

# Spatial variation in predator diel activity patterns

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*Open research:* Data and code will be deposited on Dryad upon acceptance and can currently be found at this link: <https://github.com/matt-w-rees/spatiotemporal-gams-invasive-predators>.

*Keywords:* diel activity patterns, generalised additive model, feral cat, invasive predator, intraguild predator interactions, lethal predator control, mesopredator release, red fox, spatiotemporal model

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## Spatial variation in predator diel activity patterns

### 1 ABSTRACT

2 Understanding the constraints dominant predators impose on subordinate species is important for  
3 predicting ecosystem dynamics and anticipating outcomes of predator management. Subordinate predators  
4 may avoid dominant predators in time or space, making it difficult to quantify antipredator behaviours unless  
5 joint spatiotemporal analyses are used. Here, we tested whether an invasive dominant predator (red fox  
6 *Vulpes vulpes*) alters the spatiotemporal activity of an invasive subordinate predator (feral cat *Felis catus*).  
7 We collated records of both species from 3,667 camera-traps deployed experimentally across two regions  
8 of south-eastern Australia with simplified predator guilds; foxes were poison-baited in some landscapes  
9 within each region. We used generalised additive models to quantify changes in predator spatiotemporal  
10 activity across geographic space, vegetation types, human footprint and (artificially manipulated) gradients  
11 of dominant predator activity. Foxes and cats had similar diel activity patterns when averaged across all  
12 sites, however there was important differentiation at a finer scale—cats did not reduce their spatial activity  
13 but shifted diel patterns when localised fox activity was high. Cats were crepuscular on average. However,  
14 across dry vegetation types of both regions (where foxes were nocturnal), cats shifted to diurnal behaviour  
15 with increasing fox activity. In contrast, fox activity was relatively consistent throughout the daily cycle in  
16 the wet forest; here cats avoided dawn when fox activity was high. Changes in cat diel activity patterns may  
17 facilitate spatial coexistence between these two invasive predators, potentially shifting feral cat impacts onto  
18 different native prey. It is well-appreciated that predator activity varies spatially and fluctuates throughout  
19 the daily cycle. However, our study demonstrates that diel activity patterns also vary across space, likely  
20 mediated by both landscape-context and fear. dominant predator avoidance appears to be dynamic—a key  
21 nuance which is overlooked when simply comparing the average activity overlap between two species.

**22 1. INTRODUCTION**

**23** Top predators can drive ecosystem structure and dynamics by suppressing populations of rival predators  
**24** and prey species (Prugh et al. 2009, Estes et al. 2011). Dominant predators can suppress subordinate  
**25** species directly through antagonistic interactions and predation, as well as indirectly through fear (Creel  
**26** and Christianson 2008, Allen et al. 2022). Fear-induced behavioural suppression can be as detrimental to  
**27** subordinate species as predation itself, by limiting resource acquisition and breeding success (Brown et al.  
**28** 1999, Schmitz et al. 2004, Preisser et al. 2005). Understanding how top predators—including humans—  
**29** constrain the behaviour of subordinate species is therefore important to accurately predict consequences of  
**30** predator management, such as reintroductions or lethal control (Suraci et al. 2016, Gaynor et al. 2021).

**31** Spatial and/or temporal niche partitioning may allow subordinate species to coexist with top predators  
**32** by reducing encounter-rates and resource overlap (Kronfeld-Schor and Dayan 2003). However, subordinate  
**33** species may not consistently employ avoidance behaviours because perceived predation risk is spatiotemporally  
**34** variable, and antipredator behaviours typically involve a trade-off against resource acquisition, such as limiting  
**35** or relegating activity to suboptimal places or times (Lima and Dill 1990, Lima and Bednekoff 1999). Therefore,  
**36** optimal predator avoidance strategies likely vary across heterogeneous landscapes where resource availability  
**37** (e.g., shelter, food) and perceived predation risks differ (Kauffman et al. 2007, Willems and Hill 2009, Davies  
**38** et al. 2021, Wirsing et al. 2021). For example, temporal predator avoidance may be preferable over spatial  
**39** avoidance if food is constantly available throughout the day, and vice versa. These theories are unified  
**40** under the ecology of fear concept (Brown et al. 1999), which has gained increasing attention in recent times  
**41** (Gaynor et al. 2019). However, there remains a lack of robust, empirical evidence documenting dynamic  
**42** changes in antipredator behaviour.

**43** Animal diel activity patterns are increasingly being considered alongside spatial activity and distributional  
**44** patterns. However, spatial and temporal (in regard to the daily cycle) activity patterns are still often  
**45** considered in an ad-hoc fashion. For example, by fitting separate models for spatial and temporal overlap,  
**46** or by repeating spatial analyses (e.g., resource selection functions) at different time periods such night and  
**47** day (e.g., Basille et al. 2015, Kohl et al. 2019, Smith et al. 2019, Wooster et al. 2022). Such ad-hoc  
**48** approaches make it difficult to assess the relative importance, as well as dynamic changes in spatial and  
**49** temporal processes (Suraci et al. 2022).

50 There are many approaches to modelling intraguild spatiotemporal interactions, such as time-to-encounter  
51 models and coefficients of activity overlap (Frey et al. 2017). Time-to-encounter approaches consider fine-scale  
52 avoidance or attraction by using time intervals between species detections as the response variable, although  
53 do not estimate diel activity patterns (Harmsen et al. 2009, Fancourt et al. 2019, Niedballa et al. 2019).  
54 Multispecies models have been recently developed to assess overlap in spatial and diel activity between two  
55 species (Ait Kaci Azzou et al. 2021), as well as different diel activity patterns based on the presence or  
56 absence of another species at a site (Kellner et al. 2022). Multispecies models are data-hungry and difficult  
57 to fit, but can account for imperfect detection and different types of predictor variables (e.g., Parsons et  
58 al. 2022). Given avoidance behaviours are likely dynamic (Gaynor et al. 2019), there is need for statistical  
59 approaches which jointly assess continuous shifts in spatial and diel activity patterns of one species in response  
60 to another, particularly when combined with experimental data (Suraci et al. 2022).

61 Generalised Additive Models (hereafter ‘GAMs’) are increasingly being used to estimate animal diel  
62 activity patterns and offer a flexible framework to jointly consider spatial activity. GAMs are useful to  
63 model diel activity patterns as they can implement cyclical splines—joining the end with the start of the  
64 day—as well as complexity penalties to reduce overfitting. If complex nonlinear (i.e., wiggly) effects are not  
65 statistically supported, smoothing penalties in GAMs ‘shrink’ them to a linear (i.e., no wigginess) effect,  
66 or even to a horizontal line - removing the entire effect of the predictor variable and therefore the need  
67 for additional tests of statistical significance (such as p-values and information criteria). GAMs can also  
68 capture nonlinear interactions between multiple variables with different units (i.e., ‘tensor products’), and  
69 offer the ability to share information across categorical variables through hierarchical specifications (Wood  
70 2017, Pedersen et al. 2019). However, we are only aware of one study which allowed animal diel activity  
71 to interact with predation risk as a continuous variable in a GAM (although without considering overall  
72 activity, Cunningham et al. 2019).

73 The red fox *Vulpes vulpes* (hereafter ‘fox’) and feral cat *Felis catus* (hereafter ‘cat’) have devastating  
74 impacts on native prey throughout their introduced range, implicated in the extinction of ~10 and 63 species,  
75 respectively (Doherty et al. 2016). The impacts of these invasive predators are particularly extreme on the  
76 Australian continent (Woinarski et al. 2015). Cats are more difficult to manage, and so introduced predator  
77 control programs in Australia often target only foxes (particularly through poison-baiting, Reddiex et al.  
78 2007). As foxes and cats compete for many of the same resources (Fleming et al. 2022), there is concern  
79 that lethal fox control could cause mesopredator release (Soulé et al. 1988) of cats (Glen and Dickman 2005,

80 Doherty and Ritchie 2017, Wayne et al. 2017). However, there is limited evidence that spatial cat activity  
81 increases in response to fox control (Hunter et al. 2018), although there are signs of changes in behaviour  
82 and population density (Molsher et al. 2017, Rees et al. 2023a). Other studies have investigated potential  
83 spatial and temporal interactions between these invasive predators (e.g., Roshier and Carter 2021), but not  
84 in response to fox control, or in a joint spatiotemporal framework that allows flexibility in cat avoidance  
85 behaviours with respect to differences in fox activity. Conservation managers are therefore uncertain as to  
86 whether fox control may increase the impacts of feral cats on native prey, through increases in cat density or  
87 behavioural changes which improve hunting success.

88 In this study, we first explored (1) how predator diel activity patterns vary across geographic space  
89 ('model 1'), and (2) the role of vegetation type and human footprint in predator activity patterns ('model  
90 2'). Using this knowledge to partition our dataset, we then (3) tested whether the activity of a dominant  
91 predator (fox) affected the spatiotemporal activity of a subordinate predator (cat; 'model 3'). In line with  
92 behavioural avoidance or exclusion, we predicted that cat diel activity patterns would shift towards less-risky  
93 times of day (i.e., times when fox activity was lower), and/or spatial cat activity would be lower at sites  
94 where fox activity was relatively high. We illustrate how GAMs can provide a simple framework to jointly  
95 assess spatial and temporal animal activity patterns, as well as potential species interactions.

