# Introducing the woylie (*Bettongia penicillata*) to the Swan Coastal Plain: resource availability and the impact of digging on soil water repellency

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## Abstract

The critically endangered woylie (*Bettongia penicillata*) is a small, mycophagic marsupial and is very susceptible to predation by foxes and cats. Fenced, predator-proof reserves are used as conservation tools for woylies and one such reserve occurs at Whiteman Park on the Swan Coastal Plain.  This area is not part of the woylies historic range and is therefore critical to assess the resource availability and the impact that woylies may have on the Swan Coastal Plain. By digging for fungi woylies reduce soil water repellency in heavily textured soils, but it is unknown whether this will occur on the Swan Coastal Plain. I hypothesised that on the Swan Coastal Plain, there would be a higher abundance of fungi occurring close to mycorrhizal vegetation and fungi would be less abundant in habitats that lack this vegetation. I expected woylie diggings in habitats with high amounts of organic matter would reduce soil water repellency from severe to low, and would not greatly reduce soil water repellency in habitats with little organic matter. I also expected woylies would increase their digging rate as they adapted to the wild. In March 2010, eight, captive-reared woylies were released into a soft release enclosure at Whiteman Park and their digging rate estimated by counting diggings in 10m x 2m transects over four months. In a separate 50 ha enclosure four 20m x 25m quadrats were established in each of the melaleuca, jarrah, banksia and open habitats. Simulated diggings were used to determine the effect of woylie diggings on soil water repellency using the Molarity of Ethanol Droplet test. Sequestrate fungi abundance and leaf litter depth were measured in August and September 2010 in each habitat quadrat. The digging rate of woylies increased ten fold within the first three weeks from release to reach an average rate of 22,000 diggings woylie$^{-1}$ year$^{-1}$. Simulated diggings reduced soil water repellency from severe to low in the jarrah habitat, which had the highest accumulation of leaf litter and most severely repellent topsoil. This effect was less pronounced in melaleuca and banksia habitats, and diggings increased water repellency in open habitats. After a week the water repellency in simulated diggings was no longer reduced in comparison to the surrounding soils. Eleven species of fungi were found during the study, including four underground fruiting species. Woylies will dig where fungi occurs and will reduce water repellency of soils in localised

patches, and this effect will be short lived. The low abundance of fungi on the Swan Coastal Plain indicates this habitat may not be able to support a population of woylies without supplementary feed.

## Introduction

In all areas of the world under threat from human expansion, many native species have experienced reductions in abundance and geographic range. This phenomenon is no more prevalent than in Australia with the extinctions of over 20 mammal species in the past 200 years, due to habitat removal and fragmentation, the impacts of introduced species and disease (Archer and Beale 2004; Lindenmayer 2007; Wayne 2008). When the distribution of a species is restricted to small, isolated areas of suitable habitat the risk of extinction from environmental change is heightened. An effective conservation technique to improve the future viability of an endangered species is to increase the number of separate populations (Main and Yadav 1971). This can be achieved by reintroductions: translocating animals into part of their historical range where they have become locally extinct, or introductions: expanding their range by introducing animals to locations where they previously did not occur naturally. Translocations can carry a low success rate due to reduced genetic diversity, outbreeding depression, predation by introduced species and altered resource availability (Kleiman 1989; Short *et al.* 1992). This risk is amplified with introductions, as the response of animals to the new environment is difficult to predict. Assessing environmental suitability prior to an introduction is essential to ensure long-term survival of the new population and prevent adverse effects on the environment, within the release area.

The critically endangered woylie, or brush-tailed bettong (*Bettongia penicillata ogilbyi*) was once widespread throughout Australia, but now occupies just 3% of its historical range in the south-west of Western Australia (Nelson *et al.* 1992; Start *et al.* 1995; Lindenmayer 2007; de Tores and Start 2008; Wayne *et al.* 2008). Like other Australian marsupials that fall into the critical weight range (35 g - 5.5 kg), woylies are especially susceptible to predation by introduced foxes and cats (Burbidge and McKenzie 1989; Chishlom and Taylor 2010). In the 1990s woylie populations responded positively to fox control; however, since 2001 woylie populations in the south-west of WA have declined, possibly due to the diseases *Toxoplasma* and *Trypanosoma* (Smith *et al.* 2008; Wayne 2008). Current populations of woylies are small and declining except at the Australian Wildlife Conservancy's Karakamia sanctuary near Chidlow, WA (Start *et al.* 1995; Wayne 2008). Karakamia is fenced and predator free and woylies are prolific breeders under these conditions, providing mature and captive-reared woylies for translocations to other sites. Translocations of woylies tend to fail where foxes and cats are present, making fenced, predator-proof reserves integral for successful translocations, though such reserves are rare and expensive (Short *et al.* 1992; Start *et al.* 1995; Wayne 2008).

One such reserve has been established at Whiteman Park, a recreation and conservation reserve on the Swan Coastal Plain, which provides an opportunity to expand the woylies current range and raise the public's awareness of this species. The Swan Coastal Plain is not part of the recent historical distribution of woylies with the most recent fossil evidence of this species found at the Yanchep caves and dating to 8,000-12,000 years old (Glauert 1948). The exclusion of the Swan Coastal Plain and presence of woylies on the nearby Darling scarp suggests the Swan Coastal Plain to be unsuitable woylie habitat. Woylies feed predominately on underground fungi and the abundance of this resource is essential to their survival (Christensen 1980; Zosky *et al*. 2010). In the mid 1990s a small group of woylies were illegally released at Port Kennedy, south of Rockingham WA, and subsequently starved to death over a 6 - 9 month period, as the coastal environment was deficient in underground fungi (P. Mawson pers. comm.). Investigating the abundance of underground fungi is essential in determining if the Swan Coastal Plain is a viable habitat for woylies.

Knowledge of fungi is a developing science in the south-west of WA, many species are yet to be taxonomically described and most regions have not yet been surveyed (Bougher and Syme 1998). Whiteman Park is no exception, with opportunistic surveys in 2006 uncovering one known and two undescribed species of underground fungi (Bougher *et al*. 2006 a, b). Underground fungi are mycorrhizal, forming symbiotic relationships with plant species such as *Eucalyptus* and the distribution of underground fungi in the environment directly reflects the distribution of mycorrhizal plant species (Claridge *et al.* 1993; Johnson 1994; Claridge *et al*. 2000b). I hypothesise that on the Swan Coastal Plain, the distribution and abundance of underground fungi will follow the same pattern with higher diversity and abundance of fungi occurring close to mycorrhizal trees. Subsequently fungi will be less abundant in habitats that lack trees such as grassland or cleared areas.

Underground fungi are excavated and consumed by mycophagous marsupials that will search over large areas to locate patches of fungi in the environment (Johnson 1996). Like most bettongs, woylies are ecosystem engineers and aid in the distribution of fungal spores and seeds, and create heterogeneity in the soil profile through their digging activity, which leads to the preferential flow of water and nutrients into the soil (Christensen 1980; Garkaklis *et al.* 1998, 2000, 2003; Murphy *et al.* 2005). These processes are important as many Australian soils form a water repellent (hydrophobic) surface layer created by organic matter and woylies dig to expose the underlying hydrophilic soil, allowing water to penetrate (Garkaklis *et al.* 1998, 2000; Doerr *et al.* 2000). The effect of woylie digging activity on water infiltration into the soil can be examined by comparing the top soil water repellency to the inside of the digging (Garkaklis *et al.* 1998, 2000). At Dryandra Woodland in the wheatbelt of south-west of WA, woylie diggings are critical in allowing water to flow into otherwise severely water repellent soil by exposing hydrophilic soil layers (Garkaklis *et al.* 1998, 2000). The soils at Dryandra Woodland are heavily textured with a high clay content compared to the coarse, white sands of the north-east Swan Coastal Plain (McArthur et al. 1977; Whiteman Park 2003). Soil water repellency tends to be more severe in sandy soils as the individual grains have a low surface area to volume ratio and the finite amount of organic matter available is able to coat more grains than clay based soil (Doerr *et al.* 2000). If the soils at Whiteman Park are more water repellent than those at Dryandra Woodland, the digging activity of woylies could play a vital role in allowing water to flow into the repellent sand. I expect that woylie diggings will decrease water repellency of sub surface soils on the Swan Coastal Plain and this effect will be more pronounced than at Dryandra Woodland. In addition, woylie diggings in habitats with higher amounts of organic matter, such as *Eucalyptus* woodland, should reduce the soil water repellency from severe to low when compared to habitats with little organic matter, for example open grasslands, where woylie diggings will not greatly reduce soil water repellency.

Captive reared woylies from Karakamia sanctuary were translocated into the Whiteman Park reserve. These animals had been raised in concrete floored enclosures and had therefore not had the need or opportunity to dig to find food. Donaldson and Stoddart (1994) found that Tasmanian bettongs learnt how to dig and locate fungi by smell even after being raised in concrete floored enclosures. Woylies should respond in the same manner and I expect they will increase their digging rate as they adapt to the wild.

## Materials and methods

### *Study species*

The woylie is a small mycophagous mammal in the family Potoroidae, within the superfamily Macropoidea, and is endemic to Australia (de Tores and Start 2008). Woylies are nocturnal and feed on underground fungi, which they locate by smell and dig to excavate (Christensen 1980; Lamont *et al.* 1985; Lee 2003; Garkaklis *et al.* 2004; Zosky *et al*. 2010). When fungi are seasonally less abundant they will dig for roots, tubers and bulbs (Christensen 1980). Woylies are also known to feed on sandalwood seeds and to bury, or cache, these for later use (Murphy *et al*. 2005). In their home range of 2-12 ha woylies construct nests to sleep in during the day, by carrying sticks, bark and leaves with their prehensile tail (Christensen 1980; Hide 2006). Nests are commonly located underneath the skirts of *Xanthorrhoea* bushes (Christensen 1980). Under suitable conditions, woylies are continuous breeders and females may produce three mature pouch young per year (Christensen 1980; de Tores and Start 2008).

### *Study site*

This study was conducted at Whiteman Park (-31.83S, 115.94E), which is located 15 km north-east of the city of Perth on the Swan Coastal Plain, Western Australia. This area experiences a mediterranean climate with cold-wet winters and warm-dry summers and an annual rainfall of 690 mm to 700 mm, and during 2010 the area was experiencing a particularly dry winter (BOM 2010). In 2010 Whiteman Park contains nearly 4000ha of remnant bushland, surrounded by industrial and residential development. The soils of the park are the heavily leached Bassendean sands (Whiteman Park 2003). The vegetation includes *Banksia menziesii* dominated heathlands, open Eucalypt woodlands of jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) and dense *Melaleuca rhaphiophylla* swamps (Whiteman Park 2003). Areas within Whiteman Park were cleared for the grazing of cattle during the 1930s to 1940s, but these cattle were removed when the Western Australia Planning Commission purchased the land in the 1970s (Whiteman Park 2003). The park has since been managed for conservation and revegetation of cleared land is conducted annually. Whiteman Park is a recreation and education facility as well as an important conservation park on the Swan Coastal Plain.

