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Research Article

Application of underpasses to expand nature reserves: responses of a critically endangered marsupial, the woylie, *Bettongia penicillata*

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Abstract

Despite the conservation benefits that it yields, fencing for conservation presents management challenges. One major problem is that populations in fenced reserves can increase beyond the carrying capacity of the area. This was a concern for a population of woylies, *Bettongia penicillata ogilbyi* at Whiteman Park's fenced reserve in Western Australia. Two underpasses were constructed linking the original reserve to a larger, newly established fenced reserve to provide the resident woylies with opportunities for expansion.

Underpasses were monitored with microchip readers and infrared cameras. Woylies were also tracked using GPS technology to determine if they would use the underpasses to disperse into the new area and if, in doing so, there would be a decrease in population density and associated expansion in home range size of woylies in the original reserve. The use of underpasses by woylies was clearly demonstrated with 1657 crossings by at least 51 individuals. Contrary to expectations most woylies used the underpasses to move between the two reserves, rather than permanently dispersing into the new area. Although there was an apparent decrease in population density from 3.4±0.8/ha (S.E.) to 1.36±0.08/ha (S.E.), only the core home range of males increased by 38% after the underpasses were opened. However, woylies using the underpass did shift their home ranges to incorporate the underpasses and parts of the second reserve. Findings from this study demonstrate that the use of underpasses to connect reserves separated by roads or other barriers is an effective method to manage populations limited in their expansion by natural or anthropogenic barriers.

Introduction

Despite the conservation benefits that it yields, most notably protection from predators, fencing for conservation does not come without management challenges (Richards and Short, 2003; Morris et al., 2004; Doupe et al., 2009; Gadd, 2012; de Tores and Marlow, 2012; Young et al., 2013). If poorly managed, fenced reserves may actually become a threat to the species that they are ultimately trying to conserve (Hayward and Kerley, 2009). As fenced reserves often exclude natural population-regulating factors and limit dispersal, populations within them can increase beyond the carrying capacity of the area (Long and Robley, 2004; Mayberry et al., 2010). The consequences of this may be overexploitation of resources, potentially resulting in catastrophic declines or even local extinction of the populations (Hayward and Kerley, 2009).

Overabundance following translocation of species to fenced reserves, or areas where population expansion is limited (e.g. islands), has been a significant issue in Australia (Short, 2009; Mayberry et al., 2010). Similarly, overabundance was a potential concern for an introduced population of the woylie (*Bettongia penicillata ogilbyi*) at Whiteman Park Recreation and Conservation Reserve in Western Australia.

The woylie or brush-tail bettong is a small (1–1.5 kg) potoroid marsupial that once occupied most of mainland Australia (Yeatman and Groom, 2012). Its decline following European settlement was attributed to threatening processes such as predation by foxes, *Vulpes vulpes*, and cats, *Felis catus*, habitat destruction and altered fire regimes (Wayne et al., 2013). Through extensive fox control and reintroductions, efforts made to recover the species led to its removal from the threatened fauna lists in 1996 (Start et al., 1998; Yeatman and Groom, 2012). At the time, the woylie was regarded as a success story for the conservation of native mammals (Bailey, 1996). However, an unexpected and dramatic decline in woylie numbers by up to 90% since 2001 led to it being re-listed as Critically Endangered by the IUCN, becoming the second most endangered species in the state (Woinarski and Burbidge, 2016). The exact causes of this decline are yet to be confirmed, but circumstantial evidence points to a combination of disease and predation by foxes and cats (Wayne et al., 2013). To safeguard the species' persistence, "insurance" populations were established in fenced reserves at Perup Sanctuary and Whiteman Park Recreation and Conservation Reserve, Western Australia (Yeatman and Groom, 2012). Until the exact cause of the decline and a long-term strategy for the eradication of foxes and cats have been established, maintaining populations within fenced reserves is considered the most viable conservation strategy for the woylie.

At the commencement of this study, the woylie population at Whiteman Park was estimated to be at a minimum density of 2 individuals/ha (K. Morley, unpublished data). In the confined area of the 50 ha reserve, over-population and subsequent overexploitation of resources by the woylie was likely to become a problem. Current active management practices to mitigate the potential threat of over-population in fenced populations often involve one or a combination of culling, sterilization or translocation of animals (Long and Robley, 2004). However, the woylie's critically endangered status made these options undesirable.

