

¹ Mesopredator release among invasive predators: controlling red foxes can
² increase feral cat density and alter their behaviour

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Data accessibility: Data and code will be deposited on the Dryad Digital Repository after acceptance and can be viewed here: <https://github.com/matt-w-rees/invasive-mesopredator-release>.

⁶ *Keywords:* 1080 poison, feral cat, red fox, invasive predator, intraguild predator interactions, lethal predator
⁷ control, mesopredator release, spatial capture-recapture

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8 **ABSTRACT**

- 9 1. The mesopredator release theory predicts that the density of subordinate predators will increase as
10 dominant predators decline. Persistent debate around mesopredator release in part reflects the lack of
11 robust, replicated experiments to test this theory, and use of population indices which confound changes
12 in mesopredator density and detectability. This uncertainty has immediate impacts for conservationists
13 who are faced with managing sympatric invasive predators.
- 14 2. We used replicated experimental designs and spatially-explicit models to examine whether mesopredator
15 release of the feral cat *Felis catus* occurs in response to targeted control of the introduced red fox
16 *Vulpes vulpes*. We surveyed three Control-Impact paired landscapes in a region with long-term fox
17 control (1080 poison baiting), and conducted a Before-After Control-Impact Paired-Series experiment
18 in another region. We used fox occurrence as a simple metric of fox populations and estimated feral
19 cat density with spatial mark-resight models.
- 20 3. Lethal fox control had varying effects on fox occurrence, consistent with variation in the duration and
21 intensity of poison baiting. Correspondingly, responses in feral cat density ranged from negligible to a
22 3.7-fold higher density in fox-baited landscapes. At a fine spatial scale (200 m^2), feral cat density was
23 negatively associated with fox occurrence probability across both regions. These results were consistent
24 with mesopredator release, although uncertainty was high in the region where fox control had only
25 recently commenced.
- 26 4. Feral cat detectability also varied across the (artificially-manipulated) gradients of fox occurrence
27 probability. In one region, nonlinear models indicated that feral cats had lower detection and increased
28 movement rates when foxes were uncommon, giving way to density suppression at high fox occurrence
29 probabilities.
- 30 5. Our study provides replicated, experimental evidence that dominant predator suppression can be
31 associated with a higher mesopredator density. Mesopredator release can manifest as changes in both
32 behaviour and density, distorting inference if these processes are not distinguished. Our results may help
33 explain why fox control does not consistently improve native prey persistence, suggesting integrated
34 pest management may be necessary to improve conservation outcomes.

³⁵ **1. INTRODUCTION**

³⁶ Understanding species interactions is critical for effective invasive species management (Zavaleta, Hobbs,
³⁷ & Mooney 2001). Where several invasive species co-occur, management actions that suppress the dominant
³⁸ invasive species may inadvertently benefit subordinate invasive species (Jackson 2015). For example, the
³⁹ removal of a dominant invasive predator may increase the density of subordinate invasive predators directly
⁴⁰ by reducing top-down pressure, or indirectly by increasing the availability of shared resources; often referred
⁴¹ to as mesopredator release (Soulé *et al.* 1988; Prugh *et al.* 2009). The release of subordinate invasive
⁴² predators can have serious negative implications for native taxa and ecosystem function (Doherty & Ritchie
⁴³ 2017; Takimoto & Nishijima 2022). However, integrated invasive predator management is often far more
⁴⁴ costly and less feasible than single species control, and so it is important to identify when the extra cost is
⁴⁵ justified (Bode, Baker, & Plein 2015).

⁴⁶ Most knowledge of mesopredator release stems from unreplicated ‘natural experiments’ (e.g., range
⁴⁷ contractions - Crooks & Soulé 1999) or ad-hoc management interventions (e.g., invasive species eradications -
⁴⁸ Rayner *et al.* 2007) where dominant predators have become largely absent from the system. It is particularly
⁴⁹ unclear whether mesopredator release still occurs when dominant predators are suppressed but not completely
⁵⁰ removed. The occurrence, nature (positive or negative, direct or indirect) and strength of predator interactions
⁵¹ can vary among species assemblages, environmental productivity, management regimes and other landscape
⁵² contexts (Finke & Denno 2004; Baum & Worm 2009; Ritchie & Johnson 2009). Replicating management
⁵³ programs in an experimental framework is logically challenging, but important for understanding these
⁵⁴ complexities, discriminating between plausible hypotheses and producing generalisable results to inform
⁵⁵ effective pest management (Glen & Dickman 2005; Ford & Goheen 2015).

⁵⁶ Another source of uncertainty around the mesopredator release hypothesis stems from the inability of
⁵⁷ traditional survey and modelling approaches to distinguish behavioural from numerical population processes
⁵⁸ (Anderson 2001; Hayward *et al.* 2015). Suppression of a dominant predator may simultaneously change
⁵⁹ the behaviour and the density of a mesopredator, both of which influence detection rates (Broadley *et al.*
⁶⁰ 2019). This makes it difficult to interpret observed changes in naïve indices of mesopredator activity or
⁶¹ occurrence in relation to changes in dominant predator populations, even if the study has an experimental
⁶² design. Unbiased estimates of invasive predator density are also important for setting meaningful control
⁶³ targets and inferring impacts on native prey (Moseby *et al.* 2019). Spatial capture-recapture methods offer a

64 solution by separating behavioural and observational processes from population density, estimated within a
65 defined spatial unit (Gardner, Royle, & Wegan 2009).

66 Predation by two invasive species, the red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus*
67 (hereafter ‘cat’), has played a major role in Australia’s high rates of mammalian extinction (Woinarski,
68 Burbidge, & Harrison 2015). Integrated pest management programs are rare; instead, foxes are far more
69 commonly controlled than cats, as they are more susceptible to poison baiting, have greater direct economic
70 impacts and fewer legal impediments to control (Reddiex *et al.* 2007; McLeod & Saunders 2014). Nonetheless,
71 cats are one of the most widespread and damaging vertebrate predator species (Medina *et al.* 2011; Doherty
72 *et al.* 2017; Legge *et al.* 2020). As foxes are larger-bodied (~2 kg difference) and have high dietary overlap
73 with cats (Stobo-Wilson *et al.* 2021b; Stobo-Wilson *et al.* 2021a; Woinarski *et al.* 2021), the mesopredator
74 release hypothesis (Soulé *et al.* 1988) predicts cat density, will increase as fox populations are suppressed
75 (Molsher *et al.* 2017). A mesopredator release of cats would likely dampen the conservation benefits of fox
76 control, and could even worsen outcomes for some native prey species (Takimoto & Nishijima 2022), as has
77 previously been suspected (e.g., Wayne *et al.* 2017).

78 Evidence that foxes suppress cats is inconclusive. In parts of Australia where the apex mammalian
79 predator (the dingo *Canis familiaris*) is locally extinct and introduced foxes are the largest terrestrial
80 mammalian predator, four studies found that fox control was associated with higher cat detection rates
81 (Risbey *et al.* 2000; Marlow *et al.* 2015; Norton *et al.* 2015; Stobo-Wilson *et al.* 2020). However, two other
82 studies in similar systems did not see any change (Towerton *et al.* 2011; Molsher *et al.* 2017). A further
83 study with spatial replication detected an increase at one site but not another (Davey *et al.* 2006), and
84 another observed a decrease in cat activity (Claridge *et al.* 2010). No prior studies have directly estimated
85 changes in cat density in response to fox control. More reliable and standardised population measurements
86 need to be deployed across different landscapes to understand what factors drive the variable responses of
87 cats to dominant predator control (Hayward *et al.* 2015).

88 We experimentally investigated the role of introduced foxes in top-down suppression of cat density across
89 eight landscapes within two regions of south-eastern Australia. Our experiment had a replicated Control-
90 Impact design in the region with long-term fox control, and a Before-After Control-Impact Paired-Series
91 (BACIPS) design in the region with newly implemented fox control. Foxes and cats are the only terrestrial
92 mammalian predators in these regions heavier than one kilogram. 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 focus on the associations between the two invasive predators, across an artificially-manipulated gradient of dominant predator (fox) occurrence probability. In accordance with mesopredator release theory, we predicted that: (1) fox control would be associated with higher cat densities at the landscape-scale, and (2) cat density would be negatively correlated with fox occurrence probability at a fine spatial scale (which could help explain cat responses to fox control). We based inference on direct estimates of cat density using spatially explicit mark-resight models.

¹⁰¹ **2. MATERIALS AND METHODS**

¹⁰² *2.1. Study area*

¹⁰³ We conducted our study across two regions of south-west Victoria, Australia (Fig. 1). The native
¹⁰⁴ temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and
¹⁰⁵ timber plantations. Native dingoes are now absent throughout southwest Victoria (Cairns *et al.* 2018).
¹⁰⁶ A native mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and
¹⁰⁷ extremely rare in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial
¹⁰⁸ mammalian predator guild is therefore depauperate, with foxes and cats being the primary mammalian
¹⁰⁹ terrestrial predators heavier than one kilogram; birds of prey and snakes are the only other medium-large
¹¹⁰ carnivores present.

¹¹¹ Our study landscapes in the Glenelg region were primarily lowland forest and heathy woodland. The
¹¹² area receives an average annual rainfall of 700 mm (Bureau of Meteorology 2021, Cashmore Airport) and
¹¹³ has gently undulating terrain. The region frequently experiences prescribed burns and wildfires, creating a
¹¹⁴ mosaic of fire histories and vegetation complexity. Our study landscapes in the Otway region were in the
¹¹⁵ western section of the Otway Ranges. Rainfall here is more than twice as high as the Glenelg region (Bureau
¹¹⁶ of Meteorology 2021, Cape Otway). The vegetation is a mosaic of shrubby wet forest and cool temperate
¹¹⁷ rainforest, with the northern landscape bordering on a large heathy woodland. This region rarely experiences
¹¹⁸ fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness index,
¹¹⁹ Riley, DeGloria, & Elliot 1999).

¹²⁰ Government land managers conduct ongoing targeted fox control for biodiversity conservation across
¹²¹ broad landscapes within each region (detailed in Section 2.2 below). In these landscapes, manufactured
¹²² poison baits ('FoxOff', Animal Control Technologies, Somerton) containing 3 mg of sodium fluoroacetate
¹²³ (compound 1080) are buried at a depth of 12 - 15 cm at 1-km intervals along accessible forest tracks and
¹²⁴ roads (Fig. 1). Different road densities across the two regions result in variable poison bait densities. Other
¹²⁵ large sections within each region are maintained without fox control.

