

Spatial detection modelling brings clarity to mesopredator release—changes in feral cat density and behaviour following lethal fox control

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Abstract

1. The mesopredator release hypothesis predicts that apex predator decline will cause an increase in subordinate predators. This is particularly concerning when invasive mesopredators are present, who could have devastating impacts on native prey if ‘released’ from top-down pressure. But evidence for mesopredator release is weak—few studies have used experimental designs, spatial replication or disentangled behavioural responses from numerical changes in mesopredator populations.
2. We conducted replicated field experiments to test mesopredator release in ecosystems with a simple terrestrial predator guild comprising the introduced red fox *Vulpes vulpes* and feral cat *Felis catus*. Here, conservation managers lethally suppress the larger-bodied foxes, but not feral cats. We employed a replicated Control-Impact design in one region with long-term fox control, and a Before-After Control-Impact Paired Series design in another region with newly implemented fox control. Spatial mark-resight models were fit to 63,560 camera-trap nights to characterise spatial and temporal variation in feral cat density as a function of fine scale gradients in fox occurrence, as well as the implementation of landscape scale fox control.
3. After individually identifying 137 feral cats, we found that feral cat density was highest where fox occurrence was lowest across both surveyed regions at a fine spatial scale. Feral cat responses to the implementation of broadscale fox control were not as consistent, likely owing to spatiotemporal variation in fox suppression caused by poison-baiting programs.
4. In one region we saw strong evidence of changes in feral cat detectability and movement rates due to foxes. Non-linear models revealed that this only occurred at lower fox occurrence probabilities, suggesting that feral cats can employ avoidance strategies when foxes are rare, but suffer numerical population changes when foxes are common.

34 5. *Synthesis and applications.* Our study demonstrates potential for mesopredator release following
35 the lethal apex predator control across two separate ecosystems—integrated invasive predator man-
36 agement may therefore be necessary to further protect threatened native prey. We provide another
37 example that predator interactions are context and scale-dependent but highlight that direct apex
38 predator measurements are key to accurately testing the mesopredator release hypothesis. Meso-
39 predator release can manifest in both behavioural and numerical changes, distorting inference when
40 these processes are not separated.

41 *Key words:* camera trap; *Felis catus*; invasive predator; interspecific competition; mesopredator release;
42 population density; spatial capture-recapture; spatial mark-resight; species interactions; *Vulpes vulpes*.

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 due to a reduction in direct top-down pressure or indirect benefits from an increase in the availability of shared resources; this is often referred to as mesopredator or competitor release (Crooks & Soulé, 1999; Doherty & Ritchie, 2017; Ruscoe et al., 2011). The release of subordinate invasive species, particularly predators, can have serious negative implications for native taxa and ecosystem function (Ballari et al., 2016; Courchamp et al., 1999). 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 predator interactions 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). However, the occurrence, nature (positive or negative, direct or indirect) and strength of species interactions can vary among species assemblages, predation risk, environmental productivity, management regimes and other landscape contexts (Alston et al., 2019; Finke & Denno, 2004; Hastings, 2001). Replicating management programs in an experimental framework is logistically challenging, but important for understanding these complexities, discriminating between plausible hypotheses and producing generalisable results in order to inform effective pest management (Christie et al., 2019; Glen & Dickman, 2005; Smith et al., 2020).

Unbiased estimates of invasive predator density are important to infer their impacts on native prey and set meaningful control targets (Moseby et al., 2019). Controversy around the mesopredator release hypothesis partially stems from the inability to distinguish behavioral from numerical population processes using traditional survey and modelling approaches (Hayward et al., 2015; Stephens et al., 2015). That is, the suppression of an apex predator may 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 changes in unidentified counts or presence-absence records of mesopredators in relation to the presence, absence or abundance of apex predators, even within experimentally designed studies. In contrast, spatially explicit capture-recapture methods allow you to robustly estimate predator density by

separating behavioural and observational processes from population density; however, they have seldom been used experimentally or to investigate multispecies interactions (although, see Forsyth et al., 2019).

Predation by two invasive species, the red fox *Vulpes vulpes* and feral cat *Felis catus*, has played a major role in Australia’s high rates of mammalian extinction (Woinarski et al. 2019). Integrated invasive predator management programs for these species are rare. Introduced red foxes (hereafter foxes) are far more commonly controlled than feral cats, as they are more susceptible to poison-baiting, have greater direct economic impacts and fewer legal impediments to their control (McLeod & Saunders, 2014; Reddiex et al., 2007). Nonetheless, feral cats are one of the most widespread and damaging vertebrate species (Doherty & Ritchie, 2017; Legge et al., 2020; Medina et al., 2011). As foxes are larger-bodied (~2 kg difference) and have high dietary overlap with feral cats (Catling, 1988; Glen et al., 2011; Short et al., 1999), the mesopredator release hypothesis predicts that the impacts of feral cats will increase as fox populations are suppressed (Soulé et al., 1988). 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 feral 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 feral cat detections following fox control (Marlow et al., 2015; Risbey et al., 2000; Stobo-Wilson et al., 2020). However, two other studies in similar systems did not see any change (Molsher et al., 2017; Towerton et al., 2011). One study with spatial replication detected an increase at one site but not another (Davey et al., 2006), and one study observed a decrease in feral cat activity (Claridge et al., 2010). No previous studies have directly estimated feral cat density in response to fox control.

In this study, we experimentally investigated the role of introduced foxes in top-down suppression of feral cat density in two regions of south-eastern Australia. Our experiments were based around 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 feral 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 and landscape productivity. In accordance with the mesopredator release hypothesis, we

103 predicted that (1) feral cat density would be negatively correlated with spatial fox occurrence at a fine
104 spatial scale, and (2) fox control would increase feral cat density at a landscape scale. We based inference
105 on direct estimates of feral cat density using spatially explicit mark-resight models.

2. MATERIALS AND METHODS

2.1. Study area

We conducted our study across two regions of south-west Victoria, Australia (Fig. 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 the introduced fox and feral cat being the primary functional mammalian terrestrial predators; birds of prey and snakes are the only other carnivores present.

Our study landscapes in the Glenelg region, Gunditjmara country, are primarily lowland forest (with an overstorey of *Eucalyptus obliqua* and *E. ovata*, a sparse midstorey and a fern-rich understorey) and heathy woodland (with an overstorey of *E. baxteri* s.l. and *E. willisii*, a sparse midstorey and a diverse understorey of narrow or ericoid-leaved shrubs). The terrain is gently undulating, and the region frequently experiences prescribed burns and wildfires, creating a mosaic of fire histories and vegetation complexity. The area receives an average annual rainfall of 700 mm, with average minimum temperatures of 8.1°C and maximum of 17.6°C (*Bureau of Meteorology*, 2021).

Our study landscapes in the Otway region were in the western section of the Otway Ranges, Gadubanud country. Here, the vegetation is a mosaic of shrubby wet forest and cool temperate rainforest, with an overstorey of tall eucalyptus species (primarily *E. regnans*), *Acacia melanoxylon* and *Nothofagus cunninghamii*. The midstorey is dominated by tree ferns, *Acacia verticillata*, *Pomaderris aspera* and *Olearia argophylla*. The understorey predominantly comprises a dense layer of ferns and graminoids but can be relatively sparse in steep rainforest gullies. Maximum daily temperatures average 19.3°C in summer and 9.5°C in winter; annual rainfall averages 1955 mm (*Bureau of Meteorology*, 2021). 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, averaged within a 10 m radius of each camera-trap site).

2.2. Lethal fox control

Government land managers conduct ongoing targeted fox control for biodiversity conservation across broad sections of each region. Manufactured poison baits (FoxOff, Animal Control Technologies, Somerton) containing 3 mg of sodium mono-fluoroacetate (1080) are buried at a depth of 12-15 cm at 1-km intervals along accessible forest tracks and roads (Fig. 1). Different road densities across the two regions therefore result in variable poison-bait densities. In the Glenelg region, fox-baiting in the impact landscapes has been ongoing since October 2005, with baits checked and replaced fortnightly (Robley et al., 2014). In the Otway region, 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 fox control program then lapsed for approximately six months until December 2018, when monthly bait replacement resumed for the remainder of the study (Fig. S1).

