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RESEARCH ARTICLE

Evaluation of camera placement for detection of free-ranging carnivores; implications for assessing population changes

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Abstract

1. Introduced carnivores are often cryptic, making it difficult to quantify their presence in ecosystems, and assess how this varies in relation to management interventions. Survey design should thus seek to improve detectability and maximize statistical power to ensure sound inference regarding carnivore population trends. Roads may facilitate carnivore movements, possibly leading to high detectability. Therefore, targeting roads may improve inferences about carnivore populations.

2. We assessed our ability to monitor feral cats *Felis catus* and red foxes *Vulpes vulpes* on- and off-road, with explicit consideration of the location of monitoring sites on our ability to detect population changes. We also assessed whether there was evidence of spatial or temporal interaction between these species that might influence their road-use.

3. Surveys were conducted in a conservation reserve in south-eastern Australia between 2016 and 2018. At each of 30 sites, we deployed two motion-sensor cameras, one on-road, and the other off-road. Using occupancy models, we estimated cat and fox occupancy and detectability, and conducted a power analysis to assess our ability to detect declines in occupancy under three monitoring regimes (efforts targeted equally on- and off-road, efforts targeted entirely off-road and efforts targeted entirely on-road).

4. On average, on-road detectability was seven times higher for cats and three times higher for foxes. Targeting survey effort on-road yielded the greatest power for detecting declines in both species, but our ability to detect smaller declines decreased with decreasing initial occupancy probability. No level of decline was detectable for cats

when survey efforts were targeted off-road, while only large declines (>50%) were detectable for foxes (assuming high initial occupancy probabilities). We found little evidence of spatial or temporal segregation, suggesting limited avoidance or suppression between the two species within this landscape.

5. Our results suggest that targeting monitoring on roads may be an effective approach for detecting declines in introduced carnivore populations, particularly following management intervention (e.g. lethal control), and in the face of resource limitations. We provide a framework that can help assist land managers to make informed decisions, which balance monitoring efforts and resource constraints with sufficient statistical power to assess management objectives.

1 | INTRODUCTION

Introduced mammalian carnivores are among the greatest threats to biodiversity (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016), having been associated with the decline and extinction of numerous species worldwide. In Australia, feral cats *Felis catus* and red foxes *Vulpes vulpes* have contributed to declines in many native bird and reptile populations (Doherty et al., 2016), and together have been implicated in most of the thirty mammal extinctions that have occurred since European settlement (Woinarski, Burbidge, & Harrison, 2015). This has triggered the development of various management approaches aimed at mitigating their impacts, such as predator free fencing (Legge et al., 2018), translocation to predator free islands (Abbott, 2000), guardian animals (van Bommel, 2010; van Bommel & Johnson, 2012) and lethal control (Doherty & Ritchie 2017; Doherty, Driscoll, Nimmo, Ritchie, & Spencer, 2019; Hunter, Lagisz, Leo, Nakagawa, & Letnic, 2018; Molsher, Newsome, Newsome, & Dickman, 2017). Each of these management approaches vary considerably in cost, spatial extent and effectiveness. It is therefore vital to monitor introduced carnivore populations to ensure management efforts are achieving their intended outcomes.

It can be challenging to evaluate whether management interventions are working. This is typically because cats and foxes are cryptic, they tend to occupy relatively large home-ranges, and sometimes occur in low densities (Balme, Hunter, & Slotow, 2009), leading to low detection probabilities and difficulties associated with developing feasible monitoring programmes. Several studies have shown a positive association between introduced carnivores and open or fragmented habitats (e.g. forest edges, recently burnt areas, Graham et al., 2012), which may be due to an increase in prey vulnerability or density (Hradsky et al., 2017). Roads have been shown to facilitate carnivore movement to these sites (Hradsky et al., 2017), and consequently, the proximity of traps to roads and other modified features are often considered as part of targeted carnivore surveys. Indeed, many studies have focused their efforts on roads due to perceived increases in detectability (Bubela,

Bartell, & Muller, 1998; McGregor, Legge, Potts, Jones, & Johnson, 2015; Towerton, Kavanagh, Penman, & Dickman, 2016).

Another challenge is that co-occurring species often interact, either through direct effects (i.e. interference competition and intraguild predation) or indirect effects (i.e. fear-mediated behavioural change) (Ritchie & Johnson, 2009). This is likely to affect the efficacy of multi-species monitoring programmes. For example, Hayward and Marlow (2014) suggest that subordinate carnivores avoid roads in areas where they co-occur with a more dominant (apex) carnivore. By contrast, other studies have found that both subordinate and dominant carnivores select for roads, using them frequently, and sometimes simultaneously (Mahon, Bates, & Dickman, 1998; Read & Eldridge 2010; Wysong, Iacona, Valentine, Morris, & Ritchie, 2020).

Feral cats generally occupy a mesopredator role and may be suppressed, to varying extents, by larger carnivores. For example, in parts of Australia, dingoes *Canis dingo*, Tasmanian devils *Sarcophilus harrisii* and foxes have been shown to suppress cats (Brook, Johnson, & Ritchie, 2012; Cunningham, Johnson, & Jones, 2020; Marlow et al., 2015), possibly leading to altered behaviour (Molsher et al., 2017). If this is the case, we might expect cats to be detected less in areas where larger carnivores are most active in space and time. For example, if foxes are using roads, cats might avoid them (i.e. spatial avoidance) – or use them at different times (i.e. temporal avoidance) – to reduce the probability of an encounter. Spatial avoidance behaviour would have implications for how we monitor co-occurring carnivores (Hayward & Marlow, 2014), as it means the optimal approach for monitoring a dominant carnivore would differ from that of subordinate carnivores, potentially requiring different monitoring approaches for each. By contrast, if such avoidance behaviour is not evident, or if avoidance is largely temporal rather than spatial, then a single broad approach (e.g. monitoring on roads) might adequately capture both types of carnivores, noting that the specific design may require some optimization to deal with differences in density or rates of change, which may vary between species (regardless of whether they avoid one another or not).
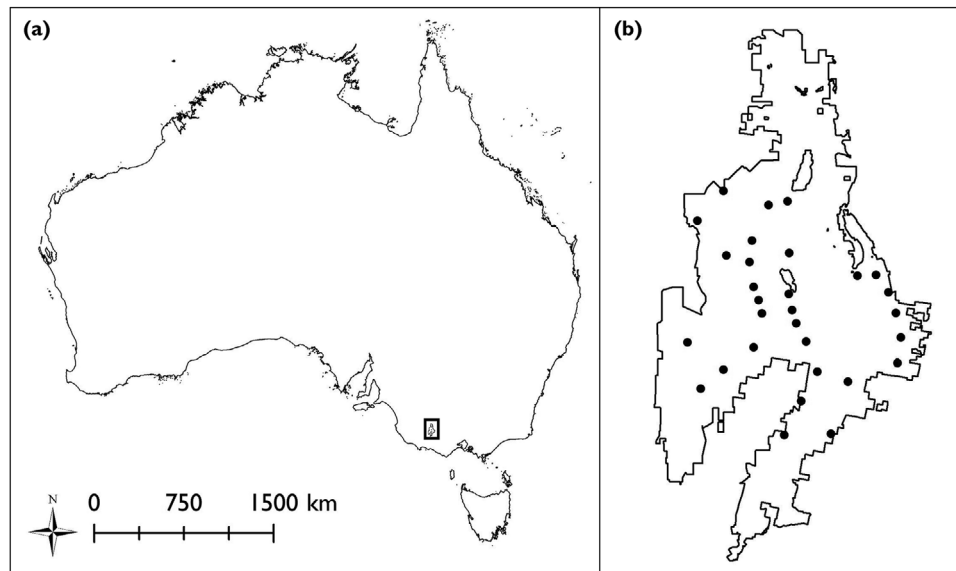
FIGURE 1 The location of the Grampians National Park relative to Australia (a) and the approximate location of paired camera sites within the Grampians National Park (b)