In 2009 to 2010 a 50 ha electric fenced, predator-proof reserve (woodlands reserve) was established within Whiteman Park for the reintroduction of native marsupials (Fig. 1). A one ha soft release enclosure was built in the south of the woodlands reserve and was the site of release for eight woylies in March 2010. The vegetation within the woodlands reserve is open woodland and can be grouped into four dominant vegetation types. These are; dense *Melaleuca* woodlands on the western edge, open *Banksia* and sheoak woodlands in the centre, open jarrah/marri woodlands to the east and also areas of open grasslands which were previously cleared for farming (Fig. 2). Four quadrats (20 m x 25 m) were randomly placed within each of the four habitat types (Fig. 1). *Xanthorrhoea preisii* is a common understorey species to all the vegetation types, except the *Melaleuca* habitat where the dense canopy only allows for a sparse undergrowth of sedges. Annual weed species are common in the woodlands reserve and include capeweed (*Arctotheca calendula*), cape tulip (*Moraea miniata*), and wild oats (*Avena fatua*). Vegetation in the woodlands reserve was last burnt in patches during spring 1981 and summer 1987-1988 (Whiteman Park 2010). During July 2010, revegetation was conducted in the open areas on the western side of the reserve. The soil within the woodlands reserve comprises Bassendean sands, though the amount of organic matter in the soil varies in the different habitats with *Melaleuca* soils being particularly moist and peaty.

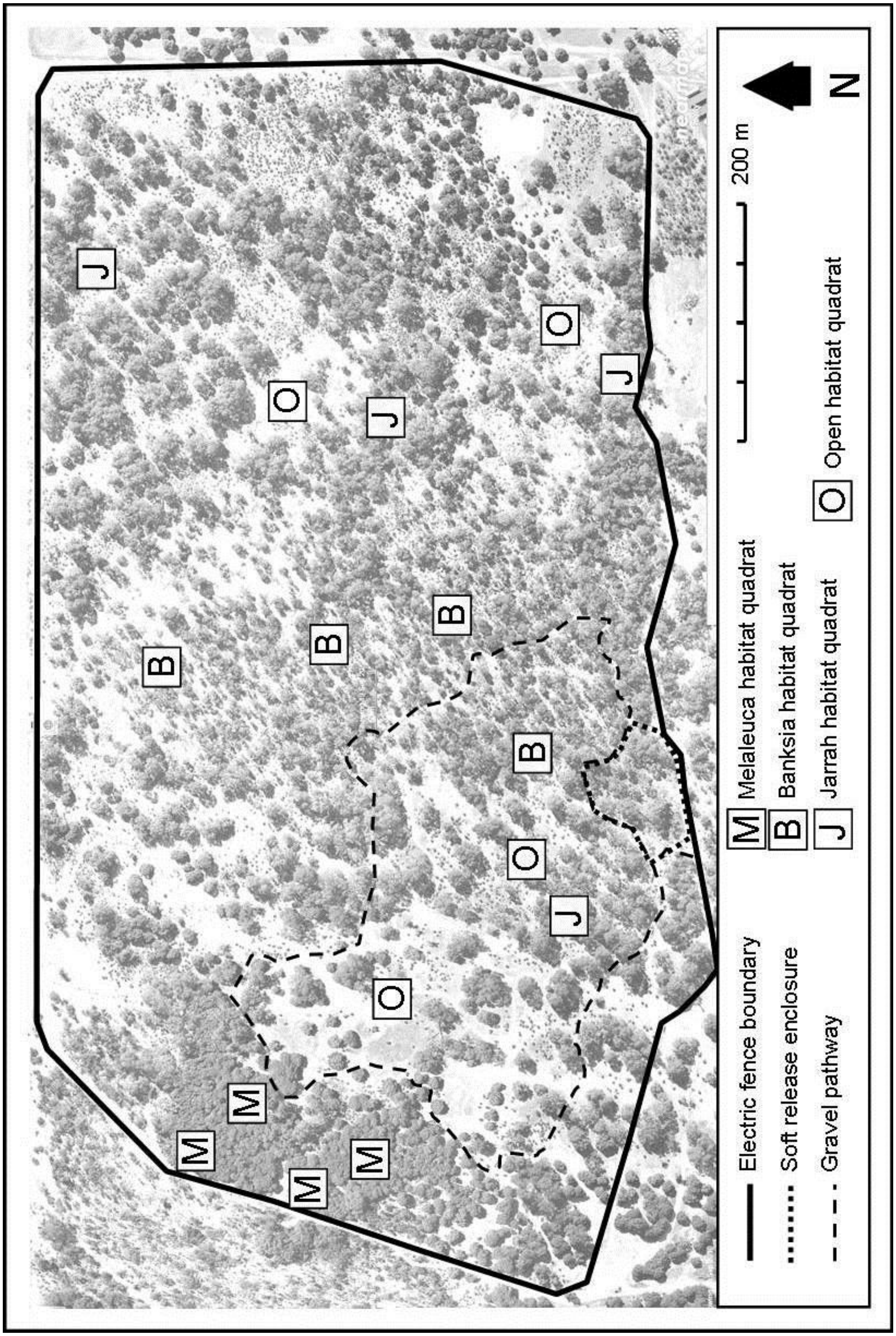

**Figure 1:** Aerial photograph of the Woodland reserve at Whiteman Park, WA showing the electric fence surrounding the reserve, the smaller soft release enclosure within and the path.

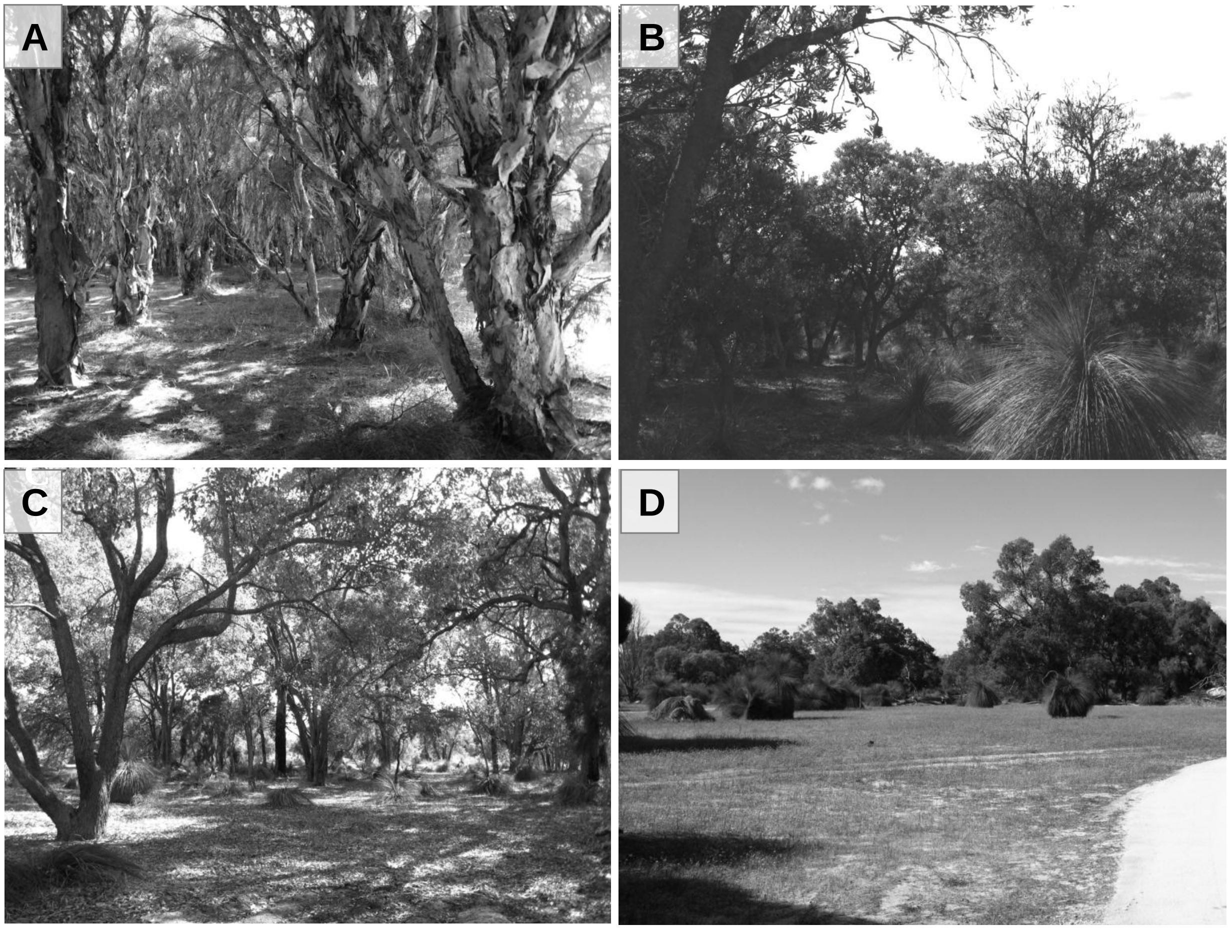

**Figure 2:** The four vegetation types in the Woodland reserve at Whiteman Park. A – melaleuca, B - jarrah/ marri, C - banksia and D - open.

### *Digging rates and soil turnover*

To estimate the digging rates of woylies and how it changed over time, the number of woylie diggings were counted in six 10 m x 2 m transects placed randomly within the soft release enclosure. After the release of eight woylies on the 23rd March 2010, diggings were counted every 4-10 days in each transect and filled in after each counting session for four months. This provided an estimate of the number of new diggings as a function of time. Woylie diggings differ in size and depth and small diggings are indistinguishable to those made by southern brown bandicoots (*Isoodon obesulus fusciventer*). While most diggings in the soft release enclosure were made by woylies, southern brown bandicoots were also present, though these animals make far fewer and significantly smaller diggings (Triggs 2004). Soil turnover was estimated by collecting the soil heap from 15 diggings of varying sizes. Soil was air dried and dry weight obtained to establish the average weight of soil turned over by woylies.

### *Soil water repellency*

Soil water repellency was measured using the Molarity of Ethanol Droplet test (MED) developed by King (1981). Droplets of ethanol solution at increments of 0.2 M are added directly to the soil and the molarity of ethanol that penetrates into the soil surface within 10 seconds is the measure of soil water repellence, or MED rating. Soils with MED ratings of 0-1.0 are classified as low water repellent, 1.2-2.2 are moderately repellent, 2.4-3.0 are severely water repellent and ratings above 3.0 are extremely water repellent (King 1981). Surface soil was gathered from 5 random locations in the soft release enclosure by collecting 10 cm x 10 cm areas to a depth of 1 cm. These soil samples were air dried and lightly sieved to remove material greater than 2 mm diameter. Five determinations of MED were conducted on each sample and the mean obtained. To measure the soil water repellency of woylie diggings, the MED test was applied to soil *in situ* (Garkaklis *et al.* 1998, 2000). Soil water repellency was measured on strategic positions common to each digging by gently removing leaf litter and debris from the soil (Fig. 3). Measures of soil water repellency are affected by soil water moisture and temperature, with MED values being highest on cool, wet soils (King 1981). Where possible soil water repellency was only measured during dry periods and after the soil had two to three days to dry after rain.

Woylies remained within the soft release enclosure during the period of my study so I used simulated diggings to measure how digging activity effects soil water repellency in each of the four habitat types. Garkaklis *et al*. (2000, 2003) used simulated woylie diggings, all to a depth of 10 cm to estimate soil water repellency and nutrient leaching over time at Dryandra woodland in the Western Australian wheatbelt. I established three 10 cm deep simulated woylie diggings in each of the habitat quadrats, giving 12 diggings per habitat type. The soil water repellency of each simulated digging was obtained on fresh and week old diggings according to the procedure used by Garkaklis *et al.* (1998, 2000). The soil water repellency of the top soil was also measured by collecting two top soil samples from each quadrat and air drying soil before measuring MED (King 1981). To gain an estimate of organic matter cover between habitat types, the litter depth and per cent litter cover was measured in six 1m$^2$ areas placed randomly within each quadrat in September 2010.

