

# Spatial variation in predator diel activity patterns – feral cats avoid red foxes in time, not space

Matthew W. Rees<sup>\*a</sup>, Brendan A. Wintle<sup>a</sup>, Jack H. Pascoe<sup>b</sup>, Mark Le Pla<sup>b</sup>, Emma K. Birnbaum<sup>b</sup>, Bronwyn A. Hradsky<sup>a</sup>

<sup>a</sup>*Quantitative & Applied Ecology Group, School of Ecosystem and Forest Science, The University of Melbourne, Parkville, VIC, Australia*

<sup>b</sup>*Conservation Ecology Centre, Otway Lighthouse Rd, Cape Otway, VIC, Australia*

**Key words:** feral cat; diel activity patterns; generalised additive model; invasive predator; intraguild predator interactions; mesopredator release; red fox; lethal predator control

---

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

<sup>1</sup> ABSTRACT

- <sup>2</sup> 1. Understanding the constraints that apex predators impose on subordinate species is important for  
<sup>3</sup> anticipating the outcomes of predator management. Subordinate predators may avoid dominant  
<sup>4</sup> predators in time or space, making it difficult to quantify changes in antipredator behaviours unless  
<sup>5</sup> joint spatiotemporal analyses are used.
- <sup>6</sup> 2. In this study, we tested whether an invasive apex predator (red fox *Vulpes vulpes*) suppresses or  
<sup>7</sup> alters the spatiotemporal activity of an invasive mesopredator (feral cat *Felis catus*).
- <sup>8</sup> 3. We surveyed these predators using 3667 camera-trap deployments across two regions of south-  
<sup>9</sup> eastern Australia; foxes were poison-baited in some landscapes within each region. The simple  
<sup>10</sup> predator guild in these regions allowed sharp focus on the interactions between these species across  
<sup>11</sup> experimental gradients of fox (apex predator) activity. We used generalised additive models to  
<sup>12</sup> quantify overall predator activity across space and fluctuations in predator activity throughout the  
<sup>13</sup> daily cycle (i.e., diel activity patterns).
- <sup>14</sup> 4. When averaged across the study region, red foxes and feral cats had very similar diel activity  
<sup>15</sup> patterns; however, there was important differentiation at a finer scale. When fox counts at a camera-  
<sup>16</sup> trap were high, feral cats did not reduce their overall activity but shifted their diel activity patterns  
<sup>17</sup> to less risky times of the day. In dry habitats of both regions, cats shifted from being nocturnal-  
<sup>18</sup> crepuscular to mostly diurnal. In wet forest habitat, fox activity was consistent throughout the diel  
<sup>19</sup> period; but when fox counts were high, cats became more nocturnal, avoiding dawn in particular.  
<sup>20</sup> Changes in cat diel activity patterns may facilitate spatial coexistence between the two invasive  
<sup>21</sup> predators, potentially shifting impacts onto different native prey species.
- <sup>22</sup> 5. It is well-appreciated that overall predator activity varies spatially and fluctuates throughout the  
<sup>23</sup> daily cycle. Our study demonstrates that diel activity patterns also vary across space, likely medi-  
<sup>24</sup> ated by both landscape context and fear. Apex predator avoidance appears to be dynamic across  
<sup>25</sup> landscapes of fear—a key nuance which is overlooked when simply comparing the average activity  
<sup>26</sup> overlap between two species or the spatial overlap of species occurrence.

27 **1. INTRODUCTION**

28 Predators shape ecosystems through both predation and the fear of predation (Creel & Christianson,  
29 2008; Ritchie & Johnson, 2009). Fear-induced behavioural suppression can be as detrimental to subordi-  
30 nate species as predation itself (Preisser et al., 2005; Schmitz et al., 2004). These non-consumptive effects  
31 of apex predator are expected to be strong drivers of mesopredator behaviour, particularly when resource  
32 competition is high (Ritchie & Johnson, 2009). A strengthening or relaxing of antipredator behaviours  
33 by mesopredators can have cascading effects across the entire ecosystem: altering population demograph-  
34 ics, species interactions, ecological function and human-wildlife coexistence (Brown et al., 1999; Estes  
35 et al., 2011; Gaynor et al., 2019; Lamb et al., 2020; Ripple & Beschta, 2004). Hence, understanding  
36 how apex predators constrain the behaviour of subordinate species is important to accurately predict the  
37 ecosystem-wide consequences of predator management, such as reintroductions or lethal control (Gaynor  
38 et al., 2021).

39 Spatial and/or temporal niche partitioning may allow predators to coexist by reducing encounter-rates  
40 and resource overlap (Kronfeld-Schor & Dayan, 2003). However, mesopredators may not consistently  
41 employ avoidance behaviours because perceived predation risk is temporally and spatially variable, and  
42 antipredator behaviours typically involve a trade-off against resource acquisition, such as limiting or  
43 relegating activity to suboptimal places or times (Lima & Bednekoff, 1999; Lima & Dill, 1990). Therefore,  
44 optimal predator avoidance strategies are likely to vary across heterogeneous landscapes where resource  
45 availability (e.g., shelter, food) and perceived predation risks differ (Kauffman et al., 2007; Willems &  
46 Hill, 2009; Wirsing et al., 2021). For example, temporal predator avoidance may be preferable over spatial  
47 avoidance if food is constantly available throughout the day, and vice versa. These concepts are unified  
48 under the ‘ecology of fear’ (Brown et al., 1999) concept, which has gained increasing attention in recent  
49 times (Gaynor et al., 2019). Notably, the mesopredator release hypothesis has recently been expanded  
50 from increases in mesopredator abundance following apex predator decline (Soulé et al., 1988) to also  
51 include changes in mesopredator behaviour (Brashares et al., 2010).

52 To accurately quantify avoidance within a predator guild, we first need to understand how the overall  
53 activity and diel activity patterns of each species varies ‘naturally’ across landscapes, particularly for  
54 species with broad distributions. It is widely recognised that the overall activity of different predator  
55 species varies across their distributions, but their diel activity patterns are often assumed to be constant.  
56 In this paper, we use the term ‘overall activity’ to refer to the number of ‘independent’ predator detections

57 at a site (offset to account for survey duration; analogous to an activity or abundance index), and ‘diel  
58 activity pattern’ to refer to fluctuations in relative activity throughout the 24-hour daily cycle. Overall  
59 activity is influenced by predator behaviour, population density and the detection process (Anderson,  
60 2001), whereas diel activity patterns are a behavioural trait (less likely to be affected by the detection  
61 process, if the survey methodology remains consistent).

62 Despite modern predator survey technologies providing time-stamped detections, detection times are  
63 commonly discarded from analyses, probably because joint modelling of overall activity and diel activity  
64 patterns is more complicated. When temporal avoidance is tested, it is usually considered in an ad-hoc  
65 fashion, by fitting separate models for spatial and temporal avoidance, or by repeating spatial analyses  
66 (e.g., resource selection functions) at different time periods (e.g., Smith et al., 2019; Basille et al., 2015;  
67 Kohl et al., 2019). However, discretising the daily cycle into categorical periods (e.g., day and night)  
68 introduces bias, assuming animals have complete step-changes in behaviour rather than progressive shifts  
69 across the daily cycle. Further, dawn and dusk are particularly important times for many predator  
70 species.

71 Generalised Additive Models (hereafter ‘GAMs’) are increasingly being used to estimate animal diel  
72 activity patterns and offer a flexible framework to jointly consider overall activity. GAMs also have other  
73 benefits, including smoothing penalties to reduce overfitting, the ability to capture nonlinear interactions  
74 between multiple variables with different units, and the ability to share information across categorical  
75 variables through hierarchical specifications (Pedersen et al., 2019; Wood, 2017). However, we are only  
76 aware of one study which allowed animal diel activity to interact with predation risk as a continuous  
77 variable in a GAM (although without considering overall activity; Cunningham et al., 2019).

78 The red fox *Vulpes vulpes* (hereafter ‘fox’; ~6 kg) and feral cat *Felis catus* (hereafter ‘cat’; ~4 kg)  
79 have devastating impacts on native prey throughout their introduced range, implicated in the extinction  
80 of ~10 and 63 species, respectively (Doherty et al., 2016). The impacts of these invasive predators have  
81 been particularly extreme on the Australian continent (Woinarski et al., 2015). Cats are more difficult to  
82 manage, and so introduced predator control programs in Australia often target only foxes (particularly  
83 through poison-baiting; Reddiex et al., 2007). As foxes and cats compete for many of the same resources,  
84 there is concern that lethal fox control could cause a mesopredator release (Soulé et al., 1988) of feral  
85 cats (Comer et al., 2020; Doherty & Ritchie, 2017; Glen & Dickman, 2005; Marlow et al., 2015; Robley  
86 et al., 2014; Wayne et al., 2017). There is some evidence that feral cats increase in activity (although

87 highly uncertain; Hunter et al., 2018), density (M.W.R, unpublished data) and alter their diets and use of  
88 space (Molsher et al., 2017) in response to fox control. Other studies have investigated potential spatial  
89 and temporal interactions between these invasive predators (e.g., Roshier & Carter, 2021), but not in  
90 response to fox control, or in a joint spatiotemporal framework that allows flexibility in cat avoidance  
91 behaviours in respect to differences in fox activity.

92 In this study, we explored how the overall activity and diel activity patterns of two competing invasive  
93 predators varied across heterogeneous landscapes, in response to (1) space and (2) vegetation types. We  
94 then investigated (3) whether cat diel activity patterns change in response to the overall level of fox  
95 activity. Our study was conducted in a simple predator system where foxes and cats are the only  
96 mammalian carnivores, and fox activity is manipulated using lethal control in some landscapes. This  
97 allowed sole focus on the interactions between these two predators, across an experimental gradient of  
98 apex predator (fox) activity. We illustrate how GAMs can provide a simple framework to jointly assess  
99 spatial and temporal animal activity patterns, as well as avoidance behaviours.

<sup>100</sup> **2. MATERIALS AND METHODS**

<sup>101</sup> *2.1. Study area and camera-trapping*

<sup>102</sup> We compiled data from multiple smaller-scale camera-trap studies across two regions in south-west  
<sup>103</sup> Victoria, Australia: the Glenelg region and Otway Ranges (Fig. 1). Introduced foxes and cats are the  
<sup>104</sup> only medium-large functional mammalian terrestrial carnivores here: native dingoes *Canis familiaris*  
<sup>105</sup> are long-absent throughout, while tiger quolls *Dasyurus maculatus* are long-absent in the Glenelg region  
<sup>106</sup> and likely functionally extinct in the Otway Ranges (last confirmed sighting in 2014). In broad sections  
<sup>107</sup> of each region, government land managers conduct ongoing targeted lethal fox control for biodiversity  
<sup>108</sup> conservation. Poison-baits containing 3 mg of sodium fluroacetate ('1080') are buried at a depth of  
<sup>109</sup> 12 - 15 cm at 1-km intervals along accessible forest tracks and roads. Different road densities result in  
<sup>110</sup> variable densities of poison-baits. Managers also frequently implement prescribed fire across both regions,  
<sup>111</sup> primarily to reduce fuel loads to prevent large wildfires.

<sup>112</sup> *2.1.1. Glenelg region*

<sup>113</sup> In the Glenelg region, large patches of natural vegetation are fragmented by pastoral farming and  
<sup>114</sup> residential properties (Fig. 1). Foxes in three distinct forest blocks in this region have been subject to  
<sup>115</sup> poison-baiting since October 2005, with fortnightly bait replacements (Robley et al., 2014). These forest  
<sup>116</sup> blocks, along with three similar, unbaited forest blocks to the north have been simultaneously surveyed  
<sup>117</sup> annually under the 'Glenelg Ark' fox control program since 2005 (40 sites per block; Robley et al., 2020).  
<sup>118</sup> Hair-tubes were used to monitor species from 2005 - 2013 (presented in Robley et al., 2014), replaced  
<sup>119</sup> by camera-traps from 2013; here we present camera-trap data from 2013 - 2019 (Robley et al., 2020).  
<sup>120</sup> We also included a further 425 camera-trap deployments at unique locations from early 2018 (M.W.R.  
<sup>121</sup> PhD surveys). This totals 2039 camera-trap deployments in the Glenelg region, collected in a control-  
<sup>122</sup> impact experimental design (foxes had been continuously controlled for at 8 - 14 years in the treatment  
<sup>123</sup> landscapes at the time of these surveys).

<sup>124</sup> *2.1.2. Otway Ranges*

<sup>125</sup> The Otway Ranges is a largely continuous patch of natural vegetation with a strong east-west rainfall  
<sup>126</sup> gradient (Fig. 1). A matrix of cool temperate rainforest and wet forest at high altitudes in the south-west

127 descend into a large heathland directly north, and into dry forests and then heathlands to the north-east.  
128 Fox-baiting commenced in small sections of the Otway Ranges in 2008 and large-scale systematic baiting  
129 began in 2016 - 2017 under the ‘Otway Ark’ program (Robley et al., 2019). For the first six weeks, poison-  
130 baits were replaced weekly, then changing to ongoing monthly bait-replacement. There was a pause in  
131 baiting for approximately six months during the second half of 2018. Fox control recommenced in late 2018  
132 with four weeks of fortnightly bait-replacement, before returning to monthly bait-replacement. A large  
133 section of the Otway Ranges to the north-west remains unbaited, but is monitored as an experimental  
134 non-treatment site (Robley et al., 2019). Otway Ark managers survey 372 camera-trap sites annually  
135 (sequentially across the region); we present one ‘before’ baiting survey and two ‘after’ baiting surveys of  
136 each site from 2016 - 2018, totalling 1113 camera-trap deployments (Robley et al., 2019). We also include  
137 data from an additional before-after control-impact surveys (one ‘before’ baiting survey and two ‘after’  
138 baiting surveys) in the western section of the Otway Ranges, conducted annually 2017 - 2019 (M.W.R  
139 PhD surveys). This added a further 195 sites and 524 camera-trap deployments.

