deer remotely, in order to attach GPS collars. I used a combination of bait stations and stalking to get within range of deer for darting (~30 m), and successfully collared just one deer. Until February 2022, darting attempts were severely restricted by personnel availability due to COVID-19. While methodological issues were due in part to the sensitivity of the dart gun and darting system (see chapter 5), the overriding difficulty was getting within range of the deer. This may be related to the sensitivity of the deer, evidenced by their nervous behaviour at bait stations and generally high degree of vigilance. As a result, even the slightest noise or movement was devastating to darting attempts. This is an important consideration for future research on Scottish red deer in which GPS collar deployment is proposed. That being said, comparisons of vigilance with other sites suggest deer in Glen Lyon may be particularly sensitive (Jayakody *et al.*, 2008; O’Neill, 2017). In North America, large-scale collaring projects are facilitated by large budgets and helicopter capture teams with net guns. This is less feasible in the UK, owing to low funding for projects and lack of qualified persons to carry out the work. This is exacerbated by restrictive licensing on wildlife handling for research. I suggest that future capture attempts in Glen

Lyon would benefit from an established winter-feeding program and means of containing deer once successfully baited, such as a corral. In summary, GPS tracking has the potential for highly valuable insights into deer movement and behaviour but requires careful planning and remains difficult in the UK.

Drone technology in the field of wildlife monitoring is rapidly advancing and could provide population level information on wildlife distribution and abundance without the need for capture (Wang, Shao and Yue, 2019; Zabel, Findlay and White, 2023). Aerial wildlife surveys are a valuable tool in population monitoring and provide high quality data. Historically, aerial surveys have been carried out by helicopter which incurs large fuel and personnel costs (Linchant *et al.*, 2015), resulting in lower frequency of surveys. In contrast, drones require relatively little expertise to fly and have low running costs. Frequent aerial surveys facilitated by cheaper drone flights could provide novel insight into fluctuations in deer distribution in relation to disturbances. In 2020, I trialled drone survey methods in Glen Lyon using a small, commercially available drone model, the Mavic Pro 4-rotor. While experts in Scotland continue to work on adapting drone technology to deer surveying (NatureScot, 2024), I experienced a number of practical challenges. Foremost amongst these was the reaction of the deer to the drone at heights up to 120 m (the legal limit). While a review of the use of drones for monitoring wildlife cites the low-disturbance nature of drones as an advantage (Christie *et al.*, 2016), this is not universal (Rebolo-Ifrán, Grilli and Lambertucci, 2019). Level of disturbance may be minimised by regulating the behaviour of the drone. I observed that deer were particularly perturbed by the drone hovering over them, while Zabel *et al.* (2023) reported no visible signs of red deer being negatively affected by drones flying at consistent height and velocity. I found hovering was sometimes necessary to distinguish the thermal signatures of deer from surrounding rocks and water that had been heated by the sun. For this reason, drone surveys using thermal cameras are often carried out early in the morning (Burke *et al.*, 2019; Kays *et al.*, 2019). Early morning drone surveys were a logistical challenge during this study due to the distances and elevation gain associated with accessing the deer, and the commitments of other data collection. Winter surveys may also contribute to reducing difficulty with thermal imaging (Zabel, Findlay and White, 2023). However, many drones are necessarily lightweight and therefore highly sensitive to weather conditions (Christie *et al.*, 2016). These drones can be blown off-course by wind and damaged by rain, and excessively cold weather reduces battery life. Weather is a significant challenge in Scottish mountain environments and researchers seeking to use drones need to factor this into their study designs.

5.10.2 Further questions

In this study, I have quantified deer responses to hillwalkers, but measuring the wider impact of these responses is outwith the scope of this thesis. There are environmental, welfare and economic consequences associated with deer disturbance behaviour and changes in deer distribution. Using a variety of methods, these could be further investigated to contribute to management of deer and outdoor recreation in Scotland, and more broadly.

What are the environmental consequences of changes in deer distribution and behaviour as a result of outdoor recreation?

The potential environmental impacts of deer are well established in the literature (Côté *et al.*, 2004; Putman *et al.*, 2011). However, population density thresholds at which these impacts become severe are less well understood (Putman *et al.*, 2011). This is likely to be especially true when deer movements are driven by temporal fluctuations in human disturbances rather than more predictable influences on movement, such as forage quality. In Scotland in particular, herbivore impacts on the environment may be exacerbated by the constraints that an anthropogenic landscape places on them (Fløjgaard *et al.*, 2022), posing further difficulty for herbivore management and conservation. I have shown that deer densities vary spatially across days of different levels of hillwalker disturbance. These results provide important context for assessing the environmental impact of red deer across the study site; that is, when deer congregate in specific areas in response to hillwalker disturbance, does this have a measurable effect on plant communities, vegetation structure, and soil integrity? By carrying out herbivore impact assessments across areas with different intensities of deer use related to hillwalker disturbance, we can quantify the indirect impacts on the environment that outdoor recreation has. This is particularly important if the areas that deer occupy when hillwalker numbers are higher (chapter 2) are associated with peatland. Peatland has been identified as highly important to conservation and climate change mitigation goals (NatureScot, 2020) but may be sensitive to trampling by deer. Larger groups of deer were observed at higher elevations, which may be related to the tendency of deer to flee uphill when disturbed (chapter 4). This may have significant consequences for the sensitive montane and arctic-alpine plant communities that characterise the upper slopes and plateaus of the study site (NatureScot, 2010).

What are the welfare consequences of deer disturbance by outdoor recreationists? Ethical, conservation, and economic considerations

The welfare consequences of disturbance of wildlife require consideration from ethical and conservation perspectives (Blumstein, 2010; Paquet and Darimont, 2010). Repeated human disturbances can significantly impact wildlife welfare by causing chronic stress (Sauerwein *et al.*, 2004), altering behaviour (Jiang, Zhang and Ma, 2007), and disrupting critical activities such as feeding (Jayakody *et al.*, 2011), and rearing young (Phillips and Alldredge, 2000). These disturbances can lead to reduced fitness and survival rates as animals expend more energy on avoidance and stress responses, leaving less for growth, reproduction, and immune function. Over time, these individual-level effects can scale up to the population level, resulting in decreased population sizes and altered community structures (Paquet and Darimont, 2010). Consequently, the welfare implications of human disturbance are important for wildlife management and conservation, in addition to an intrinsic moral responsibility to wildlife.

