Life in linear habitats: the movement ecology of an endangered mammal in a peri-urban landscape

S. J. Maclagan, T. Coates, B. A. Hradsky, R. Butryn, E. G. Ritchie.

ABSTRACT

Animal movement can be significantly altered in human-dominated landscapes such as urban and peri-urban areas, where habitat is often fragmented and/or linear. Knowledge regarding how wildlife respond to anthropogenic change is vital for informing conservation efforts in such landscapes, including the design of nature reserves and wildlife corridors. To better understand how threatened species persist and behave within human-dominated landscapes, we examined the home range and space use of the nationally endangered southern brown bandicoot Isoodon obesulus obesulus in peri-urban Melbourne, Australia's second-largest city. Specifically, we examined whether: (1) bandicoots were confined to linear strips of remnant vegetation or also made use of the broader highly modified landscape matrix; (2) the configuration of the linear vegetated strips affected home range shape; and (3) home range area differed between bandicoots living in linear strips and those in larger remnant habitat patches. We found that: (1) 71% of adult males and 33% of adult females used the matrix, but non-dispersing juveniles were entirely confined to the linear strips; males also travelled greater distances into the matrix (away from the vegetated strips) than females; (2) bandicoots had longer home ranges in narrower strips and males had longer home ranges than females; and (3) home range area for both sexes was smaller in linear strips than has been recorded in other studies in larger remnant habitats. Our study highlights the importance of retaining narrow, fragmented and modified vegetation to accommodate threatened biodiversity within human-dominated landscapes, but suggests the surrounding matrix may also offer important resources for adaptable species, such as bandicoots. Supporting off-reserve conservation of biodiversity in novel ecosystems is increasingly pertinent in our rapidly urbanizing world.

INTRODUCTION

Urbanization is a major driver of habitat destruction and modification, and hence the global extinction crisis (Aronson *et al.*, 2014). Nevertheless, certain wildlife species – including some threatened species – are able to adapt to and persist within the novel environments of cities and their peri-urban surroundings (Ives *et al.*, 2016; Maclagan *et al.*, 2018). Species may be classed as urban 'avoiders', 'adapters' or 'exploiters' depending on their level of sensitivity to anthropogenic change (McKinney, 2006; Bateman & Fleming, 2012). A broader understanding of how native species survive in highly modified environments is key to accommodating biodiversity within human-dominated landscapes – a critical issue given the globally expanding human footprint and the limited space available for conservation areas (Dearborn & Kark, 2010; Kowarik, 2011; Soanes *et al.*, 2018).

Optimal foraging theory predicts that animals will only move as much as necessary to optimize their fitness benefits and minimize their physiological costs and predation risk (Krebs, 1980). These benefits and costs can be significantly altered within human-dominated landscapes, resulting from changes in the size, shape and quality of habitats, and the composition of the broader landscape 'matrix' (Fahrig, 2007; Driscoll *et al.*, 2013; Doherty & Driscoll, 2018). In a recent global review, Tucker *et al.*, (2018) found that terrestrial mammals moved less as the strength of the 'human footprint' increased (i.e. anthropogenic effects on the structure and composition of landscapes and resources). Similarly, many studies report animals having smaller home ranges in heavily modified landscapes (Lowry *et al.*, **2013**; Salek *et al.*, **2015**). Animals may alter their movements to access new resources and/or avoid novel threats within the matrix, and this varies both between species and with the intensity of matrix development (Fahrig, **2007**; Brady *et al.*, **2011**; Lowry *et al.*, **2013**).

Linear strips of vegetation associated with waterways, property boundaries and anthropogenic linear features (e.g. roads, railway lines, drains, powerlines) are common within heavily modified landscapes (Bennett, **2003**). Although conservation is rarely their prime objective, linear strips may offer under-appreciated opportunities for biodiversity conservation, by providing a large proportion of the remaining habitat, and/or by facilitating connectivity between other habitat areas (de Lima & Gascon, **1999**; Laurance & Laurance, **1999**; Major *et al.*, **1999**; Leon & Harvey, **2006**; Wehling & Diekmann, **2009**; Pereira & Rodriguez, **2010**; Maclagan *et al.*, **2018**).

Understanding how human-dominated landscapes impact the way animals move and use space may help inform biodiversity conservation and management, such as establishing the minimum size, shape and connectivity of habitats to maintain viable wildlife populations (Allen & Singh, **2016**). Yet despite recent growth in the field of urban ecology, the number of wildlife studies in urban and peri-urban landscapes remains low in proportion to studies in relatively remote, less disturbed ecosystems – particularly considering the extent and continuing expansion of urban growth (Magle *et al.*, **2012**). Consequently, knowledge regarding how animals move in such landscapes remains limited (LaPoint *et al.*, **2015**).

To better understand how threatened species persist and behave within human-dominated landscapes, we examined the home range and space use of the nationally endangered (EPBC Act, **1999**) southern brown bandicoot *Isoodon obesulus obesulus* in peri-urban Melbourne, Australia's second-largest city. In this landscape, remnant vegetation largely occurs in narrow strips along linear features such as roads, drains and railway lines (Schmidt *et al.*, **2009**). These vegetated strips provide important habitat for the species (Maclagan *et al.*, **2018**); however, knowledge regarding the movement ecology of bandicoots within these areas remains a crucial priority to inform the ongoing management of this population (Schmidt *et al.*, **2009**).