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As a short-term solution, a larger 148 ha fenced reserve was constructed adjacent to the original reserve. Direct extension of the original reserve was not possible due to the presence of a service road, and translocation to the new reserve would have been costly and could have resulted in a genetic bottleneck. Therefore two underpasses were built to connect the two reserves without compromising the integrity of the fencing, to allow the woylies to expand to the new reserve of their own accord. The installation of underpasses was chosen because it was the most economically and logistically sound solution, it was considered less stressful for the animals (Priddel and Wheeler, 2004) and offered the advantage of maintaining the gene flow between the populations within each reserve (Corlatti et al., 2008). A large proportion of the woylie population had already been identified using Passive Integrated Transponders (PIT tags) during routine trapping in the previous years, providing us with the opportunity to record individual use of the underpasses using microchip readers (Harris et al., 2010; Chambers and Bencini, 2015). Underpasses are typically used to mitigate the negative effects of roads on wildlife. Their use and effectiveness has been studied extensively in North America and Europe, but their use in Australia is relatively recent (Harris et al., 2010). In Western Australia a number of native and introduced species readily use underpasses, including the western grey kangaroo *Macropus fuliginosus*, King's skink *Ergenia kingii*, bobtail lizard *Tiliqua rugosa*, brush-tail possum *Trichosurus vulpecula*, cat, fox, European rabbit *Oryctolagus cuniculus* and southern brown bandicoot *Isoodon obesulus fusciventer* (Harris et al., 2010; Chambers and Bencini, 2015) but no information is currently available for the woylie or other potoroids. Due to the probable high density of animals within the original reserve and evidence from previous Australian studies that demonstrate the almost-immediate use of underpasses by wildlife (Bond and Jones, 2008; Harris et al., 2010), we expected that woylies would readily use the underpasses to move into the new, unoccupied habitat of the second reserve (Efford et al., 2000).

Woylies are known to occupy defined home ranges that vary in size in response to factors such as site, habitat and population density from a minimum of 4 ha in high-density populations (>2 animals/ha) to over 65 ha in lower density populations (Sampson, 1971; Christensen, 1980; Nelson et al., 1992; Hide, 2006; Yeatman and Wayne, 2015). As the animals moved into the new reserve, we expected that population density would decrease and there would be an associated expansion in the home ranges of woylies that remained in the original reserve area to exploit the increased per capita resources (Efford et al., 2000).

Ultimately, this study aimed to seek evidence that underpasses could potentially provide a novel opportunity to mitigate some of the negative effects of fenced or otherwise enclosed reserves.

Materials and methods

To test our hypotheses we monitored the density, movements and home ranges of woylies within the original reserve over a seven-month period before and after the underpasses were opened.

Study site

This study was conducted within the Woodland Reserve at Whiteman Park, a conservation and leisure reserve located 18 km NE of Perth (31°49′49.02″ S, 115°57′0.42″ E) managed by the Western Australian Planning Commission. The ≈200 ha area comprised of two discrete reserves enclosed by a 2.2 m high electrified predator-proof fence, which is regularly checked and could not be breached by terrestrial animals for the length of this study. Stage 1 of the Woodland Reserve (50 ha) was constructed in 2009. Stage 2 (148 ha) was constructed in 2013 as an expansion of the protected area. Two underpasses separated by a distance of 270 m were built under an access road to connect the northern boundary of Stage 1 to the southern boundary of Stage 2 (Fig. 1). Each underpass consisted of a set of three tunnels, each 1.4×1.4×4 m in size. Before their opening, tunnels were blocked with mesh wire to prevent animals from using them. Due to financial restrictions limiting the availability of monitoring equipment, only one tunnel of each underpass was opened for the duration of this study.

The vegetation within the reserve comprised of remnant bushland and rehabilitated land, with *Banksia* woodland and *Melaleuca* damp land dominating in Stage 1 and heathland in Stage 2. Dominant plant species within Stage 1 included *Banksia menziesii*, *B. attenuata*, *B. ilicifolia*, *Corymbia calophylla*, *Xanthorrhoea preissii* and *Melaleuca preissii*. Dominant species within Stage 2 included *Regelia ciliata*, *Calytrix fraseri*, *Eucalyptus todtiana* and *X. preissii*.

Population density estimate

The population size and density of woylies in Woodland Reserve Stage 1 were estimated from a mark-recapture study in June 2014, before the underpasses were opened, and October 2014, six weeks after the opening of the underpasses. For each survey woylies were captured along five trapping lines that spanned the entire length of the reserve (Fig. 1). Ten treadle-operated wire cage traps (220×220×550 mm, Sheffield Wire Products, Welshpool, Western Australia), spaced about 50 m, were set for one night along each line before dusk, baited with peanuts, and draped with a hessian sack to provide protection from the elements. Traps were checked three times between 1900 hours and 2400 hours. All captured animals were identified using Passive Integrated Transponders (PIT or microchip), Trovan Unique, model ID 100, Microchips Australia, Victoria, Australia) as well as ear tags as a backup for the rare occurrence in which microchips fail (Schooley et al., 1993) and immediately released.

The population size was estimated using the program MARK (Cooch and White, 2014) and a Huggins Closed Captures model with which we tested three different models: a time varying capture probability model (M_t), a behavioural response model (M_b) and a constant capture probability model (M_0). Model averaging based on AIC weight was then used to provide an estimate of population size accounting for model uncertainty. The population density was estimated as the number of individuals per hectare. As trap lines covered the entire reserve, density could be determined without the need to estimate an effective trapping area.