2.3. 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 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 areas that have been poison-baited for foxes for more than 13 years with unbaited areas. We surveyed Cobboboonee National Park (impact) and Annya State Forest (non-impact) in January – April 2018, then Mt Clay State Forest/Narrawong Flora Reserve (hereafter ‘Mt Clay’; impact) and Hotspur State Forest (non-impact) in April – June 2018 (Fig. S1). Each grid was separated by at least 8 km, a distance very unlikely to be traversed regularly by these invasive predators (B. A. Hradsky et al., 2017b).

In the Otway region, we undertook a before-after control-impact paired series (BACIPS) study to assess changes related to the introduction of the fox control program. We deployed camera-trap grids in an impact – non-impact pair of landscapes from June to September in three years (2017, 2018, 2019), in the Great Otway National Park and Otway Forest Park (Fig. S1). Our first survey occurred approximately three months before fox-baiting began. 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 recommenced six months prior to the start of the final survey (Fig. S1). 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 (B. A. Hradsky et al., 2017b). In this study, and a concurrent study which identified individual foxes through genetic sampling (M. Le Pla et al., in review), we found no evidence that either species of predator moved between the impact and non-impact landscapes.

In each of the six survey landscapes, we deployed a grid of camera-traps (67 – 110 cameras; mean = 94), with sites spaced on average 448 m apart (range: 194 – 770 m; Fig. 1). At each site, we deployed a single Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an infrared flash and temperature-in-motion detector on a tree, facing a lure of oil-absorbing cloth doused in tuna oil (Fig. S2). More information on the camera-trapping methods is provided in Section 1.2 of the Supporting Information. Overall, we deployed 938 functional camera-traps, which operated for an average of 68 days (range: 12 – 93 days), totalling 62,415 trap nights (Table S1)

2.4. Individual feral cat identification

We sorted the cats into five categories based on their coat type: black, mackerel tabby, classic tabby, ginger and other (cats with multiple colour blends or other distinctive coats; Fig. S3). We did not attempt to identify any black cats, even the few with white splotches on their underside, as these markings could not always be seen. Within the other four coat categories, multiple observers identified individual cats based on their unique coat patterns where possible. Detailed information on this process is provided in Section 2 of the Supporting Information.

2.5. Spatial fox occurrence

We could not directly use fox presence-absence data from the camera-trap sites as an independent predictor of cat density, as spatial mark-resight models require covariate values for each grid cell in which density is estimated (see Section 2.6 below). We therefore used the fox presence-absence data for each camera-trap site to generate a spatially-interpolated layer of fox occurrence probability using binomial generalised additive mixed-effects models (Wood, 2017). These models allow efficient nonlinear spatial estimates, although, assume perfect 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 the years (using a ‘by variable’ smooth, with year as a factor). Differences in camera-trap deployment lengths were accounted for using a model offset.

2.6. Spatial mark-resight models of feral cat density

We used a spatial capture-recapture approach to estimate feral cat density (Borchers & Efford, 2008). These models consider 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. Spatial capture-recapture models commonly assume that individuals have approximately circular home ranges and spend the majority of time in the centre of their range (‘activity centre’). The probability of observing an individual therefore decreases with distance from the activity centre. Two detectability parameters govern this process: $g\theta$, the probability of detecting an individual per occasion in their activity centre, and σ : a spatial scale parameter which is related to the home range size. Multiple candidate shapes for this decline in detectability with distance from the activity centre (‘detection function’) can be modelled. We tested the half-normal and exponential detection functions in each region, carrying forward the function with the lowest Akaike’s Information Criterion score adjusted for small sample size (AICc) for all subsequent model fitting (Burnham & Anderson, 2004).

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 spatial mark-resight models typically assume unmarked individuals to be a random sample of the population, sharing the same detection process as marked individuals, and so allow density to be estimated for the entire population. Spatial mark-resight models have four categories of sightings: (1) marked individuals - detections with known identities identified to the individual level at least once each session, (2) marked but unidentifiable individuals - detections of individuals with known identities, but for which the individual could not be determined in a given session (we had no detections in this category), (3) unmarked individuals - unidentified detections which definitely do not belong to the first two categories (in our study, this category comprised black cats) and (4) mark status uncertain - detections in which

individuals cannot be identified and it is not clear whether the individual is of the marked or unmarked category.

We used closed population, sighting-only, spatial mark-resight models to estimate feral cat density using the maximum likelihood ‘secr’ R-package (Efford, 2021). Detections of the ‘mark status uncertain’ category cannot be handled in the ‘secr’ R package, we therefore added them to the unmarked detections rather than discard them (Moseby et al., 2020). We condensed detection histories of each mark category 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 camera-trap location, and estimated feral cat density across this area, with a grid cell resolution of 200 m. These habitat mask specifications were based on initial model trials and our knowledge of feral cat behaviour in these areas; the aim was to ensure density was estimated over a large enough area to encompass the activity centres of all feral cats exposed to our camera-traps, at a fine enough scale to minimise bias in density estimates.

For each region, we ran three sets of models: we (1) chose ‘base model’ covariates to carry through to subsequent model sets, (2) tested fine-scale associations between spatial fox occurrence and feral cat density, and (3) experimentally evaluated the effect of fox control on feral cat density at the landscape scale. Each of these steps is described in more detail in the following paragraphs. We assessed the relative performance of models in each set using AICc score, with models within 2 delta AICc of the top-ranked model considered equally plausible, and strongly supported compared to other candidate models (Burnham & Anderson, 2004). We expected that foxes would impact both detectability parameters for feral cats concurrently, and so always used the same parameters for $g0$ and σ within a model (Efford & Mowat, 2014).

Feral cat detectability may have decreased over each survey duration due to the lure scent fading, and density may differ across vegetation types. While we chose landscape pairs based on the similarity of ecological vegetation class groups (DELWP, 2020), there were small differences in the relative proportion of each group across landscapes. To account for this, we first condensed vegetation groups into three categories for each region: cleared land, heathy woodlands, and either lowland forests (Glenelg region only) or wet forests (Otway region only). Detailed information on this process is provided in Section 6 of the Supporting Information. We included vegetation type as a habitat mask covariate. Camera-traps were lured with tuna oil scent, which likely faded over the survey duration and potentially reduced feral

cat detectability (Rees et al., 2019). To account for this, we fit a model where g_0 had a linear trend over the survey duration for each camera-trap. We included year as a density covariate in the Otway region models to account for repeat sampling. We compared these models to a ‘null model’ without the vegetation and linear time trend covariates. We carried these covariates through to all subsequent models if their respective model had an AICc score which was lower than the null model by more than two.

To test direct associations between feral cats and foxes, we used the spatial fox occurrence estimates (detailed in the previous section) as an explanatory variable. We tested three hypotheses for each region: (1) fox occurrence only affects feral cat density, (2) fox occurrence only affects feral cat detectability (both parameters), and (3) fox occurrence affects the density and the detectability of feral cats. We included year as a feral cat density covariate in the Otway region models to account for repeat sampling. Predator associations may be nonlinear (Johnson & VanDerWal, 2009), and so we fit these three models again using regression splines (generalised additive models called within the ‘*secr*’ R-package). We assessed these three models per region relative to a null model which did not include fox occurrence covariates.

To investigate fox-baiting effects at a landscape scale, we compared the difference in feral cat density between paired non-impact and impact landscapes. We estimated density separately for each landscape (coded as a separate ‘session’) and considered statistical evidence for a difference between paired landscapes if 95% confidence intervals of the coefficient estimates of difference did not overlap zero. We used AICc scores to choose between different specifications of the detectability parameters: (1) constant, (2) an effect of fox-baiting (but with separate effects in each spatial or temporal replicate), (3) an effect of pair in the Glenelg region (due to possible seasonal differences) or an effect of year in the Otway region, (4) the combination of fox-baiting and pair/year effects, presenting the top-ranked model.

