

# **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 km<sup>2</sup>), 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.

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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.

I designed and led fieldwork to collect data for this PhD. I experimentally 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 the following volunteers: Shauni Omond, Shayne Neal, Asitha Samarawickrama, Shelley Thompson, Erin Harris, Hannah Killian, 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, Dr Pia Lentini, Prof. 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 sorted camera-trap images and identified 133 individual feral cats from this dataset, with secondary independent identifications made by Mark Le Pla and Luke Woodford.

Chapter 4 uses a subset of this dataset; the 2017 camera-trap deployments in the Otway Ranges. This dataset was used in its entirety for the other chapters, but was supplemented with additional data collected by government partner researchers (detailed below). Chapters 2 and 3 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 5 include 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*

Contributions:

Code:

#### *Chapter 3*

Contributions:

Code:

#### *Chapter 4*

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.

Contributions:

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

#### *Chapter 5*

**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.

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

**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: Predation 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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Supervisors.

Committee.

Discussions many QAEco people highly influenced this PhD. Zoï. Plus Billy.

This thesis would be very different—much worse—without the assistance of nearly 50 fieldwork volunteers. Vin and Kelly provided me a home away from home during fieldwork and some much needed employment.

Heywood DELWP office. Wes and the GA project officers: Pittsy, Thomas McKinnon, Lou, Ethan. Glenelg Ark, Arthur Rylah Institute for borrowing camera-traps. Claire Miller from PV Otway Ark.

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# Chapter 1

## General Introduction

State of the debate. How it impacts Australian ecosystem management. Background information on the ecology of case study predators in Australia.

### 1.1 Mesopredator release hypothesis

"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 (in addition to prey), Soulé *et al.* (1988) first coined 'mesopredator release'. Grounded in basic food web theory, the mesopredator release hypothesis (hereafter 'MRH') is a simple and intuitive ecological theory. So why, 33 years later, is mesopredator release 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 using experimental designs. The average mammalian predator is cryptic and occurs widely across broad habitats, at low densities. To obtain sufficient sample sizes for statistical models, a very large area needs to be surveyed intensively for predators (Royle *et al.* 2008). Even still, limited inference can be gleaned from occupancy models when nearly everywhere is suitable habitat and site occurrence probability is close to one if you monitor for long enough (Efford & Dawson 2012). Due to the large area predator populations occur over, there often aren't comparable landscapes without declines to compare against, or at least ones which are spatially independent. Without robust experimental designs, it is difficult to attribute changes in mesopredator populations to apex predator declines.

Secondly, critics argue that the MRH is 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 web of positive, negative, direct, indirect and probably nonlinear (Johnson *et al.* 2007) interactions which occur in multipredator systems (Finke & Denno 2004; Levi & Wilmers 2012; Prugh & Sivy 2020). Additionally, bottom-up processes (i.e., ecosystem productivity and prey availability) interact with top-down processes to determine the strength of mesopredator release (Elmhagen & Rushton 2007). 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. As a result, we lack key detail on the conditions which drive the occurrence and strength of mesopredator release.

Thirdly, mesopredator release remains a blurry concept because of a reliance on vague population metrics. How exactly mesopredators are expected to respond to apex predator declines and what threshold defines “release” is not clearly stipulated (Jachowski *et al.* 2020). Many of the MRH field studies reviewed by Jachowski *et al.* (2020) provided mixed support 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” and “activity” indices (Stephens *et al.* 2015). These traditional survey and statistical methods also have an ill-defined spatial and temporal resolution; this is problematic because sampling scale impacts the direction of perceived species interactions (Efford & Dawson 2012; Blanchet *et al.* 2020).

Uncertainty around the MRH hinders effective conservation management. The functioning of global ecosystems has been degraded by widespread declines in large carnivores (Ripple *et al.* 2014). Managers therefore need to predict outcomes of continued declines, improvements and reintroductions of carnivore populations. Invasive predators are also a leading causes of global biodiversity and economic declines (Bellard *et al.* 2016; Doherty *et al.* 2016) and their control—usually lethal—is a prevalent management strategy ([ref](#)). However, when multiple invasive species occur, single invasive species control often has perverse outcomes on native species, likely due to ‘release’ effects (Ballari *et al.* 2016). Invasive predators likely have greater impact on native prey relative to native predators because prey are naive to the threat invasive predators pose and lacked time to evolve antipredator behaviours (Salo *et al.* 2007; Sih *et al.* 2010). 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 its agricultural impacts (Smith 2015). Reduced distribution and density 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). Mammals in the 35 - 5500 g weight range are the preferred meal size for these invasive mesopredators and have declined most strongly since the European colonisation of Aus-

tralia (Burbidge & McKenzie 1989; Murphy & Davies 2014). However, evidence for invasive mesopredator release is contentious to say the least (Allen *et al.* 2011, 2013; Fleming *et al.* 2012; Hayward *et al.* 2015; Nimmo *et al.* 2015; Doherty & Ritchie 2017; Hunter *et al.* 2018).

The MRH considers a predator guild comprising of two species, but what happens following apex predator decline when there are multiple subordinate species? Literature around the dingo-debate hypothesises both foxes and cats to 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 have high dietary overlap (Stobo-Wilson *et al.* 2021a, b) and occupy a similar niche (Glen & Dickman 2005). Although, evidence that foxes exert top-down pressure on cats is unclear.

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 (Dexter & Murray 2009; 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 (Marlow *et al.* 2015; Doherty & Ritchie 2017; Wayne *et al.* 2017), although, Duncan *et al.* (2020) offers an alternative hypothesis regarding prey overshooting carrying capacities. Strong evidence comes from the Risbey *et al.* (2000) experiment: capture-rates of shared mammalian prey worsened with targeted fox control, but increased when both foxes and cats were suppressed. Indeed, cat activity appears to increase on average following targeted fox control, but there is considerable uncertainty around this estimate (Hunter *et al.* 2018). Interestingly, Molsher *et al.* (2017) observed no change in the 'abundance' of cats, but identified 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.

### 1.1.1 European red foxes in Australia

Europeans introduced foxes from Great Britain into Australia (at least eight times) in the early 1870's for the purpose of sport hunting (Fairfax 2019). Once established in southern Victoria, foxes spread quickly across temperate and sub-tropical mainland Australia (Fairfax 2019). Today, foxes are ubiquitous expect in tropical areas of Northern Australia (and many offshore islands).

Foxes live in family groups comprising a dominant pair and their juvenile cubs. If resource availability is high, subordinate adult offspring may also remain with the group. Fox density in Australia varies from less than 0.1 foxes per km<sup>2</sup> in semi-arid re-

gions to more than four foxes per km<sup>2</sup> in productive environments such as farmlands and wetlands. Fox 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. Foxes within the family group share a home range, but usually hunt alone. Fox home ranges are dynamic: they can drift through time, involve excursions to concentrated food resources, and change rapidly if resource availability alters or a neighbouring home range becomes vacant (it only takes 8 days - 1 month for a vacant home range to be taken over).

Foxes have a strongly seasonal lifecycle: mating occurs in mid-winter, cubs are born in spring, and offspring disperse in autumn and early winter, before breeding that season. Survival and fecundity rates vary with age and local conditions, and litter size may increase after lethal control. Sex ratios at birth usually approximate parity. The proportion of young that disperse also varies, but males are more likely to disperse than females, and disperse further on average.

Foxes typically consuming about 380 grams of food per day (ref). True generalists, they feed on a wide variety of live prey, from livestock to small arthropods, as well as carrion and fruits.

### 1.1.2 Feral cats in Australia

As a consequence of human introductions, domestic cats *Felis catus* have a near-global distribution, occurring on all continents except Antarctica and on hundreds of islands (Long 2003). Cats are successful invaders because they have versatile diets (Bonnaud et al. 2011) and habitat use (Doherty et al. 2014), high fecundity and wide thermal tolerance, and do not require free drinking water (Bradshaw et al. 2013). Domestic cats were introduced to Australia in 1788. They spread rapidly and are now found as feral populations across the entire mainland and many of the larger offshore islands.

Domestic cats become feral (hereafter ‘feral cats’) when they live independently of humans in the wild; they are termed stray cats when they depend on humans for incidental provision of food or shelter (Denny & Dickman 2010).

Cat social organisation and behaviour is highly variable. In areas with rich resources, such as rubbish tips, farms and seabird colonies, cats live in dense matrilineal societies, and dozens of cats may share a small area. Across Australia’s more typical natural environments, however, cats are largely solitary. In these environments, densities vary from 0.01 to 7 cats per km<sup>2</sup>, depending on prey availability.

Female cat home range size is likewise variable, scaling from less than 100 ha to more than 600 ha (reviewed in Hamer et al. in press), but shows the opposite relationship with productivity. Female cats have small, partially-overlapping home ranges when annual productivity is high, and large home ranges when productivity is low, provided that seasonal variation is also low; where seasonality is high, this relationship is less clear (Bengsen et al. 2016).

The home range size of male cats varies with that of females, but is larger on average because dominant males typically overlap the ranges of two to three females. Both sexes may also have ranges that partially overlap ranges of other cats of the same sex. Cats can travel far beyond their home range, particularly in response to rapid changes in resource availability (e.g. because of fire or rabbit control), and some individuals do not have a fixed home range.

Female cats attain sexual maturity from as early as 5 months, but usually at 8 - 12 months, typically once they are at least 2.5 kg in weight. Females have one to three litters of ~4 kittens each a year. The winter non-breeding period is longer in cool climates than warm ones, and so the breeding season varies from four to nine months accordingly. Dispersal behaviour is not well documented, but male cats are likely to disperse more often and further than females. Feral cat survival rates are poorly studied, especially in natural habitats. Kitten mortality rates are likely to be high, and most cats probably live no more than three to five years.

Cats eat approximately 200 g of prey a day. They use 'sit and wait' and stalking strategies to catch a wide variety of vertebrates and insects, and will also occasionally scavenge on dead animals. Individual cats may specialise on prey groups, such as birds or small mammals.

Feral cats are implicated in 26% of bird, mammal and reptile species extinctions worldwide (Doherty et al. 2016). They affect native species mostly through predation (Medina et al. 2011), but also through competition (Medina et al. 2014), disease transmission (Dubey 2008), and hybridisation (i.e. with the wildcat *Felis silvestris*; Beaumont et al. 2001). Feral cats also have socio-economic impacts, mostly as disease vectors affecting agricultural production and human health (Dubey 2008).

Cat populations are difficult to control because cats do not readily take most types of meat bait (Algar et al. 2002), but cats have been eradicated from relatively small areas using a combination of exclusion fencing, shooting, trapping, and poisoning (Moseby et al. 2009). Garrard 2020.

## 1.2 Lethal fox control

Done globally. As foxes can be relatively easily culled<sup>6</sup> (unlike feral cats<sup>7</sup>), more land is managed and resources spent on their management than any other invasive vertebrate in Australia. Predominant conservation action in Australia.

Poison baiting with 1080 (sodium fluoroacetate) is the primary fox management approach in Australia (Saunders, Gentle, & Dickman, 2010).

Threat management for vertebrate species usually involves lethal control of invasive predators—a major cause of global declines (Burbidge et al. 2012; Doherty et al. 2016). Despite this, declines regularly continue (Ballari et al. 2016; Wayne et al. 2017b). This is primarily attributed to an insufficient reduction in the density of

the controlled invasive predator (e.g. Lieury et al. 2015), or a “release” of subordinate species (e.g. Ruscoe et al. 2011). A prominent example is Australia’s widespread use of 1080 poison baits to kill canid predators, which may potentially heighten the impacts of feral cats, *Felis catus*, and overgrazing by various herbivores on threatened, native mammals (Doherty & Ritchie 2017). However, difficulties in monitoring and modelling these complex multispecies interactions has led to contention (Hayward & Marlow 2014).

Native mammal responses to fox suppression in Australia have been highly variable. Though, a temporal trend in the response of critical weight-range mammals is often observed: where populations spike in the short-term (1 - 3 years post-control)<sup>11,12</sup>, taper off closer to pre-control levels in the medium-term (5 - 15 years post-control)<sup>13–15</sup> and decline to pre-control levels or worse (including local extinctions) in the long-term (15+ years post-control)<sup>16–20</sup>. This could be explained by: (i) reduced top-down control leading to the population overshooting, then stabilising at the carrying capacity of the environment<sup>21</sup>. (ii) A mesopredator release of feral cats (particularly in regions where dingoes are absent)<sup>22</sup> due to apex predator suppression and/or increased prey availability. (iii) A release of larger herbivores (macropods and possums) due to fox suppression (increasing competition and altering habitat structure)<sup>13,22,23</sup>. (iv) compensatory responses of foxes to control (e.g. increasing reproduction rates)<sup>24</sup>, and/or learned bait aversion<sup>25,26</sup>. However, most fox control programs have not been surveyed in a way that can test these explanations, nor disentangle natural variation and the impact of other threats (e.g. drought).

Effort / lack of fox suppression Baiting at large scales (>500 km<sup>2</sup>) and high densities (5+ baits per km<sup>2</sup>) can greatly reduce fox densities, with populations remaining low for several months (Berry et al., 2014; Thomson et al., 2000). In contrast, patchy or smaller-scale control may result in little detectable change in fox density (Bengsen, 2014; Newsome, Crowther, & Dickman, 2014), or even increase fox activity or abundance through compensatory immigration (Lieury et al., 2015; Towerton, Dickman, Kavanagh, & Penman, 2016). Considerable uncertainty remains about the efficacy of low-intensity landscape-scale fox management for biodiversity conservation (Robley, Gormley, Forsyth, & Triggs, 2014; Towerton et al., 2016; Walsh, Wilson, Benshemesh, & Possingham, 2012), and the design of more effective management is hampered by a lack of tools for predicting the effects of control.

