LANDSCAPE EFFECTS OF DEER CONTROL IN ALPINE AUSTRALIA

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STATEMENT OF ORIGINALITY

I certify that the intellectual content of this thesis is the product of my own work, and that all assistance received in preparing this thesis and all sources have been acknowledged.

Eliane McCarthy, 30th June 2025

AUTHOR ATTRIBUTION STATEMENT

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Chapter 6 is being prepared for submission to an international peer-reviewed journal with co-authors Thomas Newsome, Kittikun Chris Songsomboon and Catherine E. Grueber. I co-designed the study with all other co-authors, analysed the data, and wrote the manuscript in collaboration with my co-authors.

Eliane McCarthy, 30th June 2025

ATTESTING AUTHORSHIP ATTRIBUTION STATEMENT

As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statements above are correct.

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ARTIFICIAL INTELLIGENCE STATEMENT

No content produced by generative AI tools has been used in the preparation of this thesis.

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PREFACE

This thesis is presented as a series of stand-alone manuscripts, that have been either published, in review with peer-reviewed journals or are awaiting submission for publication. Therefore, there is some unavoidable repetition between the chapters, and minor variation in the formatting and referencing styles of each chapter.

I am the primary author of all chapters included in this thesis. I have acknowledged the contribution of co-authors by listing their names at the beginning of each chapter and by using the plural “we” when referring to collaborative work. For the Introduction and Discussion, I use the singular “I” as I am the sole author of these chapters.

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This research was funded by a scholarship provided by the NSW NPWS, without which I would not have been able to complete my PhD. I also received support from the Ecological Society of Australia Holsworth Wildlife Research Endowment (2022, 2023, 2024) supporting conference attendance in Australia and overseas, fieldwork expenses and sequencing. This research was also supported by the Conservation and Wildlife Research Trust (2022) funding carcass monitoring equipment, and The University of Sydney's Postgraduate Research Support Scheme (2021, 2022, 2023), which contributed to covering the cost of fieldwork equipment and travel expenses.

TABLE OF CONTENTS

THESIS ABSTRACT

Invasive species pose a threat to biodiversity globally; and understanding their behaviour and ecology aids in developing strategies to reduce their impacts. Deer were first introduced to Australia in the mid-1800's by acclimatisation societies which sought to make Australia's fauna more like that of the Northern Hemisphere, and to distribute animals for recreation and hunting. Today, Australia's invasive deer occupy a wide range of habitats from arid woodlands to temperature and tropical rainforests. Deer are well understood to prevent bushland regeneration, alter forest composition, and have been associated with an increase in the invasive plant species.

The Australian Alps bioregion is in southeastern Australia, covering 11,000 km^2 across New South Wales (NSW), the Australian Capital Territory (ACT) and Victoria, and comprises just 0.15% of the continent, including Kosciuszko National Park. Invasive fallow deer (*Dama dama*), sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*) threaten the Australian Alps through grazing and browsing, compaction of soil and degradation of waterways, and exacerbate damage and prevent recovery in burnt areas regenerating after fire. Aerial culling from a helicopter is considered the most efficient and humane method for controlling deer over large areas, particularly in areas that are remote or with rough terrain and is commonly used to control large herbivores in the Australian Alps. My PhD project leveraged a 6-year program (2019–2025) led by NSW National Parks and Wildlife Service (NPWS) aimed at controlling deer, within a 284 km^2 study area in Kosciuszko National Park and surrounding private lands. In this PhD, I gathered data to test hypotheses around the movement and habitat preferences of fallow deer, sambar deer and red deer, the effectiveness of control efforts, the behavioural and genetic responses of deer to culling, and the effects of landscape-scale culling on vertebrate scavengers.

Fallow deer, sambar deer and red deer were captured and collared to track their movement for a period of up to two years. In **Chapter 2**, I critically evaluated the development and assessment of a method combining aerial net gunning and chemical immobilisation delivered via hand injection to capture 14 sambar deer and five red deer in two operations in Kosciuszko National Park. Captured animals were fitted with GPS collars to track their movements and activity post-capture, and I used physiological measurements to optimize animal welfare outcomes. Mortality rates were reduced between the first and second operations, likely due to a reduction of pursuit times. Activity of collared deer was lowest immediately following collaring. Overall, the method was shown to be safe and effective for capturing

sambar deer and red deer and can be used by wildlife researchers to collect spatial ecology and survival information about these species.

In **Chapter 3**, I then used the tracking data from sambar deer and red deer collared in Chapter 2, as well as similarly generated data from fallow deer, to answer questions about the three species' seasonal movement and habitat preferences in alpine and subalpine southeastern Australia. Unexpectedly, movement analyses revealed that these species had larger home ranges than conspecifics in their native ranges. I found that all three species have differentiable habitat preferences, with fallow deer spending more time in and preferentially selecting for cleared areas. All species tended to inhabit higher elevations in summer, and lower elevations in winter. I found that while fallow deer and red deer did not use burnt areas, sambar deer showed a preference for areas burnt with low to moderate and high severity in autumn and spring. I show how these patterns should be used to inform species-specific control and conservation measures, for example, burnt areas should be targeted for sambar deer control in the years after fires.

In **Chapter 4**, the focus of this thesis shifted to answering questions about how the deer population responded to the landscape-scale aerial culling effort that took place to reduce the deer population in this region in 2022 and 2023. Density estimates derived from aerial thermal surveys and relative abundance indices for the three deer species indicated that despite long term extensive culling efforts, the deer population within the region did not decrease. I investigated how fallow deer responded behaviourally to aerial control efforts, as there is uncertainty about how target species respond to the stimuli created such as the sight and sound of the helicopter, the sound of gun shots, and the disturbance related to conspecifics being shot in proximity. I used two remote camera arrays to monitor fallow deer temporal activity patterns, grouping, and movement speed before and after aerial control. I found that aerial culling was not linked to changes in grouping behaviour and movement speed, however, it was linked to decreased daytime activity and increased dusk and nighttime activity. This suggests that deer were shifting their diel activity patterns towards nocturnality during aerial culling, potentially reducing their detectability during daytime culling operations, and reducing the effectiveness of control efforts.

Post-cull, deer carcasses are left in-situ until they degrade, and in **Chapter 5**, I tested how scavengers responded to large carcass loads by monitoring carcasses post-cull. In some systems, invasive scavengers monopolise carcass resources, but native apex scavengers can also restrict the use of carcasses by rapid consumption of carcass biomass and competitive exclusion. I examined how invasive red fox (*Vulpes vulpes*) and dingo (*Canis dingo*) utilisation of carcasses varied with season and carcass species using remote camera observation on single carcasses. I also tested whether carcass density affected broader scavenger occurrence in the subalpine region of the study area using camera array data. I found that foxes scavenged on carcasses year-round, while dingoes scavenged in warmer periods. The probability of fox scavenging and occurrence decreased with increasing fallow deer carcass density, conversely, the probability of dingo scavenging increased with increasing sambar deer carcass density. Foxes exhibited temporal separation from dingoes in both their daily activity patterns and, to a greater extent, their carcass use, suggesting resource competition between the species. Nonetheless, neither fox nor dingo presences at carcass sites were linked to accelerated carcass biomass loss. Instead, biomass loss was most likely driven by warmer temperatures. The results of this study indicated that landscape-scale culling operations can impact scavenger behaviour in varied ways, and the timing of these culls affects carcass persistence time, which should be considered when planning culling operations.

In **Chapter 6**, I used population genetic analyses to test the hypothesis suggested in Chapter 4, that following the initial removal of animals from aerial culling, deer repopulated the study area from neighbouring areas, preventing sustained reductions in population size. I sampled fallow deer in the study area for two years before and two years after culling, I also sampled fallow deer throughout southeastern Australia to contextualise my findings from the study area, and used population genetic analyses, as well as movement data from collared deer, to test how deer responded to the control effort. Despite population structure remaining the same over four years of monitoring, there was an increase in effective population size and variance in heterozygosity of deer sampled in the second year following the onset of culling. Movement data indicated spatial connectivity between deer in the study area and external populations. Taken together, analyses of population genetic and movement data suggest that deer from surrounding areas were moving into the study area following culling. Although we were unable to confirm this, because deer sampled across the broader landscape surrounding the study area were not substantially genetically differentiated. On a broader scale, relatedness between populations in southeastern Australia did not align consistently with genetic separation, and some individuals separated by large distances were closely related, indicating that human-mediated dispersal may be occurring. Our findings emphasize the need to consider population connectivity and species dispersal potential when determining the appropriate scale of population control regimes.

This project found that invasive deer exhibit species-specific movement and habitat preferences, behaving differently compared to conspecifics in their native ranges, and deer and scavengers exhibit short and long term responses to aerial control. Combining movement and genetic data, the findings of this thesis clearly demonstrate that deer readily move between public and private lands, underscoring the importance of coordinated control across these areas. The findings from deer movement and scavenging data support the recommendation that management should target higher altitude subalpine regions in warmer seasons, as deer are more likely to be present in these areas in warmer periods, and carcass biomass loss is driven by warmer temperatures. Findings from genetic and movement studies indicated that the control area was not large enough to reflect the population connectivity of deer in the region, and future control efforts should evaluate the movement potential and genetic connectivity of the target species prior to control to prevent reinvasion following control. This PhD provides critical information for prioritising areas for control, optimising control efforts, and elucidates the effects of landscape-scale aerial culling on surviving deer, and the wider ecosystem.

Chapter 1: General introduction – background, research priorities and thesis aims

1.1 Invasive species management

Invasive species pose a threat to ecosystem health and diversity and understanding their ecology is imperative to reducing their impacts (Dueñas et al., 2021). Globally, invasive species are the second most common threat associated with species extinctions, behind biological resource use, and the most common threat contributing to vertebrate species extinctions since AD 1500 (Bellard et al., 2016). Aside from direct competition, invasive species are associated with reduced fitness of native species (Carmo et al., 2018; Nunes et al., 2019) and can exert competitive pressure on functionally similar native species (Brown et al., 2002). Additionally, biodiversity loss occurring as a result of invasive species competition can impact ecosystem functioning (Linders et al., 2019). Invasive species are also a key threat to agricultural productivity and food security globally (Paini et al., 2016). Critically, threats from invasive species and climate change are compounded, and interactions between these threats may exacerbate the impact of invasive species (Mainka & Howard, 2010).

Numerous lethal and non-lethal control methods exist for locally reducing population size or eradicating invasive species. The most common conventionally used lethal methods for vertebrate invasive species control are ground or aerial shooting, trapping and baiting (Doherty & Ritchie, 2017). Fencing is also a commonly used non-lethal method for preventing invasive species incursions (Smith et al., 2020). However, establishing effective invasive species control and management strategies, and maintaining the social and financial support needed for these efforts, can be challenging. Uncertainty about the parameters essential for informing management decisions, such as the initial range or abundance of the target species, generates uncertainty in forecasting or quantifying the success of control efforts (Ward et al., 2020). Additionally post-control, it is largely unknown how ecosystems may respond to the removal of invasive species, and so management strategies often adjust in response to unintended and undesirable secondary effects (Kopf et al., 2017; Prentice et al., 2019). Effective management requires collective effort and contribution across all affected areas, and in many cases, collaboration between private and public landowners (Epanchin-Niell et al., 2010). However, social perceptions around the control of invasive species vary widely, with some species garnering cultural approval and significance, disagreements surrounding the ecological impacts of a species, and welfare concerns over management strategies

(Crowley et al., 2017). Therefore, establishing and maintaining effective invasive species management strategies is fraught with complexities.

1.2 Invasive species in Australia

Australia has a long history of introductions of invasive species, stemming as far back as the introduction of the dingo (*Canis dingo*), 5–10 thousand years ago (Smith et al., 2019). However, recent species invasions, occurring since European invasion in the late 18th century, have been especially detrimental to Australia's native flora and fauna (Brown & Sax, 2004; Woinarski et al., 2015). Australia's vertebrate species are the most evolutionarily unique in the world (Holt et al., 2013). The continent's species endemism is high, with 87% of mammals, 93% reptiles, 94% of frogs and 45% of birds only occurring in Australia (Chapman, 2009). In Australia, 97 endemic species have been formally recognised as extinct since European colonisation in 1788, with the primary causes of these extinctions being habitat loss and invasive species (Woinarski et al., 2019). Invasive species management and mitigation is also a significant expense to the Australian economy (Bradshaw et al., 2021; Hoffmann & Broadhurst, 2016). Costs associated with the damage caused by invasives and their management have increased since 1970, and Australia's rate of cost increase is up to twice as high as the rate of increase globally (Bradshaw et al., 2021; Diagne et al., 2021).

1.2.1 The case of invasive deer in Australia

Deer were first introduced to Australia in the mid-1800's by acclimatisation societies, which sought to make Australia's fauna more similar to that of the Northern Hemisphere, and to distribute animals for recreation and hunting (Bentley, 1957; Rolls, 1984). Since then, continued deliberate and accidental release of deer from farms, or into natural areas for hunting, has contributed to the current population (Moriarty, 2004). Early accounts of deer management in Australia report that historically, little was done to manage or control invasive deer species (Bentley, 1957). Although 18 deer species were introduced to Australia (Van Dyck & Strahan, 2008), six are now established, and together they occupy all Australian states (Figure 1.1) and a range of ecosystems across the Australian landscape (Government of South Australia, 2023). Importantly, there is a scarcity of current research on invasive deer in Australia (Davis et al., 2016; Government of South Australia, 2023). The limited understanding of deer ecology restricts the ability of government agencies to develop effective management practices. As a consequence, developing an understanding of the abundance, movement ecology and rate of increase of deer populations inhabiting conservation areas has been identified as a research priority in Australia (Davis et al., 2016).

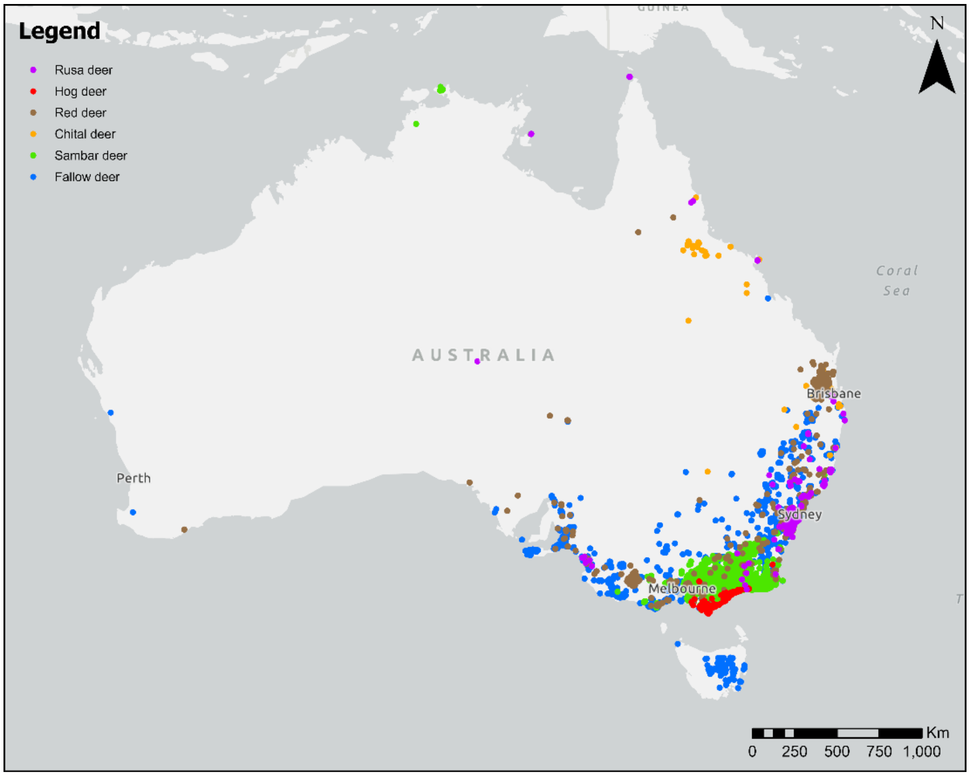

Figure 1.1: Occurrence of six invasive deer species across the Australian continent. Records from Atlas of Living Australia, downloaded 14th of March 2025 (*Atlas of Living Australia Occurrence Download*, 2025 a–f).

Internationally, deer are well understood to prevent bushland regeneration (Nugent et al., 2001; Russell et al., 2017), affect forest composition (Russell et al., 2017), and have been associated with an increase in the presence of exotic plant species (Vazquez et al., 2023). Australia's invasive deer occupy a wide range of habitats from arid woodlands to temperature and tropical rainforests (Davis et al., 2016). Anecdotal evidence suggests that deer have a negative impact on Australia's native flora and fauna, however, the full extent of their effects is unknown (Claridge, 2016). Recent Australian research on deer effects has shown that deer presence is associated with decreases in understorey cover (Wills et al., 2023), in particular, sambar deer (*Rusa unicolor*) browsing on tree ferns could decrease growth, survival and recruitment rates of the flora (Bennett, 2023). Importantly, reductions in numbers of invasive deer have been linked to improved environmental health and water quality (Comte et al., 2023). Invasive deer species also threaten Australia's agricultural industry via competition and disease spread (Cripps et al., 2019; Davis et al., 2008). Without intervention, Australia's feral deer population, having few known native predators (Davis et al., 2015), will continue to increase in geographic distribution and total population size (Burgin et al., 2015; Gormley et al., 2011; Moriarty, 2004). Invasive deer populations can grow rapidly in numbers (Cunningham et al., 2022). For example, predictive modelling of Tasmania's fallow deer (*Dama dama*) population has shown that the state's population could grow in range and number of individuals, from 30,000 in 2015 to approximately 1 million by the mid-21st century (Potts et al., 2015). Two country-wide estimates of the deer population suggest that the population has grown from 200,000 in 2004, to 1–2 million in 2022 (Government of South Australia, 2023; Moriarty, 2004).

The recently devised National Feral Deer Action Plan aims to stop the spread of and reduce the impact of large deer populations, control small populations, and protect threatened species, ecological communities and cultural assets from impact (Government of South Australia, 2023). To achieve this, the current control tools available to land managers are aerial and ground culling, trapping, baiting and exclusion fences (Davis et al., 2016; Hampton et al., 2019). Aerial culling from a helicopter is considered the most efficient and humane method for controlling deer over large areas, particularly in areas that are remote or with rough terrain (Bengsen et al., 2022; Bradshaw et al., 2023; Forsyth et al., 2013; Pulsford et al., 2022). Moreover, detection and culling rates from aerial shooting have been shown to increase substantially when aerial shooters are assisted by thermal imaging technology (Cox et al., 2023). Recreational ground shooting by hunters also occurs in many parts of Australia, however, there is a lack of evidence to support the idea that current recreational shooting regimes are effective at reducing deer populations (Bengsen & Sparkes, 2016; Comte et al., 2025). In any case, extensive and long-term control operations are required for lasting reductions in deer populations. For fallow deer, population modelling has indicated that to curb population growth, 35% of the total population (Hone et al., 2010), or 25% of the female population (Botterill-James et al., 2024) should be removed annually. Moreover, control may be more effective when deer populations are already low, for example, during a drought, when adult recruitment and survival is low (e.g., Pople et al., 2023). Previously, deer have been eradicated from Kangaroo Island (4,400 km^2) through aerial shooting (Masters et al., 2018), however eradication on the Australian mainland, over a larger geographic area and with open populations, would be more expensive and logistically complex. Therefore, current management is largely focused on controlling the spread and reducing the impacts of deer (Government of South Australia, 2023).

1.3 PhD project overview

My PhD project extended from a 6-year program (2019–2025) led by NSW National Parks and Wildlife Service (NPWS) aimed at controlling deer within Kosciuszko National Park and surrounding private lands. The wider project was funded by the NSW Environment Trust, and aimed to reduce the deer population within the study area by 70% and sustain this low population through regular control operations. In February 2022, the project commenced aerial culling operations, with the aim of reducing the population by 70% in the first year (phase 1), so that the project could monitor the effects of a severely lowered deer population for the remainder of the project (phase 2). The density of deer in the study area immediately before the onset of phase 1 was 16.4 (10.1–26.5) or an abundance of 4,652 (2,877–7,521) (values in parentheses are ± 95% confidence intervals) (Cox, 2024). In addition to controlling the deer population, NPWS aimed to develop a series of science-based recommendations for the effective control of deer throughout Australia (NSW Department of Planning Industry and Environment, 2021). My PhD project supported this work by providing an investigation into deer ecology within Alpine Australia and critically evaluating the effect of deer control on their movement, behaviour, and genetics, as well as on other animals in the broader landscape, via contemporary scientific methods and seated in perspectives from a global literature.

The Cross Tenure Feral Deer Management Project facilitated the collection of extensive monitoring datasets. I contributed to fieldwork led by the project team in which we collared and tracked 20 fallow deer, 5 red deer (*Cervus elaphus*), and 14 sambar deer for a period of up to ~2.5 years. Between 2020 and 2024, data was collected on deer density and overall species abundance from aerial thermal surveys and two remote camera arrays within the study area. Additionally, I facilitated the installation of remote cameras to directly monitor scavengers on fallow deer and sambar deer carcasses as they decomposed. Lastly, I led field teams to collect tissue samples for population genetic analysis from fallow deer and sambar deer within the study area between 2021 and 2023. I also facilitated the collection of tissue samples obtained by landholders and other government agencies between 2019 and 2023.

1.4 The study area

This study took place across a 284 km^2 study area (Figures 1.2 & 1.3). The western half of the study area forms part of the southern end of Kosciuszko National Park. Kosciuszko National Park's alpine and subalpine region is the largest in Australia (Sanecki et al., 2006), extending altitudinally from approximately 1,400 m to Australia's highest peak, Mount Kosciuszko, at 2,228 m (Green & Osborne, 2012). Continuous snow cover for at least one month of the year occurs within the subalpine zone of the study area (1,350–1,750 m ASL), while the alpine zone (above 1,750 m), is mostly above the tree line, and typically experiences continuous snow cover for at least four months of the year (MacPhee & Wilks, 2013). The study area lowers in elevation moving from west to east, and transitions into cleared pastural farmland in the eastern half, which is interspersed with patches of remnant native vegetation, and small residential areas (Department of Climate Change, Energy, the Environment and Water, 2021). Native vegetation in the study area is dominated by Eucalypt (*Eucalyptus* spp.) woodland across elevations, and alpine freshwater bogs with tussock grasslands of prickly snow grass (*Poa costiniana*) and mountain gentian (*Gentianella diemensis*) (Department of Environment and Climate Change NSW, 2007).

Figure 1.2: Map showing the location of the Cross Tenure Feral Deer Management Project study area (red point), inset map shows the extent of the study area (indicated by red boundary).

The Australian Alps are inhabited by a multitude of threatened species and ecological communities, among them, the Critically Endangered mountain pygmy-possum (*Burramys parvus*) and corroboree frog (*Pseudophryne corroboree*) (IUCN SSC Amphibian Specialist Group, 2022). Species in the region are threatened by introduced predators, including red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), which are abundant throughout the region and known to prey on native and introduced species, contributing to native species declines (Green, 2002; Woinarski et al., 2015). The region is also vulnerable to trampling and herbivory by introduced ungulate and small mammal species, including, feral horses (*Equus caballus*), three deer species (fallow, sambar, and red deer), rabbits (*Oryctolagus cuniculus*) and brown hares (*Lepus europaeus*) (Driscoll et al., 2019; Hartley et al., 2021; Wilson et al., 2022). Increases in these introduced species are associated with lower vegetation height and foliage density, higher soil compaction and bare ground cover, which have been linked to decreases in native small mammal abundance (Hartley et al., 2021; Schulz et al., 2019).

The NSW Threatened Species Scientific Committee listed herbivory and environmental degradation caused by feral deer as a key threatening process adversely affecting threatened species and ecological communities (NSW Department of Planning Industry and Environment, 2019). For example, alpine sphagnum bogs and associated fens are characteristic of the higher altitude areas of the Australian Alps and are listed as an Endangered ecological community (Department of the Environment, 2015). Deer wallowing in bogs and fens causes damage to this slow growing ecological community (Claridge, 2016), and has been shown to reduce the water quality of nearby catchments (McDowell, 2007). Deer in alpine regions are also known to cause damage via browsing, thrashing and rubbing of plants (Claridge, 2016).

Figure 1.3: Examples of landscapes and vegetation communities present in the study area, within Kosciuszko National Park, and on a private farm with remnant bushland (bottom right image).

1.5 Deer species in the study area

1.5.1 Fallow deer

Fallow deer are a medium sized deer species with variable coat colour (Figure 1.4). The species is widespread throughout Europe, and although they are thought to have been introduced across Europe from Türkiye in ancient times, their original native range and timings of introductions are unclear (Esattore et al., 2022). They are listed as a species of Least Concern on the IUCN Red List (Masseti &

Mertzanidou, 2007). In modern times, the species has been introduced to Australia, Africa, Asia, and America (De Marinis et al., 2022). In Australia, bioclimatic modelling suggests that fallow deer are well suited to Southern Australia, this suitability extends further inland on the southeastern and southwestern sides of the country (Davis et al., 2016). The present distribution of fallow deer extends across southeastern to eastern Australia and Tasmania, as well as southwestern Australia (Figure 1.1).

Figure 1.4: Two examples of female fallow deer, showing coat colour variation in the species. Images adapted from camera trap array imagery.

1.5.2 Sambar deer

Sambar deer are a large deer species (Figure 1.5), typically present in tropical regions. The species is native to Bangladesh, Bhutan, Brunei, Cambodia, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, southern China, Sri Lanka, Taiwan, Thailand, and Vietnam (Timmins et al., 2015). In 2014, sambar deer were listed as Vulnerable to extinction on the IUCN Red List, due to continual declines in sambar abundance and habitat (Timmins et al., 2015). Sambar deer are invasive in Australia, New Zealand, South Africa and the United States (Timmins et al., 2015). The first recorded introduction of sambar deer to Australia was in Tooradin, Victoria, in 1868, and sambar deer in Australia are believed to originate from Sri Lanka (Bentley, 1978). Bioclimatic analysis predicts that sambar deer are most suited to the environment of northern Australia, with the species progressively less likely to occur in areas of central and then southern Australia (Davis et al., 2016). Despite this, today, sambar deer occur throughout central and eastern Victoria, southern NSW, the Australian Capital Territory, and the Coburg peninsula in the Northern Territory (Figure 1.1; Moriarty, 2004).

1.5.3 Red deer

Red deer (*Cervus elaphus*) are a large deer species with a reddish-brown coat (Figure 1.5). The species is widespread throughout Europe and listed as Least Concern on the IUCN Red List (Lovari et al., 2018). Red deer are invasive in Australia, New Zealand and parts of South America (Lovari et al., 2018). Bioclimatic modelling suggests that red deer are well suited to much of the Australian continent, with the highest suitability for parts of central Australia, and much of Southern Australia (Davis et al., 2016). Red deer are present in southeastern to eastern Australia, with sparser occurrences in central and southwestern Australia (Figure 1.1).

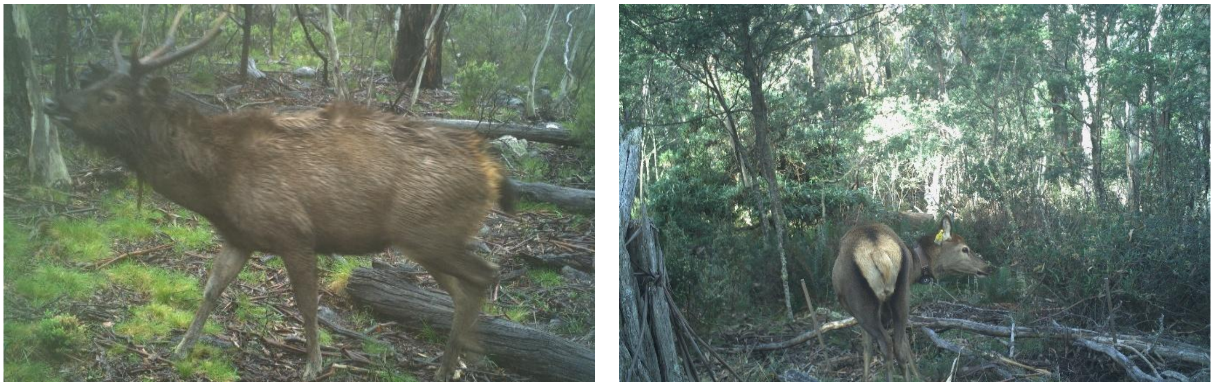

Figure 1.5: A mature male sambar deer (left), and an adult female red deer fitted with a GPS collar and ear tag (right). Images adapted from camera trap array imagery.

1.6 Research priorities

I have identified five research priorities addressed by this thesis, with the aim of expanding our current understanding of the ecology and impacts of control of invasive deer in the Australian Alps, as detailed below.

1.6.1 Deer movement and behaviour in the Australian Alps

Invasive species can exhibit unexpected characteristics in their invasive range, such as enhanced thermoregulatory ability (Kowalczyk & Zalewski, 2011) or dispersal rates (Shine, 2012). Understanding invasive species movement and habitat preferences can aid in predicting their impacts, range expansions, and in implementing effective control measures (O'Reilly-Nugent et al., 2016). For example, tracking feral goats (*Capra hircus*) in semiarid South Australia identified mallee shrubland of greater than one meter height as their preferred habitat, enabling land managers to employ additional controls at this habitat type (Moseby et al., 2021). For wild boar (*Sus scrofa*), tracking documented the first known occurrence of a long-distance dispersal of a female boar and piglets (Jerina et al., 2014). Female dispersal in that species provided a likely explanation for their high survival in fragmented habitats, indicating that management efforts should be distributed more evenly between the sexes for effective control. In the first tracking study of red deer in Australia, the species had larger home ranges at high deer densities, compared with European studies of red deer in their native range (Amos et al., 2014). Poor soil and infrequent rainfall, leading to lower resource availability, coupled with milder winters were thought to facilitate greater movement. Knowledge of feral deer movement and habitat preferences in Australia is limited, with few tracking studies examining fallow deer and red deer (e.g. Amos et al., 2014; Bengsen et al., 2024), none yet within the Australian Alps, where the unique ecosystem may be linked to unexpected deer movement. Generating an understanding of movement and habitat preferences of invasive deer in this region will allow land managers to more accurately predict their impacts and optimise control efforts.

1.6.2 Deer responses to culling

Aerial culling may be detectable by deer in the study area from the sight and sound of the helicopter and gun shots, and nearby conspecifics being shot. Humans may be referred to as a 'super predator' because of the high rate at which they kill wildlife (Darimont et al., 2015). Fear of the human super predator has been shown to outweigh fear of large carnivores (Clinchy et al., 2016), and prey species can exhibit spatial and temporal variations in behaviour because of perceived predation risk, often described as a 'dynamic landscape of fear' (Palmer et al., 2022). Therefore, understanding how a fear of culling affects animal behaviour is pertinent to culling operations, as changes in animal behaviour may affect the success of control operations or lead to undesirable management outcomes (Barton et al., 2022).

Several international studies have monitored the effect of control events on deer population dynamics and behaviour (e.g. Ikeda et al., 2019; Mysterud et al., 2020; Takeshita et al., 2017). For example, in the period during and immediately following culling activities, deer have been shown to exhibit a shift towards nocturnal activity (Ikeda et al., 2019). In another study, the majority of deer monitored during a control event were shown to leave their home ranges and move longer distances during and immediately following control events (Sunde et al., 2009). Additionally, recent Australian research focused on responses of invasive fallow deer to aerial shooting, the only known study globally on deer behavioural responses to aerial control, has shown culling induces temporary increases in movement, activity range and nocturnality (Bengsen et al., 2024). By studying changes in deer behaviour in response to extensive aerial culling operations in the study area, we can make informed recommendations for adaptive management practices that may optimise the success of control efforts.

1.6.3 Scavenger responses to culling

Introduced predators and dingoes will likely scavenge on carcasses throughout decomposition (Forsyth et al., 2014; Spencer & Newsome, 2021; Vandersteen et al., 2023). During decomposition, introduced scavengers may aid in recycling nutrients from carcasses, however this in turn supports their populations and potentially exacerbates their impacts (Newsome et al., 2021). Carcass supplementation in a desert environment has been shown to attract introduced carnivores, which scavenge on carcasses and prey on native species (Spencer et al., 2021). Similarly, provisioning carcasses in Europe has been shown to increase predator activity, whereby individuals aggregate near carcasses, in turn leading to decreased herbivore activity (Cortés-Avizanda, Carrete, et al., 2009). Importantly, carcass availability during winter, when alternative prey is limited, can stabilize and increase predator populations (Jahren et al., 2020; Needham et al., 2014).

Mass mortality events caused by natural disasters, disease or extensive culling, as in the present study, can lead to an influx of carrion in the landscape (Fey et al., 2015). Presently there is little understanding of how mass mortality events effect scavengers, though these influxes have been shown to affect the movement and population dynamics of scavengers (Handler et al., 2021), and alter food webs (Baruzzi et al., 2018). It is also important to test whether scavengers can contribute significantly to carrion removal following mass mortality events (Barton et al., 2023). If scavengers are unable to efficiently remove carcasses from the landscape, large carcass loads can subsidise pest species (Newsome et al., 2021). Therefore, monitoring the subalpine region of the study area, during and after periods of intensive culling can reveal changes in scavenger activity to discover how human-induced mass mortality events affect the abundance of scavengers and the fate of carcasses.

1.6.4 Effects of culling on deer population genetics

Aside from reducing population size, widespread culling can affect the structure and diversity of surviving populations. Populations subject to control regimes may experience changes in genetic structure (Zalewski et al., 2016), a loss of genetic variation, or unintended exploitative selection favouring particular phenotypic variants (Allendorf et al., 2008), which may influence the success of control efforts. In Australia, genetic analysis of culled feral pigs (*Sus scrofa*) over two years showed that pigs culled in the second year were genetically indistinguishable from pigs culled in the first year, indicating that the genetic population was dispersed over a larger geographic area than the control area (Cowled et al., 2006). Conversely, genetic sampling of the eastern grey squirrel (*Sciurus carolinensis*) over consecutive years of intensive culling in North Wales failed to reduce genetic diversity, and instead, following culling, genetically distinct migrant individuals reoccupied the control area (Synnott et al., 2023). The present study tests whether the extent of control was sufficient to cause a decrease in population diversity of deer, and whether the control effort was large enough to cover the spatial extent of the genetic population by examining genetic structure within the study area over multiple years. Quantifying changes in deer population diversity and structure after extensive aerial culling operations can inform the success of control and support recommendations for the optimisation of future control efforts.

1.6.5 Connectivity of deer throughout southeastern Australia

DNA from tissue samples can be used to generate valuable information about intergenerational deer movement across south-east Australia, which could not be generated from collaring data alone. For example, a genetic study of sambar deer and rusa deer dispersal ability estimated the lifetime dispersal distance for both species to be within 20 km (Hill et al., 2023). These data can also be used to inform coordinated control efforts across multiple jurisdictions, whereby land managers can undertake control at target sites as well as in locations inhabiting genetically similar populations to the target site, to prevent reinvasion following control. A previous study examining sambar deer genetics in south-eastern Australia identified three genetically distinct management units, suggesting that control efforts should be applied to each management unit independently (Davies et al., 2021). While a landscape genetic study of rusa deer (*Cervus timorensis*) showed that a railway line restricted gene flow between populations in the Illawarra region of NSW (Li-Williams et al., 2023). It is important to understand the dispersal potential and genetic connectivity of the target species, as unexpected patterns of population structure and connectivity (e.g. Burgess et al., 2022; Spencer et al., 2012) can undermine population reduction efforts.

1.7 Thesis aims and outline

1.7.1 Thesis aims

Given the context of the project, and the research priorities identified above, the project has six main aims:

1. Critically evaluate a method for the safe and efficient capture and collaring of invasive deer in alpine Australia (**Chapter 2**).
2. Test hypotheses regarding the movement and habitat preferences of invasive deer in the Australian Alps (**Chapter 3**).
3. Evaluate the effects of aerial culling on deer population size and behaviour (**Chapter 4**).
4. Examine how scavenger species respond to mass culls (**Chapter 5**).
5. Assess how deer population structure and diversity changes following extensive aerial culling in the study area (**Chapter 6**).

6. Characterise the population genetic structure and diversity of deer across southeastern Australia (**Chapter 6**).

1.7.2 Thesis outline

- In **Chapter 2**, I evaluate a method for the capture, immobilization and collaring of sambar deer and red deer using helicopter net gunning and chemical immobilization. Currently, very few methods exist for the safe and reliable capture of sambar deer, and so, this chapter describes the procedure, method refinement, and animal welfare outcomes, including post-capture movement.

- In **Chapter 3**, I use telemetry collar data from fallow deer, sambar deer and red deer to evaluate their movement and habitat preferences in the Australian Alps. I characterise and compare seasonal home ranges, movement patterns and habitat selection between species, and make recommendations for effective targeted control based on these findings.

- In **Chapter 4**, I examine the behavioural effects of aerial culling on fallow deer. I evaluate how their temporal patterns, grouping and movement speed change during aerial culling operations.

- In **Chapter 5**, I examine scavenger fallow deer and sambar deer carcass use post-cull, particularly scavenging by dingoes and foxes. I explore the effects of season, carcass density and interspecific competition on scavenging, and how scavenging on carcasses may be linked to species activity and carcass biomass loss.

- In **Chapter 6**, I examine fallow deer population genetic structure across the Australian Alps and examine how population structure and diversity might change over time because of extensive culling in the study area (see Figure 1.6 for diagrammatic representation of thesis outline and how each chapter connects together).

- In **Chapter 7**, I synthesise my findings on invasive deer in the Australian Alps and use them to make recommendations for effective control practices, and future research directions.

This study was approved by The University of Sydney Animal Ethics Committee (Project number: 2020/1844).

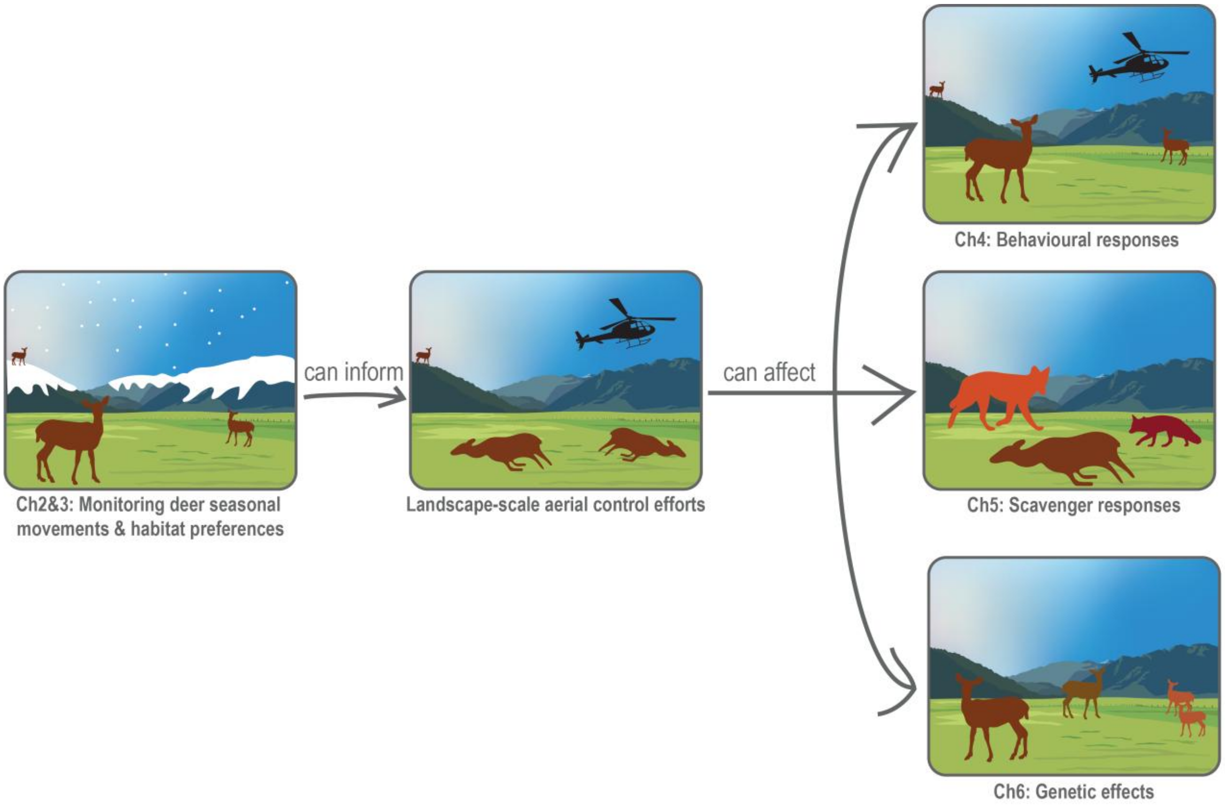

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Figure 1.6: Conceptual model showing thesis chapters and links between them.

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Chapter 2: Evaluating aerial net gunning and chemical immobilisation for capture of invasive sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*) in alpine Australia

Adult female sambar deer following collaring in subalpine Kosciuszko National Park

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2.1 Short summary

Deer are expanding in distribution and abundance in Australia, and effective deer capture methods are needed for telemetry studies of these invasive species. We assessed the use of aerial net gunning and chemical immobilisation administered via hand injection to capture and fit GPS collars to sambar deer and red deer in alpine Australia. Limited mortalities were recorded during capture, and no mortalities were recorded for 45 days post-capture. This study describes an effective method for the safe capture of sambar deer and red deer, which will assist future wildlife researchers to further refine helicopter-based capture protocols and to collect information on the spatial ecology of these species.

2.2 Abstract

Context. Deer species are expanding in distribution and abundance in Australia. There is increasing focus on the ecology of these species, but effective deer capture methods are needed for telemetry studies. **Aims.** The aims of this study were to develop, assess and refine a helicopter-based capture technique for wild sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*), based on trials in south-eastern Australia. **Methods.** We captured and collared 14 sambar deer and five red deer in two operations in Kosciuszko National Park in 2021, using a combination of aerial net gunning and chemical immobilisation delivered via hand injection. Captured animals were fitted with GPS collars to track their movements and activity post-capture. Physiological measurements were recorded as a means of assessing responses to capture and to optimise animal welfare outcomes. **Key results.** Twenty-two deer were pursued and captured with a total mortality rate of 14% (n = 3). The frequency of mortalities decreased from the first operation (17%) to the second operation (10%), largely attributed to allowable helicopter pursuit times being reduced. Post-release movement data indicated that delayed mortality due to capture did not occur. Activity of collared deer was lowest immediately following collaring, suggesting the procedure caused short-term decreases in deer activity. **Conclusions.** Aerial capture of wild sambar deer and red deer poses animal welfare risks, but these can be minimised through the refinement in net gunning and pharmacological procedures to minimise animal stress. **Implications.** This study describes an effective method for the safe capture of sambar deer and red deer, which will assist future wildlife researchers to further refine helicopter-based capture protocols and to collect spatial ecology and survival information about these species.

2.3 Introduction

Invasive species threaten biodiversity globally; and understanding their ecology is imperative to reducing their impacts (Vilà *et al.* 2011; Doherty and Ritchie 2017). In their native range, deer can affect forest composition (Russell *et al*. 2017), and high deer densities have been shown to adversely affect tree recruitment and forest regeneration (Borowski *et al*. 2021). In Australia, deer were first introduced in the 1800s, with releases commonly for hunting, and their subsequent spread has led to the establishment of wild populations in a range of ecosystems across all Australian states and mainland territories (Davis *et al*. 2016). Six deer species have now established in Australia, and some of these species have supplanted native herbivores as the dominant mammalian herbivores in a few ecosystems (Hartley *et al*. 2021). In Australia, deer have been associated with native vegetation loss and soil erosion (Ward-Jones *et al.* 2019), have the potential to transmit diseases to livestock (Cripps *et al*. 2019), and can negatively impact public health (e.g. through vehicle collisions, pollution of drinking water) (Hampton and Davis 2020). Climate matching analyses show that Australia's two largest deer species, sambar deer (*Rusa unicolor*), native to southern Asia (Timmins 2015), and red deer (*Cervus elaphus*), native to Europe and parts of central and western Asia (Lovari 2018), have the potential to extend their distribution across much of Australia (Davis *et al.* 2016). In Kosciuszko National Park, where deer and other exotic herbivores are overabundant, they have damaging impacts on biodiversity (Hartley *et al.* 2021; Ward-Jones *et al*. 2019). Australia's invasive deer populations may continue to increase in geographic distribution and total population size unless effective population control measures are undertaken (Moriarty 2004; Gormley *et al*. 2011; Burgin *et al.* 2015).

Telemetry studies offer a means of studying wild animals, including deer, that exhibit predator avoidance towards humans (Frid and Dill 2002; Stankowich 2008), and are therefore difficult to monitor through direct observation. Tracking animal movement allows researchers to gain insights into animal life survival, reproductive output, behaviour, habitat preferences, home range, dispersal, exploratory movements, and responses to environmental change (Kays *et al*. 2015). This movement data can provide information on target species mobility and rate of population spread (Alford *et al*. 2009) and can be used to prioritise areas for control by aiding in the identification of areas of preferential habitat utilisation (Moseby *et al*. 2021). During control operations, tracked individuals can also function as Judas animals (Taylor and Katahira 1988), or be monitored for their responses to culling (Spitz *et al*. 2019), informing future management efforts. Little is known about sambar deer or red deer movement and the habitat preferences they exhibit in alpine Australia (Davis *et al*. 2016; Hampton *et al.* 2019a). Capturing these large deer (sambar deer males ~ 300 kg [English 1988] and red deer males ~ 180 kg [Searle 1981]) is logistically complex and can result in unfavourable animal welfare outcomes if not undertaken carefully (Hampton *et al*. 2021).

There are very few published methods for the capture of sambar deer. Other species of cervid have been captured using physical restraint (e.g. trapping or netting) (Shury 2014), chemical restraint (e.g. darting or 'remote chemical immobilisation') (Kreeger and Arnemo 2018) or a combination of the two approaches (Hampton *et al*. 2019a). Red deer have been captured using both physical and chemical restraint across their native and introduced ranges (e.g. Roberts 2012; Amos *et al*. 2014; Becciolini *et al*. 2019; Latham *et al*. 2020). Physical restraint techniques have included helicopter net gunning and ground-based nets and box traps (Marco and Lavín 1999). Chemical restraint techniques have included helicopter (e.g. Latham *et al*. 2020) and ground-based darting (Arnemo *et al.* 1994; Amos *et al.* 2014). Helicopter net gunning has been used for red deer capture for several decades in New Zealand and was used in the 1980s in Queensland, Australia (Porter 1986). We are not aware of aerial support to capture sambar deer although in India, six sambar deer were chemically immobilised from the ground (Chatterjee *et al*. 2014) and in Taiwan, 12 sambar deer were captured using a baited ground net, and remote chemical immobilisation delivered via blowpipe (Yen *et al*. 2019). In Australia, two captive sambar deer have been captured via ground-based darting (Moore 1994). A recent review identified methods for the safe and reliable capture of sambar deer as a knowledge gap in Australian deer management (Hampton *et al.* 2019a).

Helicopter net gunning is a procedure whereby animals are entangled and captured in a weighted net fired from a gun, out of a helicopter (Yerex 2001). Ground and helicopter-based net gunning is commonly used to capture deer (Flueck *et al*. 2005; Van de Kerk *et al*. 2020), including in Australia, where the methods have previously been used to capture red deer (Porter 1986) and fallow deer (*Dama dama*) (Bengsen *et al*. 2021) from a helicopter, and trialled unsuccessfully for capturing hog deer (*Axis porcinus*) from the ground (Mayze 1990). Mortality rates resulting from net gun capture of ungulates have been shown to generally be lower than for other capture methods. For example, in one study, helicopter net gunning mortality rates were lower (0–2%) in white-tailed deer (*Odocoileus virginianus*) than for other methods (0–7% for drive nets and 1–21% for Clover traps) (Peterson *et al*. 2003). A recent study captured 27 fallow deer using a net gun from a helicopter in north-eastern New South Wales (NSW), Australia, and reported zero mortalities and no observable effects of capture on the longer-term movement and activity of collared animals (Bengsen *et al*. 2021). However, other studies report deer sustaining injuries or dying as result of net gun capture. In one study targeting white-tailed deer, 8.4% of animals sustained injuries as a result of net-gunning (Webb *et al*. 2008), and, in another study, 1.4% of animals died as a result of capture (Jacques *et al.* 2009). Helicopter net gunning is sometimes augmented by chemical restraint that may be delivered via hand injection (Ortega *et al.* 2020) or intranasal administration (Cattet *et al*. 2004). Chemical restraint is used in this way in an attempt to reduce anxiety and fear and physiological abnormalities such as hyperthermia (Thompson *et al*. 2020). However, use of chemical restraint is also associated with some negatives, such as the possibility of drug-induced lethargy (Ortega *et al*. 2020).

Reporting on the animal welfare effects of capture methods and immobilisation techniques enables researchers to identify best practice techniques and refine future practices (McMahon *et al*. 2012; Hampton *et al.* 2021). Animal capture is a high-risk activity in wildlife research, and frequently leads to animal injuries and mortalities (and injuries to human operators) (Kreeger *et al*. 1990; Webb *et al.* 2008; Latham *et al*. 2020; Hampton and Arnemo 2022). Mortalities are commonly seen during cervid capture due to processes such as ballistic trauma, hyperthermia, and capture myopathy (Beringer *et al*. 1996; Van de Kerk *et al*. 2020). In addition, in the days following capture, animals can exhibit changes in movement rates (Cattet *et al.* 2008; Northrup *et al*. 2014). It is important that wildlife practitioners aim to minimise impacts on animals, as procedures that cause adverse effects not only raise ethical concerns, but also influence animal behaviour, affecting research results.

Herein we describe the outcomes of a helicopter net gunning operation attempting to capture sambar deer and red deer across two operational periods in April 2021 (operation one), where the method was trialled, and November 2021 (operation two), where a refined method was deployed, in the mountainous subalpine area of Kosciuszko National Park, south-eastern NSW. The first operation in April 2021 served as a trial from which the methods were refined and reimplemented in November 2021 in Kosciuszko National Park, southeastern NSW. The capture method used a combination of helicopter capture and chemical immobilisation (Hampton *et al.* 2019a). Captured animals were fitted with GPS collars to track their movements and activity post-capture. Here, we focus specifically on the animal welfare outcomes during capture and use the short-term post-release movement and activity data to assess behavioural responses of collared deer and mortality. This study validates our method for the safe capture of sambar deer and red deer.

2.4 Materials and methods

2.4.1 Study site

Aerial net gunning operations took place in the southern section of Kosciuszko National Park (148.35°E 36.54°S) spanning 186 km^2 in southeastern NSW, Australia (Fig. 2.1). Operations took place over 11 days, when weather conditions were favourable (wind < 15 $km\ hr^{-1}$ and no rain), within two two-week periods in April (autumn) and November (spring) 2021. The capture area is within Australia's Snowy Mountains region, and elevation ranges from 1150 to 1917 m above sea level (NASA/METI/AIST/Japan Spacesystems and US/Japan ASTER Science Team 2019). The region is mountainous, and 32.48% of the area has a slope of 18° or greater (NSW Department of Planning and Environment 2021). Vegetation in the capture area is dominated by eucalypt woodlands with tussock grass, fern and shrubby understories, and wet open tussock grasslands (Department of Climate Change, Energy, the Environment and Water 2021). The capture area has extensive creek and river systems with multiple tributaries (Fig. 2.1). Temperature from the nearest weather station (~3 km from northern boundary of capture area) measured at 0900 and 1500 on operational days ranged from -2.4–10.6 °C in operation one, and from 4.6–12.4 °C in operation two (Bureau of Meteorology 2020). Sambar deer, fallow deer, and red deer are present within the capture area, and overall deer population density was estimated within three weeks of both aerial net gunning operations using distance sampling, via aerial thermal imaging surveys that took place across a larger area (284 km^2) of the southern section of Kosciuszko National Park, including the capture area. The first thermal survey took place during 1st–3rd of April 2021 when deer density was estimated at 15.23 ± 4.00 deer km^{-2} (18 days prior to commencement of operations), and the second thermal survey took place during 16–17th of November 2021 when deer density was estimated at 11.08 ± 2.99 deer km^{-2} (five days after completion of operations; E. O'Dwyer-Hall, unpubl. data).

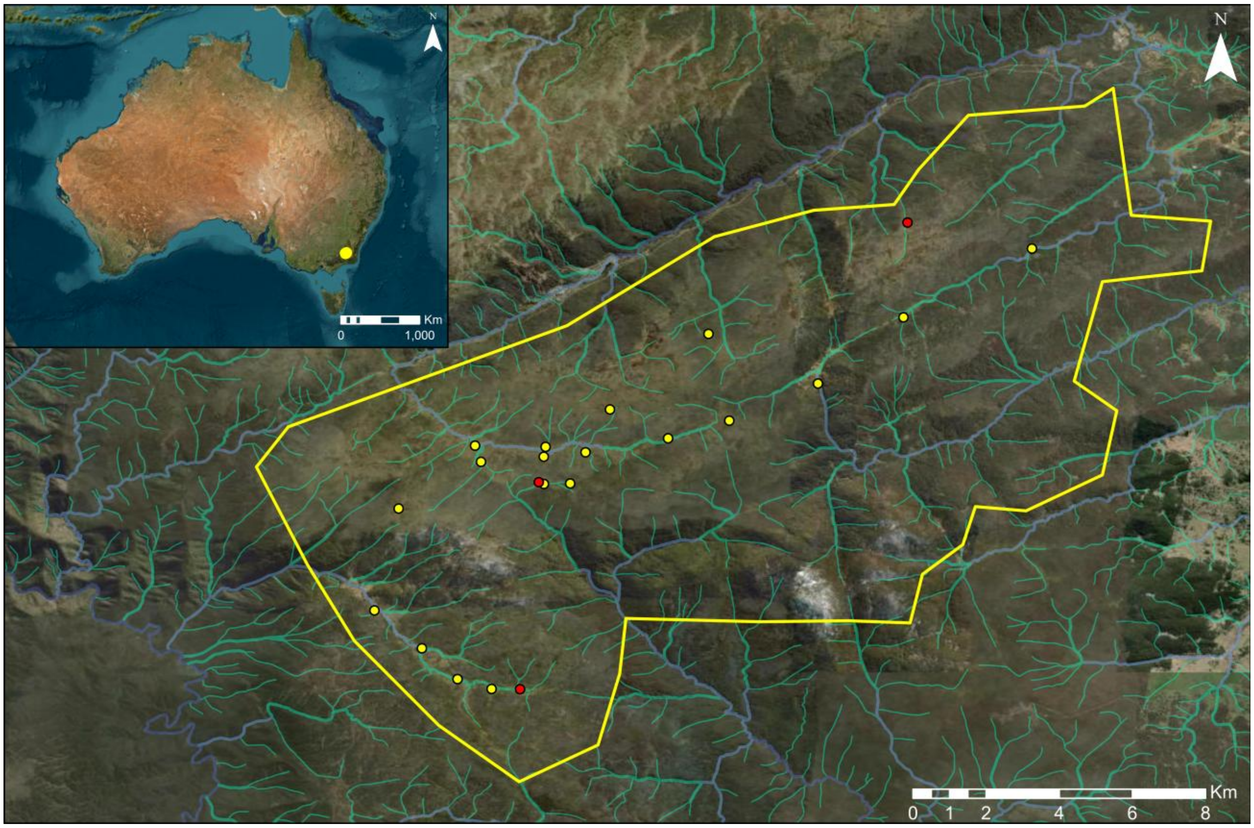

Fig. 2.1. Map of capture area, targeting sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*), in Kosciuszko National Park, Australia. Yellow bounding box indicates capture area, yellow points indicate locations of successfully captured deer, red points indicate locations of deer mortalities during capture. Watercourses are shown on map in blue (major) and green (minor). The location of the capture area relative to Australia is indicated by the frame in the top left corner. Image sources: Esri, Maxar, Earthstar Geographics.

2.4.2 Field trials

To ensure safe and effective operations, the net gun was deployed in a series of ground and aerial trials to ensure even spread of the net at operation heights 5–10 m above ground level. Running shots were also trialled on a static target to assist pilot and net gun operator to identify operational requirements prior to attempting capture of live targets.

2.4.3 Equipment and procedure

A Eurocopter AS350 B3 Squirrel helicopter crewed with pilot, navigator, and net gun operator (NSW National Parks and Wildlife Service Feral Animal Aerial Shoot Team trained shooter) was used to search the area for deer. Once a deer was sighted the pursuit phase began which was categorised into two parts.

Part one involved directing the deer toward open and reasonably level ground with an emphasis on maintaining a low level of stress and physical exertion on the deer. Part two involved a more rapid pursuit to approach within firing range and net deployment. Part one of the pursuit was limited to 10 minutes, however, for deer moving uphill, this was reduced to five minutes to reduce the likelihood of fatigue. Once the deer was in a sparsely vegetated flat area suitable for net gunning, part two commenced, which was a maximum of five minutes high intensity chase, during this time the helicopter flew at a low level (2–5 m above ground level) and speed ($\leq$ 45 km hr^{-1}). Times for each phase of the pursuit were recorded (approximate times were recorded in operation one) (Supplementary Material: Table S2.1) and ceased if the deer was observed to be panting or running unsteadily or the maximum pursuit times reached. A .308 breakaway net gun (ACE Capture, Invercargill, New Zealand) loaded with .308 blanks (22 grain, Australian Munitions ADI AP70N gunpowder) launched four 186 g weights through four barrels angled to spread a 170 × 170 mm (April) or 280 × 280 mm (November) aperture net when fired downward at heights of < 5 m (Supplementary Material: Fig. S2.1). Following an initial shot, additional nets were fired if deemed necessary by the shooter based on animal size, to further restrain the animal (Supplementary Material Table S2.1).

