

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

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

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## **1 ABSTRACT**

**2** The mesopredator release hypothesis predicts that subordinate predator density will increase as apex  
**3** predators decline. We replicated field experiments across two regions with a simple predator guild com-  
**4** prising the introduced red fox *Vulpes vulpes* and feral cat *Felis catus*. We identified 160 individual cats  
**5** from 68,504 camera-trap nights and estimated cat density using spatial mark-resight models. Targeted  
**6** lethal fox control was associated with a negligible to 3.7-fold increase in feral cat density, mirroring varia-  
**7** tion in the duration and intensity of fox suppression. Correlative models confirmed this—feral cat density  
**8** was negatively associated with fox occurrence at a fine spatial scale. We also observed changes in feral  
**9** cat detectability across the (artificial) apex predator activity gradient. Our results suggest integrated  
**10** predator management would help protect shared native prey and highlights that mesopredator release  
**11** can manifest as changes in both behaviour and density, distorting inference if these processes are not  
**12** distinguished.

<sup>13</sup> **1. INTRODUCTION**

<sup>14</sup> Understanding species interactions is critical for effective invasive species management (Zavaleta *et al.*  
<sup>15</sup> 2001). When several invasive species co-occur, management actions that suppress the dominant invasive  
<sup>16</sup> species may inadvertently benefit subordinate invasive species (Jackson 2015; Kuebbing & Nuñez 2015).  
<sup>17</sup> For example, the removal of a dominant invasive predator may increase the abundance of a subordinate  
<sup>18</sup> invasive species directly by reducing top-down pressure, or indirectly by increasing the availability of  
<sup>19</sup> shared resources; these are often referred to as mesopredator or competitor release, respectively (Crooks  
<sup>20</sup> & Soulé 1999; Ruscoe *et al.* 2011; Doherty & Ritchie 2017). The release of subordinate invasive species,  
<sup>21</sup> particularly predators, can have serious negative implications for native taxa and ecosystem function  
<sup>22</sup> (Courchamp *et al.* 1999; Ballari *et al.* 2016). However, integrated invasive predator management is often  
<sup>23</sup> far more costly and less feasible than single species control, and so it is important to identify when the  
<sup>24</sup> extra cost is justified (Bode *et al.* 2015).

<sup>25</sup> Most knowledge of mesopredator release stems from unreplicated ‘natural experiments’ (e.g. range  
<sup>26</sup> contractions - Crooks & Soulé 1999) or ad-hoc management interventions (e.g. invasive species eradica-  
<sup>27</sup> tions - Rayner *et al.* 2007). However, the occurrence, nature (positive or negative, direct or indirect)  
<sup>28</sup> and strength of predator interactions can vary among species assemblages, predation risk, environmen-  
<sup>29</sup> tal productivity, management regimes and other landscape contexts (Hastings 2001; Finke & Denno  
<sup>30</sup> 2004; Newsome *et al.* 2017; Alston *et al.* 2019). Replicating management programs in an experimental  
<sup>31</sup> framework is logically challenging, but important for understanding these complexities, discriminating  
<sup>32</sup> between plausible hypotheses and producing generalisable results to inform effective pest management  
<sup>33</sup> (Glen & Dickman 2005; Christie *et al.* 2019; Smith *et al.* 2020).

<sup>34</sup> Another source of uncertainty around the mesopredator release hypothesis stems from the inability  
<sup>35</sup> of traditional survey and modelling approaches to distinguish behavioural from numerical population  
<sup>36</sup> processes (Hayward *et al.* 2015; Stephens *et al.* 2015). Suppression of an apex predator may simultane-  
<sup>37</sup> ously change the behaviour and the density of a mesopredator, both of which influence detection rates  
<sup>38</sup> (Broadley *et al.* 2019; Rogan *et al.* 2019). This makes it difficult to interpret observed changes in naive  
<sup>39</sup> indices of mesopredator activity or occupancy in relation to changes in apex predator populations, even if  
<sup>40</sup> the study has an experimental design. Unbiased estimates of invasive predator density are also important  
<sup>41</sup> for setting meaningful control targets and inferring impacts on native prey (Moseby *et al.* 2019). Spatial  
<sup>42</sup> capture-recapture methods offer a solution by separating behavioural and observational processes from

43 population density, which is estimated within a defined spatial resolution (Borchers & Efford 2008).

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

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

63 We experimentally investigated the role of introduced foxes in top-down suppression of cat density in  
64 two regions of south-eastern Australia. Our experiments had a replicated Control-Impact design in the  
65 region with long-term fox control, and a Before-After Control-Impact Paired Series (BACIPS) design in  
66 the region with newly implemented fox control. Foxes and cats are the only functional terrestrial mam-  
67 malian predators in these regions, and each region included at least one area in which foxes were subject  
68 to continuous lethal poison-baiting (hereafter ‘impact landscape’), and a paired area where foxes were  
69 not controlled (hereafter ‘non-impact landscape’). This allowed a sharp focus on the interactions between  
70 the two invasive predators, across a gradient of apex predator (fox) occurrence. In accordance with the  
71 mesopredator release hypothesis, we predicted that: (1) cat density would be negatively correlated with  
72 fox occurrence at a fine spatial scale, and (2) fox control would increase cat density at a landscape scale.

<sup>73</sup> We based inference on direct estimates of cat density using spatially explicit mark-resight models.

<sup>74</sup> **2. MATERIALS AND METHODS**

<sup>75</sup> *2.1. Study area*

<sup>76</sup> We conducted our study across two regions of south-west Victoria, Australia (Fig. 1). The native  
<sup>77</sup> temperate forests in both regions are fragmented to varying degrees, primarily by livestock farming and  
<sup>78</sup> tree plantations. Although once widespread, native dingoes are now absent throughout, and a native  
<sup>79</sup> mesopredator, the tiger quoll *Dasyurus maculatus* is long absent from the Glenelg region and extremely  
<sup>80</sup> rare in the Otway Ranges (last sighted in 2014 despite extensive camera-trapping). The terrestrial  
<sup>81</sup> mammalian predator guild is therefore depauperate, with foxes and cats being the primary functional  
<sup>82</sup> mammalian terrestrial predators; birds of prey and snakes are the only other medium-large carnivores  
<sup>83</sup> present.

<sup>84</sup> Our study landscapes in the Glenelg region, Gunditjmara country, were primarily lowland forest and  
<sup>85</sup> heathy woodland. The area receives an average annual rainfall of 700 mm (Bureau of Meteorology 2021)  
<sup>86</sup> and has gently undulating terrain. The region frequently experiences prescribed burns and wildfires,  
<sup>87</sup> creating a mosaic of fire histories and vegetation complexity. Our study landscapes in the Otway region  
<sup>88</sup> were in the western section of the Otway Ranges on Gadubanud country. Rainfall here is more than  
<sup>89</sup> twice as high as the Glenelg region. The vegetation is a mosaic of shrubby wet forest and cool temperate  
<sup>90</sup> rainforest, with the northern landscape bordering on a large heathy woodland. This region rarely expe-  
<sup>91</sup> riences fire and is nearly ten times more rugged than the Glenelg region (based on the terrain ruggedness  
<sup>92</sup> index; Riley *et al.* 1999).

<sup>93</sup> Government land managers conduct ongoing targeted fox control for biodiversity conservation across  
<sup>94</sup> broad sections of each region. In these sections, manufactured poison baits (FoxOff, Animal Control  
<sup>95</sup> Technologies, Somerton) containing 3 mg of sodium mono-fluroacetate (1080) are buried at a depth of  
<sup>96</sup> 12-15 cm at 1-km intervals along accessible forest tracks and roads (Fig. 1). Different road densities  
<sup>97</sup> across the two regions result in variable poison-bait densities. Other large sections within each region are  
<sup>98</sup> maintained without fox control.

<sup>99</sup> 2.2. Study design and camera-trapping

<sup>100</sup> We designed experiments around the implementation of fox-baiting in each region. We simultaneously  
<sup>101</sup> surveyed one impact and one non-impact landscape within a region at a time. Each pair of impact and  
<sup>102</sup> non-impact landscapes was chosen based on similarity in vegetation groups, with the aim of maintaining  
<sup>103</sup> spatial independence with respect to predator daily movements.

<sup>104</sup> In the Glenelg region, we used a replicated control-impact design to compare three impact landscapes  
<sup>105</sup> that have been poison-baited for foxes at fortnightly intervals for more than 13 years with three paired  
<sup>106</sup> non-impact landscapes. We surveyed Cobboboonee National Park (impact) and Annya State Forest  
<sup>107</sup> (non-impact) in January – April 2018 ('replicate 1'), Mt Clay State Forest/Narrawong Flora Reserve  
<sup>108</sup> (hereafter 'Mt Clay'; impact) and Hotspur State Forest (non-impact) in April – June 2018 ('replicate 2'),  
<sup>109</sup> and Lower Glenelg National Park (LGNP) South (impact) and LGNP North (non-impact) in March –  
<sup>110</sup> May 2021 ('replicate 3'). For replicates 1 and 2, the paired landscapes were separated by at least 8 km, a  
<sup>111</sup> distance very unlikely to be traversed regularly by these invasive predators (Hradsky *et al.* 2017). LGNP  
<sup>112</sup> South and North are separated by the Glenelg river, which is impassable by terrestrial animals.

<sup>113</sup> In the Otway region, we used a before-after control-impact paired series (BACIPS) design to assess  
<sup>114</sup> changes related to the introduction of a fox control program. We deployed camera-trap grids in a pair  
<sup>115</sup> of impact – non-impact landscapes from June to September in three years (2017, 2018, 2019), in the  
<sup>116</sup> Great Otway National Park and Otway Forest Park. Our first survey occurred approximately three  
<sup>117</sup> months before fox-baiting began. Fox-baiting commenced in the impact landscape in November 2017.  
<sup>118</sup> Poison baits were replaced weekly for six weeks until December 2017, before changing to monthly bait  
<sup>119</sup> replacement until July 2018. The second survey was conducted six months after fox-baiting commenced,  
<sup>120</sup> however poison bait replacement lapsed from near the beginning of the survey until nearly three months  
<sup>121</sup> afterwards. Fox-baiting at monthly intervals recommenced in December 2018, six months prior to the  
<sup>122</sup> start of the final survey (Fig. S1). The impact and non-impact landscapes were at least 4.2 km apart  
<sup>123</sup> through dense forest, a distance unlikely to be regularly traversed by these invasive predators, although  
<sup>124</sup> possible (Hradsky *et al.* 2017). In this study, and a concurrent study which identified individual foxes  
<sup>125</sup> through genetic sampling (M. Le Pla *et al.*, in review), we found no evidence that either foxes or cats  
<sup>126</sup> moved between the impact and non-impact landscapes.

