RESEARCH ARTICLE

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Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in Australia suggests not

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Abstract

1. The role of apex predators in structuring ecosystems through the suppression of mesopredator activity and abundance is receiving increasing attention, largely due to the potential benefits for biodiversity conservation. In Australia, invasive mesopredators such as feral cats (*Felis catus*) have been identified as major contributors to Australia's mass mammal extinctions since European arrival. The introduced dingo (*Canis familiaris*) has been proposed as a novel way to suppress the impacts of feral cats, however, scientific evidence of the dingo's suppressive role is equivocal.

2. We used camera traps to investigate whether a large introduced predator (dingo) suppresses the activity of an established introduced mesopredator (feral cat) across a national park site conserving endangered species, and an agricultural site supporting cattle grazing enterprises.

3. Feral cats and dingoes exhibited marked overlap in both temporal and spatial activity, indicating coexistence. Some temporal separation was evident at the agricultural site, however, this reflected higher diurnal activity by dingoes, not a responsive shift in cat activity. Cat activity times were unrelated to dingo presence and did not differ between areas occupied by dingoes and dingo-free areas. There was no evidence of dingoes excluding cats from patches at either site, nor was there evidence of within-night fine-scale spatiotemporal avoidance of dingoes by cats.

4. Species co-occurrence models revealed dingoes had no negative effect on the probability of cat presence. The probability of detecting a cat on the national park was significantly higher in areas with dingoes than in dingo-free areas, while on agricultural land, cat detectability did not differ between areas with and without dingoes. Cats remained active, abundant and widespread across both sites, with evidence of cats hunting and breeding successfully in areas occupied by dingoes.

5. *Synthesis and applications.* Our findings indicate that feral cats can coexist with dingoes, without apparent suppression of cat activity, abundance or fitness. Proposals to reintroduce or restore dingoes and other large predators to suppress invasive mesopredators and conserve biodiversity should be carefully evaluated

on a site-by-site basis, as their ability to suppress cats and protect species of conservation significance will likely be context dependent.

1 | INTRODUCTION

Reducing the impact of invasive feral cats (*Felis catus*) is a key priority for conservation and land managers globally. In Australia, predation by feral cats is considered to be the most significant factor in Australia's recent mammalian extinctions (Woinarski, Burbidge, & Harrison, 2015) and is listed nationally as a key threatening process (Department of Environment, 2015). Cats further threaten Australian wildlife through the transmission of toxoplasmosis, a disease caused by the parasite *Toxoplasma gondii* (Dubey, 2010; Fancourt & Jackson, 2014). However, feral cat populations and their impacts remain notoriously difficult to control. Traditional techniques such as trapping, shooting and exclusion fencing can sometimes be effective at local scales, but these approaches are expensive, time-consuming and generally ineffective over large scales.

Apex predators are credited with profoundly influencing the structure and function of ecosystems, regulating biodiversity and maintaining ecosystem integrity by triggering cascading effects through lower trophic levels (Terborgh et al., 1999). The reintroduction of native wolves (*Canis lupus*) into Yellowstone National Park, USA, and the ensuing terrestrial trophic cascade among wolves, elk (*Cervus canadensis*) and quaking aspen (*Populus tremuloides*), is perhaps the best known, but intensely debated (see Fleming, 2019; Hayward, Edwards, Fancourt, Linnell, & Nilsen, 2019) example of the positive top-down influence of apex predators (Ripple, Larsen, Renkin, & Smith, 2001). To this end, the restoration or reintroduction of large and/or apex predators has been proposed to protect species of conservation significance by suppressing the abundance and activity of mesopredators (Ripple et al., 2014; Ritchie & Johnson, 2009), although due consideration is rarely given to the animal welfare impacts of such proposals (Allen et al., 2019).

In Australia, it has been suggested that large predators such as the introduced dingo (*Canis familiaris*) could provide beneficial outcomes for threatened species by suppressing the activity and abundance of introduced invasive mesopredators such as the feral cat (Brook, Johnson, & Ritchie, 2012; Dickman, Glen, & Letnic, 2009; Letnic, Koch, Gordon, Crowther, & Dickman, 2009). While dingoes occur in varying densities across most of the Australian mainland, they are subject to varying degrees of control in some areas, primarily to enable small livestock production (Fleming et al., 2014). Accordingly, the restoration or reintroduction of dingo populations into areas subjected to intensive control has been suggested as a means to suppress the impacts of feral cats on native wildlife. However, the Australian context is unique in that both dingoes and cats are introduced, raising questions as to the applicability of mesopredator suppression/release theory as demonstrated in systems with native predators.

Some studies report that dingoes have no effect on feral cat abundance (Hunter, Lagisz, Leo, Nakagawa, & Letnic, 2018; Letnic et al., 2009) whilst others claim dingoes suppress cat activity and abundance (Brook et al., 2012; Feit, Feit, & Letnic, 2019). However, the validity of these conclusions has been heavily debated, mainly due to methodological weaknesses that render study findings unreliable (Allen, Allen, & Leung, 2015; Allen et al., 2013; Fleming, Allen, & Ballard, 2012; Hayward et al., 2015; Hayward & Marlow, 2014). Most studies use unvalidated activity indices that rely on unsupported assumptions, such as track plot indices (Colman, Gordon, Crowther, & Letnic, 2014), raw camera detection rates (Brook et al., 2012) or spotlight counts (Feit et al., 2019) to infer numerical relationships between dingoes and cats. Such activity indices are often unrelated to abundance (Fancourt, 2016; Hayward & Marlow, 2014) and are plagued by detectability issues that require robust, tailored experimental design and data analyses that are rarely adopted (Ballard, Fleming, & Meek, 2018; Hayward & Marlow, 2014). Weak and/or varied methodologies have undoubtedly contributed to the increasing number of conflicting results, often at the same sites, exacerbating controversy surrounding the role of dingoes in suppressing cats (Hayward & Marlow, 2014).

