

# Invasive mesopredator release

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## Abstract

1. Background.

2. Methods.

3. Results.

4. *Synthesis and applications.*

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

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## 17 1. INTRODUCTION

18 Understanding species interactions is critical for effective invasive species management  
19 (Zavaleta et al., 2001). When several invasive species co-occur, management actions that  
20 suppress the dominant invasive species may inadvertently benefit subordinate invasive species  
21 (Jackson, 2015; Kuebbing & Nuñez, 2015). Subordinate invasive species may be released from  
22 direct top-down pressure following a decline in the dominant predator or benefit indirectly from  
23 an increase in availability of shared resources (often referred to as mesopredator or competitor  
24 release - Crooks & Soulé, 1999; Doherty & Ritchie, 2017; Ruscoe et al., 2011). The release of a  
25 subordinate invasive species, particularly predators, can have serious negative implications for  
26 native taxa and ecosystem function (Ballari et al., 2016; Courchamp et al., 1999). However,  
27 integrated predator management is often far more costly and less feasible than single species  
28 control, and so it is important to identify the extra cost if justified (Bode et al., 2015).

29 Most knowledge of predator interactions stems from unreplicated “natural experiments”  
30 (e.g. range contractions - Crooks & Soulé, 1999) or ad-hoc management interventions (e.g. in-  
31 vasive species eradications - Rayner et al., 2007). However, the occurrence, nature (positive or  
32 negative, direct or indirect) and strength of species interactions can vary among species assem-  
33 blages, predation risk, environmental productivity, management regimes, and other landscape  
34 contexts (Alston et al., 2019; Finke & Denno, 2004; Hastings, 2001). Replicating manage-  
35 ment programs in an experimental framework is logistically challenging, but important for  
36 understanding these complexities, discriminating between plausible hypotheses and producing  
37 generalisable results in order to inform effective pest management (Christie et al., 2019; Glen  
38 & Dickman, 2005; Smith et al., 2020).

39 Unbiased estimates of invasive predator density are vital for inferring native prey impacts on  
40 and for setting meaningful control targets (Moseby et al., 2019). However, controversy around  
41 the mesopredator release hypothesis has stemmed from the inability of traditional survey ap-  
42 proaches to separate behavioural and numerical population processes (Hayward et al., 2015;  
43 Stephens et al., 2015). These nonspatial approaches arbitrarily divide continuous landscapes  
44 into discrete spatial sampling units, but highly mobile predators can easily break model as-

45   sumptions by crossing these (Efford & Dawson, 2012). Additionally, the suppression of an apex  
46   predator may change the behaviour and density of a mesopredator, both of which impact detec-  
47   tion rates (Broadley et al., 2019; Rogan et al., 2019). And so, even with experimental designs,  
48   it is difficult to interpret changes in unidentified counts or presence-absence records of meso-  
49   predators in relation to apex predators. While spatially explicit capture-recapture methods  
50   have been developed to robustly estimate predator density by separating out behavioural and  
51   observational processes from population density, they have seldom been used experimentally or  
52   to investigate multispecies interactions (although, see Forsyth et al., 2019).

53    Predation by two invasive species, the red fox *Vulpes vulpes* and feral cat *Felis catus*, has  
54    played a major role in Australia’s high rates of mammalian extinction (Woinarski et al. 2019).  
55    Integrated invasive predator management programs are rare. Introduced red foxes (hereafter  
56    foxes) are far more commonly controlled than feral cats, as they are more susceptible to poison-  
57    baiting, have greater direct economic impacts and fewer legal impediments to their control  
58    (McLeod & Saunders, 2014; Reddiex et al., 2007). Nonetheless, feral cats are one of the most  
59    widespread and damaging vertebrate species (Doherty & Ritchie, 2017; Legge et al., 2020;  
60    Medina et al., 2011). As foxes are larger-bodied (~2 kg difference) and have high dietary  
61    overlap with feral cats (Catling, 1988; Glen et al., 2011; Short et al., 1999), the mesopredator  
62    release hypothesis predicts that feral cat impacts will increase as fox populations are managed  
63    (Soulé et al., 1988). This is alarming because feral cats are extremely difficult to manage in  
64    open populations (Fisher et al., 2015; Lazenby et al., 2015).

65    Evidence that foxes suppress feral cats is inconclusive (Hunter et al., 2018). In parts of Aus-  
66    tralia where the native apex mammalian predator (the dingo *Canis familiaris*) is functionally  
67    extinct and introduced red foxes are the largest terrestrial mammalian predator, four studies  
68    have observed an increase in feral cat detections following fox control (Marlow et al., 2015;  
69    Risbey et al., 2000; Stobo-Wilson et al., 2020). However, two other studies in similar systems  
70    did not see any change (Molsher et al., 2017; Towerton et al., 2011). One study with spatial  
71    replication detected an increase at one site but not another (Davey et al., 2006), and one study  
72    observed a decrease in feral cat activity (Claridge et al., 2010). No previous study has directly

73 estimated feral cat density in response to fox control.