<sup>96</sup> **2. MATERIALS AND METHODS**

<sup>97</sup> *2.1. Study area and camera-trapping*

<sup>98</sup> Our study was conducted in a simple predator system where foxes and cats are the only medium-large  
<sup>99</sup> ( $> 1$  kg) mammalian predators, and fox activity is manipulated using lethal control in some landscapes.  
<sup>100</sup> This situation allowed sole focus on the interactions between these two predators, across an experimental  
<sup>101</sup> gradient of dominant predator (fox) activity. We compiled data from multiple smaller-scale camera-trap  
<sup>102</sup> studies, each designed to experimentally assess mammal responses to fox control. Overall, we collated 5,449  
<sup>103</sup> and 2,202 independent detections of foxes and cats, respectively (separated by at least 30 minutes) from  
<sup>104</sup> 172,052 camera-trap nights (Table S2).

<sup>105</sup> We collated camera-trap data across two regions in south-west Victoria, Australia: the Glenelg region  
<sup>106</sup> and Otway Ranges (Fig. 1). Here, dingoes *Canis familiaris* are long-absent throughout, while tiger quolls  
<sup>107</sup> *Dasyurus maculatus* are long-absent in the Glenelg region and likely functionally extinct in the Otway Ranges  
<sup>108</sup> (last confirmed sighting in 2014). In broad sections of each region, government land managers conduct  
<sup>109</sup> ongoing targeted lethal fox control for biodiversity conservation (see sections below for region-specific details).  
<sup>110</sup> Poison-baits containing 3 mg of sodium fluroacetate (compound 1080) are buried at a depth of 12 - 15 cm at  
<sup>111</sup> 1-km intervals along accessible forest tracks and roads. Different road densities therefore result in variable  
<sup>112</sup> densities of poison-baits. Foxes readily dig these poison-baits often resulting in population suppression,  
<sup>113</sup> whereas it is generally accepted that cats are unlikely to consume buried fox-baits and there is no evidence  
<sup>114</sup> buried 1080 fox-baits suppresses cat populations (Risbey et al. 1997, Algar and Burrows 2004, Moseby et al.  
<sup>115</sup> 2011, Hunter et al. 2018). Managers also frequently implement prescribed fire across both regions, primarily  
<sup>116</sup> to reduce fuel loads to prevent large wildfires.

<sup>117</sup> *2.1.1. Glenelg region*

<sup>118</sup> In the Glenelg region, large patches of natural vegetation are fragmented by pastoral farming and  
<sup>119</sup> residential properties (Fig. 1). Foxes in three distinct forest blocks in this region have been subject to  
<sup>120</sup> poison-baiting since October 2005, with fortnightly bait replacements (Robley et al. 2014). These forest  
<sup>121</sup> blocks, along with three similar, unbaited forest blocks to the north have been simultaneously surveyed  
<sup>122</sup> annually under the ‘Glenelg Ark’ fox control program since 2005 (40 sites per block, Robley et al. 2020).

<sup>123</sup> Hair-tubes were used to monitor species from 2005 - 2013 (presented in Robley et al. 2014), replaced by  
<sup>124</sup> camera-traps from 2013; here we present camera-trap data from 2013 - 2019 (Robley et al. 2020). We  
<sup>125</sup> also included a further 425 camera-trap deployments at unique locations from early 2018 (M.W.R PhD  
<sup>126</sup> Surveys', Rees et al. 2023b). This totals 2,039 camera-trap deployments in the Glenelg region, collected  
<sup>127</sup> in a control-impact experimental design (foxes had been continuously controlled for at 8 - 14 years in the  
<sup>128</sup> treatment landscapes at the time of these surveys).

<sup>129</sup> *2.1.2. Otway Ranges*

<sup>130</sup> The Otway Ranges is a largely continuous patch of natural vegetation with a strong east-west rainfall  
<sup>131</sup> gradient (Fig. 1). A matrix of cool temperate rainforest and wet forest at high altitudes in the south-west  
<sup>132</sup> descend into a large heathland directly north, and into dry forests and then heathlands to the north-east.  
<sup>133</sup> Fox-baiting commenced in small sections of the Otway Ranges in 2008 and large-scale systematic baiting  
<sup>134</sup> began in 2016 - 2017 under the 'Otway Ark' program (Robley et al. 2019). For the first six weeks, poison-baits  
<sup>135</sup> were replaced weekly, then changing to ongoing monthly bait-replacement. There was a pause in baiting  
<sup>136</sup> for approximately six months during the second half of 2018. Fox control recommenced in late 2018 with  
<sup>137</sup> four weeks of fortnightly bait-replacement, before returning to monthly bait-replacement. A large section of  
<sup>138</sup> the Otway Ranges to the north-west remains unbaited, but is monitored as an experimental non-treatment  
<sup>139</sup> site (Robley et al. 2019). Otway Ark managers survey 372 camera-trap sites annually (sequentially across  
<sup>140</sup> the region); we present one 'before' baiting survey and two 'after' baiting surveys of each site from 2016 -  
<sup>141</sup> 2018, totalling 1,113 camera-trap deployments (Robley et al. 2019). We also include data from an additional  
<sup>142</sup> before-after control-impact surveys (one 'before' baiting survey and two 'after' baiting surveys) in the western  
<sup>143</sup> section of the Otway Ranges, conducted annually 2017 - 2019 (Rees et al. 2023b). This added a further 195  
<sup>144</sup> sites and 524 camera-trap deployments (Table S1).

<sup>145</sup> *2.1.3. Camera-trap set-ups*

<sup>146</sup> All camera-trap deployments consisted of a Reconyx (Holmen, Wisconsin) brand camera-trap (white or  
<sup>147</sup> infrared flash), attached to a tree or a metal picket, facing a lure. All camera-trap sites were positioned in  
<sup>148</sup> the forest interior at least 30 m away from roads. The Glenelg Ark and Otway Ark fox monitoring programs  
<sup>149</sup> positioned camera-traps at least 40 cm above ground on a tree or a metal picket and angled downwards  
<sup>150</sup> toward a lure approximately 1 - 1.5 m away (Robley et al. 2019, 2020). The lures consisted of peanut

151 butter, golden syrup and rolled oats mixed into a small ball, placed within a tea strainer or PVC pipe  
152 container and secured either to the ground, or 20 - 60 cm above ground on a wooden stake. The M.W.R  
153 PhD surveys across both regions positioned camera-traps lower on a tree (around 15 - 30 cm above the  
154 ground) angled only slightly downwards toward a tuna oil lure approximately 2 - 2.5 m away (detailed in  
155 Rees et al. 2023a). Camera-traps were active for an average of 47 days (maximum 93 days), totalling 172,052  
156 trap-nights. Camera-trap spacing averaged 867 m for Glenelg Ark, 1246 m for Otway Ark, and 444 m for the  
157 M.W.R PhD surveys (Table S1).

158 *2.2. Data preparation*

159 Analyses were conducted in R version 4.1.3 (R Core Team 2020). We first used lorelograms to identify the  
160 minimum interval to approximate independence (Iannarilli et al. 2019); this indicated that discarding repeat  
161 detections of a species within 30 minutes was sufficient to reduce temporal autocorrelation. To account for  
162 day length variation across space and time, we extracted sunrise and sunset times for each camera-trap  
163 deployment using the ‘maptools’ R-package (Bivand and Lewin-Koh 2021) and adjusted detection times to  
164 be relative to sunrise and sunset using the average double anchoring approach described by Vazquez et al.  
165 (2019). We then built a dataframe consisting of a row for each hour of the day (0 – 23), for every camera-trap  
166 deployment ( $n = 3,667$ ), recording the total number of ‘independent’ fox and feral cat detections within each  
167 hour across the camera-trap survey.

168 *2.3. Generalised additive models*

169 We modelled the total number of independent detections of each predator per hour for each camera-trap  
170 deployment (response variable) with generalised additive mixed-effect models implemented in the ‘mgcv’  
171 R-package (Wood 2017). We used the negative binomial family, as overdispersion, but not zero-inflation, was  
172 detected with a poisson distribution using the ‘DHARMA’ R-package (Hartig 2020). We specified the natural  
173 log of the number of survey days as a model offset to account for differences in camera-trap survey duration,  
174 and a random intercept for each site to account for repeat sampling for models 2 and 3 (as pseudoreplication  
175 from repeat sampling in model 1 was explicitly accounted for using the spatial term). For fox models, we  
176 also included a smooth effect of poison-bait density (number of baits within a 2.3 km radius around each  
177 camera-trap - the average maximum distance adult foxes travel from their home-range centre in these regions,  
178 Hradsky et al. 2017a) with separate responses per region to account for the effect of fox control. These

179 specifications were included in each model we fitted; models differed in their specification of the cyclical hour  
180 smooth to provide inference on variations of predator diel activity across the three questions of interest -  
181 this is detailed in the sections below. We used the ‘ggplot2’ (Wickham 2016) and ‘gratia’ (Simpson 2021)  
182 R-packages to plot models.