¹²⁶ 2.2. Study design and camera-trapping

¹²⁷ We designed experiments around the implementation of fox-baiting in each region. We simultaneously
¹²⁸ surveyed one impact and one non-impact landscape at a time. Each pair of impact and non-impact landscapes
¹²⁹ were chosen based on similarity in vegetation groups, while aiming to maximise spatial independence with
¹³⁰ respect to predator daily movements.

¹³¹ In the Glenelg region, we used a spatially replicated Control-Impact design to compare three impact
¹³² landscapes that had been poison baited for foxes at fortnightly intervals for more than 13 years with three
¹³³ paired non-impact landscapes. The pairing of these landscapes was based on similarities in vegetation
¹³⁴ classes, and specified in the original design of the Glenelg Ark monitoring program (Robley *et al.* 2014). We
¹³⁵ surveyed Cobboboonee National Park (impact) and Annya State Forest (non-impact) in January – April
¹³⁶ 2018 ('replicate 1'), Mt Clay State Forest / Narrawong Flora Reserve (hereafter 'Mt Clay'; impact) and
¹³⁷ Hotspur State Forest (non-impact) in April – June 2018 ('replicate 2'), and Lower Glenelg National Park
¹³⁸ (LGNP) South (impact) and LGNP North (non-impact) in March – May 2021 ('replicate 3'). For replicates 1
¹³⁹ and 2, the paired landscapes were separated by at least 8 km, a distance unlikely to be frequently traversed
¹⁴⁰ regularly by these invasive predators (Hradsky *et al.* 2017). Lower Glenelg National Park South and North
¹⁴¹ are separated by the Glenelg River, which is unlikely to be regularly crossed by most terrestrial animals.

¹⁴² In the Otway region, we used a Before-After Control-Impact Paired-Series (BACIPS) design to assess
¹⁴³ changes related to the introduction of a fox control program. We deployed camera-trap grids in a pair of
¹⁴⁴ impact – non-impact landscapes from June to September in three years (2017, 2018, 2019), in the Great
¹⁴⁵ Otway National Park and Otway Forest Park. Our first survey occurred approximately three months before
¹⁴⁶ fox-baiting began. Fox-baiting commenced for the first time in the impact landscape in November 2017.
¹⁴⁷ Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait
¹⁴⁸ replacement until July 2018. The second survey was conducted six months after fox-baiting commenced,
¹⁴⁹ however poison bait replacement ceased from near the beginning of the survey until nearly three months
¹⁵⁰ afterwards. Fox-baiting at monthly intervals recommenced in December 2018, six months prior to the start
¹⁵¹ of the final survey (Fig. S1). The impact (southern) and non-impact (northern) landscapes were at least
¹⁵² 4.2 km apart through dense forest. In this study, and a concurrent study which identified individual foxes
¹⁵³ through genetic sampling (Le Pla *et al.* 2022), we found no evidence that either foxes or cats moved between
¹⁵⁴ the impact and non-impact landscapes.

155 In each landscape, we established a grid of 49 – 110 sites (mean: 88). We aimed to space camera-traps
156 500 m apart, but distances ranged from 194 – 770 m (mean spacing: 448 m) due to accessibility and logistical
157 constraints. We situated each site in the forest interior, at least 30 m from roads and tracks. At each site, we
158 set up a Reconyx (Holmen, Wisconsin) infrared camera-trap on a tree, facing a tuna oil lure; see Appendix C
159 section S1.1 for details. Overall, we deployed 1,051 functional camera-traps, which operated for an average of
160 65 days (ranging 12 – 93 days), totalling 68,504 trap nights (Table 1).

161 *2.3. Individual feral cat identification*

162 We sorted the camera-trap images of cats into five categories based on coat type (Fig. S3), and identified
163 individual feral cats within each category; see Appendix C section S1.2 for details. In the Otway region, 40%
164 of cat detections were of black cats with few identifiable markings, so we did not attempt to identify any
165 black cats here. In the Glenelg region, black cats were rarer (not detected at two landscapes) and often more
166 distinctive, and so we could identify some individuals (Table 1).

167 *2.4. Fox spatial occurrence*

168 To (i) investigate effects of poison-baiting on foxes, (ii) test for negative correlations between foxes and
169 cat density (prediction 2) and (iii) account for potential effects of foxes on cat detectability, we modelled
170 fine-scale and spatially-explicit fox occurrence probabilities. We used fox occurrence probability as a simple
171 metric of fox populations in lieu of simultaneous, reliable fox density estimates. Foxes are not individually
172 identifiable from camera-trap images (Güthlin, Storch, & Küchenhoff 2014) and, while density estimates can
173 be derived from unmarked populations, their reliability remains questionable (Barker *et al.* 2018; Sun *et
al.* 2022). We modelled fox occurrence probabilities (from presence-absence records) rather than detection
174 counts as we considered this more conservative: a greater change in fox density is likely required to alter
175 occurrence. In some circumstances, predator occurrence probability scales with population density (e.g.,
176 Linden *et al.* 2017), although we acknowledge this remains unknown in our study.

178 We could not use raw fox presence-absence data from the camera-traps as a response variable for cat
179 density as spatial mark-resight models require covariate values for each grid cell in which density is estimated
180 (see Section 2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for
181 each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised

182 additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but do
183 not account for imperfect detection. Nonetheless, naïve fox occurrence probabilities may relate to how cats
184 perceive the risk of fox encounter for the survey duration.

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

191 *2.5. Spatial mark-resight models of feral cat density*

192 We used a spatial capture-recapture approach to estimate cat density (Gardner, Royle, & Wegan 2009).
193 These models use counts of detections and non-detections of individual animals at trap locations (accounting
194 for trap-specific survey effort) to estimate the location of each individual’s activity centre. They commonly
195 assume that individuals have approximately circular home ranges, spend the majority of time in the centre
196 of their range (‘activity centre’), and that the probability of observing an individual decreases with distance
197 from the activity centre. Two detectability parameters govern this process: g_0 , the probability of detecting
198 an individual per occasion in their activity centre, and sigma: a spatial scale parameter which relates to
199 home range size. Multiple candidate shapes for the decline in detectability with distance from the activity
200 centre (‘detection function’) can be modelled, although half-normal and exponential are most commonly
201 used. Spatial capture-recapture models have been extended to consider situations where not all individuals
202 in a population are identifiable (i.e., some are unmarked, Efford & Hunter 2018). These models typically
203 assume unmarked individuals to be a random sample of the population, sharing the same detection process
204 as marked individuals, allowing density to be estimated for the entire population.

205 We used sighting-only spatial mark-resight models to estimate cat density using the maximum likelihood
206 ‘secr’ R-package (Efford 2021). We used closed population models as open population spatial mark-resight
207 models have not yet been developed. Detections of the ‘mark status uncertain’ category (unidentifiable
208 cats), cannot be handled in the ‘secr’ R package; we added them to as ‘unmarked’ detections (black cats)
209 rather than discard them (following Moseby, McGregor, & Read 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 (1) chose between half-normal and exponential detection functions and (2) chose 'base model' covariates to carry through to subsequent model sets. We then (3) evaluated the effect of fox control on cat density at the landscape scale with traditional experimental approaches (prediction 1), and (4) tested for associations between fox occurrence probabilities and cat density at a fine spatial scale (prediction 2). To choose between competing model specifications, we used small-sample corrected Akaike Information Criterion (hereafter 'AIC_c') scores (Burnham & Anderson 2004); carrying forward or presenting the top-ranked model (i.e., model with the lowest AIC_c score). In addition to examining confidence intervals around estimated model coefficients, we also used AIC_c scores to assess statistical evidence; models within two AIC_c units are generally considered equivalent in terms of predictive power (Burnham & Anderson 2004). Steps two to four are described in more detail below.

The second set of models (base 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 nonlinear trend in g_0 over the survey duration for each camera-trap. We also used a range of camera-trap models which may impact detection rates (Table S1). We tested whether camera-trap model impacted cat detection rates in the Otways, but not the Glenelg region as 97% of cameras here were the HC600 model (3% were the PC900 model which primarily differ only in software settings, Seidlitz *et al.* 2020), using camera-trap model as a categorical variable ($n = 5$) on g_0 . 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 S1.5 for details. We compared these covariates as single and additive models, as well as to a 'null model' (density and detectability constant), and carried the supported covariates forward to subsequent model sets.

239 The third set of models inferred the effects of fox-baiting on cat density at a landscape scale within each
240 region using traditional experimental designs (prediction 1). We fit models which estimated cat density
241 separately for each landscape, and used AIC_c scores to choose whether to model detectability as a function of
242 predicted fox occurrence probability or constant. For the top-ranked model, we then calculated the estimated
243 difference in cat density between paired landscape surveys. We assessed the weight of statistical evidence
244 using associated confidence intervals and a p-value threshold of 0.05. In CI experiments (Glenelg region), a
245 p-value below 0.05 is achieved when the 95% confidence interval of the estimated difference does not cross
246 zero (on the natural logarithmic scale). We repeated this analysis three times in the Glenelg region, once
247 for each spatially replicated landscape pair. In BACI experiments (Otway region), changes in successive
248 estimates of difference provide inference of an effect; a p-value below 0.05 is reached once 83% confidence
249 intervals do not overlap each other (Goldstein & Healy 1995).

250 The fourth set of models directly tested the associations between fine-scale fox occurrence and cats
251 within each region (prediction 2). We tested three models where (i) fox occurrence probability affected cat
252 density, (ii) fox occurrence probability affected cat detectability (both g_0 and sigma concurrently, Efford &
253 Mowat 2014), (iii) fox occurrence probability affected both the density and the detectability of cats, against
254 the null model with no association between fox occurrence and cats. We used the spatial fox occurrence
255 probability estimates (detailed in Section 2.4) as the explanatory variable. As predator associations may be
256 nonlinear (Johnson & VanDerWal 2009), we tested these effects as linear and nonlinear terms using regression
257 splines (generalised additive models called within the ‘secr’ R-package). We included year as a cat density
258 covariate in all the Otway region models to account for repeat sampling. A limitation of this approach is
259 that uncertainty from fox occurrence probability models was not propagated into the spatial mark-resight
260 models - a full Bayesian integration of the fox occurrence analysis and the spatial mark-resight model to
261 address this is not yet implemented.