<sup>127</sup> In each landscape, we established a grid of 49 – 110 sites (mean = 88), averaging 448 m apart (range:

<sup>128</sup> 194 – 770 m). At each site, we set up a Reconyx trail camera (Reconyx, Holmen, Wisconsin) with an  
<sup>129</sup> infrared flash and temperature-in-motion detector on a tree, facing a tuna oil lure; see SI section S1 for  
<sup>130</sup> details. Overall, we deployed 1051 functional camera-traps, which operated for an average of 65 days  
<sup>131</sup> (range: 12 – 93 days), totalling 68,504 trap nights (Table S1).

<sup>132</sup> *2.3. Individual feral cat identification*

<sup>133</sup> We sorted the camera-trap images of cats into five categories based on coat type: black, mackerel  
<sup>134</sup> tabby, classic tabby, ginger and other; Fig. S3, and identified individual feral cats within each category;  
<sup>135</sup> see SI Section S2 for details. In the Otway region, 40% of cat detections were of black cats with few  
<sup>136</sup> identifiable markings, so we did not attempt to identify any black cats here. In the Glenelg region, black  
<sup>137</sup> cats were rarer (not detected at two landscapes) and often more distinctive, and so we could identify  
<sup>138</sup> some individuals (Table S1).

<sup>139</sup> *2.4. Spatial fox occurrence*

<sup>140</sup> We could not use raw fox presence-absence data from the camera-traps to predict cat density, as  
<sup>141</sup> spatial mark-resight models require covariate values for each grid cell in which density is estimated (see  
<sup>142</sup> Section 2.5). Instead, we generated a spatially-interpolated layer of the probability of fox occurrence for  
<sup>143</sup> each study landscape, using fox presence-absence data for each camera-trap site and binomial generalised  
<sup>144</sup> additive mixed-effects models (Wood 2017). These models allow efficient nonlinear spatial estimates, but  
<sup>145</sup> do not account for imperfect detection.

<sup>146</sup> We built the fox occurrence models using the ‘mgcv’ R-package (version 1.3.1; Wood 2011). We  
<sup>147</sup> modelled fox presences and absences (response variable) across space (explanatory variable) separately  
<sup>148</sup> for each region, with a duchon spline spatial smooth; these provide better predictions at the edge of  
<sup>149</sup> surveyed space than other splines (Miller & Wood 2014). In the Otway region, we included a random  
<sup>150</sup> intercept for each camera-trap site to account for repeat sampling and did not share spatial information  
<sup>151</sup> across years. Differences in camera-trap deployment lengths were accounted for using a model offset.

152    2.5. Spatial mark-resight models of feral cat density

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

166    We used closed population, sighting-only, spatial mark-resight models to estimate cat density using  
167    the maximum likelihood 'secr' R-package (Efford 2021). Detections of the 'mark status uncertain' cate-  
168    gory (unidentifiable cats), cannot be handled in the 'secr' R package; we added them to as 'unmarked'  
169    detections (black cats) rather than discard them (following Moseby *et al.* 2020). We condensed unmarked  
170    detection histories to a binary presence-absence record per each camera-trap for a 24-hour length duration  
171    ('occasion'), beginning at midday. We ran separate models for each region and treated each camera-trap  
172    grid deployment as a 'session'. We created a 4000-m buffer zone around each site (which was truncated  
173    by the river in LGNP), and estimated cat density at a 200-m grid cell resolution within this area. These  
174    habitat mask specifications were based on initial model trials and our knowledge of cat behaviour in these  
175    regions; the aim was to ensure density was estimated over a large enough area to encompass the activity  
176    centres of all cats exposed to our camera-traps, at a fine enough spatial scale to minimise bias in density  
177    estimates.

178    For each region, we ran four sets of models. We chose (1) between half-normal and exponential  
179    detection functions and (2) 'base model' covariates to carry through to subsequent model sets, (3) tested  
180    for associations between fox occurrence and cat density at a fine spatial scale, and (4) experimentally  
181    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<sub>c</sub>’) 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<sub>c</sub> 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<sub>c</sub> 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

<sup>212</sup> non-impact landscape (i.e., ‘response-ratio’) overlapped one; overlap would indicate no difference in cat  
<sup>213</sup> density. For the Otway region (BACIPS design), we assessed how much the confidence intervals around the  
<sup>214</sup> estimated difference between impact and non-impact landscapes overlapped between years; we expected  
<sup>215</sup> that the response-ratio would increase over the years, indicating an increase in cat density following the  
<sup>216</sup> introduction of fox control.

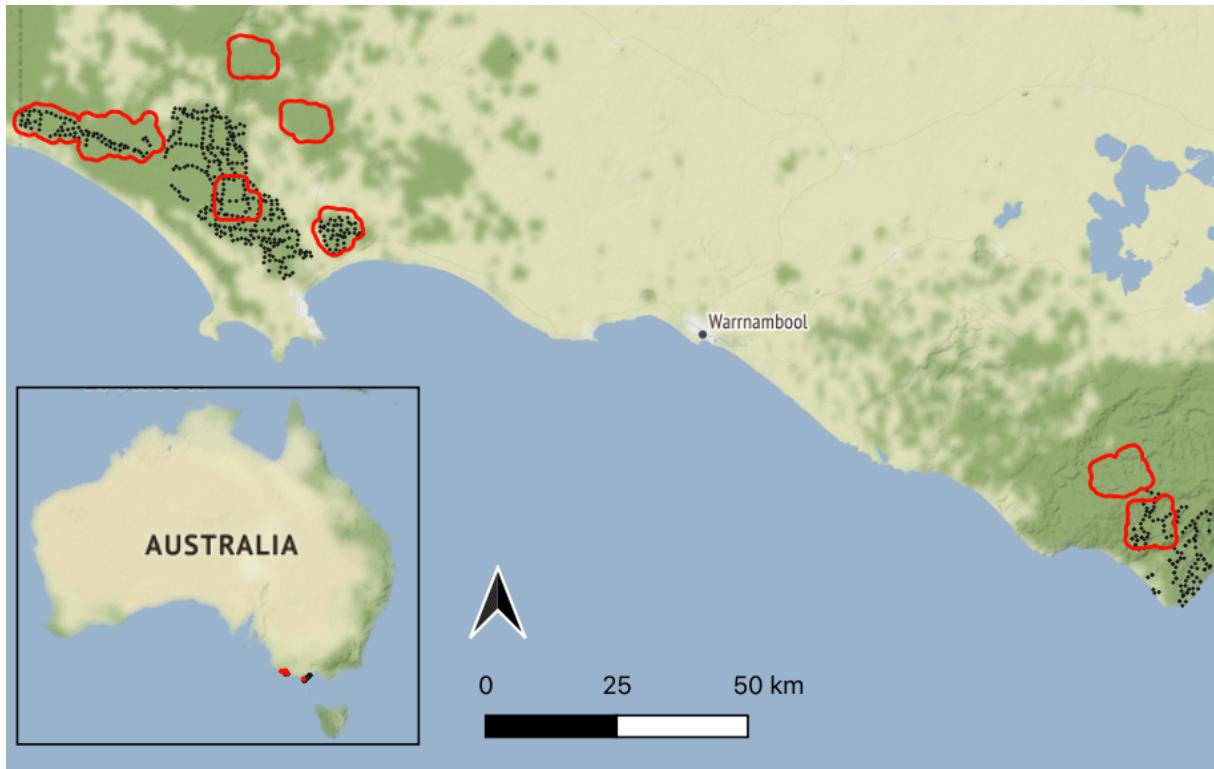


Figure 1: Locations of our eight study landscapes in south-west Victoria, Australia (red outlines). Note the two Lower Glenelg National Park landscapes in the far west are shown as one but are separated by a river. Locations of fox poison-bait stations are denoted by black dots. The Glenelg region is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

217 **3. RESULTS**

218 *3.1. Fox occurrence*

219 In the Glenelg region, there was a clear difference in fox occurrence between paired impact (poison-  
220 baited) and non-impact landscapes for replicates 1 and 3, but only a marginal difference for replicate  
221 2 (Fig. 2). In the Otway region, fox occurrence increased by 22% in the non-impact landscape, and  
222 decreased by 43% in the impact landscape over the three years (occurrence probability averaged at each  
223 camera-trap in the landscape). Fox occurrence in the Otway region was generally lower than the Glenelg  
224 region, with less fine-scale spatial variation. For example, fox occurrence was predicted to be spatially  
225 consistent across the entire Otway region in 2018 (Fig. 2). Fox model summaries and spatial standard  
226 error estimates are presented in SI Section S5.

227 *3.2. Feral cats in the Glenelg region*

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

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

239 Our hypothesis that cat density would be higher in landscapes with fox control was supported for the  
240 first and third replicate pairs: estimated cat densities were 2.5 (95% CI: 1.5 - 4.2) and 3.7 (95% CI: 1.4  
241 - 9.5) times higher in the impact landscape than the paired non-impact landscape, respectively (Fig. 5).  
242 For the second landscape pair, however, the estimated difference was positive but negligible (1.1; 95%  
243 CI: 0.69 - 1.69). At the landscape level, there was some evidence that cat detectability was affected by

244 fox occurrence; however the AIC<sub>c</sub> score was only 0.95 units better than the constant detectability model  
245 (Table S5) and the estimated effects were weak with high uncertainty. The detectability of cats in their  
246 activity centre ( $g_0$ ) tended to increase with the probability of fox occurrence (0.24; 95% CI: -0.32 - 0.80),  
247 as did sigma (0.13; 95% CI: -0.14 - 0.41).

