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Seasonal home range and habitat use of a critically endangered marsupial (*Bettongia penicillata ogilbyi*) inside and outside a predator-proof sanctuary

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Abstract. An understanding of the factors that influence the distribution of the woylie (*Bettongia penicillata ogilbyi*) at local and regional scales has been identified as a key knowledge gap, because such knowledge may assist in the recovery of this endangered species. We aimed to investigate the seasonal home-range size and habitat use of woylies to update current knowledge of the species in the context of a substantial decline. Specifically, we examined the home range and habitat use of woylies reintroduced into a sanctuary free from invasive predators and compared these data to those from an external reference site. Eight woylies inside the sanctuary and seven outside were radio-tracked in autumn 2011. The average home-range size was 65.4 (±8.2, s.e.) ha. There was little evidence to suggest any difference in home-range size between woylies inside and outside the sanctuary. Woylies were more likely to be found in the slope and low-lying valley habitats, which have greater water-holding capacity and sandier soils. These relatively large seasonal home ranges, compared with previously published estimates for the species, may be accounted for by low population density, lower seasonal food availability and clustered food distribution. Monitoring the home-range size of woylies within the sanctuary may assist in identifying the carrying capacity of the sanctuary, which has implications for how this population is managed.

Additional keywords: habitat associations, harmonic mean, kernel density, Minimum Convex Polygon.

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Introduction

An understanding of the space use and home range (HR) size of a species is important for the management of populations, contributes to investigations into population declines (Donázar *et al.* 1993; Wittmer *et al.* 2007), and can provide guidance for translocations (Ruth *et al.* 1998; Butler *et al.* 2005). An estimate of the HR size of individuals may also be useful in determining a population's carrying capacity in restricted environments such as fenced exclosures or islands (Ryan and Jamieson 1998). The movement of individuals across the landscape and the degree of overlap of territories has implications in the transmission of disease within a population (White *et al*. 1995; Kauhala and Holmala 2006). For example, populations in which there is a large degree of overlap of territories and therefore potential interaction between individuals could have a greater rate of disease transmission (White *et al*. 1995; Kauhala and Holmala 2006). Space use and utilisation of habitats can provide information about habitat preferences, which can help identify suitable translocation sites for a species.

Investigations into the role of disease and translocations to create new, or supplement existing, populations have been identified as objectives in the recovery of the woylie (*Bettongia penicillata ogilbyi*) (Yeatman and Groom 2012), a critically endangered marsupial that was once widespread across most parts of Australia (Yeatman and Groom 2012). The species has recently suffered a sudden and dramatic decline in abundance and is currently the focus of a large recovery effort (Wayne *et al*. 2013*a*, 2013*b*). Disease and predation by introduced foxes (*Vulpes vulpes*) and cats (*Felis catus*) have been implicated in the decline (Wayne *et al*. 2011, 2013*b*). Within the Upper Warren region, a centrally important area for the conservation of woylies, there has been a net loss of 95% in the six years following 2002 (Wayne *et al*. 2013*a*). An insurance population free of introduced predators was established in the Perup Sanctuary (423 ha) to conserve as much of the genetic diversity of the species as practically possible. Forty-one woylies were released into Perup Sanctuary in 2010 (Wayne *et al*. 2013*c*).

We used radio-telemetry to estimate seasonal HR size for woylies inside Perup Sanctuary and at a nearby external site. The data collected were used to identify differences in the space use and HR size of woylies between these areas to inform the management of the sanctuary and provide information for the conservation and recovery of the species.

Materials and methods

Perup Sanctuary study site

Perup Sanctuary is ~50 km east of Manjimup (34.2506°S, 116.1425°E) in the Upper Warren region of south-western Australia (Fig. 1). The sanctuary lies within Perup Nature Reserve in the southern jarrah forest Interim Biogeographic Regionalisation for Australia subregion and is managed by the Western Australian Department of Parks and Wildlife. The region has a Mediterranean-type climate with warm dry summers and cool wet winters. The area is characterised by open dry sclerophyll forest dominated by an overstorey of jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*).