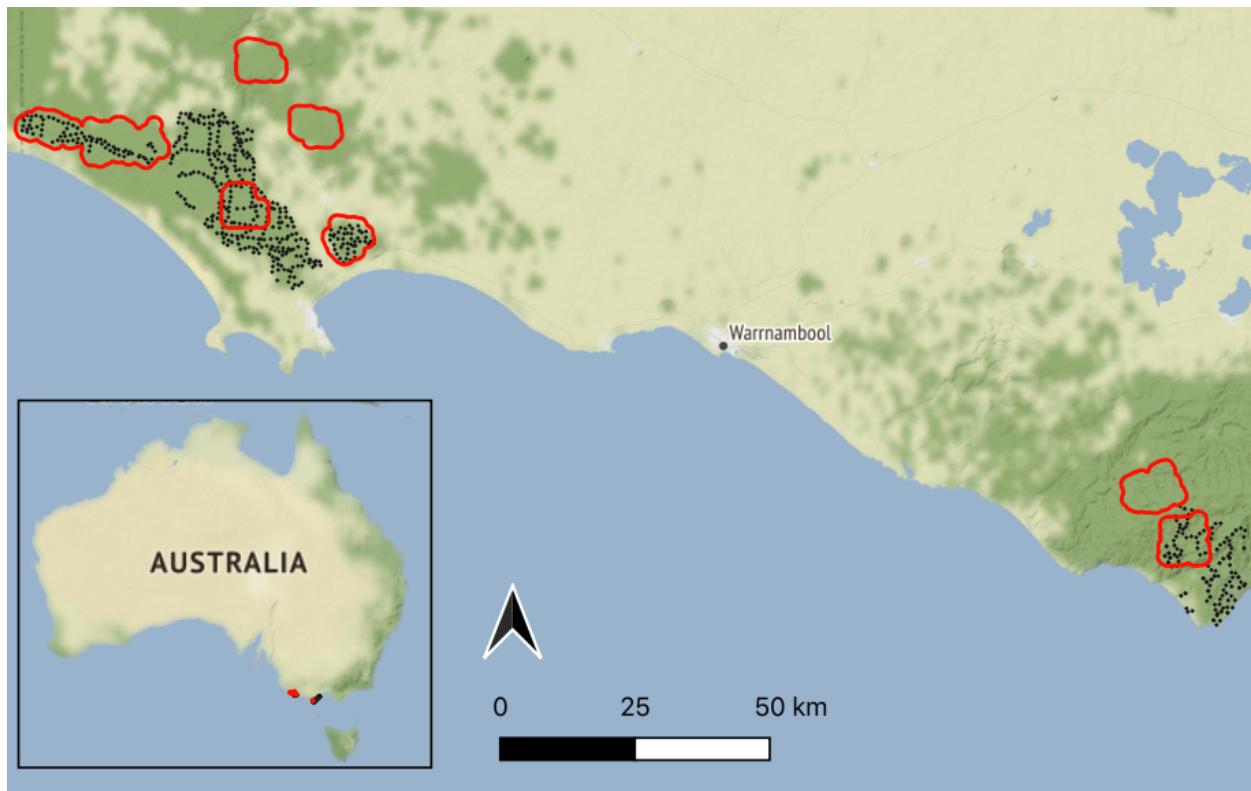


Figure 1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river (which the poison-baits closely follow along the southern bank). Locations of fox poison 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.*

262 **3. RESULTS**

263 *3.1. Glenelg region*

264 *3.1.1. Red Fox*

265 In the Glenelg region, foxes were detected at 48 – 57% of sites (i.e., naïve occupancy) within the three
266 non-impact (unbaited) landscapes (Table 1). Naïve occupancy rates were more than two and three times
267 lower in the paired impact (poison baited) landscape for replicates 1 and 3, respectively, but only 27% lower
268 in replicate 2 (Table 1). The fox spatial occurrence probability model explained 13.1% of the null deviance,
269 with an adjusted R-squared value of 0.13 (spatial standard error estimates are presented in Appendix S1.4).
270 The fox occurrence model highlighted fine-scale variation in fox occurrence probabilities within landscapes
271 (for example, fox occurrence probability was low in the centre of Mt Clay, but higher closer to the forest edge)
272 and demonstrated a strong effect of the Glenelg River in separating fox populations in the Lower Glenelg
273 National Park landscapes (Fig. 2).

274 *3.1.2. Feral cat*

275 Across the six landscapes in the Glenelg region, we recorded 251 cat detections from 32,232 camera-trap
276 nights (Table 1). We were able to identify 64% of cat detections to the individual-level; a total of 67 cats
277 (6 – 13 individuals per landscape). The exponential detector function was supported over the half-normal
278 function (Table S2). The null model was more strongly supported than models with vegetation impacts on
279 cat density and/or linear time trends on g_0 (Table S3).

280 Our prediction (1) that cat density would be higher in landscapes with fox control was supported for
281 the first and third spatial replicates: estimated cat densities were 2.5 (95% CI: 1.5 - 4.2) and 3.7 (95% CI:
282 1.4 - 9.5) times higher in the impact landscape than the paired non-impact landscape, respectively (Fig. 3).
283 There was no difference in cat density between landscape pairs in the second spatial replicate (1.1; 95% CI:
284 0.69 - 1.69; Fig. 3); this pair also had the smallest difference in naïve fox occupancy occurrence rates (Table
285 1). At the landscape-level, there was little evidence that cat detectability was associated with fox occurrence;
286 although this model ranked more highly than the constant detectability model (Table S4), the difference in
287 AICc scores was only 0.95 units and the estimated effects were weak with high uncertainty, i.e., detectability
288 (g_0): 0.24 (95% CI: -0.32 - 0.80); movement (σ): 0.13 (95% CI: -0.14 - 0.41).

289 Our prediction (2) that cat density would be negatively correlated with fox occurrence probability at a
290 fine spatial scale was supported (4.26 AIC_c units better than the null; Table S5). The top-ranked model
291 indicated that cat density declined as the probability of fox occurrence increased (-0.32; 95% CI: -0.57 -
292 -0.07; Fig. 5), and that there was no association between fox occurrence and cat detectability (Table S5).
293 Nonlinear regression splines added additional model parameters without changing predictions (Fig. 5); all
294 nonlinear models ranked below their linear counterparts (Table S5).

295 *3.2. Otway region*

296 *3.2.1. Red fox*

297 In the Otway region, the probability of fox occurrence declined by 43% over three years in the impact
298 landscape, and increased by 22% in the non-impact landscape (where they were not lethally controlled) over
299 the same period (averaged at each camera-trap site in the landscape; Fig. 2b). Fox occurrence probability in
300 the Otway region was generally lower than the Glenelg region and had less fine-scale spatial variation. For
301 example, fox occurrence was predicted to be spatially consistent across the entire Otway region in 2018 (i.e.,
302 fox occurrence probability was the same in both the impact and non-impact landscape, Fig. 2; as were naïve
303 occupancy rates, Table 1). The fox spatial occurrence model explained 27.8% of the null deviance, with an
304 adjusted R-squared value of 0.24 (spatial standard error estimates are presented in Appendix S1.4).

305 *3.2.2. Feral cat*

306 In the Otway region, we recorded 970 cat detections from 36,272 camera-trap nights (Table 1). We
307 were able to identify 53% of cat detections to the individual-level; a total of 93 cats (20 – 30 individuals
308 per landscape survey session, with some individual detected in multiple years). The exponential detector
309 function was strongly supported over the half-normal function (Table S7). The null model was more strongly
310 supported than the models with vegetation impacts on cat density, or camera-trap model or linear time
311 trends on g_0 (Table S8).

312 Our prediction (1) that fox control would be associated with higher cat densities was supported in 2019
313 (~1.5 years after fox baiting commenced), but not 2018 (six months after fox-baiting commenced, and during
314 a break in the baiting program). Within each year, there was no statistical evidence that cat densities

315 differed between the impact and non-impact landscapes (95% confidence intervals overlapped zero; Fig.
316 4a). However, a consistent upward trend in cat density in the impact landscape over three years and a
317 simultaneous downward trend in the non-impact landscape (Fig. 4a), meant that there was a significant
318 increase in cat density in the impact landscape 1.5 years after fox-baiting commenced, relative to changes in
319 the non-impact landscape (i.e., 83% CIs for the estimated difference for 2017 and 2019 do not overlap; (Fig.
320 4b). There was strong evidence that cat detectability was associated with fox occurrence probability (Table
321 S9), detailed below.

322 Our prediction (2) that cat density would be negatively correlated with fox occurrence probability at a
323 fine spatial scale had weak support. The top-ranked model included a negative linear association between
324 cat density and fox occurrence, supporting our prediction. However, statistical evidence was weak: this
325 model had similar predictive performance to a model without the association between cat density and fox
326 occurrence probability ($dAIC_c = 0.80$; Table S10). In addition, the 95% confidence interval around the linear
327 coefficient from the top-ranked model marginally overlapped zero (-0.26; 95% CI: -0.55 - 0.02). The nonlinear
328 version of this model also marginally ranked above the null model ($dAIC_c = 0.47$; Table S10). This nonlinear
329 model predicted that cat density only declined (at a steeper rate) in the mid-high range of fox occurrence
330 probability (greater than ~0.25 on the response scale; Fig. 5).

331 There was strong support for an effect of fox occurrence probability on cat detectability at a fine spatial
332 scale (Fig. 6; Table S9). Where fox occurrence probability was higher, cats were less detectable in their
333 activity centres (i.e., negative association with g_0 ; -0.69; 95% CI: -1.11 - -0.27; Fig. 6a) and ranged further
334 (i.e., positive association with sigma; coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 6b). The equivalent nonlinear
335 model predicted that detectability changes occurred only in the low-mid range of fox occurrence probabilities
336 (less than ~0.25 on the response scale; Fig. 6).

Table 1: Summary of experimental camera-trap surveys and invasive predator detections in the Glenelg and Otway regions, Australia.