While the ability of dingoes to suppress feral cat abundance remains equivocal, it has also been suggested that dingoes could potentially structure ecosystems to create predation refuges for vulnerable native species (Hayward & Marlow, 2014) by creating a 'landscape of fear' (Laundré, Hernández, & Altendorf, 2001). Conceptually, dingoes may force cats to shift their temporal and spatial activity to avoid or minimize encounter rates with dingoes (Brook et al., 2012; Feit et al., 2019), as has been observed in other native carnivore guilds (Durant, 1998). This avoidance of dingoes could potentially create cat-free refuges in space and/or time, where susceptible prey species would not be exposed to cat predation. Furthermore, if cats are restricted to sub-optimal foraging strategies to safely avoid dingoes, their foraging efficiency, fitness and fecundity may decrease, ultimately resulting in reduced cat abundance, as has been observed in other species (Lima & Dill, 1990; Linnell & Strand, 2000). However, the ability of dingoes to significantly influence the behaviour of feral cats and create cat-free refuges for prey in space or time has not been demonstrated.

The aim of this study was to investigate whether dingoes suppress feral cats by influencing their activity at different temporal

and spatial scales. We used intensive camera trap surveys and robust analytical techniques to quantify the temporal and spatial activity of sympatric dingoes and feral cats at multiple scales in semi-arid central Queensland, Australia. As the strength of any top-down control by dingoes could potentially vary in response to differing bottom-up effects (Greenville, Wardle, Tamayo, & Dickman, 2014), we surveyed dingo and cat activity across two sites with distinct land tenures, management objectives and prey communities; a nature conservation site (national park) protecting threatened species, and an agricultural site supporting cattle grazing enterprises. We asked four questions: (a) do dingoes influence the temporal activity of feral cats? (b) do dingoes influence the spatial activity of feral cats? (c) do dingoes influence the within-night fine-scale spatiotemporal activity of feral cats? and (d) do dingoes affect the probability of cat presence or cat detection? We compare and contrast our findings across sites, and discuss the implications of our findings for proposals to reintroduce or restore dingo populations to benefit biodiversity conservation.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study sites were located near the town of Dingo in the Northern Brigalow Belt bioregion of central Queensland, Australia (Figure 1). The region's climate is described as subtropical and semi-arid. The 'national park' site (−23.53°, 149.22°) was located at Taunton National Park (Scientific; TNP), home to the only significant remnant wild population of the endangered bridled nailtail wallaby (*Onychogalea fraenata*). The 116 km² park contains dense copses of remnant and regrowth brigalow (*Acacia harpophylla*) intermixed with open grassy eucalypt woodland dominated by poplar box (*Eucalyptus populnea*). The 'agricultural' site (−23.28°, 149.37°) comprised three adjoining cattle properties located approximately 30 km to the north-east of TNP (Figure 1). The grazing properties comprised a matrix of buffel grass (*Cenchrus ciliaris*) dominated pasture interspersed with patches of remnant and regrowth brigalow and grassy eucalypt woodland.

2.2 | Camera surveys

Camera traps were used to monitor feral cat and dingo activity across each site during winter 2016. Two replicate camera surveys were performed at each site for a minimum duration of 21 nights per survey (Table 1). For each survey, 90 camera traps (Reconyx HC600, Reconyx) were deployed across the national park site, and a further 90 camera traps across the agricultural site. Each site was divided into 30 grids (4 km² area). A cluster of three cameras was deployed in each grid, with one 'on-track' camera positioned adjacent to a dirt vehicle track (aiming across and along the track), and two 'off-track' cameras positioned 50–100 m away (cameras located on opposite sides of the track). Both on- and off-track cameras were used to account for any fine-scale spatial avoidance
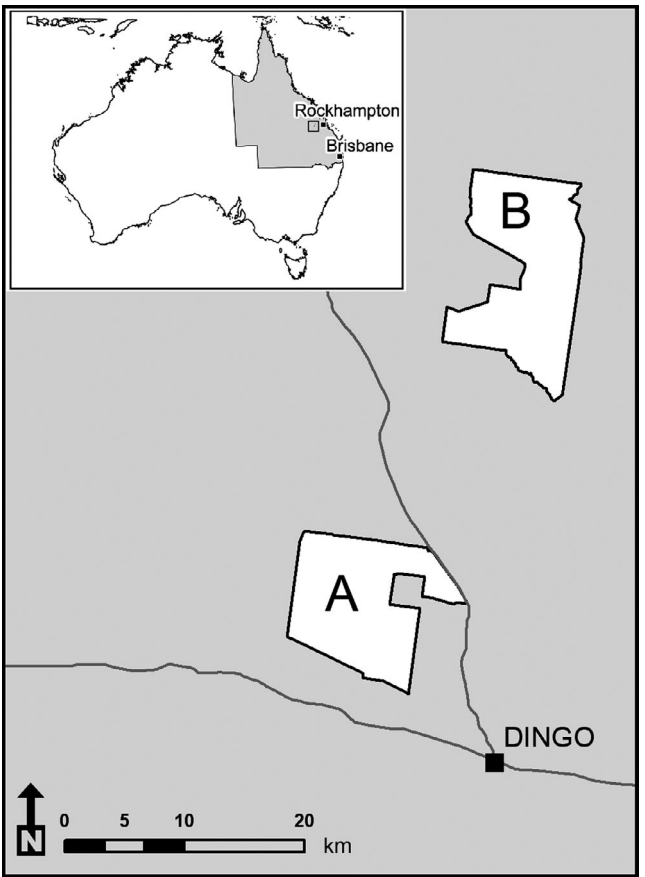

FIGURE 1 Map of study site locations. Location of national park site (A) and agricultural site (B). Inset shows location of study sites within Australia

TABLE 1 Camera survey dates for the national park and agricultural sites

Site	National park		Agricultural site
Camera trap lured?	Unlured	Lured	Lured
Survey 1	June 2016	—	July 2016
Survey 2	—	July 2016	Aug–Sept 2016

that might occur between an apex predator and a mesopredator (Fancourt, 2016). Cameras were positioned 30–40 cm above, and aimed parallel to the ground. Approximately 50 ml of tuna oil was placed on the soil in the centre of the camera's field of view on the first day to encourage animals to stay in front of the camera longer, thereby assisting with individual identification of animals. To account for the possibility that lures might negatively affect the detectability of dingoes or cats, lures were only used on three of the four surveys (first survey in national park used unlured cameras), thereby enabling a comparison in detectability between lured and unlured cameras at one site (Table 1). Cameras use passive infrared sensors to detect a heat-in-motion differential between a subject and the background temperature, and an infrared flash for night-time illumination. For each movement trigger,

cameras were programmed to repeatedly take five images in rapid succession with no delay until movement ceased.