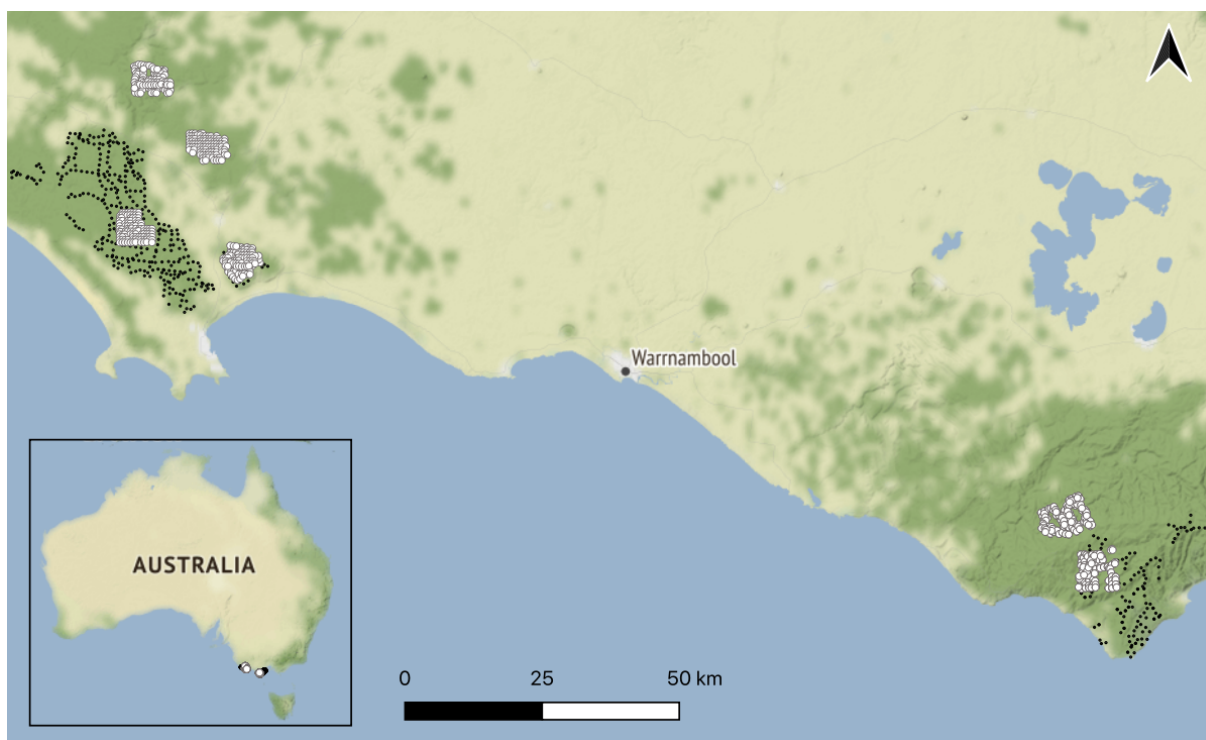


Figure 1: Locations of our six study landscapes in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots, the locations of fox poison-bait stations are denoted by smaller black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. Map tiles by Stamen Design, under CC BY 3.0, map data by OpenStreetMap, under CC BY SA.

3. RESULTS

3.1. Fox occurrence

In the Glenelg region, foxes were detected at 55% of camera-trap sites in the non-impact (unbaited) landscape and only 26% of sites in the impact (baited) landscape, for the first replicate (Annya and Cobboboonee, respectively). For the second non-impact / impact pair, the difference was smaller, with foxes detected at 48% and 35% of sites respectively (Hotspur and Mt Clay). In the Otway region, naive fox occurrence rates increased approximately 3-fold over three years in the non-impact landscape, from 0.13 in 2017, to 0.27 in 2018 and 0.43 in 2019. In contrast, in the impact landscape, naive fox occurrence rates halved over the same period, from 0.36 of sites prior to poison-baiting in 2017, to 0.27 in 2018 (fox-baiting occurred prior to, but lapsed during this survey), and 0.17 in 2019 (where fox-baiting occurred during the survey and had occurred for six months prior).

The generalised additive models of fox occurrence produced average occurrence estimates for each landscape that were largely consistent with the unadjusted naive occurrence rates. In the Glenelg region, mean fox occurrence was 0.51 (SE 0.13) and 0.34 (SE 0.12) for the first non-impact and impact replicate, with a mean estimate of 0.56 (SE 0.13) and 0.51 (SE 0.14) for the second replicate pair. In the Otway region, mean fox occurrence in the non-impact landscape changed from 0.18, 0.23, 0.36 in 2017, 2018 and 2019 (respective SEs: 0.07, 0.03, 0.11), whereas mean fox occurrence in the impact landscape changed from 0.31, 0.23, 0.18 in 2017, 2018 and 2019 (respective SEs: 0.09, 0.03, 0.08). Fine-scale spatial variation in fox occurrence was higher within the Glenelg region than the Otway region (Fig. 2). In fact, no spatial variation (i.e. a completely smooth relationship with space) was predicted for the 2018 survey data in the Otway region (Fig. 2). The fox occurrence model for the Glenelg region had an adjusted R-squared value of 0.142 and reduced null deviance by 14.8%; the model for the Otway region had an R-squared value of 0.24 and reduced null deviance by 27.8%. Model summaries and spatial standard error estimates are presented in Section 5 of the Supporting Information.

3.2. Feral cats in the Glenelg region

In the Glenelg region, we recorded 222 feral cat detections from 26,792 camera-trap nights (Table S1). Sixty-five percent of detections were feral cats with unique natural markings; the remainder were black. We were able to identify 85% of feral cat detections to the individual level; a total of 40 cats (9 –

13 individuals per grid). The exponential detector function was supported over the half-normal function (Table S2). There was no support for a linear time trend on g_0 , nor for an impact of vegetation type on feral cat density (Table S3).

At a fine spatial scale, feral cat density was negatively and linearly associated with spatial fox occurrence (coefficient -0.34; standard error 0.15; Fig. 3); feral cat detectability was not affected by fox occurrence. This model had an AICc which was 2.76 better than the null; models that included an impact of fox occurrence on detectability parameters performed worse than the null model based on AICc scores (Table S3). Regression splines did not change model predictions (Fig. 3), with all nonlinear models performing consistently worse than their linear counterparts (Table S3).

At the landscape level, feral cat density was higher in the first impact landscape than its paired non-impact landscape, but there was no difference for the second replicate (Fig. 5). The top-model in this set also had constant detectability.

3.3. Feral cats in the Otway region

In the Otway region, we recorded 1022 feral cat detections from 35,623 camera-trap nights (Table S1). Sixty-one percent of detections were feral cats with unique natural markings and we identified 86% of these, a total of 98 cats (20 – 30 per grid per year). The exponential detector function was strongly supported over the half-normal function (Table S2). There was no support for a linear time trend on g_0 , nor for an impact of vegetation type on feral cat density (Table S3).

Spatial fox occurrence was negatively correlated with feral cat density (linear model coefficient -0.26; SE 0.14; Fig. 3). There was strong support for an effect of fox occurrence on feral cat detectability (Fig. 4). Where fox occurrence was higher, feral cats were less detectable in their activity centres (i.e. negative association with g_0 ; coefficient -0.69; SE 0.21; Fig. 4A) and ranged further (i.e. positive association with σ ; coefficient 0.3; SE 0.09; Fig. 4B). The linear model and nonlinear models were indistinguishable based on AICc scores (as was also the case for the other two model specifications), with at least 10.6 AICc scores lower than the null. The shape of the nonlinear model differed from the linear model, although estimates were mostly contained within the linear model 95% confidence intervals (Fig. 3; Fig. 4).

At a landscape-scale, there was no evidence that feral cat density differed between impact and non-impact sites in any of the three years surveyed (Fig. 6A). The estimate of difference changed from a

negative value in 2017 and 2018 (i.e. feral cat density was lower in the impact site than the non-impact site) to a positive value in 2019 (when fox-baiting occurred throughout the survey duration), however 95% confidence intervals of the parameter estimates still overlapped zero (Fig. 6A). This change was due to feral cat density remaining relatively constant at the impact site between 2018 and 2019, but declining at the non-impact site over the same period (Fig. 6B). There was strong evidence that feral cat detectability differed across the three years, and in response to the fox-baiting (Table S5).