The specific aims of our study, and corresponding predictions, were:

1. Determine whether southern brown bandicoots were confined to the linear strips of vegetation or also made use of the surrounding highly modified landscape matrix, and whether this varied with sex or age. Based on the Resource Dispersion Hypothesis (Macdonald & Johnson, 2015) and the polygynous or promiscuous mating system in this species (Cockburn, 1990), we expected female home range to be governed largely by food availability, whereas males would occupy larger home ranges and move greater distances to maximize mating opportunities. Thus, we predicted males would be more likely to move into the matrix and travel greater distances away from strips than females. We also expected matrix use to reflect body-size-related differences in predation risk. Foxes and cats are thought to preferentially prey on smaller bandicoots (i.e. females and juveniles) (Dickman, 1988; Claridge *et al.*, 1991), and predation risk is likely to be higher away from the densely vegetated strips, so we again predicted greater use of the matrix by adult males vs. females or juveniles.
2. Quantify home range length of southern brown bandicoots occupying linear strips and determine whether this was related to strip width or sex. Given the linear configuration of habitat at our sites, we considered home range length (White & Garrott, 1990; Lima *et al.*, 2016) to be more meaningful than home range area for management purposes. We

predicted that home range length would decline as strip width increased to provide similar overall home range area. We also predicted that males' home ranges would be longer than females', again reflecting the mating system, and previous home range studies in this species (Broughton & Dickman, 1991; Mallick *et al*, 1998).

3. Compare home range area estimates at linear sites with those previously obtained from relatively large remnant habitat patches. We predicted that home ranges in our highly modified study area would be smaller than those previously recorded in large remnant habitats, based on patterns observed in other species in linear habitats (van der Ree *et al.*, 2001; Cale, 2003; van der Ree & Bennett, 2003; Martin *et al.*, 2007) and urban areas (Lowry *et al.*, 2013; Salek *et al.*, 2015).

MATERIALS AND METHODS

Study species and study area

The southern brown bandicoot is a medium-sized ground-dwelling marsupial (males 500–1600 g, females 400–1000 g; Braithwaite, 1995) endemic to south-eastern Australia. Once considered common, the species now occupies a patchy and reduced distribution within its former range (Brown & Main, 2010), having suffered significant population declines due to habitat loss and modification, fragmentation, inappropriate fire regimes, extensive wildfires, introduced predators and isolation of populations (Department of the Environment and Energy, 2019). Historically, southern brown bandicoots were associated with a range of native vegetation types with dense understorey; suitable habitat is now defined as any patches of native or exotic vegetation within the species' distribution with understorey vegetation structure having 50–80% average foliage density in the 0.2–1 m height range (Department of the Environment and Energy, 2019).

Our study focuses on a population of southern brown bandicoots occupying the former Koo-Wee-Rup or 'Great' Swamp, which was the largest wetland in Victoria prior to being drained from the 1870s onwards for agricultural use and to facilitate easier access to Melbourne (Yugovic & Mitchell, 2006). It is now contained within Melbourne's 'Greater Capital City Statistical Area', delineated by the Australian Government's Bureau of Statistics to reflect the 'functional extent' of the city by including the population of regular commuters (Australian Bureau of Statistics, 2016), and has a human population density of approximately 18.8 per km2 (Australian Bureau of Statistics, 2011). This peri-urban landscape comprises a mix of land uses, including small urban townships, 'rural-residential' properties (i.e. 'hobby farms'), grazing pastures, vegetable cropping and some intensive animal production (poultry farms). Remaining vegetation is concentrated in narrow linear strips along the network of drainage channels, roads and railway lines, and includes a high proportion of exotic plant species (Schmidt et al., 2009). Non-native predators of bandicoots, such as the red fox Vulpes vulpes, domestic dog Canis familiaris, and domestic and feral cat Felis catus are also common (Schmidt et al., 2009).

Despite the highly modified condition of this region, Maclagan et al. (2018) reported higher capture rates of bandicoots at five linear sites (Sites A–E in this study) than at two relatively large and intact conservation reserves nearby, indicating that linear strips can sometimes support high densities of bandicoots. They also found that most bandicoots at linear sites were resident rather than transient, that important demographic processes (breeding, recruitment of first-year adults and survival of mature adults) were occurring, and that female body condition was similar to that in intact reserves (Maclagan et al., 2018). These observations confirmed the potential for linear sites to support viable bandicoot populations in this region (Maclagan et al., 2018) and provided impetus for further research.

Study sites

Fieldwork was undertaken at seven linear sites clustered within three broad 'localities' spanning the extent of the former Koo-Wee-Rup Swamp (Yugovic & Mitchell, 2006) (38.1994°S, 145.4908°E; Fig. 1a). The region experiences mild wet winters and warm dry summers, with an average annual rainfall of 785 mm (Bureau of Meteorology, station #86314).