Following capture, the catch team helicopter landed > 100 m from the deer and proceeded quietly towards it. The deer's head was covered with a blanket and a blindfold was fitted if safe to do so. In operation two, an additional net was draped over entangled deer to provide an additional level of containment. Following this, a second helicopter with a pilot, veterinarian, veterinary nurse, and collar technician landed nearby to the catch team helicopter. Morphometric measurements (body length) were taken from recumbent sambar deer to allow estimation of body mass. Length-weight relationships were developed from adult male and female sambar deer shot and weighed in Victoria in 2012 (Table S2.1; Bartareau 2019; Watter *et al.* 2020; Hampton *et al.* 2021). We did not have access to equivalent data for red deer so body mass estimates were based on published estimates for adult male and female red deer (Amos 2015). Final estimated mass and drug doses were adapted upon visual inspection of each deer by the veterinarian (Table 2.1; Supplementary Material: Table S2.1). The veterinarian immobilised animals via intramuscular hand injection into the hindquarters. Sambar deer and red deer received medetomidine (40 mg/mL; prepared by a commercial compounding pharmacy; Bova Compounding, Caringbah, NSW, Australia) and tiletamine-zolazepam (Zoletil®; Virbac, Milperra, NSW, Australia). Medetomidine was given to all deer (~0.1 mg kg^{-1} in operations one and two), while sambar deer also received tiletamine-zolazepam (~1.0–5.0 mg kg^{-1}; Table 2.1; Supplementary Material: Table S2.1). With the exception of one animal, red deer did not receive tiletamine-zolazepam. Two considerations informed the rationale for the different approaches taken to immobilisation of sambar deer versus red deer. Studies have shown that net-gunned red deer can be safely handled without any chemical restraint (Latham *et al*. 2020), and that red deer captured via other methods can be safely handled with relatively low immobilisation doses (Wolkers *et al*. 1994). For sambar deer, however, there is little known about effective capture methods (Hampton *et al.* 2019a). In addition, owing to the much larger size of sambar deer, the risk of injury to staff was deemed to be much higher for incompletely immobilised animals (Hampton *et al.* 2019a). The tiletamine-zolazepam dose used was reduced between operations one (~2.5 mg kg^{-1}) and two (~1.0 mg kg^{-1}) (Table 2.1), in order to reduce recovery times in operation two. Following drug administration, each deer was observed until completely immobilised (recumbency), in some cases, re-administration of medetomidine and/or tiletamine-zolazepam was required if deer were incompletely immobilised (see Supplementary Material: Table S2.1). The induction time, the duration between the administration of the drugs and immobilisation being achieved, was recorded for each deer (Table 2.2; Hampton *et al.* 2021).

Table 2.1. Details for chemical immobilisation events for sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*) captured in 2021, in Kosciuszko National Park, Australia.

Collar ID	**Species**	**Sex**	**Body mass (kg)**	**Drug doses (mg/kg)**			**Physiological variables (mean)**				**Immobilisation quality score***
				Medetomidine	**Tiletamine-zolazepam**	**Atipamezole**	**HR (bpm)**	**RR (rpm)**	**SpO_2 (%)**	**Rectal temperature (°C)**	
11	Sambar	Female	163	0.22	5.20	0.77	70	42	93	37.9	3.9
7	Sambar	Male	190	0.16	5.25	0.92	70	40	83	39.6	4.0
13	Sambar	Female	159	0.13	4.72	0.79	77	23	86	39.1	4.0
12	Sambar	Female	143	0.14	7.01	1.58	85	41	84	38.5	4.0
5	Red	Female	150**	0.11	2.50	0.57	56	44	92	41.0	4.0
9	Sambar	Male	202	0.18	3.09	0.62	80	42	90	39.6	4.0
10	Red	Male	180**	0.10	NA	0.25	NR	32	86	41.4	3.5
15	Red	Female	150**	0.11	NA	0.30	75	12	89	39.3	4.0
6	Sambar	Male	160	0.12	4.69	0.69	78	32	83	38.3	4.0
8	Sambar	Male	228	0.11	5.49	0.66	65	35	81	38.8	4.0
37	Red	Female	160**	0.11	NA	0.47	66	33	89	39.7	4.0
40	Red	Male	180**	0.11	NA	0.28	77	25	91	40.2	4.0
43	Sambar	Male	181	0.12	1.10	0.56	77	37	87	39.4	4.0
35	Sambar	Female	135	0.14	1.33	0.65	80	37	91	39.8	4.0
48	Sambar	Male	193	0.13	1.09	0.59	83	34	93	39.5	3.0
49	Sambar	Male	211	0.10	1.18	0.59	85	30	95	35.3	4.0
41	Sambar	Female	138	0.18	1.45	0.82	85	35	92	38.5	2.0
47	Sambar	Male	195	0.10	0.92	0.58	84	40	86	38.5	4.0
46	Sambar	Male	237	0.11	1.06	0.58	91	30	89	38.1	4.0

For sambar deer, body mass estimates used are derived from the body mass regression relationship provided in Supplementary Material: Item S2.1. *Scoring sheet used to generate immobilization quality scores is provided in Table S2.2. **For red deer, and some sambar deer for which morphometric measurements could not be completed, so drug doses are instead derived from visual inspection body mass estimates. NR = not recorded.

Once drugs were administered and the deer was immobilised, the blanket was removed, and a blindfold was attached, allowing the capture and veterinary team to untangle and remove the nets from the animal. Hobbles were applied to front and back legs, and personnel were protected from antlers by applying antler covers (sections of ‘pool noodles’) to antler tips and/or shielding antlers using an antler protection board (see Supplementary Material: Fig. S2.1). The deer was repositioned in sternal recumbency with the pharynx higher than the rumen, nose downhill and tongue extended, to reduce the chances of regurgitation of ruminal fluid and aspiration of fluid to the lungs. The animal’s rectal temperature, heart rate, respiratory rate, and oxygen saturation (Mindray PM-60 Vet Pulse Oximeter) were recorded every five minutes until medetomidine was antagonised via administration of the reversal agent atipamezole (0.1 mg kg^{-1}) (see Supplementary Material: Table S2.1). A sterile eye lubricant was applied, and any injuries were recorded. If oxygen saturation fell below 90%, intranasal oxygen was administered. This was delivered via a size C medical oxygen bottle with an Allied Healthcare Products B&F oxygen pressure regulator in operation one, and an INHALO® medical oxygen cylinder (CD size) with an integrated oxygen regulator in operation two. Oxygen was administered at a flow rate of 1–2 L min^{-1} and was increased to 5–10 L min^{-1} if oxygen saturation fell below 85%. If oxygen saturation fell below 80%, animals were immediately given a third of a dose of the reversal agent (see below) by intramuscular injection. If the rectal temperature of a deer fell below 38.0 °C (i.e. hypothermia), the deer would be warmed using blankets, or above 40 °C (i.e. hyperthermia), the deer would be cooled using water spray and fanning (Hampton *et al.* 2022). If respiration rate fell to < 20 breaths min^{-1}, a third of a dose of atipamezole was administered. Once inspection had determined the deer was in good physical condition with no significant injuries (i.e., those that would inhibit normal movement), several morphometric measurements were taken: length from nose to the base of tail (cm), neck circumference (cm at mid neck) and full girth (cm) measurements were recorded. The veterinarian provided a qualitative immobilisation quality score for each deer (Supplementary Material: Table S2.2; Harms *et al.* 2018).

A GPS tracking collar with inbuilt mortality sensor, programmed to record animal locations hourly was then fitted (G52D Iridium, Advanced Telemetry Systems, Isanti, MN, USA). Each collar was fitted with an accelerometer, which estimated the proportion of time each collar or deer was moving between hourly fixes. Chloromide® antiseptic spray (Troy Animal Healthcare, Glendenning, NSW, Australia) was applied to any wounds. The processing time, the time between administration of the immobilising dose and the first reversal dose, was recorded for each deer (Supplementary Material: Table S2.1). Once all procedures were finalised, medetomidine was reversed with atipamezole ~0.3 mg kg^{-1} by intramuscular injection. Some deer were given further doses of atipamezole, if they did not show signs of recovering within ~15 minutes of the administration of a first dose (Supplementary Material: Table S2.1). Each of these cases were designated as a 'prolonged recovery'.

Immediately after administration of atipamezole, hobbles were removed, the blindfold was replaced with a small cloth, and catch and veterinarian teams, excluding the veterinarian, moved to > 20 m from the deer to allow it a clear path of escape upon recovery. The veterinarian remained to support and monitor the deer in sternal recumbency. When the veterinarian had assessed that the deer had recovered sufficiently, the blindfold cloth and antler protection were removed, and the veterinarian moved slowly away from the recovering deer. A firearm was available to enable immediate euthanasia to be performed should a severe adverse animal welfare event (e.g. a broken leg) result from an unsteady recovery (Hampton and Arnemo 2022). The recovery time was also recorded for each deer: the time from the first reversal dose to the time the deer was first standing (Supplementary Material: Table S2.1). This study was approved by The University of Sydney Animal Ethics Committee (Project number: 2020/1844).

2.4.4 Post-release monitoring

To measure movement and mortality for 45 days post-capture we used generalised additive models (GAMs). Previous studies evaluating post-release welfare and movement of captured deer have monitored deer movement for 30 days post-capture for mule (*Odocoileus hemionus*) and fallow deer (Northrup *et al.* 2014; Bengsen *et al.* 2021); 50 days for roe deer (*Capreolus capreolus*) (Morellet *et al.* 2009) and 45 days for red deer (Becciolini *et al.* 2019).

Data was remotely downloaded for all collars deployed on sambar deer (n = 14) and red deer (n = five) after 45 days. Mean hourly movement and activity was calculated for each deer for 1–45 days following collaring. Day one consisted of hourly data from the first 24 hours following collaring for each deer. Days 2–45 commenced at the same time each day for each deer, depending on their time of collaring on day one.

For each deer, accelerometry data was used to calculate mean proportion of time spent active per day for days 1–45 following collaring. Daily mean Euclidean distance between hourly location fixes from 1–45 days following collaring was also calculated. Then, GAMs were used to assess changes in movement and activity over the monitoring period, as the collared deer were predicted to have non-linear responses over time (Becciolini *et al.* 2019; Bengsen *et al.* 2021).

To examine trends in deer activity in the days following collaring, four GAMs were fitted, modelling changes in activity separately for males and females of the two species. The models were fitted with mean daily activity (proportion of time spent active) as the response variable, days since capture as the smooth term, and operation as an explanatory variable and multiplier in the smoothed term. Separate smooth functions were generated to model activity 1–45 days since capture for operations one and two. Models were fitted with a binomial distribution in mgcv, however, underdispersion was detected in the binomially distributed models, which was corrected using a quasi-GAM model (Zuur *et al.* 2009).

To examine changes in deer movement in the days following collaring, four GAMs were fitted, as above, with mean Euclidean distance between hourly location fixes, averaged daily, as the response variable, days since capture as the smooth term and operation as an explanatory variable and multiplier in the smoothed term. Again, separate smooth functions were generated to model mean distance between hourly location fixes, averaged daily, for the two operation periods. Models were fitted with Gaussian distributions. The response variable underwent logarithmic transformation to improve normality of the residuals. GAMs were fitted with restricted maximum likelihood and thin plate regression spline smoothers. All data wrangling and analyses were performed in R version 4.1.2, interfaced through RStudio 2021.09.1. Data visualisations were generated using ggplot2 and visreg packages. For capture outcomes and animal welfare metrics, we report descriptive statistics (means ± standard deviation and 95% confidence intervals [CIs]) to avoid performing multiple post hoc statistical tests with low power (Hampton *et al.* 2019b; Hampton *et al.* 2021). Ninety-five percent CIs were calculated using the Clopper-Pearson exact method to account for many cases in which sample sizes were small ($n < 10$) and data did not follow a normal distribution.

2.5 Results

Over the 11 days of aerial net gunning operations a total of 14 sambar deer (nine males and five females, all adult except for one yearling male) and five red deer (two males, three females, all adults) were captured and collared. A single net each was deployed on nine deer (five sambar deer, four red deer), two nets each were deployed on eight deer (seven sambar deer, one red deer), and three nets each were deployed on two deer (both sambar deer; Supplementary Material: Table S2.1).

Based on numbers of successful captures compared with total capture attempts (Table 2.2), the probability of a targeted deer being successfully collared (i.e. captured and not dying) across both operation periods was 0.21 (95% CI = 0.12–0.32) for sambar deer, and 0.31 (95% CI = 0.11–0.59) for red deer. The probability of mortality for captured deer was 0.12 (95% CI = 0.016–0.38) for sambar deer, and 0.17 (95% CI = 0.0042–0.64) for red deer. All missed shots ($n = 13$), where a net was fired but failed to capture a deer, occurred during operation one (Table 2.2). Hence, the probability of successfully capturing a sighted deer increased from 0.20 in operation one to 0.27 for operation two. Failed netting attempts during the first operation were largely due to firing in among vegetation but in operation two, nets were not fired if deer were < 10 m from heavy vegetation and larger aperture nets (280 × 280 mm) were available for stags. Mean calculated weight for male sambar deer was 199.6 ± 22.0 kg, and for female sambar deer was 147.7 ± 11.4 kg. Mean estimated weight for male red deer was 180 ± 0 kg, and for female red deer was 153.3 ± 4.7 kg.

Table 2.2. Summary of capture metrics from 11 days of aerial net gunning operations targeting sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*) over operation one (April) and operation two (November 2021), in Kosciuszko National Park, Australia. Probability of occurrence and 95% CIs are presented for each outcome. n = total number of attempts.

Capture metrics	**Operation 1**		**Operation 2**	
	Sambar (*n* = 42)	**Red (*n* = 9)**	**Sambar (*n* = 26)**	**Red (*n* = 7)**
Proportion: collaring attempts successful	0.17 (0.07–0.31)	0.33 (0.07–0.70)	0.27 (0.12–0.48)	0.29 (0.04–0.71)
Proportion: shots missed	0.29 (0.17–0.44)	0.11 (0.02–0.44)	0 (0.00–0.13)	0 (0.00–0.35)
Proportion: targeted deer that were abandoned*	0.52 (0.38–0.67)	0.44 (0.19–0.73)	0.69 (0.50–0.84)	0.71 (0.36–0.92)
Proportion: mortality at time of capture	0.12 (0.00–0.53)	0.25 (0.01–0.81)	0.12 (0.00–0.53)	0 (0.00–0.84)
Proportion: mortality post-capture	0 (0.00–0.41)	0 (0.00–0.71)	0 (0.00–0.41)	0 (0.00–0.84)
Proportion: traumatic (non-life threatening) injuries at time of capture	0.43 (0.10–0.82)	0 (0.00–0.71)	0.57 (0.18–0.90)	1.00 (0.16–1.00)
Proportion: hyperthermia	0 (0.00–0.41)	0.67 (0.09–0.99)	0 (0.00–0.41)	0.5 (0.01–0.99)
Proportion: prolonged recovery time	0.86 (0.42–1.00)	0.33 (0.01–0.91)	0 (0.00–0.41)	0.5 (0.01–0.99)
Mean induction time (min)	19 (4–34)	4 (0–9)	10 (6–14)	4 (0–13)
Mean processing time (min)	28 (16–40)	17 (12–21)	26 (23–29)	22 (22–22)
Mean recovery time (min)	47 (25–69)	44 (0–181)	10 (8–13)	11 (0–74)

*Capture attempts for targeted deer were abandoned if they were either showing signs of excessive exertion, or our threshold for maximum pursuit times was exceeded.

Refinement of procedures between operations one and two led to improvements in most (but not all) animal welfare metrics (Table 2.2). Of the 19 deer collared, two sambar deer (one in operation one and one in operation two) required a second administration of immobilisation drugs in order to achieve the desired plane of immobilisation, and one sambar deer in operation one required three administrations. All other deer (n = 16; 84%) were satisfactorily immobilised with a single injection. This trend contributed to a considerable reduction in mean induction time for sambar deer between operation one and two (Table 2.2). There was also improvement in recoveries: of the 19 deer captured and collared, six sambar deer and two red deer required two reversal doses. All other deer (n = 11; 58%) were satisfactorily reversed from a single atipamezole injection, and the frequency of prolonged recovery declined between operations one and two (Table 2.2). The was achieved largely through refinement of drug doses: higher initial doses of atipamezole were given to both species in operation two (mean doses of 0.56 mg kg^{-1} for sambar deer and 0.28 mg kg^{-1} for red deer) when compared to operation one (mean doses of 0.18 mg kg^{-1} for sambar deer and 0.22 mg kg^{-1} for red deer) (Table 2.1). This improvement was also reflected in recovery times: in operation one, the mean recovery time for sambar deer and red deer was 47 and 44 minutes, respectively; in operation two, this was reduced to 10 minutes and 11 minutes, respectively (Table 2.2). Chemical immobilisation quality was similar for all operational stages and species, with mean values of 4.0 and 3.8 for sambar deer and red deer, respectively, in operation one and 3.6 and 4.0 for sambar deer and red deer, respectively, in operation two.

2.5.1 Mortalities and injuries

Three mortalities occurred in total: two in operation one and one in operation two. The two mortalities that occurred in operation one (one sambar deer male, one red male) arose from an unknown acute cause while the animals were being pursued, with no definitive diagnosis made. As a result of these mortalities, and the presumed role that stress imposed by pursuit played in them, the maximum allowed time for phase one was reduced from 10 minutes to five minutes for operation two. In operation two, one sambar deer died at the time of capture when it became entangled in the capture net, fell into a small water body (a pond) and drowned. The yearling male was dragged from the pond and resuscitation was attempted by the navigator for 60 seconds with no response. Following this incident, aerial net gunning was not attempted on any deer < 100 m from a water body. Five male deer (four sambar deer, one red deer) sustained an antler injury during capture, and five deer (four sambar deer, one red deer) bit their tongue during capture and sustained a superficial tongue laceration (Supplementary Material: Table S2.1). No other injuries were observed (Table 2.2).

2.5.2 Post-release movement and activity

For all deer groups the mean daily activity (proportion of time spent active) tended to be lowest immediately following collaring. For red deer males, mean activity increased rapidly between days one and 10, before declining slightly, and then continuing to increase (Fig. 2.2). For red deer, mean daily activity varied from 0.10 (day one) to 0.57 (day 38) for males, and 0.22 (day two) and 0.43 (day 35) for females. For sambar deer, mean daily activity varied from 0.23 (day three) to 0.44 (day 27) for males, and 0.21 (day one) and 0.46 (day 33) for females. GAM results showed that mean daily activity for both deer species varied significantly over time for all models (red males: $F = 20.55$, $P < 0.001$, red females: $F = 14.00$, $P < 0.001$, sambar deer males: $F = 15.90$, $P < 0.001$, sambar deer females: $F = 7.84$, $P < 0.001$; Supplementary Material: Item S2.2). Mean activity in the 45 days following collaring varied significantly between operations one and two for male and female sambar deer and red female deer, with these groups showing higher levels of activity in operation two compared with operation one, red male deer activity did not vary significantly between the periods (red males: $t = -0.44$, $P = 0.662$, red females: $t = 15.06$, $P < 0.001$, sambar deer males: $t = 18.98$, $P < 0.001$, sambar deer females: $t = 5.29$, $P < 0.001$; Supplementary Material: Item S2.2).

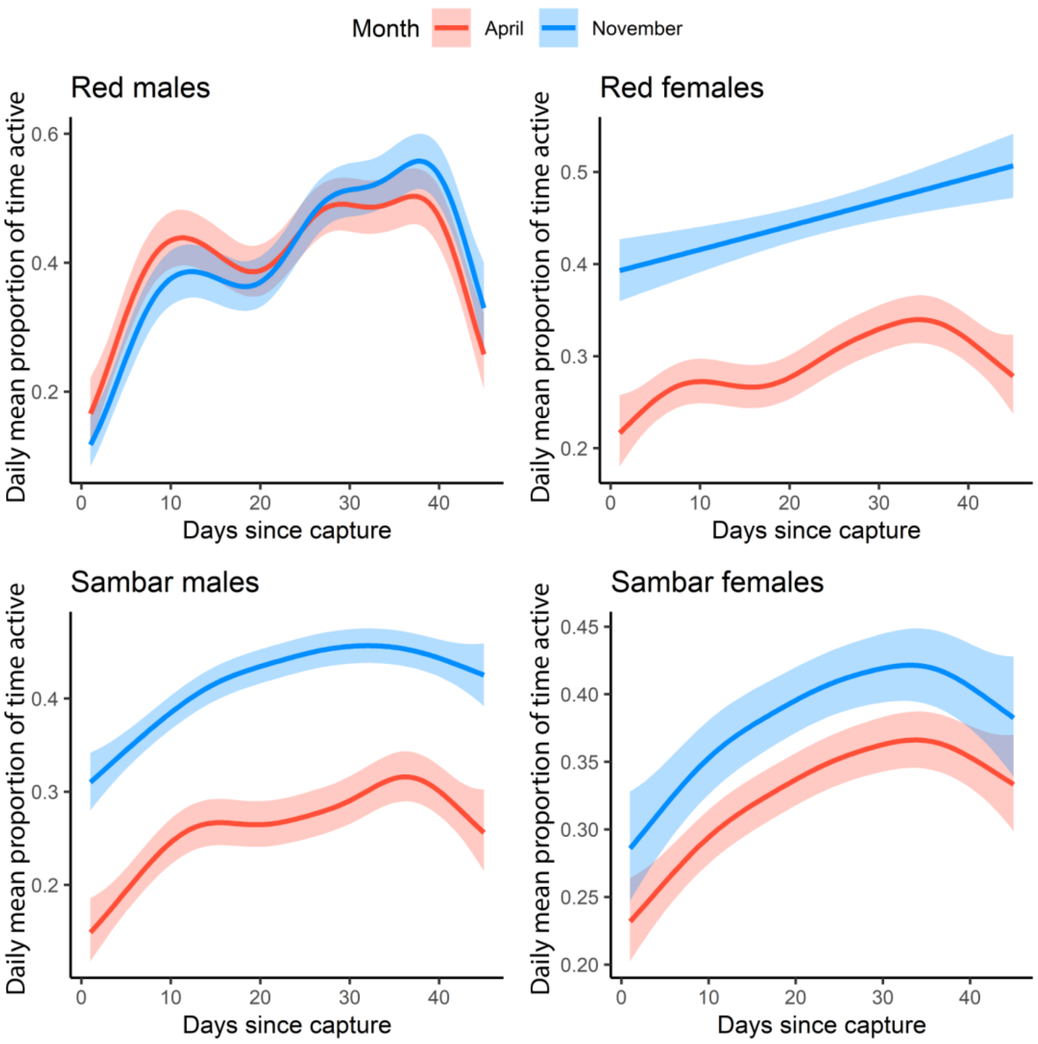

Fig. 2.2. GAM plots showing daily mean proportion of time active for 14 sambar deer (*Rusa unicolor*; nine males, five females) and five red deer (*Cervus elaphus*; two males, three females) for 1–45 days following collaring. For both species, male and females are modelled separately. Red lines represent modelled activity responses for deer collared in operation one (April), and blue lines represent responses from operation two (November). Shaded error bands show 95% confidence intervals.

Modelled movement responses showed that for red deer males, mean movement (hourly distance travelled) increased sporadically throughout the monitoring period, while for red deer females, mean movement declined for ~15 days following collaring, before increasing slightly for the remainder of the monitoring period (Fig. 2.3). For female sambar deer, and male sambar deer collared in operation one, modelled mean movement peaked immediately following collaring, then decreased in the days immediately following collaring, before plateauing around 10 days after collaring, and then remained relatively stable, with smaller positive and negative fluctuations for the remainder of the monitoring period (Fig. 2.3). This trend was less pronounced for male sambar deer collared in operation two (Fig. 2.3). These peaks in modelled movement immediately following collaring were due to some sambar deer dispersing large distances in the days following collaring, then remaining within a small area for the remainder of the monitoring period (Fig. 2.4; Supplementary Material: Fig. S2.2). Deer mean movement for red deer varied from 19 m per hour (day 4) to 400 m per hour (day 43) for males, and 12 m per hour (day two) to 187 m per hour (day one) for females. For sambar deer, mean movement varied from 21 m per hour (day three) to 143 m per hour (day one) for males, and 22 m (day four) to 118 m per hour (day one) for females. Mean movement varied significantly over time for female sambar deer, but not for male and female red and male sambar deer (red males: $F = 1.40$, $P = 0.140$, red females: $F = 1.94$, $P = 0.109$, sambar deer males: $F = 1.45$, $P = 0.240$, sambar deer females: $F = 3.90$, $P < 0.001$; Supplementary Material: Item S2.2). Mean movement in the 45 days following collaring varied significantly between the two collaring periods in all models except the model explaining female sambar deer movement (red males: $t = -3.56$, $P < 0.001$, red females: $t = 4.42$, $P < 0.001$, sambar deer males: $t = 9.39$, $P < 0.001$, sambar deer females: $t = 1.59$, $P < 0.001$; Supplementary Material: Item S2.2).

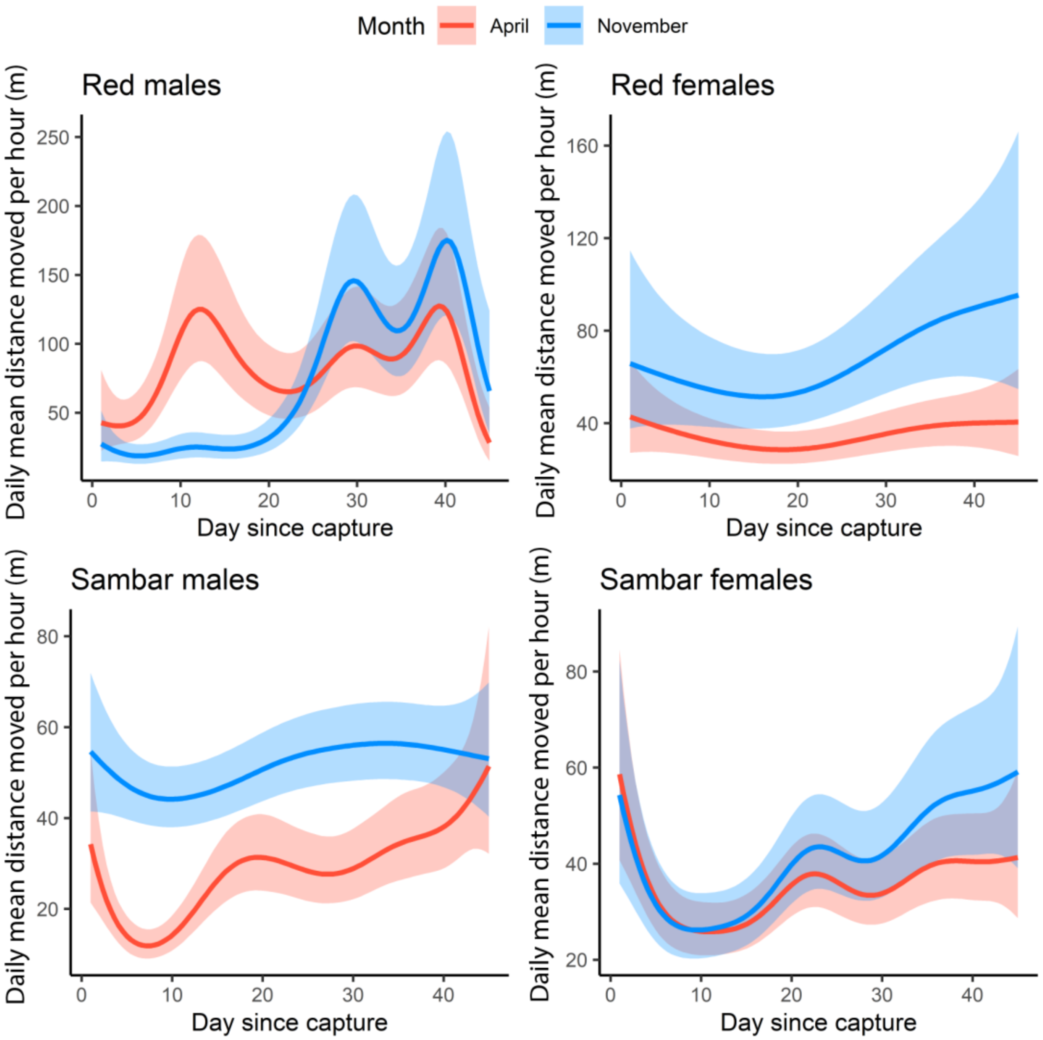

Fig. 2.3. GAM plots showing daily mean distance moved per hour for 14 sambar deer (*Rusa unicolor*; nine males, five females) and five red deer (*Cervus elaphus*; two males, three females) for 1–45 days following collaring. Sambar deer and red males and females are modelled separately. Red lines represent modelled movement responses for deer collared in operation one (April), and blue lines represent responses from operation two (November). Shaded error bands show 95% confidence intervals.

2.6 Discussion

While aerial net gunning and chemical immobilisation have previously been employed for red deer (e.g. Porter 1986; Latham *et al*. 2020), there are few reported studies employing these techniques (or any other capture methods) for sambar deer (e.g. Chatterjee *et al*. 2014; Yen *et al*. 2019). Furthermore, few studies have reported the outcomes of combining net gunning and chemical immobilisation for cervids (Ortega *et al*. 2020; McNay *et al.* 2022; Roug *et al.* 2022). Our results showed that this combination is effective for both sambar and red deer, and although mortalities occurred, we were able to considerably refine methods between our two operations and improve animal welfare outcomes.

Refinement of capture methods yielded reductions in mortalities, induction times, and recovery times for our second round of captures. There were no known mortalities at the time of capture resulting from chemical immobilisation, and post-capture, there were no mortalities during the 45-day monitoring period. However, mortality rate at the time of capture across all operations was 14% (Table 2.2). Collared deer showed acute responses but these were not sustained beyond the days immediately following collaring (Fig. 2.2 & 2.3). Activity responses of sambar deer and red deer were lowest immediately following collaring and tended to increase throughout the monitoring period (Fig. 2.2). Satellite telemetry showed that some deer moved large distances immediately following capture, and following this, movement rates were variable for the remainder of the monitoring period (Fig. 2.3).

2.6.1 Animal welfare outcomes

The overall probability of mortality during capture was 17% for red deer, and 12% for sambar deer (Table 2.2), however, small sample size meant 95% CIs were broad (see Table 2.2; Hampton *et al.* 2019b). Between operations one and two, however, the capture method was refined and the frequency of injury and mortality during capture were generally reduced (Table 2.2). In operation one, the mortalities of one sambar deer and one red deer while being chased by the helicopter led us to reduce the maximum time allowed for phase two from 10 to five minutes for operation two, in line with the maximum chase time reported for helicopter net gunning of red deer in a montane environment in New Zealand (Latham *et al.* 2020). Subsequently, no captured deer died during chases in operation two, although other factors may have been involved in the two deaths (e.g. individual susceptibility). Reductions in maximum allowed chase times have been associated with fewer animal mortalities for helicopter darting of chital deer (*Axis axis*) in a tropical environment in Australia (Amos *et al.* 2023; Hampton *et al.* 2021).

The mortality due to drowning in a small water body while entangled in a net resulted in a change to the capture method whereby animals were only pursued when tracking directly away from water. The capture method described here could potentially be adjusted or refined to suit capture attempts in environments different to the one in which we worked. Our study was in a relatively cold (compared to much of Australia) alpine environment. Should the method be deployed to capture sambar deer within their native Asian range, which is predominately tropical and sub-tropical (Timmins 2015), we suspect that sambar deer would be more susceptible to heat stress.

2.6.2 Immobilisation methods

Chemical restraint of wild Cervidae always incurs animal welfare risks at the time of capture and during the post-capture period (Dechen Quinn *et al*. 2012; Caulkett and Arnemo 2014; Ortega *et al*. 2020; Thompson *et al*. 2020). Therefore, it is important to monitor the post-release responses of animals to new or modified capture methods. Chemical immobilisation was used to mitigate the risk to human handlers but helicopter net gunning operations in northern NSW showed that fallow deer can be captured and processed safely and efficiently without the need for chemical restraint (Bengsen *et al*. 2021). However, physically restraining smaller fallow deer poses human and animal welfare risks than restraining red deer (~50–80 kgs heavier than fallow), or sambar deer (~140–200 kg heavier than fallow) (Geist and Bayer 1988). Red deer have been captured via net gunning without chemical immobilisation (Latham *et al*. 2020), and future studies could investigate applying that method in sambar deer.

Induction and recovery times were reduced for both deer species between operations one to two (Table 2.2), due to improved body mass estimation procedures and refined drug regimes. The prolonged recovery times observed in operation one were reduced in the second operation by reducing the dose of tiletamine-zolazepam (Table 2.1). The non-reversible nature of tiletamine-zolazepam has practical disadvantages related to prolonged recoveries, increased risk of associated physiological states such as hypothermia, and increased requirements for monitoring (Mayberry *et al.* 2014). Once tiletamine-zolazepam doses were reduced in November, mean recovery times were considerably reduced (10 minutes in November compared with 47 mins in April), and rapid recoveries were observed with the completely reversible immobilisation regime of medetomidine alone that was given to red deer (Table 2.1; Supplementary Material: Table S2.1). To allow comparable induction times with greater ease of administration, intranasal drug administration could be considered. Intranasal drug administration is generally easier for non-veterinarians in the field, has fewer and less severe complications, and requires less training and experience than intravenous or intramuscular drug administration (Shury *et al*. 2010).

2.6.3 Post-release behaviour

We reported on the movement and activity of collared red and sambar deer for 45 days post capture to allow for comparisons with similar studies (Northrup *et al*. 2014; Becciolini *et al*. 2019; Bengsen *et al*. 2021). While no mortalities were reported during this period, accelerometer data showed that red and sambar deer of both sexes tended to exhibit the lowest activity rates immediately following collaring. Then, throughout the monitoring period, activity rates tended to increase until 30–40 days post-collaring for both species, when activity decreased for all modelled responses, except for female red deer collared in operation two, whose activity continued to increase (Fig. 2.2). Similarly, activity increased over the first 10 days following capture, before stabilising for fallow deer captured via an aerial net gun, processed without chemical immobilisation (Bengsen *et al*. 2021). Accelerometer data may be a more sensitive indicator of mild impairment, and so, for the present study, the increase in activity over the monitoring period, may indicate that deer are recovering from impairment as a result of the collaring procedure (Bengsen *et al*. 2021).

Free-ranging deer are known to exhibit changes to movement rates and site fidelity resulting from capture and chemical immobilisation procedures (e.g. Morellet *et al*. 2009; Northrup *et al*. 2014). For male and female sambar deer, movements peaked immediately following capture and steadily decreased for ~10 days following capture and collaring before plateauing or increasing (Fig. 2.3). Some deer appeared to exhibit a disturbance response immediately following capture, like sambar deer males 49 and six, which travelled more than 12 and eight kms from their capture locations in ~7 days respectively, undertaking faster long-distance movements, interspersed with short periods of slower speed movements, before remaining within a small area and moving slower for the remainder of the monitoring period (Fig. 2.3; Fig. 2.4; Supplementary Material: Fig. S2.2). Sambar deer experiencing acute stress are known to undertake long distance movements interspersed with periods of rest (Semiadi *et al*. 1994), so capture may have contributed to increased movement rates for a short period following capture. This disturbance response was not displayed by all sambar deer, however, with sambar deer of both sexes remaining within a small distance of the capture area for the entire monitoring period, like sambar deer female 11 (Fig. 2.4). Short-term increases in movements for the period following capture have previously been reported for many Cervidae species, including moose (*Alces alces*) and male roe deer, which exhibit flight behaviour and show greater displacement from their home ranges following capture (Morellet *et al*. 2009; Neumann *et al*. 2011), as well as for an antelope species, nilgai (*Boselaphus tragocamelus*; Baumgardt *et al*. 2023). Like sambar deer, male roe deer and moose are largely solitary, and tend not to exhibit strong social bonds (Geist 1963; Hewison *et al*. 1998), and so may be more likely to move large distances following capture.

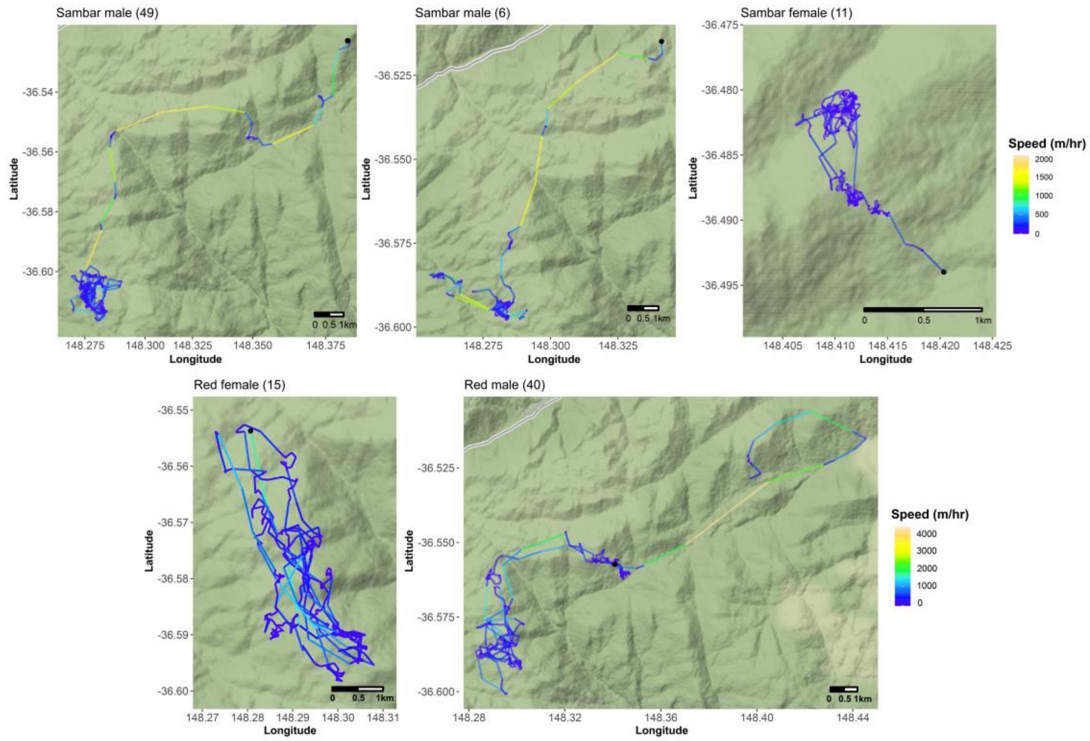

Fig. 2.4. Post-capture movements of sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*) in alpine Australia. Movement tracks are coloured according to speed (m hr^{-1}), measured as Euclidean distance between successive locations recorded hourly. Black points on maps indicate the starting point of each movement path. All movement paths are oriented north.

Comparing movement and activity rates pre- and post-capture would have allowed the delineation of movement changes due to capture (e.g. Morellet *et al*. 2009; Neumann *et al*. 2011; Northrup *et al*. 2014; Baumgardt *et al.* 2023), but was not possible in the present study. Elevated movement rates for the period immediately following collaring did not occur in red deer (Fig. 2.3), which did not move as far from their point of capture as sambar deer (Supplementary Material: Fig. S2.2), despite moving greater average maximum distances than sambar deer throughout the monitoring period (Supplementary Material: Fig. S2.2). Red deer are more social (Clutton-Brock *et al.* 1982), and may seek to reestablish social bonds following disturbance, remaining closer to their capture area, as shown for red deer female 15 and male 40 (Fig. 2.4). Conversely, post-capture movements of red deer hinds were not consistent with a flight response to move away from the capture area into forest cover for a period of ~8 days following capture (Becciolini *et al.* 2019). In the present study, low sample sizes preclude us from more definitely characterising red deer movement post-capture.

2.6.4 Conclusion

This study used an aerial net gun and chemical immobilisation to capture 14 free-ranging invasive sambar deer and five red deer in alpine Australia. The method was used across two periods, with refinement of procedures in the second period reducing mortality probability to ≦0.12, with further refinement and reduction of adverse event frequency likely to be feasible. The method presented here can be adapted and refined, to capture sambar deer and red deer within their native and invasive ranges.

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2.9 Supplementary Material

Table S2.1: Capture information, immobilisation and reversal dose information collected for each captured and collared deer: https://doi.org/10.6084/m9.figshare.21555276.

Item S2.1: Protocol used to estimate the body mass of captured sambar deer (*Rusa unicolor*) from morphometric measurements.

Male and female sambar deer body mass (BM) was estimated using relationships developed from measurements of body length (L; cm) and entire carcass mass (kg) of n = 25 adult male sambar deer and n = 11 adult female sambar deer culled in Victorian state forest in 2012–2013 (Forsyth *et al*. 2014). These relationships were estimated using least squares regression and explained 83.1% and 90.17% of the observed variation for males and females, respectively. The relationship for female sambar deer was:

$$BM = -122.9572 + (1.4919*L)$$

The relationship for male sambar deer was:

$$BM = -251.818 + (2.327*L)$$

Fig. S2.1: Images of male sambar deer (*Rusa unicolor*) taken during aerial net gun capture, and while the animal was recumbent following chemical immobilisation. In the top image, a second net is fired on the sambar deer whilst the animal is restrained by the first net. In the bottom left image, the sambar deer is fitted with a GPS tracking collar (G52D Iridium, Advanced Telemetry Systems, Isanti, MN, USA) and ear tag. The animal wears a blindfold to prevent distress to the animal during immobilisation and antler covers, to prevent harm to personnel working close to the animal during processing. In the bottom right image, a sambar deer is fitted with a blindfold, hobbles, antler covers and an antler protection board. Image credit: Rob Hunt.

Table S2.2: Immobilisation quality scoring sheet, used to rate immobilisation quality of aerially net gunned and sedated sambar (*Rusa unicolor*) and red deer (*Cervus elaphus*), adapted from Grint *et al.* (2009).

Immobilisation quality	**0**	**1**	**2**	**3**	**4**	**Score**
Spontaneous posture	Standing	Tired but standing	Lying but can rise	Lying difficulty rising	Unable to rise	
Eye reflex	Normal	Reduced	Slow, full TEL sweep	Slow, partial third eyelid sweep	Absent	
Eye position	Central/alert	Central/relaxed	Forwards/downwards but visible	Forwards/downwards & obscured by TEL	Dilated, nonresponsive	
Jaw tone	Normal	Reduced tone	Much reduced tone	Minimal tone	Absent	
Response to noise	Normal startle	Reduced startle	Relaxed	Minimal startle	Absent reaction	
Resistance in lateral recumbency	Struggling, no lateral recumbency	Some struggle, allows lateral recumbency	Min struggle Permissive	Relaxed	Absent struggle	
General attitude	Excitable	Awake and normal	Tranquil	Drowsy	Comatose	
					Mean	

Item S2.2: Model output describing post-release mean hourly distances travelled and mean activity of collared sambar (*Rusa unicolor*) and red deer (*Cervus elaphus*) in the 45 days following capture, using generalised additive models fit with thin-plate regression splines.

Sambar males (*n* = 9)

Mean hourly distance travelled

Param. Terms	**Est.**	**Std. error**	**t**	***P***
Intercept	3.29	0.05	60.48	< 0.001
Month	0.65	0.69	9.39	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***P***
s($t_{overall}$)	3.26	4.04	1.45	0.2400
s(t_{month}):April	5.02	6.16	2.83	0.0144
s(t_{month}):November	1.00	1.00	1.45	0.2286
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.29	30.6	360	

Mean activity

Param. Terms	**Est.**	**Std. error**	**t**	***P***
Intercept	-1.04	0.03	-33.85	< 0.001
Month	0.71	0.37	18.98	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***P***
s($t_{overall}$)	3.39	4.20	15.90	< 0.001
s(t_{month}):April	4.22	5.20	1.51	0.187
s(t_{month}):November	0.002	0.002	0.002	0.998
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.59	58.3	360	

Sambar females (*n* = 5)

Mean hourly distance travelled

Param. Terms	**Est.**	**Std. error**	**t**	***p***
Intercept	3.55	0.05	69.34	< 0.001
Month	0.14	0.09	1.59	0.113
Smooth Terms	**edf**	**Ref. df**	**F**	***p***
s($t_{overall}$)	5.52	6.66	3.90	< 0.001
s(t_{month}):April	1.00	1.00	2.10	0.1488
s(t_{month}):November	0.001	0.002	0.04	0.9929
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.10	12.5	270	

Mean activity

Param. Terms	**Est.**	**Std. error**	**t**	***p***
Intercept	-0.73	0.03	-26.31	< 0.001
Month	0.25	0.05	5.29	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***P***
s($t_{overall}$)	3.34	4.15	7.84	< 0.001
s(t_{month}):April	1.00	1.00	0.18	0.6720
s(t_{month}):November	< 0.001	< 0.001	0.003	0.9990
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.24	25.9	270	

Red males (*n* = 2)

Mean hourly distance travelled

Param. Terms	**Est.**	**Std. error**	**t**	***P***
Intercept	4.36	0.07	59.13	< 0.001
Month	-0.37	0.10	-3.56	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***P***
s($t_{overall}$)	6.74	7.63	1.40	0.140
s(t_{month}):April	3.68	4.38	1.21	0.411
s(t_{month}):November	1.77	2.25	0.24	0.845
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.65	70.3	90	

Mean activity

Param. Terms	**Est.**	**Std. error**	**t**	***p***
Intercept	-0.37	0.04	-8.85	< 0.001
Month	-0.03	0.06	-0.44	0.662
Smooth Terms	**edf**	**Ref. df**	**F**	***p***
s($t_{overall}$)	7.45	8.13	20.55	< 0.001
s(t_{month}):April	1.00	1.00	12.47	< 0.001
s(t_{month}):November	< 0.001	< 0.001	0.07	0.997
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.69	72.1	90	

Red females (*n* = 3)

Mean hourly distance travelled

Param. Terms	**Est.**	**Std. error**	**t**	***p***
Intercept	3.55	0.08	42.09	< 0.001
Month	0.65	0.14	4.42	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***p***
s($t_{overall}$)	2.57	3.20	1.94	0.109
s(t_{month}):April	1.00	1.00	0.74	0.392
s(t_{month}):November	< 0.001	< 0.001	0.011	0.999
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.15	17.8	135	

Mean activity

Param. Terms	**Est.**	**Std. error**	**t**	***p***
Intercept	-0.90	0.03	-31.80	< 0.001
Month	0.69	0.05	15.06	< 0.001
Smooth Terms	**edf**	**Ref. df**	**F**	***p***
s($t_{overall}$)	1.00	1.00	14.00	< 0.001
s(t_{month}):April	4.51	5.54	2.43	0.027*
s(t_{month}):November	< 0.001	< 0.001	0.001	0.999
Model fit	**R-sq (adj.)**	**Dev. (%)**	**No. obs.**	
	0.68	68.4	135	

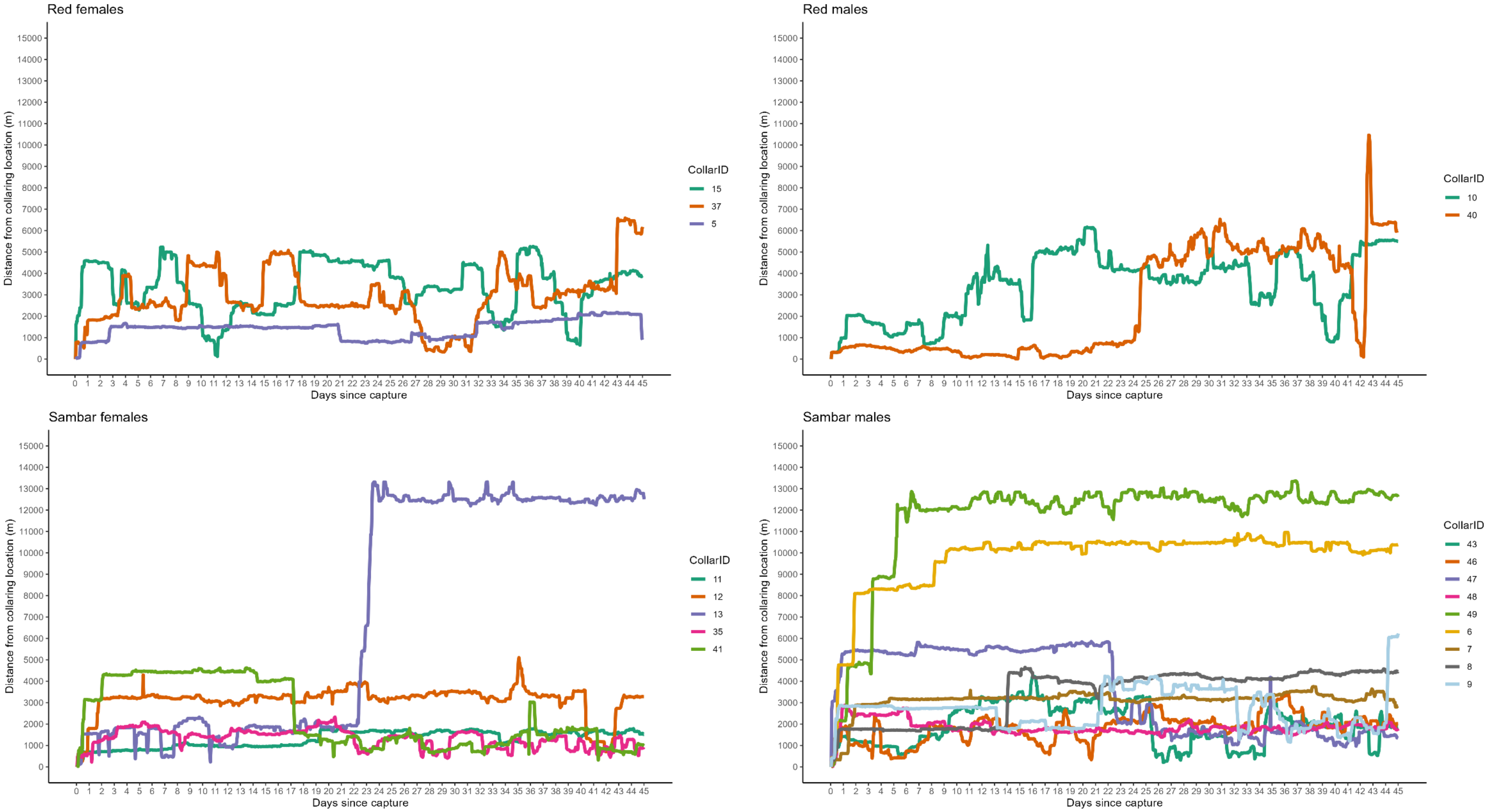

Fig. S2.2: Distances travelled from capture location for five aerially captured and collared 14 sambar deer (*Rusa unicolor*) and five red deer (*Cervus elaphus*), during a 45-day monitoring period following aerial net gunning, immobilisation, and collaring. Red and sambar deer were captured in Kosciuszko National Park, Australia in over two operation periods, in April and November 2021.

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Chapter 3: Invasive deer demonstrate species-specific niche habitat selection in the Australian Alps

Early snowfall in May, off Cascades trail, in Kosciuszko National Park

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3.1 Abstract

Australia's invasive deer populations continue to expand in abundance and distribution, yet there is limited information on their movement patterns and habitat preferences. This inhibits the prioritisation of areas for control and conservation protection. We tracked 20 fallow deer (*Dama dama*), 5 red deer (*Cervus elaphus*), and 14 sambar deer (*Rusa unicolor*) to characterise their seasonal movement and habitat preferences in alpine and subalpine southeastern Australia. Autocorrelated kernel density estimated annual home ranges ($km^2 \pm SE$) averaged 226.9 ± 54.3 for male, and 55.1 ± 46.5 for female fallow deer, 70.2 ± 35.5 for female red deer, and 25.3 ± 4.0 for male, and 80.7 (one individual) for female sambar deer. Red and sambar deer were mainly restricted to eucalyptus forest/woodland (97% of fixes for sambar, 92% for red) and native grassland (2% of fixes for sambar; 8% for red). Fallow deer, however, were more generalist, and used comparatively less eucalypt forest/woodland (73%), spending more time in cleared areas (14%), and native grasslands (13%). Seasonal resource selection functions (RSFs) showed that, relative to eucalypt forest/woodland, fallow deer preferred cleared land for all seasons except summer, heathland for all seasons except winter, and inland aquatic areas in summer. All species tended to inhabit higher elevations in summer (average: 1517 m ASL for fallow; 1709 m ASL for red; 1463 m ASL for sambar), and lower elevations in winter (average: 1344 m ASL for fallow; 1483 m ASL for red; 1102 m ASL for sambar). Additionally, seasonal RSFs showed that red deer showed a preference for higher elevations within their available range in every season except winter, when they preferred lower elevations. Of concern, we found that sambar deer showed a preference for previously burnt areas in autumn (53% of fixes) and spring (89% of fixes), preferring areas with low to moderate and high severity fire damage. Prioritising areas for control and conservation should be informed by deer movement and habitat preferences, and differences in such preferences between the three species studied herein suggest the need for tailored approaches for control to be effective in reducing their numbers and impacts on ecosystems.

3.2 Implications for managers

- Invasive fallow deer, red deer, and sambar deer in the study system exhibit different movement and habitat preferences.
- All three species move between natural areas and cleared areas, but fallow deer spend a greater proportion of time in cleared areas and thus present a greater risk to agriculture through resource competition and disease transmission to livestock.
- Control should be prioritised in accordance with seasonal movements, and should occur at higher elevations in summer, and lower elevations in the colder months.

- Sambar deer were shown to use and select for burnt areas 2–3.5 years after fire, potentially preventing revegetation and post-fire recovery. Burnt areas should be targeted for control years after fire.

3.3 Introduction

Australia is a megadiverse country (Wilson et al., 1997) but it has been severely degraded since European colonisation (Legge et al., 2023), and has among the highest native species extinction rates globally (IPBES, 2023; Woinarski et al., 2019). Colonisation led to extensive land clearing for agriculture and livestock (Bradshaw, 2012) and facilitated the human-mediated movement of invasive species into Australia, including through acclimatisation societies. These societies aimed to distribute 'useful' species and make Australia more similar to landscapes in Great Britain (Bentley, 1957; Rolls, 1984). Today, introduced species are a key contributing threat to the decline of Australia's native flora and fauna (Legge et al., 2023; Woinarski et al., 2019). Indeed, six deer species have now established across a range of ecosystems in all Australian states and territories (Davis et al., 2016). Deer browsing alters plant community composition (Wardle et al., 2001) and the exclusion of deer has been shown to lead to the recovery of forest understorey vegetation (Wills et al., 2023). Feral deer can act as reservoirs for pathogens that are transmissible to domestic livestock and other wildlife (Huaman et al., 2021). Additionally, wallowing by some deer species, including sambar deer (*Rusa unicolor*), threatens high elevation peatlands in south-eastern Australia (Comte et al., 2022).

Three species of deer, fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and sambar deer, are present within Kosciuszko National Park (hereafter KNP), a mountainous alpine and subalpine region in southeastern New South Wales (NSW), Australia (Atlas of Living Australia, 2023). Fallow deer are originally native to the Mediterranean, where they inhabit temperate forests and grasslands, Mediterranean shrubby vegetation, as well as pastures and plantations (Masseti & Mertzanidou, 2007). Red deer are native to Europe as well as western and central Asia where they inhabit woodlands, upland moors and open mountainous areas, but have also been reported along riverbanks in desert areas within their Asian range (Lovari et al., 2018). Sambar deer are the largest deer species present in Australia, and are native to southern Asia, where they utilise a wide range of habitats including arid forests, rainforests and alpine regions (Timmins et al., 2015). Sambar deer, unlike fallow deer and red deer which have synchronized breeding in autumn (Bocci et al., 2012; Davini et al., 2004), can breed year-round in their native range (Dahlan & Dawend, 2013). The Australian Alps, cover just 0.15% of the Australian continent and inhabited by many unique and range-limited flora and fauna (Kirkpatrick, 1994; Williams et al., 2014). Uncontrolled livestock grazing occurred in KNP until the mid-1900s when the National Park was created, and since then, extensive rehabilitation and revegetation works have sought to restore the region, with natural vegetation recovery slow (Good & Johnston, 2019; Scherrer & Pickering, 2005). Recent aerial thermal surveys in the region where this study took place indicate that the three wild deer species co-occur at combined densities of up to 26.2 (95% CI = 15.5–44.3) deer km^{-2} (Cox, 2024), and may cause similar damage to domestic livestock (Claridge, 2016; Davis et al., 2016). KNP is bordered by agricultural land, and feral deer use of agricultural land can lead to resource competition and disease transmission to livestock (Cripps et al., 2019; Huaman et al., 2023; Smith et al., 2012). Feral deer are subject to ground and aerial control across KNP and surrounding agricultural areas, but implementation of effective strategies could be improved with information on movement and habitat use by these species in this environment.

The need for deer control in KNP was intensified when more than 30% of the park was burnt in the 2019–2020 bushfires (Department of Planning and Environment, 2023), as invasive species including deer are known to exacerbate damage and prevent vegetation recovery in post-fire landscapes (Legge et al., 2022). Indeed, post-fire herbivory compounds the effects of fire through browsing and grazing of recovering vegetation (Smit & Coetsee, 2019), which can alter vegetation species composition, reducing richness and diversity, promoting dominant and unpalatable species (Chard et al., 2022), and delaying the restoration of carbon and nitrogen soil accumulation and recovery (Stritar et al., 2010). Ungulate responses to fire are varied, with selection for burnt areas dependent on season (Ganz et al., 2022), species (Skatter et al., 2017), and time since fire (Lashley et al., 2015). In Australia, reductions in sambar deer activity have been reported immediately following fire, with activity increasing to pre-fire levels in the years following (Forsyth et al., 2012). Australia's alpine vegetation is slow growing, and high levels of bare ground and lower vegetation cover following fire leaves burnt areas vulnerable to soil erosion and trampling for years after fire (Bridle et al., 2001; Wahren et al., 2001). Therefore, more research is needed to understand the post-fire responses of Australia's invasive deer species in order to adequately protect these systems.

Animal movement is fundamental to shaping ecological and evolutionary processes at local and ecosystem scales (Hansson et al., 2014), and invasive species have been shown to exhibit unexpected movement characteristics in their new ranges, such as increased rates of dispersal and larger home range sizes (e.g., Amos et al., 2014; Shine et al., 2021). Knowledge of feral deer movement and habitat preferences in Australia is limited, with few tracking studies examining fallow deer (e.g. Bengsen et al., 2024) and red deer (e.g. Amos, 2015; Amos et al., 2014) movement characteristics, and none within an alpine environment. Sambar deer have not previously been tracked in Australia, and so our understanding of sambar deer biology has come from camera trapping studies (e.g. Comte et al., 2022), and international tracking studies of the species within its native range (e.g. Yen et al., 2019). A better understanding of invasive species movement and habitat preferences can aid in predicting their impacts, range expansions, and in implementing effective control measures (O'Reilly-Nugent et al., 2016).

In this study, we captured fallow deer, red deer, and sambar deer within KNP and used GPS collars to examine each species' seasonal and annual home range sizes ranges. We then evaluated each species' seasonal habitat preferences using resource selection functions, evaluating preferences for elevation, slope, aspect, landcover type and distance to perennial water source. For sambar deer, we also evaluated preferences for burnt areas, as their movements overlapped recent fire affected habitat. For habitat preferences, we predicted (1) that all species would predominately inhabit eucalypt forest/woodland, the most common vegetation type in the region, but would also inhabit native grasslands and cleared areas; (2) they would all inhabit higher elevations during the summer, and lower elevations during winter, where they will be more likely to inhabit cleared grassland areas, and present a greater risk to agriculture; and (3) that sambar deer will show a preference for burnt areas compared with unburnt areas. We use the results to identify areas where deer control should be prioritised, including areas where deer are more likely to be present and areas with high ecological vulnerability.