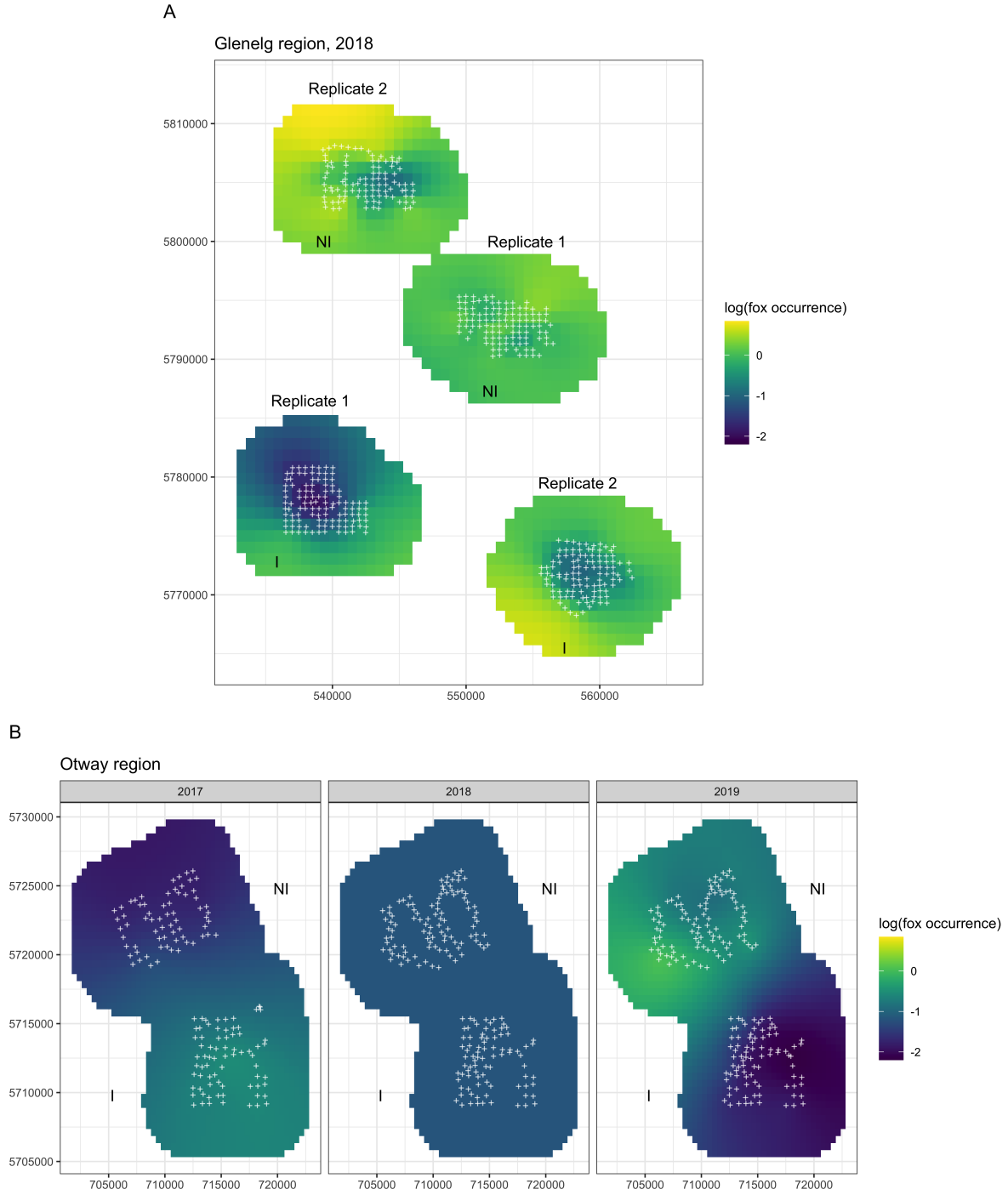


Figure 2: Predicted red fox *Vulpes vulpes* occurrence derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg (A) and Otway (B) regions, Australia. Predicted fox occurrence was used as a predictor of feral cat *Felis catus* density in the spatial mark-resight models.

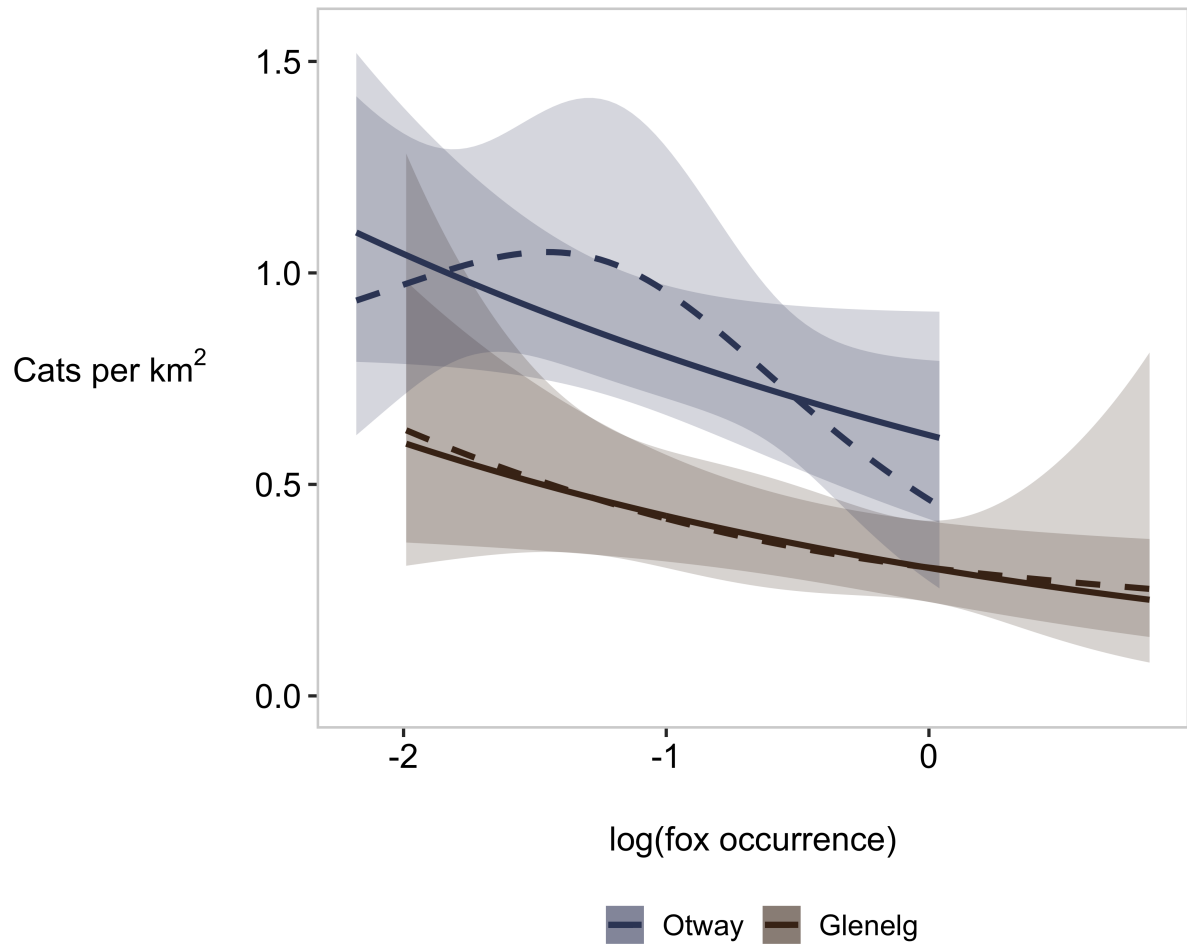


Figure 3: Linear (solid lines) and nonlinear (dashed lines) models of feral cat density and fox occurrence in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.

