Black-flanked rock-wallaby: potential for dietary competition with sympatric western grey kangaroo

Black-flanked rock-wallaby

Western grey kangaroo

(Photos: Julia Louise White)

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Author's Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

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ABSTRACT

Overabundant western grey kangaroo *Macropus fuliginosus* are known to impact agriculture, but how are they impacting threatened fauna sharing their habitat? In Paruna Wildlife Sanctuary, southwest Western Australia, kangaroos are suspected of competing with the sympatric and endangered black-flanked rock-wallaby *Petrogale lateralis lateralis*, however there is no research to support this. If kangaroos are negatively impacting rock-wallabies, kangaroo densities may need to be managed to ameliorate competitive pressures on rock-wallabies. We investigated the potential for dietary competition between *M. fuliginosus* and *P. l. lateralis* by measuring the overlap in their diets and foraging patches, as well as food resource availability. A combination of scat analysis, motion sensor camera trapping and vegetation surveys were employed. *Petrogale lateralis lateralis* diets were dominated by forbs and overlapped with those of *M. fuliginosus* which featured mostly browse and forbs (Schoener index: 0.56). Some of their shared preferred food resources were spatially and/or temporally limited. Their foraging patches also overlapped (33.9%), however these macropod species predominantly used different areas of the outcrop. Evidence over the duration of the study indicates potential for low levels of dietary competition, however the availability of shared food resources and resource partitioning suggest that *P. l. lateralis* were not being adversely impacted. In terms of the threatening processes limiting *P. l. lateralis* recovery, predation has been ranked higher than competition, a finding that is likely supported by the present study. This will likely remain true even if *M. fuliginosus* densities increase in the future. Conservation actions should therefore continue to prioritise the mitigation of predation threats to *P. l. lateralis* populations.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. GENERAL INTRODUCTION

Black-footed rock-wallabies *Petrogale lateralis* are a small to medium-sized species of macropod, of which there are three sub-species and two chromosomal races across Western Australia (WA) (Pearson 2013). All are currently threatened, with the black-flanked rock-wallaby *P. l. lateralis* listed as endangered (Department of Environment and Energy 2018). Known key threatening processes limiting the recovery of extant *P. l. lateralis* populations, in order of their significance, include predation by European red foxes *Vulpes vulpes* and feral cats *Felis catus*, habitat degradation due to weed incursion, and competition for food and refuges with introduced herbivores, namely feral goats *Capra hircus* (Burbidge et al. 2014). Furthermore, competition for food with other macropods has been identified as a potential threat (Avon Catchment Avon Catchment Council 2007; Capararo 1994; Creese et al. 2019; Read and Ward 2011).

Paruna Wildlife Sanctuary is an Australian Wildlife Conservancy (AWC) property near Perth in Western Australia that supports a translocated population of *P. l. lateralis* sourced from the Avon Wheatbelt. Maintenance of this population is a priority, but there is a paucity of information on their diet and foraging patterns, and whether sympatric western grey kangaroo *Macropus fuliginosus*, are utilising, and potentially competitively excluding them from, the same foraging resources.

This study investigated the potential for dietary competition between *P. l. lateralis* and *M. fuliginosus* by measuring dietary overlap, spatial overlap in foraging patch use, and vegetation availability. A combination of scat analysis, motion sensor camera trapping and vegetation surveys were used. This is the first study to have combined such methods to examine dietary competition. We predicted that:

- *Petrogale lateralis lateralis* and *M. fuliginosus* will exhibit some dietary overlap.

- *Petrogale lateralis lateralis* and *M. fuliginosus* will exhibit some spatial overlap in their use of foraging patches.

- *Petrogale lateralis lateralis* will predominantly forage near refuges to minimise predation risk.

2. LITERATURE REVIEW

2.1 Black-flanked rock-wallaby

2.1.1 Taxonomy and description

Petrogale lateralis consist of three sub-species: *P. lateralis lateralis*, *P. lateralis* haketti and *P. lateralis pearsoni*, and two chromosomal races: warru *P. lateralis* MacDonnell Ranges race and *P. lateralis* West Kimberley race (Pearson 2013). *Petrogale lateralis lateralis* are listed as endangered under both the federal *Environment Protection and Biodiversity and Conservation Act 1999* and state *Biodiversity Conservation Act 2016* (Department of Environment and Energy 2018).

Petrogale lateralis lateralis are dark grey-brown in colour and distinguishable by their white cheek-stripe and black feet and tail (Figure 1) (Eldridge and Close 1995; Threatened Species Scientific Threatened Species Scientific Committee 2016). Males are considerably larger than

Figure 1: Distinctive features of *Petrogale lateralis lateralis*: white cheek-stripe and black feet and tail. Photo taken at Paruna Wildlife Sanctuary (J. White).

females, weighing up to 5 kg compared to 3.8 kg for females (Eldridge and Close 1995). A suite of features enable them to swiftly navigate their rocky environments, including a strong, non-prehensile tail, powerful hind limbs, and larger hind feet, with large pads and short nails (Pentland 2014).

2.1.2 Distribution

Petrogale lateralis lateralis formerly had a wide, though patchy, distribution across WA, spanning from south of the Kimberley to southern offshore islands, as shown in Figure 2 (Pearson and Kinnear 1997). However, its distribution has severely declined since colonial settlement and the sub-species is now confined to areas of suitable rocky habitat in the Barlee, Bar Smith and Cape Ranges, Kaalpi (Calvert Range), Little Sandy Desert (Desert Queen Baths), Kalbarri National Park, Avon Wheatbelt (Nangeen Hill, Mount Caroline, Mount Stirling, Sales Rock, Tutakin Rock) and Barrow and Salisbury Islands (see Figure 2) (Burbidge et al. 2014; Threatened Species Conservation Threatened Species Scientific Committee 2016; Turpin et al. 2018).

In recent decades, populations at Durba Hills, Gardiner's Rock, Mount Shackleton and Mokenby became extinct and others were reintroduced into Avon Valley National Park, Cape Le Grande National Park, Kalbarri National Park, Paruna, Querekin Rock, and Walyunga National Park (Burbidge et al. 2014; Pearson et al. 2019; Threatened Species Conservation Threatened Species Scientific Committee 2016). The third, and most recent, translocation into Kalbarri National Park was carried out in May 2018, with animals from the largest current extant population at Nangeen Hill and Mount Caroline.
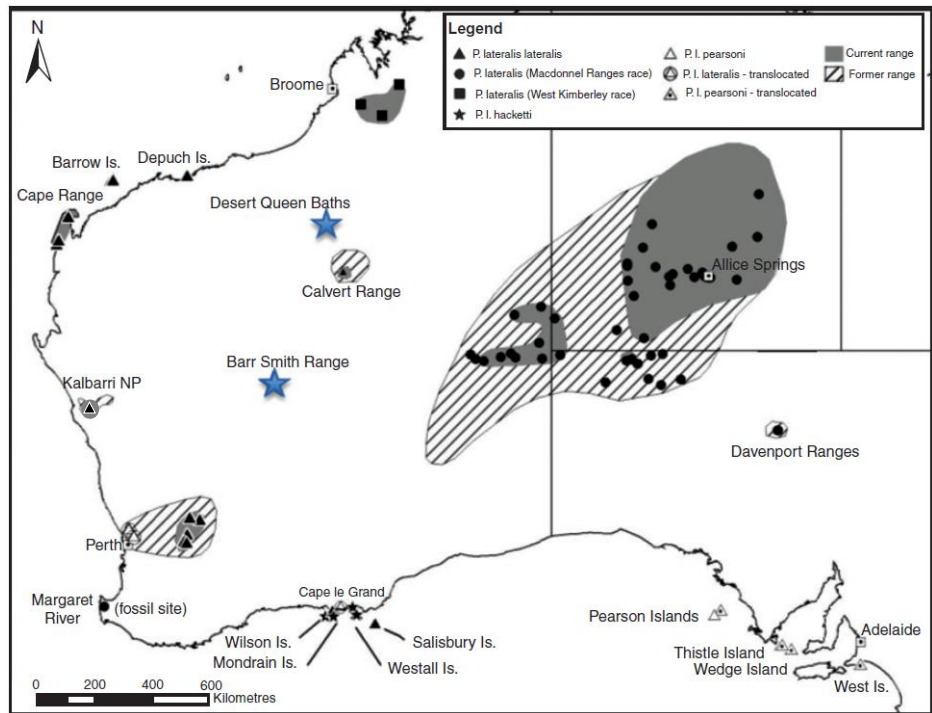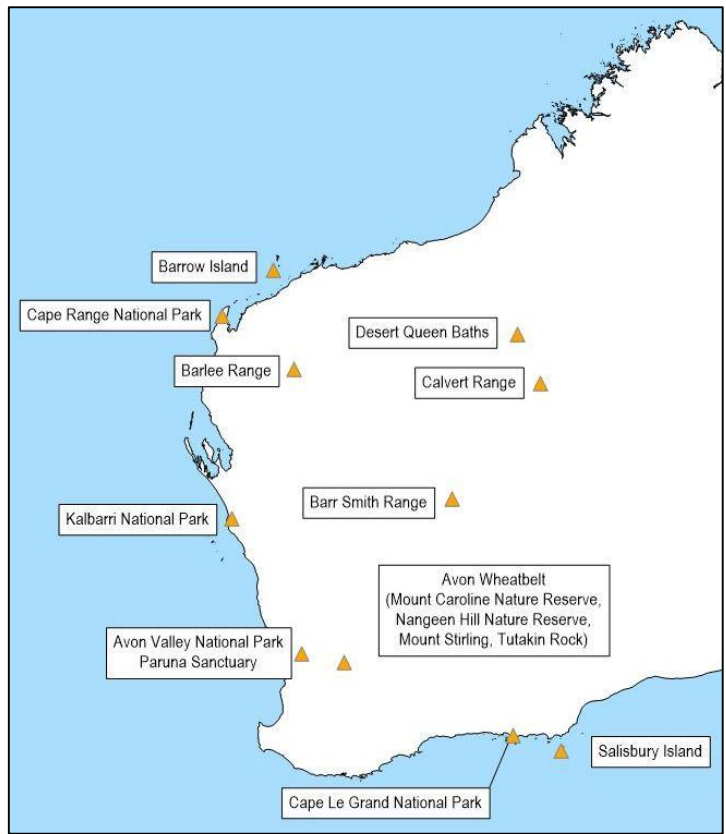
Figure 2: Distribution of *Petrogale lateralis lateralis* (triangles and blue stars) and other *Petrogale lateralis* sub-species and races, together with former ranges (hashed areas) and current ranges (solid colour) (Pearson 2013; Turpin et al. 2018).

