

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

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¹ ABSTRACT

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

²⁷ **1. INTRODUCTION**

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

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

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

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

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

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

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

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

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

¹⁰⁰ **2. MATERIALS AND METHODS**

¹⁰¹ *2.1. Study area and camera-trapping*

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

¹¹² *2.1.1. Glenelg region*

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

¹²⁴ *2.1.2. Otway Ranges*

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

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

140 *2.1.3. Camera-trap set-ups*

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

151 *2.2. Data preparation*

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

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

2.3. Generalised additive models

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

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

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

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

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

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

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

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

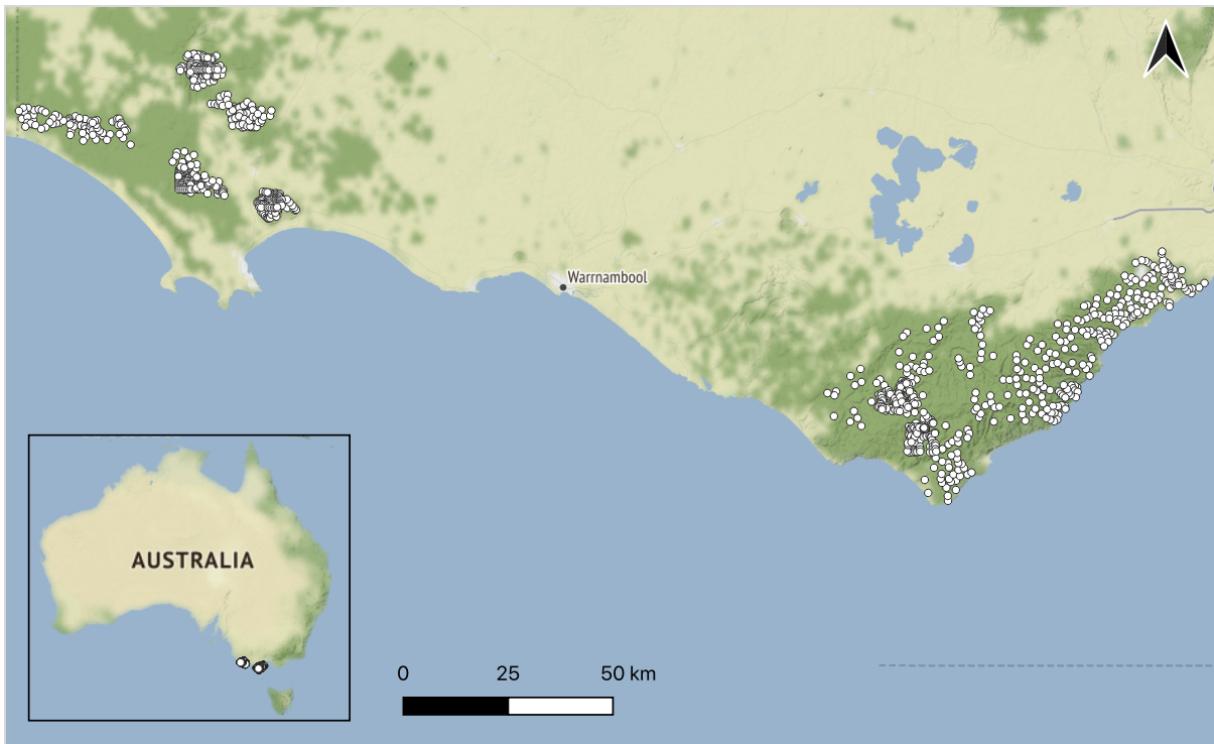


Figure 1: Locations of our study regions in south-west Victoria, Australia. The grids of camera-traps are denoted by white dots. The Glenelg region is to the west and Otway region to the east. Native vegetation is indicated by dark green, with hill shading. *Map tiles by Stamen Design, under CC BY 3.0,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

216 **3. RESULTS**

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

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

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

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

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

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

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

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

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

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

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

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

Otway Ranges: Red fox

Space-time interaction effect (excluding marginal effects)