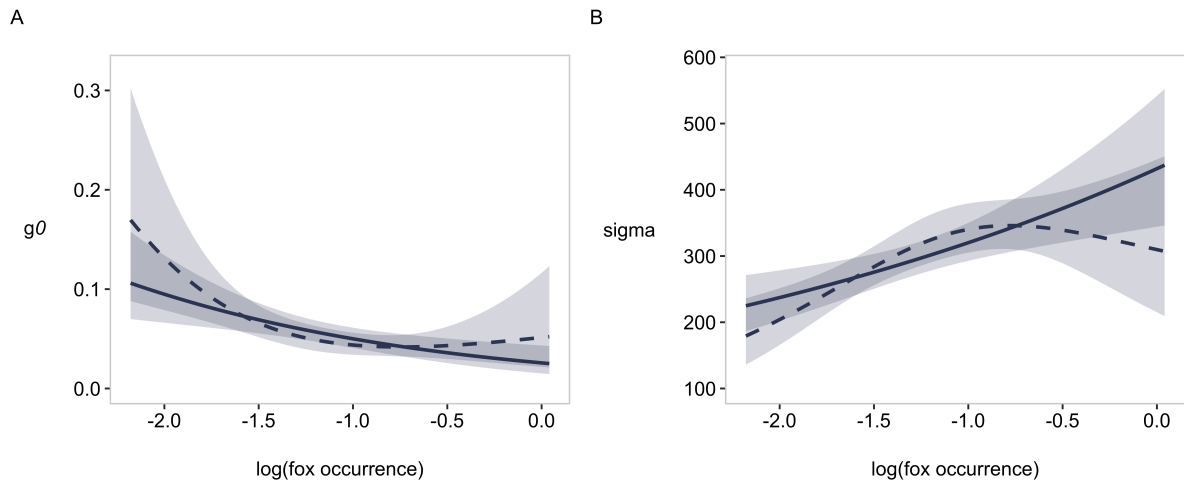


Figure 4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat detectability parameters in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0) decreased with the probability of fox occurrence (B), while sigma (which is related to home range size) increased (C). Shaded areas indicate 95% confidence intervals.

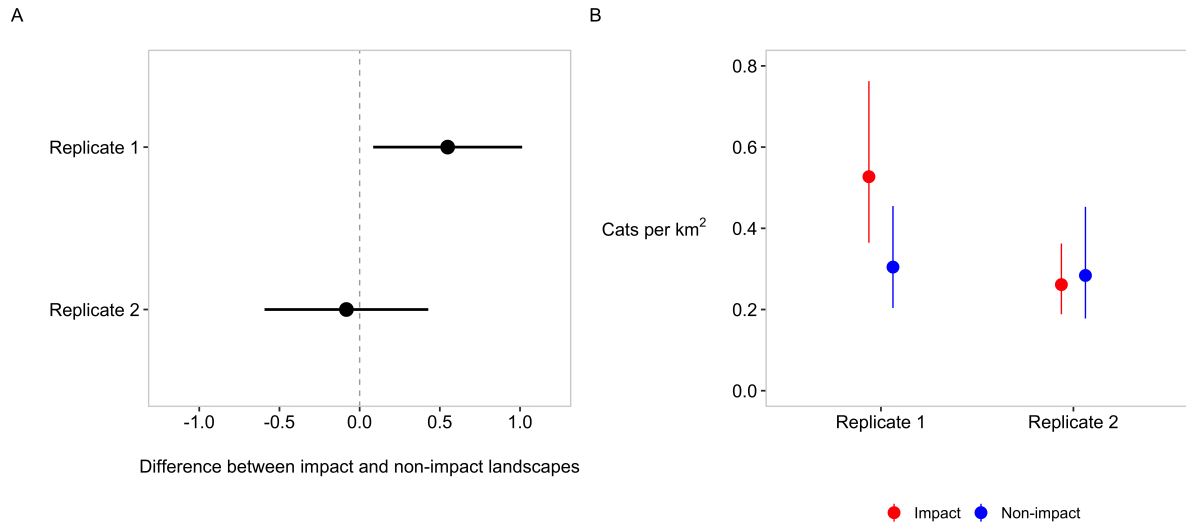


Figure 5: Estimates of difference between feral cat *Felis catus* density in impact and non-impact landscapes (A) and predicted feral cat density estimates (B) in impact and non-impact landscapes in the Glenelg region, Australia. Poison baiting for foxes has been conducted in the impact landscapes for more than 13 years. Feral cat density was higher in the impact than non-impact landscape for the first replicate pair, but not for the second replicate pair. Error bars represent 95% confidence intervals.

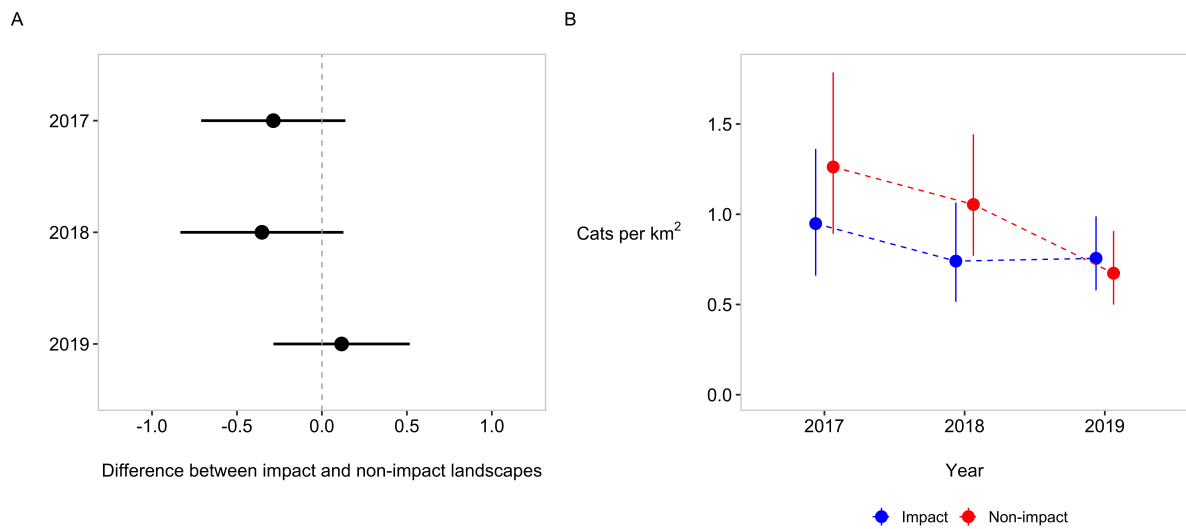


Figure 6: Estimates of difference between impact and non-impact landscapes (A) and predicted density estimates (B) in the Otway region, Australia. There was no evidence that feral cat density differed between impact and non-impact landscapes in each year surveyed). In 2017, surveys were conducted approximately two months before fox control commenced in the impact landscape (red). Error bars represent 95% confidence intervals.

4. DISCUSSION

After individually identifying 137 feral cats, we found that feral cat density was highest where fox occurrence was lowest across both surveyed regions at a fine spatial scale. However, lethal fox control did not consistently increase feral cat density at a landscape scale. This is most likely due to the fox-baiting inconsistently suppressing fox occurrence, as well as our short sampling period in the Otway region post-baiting. Our study demonstrates the potential for mesopredator release following intensive and sustained fox control, but also highlights that it is unlikely to universally occur; fox-cat interactions are 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 density from changes in detectability.

We were able to exploit a gradient in fox occurrence caused by using lethal fox control to investigate associations between feral cat density and fox occurrence at a fine spatial scale across two separate ecosystems. At this scale, we observed a similar negative association with feral cat density and fox occurrence in each ecosystem, although there was more uncertainty around the relationship in the Otway region. Across the gradient of fox occurrence, overall feral cat density was consistently higher in the Otway region than Glenelg, likely reflecting relatively high small mammal (i.e. prey) abundance (Rees et al., 2019) and lower fox occurrence at the landscape level.

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 tested this by comparing AICc scores of linear and non-linear model specifications. There was no evidence of non-linear associations between foxes and feral 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 feral 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 feral cats can successfully avoid foxes through behavioural change where foxes are rare, but this is ineffective where foxes are common. Fox avoidance strategies likely come at the expense of hunting success (Sih, 1980), which may mean that they are untenable for feral cats in the Glenelg region where small mammal abundance is relatively low (Wilson et al., 2010).