2.3 | Data analysis

All statistical analyses were performed in R version 3.4.2 (R Development Core Team, 2017).

2.3.1 | Species detections

All cat and dingo detections were recorded for each camera survey at each site. To minimize repeat captures of the same individual, a single detection event or 'activity' was treated as independent if it occurred >10 min after the last series of images for that species on that camera, unless individuals were distinguishable by unique pelage patterns, markings or colours.

2.3.2 | Effect of camera lure on probability of predator detection

Prior to pooling data from both unlured and lured surveys, we first investigated whether camera lures influenced the detectability of either dingoes or cats. We calculated the detection probability (*p*) for each species for each survey (lured, unlured) at the national park site (Table 1) using the Royle–Nichols abundance-induced heterogeneity model (Royle & Nichols, 2003) in the `unmarked` package version 0.12-3 (Fiske & Chandler, 2011). The presence or absence of a lure was included as a covariate on detection for each species.

2.3.3 | Temporal activity

To investigate whether dingoes influence the temporal activity of feral cats at the site scale, we quantified the extent to which cat and dingo temporal activity overlapped or separated at each site. To investigate whether dingoes influence cat temporal activity over finer spatial scales, we also compared the activity times of cats in grids where dingoes were present with grids where dingoes were absent within each site. We additionally compared the temporal activity of each species between sites to determine whether any observed temporal separation between predators was driven by differences in cat activity (suggesting cat activity might be influenced by dingo activity) or differences in dingo activity (suggesting cat activity was unrelated to dingo activity).

For all overlap comparisons, we created temporal activity profiles for feral cats and dingoes using the time stamp on each camera image. We fitted nonparametric kernel density curves using default smoothing parameters to characterize the probability density distribution of each species' activity pattern at each site using the `overlap` package version 0.3.2 (Meredith & Ridout, 2018a). We used the coefficient of overlapping, Δ (Weitzman, 1970), to quantify total temporal overlap between the two species, calculated as the area under the curve that is formed by taking the minimum of the two density functions at each time point. This

overlap measure ranges from 0 (no overlap, complete separation) to 1 (complete overlap, no separation). We used either the Δ_1 (*n* < 75) or Δ_4 (*n* ≥ 75) measure of overlap, depending on smaller sample size in each comparison (following Ridout & Linkie, 2009). Confidence intervals (95%) were obtained from 10,000 smoothed bootstrap samples after accounting for bootstrap bias (Meredith & Ridout, 2018b).

To test for differences in the activity times of dingoes and cats, we used the nonparametric Watson–Wheeler test to detect differences in activity peaks using the mean angle of the circular temporal data (Batschelet, 1981), using the `circular` package version 0.4-93 (Agostinelli & Lund, 2017).

2.3.4 | Spatial activity

To investigate whether dingoes exclude or negatively influence the spatial activity of feral cats, we mapped the occurrence of each species by camera grid to identify any spatial separation in predator activity. Separate maps were prepared for dingoes and cats at each site to determine whether species were active in the same areas (indicating coexistence) or in different areas (suggesting separation or exclusion).

2.3.5 | Within-night spatiotemporal activity

To investigate whether dingoes influenced the within-night spatiotemporal activity of feral cats, we examined the fine-scale spatial and temporal separation between cat and dingo detections on the same night at the same site. For each cat detection, we calculated the distance and time to the nearest dingo detection on the same night. We used ordinary least squares regression to investigate whether there was a negative relationship between distance and time between species detections (suggesting spatiotemporal avoidance of dingoes by cats). Separate regressions were performed for each site.

2.3.6 | Species co-occurrence models

We used species co-occurrence models to determine whether dingoes influenced (a) the probability of cat presence; and (b) the probability of detecting a cat. For each species, site-specific detection histories were created by recording the species' presence or absence for each camera night. A camera night was defined as the 24-hr period from 12:00:00 pm (mid-day) to 11:59:59 am on the following day. To avoid repeat detections of the same individual, a species was considered 'present' if it was detected on at least one of the three cameras in that grid on any given camera night. We used an occupancy modelling approach (MacKenzie et al., 2002) to account for the possibility that a species was present but not detected (imperfect detection), based on the species-specific detection history for each grid at each site.

For each site, we fitted a two species, static occupancy (single season) model using the `RPresence` package version 2.12.22
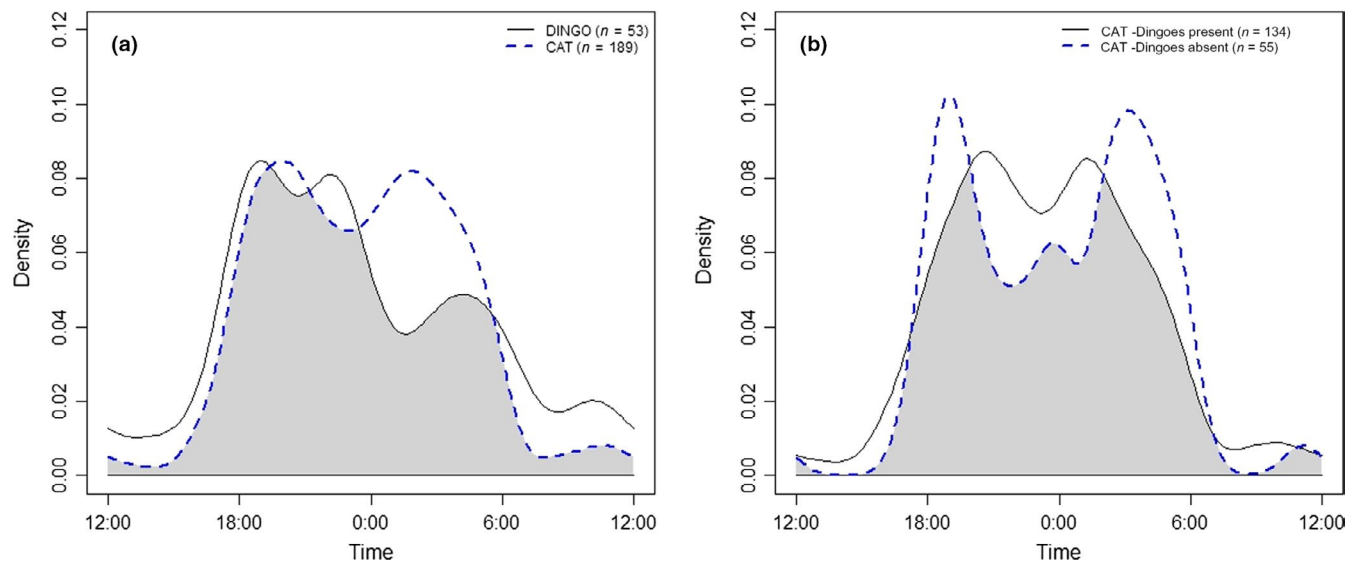
FIGURE 2 Dingo and feral cat temporal activity profiles at the national park site. Plot (a) shows overlap of dingo (solid line) and cat (dashed line) temporal activity. Plot (b) shows similarity in feral cat activity between areas with dingoes present (solid line) and areas with dingoes absent (dashed line). Shading indicates the extent of overlap/similarity in temporal activity. Sample sizes in parentheses indicate number of detection events

