

Quantifying mesopredator release: lethal control of an invasive apex predator alters feral cat density and detectability

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¹ ABSTRACT

- ² 1. The mesopredator release hypothesis predicts that subordinate predator density will increase as
³ apex predators decline. Persistent debate around mesopredator release in part reflects the lack of
⁴ robust, replicated experiments to test this theory, and the use of population indices which confound
⁵ changes in mesopredator density and detectability. This uncertainty has immediate impacts for
⁶ conservationists who are faced with managing sympatric invasive predators.
- ⁷ 2. We used replicating experimental designs and spatially explicit detection modelling to examine
⁸ whether mesopredator release of the feral cat *Felis catus* occurs in response to targeted control
⁹ of the introduced red fox *Vulpes vulpes*. We surveyed three Control-Impact paired landscapes in
¹⁰ a region with long-term fox control (1080 poison-baiting), and conducted a Before-After-Control-
¹¹ Impact Paired Series experiment in another region. We identified 160 individual feral cats from
¹² 68,504 camera-trap nights to estimate feral cat density with spatial mark-resight models.
- ¹³ 3. At a landscape scale (mean size: 169 km²), lethal fox control was associated with a range of responses
¹⁴ from a negligible to 3.7-fold increase in feral cat density. Consistent with the mesopredator release
¹⁵ hypothesis, the degree of increase corresponded with variation in the duration and intensity of fox
¹⁶ suppression. At a fine spatial scale (200 m), feral cat density had a consistent negative association
¹⁷ with fox activity across both regions.
- ¹⁸ 4. Feral cat detectability also varied across the (artificially manipulated) fox activity gradient. In one
¹⁹ region, nonlinear models indicated that feral cats exhibited avoidance behaviours when foxes were
²⁰ rare, giving way to density suppression at high fox activity.
- ²¹ 5. *Synthesis and applications.* Our study provides replicated, experimental evidence that that apex
²² predator suppression is associated with an increase in the density of a mesopredator. Mesopredator
²³ release can manifest as changes in both behaviour and density, distorting inference if these processes
²⁴ are not distinguished. Our results help explain why fox control does not consistently improve native
²⁵ prey persistence, suggesting integrated pest management may be necessary to improve conservation
²⁶ outcomes.

²⁷ **1. INTRODUCTION**

²⁸ Understanding species interactions is critical for effective invasive species management (Zavaleta,
²⁹ Hobbs, & Mooney 2001). When several invasive species co-occur, management actions that suppress
³⁰ the dominant invasive species may inadvertently benefit subordinate invasive species (Jackson 2015;
³¹ Kuebbing & Nuñez 2015). For example, the removal of a dominant invasive predator may increase the
³² abundance of a subordinate invasive species directly by reducing top-down pressure, or indirectly by
³³ increasing the availability of shared resources; these are often referred to as mesopredator or competitor
³⁴ release, respectively (Crooks & Soulé 1999; Ruscoe *et al.* 2011; Doherty & Ritchie 2017). The release
³⁵ of subordinate invasive species, particularly predators, can have serious negative implications for native
³⁶ taxa and ecosystem function (Courchamp, Langlais, & Sugihara 1999; Ballari, Kuebbing, & Nuñez 2016).
³⁷ However, integrated invasive predator management is often far more costly and less feasible than single
³⁸ species control, and so it is important to identify when the extra cost is justified (Bode, Baker, & Plein
³⁹ 2015).

⁴⁰ Most knowledge of mesopredator release stems from unreplicated ‘natural experiments’ (e.g. range
⁴¹ contractions - Crooks & Soulé 1999) or ad-hoc management interventions (e.g. invasive species eradica-
⁴² tions - Rayner *et al.* 2007). Does mesopredator release still occur when apex predators are suppressed but
⁴³ not completely removed? The occurrence, nature (positive or negative, direct or indirect) and strength
⁴⁴ of predator interactions can vary among species assemblages, predation risk, environmental productivity,
⁴⁵ management regimes and other landscape contexts (Hastings 2001; Finke & Denno 2004; Elmhagen &
⁴⁶ Rushton 2007; Newsome *et al.* 2017; Alston *et al.* 2019). Replicating management programs in an
⁴⁷ experimental framework is logically challenging, but important for understanding these complexities,
⁴⁸ discriminating between plausible hypotheses and producing generalisable results to inform effective pest
⁴⁹ management (Glen & Dickman 2005; Hayward *et al.* 2015; Christie *et al.* 2019; Smith *et al.* 2020).

⁵⁰ Another source of uncertainty around the mesopredator release hypothesis stems from the inability
⁵¹ of traditional survey and modelling approaches to distinguish behavioural from numerical population
⁵² processes (Hayward *et al.* 2015; Stephens *et al.* 2015). Suppression of an apex predator may simultane-
⁵³ ously change the behaviour and the density of a mesopredator, both of which influence detection rates
⁵⁴ (Broadley *et al.* 2019; Rogan *et al.* 2019). This makes it difficult to interpret observed changes in naive
⁵⁵ indices of mesopredator activity or occupancy in relation to changes in apex predator populations, even if
⁵⁶ the study has an experimental design. Unbiased estimates of invasive predator density are also important

57 for setting meaningful control targets and inferring impacts on native prey (Moseby *et al.* 2019). Spatial
58 capture-recapture methods offer a solution by separating behavioural and observational processes from
59 population density, which is estimated within a defined spatial resolution (Borchers & Efford 2008).

60 Predation by two invasive species, the red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus*
61 (hereafter ‘cat’), has played a major role in Australia’s high rates of mammalian extinction (Woinarski,
62 Burbidge, & Harrison 2015). Integrated pest management programs are rare; instead, foxes are far
63 more commonly controlled than cats, as they are more susceptible to poison-baiting, have greater direct
64 economic impacts and fewer legal impediments to control (Reddiex *et al.* 2007; McLeod & Saunders 2014).
65 Nonetheless, cats are one of the most widespread and damaging vertebrate predator species (Medina *et*
66 *al.* 2011; Doherty & Ritchie 2017; Legge *et al.* 2020). As foxes are larger-bodied (~2 kg difference) and
67 have high dietary overlap with cats (Stobo-Wilson *et al.* 2021a; b), the mesopredator release hypothesis
68 (Soulé *et al.* 1988) predicts that the impacts of cats on shared prey species will increase as fox populations
69 are suppressed. This is alarming because feral cats are extremely difficult to manage in open populations
70 (Fisher *et al.* 2015; Lazenby, Mooney, & Dickman 2015).