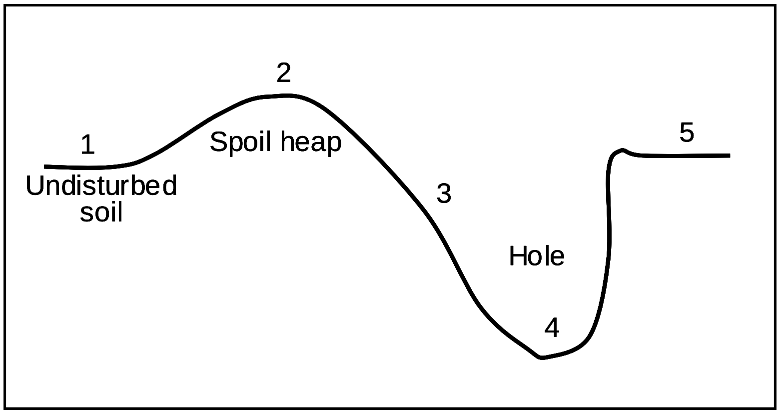

**Figure 3:** A typical woylie, Bettongia penicillata, digging showing points common to all diggings at which mean in situ water repellence is reported. 1, Soil surface; 2, spoil heap; 3, back-wall mid-point; 4, bottom of digging; 5, front of digging. Adapted from Garkaklis *et al.* (1998).

### *Fungi surveys*

The species richness and abundance of sequestrate fungi was surveyed within each of the four habitat types in the reserve in August and September 2010. Hypogeal fungi occur mostly under leaf litter but some species occur as deep as 10-15 cm under the soil surface (Bougher and Syme 1998). Fungi were surveyed by raking the soil and leaf litter to a depth of 15 cm with a three-pronged garden hoe for 100 person minutes in each habitat quadrat. The GPS coordinates of each fungi body was recorded and fungi were collected for processing and identification. Each fungi body was photographed and then air dried. Spores were examined under a compound microscope at 1000x magnification to identify fungi to genus and species level where possible. Fungi was identified using Bougher and Syme (1998) and Bougher (2009) and species identifications where confirmed by N. Bougher.

### *Data analysis*

Data analysis was conducted in Microsoft Excel and GenStat (version 11). A Bartlet's test for homogeneity of variances was conducted on the data and residual plots observed for normality prior to analysis of variance being conducted. All data were normally distributed and variances were homogenous, making analysis of variance (ANOVA) the appropriate statistical test to use. Single-factor ANOVA, with habitat type as the independent variable, was conducted on leaf litter depth and per cent litter cover. A single-factor ANOVA was also used to compare soil water repellency between positions in woylie diggings. Nested ANOVA was conducted on the top soil MED ratings with the samples and quadrats nested within habitat types. Within each habitat type fresh and week-old simulated woylie diggings were compared across the five digging positions using single-factor ANOVA.

## Results

### *Digging rate and soil turnover*

The total number of new woylie diggings increased from 0.4 diggings per night in the first two weeks after the woylies were released on the 23rd March 2010, to an average of six diggings per night in the following two months (Fig. 4A). Similarly the annual digging rate in 1 ha increased by 10 fold after the first two weeks, reaching a peak of 53,229 digs individual$^{-1}$ year$^{-1}$ in mid April, then remaining between 22,000 – 14,000 digs individual$^{-1}$ year$^{-1}$ for the remainder of the survey period (Fig. 4B). This equates to a digging rate of 47 ± 18 diggings individual$^{-1}$ night$^{-1}$ in a 1 ha area. The peak in digging rate on the 17 April is due to the short time period between that and the previous counting session when compared to the time period between other counting sessions (Fig. 4). The average annual soil turnover rate was 8.0 ± 2.6 tonnes woylie$^{-1}$ year$^{-1}$.

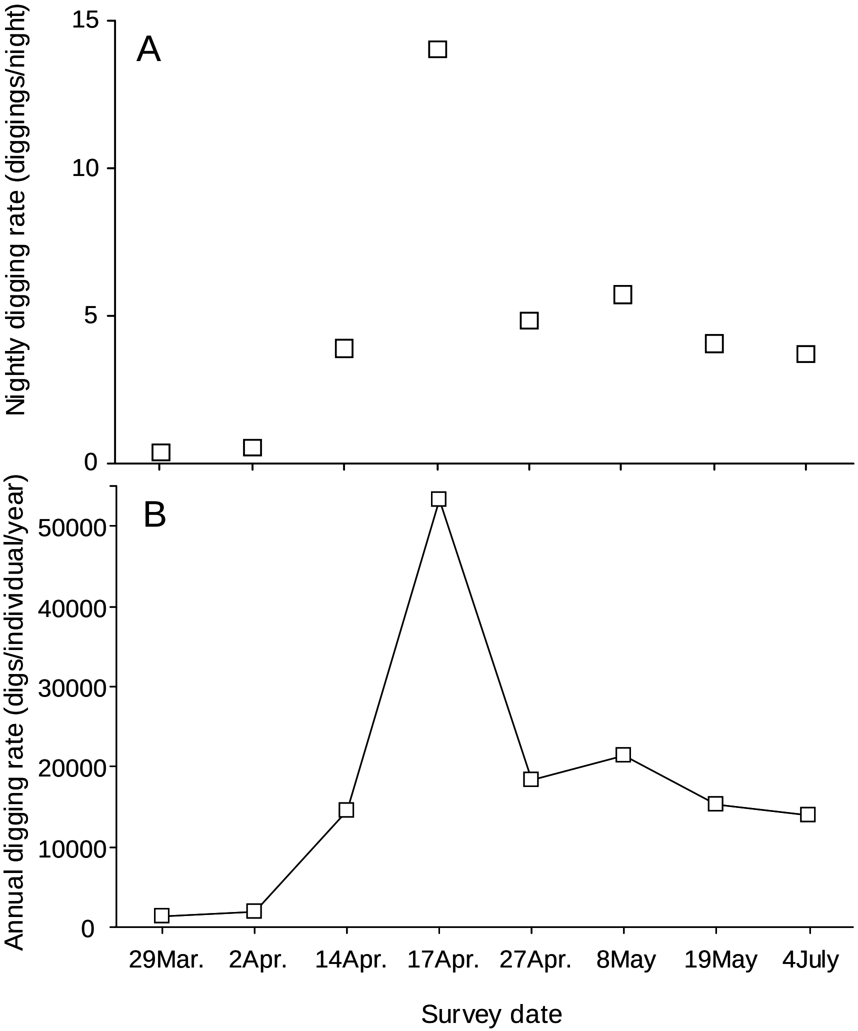

**Figure 4:** The nightly digging rate of woylies (*Bettongia penicillata ogilbyi*) in the 120 $m^2$ survey area (A), and the annual digging rate for woylies per hectare (B), at Whiteman Park on the Swan Coastal Plain, WA.

### *Soil water repellency*

In the soft release enclosure the water repellency of air dried topsoil was very low (MED = 0 ± 0, n = 16). However, the water repellency of topsoil *in situ* was severe, (MED = 2.25 ± 0.27, n = 32). The mean water repellency of subsurface soil was 43% lower than the mean surrounding surface soil (p = 0.021, Fig. 5). Subsurface soils exhibited a low to moderate water repellency while surface soils were moderate to severe. The position in the digging with the lowest soil water repellency was the spoil heap with a low mean MED value of 0.9 ± 0.28.

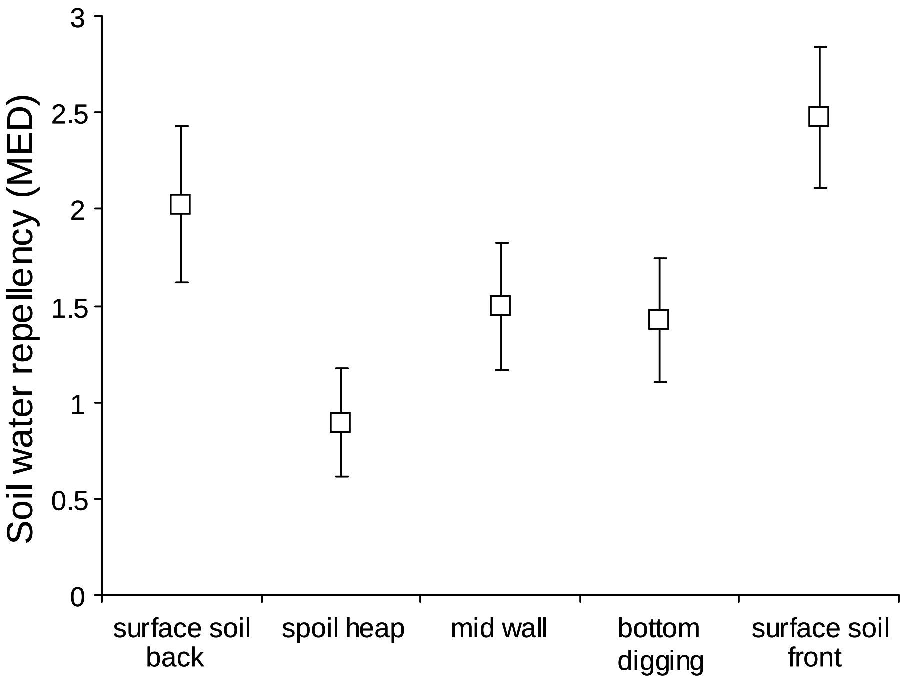

**Figure 5:** The mean soil water repellency (with standard error bars) measured in woylie (*Bettongia penicillata ogilbyi*) diggings in the soft release enclosure at Whiteman Park on the Swan Coastal Plain, WA.

### *Topsoil and organic matter*

The water repellency of air dried top soils significantly differed between habitat types and there was no significant variation between the four quadrats within habitats ($p<0.001$ and = 0.45, respectively). Jarrah habitats had severely water repellent soils, while banksia, melaleuca and open habitats had low soil water repellency ($p<0.001$, Table 1). Leaf litter depth and cover significantly differed between the four habitat types and no variation existed among quadrats within habitats. The mean leaf litter depth was highest in the jarrah quadrats, melaleuca and banksia were intermediate and open quadrats had the lowest litter depth (Table. 1, $p<0.001$). This trend was the same for the leaf litter cover, with jarrah habitats containing 88% leaf litter per square metre compared to just 13% for the open habitats (Table 1, $p<0.001$).

**Table 1:** Water repellency (mean ± standard error), litter depth (mean ± standard error) and leaf litter cover (mean ± standard error) measured in six one square metre areas in the four habitats at Whiteman Park, WA.

| Habitat | Water repellency (MED rating) | Litter depth (cm) | Litter cover (%) |
|---|---|---|---|
| Melaleuca | $0.36 \pm 0.097^{a}$ | $2.6 \pm 0.37^{ab}$ | $86.4 \pm 5.30^{ab}$ |
| Banksia | $0.94 \pm 0.119^{a}$ | $2.0 \pm 0.40^{a}$ | $71.4 \pm 5.98^{a}$ |
| Jarrah | $2.4 \pm 0.032^{b}$ | $3.8 \pm 0.33^{b}$ | $88.1 \pm 4.72^{b}$ |
| Open | $0.4 \pm 0.11^{a}$ | $0.56 \pm 0.11^{c}$ | $13.1 \pm 1.96^{c}$ |

Superscripts, a, b, and c indicate significant differences between the habitats

### *Simulated woylie diggings and soil water repellency*

Simulated woylie diggings caused a significant reduction of soil water repellency in jarrah habitats, where surface soil water repellency was moderate to severe on fresh diggings (MED = 2.1 ± 0.32) and subsurface soils were completely hydrophilic (MED = 0, $p < 0.001$, Fig. 6A). A similar pattern occurred in both melaleuca and banksia habitats where diggings decreased water repellency, but this was not significant as all soils were low to moderately repellent (Fig. 6A). Open habitats exhibited the opposite trend with water repellency being higher inside the fresh diggings compared to the surrounding surface soil ($p = 0.009$).

