

# Living with the enemy: a threatened prey species coexisting with feral cats on a fox-free island

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## Abstract

**Context.** Feral domestic cats (*Felis catus*) have contributed to substantial loss of Australian wildlife, particularly small- and medium-sized terrestrial mammals. However, mitigating cat impacts remains challenging. Understanding the factors that facilitate coexistence between native prey and their alien predators could aid better pest management and conservation actions.

**Aims.** We estimated feral cat density, examined the impact of habitat cover on long-nosed potoroos (*Potorous tridactylus tridactylus*), and assessed the spatial and temporal interactions between cats and potoroos in the ‘Bluegums’ area of French Island, south-eastern Australia.

**Materials and methods.** We operated 31 camera stations across Bluegums for 99 consecutive nights in each of winter 2018 and summer 2018/19. We used a spatially explicit capture–recapture model to estimate cat density, and two-species single-season occupancy models to assess spatial co-occurrence of cats and potoroos. We assessed the influence of vegetation cover and cat activity on potoroo activity by using a dynamic occupancy model. We also used image timestamps to describe and compare the temporal activities of the two species.

**Key results.** Bluegums had a density of 0.77 cats per km<sup>2</sup> across both seasons, although this is a conservative estimate because of the presence of unidentified cats. Cats and long-nosed potoroos were detected at 94% and 77% of camera stations, respectively. Long-nosed potoroo detectability was higher in denser vegetation and this pattern was stronger at sites with high cat activity. Cats and potoroos overlapped in their temporal activity, but their peak activity times differed.

**Conclusions.** Feral cat density at Bluegums, French Island, is higher than has been reported for mainland Australian sites, but generally lower than in other islands. Long-nosed potoroos were positively associated with cats, potentially indicating cats tracking potoroos as prey or other prey species that co-occur with potoroos. Temporal activity of each species differed, and potoroos sought more complex habitat, highlighting possible mechanisms potoroos may use to reduce their predation risk when co-occurring with cats.

**Implications.** Our study highlighted how predator and prey spatial and temporal interactions, and habitat cover and complexity (ecological refuges), may influence the ability for native prey to coexist with invasive predators. We encourage more consideration and investigation of these factors, with the aim of facilitating more native species to persist with invasive predators or be reintroduced outside of predator-free sanctuaries, exclosures and island safe havens.

**Additional keywords:** biodiversity, conservation, habitat use, introduced species, invasive species, islands, pest management, population density, predator–prey interactions, wildlife management.

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## Introduction

Since their introduction to Australia ~200 years ago, feral domestic cats (*Felis catus*) have been implicated in at least 22 native mammal extinctions and continue to endanger an estimated 75 threatened or near-threatened mammal species (Woinarski *et al.* 2015). In particular, terrestrial mammals within an intermediate body mass range (peaking ~400 g), in low-rainfall areas and not dwelling in rocky habitats are at the highest risk of cat predation (Woolley *et al.* 2019).

These mammals fall within the ‘critical weight range’ (35–5500 g), which are species considered most at risk of extinction in Australia (Burbidge and McKenzie 1989). The severity of cat impacts may be compounded by the naïveté of Australian mammals to the threat of eutherian predators (Banks and Dickman 2007), the introduction of European rabbits causing hyperpredation (Pedler *et al.* 2016), and the loss of habitat cover and complexity (Doherty *et al.* 2015b).

Protecting native fauna from invasive predators is not only important to prevent extinctions, but also to mitigate negative impacts cascading through Australian ecosystems (Clout and Russell 2007; Doherty *et al.* 2017). For instance, digging mammals, such as bandicoots, bettongs and potoroos, perform important ecological functions, including soil turnover, nutrient cycling, plant recruitment and regeneration, and mediation of fire regimes (Fleming *et al.* 2014; Halstead *et al.* 2020). However, despite cats playing a major role in the decline and extinction of many of Australia's terrestrial mammals, and, hence, the disruption or loss of their ecological functions, the management of cats and mitigation of their impacts remains challenging and often unsuccessful (Doherty *et al.* 2017).

One common approach in threatened species management is the use of predator-exclusion fencing (Dickman 2012; Legge *et al.* 2018). Although conservation fences can be very successful, they require on-going monitoring, incur high building and maintenance costs, and introduce a series of challenges by increasing the chances of inbreeding and overpopulation, and limiting dispersal (Somers and Hayward 2012; Moseby *et al.* 2018). Furthermore, with many threatened species existing in predator-free areas, there can be negative implications for future reintroductions into areas where these predators are present (Bannister *et al.* 2018; Jolly *et al.* 2018). Relying on predator exclusion could generate a negative feedback-loop whereby native species' reliance on exclusion areas inhibits anti-predator behaviour, and fewer wildlife practitioners are willing to undertake the risk of broad-scale reintroductions (Moseby *et al.* 2019).

