

Managing Interacting Invasive Predators for Biodiversity Conservation

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Abstract

Invasive predators are a major driver of global biodiversity loss. Accordingly, lethal invasive predator control is a common conservation strategy. However, despite usually being faced with multiple invasive predators, managers often implement targeted control of one species at a time due to feasibility constraints. There is concern that singular invasive predator control leads to a ‘mesopredator release’ of subordinate predators, through relaxation via direct top-down pressure and indirect competition. An invasive mesopredators release could dampen or even worsen conservation outcomes. While intuitive, evidence for mesopredator release is weak due to a lack of robust experimental designs and replication, as well as reliance on activity indices.

In this thesis, I investigated whether the lethal control of an apex invasive predator (red fox *Vulpes vulpes*) has led to a mesopredator release of a widespread subordinate invasive predator (feral cat *Felis catus*). I replicated field experiments and collated additional camera-trapping data across two regions with a simple predator guild comprising the introduced red fox and feral cat, allowing sharp focus on interactions between these species. Glenelg region with long-term fox control, Control-Impact with three replicates. Otway Ranges, BACIPS. I quantified impacts of fox control on two threatened native marsupials and assessed evidence for a mesopredator release of feral cats using multiple population metrics: site occurrence, spatiotemporal behaviour and population density.

Fox occurrence strongly declined across the gradient of 1080 poison-bait density; the maximum of 20 baits deployed in a foxes home range reduced fox occurrence by 70% consistently across both regions. However, this had basically no impact on southern brown bandicoot *Isoodon obesulus* occurrence. Long-nosed potoroo *Potorous tridactylus* occurrence increased with long-term fox-bait density in the Glenelg region, but decreased slightly in the Otway Ranges where fox control had recently commenced. Rather than being limited by foxes, habitat suitability for these threatened mammals was more strongly driven by an interaction between vegetation type and time since fire. However, not only do optimal fire regimes vary across species, but they can be entirely conflicting for the same species across different vegetation communities.

At a landscape scale (mean size: 169 km²), lethal fox control was associated with a range of responses from a negligible to 3.7-fold increase in feral cat density. Consistent with the mesopredator release hypothesis, the degree of increase corresponded

with variation in the duration and intensity of fox suppression. At a fine spatial scale (200 m), feral cat density had a consistent negative association with fox occurrence across both regions. Individual cat detectability and movement also varied across the (artificially manipulated) fox occurrence gradient. Using a larger dataset without individual identification, I saw no evidence that foxes impacted the occurrence of cats, in fact, these predators were more likely to co-occur than not in the Glenelg region. Instead, feral cats seemed to avoid foxes by shifting diel activity patterns. Where foxes are nocturnal in the Glenelg region dry vegetation types of the Otway Ranges, cats became more active during the day where fox activity was highest. In the wet vegetation types of the Otway Ranges where foxes were active consistently throughout the daily cycle; cats concentrated activity around midnight where fox activity was highest.

Another paragraph on the drivers of invasive predator occurrence and diel activity?

My thesis provides replicated, experimental evidence that apex predator suppression is associated with an increase in the density of a mesopredator. Mesopredator release can manifest as changes in both behaviour and density, distorting inference if these processes are not distinguished. Further, joint spatiotemporal models are required to adequately understand predator interactions. I provide an easily implementable, hierarchical generalised additive model framework to investigate spatiotemporal changes in species detections and share information across different contexts. Our results help explain why fox control did not consistently improve southern brown bandicoot and long-nosed potoroo occurrence, suggesting integrated pest management may be necessary to improve conservation outcomes. Until that's feasible, maintaining habitat structure through careful use prescribed fire is a priority.

Declaration

This is to certify that:

- i. the thesis comprises only their original work towards the PhD except where indicated in the preface;
- ii. due acknowledgement has been made in the text to all other material used; and
- iii. the thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Matthew W. Rees, October 2021

Preface

This preface provides a summary of the chapters in this thesis and describes my contribution to them as well as the contributions of my collaborators and supervisors.

This is a thesis with publication and comprises four ‘data’ chapters that present my PhD research (Chapters 2 - 5). Therefore there is some overlap in content and the pronoun ‘we’ is used instead of ‘I’ in recognition of the co-authors’ contributions. The General Introduction provides a brief overview of the relevant literature and outlines the key themes underlying the research, while the Synthesis describes links between the papers and places the research in a broader context.

All research presented in this thesis is predominantly my own work (i.e., I have contributed greater than 50% effort) which I completed for the purpose of this degree. I led the design, collection and collation of data, conducted all statistical analyses and led the writing of each chapter.

I deployed 425 camera-traps in the Glenelg region during 2018 (a control-impact experiment two spatial replicates), and 524 camera-trap deployments (195 unique sites) in a Before-After-Control-Impact Paired series design in the western Otway Ranges annually from 2017 to 2019. I had field assistance from: Shauni Omond, Shayne Neal, Asitha Samarawickrama, Shelley Thompson, Erin Harris, Hannah Kilian, Lani Watson, Mark Dorman, Jack Davis, Carl Roffey, Bruce Edley, Larissa Oliveira Gonçalves, Ben Lake, Chantelle Geissler, Aviya Naccarella, Emily Gronow, Harley England, David Pitts, Annie Hobby, Louise Falls, Thomas McKinnon, Jimmy Downie, Marney Hradsky, Stephanie Samson, Robin Sinclair, Asmaa Alhusainan, Kelly Forrester, Tammana Wadawani, Emily Gregg, Hannah Edwards, Adam Beck, Vishnu Memnon, Sandy Lu, Pia Lentini, Nick Golding, Emily McColl-Gausden, Nina Page, Maggie Campbell-Jones, Kyle Quinn and Jack Dickson. Surveys were conducted under University of Melbourne Animal Ethics Committee approval 1714119 and Victorian Government Department of Environment, Land Water and Planning Research Permit 10008273. I identified species and 133 individual cats from this dataset, with secondary cat identifications by Mark Le Pla and Luke Woodford.

Chapter 2 uses a subset of this dataset; the 2017 camera-trap deployments in the Otway Ranges. For the remaining data chapters, this dataset was used in its entirety and supplemented with the following datasets:

- Chapters 3 and 5 include an additional 1616 camera-trap deployments from the

Glenelg Ark fox control monitoring program (240 unique sites surveyed annually 2013-19) and 1113 from the Otway Ark fox control monitoring program (372 unique sites surveyed annually 2016-18).

- Chapter 4 includes an additional dataset from the Lower Glenelg National Park (serving as a third spatial replicate for the Control-Impact experimental design). Alan Robley designed this camera-trap layout, with Ethan Le Duc, Michael Murrell, Dylan Thomas, Rhys Weber, Chris Johansson, Lachlan Levings and Liz Beever carried out the surveys, with Luke Woodford identifying cats (all from the Victorian Government Department of Environment, Land, Water and Planning).

Publications included as part of this thesis

Chapter 2

MW Rees, JH Pascoe, BA Wintle, M Le Pla, EK Birnbaum, BA Hradsky (2019). Unexpectedly high densities of feral cats in a rugged temperate forest. *Biological Conservation*, **239**, 108287. <https://doi.org/10.1016/j.biocon.2019.108287>

Contributions: M.W.R, B.A.H and J.H.P conceived the ideas and designed the methodology; M.W.R, J.H.P, M.LP, E.K.B and B.A.H collected the data; M.W.R analysed the data with input from B.A.H and B.A.W, and led the writing of the manuscript. All authors contributed critically to the writing.

Analysis: <https://github.com/matt-w-rees/feral-cat-otways-2017-SMR>

Chapter 3

MW Rees, BA Wintle, A Robley, & BA Hradsky (In preparation). XX.

Contributions: M.W.R and B.A.H conceived the ideas; M.W.R and B.A.H collected some of the data; M.W.R analysed the data with input from B.A.H and B.A.W, and led the writing of the manuscript. All authors contributed critically to the writing.

Analysis: <https://github.com/matt-w-rees/occurrence-gams-fox-cat-sbb-lnp>

Chapter 4

MW Rees, JH Pascoe, M Le Pla, A Robley, EK Birnbaum, BA Wintle, & BA Hradsky (In review). Quantifying mesopredator release: lethal control of an invasive apex predator alters feral cat density and detectability.

Contributions: M.W.R, B.A.H, J.H.P, B.A.W and A.R conceived the ideas and designed the methodology; M.W.R, J.H.P, M.LP, E.K.B and B.A.H collected the data; M.W.R analysed the data with input from B.A.H and B.A.W, and led the writing of the

manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Analysis: <https://github.com/matt-w-rees/invasive-mesopredator-release>

Chapter 5

MW Rees, N Golding, BA Wintle, A Robley, & BA Hradsky (*In preparation*). XX.

Contributions: M.W.R and N.G conceived the ideas; M.W.R and B.A.H collected some of the data; M.W.R analysed the data with input from N.G and led the writing of the manuscript. All authors contributed critically to the writing.

Analysis: <https://github.com/matt-w-rees/spatiotemporal-gams-invasive-predator>

Other publications that I have contributed to during my candidature but are not presented in this thesis

M Le Pla, EK Birnbaum, **MW Rees**, BA Hradsky, AR Weeks, A Van Rooyen, JH Pascoe (*In review*). Genetic Sampling and an Activity Index Indicate Contrasting Outcomes of Lethal Control for an Invasive Predator

A Stobo-Wilson, BP Murphy, SM Legge, H Caceres-Escobar, DG Chapple, HM Crawford, SJ Dawson, CR Dickman, TS Doherty, PA Fleming, ST. Garnett, M Gentle, TM Newsome, R Palmer, **MW Rees**, EG Ritchie, J Speed, J Stuart, AF Suarez-Castro, E Thompson, A Tulloch, J Turpin, JCZ Woinarski (*In review*). Counting the bodies: estimating the numbers and spatial variation of Australian reptiles, birds and mammals killed by two invasive mesopredators.

A Stobo-Wilson, BP Murphy, SM Legge, DG Chapple, HM Crawford, SJ Dawson, CR Dickman, TS Doherty, PA Fleming, M Gentle, TM Newsome, R Palmer, **MW Rees**, EG Ritchie, J Speed, J Stuart, E Thompson, J Turpin, JCZ Woinarski (*In review*). Compounding and complementary carnivores: Australian bird species eaten by the introduced European red fox *Vulpes vulpes* and domestic cat *Felis catus*.

A Stobo-Wilson, BP Murphy, SM Legge, DG Chapple, HM Crawford, SJ Dawson, CR Dickman, TS Doherty, PA Fleming, M Gentle, TM Newsome, R Palmer, **MW Rees**, EG Ritchie, J Speed, J Stuart, E Thompson, J Turpin, JCZ Woinarski (2021). Reptiles as food: predation of Australian reptiles by introduced red foxes compounds and complements predation by cats. *Wildlife Research* **48**, 470-480. <https://doi.org/10.1071/WR20194>

A Stobo-Wilson, BP Murphy, HM Crawford, SJ Dawson, CR Dickman, TS Doherty, PA Fleming, M Gentle, SM Legge, TM Newsome, R Palmer, **MW Rees**, EG Ritchie, J Speed, J Stuart, E Thompson, J Turpin, JCZ Woinarski (2021). Sharing meals: Pre-

dation on Australian mammals by the introduced European red fox compounds and complements predation by feral cats. *Biological Conservation* **261** : 109284. <https://doi.org/10.1016/j.biocon.2021.109284>

H Davies, Tiwi Land Rangers, **MW Rees**, D Stokeld, AC Miller, GR Gillespie, BP Murphy (2021). Variation in feral cat density between two large adjacent islands in Australia's monsoon tropics. *Pacific Conservation Biology*. <https://doi.org/10.1071/PC20088>

MW Rees, J Carwardine, A Reeson, and J Firn (2020). Rapidly assessing cobenefits to advance threat-management alliances. *Conservation Biology*, **34**: 843-853. <https://doi.org/10.1111/cobi.13490>

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Chapter 1

General Introduction

"In the absence of large predators, smaller predators can become more abundant (mesopredator release) and, in turn, may cause the local extinction of vulnerable prey species." - Soulé *et al.* (1988).

Against a backdrop of growing evidence that top predators can apply top-down pressure on subordinate predator species, Soulé *et al.* (1988) first coined 'mesopredator release'. Soulé *et al.* (1988) found that where coyotes *Canis latrans* were absent in California, U.S.A, domestic cats *Felis catus* were more prevalent and populations of native birds succumbed to extinction. There have since been many other high profile examples of the mesopredator release across a wide-range of taxa, spanning Europe (Elmhagen & Rushton 2007), Africa (Gorman *et al.* 1998), Australia (Johnson *et al.* 2007) and in many marine systems (Baum & Worm 2009). Grounded in traditional-food web ecological theory, the mesopredator release hypothesis (hereafter 'MRH') is a simple and intuitive hypothesis. So why, 33 years later, does the MRH remain one of the most contentious hypotheses in applied ecology?

Firstly, there is a lack of replicated, robust evidence for the MRH. This is partly because predators are difficult to monitor, particularly with experimental designs. The average predator is cryptic and occurs widely across broad landscapes, at low densities. To obtain sufficient sample sizes for statistical models, a very large area needs to be surveyed intensively (Royle *et al.* 2008). There often aren't similar landscapes without apex predator declines to compare with, at least ones which are spatially independent (e.g. Dexter & Murray 2009). Without robust experimental designs, it is difficult to attribute changes in mesopredator populations to apex predator declines (Hayward *et al.* 2015).

Secondly, the MRH remains a blurry concept because of a reliance on vague population metrics. Top predators may suppress mesopredators through direct killing, resource competition and fear-induced behavioural changes (Ritchie & Johnson 2009). Mesopredator release was originally defined as a numerical increase in abundance, but has since been expanded to include changes in mesopredator distribution and behaviour following apex predator decline (Prugh *et al.* 2009). Many of the North American field studies reviewed by Jachowski *et al.* (2020) provided mixed support for MRH

because different population metrics provided conflicting inference. Jachowski *et al.* (2020) called for clearer separation of spatial, numerical and behavioural processes, which are wrapped together in commonly used “abundance” indices (Stephens *et al.* 2015). It is particularly important to account for changes in detectability because a relaxation of mesopredator behaviour may falsely signal an increase in abundance. There are few examples of mesopredator release which with direct estimates of population density; these studies have mostly used live capture-rates to infer population density, without accounting for behavioural changes which may have made individuals more trappable (e.g. Arjo *et al.* 2007; Karki *et al.* 2007; Thompson & Gese 2007; Berger *et al.* 2008; Jones *et al.* 2008). These traditional survey and statistical methods also have an ill-defined spatial resolution; this is problematic because sampling scale impacts the direction of perceived species interactions (Efford & Dawson 2012; Blanchet *et al.* 2020).

Thirdly, the MRH can be an overly simplistic representation of complex ecosystems. Most evidence for mesopredator release comes from North America and other regions with many co-occurring large carnivores (Ritchie & Johnson 2009). MRH refers to a singular, direct negative association between a dominant predator and a subordinate species, overlooking the complex webs of positive, negative, direct, indirect and probably nonlinear interactions which occur in multipredator systems (Finke & Denno 2004; Johnson *et al.* 2007; Levi & Wilmers 2012; Prugh & Sivy 2020). Additionally, bottom-up processes (i.e., ecosystem productivity and prey availability) can interact with top-down processes to determine the strength of mesopredator release and when/if it occurs at all (Elmhagen & Rushton 2007; Greenville *et al.* 2014). Intensive multispecies monitoring and complex statistical methods are therefore required to disentangle mesopredator release from the background drivers of predator populations, but this has rarely taken place. A simpler alternative is to test the MRH in ecosystems with a predator niche comprised of only two species.

We lack key detail on the conditions which drive the occurrence and strength of mesopredator release which hinders effective conservation management. The functioning of global ecosystems has been degraded by widespread declines in top predators (Heithaus *et al.* 2008; Ripple *et al.* 2014). Managers therefore need to predict outcomes of continued predator declines (Estes *et al.* 2011), as well as improvements (Chapron *et al.* 2014) and reintroductions (Baker *et al.* 2017). While native predators have undergone severe decline in recent times, some predators have spread far beyond their native ranges and become a leading cause of global biodiversity and economic declines (Bellard *et al.* 2016; Doherty *et al.* 2016). Accordingly, lethal control of invasive predators is a prevalent management strategy worldwide. However, when multiple invasive species occur, single invasive species control can often backfire and worsen outcomes for native species (Ballari *et al.* 2016). This is most likely due to release subordinate invasive species (e.g. Rayner *et al.* 2007). A better understanding of the interactions between invasive predators is key to improving conservation outcomes (Zavaleta *et al.* 2001; Doherty & Ritchie 2017).

Debate over the MRH rages in Australia—a continent which has ‘institutionalised’

poisoning predators (Philip 2019). The dingo *Canis familiaris* is Australia's native mammalian apex predator and is widely persecuted, mainly for agricultural benefits (Smith 2015). This is expected to have caused a mesopredator release of the introduced red fox *Vulpes vulpes* (hereafter 'fox') and feral cat *Felis catus* (hereafter 'cat'), in turn contributing to Australia ongoing extinction crisis (Johnson *et al.* 2007; Woinarski *et al.* 2015, 2019; Newsome *et al.* 2017). The MRH considers a predator guild comprising of two species, but what happens following apex predator decline when there are multiple subordinate species? Literature covering the dingo-debate hypothesises both foxes and cats can benefit from dingo decline. Alternative theory predicts an among-carnivore cascade (Levi & Wilmers 2012): in a dingo (~15 kg) - fox (~6 kg) - cat (~4 kg) hierarchy, dingo suppression would benefit foxes, which would in-turn disadvantage cats. Competition between these introduced predators should be high; foxes and cats occupy a similar niche (Glen & Dickman 2005) with high dietary overlap (Stobo-Wilson *et al.* 2021a, b). Although, evidence that foxes exert top-down pressure on cats is unclear (Hunter *et al.* 2018).

Strongest evidence of fox-cat interactions comes from targeted lethal fox control programs in southern parts of Australia where the medium-large carnivore guild comprises entirely of these two predators. Foxes are managed primarily for biodiversity conservation in protected areas, although few programs have demonstrated improvements and several long-term studies have reported perverse outcomes on native biodiversity (Dexter & Murray 2009; Marlow *et al.* 2015; Kinnear *et al.* 2016; Wayne *et al.* 2017; Lindenmayer *et al.* 2018; Duncan *et al.* 2020). A mesopredator release of cats is commonly suspected to be the cause, although, Duncan *et al.* (2020) offers an alternative hypothesis regarding prey overshooting carrying capacities. Indeed, cat activity appears to increase on average following targeted fox control, but this estimate is uncertain (Hunter *et al.* 2018). Notably, Molsher *et al.* (2017) observed no change in the 'abundance' of cats, but observed changes in diet and space use following fox control. No study has directly estimated feral cat density in response to fox control. Distinguishing numerical population change from behavioural changes is a clear priority to improve understanding of fox-cat interactions and mesopredator release in Australia.

My thesis aims to test the MRH using experimental designs replicated across two regions—examining the MRH from several different angles. I firstly investigated whether apex predator control effort was correlated with an increase in the occurrence of a mesopredator (Chapter 3). I secondly estimated direct changes in mesopredator density following apex predator suppression using traditional experimental designs, while accounting for changes in detectability (Chapter 4). I thirdly investigated how apex predators influenced the spatiotemporal behaviour of mesopredator through a 'landscape of fear' (Laundré *et al.* 2001) in Chapter 5. In accordance with the MRH, I hypothesised that top predator control would increase the occurrence, density and alter the behaviour of the mesopredator. These chapters highlight the different ways in which mesopredator release can manifest and how different population metrics provide different inferences on the MRH.

I tested the MRH in simple predator guilds comprising of the introduced fox and

cat. I experimentally surveyed landscapes with and without lethal fox control (1080 poison-baiting). This allowed a sharp focus on the interactions between the two invasive predators—how cats respond to artificial gradients of apex predator activity—as well as the resulting impacts on two threatened native prey species. Much of our current understanding of the basic ecology and impacts of invasive predator in Australia comes from semi-arid and arid regions; my research provides some of the first investigations of population dynamics and interactions within temperate forest ecosystems. My thesis also investigates bottom-up drivers of invasive predator and threatened native mammal occurrence, including the effect of fire across different vegetation communities, rainfall patterns and habitat fragmentation. I hope this research sheds light on optimal methods for surveillance and management of invasive predators for the benefit native species in temperate, heterogeneous landscapes.

Chapter 2

Unexpectedly high densities of feral cats in a rugged temperate forest

Abstract

Effective invasive predator management requires accurate knowledge of population density. However, density can be difficult to estimate for wide-ranging, cryptic and trap-shy species, such as the feral cat *Felis catus*. Consequently, few density estimates exist for this invasive predator of global significance, particularly from rugged, mesic or structurally complex habitats where detection is challenging. In this study, we estimated feral cat density in the wet forests and cool temperate rainforests of the Otway Ranges, south-eastern Australia, to (1) provide a density estimate for this rarely surveyed habitat type, and (2) verify predictions from a continental-scale model of feral cat density. We deployed 140 camera traps across two independent 49 km² grids and identified individual feral cats based on unique pelage markings. Using spatially explicit mark-resight models, we estimated that there were 1.14 cats km⁻² (95% CI: 0.88 – 1.47). This is more than three times the average cat density in natural environments across Australia, and at least five times higher than model-based predictions for the Otway Ranges. Such high densities of feral cats likely reflect the abundance of small native mammals and lack of apex predators in our study area. Our findings contradict the widespread assumption that feral cats occur at very low densities in mesic and rugged habitats. Underestimating the density of feral cats in these environments has significant implications for pest animal management and biodiversity conservation.

2.1 Introduction

Accurate estimates of the distribution and abundance of invasive predators are essential to determine ecosystem impacts, inform effective management and target control efforts. However, this information is difficult to obtain as predators are often cryptic, trap-shy and occur at low densities (Royle *et al.* 2008). A prominent example is the feral cat *Felis catus*, which is implicated in the extinction or decline of 430 species globally (Doherty *et al.* 2017). A better understanding of feral cat density has been highlighted as a priority for effective management of both this species and its threatened native prey (Woinarski *et al.* 2014; Legge *et al.* 2017; Moseby *et al.* 2019).

Legge *et al.* (2017) developed a continental-scale model of feral cat density for Australia which has had considerable implications for feral cat research and management. For instance, the model has been used to estimate the number of birds, reptiles and mammals killed annually across Australia by feral cats (Woinarski *et al.* 2017, 2018; Murphy *et al.* 2019). As the model estimated that there were considerably fewer feral cats in Australia than previously expected, it also casts doubt on the feasibility of Australian Federal Government's plan to cull two million feral cats between 2015 and 2020 (Doherty *et al.* 2019). Given the importance of feral cat density estimates for policy, planning and management, it is vital to verify and refine the model's predictions.

The underlying data used by Legge *et al.* (2017) had several limitations, including that feral cat density estimates were not available for any wetland, mangrove, dense heath or rainforest environments in Australia (Legge *et al.* 2017). This likely reflects the difficulty of access and ineffectiveness of traditional feral cat monitoring methods (track counts and spotlight counts) in these structurally complex habitats (Denny & Dickman 2010). Legge *et al.* (2017) highlighted the need for more site-based density surveys, particularly in these under-studied environments. Further, nearly all of the density estimates collated by Legge *et al.* (2017) were based on studies that did not identify individual cats or account for imperfect detection (i.e. the possibility that some individuals were not detected). Such methods can be unreliable when inferring across sites, times, ecological contexts and different detection methods (Edwards *et al.* 2000; Hayward *et al.* 2015), particularly for species such as cats whose densities may fluctuate substantially over time in some regions (Legge *et al.* 2017). Concurrent surveys of cats on Kangaroo Island and the adjacent Australian mainland suggests that the Legge *et al.* (2017) model may substantially underestimate this variation in density (Taggart *et al.* 2019).

Robust population density estimates for cryptic and wide-ranging species based on individual identification are now more feasible due to recent advances in technology and statistical models. Camera-traps that sense temperature-in-motion provide an efficient survey approach across diverse environments and are particularly beneficial for studies of trap-shy species with unique markings, such as feral cats (Bengsen *et al.* 2011). Concurrently, spatial mark-resight (SMR) models, an extension of spatial capture-recapture models, enable population density estimates when a portion of the population can be individually identified (Royle *et al.* 2013). These models consider

both the distribution and movement of individuals across the landscape in relation to the placement of detectors, and account for imperfect detection (Royle *et al.* 2013). The combination of camera-trap surveys to identify individuals and spatial capture-recapture methods to estimate density has shown promise for both feral and domestic cats (McGregor *et al.* 2015; Jiménez *et al.* 2017; Robley *et al.* 2017, 2018; Cove *et al.* 2018).

The small number of studies that have estimated feral cat density in the mesic regions of south-eastern Australia indicate that these habitats support few feral cats relative to other regions (Legge *et al.* 2017). However, survey effort for feral cats in these environments has been low compared to more arid regions. Our study therefore aimed to provide: (1) a density estimate for a rarely surveyed environment – a matrix of wet forest and cool temperate rainforest, and (2) an independent verification of the prediction from the Legge *et al.* (2017) continental-scale model of feral cat density for the Otway region. To achieve these aims, we undertook a camera-trap survey over 8,230 trap nights at 140 sites in the Otway Ranges, south-eastern Australia. We derived feral cat density estimates by applying SMR analysis to our camera survey data.

2.2 Methods

2.2.1 Study area

Our study was conducted in the Great Otway National Park and Otway Forest Park, Victoria, Australia (38.42°S , 142.24°E). The locality is 90 – 440 m a.s.l. and has a cool-temperate climate: maximum daily temperatures average 19.3°C in summer and 9.5°C in winter; annual rainfall averages 1955 mm (Bureau of Meteorology 2021). The vegetation is a mosaic of old-growth shrubby wet forest, wet forest and cool temperate rainforest, with an overstorey of tall eucalyptus spp. (primarily *Eucalyptus regnans*), *Acacia melanoxylon* and *Nothofagus cunninghamii*, and a midstorey dominated by tree ferns, *Acacia verticillata*, *Pomaderris aspera* and *Olearia argophylla*. The understorey predominantly comprises a dense layer of ferns and graminoids, but is relatively open in steep gullies. The terrestrial predator guild is depauperate, with the introduced red fox *Vulpes vulpes* being the only other significant competitor of feral cats. Our camera survey and other live-trapping surveys indicate an abundance of small native mammals within the study region, particularly native rats and antechinus (Banikos 2018).

2.2.2 Study design

We deployed camera traps in two grids, each approximately 49 km^2 and separated by more than five kilometres (Fig. 2.1). The northern grid comprised 67 survey sites, spaced an average of 526 m apart (86 – 848 m). The southern grid comprised 73 survey sites, spaced an average of 547 m apart (352 – 719 m). We deployed a Reconyx Hyperfire HC600 survey camera, with infrared flash and temperature-in-motion detector (Reconyx, Holmen, Wisconsin), at each site. Cameras functioned for 37 – 68 days (mean 59) from 26 June to 2 September 2017, totalling 8230 trap nights. Each camera was placed on a tree approximately 30 cm above the ground and faced towards a lure 2 – 2.5 m away. Vegetation in the camera's line of sight was cleared to prevent false triggers. The lure comprised an oil-absorbing cloth doused in tuna oil and placed inside a PVC pipe container with a mesh top. Ten to 30 small white feathers were also attached to the outside of the PVC pipe container. Each lure was fastened near the top of a one-metre wooden stake. Cameras took five immediately consecutive photographs when triggered, with no quiet period between trigger events.

2.2.3 Individual cat identification

Images of feral cats were first grouped as marked or unmarked (black) individuals. Although some black cats had small white neck/chest coat splotches, these were not always visible (cats often moved with their heads down), and so all black cats were considered unmarked to avoid double-counting. The marked portion were tabby cats with naturally unique coat markings. These were further classified into distinct groups: stripes & spots, thick swirls, other markings (ginger, distinctive breeds etc.)

and unknown (due to poor image quality). At least two independent observers identified individual cats from these groups based on matches in unique markings, predominantly on the front legs, torso and across both flanks. Observers collated folders of images of unique individuals for reference. Discrepancies between observers were reviewed together until consensus was reached. If no consensus was reached, the marked cat was considered unidentifiable.

2.2.4 Estimating population density

We used conventional SMR models for an unknown number of marked individuals (sighting-only) to estimate feral cat density. These models assume that uniquely marked cats are a random sample of the population, with the same movement ecology as unmarked cats. We fitted models using the ‘secr’ R-package (v. 3.2.1; Efford 2021) in R (v. 3.5.2; R Core Team 2020), as per Efford & Hunter (2018).

Capture histories were collapsed into 24-h occasions, beginning at midday each day (as this was the time of day with the lowest observed cat activity). We used a 3500 m buffer around the outermost coordinates of the trapping grids to ensure density was estimated over an area large enough to include the activity centres of all cats potentially exposed to our survey (Royle *et al.* 2013); this distance is larger than the estimated average maximum width of home ranges of large, male cats close to this region ($n = 3$; B.A. Hradsky, unpublished data).

In SMR models, detectability is defined by two parameters: g_0 , the probability of detecting an animal (per occasion) if a detector was to be placed in the part of its home range where most time is spent, and sigma, a spatial scale parameter relating to home range size. Animals are assumed to have approximately circular home ranges, with the probability of detection declining with distance from the home range centre. We tested three shapes of this decline in detection probability: half-normal, hazard-rate, and exponential, and used the detector function with the lowest Akaike’s Information Criterion adjusted for small sample size (AICc; Burnham & Anderson 2004) for subsequent model fitting.

As the lures may have decreased in potency over the sampling session, we tested for a linear trend in g_0 over time. We also tested whether density differed between the two grids, with and without a linear time trend. We compared these models to the null model (where detection and density were kept constant across both grids) using AICc. Overdispersal in the unmarked sightings was adjusted for as per Efford & Hunter (2018) and a spatial resolution of 0.6 of the sigma estimate was used for all models (Efford 2021).

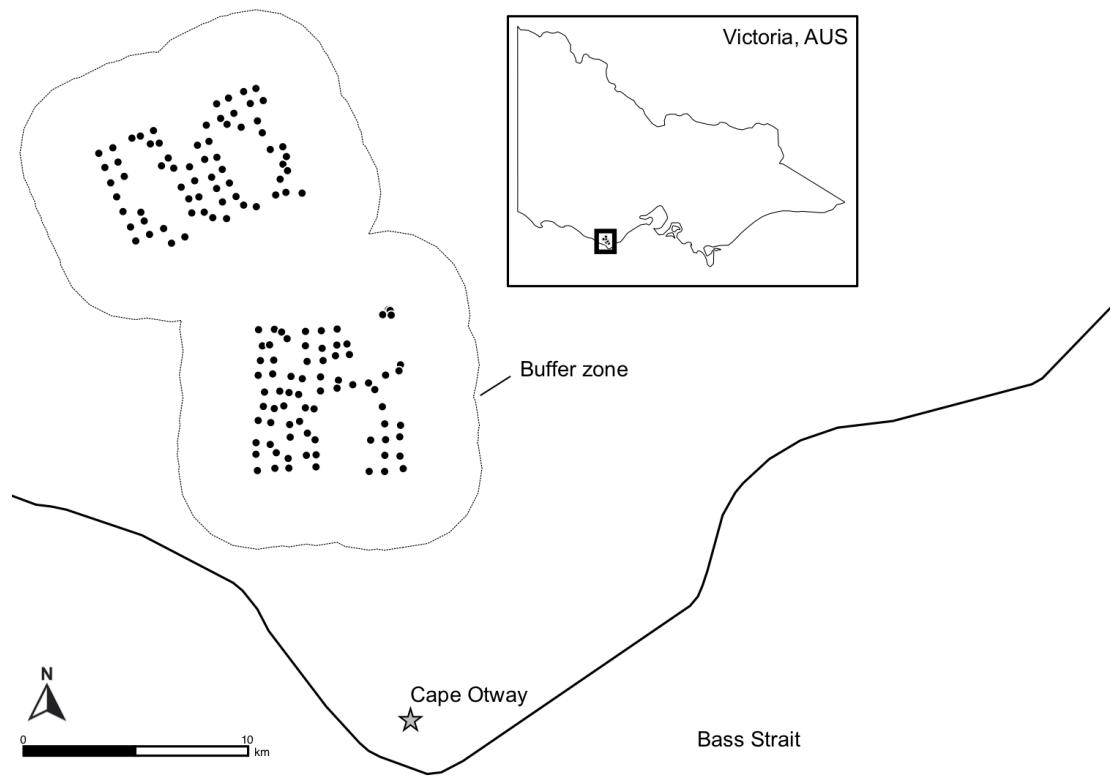


Figure 2.1: Study area, western Otway Ranges, Victoria, Australia, showing the location of the camera-trapping sites (black dots) within the 3500 m buffer zone (thin grey line).

2.3 Results

We detected feral cats at 55% of sites. Of these detections (1 detection = one or more visits of an individual/unidentifiable/unmarked cat to a camera-trap per 24-h occasion), 41% were unmarked (black) cats. Of the marked cat detections, 89% could be reliably identified to the individual-level – 47 individuals were identified. The number of detections, number of identified individuals and mean distances moved were similar across the two camera-trapping grids (Table 2.1).

The top-ranked model estimated a density of $1.14 \text{ cats km}^{-2}$ (95% CI: 0.88 – 1.47), with no difference in density between grids but a linear decrease in g_0 over time (5.7% decrease per week; Fig. A.1; Table 2.1). The second-ranked model (dAICc 1.74, Akaike weight 0.23) indicated that densities were slightly higher at the northern than southern grid, although confidence intervals overlapped substantially (Table 2.2). The hazard-rate detector function best described the rate at which detection probability changed with the distance of the camera from the centre of a cat’s home range (Table A.1). Estimates of feral cat density were robust to all model specifications, with the mean estimate varying by less than 0.2 cats km^{-2} between all models (Table 2.1).

Table 2.1: Summary of raw camera survey data for feral cats in the Otway Ranges, Victoria, Australia, 2017.

Summary statistic	southern grid	northern grid	both grids
Number of camera sites	73	67	140
Sites where cats detected (%)	51	62	55
Number of unmarked detection events	47	48	95
Number of identifiable, marked detection events	60	59	119
Number of unidentifiable, marked detection events	10	5	15
Total number of identified individuals	23	24	47
Number of cats resighted at different cameras	8	6	14
Mean recapture distance (m)	653	774	716
Maximum recapture distance (m)	905	1701	1701

Table 2.2: Comparison of spatial mark-resight models and density estimates

Model		Model comparison				Density estimate (cats km-2)			
Density	g0	K	AICc	dAICc	AICcw	grid	estimate	lcl	ucl
1 grid	T	5	1568.84	0	0.71	both	1.14	0.88	1.47
	T	6	1570.68	1.84	0.28	north	1.23	0.90	1.68
						south	1.05	0.78	1.42
1 grid	1	4	1578.37	9.53	0.01	both	1.14	0.89	1.48
	1	5	1579.66	10.82	0	north	1.25	0.91	1.72
						south	1.04	0.77	1.40

T = linear time trend

K = number of parameters estimated

AICc = Akaike's Information Criterion with small-sample adjustment

dAICc = difference between AICc of this model and the model with smallest AICc

AICcw = AICc model weight

lcl – lower 95% confidence limit

ucl – upper 95% confidence limit

2.4 Discussion

Our work provides one of the first robust estimates of feral cat density for a temperate wet forest in Australia. Our estimate of 1.14 cats km⁻² (95% CI: 0.88 – 1.47) is five times higher than that predicted by the Legge *et al.* (2017) model for this location (0.17 - 0.23 cats km⁻²), and more than three times higher than the predicted continental mean density for feral cats in ‘natural areas’ (0.27 cats km⁻²; 0.18 – 0.45 cats km⁻²; Legge *et al.* 2017). The mesic coastal areas of Australia were previously thought to support the lowest densities of feral cats across the continent, particularly rugged and wet regions, such as rainforests (Dickman 1996; Johnson 2006; Legge *et al.* 2017; McDonald *et al.* 2017). Accordingly, feral cats were believed to have relatively less impact on native species in these environments (Burbidge & Manly 2002; Doherty *et al.* 2017; Woinarski *et al.* 2017, 2018; Radford *et al.* 2018; Murphy *et al.* 2019). Our finding is therefore startling, and prompts a rethink about the threat that feral cats may pose to native fauna in mesic habitats.