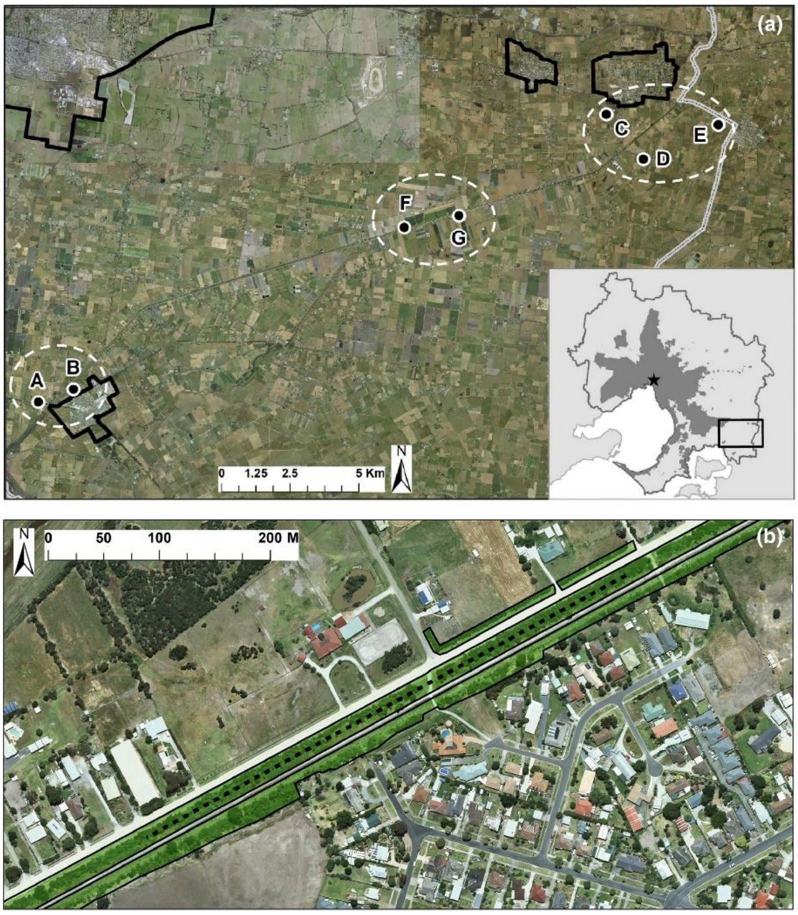

Figure 1: (a) Location of the seven field sites (A–G) from three broad 'localities' (dashed ellipses) within the former Koo-Wee-Rup Swamp region, Victoria. Melbourne's urban growth boundary is shown in black and its Greater Capital City Statistical Area is outlined in light grey. The inset shows the location of the zoomed extent (black rectangle) in relation to the city centre (black star), urban growth boundary (dark grey shading) and Greater Capital City Statistical Area (dark grey outline). (b) Example of site-level habitat configuration. At this site (B), the 'strip' (shaded green) included suitable vegetation on both sides of a road and parallel walking track. Aerial imagery shows the surrounding 'matrix' of rural residential properties to the north and urban residential properties in the Koo-Wee-Rup township to the south. The dashed line indicates the extent of the trapping transect.

Study sites were separated by at least 2 km and/or a substantial physical barrier (i.e. a large watercourse). Each consisted of a 'strip' of largely continuous roadside vegetation at least 500 m long, containing dense (i.e. approximately 50–80% average foliage density) understorey vegetation suitable for bandicoots. Sites were selected to represent the range of strip widths (16.5–56.5 m) commonly available across the region.

Vegetation comprised a mix of native and exotic plant species. Swamp paperbark *Melaleuca ericifolia* and blackwood *Acacia melanoxylon* were the dominant tree species at all sites except E and G, where the canopy was co-dominated by swamp gum *Eucalyptus ovata* (Site E) or silver wattle *Acacia dealbata* (Site G). Blackberry *Rubus fruticosus* agg. was present at all sites; other common exotic plant species included cherry plum *Prunus cerasifera*, flax-leaf broom *Genista linifolia*, kikuyu *Cenchrus clandestinus* and angled onion *Allium triquetrum*.

The 'matrix' surrounding each strip typically consisted of large rural grazing properties (>5 ha), although Sites B and E were adjoined by rural residential properties (1–3 ha) on one side, and Site B was bordered on its other side by urban residential properties (0.06–0.15 ha).

Trapping and handling

Five trapping sessions were conducted between May 2012 and October 2013, covering different stages of bandicoot breeding biology (May–Sep: pre- or early-breeding season, Oct–Dec: mid-late breeding season, Jan–Mar: largely non-breeding; Lobert & Lee, 1990). Site E was not surveyed in May–Sep 2012 and Sites F and G were only surveyed for one session (Oct–Dec 2012). Trapping was undertaken for at least four nights per session, with traps either set in the late afternoon/early evening and checked at first light (Oct–Mar), or set in the early/mid-afternoon and checked approximately 2 h after dark (May–Sep). This minimized the time between setting and checking traps (typically < 8 h, maximum < 14 h). At each site, up to 20 wire mesh cage traps (500 × 250 × 350 mm) covered with black plastic were set at 25 m intervals along a transect through the centre of the main vegetation strip (Fig. 1b). Traps were baited with peanut butter, oats and golden syrup, and hessian was provided as bedding.