An alternative approach has been the management of introduced predators in the form of culling or eradication programs. Cat eradication from islands has resulted in the significant recovery of several threatened vertebrate species (Jones *et al.* 2016). However, reducing cat populations in large, unfenced mainland sites remains difficult and has had variable success as a result of dependence on bait and trap-lure uptake (Moseby and Hill 2011; Algar *et al.* 2013). In instances where eradication is not feasible, management is commonly undertaken in the form of culling programs that aim to reduce rather than eradicate invasive predators (Doherty and Ritchie 2017). However, this form of management does not always benefit the species it is designed to protect and sometimes can even negatively affect them (Rayner *et al.* 2007; Lazenby *et al.* 2014; Marlow *et al.* 2015). This is because current culling practices are typically unselective in their approach and can result in the retention of 'problem' cats responsible for high predation rates (Moseby *et al.* 2015), or the removal of dominant cats, allowing for influxes of subordinate individuals (Lazenby *et al.* 2014). Furthermore, the success of culling programs largely depends on sustained and intensive efforts, and ongoing monitoring (Lazenby *et al.* 2014), which may not be the most efficient use of conservation funds.

With feral cats now present across 99.8% of Australia's land area (Legge *et al.* 2017), there is an urgent need to understand how we can mitigate their impacts on native fauna. Devising appropriate pest management requires an understanding of feral cat ecology, the ecology of the prey species being affected, and the relationship between cat density and impact (McGregor *et al.* 2015; Frey *et al.* 2017). Currently, this information is generally not available for most habitats and regions across Australia

(Legge *et al.* 2017). Further, native mammals vary in their ability to survive in the presence of cats (Radford *et al.* 2018; Moseby *et al.* 2019) and this should be taken into consideration by land managers. Some species cannot persist in the presence of even low cat densities (Doherty *et al.* 2017), whereas others coexist with cats in mainland habitats (Ziembicki *et al.* 2015; West *et al.* 2018) or on islands (Algar *et al.* 2011).

The long-nosed potoroo (*Potorous tridactylus tridactylus*) is one example of a threatened, native critical weight range mammal that is currently coexisting with feral cats on fox-free French Island, Victoria, Australia. It is currently unknown how this population of long-nosed potoroos is persisting in the presence of feral cats. Previous research suggests that prey able to avoid initial extinction may persist with their alien predators over many generations, enabling them to develop appropriate anti-predator behaviour (Banks *et al.* 2018). To gain a better understanding of this predator-prey relationship, we estimated cat density, examined spatial and temporal interactions between the two species, and assessed the impact of habitat cover on cat density and long-nosed potoroo activity. This information may help explain the environmental context and circumstances under which native prey species that are susceptible to invasive predators can persist in their presence. This, in turn, may provide insights that help facilitate better threatened species management outcomes, including potential species reintroductions, in the extensive areas currently occupied by invasive predators.

The specific aims and corresponding predictions of our study were as follows:

- (1) Estimate feral cat density to assess the possible numerical relationship between cat density and long-nosed potoroo persistence. Estimating a baseline density of cats on French Island can help develop thresholds at which species including long-nosed potoroos can tolerate cats where foxes are absent. We predict that cat density on French Island will be higher than on mainland Australia on the basis of a continent-wide review (Legge *et al.* 2017).
- (2) Examine the spatial interactions between cats and long-nosed potoroos. Intermediate-mass mammals (peaking ~400 g) are cat's preferred prey (Woolley *et al.* 2019); however, terrestrial mammals at a similar mass to that of long-nosed potoroos (<1500 g) are considered at high risk of cat predation (Andren *et al.* 2018; Moseby *et al.* 2019). If cats are the main predator of long-nosed potoroos on French Island, there may be a spatial relationship between the two species.
- (3) Examine the temporal interactions between cats and long-nosed potoroos. Temporal partitioning has been observed in predators (Hernandez-Santin *et al.* 2016) and, more recently, between native predators and their prey (Cunningham *et al.* 2019b). Given that cats are most likely the main predator of long-nosed potoroos on French Island (Frankham *et al.* 2011), we expected that potoroos may show fine-scale avoidance of cats by shifting their temporal activity to reduce predation risk.
- (4) Assess the impact of habitat cover (ecological refuges) on cat density and long-nosed potoroo detectability. Simplification of habitat through fire, grazing or human disturbances can exacerbate invasive predator impacts on native species (Doherty *et al.* 2015b). We, therefore, expect that dense ground cover is important for long-nosed potoroo

nesting and concealment from predators, as demonstrated in other regions of Australia for this and similar species (Holland and Bennett 2007; Andren *et al.* 2018; McHugh *et al.* 2019).

## Materials and methods

### Study area

Our study was conducted on Victoria's largest island, French Island (~170 km<sup>2</sup>), located in Western Port, south-eastern Australia. The island is mostly flat, with a maximum elevation of 98 m. The climate is mild, with an average annual maximum temperature of 18.7°C and an average annual rainfall of 696.7 mm (from nearby Rhyll weather station; Bureau of Meteorology 2018). Our study site was 'Bluegums' (~3 km<sup>2</sup>), which is located within French Island National Park (−38.398, 145.378; Fig. 1).