The high density of feral cats in our study region likely reflects the high productivity of the landscape and abundant populations of some prey species. Our study region has the highest annual rainfall in Victoria (Bureau of Meteorology 2021), and live-trapping surveys in our study site show consistent, near saturation of small mammal traps, predominantly bush rats *Rattus fuscipes* and *Antechinus spp.* (Z. Baník, unpublished data). Several images from our study confirmed that feral cats prey upon these taxa. These small mammals may be relatively robust to introduced predators due to their high fecundity and generalist habitat requirements (e.g. Banks 1999). However, by supporting high densities of feral cats, they may also facilitate high levels of predation on rarer and more vulnerable species (Smith & Quin 1996), such as the now locally extinct smoky mouse *Pseudomys fumeus* (Menkhorst & Broome 2006). Significant declines and local extinctions of other small mammals have also been reported across the eastern Otways (Wayne *et al.* 2017). Understanding temporal trends in these predator-prey dynamics and the relationships between introduced predators and their native primary and alternative prey is a key priority for future research.

The lack of apex predators and competitors in the Otway Ranges may also facilitate high feral cat densities. Dingoes *Canis familiaris*—higher order predators (Johnson *et al.* 2007)—and tiger quolls *Dasyurus maculatus*—key competitors (Glen & Dickman 2005)—are functionally extinct in the Otway Ranges. We detected foxes at 25% of sites (M. Rees, unpublished data) but the extent to which foxes exert top-down control on feral cats is unclear. Changes in feral cat abundance, behaviour and/or diet have been observed in response to fox control (Molsher *et al.* 2017; Hunter *et al.* 2018), and the relationship could be further clarified using robust density estimates under experimental manipulations of fox density.

The belief that feral cat densities in Australia are lower in mesic forests than open habitats stems partly from the lack of robust density estimates from forests, and partly from observations that cats have greater hunting success and are more detectable in open microhabitats (McGregor *et al.* 2014, 2015; Hohnen *et al.* 2016; McDonald *et al.*

2017) and select for savannah over rainforest (McGregor *et al.* 2017). However, the variation in understorey structure (from extremely dense to relatively open) in our study region potentially creates ideal shelter and foraging habitat for feral cats, which often hunt along edges between dense and open vegetation (Doherty *et al.* 2015). Our findings challenge the belief that cat density is low in mesic forests, and instead concur with the global pattern that feral cats have smaller, overlapping home ranges in productive, low-seasonal environments, resulting in higher population densities (Bengsen *et al.* 2016).

Our surveys clearly need replicating in other mesic environments before they can be generalised. Nonetheless, higher than expected densities of feral cats in mesic and complex environments would have serious implications for biodiversity conservation. Feral cats are thought to be a key driver of the recent declines of critical-weight-range mammals in northern Australia (Woinarski *et al.* 2010; Fisher *et al.* 2014; Davies *et al.* 2018). Contemporary mammal declines are also occurring in temperate Australia, including the Otway Ranges (Bilney *et al.* 2010; Wayne *et al.* 2017; Lindenmayer *et al.* 2018). A better understanding of feral cat densities in these regions is essential for identifying key threatening processes and improving management outcomes.

In conclusion, our study shows that feral cats can occur at high densities in wet forests and cool temperate rainforests, contrary to previous expectations. Further research is needed to understand the impacts of this on native mammal populations, and the mechanisms that drive spatial variation in feral cat density, including the influence of habitat type, productivity, disturbance events and interactions with other predators. New spatial capture-recapture methods will likely play a powerful role in improving understanding of the ecology of this globally-significant predator. Our work provides a strong foundation for future investigations, as our methodology allows for robust evaluations of feral cat density, particularly under experimental manipulations and population comparisons.

Chapter 3

Fire and poison-baiting manipulate invasive predator and threatened prey occurrence within temperate landscapes

Abstract

Invasive predators are often lethally controlled because of their considerable biodiversity and socioeconomic impacts. Invasive predators are resilient to low-level culling efforts, but management across broad spatiotemporal scales is expensive. Quantifying invasive predator suppression, unintended outcomes (e.g. release of subordinate invasive species) and benefits to threatened species across gradients of control effort is key to designing cost-effective control programs. However, signals may be confounded by co-occurring threats and management actions.

In this study we examined the response of four species to invasive predator management programmes across two fire-prone regions: the introduced apex predator targeted through poison-baiting (red fox *Vulpes vulpes*), an introduced mesopredator suspected to inadvertently benefit (feral cat *Felis catus*); and two threatened native mammals preyed upon by both invasive predators (southern brown bandicoot *Isoodon obesulus* and long-nosed potoroo *Potorous tridactylus*). With data from 3667 camera-trap deployments, we built hierarchical generalised additive models to estimate changes in species occurrences across (1) gradients of poison-bait density, and (2) fire history patterns among different vegetation communities, while (3) accounting for forest edge-effects.

Poison-baiting programs suppressed introduced red foxes across both regions—the degree to which depending on poison-bait density—but had highly variable impacts on threatened native prey. Fox control had no impact on southern brown bandicoot occurrence in either region, nor for potoroos in one region. However, in the other re-

gion, fox control was critical to the persistence of the long-nosed potoroo. Occurrence of both invasive predators and native prey was driven by an interaction between vegetation type and fire. Response to time since fire varied considerably, both across species and among species in different vegetation types.

Our study demonstrates how variable invasive predator control outcomes are, highlighting the importance of long-term, multispecies monitoring. Invasive predator control and prescribed fire are important tools land managers use to manipulate mammalian communities, but optimal regimes are species-specific and need to be tailored to the fine-scale landscape-context.

3.1 Introduction

Conservation managers intervene in ecosystems with the aim of stemming rapid biodiversity loss, but outcomes are rarely quantified (ref). This is integral to ensuring cost-effective allocation of conservation resources and to monitor potential unintended consequences of ecosystem intervention. However, reliable inferences about the effects of landscape-scale management are often difficult to achieve as most wildlife populations are naturally patchy and fluctuate through time due to natural drivers, co-occurring threats and concurrent management actions (Tulloch *et al.* 2016).

Management of invasive predators is a classic example (Doherty & Ritchie 2017). Because they are major drivers of global biodiversity loss, introduced predators are actively controlled—usually lethally—throughout much their non-native ranges (Bellard *et al.* 2016; Doherty *et al.* 2016). Concerningly, when multiple invasive predators co-occur, single-species control often has perverse effects on native biodiversity (Ballari *et al.* 2016). There are several possible explanations for this. Firstly, invasive predators may not be suppressed below thresholds which native prey can tolerate—predators can be remarkably resilient to low-effort culling (Sinclair *et al.* 1998; Sabo 2005; Lazenby *et al.* 2015; Moseby *et al.* 2019). Secondly, invasive predator suppression may ‘release’ subordinate invasive species which also threaten native prey (Courchamp *et al.* 1999; Ruscoe *et al.* 2011). Thirdly, native prey may not be limited solely by top-down control (Banks 1999). Quantifying invasive predator suppression, unintended outcomes and native prey responses across gradients of control effort is key to designing cost-effective invasive predator management programs (Baxter *et al.* 2008; Walsh *et al.* 2012). However, signals can still be confounded by co-occurring threats and management actions.

Quantifying impact of planned fire on introduced and native fauna is similarly complex. The effects of fire on vegetation structure are long-term (decades - centuries), nonlinear and variable across environmental conditions (Haslem *et al.* 2011). Fire can therefore drive the persistence and extinction of native fauna populations by altering food and habitat resources, particularly the dense understorey vegetation used to shelter against predation (Monamy & Fox 2000). Because post-fire regeneration of habitat structure varies across ecological communities, prey species distributed across heterogeneous landscapes can have variable responses to time since fire (Nimmo *et al.* 2014; Swan *et al.* 2015). Predators are known to increase in abundance and more heavily predate vulnerable prey when understorey vegetation is removed in the short-term following fire, however long-term effects of fire on predators are unclear (Geary *et al.* 2020a; Hradsky 2020). Predicting the long-term ramifications of fire on predators and prey is a key challenge for managers who are tasked with stemming the decline of native fauna populations while simultaneously protecting against the increasing threat of large wildfires (Clarke 2008).

Disentangling the complex and potentially interacting effects of invasive predator and fire management on native fauna is particularly pertinent to Australia, where native mammals have experienced some of the worst declines in recent world history

(Woinarski *et al.* 2019). Native mammals have declined primarily due to two introduced predators and altered fire regimes following European colonisation (Woinarski *et al.* 2015). However, habitat fragmentation certainly plays a role (May & Norton 1996) in prey declines and there is growing concern around rainfall dynamics, even in temperate ecosystems (Hale *et al.* 2016). Integrated predator management programs are rare; instead, the red fox *Vulpes vulpes* (hereafter ‘fox’) is far more commonly controlled than the feral cat *Felis catus* (hereafter ‘cat’). There is some evidence, albeit highly uncertain, that fox suppression could cause a ‘mesopredator release’ of cats (Hunter *et al.* 2018). This would help explain dramatic declines reported in native prey following long-term fox control programs in Australia (e.g., Wayne *et al.* 2017; Lindenmayer *et al.* 2018; Duncan *et al.* 2020). However, it is equally plausible that prey succumbed to co-occurring threats over time.

In this study we assessed the outcomes of two fox control programs in fire-affected regions of south-eastern Australia. We experimentally deployed 3667 camera-traps around one long-term and one recently commenced fox control programs in protected conservation areas. We accounted for the potentially nonlinear effects of fox control effort (1080 poison-bait density), variable responses to time since fire (0 - XX years) across vegetation communities, rainfall dynamics and proximity to cleared areas, on species occurrences using generalised additive models (hereafter ‘GAMs’). Quantifying apex predator suppression and testing the mesopredator release hypothesis (Crooks & Soulé 1999) are important steps towards an understanding of prey responses to lethal predator control.

3.2 Methods

3.2.1 Study species

In this study we focused on two invasive predators and two shared native mammalian prey species listed as threatened under federal legislation. The introduced predators share a similar functional niche similar and compete for many of the same resources (Glen & Dickman 2005). Both prey species are solitary, medium-sized, ground-dwelling marsupials. They nest in dense understorey vegetation during the day and turn over large quantities of soil to feed on invertebrates, plant material and fungi at night (Van Dyck & Strahan 2008).

Red fox

Introduced in the early 1870's, European red foxes (~6 kg) and are now ubiquitous across the Australian mainland except for tropical areas of the north (Fairfax 2019). Fox density varies from 0.1 foxes km^{-2} in semi-arid regions to more than four foxes km^{-2} in productive environments such as farmlands (ref). home-range size follows the opposite pattern, varying from less than 100 ha in urban and productive agricultural environments, to upwards of 2000 ha in the arid zone (ref). Foxes usually hunt alone but live in family groups comprising a dominant pair and their juvenile cubs. If resource availability is high, adult offspring may also remain with the group. Foxes have a strongly seasonal lifecycle: mating occurs in mid-winter, cubs are born in spring (average litter sizes being 3 to 6 cubs), and offspring disperse in autumn and early winter, before breeding that season. Foxes predate on and scavenge a wide variety of foods; including livestock, small arthropods and fruits (Fleming *et al.* 2021).

Feral cat

Feral cats (~4 kg) took less than a century to spread across the entire Australian continent, owing to their wide thermal tolerance without relying on free drinking water (Abbott 2008). Feral cat densities range from 0.01 to 1.5 cats km^{-2} in natural Australian environments (Legge *et al.* 2017). Female cat home-range size scale negatively with landscape productivity (Bengsen *et al.* 2016), from less than 100 ha to more than 600 ha (Hamer *et al.* n.d.). Male cat home-range size varies with that of females, but is larger on average because dominant males typically overlap the ranges of two to three females. Some individuals do not have a fixed home-range (Roshier & Carter 2021). Feral cats can breed several times a year with litters of up to five kittens (Jones & Co-man 1982). Cats are largely solitary across Australia's typical natural environments, although form dense matrilineal societies in areas with rich resources (e.g., farms, rubbish tips, seabird colonies). Feral cats are obligatory carnivores, preferring live prey but do occasionally scavenge - they do not readily take most types of meat bait (Fisher *et al.* 2015).

Southern brown bandicoot

The southern brown bandicoot (hereafter ‘SBB’; ~1.2 kg) *Isodon obesulus* is distributed in isolated populations across the southern coast of Australia and in Tasmania. SBB’s are mostly found in heathy landscapes, woodlands and dry forest type. SBB’s are solitary; home-ranges vary from 0.5 - 6 ha (Lobert 1990). Females have remarkable reproductive rates: a gestation period of 11 days, can produce two - three litters per breeding season (6 months), averaging two to four young, who become independent at age 60 days (Brown & Main 2010). Estimates of mainland SBB density average approximately 130 individuals km⁻² (Pentland 1999).

Long-nosed potoroo

The long-nosed potoroo (hereafter ‘LNP’; ~1.3 kg) *Potorous tridactylus* currently has a patchy distribution down the eastern coast of Australia from south-eastern Queensland to south-eastern South Australia, as well as the north and east coasts of Tasmania. LNP’s occur across a wide range of vegetation communities from heathlands to rainforests. Females give birth to a single young, up to four times a year, providing each with ~133 days of lactation in the pouch (Frankham *et al.* 2011). In south-west Victoria, LNP’s have a home-range size of 1.4 - 2 ha (Bennett 1987). LNP populations are generally small in size, at densities of 20 - 60 individuals km⁻², with low rates of both juvenile recruitment and individual turnover (Mason 1998; Frankham *et al.* 2011).

3.2.2 Study area and camera-trapping

We deployed and collated camera-trap data across two distinct regions in south-west Victoria, Australia: the Glenelg region and Otway Ranges (Fig. 3.1). Introduced foxes and cats are the only medium-large functional mammalian terrestrial predators across both regions: native dingoes *Canis familiaris* are long absent throughout, tiger quolls *Dasyurus maculatus* are long-absent in the Glenelg region and likely functionally extinct in the Otway Ranges (last confirmed sighting in 2014 despite extensive camera-trapping). In broad sections of each region, government land managers conduct ongoing targeted fox control for biodiversity conservation. Poison baits containing 3 mg of sodium mono-fluroacetate ('1080') are buried at a depth of 12 - 15 cm at 1-km intervals along accessible forest tracks and roads. Different road densities results in spatially variable poison-bait densities. Managers frequently implement prescribed fire across both regions.

In the Glenelg region, Gunditjmara country, large patches of natural vegetation—mostly lowland forests and heathy woodlands—are fragmented by pastoral farming and residential properties (Fig. 3.1). Foxes are subject to lethal control in three distinct forest blocks since October 2005, with fortnightly replacement of 1080 poison-baits (Robley *et al.* 2014). 40 camera-trap sites in each forest block, as well as 40 sites in three similar, unbaited forest blocks (240 sites total) to the north are simultaneously

surveyed annually under the 'Glenelg Ark' fox control program. Hair-tubes were used to monitor prey species from 2005 - 2013 (data presented in Robley *et al.* 2014), which were replaced by camera-traps in 2013 (camera-trap data from 2013-2019 is presented in this study; Robley *et al.* 2020). In early 2018, four out of the six forest block (two baited, two unbaited) were additionally surveyed with grids of 99 - 110 camera-traps (M.W.R PhD surveys). This totals 2039 camera-trap deployments in the Glenelg region, collected in a control-impact experimental design (foxes had been continuously controlled for at 8 - 13 years in the treatment landscapes during these camera-trap surveys).

The Otway Ranges, Gadubanud, Kirrae Wurrung, Gulidjan and Wadawurrung country, is a largely continuous patch of natural vegetation with a strong east-west rainfall gradient. A matrix of cool temperate rainforest and wet forest at high-altitudes in the south-west descend into a large heathland directly north, and into dry forests and then heathlands to the north-east. Fox-baiting commenced in some small sections in 2008 and large-scale systematic baiting began in 2016 - 2017 under the 'Otway Ark' program (Robley *et al.* 2019). Poison baits were initially replaced weekly for six weeks, before changing to monthly bait-replacement. There was an ~6 month pause in replacement in the second half of 2018. Fortnightly bait-replacement occurred for four weeks afterwards, then returning to monthly bait-replacement. A large section to the north-west remains unbaited, but monitored as an experimental non-treatment site. Otway Ark managers surveyed 372 sites (not simultaneously) with camera-traps annually; we present one 'before' survey and two 'after' surveys of each site from 2016 - 2018, totalling 1113 camera-trap deployments (Robley *et al.* 2019). An additional before-after control-impact (simultaneously paired series survey was conducted in the Western section of the Otway Ranges annually from 2017 - 2019 (M.W.R PhD surveys). This added a further 195 sites and 524 camera-trap deployments.

All camera-trap deployments consisted of a Reconyx (Holmen, Wisconsin) brand camera-trap (white or infrared flash), attached to a tree or a metal picket, facing a lure. One study across both regions (M.W.R PhD surveys) positioned camera-traps low on a tree (around 15 - 30 cm above the ground – angled only slightly downwards) facing a tuna oil lure approximately 2 - 2.5 m away (detailed in Rees *et al.* 2019). The Glenelg Ark and Otway Ark fox monitoring programs positioned camera-traps higher on a tree or a metal picket (at least 40 cm above ground) and angled more strongly downwards toward a lure approximately 1 - 1.5 m away (Robley *et al.* 2019, 2020). These lures consisted of peanut butter, golden syrup and rolled oats mixed into a small ball, placed within a tea strainer or PVC pipe container and secured either to the ground, or 20 - 60 cm above ground on a wooden stake. All set-ups were effective in detecting all four target species.

3.2.3 Generalised additive models

We modelled occurrence probability for each species (response variable) using binomial generalised additive mixed-effects models implemented in the 'mgcv' R-package

(Wood 2017). We specified a model offset to account for differences in camera-trap survey durations and a random effect for each unique site to account for repeat sampling. We used the same model structure and explanatory variables (detailed in the sections below) for each species. We used the double penalty model selection approach, which penalises the null space in addition to the range space (i.e. shrinking wiggly terms to linear terms) of the spline basis, meaning covariate effects can be entirely removed from the model (Marra & Wood 2011).

1080 poison-bait density

1080 poison-baits are deployed to suppress foxes and therefore benefit native prey. As cats are subordinate to foxes, they may also benefit. The degree of fox suppression is likely a function of the spatial arrangement (i.e. poison-baiting density) relative to fox home-range size and replacement schedule of 1080 baits (Fleming 1996; Benshemesh *et al.* 2020). We therefore summed the number of poison-bait stations within a 2.3 km radius around each camera-trap deployment - the average maximum distance foxes in these region travel from their home-range centre (Hradsky *et al.* 2017b). Densities ranged from 1 - 19 baits per fox-home range across both regions. We modelled a smooth function of 1080 poison-bait density with a thin plate regression spline and a factor smooth basis to model the response separately for each region. Due to wet weather impacting road conditions across both regions, some poison-bait stations are inaccessible, and so, some baits do not get replaced at times. Due to a lack of data on missing replacements, we did not account for this. There was also a ~6 month pause in bait replacement in the Otway Ranges we did not account for (the only other option was model a bait density of 0 during this time, but there very likely baits still available in these stations and this would have ignored prior fox suppression).

Time since fire and vegetation type

We expected species occurrences to differ across vegetation types and with time since fire, and to have different responses to time since fire in each different vegetation type (as post-fire regeneration occurs at different speeds; McColl-Gausden & Penman 2019; Swan *et al.* 2015); we therefore modelled an interaction between time since fire (in years; hereafter ‘TSF’) and vegetation type. We used coarse fire scar mapping provided by government managers to calculate the years since the last fire for each camera-trap deployment. We identified the Ecological Vegetation Class (hereafter “EVC”; standard units for vegetation classification in Victoria; DELWP 2020) group for each unique camera-trap site, 8 EVC groups in total. We surveyed 20 unique sites in rainforests, which are interspersed (primarily in low lying gullies) throughout wet and damp forests in the south-eastern Otway Ranges. Given the similarity and finescale interspersion of these EVC groups, and that both rarely or never experience fire, we merged them together (hereafter referred to as ‘wet forests’). We specified this using a hierarchical model structure, which estimated an average TSF response (‘global smoother’), along with EVC group-level smoothers with shared wigginess

(i.e., model GS detailed in Pedersen *et al.* 2019). This shares information on TSF responses across EVC groups and penalises functions which deviate strongly from the average response. Given these are separate smooths and the double penalty model selection was turned on; the global or group-level TSF smoothers could be removed entirely from the model if either were not supported by the data.

Recent rainfall

Changes in short-term rainfall dynamics likely impact both invasive predators and native prey (Arthur *et al.* 2012; Wilson *et al.* 2012; Paull *et al.* 2013; Greenville *et al.* 2014). We calculated the percentage difference in rainfall from the long-term median that had occurred prior to start of each camera-trap survey in six, 12, 18 and 24 month periods. For each camera-trap site, we used data from the nearest weather station ($n = 11$; Bureau of Meteorology 2021). We modelled rainfall using a thin plate regression spline and a factor smooth basis to model the response separately for each region (same specification as 1080 poison-bait density). For each species, we fit a separate model for each time period and compared them using Akaike Information Criterion (hereafter ‘AIC’) scores (Burnham & Anderson 2004).

Proximity to forest edge

Invasive predators are well-documented to prefer edges between forest and cleared land as they facilitate both efficient movement and increased hunting success (May & Norton 1996; Hradsky *et al.* 2017b; Nichols *et al.* 2019). We therefore included a smooth term (thin plate regression spline) of the minimum distance from each camera-trap site to the nearest area of non-native vegetation area. We calculated this by inverting the Department of Environment, Land, Water and Planning native vegetation extent shapefile layer and removing cleared areas smaller than 30 ha (Geary *et al.* 2020b).

3.2.4 Cumulative detection probabilities

We did not incorporate imperfect detection in the GAMs. However, we calculated the cumulative detection probability for each species by fitting an occupancy-detection model (MacKenzie *et al.* 2002) using the ‘unmarked’ R-package. We used single-season models with a random intercept for each unique site to account for repeat sampling. For foxes, we allowed detectability and occupancy parameters to vary as a binary function of fox control, but kept these parameters constant for the other species. We then calculated the probability that each species would have been detected if it was present for one to 93 days (the maximum survey duration; Garrard *et al.* 2008).

All analyses were conducted in R version 3.6.3 (R Core Team 2020).

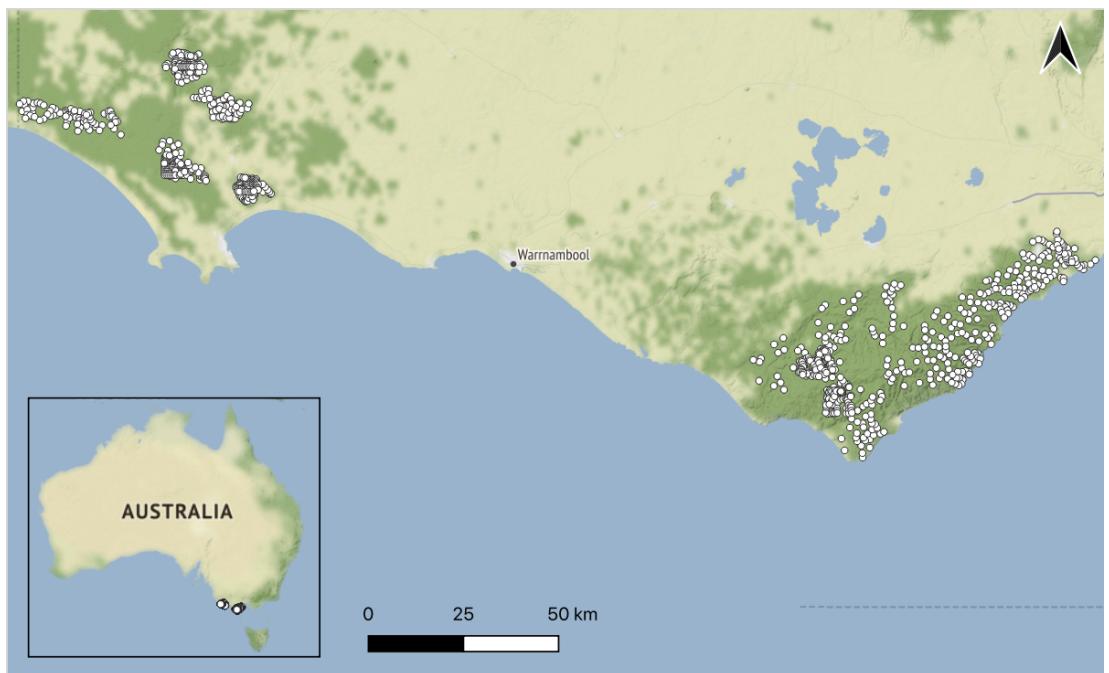


Figure 3.1: Locations of study sites in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.

3.3 Results

Overall, we deployed 3667 camera-traps (survey duration 10 - 93 days; mean 47) at 1232 unique sites across both regions - totalling 172,036 trapnights. We detected foxes on 1453 camera-traps, cats on 1010, SBBs on 394 and LNPs on 331. Predators were ubiquitous across both regions (Table 3.1). Despite being detected in all vegetation types, the majority of SBB and LNP detections took place in heathy communities. SBB's were also commonly found in lowland forests, while there were also relatively high presences of LNP's in herb-rich woodlands (Table 3.1). SBB's were largely absent from the Otway wet forests and rainforests - the few detections occurred adjacent to other vegetation types (SBB's are largely replaced by long-nosed bandicoots *Perameles nasuta* in the wet forests).

3.3.1 Generalised additive models

Despite substantially fewer presences, threatened prey GAMs had considerably better model fits than invasive predators. The fox model had an adjusted R-square value of 0.28 and explained 28% of the null deviance; the cat model had respective values of 0.25 and 26%. Adjusted R-square and deviance explained values were 0.38 and 44% for the SBB GAM, and 0.51 and 56% for the LNP GAM, respectively.

1080 poison-bait density

Fox control reduced the probability of fox occurrence by up to 88% in the Glenelg region and 70% in the Otway Ranges (Fig. 3.2a). Fox suppression scaled (negatively) approximately linearly with poison-bait density in the Otway Ranges, but nonlinearly in the Glenelg region; 6 bait stations within a fox home-range suppressed fox occurrence just as much as 7 - 13 bait stations did. Because fox occurrence probability was lower to begin with in the Otway Ranges (0.56; 95% CI: 0.49 - 0.64) relative to the Glenelg region (0.76; 95% CI: 0.70 - 0.82), foxes were suppressed by the maximum bait density (19 per fox home-range) to a similar level in both regions: a 0.17 (95% CI: 0.05 - 0.46) occurrence probability in the Otways and 0.09 (95% CI: 0.03 - 0.24) in the Glenelg region. However, there was very high uncertainty around fox suppression at 10 - 19 baits per fox home-range in the Otway Ranges.

There was no discernible effect of fox control on cat occurrence across both regions or either prey species in the Otway Ranges (Fig. 3.2b-d). In the Glenelg region, fox control had a weak positive effect on SBB occurrence (up to a 1.5-fold increase, although uncertainty around this estimate was high; Fig. 3.2c) and a strong positive effect on LNP occurrence (up to a 7-fold increase; Fig. 3.2d). In the Otway Ranges, fox-bait density was associated slightly negatively with the occurrence probability of both prey species, although uncertainty around these estimates was high (Fig. 3.2c-d).

Time since fire and vegetation type

All species responded to TSF differently across vegetation types (Fig. 3.4; 3.3). The global TSF smooth (i.e., average response) was selected out of the cat model (Fig. 3.3), indicating responses were to TSF were completely dependent on vegetation type. Foxes, SBB's and LNP's all followed an average response TSF response across the regions, with deviations across vegetation types. We observed no common patterns to TSF across species, both on average and within each vegetation type.

Foxes declined linearly with TSF on average (Fig. 3.3a), although peaked around 40 years post-fire in lowland forests. Cats had the weakest responses to TSF; occurrence was highest in both recently burnt and long-unburnt heathland areas, but the opposite response was seen in herb-rich woodlands - cat occurrence peaked around 50 years after fire (Fig. 3.4b). Irrespective of TSF, cat occurrence was lowest in heathy woodlands and lowland forests, highest in Otway wet forests.

SBB's had the strongest and most complex (i.e., wiggly) interactions with TSF, with occurrence peaking 20 and 75 years post-fire (Fig. 3.3c), although the strength of the 75 year peak varied considerably across vegetation communities (Fig. 3.4c). On average, LNP's increased linearly with TSF (Fig. 3.3d), particularly in heathy woodlands (Fig. 3.3). However, LNP's had the opposite response in herb-rich woodlands: occurrence declined with TSF.

Recent rainfall

Rainfall impacted the occurrence of invasive predators but not either native prey species. The fox model which considered rainfall deviations in the prior 18 months was ranked highest relative to the models with six, 12, and 24 month periods; at least 2.9 AIC units lower. The top-ranked model for all other species considered rainfall in a six month period. For cats, there was strong evidence this model performed better (at least 17.5 AIC units lower) than models which considered previous rainfall in longer time periods. The rainfall term was removed for both the top-ranked SBB model (at least 2.2 AIC units lower than the other models) and the three top-ranked LNP models (indistinguishable based on AIC scores).

Despite the different time periods (18 and 6 months), fox and cat occurrence followed a similar nonlinear pattern to rainfall in the Glenelg region (Fig. 3.5). Here, predator occurrence was highest when rainfall was lowest as well as in the mid-range of above average rainfall. Foxes in the Otway Ranges responded similarly to rainfall as foxes in the Glenelg region when rainfall was below average, but had opposite responses to glenelg foxes when rainfall was above average. Rainfall had no discernable effect on cat occurrence in the Otways.

Proximity to forest edge

Fox occurrence strongly declined with distance of up to two kilometres from the nearest area of non-native vegetation (Fig. 3.6a). The impact of forest edge on all other species was weak; cat occurrence slightly declined and prey species slightly increased, although there was considerable uncertainty in each of these responses (Fig. 3.6b-d).

3.3.2 Cumulative detection probabilities

All species had a greater than 75% probability of detection for the average camera-trap survey length (Fig. 3.7). Fox detectability was more than twice as low in landscapes with fox control (0.033; 95% CI: 0.030 - 0.036) than in landscapes without (0.077; 95% CI: 0.075 - 0.080). Cats were the least detectable species. Detectability of threatened prey species was high, reaching a 95% detection probability for a survey duration of 38 and 20 days for SBBs and LNPs, respectively.

Table 3.1: Number of camera-trap sites, total deployments and naive occupancy rates for red foxes, feral cats, southern brown bandicoots (SBB) and long-nosed potoroos (LNP) within Ecological Vegetation Class groups across two broad regions in south-west Victoria, Australia.

Vegetation	Region	Sites	Deployments	Fox	Cat	SBB	LNP
Dry Forest	Glenelg	25	68	0.66	0.10	0.06	0.01
	Otway	111	310	0.42	0.28	0.02	0.06
Heathland	Glenelg	40	119	0.43	0.34	0.14	0.18
	Otway	3	9	0.22	0.44	0.11	0.33
Heathy Woodland	Glenelg	154	424	0.31	0.14	0.29	0.19
	Otway	82	256	0.29	0.14	0.15	0.12
Herb-rich Woodland	Glenelg	59	372	0.50	0.27	0.02	0.12
	Otway	2	6	0.33	0.17	0.00	0.00
Lowland Forest	Glenelg	383	1046	0.46	0.18	0.17	0.05
	Otway	52	162	0.42	0.14	0.04	0.10
Swampy Scrub	Glenelg	4	10	0.60	0.50	0.00	0.00
	Otway	36	97	0.32	0.33	0.08	0.09
Wet Forest	Otway	281	780	0.31	0.54	0.01	0.07

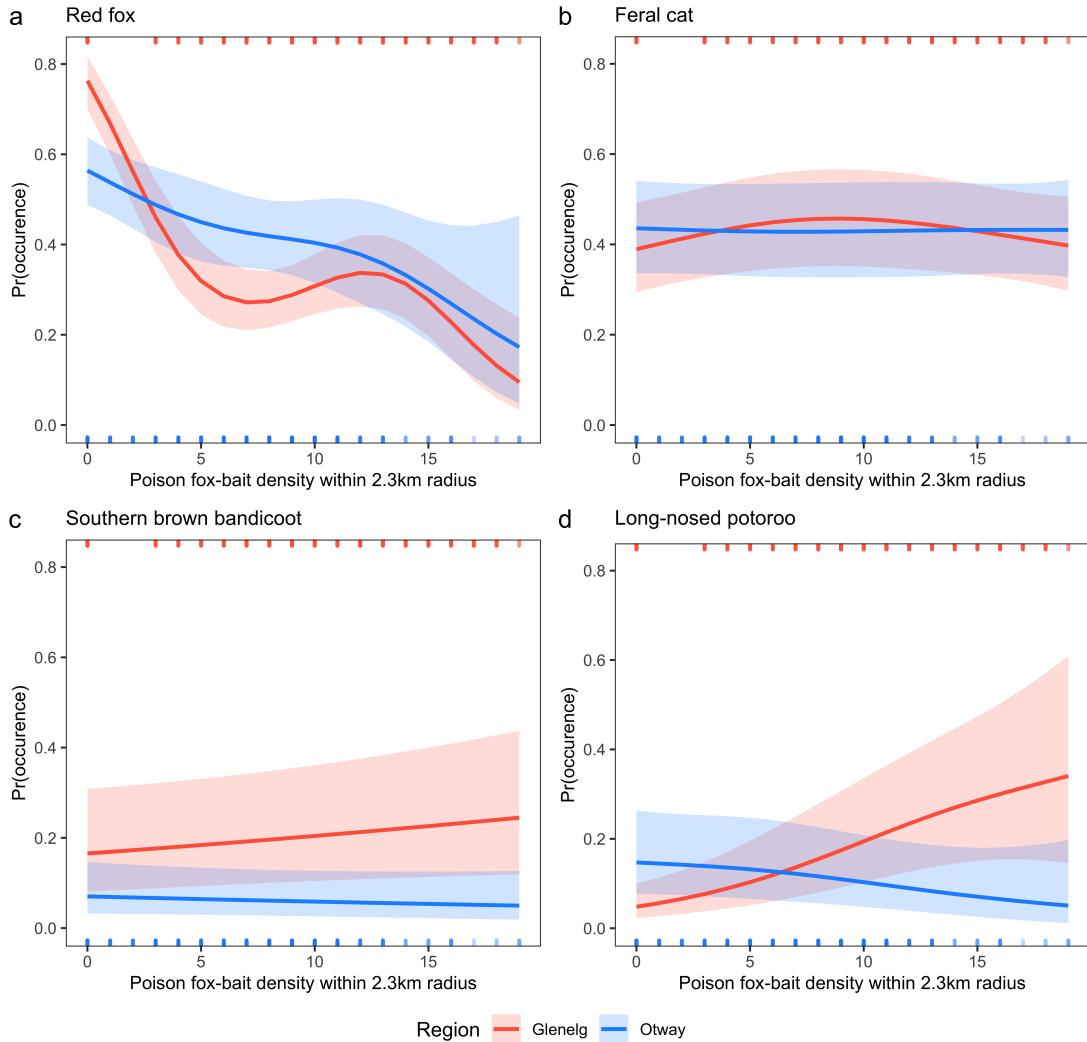


Figure 3.2: Probability of fox occurrence (a) declined with increasing 1080 poison-bait density across both the Otway Ranges (blue) and Glenelg region (red) in south-west Victoria, Australia. Feral cat occurrence probability remain unchanged across the range of fox-bait density (b). Southern brown bandicoot (d) and long-nosed potoro (e) occurrence probability increased with fox-bait density in the Glenelg region, but decreased in the Otway region—although these effects were weak with high uncertainty. Shaded regions indicate 95% confidence intervals.