71 Evidence that foxes suppress cats is inconclusive (Hunter *et al.* 2018). In parts of Australia where the
72 native apex mammalian predator (the dingo *Canis familiaris*) is functionally extinct and introduced foxes
73 are the largest terrestrial mammalian predator, four studies have observed an increase in cat detections
74 following fox control (Risbey *et al.* 2000; Marlow *et al.* 2015; Stobo-Wilson *et al.* 2020). However, two
75 other studies in similar systems did not see any change (Towerton *et al.* 2011; Molsher *et al.* 2017). A
76 further study with spatial replication detected an increase at one site but not another (Davey *et al.* 2006),
77 and another observed a decrease in cat activity (Claridge *et al.* 2010). No prior studies have directly
78 estimated cat density in response to fox control.

79 We experimentally investigated the role of introduced foxes in top-down suppression of cat density in
80 two regions of south-eastern Australia. Our experiments had a replicated Control-Impact design in the
81 region with long-term fox control, and a Before-After Control-Impact Paired Series (BACIPS) design in
82 the region with newly implemented fox control. Foxes and cats are the only functional terrestrial mam-
83 malian predators in these regions, and each region included at least one area in which foxes were subject
84 to continuous lethal poison-baiting (hereafter ‘impact landscape’), and a paired area where foxes were
85 not controlled (hereafter ‘non-impact landscape’). This allowed a sharp focus on the interactions between
86 the two invasive predators, across a gradient of apex predator (fox) occurrence. In accordance with the

⁸⁷ mesopredator release hypothesis, we predicted that: (1) cat density would be negatively correlated with
⁸⁸ fox occurrence at a fine spatial scale, and (2) fox control would increase cat density at a landscape scale.
⁸⁹ We based inference on direct estimates of cat density using spatially explicit mark-resight models.

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). The native
⁹³ temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and
⁹⁴ tree plantations. Although once widespread, native dingoes are now absent throughout, and a native
⁹⁵ mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and extremely
⁹⁶ rare in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial
⁹⁷ mammalian predator guild is therefore depauperate, with foxes and cats being the primary functional
⁹⁸ mammalian terrestrial predators; birds of prey and snakes are the only other medium-large carnivores
⁹⁹ present.

¹⁰⁰ Our study landscapes in the Glenelg region, Gunditjmara country, were primarily lowland forest and
¹⁰¹ heathy woodland. The area receives an average annual rainfall of 700 mm (Bureau of Meteorology 2021)
¹⁰² and has gently undulating terrain. The region frequently experiences prescribed burns and wildfires,
¹⁰³ creating a mosaic of fire histories and vegetation complexity. Our study landscapes in the Otway region
¹⁰⁴ were in the western section of the Otway Ranges on Gadubanud country. Rainfall here is more than
¹⁰⁵ twice as high as the Glenelg region. The vegetation is a mosaic of shrubby wet forest and cool temperate
¹⁰⁶ rainforest, with the northern landscape bordering on a large heathy woodland. This region rarely expe-
¹⁰⁷ riences fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness
¹⁰⁸ index; Riley, DeGloria, & Elliot 1999).

¹⁰⁹ Government land managers conduct ongoing targeted fox control for biodiversity conservation across
¹¹⁰ broad sections of each region. In these sections, manufactured poison baits (FoxOff, Animal Control
¹¹¹ Technologies, Somerton) containing 3 mg of sodium mono-fluroacetate (1080) are buried at a depth of
¹¹² 12-15 cm at 1-km intervals along accessible forest tracks and roads (Fig. 1). Different road densities
¹¹³ across the two regions result in variable poison-bait densities. Other large sections within each region are
¹¹⁴ maintained without fox control.

115 2.2. Study design and camera-trapping

116 We designed experiments around the implementation of fox-baiting in each region. We simultaneously
117 surveyed one impact and one non-impact landscape within a region at a time. Each pair of impact and
118 non-impact landscapes was chosen based on similarity in vegetation groups, with the aim of maintaining
119 spatial independence with respect to predator daily movements.

120 In the Glenelg region, we used a replicated control-impact design to compare three impact landscapes
121 that have been poison-baited for foxes at fortnightly intervals for more than 13 years with three paired
122 non-impact landscapes. We surveyed Cobboboonee National Park (impact) and Annya State Forest
123 (non-impact) in January – April 2018 ('replicate 1'), Mt Clay State Forest/Narrawong Flora Reserve
124 (hereafter 'Mt Clay'; impact) and Hotspur State Forest (non-impact) in April – June 2018 ('replicate 2'),
125 and Lower Glenelg National Park (LGNP) South (impact) and LGNP North (non-impact) in March –
126 May 2021 ('replicate 3'). For replicates 1 and 2, the paired landscapes were separated by at least 8 km, a
127 distance very unlikely to be traversed regularly by these invasive predators (Hradsky *et al.* 2017). LGNP
128 South and North are separated by the Glenelg river, which is impassable by terrestrial animals.

129 In the Otway region, we used a before-after control-impact paired series (BACIPS) design to assess
130 changes related to the introduction of a fox control program. We deployed camera-trap grids in a pair
131 of impact – non-impact landscapes from June to September in three years (2017, 2018, 2019), in the
132 Great Otway National Park and Otway Forest Park. Our first survey occurred approximately three
133 months before fox-baiting began. Fox-baiting commenced in the impact landscape in November 2017.
134 Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait
135 replacement until July 2018. The second survey was conducted six months after fox-baiting commenced,
136 however poison bait replacement lapsed from near the beginning of the survey until nearly three months
137 afterwards. Fox-baiting at monthly intervals recommenced in December 2018, six months prior to the
138 start of the final survey (Fig. S1). The impact and non-impact landscapes were at least 4.2 km apart
139 through dense forest, a distance unlikely to be regularly traversed by these invasive predators, although
140 possible (Hradsky *et al.* 2017). In this study, and a concurrent study which identified individual foxes
141 through genetic sampling (M. Le Pla *et al.*, in review), we found no evidence that either foxes or cats
142 moved between the impact and non-impact landscapes.