While diggings immediately reduced water repellency of subsurface soil, after a weeks time water repellency increased inside the diggings. After the melaleuca diggings had decayed over a week, the water repellency of surface and subsurface soils had increased to moderate, except the spoil heap, which remained significantly low ($p<0.001$, Fig. 6B). Similarly in jarrah habitats all subsurface soil water repellency increased within a week, especially the bottom of the digging which became moderate and significantly higher than the other low repellent sub-surface soils ($p<0.001$, Fig. 6B). There was no change in soil water repellency over time in banksia and open habitat diggings (Fig. 6B).

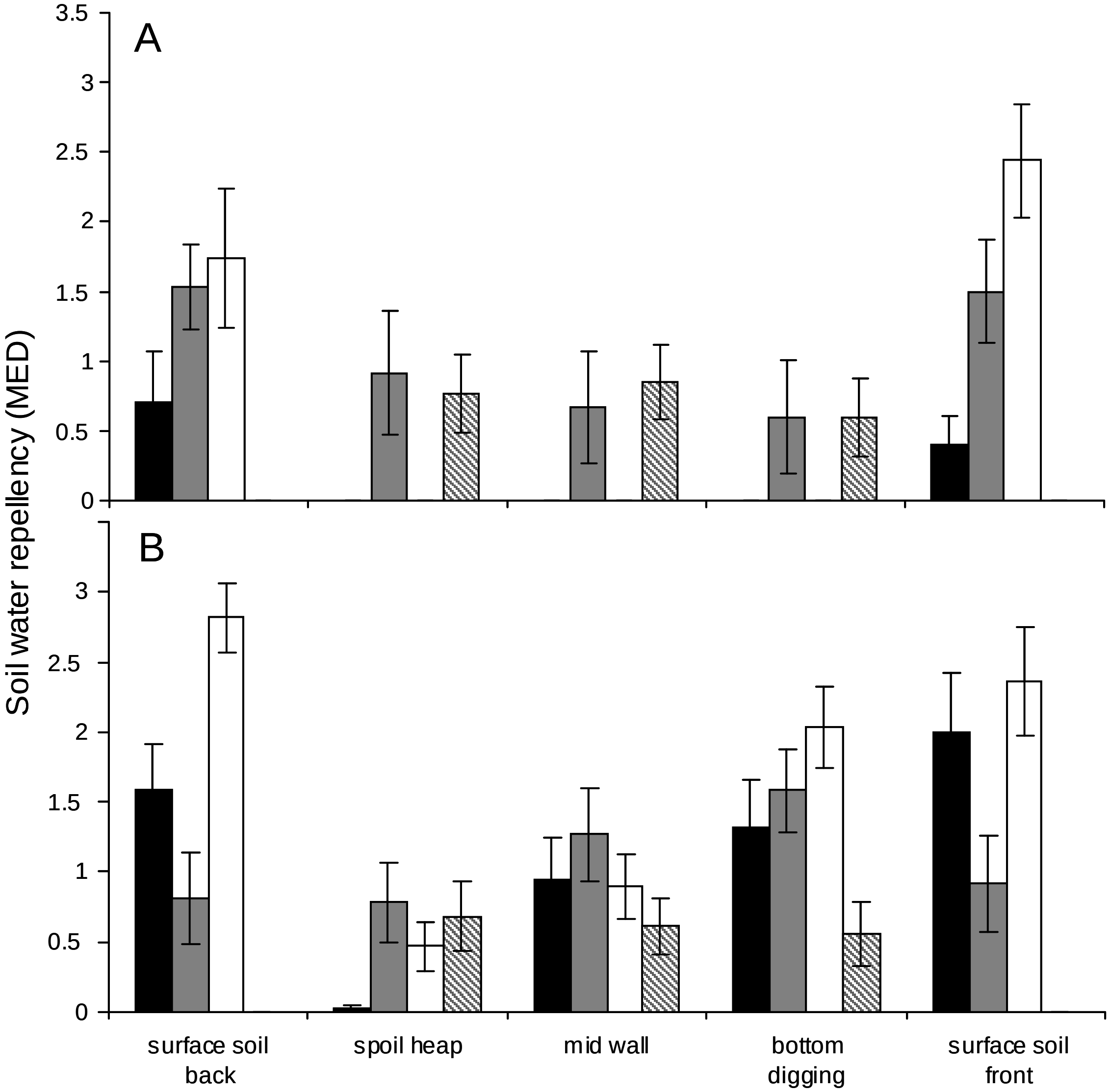

**Figure 6:** The soil water repellency (with standard error bars) measured on the five locations in the digging profile on fresh (A) and week old (B) simulated diggings in melaleuca (black), banksia (grey), jarrah (white) and open (hatched) habitats in Whiteman Park, WA. Note, where soil water repellency was completely hydrophilic (MED = 0 ± 0) the data does not appear on graphs.

### *Fungi*

Fungi surveys in August and September 2010 revealed over 11 different species of fungi in the survey area. Of these five were only identified to genus level and one was an unknown fungi. This included seven aboveground (epigeous) fruiting fungi and four underground (hypogeous) fruiting fungi (Table 2). Most epigeous fungi were found in the melaleuca habitat and included the decomposing *Aleurina ferruginea*, *Entoloma* sp., and the mycorrhizal species *Laccaria lateritia*, *Cortinarius phalarus* and *Ramaria* sp. The puffball fungi *Scleroderma cepa* was common to all habitats but most abundant in the melaleuca habitat with 80 % of the specimens collected there. *Phallus hadriani*, a decomposing stinkhorn, was found under litter in the banksia habitat in its pink staining egg stage. This stage resembles a truffle and later a long stem erupts with putrid slime at the apex. At least three different truffle species were uncovered during the surveys in the melaleuca, jarrah and banksia habitats. An underground member of the *Scleroderma* genus with a black tar-like interior occurred throughout the melaleuca habitat and was often found partially excavated by mammals. These excavated specimens had often been nibbled by animals and were infested with small white grubs. This species was also located in one of the jarrah quadrats, though it was close to a *Melaleuca rhaphiophylla* tree. Another truffle species of the genus, *Descomyces*, was found in patches of two to six fruiting bodies in two of the jarrah quadrats. This is a small white truffle and common to most *Eucalyptus* forests worldwide. A different species of the small white truffle genus, *Cystangium*, was found in two of the banksia quadrats and has not been found at Whiteman Park before. The only fungal species found in the open quadrats was the puffball, *Scleroderma cepa* and this was close to a *Xanthorrhoea* bush. All melaleuca quadrats contained truffles, but only two Banksia and two jarrah quadrats contained truffle fungi.

**Table 2:** Species list of the fungi found during August and September 2010 at Whiteman Park, WA.

| Fungi species | Form | Number found | Habitat(s) found |
|---|---|---|---|
| *Aleurina ferruginea* | Cup | >50 | melaleuca, jarrah |
| *Laccaria lateritia* | Mushroom | >20 | melaleuca |
| *Entoloma* sp. | Mushroom | 1 | melaleuca |
| *Ramaria* sp. | Coral | >30 | melaleuca |
| *Cortinarius phalarus* | Mushroom | 1 | melaleuca |
| *Scleroderma cepa* | Puffball | 10-15 | melaleuca, banksia, jarrah, open |
| *Descomyces* sp. | Truffle | 4 patches | jarrah |
| *Cystangium* sp. | Truffle | 2 | banksia |
| Underground *Scleroderma* sp. | Truffle | 4-6 patches | melaleuca, jarrah |
| *Phallus hadriani* | Phalloid | 2 patches | banksia |
| underground ascomycete | Truffle? | 1 | banksia |

## Discussion

The spatial distribution of underground fungi at Whiteman Park was limited by the distribution of woody vegetation which was in concordance with my hypothesis. Underground fungi occurred in jarrah, banksia and melaleuca habitats, but not open habitats, which presumably lacked vegetation necessary to form mycorrhizal associations with fungi. Once woylies are released into the woodlands reserve, the location of diggings should follow the distribution of fungi. Hence, woylies should spend less time foraging in the open habitats compared to the other woodland habitats.

At Perup, in the southern jarrah forests of WA, woylies preferred habitats with 50% understorey shrub density and 20-40% open spaces as they require cover to shelter from predators and to nest in during the day (Christensen 1980). This suggests that woylies will remain in habitats with *Xanthorrhoea preisii* as this is the most widespread understory species in the woodlands reserve and woylies have been known to use this species to nest in (Christensen 1980). However a recent study at Karakamia sanctuary, near Chidlow, a 270 ha predator-proofed reserve, has shown woylies forage in open paddock areas at much higher densities than in dense vegetation (Eikelboom 2010). At Scotia sanctuary in New South Whales, a 4000 ha fenced, predator free reserve, woylies foraged more under canopy cover and in deeper leaf litter than expected, presumably due to the higher amounts of fungi occurring amongst litter and close to vegetation (Pizzuto *et al.* 2007). In the absence of predation by foxes, woylies forage where food is abundant and due to the very high densities of woylies at Karakamia this includes exposed habitats (Eikelboom 2010). At Whiteman Park, possible predators of woylies include brown goshawks (*Accipiter facciatus facciatus*), southern boobook owls (*Ninox novaeseelandiae ocellata*) and wedge-tail eagles (*Aquila audax*), all observed in the park during the study and known to take bettongs (Richards and Short 1998; Priddel and Wheeler 2004). These predatory birds are likely to occur at high densities at Whiteman Park due to the abundance of rabbits. The melaleuca habitat lacked understory cover of *Xanthorrhoea preisii*, but the dense canopy of *Melaleuca rhaphiophylla* would reduce the risk of areal predation. In addition, the melaleuca habitat contained the highest abundance and species diversity of fungi, indicating higher food availability for woylies in this habitat. It is therefore likely that woylies will forage mostly in melaleuca, jarrah and banksia habitats and avoid open habitats due to the lack of food occurring there.

Simulated woylie diggings decreased soil water repellency in the melaleuca, jarrah and banksia habitats, but not the open habitat, which supported my hypothesis. The soil in jarrah habitats showed the greatest response to the simulated woylie diggings with reductions of soil water repellency inside the digging being much greater than in melaleuca and banksia habitats. Jarrah habitats also had the highest leaf litter accumulation and most water repellent topsoil. Organic matter from plants and fungi is one of the primary causes of soil water repellency and larger volumes of leaf litter increase the total organic matter in the soil (Roberts and Carbon 1972; King 1981). Sandy soils are more likely to be water repellent as the finite amount of organic matter present is able to coat more sand grains with a low surface area to volume ratio than an equivalent amount of fine particulate soil such as clay (Doerr *et al.* 2000). The soils in the melaleuca habitat contained peat which is much finer grained than the white Bassendean sands and water repellency was lower in these soils. Banksia habitats had the same soil type as jarrah, but the top layers of the soils contained a dense root mass. Organic matter from leaves and roots are the main causes of water repellency in soils, but in this case it appears that the organic matter from the highly resinous and waxy *Eucalyptus* leaves contributes to soil water repellency more than the root matter of the *Banksia* trees (Doerr *et al.* 2000). Open habitats with very little organic matter had very hydrophilic soils; but, woylies are less likely to forage in open habitats due to the lack of fungi and increased risk of predation in the open areas. On the Swan Coastal Plain, habitats with large amounts of leaf litter are more likely to have moderate to severely water repellent soils, and woylie diggings are likely to have a greater effect at reducing soil water repellency.