Underpass monitoring

The middle tunnel of the eastern-most underpass was opened on 20th August 2014, followed by the middle tunnel of the western underpass on 2nd September 2014. Each tunnel was fitted with a Passive Integrated Transponder reader consisting of a microchip decoder and two side-by-side flatbed antennae, maintained in place by a wooden frame (Dorset Identification, Aalten, Netherlands). Spaces left between the frame and the wall of the tunnel were blocked to ensure that PIT tagged animals moving through the tunnel were detected. The PIT tag readers were run from deep cycle batteries recharged by solar panels to ensure

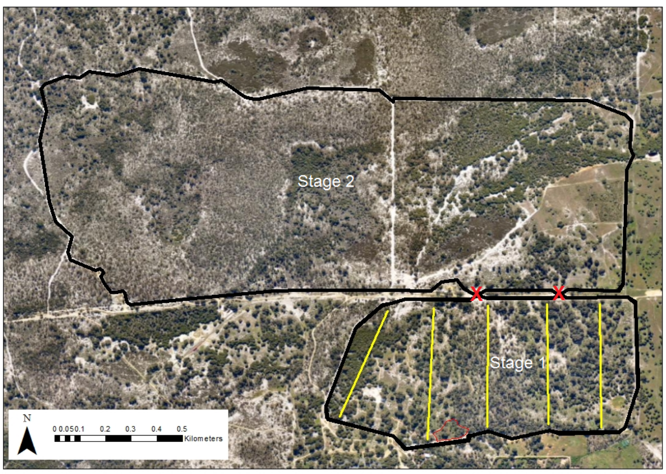

Figure 1 – Woodland Reserve Stages 1 and 2 at Whiteman Park, Western Australia. The black lines represent the boundaries of the fence, the red "X"s represent the location of the underpasses connecting the two reserves, and the yellow lines indicate the positions of the trap lines.

that they were functioning continuously for approximately two months after the underpasses were opened. Both underpasses were also fitted with two motion activated infrared cameras (Reconyx HC600, Holmen, WI, USA), attached to the roof of each entrance facing inward.

The PIT tag reader identified PIT-tagged woylies using the underpasses and the time and date of when the animal crossed. The infrared cameras recorded the use of the underpasses by woylies as well as other species. Using PIT tag records and/or photographs, crosses were classified as a 1) verified crossing 2) probable crossing or 3) investigation of entrance only. A crossing was "verified" if it had both matching photographs and PIT records or, for non-PIT tagged animals, two or more photographs from both sides of the underpass demonstrating passage from one side to the other. "Probable" crossings were those in which there was either a PIT record or a single photograph of the animal inside the underpass, but not both. "Investigations" were classified from photographs whereby animals were recorded approaching the underpass but not entering it. Multiple, frequent uses of the underpass, which could only be determined for PIT-tagged animals, implied that the individual had incorporated the underpass into its home range. However, whether or not the home ranges were modified to include the underpasses could only be confirmed for radio-collared animals.

Due to technical malfunctions, there were intermittent periods when the PIT tag readers were non-functioning. During these periods, which totalled 21 days, the underpasses were monitored only with the cameras.

Radio telemetry

Woylies were trapped for an additional night or two in February, May, and September 2014 in Woodland Reserve Stage 1 to fit them with radio collars. On these occasions only 30 traps of the three eastern-most trap lines were set because they were immediately opposite to the underpasses (Fig. 1). Traps were checked at approximately 1900 hours, 2100 hours and 2300 hours and we recorded the weight, sex, pouch status, general body condition and approximate age (juvenile, sub-adult or adult) of each captured individual. Selected adults and sub-adults were fitted with a GiPSy4 micro GPS data-logger (TechnoSmart, Italy) and a VHF radio transmitter (Sirtrack, New Zealand), attached to a fabric collar, weighing approximately 23 g. Individuals that had been first collared in February were preferentially selected at subsequent collaring events; however, re-collaring was limited by recapture rate and collaring suitability (e.g., absence of large pouch young for females). Due to the short battery life of the GPS units, collars were removed after approximately four weeks by re-trapping the collared individuals. Upon removal of collars, individuals were weighed and checked for fur loss or lesions to ensure that weight and condition had not declined. Because woylies are nocturnal (Yeatman and Groom, 2012), the GPS units were programmed to record locations every ten minutes throughout the night (from 1800 hours to 0600 hours) and only once during the day ($\approx$ 1200 hours) for up to 28 days, allowing a possible 2016 opportunities for location records. Once a week, collared individuals were tracked on foot to their nests during the day using three-elements Yagi antennas (Sirtrack, New Zealand) and R-1000 telemetry receivers (Communications Specialists Inc., Orange, California, USA). Animals were flushed from their nest to ensure that no collars were inhibiting movement or causing any obvious signs of distress (never observed), and to recover any dropped collars.