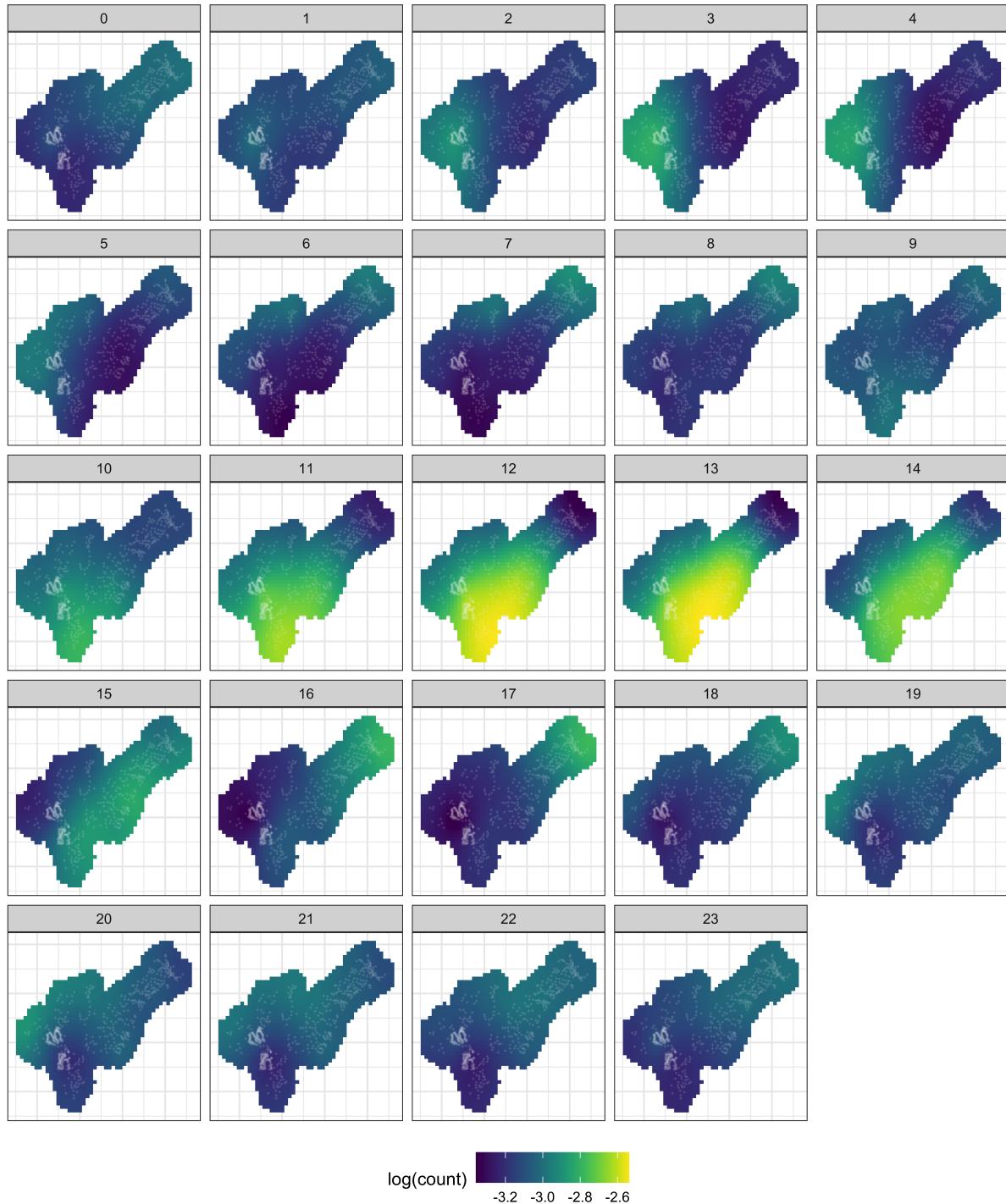


Figure 2: Interaction effect of space-time on red fox *Vulpes vulpes* activity across each hour of the day (0 - 23) in the Otway Ranges, Australia (model 1), as an example. Corresponding plots for feral cats *Felis catus* in this region, as well as both predators in the Glenelg region are provided in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