After a week the accumulation of organic matter in woylie diggings caused water repellency of subsurface soils to increase and become similarly repellent to the surrounding topsoil. The spoil heap remained the lowest area of water repellency in the digging profile as the soil was still quite aerated, though the underlying undisturbed soil would still be water repellent (Garkaklis *et al*. 1998). The increased severity of water repellency in woylie diggings over time indicates that they will only reduce soil water repellency for a short period. Several days after the digging has been made it will no longer allow for the preferential flow of water into the soil. Garkaklis *et al*. (2000) observed soil water repellency on woylie diggings as they decayed over two years at Dryandra woodland, WA. Over this time, water repellency inside the woylie diggings increased from low to severe as organic matter accumulated within them (Garkaklis *et al*. 2000). On the Swan Coastal Plain this process appears to be accelerated due to the loose nature of sandy soil and the manner it attracts a coating of organic matter. To have a significant and ongoing effect on facilitating water flow into Swan Coastal Plain soils on an environmental scale, woylies will need to be continuously active in the same area over time.

The reduction in soil water repellency from diggings by woylies on the Swan Coastal Plain will depend on the seasonal and local abundance of underground fungi as this will determine the level of digging activity. The abundance and spatial distribution of hypogeous fungi is affected by season, vegetation associations and disturbances such as fire, with fungi abundance being higher during wet periods and after fire events (Christensen 1980; Johnson 1994a; Johnson 1995; Johnson and McIlwee 1997; Bougher and Syme 1998; Vernes *et al.* 2001, 2004). At Whiteman Park the distribution of underground fungi was highly inconsistent, and most quadrats did not contain specimens. Woylies are likely to focus their foraging and digging on highly localised patches where fungi are abundant, such as the melaleuca habitat. Therefore, the effect of woylie diggings on soil water repellency will be restricted to small patches where fungi occurs and will probably not have a significant effect on the wider Swan Coastal Plain environment. The effect of woylie diggings is not limited to soil water repellency and includes the channelling and cycling of nutrients, litter and soil displacement, soil heterogeneity and the regeneration of vegetation and fungi (Garkaklis *et al*. 1998, 2000, 2003).

I hypothesised that woylie digging on the Swan Coastal Plain would reduce soil water repellency to a greater extent than what was reported by Garkaklis *et al*. (1998, 2000) at Dryandra woodland. My results indicate that this was not the case, as top soils at Whiteman Park had low to moderate water repellency, except in the jarrah habitat, compared to the severely repellent soils at Dryandra woodland (Garkaklis *et al*. 1998, 2000). These differences can be attributed to the vegetation present in each habitat type. I found severe water repellency in the jarrah habitat, with jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) as the dominant species. At Dryandra woodland the vegetation is dry sclerophyll *Eucalyptus* woodland, comprised of *E.*

*accedens*, *E. wandoo*, *E. marginata* and *C. calophylla* (Garkaklis *et al*. 1998). The vegetation at Dryandra woodland and Whiteman Park jarrah habitats contain two of the same dominant tree species, and *Eucalyptus* are known to create severe water repellency in soils due to the high amount of resins, waxes and aromatic oils in their leaves (Doerr *et al.* 2000). This similarity in habitat is most likely what elicited the same response of soils, at both locations, to woylie diggings where soils went from severe to low water repellency inside diggings. Therefore, it appears that water repellent soils will exhibit the same response to woylie diggings at Dryandra woodland only if the vegetation is dominated by *Eucalyptus* species.

The soft release enclosure in the woodlands reserve contained a mixture of jarrah and banksia habitats and my *in situ* surface soils were severely water repellent; however, the water repellency of air dried topsoil was hydrophilic, the same as open habitats. These conflicting results could be a reflection of the high levels of disturbance occurring in the vicinity of the soft release enclosure during 2009 and 2010. Construction of the woodlands reserve and soft release enclosure included the establishment of electrical fencing dug into the ground, buried pipelines for the sprinkler system, underground electrical cables for lighting, gravel pathways and revegetation work (C. Rafferty pers. comm.). This construction activity, coupled with the high density of woylies and bandicoots in the small enclosure probably led to the mixing of surface and subsurface soil layers, creating water repellent patches in subsurface soil (Garkaklis *et al*. 2000). Woylie diggings in the soft release enclosure only decreased water repellency from severe to moderate; however, I was unable to measure water repellency on diggings as soon as they were dug and even though only notably fresh diggings were used those sampled may have been a few days old. As soil water repellency quickly increases after a digging has been made this may explain why woylie diggings in the soft release enclosure did not reduce soil water repellency to low, as I had expected.

The digging rate of woylies increased after they were released and became comparable with that reported for woylies at Dryandra woodland, indicating that the captive reared woylies adapted to the wild after the first few weeks (Garkaklis *et al*. 2004). Soil turn-over by woylies at Whiteman Park was higher than the average reported by Garkaklis *et al*. (2004) and could reflect the ease at which sand is dug compared to the heavily textured soils at Dryandra woodland. Therefore, it appears that captive reared woylies are suitable for release into a natural environment that is predator free, as they are able to adapt and learn to dig for fungi quite quickly. The woylies at Whiteman Park were given supplementary feed of root vegetables, nuts and omnivore pellets (C. Rafferty pers. comm.). This was necessary as the soft release enclosure was small (one ha) and it was assumed that it could not provide enough food for eight woylies and several bandicoots. However, my study has demonstrated that underground fungi are sparse and rare in the woodlands reserve, indicating that supplementary feeding may have to continue once woylies are released into the woodlands reserve. It is possible that woylies may supplement their diet with the roots and bulbs of perennial herbs and weed species, as excavated and consumed bulbs of cape tulip were observed in the soft release enclosure. Analysis of scat contents of woylies once released into the woodlands reserve should reveal the importance of fungi and other food sources in the diet, as well as fungi species diversity.

My study has further investigated the species of fungi present at Whiteman Park since the 2006 surveys. While most of the species I found were already known to occur at Whiteman Park, I uncovered three underground fungi species and two aboveground species not previously known in the area. Of the fungi, *Scleroderma cepa* and the *Ramaria* sp. are possibly toxic to woylies (Bougher and Syme 1998). Zorsky *et al*. (2010) found 32 spore types in woylie scats at Karakamia sanctuary in Chidlow, far more than the possible nine species woylies may consume at Whiteman Park. Woylies are primarily mycophagists and fungi comprise over 70% of their diets (Christensen 1980; Zorsky *et al*. 2010). The low abundance of fungi at Whiteman Park may reflect the low rainfall over the study period, as many species of fungi fruit after rain and during wet conditions (Bougher and Syme 1998). Some species of underground fungi fruit after fire, and it has been 23 years since the last fire in the woodlands reserve (Christensen 1980; Johnson 1995; Verens *et al.* 2001, 2004). Underground fungi are now known to occur in many patches of urban vegetation in Perth, though the abundance has not been estimated at most sites (Bougher 2009).

While my study only found four species of underground fungi at Whiteman Park, I surveyed just a small fraction of the total possible habitat available. Claridge *et al*. (2000a) established that 50 m x 20 m quadrats and surveying for 100 person minutes would return the optimal number of hypogeous fungi. The chance of finding no fungi in small plots is high due to the patchy distribution of fungi in the environment (Claridge *et al*. 2000a). My quadrats were half the size so that four could fit inside the small area of melaleuca habitat available (Fig. 1). As such, it is likely that my surveying has provided a conservative estimate of the total number of underground species of fungi present in the woodlands reserve. To fully determine the diversity and seasonal abundance of fungi at Whiteman Park, surveys need to be conducted seasonally for several years, and scat contents of woylies should also be analysed.

Translocations of another critically endangered marsupial the Gilbert’s potoroo (*Potorous gilbertii*), which consumes over 90% underground fungi, have occurred in the south west of WA in the past five years (Nguyen *et al.* 2005). The Gilbert’s potoroo was only known from one location in Two People’s Bay Nature Reserve on the south coast of WA, and was translocated to another mainland site and Bald Island near Albany, WA (Bougher and Friend 2009). After two years, scat content analysis revealed potoroos on Bald island to be consuming over 20 species of fungi and 14 species were being consumed by potoroos at the mainland site (Bougher and Friend 2009). Gilbert’s potoroo were able to adapt to new environments with differing vegetation from the Two People’s Bay site as adequate fungi was available. Woylies have also been introduced to islands off the coast of South Australia and historically occurred on St Francis Island (Robinson and Smyth 1976; Start *et al*. 1995). These introductions were a success primarily due to the absence of feral predators, but also indicate that woylie populations, like Gilbert’s potoroo, can establish in new environments and will readily seek out fungi after release.

Woylies at Whiteman Park are likely to spend more time foraging in the woodland habitats as these contain the highest abundance of underground fungi. Simulated diggings have shown that woylies can reduce soil water repellency from severe to low in habitats with large accumulations of leaf litter. Therefore, woylies are likely to have a more prominent affect on the environment in these habitats, by reducing soil water repellency in patches where fungi occurs and dispersing seeds and fungal spores into new areas of the reserve. This study has provided a conservative estimate of fungi species abundance during a dry year and it is likely that this environment may yield more resources to woylies in better conditions. The successful introduction of eight captive-reared woylies into the soft release enclosure shows how quickly this species can adapt to the wild, giving a good indication that they will survive once released into the woodlands reserve. Also the establishment of woylie populations on offshore islands, which may have reduced abundances of underground fungi, shows that this species can adapt to altered resource availability. Establishing a breeding population of woylies at Whiteman Park is important for woylie conservation, as the only other healthy population of woylies in WA is at Karakamia. If the woylie population at Whiteman Park is able to flourish, then other reserves on the Swan Coastal Plain with predator-free fencing or predator control programs, can be considered as suitable translocation sites. However, introduced populations of woylies will have to be carefully monitored to ensure the animals are able to find enough food and that their foraging does not have unforseen impacts on the fungi species present on the Swan Coastal Plain. If survival of woylie populations is dependant on supplementary feeding future translocations should not be considered. The establishment of additional populations of woylies in other areas of WA, and Australia are integral to the conservation of this species as future climate change may significantly alter the abundance of fungi in some area and by increasing the woylies current range we can provide a more hopeful outlook at species survival.