Over all collaring periods we captured 118 individuals, 98 of which were fitted with collars (22 in February, 40 in May and 36 in September). Due to a combination of faulty GPS units and damage inflicted by the animals, 77 of the 98 GPS units ceased collecting usable data prematurely. As a result, only 14 and 7 individuals respectively were left with sufficient data for home range analysis for the pre- and post-opening period (Tab. 2). Not all collected locations were accurate and some were discarded according to the following criteria:

- Locations with a horizontal dilution of precision (HDOP) of more than five.
- Locations with less than three satellites present, as a minimum of three satellites is required for an accurate triangulation of location (Jensen and Jensen, 2013).
- Locations with an altitude >100 m. As Whiteman Park is between 20–50m above sea level, readings with an altitude of >100 m indicated large errors in the location data.
- Locations beyond the boundaries of the fence, when overlaying locations on a map of the reserve in ArcMap (ESRI, 2011).

Home range estimates

Home range isopleths were estimated using the Time Local Convex Hull method using the package T-LocoH (Lyons et al., 2013) in R (R Core Team, 2014). A value of s=0.0015 was chosen to calculate the time-scaled distances (TSD) between points. The *k-method* was used to identify the k^{th} nearest neighbour (k=12), where "nearest' is'determined by the TSD metric, which is influenced by s (Lyons et al., 2013). The k and s values were chosen because they were the most appropriate values to allow comparison of home ranges between individuals. The "total" home range was defined as the 95% isopleth and the 'core' home range as the 50% isopleth. The short battery lives of the GPS collars forcibly limited observations to periods of only weeks or days. As home range estimates can be affected by the length of time spent collecting data, it should be noted that the home ranges presented here are short-term estimates and therefore are likely to be underestimates.

Data analyses

All statistical analyses were carried out in the program R (R Core Team, 2014). Underpass use was analysed using a Generalised Linear Model (GLM) with a Poisson distribution and log link function, with the total number of crossings per day as the dependent variable and the number of days since opening as the independent variable (α=0.05). The mean number of crossings per hour for both underpasses combined was compared using a non-parametric Kruskal-Wallis test to account for the non-normally distributed data. If a significant difference was found (α=0.05), post-hoc analysis was done using Man-Whitney U-test with a sequential Bonferroni correction.

The size of total (95%) and core (50%) home ranges were compared between males and females using t-tests, after having tested equality of variance (α=0.05) and graphically inspected the variable distribution for normality.

Because home range size can increase with the duration of observation (Schuler and Theil, 2010), to ensure that the variation in length of monitoring between collaring periods was not affecting home range estimates, a GLM was fitted using as predictors the total number of GPS data points, number of days of collar function, collaring period and their interaction. Data for individuals that were collared during both collaring periods were taken from the second collaring period only to ensure independence in the model. Total and core home range sizes before and after the underpasses were opened were compared using t-tests (α=0.05).

Lastly, the weights of the animals before and after a collaring period and between sexes were compared with t-tests, after having tested equality of variance (α=0.05) and graphically inspected the variable distribution for normality or Mann-Whitney test when the variables were not normally distributed.

Ethics

All trapping and animal-handling procedures were approved by The University of Western Australia's Animal Ethics Committee (RA/3/100/1283) and were in accordance with the National Health and Medical Research Council's "Australian code of practice for the care and use of animals for scientific purposes" (NHMRC, 2013).

Table 1 – Frequency of use of two underpasses as detected by PIT tag readers or motion activated cameras in the Woodland Reserve at Whiteman Park (Western Australia) from August to October 2014 by woylies (*Bettongia penicillata ogilbyi*) and other species. Southern brown bandicoots and tammar wallabies are also routinely implanted with PIT tags. Values with an † indicate estimations from photography only, as the individuals could not be identified using PIT tags. Other species that did not have PIT tags could not be identified and are denoted as N/A. Reptile and bird species are described in the text.

Species	Crossings Verified	Crossings Probable	Crossings Total	Number of individuals	Investigations	Total	% use
Woylie (*Bettongia penicillata ogilbyi*)	180	1477	1657	51	70	1727	78.8
Rabbit (*Oryctolagus cuniculus*)	27	37	64	N/A	106	170	7.8
Southern brown bandicoot (*Isoodon obesulus fusciventer*)	14	156	170	8	13	183	8.4
Tammar wallaby (*Macropus eugenii*)	2	4	6	2†	38	44	2
Western grey kangaroo (*Macropus fuliginosus*)	12	2	14	N/A	35	49	2.2
Echidna (*Tachyglossus aculeatus*)	1	3	4	N/A	2	6	0.3
Reptiles	5	2	7	N/A	2	9	0.4
Birds	0	0	0	N/A	4	4	0.2
Total	397	1525	1922	N/A	270	2192	100 6

Results

Underpass use

The first use of both underpasses was recorded within two days of opening each tunnel. Over the 56 days of the study we recorded 1657 verified or probable crossings by at least 51 different individual woylies and a further 70 explorations of the entrance of the tunnels (Tab. 1). The number of crossings by an individual woylie varied from one to 125 (Fig. 2). Three individuals, of which two were sub-adults, used the underpass only once. 82% of PIT tagged woylies that had used the underpasses were still using them on the final day of study.

Other species recorded using or inspecting the underpass were the tammar wallaby *Macropus eugenii*, southern brown bandicoot, western grey kangaroo, European rabbit, echidna *Tachyglossus aculeatus*, bobtail lizard, tiger snake *Notechis scutatus*, Gould's sand monitor *Varanus gouldii*, Australian magpie *Craticus tibicen*, raven *Corvus coronoides*, Pacific black duck *Anas superciliosa* and bush-stone curlew *Burhinus grallarius* (Tab. 1).