Although I have shown that disturbance responses of red deer are both broad (shifts in distribution), and acute (fluctuations in behaviour), the physiological effects on the deer were not measured. An increasing population over the last 5 years suggests that disturbance responses have not affected population growth, though dispersal rates into the study area from outside are unknown. Even if survival rates are unaffected, deer could, speculatively, be generally smaller and weaker. This has implications for population robustness in response to additional stressors such as severe winters with high snowfall (Anderwald, Campell Andri and Palme, 2021). Additionally, economic consequences of reduced body condition also occur. Reduced carcass weights affect income from venison sales, and poor body condition affects antler size of stags (Gómez *et al.*, 2012) with potential to reduce the attractiveness of the estate to stalking clients (MacMillan, 2004). The impact of disturbance on body condition and size of red deer could be assessed using between-site comparisons of carcass weights during culls. Examining hormonal indicators of stress in faecal samples, such as glucocorticoid metabolites (FGM) or cortisol, is a non-invasive way of assessing stress levels in populations (Keay *et al.*, 2006; Sheriff *et al.*, 2011). A recent review on this method states that it can be a powerful research tool, but stresses that particular care is need to carry out analysis of samples (Palme, 2019). In the context of deer welfare in response to human disturbance, comparisons in stress hormones could be made over time as disturbance levels fluctuate (Dixon *et al.*, 2021), or between areas of differing levels of disturbance (Jachowski *et al.*, 2018).

How do the deer in Glen Lyon compare to the national and global research contexts?

Understanding the relative spatial and behavioural responses of deer across a wider population unit and between populations would provide valuable insight into context-dependent disturbance responses in red deer. This would provide a greater range of disturbance levels, aiding in parsing the effects of disturbance from other factors such as natural variation between seasons and genetics. This could be achieved by repeating the methods demonstrated in this thesis across new sites. The results from this thesis could be used to inform sampling approaches in new sites to improve the efficiency of a replicative approach and reduce sample size requirements. Alternatively, an experimental approach directly comparing controlled disturbances would provide a clear basis for statistical comparison. Distances at which animals become alert to human presence (alert distance), and flee (flight initiation distance) are commonly used to assess the sensitivity of ungulates to human disturbance (Stankowich, 2008). This particular measure has the added benefit of direct comparison with existing studies. The ability to effectively compare disturbance responses across a wide range of species and contexts globally is highly valuable due to the complexity and variability of wildlife responses to human disturbance (Tablado and Jenni, 2017).

5.11 Conclusion

This thesis has added to a growing body of literature quantifying the effects of outdoor recreation on wildlife and contributes to the ongoing discourse around land management in Scotland. Deer respond to outdoor recreation disturbance in multiple ways, as shown by this research. Red deer in the study site exhibited significant spatial and behavioural responses to disturbance by hillwalkers, but the extent of these responses depended on spatial and temporal contexts. These findings underscore the complexity of deer responses to disturbance and demonstrate the behavioural plasticity observed in deer.

In the broader context, these findings contribute to the understanding of wildlife disturbance and its implications for conservation and management. In Scotland in particular, existing research is limited, and the results of this research are highly varied. In addition, existing land use conflict around public access and deer management increases the necessity for objective research to inform discussions around management. In this research, I quantified the effects of disturbance in the study area and showed them to be substantial; however, the wider environmental and welfare implications were not measured. These remain questions for future research. Complexities and limitations in the results also emphasise the need for fine-scale, individual-based data on deer responses to disturbance, or alternative approaches to management problems. Substantial challenges remain with regard to the practicalities surrounding obtaining those data. Hurdles relating to obtaining sufficient funding, expertise, and capture methods need to be overcome to expand research in this direction. Nevertheless, by advancing our knowledge of deer responses to disturbance, this research highlights the need for effective recreation management strategies. By informing land and deer management, this research enhances our ability to manage human-wildlife interactions sustainably and promote the coexistence of multiple land uses in Scotland. The insights gained here are relevant not only to the specific context of Glen Lyon and Scotland, but also to broader efforts in wildlife conservation, globally.

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Appendix

A2: Chapter 3

A3.1 Deer spatial distribution model including observer distance

Table A3.1 Coefficients (estimate and standard error), z-value and associated degree of significance of variables included in the top model selected by AIC to explain variation in the density of deer.

Coefficients	Estimate	Std. Error	z value	*P* value	
(Intercept)	1.597	0.207	7.716	<0.001	***
Hillwalker numbers	-0.106	0.060	-1.769	0.077	.
Distance to path	0.451	0.087	5.186	<0.001	***
Topographic variation	0.306	0.061	4.988	<0.001	***
Ruggedness	0.047	0.059	0.801	0.423	
Elevation	0.326	0.079	4.149	<0.001	***
Day of year	0.174	0.058	2.970	0.003	**
Time of day	0.096	0.071	1.359	0.174	
Temperature	0.182	0.056	3.248	0.001	**
Observer distance	-0.341	0.066	-5.151	<0.001	***
Hillwalker numbers x Distance to path	0.205	0.066	3.095	0.002	**
Distance to path x Topographic variation	-0.146	0.061	-2.379	0.017	*
Hillwalker numbers x Topographic variation	-0.013	0.067	-0.192	0.848	
Hillwalker numbers x Ruggedness	0.065	0.069	0.938	0.348	
Distance to path x Day of year	0.088	0.064	1.376	0.169	
Distance to path x Time of day	-0.261	0.066	-3.932	<0.001	***