183 In this paper, we use the term ‘spatial activity’ to refer to the number of ‘independent’ predator detections  
184 at a site (offset to account for survey duration; analogous to an activity or abundance index), and ‘diel  
185 activity pattern’ to refer to fluctuations in relative activity throughout the 24-hour daily cycle. The first two  
186 models we fit explored how predator spatiotemporal activity varied across these regions, informing the best  
187 structure for our third model which tested the activity of foxes limits the spatiotemporal activity of cats  
188 (detailed in the sections below).

189 *2.3.1. How does predator diel activity patterns vary across geographic space? (model 1)*

190 To examine how the spatial activity and diel activity patterns of each predator varied across space, we fit  
191 a model for each predator which included a tensor product interaction between a spatial smooth (thin plate  
192 regression spline) and hourly smooth. This model specification allowed predators to have different activity  
193 levels across space (static across the years surveyed), as well as variation in diel activity pattern across space.  
194 Space was modelled using camera-trap coordinates and a duchon spline basis (Miller and Wood 2014).

195 *2.3.2. How does vegetation type and human footprint affect predator activity patterns? (model 2)*

196 The spatial term in model 1 estimated differences in predator activity across geographic space; we  
197 hypothesised that this was partly due to differences in vegetation type, based both on the observed spatial  
198 patterns and because vegetation type is a major driver of understorey habitat structure and prey occurrence  
199 in these regions (Swan et al. 2015, Hradsky et al. 2017b). To test whether the diel activity pattern of  
200 each predator varied among vegetation types, we identified the Ecological Vegetation Class group (hereafter  
201 ‘vegetation type’ - standard units for vegetation classification in Victoria, Department of Environment, Land,  
202 Water & Planning 2020) for each unique camera-trap site, totalling eight vegetation types. As rainforests are  
203 interspersed (primarily in low lying gullies) at fine-scales throughout wet and damp forests in the south-eastern  
204 Otway Ranges, we merged them together (hereafter referred to as ‘wet forests’). We then estimated predator  
205 activity across vegetation types using a hierarchical model specification: a global smoother for hour (i.e.,

206 average response) and group-level smoothers with shared wiggliness for the seven vegetation types ('model  
207 GS' detailed in Pedersen et al. 2019). We also fit a tensor product interaction term for hour and the human  
208 footprint index (Venter et al. 2016, 2018); as human footprint is known to impact animal activity patterns  
209 (Gaynor et al. 2018, Van Scyoc et al. 2023)

210 *2.3.3. Do feral cats avoid foxes in space or time? (model 3)*

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

220 To investigate changes in feral cat diel activity across the range of observed fox activity, we first quantified  
221 fox activity for each camera trap deployment as the total number of fox detections for the deployment  
222 divided by the number of survey days, to adjust for differences in survey duration (hereafter 'adjusted fox  
223 counts'). We modelled an interaction between hour and adjusted fox counts (as a thin plate regression spline  
224 with shrinkage - so complexity penalties could entirely remove this effect from the model if not supported),  
225 allowing cats to have nonlinear responses to both hour and adjusted fox counts. We fit separate tensor  
226 product interactions for each habitat type (using a 'by-variable' term). For a direct visual comparison to fox  
227 activity, we fit another fox model where a diel activity curve was estimated separately across each of the  
228 three habitat types.

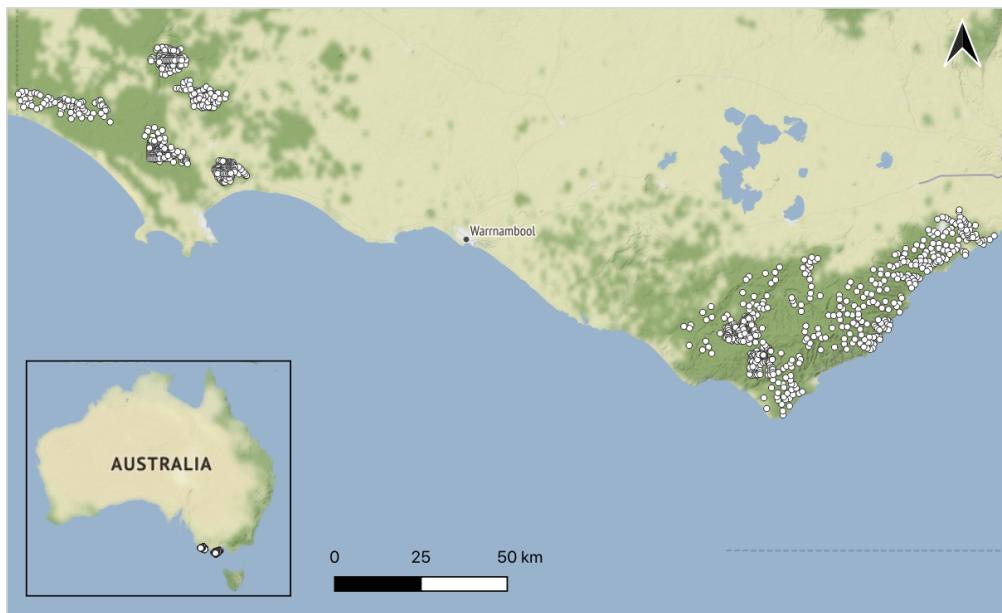


Figure 1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region ( $38^{\circ}05'54"S$   $141^{\circ}44'41"E$ ) is to the west and Otway Ranges ( $38^{\circ}57'82"S$   $141^{\circ}68'41"E$ ) to the east. Native vegetation 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..*

<sup>229</sup> **3. RESULTS**

<sup>230</sup> *3.1. Lethal suppression of foxes*

<sup>231</sup> In each model, there was a strong effect of poison fox-baiting on fox spatial activity, particularly in the  
<sup>232</sup> Glenelg region (Supporting Information Fig. S1b). Predicted fox counts on the response scale were reduced  
<sup>233</sup> by a factor of 12, 24, and 28 in the Glenelg region, as well as a factor of 13, 13, and 8 in the Otway Ranges,  
<sup>234</sup> for models 1, 2, and 3, respectively. For example, model 2 predicted fox counts in the Glenelg region to range  
<sup>235</sup> from 0.097 (95% CI: 0.077 - 0.122) in sites with no fox-baiting, to 0.004 (95% CI: 0.002 - 0.012) at sites with  
<sup>236</sup> the maximum poison-bait density; in the Otways ranging from 0.041 (95% CI: 0.033 - 0.05) - 0.008 (95% CI:  
<sup>237</sup> 0.003 - 0.020) across the gradient of poison-bait density.

<sup>238</sup> *3.2. How does predator diel activity patterns vary across geographic space? (model 1)*

<sup>239</sup> Predator activity varied considerably across space and throughout the 24-hour daily cycle, and there was  
<sup>240</sup> some variation in the predator diel activity patterns across space. On average, both predators showed similar  
<sup>241</sup> diel activity patterns, with peaks in activity around sunrise and sunset (i.e., crepuscular), although were  
<sup>242</sup> more likely to be active during the night than the day (Fig. 2i). On average, the main difference between the  
<sup>243</sup> species was that fox activity peaked just after sunset and they were less likely to be active during the day  
<sup>244</sup> than cats. Cats also tended to be more active at sunset relative to sunrise (Fig. 2i).

<sup>245</sup> The interaction between hourly and spatial smooths revealed deviations from marginal diel activity  
<sup>246</sup> pattern in space, particularly across the two regions, and within the Otway Ranges (Fig. 2). For example,  
<sup>247</sup> at midday, foxes were less active in the Glenelg region and more active across much of the Otway Ranges  
<sup>248</sup> (except for the north-east) than the average diel activity pattern. Relative to foxes, cats had slightly more  
<sup>249</sup> complex (i.e., wiggly) deviations in space from their average diel activity pattern. Most notably, cats were  
<sup>250</sup> less active during sunset and more active at midnight in the Otway Ranges relative to the Glenelg region  
<sup>251</sup> (Fig. 2).

<sup>252</sup> *3.3. How does vegetation type and human footprint affect predator activity patterns? (model 2)*

<sup>253</sup> Vegetation type had a strong influence on the spatial and diel activity patterns of foxes and cats, whereas  
<sup>254</sup> human footprint only affected fox spatial activity. Spatial levels of fox activity were similar across all

255 vegetation types, except wet forests where fox activity was considerably lower. Spatial cat activity was  
256 relatively more variable across vegetation types; lowest in heathy woodlands and highest in wet forests (Fig.  
257 3b). Diel activity patterns for foxes were similar across all vegetation type except wet forests; in wet forests,  
258 foxes were consistently active throughout the daily cycle (Fig. 3a). On the other hand, cats were mostly  
259 nocturnal (and most active) in wet forests, but largely crepuscular in all other vegetation types (Fig. 3a).

260 There was no evidence that human footprint affected diel activity patterns for either predator species;  
261 the interaction term between hour and human footprint index was removed from both models. Fox spatial  
262 activity increased linearly with the human footprint index (Supporting Information Fig. S2a), although  
263 human footprint did not impact cat spatial activity (the marginal effect of human footprint was also removed  
264 from the cat model).