## **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 km<sup>2</sup> 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<sup>-2</sup> (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 ( $38.42^{\circ}\text{S}$ ,  $142.24^{\circ}\text{E}$ ). The locality is 90 – 440 m a.s.l. and has a cool-temperate climate: maximum daily temperatures average  $19.3^{\circ}\text{C}$  in summer and  $9.5^{\circ}\text{C}$  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  $49\text{ km}^2$  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).

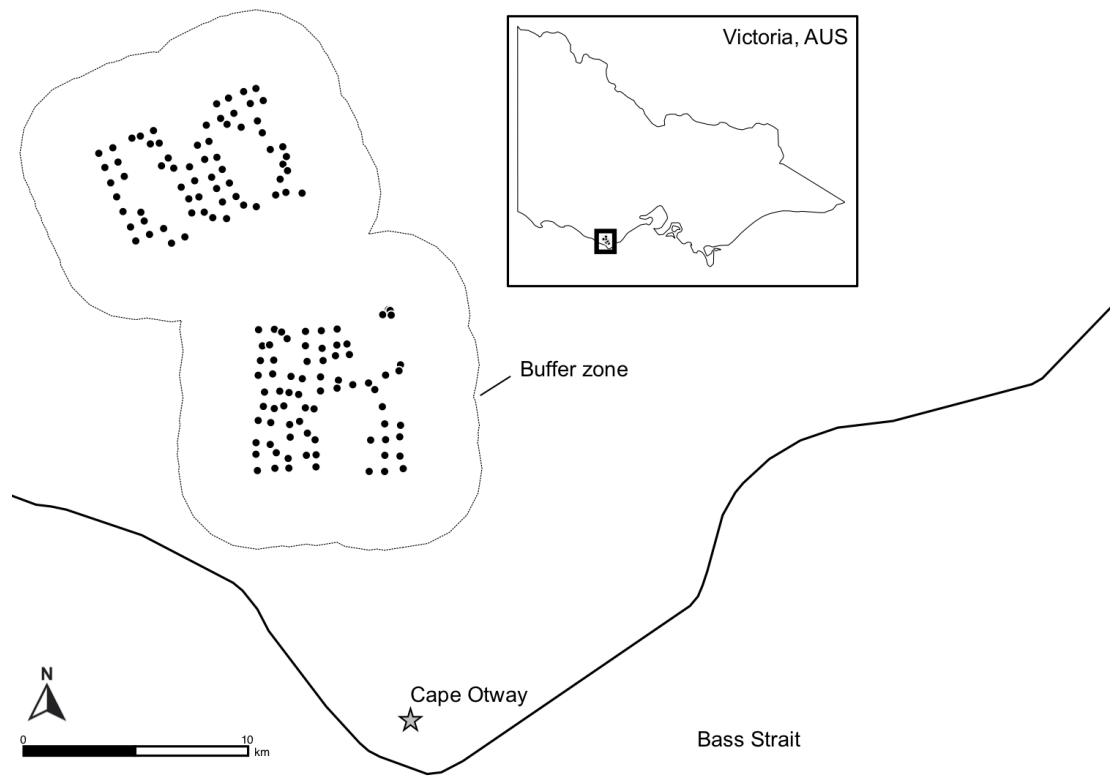


Figure 2.1: Study area, western Otway Ranges, Victoria, Australia, showing the location of the camera-trapping sites (black dots) within the 3500 m buffer zone (thin grey line).

## 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  $0.2 \text{ cats km}^{-2}$  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<sup>-2</sup> (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<sup>-2</sup>), and more than three times higher than the predicted continental mean density for feral cats in ‘natural areas’ (0.27 cats km<sup>-2</sup>; 0.18 – 0.45 cats km<sup>-2</sup>; 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

#### Background.

Invasive predators are commonly managed using lethal control because they cause biodiversity and socioeconomic losses. Invasive predators are resilient to low-level culling efforts, but lethal control across broad spatiotemporal scales is expensive. Quantifying both 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 (e.g. fire).

#### Methods.

In this study we examined the response of four species to invasive predator management in two fire-prone regions: the introduced apex predator targeted by lethal control (red fox *Vulpes vulpes*), an invasive 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 used hierarchical generalised additive models to estimate changes in species occurrences across (1) gradients of poison-bait density, as well as (2) time since fire across different vegetation communities, while (3) accounting for forest edge-effects.

#### Results

Poison-baiting suppressed foxes across both regions—the degree to which depending on poison-bait density—but had highly variable impacts on threatened native prey. In

one region, fox control was critical to the persistence of potoroos, but not bandicoots. However, more recently commenced fox control in the other region did not benefit either threatened species. This variation did not appear to be due to mesopredator release - we saw no signs of fox control impacting feral cat occurrence in either region. Vegetation type and fire were strong drivers of the entire mammal community. Heathlands and heathy woodlands are priority landscapes.

### **Sythesis**

Functionally similar predators differently.

suppression, and threatened species

quantify their suppression

low effort lethal control, or

predator control can have unintended outcomes.

Invasive predator control is a common conservation strategy but can have unintended outcomes.

responses to threat-management across heterogeneous environments Fire is near-ubiquitous drivers of mammal populations, but are seldom been accounted for when assessing fox control outcomes.

### 3.1 Introduction

Conservation managers often intervene in ecosystems with the aim of stemming rapid biodiversity loss, but the benefits of management are rarely quantified. Understanding management outcomes is essential to ensure cost-effectiveness and detect potential unintended consequences. However, reliable inference is difficult to achieve because the effects of management need to be separated from natural drivers of populations, as well impacts of co-occurring threats and management. Further, we often have a poor understanding of what drives the patchy occurrence of species within their distributions, despite being the spatial scale management usually operates at, and a common metric used to evaluate conservation strategy success.

Invasive predators are also a leading causes of global biodiversity and economic declines (Bellard *et al.* 2016; Doherty *et al.* 2016). Invasive predators can have greater impact on native prey relative to native predators because prey are naive to the threat invasive predators pose and lacked time to evolve antipredator behaviours (Salo *et al.* 2007; Sih *et al.* 2010). According, their control—usually lethal—is a prevalent management strategy worldwide ([ref](#)). However, lethal invasive predator control outcomes are notoriously inconsistent. Invasive predators can be resilient to population disturbances, including low-effort control programs. It is therefore vital to carefully monitor invasive predator control programs; both in terms of quantifying predator suppression and benefits to native biodiversity of concern.

When multiple invasive predators occur, single invasive species control often has perverse outcomes on native species (Ballari *et al.* 2016). This is likely due to ‘release’ effects of subordinate invasive predators, i.e., mesopredator release. It is therefore imperative survey the broader community to monitor unintended consequences and conservation benefits.

Australian native terrestrial mammals have experienced some of the worst declines in recent history. While habitat destruction is a key threatening process, mammalian extinctions have largely taken place within large tracts of native vegetation. These mammals perform important ecological roles - their decline can drastically impact ecosystem function. Mammals weighing between 35 and 5500 g (‘critical weight range’) have been hit hardest as they are the preferred meal size for both the red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus* (hereafter ‘cat’), introduced following European invasion more than 230 years ago. Also increasingly recognising the role of altered fire regimes. While some animals may succumb to direct mortality from fire events, most impacts are indirect through longer-term changes in food and habitat resources following fire. Interactions between invasive predators and fire.

More land in Australia has been managed for foxes than any other invasive vertebrates, primarily through continuous 1080 poison-baiting (Saunders, Gentle, & Dickman, 2010). However, native prey benefits are rarely demonstrated. This is partly because many fox control programs go unmonitored, or monitoring provides limited inference on native prey responses ([reddiex](#)), and partly because dramatic declines

and local extinctions have been reported after long-term fox control (e.g. wayne; lin-denmeyer; grampians; rock wallabies). This may be due to insufficient control effort to suppress fox to a level which benefits prey, or because fox suppression has ‘released’ feral cats (i.e., mesopredator release). However, we have little empirical evidence for either alternative. Few studies have quantified fox suppression across a gradient of control effort. Feral cats do appear to increase abundance following fox control, although there is considerable uncertainty around this (Hunter). Evaluating fox control is difficult due to co-occurring threats and management actions.

Minimising the threat of large wildfires through small-scale controlled burns to reduce fuel-loads (dried vegetative substrate) is an increasingly important role of land managers. Prescribed burning operations require juggling asset protection against the often competing needs of native species. Animals response to fire are often measured using time since the last fire event, however, post-fire regeneration varies considerably across different vegetation communities. While sample sizes often prohibit estimating fire responses across different contexts, it is imperative to inform optimal fire regimes across heterogeneous landscapes.

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.

Here, we quantified changes in invasive predator and threatened native prey occurrence across 1080 poison-bait density gradients for two broadscale fox control programs, while accounting for the effects of fire regimes. From 3667 camera-trap deployments over seven years, we were able to survey mammals across a range of environmental conditions and management contexts across two broad regions implementing fox control in south-west Victoria, Australia. We used generalised additive models to fit nonlinear relationships between fox, cat, SBB and LNP occurrence and several spatial and temporal covariates, including (1) fox-bait density, (2) time since fire across vegetation communities. We hypothesised that: (1) fox-bait density would be associated with declines in fox occurrence, increases in SBB, LNP and cat occurrence (in accordance with the mesopredator release hypothesis), (2) species occurrence would vary with time since fire, but in slightly different ways across vegetation communities. We also accounted for habitat fragmentation, hypothesising that (4) predator oc-

currence would highest closest to cleared edges, and that threatened prey occurrence would be lowest here.

## 3.2 Methods

### 3.2.1 Study area

We collated camera-trap data across the Glenelg region and Otway Ranges in south-west Victoria, Australia (Fig. 3.1). The terrestrial mammalian predator guild is depauperate throughout 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). Introduced foxes and cats are therefore the only medium-large functional mammalian terrestrial predators across both regions. The purpose of each collated study was to experimentally survey changes in the mammalian community due to fox control. 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. This allowed us to investigate fox-cat interactions across a gradient of apex predator (fox) activity and other landscape contexts. Prescribed fire is another key management action undertaken throughout both regions (except in very wet sections of Otway Ranges), primarily for asset protection.

In the Glenelg region, Gunditjmara country, natural vegetation—mostly lowland forests and heathy woodlands—is fragmented (Fig. 3.1). Foxes have been subject to lethal control in three distinct forest blocks (separated by pastoral farming and residential property) since October 2005, with 1080 poison-baits replaced fortnightly (???). Three similar, but unbaited, forest blocks to the north have been surveyed simultaneously as an experimental control (???).

The Otway Ranges, Gadubanud 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 in the high-altitude south-west descends 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. The majority of this baiting began in 2016 - 2017, although fox-baiting commenced in some small sections in 2008.

### 3.2.2 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. Camera-traps were active for an average of 47 days, totalling 172,052 trapnights. Camera-trap spacing was variable; the average minimum distance between simultaneously deployed camera-traps was 445, 853 and 1266 metres for each study. Camera-traps were de-

ployed in the Glenelg region between 2013 – 2019, and in the Otway Ranges between 2016 – 2019.

All camera-trap deployments consisted of a Reconyx (Holmen, Wisconsin) brand camera-trap (both white and infrared flash), attached to a tree or a metal picket, facing a lure. Camera-traps were set-up in two ways depending on the key aim of the project, either targeted toward predators or prey species. One study across both regions positioned camera-traps lower 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 remaining camera-traps were positioned higher on a tree or a metal picket (at least 40 cm above ground) and angled downwards more strongly - facing a lure approximately 1 - 1.5 m away. 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.

### 3.2.3 Cumulative detection probabilities

We did not incorporate imperfect detection in the GAMs. To determine the bias this may have had, we calculated the cumulative probability of detection by fitting a single season occupancy-detection model (MacKenzie *et al.* 2002). We fit these models using the ‘unmarked’ R-package with 24-hour sampling occasions. We then calculated the calculated the probability that each species would have been detected for a given survey duration (Garrard *et al.* 2008) of up to 93 days (the maximum survey duration).

### 3.2.4 Generalised additive models of species occurrence

We constructed a table with a row for each camera-trap deployment, a presence-absence column for each of the four study species, as well as additional columns for site information and explanatory variable values. 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 intercept for each unique site to account for repeat sampling. We used the same model structure for each species, because we expected all species to be effected by these explanatory variables and we aimed to contrast responses. 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).

We expected the density of 1080 poison-baits (targeted to foxes) to decrease the fox occurrence probability, and therefore increase the occurrence probability of three subordinate species. We summed the number of fox-baits 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.* 2017). We modelled this explanatory variable using a thin plate regression spline, with a factor smooth basis to model the impact separately for each region: poison-baits are replaced at different frequencies (fortnightly v.s monthly) across the regions, which has been occurring over different time scales (~7-13, 0-3 years) in the Glenelg region and Otway Ranges (respectively).

We surveyed species across a range of vegetation community types, which provide different levels of food and shelter. However, these resources are mediated by fire, but regeneration following fire occurs at different speeds across vegetation types (McColl-Gausden & Penman 2019). We expect species occurrences to differ across vegetation types and with time since fire, but to have slightly different responses to time since fire in each different vegetation type; we therefore modelled an interaction between time since fire (in years; hereafter ‘TSF’). We used coarse fire scar mapping provided by government managers to calculate the years since the last fire for each camera-trap deployment. We attached Ecological Vegetation Class (hereafter “EVC”; standard units for vegetation classification in Victoria; DELWP 2020) groups 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 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 in Pedersen *et al.* 2019). This shares information on TSF responses across groups and penalises functions which deviate strongly from the average response—increasing confidence that they are true deviations opposed to the result of sampling noise.

Long-term climate is a strong driver of species distribution in the Otway Ranges (Swan *et al.* 2021), as are short-term rainfall fluctuations in another region of south-western Victoria (Hale *et al.* 2016). We expect short-term rainfall fluctuations to have different impacts across the wide spatial gradient of average rainfall in our study sites. We therefore modelled a tensor product interaction term for spatial annual average rainfall and short-term temporal dynamics in actual rainfall. We extracted annual rainfall values (mm) from the NARCLiM dataset (1-km resolution)BCCVL database. To calculate percentage difference in short-term rainfall, we downloaded all available rainfall data from proximal weather stations ( $n = XX$ ) from Queensland Government and the Australian Bureau of Meteorology. For each species detection, we took the amount of rainfall in the previous 18 months at the nearest weather station, as well as the median rainfall over that same 18 month period since rainfall began being recorded at that weather station, and calculated the percentage difference between those two values. We chose 18 months for a comparison to Hale *et al.* (2016)).