At both underpasses, the total number of woylie crossings per day was positively correlated with time since opening (R=0.48, df=29, $p<0.001$, Fig. 3). Woylies used the underpasses continuously throughout the night, but the average number of uses was highest between 1900 hours and 2000 hours (W=9501, $p=8.4\times10^{-4}$). Underpass use dropped significantly after 0400 hours (W=20657.5, $p=7.8\times10^{-10}$) and ceased almost completely by 0600 hours, except for a rare few crossings recorded during the day (Fig. 4). Location recordings taken by the GPS collars demonstrated that woylies ventured into Stage 2 mainly at night, and most returned to Stage 1 during the day (Fig. 5).

Population estimate and density before and after the opening of the underpasses

In June 2014, before the opening of the underpasses, there were an estimated 170±40 (S.E.; 95% CI: 65–275) woylies within Woodland Reserve Stage 1, corresponding to a population density of 3.4±0.8 (S.E.) woylies per hectare. In October 2014, six weeks following the opening of the underpasses, the population of woylies in Stage 1 had decreased to an estimated 68±4 (S.E.) (95% CI: 56–79) individuals, corresponding to a population density estimate of 1.36±0.08 (S.E.) woylies per hectare. These estimations do not include any pouch young at the time of trapping.

Home range size before and after the opening of the underpasses

Unfortunately due to collar failure, with the exception of one individual, it was not possible to obtain data for the same individuals both before and after the opening of the underpasses.

Before the underpasses were opened, the average total home range size (±S.E.) of males (n=6) was 10.1±1.33 ha. This was significantly larger than that of females (n=8) at 6.8±1.04 ha (t=-1.95, df=10, p=0.03). The average core home range size of males, 2.0±0.39 ha, was also significantly larger than that of the females, 1.1±0.11 ha (t=-2.27, df=6, p=0.03).

After the underpasses were opened, the average total home range size (±SE) of males (n=3), 7.8±1.16 ha, was again significantly larger than that of females (n=4), 4.6±0.85 ha (t=3.09, df=5, p=0.013). Likewise, the average core home range for males, 3.3±0.30 ha, was also significantly larger than that of females, 0.9±0.24 ha (t=6.09, df=4 p=0.001).

The total home range sizes for both sexes following the opening of the underpasses were not significantly different from those estimated before the underpasses were opened (males: t=1.18, df=7, p=0.13; females: t=1.37, df=10, p=0.10). Similarly the core home range of females after the opening of the underpasses was not significantly different from the estimate obtained before the opening of the underpasses

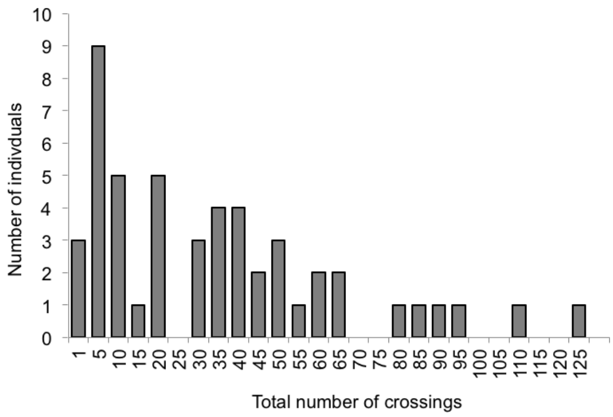

Figure 2 – Frequency distribution of crossings using the underpasses for each of the 51 PIT tagged woylies (*Bettongia penicillata ogilbyi*) from the 2nd of September to the 14th of October 2014 in the Woodland reserve at Whiteman Park (Western Australia).

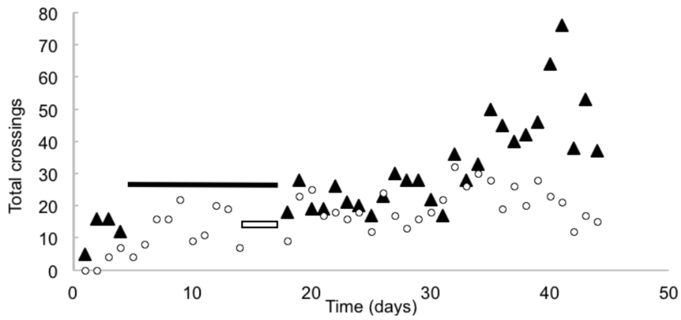

Figure 3 – Total number of underpass crossings per day made by woylies (*Bettongia penicillata ogilbyi*) since opening of the eastern-most (▲) and western-most (○) underpasses connecting two fenced areas in the Woodland Reserve at Whiteman Park (Western Australia), from the 2nd of September to the 14th of October 2014, as identified by PIT tag detection only. Lines indicate the period when the eastern (black) and western (white) PIT tag readers were not functional.