74 In this study, we experimentally investigated the role of introduced foxes in top-down sup-  
75 pression of feral cat density in two regions of south-eastern Australia. Foxes and feral cats are  
76 the only functional terrestrial mammalian predators in these regions, and each region included  
77 at least one area in which foxes were subject to continuous lethal poison-baiting (hereafter  
78 “impact landscape”), and a paired area where foxes were not controlled (hereafter “non-impact  
79 landscape”). This allowed a sharp focus on the interactions between the two invasive predators,  
80 across a gradient of apex predator (fox) occupancy and landscape productivity. We tested for  
81 a direct effect of fox control on feral cat density using traditional experimental approaches: a  
82 replicated Control-Impact design in the region with long-term fox control, and a Before-After  
83 Control-Impact Paired Series (BACIPS) design in the region with newly implemented fox con-  
84 trol. We also tested for direct associations between feral cat density and spatial fox occupancy  
85 (derived using generalised additive models) in each region, as well as investigated the relative  
86 importance of fine or broad scale fox measurements. In accordance with the mesopredator  
87 release hypothesis, we predicted that (1) fox control would increase feral cat density, and (2)  
88 feral cat density would be negatively correlated with spatial fox occupancy. We based inference  
89 on spatial mark-resight models of feral cat density and information criteria methods.

## 90 2. MATERIALS AND METHODS

### 91 2.1. Study area

92 We conducted our study across two regions of south-west Victoria, Australia (Fig. 1).  
93 The native temperate forests in both regions are fragmented to varying degrees, primarily by  
94 livestock farming and tree plantations. Although once widespread, dingoes are now absent  
95 throughout, and a native mesopredator, the tiger quoll *Dasyurus maculatus*, is long absent  
96 from the Glenelg region and recently absent in the Otway Ranges (last sighted in 2014 despite  
97 extensive camera-trapping). The terrestrial mammalian predator guild is therefore depauper-  
98 ate, with the introduced fox and feral cat being the primary functional mammalian terrestrial  
99 predators; birds of prey and snakes are the only other predators present.

100 Our study landscapes in the Glenelg region, Gunditjmara country, are primarily lowland  
101 forest (with an overstorey of *Eucalyptus obliqua* and *E. ovata*, a sparse midstorey and a fern-  
102 rich understorey) and heathy woodland (with an overstorey of *E. baxteri s.l.* and *E. willisii*, a  
103 sparse midstorey and a diverse understorey of narrow or ericoid-leaved shrubs). It has gently  
104 undulating terrain and frequently experiences prescribed burns and wildfires, creating a mosaic  
105 of fire histories and vegetation complexity. The area receives an average annual rainfall of  
106 700 mm, with average minimum temperatures of 8.1°C and maximum of 17.6°C (*Bureau of*  
107 *Meteorology*, 2021).

108 Our study landscapes in the Otway region were in the western section of the Otway Ranges,  
109 Gadubanud country. Here, the vegetation is a mosaic of shrubby wet forest and cool tem-  
110 perate rainforest, with an overstorey of tall eucalyptus species (primarily *E. regnans*), *Acacia*  
111 *melanoxylon* and *Nothofagus cunninghamii*. The midstorey is dominated by tree ferns, *Acacia*  
112 *verticillata*, *Pomaderris aspera* and *Olearia argophylla*. The understorey predominantly com-  
113 prises a dense layer of ferns and graminoids but can be relatively sparse in steep rainforest  
114 gullies. Maximum daily temperatures average 19.3°C in summer and 9.5°C in winter; annual  
115 rainfall averages 1955 mm (*Bureau of Meteorology*, 2021). This region rarely experiences fire  
116 and is nearly ten times more rugged (based on the terrain ruggedness index (Riley et al., 1999)

117 averaged within a 10 m radius of each camera-trap site).

## 118 2.2. *Lethal fox control*

119 Across broad sections of each region, government land managers conduct ongoing fox control  
120 for biodiversity conservation. Manufactured poison baits (FoxOff, Animal Control Technologies,  
121 Somerton) containing 3 mg of sodium mono-fluoroacetate (1080) are buried at a depth of 10 cm  
122 at 1-km intervals along accessible forest tracks and roads (Fig. 1). Different road densities  
123 across the two regions therefore result in variable poison-bait densities. In the Glenelg region,  
124 fox control in the impact landscapes has been ongoing since October 2005, with baits checked  
125 and replaced fortnightly (Robley et al., 2014). In the Otway region, baiting commenced in  
126 the impact landscape in November 2017. Poison baits were replaced weekly for six weeks  
127 until December 2017, before changing to monthly bait replacement until July 2018. The fox  
128 control program then lapsed for approximately six months until December 2018 due to logistical  
129 constraints, when monthly bait replacement recommenced for the duration of our study (Fig.  
130 S1).