Invasive predators are well-documented to prefer edges between forest and cleared land (refs). Mammalian prey species are also likely impacted by edges indirectly due to increased invasive predators occurrence probability, and directly due to lower level

of proximal suitable habitat (refs). We inverted the Victoria native vegetation extent shapefile from DELWP, and removed non-native vegetation areas which were smaller than 30 ha (which Hradsky ref?). For each camera-trap site, we calculated the minimum distance to non-native vegetation area. We used a thin plate regression spline for this smooth.

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

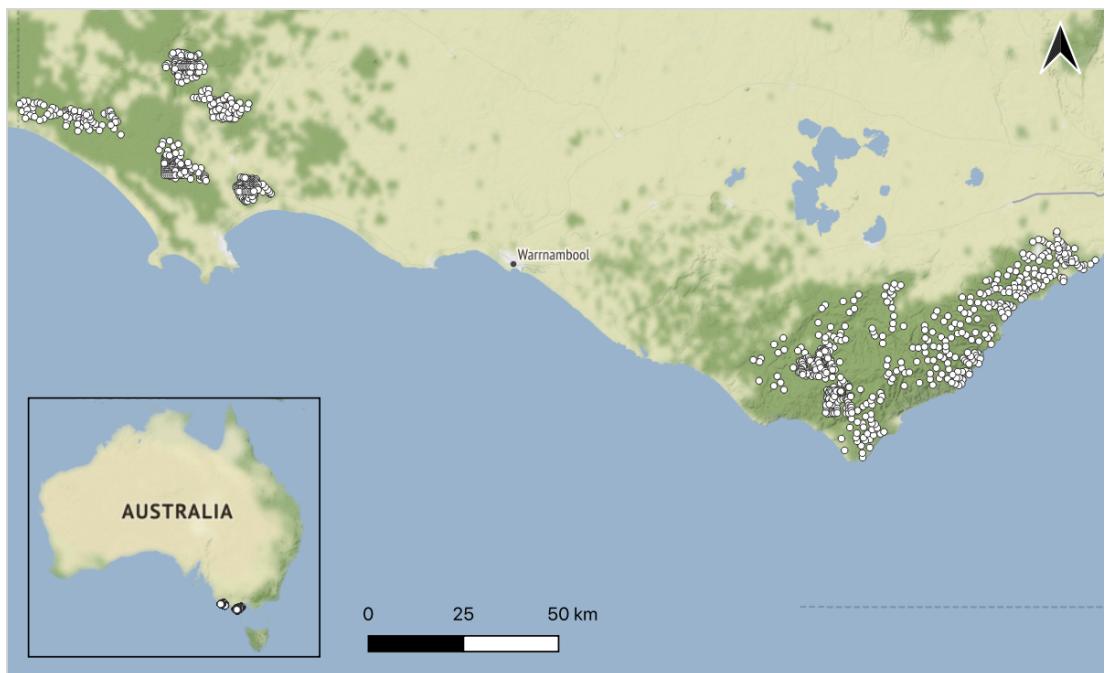


Figure 3.1: Locations of study sites in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. Map tiles by Stamen Design, under CC BY 3.0, map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

### 3.3 Results

Fox occurrence declined with increasing poison-bait density, but this relatively weak effects on the other mammal species (Fig. 3.2). The maximum poison-bait density, 9 baits per km<sup>2</sup>, reduced fox occurrence probability, consistently across both regions, by ~75% (Fig. 3.2). This was a linear decline in the Otway region, but a nonlinear shape in Glenelg with diminishing bait returns from 3 - 6 baits km<sup>-2</sup>. We saw no effect on fox control on cat occurrence across both regions. Fox-baiting slightly increased SBB and LNP occurrence in the Glenelg region, but slightly decreased their occurrence in the Otway region. The impact on SBB's was negligible; LNP's in the Glenelg region benefited the most from fox control (Fig. 3.2c-d).

Threatened species occurrence was most strongly driven by vegetation type and fire (Fig. 3.3). Despite being detected across all all vegetation communities, the majority of SBB and LNP detections took place in heathy communities; lowland forests were also important for SBB's, while herb-rich woodlands were also important for LNP's (Table C.1). However, within these vegetation communities, occurrence probability varied substantially with TSF for both threatened species. SBB's had the most complex interactions with TSF, with occurrence peaking 20 and 75 years post-fire, although the strength of the 75 year peak varied considerably across vegetation communities. Potoroo occurrence increased linearly with TSF in heathy landscapes, but decreased linearly with TSF in herb-rich woodlands. TSF on this long-term scale had a weak impact on invasive predators, and foxes were also relatively unaffected by EVC group (Fig. 3.3). Foxes, cats, and LNP's had a near-flat global function for average TSF. Foxes also had flat functions for TSF in each EVC group, whereas cats and LNP occurrence had variable relationships with TSF across the EVC groups.

Foxes were most strongly impacted by rainfall patterns; fox occurrence was highest where average long-term rainfall was lowest, but started to slightly increase again where rainfall averaged more than 1600 mm annually (Fig. ??a). Fox occurrence was also higher when rainfall in the 18 months prior to the detection was below average (Fig. ??a). In contrast, cat occurrence was highest in wettest landscapes during time with above average rainfall (Fig. ??b). Rainfall had no discernible impact on SBB's (Fig. ??c). Potoroo occurrence was strongest at sites where long-term average rainfall was high, during times with below average rainfall (Fig. ??d).

Foxes occurrence was high closest to the edge of non-native habitat, and declined linearly into the forest interior for 2 km (Fig. C.2a). Cats were mostly unaffected by this fragmentation, whereas SBB and LNP occurrence weakly increased with distance from edges, but these effects were highly uncertain (Fig. C.2).

Threatened species had better occurrence model fits than the invasive predators. The generalised additive model of fox occurrence had an adjusted R-square value of 0.29 and explained 28% of the null deviance. Respectively, these model values were 0.25 and 25% for cats; 0.38 and 44% for SBB's; 0.51 and 56% for LNP's. The occupancy-detection models revealed that, for the average camera-trap survey length, species

detection probabilities ranged from 70 - 100% (Fig. C.1). Fox detection probability was high (~95% for the average survey duration) in landscapes without fox control, but considerably lower (~65% for the average survey duration) in landscapes with fox control (assuming constant occupancy). Feral cats had the lowest detection probability. We had near-perfect detection of threatened species on camera-traps with survey durations greater than 30 days (Fig. C.1).

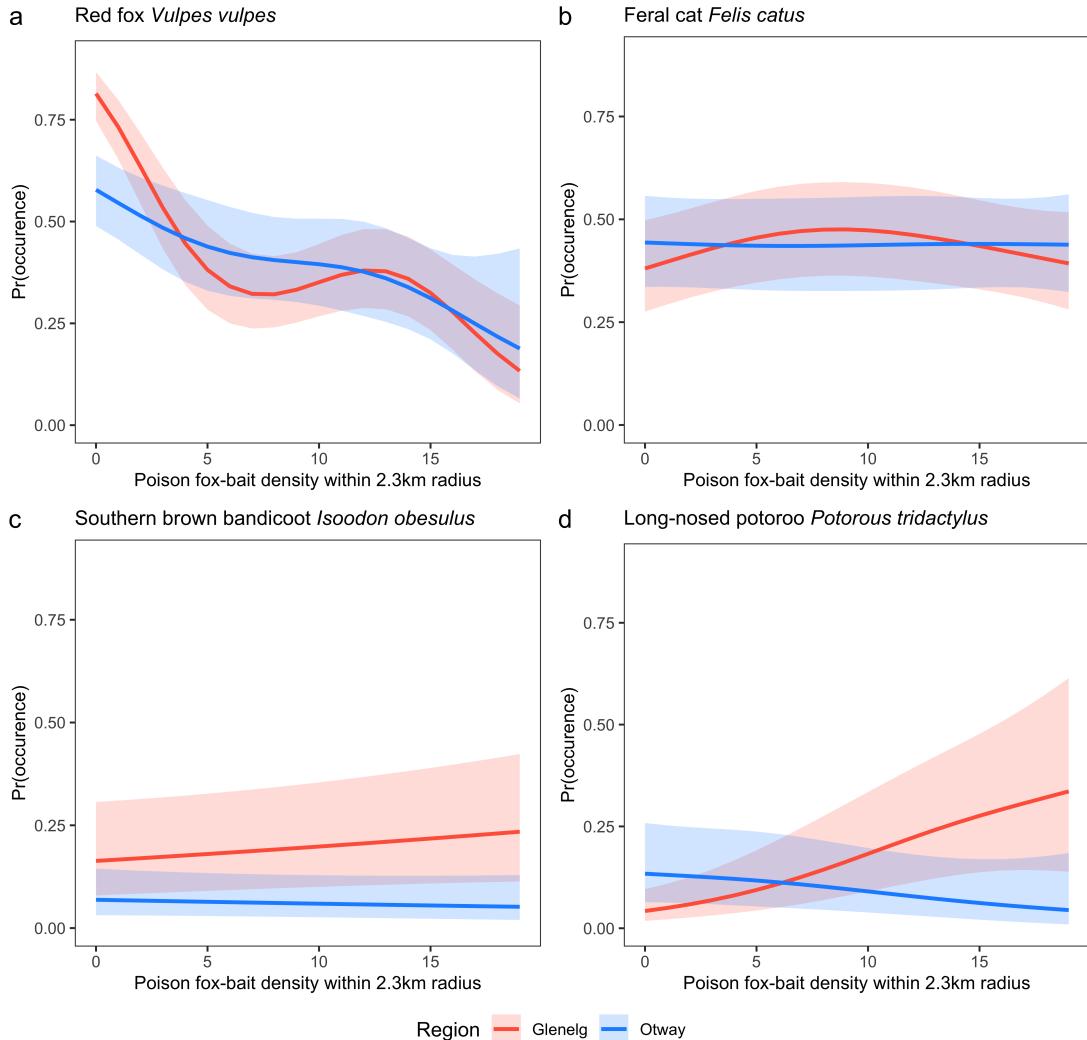


Figure 3.2: Probability of fox occurrence (a) declined with increasing 1080 poison-bait density across both the Otway Ranges (blue) and Glenelg region (red) in south-west Victoria, Australia. Feral cat occurrence probability remain unchanged across the range of fox-bait density (b). Southern brown bandicoot (d) and long-nosed potoroo (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.

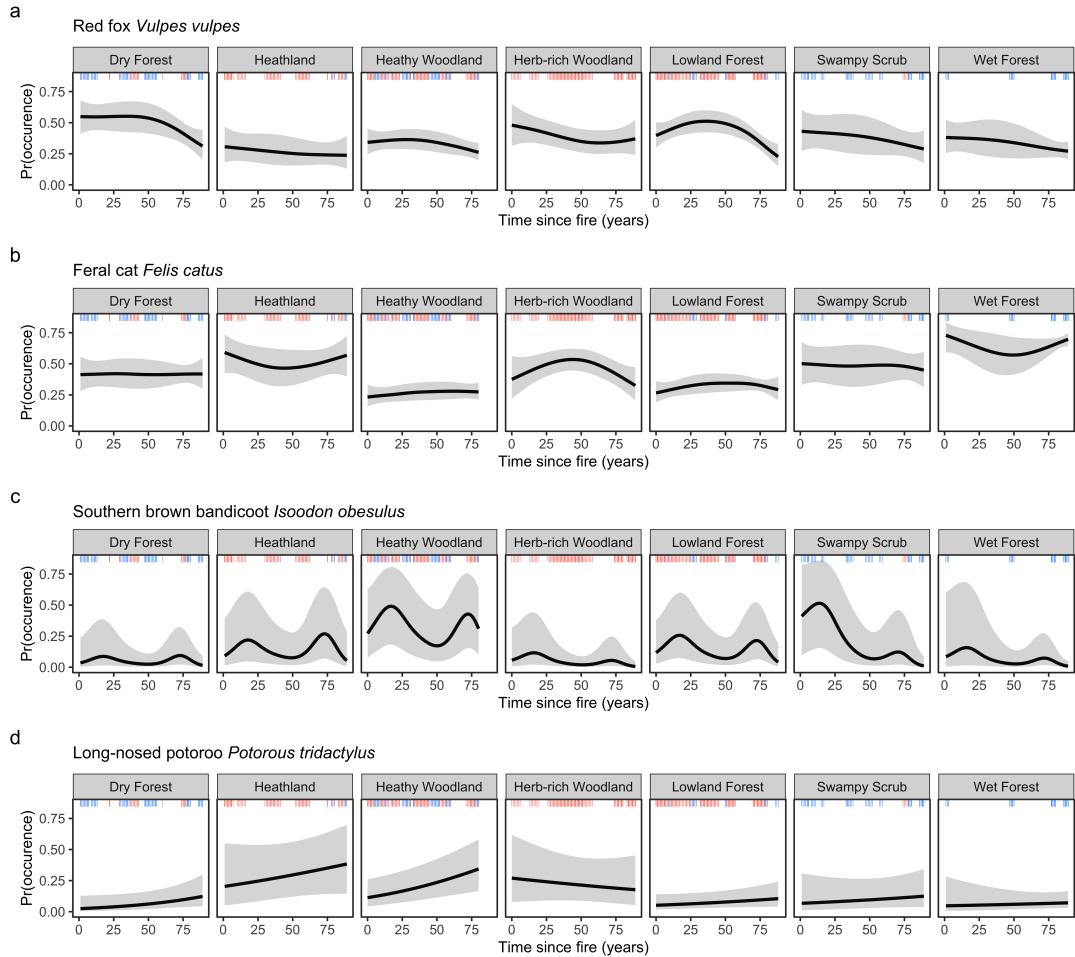


Figure 3.3: Time since fire had a weak impact on fox (a) and feral cat (b) occurrence probability in south-west Victoria, Australia. Southern brown bandicoot occurrence probability (c) peaked around 15 and 75 years following fire, although, the magnitude of both peaks differed across Ecological Vegetation 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

### 3.4 Discussion

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 main-

taining 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 healthy 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.