248 *3.3. Feral cats in the Otway region*

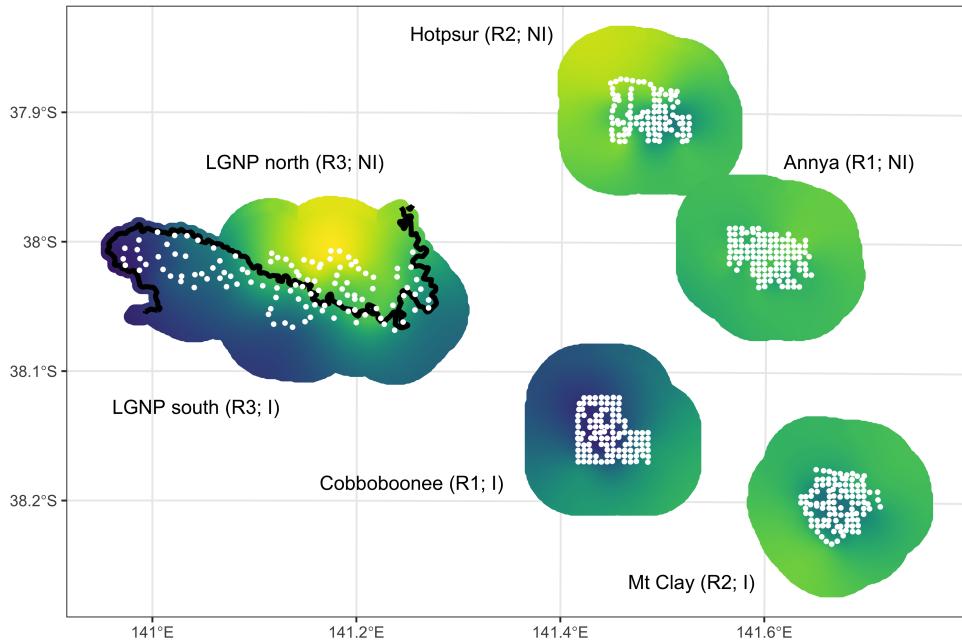
249 In the Otway region, we recorded 970 cat detections from 36,272 camera-trap nights (Table S1). We  
250 were able to identify 53% of cat detections to the individual level; a total of 93 cats (20 – 30 individuals  
251 per landscape). The exponential detector function was strongly supported over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

254 There was some evidence that cat density was negatively correlated with fox occurrence at a fine  
255 spatial scale: the two top-ranked models included a linear and a non-linear effect of fox occurrence  
256 on cat density, respectively; however, a model without a fox occurrence term received similar support  
257 (dAIC<sub>c</sub> = 0.80; Table S9). The 95% confidence interval around the linear coefficient from the top-ranked  
258 model marginally overlapped zero (-0.26; 95% CI: -0.55 - 0.02) indicating that cat density declined as  
259 fox occurrence increased in the Otways at a similar rate to Glenelg, but with slightly greater uncertainty  
260 (Fig. 3). However, the equivalent nonlinear model predicted that cat density only declined (at a steeper  
261 rate) in the mid-high range of fox occurrence probability (Fig. 3). Equivalent pairs of linear model and  
262 nonlinear models were indistinguishable based on AIC<sub>c</sub> scores (Table S9). There was also strong support  
263 for an effect of fox occurrence on cat detectability at a fine spatial scale (Fig. 4; Table S10). Where  
264 fox occurrence was higher, cats were less detectable in their activity centres (i.e., negative association  
265 with  $g_0$ ; -0.69; 95% CI: -1.11 - -0.27; Fig. 4A) and ranged further (i.e., positive association with sigma;  
266 coefficient 0.30; 95% CI: 0.13 - 0.47; Fig. 4B). The equivalent nonlinear model predicted detectability  
267 changes to have occurred only in the low-mid range of fox occurrence (Fig. 4).

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

<sup>273</sup> near-identical density estimates. These patterns continued into 2019, with cat density now somewhat  
<sup>274</sup> higher in the impact landscape than non-impact landscape. Overlap in the response ratio confidence  
<sup>275</sup> intervals for successive years was high, but the comparison between 2017 to 2019 suggests a meaningful  
<sup>276</sup> increase in cat density at the impact landscape relative to the non-impact landscape (Fig. 6B). Like the  
<sup>277</sup> fine scale model, there was strong evidence that cat detectability was impacted by fox occurrence (Table  
<sup>278</sup> S10).

(a) Glenelg region



(b) Otway region

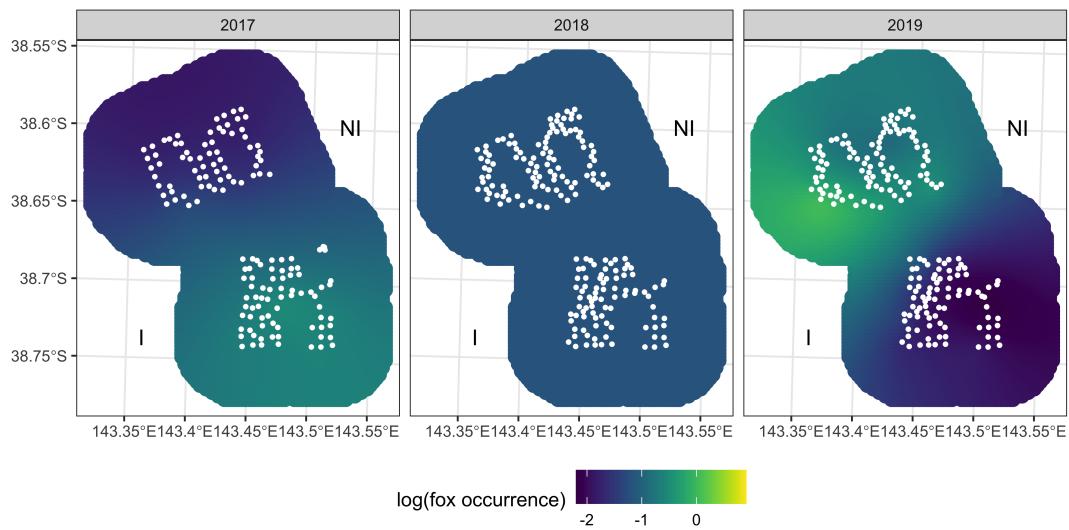


Figure 2: Predicted red fox *Vulpes vulpes* occurrence derived from generalised additive models within each impact (I) and paired non-impact (NI) landscape in the Glenelg (a) and Otway (b) regions, Australia. Predicted fox occurrence was used as a predictor of feral cat *Felis catus* density in the spatial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

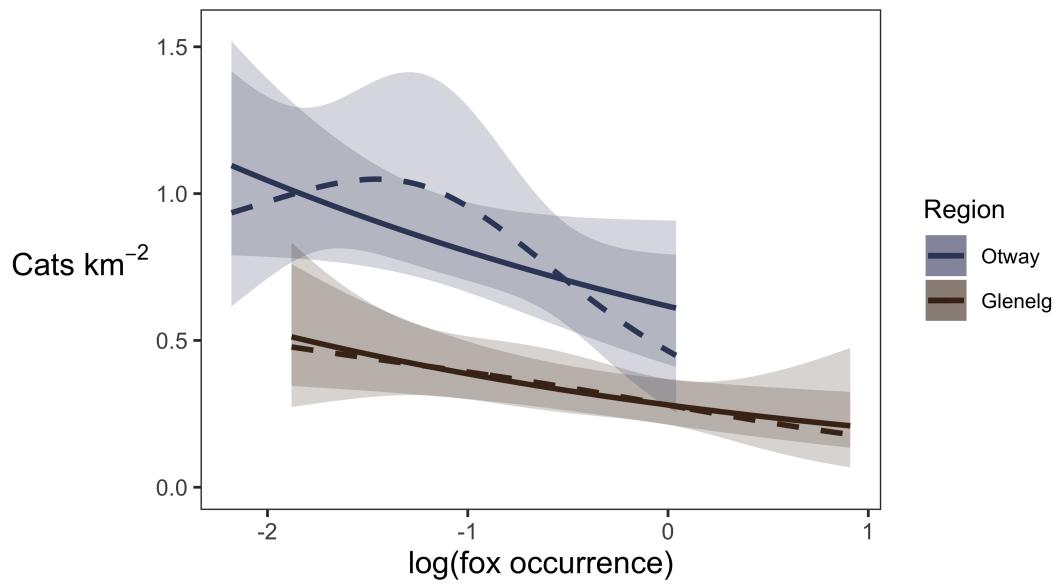


Figure 3: Linear (solid lines) and nonlinear (dashed lines) models predicted that feral cat *Felis catus* density increased with declining probability of red fox *Vulpes vulpes* occurrence (log-transformed) in the Glenelg and Otway regions, Australia. Shaded areas indicate 95% confidence intervals.

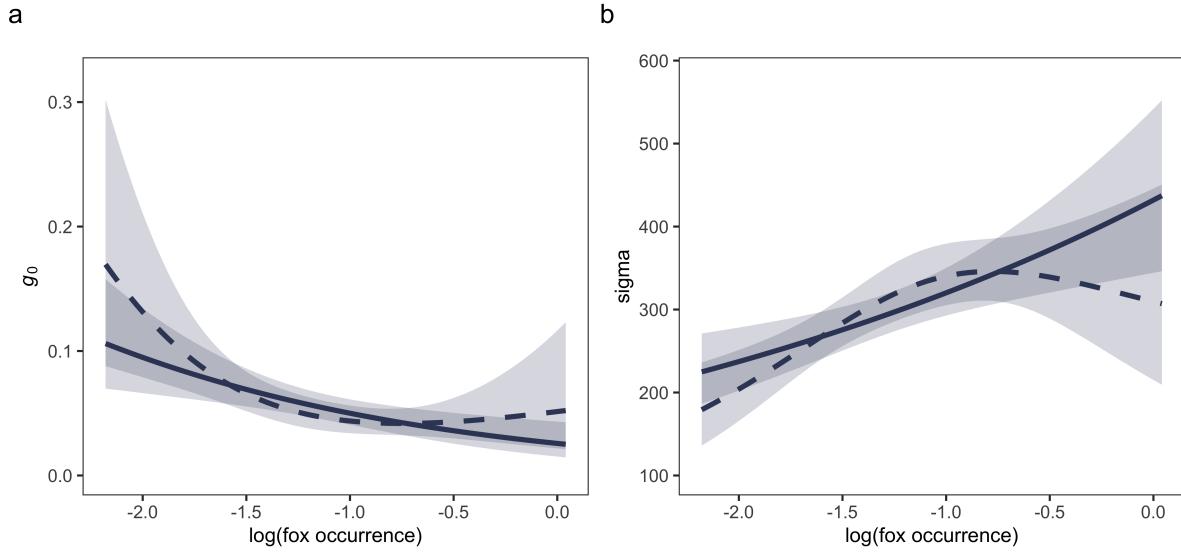


Figure 4: Linear (solid lines) and nonlinear (dashed lines) models of feral cat *Felis catus* detectability as a function of log-transformed red fox *Vulpes vulpes* occurrence in the Otway Ranges, Australia. The probability of detecting a feral cat in its activity centre per 24-hour occasion ( $g_0$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