(MacKenzie & Hines, 2018). This species co-occurrence model unifies the concepts of occurrence of different species and detection probability within a single modelling framework, thereby allowing investigation of species co-occurrence patterns (MacKenzie et al., 2017). We used four candidate models with a priori defined factors to compare whether dingoes influenced the presence and/or detectability of feral cats. Specifically: m1 ($\psi \sim$ SP, $p \sim$ SP); m2 ($\psi \sim$ SP + INT, $p \sim$ SP); m3 ($\psi \sim$ SP, $p \sim$ SP * INT_o); m4 ($\psi \sim$ SP + INT, $p \sim$ SP * INT_o), where: ψ = probability of presence, p = detection probability, SP = species effect on presence (ψ) or detection (p), INT = occurrence-level interaction between species, INT_o = detection-level interaction where the presence of one species changes the detection probability of the other species. The model averaged values were used to estimate and compare (1) the probability of cat presence (B) where dingoes are present (A) (ψ^{BA}) versus where dingoes are absent (a) (ψ^{Ba}); and (2) the probability of cat detection (B) where both cats and dingoes (A) are present (r^{BA}) versus where dingoes are absent (p^{B}) for each site.

3 | RESULTS

3.1 | Effect of camera lure on probability of predator detection

Camera trap lures had no effect on the detectability of either cats or dingoes. The probability of detecting a cat (p) did not differ between unlured (p = .052 (95% CI: 0.030–0.091)) and lured (p = .045 (95% CI: 0.026–0.077)) surveys. Similarly, there was no difference in dingo detectability between unlured (p = .029 (95% CI: 0.012–0.067)) and lured (p = .031 (95% CI: 0.012–0.077)) surveys. Accordingly, data from both surveys at the national park were subsequently pooled for further analyses.

3.2 | Temporal activity

We found no evidence that dingoes influenced cat activity times at the national park site. Cat temporal activity exhibited marked overlap with that of dingoes (Δ_1 = 0.81 (95% CI: 0.73–0.90); Figure 2a), with no significant separation between cat and dingo activity (W = 4.14, p = .126). There was also no evidence that dingoes influenced the temporal activity of cats over finer spatial scales (Δ_1 = 0.82 (95% CI: 0.70–0.91); Figure 2b), with cats remaining active at similar times regardless of whether dingoes were present or absent (W = 2.34, p = .311).

