

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

³ Matthew W. Rees^a, Jack H. Pascoe^{a,b}, Mark Le Pla^{a,b}, Alan Robley^c, Emma K. Birnbaum^b, Brendan A.
⁴ Wintle^a, Bronwyn A. Hradsky^a

^a*Quantitative and Applied Ecology Group School of Ecosystem and Forest Sciences The University of Melbourne Parkville VIC 3010 Australia*

^b*Conservation Ecology Centre Lighthouse Rd Cape Otway VIC 3233 Australia*

^c*Department of Environment Land Water and Planning Arthur Rylah Institute for Environmental Research Heidelberg VIC 3084 Australia*

5

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

*Corresponding author
Email address: matt.wayne.rees@gmail.com (Matthew W. Rees)

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 *et*
72 *al.* 2017; Legge *et al.* 2020). As foxes are larger-bodied and have high dietary overlap with cats (Stobo-Wilson
73 *et al.* 2021b; Stobo-Wilson *et al.* 2021a; Woinarski *et al.* 2021), the mesopredator release hypothesis (Soulé
74 *et al.* 1988) predicts cat density, will increase as fox populations are suppressed (Molsher *et al.* 2017). A
75 mesopredator release of cats would likely dampen the conservation benefits of fox control, and could even
76 worsen outcomes for some native prey species (Takimoto & Nishijima 2022), as has previously been suspected
77 (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. Dingoes are now absent throughout southwest Victoria (Cairns *et al.* 2018). A native
106 mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and extremely rare
107 in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial mammalian
108 predator guild is therefore depauperate, with foxes and cats being the primary mammalian terrestrial
109 predators heavier than one kilogram; birds of prey and snakes are the only other medium-large carnivores
110 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 fluroacetate
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 ('South') and non-impact ('North') landscapes were at least 4.2 km
¹⁵² apart through dense forest. In this study, and a concurrent study which identified individual foxes through
¹⁵³ genetic sampling (Le Pla *et al.* 2022), we found no evidence that either foxes or cats moved between the
¹⁵⁴ impact and non-impact landscapes.

155 In each landscape, we established an irregular grid of 49 – 110 sites (mean: 88). We broadly aimed to
156 space camera-traps 500 m apart, but randomly varied distances from 194 – 770 m (mean spacing: 448 m)
157 to achieve an irregular spacing design (Rich *et al.* 2019). Larger ‘holes’ in the grids due to accessibility
158 constraints and to increase the overall grid size. We situated each site in the forest interior, at least 30 m
159 from roads and tracks. At each site, we set up a Reconyx (Holmen, Wisconsin) infrared camera-trap on a
160 tree, facing a tuna oil lure; see Appendix C section S1.1 for details. Overall, we deployed 1,051 functional
161 camera-traps, which operated for an average of 65 days (ranging 12 – 93 days), totalling 68,504 trap nights
162 (Table 1).

163 *2.3. Individual feral cat identification*

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

169 *2.4. Fox spatial occurrence*

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

180 We could not use raw fox presence-absence data from the camera-traps as a response variable for cat
181 density as spatial mark-resight models require covariate values for each grid cell in which density is estimated

182 (see Section 2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for
183 each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised
184 additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but do
185 not account for imperfect detection. Nonetheless, naïve fox occurrence probabilities may relate to how cats
186 perceive the risk of fox encounter for the survey duration.

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

193 *2.5. Spatial mark-resight models of feral cat density*

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

207 We used sighting-only spatial mark-resight models to estimate cat density using the maximum likelihood
208 ‘secr’ R-package (Efford 2021). We used closed population models as open population spatial mark-resight
209 models have not yet been developed. Detections of the ‘mark status uncertain’ category (unidentifiable

210 cats), cannot be handled in the ‘secr’ R package; we added them to as ‘unmarked’ detections (black cats)
211 rather than discard them (following Moseby, McGregor, & Read 2020). We condensed unmarked detection
212 histories to a binary presence-absence record per each camera-trap for a 24-hour length duration (‘occasion’),
213 beginning at midday. We ran separate models for each region and treated each camera-trap grid deployment
214 as a ‘session’. We created a 4000-m buffer zone around each site (which was truncated by the river in LGNP),
215 and estimated cat density at a 200-m grid cell resolution within this area. These habitat mask specifications
216 were based on initial model trials and our knowledge of cat behaviour in these regions; the aim was to ensure
217 density was estimated over a large enough area to encompass the activity centres of all cats exposed to our
218 camera-traps, at a fine enough spatial scale to minimise bias in density estimates.

219 For each region, we ran four sets of models. We (1) chose between half-normal and exponential detection
220 functions and (2) chose ‘base model’ covariates to carry through to subsequent model sets. We then (3)
221 evaluated the effect of fox control on cat density at the landscape scale with traditional experimental
222 approaches (prediction 1), and (4) tested for associations between fox occurrence probabilities and cat
223 density at a fine spatial scale (prediction 2). To choose between competing model specifications, we used
224 small-sample corrected Akaike Information Criterion (hereafter ‘AIC_c’) scores (Burnham & Anderson 2004);
225 carrying forward or presenting the top-ranked model (i.e., model with the lowest AIC_c score). In addition
226 to examining confidence intervals around estimated model coefficients, we also used AIC_c scores to assess
227 statistical evidence; models within two AIC_c units are generally considered equivalent in terms of predictive
228 power (Burnham & Anderson 2004). Steps two to four are described in more detail below.

229 The second set of models (base models) established the base covariates for each region. We hypothesised
230 that cat detectability might decrease over each survey due to the scent of the tuna oil lure fading. To account
231 for this, we modelled a nonlinear trend in g_0 over the survey duration for each camera-trap. We also used a
232 range of camera-trap models which may impact detection rates (Table S1). We tested whether camera-trap
233 model impacted cat detection rates in the Otways, but not the Glenelg region as 97% of cameras here were
234 the HC600 model (3% were the PC900 model which primarily differ only in software settings, Seidlitz *et al.*
235 2020), using camera-trap model as a categorical variable ($n = 5$) on g_0 . We further hypothesised that cat
236 density might differ between vegetation types. We classed the vegetation into three dominant types for each
237 region: cleared land, heathy vegetation, and either dry forest (Glenelg region) or wet forest (Otway region);
238 see Appendix S1.5 for details. We compared these covariates as single and additive models, as well as to a
239 ‘null model’ (density and detectability constant), and carried the supported covariates forward to subsequent

240 model sets.

