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Habitat Selection and Movement Behaviour of Long-Nosed Potoroo in the Presence of Feral Cats

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ABSTRACT

The global biodiversity extinction crisis is attributed to a series of key threats, with the introduction and impacts of invasive predators considered among the most damaging. Given that effective large-scale lethal control is often not logistically or financially feasible, alternative solutions to promote the persistence of native wildlife most at risk of predation—critical weight range mammals—must be sought. Understanding habitat use and selection of native prey under predation pressure with widespread and common invasive predators, such as feral cats, can quantify habitat elements that may promote survival. We aimed to determine the movement behaviour of a population of critical weight range mammals persisting in the presence of feral cats. We established a trapping grid across ‘Bluegums’, French Island, in south-eastern Australia to collect morphometric, demographic and movement data by deploying GPS tracking devices on Long-nosed Potoroo (*Potorous tridactylus trisulcatus*). We used spatially explicit capture–recapture models to generate a potoroo density estimate, and autocorrelated kernel density estimators and dynamic Brownian Bridge Movement Models to examine home range and habitat use. Spatial overlap and habitat selection analyses were used to draw inferences about habitat selection and territoriality. Potoroos persisted at low densities and had large home ranges (7.3–12.5 ha). Individuals selected for structurally complex habitat and appeared reluctant to move across open areas, potentially in response to greater perceived predation risk. The fine-scale movement data in our study elucidate the extent to which potoroos rely on vegetation structure, suggesting that maintaining habitat cover and connectivity is likely to build resilience and aid potoroos and similar species to co-exist with feral cats. Given the ongoing threat feral cats pose to biodiversity, our results support the need for maintaining diverse, structurally complex vegetation to build ecosystem resilience to support improved conservation outcomes in the presence of invasive species.

1 | Introduction

The global biodiversity extinction crisis is a consequence of rapid and severe landscape change across the world; principally driven by key threats including habitat fragmentation and degradation, and the introduction of invasive species, predators and pathogens (Daszak et al. 2000; Koh et al. 2004; Pimm and Raven 2000). These human-induced changes have caused significant disruption to ecological communities and landscape connectivity (Fischer and Lindenmayer 2007; Lindenmayer et al. 1999), resulting in habitat simplification, which can exacerbate the predation pressure posed by invasive predators (Doherty et al. 2015).

Invasive mammalian predators are regarded as a significant driver of species' extinctions (Doherty et al. 2016). The feral

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cat (*Felis catus*) has a near cosmopolitan distribution and has been introduced to almost every region of the world (Doherty et al. 2014). Consequently, cats are implicated in 26% of bird, mammal and reptile extinctions (Doherty et al. 2016). Importantly, habitat structural complexity has been shown to mediate the hunting success of feral cats (McGregor et al. 2015) and could reduce their density (Hohnen et al. 2020). Hence, how we manage vegetation communities, such as through fire and grazing pressure, and the impacts of landscape modification and fragmentation can affect the survival of native wildlife.

Australia's biodiversity has been severely impacted by invasive species. Due to its geographic and evolutionary isolation, Australia's wildlife is inherently naïve to novel threats posed by anthropogenic disturbances, including introduced predators (Woinarski et al. 2015). Australia has the world's worst mammal extinction rate, with the 34 species becoming extinct in the past ~230 years amounting to 35% of the world's contemporary mammal extinctions (Woinarski, Braby, et al. 2019; Woinarski, Legge, et al. 2019). Approximately two-thirds of these extinctions have been driven by cats and foxes *Vulpes vulpes*) (Legge et al. 2018), who also threaten a further 75 species of threatened or near-threatened mammals with extinction (Woinarski et al. 2015). Furthermore, with the introduction and spread of cats across 99.8% of Australia's land area (Legge et al. 2018; Woinarski et al. 2015), many species have undergone range contraction, with an estimated 26 species confined to < 10% of their former range (Short 1998). Ground-foraging critical weight range (CWR) mammals (35–5500 g) are disproportionately represented in the extinction record and have a higher probability of extinction than other mammals (Andren et al. 2018; Burbidge and McKenzie 1989; Woinarski et al. 2015; Woolley et al. 2019). Their physical and ecological traits make these species more susceptible to predation by introduced predators such as foxes and feral cats (Andren et al. 2018; Woinarski et al. 2015; Woolley et al. 2019), explaining their high probability of decline and extinction. Consequently, Australian federal legislation lists predation by feral cats as a key threatening process (Doherty et al. 2017; Environment Protection and Biodiversity Conservation [EPBC] Act 1999; Saunders et al. 2010).

Of the 34 mammals now extinct in Australia, many of these are ground-dwelling and digging species, such as bandicoots, bilbies, bettongs and potoroos (Fleming et al. 2014). These species are considered ecosystem engineers, facilitating soil turnover, aeration and water filtration, which increases soil health and plant germination when digging for underground food sources (Frankham et al. 2011; Halstead et al. 2019; Valentine et al. 2017). Being ecological specialists, these ecosystem engineers are inherently vulnerable to decline in changing environments (Andren et al. 2018; Holland and Bennett 2007; McHugh et al. 2019). When these species are lost from ecosystems, so too are the ecological functions they perform, which can trigger trophic cascades including reduced soil turnover, increased organic matter accumulation and disruption in nutrient flow and cycling, affecting the wider functioning of the ecosystem (Clout and Russell 2008; Doherty et al. 2017, 2016). Given the history of loss of Australian mammal species, urgent action is required to slow further declines and prevent additional extinctions (Doherty et al. 2017; Smith 2013; Woinarski, Legge, et al. 2019).