The sanctuary is surrounded by a 2-m-high wire fence designed to be a barrier to foxes, cats and rabbits (*Oryctolagus cuniculus*). Construction was completed in September 2010 and was followed by an intensive program to completely remove foxes and cats. Western grey kangaroos (*Macropus fuliginosus*), brush wallabies (*Macropus irma*), all emu (*Dromaius novaehollandiae*), some brushtail possums (*Trichosurus vulpecula*) and all chuditch (*Dasyurus geoffroii*) were also removed as they were identified as potential problem species (competitors or predators) if left within the sanctuary. Forty-one woylies were sourced from the surrounding Upper Warren population and released into the sanctuary in December 2010 (Wayne *et al*. 2013*c*).

Keninup forest block study site

The Keninup forest block was used as the external (free-living) reference site. It is located ~17 km north of the sanctuary and has very similar habitat characteristics, making it an appropriate comparison site. Keninup comprises a contiguous portion (~6300 ha), and the northern extent, of Perup Nature Reserve that is bordered to the west, east and north by agricultural land. Prior to the decline, Perup Nature Reserve had high population densities of woylies (Wayne *et al*. 2013*a*), which suggests that the area has appropriate resources to support woylies. Foxes and cats are present at Keninup and preyed on several woylies that were radio-collared as part of this study (Wayne *et al*. 2013*a*).

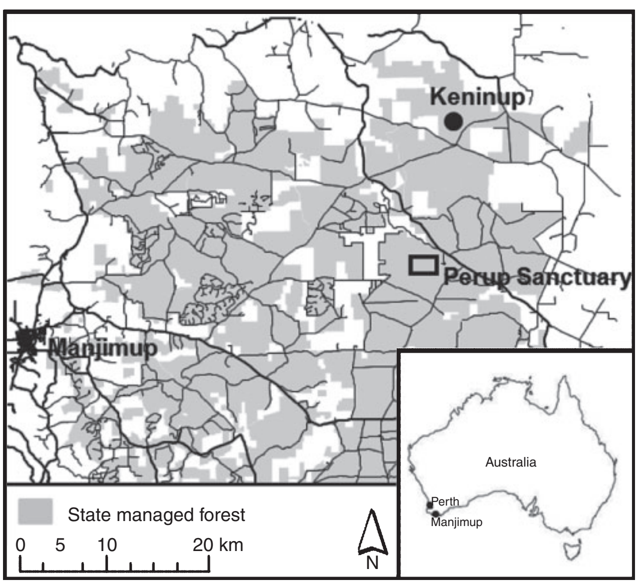

Fig. 1. Location of Perup Sanctuary and Keninup study sites in the Upper Warren region, south-western Australia.

Animal density

The density of woylies at Perup Sanctuary at the time of the study was ~0.1 ha^{-1}. Trapping and other monitoring methods immediately before the building and completion of the Perup Sanctuary indicated that no woylies were present before the translocation of 41 individuals in December 2010. The Keninup population was estimated at ~0.22 woylies ha^{-1} in 2011 based on trapping data (Wayne *et al*. 2013*a*).

Radio-tracking

All procedures were conducted following guidelines set out by the Western Australian Department of Parks and Wildlife Standard Operating Procedures 9.2 (Cage traps for live capture of terrestrial vertebrates) and 13.4 (Ground-based radio-tracking) and were approved by that department's Animal Ethics Committee. Woylies were captured in Sheffield cage traps (Sheffield Wire Products, Welshpool, WA) baited with oats, sardines and peanut butter. Only adult woylies without large pouch young were selected for collaring. Woylies were fitted with radio-transmitter collars (Sirtrack Ltd, Havelock North, NZ) weighing less than 5% of the animal's weight. Woylies at the sanctuary site had been trapped and translocated from surrounding transects in the Upper Warren region and released into the sanctuary after collaring in December 2010. Release locations were spread out across the sanctuary. Woylies at the Keninup site were trapped along transects (associated with forest tracks dissecting the area), fitted with collars and released at the point of capture in October 2010. Location fixes of individuals in the sanctuary were not collected until at least three months after release to allow animals to settle and establish a territory.