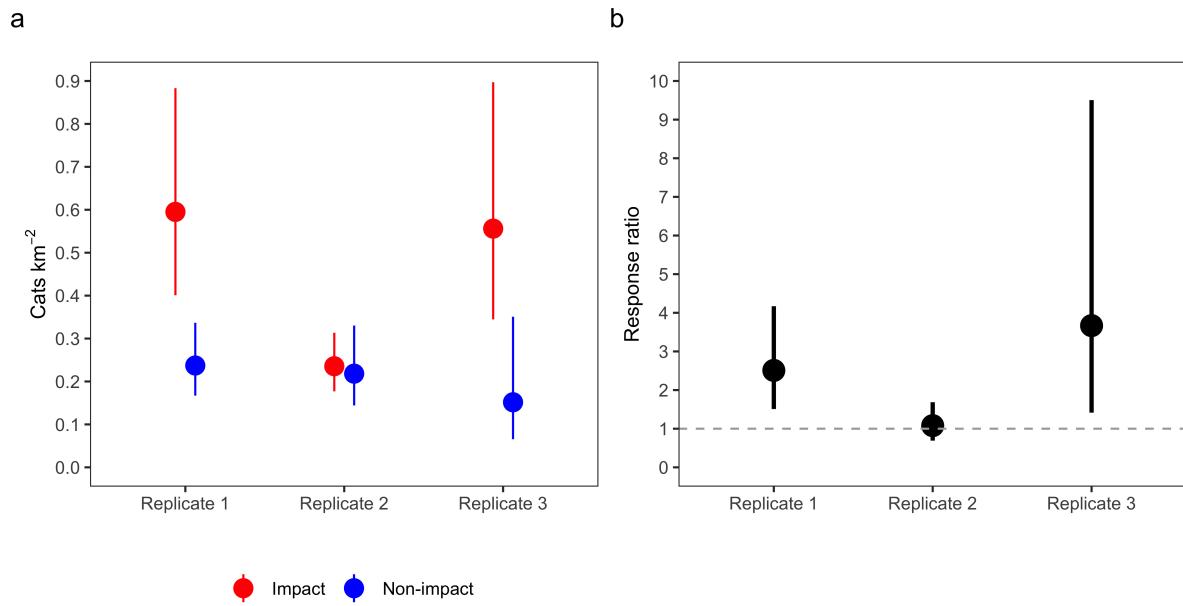


Figure 5: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the paired non-impact landscape for each replicate (b) in the Glenelg region, Australia. Poison-baiting for foxes *Vulpes vulpes* has been conducted in the impact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

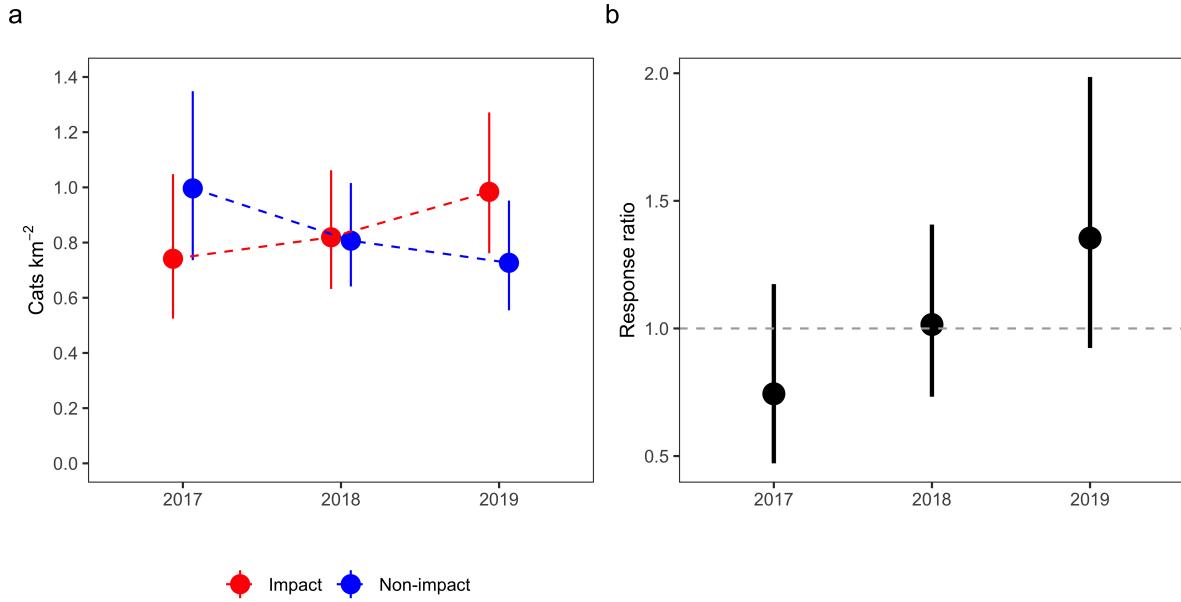


Figure 6: Landscape-scale feral cat *Felis catus* density estimates (a) and response ratio of cat density in the impact landscape relative to the non-impact landscape for each survey year (b) in the Otway region, Australia. In 2017, surveys were conducted approximately two months before lethal red fox *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.

279 **4. DISCUSSION**

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

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

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

309 2010).

310 Where fox occurrence was higher in the Otway Ranges, cats were less detectable in their activity  
311 centres and ranged further (Fig. 4). Low detectability is likely to correlate with fewer apex predator  
312 encounters, and has been observed in other predator interaction studies (e.g. Lombardi *et al.* 2017). An  
313 increase in cat ranging behaviour (sigma) with fox control supports observations made by Molsher *et al.*  
314 (2017), and may reflect a direct avoidance strategy. Animal movement rates are expected to increase  
315 in response to unpredictable threats (Riotte-Lambert & Matthiopoulos 2020). Alternatively, cats may  
316 consider foxes predictable and avoid locations they frequent, thus having to range further to obtain the  
317 same amount of food resources. In a similar forest habitat, Buckmaster (2012) observed large ‘holes’ in  
318 the home range of each GPS-collared cat; they confirmed that this was not due to an absence of prey  
319 and hypothesised that it could be due to apex predator avoidance. Regardless of the cause, variation in  
320 mesopredator detectability and movement rates with apex predator populations has serious implications  
321 for the interpretation of studies that compare relative abundance indices and spatial overlap of predator  
322 species without disentangling behaviour and detectability from density (Efford & Dawson 2012; Neilson  
323 *et al.* 2018; Stewart *et al.* 2018; Broadley *et al.* 2019).

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

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

339 mammalian prey populations two to ten years following fox control commencement (Duncan *et al.* 2020).  
340 Alternatively, top-down suppression by foxes and competition may be weaker in this highly productive  
341 environment where prey abundance was relatively high, fox occurrence was already relatively low, and  
342 overall cat densities were consistently high (Johnson & VanDerWal 2009; Greenville *et al.* 2014; Newsome  
343 *et al.* 2017). Our surveys provide important baselines against which to compare future changes in predator  
344 populations as the fox-baiting program continues.

345 Our study is among the very few which have used a direct measure of density to test mesopredator  
346 release. Previous studies have mostly used live capture-rates to infer population density, without account-  
347 ing for behavioural or detectability changes (e.g. Arjo *et al.* 2007; Karki *et al.* 2007; Thompson & Gese  
348 2007; Berger *et al.* 2008; Jones *et al.* 2008). Contention about mesopredator release has centred on such  
349 methods (Hayward *et al.* 2015); as well as unaccounted species interactions in complex predator guilds  
350 (Levi & Wilmers 2012; Jachowski *et al.* 2020). In contrast, our study tests the mesopredator release the-  
351 ory using a combined behavioural and numerical approach, in a system with a simplified carnivore guild.  
352 One limitation of our approach is that uncertainty from our fox occurrence models was not propagated  
353 into the spatial mark-resight models. A full Bayesian integration of the fox occurrence analysis and the  
354 spatial mark-resight model to address this is not yet implemented. The development of open population  
355 spatial mark-resight models would also improve parameter estimates for multi-season surveys.

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

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583 **SUPPORTING INFORMATION**

584 **S1. Field surveys**

585 In the Glenelg region, we deployed camera-traps once at a unique sites once. In the Otway region,  
586 we redeployed camera-traps in sites three times annually. All 2017 camera-sites were resurveyed each  
587 year, except for four logically challenging sites in the southern grid. In 2018, we added 16 additional  
588 sites in the southern grid, as well as 36 additional sites in the northern grid. These additional sites were  
589 resurveyed in 2019.

590 At each site, we deployed a singular remote trail camera with infrared flash and temperature-in-motion  
591 detector. The vast majority of camera-traps were Reconyx Hyperfire HC600, but a small portion was  
592 made up of both PC900 and HF2X infrared models (Reconyx, Holmen, Wisconsin). We programmed  
593 camera's to the highest sensitivity and to take five consecutive photographs when triggered (no quiet  
594 period). We attached each camera to a tree, approximately 30 cm above the ground, and facing toward a  
595 lure 2 - 2.5 metres away. The lure comprised an oil-absorbing cloth doused in tuna oil and placed inside  
596 a PVC pipe container with a mesh top. We secured each lure to the top of a 1 metre wooden stake and  
597 attached a handful of small white feathers to the outside of the PVC pipe container. Feathers were not  
598 used in the Lower Glenelg National Park survey. We cleared vegetation in the camera's line-of-sight to  
599 reduce false triggers and avoid obscuring cat coat markings in images.