265 *3.4. Do feral cats avoid foxes in space or time? (model 3)*

266 The model indicated that cats avoided foxes temporally rather than spatially (Fig. 4). Fox activity did  
267 not impact spatial cat activity in the Otway Ranges, whereas cat spatial activity slightly increased with  
268 adjusted fox counts in the Glenelg region.

269 Across all habitat types, feral cat diel activity patterns changed across gradients of fox activity (Fig.  
270 4). In the Glenelg region and Otway dry habitat types, feral cats had a nocturnal-crepuscular diel activity  
271 pattern where fox activity was low, but were most active during the day where fox activity was high. In  
272 contrast, in the wet forests of the Otway Ranges, feral cats were more strongly nocturnal when fox activity  
273 was high, avoiding dawn in particular.

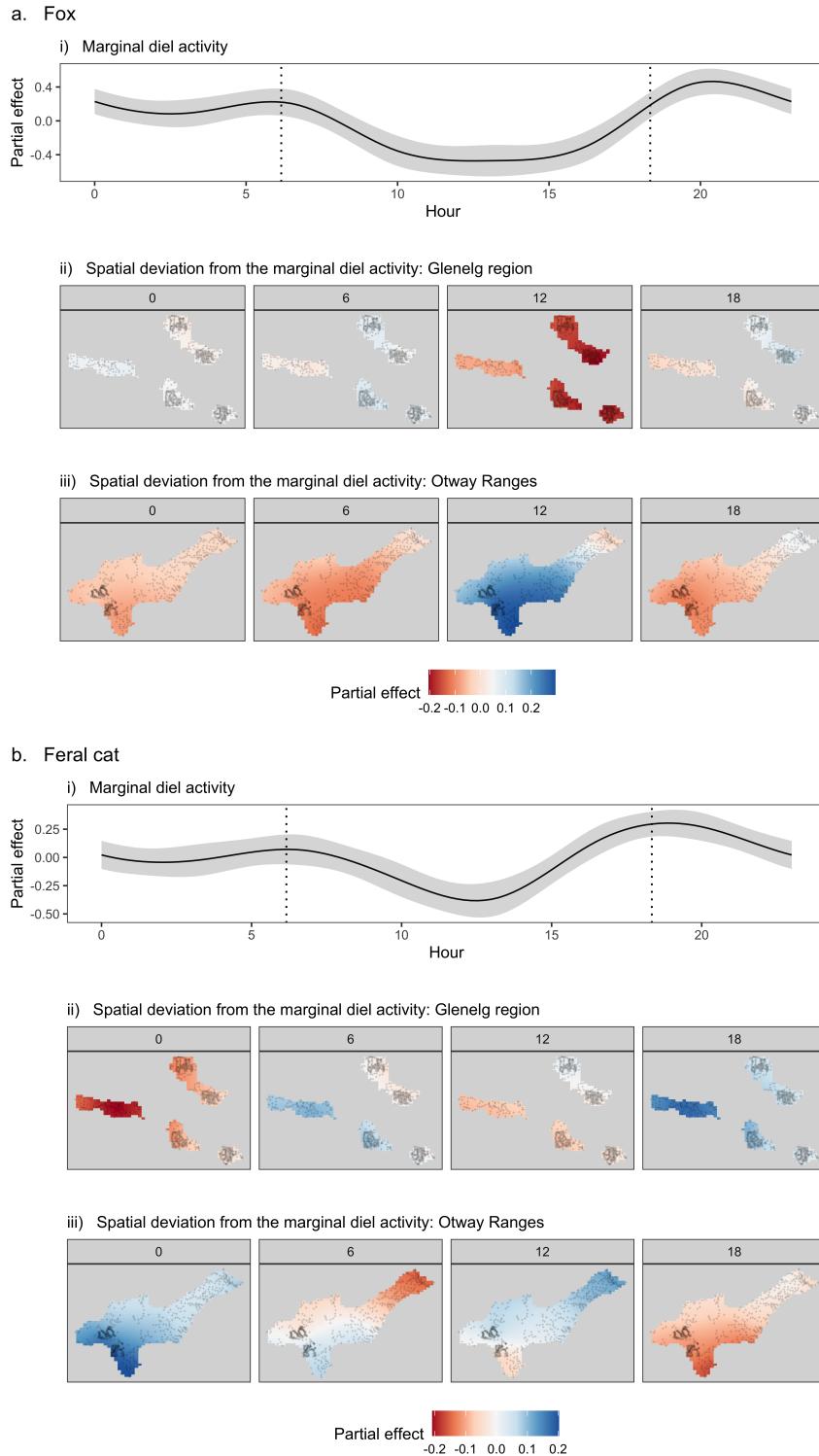


Figure 2: Marginal diel activity (i) and space-time interaction effect in the Glenelg region (ii) and Otway Ranges (iii) at midnight (0), sunrise (6), midday (12) and sunset (18) times for introduced red foxes *Vulpes vulpes* and feral cats *Felis catus*. These effects were estimated by a Generalised Additive Model with a tensor product interaction between spatial and hourly smooths, fit to camera-trap data ('model 1'). Dotted, vertical lines represent average sunrise and sunset times, shaded areas indicate 95% confidence intervals (i); black dots depict camera-trap sites (ii; iii).

a. Fox

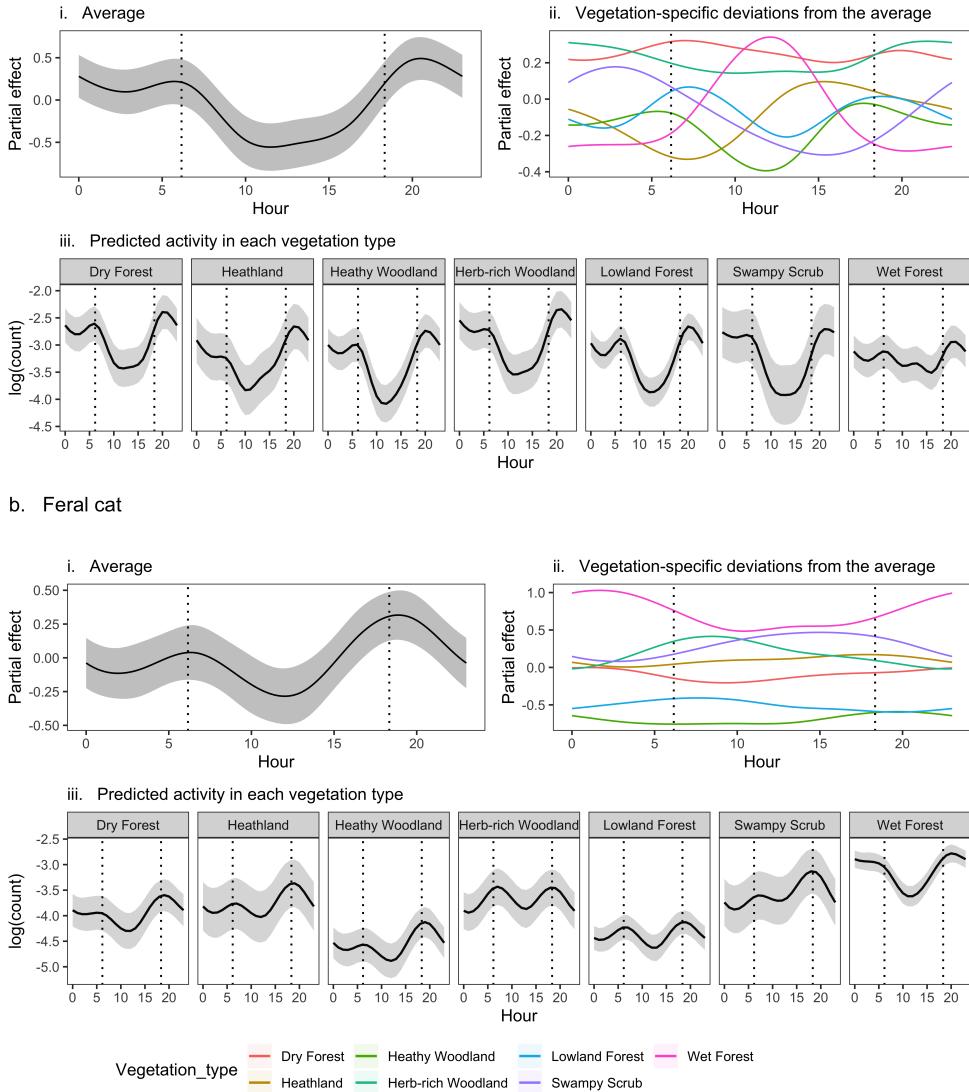


Figure 3: Red fox *Vulpes vulpes* (a) and feral cat *Felis catus* (b) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia. These effects were estimated by a hierarchical Generalised Additive Model with a global smoother for hour (i.e., average response) and group-level smoothers with shared wigginess for vegetation type (EVC groups), fit to camera-trap data ('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).