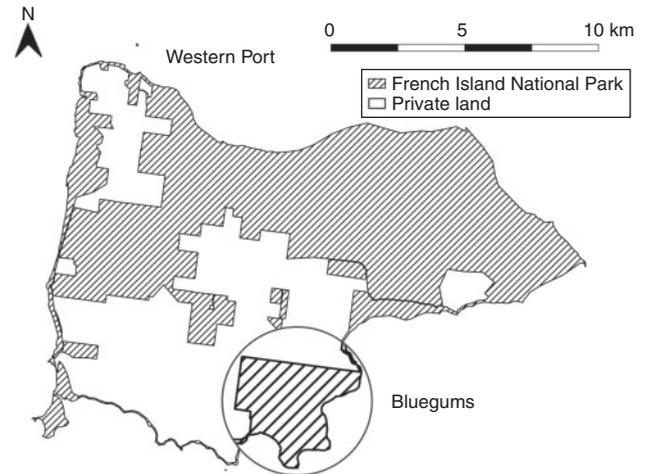
Bluegums was chosen because it has suitable habitat for a planned assisted colonisation of the mainland eastern barred bandicoot subspecies (*Perameles gunnii*, unnamed subspecies; Hill *et al.* 2018), which is currently considered *Extinct in the Wild* under the Victorian Advisory List of Threatened Vertebrate Fauna 2013. Bluegums consists of ungrazed grassland (retired pasture) and dense stands of prickly teatree (*Leptospermum continentale*), with some areas being slashed for vehicle access. The perimeter of Bluegums has denser vegetation dominated by austral bracken (*Pteridium esculentum*), messmate (*Eucalyptus obliqua*), prickly teatree (*Leptospermum continentale*) and sword-grass (*Gahnia* spp.), with scattered manna gum (*Eucalyptus viminalis*) and swamp gum (*Eucalyptus ovata*; VicFlora 2018). Apart from cats, the island lacks any other medium-sized (2–10 kg) terrestrial mammalian predators, but has multiple species of predatory birds and reptiles (DELWP 2018).

### Study species

The long-nosed potoroo is the smallest member of the Potoroidae family, with mature individuals on French Island weighing ~700–1300 g (Frankham *et al.* 2011). Long-nosed potoroos are ecological specialists that are highly susceptible to habitat loss and fragmentation (Holland and Bennett 2007; Frankham *et al.* 2014; McHugh *et al.* 2019). Their diet predominantly consists of sporocarps (truffles) of hypogeous fungi and their foraging disperses fungal spores critical for forest health (Claridge *et al.* 1993; Vernes and Jarman 2014). Previous research suggests that the long-nosed potoroo population on French Island exists at a low but stable density ( $0.33 \pm 0.01$  potoroos ha<sup>-1</sup>), with a low juvenile recruitment and turnover rate (Frankham *et al.* 2011). Currently, long-nosed potoroos are listed as *Vulnerable* under the Commonwealth *Environment Protection and Biodiversity Conservation Act* 1999 and *Threatened* in Victoria under the *Flora and Fauna Guarantee Act* 1988.

### Camera station setup

We deployed 39 infrared motion-sensing cameras (HyperFire HC600, Reconyx, Holmen, WI, USA) within Bluegums. Because density modelling relies on the ability to detect and



**Fig. 1.** Map of French Island, Victoria, south-eastern Australia, showing study site 'Bluegums'.

identify individual cats on multiple cameras, we deployed cameras at 300-m intervals to increase the likelihood of individuals being detected at more than one camera station (McGregor *et al.* 2015; Stokeld *et al.* 2015). Ideally, camera trap placements would be uniform in their distribution; however, this was not always feasible because sections of the site had thick, largely impenetrable vegetation. We accounted for this limitation by using the individual camera method in the analyses, where distance from each camera remained constant regardless of survey design (Balme *et al.* 2009). To aid identification of individual cats, we deployed two cameras at every fourth station; this maximised the chance of cats being photographed from two angles (Fig. 2; Kilshaw *et al.* 2015; McGregor *et al.* 2015). As a result, we had a total of 31 camera stations across the study area.

Cameras were mounted ~50 cm from the ground and angled slightly downward, then tested using the 'walk test' function to achieve a detection height of ~20–30 cm (the average height of a cat). Cameras were deployed for two seasons; the first deployment occurred from April to June 2018 (hereafter, 'winter'), and the second deployment from December 2018 to March 2019 (hereafter, 'summer'). For each season, cameras were deployed for 99 consecutive nights to maximise cat detections (Stokeld *et al.* 2015). All cameras were set to 'high' sensitivity and 'balanced' night mode. Cameras took five consecutive photos per trigger, with a 30-s delay period between triggers. Camera stations were passive, because cats can exhibit individual variation in lure avoidance or attraction (Kilshaw *et al.* 2015). Similarly, lures can also lose their potency through time or lead to altered activity patterns where animals are going to lures to seek out food, which can bias inferences regarding species' spatial and temporal interactions (Frey *et al.* 2017; McHugh *et al.* 2019).

