



RESEARCH ARTICLE

Investigating the effects of landscape productivity on the spatial ecology of a threatened marsupial inside feral predator exclosures

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Abstract

Landscape productivity and resource dispersion are key drivers of the movement patterns of many species. In less productive environments, home ranges are generally larger as individuals travel further to access resources. The greater bilby (*Macrotis lagotis*) has been reintroduced to several feral predator exclosures to reduce their extinction risk. Understanding how landscape productivity and resource dispersion influence bilby space use is critical to enable effective management of populations in exclosures. At two exclosures, we tested three hypotheses: 1. Bilbies would preferentially utilize habitats with sandy substrates (<20% clay content), as they are suitable for digging burrows and foraging pits; 2. Home ranges would be larger at the arid site compared to the semi-arid site due to lower productivity and patchier distribution of preferred habitats; and 3. Bilbies would travel further each night at the arid site to access preferred habitats. Rainfall was used as an indicator of productivity, and dispersion of preferred habitats as an indicator of resource dispersion. The study was undertaken during average rainfall conditions and under similar bilby population densities at both sites. GPS loggers recorded home ranges and movements of 10 bilbies at the arid site, and 11 bilbies at the semi-arid site. Seventeen of the 21 bilbies preferentially utilized habitats with sandy substrates, which were less abundant at the arid site. There were no significant differences in home range size or nightly movements between the sites for either sex. We suggest the average rainfall conditions at both sites, and the dietary flexibility of bilbies, supported the maintenance of relatively small and stable home ranges (particularly for females). The effects of landscape productivity and resource dispersion on bilby space use are more likely to be evident during extended periods of below average rainfall. Bilby home range studies during low rainfall conditions (e.g. drought) are required for the effective, long-term management of exclosure populations.

KEYWORDS

arid, conservation translocation, GPS, greater bilby, home range, reintroduction, semi-arid, threatened species

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INTRODUCTION

Understanding how individuals utilize space is a critical component of wildlife management and conservation. Yet movement of individuals is complex and influenced by a variety of factors including requirements to access food (Saïd et al., 2009; Schradin et al., 2010), shelter (Fisher, 2000), breeding sites (Campbell et al., 2013; Kelly et al., 2010) and conspecifics (e.g. for mating, passive social interaction or aggressive territory defence; Efford et al., 2016; Schoepf et al., 2015; Schradin et al., 2010). To assist with understanding animal movement, the ecological concept of 'home range' was developed by Burt (1943), which he defined as the area utilized by an individual for foraging, mating and care of their young. The definition of 'home range' has been refined over the years, and is now typically considered to be the area repeatedly used by an animal during its lifespan for all its normal behaviours and activities, excluding occasional exploratory excursions (Silva et al., 2021).

Numerous studies have shown a relationship between home range size and resource availability (McLoughlin & Ferguson, 2000). In Australia, landscape productivity and resource availability are key drivers in the movement patterns and spatial organization of several native and introduced species (Bengsen et al., 2016; Kortner et al., 2019; Newsome et al., 2017). In a study by Bengsen et al. (2016) collating data from a range of habitat types, female feral cats (*Felis catus*) had smaller home ranges in highly productive landscapes, with male home ranges scaling positively with those of females. Di Stefano et al. (2011) showed that home range size of swamp wallabies (*Wallabia bicolor*) was not only strongly correlated with the abundance of resources such as food, shelter and mates but also the spatial dispersion, or heterogeneity, of these resources (i.e. small home ranges where resources were more evenly dispersed). Similarly, in a study of northern quolls (*Dasyurus hallucatus*) in the semi-arid zone, quolls had larger activity areas where key resources (i.e. rocky habitats) were patchily dispersed throughout the landscape (Cowan et al., 2023). There are two central hypotheses that describe these relationships between home range size and the availability and dispersion of resources at the landscape-scale. Firstly, the *habitat productivity–home-range size hypothesis* (Harestad & Bunnell, 1979; McNab, 1963) predicts that within a species, home ranges will be larger in less productive environments as individuals will be required to move over larger areas to access sufficient resources for survival. Secondly, the dispersion of resources can also influence home range size. The *resource dispersion hypothesis* (Carr & Macdonald, 1986; Clutton-Brock & Harvey, 1978) states that where food resources are widely dispersed or unpredictable in abundance, individuals will occupy larger home ranges.

Arid areas generally have lower productivity than environments that receive greater rainfall, and resources tend to be more patchily distributed and less reliable due to spatial and temporal variability of rainfall (Letnic & Dickman, 2005, 2010). The ecological impact of resource patchiness and spatial/temporal variability is that individuals in arid populations may have to travel further to access resources and have larger home ranges than conspecifics in wetter/less arid areas (Fisher & Owens, 2000; Kortner et al., 2019). Consequently, individuals in arid areas may have increased energetic requirements and may experience increased conflict and territoriality over resources, particularly during periods of drought or at high population densities, leading to higher mortality and decreased fecundity (Wolff, 1997). For many arid zone species, these ecological impacts underpin their 'boom-bust' lifecycles,

where population irruptions occur during favourable seasons and are followed by dramatic declines during subsequent dry periods (Brandle & Moseby, 1999; Letnic & Dickman, 2006).

The greater bilby (*Macrotis lagotis*; hereafter 'bilby') is an endangered, nocturnal, burrowing marsupial that was once widespread across Australia, though is now restricted to the driest regions of the continent (DCCEEW, 2023; Southgate, 1990b). Bilbies once occupied more than 70% of the Australian mainland, but remaining wild populations now occupy ~20% of their former range (Bradley et al., 2015; Silcock et al., 2023; Southgate, 1990a; Southgate et al., 2007). To reduce their risk of extinction, bilbies have been reintroduced to over 15 fenced exclosures and offshore islands, free of introduced predators, in various climatic zones throughout their former range (DCCEEW, 2023; Palmer et al., 2020).

Bilbies are sexually dimorphic (males to 2500g, females to 1500g), and males adopt a roving mating strategy and may mate with multiple females within their home ranges, which, on average, spanning more than 3 km² (Miller et al., 2010; Moseby & O'Donnell, 2003). Female bilby home ranges are significantly smaller than their male counterparts, with an average female home range covering 0.18 km² in a study of bilbies reintroduced to a feral predator exclosure in arid South Australia (Moseby & O'Donnell, 2003). Bilbies are capable of breeding year-round in arid and semi-arid climates (Miller et al., 2010; Moseby & O'Donnell, 2003). They have an opportunistic foraging strategy and will exploit seed and bulb resources following rain and rely more heavily upon invertebrates when plant food resources are scarce (Bice & Moseby, 2008; Navnith et al., 2009; Southgate & Carthew, 2006). This strategy is advantageous for a species that inhabits areas where food availability is spatially and temporally variable due to unpredictable rainfall (Gibson, 2001; Morton et al., 2011; Stafford Smith & McAllister, 2008; Stafford Smith & Morton, 1990). While studies have investigated bilby home range size, movements or response to resource availability and dispersion (McRae, 2004; Moseby & O'Donnell, 2003; Southgate et al., 2007; Southgate & Carthew, 2006), there are currently no studies comparing bilby space use at sites in different climatic regions. Due to the large number of fenced bilby populations, understanding space use is important for managing both bilby populations and resources within these exclosures.

In this study, we used GPS data loggers to record and compare movements of bilbies in two fenced exclosures, one in the arid zone and the other in the semi-arid zone of Australia. The study was undertaken during a period of average rainfall conditions and under similar bilby population densities at both sites (9.26–11.26 bilbies per km²). Thus, the influence of population density and rainfall on bilby home range size was expected to be comparable at both sites. Movement data were examined to (a) improve our scientific understanding of bilby spatial ecology in exclosures to inform management of fenced populations; and (b) to test hypothesised behavioural differences at the arid site and the semi-arid site, based on differences in landscape productivity and resource dispersion. We hypothesised that: 1. Bilbies would preferentially utilize habitats with sandy substrates (<20% clay content) within the fenced exclosures as they are suitable for digging burrows and foraging pits; 2. Bilby home ranges would be larger at the arid study site versus the semi-arid site (due to the lower productivity and the patchier distribution of preferred habitats); and 3. Bilbies would travel greater distances each night at the arid study site versus the semi-arid study site (to access preferred habitats that are more patchily distributed).

METHODS

Study sites

The study was undertaken in two fenced exclosures: (1) Currawinya National Park (CNP) in the semi-arid zone of south-western Queensland (28 km² fenced exclosure), and (2) Arid Recovery (AR; Main Exclosure 14 km² fenced exclosure) situated in the arid zone of South Australia (Figure 1). Both exclosures were free of introduced predators (i.e. red foxes, feral cats) and canids during the study period. The study period at AR was from September to October 2020 (i.e. spring), and from April to May 2021 at CNP (i.e. autumn). It was not logistically possible to undertake this study during the same season at the two sites.