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

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

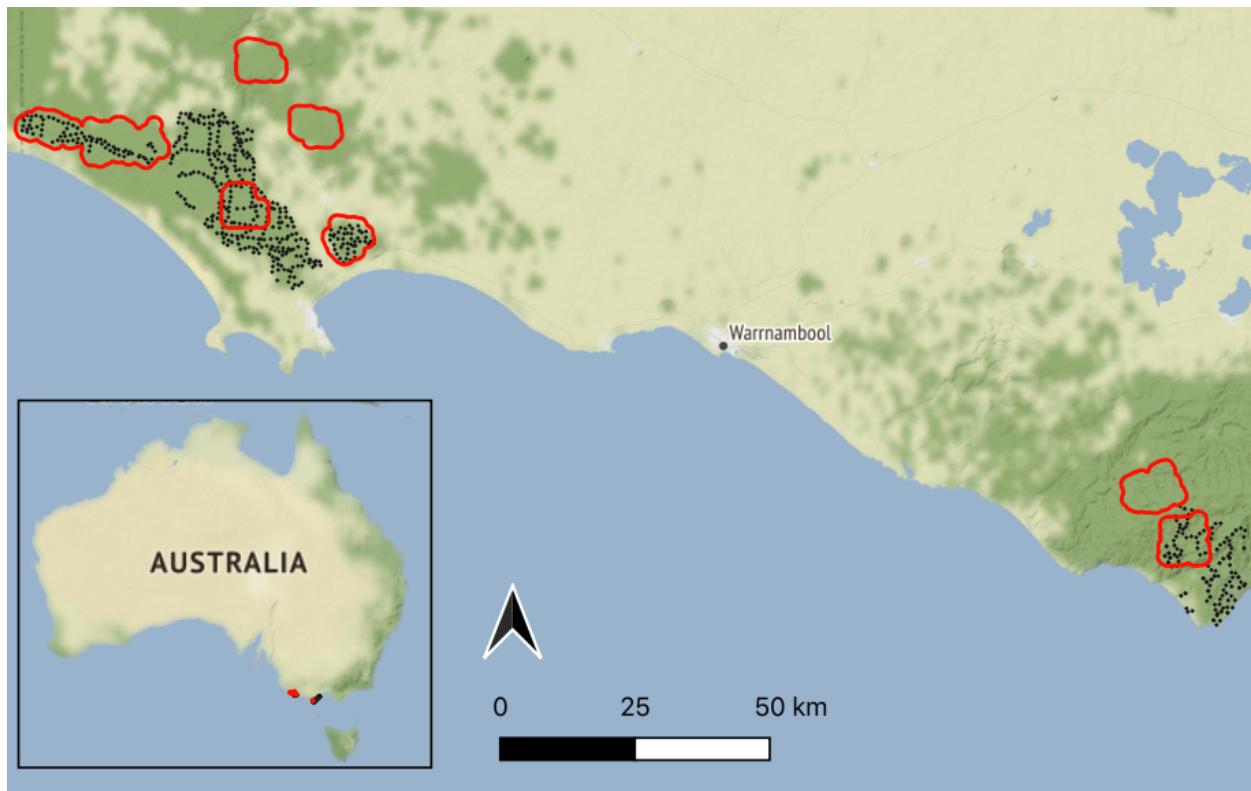


Figure 1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river (which the poison-baits closely follow along the southern bank). Locations of fox poison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

264 **3. RESULTS**

265 *3.1. Glenelg region*

266 *3.1.1. Red Fox*

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

276 *3.1.2. Feral cat*

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

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

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

297 *3.2. Otway region*

298 *3.2.1. Red fox*

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

307 *3.2.2. Feral cat*

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

314 Our prediction (1) that fox control would be associated with higher cat densities was supported in 2019
315 (~1.5 years after fox baiting commenced), but not 2018 (six months after fox-baiting commenced, and during
316 a break in the baiting program). Within each year, there was no statistical evidence that cat densities

317 differed between the impact and non-impact landscapes (95% confidence intervals overlapped zero; Fig.
318 4a). However, a consistent upward trend in cat density in the impact landscape over three years and a
319 simultaneous downward trend in the non-impact landscape (Fig. 4a), meant that there was a significant
320 increase in cat density in the impact landscape 1.5 years after fox-baiting commenced, relative to changes in
321 the non-impact landscape (i.e., 83% CIs for the estimated difference for 2017 and 2019 do not overlap; Fig.
322 4b). There was strong evidence that cat detectability was associated with fox occurrence probability (Table
323 S9), detailed below.

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

333 There was strong support for an effect of fox occurrence probability on cat detectability at a fine spatial
334 scale (Fig. 6; Table S9). Where fox occurrence probability was higher, cats were less detectable in their
335 activity centres (i.e., negative association with g_0 ; -0.69; 95% CI: -1.11 - -0.27; Fig. 6a) and ranged further
336 (i.e., positive association with sigma; coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 6b). The equivalent nonlinear
337 model predicted that detectability changes occurred only in the low-mid range of fox occurrence probabilities
338 (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

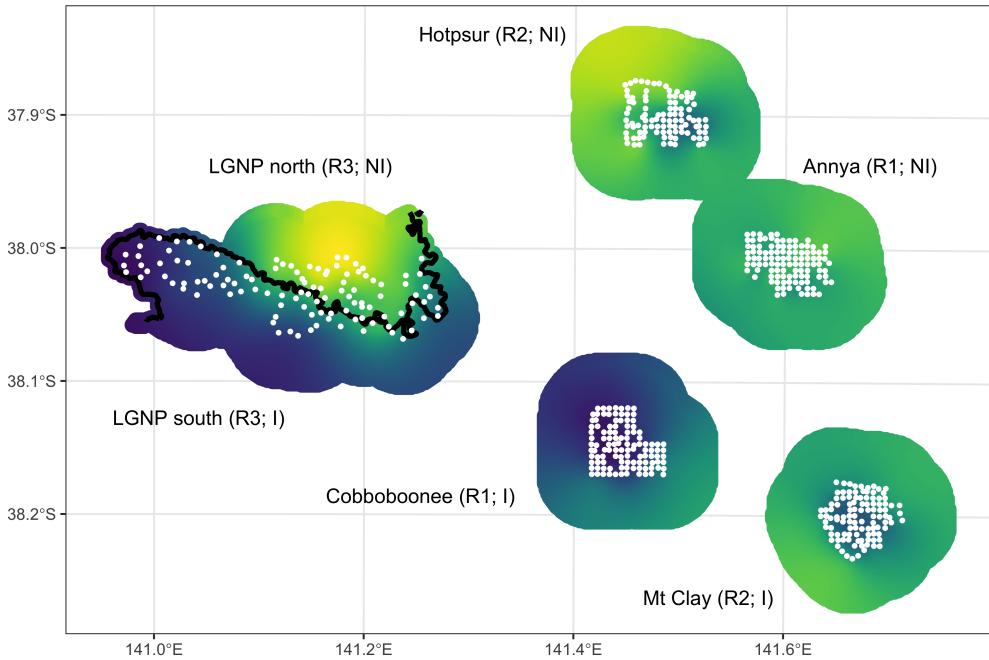
Individuals - Number of identified feral cat individuals

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

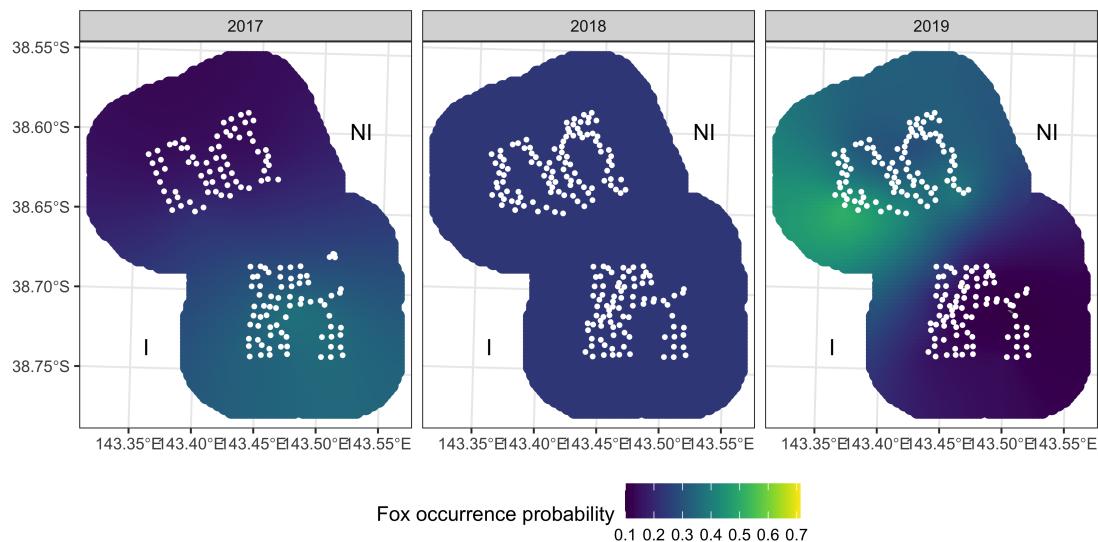


Figure 2: Predicted red fox *Vulpes vulpes* occurrence probabilities derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. White dots represent camera-trap sites. The black line (a) represents the Glenelg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