The structure and quality of habitat may hold the key to survival in ground-dwelling mammals in the presence of cats (McHugh et al. 2019). However, the relationship between ecosystem structure and predator–prey dynamics remains poorly understood (Smith 2013). Analysis of habitat selection, activity range, home range and spatial overlap through a combination of spatial and temporal data may elucidate the relationship between habitat structure and use by prey, shedding new light on how native mammals might co-exist with feral cats (Frey et al. 2017). When combined with information on population density, this information can be used to inform more targeted management actions and better conservation outcomes for CWR mammals where cats are present.

French Island, Victoria, Australia, provides an ideal opportunity to examine how Long-nosed Potoroos are persisting in the presence of feral cats. Having been isolated from the mainland for at least 8000 years (Marsden et al. 1979), French Island is the largest fox-free area in Victoria (Frankham et al. 2014). French Island is home to a population of Long-nosed Potoroos, which experiences significantly reduced interspecific competition and predation pressure compared to mainland habitats, owing to the small number of native mammals on the island (Andrew et al. 1984) and the absence of foxes (Frankham et al. 2011). Although feral and free-roaming domestic cats are present on the island, Long-nosed Potoroos still persist (Miritis et al. 2020). Past research suggests that potoroos may be minimising predation risk by avoiding cats temporally, and that potoroo detectability is not influenced by the presence of cats, indicating a lack of spatial avoidance (Miritis et al. 2020). Potoroos have been detected using both open and closed vegetation, with detectability of potoroos higher in structurally complex vegetation, with this effect intensifying at sites where cats are present (Miritis et al. 2020). Thus, there may be a relationship between the use of complex habitat and the persistence of potoroos in the presence of cats; but the extent to which the species relies on structure for this purpose remains unknown.

Our study therefore aimed to investigate the mechanism of coexistence of native prey with feral cats in isolation of the effect of additional predators. We had two primary aims:

1. Generate a potoroo density estimate for the 'Bluegums' area of French Island. Past studies indicate a tendency for this species to persist in stable, low density populations elsewhere on French Island (Long 2001; Frankham et al. 2011); we anticipate a similar pattern of persistence in Bluegums.
2. Estimate home range and quantify habitat use ('activity range') of Long-nosed Potoroos. Based on previous research, we expect potoroos will show a preference for areas with high vegetation cover (Bennett 1993; Long 2001; Seebeck 1981; Smith 2013), due to the refuge this provides from predation. Given that promiscuous mating systems are often associated with a lack of territoriality (Borremans

et al. 2014), we expect a high potential for overlap between individual activity ranges.

2 | Methods

2.1 | Study Area

French Island, located in Westernport Bay on Bunurong/Boonwurrung Country, south-eastern Victoria (38°20′S 145°22′E) is the largest island in the state at 18 000 ha (Frankham et al. 2011). Having a maximum elevation of 98 m, French Island has a mild, temperate climate with mean annual maximum and minimum temperatures of 18.7°C and 11.8°C respectively, and a mean annual rainfall of 692.6 mm (Rhyll weather station; Bureau of Meteorology 2020).

French Island is predominantly National Park, with 11 100 ha (~62%) managed for this purpose, with the remaining area primarily used for sheep and cattle grazing. The study site 'Bluegums' is in the south-eastern corner of French Island National Park. Bluegums is approximately 380 ha in size, with woodland, heath, saltmarsh and mangrove being the main vegetation types in this area (Miritis et al. 2020; VicFlora 2018) (Figure 1). More specifically, Bluegums has an interior of retired pastureland (~80 ha) and an exterior of stands of dense prickly teatree (*Leptospermu continentale*) with mossy groundcover (Groenewegen et al. 2017). While these are the predominant vegetation types, sword grass (*Gahnia* spp.), austral bracken (*Pteridium esculentum*), sweet bursaria (*Bursaria spinose*) and blackberry (*Rubus fruticosus*) also persist in smaller patches intermittently throughout (Groenewegen et al. 2017). Bluegums was selected based on past research completed by Miritis et al. (2020), which indicated high activity and co-occurrence of cats and Long-nosed Potoroos, with 94% and 77% of camera stations in Bluegums detecting cats and potoroos, respectively. In the year between Miritis et al. (2020) and this study, cat density in Bluegums remained high, with no additional control measures undertaken. In the months prior to and during this study, cat density in Bluegums was calculated at 0.587 cats per km^2 (A. Coetsee, unpublished data).

The Long-nosed Potoroo is the smallest macropodid marsupial and within the CWR, weighing just 700–1500 g (Short 1998). Like many Australian mammals, this species was once widespread but now persists in disjunct populations over a fraction of their historic range, owing to population and range declines driven by land clearing and predation since European settlement (Claridge and Barry 2000; Frankham et al. 2016; Frankham, Handasyde, et al. 2012; Short 1998).

