

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

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*Tables:* 0

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**1 ABSTRACT**

**2** Understanding the constraints that apex predators impose on subordinate species is important for  
**3** anticipating the outcomes of predator management. Subordinate predators may avoid dominant preda-  
**4** tors in time or space, making it difficult to quantify changes in antipredator behaviours unless joint  
**5** spatiotemporal analyses are used.

**6** In this study, we tested whether an invasive apex predator (red fox *Vulpes vulpes*) suppresses or  
**7** alters the spatiotemporal activity of an invasive mesopredator (feral cat *Felis catus*). We surveyed these  
**8** predators using 3667 camera-trap deployments across two regions of south-eastern Australia; foxes were  
**9** poison-baited in some landscapes within each region. The simple predator guild in these regions allowed  
**10** sharp focus on the interactions between these species across experimental gradients of fox (apex predator)  
**11** activity. We used generalised additive models to quantify overall predator activity across space and  
**12** fluctuations in predator activity throughout the daily cycle (i.e., diel activity patterns).

**13** When averaged across the study region, red foxes and feral cats had very similar diel activity patterns;  
**14** however, there was important differentiation at a finer scale. When fox counts at a camera-trap were  
**15** high, feral cats did not reduce their overall activity but shifted their diel activity patterns to less risky  
**16** times of the day. In dry habitats of both regions, cats shifted from being nocturnal-crepuscular to mostly  
**17** diurnal. In wet forest habitat, fox activity was consistent throughout the diel period; but when fox counts  
**18** were high, cats became more nocturnal, avoiding dawn in particular. Changes in cat diel activity patterns  
**19** may facilitate spatial coexistence between the two invasive predators, potentially shifting impacts onto  
**20** different native prey species.

**21** It is well-appreciated that overall predator activity varies spatially and fluctuates throughout the daily  
**22** cycle. Our study demonstrates that diel activity patterns also vary across space, likely mediated by both  
**23** landscape context and fear. Apex predator avoidance appears to be dynamic across landscapes of fear—a  
**24** key nuance which is overlooked when simply comparing the average activity overlap between two species  
**25** or the spatial overlap of species occurrence.

<sup>26</sup> **1. INTRODUCTION**

<sup>27</sup> Predators shape ecosystems through both predation and the fear of predation (Creel & Christian-  
<sup>28</sup> son 2008; Ritchie & Johnson 2009). Fear-induced behavioural suppression can be as detrimental to  
<sup>29</sup> subordinate species as predation itself (Schmitz, Krivan, & Ovadia 2004; Preisser, Bolnick, & Benard  
<sup>30</sup> 2005). These non-consumptive effects of apex predator are expected to be strong drivers of mesopredator  
<sup>31</sup> behaviour, particularly when resource competition is high (Ritchie & Johnson 2009). A strengthen-  
<sup>32</sup> ing or relaxing of antipredator behaviours by mesopredators can have cascading effects across the entire  
<sup>33</sup> ecosystem: altering population demographics, species interactions, ecological function and human-wildlife  
<sup>34</sup> coexistence (Brown, Laundré, & Gurung 1999; Ripple & Beschta 2004; Estes *et al.* 2011; Gaynor *et al.*  
<sup>35</sup> 2019; Lamb *et al.* 2020). Hence, understanding how apex predators constrain the behaviour of subordi-  
<sup>36</sup> nate species is important to accurately predict the ecosystem-wide consequences of predator management,  
<sup>37</sup> such as reintroductions or lethal control (Gaynor *et al.* 2021).

<sup>38</sup> Spatial and/or temporal niche partitioning may allow predators to coexist by reducing encounter-rates  
<sup>39</sup> and resource overlap (Kronfeld-Schor & Dayan 2003). However, mesopredators may not consistently  
<sup>40</sup> employ avoidance behaviours because perceived predation risk is temporally and spatially variable, and  
<sup>41</sup> antipredator behaviours typically involve a trade-off against resource acquisition, such as limiting or  
<sup>42</sup> relegating activity to suboptimal places or times (Lima & Dill 1990; Lima & Bednekoff 1999). Therefore,  
<sup>43</sup> optimal predator avoidance strategies are likely to vary across heterogeneous landscapes where resource  
<sup>44</sup> availability (e.g., shelter, food) and perceived predation risks differ (Kauffman *et al.* 2007; Willems  
<sup>45</sup> & Hill 2009; Wirsing *et al.* 2021). For example, temporal predator avoidance may be preferable over  
<sup>46</sup> spatial avoidance if food is constantly available throughout the day, and vice versa. These concepts are  
<sup>47</sup> unified under the ‘ecology of fear’ (Brown, Laundré, & Gurung 1999) concept, which has gained increasing  
<sup>48</sup> attention in recent times (Gaynor *et al.* 2019). Notably, the mesopredator release hypothesis has recently  
<sup>49</sup> been expanded from increases in mesopredator abundance following apex predator decline (Soulé *et al.*  
<sup>50</sup> 1988) to also include changes in mesopredator behaviour (Brashares *et al.* 2010).

<sup>51</sup> To accurately quantify avoidance within a predator guild, we first need to understand how the overall  
<sup>52</sup> activity and diel activity patterns of each species varies ‘naturally’ across landscapes, particularly for  
<sup>53</sup> species with broad distributions. It is widely recognised that the overall activity of different predator  
<sup>54</sup> species varies across their distributions, but their diel activity patterns are often assumed to be constant.  
<sup>55</sup> In this paper, we use the term ‘overall activity’ to refer to the number of ‘independent’ predator detections

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

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

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

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

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

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

<sup>99</sup> **2. MATERIALS AND METHODS**

<sup>100</sup> *2.1. Study area and camera-trapping*

<sup>101</sup> We compiled data from multiple smaller-scale camera-trap studies across two regions in south-west  
<sup>102</sup> Victoria, Australia: the Glenelg region and Otway Ranges (Fig. 1). Introduced foxes and cats are the  
<sup>103</sup> only medium-large functional mammalian terrestrial carnivores here: native dingoes *Canis familiaris*  
<sup>104</sup> are long-absent throughout, while tiger quolls *Dasyurus maculatus* are long-absent in the Glenelg region  
<sup>105</sup> and likely functionally extinct in the Otway Ranges (last confirmed sighting in 2014). In broad sections  
<sup>106</sup> of each region, government land managers conduct ongoing targeted lethal fox control for biodiversity  
<sup>107</sup> conservation. Poison-baits containing 3 mg of sodium fluroacetate ('1080') are buried at a depth of  
<sup>108</sup> 12 - 15 cm at 1-km intervals along accessible forest tracks and roads. Different road densities result in  
<sup>109</sup> variable densities of poison-baits. Managers also frequently implement prescribed fire across both regions,  
<sup>110</sup> primarily to reduce fuel loads to prevent large wildfires.

<sup>111</sup> *2.1.1. Glenelg region*

<sup>112</sup> In the Glenelg region, large patches of natural vegetation are fragmented by pastoral farming and  
<sup>113</sup> residential properties (Fig. 1). Foxes in three distinct forest blocks in this region have been subject to  
<sup>114</sup> poison-baiting since October 2005, with fortnightly bait replacements (Robley *et al.* 2014). These forest  
<sup>115</sup> blocks, along with three similar, unbaited forest blocks to the north have been simultaneously surveyed  
<sup>116</sup> annually under the 'Glenelg Ark' fox control program since 2005 (40 sites per block; Robley *et al.* 2020).  
<sup>117</sup> Hair-tubes were used to monitor species from 2005 - 2013 (presented in Robley *et al.* 2014), replaced  
<sup>118</sup> by camera-traps from 2013; here we present camera-trap data from 2013 - 2019 (Robley *et al.* 2020).  
<sup>119</sup> We also included a further 425 camera-trap deployments at unique locations from early 2018 (M.W.R.  
<sup>120</sup> PhD surveys). This totals 2039 camera-trap deployments in the Glenelg region, collected in a control-  
<sup>121</sup> impact experimental design (foxes had been continuously controlled for at 8 - 14 years in the treatment  
<sup>122</sup> landscapes at the time of these surveys).