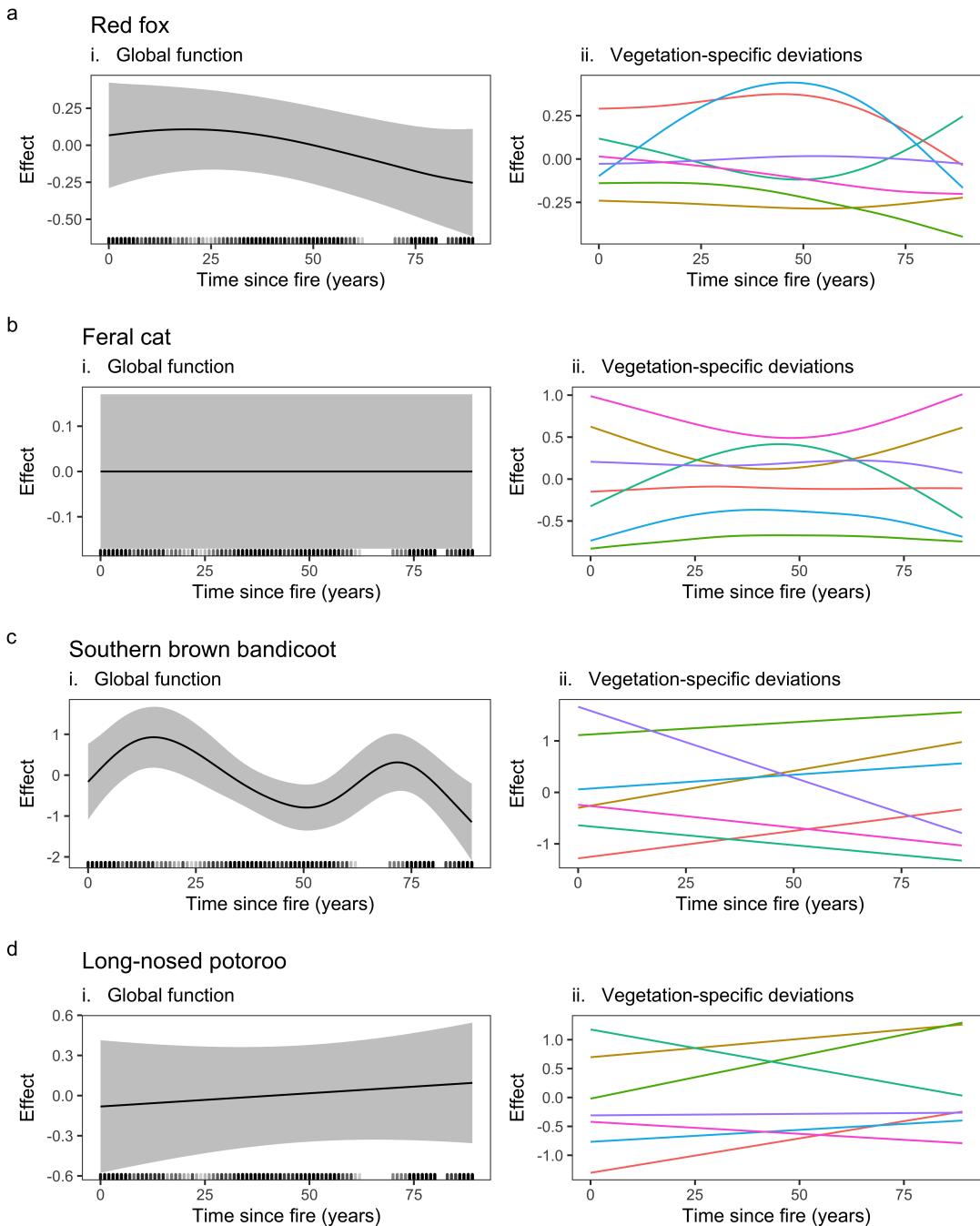


Figure 3.3: Hierarchical effects of time since fire on species occurrences across vegetation types. The global smoother (i) was selected out of the feral cat (b) model—feral cats *Felis catus* had separate responses to fire across each vegetation type. The other species had a common response to time since fire (i), and group-level deviations across all vegetation types (ii). Shaded regions indicate 95% confidence intervals.

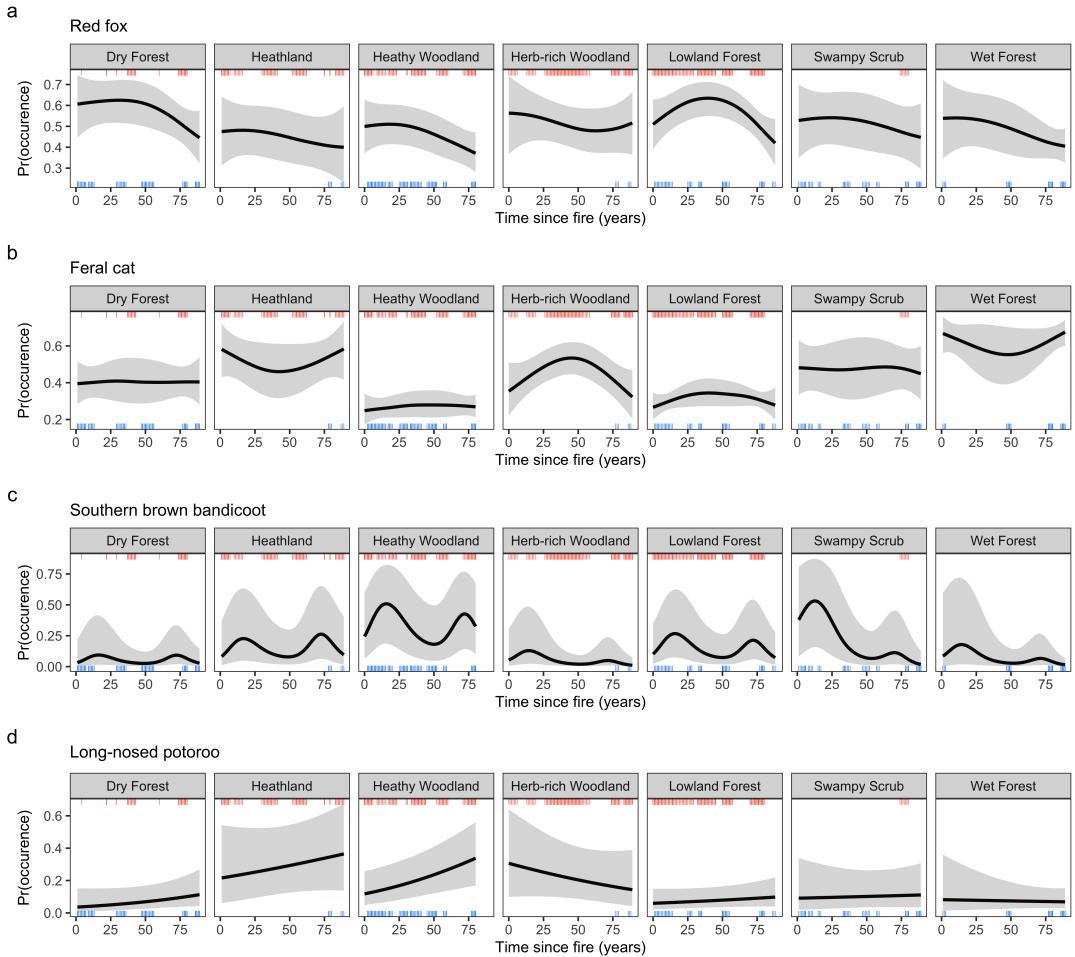


Figure 3.4: Time since fire had a weak impact on fox (a) and feral cat (b) occurrence probability in south-west Victoria, Australia. Southern brown bandicoot occurrence probability (c) peaked around 15 and 75 years following fire, although, the magnitude of both peaks differed across Ecological Vegetation Class groups. Long-nosed potoroo occurrence probability (d) linearly increased with time since fire in heathy vegetation groups, but linearly decreased with years post-fire in Herb-Rich Woodlands. Shaded regions indicate 95% confidence intervals

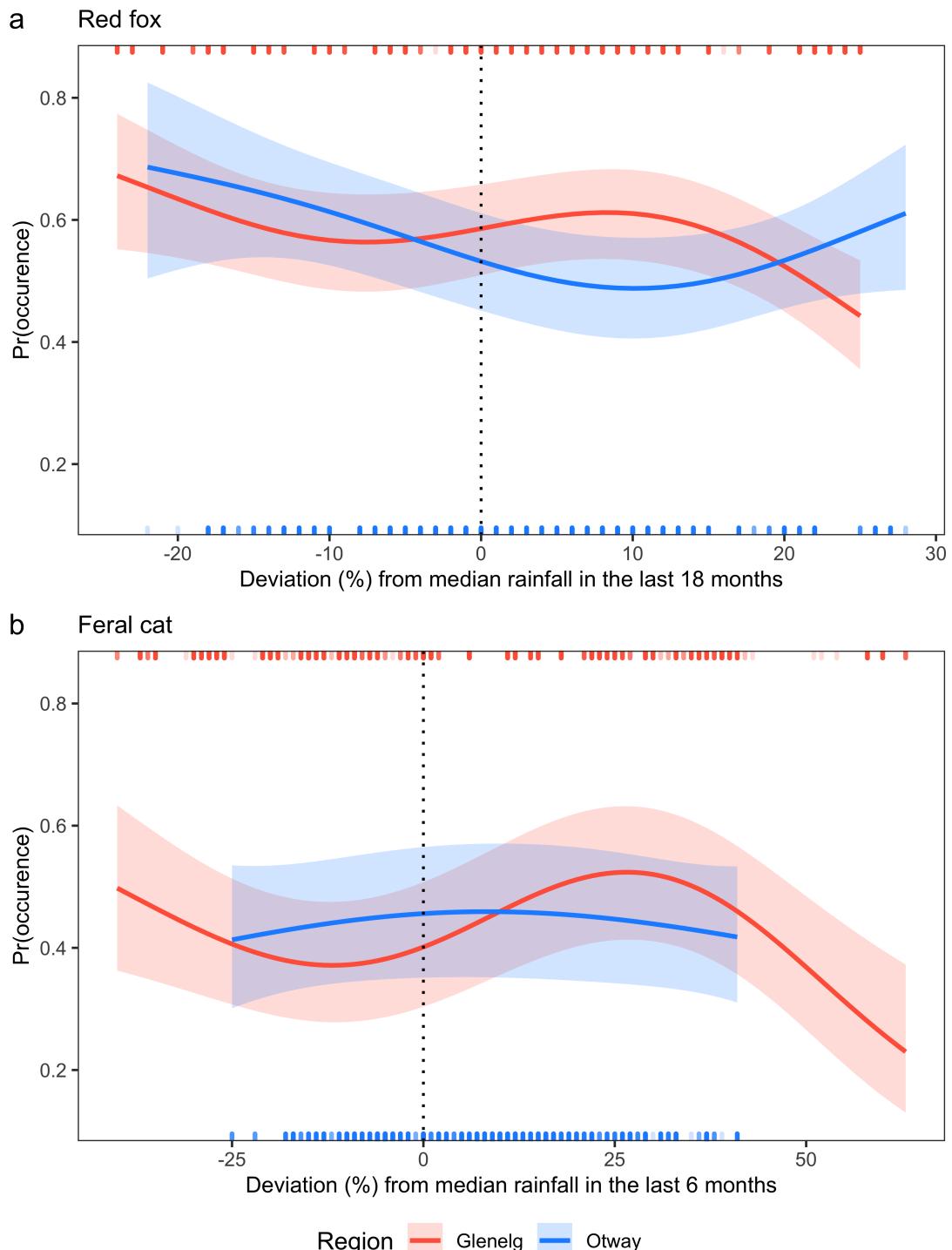


Figure 3.5: Impact of rainfall amount in the preceding 18 months (percentage difference from the long-term median) on species' occurrence probabilities in south-west Victoria, Australia. Shaded regions indicate 95% confidence intervals

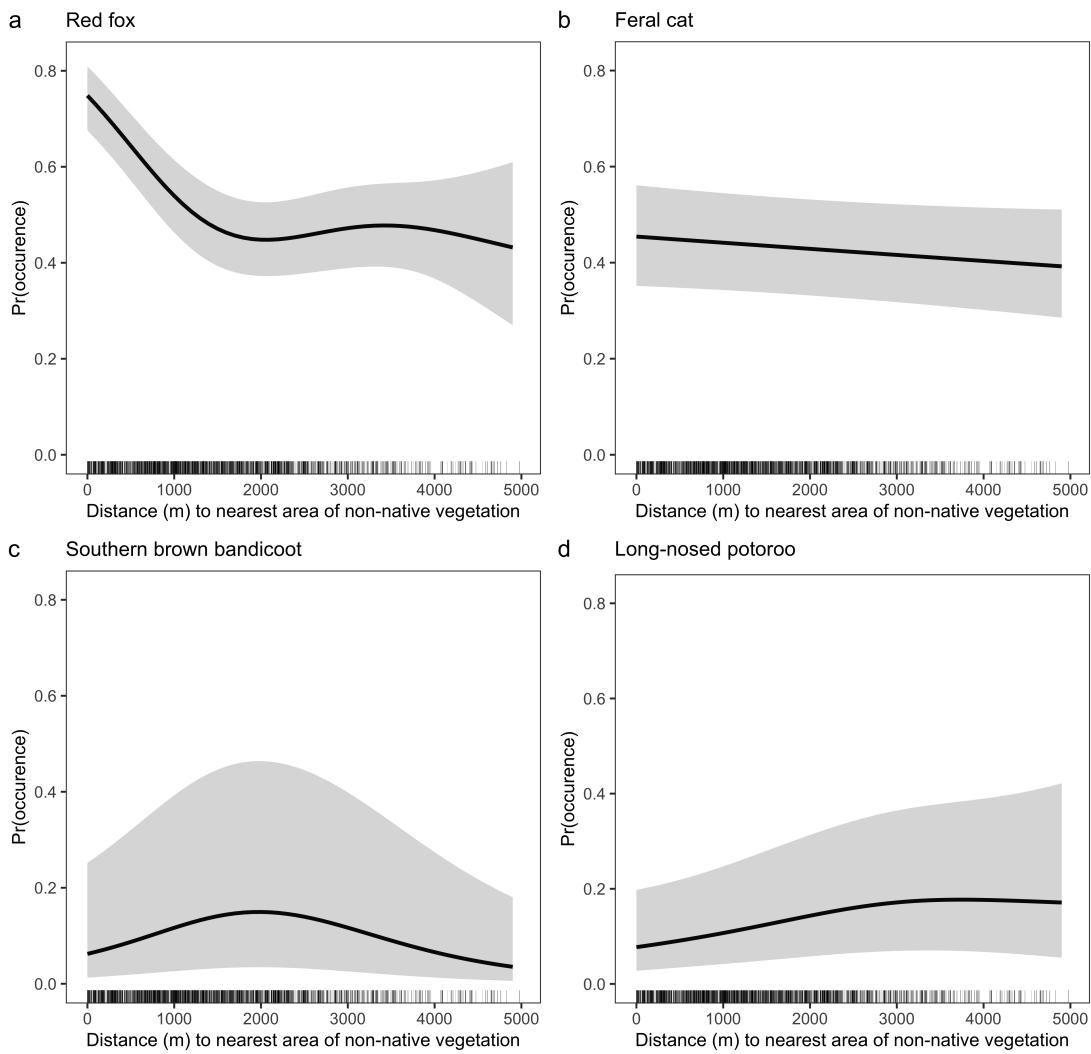


Figure 3.6: Fox occurrence probability decreased linearly for 2 km as distance to the nearest area of non-native vegetation (larger than 30 ha) increased (a). Increasing distance to non-native vegetation had a weak, positive effect on long-nosed potoroo's (d), but little-no impact on feral cats (b) and southern brown bandicoots (c) in south-west Victoria, Australia. Shaded regions indicate 95% confidence intervals.

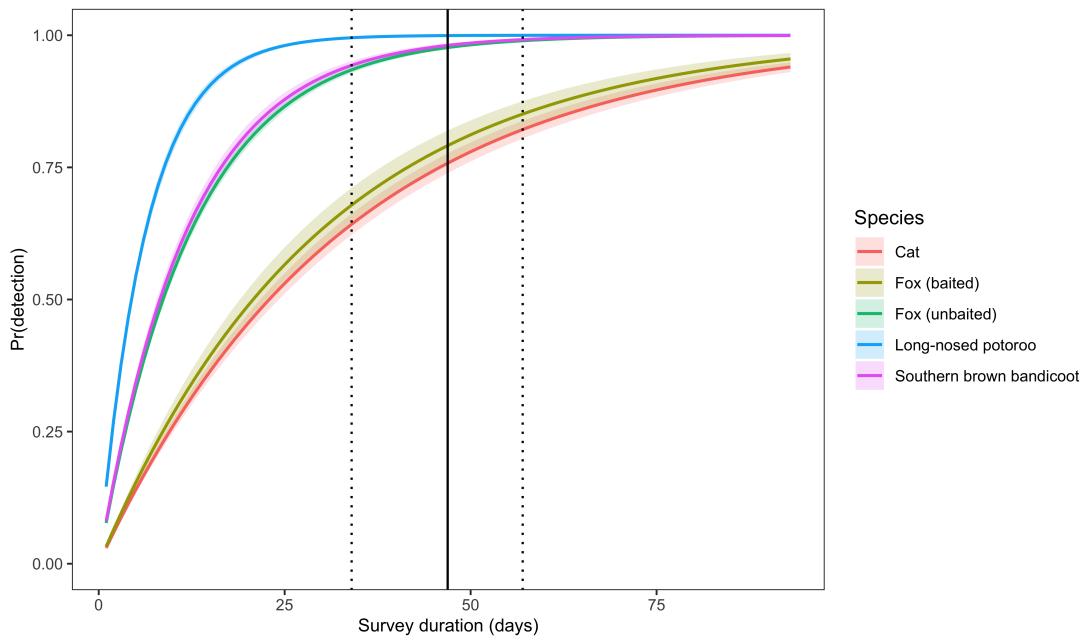


Figure 3.7: Cumulative detection probability for surveyed species averaged across all sites (solid black lines), as well as sites with fox control (solid red line) and without fox control (solid blue line). Dashed lines represent 95% confidence intervals. Vertical grey lines represent mean (solid) as well as 25% and 75% quantiles (dotted) of days camera-traps were active for.

3.4 Discussion

Identifying management effects is challenging across heterogeneous, multi-stressor systems. In our study, not only did functionally similar species respond to fire and apex predator management differently, but species themselves responded differently across landscape contexts and broad regions. Importance of species-specific monitoring and management. Luckily we've current management tools can be wielded to decrease threats (e.g. fox occurrence) and promote habitat suitability (e.g. fire). Just need considerable effort (foxes), and multispecies planning which is variable across habitat types. Assuming population-wide responses, linear responses is misleading. Many of these responses were nonlinear, reinforcing that forcing straight lines through biological processes can lead to misunderstanding [e.g., wolkovich2021simple].

Fox suppression.

Threatened species benefits to fox control.

Limitations to occupancy.

Fire - dynamic habitat. Predator responses - first evidence. Sure, directly measuring habitat structure would have been better, but managers need to plan without this information. Different species responses are surprising, overlooking species interactions.

Here we demonstrate that large reductions in invasive apex predator occurrence don't produce consistent threatened species benefits. For example, a high density of 1080 poison-baits in the Glenelg region, Australia, largely maintains the persistence of LNP's in these landscapes, but appeared to slightly worsen outcomes for this threatened species in the neighbouring Otway Ranges. Fortunately, our work demonstrates that fox control is not the only effective tool mangers have—maintaining optimal fire regimes is a high priority for threatened native mammals in temperate landscapes. However, not only do optimal fire regimes vary across species, but they can be entirely conflicting for the same species across different vegetation communities. Our work highlights the importance of fine-scale monitoring and tailoring conservation strategies to local contexts.

Ours is the study first to quantify fox suppression across a gradient of 1080 poison-bait densities. Previous studies have not considered how baiting effort varies spatially when analysing the response of foxes and other species, rather averaging across the entire fox control program. There is a huge range in bait densities and replacement schedules for fox control across Australia. Compare to other studies and bait density recommendations. The impact of poison-bait densities is relevant to the home-range size of the target species, which for foxes varies considerably (Main et al 2020) - caution needs to be taken when extrapolating to other sites. Ultimately, the best metric for fox control effectiveness is the improvement to native prey persistence.

Fox-bait density strongly correlated with fox suppression, however, the threatened species we surveyed had weak and inconsistent responses to fox-bait density. SBB's

were mostly unaffected. Perhaps this is because bandicoots may more closely follow patterns in cat populations (Catling). On the other hand, LNP's (and other macropods) often benefit the most from fox control (hunter), but only did so in the Glenelg region. The most likely explanation for the lack of positive threatened species responses in the Otway Ranges were because we only surveyed for 0 - 3 years (relative to XX-XX years post-baiting in the Glenelg region) and did not account for time-lag effects. While these species have very short recruitment periods and so have the ability to respond quickly in terms of population density, we assumed that foxes are limiting the availability in suitable habitat for CWR mammals. Rather, we found that vegetation type and TSF were strong drivers of CWR mammal habitat suitability.

Contrary to the mesopredator release hypothesis, we observed no impact of fox control on cat occurrence probability. This may be because foxes do not suppress feral cat across these region, or because occurrence is too coarse a metric to uncover interactions between these species. Cats were widespread, and of all the species, had the lowest detectability, and the other explanatory variables relatively weak effects on their occurrence. Our occurrence models threw away rich information on detection rates, masking potential behavioural and population density effects. Our work adds to the growing body of evidence that fire regimes are key to maintaining suitable habitat for small-medium sized native mammals. However, our study demonstrates that species response to fire can vary spatially. For local managers, preserving long unburnt heathy landscapes is a key management priority as they are strongholds for SBBs and LNPs. On the other hand, fresh burns in herb-rich woodland may promote LNP persistence. We saw weaker effects on the generalist invasive predators, contrary to some short-term experiments. This is unsurprising given our coarse, long-term (year) resolution, predator responses to fire and mostly finished within ~3? months. Our result suggests that managers can focus on the heightened threat of invasive predators immediately post-fire (Hradsky refs) rather than over the long-term.

Invasive predators are well-documented to prefer forest edges, this was true for foxes but not for cats in our study. For foxes, this effect lasted for 2 km into the forest interior, but no effect was detected for cats. GAMs useful for quantifying this, rather than arbitrarily defining categorical edge habitat or assuming edge effects are linear. The weak and uncertain increase in CWR mammal occurrence with distance is intuitive because there is more habitat away from edges, and less foxes.

While increasing poison-bait density can suppress foxes, Australian threatened native mammals may not benefit unless habitat structure is maintained using careful fire regimes. Failure to account for these changing environmental conditions would have produced substantial noise around the fox control effect. Improved inference will likely come from comparing a range of population metrics, such as behaviour and density. Invasive predators, fire, as well as changes to rainfall and fire regimes are pervasive biodiversity threats throughout the globe, including within protected areas. However, averaging effects across populations can be misleading because species responses vary.

3.5 GY

This effect was stronger with less uncertainty in the Glenelg region, where fortnightly poison-bait replacement had been occurring for 8 - 13 years. Fox suppression here was nonlinear: indicating 6 bait stations within a fox home-range reduced fox occurrence just as much as 7 - 13 bait stations did. In the Otway Ranges, poison-bait density had a linear, but weaker suppressive effect on foxes than in the Glenelg region. Here fox control had occurred over a shorter-term (0 - 2.5 years) with less frequent bait replacements.

Fox control is a major expenditure of Australian conservation resources, estimated at AUD 16 million per annum on fox control (McLeod 2004). It is therefore critical to ensure fox control is cost-effective in improving the persistence of threatened native prey. Foxes in Australia are primarily managed through 1080 (sodium fluoroacetate) poison-baiting (Saunders *et al.* 2010). Levels of fox suppression vary widely across studies; ranging from severe (Berry *et al.*, 2014; Thomson *et al.*, 2000) to small reductions in fox activity (Bengsen, 2014; Newsome, Crowther, & Dickman, 2014), but also increases (Lieury *et al.*, 2015; Towerton, Dickman, Kavanagh, & Penman, 2016; Marlow *et al.* 2016) - likely reflecting differences in baiting intensity. Benshemesh *et al.* (2020) is the only study to have estimated fox suppression across a gradient of baiting density; confirming that increased effort leads to greater reductions in fox activity (scat counts on malleefowl *Leipoa ocellata* mounds). However, this was estimated using linear regression across five Australian states where fox ecology (e.g. density, home-range size, behaviour) and landscape context (e.g. productivity) differs (Benshemesh *et al.* 2020). To date, managers lack empirical information on how foxes (and subordinate species) respond to varying poison-bait densities within regions (i.e., management units). To guide cost-effectiveness, it is important to ascertain whether bait density is linearly associated with fox suppression, or whether there is a threshold beyond which foxes suppression diminishes.

When multiple invasive species occur, single invasive species control often has perverse outcomes on native species (Ballari *et al.* 2016).

Experimental designs are called for to improve inference around fox control, but are not immune to these confounding effects of fire. For example Booderee, western shied... This is highlighted by the Glenelg Ark program; using a Before-After-Control-Impact paired series experimental design with three spatial replicates makes it the most robustly monitored fox control experiment in Australia. However, landscapes subject to fox control have been frequently burnt—highlighting the reality of conducting broad-scale management experiments in-situ. These confounding factors, or perhaps a mesopredator release of feral cats, may explain why two threatened native prey species, the southern brown bandicoot *Isoodon obesulus* (hereafter 'SBB') and long-nosed potoroo *Potorous tridactylus* (hereafter 'LNP'), have had an inconsistent, underwhelming response to fox control in the Glenelg region, Australia. New fox control programs are popping up - contrasting patterns of these same species may offer insight.

It is not clear whether this is the result of fox control, or due to other This is partly because many fox control programs go unmonitored, or monitoring designs provides limited inference on effects of predator management relative to other drivers (reddiex).

Prescribed burning operations often require juggling asset protection against the needs of many native species for dense vegetation.

In fact, while there is a growing body of evidence that invasive predators impacts are heightened in recently burnt areas (Meek & Saunders 2000; Green & Sanecki 2006; McGregor *et al.* 2014, 2016; Leahy *et al.* 2016; Hradsky *et al.* 2017a, b), we have a poor understanding of how long-term fire patterns impacts invasive predators (Geary *et al.* 2020a; Hradsky 2020).

Both invasive predator and native prey populations are impacted by wildfire and small-scale controlled burns used to prevent large wildfires. Animals rarely succumb to direct mortality from fire events (e.g. Garvey *et al.* 2010; Banks *et al.* 2011b; Leahy *et al.* 2015); population-level impacts usually following fire through altered food and habitat resources. Initially, fire removes understorey habitat structure prey used by prey for shelter, making hunting more efficient for predators.

Chapter 4

Quantifying mesopredator release: lethal control of an invasive apex predator alters feral cat density and detectability

Abstract

1. The mesopredator release hypothesis predicts that subordinate predator density will increase as apex predators decline. Persistent debate around mesopredator release in part reflects the lack of robust, replicated experiments to test this theory, and the use of population indices which confound changes in mesopredator density and detectability. This uncertainty has immediate impacts for conservationists who are faced with managing sympatric invasive predators.
2. We used replicating experimental designs and spatially explicit detection modelling to examine whether mesopredator release of the feral cat *Felis catus* occurs in response to targeted control of the introduced red fox *Vulpes vulpes*. We surveyed three Control-Impact paired landscapes in a region with long-term fox control (1080 poison-baiting), and conducted a Before-After-Control-Impact Paired Series experiment in another region. We identified 160 individual feral cats from 68,504 camera-trap nights to estimate feral cat density with spatial mark-resight models.
3. At a landscape scale (mean size: 169 km²), lethal fox control was associated with a range of responses from a negligible to 3.7-fold increase in feral cat density. Consistent with the mesopredator release hypothesis, the degree of increase corresponded with variation in the duration and intensity of fox suppression. At a fine spatial scale (200 m), feral cat density had a consistent negative association with fox activity across both regions.
4. Feral cat detectability also varied across the (artificially manipulated) fox activ-

ity gradient. In one region, nonlinear models indicated that feral cats exhibited avoidance behaviours when foxes were rare, giving way to density suppression at high fox activity.

5. *Synthesis and applications.* Our study provides replicated, experimental evidence that that apex predator suppression is associated with an increase in the density of a mesopredator. Mesopredator release can manifest as changes in both behaviour and density, distorting inference if these processes are not distinguished. Our results help explain why fox control does not consistently improve native prey persistence, suggesting integrated pest management may be necessary to improve conservation outcomes.

4.1 Introduction

Understanding species interactions is critical for effective invasive species management (Zavaleta *et al.* 2001). When several invasive species co-occur, management actions that suppress the dominant invasive species may inadvertently benefit subordinate invasive species (Jackson 2015; Kuebbing & Nuñez 2015). For example, the removal of a dominant invasive predator may increase the abundance of a subordinate invasive species directly by reducing top-down pressure, or indirectly by increasing the availability of shared resources; these are often referred to as mesopredator or competitor release, respectively (Crooks & Soulé 1999; Ruscoe *et al.* 2011; Doherty & Ritchie 2017). The release of subordinate invasive species, particularly predators, can have serious negative implications for native taxa and ecosystem function (Courchamp *et al.* 1999; Ballari *et al.* 2016). However, integrated invasive predator management is often far more costly and less feasible than single species control, and so it is important to identify when the extra cost is justified (Bode *et al.* 2015).

Most knowledge of mesopredator release stems from unreplicated ‘natural experiments’ (e.g. range contractions - Crooks & Soulé 1999) or ad-hoc management interventions (e.g. invasive species eradication - Rayner *et al.* 2007). Does mesopredator release still occur when apex predators are suppressed but not completely removed? The occurrence, nature (positive or negative, direct or indirect) and strength of predator interactions can vary among species assemblages, predation risk, environmental productivity, management regimes and other landscape contexts (Hastings 2001; Finke & Denno 2004; Elmhagen & Rushton 2007; Newsome *et al.* 2017; Alston *et al.* 2019). Replicating management programs in an experimental framework is logistically challenging, but important for understanding these complexities, discriminating between plausible hypotheses and producing generalisable results to inform effective pest management (Glen & Dickman 2005; Hayward *et al.* 2015; Christie *et al.* 2019; Smith *et al.* 2020).

Another source of uncertainty around the mesopredator release hypothesis stems from the inability of traditional survey and modelling approaches to distinguish behavioural from numerical population processes (Hayward *et al.* 2015; Stephens *et al.* 2015). Suppression of an apex predator may simultaneously change the behaviour and the density of a mesopredator, both of which influence detection rates (Broadley *et al.* 2019; Rogan *et al.* 2019). This makes it difficult to interpret observed changes in naive indices of mesopredator activity or occupancy in relation to changes in apex predator populations, even if the study has an experimental design. Unbiased estimates of invasive predator density are also important for setting meaningful control targets and inferring impacts on native prey (Moseby *et al.* 2019). Spatial capture-recapture methods offer a solution by separating behavioural and observational processes from population density, which is estimated within a defined spatial resolution (Borchers & Efford 2008).

Predation by two invasive species, the red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus* (hereafter ‘cat’), has played a major role in Australia’s high rates of

mammalian extinction (Woinarski *et al.* 2015). Integrated pest management programs are rare; instead, foxes are far more commonly controlled than cats, as they are more susceptible to poison-baiting, have greater direct economic impacts and fewer legal impediments to control (Reddiex *et al.* 2007; McLeod & Saunders 2014). Nonetheless, cats are one of the most widespread and damaging vertebrate predator species (Medina *et al.* 2011; Doherty & Ritchie 2017; Legge *et al.* 2020). As foxes are larger-bodied (~2 kg difference) and have high dietary overlap with cats (Stobo-Wilson *et al.* 2021a, b), the mesopredator release hypothesis (Soulé *et al.* 1988) predicts that the impacts of cats on shared prey species will increase as fox populations are suppressed. This is alarming because feral cats are extremely difficult to manage in open populations (Fisher *et al.* 2015; Lazenby *et al.* 2015).

Evidence that foxes suppress cats is inconclusive (Hunter *et al.* 2018). In parts of Australia where the native apex mammalian predator (the dingo *Canis familiaris*) is functionally extinct and introduced foxes are the largest terrestrial mammalian predator, four studies have observed an increase in cat detections following fox control (Risbey *et al.* 2000; Marlow *et al.* 2015; Stobo-Wilson *et al.* 2020a). However, two other studies in similar systems did not see any change (Towerton *et al.* 2011; Molsher *et al.* 2017). A further study with spatial replication detected an increase at one site but not another (Davey *et al.* 2006), and another observed a decrease in cat activity (Claridge *et al.* 2010). No prior studies have directly estimated cat density in response to fox control.

We experimentally investigated the role of introduced foxes in top-down suppression of cat density in two regions of south-eastern Australia. Our experiments had a replicated Control-Impact design in the region with long-term fox control, and a Before-After Control-Impact Paired Series (BACIPS) design in the region with newly implemented fox control. Foxes and cats are the only functional terrestrial mammalian predators in these regions, and each region included at least one area in which foxes were subject to continuous lethal poison-baiting (hereafter ‘impact landscape’), and a paired area where foxes were not controlled (hereafter ‘non-impact landscape’). This allowed a sharp focus on the interactions between the two invasive predators, across a gradient of apex predator (fox) occurrence. In accordance with the mesopredator release hypothesis, we predicted that: (1) cat density would be negatively correlated with fox occurrence at a fine spatial scale, and (2) fox control would increase cat density at a landscape scale. We based inference on direct estimates of cat density using spatially explicit mark-resight models.

4.2 Methods

4.2.1 Study area

We conducted our study across two regions of south-west Victoria, Australia (Fig. 4.1). The native temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and tree plantations. Although once widespread, native dingoes are now absent throughout, and a native mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and extremely rare in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial mammalian predator guild is therefore depauperate, with foxes and cats being the primary functional mammalian terrestrial predators; birds of prey and snakes are the only other medium-large carnivores present.

Our study landscapes in the Glenelg region, Gunditjmara country, were primarily lowland forest and heathy woodland. The area receives an average annual rainfall of 700 mm (Bureau of Meteorology 2021) and has gently undulating terrain. The region frequently experiences prescribed burns and wildfires, creating a mosaic of fire histories and vegetation complexity. Our study landscapes in the Otway region were in the western section of the Otway Ranges on Gadubanud country. Rainfall here is more than twice as high as the Glenelg region. The vegetation is a mosaic of shrubby wet forest and cool temperate rainforest, with the northern landscape bordering on a large heathy woodland. This region rarely experiences fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness index; Riley *et al.* 1999).

Government land managers conduct ongoing targeted fox control for biodiversity conservation across broad sections of each region. In these sections, manufactured poison baits (FoxOff, Animal Control Technologies, Somerton) containing 3 mg of sodium mono-fluroacetate (1080) are buried at a depth of 12-15 cm at 1-km intervals along accessible forest tracks and roads (Fig. 4.1). Different road densities across the two regions result in variable poison-bait densities. Other large sections within each region are maintained without fox control.

4.2.2 Study design and camera-trapping

We designed experiments around the implementation of fox-baiting in each region. We simultaneously surveyed one impact and one non-impact landscape within a region at a time. Each pair of impact and non-impact landscapes was chosen based on similarity in vegetation groups, with the aim of maintaining spatial independence with respect to predator daily movements.

In the Glenelg region, we used a replicated control-impact design to compare three impact landscapes that have been poison-baited for foxes at fortnightly intervals for more than 13 years with three paired non-impact landscapes. We surveyed Cobbo-

boonee National Park (impact) and Annya State Forest (non-impact) in January – April 2018 ('replicate 1'), Mt Clay State Forest/Narrawong Flora Reserve (hereafter 'Mt Clay'; impact) and Hotspur State Forest (non-impact) in April – June 2018 ('replicate 2'), and Lower Glenelg National Park (LGNP) South (impact) and LGNP North (non-impact) in March – May 2021 ('replicate 3'). For replicates 1 and 2, the paired landscapes were separated by at least 8 km, a distance very unlikely to be traversed regularly by these invasive predators (Hradsky *et al.* 2017b). LGNP South and North are separated by the Glenelg river, which is impassable by terrestrial animals.

In the Otway region, we used a before-after control-impact paired series (BACIPS) design to assess changes related to the introduction of a fox control program. We deployed camera-trap grids in a pair of impact – non-impact landscapes from June to September in three years (2017, 2018, 2019), in the Great Otway National Park and Otway Forest Park. Our first survey occurred approximately three months before fox-baiting began. Fox-baiting commenced in the impact landscape in November 2017. Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait replacement until July 2018. The second survey was conducted six months after fox-baiting commenced, however poison bait replacement lapsed from near the beginning of the survey until nearly three months afterwards. Fox-baiting at monthly intervals recommenced in December 2018, six months prior to the start of the final survey (Fig. C.1). The impact and non-impact landscapes were at least 4.2 km apart through dense forest, a distance unlikely to be regularly traversed by these invasive predators, although possible (Hradsky *et al.* 2017b). In this study, and a concurrent study which identified individual foxes through genetic sampling (M. Le Pla *et al.*, in review), we found no evidence that either foxes or cats moved between the impact and non-impact landscapes.

In each landscape, we established a grid of 49 – 110 sites (mean = 88), averaging 448 m apart (range: 194 – 770 m). At each site, we set up a Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an infrared flash and temperature-in-motion detector on a tree, facing a tuna oil lure; see Appendix C section C.1 for details. Overall, we deployed 1051 functional camera-traps, which operated for an average of 65 days (range: 12 – 93 days), totalling 68,504 trap nights (Table C.1).

4.2.3 Individual feral cat identification

We sorted the camera-trap images of cats into five categories based on coat type: black, mackerel tabby, classic tabby, ginger and other; Fig. C.3, and identified individual feral cats within each category; see Appendix C section C.2 for details. In the Otway region, 40% of cat detections were of black cats with few identifiable markings, so we did not attempt to identify any black cats here. In the Glenelg region, black cats were rarer (not detected at two landscapes) and often more distinctive, and so we could identify some individuals (Table C.1).