Woylies at both sites were radio-tracked at night using Yagi hand-held antennae (Titley Electronics, Ballina, NSW) during March and April 2011. Location fixes of individuals were taken using biangulation between 1900 and 0300 hours. For each location fix, a bearing of that location was taken from two positions within the study area simultaneously. The point at which these two bearings intersected was recorded as the location of the animal at that time. An estimate of the error associated with each location fix was calculated using a blind test where a dummy collar was placed in a known location and the biangulation procedure was conducted on the dummy collar. The distance between the known and estimated location was measured using ArcMap GIS (ESRI 2011). The dummy test was conducted at 23 different locations. We attempted to simulate as close as possible the actual conditions for fixing woylie locations by running the dummy test in the same bushland in which woylies were tracked, placing the collar at ground level amongst vegetation and taking bearings at a comparable distance (based on signal strength).

Fixes were taken on the woylies no less than 30 min apart and the number of fixes taken per individual per night ranged between 1–8. This was deemed an appropriate length of time to ensure fixes were independent as woylies are capable of rapid movement across the landscape (pers. obs.) and a closely related species (*Bettongia gaimardi*) has been recorded moving 500–600 m within 30-min intervals (Taylor 1993).

Home range estimation and analyses

Location fixes of individuals were calculated using Locate II software (Nams 2006). Fixes were then analysed using RANGES 8 ver. 2.5 (Kenward *et al*. 2008) and plotted using ArcMap GIS (ESRI 2011). Home ranges were calculated using kernel density (Worton 1995), harmonic mean (Dixon and Chapman 1980) and minimum convex polygon (MCP) (Mohr 1947) methods. We used 95% of fixes for the kernel density and harmonic mean methods and 100% of fixes for the MCP method. Boulanger and White (1990) identified the harmonic mean method as the best performing estimate compared with MCP, Koeppl ellipse, Jennrich and Turner ellipse, and the Fourier series methods. Following that study, Seaman and Powell (1996) compared the kernel density estimate to the harmonic mean and found that kernel density with a fixed smoothing multiplier was the least biased method but that kernel density estimates calculated from small sample sizes (<50 samples) would overestimate HR size. MCP estimates have been commonly used for previous estimates of woylie HR size, meaning that it may be difficult to compare the results of this study to past estimates without the inclusion of this method. With this information in mind, this study included kernel density, MCP and harmonic mean estimates to minimise the impact of small sample size and allow some comparison between previous studies. For the kernel density method, a ratio of least-squares cross-validation to a reference smoothing factor ($h_{\text{lscv}}/h_{\text{ref}}$) was used as the smoothing multiplier to avoid overestimation of range size (Wauters *et al*. 2007). Incremental area analysis was conducted for each HR to identify whether the estimated range size had stabilised. This was considered to be the case when additional location fixes did not increase the size of the range and the incremental plot reached an asymptote. All ranges reached an asymptote at an average of 66% (s.e. = 5) of the total number of fixes and the minimum number of fixes used for HR calculation was 27, with a mean of 34 (s.e. = 1.2).

Overlap of individual home ranges

The percentage of an animal's HR that included the HR of another collared animal was calculated to quantify the degree of potential interactions between woylies. This area was calculated using ArcMap software.

Habitat use

Satellite imagery and vegetation maps based on the classifications of Havel and Mattiske (2000) were used to identify the vegetation type associated with each location fix. Habitat use was analysed only at Perup to get an accurate measure of the total available habitats (i.e. the total area of each habitat type within the fenced area). A Chi-square test was used to compare the observed number of fixes within each habitat type to the expected number of fixes if the distribution across habitats was random. There are six vegetation types, as described by Havel and Mattiske (2000), within Perup Sanctuary: Carbarup, Bevan 2, Yerraminnup, Yerraminnup Flat, Catterick and Corbalup 2. The distribution of woylie locations within the sanctuary was not biased, based on trap location, as these animals were released into the sanctuary (with radio-collar attached) from an external site. The habitat preferences recorded represent the distribution of individuals several months after being introduced to a novel site.