There was some temporal separation evident between cats and dingoes at the agricultural site, however, this was due to increased diurnal activity by dingoes rather than cats avoiding dingoes. Cats and dingoes exhibited considerable overlap in temporal activity across the site (Δ_1 = 0.61 (95% CI: 0.46–0.69); Figure 3a), although peak activity times differed for each species (W = 38.32, p < .001). Cats were predominantly nocturnal while dingoes exhibited bimodal peaks in activity around dusk and late morning (Figure 3a). Notwithstanding these differences, dingoes did not appear to influence cat activity times (Δ_4 = 0.87 (95% CI: 0.84–0.97); Figure 3b), as cat temporal activity remained consistent regardless of whether dingoes were present or absent (W = 0.89, p = .641; Figure 3b). Cat temporal activity at the agricultural site was also consistent with activity times observed at the national park site (Δ_4 = 0.89 (95% CI: 0.84–0.95)); Figure 4a), with no difference in peak activity times observed across sites (W = 3.05, p = .218). In contrast, while there was some similarity in dingo temporal activity across sites (Δ_1 = 0.69 (95% CI: 0.55–0.80)), there were significant differences in peak activity times (W = 11.38, p = .003); Figure 4b), with dingoes being more diurnally active at the agricultural site and more nocturnal at the national park site. Given cat temporal activity remained consistent across sites,
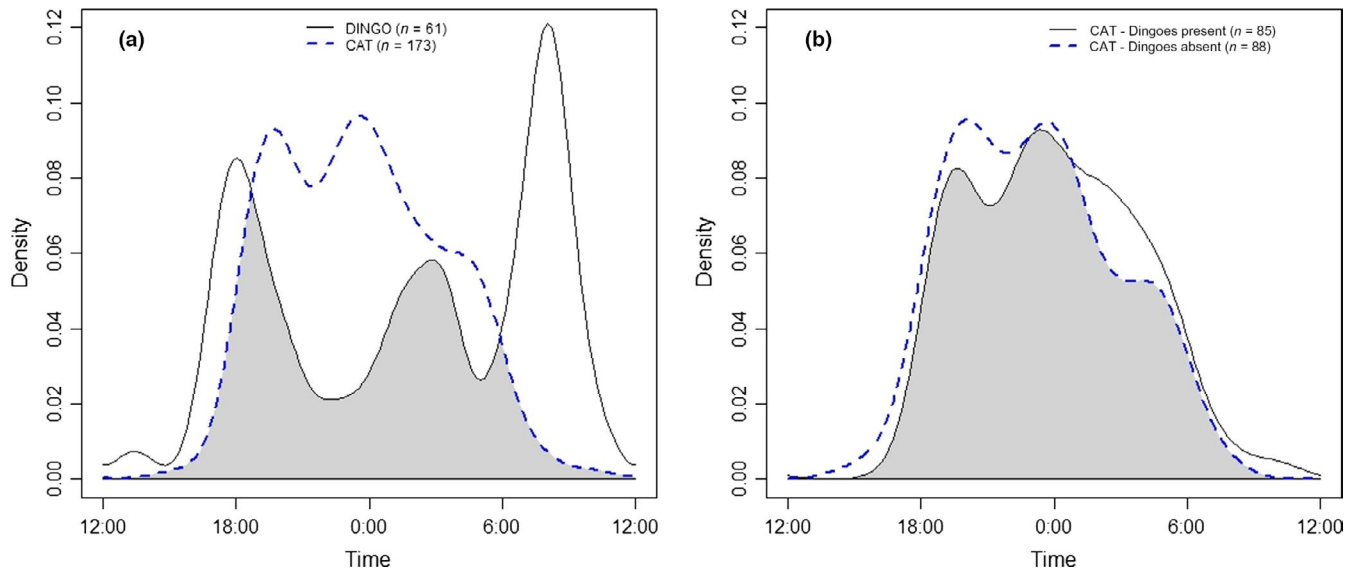
FIGURE 3 Dingo and feral cat temporal activity profiles at the agricultural site. Plot (a) shows overlap of dingo (solid line) and cat (dashed line) temporal activity. Plot (b) shows similarity in feral cat activity between areas with dingoes present (solid line) and areas with dingoes absent (dashed line). Shading indicates the extent of overlap/similarity in temporal activity. Sample sizes in parentheses indicate number of detection events
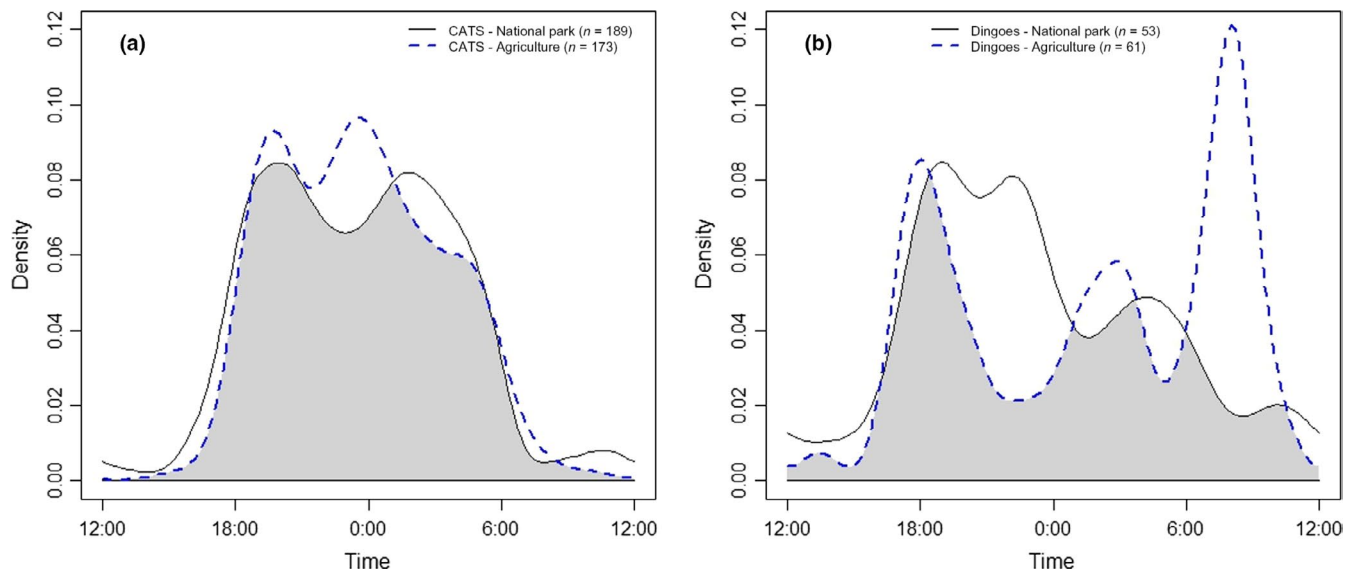

FIGURE 4 Comparison of (a) feral cat and (b) dingo temporal activity profiles across sites. Solid line shows temporal activity at the national park site and dashed line shows temporal activity at the agricultural site. Shading indicates the extent of temporal activity overlap/similarity for (a) cats or (b) dingoes across sites. Sample sizes in parentheses indicate number of detection events for each species at each site

regardless of whether dingoes were present or absent, and regardless of when dingoes were active, the observed separation between cat and dingo activity at the agricultural site (Figure 3a) reflects a difference in dingo activity times (Figure 4b), not a responsive shift in cat activity (Figure 4a).

3.3 | Spatial activity

We found no evidence that dingoes excluded feral cats from any areas on either site. At the national park site, dingoes were

detected across 60% (18/30 grids) of the site, with activity concentrated into the northern and western parts of the site (Figure 5). Cats were not restricted to dingo-free areas in the south-east of the site. Cats were detected in 93% (28/30) of grids, indicating that cats were widespread across the site, regardless of whether dingoes were present or absent (Figure 5). Several images of kittens and sub-adult cats were captured in grids with high dingo activity, suggesting that cats are successfully breeding and rearing young in parts of the park where dingoes were present. Many cameras in these areas also captured images of cats carrying large
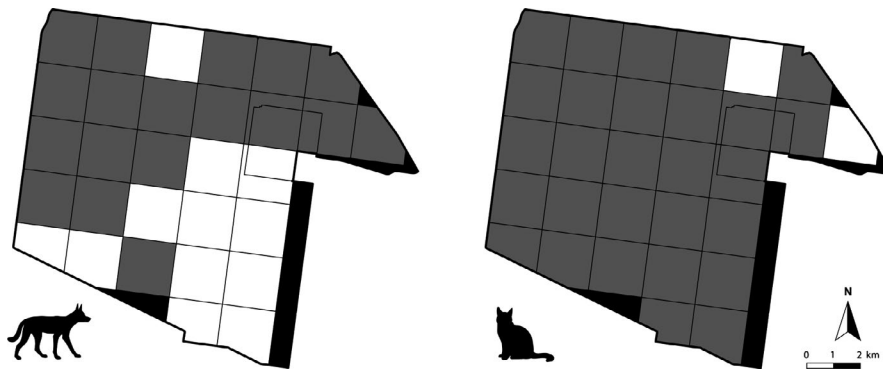
FIGURE 5 Spatial activity of dingoes (left) and feral cats (right) across the national park site. Grey shading indicates grids where each species was detected. White shading indicates surveyed grids where the species was not detected. Black shading indicates areas not surveyed

prey, including black-striped wallabies (*Macropus dorsalis*), common brushtail possums (*Trichosurus vulpecula*), European rabbits (*Oryctolagus cuniculus*) and rufous bettongs (*Aepyprymnus rufescens*), suggesting that the presence of dingoes is not restricting cats from hunting successfully.