## 131 2.3. *Study design and camera-trapping*

132 We designed experiments around the implementation of fox poison-baiting in each region.  
133 We simultaneously surveyed one impact and one non-impact landscape at a time using camera-  
134 traps. Each landscape pair was chosen based on similarity in landscape context, namely vege-  
135 tation groups, with the aim of maintaining spatial independence with respect to predator range  
136 movements.

137 In the Glenelg region, we used a replicated control-impact design to test for differences in  
138 areas that have been poison-baited for foxes for more than 13 years compared with unbaited  
139 areas. We deployed a pair of camera-trapping grids in Cobboboonee National Park (impact)  
140 and Annya State Forest (non-impact) in January – April 2018, then moved these cameras to  
141 Mt Clay State Forest/Narrawong Flora Reserve (hereafter “Mt Clay”; impact) and Hotspur

142 State Forest (non-impact) in April – June 2018 (Fig. S3). Each grid was separated by at least  
143 8 km, a distance very unlikely to be traversed regularly by these invasive predators (Hradsky  
144 et al., 2017).

145 In the Otway region, we undertook a BACIPS study to assess changes related to the intro-  
146 duction of the fox control program. We deployed camera-trap grids in an impact – non-impact  
147 pair of landscapes in June – September from 2017 to 2019, in the Great Otway National Park  
148 and Otway Forest Park (Fig. S1). Our first survey occurred approximately three months be-  
149 fore fox-baiting began. The second survey was conducted six months post-commencement of  
150 fox-baiting, however poison bait replacement lapsed at the beginning of the survey until nearly  
151 three months afterwards (Fig. S1). Fox-baiting recommenced six months prior to the start of  
152 the final survey (Fig. S1). The impact and non-impact landscapes were at least 4.2 km apart, a  
153 distance unlikely to be traversed by these invasive predators, although possible (Hradsky et al.,  
154 2017). In this study, and a concurrent study which identified individual foxes through genetic  
155 sampling (M. Le Pla, in review), we found no evidence of either species of predator moving  
156 between these landscapes.

157 In each of the six survey landscapes, we deployed a grid of camera-traps (67 – 110 cameras;  
158 mean = 94), with sites spaced on average 448 m apart (range: 194 – 770 m; Fig. 1). At each  
159 site, we deployed a single Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an infrared  
160 flash and temperature-in-motion detector on a tree, facing a lure of oil-absorbing cloth doused  
161 in tuna oil (Fig. S2). More information on the camera-trapping methods is provided in Section  
162 1.2 of the Supporting Information. Overall, we deployed 938 functional camera-traps, which  
163 operated for an average of 68 days (range: 12 – 93 days), totalling 62,415 trap nights (Table 1)  
164 across a total study duration of five months and three years in the Glenelg and Otways regions  
165 respectively (Fig. S1).

#### 166 2.4. Individual feral cat identification

167 We added a species metadata tag for each camera-trap image, compiled species record tables  
168 and extracted feral cat photos for individual identification using the “camtrapR” R package

169 (Niedballa et al., 2016). We sorted the cats into five categories based on their coat type:  
170 black, spotty tabby, swirly tabby, ginger and other (cats with multiple colour blends or other  
171 distinctive coats; Fig. S3). We did not attempt to identify any black cats, even the few with  
172 white splotches on their underside, as these markings could not always be seen. Within the  
173 other four coat categories, multiple observers identified individual cats based on their unique  
174 coat patterns where possible. Detailed information on this process is provided in Section 2 of  
175 the Supporting Information.

## 176 2.5. *Spatial fox occupancy*

177 Spatial mark-resight models require density covariate values for each grid cell density is  
178 estimated across (or a single value for the entire session - each camera-trap grid deployment  
179 in our case), and so we could not directly use the fox data from the camera-trap sites as  
180 independent variables. We therefore used the presence-absence data for each camera-trap site to  
181 generate a spatially-interpolated layer of fox occupancy probability using binomial generalised  
182 additive models (Wood, 2017). We did so using the “mgcv” R package (version 1.3.1; Wood,  
183 2011). We modelled fox presences and absences (response variable) across space (explanatory  
184 variable) separately for each region, with a duchon spline spatial smooth as these provide better  
185 predictions at the edge of surveyed space than other splines (Miller & Wood, 2014). In the  
186 Otway region, we included a random intercept for each camera-trap site to account for repeat  
187 sampling and did not share spatial information across the years (using a “by variable” smooth  
188 with year as a factor). Differences in camera-trap deployment lengths were accounted for using  
189 a model offset. We did not use occupancy-detection models because factors which impact fox  
190 detectability on camera-traps may also impact fox detectability to feral cats - which is more  
191 important than predictive performance in this context. We predicted GAM estimates into the  
192 respective spatial mark-resight habitat mask and trapfile (detailed below).