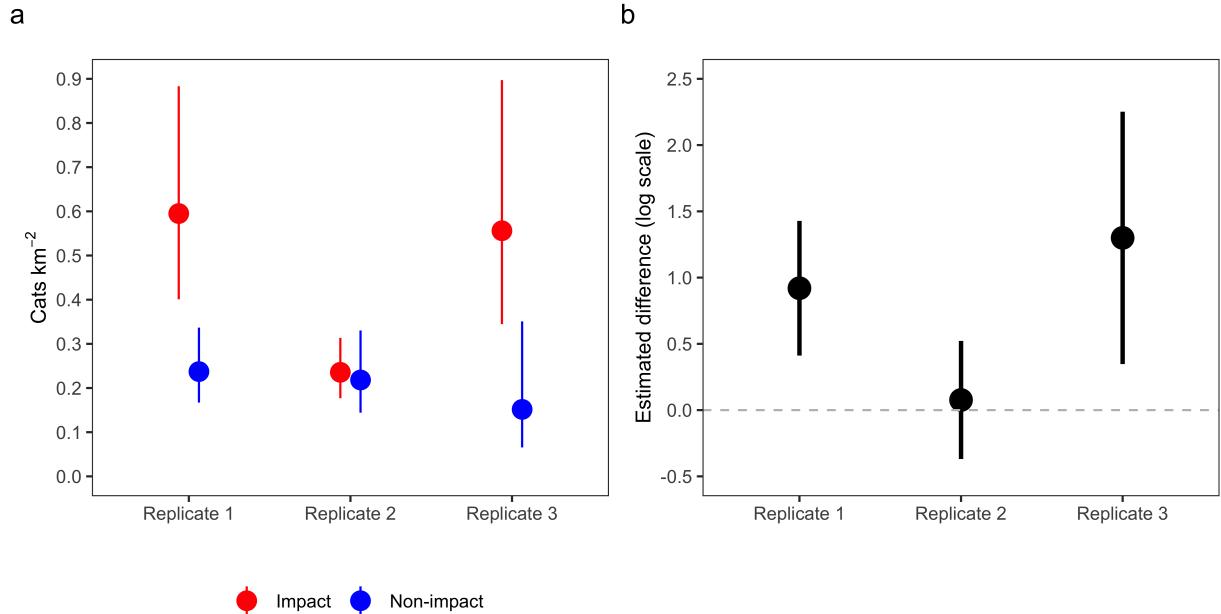


Figure 3: Feral cat *Felis catus* density in response to long-term fox control in the Glenelg region, Australia (replicated Control-Impact analysis). Poison baiting for foxes *Vulpes vulpes* had been conducted continuously in the impact landscapes for more than 13 years for the first two replicates, 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 ($p < 0.05$).

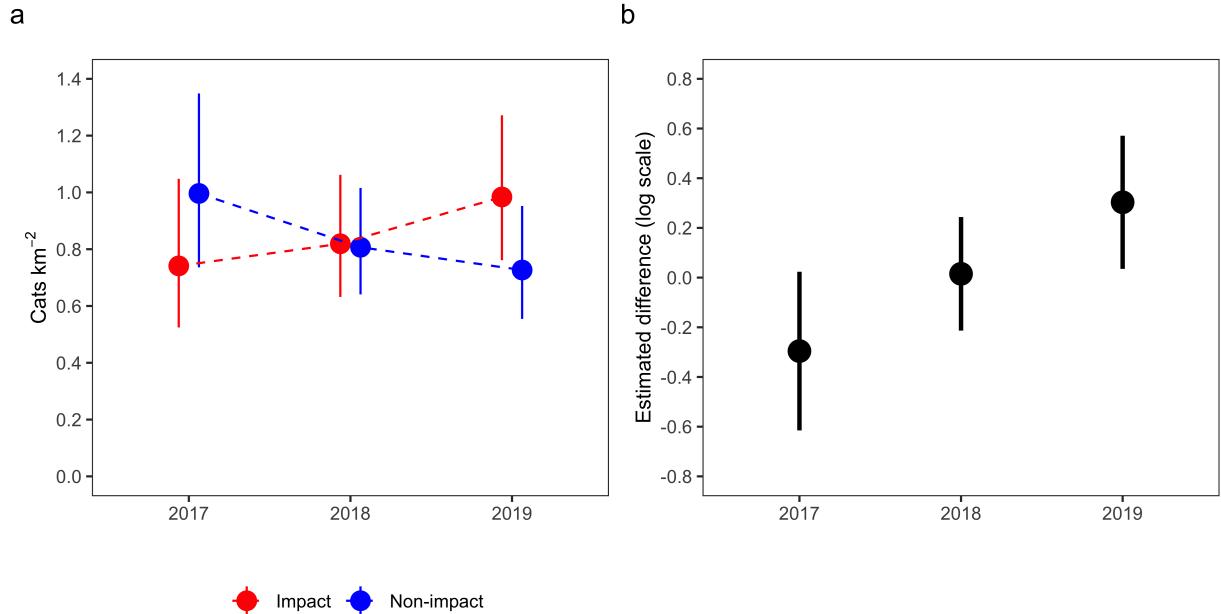


Figure 4: Feral cat *Felis catus* density in response to fox control in the Otway Ranges, Australia (Before-After Control-Impact Paired-Series analysis). The 2017 surveys were conducted approximately two months before lethal red fox *Vulpes vulpes* control began in the impact landscape. Baiting ceased 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 ($p < 0.05$).

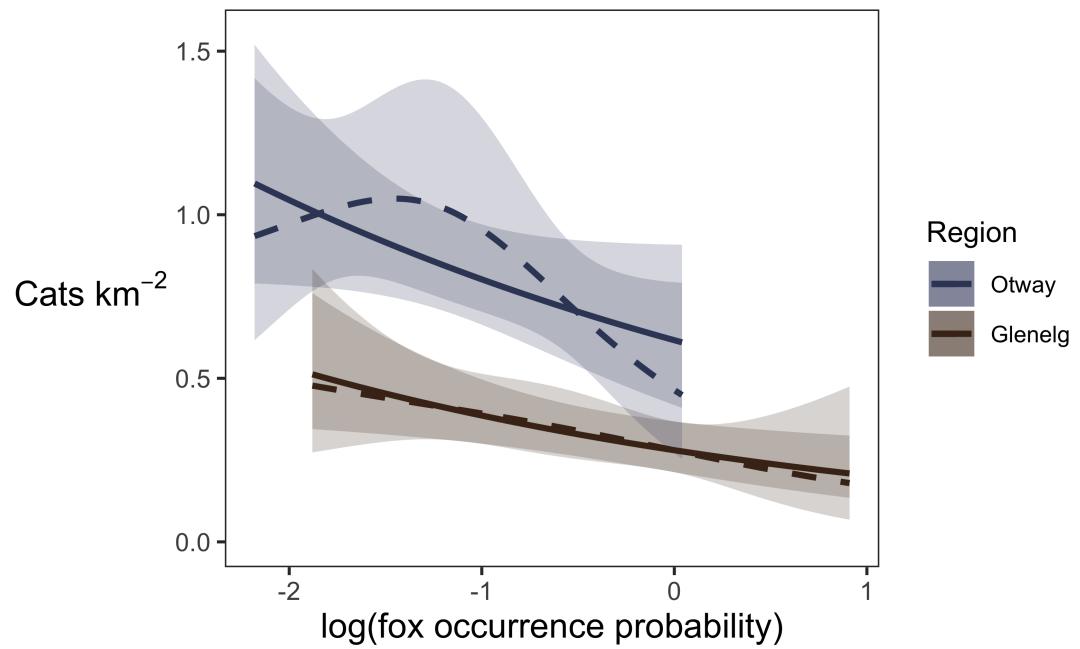


Figure 5: Feral cat *Felis catus* density in relation to the probability of red fox *Vulpes vulpes* occurrence, Glenelg and Otway regions, Australia. Lines show estimates from top-ranked linear (solid) and nonlinear (dashed) models, shaded areas indicate 95% confidence intervals

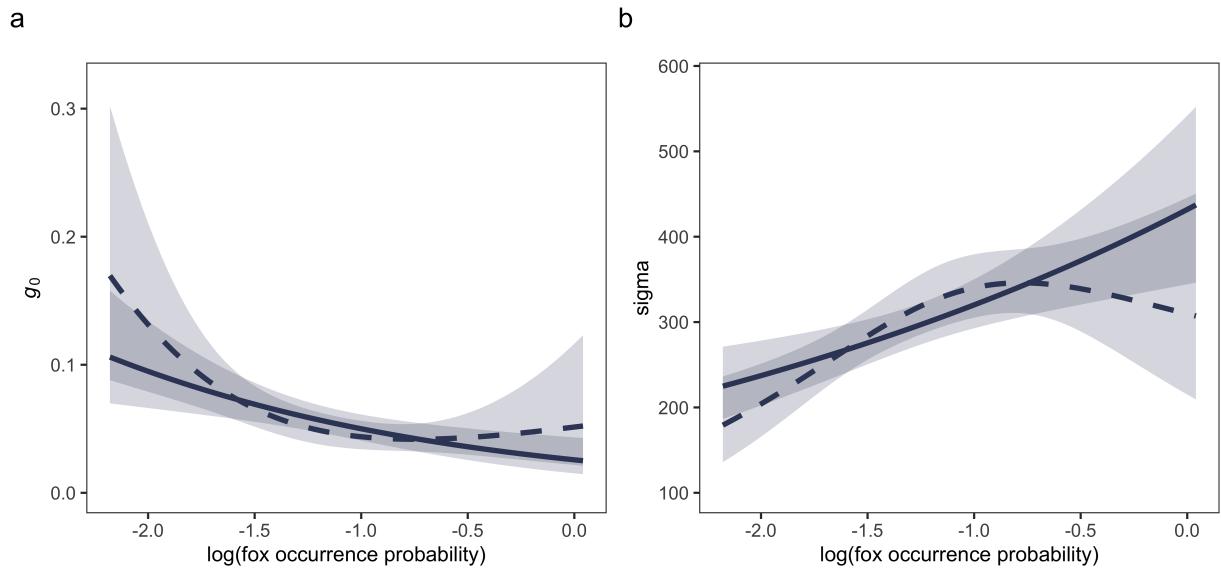


Figure 6: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-scaled red fox *Vulpes vulpes* occurrence probability in the Otway region, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0)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