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Fourth Year Project Literature Review
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# Mycophagy in Australian mammals: Environmental implications

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# Table of Contents

# 1. Abstract

Underground (hypogeous) fungi occur in association with plants and are consumed by mycophagous mammals. In Australia where the soils are nutrient poor, there is a high diversity of hypogeous fungi which forms an important food item for marsupials in the family Potoroidae. Potoroids are important vectors for spore dispersal of hypogeous fungi and may help to accelerate habitat regeneration after fire as they inoculate plants with fungal spores in their scats. The consumption of hypogeous fungi by potoroids varies with season, vegetation characteristics, landscape position and soil type. Potoroids alter the soil profile with their diggings, increasing water infiltration into the soil, nutrient leaching and the accumulation of organic matter and fungal hyphae. The woylie (*Bettongia penicillata* Gray 1837), is a mycophagous marsupial with a distribution that is now restricted to reserves in the south-west of Western Australia. Woylie activity affects the environment by altering soil water repellency, through digging, and dispersing native plant seeds in 'caches'. Woylie populations have declined because of land clearing, introduced predators and disease, leaving many ecosystems without this important disperser of spores and seeds. In the past, translocations of woylies have tended to fail due to predation, but it is also important to assess the habitat suitability and abundance of hypogeous fungi before translocating. A predator-free reserve in Whiteman Park, on the Swan Coastal Plain, is now home to eight translocated woylies, though the suitability of the habitat and woylie impact on the environment is unknown. I hypothesise woylies will forage according to the distribution of fungi within the habitat and their diggings will increase water infiltration into the soil.

# 2. Introduction

Australia is an ancient country with heavily weathered soils that are low in nutrients, especially nitrogen. Many native plants, especially *Eucalyptus* species have formed symbiotic relationships with mycorrhizal fungi to help them take up the little nutrients available in the soil (Johnson 1996). The fruiting bodies or sporocarps of ectomycorrhizal fungi fruit underground. Where this underground, or hypogeous, fungi occurs in Australia, it forms the diet of a range of small to medium sized mammals, particularly those in the family Potoroidae (Christensen 1980; Johnson

1996; Johnson and McIlwee 1997). These mycophagous marsupials dig to uncover hypogeous sporocarps (Triggs 2004). The importance of hypogeous fungi in the diet of mycophagous mammals varies according to seasonal abundance, the occurrence of fire, vegetation and landscape patterns (Christensen 1980; Claridge *et al.* 1993 Johnson 1994a, 1995; Johnson and McIlwee 1997; Verens *et al.* 2001, 2004). Mycophagous mammals are important dispersal vectors for the spores of hypogeous fungi, as spores pass through the digestive tract and are deposited in the animal's scats within its foraging range (Christensen 1980; Lamont *et al.* 1985; Claridge *et al.* 1992; Colgan and Claridge 2002). An important tripartite relationship exists between bettongs, hypogeous fungi and fire in Australian ecosystems, as bettongs increase the rate of plant inoculation of fungal spores after fire events (Johnson 1995; Vernes *et al.* 2004).

Mycophagous mammals in Australia are important ecosystem engineers; however, many have suffered declines in their distributions since European settlement (Start *et al.* 1995; Short and Turner 1999; Nguyen *et al*. 2005). The woylie, or brushed-tailed bettong (*Bettongia penicillata* Gray 1837), has suffered similar reductions in population numbers and fenced, predator-proof reserves appear to be the only locations it can be translocated successfully (Start *et al.* 1995; Wayne 2008). Woylies play an important role in the environment by facilitating the dispersal of fungi and some plant species as well as altering soil characteristics with their diggings (Christensen 1980; Garkaklis *et al.* 1998, 2000, 2003; Murphy *et al.* 2005). The decline of woylies from their previous range has important implications in the dispersal of fungi and seedling recruitment in locations where the woylie are now locally extinct.

In this review, I give a brief history of woylie biology and declines in Western Australia. I highlight the importance of mycophagous mammals in the dispersal of hypogeous fungi and how the dietary composition and foraging activity of these mammals is affected by environmental factors. I discuss how digging by these animals can alter the environment, particularly focussing on their effect on water flow into the soil. Using the evidence given I provide hypotheses regarding the impact that woylies will have on the Swan Coastal Plain.

## 3. Woylie biology and conservation

The woylie is a small mycophagous mammal in the Family Potoroidae, within the superfamily Macropoidea, and are endemic to Australia (de Tores and Start 2008). Woylies are nocturnal and feed predominantly on underground (hypogeous) fungi, which they locate by smell and excavate by digging (Christensen 1980; Lamont *et al.* 1985; Lee 2003; Garkaklis *et al.* 2004). These animals have evolved large cutting premolars to break open the tough outer shell of fungi sporocarps (Keast 1968). Woylies reside in nests during the day, which they build by carrying sticks and leaves with their tail. These nests are commonly located underneath *Xanthorrhoea* bushes (Christensen 1980). Under suitable conditions, woylies are continuous breeders and females may produce three mature pouch young per year (Christensen 1980; de Tores and Start 2008). The woylie is currently classified as critically endangered by the IUCN redlist criteria (Wayne *et al.* 2008). Like other Australian marsupials that fall into the critical weight range, woylies are especially susceptible to predation by introduced foxes and cats (Burbidge and McKenzie 1989).

### *3.1 Distribution and declines*

The historical distribution of woylies includes most of mainland Australia, but like many other medium sized marsupials in Australia, the woylie has suffered declines in its distribution since European settlement (Fig. 1; Start *et al.* 1995). These declines have been attributed to habitat reduction by land clearing, predation from introduced predators, competition with feral herbivores, and more recently disease, most importantly *Toxoplasma* and *Trypanosoma* (Start *et al.* 1995; de Tores and Start 2008; Wayne 2008). Conservation efforts in the past have included translocating woylies to areas of suitable habitat where they had become locally extinct, or were present in very low numbers, which has included the establishment of several island populations (Delroy *et al*. 1986). Many of the translocations to mainland sites were unsuccessful due to predation by foxes and cats, as well as the recent onset of disease (Short *et al.* 1992; Wayne 2008). Woylies now only occur in a few locations in the south-west of Western Australia, and some translocated populations in eastern Australia (Start *et al.* 1995). Fenced, predator-proof areas of suitable habitat for woylies are important for the conservation of this species, and to extend its possible distribution (Start *et al.* 1995).

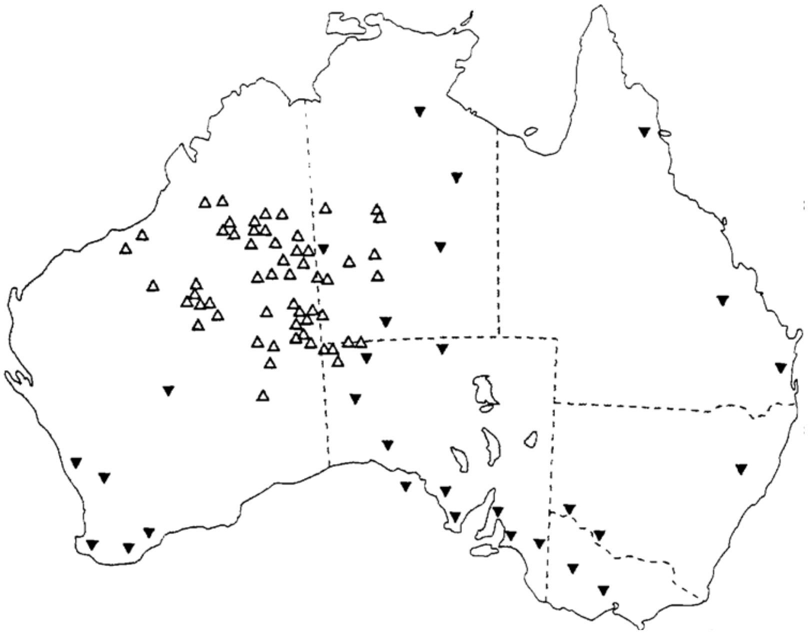

**Figure 7:** Historic distribution of woylies (*Bettongia penicillata*) from Finlayson (1985) ▼, and Aboriginal records, ∆. From: Start *et al*. (1995).

Declining, yet significant, populations of woylies in the south west of Western Australia occur in Dryandra Woodland, Perup, Tutanning and Batalling where the population is particularly low (Fig. 2; Start *et al.* 1995; Wayne 2008). The only stable population of woylies in the south-west of WA occurs at the Australian Wildlife Conservancy's Karakamia sanctuary near Chidlow (Wayne 2008). Successful translocations of woylies have only occurred when the threat of predation has been removed and fenced reserves are considered the only viable locations for translocation. It is unknown whether such fenced, predator free reserves on the Swan Coastal Plain will support a population of woylies due to the sandy soil and coastal vegetation. In the mid 1990s a small group of woylies were illegally released at Port Kennedy, south of Rockingham WA, and subsequently starved to death due to the coastal environment lacking hypogeous fungi (P. Mawson pers. comm.). However, it is unknown whether other areas on the Swan Coastal Plain, further east, could provide woylies with enough suitable food. The availability of resources has also been suggested as a factor contributing to woylie declines, with large-scale fungi now surveys being conducted in the Perup region of Western Australia, to test this hypothesis (Rodda *et al*. 2008). The suitability of the Swan Coastal Plain for translocated woylie populations needs to be assessed in terms of hypogeous fungi abundance, to estimate translocation success.

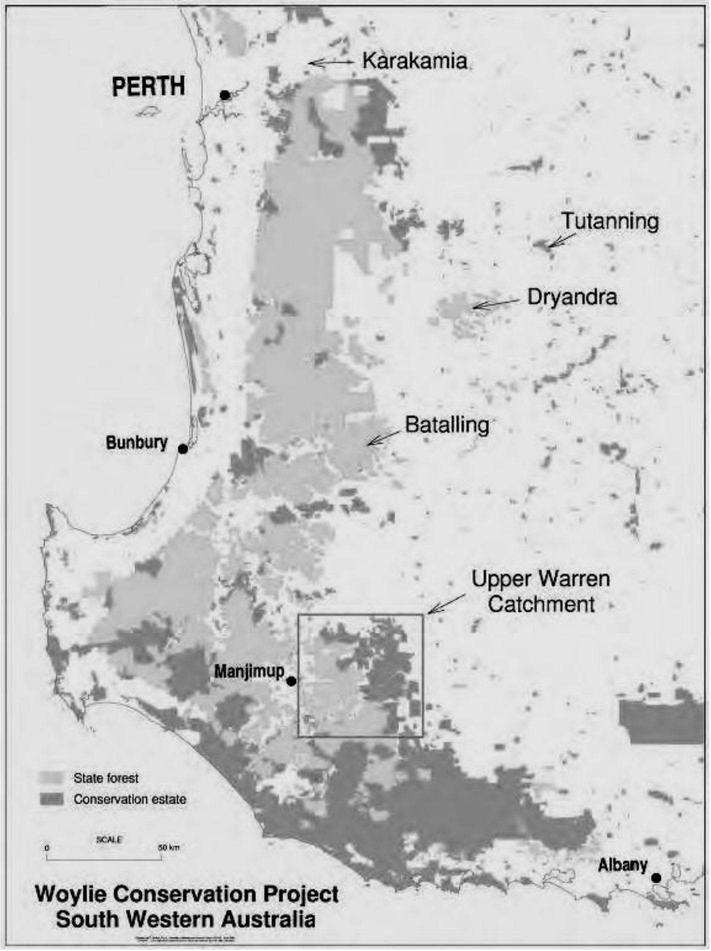

**Figure 8:** The distribution of important woylie populations in the south-west of Western Australia. From Wayne (2008)

## 4. Mycophagy in mammals

Where hypogeous fungi occur in the environment, they commonly form part of the diet of small mammals (Johnson 1996; Bertolino *et al.* 2004). Most species that consume hypogeous fungi, such as the northern brown bandicoot and red squirrel, are not purely mycophagous and tend to consume hypogeous fungi as an alternative food source, when abundant (McIlwee and Johnson 1998; Bertolino *et al.* 2004). However, many marsupials in the family Potoroidae (bettongs and potoroos) appear to be primarily mycophagous with hypogeous fungi comprising 50-90% of the diet (Christensen 1980; Taylor 1992; Johnson and McIlwee 1997; McIlwee and Johnson 1998; Vernes *et al.*2001; Nguyen *et al.* 2005). The fruiting bodies of hypogeous fungi, sporocarps, emit a strong odour that is easily located by foraging mammals (Donaldson and Stoddart 1994).