193 2.6. *Spatial mark-resight models of feral cat density*

194 We used a spatial capture-recapture approach to estimate feral cat density (Borchers &  
195 Efford, 2008). These models consider counts of detections and non-detections of individual  
196 animals at trap locations (accounting for trap-specific survey effort) to estimate the location of  
197 each individual’s activity centre. These models generally assume that individuals have approx-  
198 imately circular home ranges and spend the majority of time in the centre of which (“activity  
199 centre”). The probability of observing an individual therefore decreases with distance from  
200 the activity centre. Two detectability parameters govern this process:  $g_0$ , the probability of  
201 detecting an individual per occasion in their activity centre and  $\sigma$ : a spatial scale param-  
202 eter which is relative to the home range size. Multiple candidate shapes for this decline in  
203 detectability with distance from the activity centre (“detection function”) can be modelled.

204 Spatial capture-recapture models have been extended to consider situations where not all  
205 individuals in a population are identifiable (i.e. marked) (Chandler & Royle 2013). These spa-  
206 tial mark-resight models typically assume unmarked individuals to be a random sample of the  
207 population, sharing the same detection process as marked individuals, and so allow density to  
208 be estimated for the entire population. Spatial mark-resight models have four categories of  
209 sightings: (1) marked individuals - detections with known identities identified to the individ-  
210 ual level at least once each session, (2) marked but unidentifiable individuals - detections of  
211 individuals with known identities, but for which the individual could not be determined in a  
212 given session (we had no detections in this category), (3) unmarked individuals - unidentified  
213 detections which definitely do not belong to the first two categories (in our study, this category  
214 comprised black cats) and (4) mark status uncertain - detections in which individuals cannot  
215 be identified and it is not clear whether the individual is of the marked or unmarked category.

216 We used closed population, sighting-only, spatial mark-resight to estimate feral cat density  
217 using the maximum likelihood “secr” R package (Efford, 2021). Detections of the “mark status  
218 uncertain” category cannot be handled in the “secr” R package, we therefore added them to the  
219 unmarked detections rather than discard them (Moseby et al., 2020). We condensed detection  
220 histories of each mark category to a binary presence-absence record per each camera-trap for

221 a 24-hour length duration (“occasion”), beginning at midday. We ran separate models for  
222 each region and treated each camera-trap grid deployment as a “session”. We created a 4000  
223 metre buffer zone around each camera-trap location to estimate feral cat density across, with  
224 a grid cell resolution of 200 metres. These habitat mask specifications were based on initial  
225 models and our knowledge of feral cats in these area - ensuring density is estimated over a large  
226 enough area to encompass the activity centres of all feral cats exposed to our camera-traps,  
227 at a fine enough scale to minimise bias in density estimates. We tested the half-normal and  
228 exponential detection functions in each region, carrying forward the function with the lowest  
229 Akaike’s Information Criterion score adjusted for small sample size (AICc) for all subsequent  
230 model fitting (Burnham & Anderson, 2004).

231 For each region, we ran three sets of models: (1) to choose the best “null model” to carry  
232 through into other model sets (2) to experimentally evaluate the effect of fox control on feral cat  
233 density, and (3) test fine-scale association between spatial fox occupancy and feral cat density.  
234 We assessed the relative performance of models in each set using AICc score, with models  
235 within 2 delta AICc of the top-ranked model considered strongly supported compared to the  
236 other candidate models (Burnham & Anderson, 2004).

237 We compared four candidate “null models” (1) for each region. The first model (1A) was  
238 the simplest - density and detectability parameters were held constant. Model 1B included an  
239 effect of vegetation group on feral cat density (with detectability parameters constant). For  
240 this model, we condensed Ecological Vegetation Class groupings (DELWP, 2020) into three  
241 categories for each region: cleared land, heathy woodlands, lowland forests (Glenelg region  
242 only) and wet forests (Otways region only). Detailed information on this process is provided in  
243 Section X of the Supporting Information. Model 1C included a linear time trend on  $g_0$ , keeping  
244 density and sigma constant - because the potency of the tuna oil lure likely decreased over the  
245 survey duration (Rees et al., 2019). The fourth model (1D) was a combination of model 1B  
246 and 1C: density  $\sim$  vegetation group,  $g_0 \sim T$ , sigma  $\sim 1$ .

