

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 *melanoxydon* 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 σ : 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 ~ 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

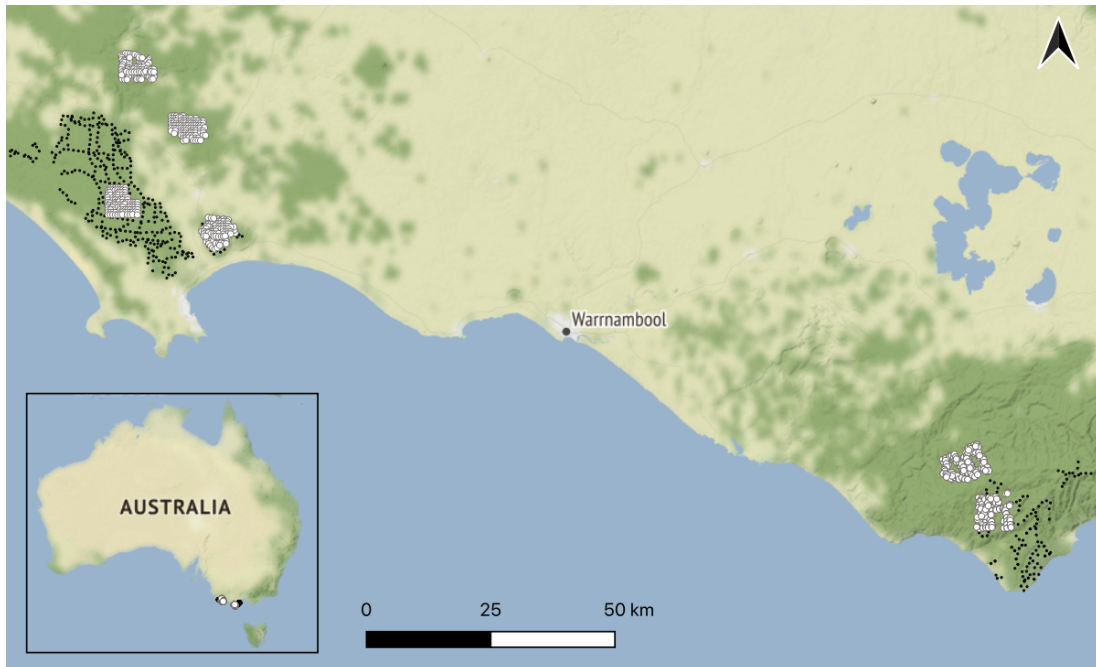


Figure 1: Locations of our six study landscapes in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots, the locations of fox poison-bait stations are denoted by smaller black dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated 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 σ 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.