Upon capture, bandicoots were placed into cloth bags, weighed, measured, sexed and permanently marked with a Passive Integrated Transponder (Trovan, www.trovan.com). Individuals were classified as juvenile or adult based on sex, mass and time of year as per Maclagan *et al.* (2018). A single-stage Very High Frequency (VHF) transmitter was attached to the tail, unless the bandicoot had pouch-young at an advanced stage (to reduce the risk of abandonment of young), lacked a tail, or appeared sickly or injured. Various sizes of single-stage transmitters (1.1–3.75 g) with whip antennas (150–220 mm long) were used (Sirtrack, www.sirtrack.co.nz; or Advanced Telemetry Systems, www.atstrack.com), with transmitters selected to be no wider than the tail and to weigh <5% of body mass. The attachment method (developed by N. Hughes, personal communication) was as follows: (1) a bead of flexible contact adhesive (*Selley's Kwik Grip*) was placed on top of the tail base; (2) a layer of flexible breathable tape (*Fixomull*) was laid around the tail over the glue; (3) another bead of glue was applied and the transmitter placed on top with the antenna running along the length of the tail; and (4) 1–2 layers of paper tape (*Micropore*) were wrapped around both the tail and transmitter. Tail-mounted transmitters generally remained attached for 2–4 weeks (maximum 5 weeks) before falling off naturally. Following transmitter attachment, animals were released at the point of capture.

Radio-tracking and location data

Individuals were radio-tracked for up to 4 weeks using a handheld VHF receiver (*Ultra*, Sirtrack) and three-element folding Yagi antenna (Advanced Telemetry Systems). When bandicoots travelled longer distances, a vehicle-mounted omni-directional whip antenna (Titley Scientific, www.titley-scientific.com) was used to establish the general location before radio-tracking commenced on foot. The animal was approached as closely as possible without disturbing it (generally 3–10 m), and the location marked with a handheld GPS (Garmin 62SC, www.garmin.com). If there was any doubt regarding whether the animal was inside the strip, we radio-tracked from the opposite side to confirm. The angle and estimated distance to the animal (based on signal strength) was used to adjust GPS locations once uploaded into the computer GIS mapping software, ArcMap version 10.1 (ESRI, 2012). Locations were conservatively estimated as being accurate to within 3 m, due to the high accessibility of the sites. If a radio-transmitter dislodged prematurely, traps were set close to the last known location or identified nest site(s) to re-trap the animal and re-attach the radio-transmitter.

Although we observed some individual-level variation in activity patterns (i.e. some bandicoots were largely diurnal while others were predominantly nocturnal), activity generally peaked around dusk. Thus, radio-tracking was concentrated between mid-day and midnight to maximize data capture from active individuals. Up to five independent locations were obtained for each animal per 24 h period. Locations were considered independent if at least 1 h had elapsed between fixes (preliminary data showed that bandicoots could traverse the entire length of their home range within this time), and one of the following additional conditions was met (ensuring that only one nest location was obtained for each nesting period):

1. The animal had moved > 3 m; or
2. The animal had not moved, but there was evidence it was not in a nest (i.e. seen or heard foraging or moving about and not simply flushed from a nest); or
3. The animal had not moved, but at least 18 h had passed (ensuring at least one nesting/activity cycle had elapsed), and the animal was known to move again at a later time (i.e. animal was alive and transmitter functioning).

Matrix use

To determine whether bandicoots used the highly modified matrix, and whether sex or age affected matrix use, we classed each location as ‘strip’ or ‘matrix’. ‘Strips’ of native vegetation were defined in ArcMap (ESRI, 2012), using aerial photos and site knowledge, and comprised multiple parallel polygons if suitable vegetation occurred on both sides of a linear feature (i.e. road, railway line, walking track; Fig. 1b). All locations outside the strip were classified as ‘matrix’.

Bandicoots were considered to use the matrix if they had at least 10 locations overall, and at least one of these occurred within the matrix. The bandicoot’s distance into the matrix was calculated as its perpendicular distance from the strip. No juveniles used the matrix. To test whether sex affected the likelihood of matrix use of adult bandicoots, we used generalized linear mixed models with logit-link functions and binomial errors (individuals were coded as 1 if they used the matrix at least once or 0 if all location were within the strip). To test whether sex affected the distance travelled into the matrix, we used linear mixed models (see Model selection, below). Distances were log10-transformed to improve the normality and homoscedasticity of the residuals.

Home range length

To examine the effect of strip-width and sex on home range length, we calculated home range length for adult bandicoots that had a substantial majority (defined as ≥75%) of their locations within the strip, and only used one linear strip. Home range length was not meaningful for individuals that intensely used the matrix or the intersection between perpendicular strips (e.g. at road junctions). Lengths were calculated by perpendicularly ‘snapping’ strip locations to a central line using ArcMap (ESRI, 2012), then measuring the length of the 95% closest locations (i.e. excluding the outlying 5%) using XTools Pro version 12.1 (XTools, 2012). A diagrammatic representation of this process is shown in Supporting Information Figure S1. Although the peripheral parts of an individual's home range may be necessary for biological requirements, comparing 95% home range lengths reduces undue bias from infrequently used locations (Kenward, 2001).

To determine the minimum number of locations required to adequately estimate home range length, we generated incremental home range length plots (sensu Harris et al., 1990) for animals with >50 strip locations (range: 54–81). Home range length began to plateau by 20 locations, with 90% of the total home range length reached at 10–20 locations (Supporting Information Figure S2). Therefore, we included all individuals with ≥20 strip locations in the home range length analysis. All animals appeared to be resident, based on the incremental area curves of home range length (e.g. Supporting Information Figure S2) and the consistency of their locations between tracking seasons (S. Maclagan, unpublished data).

We used linear mixed models to quantify the single, additive and interactive effects of strip-width and sex on home range length of adult bandicoots (see Model selection, below). 'Strip width' for each site was calculated as the average width of the strip at 10 equally spaced points (excluding the width of any linear feature). Home range length data were $\log_{10}$-transformed to improve the normality and homoscedasticity of the residuals.