Region	Landscape	Replicate	Treatment	Start date	End date	Camera-traps	Trap-nights	Red fox		Feral cats (max. 1 detection per 24-hr)				Total detections
								Naïve occupancy	Individuals	Moves	Prop. unidentified	Prop. unmarked		
Glenelg	Cobboboonee	1	impact	2018-02-13	2018-04-29	110	7752	0.26	13	19	0.11	0.46	81	
	Annya	1	non-impact	2018-01-26	2018-04-13	110	8000	0.55	9	11	0.07	0.43	46	
	Mt Clay	2	impact	2018-04-30	2018-06-27	106	5451	0.35	10	16	0.13	0.00	38	
	Hotspur	2	non-impact	2018-04-16	2018-06-21	99	6085	0.48	8	12	0.08	0.34	38	
	LGNP South	3	impact	2021-03-25	2021-05-12	64	2842	0.17	21	4	0.00	0.00	37	
	LGNP North	3	non-impact	2021-03-30	2021-05-14	49	2102	0.57	6	3	0.00	0.00	11	
	Otways	South	1	impact	2017-06-23	2017-08-30	73	4543	0.36	20	18	0.04	0.42	114
Otways	North	1	non-impact	2017-07-05	2017-09-02	67	3565	0.13	26	12	0.07	0.40	114	
	South	2	impact	2018-06-28	2018-09-13	85	6077	0.27	24	37	0.11	0.39	151	
	North	2	non-impact	2018-07-09	2018-09-21	103	7099	0.27	30	32	0.07	0.38	164	
	South	3	impact	2019-06-07	2019-09-17	86	7150	0.17	25	69	0.11	0.27	214	
	North	3	non-impact	2019-06-13	2019-09-15	99	7838	0.43	27	39	0.10	0.47	213	

Note:

Naïve occupancy - proportion of camera-trap sites which detected foxes

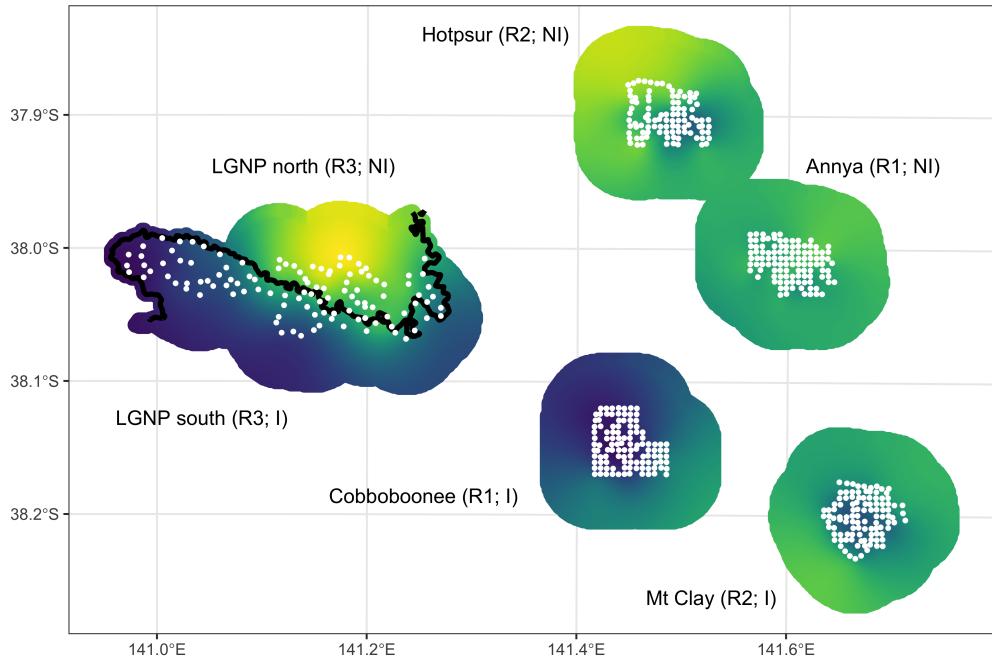
Individuals - Number of identified feral cat individuals

Moves - successive recaptures of individuals at different sites

Prop. unidentified - proportion of feral cat detections in the 'marked' spatial mark-resight category which could not be identified to the individual-level

Prop. unmarked - proportion of feral cat detections in the 'unmarked' spatial mark-resight category

(a) Glenelg region



(b) Otway region

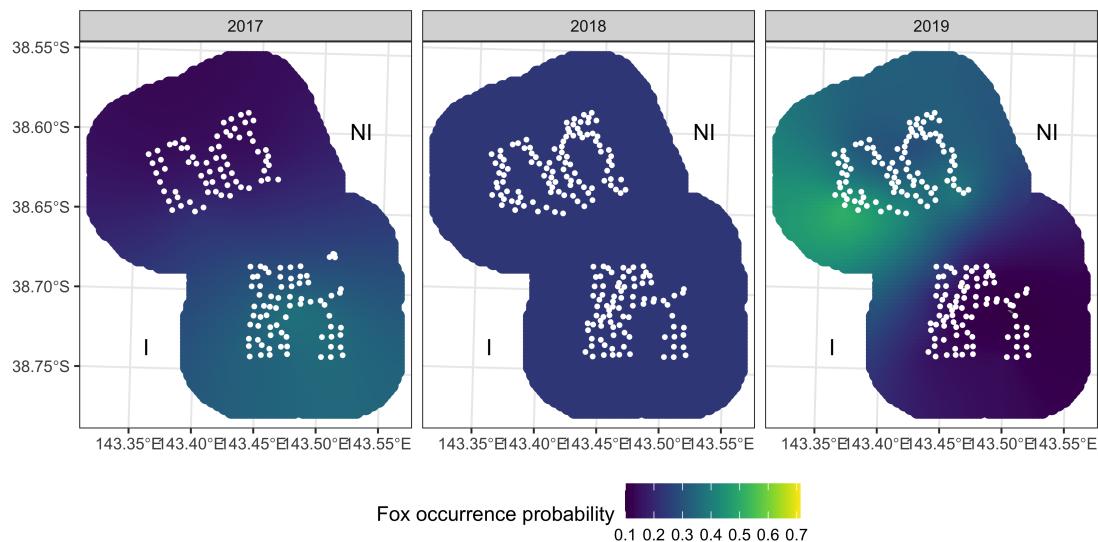


Figure 2: Predicted red fox *Vulpes vulpes* occurrence probabilities derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. White dots represent camera-trap sites. The black line (a) represents the Glenelg River which separates the impact (south) and non-impact (north) landscape pair in the Lower Glenelg National Park.

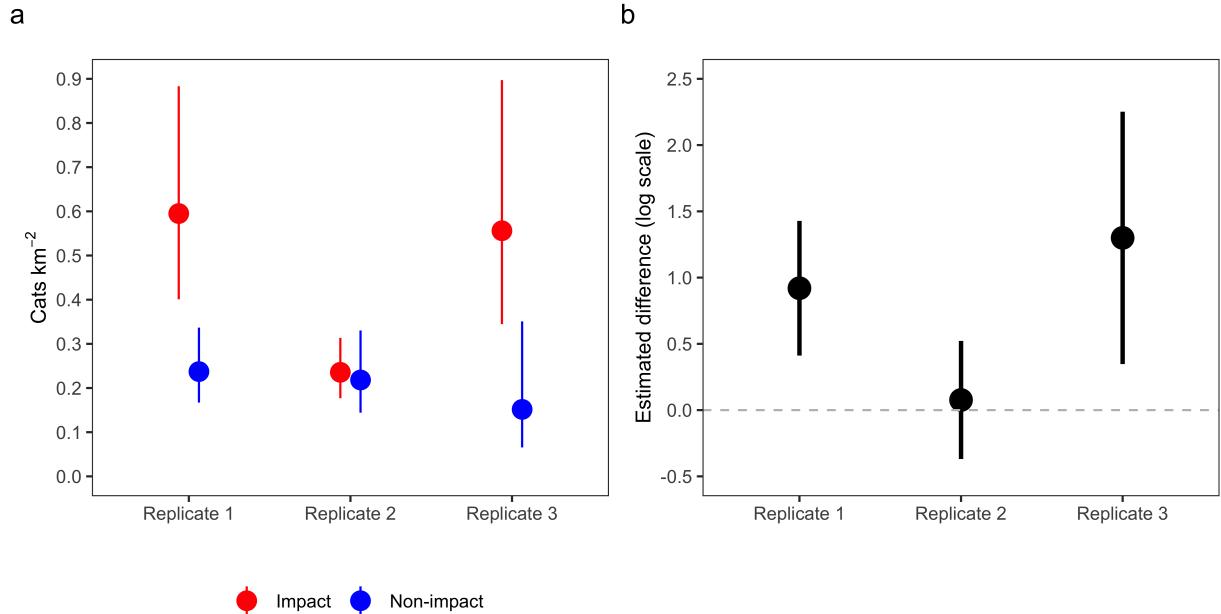


Figure 3: Feral cat *Felis catus* density in response to long-term fox control in the Glenelg region, Australia (replicated Control-Impact analysis). Poison baiting for foxes *Vulpes vulpes* had been conducted continuously in the impact landscapes for more than 13 years for the first two replicates, and 16 years for the third replicate. (a) Cat density estimates with 95% confidence intervals for each landscape derived from spatial mark-resight models. (b) Estimates of difference in cat density (impact landscape relative to the paired non-impact landscape) for each replicate. Error bars show 95% confidence intervals. In (b), confidence intervals that do not overlap 0 (grey dashed line) indicate that that cat density was higher in the impact landscape than the associated non-impact landscape ($p < 0.05$).