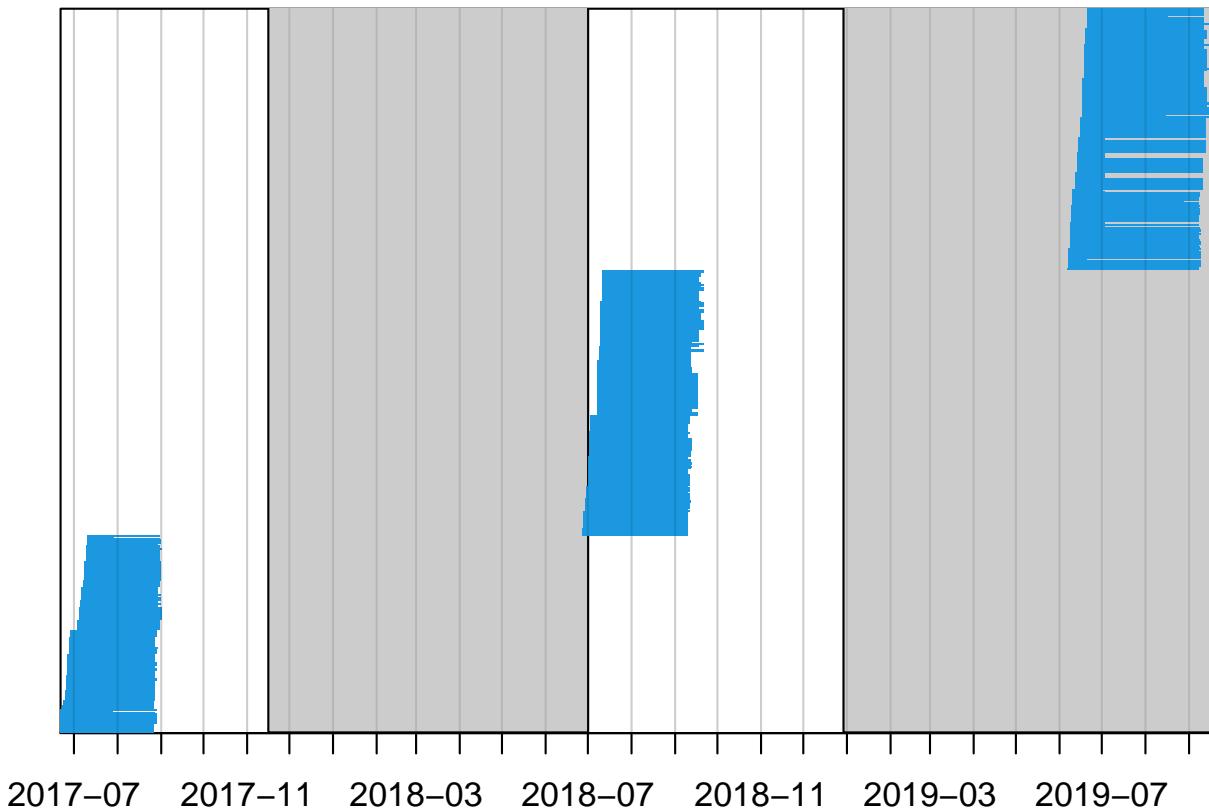


Figure S1: Camera-trap operation times in the Otway region, Australia. Each blue horizontal line represents one camera-trap deployment. Grey shading indicates periods of fox control in the impact landscape.



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

600 **S2. Individual cat identification**

601 We first labelled every camera-trap image with a species metadata tag using DigiKam software. We  
602 also added metadata tags for each cat coat type: black, mackerel tabby, classic tabby, ginger and other  
603 (coats with multiple colour blends; Fig. 3). This allowed us to summarise species records and extract cat  
604 images using the ‘camtrapR’ R-package (Niedballa *et al.* 2016).

605 We considered all black cats to be of the ‘unmarked’ category in spatial mark-resight models - even  
606 the few with white splotches on their underside (as these couldn’t always be seen as cats move with their  
607 head down).

608 In the remaining coat categories where possible, we identified individual cats based on their unique  
609 coat markings. The ability to identify individuals substantially increased as the image library for each cat  
610 increased. Therefore we made the easiest identifications first to build up these libraries, before making  
611 decisions on the less obvious detections. We examined and matched all coat markings seen between two  
612 particular deflections. Markings on the front legs were the most useful for ID’s as the patterns do not  
613 skew as much with different body positions. On the whole, unidentifiable detections were mainly due to  
614 only part of a cat appearing in the frame, or because photos were blurry (because of cat movement or a  
615 foggy camera lens).

616 We were left with a small number of instances (less than ten) where only left or right flanks could be  
617 seen. In this case, the side with the most repeat detections was labelled as an individual, whereas the  
618 side with the least number of detections was considered unidentifiable. Additionally, an extremely small  
619 portion of cats in the Otways had ginger coats. When ginger coats are photographed with an infrared  
620 flash, they become overexposed and no markings can be seen (see the image in bottom-right corner in Fig.  
621 S3). We only had one detection of a ginger cat without an infrared coat. Therefore, if there were multiple  
622 ginger cat detections in a single grid, we treated them in the same way as one-sided flank detections.

623 One observer identified the 2018 feral cats in the Glenelg region (MR) and the 2021 Lower Glenelg Na-  
624 tional Park cats (Luke Woodford). In the 2017 and 2018 Otway datasets (where there were substantially  
625 more cat detections and fewer distinct coat patterns) two independent observers identified individual  
626 cats and discrepancies between observers were reviewed together until consensus was reached (MR, MLP,  
627 BH). If no consensus was reached, the cat was considered unidentifiable. In the 2019 Otway dataset,

628 many of the identified cats were sighted in the previous surveys – these larger individual libraries meant  
629 that cats could be identified more easily so only one observer was necessary (MR). We also made use of  
630 additional cat images taken within the Otway region grids (just before each of our surveys) by white flash  
631 camera-traps from another study (Zoï Banikos, unpublished data). This provided additional and higher  
632 quality images (due to the white flash) of individuals in the photo library for identifications.

633 We were therefore left with three groups of cats: unmarked (black cats), marked (cats which could  
634 be identified to the individual-level with complete certainty) and mark status unknown (cats which were  
635 not black, but couldn't be identified to the individual level with complete certainty).

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



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

<sup>639</sup> **S3. Summary statistics**

Table S1: Summary of camera-trap survey effort and feral cat detections.

| Landscape  | Cameras | Trapnights | Cats | Moves | Detections (max. 1 per 24-hr) |              |          |
|------------|---------|------------|------|-------|-------------------------------|--------------|----------|
|            |         |            |      |       | Identified                    | Unidentified | Unmarked |
| Annya      | 110     | 8000       | 9    | 11    | 23                            | 3            | 20       |
| Cobbob     | 110     | 7752       | 13   | 19    | 35                            | 9            | 37       |
| Hotspur    | 99      | 6085       | 8    | 12    | 22                            | 3            | 13       |
| Mt Clay    | 106     | 5451       | 10   | 16    | 33                            | 5            | 0        |
| LGNP north | 49      | 2102       | 6    | 3     | 11                            | 0            | 0        |
| LGNP south | 64      | 2842       | 21   | 4     | 37                            | 0            | 0        |
| North 2017 | 67      | 3565       | 26   | 12    | 60                            | 8            | 46       |
| South 2017 | 73      | 7099       | 20   | 18    | 62                            | 4            | 48       |
| North 2018 | 103     | 7838       | 30   | 32    | 90                            | 12           | 62       |
| South 2018 | 85      | 4543       | 24   | 37    | 75                            | 17           | 59       |
| North 2019 | 99      | 6077       | 27   | 39    | 90                            | 22           | 101      |
| South 2019 | 86      | 7150       | 25   | 69    | 133                           | 23           | 58       |

640 **S4. Feral cat detection plots**

641 *S4.1. Glenelg region*

642 *S4.1.1. Replicate 1*

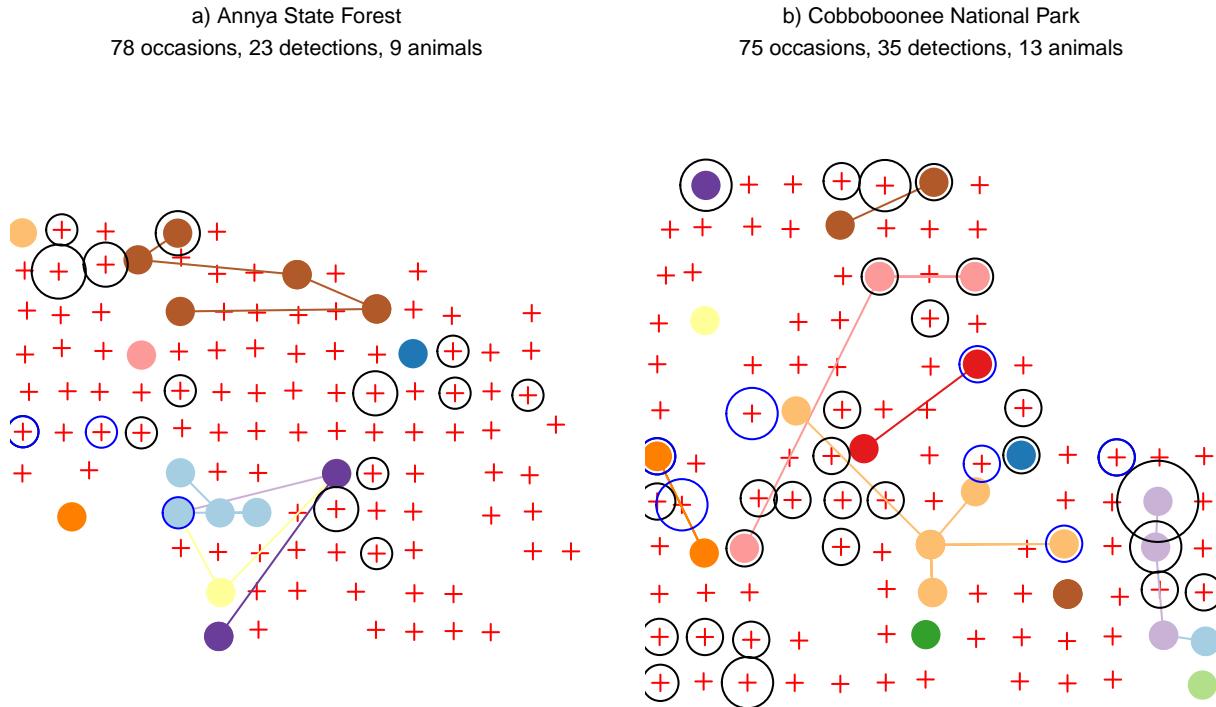


Figure S4: Feral cat detections in the first replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles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