A4: Chapter 4

Appendix 4.1 Behavioural observation locations and dates

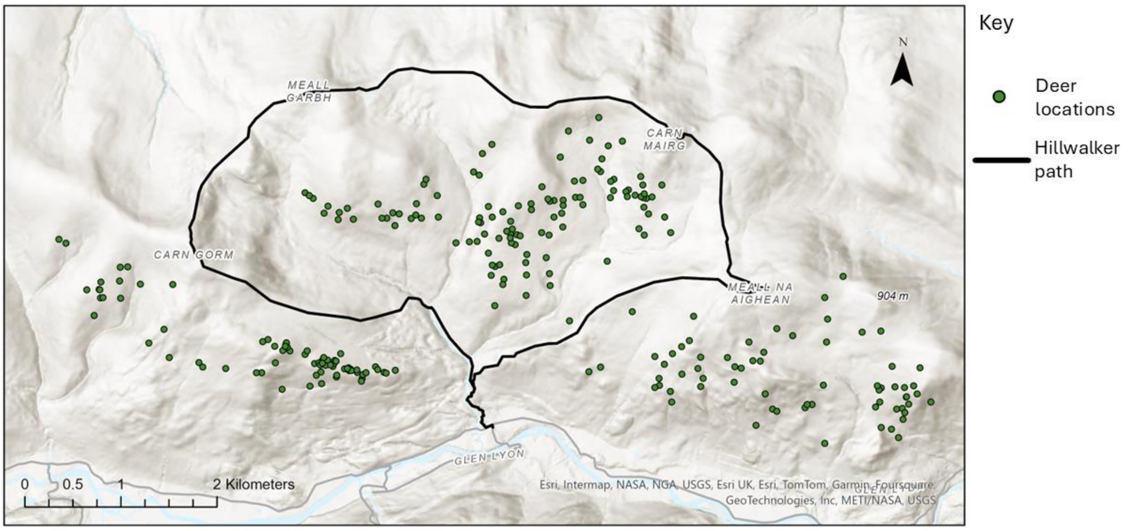

Figure A.4.1 Map of all locations of behavioural observations

Table A.4.1 Table of the dates and times associated with behavioural observations, and the sections of the study site they were located within (C = Centre, E = East, W = West).

ObsID	Date	Time	Section	ObsID	Date	Time	Section
O0057	12/06/2020	16:17	C	O2428	16/09/2021	14:00	E
O0065	14/06/2020	10:58	E	O2427	16/09/2021	13:57	E
O0103	17/06/2020	12:15	C	O2441	17/09/2021	09:09	W
O0104	17/06/2020	12:15	C	O2442	17/09/2021	09:09	W
O0109	17/06/2020	15:10	E	O2506	19/09/2021	12:24	C
O0110	17/06/2020	15:10	E	O2514	19/09/2021	15:39	W
O0179	21/06/2020	12:24	E	O2515	19/09/2021	15:39	W
O0186	23/06/2020	13:05	C	O2516	19/09/2021	16:00	W
O0188	23/06/2020	13:05	C	O2573	22/09/2021	12:00	E
O0187	23/06/2020	14:20	C	O2583	23/09/2021	11:27	C
O0217	25/06/2020	15:05	W	O2599	24/09/2021	10:51	C
O0216	25/06/2020	15:05	W	O2600	24/09/2021	10:51	C
O0220	27/06/2020	10:51	C	O2604	24/09/2021	10:51	C
O0239	17/07/2020	10:46	W	O2646	26/09/2021	12:54	E
O0247	17/07/2020	14:50	W	O2645	26/09/2021	12:45	E
O0253	18/07/2020	08:27	W	O2650	28/09/2021	16:18	C
O0270	19/07/2020	11:03	C	O2648	28/09/2021	10:24	W
O0270_O0272	19/07/2020	12:33	C	O2649	28/09/2021	10:24	W
O0271	19/07/2020	15:51	C	O2654	29/09/2021	11:27	E
O0272	19/07/2020	10:55	C	O2655	29/09/2021	11:27	E
O0274	20/07/2020	09:02	W	O2778	30/05/2022	13:06	C

O0292	20/07/2020	15:07	W	O2785	31/05/2022	12:30	C
O0354	23/07/2020	15:31	E	O2785.1	31/05/2022	12:54	C
O0355	23/07/2020	16:09	E	O2785.2	31/05/2022	12:54	C
O0375	25/07/2020	16:22	E	O2785.3	31/05/2022	12:54	C
O0372	25/07/2020	13:09	E	O2785.4	31/05/2022	13:12	C
O0371	25/07/2020	13:09	E	O2786	31/05/2022	16:12	E
O0371_O0374	25/07/2020	15:51	E	O2799	03/06/2022	09:27	C
O0374	25/07/2020	15:33	E	O2800	03/06/2022	12:27	W
O0427	28/07/2020	12:04	W	O2801	04/06/2022	12:27	W
O0476	30/07/2020	09:55	E	O2929	05/06/2022	09:03	W
O0484	31/07/2020	14:06	C	O2930	05/06/2022	09:03	W
O0484.1	31/07/2020	14:37	C	O2927	05/06/2022	09:03	W
O0484.2	31/07/2020	14:37	C	O2931	05/06/2022	14:51	W
O0481	31/07/2020	10:41	E	O2818	13/06/2022	10:54	C
O0547	03/08/2020	09:37	C	O2819	13/06/2022	15:39	C
O0548	03/08/2020	09:46	C	O2822	14/06/2022	15:32	E
O0548_O0549	03/08/2020	10:13	C	O2823	14/06/2022	16:57	E
O0549	03/08/2020	09:37	C	O2858	17/06/2022	15:51	E
O0553	03/08/2020	13:17	C	O2862	18/06/2022	10:54	C
O0573	06/08/2020	15:59	W	O3360	18/06/2022	11:00	C
O0574	06/08/2020	15:59	W	O3362	18/06/2022	13:27	E
O0572	06/08/2020	13:14	W	O2866	18/06/2022	15:15	W
O0576	24/08/2020	14:32	E	O2867	18/06/2022	15:24	W
O0600	28/08/2020	09:41	W	O2889	20/06/2022	11:30	W
O0607	28/08/2020	11:39	W	O2896	21/06/2022	15:57	C
O0608	28/08/2020	14:08	W	O2919	23/06/2022	10:36	C
O4058	28/08/2020	16:27	W	O2918	23/06/2022	10:36	C
O0666	30/08/2020	12:54	C	O2914	23/06/2022	08:30	W
O0664	30/08/2020	12:24	C	O2915	23/06/2022	08:39	W
O4059	31/08/2020	18:08	C	O2915_O2915	23/06/2022	08:54	W
O0700	31/08/2020	14:17	W	O2916	23/06/2022	08:39	W
O0876	06/09/2020	09:58	W	O2917	23/06/2022	08:39	W
O4041	06/09/2020	11:24	W	O2924	24/06/2022	12:33	C
O4044	06/09/2020	14:45	W	O3973	24/06/2022	12:33	C
O0890	08/09/2020	11:25	C	O2925	24/06/2022	14:27	C
O0892	08/09/2020	11:25	C	O3363	25/06/2022	08:42	W
O0891	08/09/2020	11:25	C	O3364	25/06/2022	08:42	W
O4057	10/09/2020	09:32	C	O2933	10/07/2022	15:33	C
O0947	10/09/2020	09:32	C	O2938	11/07/2022	10:54	C
O0948	10/09/2020	09:38	C	O2975	13/07/2022	11:24	E