Results

Home range estimation

Eight woylies in Perup Sanctuary (four female and four male) and seven woylies at Keninup (two female and five male) were radio-collared and tracked in March and April 2011 (Table 1). There was no evidence to support a difference in the HR size between sites using any of the three methods (Table 1). Because all three methods gave similar average estimates (kernel density = 65.4 ha, MCP = 79.1 ha, harmonic mean = 69.2 ha), all further results are presented using the kernel density value only. Pooling the data from both sites, there was no evidence to support a difference between the HR sizes of males and females (t = –0.79, d.f. = 13, P = 0.). The HR size of individuals ranged from 27.5 ha (PS2) to 141.0 ha (K5), with an average of 65.4 ha (s.e. = 8.2) (Table 1). The HR plots at Perup appear to be grouped in the south-west corner of the sanctuary (Fig. 2). The linear nature of the HR plots at Keninup (Fig. 3) are likely to be an artefact of the sampling procedure as fixes were taken from existing tracks within the site.

Error test

The mean error associated with the biangulation method for determining an animal's location was estimated to be 115 ± 21 m. A *t*-test comparing the known GPS coordinates with the estimated positions found no evidence to support a difference (t = 0.19, d.f. = 22, P = 0.84). The HR size calculated using the known locations was estimated to be 33.4 ha. This was 16.7% larger than the HR calculated using the estimated locations (27.7 ha).

Overlap of individuals

There was no evidence to suggest a difference in the percentage of overlap of home ranges between Perup and Keninup (t = 0.03, d.f. = 13, P = 0.97). The average overlap for both sites was 77.5% (s.e. = 5.26) (Table 1). The maximum overlap was 100%, calculated from a female woylie at Perup (PS2) and a male woylie at Keninup (K4). The minimum overlap was 35.2%, calculated from a male woylie at Keninup (K7). On average, females shared 87.5% (s.e. = 4.64) of their HR with another animal compared with 70.8% (s.e. = 7.62) for males, but this difference was not significant (t = 1.63, d.f. = 13, P = 0.12).

Habitat use

The distribution of location fixes of woylies was not random across each habitat type (χ^2 = 192.2, P < 0.001). Yerraminnup and Yerraminnup Flat habitats had a greater number of fixes than was expected on the basis of the availability of these habitats in the sanctuary (Fig. 4). In contrast, Carbarup, Bevan 2, Catterick and Corbalup 2 had a lower than expected number of fixes on the basis of their availability.

Table 1. Summary of home ranges of radio-tracked woylies at Perup (PS) and Keninup (KEN) sites
Individuals were tracked between March and April 2011. Home-range estimates (ha) were calculated using harmonic mean (HM95%), minimum convex polygon (MCP100%) and kernel density (KD95%) estimates. The percentage overlap was calculated from the kernel density estimate

Site	Animal	Sex	No. of fixes	Harmonic mean	MCP	Kernel density	% Overlap
PS	PS1	F	42	60.0	68.8	41.5	77.5
	PS2	F	41	48.2	70.9	27.5	59.6
	PS3	F	30	64.3	80.6	68.3	73.8
	PS4	F	34	45.8	59.9	42.6	100.0
	PS5	M	27	64.5	67.4	66.5	99.4
	PS6	M	42	118.3	131.8	114.9	75.1
	PS7	M	37	117.3	126.1	81.8	71.9
	PS8	M	34	24.4	38.3	29.9	88.3
	Mean ± s.e.		35.9 ± 1.2	67.8 ± 11.8	80.5 ± 11.4	59.1 ± 10.5	77.7 ± 6.2
KEN	K1	F	36	54.7	64.0	70.5	85.0
	K2	F	33	88.4	92.4	93.5	100.0
	K3	M	34	38.0	40.1	42.3	96.2
	K4	M	37	105.1	114.3	54.1	98.8
	K5	M	31	77.8	85.7	141.0	61.0
	K6	M	37	48.9	67.9	61.5	77.7
	K7	M	28	82.8	78.2	45.3	38.1
	Mean ± s.e.		33.7 ± 1.3	70.8 ± 9.1	77.5 ± 8.9	72.6 ± 13.1	77.3 ± 9.3
	Combined average		34 ± 1.2	69.2 ± 7.4	79.1 ± 7.1	65.4 ± 8.2	77.5 ± 5.3