339 **4. DISCUSSION**

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

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

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

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

375 Secondly, foxes may have a weaker suppressive effect on cats in the highly productive Otway region than
376 the dry forests of Glenelg. Fox occurrence was already relatively low prior to fox control in the Otways
377 compared to Glenelg (Fig. 2). Additionally, competition theory predicts competitive interactions to be
378 weaker with high prey availability: there may be less imperative for foxes to be aggressive towards or prey
379 upon cats when there is enough food to share (Dickman 1996; Johnson & VanDerWal 2009; Greenville
380 *et al.* 2014; Sogliani & Mori 2019). Conversely, foxes may have a higher capacity to maintain vigilance
381 against cats when they are not food stressed, and top-down control from dominant predators could be the
382 primary limiting factor for feral cats (a generalist mesopredator) in resource-rich environments (Oksanen
383 & Oksanen 2000; Feit, Feit, & Letnic 2019). Prey availability is likely a strong mediator of mesopredator
384 release, although it remains unclear whether mesopredator release would be stronger where prey availability
385 is low or high—severely limiting our ability to predict mesopredator release across different landscapes.

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

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

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

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

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

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

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

445 **ACKNOWLEDGEMENTS**

446 We acknowledge and pay respect to the Gunditjmara and Gadabanut Peoples on whose traditional lands
447 this study took place. This experiment was conducted in cooperation with the Glenelg Ark (Department
448 of Environment, Land Water and Planning) and Otway Ark (Parks Victoria) working groups. Surveys
449 were conducted under University of Melbourne Animal Ethics Committee approval 1714119 and Victorian
450 Government Department of Environment, Land Water and Planning Research Permit 10008273. Ethan Le
451 Duc, Michael Murrell, Dylan Thomas, Rhys Weber, Chris Johansson, Lachlan Levings and Liz Beever carried
452 out the Lower Glenelg National Park surveys, with Luke Woodford identifying cats. We are grateful to
453 our field assistants: Shauni Omond, Shayne Neal, Asitha Samarawickrama, Shelley Thompson, Erin Harris,
454 Hannah Killian, Lani Watson, Mark Dorman, Jack Davis, Carl Roffey, Bruce Edley, Larissa Oliveira Gonçalves,
455 Ben Lake, Chantelle Geissler, Aviya Naccarella, Emily Gronow, Harley England, David Pitts, Annie Hobby,
456 Louise Falls, Thomas McKinnon, Jimmy Downie, Marney Hradsky, Stephanie Samson, Robin Sinclair,
457 Asmaa Alhusainan, Kelly Forrester, Tammana Wadawani, Emily McColl-Gausden, Emily Gregg, Hannah
458 Edwards, Adam Beck, Vishnu Memnon, Sandy Lu, Pia Lentini, Nick Golding, Emily McColl-Gausden, Nina
459 Page, Maggie Campbell-Jones, Kyle Quinn and Jack Dickson. This manuscript was improved by comments
460 from William Geary, two PhD examiners and three peer-reviewers. Joanne Potts also provided advice
461 on fitting spatial mark-resight models. Our study was generously supported by the Conservation Ecology
462 Centre, the Victorian Government Department of Environment, Land Water and Planning, Arthur Rylah
463 Institute for Environmental Research, Parks Victoria, Holsworth Wildlife Research Endowment – Equity
464 Trustees Charitable Foundation and Ecological Society of Australia, the Australian Government’s National
465 Environmental Science Program through the Threatened Species Recovery Hub, and ARC Linkage Project
466 LP170101134. M.W.R also received support from an Australian Government Research Training Program
467 Scholarship.

468 REFERENCES

- 469 Alston, J., Maitland, B., Brito, B., Esmaeili, S., Ford, A., Hays, B., Jesmer, B., Molina, F. & Goheen, J.
470 (2019) Reciprocity in restoration ecology: When might large carnivore reintroduction restore ecosystems?
471 *Biological Conservation*, **234**, 82–89.
- 472 Anderson, D.R. (2001) The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin*,
473 1294–1297.
- 474 Arjo, W.M., Gese, E.M., Bennett, T.J. & Kozlowski, A.J. (2007) Changes in kit fox–coyote–prey relationships
475 in the Great Basin Desert, Utah. *Western North American Naturalist*, **67**, 389–401.
- 476 Barker, R.J., Schofield, M.R., Link, W.A. & Sauer, J.R. (2018) On the reliability of n-mixture models for
477 count data. *Biometrics*, **74**, 369–377.
- 478 Baum, J.K. & Worm, B. (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal*
479 *of Animal Ecology*, **78**, 699–714.
- 480 Berger, K.M., Gese, E.M. & Berger, J. (2008) Indirect effects and traditional trophic cascades: A test
481 involving wolves, coyotes, and pronghorn. *Ecology*, **89**, 818–828.
- 482 Bode, M., Baker, C.M. & Plein, M. (2015) Eradicating down the food chain: Optimal multispecies eradication
483 schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, **52**, 571–579.
- 484 Broadley, K., Burton, A.C., Avgar, T. & Boutin, S. (2019) Density-dependent space use affects interpretation
485 of camera trap detection rates. *Ecology and Evolution*, **9**, 14031–14041.
- 486 Buckmaster, A.J. (2012) *Ecology of the Feral Cat (*Felis Catus*) in the Tall Forests of Far East Gippsland*.
487 PhD thesis, School of Biological Sciences; University of Sydney.
- 488 Bureau of Meteorology. (2021) Climate data online, <http://www.bom.gov.au/climate/data/>
- 489 Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: Understanding AIC and BIC in model
490 selection. *Sociological Methods & Research*, **33**, 261–304.
- 491 Cairns, K.M., Shannon, L.M., Koler-Matznick, J., Ballard, J.W.O. & Boyko, A.R. (2018) Elucidating
492 biogeographical patterns in australian native canids using genome wide SNPs. *PLoS One*, **13**, e0198754.
- 493 Claridge, A.W., Cunningham, R.B., Catling, P.C. & Reid, A.M. (2010) Trends in the activity levels of
494 forest-dwelling vertebrate fauna against a background of intensive baiting for foxes. *Forest Ecology and*
495 *Management*, **260**, 822–832.
- 496 Comer, S., Clausen, L., Cowen, S., Pinder, J., Thomas, A., Burbidge, A.H., Tiller, C., Algar, D. &
497 Speldewinde, P. (2020) Integrating feral cat (*Felis catus*) control into landscape-scale introduced predator
498 management to improve conservation prospects for threatened fauna: A case study from the south coast