CNP (semi-arid zone) has a mean annual rainfall of 294.8 mm, while AR (arid zone) has a mean annual rainfall of 139.2 mm (Figure 2). Both exclosures recorded 'average' rainfall in the 12 months prior to the tracking periods (i.e. as defined by the Bureau of Meteorology as rainfall between 30th and 80th percentiles for a 12-month period; Bureau of Meteorology, 2023). CNP recorded 344.8 mm (66th percentile) in the 12 months prior to tracking (April 2020–March 2021) and 304.5 mm (57th percentile) between 12 and 24 months prior to tracking (April 2019–March 2020; Bureau of Meteorology, 2022). At AR, 109.0 mm (32nd percentile) was recorded in the 12 months prior to tracking (October 2019–September 2020), and below average rainfall of 54.8 mm (11th percentile) was recorded in the 12–24 months prior to tracking (October 2018–September 2019; Bureau of Meteorology, 2021). During 2018–2019 both sites experienced drought conditions, which was followed by rainfall in 2020 signalling a shift from drought conditions to average rainfall conditions (Figure 2).

Bilbies were reintroduced to CNP in multiple releases between April 2019 and April 2021, and the population was in the growth phase during this study (i.e. high rates of population increase until carrying capacity

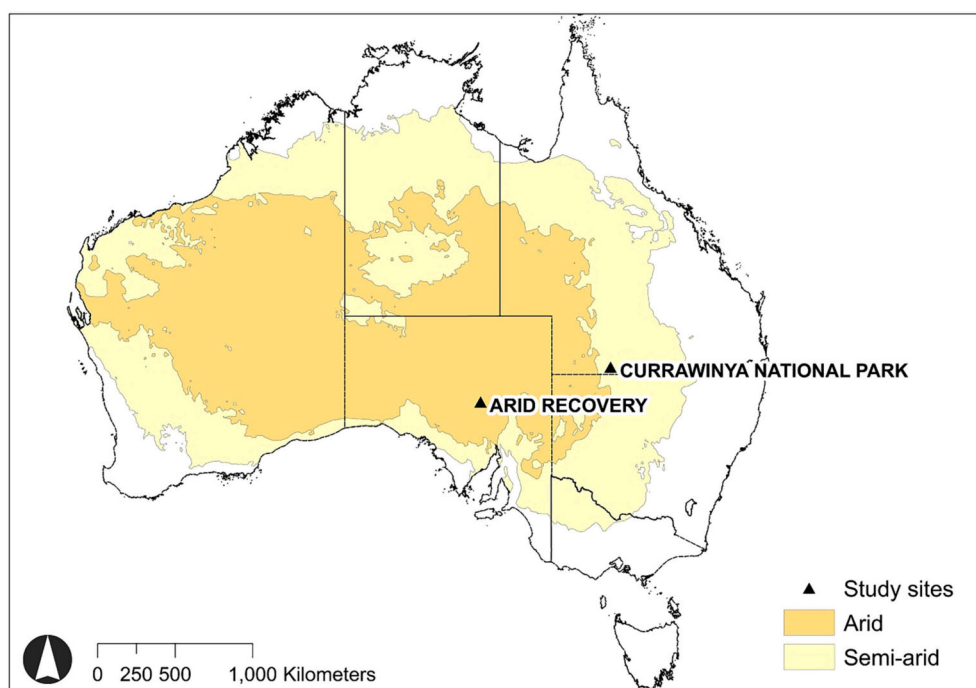


FIGURE 1 Location of the two study sites (both fenced exclosures), Arid Recovery in the arid zone of South Australia, and Currawinya National Park in the semi-arid zone of Queensland.

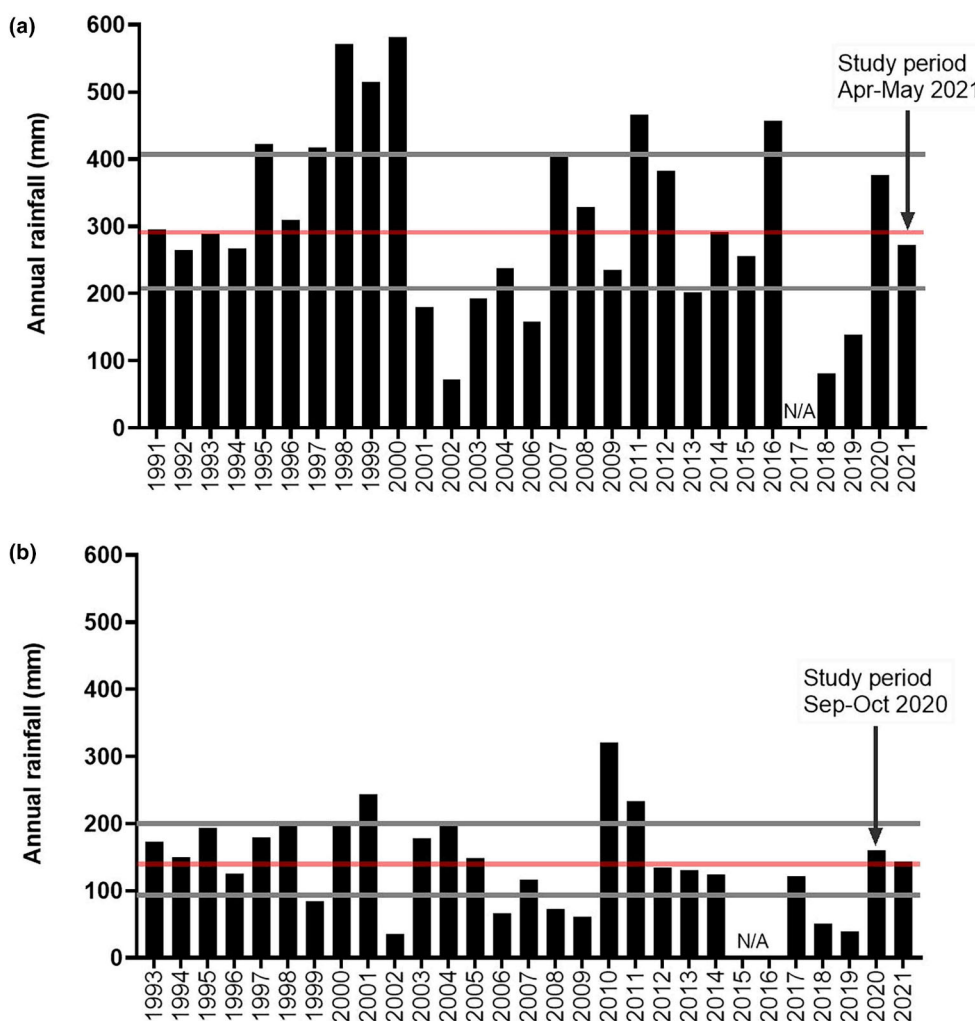


FIGURE 2 Annual rainfall recorded over the last ~30 years at (a) Bureau of Meteorology (BoM) weather station 44 181 at the Paroo River in Hungerford, Queensland (8 km south of CNP); and (b) BoM weather station 016096 at the Olympic Dam Aerodrome, South Australia (9.8 km south of AR). The red lines on the graphs indicate the mean annual rainfall for the stations (from 1884 to 2021 for the Paroo River weather station, and from 1993 to 2021 for the Olympic Dam Aerodrome weather station). The lower grey lines are the 30th percentiles for annual rainfall (i.e. 30% of all annual rainfall totals fall below this line), and the upper grey lines are the 80th percentiles for annual rainfall at each station. Annual rainfall totals falling between these two percentiles are considered ‘average’ rainfall years by BoM (Bureau of Meteorology, 2023).

reached; IUCN/SSC, 2013). At AR, bilbies were reintroduced in 2000 and the population has been supplemented several times since the initial release (Moseby, Hill, & Read, 2009). The population was in the regulation phase during this study (i.e. lower rates of population increase compared to growth phase due to increased population density; IUCN/SSC, 2013). We calculated population density estimates immediately prior to the commencement of tracking periods at each enclosure using spatially explicit capture-recapture (SECR) methods and track count data as a secondary validation method. Similar population density estimates were obtained for the enclosures, with 11.26 bilbies per km² at CNP and 9.26 bilbies per km² at AR (C. Arkinstall, unpublished data).