Where fox occurrence was higher in the Otway Ranges, feral cats were less detectable in their activity

centres and ranged further (Fig. 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). Sigma scaling with fox occurrence probability 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, feral cats may consider foxes predictable and avoid locations they frequent, thus having to range further to cover the same home-range area. In forests similar to the Otway region, Buckmaster (2012) observed large ‘holes’ in the home-range of each GPS collared feral cat; they confirmed that this was not due to an absence of prey and so hypothesised that it could be due to apex predator avoidance. On the other hand, sigma scaling with fox occurrence probability may be an indirect effect - a symptom of the change in feral cat density. Feral cat density was lowest where fox occurrence was highest, and animals, including feral cats, tend to have larger home ranges at low densities (Bengsen et al., 2016). Regardless of the mechanism, apex predator-dependent movement rates has serious implications for the interpretation of studies which compare the relative abundance (without disentangling behaviour and detectability from density) and spatial overlap of predator species (Broadley et al., 2019; Efford & Dawson, 2012; Neilson et al., 2018; Stewart et al., 2018).

Feral cat density in the Glenelg region was similar across three out of the four landscapes surveyed (Fig. 5). This is unsurprising given that landscape-wide fox occurrence estimates varied by less than 10% across these three landscapes, despite a long-term fox baiting program at Mt Clay. In contrast, feral cat density was at least 67% higher in the other impact (baited) landscape (Cobboboonee), and average fox occurrence was around 31% lower. Fox baiting may be more effective at reducing fox occurrence at Cobboboonee where the camera-trap grid is largely surrounded by mostly fox-baited forest, than Mt Clay which is nearly entirely surrounded by unbaited farmland (Fig. 1). Landscape feral cat density estimates are averaged across the entire camera-trap grid interior and surrounding 4 km buffer zone. Hradsky et al. (2019) predicted that extending poison-baits 1 km into the adjacent farmland would more than halve fox density inside Mt Clay. Studies of fox-cat (and other predator-predator) interactions often rely solely on 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 response of subordinate species (Salo et al., 2010).

We saw no evidence that feral cat density differed between impact and non-impact landscapes in the Otway region (Fig. 6). There may not have been an effect because fox occurrence was already low prior

to fox control commencing (Fig. 2). The non-linear correlative model predicted feral cat density to be unaffected by fox occurrence at such low levels (Fig. 3). However, we did see a small increase in feral cat density in the impact landscape relative to the non-impact landscape during our final survey in 2019. Our short sampling period post-baiting may have not allowed enough time for changes to manifest in the adult population, as foxes possibly suppress cats through lowered breeding and recruitment rates (Ritchie & Johnson, 2009). Despite high feral cat density, the high proportion of unmarked cats in the Otway region, and complex detectability covariates reduced our ability to demonstrate statistical evidence for weak fox-baiting effects. Our surveys here provide an important baseline for which to compare future changes in predators and prey against, particularly once fox-baiting has occurred over a longer (and more consistent) time frame.

Our study has several limitations. It is unclear whether foxes may suppress feral cats directly through top-down control, or indirectly through competition for shared prey. Instead of responding directly to foxes, feral cats may have responded to fox-induced impacts on native prey (Stobo-Wilson et al., 2020). However, vegetation type is a strong predictor of native prey occurrence within these regions (B. A. Hradsky et al., 2017a), and we saw no evidence that vegetation type impacted feral cat density. Rather than avoidance or exclusion, negative correlation between foxes and feral cats may reflect differences in niche preference. However, this is less likely to be an issue for our study because foxes were artificially suppressed using lethal control. Uncertainty from our fox occurrence models was not propagated into the spatial mark-resight models, however, a full Bayesian integration of the fox occurrence analysis and the spatial mark-resight model is not yet implemented. The development of open population spatial mark-resight models would also improve parameter estimates for multi-season surveys.

Our study is among the very few which have tested the mesopredator release in terms of changes in the density of the mesopredator population through direct measurement of density. Previous studies have mostly used live capture-rates to infer population density, without accounting for behavioural or detectability changes (Arjo et al., 2007; Berger et al., 2008; Jones et al., 2008; Karki et al., 2007; Thompson & Gese, 2007). Contention about mesopredator release has centred on such methods (Hayward & Marlow, 2014); as well unaccounted species interactions in complex predator guilds (Jachowski et al., 2020; Levi & Wilmers, 2012). In contrast, our study tests the mesopredator release theory using a combined behavioural and numerical approach, in a simple system with only two carnivore species.

We saw behavioural and numerical responses consistent with a mesopredator release of feral cats,

420 although numerical changes were only consistently observed at a finescale. This may explain why pest
421 management that only targets foxes—one of the most prevalent conservation actions in Australia—does not
422 consistently improve native prey persistence (Dexter & Murray, 2009; Duncan et al., 2020; Lindenmayer
423 et al., 2018; Wayne et al., 2017). However, more evidence is required to unequivocally prove that lethal
424 fox control consistently causes increases in feral cat density. Regardless, there will be circumstances where
425 targeted fox control is worthwhile because some native prey species are more susceptible to foxes than
426 feral cats (Stobo-Wilson et al., 2021). A more integrated approach to invasive predator management,
427 whereby both foxes and feral cats are simultaneously or otherwise optimally controlled together could
428 substantially improve biodiversity outcomes (Comer et al., 2020; Risbey et al., 2000). If this is not
429 feasible, changes in invasive mesopredator density and the outcomes for prey species should be closely
430 monitored with triggers for ceasing invasive apex predator control or commencing integrated management
431 if single-species control proves counterproductive for conservation of threatened prey species.

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6. AUTHORS' 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 and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

7. OPEN RESEARCH

Raw data and code are on Github link xx.

Data will be deposited on the Dryad Digital Repository after acceptance.

REFERENCES

- Alston, J., Maitland, B., Brito, B., Esmaeili, S., Ford, A., Hays, B., Jesmer, B., Molina, F., & Goheen, J. (2019). Reciprocity in restoration ecology: When might large carnivore reintroduction restore ecosystems? *Biological Conservation*, *234*, 82–89.
- Arjo, W. M., Gese, E. M., Bennett, T. J., & Kozlowski, A. J. (2007). CHANGES IN KIT FOX–COYOTE–PREY RELATIONSHIPS IN THE GREAT BASIN DESERT, UTAH. *Western North American Naturalist*, *67*(3), 389–401. [https://doi.org/10.3398/1527-0904\(2007\)67%5B389:CIKFRI%5D2.0.CO;2](https://doi.org/10.3398/1527-0904(2007)67%5B389:CIKFRI%5D2.0.CO;2)
- Ballari, S. A., Kuebbing, S. E., & Nuñez, M. A. (2016). Potential problems of removing one invasive species at a time: A meta-analysis of the interactions between invasive vertebrates and unexpected effects of removal programs. *PeerJ*, *4*, e2029.
- Bengsen, A. J., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P. J. S., Friend, J. A., Johnston, M., McGregor, H., Moseby, K., & Zewe, F. (2016). Feral cat home-range size varies predictably with landscape productivity and population density. *Journal of Zoology*, *298*(2), 112–120. <https://doi.org/https://doi.org/10.1111/jzo.12290>
- Berger, K. M., Gese, E. M., & Berger, J. (2008). Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology*, *89*(3), 818–828. <https://doi.org/https://doi.org/10.1890/07-0193.1>
- Bode, M., Baker, C. M., & Plein, M. (2015). Eradicating down the food chain: Optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, *52*(3), 571–579.
- Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, *64*(2), 377–385.
- Broadley, K., Burton, A. C., Aygar, T., & Boutin, S. (2019). Density-dependent space use affects interpretation of camera trap detection rates. *Ecology and Evolution*, *9*(24), 14031–14041.
- Buckmaster, A. J. (2012). *Ecology of the feral cat (felis catus) in the tall forests of far east gipps-*

land [PhD thesis, University of Sydney.; School of Biological Sciences; University of Sydney.; School of
Biological Sciences]. <http://hdl.handle.net/2123/8123>

Bureau of meteorology. (2021). Climate Data Online URL; (accessed May 2021). <http://www.bom.gov.au/climate/data/>

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding aic and bic in
model selection. *Sociological Methods & Research*, 33(2), 261–304.