4.2.4 Spatial fox occurrence

We could not use raw fox presence-absence data from the camera-traps to predict cat density, as spatial mark-resight models require covariate values for each grid cell in which density is estimated (see Section 4.2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but do not account for imperfect detection.

We built the fox occurrence models using the ‘mgcv’ R-package (version 1.3.1; Wood 2011). We modelled fox presences and absences (response variable) across space (explanatory variable) separately for each region, with a duchon spline spatial smooth; these provide better predictions at the edge of surveyed space than other splines (Miller & Wood 2014). In the Otway region, we included a random intercept for each camera-trap site to account for repeat sampling and did not share spatial information across years. Differences in camera-trap deployment lengths were accounted for using a model offset.

4.2.5 Spatial mark-resight models of feral cat density

We used a spatial capture-recapture approach to estimate cat density (Borchers & Efford 2008). These models use counts of detections and non-detections of individual animals at trap locations (accounting for trap-specific survey effort) to estimate the location of each individual’s activity centre. They commonly assume that individuals have approximately circular home ranges, spend the majority of time in the centre of their range (‘activity centre’), and that the probability of observing an individual decreases with distance from the activity centre. Two detectability parameters govern this process: g_0 , the probability of detecting an individual per occasion in their activity centre, and sigma: a spatial scale parameter which relates to home range size. Multiple candidate shapes for the decline in detectability with distance from the activity centre (‘detection function’) can be modelled. Spatial capture-recapture models have been extended to consider situations where not all individuals in a population are identifiable (i.e., some are unmarked; Chandler & Royle 2013). These models typically assume unmarked individuals to be a random sample of the population, sharing the same detection process as marked individuals, allowing density to be estimated for the entire population.

We used closed population, sighting-only, spatial mark-resight models to estimate cat density using the maximum likelihood ‘secr’ R-package (Efford 2021). Detections of the ‘mark status uncertain’ category (unidentifiable cats), cannot be handled in the ‘secr’ R package; we added them to as ‘unmarked’ detections (black cats) rather than discard them (following Moseby *et al.* 2020). We condensed unmarked detection histories to a binary presence-absence record per each camera-trap for a 24-hour length duration (‘occasion’), beginning at midday. We ran separate models for each region

and treated each camera-trap grid deployment as a ‘session’. We created a 4000-m buffer zone around each site (which was truncated by the river in LGNP), and estimated cat density at a 200-m grid cell resolution within this area. These habitat mask specifications were based on initial model trials and our knowledge of cat behaviour in these regions; the aim was to ensure density was estimated over a large enough area to encompass the activity centres of all cats exposed to our camera-traps, at a fine enough spatial scale to minimise bias in density estimates.

For each region, we ran four sets of models. We chose (1) between half-normal and exponential detection functions and (2) ‘base model’ covariates to carry through to subsequent model sets, (3) tested for associations between fox occurrence and cat density at a fine spatial scale, and (4) experimentally evaluated the effect of fox control on cat density at the landscape scale. Each step is described in more detail below. We compared competing models using small-sample corrected Akaike Information Criterion (hereafter ‘ AIC_c ’) scores (Burnham & Anderson 2004) and examined the confidence intervals around estimated model coefficients. Each step is described in more detail below.

The second set of models established the base covariates for each region. We hypothesised that cat detectability might decrease over each survey due to the scent of the tuna oil lure fading. To account for this, we modelled a linear trend in g_0 over the survey duration for each camera-trap. We further hypothesised that cat density might differ between vegetation types. We classed the vegetation into three dominant types for each region: cleared land, heathy vegetation, and either dry forest (Glenelg region) or wet forest (Otway region); see Appendix C section C.6 for details. We compared these covariates as single and additive models, as well as to a ‘null model’ (density and detectability constant) - carrying supported covariates forward to subsequent model fits.

The third set of models directly tested the associations between fox occurrence and cats within each region. We tested three hypotheses for each region: (i) fox occurrence only affects cat density, (ii) fox occurrence only affects cat detectability (both g_0 and sigma concurrently; Efford & Mowat 2014), (iii) fox occurrence affects the density and the detectability of cats, against (iv) the null hypothesis that there was no association between fox occurrence and cats. We used the spatial fox occurrence estimates (detailed in Section 4.2.4) as the explanatory variable. As predator associations may be nonlinear (Johnson & VanDerWal 2009), we tested these effects as linear and non-linear terms using regression splines (generalised additive models called within the ‘secr’ R-package). We included year as a cat density covariate in all the Otway region models to account for repeat sampling and compared to a null model without any fox occurrence effects using AIC_c scores.

The fourth set of models examined the effects of fox-baiting at a landscape scale within each region. We fitted a model that estimated cat density separately for each landscape, and used AIC_c scores to choose whether to model detectability as a function of predicted fox occurrence (as per hypothesis ii in the second set of models above)

or constant. We then derived the response ratio (estimated difference in cat density in the impact landscape relative to the paired non-impact landscape, back-transformed to the response scale) for the top-ranked model. We used visual inspection of the 95% confidence intervals around the density estimates to evaluate whether fox control increased cat density at a landscape level (Cumming & Finch 2005). For the Glenelg region (replicated control-impact design), we assessed whether each confidence interval around the relative difference in cat density in the impact landscape to the paired non-impact landscape (i.e., ‘response-ratio’) overlapped one; overlap would indicate no difference in cat density. For the Otway region (BACIPS design), we assessed how much the confidence intervals around the estimated difference between impact and non-impact landscapes overlapped between years; we expected that the response-ratio would increase over the years, indicating an increase in cat density following the introduction of fox control.

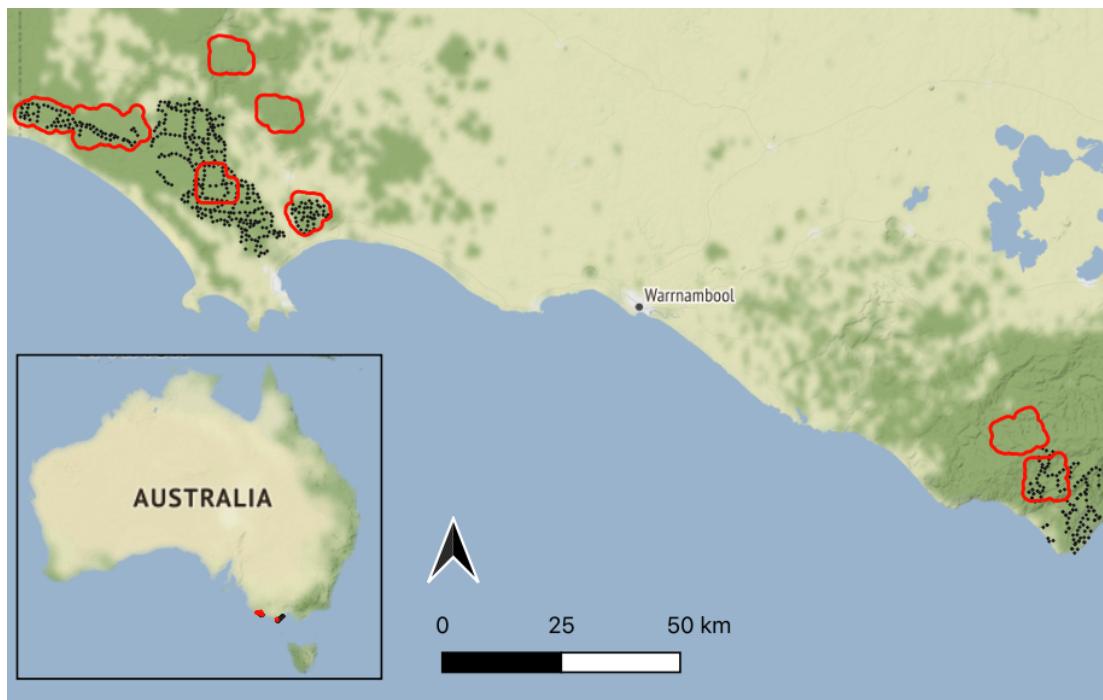


Figure 4.1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river. Locations of fox poison-bait stations are denoted by black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.*

4.3 Results

4.3.1 Fox occurrence

In the Glenelg region, there was a clear difference in fox occurrence between paired impact (poison-baited) and non-impact landscapes for replicates 1 and 3, but only a marginal difference for replicate 2 (Fig. 4.2). In the Otway region, fox occurrence increased by 22% in the non-impact landscape, and decreased by 43% in the impact landscape over the three years (occurrence probability averaged at each camera-trap in the landscape). Fox occurrence in the Otway region was generally lower than the Glenelg region, with less fine-scale spatial variation. For example, fox occurrence was predicted to be spatially consistent across the entire Otway region in 2018 (Fig. 4.2). Fox model summaries and spatial standard error estimates are presented in Appendix C section C.5.

4.3.2 Feral cats in the Glenelg region

Across the six landscapes in the Glenelg region, we recorded 251 cat detections from 32,232 camera-trap nights (Table C.1). We were able to identify 64% of cat detections to the individual level; a total of 67 cats (6 – 13 individuals per landscape). The exponential detector function was supported over the half-normal function (Table C.2). The null model was more strongly supported than models with vegetation impacts on cat density and/or linear time trends on g_0 (Table C.3).

At a fine spatial scale, the model with a linear relationship between fox occurrence and cat density was strongly supported (AIC_c 2.76 better than the null; Table C.4). It indicated that cat density declined as fox occurrence increased (-0.32; 95% CI: -0.57 - -0.07; Fig. 4.3). There was no evidence of an impact of fox occurrence on cat detectability (Table C.4). Regression splines added additional model parameters without changing predictions (Fig. 4.3), and so, all nonlinear models ranked below their linear counterparts (Table C.4).

Our hypothesis that cat density would be higher in landscapes with fox control was supported for the first and third replicate pairs: estimated cat densities were 2.5 (95% CI: 1.5 - 4.2) and 3.7 (95% CI: 1.4 - 9.5) times higher in the impact landscape than the paired non-impact landscape, respectively (Fig. 4.5). For the second landscape pair, however, the estimated difference was positive but negligible (1.1; 95% CI: 0.69 - 1.69). At the landscape level, there was some evidence that cat detectability was affected by fox occurrence; however the AIC_c score was only 0.95 units better than the constant detectability model (Table C.5) and the estimated effects were weak with high uncertainty. The detectability of cats in their activity centre (g_0) tended to increase with the probability of fox occurrence (0.24; 95% CI: -0.32 - 0.80), as did sigma (0.13; 95% CI: -0.14 - 0.41).

4.3.3 Feral cats in the Otway region

In the Otway region, we recorded 970 cat detections from 36,272 camera-trap nights (Table C.1). We were able to identify 53% of cat detections to the individual level; a total of 93 cats (20 – 30 individuals per landscape). The exponential detector function was strongly supported over the half-normal function (Table C.7). The null model was more strongly supported than the models with vegetation impacts on cat density and/or linear time trends on g_0 (Table C.8).

There was some evidence that cat density was negatively correlated with fox occurrence at a fine spatial scale: the two top-ranked models included a linear and a non-linear effect of fox occurrence on cat density, respectively; however, a model without a fox occurrence term received similar support ($dAIC_c = 0.80$; Table C.9). The 95% confidence interval around the linear coefficient from the top-ranked model marginally overlapped zero (-0.26; 95% CI: -0.55 - 0.02) indicating that cat density declined as fox occurrence increased in the Otways at a similar rate to Glenelg, but with slightly greater uncertainty (Fig. 4.3). However, the equivalent nonlinear model predicted that cat density only declined (at a steeper rate) in the mid-high range of fox occurrence probability (Fig. 4.3). Equivalent pairs of linear model and nonlinear models were indistinguishable based on AIC_c scores (Table C.9). There was also strong support for an effect of fox occurrence on cat detectability at a fine spatial scale (Fig. 4.4; Table C.10). Where fox occurrence was higher, cats were less detectable in their activity centres (i.e., negative association with g_0 ; -0.69; 95% CI: -1.11 - -0.27; Fig. 4.4A) and ranged further (i.e., positive association with sigma; coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 4.4B). The equivalent nonlinear model predicted detectability changes to have occurred only in the low-mid range of fox occurrence (Fig. 4.4).

Our hypothesis that cat density in the impact landscape would increase relative to the non-impact landscape with fox control was supported, however there was considerable uncertainty. Cat density tended to be lower in the impact than non-impact landscape prior to fox-baiting (i.e., in 2017), although the confidence intervals for the two density estimates overlapped substantially (Fig. 4.6). In 2018, cat density decreased in the non-impact landscape and increased in the impact landscape, converging to near-identical density estimates. These patterns continued into 2019, with cat density now somewhat higher in the impact landscape than non-impact landscape. Overlap in the response ratio confidence intervals for successive years was high, but the comparison between 2017 to 2019 suggests a meaningful increase in cat density at the impact landscape relative to the non-impact landscape (Fig. 4.6B). Like the fine scale model, there was strong evidence that cat detectability was impacted by fox occurrence (Table C.10).

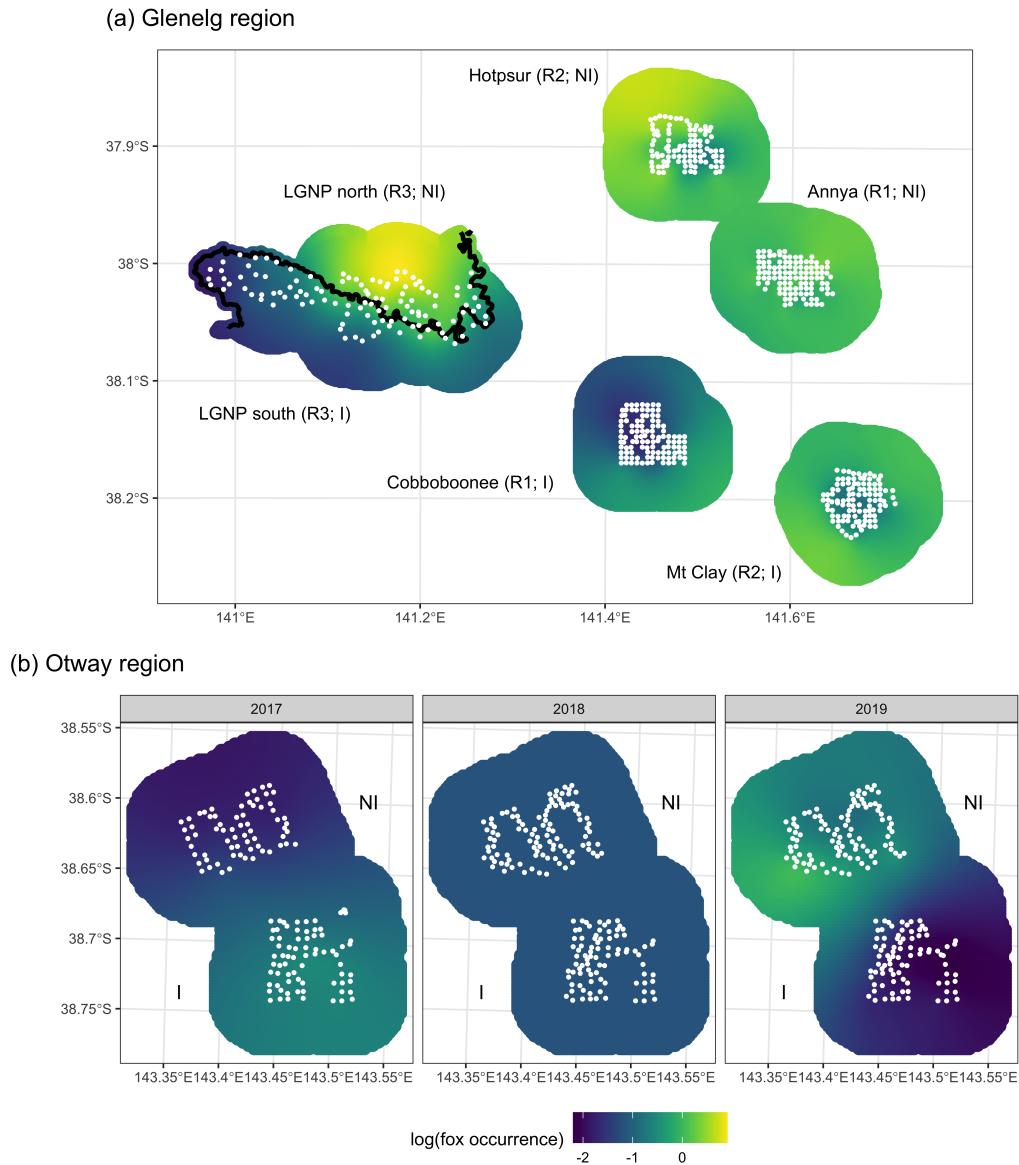


Figure 4.2: Predicted red fox *Vulpes vulpes* occurrence derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. White dots represent camera-trap sites. Predicted fox occurrence was used as a predictor of feral cat *Felis catus* density in the spatial mark-resight models.

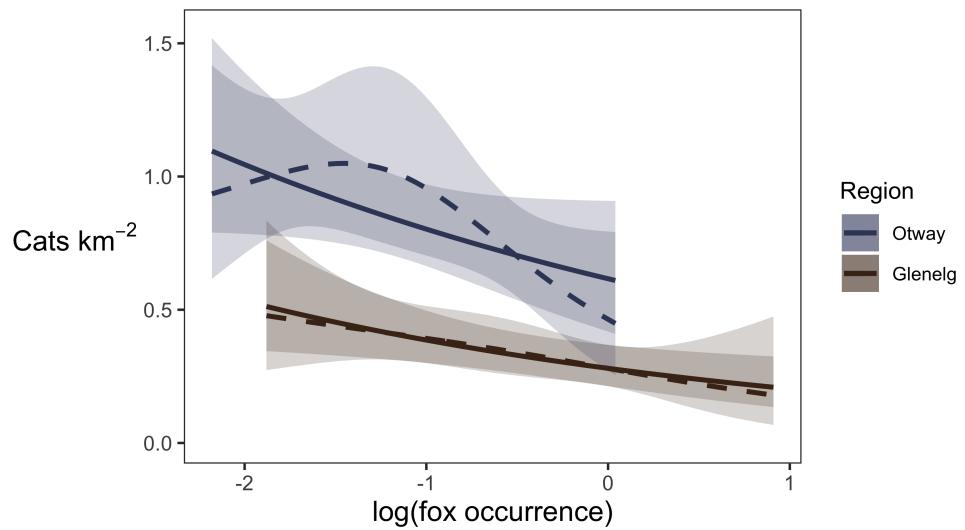


Figure 4.3: Linear (solid lines) and nonlinear (dashed lines) models predicted that feral cat *Felis catus* density increased with declining probability of red fox *Vulpes vulpes* occurrence (log-transformed) in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.

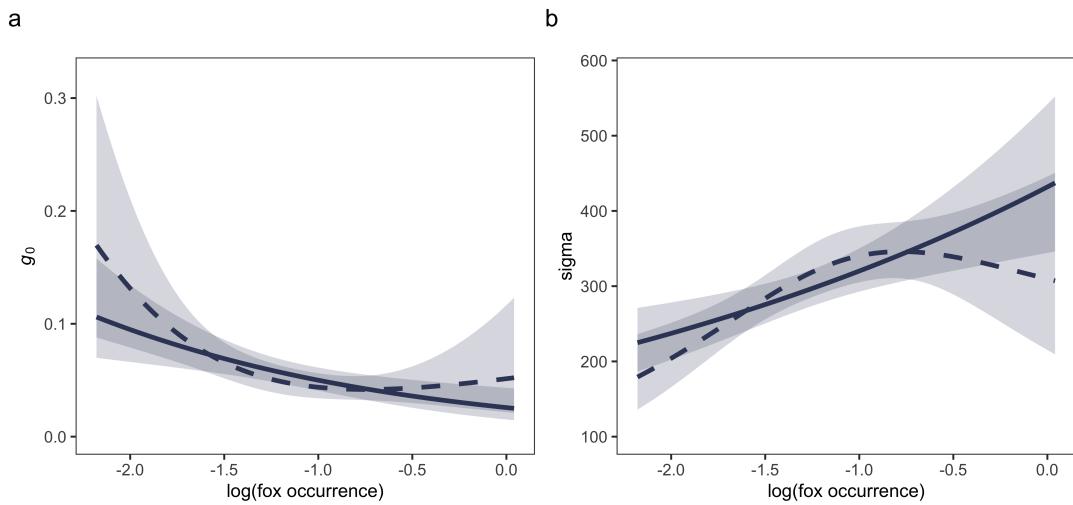


Figure 4.4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-transformed red fox *Vulpes vulpes* occurrence in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0) decreased with the probability of fox occurrence (a), while sigma (which is related to home range size; exponential detection function) increased (b). Shaded areas indicate 95% confidence intervals.

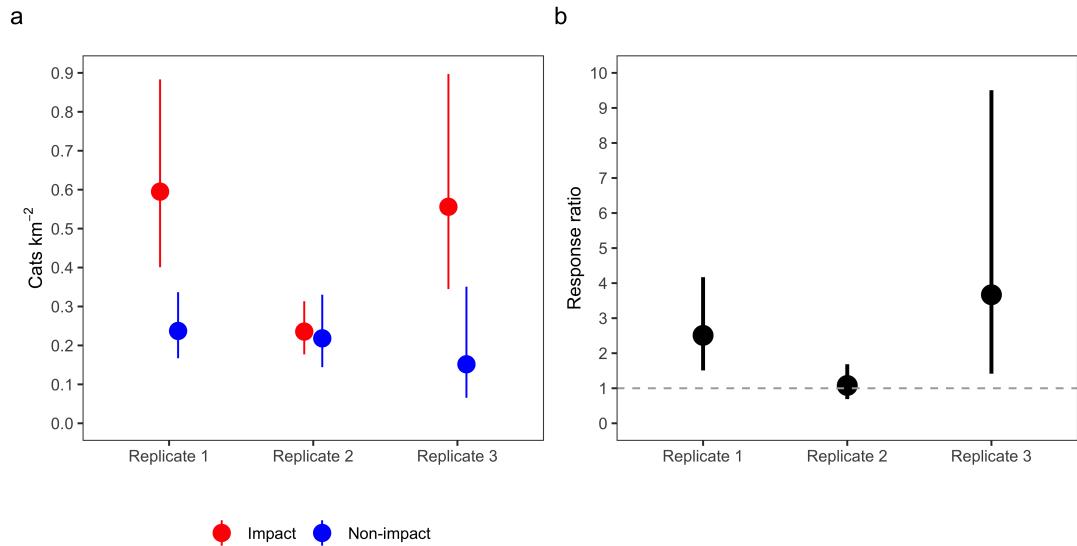


Figure 4.5: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the paired non-impact landscape for each replicate (b) in the Glenelg region, Australia. Poison-baiting for foxes *Vulpes vulpes* has been conducted in the impact landscapes for more than 13 years. Grey dashed line represents no difference between the paired landscapes. Error bars represent 95% confidence intervals.

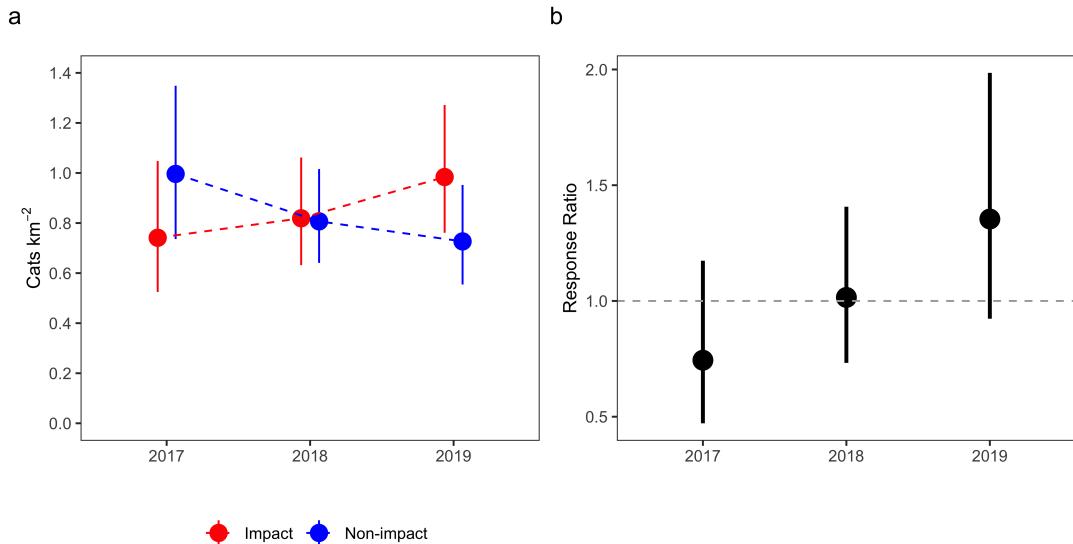


Figure 4.6: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the non-impact landscape for each survey year (b) in the Otway region, Australia. In 2017, surveys were conducted approximately two months before lethal red fox *Vulpes vulpes* control commenced in the impact landscape; control lapsed for six months prior to the 2018 survey. Error bars represent 95% confidence intervals. Overlap with the grey dashed line in (b) represents no difference in density between the paired landscapes for that year; the proportion overlap between response ratio confidence intervals across years provides evidence for a change in difference.

4.4 Discussion

Our study is one of the first to provide replicated, experimental evidence that apex predator suppression can increase mesopredator population density. Our study provides two lines of evidence that foxes can exert top-down control on feral cats in the forests of south-eastern Australia: feral cat density was (1) higher where fine-scale fox occurrence probability was lowest, and (2) commonly higher in landscapes where fox control occurred. This is alarming because targeted fox control is a widely used conservation strategy; this unintended consequence could dampen benefits to native prey and even further threaten these species. However, as our findings highlight, mesopredator release of cats following fox control is unlikely to occur universally; the degree of fox suppression varies and fox-cat interactions are likely to be context and scale-dependent. More broadly, our study illustrates how correlative and experimental approaches provide complementary lines of evidence when investigating interactions between predator species, and the importance of disentangling changes in population density from changes in detectability.

We were able to exploit a gradient in fox occurrence caused by lethal control to investigate associations between cat density and fox occurrence at a fine spatial scale across two separate regions. At this scale, we observed a consistently negative association between cat density and fox occurrence, supporting our first hypothesis, although there was more uncertainty around the relationship in the Otway region. We acknowledge that it could also simply reflect differences in niche preference, rather than foxes excluding cats or cats avoiding foxes. However, we consider this unlikely given we observed the relationship across an artificial gradient of fox occurrence caused by lethal control.

There is contention around whether linear regression is appropriate for investigating correlations between different predator species, as subordinate predators may only be suppressed when apex predator abundance is high (Johnson & VanDerWal 2009). We found no evidence of non-linear associations between foxes and cats in the Glenelg region, while linear and non-linear models performed equally well in the Otway region. Non-linear models in the Otway region predicted that cat density declined only in the mid-high range of fox occurrence, while behavioural changes were seen in the low-mid range of fox occurrence. Perhaps cats can successfully avoid foxes through behavioural change where foxes are rare, but this is ineffective where foxes are common. This could explain the lack of evidence for foxes impacting cat detectability in the Glenelg region where fox occupancy is relatively high. Alternatively, behavioural changes may be untenable for cats in the Glenelg region because small mammal abundance is relatively low and fox avoidance strategies likely come at the expense of hunting success (Sih 1980; Wilson *et al.* 2010).

Where fox occurrence was higher in the Otway Ranges, cats were less detectable in their activity centres and ranged further (Fig. 4.4). Low detectability is likely to correlate with fewer apex predator encounters, and has been observed in other predator interaction studies (e.g. Lombardi *et al.* 2017). An increase in cat ranging behaviour

(sigma) with fox control supports observations made by Molsher *et al.* (2017), and may reflect a direct avoidance strategy. Animal movement rates are expected to increase in response to unpredictable threats (Riotte-Lambert & Matthiopoulos 2020). Alternatively, cats may consider foxes predictable and avoid locations they frequent, thus having to range further to obtain the same amount of food resources. In a similar forest habitat, Buckmaster (2012) observed large ‘holes’ in the home range of each GPS-collared cat; they confirmed that this was not due to an absence of prey and hypothesised that it could be due to apex predator avoidance. Regardless of the cause, variation in mesopredator detectability and movement rates with apex predator populations has serious implications for the interpretation of studies that compare relative abundance indices and spatial overlap of predator species without disentangling behaviour and detectability from density (Efford & Dawson 2012; Neilson *et al.* 2018; Stewart *et al.* 2018; Broadley *et al.* 2019).

In the Glenelg region where fox-baiting had occurred for more than 13 years, feral cat density was considerably higher in two out of three distinct landscapes than in similar, unbaited landscapes. The outlier is most likely due to limited suppression of foxes at Mt Clay despite ongoing fox control (Fig. 4.2). Mt Clay is a small forest block surrounded entirely by unbaited farmland. Simulation modelling indicates that the size of the baited area is a key driver of the degree of reduction in the fox population (Hradsky *et al.* 2019; Francis *et al.* 2020). Studies of fox-cat (and other predator-predator) interactions often use the presence of a management program as a proxy for lower apex predator abundance and distribution (e.g. Hunter *et al.* 2018). Our findings strongly indicate the need to directly measure the apex predator population in order to reliably interpret the responses of subordinate species (Salo *et al.* 2010).

In the Otway region, we observed a weaker-but increasing–effect of fox control on cat density, to be expected from a recently commenced and less intensive fox-baiting program. The short duration of baiting in the Otway region may mean that changes in adult cat density are yet to fully manifest as foxes potentially suppress cats by reducing recruitment rates. Cats may also respond to an increase in shared prey availability following fox suppression (Stobo-Wilson *et al.* 2020a). A time-lagged release of cats following fox control would explain eruptions and subsequent crashes commonly observed in shared mammalian prey populations two to ten years following fox control commencement (Duncan *et al.* 2020). Alternatively, top-down suppression by foxes and competition may be weaker in this highly productive environment where prey abundance was relatively high, fox occurrence was already relatively low, and overall cat densities were consistently high (Johnson & VanDerWal 2009; Greenville *et al.* 2014; Newsome *et al.* 2017). Our surveys provide important baselines against which to compare future changes in predator populations as the fox-baiting program continues.

Our study is among the very few which have used a direct measure of density to test mesopredator release. Previous studies have mostly used live capture-rates to infer population density, without accounting for behavioural or detectability changes (e.g. Arjo *et al.* 2007; Karki *et al.* 2007; Thompson & Gese 2007; Berger *et al.* 2008; Jones

et al. 2008). Contention about mesopredator release has centred on such methods (Hayward *et al.* 2015); as well as unaccounted species interactions in complex predator guilds (Levi & Wilmers 2012; Jachowski *et al.* 2020). In contrast, our study tests the mesopredator release theory using a combined behavioural and numerical approach, in a system with a simplified carnivore guild. One limitation of our approach is that uncertainty from our fox occurrence models was not propagated into the spatial mark-resight models. A full Bayesian integration of the fox occurrence analysis and the spatial mark-resight model to address this is not yet implemented. The development of open population spatial mark-resight models would also improve parameter estimates for multi-season surveys.

The results of our study may explain why pest management that only targets foxes—one of the most prevalent conservation actions in Australia—does not consistently improve native prey persistence (Dexter & Murray 2009; Robley *et al.* 2014; Wayne *et al.* 2017; Lindenmayer *et al.* 2018; Duncan *et al.* 2020). More evidence is required to understand the circumstances in which lethal fox control increases cat density, particularly the role of baseline fox and prey densities. A more integrated approach to invasive predator management, where foxes and cats are simultaneously or otherwise optimally controlled could substantially improve biodiversity outcomes (Risbey *et al.* 2000; Comer *et al.* 2020). If this is not feasible, changes in invasive mesopredator density and the outcomes for native prey species should be closely monitored as part of any control program for invasive apex predators, with triggers for ceasing apex predator control or commencing integrated management if single-species control proves counterproductive for the conservation of threatened prey species.

Chapter 5

Spatiotemporal shifts in predator behaviour across habitats, individuals and threats.

Abstract

Most animals have to trade-off resource acquisition against avoiding top predators in space or time. This is likely to be particularly difficult to balance when subordinate species occupy a similar function niche to the apex predator - when resource competition is high. The decline of a top predator may therefore alter the spatial or temporal behaviour of a subordinate species by relaxing the suppressive effects of fear. However, this is difficult to understand or predict because there are not many statistical approaches which consider joint consider animal behaviour across space and time (as in the 24-hour cycle).

In this study, we investigated whether the lethal suppression of an introduced apex predator (red fox *Vulpes vulpes*) led to a behavioural release of a subordinate invasive mesopredator (feral cat *Felis catus*). We experimentally monitored predators across two red fox control programs in temperate south-eastern Australia, using 3667 camera-trap deployments. We used generalised additive models to estimate how the spatiotemporal activity of invasive predators vary across heterogeneous landscapes, as well as investigate whether feral cat activity changes across (artificially manipulated) fox activity gradients, and how diel activity varies across individual cats.

We observed patterns consistent with top-down behavioural suppression: across three replicates, feral cats altered diel—not spatial—patterns to less risky times of the day when red fox activity was high. Temporal avoidance of foxes was flexible; presumably dependent on fox diel activity patterns. This ranged from subtle shifts (concentrating activity around the least risky times) to near reversal of diel activity - from mostly nocturnal to diurnal activity. Changes in diel activity may facilitate spatial

coexistence between these two invasive predators, although is likely to alter feral cat impacts on native prey.

Our study highlights the importance of considering spatiotemporal patterns avoidance together and we provide a flexible generalised additive modelling framework for assessing variation in spatiotemporal animal behaviour. Notably, apparent diel avoidance behaviours depended on finescale spatial risk of top predator encounter. Averaging predator behaviour across heterogenous landscapes can overlook considerable behavioural variation. Similarly, estimating spatial and temporal overlap between two species can overlook finescale interactions.

5.1 Introduction

Top predators shape ecosystems through predation as well as the fear of predation-regulating both the number of individuals and the spatiotemporal behaviour of subordinate species (Ritchie & Johnson 2009). Some posit that behavioural suppression can be more detrimental to populations of subordinate species (both smaller ‘mesopredators’ and prey) than predation itself (ref). Antipredator behaviour may not only reduce individual and population-level fitness, but alter species interactions, ecological functions and human-wildlife coexistence (e.g. Lamb *et al.* 2020). Understanding how top predators constrain the behaviour of subordinate species is a key component of predicting ecosystem-wide consequences of predator management, such as reintroductions and lethal control.

Subordinate species can limit or change their use of the spatial and temporal (i.e., daily cycle) niches to avoid predators in space and/or time. For example, following the reintroduction of wolves *Canis lupus* in Yellowstone National Park, elk *Cervus elaphus* shifted the time of day they used risky, open landscapes (Kohl *et al.* 2019). Because precautionary avoidance of predators can be costly and predation risk is spatiotemporally variable, animals likely have flexible antipredator responses (Sih *et al.* 2000; Berger *et al.* 2001). There is a trade-off between predator avoidance and resource acquisition (Sih 1992), and so, animals may have to readjust spatiotemporal behaviour to balance this trade-off across heterogeneous landscapes. Limited inference around avoidance behaviours can be drawn from studies which only consider one spatial or temporal dimension, or assume predator avoidance to be constant.

Further, behavioural avoidance decisions can vary from individual to individual (Quinn *et al.* 2012; Bonnot *et al.* 2014; Basille *et al.* 2015). Variation may due to population demographics (e.g. age, sex), threat naivety, resource-preferences, learned culture (refs). Understanding variation in behavioural traits is important because populations with high individual heterogeneity may be more adaptable to threats (Wolf & Weissing 2012) or resistant to management (Swan *et al.* 2017). Behavioural traits also impact ecosystem function. For example, a diurnal predator likely preys on different species than nocturnal counterparts. Even when information on individual diel activity patterns is available, studies predominantly estimate these patterns at the population-level due to small sample sizes (e.g., Kohl *et al.* 2019).

The decline of top predators is expected to cause a ‘mesopredator release’ of subordinate predators, which could potentially lead to localised prey extinctions (Crooks & Soulé 1999; Prugh *et al.* 2009). There is particular concern around mesopredator release in ecosystems with multiple sympatric introduced predators (Doherty & Ritchie 2017). For example, the red fox *Vulpes vulpes* (hereafter ‘fox’; ~6 kg) and feral cat *Felis catus* (hereafter ‘cat’; ~4 kg) have devastating impacts on native prey throughout their introduced range, implicated in the decline of XX and XX species, respectively (Doherty *et al.* 2016). Cats are more difficult to manage, and so, foxes are far more commonly controlled with lethal techniques (namely poison-baiting). There is some evidence that cats, who compete for many of the same resources as foxes (Glen & Dick-

man 2005), can increase in density and change behaviour following fox control (Rees et al. in review; Molsher *et al.* 2017). Other studies have investigated behavioural interactions between these invasive predators (e.g., Roshier & Carter 2021), but not in a joint spatiotemporal framework or where cat avoidance behaviours are allowed flexibility in respect to fox encounter probability.