Both enclosures contain habitats that are representative of the surrounding landscape and contain the dominant vegetation types that occur within the local area (Figure 3). The fenced enclosure at CNP encompasses mixed shrublands on sandy soils, mulga shrublands, small sparsely vegetated claypans and larger claypans fringed by black box (*Eucalyptus largiflorens*). The Main Enclosure at AR is characterized by longitudinal sand

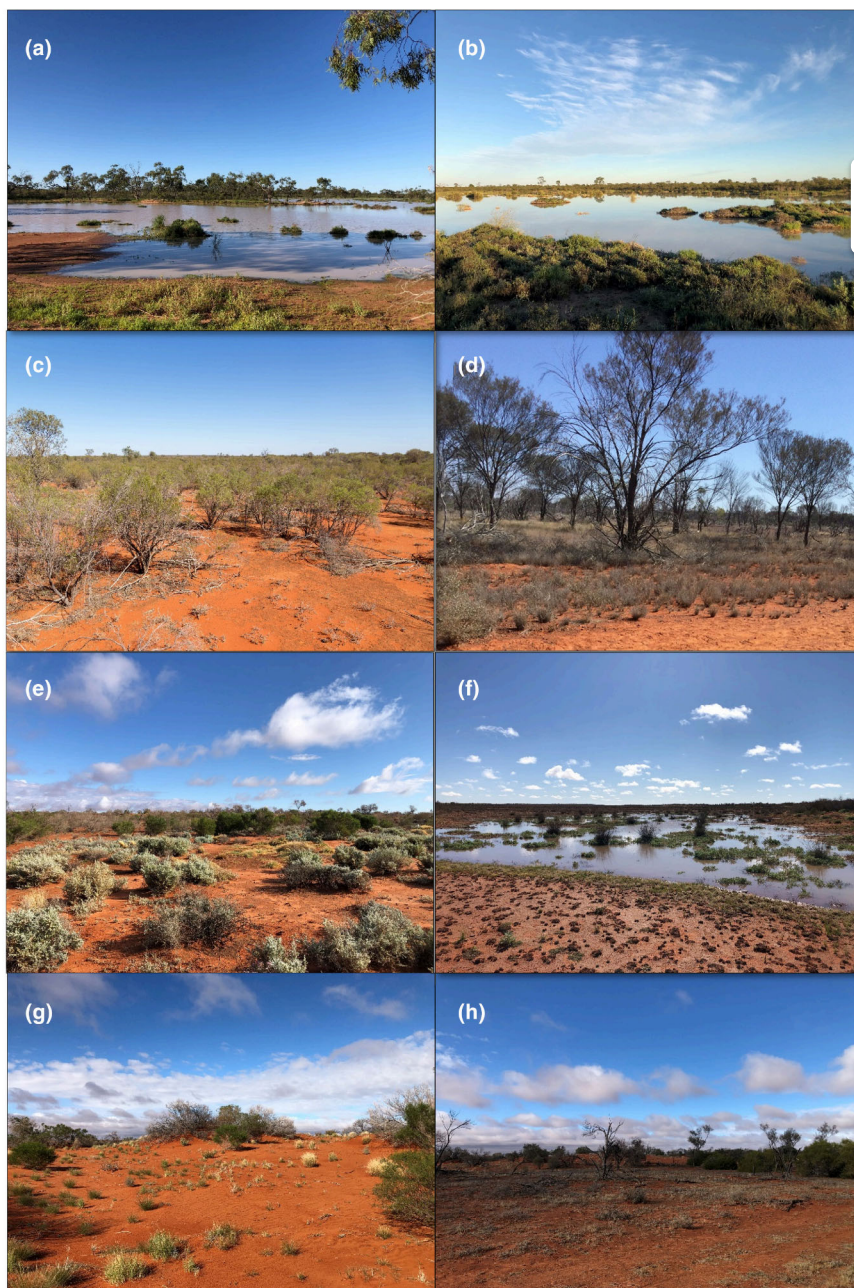


FIGURE 3 Habitat types present within the enclosures, including (a) claypan fringed by black Box (*Eucalyptus largiflorens*), (b) claypan, (c) shrublands, (d) mulga (*Acacia aneura*) shrublands, (e) swale, (f) swamp, (g) sand dune and (h) sand plain.

dunes and interdunal swales, with a small number of claypans and vegetated swamps scattered throughout the enclosure.

Bilby capture and tracking

Initial capture of bilbies at CNP was via cage traps set adjacent to the existing track network. Trapping was undertaken over six nights in Autumn 2021 (15–20 March), and bilbies were monitored until late April. At AR, bilbies were captured by burrow trapping (McGregor & Moseby, 2014) and hand netting over seven nights in spring 2020 (8–14 September), and study animals were monitored until late October. An additional female bilby was

captured at AR during the tracking period; this female was included in the study with a delayed tracking period from late November to mid December 2020.

We taped a PinPoint 120 GPS logger (Lotek Wireless Inc., United Kingdom) and a VHF transmitter (A2480 model, Advanced Telemetry Systems Inc., United States of America) to the tail of captured bilbies, as described in Cornelsen et al. (2021). The combined weight of the GPS and VHF units, and tape, was 8.9g. The smallest bilby included in the study weighed 610g (AR female), with the attachment weight approximately 1.45% of the bilby's total body weight. Following attachment and examination, bilbies were released at their initial capture location.

GPS loggers were scheduled to collect hourly fixes throughout the night for up to 25 nights. The first nightly fixes were scheduled for approximately 1 h after sunset, with 11 hourly fixes collected each night (CNP: 19:00–06:00; AR: 19:30–06:30). Where the GPS loggers were not able to obtain a valid fix within 40 seconds, they were set to shut down ('timeout') until the next scheduled fix to conserve battery life. The VHF transmitters were in operation for the duration of the tracking period to enable bilbies to be radiotracked daily (where possible) to diurnal burrows. At the end of the study period, bilbies were recaptured, and GPS and VHF units removed.

Stationary GPS logger test

A stationary test of six GPS loggers was undertaken prior to deployment on the bilbies, to examine the relationship between the GPS logger horizontal dilution of precision (HDOP) values and on-ground accuracy. Site conditions such as vegetation cover and terrain can impact satellite acquisition and positional accuracy of location fixes, therefore understanding the relationship between HDOP values and on-ground positional accuracy is considered best practice for studies utilizing GPS data (Matthews et al., 2013; Recio, Mathieu, Denys, et al., 2011).

Six GPS loggers were placed at a known geographical location in CNP (the stationary test location), as measured with a differential GPS (accuracy to within 10mm). Loggers recorded hourly fixes from 7:30 PM to 6:30 AM for nine consecutive nights. Accuracy of the fixes was then determined in ArcMap 10.8 (ESRI Inc., USA). The results of the stationary test were used to inform the selection of GPS data for habitat use and nightly movement analyses.

Habitat availability, dispersion and use

Habitat availability at each enclosure was calculated using fine-scaled habitat maps developed for each site. We measured the geographical spread of habitat types (including preferred habitats identified from GPS data) within each enclosure as an indicator of resource dispersion. We used the 'landscapemetrics' package in R (Hesselbarth et al., 2019) to assess several measures of habitat dispersion. This open-source package includes a wide array of landscape metrics commonly used in studies of animal movement, habitat use and ranging behaviour (Bista et al., 2021; Gardiner et al., 2019; Hesselbarth et al., 2019; Jackson & Fahrig, 2014). The dispersion of habitat types (including preferred habitats) in each enclosure was examined using two aggregation metrics: (1) 'CLUMPY' (clumpiness index) and (2) 'ENN_MN' (mean Euclidean nearest neighbour distance; Hesselbarth et al., 2019; McGarigal et al., 2015). The clumpiness index measures the degree to which patches of the same habitat type are aggregated on a scale



from -1 (maximally disaggregated) to 1 (maximally clumped; McGarigal et al., 2015). The mean Euclidean nearest neighbour distance is a measure (in metres) of the shortest straight-line distance between two habitat patches (edge-to-edge) of the same type (McGarigal et al., 2015). We described the landscape-level habitat characteristics for each enclosure using 'CONTAG' (contagion index; Hesselbarth et al., 2019; McGarigal et al., 2015). The contagion index measures the extent to which habitat types are aggregated (or clumped) at the landscape-level, as a percentage (Fan & Myint, 2014; McGarigal et al., 2015). This measure accounts for both interspersions (the intermixing of different habitat types) and dispersion (the distribution of each habitat type across the landscape), with higher contagion indices indicating habitats are less intermixed and less evenly distributed across the landscape.

To assess bilby habitat use within each enclosure, we intersected autocorrelated kernel density estimate (AKDE) home ranges and GPS fixes ($\text{HDOP} \leq 4.0$) with habitat maps. We also recorded habitat type for diurnal burrow locations during radiotracking.

Home range size and nightly ranges

Home ranges were calculated using AKDE in 'ctmm' package (Calabrese et al., 2016) in R (R Core Team, 2023). We followed the workflow outlined in Calabrese et al. (2016) with the additional step of modelling the device-specific GPS logger error, as outlined in Noonan et al. (2019). As the positional error (in metres) of each GPS fix was modelled and accounted for in 'ctmm' home range analyses, fixes of all HDOP values were included.