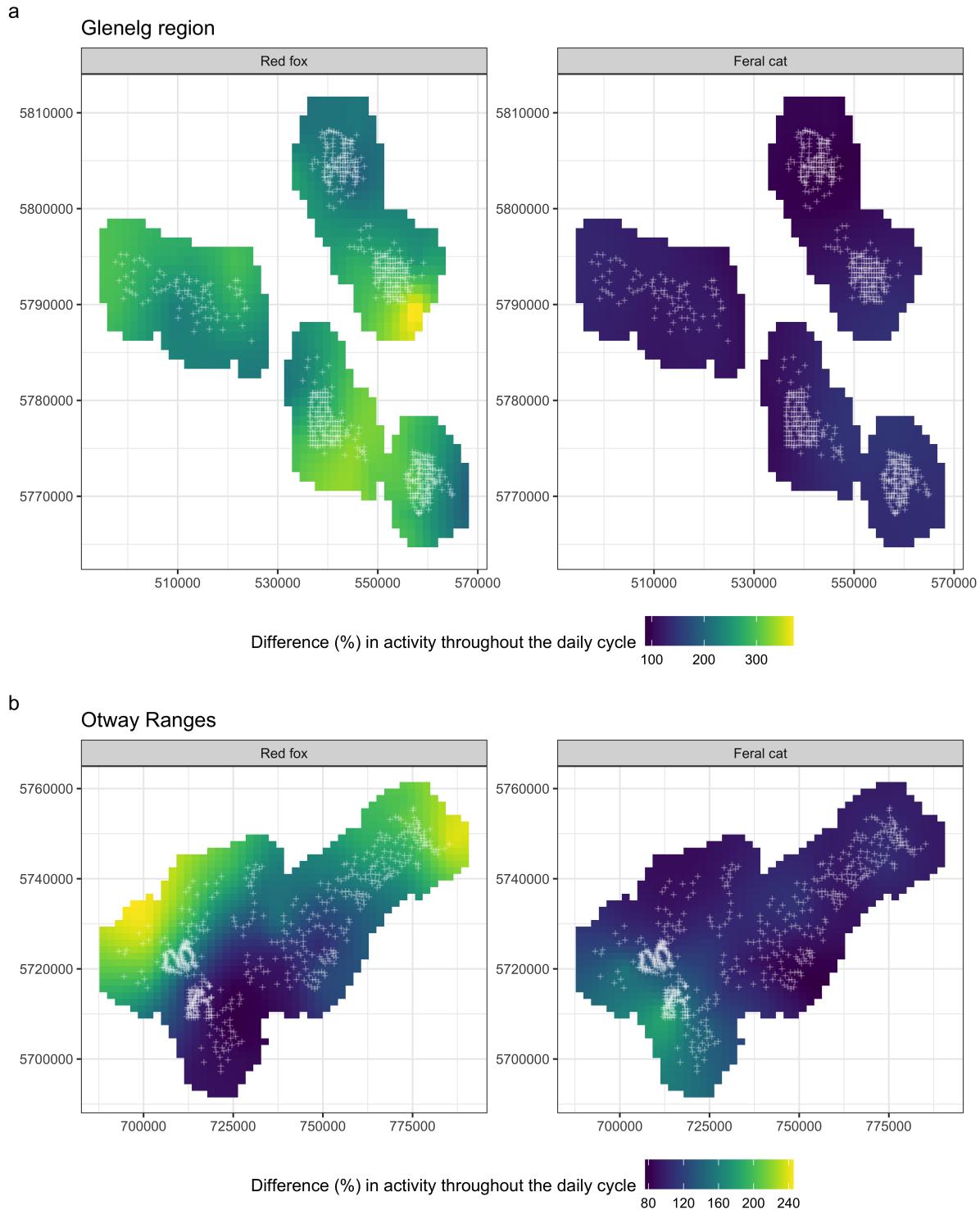
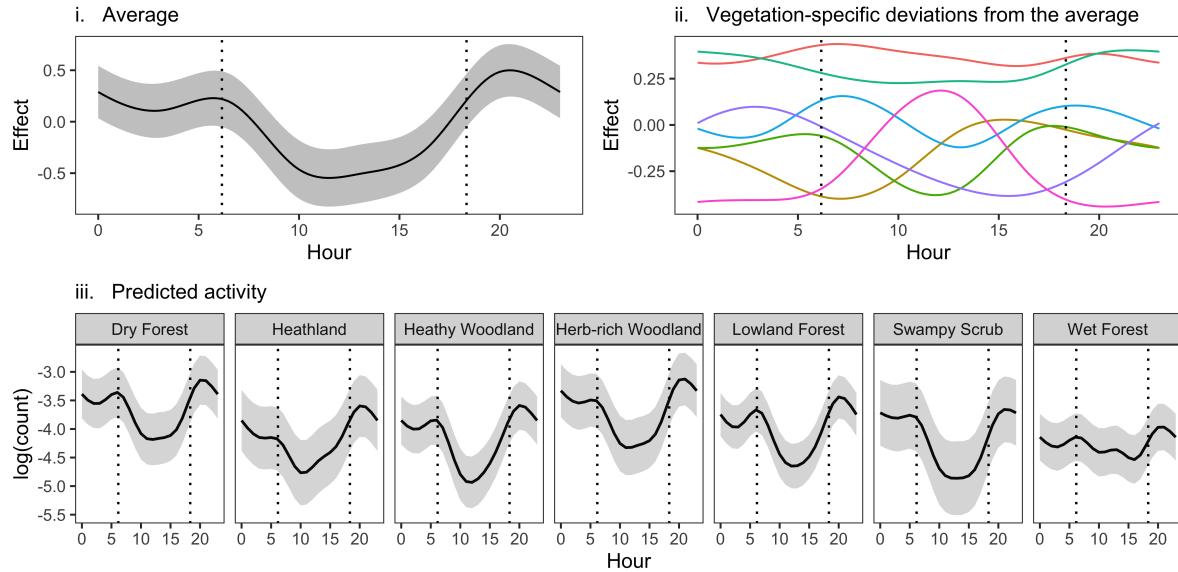