#### 140 2.1.3. Camera-trap set-ups

141 All camera-trap deployments consisted of a Reconyx (Holmen, Wisconsin) brand camera-trap (white  
142 or infrared flash), attached to a tree or a metal picket, facing a lure. The Glenelg Ark and Otway Ark  
143 fox monitoring programs positioned camera-traps at least 40 cm above ground on a tree or a metal picket  
144 and angled downwards toward a lure approximately 1 - 1.5 m away (Robley et al., 2019, 2020). The  
145 lures consisted of peanut butter, golden syrup and rolled oats mixed into a small ball, placed within a tea  
146 strainer or PVC pipe container and secured either to the ground, or 20 - 60 cm above ground on a wooden  
147 stake. The M.W.R. PhD surveys across both regions positioned camera-traps lower on a tree (around 15  
148 - 30 cm above the ground) angled only slightly downwards toward a tuna oil lure approximately 2 - 2.5  
149 m away (detailed in Rees et al., 2019). Camera-traps were active for an average of 47 days (maximum  
150 93 days), totalling 172,052 trap-nights.

#### 151 2.2. Data preparation

152 All data analysis was conducted in R version 3.6.3 (R Core Team, 2020). We first used lorelograms  
153 to identify the minimum interval to approximate independence (Iannarilli et al., 2019); this indicated  
154 that discarding repeat detections of a species within 30 minutes was sufficient to reduce temporal auto-

correlation. To account for day length variation across space and time, we extracted sunrise and sunset times for each camera-trap deployment using the ‘maptools’ R-package (Bivand & Lewin-Koh, 2021) and adjusted detection times to be relative to sunrise and sunset using the average double anchoring approach described by Vazquez et al. (2019). We then built a dataframe consisting of a row for each hour of the day (0 – 23), for every camera-trap deployment ( $n = 3667$ ), recording the total number of ‘independent’ fox and feral cat detections within each hour across the camera-trap survey.

### 2.3. Generalised additive models

We modelled the total number of independent detections of each predator per hour for each camera-trap deployment (response variable) with generalised additive mixed-effect models implemented in the ‘mgcv’ R-package (Wood, 2017). We used the negative binomial family, as overdispersion, but not zero-inflation, was detected with a poisson distribution using the ‘DHARMA’ R-package (Hartig, 2020). We specified the natural log of the number of survey days as a model offset to account for differences in camera-trap survey duration, and a random intercept for each site to account for repeat sampling. For fox models, we also included a smooth effect of poison-bait density with separate responses per region to account for the effect of fox control (all figures in this manuscript are derived from fox models predicted to a no fox-baiting scenario). This formed the base model specification for each model we fitted; models differed in their specification of the cyclical hour smooth to provide inference on variations of predator diel activity across the four questions of interest; this is detailed in the sections below.

#### 2.3.1. How does predator overall activity and diel activity patterns vary across space? (model 1)

To examine how the overall activity and diel activity patterns of each predator varied across space, we fit a model for each predator which included a tensor product interaction between a spatial smooth and hourly smooth. This allowed predators to have different activity levels across space (static across the years surveyed), as well as variation in diel activity pattern across space. Space was modelled using camera-trap coordinates and a duchon spline basis (Miller & Wood, 2014). To examine how the relative strength of diel activity patterns changed across space, we plotted the percentage increase from the minimum to maximum activity estimate within the daily cycle for each predicted location (hereafter referred to as ‘diel activity pattern strength’).

182    2.3.2. How does predator overall activity and diel activity patterns vary across vegetation types? (model  
183            2)

184       Predator activity varied across space; we hypothesised that this was partly due to differences in  
185       vegetation type, based both on the observed spatial patterns and because vegetation type is a major  
186       driver of understorey habitat structure and prey occurrence in these regions (Hradsky et al., 2017; Swan  
187       et al., 2015). To test whether the diel activity pattern of each predator varied among vegetation types,  
188       we identified the Ecological Vegetation Class group (hereafter “vegetation type”; standard units for  
189       vegetation classification in Victoria; Department of Environment, Land, Water & Planning, 2020) for  
190       each unique camera-trap site, totalling eight vegetation types. As rainforests are interspersed (primarily  
191       in low lying gullies) at fine-scales throughout wet and damp forests in the south-eastern Otway Ranges,  
192       we merged them together (hereafter referred to as ‘wet forests’). We then estimated predator activity  
193       across vegetation types using a hierarchical model specification: a global smoother for hour (i.e., average  
194       response) and group-level smoothers with shared wigginess for the seven vegetation types (“model GS”  
195       detailed in Pedersen et al., 2019). We also included a random effect to account for differences in overall  
196       activity levels between the two regions.

197    2.3.3. Do feral cats avoid foxes in space or time? (model 3)

198       Fox diel activity across vegetation types showed strong similarity between all vegetation types except  
199       wet forests. To examine whether cats avoid foxes in space or time, we therefore modelled fox-induced  
200       changes in feral cat diel activity separately for wet forest and dry vegetation types. We further split dry  
201       vegetation types by region for replication. We refer to the resulting variable as ‘habitat type’, which  
202       had three levels: (i) wet forests and rainforests in the western Otway Ranges ('wet\_otways'), (ii) dry  
203       vegetation types in the Otway Ranges ('dry\_otways') and (iii) dry vegetation types in the Glenelg region  
204       ('dry\_glenelg'). We hypothesised that cats would avoid foxes in time by becoming more diurnal in dry  
205       vegetation types where foxes were mostly nocturnal, but not in wet forests where fox activity showed  
206       little variation across the daily cycle.

207       To investigate changes in feral cat diel activity across the range of observed fox activity, we first  
208       quantified fox activity for each camera trap deployment as the total number of fox detections for the  
209       deployment divided by the number of survey days, to adjust for survey duration (hereafter ‘adjusted fox  
210       counts’). We modelled an interaction between hour (cyclical spine) and adjusted fox counts (thin plate

211 regression spline with shrinkage - meaning fox effects could be entirely removed from the model if not  
212 supported by sufficient data), allowing cats to have nonlinear responses to both hour and adjusted fox  
213 counts. We fit separate tensor product interactions for each habitat type (using a ‘by-variable’ term).  
214 For a direct visual comparison to fox activity, we fit another fox model where a diel curve was estimated  
215 separately across each of the three habitat types.

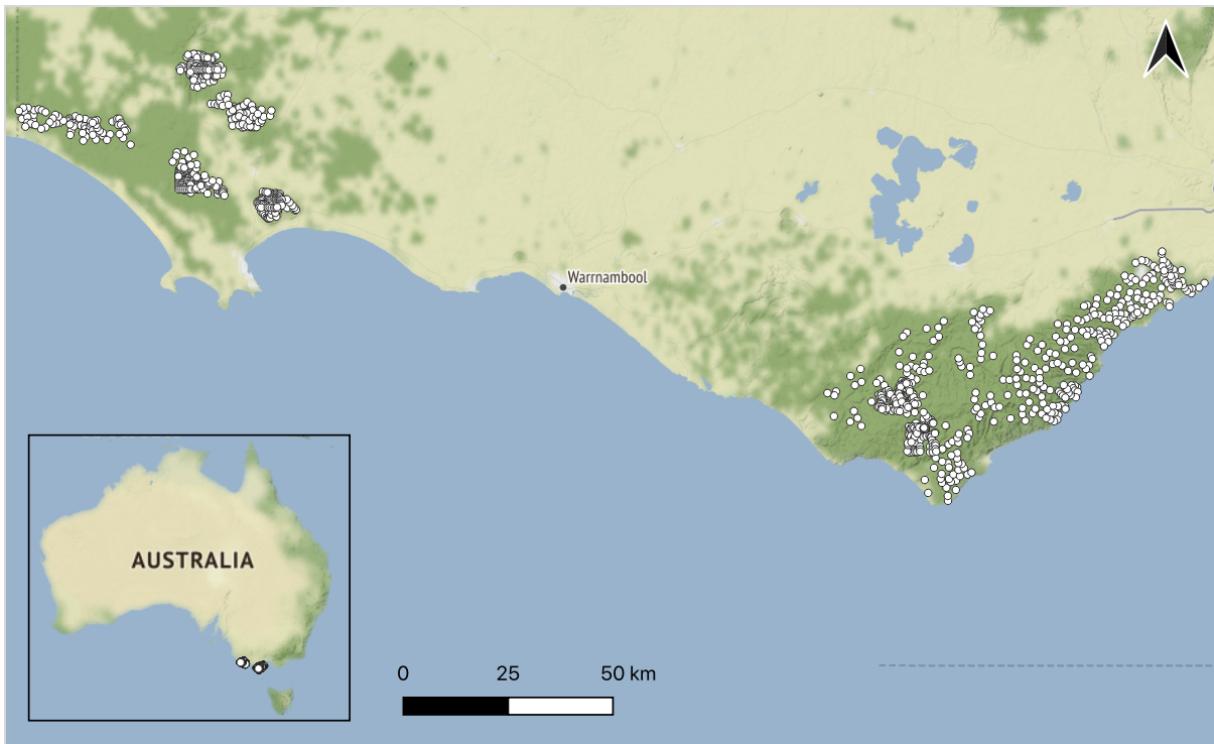


Figure 1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0,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

216 **3. RESULTS**

217 Overall, we collated 5449 and 2202 independent detections of foxes and cats, respectively (separated  
218 by at least 30 minutes) from 172,052 camera-trap nights (Table S1).

219 *3.0.1. How does predator overall activity and diel activity patterns vary across space? (model 1)*

220 Predator activity varied considerably across space and throughout the 24-hour daily cycle, and there  
221 was some variation in the predator diel activity patterns across space. On average, both predators showed  
222 similar diel activity patterns: mostly nocturnal with peaks in activity around sunrise and sunset (i.e.,  
223 crepuscular; Fig. 4i). The main difference between the species was that fox activity peaked just after  
224 sunset and they were less likely to be active during the day than cats. Cats also tended to be more active  
225 at sunset relative to sunrise.

226 Diel activity pattern strength also differed between the species. Fox activity was concentrated strongly  
227 at particular times of the day, especially in the Glenelg region where activity varied by up to 371%  
228 throughout the daily cycle (Fig. 3a). Feral cats had relatively more consistent activity throughout the  
229 daily cycle and across regions; the maximum difference in cat activity throughout the daily cycle for any  
230 given location was 185%.

231 Variation in diel activity patterns across space, as well as differences in overall activity between the  
232 predators, was strongest in the Otway Ranges. For example, overall fox activity (Fig. S8) and diel  
233 activity pattern strength (Fig. 3b) were lowest in the south-west Otway Ranges, while feral cat overall  
234 activity (Fig. S9) and diel activity pattern strength (Fig. 3b) were highest in that subregion.

235 *3.0.2. How does predator overall activity and diel activity patterns vary across vegetation types? (model  
236 2)*

237 Overall levels of fox activity were similar across all vegetation types, except wet forests where fox  
238 activity was considerably lower. Overall cat activity was more variable across vegetation types; lowest in  
239 heathy woodlands and highest in wet forests (Fig. 4b).

240 Diel activity patterns for foxes were similar across all vegetation type except wet forests; in wet  
241 forests, foxes were consistently active throughout the daily cycle (Fig. 4a). On the other hand, cats were

<sup>242</sup> nocturnal (and most active) in wet forests, but largely crepuscular in all other vegetation types (Fig. 4b).  
<sup>243</sup> For both predators, the random effect for region (Glenelg or Otways) in the vegetation models shrank to  
<sup>244</sup> near-zero, indicating all variation between the regions was explained by the vegetation covariate and site  
<sup>245</sup> random intercept.

<sup>246</sup> *3.0.3. Do feral cats avoid foxes in space or time? (model 3)*

<sup>247</sup> Cat spatial activity was relatively unaffected by the fox activity in both habitat types of the Otway  
<sup>248</sup> Ranges; and, if anything, increased with increasing adjusted fox counts in the Glenelg region (Fig. 5),  
<sup>249</sup> indicating cats did not avoid foxes spatially.

<sup>250</sup> Across all habitat types, feral cat diel activity patterns changed across the gradient of fox activity  
<sup>251</sup> (Fig. 5). In the Glenelg region and Otway dry habitat types, feral cats had a nocturnal-crepuscular diel  
<sup>252</sup> activity pattern where fox activity was low, but were most active during the day where fox activity was  
<sup>253</sup> high. In contrast, in the wet forests of the Otway Ranges, feral cats were more strongly nocturnal when  
<sup>254</sup> fox activity was high.