There are few statistical approaches which consider animal activity in a joint spatiotemporal framework (temporal as in the daily cycle). Instead, ‘landscapes of fear’ (Gaynor *et al.* 2019) are usually modelled in an ad-hoc fashion: separate models for spatial and temporal avoidance, or by repeating spatial analyses (namely resource selection functions) at different time periods (e.g., Smith *et al.* 2019; Basille *et al.* 2015; Kohl *et al.* 2019) and vice versa (refs). However, discretising the daily cycle into categorical periods (e.g., day and night) introduces bias and assumes animals to have a complete step-changes in behaviour, rather than progressive changes across the daily cycle. Generalised additive models (hereafter ‘GAMs’) are increasingly being used to estimate animal diel activity patterns with cyclical splines - matching up the late night to early morning. There are many other benefits to GAMs, including smoothing penalties to reduce overfitting, nonlinear interactions of multiple variables with different units (‘tensor products’) and hierarchical specifications to share information across groups (Wood 2017; Pedersen *et al.* 2019). However, we are only aware of one study which allowed animal diel activity to interact with a continuous variable such as predation risk in a GAM (without incorporating spatial activity; Cunningham *et al.* 2019).

Here we illustrate how generalised additive models can be used to jointly assess spatial and temporal animal activity patterns, using two competing invasive predators as a case-study: foxes and cats. We investigated how the diel activity patterns of each predator vary across (1) space and (2) vegetation types, as well as (3) in response to fox spatial activity for cats and (4) among individual cats. We tested this in a simple predator system where only cats and foxes occur, and fox activity is manipulated using lethal control. This allowed sole focus on the interactions between these two predators, across an artificial gradient of apex predator (fox) activity.

5.2 Methods

We collated camera-trap data from three studies across two distinct regions in south-west Victoria, Australia: the Glenelg region and Otway Ranges (Fig. 5.1). Introduced foxes and cats are the only medium-large functional mammalian terrestrial predators across both regions: native dingoes *Canis familiaris* are long absent throughout, tiger quolls *Dasyurus maculatus* are long-absent in the Glenelg region and likely functionally extinct in the Otway Ranges (last confirmed sighting in 2014 despite extensive camera-trapping). In broad sections of each region, government land managers conduct ongoing targeted fox control for biodiversity conservation. Poison baits containing 3 mg of sodium mono-fluroacetate ('1080') are buried at a depth of 10 cm at 1-km intervals along accessible forest tracks and roads.

In the Glenelg region, Gunditjmara country, large patches of natural vegetation—mostly lowland forests and heathy woodlands—are fragmented by pastoral farming and residential properties (Fig. 5.1). Foxes have been subject to lethal control in three distinct forest blocks since October 2005, with 1080 poison-baits replaced fortnightly (Robley *et al.* 2014). Three similar, but unbaited, forest blocks to the north are surveyed simultaneously as an experimental control (Robley *et al.* 2020).

The Otway Ranges, Gadubanud and Wadawurrung country, is a largely continuous patch of natural vegetation with a strong east-west rainfall gradient. A matrix of cool temperate rainforest and wet forest at high-altitudes in the south-west descend into a large heathland directly north, and into dry forests and then heathlands to the north-east. Foxes are controlled through 1080 poison-baits with monthly replacement across most of the Otway Ranges, but a large section to the north-west remains unbaited. Fox-baiting commenced in some small sections in 2008 but the majority of baiting began in 2016 - 2017.

5.2.1 Camera-trap surveys

We compiled camera-trap data from three distinct studies across the two regions; totalling 3667 deployments of camera-traps at 1232 camera-trap sites. The purpose of each study was to quantify changes in the mammalian community due to fox control. Fox control had been occurring in treatment landscapes for 8 - 14 years by the time of these camera-trap surveys; sites in the Otways Ranges were surveyed initially before and up to 3 years following the commencement of fox control.

All camera-trap deployments consisted of a Reconyx (Holmen, Wisconsin) brand camera-trap (white or infrared flash), attached to a tree or a metal picket, facing a lure. One study across both regions (M.W.R PhD surveys; 949 deployments at 620 unique sites) positioned camera-traps low on a tree (around 15 - 30 cm above the ground – angled only slightly downwards) facing a tuna oil lure approximately 2 - 2.5 m away (detailed in Rees *et al.* 2019). The others two studies (Glenelg Ark and Otway Ark fox control program annual monitoring; 1616 camera-trap deployments at 240 sites

and 1113 deployments from 372 sites, respectively) positioned camera-traps higher on a tree or a metal picket (at least 40 cm above ground) and angled more strongly downwards toward a lure approximately 1 - 1.5 m away (Robley *et al.* 2020). These lures consisted of peanut butter, golden syrup and rolled oats mixed into a small ball, placed within a tea strainer or PVC pipe container and secured either to the ground, or 20 - 60 cm above ground on a wooden stake. All set-ups were effective in detecting both predator species.

Camera-traps were active for an average of 47 days, totalling 172,052 trap-nights. Camera-trap spacing was variable; the average minimum distance between simultaneously deployed camera-traps was 445 m, 853 m and 1266 m, respectively. Camera-traps were deployed in the Glenelg region between 2013 – 2019, and in the Otway Ranges between 2016 – 2019.

5.2.2 Data preparation

All data analysis was conducted in R version 3.6.3 (R Core Team 2020). We first created a table of species detections and deployment information (coordinates, dates) for each camera-trap deployment. We then used lorelograms to identify the minimum interval to approximate independence (Iannarilli *et al.* 2019); this indicated discarding repeat detections of a species within 30 minutes was sufficient to reduce temporal autocorrelation. To account for day length variation across space and time, we extracted sunrise and sunset times for each camera-trap deployment using the ‘maptools’ R-package (Bivand & Lewin-Koh 2021) and adjusted detection times to be relative to sunrise and sunset using the average double anchoring approach described by Vazquez *et al.* (2019). Using the ‘reshape’ R-package (Wickham 2007), we manipulated the detection table into a dataframe with a row for each hour of the day, for every camera-trap deployment, recording the total number of ‘independent’ fox and feral cat detections within each hour for the entire camera-trap survey duration.

We identified the mapped Ecological Vegetation Class group (“EVC”; DELWP 2020) at each camera-trap location. Eight EVC groups types were surveyed in both regions, although to varying degrees (Table 1). In the Otway region, rainforests are finely interspersed (primarily in low lying gullies) throughout wet and damp forests, and so we merged these groups (hereafter ‘wet forests’). To account for fox control, we calculated the number of poison fox-baits within a 2.3 km radius around each camera-trap for each deployment; this is the average maximum distance foxes in these regions travel from their home range centre (Hradsky *et al.* 2017b). To investigate changes in feral cat diel activity in response to counts of foxes, we calculated the total number of fox detections for each camera-trap deployment, divided by the log of the number of survey days to account for differences in camera-trap survey durations (hereafter ‘adjusted fox counts’).

5.2.3 Generalised additive models

GAMs are essentially generalised linear models with added smoothing functions to allow nonlinear relationships between response and explanatory variables (Wood 2017). The daily cycle of diel activity can be binned into discrete intervals (e.g., hour) and a smooth function of animal activity fitted using a cyclic cubic spline basis where end points of the spline join (e.g., last and first hour of the day). A maximum wigginess is specified and complexity penalised (ultimately to a linear function) to avoid overfitting.

We modelled the total count of each predator for each camera-trap deployment (response variable) with generalised additive mixed-effect models implemented in the ‘mgcv’ R-package (Wood 2017). We used the negative binomial family as overdispersion, but not zero-inflation, was detected using the ‘DHARMA’ R-package (Hartig 2020). We specified a model offset to account for differences in camera-trap survey duration, and a random intercept for each site to account for repeat sampling. For fox models only ($n = 2$), we included a smooth effect of poison-bait density using a thin plate regression spline basis. This formed the base model specification for each model we fitted; models differed in their specification of the cyclical hour smooth in order to provide inference on variations of predator diel activity across the four questions of interest identified in our aims; detailed in the sections below. We plotted models using ‘ggplot2’ and ‘gratia’ R-packages (Wickham 2016; Simpson 2021).

Spatial variation in predator activity

We fit a model for each predator which included a tensor product interaction between a spatial smooth and hourly smooth. This allowed predators to have different activity levels across space (static across the years surveyed), as well as a variation in diel activity across space. Space was modelled using camera-trap coordinates and a duchon spline basis (Miller & Wood 2014). To compare how much activity patterns varied across the daily cycle between locations (relative diel activity pattern strengths), we plotted the percentage increase from the minimum to maximum activity estimate for every predicted location.

Variation in predator activity across vegetation types

We estimated predator diel activity across EVC groups using a hierarchical model specification: a global smoother for hour and group-level smoothers with shared wigginess for the seven EVC groups (i.e. model GS in Pedersen *et al.* 2019). We included a random effect to account for overall differences between the two regions.

Feral cat spatiotemporal avoidance of foxes

Analysis of fox diel activity across EVC groups showed strong similarity between all vegetation groups except wet forests. We hypothesised that cats would temporally avoid foxes by becoming more diurnal in dry vegetation groups where foxes were mostly nocturnal, but not in wet forests where fox activity had little variation across the daily cycle. We therefore modelled fox-induced changes in feral cat diel activity separately for wet and dry vegetation groups. We further split dry vegetation groups by region for replication. We refer to the resulting variable as ‘habitat type’, which had three levels: (i) wet forests and rainforests in the western Otway Ranges (‘wet_otways’), (ii) dry EVC groups of the Otway Ranges (‘dry_otways’) and (iii) the Glenelg region (‘dry_glenelg’).

We used a tensor product of hour and adjusted fox counts smooths to model feral cat diel activity across the range of observed fox activity. We specified this with a by-variable factor smooth to model separate responses for each habitat type. We modelled adjusted fox counts using a thin plate regression spline with shrinkage to penalise the null space in addition to the range space (i.e. shrinking wiggly terms to linear functions) of the spline basis, meaning fox effects could be entirely removed from the model (while the hourly curves could be shrunk to a flat line due the inbuilt range space penalty; Marra & Wood 2011). This model specification allowed five different scenarios: that there was (1) no effect of hour or foxes on feral cats (2) a static hourly effect only, (3) a spatial response to foxes only, (4) a spatial response to foxes and an unrelated static hourly effect, or (5) a spatial response to foxes and an hourly effect which changes across the range of fox counts. We also included a separate spatial smooth (using a duchon spline) to account for the effect of unmodelled environmental covariates (including overall differences in spatial activity between regions) and spatial autocorrelation.

Individual variation in feral cat diel activity

One of the collated datasets identified individual cats based on unique pelage patterns across the wet forests of the western Otway Ranges and four forest blocks in the Glenelg region (Chapter 4). We used this dataset to model individual heterogeneity in cat diel activity using a hierarchical model specification. This included a global smoother which estimated the average diel activity for all detected cats (including unidentifiable cats), along with group-level smoothers for each identified individual, with a common wiggliness (i.e. model GS in Pedersen *et al.* 2019). This model structure penalises functions which deviate strongly from the average response; individual with few detections should take the shape of the global response.

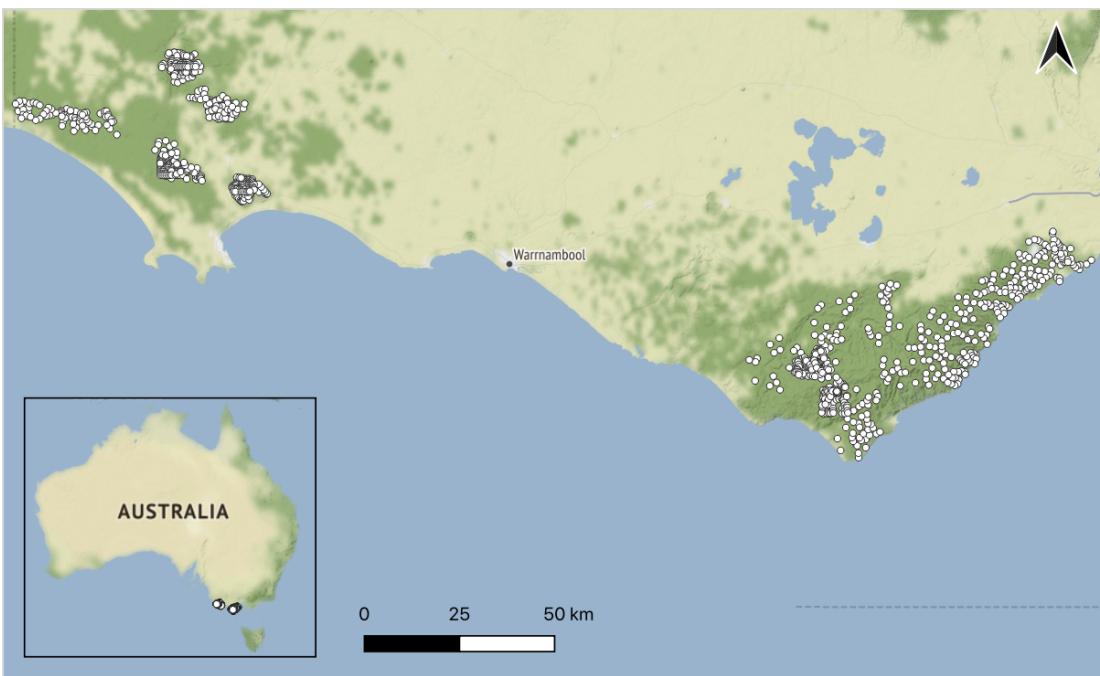


Figure 5.1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.*

5.3 Results

Overall, we collated 5449 and 2202 ‘independent’ (separated by at least 30 minutes) detections of foxes and cats, respectively (Table 5.1. The models explained 18.1 - 35.2% of null deviance ($n = 7$) (**Or spell out for each model is the corresponding section below?**).

Spatial variation in predator activity

Diel activity strength varied across space for both predators (Fig. 5.2). Fox activity was concentrated strongly at particular times of the day, especially in the Glenelg region where activity varied by up to 371% throughout the daily cycle. Feral cats had relatively more consistent activity throughout the daily cycle and across regions; the maximum difference in cat activity throughout the daily cycle for any given location was 185%. Both predators had similar spatial patterns in diel activity strength across space in the Glenelg region, but seemingly opposing patterns in the Otway Ranges. For example, fox diel activity strength was lowest in the wet forests of south-west Otway Ranges, where feral cat diel strength was highest (Fig. 5.2).

Variation in predator activity across vegetation types

On average, both predators occupied similar times of the day—mostly nocturnal with activity peaks around sunrise and sunset (i.e., crepuscular; Fig. 5.3i). The main difference was that fox activity peaked after sunset and they were less likely to be active during the day relative to cats. For foxes, little variation in this pattern was shown across all EVC groups except wet forests, where foxes were nearly as active during the day as they were at night (Fig. 5.3a). On the other hand, cats were nocturnal (and most abundant) in wet forests, but largely crepuscular in all other EVC groups (Fig. 5.3b). Cats tended to be more active at sunset than sunrise. For both predators, the random effect for region (Glenelg or Otways) in the vegetation models shrank to near-zero effect, indicating all variation between the regions was explained by the vegetation covariate and site random intercept. Fox activity similar across EVC groups, except was lower in wet forests. Relative to foxes, cat activity was more variable across EVC groups; lowest in heathy woodlands and highest in wet forests (Fig. 5.3b).

Feral cat spatiotemporal avoidance of foxes

Across all habitat type replicates, feral cats diel patterns changed across the gradient of fox activity (Fig. 5.4). In the Glenelg region and dry Otway habitat types, feral cats had a nocturnal-crepuscular diel patterns where fox activity was low, but were most active during the day where fox activity was high. In contrast, in the wet forests of the Otway Ranges, feral cats were more strongly nocturnal when fox activity was high. Cat spatial activity was relatively unaffected by the fox activity gradient in both

habitat types of the Otway Ranges, but increased with the number of fox detections in the Glenelg region (Fig. 5.4), indicating cats did not avoid foxes spatially.

Individual variation in feral cat diel activity

We had data from 39 individual cats in the Glenelg region and 94 individuals in the western Otway Ranges. Individual heterogeneity in cat diel activity patterns was higher in the Glenelg region than the Otway Ranges (Fig. 5.5). In the Glenelg region, the average diel activity pattern was shrunk to an almost flat line; diel activity curves were estimated nearly separately for each individual (although individuals with few detections were heavily penalised towards a flat line). In the western Otway Ranges, feral cats on average were nocturnal; individuals mostly deviated with different activity peaks near sunrise and sunset times or the strength of diel activity (i.e., difference between high and low activity throughout the daily cycle).

Table 5.1: Summary of the number of camera-trap deployments, unique survey sites and 'independent' counts of invasive predator detections across Ecological Vegetation Class groups within the Glenelg and Otway regions, south-west Victoria, Australia.

Vegetation	Region	Sites	Deployments	Fox counts	Cat counts
Dry Forest	Glenelg	25	69	347	9
	Otways	111	314	341	158
Heathland	Glenelg	40	119	265	59
	Otways	3	9	8	6
Heathy Woodland	Glenelg	154	424	574	96
	Otways	82	256	160	66
Herb-rich Woodland	Glenelg	59	373	863	198
	Otways	2	6	3	2
Lowland Forest	Glenelg	383	1046	1900	290
	Otways	52	163	190	35
Swampy Scrub	Glenelg	4	10	19	8
	Otways	36	98	64	88
Wet Forest	Otways	281	780	715	1187
Total		1232	3667	5449	2202

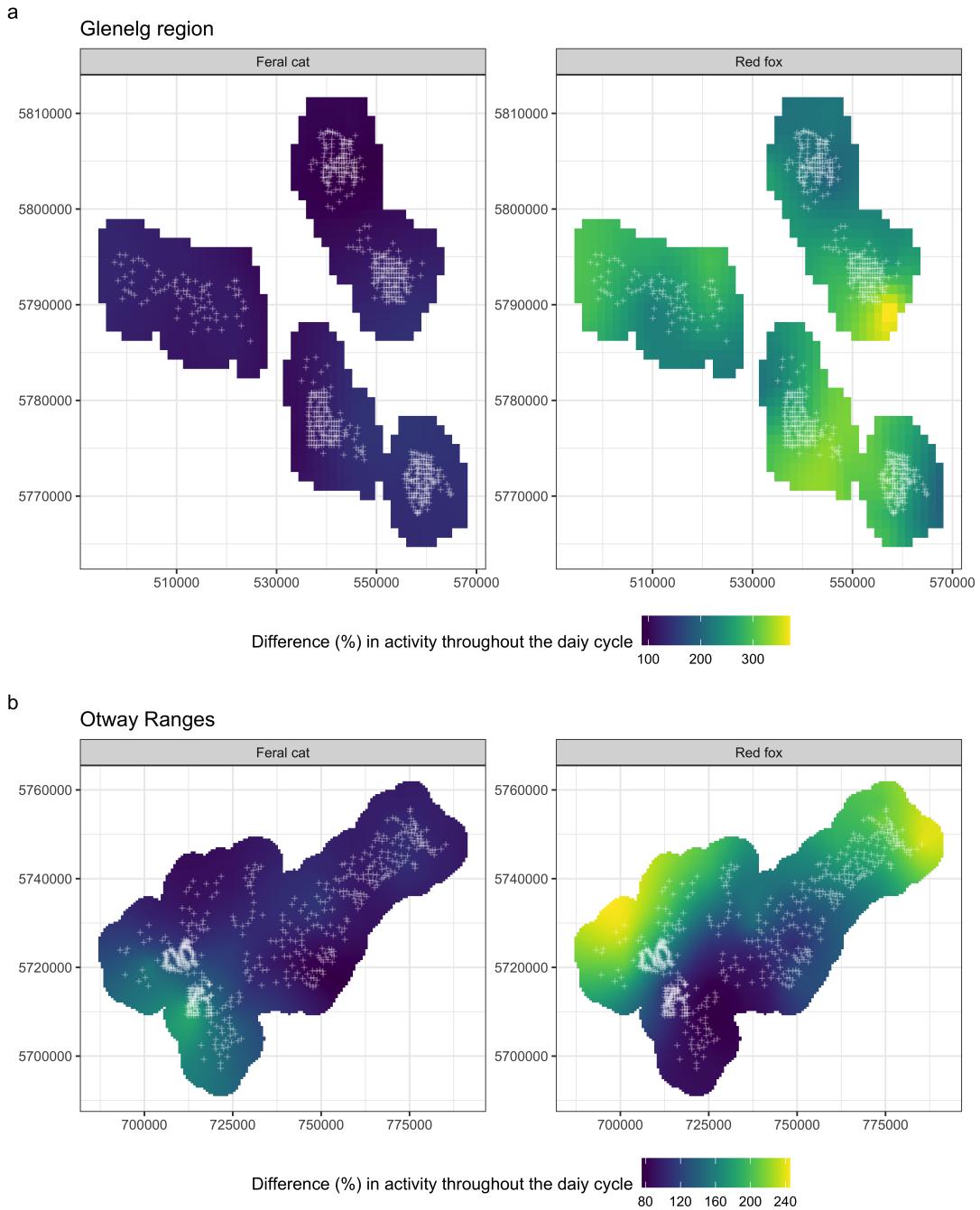
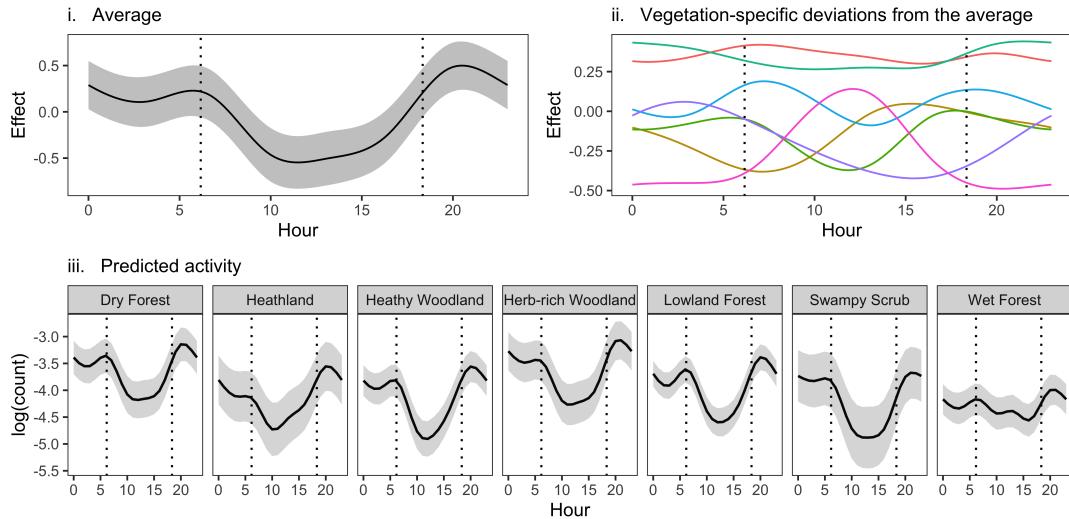


Figure 5.2: The strength of diel activity patterns of two invasive predators varied within the two study regions in south-west Victoria, Australia. White crosses depict unique camera-trap sites; colour brightness scales with increasing percentage difference between the minimum and maximum activity estimate over the 24-hour cycle for each location. Red foxes *Vulpes vulpes* (a, c) concentrated their activity during particular times of the day, especially in the Glenelg region (a) and the drier parts of the Otways (c), whereas feral cat *Felis catus* activity was relatively consistent activity throughout the daily cycle (b, d).

a. Fox



b. Feral cat

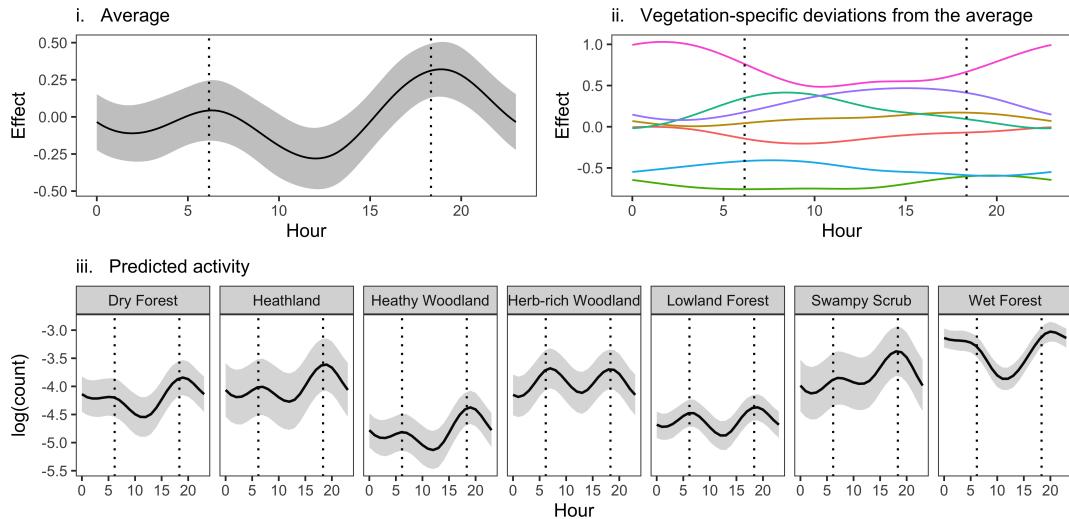


Figure 5.3: Red foxes *Vulpes vulpes* (a) and feral cat *Felis catus* (B) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia. Dotted, vertical lines represent average sunrise and sunset times. Shaded areas indicate 95% confidence intervals. Both invasive predators had a crepuscular to nocturnal diel activity pattern on average, with slight deviations across the drier EVC groups and large deviations in wet forests (ii; wet forests shown as pink line). The overall level of activity was relatively consistent across EVC groups for foxes (a – iii), whereas it differed substantially for feral cats (b - iii)

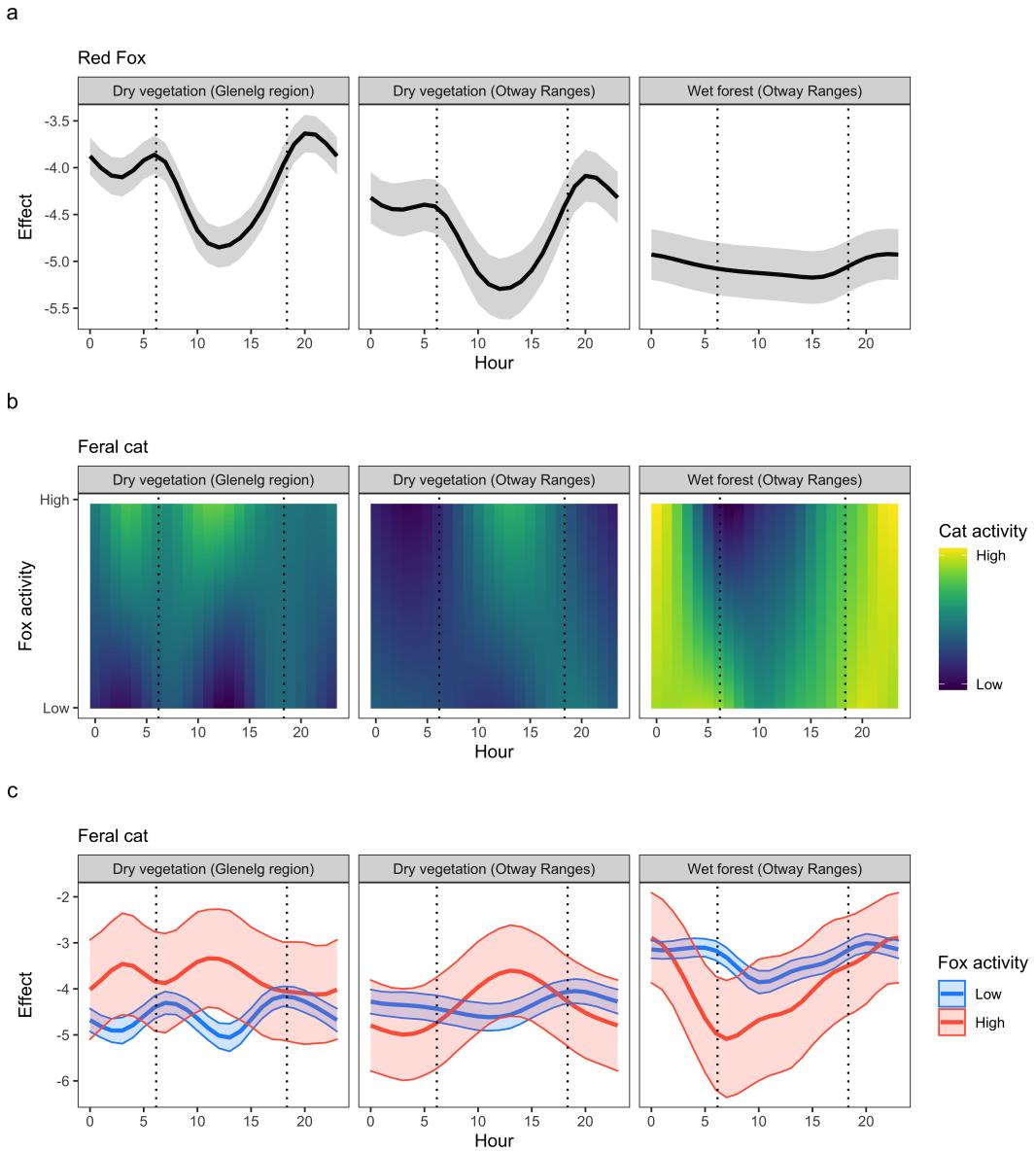


Figure 5.4: Variation in mean feral cat *Felis catus* activity (a) and associated uncertainty estimates (b) in response to count of 'independent' red fox *Vulpes vulpes* detections (log-transformed and survey effort adjusted) across each 'habitat type' in south-west Victoria, Australia. Grey vertical lines represent average sunrise and sunset times. In the Glenelg region, there were more feral cat detections where there were more fox detections, but cat peak diel activity shifted from crepuscular night to pre-dawn and midday (a). In the Otway Ranges, feral cat activity also peaked during the day where fox activity was high in dry vegetation types (b), but was more nocturnal where fox activity was high in the rainforests and wet forests (c).

a. Glenelg region

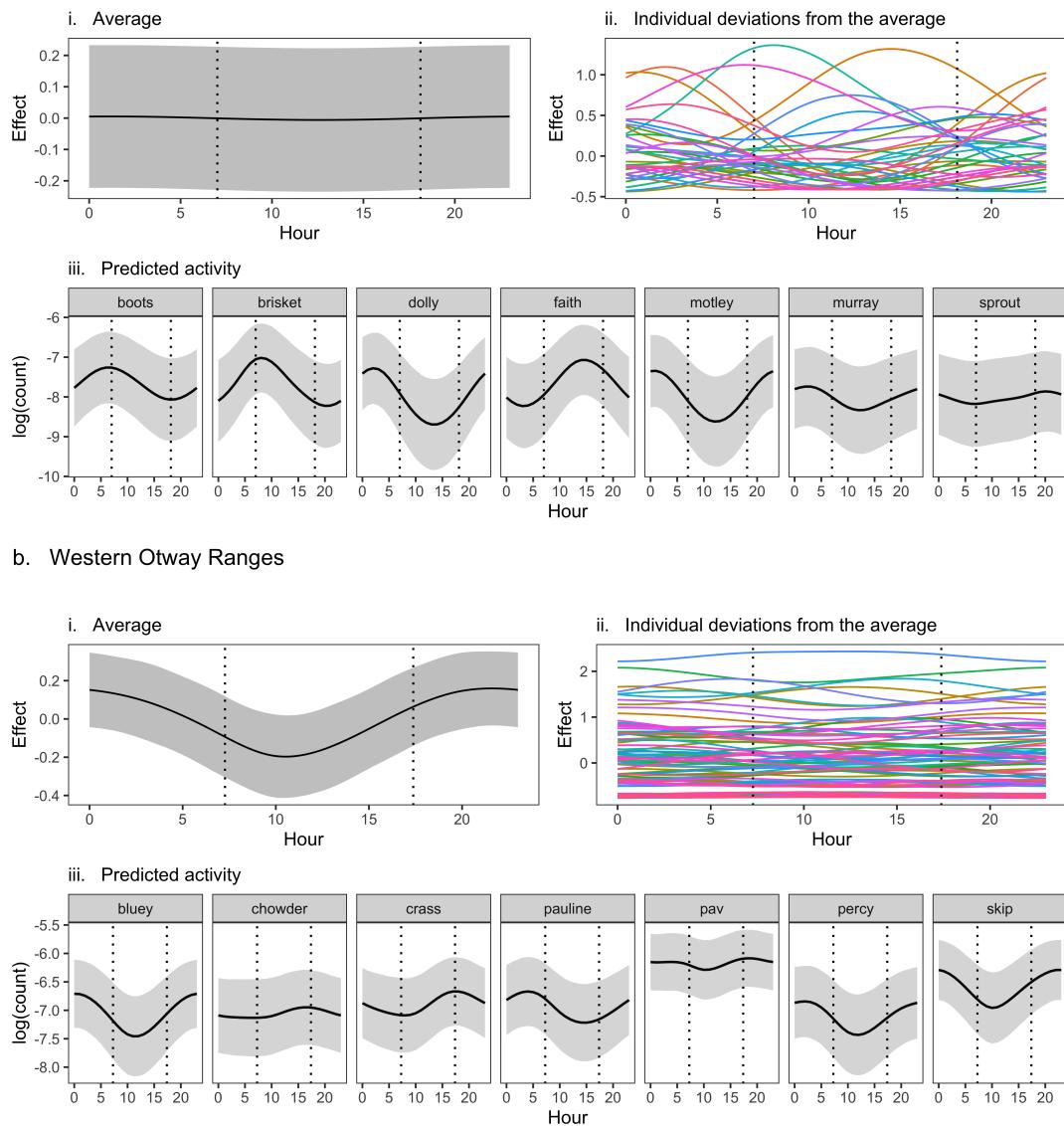


Figure 5.5: Individual heterogeneity in feral cat *Felis catus* diel activity across the Glenelg region (a; 39 identified individuals) and wet forests of the western Otway Ranges (b; 94 identified individuals) in south-west Victoria, Australia. As an example, the predicted activity of the seven individuals with the most detections in each region are shown in (iii). Dotted, vertical lines represent average sunrise and sunset times. Shaded areas indicate 95% confidence intervals. The global function of feral cat diel activity in the Glenelg region was almost a flat line, signalling high individual variation (deviations can therefore be interpreted directly as unique diel patterns). In the Otway wet forests, feral cats were on average nocturnal, individuals mostly deviated with different activity peaks near sunrise and sunset times.

5.4 Discussion

Animal diel activity patterns can be complex; varying across individuals, habitat types and threat-levels. Despite telling an important story about how animals interact with each other and the environment, detection times are commonly discarded from statistical analyses. But even when considered, circadian rhythms are predominantly modelled at the population-level, overlooking behavioural syndromes which can affect fitness, survival and ecosystem-impacts. In our study, sympatric invasive predators had similar diel activity patterns when averaged across broad regions (i.e., high circular overlap; Roshier & Carter 2021), but behaviours varied considerably within landscapes, as revealed by our joint spatiotemporal modelling framework. Fox activity was strongly tied to the daily cycle, but differed across dry (nocturnal behaviour) and wet (cathemeral behaviour) vegetation communities. At sites with high fox activity, subordinate feral cats shifted activity to less risky times-of-the-day, likely facilitating spatial coexistence (Carothers & Jaksic 1984). Considering changes in animal activity throughout the daily cycle provides important context for understanding species interactions, which is key for effective ecosystem management (Gaynor *et al.* 2021).

In our study, simply comparing average diel activity overlap between two species (Ridout & Linkie 2009) would have been misleading for two reasons. Firstly, apex predator temporal avoidance strategies were not consistently employed, but dependent on encounter risk. Secondly, temporal avoidance was dynamic, depending on the spatially variable diel patterns of the apex predator. Few studies have demonstrated predator-induced shifts in diel activity such as these (Kronfeld-Schor & Dayan 2003), but notably, ship rats *Rattus norvegicus* were also found to switch from nocturnal to diurnal behaviour in response to fox activity (Fenn & Macdonald 1995). In the wet forests of the Otway Ranges, cats exposed to high fox activity levels concentrated their activity away from sunset and sunrise towards midnight, despite a diurnal shift appearing to similarly reduce the risk of a fox encounter. We expect becoming more nocturnal to be favourable over a diurnal shift because this is when prey are most active here and cats would be least visible (as most cats here had black or dark coloured coats; Graipel *et al.* 2014).