In this study, we assessed our ability to effectively monitor cats and foxes in the Grampians National Park (GNP), an area of high biodiversity and conservation value in central-west Victoria, Australia. We used motion sensor cameras to test whether cat and fox detectability was greater on-road compared with off-road habitats, with explicit consideration of how this affects our ability to detect changes in occupancy. We also assessed whether there was any evidence of spatial or temporal interaction between cats and foxes that may influence their road-use. While we acknowledge that red foxes are native in a substantial proportion of their global distribution, our focus here is in the context of invasive species management. Broadly, we seek to inform and aid improvement in the ways these species are surveyed, given the widespread distribution and environmental damage caused by introduced mammalian carnivores globally. Nevertheless, our results may be applicable to other contexts where land managers are interested in monitoring changes in native fox populations, or for other native terrestrial carnivores.

2 | MATERIALS AND METHODS

2.1 | Study location

The GNP encompasses an area of ~168,000 ha in south-eastern Australia, approximately 260 km west of Melbourne (Figure 1a). The park has high floral and faunal diversity. It supports at least 105 vertebrate species, 89 of which are native to the region, and 12 of which are currently threatened in Victoria (under the Flora and Fauna Guarantee Act, 1988). Cats and foxes have long been established in the Grampians (likely >150 years; Dickman, 1996), and their impacts on biodiversity are of great concern. Fox poison baiting (buried 1080 baits along road networks) was first implemented in 1996, triggered by declines in the only population of the critically endangered brush-tailed

rock-wallaby *Petrogale penicillata* within this park. A more systematic approach to baiting was introduced in 2002, shifting from perimeter baiting to large-scale ground baiting across 78,000 ha of the park. To date, this programme has been expanded to 226,000 ha and includes surrounding state forest, state park and some key areas of private land. There is currently no attempt to control feral cats in the area (as of March 2020) due to the previously limited control techniques permissible in Victoria (but note that lethal control is planned for the future).

2.2 | Survey design

Sites were selected to complement an ongoing, long-term ecological study of small mammals aimed at assessing their responses to wildfire and underlying climatic conditions (see Hale et al., 2016). Thirty of 36 sites associated with Hale et al. (2016) were sampled (Figure 1b), with each site comprising a pair of cameras (XR6 Ultrafire, Reconyx, Wisconsin, USA):

1. an 'off-road' camera, located away from roads and tracks within the centre of the mammal live-trapping grids used in Hale et al. (2016); and
2. an 'on-road' camera, located nearby but immediately adjacent to the nearest roads or tracks.

There were 60 cameras spread across the 30 sites in total (i.e. two cameras at each of the 30 sites). The distance between the on- and off-road cameras within each site was ~193 m on average (ranging from 75 to 603 m), which was considered small enough to ensure a high probability that both cameras were present within an individual's home-range, based on a review of the literature on fox and cat home range size in Australia (Carter, Luck, & McDonald, 2012; Hradsky, 2016;

Molsher et al., 2017; Moseby, Stott, & Crisp, 2009). Neighbouring sites were separated by at least 2 km.

Cameras were mounted to a metal fence post if placed off-road or a security post (within security boxes, design adapted from Meek, Ballard, & Fleming, 2013) if placed on-road (to minimize incidence of theft). Cameras were positioned facing south, tilted slightly down and 90–100 cm above the ground to ensure a focal point 5–6 m away from the device and to minimize false triggers associated with sun glare (as recommended by Meek, Ballard, & Fleming, 2012 for targeting introduced carnivores). All cameras were set up passively (i.e. no lure), as we were interested in determining the ability of each camera to pick up natural carnivore movements through the landscape, which would be confounded if individuals were lured to cameras. Camera sensitivity was set to high with a quiet period of 5 seconds and a one second delay between images, reflecting the fastest trigger time and lowest delay for this model of camera (Meek et al., 2012). Each event was set to capture three images at a low resolution (3MP) to save battery life. Vegetation within the range of the focal point was cleared at off-road cameras to minimize the event of false triggers and to ensure ease in species identification. Given that cats and foxes are known to readily use both open and closed habitats (Graham et al., 2012; Hradsky et al., 2017; Towerton, Penman, Kavanagh, & Dickman, 2011; Towerton, Kavanagh, Penman, & Dickman, 2016), we did not expect this to alter the behaviour of either species. All cameras were deployed for a minimum of 60 nights, and on-road batteries checked and replaced if necessary mid-survey (due to an increase in triggers associated with vehicle traffic).

Each three-photo sequence was treated as a single point in time and an event was defined as a set of images separated by 5 minutes – this was considered adequate, as cat and fox resident times (i.e. the amount of time spent within the focal view of the camera) were short, and in most cases limited to a single three-photo sequence. We consider that individuals had no incentive to remain at camera stations and were likely to be passing through.

Images were processed using C_{PW} Photo Warehouse, a custom Microsoft Access application designed to facilitate archiving, identifying, summarizing and analysing photo data collected from remote wildlife cameras (Ivan & Newkirk, 2016).

We sampled cat and fox populations in the GNP across five discrete seasons: (i) late July to early September 2016 (hereon referred to as winter 2016); (ii) early March to early May 2017 (autumn 2017); (iii) early November 2017 to early January 2018 (spring 2017); (iv) late April to early August 2018 (autumn 2018); and (v) early October to late December 2018 (spring 2018) to capture natural fluctuations in predator distribution through time and seasonally.