Note: The Depuch Island population has since gone extinct.

2.1.3 Habitat requirements

Petrogale taxa differ from other macropods in that they are refuge-dependent and typically only occur in rocky habitats such as cliffs, gorges and outcrops (Tuft et al. 2011b). Rocky substrates must be structurally complex (Pentland 2014), featuring crevices, extensive multi-entranced caves and overhangs to support *P. l. lateralis* (Pearson 2013). Such features provide protection from thermal extremes and predators, with the former being especially important in times of increased light intensity (sun or moon) or wind velocity (Pentland 2014). Refuges also offer shelter from precipitation and a secure place for courtship and raising young (Pentland 2014).

Rock outcrops, with their geology, topography and superior water storage, support vegetation communities that are distinct from, and more productive than, the surrounding vegetation (Hunter and Clarke 1998). Greater water availability allows food resources for *Petrogale* taxa to persist in dry conditions for longer, thereby supporting their nutritional requirements through drought periods (Tuft et al. 2011b). Their water requirements are usually satisfied through their diet (Pentland 2014), however they will drink free water in dry conditions (Lim and Giles 1987; Pearson 2013; Pentland 2014).

In addition to the presence of rock structural components, the proximity of particular vegetation communities to refuges also determines if habitat can support *P. l. lateralis* (Chauvin 2015; Pearson 2013). Vegetation must comprise palatable grasses, herbs and forbs, and be close enough to refuges for foraging *P. l. lateralis* to evade predation (Pearson 2013).

2.1.4 Foraging and dispersal patterns

Petrogale taxa are crepuscular or nocturnal central place foragers (Sharp 2009); returning to a central location between foraging trips (Boyd et al. 2014). Consequently, they exhaust the foraging

patches closest to their central location and then progressively move to those further away until costs (time, energy and predation risk) outweigh energy returns (food quality and quantity) (Orians 1979). This strategy constrains them from choosing the optimum foraging patches (Bakker et al. 2005) that yield maximum energy returns at minimum cost (Chauvin 2015; Olsson and Bolin 2014; Pentland 2014).

A perceived risk of predation while foraging has been reported to further constrain their behaviour (Bakker et al. 2005), including the distance they travel from their refuge to forage (Banks et al. 1999) and the time they spend foraging (Jacob and Brown 2000). Pentland (2014) observed that *P. l. lateralis* at Nangeen Hill presented signs of predation-induced fear in response to predator presence (principally foxes) and reduced their foraging time and foraging range to <35 m from their refuge, despite there being superior foraging patches further away. The eradication (through baiting) and exclusion of predators (through fencing), from this location has since corresponded with an expansion in their foraging range to encompass such patches (Chauvin 2015). Burbidge (2008) suggested that absence of predators from Barrow Island was also responsible for resident *P. l. lateralis* expanding their ranges; venturing as far as 1.4 km from their refuges.

Petrogale lateralis lateralis display strong signs of site fidelity (Pentland 2014), but are also capable of independently dispersing to colonise vacant habitat (Pearson 2013). Their presence was recorded in Kokerbin Nature Reserve (Avon Wheatbelt) in 2004 (Avon Catchment Avon Catchment Council 2007) despite the population having been deemed extinct by the 1980s (Kinnear et al. 1988). Freegard and Orell (2005) determined that this was the result of a small group having dispersed 8 km from Gundaring Nature Reserve.

2.1.5 Dietary composition and selectivity

Petrogale lateralis lateralis have a specialised dentition and forestomach capable of bacterial fermentation of cellulose, which enables them to consume and digest high fibre and silica

containing plant material (Tyndale-Biscoe 2005). This provides them with the flexibility to both graze and browse on a wide range of plant groups and species (Chauvin 2015), thereby facilitating their survival in a range of habitats and climatic zones; from limestone gorges with grassland in the arid north to granite outcrops amongst forest and woodland in the temperate south.

Only two studies have directly investigated *P. l. lateralis* dietary composition (Chauvin 2015; Creese et al. 2019), with one of these also examining dietary selectivity (Chauvin 2015). Dietary compositions are spatially variable, differing between populations in the northern (Cape Range National Park) (Creese et al. 2019) and southern (Avon Wheatbelt and Avon Valley National Park) parts of WA (Chauvin 2015) (Figure 2).

Petrogale lateralis lateralis in Cape Range National Park have diets consisting of mostly dicot species (60-70%) (Creese et al. 2019), whereas those in the Avon Wheatbelt have diets comprising predominantly monocot species (66.2%) (Chauvin 2015). The diets of *P. l. lateralis* in Avon Valley National Park varied to a lesser extent, containing close to even proportions of plant classes (56.4% monocots, 42.2% dicots) (Chauvin 2015). In terms of plant functional groups, the southern populations consume predominantly grass, followed by forbs, browse, sedges and ferns (Chauvin 2015). Weed species are regularly consumed, with annual veldt grass *[1]Erharta longiflora* accounting for 28.2% of dietary intake in the Avon Wheatbelt, compared to 17.6% of false brome *Brachypodium distachyon* in Avon Valley National Park (Chauvin 2015). Cape weed *Arctotheca calendula* has also been consumed in the Avon Wheatbelt (Nangeen Hill) (Pentland 2014). The spatial variation in dietary compositions is largely due to the considerably different vegetation compositions, and accordingly food resources available, between locations (Chauvin 2015; Creese et al. 2019).

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[1]Asterisks indicate invasive weed species

Dietary compositions are also temporally variable within select populations. Rock-wallabies adjust their feeding strategies from grazing (on grasses and herbs in the wet season) to browsing (in the dry season) in response to changes in food availability around their refuges (Tuft et al. 2011b): *P. lateralis* MacDonnell Ranges race (Capararo 1994), nabarlek *P. assimilis*, short-eared rock-wallaby *P. brachyotis* (Telfer and Bowman 2006), brush-tailed rock-wallaby *P. penicillata* (Tuft et al. 2011b), and yellow-footed rock-wallaby *P. xanthopus* (Copley and Robinson 1983; Dawson and Ellis 1979). Contrastingly, *P. l. lateralis* in Cape Range National Park were instead reported to consistently consume similar proportions of plant functional groups (browse, fern/sedge, forbs, grasses, herbs and orchid/lily) across seasons (Creese et al. 2019).

Dietary preferences and availability of different plant groups determine dietary composition (Sprent and McArthur 2002). *Petrogale lateralis lateralis* in the Avon Wheatbelt and Avon Valley National Park have been reported to exhibit a degree of dietary preference, consuming a greater proportion of several monocot and dicot plant species compared with that available in the vegetation (Chauvin 2015).

2.1.6 Key threatening processes

2.1.6.1 Predation by foxes

Fox predation has been a strong driver of the decline of Australian critical weight range (0.035 – 5.5kg) mammals, including *P. l. lateralis* (Johnson and Isaac 2009; Kinnear et al. 2010; Kinnear et al. 1988; Kinnear et al. 1998). Several *P. l. lateralis* populations, including those on Depuch Island and Gardiner's Rock, were driven to extinction by fox predation and single individual foxes are capable of causing devastating effects (Short et al. 2002), initially targeting juveniles, sub-adults and females with large pouch young (Kinnear et al. 1984; Pentland 2014).

A sequence of studies determined that fox predation directly restricted the size and distribution of the Mount Caroline, Mount Stirling, Nangeen Hill, Sales Rock, Tutakin and Querekin *P. l. lateralis* populations in the Avon Wheatbelt (Kinnear et al. 1988; Kinnear et al. 1998). These populations had remained moderately static or declined from 1979 to 1982 for unknown reasons, but signs pointed to fox predation (Kinnear et al. 1988). Fox control undertaken over subsequent years (1983 to 1986) at two sites (Mount Caroline and Nangeen Hill) led to an increase in resident *P. l. lateralis* numbers, by 138 (223%), and also resulted in increased habitat use (Kinnear et al. 1988). Predictably, resident *P. l. lateralis* numbers at the two sites not exposed to fox control (Tutakin and Querekin) declined by 14 (85%) (Kinnear et al. 1988). The study was repeated from 1986 to 1990 and further population increases resulted (Kinnear et al. 1998).