### Density estimate

We created capture histories for each of the winter and summer survey periods, where we included individual cats and their corresponding daily camera trap visits (occasions) for each



Fig. 2. Anterior and lateral perspective of a cat captured at a station with two cameras.

station. We defined the time interval between occasions as 24 h. Individual cats were identified on the basis of differences in morphological features, including coat colour, number and positions of stripes and patches on coat, distinct markings (e.g. black cat with white neck patch), and tail length and thickness relative to body. Cats that could not be confidently identified on the basis of these criteria were excluded from the analysis. Kittens were also excluded because they are dependent on an adult for survival.

Density was estimated using a spatially explicit capture–recapture model using the ‘secr’ package in R (R Core Team 2017; Efford 2019). One of the requirements of this model is to have a sufficient number of recaptures of individual cats where sufficient recaptures is defined as  $>1$  (Efford *et al.* 2009). This recapture rate was calculated by dividing the mean number of recaptures ( $r$ ) by the number of individual cats ( $n$ ; Efford *et al.* 2009). To aid the estimation of the model parameters, we created a home-range buffer around each camera station using QGIS (QGIS Development Team 2019). This buffer was based on mean maximum cat home-range size. We chose a mean maximum cat home-range of 5.1 km<sup>2</sup> on the basis of previous research by Luna-Mendoza *et al.* (2011) who determined feral cat home-range on an island which had an area, climate and vegetation type similar to those of French Island. On the basis of this home-range, we calculated a buffer radius of 1274.5 m (assuming a circular home-range of 5.1 km<sup>2</sup>), took the outer-most limit of the buffer and applied it to each of the camera stations.

The second assumption of the capture–recapture model is that every cat has a centroid home range and that the probability of detecting an individual decreases as distance between their home-range centre and camera trap increases (Krebs *et al.* 2011). To estimate this detection probability, we determined which functional form (half-normal or hazard rate) best fit the observed data. The detection function describes the decline in detection probability with distance from the home-range centre (Efford 2019). Using the optimal detection function, we assessed the influence of vegetation cover on feral cat density. Vegetation cover was estimated as the mean normalised vegetation difference index (NDVI) within a 50-m buffer around each camera station. We calculated NDVI using Sentinel 2 satellite imagery from the 7 February 2018 at a resolution of 10 m. Mean NDVI values ranged between 0.33 and 0.62, with higher values

representing higher environmental productivity. The preferred detection model was selected on the basis of Akaike’s information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We also calculated the AIC weights ( $w$ ), which represented the proportional weight for each model (Burnham and Anderson 2002). The ‘best’ model was chosen on the basis of the lowest AIC score. We then fitted a density model using NDVI to assess whether this habitat covariate had a statistical influence on cat density. The NDVI model was compared with the previously preferred model using AICc. We used the ‘best’ model to determine cat density with lower and upper 95% confidence intervals.

#### Assessing spatial relationships

We used two-species single-season occupancy models to assess spatial co-occurrence between cats and potoroos. We developed nightly detection histories (presence or absence within 24 h) for cats and long-nosed potoroos across the 99 sampling nights. We fitted models in PRESENCE version 12.22 (MacKenzie and Hines 2018) to calculate the probability of occupancy (estimated occupancy), which accounts for imperfect detection. Using this model, we assessed whether the presence of cats influenced the detection probability of long-nosed potoroos. We compared a ‘full’ model and ‘reduced’ models (MacKenzie *et al.* 2018). These three models compare estimated detection probability of potoroos ( $pB$ ) with the detection probability given that cats are present and detected ( $rBA$ ) versus when cats are present but not detected ( $rBa$ ; where A = cat and B = long-nosed potoroo).

The full model estimates the detection probability independently, whereas the reduced model assumes that the detection probabilities of potoroos are the same irrespective of whether or not cats are present and detected or present and not detected ( $rBA = rBa$ ), and irrespective of whether cats are detected ( $pB = rBA = rBa$ ; MacKenzie *et al.* 2018). We also calculated a species interaction factor (SIF), which is an absolute measure of co-occurrence and determined the direction of interaction for the two species (MacKenzie *et al.* 2018). A negative SIF value suggests that species occupancy is not the result of interaction between the two species, whereas a positive SIF value suggests that occupancy differences are the result of interaction (Hernandez-Santin *et al.* 2016). We selected for the best model by using AIC. Our sites were not independent for the detection of cats, meaning that we do not meet the assumption for the

occupancy parameter of the model. We report the site occupancy of cats (psiA), occupancy of potoroos given that cats are present (psiBA) and occupancy given that cats are absent (psiBa) from the best detection model; however, these occupancy results should be interpreted with caution. Individual models were run for each season.

To further explore how potoroo occupancy is influenced by spatial variables, we used a dynamic (multi-season) occupancy model to assess the role of NDVI and cat activity (the number of 10-min presences of a cat per day per site). Using the unmarked package in R (Fiske and Chandler 2011), we fitted models with NDVI, cat activity and their interaction as covariates of either detection probability, occupancy, or both. We compared the three models using AICc and plotted model estimated relationships with 95% confidence intervals to make inferences.