O0956	12/09/2020	10:53	E	O2976	13/07/2022	11:24	E
O0988	28/09/2020	09:36	E	O2977	13/07/2022	14:12	E
O0989	28/09/2020	16:17	E	O2978	14/07/2022	11:27	C
O0990	28/09/2020	16:17	E	O2980	14/07/2022	12:21	C
O0991	28/09/2020	16:54	E	O2982	15/07/2022	12:30	C
O1055	01/10/2020	12:59	C	O3042	21/07/2022	08:57	W
O1056	01/10/2020	15:17	C	O3043	21/07/2022	08:48	W
O1068	02/10/2020	11:41	C	O4060	21/07/2022	08:34	W
O1070	02/10/2020	11:47	C	O4061	21/07/2022	11:57	W
O1129	06/10/2020	12:30	W	O3045	21/07/2022	14:15	W
O1126	06/10/2020	11:54	W	O3046	21/07/2022	15:12	W
O1390	05/06/2021	08:49	C	O3048	22/07/2022	11:39	E
O1391	05/06/2021	08:49	C	O3051	24/07/2022	14:36	E
O1470	08/06/2021	15:21	C	O3061	25/07/2022	12:21	C
O1471	09/06/2021	14:06	E	O3055	26/07/2022	08:45	W
O1472	09/06/2021	14:24	E	O3056	26/07/2022	08:51	W
O1475	10/06/2021	14:10	C	O3065	27/07/2022	11:39	C
O1483	11/06/2021	11:52	W	O3063	27/07/2022	11:39	C
O1498	13/06/2021	14:12	E	O3068	10/08/2022	15:00	E
O1499	13/06/2021	14:39	E	O3107	14/08/2022	12:00	C
O1578	16/06/2021	18:00	C	O3103	14/08/2022	08:15	W
O1639	18/06/2021	10:57	W	O3104	14/08/2022	08:18	W
O1637	18/06/2021	08:45	W	O3105	14/08/2022	08:36	W
O1638	18/06/2021	08:45	W	O3105.1	14/08/2022	10:27	W
O1640	18/06/2021	11:39	W	O3105.2	14/08/2022	10:27	W
O1706	21/06/2021	11:00	C	O3106	14/08/2022	08:39	W
O1707	21/06/2021	11:21	C	O3148	18/08/2022	10:12	C
O1721	12/07/2021	11:39	C	O3150	18/08/2022	10:12	C
O1801	14/07/2021	14:06	W	O3149	18/08/2022	10:12	C
O1802	14/07/2021	14:06	W	O3152	18/08/2022	12:24	E
O1823	15/07/2021	13:30	W	O3153	18/08/2022	12:54	E
O1825	15/07/2021	16:03	W	O3154	18/08/2022	13:27	E
O1907	19/07/2021	13:57	C	O3160	19/08/2022	13:21	E
O1925	20/07/2021	14:30	C	O3157	19/08/2022	09:15	E
O1926	20/07/2021	14:30	C	O3159	19/08/2022	13:30	E
O1931	21/07/2021	13:51	C	O3167	20/08/2022	13:12	C
O1930	21/07/2021	13:51	C	O3168	20/08/2022	13:54	C
O1930_O1931	21/07/2021	13:42	C	O3193	22/08/2022	11:00	W
O1928	21/07/2021	11:15	C	O3198	23/08/2022	12:36	C
O1929	21/07/2021	11:15	C	O3199	23/08/2022	12:45	C
O1986	23/07/2021	12:57	W	O3200	23/08/2022	14:03	C
O1989	23/07/2021	12:57	W	O3196	23/08/2022	15:30	W
O1991	23/07/2021	12:57	W	O3228	25/08/2022	08:45	W
O1992	23/07/2021	14:03	W	O3229	25/08/2022	09:00	W

O2004	24/07/2021	15:36	C	O3234	09/09/2022	14:09	C
O2003	24/07/2021	15:36	C	O3267	11/09/2022	14:00	C
O2045	26/07/2021	11:15	E	O3291	14/09/2022	13:00	C
O2046	26/07/2021	11:12	E	O3293	14/09/2022	16:30	E
O2048	27/07/2021	08:30	W	O3292	14/09/2022	15:21	E
O3993	11/08/2021	19:12	E	O3302	15/09/2022	13:39	W
O3992	11/08/2021	19:00	W	O3319	18/09/2022	14:15	C
O3997	12/08/2021	14:45	C	O3320	19/09/2022	11:00	C
O2145	15/08/2021	12:03	C	O3321	19/09/2022	11:00	C
O2169	16/08/2021	14:30	W	O3323	19/09/2022	11:51	C
O2233	18/08/2021	14:12	E	O3324	19/09/2022	15:42	W
O2232	18/08/2021	11:06	E	O3326	21/09/2022	14:27	E
O2236	20/08/2021	10:18	C	O3327	21/09/2022	14:27	E
O2292	23/08/2021	13:30	E	O3325	21/09/2022	13:57	E
O2365	26/08/2021	13:09	W	O3329	22/09/2022	12:12	W
O3994	12/09/2021	13:12	C	O3330	22/09/2022	14:15	W
O3995	12/09/2021	13:18	C				

Appendix 4.2 Figures of significant effects on deer activity levels

Groups with a higher proportion of calves were more likely to be active (Figure A.4.2A). Proportion of active deer decreased as sun hours increased (Figure A.4.2B), and increased with increasing windspeed (Figure A.4.2C).