Home range area

To compare the home range size of bandicoots in our study with estimates from other studies on *I. obesulus* in larger remnant habitat patches (there are no such patches within our immediate study area), we calculated home range area using the 95% Minimum Convex Polygon (MCP) method in the 'adehabitat' package (Calenge, 2006) in R version 3.3.1 (R Core Team, 2016). MCPs produce more reliable results than probabilistic models when sample sizes are small (Laver & Kelly, 2008), and kernel density estimate methods can overestimate the size of irregular home range shapes, including those that are linear (Downs & Horner, 2008). The MCP method is also the most consistent with previous *I. obesulus* studies in remnant habitats (Table 2).

To determine the minimum number of locations needed to adequately estimate 95% MCPs, we generated incremental plots for animals with >50 locations (range: 54–117). True asymptotes were not reached, but rates of increase generally slowed above 30 locations (Supporting Information Figure S3). There was no evidence of a relationship between sampling effort and home range area for adults of either sex with ≥30 locations (Spearman rank correlations: males: r = 0.07, P = 0.83, n = 13; females: r = 0.29, P = 0.43, n = 10). Therefore, we deemed 30 locations an acceptable minimum for our purposes. This number may underestimate true home range area, but is larger than that used in previous *I. obesulus* studies (Table 2).

We used linear mixed models to test for an effect of sex on home range area. Data were $\log_{10}$-transformed to improve the normality and homoscedasticity of the residuals.

Model selection

For each analysis, the random structure in the mixed models accounted for the spatial nesting (and where applicable, repeated measurements of an individual) in our design. To determine the most appropriate random structure for each model set, we fitted the full fixed model (all possible fixed effects and their interactions) and compared the level of support for models with different (or no) random structures, using Akaike's information criterion adjusted for small sample size (AIC_c) and associated Akaike model weights (Zuur *et al.*, 2009).

The candidate random intercept structures were 'locality', 'individual' and 'individual within locality' for distance into the matrix, and 'locality' for probability of matrix use, home range length and home range area. Sample sizes were insufficient to use 'site' rather than 'locality' as the spatial grouping variable. Results of random structure selection are presented in Supporting Information Table S1.

We then used the highest-ranked random structure to compare the candidate fixed effects models to each other and a null (intercept-only) model. The model with the lowest AIC_c is considered the 'best' in the set, while others within 2 AIC_c units also have substantial support (Burnham & Anderson, 2002). Model sets are shown in Table 1.

Table 1. Candidate models and model selection results for the movement ecology of southern brown bandicoots *Isoodon obesulus obesulus* in the former Koo-Wee-Rup Swamp region, Victoria, Australia

Response variable	Candidate model	logLik	ΔAIC_c	Akaike weight	R^2m	R^2c
Probability of using matrix	~Sex	−28.22	0.00	0.87	0.14	–
	~1	−31.19	3.74	0.13	0.00	–
Distance into matrix[a]	~Sex + (1|Individual)	−54.38	0.00	0.81	0.16	0.73
	~1 + (1|Individual)	−56.87	2.92	0.19	0.00	0.72
Home range length[a]	Strip width + Sex	13.36	0.00	0.82	0.66	–
	Strip width × Sex	13.41	3.13	0.17	0.65	–
	Strip width	7.67	8.46	0.01	0.48	–
	~1	−0.39	21.96	0.00	0.00	–
	Sex	0.53	22.75	0.00	0.07	–
Home range area[a]	~Sex	−9.99	0.00	0.65	0.15	–
	~1	−11.92	1.2	0.35	0.00	–

Outputs shown are log likelihood (logLik), the difference in Akaike's information criterion adjusted for small sample size between the model and the best model (ΔAIC_c), and the likelihood of the model being the best in the set (Akaike weight). Model fit is indicated by the marginal (R^2m; fixed effects only) and, if applicable, conditional (R^2c; full model including random structure) R^2. [a] $\log_{10}$-tranformed.

All models were fitted in R version 3.3.1 (R Core Team, 2016). Generalized linear mixed models and linear mixed models were fitted using the package ‘lme4’ (Bates et al., 2015). Models without a random structure were run as generalized linear or linear models in the base package, as applicable. As a measure of model fit, we produced conditional and marginal R2 (Nakagawa & Schielzeth, 2013) using the package MuMIn (Barton, 2016).

RESULTS

We obtained ≥10 independent locations ($\bar{x} \pm$ se: 33.0 ± 19.5) for 56 bandicoots, including 46 adults (31 males, 15 females) and 10 juveniles (5 males, 5 females). An example of the radio-tracking data is shown in Fig. 2. Of the total 1849 locations, 84% (*n* = 1546) occurred within the vegetated strips and the remaining 16% (*n* = 303) occurred within the matrix. The maximum length of strip traversed within a single night was 1200 m for a male and 450 m for a female.

Figure 2: Radio-tracking data for four adult southern brown bandicoots *Isoodon obesulus obesulus* radio-tracked at Site B during Jun–Jul 2013. The yellow dots represent data from an adult male while the other three colours represent adult females.

Most bandicoots overlapped spatially with others, of both the same and opposite sex. Within sexes, there was at least partial overlap among ≥85% of females (*n* = 13) and ≥52% of males (*n* = 23). In comparison, ≥71% of females (*n* = 14) and ≥75% of males (*n* = 16) overlapped at least partially with individuals of the opposite sex. These estimates only include adults that were tracked concurrently with at least one individual of the relevant sex.