143 In each landscape, we established a grid of 49 – 110 sites (mean = 88), averaging 448 m apart (range:

¹⁴⁴ 194 – 770 m). At each site, we set up a Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an
¹⁴⁵ infrared flash and temperature-in-motion detector on a tree, facing a tuna oil lure; see SI section S1 for
¹⁴⁶ details. Overall, we deployed 1051 functional camera-traps, which operated for an average of 65 days
¹⁴⁷ (range: 12 – 93 days), totalling 68,504 trap nights (Table S1).

¹⁴⁸ *2.3. Individual feral cat identification*

¹⁴⁹ We sorted the camera-trap images of cats into five categories based on coat type: black, mackerel
¹⁵⁰ tabby, classic tabby, ginger and other; Fig. S3, and identified individual feral cats within each category;
¹⁵¹ see SI Section S2 for details. In the Otway region, 40% of cat detections were of black cats with few
¹⁵² identifiable markings, so we did not attempt to identify any black cats here. In the Glenelg region, black
¹⁵³ cats were rarer (not detected at two landscapes) and often more distinctive, and so we could identify
¹⁵⁴ some individuals (Table S1).

¹⁵⁵ *2.4. Spatial fox occurrence*

¹⁵⁶ We could not use raw fox presence-absence data from the camera-traps to predict cat density, as
¹⁵⁷ spatial mark-resight models require covariate values for each grid cell in which density is estimated (see
¹⁵⁸ Section 2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for
¹⁵⁹ each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised
¹⁶⁰ additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but
¹⁶¹ do not account for imperfect detection.

¹⁶² We built the fox occurrence models using the ‘mgcv’ R-package (version 1.3.1; Wood 2011). We
¹⁶³ modelled fox presences and absences (response variable) across space (explanatory variable) separately
¹⁶⁴ for each region, with a duchon spline spatial smooth; these provide better predictions at the edge of
¹⁶⁵ surveyed space than other splines (Miller & Wood 2014). In the Otway region, we included a random
¹⁶⁶ intercept for each camera-trap site to account for repeat sampling and did not share spatial information
¹⁶⁷ across years. Differences in camera-trap deployment lengths were accounted for using a model offset.

168 2.5. Spatial mark-resight models of feral cat density

169 We used a spatial capture-recapture approach to estimate cat density (Borchers & Efford 2008). These
170 models use counts of detections and non-detections of individual animals at trap locations (accounting for
171 trap-specific survey effort) to estimate the location of each individual's activity centre. They commonly
172 assume that individuals have approximately circular home ranges, spend the majority of time in the
173 centre of their range ('activity centre'), and that the probability of observing an individual decreases with
174 distance from the activity centre. Two detectability parameters govern this process: g_0 , the probability
175 of detecting an individual per occasion in their activity centre, and sigma: a spatial scale parameter
176 which relates to home range size. Multiple candidate shapes for the decline in detectability with distance
177 from the activity centre ('detection function') can be modelled. Spatial capture-recapture models have
178 been extended to consider situations where not all individuals in a population are identifiable (i.e., some
179 are unmarked; Chandler & Royle 2013). These models typically assume unmarked individuals to be a
180 random sample of the population, sharing the same detection process as marked individuals, allowing
181 density to be estimated for the entire population.

182 We used closed population, sighting-only, spatial mark-resight models to estimate cat density using the
183 maximum likelihood 'secr' R-package (Efford 2021). Detections of the 'mark status uncertain' category
184 (unidentifiable cats), cannot be handled in the 'secr' R package; we added them to as 'unmarked' detec-
185 tions (black cats) rather than discard them (following Moseby, McGregor, & Read 2020). We condensed
186 unmarked detection histories to a binary presence-absence record per each camera-trap for a 24-hour
187 length duration ('occasion'), beginning at midday. We ran separate models for each region and treated
188 each camera-trap grid deployment as a 'session'. We created a 4000-m buffer zone around each site (which
189 was truncated by the river in LGNP), and estimated cat density at a 200-m grid cell resolution within
190 this area. These habitat mask specifications were based on initial model trials and our knowledge of cat
191 behaviour in these regions; the aim was to ensure density was estimated over a large enough area to
192 encompass the activity centres of all cats exposed to our camera-traps, at a fine enough spatial scale to
193 minimise bias in density estimates.

194 For each region, we ran four sets of models. We chose (1) between half-normal and exponential
195 detection functions and (2) 'base model' covariates to carry through to subsequent model sets, (3) tested
196 for associations between fox occurrence and cat density at a fine spatial scale, and (4) experimentally
197 evaluated the effect of fox control on cat density at the landscape scale. Each step is described in

more detail below. We compared competing models using small-sample corrected Akaike Information Criterion (hereafter ‘AIC_c’) scores (Burnham & Anderson 2004) and examined the confidence intervals around estimated model coefficients. Each step is described in more detail below.

The second set of models established the base covariates for each region. We hypothesised that cat detectability might decrease over each survey due to the scent of the tuna oil lure fading. To account for this, we modelled a linear trend in g_0 over the survey duration for each camera-trap. We further hypothesised that cat density might differ between vegetation types. We classed the vegetation into three dominant types for each region: cleared land, heathy vegetation, and either dry forest (Glenelg region) or wet forest (Otway region); see see SI section S6 for details. We compared these covariates as single and additive models, as well as to a ‘null model’ (density and detectability constant) - carrying supported covariates forward to subsequent model fits.

The third set of models directly tested the associations between fox occurrence and cats within each region. We tested three hypotheses for each region: (i) fox occurrence only affects cat density, (ii) fox occurrence only affects cat detectability (both g_0 and sigma concurrently; Efford & Mowat 2014), (iii) fox occurrence affects the density and the detectability of cats, against (iv) the null hypothesis that there was no association between fox occurrence and cats. We used the spatial fox occurrence estimates (detailed in Section 2.4) as the explanatory variable. As predator associations may be nonlinear (Johnson & VanDerWal 2009), we tested these effects as linear and non-linear terms using regression splines (generalised additive models called within the ‘secr’ R-package). We included year as a cat density covariate in all the Otway region models to account for repeat sampling and compared to a null model without any fox occurrence effects using AIC_c scores.