Despite fox control programs at Nangeen Hill, invading foxes continued to adversely impact resident *P. l. lateralis* by generating a state of fear within them (Kinnear et al. 2010; Pentland 2014). This in turn restricted *P. l. lateralis* foraging time and foraging range, which eventually resulted in overgrazing, resource depletion and soil degradation (Kinnear et al. 2010; Pentland 2014). In response, a predator-proof fence was installed around Nangeen Hill in 2013, and all predators removed from within the enclosure, which has led to an expansion in the resident *P. l. lateralis* foraging range (R. Boyland, WWF Australia, pers. comm.; Chauvin 2015).

2.1.6.2 Predation by feral cats

Feral cat predation has surpassed fox predation to become the greatest threat to Australian critical weight range mammals (Burbidge et al. 2014). Predation of allied rock-wallabies *P. assimilis* (Spencer 1991), *P. xanthopus* (Lapidge 2000) and *P. lateralis* MacDonnell Ranges race (Read et al. 2019; Ruykys 2011; Ward et al. 2011) by feral cats has been reported, but their impact on *P. l. lateralis* is poorly documented. A study of the diets of feral cats in the Northern Territory discovered *P. l. lateralis* remains in their stomach contents (Paltridge et al. 1997), and there have been similar

findings at Mt Caroline in the Avon Wheatbelt (Hegglun 2018; H. Crawford, pers. comm.). It could not be confirmed that the cats made the kills, however they have been frequently recorded intruding into *P. l. lateralis* refuges by camera traps (Pentland 2014).

Long-term feral cat control at Kaalpi (Calvert Range, Little Sandy Desert) corresponding with increased resident *P. l. lateralis* numbers strongly suggests that feral cat predation is a restricting factor (Burbidge et al. 2014). The impact of feral cats on *P. l. lateralis* may be exacerbated through fox suppression, which reduces interference and dietary competition (mesopredator release) (Johnson 2006).

2.1.6.3 Habitat degradation due to weed incursion

Weeds have played a major role in the loss of Australia's biodiversity due to their ability to invade ecosystems and out-compete their native species, thereby altering their species' composition, function and structure (Yates and Hobbs 1997). The long-term impact of weed encroachment on *P. l. lateralis* habitat is poorly known, although a study at Nangeen Hill has shed some light (Pentland 2014). Nangeen Hill is one of several isolated pockets of *P. l. lateralis* habitat remaining after extensive clearing for agriculture in the Avon Wheatbelt. Fragmented habitats are vulnerable to weed incursion because of its increased exposure to dispersing weed seeds (Adair 1995), high edge-to-area ratio (Panetta and Hopkins 1991), and susceptibility to exogenous disturbances that promote weed establishment (Adair 1995), such as nutrient enrichment, grazing by introduced herbivores, soil disturbance, and secondary salinity (Yates and Hobbs 1997).

Heavy overgrazing by resident *P. l. lateralis* within their restricted foraging range led to the incursion of weeds (Pentland 2014). *Arctotheca calendula* and ice plant *Cleretum papulosum* rapidly outcompeted native grasses within 25 m of the refuge at Nangeen Hill and changed the vegetation structure (Pentland 2014), reducing foraging resources available to *P. l. lateralis* (Pearson 2013).

Buffel grass *Cenchrus ciliaris is another weed with the potential to impact *P. l. lateralis*, given its documented ability to also out-compete grasses and promote very hot wildfires that can destroy key food resources for *P. lateralis* MacDonnell Ranges populations (Biosecurity Biosecurity SA 2012; Read and Ward 2011). In addition to weeds, introduced herbivores also invade and adversely impact *P. l. lateralis* and their habitat (Pearson 2013).

2.1.6.4 Dietary competition with introduced herbivores

Introduced herbivores, including feral goats, feral camels *Camelus dromedarius*, European rabbits *Oryctolagus cuniculus*, and domestic sheep *Ovis aries* and cattle *Bos taurus*, have detrimentally impacted native flora and fauna across Australia. In particular, their foraging within *Petrogale* spp. habitat can promote weed incursions and also reduce food resources available to *Petrogale* spp. (Pearson 2013; Pearson *et al.* 2019). For example, feral goats in Kalbarri National Park caused vegetation communities to become dominated by plant species unpalatable to *P. l. lateralis* (Pearson 2013). This resulted in the *P. l. lateralis* population declining to near local extinction levels (Pearson 2013).

Feral goats have a competitive advantage due to their adaptability to harsh environments, versatile foraging habits (Lu 1988) and high reproductive potential (Department of the Environment 2008). Further competitive advantage comes from their having a much larger home range (Creese et al. 2019) and body size compared to *P. l. lateralis*, and the ability to feed while balancing on their hind legs, thereby accessing food at a greater range of heights from the ground (Dawson and Ellis 1979). A study in Cape Range National Park (Creese et al. 2019) suggested that exploitation and interference competition between feral goats and *P. l. lateralis* was occurring based on the significant dietary overlap recorded and an observation of goats disturbing natural *P. l. lateralis* activity. Other studies of feral goats and *P. xanthopus* in Queensland (Gordon et al. 1990) and New

South Wales (Dawson and Ellis 1979) also reported significant dietary overlap and competition across seasons, with Dawson and Ellis (1979) recording a peak in dietary overlap in the dry season.

2.1.6.5 Dietary competition with native herbivores: western grey kangaroo

Sympatric native herbivores, particularly macropods, can also be a source of competition for rock-wallabies. *Macropus fuliginosus* are sympatric with *P. l. lateralis* across their range (Morris 2000; Palmer 2017b; Pentland 2014). *Macropus fuliginosus* are large macropods, weighing up to 72 kg (Leishman 2014a), widely distributed across Australia (Dawson 2012). While the species has suffered habitat loss to cropping and urbanisation in some areas, in other areas it has increased in density from the provision of watering points, establishment of improved pasture, and

Figure 3: Distribution of *Macropus fuliginosus* (IUCN Red List 2019). *Macropus fuliginosus* have a widespread distribution, which spans the southern half of Australia, including western New South Wales and southern central Queensland (Department of Parks and Wildlife 2013) and includes areas subject to uniform or winter rainfall (Caughley et al. 1987).

suppression of dingoes *Canis familiaris* (Dawson 2012). The species occupies a broad range of disparate habitats, including forest, woodland, shrubland and heathland (Schmidt et al. 2010), and the density at which they occur is generally correlated with habitat heterogeneity (Coulson 1993). Heterogenous habitats are more likely to support their shelter and food requirements (Short et al. 1983).

Macropus fuliginosus are nocturnal foragers (Leishman 2014a); sheltering from the elements during the day, before moving to open, grassy areas to feed at night (Dawson 2012). They depend on crypsis in dense vegetation, clear lines of sight and superior speed to escape predators (Le Mar and Mcarthur 2005). The species is predominantly sedentary and has a foraging range of between 33 and 70 ha (Arnold et al. 1992), with more mobile individuals also moving greater distances; up to 85 km (Priddel et al. 1988).

Macropus fuliginosus have a specialised dentition for preferentially grazing grass, however they also consume browse and forbs (Barker 1987; Leishman 2014a). Their ability to survive on protein deficient grass and fibre rich browse has been attributed to their large size (Dawson 1989) and nitrogen recycling abilities (Hume 1999). *Macropus fuliginosus* diet consists of both monocot and dicot species (Halford et al. 1984; Norbury 1987; Wann and Bell 1997), with proportions of each group varying likely according to their relative abundance (Shepherd et al. 1997) across seasons and vegetation types (Table 1). In Victoria, grasses account for 75% of dietary intake when they dominate the vegetation. As abundance declines with changing seasonal conditions, *M. fuliginosus* accordingly switch their diets to incorporate considerably more browse and forbs (Table 1). Populations in New South Wales and Queensland exhibit similar dietary shifts (Table 1).

Table 1: Comparison of plant classes predominantly consumed by *Macropus fuliginosus* across seasons and locations

Location	Vegetation type	Season	Plant class		Reference
			Monocots	Dicots	
WA: Harry Waring Marsupial Reserve	Grass, sedge and shrub dominated associations	All seasons	✓		(Algar 1986)
WA: Whiteman Park	Eucalyptus, Melaleuca and Banksia woodlands and forest	All seasons		✓	(Wann and Bell 1997)
WA: Perup Nature Reserve	Eucalyptus open forest	Autumn to Spring		✓	(Shepherd et al. 1997).
NSW	Mulga Acacia aneura woodland	Spring	✓		(Wilson 1991)
	Arid rangelands	Winter	✓		
		Summer		✓	(Barker 1987)
QLD	Arid rangelands	Winter	✓		
		Summer		✓	
VIC	Mixed pasture	Winter	✓		(Norbury 1987)
		Summer		✓	

Dietary overlap between sympatric herbivores points to possible competition for food resources (Dawson and Ellis 1996), however it's just one of a number of influential factors at play. There must also be spatial overlap in foraging patch use, and a limited availability of preferred food resources within the vegetation, for competition to occur (Creese et al. 2019; Wilson 1991). *Macropus fuliginosus* do not experience the same spatial constraints as *P. l. lateralis*, allowing them greater access to available food resources (Tuft et al. 2011a). As such, there is potential for interspecific spatial and dietary overlap, as well as exploitation and interference competition.