2.3 | Statistical analysis

We used single-season occupancy models (MacKenzie et al., 2002) to estimate occupancy and detection probabilities of cats and foxes in the GNP. We summarized camera observations into 24-hour detection histories, considering each sampling night at each camera one detection attempt. Models are formulated in terms of parameters ψ_i and p_{ij},

where ψ_i is the probability that site i is occupied by the species of interest p_{ij} is the probability of detecting the species at site i during survey j, conditional upon it being present. In its basic formulation, the model structure assumes independence among sites and detections, no changes in the occupancy status of sites (i.e. sites are 'closed' – either occupied or empty – across the whole survey period) and no false positive records.

Where sites are spaced too close together with respect to the territorial patterns of the target species (e.g. where the home-range of an individual overlaps with more than one camera), modelled estimates of occupancy and detectability may be biased (MacKenzie & Bailey, 2004). Given the large home-range sizes of cats and foxes in Australia (Carter et al., 2012; Molsher, Dickman, Newsome, & Müller, 2005), there would be potential for us to violate the assumption of independence of sites if we considered every camera trap a separate site, especially those within a single pair. Therefore, we instead fit three separate models to the data: (i) where detections were pooled across both cameras within a pair (i.e. pooling off- and on-road detections for a given night); (ii) using only off-road detections; and (iii) using only on-road detections.

While sites (i.e. pairs of cameras) were typically spaced >2 km apart, this too may be insufficient to ensure independence: a study conducted elsewhere in southern Australia (within similar habitat) showed that fox home-range sizes were up to 7 km in length (Hradsky et al., 2017). The placement of cameras on tracks and roads could also increase the risk of non-independence among sites (Hines et al., 2010), given these carnivores have been shown to move large distances along roads over short time periods (Hradsky et al., 2017). No data are available on cat or fox home-range within the GNP, so we tested whether potential violation of this assumption was likely to influence our modelled outputs of occupancy and detectability by fitting models to a subset of data, including only information from on-road cameras spaced >7 km apart (in any straight-line direction).

Similarly, where sites are not closed, modelled outputs may be biased (MacKenzie & Bailey, 2004). However, complete closure is difficult to achieve, particularly so for dynamic environments in continuous habitat, and where the species of interest are mobile (Steenweg, Hebblewhite, Whittington, Lukacs, & McKelvey, 2017). One proposed solution for dealing with potential violations of closure is to redefine the estimated parameter from occupancy (i.e. the probability of occurrence at a given site) to use (i.e. the probability of use of a given site) (Latif, Ellis, & Amundson, 2016). We apply this definition of occupancy here.

Models were fitted within the maximum-likelihood framework for inference using the package 'unmarked' (Chandler et al. 2020) in R (R Core Team, 2019). We did not include any predictors of occupancy or detectability due to small sample sizes and issues associated with model convergence. Additionally, we did not consider multi-season models (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) because we were not interested in extinction and colonization dynamics, but rather typical detection probabilities.

Using the fitted detection probabilities obtained from each model, we calculated the probability of detecting each species at site i at least once after k repeat visits as $p^* = 1 - (1 - p)^k$, where p^* is the cumulative detection probability.

2.4 | Power analysis

Power analysis allows us to determine whether a given design has the potential to produce a statistically significant result when the effect size (in this case, a change in occupancy) is biologically important. Guillera-Arroita and Lahoz-Monfort (2012) provide approximations (Equation 1) to calculate how the power of a given study design changes depending on the allocation of survey effort (i.e. number of sites and trap nights).

The probability of observing a significant difference in occupancy (i.e. power), given a significance level of α, is

$$
G = 1 - \beta = \left\{ 1 - \Phi \left(\frac{z_{\alpha/2} \sqrt{\sigma_1^2 + \sigma_2^2} - (\psi_1 - \psi_2)}{\sqrt{\sigma_1^2 + \sigma_2^2}} \right) \right\}
$$

$$
+ \Phi \left(\frac{-z_{\alpha/2} \sqrt{\sigma_1^2 + \sigma_2^2} - (\psi_1 - \psi_2)}{\sqrt{\sigma_1^2 + \sigma_2^2}} \right) \tag{1}
$$

where β is the probability of performing a type II error (i.e. not detecting an effect of a given magnitude when one has occurred), ψ_1 and ψ_2 are the true underlying occupancy probabilities in time 1 and 2, $\Phi(x)$ is the cumulative distribution function for the standard normal distribution, $z_{\alpha/2}$ is the upper $100\alpha/2$-percentage point for the standard normal distribution (e.g. 1.96 for $\alpha = 0.05$), $\sigma_i^2 = \psi_i(1 - \psi_i + F_i)/S_i$ is the variance of the occupancy estimator and $F = (1 - p^*)/\{p^* - kp(1 - p)^{(k-1)}\}$.

We defined R to be the proportional difference in occupancy, so that $\psi_2 = \psi_1 (1 - R)$, with $R > 0$ representing a decline. For a given R, the power to detect the decline increases both as the number of sampling sites (S) and the number of repeat visits (k) increases.

Here we apply Equation (1) to the fitted estimates of detectability obtained from the occupancy models to test our capacity to detect a decline in occupancy under three hypothetical monitoring regimes. To test the influence of declining occupancy on our ability to detect a response, we consider three initial starting occupancy probabilities: (i) low (i.e. $\psi^1 = 0.3$); (ii) moderate (i.e. $\psi^1 = 0.5$); and (iii) high (i.e. $\psi^1 = 0.8$). We assume a standard sampling design with k trap nights, across S sites, and fitted pooled, off- and on-road estimates of detectability as averaged across the five sampling occasions; winter 2016, autumn 2017, spring 2017, autumn 2018 and spring 2018. Our calculations assume that two datasets are collected: one at time 1 and one at time 2. The datasets are then analysed and their estimated occupancy probabilities with associated uncertainties compared, to assess whether there is evidence of a decline between the two times considered. We apply this approach to the following three scenarios:

1. *Pilot*: 30 sites sampled, with two cameras deployed at each site (one on-road and one off-road) for a minimum of 60 nights (as in the present study);

2. *Scenario A*: 60 sites sampled, with one camera deployed at each site (off-road) for a minimum of 60 nights (effort targeted entirely off-road); and

3. *Scenario B*: 60 sites sampled, with one camera deployed at each site (on-road) for a minimum of 60 nights (effort targeted entirely on-road).