Similar spatial overlap was observed at the agricultural site, with no evidence of any exclusion or spatial separation between dingoes and cats (Figure 6). Dingoes were detected across 60% (18/30 grids) of the site, while feral cats remained widespread, being detected in 93% (28/30) of grids (Figure 6).

3.4 | Within-night spatiotemporal activity

There was no evidence of within-night fine-scale spatiotemporal avoidance of dingoes by cats (Figure 7). Distance and time between dingo and cat detections were not inversely related at either the national park site (R^2 = .011, p = .202) or the agricultural site (R^2 = .001, p = .806).

3.5 | Species co-occurrence models

Dingoes did not influence the probability of cat presence, nor did they negatively affect the probability of cat detection at either site

(Figure 8). At the national park site (Figure 8a,c), the probability of cat presence did not differ between areas where dingoes were present (ψ^{BA} = 0.93 (95% CI: 0.46–0.99)) and areas where dingoes were absent (ψ^{Ba} = 0.95 (95% CI: 0.39–0.99)), and the probability of detecting a cat was actually higher in areas occupied by dingoes (r^{BA} = 0.18 (95% CI: 0.14–0.24)) than in dingo-free areas (p^B = .03 (95% CI: 0.01–0.08)).

We found similar, non-negative effects at the agricultural site (Figure 8b,d). The probability of cat presence in areas occupied by dingoes (ψ^{BA} = 0.80 (95% CI: 0.36–0.96)) did not differ from dingo-free areas (ψ^{Ba} = 0.69 (95% CI: 0.09–0.98)). Similarly, the probability of detecting a cat did not differ between areas occupied by dingoes (r^{BA} = 0.11 (95% CI: 0.07–0.17)) and dingo-free areas (p^B = .06 (95% CI: 0.02–0.19)).

4 | DISCUSSION

We found no evidence that the top-down effects exerted by an introduced apex predator influenced the activity of an invasive mesopredator. Dingoes and cats coexisted at both the national park site and the agricultural site, with cats abundant, widespread and active in sympatry with dingoes across both sites. Dingoes did not exclude feral cats from any areas (Figures 5 and 6), nor did they
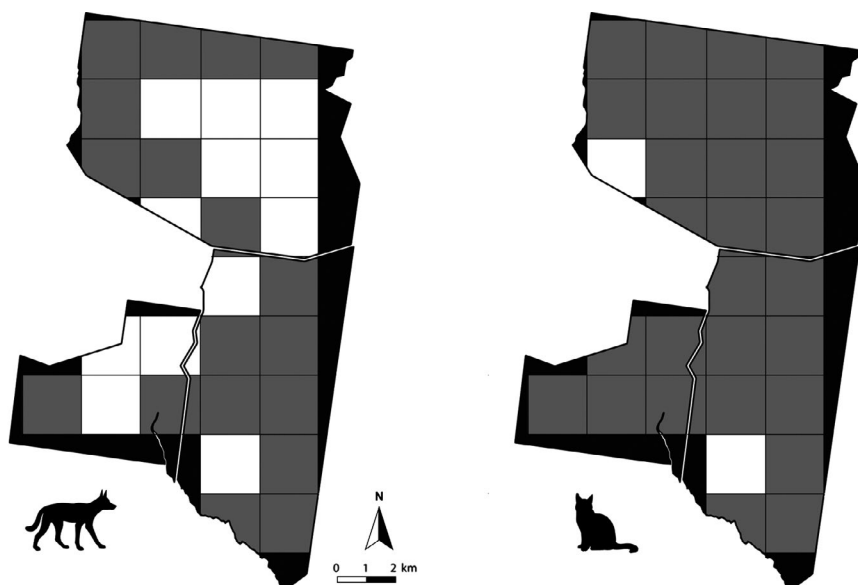

FIGURE 6 Spatial activity of dingoes (left) and feral cats (right) across the agricultural site. Grey shading indicates grids where each species was detected. White shading indicates surveyed grids where the species was not detected. Black shading indicates areas not surveyed
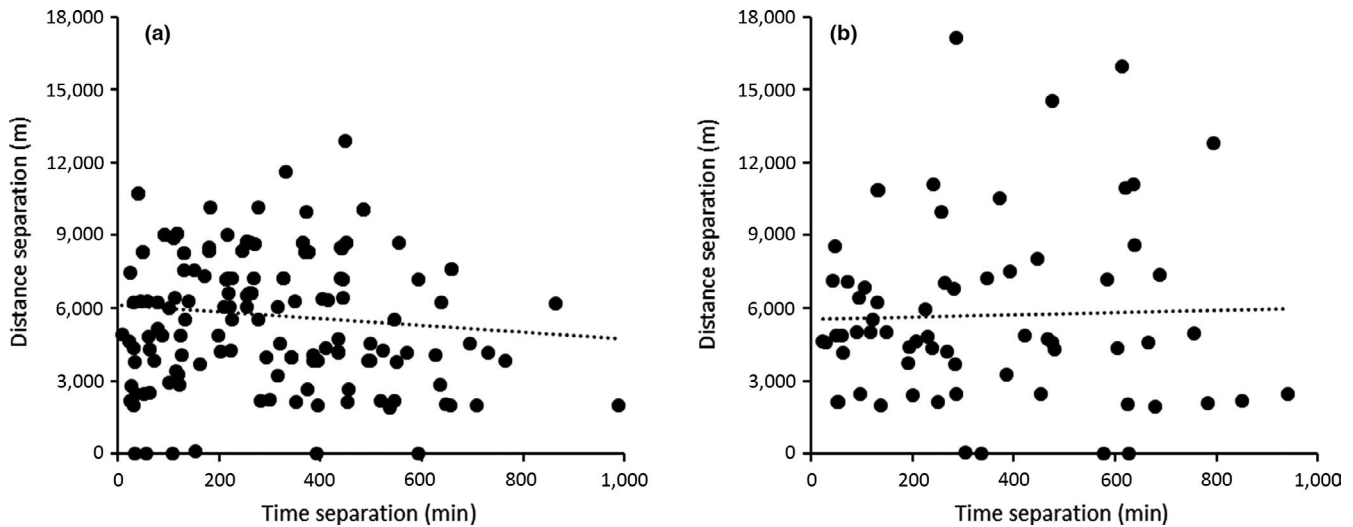
FIGURE 7 Cat detections categorized by distance and time to nearest dingo detection within the same night. Each data point represents a single feral cat detection at (a) the national park site; and (b) the agricultural site. Dashed line represents ordinary least squares regression line