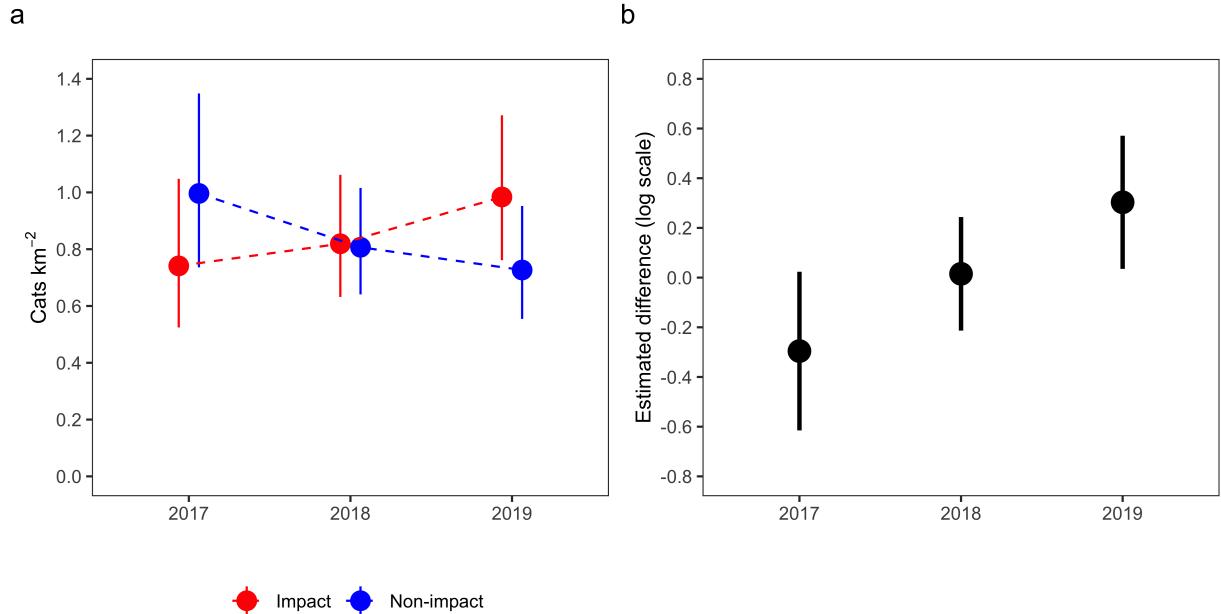


Figure 4: Feral cat *Felis catus* density in response to fox control in the Otway Ranges, Australia (Before-After Control-Impact Paired-Series analysis). The 2017 surveys were conducted approximately two months before lethal red fox *Vulpes vulpes* control began in the impact landscape. Baiting ceased July - November 2018 before resuming approximately five months prior to the 2019 survey. (a) Cat density estimates with 95% confidence intervals for each survey, derived from spatial mark-resight models. (b) Estimates of the difference (on the natural logarithmic scale) between landscape pairs in each survey year (impact landscape relative to the non-impact landscape) with 83% confidence intervals. In (b), confidence intervals that do not overlap each other (visualised horizontally) indicates evidence for a change in cat density at the impact landscape relative to change at the non-impact landscape ($p < 0.05$).

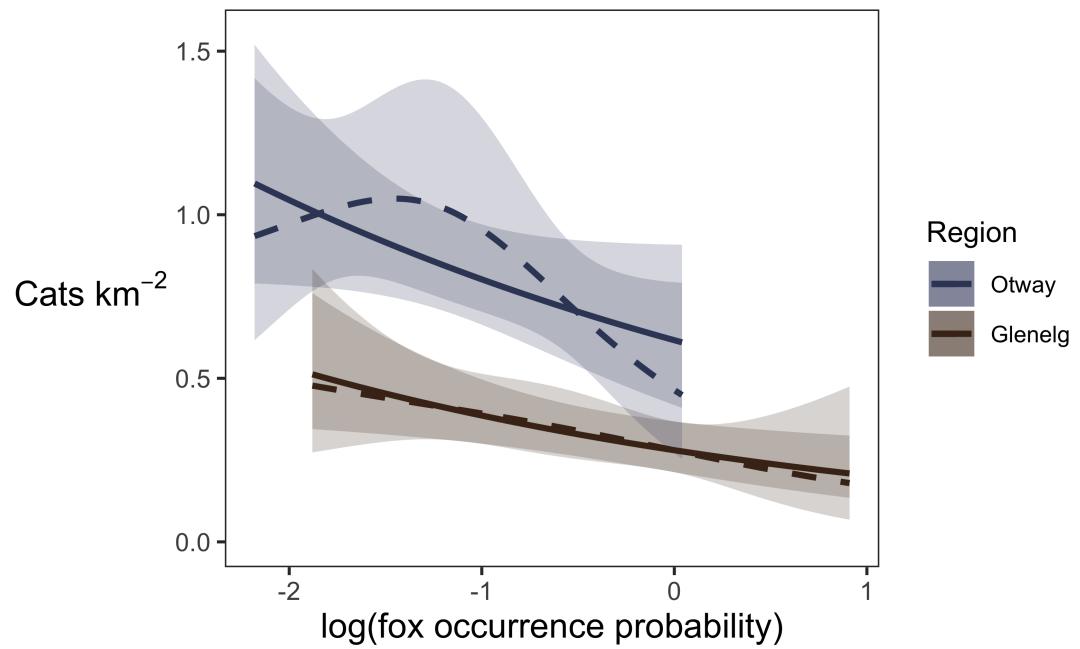


Figure 5: Feral cat *Felis catus* density in relation to the probability of red fox *Vulpes vulpes* occurrence, Glenelg and Otway regions, Australia. Lines show estimates from top-ranked linear (solid) and nonlinear (dashed) models, shaded areas indicate 95% confidence intervals

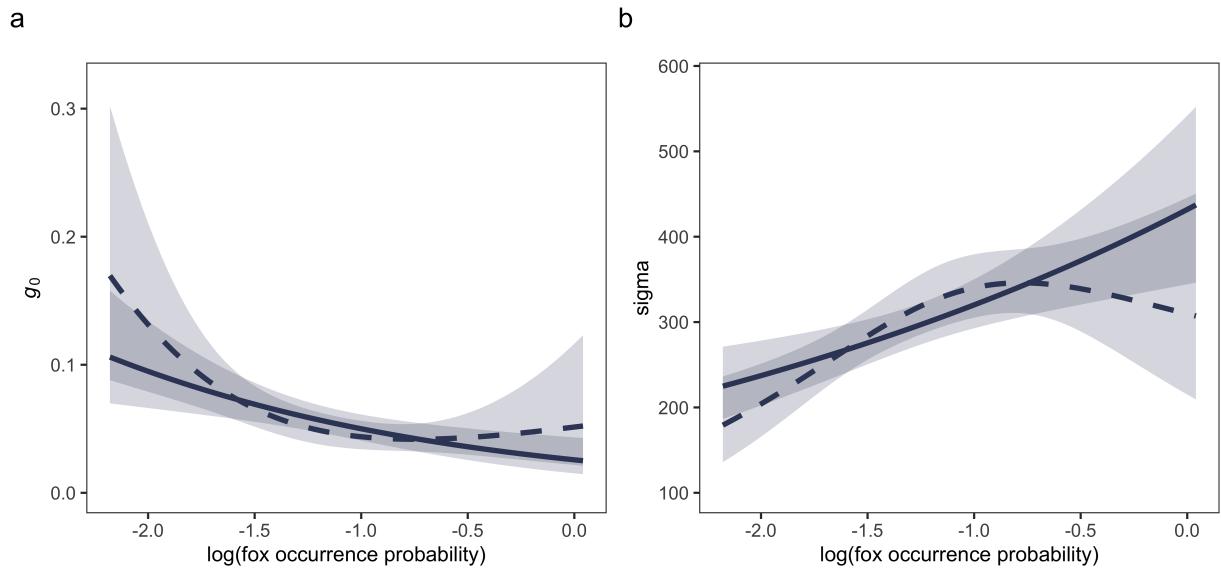


Figure 6: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-scaled red fox *Vulpes vulpes* occurrence probability in the Otway region, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0) 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.

³³⁷ **4. DISCUSSION**

³³⁸ Our study is one of the first to provide replicated, experimental evidence that dominant predator
³³⁹ suppression is associated with higher mesopredator densities. We provide two lines of evidence that foxes
³⁴⁰ can exert top-down control on feral cats in the forests of south-eastern Australia: feral cat density was (1)
³⁴¹ commonly higher in landscapes where fox control occurred, and (2) higher where fine-scale fox occurrence
³⁴² probability was lowest, although this association was only weakly supported in the Otway region. Targeted
³⁴³ fox control is a widely used conservation strategy in Australia, and so unintended mesopredator release of
³⁴⁴ feral cats is concerning, as it is likely to increase impacts on some native prey (e.g., Marlow *et al.* 2015).
³⁴⁵ More broadly, our study illustrates how experimental (landscape-scale) and correlative (fine-scale) approaches
³⁴⁶ provide complementary lines of evidence when investigating interactions between predator species, and
³⁴⁷ highlights the importance of disentangling changes in mesopredator density from changes in detectability.

³⁴⁸ In the Glenelg region where fox-baiting had occurred for more than 13 years, feral cat density was
³⁴⁹ considerably higher in two out of three baited landscapes than their unbaited pairs. The lack of difference
³⁵⁰ for Pair 2 was likely due to limited suppression of foxes at Mt Clay despite ongoing fox control (Fig. 2a). Mt
³⁵¹ Clay is a small forest block surrounded entirely by unbaited farmland; simulation modelling indicates that
³⁵² the size of the baited area is a key driver of the degree of reduction in the fox population (Francis, Robley, &
³⁵³ Hradsky 2020), including at Mt Clay (Hradsky *et al.* 2019). There was also strong support for a negative
³⁵⁴ association between cat density and fox occurrence probability at a fine spatial scale in this region, consistent
³⁵⁵ with the mesopredator release hypothesis. Studies of fox-cat (and other intraguild predator) interactions
³⁵⁶ often use the presence of a management program as a proxy for dominant predator suppression (e.g., Hunter
³⁵⁷ *et al.* 2018). Our findings indicate the need to directly measure the dominant predator population in order
³⁵⁸ to reliably interpret the responses of subordinate species (Salo *et al.* 2010).

³⁵⁹ In the Otway region, cat density had increased significantly in the impact landscape two years after baiting
³⁶⁰ commenced, relative to changes in the non-impact landscape. However, this increase was relatively small
³⁶¹ compared to differences between cat densities in impact and non-impact landscapes in Glenelg. Evidence
³⁶² for a fine-scale negative association with fox occurrence was also much weaker. There are two possible
³⁶³ explanations for this. Firstly, changes in fox and adult cat density may not have fully manifested yet. Fox
³⁶⁴ occurrence rates in the impact landscape continued to decline over our three years of surveys. We found
³⁶⁵ some evidence for a sequential response: a reduction in foxes occurrence probability may relax cat behaviour,

366 potentially improving hunting success, leading to higher recruitment rates, subsequently higher cat densities.
367 Also, younger cats are more vulnerable to fox predation than adult cats (Sogliani & Mori 2019), and so
368 foxes may have a greater impact on recruitment rates than the adult population, leading to a delayed effect
369 on density. Further, cats may respond to an increase in shared prey availability following fox suppression
370 (Stobo-Wilson *et al.* 2020). A time-lagged release of cats following fox control would explain eruptions and
371 subsequent crashes commonly observed in shared mammalian prey populations two to ten years following fox
372 control commencement (Duncan *et al.* 2020).