Our three scenarios considered some of the trade-offs in sampling design for increasing statistical power, specifically by: (i) increasing the number of sample sites (Scenario A and B); and (ii) increasing the number of detectors (i.e. cameras) at a given site to maximize the chance of an encounter (Pilot). We assume a standard sampling duration of 60 nights for all three scenarios because this was sufficient for obtaining high confidence (>95%) that failure to record a cat or fox on a camera reflects a true absence (based on pooled detection histories across on- and off-road cameras; see Results), and because longer survey durations are likely to increase the probability of changes to the occupancy status of sites (and thus are more likely to violate the closure assumption). The number of sites sampled was capped based on what could be realistically implemented within the study area based on logistical (e.g. maintaining appropriate spatial distance and replication within the boundaries of the park) and financial (e.g. resources to cover equipment and personnel costs) constraints.

For all of our analyses, we set alpha (α) to 0.05 and beta (β) to 0.95. This assumes equal importance is given to the probability of performing a Type I error (detecting a false decline) as to the probability of performing a Type II error (not detecting a decline when one has occurred) (Di Stefano, 2003).

2.5 | Temporal interactions

To examine temporal avoidance between cats and foxes, we created temporal activity profiles across each sampling season using timestamps from camera photos ('overlap' package in R; Meredith & Ridout, 2018). This analysis considered only temporal interactions at on-road cameras, due to data limitations (i.e. there were too few off-road detections in some seasons to allow analysis). We plotted the smooth kernel density functions to create a probability density distribution for each species activity pattern and calculated the coefficient of overlap (Δ), which measures the total overlap between the two species temporal activity distributions (ranging from 0 or no overlap to 1 or complete overlap). We calculated 95% confidence intervals using 5000 smoothed bootstrap samples for each species (after adjusting for bootstrap bias; Meredith & Ridout, 2018). We used the estimator Δ_4 for inference, because simulation studies conducted by Ridout and Linkie (2009) and Meredith and Ridout (2018) found that this was the best performing option when the smaller of the two samples was >75.

To further explore the similarity between cat and fox activity patterns, we used Mardia–Watson–Wheeler tests ('Circular' package in R;
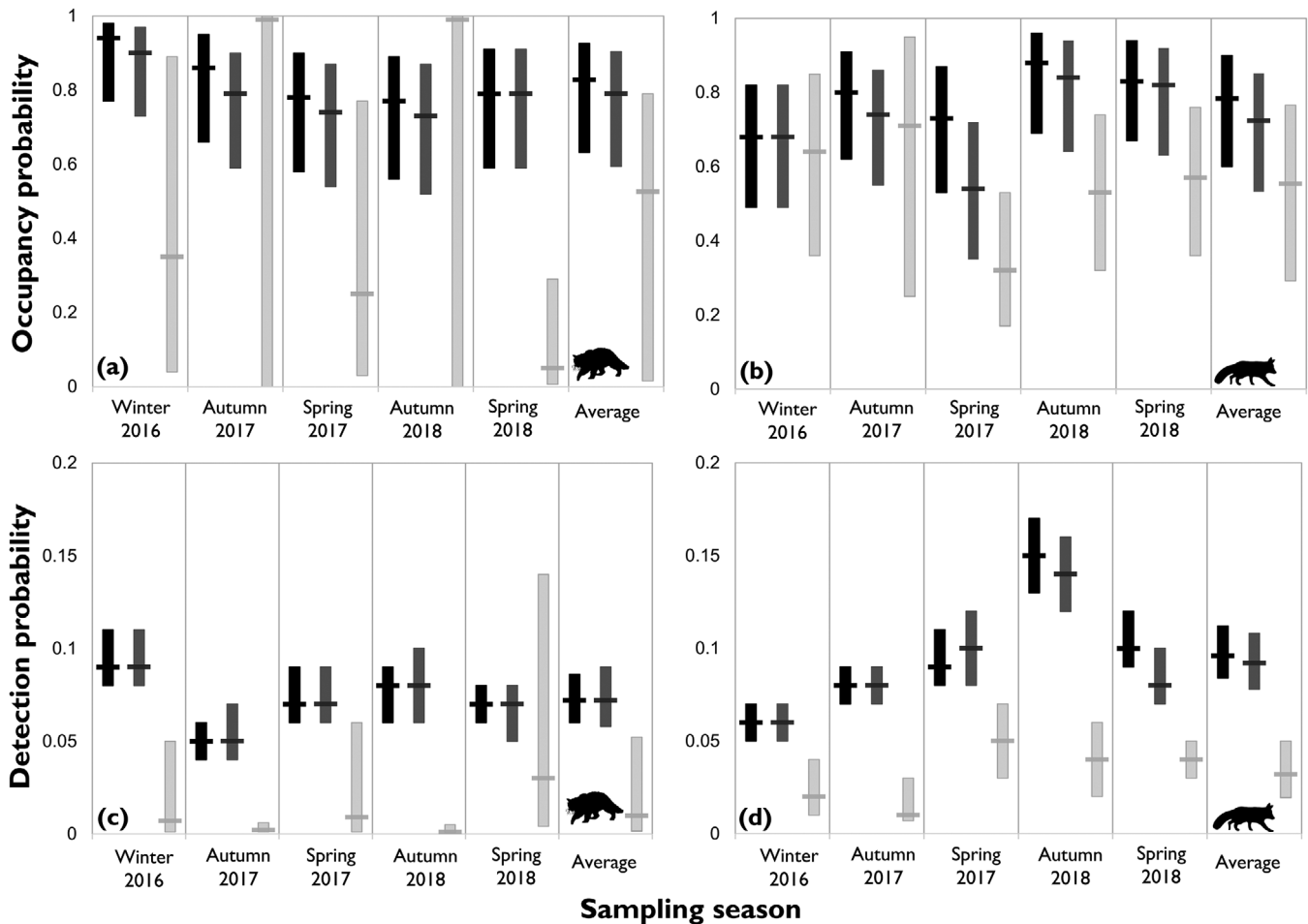
FIGURE 2 Occupancy (a, b) and detection (c, d) probabilities pooled across on- and off-road locations (black), on-road (dark grey) and off-road (light grey) for feral cats *Felis catus* (left) and red foxes *Vulpes vulpes* (right) in the Grampians National Park, south-eastern Australia. Occupancy and detection probabilities are provided for five sampling occasions: winter 2016, autumn 2017, spring 2017, autumn 2018 and spring 2018, as well as for the average across all seasons. Shaded bars indicate lower and upper confidence intervals. Estimates are derived from single-season occupancy models and assume occupancy and detectability remain constant across sites.