### Assessing temporal activity

We developed a series of ‘events’ for cats and long-nosed potoroos where an ‘event’ represented detections of the same species within a 10-min period at a single camera station. Single events could have been made up of multiple detections. We extracted the timestamps within the image metadata to assess the temporal activity of cats and long-nosed potoroos, and potential evidence of interactions over a 24-h period. We converted image timestamps into radians, because time of day is a circular (periodic) random variable. We then generated activity curves for the two species using the ‘overlap’ package in R (Ridout and Linkie 2009; R Core Team 2017). This package allowed us to fit a kernel-density function to analyse activity through a circular inferential statistical approach (Frey *et al.* 2017).

The kernel density function of the ‘overlap’ package (Ridout and Linkie 2009) allowed us to estimate a symmetrical coefficient of overlap ( $\Delta$ ) between cats and long-nosed potoroos, using the total variation distance function (Ridout and Linkie 2009). We then estimated the precision of  $\Delta$  by bootstrapping the dataset 10 000 times, resulting in an overlap range of 0–1, where 0 represents no overlap and 1 represents complete overlap. As  $\Delta$  is a relative measure (Ridout and Linkie 2009), interspecific differences between cat and long-nosed potoroo activity patterns were also tested for statistical significance by using the non-parametric circular Mardia–Watson–Wheeler (MWW) statistical test (Frey *et al.* 2017). The cat data showed a crepuscular activity curve (i.e. bimodal), but the MWW test assumes a unimodal distribution of activity (Frey *et al.* 2017). We, therefore, created a secondary sampling structure where we split cat and long-nosed potoroo peak activities into diurnal and nocturnal periods. These two activity periods were then compared for the two species for both seasons.

## Results

### Cat density

Of the 586 adult-cat detections across both seasons, 68% of cats were confidently identified as individuals and given unique identification numbers; detections that were ambiguous (32%) were not included in the analysis. This resulted in 13 individual cats with a recapture rate of 2.54 ( $n/r = 33/13$ ). Of the 13 individuals, two were identified as potentially being free-ranging owned cats, but we did not exclude them from the

analysis. The hazard rate detection function (AICc = 4068.62,  $w = 1$ ) was supported over the half-normal function (4092.53, 0). The model including NDVI as a covariate of cat density was not well supported (4071.80, 0.17); thus, the baseline model with the hazard rate detection function was used to estimate cat density as 0.77 cats per km<sup>2</sup> (95% CI: 0.48–1.21), which was the same across both seasons. This is a conservative estimate because of the exclusion of unidentifiable cats.

### Cat and long-nosed potoroo detections

Cats, including kittens, were detected 610 times across both seasons and had a naïve occupancy of 94% (winter: 84%; summer 90%). Three detections showed cats with long-nosed potoroos in their mouths at night. Long-nosed potoroos were detected 938 times and had a naïve occupancy of 77% (winter: 74%; summer: 77%). Cats were not detected at two camera stations, both of which had high vegetation cover (NDVI = 0.51 or more). Long-nosed potoroos were not detected at seven camera stations. Four of those were near the track in the centre of Bluegums, which is dominated by retired pasture. Long-nosed potoroos had a higher number of detections on the perimeter of Bluegums where NDVI was generally higher, whereas cats had a higher number of detections along the road and track (Fig. 3).

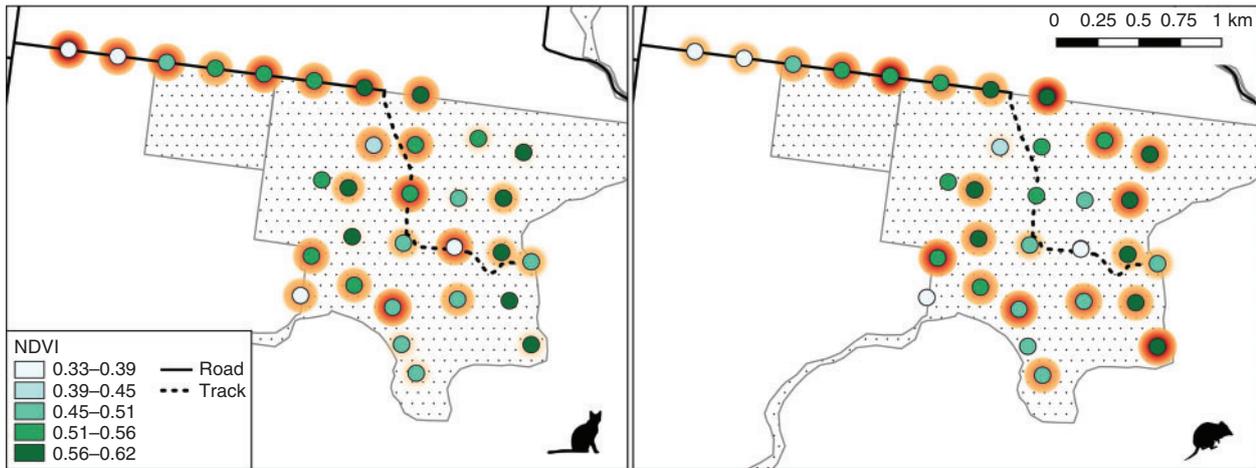
### Cat and long-nosed potoroo spatial interactions