<sup>643</sup> S4.1.2. Replicate 2

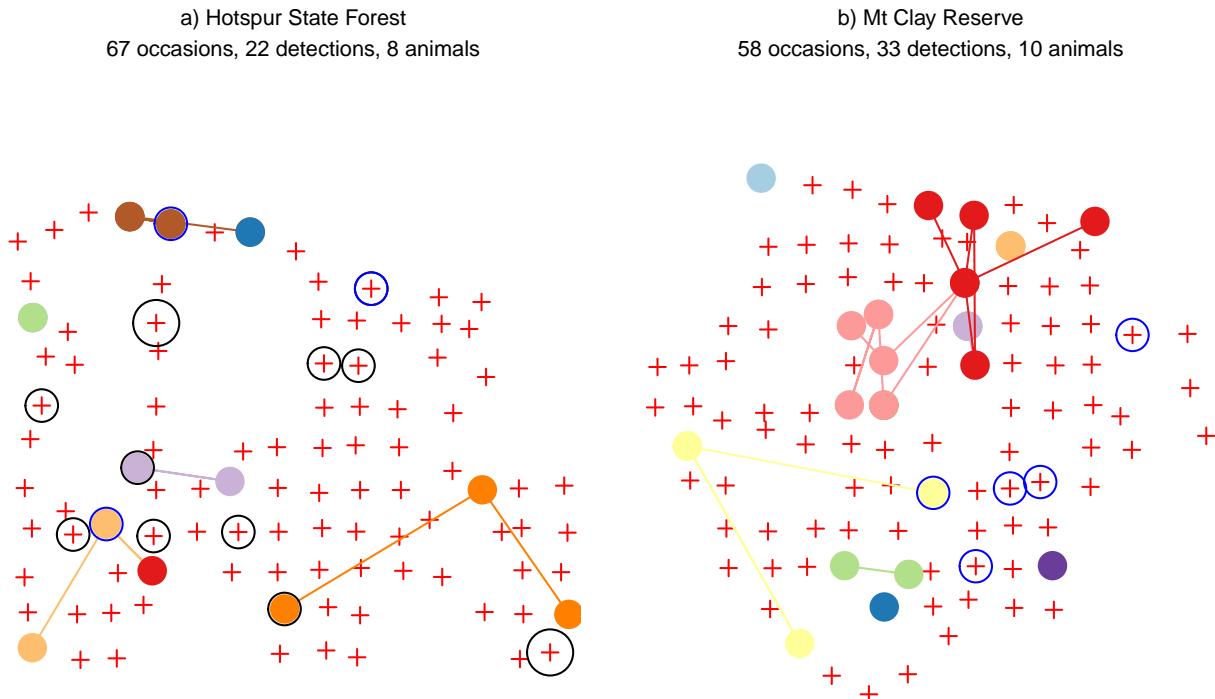


Figure S5: Feral cat detections in the second replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles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

644 S4.1.3. Replicate 3

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

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

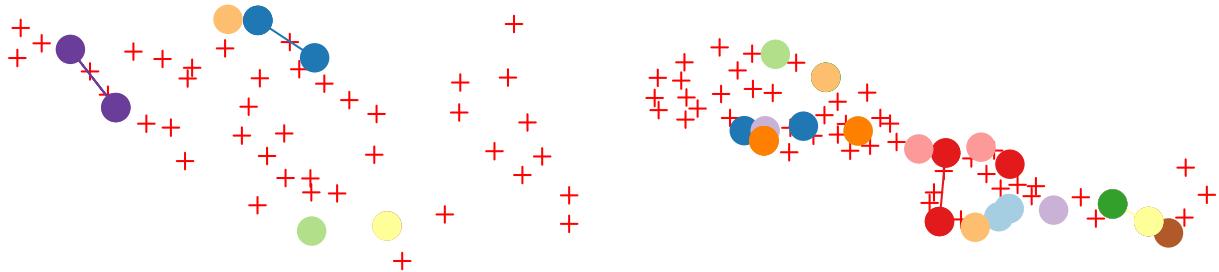


Figure S6: Feral cat detections in the third replicate grid pair in the Glenelg region, Australia. Camera-traps are indicated by red crosses. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control does not occur in the north (a) but does in the south (b).

645 S4.2. *Otway region*

646 S4.2.1. 2017

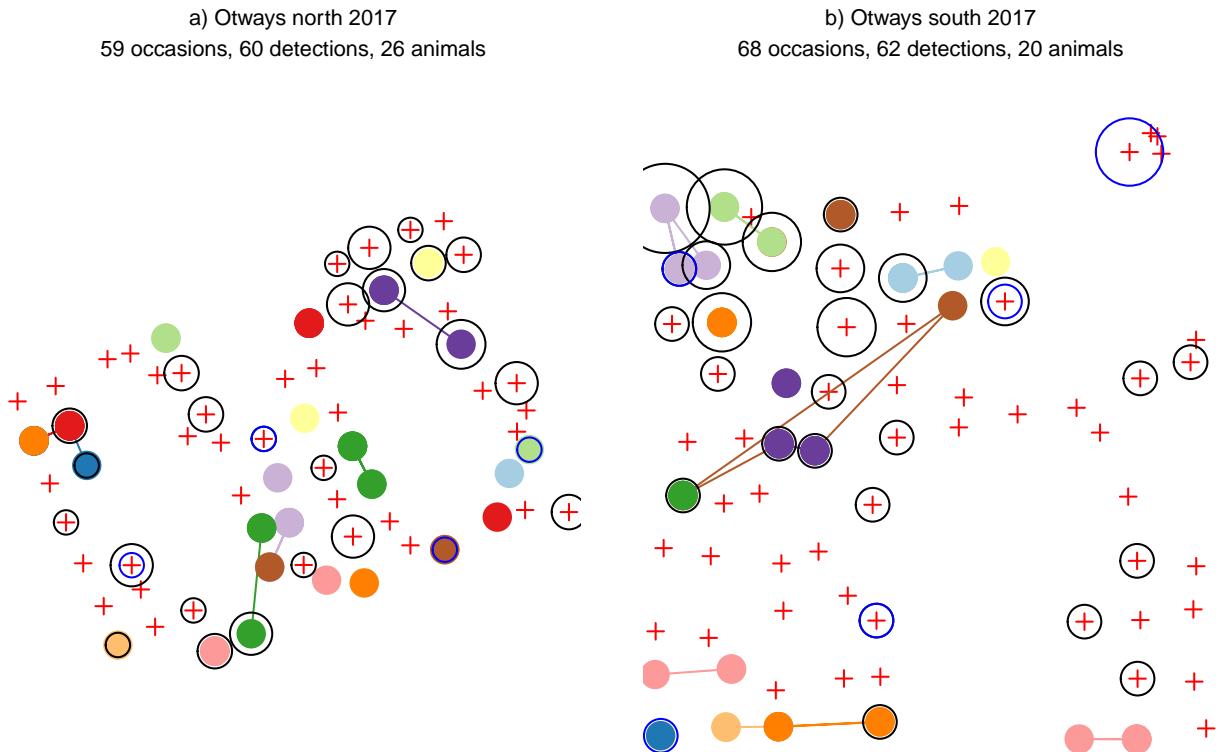


Figure S7: Feral cat detections in the Otway region, Australia, 2017. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling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

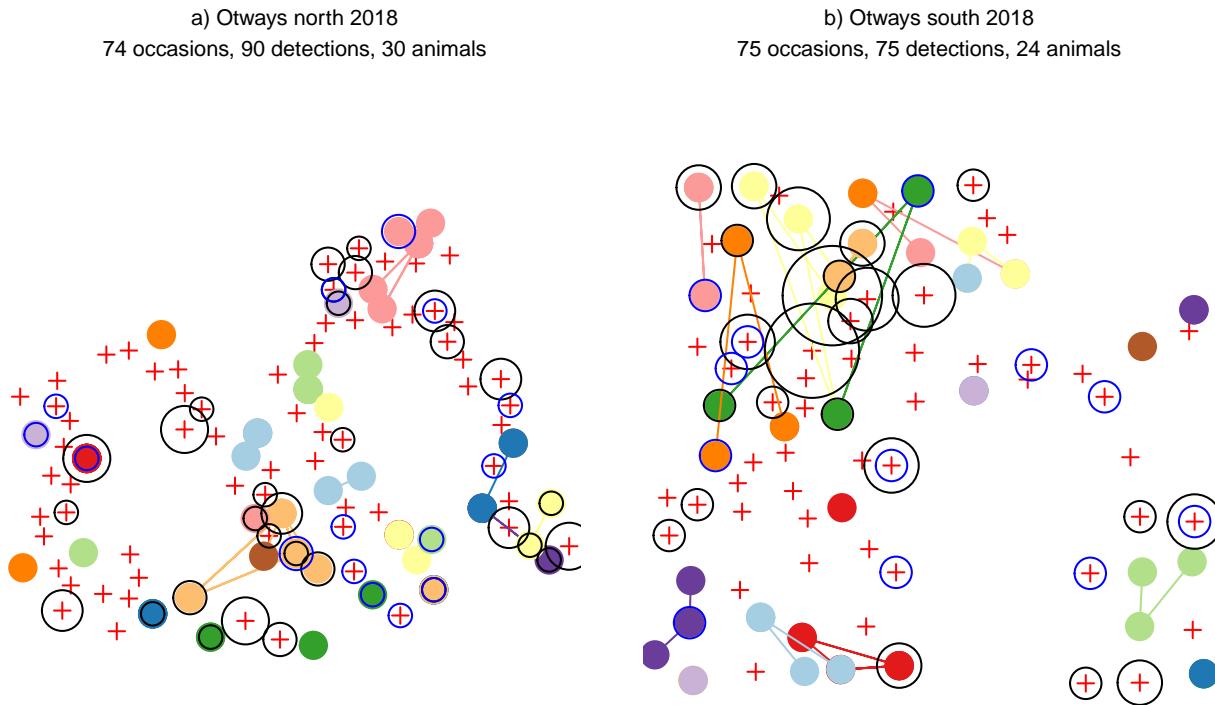


Figure S8: Feral cat detections in the Otway region, Australia, 2018. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling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