- 499 of Western Australia. *Wildlife Research*, **47**, 762–778.
- 500 Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system.
- 501 *Nature*, **400**, 563–566.
- 502 Davey, C., Sinclair, A., Pech, R.P., Arthur, A.D., Krebs, C.J., Newsome, A., Hik, D., Molsher, R. & Allcock,
- 503 K. (2006) Do exotic vertebrates structure the biota of Australia? An experimental test in New South
- 504 Wales. *Ecosystems*, **9**, 992–1008.
- 505 Department of Environment, Land, Water & Planning. (2020) Bioregions and EVC Benchmarks, <https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks>
- 506 Dexter, N. & Murray, A. (2009) The impact of fox control on the relative abundance of forest mammals in
- 507 East Gippsland, Victoria. *Wildlife Research*, **36**, 252–261.
- 508 Dickman, C.R. (1996) *Overview of the Impacts of Feral Cats on Australian Native Fauna*. Australian Nature
- 509 Conservation Agency.
- 510 Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G. & Woinarski, J.C.Z. (2017) Impacts
- 511 and management of feral cats (*Felis catus*) in Australia. *Mammal Review*, **47**, 83–97.
- 512 Doherty, T.S. & Ritchie, E.G. (2017) Stop jumping the gun: A call for evidence-based invasive predator
- 513 management. *Conservation Letters*, **10**, 15–22.
- 514 Duncan, R.P., Dexter, N., Wayne, A. & Hone, J. (2020) Eruptive dynamics are common in managed mammal
- 515 populations. *Ecology*, **101**, e03175.
- 516 Efford, M.G. (2021) secr: spatially explicit capture-recapture models. R package version 4.4.4, <http://CRAN.R-project.org/package=secr>
- 517 Efford, M.G. & Dawson, D.K. (2012) Occupancy in continuous habitat. *Ecosphere*, **3**, 1–15.
- 518 Efford, M.G. & Hunter, C.M. (2018) Spatial capture–mark–resight estimation of animal population density.
- 519 *Biometrics*, **74**, 411–420.
- 520 Efford, M.G. & Mowat, G. (2014) Compensatory heterogeneity in spatially explicit capture–recapture data.
- 521 *Ecology*, **95**, 1341–1348.
- 522 Feit, B., Feit, A. & Letnic, M. (2019) Apex predators decouple population dynamics between mesopredators
- 523 and their prey. *Ecosystems*, **22**, 1606–1617.
- 524 Finke, D.L. & Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature*, **429**, 407–410.
- 525 Ford, A.T. & Goheen, J.R. (2015) Trophic cascades by large carnivores: A case for strong inference and
- 526 mechanism. *Trends in Ecology & Evolution*, **30**, 725–735.
- 527 Francis, L., Robley, A. & Hradsky, B. (2020) *Evaluating Fox Management Strategies Using a Spatially*

- 530 *Explicit Population*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 304.
531 Department of Environment, Land, Water; Planning, Heidelberg, Victoria.
- 532 Gardner, B., Royle, J.A. & Wegan, M.T. (2009) Hierarchical models for estimating density from DNA
533 mark–recapture studies. *Ecology*, **90**, 1106–1115.
- 534 Glen, A.S. & Dickman, C.R. (2005) Complex interactions among mammalian carnivores in Australia, and
535 their implications for wildlife management. *Biological Reviews*, **80**, 387–401.
- 536 Goldstein, H. & Healy, M.J. (1995) The graphical presentation of a collection of means. *Journal of the Royal
537 Statistical Society: Series A (Statistics in Society)*, **158**, 175–177.
- 538 Greenville, A.C., Wardle, G.M., Tamayo, B. & Dickman, C.R. (2014) Bottom-up and top-down processes
539 interact to modify intraguild interactions in resource-pulse environments. *Oecologia*, **175**, 1349–1358.
- 540 Güthlin, D., Storch, I. & Küchenhoff, H. (2014) Is it possible to individually identify red foxes from
541 photographs? *Wildlife Society Bulletin*, **38**, 205–210.
- 542 Hamer, R.P., Gardiner, R.Z., Proft, K.M., Johnson, C.N. & Jones, M.E. (2021) A triple threat: High
543 population density, high foraging intensity and flexible habitat preferences explain high impact of feral
544 cats on prey. *Proceedings of the Royal Society B*, **288**, 20201194.
- 545 Hayward, M.W., Boitani, L., Burrows, N.D., Funston, P.J., Karanth, K.U., MacKenzie, D.I., Pollock, K.H.
546 & Yarnell, R.W. (2015) Ecologists need robust survey designs, sampling and analytical methods. *Journal
547 of Applied Ecology*, **52**, 286–290.
- 548 Hradsky, B.A., Kelly, L.T., Robley, A. & Wintle, B.A. (2019) FoxNet: An individual-based model framework
549 to support management of an invasive predator, the red fox. *Journal of Applied Ecology*, **56**, 1460–1470.
- 550 Hradsky, B.A., Robley, A., Alexander, R., Ritchie, E.G., York, A. & Di Stefano, J. (2017) Human-modified
551 habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes*. *Scientific Reports*, **7**,
552 1–12.
- 553 Hunter, D.O., Lagisz, M., Leo, V., Nakagawa, S. & Letnic, M. (2018) Not all predators are equal: A
554 continent-scale analysis of the effects of predator control on Australian mammals. *Mammal Review*, **48**,
555 108–122.
- 556 Jachowski, D.S., Butler, A., Eng, R.Y.Y., Gigliotti, L., Harris, S. & Williams, A. (2020) Identifying
557 mesopredator release in multi-predator systems: A review of evidence from North America. *Mammal
558 Review*, **50**, 367–381.
- 559 Jackson, M.C. (2015) Interactions among multiple invasive animals. *Ecology*, **96**, 2035–2041.
- 560 Johnson, C.N. & VanDerWal, J. (2009) Evidence that dingoes limit abundance of a mesopredator in eastern

- 561 Australian forests. *Journal of Applied Ecology*, **46**, 641–646.
- 562 Jones, K.L., Van Vuren, D.H. & Crooks, K.R. (2008) Sudden Increase in a Rare Endemic Carnivore: Ecology
563 of the Island Spotted Skunk. *Journal of Mammalogy*, **89**, 75–86.
- 564 Karki, S.M., Gese, E.M. & Klavetter, M.L. (2007) Effects of coyote population reduction on swift fox
565 demographics in Southeastern Colorado. *The Journal of Wildlife Management*, **71**, 2707–2718.
- 566 Le Pla, M.N., Birnbaum, E.K., Rees, M.W., Hradsky, B.A., Weeks, A.R., Van Rooyen, A. & Pascoe, J.H.
567 (2022) Genetic sampling and an activity index indicate contrasting outcomes of lethal control for an
568 invasive predator. *Austral Ecology*.
- 569 Legge, S., Taggart, P.L., Dickman, C.R., Read, J.L. & Woinarski, J.C. (2020) Cat-dependent diseases cost
570 Australia AU \$6 billion per year through impacts on human health and livestock production. *Wildlife
571 Research*, **47**, 731–746.
- 572 Letnic, M., Greenville, A., Denny, E., Dickman, C.R., Tischler, M., Gordon, C. & Koch, F. (2011) Does a
573 top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology
574 and Biogeography*, **20**, 343–353.
- 575 Levi, T. & Wilmers, C.C. (2012) Wolves–coyotes–foxes: A cascade among carnivores. *Ecology*, **93**, 921–929.
- 576 Linden, D.W., Fuller, A.K., Royle, J.A. & Hare, M.P. (2017) Examining the occupancy–density relationship
577 for a low-density carnivore. *Journal of applied ecology*, **54**, 2043–2052.
- 578 Lindenmayer, D.B., Wood, J., MacGregor, C., Foster, C., Scheele, B., Tulloch, A., Barton, P., Banks,
579 S., Robinson, N., Dexter, N., O'Loughlin, L.S. & Legge, S. (2018) Conservation conundrums and the
580 challenges of managing unexplained declines of multiple species. *Biological Conservation*, **221**, 279–292.
- 581 Lombardi, J.V., Comer, C.E., Scognamillo, D.G. & Conway, W.C. (2017) Coyote, fox, and bobcat response to
582 anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems*, **20**, 1239–1248.
- 583 Marlow, N.J., Thomas, N.D., Williams, A.A., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J. & Berry,
584 O. (2015) Cats (*Felis catus*) are more abundant and are the dominant predator of woylies (*Bettongia
585 penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology*, **63**, 18–27.
- 586 McLeod, S.R. & Saunders, G. (2014) Fertility control is much less effective than lethal baiting for controlling
587 foxes. *Ecological Modelling*, **273**, 1–10.
- 588 Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Le Corre,
589 M., Horwath, S.V. & Nogales, M. (2011) A global review of the impacts of invasive cats on island
590 endangered vertebrates. *Global Change Biology*, **17**, 3503–3510.
- 591 Miller, D.L. & Wood, S.N. (2014) Finite area smoothing with generalized distance splines. *Environmental*