Dietary and spatial overlap between *M. fuliginosus* and *P. l. lateralis* has not been investigated, despite their sharing of foraging habitat in the Avon Wheatbelt (Pentland 2014; Willers et al. 2011) and Paruna (Lin 2011; Palmer 2017a). A degree of dietary and spatial overlap is envisaged to occur, at least in the dry season, for several reasons.

First, comparison of their diets (Chauvin 2015; Wann and Bell 1997) reveals that their grass, forb and browse intakes (Table 2) follow similar temporal patterns, and include some congeneric plants. The plant functional groups consumed by *P. l. lateralis* and *M. fuliginosus* (Table 2) highlights possible dietary overlap.

Table 2: **Comparison of plant functional groups consumed by *P. l. lateralis* and *M. fuliginosus*. Data reviewed from various literature sources (Bamford et al. 2009; Barker 1987; Chauvin 2015; Creese et al. 2019).**

Plant Functional Group	*P. l. lateralis*	*M. fuliginosus*
Grasses	✓	✓
Forbs †	✓	✓
Browse	✓	✓
Sedges	✓	✓
Ferns	✓	

† Includes Plants with stellate trichomes (including Ptilotus, Solanum, Sida, and Abutilon spp.)

Second, there is dietary and spatial overlap between *P. l. lateralis* in Cape Range National Park and euro *Osphranter robustus erubescens*; another large sympatric macropod (Creese et al. 2019; Leishman 2014b). Herbivores consistently consume a number of the same plant species and exploit the same foraging patches, across summer and winter (Creese et al. 2019). Based on this, and the fact that food resources are spatially limited due to the variable vegetation structure within gorges (dense on the floor to scattered on the walls and around refuges), interspecific dietary competition could be occurring between *P. l. lateralis* and *O. r. erubescens* (Creese *et al.* 2019). Several studies have documented dietary overlap between *O. robustus* and other *Petrogale* taxa: *P. lateralis* MacDonnell Ranges race (Capararo 1994; Geelen 1999), *P. penicillata* (Tuft 2005), and *P. xanthopus* (Dawson and Ellis 1979). Dietary overlap temporally varies; being higher in winter (45%) than summer (25%) between *O. r. erubescens* and *P. lateralis* MacDonnell Ranges in the

Northern Territory (Capararo 1994). By contrast, dietary overlap between *O. r. robustus* and *P. xanthopus* in New South Wales Dawson and Ellis (1979) peaks in the dry season when vegetation conditions are poorest (39%) rather than the wet season when vegetation is most abundant.

Third, *M. fuliginosus* have dietary overlap with another sympatric small macropod; black-gloved wallaby *Notamacropus irma*(Wann and Bell 1997), as well as domestic sheep (Wilson 1991). A number of studies have reported dietary overlap between eastern grey kangaroo *M. giganteus* and sympatric marsupials: *P. penicillata* (Tuft 2005), red-bellied pademelon *Thylogale billardierii* (Le Mar and Mcarthur 2005), swamp wallaby *Wallabia bicolor* (Davis et al. 2008), common wombat *Vombatus ursinus* (Davis et al. 2008) and northern hairy-nosed wombat *Lasiorhinus krefftii* (Woolnough and Johnson 2000).

2.2 Methods of assessing aspects informing dietary competition

2.2.1 Foraging habitat use

Scat counting can be an efficient, cost-effective and non-invasive method (Garrote *et al.* 2014; Johnson *et al.* 1987) for assessing foraging habitat use by macropods as they mostly defecate while feeding (Telfer *et al.* 2006). However, this method is limited in that it depends on all scats being detectable and identifiable. This can prove difficult when groundcover is high (Woolnough and Johnson 2000), and when sympatric species have similar scat morphologies (Davison *et al.* 2002). In these circumstances, motion sensor camera trapping can be a suitable alternative (Turpin and Bamford 2015; Turpin *et al.* 2018).

Motion sensor camera trapping is equally non-invasive and a particularly effective method for detecting cryptic species or those that occur in low numbers (Doody *et al.* 2012; Turpin and Bamford 2015; Turpin *et al.* 2018). Although potentially more labour intensive than scat counting (Newey *et al.* 2015), camera trapping can collect a wider range of data pertaining to foraging activity (i.e.

temperature, time, weather and lunar phase: Reconyx 2011; Richardson *et al.* 2018), continuously over several months (Swann *et al.* 2004). Practical challenges associated with this technology can arise in the form of false positive images, devices re-setting themselves and difficulties extracting usable metadata (Newey *et al.* 2015). False negatives can also occur (Newey *et al.* 2015) when animals remain largely stationary, such as during intensive browsing sessions.

2.2.2 Dietary analysis

Several methods can be used to assess the botanical composition of herbivore diets, including scat analysis, stomach content analysis, mouth content analysis, stable isotope analysis, and direct observation of feeding. The strengths and limitations of each are discussed below and shown in Table 3.

Scat analysis is the most commonly used method and involves examining the epidermal features of undigested plant fragments in scats. It requires minimal disturbance to animals, and can therefore be broadly applied, particularly for species of conservation significance, and those prone to severe stress and capture myopathy (Wann and Bell 1997). This method has a couple of limitations. First, it again depends on the identifiability of scats of various species (Dawson and Ellis 1979). This can prove difficult when sympatric species have similar scat morphologies (Davison *et al.* 2002). Second, scat analysis relies on the assumption that epidermal tissues survive digestion (Dawson and Ellis 1979) and so the proportions of plant species found within pellets are equal to the proportions in which they were consumed (Storr 1961). The extent to which this holds true varies across plant functional groups, with the epidermis of browse (lignified), stellate plants (distinctive trichomes) and grass (silica bodies) being more resistant to digestive processes than that of forbs (Horsup and Marsh 1992), and this creates bias in estimated relative abundances of consumed plants (Creese et al. 2019).

Stomach content analysis is a similar method to scat analysis; examining the same features, although of less digested plant fragments, and so produces results that have less bias associated with the differential digestion rates of plant species (Davis et al. 2008; Sprent and McArthur 2002). The major limitation for this method is that it requires the death of the subject animal so is unacceptable for application to conservation significant species. Like scat analysis, it provides a snapshot of plant material consumed in the short term (24 to 48 hours prior to collection) (McMillan et al. 2010).

Stable isotope analysis can be used to determine the short to long term diet of herbivores based on the ratios of stable isotopes of carbon and nitrogen ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in samples of faeces (e.g. Horsup and Marsh 1992), blood and hair (e.g. McMillan et al. 2010). Plant functional groups vary in their stable isotopic signatures, depending on their photosynthetic pathways (McMillan et al. 2010), and their individual contribution to a herbivore's diet is indicated by the measured $^{13}C/^{12}C$ value (Horsup and Marsh 1992). This method can also be affected by differential digestibility if scat samples are used, although results have less bias than those of scat and stomach content analysis because the epidermis is not required for determination of plant functional group (Horsup and Marsh 1992).

Direct observation of feeding can be used in conjunction with the aforementioned methods to support findings (e.g. Creese et al. 2019; Horsup and Marsh 1992). This method is limited in that it only allows the observer to infer consumption of a particular plant functional group or species at the time of observation (McMillan et al. 2010). Furthermore, identification of different plant species while they are being eaten at night can prove difficult, with some, such as browse, being more easily identifiable than groundcover forbs and grasses (Horsup and Marsh 1992).

Table 3: Comparison of the strengths of aspects of diet analysis methods

Aspect	Method				
	Scat analysis	Stomach contents analysis	Mouth contents analysis	Stable isotope analysis	Direct observation of feeding
Precision of estimate	✓✓	✓✓✓	✓✓✓	✓✓✓	✓
Conservation significant fauna application	✓	✗	✓	✓	✓
Stress or capture myopathy prone fauna application	✓	NA	✗	✓	✓
Highly digestible plant fragment detection capability	✓	✓✓	✓✓	NA	NA
Time span	✓✓	✓✓	✓✓	✓✓✓	✓

3. RESEARCH PAPER

3.1. Abstract

Overabundant western grey kangaroo *Macropus fuliginosus* are known to impact agriculture, but how are they impacting threatened fauna sharing their habitat? In Paruna Wildlife Sanctuary, southwest Western Australia, kangaroos are suspected of competing with the sympatric and endangered black-flanked rock-wallaby *Petrogale lateralis lateralis*, however there is no research to support this. If kangaroos are negatively impacting rock-wallabies, kangaroo densities may need to be managed to ameliorate competitive pressures on rock-wallabies. We investigated the potential for dietary competition between *M. fuliginosus* and *P. l. lateralis* by measuring the overlap in their diets and foraging patches, as well as food resource availability. A combination of scat analysis, motion sensor camera trapping and vegetation surveys were employed. *Petrogale lateralis lateralis* diets were dominated by forbs and overlapped with those of *M. fuliginosus* which featured mostly browse and forbs (Schoener index: 0.56). Some of their shared preferred food resources were spatially and/or temporally limited. Their foraging patches also overlapped (33.9%), however these macropod species predominantly used different areas of the outcrop. Evidence over the duration of the study indicates potential for low levels of dietary competition, however the availability of shared food resources and resource partitioning suggest that *P. l. lateralis* were not being adversely impacted. In terms of the threatening processes limiting *P. l. lateralis* recovery, predation has been ranked higher than competition, a finding that is likely supported by the present study. This will likely remain true even if *M. fuliginosus* densities increase in the future. Conservation actions should therefore continue to prioritise the mitigation of predation threats to *P. l. lateralis* populations.