Lund & Agostinelli, 2015). This method detects differences in the mean angle or angular variance of circular temporal data, indicating activity peaks. It assumes no repeat data, so we altered identical records by 0.001 degrees (i.e. 0.24 seconds) as per Fancourt, Hawkins, Cameron, Jones, and Nicol (2015).

3 | RESULTS

3.1 | Model assumptions

There was little difference between estimates of occupancy and detectability obtained from models fit to all of the available on-road data, compared with models fit to a subset of the on-road data (taken from cameras spaced >7 km apart) (see Supplementary Material S1). Given that these differences are likely to have a negligible influence on the outcomes of this study, we use the estimates of occupancy and

detectability computed using all of the available on-road data for further inference.

3.2 | Occupancy and detectability

We obtained >60 nights of data from all 30 paired sites (at both camera locations) in winter 2016 and autumn 2017. Due to theft and/or malfunctioning, some sites were excluded in spring 2017 (26 paired sites analysed), autumn 2018 (25 paired sites analysed) and in spring 2018 (27 paired sites analysed).

Cat and fox occupancy was relatively high over the duration of the study (based on data pooled across on- and off-road cameras), with probabilities ≥0.77 and ≥0.68, respectively (Figure 2a and 2b). There was little evidence to suggest a significant difference among seasons or locations for either species, based on broadly overlapping confidence intervals in almost all cases (Figure 2a and 2b). Off-road
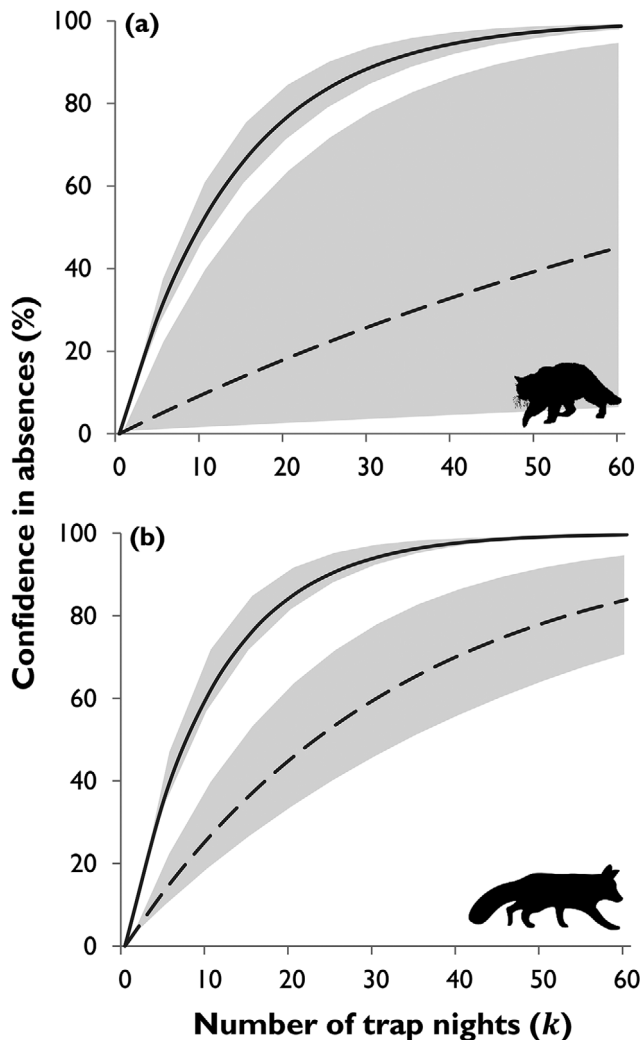
FIGURE 3 The probability of detecting (a) feral cats *Felis catus* and (b) red foxes *Vulpes vulpes* on-road (solid line) and off-road (dashed line) after *k* trap nights in the Grampians National Park, south-eastern Australia. Detectability is averaged across five sampling seasons (winter 2016, autumn 2017, spring 2017, autumn 2018 and spring 2018) and shading indicates upper and lower 95% confidence intervals.

occupancy was typically lower for cats and foxes compared to pooled and on-road occupancy (with some exceptions); however, the off-road estimates were almost always more imprecise, suggesting a high level of uncertainty in the modelled outputs (particularly so for cats, Figure 2a and 2b).

Detectability varied considerably between on- and off-road locations (Figure. 2c and 2d), improving significantly for both cats (sevenfold) and foxes (threefold) on-road (Figure 3). There was almost no difference between the pooled and on-road detectability for cats among seasons (Figure 2c), suggesting that the off-road cameras provided little additional benefit in terms of detecting this species. There were some differences in the pooled and on-road detectability for foxes among seasons (Figure 2d); however, this was not significant (evident by overlapping confidence intervals). When targeted on-road or when

pooled across locations, both predators could be detected with >95% confidence in areas where they were present with <60 trap nights (42 trap nights required for cats and 29–32 trap-nights required for foxes, Table 1). By contrast, 299 trap-nights (cats) and 99 trap-nights (foxes) were required to obtain 95% confidence in absences for cameras deployed off-road (Table 1).

The off-road detectability for cats was unusually high in spring 2018 compared with previous estimates (Figure 2c), despite being recorded only twice at one off-road camera (see Supplementary Material S2). However, the confidence intervals were wide (ranging from 0.004 to 0.14, Figure 2c). Notably, a greater level of precision (evident by narrower confidence intervals, Figure 2c) can be inferred for the off-road detectability of cats in all other seasons, where more detections were recorded across a greater number of cameras (Supplementary Material S2).

3.3 | Power analysis

Power to detect declines in occupancy varied among monitoring regimes, species and according to initial starting occupancy probabilities (ψ^1). Scenario B (effort targeted entirely on-road) yielded the greatest power for detecting declines in both cats and foxes under all values of ψ^1. Scenario A (effort targeted entirely off-road) yielded the least power for detecting declines in cats, however performed better than the Pilot scenario for detecting declines in foxes (Figure 4).

As ψ^1 increased, our ability to detect a response also increased, leading to greater power for detecting declines of smaller magnitudes. For example, when $\psi^1 = 0.3$, only large declines (i.e. >80%) could be detected with ≥95% confidence for both species, and only when survey efforts were targeted entirely on-road (i.e. under Scenario B, Figure 4). By contrast, when $\psi^1 = 0.8$, more moderate declines (e.g. 40%) were detectable with >95% confidence for both species (under Scenario B, Figure 4).