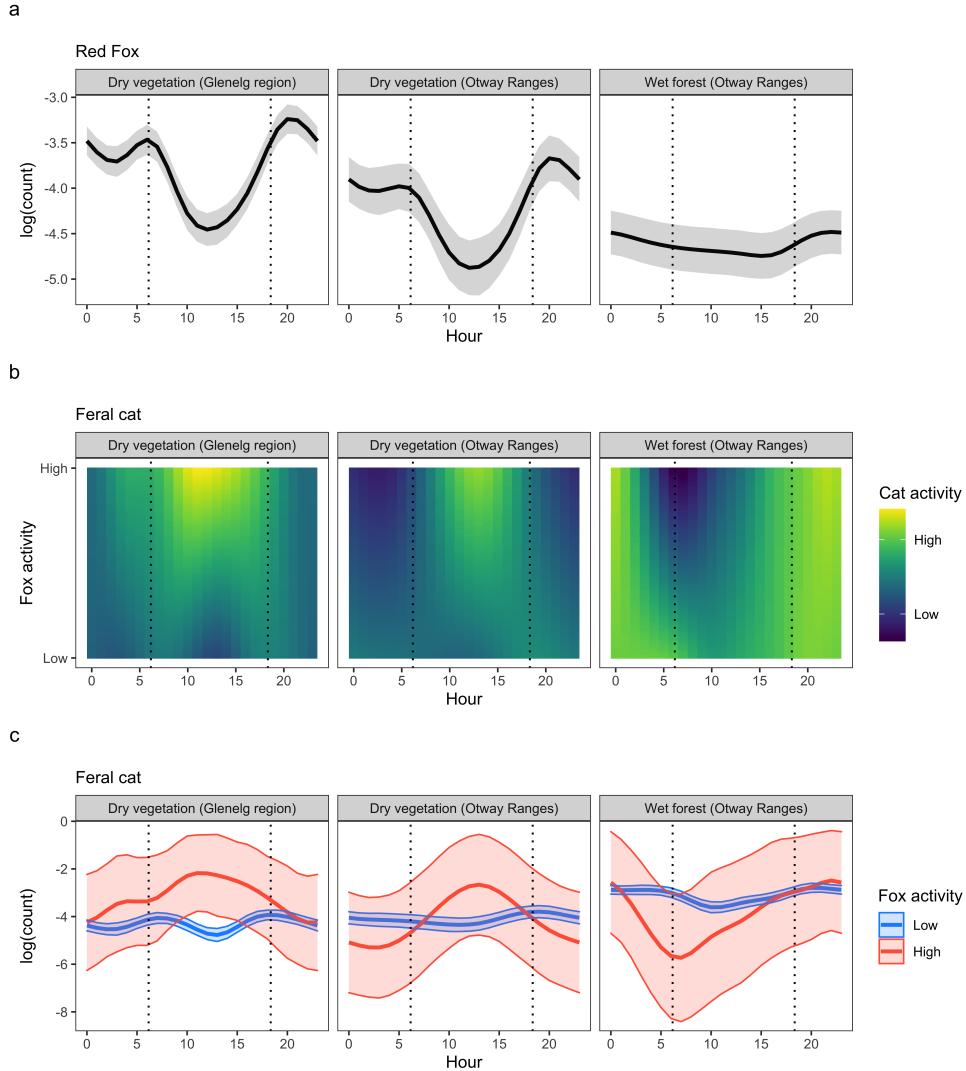


Figure 4: Red fox *Vulpes vulpes* diel activity patterns (a), as well as variation in feral cat *Felis catus* diel activity patterns in response to counts of 'independent' fox detections (log-transformed and survey effort adjusted) across each habitat type in south-west Victoria, Australia (b; c). Effects were estimated by a Generalised Additive Model with a tensor product interaction between hour (cyclical spine) and fox counts adjusted for survey length at each camera-trap ('fox activity'; 'model 3'), fit to camera-trap data. Panels B and C present the same model in two different ways: (b) cat diel activity across the entire continuum of fox activity, (c) cat diel activity patterns at the minimum and maximum fox activity, with associated 95% confidence intervals (shaded bands). 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).

<sup>274</sup> **4. DISCUSSION**

<sup>275</sup> A key question in ecological theory is whether animals are evolutionarily hardwired to occupy particular  
<sup>276</sup> temporal niches, or have circadian rhythms that are responsive to changing environmental conditions and  
<sup>277</sup> interactions with other species (Schoener 1974, Daan 1981, Lima and Dill 1990). Here we demonstrate that  
<sup>278</sup> diel activity patterns are not fixed, but vary across space based on landscape context and fear. In our study,  
<sup>279</sup> sympatric invasive predators had similar diel activity patterns when averaged across broad regions (i.e., high  
<sup>280</sup> circular overlap, as did Roshier and Carter 2021), but behaviours varied considerably within landscapes.  
<sup>281</sup> Foxes were nocturnal in dry habitat types, but showed little variation in activity through the daily cycle  
<sup>282</sup> in wet forests (Fig. 3a). In contrast, cats were mostly nocturnal in wet forests but crepuscular in dry  
<sup>283</sup> vegetation types (Fig. 3b). Within broad habitat types, cats altered their diel activity patterns at sites  
<sup>284</sup> with higher fox activity towards less-risky times of day (i.e., times when fox activity was lower), however we  
<sup>285</sup> found no signs of foxes suppressing cat spatial activity (Fig. 4). Control programs that reduce invasive fox  
<sup>286</sup> activity may therefore shift cat diel activity patterns, which in turn may alter cat impacts on native prey  
<sup>287</sup> species. Quantifying changes in diel activity patterns provides important context for understanding species  
<sup>288</sup> interactions, which is key for effective ecosystem management (Gaynor et al. 2021).

<sup>289</sup> Shifting diel activity patterns may facilitate spatial coexistence of dominant and subordinate species  
<sup>290</sup> (Carothers and Jakšić 1984). For cats, altering diel activity patterns to less-preferred times of day may  
<sup>291</sup> be worthwhile to persist in high-quality habitat. There have been an increasing number of studies which  
<sup>292</sup> document slight changes in diel activity peaks of subordinate species in response to dominant predators,  
<sup>293</sup> but few studies have demonstrated predator-induced reversals in diel activity (Kronfeld-Schor and Dayan  
<sup>294</sup> 2003). Notably, ship rats *Rattus norvegicus* were also found to switch from nocturnal to diurnal behaviour in  
<sup>295</sup> response to fox activity (Fenn and Macdonald 1995) and a similar nocturnal-diurnal shift was observed in  
<sup>296</sup> American mink *Neovison vison* following the recolonisation of native predators (Harrington et al. 2009). Our  
<sup>297</sup> study is particularly unique in that we replicated this behaviour across two separate regions with experimental  
<sup>298</sup> manipulation, although there was considerable uncertainty in cat diel activity patterns where fox activity  
<sup>299</sup> was highest (because there were fewer sites with high fox activity relative to low).

<sup>300</sup> For cats in our study, a switch to diurnal behaviour where fox activity was high in the dry vegetation  
<sup>301</sup> types may have been facilitated by the higher abundance of reptiles in these habitat types relative to wet  
<sup>302</sup> forests (which are mostly diurnal, Woinarski et al. 2018). At wet forest sites with high fox activity, cats

303 concentrated their activity away from sunrise and sunset towards midnight, despite a diurnal shift appearing  
304 to similarly reduce the risk of a fox encounter. In this situation, we expect becoming more nocturnal to be  
305 favourable over a diurnal shift because this is when small mammals are active and cats would be least visible  
306 to foxes (cats here mostly had black or grey coats, Rees et al. 2023a). Spatial fox activity was twice as low  
307 in the wet forests relative to dry habitat types, and so cats were likely under less pressure to radically alter  
308 their diel activity patterns. Understanding how these potential avoidance behaviours impacts native prey is  
309 a key research priority to improve invasive predator management.

310 Cats appeared to avoid foxes in time, but we saw no evidence of spatial avoidance (i.e. no fine-scale  
311 negative association between fox and cat spatial activity. In fact, there was some evidence that cat and  
312 fox spatial activity was positively correlated in the Glenelg region, suggesting temporal partitioning may  
313 facilitate predator co-abundance in quality habitat. Nonetheless, cats may have still avoided foxes spatially,  
314 but transiently on the scale of hours to days, or at finer spatial scales than most camera-trap studies can  
315 detect (and which telemetry studies can highlight, e.g., Kohl et al. 2019, Smith et al. 2019). Short-term  
316 spatial avoidance is quite plausible given foxes mark territories using scats and odours, which cats could  
317 tangibly associate with high risk shortly after. Subordinate predators may prefer temporal avoidance of  
318 dominant predators (changing diel patterns or transient site avoidance) over longer-term site avoidance when  
319 both species have similar resource requirements and share many prey species.

320 Many species increase nightly activity to avoid humans (Gaynor et al. 2018, Van Scyoc et al. 2023),  
321 however we effect of human footprint on either predator species on our study. This is somewhat unsurprising  
322 given there was little variation in human activity among our sites; we studied predators within rugged  
323 conservation reserves largely free from human pressures (our camera-trap sites encompassed only the lower  
324 32% of the total human footprint index range). On the other hand, foxes within our study region often select  
325 for human-modified features more during night than day (Hradsky et al. 2017a). Subordinate predators  
326 may still prefer to avoid dominant (animal) predators over humans, even when this decision leads to higher  
327 mortality rates (Prugh et al. 2023).