<sup>123</sup> *2.1.2. Otway Ranges*

<sup>124</sup> The Otway Ranges is a largely continuous patch of natural vegetation with a strong east-west rainfall  
<sup>125</sup> gradient (Fig. 1). A matrix of cool temperate rainforest and wet forest at high altitudes in the south-west

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

141 *2.1.3. Camera-trap set-ups*

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

152 *2.2. Data preparation*

153 All data analysis was conducted in R version 3.6.3 (R Core Team 2020). We first used lorelograms  
154 to identify the minimum interval to approximate independence (Iannarilli *et al.* 2019); this indicated  
155 that discarding repeat detections of a species within 30 minutes was sufficient to reduce temporal auto-  
156 correlation. To account for day length variation across space and time, we extracted sunrise and sunset  
157 times for each camera-trap deployment using the ‘maptools’ R-package (Bivand & Lewin-Koh 2021) and  
158 adjusted detection times to be relative to sunrise and sunset using the average double anchoring approach  
159 described by Vazquez *et al.* (2019). We then built a data frame consisting of a row for each hour of the  
160 day (0 – 23), for every camera-trap deployment ( $n = 3667$ ), recording the total number of ‘independent’  
161 fox and feral cat detections within each hour across the camera-trap survey.

162 *2.3. Generalised additive models*

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

174 *2.3.1. How does predator overall activity and diel activity patterns vary across space? (model 1)*

175 To examine how the overall activity and diel activity patterns of each predator varied across space,  
176 we fit a model for each predator which included a tensor product interaction between a spatial smooth  
177 and hourly smooth. This allowed predators to have different activity levels across space (static across  
178 the years surveyed), as well as variation in diel activity pattern across space. Space was modelled using  
179 camera-trap coordinates and a duchon spline basis (Miller & Wood 2014). To examine how the relative

180 strength of diel activity patterns changed across space, we plotted the percentage increase from the  
181 minimum to maximum activity estimate within the daily cycle for each predicted location (hereafter  
182 referred to as ‘diel activity pattern strength’).

183 *2.3.2. How does predator overall activity and diel activity patterns vary across vegetation types? (model*  
184 *2)*

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

198 *2.3.3. Do feral cats avoid foxes in space or time? (model 3)*

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

208 To investigate changes in feral cat diel activity across the range of observed fox activity, we first  
209 quantified fox activity for each camera trap deployment as the total number of fox detections for the  
210 deployment divided by the number of survey days, to adjust for survey duration (hereafter ‘adjusted fox  
211 counts’). We modelled an interaction between hour (cyclical spine) and adjusted fox counts (thin plate  
212 regression spline with shrinkage - meaning fox effects could be entirely removed from the model if not  
213 supported by sufficient data), allowing cats to have nonlinear responses to both hour and adjusted fox  
214 counts. We fit separate tensor product interactions for each habitat type (using a ‘by-variable’ term).  
215 For a direct visual comparison to fox activity, we fit another fox model where a diel curve was estimated  
216 separately across each of the three habitat types.

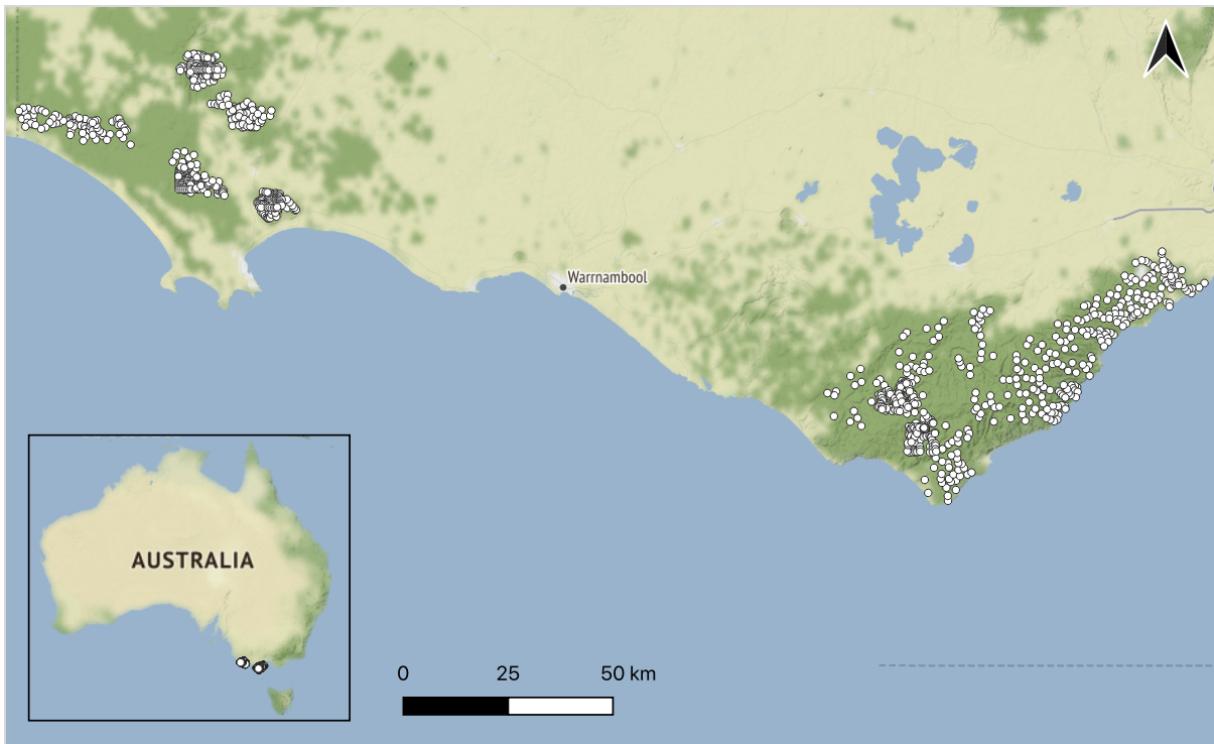


Figure 1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0,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

217 **3. RESULTS**

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

220 *3.0.1. How does predator overall activity and diel activity patterns vary across space? (model 1)*

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

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

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

236 *3.0.2. How does predator overall activity and diel activity patterns vary across vegetation types? (model  
237 2)*

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

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

<sup>243</sup> nocturnal (and most active) in wet forests, but largely crepuscular in all other vegetation types (Fig. 4b).  
<sup>244</sup> For both predators, the random effect for region (Glenelg or Otways) in the vegetation models shrank to  
<sup>245</sup> near-zero, indicating all variation between the regions was explained by the vegetation covariate and site  
<sup>246</sup> random intercept.

<sup>247</sup> *3.0.3. Do feral cats avoid foxes in space or time? (model 3)*

<sup>248</sup> Cat spatial activity was relatively unaffected by the fox activity in both habitat types of the Otway  
<sup>249</sup> Ranges; and, if anything, increased with increasing adjusted fox counts in the Glenelg region (Fig. 5),  
<sup>250</sup> indicating cats did not avoid foxes spatially.

<sup>251</sup> Across all habitat types, feral cat diel activity patterns changed across the gradient of fox activity  
<sup>252</sup> (Fig. 5). In the Glenelg region and Otway dry habitat types, feral cats had a nocturnal-crepuscular diel  
<sup>253</sup> activity pattern where fox activity was low, but were most active during the day where fox activity was  
<sup>254</sup> high. In contrast, in the wet forests of the Otway Ranges, feral cats were more strongly nocturnal when  
<sup>255</sup> fox activity was high.