### Otway Ranges: Red fox

Space-time interaction effect (excluding marginal effects)

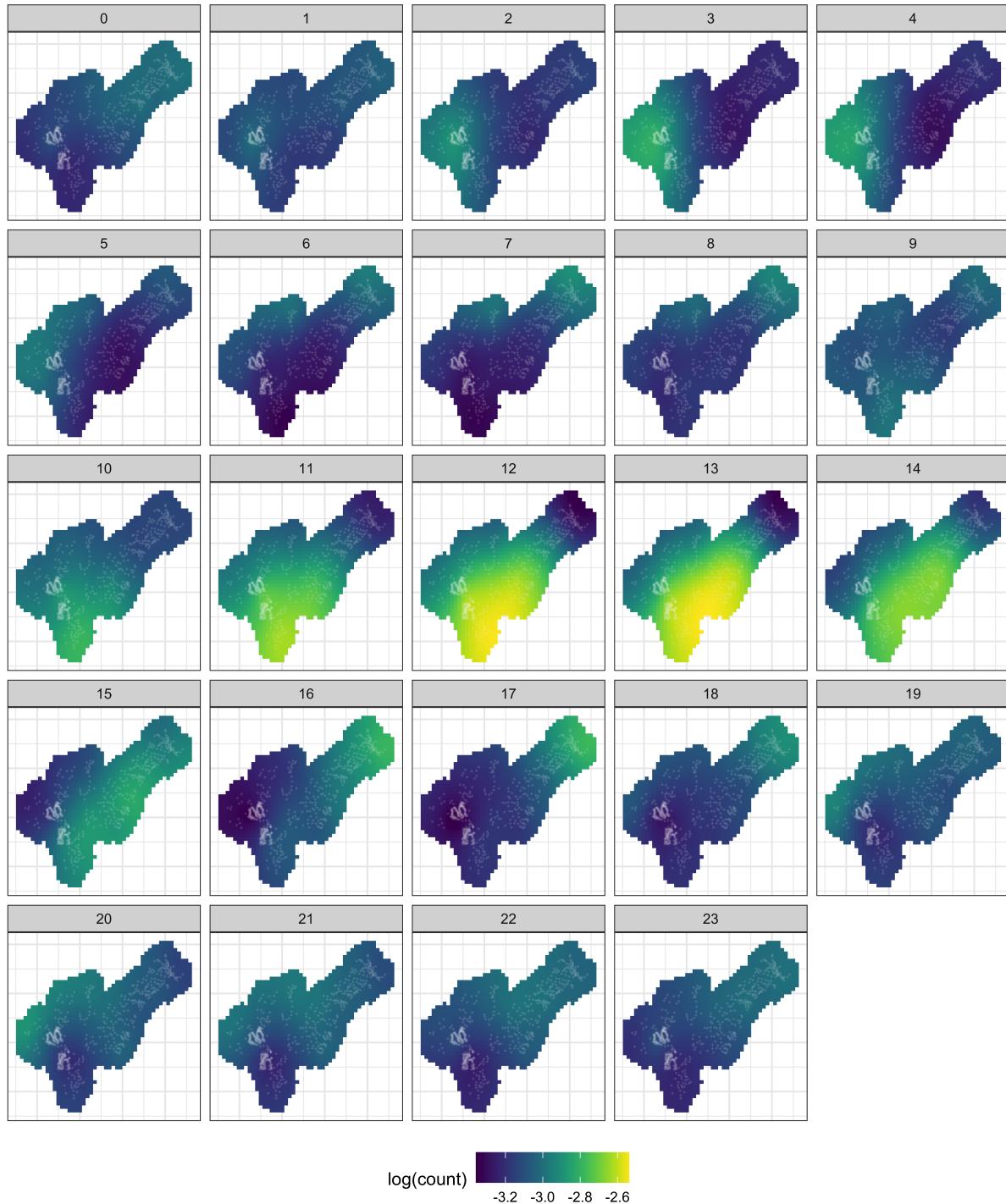


Figure 2: Interaction effect of space-time on red fox *Vulpes vulpes* activity across each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1), as an example. Corresponding plots for feral cats *Felis catus* in this region, as well as both predators in the Glenelg region are provided in the Supporting Information, as are the marginal effects of space and time. White crosses depict unique camera-trap sites.

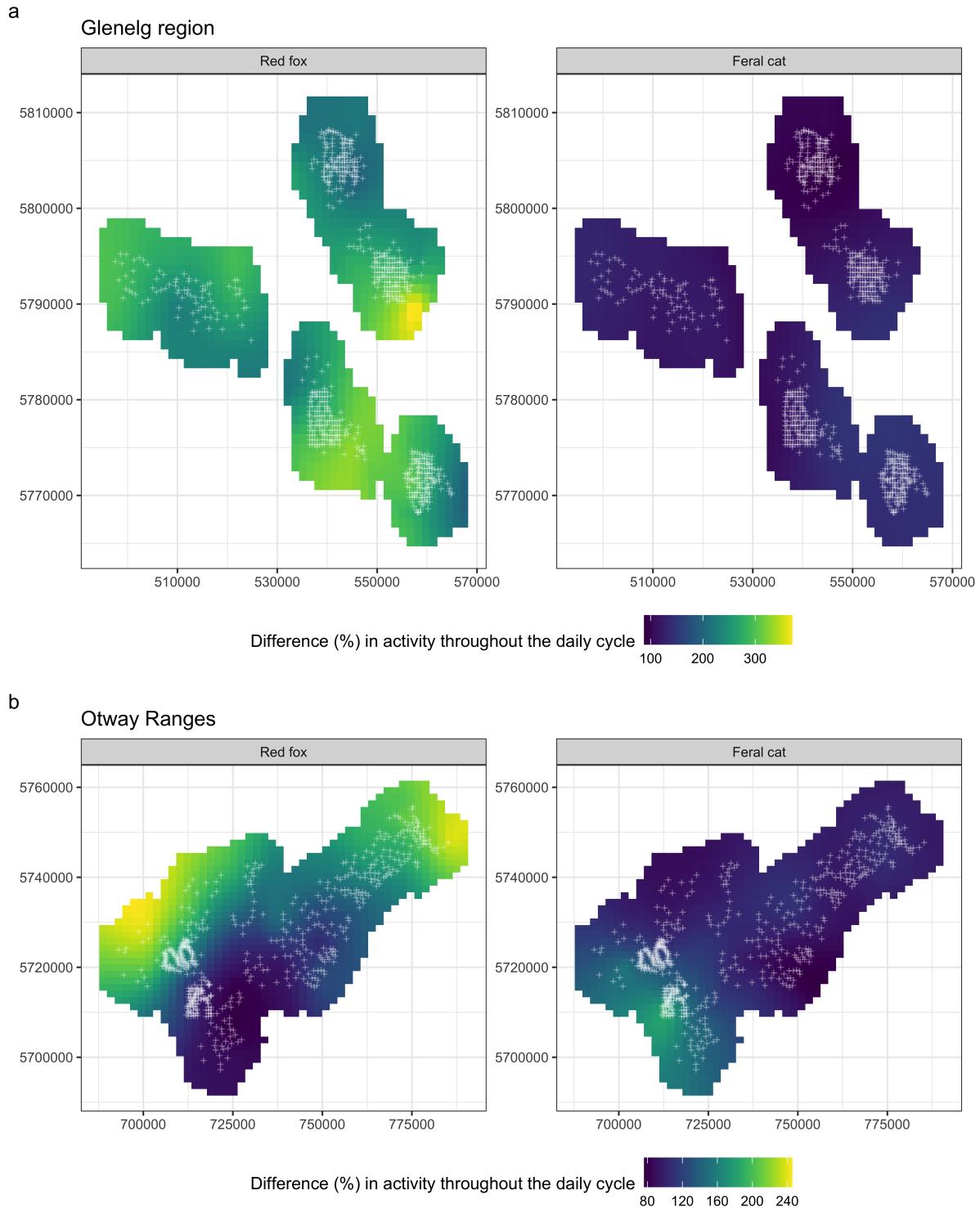
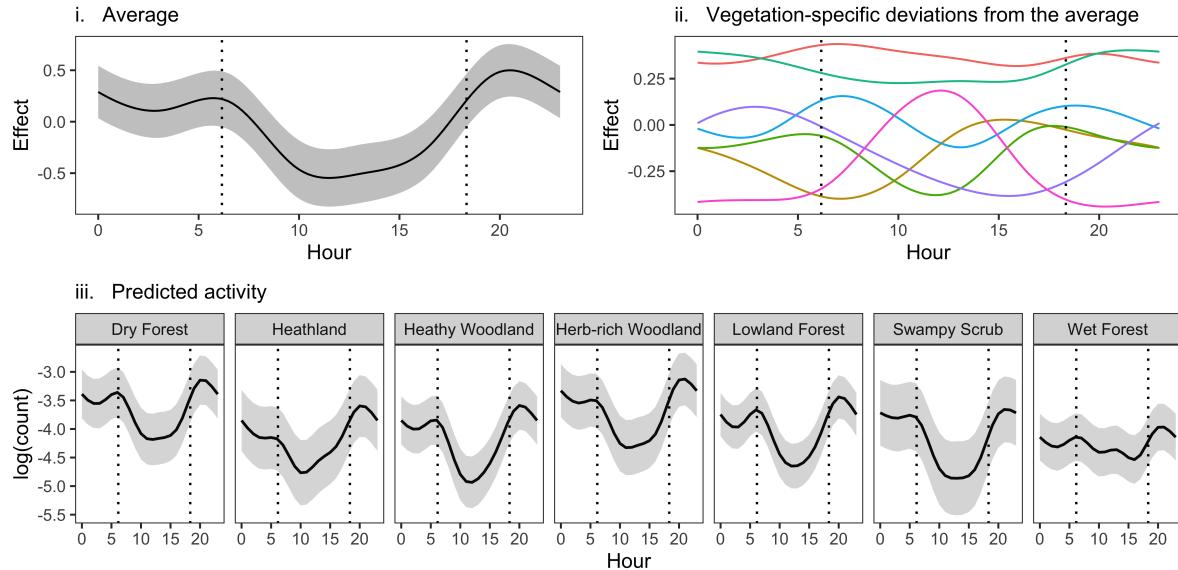


Figure 3: The strength of diel activity patterns of two invasive predators varied within the two study regions in south-west Victoria, Australia (model 1). White crosses depict unique camera-trap sites; colour brightness scales with increasing percentage difference between the minimum and maximum activity estimate over the 24-hour cycle for each location. Red foxes *Vulpes vulpes* (a, c) concentrated their activity during particular times of the day, especially in the Glenelg region (a) and the drier parts of the Otways (c), whereas feral cat *Felis catus* activity was relatively consistent activity throughout the daily cycle (b, d).

a. Fox



b. Feral cat

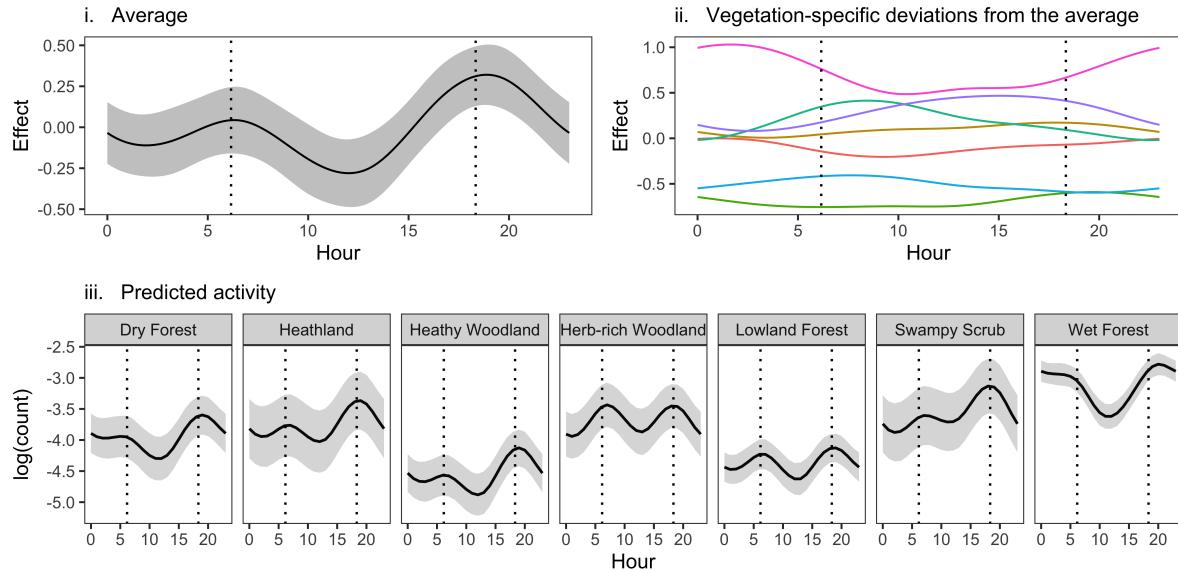
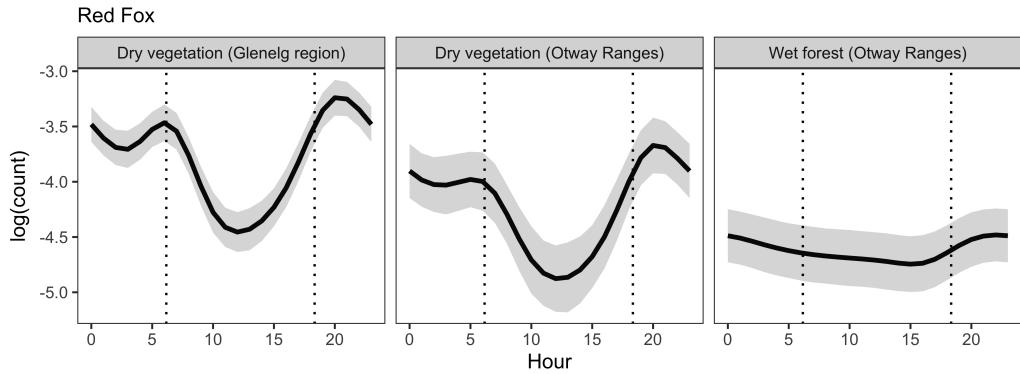
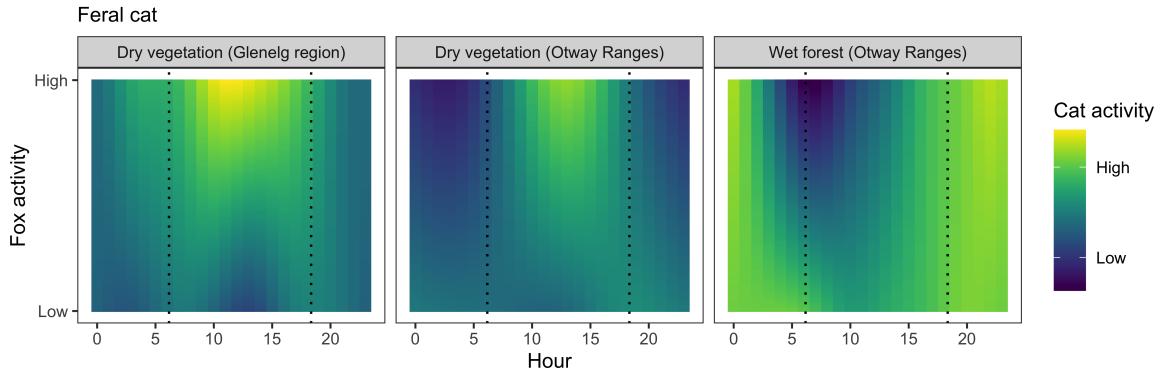