3.4 Methods

3.4.1 Study area

This study took place in the Australian Alps, in an area within and surrounding KNP, on the Country of the Ngarigo People, between April 2021 and May 2023. Elevation in this area, defined as a 20 km radius around the minimum convex polygon (MCP) of all deer location fixes generated (see below), averages 1007 m and ranges from 123–2227 m above sea level (ASL). Slope averages 10° and ranges from 0–90°, aspect averages 136° and ranges from -1–360°, and distance to a perennial water source averages 697 m and ranges from 0–3548 m. Vegetation is dominated by eucalyptus forests and woodlands with tussock grass, fern and shrubby understories, and wet open tussock grasslands, interspersed with some shrubland and heathland. Some of the area has been cleared for agricultural and residential settlements (Figure 3.1). Continuous snow cover for at least one month of the year occurs within the subalpine zone of the study area (1350–1750 m ASL), while the alpine zone (above 1750 m), is mostly above the tree line, and typically experiences continuous snow cover for at least four months of the year (MacPhee & Wilks, 2013; Sanecki et al., 2006). The mean monthly maximum temperature at Thredbo Top Station (Latitude: -36.49, Longitude: 148.29, 1957 m ASL), centrally located within the study area, ranged from -0.1 °C in July 2022, to 17.3 °C in January 2022 (Bureau of Meteorology, 2023a), and monthly total precipitation during the monitoring period ranged from

22.6 mm in April 2021 to 386 mm in October 2022, with the lowest precipitation typically occurring over winter and summer and the highest over spring (Bureau of Meteorology, 2023b).

3.4.2 Deer capture and collaring

Deer of all three species were captured and collared using aerial net gunning from a helicopter, with sedation administered via hand injection, and a GPS tracking collar with inbuilt mortality sensor fitted (G52D Iridium, Advanced Telemetry Systems, Isanti, MN, USA) (see McCarthy et al., 2023). The smaller fallow deer were additionally captured in collapsible clover traps set up along game trails. Once set, clover traps were checked daily for trapped deer. If a deer was captured, the animal remained conscious, physically restrained by at least two personnel while a GPS collar was fitted.

In total, 20 fallow deer (11 males, 9 females), 5 red deer (2 males, 3 females), and 14 sambar deer (9 males, 5 females), were collared between April 2021 and December 2022. All collars were programmed to record animal locations hourly. Lowered activity for approximately 10 days following collaring has been reported for fallow deer (Bengsen et al., 2021) red deer and sambar deer, while some sambar deer have been shown to undertake long-distance movements immediately following collaring (McCarthy et al., 2023). Therefore, the first ten days of data following collaring were excluded from analyses to allow the deer to resume normal behaviours. Deer in the following analyses were monitored for between three and 25 months, from April 2021 to May 2023.

3.4.3 Home ranges

The study area (Figure 3.1) is characterised by strong seasonal variations in temperature and precipitation between four annual seasons - summer (December–February); autumn (March–May); winter (June–August) and spring (September–November). Therefore, for all seasonal home range and habitat preference analyses, movement data was broken up into these four seasons. Deer were included in the seasonal home range analyses only if they were monitored for the entire three-month period of a given season. For the home range calculations for each individual, all datapoints with horizontal dilution of precision (HDOP) greater than 2.5 or where HDOP could not be calculated were filtered from the dataset. If a single individual had more than 25% location fixes with a HDOP greater than 2.5 or missing, corresponding to ~22 days of unreliable data for a single season, and ~91 days for a yearly home range estimate, then the home range for this individual for this period(s) was not calculated (see Table S3.1).

Seasonal home ranges for each deer were calculated by modelling the GPS movement data as a continuous-time stochastic process, which models movement data assuming the animal is moving continuously and accounts for randomness in animal movement (Calabrese et al., 2016). We calculated seasonal 95% home range contours for all range resident individuals using the R package *ctmm* v1.2.0 (Calabrese et al., 2016). Individuals that occupied the same area continuously throughout the monitoring period were termed 'range resident' (Mueller & Fagan, 2008). To do so, variograms, which visualise the average square distance travelled by each individual within their monitoring period, were used to assess the range residency of each individual. From visual assessment of variograms, if the semi-variance values reached an asymptote or flattened, before or at three months of monitoring, the individual was determined to be a range resident, and home range estimates were only generated for these individuals as range residency is an assumption of home range estimation (following Calabrese et al., 2016; Silva et al., 2021). For each range resident individual, perturbative hybrid residual maximum likelihood estimation, a model parameter estimation method, was used to determine which stationary movement model was most appropriate for each individual based on whether the data was autocorrelated or independently distributed. The models used were the independent and identically distributed (IID) null model, which is used when the animal has no autocorrelation, the Ornstein-Uhlenbeck (OU) model, which is suitable for data with autocorrelation in animal position, and the Ornstein-Uhlenbeck-F model (OUF), which is suitable when there is autocorrelation in animal position and velocity. Additionally, models were anisotropic if autocorrelation varied with direction (see Silva et al., 2021). The most appropriate movement model for each individual was selected based on AIC_C using the ctmm.select function (Calabrese et al., 2016) (Table S3.1). Then the 95% home range contour and 95% confidence intervals were quantified, via weighted autocorrelated kernel density estimation (wAKDE), for each deer, using model selected in the previous step.

The seasonal 100% MCP 'movement extent' was then calculated for all individuals, including those that were not range resident, as a measure of each animal's total movement range, using the *adehabitatHR* package v0.4.21. These statistics allow comparison of home range sizes generated here with earlier studies, as the MCP method is widely used, and the range residence assumption is often not tested (Calenge, 2007; Laver & Kelly, 2008; Silva et al., 2021).

Then, to determine whether seasonal home range or movement extent (response variables) were affected by monitoring year (predictor variable), linear mixed models with Gaussian distributions and individual ID as a random effect were constructed for each species using the *nlme* package v3.1.153 (Pinheiro et al., 2016). To assess the normality and heteroscedasticity of the models, graphs of residuals against fitted values and explanatory variables were generated, and residuals fanned out as fitted values and explanatory variables increased, indicating that the residuals were heteroscedastic for all models. In response to this, the response variables were natural log transformed, and following the transformation, the residuals were homoscedastic for all models. The final models were fitted with the log of movement extent as the response variable, and included sex and season in addition to year as fixed effects. Statistical significance was inferred at α = 0.05. We report the beta coefficients, standard errors, and p values for the fixed effects in each model.

Annual home ranges and movement extents were calculated using the wAKDE and MCP methods described above, and included location fixes from April 2021–November 2023; deer were included in the analyses only if they were monitored for an entire year. If individuals were monitored for two years, an annual home range was calculated for each year and results averaged by species and sex. The effect of year on annual home ranges could not be tested because individuals were monitored over different year-long periods, depending on when each individual was first collared.

3.4.4 Movement activity

To discern patterns in the movement activity of each species and sex throughout the year, we calculated the mean daily Euclidean distance between hourly location fixes for all individuals. Where individuals were monitored for more than one year, distances travelled were averaged between years to generate one resulting value for each calendar day. The mean values for each individual were then averaged to generate a mean for each calendar day for each species and sex.

3.4.5 Seasonal variation in elevational use

We calculated the mean elevation used by fallow deer, sambar deer and red deer for each season and fitted linear mixed models to determine how elevational usages changed between seasons, described below. For these models and the resource selection functions (RSFs) described below, deer were excluded from the analyses if they were monitored for less than two months in a given season. For all analyses, all datapoints with HDOP greater than 2.5 or where HDOP could not be calculated, were filtered from the dataset, resulting in the removal of 2.8% or 8755 datapoints from the total dataset (similar to Stewart et al., 2022).

To determine whether the mean elevation used for each season by each individual (response variable) was affected by season (predictor variable), linear mixed models with Gaussian distributions and individual ID as a random effect were constructed for each species using the *nlme* package v3.1.153 (Pinheiro et al., 2016). For these models, we applied a weight equal to the number of observations contributing to each seasonal mean elevation, so that averaged observations with higher numbers of observations contributing to their means for each season were weighed higher. Model assumptions were assessed by examining residual plots against fitted values and explanatory variables to check for normality and heteroscedasticity. Statistical significance was inferred at α = 0.05. We report the beta coefficients, standard errors, and p values for the fixed effects in each model.

3.4.6 Seasonal habitat selection

We used RSFs to examine habitat selection within each deer's seasonal movement extent in relation to a set of environmental covariates relevant to deer ecology (third order habitat selection; Johnson, 1980). The environmental variables included in the RSF model were elevation, slope, aspect, landcover type, distance to perennial water source and burnt area. Burnt area was only included in RSFs for the four sambar deer which had available habitat in and used fire affected habitat as fallow deer, and red deer and all other sambar deer did not have any fire affected habitat in their available habitat in any season (Figure 3.1). The aspect of the slope of each location clockwise from north was categorised into eight levels, north (0–22° and 338–360°), northeast (23–67°), east (68–112°), southeast (113–157°), south (158–202°), southwest (203–247°), west (248–292°) and northwest (293–337°). Vegetation was classified into six types: cleared (including cleared areas, non-native vegetation and buildings, this landcover type is predominantly pasture in our study area), eucalyptus forest/woodland (consisting of forests and woodlands dominated by Eucalyptus species with a projective foliage cover of 10–70%), native grassland (consisting of tussock grasslands and other grasslands, herblands, sedgelands and rushlands), inland aquatic (permanent water bodies, as well as areas which are subject to inundation or have ephemeral streams), shrubland (consisting of acacia and other shrubland) and heath (Table S3.2). Rasters were resampled to 100 m resolution using nearest neighbour resampling in ArcGIS Pro 3.1 (Environmental Systems Research Institute, 2020). Reference categories for categorical variables were 'eucalypt forest/woodland' for landcover type, 'east' for aspect, and 'no fire' for burnt area. For all species, sexes were analysed together, as small sample sizes did not facilitate analysis of the effect of sex on habitat selection.

To define availability, we generated 10 random 'available' locations for each GPS location within the seasonal 100% MCP for each individual, then the values of each environmental covariate were extracted for all used and random points using R package *amt* v0.2.1.0 (Signer et al., 2019). For deer that were monitored over multiple years, a separate MCP was generated for each successive season that the animal was monitored, and available points were generated for each MCP. Then, data from each animal was combined into one resulting seasonal dataset for each deer species.

Prior to model fitting, all numerical variables were checked for collinearity using the Pearson correlation coefficient prior to analyses, with 0.7 considered the threshold for correlation, and no variables were correlated. All continuous covariates were scaled and centred, and available points were weighted by 1000 (Muff et al., 2020).

The method outlined by Muff et al. (2020) was used to fit RSFs as generalized linear mixed effects models (GLMMs) with a binomial distribution and a large, fixed variance using the glmmTMB function in the *glmmTMB* package v1.1.7 interfaced through a high-performance computer (Brooks et al., 2017). These RSFs examined the effect of each environmental variable on the binary response variable that was either a true location used by a deer ("case" = 1), or a random location within the individual's seasonal movement extent ("case" = 0). Each combination of deer species and season was modelled separately ($N = 12$). We included individual as a random effect, and random slopes for each covariate to account for variation in responses among individual deer (Muff et al., 2020). The global model that was run for each species and season is given below:

case ~ elevation + slope + distance to water + vegetation type + aspect + (1 | ID) + (0 + elevation | ID) + (0 + slope | ID) + (0 + distance to water | ID) + (0 + vegetation type | ID) + (0 + aspect | ID)

First, we fitted the global models and checked for model convergence issues. If a global model did not converge, we examined the full set of sub-models to identify which variables or their random slopes might be causing non-convergence. For all models, random slopes for the categorical variables vegetation type and aspect had a variance close to zero, which led to model convergence issues, so these random slopes were removed from all global models and all sub-models (as in Hooven et al., 2023). To evaluate model fit, we compared AIC_C values of the global model and full sub model sets and selected the model with the lowest AIC_C value for each season and species, using *AICcmodavg* (Mazerolle, 2023). To determine the effect of each environmental variable on deer resource selection, we examined the β coefficients and confidence intervals of each environmental variable in the best fitting model. Here, model inference was drawn from the magnitude of effect size and their corresponding confidence intervals.

3.4.7 Burn severity selection by sambar deer

An area in the north-west of the study area was burnt with low to very high intensity during extensive bushfires between December 2019–January 2020 (Figure 3.1; Department of Planning and Environment, 2023). Step selection functions (SSFs) were evaluated to examine sambar deer movement decision-making in their use of fire affected areas and their burn-severity preferences. Only four collared sambar deer (3 males, 1 female) had available habitat in burnt area, therefore all other animals were excluded from this analysis. To examine fine-scale sambar deer preferences when they were close to burnt areas, location data was subset to include only locations within 500 m of burnt areas. Some collars recorded location information less frequently than hourly towards the end of their life, so location data were resampled to 8 hours for consistency between individuals. Then, 100 random steps were generated for each used step by drawing from a gamma distribution of step lengths (rate = 430.256, shape = 0.984) and a von Mises distribution of turn angles (mean = 0.003, kappa = 0.093). The parameters of each distribution were calculated using packages *MASS* v7.3-64 (Ripley et al., 2025), and *circular* v0.5-1 (Lund et al., 2024). Fire-severity scores; 'no data' (unknown fire status, likely due to cloud contamination in imagery within a fire extent [W. Dorrington, personal communication, September 5, 2023]), ‘unburnt’, ‘low–moderate’ (burnt understory, unburnt canopy), ‘moderate’ (partial canopy scorch), ‘high’ (complete canopy scorch, partial canopy consumption), or ‘very high’ (full canopy consumption) were extracted for all steps at the end point of each step using a Fire Extent and Severity map (Table S3.2), and ‘unburnt’ was selected as the reference category. Individuals were modelled separately using conditional logistic regression models in the *survival* package v.3.8.3 (Therneau et al., 2023). To infer group-level responses, we calculated inverse-variance weighted averages of the coefficients across individuals, we calculated confidence intervals from the average weighted estimates. One female sambar deer (ID: 049818) was excluded from model averaged estimates due to model convergence issues, likely due to low sampling of the very high severity burn class by this individual. The statistical significance of results was inferred if the confidence intervals of the model did not include zero. All statistical analyses were conducted in R (R Core Team, 2021) interfaced via RStudio Desktop (v. 4.3.2).

3.5 Results

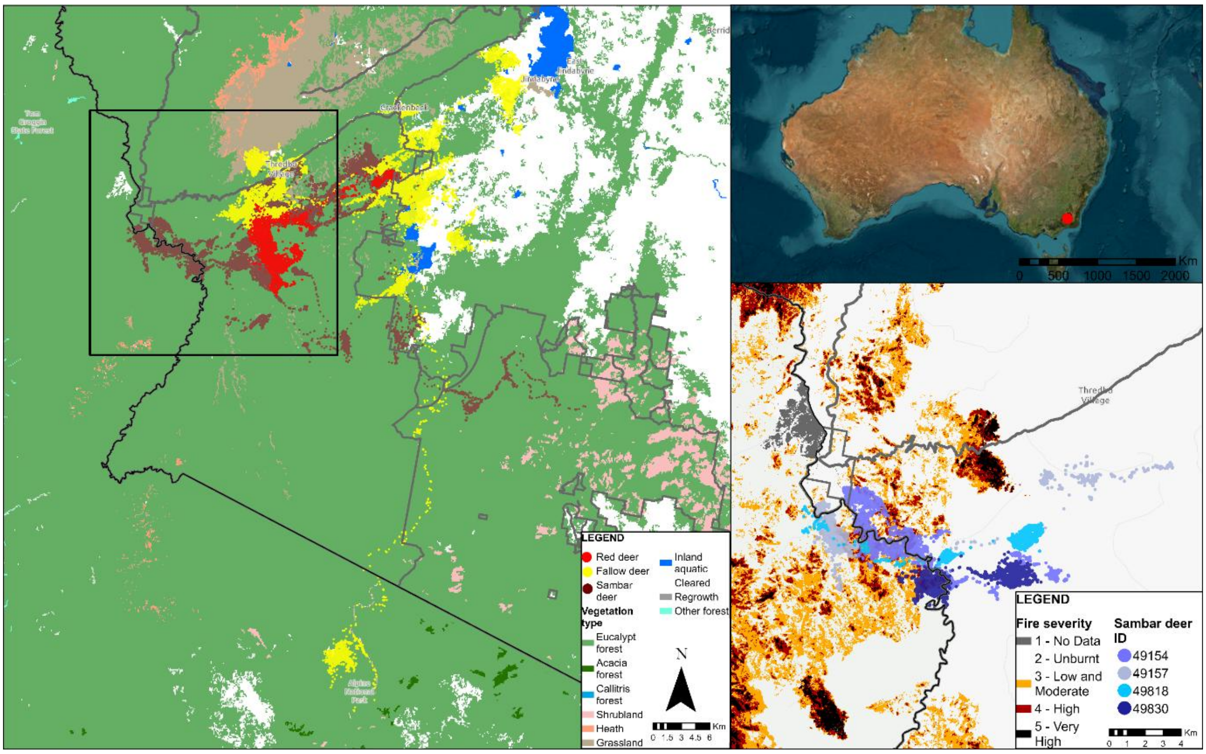


Figure 3.1: Left: Map of study area, depicting sambar deer (*Rusa unicolor*; brown points; $N = 14$), red deer (*Cervus elaphus*; red points; $N = 5$) and fallow deer (*Dama dama*; yellow points; $N = 14$) GPS locations between April 2021 and May 2023, in and around southern Kosciuszko National Park, Australia. The black line indicates the NSW Victoria border, the grey lines indicate the borders of Kosciuszko National Park. The black extent indicator shows the area displayed in the bottom right image. Top right: The location of the study area relative to Australia is indicated by the red dot. Bottom right: Location fixes of the four sambar deer (*Rusa unicolor*) between April 2021–May 2023 which used areas burnt in the 2019–2020 fires which affected parts of the alpine region in NSW and eastern Victoria. Image sources: Esri, Maxar, Earthstar Geographics.

3.5.1 Animals monitored

In total, location data from 13 sambar (8 males, 5 females), 5 red (2 males, 3 females), and 14 fallow deer (7 males, 7 females), were included in this study. Of the 14 sambar deer collared, one deer was excluded due to unconfirmed mortality/collar malfunction less than two months following collaring. Of the 20 fallow deer collared, six were excluded from the analysis, two because of confirmed mortality by a human hunter, and four because of unconfirmed mortality/collar malfunction less than two months after capture.

3.5.2 Home ranges and movement activity

Year of monitoring did not have an effect on the resulting seasonal movement extent and home ranges of fallow deer, red deer or sambar deer (Table S3.3). Therefore, mean seasonal home ranges are presented with data from 2021–2023, with seasonal home ranges combined across years to generate means and standard errors (Table S3.4). We found that fallow deer home ranges and movement extents were highest in spring and autumn for males, while for females, movement extents were smallest in winter but stable across the other seasons, while home ranges were smallest in spring but stable across the other seasons (Figure 3.2). For red deer, movement extents and home ranges were highest in summer (and autumn for movement extent) for males, while for females, movement extent and home range was lowest in winter and relatively stable across the other seasons (Figure 3.2). For fallow deer and red deer, acute increases in movement activity were recorded in April, in alignment with the breeding season (rut; Figures S3.1–S3.3). For sambar deer, male movement extent was highest in autumn and winter and home range was highest in spring and autumn, for females, movement extent was relatively stable throughout the year, while home range was highest in autumn and relatively stable across the other seasons (Figure 3.2; Table S3.4).

Fallow deer males had an annual home range of 226.9 ± 54.3 km ($N = 4$), and a movement extent of 78.2 ± 5.9 km ($N = 5$), while females had a home range of 55.1 ± 46.5 km ($N = 3$), and a movement extent of 50.2 ± 14.1 km ($N = 7$; Table S3.4). No red deer males were monitored for a full year, so only female red deer annual home range is reported and was 70.2 ± 35.5 km ($N = 4$), female red deer annual movement extent was 35.3 ± 5.2 km ($N = 4$; Table S3.4). Sambar deer males had an annual home range of 25.3 ± 4.0 km ($N = 2$) and a movement extent of 111.9 ± 56.7 km ($N = 5$), sambar deer females had a home range of 80.7 km ($N = 1$), and a movement extent of 64.9 ± 3.3 km ($N = 3$; Table S3.4).

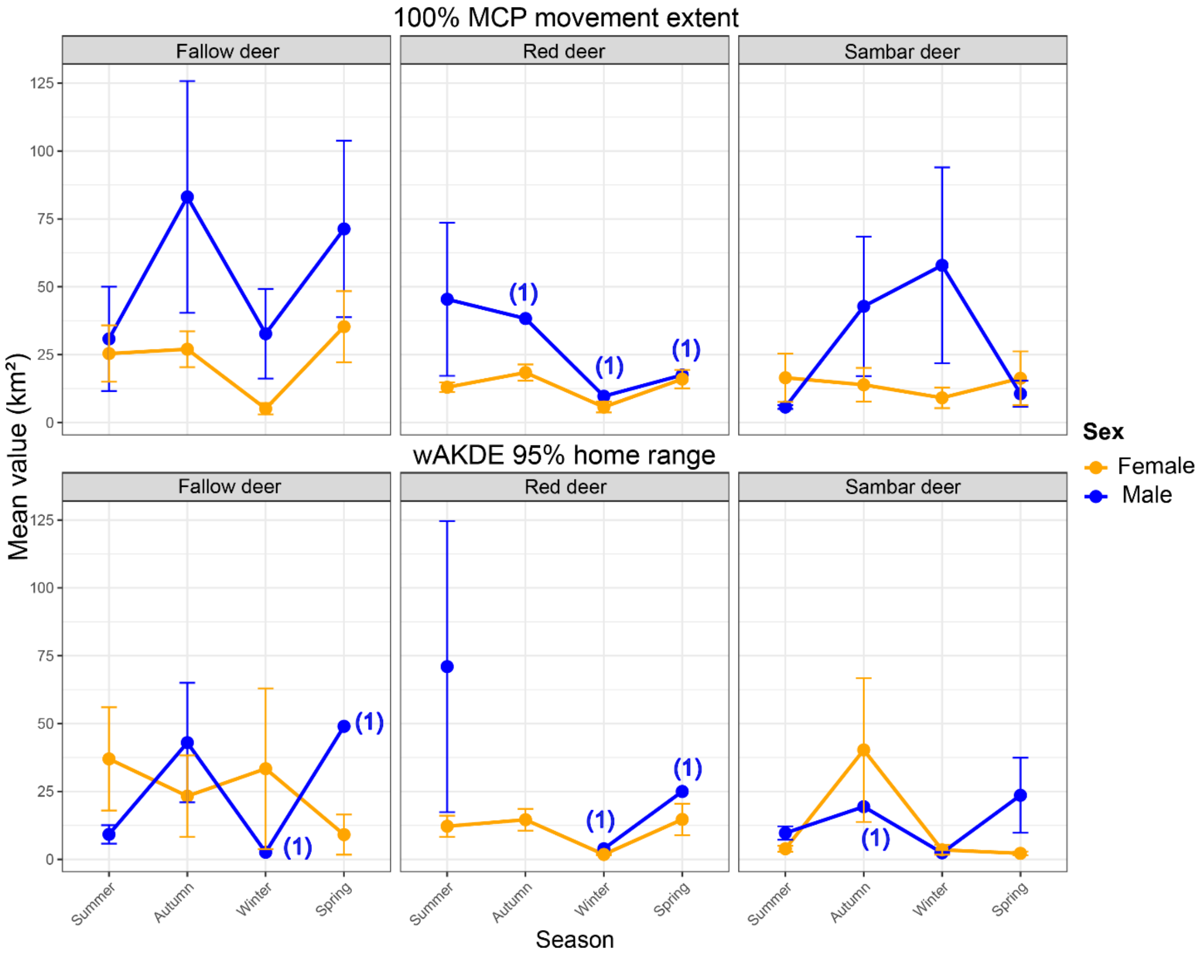


Figure 3.2: Seasonal mean movement extents (100% minimum convex polygons; top row) and home ranges (95% weighted autocorrelated kernel density estimates; bottom row) of fallow deer, red deer and sambar deer males (blue) and females (orange) in a subalpine area of Kosciuszko National Park, Australia. Points with a (1) beside them indicate that only one animal contributed to the estimate for that season.

3.5.3 Seasonal habitat preferences

For fallow deer, the mean elevation used in summer was 1517 m ASL (Q1: 1235 m, Q3: 1762 m) the mean slope used was 11° (Q1: 6°, Q3: 14°), in autumn this reduced to 1449 m (Q1: 1187 m, Q3: 1740 m), and the mean slope used was 11° (Q1: 6°, Q3: 15°). By winter, they used a mean elevation of 1334 m (Q1: 1151 m, Q3: 1520 m) and mean slope used increased to 16° (Q1: 9°, Q3: 22°). Fallow deer remained at a similar elevational range in spring (mean: 1334 m, Q1: 1157 m, Q3: 1560 m), and used a mean slope of 11° (Q1: 6°, Q3: 16°).The linear mixed model evaluating between-season elevational usage fallow deer showed that showed that the mean elevation used by the species was significantly lower in winter ($\beta = -205.013$, SE = 95.322) compared with summer (Table S3.5).

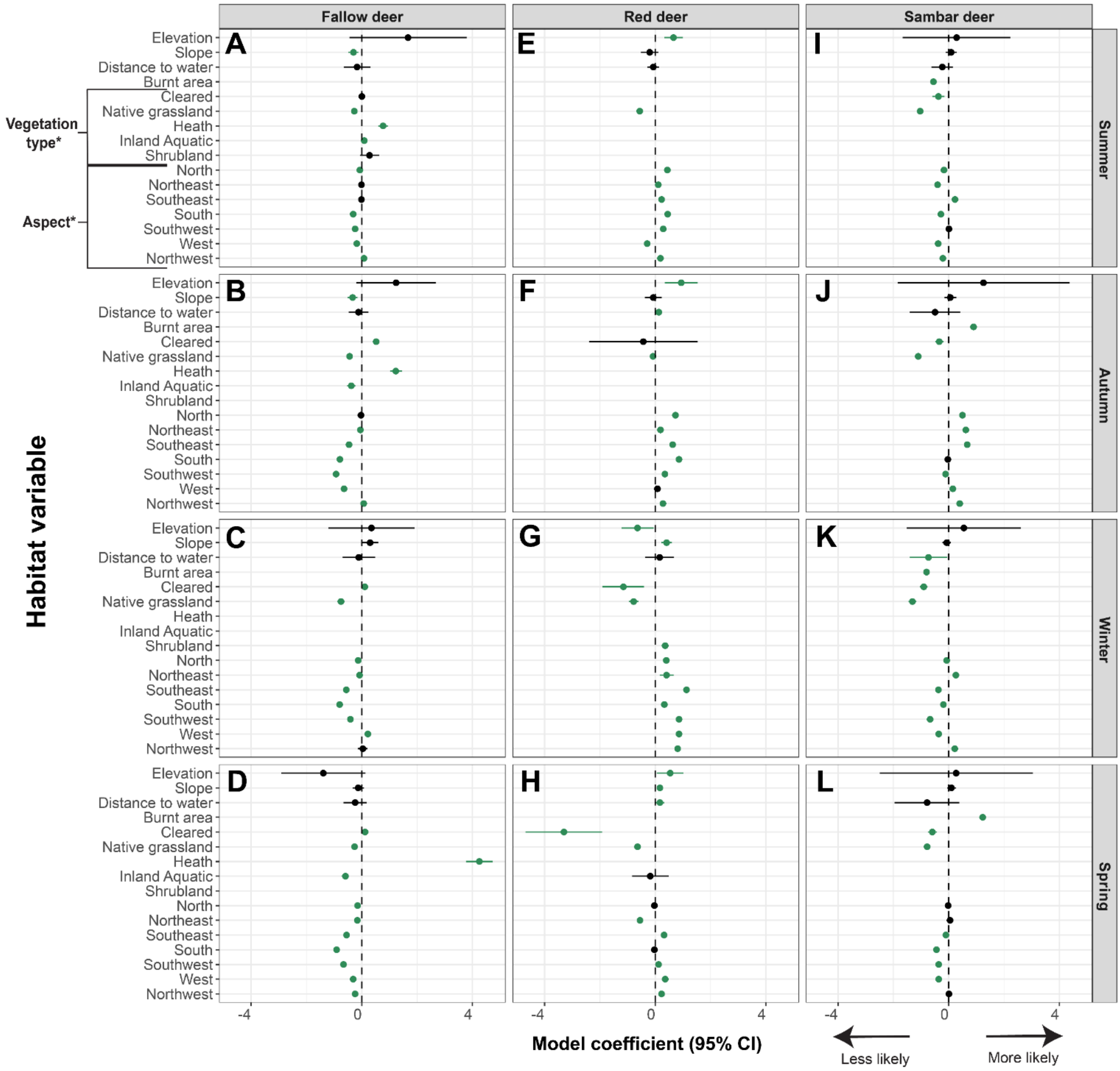
For RSFs for all seasons and species, the global model was the best performing model, with $\Delta AIC_C \geq 3$ when compared to the next best competing sub-model (Table S3.6). For fallow deer, seasonal RSFs indicated that they had no elevational preference within their seasonally available ranges (Figure 3.3 A–D), but they showed a preference for gentler slopes in summer and autumn (Figure 3.3 A, B; Table S3.6). Fallow deer showed no clear preference for proximity to water in any season (Figure 3.3 A–D). The majority of vegetation used by fallow deer was eucalypt forest/woodland, however, in summer, fallow deer preferred heath and inland aquatic areas, and avoided native grasslands (Figure 3.3A; Figure 3.4). In autumn, fallow deer preferred cleared areas and heath, and avoided inland aquatic areas and native grasslands (Figure 3.3B). In winter, fallow deer were never located in heath, inland aquatic areas, or shrubland. They preferred cleared areas compared to eucalypt forest/woodland and avoided native grassland (Figure 3.3C). By spring, fallow deer showed a preference for cleared areas and heath, and avoidance for native grassland and inland aquatic areas (Figure 3.3D). In summer and autumn, fallow deer preferred east and north facing slopes (Figure 3.3A, B), in winter they preferred east and west facing slopes (Figure 3.3C), and in spring they preferred east facing slopes (Figure 3.3D; Table S3.6).

For red deer, the mean elevation used in summer was 1709 m ASL (Q1: 1672 m, Q3: 1759 m), the mean slope used was 13° (Q1: 8°, Q3: 17°). In autumn the mean elevation used reduced to 1672 m (Q1: 1616 m, Q3: 1778 m) and the mean slope used was 14° (Q1: 8°, Q3: 19°). In winter the mean elevation used reduced again to 1483 m (Q1: 1348 m, Q3: 1636 m), and the mean slope used increased to 21° (Q1: 17°, Q3: 25°). In spring, the mean elevation used increased to 1633 m (Q1: 1607 m, Q3: 1749 m), and the mean slope used decreased to 14° (Q1: 8°, Q3: 19°). The linear mixed model evaluating between-season elevational usage by red deer showed that the mean elevation used by the species was significantly lower in winter ($\beta = -218.230$, SE = 44.853), compared with summer (Table S3.5).

Seasonal RSFs indicated that red deer showed a strong preference for higher elevations within their seasonally available habitats for all seasons except winter, where they showed a preference for lower elevations (Figure 3.3 E–H). Red deer preferred steeper slopes in winter and spring (Figure 3.3 G–H; Table S3.6); in spring and autumn, they showed a preference for habitats away from continuous waterbodies (Figure 3.3 F, H). The majority of vegetation used by red deer was eucalypt forest/woodland, which red preferred in all seasons, compared to other used habitat types, cleared areas and native grasslands (Figure 3.3 E–H; Figure 3.4). In winter, red deer used and selected for shrubland (Figure 3.3G). In spring, red deer used inland aquatic areas, which they did not show a preference for compared to other used habitat types (Figure 3.3H). In summer and autumn, red deer avoided east and west facing slopes, preferring south and north facing slopes (Figure 3.3 E&F). In winter, they showed the strongest preference for southeast and west facing slopes; Figure 3.3G). By spring, they showed a strong preference for southeast, and west facing slopes (Figure 3.3H; Table S3.6).

For sambar deer, in summer the mean elevation used was 1463 m ASL (Q1: 1461 m, Q3: 1695 m) and the mean slope used was 15° (Q1: 9, Q3: 20°). In autumn, the mean elevation used was 1353 m (Q1: 854 m, Q3: 1693 m), and the mean slope used was 16° (Q1: 10, Q3: 20°). In winter, the mean elevation used reduced to 1102 m (Q1: 683 m, Q3: 1457 m), and the mean slope used was 18° (Q1: 11, Q3: 24°). In spring, the mean elevation used was 1162 m (Q1: 743 m, Q3: 1433 m), and the mean slope used was 17° (Q1: 11°, Q3: 23°). The linear mixed model evaluating between-season elevational usage by sambar deer showed that the mean elevation used by the species was significantly lower in winter (β = -496.106, SE = 84.029) and spring (β = -434.214, SE = 103.587), compared with summer (Table S3.5).

Seasonal RSFs indicated that sambar deer showed no substantial elevation or slope preferences within their seasonally available ranges (Figure 3.3 I–L; Table S3.6). In winter, sambar deer preferred locations closer to perennial water sources comparatively with what was available within their available ranges (Figure 3.3 K). The majority of vegetation used by sambar deer was eucalypt forest/woodland, which sambar preferred in all seasons, compared to other used habitat types, cleared areas and native grasslands (Figure 3.3 I–L; Figure 3.4). In summer, sambar deer preferred east and southeast facing slopes (Figure 3.3I). In autumn, they selected for north and northeast facing and southeast facing slopes (Figure 3.3J). In winter and spring, they selected for northeast, east and northwest facing slopes (Figure 3.3 K,L). In summer and winter, the four sambar deer that used fire affected habitat, avoided burnt areas, but selected for burnt areas in autumn and spring (Figure 3.3 I–L; Table S3.6).



*For all resource selection functions, 'eucalypt forest/woodland' was the reference vegetation type, 'east' was the reference aspect, and 'no fire' was the reference burnt area class. Selection coefficients presented here represent preferences for each vegetation type and aspect, and 'burned' for burnt area, relative to the reference type for each variable.

Figure 3.3: Selection coefficients (β parameter estimates) and 95% confidence intervals of generalized linear mixed effects resource selection functions, modelling the habitat preferences of fallow deer, red deer, and sambar deer in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. Coefficients coloured green have confidence intervals that do not include zero. For continuous variables, the direction of the coefficient indicates whether a species was more (coefficient above zero) or less (coefficient below zero) likely to be present at higher values of each variable. For categorical variables, the direction of the coefficient indicates whether the species was more (coefficient above zero) or less likely (coefficient below zero) to be present in that category relative to the reference class. Where a selection coefficient is not present, this habitat type was not experienced by any collared animal of that species for that season.

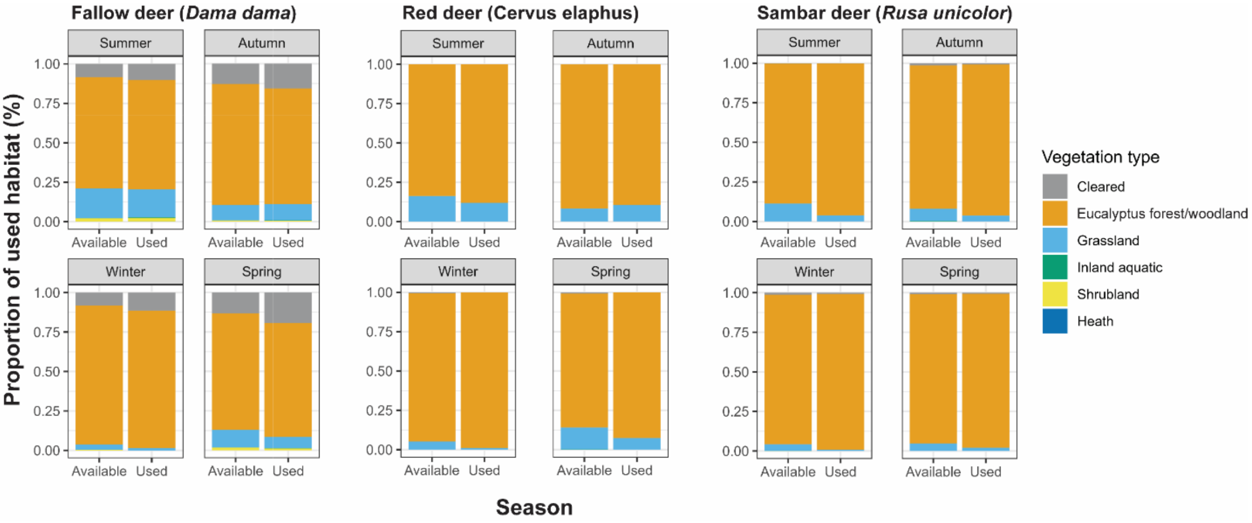


Figure 3.4: The proportion of used versus available habitat types for three species of feral deer, fallow deer, red deer, and sambar deer, which are present in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia between April 2021 and May 2023.

3.5.4 Burnt severity selection by sambar deer

For the three sambar deer that were included in this analysis, individual preferences were variable, with one individual selecting for low to moderate and high severity burnt areas, and one individual selecting for low to moderate burnt areas, the third individual did not show a preference (Table S3.7). The inverse distance weighted average selection coefficients of the step selection functions run for each individual showed that when these individuals were within 500 m of burnt habitat, they preferentially inhabited areas that were burnt in the 2019–2020 fires with low to moderate and high severity intensity (Figure 3.5).

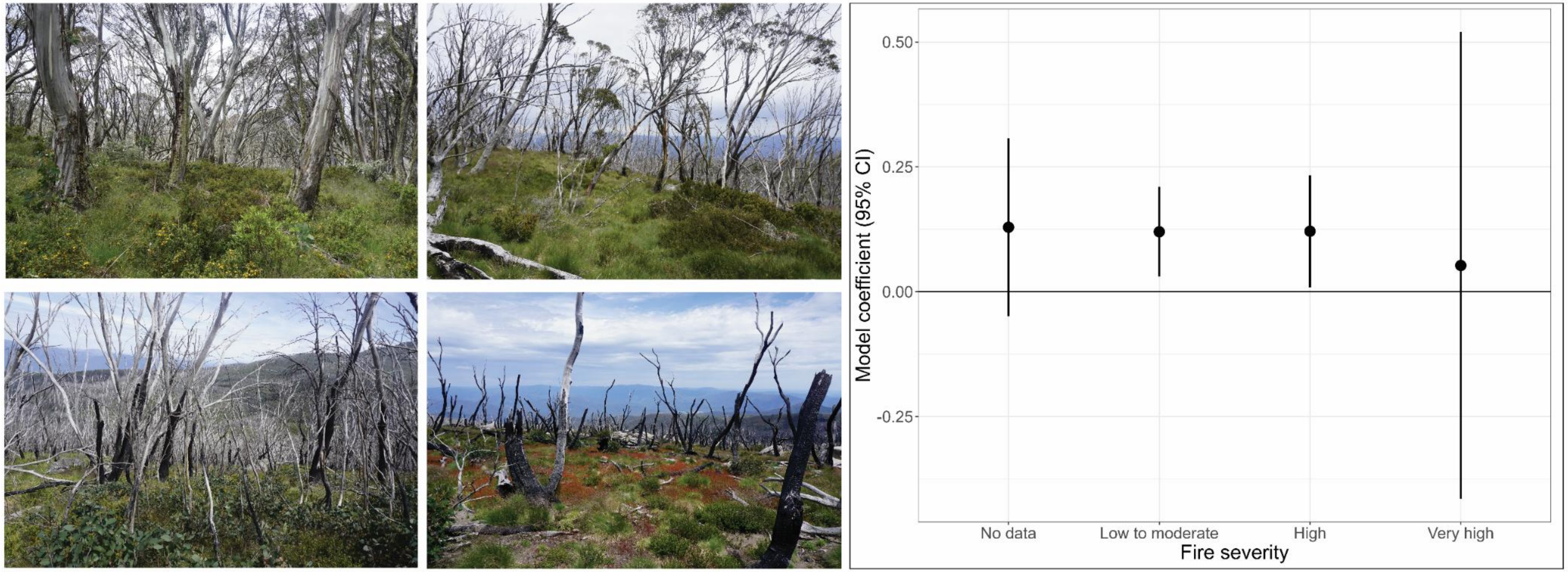


Figure 3.5: Left: Images of landscape affected by the 2019–2020 fires in the region, showing unburnt (top left), low to moderate severity (top right), high severity (bottom left) and very high severity burnt forest (bottom right); all images were taken in December 2023. Burn severity data source: Department of Planning and Environment, 2023. Right: Averaged step selection function coefficients and 95% confidence intervals of burn severity class preference relative to unburnt areas (the reference class) of GPS collared sambar deer between 2021–2023 in the Snowy Mountains region of southeastern Australia, when within 500 m of a burnt area. The three individuals were modelled separately using conditional logistic regressions, and coefficients were inverse-variance averaged for group level inferences.

3.6 Discussion

In this study, we sought to understand fallow deer, sambar deer and red deer habitat preferences based on home range and movement data, so that control efforts can be more precisely targeted to at-risk environmentally sensitive areas and locations where deer are most likely to be present. Sample sizes for all three species, particularly red deer, were low, so our findings may not be representative of the species, nonetheless, our study provides insight into habitat use by invasive deer within the Australian Alps. As predicted, (1) all species mainly inhabited eucalypt forest/woodland, however, while red deer and sambar deer inhabited eucalypt forest/woodland more than 90% of the time, fallow deer were more varied in their habitat use, and spent time in cleared areas, heathland, and inland aquatic areas. (2) All species tended to inhabit higher elevations in summer, and lower elevations in winter, with all species using significantly lower mean elevations in winter compared to summer, and for sambar deer, in spring compared to summer. Additionally, within their seasonally available ranges, red deer selected for higher elevations in summer, autumn and spring, but lower elevations in winter. (3) fallow deer and red deer did not inhabit burnt areas, and while only four sambar deer used burnt areas, these sambar deer preferentially inhabited these areas in spring and autumn, selecting for low to moderate and high severity burnt areas. The three invasive deer species found in alpine Australia display distinct seasonal movement patterns and habitat preferences. Recognising and understanding these differences is crucial when devising control programs and prioritising conservation efforts.

3.6.1 Fallow deer home range and habitat use

Annual home range estimates of fallow deer in this study exceeded prior estimates from the USA (Morse et al., 2009), Poland (Borkowski & Pudełko, 2007), and Italy (Ciuti et al., 2003; Davini et al., 2004). Seasonal home ranges recorded in this study were also considerably larger than previously reported estimates from Poland (Borkowski & Pudełko, 2007) and Italy (Ciuti et al., 2003; Davini et al., 2004) across all seasons. Fallow deer in our study had the largest home ranges in spring for males, and in summer for females (Figure 3.2; Table S3.4). Previous research on fallow deer in Italy, within the native range of fallow deer, showed that that home range was largest in autumn for both sexes (Borkowski & Pudełko, 2007; Ciuti et al., 2003). Despite home ranges not being largest in autumn in this study, male movement extents were largest in autumn (Figure 3.2), suggesting non range residents were undertaking longer distance movements. Additionally, we saw a spike in male activity, or mean hourly distances travelled, in April (during autumn), which coincides with the breeding season (rut; Figure S3.1), when adult males are known to follow and defend groups of females and fight with other males (Alvarez et al., 1990; Jennings et al., 2013).

In our study area, fallow deer appeared to be a more generalist species than red deer and sambar deer, inhabiting a wider variety of habitat types (Figure 3.3 A–D). Fallow deer also showed a preference for inland aquatic areas in summer (Figure 3.3A; Figure 3.4). Although we could not uncover what fallow were using these aquatic areas for, swimming has been reported in Persian fallow deer (Khademi, 2014). While fallow deer were shown to avoid native grasslands, they did use native grasslands more often than their heterospecifics, particularly in summer (Figure 3.3A; Figure 3.4). Fallow deer also used a higher proportion of cleared land in all seasons compared with sambar deer and red deer, selecting for cleared areas in autumn, winter and spring (Figure 3.3 B–D; Figure 3.4). Fallow deer are known to be opportunistic generalist grazers and browsers (Davis et al., 2023), and are highly adaptable to seasonal food availability (Esattore et al., 2022). They browse on lower quality food while snow covers ground vegetation during the European winter (Kamler & Homolka, 2011), and graze on crops and pasture in agricultural areas in Australia (Bentley, 1998; Davis et al., 2023; Hall & Gill, 2005). Their adaptable dietary requirements and use of a variety of vegetation types in alpine Australia suggest that fallow deer present a widespread risk and should be targeted for control in a variety of habitat types in the Australian Alps.

3.6.2 Red deer home range and habitat use

Like fallow deer, red deer home range estimates from this study were considerably larger than previous estimates of red deer home range from Australia and abroad (Amos et al., 2014; Catt & Staines, 1987; Jerina, 2012; Reinecke et al., 2014). In Queensland, in a low elevation subtropical environment, red deer had home ranges that were lowest during the rut (6 km^2 for males and ~ 1 km^2 for females) for one year and second lowest behind summer for another year. The one male in our study that was monitored during the autumn period was not range resident and had a movement range almost twofold the mean summer range for males (Figure 3.2; Table S3.4). The mean movement extent of red deer females in this study also peaked in autumn (Figure 3.2; Table S3.4), where only three of five individuals were range resident, and like fallow deer, male red deer also had a peak in movement activity between late March and early April (Figure S3.2). Heightened activity during the rut for red deer males is well documented and increases mating success (Csányi et al., 2022). Previous research has shown that females may also make extraordinary movements when in oestrus during the rut, potentially to pursue novel matings (Stopher et al., 2011), however, we did not see a peak in activity for female red deer during this period (Figure S3.2). This may be because the red deer population has a restricted range within the study area (suggested in Figure 3.1) and movements outside of this range would not lead to novel matings. Tracking greater numbers of red deer or conducting indirect sampling (either through camera trapping or faecal pellet surveys) would establish the total movement range of the red deer population within the study area, and if they were locally confined, control could aim for local eradication.

In summer, red deer tended to inhabit higher elevations than the other two species, and had no cleared land within their used habitat, indicating that all individuals remained within the national park for the duration of the season, despite the summer home range being the largest seasonal home range for male red deer (Figure 3.2; Figure 3.3E; Figure 3.4). This peak in home range size in summer has previously been reported for male red deer in Europe (Clutton-Brock et al., 1982; Georgii & Schröder, 1983), but was not found for red deer in subtropical Australia (Amos et al., 2014). In areas with more extreme seasonal and temperature variation, like our study area in alpine and subalpine KNP and surrounds, red deer may behave more similarly to their European conspecifics, and may seek out habitats that maximise energy gains in summer, in preparation for the rut, as seen in Europe (Bocci et al., 2012). For autumn, winter, and spring, red deer in our study continued to occupy higher mean elevations than the other two species, and used a more limited range of vegetation types than fallow, using predominantly eucalypt forest/woodland, but also native grassland, cleared lands (in all seasons except summer) and inland aquatic areas (in spring). Previous research indicates that the likelihood of red deer presence on agricultural land decreases with distance to forest (Månsson et al., 2021), similarly, while red deer in this study did use a small proportion of cleared land close to subalpine KNP, they used cleared areas the least of the three species studied. Red deer predominantly inhabited the high elevation forested areas within KNP, these results suggest that control targeting this species in the summer may be most efficient, as red deer are likely to be within the national park and not on private property.

3.6.3 Sambar deer home range and habitat use

Sambar deer are reported to be mainly sedentary (Leslie, 2011) and we saw that home ranges of range resident males and females tended to be lower than for the other two species for range resident males in all seasons except summer, and range resident females in summer and spring (Figure 3.2; Table S3.4). Despite this, annual movement extents of non-range residents were the largest of the three species, and markedly larger than other previously reported annual home range estimates for the species in Taiwan (Yen et al., 2019), India (Sankar, 1994), and the USA (Richardson, 1972; Shea, 1986). Notably, home ranges for all three species were larger than several other earlier reported estimates of their conspecifics in other regions. In tracking efforts with a small effective sample size, conventional home range estimators have been shown to markedly underestimate home range size, so in this study we used an AKDE home range estimator to mitigate this effect (Silva et al., 2021), and this may have also contributed to the larger home ranges we found. Notably however, invasive species at the invasion front have been reported to exhibit larger daily movement distances than conspecifics in their native ranges (Shine et al., 2021), as well as larger exploratory home ranges compared to those in longer established areas (Burstal et al., 2020). The larger home ranges we report in this study could also potentially be a function of low resource density and preferrable habitat within the study region, as higher forage quality (Tomaszewski et al., 2022) and productivity (Bjørneraas et al., 2012) have been associated with smaller home range sizes.

Sambar deer exhibited seasonal movement patterns, moving to lower elevations in winter, compared with their summer range (Table S3.5); this behaviour has been reported for sambar deer in Australia (Comte et al., 2022; Greene, 2022), as well as within their native range (Yen et al., 2019). Across the monitoring period however, sambar deer location fixes ranged from elevations between 123 and 2046 m above sea level, and they tended to utilise lower mean elevations than the other two species throughout the seasons, despite lower available elevations not being selected for within their seasonally-available range in any season (Figure 3.3 I–L). Sambar deer may be occupying lower elevations than the other two species because they are a predominantly tropical species, and have a lighter weight coat and lower capacity for heat production than the other species (Semiadi et al., 1996). Unlike the other two species, sambar deer are known to mate year-round closer to the equator, within their native ranges (Dahlan & Dawend, 2013). However, further from the equator they may have a more distinct breeding season, for example, in alpine and subalpine Victoria, peak rutting occurs in spring (Watter et al., 2020). However, in this study, unlike the other two species, there are no visually distinct peaks in sambar distances travelled throughout the year that may be indicative of altered activity due to breeding, suggesting they exhibit a broad breeding pattern in this study (Figure S3.3). While fallow deer and red deer exhibit heightened activity during the autumn rut, sambar deer maintain relatively consistent activity levels throughout the year, and instead, their movements are more likely dictated by seasonally-dependent habitat selection.

Sambar deer showed a preference for areas closer to perennial water sources in winter, for other seasons, estimates suggested a preference, but were not reliable due to high variance (Figure 3.3 I–L). In Victoria, sambar deer presence and density has previously been correlated with closeness to water, as these areas likely support higher quality forage (Fedrigo et al., 2024; Forsyth et al., 2009; Sotorra et al., 2020), however, another study in subalpine Victoria suggests lower activity of sambar deer close to watercourses (Comte et al., 2022). Sambar deer used the most limited range of vegetation types, using only eucalypt forest/woodland, native grassland and cleared area throughout the monitoring period, showing a strong preference for eucalypt forest/woodland for all seasons (Figure 3.3 I–L, Figure 3.4). Sambar deer are known to be forest dwelling, and have previously been reported to only enter open areas at night to feed (Porwal et al., 1996), despite this, open habitats are thought to be important feeding habitats for sambar deer (Forsyth et al., 2009). Our study indicates that sambar deer exhibit a preference for forested regions near water sources. Sambar deer may therefore pose a heightened risk to waterways, with greater potential for damage through trampling and wallowing (as in Comte et al., 2023). Consequently, targeted control measures in proximity to subalpine and alpine wetlands and waterways should be considered to safeguard these ecosystems.

In autumn and spring of 2021–2023, sambar with available habitats intersecting fire-affected areas in the 2019–2020 megafires showed a preference for burnt areas 2–3.5 years post-fire (Figure 3.3 J & L). Step-selection functions showed that, compared with unburnt areas, sambar deer preferred low to moderate (burnt understory and unburnt canopy) and high severity (complete understory scorch, partial canopy consumption) burnt areas (Figure 3.5; Department of Planning and Environment, 2023). Previous studies of sambar deer in Australia show that populations were substantially reduced immediately following fire, but that burnt habitat was reoccupied 1.3–2 years post fire (Forsyth et al., 2012). Post-fire successional changes in vegetation may provide higher quantities of high-quality forage and denser understorey for shelter, which sambar may be selecting for (Downes, 1983; Fuhlendorf et al., 2009); this has previously been shown for elk in north America (Bailey & Whitlam, 2002). Post-fire herbivory can prevent the regeneration of native vegetation, and alter plant community composition (Tuft et al., 2012). Sambar deer are known to eat invasive plant species, such as Hawkweed (*Pilosella* spp.), in Alpine areas (Quin et al., 2023), and so could potentially aid in the colonisation of invasive plant species in fire affected areas in Australia via seed dispersal. Future research on plant species preferred by sambar deer post-fire could clarify vulnerability to herbivory and trampling in native species and identify invasive species at risk of dispersal by sambar deer. This information could aid in prioritising control efforts for at-risk ecological communities.

3.6.4 Management implications for invasive deer

In Australia, limited knowledge of invasive deer movement potential, interactions with threatened habitats, and their agricultural impact prevents the development of targeted management approaches (Davis et al., 2016). Knowledge of deer movement and habitat preferences should be used to develop scientifically-informed control programs (as described in Comte et al., 2022; Forsyth et al., 2010; Latham et al., 2015). All three deer species studied herein exhibited seasonal altitudinal migration, inhabiting higher elevations in summer, and moving to lower elevations in winter. This pattern is reflected in the mean elevations used by all three species, and statistical testing supported this seasonal shift for all three species (Table S3.5). Therefore, we recommend control be prioritised in accordance with seasonal movements, and should occur at higher elevations in summer, and lower elevations in the colder months (previously proposed for sambar deer in alpine Australia in Comte et al., 2022). In the colder months we saw that the three species had lowered activity and small seasonal home ranges, and had the lowest proportion of fixes in native grassland. Therefore, as animals will be less active, they may be less visible and more difficult to target in aerial shooting operations, and control during the colder months may be less effective, although lower temperatures would be more favourable for thermal aerial culling operations (Cox et al., 2023). Our habitat selection analyses imply that we can selectively target species by targeting specific habitats, for example, control on cleared or agricultural areas, may more likely result in a population reduction for fallow deer, as they occupy cleared areas more often than the other two species, particularly in autumn, and to a lesser extent, winter and spring, when they exhibit the strongest selection for cleared areas. The effectiveness of targeting preferred vegetation types for deer population control should be formally evaluated for our study area. Moreover, fallow deer movement between agricultural land and adjacent national park creates the opportunity for dispersal of plants, including invasive species, between the two zones, and of particular concern would be the movement of plants from the agricultural areas to the national park (Claridge et al., 2016). Fallow deer are also more likely to be vectors of disease to domestic animals and livestock, particularly in the warmer months when they are more likely to move between agricultural and wilderness areas (Pacioni et al., 2022). Critically, control efforts typically target burnt areas immediately after fire, where the open postfire canopy improves visibility (Rumpff et al., 2023), however, deer populations have been shown to decrease in burnt areas immediately postfire and increase in the years following (Forsyth et al., 2012). In addition to post-fire control, burnt areas should therefore be targeted in the years following a fire, when invasive herbivores, like sambar deer, use burnt areas, and likely increase damage and prevent regeneration and post-fire recovery.

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3.9 Supplementary Material

Table S3.1: Online spreadsheet that includes a tracking summary for each individual, detailing tracking duration, number of locations received and reason for collar failure where appropriate. Also includes seasonal and annual individual weighted autocorrelated kernel density estimates (95% wAKDEs) home ranges, and upper and lower home range estimates, effective and absolute sample sizes and home range models used, as well as minimum convex polygon (100% MCPs) movement extents for each collared deer that was tracked for more than two months of each season for each year they were monitored. The dataset is downloadable here: https://doi.org/10.6084/m9.figshare.24531406.v1

Table S3.2: Habitat variables used in resource selection functions and step selection functions evaluating fallow deer, red deer, and sambar deer habitat preferences in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. Habitat variables were derived from the sources provided below for the minimum convex polygon of all deer locations with a 20 km buffer.

Type	**Variable name (units)**	**Description**	**Resolution (m)**	**Source & access date**
Topography	Elevation (metres)	Digital elevation model (DEM)	100	Victoria: Vicmap Elevation DEM 10m (Department of Energy Environment and Climate Action, 2023) Accessed 17th July 2023. New South Wales: NSW Elevation Data Service (Department of Customer Service, 2023a) Accessed 17th July 2023.
	Slope (degrees)	Derived from DEM using the Slope tool in ArcGIS Pro 3.1.		
	Aspect	Derived from DEM using the Aspect tool in ArcGIS Pro 3.1.		
	Distance to water (m)	A distance to feature raster layer was derived in ArcGIS Pro 3.1 using the Distance Accumulation tool. The layer was derived from features where the variable 'hydronamet' = 'river', 'rivulet', 'creek' and 'gully' for the New South Wales dataset (NSW Hydrology) and the variable 'FTYPE_CODE' = 'watercourse_river' and 'connector_river' for the Victoria dataset (Vicmap Hydro). Ephemeral and minor water bodies were	1:25000 (scale)	Victoria: Vicmap Hydro (Department of Transport and Planning, 2023) Accessed 17th July 2023. New South Wales: NSW Hydrography – SEED

		excluded for the resulting raster. For New South Wales, features where the variable ‘hydronamet’ = ‘backwater’, ‘gulch’, ‘hollow’ and ‘bog’ were excluded. For Victoria, features where the variable ‘FTYPE_CODE’ = ‘connector_stream’, ‘watercourse_channel_drain’, ‘watercourse_stream’ and ‘connector_channel_drain’ were excluded.		(Department of Customer Service, 2023b) Accessed 17th July 2023.
Landcover	Vegetation type	Dataset consists of 32 vegetation groups and one ‘unknown/no data’ group. Groups are delineated by a Major Vegetation Group (MVG) number, MVG groups were combined to form 12 major groups, these groups and the MVG groups they were derived from a provided in parentheses: eucalyptus forest/woodland (2,3,5,11); acacia forest (6); Callitris forest (7); other forest (10); shrubland (16, 17); heath (18); native grasslands (19, 21); inland aquatic (24); cleared (25); unknown (26, 99); naturally bare (27) and regrowth (29). The lookup table for this dataset is available here: https://www.dcceew.gov.au/environment/land/native-vegetation/national-vegetation-information-system/data-products#mvg60.	100	Australia - Present Major Vegetation Groups - NVIS Version 6.0 (Albers 100m Analysis Product) (Department of Climate Change, Energy, the Environment and Water, 2023) Accessed 17th July 2023.
	Burn severity	Source dataset provides yearly burnt areas from 2016 onwards. No burns are recorded in the study area outside of the 2019–2020 fire season, where a section in the northwest of the study area was burnt. The burn severity	Derived from Sentinel-2 MSI: Multispectral Instrument, Level 2A. Products range from 10–	Fire Extent and Severity Mapping (FESM) – SEED (Department of Planning and

	in this area ranged was rated from 0–5 with 0 being unburnt, 5 being extreme (canopy consumption) and 1 being low (burnt understory with unburnt canopy), this layer was used for the step selection functions for sambar deer. This layer was used for step selection functions to evaluate burnt area selection by sambar deer.	60 m resolution - resampled to 100.	Environment, 2023) Accessed 17th July 2023.
Burn area	Burn ratings 1–5 were merged to form a binary layer depicting burnt and unburnt area for the resource selection functions for sambar deer, which included burn area as a variable.	Derived from Sentinel-2 MSI: Multispectral Instrument, Level 2A. Products range from 10–60 m resolution - resampled to 100m.	Fire Extent and Severity Mapping (FESM) - SEED (Department of Planning and Environment, 2023) Accessed 17th July 2023.