### Otway Ranges: Red fox

Space-time interaction effect (excluding marginal effects)

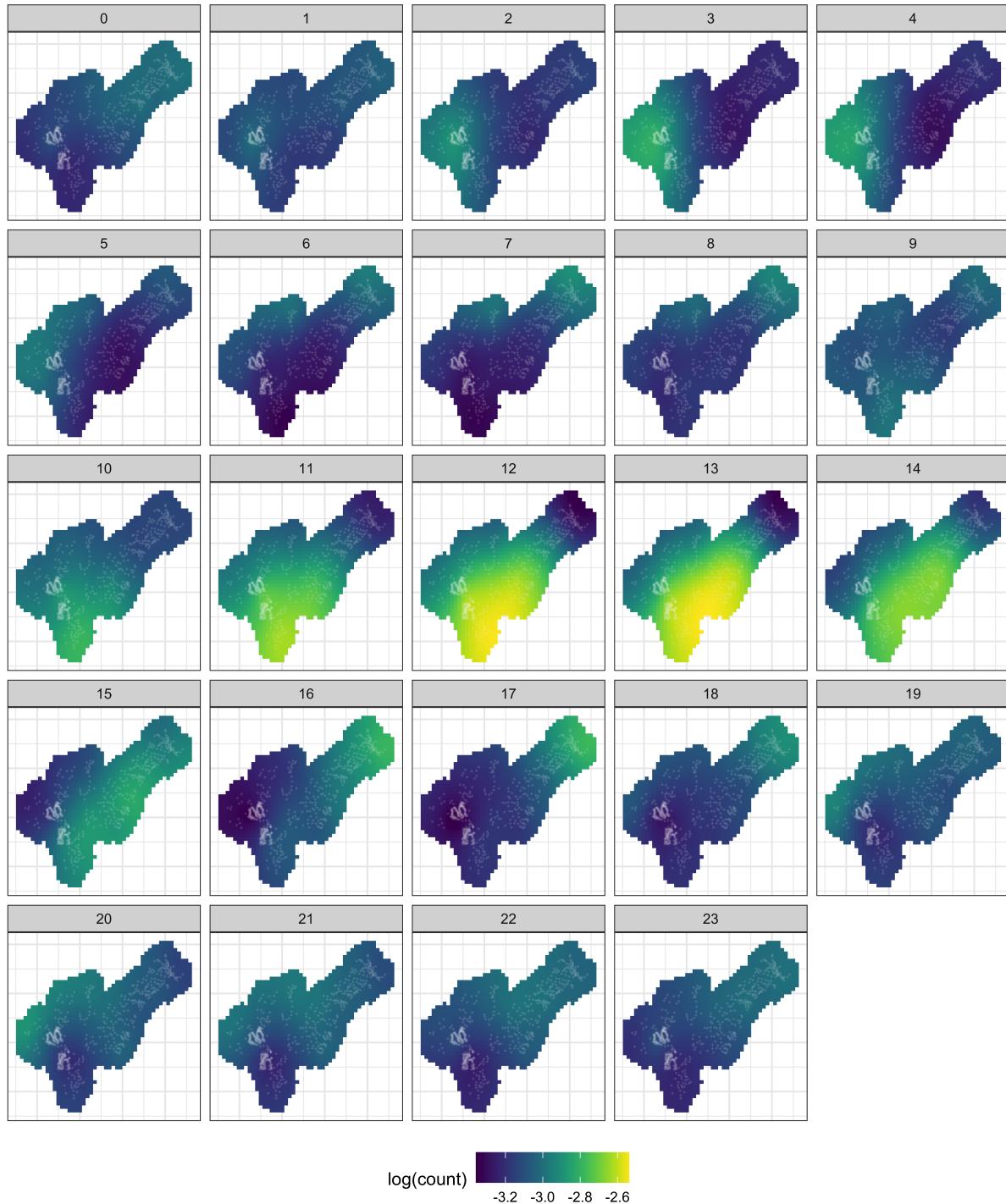


Figure 2: Interaction effect of space-time on red fox *Vulpes vulpes* activity across each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1), as an example. Corresponding plots for feral cats *Felis catus* in this region, as well as both predators in the Glenelg region are provided in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

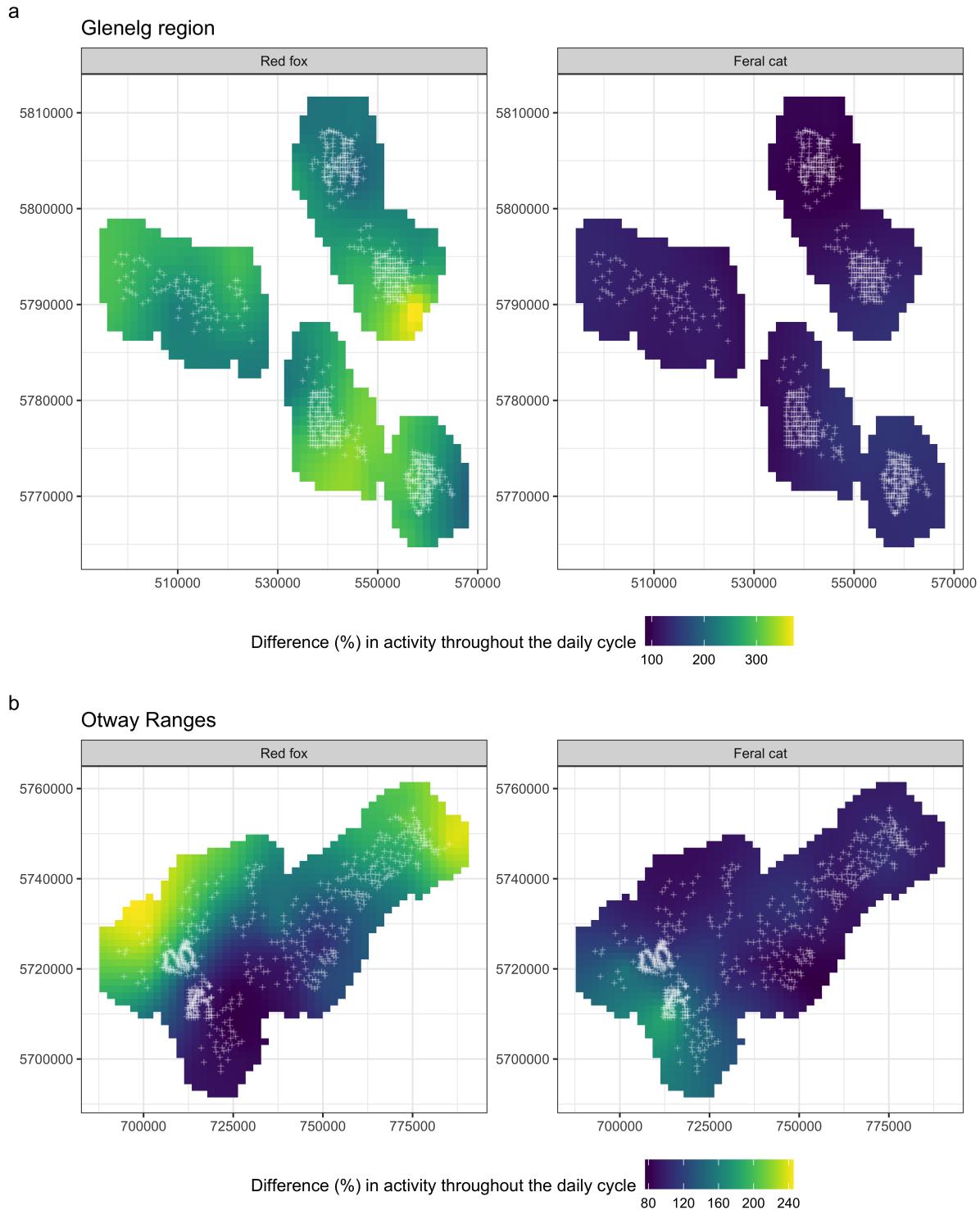
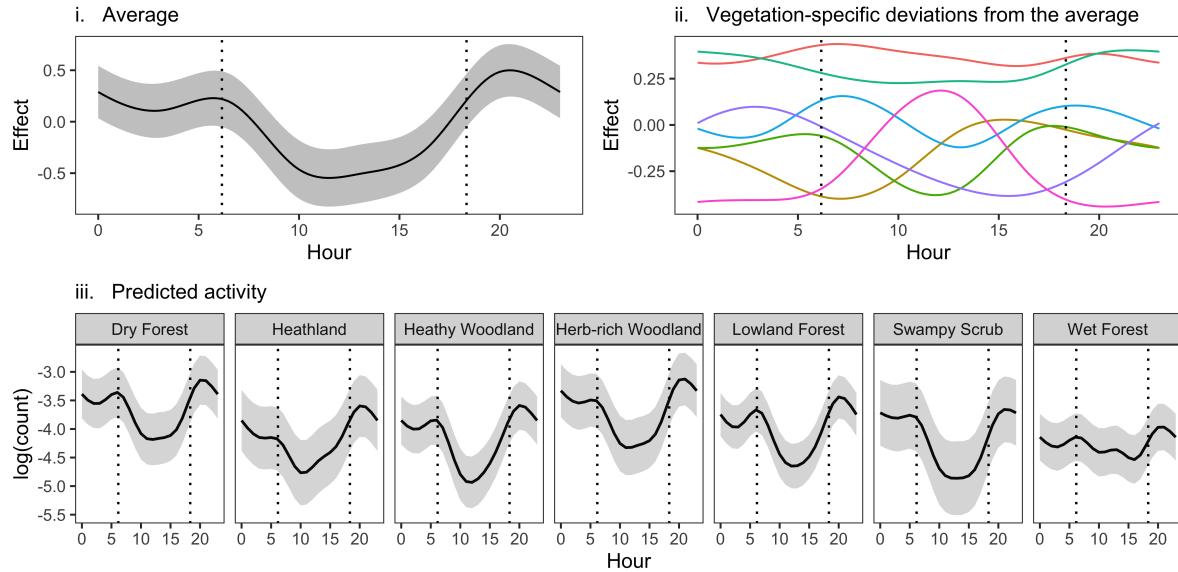