328 A distinction of our study from others is that we modelled potential avoidance behaviours in a simple  
329 predator guild, where dominant predator activity was artificially manipulated (suppressed by up to 21-fold).  
330 The simple predator guild removes bias from unmodelled impacts of other predators in the system (Levi and  
331 Wilmers 2012). Artificial manipulation of the dominant predator also reduces potential bias from differences

332 in niche preferences between the predator species. We also included replication across different habitat  
333 types. However, because our study did not consider associations with prey species, we cannot distinguish  
334 whether changes in cat diel activity patterns were the result of direct fox avoidance or indirect associations  
335 with shared prey. For example, low fox activity may promote the availability of a preferred shared prey  
336 species with a diel pattern which differs from those of cats on average, and as a result, cats might shift  
337 diel activity patterns at sites with low fox activity to more closely match those of the more abundant prey  
338 species. We would expect introduced European rabbits *Oryctolagus cuniculus* and hares *Lepus europaeus*  
339 (which are diurnal) to be particularly likely to induce such a response in dry vegetation types (McGregor et  
340 al. 2020, Stobo-Wilson et al. 2020), however, rabbits and hares are rare within the natural vegetation of  
341 the landscapes we surveyed (only ever being detected at 40 of 1,232 sites) and there is little evidence that  
342 predation by foxes suppresses rabbit populations (Norbury and Jones 2015, Scroggie et al. 2018).

343 Flexible antipredator behaviours make evolutionary sense, but have been rarely demonstrated in terms of  
344 spatiotemporal predator avoidance, because this often requires manipulative experiments or at least more  
345 complicated models (although, see Relyea 2003, Brown et al. 2013, Cunningham et al. 2019). Our study  
346 demonstrates that GAMs offer a powerful tool for modelling continuous shifts in animal activity across  
347 both space and time, capable of capturing complex interactions and sharing information across categorical  
348 variables. We are only aware of one study which allowed animal diel activity to interact with predation risk  
349 as a continuous variable in a GAM (although without allowing for nonlinear shifts via a tensor product or  
350 jointly considering spatial activity, Cunningham et al. 2019). Further, complexity penalties are particularly  
351 beneficial in assessing spatiotemporal responses, because they are less prone to spurious estimates from small  
352 sample sizes or noisy data, and allow multiple hypotheses to be tested within one model without the need for  
353 ad-hoc significance testing (e.g., running a separate model for each scenario and comparing with Information  
354 Criteria). For example, our model specification allowed cats to respond to fox activity with (a) nonlinear  
355 shifts in both spatial and diel activity (as was observed in the Glenelg region), (b) nonlinear shifts in spatial  
356 but not diel activity, (c) nonlinear shifts in diel but not spatial activity (as was observed in both habitat  
357 types of the Otway Ranges), as well as their respective linear counterparts and also different linear-nonlinear  
358 combinations of the first scenario ('model 3'). **ADD CLOSER**

359 The alternative approach of simply comparing average diel activity overlap between two species (Ridout  
360 and Linkie 2009) would have been misleading for two reasons. Firstly, predator diel activity patterns  
361 varied 'naturally' across heterogeneous landscapes (requiring avoidance to be tested in wet forests and

362 dry vegetation types separately, Fig. 3). Secondly, dominant predator temporal avoidance strategies were  
363 not consistently employed, but depended on spatial dominant predator activity and habitat type (Fig. 4).  
364 Despite their underlying statistical complexity, GAMs in the ‘mgcv’ R-package are straightforward to fit.  
365 Our GAM framework for modelling spatiotemporal activity can be used on any species with time-stamped  
366 detections, including datasets with categorical or continuous covariates and hierarchical groupings. However,  
367 like many other spatiotemporal approaches such as time-to-encounter models, a key limitation is that our  
368 GAM approach did not separate the observation processes from the state process. Integrating GAM-like  
369 functions into recently developed multispecies spatiotemporal models (e.g., Kellner et al. 2022) would be  
370 highly advantageous.

371 Animal diel activity patterns can be complex, varying across space, habitat types and threat-levels  
372 (McCann et al. 2017). Despite telling an important story about how animals interact with each other and the  
373 environment, detection times are commonly discarded from statistical analyses of camera-trap data. When  
374 considered, diel activity patterns are predominantly estimated at the population-level, overlooking finer-scale  
375 behaviours that can affect fitness, survival and ecosystem-impacts. Our results demonstrate the importance  
376 of (a) considering diel activity in regards to species interactions, (b) modelling changes in animal behaviour  
377 rather than overlap with other species, and (c) testing avoidance behaviours within a joint spatiotemporal  
378 framework. Our study adds to the growing body of evidence that dominant predators may cause fear which  
379 is powerful enough to reverse the diel activity patterns of subordinate species (Kronfeld-Schor and Dayan  
380 2003), and crucially, demonstrates that these effects are habitat-dependent.

381 REFERENCES

- 382 Ait Kaci Azzou, S. et al. 2021. A sparse observation model to quantify species distributions and their overlap  
383 in space and time. - *Ecography* 44: 928–940.
- 384 Algar, D. and Burrows, N. 2004. Feral cat control research: Western shield review–february 2003. -  
385 Conservation Science Western Australia in press.
- 386 Allen, M. C. et al. 2022. Fear of predators in free-living wildlife reduces population growth over generations.  
387 - *Proceedings of the National Academy of Sciences* 119: e2112404119.
- 388 Basille, M. et al. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution.  
389 - *Ecology* 96: 2622–2631.
- 390 Bivand, R. and Lewin-Koh, N. 2021. Maptools: Tools for handling spatial objects.
- 391 Brown, J. S. et al. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. -  
392 *Journal of Mammalogy* 80: 385–399.
- 393 Brown, G. E. et al. 2013. Phenotypically plastic neophobia: A response to variable predation risk. -  
394 *Proceedings of the Royal Society B: Biological Sciences* 280: 20122712.
- 395 Carothers, J. H. and Jakšić, F. M. 1984. Time as a niche difference: The role of interference competition. -  
396 *Oikos*: 403–406.
- 397 Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. - *Trends in  
398 Ecology & Evolution* 23: 194–201.
- 399 Cunningham, C. X. et al. 2019. Temporal partitioning of activity: Rising and falling top-predator abundance  
400 triggers community-wide shifts in diel activity. - *Ecography* 42: 2157–2168.
- 401 Daan, S. 1981. Adaptive daily strategies in behavior. - In: *Biological rhythms*. Springer Publishing, pp.  
402 275–298.
- 403 Davies, A. B. et al. 2021. Spatial heterogeneity facilitates carnivore coexistence. - *Ecology* 102: e03319.
- 404 Department of Environment, Land, Water & Planning 2020. Bioregions and EVC Benchmarks.
- 405 Doherty, T. S. and Ritchie, E. G. 2017. Stop jumping the gun: A call for evidence-based invasive predator  
406 management. - *Conservation Letters* 10: 15–22.
- 407 Doherty, T. S. et al. 2016. Invasive predators and global biodiversity loss. - *Proceedings of the National  
408 Academy of Sciences* 113: 11261–11265.
- 409 Estes, J. A. et al. 2011. Trophic downgrading of planet earth. - *Science* 333: 301–306.
- 410 Fancourt, B. A. et al. 2019. Do introduced apex predators suppress introduced mesopredators? A multiscale  
411 spatiotemporal study of dingoes and feral cats in Australia suggests not. - *Journal of Applied Ecology* 56:

- 412        2584–2595.
- 413    Fenn, M. G. and Macdonald, D. W. 1995. Use of middens by red foxes: Risk reverses rhythms of rats. -  
414        Journal of Mammalogy 76: 130–136.
- 415    Fleming, P. A. et al. 2022. Distinctive diets of eutherian predators in australia. - Royal Society Open Science  
416        in press.
- 417    Frey, S. et al. 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap  
418        data: Challenges and opportunities. - Remote Sensing in Ecology and Conservation 3: 123–132.
- 419    Gaynor, K. M. et al. 2018. The influence of human disturbance on wildlife nocturnality. - Science 360:  
420        1232–1235.
- 421    Gaynor, K. M. et al. 2019. Landscapes of fear: Spatial patterns of risk perception and response. - Trends in  
422        Ecology & Evolution 34: 355–368.
- 423    Gaynor, K. M. et al. 2021. An applied ecology of fear framework: Linking theory to conservation practice. -  
424        Animal Conservation 24: 308–321.
- 425    Glen, A. S. and Dickman, C. R. 2005. Complex interactions among mammalian carnivores in Australia, and  
426        their implications for wildlife management. - Biological Reviews 80: 387–401.
- 427    Harmsen, B. J. et al. 2009. Spatial and Temporal Interactions of Sympatric Jaguars (*Panthera onca*) and  
428        Pumas (*Puma concolor*) in a Neotropical Forest. - Journal of Mammalogy 90: 612–620.
- 429    Harrington, L. A. et al. 2009. The impact of native competitors on an alien invasive: Temporal niche shifts  
430        to avoid interspecific aggression. - Ecology 90: 1207–1216.
- 431    Hartig, F. 2020. DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models.
- 432    Hradsky, B. A. et al. 2017a. Human-modified habitats facilitate forest-dwelling populations of an invasive  
433        predator, *Vulpes vulpes*. - Scientific Reports 7: 1–12.
- 434    Hradsky, B. A. et al. 2017b. Bayesian networks elucidate interactions between fire and other drivers of  
435        terrestrial fauna distributions. - Ecosphere 8: e01926.
- 436    Hunter, D. O. et al. 2018. Not all predators are equal: A continent-scale analysis of the effects of predator  
437        control on Australian mammals. - Mammal Review 48: 108–122.
- 438    Iannarilli, F. et al. 2019. Using lorelograms to measure and model correlation in binary data: Applications  
439        to ecological studies. - Methods in Ecology and Evolution 10: 2153–2162.
- 440    Kauffman, M. J. et al. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey  
441        system. - Ecology Letters 10: 690–700.
- 442    Kellner, K. F. et al. 2022. A two-species occupancy model with a continuous-time detection process reveals