3.2. Introduction

Western grey kangaroo *M. fuliginosus* populations can reach high densities in woodlands and forests adjacent to pasture or crops (Coulson et al. 1999), especially following the suppression of dingos (Dawson 2012) and, to a lesser extent, foxes (which prey on young-at-heel: Arnold et al. 1991; Banks 2001; Banks et al. 2000; Chang 2001). This can have adverse impacts on agriculture, particularly when *M. fuliginosus* compete with sheep for food (Wilson 1991). Overabundance of kangaroos can also be detrimental for the natural environment. For example, Neave and Tanton (1989) found that *M. fuliginosus* grazing reduced the height of vegetation in Tidbinbilla Nature Reserve (Australian Capital Territory) to the extent that it was no longer suitable habitat for certain birds and invertebrates. Their large body size (weighing up to 72 kg: Leishman 2014a) lowers their predation risk, and this combined with their broad diet of grasses, forbs, browse and sedges (Algar 1986; Barker 1987; Norbury 1987; Shepherd et al. 1997; Wann and Bell 1997), gives *M. fuliginosus* a competitive advantage over smaller sympatric macropods (Tuft et al. 2011a), such as the endangered black-flanked rock-wallaby *Petrogale lateralis lateralis* (weighing up to 5 kg: Eldridge and Close 1995).

Petrogale lateralis lateralis are a small to medium-sized macropod (up to 5 kg males, 3.8 kg females: Eldridge and Close 1995) occurring in areas of suitable rocky habitat across WA (Pearson 2013). Populations of the sub-species have declined predominantly due to predation by foxes and feral cats, habitat degradation from weed incursion, and dietary competition from introduced herbivores like feral goats (Burbidge et al. 2014). However, additional dietary competition from native herbivores is suspected to also contribute. That being said, dietary competition can only occur if three aspects are observed: 1) dietary overlap, 2) spatial overlap in foraging patch use, and 3) limited field availability of preferred food resources (Creese et al. 2019; Wilson 1991).

While several studies have examined the respective diets and foraging patterns of *P. l. lateralis* and *M. fuliginosus* across their ranges (Algar 1986; Arnold *et al.* 1992; Barker 1987; Chauvin 2015; Creese *et al.* 2019; Halford *et al.* 1984; Norbury 1987; Pentland 2014; Priddel *et al.* 1988; Shepherd *et al.* 1997; Wann and Bell 1997; Wilson 1991), no studies have investigated any of the aspects informing dietary competition between sympatric populations of these species across southern Western Australia. A comparison of studies undertaken in southern Western Australia shows that *P. l. lateralis* diets are similar to those of *M. fuliginosus*; featuring the same plant functional groups, some congeneric plants, and following similar temporal patterns in terms of proportions of groups consumed across seasons (Chauvin 2015; Pentland 2014; Wann and Bell 1997).

Previous studies have reported dietary and spatial overlap between other sympatric macropods and *P. l. lateralis* or *M. fuliginosus*. Creese et al. (2019) found that *P. l. lateralis* and euro *Osphranter robustus erubescens* in Cape Range National Park consume some of the same plants and forage within the same patches. In light of food resources being spatially limited, the study suggested possible dietary competition between these two species (Creese et al. 2019). Other studies have found that *M. fuliginosus* consume a similar range of plants as black-gloved wallaby *N. irma* in Whiteman Park (Wann and Bell 1997) and *N. irma* and tammar wallaby *Notamacropus eugenii* in Perup Nature Reserve (Shepherd et al. 1997).

Petrogale lateralis lateralis are crepuscular or nocturnal central place foragers (Sharp 2009), returning to a central rock refuge between foraging trips (Boyd et al. 2014) for protection from predators and thermal extremes (Pentland 2014). Their foraging behaviour is therefore inherently restricted and can be even further constrained by a perceived risk of predation (Pentland 2014). *Macropus fuliginosus* do not face these same spatial constraints and consequently have much larger home ranges (33 to 70 ha: Arnold et al. 1992). This offers them an added competitive advantage over *P. l. lateralis*, as they are able to forage further to obtain the food they require (Tuft et al. 2011a).

Paruna Wildlife Sanctuary (Paruna) in southwest Western Australia supports a population of translocated *P. l. lateralis* that are sympatric with *M. fuliginosus*. The conservation and management of this population is dependent on reducing potentially detrimental factors, including dietary competition with *M. fuliginosus.* This study investigated the potential for dietary competition between *P. l. lateralis* and *M. fuliginosus* by measuring dietary overlap, spatial overlap in foraging patch use, and vegetation availability. A combination of scat analysis, motion sensor camera trapping and vegetation surveys were used. This is the first study to have combined such methods to examine dietary competition. We predicted that:

1. *Petrogale lateralis lateralis* and *M. fuliginosus* will exhibit some dietary overlap.

2. *Petrogale lateralis lateralis* and *M. fuliginosus* will exhibit some spatial overlap in their use of foraging patches.

3. *Petrogale lateralis lateralis* will predominantly forage near refuges to minimise predation risk.

3.3. Methods

3.3.1 Study area

Paruna Wildlife Sanctuary (31°40´S, 116°8´E) is located in the Avon Valley, ~45 km north-east of Perth in Western Australia (Figure 4). The 1,950 ha sanctuary is managed by the Australian Wildlife Conservancy and functions as a wildlife corridor between Avon Valley National Park and Walyunga National Park. Erosion of the valley slopes has resulted in shallow soils and many exposed underlying granite and dolerite dykes (Australian Wildlife Conservancy 1998). The sanctuary experiences warm, dry summers and cool, wet winters and receives an average rainfall of 655 mm (Bureau of Meteorology 2019).

Petrogale lateralis lateralis have been translocated to a rock outcrop within the sanctuary (the "release site") and have subsequently colonised a second rock outcrop (the "new site"). Both sites provide rock refuges for *P. l. lateralis* within boulder piles over granite outcrops (Lin 2011), however those at the release site are more structurally complex; featuring more crevices, extensive multi-entranced caves and overhangs (Pearson 2013). Vegetation transitions from closed heath and/or herblands on the outcrops to open eucalypt woodlands over shrublands on the slopes (Australian Wildlife Conservancy 1998).
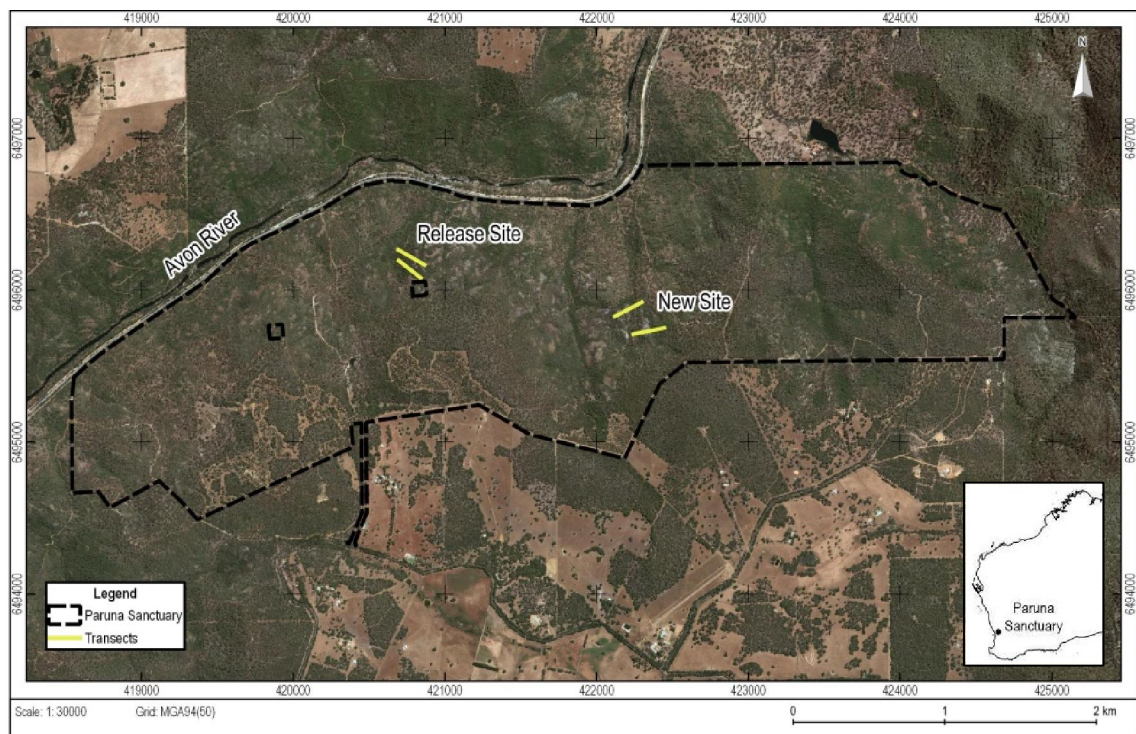
Figure 4:   **Map of Paruna Wildlife Sanctuary outcrops and transects, and location within Western Australia**