We observed surprising effects of rainfall on mammal occurrence. Feral cats were the exception, who's occurrence probability increased with both short and long-term rainfall. On the other hand, foxes, who had the strongest interaction with rainfall patterns, had higher occurrence probabilities with low rainfall. These responses may reflect different prey preferences. In a neighbouring region, Grampians, small mammals (rodent, antechinus) abundance followed short-term rainfall patterns - this increase in prey availability could explain cats occurring where rainfall is high. Foxes - I dunno? SBB's occurrence was not impacted by rainfall, LNP occurrence increased during dry periods within areas with high long-term rainfall averages. More effort is required to tease apart rainfall effects on mammal communities in these temperate landscapes. Directly quantifying time lag-effects with rainfall should be a future research priority, as should investigating interactive effects between species.

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.

## **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 km<sup>2</sup>), 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.* 2017). 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. D.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.* 2017). 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 D.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 D.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. D.3, and identified individual feral cats within each category; see Appendix C section D.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 D.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 D.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.

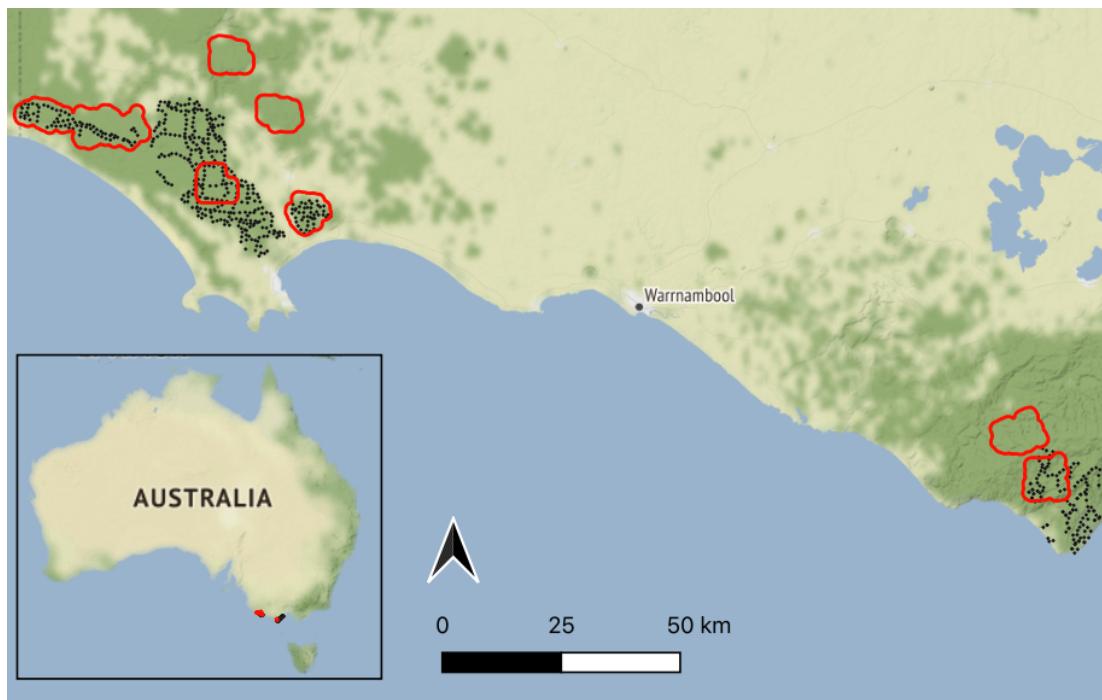


Figure 4.1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river. Locations of fox poison-bait stations are denoted by black dots. The Glenelg region 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 D.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 D.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 D.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 D.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 D.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 D.4). Regression splines added additional model parameters without changing predictions (Fig. 4.3), and so, all nonlinear models ranked below their linear counterparts (Table D.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 D.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 D.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 D.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 D.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 D.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 D.9). There was also strong support for an effect of fox occurrence on cat detectability at a fine spatial scale (Fig. 4.4; Table D.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 D.10).

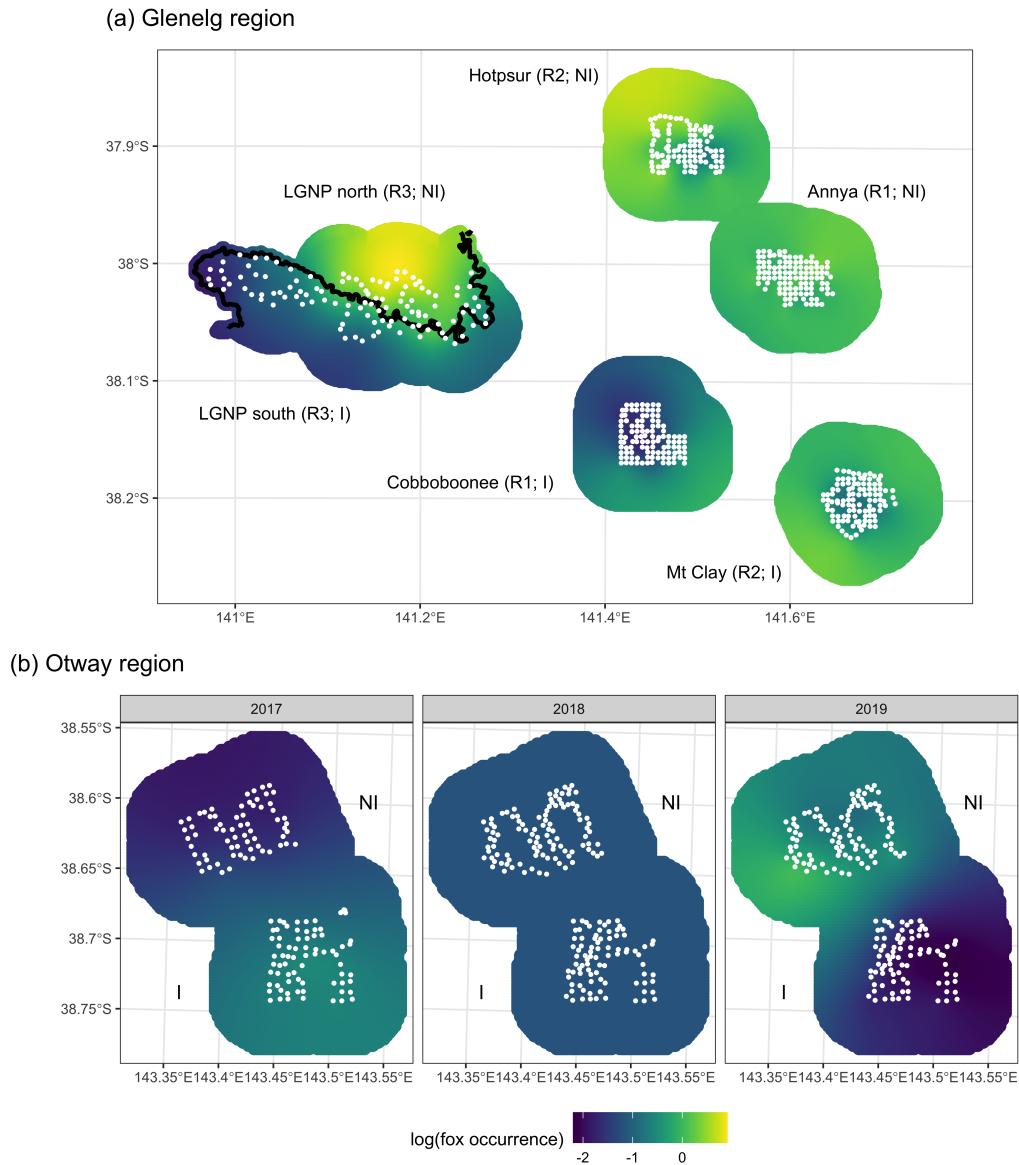


Figure 4.2: Predicted red fox *Vulpes vulpes* occurrence derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. White dots represent camera-trap sites. Predicted fox occurrence was used as a predictor of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

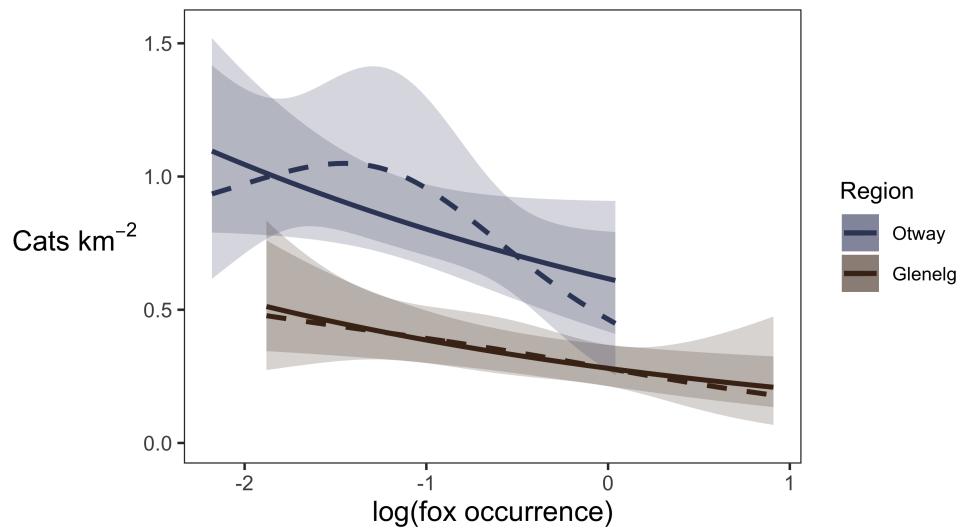


Figure 4.3: Linear (solid lines) and nonlinear (dashed lines) models predicted that feral cat *Felis catus* density increased with declining probability of red fox *Vulpes vulpes* occurrence (log-transformed) in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.

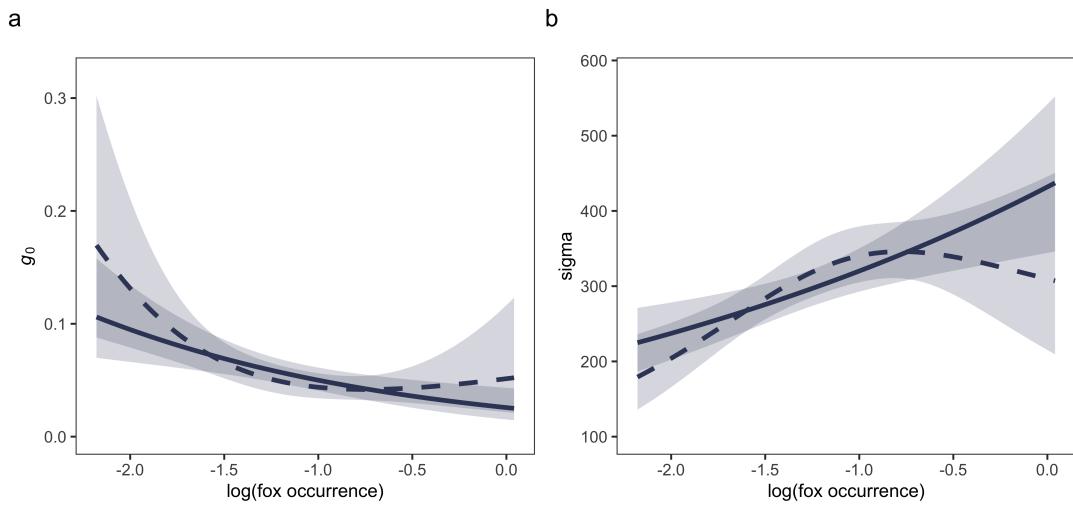


Figure 4.4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-transformed red fox *Vulpes vulpes* occurrence in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion ( $g_0$ ) 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.