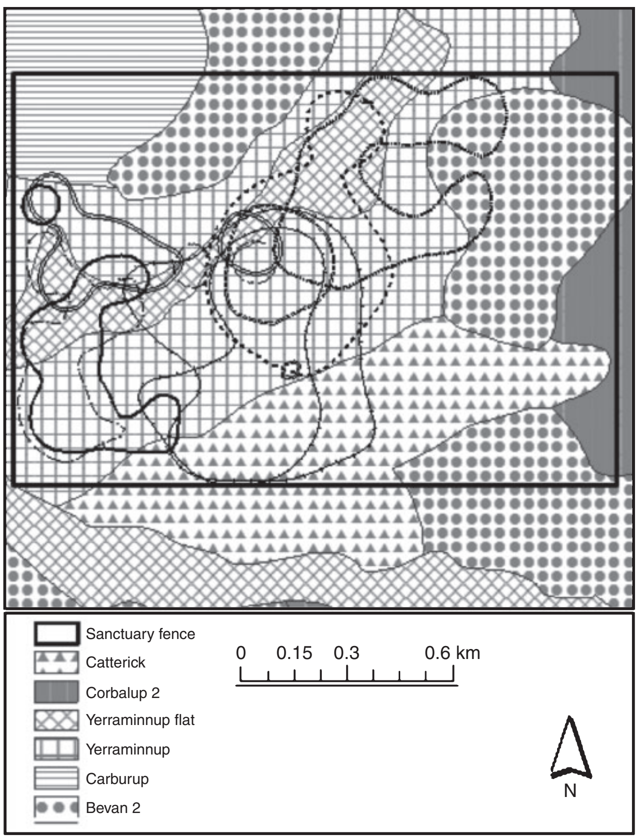

Fig. 2. Home-range plots of four female and four male woylies at Perup Sanctuary study site using kernel density estimates with associated vegetation types.

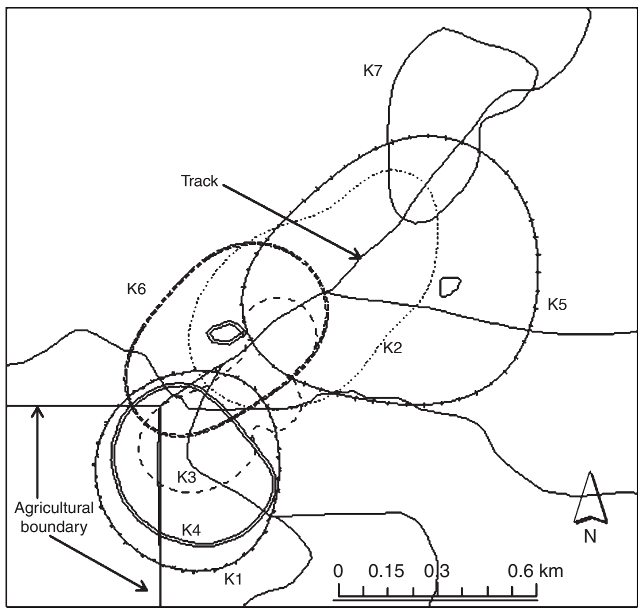

Fig. 3. Home-range plots of two female and five male woylies at Keninup study site using kernel density estimates. The agricultural boundary is a 1-m-high wire fence that is permeable to woylies.

Discussion

The average seasonal HR size for woylies in the Upper Warren was 65.4 ha. This is larger than other previously recorded estimates for the species (29 ha: Sampson 1971; 8.1 ha: Christensen 1977) but comparisons between studies are difficult as there is variability in the method of calculating HR size,

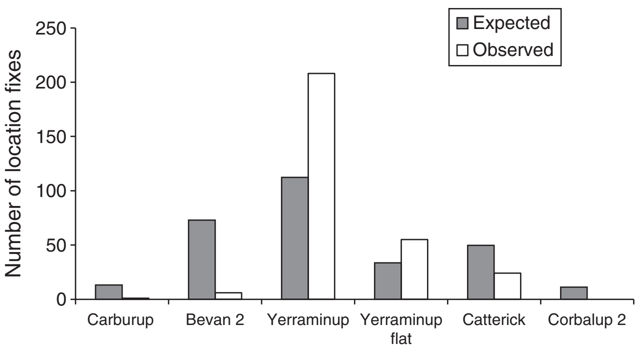

Fig. 4. The number of observed and expected location fixes for woylies within Perup Sanctuary according to habitat type.