negatively influence cat presence (Figure 8). Cat temporal activity remained consistent regardless of whether dingoes were present or absent (Figures 2b and 3b), regardless of when dingoes were active (Figure 2a), and regardless of land tenure (Figure 4a). There was some temporal separation evident between cats and dingoes at the agricultural site (Figure 3a), however, this was clearly due to higher diurnal activity by dingoes (Figure 4b) rather than cats altering their activity to avoid dingoes (Figure 4a). Collectively, our findings suggest that proposals to use dingoes to protect species of conservation significance by controlling feral cat activity, despite assertions to the contrary (Brook et al., 2012; Dickman et al., 2009; Letnic et al., 2009), are unsupported.

The inability of dingoes to exclude cats from any patches suggests that dingoes do not create spatial predation refuges for cat-susceptible wildlife. Our findings are consistent with studies in arid environs where even after intensive control efforts, cats and introduced red foxes (*Vulpes vulpes*) were still present, despite the heavy presence of dingoes (Bannister, 2014). The dingo arrived in Australia around 3,250–5,000 years ago (Jackson et al., 2019) while feral cats were only introduced to Australia around 200 years ago. This incursion, spread and establishment of feral cats across the entire country by around 1890 (Abbott, 2008), and the extinctions of native species that ensued (Woinarski et al., 2015), all occurred in the presence of dingoes (before dingo populations were subjected to modern-day control efforts in some areas; Allen et al., 2015). As dingoes were clearly unable to prevent low numbers of cats from breeding, expanding their range, and establishing across the entire continental land mass, it is extremely unlikely that they could now exclude or reduce the impacts of the estimated 2.1–6.3 million feral cats (Legge et al., 2017) that occur today. Despite a range of localized control efforts, feral cats still occur across >99.8% of Australia's land area (Legge et al., 2017), indicating that dingoes have been unable to exclude cats from any parts of the continent. While dingoes could potentially exclude cats over finer spatial scales, our study found

that was not the case (Figures 5–7). This combined evidence raises questions about the premise on which proposed restoration or reintroductions of dingoes are based.

The failure of dingoes to influence the temporal activity of feral cats (Figures 2–4) further suggests that dingoes do not create cat-free temporal refuges for vulnerable wildlife. In contrast, Brook et al. (2012) concluded that the reduced activity by dingoes at dusk was associated with higher cat activity at dusk on properties where dingoes were controlled. However, extracting values from figure 5 in Brook et al. (2012), the proportion of cat activity in the 4 hr after sunset did not differ between properties with (~40%) and without ~(37%) dingo control, and there was no significant difference in peak activity times for cats between properties with and without dingo control ($p = .053$, page 1282). Brook et al. (2012) also inferred that increased separation between cat and dingo temporal activity observed at properties where dingoes were controlled was 'feral cats responding to reduced dingo presence' (page 1284). However, their observed increased temporal separation was due to differences in dingo activity ($p < .001$, page 1282), not a shift in cat activity ($p = .053$, page 1282). Accordingly, despite their conclusions to the contrary, the findings of Brook et al. (2012) actually support our findings that cat temporal activity remained consistent, regardless of differences in dingo activity. We suggest the different temporal activity of dingoes between sites likely reflects differences in prey activity at those sites. For example, the predominant nocturnal activity of dingoes at the national park site matches the nocturnal activity of the wallabies, possums and bettongs frequently detected across the site, whereas the higher diurnal activity of dingoes at the agricultural site closely matches the activity of eastern grey kangaroos (*Macropus giganteus*) that dominate this site (B. Fancourt, unpublished data). More detailed comparisons of predator and prey activity are required to confirm reasons for the observed differences in dingo temporal activity across sites.
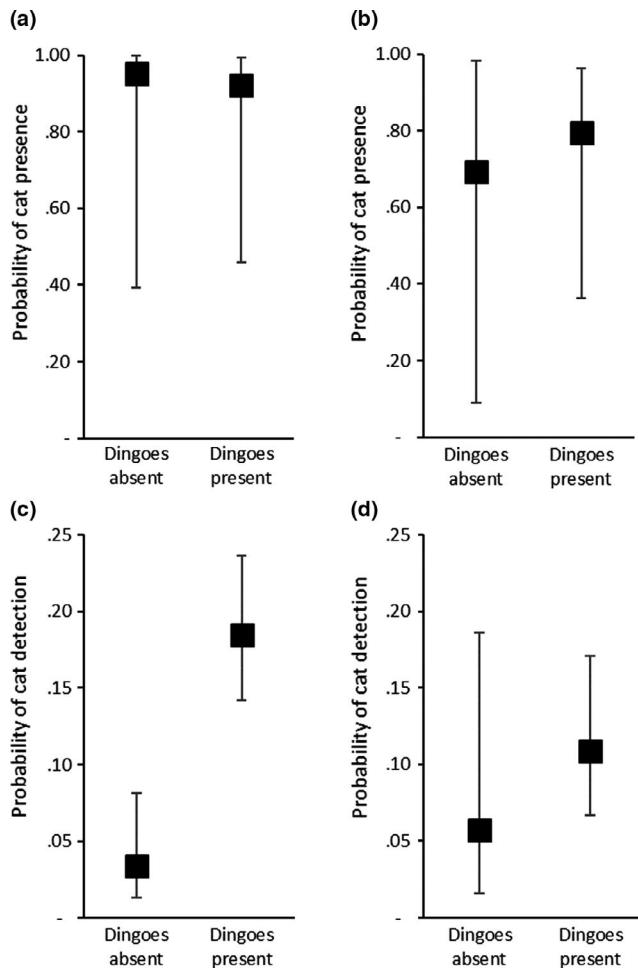
(a)