A sampling regime that targets foxes off-road is capable of detecting declines in occupancy, but only of magnitudes greater than 50% (with ≥95% confidence) assuming high ψ^1 (i.e. ≥0.8, Figure 4). No magnitude of decline was detectable for cats with ≥95% confidence when survey effort was targeted entirely off-road (Figure 4). For foxes, larger ψ^1 probabilities lead to smaller improvements in power under Scenario A (effort targeted entirely off-road), compared with the Pilot Scenario (effort targeted equally across both locations), which suggests that there is a significant trade-off with respect to the number of sites sampled and the number of detectors (i.e. cameras) at each site. For example, under smaller values of ψ^1 (i.e. 0.3, Figure 4), improvements in statistical power may be gained by increasing the number of sites sampled.

3.4 | Temporal predator interactions

There was a high degree of temporal overlap (≥0.78) between cats and foxes at on-road cameras across all sampling seasons (Supplementary

TABLE 1 The number of repeat trap nights (k) required for detecting feral cats *Felis catus* and red foxes *Vulpes vulpes* in the Grampians National Park, south-eastern Australia, with 80, 90 and 95% confidence and lower (LCI) and upper (UCI) confidence intervals

		80% confidence			90% confidence			95% confidence		
		k	LCI	UCI	k	LCI	UCI	k	LCI	UCI
Cat	Pooled	23	18	26	32	25	38	42	32	49
	Off-road	161	32	1,609	230	45	2,302	299	59	2,995
	On-road	23	18	26	32	25	38	42	32	49
Fox	Pooled	16	14	20	22	20	28	29	26	36
	Off-road	53	32	80	76	45	114	99	59	149
	On-road	18	14	20	25	20	28	32	26	36

Based on estimates of detectability as averaged across five sampling seasons (winter 2016, autumn 2017, spring 2017, autumn 2018, spring 2018) for the pooled, off-road and on-road locations. All values are rounded up to the nearest whole number.
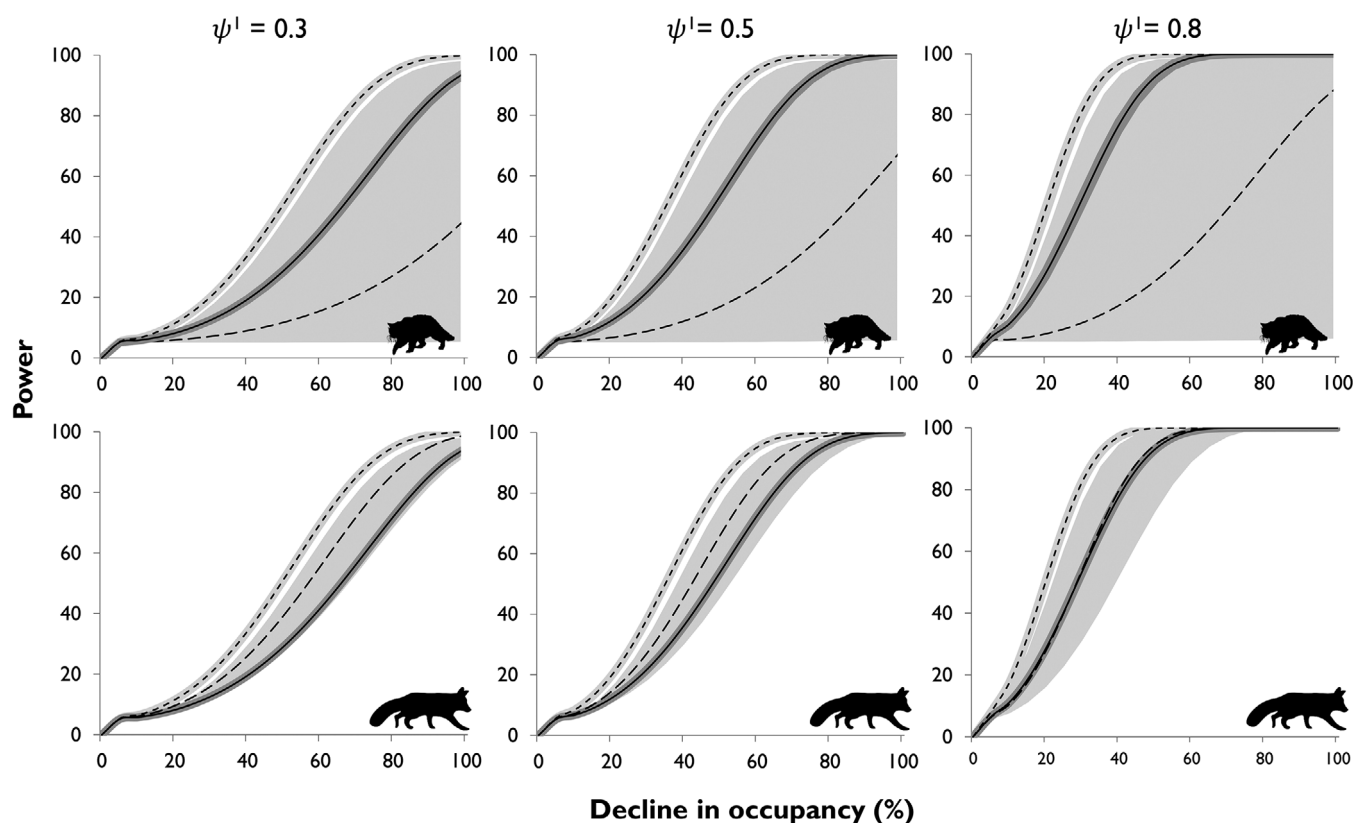

FIGURE 4 The power to detect declines in feral cat *Felis catus* (top) and red fox *Vulpes vulpes* (bottom) occupancy in the Grampians National Park, south-eastern Australia, under three initial starting occupancy probabilities (ψ^1), and three different monitoring regimes with varying predator detectability: (i) Pilot (effort targeted on- and off-road, solid line); (ii) Scenario A (effort targeted entirely off-road, dashed line); and (iii) Scenario B (effort targeted entirely on-road, dotted line). Shading indicates lower and upper 95% confidence bounds and alpha (α) is set to 0.05.