Figure 3: The strength of diel activity patterns of two invasive predators varied within the two study regions in south-west Victoria, Australia (model 1). White crosses depict unique camera-trap sites; colour brightness scales with increasing percentage difference between the minimum and maximum activity 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

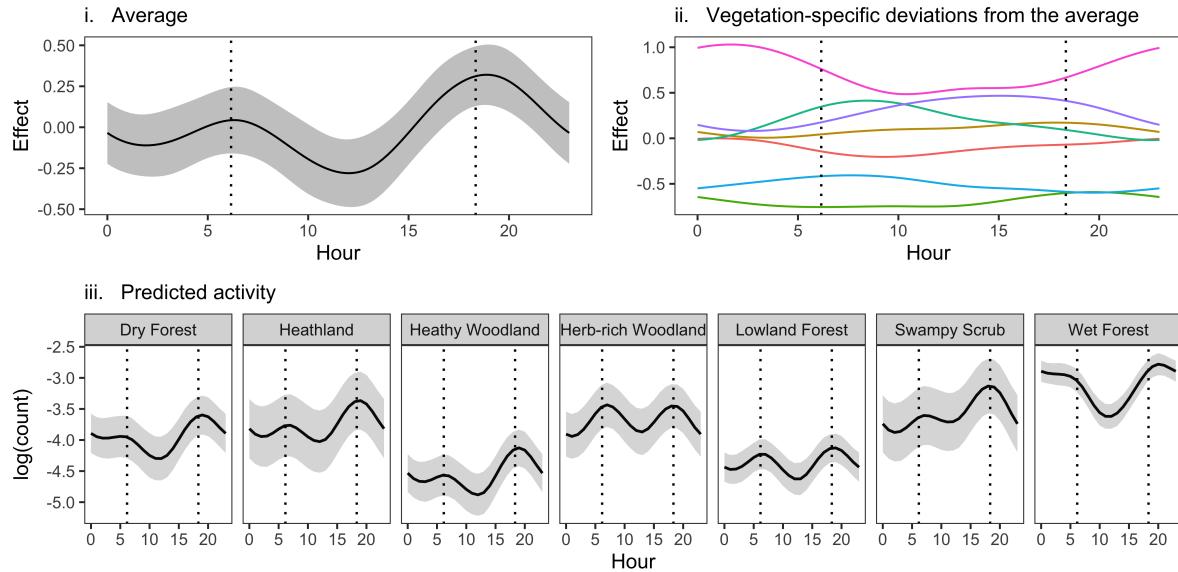
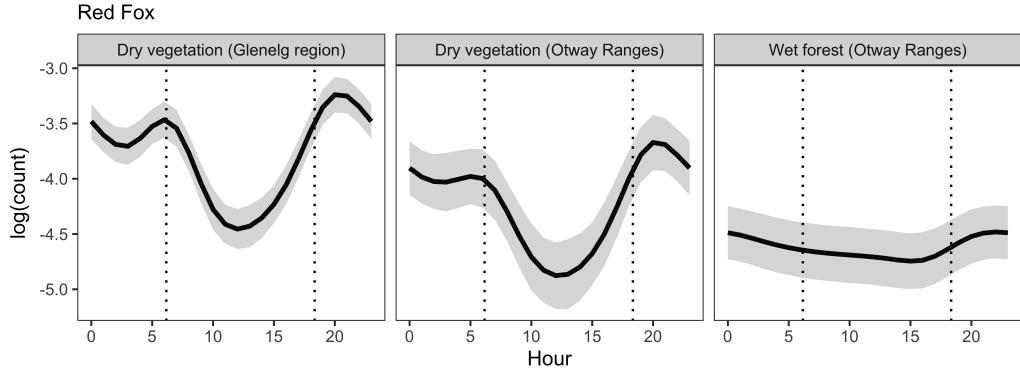
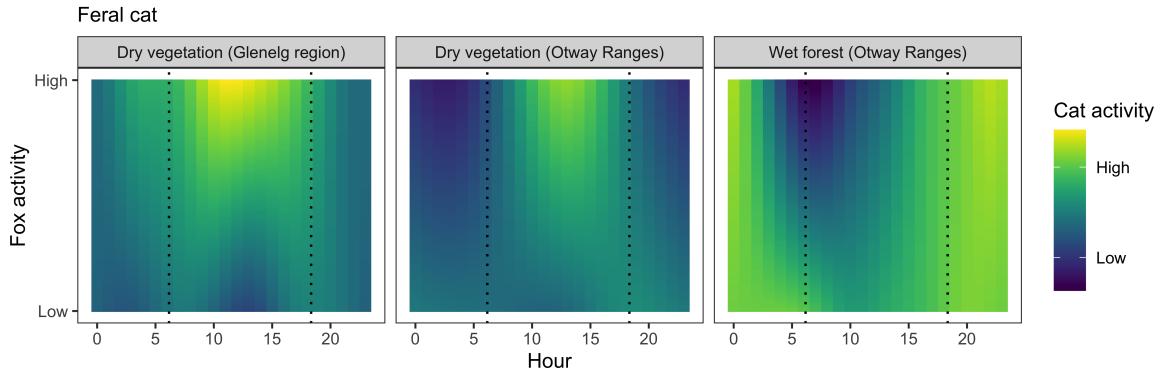


Figure 4: Red foxes *Vulpes vulpes* (a) and feral cat *Felis catus* (B) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia (model 2). Dotted, vertical lines represent average sunrise and sunset times. Shaded areas 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

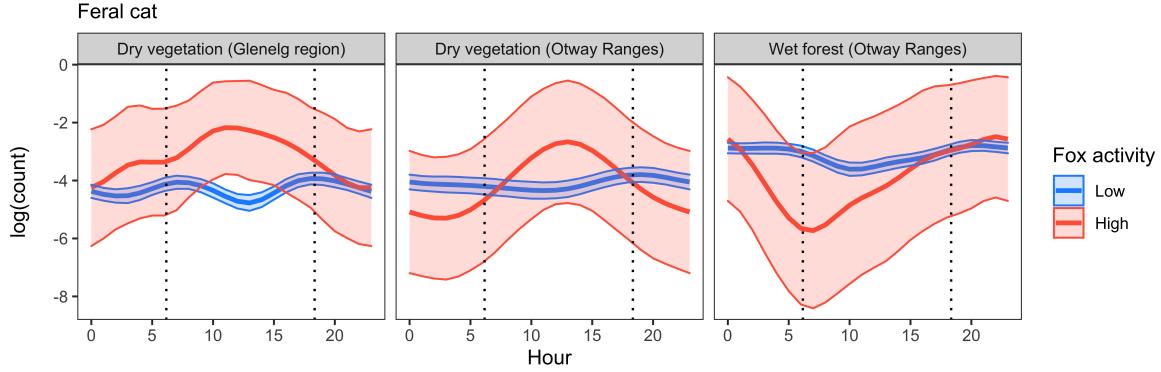


Figure 5: Variation in mean feral cat *Felis catus* activity (a) and associated uncertainty estimates (b) in response to count of 'independent' red fox *Vulpes vulpes* detections (log-transformed and survey effort adjusted) across each 'habitat type' in south-west Victoria, Australia (model 3). Grey 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).

256 **4. DISCUSSION**

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

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

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

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

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

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

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

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

346 ACKNOWLEDGEMENTS

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**508 Supporting Information**

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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.