- 592 and *Ecological Statistics*, **21**, 715–731.
- 593 Molsher, R., Newsome, A.E., Newsome, T.M. & Dickman, C.R. (2017) Mesopredator management: Effects
594 of red fox control on the abundance, diet and use of space by feral cats. *PLoS One*, **12**, e0168460.
- 595 Moseby, K.E., Letnic, M., Blumstein, D.T. & West, R. (2019) Understanding predator densities for successful
596 co-existence of alien predators and threatened prey. *Austral Ecology*, **44**, 409–419.
- 597 Moseby, K., McGregor, H. & Read, J. (2020) Effectiveness of the felixer grooming trap for the control of
598 feral cats: A field trial in arid South Australia. *Wildlife Research*, **47**, 599–609.
- 599 Norton, M.A., Prentice, A., Dingle, J., French, K. & Claridge, A.W. (2015) Population characteristics and
600 management of the long-nosed potoroo (*Potorous tridactylus*) in high-quality habitat in the Southern
601 Highlands of New South Wales. *Australian Mammalogy*, **37**, 67–74.
- 602 Oksanen, L. & Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *The
603 American Naturalist*, **155**, 703–723.
- 604 Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009)
605 The rise of the mesopredator. *Bioscience*, **59**, 779–791.
- 606 Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. (2007) Spatial heterogeneity of
607 mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences*,
608 **104**, 20862–20865.
- 609 Reddiex, B., Forsyth, D.M., McDonald-Madden, E., Einoder, L.D., Griffioen, P.A., Chick, R.R. & Robley,
610 A.J. (2007) Control of pest mammals for biodiversity protection in Australia. I. Patterns of control and
611 monitoring. *Wildlife Research*, **33**, 691–709.
- 612 Rich, L.N., Miller, D.A., Muñoz, D.J., Robinson, H.S., McNutt, J.W. & Kelly, M.J. (2019) Sampling design
613 and analytical advances allow for simultaneous density estimation of seven sympatric carnivore species
614 from camera trap data. *Biological Conservation*, **233**, 12–20.
- 615 Riley, S.J., DeGloria, S.D. & Elliot, R. (1999) Index that quantifies topographic heterogeneity. *Intermountain
616 Journal of Sciences*, **5**, 23–27.
- 617 Riotte-Lambert, L. & Matthiopoulos, J. (2020) Environmental predictability as a cause and consequence of
618 animal movement. *Trends in Ecology & Evolution*, **35**, 163–174.
- 619 Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S. & Wright, I.W. (2000) The impact of cats and foxes
620 on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife
621 Research*, **27**, 223–235.
- 622 Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conserva-

- 623 tion. *Ecology Letters*, **12**, 982–998.
- 624 Robley, A., Gormley, A.M., Forsyth, D.M. & Triggs, B. (2014) Long-term and large-scale control of the
625 introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation*,
626 **180**, 262–269.
- 627 Salo, P., Banks, P.B., Dickman, C.R. & Korpimäki, E. (2010) Predator manipulation experiments: Impacts
628 on populations of terrestrial vertebrate prey. *Ecological Monographs*, **80**, 531–546.
- 629 Seidlitz, A., Bryant, K.A., Armstrong, N.J., Calver, M. & Wayne, A.F. (2020) Optimising camera trap
630 height and model increases detection and individual identification rates for a small mammal, the numbat
631 (*myrmecobius fasciatus*). *Australian Mammalogy*, **43**, 226–234.
- 632 Sih, A. (1980) Optimal behavior: Can foragers balance two conflicting demands? *Science*, **210**, 1041–1043.
- 633 Soglianai, D. & Mori, E. (2019) ‘The fox and the cat’: Sometimes they do not agree. *Mammalian Biology*, **95**,
634 150–154.
- 635 Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of
636 rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, **2**, 75–92.
- 637 Stobo-Wilson, A.M., Brandle, R., Johnson, C.N. & Jones, M.E. (2020) Management of invasive mesopredators
638 in the Flinders Ranges, South Australia: Effectiveness and implications. *Wildlife Research*, **47**, 720–730.
- 639 Stobo-Wilson, A.M., Murphy, B.P., Crawford, H.M., Dawson, S.J., Dickman, C.R., Doherty, T.S., Fleming,
640 P.A., Gentle, M.N., Legge, S.M., Newsome, T.M., Palmer, R., Rees, M.W., Ritchie, E.G., Speed, J.,
641 Stuart, J.-M., Thompson, E., Turpin, J. & Woinarski, J.C.Z. (2021a) Sharing meals: Predation on
642 Australian mammals by the introduced European red fox compounds and complements predation by feral
643 cats. *Biological Conservation*, **261**, 109284.
- 644 Stobo-Wilson, A.M., Murphy, B.P., Legge, S.M., Chapple, D.G., Crawford, H.M., Dawson, S.J., Dickman,
645 C.R., Doherty, T.S., Fleming, P.A., Gentle, M. & others. (2021b) Reptiles as food: Predation of Australian
646 reptiles by introduced red foxes compounds and complements predation by cats. *Wildlife Research*, **48**,
647 470–480.
- 648 Sun, C., Burgar, J.M., Fisher, J.T. & Burton, A.C. (2022) A cautionary tale comparing spatial count
649 and partial identity models for estimating densities of threatened populations. *Global Ecology and
650 Conservation*, e02268.
- 651 Takimoto, G. & Nishijima, S. (2022) A simple theory for the mesopredator release effect: When does an
652 apex predator protect their shared prey from a mesopredator? *Oikos*, e09021.
- 653 Thompson, C.M. & Gese, E.M. (2007) Food webs and intraguild predation: Community interactions of a

- 654 native mesocarnivore. *Ecology*, **88**, 334–346.
- 655 Towerton, A.L., Penman, T.D., Kavanagh, R.P. & Dickman, C.R. (2011) Detecting pest and prey responses
656 to fox control across the landscape using remote cameras. *Wildlife Research*, **38**, 208–220.
- 657 Wayne, A.F., Maxwell, M.A., Ward, C.G., Wayne, J.C., Vellios, C.V. & Wilson, I.J. (2017) Recoveries and
658 cascading declines of native mammals associated with control of an introduced predator. *Journal of*
659 *Mammalogy*, **98**, 489–501.
- 660 Wilson, R.R., Blankenship, T.L., Hooten, M.B. & Shivik, J.A. (2010) Prey-mediated avoidance of an intraguild
661 predator by its intraguild prey. *Oecologia*, **164**, 921–929.
- 662 Woinarski, J.C.Z., Burbidge, A.A. & Harrison, P.L. (2015) Ongoing unraveling of a continental fauna: Decline
663 and extinction of Australian mammals since European settlement. *Proceedings of the National Academy*
664 *of Sciences*, **112**, 4531–4540.
- 665 Woinarski, J.C.Z., Stobo-Wilson, A.M., Crawford, H.M., Dawson, S.J., Dickman, C.R., Doherty, T.S., Fleming,
666 P.A., Garnett, S.T., Gentle, M.N., Legge, S.M. & others. (2021) Compounding and complementary
667 carnivores: Australian bird species eaten by the introduced european red fox (*Vulpes vulpes*) and domestic
668 cat (*Felis catus*). *Bird Conservation International*, 1–17.
- 669 Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semi-
670 parametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical*
671 *Methodology)*, **73**, 3–36.
- 672 Wood, S.N. (2017) *Generalized Additive Models: An Introduction with r*. CRC press.
- 673 Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001) Viewing invasive species removal in a whole-ecosystem
674 context. *Trends in Ecology & Evolution*, **16**, 454–459.