Shifting diel activity patterns may allow the spatial coexistence of dominant and subordinate species (Carothers & Jaksic 1984; Kronfeld-Schor & Dayan 2003). Cats and foxes have similar requirements (Glen & Dickman 2005; Stobo-Wilson *et al.* 2021a, b), and so, altering preferred circadian rhythms may be worthwhile to persist in high-quality habitat. We observed no spatial association between cats and foxes in the Otways, and a slightly positive correlation between the predators in the Glenelg region (Fig. 5.4). Without jointly modelling changes in diel activity, we would have inferred no impact of apex predators on feral cats, like others previously have (e.g., Fancourt *et al.* 2019; Stobo-Wilson *et al.* 2020b). Understanding behavioural change impacts on native prey is a key future research priority to improve invasive predator management.

Individual cats in the Glenelg region had more variation than similarity in diel ac-

tivity patterns, whereas cats in the wet forests of the Otway Ranges were mostly nocturnal, with relatively slight deviations across individuals. This result is unsurprising for two reasons. Firstly, cats were identified to the individual-level across a larger area with more heterogeneous vegetation types in the Glenelg region. Secondly, more drastic changes in diel activity were attributable to the threat of foxes in the Glenelg region relative the wet forests of the Otway Ranges. One question arising from this is whether individuals themselves have dynamic diel patterns (or spatial patterns for that matter), or whether individual variation is due to the unique spatial context of an animals home range. Estimating diel activity separately for individual animals facilitates identification of common behavioural syndromes, which is particularly useful when individual demographics (e.g., age, sex) are unknown.

Generalised additive models provide a flexible joint approach to modelling spatiotemporal activity. Previous spatiotemporal studies of predator avoidance have largely relied on repeating analyses (name resource selection functions) at different periods of the daily cycle (e.g., Smith *et al.* 2019; Basille *et al.* 2015; Kohl *et al.* 2019). Here we demonstrate how GAMs can model continuous shifts in activity across both space and time, with complex variable interactions and information sharing. Smoothing penalties make GAMs more closely aligned with null hypothesis testing; the null hypothesis being that there are no diel patterns in activity and, for hierarchical specifications, different groups all follow the same average diel pattern. This makes diel GAMs more robust than separately fit models for categorical time periods and kernel density estimation, in which noisy data can produce spurious estimates (Iannarilli *et al.* 2019). Despite the added complexity, GAMs in the ‘mgcv’ R-package are straightforward to fit. For individually identifiable species, the Distiller *et al.* (2020) spatial capture-recapture model offers an extremely powerful extension of GAMs to disentangle behavioural and numerical population effects, although at considerable computational costs and data requirements.

Our study adds to the limited body of evidence that top predators can produce a landscape of fear which is powerful enough to reverse the circadian rhythms of subordinate species (Kronfeld-Schor & Dayan 2003). A key distinction of our study is that we modelled avoidance behaviours in a simple predator guild, where apex predator activity was artificially manipulated, reducing bias from differences in niche preferences or the unmodelled impacts of other predators in the system. We also included replication across different habitat types, revealing flexible predator behaviour and dynamic species interactions. Our results demonstrate the importance of (a) considering diel activity in regards to species interactions, (b) modelling *changes* in animal behaviour rather than overlap with other species, and (c) testing avoidance behaviours within a joint spatiotemporal framework. Our GAM framework for modelling spatiotemporal activity can be used on any species with time-stamped detections, covariates and hierarchical groupings.

5.5 GY

However, predator interaction studies often investigate spatial avoidance but overlook diel activity - the distribution of activity throughout the daily cycle (Kronfeld-Schor & Dayan 2003). Animals must allocate particular times of the day to rest, forage, socialise and reproduce, which are traded-off against threat avoidance (e.g., predation) and deterrence against resource loss (i.e. inter and intraspecific competition; Kronfeld-Schor *et al.* 2013; Fraser & Metcalfe 1997; Creel & Christianson 2008). Because of spatial variation in resources and predation risk, animals may adjust diel behaviour to balance this trade-off across heterogeneous landscapes.

A variety of statistical approaches are used to model diel behaviour separately across different categorical contexts, but few allow continuous *changes* in diel activity (Frey *et al.* 2017). Kernel density estimation is most commonly used and provides a coefficient of overlap between two diel curves (i.e., temporal overlap between two species or one species in two categorical contexts; Ridout & Linkie 2009). Kernel density estimation does not incorporate explanatory variables and is susceptible to noisy estimates from small sample sizes (Frey *et al.* 2017; Iannarilli *et al.* 2019). To account for the spatiotemporal nature of avoidance behaviours, temporal overlap coefficients are increasingly being joined with spatial overlap coefficients (e.g., Ait Kaci Azzou *et al.* 2021; Farris *et al.* 2020). However, overlap coefficients do not account for behavioural changes which are employed or enhanced under heightened threat-levels (Lima & Dill 1990; Blanchet *et al.* 2020). Straightforward, integrated methods for examining dynamic changes in spatiotemporal animal behaviour are needed.

An increasingly popular method to estimate diel activity patterns are Generalised Additive Models (hereafter ‘GAMs’). GAMs have smoothing functions to avoid overfitting and can incorporate interactions between explanatory variables (both categorical and numerical; Wood 2017), however, there are few examples of activity curves interacting with continuous covariates (although see Cunningham *et al.* 2019). This may because these features aren’t widely known, or due to concerns that sample sizes are too small to fit separate diel curves to different groups or contexts (e.g. individuals or categorical environmental conditions). However, hierarchical GAMs can estimate separate functions while sharing information across categorical groups (Pedersen *et al.* 2019). Hierarchical GAMs estimate an average functional response and group-level functions which are penalised as they deviate from the average - providing confidence that they are true deviations rather than artefacts of noisy data (Pedersen *et al.* 2019).

A key question in ecological theory is whether animals are evolutionary hardwired to occupy particular temporal niches, or have circadian rhythms which are responsive to changing environmental conditions and interactions with other species (Schoener 1974; Daan 1981; Lima & Dill 1990).

Predator avoidance involves altering or reducing use of spatial and temporal niches. This perception of spatial variation in predation risk, i.e., ‘the landscape of fear’, is crit-

ical to understand–antipredator behaviours may have larger impacts on populations of subordinate species than predation itself (Gaynor *et al.* 2019).

This is complicated by individual variation - both in perceived risks / benefits and reactions to the same threats.

subordinate species responses may vary across individuals due to personality traits or across landscape-contexts due to different environmental conditions and species interactions. Understanding variation in behaviour is often thought of in an evolutionary context, but has tangible implications for applied wildlife management, particularly the control of introduced predators.

predator cues and landscape context, behavioural choices likely vary across individuals due to personality trait differences (Quinn *et al.* 2012; Bonnot *et al.* 2014; Basille *et al.* 2015; Lamb *et al.* 2020). Populations with high individual heterogeneity in spatiotemporal behaviour may be more adaptable to threats (Wolf & Weissing 2012) and resistant to management (Swan *et al.* 2017).

Personality may change, predator management and impacts.

Chapter 6

Synthesis

text

References

- Abbott, I. (2008). The spread of the cat, *felis catus*, in australia: Re-examination of the current conceptual model with additional information. *Conservation Science Western Australia*, 7.
- Ait Kaci Azzou, S., Singer, L., Aebsicher, T., Caduff, M., Wolf, B. & Wegmann, D. (2021). A sparse observation model to quantify species distributions and their overlap in space and time. *Ecography*, 44, 928–940.
- Alston, J., Maitland, B., Brito, B., Esmaeili, S., Ford, A. & Hays, B. *et al.* (2019). Reciprocity in restoration ecology: When might large carnivore reintroduction restore ecosystems? *Biological conservation*, 234, 82–89.
- Arjo, W.M., Gese, E.M., Bennett, T.J. & Kozlowski, A.J. (2007). Changes in kit fox-coyote-prey relationships in the Great Basin Desert, Utah. *Western North American Naturalist*, 67, 389–401.
- Arthur, A.D., Catling, P.C. & Reid, A. (2012). Relative influence of habitat structure, species interactions and rainfall on the post-fire population dynamics of ground-dwelling vertebrates. *Austral Ecology*, 37, 958–970.
- Baker, C.M., Gordon, A. & Bode, M. (2017). Ensemble ecosystem modeling for predicting ecosystem response to predator reintroduction. *Conservation Biology*, 31, 376–384.
- Ballari, S.A., Kuebbing, S.E. & Nuñez, M.A. (2016). Potential problems of removing one invasive species at a time: A meta-analysis of the interactions between invasive vertebrates and unexpected effects of removal programs. *PeerJ*, 4, e2029.
- Banikos, Z. (2018). Responses of critical weight range digging mammals to a fox control program in south-eastern Australia. Master's thesis. University of Melbourne; School of BioSciences.
- Banks, P.B. (1999). Predation by introduced foxes on native bush rats in Australia: Do foxes take the doomed surplus? *Journal of Applied Ecology*, 36, 1063–1071.
- Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.-P. & Courtois, R. (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96, 2622–2631.

- Baum, J.K. & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78, 699–714.
- Baxter, P.W., Sabo, J.L., Wilcox, C., McCarthy, M.A. & Possingham, H.P. (2008). Cost-effective suppression and eradication of invasive predators. *Conservation Biology*, 22, 89–98.
- Bellard, C., Genovesi, P. & Jeschke, J. (2016). Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152454.
- Bengsen, A., Butler, J. & Masters, P. (2011). Estimating and indexing feral cat population abundances using camera traps. *Wildlife Research*, 38, 732–739.
- Bengsen, A.J., Algar, D., Ballard, G., Buckmaster, T., Comer, S. & Fleming, P.J.S. et al. (2016). Feral cat home-range size varies predictably with landscape productivity and population density. *Journal of Zoology*, 298, 112–120.
- Bennett, A. (1987). Conservation of mammals within a fragmented forest environment: The contributions of insular biogeography and autecology. *Nature conservation: the role of remnants of native vegetation*, 41–52.
- Benshemesh, J., Southwell, D., Barker, R. & McCarthy, M. (2020). Citizen scientists reveal nationwide trends and drivers in the breeding activity of a threatened bird, the malleefowl (*leipoa ocellata*). *Biological Conservation*, 246, 108573.
- Berger, J., Swenson, J.E. & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: Conservation lessons from pleistocene extinctions. *Science*, 291, 1036–1039.
- Berger, K.M., Gese, E.M. & Berger, J. (2008). Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology*, 89, 818–828.
- Bilney, R.J., Cooke, R. & White, J.G. (2010). Underestimated and severe: Small mammal decline from the forests of south-eastern Australia since European settlement, as revealed by a top-order predator. *Biological Conservation*, 143, 52–59.
- Bivand, R. & Lewin-Koh, N. (2021). *Maptools: Tools for handling spatial objects*.
- Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23, 1050–1063.
- Bode, M., Baker, C.M. & Plein, M. (2015). Eradicating down the food chain: Optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, 52, 571–579.
- Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L. & Cargnelutti, B. et al. (2014). Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology*, 26, 105–114.
- Borchers, D.L. & Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64, 377–385.

- Broadley, K., Burton, A.C., Avgar, T. & Boutin, S. (2019). Density-dependent space use affects interpretation of camera trap detection rates. *Ecology and evolution*, 9, 14031–14041.
- Brown, G.W. & Main, M.L. (2010). National recovery plan for the southern brown bandicoot (*Isoodon obesulus obesulus*). *Victorian Government Department of Sustainability and Environment (DSE): Melbourne, Australia*.
- Buckmaster, A.J. (2012). Ecology of the feral cat (*Felis catus*) in the tall forests of far east gippsland. PhD thesis. University of Sydney.; School of Biological Sciences; University of Sydney.; School of Biological Sciences.
- Burbidge, A.A. & Manly, B.F.J. (2002). Mammal extinctions on Australian islands: Causes and conservation implications. *Journal of Biogeography*, 29, 465–473.
- Bureau of Meteorology. (2021). Climate data online.
- Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological methods & research*, 33, 261–304.
- Carothers, J.H. & Jakšić, F.M. (1984). Time as a niche difference: The role of interference competition. *Oikos*, 403–406.
- Chandler, R.B. & Royle, J.A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, 7, 936–954.
- Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D. & Andrén, H. *et al.* (2014). Recovery of large carnivores in europe's modern human-dominated landscapes. *science*, 346, 1517–1519.
- Christie, A.P., Amano, T., Martin, P.A., Shackelford, G.E., Simmons, B.I. & Sutherland, W.J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *Journal of Applied Ecology*, 56, 2742–2754.
- Claridge, A.W., Cunningham, R.B., Catling, P.C. & Reid, A.M. (2010). Trends in the activity levels of forest-dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest Ecology and Management*, 260, 822–832.
- Clarke, M.F. (2008). Catering for the needs of fauna in fire management: Science or just wishful thinking? *Wildlife Research*, 35, 385–394.
- Comer, S., Clausen, L., Cowen, S., Pinder, J., Thomas, A. & Burbidge, A.H. *et al.* (2020). Integrating feral cat (*felis catus*) control into landscape-scale introduced predator management to improve conservation prospects for threatened fauna: A case study from the south coast of Western Australia. *Wildlife Research*, 47, 762–778.
- Courchamp, F., Langlais, M. & Sugihara, G. (1999). Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology*, 68, 282–292.
- Cove, M.V., Gardner, B., Simons, T.R., Kays, R. & O'Connell, A.F. (2018). Free-ranging

- domestic cats (*Felis catus*) on public lands: Estimating density, activity, and diet in the florida keys. *Biological Invasions*, 20, 333–344.
- Creel, S. & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23, 194–201.
- Crooks, K.R. & Soulé, M.E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563–566.
- Cumming, G. & Finch, S. (2005). Inference by eye: Confidence intervals and how to read pictures of data. *American psychologist*, 60, 170.
- Cunningham, C.X., Scoleri, V., Johnson, C.N., Barmuta, L.A. & Jones, M.E. (2019). Temporal partitioning of activity: Rising and falling top-predator abundance triggers community-wide shifts in diel activity. *Ecography*, 42, 2157–2168.
- Daan, S. (1981). Adaptive daily strategies in behavior. In: *Biological rhythms* (ed. Aschoff, J.). Springer US, Boston, MA, pp. 275–298.
- Davey, C., Sinclair, A., Pech, R.P., Arthur, A.D., Krebs, C.J. & Newsome, A. *et al.* (2006). Do exotic vertebrates structure the biota of Australia? An experimental test in new south wales. *Ecosystems*, 9, 992–1008.
- Davies, H.F., McCarthy, M.A., Firth, R.S., Woinarski, J.C., Gillespie, G.R. & Andersen, A.N. *et al.* (2018). Declining populations in one of the last refuges for threatened mammal species in northern Australia. *Austral Ecology*, 43, 602–612.
- DELWP. (2020). *Bioregions and evc benchmarks*. Available at: <https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks>. Last accessed.
- Denny, E.A. & Dickman, C. (2010). Review of cat ecology and management strategies in Australia. *Invasive Animals Cooperative Research Centre, Canberra*.
- Dexter, N. & Murray, A. (2009). The impact of fox control on the relative abundance of forest mammals in east gippsland, victoria. *Wildlife Research*, 36, 252–261.
- Dickman, C.R. (1996). *Overview of the impacts of feral cats on Australian native fauna*. Australian Nature Conservation Agency Canberra.
- Distiller, G.B., Borchers, D.L., Foster, R.J. & Harmsen, B.J. (2020). Using continuous-time spatial capture–recapture models to make inference about animal activity patterns. *Ecology and Evolution*, 10, e6822.
- Doherty, T.S., Bengsen, A.J. & Davis, R.A. (2015). A critical review of habitat use by feral cats and key directions for future research and management. *Wildlife Research*, 41, 435–446.
- Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G. & Woinarski, J.C. (2017). Impacts and management of feral cats (*Felis catus*) in Australia. *Mammal Review*, 47, 83–97.

- Doherty, T.S., Driscoll, D.A., Nimmo, D.G., Ritchie, E.G. & Spencer, R.-J. (2019). Conservation or politics? Australia's target to kill 2 million cats. *Conservation Letters*, 12, e12633.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G. & Dickman, C.R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, 113, 11261–11265.
- Doherty, T.S. & Ritchie, E.G. (2017). Stop jumping the gun: A call for evidence-based invasive predator management. *Conservation Letters*, 10, 15–22.
- Duncan, R.P., Dexter, N., Wayne, A. & Hone, J. (2020). Eruptive dynamics are common in managed mammal populations. *Ecology*, 101, e03175.
- Edwards, G., De Preu, N., Shakeshaft, B. & Crealy, I. (2000). An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research*, 27, 143–149.
- Efford, M.G. (2021). *Secr: Spatially explicit capture-recapture models. R package version 4.4.4*. Available at: <http://CRAN.R-project.org/package=secr>. Last accessed.
- Efford, M.G. & Dawson, D.K. (2012). Occupancy in continuous habitat. *Ecosphere*, 3, 1–15.
- Efford, M.G. & Hunter, C.M. (2018). Spatial capture–mark–resight estimation of animal population density. *Biometrics*, 74, 411–420.
- Efford, M.G. & Mowat, G. (2014). Compensatory heterogeneity in spatially explicit capture–recapture data. *Ecology*, 95, 1341–1348.
- Elmhagen, B. & Rushton, S.P. (2007). Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters*, 10, 197–206.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J. & Bond, W.J. *et al.* (2011). Trophic downgrading of planet earth. *science*, 333, 301–306.
- Fairfax, R.J. (2019). Dispersal of the introduced red fox (*vulpes vulpes*) across australia. *Biological Invasions*, 21, 1259–1268.
- Fancourt, B.A., Cremasco, P., Wilson, C. & Gentle, M.N. (2019). Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in australia suggests not. *Journal of Applied Ecology*, 56, 2584–2595.
- Farris, Z.J., Gerber, B.D., Karpanty, S., Murphy, A., Wampole, E. & Ratelolahy, F. *et al.* (2020). Exploring and interpreting spatiotemporal interactions between native and invasive carnivores across a gradient of rainforest degradation. *Biological Invasions*, 22, 2033–2047.

- Fenn, M.G. & Macdonald, D.W. (1995). Use of middens by red foxes: Risk reverses rhythms of rats. *Journal of Mammalogy*, 76, 130–136.
- Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 407–410.
- Fisher, D.O., Johnson, C.N., Lawes, M.J., Fritz, S.A., McCallum, H. & Blomberg, S.P. *et al.* (2014). The current decline of tropical marsupials in Australia: Is history repeating? *Global Ecology and Biogeography*, 23, 181–190.
- Fisher, P., Algar, D., Murphy, E., Johnston, M. & Eason, C. (2015). How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? *Applied Animal Behaviour Science*, 173, 88–96.
- Fleming, P.A., Crawford, H.M., Stobo-Wilson, A.M., Dawson, S.J., Dickman, C.R. & Dundas, S.J. *et al.* (2021). Diet of the introduced red fox *vulpes vulpes* in australia: Analysis of temporal and spatial patterns. *Mammal Review*, 51, 508–527.
- Fleming, P.J. (1996). Ground-placed baits for the control of wild dogs: Evaluation of a replacement-baiting strategy in north-eastern new south wales. *Wildlife Research*, 23, 729–740.
- Francis, L., Robley, A. & Hradsky, B. (2020). *Evaluating fox management strategies using a spatially explicit population*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 304. Department of Environment, Land, Water; Planning, Heidelberg, Victoria.
- Frankham, G.J., Reed, R.L., Fletcher, T.P. & Handasyde, K.A. (2011). Population ecology of the long-nosed potoroo (*Potorous tridactylus*) on french island, victoria. *Australian Mammalogy*, 33, 73–81.
- Fraser, N.H.C. & Metcalfe, N.B. (1997). The costs of becoming nocturnal: Feeding efficiency in relation to light intensity in juvenile atlantic salmon. *Functional Ecology*, 11, 385–391.
- Frey, S., Fisher, J.T., Burton, A.C. & Volpe, J.P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, 3, 123–132.
- Garrard, G.E., Bekkessy, S.A., McCarthy, M.A. & Wintle, B.A. (2008). When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, 33, 986–998.
- Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. (2019). Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, 34, 355–368.
- Gaynor, K.M., Cherry, M.J., Gilbert, S.L., Kohl, M.T., Larson, C.L. & Newsome, T.M. *et*

- al.* (2021). An applied ecology of fear framework: Linking theory to conservation practice. *Animal Conservation*, 24, 308–321.
- Geary, W.L., Doherty, T.S., Nimmo, D.G., Tulloch, A.I.T. & Ritchie, E.G. (2020a). Predator responses to fire: A global systematic review and meta-analysis. *Journal of Animal Ecology*, 89, 955–971.
- Geary, W.L., Hradsky, B.A., Robley, A. & Wintle, B.A. (2020b). Predators, fire or resources: What drives the distribution of herbivores in fragmented mesic forests? *Austral Ecology*, 45, 329–339.
- Glen, A.S. & Dickman, C.R. (2005). Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological reviews*, 80, 387–401.
- Gorman, M.L., Mills, M.G., Raath, J.P. & Speakman, J.R. (1998). High hunting costs make african wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, 391, 479–481.
- Graipel, M., Oliveira-Santos, L., Goulart, F., Tortato, M., Miller, P. & Cáceres, N. (2014). The role of melanism in oncillas on the temporal segregation of nocturnal activity. *Brazilian Journal of Biology*, 74, S142–S145.
- Green, K. & Sanecki, G. (2006). Immediate and short-term responses of bird and mammal assemblages to a subalpine wildfire in the snowy mountains, australia. *Austral Ecology*, 31, 673–681.
- Greenville, A.C., Wardle, G.M., Tamayo, B. & Dickman, C.R. (2014). Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia*, 175, 1349–1358.
- Hale, S., Nimmo, D.G., Cooke, R., Holland, G., James, S. & Stevens, M. *et al.* (2016). Fire and climatic extremes shape mammal distributions in a fire-prone landscape. *Diversity and Distributions*, 22, 1127–1138.
- Hamer, R., Andersen, G., Hradsky, B., Troy, S., Gardiner, R. & Johnson, C. *et al.* (n.d.). Differing effects of productivity on home-range size and population density of a native and an invasive mammalian carnivore.
- Hartig, F. (2020). DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models.
- Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A. & Taylor, R.S. *et al.* (2011). Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, 48, 247–256.
- Hastings, A. (2001). Transient dynamics and persistence of ecological systems. *Ecology Letters*, 4, 215–220.
- Hayward, M.W., Boitani, L., Burrows, N.D., Funston, P.J., Karanth, K.U. & MacKenzie,

- D.I. *et al.* (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, 52, 286–290.
- Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in ecology & evolution*, 23, 202–210.
- Hohnen, R., Tuft, K., McGregor, H.W., Legge, S., Radford, I.J. & Johnson, C.N. (2016). Occupancy of the invasive feral cat varies with habitat complexity. *PLoS One*, 11, e0152520.
- Hradsky, B.A. (2020). Conserving australia's threatened native mammals in predator-invaded, fire-prone landscapes. *Wildlife Research*, 47, 1–15.
- Hradsky, B.A., Kelly, L.T., Robley, A. & Wintle, B.A. (2019). FoxNet: An individual-based model framework to support management of an invasive predator, the red fox. *Journal of Applied Ecology*, 56, 1460–1470.
- Hradsky, B.A., Mildwaters, C., Ritchie, E.G., Christie, F. & Di Stefano, J. (2017a). Responses of invasive predators and native prey to a prescribed forest fire. *Journal of Mammalogy*, 98, 835–847.
- Hradsky, B.A., Robley, A., Alexander, R., Ritchie, E.G., York, A. & Di Stefano, J. (2017b). Human-modified habitats facilitate forest-dwelling populations of an invasive predator, (*Vulpes vulpes*). *Scientific Reports*, 7, 1–12.
- Hunter, D.O., Lagisz, M., Leo, V., Nakagawa, S. & Letnic, M. (2018). Not all predators are equal: A continent-scale analysis of the effects of predator control on Australian mammals. *Mammal Review*, 48, 108–122.
- Iannarilli, F., Arnold, T.W., Erb, J. & Fieberg, J.R. (2019). Using lorelograms to measure and model correlation in binary data: Applications to ecological studies. *Methods in Ecology and Evolution*, 10, 2153–2162.
- Jachowski, D.S., Butler, A., Eng, R.Y.Y., Gigliotti, L., Harris, S. & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: A review of evidence from north america. *Mammal Review*, 50, 367–381.
- Jackson, M.C. (2015). Interactions among multiple invasive animals. *Ecology*, 96, 2035–2041.
- Jiménez, J., Nuñez-Arjona, J.C., Rueda, C., González, L.M., García-Domínguez, F. & Muñoz-Igualada, J. *et al.* (2017). Estimating carnivore community structures. *Scientific reports*, 7, 1–10.
- Johnson, C. (2006). *Australia's mammal extinctions: A 50,000-year history*. Cambridge University Press.
- Johnson, C.N., Isaac, J.L. & Fisher, D.O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: Dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences*, 274, 341–346.

- Johnson, C.N. & VanDerWal, J. (2009). Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology*, 46, 641–646.
- Jones, E. & Coman, B. (1982). Ecology of the feral cat, (*Felis catus* (L.)), in south-eastern Australia II.* Reproduction. *Wildlife Research*, 9, 111–119.
- Jones, K.L., Van Vuren, D.H. & Crooks, K.R. (2008). Sudden Increase in a Rare Endemic Carnivore: Ecology of the Island Spotted Skunk. *Journal of Mammalogy*, 89, 75–86.
- Karki, S.M., Gese, E.M. & Klavetter, M.L. (2007). Effects of coyote population reduction on swift fox demographics in southeastern Colorado. *The Journal of Wildlife Management*, 71, 2707–2718.
- Kinnear, J.E., Pentland, C., Moore, N. & Krebs, C. (2016). Fox control and 1080 baiting conundrums: Time to prepare for a crispr solution. *Australian Mammalogy*, 39, 127–136.
- Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W. & White, P.J. *et al.* (2019). Do prey select for vacant hunting domains to minimize a multi-predator threat? *Ecology Letters*, 22, 1724–1733.
- Kronfeld-Schor, N., Bloch, G. & Schwartz, W.J. (2013). Animal clocks: When science meets nature. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131354.
- Kronfeld-Schor, N. & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual review of ecology, evolution, and systematics*, 34, 153–181.
- Kuebbing, S.E. & Nuñez, M.A. (2015). Negative, neutral, and positive interactions among nonnative plants: Patterns, processes, and management implications. *Global Change Biology*, 21, 926–934.
- Lamb, C.T., Ford, A.T., McLellan, B.N., Proctor, M.F., Mowat, G. & Ciarniello, L. *et al.* (2020). The ecology of humancarnivore coexistence. *Proceedings of the National Academy of Sciences*, 117, 17876–17883.
- Laundré, J.W., Hernández, L. & Altendorf, K.B. (2001). Wolves, elk, and bison: Reestablishing the “landscape of fear” in yellowstone national park, usa. *Canadian Journal of Zoology*, 79, 1401–1409.
- Lazenby, B.T., Mooney, N.J. & Dickman, C.R. (2015). Effects of low-level culling of feral cats in open populations: A case study from the forests of southern tasmania. *Wildlife Research*, 41, 407–420.
- Leahy, L., Legge, S.M., Tuft, K., McGregor, H.W., Barmuta, L.A. & Jones, M.E. *et al.* (2016). Amplified predation after fire suppresses rodent populations in australia’s tropical savannas. *Wildlife Research*, 42, 705–716.
- Legge, S., Murphy, B.P., McGregor, H., Woinarski, J.C.Z., Augusteyn, J. & Ballard, G. *et al.* (2017). Enumerating a continental-scale threat: How many feral cats are in australia? *Biological Conservation*, 206, 293–303.

- Legge, S., Taggart, P.L., Dickman, C.R., Read, J.L. & Woinarski, J.C. (2020). *Wildlife Research*, 47, 731–746.
- Levi, T. & Wilmers, C.C. (2012). Wolves–coyotes–foxes: A cascade among carnivores. *Ecology*, 93, 921–929.
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian journal of zoology*, 68, 619–640.
- Lindenmayer, D.B., Wood, J., MacGregor, C., Foster, C., Scheele, B. & Tulloch, A. *et al.* (2018). Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biological Conservation*, 221, 279–292.
- Lobert, B. (1990). Home range and activity period of the southern brown bandicoot (*Isoodon obesulus*) in a victorian heathland. *Bandicoots and Bilbies'.*(Eds JH Seebeck, PR Brown, RL Wallis and CM Kemper.) pp, 319–325.
- Lombardi, J.V., Comer, C.E., Scognamillo, D.G. & Conway, W.C. (2017). Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems*, 20, 1239–1248.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.
- Marlow, N.J., Thomas, N.D., Williams, A.A., Macmahon, B., Lawson, J. & Hitchen, Y. *et al.* (2015). Cats (*Felis catus*) are more abundant and are the dominant predator of woylies (*bettongia penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology*, 63, 18–27.
- Marra, G. & Wood, S.N. (2011). Practical variable selection for generalized additive models. *Computational Statistics & Data Analysis*, 55, 2372–2387.
- Mason, R.J. (1998). Habitat use and population size of the long-nosed potoroo, (*Potorous tridactylus*) (marsupialia: Potoroidae) in a coastal reserve, north-eastern new south wales. *Australian Mammalogy*, 20, 35–42.
- May, S.A. & Norton, T. (1996). Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in australian forest ecosystems. *Wildlife Research*, 23, 387–400.
- McColl-Gausden, S.C. & Penman, T.D. (2019). Pathways of change: Predicting the effects of fire on flammability. *Journal of Environmental Management*, 232, 243–253.
- McDonald, P.J., Nano, C.E.M., Ward, S.J., Stewart, A., Pavay, C.R. & Luck, G.W. *et al.* (2017). Habitat as a mediator of mesopredator-driven mammal extinction. *Conservation Biology*, 31, 1183–1191.
- McGregor, H.W., Cliff, H.B. & Kanowski, J. (2017). Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildlife Research*, 43, 623–633.

- McGregor, H.W., Legge, S., Jones, M.E. & Johnson, C.N. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PloS one*, 9, e109097.
- McGregor, H.W., Legge, S., Jones, M.E. & Johnson, C.N. (2016). Extraterritorial hunting expeditions to intense fire scars by feral cats. *Scientific reports*, 6, 1–7.
- McGregor, H.W., Legge, S., Potts, J., Jones, M.E. & Johnson, C.N. (2015). Density and home range of feral cats in north-western Australia. *Wildlife Research*, 42, 223–231.
- McLeod, S.R. & Saunders, G. (2014). Fertility control is much less effective than lethal baiting for controlling foxes. *Ecological Modelling*, 273, 1–10.
- Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S. & Josh Donlan, C. *et al.* (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, 17, 3503–3510.
- Meek, P.D. & Saunders, G. (2000). Home range and movement of foxes (*vulpes vulpes*) in coastal new south wales, australia. *Wildlife Research*, 27, 663–668.
- Menkhorst, P. & Broome, L. (2006). *Background and implementation information for the smoky mouse *Pseudomys fumeus*: National recovery plan*. Department of Sustainability; Environment.
- Miller, D.L. & Wood, S.N. (2014). Finite area smoothing with generalized distance splines. *Environmental and ecological statistics*, 21, 715–731.
- Molsher, R., Newsome, A.E., Newsome, T.M. & Dickman, C.R. (2017). Mesopredator management: Effects of red fox control on the abundance, diet and use of space by feral cats. *PLoS One*, 12, e0168460.
- Monamy, V. & Fox, B.J. (2000). Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. *Austral Ecology*, 25, 580–587.
- Moseby, K.E., Letnic, M., Blumstein, D.T. & West, R. (2019). Understanding predator densities for successful co-existence of alien predators and threatened prey. *Austral Ecology*, 44, 409–419.
- Moseby, K., McGregor, H. & Read, J. (2020). Effectiveness of the felixer grooming trap for the control of feral cats: A field trial in arid South Australia. *Wildlife Research*, 47, 599–609.
- Murphy, B.P., Woolley, L.-A., Geyle, H.M., Legge, S.M., Palmer, R. & Dickman, C.R. *et al.* (2019). Introduced cats (*Felis catus*) eating a continental fauna: The number of mammals killed in Australia. *Biological Conservation*, 237, 28–40.
- Neilson, E.W., Avgar, T., Burton, A.C., Broadley, K. & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*, 9, e02092.
- Newsome, T.M., Greenville, A.C., Ćirović, D., Dickman, C.R., Johnson, C.N. & Kro-

- fel, M. *et al.* (2017). Top predators constrain mesopredator distributions. *Nature communications*, 8, 1–7.
- Nichols, M., Ross, J., Glen, A.S. & Paterson, A.M. (2019). An evaluation of systematic versus strategically-placed camera traps for monitoring feral cats in new zealand. *Animals*, 9, 687.
- Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016). CamtrapR: An r package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7, 1457–1462.
- Nimmo, D.G., Kelly, L.T., Farnsworth, L.M., Watson, S.J. & Bennett, A.F. (2014). Why do some species have geographically varying responses to fire history? *Ecography*, 37, 805–813.
- Paull, D.J., Mills, D.J. & Claridge, A.W. (2013). Fragmentation of the southern brown bandicoot (*Isoodon obesulus*): Unraveling past climate change from vegetation clearing. *International Journal of Ecology*, 2013.
- Pedersen, E.J., Miller, D.L., Simpson, G.L. & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876.
- Pentland, C. (1999). Population dynamics of the southern brown bandicoot (*Isoodon obesulus*) on Ellen Brook Reserve. Honours Thesis. Edith Cowan University.
- Philip, J. (2019). The Institutionalisation of Poison: A historical review of vertebrate pest control in Australia, 1814 to 2018. *Australian Zoologist*, 40, 129–139.
- Prugh, L.R. & Sivy, K.J. (2020). Enemies with benefits: Integrating positive and negative interactions among terrestrial carnivores. *Ecology Letters*, 23, 902–918.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J. & Laliberte, A.S. *et al.* (2009). The rise of the mesopredator. *Bioscience*, 59, 779–791.
- Quinn, J.L., Cole, E., Bates, J., Payne, R. & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1919–1926.
- Radford, J.Q., Woinarski, J.C., Legge, S., Baseler, M., Bentley, J. & Burbidge, A.A. *et al.* (2018). Degrees of population-level susceptibility of Australian terrestrial non-volant mammal species to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). *Wildlife Research*, 45, 645–657.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. (2007). Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences*, 104, 20862–20865.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reddiex, B., Forsyth, D.M., McDonald-Madden, E., Einoder, L.D., Griffioen, P.A. &

- Chick, R.R. *et al.* (2007). Control of pest mammals for biodiversity protection in Australia. I. Patterns of control and monitoring. *Wildlife Research*, 33, 691–709.
- Rees, M.W., Pascoe, J.H., Wintle, B.A., Le Pla, M., Birnbaum, E.K. & Hradsky, B.A. (2019). Unexpectedly high densities of feral cats in a rugged temperate forest. *Biological Conservation*, 239, 108287.
- Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337.
- Riley, S.J., DeGloria, S.D. & Elliot, R. (1999). Index that quantifies topographic heterogeneity. *intermountain Journal of sciences*, 5, 23–27.
- Riotte-Lambert, L. & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology & Evolution*, 35, 163–174.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G. & Hebblewhite, M. *et al.* (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.
- Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S. & Wright, I.W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research*, 27, 223–235.
- Ritchie, E.G. & Johnson, C.N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998.
- Robley, A., Gormley, A.M., Forsyth, D.M. & Triggs, B. (2014). Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation*, 180, 262–269.
- Robley, A., Moloney, P., Stringer, L. & Donald, S. (2020). *Glenelg ark 2005–2019: Long-term predator and native mammal response to predator control*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 318. Department of Environment, Land, Water; Planning, Heidelberg, Victoria.
- Robley, A., Moloney, P. & Team, P.V.W.C.D. (2019). *Glenelg ark 2005–2019: Long-term predator and native mammal response to predator control*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 299. Department of Environment, Land, Water; Planning, Heidelberg, Victoria.
- Robley, A., Ramsey, D.S. & Woodford, L. (2018). *Estimating population changes in wild dogs, feral cats and foxes in relation to an aerial baiting operation in eastern victoria*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 292. Department of Environment, Land, Water; Planning, Heidelberg, Victoria.
- Robley, A., Ramsey, D.S., Woodford, L., Taglierini, A., Walker, J. & Sloane, P. *et al.* (2017). *Towards a feral cat management strategy for Hattah-Kulkyne National Park: Estimation of feral cat density and bait uptake rates, and comparison of management strategies*.

Arthur Rylah Institute for Environmental Research Technical Report Series No. 281.
Department of Environment, Land, Water; Planning, Heidelberg, Victoria.