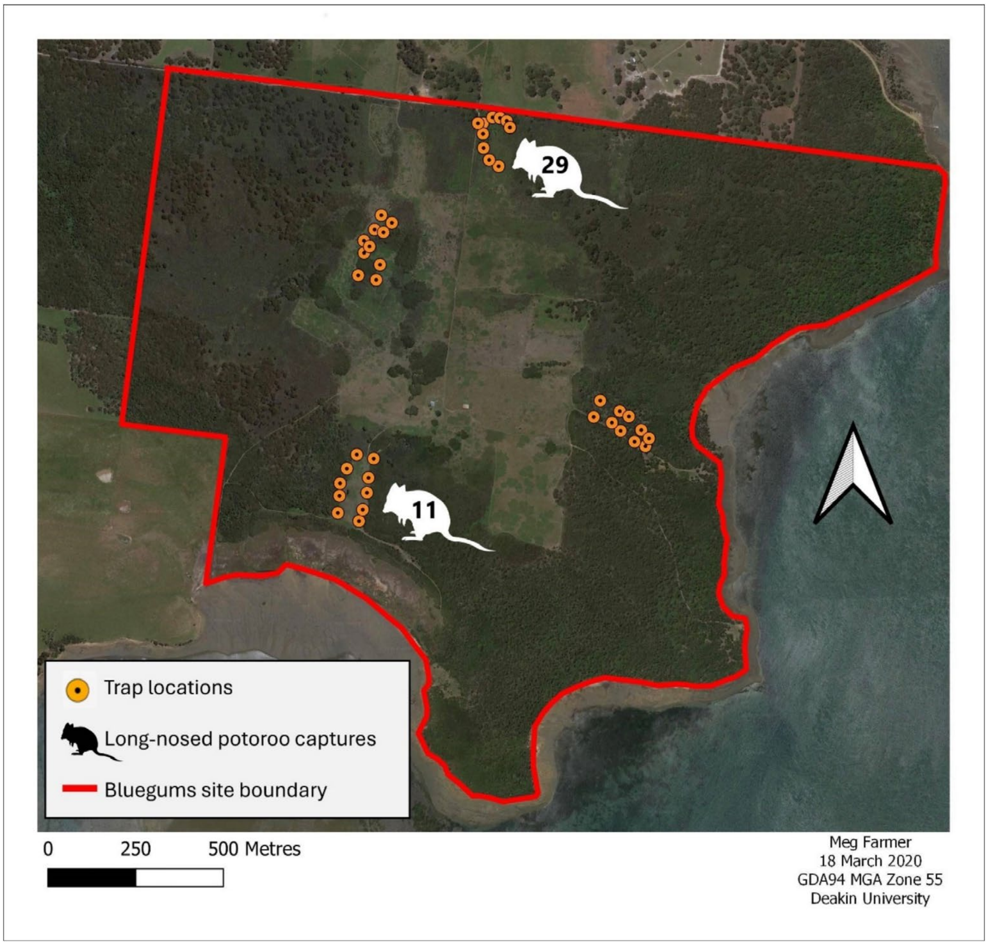

FIGURE 1 | Long-nosed Potoroo (*Potorous tridactylus trisulcatus*) trapping grid and captures in 'Bluegums', French Island National Park, south-eastern Australia. Sites are labelled A-D, clockwise from top left. Long-nosed Potoroos denote sites where potoroos were captured, with the enclosed number indicating the total captures at each site. Light green vegetation in the centre represents retired, open pasture.

In comparison to larger macropods, potoroos are relatively understudied, owing to their small size, cryptic nature and propensity to occur in dense undergrowth, which makes observational studies difficult (Frankham, Reed, et al. 2012). Consequently, there is neither long-term population data available on the species (Frankham, Reed, et al. 2012), nor detailed information on their habitat use and preferences (Norton, French, et al. 2011).

2.2 | Trapping Grid

Potential trapping locations were identified based on detection of Long-nosed Potoroo on camera traps deployed across Bluegums, which identified potoroos at 24 camera locations, constituting 77% of camera sites (Miritis et al. 2020). Use of known locations is preferable over deploying a grid across the entirety of Bluegums to increase chances of trap success, given the difficulty in catching this species previously (Frankham et al. 2011; Gloury 2008). These potential sites broadly represented a gradient from open to closed vegetation based on satellite imagery and in-field assessments, with the aim of sampling a range of compositions to target individuals using a different combination of habitat attributes (Figure S1).

Within these broad categories, we selected four trapping sites with a mixture of different vegetation types, across a gradient of vegetation density, from cleared to high structure. In order of clearest to most structured habitat, this included open retired pasture (Site A), open woodland with fragmented sedge understorey (Site C), remnant woodland with dense bracken understorey (Site B) and dense tea tree stands (Site D; Figure S1). Trapping locations were selected such that they were equally spread across the site to facilitate density estimation (Figure 1). Ten wire cage traps (50 × 18 × 20 cm) were deployed at each trapping location in two transects of five, with 20–50 m spacing between traps with a minimum distance of 350 m between trapping sites (Figure 1). This configuration was chosen to maximise the trapping area, while also ensuring that all animals would not be in traps for more than 5 h.

2.3 | Trapping Data

On average, we trapped twice a month between October 2019 and mid-January 2020 (DELWP permit number 10009179; approved by Deakin University Animal Ethics Committee, project ID B19-2019). Each trapping occasion consisted of two to six nights (an average of four) of trapping, making a total of 960 effective trapping nights. Traps were set 3 h prior to dusk to target activity peaks of potoroos and reduce the chances of catching diurnally active species (Miritis et al. 2020). Traps were baited with a mixture of peanut butter, rolled oats, honey and vanilla extract. Trap checking commenced approximately 2 h after dusk.

Captured individuals were transferred to a calico bag for handling. Potoroos were weighed, the head and pes lengths measured, body condition scored (good, average, poor) and reproductive condition assessed (i.e., presence of pouch young or lactating teats). All potoroos were microchipped on first capture with an 11 × 2 mm Passive Integrated Transponder (PIT tag) inserted between the shoulder blades.