Material S3). Both species were most active between dusk and dawn, although cats did show a moderate level of diurnal activity in winter 2016 (Figure 5a). There was some evidence to suggest differences in peak cat and fox activities in winter 2016 ($w = 13.93$, $p < 0.01$), with cat activity peaking just before dusk, then steadily declining, while fox activity remained relatively steady between dusk and dawn (Figure 5a, Supplementary Material S3); autumn 2017 ($w = 6.69$, $p = 0.04$),

with fox activity peaking around midnight, and cat activity remaining relatively steady between dusk and dawn (Figure 5b, Supplementary Material S3); spring 2017 ($w = 10.20$, $p = <0.01$), with fox activity peaking after dusk, and cat activity peaking after midnight (Figure 5c, Supplementary Material S3); and autumn 2018 ($w = 11.47$, $p = <0.01$), with foxes exhibiting two main peaks (around dusk and midnight), and cat activity peaking around dusk (Figure 5d, Supplementary Material
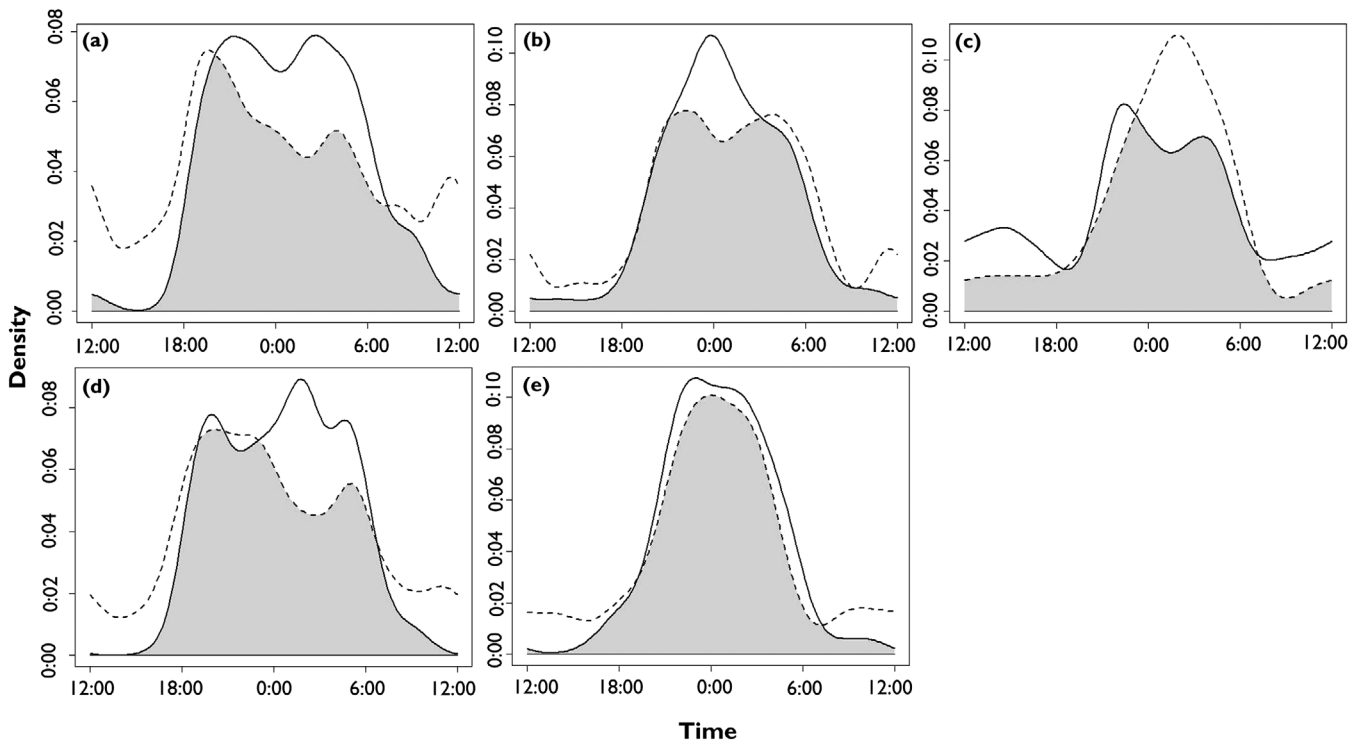
FIGURE 5 Overlap in feral cat *Felis catus* (dashed line) and red fox *Vulpes vulpes* (solid line) activity times in the Grampians National park, south-eastern Australia, across five sampling seasons: (a) winter 2016; (b) autumn 2017; (c) spring 2017; (d) autumn 2018; and (e) spring 2018. Grey shading indicates overlap.

S3). There was no evidence to suggest a difference in peak activity times in spring 2018 ($w = 0.54$, $p = 0.76$, Figure 5e, Supplementary Material S3).

4 | DISCUSSION

The development and implementation of sound monitoring programmes is integral to cost-efficient and ecologically effective wildlife management and conservation (Robinson et al., 2018). Here we demonstrate that monitoring cat and fox populations using road and track networks in natural landscapes improves our ability to detect both species, leading to improved precision around modelled estimates, increased statistical power and consequently allowing for detection of smaller changes in species occupancy. While we acknowledge that this approach is likely to have some limitations (i.e. limited inference about predator–prey interactions, or carnivore habitat use at off-road sites), we highlight that such large differences in detection rates are likely to have major implications on the quality of data collected, and subsequently, the types of analyses that can be performed. As we show here, data limitations (in this case associated with an off-road approach to monitoring) can lead to inability to perform a given analysis (i.e. temporal activity), uncertainty in modelled estimates (low precision), low power for detecting changes in populations (especially if initial population sizes are small) and potentially poor ecological inference.

Average cat and fox occupancy estimates were relatively high (≥ 0.53) regardless of the underlying data (i.e. pooled, off-road or on-road), which contrasts with previous estimates from this landscape. Robley et al. (2012) estimated cat occupancy to be approximately 0.17 (SE ± 0.046) in areas of high conservation value, while a broader survey across a larger area estimated fox occupancy to be approximately 0.28 (SE ± 0.086), figures of which are considerably lower than our comparable off-road estimates. While this could be due to genuine differences in occupancy, another explanation is that the cameras in that study were deployed for an insufficient period of time (~23 days for cats and ~28 days for foxes) to enable high confidence that these species would be detected if they were present. Indeed, the authors of that report suggest that the cumulative detection probability did not exceed 67% on average (noting that detectability varied according to location, and for foxes was more likely closer to roads). In both cases, although to a lesser extent in Robley et al. (2012) (likely due to a larger sample size), the confidence limits around the occupancy estimates were broad, indicating moderate to high rates of imprecision, and thus should be interpreted with caution.