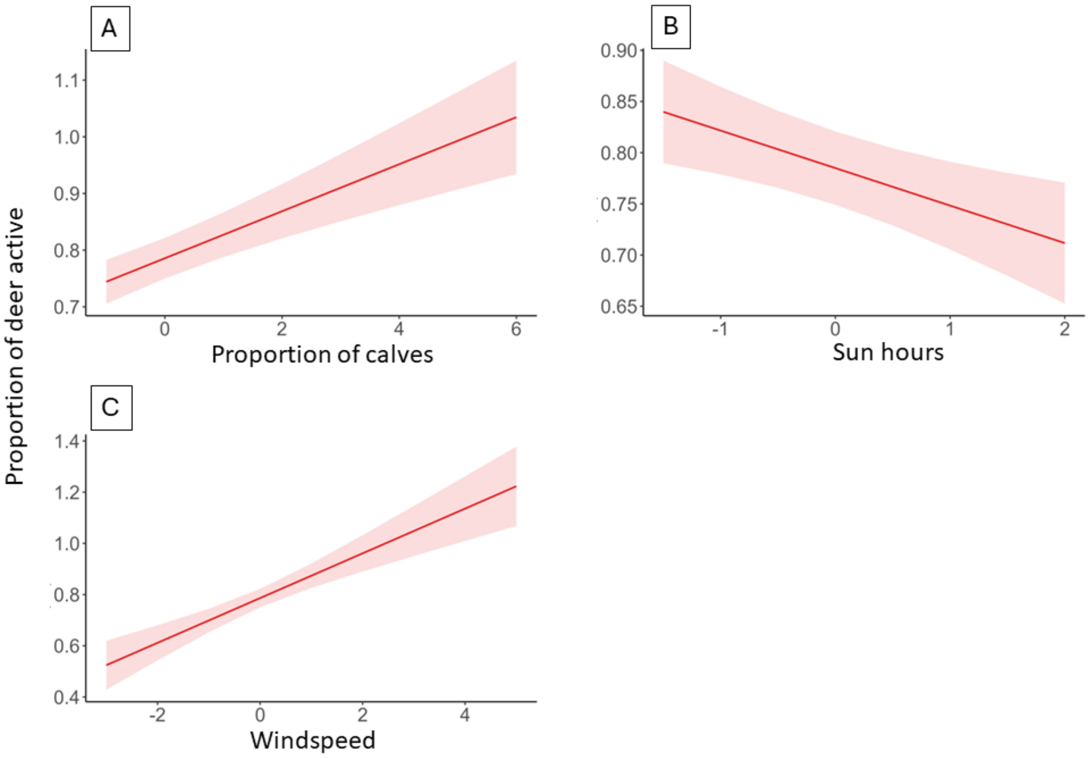

Figure A.4.2. Effects of A) proportion of calves in a group, B) sun hours, and C) windspeed on the proportion of active deer in a group.

Appendix 4.3. Figure of the effect of elevation on probability of acute disturbance behaviour

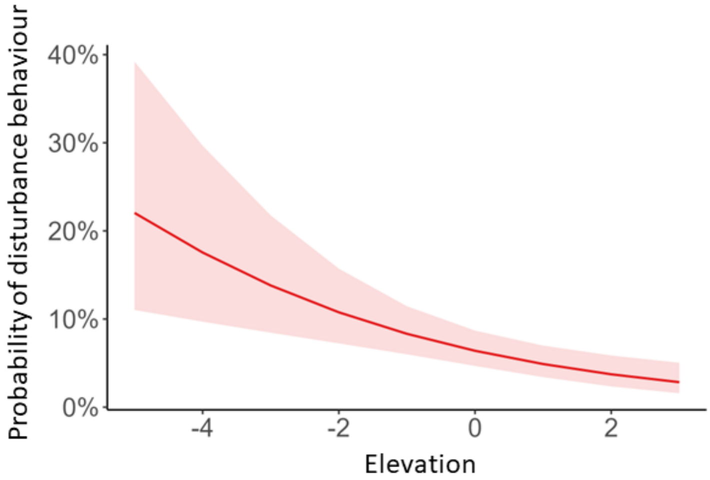

Figure A.4.3. The effect of elevation on probability of disturbance behaviour.

Appendix 4.4. Figures of significant effects on deer group size 1

Overall, group size decreased with terrain ruggedness (Figure A.4.4A). Day of year interacted with topographic variation, indicating that early in the season group sizes were larger where topographic variation was greater (Figure A.4.4B). This effect diminished as the season went on.

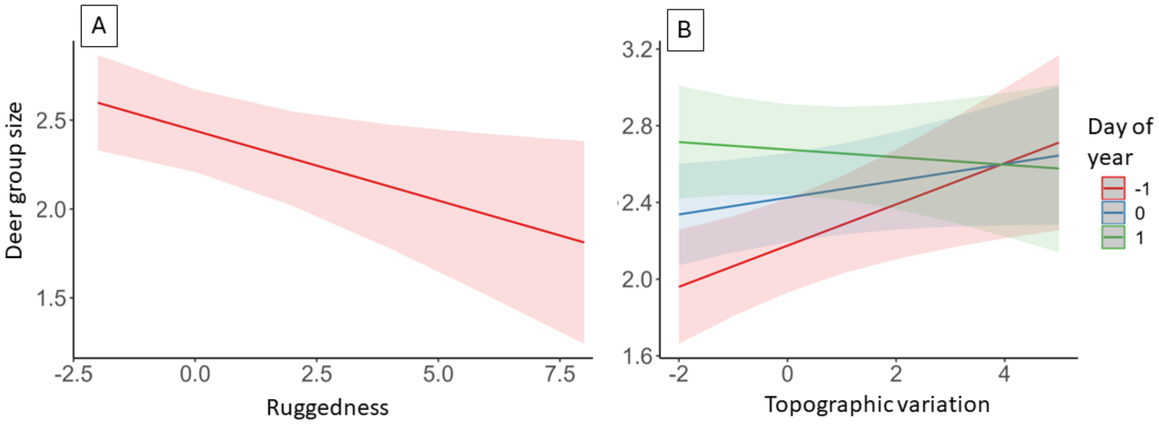

Figure A.4.4. The effect of ruggedness on deer group size (A), and the interacting effect of topographic variation and day of year on deer group size (B).

Appendix 4.5. Figures of significant effects on deer group size 2

Group size increased with increasing elevation (Figure A.4.5.A) and temperature (Figure A.4.5.B), and decreased towards dawn and dusk (Figure A.4.5.C).