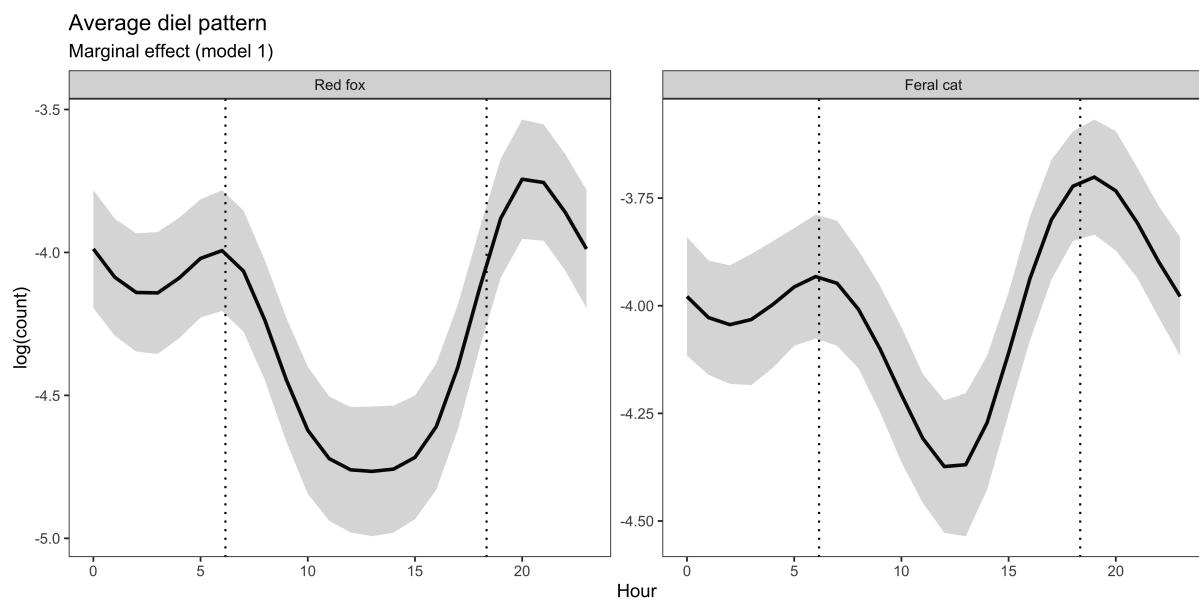


Figure S1: Marginal effect of time (model 1) on predators across both study regions in south-west Victoria, Australia.  
White crosses depict unique camera-trap sites

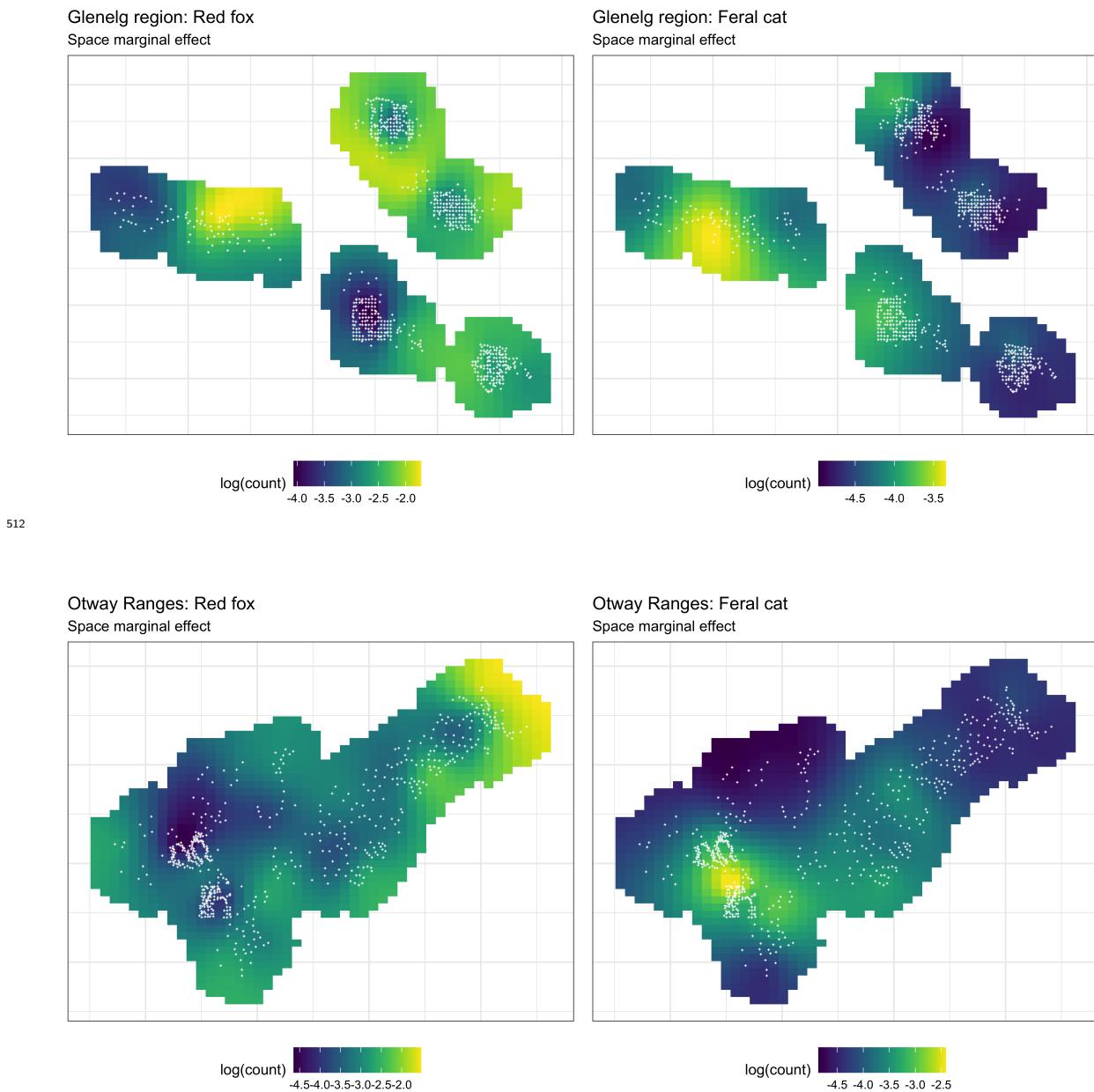


Figure S2: Marginal effect of space on predators across south-west Victoria, Australia (model 1). White crosses depict unique camera-trap sites

### Glenelg region: Red fox

Space-time interaction effect (excluding marginal effects)