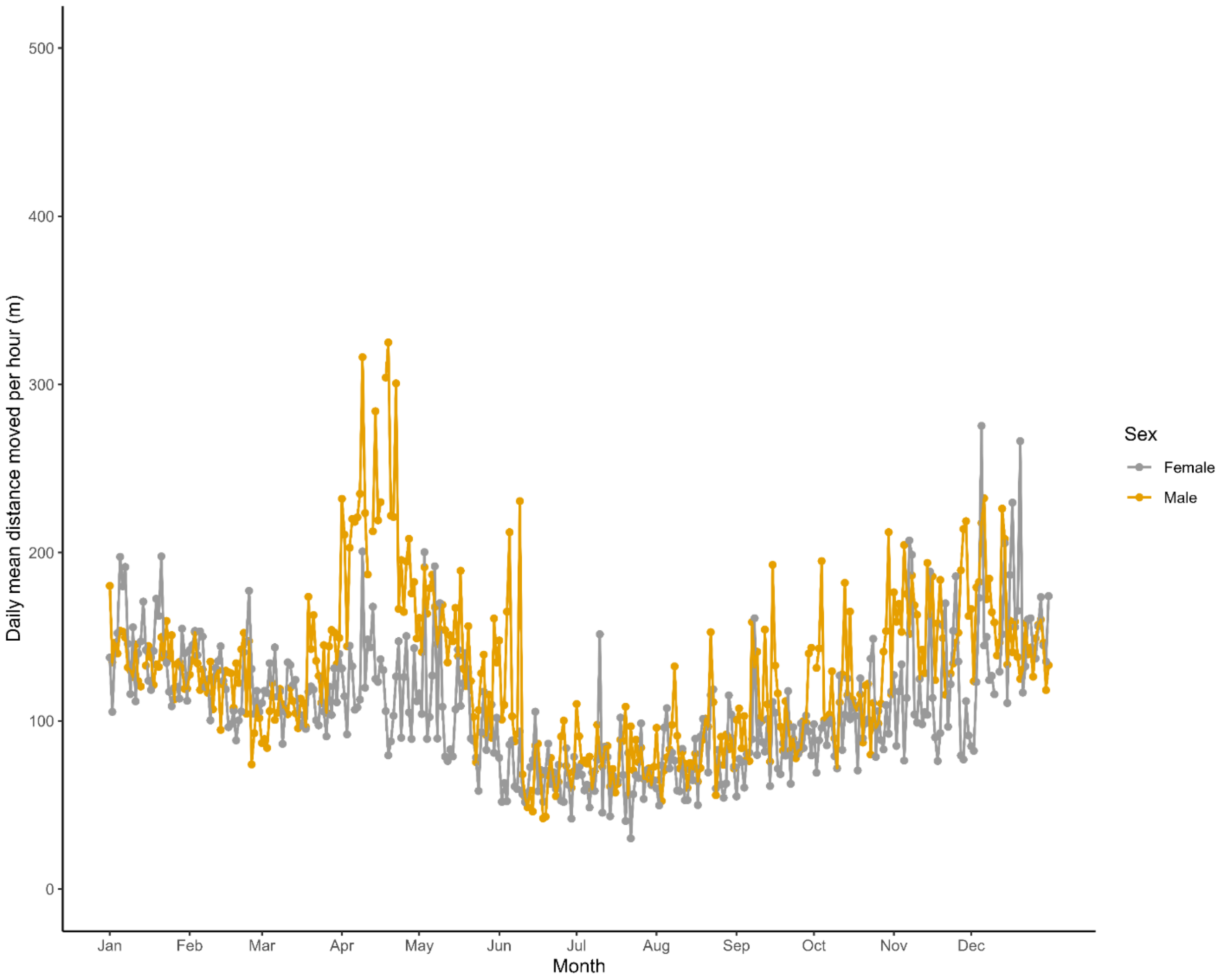

Figure S3.1: Average daily mean distances moved per hour for fallow deer (*Dama dama*) of both sexes in the Snowy Mountains region, in southeastern Australia. Animals were monitored from April 2021 to May 2023

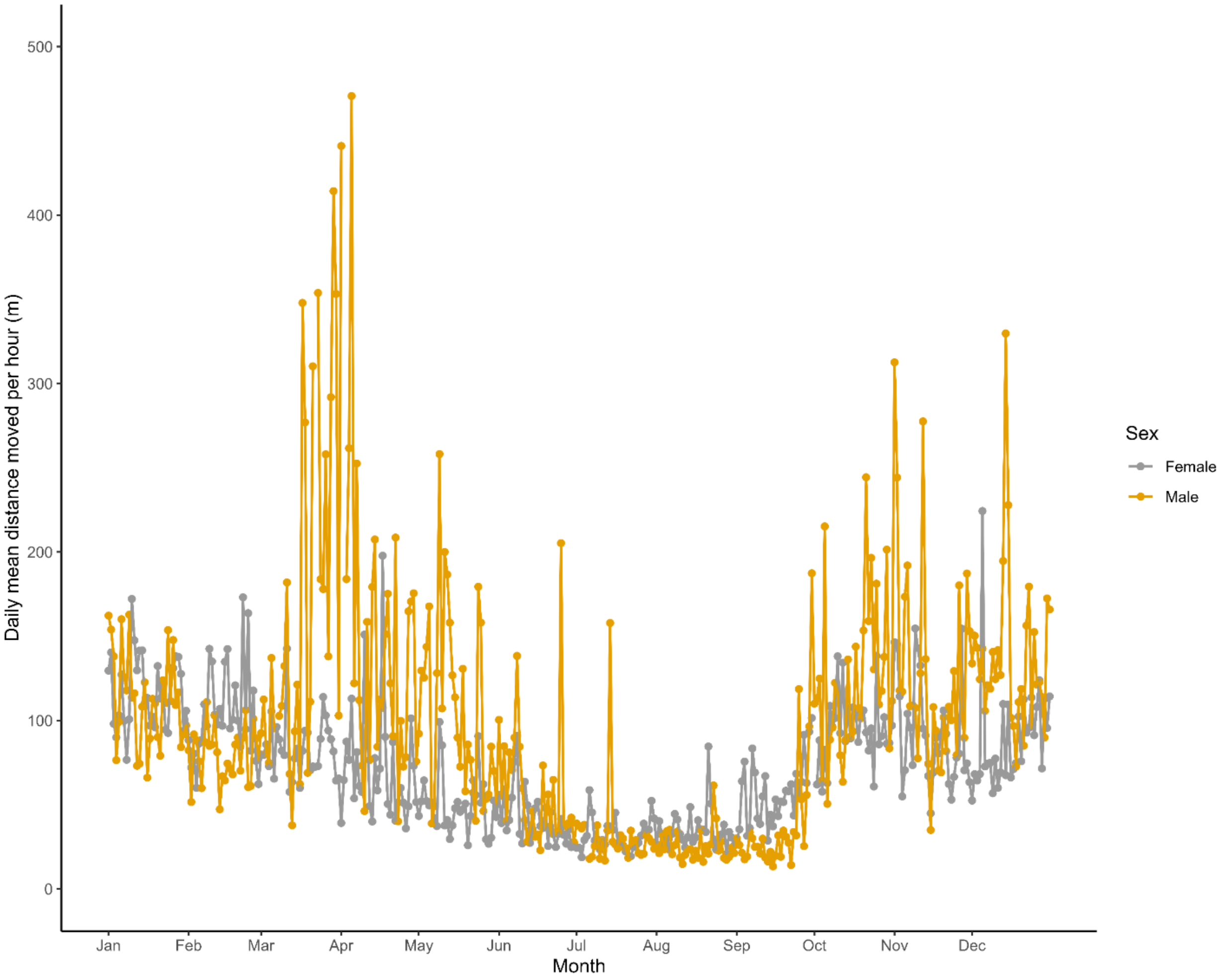

Figure S3.2: Average daily mean distances moved per hour for red deer (*Cervus elaphus*) of both sexes in the Snowy Mountains region, in southeastern Australia. Animals were monitored from April 2021 to May 2023.

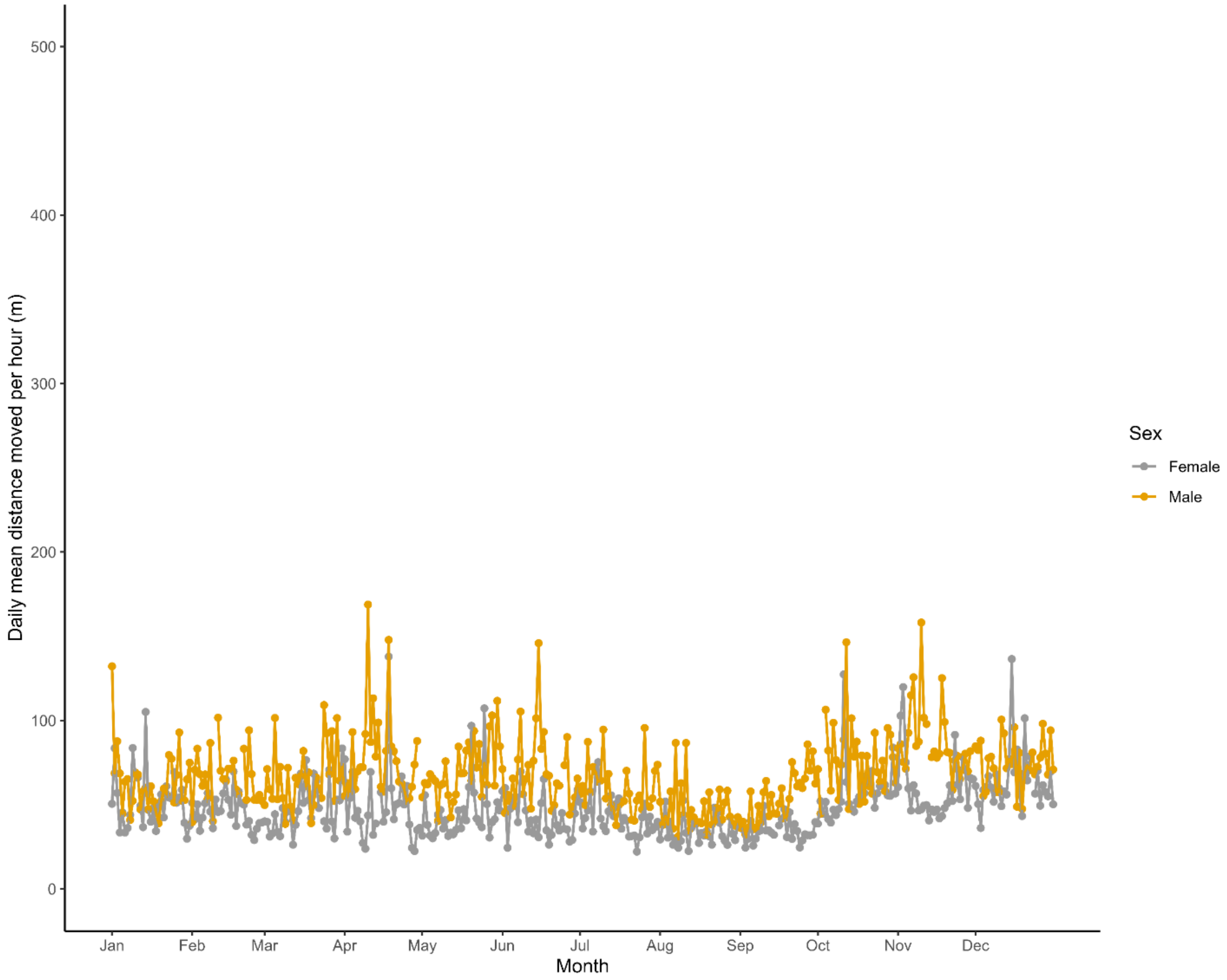

Figure S3.3: Average daily mean distances moved per hour for sambar deer (*Rusa unicolor*) of both sexes in the Snowy Mountains region, in southeastern Australia. Animals were monitored from April 2021 to May 2023.

Table S3.3: Model summaries of the linear mixed effects models run to evaluate the effect of sex, year, and season on home range (wAKDE estimates) and movement extent (from MCP estimates) for fallow deer, red deer and sambar deer in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. The reference level for season is 'autumn', and for sex it is 'female'.

	Response variable					
	log(HR)			log(HR)		
	wAKDE home range			**MCP movement extent**		
Fixed effects (β parameter estimates)	Fallow deer	Red deer	Sambar deer	Fallow deer	Red deer	Sambar deer
Sex: male	0.238	1.339	0.917**	1.098*	0.993	0.60
Standard error	(0.545)	(0.965)	(0.387)	(0.591)	(0.434)	(0.57)
Year	1.209	-0.010	-0.515	0.626*	0.046	0.57
Standard error	(0.687)	(0.230)	(0.446)	(0.342)	(0.239)	(0.43)
Season: Spring	0.295	0.491	-2.082**	0.463	-0.258	-0.10
Standard error	(1.049)	(0.403)	(0.712)	(0.409)	(0.389)	(0.72)
Season: Summer	1.024	0.247	-2.249**	-0.222	-0.299	-0.29
Standard error	(1.050)	(0.384)	(0.783)	(0.437)	(0.373)	(0.67)
Season: Winter	0.140	-0.914*	-2.626***	-0.758*	-1.335***	-0.70
Standard error	(1.049)	(0.466)	(0.783)	(0.421)	(0.360)	(0.58)
Constant	-2,442.215	21.872	1043.879	-1,263.347*	-90.432	-1141.18
Standard error	(1,389.018)	(465.805)	(900.829)	(692.060)	(483.875)	(863.64)
Observations	31	18	26	47	24	45
Log Likelihood	-48.878	-14.194	-32.075	-63.872	-20.163	-70.17
Akaike Inf. Crit.	113.755	44.388	80.151	143.744	56.325	156.34
Bayesian Inf. Crit.	123.506	48.268	88.117	157.452	63.448	169.75
Note:	*p < 0.1; **p < 0.05; ***p < 0.01					

Table S3.4: Average home ranges and standard errors for fallow deer, red deer and sambar deer in the south-eastern Australian Alps, in Kosciuszko National Park and surrounding land. wAKDE 95% home range was only calculated for range-resident individuals, 100% MCP movement extent was calculated for all individuals, including those that were not range residents. Home ranges are pooled for monitoring years 2021–2023. Seasonal and annual mean home ranges and standard errors (SE) are presented for each species and sex.

Species	**Season**	**Sex**	**Mean wAKDE 95% home range (km^2) ± SE**	**Mean 100% MCP movement extent (km^2) ± SE**
Fallow deer	Summer	Male	9.2 ± 3.4 (n = 7)	30.8 ± 19.2 (n = 8)
		Female	37.0 ± 19.0 (n = 8)	25.4 ± 10.4 (n = 8)
	Autumn	Male	43.0 ± 22.0 (n = 3)	83.1 ± 42.7 (n = 7)
		Female	23.3 ± 15.0 (n = 5)	27.0 ± 6.6 (n = 9)
	Winter	Male	2.6 (n = 1)	32.7 ± 16.5 (n = 3)
		Female	33.4 ± 29.6 (n = 3)	5.1 ± 2.1 (n = 3)
	Spring	Male	49.0 (n = 1)	71.3 ± 32.5 (n = 4)
		Female	9.1 ± 7.4 (n = 3)	35.3 ± 13.1 (n = 5)
	Annual	Male	226.9 ± 54.3 (n = 4)	78.2 ± 5.9 (n = 5)
		Female	55.1 ± 46.5 (n = 3)	50.2 ± 14.1 (n = 7)
Red deer	Summer	Male	71.0 ± 53.6 (n = 2)	45.4 ± 28.2 (n = 2)
		Female	12.2 ± 3.9 (n = 5)	13.0 ± 1.8 (n = 5)
	Autumn	Male	No individuals	38.3 (n = 1)
		Female	14.6 ± 4.0 (n = 3)	18.4 ± 3 (n = 5)
	Winter	Male	3.9 (n = 1)	9.7 (n = 1)
		Female	1.8 ± 0.3 (n = 2)	5.7 ± 2 (n = 5)
	Spring	Male	25.0 (n = 1)	17.5 (n = 1)
		Female	14.7 ± 5.8 (n = 4)	16.0 ± 3.4 (n = 4)
	Annual	Male	No individuals	No individuals
		Female	70.2 ± 35.5 (n = 4)	35.3 ± 5.2 (n = 4)
Sambar deer	Summer	Male	9.7 ± 2.5 (n = 6)	5.7 ± 0.7 (n = 6)
		Female	3.9 ± 1.1 (n = 4)	16.5 ± 8.9 (n = 6)
	Autumn	Male	19.4 (n = 1)	42.82 ± 25.72 (n = 6)
		Female	40.3 ± 26.5 (n = 3)	13.9 ± 6.2 (n = 4)
	Winter	Male	2.4 ± 0.3 (n = 2)	57.9 ± 36.1 (n =7)
		Female	3.5 ± 1.8 (n = 3)	9.1 ± 3.8 (n = 6)
	Spring	Male	23.6 ± 13.8 (n = 4)	10.6 ± 4.8 (n = 5)

	Female	2.2 ± 0.7 (n = 3)	16.3 ± 9.9 (n = 5)
Annual	Male	25.3 ± 4.0 (n = 2)	111.9 ± 56.7 (n = 5)
	Female	80.7 (n = 1)	64.9 ± 3.3 (n = 3)

Table S3.5: Model summaries of the linear mixed effects models, run to evaluate the effect of season on mean elevation used by fallow deer, red deer and sambar deer in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. The reference level for season is ‘summer’.

Mean elevation used (Response variable)			
Fixed effects (β parameter estimates)	Fallow deer	Red deer	Sambar deer
Season: Autumn	-76.994	-19.803	-60.257
Standard error	92.469	39.373	92.291
Season: Winter	-205.013**	-218.230***	-496.106***
Standard error	95.322	44.853	84.029
Season: Spring	-98.244	-45.905	-434.214***
Standard error	87.959	44.678	103.587
Constant	1413.557***	1700.869***	1557.119***
Standard error	84.645	25.623	92.169
Observations	40	15	34
Log likelihood	-256.501	-63.687	-213.121
Akaike Inf. Crit.	525.002	139.374	438.243
Bayesian Inf. Crit.	534.503	141.762	446.650
Note: *p < 0.1; **p < 0.05; ***p < 0.01			

Table S3.6: Selection coefficients (β parameter estimates) and 95% confidence intervals of generalised linear mixed effects resource selection functions, modelling the habitat preferences of fallow deer, red deer, and sambar deer in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia. For selection coefficients reported as 'NA', no individuals of the species inhabited that habitat type during the season.

											Vegetation type*						**Aspect***				
Species	**Season**	**Number of individuals**	**Number of true locations**	**Intercept****	**Elevation**	**Slope**	**Distance to water**	**Cleared**	**Native grassland**	**Heath**	**Inland Aquatic**	**Shrubland**	**North**	**Northeast**	**Northwest**	**South**	**Southeast**	**Southwest**	**West**	**Burnt area**	**ΔAIC$_C$ from the next best model**
Fallow deer	**Summer**	14	32902	-0.0008	1.67 (-0.44, 3.79)	-0.30 (-0.49, -0.12)	-0.17 (-0.65, 0.32)	0.004 (-0.05, 0.06)	-0.27 (-0.30, -0.23)	0.77 (0.60, 0.94)	0.09 (0.003, 0.18)	0.28 (-0.06, 0.63)	-0.07 (-0.11, -0.02)	-0.01 (-0.06, 0.03)	0.08 (0.03, 0.13)	-0.31 (-0.35, -0.26)	-0.01 (-0.06, 0.03)	-0.24 (-0.28, -0.19)	-0.18 (-0.22, -0.14)	NA	318.98
	Autumn	12	33613	-0.01	1.24 (-0.20, 2.67)	-0.33 (-0.51, -0.16)	-0.12 (-0.47, 0.24)	0.52 (0.47, 0.56)	-0.44 (-0.48, -0.40)	1.23 (1.02, 1.45)	-0.38 (-0.53, -0.23)	NA	-0.03 (-0.08, 0.01)	-0.05 (-0.09, -0.02)	0.07 (0.01, 0.12)	-0.79 (-0.84, -0.75)	-0.46 (-0.50, -0.42)	-0.93 (-0.98, -0.88)	-0.64 (-0.68, -0.61)	NA	1199.88
	Winter	9	14698	-0.02	0.35 (-1.21, 1.91)	0.30 (-0.01, 0.60)	-0.11 (-0.69, 0.48)	0.11 (0.05, 0.17)	-0.75 (-0.89, -0.61)	NA	NA	NA	-0.13 (-0.21, -0.05)	-0.08 (-0.14, -0.01)	0.04 (-0.14, 0.21)	-0.80 (-0.87, -0.72)	-0.56 (-0.64, -0.49)	-0.41 (-0.50, -0.32)	0.22 (0.16, 0.27)	NA	181.62
	Spring	11	19653	-0.0005	-1.39 (-2.91, 0.13)	-0.13 (-0.33, 0.08)	-0.24 (-0.66, 0.18)	0.12 (0.07, 0.16)	-0.26 (-0.32, -0.19)	4.25 (3.77, 4.73)	-0.59 (-0.73, -0.46)	NA	-0.15 (-0.21, -0.09)	-0.16 (-0.21, -0.11)	-0.24 (-0.33, -0.14)	-0.91 (-0.98, -0.85)	-0.55 (-0.60, -0.49)	-0.66 (-0.72, -0.59)	-0.31 (-0.35, -0.27)	NA	318.66
Red deer	**Summer**	5	14679	-0.0001	0.66 (0.33, 1.00)	-0.20 (-0.52, 0.12)	-0.07 (-0.28, 0.14)	NA	-0.56 (-0.61, -0.50)	NA	NA	NA	0.44 (0.37, 0.51)	0.11 (0.04, 0.18)	0.19 (0.11, 0.28)	0.45 (0.38, 0.51)	0.23 (0.16, 0.30)	0.29 (0.22, 0.36)	-0.29 (-0.36, -0.22)	NA	458.1
	Autumn	4	12896	-0.0002	0.94 (0.34, 1.53)	-0.07 (-0.38, 0.23)	0.13 (0.07, 0.19)	-0.43 (-2.39, 1.53)	-0.08 (-0.14, -0.02)	NA	NA	NA	0.73 (0.65, 0.81)	0.19 (0.11, 0.28)	0.28 (0.18, 0.39)	0.86 (0.79, 0.93)	0.63 (0.56, 0.70)	0.35 (0.27, 0.43)	0.08 (-0.0008, 0.16)	NA	3.06
	Winter	4	11722	-0.0002	-0.64 (-1.22, -0.06)	0.41 (0.22, 0.60)	0.16 (-0.36, 0.68)	-1.15 (-1.90, -0.40)	-0.78 (-0.96, -0.60)	NA	NA	NA	0.36 (0.23, 0.48)	0.40 (0.33, 0.48)	0.41 (0.16, 0.67)	0.81 (0.72, 0.89)	0.33 (0.24, 0.42)	1.13 (1.05, 1.21)	0.86 (0.77, 0.94)	NA	101.72
	Spring	3	10743	-0.0003	0.54 (0.06, 1.02)	0.17 (0.06, 0.28)	0.17 (0.004, 0.33)	-3.30 (-4.69, -1.92)	-0.64 (-0.71, -0.56)	NA	-0.18 (-0.84, 0.48)	NA	-0.03 (-0.12, 0.05)	-0.55 (-0.64, -0.46)	0.23 (0.14, 0.33)	-0.03 (-0.11, 0.05)	0.32 (0.25, 0.40)	0.12 (0.04, 0.20)	0.36 (0.29, 0.43)	NA	256.42
Sambar deer	**Summer**	11	28515	-0.0006	0.29 (-1.66, 2.23)	0.09 (-0.11, 0.29)	-0.23 (-0.62, 0.15)	-0.37 (-0.59, -0.15)	-1.03 (-1.10, -0.96)	NA	NA	NA	-0.17 (-0.23, -0.11)	-0.40 (-0.47, -0.33)	-0.21 (-0.27, -0.15)	-0.28 (-0.33, -0.22)	0.23 (0.18, 0.28)	0.01 (-0.04, 0.06)	-0.38 (-0.43, -0.33)	-0.55 (-0.66, -0.43)	75.97
	Autumn	7	20887	-0.01	1.26 (-1.84, 4.37)	0.06 (-0.15, 0.28)	-0.49 (-1.40, 0.42)	-0.34 (-0.49, -0.18)	-1.10 (-1.18, -1.03)	NA	NA	NA	0.50 (0.43, 0.57)	0.62 (0.56, 0.69)	0.40 (0.33, 0.47)	-0.03 (-0.10, 0.03)	0.67 (0.61, 0.73)	-0.11 (-0.18, -0.05)	0.15 (0.09, 0.22)	0.90 (0.77, 1.02)	245.41
	Winter	11	28721	-0.01	0.55 (-1.51, 2.60)	-0.07 (-0.23, 0.08)	-0.73 (-1.40, -0.06)	-0.90 (-1.04, -0.77)	-1.31 (-1.45, -1.17)	NA	NA	NA	-0.07 (-0.12, -0.01)	0.26 (0.21, 0.30)	0.22 (0.17, 0.28)	-0.19 (-0.24, -0.15)	-0.37 (-0.42, -0.33)	-0.67 (-0.73, -0.61)	-0.36 (-0.40, -0.31)	-0.80 (-0.85, -0.75)	951.41
	Spring	9	23638	-0.0007	0.27 (-2.49, 3.04)	0.10 (-0.06, 0.26)	-0.78 (-1.96, 0.39)	-0.59 (-0.75, -0.43)	-0.78 (-0.87, -0.68)	NA	NA	NA	-0.02 (-0.08, 0.04)	0.05 (-0.00, 0.11)	0.01 (-0.06, 0.07)	-0.44 (-0.49, -0.39)	-0.10 (-0.15, -0.06)	-0.36 (-0.42, -0.30)	-0.36 (-0.41, -0.31)	1.23 (1.14, 1.32)	360.2

*For all resource selection functions, 'eucalypt forest/woodland' was the reference vegetation type, 'east' was the reference aspect, and 'no fire' was the reference burnt area class. Selection coefficients presented here represent preferences for each vegetation type and aspect relative to the reference type for each variable. **Intercept variance is not presented here as model intercepts were fit with fixed variance of 10^6 (as in Muff et al., 2020).

Table S3.7: Selection coefficients (β parameter estimates), summary statistics and inverse variance weightings used to calculated weighted coefficients of conditional logistic regressions to model sambar deer fire severity preferences when within 500 m of a burnt area in the Snowy Mountains region, in and around Kosciuszko National Park, in southeastern Australia.

Sambar deer ID (number of true steps)	**Fire severity score**	**β parameter estimate**	**Standard error**	**z-score**	**Inverse variance weighting**
49154 (n = 2680)	No data	0.180	0.122	1.475	67.208
	Low to moderate	0.112**	0.0543	2.057	339.185
	High	0.172***	0.0641	2.687	243.184
	Very high	-0.145	0.323	-0.449	9.610
49157 (n = 518)	No data	-4.139***	1.450	-2.854	0.476
	Low to moderate	0.244**	0.111	2.202	81.383
	High	-0.149	0.200	-0.746	25.009
	Very high	0.299	0.472	0.634	4.496
49830 (n = 607)	No data	-0.111	0.154	-0.720	42.106
	Low to moderate	-0.0316	0.140	-0.225	50.774
	High	-0.0221	0.173	-0.127	33.350
	Very high	0.278	0.536	0.520	3.485

Note: $^{*}p < 0.1$; $^{**}p < 0.05$; $^{***}p < 0.01$

Chapter 4: Aerial culling alters activity patterns but not grouping or movement in invasive fallow deer

Aerial shooters prepared for take-off in a ParkAir helicopter

A slightly revised version of this chapter is in review in *Journal of Applied Ecology* as: McCarthy, E.D., Grueber, C.E., Cox, T.E., Lai, B., Tomkins, E., Janes, M., Cass, J., Kuner, C., Whittaker, C., Newsome, T. M. (2025) Aerial culling alters activity patterns but not grouping or movement in invasive fallow deer. I co-designed the study with all other co-authors, analysed the data, and wrote the manuscript in collaboration with my co-authors.

4.1 Abstract

1. Predation has been widely documented to impact prey behaviour, group dynamics and habitat selection, ultimately influencing individual fitness, population dynamics, and even trophic cascades. Such outcomes could also occur when humans manage wildlife populations through lethal control, but lethal control techniques vary widely, making responses by the target species difficult to predict. Aerial or helicopter-based culling is a common method used to kill animals over a large area, but little is known about how target species respond to the stimuli created by the sight and sound of the helicopter, the sound of gun shots, and the disturbance related to conspecifics being shot in proximity.
2. Here we investigate the effects of aerial culling on invasive fallow deer (*Dama dama*) in an alpine region of south-east Australia. We used two large-scale remote camera arrays to monitor fallow deer temporal activity patterns, grouping, and movement speed during and outside of aerial control periods.
3. We found that aerial culling did not cause major changes in grouping or movement speed, however, the operations were linked to short term decreases in deer activity, particularly during the day, coupled with relative increases in activity for the dusk and night-time periods. This suggests that fallow deer were shifting their diel activity patterns towards dusk during aerial culling.
4. *Synthesis and applications*: Though a common technique employed for the control of medium- to large-bodied invasive species, there is limited research on the effect of aerial culling on the target species from both a population and behavioural standpoint. In our study, aerial control induced short-term temporal shifts in behaviour, suggesting future research could examine how management efforts can take advantage of this behaviour to achieve sustained population reductions.

4.2 Introduction

Spatial and temporal variations in animal behaviour can occur because of perceived and real predation risk, potentially affecting the fitness and population dynamics of species, and in turn initiating behaviourally-mediated trophic cascades (Palmer et al., 2022). Such antipredator behaviour is measurable in levels of vigilance (Jayakody et al., 2008), group size (Beauchamp, 2003), temporal changes in activity (Crawford et al., 2021) and changes in space use and habitat selection (Laundre et al., 2010). These effects have been documented across a wide variety of taxonomic groups and impose numerous costs on prey species (Zanette & Clinchy, 2019).

Where humans manage populations of wildlife, there may be additional forms of avoidance by the target species (Darimont et al., 2015). Hunting, for instance, has been shown to initiate changes in species' movement patterns (Cleveland et al., 2012), and group size (Proffitt et al., 2009), and ground-based culling is associated with shifts in diel activity (Comte et al., 2022). Due to technological advancements, humans are also capable of killing wildlife at high rates (Darimont et al., 2015) such that animals have been shown to exhibit stronger predator avoidance behaviours towards humans than towards large carnivores (Clinchy et al., 2016). Understanding how human intervention affects animal behaviour is therefore pertinent to the ongoing use of hunting and targeted culling operations for native and introduced species (Darimont et al., 2015).

Aerial culling is a highly efficient and commonly used method for the control of medium- to large-bodied invasive or overabundant species (Bradshaw et al., 2023). In aerial culling operations using helicopters, the pilot flies at a higher altitude searching for targets, and then manoeuvres into a position suitable for shooting the target. An aerial culling operation may be detectable by an animal through the sight and sound of the helicopter, the sound of gun shots, and the disturbance related to conspecifics being shot in close proximity. Thus, while ground-based hunting and culling operations may only come into direct contact with a few individuals within a population, aerial culling may initiate anti-predator behaviour across a greater proportion of the species population (Suraci et al., 2019). Yet, despite its widespread use, only five articles of primary research have examined the effect of aerial culling on ungulate behaviour (Bengsen et al., 2024; Bengsen et al., 2025; Campbell et al., 2010; Campbell et al., 2012; Dexter, 1996). A previous article focusing on fallow deer responses found that aerial culling resulted in temporary increases in movement speeds and nocturnality (Bengsen et al., 2024), but such effects may vary depending on the intensity of culling and the associated landscapes in which the target species are in. Notably, previous studies of aerial culling effects on ungulate behaviour have relied on animal tracking data and assessed movement changes, and no previous studies have investigated how aerial culling affects ungulate sociality.

In Australia, invasive deer have a detrimental environmental impact via browsing, trampling and antler-rubbing (Davis et al., 2016). In slow-growing alpine areas, increases in introduced ungulates have been associated with lower vegetation height and foliage density and higher soil compaction (Hartley et al., 2021). As such, human-mediated control is often used to reduce deer densities and their associated impacts (Bengsen et al., 2020). Aerial culling is considered an effective landscape-scale control tool for deer, especially in remote locations (Bradshaw et al., 2023; Pulsford et al., 2022). Therefore, there is a need to quantify the effects of aerial culling on the behaviour, and subsequent mitigation of the impacts, of these target species and to improve management effectiveness.

Here we leveraged an extensive culling effort across 284 km^2, aimed at substantially reducing the deer population within the study area to test the impact of aerial culling on the behaviour of a target invasive species, fallow deer (*Dama dama*). First, we estimate changes in population size over the study period from aerial thermal surveys and camera-derived relative detection indices. Then, we evaluate whether fallow deer respond to the presence of aerial control given it generates strong visual and audio cues. Specifically, we test whether fallow deer 1) have reduced activity during and immediately following aerial culling operations, 2) exhibit decreased daytime activity when aerial control occurs, and in turn have increased nocturnal, dusk and dawn activity, 3) are more likely to form groups as an antipredator response, and 4) exhibit increased movement speed during and immediately after shooting. We predict that these effects are strongest during the daytime, while aerial culling is occurring. To address these predictions, we utilised two large camera arrays, which enabled us to study sociality, movement and diel activity simultaneously over a large geographic area.

4.3 Methods

4.3.1 Study area and species

This research took place within and surrounding Kosciuszko National Park in south-eastern Australia (Fig. 4.1), on the Country of the Ngarigo People. Recreational hunting is not permitted in the National Park, but introduced species are targeted via Government-managed culling programs. Ground-based recreational hunting does occur on the private farmland in the east of the study area, but not in a coordinated manner. Elevation in this area ranges from approximately 1000 to 2000 m AGL (NASA/METI/AIST/Japan Spacesystems and US/Japan ASTER Science Team, 2019). The lower elevation eastern side of the study area is predominantly cleared pastoral farmland, interspersed with patches of remnant native vegetation, and small residential areas (Australian Government Department of Climate Change, Energy, the Environment and Water, 2021). Vegetation across the study area is dominated by Eucalypt (Eucalyptus sp.) woodland, and at higher elevations, alpine freshwater bogs with tussock grasslands of prickly snow grass (Poa costiniana) and mountain gentian (Gentianella diemensis; Department of Environment and Climate Change NSW, 2007). Continuous snow cover for at least one month of the year occurs within the subalpine zone of the study area (1350–1750 m ASL), while the alpine zone (above 1750 m), is mostly above the tree line, and typically experiences continuous snow cover for at least four months of the year (MacPhee & Wilks, 2013). From 2020–2023, the mean monthly maximum temperature at Thredbo Village station (1380 m ASL), ranged from 5.1 °C in July 2022, to 23.8 °C in January 2020 (Bureau of Meteorology, 2024). The study species, fallow deer, are a medium-sized deer species, and are known to inhabit both agricultural areas and sub-alpine and alpine protected areas in the region (McCarthy et al., 2025). Group size is variable, and males are found in small groups of less than five throughout the year, except for during the rut when they are solitary (Thirgood, 1990). Females are typically found in groups, except during parturition, when group size decreases and individuals may be solitary (Thirgood, 1990).

4.3.2 Camera data collection

There were two camera trap arrays within the study site (Fig. 4.1), the Big Boggy array had 46 cameras and was situated in a high elevation sub-alpine area. The Interface array had 48 cameras and was situated in a lower elevation montane area, on the boundary between Kosciuszko National Park and private agricultural land (Fig. 4.1). Both arrays functioned continuously from May 2020 until November 2023. Within each array, each camera (Reconyx HyperFire 2, Holmen, USA) was 600–700 m apart (Fig. 4.1) and fixed to a mature tree at 1.5 m above the ground. Wooden stakes were set up 2 m apart, 1 m from the centre of the camera field of view on either side, 6 m from the camera, to demarcate a standardised detection zone. Cameras were aimed at the midpoint between the two posts. Images captured when the animal remained outside of this zone were removed prior to analyses (similar to Bengsen et al., 2022). Cameras were programmed for passive infrared motion detection with high sensitivity and no white flash, and captured 10 images per detection in rapid succession with no quiet period between detections.

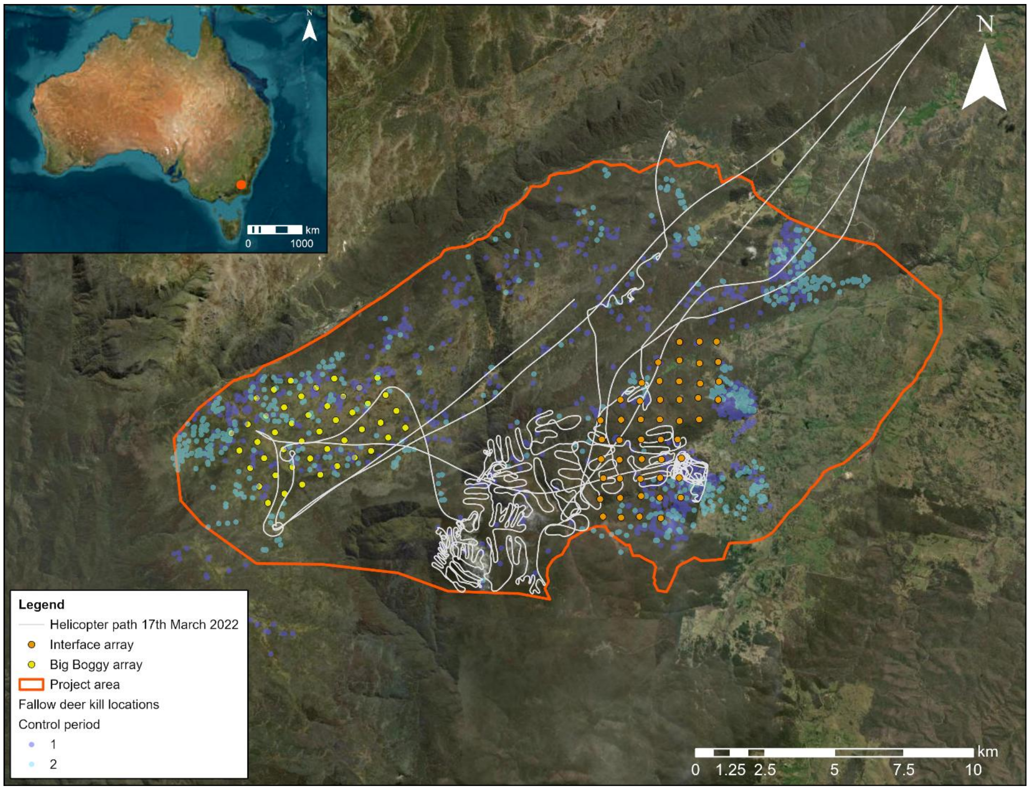

Figure 4.1: Study area showing locations of the two camera arrays, all fallow deer culled during the study, and an example helicopter flight path on the 17th of March 2022 (main image). Forty-two days of aerial control via helicopter occurred from February 2021 – May 2022 and November 2022 – March 2023. Inset map shows the study area (red point).

4.3.3 Camera data processing

We manually tagged all images with species and group size information in ExifPro version 2.1.0 (Kowalski, 2015). To limit autocorrelation, multiple photographs of the same presumptive individual or group of individuals (photographs taken < 5 min apart) were removed prior to analysis. Histograms of fallow deer activity were inspected to confirm that this was an appropriate breakpoint. Image tag data were extracted using R package recocam v1.1.0 (Raghunath et al., 2019), with one entry per detection event. Camera operability matrices were generated using camtrapR v2.3.0 (Niedballa et al., 2016).

4.3.4 Aerial control

Forty-two days of aerial control via helicopter occurred across a 407-day period (14 February 2022 – 28 March 2023) from February 2021 – May 2022 and November 2022 – March 2023 (outside of the period when snow was likely to occur). Shooting was conducted using a .308 semi-automatic rifle, out of an AS350 B3 Écureuil (Squirrel) helicopter (Aerospatiale, France). Fallow deer, red deer (Cervus elaphus) and sambar deer (Rusa unicolor) were targeted for culling. On most aerial control days, culling took place across the area covered by both camera arrays (Fig. 4.1), but the extent of culling activity and the number of deer culled varied between the camera arrays from day to day. Culling took place during daylight hours (see below).

4.3.5 Background population size and species composition monitoring

To estimate deer population size changes throughout aerial control, deer density and abundance were estimated using distance sampling over nine aerial thermal surveys which occurred between May 2020 and November 2023, outside of shooting periods (method provided in Appendix Item 4.1). As species differentiation is not possible from thermal imagery used in aerial surveys, estimates are inclusive of all deer species present within the study site. Therefore, to provide a proxy for the relative abundance of each species, we also calculated species' relative detection indices for 2020–2023 (the standardised average monthly number of detections per camera; method described in Appendix Item 4.2) and the number of each species culled.

4.3.6 Effect of culling on fallow deer behaviour

To examine the short-term effects of culling on deer behaviour, the camera array dataset was limited to the period 1 November 2021 to 28 March 2023, excluding data from June to October 2022 when shooting did not occur. Data collected between November 2021 and May 2022 was designated period 1 and data collected from November 2022 to March 2023 was designated period 2.

Previous research has shown that the effects of shooting on deer behaviour can last for as little as two days (Pecorella et al., 2016), up to an average of six days (Sunde et al., 2009). Therefore, a camera detection event was classified as 'within shooting period' if it occurred on a day of aerial culling or in the seven days following. All remaining days were classified as 'outside of shooting period'.

For all models, fallow deer activity on camera arrays was analysed in four discrete time periods: day, night, dusk, and dawn. We extracted sunrise and sunset times for each day using the R package activity v.1.3.4 (Rowcliffe, 2023). Day was defined as one hour after sunrise to one hour before sunset, night was defined as one hour after sunset to one hour before sunrise, dawn was defined as one hour before and after sunrise, and dusk was defined as one hour before and after sunset, as in Smith et al. (2019).

4.4 Statistical analysis

4.4.1 Temporal activity (Predictions 1 and 2)

We fitted a generalised linear mixed model (GLMM) to evaluate the short-term effect of shooting on the overall activity and temporal activity of fallow deer (model 1). Model 1 used the number of events across each array for each time of day as the response variable. Fixed predictor variables were shooting status (1 for within shooting period, 0 for outside of shooting period), time of day (categorical: day [reference category], night, dusk or dawn); the interaction between shooting status and time of day; and array. To account for temporal variation over the study period, random effects were used for shooting period and month. We included two offset terms to account for variation in sampling opportunity: the natural logarithm of the length (hours) of each time-of-day period (i.e. dawn, dusk, etc) for each day, and the natural logarithm of the number of cameras (from 30 to 44 for each array) that were functioning for each array for each day.

To determine how temporal activity changed with days since shooting, we fitted a second GLMM (model 2). For this model, the 'outside of shooting' data were excluded, and shooting status was a continuous predictor variable where day 0 represented an active aerial culling day, and days 1–7 represented 1–7 days following a day of aerial culling, so that changes in deer behaviour could be measured throughout the post-cull periods. Here, response variable, fixed predictor variables, random effects and offset terms were the same as in model 1. Models 1 and 2 were both fitted with negative binomial distribution with quadratic parameterisation to account for overdispersion.

4.4.2 Grouping (Prediction 3)

For each camera trap event, we coded fallow deer as either 'alone' (one individual sighted), or 'in a group', (more than one individual sighted). We fitted a GLMM with binomial distribution to determine the effect of shooting on fallow deer grouping behaviour (model 3). Here, grouping status was the binary response variable ('0' coded for alone, '1' for in a group); fixed and random effects were the same as model 1.

We fitted a second GLMM to determine whether grouping behaviour changed with days since shooting (model 4). Here, the response variable was the same as in model 3, fixed predictor variables and random effects were the same as model 1, and shooting status was coded 0–7 as in model 2.

4.4.3 Movement speed (Prediction 4)

Staying time, i.e. the amount of time an animal spends within the field of view of a camera trap, is inversely proportional to, and often used as a proxy for, movement speed (Nakashima et al., 2018; Palencia et al., 2022; Rowcliffe et al., 2016). Therefore, we fitted a linear mixed model (LMM) to determine the effect of shooting on fallow deer staying time (model 5). Staying time of each event (in seconds) was the rounded continuous response variable; fixed and random effects were the same as model 1. To account for small differences in the shutter speed of the cameras, which may contribute to small differences in detected staying times, we analysed staying time data in 10-second intervals, such that staying times between 1–10 seconds were reported as 10 seconds, staying times between 11–20 seconds were reported as 20 seconds, etc, up to a maximum of 5580 seconds.

We fitted a second LMM to determine how staying time changed with days since shooting (model 6). Here, the binary response variable was the same as in model 5, fixed and random effects were the same as model 1, and shooting status was coded 0–7 as in model 2. For both models, we log transformed the response variable as a Pearson residual plot indicated that the models were heteroscedastic and fitted the model with Gaussian error.

All analyses were conducted in R version 4.1.2, interfaced through Rstudio (R Core Team, 2021). We constructed mixed models using the lme4 v1.1.35.1 and glmmTMB v1.1.8 (Bates et al., 2015; Brooks et al., 2017). Model outputs were summarised using lmerTest v3.1–3 (Kuznetsova et al., 2017) and model predictions generated using sjPlot v2.8.14 (Lüdecke et al., 2024). Diel activity patterns were characterised using kernel density estimation from the stats package v4.1.2 (R Core Team, 2021) and circular data was prepared for visualisation using the circular package v0.5.0 (Lund et al., 2024). Packages DHARMa v0.4.6 (Hartig & Lohse, 2022) and ggplot2 v3.5.1 (Ginestet, 2011) were used for model and effects visualisation. The statistical significance of model parameter estimates was inferred at $\alpha = 0.05$.

4.5 Results

4.5.1 Background population monitoring

The comparison of species' relative detection indices and the numbers of each species culled indicated that fallow deer were the most abundant deer species throughout the site, and that red and sambar deer occurred at much lower abundances (Fig. S4.2). Over the study period, 1464 fallow deer were culled, including 893 in period 1 and 571 in period 2, comprising 88% of kills across all operations (Fig. 4.1). Aerial thermal surveys covering the entire study area, and relative detection indices derived from the interface camera array data indicated that both the overall deer population and the fallow deer population in the Interface area remained relatively stable, with some consistent seasonal fluctuations, despite an increase in maximum relative detections between the 2021–2022 summer period and the 2022–2023 summer period (Figs 2A, C, Table S4.1). While for the Big Boggy array, relative detections were highly seasonal, with abundance lowest during the colder months. For the Big Boggy, there was a decrease in the maximum relative detections observed between the 2021–2022 summer period and the 2022–2023 summer period (Fig. 4.2B). Shooting occurred on 27 of 212 days in period 1 and 15 of 148 days in period 2. During the two shooting periods, the Interface and Big Boggy arrays captured 7508 independent events of fallow deer (Interface = 4534, Big Boggy = 2974). In shooting period 1; 1075 events occurred within seven days of shooting, and 3401 events occurred outside of shooting periods. In shooting period 2; 770 events occurred within seven days of shooting, and 2262 events occurred outside of shooting periods (Fig. S4.3).

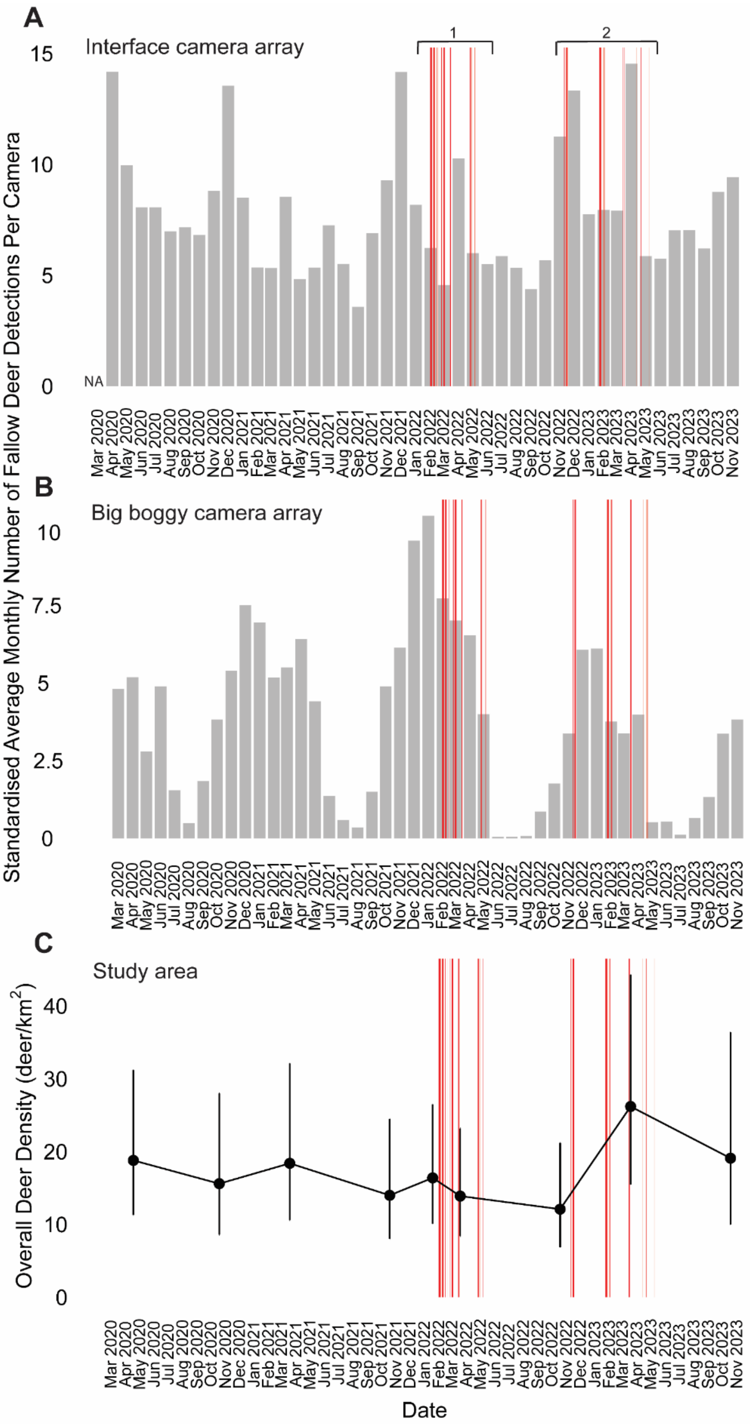

Figure 4.2: Fallow deer standardised average monthly number of detections per camera across the Interface (A) and Big Boggy (B) camera arrays from March 2020 to November 2023. Deer density estimates derived from nine aerial thermal surveys of the study area between May 2020 and November 2023 (C). Vertical red lines indicate the dates of aerial culling included in behavioural analyses. Numbers at top of figure indicate shooting periods 1 and 2.

4.5.2 Temporal activity (Predictions 1 and 2)

During and up to 7 days following an aerial culling event, the number of detection events overall tended to be lower than outside of shooting events (Fig. 4.3A; Table S4.2A). During the shooting periods, the number of detection events was higher during dusk (Fig. 4.3A; Table S4.2A) and night periods (Fig. 4.3A; Table S4.2A), relative to the change in the day period. The number of detections was higher across all periods for the Interface compared to the Big Boggy array (Fig. 4.3A; Table S4.2A). Kernel density estimation visualisation showed that fallow deer were crepuscular and were most active during dawn and dusk between November and May (Fig. 4.4; Fig. S4.4). There were also fewer detection events at night (Fig. 4.3A; Table S4.2A), and more during dawn (Fig. 4.3A; Table S4.2A) and dusk (Fig. 4.3A; Table S4.2A), compared to the day period. No statistically significant effects on temporal activity were observed for the interaction between days since shooting and time of day (model 2).

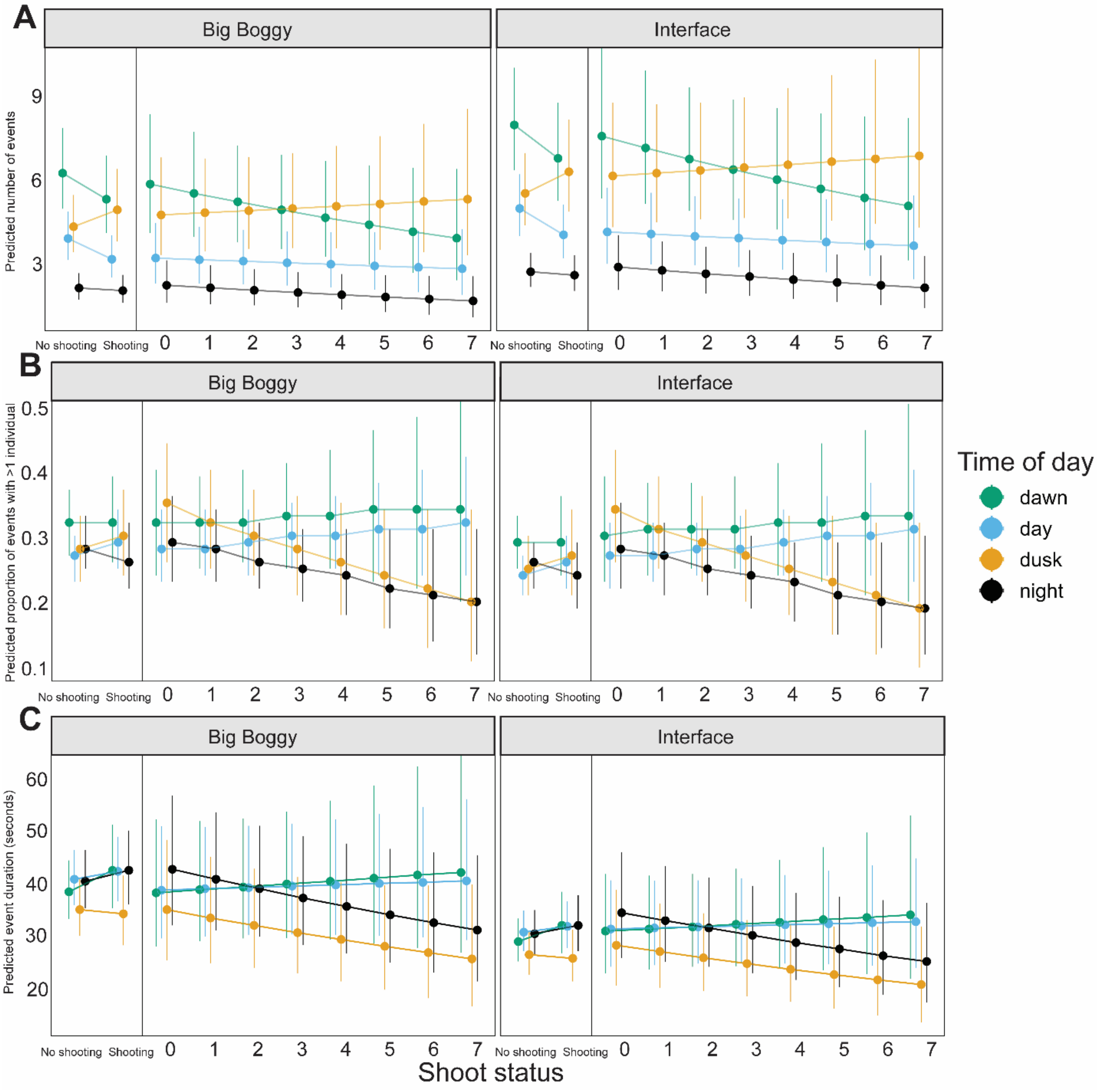

Figure 4.3: The effect of aerial culling on temporal activity of fallow deer (Dama dama) (A), grouping (B) and staying time and (C), broken up by each level of predictor variables ‘array’ and ‘time of day’. For each plot, the box on the left-hand side shows the predictions for periods during and up to 7 days following an aerial culling event, labelled ‘shooting’, or outside of these periods, labelled ‘No shooting’. The box on the right-hand side shows the predictions for the day of shooting, ‘0’, and 1–7 days following shooting, labelled 1–7. For plot A, predictions are based on 46 working cameras in each array, and 8-hour timeframes for each time of day.

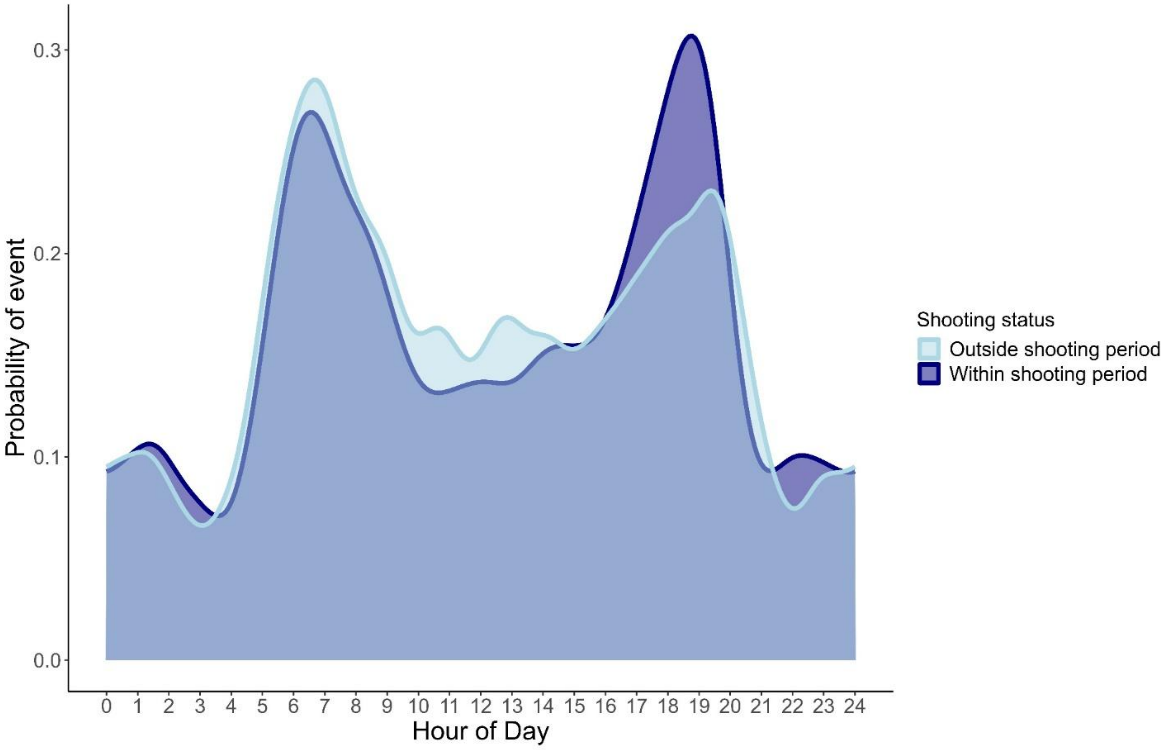

Figure 4.4: Kernel density estimates of the diel activity patterns of fallow deer (Dama dama) between November 2021 – May 2022 and November 2022 – May 2023 for outside of aerial culling periods (light blue) and during aerial culling periods (dark blue).