Figure 4: Red foxes *Vulpes vulpes* (a) and feral cat *Felis catus* (B) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia (model 2). Dotted, vertical lines represent average sunrise and sunset times. Shaded areas indicate 95% confidence intervals. Both invasive predators had a crepuscular to nocturnal diel activity pattern on average, with slight deviations across the drier EVC groups and large deviations in wet forests (ii; wet forests shown as pink line). The overall level of activity was relatively consistent across EVC groups for foxes (a – iii), whereas it differed substantially for feral cats (b - iii).

a



b



c

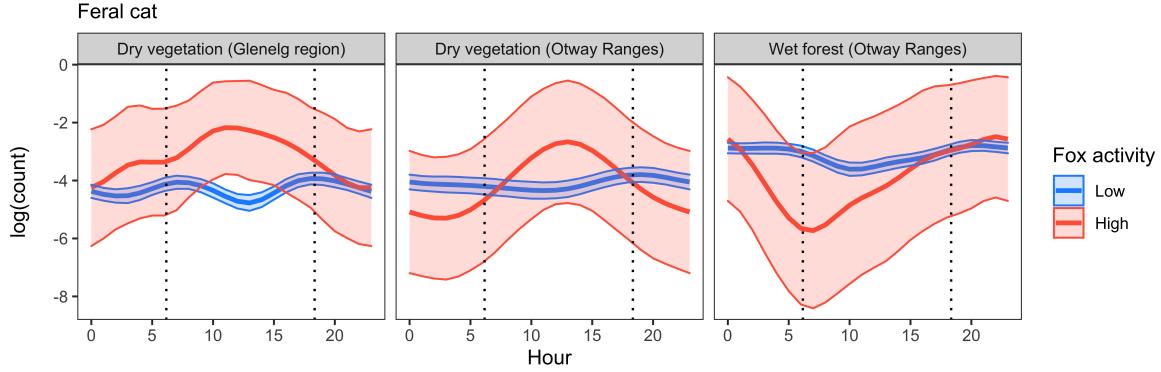


Figure 5: Variation in mean feral cat *Felis catus* activity (a) and associated uncertainty estimates (b) in response to count of 'independent' red fox *Vulpes vulpes* detections (log-transformed and survey effort adjusted) across each 'habitat type' in south-west Victoria, Australia (model 3). Grey vertical lines represent average sunrise and sunset times. In the Glenelg region, there were more feral cat detections where there were more fox detections, but cat peak diel activity shifted from crepuscular night to pre-dawn and midday (a). In the Otway Ranges, feral cat activity also peaked during the day where fox activity was high in dry vegetation types (b), but was more nocturnal where fox activity was high in the rainforests and wet forests (c).

255 **4. DISCUSSION**

256 A key question in ecological theory is whether animals are evolutionary hardwired to occupy particular  
257 temporal niches, or have circadian rhythms that are responsive to changing environmental conditions and  
258 interactions with other species (Daan, 1981; Lima & Dill, 1990; Schoener, 1974). Here we demonstrate  
259 that diel activity patterns are not fixed, but vary across space based on landscape context and fear. In our  
260 study, sympatric invasive predators had similar diel activity patterns when averaged across broad regions  
261 (i.e., high circular overlap; Fig. S1; as did Roshier & Carter, 2021), but behaviours varied considerably  
262 within landscapes. Fox daily activity patterns were most strongly tied to the daily cycle in dry habitat  
263 types, but showed little diel activity pattern in the wet forests (Fig. 4a). In contrast, cats were mostly  
264 nocturnal in wet forests but crepuscular in dry vegetation types (Fig. 4b). Within broad habitat types,  
265 cats altered their diel activity patterns at sites with higher fox activity (Fig. 5). Control programs that  
266 reduce invasive fox activity are therefore likely to change cat diel activity patterns, which in turn may  
267 alter cat impacts on native prey species. Quantifying changes in diel activity patterns provides important  
268 context for understanding species interactions, which is key for effective ecosystem management (Gaynor  
269 et al., 2021).

270 Shifting diel activity patterns may facilitate spatial coexistence of dominant and subordinate species  
271 (Carothers & Jakšić, 1984). For cats, altering diel activity patterns to less-preferred times of day may be  
272 worthwhile to persist in high-quality habitat. Few studies have demonstrated predator-induced shifts in  
273 diel activity (Kronfeld-Schor & Dayan, 2003), but notably, ship rats *Rattus norvegicus* were also found to  
274 switch from nocturnal to diurnal behaviour in response to fox activity (Fenn & Macdonald, 1995) and a  
275 similar nocturnal-diurnal shift was observed in American mink *Neovison vison* following the recolonisation  
276 of native predators (Harrington et al., 2009). For cats in our study, a switch to diurnal behaviour where  
277 fox activity was high in the dry vegetation types may have been facilitated by the higher abundance of  
278 reptiles in these habitat types relative to wet forests (which are mostly diurnal; Woinarski et al., 2018).  
279 At wet forest sites with high fox activity, cats concentrated their activity away from sunrise and sunset  
280 towards midnight, despite a diurnal shift appearing to similarly reduce the risk of a fox encounter. In  
281 this situation, we expect becoming more nocturnal to be favourable over a diurnal shift because this is  
282 when small mammals are active and cats would be least visible to foxes (cats here mostly had black or  
283 grey coats). Overall fox activity was twice as low in the wet forests relative to dry habitat types, and  
284 so cats were likely under less pressure to radically alter their diel activity patterns. Understanding how

285 these potential avoidance behaviours impacts native prey is a key research priority to improve invasive  
286 predator management.

287 Cats may have avoided foxes in time, but we saw no sign of spatial avoidance (i.e. no fine-scale negative  
288 association between fox and cat overall activity (Fig. 5b:c). Overlap in spatial activity at fine scales (i.e.,  
289 at the level of camera-trap sites) may have been facilitated by temporal avoidance (Kronfeld-Schor &  
290 Dayan, 2003). However, we considered spatial avoidance across the entire survey duration (averaging  
291 47 days). Cats may indeed avoid foxes spatially, but transiently on the scale of hours to days—after  
292 all, how is a cat to know where to avoid a fox without encountering signs of one? Short-term spatial  
293 avoidance is quite plausible given foxes mark territories using scats and odours, which cats could tangibly  
294 associate with high risk shortly after. Temporary spatial avoidance could be tested using decay curves  
295 (e.g., Niedballa et al., 2019). Alternatively, no sign of spatial avoidance between these invasive predators  
296 could also be an artefact of the quality of camera set-up and hence detectability. The 3667 camera-  
297 traps were deployed by numerous people, and the quality of set-ups differed considerably in terms of  
298 detecting predators. Camera-traps that angled only slightly downwards, rather than upwards or strongly  
299 downwards, seemed most effective at detecting both predator species (M.W Rees, personal observation).  
300 Predator interactions are routinely inferred through spatial associations between species; however such  
301 analyses are subject to numerous pitfalls which can make inference unreliable (reviewed in Blanchet et  
302 al., 2020).

303 A distinction of our study from others is that we modelled potential avoidance behaviours in a simple  
304 predator guild, where apex predator activity was artificially manipulated. This reduces potential bias  
305 from differences in niche preferences and the unmodelled impacts of other predators in the system. We  
306 also included replication across different habitat types. However, because our study did not consider  
307 associations with prey species, we cannot distinguish whether changes in cat diel activity patterns were  
308 the result of direct fox avoidance or indirect associations with shared prey. For example, low fox activity  
309 may promote the availability of a preferred shared prey species with a diel pattern which differs from those  
310 of cats on average, and as a result, cats might shift diel activity patterns at sites with low fox activity  
311 to more closely match those of the more abundant prey species. We would expect introduced European  
312 rabbits *Oryctolagus cuniculus* and hares *Lepus europaeus* (which are diurnal) to be particularly likely  
313 to induce such a response in dry vegetation types (McGregor et al., 2020; Stobo-Wilson et al., 2020),  
314 however, rabbits and hares are rare within the natural vegetation of the landscapes we surveyed (only  
315 ever being detected at 40 of 1232 sites) and there is little evidence that predation by foxes suppresses

316 rabbit populations (Norbury & Jones, 2015; Scroggie et al., 2018). While of particular interest, whether  
317 temporal fox-cat interactions are direct or indirect does not change the resulting impact on native prey,  
318 and hence the outcomes of fox management.

319 Flexible antipredator behaviours make evolutionary sense, but have been rarely demonstrated in terms  
320 of spatiotemporal predator avoidance (although, see Relyea, 2003; Brown et al., 2013; Cunningham et  
321 al., 2019), because this often requires manipulative experiments or at least more complicated models  
322 (Kronfeld-Schor & Dayan, 2003). Our study demonstrates that GAMs offer a powerful tool for modelling  
323 continuous shifts in animal activity across both space and time, capable of capturing complex interactions  
324 and sharing information across categorical variables. The inbuilt smoothing penalties are another benefit  
325 of GAMs over kernel density estimation (Ridout & Linkie, 2009), in which noisy data can produce spurious  
326 estimates (Frey et al., 2017; Iannarilli et al., 2019). The alternative approach of simply comparing  
327 average diel activity overlap between two species (Ridout & Linkie, 2009) would have been misleading for  
328 two reasons. Firstly, predator diel activity patterns varied ‘naturally’ across heterogeneous landscapes  
329 (requiring avoidance to be tested in wet forests and dry vegetation types separately; Fig. 4). Secondly,  
330 apex predator temporal avoidance strategies were not consistently employed, but depended on overall apex  
331 predator activity and vegetation type (Fig. 5). Despite their underlying statistical complexity, GAMs  
332 in the ‘mgcv’ R-package are straightforward to fit. Our GAM framework for modelling spatiotemporal  
333 activity can be used on any species with time-stamped detections, including datasets with categorical or  
334 continuous covariates and hierarchical groupings.

335 Animal diel activity patterns can be complex, varying across space, habitat types and threat-levels.  
336 Despite telling an important story about how animals interact with each other and the environment, de-  
337 tection times are commonly discarded from statistical analyses of camera-trap data. In the rare instances  
338 that they are considered, diel activity patterns are predominantly estimated at the population-level,  
339 overlooking finer-scale behaviours that can affect fitness, survival and ecosystem-impacts. Our results  
340 demonstrate the importance of (a) considering diel activity in regards to species interactions, (b) mod-  
341 elling changes in animal behaviour rather than overlap with other species, and (c) testing avoidance  
342 behaviours within a joint spatiotemporal framework. Our study adds to the limited body of evidence  
343 that top predators can produce a landscape of fear which is powerful enough to reverse the diel activity  
344 patterns of subordinate species (Kronfeld-Schor & Dayan, 2003).

<sup>345</sup> **ACKNOWLEDGEMENTS**

<sup>346</sup> We acknowledge the Gunditjmara and Eastern Maar peoples on whose traditional lands this study took  
<sup>347</sup> place. We thank Nick Golding, who inspired the use of GAMs in this paper and provided statistical advice.  
<sup>348</sup> We are grateful to Alan Robley, the Department of Environment, Land, Water, and Planning (DELWP)  
<sup>349</sup> Heywood team and Parks Victoria West Coast District Team for sharing camera-trapping datasets. The  
<sup>350</sup> M.W.R PhD surveys were conducted under University of Melbourne Animal Ethics Committee approval  
<sup>351</sup> 1714119.5 and Victorian Government DELWP Research Permit 10008273, with the assistance of Shauni  
<sup>352</sup> Omond, Shayne Neal, Asitha Samarawickrama, Shelley Thompson, Erin Harris, Hannah Killian, Lani  
<sup>353</sup> Watson, Mark Dorman, Jack Davis, Carl Roffey, Bruce Edley, Larissa Oliveira Gonçalves, Ben Lake,  
<sup>354</sup> Chantelle Geissler, Aviya Naccarella, Emily Gronow, Harley England, David Pitts, Annie Hobby, Louise  
<sup>355</sup> Falls, Thomas McKinnon, Jimmy Downie, Marney Hradsky, Stephanie Samson, Robin Sinclair, Asmaa  
<sup>356</sup> Alhusainan, Kelly Forrester, Tammana Wadawani, Emily Gregg, Hannah Edwards, Adam Beck, Vishnu  
<sup>357</sup> Memnon, Sandy Lu, Pia Lentini, Nick Golding, Emily McColl-Gausden, Nina Page, Maggie Campbell-  
<sup>358</sup> Jones, Kyle Quinn and Jack Dickson. This study was generously supported by the Conservation Ecology  
<sup>359</sup> Centre, the Victorian Government DELWP, Parks Victoria, Holsworth Wildlife Research Endowment –  
<sup>360</sup> Equity Trustees Charitable Foundation and Ecological Society of Australia, Australian Research Council  
<sup>361</sup> Linkage Project LP170101134, and the Australian Government's National Environmental Science Pro-  
<sup>362</sup> gram through the Threatened Species Recovery Hub. M.W.R also received funding from an Australian  
<sup>363</sup> Government Research Training Program Scholarship and a Victorian Government DELWP top-up schol-  
<sup>364</sup> arship.