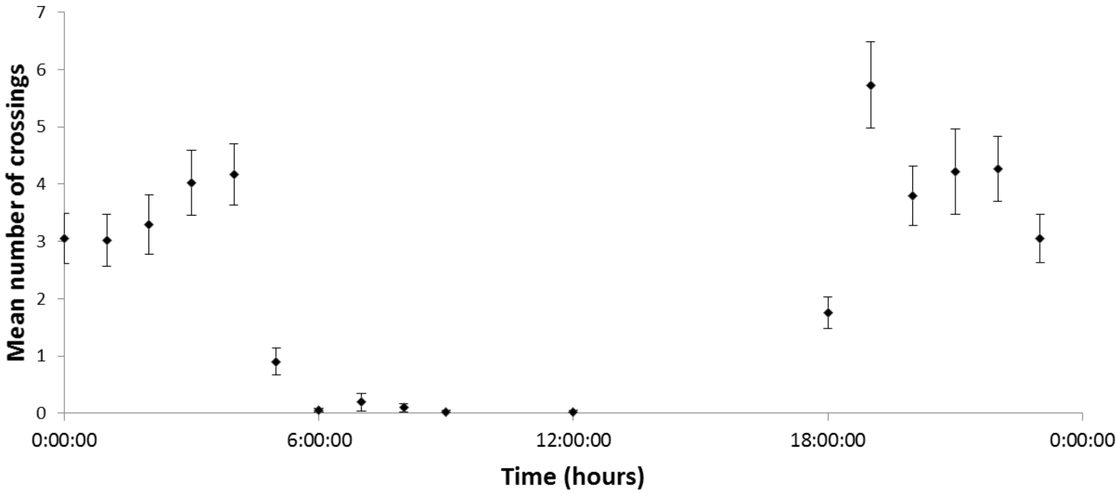

Figure 4 – Mean number of underpass crossings per hour (±SE) by woylies (*Bettongia penicillata ogilbyi*) as identified by PIT tag readers, for both underpasses from 2 September to 14 October 2014 in the Woodland Reserve at Whiteman Park, Western Australia.

(t=-0.71, df =10, p=0.75). However, the core home range size of males increased by 38% after the underpasses were opened (t=-2.07, df=7, p=0.03). All males and one female using the underpasses incorporated one of the underpasses and part of Woodland Reserve Stage 2 in their home ranges (Table 2). Only one animal (a male) was recorded in Stage 2 for several days, possibly having permanently dispersed in the new area.

Output from the GLM model indicated that neither the total number of data points nor the length of data collection had any significant influence on home range size between collaring periods.

On average, adult woylies weighed 1.1±0.04 kg and there was no significant difference in weight between sexes (t=-0.005, df=12, p=0.5) or before (1.1±0.04) and after (1.1±0.08) they had been wearing collars (W=56.5,p=0.25).

Discussion

As hypothesised, woylies readily used the underpasses, even though they did not seem to have permanently dispersed into Stage 2. Therefore our study provides evidence that underpasses can be successfully adopted to connect fenced reserves. We did not detect any change in the average home range size of woylies, except for males at the core home range level. However, we acknowledge that our power may have been hampered by the small sample size due to the high rate of failure of the GPS collars.

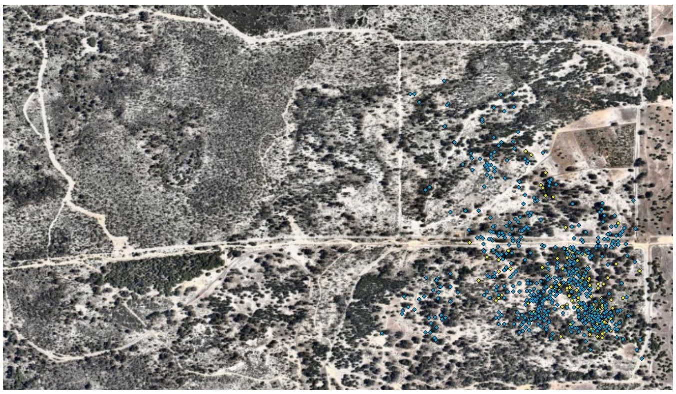

Figure 5 – GPS locations of collared woylies (*Bettongia penicillata ogilbyi*) in Stage 1 and 2, taken in September 2014 in the Woodland Reserve at Whiteman Park, after the underpasses were open. Blue dots represent locations taken at night (between 1800 and 0600 hours) and yellow represent locations taken during day (at 1200 hours).

Underpass use

The hypothesis that woylies would use the underpasses as soon as they were opened was supported, with the first recorded passage occurring only two days after each underpass was opened. This finding is in agreement with other Australian studies that showed that wildlife used underpasses shortly following construction (Bond and Jones, 2008; Harris et al., 2010), but it contrasts with international studies in which wildlife took months to years before they started using underpasses (Clevenger and Waltho, 2005; Mata et al., 2005).