3.3.2   Vegetation availability

Vegetation surveys were undertaken from September to October 2018 at both outcrops to compare the availability of potential food resources. Four transects (100 m each) were laid at each outcrop, beginning near rock refuges and extending upslope and downslope (Figure 4). Quadrats (5 x 5 m) were established at 20 m intervals along the linear transects (11 quadrats per transect for a total of 44 quadrats); three quadrats were within 20 m of the refuge, four upslope and four downslope of

the refuge. Within quadrats, percentage cover of each plant species with foliage up to 1 m above ground level (and thereby accessible to *P. l. lateralis*) was recorded using a modified Braun-Blanquet cover-abundance scale (Braun-Blanquet 1932). Plant species were classified into functional groups: browse (i.e. woody shrubs and trees), grass, forb, fern and sedge. Specimens were collected to create a plant reference library. Other observations recorded for quadrats include topography, vegetation type and density versus bare rock, canopy cover and nearby shelter points (boulder piles that provide temporary protection within the forging range: Tuft et al. 2011a).

3.3.3   Plant reference library

A plant reference library was created for each plant species recorded from the survey quadrats. A permanent slide of leaf and/or stem epidermis was created using a modified methodology from Chauvin (2015). Small sections of leaf and stem were placed in a beaker and boiled in 5 mL of 10% chromic acid (H_2CrO_4) and 5 mL of 10% nitric acid (HNO_3) to digest away mesophyll. Once only epidermal fragments remained, residual acid was extracted from the beaker, before adding water with a few drops of concentrated ammonia. Solution was then again extracted, before adding Gentian Violet in 95% ethanol to soak for 30 min. Stained material was washed in water and dehydrated through a series of ethanol solutions (50%, 70% and 95%). Epidermal fragments were transferred to a microscope slide, soaked in xylene and sealed with a coverslip coated in Depex mounting solution. Photographs (at 100x, 200x and 400x optical magnifications) of each slide were taken to aid identification of epidermal fragments in scats.

3.3.4   Scat analysis

Scats for *P. l. lateralis* and *M. fuliginosus* were collected for diet analysis at each quadrat at the same time vegetation surveys were undertaken. The dissimilar size and shape of scats from each species made them distinguishable from each other; *P. l. lateralis* scats have a tapered cylindrical

shape (Tuft et al. 2011b), while *M. fuliginosus* scats are larger and round in shape. Scats were frozen in paper bags before being air dried for analysis.

A total of 20 scats were processed for analysis; five from each species from each of the two transects at the release site outcrop (no *P. l. lateralis* scats could be found at the new site). For each scat, a permanent slide of epidermal fragments was created using a modified methodology from Chauvin (2015). Scats were broken up using a mortar and pestle before being transferred a grinder for 2 min. Samples were transferred into conical flasks with 25 mL of 30% hydrogen peroxide (H_2O_2), two drops of 5% sodium diphosphate ($Na_4P_2O_7$) solution and two drops of concentrated ammonia (NH_3), and heated for ~12 h at 65°C. Samples were then transferred into centrifuge tubes, centrifuged (3,000 rpm) for 10 min, and washed in ethanol (helped by further centrifuging) before being soaked in Gentian Violet in 95% ethanol for 30 min. Stained material was transferred to a 32 mm sieve and washed and dehydrated through a series of ethanol solutions (50%, 70% and 95%). A subsample of epidermal fragments from each sample was taken and spread evenly across a microscope slide, soaked in xylene and sealed with a coverslip coated in Depex mounting solution.

Slides of epidermal fragments were analysed using a point quadrat sampling method at 100x optical magnification whereby, for each field of view, the fragments occurring under the cross-hairs of a 10x10 grid eyepiece graticule were identified and counted (Poole et al. 2014). This methodology accounts for the size of the fragment (which will be proportional to the number of times that fragment occurs under graticule cross-hairs) (Poole et al. 2014). To ensure even sampling intensity between samples, the field of view was moved across the microscope slide in a linear fashion until 200 fragment-graticule intersections had been recorded for each sample (Poole et al. 2014). Photographs of each field of view were taken to aid this process. Where possible, fragments were identified to species, genus or family level through cross-referencing with the key diagnostic characteristics of plant species in the reference collection. Where this wasn't possible,

fragments were classed as unknown Poaceae, unknown monocot, unknown dicot or unknown fragment.

3.3.5 Camera trapping

Motion sensor camera traps (Reconyx Hyperfire HC500) were deployed to monitor all foraging activity within quadrats at both outcrops between September and December 2018. For each quadrat, a single camera was mounted to trees or metal stakes 0.3-0.5 m above ground level at a sufficient distance away to ensure the field of view included the entire quadrat. Settings were fixed to rapid fire (five photos after every trigger, with no delay) and camera maintenance (battery and memory card replacement) was undertaken every six weeks. Photos were processed in Windows Photo Viewer and ExifPro Image Viewer version 2.1 (Kowalski and Kowalski 2000), and the metadata of every fifth photo of each sequence (representing a single trigger) was exported. Sequential captures of the same species within 5 min were classified as a single capture event unless multiple individuals were visible in the same photo (classified as multiple capture events). 5 min was chosen with the knowledge that kangaroos can linger for some time while foraging but also can move very quickly past cameras (Green-Barber and Old 2018). Camera trap photos capturing *P. l. lateralis* and *M. fuliginosus* consuming particular plant species were also used to support scat analysis.

3.3.6 Data analysis

Vegetation availability at the two outcrops was compared using non-metric multidimensional scaling (nMDS) comparing the percentage cover of each plant species at each outcrop with predictor variables outcrop ('release' and 'new' sites) and location (refuge, upslope and downslope), followed by one-way analysis of similarity (ANOSIM) and a similarity percentage (SIMPER) (PAST 3.0) (Hammer and Harper 2013). The SIMPER determined the contribution of each plant species to the differences found by the nMDS and ANOSIM.

Dietary compositions of *P. l. lateralis* and *M. fuliginosus* were compared using nMDS comparing the counts of epidermal fragments of each plant species in the scats of each macropod species and analysed using a two-way PERMANOVA with species and location as predictor variables. Dietary overlap between *P. l. lateralis* and *M. fuliginosus* was quantified using the Schoener index (Schoener 1968):

$$\alpha = 1 - 0.5 * \sum \left(\left| P_{xi} - P_{yi} \right| \right) \qquad \text{eq. 1}$$

where Pxi is the proportion of plant species i in the diet of *P. l. lateralis* and Pyi is the proportion of plant species i in the diet of M. fuliginosus. Values range from 0 (no overlap) to 1 (total overlap), with values >0.6 considered as indication of significant diet overlap (Creese et al. 2019; Wallace and Ramsey 1983).

Dietary selectivity of *P. l. lateralis* and *M. fuliginosus* was quantified using Ivlev's Selectivity Index (Lechowicz 1982):

$$E_i = (r_i - p_i) / (r_i + p_i) \qquad \text{eq. 2}$$

where ri is the proportion of plant species i in the diets of either *P. l. lateralis* or *M. fuliginosus* and pi is the abundance of plant species i in the field. The Ei was rounded to -1, 0 or 1, with -1 signifying avoidance, 0 signifying use in proportion to availability and 1 signifying selection (Poole et al. 2014).

Spatial overlap in foraging patch use between *P. l. lateralis* and *M. fuliginosus* was measured by adding the standardised proportions of photo captures of each species at different locations. The distribution of *P. l. lateralis* and *M. fuliginosus* foraging activity across the outcrops; represented as proportions of independent camera trap events (captures) of each species at different locations, was assessed using Pearson's chi-square tests:

$$\chi 2 = \sum \frac{(\text{observed} - \text{expected})^2}{\text{expected}} \qquad \text{eq. 3}$$

Expected values were calculated based on the assumption that there was no difference in the proportion of captures of each species by location. *P. l. lateralis* captures at the new site were excluded from all statistical analyses because only three captures of the same individual were recorded.

Temporal overlap in foraging activity between *P. l. lateralis* and *M. fuliginosus* was measured using the timestamp record from photo captures in the Overlap package version 0.3.2 (Meredith and Ridout 2018). Coefficient of overlap values (Δ) range from 0 (no overlap) to 1 (total overlap). The Δ4 estimator was used because the sample size was greater than 75 (Meredith and Ridout 2018), and 95% confidence intervals were estimated from 10,000 smoothed bootstrap samples, after correcting for the bootstrap bias (Dawson et al. 2018). To determine the significance of the Δ value, a Mardia-Watson-Wheeler test (Batschelet 1981) was performed in the Circular package version 0.4-93 (Lund et al. 2017). This test assumes no repeat data so captures recorded at identical times were adjusted by 0.86 seconds (adjusting by 0.00001 resulted in 0.86 s). All statistical tests of temporal patterns were performed in R version 1.1.442 (R Core Team 2012). In addition, we also examined a range of variables including whether or not a quadrat: occurred within 20 m of a refuge (large rock or boulder pile), had a dense understorey, and/or had any canopy cover.