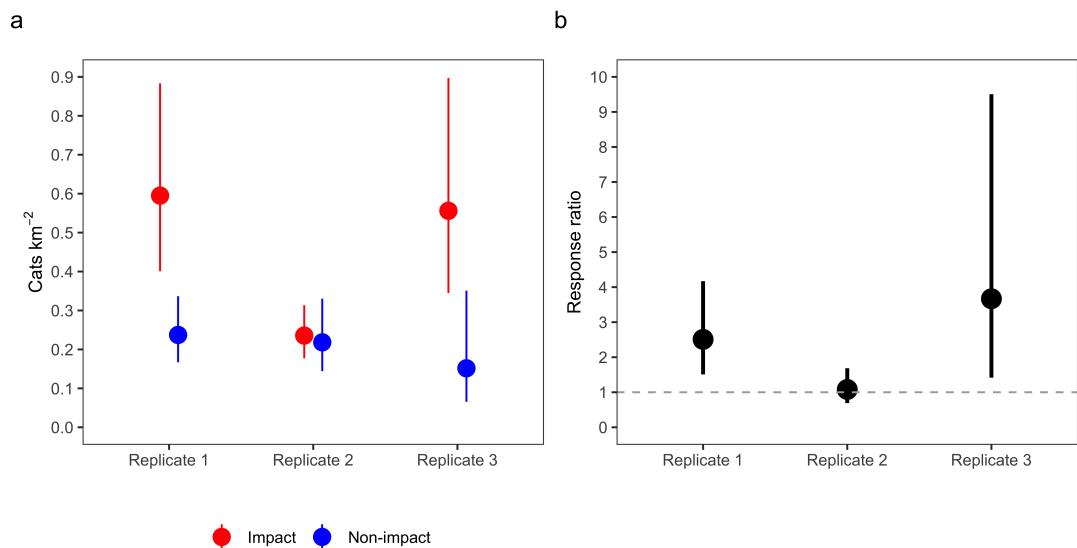


Figure 4.5: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the paired non-impact landscape for each replicate (b) in the Glenelg region, Australia. Poison-baiting for foxes *Vulpes vulpes* has been conducted in the impact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

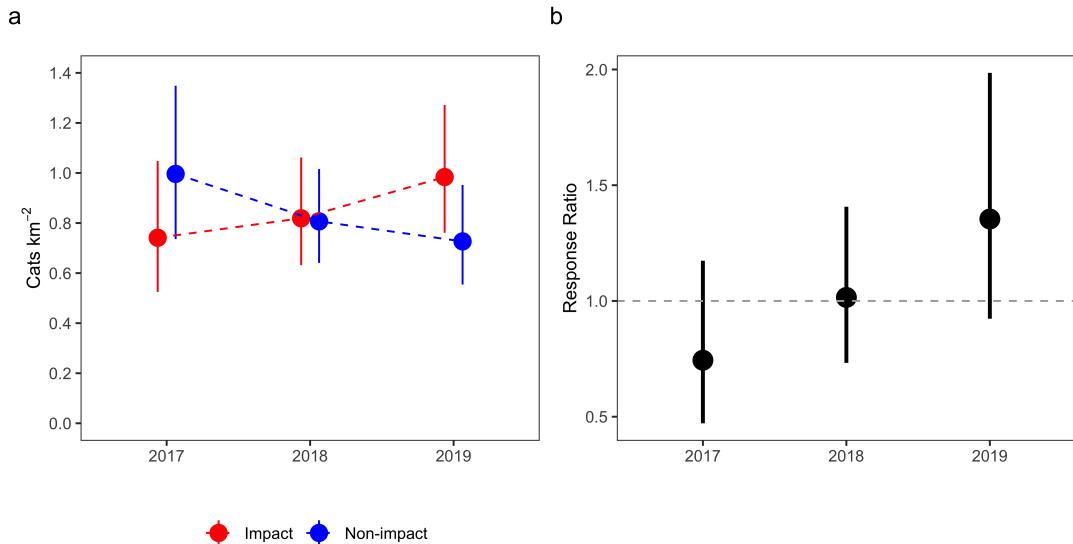


Figure 4.6: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the non-impact landscape for each survey year (b) in the Otway region, Australia. In 2017, surveys were conducted approximately two months before lethal red 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**

## 5.1 Introduction

Diel activity patterns - the distribution of activity throughout the daily cycle - are an important but overlooked aspect of behavioural ecology (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). 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). This is important to understand because constrained diel activity can incur fitness costs to individuals and populations (e.g., Lamb *et al.* 2020).

Predators shape ecosystems through both predation and the fear of predation-regulating the number of individuals and the spatiotemporal behaviour of subordinate species (Ritchie & Johnson 2009). The 'landscape of fear' refers to an animal's perception of spatial variation in predation risk, which can drive spatiotemporal behaviours (Gaynor *et al.* 2019). For example, elk *Cervus elaphus* in Yellowstone National Park use risky, open parts of the landscape when the activity of reintroduced wolves *Canis lupus* is low (Kohl *et al.* 2019). Even when faced with the same 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).

Diel activity patterns are increasingly considered as technology like telemetry devices and camera-traps have become more widely available (Lashley *et al.* 2018). Telemetry devices provide high resolution data at the individual-level, however, resource constraints generally limit these studies to few individuals and target personalities susceptible to physical capture (Biro & Dingemanse 2008). Camera-traps are particularly useful because they provide a more balanced view of the entire population and can detect multiple species, providing inference on ecological differences and species interactions (Harmsen *et al.* 2009). However, individual-level inference from camera-trap images is limited to species with unique markings. For example, Distiller *et al.* (2020) recently used camera-traps to individually identify jaguars and estimate sex difference in diel activity patterns. 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).

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 den-

sity 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).

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. The red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus* (hereafter ‘cat’) have some of the widest distributions of any carnivores, and co-occur across most of their global range. Because of their devastating impacts on native prey in their introduced range, understanding differences in their behavioural ecology across space, and how foxes may impact feral cat behaviour is key to effective management (Doherty & Ritchie 2017). Numerous studies have investigated environmental drivers and interactions between these invasive predators (e.g., Molsher *et al.* 2017; Roshier & Carter 2021), but not in a joint spatiotemporal framework. 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.* 2017). 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.

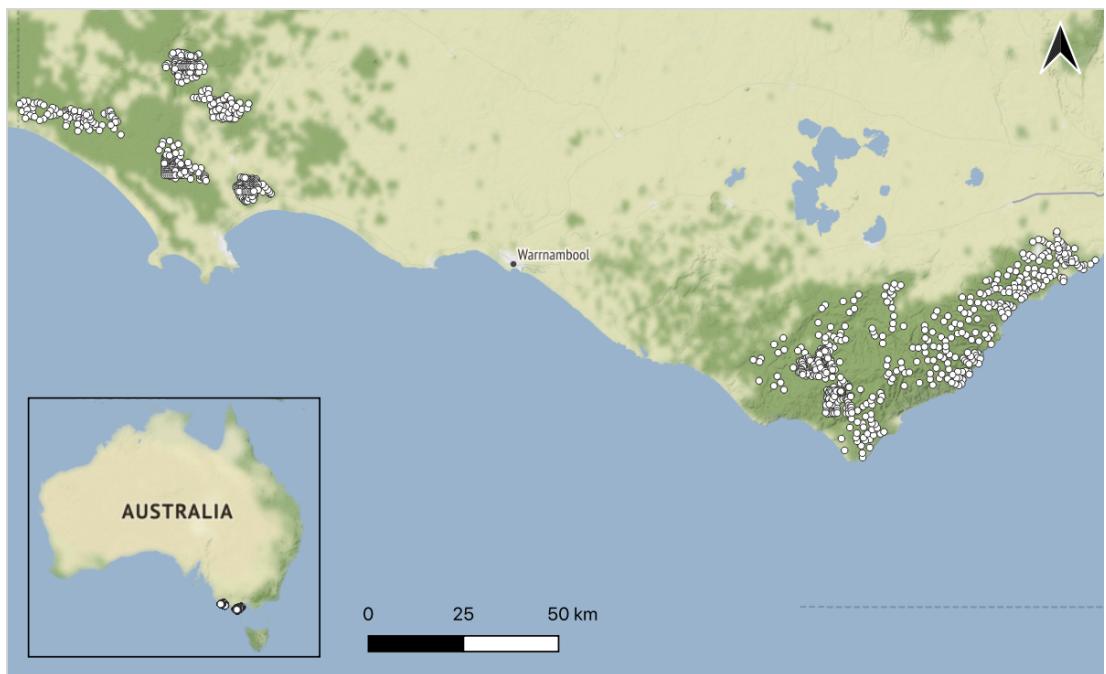


Figure 5.1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 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
<b>Total</b>		<b>1232</b>	<b>3667</b>	<b>5449</b>	<b>2202</b>

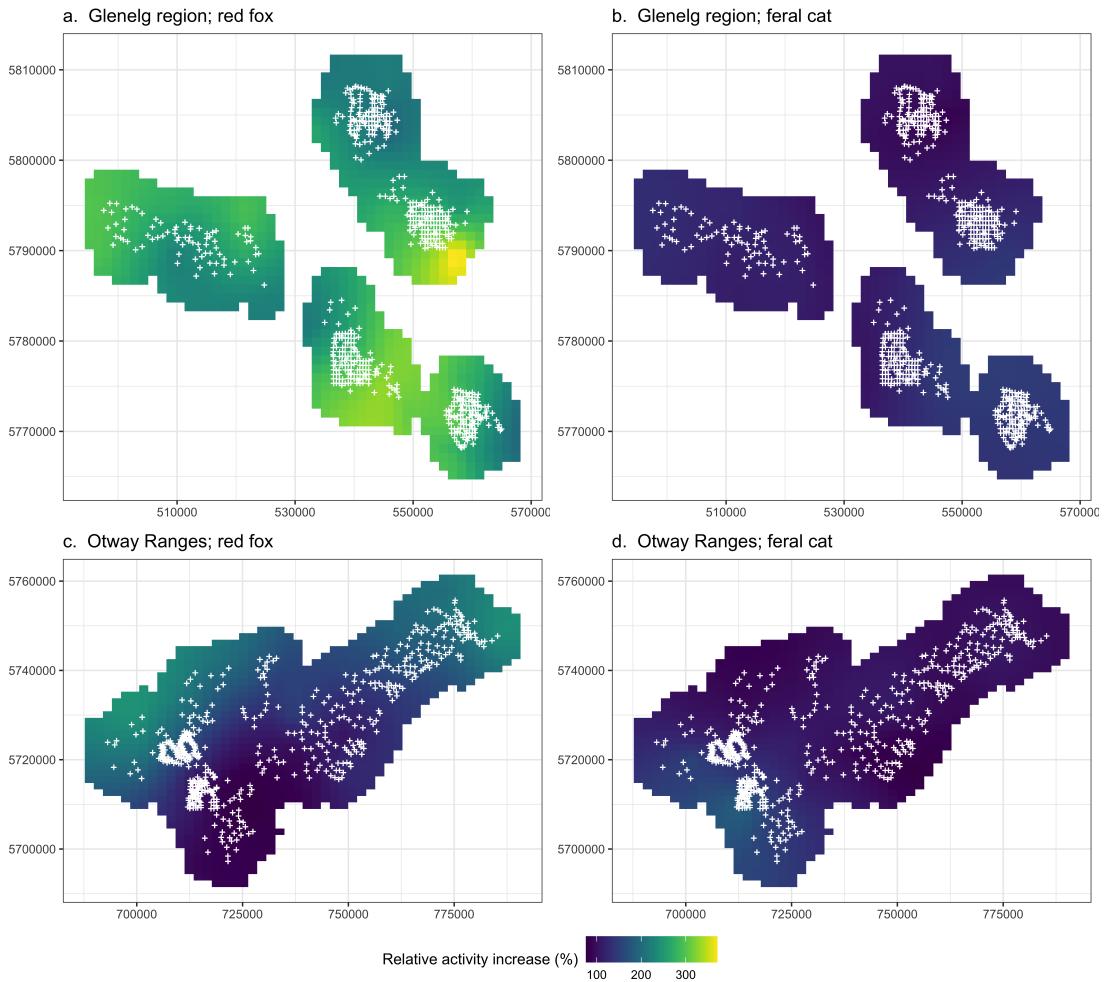
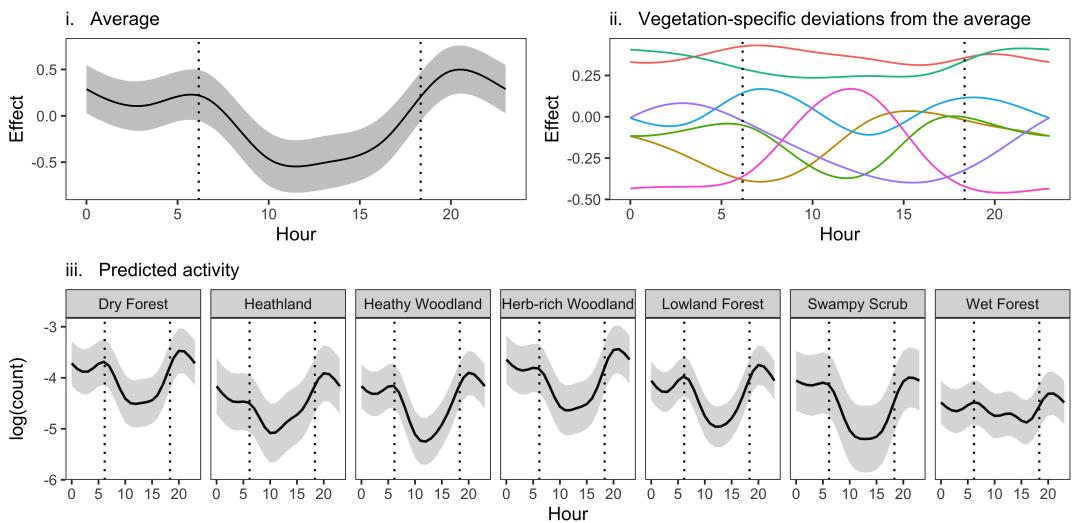


Figure 5.2: The strength of diel activity patterns of two invasive predators varied within the two study regions in south-west Victoria, Australia. White crosses depict unique camera-trap sites; colour brightness scales with increasing percentage difference between the minimum and maximum activity estimate 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

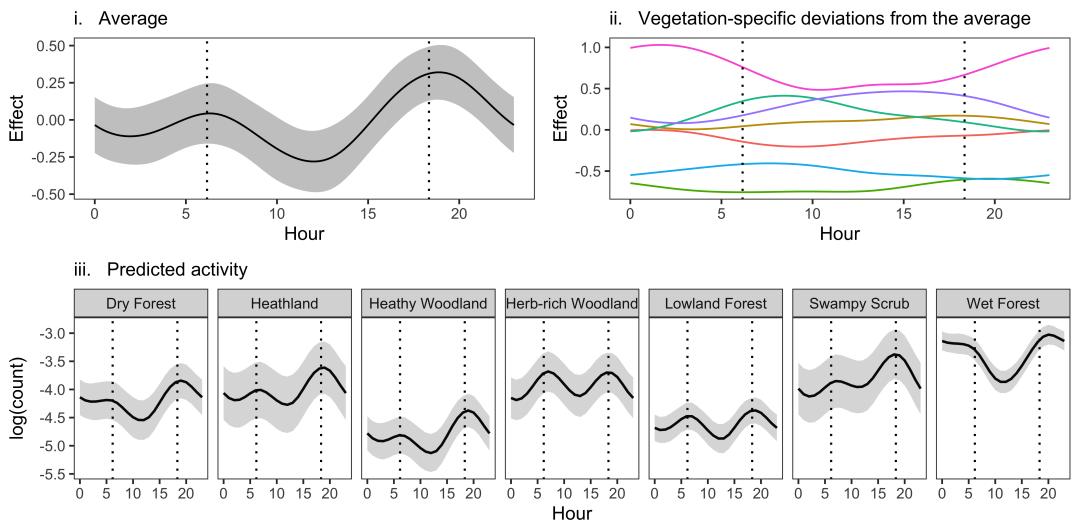


Figure 5.3: Red foxes *Vulpes vulpes* (a) and feral cat *Felis catus* (B) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia. Dotted, vertical lines represent average sunrise and sunset times. Shaded areas indicate 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)