- 443 spatial and temporal interactions. - *Journal of Agricultural, Biological and Environmental Statistics* 27:  
444 321–338.
- 445 Kohl, M. T. et al. 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat? -  
446 *Ecology Letters* 22: 1724–1733.
- 447 Kronfeld-Schor, N. and Dayan, T. 2003. Partitioning of time as an ecological resource. - *Annual Review of  
448 Ecology, Evolution, and Systematics* 34: 153–181.
- 449 Levi, T. and Wilmers, C. C. 2012. Wolves–coyotes–foxes: A cascade among carnivores. - *Ecology* 93: 921–929.
- 450 Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: A review and  
451 prospectus. - *Canadian Journal of Zoology* 68: 619–640.
- 452 Lima, S. L. and Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: The  
453 predation risk allocation hypothesis. - *The American Naturalist* 153: 649–659.
- 454 McCann, N. P. et al. 2017. Temporal scaling in analysis of animal activity. - *Ecography* 40: 1436–1444.
- 455 McGregor, H. et al. 2020. The short-term response of feral cats to rabbit population decline: Are alternative  
456 native prey more at risk? - *Biological Invasions* 22: 799–811.
- 457 Miller, D. L. and Wood, S. N. 2014. Finite area smoothing with generalized distance splines. - *Environmental  
458 and Ecological Statistics* 21: 715–731.
- 459 Molsher, R. et al. 2017. Mesopredator management: Effects of red fox control on the abundance, diet and  
460 use of space by feral cats. - *PLoS One* 12: e0168460.
- 461 Moseby, K. et al. 2011. The use of poison baits to control feral cats and red foxes in arid South Australia II.  
462 Bait type, placement, lures and non-target uptake. - *Wildlife Research* 38: 350–358.
- 463 Niedballa, J. et al. 2019. Assessing analytical methods for detecting spatiotemporal interactions between  
464 species from camera trapping data. - *Remote Sensing in Ecology and Conservation* 5: 272–285.
- 465 Norbury, G. and Jones, C. 2015. Pests controlling pests: Does predator control lead to greater European  
466 rabbit abundance in Australasia? - *Mammal Review* 45: 79–87.
- 467 Parsons, A. W. et al. 2022. The effect of urbanization on spatiotemporal interactions between gray foxes and  
468 coyotes. - *Ecosphere* 13: e3993.
- 469 Pedersen, E. J. et al. 2019. Hierarchical generalized additive models in ecology: An introduction with mgcv.  
470 - *PeerJ* 7: e6876.
- 471 Preisser, E. L. et al. 2005. Scared to death? The effects of intimidation and consumption in predator–prey  
472 interactions. - *Ecology* 86: 501–509.
- 473 Prugh, L. R. et al. 2009. The rise of the mesopredator. - *Bioscience* 59: 779–791.

- 474 Prugh, L. R. et al. 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. -  
475 Science 380: 754–758.
- 476 R Core Team 2020. R: A language and environment for statistical computing. - R Foundation for Statistical  
477 Computing.
- 478 Reddiex, B. et al. 2007. Control of pest mammals for biodiversity protection in Australia. I. Patterns of  
479 control and monitoring. - Wildlife Research 33: 691–709.
- 480 Rees, M. W. et al. 2023a. Mesopredator release among invasive predators: Controlling red foxes can increase  
481 feral cat density and alter their behaviour. - Journal of Applied Ecology 60: 1100–1114.
- 482 Rees, M. W. et al. 2023b. Data from: Mesopredator release among invasive predators: Controlling red foxes  
483 can increase feral cat density and alter their behaviour.
- 484 Relyea, R. A. 2003. Predators come and predators go: The reversibility of predator-induced traits. - Ecology  
485 84: 1840–1848.
- 486 Ridout, M. S. and Linkie, M. 2009. Estimating overlap of daily activity patterns from camera trap data. -  
487 Journal of Agricultural, Biological, and Environmental Statistics 14: 322–337.
- 488 Risbey, D. A. et al. 1997. Control of feral cats for nature conservation. I. Field tests of four baiting methods.  
489 - Wildlife Research 24: 319–326.
- 490 Robley, A. et al. 2014. Long-term and large-scale control of the introduced red fox increases native mammal  
491 occupancy in Australian forests. - Biological Conservation 180: 262–269.
- 492 Robley, A. et al. 2019. The Otway Ark: response of predators and native species 2016–2018.
- 493 Robley, A. et al. 2020. Glenelg Ark 2005–2019: long-term predator and native mammal response to predator  
494 control.
- 495 Roshier, D. A. and Carter, A. 2021. Space use and interactions of two introduced mesopredators, european  
496 red fox and feral cat, in an arid landscape. - Ecosphere 12: e03628.
- 497 Schmitz, O. J. et al. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. - Ecology  
498 Letters 7: 153–163.
- 499 Schoener, T. W. 1974. The compression hypothesis and temporal resource partitioning. - Proceedings of the  
500 National Academy of Sciences 71: 4169–4172.
- 501 Scroggie, M. P. et al. 2018. Invasive prey controlling invasive predators? European rabbit abundance does  
502 not determine red fox population dynamics. - Journal of Applied Ecology 55: 2621–2631.
- 503 Simpson, G. L. 2021. gratia: Graceful 'ggplot'-based graphics and other functions for GAMs fitted using  
504 'mgcv'.

- 505 Smith, J. A. et al. 2019. Integrating temporal refugia into landscapes of fear: Prey exploit predator downtimes  
506 to forage in risky places. - *Oecologia* 189: 883–890.
- 507 Soulé, M. E. et al. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban  
508 habitat islands. - *Conservation Biology* 2: 75–92.
- 509 Stobo-Wilson, A. M. et al. 2020. Management of invasive mesopredators in the Flinders Ranges, South  
510 Australia: Effectiveness and implications. - *Wildlife Research* 47: 720–730.
- 511 Suraci, J. P. et al. 2016. Fear of large carnivores causes a trophic cascade. - *Nature communications* 7: 1–7.
- 512 Suraci, J. P. et al. 2022. Beyond spatial overlap: Harnessing new technologies to resolve the complexities of  
513 predator-prey interactions. - *Oikos*: e09004.
- 514 Swan, M. et al. 2015. Predicting faunal fire responses in heterogeneous landscapes: The role of habitat  
515 structure. - *Ecological Applications* 25: 2293–2305.
- 516 Van Scoyoc, A. et al. 2023. The influence of human activity on predator-prey spatiotemporal overlap. - *The*  
517 *Journal of Animal Ecology* 92: 1124—1134.
- 518 Vazquez, C. et al. 2019. Comparing diel activity patterns of wildlife across latitudes and seasons: Time  
519 transformations using day length. - *Methods in Ecology and Evolution* 10: 2057–2066.
- 520 Venter, O. et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for  
521 biodiversity conservation. - *Nature communications* 7: 12558.
- 522 Venter, O. et al. 2018. Last of the wild project, version 3 (LWP-3): 2009 human footprint, 2018 release.
- 523 Wayne, A. F. et al. 2017. Recoveries and cascading declines of native mammals associated with control of an  
524 introduced predator. - *Journal of Mammalogy* 98: 489–501.
- 525 Wickham, H. 2016. *ggplot2: Elegant graphics for data analysis*. - Springer-Verlag New York.
- 526 Willems, E. P. and Hill, R. A. 2009. Predator-specific landscapes of fear and resource distribution: Effects  
527 on spatial range use. - *Ecology* 90: 546–555.
- 528 Wirsing, A. J. et al. 2021. The context dependence of non-consumptive predator effects. - *Ecology Letters*  
529 24: 113–129.
- 530 Woinarski, J. C. Z. et al. 2015. Ongoing unraveling of a continental fauna: Decline and extinction of  
531 Australian mammals since European settlement. - *Proceedings of the National Academy of Sciences* 112:  
532 4531–4540.
- 533 Woinarski, J. C. Z. et al. 2018. How many reptiles are killed by cats in Australia? - *Wildlife Research* 45:  
534 247–266.
- 535 Wood, S. N. 2017. *Generalized additive models: An introduction with r*. - CRC press.