Catling, P. (1988). Similarities and contrasts in the diets of foxes, *vulpes vulpes*, and cats, *felis catus*,
relative to fluctuating prey populations and drought. *Wildlife Research*, 15(3), 307–317.

Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland, W. J.
(2019). Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *Journal
of Applied Ecology*, 56(12), 2742–2754.

Claridge, A. W., Cunningham, R. B., Catling, P. C., & Reid, A. M. (2010). Trends in the activity
levels of forest-dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest
Ecology and Management*, 260(5), 822–832.

Comer, S., Clausen, L., Cowen, S., Pinder, J., Thomas, A., Burbidge, A. H., Tiller, C., Algar, D., &
Speldewinde, P. (2020). Integrating feral cat (*felis catus*) control into landscape-scale introduced predator
management to improve conservation prospects for threatened fauna: A case study from the south coast
of western australia. *Wildlife Research*, 47(8), 762–778.

Courchamp, F., Langlais, M., & Sugihara, G. (1999). Cats protecting birds: Modelling the meso-
predator release effect. *Journal of Animal Ecology*, 68(2), 282–292.

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented
system. *Nature*, 400(6744), 563–566.

Davey, C., Sinclair, A., Pech, R. P., Arthur, A. D., Krebs, C. J., Newsome, A., Hik, D., Molsher, R.,
& Allcock, K. (2006). Do exotic vertebrates structure the biota of australia? An experimental test in
new south wales. *Ecosystems*, 9(6), 992–1008.

DELWP. (2020). *Bioregions and evc benchmarks*. Victorian Government Department of Environ-

ment, Land, Water; Planning, Melbourne. Accessed June 2021). <https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks>

Dexter, N., & Murray, A. (2009). The impact of fox control on the relative abundance of forest mammals in east gippsland, victoria. *Wildlife Research*, *36*(3), 252–261.

Doherty, T. S., & Ritchie, E. G. (2017). Stop jumping the gun: A call for evidence-based invasive predator management. *Conservation Letters*, *10*(1), 15–22.

Duncan, R. P., Dexter, N., Wayne, A., & Hone, J. (2020). Eruptive dynamics are common in managed mammal populations. *Ecology*, *101*(12), e03175.

Efford, M. G. (2021). *Secr: Spatially explicit capture-recapture models*. R package version 4.4.4. (accessed June 2021). <http://CRAN.R-project.org/package=secr>

Efford, M. G., & Dawson, D. K. (2012). Occupancy in continuous habitat. *Ecosphere*, *3*(4), 1–15.

Finke, D. L., & Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature*, *429*(6990), 407–410.

Fisher, P., Algar, D., Murphy, E., Johnston, M., & Eason, C. (2015). How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? *Applied Animal Behaviour Science*, *173*, 88–96.

Forsyth, D. M., Ramsey, D. S., & Woodford, L. P. (2019). Estimating abundances, densities, and interspecific associations in a carnivore community. *The Journal of Wildlife Management*, *83*(5), 1090–1102.

Glen, A., Pennay, M., Dickman, C., Wintle, B., & Firestone, K. (2011). Diets of sympatric native and introduced carnivores in the barrington tops, eastern australia. *Austral Ecology*, *36*(3), 290–296.

Glen, A. S., & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in australia, and their implications for wildlife management. *Biological Reviews*, *80*(3), 387–401.

Hastings, A. (2001). Transient dynamics and persistence of ecological systems. *Ecology Letters*, *4*(3), 215–220.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, K. U., MacKenzie, D. I., Pollock, K. H., & Yarnell, R. W. (2015). Ecologists need robust survey designs, sampling and analytical methods. *Journal of Applied Ecology*, 52(2), 286–290.

Hayward, M. W., & Marlow, N. (2014). Will dingoes really conserve wildlife and can our methods tell? *Journal of Applied Ecology*, 51(4), 835–838. <https://doi.org/https://doi.org/10.1111/1365-2664.12250>

Hradsky, B. A., Kelly, L. T., Robley, A., & Wintle, B. A. (2019). FoxNet: An individual-based model framework to support management of an invasive predator, the red fox. *Journal of Applied Ecology*, 56(6), 1460–1470.

Hradsky, B. A., Penman, T. D., Ababei, D., Hanea, A., Ritchie, E. G., York, A., & Di Stefano, J. (2017a). Bayesian networks elucidate interactions between fire and other drivers of terrestrial fauna distributions. *Ecosphere*, 8(8), e01926. <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1926>

Hradsky, B. A., Robley, A., Alexander, R., Ritchie, E. G., York, A., & Di Stefano, J. (2017b). Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *vulpes vulpes*. *Scientific Reports*, 7(1), 1–12. <https://doi.org/https://doi.org/10.1890/11-0165.1>

Hunter, D. O., Lagisz, M., Leo, V., Nakagawa, S., & Letnic, M. (2018). Not all predators are equal: A continent-scale analysis of the effects of predator control on australian mammals. *Mammal Review*, 48(2), 108–122.

Jachowski, D. S., Butler, A., Eng, R. Y. Y., Gigliotti, L., Harris, S., & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: A review of evidence from north america. *Mammal Review*, 50(4), 367–381. <https://doi.org/https://doi.org/10.1111/mam.12207>

Jackson, M. C. (2015). Interactions among multiple invasive animals. *Ecology*, 96(8), 2035–2041.

Johnson, C. N., & VanDerWal, J. (2009). Evidence that dingoes limit abundance of a mesopredator in eastern australian forests. *Journal of Applied Ecology*, 46(3), 641–646. <https://doi.org/https://doi.org/10.1111/j.1365-2664.2009.01650.x>

Jones, K. L., Van Vuren, D. H., & Crooks, K. R. (2008). Sudden Increase in a Rare Endemic Carnivore:

561 Ecology of the Island Spotted Skunk. *Journal of Mammalogy*, 89(1), 75–86. <https://doi.org/10.1644/07->
562 MAMM-A-034.1

563 Karki, S. M., Gese, E. M., & Klavetter, M. L. (2007). Effects of coyote population reduction on swift
564 fox demographics in southeastern colorado. *The Journal of Wildlife Management*, 71(8), 2707–2718.
565 <https://doi.org/https://doi.org/10.2193/2006-275>

566 Kuebbing, S. E., & Nuñez, M. A. (2015). Negative, neutral, and positive interactions among nonnative
567 plants: Patterns, processes, and management implications. *Global Change Biology*, 21(2), 926–934.

568 Lazenby, B. T., Mooney, N. J., & Dickman, C. R. (2015). Effects of low-level culling of feral cats in
569 open populations: A case study from the forests of southern tasmania. *Wildlife Research*, 41(5), 407–420.

570 Legge, S., Taggart, P. L., Dickman, C. R., Read, J. L., & Woinarski, J. C. (2020). *Wildlife Research*,
571 47(8), 731–746.

572 Levi, T., & Wilmers, C. C. (2012). Wolves–coyotes–foxes: A cascade among carnivores. *Ecology*,
573 93(4), 921–929. <https://doi.org/https://doi.org/10.1890/11-0165.1>

574 Lindenmayer, D. B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks,
575 S., Robinson, N., Dexter, N., O’Loughlin, L. S., & Legge, S. (2018). Conservation conundrums and the
576 challenges of managing unexplained declines of multiple species. *Biological Conservation*, 221, 279–292.
577 <https://doi.org/https://doi.org/10.1016/j.biocon.2018.03.007>

578 Lombardi, J. V., Comer, C. E., Scognamillo, D. G., & Conway, W. C. (2017). Coyote, fox, and bobcat
579 response to anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems*, 20(6),
580 1239–1248.

581 Marlow, N. J., Thomas, N. D., Williams, A. A., Macmahon, B., Lawson, J., Hitchen, Y., Angus,
582 J., & Berry, O. (2015). Cats (*felis catus*) are more abundant and are the dominant predator of woylies
583 (*bettongia penicillata*) after sustained fox (*vulpes vulpes*) control. *Australian Journal of Zoology*, 63(1),
584 18–27.