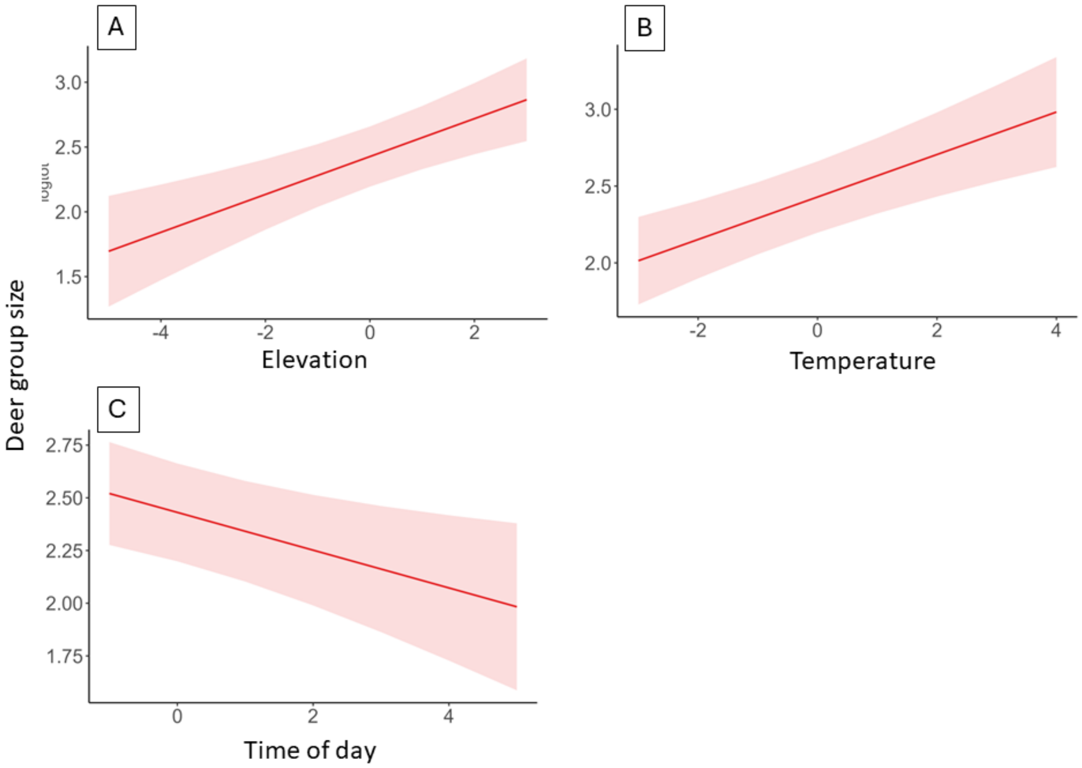

Figure A.4.5. The effects of A) elevation, B) temperature, and C) time of day on deer group size.

Appendix 4.6 Figures of significant effects on deer group aggregation 1

Deer were more likely to be highly aggregated at low elevations compared to high (Figure A.4.6A). Large groups were more likely to be dispersed, and small groups were more likely to be highly aggregated (Figure A.4.6B). Small groups showed the least variation in degree of aggregation, and as groups got larger the confidence interval was wider.

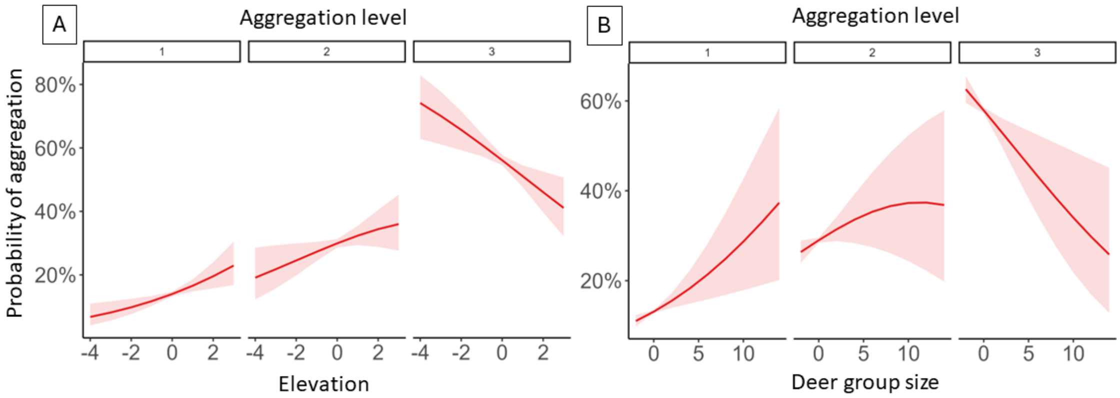

Figure A.4.6. Effects of A) elevation, and B) deer group size on probability of deer being either dispersed (aggregation level 1) to highly aggregated (aggregation level 3).

Appendix 4.7 Figures of significant effects on deer group aggregation 2

Group behaviour was generalised as settled or unsettled, according to whether behaviours were occurring in one place, or while travelling. Group behaviour was also considered in terms of resting versus all other behaviours. Higher probabilities of being aggregated were associated with deer groups displaying unsettled behaviour (Figure A.4.7A) and deer groups where the dominant behaviour was resting (Figure A.4.7B). Deer groups that were either resting, grazing, or both resting and grazing were more likely to be dispersed. However, when the behaviours were categorised as resting or not, deer were more likely to be dispersed when resting was not representative of the majority of the group.

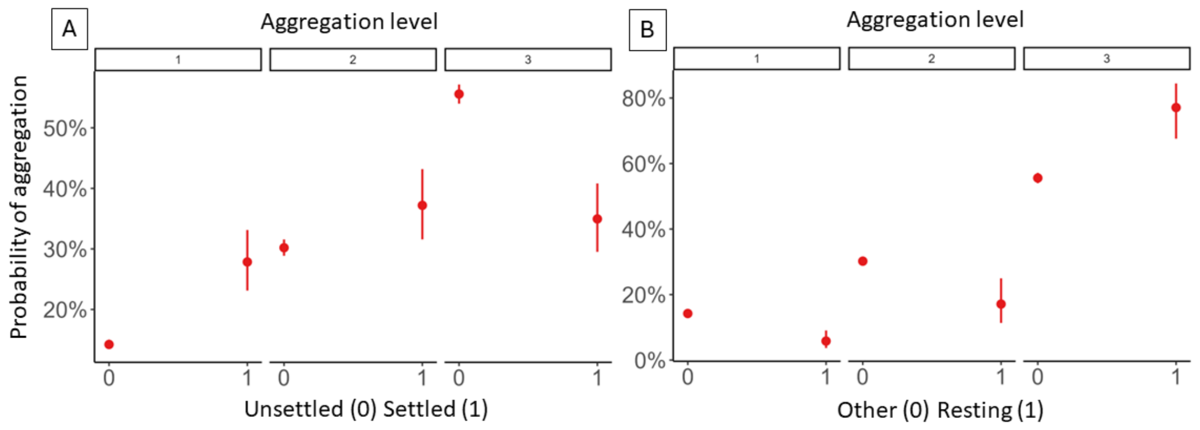

Figure A.4.7. Probability of degree of deer aggregation during behaviours A) settled, where 0 represents unsettled behaviours (moving, moving + grazing, running, alert) and 1 represents settled behaviours (resting, resting + grazing and grazing), and B) resting, where 0 represents all observations where resting was not the majority group behaviour, and 1 represents observations where the majority of the deer were resting.