<sup>365</sup> **CONFLICT OF INTEREST**

<sup>366</sup> The authors declare no conflicts of interest.

<sup>367</sup> **AUTHOR CONTRIBUTIONS**

<sup>368</sup> M.W.R conceived the ideas and designed the methodology; M.W.R, J.H.P, M.LP, E.K.B and B.A.H  
<sup>369</sup> collected some of the data; M.W.R analysed the data with input from B.A.H and B.A.W, and led the

<sup>370</sup> writing of the manuscript. All authors contributed critically to the drafts and gave final approval for  
<sup>371</sup> publication.

<sup>372</sup> **DATA AVAILABILITY**

<sup>373</sup> Data and code will be deposited on the Dryad Digital Repository after acceptance and can be viewed  
<sup>374</sup> here: <https://github.com/matt-w-rees/spatiotemporal-gams-invasive-predators>.

375 REFERENCES

- 376      Anderson, D. R. (2001). The need to get the basics right in wildlife field studies. *Wildlife Society*  
377      *Bulletin*, 1294–1297. [https://doi.org/https://doi.org/10.2307/3784156](https://doi.org/10.2307/3784156)
- 378      Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J.-P., & Courtois, R. (2015).  
379      Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96(10),  
380      2622–2631. [https://doi.org/https://doi.org/10.1890/14-1706.1](https://doi.org/10.1890/14-1706.1)
- 381      Bivand, R., & Lewin-Koh, N. (2021). *Maptools: Tools for handling spatial objects*. <https://CRAN.R-project.org/package=maptools>
- 383      Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological  
384      interactions. *Ecology Letters*, 23(7), 1050–1063. [https://doi.org/https://doi.org/10.1111/ele.13525](https://doi.org/10.1111/ele.13525)
- 385      Brashares, J. S., Prugh, L. R., Stoner, C. J., & Epps, C. W. (2010). Ecological and conservation  
386      implications of mesopredator release. In *Trophic cascades: Predators, prey, and the changing dynamics*  
387      of nature (pp. 221–240). Island Press.
- 388      Brown, G. E., Ferrari, M. C., Elvidge, C. K., Ramnarine, I., & Chivers, D. P. (2013). Phenotypically  
389      plastic neophobia: A response to variable predation risk. *Proceedings of the Royal Society B: Biological*  
390      *Sciences*, 280(1756), 20122712. [https://doi.org/https://doi.org/10.1098/rspb.2012.2712](https://doi.org/10.1098/rspb.2012.2712)
- 391      Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game  
392      theory, and trophic interactions. *Journal of Mammalogy*, 80(2), 385–399. [https://doi.org/https://doi.org/10.2307/1383287](https://doi.org/10.2307/1383287)
- 394      Carothers, J. H., & Jakšić, F. M. (1984). Time as a niche difference: The role of interference compe-  
395      tition. *Oikos*, 403–406. [https://doi.org/https://doi.org/10.2307/3544413](https://doi.org/10.2307/3544413)
- 396      Comer, S., Clausen, L., Cowen, S., Pinder, J., Thomas, A., Burbidge, A. H., Tiller, C., Algar, D.,  
397      & Speldewinde, P. (2020). Integrating feral cat (*Felis catus*) control into landscape-scale introduced  
398      predator management to improve conservation prospects for threatened fauna: A case study from the  
399      south coast of Western Australia. *Wildlife Research*, 47(8), 762–778. [https://doi.org/https://doi.org/10.1071/WR19217](https://doi.org/10.1071/WR19217)

- 401 Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends*  
402 in *Ecology & Evolution*, 23(4), 194–201. [https://doi.org/https://doi.org/10.1016/j.tree.2007.12.004](https://doi.org/10.1016/j.tree.2007.12.004)
- 403 Cunningham, C. X., Scoleri, V., Johnson, C. N., Barmuta, L. A., & Jones, M. E. (2019). Temporal  
404 partitioning of activity: Rising and falling top-predator abundance triggers community-wide shifts in diel  
405 activity. *Ecography*, 42(12), 2157–2168. <https://doi.org/https://doi.org/10.1111/ecog.04485>
- 406 Daan, S. (1981). Adaptive daily strategies in behavior. In *Biological rhythms* (pp. 275–298). Springer  
407 Publishing. [https://doi.org/10.1007/978-1-4615-6552-9\\_15](https://doi.org/10.1007/978-1-4615-6552-9_15)
- 408 Department of Environment, Land, Water & Planning. (2020). *Bioregions and EVC Benchmarks*.  
409 Victorian Government Department of Environment, Land, Water; Planning, Melbourne. Accessed June  
410 2021). <https://www.environment.vic.gov.au/biodiversity/bioregions-and-evc-benchmarks>
- 411 Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators  
412 and global biodiversity loss. *Proceedings of the National Academy of Sciences*, 113(40), 11261–11265.  
413 <https://doi.org/10.1073/pnas.1602480113>
- 414 Doherty, T. S., & Ritchie, E. G. (2017). Stop jumping the gun: A call for evidence-based invasive  
415 predator management. *Conservation Letters*, 10(1), 15–22. <https://doi.org/https://doi.org/10.1111/conl.12251>
- 417 Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R.,  
418 Essington, T. E., Holt, R. D., Jackson, J. B., & others. (2011). Trophic downgrading of planet earth.  
419 *Science*, 333(6040), 301–306. <https://doi.org/https://doi.org/10.1126/science.1205106>
- 420 Fenn, M. G., & Macdonald, D. W. (1995). Use of middens by red foxes: Risk reverses rhythms of  
421 rats. *Journal of Mammalogy*, 76(1), 130–136. <https://doi.org/https://doi.org/10.2307/1382321>
- 422 Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns  
423 and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing*  
424 in *Ecology and Conservation*, 3(3), 123–132. <https://doi.org/https://doi.org/10.1002/rse2.60>
- 425 Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes  
426 of fear: Spatial patterns of risk perception and response. *Trends in Ecology & Evolution*, 34(4), 355–368.

- 427 <https://doi.org/https://doi.org/10.1016/j.tree.2019.01.004>
- 428     Gaynor, K. M., Cherry, M. J., Gilbert, S. L., Kohl, M. T., Larson, C. L., Newsome, T. M., Prugh,  
429     L. R., Suraci, J. P., Young, J. K., & Smith, J. A. (2021). An applied ecology of fear framework:  
430     Linking theory to conservation practice. *Animal Conservation*, 24(3), 308–321. <https://doi.org/https://doi.org/10.1111/acv.12629>
- 432     Glen, A. S., & Dickman, C. R. (2005). Complex interactions among mammalian carnivores in  
433     Australia, and their implications for wildlife management. *Biological Reviews*, 80(3), 387–401. <https://doi.org/https://doi.org/10.1017/S1464793105006718>
- 435     Harrington, L. A., Harrington, A. L., Yamaguchi, N., Thom, M. D., Ferreras, P., Windham, T. R., &  
436     Macdonald, D. W. (2009). The impact of native competitors on an alien invasive: Temporal niche shifts  
437     to avoid interspecific aggression. *Ecology*, 90(5), 1207–1216. <https://doi.org/https://doi.org/10.1890/08-0302.1>
- 439     Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression  
440     models*. <https://CRAN.R-project.org/package=DHARMa>
- 441     Hradsky, B. A., Penman, T. D., Ababei, D., Hanea, A., Ritchie, E. G., York, A., & Di Stefano, J.  
442     (2017). Bayesian networks elucidate interactions between fire and other drivers of terrestrial fauna dis-  
443     tributions. *Ecosphere*, 8(8), e01926. <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1926>
- 445     Hunter, D. O., Lagisz, M., Leo, V., Nakagawa, S., & Letnic, M. (2018). Not all predators are equal:  
446     A continent-scale analysis of the effects of predator control on Australian mammals. *Mammal Review*,  
447     48(2), 108–122. <https://doi.org/https://doi.org/10.1111/mam.12115>
- 448     Iannarilli, F., Arnold, T. W., Erb, J., & Fieberg, J. R. (2019). Using lorelograms to measure and  
449     model correlation in binary data: Applications to ecological studies. *Methods in Ecology and Evolution*,  
450     10(12), 2153–2162. <https://doi.org/https://doi.org/10.1111/2041-210X.13308>
- 451     Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., & Boyce, M. S. (2007).  
452     Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*,  
453     10(8), 690–700. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2007.01059.x>

- 454 Kohl, M. T., Ruth, T. K., Metz, M. C., Stahler, D. R., Smith, D. W., White, P. J., & MacNulty,  
455 D. R. (2019). Do prey select for vacant hunting domains to minimize a multi-predator threat? *Ecology*  
456 *Letters*, 22(11), 1724–1733. <https://doi.org/https://doi.org/10.1111/ele.13319>
- 457 Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. *Annual*  
458 *Review of Ecology, Evolution, and Systematics*, 34(1), 153–181. <https://doi.org/https://doi.org/10.1146/>  
459 [annurev.ecolsys.34.011802.132435](http://annurev.ecolsys.34.011802.132435)
- 460 Lamb, C. T., Ford, A. T., McLellan, B. N., Proctor, M. F., Mowat, G., Ciarniello, L., Nielsen, S. E.,  
461 & Boutin, S. (2020). The ecology of human-carnivore coexistence. *Proceedings of the National Academy*  
462 *of Sciences*, 117(30), 17876–17883. <https://doi.org/10.1073/pnas.1922097117>
- 463 Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior:  
464 The predation risk allocation hypothesis. *The American Naturalist*, 153(6), 649–659. <https://doi.org/>  
465 <https://doi.org/10.1086/303202>
- 466 Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and  
467 prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. <https://doi.org/https://doi.org/10.1139/z90->  
468 092
- 469 Marlow, N. J., Thomas, N. D., Williams, A. A., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J.,  
470 & Berry, O. (2015). Cats (*Felis catus*) are more abundant and are the dominant predator of woylies  
471 (*Bettongia penicillata*) after sustained fox (*Vulpes vulpes*) control. *Australian Journal of Zoology*, 63(1),  
472 18–27.
- 473 McGregor, H., Moseby, K., Johnson, C. N., & Legge, S. (2020). The short-term response of feral  
474 cats to rabbit population decline: Are alternative native prey more at risk? *Biological Invasions*, 22(2),  
475 799–811. <https://doi.org/https://doi.org/10.1007/s10530-019-02131-5>
- 476 Miller, D. L., & Wood, S. N. (2014). Finite area smoothing with generalized distance splines. *Envi-*  
477 *ronmental and Ecological Statistics*, 21(4), 715–731.
- 478 Molsher, R., Newsome, A. E., Newsome, T. M., & Dickman, C. R. (2017). Mesopredator management:  
479 Effects of red fox control on the abundance, diet and use of space by feral cats. *PLoS One*, 12(1), e0168460.  
480 <https://doi.org/https://doi.org/10.1371/journal.pone.0168460>

481 Niedballa, J., Wilting, A., Sollmann, R., Hofer, H., & Courtiol, A. (2019). Assessing analytical  
482 methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote*  
483 *Sensing in Ecology and Conservation*, 5(3), 272–285. <https://doi.org/https://doi.org/10.1002/rse2.107>

484 Norbury, G., & Jones, C. (2015). Pests controlling pests: Does predator control lead to greater  
485 European rabbit abundance in Australasia? *Mammal Review*, 45(2), 79–87. <https://doi.org/https://doi.org/10.1111/mam.12034>

487 Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive  
488 models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876. <https://doi.org/https://doi.org/10.7717/peerj.6876>

490 Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation  
491 and consumption in predator-prey interactions. *Ecology*, 86(2), 501–509. <https://doi.org/https://doi.org/10.1890/04-0719>

493 R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for  
494 Statistical Computing. <https://www.R-project.org/>

495 Reddiex, B., Forsyth, D. M., McDonald-Madden, E., Einoder, L. D., Griffioen, P. A., Chick, R. R.,  
496 & Robley, A. J. (2007). Control of pest mammals for biodiversity protection in Australia. I. Patterns  
497 of control and monitoring. *Wildlife Research*, 33(8), 691–709. <https://doi.org/https://doi.org/10.1071/WR05102>

499 Rees, M. W., Pascoe, J. H., Wintle, B. A., Le Pla, M., Birnbaum, E. K., & Hradsky, B. A. (2019).  
500 Unexpectedly high densities of feral cats in a rugged temperate forest. *Biological Conservation*, 239,  
501 108287. <https://doi.org/https://doi.org/10.1016/j.biocon.2019.108287>

502 Relyea, R. A. (2003). Predators come and predators go: The reversibility of predator-induced traits.  
503 *Ecology*, 84(7), 1840–1848. [https://doi.org/https://doi.org/10.1890/0012-9658\(2003\)084%5B1840:PCAPGT%5D2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2003)084%5B1840:PCAPGT%5D2.0.CO;2)

505 Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera  
506 trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337. <https://doi.org/https://doi.org/10.1198/jabes.2009.08038>