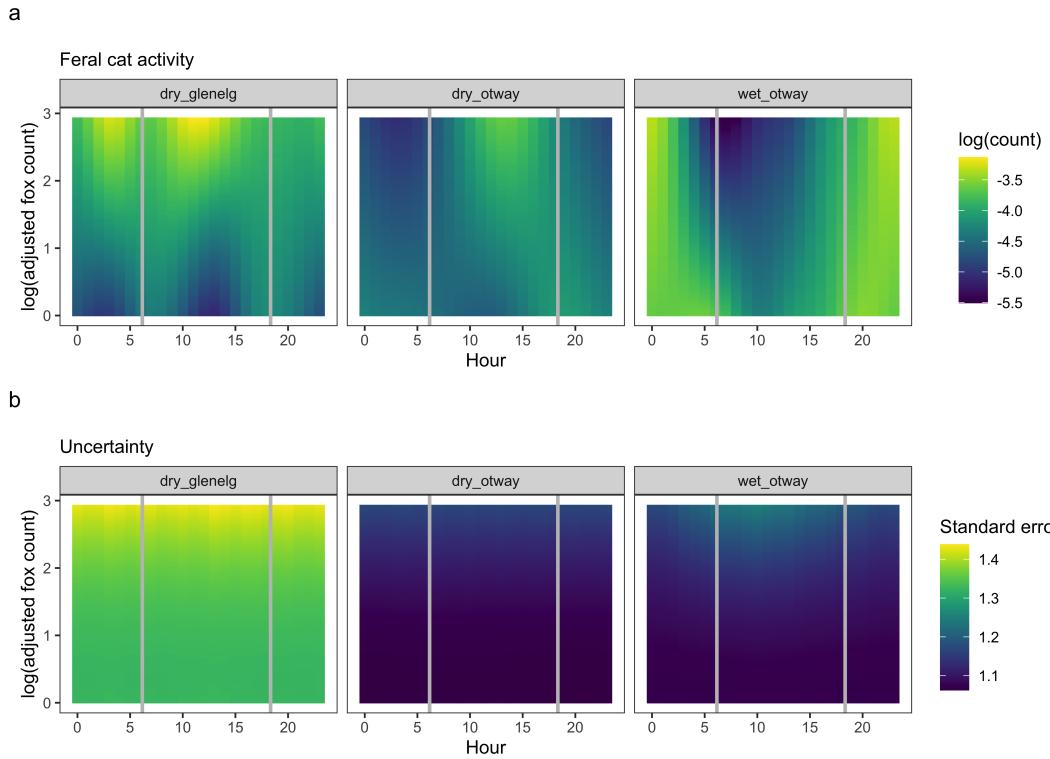
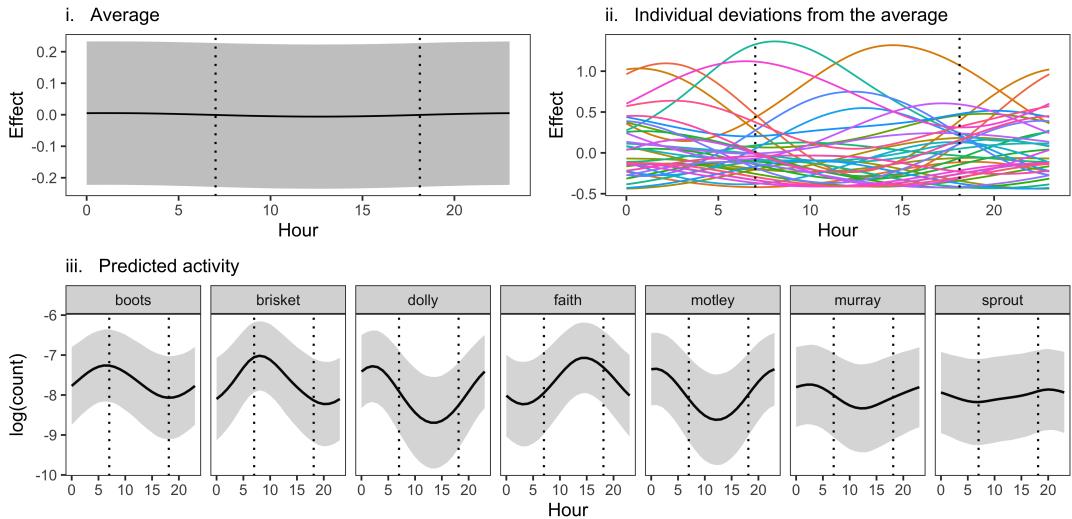


Figure 5.4: Variation in mean feral cat *Felis catus* activity (a) and associated uncertainty estimates (b) in response to count of 'independent' red fox *Vulpes vulpes* detections (log-transformed and survey effort adjusted) across each 'habitat type' in south-west Victoria, Australia. Grey vertical 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



b. Western Otway Ranges

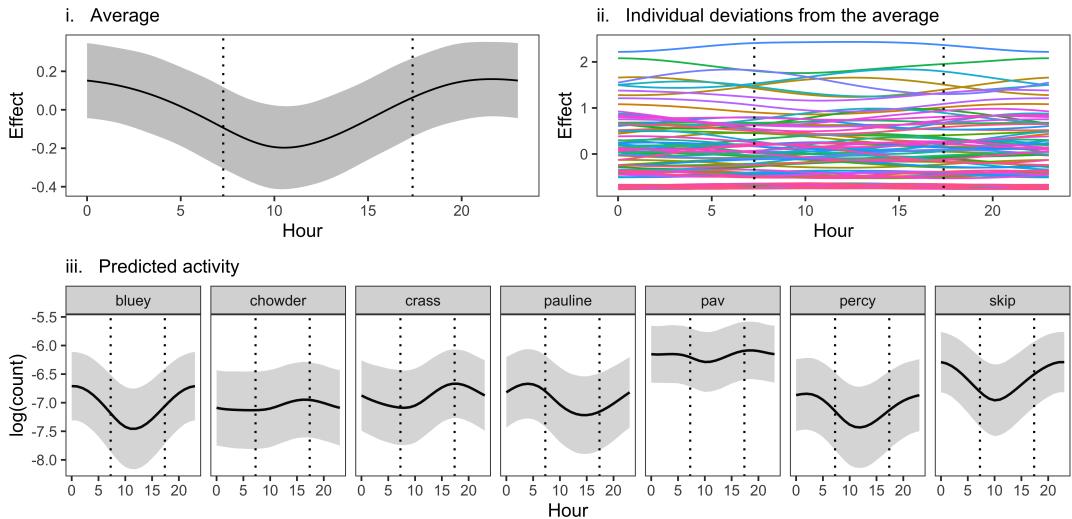


Figure 5.5: Individual heterogeneity in feral cat *Felis catus* diel activity across the Glenelg region (a; 39 identified individuals) and wet forests of the western Otway Ranges (b; 94 identified individuals) in south-west Victoria, Australia. As an example, the predicted activity of the seven individuals 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 & Jakšić 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 & Jakšić 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.



## **Chapter 6**

# **Synthesis**

text



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## **Appendix A**

## **Supporting Information: Chapter 2**

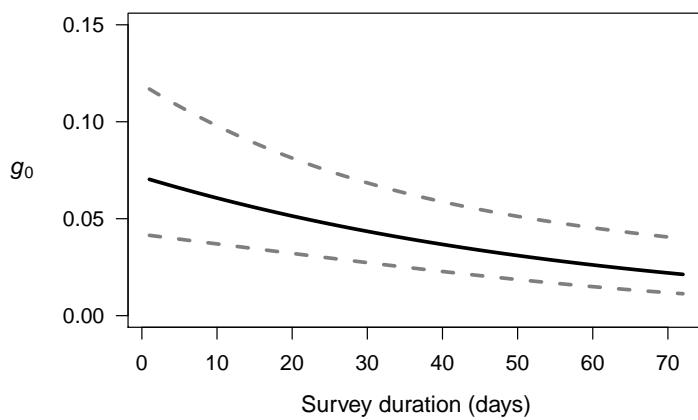


Figure A.1: The AICc-best model linear trend in  $g_0$  values (probability of daily detection in activity centre) throughout the survey. Grey dashed lines indicate 95% confidence intervals.

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	AICcwt	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

AICcwt - 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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## ARTICLE INFO

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*Felis catus*

Invasive predator

Population density

Spatial capture-recapture

Spatial mark-resight

## 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 km<sup>2</sup> 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<sup>-2</sup> (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.

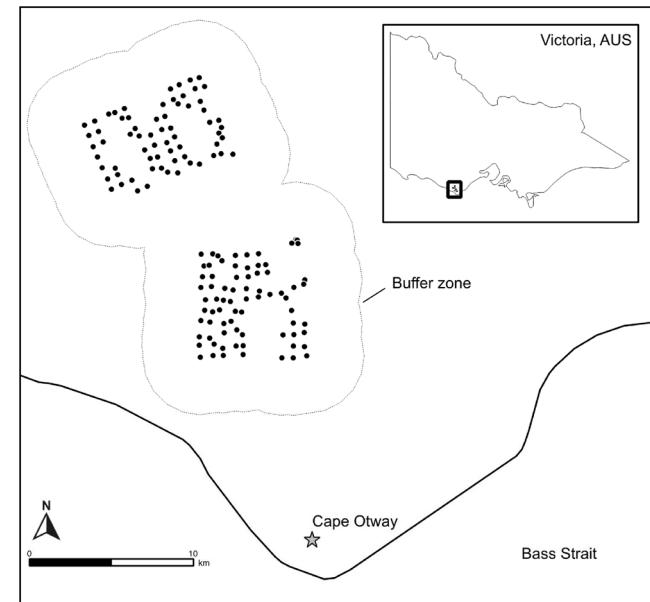
## 2. Methods

### 2.1. Study area

Our study was conducted in the Great Otway National Park and Otway Forest Park, Victoria, Australia ( $38.42^{\circ}$ S,  $142.24^{\circ}$ E). The locality is 90–440 m a.s.l. and has a cool-temperate climate: maximum daily temperatures average  $19.3^{\circ}$ C in summer and  $9.5^{\circ}$ 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  $49\text{ km}^2$  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  $\sigma$ , 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; 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  $\sigma$  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  $\text{km}^{-2}$  (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, Akaike 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  $\text{km}^{-2}$  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  $\text{km}^{-2}$  (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  $\text{km}^{-2}$ ), and more than three times higher than the predicted continental mean density for feral cats in 'natural areas' (0.27 cats  $\text{km}^{-2}$ ; 0.18–0.45 cats  $\text{km}^{-2}$ ) (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 $\text{km}^{-2}$ )				
	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.

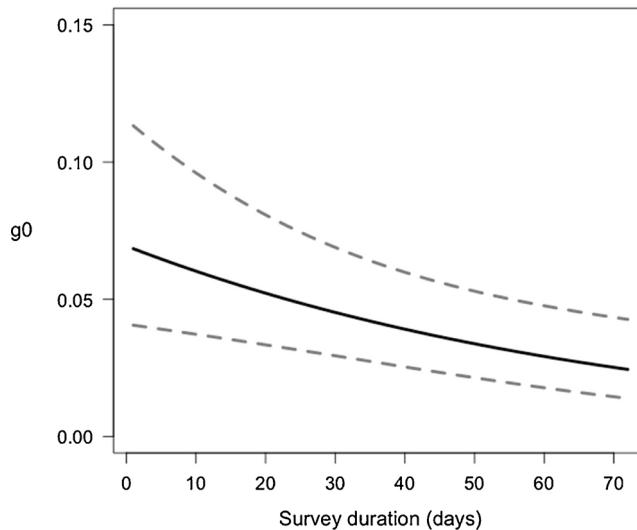
#### Declaration of Competing Interest

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.