collection and number of location fixes, sample size of animals, population density and season in which the study was undertaken. These factors are known to impact the resulting estimate of HR size (Boulanger and White 1990; Fisher and Owens 2000), which suggests that HR estimates must be considered in association with these factors when applying estimates to populations under different conditions. Previous estimates for the species are unlikely to be as relevant to current free-ranging populations because of the recent substantial decline in woylie abundance. The current study provides an updated estimate for woylie HR size in a free-ranging population at Keninup and the critically important Perup Sanctuary, which can be utilised specifically for the management of the sanctuary and in the broader context of the recovery of the species.

The large HR estimates in the low-density populations at Perup and Keninup support the hypothesis of an inverse relationship between density and HR (Wolff 1985; Erlinge *et al*. 1990; Denton and Beebee 1993). This relationship is driven by the territorial nature of male woylies (Sampson 1971; Christensen 1977) and mate-searching behaviour, which at low population densities would require animals to travel greater distances before an interaction with another woylie would occur. In 2010, Yeatman (unpubl. data) calculated an average HR size using kernel density of 14.6 ha for five woylies at Karakamia Wildlife Sanctuary, which is a high-density population (~2 woylies ha^{-1}) (Wayne *et al*. 2013*a*) to date unaffected by the decline (Yeatman and Groom 2012). This estimate is less than one-third of the population size calculated for woylies in the Upper Warren. In terms of the future management of Perup Sanctuary, where the density of woylies has substantially increased since the completion of this study (as of October 2013 the density within the sanctuary was ~1 woylie ha^{-1}) and is likely to increase further, the territorial behaviour of male woylies may act as a limiting factor and potentially contribute to a carrying capacity within the sanctuary. If this is the case, monitoring the HR size of woylies within the sanctuary may assist in identifying the carrying capacity of the sanctuary, which has important implications for how the woylie population is managed. Understanding the factors that limit population size is necessary for management to maintain a healthy, viable insurance population, which can continue to contribute to the recovery of the species.

Patterns of HR size in eutherian mammals show a positive relationship with body mass (McNab 1963; Harestad and Bunnell 1979). Fisher and Owens (2000) demonstrated that climate, average rainfall in particular, played a greater role in determining the HR size of female macropods and that body size, diet and density were less important factors. This supports the findings of the current study, which was conducted when availability of fungi was at its lowest due to the seasonal drought in summer/autumn (Johnson 1994; Danks *et al*. 2013). The ephemeral nature and patchy distribution of their primary food source means that woylies may be required to move relatively large distances to find food even during the more productive fungi seasons (Bougher 1994; Tedersoo *et al*. 2003). The patchy distribution of fungal sporocarps was identified by Taylor (1993) and Vernes and Pope (2001) as a contributing factor to the large HR sizes recorded for *B. gaimardi* and *B. tropica*, respectively. The current study's estimate of HR is likely to be at the upper end of a scale of home-range sizes, which may change throughout an animal's life depending on the seasonal availability of food (Claridge 2002; Danks *et al*. 2013) and the density of the population at that time. A limitation of this study is that data were recorded during only one season. Additional estimates recorded during multiple seasons would improve the robustness of our estimate of woylie HR size across seasons and strengthen our understanding of the processes influencing HR size.

This study used three methods of calculating HR size to account for potential overestimates due to the smaller number of fixes taken per individual and to be comparable with previous studies. Despite the differing methodologies, the kernel density, harmonic mean and MCP estimates were all very similar, with average values ranging between 65.4 and 79.1 ha. The MCP method tended to yield slightly larger estimates of HR, particularly at Perup. As harmonic mean and kernel density allow for the determination of core areas of activity (i.e. areas with a greater density of points) whereas MCP does not (Lawson and Rodgers 1997), this may account for the slightly larger MCP estimates at each site. Studies by Boulanger and White (1990) and Worton (1995) suggest that harmonic mean and kernel density methods provide more accurate estimates of HR size than the MCP method. This is in contrast to Wauters *et al*. (2007), who found that kernel density (using a h_{lscv}/h_{ref} smoothing multiplier, as was applied in this study) gave similar estimates to the MCP method and recommended the use of both of these estimates in future studies.