The fourth set of models examined the effects of fox-baiting at a landscape scale within each region. We fitted a model that estimated cat density separately for each landscape, and used AIC_c scores to choose whether to model detectability as a function of predicted fox occurrence (as per hypothesis ii in the second set of models above) or constant. We then derived the response ratio (estimated difference in cat density in the impact landscape relative to the paired non-impact landscape, back-transformed to the response scale) for the top-ranked model. We used visual inspection of the 95% confidence intervals around the density estimates to evaluate whether fox control increased cat density at a landscape level (Cumming & Finch 2005). For the Glenelg region (replicated control-impact design), we assessed whether each confidence interval around the relative difference in cat density in the impact landscape to the paired

²²⁸ non-impact landscape (i.e., ‘response-ratio’) overlapped one; overlap would indicate no difference in cat
²²⁹ density. For the Otway region (BACIPS design), we assessed how much the confidence intervals around the
²³⁰ estimated difference between impact and non-impact landscapes overlapped between years; we expected
²³¹ that the response-ratio would increase over the years, indicating an increase in cat density following the
²³² introduction of fox control.

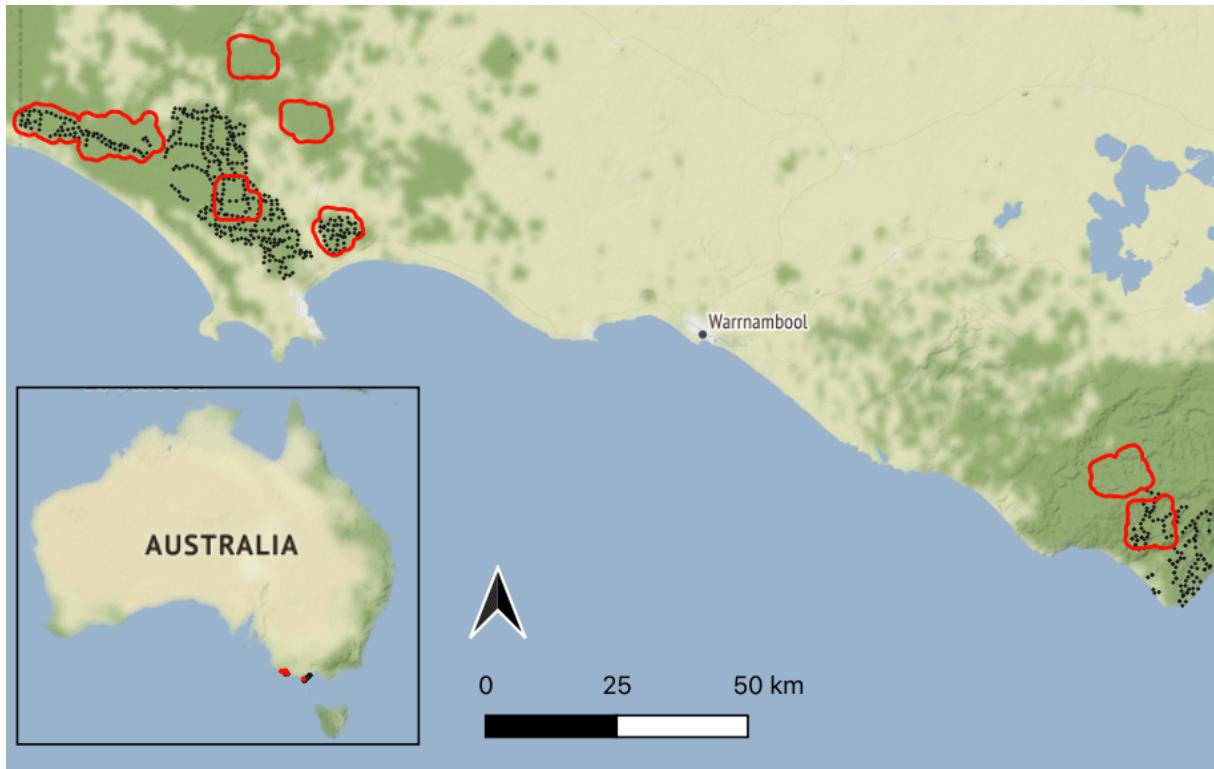


Figure 1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river. Locations of fox poison-bait stations are denoted by black dots. The Glenelg region is 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.*

233 **3. RESULTS**

234 *3.1. Fox occurrence*

235 In the Glenelg region, there was a clear difference in fox occurrence between paired impact (poison-
236 baited) and non-impact landscapes for replicates 1 and 3, but only a marginal difference for replicate
237 2 (Fig. 2). In the Otway region, fox occurrence increased by 22% in the non-impact landscape, and
238 decreased by 43% in the impact landscape over the three years (occurrence probability averaged at each
239 camera-trap in the landscape). Fox occurrence in the Otway region was generally lower than the Glenelg
240 region, with less fine-scale spatial variation. For example, fox occurrence was predicted to be spatially
241 consistent across the entire Otway region in 2018 (Fig. 2). Fox model summaries and spatial standard
242 error estimates are presented in SI Section S5.

243 *3.2. Feral cats in the Glenelg region*

244 Across the six landscapes in the Glenelg region, we recorded 251 cat detections from 32,232 camera-
245 trap nights (Table S1). We were able to identify 64% of cat detections to the individual level; a total
246 of 67 cats (6 – 13 individuals per landscape). The exponential detector function was supported over
247 the half-normal function (Table S2). The null model was more strongly supported than models with
248 vegetation impacts on cat density and/or linear time trends on g_0 (Table S3).

249 At a fine spatial scale, the model with a linear relationship between fox occurrence and cat density
250 was strongly supported (AIC_c 2.76 better than the null; Table S4). It indicated that cat density declined
251 as fox occurrence increased (-0.32; 95% CI: -0.57 - -0.07; Fig. 3). There was no evidence of an impact
252 of fox occurrence on cat detectability (Table S4). Regression splines added additional model parameters
253 without changing predictions (Fig. 3), and so, all nonlinear models ranked below their linear counterparts
254 (Table S4).

255 Our hypothesis that cat density would be higher in landscapes with fox control was supported for the
256 first and third replicate pairs: estimated cat densities were 2.5 (95% CI: 1.5 - 4.2) and 3.7 (95% CI: 1.4
257 - 9.5) times higher in the impact landscape than the paired non-impact landscape, respectively (Fig. 5).
258 For the second landscape pair, however, the estimated difference was positive but negligible (1.1; 95%
259 CI: 0.69 - 1.69). At the landscape level, there was some evidence that cat detectability was affected by

260 fox occurrence; however the AIC_c score was only 0.95 units better than the constant detectability model
261 (Table S5) and the estimated effects were weak with high uncertainty. The detectability of cats in their
262 activity centre (g_0) tended to increase with the probability of fox occurrence (0.24; 95% CI: -0.32 - 0.80),
263 as did sigma (0.13; 95% CI: -0.14 - 0.41).