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#### 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 <sup>-2</sup> )		
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

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## **Appendix C**

### **Supporting Information: Chapter 3**

Table C.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

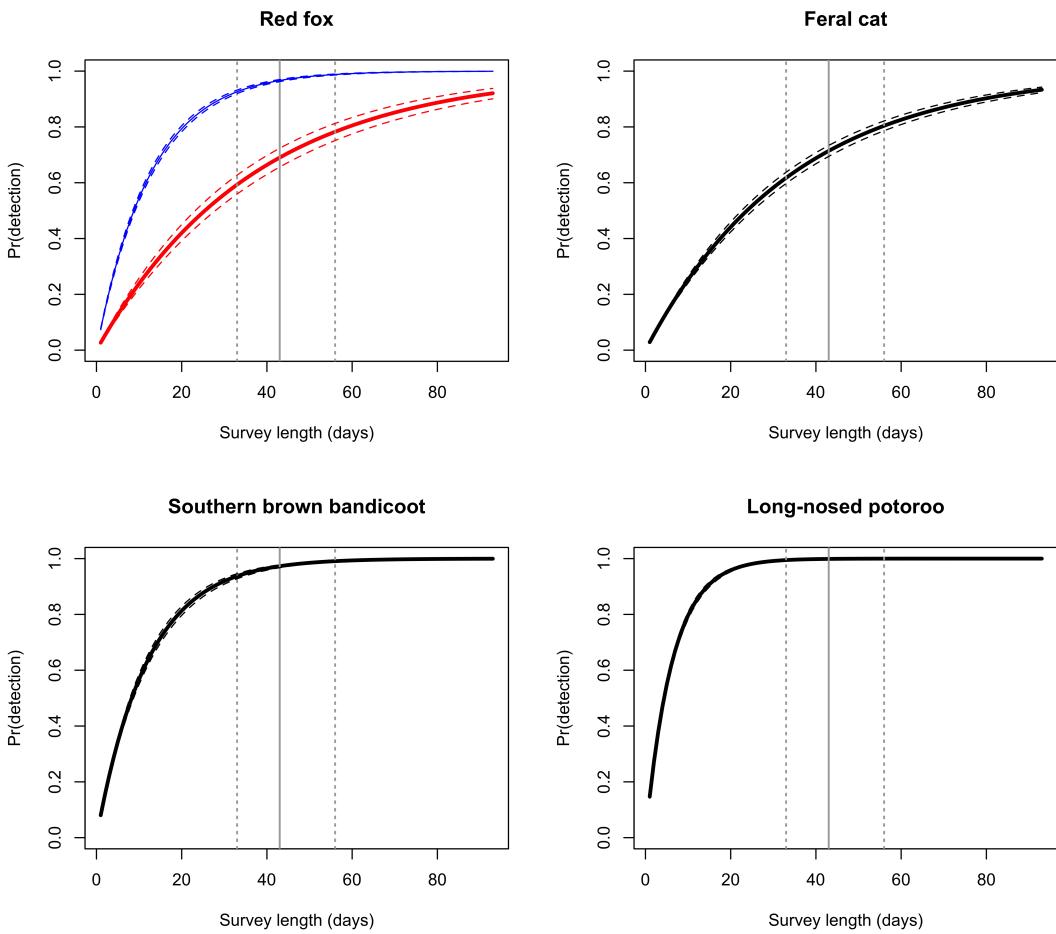


Figure C.1: Cumulative detection probability for surveyed species averaged across all sites (solid black lines), as well as sites with fox control (solid red line) and without fox control (solid blue line). Dashed lines represent 95% confidence intervals. Vertical grey lines represent mean (solid) as well as 25% and 75% quantiles (dotted) of days camera-traps were active for.

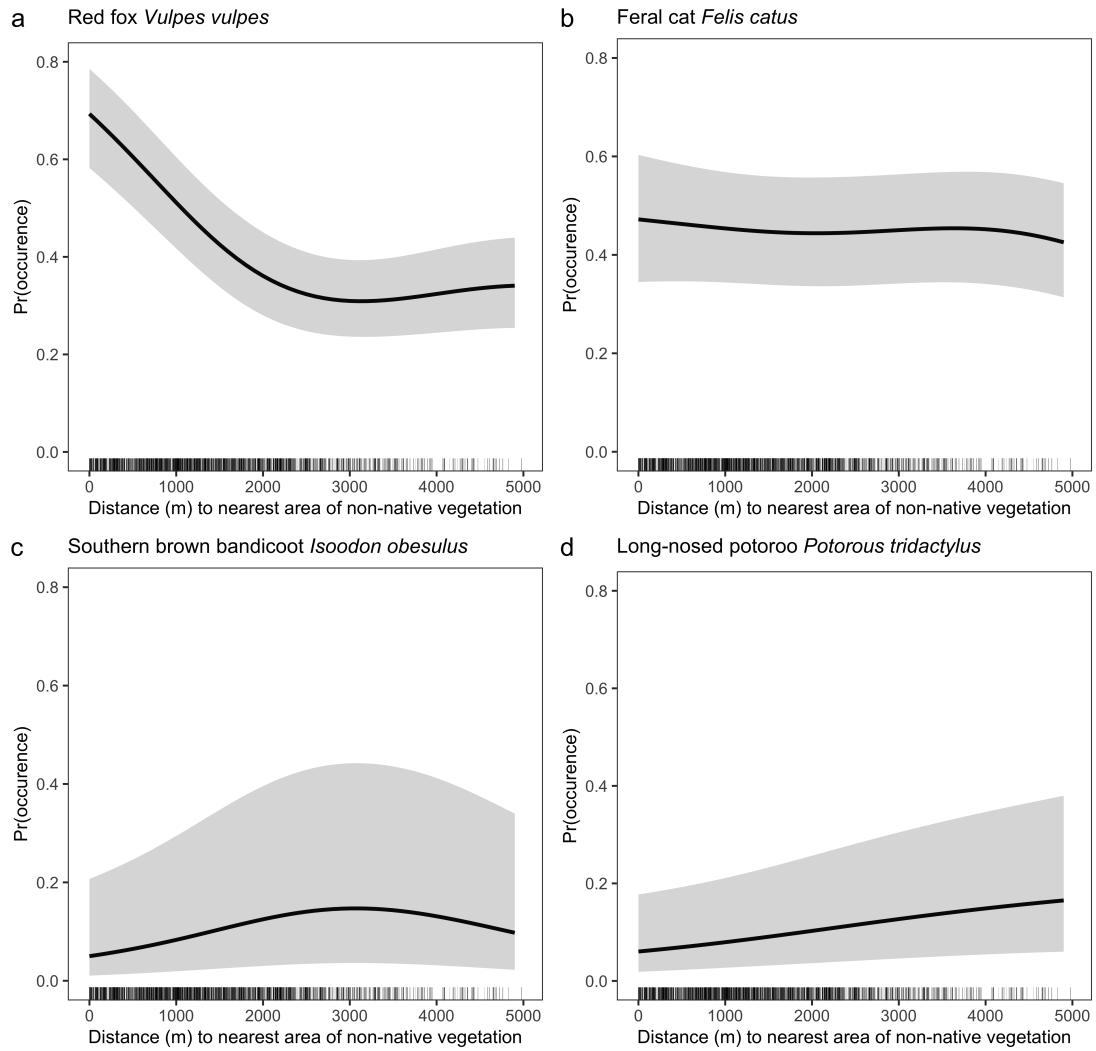


Figure C.2: Fox occurrence probability decreased linearly for 2 km as distance to the nearest area of non-native vegetation (larger than 30 ha) increased (a). Increasing distance to non-native vegetation had a weak, positive effect on long-nosed potoroo's (d), but little-no impact on feral cats (b) and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

## **Appendix D**

### **Supporting Information: Chapter 4**

## D.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.

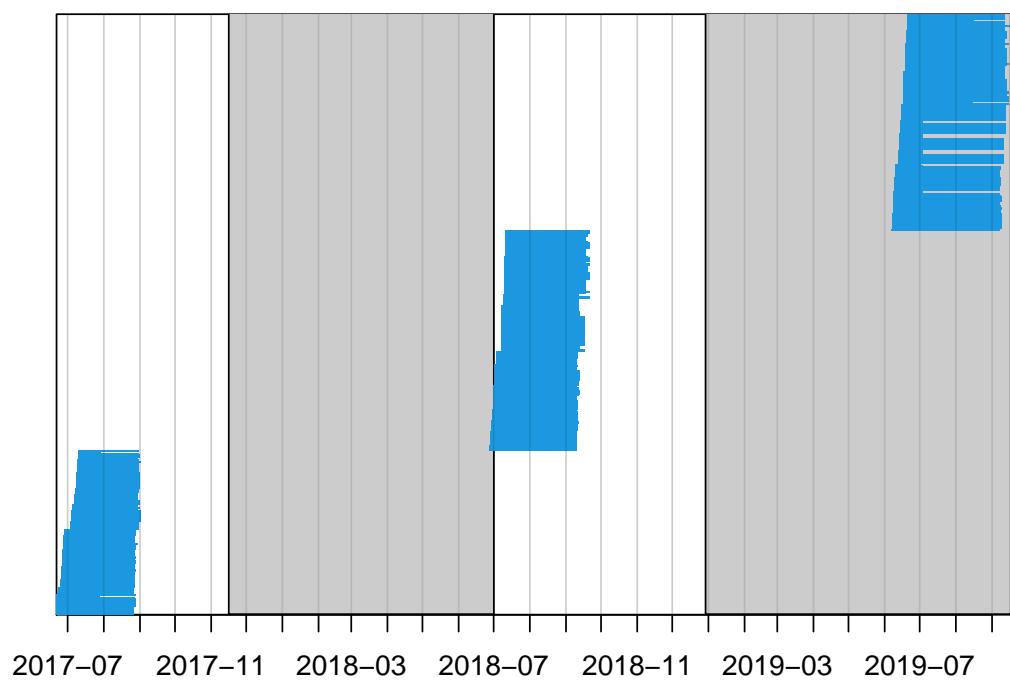


Figure D.1: Camera-trap operation times in the Otway region, Australia. Each blue horizontal line represents one camera-trap deployment. Grey shading indicates periods of fox control in the impact landscape.



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

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

### D.3 Summary statistics

Table D.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

## D.4 Feral cat detection plots

### D.4.1 Glenelg region

#### Replicate 1

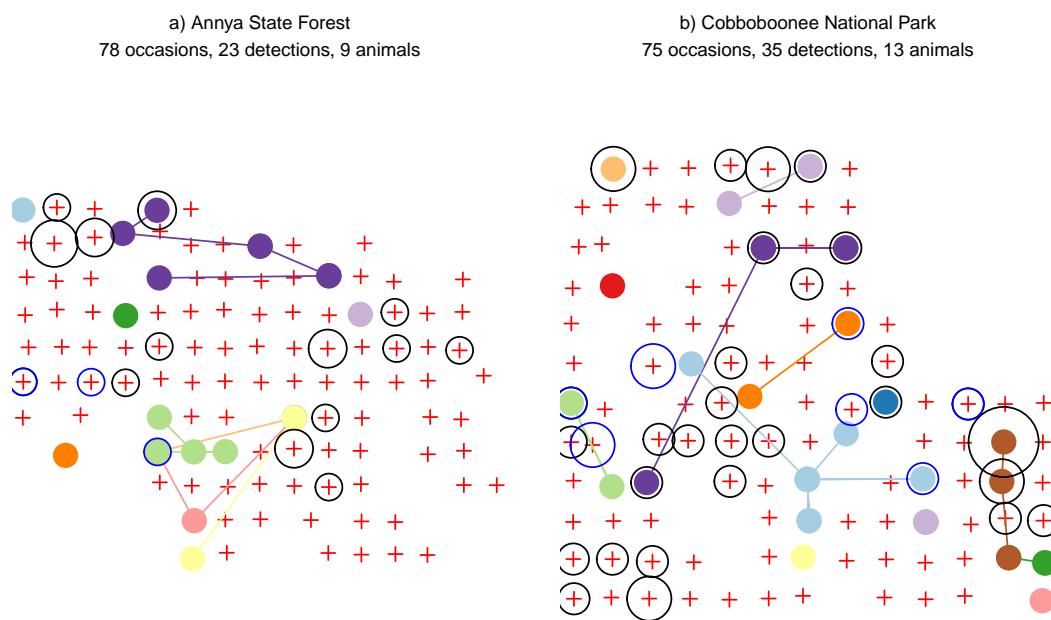


Figure D.4: Feral cat detections in the first replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles 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

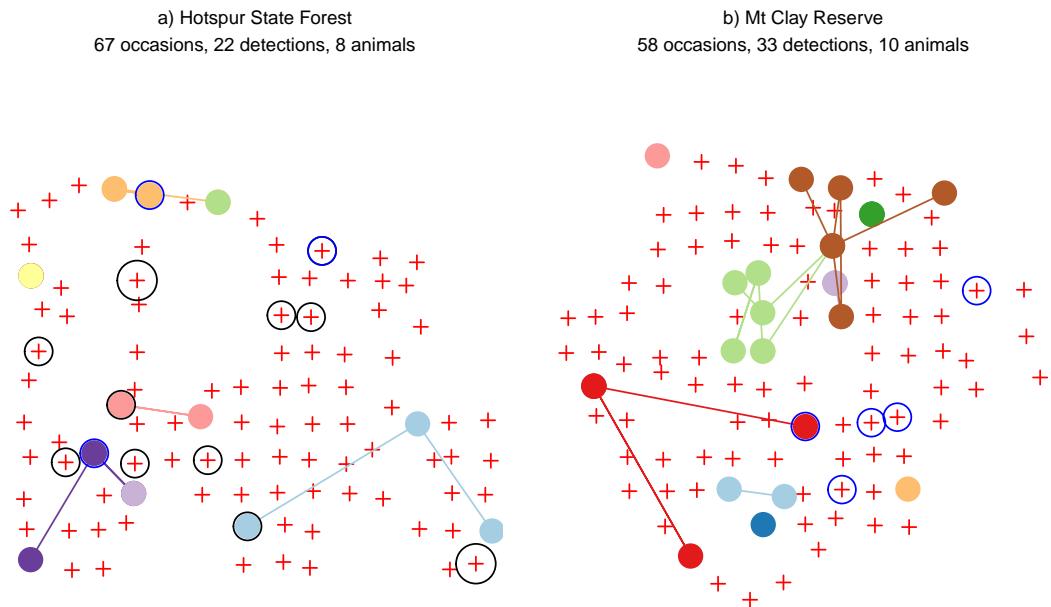
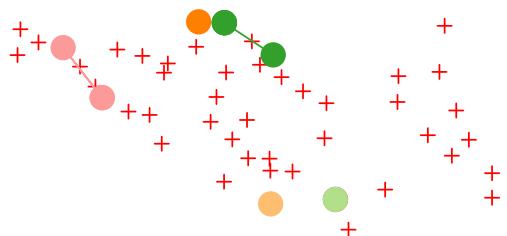


Figure D.5: Feral cat detections in the second replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles 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

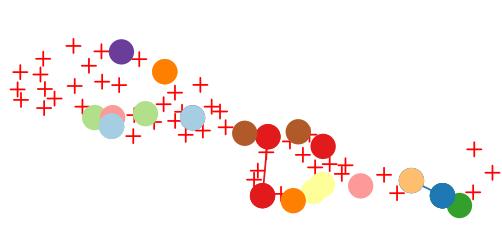


Figure D.6: Feral cat detections in the third replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles 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).