(b)

(c)

(d)

FIGURE 8 Effect of dingo presence on the probability of cat presence and detectability. Plots show species cooccurrence model estimates of the effect of dingo presence on (a) probability of cat presence at the national park site; (b) probability of cat presence at the agricultural site; (c) probability of cat detection at the national park site and (d) probability of cat detection at the agricultural site. Error bars show 95% confidence intervals

We found no evidence that despite close coexistence with dingoes, cats suffered any loss of fitness. We recorded numerous images of cats walking past cameras with large prey species, including wallabies, possums and bettongs, suggesting cats are still hunting effectively in areas with high dingo activity. Cats with kittens of various ages were also recorded on cameras in areas with high dingo activity, suggesting that cats are still breeding and successfully rearing young in the presence of dingoes, although the frequency with which this occurs could not be quantified from this study. Cat densities at the national park site (0.43 cats/km^2; Legge et al. (2017 table B1)) were actually 59% higher than the national average of 0.27 cats/km^2 (Legge et al., 2017), suggesting that dingoes are failing to reduce cat densities either directly or through reduced fitness and fecundity of cats. Even if dingoes are having unquantified effects on cat fitness, this has not translated into reduced cat abundance.

There are several possible explanations for our finding that dingoes do not appear to influence cat activity. First, the pervasiveness of feral cats in the presence of dingoes suggests that cats are unperturbed by dingoes at these sites. The observed significant overlap in both temporal and spatial activity creates a high probability that cats would encounter dingoes on a regular basis. Cats have likely adapted appropriate anti-predator responses to avoid dingoes, without altering when or where they are active. Observations of cats climbing trees (McGregor, Hampton, Lisle, & Legge, 2016; B. Fancourt, pers. obs.) or retreating to rock crevices (McGregor et al., 2016) to escape cat detection dogs, provides an insight as to how cats behave when confronted with a canid. We suggest that the ready availability of large trees across both of our sites would assist cats to temporarily seek refuge from passing dingoes. But differing habitat complexity can provide different levels of predation risk (Lima & Dill, 1990), suggesting that cats might be more vulnerable to dingoes in arid environments where trees are more sparsely distributed or absent. However, the ongoing persistence of cats in arid central Australia despite a heavy presence of dingoes (Bannister, 2014) suggests that cats are able to successfully use alternative forms of refuge, perhaps rabbit warrens or rock crevices (where available), in different environs. More detailed analysis of the fine-scale spatial activity of sympatric dingoes and cats is needed to elucidate how cats coexist with dingoes in such environments.

Second, the strength of any top-down effects by dingoes could be density dependent, with stronger effects at higher dingo densities and weaker effects at lower densities (Feit et al., 2019). Newsome et al. (2017) contend that the strength of top-down effects weakens as an apex predator's density decreases towards the edge of its range. However, dingoes are well established at both of our study sites, which are located in areas recording some of the highest abundance indices for dingoes (per Newsome et al., 2017). Dingo predation is also considered the major cause of adult mortality of the endangered bridled nailtail wallaby at the national park site (Fisher, Blomberg, & Hoyle, 2001). Accordingly, further increasing dingo densities at this site may have catastrophic outcomes for the species' ongoing conservation. As noted by Moseby, Neilly, Read, and Crisp (2012) and Allen and Fleming (2012), if the density of dingoes required to adequately suppress feral cats is too high, then any purported benefit to wildlife would be negated by increased predation rates by dingoes, rendering such approaches futile for conserving biodiversity. Increasing dingo densities in agricultural areas would also increase conflict with farmers due to increased attacks on livestock, particularly sheep (Fleming et al., 2014).

Third, the strength of top-down effects is thought to be dependent on the relative strength of bottom-up effects, with apex predators exerting stronger influence on mesopredators when prey is scarce and weak influence when prey is abundant (Greenville et al., 2014). In contrast, Feit et al. (2019) argued that top-down effects were dependant on the density of the apex predator, regardless of prey availability. This inconsistency is likely a function of the methods employed; both studies used uncorrected raw activity indices (number of camera detections and spotlight counts respectively) that do not incorporate detectability and are considered unreliable indicators of abundance (Fancourt, 2016;

Hayward & Marlow, 2014). In the current study, the absence of foxes from the national park site allows the persistence of many critical weight range ('CWR') prey species (35–5,500 g; Burbidge & McKenzie, 1989) that are highly susceptible to fox predation and hence are typically rare where foxes occur. While foxes were also absent from the agricultural site, the heavily modified grazing environment at this site had increased the suitability for cattle (*Bos indicus*) while CWR prey species were rare (B. Fancourt, unpublished data). Despite this contrast in prey availability, we found no influence of dingoes on cat activity, suggesting that the absence of any observed top-down effects by dingoes was not a function of prey availability.

Care should be taken in extrapolating our findings to other sites in different environs. Due to the large scale required for each site, and the intensity with which each site was monitored, our study was necessarily limited to two large-scale sites. We selected sites located in close geographical proximity and monitored both sites concurrently to minimize differences in environmental conditions that may have otherwise confounded our findings. The addition of further replicate sites would have unavoidably resulted in temporal and spatial mismatches, potentially introducing additional environmental effects that could not be controlled. Our study was also limited to winter, and as such, it is possible that results may differ in different seasons, as observed in Wang and Fisher (2012).

Our study reveals that despite assertions to the contrary, dingoes did not suppress the spatial or temporal activity of feral cats. Cats not only coexisted with dingoes, they remained abundant, active and widespread across the landscape. Dingoes did not appear to structure ecosystems to create predation refuges for cat-susceptible species. We suggest that proposals to restore or reintroduce apex predators such as dingoes to conserve biodiversity should be carefully evaluated on a site-by-site basis, as their ability to suppress cats and protect species of conservation significance will likely be context dependent.

AUTHORS' CONTRIBUTIONS

B.A.F. conceived the ideas and designed methodology. B.A.F., C.W. and P.C. collected the data. B.A.F. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6hb0063 (Fancourt, Cremasco, Wilson, & Gentle, 2019).

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