585 McLeod, S. R., & Saunders, G. (2014). Fertility control is much less effective than lethal baiting for
586 controlling foxes. *Ecological Modelling*, 273, 1–10.

587 Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S.,
588 Le Corre, M., Horwath, S. V., & Nogales, M. (2011). A global review of the impacts of invasive cats on
589 island endangered vertebrates. *Global Change Biology*, 17(11), 3503–3510.

590 Miller, D. L., & Wood, S. N. (2014). Finite area smoothing with generalized distance splines. *Envi-*
591 *ronmental and Ecological Statistics*, 21(4), 715–731.

592 Molsher, R., Newsome, A. E., Newsome, T. M., & Dickman, C. R. (2017). Mesopredator management:
593 Effects of red fox control on the abundance, diet and use of space by feral cats. *PLoS One*, 12(1), e0168460.

594 Moseby, K. E., Letnic, M., Blumstein, D. T., & West, R. (2019). Understanding predator densities
595 for successful co-existence of alien predators and threatened prey. *Austral Ecology*, 44(3), 409–419.

596 Moseby, K., McGregor, H., & Read, J. (2020). Effectiveness of the felixer grooming trap for the
597 control of feral cats: A field trial in arid south australia. *Wildlife Research*, 47(8), 599–609.

598 Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K., & Boutin, S. (2018). Animal movement
599 affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*,
600 9(1), e02092. <https://doi.org/https://doi.org/10.1002/ecs2.2092>

601 Rayner, M. J., Hauber, M. E., Imber, M. J., Stamp, R. K., & Clout, M. N. (2007). Spatial hetero-
602 geneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy*
603 *of Sciences*, 104(52), 20862–20865.

604 Reddiex, B., Forsyth, D. M., McDonald-Madden, E., Einoder, L. D., Griffioen, P. A., Chick, R. R.,
605 & Robley, A. J. (2007). Control of pest mammals for biodiversity protection in australia. I. Patterns of
606 control and monitoring. *Wildlife Research*, 33(8), 691–709.

607 Rees, M., Pascoe, J., Wintle, B., Le Pla, M., Birnbaum, E., & Hradsky, B. (2019). Unexpectedly high
608 densities of feral cats in a rugged temperate forest. *Biological Conservation*, 239, 108287.

609 Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). Index that quantifies topographic heterogeneity.
610 *Intermountain Journal of Sciences*, 5(1-4), 23–27.

611 Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and con-
612 sequence of animal movement. *Trends in Ecology & Evolution*, 35(2), 163–174. <https://doi.org/https://doi.org/10.1016/j.tree.2019.11.008>

613 //doi.org/10.1016/j.tree.2019.09.009

614 Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S., & Wright, I. W. (2000). The impact of cats and
615 foxes on the small vertebrate fauna of heirisson prong, western australia. II. A field experiment. *Wildlife*
616 *Research*, 27(3), 223–235. <https://doi.org/https://doi.org/10.1071/WR98092>

617 Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodi-
618 versity conservation. *Ecology Letters*, 12(9), 982–998. [https://doi.org/https://doi.org/10.1111/j.1461-](https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01347.x)
619 0248.2009.01347.x

620 Robley, A., Gormley, A. M., Forsyth, D. M., & Triggs, B. (2014). Long-term and large-scale control of
621 the introduced red fox increases native mammal occupancy in australian forests. *Biological Conservation*,
622 180, 262–269.

623 Rogan, M. S., Balme, G. A., Distiller, G., Pitman, R. T., Broadfield, J., Mann, G. K., Whittington-
624 Jones, G. M., Thomas, L. H., & O’Riain, M. J. (2019). The influence of movement on the occupancy-
625 density relationship at small spatial scales. *Ecosphere*, 10(8), e02807.

626 Ruscoe, W. A., Ramsey, D. S., Pech, R. P., Sweetapple, P. J., Yockney, I., Barron, M. C., Perry, M.,
627 Nugent, G., Carran, R., Warne, R., & others. (2011). Unexpected consequences of control: Competitive
628 vs. Predator release in a four-species assemblage of invasive mammals. *Ecology Letters*, 14(10), 1035–
629 1042.

630 Salo, P., Banks, P. B., Dickman, C. R., & Korpimäki, E. (2010). Predator manipulation experiments:
631 Impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, 80(4), 531–546. <https://doi.org/https://doi.org/10.1890/09-1260.1>

633 Short, J., Calver, M. C., & Risbey, D. A. (1999). The impact of cats and foxes on the small vertebrate
634 fauna of heirisson prong, western australia. I. Exploring potential impact using diet analysis. *Wildlife*
635 *Research*, 26(5), 621–630.

636 Sih, A. (1980). Optimal behavior: Can foragers balance two conflicting demands? *Science*, 210(4473),
637 1041–1043. <https://doi.org/10.1126/science.210.4473.1041>

638 Smith, J. A., Suraci, J. P., Hunter, J. S., Gaynor, K. M., Keller, C. B., Palmer, M. S., Atkins, J. L.,

- 639 Castañeda, I., Cherry, M. J., Garvey, P. M., & others. (2020). Zooming in on mechanistic predator–
640 prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological
641 interactions. *Journal of Animal Ecology*, 89(9), 1997–2012.
- 642 Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., & Hill, S. (1988). Reconstructed
643 dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*,
644 2(1), 75–92.
- 645 Stephens, P. A., Pettorelli, N., Barlow, J., Whittingham, M. J., & Cadotte, M. W. (2015). *Manage-*
646 *ment by proxy? The use of indices in applied ecology*. Wiley Online Library.
- 647 Stewart, F. E. C., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2018). Species occurrence data reflect
648 the magnitude of animal movements better than the proximity of animal space use. *Ecosphere*, 9(2),
649 e02112. <https://doi.org/https://doi.org/10.1002/ecs2.2112>
- 650 Stobo-Wilson, A. M., Brandle, R., Johnson, C. N., & Jones, M. E. (2020). Management of invasive
651 mesopredators in the flinders ranges, south australia: Effectiveness and implications. *Wildlife Research*,
652 47(8), 720–730.
- 653 Stobo-Wilson, A. M., Murphy, B. P., Legge, S. M., Chapple, D. G., Crawford, H. M., Dawson, S.
654 J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Gentle, M., & others. (2021). Reptiles as food:
655 Predation of australian reptiles by introduced red foxes compounds and complements predation by cats.
656 *Wildlife Research*. <https://doi.org/https://doi.org/10.1071/WR20194>
- 657 Thompson, C. M., & Gese, E. M. (2007). Food webs and intraguild predation: Community interac-
658 tions of a native mesocarnivore. *Ecology*, 88(2), 334–346. [https://doi.org/https://doi.org/10.1890/0012-](https://doi.org/https://doi.org/10.1890/0012-9658(2007)88%5B334:FWAIPC%5D2.0.CO;2)
659 [9658\(2007\)88%5B334:FWAIPC%5D2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2007)88%5B334:FWAIPC%5D2.0.CO;2)
- 660 Towerton, A. L., Penman, T. D., Kavanagh, R. P., & Dickman, C. R. (2011). Detecting pest and prey
661 responses to fox control across the landscape using remote cameras. *Wildlife Research*, 38(3), 208–220.
- 662 Wayne, A. F., Maxwell, M. A., Ward, C. G., Wayne, J. C., Vellios, C. V., & Wilson, I. J. (2017).
663 Recoveries and cascading declines of native mammals associated with control of an introduced predator.
664 *Journal of Mammalogy*, 98(2), 489–501. <https://doi.org/10.1093/jmammal/gyw237>

- 665 Wilson, R. R., Blankenship, T. L., Hooten, M. B., & Shivik, J. A. (2010). Prey-mediated avoidance
666 of an intraguild predator by its intraguild prey. *Oecologia*, 164(4), 921–929.
- 667 Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of
668 semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical*
669 *Methodology)*, 73(1), 3–36.
- 670 Wood, S. N. (2017). *Generalized additive models: An introduction with r*. CRC press.
- 671 Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-
672 ecosystem context. *Trends in Ecology & Evolution*, 16(8), 454–459.