Detection probability of long-nosed potoroos when cats were present was equal to when cats were not present, in both seasons (i.e.  $pB = rBA = rBa$ ; winter: AIC = 3589.37,  $w = 1$ ; summer: AIC = 3644.57,  $w = 1$ ). This indicates that the presence of cats did not influence the detection probability of long-nosed potoroos. Winter occupancy of long-nosed potoroos when cats were present was slightly less (psiBA = 0.73, 95% CI: 0.53–0.87) than that when cats were absent (psiBa = 0.80, 0.31–0.97). Whereas summer occupancy of potoroos when cats were present was greater (psiBA = 0.78, 0.59–0.90) than that when cats were absent (psiBa = 0.50, 0.12–0.88). Cats and potoroos had a positive co-occurrence value for both seasons (winter SIF = 0.98; summer SIF = 1.05), suggesting that long-nosed potoroo station occupancy was higher where cats were present.

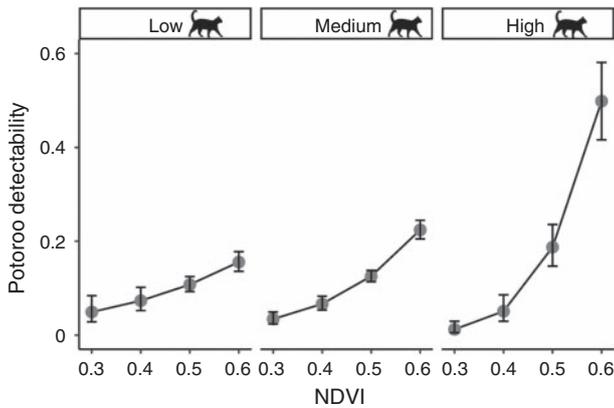
The dynamic occupancy model with an interactive effect of NDVI and cat activity on potoroo detection probability was more strongly supported (AICc  $w = 0.97$ ) than were models where occupancy ( $\Delta$ AICc = 146.17,  $w = 0.00$ ), or both occupancy and detectability (6.88, 0.03), varied according to NDVI interacting with cat activity. There were clear effects of NDVI (estimate = 4.23, 95% CI = 2.01–6.46), cat activity (–15.14, –24.20–6.08) and their interaction (34.6, 18.11–51.08). Potoroo detectability increased with an increasing NDVI and this effect was much stronger when cat activity was highest (Fig. 4).

### Cat and long-nosed potoroo temporal interactions

Over both seasons, cats had a crepuscular activity curve, with a major peak in activity around dusk and another smaller, but clear, activity peak in the hours near dawn. Long-nosed potoroos had a nocturnal activity curve where activity increased in the first few hours following dusk (Fig. 5). Cats and long-nosed potoroos shared 64% of their temporal activity in winter (95% CI = 0.57–0.69) and 76% in summer (0.68–0.80). Long-nosed



**Fig. 3.** Map of Bluegums, showing mean normalised vegetation difference index (NDVI) at each camera station. Heat-map underlay denotes frequency of cat (*Felis catus*) and long-nosed potoroo (*Potorous tridactylus tridactylus*) detections for both seasons (winter and summer combined).



**Fig. 4.** Changes in potoroo detectability as a function of mean normalised vegetation difference index (NDVI; x-axis) at sites with low, medium or high cat activity. Cat activity is measured as the number of 10-min presences of a cat per day per site. Low activity represents the minimum recorded (0), medium is the mean (0.08) and high is the maximum (0.3). Points are model predicted estimates with 95% confidence intervals.

potoroos showed a difference in their peak activity time from that of cats for both the diurnal (winter:  $W = 57.782, P < 0.001$ ; summer:  $W = 17.641, P < 0.001$ ) and nocturnal (winter:  $W = 35.936, P < 0.001$ ; summer:  $W = 9.9125, P = 0.01$ ) activity periods. When evening cat activity started to subside about 1900 hours in winter, long-nosed potoroo activity continued to increase and peaked about 2130 hours (Fig. 5). In summer, cat activity still peaked early in the night about 2030 hours and started to subside at 2100 hours, then showed a minor, but clear, increase during long-nosed potoroo peak activity (0100 hours) and at dawn.