- 508 Ripple, W. J., & Beschta, R. L. (2004). Wolves and the ecology of fear: Can predation risk structure  
509 ecosystems? *BioScience*, 54(8), 755–766. [https://doi.org/https://doi.org/10.1641/0006-3568\(2004\)054%5B0755:WATEOF%5D2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054%5B0755:WATEOF%5D2.0.CO;2)
- 511 Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodi-  
512 versity conservation. *Ecology Letters*, 12(9), 982–998. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- 514 Robley, A., Gormley, A. M., Forsyth, D. M., & Triggs, B. (2014). Long-term and large-scale control of  
515 the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation*,  
516 180, 262–269. <https://doi.org/https://doi.org/10.1016/j.biocon.2014.10.017>
- 517 Robley, A., Moloney, P., & Parks Victoria West Coast District Team. (2019). *The Otway Ark: response of predators and native species 2016–2018*. Arthur Rylah Institute for Environmental Research  
518 Technical Report Series No. 299. Department of Environment, Land, Water; Planning, Heidelberg,  
519 Victoria.
- 521 Robley, A., Moloney, P., Stringer, L., & Donald, S. (2020). *Glenelg Ark 2005–2019: long-term predator and native mammal response to predator control*. Arthur Rylah Institute for Environmental Research  
522 Technical Report Series No. 318. Department of Environment, Land, Water; Planning, Heidelberg,  
523 Victoria.
- 525 Roshier, D. A., & Carter, A. (2021). Space use and interactions of two introduced mesopredators, European red fox and feral cat, in an arid landscape. *Ecosphere*, 12(7), e03628. <https://doi.org/https://doi.org/10.1002/ecs2.3628>
- 528 Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated  
529 indirect interactions. *Ecology Letters*, 7(2), 153–163. <https://doi.org/https://doi.org/10.1111/j.1461-0248.2003.00560.x>
- 531 Schoener, T. W. (1974). The compression hypothesis and temporal resource partitioning. *Proceedings  
532 of the National Academy of Sciences*, 71(10), 4169–4172. <https://doi.org/10.1073/pnas.71.10.4169>
- 533 Scroggie, M. P., Forsyth, D. M., McPhee, S. R., Matthews, J., Stuart, I. G., Stamation, K. A.,  
534 Lindeman, M., & Ramsey, D. S. (2018). Invasive prey controlling invasive predators? European rabbit

- 535 abundance does not determine red fox population dynamics. *Journal of Applied Ecology*, 55(6), 2621–  
536 2631. [https://doi.org/https://doi.org/10.1111/1365-2664.13253](https://doi.org/10.1111/1365-2664.13253)
- 537 Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019). Integrating  
538 temporal refugia into landscapes of fear: Prey exploit predator downtimes to forage in risky places.  
539 *Oecologia*, 189(4), 883–890. [https://doi.org/https://doi.org/10.1007/s00442-019-04381-5](https://doi.org/10.1007/s00442-019-04381-5)
- 540 Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., & Hill, S. (1988). Reconstructed  
541 dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*,  
542 2(1), 75–92. <https://doi.org/https://doi.org/10.1111/j.1523-1739.1988.tb00337.x>
- 543 Stobo-Wilson, A. M., Brandle, R., Johnson, C. N., & Jones, M. E. (2020). Management of invasive  
544 mesopredators in the Flinders Ranges, South Australia: Effectiveness and implications. *Wildlife Research*,  
545 47(8), 720–730. <https://doi.org/https://doi.org/10.1071/WR19237>
- 546 Swan, M., Christie, F., Sitters, H., York, A., & Di Stefano, J. (2015). Predicting faunal fire responses  
547 in heterogeneous landscapes: The role of habitat structure. *Ecological Applications*, 25(8), 2293–2305.  
548 <https://doi.org/https://doi.org/10.1890/14-1533.1>
- 549 Vazquez, C., Rowcliffe, J. M., Spoelstra, K., & Jansen, P. A. (2019). Comparing diel activity patterns  
550 of wildlife across latitudes and seasons: Time transformations using day length. *Methods in Ecology and*  
551 *Evolution*, 10(12), 2057–2066. <https://doi.org/https://doi.org/10.1111/2041-210X.13290>
- 552 Wayne, A. F., Maxwell, M. A., Ward, C. G., Wayne, J. C., Vellios, C. V., & Wilson, I. J. (2017).  
553 Recoveries and cascading declines of native mammals associated with control of an introduced predator.  
554 *Journal of Mammalogy*, 98(2), 489–501. <https://doi.org/10.1093/jmammal/gyw237>
- 555 Willems, E. P., & Hill, R. A. (2009). Predator-specific landscapes of fear and resource distribution:  
556 Effects on spatial range use. *Ecology*, 90(2), 546–555. <https://doi.org/https://doi.org/10.1890/08-0765.1>
- 557 Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P., & Schmitz, O. J. (2021). The context  
558 dependence of non-consumptive predator effects. *Ecology Letters*, 24(1), 113–129. <https://doi.org/https://doi.org/10.1111/ele.13614>
- 560 Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental

- 561 fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the*  
562 *National Academy of Sciences*, 112(15), 4531–4540. <https://doi.org/10.1073/pnas.1417301112>
- 563 Woinarski, J. C. Z., Murphy, B., Palmer, R., Legge, S., Dickman, C., Doherty, T., Edwards, G.,  
564 Nankivell, A., Read, J., & Stokeld, D. (2018). How many reptiles are killed by cats in Australia? *Wildlife*  
565 *Research*, 45(3), 247–266. <https://doi.org/https://doi.org/10.1071/WR17160>
- 566 Wood, S. N. (2017). *Generalized additive models: An introduction with r*. CRC press.

## **SUPPORTING INFORMATION**

*Spatial variation in predator diel activity patterns – feral cats avoid red foxes in time, not space*

MW Rees, BA Wintle, JH Pascoe, M Le Pla, EK Birnbaum & BA. Hradsky

Table S1: Summary of the number of camera-trap deployments, unique survey sites and 'independent' counts of invasive predator detections across Ecological Vegetation Class groups within the Glenelg and Otway regions, south-west Victoria, Australia.

Vegetation	Region	Sites	Deployments	Fox counts	Cat counts
Dry Forest	Glenelg	25	69	347	9
	Otways	111	314	341	158
Heathland	Glenelg	40	119	265	59
	Otways	3	9	8	6
Heathy Woodland	Glenelg	154	424	574	96
	Otways	82	256	160	66
Herb-rich Woodland	Glenelg	59	373	863	198
	Otways	2	6	3	2
Lowland Forest	Glenelg	383	1046	1900	290
	Otways	52	163	190	35
Swampy Scrub	Glenelg	4	10	19	8
	Otways	36	98	64	88
Wet Forest	Otways	281	780	715	1187
<b>Total</b>		<b>1232</b>	<b>3667</b>	<b>5449</b>	<b>2202</b>

Table S2: Generalised additive model summaries for invasive predator spatiotemporal activity in south-west Victoria, Australia.

Species	Model	EDF	dev.expl	r.sq
fox	1_spatial	772.6469	0.3514	0.1170
fox	2_vegetation_type	766.1054	0.3498	0.1155
fox	3_habitat_type	768.2692	0.3487	0.1139
cat	1_spatial	562.9236	0.2314	0.0772
cat	2_vegetation_type	566.7562	0.2300	0.0769
cat	3_fox_by_habitat_type	585.8580	0.2317	0.0779

*Note:*

EDF - estimated degrees of freedom of all model terms.

dev.expl - proportion of the null deviance explained by the model.

r.sq - adjusted r-squared value.

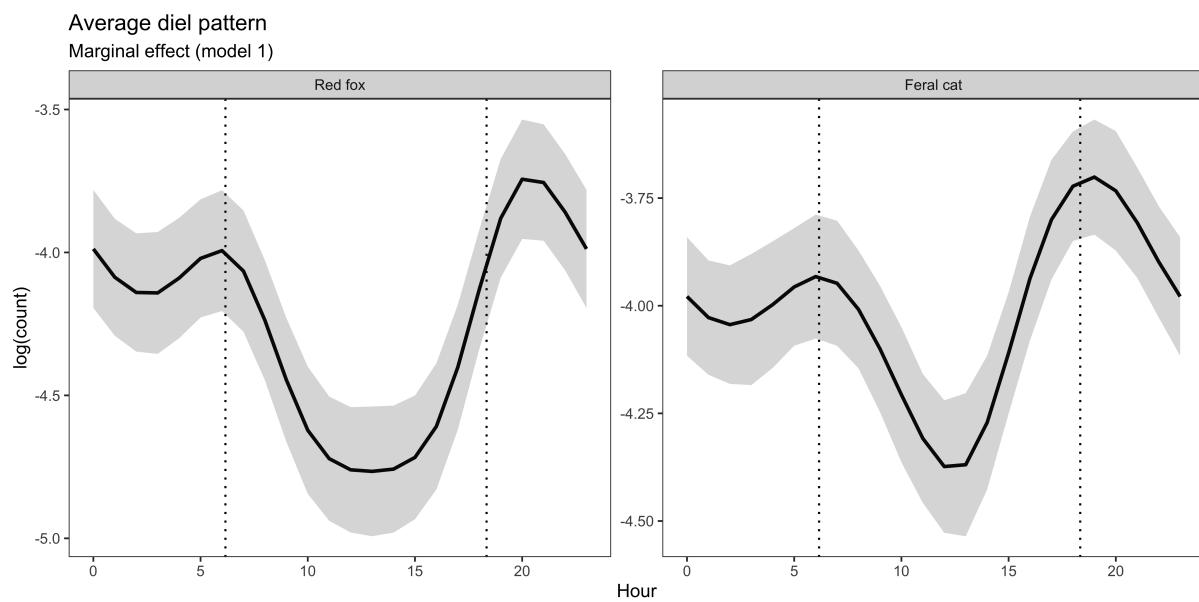


Figure S1: Marginal effect of time (model 1) on predators across both study regions in south-west Victoria, Australia.  
White crosses depict unique camera-trap sites

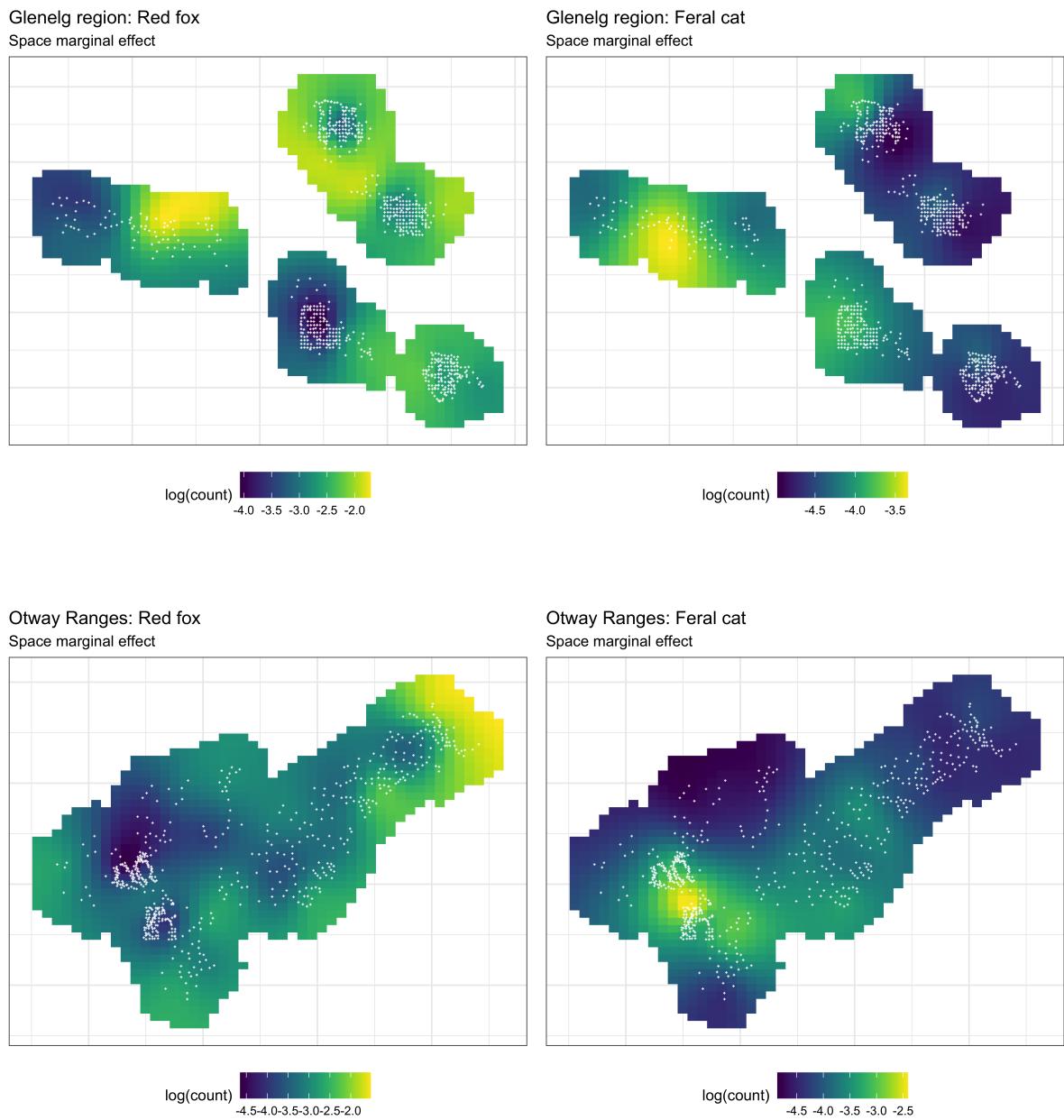


Figure S2: Marginal effect of space on predators across south-west Victoria, Australia (model 1). White crosses depict unique camera-trap sites