The sporocarps of hypogeous fungi have a low nutritional value for small hindgut fermenting mammals, as they are unable to transform non-protein nitrogen into useable forms and many of the nutrients are passed undigested (Cork and Kenagy 1989). Therefore, hypogeal fungi are usually consumed by hindgut fermenting species when abundant due to the low energetic cost of location and excavation of sporocarps (Claridge and Cork 1994; McIlwee and Johnson 1998). Other foods, including; fruit, grass and invertebrates are also consumed by hindgut fermenters to fulfil their nutritional requirements (McIlwee and Johnson 1998; Bertolino *et al.* 2004). Potoroid marsupials are mammals with foregut fermentation and are therefore able to extract more of the available nutrients from hypogeous fungi, than the smaller hindgut fermenting species (Claridge and Cork 1994; Johnson 1994b; Jonson 1996). Bettongs and potoroos are able to digest the nutrients contained in the cell walls of sporocarps using fermenting bacteria in the forestomach, while animals with more simple digestive tracts are not able to utilise the potential energy from hypogeous fungi (Claridge and Cork 1994). Johnson (1998) found hypogeous fungi provided Tasmanian bettongs (*Bettongia gaimardi*) with a surplus of the energy required for lactation, and the digestibility of nitrogen from fungi consumed by the long-nosed potoroo (*Potorous tridactylus)* was 72% (Claridge and Cork 1994). The digestibility of nitrogen from sporocarps consumed by the hindgut fermenting ground squirrel (*Spermophilus saturates*) was only 56% in comparison (Cork and Kenagy 1989). Claridge and Cork (1994) also demonstrated the metabolic energy intake of *P. tridactylus* fed on a diet of *Mesophellia glauca* was 73% of their daily field energy requirements. Though this represents only one species of fungi of the 50 known to be consumed by *P. tridactylus*, and the animals used in this study did not expend energy to obtain food, it nevertheless demonstrates that hypogeous fungi is an important food item for mycophagous marsupials. Christensen (1980) concluded *Mesophellia* sporocarps were suitable for woylies to obtain their nutritional requirements, with more nitrogen and phosphorus, and a high fat content when compared to jarrah leaves consumed by the similarly sized brush-tailed possum (*Trichosurus vulpecula*).

### *4.1 Problems associated with scat content analysis*

The diet of mycophagous mammals is most frequently determined by scat content analysis. Scats are collected by trapping the target species, and collecting scats from the base of traps. In some cases, dung beetles bury scats before they are collected by researchers which may reduce sample size (Taylor 1992). Scats are examined for macroscopic content, plant material, and microscopic content, which includes spores of hypogeal fungi. In many areas of the world the diversity of hypogeous fungi in the environment is poorly known and not all spore types in the scats can be identified, or many species may be grouped into a common 'type' due to similarities in form (Taylor 1992; Nguyen *et al.* 2005). Inadequate species identification could lead to the underestimation of different fungal species consumed, their abundance in the environment or the overall importance of fungi as a food source. Given that scats contain large quantities of low digestible material and low quantities of highly digestible material this could lead to the overestimation or underestimation of some components in the diet (McIlwee and Johnson 1998). This may be the case for hindgut fermenting species, which are unable to digest large amounts of plant and fungi material. McIlwee and Johnson (1998) used stable isotope analysis and scat content analysis to determine the diets of mycophagous mammals in Australia. They found that stable isotope analysis correlated to the data obtained from scat analysis, but were also able to examine the importance of hypogeous fungi in nitrogen and carbon assimilation compared to other foods. Therefore, scat content analysis, though it has some limitations, should provide a relatively robust idea of the dietary content of mycophagous mammals.

## 5. Consumption of fungi and environmental factors

The consumption of hypogeous fungi by mycophagous mammals is dependent on the environment. Foraging and the diets of mycophagous mammals can be determined by scat content analysis and digging activity. Digging activity can also be used to determine population size (Mallick *et al.* 1997). The foraging activity can be examined over temporal and environmental gradients by establishing fixed quadrats and transects, while seasonal fluctuations in the diet are determined by trapping animals over time and collecting scats from traps.

Ectomycorrhizal fungi are associated with particular species of symbiotic plants, usually *Eucalyptus* species, and are found in higher abundance near the host plants (Johnson 1994a). Where fungi are not distributed within the environment at random, the digging patterns of mycophagous mammals reflect this, as they do not dig at random, but when they locate sporocarps by olfactory cues (Donaldson and Stoddart 1994). Vegetation characteristics therefore determine foraging patterns by mycophagous mammals as the type of vegetation present and its structure determines the location, abundance and species of hypogeous fungi. The Tasmanian bettong (*Bettongia gaimardi*) showed higher digging densities closer to mature *Eucalyptus tenuiramus* and increasing stem density of this species (Johnson 1994a). This pattern demonstrates that food density, as shown by digging density, is directly related to stem density of *E. tenuiramus* in *B. gaimardi* habitats (Johnson 1994a). Understorey cover did not have any effect on the foraging of *B. gaimardi*, showing that food abundance is the primary factor determining foraging activity. This contrasts to woylies in Perup Western Australia, which specifically prefer habitats with over 50% understorey shrub density with 20-40% open spaces (Christensen 1980). The difference between the understorey cover preferences between these two species could be due to the threat of predation, foxes and feral cats being common in the Perup region, while absent in Tasmania at the time of Johnson’s (1994a) study. However, it is also likely that at Perup shrub density also reflects fungi abundance hence focusing woylie activity in these areas.

Position in the landscape can also alter the distribution of diggings by mycophagous mammals. Long-nosed potoroos *(Potorous tridactylus)* utilise different parts of the landscape depending on the seasonal abundance of food and had higher digging densities on sheltered mid-slope sites and gullies compared to exposed sites and ridges (Claridge *et al.* 1993). During hotter months, *Mesophellia* fungi species occur in association with *Eucalyptus* on midslopes and in wetter months the fungi *Zelleromyces daucinus,* appears to be common in gully sites (Claridge *et al.* 1993). *P. tridactylus* take advantage of the seasonal variation of fungi in their habitat by foraging over different parts of the landscape in different seasons. The diggings of woylies were most often associated with sandy-loam soils at Perup, in the southern jarrah forest of Western Australia, though this was also associated with heartleaf, *Gastrolobium bilobum,* thickets (Christensen 1980). These woylies exhibited seasonal variation in the foraging on ridges and gully sites which probably reflects seasonal abundance in hypogeous fungi. Christensen (1980) also noted woylies from Tutanning, in the central wheatbelt, had a much higher content of plant material in their diet compared to woylies from Perup. The reason for this remains unknown, but is probably due to differences in vegetation, soil type or landscape patterns.

Seasonality is probably the primary factor determining hypogeous fungi abundance and diversity. In northern Queensland, the composition of different fungal taxa consumed by the northern bettong (*Bettongia tropica*) was strongly influenced by season, although the contribution of fungi to the diet did not change over time (Johnson and McIlwee 1997; Vernes *et al.* 2001). The amount of supplementary foods, such as lily bulbs, grasses and root and tubers, in the diet of *B. tropica* reflected their seasonal abundance, with lilies being consumed more in the wet season and roots and tubers more in the dry season (Vernes *et al.* 2001). Similarly, the dietary composition of the Tasmanian bettong (*Bettongia gaimardi*) is seasonal, as the bettongs are exclusively mycophagists when hypogenous fungi is abundant during spring, but supplement their diet with other fruit, plant material and invertebrates, when these are abundant at other times of the year (Taylor 1992; Johnson 1994a; Fig. 1). The dietary composition of woylies also changes with season, with the proportion of *Mesophellia* species in the diet changing during the year, with a peak in summer (Christensen 1980).

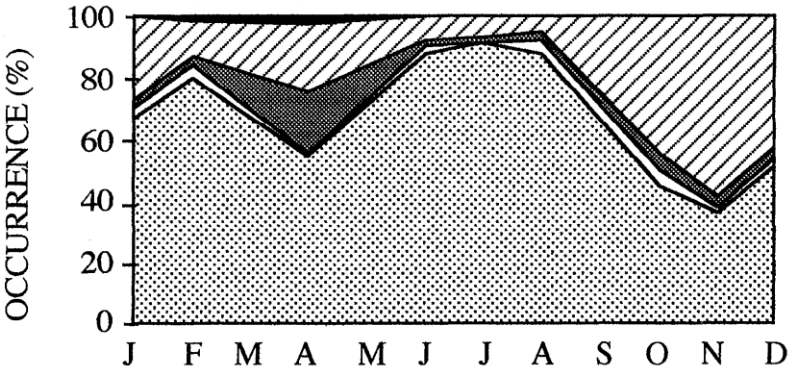

**Figure 9:** The seasonal diet composition of the Tasmanian bettong (*Bettongi gaimardi*), a typical mycophagous marsupial. Fungi (light stippling) is the prominent food source, then fruit (cross-hatching), then leaf (heavy stippling). Both invertebrates (unshaded) and tubers (filled) are consumed in low amounts. From Johnson (1994b).

Foraging activity and dietary composition are also determined by disturbances, with fire being a very prominent factor in Australian ecosystems. The effect of fire on the consumption of hypogeous fungi by potoroid marsupials has been studied for several species in Australia (Christensen 1980; Johnson 1995; Verens *et al.* 2001, 2004). Fire results in lower species diversity of hypogeous fungi at burnt sites, but hypogeous fungi is still a prominent food source in the diet of bettongs following fire (Christensen 1980; Johnson 1996; Vernes *et al.* 2001). Fire stimulates the growth of fungi in the family Mesophelliaceae, and *Mesophellia* species abundance peaks a few weeks after fire (Vernes *et al.* 2001). After fire, the digging rate of *Bettongia tropica* did not increase, instead foraging shifted from unburnt to burnt sites, exploiting the larger resource of fungi (Vernes *et al.* 2004). A similar pattern was reported in Tasmania where sporocarp production increased after fire, due to increases in the growth of fungi in the family Mesophelliaceae mainly the species of *Mesophellia*, *Castoreum* and *Nothocastoreum* (Johnson 1995). Body condition and the number of diggings by woylies increased after fire, as did the proportion of *Mesophellia* consumed, further demonstrating the pattern of increased fungal abundance after fire (Christensen 1980; Lamont *et al.* 1985).

The variation in dietary composition over landscape, seasonal and temporal scales has been studied extensively for several species of Australian mycophagous marsupials. The effect of fire and seasonal changes in the diet of woylies at Perup, Western Australia, was reported by Christensen (1980), but it is unknown whether the diet of woylies differs seasonally at other locations in the south west, including the Swan Coastal Plain. Woylies preferred to forage in the relatively fertile sandy-loam soils at Perup, and the soils of the Swan Coastal plain are infertile sands, though whether it is the soil type or vegetation associations present that determine food availability of woylies is unknown.