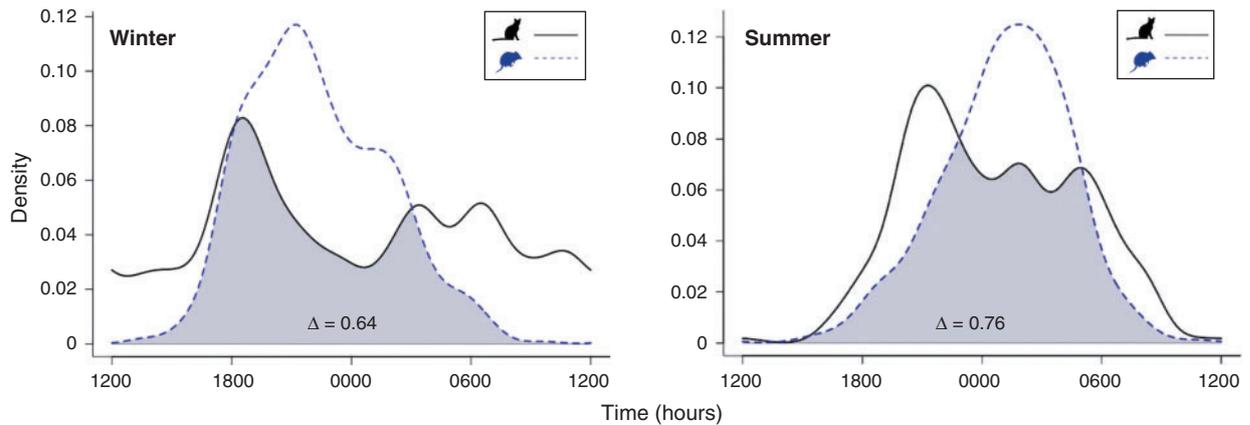
**Discussion**

Understanding potential environmental and behavioural mechanisms that may affect the coexistence of native prey and invasive predators has important implications for biodiversity

conservation, and pest and wildlife management. In our study, we found that (1) the cat population density in Bluegums was 0.77 cats per km<sup>2</sup>, (2) long-nosed potoroo spatial occupancy was positively associated with the presence of cats, but their activity typically decreased with an increasing cat activity, (3) cats and long-nosed potoroos overlapped in their temporal activity, but their peak activity times differed, and (4) long-nosed potoroo detectability was higher in denser vegetation cover and this effect was stronger in areas of high cat activity. In the absence of foxes, potoroos are currently coexisting with feral cats, and multiple factors (a ‘moderate’ cat density, temporal avoidance and predation-risk minimisation, and refuge availability) are likely to be important. These factors require further and urgent examination in this and other ecosystems, to help guide the conservation of native wildlife outside of invasive predator-free areas.

*Cat density*

We showed that long-nosed potoroos in Bluegums, French Island, are coexisting with an estimated cat population density of 0.77 cats per km<sup>2</sup>. This density is higher than that tolerated by similar-sized or larger critical weight range mammals, such as the burrowing bettong (*Bettongia lesueur*) and greater bilby (*Macrotis lagotis*), which in the study by Moseby et al. (2019) tolerated a cat density of up to 0.46 cats per km<sup>2</sup> inside a fenced reserve, notably in an area of more open vegetation. Similar to our study, this estimate was in the absence of other mammalian predators (e.g. foxes), and it is important to note that the incursion of a fox (*Vulpes vulpes*) in the Moseby et al. (2019) study resulted in the collapse of the burrowing bettong population. Our estimate is also similar to that of McTier (2000) who estimated cat density in southern French Island (including Bluegums) as 0.4–1.1 cats km<sup>2</sup> (midpoint 0.75). Relative to the rest of Australia, cats in Bluegums occur at a higher density than in mainland locations (Legge et al. 2017), and this may be due to the absence of medium-sized or larger mammalian predators that have been shown to suppress cats (Risbey et al. 2000; Marlow et al. 2015), or because of higher food availability on islands (Legge et al. 2017). However, cat density at Bluegums



**Fig. 5.** Temporal activity of cats (*Felis catus*) and long-nosed potoroos (*Potorous tridactylus tridactylus*) for winter and summer. Overlap coefficient ( $\Delta$ ) denotes the area shaded in grey.

was lower than that on smaller fox-free islands (e.g. Phillip Island and Macquarie Island, although cats were eradicated from the latter in 2000), which is consistent with the negative relationship between cat densities and island size demonstrated by Legge *et al.* (2017).

#### Habitat structure, use and predation risk

Vegetation cover as reflected by NDVI did not appear to influence cat density, being similar to the findings of Legge *et al.* (2017). However, potoroos detectability increased with an increasing vegetation cover (NDVI) and, at higher cat activity levels, the role of vegetative cover appears to be increasingly important. A study from south-western Victoria concluded that long-nosed potoroos require a mosaic of habitats that include dense cover for diurnal shelter, and open, less dense vegetation for nocturnal foraging (Bennett 1993). However, foraging habitat may be selected not only for its profitability, but also in terms of its predation risk. When the best feeding areas are also the most dangerous, prey species may trade off resource gain to avoid predation risk by altering where they forage (Lima and Dill 1990; McHugh *et al.* 2019). Previous research has shown that the introduction of a predator species to an island population increased the risk-sensitive foraging behaviour of its prey species (Cunningham *et al.* 2019a). Frankham *et al.* (2011) reported that potoroos on French Island rarely moved out of mature remnant vegetation into disturbed areas with a lower vegetation cover. Our results suggest that where cats are more active, potoroos may be selecting for more complex vegetation where predation risk is presumably lower (see McGregor *et al.* 2015). On the basis of the described foraging behaviour of long-nosed potoroos, foraging would be expected to occur in the more open vegetation of Bluegums, and, so, our results may indicate a shift in behaviour in response to cats. If cats are eradicated from French Island, these results provide an opportunity for future research to quantify possible shifts in potoroos habitat use with shifts in predation risk. Furthermore, our results may suggest that complex habitat may serve as a refuge from predation for potoroos, which may be facilitating their coexistence with cats. Although this possibility requires further examination, the higher detection rate of potoroos in denser vegetation does highlight the importance of

vegetation cover for this species, as has been suggested for other species (Doherty *et al.* 2015b; Reside *et al.* 2019).