4.5.3 Grouping (Prediction 3)

Fallow deer were more likely to be in a group during the dawn period compared to the day period (Fig. 4.3B; Table S4.2B), and less likely to be in a group in the Interface array compared to the Big Boggy array (Fig. 4.3B; Table S4.2B). No significant relationships were observed for the interaction between time of day and shooting status.

For model 4, the full model failed to converge so we reduced model complexity by removing one random effect at a time. The model including month but excluding period was a better fit (ΔAIC >2) than the converse, therefore, we excluded the random effect of period from model 4. With increasing days since shooting event, fallow deer showed a decreasing tendency to be detected in a group during the night (Fig. 4.3B; Table S4.2B) and dusk periods (Fig. 4.3B; Table S4.2B), though these effects were only approaching significance ($p < 0.1$).

4.5.4 Movement speed (Prediction 4)

Fallow deer had a shorter staying-time for the dusk period compared to the day period (Fig. 4.3C; Table S4.2C), and in the Interface array compared to the Big Boggy array (Fig. 4.4C; Table S4.2C). There were no other significant interactions between the effects of shooting and time of day on staying-time for models 5 and 6.

4.6 Discussion

When humans manage wildlife populations, the target species may adopt behaviours to avoid being detected (Darimont et al., 2015). Such behaviours may influence the effectiveness of management aimed at reducing the abundance of a target species. Understanding how human-mediated aerial culling affects animal behaviour is therefore important, given the ongoing use of targeted culling operations for controlling invasive species. In this study, aerial culling was linked to short-term decreases in deer activity, supporting prediction 1. Additionally, culling was associated with short-term shifts in fallow deer temporal activity, supporting prediction 2. However, our results suggest that aerial culling at the intensity undertaken induced limited behavioural effects on the target population of fallow deer, including no effect on grouping behaviour or movement speed, failing to support predictions 3 and 4.

Prey species may exert proactive behaviours to avoid predators in both space and time (Palmer et al., 2022). In our study, decreases in fallow deer daytime activity during the shooting periods were coupled with short-term increased activity during dusk and night (Fig. 4.3A), suggesting they adapted their behaviour to avoid daytime aerial culling. In deer, predation risk by non-human predators contributes to changes in diel activity patterns (Crawford et al., 2021; Esattore et al., 2023). Recently in Australia, both ground-based culling of invasive sambar deer (Comte et al., 2022), and aerial culling of fallow deer (Bengsen et al., 2024), has been found to have a similar effect, with deer shifting their behaviour towards nocturnality during control periods. Shifts toward nocturnality also occur in response to various non-lethal forms of human disturbance, such as agricultural activities, hiking, and vehicles (Gaynor et al., 2018). Therefore, species' responses to novel forms of human disturbance should be considered when planning and implementing wildlife management and control activities.

Group formation is often considered an adaptive response to evolutionary pressure from predation via enhanced predator detection (Sorato et al., 2012), allowing for group cooperative defence (Grovenburg et al., 2012) and for reduced vigilance (Beauchamp, 2013). As such, group formation may allow for increased foraging intensity (Fortin et al., 2004), which may lead to greater damage to vegetation by exotic herbivores (Ramirez et al., 2018). Research examining the effect of human predators on animal group size is limited; however, red deer will disaggregate in response to rising predation risk from wolves and humans (Proffitt et al., 2009). Despite no significant relationship being observed, fallow deer in our study showed an increasing propensity to group during the day, with a concomitant decreasing propensity to group at dusk or at night, following aerial culling (Fig. 4.3B; model 4). Increased grouping behaviour for days of active aerial culling (day 0; Table S4.2B: model 4) may have also been a short-term adaptive response to aerial culling and any risks associated with it. Perceived predation risk in deer and its effect on group size may therefore be temporally adaptive (Delisle et al., 2023), with the strongest effect on behaviour during the day. This pattern highlights the importance of accounting for time of day when evaluating animal responses to humans.

Prey movement facilitates predator-prey interactions, and decreased movement speeds can lead to reduced predator-prey encounters (Keim et al., 2021). Conversely, when animals exert anti-predator behaviour, increased movement can result from avoiding spatially risky areas (Basille et al., 2015). Such movement responses may occur as instantaneous reactions to predator detection or persist over longer periods due to chronic increases in predation risk (Picardi et al., 2019). In our study, we did not detect any changes in staying time or movement rates as a result of aerial culling, although slight temporal variability was observed (Fig. 4.3C; Table S4.2A). In a previous study, ground-based culling resulting in the eradication of > 2,000 reindeer (Rangifer tarandus) infected with chronic wasting disease led to daytime movements 60% greater than seasonally comparable post-cull periods in previous years (Mysterud et al., 2020). That study made use of a 10-year dataset characterised by long periods of continuous culling pressure spanning 1–4 months, so, it is possible that behavioural observations made during longer periods of sustained and more intensive aerial control may increase the detectability and precision of the weak effects we observed.

Deer detections during aerial culling and for the 7 days following were lower than outside of periods of shooting (Fig. 4.3A; Table S4.2A). However, the aerial thermal survey density estimates and relative detection indices generated in this study did not have sufficient temporal detail to enable us to determine whether these changes were directly linked to numbers of animals killed or other factors (Fig. 4.2; Table S4.1). Alongside changes in movement rates, ground-based hunting has been shown to trigger changes in movement ranges, as target species may flee areas subject to control (Sunde et al., 2009). Animals may use novel areas at the perimeter of their range (Mysterud et al., 2020) or increase home range sizes when subject to intensive control (Riordan et al., 2011), potentially moving to areas perceived as low-risk compared to areas were active culling is occurring (Tolon et al., 2009). Although a recent study of fallow deer movement responses to aerial control found no evidence for deer leaving their pre-control ranges during or immediately after aerial shooting (Bengsen et al., 2024). In our study, short-term decreases in deer activity may be due to deer shifting their movement ranges outside of the aerial culling operational zone. Alternatively, short-term decreases in activity may be directly due to numbers killed, and subsequent increases in activity following culling might reflect new deer moving into the site (Takeshita et al., 2017). Population genetic approaches (similar to Synnott et al., 2023), GPS tracking of targeted animals (Bengsen et al., 2024), or a database of individually recognisable individuals from camera trap imagery, could be used to estimate immigration and emigration rates following culling. Such data would clarify whether changes in deer density and abundance within a control site are influenced by movement patterns in addition to control efforts.

Our findings suggest that invasive deer can perceive and respond to aerial culling by exhibiting behavioural adaptations in the short-term. Importantly, reduced activity of deer during daytime aerial culling operations may decrease the detectability of target species from an aircraft, as deer activity has previously been linked to detectability during aerial thermal surveys (Zabransky et al., 2016). This may reduce the impact and increase the effort and costs of wildlife management efforts. Though the use of thermal imaging to aid in the detectability of stationary animals may mitigate against this effect (Cox et al., 2023). Thermal-assisted ground-based control commencing at dusk could also be considered alongside daytime aerial control to take advantage of increased deer activity during the dusk and night periods. Aerial culling operations could investigate how diel activity patterns change throughout the course of a culling event, and when animal behaviour returns to pre-culling levels once operations have ceased, to help determine the optimal timing between culling events in long-term operations. Understanding whether long-term shifts can occur under different intensities of control would also help determine the need to change management approaches in the future. Continuously altering the timing, duration and location of culling during long term operations may decrease the spatio-temporal predictability of refugia (Cleveland et al., 2012), which may minimise behavioral changes in the target species during culling operations. Conversely, it has also been suggested that introducing year-round culling, where feasible, may also reduce the predictability of management efforts and may reduce overall antipredator behaviour in the long-term (Cromsigt et al., 2013). Future studies could examine the effectiveness of these alternative management strategies for reducing target species populations, and may also aim to examine the effects of aerial shooting across different environments and between sexes, as previous research has shown that these effects can vary depending on these factors (Bengsen et al., 2024).

Human encroachment and anthropogenic impacts on natural systems, including the spread of invasive species, coupled with the extirpation of native predator populations, has facilitated the need for wildlife management practices that curb invader impacts (Dueñas et al., 2021). For overabundant and invasive large mammal species, aerial control is one of the most widely deployed control methods (Bradshaw et al., 2023; Cox et al., 2023). Ultimately, if the goal is to reduce the numbers and impacts of invasive species, it is critical to understand how target species respond to management efforts. Our study adds to the literature demonstrating that deer populations can shift their behaviour in response to culling operations (e.g. Bengsen et al., 2024; Comte et al., 2022; Mysterud et al., 2020), suggesting a need to examine how management efforts can take advantage of this behaviour to achieve sustained population reduction.

4.7 Acknowledgments

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4.9 Supplementary Material

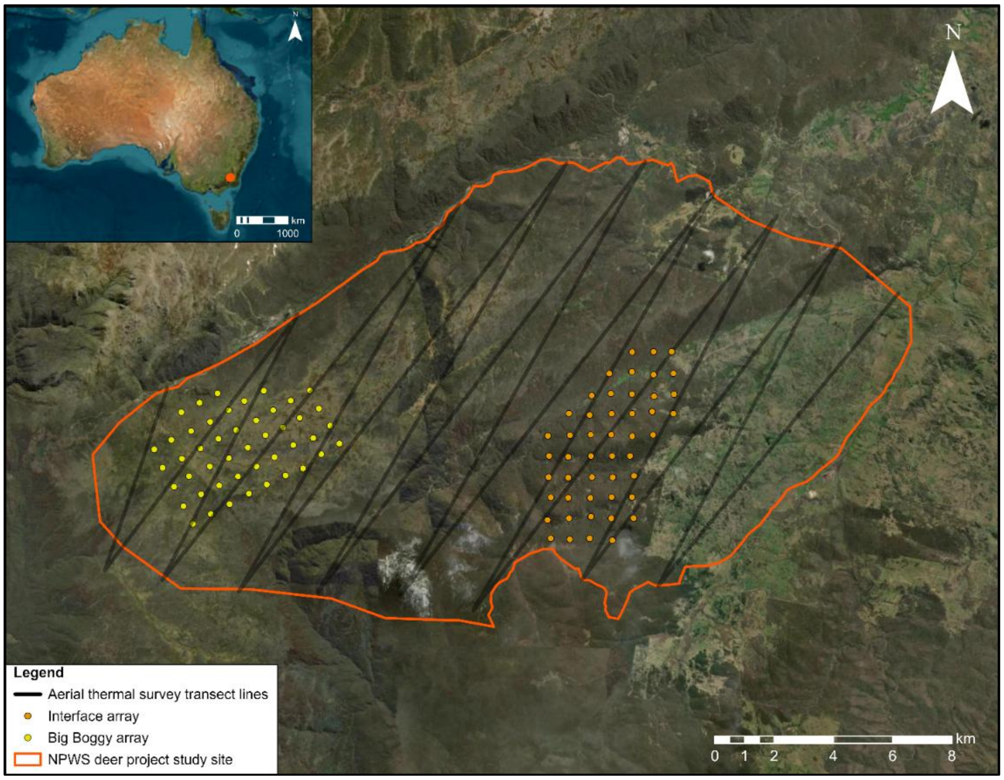

Figure S4.1: Map showing the study area boundaries, the locations of the Interface and Big Boggy camera arrays, and the aerial thermal survey transects (main image). Inset map shows the location of the study area (red point).

Appendix Item 4.1: Method for collecting and analysing thermal survey imagery

Aerial thermal surveys consisted of 16 transects spaced approximately 2.5km apart in a zig zag formation (Figure S1). The helicopter flew at variable speed (30–35 knots over dense habitat, 35–40 knots over sparse or open habitat) at 220 feet. The strip width was 105.7 m. All thermal imagery was collected with a Sierra-Olympic Vayu HD (generation 1) uncooled microbolometer array (hereafter referred to as "the Vayu"). The Vayu has a 24 x 14.5 mm sensor that produces a 1920 x 1200-pixel image and has a refresh rate of > 60 Hz. We viewed survey output from the thermal imager on a Blackmagic Video Assist 7" 3G monitor (https://blackmagicdesign.com/au/products/blackmagicvideoassist). All video was collected and processed as "white-hot" grayscale imagery. Surveys were conducted in the first two hours from first light, and the last 1.5 hours before last light to maximise optimal thermal conditions. The Vayu was mounted to a Ronin MX gimbal (https://www.dji.com/au/ronin-mx) for image stabilization and to ensure a fixed camera angle relative to the ground. The gimbal was mounted to the open-door frame of an AS350 Squirrel helicopter. Thermal footage was recorded through the Blackmagic on to an external hard drive for later review.

For thermal imagery review, the bottom of the field of view of the imager was considered the zero line. Footage was viewed using VLC media player 3.0.8 and detections were logged using a custom-built AutoHotKey application ClickPosition. ClickPosition logs the position of the animal in the field of view, along with the general species (e.g. deer, pig), density, vegetation class and time of detection. This information was transcribed to a custom Microsoft Excel® workbook which calculated the precise (+/- 1 m) distance from the zero line (assuming flat terrain) using the time-stamped tracklog including GPS coordinates and height-above-ground values. Outputs from the workbook include a CSV file of detections, and a KML file including species and group size for mapping.

Population density and abundance estimates were generated using the Distance package v1.0.9 (Miller et al., 2019) in R. We used conventional distance sampling analysis for thermal surveys as there was only one "observer" (one imager). We included habitat (and site where required) as covariates in the model where the key function was not uniform. Survey data were pooled over time, thus increasing the number of detections used to generate estimates over subsequent surveys.

Appendix Item 4.2: Method for calculating deer relative activity over time

Detection rates of white-tailed deer (Odocoileus virginianus) and sambar deer (Rusa unicolor) on camera traps have been shown to be positively correlated with densities derived from spatial mark-resight models (Bengsen et al., 2022; Parsons et al., 2017). Therefore, we used relative detection indices as an estimator of relative abundance in this study. To generate a relative detection index for fallow deer (the average number of detections per active camera per month – Figures 9–11), species detection histories were generated using camtrapR v2.3.0 (Niedballa et al., 2016) using all March 2020 – November 2023 data. Then, the total number of cameras working each day was calculated, and the total number of detections per day was divided by the total number of cameras working for that day to generate a standardised number of events per day per active camera. The average number of events per month per active camera was then generated by summing the events per day for each month for each camera, and then calculating the mean for all active cameras.

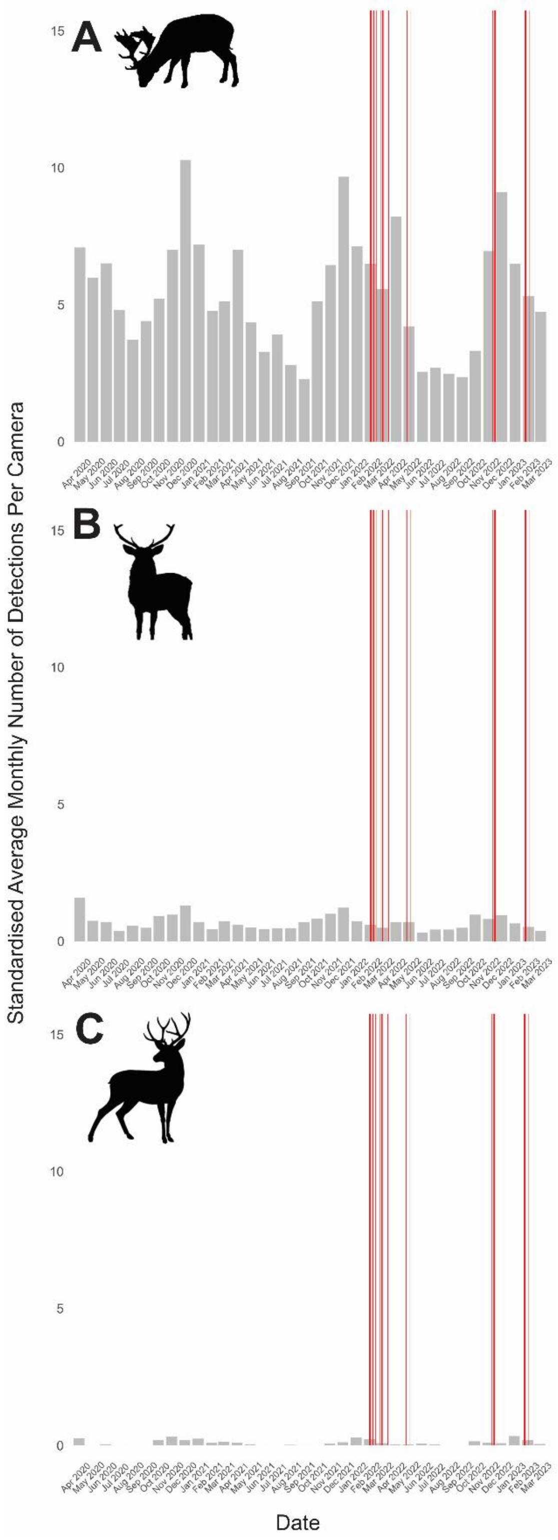

Figure S4.2: Fallow deer (A), sambar deer (B) and red deer (C) standardised average monthly number of detections per camera across the Big Boggy and Interface camera arrays from April 2020 to March 2023.

Table S4.1: Density and abundance estimates for deer throughout the project site (284 km2). Transect detections show how many of the transects within that area had detections compared to the total transects in the project area. Upper and lower confidence limits (±95%) are provided for the abundance and density estimates in parentheses.

Survey	**Transects Detections (/16)**	**Detections**	**Deer sighted**	**Estimated density (deer/km^2)**	**Estimated abundance**	**Coefficient of variation**
May 2020	13	143	231	18.8 (11.3–31.2)	5326 (3201–8864)	25
November 2020	15	98	265	15.6 (8.6–28.0)	4419 (2452–7963)	28
April 2021	15	118	317	18.4 (10.6–32.1)	5233 (3008–9106)	27
November 2021	12	94	218	14.0 (8.0–24.5)	3975 (2272–6954)	27
February 2022	13	123	283	16.4 (10.1–26.5)	4652 (2877–7521)	23
April 2022	15	107	240	13.9 (8.4–23.2)	3959 (2378–6591)	24
November 2022	15	84	209	12.1 (6.9–21.2)	3444 (1971–6018)	27
April 2023	16	185	452	26.2 (15.5–44.3	7449 (4408–12587)	25
November 2023	14	130	319	19.1 (10.0–36.4)	5429 (2849–10348)	31

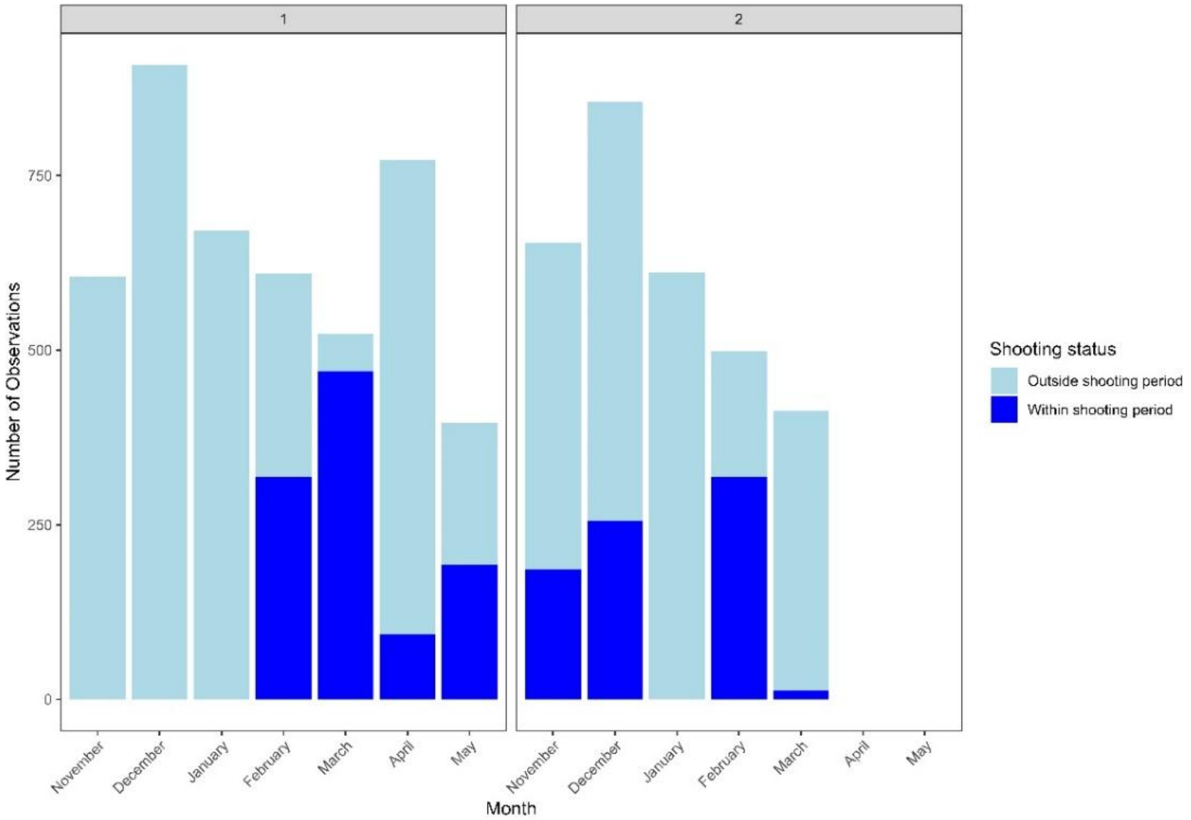

Figure S4.3: Number of detections of fallow deer for the Big Boggy and Interface camera arrays shown for each month, shooting period, and shooting status, where 'within shooting period' represents periods during and up to 7 days following an aerial culling event.

Table S4.2: Summary results for the models evaluating the effect of aerial culling on fallow deer behavioural characteristics diel activity, grouping and staying time. Models 1, 3 and 5 evaluate the effect of aerial culling on these behavioural characteristics for periods during and up to 7 days following an aerial culling event, compared with outside of shooting events. Models 2, 4 and 6 evaluate the effect of aerial culling on behavioural characteristics separately for the day of aerial culling and each of the seven days following.

Parameter	**Estimate**	**p-value**	**Standard error**	**Confidence interval**
Temporal activity				
1: (Intercept)	-4.563	$< 2 \times 10^{-16}$	0.114	(-4.785, -4.340)
1: Shooting[1]	-0.210	0.001	0.066	(-0.338, -0.081)
1: Array[2]	0.247	3.41×10^{-13}	0.034	(0.180, 0.314)
1: Time of day: night[3]	-0.616	$< 2 \times 10^{-16}$	0.051	(-0.716, -0.517)
1: Time of day: dawn[3]	0.481	$< 2 \times 10^{-16}$	0.054	(0.376, 0.586)
1: Time of day: dusk[3]	0.103	0.080	0.059	(-0.012, 0.217)
1: Shooting x time of day: night	0.162	0.092	0.096	(-0.027, 0.351)
1: Shooting x time of day: dawn	0.037	0.725	0.106	(-0.170, 0.244)
1: Shooting x time of day: dusk	0.350	0.001	0.110	(0.134, 0.564)
1: Random effects:	Variance	Standard Deviation		
Month	0.048	0.218		
Period	0.009	0.095		
2: (Intercept)	-4.760	$< 2 \times 10^{-16}$	0.172	(-5.096, -4.423)
2: Shooting[4]	-0.018	0.516	0.027	(-0.071, 0.036)
2: Array[2]	0.257	2.35×10^{-4}	0.070	(0.120, 0.394)
2: Time of day: night[3]	-0.371	0.001	0.115	(-0.596, -0.145)
2: Time of day: dawn[3]	0.603	1.62×10^{-6}	0.126	(0.356, 0.849)
2: Time of day: dusk[3]	0.407	0.002	0.130	(0.153, 0.662)

2: Shooting x time of day: night	-0.026	0.512	0.039	(-0.103, 0.051)
2: Shooting x time of day: dawn	-0.039	0.381	0.044	(-0.125, 0.048)
2: Shooting x time of day: dusk	0.032	0.462	0.043	(-0.053, 0.117)
2: Random effects:	Variance	Standard Deviation		
Month	0.102	0.319		
Period	0.007	0.083		
Grouping				
3: (Intercept)	-0.999	$< 2 \times 10^{-16}$	0.092	(-1.189, -0.786)
3: Shooting[1]	0.113	0.220	0.093	(-0.069, 0.294)
3: Array[2]	-0.154	0.006	0.056	(-0.263, -0.045)
3: Time of day: night[3]	0.089	0.269	0.081	(-0.070, 0.247)
3: Time of day: dawn[3]	0.235	0.007	0.087	(0.062, 0.405)
3: Time of day: dusk[3]	0.061	0.559	0.105	(-0.147, 0.265)
3: Shooting x time of day: night	-0.225	0.141	0.153	(-0.527, 0.074)
3: Shooting x time of day: dawn	-0.079	0.653	0.175	(-0.424, 0.263)
3: Shooting x time of day: dusk	-0.023	0.903	0.190	(-0.397, 0.348)
3: Random effects:	Variance	Standard Deviation		
Month	0.028	0.167		
Period	0.002	0.043		
4: (Intercept)	-0.951	8.64×10^{-11}	0.147	(-1.269, -0.674)
4: Shooting[4]	0.027	0.438	0.035	(-0.042, 0.095)
4: Array[2]	-0.055	0.621	0.112	(-0.275, 0.165)
4: Time of day: night[3]	0.068	0.689	0.170	(-0.268, 0.400)
4: Time of day: dawn[3]	0.183	0.352	0.196	(-0.206, 0.564)
4: Time of day: dusk[3]	0.317	0.125	0.207	(-0.093, 0.719)

4: Shooting x time of day: night	-0.097	0.105	0.059	(-0.215, 0.019)
4: Shooting x time of day: dawn	-0.011	0.874	0.069	(-0.148, 0.123)
4: Shooting x time of day: dusk	-0.135	0.061	0.072	(-0.280, 0.004)
4: Random effects:	Variance	Standard Deviation		
Month	0.020	0.141		
Period	-	-		
Staying time				
5: (Intercept)	1.403	4.11 x 10^{-9}	0.067	(1.269, 1.541)
5: Shooting[1]	0.037	0.446	0.048	(-0.057, 0.134)
5: Array[2]	-0.285	$< 2 \times 10^{-16}$	0.029	(-0.343, -0.226)
5: Time of day: night[3]	-0.006	0.887	0.043	(-0.090, 0.078)
5: Time of day: dawn[3]	-0.063	0.176	0.047	(-0.154, 0.028)
5: Time of day: dusk[3]	-0.155	0.004	0.055	(-0.262, -0.048)
5: Shooting x time of day: night	0.013	0.876	0.082	(-0.149, 0.174)
5: Shooting x time of day: dawn	0.070	0.463	0.095	(-0.117, 0.255)
5: Shooting x time of day: dusk	-0.073	0.479	0.103	(-0.275, 0.129)
5: Random effects:	Variance	Standard Deviation		
Month	0.021	0.146		
Period	6.04 x 10^{-4}	0.025		
6: (Intercept)	1.351	2.92 x 10^{-4}	0.141	(1.043, 1.639)
6: Shooting[4]	0.007	0.709	0.020	(-0.034, 0.046)
6: Array[2]	-0.215	5.74 x 10^{-4}	0.062	(-0.341, -0.095)
6: Time of day: night[3]	1.034	0.275	0.095	(-0.081, 0.289)
6: Time of day: dawn[3]	-0.026	0.848	0.108	(-0.229, 0.193)
6: Time of day: dusk[3]	-0.101	0.395	0.118	(-0.332, 0.131)

6: Shooting x time of day: night	-0.054	0.088	0.032	(-0.116, 0.008)
6: Shooting x time of day: dawn	0.012	0.760	0.038	(-0.064, 0.085)
6: Shooting x time of day: dusk	-0.060	0.120	0.039	(-0.136, 0.016)
6: Random effects:	Variance	Standard Deviation		
Month	0.056	0.237		
Period	0.009	0.096		

[1]’Within shooting period’ was the reference category. [2]’Interface array’ was the reference category. [3]’Day’ was the reference category. [4]Continuous variable with range 1–7.

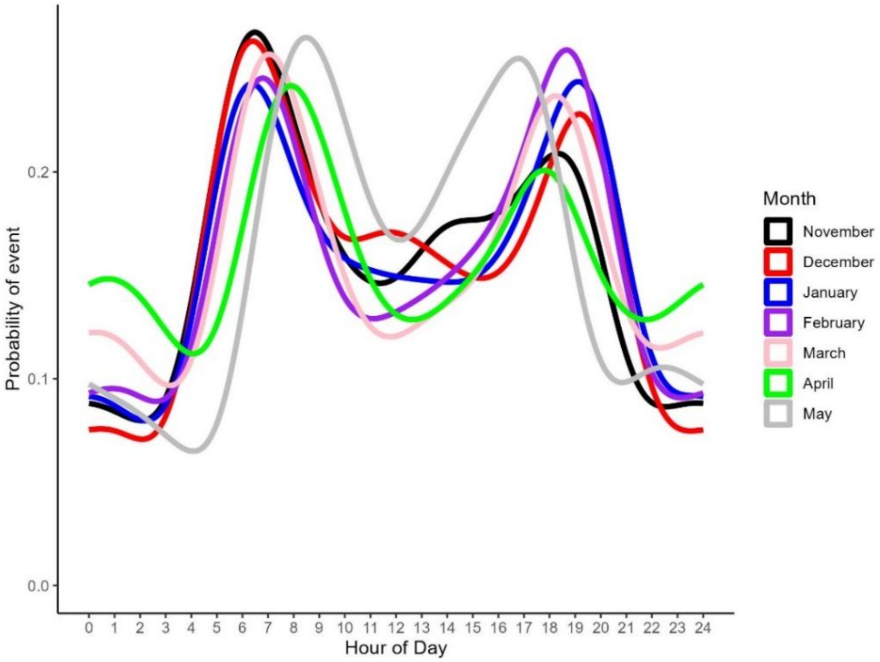

Figure S4.4: Kernel density estimates of the diel activity patterns of fallow deer (Dama dama) between November 2021 – May 2022 and November 2022 – May 2023, broken up by month.

References for Supplementary Material

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Chapter 5: Mammalian scavenger responses to mass herbivore culls

Canid footprints in the snow in subalpine Kosciuszko National Park

A slightly revised version of this chapter is in review in *Ecosphere* as: McCarthy, E.D., Grueber, C.E., Newsome, T. M. (2025) Mammalian scavenger responses to mass herbivore culls. I co-designed the study with all other co-authors, analysed the data, and wrote the manuscript in collaboration with my co-authors.

5.1 Abstract

Animal carcasses are exploited by a range of scavenger species, but little is known about scavenger responses to the presence of large carcass loads following mass culling events. In some systems, invasive scavengers may monopolize these carcass resources, but native apex scavengers could also restrict the use of carcasses by invasive species by consuming carcass biomass or competitive exclusion. Yet, these relationships may also change depending on the species of carcasses available and the habitats and seasons in which they fall. Here we assess the utilisation of carcasses by an invasive mesoscavenger, the red fox (*Vulpes vulpes*) and a long-established apex scavenger, the dingo (*Canis dingo*), following multiple culling events in subalpine Australia that resulted in a total of 500 fallow deer (*Dama dama*), 111 sambar deer (*Rusa unicolor*), and 12 red deer (*Cervus elaphus*) culled within a localized area. Fifty-five of these deer carcasses were monitored to assess carcass utilization and behaviour of the target scavenger species, and their broader activity responses were assessed via a camera array in the surrounding landscape. We found that foxes utilized carcasses year-round, while dingoes mostly utilized carcasses in warmer periods. At the single carcass level, the probability of fox scavenging per day at each carcass decreased from 3.2% to 0.2% from densities of 1 to 35 fallow deer carcasses/km^2, while the probability of dingo scavenging per day at each carcass increased from 1.3% to 14.2% from densities of 1 to 10 sambar deer carcasses/km^2. Across the broader landscape, the probability of fox occurrence per day at each camera decreased from 1.2% to 0.1% from densities of 1 to 30 fallow deer carcasses/km^2, whereas dingoes were more influenced by season than carcass density. Foxes exhibited temporal separation from dingoes in both their daily activity patterns and, to a greater extent, their carcass use, suggesting resource competition between the species. Nonetheless, neither fox nor dingo presences at carcass sites were linked to accelerated carcass biomass loss. Instead, carcass biomass loss was driven by warmer temperatures when insect scavengers are more active, with 40% of carcasses culled outside of early summer not reaching 90% biomass loss within the ~6-month monitoring period. Overall, these results indicate that landscape-scale culling operations can impact scavenger feeding behaviours and activity patterns in varied ways, and that the timing of such culls can impact the persistence of large carcass load.

5.2 Introduction

The decomposition of organic matter, including carrion, is fundamental for nutrient and energy cycling in all ecosystems (Swift et al., 1979). The decomposition process is driven by environmental conditions (Turner et al., 2017; Vandersteen et al., 2023), detritus or carrion traits (Moleón et al., 2015; Pardo-Barquín et al., 2019), the assemblages and abundance of detritovores, and other vertebrate and invertebrate scavengers present, and interactions among these factors (Newsome et al., 2021). Within an ecosystem, detritus and carrion biomass distribution is typically spatiotemporally patchy. However, mass mortality events, triggered by adverse environmental conditions, disease epidemics, or widespread culling, can lead to an influx of carrion in the landscape (Fey et al., 2015). Understanding how scavenger species respond to and utilize carrion during periods of high resource availability is important because it can affect the movement and population dynamics of scavenger species (Handler et al., 2021; White, 2010), influence the distribution and abundance of the prey species of facultative scavengers (Cortés-Avizanda, Selva, et al., 2009; Moleón et al., 2014; Rees et al., 2020) and alter food web dynamics (Baruzzi et al., 2018; Wilson & Wolkovich, 2011).

Within scavenger guilds, larger apex scavengers typically consume carrion at the fastest rate (Gutiérrez-Cánovas et al., 2020), and outcompete other vertebrates for carrion resources (Newsome et al., 2024). As a consequence, less efficient midsized mesoscavengers may increase carrion use in the absence of apex scavengers (Morales-Reyes et al., 2017; O'Bryan et al., 2019). Conversely, apex predators can also facilitate scavenging by mesoscavengers. For example, in a temperate European forest, wolves (*Canis lupus*) facilitated scavenging on bison (*Bison bonasus*) carcasses by red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*), by tearing apart the bison's thick skin to expose the flesh, which was otherwise inaccessible to smaller scavengers (Selva et al., 2003). Yet, little is known about how these dynamics might be affected by increasing carcass size, or increasing carcass load, for example, from a mass-mortality event (Barton et al., 2023). Increases in carcass biomass have been linked to increased rates of vertebrate scavenging generally (Moleón et al., 2015), and increased interspecific activity overlap among scavengers (Baruzzi et al., 2022). Thus, as more carcasses become accessible to scavengers, competition among scavengers may decrease (Selva et al., 2003).

At a broader landscape scale, scavengers may also respond to the availability and density of carrion. However, the results are varied from the few studies to date. For example, a study examining scavenger carcass use and distribution in the landscape following a mass drowning event found that vultures within 30 km of the carcasses rarely visited the resource, suggesting carrion availability was not directly driving scavenger distributions (Handler et al., 2021). Similarly, over long time scales, the population growth rate of a facultative scavenger has been shown to be unaffected by the availability of prey carrion in the landscape (Sidous et al., 2024). In contrast, provisioning large herbivore carcasses has been shown to rapidly increase local abundances of scavenging corvids (Rees et al., 2020; White, 2010). Furthermore, the local density of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) carcasses has been shown to be a strong predictor of vulture presence at roosts (Mateo-Tomás & Olea, 2010). Although studies are limited, differing responses of scavengers to large carcass loads could reflect the carcass type available, as scavenger-specific differences in carrion utilization are known to exist among carcass types (Olson et al. 2016). Moreover, scavengers with certain feeding strategies, such as being more or less social, have also been found to influence feeding patterns at sites with high carrion loads, with group sizes and number of individuals feeding increasing for more social feeders (Baruzzi et al., 2022). These findings have led to calls to better understand the range of scavenger responses to large carcass loads, but also to assess whether scavengers can contribute significantly to carrion removal following mass mortality events (Barton et al., 2023). If the scavengers cannot efficiently remove the carcasses, it may increase the risk of large carcass loads subsidizing pest species, altering nutrient cycling or leading to disease spread (Newsome et al., 2021).

One challenge of studying mass mortality events is that they can be sporadic in time and place, making it difficult to assess scavenger use of the carcasses and their broader landscape response to the nutrient pulse. However, when these events arise from large scale culling operations, there are opportunities to set up field experiments. The Australian Alps bioregion, a mountainous alpine and subalpine area in southeastern Australia (Costin, 2000), is an ideal location for assessing mammalian scavenger responses to mass culling. Three invasive deer species are present in this region: fallow deer (*Dama dama*), sambar deer (*Rusa unicolor*) and red deer. As such, culling is widespread, and aerial culling is commonly deployed as an efficient landscape-scale control tool for large invasive herbivores in this region (e.g. Pulsford, Roberts, and Elford 2022). Carcasses are usually not removed during aerial culling operations and remain in place until their decomposition (Hampton et al., 2022). Invasive mesoscavenger the red fox, and longer established apex scavenger the dingo (*Canis dingo*) are known to scavenge on deer carcasses (Forsyth et al., 2014; Woodford et al., 2021). Previous research in the region has shown that scavenging is highest in winter and spring (Vandersteen et al., 2023), while biomass loss is fastest in warm periods (Spencer & Newsome, 2021), and that mesoscavengers monopolise carcass resources (Vandersteen et al., 2023). Where present, however, the dingo, could play a role in reducing mesoscavenger carcass use, either by rapid removal of carcass biomass, or by deterring them from utilising carrion (Newsome et al., 2024). More broadly, foxes have been shown to exhibit patterns of spatiotemporal avoidance towards dingoes (Schroeder et al., 2015; Wooster et al., 2021), and so, this behaviour may also be detectable around carrion resource hotspots (Forsyth et al., 2014). Thus, the presence of these scavengers and deer culling in the Australian Alps allows examination of how intensive human-mediated culling affects scavenger carcass use, scavenger activity in the broader, as well as the roles of these scavengers in accelerating carcass biomass loss, and how environmental conditions interact with these effects.

Taking advantage of this opportunity in the Australian Alps, we propose that scavenger carcass use will be mediated by apex-mesoscavenger dynamics, and a range of environmental factors and carrion characteristics, and that carcass load will trigger changes in scavenging rates and scavenger local distributions. Specifically, we first predicted that visitations to carcasses and scavenging will be higher for foxes compared to dingoes (Vandersteen et al., 2023), higher in cooler periods for both foxes and dingoes (Vandersteen et al., 2023), and for larger carcasses and higher carcass densities (Mateo-Tomás et al., 2019; Moleón et al., 2015), and will decrease with time since death (H[Hypothesis] 1). Secondly, we predicted that carcass density across the landscape will influence fox and dingo distributions, with higher activity for both species in areas with higher carcass loads, with this effect being stronger for larger-sized carcasses (H2) (Mateo-Tomás et al., 2019; Rees et al., 2020; White, 2010). Thirdly, at both the carcass and landscape level, we predicted that dingo presence will influence fox activity, resulting in temporal avoidance between dingoes and foxes, with this effect being more pronounced at carcasses due to competitive exclusion within a localised area (H3) (Forsyth et al., 2014; Schroeder et al., 2015; Wooster et al., 2021). Finally, despite extensive carcass visitations, we predicted that scavenging by foxes and dingoes will have limited effect on carcass biomass loss due to the high number of carcasses in the landscape, and will instead be faster in higher temperatures (Spencer & Newsome, 2021), and for smaller carcasses (H4).

5.3 Methods

5.3.1 Study area

This study took place in Australia's Alpine region, in an area within Kosciuszko National Park, on the Country of the Ngarigo People, in south-east New South Wales. Recreational hunting is not permitted in the National Park, but introduced species are targeted via Government-run culling programs. Elevation across the study area ranged from 1568–1875 m, and elevation across the carcass cameras ranged from 1618–1841 m. Vegetation is dominated by eucalypt woodlands with tussock grass, fern and shrubby understories, and wet open tussock grasslands, interspersed with some shrubland and heathland. Continuous snow cover for at least one month of the year occurs within the subalpine zone of the study area (below 1750 m ASL), while the alpine zone, (above 1750 m ASL), is mostly above the tree line, and typically experiences continuous snow cover for at least four months of the year (MacPhee & Wilks, 2013; Sanecki et al., 2006). During the study, in early winter, monthly mean temperature ranged from 5.1 (July 2022) to 13.7 (November 2022), and for early summer ranged from 9.0 (May 2023) to 21.4 (January 2023). In late summer, monthly mean temperature ranged from 9.0 (May 2023) to 20.9 (February 2023) (Bureau of Meteorology, 2024).

5.3.2 Aerial control

Twenty-three days of aerial control was conducted by one helicopter across a 378-day period (9 May 2022–22 May 2023), outside of the period when snow was likely to occur (June–October). Shooting was conducted using a .308 semi-automatic rifle, out of an AS350 B3 Écureuil (Squirrel) helicopter (Aerospatiale, France). Fallow deer, red deer and sambar deer were targeted for culling. These deer typically weight 150–200 kg for sambar deer, 150–180 kg for red deer (McCarthy et al., 2023), and 40–80 kg for fallow deer (Geist & Bayer, 1988). Within each shooting period, the majority of the study area was subjected to aerial culling. The location of each culled deer was recorded by personnel on the helicopter at the time of shooting

5.3.3 Camera array

An array of 46 cameras was situated in the study area, where the majority of the aerial culling took place. Each camera was spread 600–700 m apart in a grid (Figure 5.1). Camera traps (model: Reconyx HyperFire 2; Professional Reconyx Inc., Holmen, WI, USA) were set at 1.5 m above the ground tied to a mature tree, facing south, to minimise the effect of the sun on the camera. The cameras were setup to capture non-native and native herbivores, such as horses (*Equus caballus*), and swamp wallabies (*Wallabia bicolor*), and scavengers, such as dingoes, foxes and cats (*Felis catus*). In-field testing determined that, at night, fallow-sized deer would reliably trigger the camera if they came within a ~37° detection angle at a distance of less than 6 m from the camera. Therefore, wooden stakes of 1 m length were set up 2 m apart, 1 m from the centre of the camera field of view on either side, at a distance of 6 m from the camera, marking the point at which animals were detectable by the camera at night. Images captured during the day where the animal remained outside of this zone for the entire capture period were removed from downstream processing, to calibrate the detectability of daytime and nighttime detections. Cameras were programmed for passive infrared motion detection with high sensitivity, and captured 10 images per detection in rapid succession. There was no quiet period between detections.

The camera array functioned continuously between May 2022 and November 2023, and camera data were downloaded twice yearly; however, some cameras did not run for the entire monitoring period as it was not always possible to check cameras prior to the batteries going flat, and cameras were sometimes disturbed by animals. Due to camera failures, or memory cards filling up before download, there was some minor variation in sampling effort, which was accounted for in statistical modelling where necessary.

5.3.4 Carcass camera monitoring

Carcass scavenger use and biomass loss were monitored within and surrounding the camera array, up to 2.8 km from the nearest array camera, at fifty-six carcasses across three seasonal deployments (Figure 5.1). Early winter monitoring commenced in May 2022, with the deployment of remote cameras monitoring 13 fallow deer and 8 sambar deer carcasses. Early summer monitoring commenced between November and December 2022, when 14 fallow deer and two sambar deer carcasses were monitored. The late summer deployment commenced between February and March 2023, when 9 fallow deer carcasses and 10 sambar deer carcasses were monitored. For these carcasses, monitoring commenced between two and 144 hours post death, and carcasses were remotely monitored for up to 180 days following animal death. One remote camera monitoring a sambar deer carcass deployed in the late summer period malfunctioned for the entire monitoring period and was excluded from downstream analyses.

Within each deployment season, carcass monitoring sites were established a minimum of 100 m from the nearest sites monitored within the same season. Maintaining greater distances between monitored carcasses was not possible due to high densities of carcasses within the study area. Each carcass remained in situ at the place of death, intact with exception of bullet entry and exit wounds. A Reconyx HyperFire 2 camera trap was attached to a tree or a free-standing star picket 3–4 m from the carcass. Cameras were programmed for passive infrared motion detection with high sensitivity, and captured 10 images per detection in rapid succession. There was no quiet period between detections. Canopy cover at each site was rated as either open or closed, open canopy habitats had no tree cover over the carcass and were at least 20 m away from densely forested areas, closed canopy habitats had more than 20% canopy cover over the carcass, as in Spencer & Newsome (2021). Canopy cover and proportion tree cover were included as predictor variables in the statistical models, as vegetation cover has previously been shown to affect scavenging activity and biomass loss (Spencer & Newsome, 2021), as well as landscape-scale habitat selection (Cagnacci et al., 2004; Wysong et al., 2020).

To quantify carcass persistence rates, time lapse photo imagery, captured at 13:00 each day, was used to estimate carcass biomass loss-rate. The dates of 50% and 90% biomass loss were recorded for each carcass through an assessment of time lapse photos and, where possible, carcass persistence rates were verified using in-field observations.

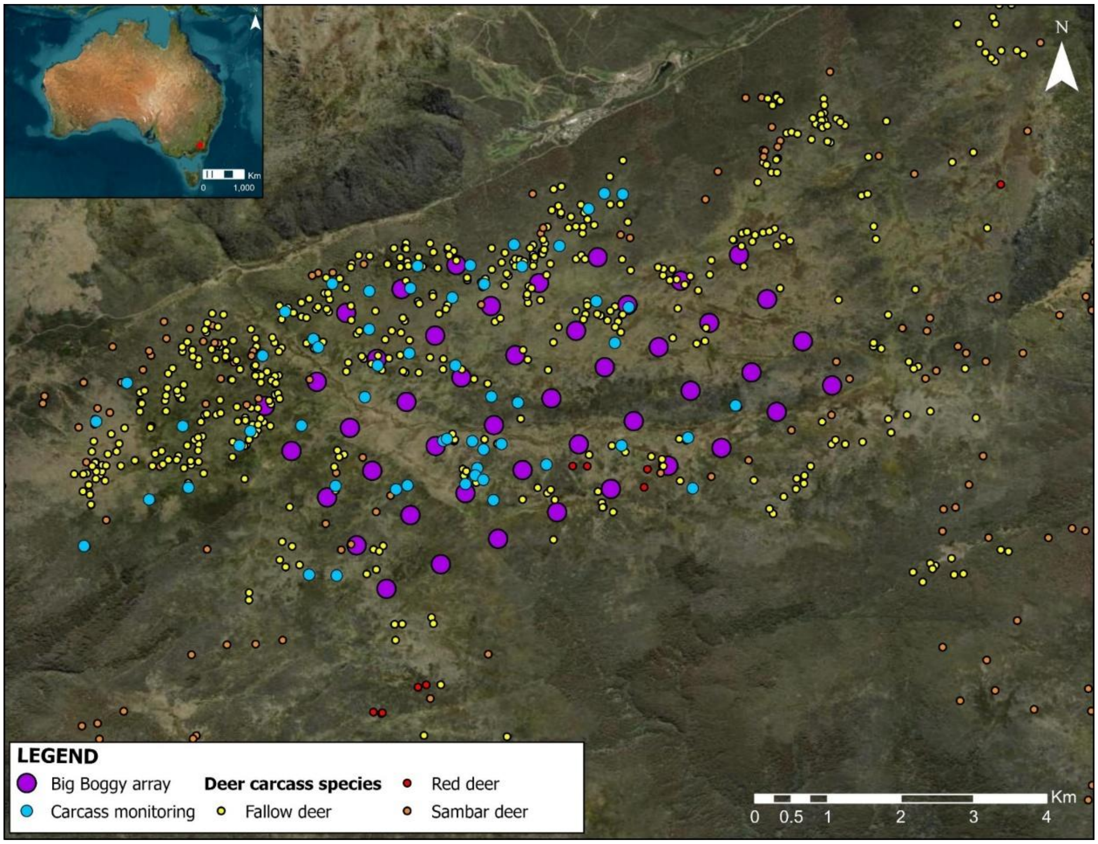

Figure 5.1: Map showing the study area the locations of all array cameras (purple points), locations of fallow deer (yellow points), sambar deer (orange points) and red deer (red points) aerially culled between the 9th of May 2022 and the 22nd of May 2023, and the locations of the 56 carcasses that were monitored (blue points). Inset map shows the location of the study, in a subalpine area of Kosciuszko National Park, Australia (red point).

5.3.5 Camera data processing

5.3.5.1 Camera array

All images were tagged in ExifPro 2.1.0 (https://github.com/mikekov/ExifPro) to species (where identifiable) based on manual identification in photos. To ensure independence, subsequent photographs of the same presumptive individual or group of individuals (photographs taken < 5 min apart) were removed prior to analysis. Histograms of dingo and fox activity were inspected to confirm that this was an appropriate breakpoint. If an animal was detected, but it did not come within the 6 m detection zone, the detection was excluded from downstream processing so that the detection zone was standardized for day and night detections. Image tag data were extracted using R package *recocam* v1.0.0.0 (Raghunath et al., 2019), with one entry per detection event.

5.3.5.2 Carcass monitoring cameras

All images were tagged using Digikam v7.9.0 (Gilles et al., 2018). Each event was tagged to species level, then, an event was characterised as a scavenging event if the species scavenged on the carcass in at least one of the remote-camera images from that event, otherwise the event was characterised as an investigation event. To ensure independence, subsequent photographs of the same presumptive individual or group of individuals (photographs taken < 10 min apart) were removed prior to analysis (following Spencer & Newsome, 2021; Vandersteen et al., 2023). For camera arrays and carcass monitoring cameras, camera operability matrices were generated using *camtrapR* v2.3.0 (Niedballa et al., 2016).

5.3.6 Statistical analyses

5.3.6.1 Carcass visitations over time

We summarised the number of feeding events for each scavenger species and plotted histograms of daily scavenging events over time, from one to 185 days post death.

We tested the determinants of dingo and fox carcass visitation rates (H1). The response variable was the number of visitation events per month for each scavenger (dingoes and foxes modelled separately). Visitation rates were estimated using generalised additive mixed models (GAMMs), because temporal variation in visitation events is not likely to be monotypic over time (as in Dawson et al., 2022). Our fixed predictor variables were carcass species, deployment season, and months since death. Carcass species was a categorical predictor for the two deer species (fallow deer [reference category], sambar deer). Months since death (a continuous integer value; rounded down to the nearest whole month) was modelled as a tensor product smooth, with separate smooths fitted for each season (early winter, early summer, late summer). The categorical random effect was carcass ID (1–51; ordered by deployment date). For this analysis, four carcasses were excluded because they were not monitored for > 3 days (10%) of any month. An offset term for the number of days each carcass monitoring camera was active for each month (natural log transformed) was also included. For foxes, the GAMM was fitted using a negative binomial error distribution with a log link function, because the response variable was overdispersed when fitted with a poisson error distribution. For dingoes, the GAMM was fitted using a zero-inflated poisson error distribution (ziP) because the response variable was overdispersed, and dingo visitation rates were low overall, leading to an excess of months with zero visitations. GAMMs were fitted with the *mgcv* package v1.8-42 (Wood, 2023). The statistical significance of parameter estimates, relative to a null hypothesis of no effect, was inferred at $\alpha = 0.05$.

5.3.6.2 Effect of carcass density on scavenging probability

We tested the determinants of dingo and fox carcass scavenging rates (H1). The response variable was the presence or absence of scavenging for each day of carcass camera deployment up to 5 months post deployment (binary variable; dingoes and foxes modelled separately). Scavenging probability was estimated using generalised linear models (GLMs) as the likelihood of scavenging was expected to increase linearly with carcass density. We performed model selection and averaging based on AIC; our fixed predictor variables were fallow deer carcass density, sambar deer/red deer carcass density, canopy cover, carcass species and the interaction between deployment season and months since death. For the carcass density calculations, sambar deer and red deer were combined here and for the analysis below, because they are similar in size and only a low number of red deer were shot. Carcass density was calculated for a 375 m circular buffer around each monitored carcass, consistent with camera array carcass density estimates generated below. Carcasses were included in density estimates from the date they were shot, up to the median days to 90% biomass loss for each monitoring period (values presented in results). The resultant carcass density for each day was expressed as a continuous non-integer value (carcasses km^{-2}). Canopy cover was a categorical predictor for either open or closed canopy (reference category; canopy characterisation is described under 'Carcass camera monitoring'). Carcass species was a categorical predictor for the two deer species (fallow deer [reference category], sambar deer). Deployment season was a categorical predictor for the three seasonal deployments (early winter, early summer [reference category], late summer) and months since death was a categorical predictor (0–5; rounded down for each day to the nearest whole month). For this analysis, 3 of the 55 monitored carcasses were excluded, because they were monitored for less than two days in total. Predictor variables were standardised prior to model selection and averaging (Gelman, 2008; Grueber et al., 2011). Model selection was based on Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson, 2004), using the *MuMIn* package v1.46.0 (Barton, 2019). Models within ΔAICc < 2 of the best-fitting model were averaged using the 'zero' method (Grueber et al., 2011; Nakagawa & Freckleton, 2011). For the model predicting the determinants of dingo scavenging, the interaction between deployment season and months since death inhibited convergence (likely because some months had very few or no dingo observations) and was removed. Statistical inference was based on parameter effect sizes, their confidence intervals, and the relative importance (sum of Akaike weights) of each predictor (values equal to 1).

5.3.6.3 Effect of carcass density on scavenger distribution

We tested the determinants of fox and dingo distributions across the culling area (H2). The response variable was the presence or absence of a fox/dingo for each day and each camera in the array between the 10th of May 2022 and the 23rd of November 2023 (binary variable; dingoes and foxes modelled separately). The date range begins one day after the start of culling, and ends 185 days after the end of culling. Scavenger distribution was estimated using generalised linear mixed models (GLMMs) as the likelihood of scavenger detection was expected to increase linearly with carcass density. As above, model selection and averaging was performed, our fixed predictor variables were fallow deer carcass density, sambar deer/red deer carcass density, tree cover and season. The carcass density for each day and camera was generated as in the previous analysis, and expressed as a continuous non-integer value (carcasses km^{-2}). Cameras in the camera array were spaced 600–700 m apart, and we calculated density estimates within a 375 m radius of each camera, to ensure that carcasses only contributed to the density estimates for a single camera. Tree cover was derived from the 5 m resolution New South Wales (NSW) Woody Vegetation Extent 2011 dataset for the area surrounding the camera array (NSW Department of Climate Change, Energy, the Environment and Water 2011). For each camera, the proportion of tree cover within a 375 m circular buffer around each monitored carcass was calculated for each monitoring day, the resultant tree cover variable was expressed as a percentage. Season was a categorical predictor for the four Australian seasons (summer [reference category]: December–February; autumn: March–May; winter: June–August; Spring: September–November). The categorical random effect was camera ID (1–46). We performed predictor variable standardisation, model selection and averaging, and statistical inference, as described above. For this analysis, and the one described above, mixed models were constructed using the *lme4* package v1.1-32 (Bates et al., 2014), predictor variables were standardised using the *arm* package (Gelman et al., 2009). Packages *DHARMa* v0.4.6, *ggplot2* v3.5.1 and *ggbreak* v0.1.2 were used for model and effects visualisation (Hartig, 2018; Wickham, 2016; Xu et al., 2021).

5.3.6.4 Temporal activity of scavengers

We examined differences between the temporal activity patterns of foxes and dingoes while scavenging, and across the culling area (H3). First, we calculated a coefficient of overlap (hereafter referred to as ‘overlap’; a continuous variable between 0 and 1, where 1 indicates identical activity patterns and 0 indicates no overlap) between the diel activity curves of foxes and dingoes for detections at carcass cameras and array cameras. We then calculated overlap for the diel activity curves of detections at carcass cameras compared with array cameras (calculated separately for foxes and dingoes). For this analysis, carcass camera data were subset by seasonal deployment, to calculate the overlap for each season. Camera array data were subset into three 6-month periods overlapping with carcass monitoring periods. The starting time of each detection event was used as the input for detection time, and converted to radians. Then, diel activity patterns were characterised using kernel density estimation with either the Dhat4 (for samples > 50), or the Dhat1 estimator (for samples < 50). Overlap was calculated using the *overlap* package v0.3.4 (Meredith et al., 2024). Confidence intervals (95%) were obtained from 10,000 smoothed bootstrap samples. We then used the nonparametric Watson's two-sample test of homogeneity to test for between species and between camera type differences in temporal activity. We used the *circular* package v0.5-0 to run this test and to prepare data for visualisation (Lund et al., 2023). The statistical significance of parameter estimates, relative to a null hypothesis of no effect, was inferred at $\alpha = 0.05$.

5.3.6.5 Effect of scavenger activity on biomass loss

We examined the extent to which fox and dingo scavenging contributed to carcass biomass loss (H4). The response variable was the time taken in days to 90% biomass loss for the early summer deployment, and 50% biomass loss for the late summer and early winter deployments. These two different endpoints were used because biomass loss was much slower in early winter and late summer (see Results). We used Cox proportional hazards models to perform survival analyses to assess the determinants of biomass loss (modelled separately for each season). Six of the 55 carcasses (4 from early summer, 2 from late summer) were monitored for less than 14 days (the fastest time to 10% biomass remaining) and were removed from this analysis. Our fixed predictor variables were the presence of fox scavenging, the presence of dingo scavenging, canopy cover and carcass species. We also included overall scavenging rate and scavenger species richness for all scavenger species, to evaluate the effect of all scavenger species on biomass loss, in case other species besides foxes and dingoes were significant contributors to biomass loss. The presence of fox scavenging was a binary predictor variable, and carcasses that were scavenged by a fox one or more times within the median survival time to 90% or 50% biomass loss for each season (see results) were assigned a value of 1. Similarly, the presence of dingo scavenging was included as a separate binary predictor variable, following the criteria described above. Canopy cover was a categorical predictor for either open or closed canopy (reference category; canopy characterisation is described under 'Carcass camera monitoring'). For all species observed scavenging, scavenging rate (number of feeding events/number of days camera active) and scavenger species richness (number of species observed feeding on carcass) were continuous predictors. For the model evaluating the predictors of biomass loss for the early summer deployment, canopy cover was excluded from the initial models because only 2/12 monitored carcasses were in a closed canopy environment. Carcass species was a categorical predictor for the two deer species (fallow deer [reference category], sambar deer). For the late summer deployment, month of deployment was included as a categorical random effect with two levels (February, March), because carcasses were deployed over a period of 53 days. We performed model selection and averaging as described above to determine the predictors that best explained biomass loss. To visualize the results of these analyses, we separated data into carcasses where dingo and fox scavenging did and did not occur, as well as open and closed canopy, and sambar deer and fallow deer carcass treatments. We then presented Kaplan-Meier estimates of the survival function comparing the four survival curves for each seasonal deployment using *ggsurvfit* v1.1.0 (Sjoberg et al., 2024). For continuous predictors, we constructed survival area plots for each seasonal deployment using *contsurvplot* v0.2.1 (Denz, 2023). The package *survival* v3.7-0 was used to run the Cox proportional hazards models and test the proportional hazards assumption for all models (Therneau et al., 2023). Statistical inference was based on confidence intervals, and the relative importance (sum of Akaike weights) of each predictor variable (values equal to 1). All analyses were conducted in R version 4.1.2, interfaced through Rstudio (R Core Team, 2021).