373 Secondly, foxes may have a weaker suppressive effect on cats in the highly productive Otway region than
374 the dry forests of Glenelg. Fox occurrence was already relatively low prior to fox control in the Otways
375 compared to Glenelg (Fig. 2). Additionally, competition theory predicts competitive interactions to be
376 weaker with high prey availability: there may be less imperative for foxes to be aggressive towards or prey
377 upon cats when there is enough food to share (Johnson & VanDerWal 2009; Greenville *et al.* 2014; Sogliani
378 & Mori 2019). Conversely, foxes may have a higher capacity to maintain vigilance against cats when they are
379 not food stressed, and top-down control from dominant predators could be the primary limiting factor for
380 feral cats (a generalist mesopredator) in resource-rich environments (Oksanen & Oksanen 2000; Feit, Feit,
381 & Letnic 2019). Prey availability is likely a strong mediator of mesopredator release, although it remains
382 unclear whether mesopredator release would be stronger where prey availability is low or high—severely
383 limiting our ability to predict mesopredator release across different landscapes.

384 Because subordinate predators may only be suppressed when dominant predator abundance is high, there
385 is contention around whether linear regression is appropriate for investigating correlations between different
386 predator species (Johnson & VanDerWal 2009; Letnic *et al.* 2011). We found no evidence of nonlinear
387 associations between foxes and cats in the Glenelg region, while linear and nonlinear models performed
388 equally well in the Otway region. Nonlinear models in the Otway region predicted that cat density declined
389 only in the mid-high range of fox occurrence (Fig. 5), while behavioural changes were seen in the low-mid
390 range of fox occurrence probability (Fig. 6). Perhaps cats can successfully avoid foxes through behavioural
391 change where foxes are rare, but this is ineffective where foxes are common. This could explain the lack
392 of evidence for foxes impacting cat detectability in the Glenelg region where fox occupancy was relatively
393 high. Alternatively, behavioural changes may be untenable for cats in the Glenelg region because small
394 mammal abundance is relatively low (M.Rees, unpublished data) and fox avoidance strategies likely come at
395 the expense of hunting success (Sih 1980; Wilson *et al.* 2010). Negative spatial associations between species

396 may simply reflect differences in niche preference rather than exclusion or avoidance, although is less likely in
397 our case given we observed the relationship across an artificial gradient of fox occurrence probability caused
398 by lethal control.

399 In the Otway region, we observed seemingly opposing trends in fox occurrence probabilities and cat
400 densities in the impact and non-impact landscapes over time (Fig. 2b; Fig. 4). We are unsure what drove
401 the increase in fox occurrence probability in the non-impact landscape and whether it was related to fox
402 control in the nearby impact landscape. The effects observed in our BACIPS study may therefore only partly
403 be due to mesopredator release in the strict sense (i.e., due to fox suppression in the impact landscape),
404 although may demonstrate reciprocity in responses of cats to both increases and declines in foxes, which
405 is rarely observed (Alston *et al.* 2019). Perhaps changes in the non-impact landscape were due to changes
406 in prey availability, however we do not expect large fluctuations in prey here given the low seasonality and
407 consistent climatic conditions relative to other parts of the country.

408 Where fox occurrence probabilities were higher at a fine spatial scale in the Otway Ranges, cats were
409 less detectable in their activity centres and ranged further (Fig. 6). Low detectability is likely to correlate
410 with fewer dominant predator encounters, and has been observed in other predator interaction studies (e.g.,
411 Lombardi *et al.* 2017). An increase in cat ranging behaviour (sigma) with fox control supports observations
412 made by Molsher *et al.* (2017) using telemetry, and may reflect a direct avoidance strategy. Animal movement
413 rates are expected to increase in response to unpredictable threats (Riotte-Lambert & Matthiopoulos 2020).
414 Alternatively, cats may consider foxes predictable and avoid locations they frequent, thus having to range
415 further to obtain the same amount of food. In a similar forest habitat, Buckmaster (2012) observed large
416 ‘holes’ in the home range of each GPS-collared cat; they confirmed that this was not due to an absence
417 of prey and hypothesised it was due to dominant predator avoidance. In contrast, cats in another similar
418 forest habitat without foxes or dingoes have compact home ranges within which intensity of use is reasonably
419 uniformly spread, (Hamer *et al.* 2021), suggesting this to be an optimal strategy for cats. Regardless of the
420 cause, changes in mesopredator detectability and movement rates when dominant predators are suppressed
421 have serious implications for the interpretation of studies that simply compare relative activity, occurrence or
422 spatial overlap indices of predator species (Efford & Dawson 2012; Broadley *et al.* 2019).

423 Our findings may explain why pest management that only targets foxes—one of the most prevalent
424 conservation actions in Australia—does not consistently improve native prey persistence (Dexter & Murray

425 2009; Robley *et al.* 2014; Wayne *et al.* 2017; Lindenmayer *et al.* 2018; Duncan *et al.* 2020). More evidence is
426 required to understand the circumstances in which lethal fox control increases cat density, particularly the
427 role of baseline fox and prey densities. A more integrated approach to invasive predator management, where
428 foxes and cats are simultaneously or otherwise optimally controlled could substantially improve biodiversity
429 outcomes (Risbey *et al.* 2000; Comer *et al.* 2020). If this is not feasible, changes in invasive mesopredator
430 density and native prey populations should be closely monitored as part of invasive predator control programs,
431 with triggers for ceasing dominant predator control or commencing integrated management if single-species
432 control proves counter-productive for threatened native prey.

433 This study is among very few which have used a direct measure of density to test mesopredator release.
434 Previous studies have mostly used live capture-rates to infer population density, without accounting for
435 behavioural or detectability changes (e.g., Arjo *et al.* 2007; Karki, Gese, & Klavetter 2007; Thompson &
436 Gese 2007; Berger, Gese, & Berger 2008; Jones, Van Vuren, & Crooks 2008). Contention about mesopredator
437 release has centred on such methods (Hayward *et al.* 2015), as well as unaccounted species interactions
438 in complex predator guilds (Levi & Wilmers 2012; Jachowski *et al.* 2020). In contrast, our study tests
439 the mesopredator release theory using a combined behavioural and numerical approach, in a system with
440 a simplified carnivore guild. Further replication of our approach in new landscapes, as well as explicitly
441 accounting for dominant predator density, prey availability and landscape productivity is a priority for
442 improving understanding of mesopredator release.

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668 **SUPPORTING INFORMATION**

669 *S1.1. Field surveys*

670 In the Glenelg region, we deployed camera-traps once at each site. In the Otway region, we redeployed
671 camera-traps annually for three years. For the Otway region, all 2017 camera-sites were resurveyed each
672 year, except for four logically challenging sites in the southern grid. In 2018, we also added 16 sites in the
673 southern grid, and 36 sites in the northern grid. All 2018 sites were resurveyed in 2019.

674 At each site, we deployed a single Reconyx (Holmen, Wisconsin) branded camera-trap with passive
675 infrared sensor that detects a thermal differential between the subject and the background temperature. The
676 majority of camera-traps were Reconyx Hyperfire HC600 (97% in the Glenelg region; 78% in the Otway
677 Ranges). In the Glenelg region, PC900's were deployed at the remainder of sites (3%). In the Otway Ranges,
678 PC900, PC800, HC500 and HF2X models were also used (Table S1). We programmed cameras to the 'high
679 sensitivity' setting and to take five consecutive photographs when triggered (no 'quiet period'). We attached
680 each camera to a tree, approximately 30 cm above the ground, facing toward a lure 2 - 2.5 m away. The lure
681 comprised an oil-absorbing cloth doused in tuna oil, placed inside a PVC pipe container with a mesh top.
682 We secured each lure to the top of a 1-m wooden stake and attached a handful of small white feathers to
683 the outside of the PVC pipe container. Feathers were not used in the Lower Glenelg National Park survey.
684 We cleared vegetation from the camera's line-of-sight to reduce false triggers and avoid obscuring cat coat
685 markings.

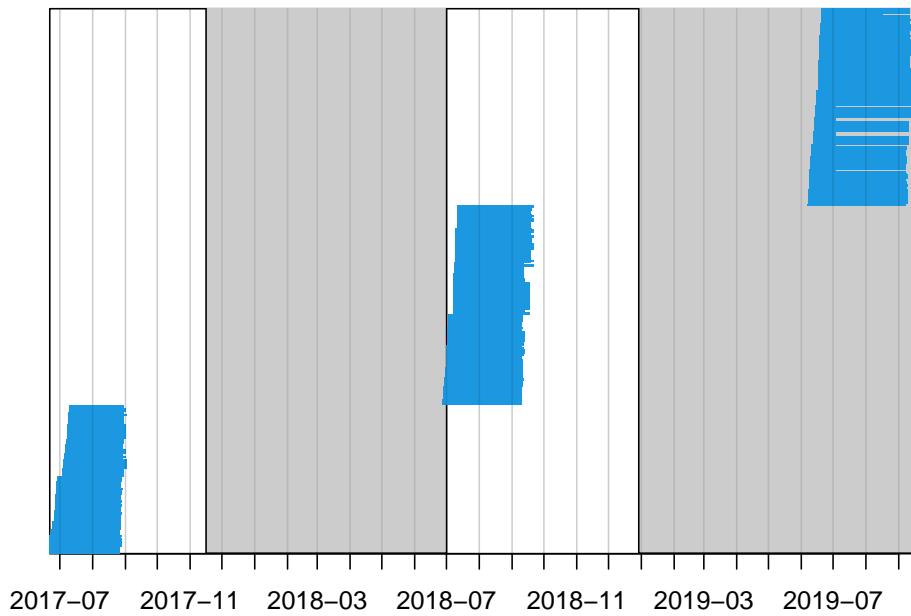


Figure S1: Camera-trap operation times in the Otway region, Australia. Each blue horizontal line represents one camera-trap deployment. Grey shading indicates periods of fox control in the impact landscape.

Table S1: Frequency of different Reconyx camera-trap models used in surveys

Region	Camera model	Frequency
Glenelg	HC600 HYPERFIRE	413
Glenelg	PC900 PROFESSIONAL	12
Otway	HC600 HYPERFIRE	405
Otway	HYPERFIRE 2 COVERT	59
Otway	PC900 PROFESSIONAL	34
Otway	HC500 HYPERFIRE	9
Otway	PC800 PROFESSIONAL	6



Figure S2: Example of a typical camera-trap set-up in the Otway region, Australia.