264 *3.3. Feral cats in the Otway region*

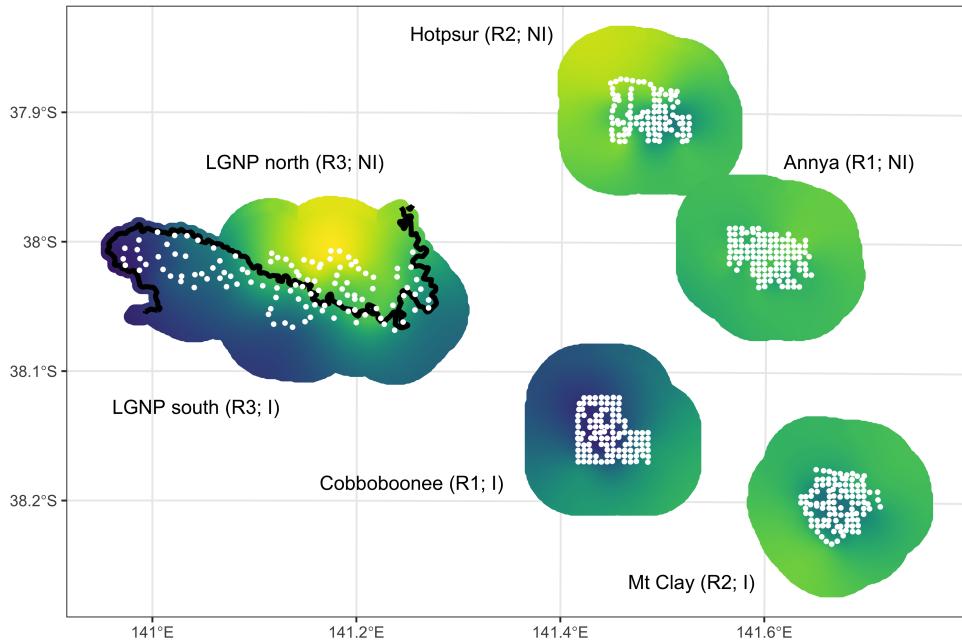
265 In the Otway region, we recorded 970 cat detections from 36,272 camera-trap nights (Table S1). We
266 were able to identify 53% of cat detections to the individual level; a total of 93 cats (20 – 30 individuals
267 per landscape). The exponential detector function was strongly supported over the half-normal function
268 (Table S7). The null model was more strongly supported than the models with vegetation impacts on
269 cat density and/or linear time trends on g_0 (Table S8).

270 There was some evidence that cat density was negatively correlated with fox occurrence at a fine
271 spatial scale: the two top-ranked models included a linear and a non-linear effect of fox occurrence
272 on cat density, respectively; however, a model without a fox occurrence term received similar support
273 (dAIC_c = 0.80; Table S9). The 95% confidence interval around the linear coefficient from the top-ranked
274 model marginally overlapped zero (-0.26; 95% CI: -0.55 - 0.02) indicating that cat density declined as
275 fox occurrence increased in the Otways at a similar rate to Glenelg, but with slightly greater uncertainty
276 (Fig. 3). However, the equivalent nonlinear model predicted that cat density only declined (at a steeper
277 rate) in the mid-high range of fox occurrence probability (Fig. 3). Equivalent pairs of linear model and
278 nonlinear models were indistinguishable based on AIC_c scores (Table S9). There was also strong support
279 for an effect of fox occurrence on cat detectability at a fine spatial scale (Fig. 4; Table S10). Where
280 fox occurrence was higher, cats were less detectable in their activity centres (i.e., negative association
281 with g_0 ; -0.69; 95% CI: -1.11 - -0.27; Fig. 4A) and ranged further (i.e., positive association with sigma;
282 coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 4B). The equivalent nonlinear model predicted detectability
283 changes to have occurred only in the low-mid range of fox occurrence (Fig. 4).

284 Our hypothesis that cat density in the impact landscape would increase relative to the non-impact
285 landscape with fox control was supported, however there was considerable uncertainty. Cat density
286 tended to be lower in the impact than non-impact landscape prior to fox-baiting (i.e., in 2017), although
287 the confidence intervals for the two density estimates overlapped substantially (Fig. 6). In 2018, cat
288 density decreased in the non-impact landscape and increased in the impact landscape, converging to

²⁸⁹ near-identical density estimates. These patterns continued into 2019, with cat density now somewhat
²⁹⁰ higher in the impact landscape than non-impact landscape. Overlap in the response ratio confidence
²⁹¹ intervals for successive years was high, but the comparison between 2017 to 2019 suggests a meaningful
²⁹² increase in cat density at the impact landscape relative to the non-impact landscape (Fig. 6B). Like the
²⁹³ fine scale model, there was strong evidence that cat detectability was impacted by fox occurrence (Table
²⁹⁴ S10).

(a) Glenelg region



(b) Otway region

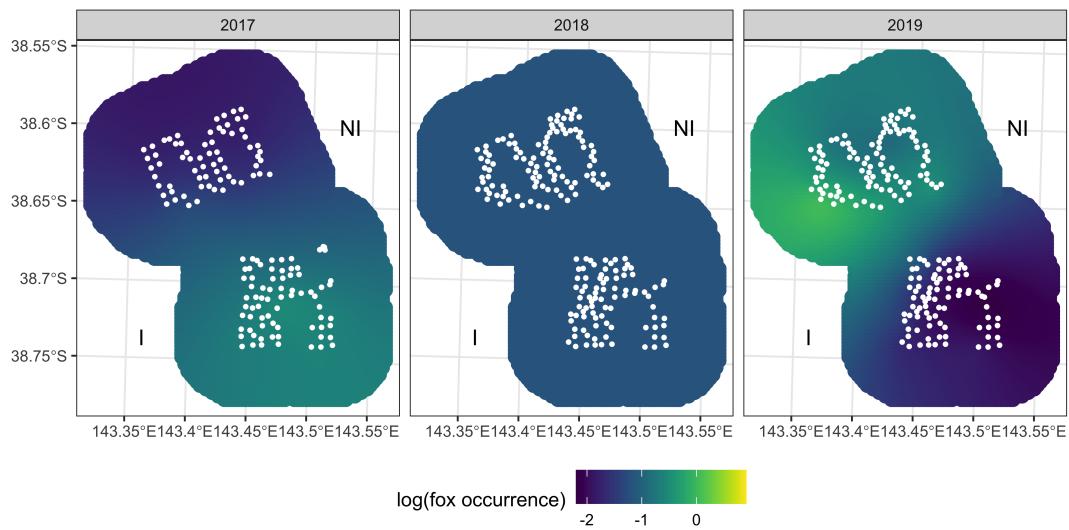


Figure 2: Predicted red fox *Vulpes vulpes* occurrence derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. Predicted fox occurrence was used as a predictor of feral cat *Felis catus* density in the spatial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