Bandicoots frequently used vegetation on both sides of linear features such as roads and tracks, many as part of their daily movement paths. Gap-crossing ability appeared to vary between individuals. Both adult and juvenile bandicoots crossed a 2.5 m wide gravel walking trail and 2 m wide drain with slow-flowing water at Site B, a 5 m wide disused railway line at Site A, and a 10.5 m wide active railway line (with culverts underneath the track) at Site E. Adults of both sexes also crossed the 5–7 m wide gravel roads present at Sites A, B, C, D and G. However, only a single adult male was ever observed crossing one of the 7 m wide bitumen roads present at Sites E and F, and no individual crossed the 9 m wide fast-flowing waterway adjacent Sites F and G. No juveniles were recorded crossing roads.

Matrix use

Males were more likely than females to use the matrix (coef ± se: 1.59 ± 0.68; Table 1), with 71% of males (*n* = 31) and 33% of females (*n* = 15) recorded in the matrix at least once. Males also travelled further into the matrix than females (coef ± se: 0.52 ± 0.20; Table 1). The median (min–max) distance travelled into the matrix was 76.1 (3.5–613.3) m for males and 29.7 (1.3–57.0) m for females. We did not observe any juveniles using the matrix, despite obtaining a total of 203 locations from ten individuals.

Bandicoots in the matrix were often found close to the feeding places of domestic animals (e.g. rabbits, caged birds, chickens, pigs, sheep, cats, dogs). Local landholders suggested that some bandicoots regularly accessed food provided for domestic pets or livestock.

Some bandicoots also nested in the matrix: among individuals that used the matrix, 18% of the nesting sites we located (*n* = 50) were outside strips. This may underestimate the true number because limited access in the matrix made it more difficult to locate nests than in strips. Matrix nests were typically situated under houses, sheds or piles of refuse, but one nest was found under a clump of *Agapanthus* in a residential garden. Nest sites within strips tended to occur where groundcover vegetation was particularly dense, but did not appear to be limited by a lack of taller vegetation – for example, a number of nests occurred in dense *Kikuyu* grass directly adjacent to the roadside and subject to regular slashing.

Home range length

We calculated home range lengths for 24 adult and 5 juvenile bandicoots that had at least 75% of their locations within the strip (Table 2). Among adult bandicoots, there was strong support for an effect of strip width (coef ± se: −0.01 ± 0.00) and sex (0.22 ± 0.06) on home range length, with the additive model most highly ranked (Table 1). Home ranges were shorter in wider strips, and males had longer home ranges than females (Fig. 3). Juveniles tended to have shorter home ranges than adults (Table 2). We were unable to explore the effects of strip width or sex on juvenile home-range length due to the small sample size.

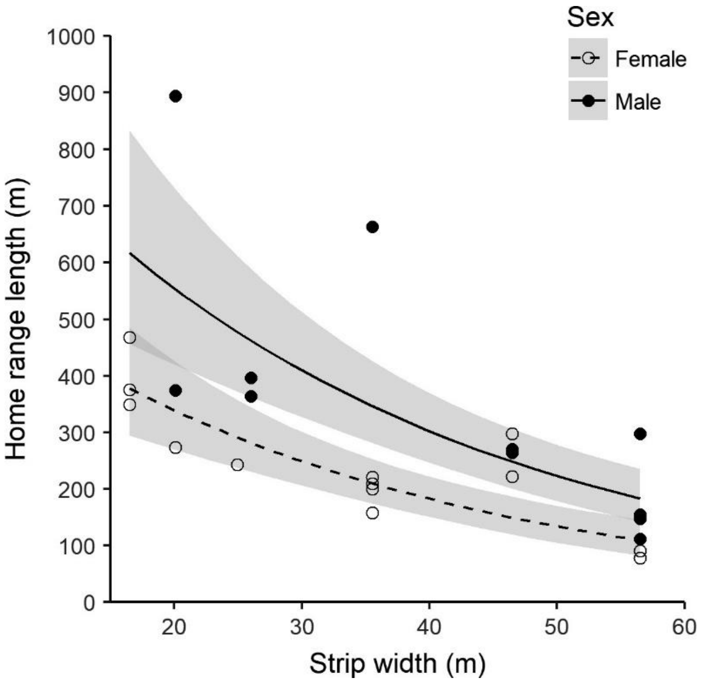

Figure 3: Relationship between strip width, sex and home range length from the top-ranked model for adult southern brown bandicoots *Isoodon obesulus obesulus* occupying linear strips of vegetation in the former Koo-Wee-Rup Swamp region, Victoria, Australia. Strip-width has been back-transformed to facilitate interpretation.

Table 2: Home range lengths of southern brown bandicoots *Isoodon obesulus obesulus* occupying linear strips of vegetation in the former Koo-Wee-Rup Swamp region, Victoria, Australia.

Demographic group	*n*	Home range length (m)	
		$\bar{x}$ ± se	min–max
Adult males	11	358 ± 71	111–893
Adult females	13	245 ± 31	78–468
Juvenile males	1	84	–
Juvenile females	4	169 ± 56	52–278

Home range area

We calculated home range area for 23 adult bandicoots (13 males, 10 females) with ≥30 locations. There was weak evidence that males had larger home ranges than females (coef ± se: 0.32 ± 0.16; Table 1). Home range sizes are shown in Table 3, along with values from previous studies.