5.4 Results

Over the 561-day period between 9th of May 2022 and 23rd of November 2023, a total of 500 fallow deer, 111 sambar deer, and 12 red deer were culled within the culling area (up to 3 km from the camera array). Of the 56 carcass monitoring sites set up, remote camera data was collected from 55. The working carcass monitoring cameras functioned for a total of 6925 trap nights, for a mean time of 129.0 ± 51.8 (SD) nights per camera.

Species that scavenged on carcasses included the Australian raven (N = 5317; *Corvus coronoides*), bush rat (N = 257; *Rattus fuscipes*), wedge-tailed eagle (N = 69; *Aquila audax*), wild boar (N = 31; *Sus scrofa*), Australian magpie (feeding events [N] = 30; *Gymnorhina tibicen*), grey currawong (N = 7; *Strepera versicolor*), common brushtail possum (N = 6; *Trichosurus vulpecula*), common ringtail possum (N = 4; *Pseudocheirus peregrinus*), brown falcon (N = 3; *Falco berigora*), emu (N = 3; *Dromaius novaehollandiae*), spotted-tail quoll (N = 1; *Dasyurus maculatus*), dingo and fox (Figure S5.1).

For the focal species, foxes investigated 39 carcasses for a total of 6.2 hours and scavenged on 27 carcasses (8 from early winter deployment, 6 from early summer deployment and 13 from late summer deployment), over 229 events, for a total of 31.9 hours. Dingoes investigated 22 carcasses for a total of 2.5 hours and scavenged on 23 carcasses (8 from early winter deployment, 8 from early summer deployment and 7 from late summer deployment), over 113 events, for a total of 31.8 hours.

5.4.1 Carcass visitations over time

For foxes, in the early winter deployment, visitation events increased steadily over time from 0–6 months post deployment at both sambar deer and fallow deer carcasses (Figure 5.2A). For the early summer deployment, visitation events by foxes at fallow deer carcasses peaked approximately 2 months post deployment before decreasing for the remainder of the monitoring period, while visitation events to sambar deer carcasses peaked approximately 5 months post deployment (Figure 5.2B). For the late summer deployment, visitation events to fallow deer carcasses remained low and stable throughout the monitoring period, while visitation events to sambar deer carcasses peaked immediately following deployment, then decreased to a minimum approximately 3.5 months post deployment, before increasing again to a maximum at 6 months post deployment (Figure 5.2C). Visitations by foxes to carcasses were predicted by statistically significant interactions between season and months since death for the early winter (edf = 1.00, $p < 0.001$) and late summer deployments (edf = 2.77, $p < 0.001$), but not the early summer deployment (edf = 1.00, $p = 0.695$; deviance explained 55.6%; Table S5.1). Fox visitations to sambar deer carcasses were significantly higher than visitation events at fallow deer carcasses ($z = 3.117$, $p = 0.001$; Table S5.1). This relationship was observed for all months since death in all seasons, except for up to month 4 of the early summer deployment, where visitation events to fallow deer carcasses exceeded visitation events at sambar deer carcasses (Figure 5.2 A–C).

For dingoes, in the early winter deployment, visitation events were low until approximately 4 months post deployment in late winter, when they increased (Figure 5.2D). Visitation events by foxes peaked 5–6 months after carcass deployment for both sambar deer and fallow deer carcasses (Figure 5.2D). For the early summer deployment, visitation events by dingoes peaked 0–2 months post deployment and decreased for the remainder of the monitoring period (Figure 5.2E). For the late summer deployment, visitation events peaked immediately post deployment, and then decreased steadily until approximately 3 months post deployment, they then remained low for the remainder of the monitoring period (Figure 5.2F). Visitations by dingoes to carcasses were predicted by statistically significant interactions between season and months since death for all monitoring seasons (early winter: edf = 3.00, $p < 0.001$; early summer: edf = 2.60, $p = 0.008$; late summer: edf = 3.31, $p < 0.001$; deviance explained = 77.6%; Table S5.1). Dingo visitations to sambar deer carcasses were significantly higher than visitation events at fallow deer carcasses ($z = 2.057$, $p = 0.040$; Table S5.1), a pattern that was consistent across all seasons.

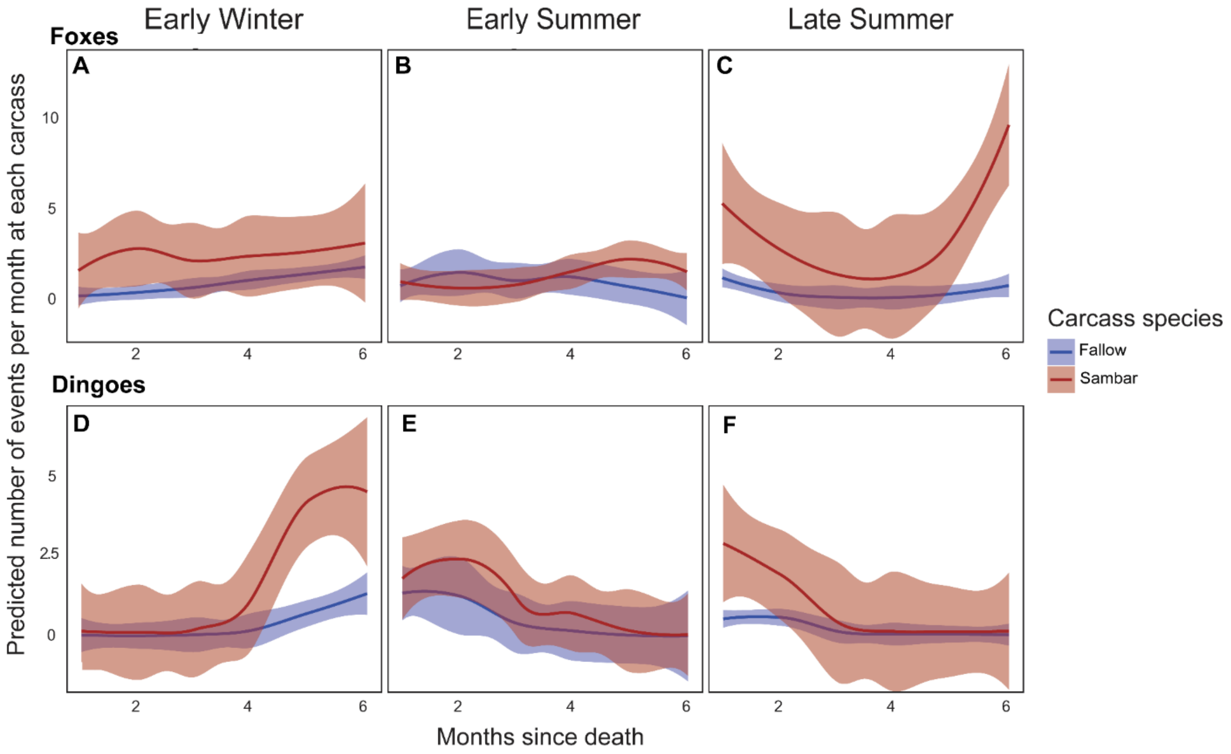

Figure 5.2: Generalised additive mixed model plots showing the predicted number of visitation events by red foxes (*Vulpes vulpes*; top row) and dingoes (*Canis dingo*; bottom row) to fallow deer (*Dama dama*; blue; *N* = 32) and sambar deer (*Rusa unicolor*; brown; *N* = 19) carcasses across three seasonal periods commencing early summer, late summer and early winter, from 1 to 6 months post carcass death (Table S5.1). Shaded areas represent ± 95% confidence intervals, full model output provided in Table S5.1 A–C. Deer were culled during an aerial culling effort in a subalpine area of Kosciuszko National Park, Australia.

5.4.2 Effect of carcass density on scavenging probability

In the culling area surrounding the camera array, a total of 223 deer were culled within the 375 m radius buffer. Deer carcass density ranged from 0 to 33.56 deer/km² for fallow deer carcasses and 0 to 9.06 deer/km² for sambar deer/red deer carcasses. The probability of fox scavenging was lower at carcasses with an open canopy (β = -1.371, SE = 0.219, SW (sum of Akaike weights) = 1; Table S5.2), and with higher surrounding fallow deer carcass densities (β = -1.430, SE = 0.295, SW = 1; Figure 5.3A; Table S5.2). For the late summer deployment, the probability of scavenging was lower for the third (β = -1.557, SE = 0.644; Table S5.2) and fourth (β = -1.220, SE = 0.576, SW = 1; Table S5.2) months following deployment (see Table S5.3 for model selection table). The probability of dingo scavenging was higher at carcasses with higher surrounding sambar deer carcass densities (β = 1.453, SE = 0.238, SW = 1; Figure 5.3B; Table S5.2), and was lower during the early winter (β = -1.605, SE = 0.398; Table S5.2), and late summer deployments (β = -0.672, SE = 0.343, SW = 1; Table S5.2), compared to the early summer deployment.

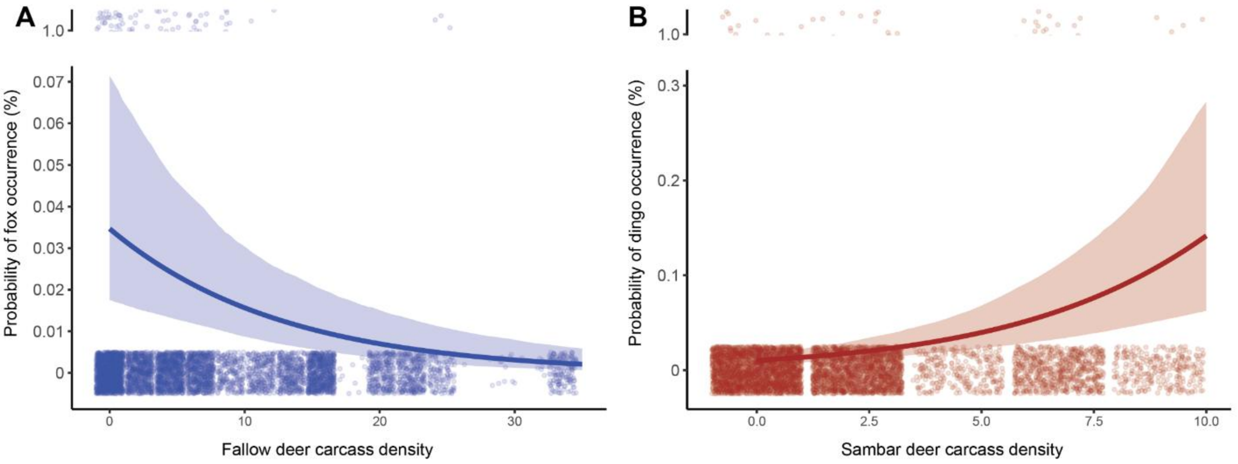

Figure 5.3: Predicted probabilities of red fox (*Vulpes vulpes*; A) and dingo (*Canis dingo*; B) detections at a single carcass camera per day based on the density of fallow deer carcasses (per km^2; *Dama dama*; A; blue) and sambar deer carcasses (*Rusa unicolor*; B; brown), following aerial culling in a subalpine area of Kosciuszko National Park, Australia. Predicted effects are taken at the mean of all other model parameters (density of fallow/sambar deer carcasses, canopy cover, carcass species, deployment season and months since death). Shaded areas represent ± 95% confidence intervals. Points at 0 and 1 are numbers of fox detections and non-detections for each trapping day, points are plotted with semi-transparency to indicate data density, total *N* = 6630, for foxes: 0 = 6,510, 1 = 120; for dingoes 0 = 6,565, 1 = 65; full model output at Table S5.2).

5.4.3 Effect of carcass density on scavenger distribution

Between the 10th of May 2022 and the 23rd of November 2023, a total of 22,270 trap nights across the camera array provided data: 3,759 trap nights in summer, 3,980 in autumn, 7,718 in winter and 6,813 in spring. During the entire period there were 460 detections of dingoes and 1,848 detections of foxes. The probability of a fox occurrence was more likely in all seasons compared to summer (autumn: β = 0.631, SE = 0.151; spring: β = 0.359, SE = 0.141; winter: β = 0.384, SE = 0.143, SW = 1; Figure 5.4A; Table S5.4), and decreased with increasing fallow deer carcass density (β = -0.806, SE = 0.155, SW = 1; Figure S5.2; Table S5.4; see Table S5.5 for model selection table). The probability of a dingo occurrence was less likely in winter (β = -1.194, SE = 0.242), and autumn (β = -0.708, SE = 0.260, SW = 1; Figure 5.4B; Table S5.4), compared to summer.

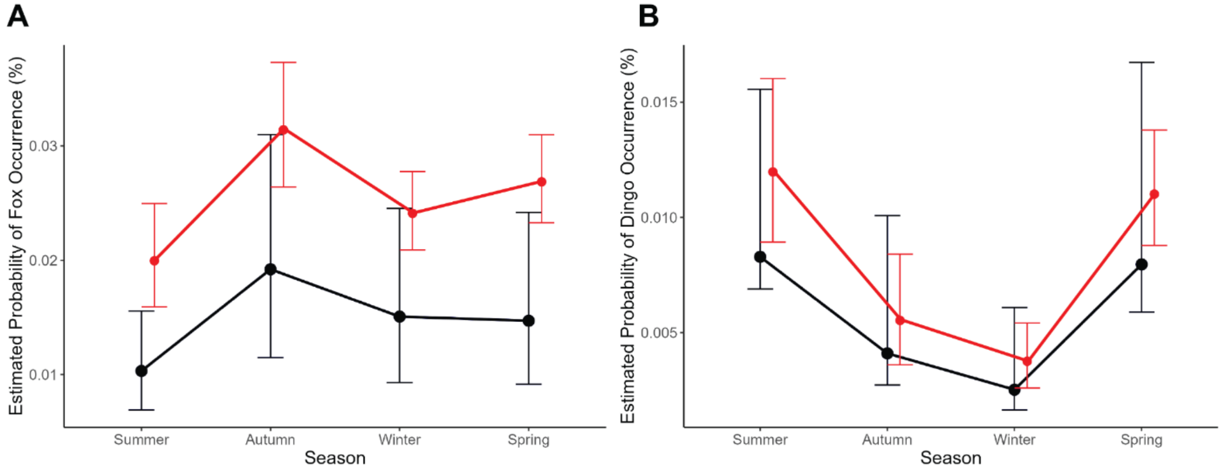

Figure 5.4: Predicted probabilities and bootstrapped 95% confidence intervals (black) and observed proportions with 95% confidence intervals (red) of (A) red fox (*Vulpes vulpes*; $N = 1{,}848$) and (B) dingo (*Canis dingo*; B; $N = 460$) detections at a single carcass camera per day for each season, following aerial culling in a subalpine area of Kosciuszko National Park, Australia, between May 2022, and November 2023. Predicted effects are taken at the mean of all other continuous predictors (density of fallow/sambar deer carcasses and tree cover; full model output at Table S5.4).

5.4.4 Temporal activity of scavengers

Foxes were largely nocturnal across all deployment seasons (Figure 5.5). Dingoes shifted between diurnal activity in the early winter deployment (Figure 5.5A, B), and towards nocturnality in the early summer and late summer deployments, with activity peaks in the morning and afternoon in early summer on the carcass camera (Figure 5.5B, E), and in late summer on the camera array (Figure 5.5F). Dingo activity on carcass cameras for the late summer deployment was largely nocturnal (Figure 5.5C). The overlap (Δ) between the activity of foxes and dingoes was lower at carcass cameras than across the camera array for the early winter and early summer deployments (Figure 5.5A, B, D, E), but was higher at carcass cameras than across the camera array for the late summer deployment (Figure 5.5C, F).

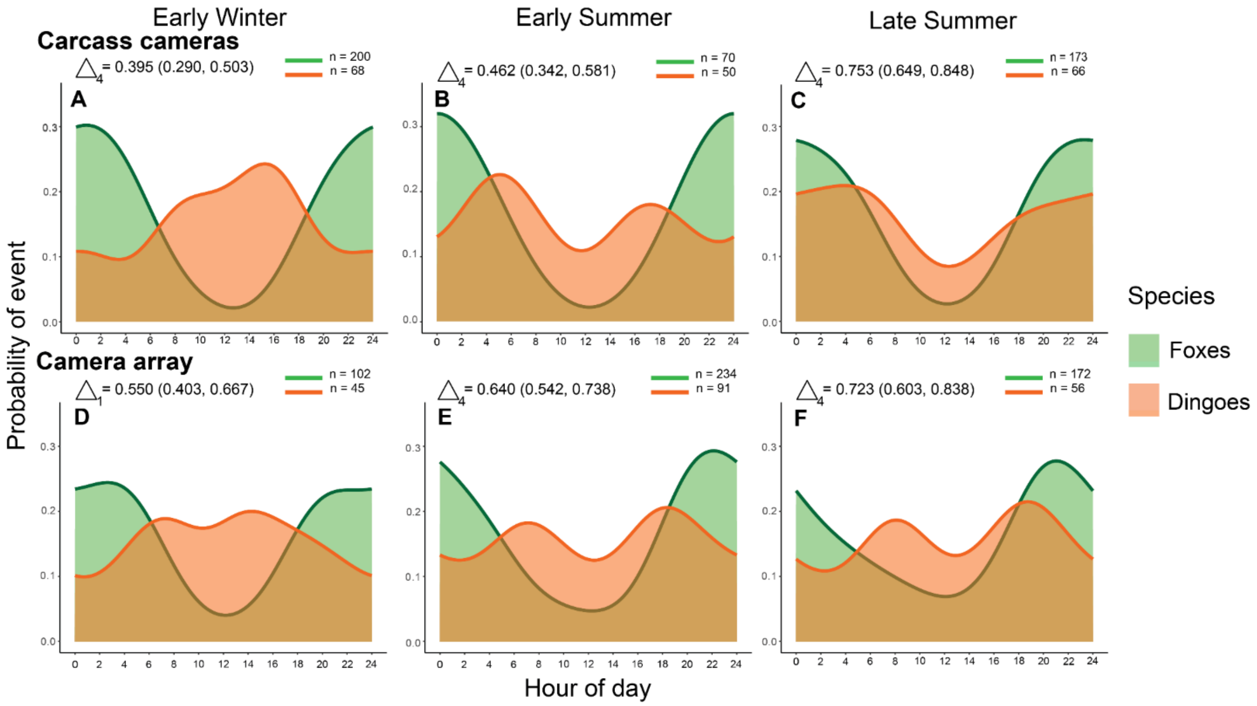

Figure 5.5: Density plots showing the overlap in temporal activity of red foxes (*Vulpes vulpes*; green) and dingoes (*Canis dingo*; orange) at carcass cameras (scavenging and investigation events) and camera array cameras for carcass deployments commencing in early winter, early summer and late summer following aerial culling in subalpine Kosciuszko National Park. The coefficient of overlap (Δ), estimator (1–4) and bootstrapped 95% confidence intervals are presented, sample sizes indicate the number of detection events for each species at each camera type. Full model output at Table S5.6.

Watson's Two-Sample Tests of Homogeneity revealed that foxes tended to be more nocturnal than dingoes at carcass cameras and across the camera array for all monitoring periods (Figure 5.5; Table S5.6). Foxes also tended to be more nocturnal at carcass cameras compared with across the camera array for all monitoring periods (Figure 5.5; Table S5.6). For dingoes, diel activity at carcass cameras and the camera array for the early winter and early summer deployment periods was not significantly different (Figure 5.5A, B, D, E). However, for the late summer deployment, dingoes tended to be more nocturnal at carcass cameras compared with across the camera array (Figure 5.5C, F; Table S5.6).

5.4.5 Effect of scavenger activity on biomass loss

Only 7/21 carcasses in the early winter period, and 8/16 carcasses in the late summer period reached 90% biomass loss within the ~6-month monitoring periods. Therefore, days to 50% biomass loss is reported for these periods, and days to 90% biomass loss is reported for the early summer deployment, when carcasses decomposed more rapidly. Despite this, persistence data were right censored, meaning some carcasses did not reach 90% or 50% biomass loss by the end of the monitoring period (9/21 censored for early winter, 2/12 censored for early summer and 1/16 censored for late summer).

The median time taken for carcasses to decompose to 50% biomass loss for the carcasses monitored in the early winter deployment was 142 days (range: 123–153 days) for fallow deer, and 131 days (range: 118–144) for sambar deer, for the late summer deployment it was 20 days (range: 8–28 days) for fallow deer, and 30 days (range: 10–138 days) for sambar deer. The median time taken for carcasses to decompose to 90% biomass loss for carcasses monitored in the early winter deployment was 167 days (range: 130–177 days) for fallow deer and 164 days (only one individual) for sambar deer, for the early summer deployment it was 81 days (range: 14–87 days) for fallow deer, and 87 days (range: 11–165 days) for sambar deer, and for the late summer deployment it was 155 days (range: 46–219 days) for fallow deer, and 207 days (range: 58–213 days) for sambar deer.

For the early winter deployment, carcasses in an open canopy environment lasted longer than carcasses that were in a closed canopy environment (Figure 5.6B). In the same season, carcasses with a higher overall scavenging rate lasted longer (Figure 5.6E; Table S5.7). There were no other significant associations between the predictor variables and biomass loss for the models run for each seasonal deployment (Figure 5.6; Table S5.7; full model selection table is presented in Table S5.8).

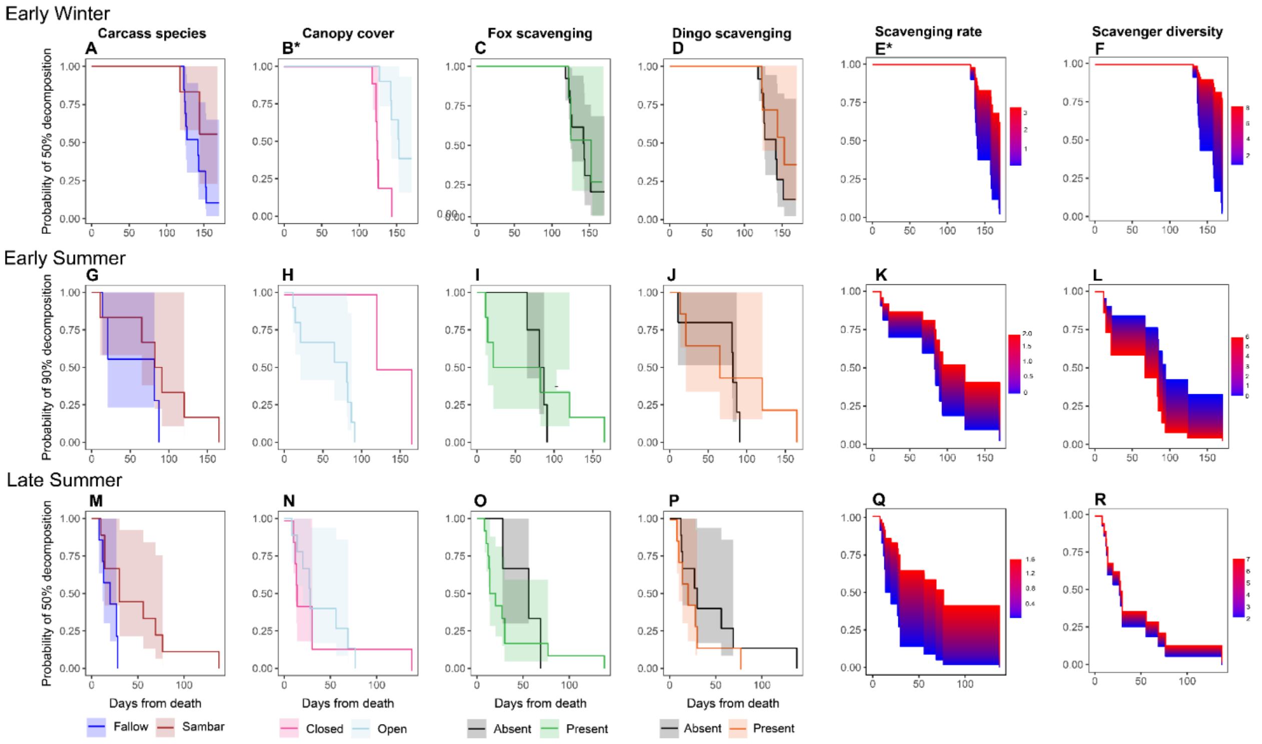

Figure 5.6: Kaplan-Meier and survival area plots of the survival function for deer carcass biomass loss for early winter (*N* = 21), early summer (*N* = 12), and late summer (*N* = 16) deployments, following aerial culling in subalpine Kosciuszko National Park. Plots indicate the effect of carcass species (sambar deer; *Rusa unicolor*, or fallow deer; *Dama dama*), canopy cover, the presence of red fox (*Vulpes vulpes*) and dingo (*Canis dingo*) scavenging, as well as species scavenging rate and scavenger diversity for all species that scavenged. Shading indicates 95% confidence intervals. The variables that had a significant effect on carcass persistence are indicated by an asterisk beside their panel labels. Full model output at Table S5.7.

5.5 Discussion

Animal mass mortality events are increasing in frequency and magnitude globally (Fey et al., 2015). These events may lead to an influx of carrion in the landscape, yet little is known about how this affects scavenger guilds (Barton et al., 2023; Baruzzi et al., 2022). Here we evaluated the behavioural and population-level responses of a widespread invasive mesoscavenger, the fox, and longer established apex scavenger, the dingo, to extensive carcass supplementation akin to a mass mortality event. We found that foxes visited carcasses year-round, including throughout winter, while dingo visitation was limited to warmer months, and that foxes and dingoes visited sambar deer carcasses more often than fallow deer carcasses, partially supporting hypothesis H1. Carcass density affected scavenging and occurrence rates, with higher rates of scavenging by dingoes in areas with higher sambar deer carcass densities, and lower rates of scavenging and occurrence by foxes in areas with higher fallow deer carcass density, providing partial support for H1 and H2, respectively. However, despite visitations to carcasses being higher at larger sambar deer carcasses compared with smaller fallow deer carcasses, actual feeding (scavenging) was not more likely at sambar deer carcasses, refuting H2. Foxes demonstrated temporal separation from dingoes in both their activity patterns and, to a greater extent, their use of carcasses, supporting the hypothesis of resource competition between the species (H3). Despite extensive scavenging on carcasses, scavenging by dingoes and foxes, and scavenging rate by all scavenger species did not accelerate carcass biomass loss, indicating limited capacity for vertebrate scavengers in the system to help remove large carcass loads from the environment, supporting H4 (Figure 5.7). Instead, carcass biomass loss was accelerated in warmer temperatures. Below we discuss the implications of our findings and iterate the importance of understanding scavenger dynamics in response to carcass load, type and season.

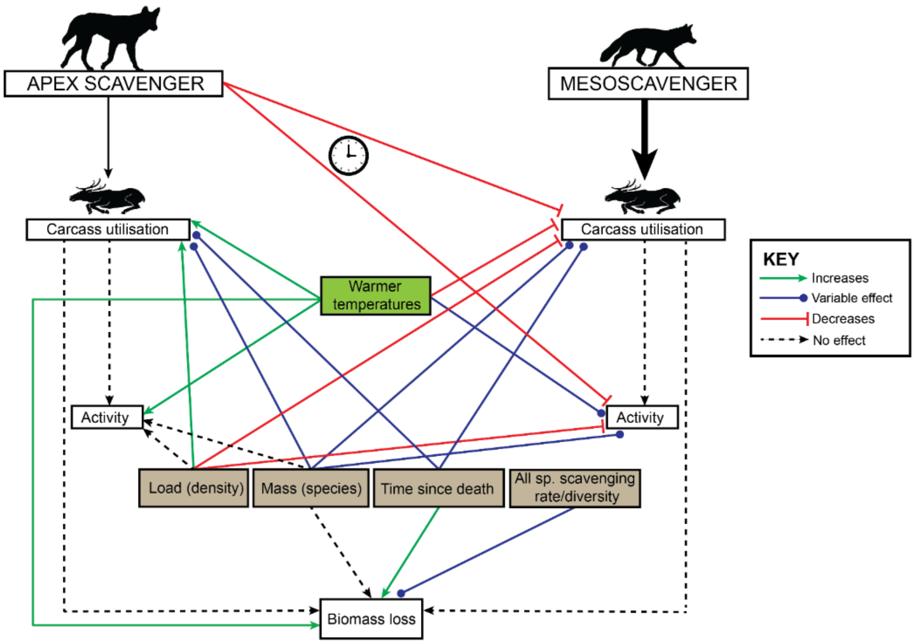

Figure 5.7: Observed relationships between foxes and dingoes and carcass utilization (visitations and scavenging) following a mass herbivore cull, which contributes to biomass loss on a local scale, and increases in activity on a landscape scale, and how these processes are affected by temperature and carrion characteristics (brown boxes).

Dingoes scavenged on fewer carcasses but had a similar total scavenging time compared to foxes. Dingo carcass visitation was also highly seasonally dependent, with visitations highest outside of the cooler months (Figure 5.2 D–F), similar to other Australian studies of the species (Spencer & Newsome, 2021; Vandersteen et al., 2023). Although there is often a general trend of increased vertebrate scavenging in winter (e.g. Selva et al. 2005; Vandersteen et al. 2023), studies of wolves in environments where snow falls in winter have reported higher scavenging rates during summer, possibly due to increased proliferation of carcass odour in warmer conditions, facilitating easier detection (Bassi et al., 2018). Further to this, wolves may be less reliant on carrion during winter, as extreme weather can worsen prey body condition and make prey more vulnerable to predation (Metz et al., 2012). In our study, dingo occurrence also followed a seasonal pattern, with occurrence (Figure 5.4; Table S5.4), as well as relative abundance (Figure S5.3) lowest over winter for most monitoring years. Reduced visitations and scavenging on carcasses may reflect seasonal movements by the species to lower elevations with the onset of winter. However, in an area nearby to the current study area, longer-term tracking revealed that dingoes remained within their home ranges across seasons (Claridge et al., 2009). Moreover, dingoes have previously been shown to persist in areas during significant snowfall (Robley et al., 2010). Lower dingo occurrences during winter (Figure 5.4B) may be a function of lower dingo activity during this period, rather than reduced presence in the study area. This coincides with pregnancy and whelping, when the pack may be practicing alloparental behaviour and remaining close to the natal den (Thomson, 1992). Dingo visitations to carcasses were highest in the early-winter deployment, in spring, when carcasses were ~5 months old (Figure 5.2D). During this period, many of the visitation and scavenging events were by packs of dingo pups, likely born during the winter (Figure S5.4), similar to Forsyth et al. (2014). Carcasses may present an easily accessible food source to young scavengers, like dingo pups, who are not yet learned predators (Thomson, 1992). Wolves are known to kill and carry prey to pups during pup-rearing (Mech et al., 1999), and so, dingoes may similarly utilise carcasses as a supplemental food source during periods of parental care. Nonetheless, apex scavenging by dingoes appears to be seasonally-mediated in a subalpine environment, with very low activity in winter and high activity in warmer periods.

Prey kill and consumption rates of Canidae are positively correlated with body mass (Emerson et al., 2025), and foxes, a smaller member of the Canidae family than dingoes, may therefore be less reliant on live prey than dingoes, and more reliant on carrion as a food source. In our study, foxes visited carcasses year-round and were more active that dingoes throughout winter, with visitation events increasing over winter (Figure 5.2A). Foxes have been shown to increase scavenging as temperatures decrease during the winter (De Pelsmaeker et al., 2024; Selva et al., 2005). Moreover, in a study examining fox diet in a moose (*Alces alces*) hunting area, scavenging on moose carcasses over winter was a main foraging activity (Needham et al., 2014). Fox movements are theorised to be associated with carrion availability (Cagnacci et al., 2004; Lovari et al., 1994). On a landscape scale, long-term increases in the availability of ungulate carcasses over winter has been linked to increases in the abundance of fox populations (Jahren et al., 2020; Selås & Vik, 2006). In our study, deer carcasses are clearly utilised by foxes, but the extent to which it increases their population growth is unknown. However, in other Australian studies, food availability has been linked to increased body mass (Stepkovitch et al., 2019) and population growth (Read & Bowen, 2001) in foxes. Therefore, widespread carcass supplementation that occurs during culling operations may support the growth of fox populations. Increased carrion availability has been associated with increased rates of predation to vulnerable prey species (Moleón et al., 2014; Tobajas et al., 2022). As an invasive species in Australia, foxes prey on and compete with native species (Fleming et al., 2021; Saunders et al., 2010), and have been implicated in the decline and extinction of Australia's native species (Woinarski et al., 2015). Therefore, it is imperative to consider the flow-on effects of culling on fox population growth in case it exacerbates their impacts.

We found an association between higher fallow deer carcass density and a lower probability of fox scavenging and occurrence (Figure 5.3A; Figure S5.2; Table S5.4). There is a well-established relationship between ungulate presence and subsequent carcass availability and fox abundance in large-scale multi-year studies (Carricondo-Sanchez et al., 2016; Henden et al., 2014; Selås & Vik, 2006). However, our study, which examined fine-scale carcass distribution over a shorter time frame, suggests that foxes do not preferentially visit areas with higher fallow deer carcass densities. This may be because there were high densities of fallow deer carcasses throughout the camera array (Figure 5.1), and foxes did not have to seek out areas with the highest densities to scavenge. An alternative explanation is that when carcasses are in lower densities, foxes experience competition for resources from conspecifics and other scavenger species, and so foxes can dominate low-density resources. This has been observed for coyotes in North America, which scavenged on sparsely-distributed carcasses and not highly-concentrated hunter kills (Wilmers et al., 2003). In contrast, sambar carcass densities across the camera array were markedly lower (Figure 5.1), and scavengers may have needed to move greater distances to exploit sambar deer carcasses. Indeed, we found that dingo scavenging was higher in areas with higher sambar carcass density, however we did not find that scavenging was more likely for sambar deer carcasses compared to fallow deer carcasses for dingoes (Figure 5.3B; Table S5.4). Long-term increases in sambar deer abundance have previously been linked to increases in sambar deer presence in dingo (and fox) scats (Forsyth et al., 2018), and in this study, dingo activity at carcasses was higher at sambar deer carcasses compared with fallow deer carcasses across all monitoring periods (Figure 5.2 D–F). Scavenging time (Vandersteen et al., 2023), species abundance and richness and scavenger efficiency is known to be higher at larger carcasses (Moleón et al., 2015), potentially because larger carcasses are more visually conspicuous (DeVault et al., 2004), and may also emit stronger odours which attract scavengers (Naves-Alegre et al., 2022). Despite this, in our study, an influx of carcasses in the landscape following culling was not linked to marked immediate changes in the relative abundances of foxes or dingoes across the camera array (Figure S5.3). This suggests that carcasses only influenced local population distribution, though longer-term monitoring may have yielded detectable effects on population growth because of carcass supplementation.

Apex scavengers have the ability to locate and rapidly consume carcasses, and may influence carcass utilisation by smaller scavengers (Newsome et al., 2021). There are multiple lines of evidence suggesting that dingoes suppress fox populations (Letnic et al., 2012), through direct competition (Moseby et al., 2012); or temporal (McHugh et al., 2022; Wooster et al., 2022) and spatial partitioning (Schroeder et al., 2015) of activity in areas where they co-occur. In our study, foxes were mostly nocturnal across all monitoring seasons, whereas dingo activity shifted seasonally, being mostly diurnal during the early winter monitoring period, but shifting toward nocturnality in early summer and late summer (Figure 5.5). We found there was fox and dingo temporal separation at carcass cameras and the camera array; combined with increased nocturnality by foxes at carcass cameras compared with across the camera array (Figure 5.5; Table S5.6). Further to this, temporal separation between the species appears to be strongest at carcass resources, as temporal overlap between foxes and dingoes was lower at carcass cameras compared with the camera array for two of three seasons (Figure 5.5). This supports the hypothesis that foxes shift their temporal activity and resource use to avoid dingoes, and aligns with previous research demonstrating temporal separation in localised resource use between foxes and dingoes at sambar deer carcasses (Forsyth et al., 2014), and spatial separation of foxes and dingoes at water resources (Brawata & Neeman, 2011). High temporal overlap between the species for carcass use and activity during the late summer deployment (Figure 5.5 C, F) may have been due to reduced resource competition between the species, as dingo carcass visitations remained low throughout the late summer deployment, while fox visitations peaked at the start of the late summer deployment and remained high throughout much of the deployment (Figure 5.2C). This suggests either that dingo activity was low in the study region (Figure S5.3), or that dingoes were selecting alternative food sources during this period.

Despite extensive scavenging by foxes and dingoes, these species did not affect carcass biomass loss in any season (Figure 5.6). Furthermore, all species scavenging rate and scavenger diversity did not increase biomass loss (Figure 5.6). However, frequent scavenging by mammalian scavengers, like dingoes, can accelerate biomass loss under certain conditions, for example, in a temperate forest, where 63% of carcasses were scavenged by dingoes (Spencer & Newsome, 2021). Large mammal scavenging in our study may have been too infrequent to impact carcass loss rates. In this study, dingoes scavenged on 42% of carcasses, and dingo scavenging on carcasses in a nearby area has been reported as low as 15%

(Vandersteen, 2022). We did see that canopy cover affected biomass loss in early winter, when biomass loss was faster under closed canopies compared to open canopy environments (Figure 5.6B). From observations of time-lapse imagery, carcasses in open environments were more often covered in snow over winter, and so, snow cover may have preserved carcasses for longer periods, or decreased odour cues (Bartel et al., 2023). Notably also, some carcasses in open canopy bog environments appeared to have mummified over winter, with skin, hair and structure very well preserved (Figure S5.5). This phenomenon is similar to findings from the Antarctic Peninsula, where carcasses remained unchanged and were mummified over a ten-year monitoring period (Nývlt et al., 2016). In addition, we found limited evidence to support the hypothesis that biomass loss would be faster for smaller carcasses (Figure 5.6 A,G,M; similar to Müller et al., 2024), despite other previous research linking greater body mass to longer persistence (Flint et al., 2010; Santos et al., 2016). Instead, carcass persistence varied by season, with longer persistence in early winter and late summer compared to the early summer deployment (Figure 5.6), likely due to insect activity accelerating biomass loss (Barton & Evans, 2017).

5.5.1 Conclusion

Overall, this study revealed that human-induced mass mortality events and resulting carcass subsidies can substantially impact scavenger feeding behaviours and local distributions. However, apex scavenger the dingo, and mesoscavenger the fox, exhibited distinct seasonal and diel patterns of carcass utilisation (Figure 5.7), which may be influenced by carcass species abundances, nutritional requirements and interspecific competition. We found some evidence to support an effect of carcass size and density on rates of carcass visitations and scavenging, as well as landscape-scale distribution, but these effects differed between dingoes and foxes. Critically, this study indicates that invasive foxes were common scavengers on deer carcasses, and if carcass presence is a concern in the landscape, then culling should occur in early summer, when carcass biomass loss is accelerated (likely by the presence of insects). This may reduce the likelihood of prolonged food sources support problematic overwintering species, like foxes. Longer-term landscape-scale monitoring following mass carcass subsidies could also reveal whether culling can lead to sustained changes in scavenger guild populations.

5.6 Acknowledgements

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5.8 Supplementary Material

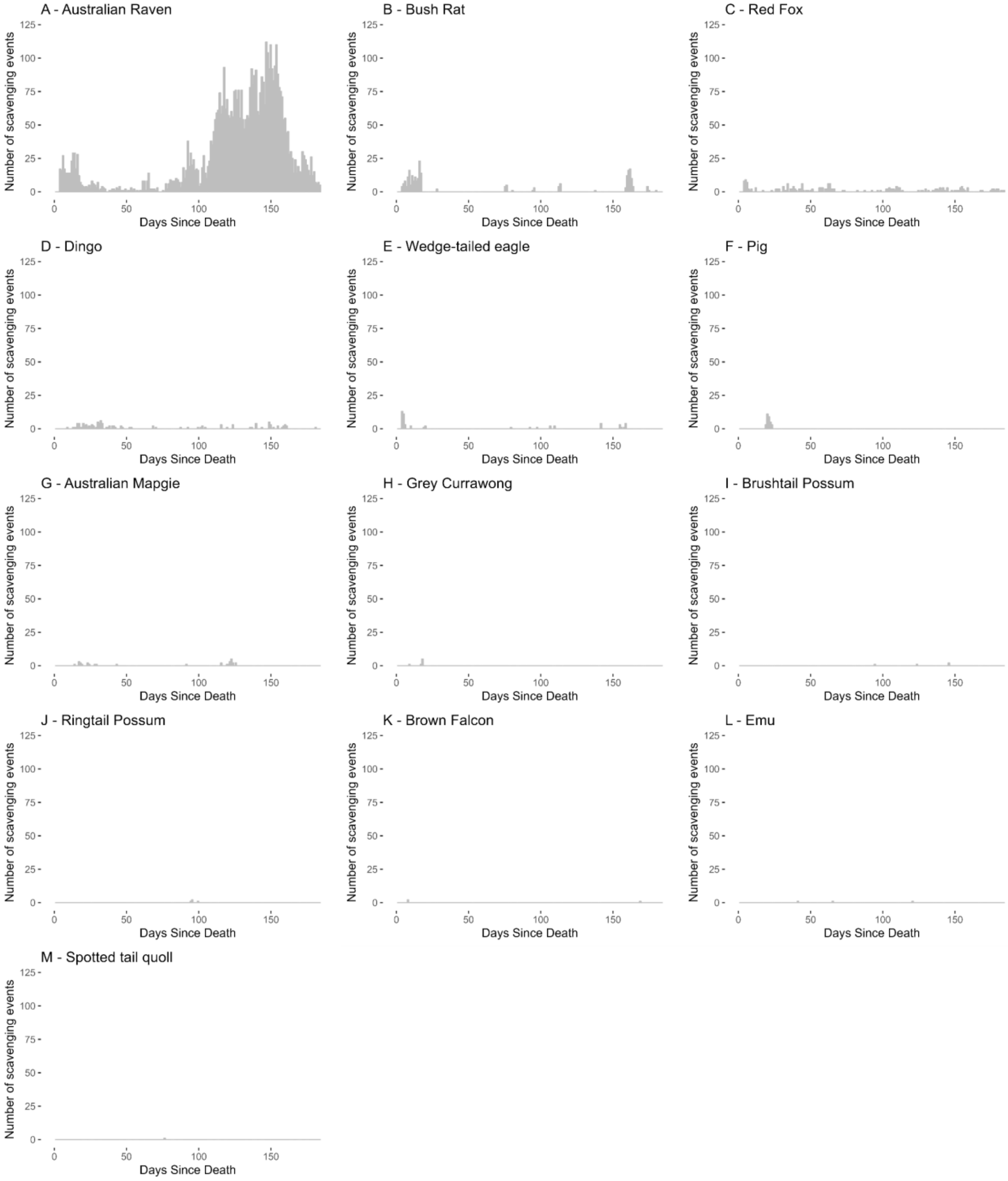

Figure S5.1: Histograms of the number of feeding events (seasonal deployments are pooled) by all scavenger species which scavenged on fallow deer (*Dama dama*) and sambar deer (*Rusa unicolor*) carcasses in subalpine Kosciuszko National Park from 0–185 days post death (bin number = 185).

Table S5.1: Results from generalised additive mixed models (GAMMs) evaluating patterns in visitation events to sambar deer and fallow deer carcasses over time for red foxes (*Vulpes vulpes*) and dingoes (*Canis dingo*) for each deployment season. GAMMs are fit with tensor product smooths.

Table S5.1(a) – Parameter terms for the GAMMs.

Species	**Parameter terms**	**Estimate**	**Standard error**	**z-value**	**p-value**
Foxes	*(Intercept)*	-3.918	0.2914	-13.45	< 0.001
	Species	1.269	0.4072	3.117	0.00183
Dingoes	*(Intercept)*	-5.010	0.4309	-11.63	< 0.001
	Species	1.148	0.5583	2.057	0.0397

Table S5.1(b) – Tensor product smooth terms for the GAMMs.

Species	**Smooth terms**	**edf**	**Reference edf**	**Chi-square statistic**	**p-value**
Foxes	te($_{months}$):season–early winter	1.00	1.001	15.63	< 0.001
	te($_{months}$):season–early summer	1.00	1.000	0.154	0.695
	te($_{months}$):season–late summer	2.77	3.255	20.45	< 0.001
	s($_{\text{station}}$)	30.70	49.00	83.73	< 0.001
Dingoes	te($_{months}$):season–early winter	2.997	3.428	47.45	< 0.001
	te($_{months}$):season–early summer	2.059	2.488	10.63	7.73×10^{-3}
	te($_{months}$):season–late summer	3.306	3.706	35.41	< 0.001
	s($_{\text{station}}$)	29.79	49.00	129.5	< 0.001

Table S5.1(c) – Model fit results for the GAMMs.

Species	**R-squared (adjusted)**	**Deviation explained (%)**	**Number of observations**
Foxes	-0.117	55.6	249
Dingoes	-	77.6	249

Table S5.2: Results from generalised linear models evaluating the relationship between fox and dingo scavenging on monitored sambar deer and fallow deer carcasses and the densities of fallow deer and sambar deer carcasses, deployment season (and the interaction with months since death for foxes) and canopy cover. All results are full averages from the averaged models.

Model (*N* = observations)	**Variable**	**Estimate[1]**	**Standard error**	**Adjusted standard error**	**Confidence intervals (2.5%, 97.5%)**	**Relative importance (sum of Akaike weights)**
Probability of dingo scavenging (*N* = 6,630)	(Intercept)	-3.999	0.2586	0.2586	(-4.506, -3.492)	-
	Density: sambar carcasses	1.453	0.2375	0.2376	(0.9877, 1.919)	1
	Season: early winter[2]	-1.605	0.3979	0.3980	(-2.385, -0.8247)	1
	Season: late summer	-0.6718	0.3425	0.3426	(-1.343, -0.0003216)	1
	Carcass species: sambar	-0.03151	0.1565	0.1565	(-0.8008, 0.4733)	0.19
	Density: fallow carcasses	-0.01078	0.1320	0.1320	(-0.6742, 0.5497)	0.17
	Canopy	-0.008105	0.1122	0.1122	(-0.5701, 0.4760)	0.17
Probability of fox scavenging (*N* = 6,630)	(Intercept)	-4.074	0.3131	0.3131	(-4.687, -3.460)	-
	Density: sambar carcasses	0.02809	0.1789	0.1789	(-0.5219, 0.7034)	0.31
	Canopy: open	-1.371	0.2194	0.2194	(-1.801, -0.9413)	1
	months_since_deployment0:Seasonearly summer	0.6824	0.6496	0.6497	(-1.956, 0.5910)	1
	months_since_deployment1:Seasonearly summer -	-0.1952	0.6553	0.6554	(-1.480, 1.089)	1
	months_since_deployment2:Seasonearly summer	-0.5826	0.6504	0.6505	(-1.858, 0.6923)	1

	months_since_deployment3:Seasonearly summer	-0.6638	0.5879	0.5880	(-1.816, 0.4888)	1
	months_since_deployment4:Seasonearly summer	-0.3370	0.5872	0.5873	(-1.488, 0.8140)	1
	months_since_deployment5:Seasonearly summer	-0.8527	1.053	1.0523	(-2.916, 1.211)	1
	months_since_deployment0:Seasonearly winter	-0.9063	0.5364	0.5365	(-1.958, 0.1452)	1
	months_since_deployment1:Seasonearly winter	0.6872	0.4803	0.4803	(-1.629, 0.2542)	1
	months_since_deployment2:Seasonearly winter	-0.8672	0.5407	0.5408	(-1.927, 0.1928)	1
	months_since_deployment3:Seasonearly winter	0.06542	0.4331	0.4332	(-0.7836, 0.9145)	1
	months_since_deployment4:Seasonearly winter	0.7653	0.4666	0.4667	(-0.1495, 1.680)	1
	months_since_deployment5:Seasonearly winter	0.4980	0.4751	0.4752	(-0.4333, 1.429)	1
	months_since_deployment0:Seasonlate summer	0.01948	0.4074	0.4074	(-0.7791, 0.8181)	1
	months_since_deployment1:Seasonlate summer	0.2564	0.3813	0.3813	(-0.4910, 1.004)	1
	months_since_deployment2:Seasonlate summer	-1.557	0.6437	0.6438	(-2.819, -0.2950)	1
	months_since_deployment3:Seasonlate summer	-1.220	0.5758	0.5759	(-2.348, -0.09091)	1

	months_since_deployment4:Seasonlate summer	-0.6585	0.4736	0.4737	(-1.587, 0.2699)	1
	months_since_deployment5:Seasonlate summer	NA	NA	NA	NA	NA
	Carcass species: sambar	0.2138	0.2676	0.2677	(-0.1081, 0.8773)	0.56
	Density: fallow carcasses	-1.430	0.2950	0.2951	(-2.009, -0.8520)	1

[1]Effect sizes have been standardised on two SD. [2]Early summer was the reference category.

Table S5.3: Model selection table from generalised linear models evaluating the factors affecting the probability of dingo and fox scavenging, including the density of fallow deer and sambar deer carcasses, canopy cover, carcass species, and deployment season (and an interaction with months since death for foxes). Where there were > 10 models included in model selection, only the first 10 models with the lowest AIC are presented. For each resulting model, the response variables included in the model are shown in bold, where multiple models are in bold, there were multiple competing models and we performed model averaging.

Response	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**Model weight (w_i)**
Variables predicting dingo scavenging	**Density of sambar carcasses + season**	4	-341.8	691.6	0.00	0.371
	Carcass species + density of sambar carcasses + season	5	-341.7	693.4	1.75	0.155
	Density of fallow carcasses + density of sambar carcasses + season	5	-341.8	693.6	1.96	0.139
	Canopy + density of sambar carcasses + season	5	-341.8	693.6	1.97	0.139
	Canopy + carcass species + density of sambar carcasses + season	6	-341.6	695.3	3.61	0.061
	Carcass species + density of fallow carcasses + density of sambar carcasses + season	6	-341.7	695.3	3.70	0.058
	Canopy + density of fallow carcasses + density of sambar carcasses + season	6	-341.8	695.6	3.93	0.052
	Canopy + carcass species + density of fallow carcasses + density of sambar carcasses + season	7	-341.6	697.2	5.54	0.023
Variables predicting fox scavenging	**Canopy + carcass species + density of fallow carcasses + months since death:deployment season**	21	-540.5	1123.1	0.00	0.354
	Canopy + density of fallow carcasses + months since death:deployment season	20	-541.8	1122.8	0.71	0.249
	Canopy + density of fallow carcasses + density of sambar carcasses + months since death:deployment season	21	-541.4	1125.0	1.87	0.139
	Canopy + carcass species + density of fallow carcasses + density of sambar carcasses months since death: deployment season	22	-540.5	1125.1	1.99	0.131

	Canopy + density of fallow carcasses	3	-560.4	1126.8	3.67	0.056
	Canopy + carcass species + density of fallow carcasses	4	-559.9	1127.8	4.69	0.034
	Canopy + density of fallow carcasses + density of sambar carcasses	4	-560.3	1128.5	5.46	0.023
	Canopy + carcass species + density of fallow carcasses + density of sambar carcasses	5	-559.9	1129.8	6.67	0.013

Table S5.4: Results from generalised linear mixed models evaluating the relationship between fox and dingo detections on camera array cameras and the densities of fallow deer and sambar deer carcasses, season and tree cover. All results are full averages from the averaged models.

Model (*N* = observations)	**Variable**	**Estimate[1]**	**Standard error**	**Adjusted standard error**	**Confidence intervals (2.5%, 97.5%)**	**Relative importance (sum of Akaike weights)**
Probability of dingo detection (*N* = 22,270)	(Intercept)	-4.785	0.2142	0.2142	(-5.205, -4.365)	-
	Density: sambar carcasses	0.2884	0.1505	0.1505	(-0.006592, 0.5834)	0.78
	seasonAutumn[2]	-0.7081	0.2598	0.2598	(-1.217, -0.1988)	1
	seasonSpring	-0.0406	0.1906	0.1906	(-0.4142, 0.3330)	1
	seasonWinter	-1.194	0.2419	0.2412	(-1.669, -0.7202)	1
	tree_cover	0.5851	0.3131	0.3131	(-0.02863, 1.199)	0.77
	Density: fallow carcasses	0.0316	0.1759	0.1759	(-0.3132, 0.3764)	0.15
Probability of fox detection (*N* = 22,270)	(Intercept)	-4.564	0.2095	0.2095	(4.974, -4.153)	-
	Density: fallow carcasses	-0.8056	0.1550	0.1550	(-1.109, -0.502)	1
	seasonAutumn[1]	0.6307	0.151	0.151	(0.3348, 0.9266)	1
	seasonSpring	0.3590	0.1408	0.1408	(0.0830, 0.6350)	1
	seasonWinter	0.3837	0.1434	0.1434	(0.1026, 0.6647)	1
	tree_cover	0.3597	0.3398	0.3398	(-0.3063, 1.0258)	0.31
	Density: sambar carcasses	0.02991	0.1420	0.1420	(-0.2484, 0.3082)	0.19

[1] Effect sizes have been standardised on two SD. [2] Summer was the reference category.

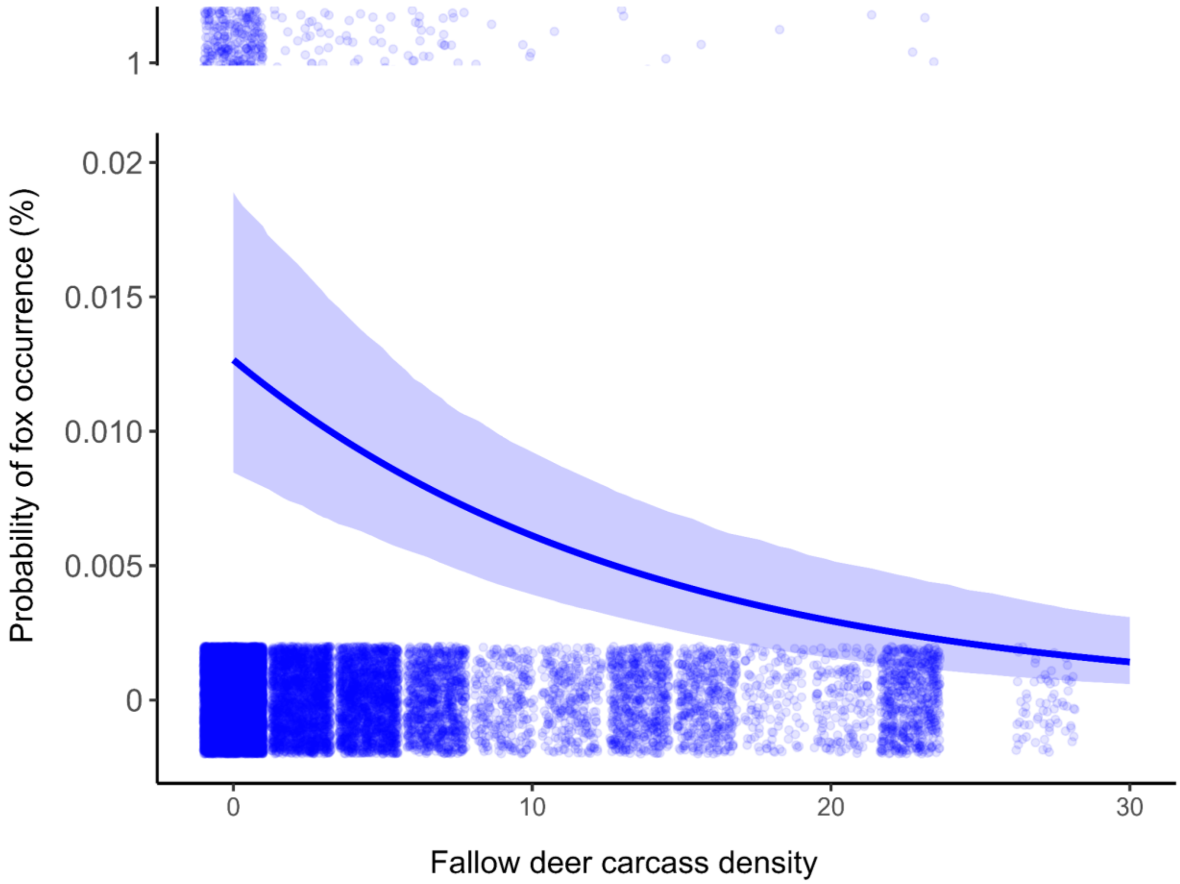

Figure S5.2: Predicted probabilities of fox detections at a single array camera per day based on the density of fallow deer carcasses, following aerial culling in a subalpine area of Kosciuszko National Park, Australia. Predicted effects are taken at the mean of all other model parameters (density of fallow/sambar deer carcasses, tree cover, season, camera station). Points at 0 and 1 are numbers of fox detections and non-detections for each trapping day, points are plotted with semi-transparency to indicate data density, total *N* = 22,270, 0 = 21,701, 1 = 569). For the random effect for camera station, the mean number of trapping nights per camera was 484 ± 109 (SD).

Table S5.5: Model selection table from generalised linear mixed models evaluating the factors affecting the probability of dingo and fox detection on the camera array cameras, including the density of fallow deer and sambar deer carcasses, tree cover, and deployment season. Where there were > 10 models included in model selection, only the first 10 models with the lowest AIC are presented. For each resulting model, the response variables included in the model are shown in bold, where multiple models are in bold, there were multiple competing models and we performed model averaging.