<sup>536</sup> Wooster, E. I. et al. 2022. Predator protection dampens the landscape of fear. - Oikos: e09059.

<sup>537</sup> SUPPORTING INFORMATION

Table S1: Summary of experimental camera-trap survey designs around fox control in south-west Victoria, Australia.

Region	Source	Block	Treatment	Surveys	Year from	Year to	Sites	Min. spacing (m)	Mean spacing (m)	Max spacing (m)
Glenelg	Glenelg Ark	Annya	non-treatment	7	2013	2019	40	683	988	1509
Glenelg	Glenelg Ark	Hotspur	non-treatment	7	2013	2019	40	335	817	1319
Glenelg	Glenelg Ark	LGNP N	non-treatment	7	2013	2019	40	275	687	1828
Glenelg	Glenelg Ark	Cobboboonee	treatment	7	2013	2019	40	362	982	2351
Glenelg	Glenelg Ark	LGNP S	treatment	7	2013	2019	40	502	1120	2686
Glenelg	Glenelg Ark	Mt Clay	treatment	7	2013	2019	40	178	607	1068
Glenelg	MWR PhD	Annya	non-treatment	1	2018	2018	110	307	469	623
Glenelg	MWR PhD	Hotspur	non-treatment	1	2018	2018	99	242	428	594
Glenelg	MWR PhD	Cobboboonee	treatment	1	2018	2018	110	274	452	509
Glenelg	MWR PhD	Mt Clay	treatment	1	2018	2018	106	209	445	671
Otways	MWR PhD	North	non-treatment	3	2017	2019	104	238	434	714
Otways	MWR PhD	South	treatment	3	2017	2019	91	86	436	717
Otways	Otway Ark	FA4	non-treatment	3	2017	2019	73	634	1560	4150
Otways	Otway Ark	FA1	treatment	3	2016	2018	80	277	996	1825
Otways	Otway Ark	FA2	treatment	3	2016	2018	80	638	938	1865
Otways	Otway Ark	FA3	treatment	3	2016	2018	140	739	1491	3514

Table S2: 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 S3: Generalised additive model summaries for invasive predator spatiotemporal activity in south-west Victoria, Australia.

Species	Model	EDF	dev.expl	r.sq
fox	1_spatial	98.0605	0.0657	0.0137
fox	2_vegetation_type	752.9670	0.3496	0.1155
fox	3_habitat_type	757.1467	0.3486	0.1138
cat	1_spatial	78.4323	0.1110	0.0367
cat	2_vegetation_type	566.7735	0.2301	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.

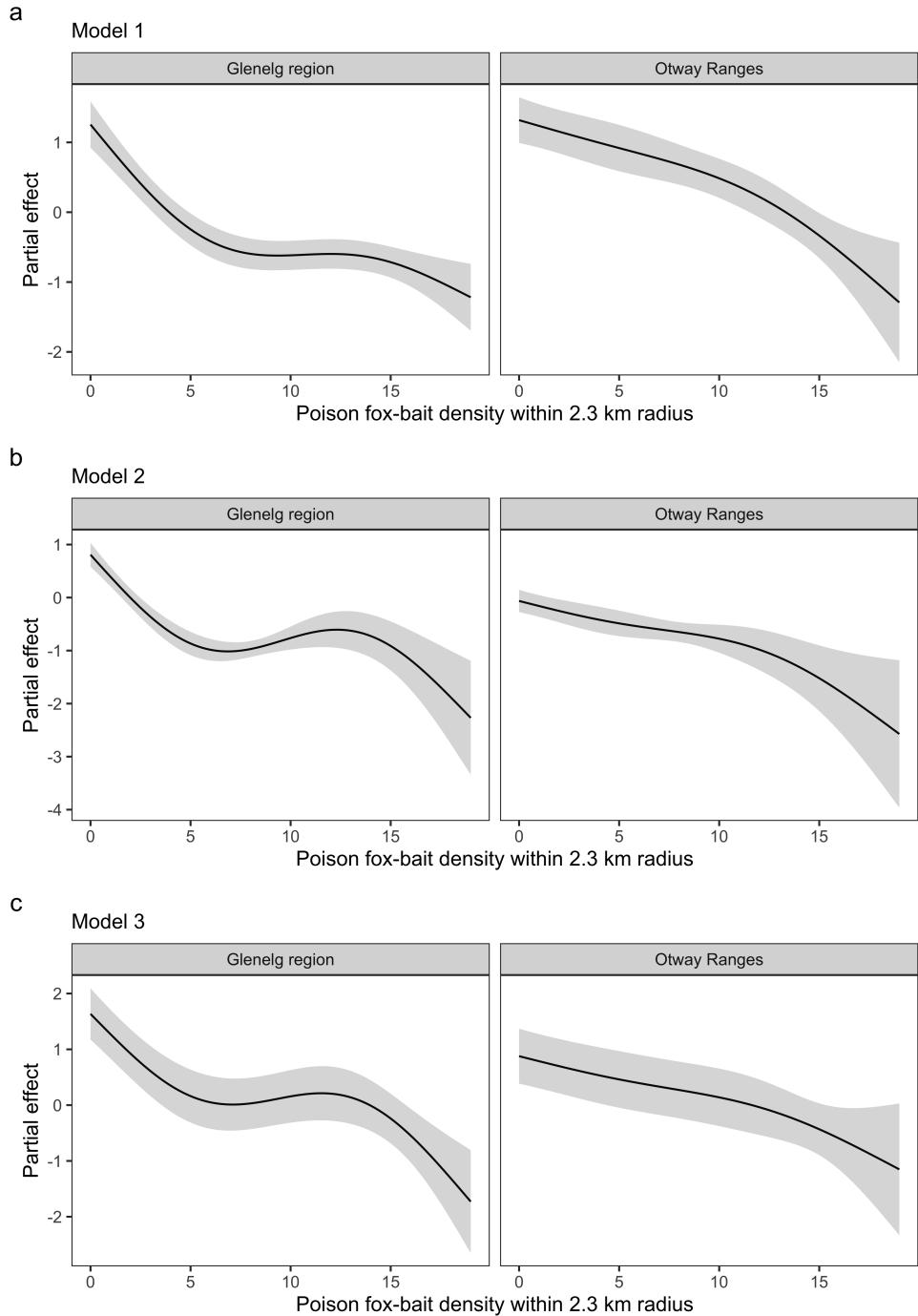


Figure S1: Effects of 1080 poison-bait density on the spatial activity of red foxes *Vulpes vulpes*, derived from each model (model 1: spatial, model 2: vegetation group / human footprint, model 3: habitat type). Shaded areas indicate 95% confidence intervals.

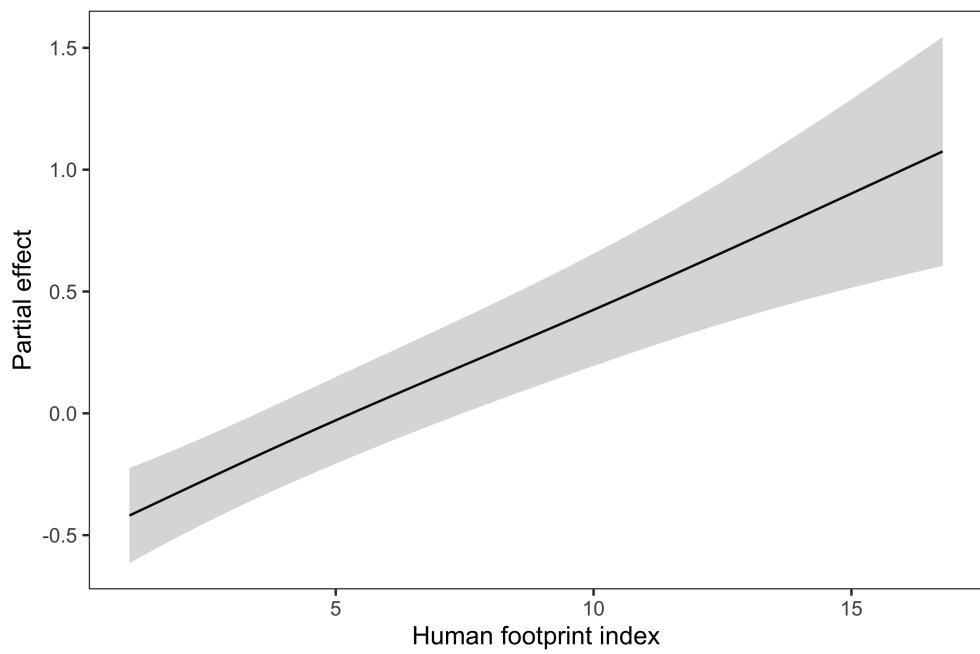


Figure S2: Effects human footprint index on the spatial activity of red foxes *Vulpes vulpes*. (model 2). The interaction effect of human foot print and fox diel activity pattern was removed from this model. Both the marginal and interactive effect of human footprint was removed for feral cats *Felis catus*). Shaded areas indicate 95% confidence intervals.