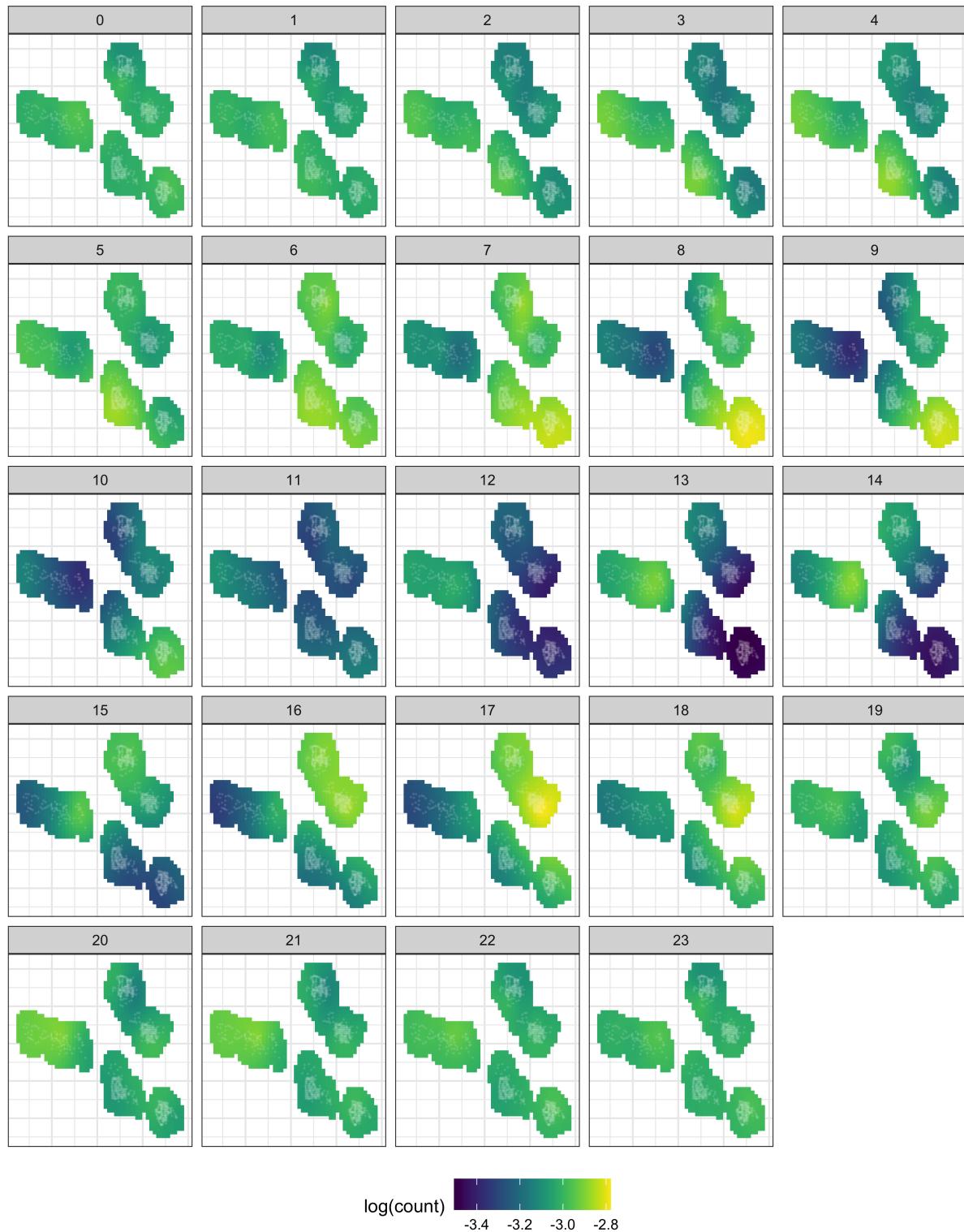


Figure S3: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites.

Glenelg region: Feral cat

Space-time interaction effect (excluding marginal effects)

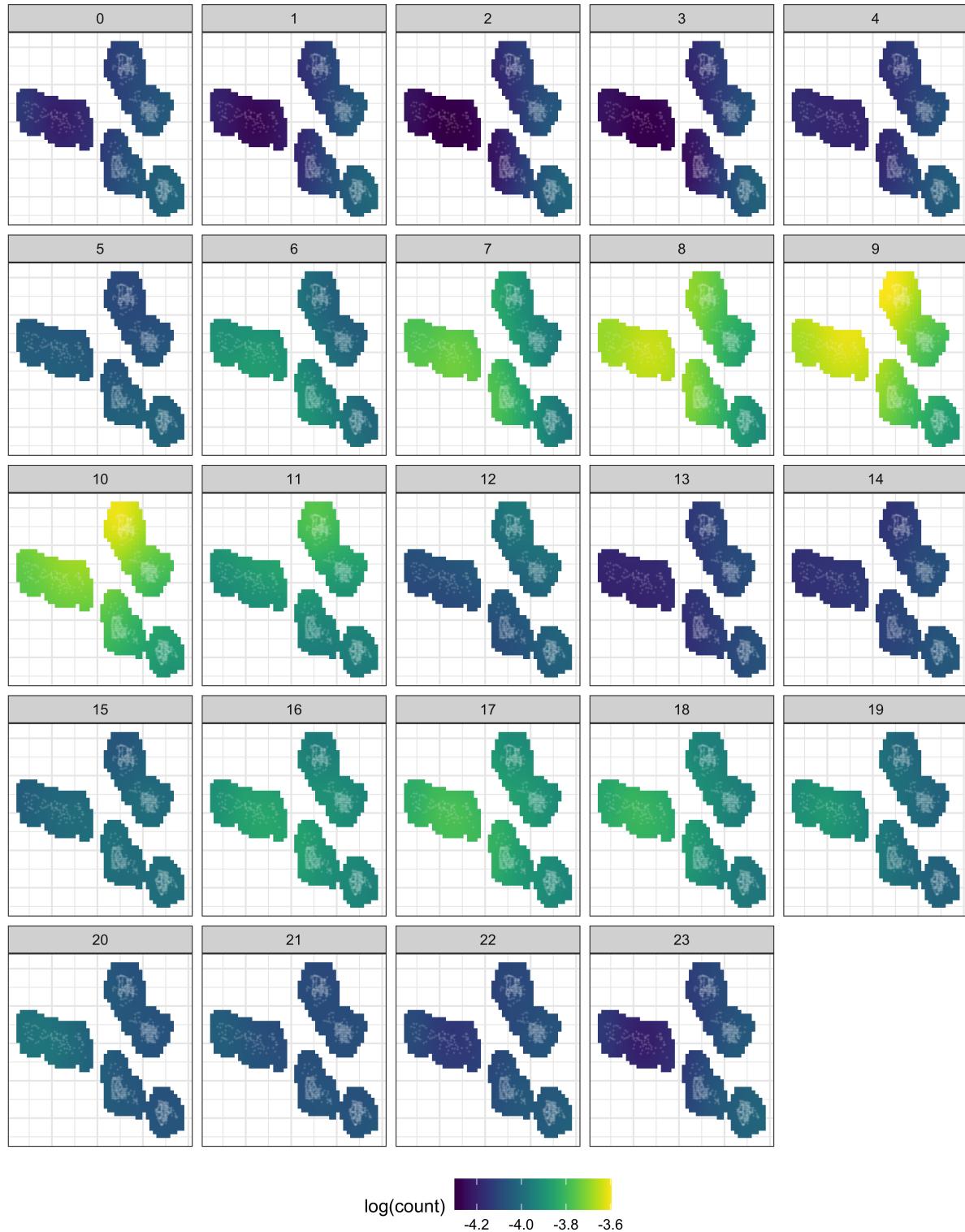


Figure S4: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites.

### Otway Ranges: Feral cat

Space-time interaction effect (excluding marginal effects)

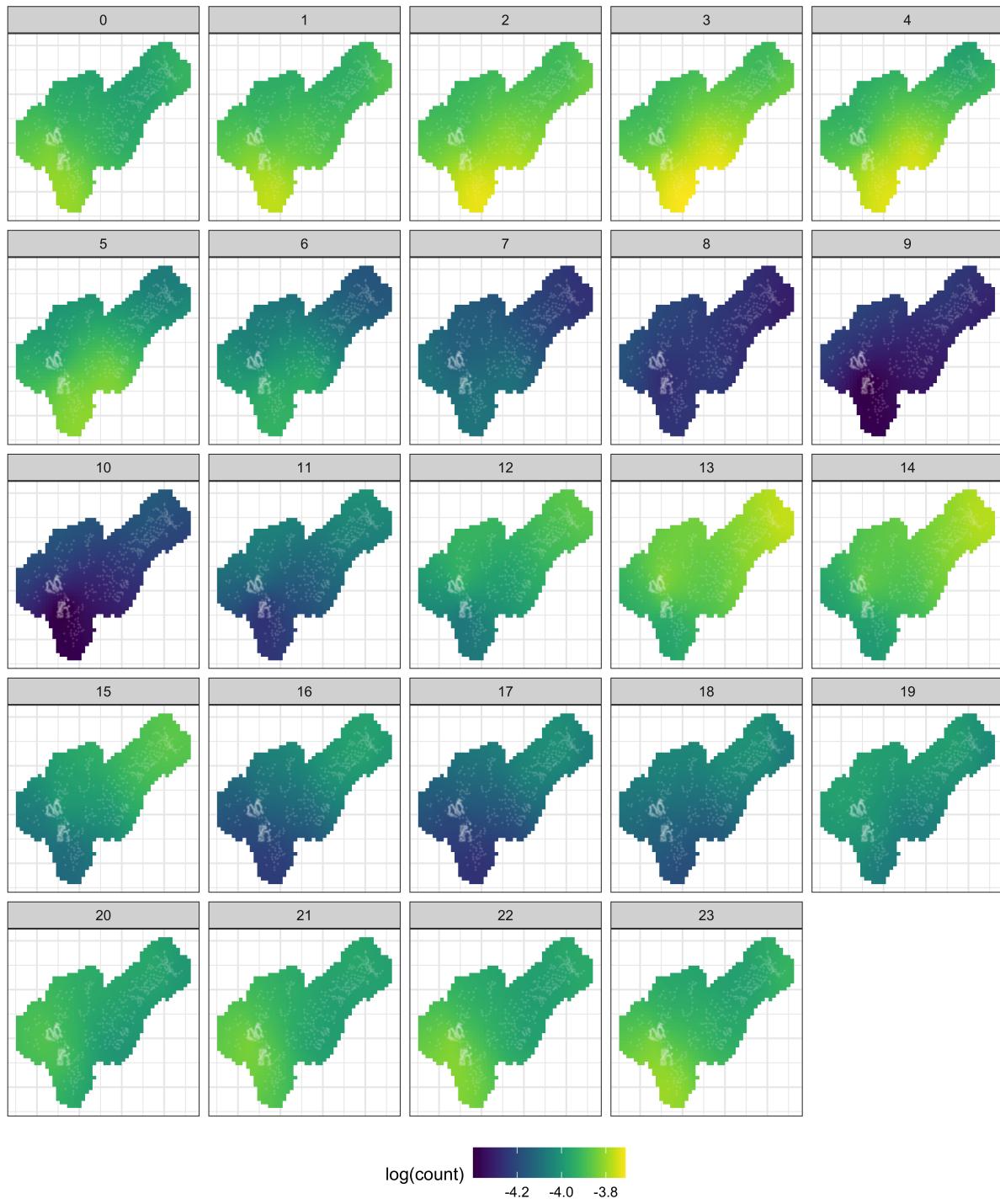


Figure S5: Interaction effect of space-time on feral cat *Felis catus* activity across each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites.