In December 2019, when individuals were consistently being recaught, we deployed tracking devices to assess their movement behaviour. We fitted potoroos with GPS tags (igot-U) coupled with VHF transmitters (Biotrack PIP3 VHF radio-transmitters (< 1.0 g) with a 150-mm whip antenna) to enable retrieval. To reduce weight and bulk, Igot-Us were repackaged in epoxy resin and shrink wrap, as outlined by Allan et al. (2013). The VHF transmitter was securely attached to the top side of the Igot-U using a 3-cm piece of Elastoplast tape. The total weight of this package was ~25 g (~2% of the average adult body mass of French Island potoroos 1239.3 g). Each Igot-U was programmed to take a reading of the animal's location every 10 min, increasing in frequency to every minute if it detected the animal moving at a velocity equal to or greater than 10 km/h. These settings were to prolong battery life by reducing the number of readings while movement was minimal (e.g., at rest), but still capture even short duration, high-energy movements of the animal, revealing their fine-scale habitat use. Each unit was attached to the base of the tail using a combination of leukoplast and elastoplast tape, as outlined by Smith (2013). We fitted seven individuals (five males and two females) with transmitters over the course of this study. Transmitters were removed (on average) after 16 days upon recapture using a citrus-based oil. When a potoroo could not be recaptured, the units were located using the VHF transmitter and a directional antenna once the device had become detached from the individual (approximately 3 weeks). No individual was tracked more than once during this study.

2.4 | Data Analysis

We estimated the density of the potoroo population using a spatially explicit capture–recapture (SECR) model, in the 'secr' package in R (R Core Team 2017; Efford 2020). We used a habitat mask to restrict the density estimation to Bluegums only. This model relates the probability of detecting a potoroo at a particular detector (trap) to the distance of the trap from the centre point of the animal's activity range, where the probability of detection decreases with increasing distance from this centre point (Efford 2020). We first tested which detection function best fit our observed data; comparing the half normal, hazard rate and exponential functional forms to see which best described this decline in detection probability. We used the Akaike Information Criterion corrected for small sample sizes (AIC_c) to determine the best supported functional form, with any model with an ΔAIC score below two considered to have support. The model with the lowest AIC_c score was considered the best supported detection function and thus was used in all subsequent models.

A SECR model estimates three parameters: D (density), g0 and sigma. The terms g0 and sigma are variables in the detection function; in the context of our study, g0 relates to the probability of catching a potoroo if a trap (detector) is placed in the area where it spends the most time, and sigma is a spatial variable which relates to the individual potoroo's activity range size. We held density constant and tested three potential influences on the detection probability of potoroos: a learned response affecting g0; a learned response affecting g0 and sigma; and a site-learned response. A learned response (b) is at an individual level, where the probability of capture changes following the first capture. In a site-learned response (k), the ability to capture individuals at a site may increase over time following the first capture of individuals at that site (in essence, individuals becoming 'trap happy' rather than 'trap shy'). Each of these three variables were tested because we recognised that there was potential for a learned response at a site or individual level to influence an animal's detectability (Chitty and Kempson 1949; Getz 1961; Tasker and Dickman 2001), thus helping explain potoroo abundance. As above, the best supported model was determined by comparison of AIC_c scores.

Factors such as dense vegetation cover and an animal's orientation can decrease the accuracy with which a GPS location can be triangulated and thus increase the error margin associated with the fix (Allan et al. 2018; Williams et al. 2012). This is reflected in the estimated horizontal position error (EHPE) value in the data obtained from the GPS units (Allan et al. 2018). Recognising this, we deployed six Igot-Us in a stationary GPS test to ascertain if there was a difference in error rate at different vegetation densities. Igot-Us were deployed at known locations in Bluegums, stratified across a gradient from closed, dense vegetation to open, retired pasture. No substantive difference in error rate was found between different vegetation densities. From this test, we decided that any readings with an EHPE of > 50 m were too uncertain and therefore excluded them from the dataset. Core areas in activity range estimates should represent areas with the highest probability of use (Burt 1943; Seaman and Powell 1990). However, repeated readings where an individual is stationary for a length of time, such as while nesting, are likely to inflate core estimates. To reduce the influence of regular usage of a nest site, repeat readings during daylight hours, when individuals were most likely to be resting in nests, were classified as nesting site repeats and were removed. The removal of these fixes does not rarify points but recognises and reduces the potential for inaccuracies introduced by repeat nest site use in home range estimates and habitat use analyses.

To estimate the home range of each individual we fitted continuous time movement models and generated 95% utilisation distribution estimates using an optimally weighted autocorrelated kernel density estimator (wAKDE) in the 'ctmm' package in R (version 1.2.1; Calabrese et al. 2016; Fleming and Calbrese 2023; Fleming et al. 2015). This approach was selected as it accounts for the many complexities of modern GPS data, including autocorrelation, small sample sizes, irregular sampling regimes and measurement errors (Fleming et al. 2019; Noonan et al. 2019; Silva et al. 2021).

While range estimators such as wAKDEs are ideal for describing an individual's space use as it pertains to the classical definition of home range (Burt 1943), occurrence estimators such as dynamic Brownian Bridge movement models (dBBMM) can be effectively used to study an animal's movement within a given period (Noonan et al. 2019). Occurrence estimators provide a more effective way to answer specific questions about an animal's movement ecology within a given study period, such as landscape features visited, habitat and corridor use and overlap of individuals (Alston et al. 2022). Thus, we fitted dBBMM in the 'move' package in R (R Core Team 2017) to determine the specific space use of individuals during our study, hereafter referred to as 'activity range'. This model was selected because it accounts for time between successive locations in the utilisation distribution, where readings are taken in quick succession and therefore locations are serially correlated (Walter et al. 2015). To be confident that the calculated activity range is representative of the total area used by each individual, we conducted an incremental area analysis in R (R Core Team 2017). We also used the 'adehabitatHR' package in R to calculate the 95% Minimum Convex Polygon (MCP) to allow us to compare our results directly to previous studies.