Table 3: Home range area estimates for the southern brown bandicoot *Isoodon obesulus* from this study and from previous studies.

Study	Landscape type	Mean home range (ha) (min–max)		Sample size		Home range estimation method	Type of location data	Min. no. loc.
		Male	Female	M	F			
This study	Peri-urban	1.66 (0.27–4.8)	0.75 (0.08–1.54)	13	10	95% MCP	Radio-tracking	30
Robinson *et al.* (2018)a	Remnant	15.2	4.6	5	6	95% MCP	Radio-tracking	28
Stava (2005)	Remnant	2.74	1.76	6	6	95% MCP	Radio-tracking	–
Broughton & Dickman (1991)	Remnant	2.34	1.83	75	60	100% MCP	Spool-and-line, pigment tracking, trapping grid	10
Copley *et al.* (1990)	Remnant	2.1	1.5	10	11	Grid cell	Trapping grid	10
Lobert (1990)b	Remnant	1.55 (0.79–2.50)	1.1	3	1	90% 'Centre of Activity' isopleth	Radio-tracking	14
Mallick *et al.* (1998)	Rural	6.95 (5.0–8.9)	3.28 (0.8–5.6)	2	5	95% MCP	Trapping grid	8

Study	Landscape type	Mean home range (ha) (min–max)		Sample size		Home range estimation method	Type of location data	Min. no. loc.
		Male	Female	M	F			
Heinsohn (1966)	Rural	5.3 (4.3–6.6)	2.3	4	1	100% MCP	Trapping grid	6

MCP, Minimum Convex Polygon. [a] Animals recently translocated. [b] Animals radio-tracked for 1–3 days only.

Aside from one study where animals were only tracked for a very short period (Lobert, 1990), our home range area estimates were smaller than those previously reported for I. obesulus in any habitat type, including both relatively large patches of remnant vegetation and more open rural landscapes. We also recorded the smallest home ranges for individual I. obesulus of each sex ever reported.

DISCUSSION

Anthropogenic landscape change can affect wildlife in many ways, including by altering individuals' movement and space use. In our human-dominated and highly modified study area, we found that southern brown bandicoots: (1) predominately remained within strips of dense vegetation, but some adults – particularly males – also moved considerable distances into the landscape matrix; (2) aligned their home ranges with the configuration of vegetation, with individuals in narrower strips having longer home ranges; and (3) had smaller home ranges than those previously recorded in larger remnant habitats.

Matrix use

Bandicoots generally concentrated their activity within the vegetated strips, indicating an overall preference for dense vegetation cover. However, at least two thirds of adult males and one third of adult females also used the surrounding landscape matrix. This suggests the matrix may offer important resources, such as novel food and/or shelter. We suspect anthropogenic food is the stronger of these two drivers, as animals were often tracked to properties where domestic animal food was available. Exploitation of anthropogenic food is common among opportunistic mammal species in urbanized landscapes throughout the world (Fedriani *et al.*, 2001; Newsome *et al.*, 2015), including bandicoots (FitzGibbon & Jones, 2006; Hillman & Thompson, 2016).

As predicted, male bandicoots were more likely to use the matrix than females or juveniles, with juveniles never recorded in the matrix. Males also travelled further from strips than females. These differences were expected based on the polygynous or promiscuous mating system (Cockburn, 1990) and body size-related differences in predation risk; foxes and cats are thought to preferentially prey on smaller bandicoots (i.e. females and juveniles) (Dickman, 1988; Claridge *et al.*, 1991). Such differences in predation risk are consistent with observed patterns of sex-ratio bias in *I. obesulus*: female-biased populations are generally confined to areas where exotic predators are excluded, whereas most other populations are male-biased (Pentland, 1999; Maclagan *et al.*, 2018). At our sites, there were more males than females (Maclagan *et al.*, 2018), which could reflect a higher predation risk for females, as is common in many species (Boukal *et al.*, 2008), and is implicated in sex-based differences in habitat preference for various taxa (Ruckstuhl & Neuhaus, 2002). Experimental manipulation of predator abundance and resource quality could further elucidate the drivers of these observations. Future research could also investigate seasonal differences in space use by male and female bandicoots.

The apparent reluctance of juvenile bandicoots to leave the vegetated strips could have important implications for dispersal and gene flow. Bandicoots are most likely to disperse as juveniles (Cockburn, 1990), as is typical in most mammals (Greenwood, 1980). None of the juveniles in our study dispersed during the tracking period, and further research into habitat selection during dispersal is required. Nonetheless, confinement of their non-dispersal activity to densely vegetated linear strips suggests that structural connectivity of habitat is also likely to be important during dispersal.

Home range length

As predicted, home range length declined with increasing strip width, suggesting that bandicoots require a minimum area to meet their needs, and must adopt more elongated home ranges to achieve this in narrower strips. Likewise, black bears *Ursus americanus* on a linear island occupied more elongated home ranges in the narrower parts of the island (Lindzey & Meslow, 1977). Brush-tailed phascogales (van der Ree *et al.*, 2001), squirrel gliders (van der Ree & Bennett, 2003), mountain brushtail possums (Martin *et al.*, 2007) and white-browed babblers (Cale, 2003) also have longer home ranges in strips of roadside vegetation than large habitat patches, although none of these studies investigated the relationship between home range length and strip width. An important implication of this relationship is that narrower strips may impose greater energetic costs due to increased travel distances, and thus become unviable habitat for bandicoots below a minimum width.