Response	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**Model weight (w_i)**
Variables predicting dingo occurrence	**Density of sambar carcasses + season + tree cover**	7	-948.4	1910.9	0.00	0.302
	Density of sambar carcasses + season	6	-950.0	1912.0	1.16	0.169
	Season + tree cover	6	-950.0	1912.1	1.23	0.163
	Density of fallow carcasses + density of sambar carcasses + season + tree cover	8	-948.4	1912.8	1.97	0.113
	Season	5	-951.7	1913.5	2.64	0.081
	Density of fallow carcasses + season + tree cover	7	-949.9	1913.8	2.96	0.069
	Density of fallow carcasses + density of sambar carcasses + season	7	-950.0	1913.9	3.06	0.065
	Density of fallow carcasses + season	6	-951.5	1915.0	4.17	0.038
Variables predicting fox occurrence	**Density of fallow carcasses + season**	6	-2424.0	4859.9	0.00	0.445
	Density of fallow carcasses + season + tree cover	7	-2423.4	4860.8	0.92	0.281
	Density of fallow carcasses + density of sambar carcasses + season	7	-2423.9	4861.9	1.96	0.167
	Density of fallow carcasses + density of sambar carcasses + season + tree cover	8	-2423.4	4862.8	2.90	0.105
	Density of fallow carcasses	3	-2432.8	4871.5	11.58	0.001

	Density of fallow carcasses + tree cover	4	-2432.3	4872.6	12.68	0.001
	Density of fallow carcasses + density of sambar carcasses	4	-2432.7	4873.3	13.41	0.001

Table S5.6: Results from Watson's Two-Sample Tests of Homogeneity evaluating differences in the distribution of temporal activity between foxes and dingoes at carcass cameras and camera array cameras (1), and differences in the temporal activity of each species between the camera types for each seasonal deployment, for each species (2). Sample sizes for each test are given in Figure 5.5.

Comparison	**Subject**	**Season**	**Test statistic**[1]
(1) Dingoes compared with foxes	Carcass cameras	Early winter	1.8162***
		Early summer	1.2407***
		Late summer	0.4062***
	Camera array	Early winter	0.757***
		Early summer	1.0555***
		Late summer	0.4083***
(2) Carcass cameras compared with camera array	Foxes	Early winter	0.273**
		Early summer	0.4553***
		Late summer	0.3384**
	Dingoes	Early winter	0.0734 ($p < 0.1$)
		Early summer	0.0884 ($p < 0.1$)
		Late summer	0.2543*

[1] Asterisks on test statistics indicate level of significance, where *$p < 0.05$; **$p < 0.01$ and ***$p < 0.001$

Table S5.7: Results from Cox proportional hazards models evaluating differences in carcass persistence time depending on canopy, carcass species, the presence or absence of fox and dingo scavenging, and all species scavenging rate and scavenger diversity for each seasonal deployment (early winter, early summer, and late summer). Results for each season are full averages from the averaged models.

Deployment season: biomass loss measure (*N* = carcasses)	**Variable**	**Estimate**	**Hazard ratio***	**Standard error**	**Confidence intervals (2.5%, 97.5%)**	**Relative importance (sum of Akaike weights)**
Early winter: days to 50% biomass loss (*N* = 21)	**Canopy: open**	-4.358	0.013	1.320	(-6.946, -1.771)	1
	Carcass species: Sambar	-0.576	0.562	1.074	(-4.124, 0.403)	0.31
	Scavenging rate	-1.590	0.204	0.670	(-2.903, -0.277)	1
	Scavenger diversity	-0.166	0.847	0.330	(-1.314, 0.090)	0.27
	Dingo scavenging	-0.108	0.898	0.390	(-2.379, 0.517)	0.12
Early summer: days to 90% biomass loss (*N* = 12)	Fox scavenging	-3.508	0.030	3.113	(-9.857, -0.447)	0.68
	Scavenger diversity	1.923	6.841	1.660	(0.424, 5.225)	0.68
	Scavenging rate	-9.160	0.0001	8.196	(-25.991, -0.912)	0.68
Late summer: days to 50% biomass loss (*N* = 16)	Canopy: open	-0.555	0.574	0.823	(-2.8373312, 0.134841850)	0.41
	Carcass species: Sambar	-1.361	0.256	0.907	(-3.1179791, -0.006323235)	0.87

	Scavenging rate	-0.653	0.520	0.766	(-2.4840071, 0.255663923)	0.59
	Fox scavenging	0.098	1.103	0.359	(-0.4584528, 2.230186461)	0.11

*Hazard ratio = exp(Estimate) - estimates the magnitude of the effect. [1]Top ranked model was > 2 delta AICc from the next top model; no averaging undertaken.

Table S5.8: Model selection table from Cox proportional hazards models evaluating differences in carcass persistence time depending on canopy, carcass species, the presence or absence of fox and dingo scavenging, and scavenging rate and scavenger diversity for each seasonal deployment (early winter, early summer, and late summer). Where there were > 10 models included in model selection, only the first 10 models with the lowest AIC are presented. For each resulting model, the response variables included in the model are shown in bold, where multiple models are in bold, there were multiple competing models and we performed model averaging.

Response	**Model**	**df**	**logLik**	**AICc**	**ΔAICc**	**w_i**
Early winter: days to 50% biomass loss	**Canopy + carcass species + scavenging rate (-1.522)**	**3**	**-16.309**	**41.6**	**0.00**	**0.184**
	Canopy + scavenging rate (-1.722)	**2**	**-18.164**	**41.7**	**0.04**	**0.180**
	Canopy + scavenger diversity (-0.612) + scavenging rate (-1.498)	**3**	**-16.442**	**41.9**	**0.27**	**0.161**
	Canopy + dingo feeding + scavenging rate (-1.637)	**3**	**-17.293**	**43.6**	**1.97**	**0.069**
	Canopy + carcass species + scavenger diversity (0.460) + scavenging rate (-1.420)	4	-15.152	44.0	2.40	0.055
	Canopy + fox feeding + scavenging rate (-1.716)	3	-17.770	44.5	2.92	0.043
	Canopy + carcass species + dingo feeding + scavenging rate (-1.551)	4	-15.444	44.6	2.98	0.041
	Canopy + carcass species + fox feeding + scavenging rate (-1.483)	4	-15.559	44.8	3.21	0.037
	Canopy + scavenger diversity (-0.691)	2	-19.750	44.8	3.22	0.037
	Canopy + carcass species	2	-19.756	44.8	3.23	0.037

Early summer: days to 90% biomass loss	**Fox feeding + scavenger diversity (2.824) + scavenging rate (-13.450)**	**3**	**-9.729**	**29.5**	**0.00**	**0.294**
	Null model	**0**	**-15.487**	**31.0**	**1.52**	**0.138**
	Carcass species	1	-14.768	32.0	2.58	0.081
	Scavenger diversity (0.189)	1	-15.103	32.7	3.25	0.058
	Dingo feeding	1	-15.196	32.9	3.43	0.053
	Scavenging rate (-0.452)	1	-15.391	33.3	3.82	0.043
	Scavenger diversity (0.633) + scavenging rate (-3.236)	2	-13.810	33.3	3.88	0.042
	Fox feeding	1	-15.482	33.5	4.01	0.040
	Dingo feeding + scavenger diversity (0.330)	2	-14.280	34.3	4.82	0.026
	Dingo feeding + fox feeding + scavenger diversity (2.973) + scavenging rate (-14.270)	4	-9.255	34.5	5.05	0.023
Late summer: days to 50% biomass loss	**Canopy + carcass species + scavenging rate (-1.404)**	**3**	**-23.371**	**54.7**	**0.00**	**0.116**
	Carcass species	**1**	**-26.099**	**55.7**	**0.91**	**0.074**
	Carcass species + scavenging rate (-0.760)	**2**	**-25.479**	**55.9**	**1.14**	**0.065**

	Scavenging rate (-0.911)	**1**	**-27.050**	**56.4**	**1.64**	**0.051**
	Canopy + carcass species	**2**	**-24.747**	**56.5**	**1.80**	**0.047**
	Carcass species + fox feeding	**2**	**-25.064**	**56.7**	**1.95**	**0.044**
	Canopy + scavenging rate (-1.405)	2	-25.989	56.9	2.16	0.039
	Null model	0	-28.160	57.2	2.44	0.034
	Carcass species + scavenging rate (-0.782)	3	-24.614	57.2	2.49	0.033
	Carcass species + dingo feeding	2	-26.234	57.4	2.65	0.031

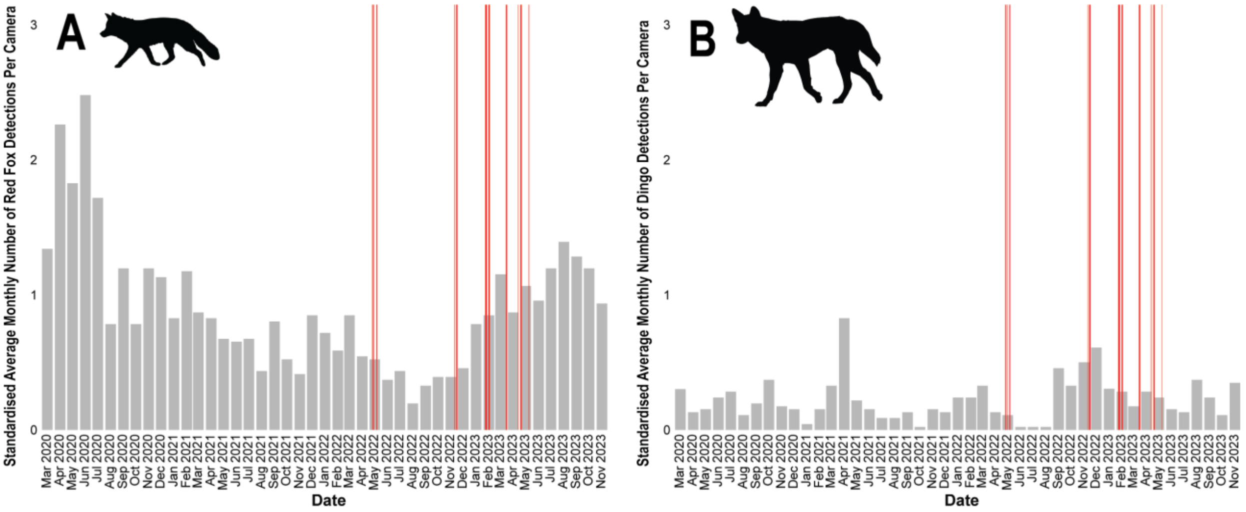

Figure S5.3: Fox (A) and dingo (B) standardised average monthly number of detections per camera across the Kosciuszko National Park camera array from March 2020 to November 2023. Method was calculated as in Chapter 4.

Figure S5.4: Juvenile dingoes scavenge on a 5-month old sambar deer carcass, culled during an aerial shooting program in subalpine Kosciuszko National Park, Australia.

Figure S5.5: A sambar deer carcass in a subalpine Sphagnum shrub bog in Kosciuszko National Park in late October 2022, animal was culled in late May 2022. Upon visual inspection, carcass appeared to have mummified and had undergone limited biomass loss, likely due to persistent snow cover over winter.

Chapter 6: Genetic effects of culling fallow deer in southeastern Australia

View from the Main Range, Kosciuszko National Park

This chapter is being prepared for submission to an international peer-reviewed journal with co-authors Thomas Newsome, Kittikun Chris Songsomboon and Catherine E. Grueber.

6.1 Abstract

Invasive deer in Australia are increasing both in number and in geographical range. These deer contribute to the degradation of natural and agricultural areas by dispersing invasive plants, hindering plant recruitment, altering forest structure, and competing with livestock for resources. To mitigate these impacts, aerial culling is commonly deployed to reduce population sizes of invasive deer. When successful, there are likely to be shifts in the species' population genetic structure and diversity that reflect a declining or disturbed population. However, a recent extensive culling effort in the Australian Alps, in which 1,464 fallow deer (*Dama dama*) were removed from a localised area (284 km^2) over two years, did not significantly reduce the number of deer as measured using aerial thermal surveys; it is unclear why a reduction in deer numbers was not observed. A plausible hypothesis is that, after animals were removed, deer repopulated the site from neighbouring areas. Here we test this hypothesis, using population genetic and movement analyses. We found some evidence for a change in population diversity across the two-year culling period. For example, in year two of culling operations we saw an increase in effective population size and variance in heterozygosity of deer sampled within the study area, consistent with the hypothesis that, following removal of deer, new individuals repopulated from adjacent areas. This hypothesis is also consistent with GPS tracking data reported herein, which indicated movement of deer among the study area and external populations. We were unable to confirm our repopulation hypothesis using population genetic structure data, because animals across the relevant landscape distances were not substantially genetically differentiated. Across a broader geographic range, genetic separation was also not consistently aligned with geographic separation, and some individuals separated by large distances were closely related. This suggests human-mediated translocation may also be occurring or have occurred in the recent past. Our findings underscore the need to integrate population connectivity when determining the appropriate scale of population control regimes.

6.2 Introduction

Invasive species threaten biodiversity (Cameron et al., 2016; Vilà et al., 2011), ecosystem function (Gallardo et al., 2016; Walsh et al., 2016), and agricultural productivity globally (Paini et al., 2016). Consequently, invasive species are culled to lower population sizes, or with the aim of eradication (Comte et al., 2023; Jones et al., 2016). However, the success of control efforts is often uncertain (Ward et al., 2020). Furthermore, culling species can have unexpected secondary effects (Prentice et al., 2019), such as affecting the behaviour of target animals, triggering changes in temporal activity (Chapter 4), social structure (Downing et al., 2023), movement range (Riordan et al., 2011; Sunde et al., 2009) and mate choice (Rutledge et al., 2012). In an area where the density of a culled species is reduced, animals may repopulate the site from surrounding areas (Kierepka et al., 2017; Takeshita et al., 2017). Therefore, it is important to ensure the scale of control reflects the dispersal and connectivity of the target species, as unexpected patterns of population structure and connectivity (Burgess et al., 2022; Spencer et al., 2012) can undermine population reduction efforts.

The effects of population management efforts are commonly studied with ecological and field monitoring (e.g. Bengsen et al., 2024; Downing et al., 2023). However, genetic studies can also help inform population size change, shifts in animal movement and metapopulation structure. For example, long-term monitoring of invasive grey squirrels (*Sciurus carolinensis*) has revealed that despite extensive culling efforts, genetic diversity of the population in the target area has remained unchanged. This is most likely because new genetically distinct animals are moving into the study area following control and thus maintaining genetic diversity of the population in the area (Synnott et al., 2023). Furthermore, fitness advantages resulting from altered population structure can lead to accelerated range expansion (Wagner et al., 2017). Alternatively, when culling efforts lead to a loss of genetic diversity, this likely indicates that gene flow is restricted because a population is isolated, which could potentially accelerate population decline (Allendorf et al., 2008; Zalewski et al., 2016). Therefore, monitoring genetic changes in a managed species can complement field-based ecological monitoring and inform management efforts.

Deer were first introduced to Australia in the mid-1800's for hunting, and since then, continued release of deer from farms and translocations between wild populations have led to the establishment of wild populations of six species (Davis et al., 2016). Research has shown that selective browsing by deer can contribute to the dispersal of invasive plants (Forsyth & Davis, 2011), hinder plant recruitment (Bennett, 2023), and alter the structure of forests (Wills et al., 2023). Deer occurrence may also be associated with reductions in the occurrence of small mammals (Pedersen et al., 2014). Consequently, designing effective deer management practices (Green & Grosholz, 2021; Kopf et al., 2017), and forecasting and preventing future deer invasions are research priorities (Le Roux & Wieczorek, 2009; Pili et al., 2024). Aerial culling is commonly deployed to control deer in Australia, and considered an effective landscape-scale control tool for large herbivores, particularly in remote locations (Bengsen et al., 2022; Bradshaw et al., 2023; Pulsford et al., 2022). A large-scale aerial control program targeting deer was recently undertaken in the region, across both Kosciuszko National Park and adjacent private agricultural land, in response to growing concern over increases in deer abundance, and possible environmental damage and threats to agriculture (NSW Department of Planning Industry and Environment, 2021). However, thermal aerial surveys indicated that the extensive culling effort failed to reduce the number of deer in the area (Chapter

4). Here we use genetic analyses of fallow deer (*Dama dama*; hereafter 'deer') structure and diversity and deer tracking data to investigate why a sustained population reduction was not observed.

Given that a sustained population decline was not detected, we hypothesise that culling efforts did induce an initial population decline, but that new animals moved into the area promptly, preventing sustained local population reductions. In this case, we predict that population genetic diversity of animals at the site will remain the same or increase, and that measures of population structure across the broader area will decrease. Alternatively, it is plausible that despite culling efforts – the population size detectable within the study area remained the same and deer movement did not change (i.e. that a failure to detect a statistically significant population decline truly reflects an unchanged population). If true, we predict that our genetic data will show no change in population genetic diversity nor structure. Finally, it is also plausible that the population declined, but that no new animals moved into our study area, in which case we would predict a decrease in population diversity and no change in structure. However, we expect that this latter hypothesis is the least likely, because thermal aerial surveys suggested the population size did not decrease. In this study, our population genetic data are supported by tracking data from 16 deer initially tracked within our study area. We use this data to evaluate the potential for connectivity between our study area and external populations. To contextualise the diversity and structure of deer within the study area, we also assess the diversity and structure of other deer populations across New South Wales (NSW) and the Australian Capital Territory (ACT), in the regions surrounding the study area. In this study, combining movement and population genetic data provided detailed insights to test our hypotheses and inform future management.

6.3 Methods

6.3.1 Study area description

The study area is 284 km^2, and approximately 12 km long and 28 km wide (Figure 6.1). The western half of the study area forms part of the southern end of Kosciuszko National Park (National Park population). Native vegetation in the park is dominated by Eucalypt (*Eucalyptus* spp.) woodland and alpine tussock grassland (Department of Environment and Climate Change NSW, 2007). The area decreases in elevation moving from west to east, and transitions into pastural farmland in the eastern half (private population), which is interspersed with patches of remnant native vegetation, and small residential areas.

6.3.2 Control effort

The population of deer (including fallow deer, sambar deer [*Rusa unicolor*] and red deer [*Cervus elaphus*]) was estimated at a density of 16.4 deer/km^2 (± 95% CI: 10.1–26.5 deer/km^2) or ~4,652 (± 95% CI: 2,877–7,521) individuals within the study area, through aerial thermal surveys immediately prior to control in February 2022. Fallow deer were the most abundant deer species in the study area (Figure S4.2)

Forty-eight days of aerial control via helicopter occurred across a 460-day period (14 February 2022–19 May 2023) from February 2021–May 2022 (27 days) and November 2022–May 2023 (21 days) in summer, autumn and spring, outside of the period when snow was likely to occur. Fallow deer, red deer and sambar deer were targeted for culling. On most aerial control days, culling took place across both the National Park and private population areas (Figure 6.1), but the extent of culling activity and the number of deer culled varied between the areas from day to day. Over the study period, 1,575 fallow deer were culled, including 1,117 in period 1 and 458 in period 2 (Table 6.1). Fallow deer comprised 82% of kills across all operations.

Aerial thermal surveys covering the entire study area indicate that the overall deer population remained relatively stable, with some consistent seasonal fluctuations between 2020 and 2023 (Figure 4.2). Following control, in November 2023, deer density was not reduced throughout the study area, and the population of deer was estimated at a density of 19.1 deer/km^2 (± 95% CI: 10.0–36.4 deer/km^2) or ~5,429 (± 95% CI: 2,849–10,348) individuals within the study area.

6.3.3 Sampling distribution

Between 2019 and 2023, deer ear tissue samples were collected during ground and aerial culling operations conducted by government agencies and private landholders in NSW and the ACT. Samples were also collected opportunistically, for example, from roadkill and during collaring of deer within the study area. Tissue samples were collected using commercially available Allflex Tissue Sampling Units (TSUs, Allflex Australia Pty Ltd, Capalaba, Queensland). For each sampled animal we recorded sex, life stage (adult or juvenile), sampling date and location. Samples were stored at 2 °C in TSUs between collection and extraction.

National Park samples (N = 106) were collected within the study area boundaries, within Kosciuszko National Park; private samples (N = 138) were collected within the study area boundaries on private land, predominantly farmland (Figure 6.1). An additional 155 samples were collected from throughout NSW and the ACT (Figure 6.1; details in Table S6.1).

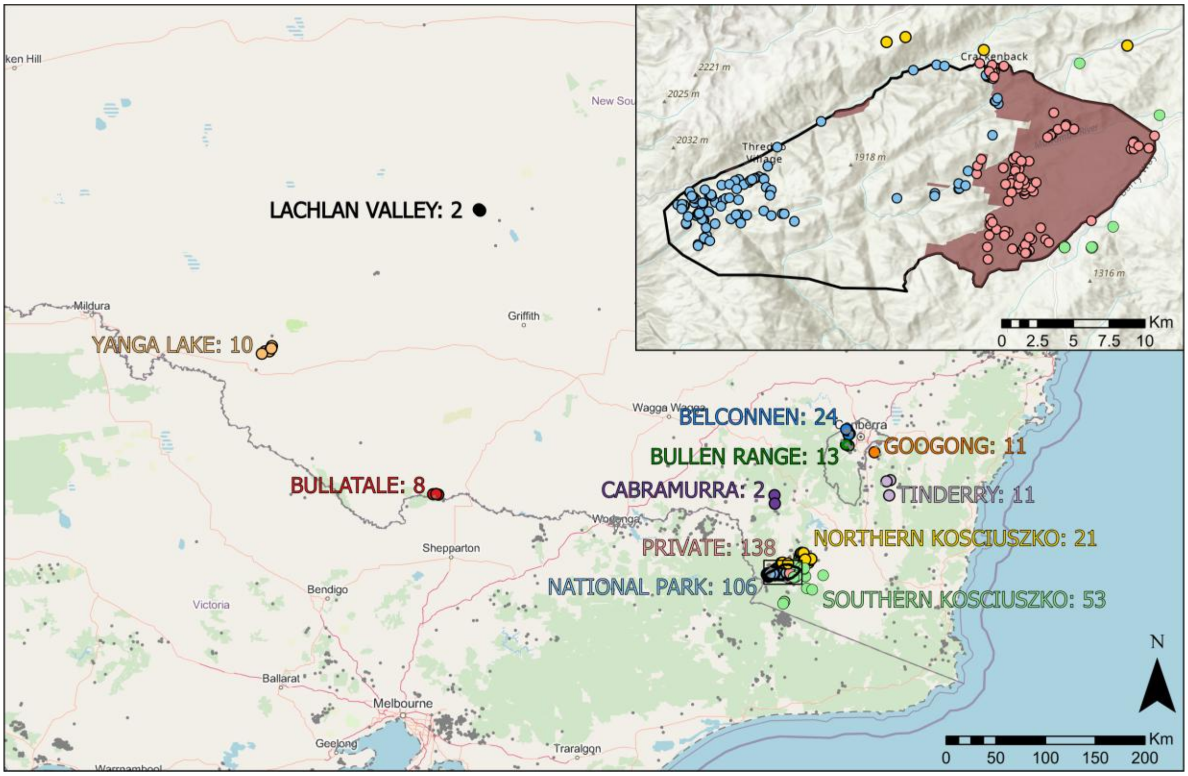

Figure 6.1: Fallow deer tissue sample distribution of the 400 samples collected across NSW and the ACT (excluding duplicates). Samples were collected external to the study area opportunistically and as part of ongoing culling operations between 2019 and 2023. Smaller grey points indicate occurrence records of fallow deer from Atlas of Living Australia (Atlas of Living Australia Occurrence Download, 2025). Inset map shows the distribution of National Park and private samples (private area indicated by brown area within the study area boundaries). These samples were collected opportunistically and across 460 days of aerial culling within the study area (black boundaries).

6.3.4 DNA extraction and sequencing

Tissue samples from a total of 406 deer were prepared for reduced-representation sequencing. For 48 samples, DNA was extracted using the Isolate II Genomic DNA kit (Bioline Pty Ltd) following manufacturer instructions, except that digestion incubation was run overnight. We quantified DNA concentration using a Nanodrop 2000 Spectrophotometer (ThermoFisher Scientific). We then assessed extraction quality via 1% agarose 1× Tris-acetate-Ethylenediaminetetraacetic acid (TAE) gel electrophoresis (Astral Scientific), using SYBR safe DNA gel stain (ThermoFisher Scientific); gels were run for 30 minutes at 100 V. For the remaining 375 samples, Diversity Arrays Technology Pty Ltd., Australia; hereafter DArT, performed DNA extraction and sample quality checks.

Across a total of five sequencing places, we included 12 intraplate and 5 interplate replicates (Table S6.2), to a total of 423 DNA samples submitted for DArTseq. Restriction enzyme NlaIII was used to fragment DNA, which was then sequenced using an Illumina Hiseq 2500, targeting 2.5 million reads per sample. Reads were aligned to the fallow deer reference genome (GenBank BioProject PRJNA905851; Barnard et al., 2023).

DArT in-house filtering returned a total of 9,348 SNP loci across our full dataset. Further filtering was conducted using the package *dartR* v2.9.7 (Gruber et al., 2018). We removed SNPs with a read depth lower than 5 or higher than 50, with < 99% reproducibility according to DArT internal controls and < 95% call rate. We removed 6 samples that were sequenced for another study but which did not have relevant metadata for the current study. Prior to additional filtering, we evaluated genotyping concordance between our technical replicates and found they had a mean error rate of 0.54% for intraplate replicates and 2.20% for interplate replicates (Table S6.2). We removed 67 loci from the entire dataset that showed > 1 replication errors, and then removed samples representing our technical replicates (one replicate of each pair chosen at random). We removed SNPs on sex chromosomes, and those which had an unknown chromosomal assignment, based on chromosome assignment of reference genome (Barnard et al., 2023). We removed one individual with a genotyping call rate < 80%, all other individuals had a call rate > 90% (mean = 99%). Loci were filtered based on a minor allele frequency across the entire of 0.00376 (3/2N individuals), to reduce the probability of retaining false alleles resulting from sequencing errors while retaining potential for detecting rare or population-specific alleles. The final filtered dataset comprised 2,279 loci and 399 individuals (Figure 6.1).

6.3.5 Genetic analyses

6.3.5.1 Pre-cull population structure

To determine the number of deer populations across the study area, we used a Bayesian clustering approach with STRUCTURE v2.3.4 (Pritchard et al., 2000), implemented via *dartR*, focussed on samples from the National Park and private sampling areas collected before the onset of culling in February 2022 (N = 94). To quantify the likelihood of the number of populations (k) for each value from 1 to 5, we used 3 independent runs with 10,000 burn-in and 50,000 MCMC iterations for each value of k. The preferred value of k was determined using the change in the second order of likelihood, Δk (Evanno et al., 2005). We then summarised the individual ancestries for the preferred value of k.

6.3.5.2 Genetic effect of culling

We compared the structure and diversity of the deer population at the National Park and private sampling areas before and during extensive culling operations using samples that were collected prior to culling versus during culling operations. Based on results of the STRUCTURE analysis (see Results), samples from the National Park and private areas were combined for each period. Samples were analysed in four time periods: two one-year periods prior to culling ('-1' and '0'), and two one-year periods after the onset of culling in February 2022 ('1' and '2'; Table 6.1).

Table 6.1: Sample sizes of fallow deer sampled prior to and during aerial culling operations within the study area within and near to Kosciuszko National Park, NSW, grouped by sampling period, sex (m = male; f = female; u = unknown) and sampling location. Period refers to the date of sample collection in relation to culling, which began in February 2022.

Period	**Kosciuszko National Park (National Park; *N* samples)**	**Private land (private; *N* samples)**
-1 (January 2020–January 2021)	1 (m = 0; f = 1)	61 (m = 35; f = 25; u = 1)
0 (February 2021–January 2022)	9 (m = 6; f = 3)	23 (m = 15; f = 8)
1 (February 2022–January 2023)	38 (m = 15; f = 23)	34 (m = 15; f = 17; u = 2)
2 (February 2023–May 2023)	58 (m = 30; f = 26; u = 2)	20 (m = 4; f = 16)

To visualise differences in population structure in the study area between time periods (total $N = 244$ across all time periods), we performed a Pearson principal component analysis (PCA) with plotted individuals classified by period, using *dartR*. To quantify temporal changes in allele frequencies, we calculated the pairwise fixation index (F_{ST}; Weir & Cockerham, 1984) between periods for the study area using *dartR*, based on the implementation in the *StAMPP* package (Pembleton et al., 2013). 95% confidence intervals were estimated via loci bootstrapping using the *HIERFSTAT* v0.5-11 package (Goudet, 2005).

To quantify temporal changes in individual-level diversity of deer at our study area, we focused on mean standardised multilocus heterozygosity (sMLH) using the package *inbreedR* v0.3.3 (Stoffel et al., 2016). sMLH is a measure of individual heterozygosity that is standardised across all loci and individuals and so is more suitable than H_O for observing relative changes over time (Wright et al., 2022). Change in sMLH was modelled via linear regression using the package *stats* v3.6.2 (R Core Team, 2016). For this test, sMLH was the response variable, and sampling period was the categorical predictor variable, with sampling period '-1' as the reference level (Table 6.1). We also calculated observed heterozygosity (H_O), as it is a more widely used statistic.

Next, we quantified temporal changes in population-level diversity. We calculated unbiased expected heterozygosity (UH_E), and population-level inbreeding (F_{IS}), using *dartR*. We used bootstrapping across loci (1,000 replicates) to evaluate 95% confidence intervals (CIs) for UH_E and F_{IS} using the package *boot* v1.3.30. We calculated effective population size (N_e) for each period for a random subset of individuals rarefied to the lowest period sample size ($N = 32$) using NeEstimator v2.1 interfaced through *dartR* (Do et al., 2014), without removing singleton alleles and 95% CIs estimated via jackknife resampling.

To further investigate changes in within-population diversity and structure, we estimated relatedness among all sampled deer at the study site ($N = 244$) using EMIBD9 v1.1.0.0 (Wang, 2022) interfaced through *dartR*. This method is optimised for small samples and samples with a high proportion of close relatives. For this analysis, the estimator was run with inbreeding not allowed so that estimates aligned with kinship coefficient relatedness thresholds and were more conservative (Speed & Balding, 2015; Wang, 2022). We calculated the mean kinship of each individual relative to others *within* each sampling period (mean within-period kinship coefficient), as well as the mean kinships *between* individuals identified at each sampling period, both with corresponding standard deviations. The latter was evaluated by averaging the kinships of all possible pairs of individuals across each combination of periods. We also calculated the standardised number of relationships for each period, which was the number of second-order relationships among individuals in each period divided by the total number of pairwise comparisons between individuals for that period (number of possible relationships). We referred to the relatedness thresholds and confidence intervals provided in Speed & Balding (2015) (relatedness threshold = 0.25 [0.204, 0.296]: equivalent to first order relationship - parent/offspring/sibling; relatedness threshold = 0.125 [0.092, 0.158]: equivalent to second-order relationship grandparent/grandchild, aunt/uncle/niece/nephew, half-sibling). We then tested for statistically significant change over time in the kinship among individuals across the four sampling periods using linear regression as above. For this test, the mean within-period kinship coefficient of each individual was the response variable, sampling period was the categorical predictor variable, and sampling period '-1' was the reference level (Table 6.1). The statistical significance of results for linear models was inferred at $\alpha = 0.05$.

6.3.5.3 Genetic structure across southeastern Australia

For all further analyses, we combined all samples from Kosciuszko National Park and private land across the four periods into a single population called study area ($N = 244$), based on the results of the previous analysis (see Results).

We performed a PCA to visualise genetic differences between populations of deer sampled across NSW and the ACT (*N* = 399). To quantify the diversity and differences between populations, we calculated sMLH, H_o, UH_E and F_{IS} for each population, as defined by sampling locality, and calculated F_{ST} between each pair of populations (and 95% confidence intervals for each metric), using methods described above.

To evaluate relatedness within and between populations, we estimated relatedness among deer using EMIBD9, as above. We calculated mean kinship coefficients within and between each population. We then inferred first and second order relationships between populations using kinship coefficient relatedness thresholds and confidence intervals, as described above.

To investigate deer genetic dispersal potential compared to movement data, we performed global spatial autocorrelation analyses (Smouse & Peakall, 1999), for males and females separately, in *dartR*. Individuals with unknown sex and juveniles were excluded, additionally, individuals sampled from Lachlan Valley and Cabramurra were excluded due to small sample sizes. To examine spatial autocorrelation across all sampled individuals, custom distance classes were used – ranging from close distances (1 km) to represent our study area of interest, and intermediate distances to complement GPS monitoring and genetic sampling up to 600 km, the maximum distance between samples, informed by the movement analyses (see below). However, it is important to note that although we had high resolution of samples for distances up to ~40 km, sampling was limited at greater distances in terms of both animals and populations (Table 6.5). Genetic distances were calculated from a Euclidean distance matrix of individuals. The null hypothesis of no spatial autocorrelation (i.e. that deer are not spatially structured across the sampling area) was tested using 1,000 random permutations, with 95% confidence intervals around the spatial correlation coefficients estimated using 1,000 bootstraps. We visualised results for all analyses using R packages *ggplot2* v3.5.1 (Ginestet, 2011) and *ggpubr* v0.6.0 (Kassambara, 2018). All filtering and analyses were conducted in R version 4.1.2, interfaced through RStudio (R Core Team, 2021).

6.3.6 Movement potential

To evaluate natural dispersal potential for deer, and to inform expected spatial connectivity for population genetics analyses, we used data from GPS-collared fallow deer within the study area. 20 deer (11 males, 9 females) were captured and collared using aerial net gunning or clover trapping. To restrain deer during capture, for aerial net gunning, the net was released from a helicopter and sedation was administered via hand injection from the ground. For clover trapping, deer were restrained by a minimum of two personnel. Captured deer were fitted with a GPS tracking collar, programmed to record locations hourly

(G52D Iridium, Advanced Telemetry Systems, Isanti, MN, USA; for more details of collaring procedure see McCarthy et al., 2023). This study was approved by The University of Sydney Animal Ethics Committee (Project number: 2020/1844).

Abnormal activity (e.g. long distance movements) for approximately 10 days following collaring has been reported for deer captured and collared via aerial net gunning (McCarthy et al., 2023). Therefore, the first ten days of data following collaring were excluded. We also filtered from the dataset all locations with a horizontal dilution of precision (HDOP) > 2.5, or where HDOP could not be calculated. Then, for each full year each deer was monitored, we calculated the yearly mean and maximum displacement from their starting location using the package *move2* v0.4.4, and generated means for males and females (Kranstauber et al., 2024). Deer monitored for less than a full year were excluded from averages. We also generated figures showing net displacement over time for each individual.

6.4 Results

6.4.1 Pre-cull population structure

Based on likelihood statistics, the best-supported number of genetic populations of deer in the study area pre-cull was two (STRUCTURE analysis: $\Delta k = 67.0$), but all individuals were majority assigned to population 1, suggesting a single panmictic population (Figure 6.2). Individuals with the greatest evidence of possible admixture ($N = 6$ with population 2 assignment > 10%) were only found in the private population (Figure 6.2).

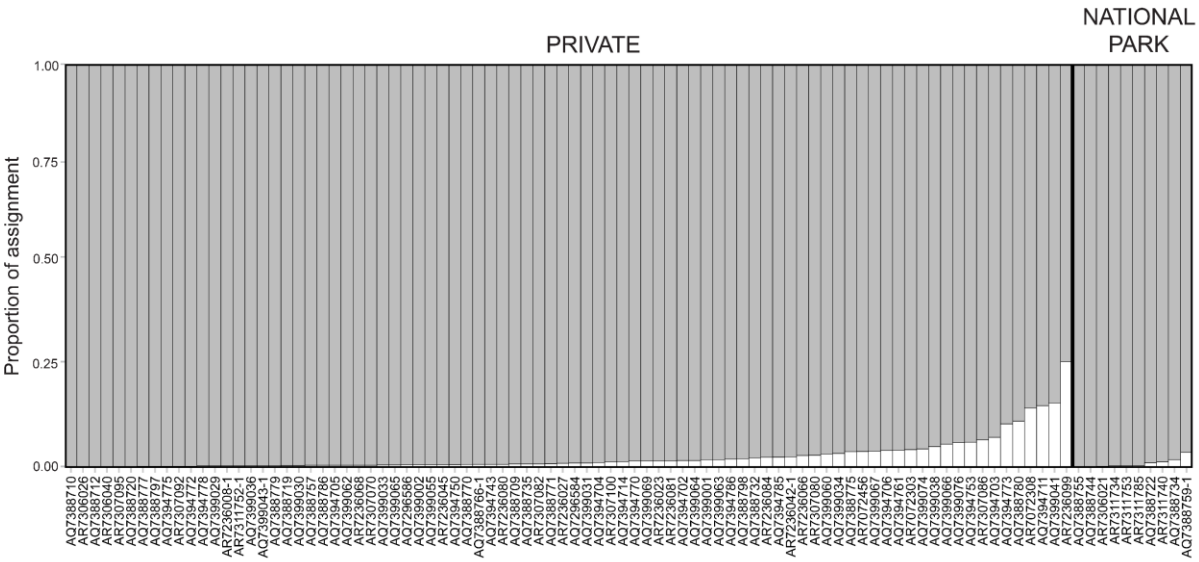

Figure 6.2: STRUCTURE plot for all fallow deer sampled in the study area (*N* = 94; 2,168 polymorphic loci), from populations National Park and private, collected before the onset of culling in February 2022. Each deer is represented by a single vertical bar. The best fit for k was k = 2 (Table S6.3).

6.4.2 Population genetic effect of culling

The PCA showed no genetic separation among the four sampling periods (Figure S6.1). Similarly, pairwise F_{ST} indicated no change in allele frequencies across the four year-long sampling periods pre and post cull (Table 6.2).

Table 6.2: Pairwise F_{ST} with bootstrapped 95% upper and lower confidence intervals (blue text below the diagonal) and kinship coefficients with standard deviation (SD; black text above the diagonal) comparing genetic differentiation of 244 fallow deer with 2,230 polymorphic loci, sampled between periods before the onset of culling (periods -1 & 0), and after the onset of culling (periods 1 & 2), defined in Table 6.1. Samples were collected from within the study area within and near to Kosciuszko National Park, NSW.

Period (*N* = number of individuals)	***N***	-1	0	1	2	**Mean within-period kinship coefficient (SD)**
-1	62	-	0.028 (0.020)	0.027 (0.018)	0.028 (0.018)	**0.028 (0.021)**
0	32	0.003 (0.002, 0.003)	-	0.028 (0.018)	0.030 (0.021)	**0.029 (0.024)**
1	72	0.001 (< 0.001, 0.002)	0.001 (< 0.001, 0.002)	-	0.028 (0.019)	**0.028 (0.021)**
2	78	0.002 (< 0.001, 0.002)	< 0.001 (< 0.001, 0.002)	0.001 (< 0.001, 0.002)	-	**0.029 (0.022)**
Mean F_{ST} of period to all other periods (SD)	-	**0.002 (< 0.001)**	**0.001 (< 0.001)**	**0.001 (< 0.001)**	**0.001 (< 0.001)**	-

Mean sMLH of deer within the study area was highest for period -1, the period up to one year before the onset of culling, then decreased in period 0, and increased and was stable between periods 1 and 2, in the first and second years of culling (Table 6.3). There was a statistically significant difference in sMLH between periods -1 and 0 ($\beta = -0.028$, SE = 0.013, but there was no difference between periods -1 and 1 ($\beta = -0.011$, SE = 0.010) and -1 and 2 ($\beta = -0.011$, SE = 0.010) (Figure 6.3A; Table S6.4). H_O followed a similar pattern, being highest in period -1, then decreasing in period 0, increasing in period 1 and decreasing slightly again, but with high variance, in period 2 (Table S6.5).

Population-level UH_E followed a similar pattern to H_O (Table 6.3). F_{IS} remained very close to zero across the four periods (Table 6.3). N_e decreased between periods -1 and 0, and 0 and 1, and was highest, with high variance in period 2 (Figure 6.3C; Table 6.3).

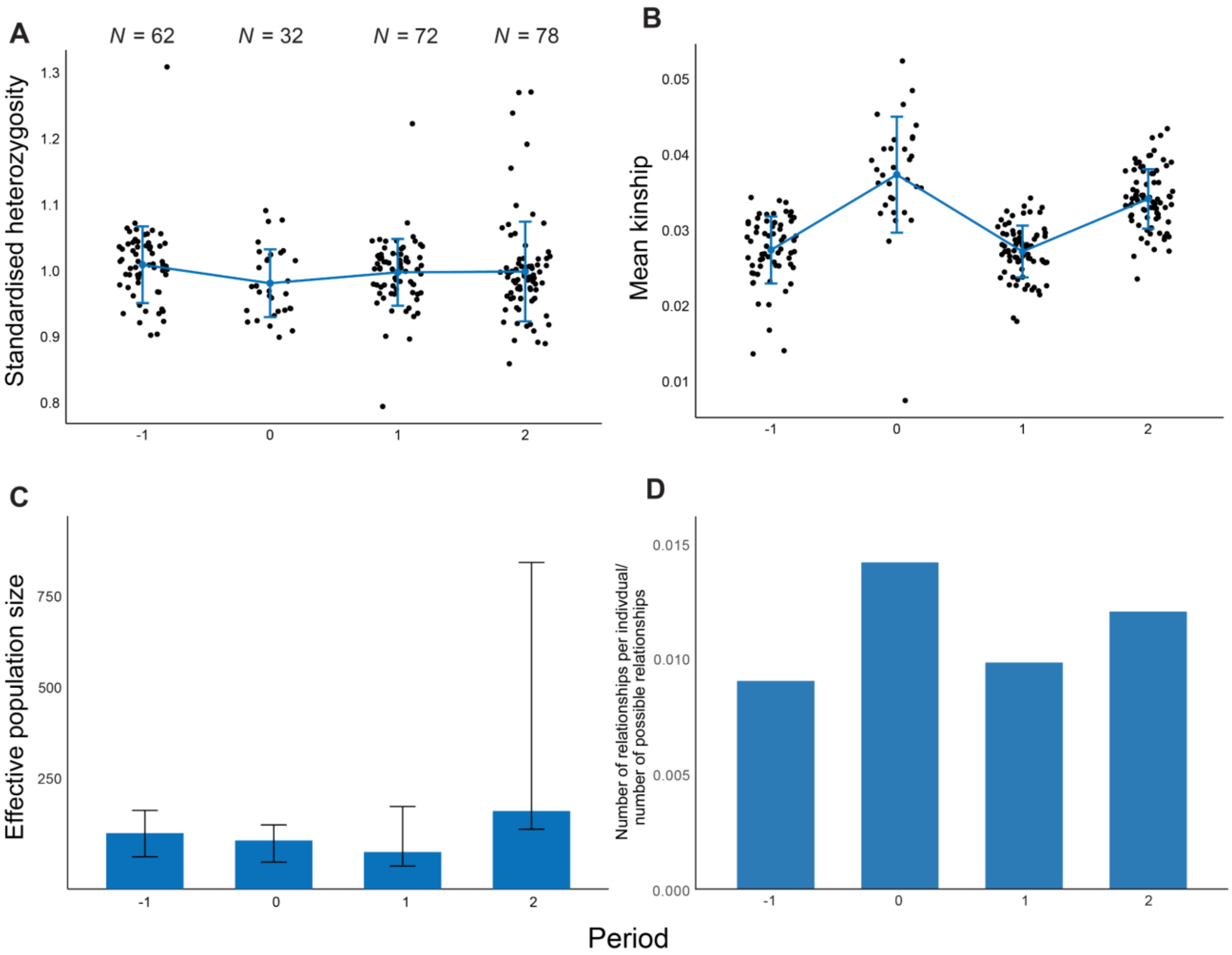

Figure 6.3: (A) standardised multilocus heterozygosity (sMLH) ± standard deviation, (B) mean kinship to all other individuals in the study area from all periods ± standard deviation, (C) effective population size ($N_{e;}$ for each period, N_e was calculated for a random subset of individuals rarefied to the lowest sample size [$N = 32$]), and (D) the standardised number of relationships for each period for fallow deer sampled over year-long periods before (periods -1 and 0), and after (periods 1 and 2) the onset of shooting (defined in Table 6.1). Points in A and B are jittered on the x-axis (width = 0.2).

Table 6.3: Genetic diversity indices for 244 fallow deer, with 2,230 polymorphic loci, sampled within each year-long period pre-cull ('-1' and '0') and after the onset of culling ('1' and '2') (defined in Table 6.1) within the study area near to Kosciuszko National Park, NSW. Values in parentheses are 95% upper and lower 95% confidence intervals.

Period	***N***	**polyLoc**[1]	**sMLH**[2]	**UH$_E$**[3]	**F$_{IS}$**[4]
-1	62	2129	1.009 (0.996, 1.025)	0.308 (0.299, 0.313)	0.007 (0.002, 0.013)
0	32	2074	0.981 (0.965, 0.998)	0.303 (0.291, 0.305)	0.024 (0.017, 0.032)
1	72	2127	0.998 (0.986, 1.009)	0.308 (0.299, 0.313)	0.018 (0.012, 0.023)
2	78	2125	0.999 (0.982, 1.015)	0.305 (0.297, 0.310)	0.008 (0.003, 0.013)

1. polyLoc = number of polymorphic loci; 2. sMLH = mean standardised multilocus heterozygosity, standardised across all loci and individuals (*N* = 244); 3. UH$_E$ = unbiased expected heterozygosity; 4. F$_{IS}$ = population-level inbreeding coefficient.

Mean kinship was very similar within periods as well as between periods (Table 6.2). The linear model evaluating changes in the mean kinship of individuals in each period to all other individuals in the same period indicated that there was a statistically significant difference in mean kinship between periods -1 and 0 ($\beta = 0.010$, SE = 0.001), and periods -1 and 2 ($\beta = 0.007$, SE = 0.001), but not between periods -1 and 1 ($\beta = -0.0002$, SE = 0.001) (Table S6.4, Figure 6.3B). The standardised number of relationships for each period followed a similar pattern to mean kinship (Figure 6.3D).

6.4.3 Genetic structure across southeastern Australia

Relatedness between the study area and Northern Kosciuszko populations was very similar within and between populations. From the PCA comparing all populations, there was little separation between the study area population and the Northern Kosciuszko and Southern Kosciuszko populations (Figure 6.4). However, some individuals sampled in the Southern Kosciuszko and study area populations grouped close to the cluster formed by the Lachlan Valley, Bullatale and Yanga Lake (all Western NSW), and the Cabramurra populations (Figure 6.4). This cluster overlapped with another cluster, which was spread out across PC1, with Tinderry samples spread between the two clusters. The third cluster consisted of the Bullen Range and Googong populations, and two individuals from the Belconnen population (both yearling males). The remainder of individuals sampled from the Belconnen population grouped in a tight cluster distinctly separated from other groups on PC1 and PC2. Overall, the variance explained by the PC ordination was low, with the first two PCs explaining a total of 10.7% variation (Figure 6.4). Between population pairwise F$_{ST}$ reflected the relationships of the PCA, and showed that the study area, Northern and Southern Kosciuszko populations were very similar (Table 6.4). Southern Kosciuszko had higher relatedness to the study area and Northern Kosciuszko populations compared to within its own population (Table 6.4).

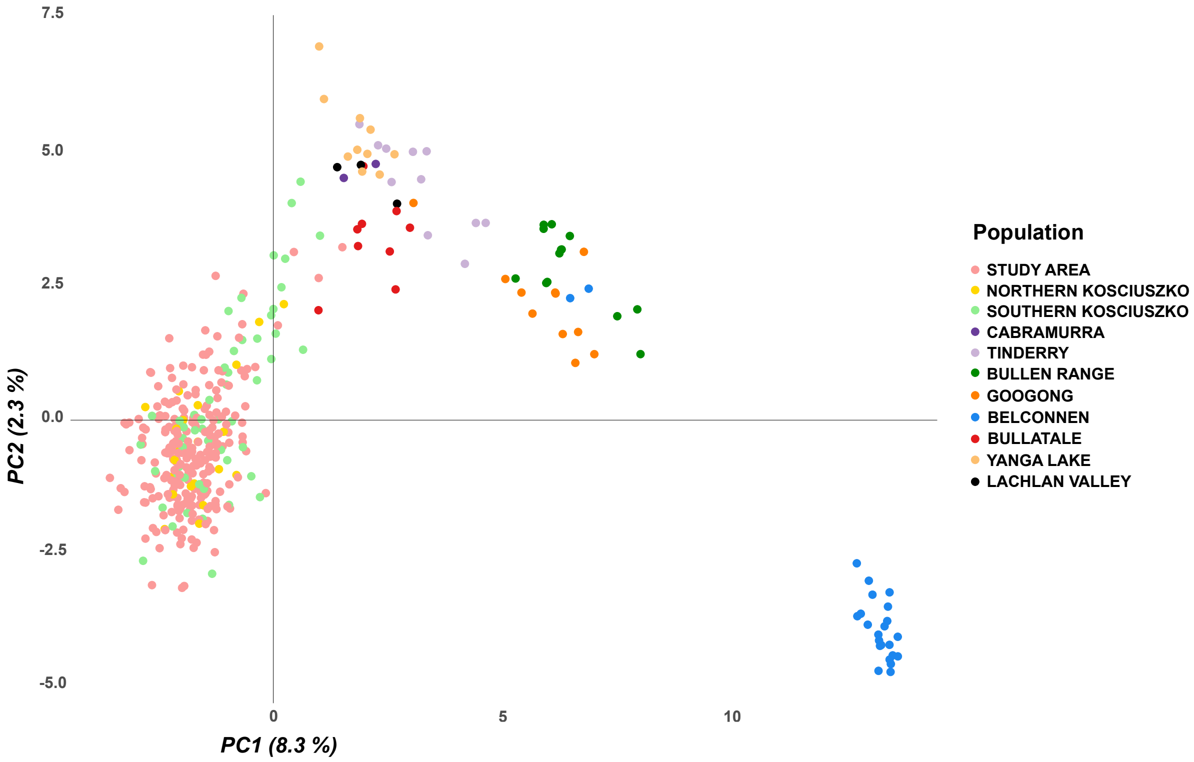

Figure 6.4: Principal coordinate plot showing genetic differentiation of fallow deer populations sampled across NSW and the ACT (key ordered as in Table 6.5), composed of a total of 399 individuals with 2,273 polymorphic loci. PC1 and PC2 explain 8.3% and 2.3% of the total variance, respectively.

Table 6.4: Pairwise F_{ST} with bootstrapped 95% upper and lower confidence intervals (blue) and mean kinship coefficients with standard deviations (black) of 14 fallow deer populations composed a total of 399 individuals with 2,279 polymorphic loci, sampled across NSW and the ACT (ordered as in Table 6.5).

Population (*N* = number of individuals)	*N* (F_{ST})	Study area	Northern Kosciuszko	Southern Kosciuszko	Cabramurra	Tinderry	Bullen Range	Googong	Belconnen	Bullatale	Yanga Lake	Lachlan Valley	**Mean within-population kinship coefficient (SD)**
***N* (Kinship)**	-	29,646	210	1,378	1	55	78	55	276	28	45	1	-
Study area	244	-	0.072 (0.019)	0.065 (0.019)	0.030 (0.010)	0.031 (0.010)	0.026 (0.010)	0.029 (0.011)	0.014 (0.008)	0.036 (0.011)	0.036 (0.012)	0.017 (0.008)	**0.072 (0.020)**
Northern Kosciuszko	21	< 0.001 (< -0.001, 0.002)	-	0.067 (0.019)	0.032 (0.009)	0.032 (0.010)	0.029 (0.010)	0.031 (0.010)	0.016 (0.008)	0.038 (0.010)	0.039 (0.011)	0.017 (0.005)	**0.074 (0.019)**
Southern Kosciuszko	53	0.003 (0.003, 0.004)	< 0.001 (< 0.001, 0.002)	-	0.036 (0.012)	0.057 (0.009)	0.032 (0.012)	0.032 (0.011)	0.019 (0.010)	0.040 (0.012)	0.042 (0.016)	0.023 (0.014)	**0.063 (0.021)**
Cabramurra	2	0.074 (0.063, 0.086)	0.071 (0.059, 0.083)	0.052 (0.040, 0.063)	-	0.057 (0.009)	0.055 (0.011)	0.049 (0.009)	0.030 (0.010)	0.044 (0.011)	0.061 (0.012)	0.064 (0.007)	**0.044 (0)**
Tinderry	11	0.120 (0.111, 0.128)	0.125 (0.115, 0.135)	0.109 (0.101, 0.117)	0.098 (0.084, 0.111)	-	0.061 (0.015)	0.074 (0.020)	0.070 (0.021)	0.049 (0.011)	0.049 (0.011)	0.037 (0.009)	**0.157 (0.030)**
Bullen Range	13	0.143 (0.134, 0.151)	0.149 (0.140, 0.158)	0.130 (0.122, 0.139)	0.132 (0.116, 0.147)	0.171 (0.160, 0.182)	-	0.090 (0.025)	0.141 (0.028)	0.054 (0.013)	0.054 (0.012)	0.036 (0.008)	**0.182 (0.043)**

Googong	11	0.130 (0.122, 0.139)	0.135 (0.126, 0.145)	0.120 (0.112, 0.129)	0.127 (0.112, 0.143)	0.142 (0.132, 0.152)	0.141 (0.131, 0.151)	-	0.127 (0.027)	0.054 (0.014)	0.061 (0.012)	0.034 (0.007)	**0.166 (0.051)**
Belconnen	24	0.250 (0.328, 0.261)	0.298 (0.285, 0.311)	0.257 (0.246, 0.270)	0.369 (0.348, 0.389)	0.307 (0.293, 0.323)	0.214 (0.201, 0.227)	0.228 (0.213, 0.241)	-	0.051 (0.013)	0.037 (0.011)	0.034 (0.009)	**0.295 (0.071)**
Bullatale	8	0.111 (0.103, 0.120)	0.112 (0.103, 0.122)	0.099 (0.090, 0.108)	0.124 (0.109, 0.139)	0.165 (0.154, 0.176)	0.172 (0.161, 0.184)	0.164 (0.153, 0.177)	0.323 (0.318, 0.349)	-	0.069 (0.011)	0.032 (0.006)	**0.163 (0.047)**
Yanga Lake	10	0.094 (0.088, 0.101)	0.094 (0.087, 0.102)	0.079 (0.073, 0.085)	0.064 (0.051, 0.077)	0.136 (0.126, 0.147)	0.152 (0.142, 0.162)	0.129 (0.120, 0.139)	0.324 (0.309, 0.339)	0.115 (0.106, 0.124)	-	0.047 (0.008)	**0.133 (0.051)**
Lachlan Valley	2	0.171 (0.157, 0.185)	0.177 (0.161, 0.192)	0.153 (0.138, 0.167)	0.141 (0.121, 0.164)	0.215 (0.197, 0.232)	0.248 (0.230, 0.267)	0.235 (0.218, 0.253)	0.438 (0.418, 0.459)	0.231 (0.214, 0.248)	0.176 (0.159, 0.192)	-	**0.284 (0)**
Mean F_{ST} of population to all other populations (SD)	-	**0.110**	**0.116**	**0.100**	**0.125**	**0.159**	**0.165**	**0.155**	**0.302**	**0.163**	**0.136**	**0.218**	-

Relative to the other southeastern Australian populations, the study area had high mean sMLH, similar to the Northern and Southern Kosciuszko and Yanga Lake populations (Table 6.5). The study area had the third highest UH_E, exceeded only by the Southern Kosciuszko and Cabramurra population (Table 6.5). F_{IS} for the study area was the same as the Northern Kosciuszko population and was relatively low compared to other populations (Table 6.5; see Table S6.6 for H_O for each population).

Table 6.5: Genetic diversity indices for 399 fallow deer, with 2,279 polymorphic loci, sampled across NSW and the ACT (ordered by distance from study area). Values in parentheses are 95% upper and lower 95% confidence intervals.

Population (*N* = number of individuals)	**Approximate distance from study area (km)**	***N***	**polyLoc**[1]	**sMLH**[2]	**$\mathrm{UH_E}$**[3]	**$\mathrm{F_{IS}}$**[4]
Study area	-	244	2230	1.032 (1.020, 1.040)	0.300 (0.293, 0.308)	**0.016 (0.012, 0.020)**
Northern Kosciuszko	1–16	21	1976	1.024 (1.002, 1.048)	0.296 (0.289, 0.304)	**0.016 (0.007, 0.025)**
Southern Kosciuszko	1–25	53	2166	1.018 (0.998, 1.036)	0.305 (0.297, 0.311)	**0.039 (0.033, 0.046)**
Cabramurra	60–70	2	1391	1.118 (1.089, 1.146)	0.337 (0.326, 0.348)	**0.029 (0.007, 0.050)**
Tinderry	120–130	11	1684	0.924 (0.879, 0.973)	0.269 (0.260, 0.277)	**0.024 (0.010, 0.038)**
Bullen Range	130–140	13	1584	0.916 (0.889, 0.943)	0.252 (0.244, 0.260)	0.010 (-0.004, 0.022)
Googong	140–150	11	1652	0.854 (0.777, 0.920)	0.251 (0.243, 0.260)	**0.061 (0.048, 0.074)**
Belconnen	160–170	24	1471	0.647 (0.617, 0.682)	0.165 (0.157, 0.172)	**0.060 (0.046, 0.0734)**
Bullatale	290–300	8	1605	0.999 (0.973, 1.029)	0.272 (0.263, 0.280)	**-0.021 (-0.034, -0.007)**
Yanga Lake	460–470	10	1808	1.020 (1.006, 1.034)	0.288 (0.280, 0.297)	-0.003 (-0.018, 0.010)
Lachlan Valley	430–440	2	1119	1.147 (1.142, 1.151)	0.276 (0.264, 0.289)	**-0.171 (-0.187, -0.157)**

1. polyLoc = number of polymorphic loci; 2. sMLH = mean standardised multilocus heterozygosity, standardised across all loci and individuals (*N* = 399); 3. $\mathrm{UH_E}$ = unbiased expected heterozygosity; 4. $\mathrm{F_{IS}}$ = population-level inbreeding coefficient, values are in **bold** where confidence intervals do not include zero.

Comparing kinship values to relatedness thresholds suggested that between populations, there were 9 first-order relationships detected, separated by distances ranging from 4.2 to 41.5 km (mean ± SD = 20.7 ± 11.6 km; Table S6.7), which is within the plausible natural yearly dispersal distance for fallow deer (see below; Figure 6.5). Between populations there were also 2,517 second-order relationships detected, separated by distances ranging from 0.9 to 494.5 km (mean (SD) = 22.8 ± 29.4 km; Figure S6.2).

Spatial autocorrelation analyses showed that for distance classes less than 40 km, both male and female deer were positively autocorrelated, meaning they were more likely to be related at these distances than expected by chance, similar to the maximum movement of tracked male deer (55.24 km) (Figure 6.5B; Figure S6.3). For distance classes between 50–600km, some showed positive autocorrelation, some negative, and several exhibited no statistically significant autocorrelation Figure S6.3).

6.4.4 Movement potential

The movement ranges of collared deer extended outside of the study area (Figure 6.5A). For deer collared for a full year, the mean maximum displacement from their starting location in the first year of collaring was 16.13 ± 5.98 km ($N = 4$) for males and 11.78 ± 6.87 km (SD; $N = 7$) for females. In the second year of collaring the mean maximum displacement from their starting location was 19.90 ± 2.77 km ($N = 2$) for males and 15.26 ± 10.00 km for females ($N = 4$). Only one female deer was collared for a full third year, and their maximum displacement from their starting location was 19.92 km (Figures 6B & 6C).