GPS data for each bilby were plotted in 'ctmm' to identify and remove any obviously erroneous locations from the data set (i.e. fixes outside of the fenced enclosures). Empirical variograms were reviewed for each bilby to determine if they exhibited range-residency and were suitable for home range analyses. Movement models were fitted using maximum likelihood. We ranked the movement models for each individual using corrected Akaike Information Criterion (AIC_c) (Brewer et al., 2016; Burnham & Anderson, 2002). The top ranked movement model was selected and used to condition home range analyses in 'ctmm'. AKDE 95% and 50% isopleths were used for area calculations (clipped to the enclosure fence where required). Home ranges were also estimated using incremental area analysis and the minimum convex polygon (MCP) method in Ranges 9.0 (Anatrack Ltd., UK), to enable comparison with previous bilby home range and movement studies (McRae, 2004; Moseby & O'Donnell, 2003).

Nightly home ranges (100% MCP) were calculated where three or more highly accurate fixes ($\text{HDOP} \leq 4.0$) were obtained per individual per night.

Nightly movements

We calculated mean nightly distance travelled and maximum nightly distance travelled where there were at least three GPS fixes ($\text{HDOP} \leq 4.0$) per night, and where fixes were not more than 3h apart. We excluded nights where these criteria were not met.

Data analyses

Data were processed and visually inspected in R for normality prior to statistical analysis. Where data were normally distributed, we used t -tests with

Welch's correction and *t*-tests to test for significant differences in sample means and variances. For non-normally distributed data, Wilcoxon rank sum tests were used. For habitat use analyses we used Chi-squared tests in R to compare observed and expected GPS fixes per habitat type, with *p*-values calculated using Monte Carlo simulations in R where sample sizes were small (i.e. less than five fixes for a habitat type). Chi-squared tests were also used to compare mean burrows use between the study sites and sexes. Statistical power analyses were conducted for all statistical tests in R package 'pwr' (Champely, 2020), with Cohen's *d* of 0.5 (medium-sized effect based on results from Moseby and O'Donnell (2003) and initial results from CNP; Cohen, 1988), and significance level set to 0.05.

RESULTS

Stationary GPS logger test

The mean proportion of valid fixes (i.e. three or more satellites visible to the logger) relative to scheduled fixes for all GPS loggers was 0.98 (\pm SE 0.02, $n=6$), with a range of 0.88–1.00 (Table 1). The proportion of valid fixes with a HDOP of 4.0 or less was 0.88 on average (\pm SE 0.07, $n=6$), and five of the six units had a valid fix proportion higher than 0.90. The stationary logger tests showed that valid fixes with a HDOP of ≤ 4.0 were an average of 5.31 m from the known location (\pm SE 0.26 m, $n=628$) and 87% were accurate to within 10 m (Table 1).

GPS logger field performance

We collected GPS data for 21 bilbies during the study period, including 11 bilbies from CNP (5F:6M) and 10 bilbies from AR (4F:6M; Table S1; Appendix S1). Four additional GPS loggers were attached to bilbies at CNP (1F:3M); however, they detached before collecting adequate location fixes for inclusion in this study. There were no significant animal welfare issues associated with the tail attachments, only minor rubbing on the dorsal surface of the tail was observed in a small number of bilbies. Of the successfully deployed GPS units, location fixes were collected for a minimum of 20 days (233 scheduled GPS fixes) to a maximum of 41 days (384 scheduled GPS fixes; Table S1; Appendix S1).

The proportion of valid location fixes obtained from the total scheduled fixes ranged from 0.64 to 0.87 (mean of $0.76 \pm$ SE 0.01; Table S1; Appendix S1). Approximately, two-thirds of all invalid fixes (i.e. scheduled fixes where a location was not able to be obtained) were recorded during the first hour or in the last 2 h of the nightly fix schedule (61% of invalid fixes at CNP, 63% at AR). It is likely that bilbies were down burrows when these fixes were attempted, and satellites were not within visible range of the loggers. On average, the proportion of valid fixes for each bilby with a HDOP ≤ 4.0 was 0.94 (SE ± 0.01 , range 0.85–0.97). Based on the results of the stationary test, these fixes were considered highly spatially accurate and suitable for home range and movement calculations.

Habitat availability, dispersion and use

The habitat and substrate types represented in the enclosures ranged from sand dunes and shrublands with sandy soils (5–20% clay), to harder clay soils associated with swales, swamps and claypans ($>35\%$ clay; Table 2).

TABLE 1 Results of stationary GPS logger test conducted at Currawinya National Park (CNP) for six loggers situated at a known test location.

Fix schedule and number of nights	Number of scheduled fixes	Valid GPS fixes (proportion of valid fixes)	Proportion of GPS fixes with HDOP ≤ 4.0	Distance from stationary test location for all GPS fixes with HDOP ≤ 4.0
19:30–06:30 9 nights	642	628 (0.98)	Mean: 0.88 (\pm SE 0.07) Range: 0.52–0.99	Mean: 5.31 m (\pm SE 0.26 m) Interquartile range: 1.73–6.81 m Proportion of fixes <10 m from the test location: 0.87 Maximum distance: 58.46 m

TABLE 2 Habitat types and texture of dominant substrate at Currawinya National Park (CNP) and Arid Recovery (AR).

Site	Habitat type	Texture classification of dominant substrate ^a	Percentage of habitat available in enclosure	Percentage of pooled GPS fixes	Habitat and landscape measures		
					Clumpiness index (scale from -1 to 1)	Mean Euclidean nearest neighbour distance (m)	Contagion index (%)
CNP	Claypan	Clay loam to clay (>35% clay)	3.1%	0.6%	0.764	170	57.0
	Claypan with <i>Eucalyptus largiflorens</i>	Clay loam to clay (>35% clay) with fine sand to sandy loam (5–20% clay) at the edges	17.7%	10.4%	0.860	128	
	Mulga shrublands	Fine sand, sandy loam or silty loam (5–20% clay)	12.0%	13.3%	0.979	1149	
AR	Shrublands	Fine sand, sandy loam or silty loam (5–20% clay)	67.2%	75.7%	0.865	58	
	Claypan	Sandy clay to clay (>35% clay)	0.6%	0.2%	0.883	320	60.4
	Sand dune	Fine sand (5–10% clay)	31.7%	60.6%	0.880	96	
	Sandplain	Sandy loam to sandy clay loam (10–25% clay)	8.3%	6.0%	0.858	135	
	Swale	Sandy clay (35–40% clay)	58.5%	30.4%	0.875	82	
	Swamp	Sandy clay to clay (>35% clay)	1.0%	2.7%	0.947	698	

Note: The percentage of each habitat type, the percentage of pooled GPS fixes, habitat and landscape measures are outlined for each enclosure.

^aTexture classification derived from Dunwoody (2009) for CNP, and James and Eldridge (2007) and Kinhill-Stearns Roger Joint Venture (1982) for AR.

GPS fixes were recorded in all habitat types at both exclosures (Figure S1: Appendix S1), but clear preferences were detected. When all logged data were examined together, Chi-squared tests showed that the spatial distribution of nightly GPS fixes was not proportional to habitat availability inside the fenced exclosures (CNP $\chi^2=131.59$, d.f.=3, $p<0.0001$; AR $\chi^2=1001.40$, d.f.=4, $p<0.0001$; Table S2: Appendix S1). The statistical power of these Chi-squared tests to detect a medium effect size (Cohen's $d=0.5$) was equal to 1 at the 0.05 significance level.

At CNP, the most utilized habitat was shrubland (~76% of pooled fixes), which accounted for 67.2% of available area inside the fence. At AR, sand dune habitat was the most utilized (~61% of pooled fixes), which accounted for 31.7% of available area. Claypan habitat was the least utilized habitat at both exclosures, accounting for 0.6% (CNP) and 0.2% (AR) of the pooled GPS fixes, despite representing 3.1% (CNP) and 0.6% (AR) of available area. Swale habitat at AR covered 58.5% of the fenced exclosure; however, it was significantly underutilized with approximately 30% of the pooled GPS fixes recorded in the swales.

When Chi-squared tests were restricted to available habitat within each bilby's home range, the results showed there was considerable variation in habitat preferences amongst individuals (Table S2: Appendix S1). The statistical power of these individual Chi-squared tests to detect a medium effect size (Cohen's $d=0.5$) was 0.9 at the 0.05 significance level. Only two bilbies at CNP (CF5 Shell and CM1 Cooper) and one bilby at AR (AF8 Bonnie) had nightly GPS fixes proportional to the habitat available within their 95% AKDE home ranges. The majority of the nocturnal GPS fixes at AR were in sand dune habitat, accounting for more than 50% of fixes for all except one of the bilbies. At CNP, the majority of GPS fixes were in shrublands habitat, with eight of the 11 bilbies having 70% or more of their nightly fixes in this habitat type. Therefore, the preferred habitat types were sand dunes at AR and shrublands at CNP. The lowest proportion of GPS fixes was recorded in the claypan habitat at both sites, accounting for between 0 and 3% of fixes for each bilby.