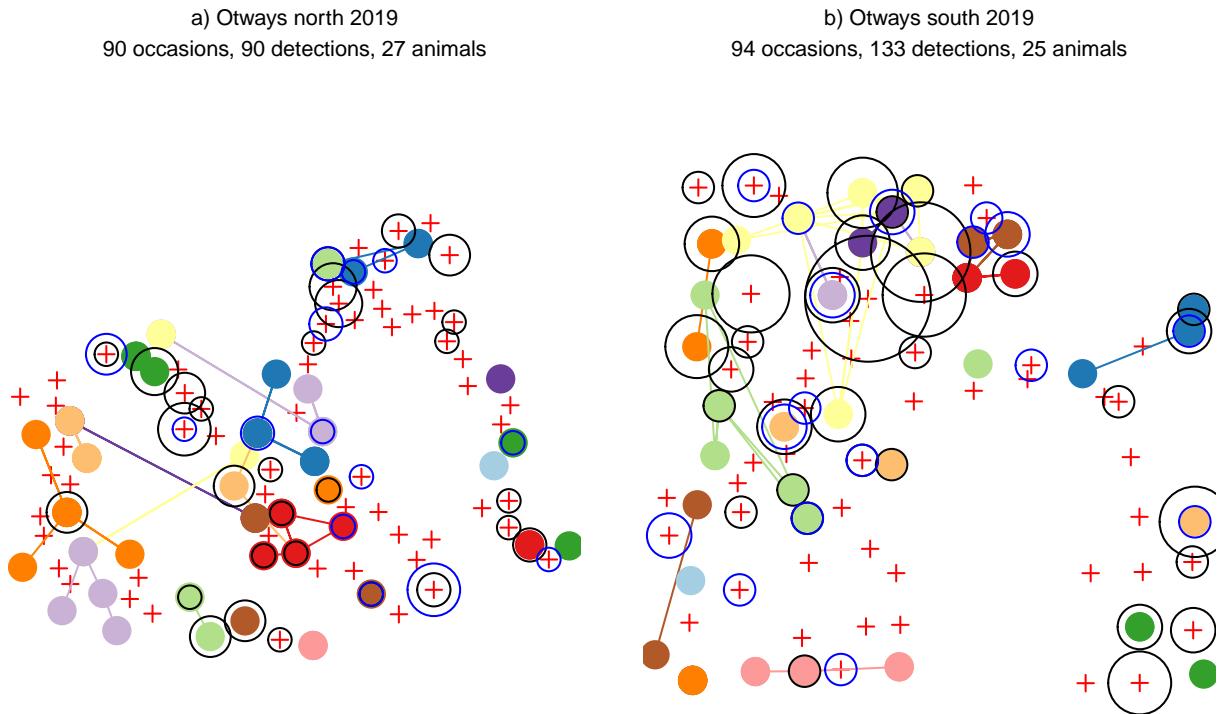


Figure S9: Feral cat detections in the Otway region, Australia, 2019. Solid fill coloured circles represent identified cats with lines indicating observed movements. Black open circles indicate black cat detections; blue circles indicate unidentifiable tabby cat detections, with circle radius scaling positively with the number of daily detections. Fox control occurred in the northern landscape (a) during this survey, but not the southern landscape (b).

649 **S5. Fox spatial occurrence**

650 *S5.1. Glenelg region*

```
651 ##
652 ## Family: binomial
653 ## Link function: logit
654 ##
655 ## Formula:
656 ## fox ~ s(x, y, bs = "ds", m = c(1, 0.5), k = 200) + offset(log(survey_duration))
657 ##
658 ## Parametric coefficients:
659 ##           Estimate Std. Error z value Pr(>|z|)
660 ## (Intercept) -4.53965   0.09293 -48.85 <2e-16 ***
661 ## ---
662 ## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
663 ##
664 ## Approximate significance of smooth terms:
665 ##          edf Ref.df Chi.sq p-value
666 ## s(x,y) 25.58    199  61.78 9.75e-07 ***
667 ## ---
668 ## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
669 ##
670 ## R-sq.(adj) =  0.126  Deviance explained = 13.1%
671 ## fREML = 845.52  Scale est. = 1             n = 538
```

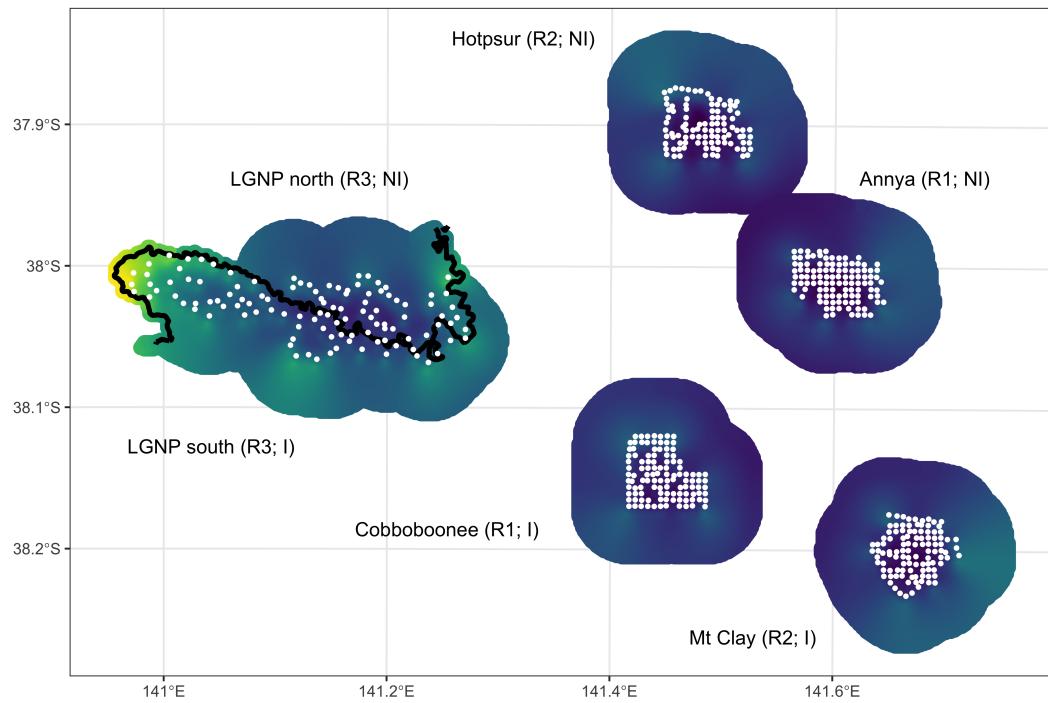


Figure S10: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Glenelg region, Australia.

672 *S5.2. Otway Region*

```
673 ##  
674 ## Family: binomial  
675 ## Link function: logit  
676 ##  
677 ## Formula:  
678 ## fox ~ year + s(x, y, by = year, bs = "ds", m = c(1, 0.5), k = 100) +  
679 ##     s(station, bs = "re") + offset(log(survey_duration))  
680 ##  
681 ## Parametric coefficients:  
682 ##             Estimate Std. Error z value Pr(>|z|)  
683 ## (Intercept) -5.283154   0.230023 -22.968 <2e-16 ***  
684 ## year2018    0.004643   0.277696   0.017   0.987  
685 ## year2019    0.037119   0.282270   0.132   0.895  
686 ## ---  
687 ## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1  
688 ##  
689 ## Approximate significance of smooth terms:  
690 ##             edf Ref.df Chi.sq p-value  
691 ## s(x,y):year2017 2.688e+00    99  8.096 0.010597 *  
692 ## s(x,y):year2018 2.494e-05    99  0.000 0.506341  
693 ## s(x,y):year2019 6.148e+00    99 22.262 0.000380 ***  
694 ## s(station)      5.366e+01   194 75.723 0.000116 ***  
695 ## ---  
696 ## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1  
697 ##  
698 ## R-sq.(adj) =  0.24 Deviance explained = 27.8%  
699 ## fREML = 763.36 Scale est. = 1 n = 513
```

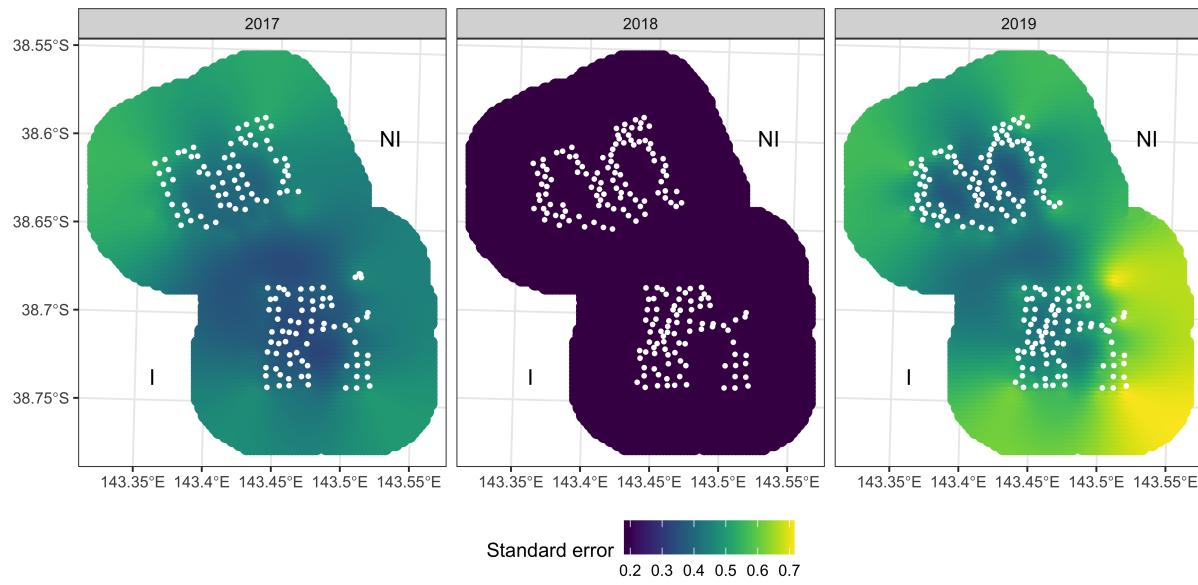


Figure S11: Standard error estimate of log fox occurrence probability derived from generalised additive models within each impact (I) and associated non-impact (NI) landscape in the Otway region, Australia.

700 **S6. Vegetation categories**

701 We condensed the main Ecological Vegetation Class groupings (DELWP 2020) present into three  
702 categories for each region: cleared land, heathy woodlands, lowland forests (Glenelg region only) and  
703 wet forests (Otways region only). We merged similar groups to reduce the number of categories for each  
704 region. In the Glenelg region, we merged dry forests with lowland forests. In the Otway region, we  
705 merged rainforests with wet forests, as well as merged dry forests and heathy woodlands.