- Rogan, M.S., Balme, G.A., Distiller, G., Pitman, R.T., Broadfield, J. & Mann, G.K. *et al.* (2019). The influence of movement on the occupancy–density relationship at small spatial scales. *Ecosphere*, 10, e02807.
- Roshier, D.A. & Carter, A. (2021). Space use and interactions of two introduced mesopredators, european red fox and feral cat, in an arid landscape. *Ecosphere*, 12, e03628.
- Royle, J.A., Chandler, R.B., Sollmann, R. & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.
- Royle, J.A., Stanley, T.R. & Lukacs, P.M. (2008). Statistical modeling and inference from carnivore survey data. *Noninvasive survey methods for carnivores*, 293–312.
- Ruscoe, W.A., Ramsey, D.S., Pech, R.P., Sweetapple, P.J., Yockney, I. & Barron, M.C. *et al.* (2011). Unexpected consequences of control: Competitive vs. Predator release in a four-species assemblage of invasive mammals. *Ecology Letters*, 14, 1035–1042.
- Sabo, J.L. (2005). Stochasticity, predator–prey dynamics, and trigger harvest of nonnative predators. *Ecology*, 86, 2329–2343.
- Salo, P., Banks, P.B., Dickman, C.R. & Korpimäki, E. (2010). Predator manipulation experiments: Impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, 80, 531–546.
- Saunders, G.R., Gentle, M.N. & Dickman, C.R. (2010). The impacts and management of foxes *vulpes vulpes* in australia. *Mammal Review*, 40, 181–211.
- Schoener, T.W. (1974). The compression hypothesis and temporal resource partitioning. *Proceedings of the National Academy of Sciences*, 71, 4169–4172.
- Sih, A. (1980). Optimal behavior: Can foragers balance two conflicting demands? *Science*, 210, 1041–1043.
- Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *The American Naturalist*, 139, 1052–1069.
- Sih, I., Ziembka, I. & Harding, K. (2000). New insights on how temporal variation in predation risk shapes prey behavior. *Trends in ecology & evolution*, 15, 3—4.
- Simpson, G.L. (2021). *Gratia: Graceful 'ggplot'-based graphics and other functions for gams fitted using 'mgcv'*.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P. & Newsome, A.E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, 12, 564–575.
- Smith, A.P. & Quin, D.G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation*, 77, 243–267.

- Smith, B. (2015). *The dingo debate: Origins, behaviour and conservation*. Csiro Publishing.
- Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J. & Middleton, A.D. (2019). Integrating temporal refugia into landscapes of fear: Prey exploit predator downtimes to forage in risky places. *Oecologia*, 189, 883–890.
- Smith, J.A., Suraci, J.P., Hunter, J.S., Gaynor, K.M., Keller, C.B. & Palmer, M.S. *et al.* (2020). Zooming in on mechanistic predator-prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological interactions. *Journal of Animal Ecology*, 89, 1997–2012.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, 2, 75–92.
- Stephens, P.A., Pettorelli, N., Barlow, J., Whittingham, M.J. & Cadotte, M.W. (2015). Management by proxy? The use of indices in applied ecology. *Journal of Applied Ecology*, 52, 1–6.
- Stewart, F.E.C., Fisher, J.T., Burton, A.C. & Volpe, J.P. (2018). Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere*, 9, e02112.
- Stobo-Wilson, A.M., Brandle, R., Johnson, C.N. & Jones, M.E. (2020a). Management of invasive mesopredators in the Flinders Ranges, South Australia: Effectiveness and implications. *Wildlife Research*, 47, 720–730.
- Stobo-Wilson, A.M., Murphy, B.P., Crawford, H.M., Dawson, S.J., Dickman, C.R. & Doherty, T.S. *et al.* (2021a). Sharing meals: Predation on Australian mammals by the introduced european red fox compounds and complements predation by feral cats. *Biological Conservation*, 261, 109284.
- Stobo-Wilson, A.M., Murphy, B.P., Legge, S.M., Chapple, D.G., Crawford, H.M. & Dawson, S.J. *et al.* (2021b). Reptiles as food: Predation of Australian reptiles by introduced red foxes compounds and complements predation by cats. *Wildlife Research*, 48, 470–480.
- Stobo-Wilson, A.M., Stokeld, D., Einoder, L.D., Davies, H.F., Fisher, A. & Hill, B.M. *et al.* (2020b). Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal australia. *Diversity and Distributions*, 26, 832–842.
- Swan, G.J.F., Redpath, S.M., Bearhop, S. & McDonald, R.A. (2017). Ecology of problem individuals and the efficacy of selective wildlife management. *Trends in Ecology & Evolution*, 32, 518–530.
- Swan, M., Christie, F., Sitters, H., York, A. & Di Stefano, J. (2015). Predicting faunal fire responses in heterogeneous landscapes: The role of habitat structure. *Ecological Applications*, 25, 2293–2305.
- Taggart, P.L., Fancourt, B.A., Bengsen, A.J., Peacock, D.E., Hodgens, P. & Read, J.L. *et al.*

- al.* (2019). Evidence of significantly higher island feral cat abundance compared with the adjacent mainland. *Wildlife Research*, 46, 378–385.
- Thompson, C.M. & Gese, E.M. (2007). Food webs and intraguild predation: Community interactions of a native mesocarnivore. *Ecology*, 88, 334–346.
- Towerton, A.L., Penman, T.D., Kavanagh, R.P. & Dickman, C.R. (2011). Detecting pest and prey responses to fox control across the landscape using remote cameras. *Wildlife Research*, 38, 208–220.
- Tulloch, A.I.T., Mortelliti, A., Kay, G.M., Florance, D. & Lindenmayer, D. (2016). Using empirical models of species colonization under multiple threatening processes to identify complementary threat-mitigation strategies. *Conservation Biology*, 30, 867–882.
- Van Dyck, S. & Strahan, R. (2008). *The mammals of australia*. New Holland Pub Pty Limited.
- Vazquez, C., Rowcliffe, J.M., Spoelstra, K. & Jansen, P.A. (2019). Comparing diel activity patterns of wildlife across latitudes and seasons: Time transformations using day length. *Methods in Ecology and Evolution*, 10, 2057–2066.
- Walsh, J.C., Wilson, K.A., Benshemesh, J. & Possingham, H.P. (2012). Unexpected outcomes of invasive predator control: The importance of evaluating conservation management actions. *Animal Conservation*, 15, 319–328.
- Wayne, A.F., Maxwell, M.A., Ward, C.G., Wayne, J.C., Vellios, C.V. & Wilson, I.J. (2017). Recoveries and cascading declines of native mammals associated with control of an introduced predator. *Journal of Mammalogy*, 98, 489–501.
- Wickham, H. (2007). Reshaping data with the reshape package. *Journal of Statistical Software*, 21, 1–20.
- Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.
- Wilson, B.A., Valentine, L.E., Reaveley, A., Isaac, J. & Wolfe, K.M. (2012). Terrestrial mammals of the gnangara groundwater system, western australia: History, status, and the possible impacts of a drying climate. *Australian Mammalogy*, 34, 202–216.
- Wilson, R.R., Blankenship, T.L., Hooten, M.B. & Shivik, J.A. (2010). Prey-mediated avoidance of an intraguild predator by its intraguild prey. *Oecologia*, 164, 921–929.
- Woinarski, J., Burbidge, A. & Harrison, P. (2014). *The action plan for Australian mammals 2012*. Commonwealth Scientific; Industrial Research Organization Publishing
- Woinarski, J.C., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A.D. & Hill, B. *et al.* (2010). Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research*, 37, 116–126.
- Woinarski, J.C.Z., Braby, M.F., Burbidge, A.A., Coates, D., Garnett, S.T. & Fensham,

- R.J. *et al.* (2019). Reading the black book: The number, timing, distribution and causes of listed extinctions in australia. *Biological Conservation*, 239, 108261.
- Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences*, 112, 4531–4540.
- Woinarski, J.C.Z., Murphy, B.P., Legge, S.M., Garnett, S.T., Lawes, M.J. & Comer, S. *et al.* (2017). How many birds are killed by cats in Australia? *Biological Conservation*, 214, 76–87.
- Woinarski, J., Murphy, B., Palmer, R., Legge, S., Dickman, C. & Doherty, T. *et al.* (2018). How many reptiles are killed by cats in Australia? *Wildlife Research*, 45, 247–266.
- Wolf, M. & Weissing, F.J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27, 452–461.
- Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 3–36.
- Wood, S.N. (2017). *Generalized additive models: An introduction with r*. CRC press.
- Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, 16, 454–459.

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Appendix A

Supporting Information: Chapter 2

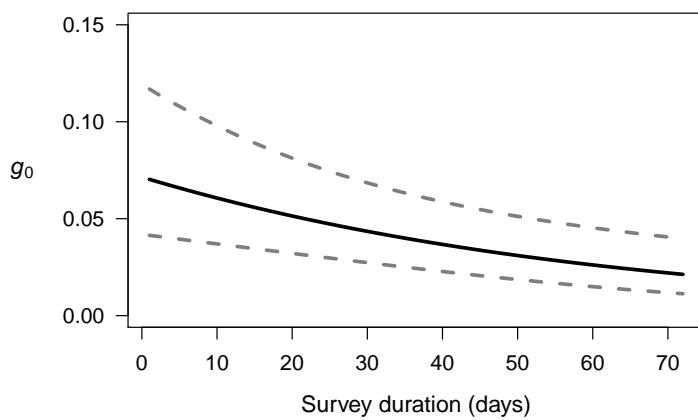


Figure A.1: The AICc-best model linear trend in g_0 values (probability of daily detection in activity centre) throughout the survey. Grey dashed lines indicate 95% confidence intervals.

Table A.1: Model selection table and density estimates for different detection function shapes for spatial mark-resight models.

Detector function	Model comparison				Density estimate (cats km-2)		
	K	AICc	dAICc	AICcw	estimate	lcl	ucl
hazard-rate	4	2359.59	0.00	0.7	1.15	0.93	1.42
exponential	3	2361.25	1.66	0.3	1.19	0.96	1.49
halfnormal	3	2373.30	13.72	0.0	1.12	0.93	1.35

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcw - AICc model weight

lcl – lower 95% confidence limit

ucl – upper 95% confidence limit

Appendix B

Chapter 2 publication



Short communication

Unexpectedly high densities of feral cats in a rugged temperate forest

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ABSTRACT

Effective invasive predator management requires accurate knowledge of population density. However, density can be difficult to estimate for wide-ranging, cryptic and trap-shy species, such as the feral cat *Felis catus*. Consequently, few density estimates exist for this invasive predator of global significance, particularly from rugged, mesic or structurally complex habitats where detection is challenging. In this study, we estimated feral cat density in the wet forests and cool temperate rainforests of the Otway Ranges, south-eastern Australia, to (1) provide a density estimate for this rarely surveyed habitat type, and (2) verify predictions from a continental-scale model of feral cat density. We deployed 140 camera traps across two independent 49 km² grids and identified individual feral cats based on unique pelage markings. Using spatially explicit mark-resight models, we estimated that there were 1.14 cats km⁻² (95% CI: 0.89–1.47). This is more than three times the average cat density in natural environments across Australia, and at least five times higher than model-based predictions for the Otway Ranges. Such high densities of feral cats likely reflect the abundance of small native mammals and lack of apex predators in our study area. Our findings contradict the widespread assumption that feral cats occur at very low densities in mesic and rugged habitats. Underestimating the density of feral cats in these environments has significant implications for pest animal management and biodiversity conservation.

1. Introduction

Accurate estimates of the distribution and abundance of invasive predators are essential to determine ecosystem impacts, inform effective management and target control efforts. However, this information is difficult to obtain as predators are often cryptic, trap-shy and occur at low densities (Royle et al., 2008). A prominent example is the feral cat *Felis catus*, which is implicated in the extinction or decline of 430 species globally (Doherty et al., 2016b). A better understanding of feral cat density has been highlighted as a priority for effective management of both this species and its threatened native prey (Burbidge et al., 2012; Legge et al., 2017; Moseby et al., 2018).

Legge et al. (2017) developed a continental-scale model of feral cat density for Australia which has had considerable implications for feral cat research and management. For instance, the model has been used to estimate the number of birds, reptiles and mammals killed annually across Australia by feral cats (Woinarski et al., 2017, 2018; Murphy et al., 2019). As the model estimated that there were considerably fewer feral cats in Australia than previously expected, it also cast doubt on the feasibility of Australian Federal Government's plan to cull two million feral cats between 2015 and 2020 (Doherty et al., 2019). Given the

importance of feral cat density estimates for policy, planning and management, it is vital to verify and refine the model's predictions.

The underlying data used by Legge et al. (2017) had several limitations, including that feral cat density estimates were not available for any wetland, mangrove, dense heath or rainforest environments in Australia (Legge et al., 2017). This likely reflects the difficulty of access and ineffectiveness of traditional feral cat monitoring methods (track counts and spotlight counts) in these structurally complex habitats (Denny and Dickman, 2010). Legge et al. (2017) highlighted the need for more site-based density surveys, particularly in these under-studied environments. Further, nearly all of the density estimates collated by Legge et al. (2017) were based on studies that did not identify individual cats or account for imperfect detection (i.e. the possibility that some individuals were not detected). Such methods can be unreliable when inferring across sites, times, ecological contexts and different detection methods (Edwards et al., 2000; Hayward et al., 2015), particularly for species such as cats whose densities may fluctuate substantially over time in some regions (Legge et al., 2017). Concurrent surveys of cats on Kangaroo Island and the adjacent Australian mainland suggests that the Legge et al. (2017) model may substantially underestimate this variation in density (Taggart et al., 2019).

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Robust population density estimates for cryptic and wide-ranging species based on individual identification are now more feasible due to recent advances in technology and statistical models. Camera-traps that sense temperature-in-motion provide an efficient survey approach across diverse environments and are particularly beneficial for studies of trap-shy species with unique markings, such as feral cats (Bengsen et al., 2012). Concurrently, spatial mark-resight (SMR) models, an extension of spatial capture-recapture models, enable population density estimates when a portion of the population can be individually identified (Royle et al., 2013). These models consider both the distribution and movement of individuals across the landscape in relation to the placement of detectors, and account for imperfect detection (Royle et al., 2013). The combination of camera-trap surveys to identify individuals and spatial capture-recapture methods to estimate density has shown promise for both feral and domestic cats (Cove et al., 2017; Jiménez et al., 2017; McGregor et al., 2015b, 2016; Robley et al., 2017, 2018).

The small number of studies that have estimated feral cat density in the mesic regions of south-eastern Australia indicate that these habitats support few feral cats relative to other regions (Legge et al., 2017). However, survey effort for feral cats in these environments has been low compared to more arid regions. Our study therefore aimed to provide: (1) a density estimate for a rarely surveyed environment – a matrix of wet forest and cool temperate rainforest, and (2) an independent verification of the prediction from Legge et al.'s (2017) continental-scale model of feral cat density for the Otway region. To achieve these aims, we undertook a camera-trap survey over 8230 trap nights at 140 sites in the Otway Ranges, south-eastern Australia. We derived feral cat density estimates by applying SMR analysis to our camera survey data.

2. Methods

2.1. Study area

Our study was conducted in the Great Otway National Park and Otway Forest Park, Victoria, Australia (38.42° S, 142.24° E). The locality is 90–440 m a.s.l. and has a cool-temperate climate: maximum daily temperatures average 19.3° C in summer and 9.5° C in winter; annual rainfall averages 1955 mm (Bureau of Meteorology, 2019). The vegetation is a mosaic of old-growth shrubby wet forest, wet forest and cool temperate rainforest, with an overstorey of tall eucalyptus spp. (primarily *Eucalyptus regnans*), *Acacia melanoxylon* and *Nothofagus cunninghamii*, and a midstorey dominated by tree ferns, *Acacia verticillata*, *Pomaderris aspera* and *Olearia argophylla*. The understorey predominantly comprises a dense layer of ferns and graminoids, but is relatively open in steep gullies. The terrestrial predator guild is depauperate, with the introduced red fox *Vulpes vulpes* being the only other significant competitor of feral cats. Our camera survey and other live-trapping surveys indicate an abundance of small native mammals within the study region, particularly native rats and antechinus (Banikos, 2018).

2.2. Study design

We deployed camera traps in two grids, each approximately 49 km^2 and separated by more than five kilometres (Fig. 1). The northern grid comprised 67 survey sites, spaced an average of 526 m apart (86–848 m). The southern grid comprised 73 survey sites, spaced an average of 547 m apart (352–719 m). We deployed a Reconyx Hyperfire HC600 survey camera, with infrared flash and temperature-in-motion detector (Reconyx, Holmen, Wisconsin), at each site. Cameras functioned for 37–68 days (mean 59) from 26 June to 2 September 2017, totalling 8230 trap nights. Each camera was placed on a tree approximately 30 cm above the ground and faced towards a lure 2–2.5 m away. Vegetation in the camera's line of sight was cleared to prevent false

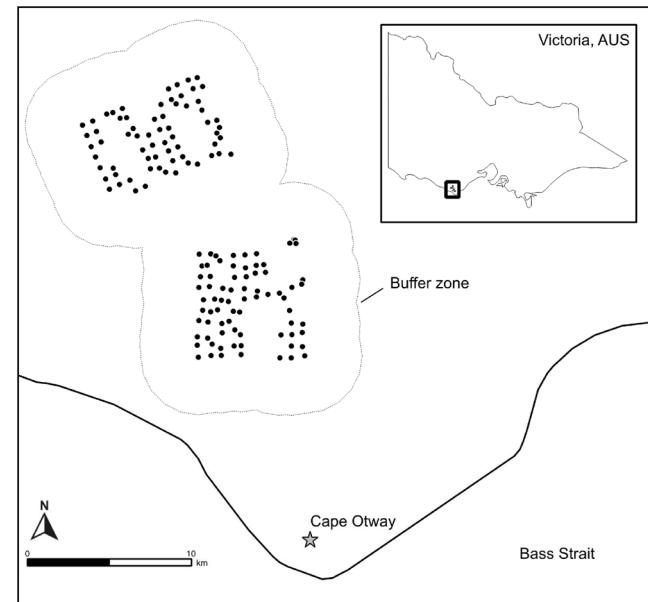


Fig. 1. Study area, western Otway Ranges, Victoria, Australia, showing the location of the camera trapping sites (black dots) within the 3500 m buffer zone (thin grey line).

triggers. The lure comprised an oil-absorbing cloth doused in tuna oil and placed inside a PVC pipe container with a mesh top. Ten to 30 small white feathers were also attached to the outside of the PVC pipe container. Each lure was fastened near the top of a one-metre wooden stake. Cameras took five immediately consecutive photographs when triggered, with no quiet period between trigger events.

2.3. Individual cat identification

Images of feral cats were first grouped as marked or unmarked (black) individuals. Although some black cats had small white neck/chest coat splotches, these were not always visible (cats often moved with their heads down), and so all black cats were considered unmarked to avoid double-counting. The marked portion were tabby cats with naturally unique coat markings. These were further classified into distinct groups: stripes & spots, thick swirls, other markings (ginger, distinctive breeds etc.) and unknown (due to poor image quality). At least two independent observers identified individual cats from these groups based on matches in unique markings, predominantly on the front legs, torso and across both flanks. Observers collated folders of images of unique individuals for reference. Discrepancies between observers were reviewed together until consensus was reached. If no consensus was reached, the marked cat was considered unidentifiable.

2.4. Estimating population density

We used conventional SMR models for an unknown number of marked individuals (sighting-only) to estimate feral cat density. These models assume that uniquely marked cats are a random sample of the population, with the same movement ecology as unmarked cats. We fitted models using the "secr" package (v. 3.2.1; Efford, 2019) in R (v. 3.5.2; R Core Team, 2017), as per Efford and Hunter (2017).

Capture histories were collapsed into 24-h occasions, beginning at midday each day (as this was the time of day with the lowest observed cat activity). We used a 3500 m buffer around the outermost coordinates of the trapping grids to ensure density was estimated over an area large enough to include the activity centres of all cats potentially exposed to our survey (Royle et al., 2013); this distance is larger than the estimated average maximum width of home ranges of large, male

cats close to this region ($n = 3$; B.A. Hradsky, unpublished data).

In SMR models, detectability is defined by two parameters: g_0 , the probability of detecting an animal (per occasion) if a detector was to be placed in the part of its home range where most time is spent, and σ , a spatial scale parameter relating to home range size. Animals are assumed to have approximately circular home ranges, with the probability of detection declining with distance from the home range centre. We tested three shapes of this decline in detection probability: half-normal, hazard-rate, and exponential, and used the detector function with the lowest Akaike's Information Criterion adjusted for small sample size (AICc; Buckland et al., 1997) for subsequent model fitting.

As the lures may have decreased in potency over the sampling session, we tested for a linear trend in g_0 over time. We also tested whether density differed between the two grids, with and without a linear time trend. We compared these models to the null model (where detection and density were kept constant across both grids) using AICc. Overdispersion in the unmarked sightings was adjusted for as per Efford and Hunter (2017) and a spatial resolution of 0.6 of the σ estimate (Efford, 2017) was used for all models.

3. Results

We detected feral cats at 55% of sites. Of these detections (1 detection = one or more visits of an individual/unidentifiable/unmarked cat to a camera-trap per 24-h occasion), 41% were unmarked (black) cats. Of the marked cat detections, 89% could be reliably identified to the individual-level – 47 individuals were identified. The number of detections, number of identified individuals and mean distances moved were similar across the two camera-trapping grids (Table 1).

The top-ranked model estimated a density of 1.14 cats km^{-2} (95% CI: 0.89–1.47), with no difference in density between grids but a linear decrease in g_0 over time (5.7% decrease per week; Fig. A1); Table 2. The second-ranked model (dAICc 1.74, Akaiae weight 0.23) indicated that densities were slightly higher at the northern than southern grid, although confidence intervals overlapped substantially (Table 2). The hazard-rate detector function best described the rate at which detection probability changed with the distance of the camera from the centre of a cat's home range (Table A1). Estimates of feral cat density were robust to all model specifications, with the mean estimate varying by less than 0.2 cats km^{-2} between all models (Table 1).

4. Discussion

Our work provides one of the first robust estimates of feral cat density for a temperate wet forest in Australia. Our estimate of 1.14 cats km^{-2} (95% CI: 0.89–1.47) is five times higher than that predicted by the Legge et al. (2017) model for this location (0.17–0.23 cats km^{-2}), and more than three times higher than the predicted continental mean density for feral cats in 'natural areas' (0.27 cats km^{-2} ; 0.18–0.45 cats km^{-2}) (Legge et al., 2017). The mesic coastal areas of Australia were

Table 2

Comparison of spatial mark-resight models and density estimates. T = linear time trend; K = number of parameters estimated; AICc = Akaike's Information Criterion with small-sample adjustment; dAICc = difference between AICc of this model and the model with smallest AICc; AICcwt = AICc model weight; lcl – lower 95% confidence limit; ucl – upper 95% confidence limit.

Model	Model comparison					Density estimate (cats km^{-2})				
	Density	g_0	K	AICc	dAICc	AICcwt	grid	estimate	lcl	ucl
–	T	5	2412.2	0	0.68		both	1.14	0.89	1.47
grid	T	6	2414.0	1.748	0.29		northern	1.25	0.90	1.75
–	–	4	2419.0	6.781	0.02		southern	1.06	0.80	1.41
grid	–	5	2421.1	8.884	0.01		both	1.14	0.88	1.48
							northern	1.21	0.88	1.68
							southern	1.08	0.81	1.45

previously thought to support the lowest densities of feral cats across the continent, particularly rugged and wet regions, such as rainforests (Dickman, 1996; Johnson, 2006; Legge et al., 2017; McDonald et al., 2017). Accordingly, feral cats were believed to have relatively less impact on native species in these environments (Burbidge and Manly, 2002; Doherty et al., 2016a; Woinarski et al., 2017, 2018; Radford et al., 2018; Murphy et al., 2019). Our finding is therefore startling, and prompts a rethink about the threat that feral cats may pose to native fauna in mesic habitats.

The high density of feral cats in our study region likely reflects the high productivity of the landscape and abundant populations of some prey species. Our study region has the highest annual rainfall in Victoria (BOM, 2019), and live-trapping surveys in our study site show consistent, near saturation of small mammal traps, predominantly bush rats, *Rattus fuscipes*, and antechinus *Antechinus* spp. (Z. Banikos, unpublished data). Several images from our study confirmed that feral cats prey upon these taxa. These small mammals may be relatively robust to introduced predators due to their high fecundity and generalist habitat requirements (e.g. Banks, 1999). However, by supporting high densities of feral cats, they may also facilitate high levels of predation on rarer and more vulnerable species (Smith and Quin, 1996), such as the now locally extinct smoky mouse *Pseudomys fumeus* (Menkhorst and Broome, 2008). Significant declines and local extinctions of other small mammals have also been reported across the eastern Otways (Wayne et al., 2017). Understanding temporal trends in these predator-prey dynamics and the relationships between introduced predators and their native primary and alternative prey is a key priority for future research.

The lack of apex predators and competitors in the Otway Ranges may also facilitate high feral cat densities. Dingoes *Canis dingo*—higher order predators (Johnson et al., 2007)—and tiger quolls *Dasyurus maculatus*—key competitors (Glen and Dickman, 2005)—are functionally extinct in the Otway Ranges. We detected foxes at 25% of sites (M.

Table 1

Summary of raw camera survey data for feral cats in the Otway Ranges, Victoria, Australia, 2017.

Summary statistic	southern grid	northern grid	both grids
Number of camera sites	73	67	140
Sites where cats detected (%)	51	62	55
Number of unmarked detection events	47	48	95
Number of identifiable, marked detection events	60	59	119
Number of unidentifiable, marked detection events	10	5	15
Total number of identified individuals	23	24	47
Number of cats resighted at different cameras	8	6	14
Mean recapture distance (m)	653	774	716
Maximum recapture distance (m)	905	1701	1701

Rees, unpublished data) but the extent to which foxes exert top-down control on feral cats is unclear. Changes in feral cat abundance, behaviour and/or diet have been observed in response to fox control (Molsher et al., 2017; Hunter et al., 2018), and the relationship could be further clarified using robust density estimates under experimental manipulations of fox density.

The belief that feral cat densities in Australia are lower in mesic forests than open habitats stems partly from the lack of robust density estimates from forests, and partly from observations that cats have greater hunting success and are more detectable in open microhabitats (Hohen et al., 2016; McDonald et al., 2016; McGregor et al., 2014, 2015a) and select for savannah over rainforest. However, the variation in understorey structure (from extremely dense to relatively open) in our study region potentially creates ideal shelter and foraging habitat for feral cats, which often hunt along edges between dense and open vegetation (Doherty et al., 2015). Our findings challenge the belief that cat density is low in mesic forests, and instead concur with the global pattern that feral cats have smaller, overlapping home ranges in productive, low-seasonal environments, resulting in higher population densities (Bengsen et al., 2016).

Our surveys clearly need replicating in other mesic environments before they can be generalised. Nonetheless, higher than expected densities of feral cats in mesic and complex environments would have serious implications for biodiversity conservation. Feral cats are thought to be a key driver of the recent declines of critical-weight-range mammals in northern Australia (Woinarski et al., 2010; Fisher et al., 2014; Davies et al., 2018). Contemporary mammal declines are also occurring in temperate Australia, including the Otway Ranges (Bilney et al., 2010; Wayne et al., 2017; Lindenmayer et al., 2018). A better understanding of feral cat densities in these regions is essential for identifying key threatening processes and improving management outcomes.

In conclusion, our study shows that feral cats can occur at high densities in wet forests and cool temperate rainforests, contrary to

previous expectations. Further research is needed to understand the impacts of this on native mammal populations, and the mechanisms that drive spatial variation in feral cat density, including the influence of habitat type, productivity, disturbance events and interactions with other predators. New spatial capture-recapture methods will likely play a powerful role in improving understanding of the ecology of this globally-significant predator. Our work provides a strong foundation for future investigations, as our methodology allows for robust evaluations of feral cat density, particularly under experimental manipulations and population comparisons.

Declaration of Competing Interest

The authors confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

Acknowledgements

We acknowledge the Gadabanud people on whose traditional lands this study took place. Surveys were conducted under University of Melbourne Animal Ethics Committee approval 1714119.5 and Victorian Government Department of Environment, Land Water and Planning Research Permit 10008273. We thank Luke Woodford and Hugh McGregor for contributing to cat identification, and Shauni Omond, Shayne Neal, Asitha Samarakrama, Shelley Thompson, Lani Watson, Mark Dorman, Jack Davis, Carl Roffey, Bruce Edley and Larissa Oliveira Gonçalves for fieldwork assistance. This study was generously supported by the Conservation Ecology Centre, the Victorian Government Department of Environment, Land Water and Planning, Parks Victoria, and the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub. MR also receives support from an Australian Government Research Training Program Scholarship.

Appendix A

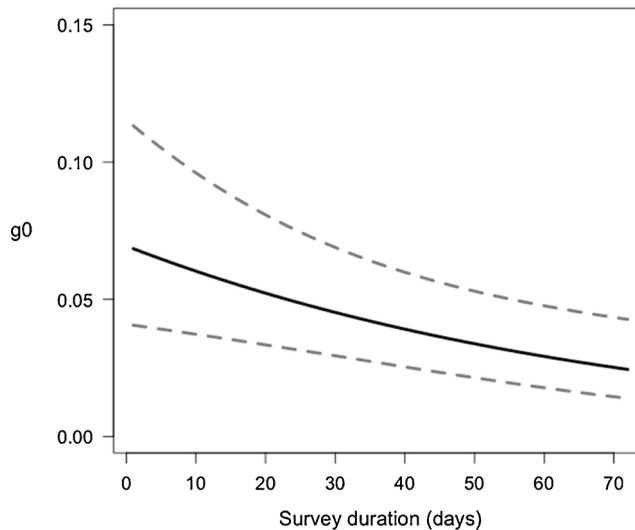


Fig. A1. The AICc-best model linear trend in g_0 values (probability of daily detection in activity centre) throughout the survey. Grey dashed lines indicate 95% confidence intervals.

Table A1

Model selection table and density estimates for different detector functions shapes for spatial mark-resight models. K = number of parameters estimated; AICc = Akaike's Information Criterion with small-sample adjustment; dAICc = difference in AICc from top-ranked model; AICcw = AICc model weight; lcl – lower 95% confidence limit; ucl – upper 95% confidence limit.

Model comparison					Density estimate (cats km ⁻²)		
Detector function	K	AICc	dAICc	AICcw	estimate	lcl	ucl
hazard-rate	4	3198.01	0.00	0.75	1.14	0.92	1.41
exponential	3	3212.03	2.203	0.25	1.18	0.94	1.46
halfnormal	3	3200.22	14.018	0.00	1.11	0.92	1.34

References

- Banikos, Z., 2018. Responses of Critical Weight Range Digging Mammals to a Fox Control Program in South-eastern Australia. Masters Thesis. University of Melbourne, Parkville, Vic., Australia.
- Banks, P.B., 1999. Predation by introduced foxes on native bush rats in Australia: do foxes take the doomed surplus? *J. Appl. Ecol.* 36 (6), 1063–1071.
- Bengsen, A., Butler, J., Masters, P., 2012. Estimating and indexing feral cat population abundances using camera traps. *Wildl. Res.* 38, 732–739.
- Bengsen, A.J., et al., 2016. Feral cat home-range size varies predictably with landscape productivity and population density. *J. Zool.* 298, 112–120.
- Bilney, R.J., Cooke, R., White, J.G., 2010. Underestimated and severe: small mammal decline from the forests of south-eastern Australia since European settlement, as revealed by a top-order predator. *Biol. Conserv.* 143, 52–59.
- Buckland, S.T., Burnham, K.P., Augustin, N.H., 1997. Model selection: an integral part of inference. *Biometrics* 53, 603–618.
- Burbidge, A., Harrison, P., Woinarski, J., 2012. The Action Plan for Australian Mammals 2012. CSIRO Publishing, Collingwood, Australia.
- Burbidge, A., Manly, B.F.J., 2002. Mammal extinctions on Australian islands: causes and conservation implications. *J. Biogeogr.* 29, 465–473.
- Bureau of Meteorology, 2019. Climate Data Online URL <http://www.bom.gov.au/climate/data/index.shtml> (accessed May 2019).
- Cove, M.V., Gardiner, B., Simons, T.R., Kays, R., O'Connell, A.F., 2017. Free-ranging domestic cats (*Felis catus*) on public lands: estimating density, activity, and diet in the Florida keys. *Biol. Invasions* 20 (2), 333–344.
- Davies, H.F., et al., 2018. Declining populations in one of the last refuges for threatened mammal species in northern Australia. *Austral Ecol.* 43, 602–612.
- Denny, E.A., Dickman, C.R., 2010. Review of Cat Ecology and Management Strategies in Australia. Invasive Animals Cooperative Research Centre, Canberra.
- Dickman, C.R., 1996. Overview of the Impacts of Feral Cats on Australian Native Fauna. Australian Nature Conservation Agency, Canberra.
- Doherty, T.S., Bengsen, A.J., Davis, R.A., 2015. A critical review of habitat use by feral cats and key directions for future research and management. *Wildl. Res.* 41, 435–446.
- Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G., Woinarski, J.C.Z., 2016a. Impacts and management of feral cats *Felis catus* in Australia. *Mamm. Rev.* 47, 1–15.
- Doherty, T.S., Driscoll, D.A., Nimmo, D.G., Ritchie, E.G., Spencer, R.-J., 2019. Conservation or politics? Australia's target to kill 2 million cats. *Conserv. Lett.*, e12633.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016b. Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci.* 113, 11261–11265.
- Edwards, G.P., De Preu, N.D., Shakeshaft, B.J., Crealy, I.V., 2000. An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildl. Res.* 27, 143–149.
- Efford, M., 2017. Habitat Masks in the Package Secr. Retrieved July 18, 2019, from. <https://www.otago.ac.nz/density/pdfs/secr-habitatmasks.pdf>.
- Efford, M.G., 2019. Secr: Spatially Explicit Capture-recapture Models. R Package Version 3.2.1. <https://CRAN.R-project.org/package=secr>.
- Efford, M.G., Hunter, C.M., 2017. Spatial capture-mark-resight estimation of animal population density. *Biometrics* 74 (2), 411–420.
- Fisher, D.O., et al., 2014. The current decline of tropical marsupials in Australia: Is history repeating? *Glob. Ecol. Biogeogr.* 23, 181–190.
- Glen, A.S., Dickman, C.R., 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biol. Rev. Camb. Philos. Soc.* 80, 387–401.
- Hayward, M.W., Boitani, L., Burrows, N.D., Funston, P.J., Karanth, K.U., Mackenzie, D.I., Pollock, K.H., Yarnell, R.W., 2015. Ecologists need robust survey designs, sampling and analytical methods. *J. Appl. Ecol.* 52, 286–290.
- Hohnen, R., Tuft, K., McGregor, H.W., Legge, S., Radford, I.J., Johnson, C.N., 2016. Occupancy of the invasive feral cat varies with habitat complexity. *PLoS One* 11, e0152520.
- Hunter, D.O., Lagisz, M., Leo, V., Nakagawa, S., Letnic, M., 2018. Not all predators are equal: a continent-scale analysis of the effects of predator control on Australian mammals. *Mamm. Rev.* 48 (2), 108–122.
- Jiménez, J., Nuñez-Arjona, J.C., Rueda, C., González, L.M., García-Domínguez, F., Muñoz-Igualada, J., López-Bao, J.V., 2017. Estimating carnivore community structures. *Sci. Rep.* 7, 41036.
- Johnson, C., 2006. Australia's Mammal Extinctions: a 50,000-year History. Cambridge University Press, Cambridge, England.
- Johnson, C.N., Isaac, J.L., Fisher, D.O., 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proc. R. Soc. Lond., B, Biol. Sci.* 274, 341–346.
- Legge, S., et al., 2017. Enumerating a continental-scale threat: How many feral cats are in Australia? *Biol. Conserv.* 206, 293–303.
- Lindenmayer, D.B., et al., 2018. Conservation conundrums and the challenges of managing unexplained declines of multiple species. *Biol. Conserv.* 221, 279–292.
- McDonald, P.J., Nano, C.E.M., Ward, S.J., Stewart, A., Pavay, C.R., Luck, G.W., Dickman, C.R., 2017. Habitat as a mediator of mesopredator-driven mammal extinction. *Conserv. Biol.* 31, 1183–1191.
- McDonald, P.J., Stewart, A., Schubert, A.T., Nano, C.E.M., Dickman, C.R., Luck, G.W., 2016. Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildl. Res.* 43, 121–129.
- McGregor, H.W., Legge, S., Jones, M.E., Johnson, C.N., 2014. Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS One* 9 (10), e109097.
- McGregor, H.W., Legge, S., Jones, M.E., Johnson, C.N., 2015a. Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS One* 10, e0133915.
- McGregor, H.W., Legge, S., Potts, J., Jones, M.E., Johnson, C.N., 2015b. Density and home range of feral cats in north-western Australia. *Wildl. Res.* 42, 223–231.
- McGregor, H.W., Cliff, H.B., Kanowski, A.J., 2016. Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildlife Research* 43 (8), 623–633.
- Menkhorst, P., Broome, L., 2008. National Recovery Plan for the Smoky Mouse (*Pseudomys Fumeus*). Department of Sustainability and Environment, Melbourne.
- Molsher, R., Newsome, A.E., Newsome, T.M., Dickman, C.R., 2017. Mesopredator management: effects of red fox control on the abundance, diet and use of space by feral cats. *PLoS One* 12, 1–15.
- Moseby, K.E., Letnic, M., Blumstein, D.T., West, R., 2018. Understanding predator densities for successful co-existence of alien predators and threatened prey. *Austral Ecol.* 44 (3), 1–11.
- Murphy, B.P., et al., 2019. Introduced cats (*Felis catus*) eating a continental fauna: the number of mammals killed in Australia. *Biol. Conserv.* 237, 28–40.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0 <https://www.R-project.org>.
- Radford, J.Q., et al., 2018. Degrees of population-level susceptibility of Australian terrestrial non-volant mammal species to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). *Wildl. Res.* 45, 645–657.
- Robley, A., Ramsey, D., Woodford, L., Taglierini, A., Walker, J., Sloane, P., Luitjes, M., 2017. Towards a Feral Cat Management Strategy for Hattah-Kulkyne National Park: Estimation of Feral Cat Density and Bait Uptake Rates, and Comparison of Management Strategies. Arthur Rylah Institute for Environmental Research, Heidelberg.
- Robley, A., Ramsey, D., Woodford, L., 2018. Estimating Population Changes in Wild Dogs, Feral Cats and Foxes in Relation to an Aerial Baiting Operation in Eastern Victoria. Arthur Rylah Institute for Environmental Research, Heidelberg.
- Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2013. Spatial Capture-Recapture. Academic Press, Cambridge, Massachusetts.
- Royle, J.A., Stanley, T.R., Lukacs, P.M., 2008. Statistical modeling and inference from carnivore survey data. Noninvasive Survey Methods for Carnivores. Island Press, Washington, DC, USA, pp. 293–312.
- Smith, A.P., Quin, D.G., 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biol. Conserv.* 77 (2–3), 243–267.
- Taggart, P.L., et al., 2019. Evidence of significantly higher island feral cat abundance compared to the adjacent mainland. *Wildl. Res.* 46 (5), 378–385.
- Wayne, A.F., Wilson, B.A., Woinarski, J.C.Z., 2017. Falling apart? Insights and lessons from three recent studies documenting rapid and severe decline in terrestrial mammal assemblages of northern, south-eastern and southwestern Australia. *Wildl. Res.* 44 (2), 114–126.
- Woinarski, J.C.Z., et al., 2017. How many birds are killed by cats in Australia? *Biol. Conserv.* 214, 76–87.
- Woinarski, J.C.Z., Armstrong, M., Brennan, K., Fisher, A., Griffiths, A.D., Hill, B., Milne, D.J., Palmer, C., Ward, S., Watson, M., 2010. Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildl. Res.* 37, 116–126.
- Woinarski, J.C.Z., Murphy, B.P., Palmer, R., Legge, S.M., Dickman, C.R., Doherty, T.S., Edwards, G., Nankivell, A., Read, J.L., Stokeld, D., 2018. How many reptiles are killed by cats in Australia? *Wildl. Res.* 45, 247–266.