3.4. Results

3.4.1 Vegetation availability

A combined total of 101 plant species were recorded across the outcrops (release site = 67, new site = 93). Of these, 9 were only recorded at the release site and 35 were unique to the new site (Table 5). Vegetation availability was significantly different between outcrops (ANOSIM, R = 0.24, p = 0.0003) and also the location (refuge, upslope and downslope) on outcrops (ANOSIM, R = 0.23, p = 0.0001; Figure 5).
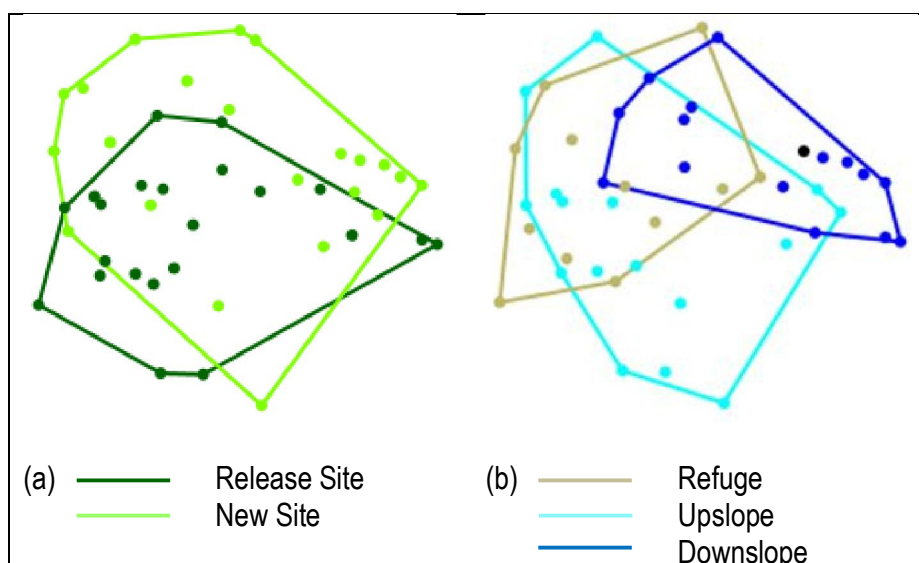
Figure 5: Non-metric MDS ordination comparing vegetation availability (a) at the outcrops and (b) location in respect to the refuge in Paruna Wildlife Sanctuary

Browse species *Trymalium odoratissimum odoratissimum* and *Darwinia citriodora* contributed most of the difference in vegetation availability between outcrops and locations. *Trymalium odoratissimum odoratissimum* was present at both outcrops, mostly occurring downslope of the refuge (SIMPER, 26% relative availability downslope vs 7% upslope and 5% at the refuge) and was the most available species at the new site (15.5% relative availability). *Darwinia citriodora* was only present at the release site where it was the most available plant species (13.2% relative availability), mostly occurring near and upslope of the refuge (SIMPER, 11% relative availability near the refuge and 9% upslope, vs 1% downslope).

In terms of plant functional groups, forbs were the most available at both outcrops, followed by browse, grasses, ferns and sedges. The new site had more forbs (55% vs 45% relative availability), grasses (18% vs 13% relative availability) and sedges (1% vs <1% relative availability), whereas the release site had more browse (34% vs 22% relative availability) and ferns (7% vs 4% relative availability).

3.4.2   Dietary compositions and selectivity

Most (76%) of all plant fragments in scats could be identified to at least family level, with 10% being unknown Poaceae spp., 18% unknown monocots, 4% unknown dicots and 2% unknown fragments. *Petrogale lateralis lateralis* scats comprised a total of seven plant species and were dominated by monocots (65.6%), with dicots contributing 26.3% and pteridophytes 7.3% (Table 5). Forbs were the most observed (49.8% occurrence) plant functional group in *P. l. lateralis* scats (on account of *B. sphaerocephala* being classified as a forb), followed by grasses (12.8% occurrence), ferns (7.3% occurrence) and browse (3.1% occurrence). *Petrogale lateralis lateralis* selected for (Ei = 1) two plant species (pincushions *Borya sphaerocephala* and bellardia **Bellardia trixago*), avoided one species (*T. o. odoratissimum*), and consumed four species in proportion to their availability (rock fern *Cheilanthes austrotenuifolia*, **E. longiflora* (Figure 6), common sowthistle **Sonchus oleraceus* and early hair grass **Aira praecox*) (Table 5). *Borya sphaerocephala* was the most common plant species in *P. l. lateralis* scats (31.7% occurrence), followed by **B. trixago* (15.6% occurrence), *C. austrotenuifolia* (7.3% occurrence) and **E. longiflora* (7.0% occurrence).

Figure 6: *Petrogale lateralis lateralis* herbivory of **Ehrharta longiflora*

Macropus fuliginosus scats consisted of a total of 13 plant species and featured marginally more dicots (47.8%) than monocots (42.2%), with pteridophytes contributing 7.4% (Table 5). In terms of plant functional groups in their scats, browse was the most common (22.9% occurrence), followed by forbs (12.5% occurrence), grasses (9.0% occurrence) and ferns (7.4% occurrence). *Macropus fuliginosus* selected for six species (**S. oleraceus* Figure 7, yellow autumn lily *Tricoryne elatior*, powderbark wandoo *Eucalyptus accedens*, **B. trixago*, *B. sphaerocephala* and morning iris *Orthrosanthus laxus*), and consumed seven species in proportion to their field availability *T. o. odoratissimum* (14.9% occurrence), *C. austrotenuifolia* (7.4% occurrence), **E. longiflora* (4.0% occurrence; Figure 7), graceful honeymyrtle *Melaleuca radula* (1.7% occurrence), foxtail mulga grass *Neurachne alopecuroidea* (1.3% occurrence), zamia *Macrozamia riedlei* (0.6% occurrence) and snail hakea *Hakea cristata* (0.4% occurrence). **Sonchus oleraceus* was the most common food plant species in *M. fuliginosus* scats (17% occurrence), followed by *T. o. odoratissimum* (14.9% occurrence), *C. austrotenuifolia* (7.4% occurrence) and *T. elatior* (6.0% occurrence).

Figure 7: *Macropus fuliginosus* herbivory of **Ehrharta longiflora* (left) and
*Sonchus oleraceus (right)

3.4.3   Dietary overlap

There was some dietary overlap between *P. l. lateralis* and *M. fuliginosus* (Schoener index, α =
0.56), with six plant species featuring in both of their diets: **B. trixago*, *B. sphaerocephala*,
C. austrotenuifolia, **E. longiflora*, **S. oleraceus* and *T. o. odoratissimum* (Table 5). Overall dietary
compositions were, however, significantly different (PERMANOVA, F = 5.63, p = 0.001) (Figure 8).
Borya sphaerocephala contributed most of the difference (SIMPER 27.4%), followed by
*S. oleraceus (SIMPER 15.5%), *T. o. odoratissimum* (SIMPER 13.0%) and **B. trixago* (SIMPER
12.4%).
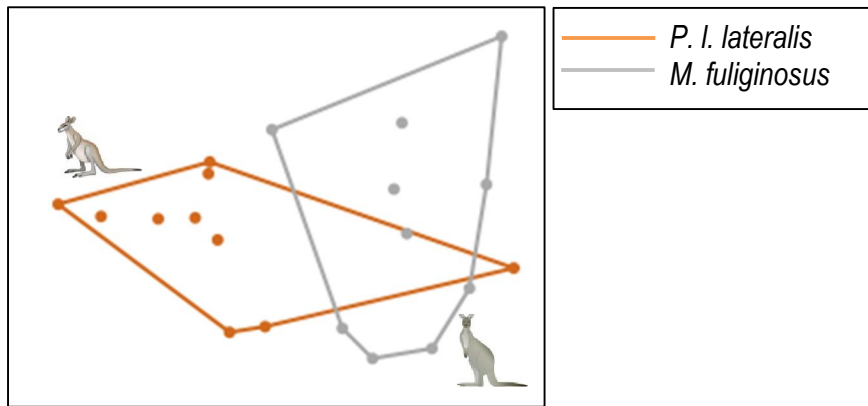
Figure 8: Non-metric MDS ordination comparing dietary compositions of *Petrogale lateralis lateralis* and *Macropus fuliginosus* at Paruna Wildlife Sanctuary

3.4.4 Spatial overlap in foraging patch use

A total of 115 *P. l. lateralis* (release site = 112, new site = 3) and 622 *M. fuliginosus* (release site = 308, new site = 314) independent photo captures were recorded across a total of 128 trap nights. During this time, a total of three fox (new site only) and 34 feral cat (release site = 14, new site = 20) independent photo captures were also recorded. At least three different feral cat individuals, including a kitten, were identified from photos. All *P. l. lateralis* captures at the new site were of the same individual and the low number of captures precluded the carrying out of statistical analyses for this outcrop.