The degree of overlap in the activity ranges of individuals at each site was measured using the utilisation distribution overlap index (UDOI) proposed by Fieberg and Kochanny (2005), using the 'adehabitatHR' package in R (Calenge 2006; R Core Team 2017). These were calculated for each trapping site individually, as there was no between-site overlap of potoroo activity range. Unlike crude indexes of spatial segregation such as percentage spatial overlap, UDOI takes into consideration the actual utilisation distributions of the two animals, to provide an index of the degree of space sharing occurring (Huck and Fernandez-Duque 2017; Naro-Maciel et al. 2018). UDOI ranges from 0 (no overlap) to 1 (complete overlap) where both utilisation distributions are uniform (Fieberg and Kochanny 2005). UDOI values > 1 are also possible, which indicates non-uniform utilisation distributions and a high degree of overlap (Fieberg and Kochanny 2005).

To determine the habitat selection by each individual, we conducted a K-select analysis to understand if potoroos select for different habitats. A K-select (Type III) analysis considers the home range of the individual (calculated via the MCP) to quantify the habitat elements available at the individual level (Aebischer et al. 1993). This is important when testing the marginality of the individual (the difference between the available habitat and the habitat used), where longer marginality indicates greater selection for particular habitat. We conducted our K-select analysis using the 'adehabitatHS' package in R (Calenge 2006; R Core Team 2017), using the two variables 'structure' and 'cleared'. We used satellite imagery sourced from Google Maps to classify Bluegums into open areas and areas of high structural complexity in ArcGIS (ESRI 2014). Remnant woodland or revegetated areas characterised by dense understorey were classified as 'structure', while open areas of retired pastureland were classified as 'cleared'. To recognise the potential for error in classifying areas, as well as the potential for error in obtaining GPS fixes in dense vegetation, each habitat layer was buffered by 5 m, accounting for an interface of habitats where there is potential for the individual to be using either habitat (Beilharz and Whisson 2016). Each GPS fix could subsequently be classified as being in either structure or cleared areas. We ran a principal component analysis (PCA) to look for commonalities among our variables; to identify trends in habitat selection based on the habitat that is available to the individual (structure or cleared). In testing each individual's habitat selection, we used a Bonferroni-corrected significance value (0.0125) to reduce the Type I error rate resulting from multiple comparisons.

3 | Results

We conducted 960 effective trap nights from October to January, resulting in a trap success of 4.38%. A total of 10 individuals, 7 males and 3 females, were captured, and these captures were restricted to two main sites (Sites B and D), with 29 and 11 total captures (inclusive of recaptures), respectively (Figure 1).

On average, males were found to weigh more than females, with male weights ranging from 1061 to 1415 g with an average male weight of 1259.9 ± 51.3 g SD (Table S1). Females weighed between 1146 and 1240 g, with an average female weight of 1191 ± 27.2 g SD (Table S1). The overall condition of assessed individuals was good, with only one female's body condition considered 'average' (Table S1).

3.1 | Density Estimation

The half normal detection function was strongly supported and therefore used in all subsequent models (AIC $w_i = 0.858$, Table S2). We found no support for a learned response at a site or individual level (Table S3), suggesting that none of the variable combinations had a significant influence on potoroo capture rates or density. We used our best supported model to calculate a density estimate of 0.22 potoroos/ha (95% CI: 0.075–0.575). Given the retired pastureland interior of Bluegums, and the aversion of potoroos to open spaces (identified by our results below), it is unlikely that potoroos are homogeneously distributed across the site. Recognising this, we have excluded the ~80 ha of pasture from our population estimate, giving an effective habitat size of 300 ha and a population estimate of approximately 66 potoroos in Bluegums (95% CI: 22.5–172.5).

3.2 | GPS Data Analysis

While transmitters were initially attached to seven individuals, due to equipment failure (two failing to collect any data, and one collecting insufficient data for analysis) we were only able to retrieve adequate data for analysis from four of these transmitters. All four transmitters were attached to males, each for between 6 nights and 14 nights, depending on when individuals were recaptured. Potoroo home ranges (wAKDE) varied from 7.3 to 12.5 ha, with an average home range size of 9.55 ± 1.22 ha SE. MCP calculations resulted in smaller home range estimates (Table S4). Potoroo activity ranges (dBBMM) varied from 8.19 ha to 15.14 ha, with an average activity range size of 10.80 ± 1.66 ha SE (Table S4).

Our incremental area analysis revealed that the activity range size of individuals 7D47882F and 7D4FC7B reached an asymptote, suggesting that no additional GPS fixes would have increased our activity range calculation (Figure S2). Activity ranges of 7D46301 and 7D4CD22 were still increasing, suggesting that some additional fixes may have slightly changed our estimates (Figure S2).

3.3 | Spatial Overlap Analysis

Degree of activity range overlap between individuals was found to vary between sites. Site B reported little overlap in the utilisation distributions of both individuals relative to uniform space use, with a UDOI value of 0.14 (Figure 2). Contrastingly, those individuals at site D (the southernmost trapping location) had a much higher degree of spatial overlap, with a UDOI value of 0.76 indicating a greater similarity between the two utilisation distributions, thus suggesting a high level of space sharing between individuals (Figure 2).

FIGURE 2 | Overview of the distribution of four Long-nosed Potoroo (*Potorous tridactylus trisulcatus*) activity ranges (dBBMM) in Bluegums, French Island, south-eastern Australia.

3.4 | Habitat Selection Analysis

Potoroos showed a strong preference ($p = 0.005$) for structurally complex habitats. Two animals showed particularly strong selection towards structure ($p = 0.005$ for both), but all individuals displayed a positive association with more complex areas.