Also in line with predictions, male bandicoots had longer home ranges than females, presumably to increase access to mates. This is consistent with the observations of larger male home ranges in previous studies on this species (Broughton & Dickman, 1991; Mallick *et al.*, 1998).

Home range area

As predicted, the home ranges we observed were smaller than any previously recorded for this species. This finding is consistent with a general trend for mammals to show reduced home ranges in urban areas (Lowry *et al.*, 2013; Salek *et al.*, 2015) – for example, raccoon *Procyon lotor* (Prange *et al.*, 2004), key deer *Odocoileus virginianus clavium* (Harveson *et al.*, 2007), badger *Meles meles* (Davison *et al.*, 2009), stonemarten *Martes foina* (Herr *et al.*, 2009) and red fox *Vulpes vulpes* (Tolhurst *et al.*, 2016; Fiderer *et al.*, 2019).

Tucker *et al.* (2018) proposed two non-exclusive mechanisms to explain reduced animal movements in areas highly impacted by humans: (1) movement barriers (such as habitat change and fragmentation), and (2) reduced movement requirements due to enhanced resources (such as crops, supplemental feeding, and water sources). In our study, bandicoot activity was predominantly concentrated within linear vegetated strips, indicating a potential constraining effect of the matrix on bandicoot movement (particularly for juveniles and females). However, reduced movement requirements due to increased and novel resources are also likely. Previous research has revealed a negative relationship between home range size and population density in *I. obesulus* (Heinsohn, 1966; Lobert, 1990; Broughton & Dickman, 1991; Mallick *et al.*, 1998; Pentland, 1999), and density in turn is positively correlated with abundance of invertebrate prey (Lobert, 1985; Broughton & Dickman, 1991; Packer, 2014). Bandicoots were in particularly high density at our sites, possibly due to the availability of novel resources provided by exotic plant species (e.g. blackberry, *Rubus fruticosus* agg.) and anthropogenic food and/or water resources, or the relatively fertile and productive soil found in the Koo-Wee-Rup Swamp region (Maclagan *et al.*, 2018). Increased and/or more stable food resources are thought to be associated with the smaller home ranges of many other urban animals around the world, including threatened species (Harveson *et al.*, 2007; Lowry *et al.*, 2013; Salek *et al.*, 2015; Tucker *et al.*, 2018). A possible implication of the small home ranges, high density and high overlap of individuals at our study sites could be increased transmission of parasites or diseases between individuals (e.g. Quinn & Whisson, 2005).

Management recommendations

Based on our findings, southern brown bandicoots in the former Koo-Wee-Rup Swamp region may be classed as urban 'adapters', as they remain dependent on natural resources (i.e. vegetated strips), but are also capable of using anthropogenic resources (McKinney, 2006). We provide the following management recommendations to support the ongoing conservation of this adaptable species in peri-urban Melbourne:

1. Vegetated strips along linear infrastructure should be maintained at a minimum width of 30 m, including both sides of gravel roads, but not bitumen roads or other impassable features such as deep waterways. This configuration allows relatively compact home ranges and therefore minimizes energetic demands from excessively elongated home ranges.

2. Where a width of ≥30 m is not achievable, narrower strips should also be considered important for bandicoots. Strips as narrow as 16.5 m have been found to support resident individuals (Maclagan *et al.*, 2018).

3. Gaps in the habitat network should be minimized, noting that even 7 m wide bitumen roads appear to act as barriers to adult movement, or 7 m wide gravel roads to juvenile movement. Culverts or other crossing structures may be useful in cases where such gaps cannot be avoided.

4. For 30 m wide vegetated strips, gaps should be ≥500 m apart to accommodate at least one male and two female home ranges; gaps should be further apart in narrower strips.

5. Any weed management (e.g. blackberry poisoning) in linear strips should consider potential impacts on bandicoot habitat values. Weed control should be done gradually and cautiously, replacing exotic plants with fast-growing native species that create dense understorey.

6. To reduce predation risk, domestic cats should be confined and foxes and feral cats controlled. This should be conducted using an integrated, whole-of-ecosystem approach to avoid potential unintended, negative outcomes (Doherty & Ritchie, 2017).

7. The permeability and habitat value of the matrix may be enhanced by encouraging the planting of dense understorey species in private gardens and public spaces (e.g. parks, roadside curbs).

8. Ongoing population monitoring should be undertaken to inform adaptive management of bandicoots.

Key priorities for further research include:

1. Assessing the impact(s) of human-provisioned food on bandicoot health and behaviour.
2. Determining what factors influence habitat selection and matrix use by dispersing juveniles.
3. Related with (2), examining how habitat connectivity and matrix composition affect gene flow and bandicoot population viability (landscape genetics).

In conclusion, our study highlights the likely underappreciated value that narrow, fragmented and modified areas of vegetation can have for accommodating wildlife, including threatened species, in human-dominated landscapes. It also suggests the surrounding matrix may offer important resources for adaptable species, such as bandicoots. Understanding how anthropogenic landscape change influences the way animals move and use space is increasingly important as we seek ways to better support off-reserve biodiversity conservation in novel ecosystems arising from widespread and increasing urbanization.

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