686 *S1.2. Individual cat identification*

687 We first labelled every camera-trap image with a species metadata tag using DigiKam software. For cat
688 images, we also added metadata tags for each cat coat type: black, mackerel/spotted tabby, classic tabby,
689 ginger and other (coats with multiple colour blends; Fig. 3). This allowed us to summarise species records
690 and extract cat images using the ‘camtrapR’ R-package (Niedballa, *et al.* (2016). camtrapR: an R package
691 for efficient camera trap data management. *Methods in Ecology and Evolution*, 7(12), 1457-1462).

692 In the Otway Ranges, we considered all black cats to be of the ‘unmarked’ category in spatial mark-resight
693 models - even the few with white splotches on their underside (as these couldn’t always be seen as cats move
694 with their head down). In the Glenelg region, black cats were rarer (not detected at two landscapes) and
695 often more distinctive, and so we could feasibly identify some individuals.

696 For each of the ‘marked’ coat categories, we identified individual cats based on their unique pelage
697 markings where possible. Our ability to identify individuals substantially increased as the image library for
698 each cat increased. Therefore we made the easiest identifications first to build up these libraries, before
699 making decisions on the less obvious detections. We examined and matched all coat markings seen between
700 two particular detections. Markings on the front legs were the most useful for identification as the patterns
701 do not skew as much with different body positions. Unidentifiable detections were mainly due to only part of
702 a cat appearing in the frame or because photos were blurry (because of cat movement or a foggy camera
703 lens).

704 In a small number of instances (less than ten), only left or right flanks were ever seen. For these cases, the
705 side with the most repeat detections was labelled as an individual, whereas the side with the least number
706 of detections was considered unidentifiable. Additionally, an extremely small portion of cats in the Otway
707 region (no cats detected in Glenelg had ginger coats). When ginger coats are photographed with an infrared
708 flash, they become overexposed and no markings can be seen (see the image in bottom-right corner in Fig.
709 S3). Therefore, if there were multiple ginger cat detections in a single grid, we treated them in the same way
710 as one-sided flank detections.

711 For the Glenelg region, one observer identified the feral cats from landscape pairs 1 and 2 (MR) and pair 3
712 (Luke Woodford). For the 2017 and 2018 Otway datasets (where there were substantially more cat detections
713 and fewer distinct coat patterns), two independent observers identified individual cats and discrepancies

714 between observers were reviewed together until consensus was reached (MR, MLP, BH). If no consensus was
715 reached, the cat was considered unidentifiable. In the 2019 Otway dataset, many of the identified cats were
716 sighted in the previous surveys, making it easier to identify individuals, and only one observer was used (MR).
717 We supplemented our image libraries for each individual cat with images from additional camera-trap surveys
718 conducted within the Otway region grids (just before each of our surveys) using white flash camera-traps
719 (Zoï Banikos, unpublished data).

720 This process left us with three groups of cats: unmarked, marked (cats which could be identified to the
721 individual-level with complete certainty) and mark status unknown (marked cats which couldn't be identified
722 to the individual-level with complete certainty).

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



Figure S3: Feral cat coat categories from left-right, top-bottom: mackerel/spotted tabby, classic tabby, other, black, ginger and ginger with infrared flash.

726 S1.3. Feral cat detection plots

727 S1.3.1. Glenelg region

728 S1.3.1.1. Replicate 1.

729

730

a) Annya State Forest
78 occasions, 23 detections, 9 animals

b) Cobboboonee National Park
75 occasions, 35 detections, 13 animals

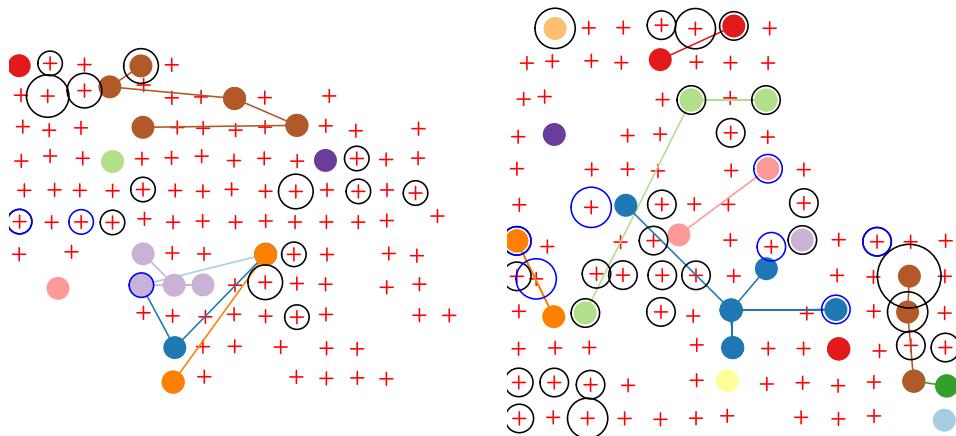


Figure S4: Feral cat detections in the first replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in Annya (a; non-impact) but does in Cobboboonee (b; impact).

731 S1.3.1.2. Replicate 2.

732

733

a) Hotspur State Forest
67 occasions, 22 detections, 8 animals

b) Mt Clay Reserve
58 occasions, 33 detections, 10 animals

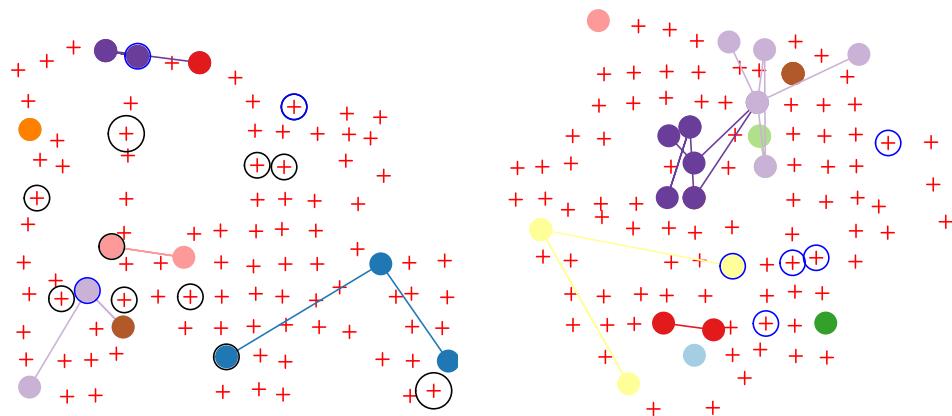


Figure S5: Feral cat detections in the second replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in Hotspur (a; non-impact) but does in Mt Clay (b; impact).

⁷³⁴ S1.3.1.3. Replicate 3.

⁷³⁵

⁷³⁶

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

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

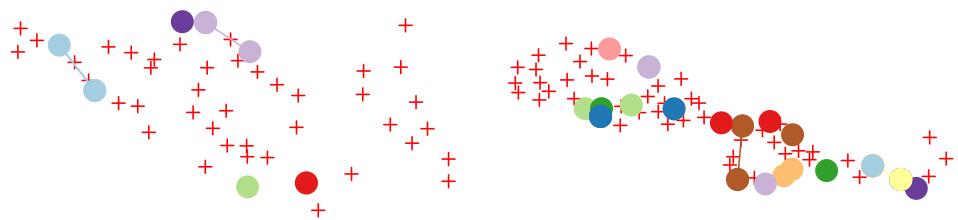


Figure S6: Feral cat detections in the third replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Fox control does not occur in the north (a; non-impact) but does in the south (b; impact) of Lower Glenelg National Park.

⁷³⁷ S1.3.2. *Otway region*

⁷³⁸ S1.3.2.1. *2017.*

⁷³⁹

⁷⁴⁰

a) Otways north 2017
59 occasions, 60 detections, 26 animals

b) Otways south 2017
68 occasions, 62 detections, 20 animals

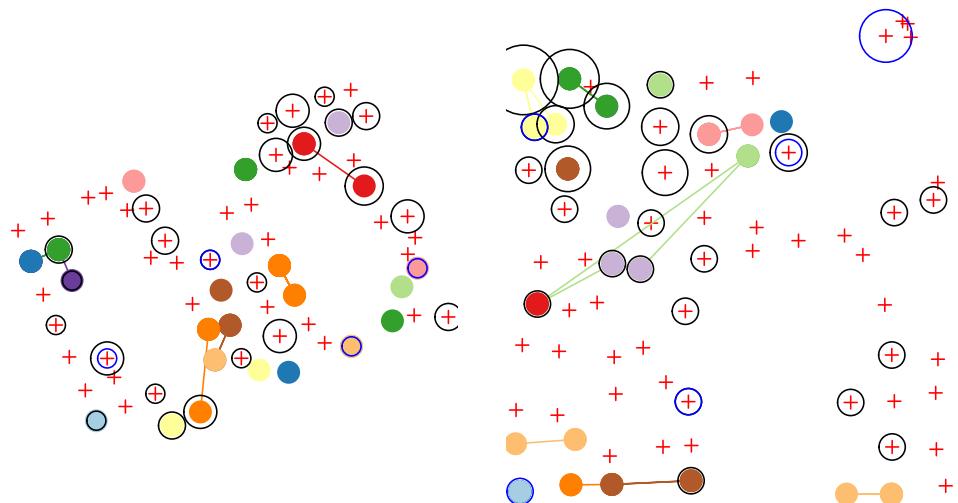


Figure S7: Feral cat detections in the Otway region, Australia, 2017. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control did not occur in either of the landscapes during this time.

741 S1.3.2.2. 2018.

742

743

a) Otways north 2018
74 occasions, 90 detections, 30 animals

b) Otways south 2018
75 occasions, 75 detections, 24 animals

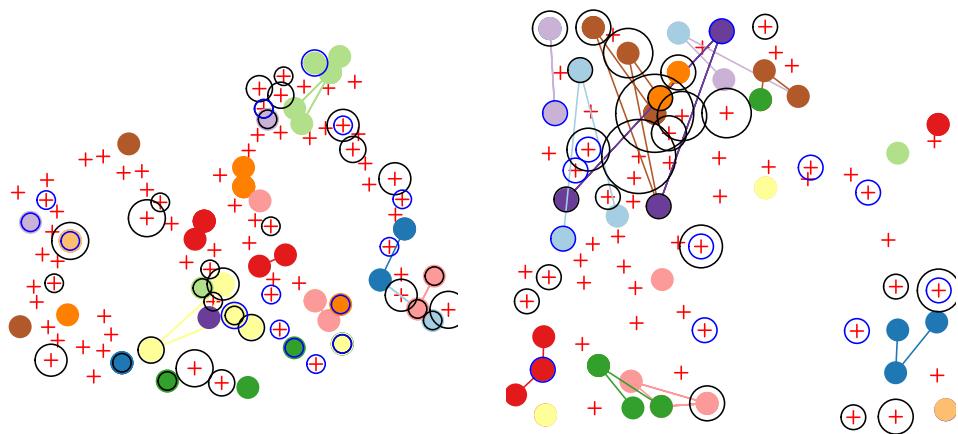


Figure S8: Feral cat detections in the Otway region, Australia, 2018. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control did not occur in the north landscape (a; non-impact),. Fox control occurred, but lapsed just prior to the survey in the south landscape (b; impact).