#### Cat and long-nosed potoroos spatial interactions

Long-nosed potoroos occupancy was greater in the presence of cats. This positive spatial relationship is likely to be due to the widespread distribution of cats across our study site, and a general lack of sites where long-nosed potoroos were present without cats. However, it is also plausible that cats are actively tracking potoroos as prey or other prey species that co-occur with potoroos. Although this observed relationship does not necessarily represent a causal link, evidence in support of this hypothesis was multiple camera trap images showing cats carrying young long-nosed potoroos in their mouths. These potoroos were likely to have recently been killed by the same cats rather than scavenged, because scavenging is typically rare in cats (Doherty *et al.* 2015a). These results are consistent with a previous study, suggesting that low long-nosed potoroos juvenile recruitment on French Island may be the result of juveniles and subadults being preyed on by cats (Frankham *et al.* 2011). However, this low recruitment may also be the result of intrinsic population regulation because French Island is a fragmented landscape, and remnant patches of National Park suitable for long-nosed potoroos may have reached their carrying capacity or may be restricted by limited dispersal pathways. Further work examining potoroos population ecology, movement and genetics should investigate these possibilities and their potential conservation consequences.

#### Cat and long-nosed potoroos temporal interactions

Cats exhibited a largely crepuscular activity pattern with peak activity just after dusk but also in the early hours of the morning. Previous research examining two different island cat populations in the USA found that the island with a large population of owned cats showed crepuscular activity, whereas an island with mostly feral cats coexisting with other land predators showed mostly nocturnal activity (Cove *et al.* 2018). The study concluded that crepuscular activity was most likely to be due to owned cats exhibiting peak activity when first being let out in the morning and before coming inside at night, and nocturnal activity on the

island with predominantly feral cats was most likely the result of intraguild avoidance of other predators by cats (Cove *et al.* 2018). Furthermore, Hernandez-Santin *et al.* (2016) concluded that feral cats were mostly nocturnal and peak activities were lowered in the presence of dingoes. In our study, crepuscular activity may have been observed because there is an absence of other mammalian predators (e.g. foxes, dingoes, and domestic dogs) to influence their behaviour. In contrast, long-nosed potoroos were largely nocturnal, with peak activity occurring in the first few hours after dusk, which has been observed also in other studies (Claridge *et al.* 2007; Frankham *et al.* 2011).

We found that long-nosed potoroos and feral cats shared more than half of their temporal activity in both seasons; however, their peak activity times were different. Most notably, peak activity of long-nosed potoroos increased after cat activity started to subside, and this pattern was consistent despite the actual peak activity times changing for both species between sampling periods (from winter to summer). Although correlation does not equate causation, the temporal differences observed in the present study provided a clue to one mechanism (fine-scale avoidance of predation risk) by which long-nosed potoroos may persist in the presence of cats. This has been observed in other Australian species where the introduction of a native predator was associated with a higher increase in temporal niche partitioning by its prey (Cunningham *et al.* 2019b).

## Conclusions

The strong selective pressure of predation has resulted in morphological and behavioural changes in many species over evolutionary time; however, a growing body of research suggests that prey are able to assess predation risk and adaptively alter their behaviour to reduce predation risk over their lifetimes (Lima and Dill 1990). Although predation can initially be high, some prey may persist long enough to adopt antipredator mechanisms, ensuring their survival over generations (Banks *et al.* 2018; Cunningham *et al.* 2019a). Our study has provided a new understanding of how a threatened and critical weight range mammal may persist in the presence of an introduced predator (feral cats). If cats are eradicated from French Island, quantifying shifts in temporal and spatial behaviour of long-nosed potoroos and other potential prey would provide an opportunity for stronger inference regarding habitat use and predator avoidance.

Currently, the likelihood of cats being completely eradicated from mainland Australia is very low (Doherty *et al.* 2017). It is, therefore, important to explore alternative management practices for reducing cat impacts on native wildlife, and to conserve species within their natural distribution. Cat eradication is likely to benefit many of French Island's native species. However, we have shown that in the case of long-nosed potoroos, and possibly for other species able to tolerate cats at certain densities and in particular habitats, complete cat exclusion may not be necessary and cat presence may be important for conserving populations that can coexist with alien predators. Long-nosed potoroos are currently listed as threatened in Victoria. Having a 'cat-savvy' insurance population that can coexist in the presence of this alien predator and, therefore, potentially be used as a source for translocations to other areas has great value. More broadly, our study emphasised that there are scenarios in which

ground-dwelling, critical weight range mammals can coexist in the presence of cats, suggesting that conservation of some native species may be achievable in circumstances where cat eradication is not feasible.

## Conflicts of interest

Tim Doherty was a guest Associate Editor for the Special Issue. Despite this relationship, he did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Wildlife Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors have no further conflicts of interest to declare.

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