247 We compared two types of experimental models on feral cat density (2) to their respective  
248 null model in each region. The first was a standard control-impact or before-after-control impact

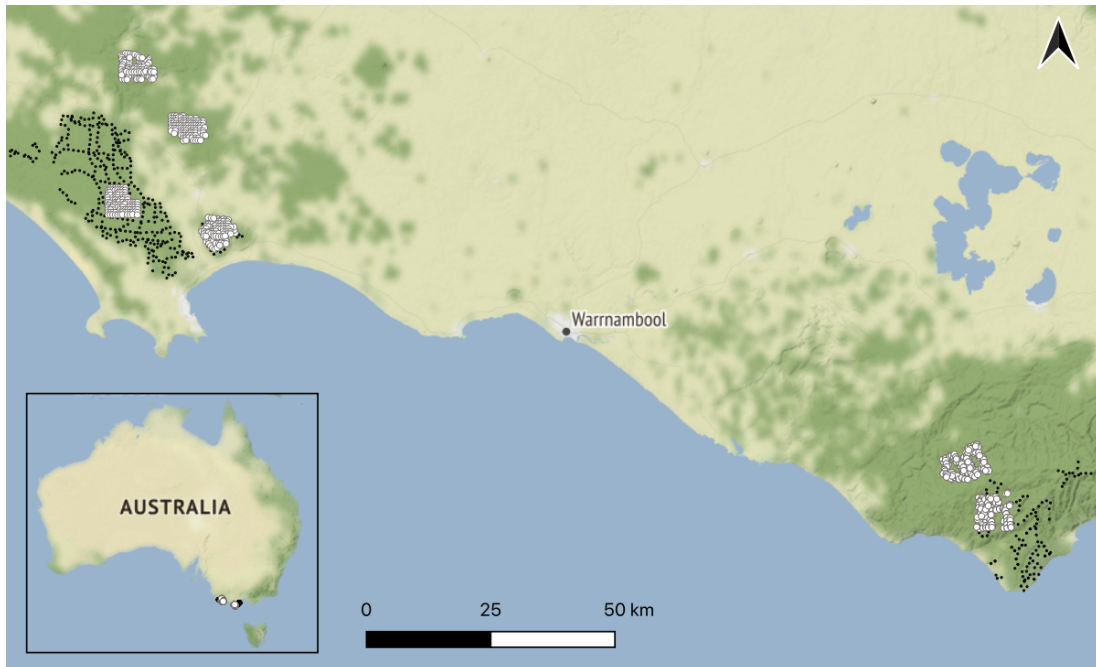


Figure 1: Locations of our six study landscapes in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots, the locations of fox poison-bait stations are denoted by smaller black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated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

249 model specification in the Glenelg and Otways regions respectively - with the effect of fox-  
 250 baiting averaged across space and time replicates. The second experimental models modelled  
 251 fox-baiting effects separately for each space and time replicate in the Glenelg and Otways regions  
 252 respectively. We ran these models twice: once where detectability was constant, and another  
 253 where detectability parameters mirrored the respective density parameter specification.

254 In the Glenelg region, we fit a standard control-impact model using a binary impact (fox-  
 255 baited) or non-impact categorical covariate. In the Otway Ranges, we fit a standard before-  
 256 after-control-impact model with an interaction between landscape (impact or non-impact) and  
 257 time period (before [2017] or after [2018-19] poison-baiting began).

258 We expected that foxes would impact both detectability parameters for feral cats concur-  
 259 rently, and so, always specified  $g_0$  and  $\sigma$  consistently (Efford & Mowat, 2014).

### 3. RESULTS

Table 1: Camera-trap surveys and feral cat spatial capture-recapture summary statistics.

Land- scape	Fox control?	Camera- traps	Trap nights	Identified cats	Identified detections	Unidentified detections	Unmarked detections
Annya	no	110	8000	9	23	3	20
Cobbob	yes	110	7752	13	35	9	37
Hotspur	no	99	6085	8	22	3	13
Mt Clay	yes	106	5451	10	33	5	0
South 2017	no	73	3565	20	62	8	46
North 2017	no	67	7099	26	60	4	48
South 2018	yes	85	7838	24	75	12	62
North 2018	no	103	4543	30	90	17	59
South 2019	yes	86	6077	25	133	22	101
North 2019	no	99	7150	27	90	23	58