Figure 3: The strength of diel activity patterns of two invasive predators varied within the two study regions in south-west Victoria, Australia (model 1). White crosses depict unique camera-trap sites; colour brightness scales with increasing percentage difference between the minimum and maximum activity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

a. Fox



b. Feral cat

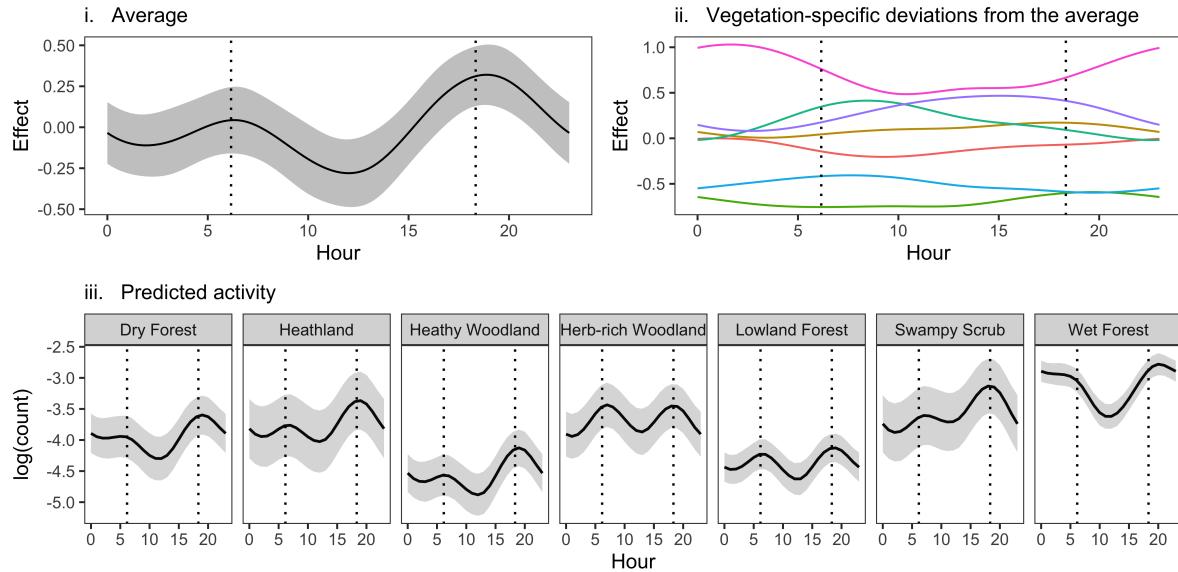
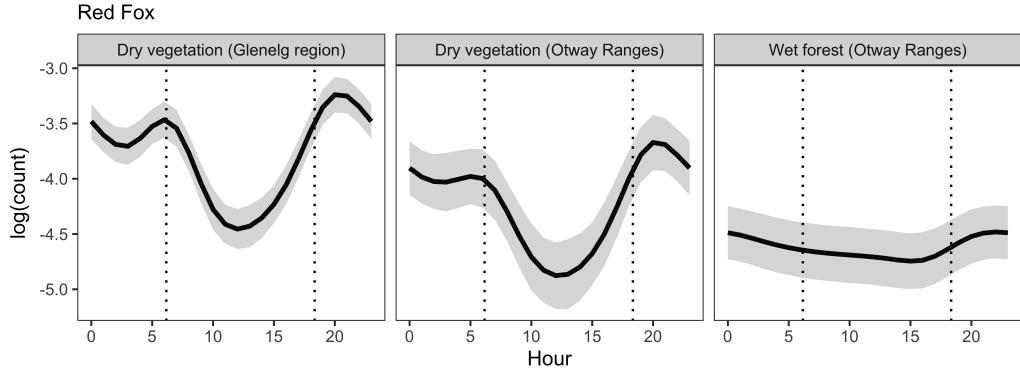
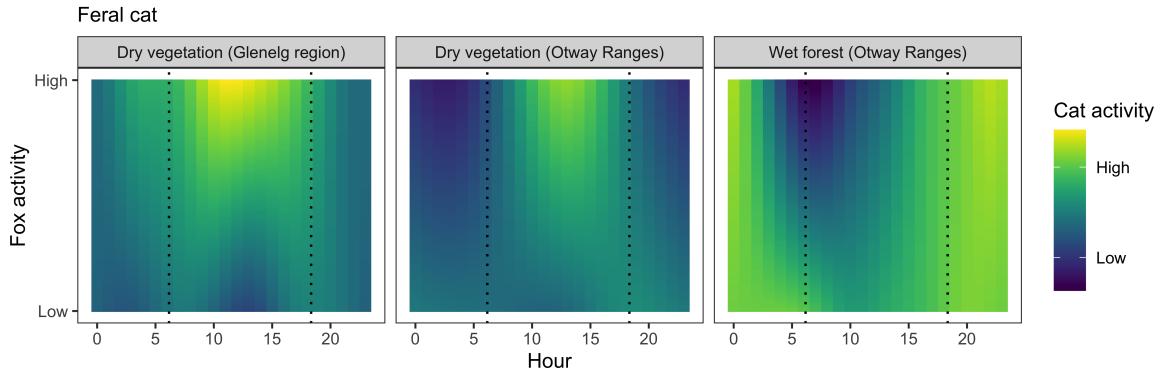