## 6. The role of mycophagous mammals in the ecosystem

Mycophagous mammals are the primary dispersal vectors for the spores of hypogeous fungi. As these fungi exist under the soil surface there is little opportunity for wind dispersal, and fungi rely almost exclusively on the transportation of spores by mammals (Johnson 1996). Mycophagous mammals consume hypogeous fungi sporocarps, which includes the structure containing spores. These spores survive the digestive process and are dispersed in the animal's scats, providing spores with added nutrition (Christensen 1980; Lamont *et al.* 1985; Claridge *et al.* 1992; Colgan and Claridge 2002). Dung beetles may also assist by burying the mammal scats under the soil surface, hence allowing fungal growth and reducing the risk of desiccation (Christensen 1980; Johnson 1996). Since fungal sporocarps are associated with the roots of host plants, for example

*Eucalyptus* species, foraging by bettongs is concentrated about these areas, ensuring that fungal spores are deposited close to suitable habitat (Johnson 1996). Mycophagous mammals provide an efficient form of spore dispersal as these mammals have large foraging ranges (woylie 2-12ha, Christensen 1980; Hyde 2006) and are able to disperse fungi much larger distances than wind (Johnson 1996).

This co-evolutionary relationship between mycophagous mammals and hypogeous fungi is especially important for habitat regeneration after fire in Australia. Since fire promotes the fruiting of fungi in the family Mesophelliaceae, this in turn increases the foraging by potoroid marsupials (Christensen 1980; Johnson 1995; Vernes *et al.* 2004). This process results in the rapid dispersal of ectomycorrhizal fungi into burnt habitat, facilitating habitat regeneration as the process of inoculation of plants with ectomycorrhizal fungi is accelerated (Johnson 1995). Hypogeous fungi have a high nitrogen content, and in the infertile soils of jarrah forest, this is especially important, as the stimulation of fungal growth after fire contributes significant nitrogen to the ecosystem (Christensen 1980; Johnson 1995).

The dispersal activity of mycophagous mammals is not just limited to the spores of hypogeous fungi. Woylies in the south west of Australia have been observed to partake in seed caching behaviour (Christensen 1980; Murphy *et al.* 2005). Woylies collected *Gastrolobium* seed and wheat from traps, which they randomly buried, presumably for later excavation (Christensen 1980). Woylies were also found to be important vectors in the dispersal of sandalwood *Santalum spicatum*, which have large seeds that can only be dispersed by animals (Murphy *et al.* 2005). There were significantly more sandalwood seedlings and saplings further from the parent plant in Dryandra Woodland, where woylies are present compared to Wickepin, which is further inland than Dryandra, where woylies are extinct. Seed caching behaviour of *S. spicatum* seeds was directly observed by Murphy *et al.* (2005), with woylies burying seeds in random locations, and consuming some of the seeds. Woylies appear to be important in the seed dispersal of *S. spicatum*, possibly explaining the reductions of sandalwood recruitment in areas where the woylie has become extinct.

Not only do mycophagous mammals in Australia play an important part in dispersal and habitat regeneration after fire, their diggings create a disturbance to the soil which is an important environmental process. Diggings create heterogeneity in the soil profile and alter other soil characteristics (Garkaklis *et al.* 1998). As woylie diggings decay, organic matter accumulates inside them as well as fungal hyphae, allowing a redistribution of nutrients under the surface layer of the soil (Garkaklis *et al.* 2000). In environments where the soil is water repellent, animal diggings can create areas of higher water infiltration and allow water to penetrate under the top layer of soil (Fig. 2; Garkaklis *et al.* 1998, 2004). The heightened water infiltration lead to increased leaching of soil nitrate, ammonium and sulfur in Dryandra woodland (Garkaklis *et al.* 2003). These nutrients were found at lower concentrations inside decaying diggings due to leaching use by fungi and bacteria that grow inside diggings (Garkaklis *et al.* 2003). In these two studies, Garkaklis *et al.* (2000, 2003) used simulated woylie diggings to obtain the exact age of the digging; however, this procedure may have yielded results exhibiting less variation than would occur naturally inside real woylie diggings.

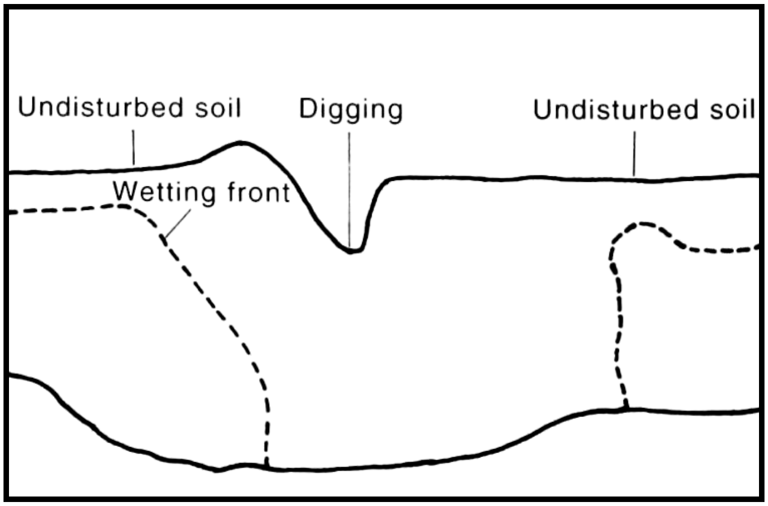

**Figure 10:** The pattern of water infiltration after rainfall inside the digging of a woylie (*Bettongia penicillata*).

## 7. Soil water repellency in Australian soils

Soil water repellency occurs when water does not freely drain into the soil but remains on the surface. This phenomenon is caused by water repellent, hydrophobic, substances, which are layered on top of or mixed with water loving, hydrophilic substances (Doerr *et al.* 2000).

Hydrophobic components in the soil are composed of organic matter from decaying plant material, fungal hyphae, and microorganisms (Roberts and Carbon 1972; King 1981). Generally, the more humus present layered on top of the soil the higher the water repellency. Most Australian soils are prone to a degree of soil water repellency, due to *Eucalyptus* having a high amount of resins, waxes and aromatic oils (Doerr *et al.* 2000). King (1981) also reported severe to extreme water repellency of soils under *Xanthorrhoea* bushes. Soil water repellency tends to be more severe in sandy soils, as the individual grains have a low surface area to volume ratio and the finite amount of organic matter is able to coat more grains than clay based soil (Doerr *et al.* 2000).

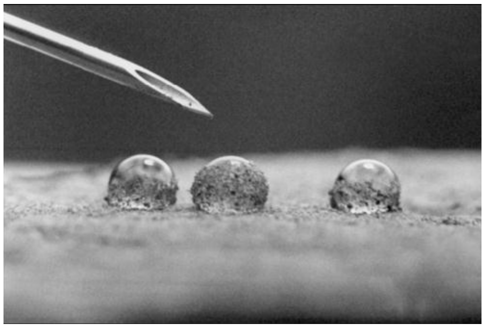

**Figure 11:** Soil water repellency; water droplets remaining on the surface of an extremely water repellent soil, a hypodermic needle is shown for scale. From Doerr *et al.* (2000).

One method of measuring soil water repellency is the molarity of ethanol droplet (MED) technique by King (1981). Droplets of ethanol solution at concentrations of 0.2 M increments are added to the soil and the molarity of ethanol to penetrate into the soil surface within 10 seconds is the measure of soil water repellence. Soils with a low MED have low water repellency and the higher the MED the more water repellent, and MED values of over 3.5 M are extremely water repellent (King 1981). Measures of water repellency are affected by soil water moisture and temperature, with MED values being highest on cool, wet soils. Therefore, to standardise measurements, King (1981) suggested all measures of soil water repellency should be conducted on oven or air-dried soils, otherwise soils measured during winter will appear more water repellent.

Garkaklis *et al.* (1998, 2000) have reported the effect of woylie diggings on soil water repellency at Dryandra Woodland, in the wheatbelt. In this ecosystem, soil was severely water repellent averaging 2.5 M, and woylie diggings created patches of lower water repellency, average 0.4 M

(Garkaklis *et al.* 1998, 2000). Garkaklis *et al.* (1998, 2000) measured water repellency *in situ*, indicating that temperature and soil moisture at the time of measurement were not standardised, possibly increasing the variation of the results. Water repellency was measured in 20 simulated woylie diggings as they decayed, and after three years, soils returned to the severe level of repellency of the surface soil (Garkaklis *et al.* 2000). The increased water repellency inside the diggings over time was due to the accumulation of organic matter and the growth of fungal hypae (Garkaklis *et al*. 2000). However, only 20 simulated woylie diggings were used in this study, a relatively low sample size considering the relative ease of constructing simulated diggings compared to locating a large number of natural woylie diggings of known age. A larger sample size would have been wise, to account for spatial and temporal variation, as well as the accumulation of different materials inside the digging.

## 8. Conclusion

Hypogeous fungi occur in nutrient poor environments where it forms symbiotic relationships with plants. These plant and fungal associations are common in Australia where the soils are infertile and low in nitrogen. The fruiting bodies of hypogeous fungi, sporocarps, form the diet of mycophagous mammals, which must excavate these by digging. Animals that consume hypogeous fungi are important vectors for the dispersal of fungal spores. Without these mammals, dispersal and recruitment rates of ectomycorrhizal fungi might be much lower, possibly reducing the nutrients available to plants.

Mycophagous marsupials in Australia, in the family Potoroidae, occur in the many environments where hypogeous fungi exist, from Tasmania, to tropical Queensland and the south west of Western Australia. These marsupials have all suffered declines in their distributions since European settlement, due to habitat loss and predation from introduced predators. The symbiotic role of mycophagous marsupial in ecosystem functioning has been lost in many areas of Australia where they are now locally extinct. The reduction of the range of the woylies in Western Australia is already believed to have reduced the recruitment of native sandalwood trees *Santalum spicatum*, as woylies are no longer present to disperse these seeds. Translocating woylies into many areas of their previous distribution is unlikely to be successful due to habitat loss, predation by foxes and the onset of disease. This makes fenced, predator free reserves integral to the continued persistence of the species.

Hypogeous fungi comprise the majority of a mycophagous mammal's diet, though this alters seasonally and with vegetation characteristics. In Perup in the south-west of Western Australia, woylies foraged over a range of vegetation types, but other species of bettongs foraging reflected hypogeous fungi abundance. The abundance and distribution of fungi on the Swan Coastal Plain is poorly known and whether woylies exhibit any patterns to their foraging remains to be determined. A fenced, predator free reserve in Whiteman Park on the east of the Swan Coastal plain exhibits a variety of vegetation types, including jarrah, *Banksia*, *Melaleuca* and open areas, all with an understorey of *Xanthorrhoea*. Since the distribution of fungi is not known for this particular reserve, it is difficult to predict which species of plant will be associated with woylie foraging. I hypothesise that woylies foraging will reflect the distribution and abundance of hypogeous fungi. The sporocarps of fungi are known to occur in patches, and woylies locate these by smell, I believe that woylie diggings will be clumped in areas where the fungi occurs and areas without fungi will be characterised by little to no diggings.

At Dryandra, in the wheatbelt, where the soils are heavily textured with a high clay content, woylie diggings reduced soil water repellency compared to the surrounding soil. Soils on the Swan Coastal plain are coarse sands, compared to Dryandra soils and are extremely water repellent. It is likely that woylie diggings will decrease soil water repellency from extreme to low by their digging on Swan Coastal Plain sands. This will then lead to the preferential flow of water into the soil.

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