*Note: There is a maximum of one detection per each 24-hour occasion.*

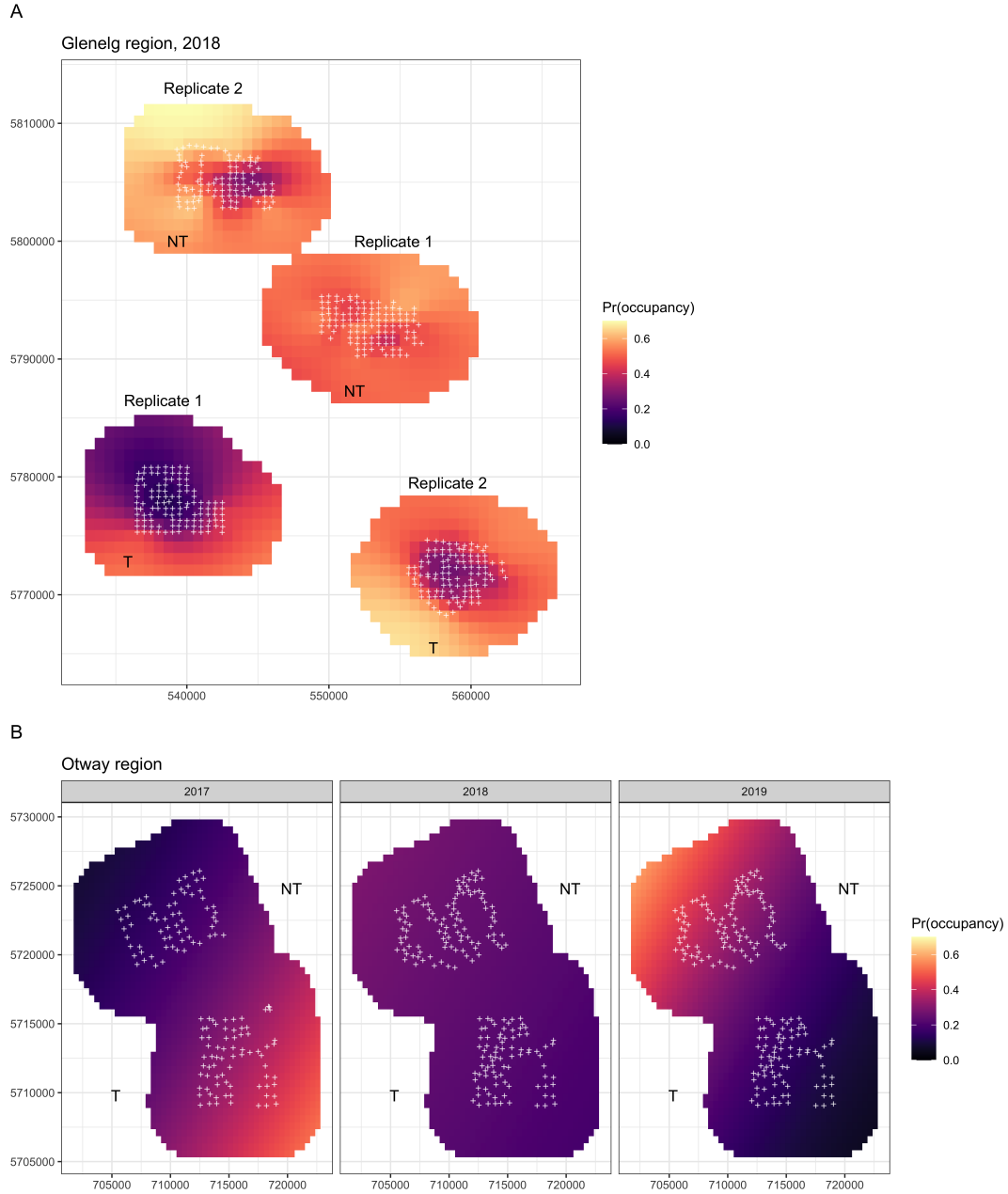


Figure 2: Fox probability of occupancy derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg (A) and Otways (B) regions. Estimates were used as predictor variables in the feral cat spatial mark-resight models.

Table 2: Akaike’s Information Criterion values adjusted for small sample size for top-5 ranked feral cat density models in each region (ordered in decreasing AICc scores).

Region	Density	Detectability	Parameters	logLik	dAICc	AICcwt
Glenelg	fox_occ_avg	1	4	-985.5	0	0.64
Glenelg	fox_occ_avg	fox_occ_avg	6	-984.4	3.35	0.12
Glenelg	pair *	1	6	-985	4.4	0.07
	foxbaited_01					
Glenelg	pair +	1	5	-986.5	4.75	0.06
	foxbaited_01					
Glenelg	fox_occ	1	4	-988.3	5.65	0.04
Glenelg	foxbaited_01	1	4	-988.9	6.91	0.02
Otways	fox_occ	fox_occ	6	-3543	0	0.37
Otways	1	fox_occ	5	-3545	1.58	0.17
Otways	1	fox_occ_avg	5	-3545	2.27	0.12
Otways	fox_occ_avg	fox_occ_avg	6	-3544	2.44	0.11
Otways	1	foxbaited_01	5	-3546	3.64	0.06
Otways	grid +	foxbaited_01	7	-3544	3.8	0.06
	before_after					
Otways	foxbaited_01	foxbaited_01	6	-3545	3.89	0.05
Otways	grid *	foxbaited_01	8	-3543	5.76	0.02
	before_after					
Otways	grid + year	foxbaited_01	8	-3543	5.89	0.02
Otways	fox_occ	1	4	-3548	6.65	0.01