The large degree of HR overlap at both the Perup and Keninup sites (77.5%) is similar to earlier findings (e.g. 64% by Christensen 1977). Even at relatively low densities, these results indicate that there is the potential for a high degree of interaction between individuals. The estimates of HR overlap would be an absolute minimum as they only account for radio-collared individuals and there would be other uncollared animals sharing the ranges studied here. The high likelihood of interaction means there may be a greater potential for disease transfer, which has been implicated in the recent decline of the species (Thompson *et al*. 2013).

Habitat preferences by woylies in the Perup Sanctuary were apparent, with a strong bias in favour of Yerraminnup and Yerraminnup Flat habitats. These sites are found on the slopes and in low-lying valleys, respectively and have relatively greater water-holding capacity compared with other habitats such as Bevan 2 (Havel and Mattiske 2000). Zosky (2011) found a positive relationship between soil moisture content and sporocarp abundance in the Upper Warren, suggesting that woylies may preferentially visit the lower-lying habitats as these areas have a greater abundance of food. The number of fixes within the Yerraminnup Flat sites is unexpected. Although these sites can store soil moisture, they support fewer *Eucalyptus* species and mostly consist of thickets of *Melaleuca viminea*, which is not known to support the growth of hypogeous fungi upon which the woylies predominantly feed (Claridge 2002). It could be that there are small amounts of fungi associated with the few *Eucalyptus* species in these areas, woylies are feeding on other foods or that woylies are just travelling through this habitat as they move between adjacent Yerraminnup sites.

It is less clear why woylies were rarely found in Carbarup, Bevan 2, Catterick or Corbalup 2. All habitats within the sanctuary (excluding Yerraminnup Flat) have many ectomycorrhizal *Eucalyptus* species and the vegetation in these habitats, although different, would still be expected to provide the necessary resources for woylies. The soft sandy topsoil is one particular characteristic of Yerraminnup that distinguishes it from the other habitats within the sanctuary that have higher bulk density soils such as the clay substrates in the Yerraminnup Flat sites and the compacted lateritic soils in the Bevan 2 habitat. The sandy soil at the Yerraminnup sites would be much easier to dig and so woylies may be better able to access underground fungi. Time spent digging would need to be minimised in order to optimise energetics and so although fungi may be available in other habitats, foraging in areas that are easier to dig provides the greatest benefit (Holcroft and Herrero 1984). This may explain the lower than expected number of location fixes in the Carbarup, Bevan 2, Catterick and Corbalup 2 habitats and the apparent preference for Yerraminnup. As the density of woylies within the sanctuary increases, woylies may be forced to forage in the less preferred habitats as competition for resources increases.

It may be that the distribution of activity between habitats varies seasonally based on changes in the availability of different species of fungi (Zosky 2011) or the degree of compaction of soil (Claridge *et al*. 1993). After heavy winter rains, soil becomes more friable and is easier to dig. At this time of year, woylies may be able to access fungi more easily in the highly compacted habitats such as Bevan 2, allowing them to utilise a greater number of habitats. To identify any interaction between season and habitat preferences, woylies would need to be tracked over multiple seasons with associated measures of fungal abundance recorded during each season and in each habitat.

Conclusion

This study provides a current estimate of a seasonal HR size for wild free-ranging and ‘semi-confined’ woylies in low-density populations. HR estimates are dependent on many factors and, as a result, should be considered only as a general area of activity. The limitations of these estimates and the potential for variation based on population and seasonal factors means that comparison between studies should be undertaken with caution. In the context of a recent population decline, this study provides information on space use and habitat associations that can be used in the management of the insurance population in Perup Sanctuary and in the consideration of translocation sites used in the recovery of the species.

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