The geographical spread of habitat types in both exclosures showed a trend towards habitats being more clumped than dispersed, with the clumpiness index for all habitat types being >0.7 (Table 2). The preferred habitat type at AR had a higher clumpiness index (sand dunes, 0.883) than the preferred habitat type at CNP (shrublands, 0.865), indicating that the preferred habitat at CNP is marginally less clumped than preferred habitat at AR (Table 2). The percentage area of the preferred shrubland habitat at CNP (67.2%) was more than twice the percentage area of the preferred sand dune habitat at AR (31.7%), so although the clumpiness indices are relatively similar there was more preferred habitat available at CNP. The mean Euclidean nearest neighbour distance (i.e. mean straight-line distance from edge-to-edge of patches of the same habitat type) for sand dunes at AR was 96m, which was more than 1.5 times greater than the 58m for shrublands at CNP (Table 2). This shows that there is a greater mean distance between patches of preferred habitat at AR compared to CNP. At the landscape level, the contagion index at CNP (57.0%) was lower than at AR (60.4%), indicating that the different habitat types at CNP have a higher proportion of intermixing (i.e. more heterogeneous) and are more evenly distributed throughout the exclosure than at AR (Table 2).

We radiotracked bilbies to diurnal burrow locations at least every 3 days for between 9 and 32 days. Sixty burrows were recorded being used by bilbies at CNP and 65 burrows at AR (Table S3: Appendix S1). There was no significant difference in the mean number of burrows between both sexes and sites ($\chi^2=0.32$, d.f.=3, $p=0.57$). At CNP, 85% (51 burrows) of the

recorded burrows were in shrubland habitat and a further 13% (8 burrows) in mulga shrubland habitat. A single burrow was recorded under the *E. largiflorens* canopy fringing a claypan at CNP, which was used by one male on several occasions. At AR, 97% of the recorded burrows were in the sand dunes. Sand is the dominant soil substrate in both the shrublands habitat at CNP and the dunes at AR. Single burrows were recorded in both the swale and sandplain habitat at AR, both of which were only occupied by male bilbies on a single occasion. No bilby burrows were recorded in claypans at either site.

Home range size

Using the GPS data collected during this study, we were able to calculate AKDE home ranges for 11 bilbies from CNP (5F:6M) and 10 bilbies from AR (4F:6M; Figure 4, Table 3). There were no significant differences in the mean 95% AKDE home ranges between AR bilbies (females 29.02 ha \pm 7.75, males 245.58 ha SE \pm 154.97) and CNP bilbies (females 20.80 ha SE \pm 2.94, males 216.74 ha SE \pm 54.19; females $W=13$, $p=0.56$; males $W=11$, $p=0.31$; Figure 5a). The 50% AKDE home ranges were not significantly different at AR (females 7.53 ha SE \pm 2.41, males 64.57 ha SE \pm 43.70) compared to CNP (females 5.73 ha SE \pm 1.20, males 55.29 ha SE \pm 17.82; females $W=12.5$, $p=0.54$; males $W=12$, $p=0.39$).

Male 95% and 50% AKDE home ranges were significantly larger than female home ranges at both exclosures (CNP 95% $W=0$, $p=0.01$; CNP 50% $W=2$, $p=0.02$; AR 95% $W=24$, $p=0.01$; AR 50% $W=24$, $p=0.01$). The mean male 95% AKDE home range at CNP was more than 10 times larger than the mean female home range at CNP, and the mean male home range at AR was more than nine times larger than the mean female home ranges at AR (Table 3).

The statistical power of the Wilcoxon rank sum tests to detect medium-sized differences (Cohen's $d=0.5$) in home range size between groups was low for all comparisons (i.e. power <0.2). This is due to the small sample sizes in each group (4–6 bilbies per group).

Males at both sites exhibited large home range size variation, but the AR male home ranges (\pm SD 379.60 ha) were significantly more variable than the CNP males (\pm SD 132.73 ha; $F_{5,5}=0.12$, $p=0.04$). The largest home range recorded was 1019.51 ha (AKDE 95%) for an AR male (AM7 Zeb), at more than 2.5 times the size of the second largest male home range (CNP, CM4 Moc) and more than eight times the size of all other AR male home ranges (Table 3). The fixes for this male were clustered in 4–5 disparate areas inside the fenced exclosure, whereas other AR males generally had only 1–2 clusters of fixes within their home range. The smallest male home range recorded was for a sub-adult male bilby at CNP, that also had the lowest body mass (875 g) of the males tracked at CNP (mean CNP male body mass 1750.8 g, SE \pm 244.0 g). Variance in female home ranges did not differ significantly between the two sites (AR females \pm SD 15.49 ha; CNP females \pm SD 6.25 ha; $F_{4,3}=0.16$, $p=0.11$).

Female home range sizes were significantly less variable than male home ranges, with male home range standard deviation (\pm SD 271.54 ha) more than 24 times larger than for females (\pm SD 11.37 ha; $F_{8,11}=0.002$, $p<0.001$). An AR female had the smallest home range at 13.99 ha, with only one other bilby (CNP female, CF1 Balonne) with a home range less than 15 ha (Table 3). The largest home range for a female was at AR with a range of 50.11 ha. This female's home range was inflated by the inclusion of a large open claypan despite none of her GPS fixes located in the claypan itself.

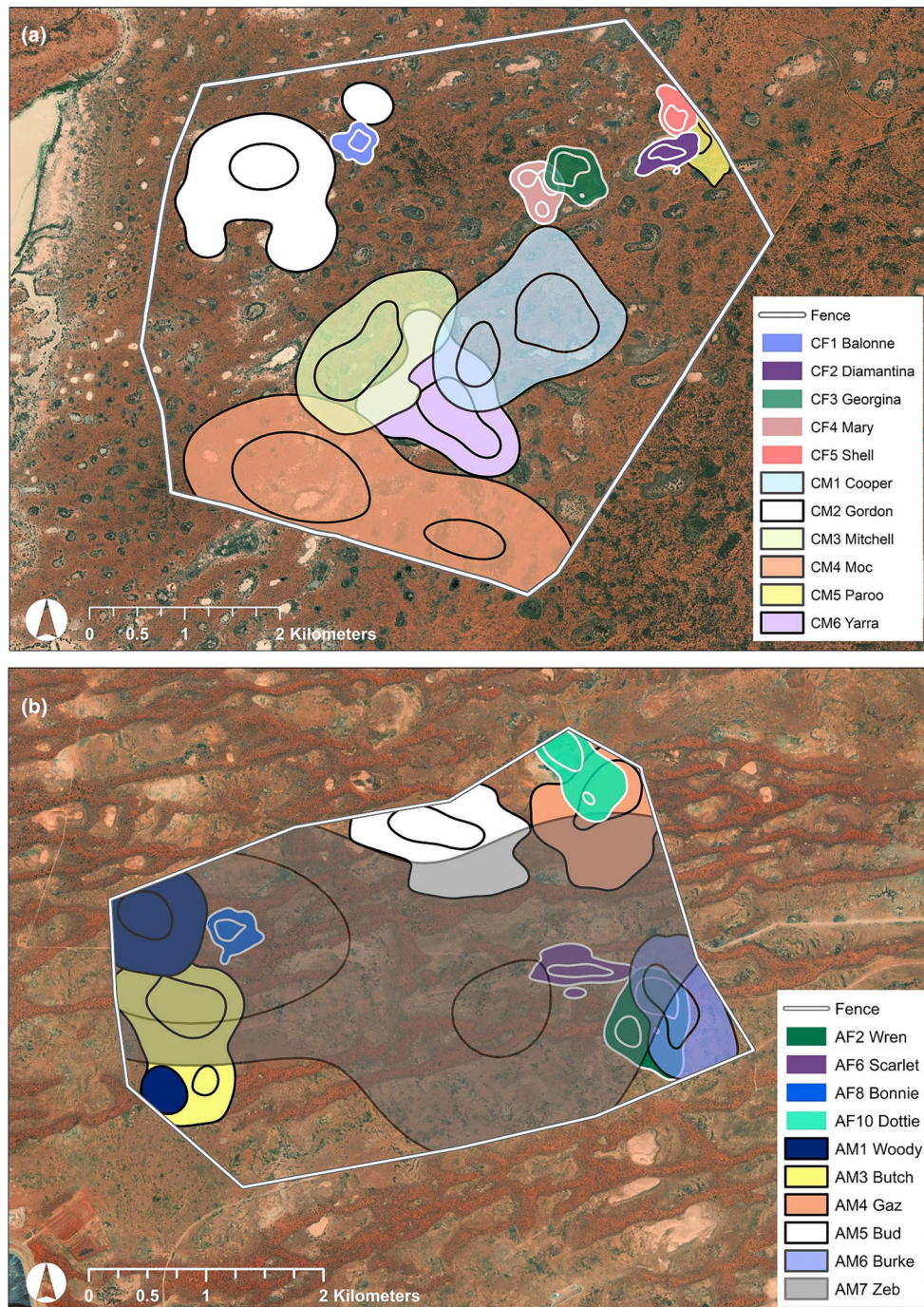


FIGURE 4 Home ranges (50% and 95% autocorrelated kernel density estimate isopleths) of the bilbies at (a) Currawinya National Park and (b) Arid Recovery. Male home range polygons are outlined in black, and female home range polygons are outlined in white.