Appendix 4.8 Figures of significant effects on deer group size aggregation 2

Weather affected the degree of aggregation in deer groups. Probability of deer being highly aggregated was notably greater when there was more rain (Figure A.4.8A), and increased slightly as amount of sun increased (Figure A.4.8B).

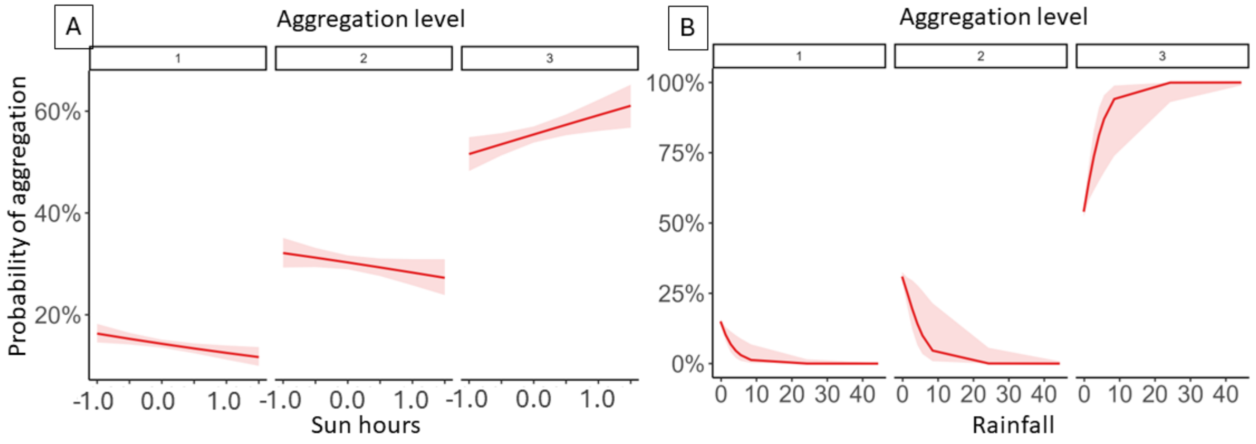

Figure A.4.8. The effects of A) sun hours, and B) rainfall (as sum amount of rain) on the probability of deer being either dispersed (aggregation level 1) to highly aggregated (aggregation level 3).

Appendix: Chapter 5

A5.1 Deer darting capture protocol

DARTING

- Avoid darting in windy conditions, never in strong wind or a gust
- Use rangefinder to get distance, recommended max 30m shot
- Load pre-prepared dart
- Set pressure on dart gun according to chart
- Aim for the large muscle in the thigh
- Make sure target is still, preferably standing side on to avoid hitting at an angle and the dart bouncing out.
- Have second dart available if needed, but preferable to just leave the deer if first dose insufficient (so long as dart comes back out)

APPROACH

- Wait until deer is lying down – normally 6-8 minutes after darting. Then wait for additional few minutes. If in doubt, wait until confident fully anaesthetised (up to 15 minutes)
- Monitor as soon as can see her breathing
- Approach quietly from behind
- First touch light contact on hindquarters to ensure fully anaesthetised

AT THE DEER

- Put on blindfold
- ABC and assess depth of anaesthetic (simultaneaously with 3 people)
- Re-position (sternal recumbency)
- Can rest head on someone’s backpack to ensure flow of saliva (ears higher than heart and nose pointing down)
- Cotton wool in ears
- Remove dart and check for damage (check that there’s no drug left/fully depressurised before removing)
- Wound spray
- Replace safety cap on dart and put away
- Monitoring vitals (to be done periodically throughout)
- Breathing: breaths per min and pattern (aim minimum every 5 mins for vitals)
- Heart rate/pulse
- Temperature: should be between 38.5^{o}C and 39.5^{o}C (40.5 is hyperthermia)
- Record time of measurement and values on monitoring chart
- Tagging
- Locate space for tag in **left** ear, between the two veins, by feeling with fingers
- Place tag with pointy part on outside of the ear and squeeze firmly to lock in tag.
- Repeat on right ear for Do Not Eat tag, low down with tag fold close to ear edge.
- Record tag ear and colour + any other tag markings
- Fitting collar
- Remove fitting hardware and place collar around neck

- Adjust to correct size, ensuring fit is a comfortable 2-fingers (not tight) gap at location indicated by collar-fitting guide (mid-neck)
- Replace fitting hardware loosely
- Keeping belt against the battery pack (as if tightened), move collar and settle into locations as much as possible to confirm fit
- Tighten bolts (tight)
- Remove magnet from drop-off
- Remove magnet from battery pack
- Check VHF beacon (if have receiver)
- Blood sampling (only attempt if sedation is good – needs to be done before fitting collar)
- Pull rubber cover off vacutainer needle, screw into holder and get tubes ready
- Turn neck around to the right so neck ~90 degrees (exposing the left side of the neck)
- Place thumb/fingers in jugular groove a base of the neck to raise the vein
- Tap or feel above thumb to feel the blood moving, redo if need to feel the difference.
- When confident you can feel the vein, insert needle into vein and up a bit at an angle with one positive movement (to avoid making the vein wobble and losing it).
- If successful, there will be blood.
- Do not let the needle slip out, so hold in place with the same hand that the needle was inserted with (right if right-handed). Keep this hand pressed against the deer's neck throughout.
- Starting with the red-top, push tubes into holder until it clicks (push against hand not deer's neck)
- Let blood come into vacutainer tubes until it stops (line on Silvia's, ~6ml on purple and red-tops).
- May need to raise the vein again to make sure enough blood flows.
- Mix the RNA and purple top tubes immediately by turning over and back ~10x
- (Back-up method use 19G 1" needle and 20ml syringe – purple and red-top only)

LEAVING THE DEER

- Magnets off collar check
- Kit packed
- Photograph collar and ears (if not already done and if there's time)
- Position deer so pointing towards a safe exit route (preferably with people between deer and any potential hazards, facing uphill)
- Cotton wool out
- Blindfold off but hold in place
- Administer reversal (3ml atipamezole IM)
- Hold head up until deer is coming around – indicated by starting to fight being held, showing resistance, stopping snaking their head
- Leave vicinity quickly and quietly