744 S1.3.2.3. 2019.

745

746

a) Otways north 2019
90 occasions, 90 detections, 27 animals

b) Otways south 2019
94 occasions, 133 detections, 25 animals

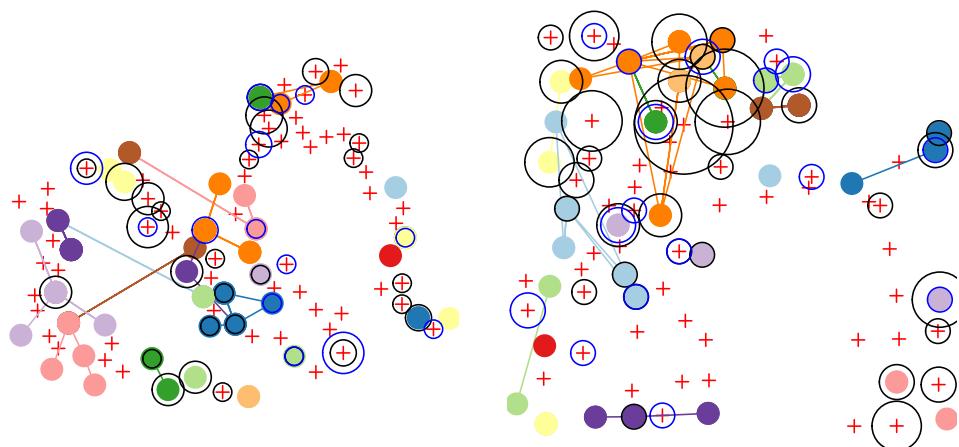


Figure S9: Feral cat detections in the Otway region, Australia, 2019. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control did not occur in the north landscape (a; non-impact); foxes were controlled in the south landscape (b; non-impact) during this survey.

⁷⁴⁷ *S1.4. Fox spatial occurrence*

⁷⁴⁸ *S1.4.1. Glenelg region*

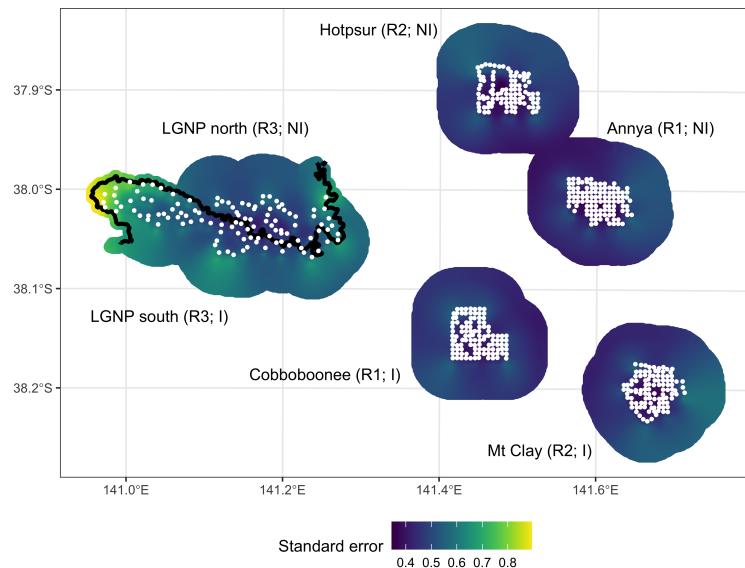


Figure S10: Standard error estimates around red fox occurrence probabilities derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg region, Australia. White dots represent camera-traps.

⁷⁴⁹ S1.4.2. *Otway Region*

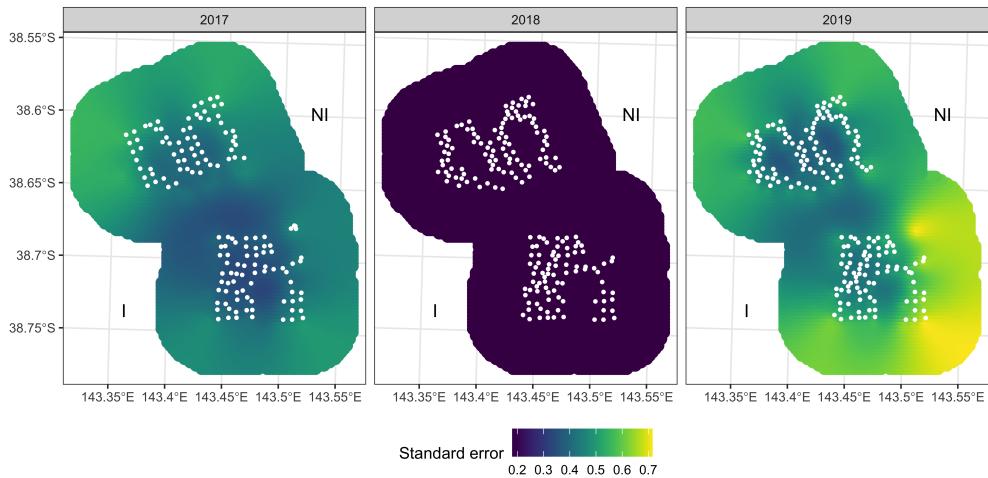


Figure S11: Standard error estimates around red fox occurrence probabilities derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape survey session in the Otway region, Australia. White dots represent camera-traps.

750 *S1.5. Vegetation categories*

751 We condensed the main Ecological Vegetation Class groupings (Department of Environment, Land, Water
752 & Planning 2020) into three categories for each region by merging similar groups. In the Glenelg region, we
753 merged dry forests with lowland forests. In the Otway region, we merged rainforests with wet forests, as well
754 as merged dry forests and heathy woodlands. This resulted in three categories for each region: cleared land,
755 heathy woodlands, and lowland forests (Glenelg region only) or wet forests (Otways region only).

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

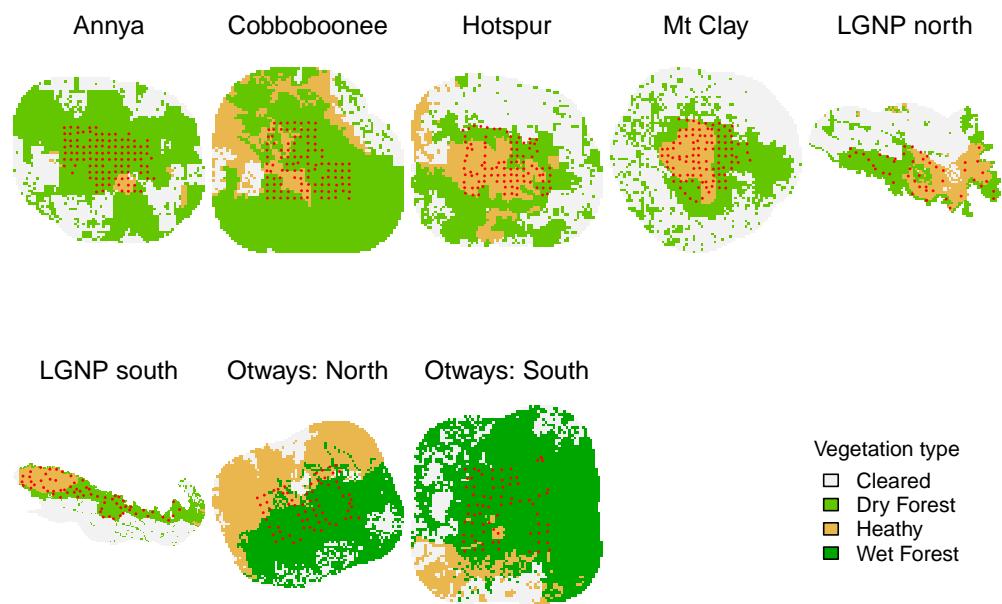


Figure S12: Condensed Ecological Vegetation Class groups in each study landscape used as habitat mask covariates in spatial mark-resight models (base models).

760 S1.6. Spatial mark-resight models

761 S1.6.1. Glenelg region

Table S2: 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	3532.04	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 S3: 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	0.39
D~vegetation g0~1 sigma~1	5	-1307.68	2625.37	2626.35	0.12	0.37
D~vegetation g0~s(T) sigma~1	7	-1306.25	2626.50	2628.40	2.16	0.13
D~1 g0~s(T) sigma~1	5	-1308.83	2627.66	2628.64	2.41	0.12

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

s(T) - nonlinear time trend smooth with three knots (g0 only)

Table S4: 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~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 S5: 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~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) - nonlinear smooth of fox_occ with three knots

Table S6: 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

⁷⁶² *S1.6.2. Otway region*

Table S7: 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 S8: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 2.

Model	K	logLik	AIC	AICc	dAICc	AICcwt
D~year g0~1 sigma~1	5	-3550.63	7111.26	7111.67	0.00	0.51
D~year g0~s(T, k = 3) sigma~1	7	-3548.91	7111.82	7112.59	0.92	0.32
D~year + vegetation g0~1 sigma~1	7	-3550.04	7114.08	7114.86	3.19	0.10
D~year + vegetation g0~s(T, k = 3) sigma~1	9	-3548.32	7114.64	7115.90	4.23	0.06
D~year g0~model sigma~1	9	-3550.42	7118.84	7120.11	8.44	0.01
D~year g0~s(T, k = 3) + model sigma~1	11	-3548.65	7119.30	7121.18	9.51	0.00
D~year + vegetation g0~model sigma~1	11	-3549.84	7121.69	7123.57	11.90	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

s(T, k = 3) - nonlinear time trend (g0 only)

model - Reconyx camera-trap model

Table S9: 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~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 S10: 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~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) - nonlinear smooth of fox_occ with three knots

Table S11: 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