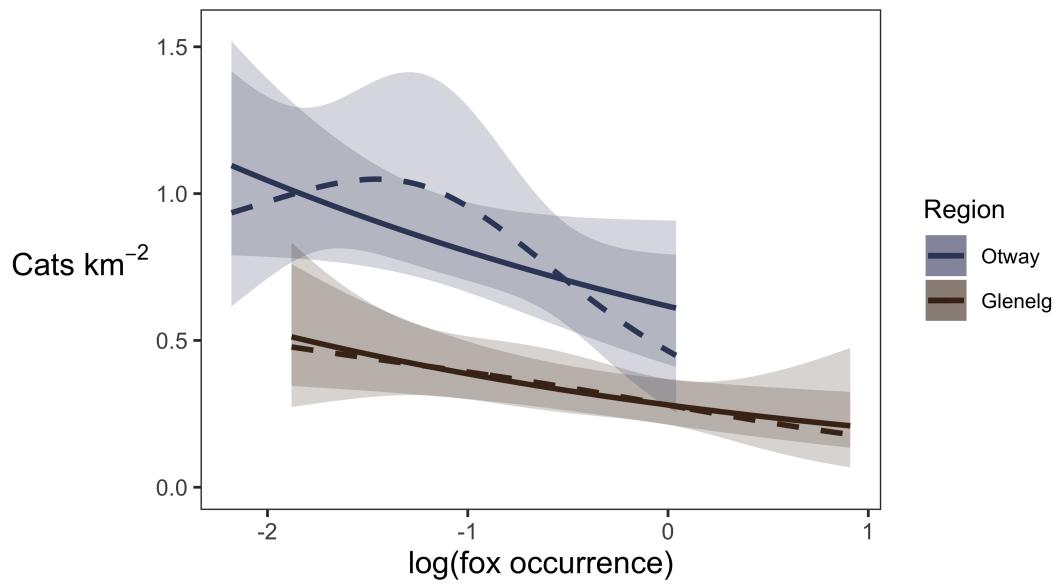


Figure 3: Linear (solid lines) and nonlinear (dashed lines) models predicted that feral cat *Felis catus* density increased with declining probability of red fox *Vulpes vulpes* occurrence (log-transformed) in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.

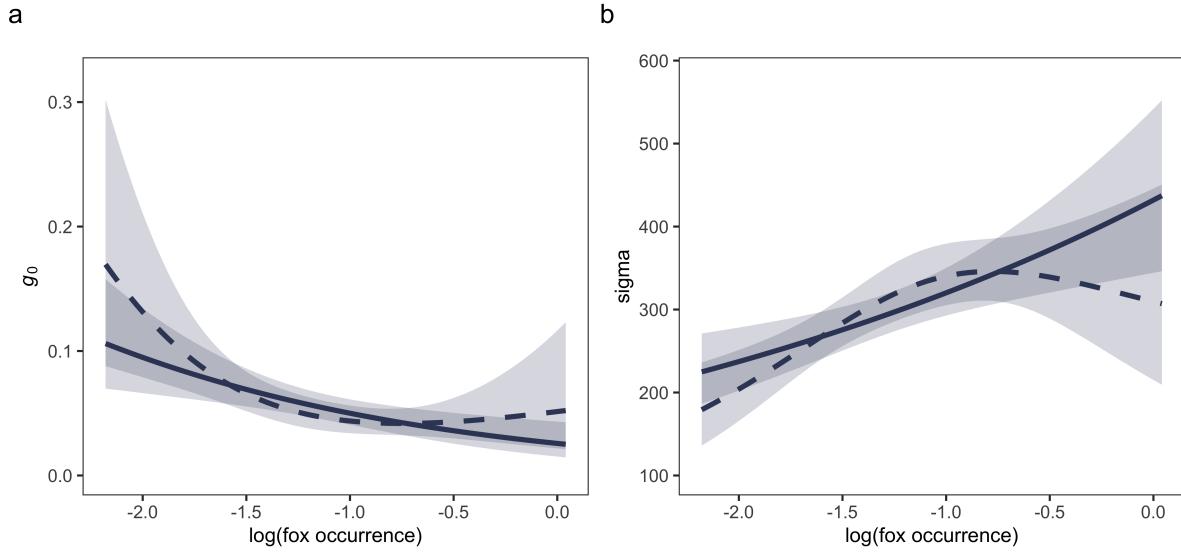


Figure 4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-transformed red fox *Vulpes vulpes* occurrence in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion (g_0) decreased with the probability of fox occurrence (a), while σ (which is related to home range size; exponential units) increased (b). Shaded areas indicate 95% confidence intervals.