Over a third of the population, as estimated in June, was recorded using the underpass at least once. Relative to time-frame, the proportion of individuals using the underpasses and frequency of use was higher than in any other Australian study (Taylor and Goldingay, 2003; Harris et al., 2010; Crook et al., 2013; Chambers and Bencini, 2015) and many overseas studies (Foster and Humphrey, 1995; Ng et al., 2003; Kleist et al., 2007; Braden et al., 2008) although this is likely to have been exacerbated by the fencing limiting movement elsewhere. Similar to the initial results of other studies, the number of crossings increased significantly with time since opening (Kleist et al., 2007; Braden et al., 2008; Harris et al., 2010). While the first woylies to use the underpass were mostly males, females soon became frequent users and the total number of males and females using the underpasses was approximately equal.

Contrary to our original expectation, the high number of crossings by multiple individuals suggests that most woylies recorded using the underpass did not permanently move into Woodland Reserve Stage 2, but rather used the underpasses to travel back and forth between reserves. This is supported by evidence of woylies being recorded in Stage 2 more frequently during the night than during the day (Fig. 5). It is likely that woylies were travelling to Stage 2 early in the night to forage for food, but returning to their pre-existing nesting sites in Stage 1 before sunrise (Fig. 4). During feeding activities woylies make a large number of small diggings in search of their major food source, hypogeous fruiting bodies of ectomychorrizal fungi (Christensen, 1980; Lamont et al., 1985; Garkaklis, 2001). The observation of numerous diggings in Stage 2 and records of collared individuals using the underpasses at night and then radio-tracked to their nests in Stage 1 the following day, also support the notion that woylies were using Stage 2 to forage but returned to rest in their original nesting sites in Stage 1 during the day rather than dispersing permanently into Stage 2.

This is not surprising given the short duration of our study. Despite the potential advantages of permanently dispersing into the new area, such as decreased competition for resources, dispersal can also carry high costs, which may have outweighed the potential advantages (Janmaat et al., 2009). Woylies are known to have high fidelity to nesting areas and may prefer to return to pre-existing nests, which are built by actively carrying nesting material with the tail and are important

Table 2 – Weight (kg), number of days collared, number of locations and total (95% isopleth) and core (50% isopleth) home ranges (HR) of woylies before and after opening of underpasses in the Woodland reserve at Whiteman Park, Western Australia. The percentage of total home range in Stage 2 (WR2) in September 2014, after the underpasses were opened indicates that animals expanded their home range to include the underpasses and part of the second reserve. Individuals that had used an underpass at least once are indicated with †.

				Home range size (ha)		
Sex and ID	**Weight (kg)**	**Collar days**	**Locations**	**Total**	**Core**	**% total HR in WR2**
BEFORE						
F1	1.14	17	247	3.68	1.38	-
F2	1.17	10	96	3.95	1.3	-
F3	1.12	19	384	4.98	0.79	-
F4	1.34	15	231	5.41	1.07	-
F5	0.96	6	83	5.7	0.7	-
F6	1.37	10	91	9.47	1.39	-
F7	1.03	28	836	10.07	0.79	-
F8	1.1	11	107	11.04	1.4	-
Mean(±SE) Females	**1.2(±0.05)**	**14.5(±2.44)**	**259.4(±90.47)**	**6.8(±1.04)**	**1.1(±0.11)**	**N/A**
M1	0.92	9	181	6.77	1.17	-
M2	1.17	8	101	6.9	1.15	-
M3	1.09	21	294	8.36	2.39	-
M4	1.35	18	223	10.88	2.98	-
M5	1.14	25	423	12.97	3.22	-
M6	1.25	5	88	14.57	1.24	-
Mean(±SE) Males	**1.2(±0.06)**	**14.3(±3.03)**	**218.3(±51.57)**	**10.1(±1.33)**	**2.0(±0.39)**	**N/A**
AFTER						
F9	0.88	13	85	2.27	0.69	0
F10	0.9	19	176	4.48	0.77	0
F4†	1.34	11	85	5.36	0.65	0
F11†	-	5	56	6.24	1.65	5
Mean(±SE) Females	**1.0(±0.15)**	**12(±2.89)**	**100.5(±26.08)**	**4.6(±0.85)**	**0.9(±0.24)**	**1.3(±1.25)**
M9†	1.13	5	50	8.15	2.92	42
M10†	0.89	15	93	7.68	3.04	14
M11†	1.21	11	78	7.43	3.88	11
Mean(±SE) Males	**1.1(±0.10)**	**10.3(±2.91)**	**73.7(±12.60)**	**7.8(±0.21)**	**3.3(±0.30)**	**22.3 (±9.87)**

resources used both for predator protection and to help maintain constant metabolic energy requirements (Sampson, 1971; Christensen and Leftwich, 1980). Therefore younger or subordinate individuals may be more likely to disperse permanently than older individuals. Indeed, two of the three individuals that used the underpasses only once and presumably emigrated into Stage 2 were sub-adults. Further indirect evidence that new recruits may be dispersing in Stage 2 is that the proportion of new individuals trapped in October (5%) was less than half of the proportion trapped in June (12%) before the underpasses were opened. However, the known difficulty in trapping juveniles of this species (Pacioni 2010) has limited our capacity to conclusively validate this hypothesis.