Otway Ranges: Red fox

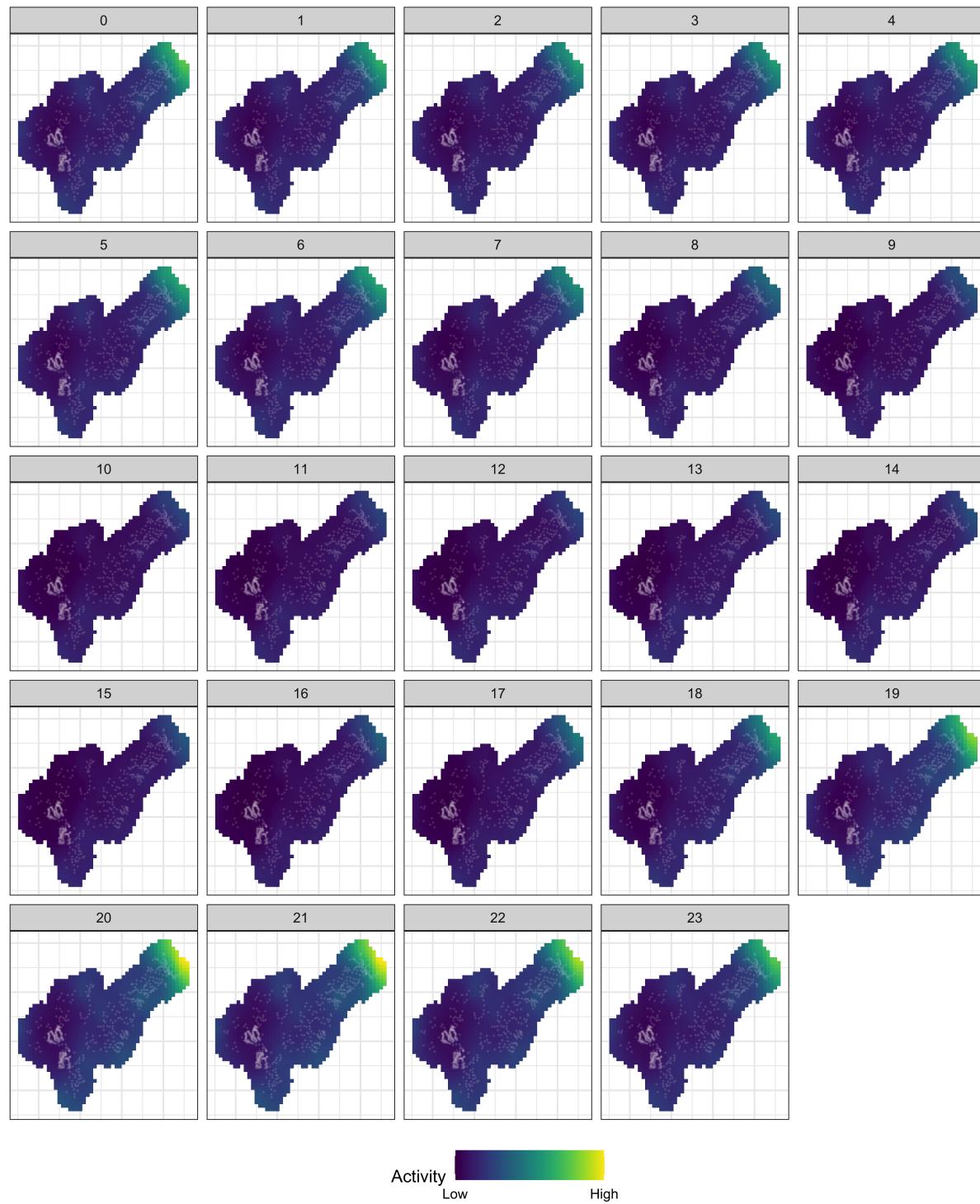


Figure S6: Overall spatial activity of red foxes *Vulpes vulpes* for each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites

## Glenelg region: Feral cat

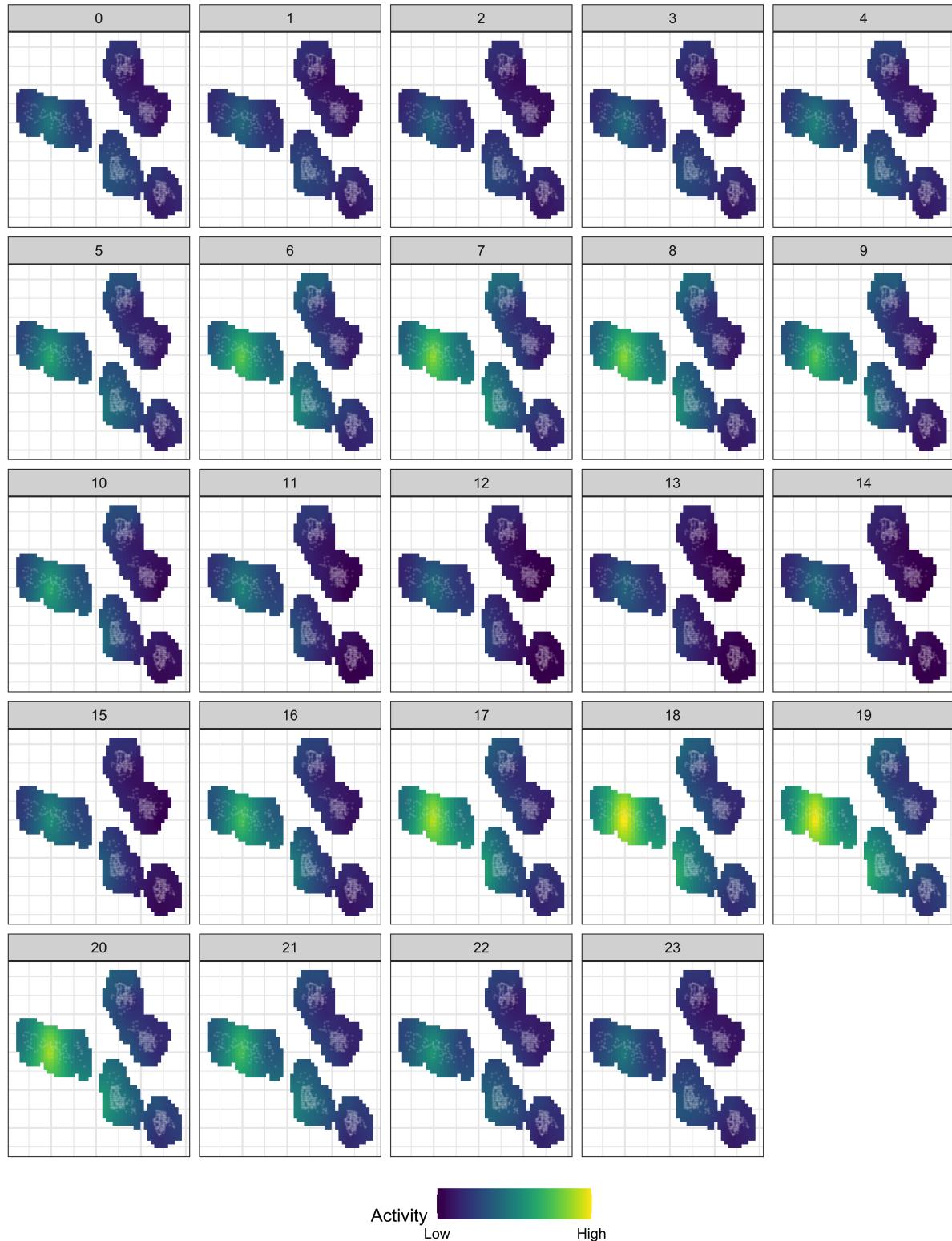


Figure S7: Overall spatial activity of feral cats *Felis catus* for each hour of the day (0 - 23) in the Glenelg region, Australia (model 1). White crosses depict unique camera-trap sites