Our results provide strong support for a positive association between introduced predators and roads, adding to the growing body of evidence that suggests a significant positive effect of roads on predator activity (Carter, Potts, & Roshier, 2019; Dawson et al., 2018; Raiter, Hobbs, Possingham, Valentine, & Prober, 2018; Wysong et al., 2020). The potential for roads to facilitate predator movements has been widely reported in the literature, with several studies

documenting the frequent use of roads by predators (Bischof, Gjeves-tad, Ordiz, Eldegard, & Milleret, 2019; Read et al., 2015) and others deliberately targeting roads to enhance the likelihood of capture (Bubela et al., 1998; McGregor et al., 2015; Towerton et al., 2016). However, there remains some disagreement about whether co-occurring predators should both use roads preferentially (Haywood & Marlow, 2014; Mahon et al., 1998; Nimmo, Watson, Forsyth, & Bradshaw, 2015; Read & Eldridge, 2010), and this is likely to be context dependent. While we did find some evidence of temporal segregation of cats and foxes (evident in significant differences in peak activity times in all but one season), they overlapped considerably in their activity. This, coupled with high spatial overlap (i.e. both species showing a strong preference for roads), provides little support for competitor avoidance or suppression within this landscape. One possibility is that ongoing baiting directed at foxes could be suppressing their numbers sufficiently to allow for temporal and spatial co-occurrence of cats. For example, Johnson and VanDerWal (2009) demonstrated that the relationship between dingoes and foxes is likely to be triangular in shape (i.e. dingoes and foxes can co-occur, but dingo abundance generally sets the upper limit on the abundance that foxes can reach). Another possible explanation is that in the relatively structurally complex landscape of our study, cats can easily retreat to shrubs or up trees if they encounter a fox.

A notable result of this study is that cats and (particularly) foxes appear to be widespread across the GNP despite an extensive and ongoing fox baiting programme. While this could suggest that the baiting programme is not achieving its intended aim of reducing the fox population to a sufficient level to alleviate predation on native wildlife, it is possible that occupancy is too coarse a metric for measuring success in management interventions, and it cannot reliably inform possible changes in population abundance. For example, lethal control may be reducing fox densities sufficiently to allow some predation relief on native prey species without significant reductions in site occupancy. Thus, while occupancy modelling can answer some questions, this approach is likely to overlook important relationships that require more detailed information (Nimmo et al., 2015). Other methods (e.g. spatial count, spatial-presence-absence), which can be used to measure predator densities in unmarked populations (i.e. where some or all individuals cannot be confidently identified), are likely to be more useful for teasing apart these types of relationships (Chandler & Royle, 2013; Ramsey, Caley, & Robley, 2015). These approaches have different survey requirements and assumptions (e.g. detectors must be spaced at a distance relative to the home-range of the target species so that a single individual is exposed to multiple detectors) and perform best with minimal bias when there are a high number of detections across each sample (i.e. >10) (Ramsey et al., 2015). So careful consideration must be given to survey design to ensure it is capable of answering the specific question at hand.

A primary challenge of monitoring programmes is ensuring there is adequate power for detecting effects of varying magnitudes (Guillera-Arroita & Lahoz-Monfort, 2012). This is further complicated by the fact that species vary in their detectability, distribution and abundance across landscapes. Improving power can be achieved by increasing the sampling effort (i.e. the number of sites or survey nights); however, this is typically limited by financial and logistical constraints (Field, Tyre, & Possingham, 2005; Joseph, Field, Wilcox, & Possingham, 2006), and in an occupancy context, may have implications for the accuracy of inferences made. For example, while increasing the number of survey nights may well improve power for detecting smaller declines, longer survey durations are more likely to violate the closure assumption (e.g. individuals could be born, die or migrate, leading to changes in the occupancy status of sites), which could lead to biased estimates (MacKenzie & Bailey, 2004). Similarly, increasing the number of sites can increase the risk of spatial non-independence, particularly in study regions that are limited in extent (such as the GNP). Therefore, there is a trade-off when considering a sampling design that can be implemented at realistic temporal and spatial time-scales, whilst still providing an acceptable level of confidence in detecting changes through time (Guillera-Arroita & Lahoz-Monfort, 2012).

The sampling regimes considered in this study were designed with financial and logistical constraints in mind; all three regimes could be realistically implemented within the GNP. However, there was great variability in statistical power for detecting changes in predator occupancy among the three regimes. These differences in statistical power have real-world implications. For example, in our study region, a sampling regime designed to solely target off-road habitats before and after lethal cat control may not detect an effect, and consequently conclude that management was ineffective. However, such a regime is highly unlikely to detect a decline (of any magnitude, assuming one occurs) in cats with a reasonable level of confidence. Similarly, van Hespen, Hauser, Benshemesh, Rumpff, and Lahoz-Monfort (2019) demonstrated through simulation modelling that small changes in environmental factors, budget constraints and monitoring design can affect the chances of a monitoring programme successfully achieving its intended outcomes. These are crucial considerations for developing effective monitoring programmes, yet there are relatively few examples in the published peer-reviewed literature where power analysis has been used to inform carnivore monitoring (but see Ramsey et al., 2017; Travaini et al., 2010; van Hespen et al., 2019).

Another crucial consideration is that as occupancy declines, our ability to detect a response also declines (as we have shown here), and so too might the detectability of the target species. When occupancy and detectability probabilities are low, more survey effort is required to detect a decline of a given magnitude, and so the choice of survey design becomes even more important.

While on-road sampling is likely to be an effective approach for determining whether carnivore populations are declining in response to management interventions, it too has its limitations. Little inference can be gained about the functional role of introduced carnivores across the entire landscape; for example, the presence of a cat or fox at a road site does not necessarily mean that they are using the adjacent vegetation. Restricting sampling entirely to roads and tracks may also limit the opportunity for concurrent predator–prey monitoring, and in turn, our ability to gain insight into predator–prey relationships. This is a fundamental question, given that predator control programmes are often implemented to protect native species. Answering these questions will

likely require additional and complementary approaches (such as by combining diet, movement and camera trapping studies, see Hradsky, 2016), far greater survey effort and targeted monitoring across the entire landscape. Without some measure of impact (i.e. do introduced predators reduce native prey populations), or response (i.e. is the management intervention achieving its' intended aim of protecting native species), such lethal control programmes are difficult to justify (van Eeden, Dickman, Ritchie, & Newsome, 2017).

Nevertheless, our results suggest that surveys targeting roads – especially when resources may be limited – can be an efficient approach for determining if landscape-scale lethal control is effective. We urge others to consider the importance of this for other ecosystems where carnivore monitoring and management occurs.

AUTHORS' CONTRIBUTIONS

HMG, EGR, MS, DGN, RD and BT conceived the ideas and designed the methodology; BT and DS collected the data; HMG analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Sample R code for the power analysis conducted as part of this study is available online as supplementary material in Guillera-Arroita and Lahoz-Monfort (2012). The data used to produce the results reported in this study are available for download from figshare: https://doi.org/10.6084/m9.figshare.12494153 (Geyle et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.