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

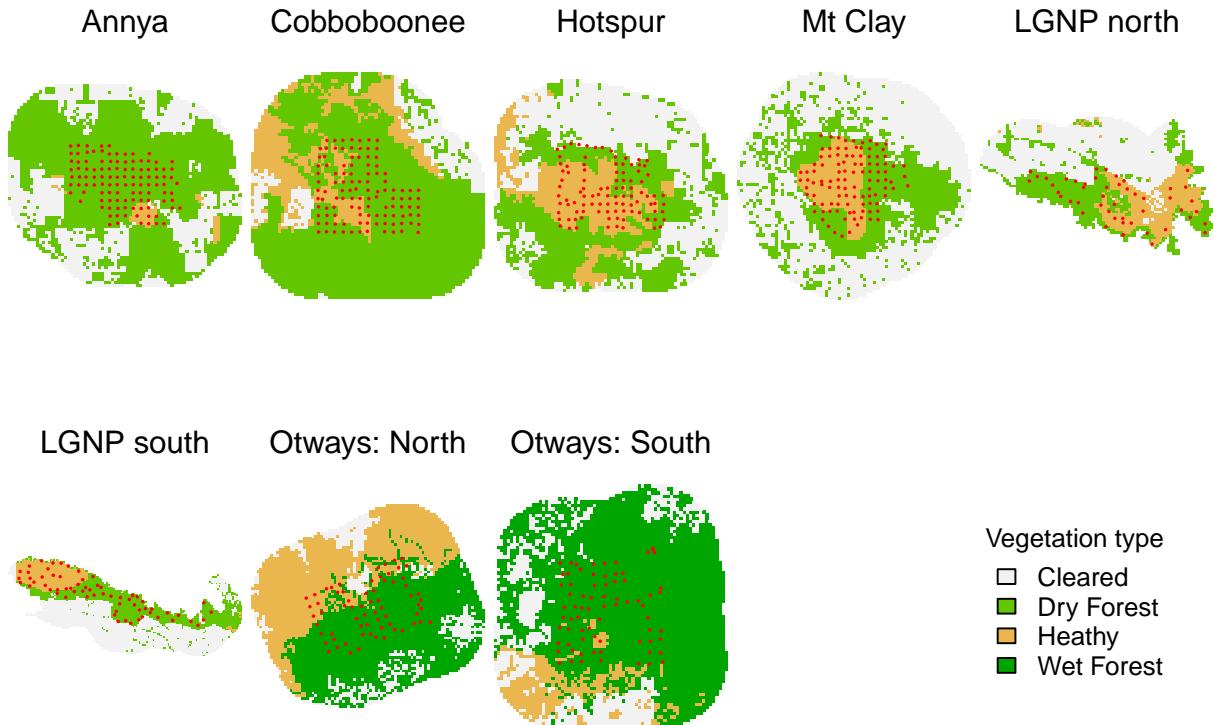


Figure S12: Condensed Ecological Vegetation Class groups used as habitat mask covariates in spatial mark-resight models.

<sup>710</sup> **S7. Spatial mark-resight models**

<sup>711</sup> *S7.1. Glenelg region*

Table S2: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 1.

| Detector function | K | logLik   | AIC     | AICc    | dAICc | AICcwt |
|-------------------|---|----------|---------|---------|-------|--------|
| exponential       | 3 | -1745.99 | 3497.99 | 3498.37 | 0.00  | 1      |
| half-normal       | 3 | -1763.02 | 3532.05 | 3532.43 | 34.06 | 0      |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

Table S3: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 2.

| Model                     | K | logLik   | AIC     | AICc    | dAICc | AICcwt |
|---------------------------|---|----------|---------|---------|-------|--------|
| D~1 g0~1 sigma~1          | 3 | -1309.93 | 2625.85 | 2626.23 | 0.00  | 0.32   |
| D~vegetation g0~1 sigma~1 | 5 | -1307.68 | 2625.37 | 2626.35 | 0.12  | 0.30   |
| D~vegetation g0~T sigma~1 | 6 | -1306.89 | 2625.77 | 2627.17 | 0.94  | 0.20   |
| D~1 g0~T sigma~1          | 4 | -1309.32 | 2626.65 | 2627.29 | 1.06  | 0.19   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

T - linear time trend (g0 only)

Table S4: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 3.

| Model                                       | K | logLik   | AIC     | AICc    | dAICc | AICcwt |
|---------------------------------------------|---|----------|---------|---------|-------|--------|
| D~fox_occ g0~1 sigma~1                      | 4 | -1306.67 | 2621.33 | 2621.98 | 0.00  | 0.49   |
| D~fox_occ g0~fox_occ sigma~fox_occ          | 6 | -1304.97 | 2621.94 | 2623.34 | 1.36  | 0.25   |
| D~s(fox_occ) g0~1 sigma~1                   | 5 | -1306.61 | 2623.21 | 2624.20 | 2.22  | 0.16   |
| D~1 g0~1 sigma~1                            | 3 | -1309.93 | 2625.85 | 2626.23 | 4.26  | 0.06   |
| D~s(fox_occ) g0~s(fox_occ) sigma~s(fox_occ) | 9 | -1303.41 | 2624.81 | 2627.97 | 5.99  | 0.02   |
| D~1 g0~fox_occ sigma~fox_occ                | 5 | -1309.41 | 2628.82 | 2629.80 | 7.82  | 0.01   |
| D~1 g0~s(fox_occ) sigma~s(fox_occ)          | 7 | -1307.91 | 2629.81 | 2631.71 | 9.73  | 0.00   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox\_occ - fine-scale occurrence probability of foxes derived from generalised additive models

s(fox\_occ) - non-linear smooth of fox\_occ with three knots

Table S5: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Glenelg region; model set 4.

| Model                              | K  | logLik   | AIC     | AICc    | dAICc | AICcwt |
|------------------------------------|----|----------|---------|---------|-------|--------|
| D~session g0~fox_occ sigma~fox_occ | 10 | -1297.46 | 2614.93 | 2618.86 | 0.00  | 0.62   |
| D~session g0~1 sigma~1             | 8  | -1300.66 | 2617.32 | 2619.80 | 0.95  | 0.38   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox\_occ - fine-scale occurrence probability of foxes derived from generalised additive models

session - landscape (n = 6)

Table S6: Feral cat density per square kilometre as estimated by the AICc top-ranked model in the Glenelg region, Australia.

| Landscape   | Estimate | 5% CI | 95% CI | Treatment  | Replicate |
|-------------|----------|-------|--------|------------|-----------|
| Annya       | 0.24     | 0.17  | 0.34   | Non-impact | 1         |
| Cobboboonee | 0.60     | 0.40  | 0.88   | Impact     | 1         |
| Hotspur     | 0.22     | 0.14  | 0.33   | Non-impact | 2         |
| Mt Clay     | 0.24     | 0.18  | 0.31   | Impact     | 2         |
| LGNP north  | 0.15     | 0.07  | 0.35   | Non-impact | 3         |
| LGNP south  | 0.56     | 0.34  | 0.90   | Impact     | 3         |

Table S7: Akaike's Information Criterion values for detector functions in the Otway region, Australia; model set 1.

| Detector function | K | logLik   | AIC      | AICc     | dAICc  | AICcwt |
|-------------------|---|----------|----------|----------|--------|--------|
| exponential       | 3 | -5591.00 | 11188.01 | 11188.17 | 0.00   | 1      |
| half-normal       | 3 | -5743.26 | 11492.52 | 11492.69 | 304.52 | 0      |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

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

| Model                            | K | logLik   | AIC     | AICc    | dAICc | AICcwt |
|----------------------------------|---|----------|---------|---------|-------|--------|
| D~year g0~1 sigma~1              | 5 | -3550.63 | 7111.26 | 7111.67 | 0.00  | 0.48   |
| D~year g0~T sigma~1              | 6 | -3549.83 | 7111.67 | 7112.25 | 0.57  | 0.36   |
| D~year + vegetation g0~1 sigma~1 | 7 | -3550.04 | 7114.08 | 7114.86 | 3.19  | 0.10   |
| D~year + vegetation g0~T sigma~1 | 8 | -3549.24 | 7114.48 | 7115.49 | 3.82  | 0.07   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

T - linear time trend (g0 only)

Table S9: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 3.

| Model                                              | K  | logLik   | AIC     | AICc    | dAICc | AICcwt |
|----------------------------------------------------|----|----------|---------|---------|-------|--------|
| D~year + fox_occ g0~fox_occ sigma~fox_occ          | 8  | -3541.80 | 7099.59 | 7100.60 | 0.00  | 0.33   |
| D~year + s(fox_occ) g0~s(fox_occ) sigma~s(fox_occ) | 11 | -3538.59 | 7099.19 | 7101.07 | 0.47  | 0.26   |
| D~year g0~s(fox_occ) sigma~s(fox_occ)              | 9  | -3541.07 | 7100.13 | 7101.40 | 0.80  | 0.22   |
| D~year g0~fox_occ sigma~fox_occ                    | 7  | -3543.44 | 7100.87 | 7101.65 | 1.05  | 0.19   |
| D~year + fox_occ g0~1 sigma~1                      | 6  | -3548.26 | 7108.51 | 7109.09 | 8.49  | 0.00   |
| D~year + s(fox_occ) g0~1 sigma~1                   | 7  | -3547.47 | 7108.94 | 7109.72 | 9.12  | 0.00   |
| D~year g0~1 sigma~1                                | 5  | -3550.63 | 7111.26 | 7111.67 | 11.07 | 0.00   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox\_occ - fine-scale occurrence probability of foxes derived from generalised additive models

s(fox\_occ) - non-linear smooth of fox\_occ with three knots

Table S10: Akaike's Information Criterion values adjusted for small sample size for feral cat density models in the Otway region; model set 4.

| Model                              | K  | logLik   | AIC     | AICc    | dAICc | AICcwt |
|------------------------------------|----|----------|---------|---------|-------|--------|
| D~session g0~fox_occ sigma~fox_occ | 10 | -3541.77 | 7103.55 | 7105.11 | 0.00  | 0.99   |
| D~session g0~1 sigma~1             | 8  | -3548.37 | 7112.73 | 7113.74 | 8.63  | 0.01   |

K - number of parameters

AICc - Akaike's Information Criterion with small-sample adjustment

dAICc - difference between AICc of this model and the model with smallest AICc

AICcwt - AICc model weight

fox\_occ - fine-scale occurrence probability of foxes derived from generalised additive models

session - landscape by year (n = 6)

Table S11: Feral cat density per square kilometre as estimated by the AICc top-ranked model in the Otway region, Australia.

| Landscape  | Estimate | 5% CI | 95% CI | Treatment  | Year |
|------------|----------|-------|--------|------------|------|
| north 2017 | 1.00     | 0.74  | 1.35   | Non-impact | 2017 |
| south 2017 | 0.74     | 0.52  | 1.05   | Impact     | 2017 |
| north 2018 | 0.81     | 0.64  | 1.02   | Non-impact | 2018 |
| south 2018 | 0.82     | 0.63  | 1.06   | Impact     | 2018 |
| north 2019 | 0.73     | 0.55  | 0.95   | Non-impact | 2019 |
| south 2019 | 0.98     | 0.76  | 1.27   | Impact     | 2019 |