675 **SUPPORTING INFORMATION**

676 *S1.1. Field surveys*

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

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

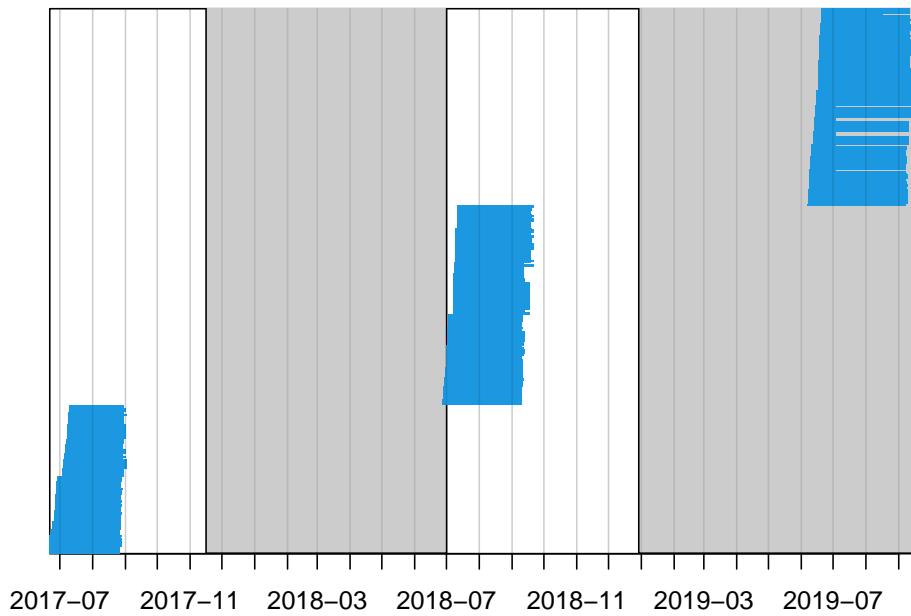


Figure S1: Camera-trap operation times in the Otway region, Australia. Each blue horizontal line represents one camera-trap deployment. Grey shading indicates periods of fox control in the impact landscape.

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.

693 *S1.2. Individual cat identification*

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

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

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

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

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

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

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

730 We ignored the few detections of cats which were obviously young enough to be dependent on a parent,
731 as these kittens do not have independent activity centres or movements and were not yet recruited into the
732 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.

733 S1.3. Feral cat detection plots

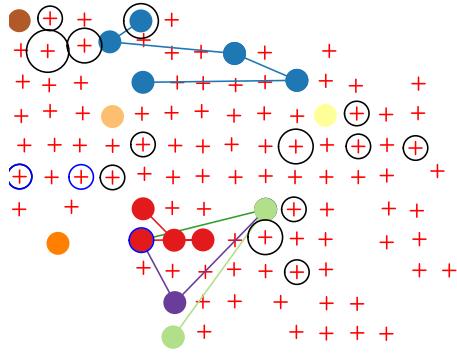
734 S1.3.1. Glenelg region

735 S1.3.1.1. Replicate 1.

736

737

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



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

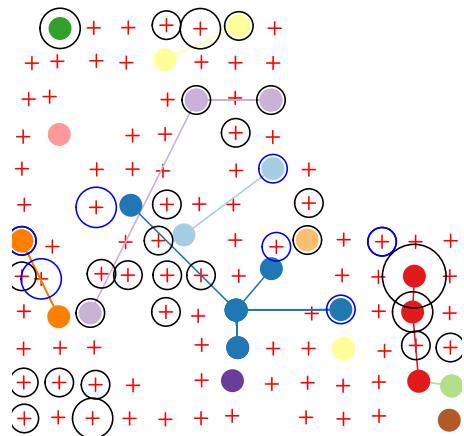


Figure S4: Feral cat detections in the first replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles 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).

738 S1.3.1.2. Replicate 2.

739

740

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

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

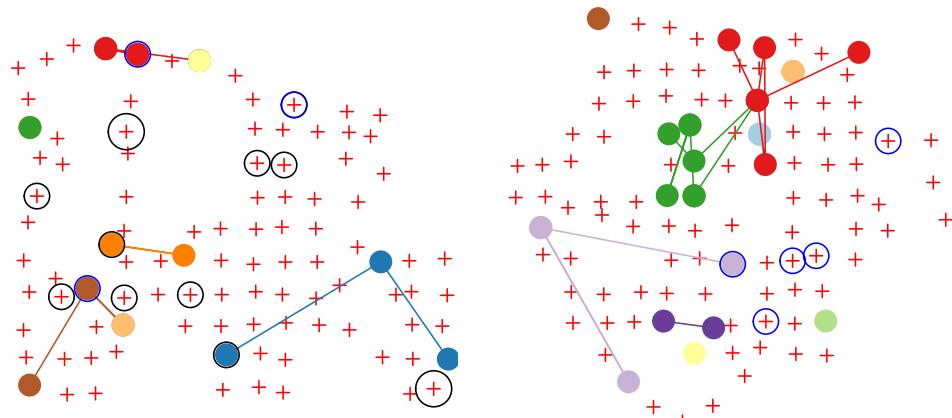


Figure S5: Feral cat detections in the second replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles 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).

741 S1.3.1.3. Replicate 3.

742

743

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

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

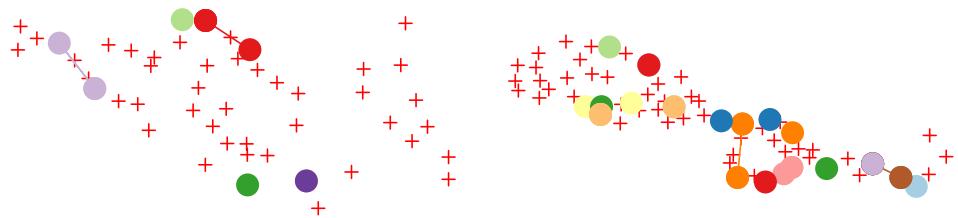


Figure S6: Feral cat detections in the third replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Fox control does not occur in the north (a; non-impact) but does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

744 S1.3.2. *Otway region*

745 S1.3.2.1. 2017.

746

747

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

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

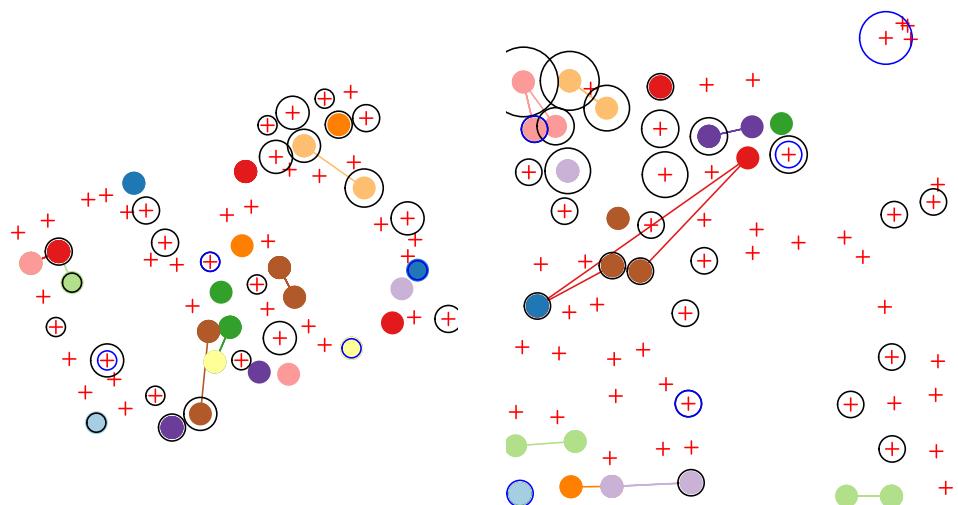


Figure S7: Feral cat detections in the Otway region, Australia, 2017. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling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

748 S1.3.2.2. 2018.

749

750

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

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

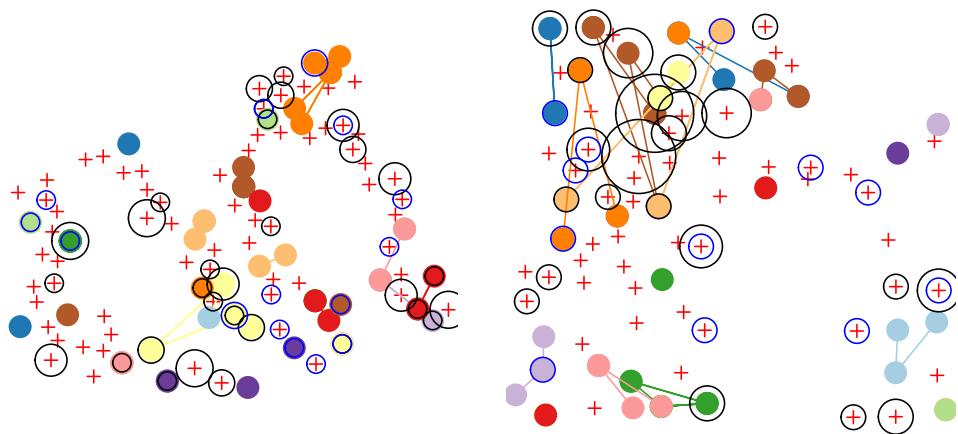


Figure S8: Feral cat detections in the Otway region, Australia, 2018. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling 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).