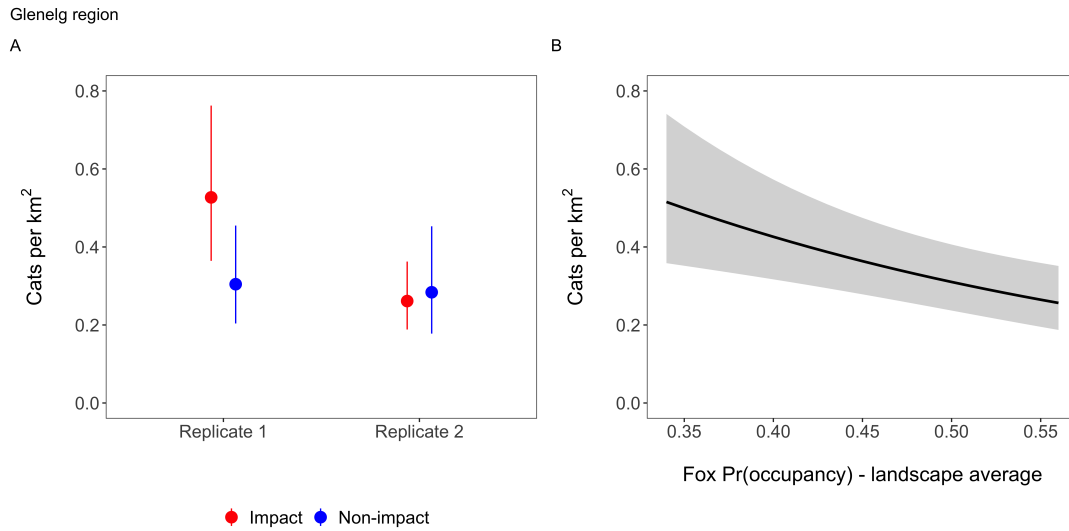


Figure 3: Best-ranked experimental (A) and correlative (B) models of feral cat density in the Glenelg region, Australia. There was statistical evidence (i.e., 95% confidence intervals of the parameter estimates did not overlap zero) that feral cat density was higher in the landscape with fox-baiting (impact) than the associated landscape without fox-baiting (non-impact) for the first replicate, but not for the second replicate (A). The best-ranked model predicted that feral cat density declined with the probability of fox occupancy at the landscape level (B). Error bars and the shaded region indicate 95% confidence intervals.





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## 7. AUTHORS' CONTRIBUTIONS

M.W.R, B.H, J.H.P, B.A.W and A.R conceived the ideas and designed methodology; M.W.R, J.H.P, M.LP, E.K.B and B.H collected the data; M.W.R analysed the data; M.W.R led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## 290 **8. OPEN RESEARCH**

291     Raw data and code are on Github link xx.

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

## 293 REFERENCES

- 294 Alston, J., Maitland, B., Brito, B., Esmaceli, S., Ford, A., Hays, B., Jesmer, B., Molina,  
295 F., & Goheen, J. (2019). Reciprocity in restoration ecology: When might large carnivore  
296 reintroduction restore ecosystems? *Biological Conservation*, 234, 82–89.
- 297 Ballari, S. A., Kuebbing, S. E., & Nuñez, M. A. (2016). Potential problems of removing  
298 one invasive species at a time: A meta-analysis of the interactions between invasive vertebrates  
299 and unexpected effects of removal programs. *PeerJ*, 4, e2029.
- 300 Bode, M., Baker, C. M., & Plein, M. (2015). Eradicating down the food chain: Opti-  
301 mal multispecies eradication schedules for a commonly encountered invaded island ecosystem.  
302 *Journal of Applied Ecology*, 52(3), 571–579.
- 303 Borchers, D. L., & Efford, M. G. (2008). Spatially explicit maximum likelihood methods  
304 for capture–recapture studies. *Biometrics*, 64(2), 377–385.
- 305 Broadley, K., Burton, A. C., Avgar, T., & Boutin, S. (2019). Density-dependent space use  
306 affects interpretation of camera trap detection rates. *Ecology and Evolution*, 9(24), 14031–  
307 14041.
- 308 *Bureau of meteorology*. (2021). Climate Data Online URL; (accessed May 2021). <http://www.bom.gov.au/climate/data/>  
309
- 310 Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding aic and  
311 bic in model selection. *Sociological Methods & Research*, 33(2), 261–304.
- 312 Catling, P. (1988). Similarities and contrasts in the diets of foxes, *vulpes vulpes*, and cats,  
313 *felis catus*, relative to fluctuating prey populations and drought. *Wildlife Research*, 15(3),  
314 307–317.
- 315 Christie, A. P., Amano, T., Martin, P. A., Shackelford, G. E., Simmons, B. I., & Sutherland,  
316 W. J. (2019). Simple study designs in ecology produce inaccurate estimates of biodiversity

317 responses. *Journal of Applied Ecology*, 56(12), 2742–2754.