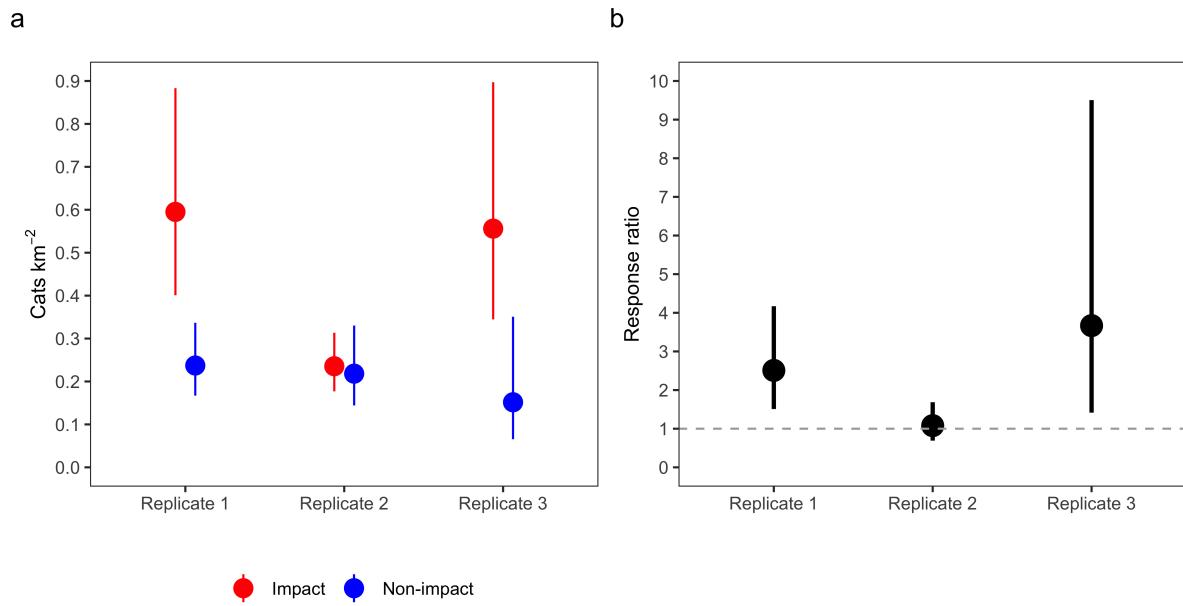


Figure 5: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the paired non-impact landscape for each replicate (b) in the Glenelg region, Australia. Poison-baiting for foxes *Vulpes vulpes* has been conducted in the impact landscapes for more than 13 years. Grey dashed line represents no difference between the paired landscapes. Error bars represent 95% confidence intervals.

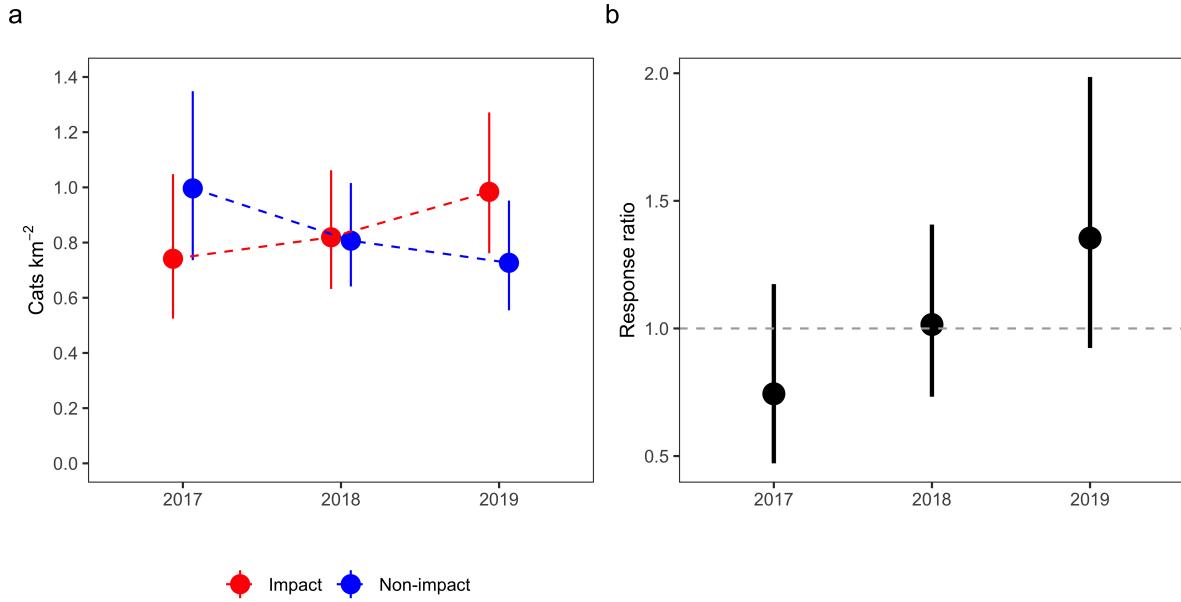


Figure 6: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the non-impact landscape for each survey year (b) in the Otway region, Australia. In 2017, surveys were conducted approximately two months before lethal red fox *Vulpes vulpes* control commenced in the impact landscape; control lapsed for six months prior to the 2018 survey. Error bars represent 95% confidence intervals. Overlap with the grey dashed line in (b) represents no difference in density between the paired landscapes for that year; the proportion overlap between response ratio confidence intervals across years provides evidence for a change in difference.

²⁹⁵ **4. DISCUSSION**

²⁹⁶ Our study is one of the first to provide replicated, experimental evidence that apex predator suppression
²⁹⁷ can increase mesopredator population density. Our study provides two lines of evidence that foxes
²⁹⁸ can exert top-down control on feral cats in the forests of south-eastern Australia: feral cat density was
²⁹⁹ (1) higher where fine-scale fox occurrence probability was lowest, and (2) commonly higher in landscapes
³⁰⁰ where fox control occurred. This is alarming because targeted fox control is a widely used conservation
³⁰¹ strategy; this unintended consequence could dampen benefits to native prey and even further threaten
³⁰² these species. However, as our findings highlight, mesopredator release of cats following fox control is
³⁰³ unlikely to occur universally; the degree of fox suppression varies and fox-cat interactions are likely to
³⁰⁴ be context and scale-dependent. More broadly, our study illustrates how correlative and experimental
³⁰⁵ approaches provide complementary lines of evidence when investigating interactions between predator
³⁰⁶ species, and the importance of disentangling changes in population density from changes in detectability.

³⁰⁷ We were able to exploit a gradient in fox occurrence caused by lethal control to investigate associations
³⁰⁸ between cat density and fox occurrence at a fine spatial scale across two separate regions. At this scale,
³⁰⁹ we observed a consistently negative association between cat density and fox occurrence, supporting our
³¹⁰ first hypothesis, although there was more uncertainty around the relationship in the Otway region. We
³¹¹ acknowledge that it could also simply reflect differences in niche preference, rather than foxes excluding
³¹² cats or cats avoiding foxes. However, we consider this unlikely given we observed the relationship across
³¹³ an artificial gradient of fox occurrence caused by lethal control.