## Glenelg region: Red fox

Space-time interaction effect (excluding marginal effects)

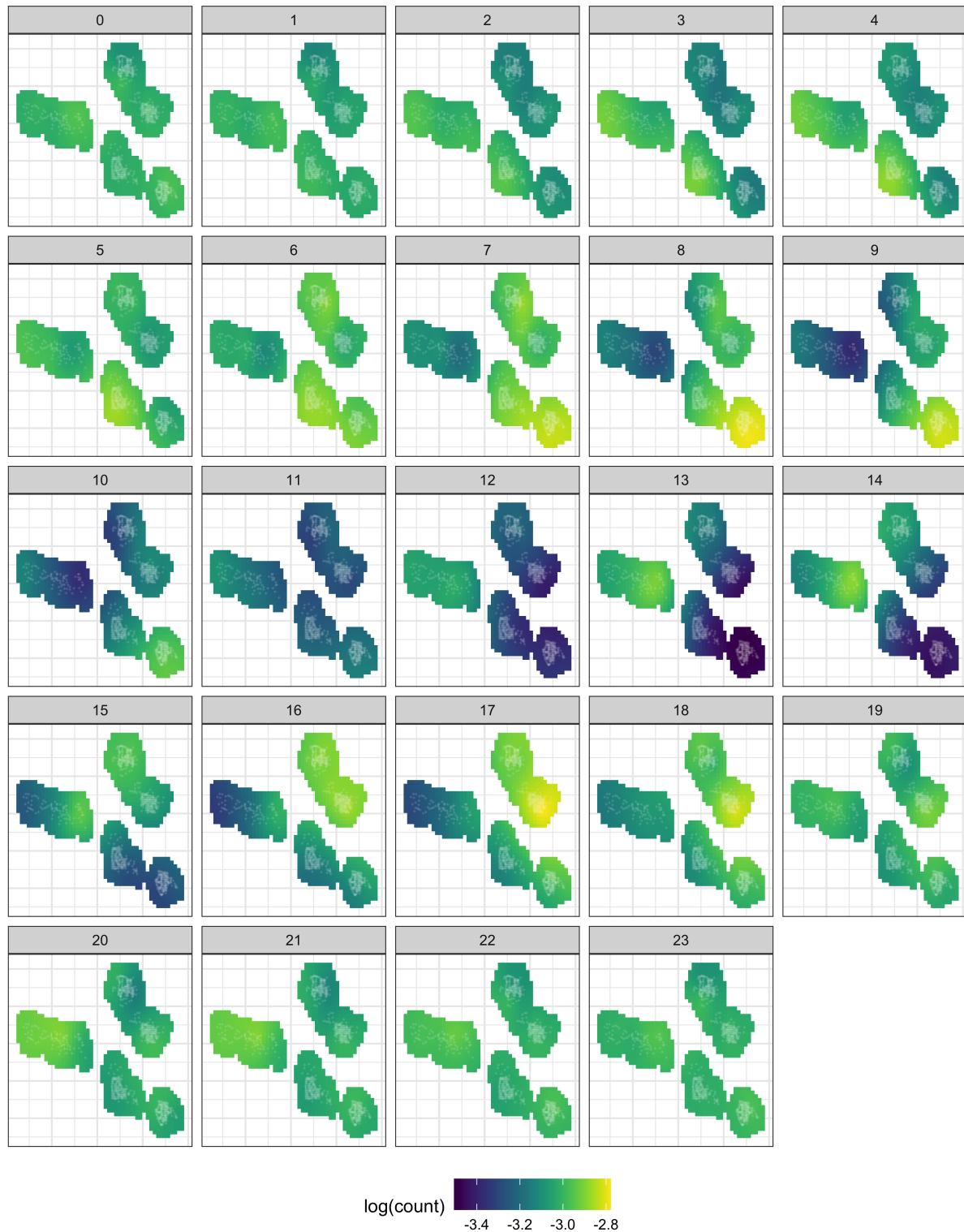


Figure S3: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites.

Glenelg region: Feral cat

Space-time interaction effect (excluding marginal effects)

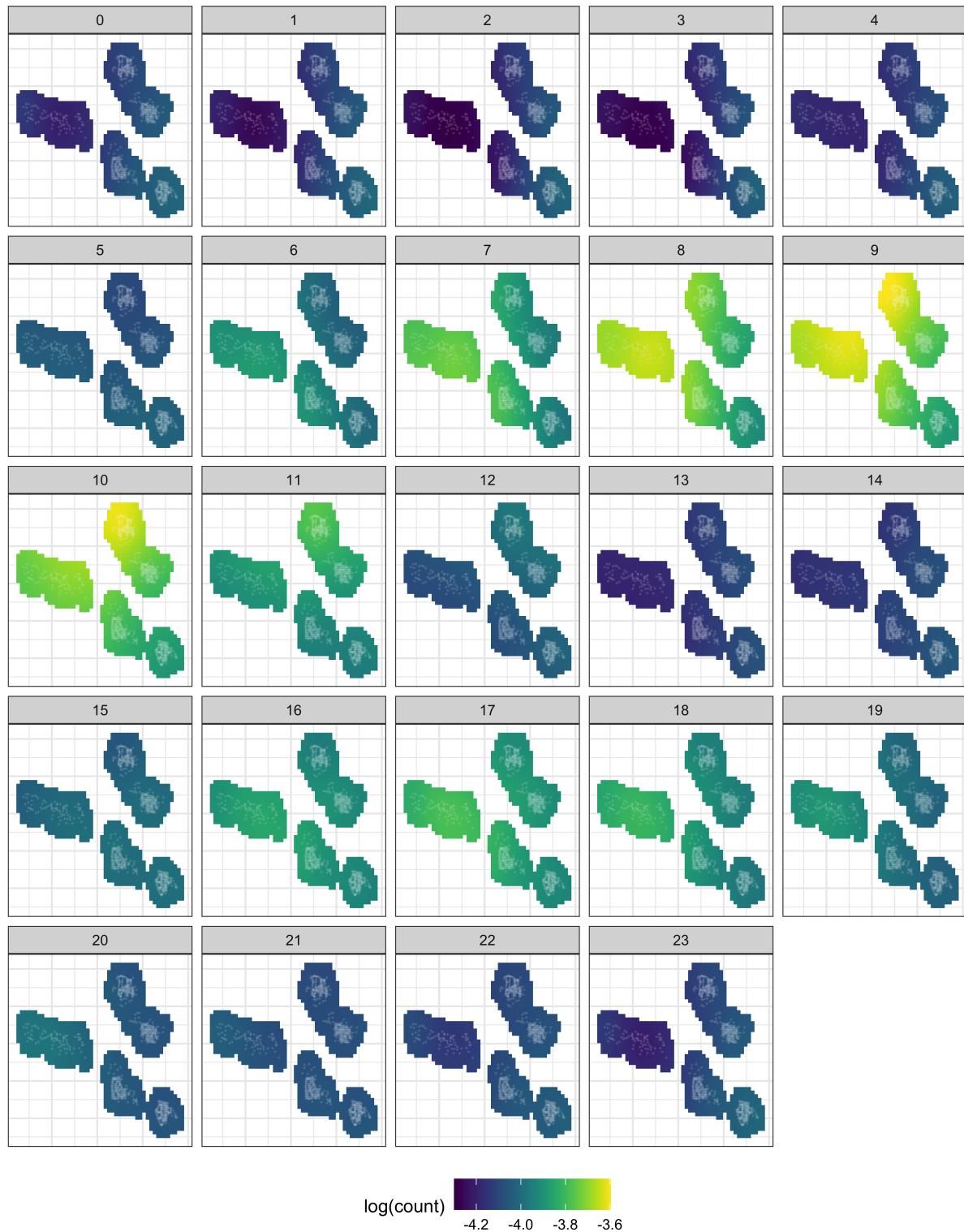


Figure S4: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites.

### Otway Ranges: Feral cat

Space-time interaction effect (excluding marginal effects)

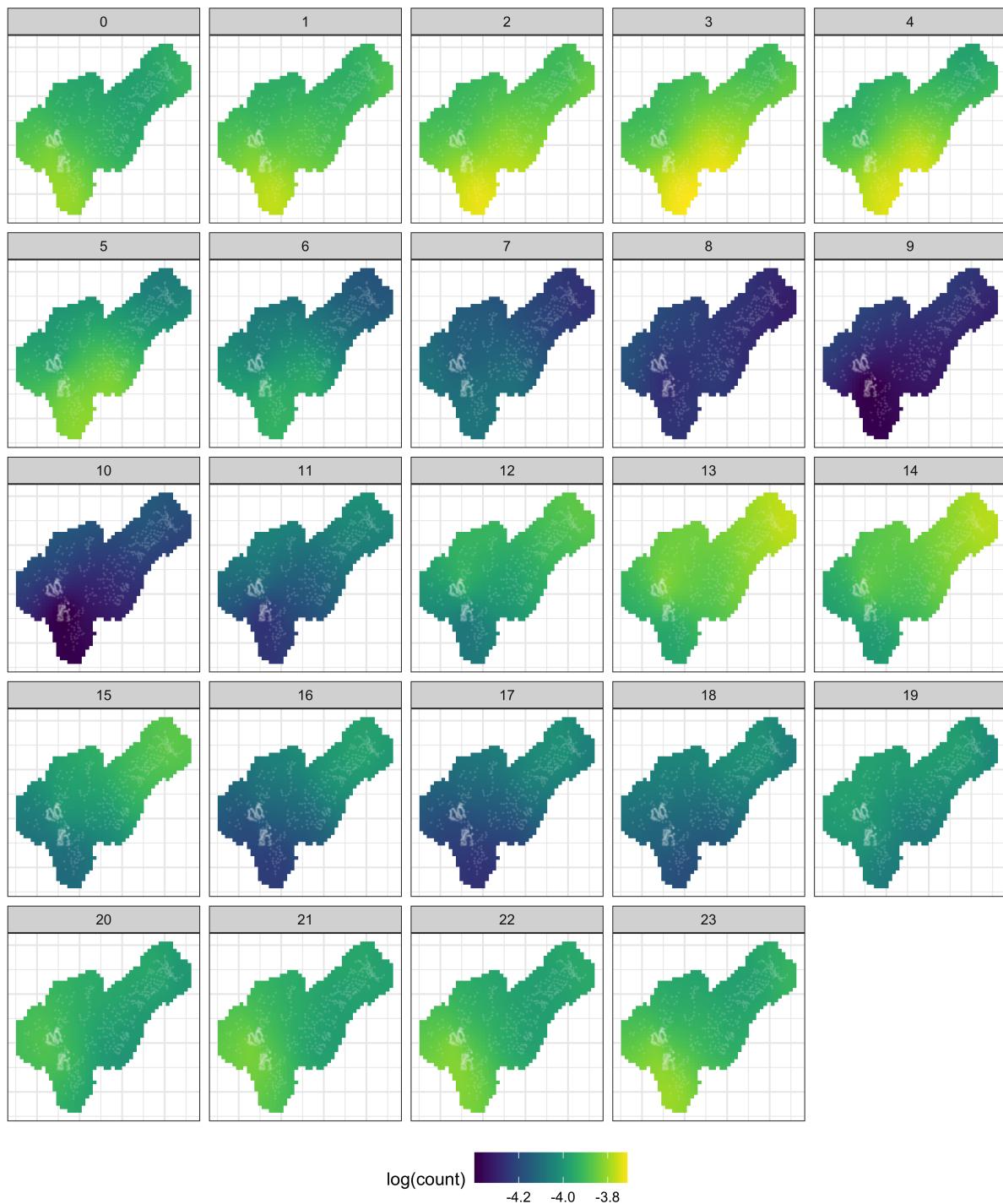


Figure S5: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites.