The maximum recorded displacement from a starting location was a male deer which travelled at least 55.24 km from its starting location in its first year of collaring, this individual was tracked for 329 days before collar malfunction (Figures 2A: blue; Figure 6.5B). The maximum recorded displacement for a female deer was 26.20 km in its second year of collaring, this individual was tracked for a total of 838 days (Figures 6A: orange; Figure 6.5B). For deer collared for a full year, the lowest maximum displacement from the starting location recorded for a male was 8.86 km in its first year of collaring (Figure 6.5B), the lowest maximum displacement recorded for a female was 2.09 km in its second year of collaring (Figure 6.5C).

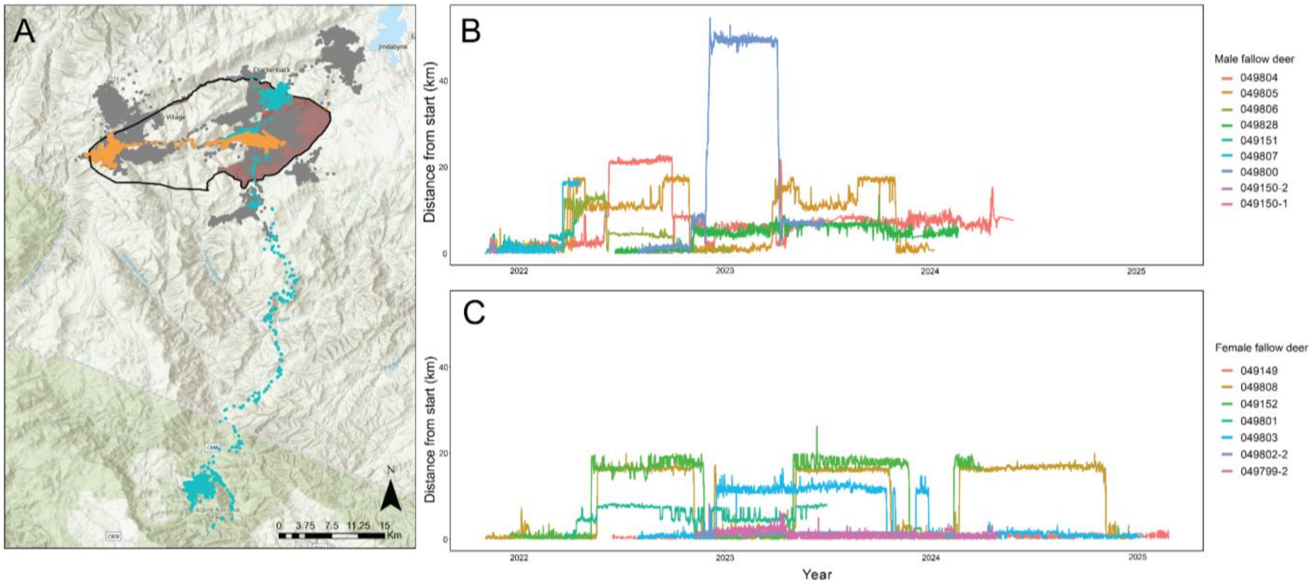

Figure 6.5: (A) Movements of the 16 collared fallow deer (*Dama dama*; grey), originally collared in the study area in southern Kosciuszko National Park. Male deer with ID: 049800 had the highest maximum displacement from its starting position overall (locations path shown in blue), female deer with ID: 049152 had the highest maximum displacement from its starting position for a female (locations shown in orange). (B) shows net displacement over time for collared male deer (*N* = 9), and (C) shows net displacement over time for collared female deer (*N* = 7).

6.5 Discussion

This study examined the effects of extensive culling on an invasive deer population in south-eastern Australia, via investigating changes to connectivity, diversity and movement potential of populations throughout the region. Following the onset of culling, there was limited change in sMLH, F_{IS} and population structure over time. However, in year 2 of culling, we saw an increase in effective population size and variance in heterozygosity of deer sampled within the study area, consistent with the hypothesis that, following removal of deer from the study area, new individuals repopulated promptly from adjacent areas. Supporting this interpretation, we found that deer exhibited large movement ranges and moved between the study area and external populations. Below we discuss the implications of our findings and make recommendations for invasive deer management and control.

We found that sustained aerial culling throughout the study area did not cause appreciable changes in UH_E nor F_{IS}, as these remained similar to other populations over time (Tables 2 & 4; Figure S6.1; Table S6.4). Notably however, the increase in the point estimate and variance of N_e in period 2, likely due to the sampling of individuals with higher sMLH in this period, suggests increased genetic diversity in the second year of culling (Figure 6.3 A & C). Increased N_e may prevent any inbreeding depression that could occur because of culling-induced population reductions. Genetic mixing in species of conservation concern has been shown to increase heterozygosity of the recipient population, which in turn, is the strongest predictor of increased population fitness following the intervention (Hoffmann et al., 2021). For example, despite having a low population size, low-latitude killer whales (*Orcinus orca*) maintain higher heterozygosity and effective population size than larger populations at higher latitudes, likely due to sporadic admixture with other populations during migration (Reeves et al., 2025). Therefore, in the present study, higher effective population size from likely admixture with surrounding populations in the second year of culling may be linked to increased population fitness in future generations. However, it is important to acknowledge that in this study, we only saw limited population genetic change in the final monitoring period (Figure 6.3). This may be because the magnitude of the change was low, or it was too soon following the onset of culling to detect a more substantial change in population diversity, as there is a time lag between disturbance events and the genetic response (Gargiulo et al., 2025). Therefore, longer-term monitoring is required to determine whether increases in heterozygosity and effective population size are sustained over time, and whether they lead to changes in other population demographic and health parameters.

Deer in southern and northern Kosciuszko were genetically indistinguishable from those within the study area (Table 6.4; Figure 6.4), likely due to the movement of deer in and out of the study area (Figure 6.5) and genetic connectivity among the populations (Figure S6.2). This observation provides further support for the hypothesis that deer moved into the study area and repopulated following control. A similar study examining culling of feral pigs (*Sus scrofa*) also showed that pigs culled each year were genetically similar. Here, the recovery of the pig population was attributed to pigs moving into the area from nearby genetically similar populations following control (Cowled et al., 2006). In the present study, the finding that deer within the study area are genetically indistinguishable from deer in surrounding populations indicates that the genetic connectivity of deer in this region is more expansive than the study area. Therefore, if control is to drive sustained population and genetic diversity reductions, management should be implemented on a much broader spatial scale.

Knowledge of the natural dispersal potential of the species supports management across spatial scales that align with the species' movement range (described for other invasive deer species in Burgess et al., 2022; Davies et al., 2021; Hill et al., 2023), while also accounting for connectivity between populations. In this study, we observed that at shorter distances, deer relatedness was mediated by the natural movement and migration ranges of the species (Figure S6.3; Table S6.7). The current results from movement data suggest that the yearly dispersal potential of deer within the study area is likely up to 50 km (Figure 6.5). Previous estimates of long-term fallow deer range expansion in their invasive range were much lower and averaged 0.4 km/year in Tasmania, Australia (Cunningham et al., 2022) and 0.8 km/year in New Zealand (Caughley, 1963). The home ranges of the fallow deer tracked in this study have also been larger than previously recorded estimates from the USA and Europe (see Chapter 3), and so, fallow deer in this study apparently have much higher dispersal potential than the species in their other ranges. For the study area, our data support the recommendation introduced above, that management should be implemented at a broader scale, reflecting an updated understanding on the movement potential of the species.

The distances between some closely related individuals far exceeded yearly dispersal distances of fallow deer (Figure 6.5; Figure 6.4; Table 6.4; Figure S6.3). For example, some individuals were genetically similar despite being separated by large distances of up to ~275 km (Bullatale to Cabramurra) and ~375 km (Lachlan Valley to Cabramurra). Given that these patterns do not follow natural patterns of dispersal (Figure 6.5; Figure S6.3), where relatedness is expected to decrease with increasing geographic distance (Wright, 1943), human-mediated dispersal may be occurring. Human-mediated dispersal may occur either for the purpose of stocking areas for hunting (Frantz et al., 2006; Spencer & Hampton, 2005), or from farming, where animals were translocated and then released either intentionally or accidentally (Tabak et al., 2017). Population supplementation can facilitate admixture and thus increase genetic diversity, and can result in more rapid increases in range size (Wagner et al., 2017; Wilson et al., 2009). A simulation study of fallow deer in Australia showed that high-diversity individuals entering an inbred population would likely lead to increased rates of population growth for that recipient population (White et al., 2024). We recommend assembling a more comprehensive sample set and evaluating genetic connectivity across southeastern NSW to confirm potential translocation sites, as translocations may provide unintended advantages for invasive deer and undermine control efforts. Additional samples collected systematically across NSW could also be used to conduct more detailed spatial autocorrelation analyses for a more complete understanding of dispersal at large distances.

6.5.1 Conclusion and management implications

This study integrated genetic and movement data to investigate the effects of extensive culling operations in alpine southeastern Australia, and examined population diversity and connectivity across a broader geographic range. In year 2 of culling, we found some evidence for an increase in population diversity. This was consistent with our hypothesis that following extensive control, new deer repopulated the area from surrounding areas. Consistent with this hypothesis, movement data showed that deer had the potential to move outside of the study area, and that there was movement between the study area and external populations. However, we could not confirm whether deer from outside of the study area were moving in following control, as the genetic structure of deer in the study area population and external populations was indistinguishable. Our findings also show that the natural and unnatural movement of individuals between populations can maintain genetic connectivity, underscoring the need to consider connectivity between populations, as even limited dispersal can increase genetic diversity and the overall health of populations. For appreciable changes in population size, which may be reflected in the genetic composition of a population, we recommend expanding control over a larger area, informed by connectivity between local populations, and the dispersal potential of the species.

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6.8 Supplementary Material

Table S6.1: Fallow deer tissue sample distribution of the 155 samples collected across NSW and the ACT (excluding duplicates). Samples were collected external to the study area opportunistically and as part of ongoing culling operations.

Location	***N* samples**	**Location details**
Northern Kosciuszko	21	North of the Alpine Way, a major road defining the northern boundary of the study area, up to 16 km from the study area boundary.
Southern Kosciuszko	53	South of the Alpine way, up to 25 km from the study area boundary.
Cabramurra	2	Within 13 km of Cabramurra, NSW.
Tinderry	11	Within 11 km of the boundary of Tinderry Nature Reserve, NSW.
Googong	11	Within 1 km of the town of Googong, NSW.
Bullen Range	13	Within 2 km of Bullen Range Nature Reserve, ACT.
Belconnen	24	In Woodstock Nature Reserve and Lower Molonglo Nature Reserve, within 5 km of Belconnen, ACT.
Lachlan Valley	2	Within Lachlan Valley National Park, NSW.
Yanga Lake	10	Within Yanga Lake National Park, NSW.
Bullatale	8	Within Murray Valley National Park, NSW.

Table S6.2: Error rates between intra-plate (*N* = 12) and inter-plate (*N* = 5) technical replicates for DArTseq of fallow deer (total number of loci = 3,869). Error rates were calculated prior to stringent filtering (see Methods).

Sample ID	Population	Type	Called Loci	Error rate (%)
AQ7388766	private	Inter	3802	7.50
AQ7399043	private	Intra	3758	1.33
AR7233189	private	Inter	3860	1.17
AR7307100	private	Inter	3854	1.06
AR7311752	private	Intra	3767	1.01
AR7306583	National Park	Inter	3864	0.88
AR7311722	private	Intra	3834	0.83
AR7311710	private	Intra	3856	0.67
AR7260397	Northern Kosciuszko	Intra	3853	0.55
AR7236008	private	Intra	3857	0.41
AR7072336	Southern Kosciuszko	Inter	3864	0.41
AR7260332	Northern Kosciuszko	Intra	3863	0.39
AR7318470	National Park	Intra	3869	0.36
AR7236042	private	Intra	3869	0.28
AR7318403	National Park	Intra	3853	0.26
AQ7388759	National Park	Intra	3869	0.21
AR7311749	National Park	Intra	3867	0.21

Table S6.3: Evanno table for all fallow deer sampled in the study area (*N* = 94; 2168 polymorphic loci), from populations National Park and private, collected before the onset of culling in February 2022. Shows that the best fit for the number of populations was k = 2.

k	reps	mean.ln.k	sd.ln.k	ln.pk	ln.ppk	delta.k
1	3	-198363.5	4.5	NA	NA	NA
2	3	-198074.2	8.0	289.3	538.2	67.0
3	3	-198323.1	21.5	-248.9	47.4	2.2
4	3	-198524.5	68.1	-201.5	28.1	0.4
5	3	-198754.1	61.7	-229.6	NA	NA

Table S6.4: Results from linear models evaluating changes in standardised multilocus heterozygosity (sMLH) and mean kinship over year-long periods before (-1 and 1), and after (1 and 2) the onset of shooting. The reference level for the period is '-1'.

Model (*N* = observations)	Variable	Estimate	Standard error	t value	p value
Standardised multilocus heterozygosity (sMLH; *N* = 244)	(Intercept)	1.009	0.008	129.245	< 0.001
	Period 0	-0.028	0.013	-2.089	**0.038**
	Period 1	-0.011	0.011	-1.082	0.280
	Period 2	-0.011	0.010	-0.987	0.325
Mean kinship (*N* = 244)	(Intercept)	0.028	0.0006	47.084	< 0.001
	Period 0	0.010	0.001	9.979	**< 0.001**
	Period 1	-0.0002	0.001	-0.258	0.797
	Period 2	0.007	0.001	8.662	**< 0.001**

Table S6.5: Additional genetic diversity indices for 244 fallow deer, with 2,230 polymorphic loci, sampled within each year-long period pre-cull ('-1' and '0') and after the onset of culling ('1' and '2') within the study area near to Kosciuszko National Park, NSW.$_1$ Values in parentheses are 95% upper and lower 95% confidence intervals.

Period	**H_O[1]**	**N_e[2] (*N* = 32 for each period)**
-1 (*N* = 62)	0.308 (0.301, 0.316)	153.4 (88.6, 215.9)
0 (*N* = 32)	0.295 (0.288, 0.302)	133.3 (73.7, 176.1)
1 (*N* = 72)	0.303 (0.296, 0.311)	101.6 (63.3, 226.5)
2 (*N* = 78)	0.304 (0.297, 0.311)	214.2 (164.1, 896.8)

1. H_O = observed heterozygosity, 2. N_e = effective population size

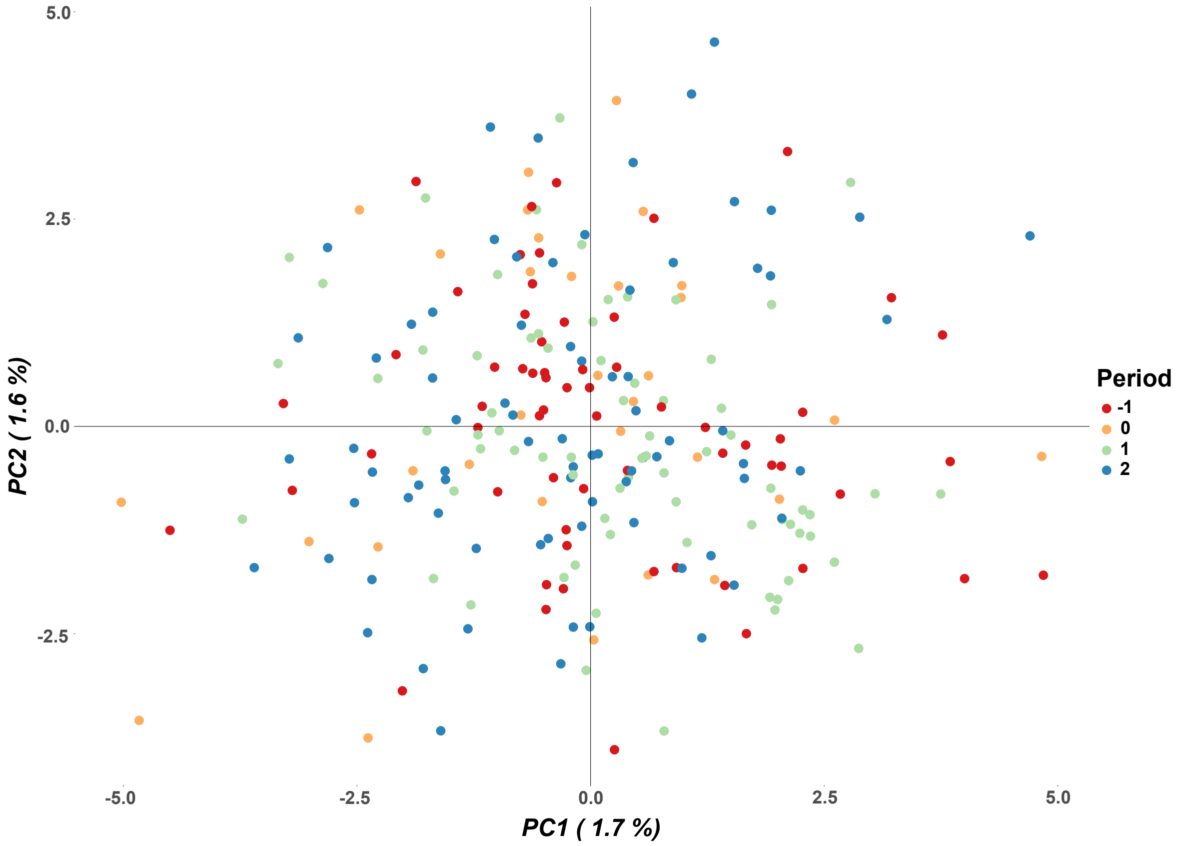


Figure S6.1: Principal coordinate plot showing no genetic differentiation between fallow deer sampled between periods before the onset of culling (periods -1 [$N = 62$] & 0 [$N = 32$]), and after the onset of culling (periods 1 [$N = 72$] & 2 [$N = 78$]), with 2,230 polymorphic loci. Samples were collected from within the study area within and near to Kosciuszko National Park, NSW. PC1 and PC2 explain 1.7% and 1.6% of the total variance, respectively.

Table S6.6: Additional genetic diversity indices for 399 fallow deer, with 2,279 polymorphic loci, sampled across NSW and the ACT. Values in parentheses are 95% upper and lower 95% confidence intervals.

Population	**Ho[1]**
Study area (*N* = 244)	0.297 (0.290, 0.304)
Belconnen (*N* = 24)	0.161 (0.152, 0.168)
Bullatale (*N* = 8)	0.279 (0.269, 0.289)
Bullen Range (*N* = 13)	0.251 (0.242, 0.260)
Cabramurra (*N* = 2)	0.326 (0.312, 0.339)
Googong (*N* = 11)	0.233 (0.224, 0.242)
Lachlan Valley (*N* = 2)	0.332 (0.316, 0.348)
Northern Kosciuszko (*N* = 21)	0.293 (0.285, 0.301)
National Park (*N* = 106)	0.293 (0.286, 0.301)
Private (*N* = 138)	0.300 (0.293, 0.307)
Southern Kosciuszko (*N* = 53)	0.293 (0.285, 0.300)
Tinderry (*N* = 11)	0.263 (0.254, 0.271)
Yanga Lake (*N* = 10)	0.291 (0.281, 0.300)

1. Ho = observed heterozygosity

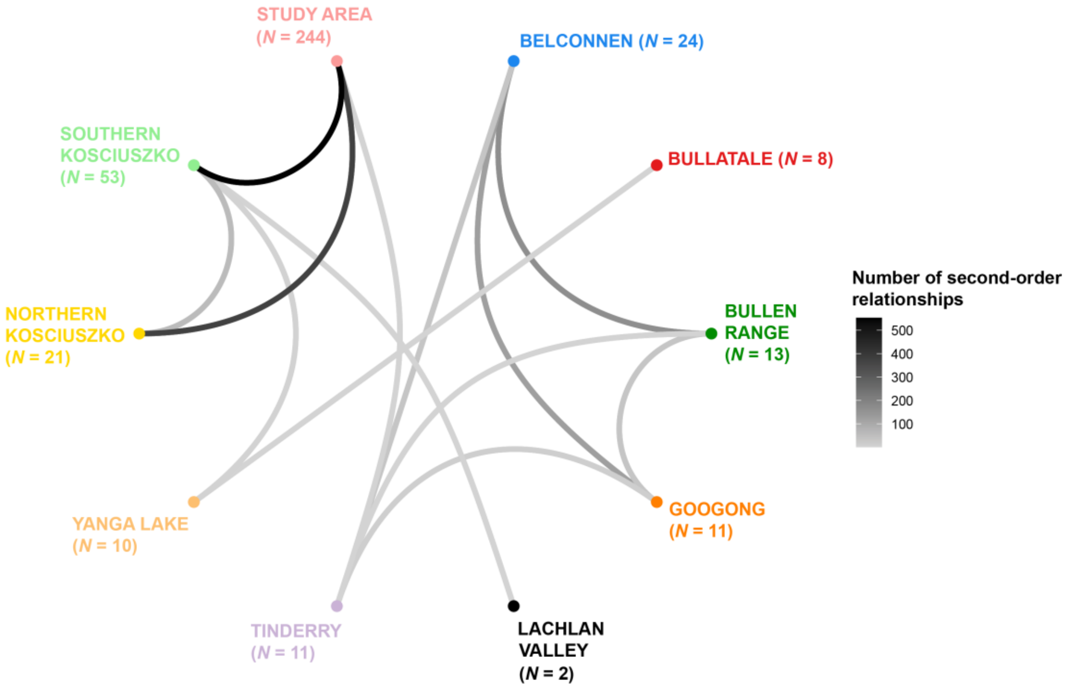


Figure S6.2: Genetic network showing number of second-order relationships detected between 11 populations of 399 fallow deer, with 2,279 polymorphic loci, sampled across NSW and the ACT. Cabramurra is not presented here because there were no second-order relationships detected between samples from Cabramurra and other populations.

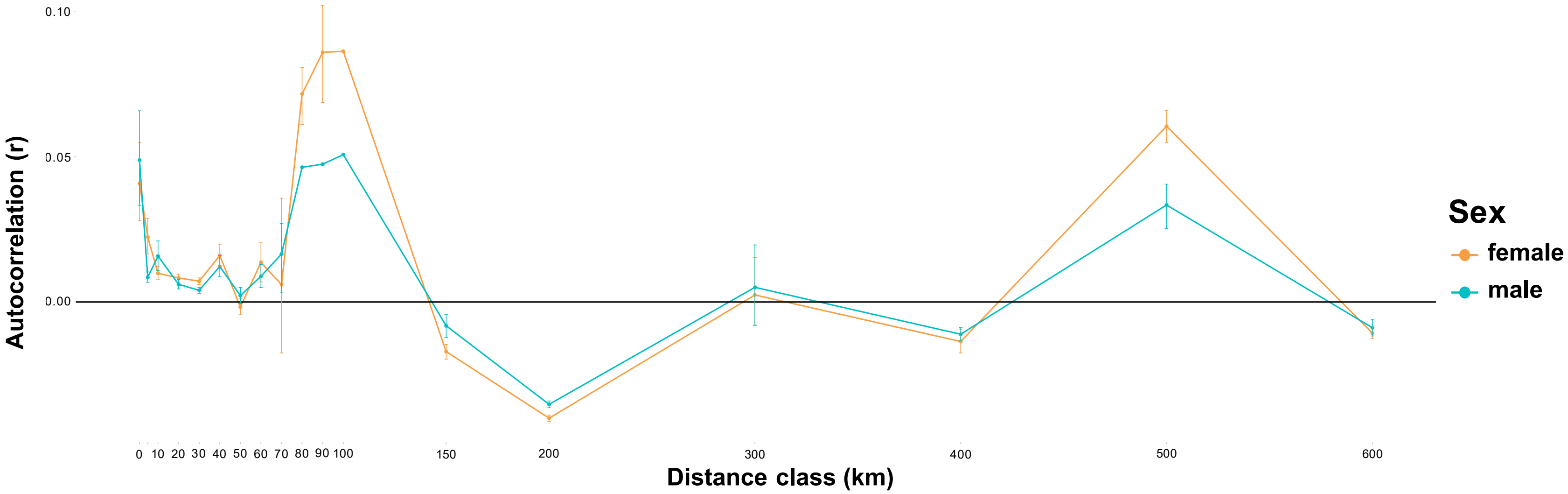


Figure S6.3: Auto-correlogram showing spatial autocorrelation between 286 fallow deer with 2,258 polymorphic loci, sampled in populations in southeastern Australia. Fallow deer males (*N* = 145; blue) and females (*N* = 141; orange) are sampled across 18 distance classes with endpoints between 1 km and 600 km. Error bars show the 95% confidence intervals, estimated via bootstrapping. Spatial autocorrelation analyses showed that for distance classes less than 40 km, both male and female fallow deer were positively autocorrelated. However, this trend tended to decrease with increasing distance class, and at distance class < 50 km, both sexes were not autocorrelated. However, at distance classes between < 60 and < 100 km, males and females were again positively autocorrelated, which exceeds the maximum movement potential for fallow deer. However, at distance class < 70 km, both sexes were not autocorrelated. At distances < 150 km and < 200 km, both sexes were negatively autocorrelated. At < 300 km, neither was autocorrelated. At < 400 km, both were negatively autocorrelated, then positively at < 500 km, and negatively again at < 600 km (Tables S3 & S4). Upper and lower limits for autocorrelation estimates could not be calculated for comparisons at the < 100 km distance class for females (Table S6.8), and the < 80, 90 and 100 km distance classes for males, due to low numbers of individuals for comparisons (Table S6.9).

Table S6.7: Fallow deer first-order relatives (plausible parent-offspring or full siblings) detected between populations within southeastern Australia (N = 399), from 2,279 polymorphic loci using EMIBD9 relatedness estimation. 305 pairs of within-population first-order relatives not shown.

Kinship coefficient	**Populations of relatives**	**Sample IDs**	**Sexes**	**Age classes**	**Distance between samples (km)**
0.317	Belconnen	Fallow-021	male	juvenile	16.5
	Bullen Range	Fallow-019	female	adult	
0.272	Study area	AR7307092	male	adult	4.2
	Southern Kosciuszko	AQ7394725	unknown	unknown	
0.272	Study area	AR7260376	female	adult	28.0
	Southern Kosciuszko	AR7236093	male	adult	
0.262	Study area	AQ7399034	male	adult	15.0
	Southern Kosciuszko	AR7306586	male	yearling	
0.261	Study area	AR7260347	male	adult	36.2
	Northern Kosciuszko	AR7261100	male	yearling	
0.251	Southern Kosciuszko	AR7236088	male	yearling	41.5
	Study area	AR7260312	male	yearling	
0.222	Bullen Range	Fallow-010	unknown	unknown	15.2
	Belconnen	Fallow-021	male	juvenile	
0.207	Bullen Range	Fallow-006	unknown	unknown	14.5
	Belconnen	Fallow-054	female	adult	
0.206	Belconnen	Fallow-032	male	adult	15.2
	Bullen Range	Fallow-006	unknown	unknown	

Table S6.8: Results from spatial autocorrelation analysis for female fallow deer (*N* = 141; 2,258 polymorphic loci) sampled from populations across the NSW and the ACT[1].

Bin	Number of pairwise comparisons (*N*)	U-AcC	Correction	C-AcC	C-AcC LL	C-AcC UL	U-LL for the null hypothesis of no SAc	U-UL for the null hypothesis of no SAc	C-LL for the null hypothesis of no SAc	C-UL for the null hypothesis of no SAc	p-value
1000	312	0.034	0.007	0.041	0.028	0.055	-0.012	0.000	-0.005	0.007	0.00
5000	878	0.015	0.007	0.022	0.017	0.029	-0.010	-0.004	-0.003	0.003	0.00
10000	1277	0.003	0.007	0.010	0.008	0.012	-0.010	-0.004	-0.003	0.003	0.00
20000	1968	0.001	0.007	0.008	0.007	0.010	-0.009	-0.005	-0.002	0.002	0.00
30000	1646	< 0.001	0.007	0.007	0.006	0.008	-0.010	-0.005	-0.002	0.002	0.00
40000	601	0.009	0.007	0.016	0.012	0.020	-0.011	-0.004	-0.003	0.004	0.00
50000	241	-0.009	0.007	-0.002	-0.004	0.001	-0.012	-0.001	-0.005	0.006	0.258
60000	91	0.006	0.007	0.014	0.007	0.020	-0.016	0.003	-0.009	0.010	0.011
70000	7	-0.001	0.007	0.006	-0.018	0.036	-0.036	0.041	-0.029	0.049	0.335
80000	10	0.064	0.007	0.072	0.061	0.081	-0.035	0.029	-0.028	0.036	0.003

90000	14	0.079	0.007	0.086	0.069	0.102	-0.032	0.021	-0.025	0.028	0.002
100000	4	0.079	0.007	0.086	NA	NA	-0.043	0.050	-0.036	0.058	0.02
150000	233	-0.024	0.007	-0.017	-0.020	-0.015	-0.012	-0.002	-0.005	0.005	0.001
200000	1741	-0.047	0.007	-0.040	-0.041	-0.039	-0.009	-0.006	-0.002	0.001	0.00
300000	37	-0.005	0.007	0.002	-0.008	0.015	-0.021	0.008	-0.014	0.015	0.344
400000	118	-0.021	0.007	-0.014	-0.018	-0.009	-0.010	-0.005	-0.003	0.003	0.001
500000	17	0.053	0.007	0.060	0.055	0.066	-0.024	0.011	-0.017	0.018	0.002
600000	601	-0.018	0.007	-0.011	-0.013	-0.009	-0.009	-0.006	-0.002	0.001	0.00

1. AcC = autocorrelation coefficient, U = uncorrected, C = corrected, LL = lower limits, UL = upper limits, Sac = spatial autocorrelation.

Table S6.9: Results from spatial autocorrelation analysis for male fallow deer (*N* = 145; 2,258 polymorphic loci) sampled from populations across the NSW and the ACT[1].

Bin	Number of pairwise comparisons (*N*)	U-AcC	Correction	C-AcC	C-AcC LL	C-AcC UL	U-LL for the null hypothesis of no SAc	U-UL for the null hypothesis of no SAc	C-LL for the null hypothesis of no SAc	C-UL for the null hypothesis of no SAc	p-value
1000	274	0.042	0.007	0.049	0.033	0.066	-0.012	0.000	-0.005	0.007	0.000
5000	1356	0.002	0.007	0.008	0.007	0.010	-0.009	-0.005	-0.002	0.002	0.000
10000	906	0.009	0.007	0.016	0.011	0.021	-0.010	-0.004	-0.003	0.003	0.000
20000	1139	-0.001	0.007	0.006	0.004	0.008	-0.009	-0.005	-0.002	0.002	0.000
30000	2609	-0.003	0.007	0.004	0.003	0.005	-0.009	-0.006	-0.002	0.001	0.000
40000	799	0.005	0.007	0.012	0.009	0.016	-0.010	-0.004	-0.003	0.003	0.000
50000	383	-0.005	0.007	0.002	-0.001	0.005	-0.011	-0.003	-0.004	0.004	0.132
60000	247	0.002	0.007	0.009	0.005	0.013	-0.012	-0.002	-0.005	0.005	0.003
70000	11	0.010	0.007	0.017	0.003	0.027	-0.030	0.026	-0.023	0.033	0.057
80000	5	0.039	0.007	0.046	NA	NA	-0.043	0.025	-0.036	0.032	0.017

90000	3	0.040	0.007	0.047	NA	NA	-0.045	0.043	-0.038	0.050	0.027
100000	5	0.044	0.007	0.051	NA	NA	-0.042	0.025	-0.035	0.032	0.017
150000	150	-0.015	0.007	-0.008	-0.012	-0.004	-0.013	-0.001	-0.006	0.006	0.006
200000	1684	-0.042	0.007	-0.035	-0.036	-0.034	-0.008	-0.006	-0.001	0.001	0.000
300000	35	-0.002	0.007	0.005	-0.008	0.020	-0.022	0.008	-0.015	0.015	0.186
400000	357	-0.018	0.007	-0.011	-0.013	-0.009	-0.009	-0.005	-0.002	0.002	0.000
500000	60	0.026	0.007	0.033	0.025	0.040	-0.017	0.003	-0.011	0.009	0.000
600000	327	-0.016	0.007	-0.009	-0.012	-0.006	-0.009	-0.005	-0.002	0.002	0.000

1. AcC = autocorrelation coefficient, U = uncorrected, C = corrected, LL = lower limits, UL = upper limits, Sac = spatial autocorrelation.

Chapter 7: General Discussion

7.1 Thesis overview

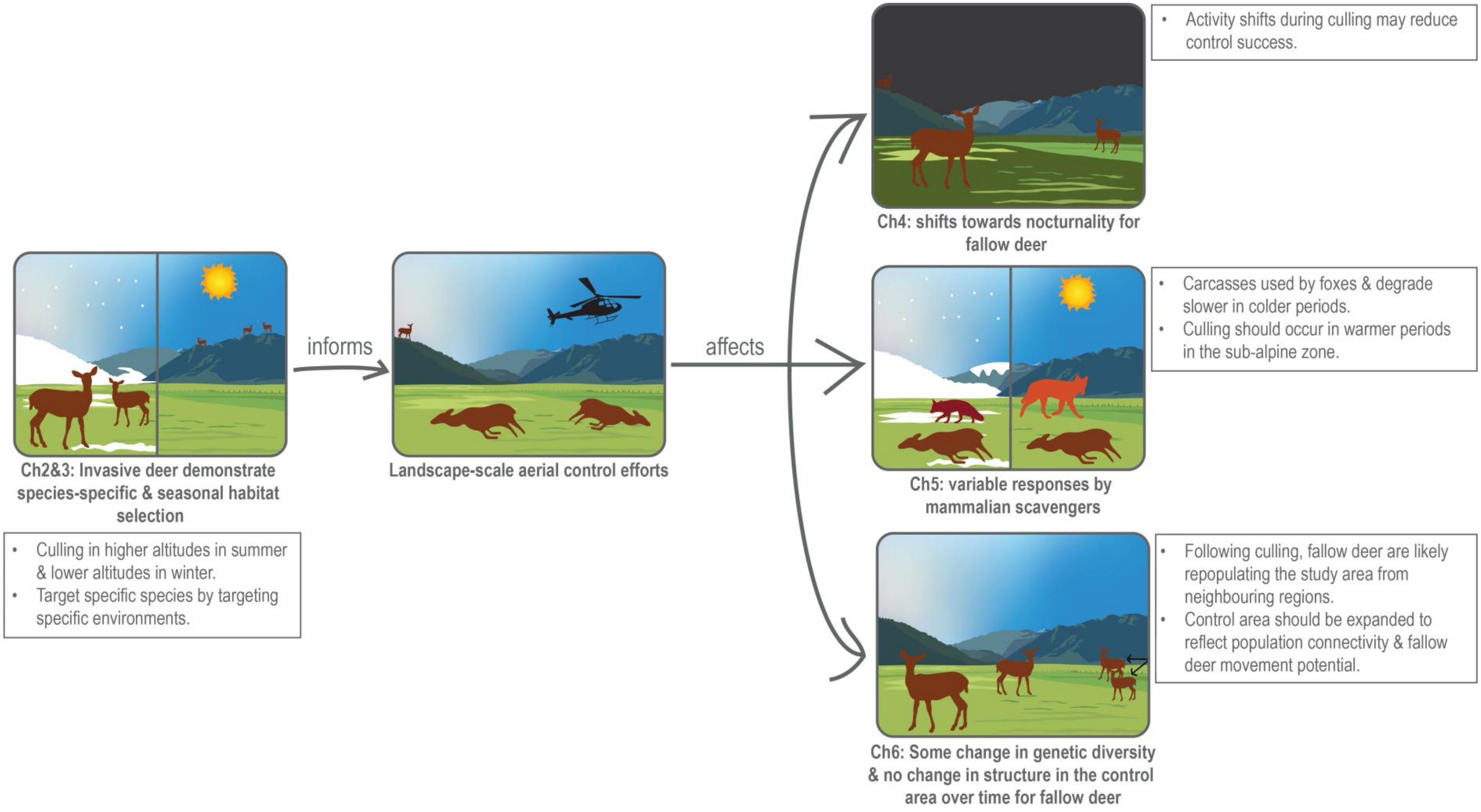
This thesis aimed to establish an understanding of the effects of invasive deer control in the Australian Alps. The data collection and analysis for this project complemented an ongoing extensive aerial control effort of deer in southern Kosciuszko National Park and privately managed land adjacent to the park, predominantly cleared farmland, with the aim of providing findings to aid existing and future control efforts. This thesis explored deer movement and habitat preferences, and how we might learn from these to inform control. I then investigated fallow deer behavioural responses to control, and post-cull, examined scavenger responses, as well as genetic responses of fallow deer (*Dama dama*) (Figure 7.1).

In **Chapter 2**, I assessed the method for capturing sambar deer (*Rusa unicolor*) and red deer (*Cervus elaphus*), via aerial net gunning and chemical immobilisation. I then examined the incidence of mortalities and movement responses of collared animals for 45 days post-collaring. The method was shown to be safe and effective, especially following refinements made to the initial protocol, such as reducing allowable pursuit times, to reduce animal stress. In **Chapter 3**, I tested hypotheses surrounding the movement patterns and habitat preferences of deer in the Australian Alps, an area which has not yet been studied widely. I used tracking data from fallow deer, sambar deer and red deer to characterise their home ranges, seasonal movements, and habitat selection. I found that all three species tended to have larger home ranges than their conspecifics within their native ranges. Fallow deer showed a stronger preference for cleared areas compared to the other two species, potentially posing a greater agricultural risk, through disease transmission and resource competition with livestock. I made recommendations for more effective control based on seasonal and species-specific habitat preferences in the region. For example, all three species exhibited seasonal altitudinal migration, and control should be conducted in accordance with their seasonal movements. Critically, sambar deer selected for burnt areas years after fire and should be targeted for control in these areas.

In the following chapters, I investigated the effects of landscape-scale aerial control triggering mass-mortality events, and how this affected the target species in the short and long term, as well as scavengers in the landscape. In **Chapter 4**, I investigated the effects of aerial culling on overall deer population size, as well as fallow deer behaviour, specifically their movement speed, group size and diel activity patterns during and immediately following an aerial control effort. I found that aerial control did not reduce overall deer density and was not linked to changes in movement speed or group size. Aerial control was however linked to increased activity for dusk and night-time periods, coupled with decreased activity during the day. This suggests that fallow deer may perceive and respond to aerial culling by exhibiting a short-term behavioural adaptation, which should be accounted for when designing aerial control operations.

In **Chapter 5**, I examined the responses of scavengers to mass herbivore culls in the weeks and months post-cull and focused specifically on the two largest mammalian species that scavenged on deer carcasses, red foxes (*Vulpes vulpes*) and dingoes (*Canis dingo*). Foxes and dingoes exhibited different patterns of carcass utilisation, with foxes scavenging on carcasses year-round, including throughout winter, while dingoes scavenged mainly in spring and summer. I found that foxes were less likely to occur and to scavenge on carcasses in areas with high densities of fallow deer carcasses. However, dingoes were more likely to scavenge in areas with high sambar deer carcass densities, but, across the camera array, carcass densities did not affect their occurrence. Foxes and dingoes also exhibited contrasting daily activity patterns and showed temporal separation in their scavenging on carcasses. Nonetheless, neither fox nor dingo carcass use were associated with accelerated biomass loss, instead biomass loss appeared to be driven by warmer temperatures. These findings underscore the importance of conducting aerial control in in warmer months in alpine regions so carcasses persist for shorter periods of time and do not provide a supplemental food source for invasive scavengers in the winter.

In **Chapter 6**, I evaluated longer-term genetic responses of fallow deer to culling, monitoring deer for two years prior to and two years after the commencement of landscape-scale control. In the second year following the commencement of culling, I found some evidence for an increase in population diversity, supporting the hypothesis that following immediate population reductions after control, deer from neighbouring areas moved in and repopulated the area. This hypothesis aligned with movement data, which showed that deer movement ranges extended well beyond the bounds of the study area. These findings emphasise the need to consider population connectivity when determining the scale of population control regimes.



- Culling in higher altitudes in summer & lower altitudes in winter.
- Target specific species by targeting specific environments.

- Activity shifts during culling may reduce control success.

- Carcasses used by foxes & degrade slower in colder periods.
- Culling should occur in warmer periods in the sub-alpine zone.

- Following culling, fallow deer are likely repopulating the study area from neighbouring regions.
- Control area should be expanded to reflect population connectivity & fallow deer movement potential.

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Figure 7.1: Summary of key findings and management implications for each chapter.

7.2 Key management findings and recommendations

7.2.1 Deer readily move between cleared areas and national park

Genetic analyses (Chapter 6) demonstrated that there was no barrier to genetic connectivity for fallow deer between the lower-altitude, predominantly pastoral private land and subalpine Kosciuszko National Park, within the study area. This result corroborates findings from deer movement data (Chapter 3) which showed that fallow deer selectively inhabited cleared areas in autumn, winter, and spring, while exhibiting seasonal altitudinal migration, occupying higher altitudes in summer (predominantly national park) and lower altitudes in winter.

Deer near to a forest pasture interface are known to move between habitats for feeding and disturbance avoidance (Månsson et al., 2021; Menichetti et al., 2019). Fallow deer particularly, have been shown to have high dietary flexibility and adaptability in diverse environments (Esattore et al., 2022). Importantly, deer movement between agricultural land and adjacent national park creates the opportunity for dispersal of plants, including invasive species, between the two zones, and of particular concern would be the movement of plants from the agricultural areas to the national park (Claridge, 2016). Additionally, fallow deer may be vectors of disease to domestic animals and livestock, and in high densities could exert strong competitive pressure on livestock, reducing stock carrying capacity (Davis et al., 2023; Pacioni et al., 2022). This finding further supports the need for cross-tenure and cross-jurisdictional management efforts, targeting invasive deer on pastural land adjacent to national parks, mitigating their ecological and economic impacts.

A supplementary result identified during the analysis of camera array data (Chapter 4) was that there tended to be more detections of female deer compared to male deer for the Interface camera array (closer to farmland), and more detections of male deer compared to female deer for the Big Boggy camera array (higher altitude) (Figure 7.2). This result was fairly consistent between fallow deer and sambar deer, and across all monitoring periods from 2020–2023. This suggests that there may be a higher male:female ratio in the higher altitude subalpine national park, and a higher female:male ratio in the lower altitude predominately cleared montane region of the study area. Sexual segregation may occur because of different priorities for males and females, the predation risk hypothesis predicts that females prioritise avoiding predation and offspring safety, while males prioritise energy intake in anticipation for breeding competition (Crawford et al., 2021). The lower-altitude farmland may be perceived as lower risk by females raising young, perhaps because there are lower numbers of potential predators (dingoes and foxes) due to long-standing lethal baiting (R. Hunt, personal communication, March 5, 2022). Though our understanding of dingo and fox predation on deer is limited, and increases in deer abundances have previously been linked to increases in deer in the scat of both species, it is unclear whether this results from predation or scavenging (Forsyth et al., 2018). In any case, a higher female:male ratio on farmland could lead to a higher rate of population growth with more reproducing females. However, raw numbers of detections reported here do not account for the activity levels of the deer, and may represent many camera triggers by one deer, or a small number of deer. Furthermore, we may expect detections of males to be higher across both arrays given that fallow deer and sambar deer had higher movement rates for some periods throughout the calendar year (Figure S3.1; Figure S3.3). However, given we see higher detections of female fallow deer and sambar deer for the Interface array compared with the Big Boggy array across monitoring periods, I expect that the trend reported here would be consistent even after accounting for differences in movement speeds between the sexes. This additional finding further underscores the importance of control occurring on farmland adjacent to national parks and protected areas, as populations in these areas may have a higher reproductive potential, which could threaten agricultural productivity.

Critically, cross-tenure management efforts coordinated across public and private lands require substantial private landholder support. However, maintaining stakeholder and community support has been identified as one of the five key challenges of long-term invasive mammal management (Mill et al., 2020). Maintaining private landholder participation was a key challenge in the Cross Tenure Feral Deer Management Project. The project relied on cooperation from private landholders in the study area for access to their properties for aerial shooting operations and camera array deployment and servicing. Throughout the life of the project, the project lost support from some landowners, who declined permission for further aerial shooting on their property. As such, less aerial culling could be conducted across private land in the later stages of the project. Where cross-tenure management is important, projects should provide strong evidence that management activities will serve landholder interests, as well as a transparent system for evaluating and reporting on the progress of the project (Hare et al., 2021). Importantly, in Australia, public support for non-lethal management options has been shown to be higher than for lethal management options (van Eeden et al., 2019). Therefore, if landowners are unwilling to have lethal control on their property, wildlife managers could consider private landowner willingness for non-lethal deer damage mitigation measures, such as exclusion fencing (Forsyth, 2023). Culling efforts should have a strong scientific basis, clear benefits for stakeholders, and transparent reporting to promote long-term landholder support.

Figure 7.2: Numbers of fallow deer (top) and sambar deer (bottom) detections for each monitoring period at the Big Boggy and Interface camera arrays, broken down into numbers of adult and yearling males and females.

7.2.2 Culling should occur in summer in the subalpine zone

Findings from movement and scavenging data (Chapters 3 & 5) support the recommendation that in subalpine areas, culling should occur in warmer months. Movement data showed that all three deer species tended to inhabit higher elevations in summer and lower elevations in winter, and for sambar deer, lower elevations in spring compared to summer as well. Therefore, if all three species are more likely to occur in the subalpine zone in warmer seasons, aerial control efforts may remove higher numbers of deer during these periods compared to cooler seasons. Looking at the landscape-scale effects of mass culling in the weeks and months post-cull, I found that deer culled during warmer seasons break down quicker, likely due to warmer temperatures facilitating higher insect activity which accelerates biomass loss (Chapter 5) (Barton & Evans, 2017). Importantly, I found that deer carcasses just before the onset of winter provided a supplemental food source for foxes throughout the winter period (Figure 5.2). Foxes are known to increase scavenging during the winter (De Pelsmaeker et al., 2024; Selva et al., 2005), and so, widespread carcass supplementation just before or during colder seasons may support the growth of fox populations. Additionally, in the Australian Alps, carcass supplementation in cooler periods may support other invasive scavengers, providing a supplemental food source for invasive pigs (*Sus scrofa*) which increase scavenging during cooler periods (Kane, 2020), and enabling overwintering of European wasp nests (Cairncross et al., 2022). Conversely, if deer are culled during warmer seasons, they will breakdown quickly and be available for scavenging by foxes and other invasive scavengers for shorter time periods. Culling deer during warmer seasons in the subalpine zone aligns with deer movements and promotes accelerated carcass breakdown, preventing longer periods of scavenging by foxes and other invasive scavengers. However, it is important to consider the timing of deer birthing in the region, as fallow deer and red deer commonly give birth during the early summer period after a gestational period of ~7.5 months (Tuckwell, 2003), while sambar deer give birth year-round (Dahlan & Dawend, 2013). Therefore, culling before fallow deer and red deer give birth in late spring may balance animal welfare with ecological objectives.

7.2.3 Control should reflect population connectivity

From camera array data I found that during and for the 7 days following aerial culling, deer detections were lower than outside of shooting periods, despite aerial control efforts not achieving a long-term population reduction from aerial thermal survey density estimates and relative activity indices (Chapter 4) (Figure 4.2). I postulated that these decreases were linked to reductions in the number of deer in the study area from aerial shooting, and that subsequent increases in deer detections were due to deer from neighbouring regions moving into the study area. I used population genetic analyses to test this hypothesis (Chapter 6), and found that while population structure did not change as a result of culling, population diversity increased in the second year following the onset of culling (Figure 6.3). This finding was consistent with the hypothesis that new deer repopulated the study area from neighbouring areas following control and suggests that the study and control area was not large enough to reflect the population connectivity of the target species.

At the commencement of the project, the project team did not have information on the movements and genetic connectivity of the three deer species. Therefore, the boundaries of the Cross Tenure Feral Deer Management Project study area were established to include an area in Kosciuszko National Park where fallow deer, sambar deer and red deer were known to co-occur, and to include some private farmland, to aid in the development of strategies for deer control on private land (NSW Department of Planning Industry and Environment, 2021). However, the project did not have adequate information about how large the project area should be, and findings from movement data in this PhD suggest that the project area should have been much larger. In this PhD, I found that overall, the home ranges for all three species were larger than many other previously recorded home ranges from conspecifics in other regions (Chapter 3). Some collared deer also exhibited very long-distance movements (Chapter 6). Notably, there was a sighting of a collared female sambar deer in Green Cape in southeastern New South Wales (NSW) (~170 km from the initial collaring location in southern Kosciuszko National Park). This was likely a sambar deer collared during aerial net gunning and collaring operations in 2021 and 2022, as no other sambar deer collaring has been recorded in Australia, and several collars on female sambar deer stopped transmitting location data before the collar's automatic drop-off date, so the locations of these deer are not known. However, I could not confirm that this was a deer collared by the deer team as the animal did not have any identifying features and the deer could not be captured for identification. Coordinating control over a larger area would likely have reduced the deer population across a larger area and prevented incursions from deer outside of the study area following control.

Previous genetic structure analyses of invasive rusa deer (*Rusa timorensis*) and sambar deer across southeastern Australia (Hill et al., 2023) and at the smaller scale, across the Illawarra region, NSW (Li-Williams et al., 2023), have identified distinct regional genetic variation in these species. This has facilitated the identification of genetic management units so that control can be coordinated across genetically connected areas. Given we now know that fallow deer genetic connectivity extends well beyond the study area (Chapter 6), systematic sampling of individuals at set distances from the study area could provide more detailed information on genetic connectivity among deer in the study area, and in southern and northern Kosciuszko. Additionally, the area between the Kosciuszko region and the Australian Capital Territory (ACT), and south of the study area were not sampled, and sampling of these regions would have facilitated a more complete understanding of the dispersal potential and connectivity of fallow deer in southeastern Australia. More detailed sampling across a larger geographic area would allow researchers to identify the origin of new populations, arising either through natural or human-mediated dispersal, soon after they are detected. Future management efforts could then conduct coordinated control across all genetically connected regions to reduce reinvasion following control, and achieve greater and longer lasting reductions in overall deer density (as suggested by Hill et al., 2023).

7.2.4 Dissemination of research before control commences may increase success of control efforts

Initially, the Cross Tenure Feral Deer Management Project aimed to reduce the deer population within the study area by 70% in the first year of control in 2022 (phase 1). They then aimed to sustain this low population through regular control operations until 2027 and monitor the effects of a severely lowered deer population for the remainder of the project (phase 2). Despite extensive culling efforts, aerial thermal surveys indicated that the population remained relatively stable during phase 1, and in the years following (Chapter 4). The project was unable to demonstrate a maintained decline in deer numbers throughout the project area, and did not commence phase 2. As a result, the project could not fulfill its original goals for phase 2, which were reliant on the 70% population reduction being achieved, and the project ended two years before its originally intended end, in 2025. The original goals of the project post-population knockdown (phase 2) included trialling control techniques to maintain reduced population levels, assessing the ongoing costs of sustaining the population reduction, and assessing agricultural and environmental benefits of deer population reduction (NSW Department of Planning, Industry and Environment, 2021). My PhD commenced seven months before the onset of control, had my PhD commenced sooner, I may have been able to deliver findings from movement and genetic analyses prior to the onset of control that could have informed how control was conducted. For example, I could have informed the project team of the female bias on the Interface camera array and advised that control be prioritised more in this area. From movement data (Chapter 3), I could have advised that control be conducted in the subalpine region during the summer, as more deer were likely to be present in the region. Moreover, insights from movement and genetic analyses (Chapters 3 & 6) could have informed recommendations for expanding the control area. Disseminating these findings sooner may have led to higher numbers of deer being shot and more sustained reductions in numbers of deer in the study area. Critically however, delaying invasive species control while research is undertaken could allow for to increases in target populations and continual environmental degradation, ultimately increasing the magnitude of mitigation required. Therefore, if feasible, I recommend that site-specific research be conducted early enough to inform decision-making prior to the implementation of extensive control actions for landscape-scale invasive species control programs.

7.3 Future directions

7.3.1 Research on sambar deer and red deer responses to control

Fallow deer were the focal species for Chapters 4 and 6, which examined behavioural responses during control and longer-term population genetic responses following control. They were selected because they were the most abundant species in the study area, enabling the most comprehensive analyses. However, future studies could examine behavioural responses of sambar deer and red deer to control. We might expect sambar deer to be more predator averse, as they may have had more recent exposure to large predators in their native range (Bhattarai & Kindlmann, 2018), and therefore have a stronger antipredator response to control. Previous research on sambar deer abundance throughout control has shown that during and after ground shooting operations, sambar deer abundance lowers initially, but increases again soon after the cessation of culling (Bennett et al., 2015). This may suggest that sambar deer in the present project were deterred from the site during culling and shifted their movement ranges. Alternatively, the perceived population reduction may have been due to actual numbers of deer killed and increases in deer numbers following control was due to new deer moving into the area (Chapter 6). Previous research on red deer movement responses to ground shooting showed that time spent outside of home range increases, and red deer are more likely to use areas with high tree density and canopy cover during the hunting season (Meisingset et al., 2022). Importantly, the responses of sambar deer and red deer to aerial shooting have not yet been studied, findings from this research may aid in planning for future control efforts.

In the longer term, examining the genetic responses of sambar deer and red deer to culling operations may provide alternative insights into the effect of culling on invasive deer, as these species were present in lower abundances in the study area. We may expect that sambar deer, which have similarly large home ranges to fallow deer exhibit similar responses to fallow deer, and soon after control, new deer from surrounding areas move in and repopulate the study area. However, if sambar deer have lower abundances than fallow deer throughout the region, we may expect that they also have lower overall genetic diversity than fallow deer, and so, we may not see the same increase in genetic diversity in the study area in the years following control. Conversely, red deer are in the lowest abundance in the study area and have the smallest home ranges (Chapter 3). Therefore, red deer might be more likely to experience a population bottleneck following control. Historically, habitat fragmentation and hunting pressure has led to a loss of genetic diversity and genetic drift in native Scandinavian red deer populations

(Haanes et al., 2011; Rosvold et al., 2012). Recent culling of genetically isolated sitka black-tailed deer (*Odocoileus hemionus sitkensis*) within the Haida Gwaii archipelago has led to a loss of within-island genetic variation and an increase in between-island genetic differentiation (Burgess et al., 2022). For red deer in Kosciuszko National Park, which are range restricted and likely also genetically isolated, we might expect similar findings.

7.3.2 Consider longer term monitoring of target population and wider ecological responses to control

Short-term monitoring of fallow deer behavioural responses to control revealed shifts in their diel activity patterns during aerial control operations (Chapter 4). However, long-term behavioural shifts may also occur following widespread control. For example, anthropogenic disruption of social structures during culling of African elephants (*Loxodonta africana*) was linked to decreased social familiarity decades after the cessation of culling (Shannon et al., 2013). Culling European badgers (*Meles meles*) to prevent bovine tuberculosis increased their short-term movement ranges, likely leading to disease transmission across larger areas in the longer-term, due to direct contact between greater numbers of individuals and social stress-induced immunosuppression (Riordan et al., 2011). For deer in our study area, it is not known how the relatively short-term changes in diel activity and population diversity will go on to affect changes in the deer population in the long term.

Long-term post-control monitoring can also help identify any effects of culling on broader ecosystem health. In the present study, while dingo and fox abundances did not appear to increase with carcass supplementation after the onset of culling, carcasses may have affected the abundances and distributions of other scavenger species, and nutrient recycling from carcasses into soil may have affected changes in plant health and species composition (Quaggiotto et al., 2019). A global review of studies evaluating the ecological recovery following invasive species removal found positive or mixed outcomes for the majority of studies, but for 31% of studies, removal led to negative ecological outcomes, or ecological recovery did not occur (Prior et al. 2018). Control programs can fail to predict and manage unintended outcomes for native species and whole ecosystems occurring as a direct or indirect result of the invasive species decline (Kopf et al. 2017). Importantly, invasive species control can disrupt food webs. This may occur, for example, because an invasive species functions as a prey species for an invasive predator, and when the invasive species is suppressed, the predator switches prey to a native species (Lurgi et al. 2018; Cliff et al. 2020). Control of invasive species may also have unintended negative consequences for native species which rely on habitat provided by invasive species for their survival, as is the case for the endangered California clapper rail (*Rallus longirostris obsoletus*), which nests in invasive hybrid

Spartina, and whose population declined following Spartina control (Lampert et al. 2014). Therefore, it is important that invasive species control programmes undergo long-term ecosystem impact assessments after their implementation (Kopf et al. 2017).

7.3.3 Determine culling targets for effective population knockdown

Future culling efforts should be informed by modelling of deer population dynamics to determine the amount of culling required to achieve reductions in population size. From age at first reproduction, and annual fecundity, the annual population growth rates for fallow deer and sambar deer have been predicted to be 0.45 (95% credible intervals [CI]: 0.13–1.18) for fallow deer, and 0.55 (0.16–1.43) for sambar deer (Hone et al., 2010). Then, the estimated annual proportion of animals to remove to stop population growth has been shown to be 0.34 (0.12–0.69) for fallow deer, and 0.4 (0.14–0.76) for sambar deer (Hone et al., 2010). Aerial survey density estimates and relative abundance indices strongly suggest that the culling effort described in the present study was not able to remove the annual proportion of animals required to stop population growth. To achieve a sustained reduction in population size, proportions of animals culled in the population would have needed to exceed these values.

In addition to breeding biology, population dynamics models integrating species sociality and rates of immigration and emigration, can provide us with population size predictions under different culling effort scenarios and should be used to inform future culling efforts. In Tasmania, a population model has been developed to predict future state-wide invasion patterns for fallow deer under different culling and habitat suitability scenarios (Botterill-James et al., 2024). Modelling of culling scenarios also allows for adjustment of the sex ratio of animals removed from the environment. Modelling of different population reduction scenarios for chital deer (*Axis axis*) in Hawai'i revealed that selective removal of males was not just inefficient, but also counterproductive to reaching population reduction goals (Hess & Judge, 2021). The Deer Population Projection Tool, a web tool developed to determine appropriate cull targets for deer in Scotland, accounts for current population size, numbers of deer culled, survival probabilities, fecundity, and sex ratios to project deer population size and density in an area of interest for up to 5 years (Sutherland et al., 2025). However, this model assumes a closed population and does not account for deer movement into the area following culling and may overestimate population reductions from culling (Sutherland et al., 2025). Additionally, population genetic modelling conducted alongside population size modelling could elucidate whether declines in population size were sufficient to drive concurrent decreases in genetic diversity and viability. For example, culling of reindeer (*Rangifer tarandus*) to handle the spread of chronic wasting disease under different harvest scenarios allowed researchers to determine which demographic to focus culling efforts on to achieve the target population reduction, whilst minimising a reduction in effective population size (Kvalnes et al., 2024). Importantly, combining spatial and genetic analyses allows researchers to determine how landscape features affect gene flow, enabling the development of spatially explicit strategies for maximally efficient and humane control operations (similar to Li-Williams et al., 2023). Future control efforts should incorporate population modelling, informed by species biology, sociality, movement rates and spatial data, to determine annual cull targets needed to achieve population suppression goals.

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