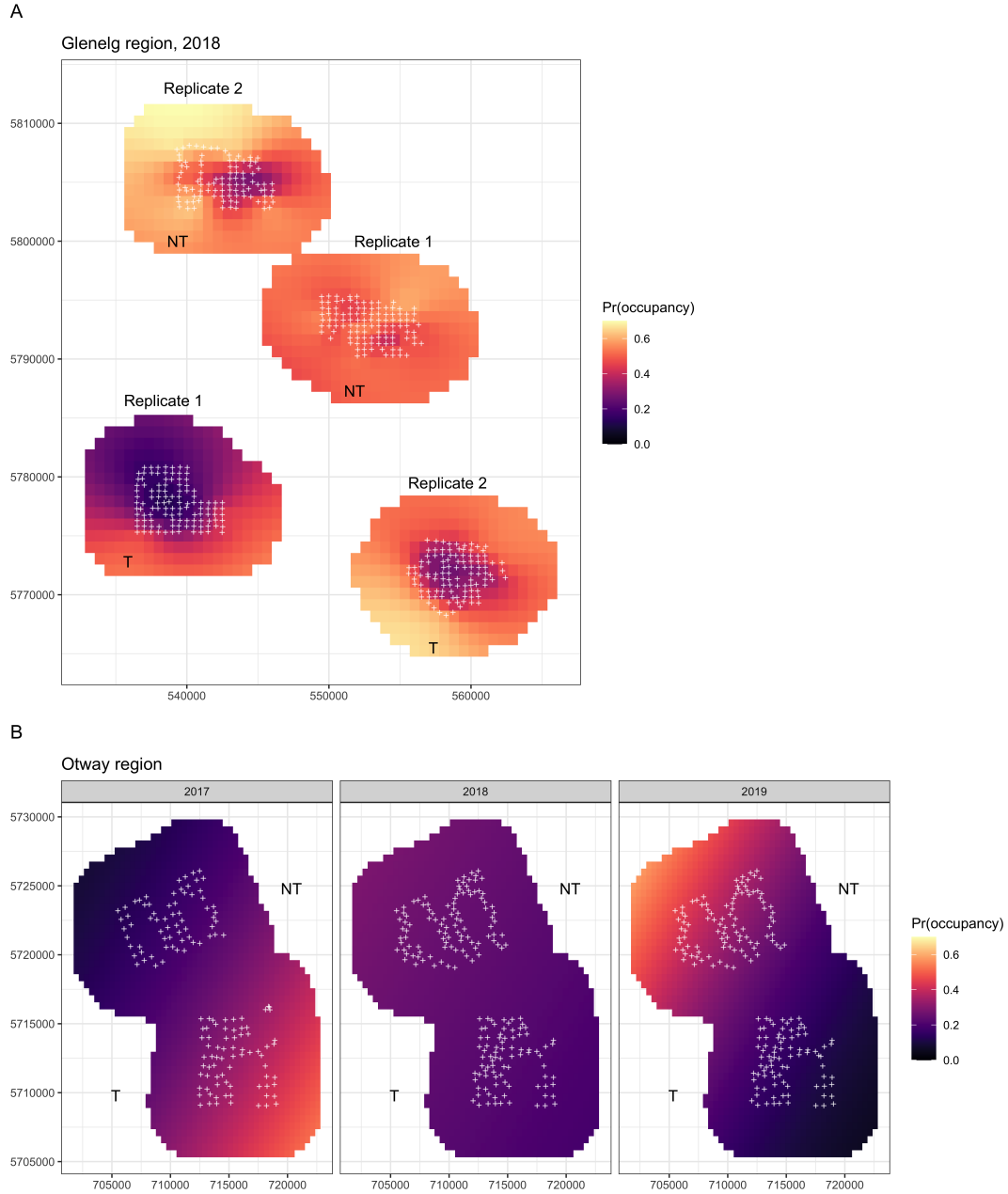


Figure 2: Fox probability of occupancy derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg (A) and Otways (B) regions. Estimates were used as predictor variables in the feral cat spatial mark-resight models.

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

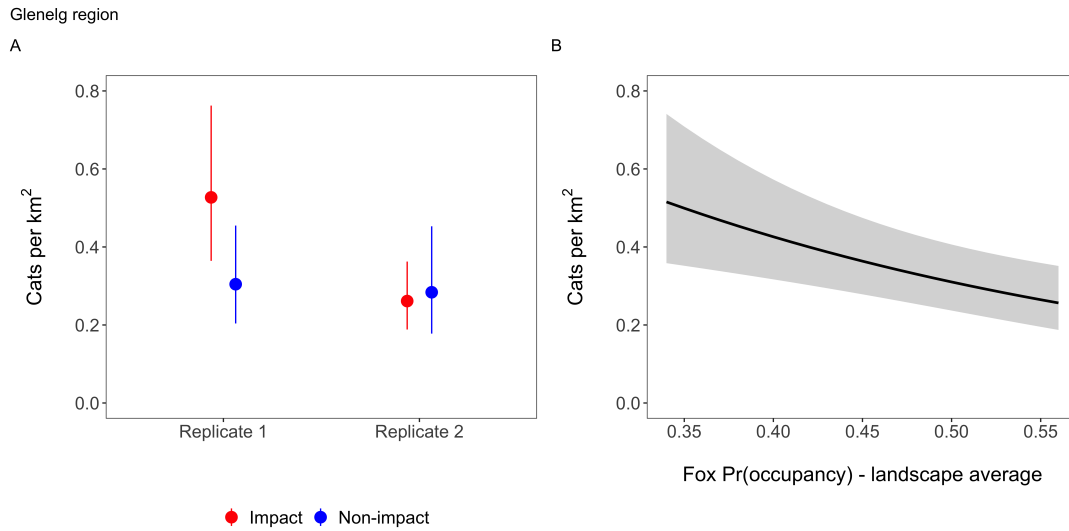


Figure 3: Best-ranked experimental (A) and correlative (B) models of feral cat density in the Glenelg region, Australia. There was statistical evidence (i.e., 95% confidence intervals of the parameter estimates did not overlap zero) that feral cat density was higher in the landscape with fox-baiting (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.

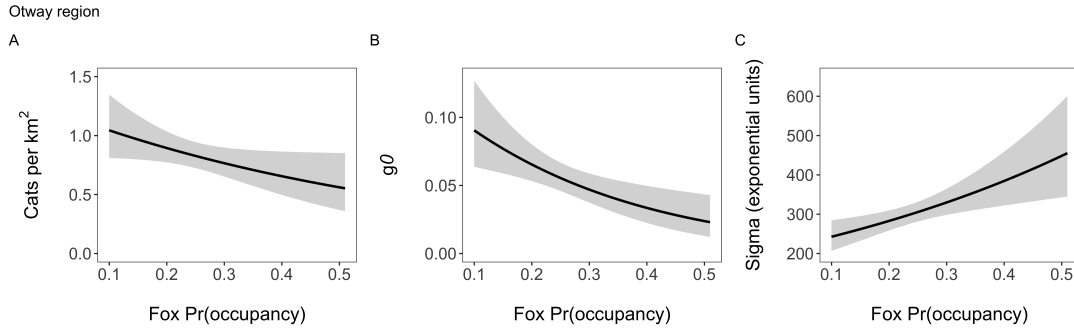


Figure 4: Best-ranked model of feral cat density in the Otway region, Australia. The best-ranked model predicted that feral cat density declined with the probability of fox occupancy (B). This model also predicted that the probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0) increased with the probability of fox occupancy (B), while sigma (which is related to home range size) increased (C). Shaded regions indicate 95% confidence intervals.

263

5. CONCLUSIONS

264 6. ACKNOWLEDGEMENTS

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285 7. AUTHORS' CONTRIBUTIONS

286 M.W.R, B.H, J.H.P, B.A.W and A.R conceived the ideas and designed methodology; M.W.R,
287 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 writ-
288 ing of the manuscript. All authors contributed critically to the drafts and gave final approval
289 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.

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