## D.4.2 Otway region

2017

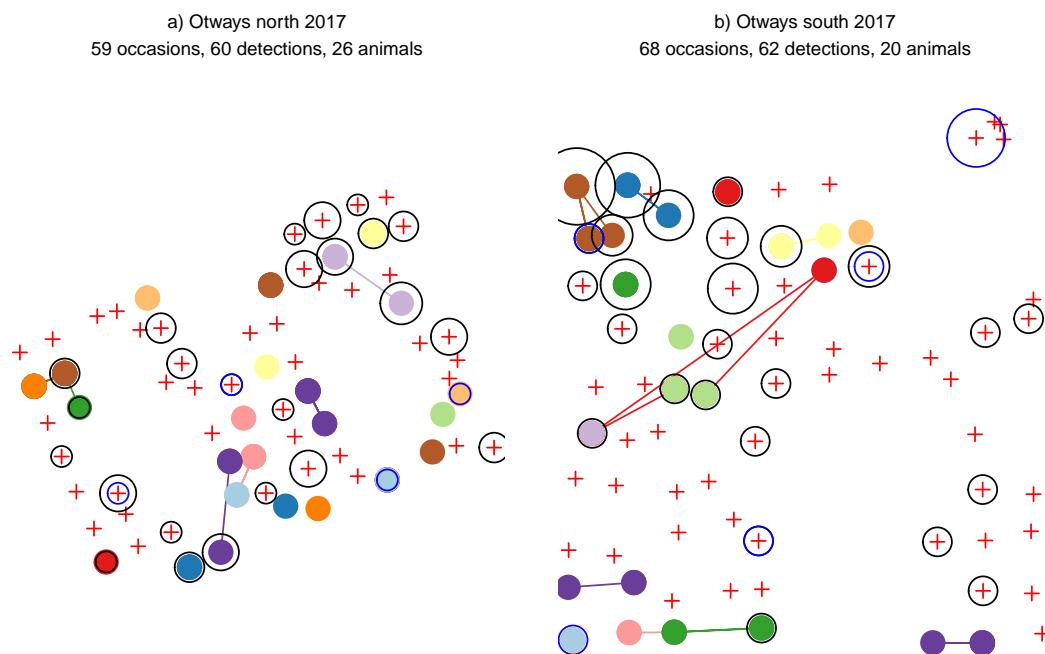


Figure D.7: Feral cat detections in the Otway region, Australia, 2017. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling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

2018

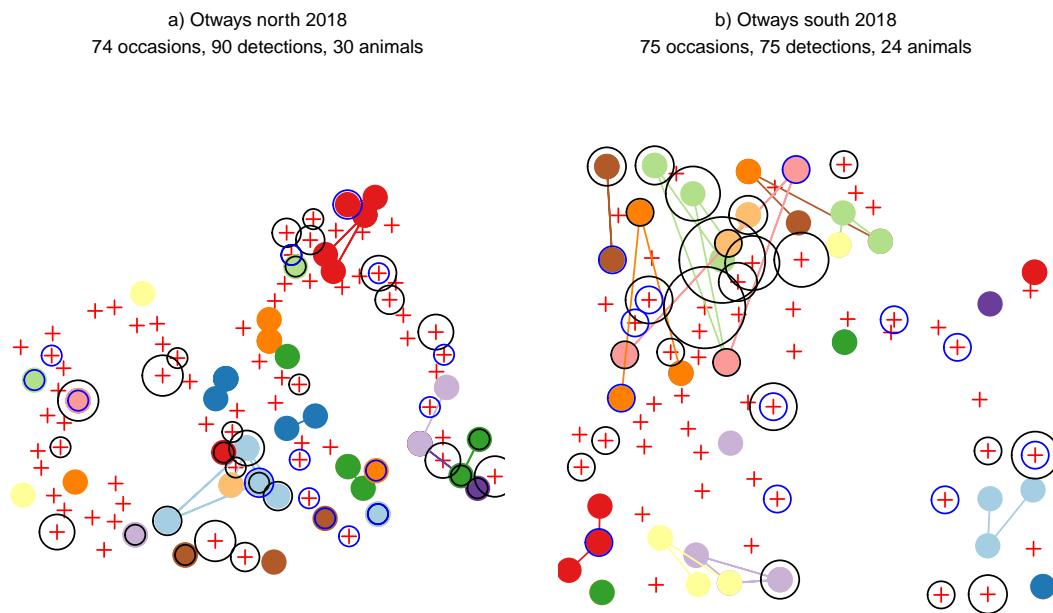


Figure D.8: Feral cat detections in the Otway region, Australia, 2018. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling 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

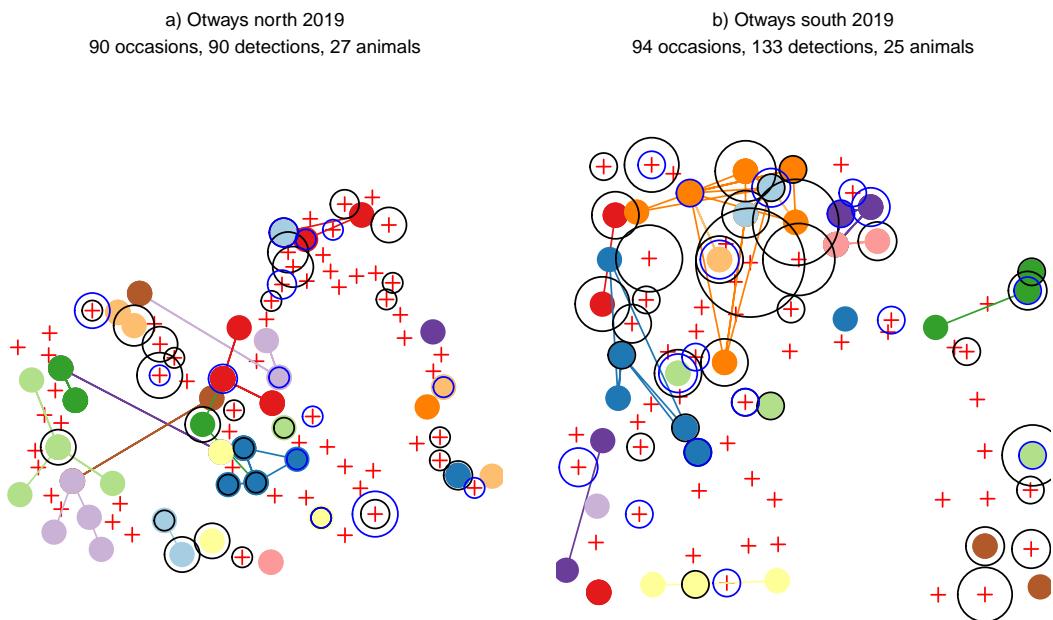


Figure D.9: Feral cat detections in the Otway region, Australia, 2019. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling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

## D.5 Fox spatial occurrence

### D.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

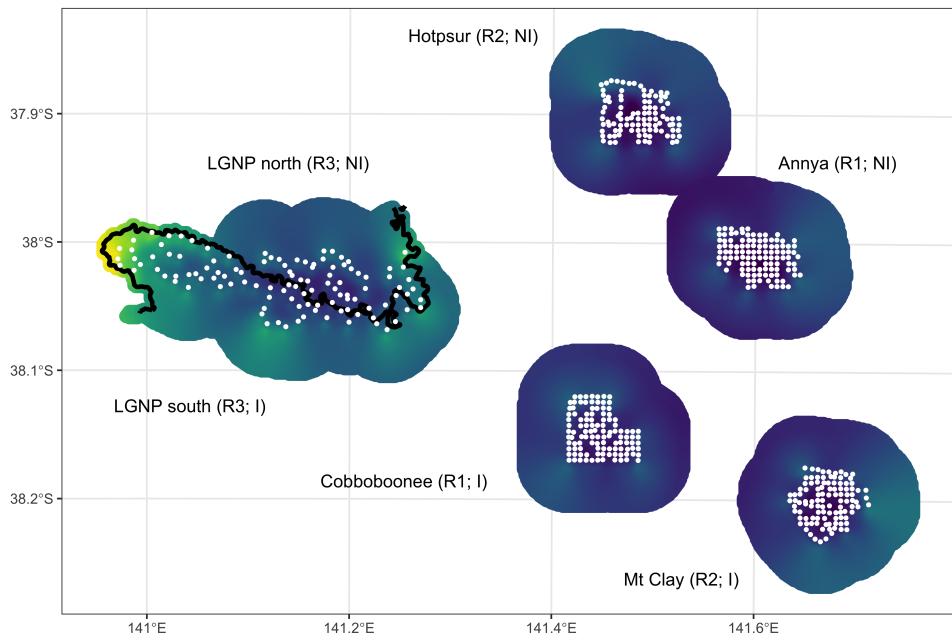


Figure D.10: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg region, Australia.

## D.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

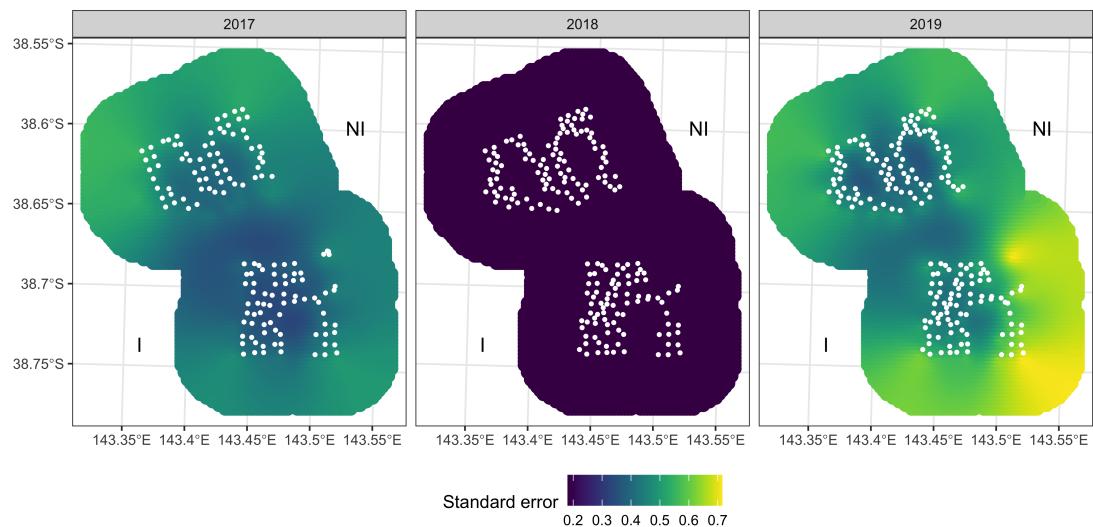


Figure D.11: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Otway region, Australia.

## D.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.

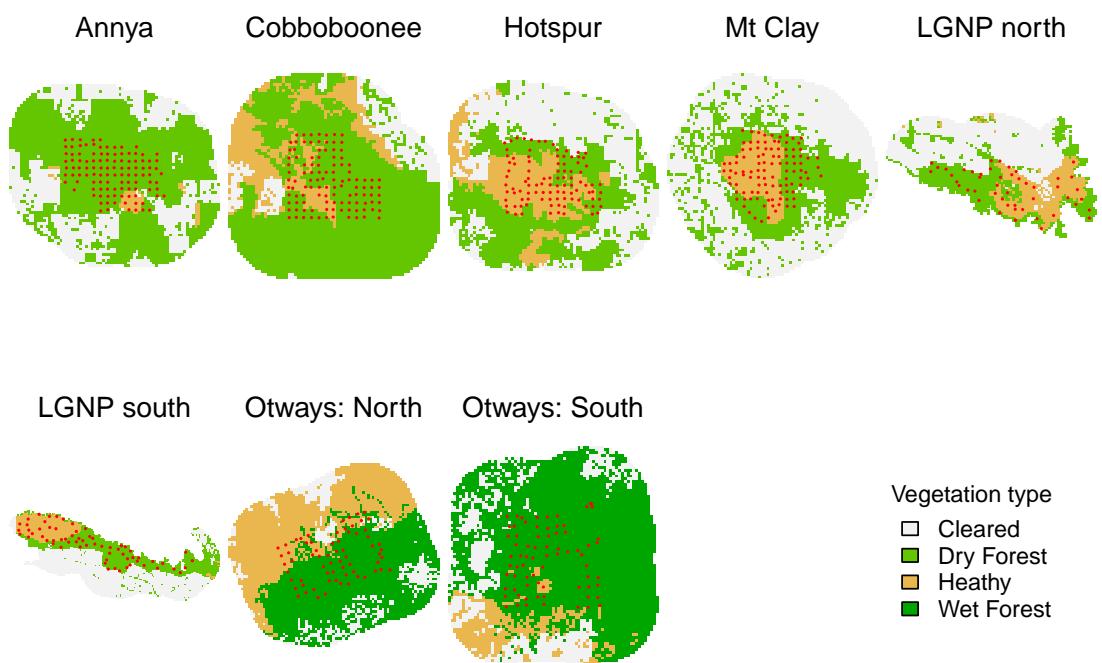


Figure D.12: Condensed Ecological Vegetation Class groups used as habitat mask covariates in spatial mark-resight models.

## D.7 Spatial mark-resight models

### D.7.1 Glenelg region

Table D.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 D.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 D.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 D.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 D.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

### D.7.2 Otway region

Table D.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 D.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 g <sup>0</sup> 1 sigma <sup>~</sup> 1	5	-3550.63	7111.26	7111.67	0.00	0.48
D~year g <sup>0</sup> T sigma <sup>~</sup> 1	6	-3549.83	7111.67	7112.25	0.57	0.36
D~year + vegetation g <sup>0</sup> 1 sigma <sup>~</sup> 1	7	-3550.04	7114.08	7114.86	3.19	0.10
D~year + vegetation g <sup>0</sup> T sigma <sup>~</sup> 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 D.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 D.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 D.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