Nightly ranges

The mean nightly MCP ranges for males were significantly larger than females at both CNP and AR (CNP $t = -3.92$, d.f. = 5.26, $p = 0.01$; AR $t = -3.95$, d.f. = 7.40, $p = 0.005$). The mean nightly MCP range for females at AR (7.35 ha) was not significantly different to the mean for females at CNP (5.26 ha; $t = -0.79$, d.f. = 3.56, $p = 0.48$; Table 4, Figure 5b). There was no significant difference between the mean male nightly MCP range at AR

TABLE 3 Home range estimates in hectares for bilbies (*Macrotis lagotis*) at Currawinya National Park (CNP) and Arid Recovery (AR).

Site	Sex	ID	Home range area		
			AKDE 50% (ha)	AKDE 95% (ha)	MCP 95% (ha)
CNP	Female	CF1 Balonne	3.17	14.38	11.49
		CF2 Diamantina	3.97	18.32	22.03
		CF3 Georgina	9.24	29.89	20.58
		CF4 Mary	7.91	25.36	19.75
		CF5 Shell	4.36	16.04	12.63
		Mean (\pm SE)	5.73 (\pm 1.20)	20.80 (\pm 2.94)	17.30 (\pm 2.18)
	Male	CM1 Cooper	77.26	246.77	172.99
		CM2 Gordon	27.21	224.21	152.09
		CM3 Mitchell	51.33	194.39	161.01
		CM4 Moc	130.22	438.38	373.02
CM5 Paroo		6.71	29.53	21.27	
	Mean (\pm SE)	55.29 (\pm 17.82)	216.74 (\pm 54.19)	173.13 (\pm 46.12)	
AR	Female	AF2 Wren	13.98	50.11	34.35
		AF6 Scarlet	4.66	22.05	18.20
		AF8 Bonnie	3.17	13.99	12.73
		AF10 Dottie	8.32	29.91	29.93
		Mean (\pm SE)	7.53 (\pm 2.41)	29.02 (\pm 7.75)	23.80 (\pm 5.02)
	Male	AM1 Woody	14.82	69.43	80.99
		AM3 Butch	29.54	122.68	122.64
		AM4 Gaz	22.41	90.24	84.06
		AM5 Bud	19.73	95.29	91.13
		AM6 Burke	18.06	76.31	59.07
AM7 Zeb		282.84	1019.51	583.47	
	Mean (\pm SE)	64.57 (\pm 43.70)	245.58 (\pm 154.97)	170.23 (\pm 83.07)	

(28.20 ha) and CNP (24.18 ha; $t = -0.56$, d.f. = 9.98, $p = 0.59$). The statistical power of these tests to detect medium-sized differences (Cohen's $d = 0.5$) in nightly range size between the groups was low for all comparisons (i.e. power < 0.2).

Nightly movements

Mean nightly distance travelled

Males travelled significantly further each night than females at both CNP (males 2083.59 m; females 1290.52 m) and AR (males 2632.82 m; females 1317.66 m; CNP $t = -3.00$, d.f. = 6.68, $p = 0.02$; AR $t = -6.06$, d.f. = 5.93, $p = 0.001$). The mean nightly distance travelled by males at AR was more than 500 m further than the mean for CNP males, however the means were not significantly different ($t = -2.00$, d.f. = 7.51, $p = 0.08$). All males at AR moved more than 2 km per night on average, whereas at CNP two of the males had nightly means of less than 2 km per night. The mean nightly distance travelled by females at the two exclosures were not significantly different ($t = -0.13$, d.f. = 4.95, $p = 0.90$).

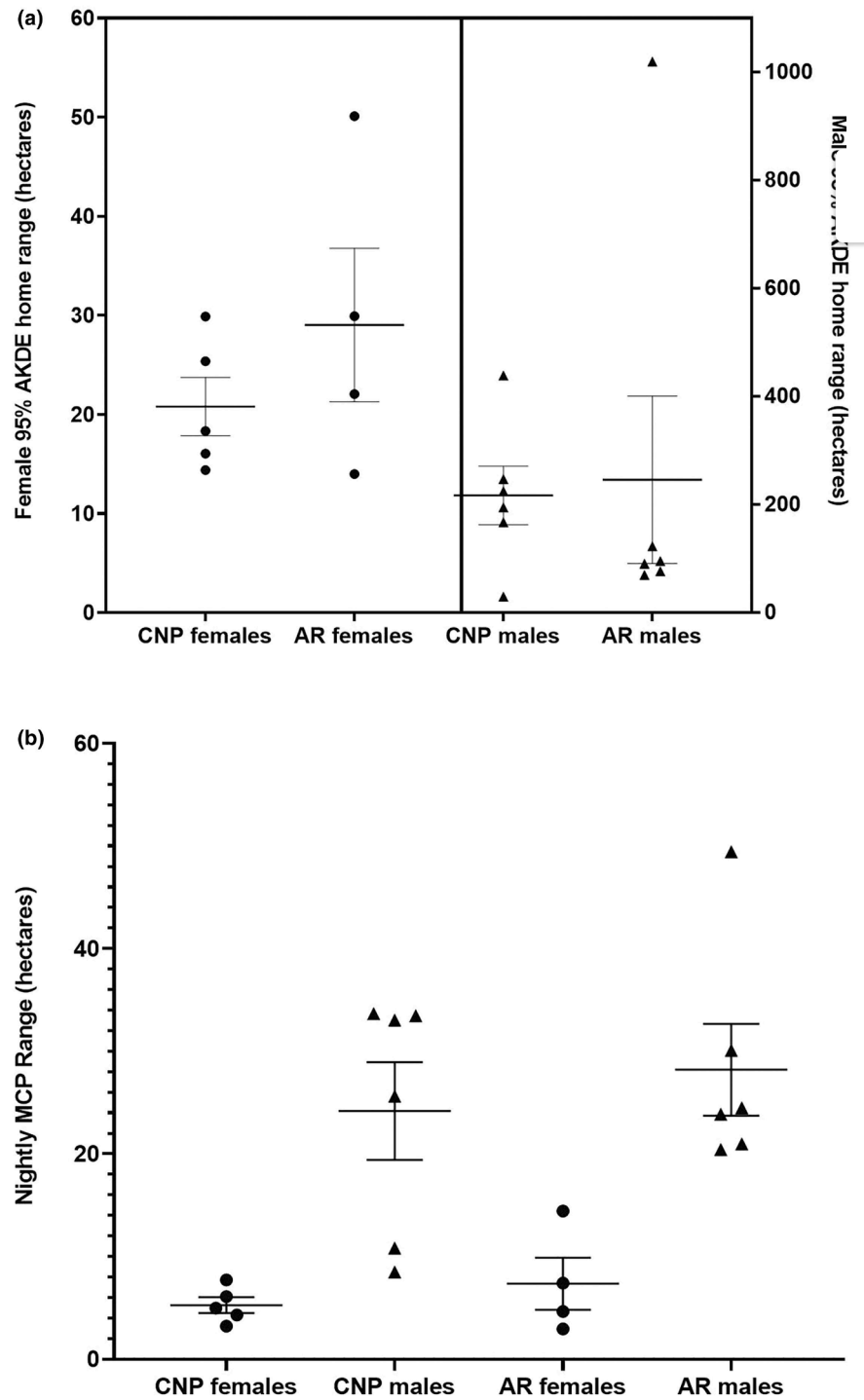


FIGURE 5 (a) Mean 95% autocorrelated kernel density estimate (AKDE) home ranges (\pm SE) for male (right panel) and female (left panel) bilbies at Currawinya National Park (CNP) and Arid Recovery (AR) and (b) mean nightly minimum convex polygon (MCP) range size (\pm SE) for male and female bilbies at CNP and AR.