Home range characteristics and population density prior to the opening of the underpass

The size and density of the woylie population in Woodland Reserve Stage 1 before the opening of the underpasses was much larger than the estimate of 2/ha suggested at the outset of the study. Population densities for the woylie in fenced reserves have been found to range from 0.05 to 4.8 woylies per ha, depending on site and habitat type (Freegard, 2007). With a population close to the maximum density recorded for the species, and no means of dispersing, it is clear that the woylie population in Stage 1, prior to the opening of the underpasses, was approaching the carrying capacity of the area.

The density and associated home range characteristics of the woylie population in Woodland Reserve Stage 1, prior to the opening of the underpass are in agreement with Hixon (1980) and Schoener (1983) who found that home range size decreases with an increase in population density as animals compete for resources.

Change in population density and home ranges following the opening of the underpasses

The hypothesis that there would be a reduction in the population density of woylies in Woodland Reserve Stage 1 following the opening of the underpasses was supported, with the population estimate apparently decreasing by 60% although the CIs between the two estimates were overlapping. Despite this lack of significance, the reduction trend in the density of the population, together with the evidence provided by the radio tracking and microchip readers, demonstrates the efficacy of the use of underpasses. Considering the short-term nature of this study, it is unlikely that there could have been a true "decline" in population due to increased mortality, and even more unlikely that such a decline would have gone unnoticed because Whiteman Park staff monitored the reserve routinely. While we acknowledge that it would have been ideal to estimate the population density in Stage 2, which was not possible due to time and resource limitations, we argue that the reduction in density in Stage 1 reflects the fact that the same number of woylies became spread over the two reserves, as documented by their frequent use of the underpasses and the observation of diggings in Stage 2.

We were only able to demonstrate an expansion in the core home ranges for males following the opening of the underpasses. Considering the few data collected due to the systematic failure of the radio collars, we cannot rule out that the lack of expansion in the size of the home ranges could be the result of limited statistical power. Despite this, our results suggest that individuals using the underpass shifted their home ranges to incorporate the underpasses and parts of Stage 2, without permanently emigrating. This finding is similar to that of Christensen (1980) who reported that although the home range sizes of woylies remained the same following a fire, some individuals shifted their home ranges to incorporate nearby unburnt habitat, these individuals being young males. Without the ability to study the same individuals before and after the underpasses were opened, we were unable to quantify shifts in the home ranges of individuals, but our results suggest that woylies largely remained faithful to their nesting sites. In support of this, Christensen (1980) reported that woylies in his study largely remained close to their nesting sites because of their innate fidelity to the area.

As this was a short-term study, it may also be that changes in total home range size may have not yet been detectable, as there had not been enough time to allow sufficient dispersal into Stage 2. Indeed, Christensen (1980) found that the few expansions in woylies' home ranges that occurred within his study were made very slowly, with a gradual "probing" extension of home range area by limited explorations, which has been also reported for a variety of taxa (Gamble et al., 2007; Janmaat et al., 2009). As well as visiting Stage 2 to feed, it may be that woylies were gradually exploring the area and males are more inclined to exploration (Christensen, 1980), also as shown by the fact that they were first to use the underpasses. We predict that new individuals will begin to disperse into Stage 2 as they leave their mothers to establish their own nesting sites and home ranges. It would be sensible to monitor Stage 2 in the future to see if this prediction is correct and to detect potential long-term changes in home ranges.

Management implications

This study has provided evidence that underpasses are an effective and relatively novel strategy for managing fenced populations. Through the use of underpasses, animals in Whiteman Park's Woodland Reserve have been given the opportunity to start dispersing into a new area of their own accord. This management strategy has fewer risks and is more desirable than other options for fenced populations such as culling, sterilisation or translocation. Due to their critically endangered status, conservation of the woylie will continue to be carried out in fenced reserves for the foreseeable future. Therefore, managing the potential negative effects of fencing is critically important to ensure that the already severely depleted woylie populations do not decline any further. While in this study we focused on application of underpasses for the woylie in fenced reserves, the benefits discussed above are also potentially relevant for the management of other species in habitats where their expansion is limited by natural or anthropogenic barriers.

The management of multiple fenced reserves connected by structures such as underpasses also would provide unique opportunities to manage unforeseen circumstances or catastrophes more effectively by providing the ability to isolate certain areas. For example, being able to close off areas to quarantine the spread of disease or to isolate predators should they breach the fence could potentially be very beneficial from a management point of view. Indeed, soon after the end of this study a fire burnt large areas of the reserve, and the gates had to be opened to offer an escape route for the animals. As underpasses are placed under roads that are natural firebreaks they could offer safe passage to areas unaffected by fire should a fire affect only part of a reserve system. Where applicable, this strategy should be employed for the management of fenced populations in the future. In the planning and construction of future fenced reserves, developers could consider sub-dividing areas into discrete areas connected by underpasses. In the example of woylies at Whiteman Park, indeed, a third fenced reserve area is being planned for the expansion of current populations and the addition of new species.

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