### Otway Ranges: Red fox

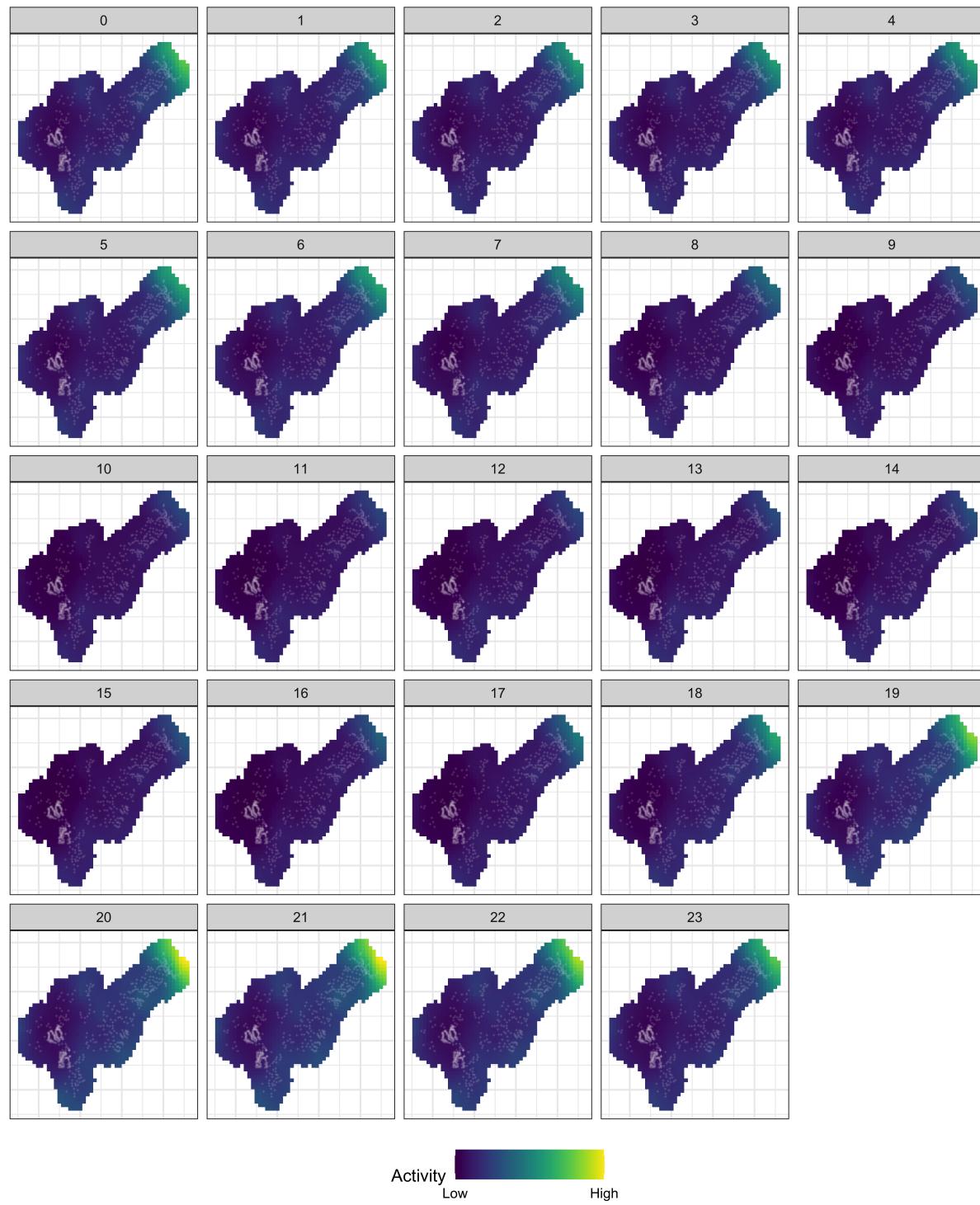


Figure S8: Overall spatial activity of red foxes *Vulpes vulpes* for each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites

Otway Ranges: Feral cat

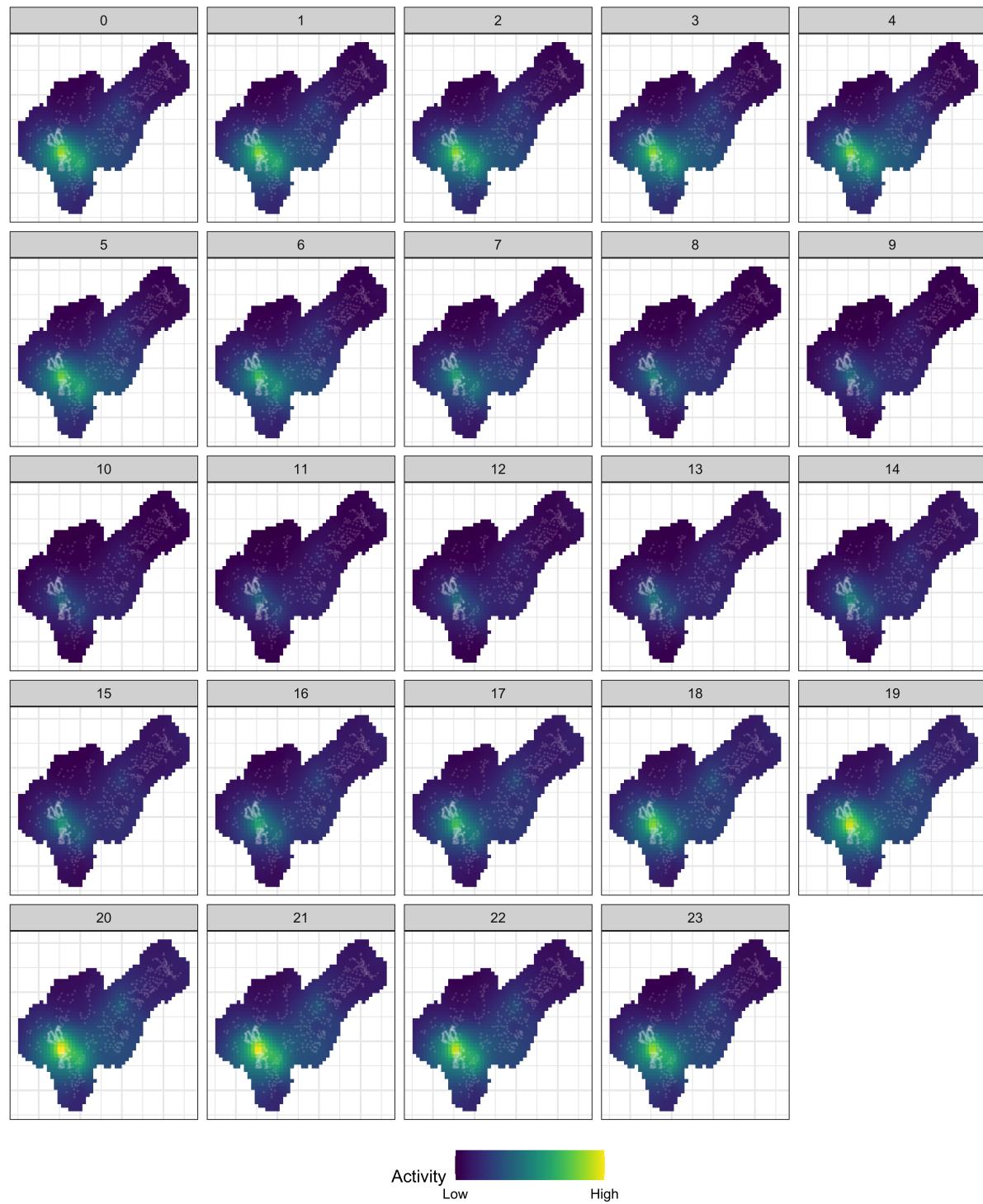


Figure S9: Overall spatial activity of feral cats *Felis catus* for each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1). White crosses depict unique camera-trap sites