When plotted over a satellite image of Bluegums, and for those individuals captured at site B, it becomes apparent that each individual's activity range is restricted almost entirely to areas of higher vegetation cover (Figure 3), with some limited movement into open areas (Figure 3). Darker areas in the activity range indicate areas of high frequency of visitation by these individuals, and for both individuals at site B this core area is restricted to dense vegetation (Figure 3).

For those individuals trapped at site D, the activity range demonstrates that the two individuals vary in the extent to which they are willing to venture out into the open (Figure 4). One potoroo (Figure 4; left) has an activity range much greater in size—7.22 ha larger than its counterpart—and which incorporates the open area between two habitat patches (Figure 4). However, it must be noted that movements across this less-hospitable area appear to be concentrated through the strip of vegetation at the top of its range, and core areas of high visitation frequency are still restricted to more densely vegetated areas (Figure 4; left).

4 | Discussion

Knowledge of the mechanisms by which native prey may be able to coexist with invasive predators—both behavioural and environmental—is vital for informing improved biodiversity conservation outcomes (Miritis et al. 2020). Understanding animal ecology, movement patterns and associated inferences regarding habitat preferences underpins our ability to understand species' responses to environmental change, including habitat modification and introduced predators (Allan et al. 2018; Graham et al. 2012; Hradsky et al. 2017). Through examining these patterns, our study found that (1) potoroos

FIGURE 3 | Activity ranges (dBBMM) for individual Long-nosed Potoroos (*Potorous tridactylus trisulcatus*) 7D4CD22 (left) and individual 7D47882F (right) at site B in Bluegums, French Island, south-eastern Australia. Darker colours indicate areas of higher visitation frequency.

FIGURE 4 | Activity ranges for individual Long-nosed Potoroos (*Potorous tridactylus trisulcatus*) 7D46301 (left) and individual 7D4FC7B (right) at site D in Bluegums, French Island, south-eastern Australia. Darker colours indicate areas of higher visitation frequency. The white arrow indicates a movement corridor across open areas.

captured in Bluegums appear overall to be in good health; (2) the estimated population density in Bluegums is 0.22/ha; (3) the average male home range size is 9.55 ha; (4) the degree of activity range overlap was up to 0.76, indicating high space use sharing and low territoriality between males; and (5) potoroos displayed an overall trend for selection of structurally complex habitat and a reluctance to move across open areas. The persistence of potoroos in the presence of cats may be due to dense vegetation providing refuges from predation risk (Reside et al. 2019), and potoroos avoiding cats temporally (Miritis et al. 2020). Therefore, increasing cover and connectivity of habitat patches will likely enhance the ability of this species to coexist alongside feral cats.

4.1 | Morphometric and Demographic Data

Our potoroo trapping success of 4.38% is congruent with others, reporting a range of < 0.05%–10% (Bennett and Baxter 1989; Frankham et al. 2011). This reluctance of potoroos to enter traps could reflect their timid nature, which has resulted in a scarcity of information on the state of wild populations (Frankham et al. 2011; Frankham, Reed, et al. 2012). We caught twice the number of males than females in this study. This trend is unlikely to be reflective of an actual sex bias in the population but, rather, a result of females having smaller home ranges than males (Bennett 1989; Kitchener, unpublished data, 1967; Long 2001) and thus having a lower probability of encountering traps (Norton, Claridge, et al. 2011).

Individuals caught weighed between 1061.0 and 1415.2 g, with females lighter than males, although this was only by a small margin (68.8 g difference). This trend has been observed in other studies, in which individuals range from 700 to 1500 g (Frankham et al. 2011; Norton, Claridge, et al. 2011; R. Reed, unpublished data, 2006). This lack of pronounced sexual-size dimorphism is common in small, solitary macropods: female oestrus cycles are asynchronous and unpredictable, so males secure paternity by maintaining an intimate knowledge of the nesting sites and reproductive status of females within their range (Frederick and Johnson 1996; Jarman 1991). Consequently, there are fewer confrontation-based, aggressive encounters between males, which reduces the selective pressure for males to become larger; thus, males and females are more monomorphic in this species (Frankham, Reed, et al. 2012; Jarman 1991).

4.2 | Population Density

Our finding that Long-nosed Potoroos are persisting at a low density in Bluegums supports Frankham et al. (2011), who documented the species at 0.33 ± 0.01 potoroos/ha at another French Island study site and (Claridge et al. 2007) between 0.2 and 2.6/ha elsewhere. The documented tendency of the species to form stable, low density populations (Frankham et al. 2011; Long 2001; Smith 2013) is poorly understood, and we may have expected a higher density population to be recorded in this study, given the absence of foxes and fewer interspecific competitors in comparison to the mainland (Frankham et al. 2011). Low density populations present a suite of problems to managers (Smith 2013). It is beyond the scope of this study to establish the causality of the observed low population density; however, we present three possible explanations: a low carrying capacity at the site, as dictated by its climatic conditions; low density as a habitat availability and suitability-driven response; as a predator-driven condition (Frankham et al. 2011); or a combination thereof.

Prolonged drought conditions across south-eastern Australia in the years preceding this study (Bureau of Meteorology 2020) likely reduced the carrying capacity of the site for potoroos, as drought conditions are known to cause declines in CWR mammals (Lupone et al. 2024). This reduced carrying capacity was likely exacerbated by the presence of feral cats, a known predator of potoroos on the island. Additionally, sporocarp production is favoured by above-average rainfall conditions in spring, summer and autumn (Beaton et al. 1984). Thus, prolonged drought conditions may have resulted in a scarcity of this key resource, leading to population declines.

The observed low population densities may also reflect the dietary dependence of potoroos on hypogeal fungi, a widely yet irregularly distributed resource (Bennett and Baxter 1989; Claridge and May 1994). The availability of appropriate habitat to support the growth of such fungi may constrain the ability of the species to reach higher population densities. In which case, fragmentation and loss of important microhabitat elements can reduce the carrying capacity of a site and potentially result in declines (Frankham et al. 2011). This is particularly true in species such as potoroos that rely on areas of high vegetation complexity (Bennett 1993; Claridge et al. 2007; Holland and Bennett 2007; Le Pla et al. 2024a; Miritis et al. 2020; Seebeck 1981). Bluegums is managed as a National Park; however, its historic conversion to farmland with European settlement is likely to have a legacy effect on vegetation composition, connectivity, and soil structure (Cuddington 2011); consequently, the site may be unable to sustain higher densities of potoroos in its current state.

Direct predation by feral cats may be acting as a form of sustainable harvest of potoroos, maintaining the species at low densities. Previous camera trapping data in Bluegums indicate that feral cats and potoroos overlap spatially and temporally, and images have recorded potoroo predation by cats (Miritis et al. 2020). Top-down population regulation is well documented in other species and ecosystems (Estes et al. 2011; Ritchie and Johnson 2009) and, given that cats fill the apex predator role on French Island (Miritis et al. 2020), it is possible that our observations follow a similar pattern.

A combination of these bottom-up and top-down factors are likely working in synergy, restricting population size and density. Under such a scenario, sub-optimal habitats and conditions are made even less suitable by the presence of cats and a 'landscape of fear', so that movement between patches is restricted and access to habitat and resources diminished, reducing the site's carrying capacity (Lima and Dill 1990; McHugh et al. 2019). Further research is required to verify and explore these relationships.

4.3 | Movement Behaviour

Studying the area traversed by an individual to fulfil its energetic and reproductive requirements can provide insights into which habitat attributes are essential for survival (Burt 1943; McTier 2000; Claridge and Barry 2000). Very few other studies have used GPS to track Long-nosed Potoroos (Le Pla et al. 2024a, 2024b), with all other Victorian studies using VHF tracking (Long 2001) or trapping success (Bennett 1987) to quantify ranging behaviour. Along with the use of MCPs and kernel density estimators, this difference in approach is the likely cause of significantly lower ranging behaviour estimates generated by these studies (1.4–2.9 ha in females and 2.0 and 4.0 ha in males) (Bennett 1987; Long 2001). Our MCP results indicate ranges closer to those previously reported (3.56–7.75 ha; Table S4). GPS tracking provides more fine-scale data than these approaches, which can result in a more accurate representation of the ranging behaviour of the individual (Walter et al. 2015). Our dBBMM analyses of potoroo activity ranges are more congruent with the findings of Le Pla et al. (2024a), who generated a mean male home range of 13.73 ha using dBBMMs. Models such as AKDEs, which explicitly deal with the biases inherent in GPS datasets, represent further improvements in our ability to estimate an animal's home range (Alston et al. 2022; Fleming et al. 2015; Silva et al. 2021). Using this approach, Le Pla et al. (2024b) generated comparable results to ours, with a mean male home range size of 14.17 ha, indicating that Long-nosed Potoroo ranging behaviour may be greater than previously thought.

The availability and distribution of key resources (water and food availability) and biotic factors (competition and predation) all contribute to determining a species' space use (Borremans et al. 2014; Endries and Adler 2005; Ostfeld 1985). In some cases, activity range may be indicative of habitat quality, as mean activity range size is negatively correlated with resource availability (Borremans et al. 2014; Endries and Adler 2005; Mares and Lacher 1987). Theoretically, resource-rich environments should allow species to reach higher population densities than resource-poor environments (Adler et al. 1997; Borremans et al. 2014; Mares and Lacher 1987). Therefore, the combination of low population density and large activity ranges in the potoroo population may indicate low resource availability in Bluegums. Likewise, large home ranges may be a consequence of irregularly distributed food sources such as hypogeal fungi (Adler et al. 1997).

Predation risk by feral cats may also influence potoroo activity ranges. In the presence of predators, animals may use sub-optimal habitats with lower predation risk rather than optimal habitats with higher predation risk (Lima and Dill 1990; McHugh et al. 2019). A trade-off between food and safety (Lima and Dill 1990) may see potoroos increase activity range size to fulfil their resource requirements. Our habitat selection analysis supports this hypothesis, with individuals showing selection for structural complexity over more open areas. Bennett (1993) showed that potoroos used a mosaic of open and closed habitats to fulfil their foraging and nesting requirements. However, we found potoroos had a strong selection towards structurally complex habitats, with all but one of the activity ranges entirely within closed habitats, and all four core ranges restricted to areas of complex habitat (Figures 3 and 4). Given that cats have greater hunting success in, and therefore preferentially use, areas with a mix of open and closed habitat (Hohnen et al. 2016; McGregor et al. 2015), potoroos may be limiting their movements within more open habitats to reduce predation risk.