Maximum nightly distance

Males at AR had significantly larger maximum nightly distances (mean 5192.93m) compared to CNP males (mean 3563.90m; $t = -2.97$, d.f. = 9.12, $p = 0.02$). All the maximum nightly movements recorded for CNP males were less than 5km, whereas at AR four of the six males had maximum nightly movements exceeding 5km (Table 4). There were no significant

TABLE 4 Number of nights tracked, mean number of GPS fixes per night, mean nightly distance travelled, maximum nightly distance travelled for bilbies (*Macrotis lagotis*) tracked at Currawinya National Park (CNP) and Arid Recovery (AR).

Site	Sex	ID	Number of nights	Mean steps per night	Mean nightly distance travelled (m) (±SE)	Minimum nightly distance (m)	Maximum nightly distance (m)
CNP	Female	CF1 Balonne	22	9.32	933.87 (±46.55)	593.78	1429.30
		CF2 Diamantina	24	9.00	1340.16 (±65.38)	622.89	1809.19
		CF3 Georgina	18	8.72	1487.01 (±84.91)	876.87	2047.58
		CF4 Mary	19	9.37	1481.25 (±59.42)	1104.02	2096.37
		CF5 Shell	19	9.11	1210.30 (±95.49)	676.57	2046.22
		Mean (±SE)	20.4	9.10	1290.52 (±102.73)	774.83 (±95.99)	1885.73 (±124.60)
AR	Male	CM1 Cooper	22	9.50	2514.85 (±167.27)	1413.45	4307.24
		CM2 Gordon	22	7.91	1060.41 (±92.14)	291.62	2183.01
		CM3 Mitchell	21	9.19	2479.21 (±129.27)	1476.94	3706.40
		CM4 Moc	23	8.83	2530.83 (±230.56)	165.19	4182.55
		CM5 Paroo	18	9.50	1679.10 (±145.01)	756.25	3153.78
		CM6 Yarra	22	9.73	2237.12 (±158.21)	836.67	3850.40
		Mean (±SE)	20.8	9.09	2083.59 (±243.35)	823.35 (±233.31)	3563.90 (±322.11)

(Continues)

TABLE 4 (Continued)

Site	Sex	ID	Number of nights	Mean steps per night	Mean nightly distance travelled (m) (\pm SE)	Minimum nightly distance (m)	Maximum nightly distance (m)
AR	Female	F2 Wren	22	7.68	1792.35 (\pm 118.18)	765.22	3090.26
		F6 Scarlet	23	8.74	1317.39 (\pm 85.51)	383.17	2004.00
		F8 Bonnie	24	7.58	947.33 (\pm 63.79)	153.39	1534.39
		F10 Dottie	21	7.14	1213.55 (\pm 54.48)	666.43	1581.15
	Mean (\pm SE)		22.5	7.79	1317.66 (\pm 176.38)	492.05 (\pm 138.92)	2052.45 (\pm 361.70)
	Male	M1 Woody	22	8.77	2130.75 (\pm 306.58)	951.65	6634.22
		M3 Butch	31	8.84	2532.67 (\pm 190.27)	274.90	5096.92
		M4 Gaz	21	8.95	2873.69 (\pm 139.45)	1769.33	3963.35
		M5 Bud	18	9.61	2627.73 (\pm 203.13)	1397.16	4412.06
		M6 Burke	29	8.86	2603.17 (\pm 162.96)	1195.80	5141.98
		M7 Zeb	31	8.77	3028.90 (\pm 249.35)	633.72	6179.06
	Mean (\pm SE)		25.33	8.97	2632.82 (\pm 126.22)	1037.09 (\pm 219.24)	5192.93 (\pm 415.17)

differences in the maximum nightly distances travelled by females at AR (mean 2052.45 m) and CNP (mean 1885.73 m; $t = -0.44$, d.f. = 3.72, $p = 0.69$). The maximum nightly distances travelled for females at the two sites ranged between approximately 1.5 and 3 km. The statistical power of the T-tests to detect medium-sized differences (Cohen's $d = 0.5$) for either mean or maximum nightly distances between groups was low for all comparisons (i.e. power < 0.2).

DISCUSSION

In this study, we investigated the links between bilby movement and 1. landscape productivity (using rainfall as an indicator); and 2. resource dispersion (using habitat distribution as an indicator), at two fenced predator-proof exclosures. Fenced predator-proof exclosures have been used as a conservation tool for bilbies since the 2000s, but there is limited published literature pertaining to bilby behavioural ecology at these sites (Bradley et al., 2015; DCCEEW, 2023; Palmer et al., 2020). Monitoring of bilby space use in exclosures is important for identifying key resources, habitats, thresholds for overabundance, resource limitation and potential ecosystem impacts (Finlayson & Moseby, 2004; Moseby et al., 2018).

Habitat availability, dispersion and use

A key aim of this study was to determine if bilbies preferentially utilized specific habitats within the two exclosures. Although bilbies were constrained by fences, both exclosures were large ($> 10 \text{ km}^2$) and contained all of the main habitat types that occurred within the adjacent landscape. We hypothesised that bilbies would prefer habitats with sandy substrates ($< 20\%$ clay content) as they are more suitable for digging burrows and foraging pits compared to harder, clay-dominated substrates, as has been found in previous studies (Mayhew, 2006; Moseby & O'Donnell, 2003). In support of our hypothesis, we found that $\sim 80\%$ of the bilbies we tracked preferentially utilized habitats with sandy substrates in their home ranges (i.e. shrublands at CNP and sand dunes at AR). Studies of wild bilby populations have also shown that bilbies are predominantly associated with softer, sandier substrates in areas they occupy (Burrows et al., 2012; Lohr et al., 2021).

Nearly, all the burrows used by bilbies during this study were in habitats with sandy substrate (i.e. sand dunes, shrublands and mulga shrublands), and there were no significant differences in the mean of burrows used by males or females, or between the sites. Bilbies have a limited ability to withstand heat stress, and therefore shelter in deep burrows ($\sim 2\text{--}3 \text{ m}$ below ground) which provide a stable thermal environment during the day (Gibson & Hume, 2000). However, digging such deep burrows is energetically expensive and bilbies have a far higher field metabolic rate (FMR; i.e. total energy expenditure) than expected for an arid-dwelling mammal (Gibson & Hume, 2004; Johnson & Johnson, 1983; Smyth & Philpott, 1968). As such, bilbies may preferentially select to burrow in soft, sandy substrate to reduce energy expenditure, particularly as they maintain several burrows within their home range (Berris et al., 2021; Moseby & O'Donnell, 2003). Similarly, foraging in sandy substrates would reduce the energetic costs compared to foraging in harder clay soil. Predation risk may also be lowered when foraging in sandy habitats due to the higher density of burrows that bilbies can escape to when in the presence of a predator, as has been observed in several species of arid-dwelling gerbils (Kotler et al., 2001; Ziv et al., 1995). For example, field studies of three gerbil species (*Gerbillus*



allenbyi, *G. dasyurus* and *G. pyramidum*) in the Negev Desert, Israel, revealed multiple benefits to foraging in sand dunes compared to the hard loess plateaus: (1) food resources can be recovered more efficiently as it is easier to dig in soft sand; (2) sand on the dunes is shifted by wind each day exposing new food resource patches; and (3) predation risk is lowered due to the high density of burrows on the dunes, to which gerbils can retreat (Ziv et al., 1995). We suggest that bilbies preferentially utilize habitats with sandy substrates for these same reasons. Therefore, we recommend that when assessing potential sites for future bilby reintroductions, practitioners quantify the area of suitable burrowing and foraging habitat, as this will likely influence the availability of food resources and predation risk.

At CNP, the preferred shrubland habitat (67% of enclosure area) was more evenly dispersed throughout the enclosure, with a lower mean distance between patches, compared to the sand dunes at AR (32% of enclosure area). Due to the more even dispersion and increased availability of preferred habitat at CNP, GPS fixes for bilbies tended to be more evenly distributed within their home ranges, particularly the female bilbies. Conversely, most bilbies at AR had clusters of GPS fixes on multiple sand dunes with comparatively fewer fixes on the interconnecting swales, resulting in the uneven use of habitats within their home ranges. Studies of a range of mammal species have shown that individuals typically have larger home ranges in areas of low habitat/resource heterogeneity (Beier & McCullough, 1990; Di Stefano et al., 2011; Kie et al., 2002; Martin & Martin, 2007). Thus, based on the results of our study and these previous studies, it is reasonable to expect larger bilby home ranges at AR compared to CNP, due to the more uneven distribution of preferred burrowing and foraging habitat at AR.

Home range size

The second hypothesis we tested was that bilby home range size would be larger in the more arid environment at AR, due to lower landscape productivity and the patchier distribution of resources. We used rainfall as an indicator of landscape productivity, and we measured the patchiness of preferred habitats as an indicator of resource dispersion. During the study, population density at both enclosures was comparable (11.26 bilbies per km² at CNP and 9.26 bilbies per km² at AR) and rainfall in the preceding 12 months was 'average' at each site (between 30th and 80th percentiles). Conditions were therefore appropriate for a comparison of home range and movements between the arid and semi-arid enclosures.