### Otway Ranges: Red fox

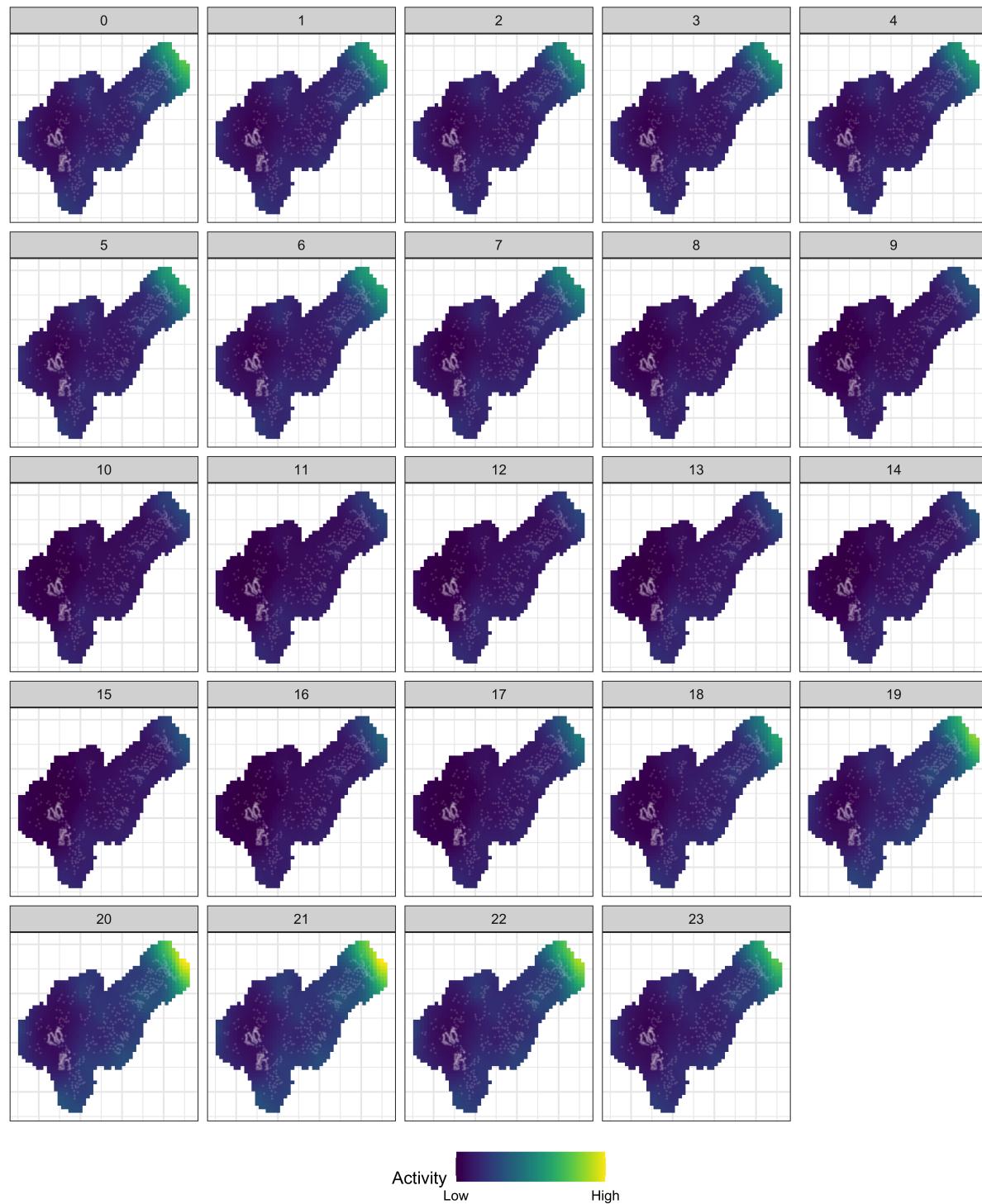


Figure S6: Overall spatial activity of red foxes *Vulpes vulpes* for each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites

Glenelg region: Feral cat

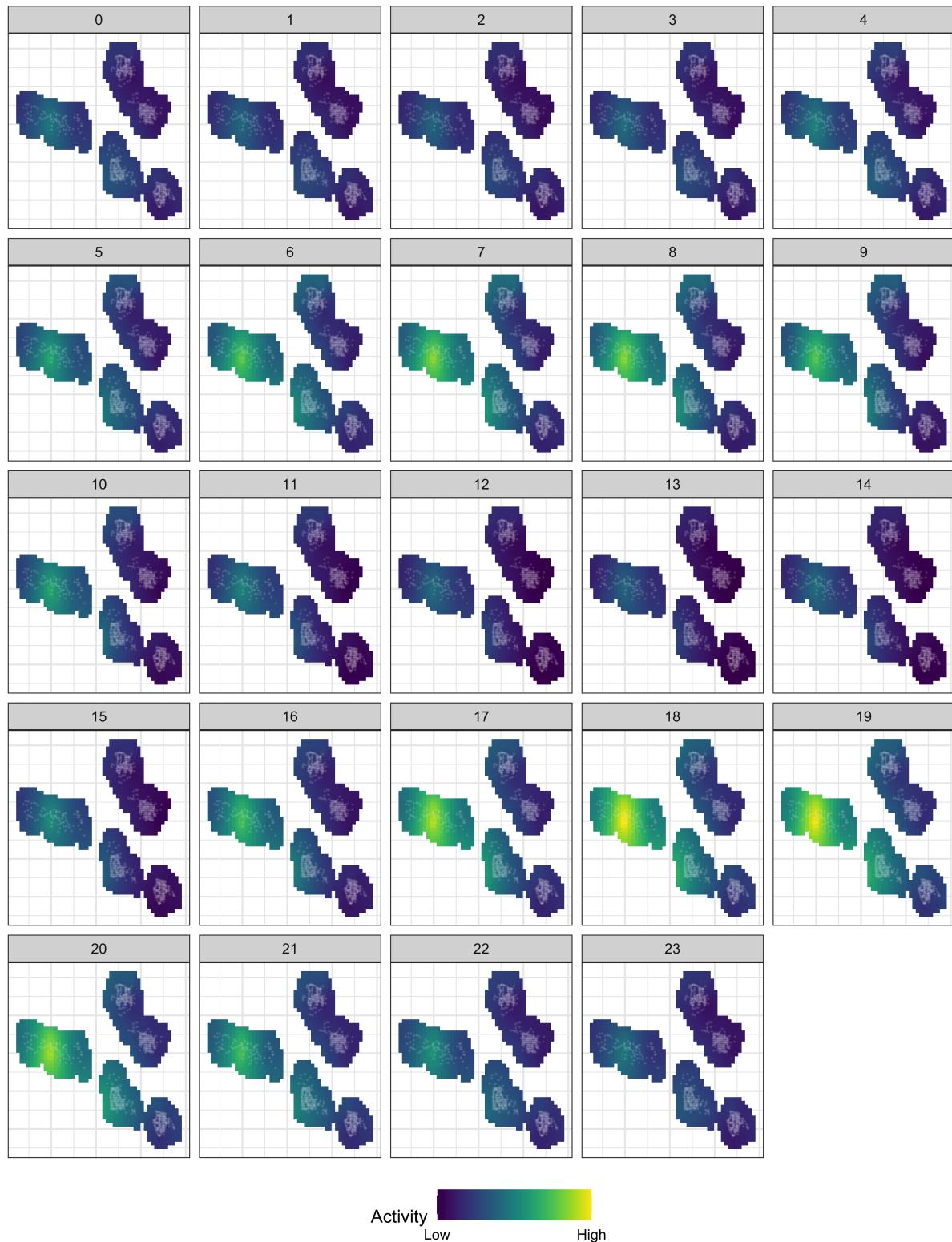


Figure S7: Overall spatial activity of feral cats *Felis catus* for each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites

### Otway Ranges: Red fox

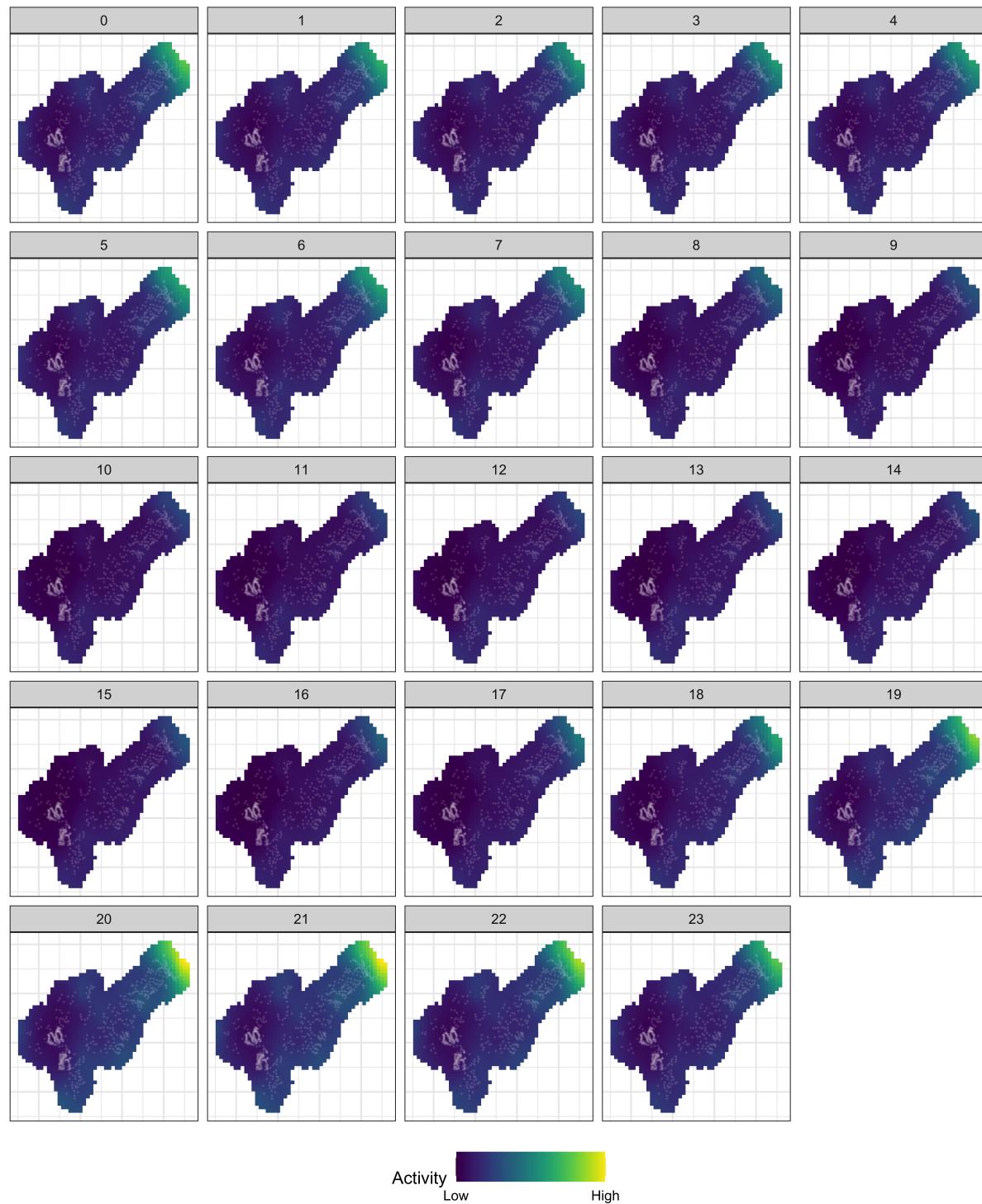


Figure S8: Overall spatial activity of red foxes *Vulpes vulpes* for each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites

Otway Ranges: Feral cat

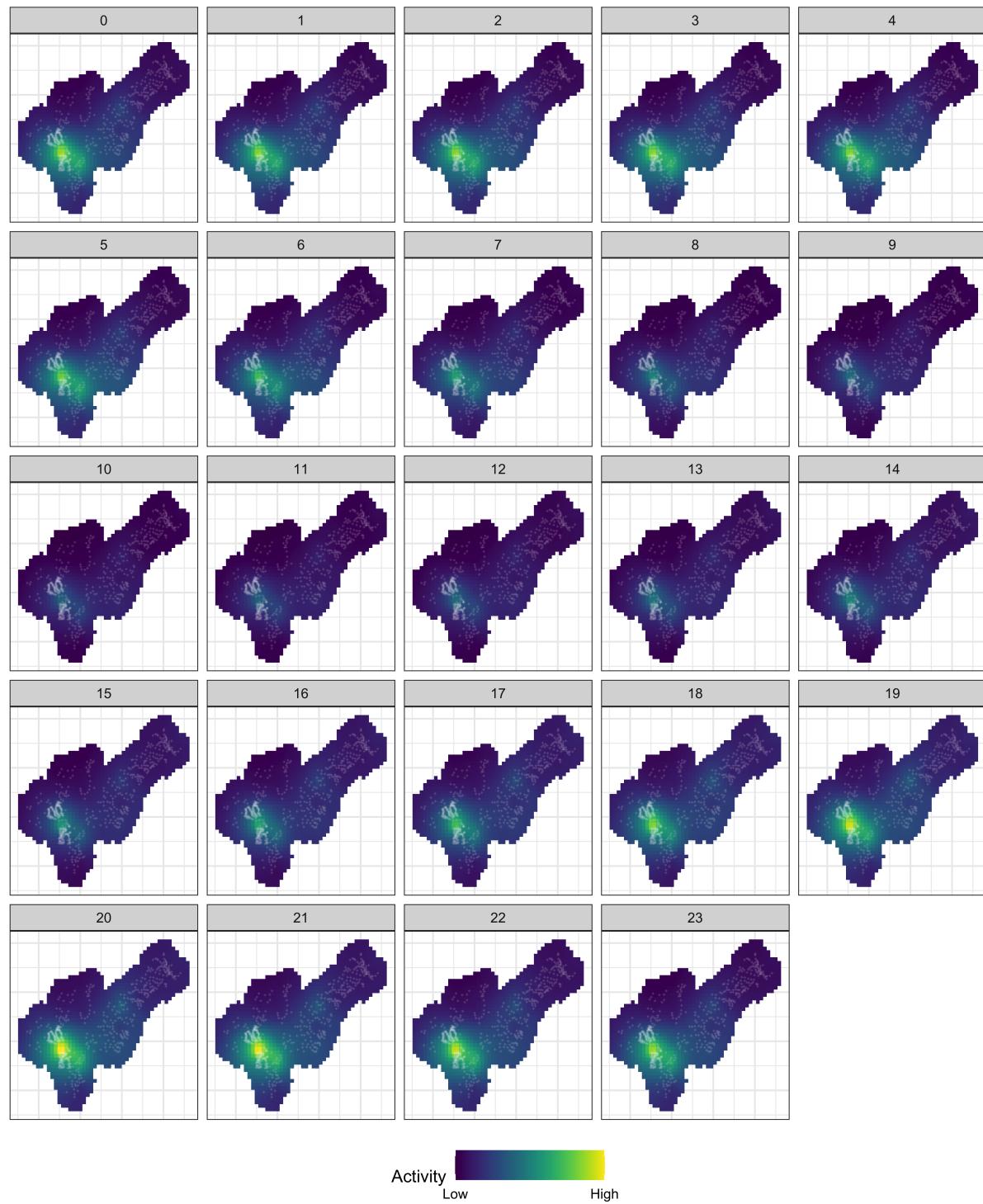


Figure S9: Overall spatial activity of feral cats *Felis catus* for each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites