

Movement and ranging behaviour of long-nosed potoroos (*Potorous tridactylus*) in south-west Victoria, Australia

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ABSTRACT

Context. A comprehensive understanding of movements and space use can underpin the effective management of threatened species. GPS dataloggers can collect large amounts of high-quality movement data, and recent advances in statistical approaches allow for robust estimates of home range size to be generated. Until recently, technological and practical constraints have generally restricted the collection of movement data via GPS dataloggers to larger species. However, reductions in the size and weight of GPS dataloggers now allow for this technology to be applied to smaller species. **Aims.** The aim of this study was to describe the home range and movement patterns of a nationally vulnerable, native Australian ground-dwelling mammal, the long-nosed potoroo (*Potorous tridactylus*), in south-west Victoria, mainland Australia. **Methods.** We attached GPS dataloggers to 40 long-nosed potoroos between 2020 and 2022 and estimated home range size using dynamic Brownian Bridge movement models. We evaluated the influence of physiological factors such as body mass and sex on home range size and described patterns of home range overlap between and within sexes. **Key results.** Mean home range sizes were estimated to be 13.73 ha (95% CI: 10.9–16.6) and 6.67 ha (95% CI: 5.49–7.85) for males and females respectively. Home range size scaled with body mass in males but not females, and ranges were largely overlapping – although there was some evidence of intrasexual spatial partitioning of core range areas in females. **Conclusions.** Ours is the first application of GPS dataloggers to this species, and our home range estimates are over twice as large as other reported estimates for mainland Australia. Long-nosed potoroos may range across larger areas than previously predicted on mainland Australia. **Implications.** This knowledge may be used to optimise the management of long-nosed potoroo populations before and after fire – a key threatening process for this species. Our study highlights the value of integrating GPS dataloggers and robust home range estimators when describing the movement ecology of a population.

Keywords: behaviour, conservation management, endangered species, geographical range, locomotion, reproductive strategy, spatial ecology, threatened species.

Introduction

The movement of an animal influences many aspects of its ecology, from individual fitness and reproductive success to population dynamics, geneflow, and species distributions (Bohonak 1999; Bowler and Benton 2005; Elith and Leathwick 2009). Therefore, a detailed understanding of animal movements is fundamental to developing and enacting effective conservation strategies. For example, prior knowledge of home range size can be used to ensure survey sites are spatially independent for occupancy modelling (MacKenzie *et al.* 2002), a practice often used to monitor populations of conservation concern through time (Ahumada *et al.* 2013), or before and after a management intervention such as fire (Pons *et al.* 2003) or invasive predator control (Robley *et al.* 2014). This same knowledge can be used to parameterise sophisticated decision support tools, such as agent-based models

(DeAngelis and Mooij 2005; Hradsky *et al.* 2019), to model the potential benefits and consequences of different management regimes. Finally, home range estimates may be used as informative priors for density estimation when individuals are able to be uniquely identified using spatially explicit capture–recapture modelling within a Bayesian framework (Royle *et al.* 2013). Despite these benefits, a detailed understanding of home range size for many species is lacking.

Historically, insight into an animal's home range was generated either through direct observation (if they were individually identifiable), from capture locations (Kitchener 1973), or by attaching very high frequency (VHF) transmitters to individuals and relocating them using a VHF receiver (Long 2001). Both approaches are often characterised by small sample sizes, logistical challenges, and analytical issues. More recently, Global Positioning System (GPS) loggers that are physically attached to an animal are increasingly being used to generate high-volume and high-quality movement data (Cagnacci *et al.* 2010; Hebblewhite and Haydon 2010; Tomkiewicz *et al.* 2010). Although weight restrictions have historically limited the application of this technology to medium- to large-sized animals (Merrill and Mech 2003; Dussault *et al.* 2005), technological advances reducing the size and weight of GPS loggers have expanded the suite of species that can be tracked using GPS loggers (Price-Rees *et al.* 2013; Stevenson *et al.* 2013; Zhang *et al.* 2019).

A wide range of analytical approaches have been developed to take advantage of ever-increasing sample sizes of animal locations. The most basic of these, the minimum convex polygon (MCP), remains commonly used despite its shortcomings (Harris *et al.* 1990; Börger *et al.* 2006), because it allows for comparison of home range areas with older studies (Nilsen *et al.* 2008). Kernel density estimators (KDE) represent an advance on polygon-based estimators, because they use the density of fixes to estimate the area an animal ranges in addition to how intensely different areas are used, referred to as a utilisation distribution (UD) (Worton 1989; Kranstauber *et al.* 2012). KDEs commonly ignore the temporal structure of a movement dataset and often require fixes to originate from a regular sampling schedule or to be temporally independent (Fieberg 2007; Kranstauber *et al.* 2012). More recently, the development of the dynamic Brownian bridge movement model (hereafter referred to as 'dBBMM') has further improved upon traditional KDEs by incorporating both temporal and spatial structures of tracking data (Horne *et al.* 2007; Kranstauber *et al.* 2012). This development allows for variable movement patterns and irregular fix schedules, better capturing movement pathways compared with traditional KDE estimators (Horne *et al.* 2007; Kranstauber *et al.* 2012).

The long-nosed potoroo (*Potorous tridactylus* – hereafter 'potoroo') is a cryptic and largely nocturnal species that utilises dense vegetation, making direct observations difficult (Bennett 1993; Claridge *et al.* 2007; Norton *et al.* 2010). Despite belonging to a faunal group that has been highly

disadvantaged by the landscape changes and introduction of invasive predators that followed European invasion in Australia (Burbidge and McKenzie 1989; Woinarski *et al.* 2015), the behaviour and movements of this species remains poorly understood. Potoroos are considered solitary yet non-territorial (Seebeck *et al.* 1989; Long 2001), and occur in a patchy distribution along the eastern coast of Australia, from south-eastern Queensland through to the south-eastern coast of South Australia and Tasmania (Johnston 2008). Their small size and generally low trapping success have likely contributed to the small number of studies that describe their home range.

In addition to the myriad of ecological factors that can influence potoroo movements and behaviour (Claridge *et al.* 1992; Bennett 1993; Norton *et al.* 2011), variability in survey technique, analytical approach, and sample sizes among the few studies that have estimated potoroo home range size makes direct comparisons challenging. For example, one study of Tasmanian potoroos reported home ranges of 19.4 ha for males and 5.2 ha for females using trapping data and MCP's (Kitchener 1973), whereas a study of Victorian potoroos reported much smaller home ranges (4 ha for males and 2.9 ha for females) based on similar sample sizes but using VHF tracking and a KDE estimator (Long 2001). Another potential reason for this discrepancy may be due to the considerable variation in body mass displayed by potoroos throughout its geographic range (Norton *et al.* 2010; Frankham *et al.* 2011). Individuals in south-west Victoria are among the smallest described, whereas Tasmanian potoroos weigh almost twice as much on average (Hird 1996; Long 2001; Frankham *et al.* 2011). Regardless, females are consistently estimated to have smaller ranges than males (Kitchener 1973; Hird 1996; Long 2001), a characteristic potoroos share with many other macropod species (Fisher and Owens 2000). To date, there have been no reported instances of GPS datalogger technology being used to generate home range estimates for potoroos, and no instances of more sophisticated home range estimators being used to estimate the home range size of this species.

Here we present the first study to use GPS dataloggers to estimate the home range size of potoroos. Our aim was to provide robust estimates of home range size, evaluate the influence of physiological factors such as body mass and sex on home range size, and describe patterns of home range overlap between and within sexes, in a population of potoroos in south-west Victoria, mainland Australia.

Materials and methods

Site description

Our study was conducted in the western Heathy Woodlands of the Great Otway National Park (38.54S, 143.47E), Victoria, Australia (Fig. 1). This locality is 130–250 m above sea

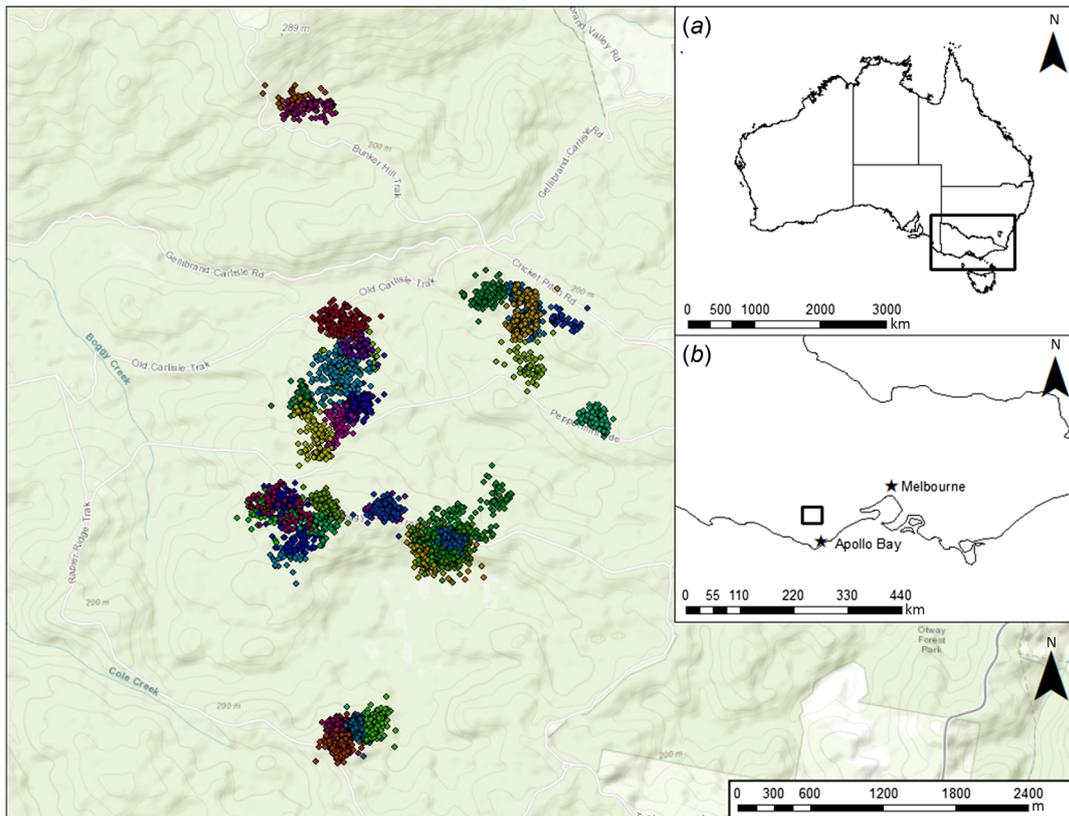


Fig. 1. Study area and location of all potoroo fixes collected during this study in reference to (a) Australia and (b) Victoria.

level and has a mild, temperate climate: maximum daily temperatures average 26.1°C in summer and 11.6°C in winter; annual rainfall averages 538 mm with more rainfall in winter and spring (June to November) relative to the warmer months of summer and autumn (December to May) (Bureau of Meteorology 2020). The overstorey is dominated by *Eucalyptus baxterii* and *E. obliqua*, with a mid-storey dominated by *Banksia marginata*, *Epacris impressa*, *Xanthorrhoea australis*, and *Leptospermum continentale*, with *Melaleuca squarosa* becoming the dominant mid-storey species in drainage lines. The understorey predominantly comprises a diverse array of herbs, graminoids, and lichens.

Live trapping, processing, and collar attachment of potoroos

Potoroos were live-trapped using wire mesh cage traps (approximately 72 cm long × 31 cm high × 31 cm wide) in seven 'blocks' broadly distributed throughout our study region between 2020 and 2022. Survey timing varied each year between March and August, with the majority of collar deployments taking place between late autumn and winter (May–August). Traps were baited using a traditional bait ball consisting of peanut butter, rolled oats, and golden syrup, and set in what was assessed as desirable habitat for potoroos.

Traps were open continuously and checked each day at dawn and dusk. Captured potoroos were transferred to a soft cloth capture bag for further processing.

Potoroos were handled by experienced individuals to identify, mark, weigh, measure, sex, and attach or remove GPS collars to minimise stress to individuals during processing. Females were examined for reproductive status, and the developmental stage of any pouch young was recorded. Females with large, furred pouch young were released immediately and were not included in this study. All other potoroos were implanted with a uniquely coded Trovan microchip between their shoulder blades to allow for individual identification in subsequent captures. Non-target species captured in cage traps were processed as described above with the exception of microchip implanting and GPS collar attachment.

We attached a 20-g LiteTrack20 GPS collar (<https://www.lotek.com/products/litetrack-20/>) to potoroos that exceeded 500 g, so that the weight of the collars represented less than 4% of their body mass. The collars were attached using a 4-mm wide plastic cable-tie around the neck. Although this specific approach of using cable ties had not been previously attempted for potoroos, the use of cable ties as collar attachment mechanisms has been highly successful in terms of retention time and welfare outcomes for species of similar

size and body shape (Coetsee *et al.* 2016). Collars were attached to alert animals, with a collar attachment time of approximately 2–4 min on average. Mean handling time was <10 min.

During 2020 deployments, GPS collars were programmed to collect fixes at half-hourly intervals during the night (1800–0600 hours) and 3-hourly intervals during the day (0600–1800 hours). Initial data collected during these deployments suggested potoroos were more active during the day than expected. Therefore, GPS collars in the 2021–22 deployments were programmed to collect fixes at hourly intervals continuously throughout the 24-h diel period. We retrieved all the collars during this study by recapturing individuals still fitted with dataloggers at the end point of battery life.

Data cleaning and pre-processing

The exclusion or correction of location errors after GPS data have been collected is a crucial first step to estimating home ranges. The primary goal of this screening step is to remove inaccurate locations, which can introduce bias and wrong conclusions, while retaining as many plausible locations as possible to improve statistical power and sample sizes (Bjørneraas *et al.* 2010). We discarded location data collected during the first night after collar attachment to ensure any short-term behavioural changes resulting from capture and collar attachment would not introduce bias into space use and home range estimates. Screening methods based upon the number of satellites, the geometry of those satellites (commonly represented by a measure called dilution of precision or DOP), or a combination of both are commonly used; however, these methods can lead to large data reductions without eliminating all obviously erroneous locations (D'eon and Delparte 2005; Bjørneraas *et al.* 2010). Alternative screening methods based upon identifying locations arising from unrealistic movement patterns have recently been developed and are increasingly being used to screen GPS datasets (Bjørneraas *et al.* 2010; McGregor *et al.* 2014). As per Bjørneraas *et al.* (2010), data were screened to remove fixes that reflected a turning angle of 170–190° and travelling speeds >1.5 km/h (indicating an erroneous 'spike' in movement), or that exceeded a mean distance of 300 m and median distance of 600 m from a moving window of 10 fixes.

Home range estimation

To ensure only individuals that displayed range residency were included in home range estimation, we first assessed range residency of all individuals via variogram analysis (Fleming *et al.* 2014). This exploratory analysis plots the semi-variance in positions as a function of the time lag separating observations, with individuals displaying range-resident behaviour showing clear asymptotes over longer

time lags (Calabrese *et al.* 2016). All animals fulfilled this criterion (Supplementary Figs S1–S3).

We then fitted dBBMMs to estimate the 95% and 50% UD areas for all individuals. Brownian bridge movement models (BBMM) represent an improvement upon KDE-based methods to estimate the UD of an individual, because they incorporate information about the movement path rather than just individual points and provide an estimate of an individual's mobility referred to as the Brownian motion variance (σ^2m) (Horne *et al.* 2007; Kranstauber *et al.* 2012). The σ^2m parameter contains information on both how straight a movement path is as well as how the path varies in speed and scale of movements (Kranstauber *et al.* 2012). However, while BBMMs produce a single estimate of σ^2m for the entire movement path, dBBMMs allow σ^2m to vary within a moving window of fixes, better representing the realistic variance in an animal's movement path characteristics as they transition between different behavioural states (i.e. active and resting) (Kranstauber *et al.* 2012). We fitted dBBMMs for each potaroo following the recommendations of Kranstauber *et al.* (2012) using an estimated location error of 15 m, window size of 11 (equivalent to 11 h), and a margin of 5 (equivalent to 5 h) to account for potential diurnal versus nocturnal movement pattern differences. Additionally, we also conducted an asymptote analysis to determine the sensitivity of dBBMMs to sample size (Figs S4–S6).

Factors influencing nocturnal movements and home range size

We examined the influence of body mass and sex on 95% dBBMM range areas using generalised linear models (GLMs) with a Gamma distribution and log link function. A Gamma distribution was chosen as our response variable, and home range size in hectares was continuous, right skewed and had only positive values (Zuur *et al.* 2009). We compared support for body mass and sex individually, alongside their respective additive and interactive models, and a null model using Akaike's Information Criterion corrected for small sample size (AICc) (Buckland *et al.* 1997). Models within 2 AICc units of the top-ranked model were considered equally plausible. We initially included a random intercept with block (seven levels: PP, GVR, BC, CH6, CH4, CH3, and CH2) nested within year (three levels: 2020, 2021 and 2022) to account for any potential spatial and temporal variation in home range sizes within our study design. To evaluate the need for this random intercept, we compared the AICc value of our most complex fixed effects ($mass \times sex$) fitted as generalised linear mixed model (GLMM) with the AICc value of the same fixed effects fitted as a GLM without these random effects (Zuur *et al.* 2009). Because the model without random effects was more strongly supported ($\Delta AICc = 3.08$), the random effects were discarded and the analysis run using GLMs instead (Bolker *et al.* 2009). Additionally, we also included the number of fixes and deployment duration as

fixed effects, but because there was little evidence that these factors significantly influenced home range sizes, these factors were discarded. In total, we had five candidate models. Fitted GLMs were assessed for overdispersion via simulation (Hartig 2020), with no evidence of overdispersion detected.

Home range overlap

Intra- and intersexual home range overlap (%) was described by comparing the degree to which 95% and 50% dBBMM home range areas overlapped among all individuals that co-occurred in the same area using the intersect feature in ArcMap. Proportional overlap (%) for each pair of co-occurring individuals (e.g. hypothetical individuals A and B) was derived as $[(\text{area}_{AB}/\text{home range}_A)(\text{area}_{AB}/\text{home range}_B)]^{0.5}$, where area_{AB} is the area of overlap of the co-occurring individuals and home range_A and home range_B are the home ranges of individuals A and B, respectively (Atwood and Weeks 2003).

Software

Variograms were generated using the 'ctmm' package (v 1.0.0, Fleming and Calabrese 2022), dBBMMs were fitted using the 'move' package (v 4.0.2, Kranstauber *et al.* 2020), GLMMs were fitted using the 'lme4' package (v 1.1-23; Bates *et al.* 2015), GLMs were fitted in the R programming environment (v. 3.6.1; R Core Team 2021), and residual diagnostics and overdispersion in fitted models were assessed using the 'DHARMA' package (v. 0.3.2.0; Hartig 2020). Home range overlap was undertaken using ArcMap (v 10.6).

Results

We successfully captured and attached GPS collars to 39 individual potoroos (23 males and 16 females) (Figs 1 and 2, Table 1). Although traps were open continuously, no potoroos were captured during the day. One collar failed to successfully collect any GPS fixes and was discarded from this study. Collar deployments are described in the Supplementary Information (Tables S1–S3). Beyond minor hair loss around the neck of some individuals, no observable negative effects of collar attachment, such as loss of body mass, were observed. Individuals varied in mass, but a two-sample Wilcoxon rank sum test revealed there was no significant difference in mean body mass between males and females ($w = 219$, $P = 0.16$). Males weighed 805 g (95% CI: 748–860) and females weighed 765 g (95% CI: 705–815) on average.

Given any animal larger than 500 g was suitable for inclusion in our study, it is likely our sample included both resident adults as well as subadults yet to disperse (Table 1). Halfway through deployment, one male ('Doody') began to display extra-territorial movements and eventually dispersed into adjacent habitat approximately 2 km away. Therefore, only movement data before the first example of potential

dispersal movement behaviour (assessed visually and characterised by marked departures from previously consistent movement patterns) were included in further analysis. The dispersal behaviour we observed in one individual male weighing 620 g (Doody) concurs with the suggestion of Hughes (1964) that males weighing less than 640 g are likely to be subadults. However, because Hughes (1964) based his study upon Tasmanian potoroos, which are larger on average relative to the potoroos found in south-eastern Australia, it is possible that potoroos in our study region could reach sexual maturity at lower body masses. Four of the 23 males and three of the 15 females included in this study were deemed to be subadults according to this criterion. An additional two-sample Wilcoxon rank sum test with subadults removed from the sample again suggested no significant difference in mean body mass between adult males and females ($w = 158$, $P = 0.08$). Individuals were tracked for an average of 14 days (range: 4–41 days). After data cleaning, 7534 fixes (range: 43–843 fixes per individual) were available for home range analysis.

Home ranges were roughly circular and the predicted 95% and 50% ranges of potoroos varied substantially among individuals (Fig. 2, Table 1). The largest 95% dBBMM range was predicted for the male 'Snape' (29.50 ha), and the smallest 95% dBBMM range was predicted for the female 'Black Widow' (3.44 ha). The average 95% dBBMM range was 13.73 ha (95% CI: 10.9–16.6) for males and 6.67 ha (95% CI: 5.49–7.85) for females. The average 95% dBBMM range across individuals was 10.94 ha (95% CI: 8.86–13.00).

The largest 50% dBBMM range was predicted for the male 'Snape' (8.00 ha) and the smallest 50% dBBMM range was predicted for the female 'Frenchie' (0.62 ha). The average 50% dBBMM range was 2.92 ha (95% CI: 2.20–3.64) for males and 1.23 ha (95% CI: 1.02–1.44) for females. The average 50% dBBMM range across individuals was 2.25 ha (95% CI: 1.74–2.76).

There was strong evidence that both body mass and sex influenced the home range size of potoroos in our study. Models that included both body mass and sex, either additively or interactively, were more supported relative to models that only included one of these covariates (Table 2). Estimates from the top-ranked model suggested that the influence of body mass on home range size depended on sex. Body mass had no detectable influence on home range size in females, but it had a positive influence on males (Fig. 3).

There were 24 occasions where male and female 95% ranges overlapped, 23 occasions where male ranges overlapped with other males, and six occasions where female ranges overlapped with other females (Fig. 2). There was little evidence of exclusive 95% ranges among individuals or between sexes (Figs 2 and 3). Where individuals of the same sex co-occurred, 95% area overlap was 38.8% (95% CI: 29.0–48.6) for males and 47.1% (95% CI: 33.2–61.0) for females (Table S4–S9). Although samples sizes were small, there was some evidence that adult males may potentially

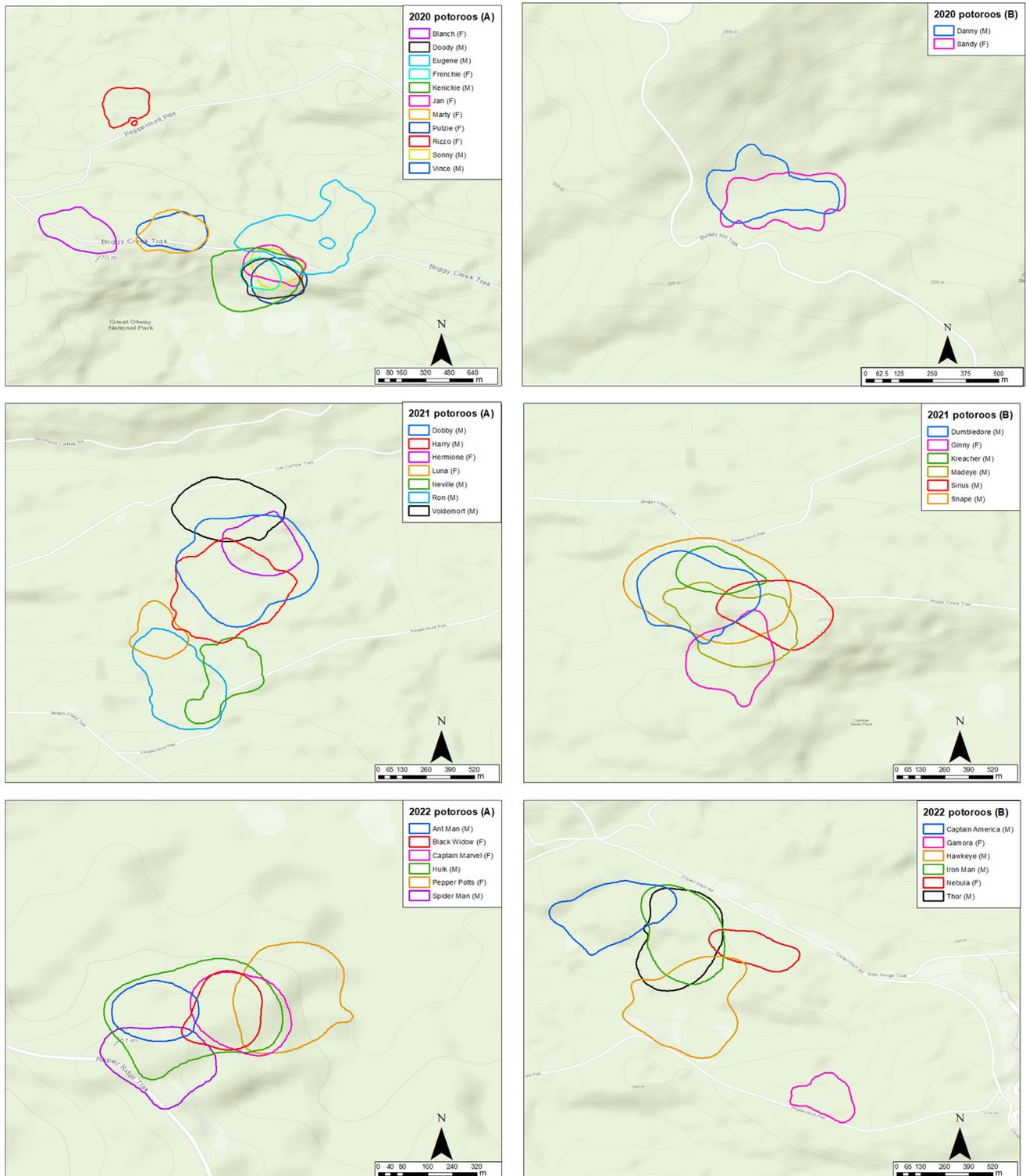


Fig. 2. 95% home ranges of long-nosed potoroos collared in 2020 (top two panels), 2021 (middle panels) and 2022 (bottom panels), as estimated by dBBMM analysis.

orient their 95% ranges to maximise overlap with multiple female 95% ranges. For example, one male (‘Kenickie’) had a home range area that almost completely overlapped the

entirety of three different female ranges, and another (‘Hulk’) had a home range area that almost completely overlapped the entirety of two different female ranges.

Table 1. Summary statistics of collared long-nosed potoroos.

| ID | Year | Sex | Mass (g) | Fixes | dBBMM range (ha) | |
|--------------------|------|-----|----------|-------|------------------|-------|
| | | | | | 50% | 95% |
| Blanch | 2020 | F | 620 | 158 | 1.29 | 8.49 |
| Frenchie | 2020 | F | 540 | 646 | 0.62 | 3.52 |
| Jan | 2020 | F | 790 | 48 | 1.62 | 6.13 |
| Marty | 2020 | F | 880 | 128 | 1.49 | 8.12 |
| Putzie | 2020 | F | 820 | 786 | 1.17 | 7.09 |
| Rizzo | 2020 | F | 720 | 205 | 0.70 | 5.20 |
| Sandy | 2020 | F | 880 | 95 | 1.76 | 8.00 |
| Danny | 2020 | M | 880 | 81 | 1.37 | 8.53 |
| Doody ^A | 2020 | M | 620 | 452 | 1.24 | 6.55 |
| Eugene | 2020 | M | 900 | 157 | 4.09 | 23.10 |
| Kenickie | 2020 | M | 960 | 843 | 4.45 | 16.21 |
| Sonny | 2020 | M | 640 | 539 | 1.16 | 5.50 |
| Vince | 2020 | M | 680 | 108 | 1.35 | 7.40 |
| Ginny | 2021 | F | 670 | 43 | 1.73 | 12.51 |
| Hermione | 2021 | F | 670 | 111 | 1.29 | 8.35 |
| Luna | 2021 | F | 770 | 186 | 1.12 | 5.08 |
| Dobby | 2021 | M | 820 | 93 | 5.84 | 26.13 |
| Dumbledore | 2021 | M | 860 | 105 | 3.89 | 17.63 |
| Harry | 2021 | M | 780 | 206 | 4.72 | 20.29 |
| Kreacher | 2021 | M | 660 | 107 | 1.36 | 6.56 |
| Madeye Moody | 2021 | M | 960 | 100 | 2.74 | 17.21 |
| Neville | 2021 | M | 820 | 106 | 1.80 | 8.55 |
| Ron | 2021 | M | 850 | 135 | 2.04 | 14.40 |
| Sirius | 2021 | M | 840 | 93 | 2.80 | 12.81 |
| Snape | 2021 | M | 820 | 64 | 8.00 | 29.50 |
| Voldemort | 2021 | M | 950 | 182 | 2.89 | 12.38 |
| Black Widow | 2022 | F | 620 | 163 | 1.07 | 3.89 |
| Captain Marvel | 2022 | F | 800 | 198 | 0.95 | 5.28 |
| Gamora | 2022 | F | 840 | 202 | 0.63 | 4.60 |
| Nebula | 2022 | F | 860 | 52 | 1.11 | 5.60 |
| Pepper Potts | 2022 | F | 860 | 90 | 1.87 | 8.21 |
| Ant Man | 2022 | M | 520 | 129 | 0.79 | 3.44 |
| Captain America | 2022 | M | 800 | 163 | 2.45 | 12.92 |
| Hawkeye | 2022 | M | 860 | 77 | 2.25 | 19.27 |
| Hulk | 2022 | M | 1000 | 182 | 2.91 | 12.14 |
| Iron Man | 2022 | M | 880 | 155 | 3.85 | 14.46 |
| Spider Man | 2022 | M | 520 | 190 | 1.14 | 5.40 |
| Thor | 2022 | M | 900 | 156 | 4.04 | 15.43 |

ID, Year, Sex, Mass (g), and the number of GPS fixes available after data cleaning for potoroos collared during this study. Home ranges are derived by fitting dynamic Brownian Bridge movement models (dBBMM). Areas are presented in hectares.

^AAnimal demonstrated dispersal behaviour – only fixes prior to dispersal are included in this summary.

Table 2. Generalised linear models of factors influencing long-nosed potoroos 95% home range size as predicted by dynamic Brownian bridge movement models.

| Rank | Model | Parameters | LogLk | ΔAICc | AICcwt |
|------|--------------------|------------|---------|-------|--------|
| 1 | Range ~ mass × sex | 5 | -100.83 | 0.00 | 0.84 |
| 2 | Range ~ mass + sex | 4 | -103.83 | 3.32 | 0.15 |
| 3 | Range ~ sex | 3 | -109.48 | 12.13 | 0.01 |
| 4 | Range ~ mass | 3 | -110.52 | 14.21 | 0.00 |
| 5 | Range ~ 1 | 2 | -118.29 | 27.39 | 0.00 |

Models are defined in terms of whether home range size (*Range*) was constant (*1*), varied according to body mass (*mass*), sex (*sex*), an additive effect of body mass and sex (*mass + sex*), or an interactive effect of body mass and sex. Log likelihood (LogLk), change in AICc (ΔAICc), and AICc weight (AICcwt) follow Burnham and Anderson 2002.

There were 12 occasions where male and female 50% ranges overlapped, eight occasions where male 50% ranges overlapped with other males, and four occasions where female 50% ranges overlapped with other females. There was little evidence of consistently distinct 50% core areas between males and females. Where males and females co-occurred, their 50% range overlap was 32.9% (95% CI: 20.4–45.4) on average. In contrast, there was some evidence of distinct 50% core areas among females (Fig. 4a) but not males (Fig. 4b). Where individuals of the same sex co-occurred, 50% range overlap was 28.6% (95% CI: 14.4–42.8) on average for males and 12.7% (95% CI: 0–33.7) on average for females – although sample sizes for co-occurring females were small.

Discussion

Our home range estimates of 13.73 ha (95% CI: 10.9–16.6) and 6.67 ha (95% CI: 5.49–7.85) for male and female potoroos, respectively, are more than twice as large as previous estimates reported in the literature for Victorian potoroos (Long 2001, Table 3). They are also the first to be produced for this species using GPS dataloggers and dynamic Brownian bridge movement models. Our results suggested that the influence of body mass on potoroos home range size depended on sex. Body mass had no detectable influence on home range size in females but a positive influence in males (Table 3, Fig. 3). Contrary to elsewhere throughout their range (Norton *et al.* 2010; Frankham *et al.* 2011) and similarly to studies nearby (Bennett 1987), we observed no substantial differences in body mass between male and female potoroos. Prior trapping surveys in the same area suggest the body mass of male and females used in our analysis were typical for potoroos in this region (Le Pla, unpubl.data).

The discrepancy between male and female potoroos ranges at larger mass, despite no significant differences in body mass between sexes, suggest that this difference is not driven by the

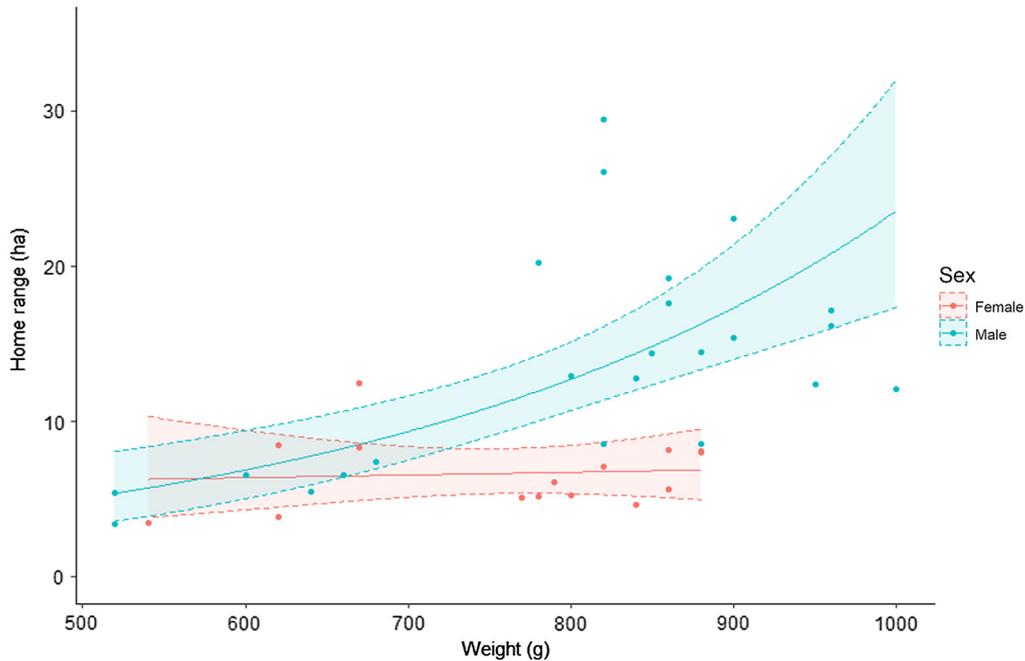


Fig. 3. Predicted relationship between home range size and body mass for male and female long-nosed potoroos. Shaded areas indicate 95% confidence intervals.

increased energetic requirements that coincide with increasing body mass (McNab 1963; Lindstedt *et al.* 1986; Swihart *et al.* 1988). Indeed, given the largely similar range sizes we observed in females of all masses (Fig. 3), it is likely that a range of 6–7 ha is large enough to allow females and younger males to find sufficient food and shelter with minimum risk and energy expenditure in our study area (Sandell 1989; Fisher and Owens 2000). Rather, the intersexual home range overlap patterns observed in our study imply resident adult male potoroos may range across larger areas to maximise their range overlap with nearby females. Potoroos are continuous breeders with asynchronous oestrous cycles (Hughes 1964), and male reproductive success may be linked to a male's ability to regularly assess the sexual status of nearby females (Long 2001; Frankham *et al.* 2012). Maximising intersexual spatial overlap may provide males with greater access to females, which in turn could provide males with detailed knowledge of female movements and potentially improve their reproductive fitness (Schwagmeyer 1988; Long 2001). For example, in a study on French Island, Victoria, male potoroos that successfully sired young also demonstrated a high degree of spatial overlap with the mothers of their offspring (Frankham *et al.* 2012). This behaviour may be common within our study region – we observed several large male ranges almost entirely overlapping co-occurring female ranges, and it is not uncommon for both male and female potoroos to be detected together on camera traps (Le Pla, unpubl. data).

The substantial difference in mean body mass between these populations of potoroos is often proposed as an

explanation for why Tasmanian home range estimates are larger than Victorian estimates (Table 3; Kitchener 1973; Long 2001). Further, the Victorian and Tasmanian populations have been separated for over 2 million years (Frankham *et al.* 2016), potentially resulting in demographic differences influencing a range of characteristics, including home range size.

Substantial differences in sample sizes and methodological approaches may go some way to explaining the variability in potoroos home range estimates. For example, although the studies of Johnson (1988) and Hird (1996) were conducted at the same location and both used trapping data to estimate home range size, Johnson's choice of estimator (MCP) is more vulnerable to biases compared with the estimator used by Hird (KDE) (Börger *et al.* 2006). At small sample sizes, such as those that characterise trapping datasets, MCPs tend to underestimate home range sizes relative to methods that estimate a UD (Girard *et al.* 2002; Börger *et al.* 2006; Fleming *et al.* 2019). Indeed, MCP estimates of potoroos ranges are consistently lower than those predicted using a KDE approach in both Tasmania and mainland Australia (except for Kitchener 1973; Table 3). Because all home range estimates of Tasmanian potoroos have been based upon trapping locations (Table 3), it is possible, much like we observed in our study, that Tasmanian potoroos also range across larger areas than previously predicted. If so, it is also possible that a latitudinal gradient in potoroos home range size exists and has gone undetected due to methodological and analytical differences among studies. Future studies that incorporate GPS tracking of Tasmanian potoroos will be helpful in determining if this is indeed the case.

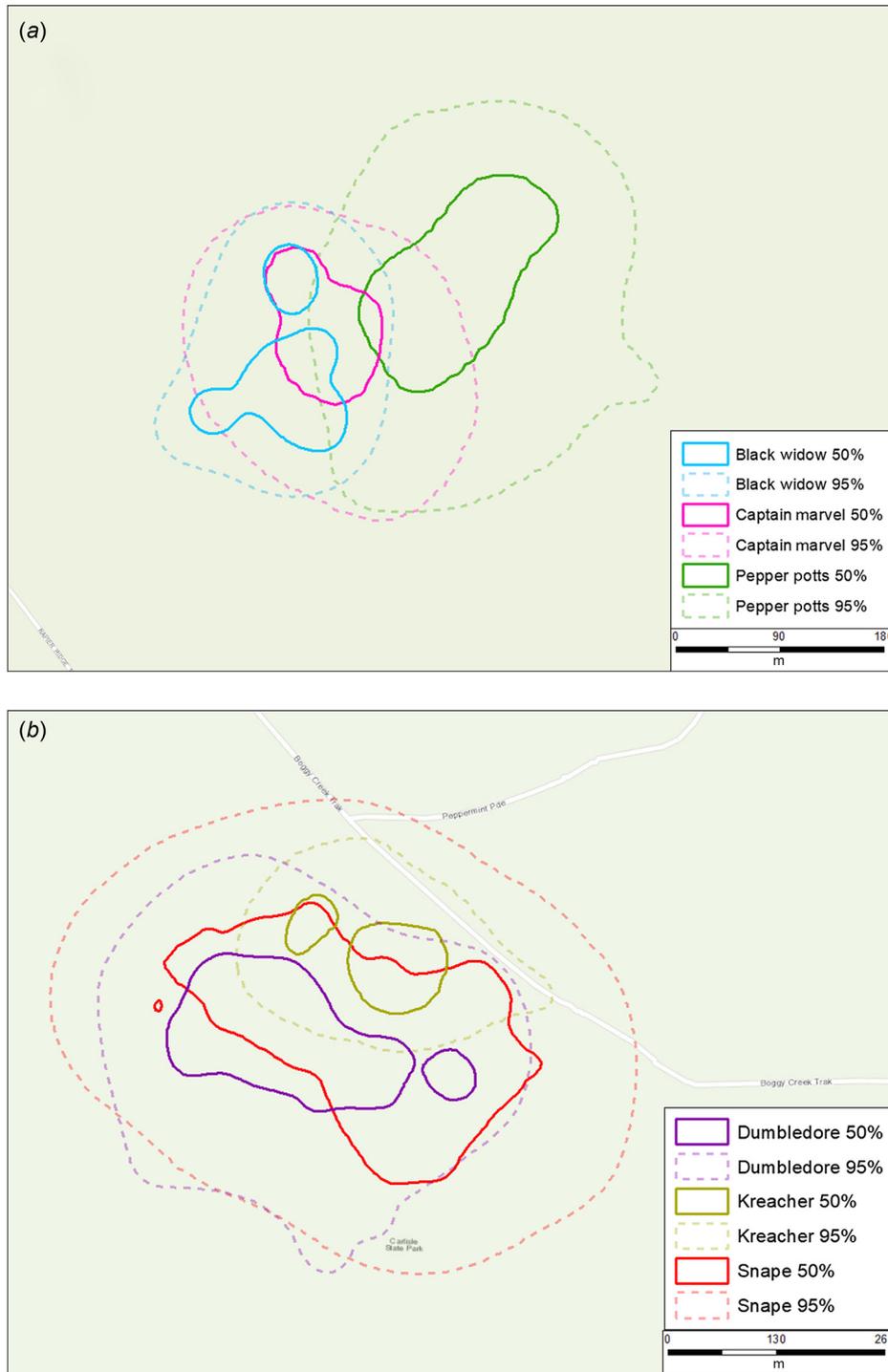


Fig. 4. 50% (solid lines) and 95% (dotted lines) home ranges of co-occurring (a) female and (b) male long-nosed potoroos.

Additionally, landscape context may also play a significant role in determining home range size and arrangement in potoroos. For example, the studies of Bennett (1987) and Long (2001) were undertaken within a relatively small habitat patch surrounded by cleared agricultural land, whereas past Tasmanian studies and our study were conducted in much

larger, contiguously connected habitat patches (Kitchener 1973; Johnson 1988; Hird 1996). Potoroos often display a reluctance to use cleared agricultural landscapes, so this difference in landscape context may be partially responsible for the smaller and potentially more constrained home ranges described by Bennett (1987) and Long (2001). Fine-scale

Table 3. Comparison of home range size of long-nosed potoroos with published and unpublished data from other populations.

| Population | Mass \pm s.e. (g) | | Survey type | Range estimator | n | | Range size (ha) | | Reference |
|------------|---------------------|---------------|-------------|-----------------|----|----|-----------------|-----|------------------|
| | ♂ | ♀ | | | ♂ | ♀ | ♂ | ♀ | |
| Tasmania | – | – | Trap | MCP | 5 | 5 | 19.2 | 5.2 | Kitchener (1973) |
| Tasmania | – | – | Trap | MCP | 10 | 1 | 4.4 | 0.9 | Johnson (1988) |
| Tasmania | 1420 \pm 43 | 1190 \pm 67 | Trap | KDE | 16 | 8 | 10.8 | 5.7 | Hird (1996) |
| Victoria | 789 \pm 77 | 777 \pm 86 | Trap | MCP | 6 | 6 | 2.0 | 1.5 | Bennett (1987) |
| Victoria | 781 \pm 37 | 689 \pm 20 | VHF | KDE | 5 | 7 | 4.0 | 2.9 | Long (2001) |
| Victoria | 805 \pm 28 | 765 \pm 31 | GPS | dBBMM | 23 | 15 | 13.7 | 6.7 | This study |

Trap, data generated through trapping; VHF, data generated through tracking of animals with VHF data logger attached; GPS, data generated via attachment of GPS datalogger to individuals; MCP, Minimum Convex Polygon; KDE, Kernel Density Estimator; dBBMM, Dynamic Brownian bridge movement model.

differences in availability, arrangement of suitable habitat (Bennett 1993; Norton *et al.* 2011), and access to key food resources (Bennett and Baxter 1989; Claridge *et al.* 1993; Claridge and Cork 1994) also likely play a pivotal role in determining the size and spatial arrangement of potoroos home ranges. We recommend similar research into the movement ecology of potoroos populations, particularly those at different latitudes (e.g. Barren Grounds and Booderee, NSW; Norton *et al.* 2010, 2011; Hall *et al.* 2021) and in different habitats (e.g. sub-tropical Queensland; McHugh *et al.* 2019, 2020) before generalising our estimates of home range size to other landscapes.

The lack of exclusive 95% inter- or intrasexual ranges in our study supports the notion of potoroos being solitary yet non-territorial (Bennett 1987; Long 2001; Norton *et al.* 2010). We observed several examples of larger males (e.g. >800 g) demonstrating patterns of high overlap of both 50% and 95% ranges (Fig. 4b), and larger male potoroos often had ranges that encapsulated large proportions of smaller male ranges. In contrast, although sample sizes were small, the limited overlap of 50% 'core' activity areas observed among females suggests female potoroos may display some degree of spatial partitioning of activity (Fig. 4a). This arrangement could be driven by resource or shelter availability (Bennett and Baxter 1989; Bennett 1993) and has been observed in potoroos populations elsewhere (Norton *et al.* 2010; Frankham *et al.* 2014). Although it is likely these females are closely related, (female potoroos have been shown to be highly philopatric in other studies; Frankham *et al.* 2012, 2014), the behavioural mechanisms that underpin exactly how female potoroos partition these core areas remain unknown and beyond the scope of our data. Moreover, because we were unable to attach GPS dataloggers to females with large pouch young in our study, this apparent partitioning may simply be an artifact of excluding these individuals from our sample. Attaching GPS dataloggers to more co-occurring female potoroos, collecting movement data at more frequent intervals, and incorporating additional data streams (e.g. accelerometers) could allow for the classification of fine-scale movement behaviours and provide researchers with the ability to discern movements patterns

associated with different behaviours (e.g. foraging or reproductive movements) (Langrock *et al.* 2012; Bennison *et al.* 2017). This approach would allow for the detailed description of encounters among individual potoroos and the context in which these encounters occur.

The primary limitations of our study were the variable fix success (i.e. variation in the proportion of attempted fixes that each GPS datalogger was able to successfully record as a location but were not removed through data screening), our inability to attach GPS dataloggers to females with pouch young, and the short duration of deployments. Fix success may be influenced by many factors (e.g. topography, fix interval, habitat characteristics; Cain *et al.* 2005), and fix success varied widely among individual GPS dataloggers in our study. For example, one GPS datalogger failed to record any fixes whatsoever, whereas another produced an overall average fix success of 88.7%. Similarly, fix success also varied temporally for individual dataloggers throughout their deployments. For example, one GPS datalogger's daily fix success ranged between 8% and 80%. Despite this variability in fix success, because dBBMMs explicitly incorporate both spatial and temporal features of an individual's path when estimating the UD, this approach can robustly estimate the UD even with variable fix success (Kranstauber *et al.* 2012). Additionally, although capture rates of male and female potoroos in our study region are generally even (Le Pla, unpubl. data), the inability to attach GPS dataloggers to female potoroos with large pouch young resulted in more males than females being included in our study (Table 1). This reduced the opportunity to describe occasions where female potoroos co-occurred and limited our ability to assess the degree to which co-occurring female 95% and 50% ranges overlapped. Finally, the relatively short duration of deployments (4–41 days) precluded any investigation into how potoroos movements may change through time. Given the potoroos' propensity for exploiting hypogean fungi (Bennett and Baxter 1989; Claridge and Cork 1994), it is possible potoroos may alter the size and spatial arrangement of their ranges in response to drivers of this seasonally available food resource.

Inappropriate fire regimes are a key threatening process for potoroos (Woinarski *et al.* 2014) because they often tend to inhabit environments that are burnt, through both prescribed burning and wildfire. For example, the recent ‘Black Summer’ wildfires (which took place during summer 2019–2020) in Australia burnt a substantial proportion of the long-nosed potoroo distribution (Legge *et al.* 2022; Ward *et al.* 2022), and a recent meta-analysis identified potoroos as one of nine mammal species consistently negatively affected by fire (Pocknee *et al.* 2023). Further, there is mounting evidence that potoroos may be particularly vulnerable to predation by invasive predators immediately after fire (Smith 2013; Robley *et al.* 2016; Hradsky 2020; Le Pla, unpubl. data). Estimates of potoroo home range size can directly inform the management of this functionally important (Claridge *et al.* 1992), yet nationally vulnerable, species after fire. For example, robust pre-fire home range size estimates could be used to assess the suitability of unburnt patches post-fire. Indeed, the small scale of burnt patches (<2 ha) relative to assumed potoroo home ranges (~6 ha) was proposed as a primary reason for the lack of negative impact of planned burns on potoroos in sub-tropical Queensland (McHugh *et al.* 2020). Identifying where to prioritise recovery efforts (i.e. post-fire predator management), understanding the carrying capacity of the landscape as it recovers, and informing the ideal size of – and distance between – unburnt habitat patches to leave remaining within a prescribed burn scar to maintain viable populations of potoroos in the landscape post-fire are all potential ways land managers could use home range data to improve the management of potoroos in fire-prone landscapes.

Our results demonstrate the value of integrating GPS loggers and robust home range estimators to describe the movement ecology of a small, vulnerable native Australian marsupial. We highlight the potential that home ranges of potoroos may be larger than previously expected in mainland Australia and provide further evidence that males may arrange their ranges to maximise reproductive opportunities. Given their highly variable body size and the diverse array of habitats inhabited by this species, there would be value in conducting similar research into the movement ecology of potoroos elsewhere throughout their distribution. Doing so would determine if the patterns of movement and range overlap observed in our study are consistent or vary according to different habitat types, body sizes, and landscape contexts. Improving our understanding of how range size and overlap vary within potoroo populations can inform targeted management actions before and after fire – a key threatening process for this threatened marsupial.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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