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

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

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

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

328 DELWP. (2020). *Bioregions and evc benchmarks*. Victorian Government Department  
329 of Environment, Land, Water; Planning, Melbourne. Accessed June 2021). [https://www.](https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks)  
330 [environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks](https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks)

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

333 Efford, M. G. (2021). *Secr: Spatially explicit capture-recapture models*. R package version  
334 4.4.4. (accessed June 2021). <http://CRAN.R-project.org/package=secr>

335 Efford, M. G., & Dawson, D. K. (2012). Occupancy in continuous habitat. *Ecosphere*, 3(4),  
336 1–15.

337 Finke, D. L., & Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature*,  
338 429(6990), 407–410.

339 Fisher, P., Algar, D., Murphy, E., Johnston, M., & Eason, C. (2015). How does cat be-  
340 haviour influence the development and implementation of monitoring techniques and lethal

341 control methods for feral cats? *Applied Animal Behaviour Science*, 173, 88–96.

342 Forsyth, D. M., Ramsey, D. S., & Woodford, L. P. (2019). Estimating abundances, densities,  
343 and interspecific associations in a carnivore community. *The Journal of Wildlife Management*,  
344 83(5), 1090–1102.

345 Glen, A., Pennay, M., Dickman, C., Wintle, B., & Firestone, K. (2011). Diets of sympatric  
346 native and introduced carnivores in the barrington tops, eastern australia. *Austral Ecology*,  
347 36(3), 290–296.

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

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

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

355 Hradsky, B. A., Robley, A., Alexander, R., Ritchie, E. G., York, A., & Di Stefano, J. (2017).  
356 Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *vulpes*  
357 *vulpes*. *Scientific Reports*, 7(1), 1–12.

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

361 Jackson, M. C. (2015). Interactions among multiple invasive animals. *Ecology*, 96(8), 2035–  
362 2041.

363 Kuebbing, S. E., & Nuñez, M. A. (2015). Negative, neutral, and positive interactions among  
364 nonnative plants: Patterns, processes, and management implications. *Global Change Biology*,

365 21(2), 926–934.

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

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

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

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

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

380 Miller, D. L., & Wood, S. N. (2014). Finite area smoothing with generalized distance splines.  
381 *Environmental and Ecological Statistics*, 21(4), 715–731.

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

385 Moseby, K. E., Letnic, M., Blumstein, D. T., & West, R. (2019). Understanding predator  
386 densities for successful co-existence of alien predators and threatened prey. *Austral Ecology*,  
387 44(3), 409–419.

388 Moseby, K., McGregor, H., & Read, J. (2020). Effectiveness of the felixer grooming trap for

the control of feral cats: A field trial in arid south australia. *Wildlife Research*, 47(8), 599–609.

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). CamtrapR: An r package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7(12), 1457–1462.

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

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

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

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

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S., & Wright, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of heirisson prong, western australia. II. A field experiment. *Wildlife Research*, 27(3), 223–235.

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

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

Ruscoe, W. A., Ramsey, D. S., Pech, R. P., Sweetapple, P. J., Yockney, I., Barron, M. C.,

- 413 Perry, M., Nugent, G., Carran, R., Warne, R., & others. (2011). Unexpected consequences of  
414 control: Competitive vs. Predator release in a four-species assemblage of invasive mammals.  
415 *Ecology Letters*, 14(10), 1035–1042.
- 416 Short, J., Calver, M. C., & Risbey, D. A. (1999). The impact of cats and foxes on the small  
417 vertebrate fauna of heirisson prong, western australia. I. Exploring potential impact using diet  
418 analysis. *Wildlife Research*, 26(5), 621–630.
- 419 Smith, J. A., Suraci, J. P., Hunter, J. S., Gaynor, K. M., Keller, C. B., Palmer, M. S.,  
420 Atkins, J. L., Castañeda, I., Cherry, M. J., Garvey, P. M., & others. (2020). Zooming in on  
421 mechanistic predator–prey ecology: Integrating camera traps with experimental methods to  
422 reveal the drivers of ecological interactions. *Journal of Animal Ecology*, 89(9), 1997–2012.
- 423 Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., & Hill, S. (1988). Re-  
424 constructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands.  
425 *Conservation Biology*, 2(1), 75–92.
- 426 Stephens, P. A., Pettorelli, N., Barlow, J., Whittingham, M. J., & Cadotte, M. W. (2015).  
427 *Management by proxy? The use of indices in applied ecology*. Wiley Online Library.
- 428 Stobo-Wilson, A. M., Brandle, R., Johnson, C. N., & Jones, M. E. (2020). Management of  
429 invasive mesopredators in the flinders ranges, south australia: Effectiveness and implications.  
430 *Wildlife Research*, 47(8), 720–730.
- 431 Towerton, A. L., Penman, T. D., Kavanagh, R. P., & Dickman, C. R. (2011). Detecting  
432 pest and prey responses to fox control across the landscape using remote cameras. *Wildlife*  
433 *Research*, 38(3), 208–220.
- 434 Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood  
435 estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society:*  
436 *Series B (Statistical Methodology)*, 73(1), 3–36.
- 437 Wood, S. N. (2017). *Generalized additive models: An introduction with r*. CRC press.



438       Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in  
439   a whole-ecosystem context. *Trends in Ecology & Evolution*, 16(8), 454–459.