Figure 4: Red foxes *Vulpes vulpes* (a) and feral cat *Felis catus* (B) diel activity patterns overall (i) and across different Ecological Vegetation Class (EVC) groups (ii, iii) in south-west Victoria, Australia (model 2). Dotted, vertical lines represent average sunrise and sunset times. Shaded areas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

a



b



c

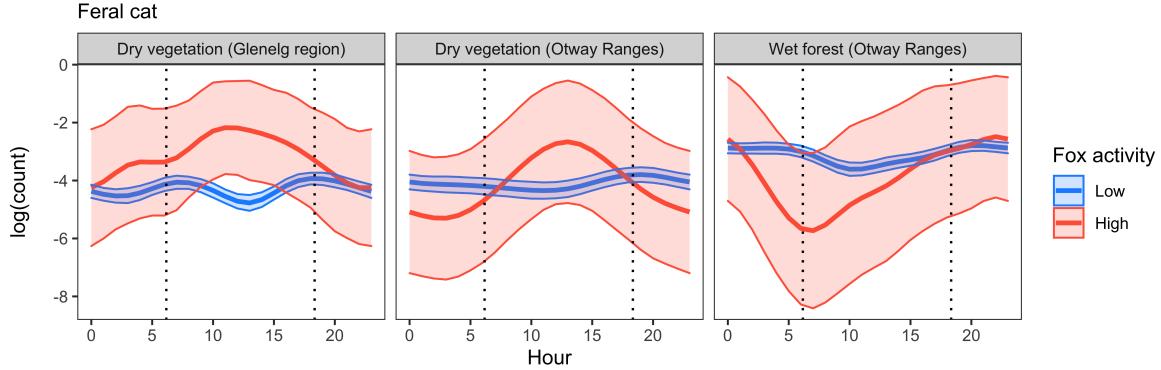


Figure 5: Variation in mean feral cat *Felis catus* activity (a) and associated uncertainty estimates (b) in response to count of 'independent' red fox *Vulpes vulpes* detections (log-transformed and survey effort adjusted) across each 'habitat type' in south-west Victoria, Australia (model 3). Grey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

255 **4. DISCUSSION**

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

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

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

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

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

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

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

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

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³⁶⁵ **CONFLICT OF INTEREST**

³⁶⁶ The authors declare no conflicts of interest.

³⁶⁷ **AUTHOR CONTRIBUTIONS**

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

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

³⁷² **DATA AVAILABILITY**

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

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