Appendix C

Supporting Information: Chapter 4

C.1 Field surveys

In the Glenelg region, we deployed camera-traps once at a unique sites once. In the Otway region, we redeployed camera-traps in sites three times annually. All 2017 camera-sites were resurveyed each year, except for four logically challenging sites in the southern grid. In 2018, we added 16 additional sites in the southern grid, as well as 36 additional sites in the northern grid. These additional sites were resurveyed in 2019.

At each site, we deployed a singular remote trail camera with infrared flash and temperature-in-motion detector. The vast majority of camera-traps were Reconyx Hyperfire HC600, but a small portion was made up of both PC900 and HF2X infrared models (Reconyx, Holmen, Wisconsin). We programmed camera's to the highest sensitivity and to take five consecutive photographs when triggered (no quiet period). We attached each camera to a tree, approximately 30 cm above the ground, and facing toward a lure 2 - 2.5 metres away. The lure comprised an oil-absorbing cloth doused in tuna oil and placed inside a PVC pipe container with a mesh top. We secured each lure to the top of a 1 metre wooden stake and attached a handful of small white feathers to the outside of the PVC pipe container. Feathers were not used in the Lower Glenelg National Park survey. We cleared vegetation in the camera's line-of-sight to reduce false triggers and avoid obscuring cat coat markings in images.

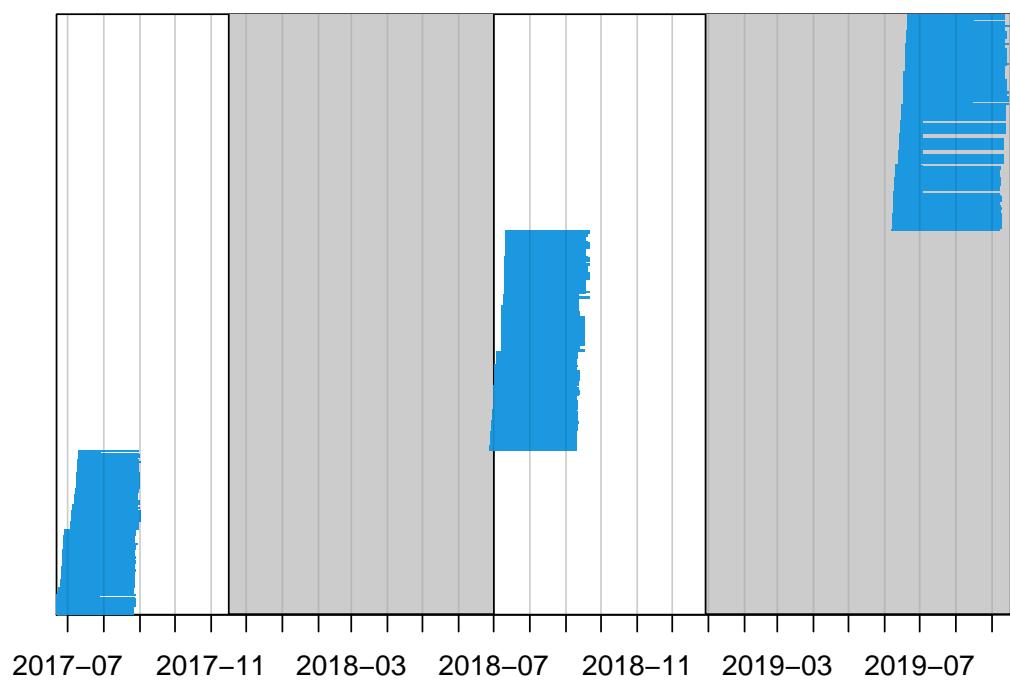


Figure C.1: Camera-trap operation times in the Otway region, Australia. Each blue horizontal line represents one camera-trap deployment. Grey shading indicates periods of fox control in the impact landscape.



Figure C.2: Example of a typical camera-trap set-up in the Otway region, Australia.

C.2 Individual cat identification

We first labelled every camera-trap image with a species metadata tag using DigiKam software. We also added metadata tags for each cat coat type: black, mackerel tabby, classic tabby, ginger and other (coats with multiple colour blends; Fig. 3). This allowed us to summarise species records and extract cat images using the ‘camtrapR’ R-package (Niedballa *et al.* 2016).

We considered all black cats to be of the ‘unmarked’ category in spatial mark-resight models - even the few with white splotches on their underside (as these couldn’t always be seen as cats move with their head down).

In the remaining coat categories where possible, we identified individual cats based on their unique coat markings. The ability to identify individuals substantially increased as the image library for each cat increased. Therefore we made the easiest identifications first to build up these libraries, before making decisions on the less obvious detections. We examined and matched all coat markings seen between two particular deflections. Markings on the front legs were the most useful for ID’s as the patterns do not skew as much with different body positions. On the whole, unidentifiable detections were mainly due to only part of a cat appearing in the frame, or because photos were blurry (because of cat movement or a foggy camera lens).

We were left with a small number of instances (less than ten) where only left or right flanks could be seen. In this case, the side with the most repeat detections was labelled as an individual, whereas the side with the least number of detections was considered unidentifiable. Additionally, an extremely small portion of cats in the Otways had ginger coats. When ginger coats are photographed with an infrared flash, they become overexposed and no markings can be seen (see the image in bottom-right corner in Fig. S3). We only had one detection of a ginger cat without an infrared coat. Therefore, if there were multiple ginger cat detections in a single grid, we treated them in the same way as one-sided flank detections.

One observer identified the 2018 feral cats in the Glenelg region (MR) and the 2021 Lower Glenelg National Park cats (Luke Woodford). In the 2017 and 2018 Otway datasets (where there were substantially more cat detections and fewer distinct coat patterns) two independent observers identified individual cats and discrepancies between observers were reviewed together until consensus was reached (MR, MLP, BH). If no consensus was reached, the cat was considered unidentifiable. In the 2019 Otway dataset, many of the identified cats were sighted in the previous surveys – these larger individual libraries meant that cats could be identified more easily so only one observer was necessary (MR). We also made use of additional cat images taken within the Otway region grids (just before each of our surveys) by white flash camera-traps from another study (Zoï Banikos, unpublished data). This provided additional and higher quality images (due to the white flash) of individuals in the photo library for identifications.

We were therefore left with three groups of cats: unmarked (black cats), marked (cats

which could be identified to the individual-level with complete certainty) and mark status unknown (cats which were not black, but couldn't be identified to the individual level with complete certainty).

We ignored the few detections of cats which were obviously young enough to be dependent on a parent, as these kittens do not have independent activity centres or movements and were not yet recruited into the adult population.



Figure C.3: Feral cat coat categories from left-right, top-bottom: black, mackerel tabby, classic tabby, other, black, ginger and ginger with infrared flash.

C.3 Summary statistics

Table C.1: Summary of camera-trap survey effort and feral cat detections.

Landscape	Cameras	Trapnights	Cats	Moves	Detections (max. 1 per 24-hr)		
					Identified	Unidentified	Unmarked
Annya	110	8000	9	11	23	3	20
Cobbob	110	7752	13	19	35	9	37
Hotspur	99	6085	8	12	22	3	13
Mt Clay	106	5451	10	16	33	5	0
LGNP north	49	2102	6	3	11	0	0
LGNP south	64	2842	21	4	37	0	0
North 2017	67	3565	26	12	60	8	46
South 2017	73	7099	20	18	62	4	48
North 2018	103	7838	30	32	90	12	62
South 2018	85	4543	24	37	75	17	59
North 2019	99	6077	27	39	90	22	101
South 2019	86	7150	25	69	133	23	58

C.4 Feral cat detection plots

C.4.1 Glenelg region

Replicate 1

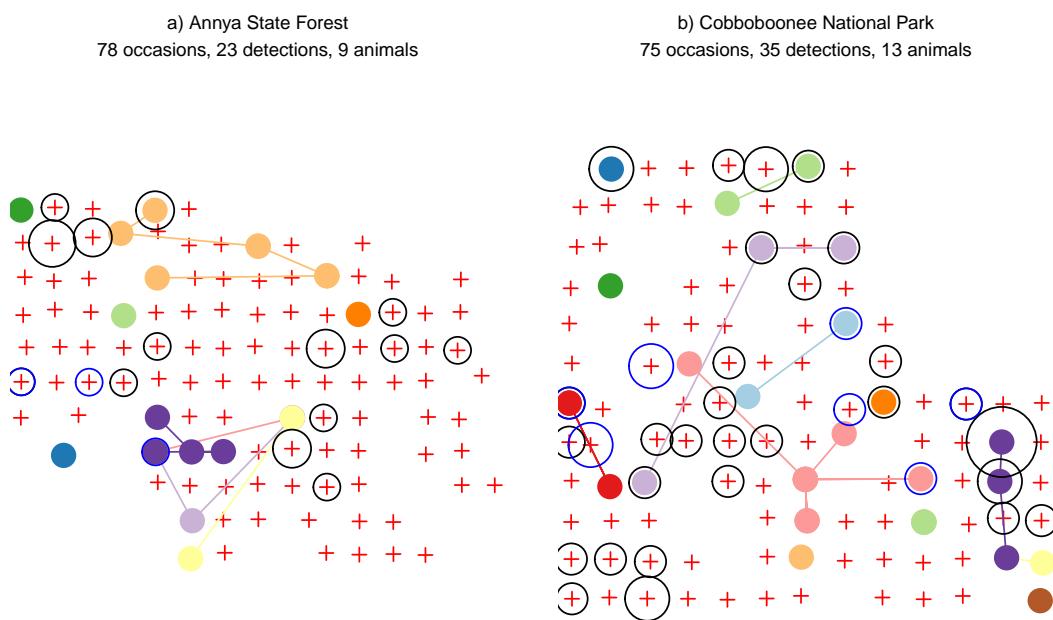


Figure C.4: Feral cat detections in the first replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in Annya (a) but does in Cobboboonee (b).

Replicate 2

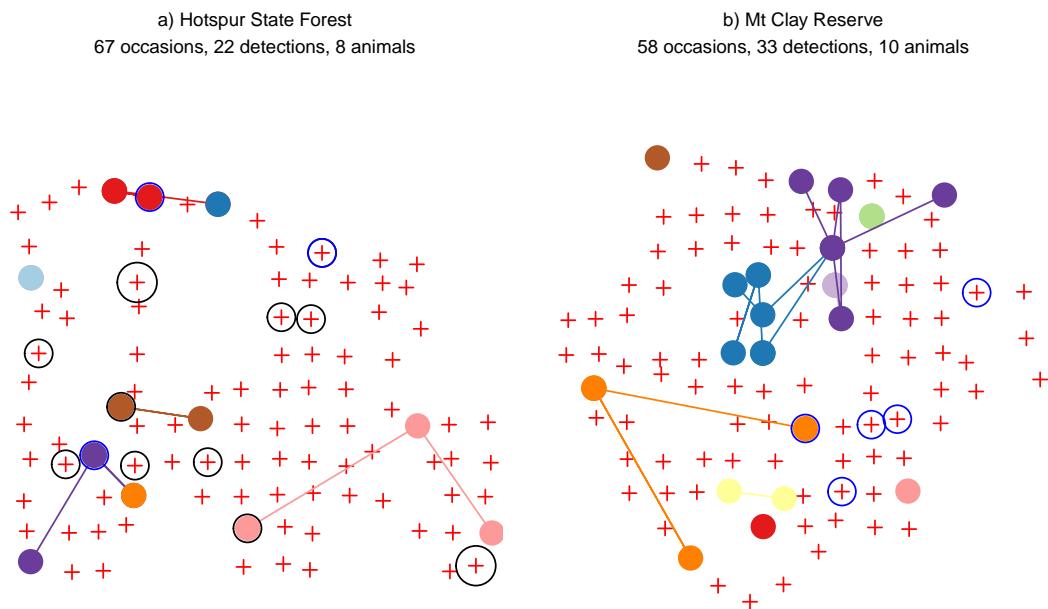
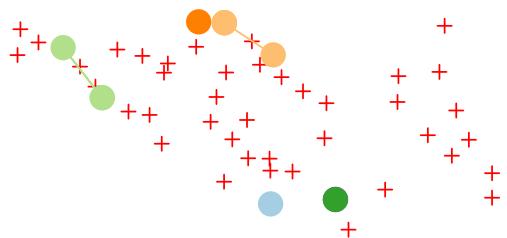


Figure C.5: Feral cat detections in the second replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in Hotspur (a) but does in Mt Clay (b).

Replicate 3

a) Lower Glenelg National Park – north
41 occasions, 11 detections, 6 animals



a) Lower Glenelg National Park – south
43 occasions, 37 detections, 21 animals

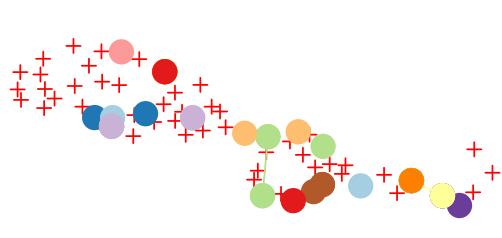


Figure C.6: Feral cat detections in the third replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in the north (a) but does in the south (b).

C.4.2 Otway region

2017

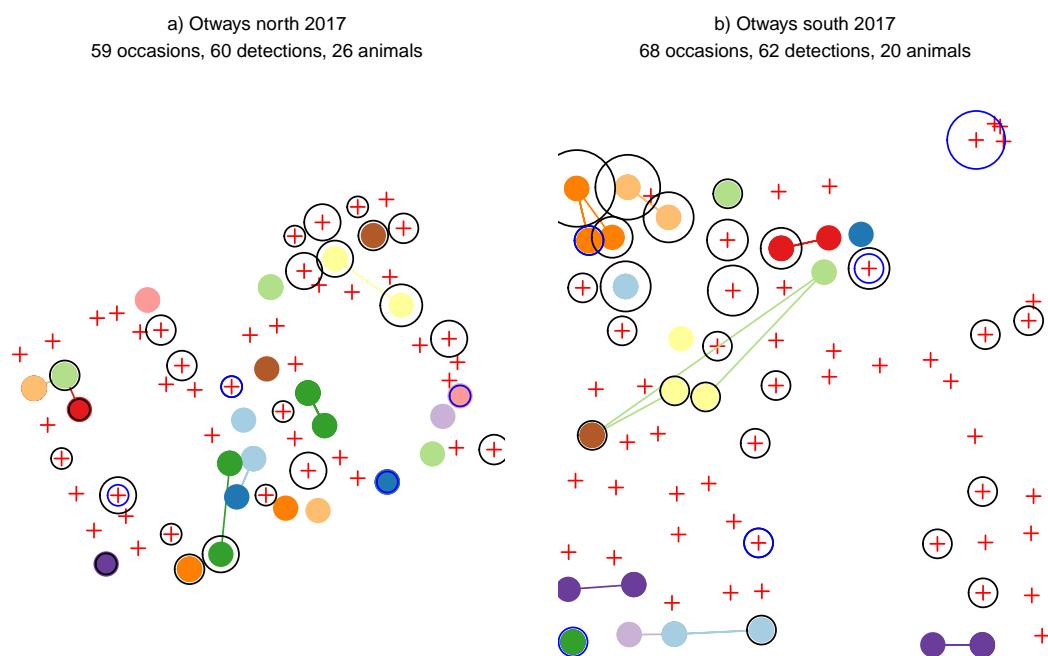


Figure C.7: Feral cat detections in the Otway region, Australia, 2017. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control did not occur in either of the landscapes during this time.

2018

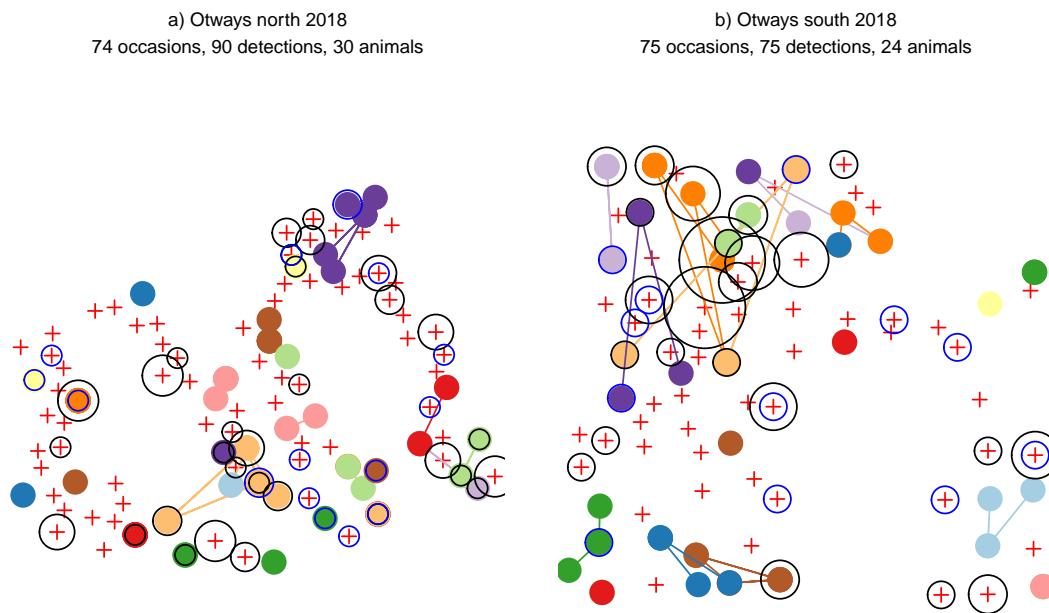


Figure C.8: Feral cat detections in the Otway region, Australia, 2018. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control had occurred, but lapsed just prior to the survey in the northern landscape (a), and did not occur in the southern landscape (b).

2019

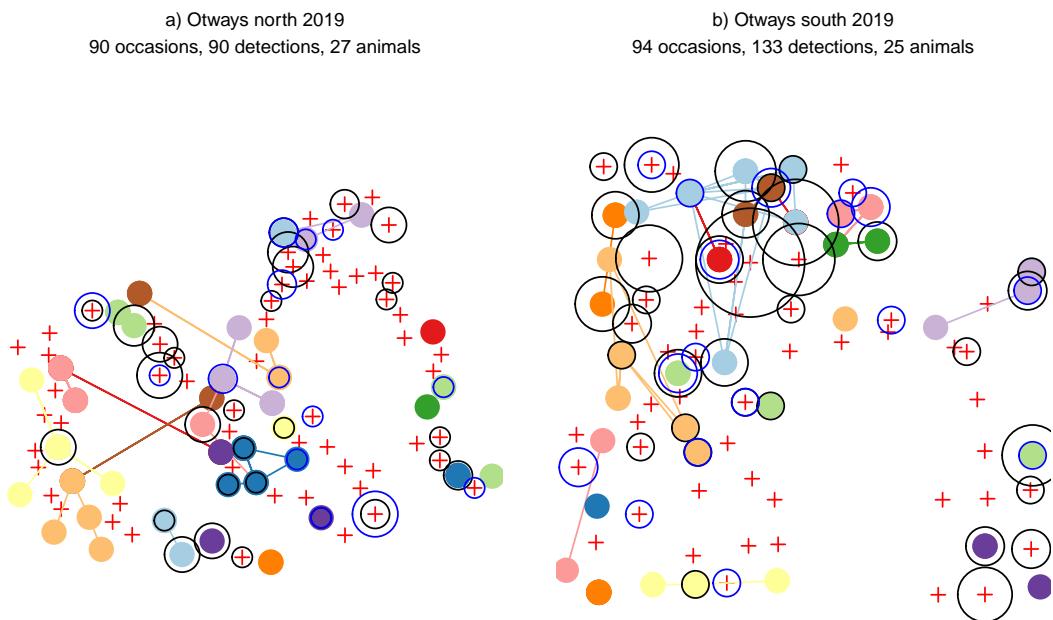


Figure C.9: Feral cat detections in the Otway region, Australia, 2019. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control occurred in the northern landscape (a) during this survey, but not the southern landscape (b).

C.5 Fox spatial occurrence

C.5.1 Glenelg region

```
Family: binomial
Link function: logit

Formula:
fox ~ s(x, y, bs = "ds", m = c(1, 0.5), k = 200) + offset(log(survey_duration))

Parametric coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -4.53965    0.09293 -48.85   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:
        edf Ref.df Chi.sq p-value
s(x,y) 25.58     199  61.78 9.75e-07 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) =  0.126  Deviance explained = 13.1%
fREML = 845.52  Scale est. = 1           n = 538
```

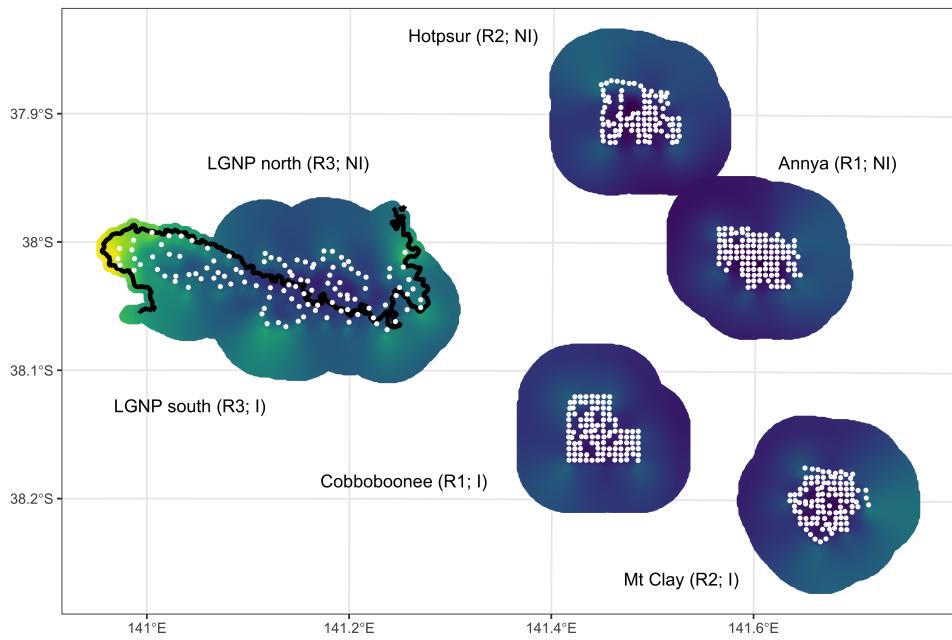


Figure C.10: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg region, Australia.

C.5.2 Otway Region

Family: binomial

Link function: logit

Formula:

```
fox ~ year + s(x, y, by = year, bs = "ds", m = c(1, 0.5), k = 100) +
  s(station, bs = "re") + offset(log(survey_duration))
```

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-5.283154	0.230023	-22.968	<2e-16 ***
year2018	0.004643	0.277696	0.017	0.987
year2019	0.037119	0.282270	0.132	0.895

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value
s(x,y):year2017	2.688e+00	99	8.096	0.010597 *
s(x,y):year2018	2.494e-05	99	0.000	0.506341
s(x,y):year2019	6.148e+00	99	22.262	0.000380 ***
s(station)	5.366e+01	194	75.723	0.000116 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.24 Deviance explained = 27.8%

fREML = 763.36 Scale est. = 1 n = 513

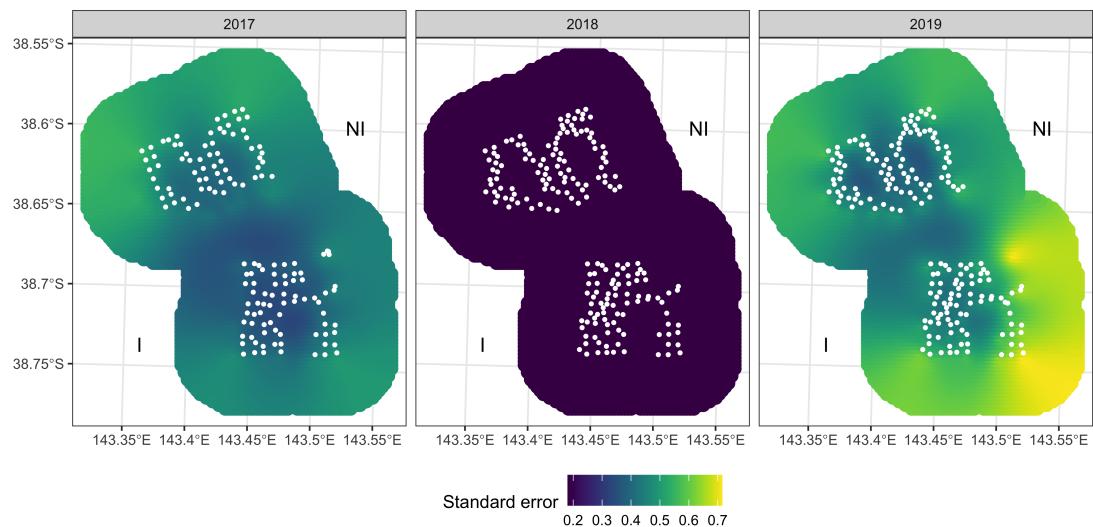


Figure C.11: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Otway region, Australia.

C.6 Vegetation categories

We condensed the main Ecological Vegetation Class groupings (DELWP 2020) present into three categories for each region: cleared land, heathy woodlands, lowland forests (Glenelg region only) and wet forests (Otways region only). We merged similar groups to reduce the number of categories for each region. In the Glenelg region, we merged dry forests with lowland forests. In the Otway region, we merged rainforests with wet forests, as well as merged dry forests and heathy woodlands.

A very small proportion of other Ecological Vegetation Class groupings were present in the habitat masks: riparian scrubs or swampy scrubs and woodlands, coastal scrubs grasslands and woodlands, wetlands, riverine grassy woodlands or forests, plains woodlands or forests, herb-rich woodlands. We removed these groups, and interpolated cell values from the nearest of the three vegetation categories.

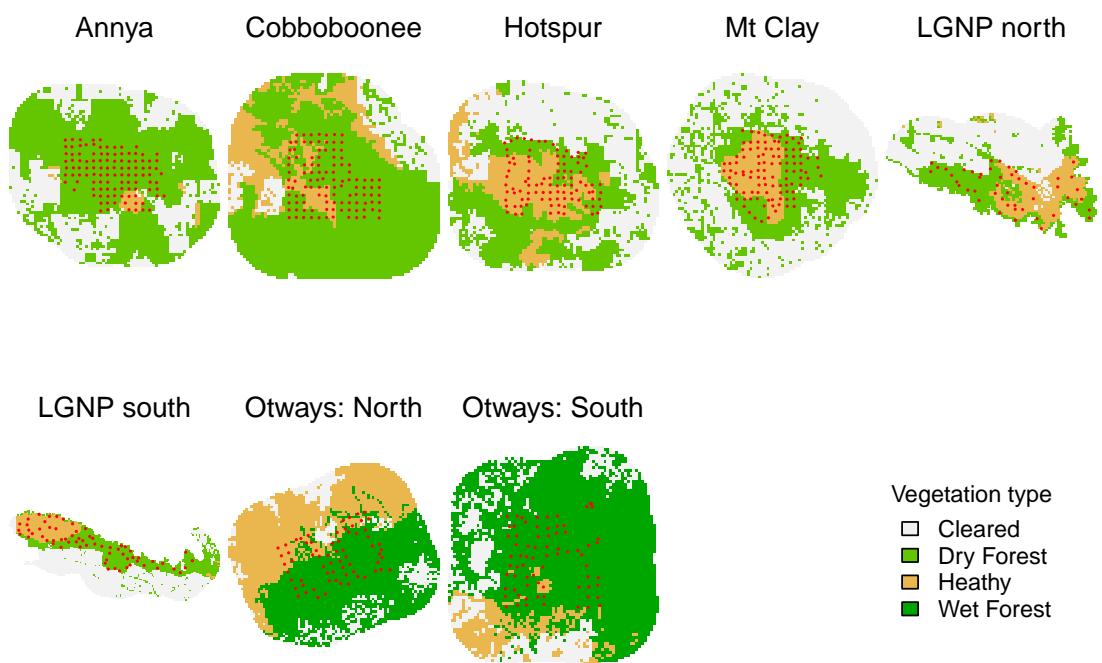


Figure C.12: Condensed Ecological Vegetation Class groups used as habitat mask covariates in spatial mark-resight models.

C.7 Spatial mark-resight models

C.7.1 Glenelg region

Table C.2: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 1.

Detector function	K	logLik	AIC	AICc	dAICc	AICcwt
exponential	3	-1745.99	3497.99	3498.37	0.00	1
half-normal	3	-1763.02	3532.05	3532.43	34.06	0

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

Table C.3: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 2.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~1 g0~1 sigma~1	3	-1309.93	2625.85	2626.23	0.00	0.32
D~vegetation g0~1 sigma~1	5	-1307.68	2625.37	2626.35	0.12	0.30
D~vegetation g0~T sigma~1	6	-1306.89	2625.77	2627.17	0.94	0.20
D~1 g0~T sigma~1	4	-1309.32	2626.65	2627.29	1.06	0.19

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

T - linear time trend (g0 only)

Table C.4: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 3.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~fox_occ g0~1 sigma~1	4	-1306.67	2621.33	2621.98	0.00	0.49
D~fox_occ g0~fox_occ sigma~fox_occ	6	-1304.97	2621.94	2623.34	1.36	0.25
D~s(fox_occ) g0~1 sigma~1	5	-1306.61	2623.21	2624.20	2.22	0.16
D~1 g0~1 sigma~1	3	-1309.93	2625.85	2626.23	4.26	0.06
D~s(fox_occ) g0~s(fox_occ) sigma~s(fox_occ)	9	-1303.41	2624.81	2627.97	5.99	0.02
D~1 g0~fox_occ sigma~fox_occ	5	-1309.41	2628.82	2629.80	7.82	0.01
D~1 g0~s(fox_occ) sigma~s(fox_occ)	7	-1307.91	2629.81	2631.71	9.73	0.00

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox_occ - fine-scale occurrence probability of foxes derived from generalised additive models

s(fox_occ) - non-linear smooth of fox_occ with three knots

Table C.5: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 4.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~session g0~fox_occ sigma~fox_occ	10	-1297.46	2614.93	2618.86	0.00	0.62
D~session g0~1 sigma~1	8	-1300.66	2617.32	2619.80	0.95	0.38

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox_occ - fine-scale occurrence probability of foxes derived from generalised additive models

session - landscape (n = 6)

Table C.6: Feral cat density per square kilometre as estimated by the AICc top-ranked model in the Glenelg region, Australia.

Landscape	Estimate	5% CI	95% CI	Treatment	Replicate
Annya	0.24	0.17	0.34	Non-impact	1
Cobboboonee	0.60	0.40	0.88	Impact	1
Hotspur	0.22	0.14	0.33	Non-impact	2
Mt Clay	0.24	0.18	0.31	Impact	2
LGNP north	0.15	0.07	0.35	Non-impact	3
LGNP south	0.56	0.34	0.90	Impact	3

C.7.2 Otway region

Table C.7: Akaike's Information Criterion values for detector functions in the Otway region, Australia; model set 1.

Detector function	K	logLik	AIC	AICc	dAICc	AICcwt
exponential	3	-5591.00	11188.01	11188.17	0.00	1
half-normal	3	-5743.26	11492.52	11492.69	304.52	0

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

Table C.8: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 2.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~year g0~1 sigma~1	5	-3550.63	7111.26	7111.67	0.00	0.48
D~year g0~T sigma~1	6	-3549.83	7111.67	7112.25	0.57	0.36
D~year + vegetation g0~1 sigma~1	7	-3550.04	7114.08	7114.86	3.19	0.10
D~year + vegetation g0~T sigma~1	8	-3549.24	7114.48	7115.49	3.82	0.07

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

T - linear time trend (g0 only)

Table C.9: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 3.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~year + fox_occ g0~fox_occ sigma~fox_occ	8	-3541.80	7099.59	7100.60	0.00	0.33
D~year + s(fox_occ) g0~s(fox_occ) sigma~s(fox_occ)	11	-3538.59	7099.19	7101.07	0.47	0.26
D~year g0~s(fox_occ) sigma~s(fox_occ)	9	-3541.07	7100.13	7101.40	0.80	0.22
D~year g0~fox_occ sigma~fox_occ	7	-3543.44	7100.87	7101.65	1.05	0.19
D~year + fox_occ g0~1 sigma~1	6	-3548.26	7108.51	7109.09	8.49	0.00
D~year + s(fox_occ) g0~1 sigma~1	7	-3547.47	7108.94	7109.72	9.12	0.00
D~year g0~1 sigma~1	5	-3550.63	7111.26	7111.67	11.07	0.00

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox_occ - fine-scale occurrence probability of foxes derived from generalised additive models

s(fox_occ) - non-linear smooth of fox_occ with three knots

Table C.10: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 4.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~session g0~fox_occ sigma~fox_occ	10	-3541.77	7103.55	7105.11	0.00	0.99
D~session g0~1 sigma~1	8	-3548.37	7112.73	7113.74	8.63	0.01

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox_occ - fine-scale occurrence probability of foxes derived from generalised additive models

session - landscape by year (n = 6)

Table C.11: Feral cat density per square kilometre as estimated by the AICc top-ranked model in the Otway region, Australia.

Landscape	Estimate	5% CI	95% CI	Treatment	Year
north 2017	1.00	0.74	1.35	Non-impact	2017
south 2017	0.74	0.52	1.05	Impact	2017
north 2018	0.81	0.64	1.02	Non-impact	2018
south 2018	0.82	0.63	1.06	Impact	2018
north 2019	0.73	0.55	0.95	Non-impact	2019
south 2019	0.98	0.76	1.27	Impact	2019