We did not record larger home ranges for males or females at AR compared to CNP. This may have been influenced by the favourable environmental conditions during the study period, and the low statistical power to detect moderate-sized differences due to small sample sizes. In the year prior to the study, rainfall conditions were average for both sites, and were preceded by a drought. The ecosystems at both sites were likely responding to the increased rainfall with a 'boom' of resources (Letnic & Dickman, 2006). Bilbies are omnivorous and utilize an opportunistic feeding strategy to exploit temporarily abundant food resources in otherwise unpredictable climates (Bice & Moseby, 2008; Gibson & Hume, 2004; Southgate & Carthew, 2006). As such, they would likely have a higher probability of encountering food resources in the landscape compared to a dietary specialist (Duncan et al., 2015; Gompper & Gittleman, 1991). We suggest that this dietary flexibility enabled the bilbies in our study to obtain adequate food resources from relatively small and stable home ranges at both study sites, due to the favourable environmental conditions in the 12

months preceding the study. However, extended periods of low rainfall may result in the exhaustion of some food resources within their ranges and the need to travel to other habitat patches to meet their energetic requirements (Bengsen et al., 2016; Sandell, 1989).

Many species in arid regions have 'drifting' home ranges because rainfall and food availability are unpredictable (Daly & Daly, 1974; Morton, 1978). Drifting ranges are often characterized by temporarily localized movements and shifts away from these ranges in response to changes in food availability (Morton, 1978). Drifting home ranges have been observed in several Dasyuridae species in Australia, sand rats (*Psammomys obesus*) in North Africa and Patagonian maras (*Dolichotis patagonum*) in the deserts of Argentina (Daly & Daly, 1974; Morton, 1978; Taber & Macdonald, 1992). Bilbies may also adopt drifting home ranges in response to the unpredictable environmental conditions across much of their current range. This would explain the movement patterns we observed during our study of relatively small, stable and comparable home range sizes at both study sites, under reasonably favourable environmental conditions. However, longer term studies of bilby home range size are required to confirm this hypothesis. Further, we recommend that our study methodology is replicated at other arid and semi-arid sites following prolonged periods of low rainfall when food resources diminish, to determine if bilbies shift or expand their home ranges. These studies will provide further insight into the movements of bilbies and their home ranges in response to landscape productivity in different climatic zones. Undertaking similar studies on wild bilby populations would be beneficial, as we acknowledge that bilby movements at our study sites were constrained to the area inside the enclosures and may not be directly translatable to wild/unfenced populations.

Male home ranges were significantly larger than females at both sites, which is consistent with previous bilby movement studies and the pattern of space use for males in an overlapping promiscuous mating system (McRae, 2004; Miller et al., 2010; Moseby & O'Donnell, 2003; Southgate & Possingham, 1995). Males at both sites exhibited large home range size variation, with larger variability observed in the AR male home ranges (\pm SD 379.60 ha) than the CNP males (\pm SD 132.73 ha), though this was largely influenced by a single male at AR (AM7, Zeb). However, it is not uncommon for males in a polygynous/promiscuous mating system to have large and/or variable ranges (Bengsen et al., 2012, 2016; Moseby, Stott, & Crisp, 2009).

For females in this study, access to suitable burrowing substrate (i.e. sandy soils) clearly determined the location of their home ranges. This was particularly evident for females at AR, where female home range cores and GPS fixes were strongly associated with a defined area of the sand dune habitat. Based on our results, the dispersion of habitats suitable for burrowing will directly influence the dispersion of females within the enclosures. Whereas male home range size is more likely to be dictated by the density and location of females and indirectly by habitat dispersion (due to its effect on female home range location; Clutton-Brock & Harvey, 1978; Martin & Martin, 2007; Miller et al., 2010). This pattern of spatial organization has also been observed in other Australian mammals, such as the echidna (*Tachyglossus aculeatus*) and the mountain brushtail possum (*Trichosurus cunninghami*; Martin & Martin, 2007; Sprent & Nicol, 2012).

Moseby and O'Donnell (2003) is currently the only published study reporting stable bilby home range areas (i.e. home range reached an asymptote). Other studies have reported short-term area use or burrow ranges (Berris et al., 2021; McRae, 2004), both of which are likely to underestimate home range size. Moseby and O'Donnell (2003) collected home range data for bilbies at AR during the initial reintroduction to the enclosure in 2000, where mean female home range size was 18 ha and mean male home

range size was 316 ha. The mean 95% MCP home range size for females in this study (17.3 ha at CNP, 23.8 ha at AR) was comparable to the home ranges reported by Moseby and O'Donnell (2003). Mean male home range size recorded at AR in 2000 was ~1.8 times larger than that recorded during this study (173.1 ha at CNP, 170.2 ha at AR). The larger male home range recorded at AR in 2000 may have been due to a lower density of bilbies in the enclosure as this was during the initial reintroduction phase (~2 bilbies per km² in 2000 [K. Moseby, unpublished data], 9.26 bilbies per km² during this study). At lower population densities and where females are highly dispersed, male bilbies likely travel further and cover larger areas in search of mating opportunities, thus resulting in larger home ranges (Clutton-Brock, 1989). This pattern of space use has also been observed in grey-tailed voles (*Microtus canicaudus*), where male voles had larger home ranges at lower population densities (Bond & Wolff, 1999).

Nightly ranges and movements

The third hypothesis we tested was that bilbies at the arid site would travel further each night, compared to the semi-arid site, to access preferred habitats that were more patchily distributed. As we expected, the distribution of preferred habitat at AR was more clumped with larger distances between patches compared to CNP. Further, there was almost twice the proportion of preferred habitat at CNP compared to AR. There were no significant differences in the male or female nightly ranges of bilbies at AR and CNP. This may have been due to an abundance of resources at both sites after drought-breaking rain and/or the small sample size.

GPS loggers

This study is one of the first to report on the use of GPS loggers on bilbies, which have traditionally been studied with VHF radio transmitters. The loggers enabled the collection of detailed, spatially accurate data sets that were used to examine habitat preferences and space use at different scales. These loggers significantly reduced the cost and effort required to track individuals compared to radiotracking, with only a small proportion of the tail-mounted attachments (16%) detaching before sufficient fixes were collected (Matthews et al., 2013; Recio, Mathieu, Maloney, & Seddon, 2011; Tomkiewicz et al., 2010). We observed only minor rubbing of the skin in a small number of attachments, but no major injuries, as has been reported for other types of attachments in peramelids (Coetsee et al., 2016). We recommend the use of similar GPS loggers in future studies of bilbies as they provide detailed data and improve efficiency of data collection.

CONCLUSIONS

Our data supported our hypothesis that bilbies would preferentially utilize sandy substrates within the enclosures for foraging and burrowing. Seventeen of the 21 bilbies we tracked at the two sites preferentially utilized sand dunes, shrublands or mulga shrublands – all habitats with sandy substrates. Bilbies at both sites burrowed almost exclusively in sandy substrate. Future reintroductions of the bilby should consider the availability and dispersion of habitats with sandy substrates at proposed release sites.

We did not identify significant differences in home range size or nightly ranges between the sites for either sex, despite the patchier distribution

of preferred habitats at the arid site. However, this study makes a valuable contribution to the limited published information available on the home range size and movements of bilbies in fenced exclosures. Our results indicate that female bilby home range and movements are more likely to be directly influenced by the dispersion and availability of resources (e.g. habitat suitable for burrowing) compared to males. We recommend that similar studies are replicated at other arid (e.g. Sturt National Park) and semi-arid exclosures (e.g. Mallee Cliffs, Scotia and Mount Gibson sanctuaries), where bilbies have been reintroduced and populations have established. Furthermore, undertaking studies of a similar nature during periods of low rainfall, and when landscape productivity is low, will provide further insight on how male and female bilbies utilize space when resources are limited. We view this information as critical to the effective, long-term management of bilby populations at both sites, and informative for other exclosures and offshore islands where bilbies have been reintroduced.

AUTHOR CONTRIBUTIONS

Cassandra M. Arkininstall: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); project administration (supporting); resources (lead); software (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Sean I. FitzGibbon:** Conceptualization (equal); funding acquisition (lead); methodology (supporting); project administration (lead); resources (supporting); supervision (lead); writing – original draft (supporting); writing – review and editing (equal). **Brianna Coulter:** Conceptualization (equal); investigation (supporting); writing – original draft (supporting); writing – review and editing (equal). **Katherine E. Moseby:** Conceptualization (equal); methodology (supporting); resources (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (equal). **Peter J. Murray:** Conceptualization (equal); methodology (supporting); resources (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support this study are available from the corresponding author on reasonable request.

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