³¹⁴ There is contention around whether linear regression is appropriate for investigating correlations
³¹⁵ between different predator species, as subordinate predators may only be suppressed when apex predator
³¹⁶ abundance is high (Johnson & VanDerWal 2009). We found no evidence of non-linear associations
³¹⁷ between foxes and cats in the Glenelg region, while linear and non-linear models performed equally well
³¹⁸ in the Otway region. Non-linear models in the Otway region predicted that cat density declined only in
³¹⁹ the mid-high range of fox occurrence, while behavioural changes were seen in the low-mid range of fox
³²⁰ occurrence. Perhaps cats can successfully avoid foxes through behavioural change where foxes are rare,
³²¹ but this is ineffective where foxes are common. This could explain the lack of evidence for foxes impacting
³²² cat detectability in the Glenelg region where fox occupancy is relatively high. Alternatively, behavioural
³²³ changes may be untenable for cats in the Glenelg region because small mammal abundance is relatively
³²⁴ low and fox avoidance strategies likely come at the expense of hunting success (Sih 1980; Wilson *et al.*

325 2010).

326 Where fox occurrence was higher in the Otway Ranges, cats were less detectable in their activity
327 centres and ranged further (Fig. 4). Low detectability is likely to correlate with fewer apex predator
328 encounters, and has been observed in other predator interaction studies (e.g. Lombardi *et al.* 2017). An
329 increase in cat ranging behaviour (sigma) with fox control supports observations made by Molsher *et al.*
330 (2017), and may reflect a direct avoidance strategy. Animal movement rates are expected to increase
331 in response to unpredictable threats (Riotte-Lambert & Matthiopoulos 2020). Alternatively, cats may
332 consider foxes predictable and avoid locations they frequent, thus having to range further to obtain the
333 same amount of food resources. In a similar forest habitat, Buckmaster (2012) observed large ‘holes’ in
334 the home range of each GPS-collared cat; they confirmed that this was not due to an absence of prey
335 and hypothesised that it could be due to apex predator avoidance. Regardless of the cause, variation in
336 mesopredator detectability and movement rates with apex predator populations has serious implications
337 for the interpretation of studies that compare relative abundance indices and spatial overlap of predator
338 species without disentangling behaviour and detectability from density (Efford & Dawson 2012; Neilson
339 *et al.* 2018; Stewart *et al.* 2018; Broadley *et al.* 2019).

340 In the Glenelg region where fox-baiting had occurred for more than 13 years, feral cat density was
341 considerably higher in two out of three distinct landscapes than in similar, unbaited landscapes. The
342 outlier is most likely due to limited suppression of foxes at Mt Clay despite ongoing fox control (Fig. 2).
343 Mt Clay is a small forest block surrounded entirely by unbaited farmland. Simulation modelling indicates
344 that the size of the baited area is a key driver of the degree of reduction in the fox population (Hradsky *et*
345 *al.* 2019; Francis, Robley, & Hradsky 2020). Studies of fox-cat (and other predator-predator) interactions
346 often use the presence of a management program as a proxy for lower apex predator abundance and
347 distribution (e.g. Hunter *et al.* 2018). Our findings strongly indicate the need to directly measure the
348 apex predator population in order to reliably interpret the responses of subordinate species (Salo *et al.*
349 2010).

350 In the Otway region, we observed a weaker-but increasing-effect of fox control on cat density, to
351 be expected from a recently commenced and less intensive fox-baiting program. The short duration of
352 baiting in the Otway region may mean that changes in adult cat density are yet to fully manifest as
353 foxes potentially suppress cats by reducing recruitment rates. Cats may also respond to an increase in
354 shared prey availability following fox suppression (Stobo-Wilson *et al.* 2020). A time-lagged release of

355 cats following fox control would explain eruptions and subsequent crashes commonly observed in shared
356 mammalian prey populations two to ten years following fox control commencement (Duncan *et al.* 2020).
357 Alternatively, top-down suppression by foxes and competition may be weaker in this highly productive
358 environment where prey abundance was relatively high, fox occurrence was already relatively low, and
359 overall cat densities were consistently high (Johnson & VanDerWal 2009; Greenville *et al.* 2014; Newsome
360 *et al.* 2017). Our surveys provide important baselines against which to compare future changes in predator
361 populations as the fox-baiting program continues.

362 Our study is among the very few which have used a direct measure of density to test mesopredator re-
363 lease. Previous studies have mostly used live capture-rates to infer population density, without accounting
364 for behavioural or detectability changes (e.g. Arjo *et al.* 2007; Karki, Gese, & Klavetter 2007; Thomp-
365 son & Gese 2007; Berger, Gese, & Berger 2008; Jones, Van Vuren, & Crooks 2008). Contention about
366 mesopredator release has centred on such methods (Hayward *et al.* 2015); as well as unaccounted species
367 interactions in complex predator guilds (Levi & Wilmers 2012; Jachowski *et al.* 2020). In contrast, our
368 study tests the mesopredator release theory using a combined behavioural and numerical approach, in a
369 system with a simplified carnivore guild. One limitation of our approach is that uncertainty from our fox
370 occurrence models was not propagated into the spatial mark-resight models. A full Bayesian integration
371 of the fox occurrence analysis and the spatial mark-resight model to address this is not yet implemented.
372 The development of open population spatial mark-resight models would also improve parameter estimates
373 for multi-season surveys.

374 The results of our study may explain why pest management that only targets foxes—one of the most
375 prevalent conservation actions in Australia—does not consistently improve native prey persistence (Dexter
376 & Murray 2009; Robley *et al.* 2014; Lindenmayer *et al.* 2018; Duncan *et al.* 2020; Wayne *et al.* 2017).
377 More evidence is required to understand the circumstances in which lethal fox control increases cat
378 density, particularly the role of baseline fox and prey densities. A more integrated approach to invasive
379 predator management, where foxes and cats are simultaneously or otherwise optimally controlled could
380 substantially improve biodiversity outcomes (Risbey *et al.* 2000; Comer *et al.* 2020). If this is not
381 feasible, changes in invasive mesopredator density and the outcomes for native prey species should be
382 closely monitored as part of any control program for invasive apex predators, with triggers for ceasing apex
383 predator control or commencing integrated management if single-species control proves counterproductive
384 for the conservation of threatened prey species.

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