POST-REVIVAL

- Observe deer until back on its feet
- Take notes on recovery and timings
- Fill in any blanks on datasheet

A5.2 Replacement, Reduction, Refinement

Replacement

The specific focus of the research is on the red deer in its natural habitat. It would not be meaningful to substitute it with another species. Direct observation, pellet group (dung) surveys to indicate space use, camera trapping are possible alternatives to animal use. However, this project will investigate deer movement and behaviour in time and space. An equal focus on temporal variation in movements means that typical spatial distribution methods, such as pellet surveys, are insufficient. Given our interest in direct, short-term responses to mobile stimuli, as well as the spatial scale over which we are working, camera trapping also has limited value. Alternatives such as direct observations are limited by observer bias, difficulty in tracking multiple animals over large distances, potential influence of observer presence on the deer, and the amount of time required. By using GPS collars, the project limits interaction with the deer to a short capture operation, whilst maximising data quality and quantity to build a comprehensive response to our research questions.

Reduction

We have been guided by precedents among published studies employing the same techniques, and by our calculations of the number of animals needed to supply enough data to answer our research questions robustly. We are focusing on a specific demographic group (females of breeding age) to minimise unwanted variation between subjects, thereby minimising required sample sizes. We are also using collars made by a reputable company and the model is well tested in the field. Prior to deployment, all collars will be rigorously tested to ensure working condition. Data obtained from the collared animals will be maximised by supplementing it with data from additional sources (including pellet group surveys, direct observations, camera trapping and vegetation surveys) to complement GPS and behavioural data from the collars. All functions of the collars will be utilised, including the built-in accelerometer that indicates activity levels and head position, and the VHF beacon for relocations in the field. The GPS data, themselves, will provide multiple data analysis options to answer the research questions. For example, GPS locations can provide information on temporal distributions, in addition to a subset of the locations being used to determine habitat selection. GPS and activity data can also be combined to look at activity in response to specific disturbance events. Taken together, these features of the collars mean that we will need to collar fewer animals to gather large quantities of data to provide a robust answer to our research questions.

Additional measures include the use of data from related studies, that allow us to run computer simulations to bolster our confidence that the number of animals used will be adequate.

Refinement

Red deer have been chosen for this study because they are the only relevant species in the context of the research question, with alternatives such as domestic ungulates or farmed deer unsuitable. Red deer, and other wild deer species, are commonly and successfully used in similar research projects involving capture and fitting GPS collars.

Methods for capture have been developed with veterinary advice to ensure they are the most refined for the purpose, including anaesthesia with recommended drug doses and combinations. A number of further steps will be taken to minimise animal suffering and stress during the capture procedure and immediately thereafter, and for the duration of collar deployment (which will not exceed 12 months).

The protocol will be conducted by vets and will only be conducted by other suitably qualified personnel if the vets are satisfied of their competency by repeat performance under supervision.

Capture and collaring will take place in winter. Collaring in winter reduces the risk of heat stress in anaesthetised deer, whilst doing so before the latter stages of the winter period ensures that animals are not in poor condition as a result of prolonged exposure to low food availability and low temperatures, and further avoids the risk of compromising the welfare of females during advanced stages of gestation.

The primary method of capture is to use a dart gun to administer the anaesthetic to an unconfined animal. Veterinary advice is that, to ensure that enough animals can be captured, it is possible that clover traps could be used to confine the deer for a short amount of time. If confinement is deemed necessary, it will be limited to 12 hours, during which time the deer will not suffer from dehydration and appropriate feed will be available. If remote darting is not practical, anaesthetic will be administered intramuscularly to an animal once safely restrained.

During the capture, every effort will be made to minimise stress to the deer. The deer will first be approached from behind whilst watching for eye, ear and head movements that can signal consciousness. First contact with the deer will be a light touch to the hind quarters so that the response can be safely observed, and a blindfold will be put on over the deer’s eyes to minimise external stimuli. The dart wound will be treated prior to the commencement of other procedures. To reduce likelihood of injury on releasing the deer, all persons will move away from the deer, allowing the deer an obvious escape route, clear from obstacles, and in the direction the deer is facing.

The use of automated drop-off mechanisms on the collars ensures that the collars can be collected using the VHF beacon without the need for recapture of the study animals.

A5.3. Proportions of vigilant deer from hill scans

Table A.5.3 The mean percentage of deer vigilant during group scan sampling of hill deer overall, on days when the number of hillwalkers was below average (quiet days), and on days when the number of hillwalkers was equal to or above average (busy days).

	Percentage of vigilant deer
All observations	47.4%
Quiet days	44.6%
Busy days	51.6%

A5.4. Collared deer vigilance model

Table. A.5.4 Results of binomial GLM. Estimate, standard error and z value, and associated significance.

	Estimate	Std. Error	z value	*P*-value
(Intercept)	1.7670	0.0317	55.8410	<0.001 ***
Dynamic body acceleration	-68.7800	0.3243	-212.0750	<0.001 ***
Month2	0.1910	0.0258	7.4170	<0.001 ***
Month3	0.1999	0.0244	8.1980	<0.001 ***
Month4	0.2886	0.0801	3.6040	<0.001 ***
Month5	0.1605	0.0219	7.3320	<0.001 ***
Month6	0.1102	0.0221	4.9840	<0.001 ***
Month7	-0.3445	0.0247	-13.9750	<0.001 ***
Month8	0.0142	0.0262	0.5430	0.587223
Month9	0.3089	0.0269	11.5010	<0.001 ***
Month10	0.7908	0.0261	30.3460	<0.001 ***
Month11	0.6625	0.0268	24.7370	<0.001 ***
Month12	0.4410	0.0206	21.3970	<0.001 ***
Distance to woodland	-0.0023	0.0001	-27.7040	<0.001 ***
Distance to buildings	-0.0017	0.0001	-22.7290	<0.001 ***
Time period_night	-1.6120	0.0208	-77.6160	<0.001 ***
Time_period_dawn/dusk	-0.7307	0.0266	-27.5050	<0.001 ***
Distance to roads	0.0011	0.0001	16.7410	<0.001 ***
Distance to buildings x Time period_night	0.0020	0.0001	39.1310	<0.001 ***
Distance to buildings x Time period_dawn/dusk	0.0013	0.0001	20.4980	<0.001 ***