Degree of spatial overlap of individuals was different for each site in our study. The high overlap of individuals at site D suggests that, although male Long-nosed Potoroos are solitary, they do not appear to be territorial (Long 2001; Norton, Claridge, et al. 2011). This result is congruent with what is known of individual associations within promiscuous mating systems (Borremans et al. 2014). However, intrasexual overlap in males has been significantly lower in the past (Bennett 1987; Heinsohn 1968). Spatial or temporal differences in resource availability may be driving this discrepancy, or the broad-scale approaches of previous studies (Bennett 1987; Jarman 1991; Long 2001) may have underestimated overlap. Contrastingly, the minimal overlap of individuals at site B supports the low degree of male overlap recorded by Bennett (1987). This discrepancy in our results may be a function of small sample size or differences in habitat elements and quality between the two sites (Borremans et al. 2014; Endries and Adler 2005). For instance, the greater proximity of open space in site D may be constraining potoroos to closed areas as a response to reduce predation risk, causing a greater degree of overlap.

We believe the selection of closed habitat by potoroos is a predator avoidance strategy, rather than these areas being resource rich. This is due to fungal sporocarps requiring light to grow, so areas with a less complex understorey support a greater diversity of hypogeal fungi (Bennett 1993). Furthermore, under the 'landscape of fear hypothesis', individuals minimise time spent in areas where perceived predation risk is high, and thus habitat use may not indicate what is 'best' habitat for foraging, but simply least dangerous (Lima and Dill 1990; McHugh et al. 2019; Norton, French, et al. 2011). Increased structural complexity limits the hunting success of cats (Doherty et al. 2016; McGregor et al. 2015), so this habitat selection is most likely based on the refuge that cover provides from predation, as has been observed in other small mammal species (Andren et al. 2018; Holland and Bennett 2007; Lima and Dill 1990; McHugh et al. 2019; Norton, French, et al. 2011; Short 1998). We also note the presence of birds of prey, such as the Wedge-tailed Eagle (*Aquila audax*) and Barn Owl (*Tyto alba javanica*) have been detected in Bluegums preying on potoroos (A. Coetsee, unpublished data), and thus potoroo use of closed vegetation may also reflect an effort to evade aerial predators. While these native predators may be contributing to the landscape of fear at play, given the high density of cats at the site (Miritis et al. 2020), we propose that they are likely a key driver of this behaviour, given their hunting preferences (Doherty et al. 2016; McGregor et al. 2015). Hence, habitat fragmentation could have significant ramifications for Long-nosed Potoroos, which are known to be poor dispersers (Frankham et al. 2014, 2016; Holland and Bennett 2007) and have displayed significant reluctance to venture into areas of lower vegetation cover (Andren et al. 2018; Frankham et al. 2011).

4.4 | Study Limitations and Recommendations

We acknowledge the limitations inherent in only measuring the home and activity ranges of one sex. The 'females in space' hypothesis purports that the abundance and distribution of food is the key determinant of reproductive success in females (Martin and Martin 2007), while reproductive success of males is determined by access to receptive females (Ostfeld 1990). Thus, female home ranges may provide a more accurate picture of the home range required to fill resource requirements (Ostfeld 1990), and the large home ranges of males in this and other studies (Kitchener 1967; Le Pla et al. 2024a; Long 2001) may reflect the promiscuous mating system of potoroos (Frankham, Reed, et al. 2012). Further concurrent GPS tracking of individuals of both sexes at multiple sites to gain an understanding of the influence of habitat type, predator abundance and risk, and seasonally available resources such as fungi (Adler et al. 1997; Bowie 2007; Claridge and Barry 2000) on habitat use and degree of spatial overlap between individuals is therefore recommended. Future comparison of this study with data collected post-cat eradication on French Island would be beneficial to experimentally quantify the impact of cats on CWR mammal behaviour and habitat use and confirm the use of structure as a predator avoidance mechanism. It would also be beneficial to conduct a population viability analysis under current conditions, compared to if habitat and predation rates were changed to further elucidate the capacity of potoroos to co-exist with cats, and the role of vegetation in ensuring potoroo survival.

4.5 | Management Actions

Vegetation management to maximise cover and connectivity may encourage predator-avoidance behaviours and facilitate persistence in this species. Such long-term initiatives that promote co-existence with introduced predators may provide a more viable, effective and holistic approach to addressing invasive predator impacts beyond just lethal control and should therefore increasingly be considered as a component of predator abatement plans (Doherty et al. 2015). Given that many CWR mammal populations now persist as 'islands' of fragmented habitat (Frankham 1998), French Island provides an opportunity to trial the potential conservation benefits of restoring ecological resilience in vegetation communities. Furthermore, an understanding of the co-occurrence of individuals in a given area may inform management decisions and assist in cost–benefit analyses regarding habitat alteration to increase resource availability (Claridge and Barry 2000).

5 | Conclusion

Introduced predators pose a significant threat to biodiversity worldwide through direct predation, disease transmission and trophic cascades. Yet broadscale eradication of these predators is not practically or financially feasible in most cases, and thus alternative solutions that enhance the capacity for native prey to persist alongside introduced predators must be sought. Our study is one of very few to use fine-scale GPS data to analyse the home range, activity and habitat selection of the Long-nosed Potoroo, a critical weight range mammal, to reveal movement behaviour that may reduce their predation risk by feral cats. The strong reliance on structure by this species suggests that management to maintain habitat cover and connectivity is likely to be important in encouraging predator-avoidance behaviours. Incorporating habitat management into predator abatement plans should therefore increasingly be considered to facilitate the persistence of native prey species, especially where lethal control is ineffective.

Author Contributions

Meg Farmer: conceptualization, data curation, formal analysis, investigation, methodology, writing – original draft, writing – review and editing. **Anthony R. Rendall:** conceptualization, data curation, formal analysis, investigation, supervision, writing – original draft, writing – review and editing. **Amy Coetsee:** conceptualization, investigation, supervision, writing – review and editing. **Euan G. Ritchie:** conceptualization, resources, supervision, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and statistical outputs are available upon request from Deakin University.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.