751 S1.3.2.3. 2019.

752

753

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

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

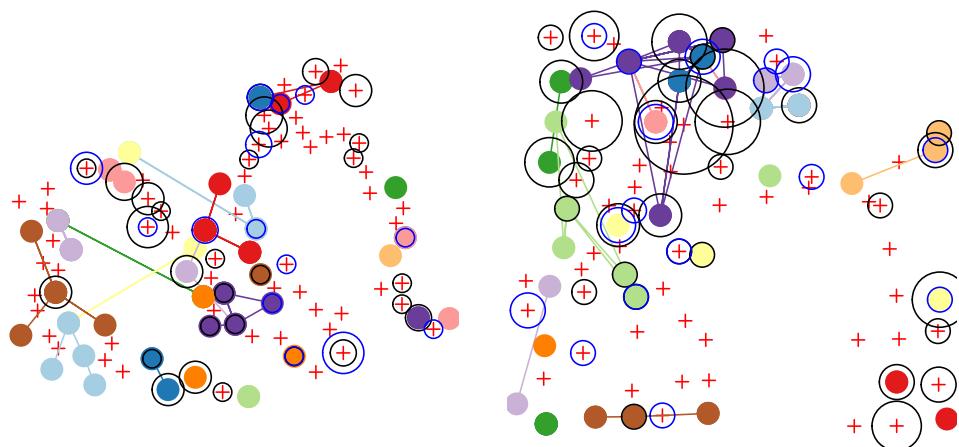


Figure S9: Feral cat detections in the Otway region, Australia, 2019. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling 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.

⁷⁵⁴ *S1.4. Fox spatial occurrence*

⁷⁵⁵ *S1.4.1. Glenelg region*

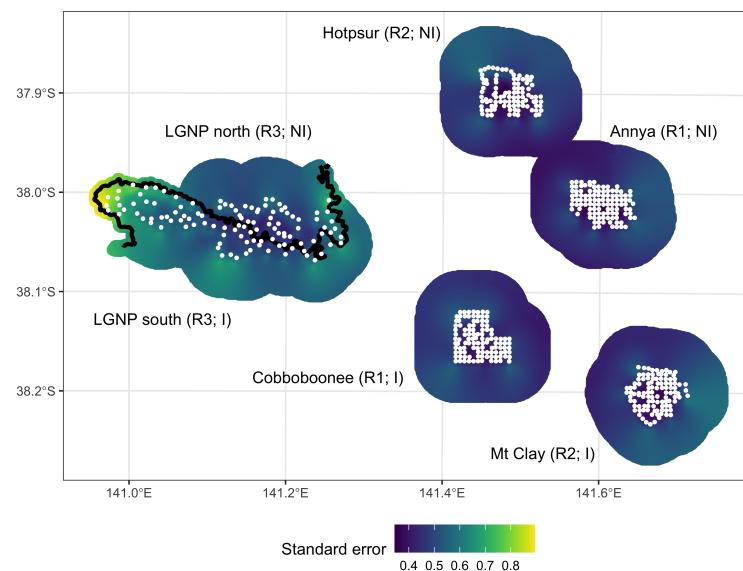


Figure S10: Standard error estimates around red fox occurrence probabilities derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg region, Australia. White dots represent camera-traps.

⁷⁵⁶ S1.4.2. *Otway Region*

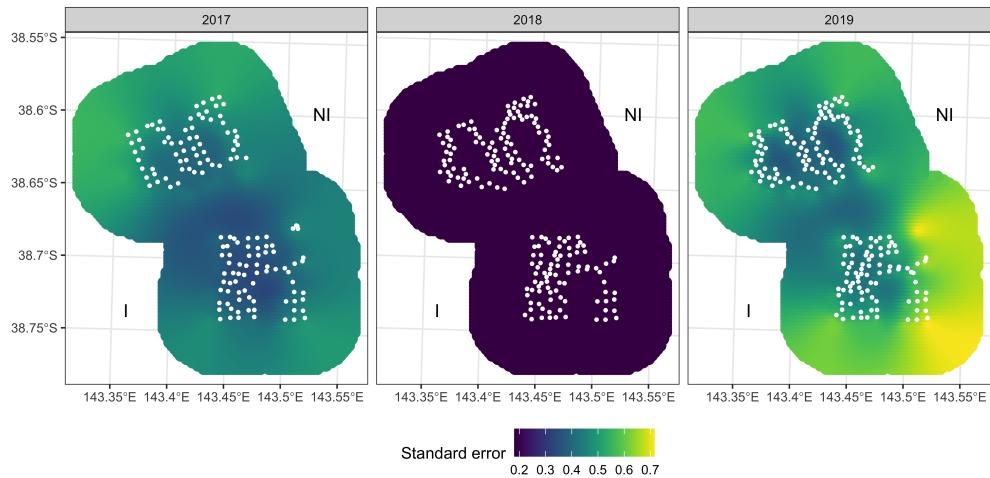


Figure S11: Standard error estimates around red fox occurrence probabilities derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape survey session in the Otway region, Australia. White dots represent camera-traps.

⁷⁵⁷ *S1.5. Vegetation categories*

⁷⁵⁸ We condensed the main Ecological Vegetation Class groupings (Department of Environment, Land, Water
⁷⁵⁹ & Planning 2020) into three categories for each region by merging similar groups. In the Glenelg region, we
⁷⁶⁰ merged dry forests with lowland forests. In the Otway region, we merged rainforests with wet forests, as well
⁷⁶¹ as merged dry forests and heathy woodlands. This resulted in three categories for each region: cleared land,
⁷⁶² heathy woodlands, and lowland forests (Glenelg region only) or wet forests (Otways region only).

⁷⁶³ A very small proportion of other Ecological Vegetation Class groupings were present in the habitat masks:
⁷⁶⁴ riparian scrubs or swampy scrubs and woodlands, coastal scrubs grasslands and woodlands, wetlands, riverine
⁷⁶⁵ grassy woodlands or forests, plains woodlands or forests, herb-rich woodlands. We removed these groups,
⁷⁶⁶ and interpolated cell values from the nearest of the three vegetation categories.

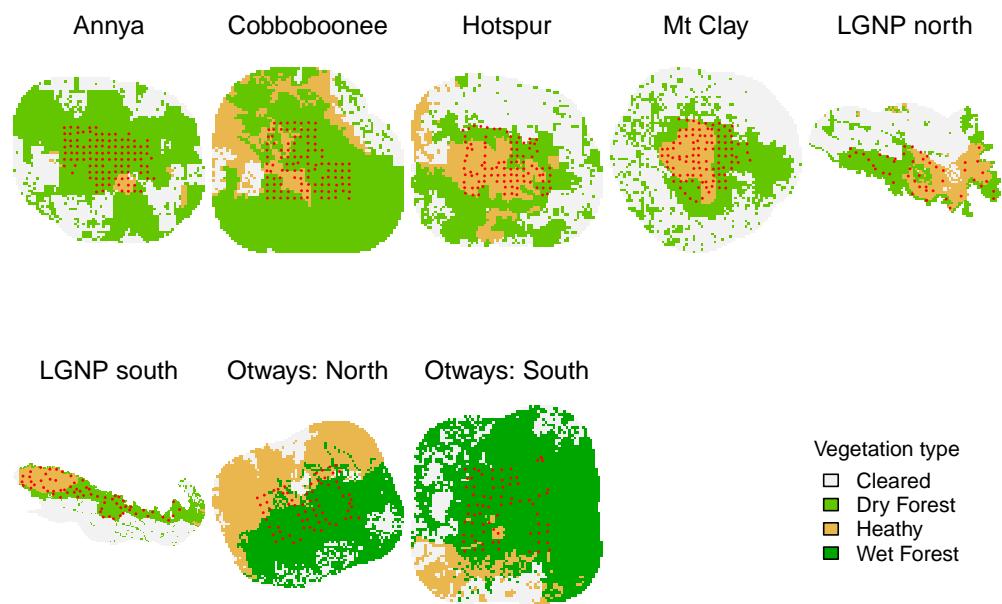


Figure S12: Condensed Ecological Vegetation Class groups in each study landscape used as habitat mask covariates in spatial mark-resight models (base models).

⁷⁶⁷ *S1.6. Spatial mark-resight models*

⁷⁶⁸ *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

769 *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