There was some spatial overlap in foraging patch use between *P. l. lateralis* and *M. fuliginosus* at the release site (33.9%; Figure 9 and Figure 10). Herbivore foraging activity was disproportionate (percentage of total captures for each species) with location (transect 1: χ^2_2= = 53.11, p < 0.001 and transect 2: χ^2_2= 103.12, p < 0.001). *Petrogale lateralis lateralis* captures were mostly near the refuge (53% of captures of this species) or downslope of the refuge (33%), with very few captures upslope of the refuge (3%) (Table 4 and Figure 10). By contrast, *M. fuliginosus* captures were predominantly upslope of the refuge (47% of captures of this species), with fewer downslope of the

refuge (19%) or near the refuge (13%) (Table 4 and Figure 10). At the new site, *M. fuliginosus* captures were similarly fewest at the refuge (15%), but highest downslope of the refuge (36%) rather than upslope of the refuge (27%) (Table 4 and Figure 10).
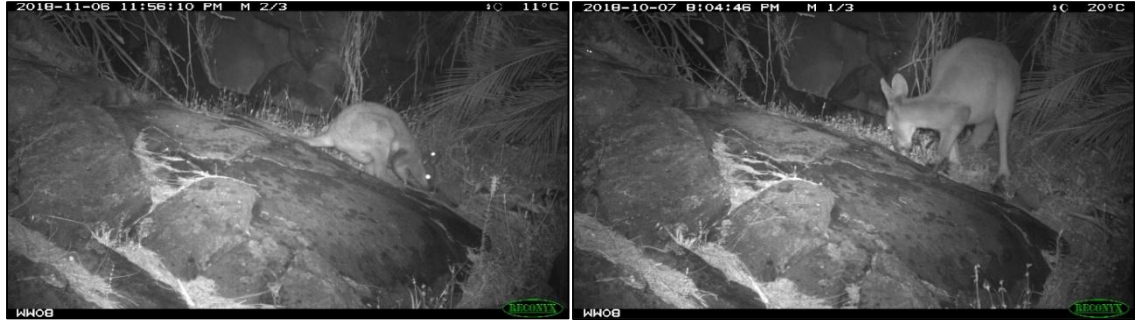
Figure 9: *Petrogale lateralis lateralis* **(left) and** *Macropus fuliginosus* **(right) captured using the same foraging patch in Paruna Wildlife Sanctuary**

In addition to spatial overlap, there was also temporal overlap in foraging activity between *P. l. lateralis* and *M. fuliginosus*, with both species foraging across the release site outcrop from dusk until dawn (Figure 11). However, time spent foraging and peak foraging times varied. *Petrogale lateralis lateralis* predominantly began foraging just before dusk (17:00 h) and ended mid-morning (09:00 h), peaking between 20:00-21:00 h and then again at midnight (00:00 h). By contrast, *M. fuliginosus* foraged throughout the day and night, peaking at 07:00 h, then between 18:00-19:00 h, and again around midnight (00:00-01:00 h) (Figure 11).
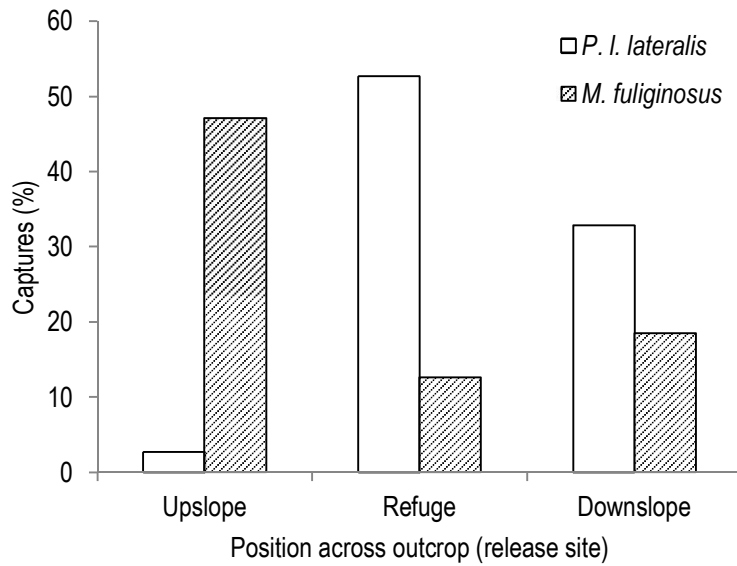
Figure 10: **Proportion of captures of *Petrogale lateralis lateralis* and *Macropus fuliginosus* across the release site outcrop in Paruna Wildlife Sanctuary**
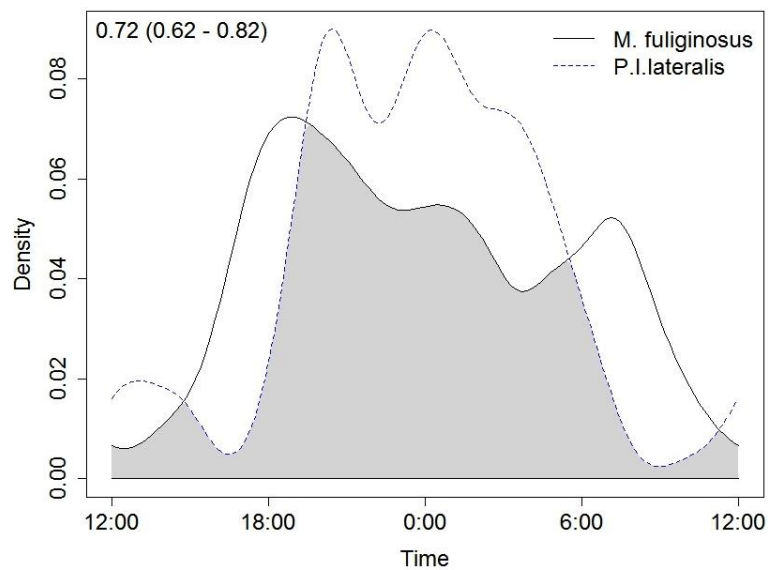
Figure 11: **Temporal overlap in foraging activity between *Petrogale lateralis lateralis* and *Macropus fuliginosus* across the release site outcrop in Paruna Wildlife Sanctuary**

Shaded area indicates temporal overlap. Value in the top left hand corner represents the proportion overlap in temporal activity (with the 95% confidence interval in brackets).

Table 4: Photo captures of *Petrogale lateralis lateralis* and *Macropus fuliginosus* across the outcrops in Paruna Wildlife Sanctuary

			Upslope				Refuge			Downslope				Total	Chi-square	
			Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10	Q11		χ^2	p
M. fuliginosus	RS	T1	11	17	26	20	12	1	11	12	1	7	4	122	54.9	<0.001
		T2	30	62	5	22	15	0	0	7	43	2	0	186	250.5	<0.001
	NS	T3	6	40	8	13	19	11	0	5	23	0	3	128	122.4	<0.001
		T4	6	6	20	6	5	5	28	21	30	21	38	186	84.2	<0.001
P. l. lateralis	RS	T1	0	0	0	3	2	15	6	9	7	13	6	61	26.4	<0.001
		T2	0	0	1	0	1	35	0	6	5	3	0	51	52.8	<0.001
	NS	T3	0	0	0	0	0	0	0	0	0	0	0	0	NA	NA
		T4	0	0	0	0	0	3	0	0	0	0	0	3	NA	NA

RS = release site, NS = new site, Q = quadrat, T = transect. NA = data not suitable for analysis because only a single P. l lateralis individual was captured at the new site. The darker coloured shading indicates higher numbers of captures.

38

Table 5: Relative abundance of plant species at the outcrops in Paruna Wildlife Sanctuary compared to within *Petrogale lateralis lateralis* and *Macropus fuliginosus* scats

Plant			Relative availability (%)		*P. l. lateralis*		M. fuliginosus	
Class Functional group	Family	Species	Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Monocot								
Forb	Asparagaceae	*Dichopogon capillipes*	0.6	1.0	0.0	-1	0.0	-1
Forb	Asparagaceae	*Thysanotus manglesianus*	0.1	0.1	0.0	-1	0.0	-1
Forb	Boryaceae	*Borya sphaerocephala*	0.2	0.8	31.7	1	1.3	1
Sedge	Cyperaceae	*Lepidosperma* sp. 1	0.0	0.0	0.0	-1	0.0	-1
Sedge	Cyperaceae	*Lepidosperma* sp. 2	0.0	0.0	0.0	-1	0.0	-1
Sedge	Cyperaceae	*Schoenus nanus*	0.0	0.8	0.0	-1	0.0	-1
Forb	Haemodoraceae	*Haemodorum* sp.	0.2	0.2	0.0	-1	0.0	-1
Forb	Hemerocallidaceae	*Caesia micrantha*	0.3	1.0	0.0	-1	0.0	-1
Forb	Hemerocallidaceae	*Tricoryne elatior*	0.1	0.3	0.0	-1	6.0	1
Forb	Hypoxidaceae	*Pauridia occidentalis*	0.7	0.4	0.0	-1	0.0	-1
Forb	Iridaceae	*Orthrosanthus laxus*	0.0	0.1	0.0	-1	0.7	1
Forb	Iridaceae	*Romulea rosea*	3.2	3.9	0.0	-1	0.0	-1
Forb	Orchidaceae	*Caladenia flava*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Leptoceras menziesii*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Prasophyllum macrostachyum*	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Prasophyllum* sp.	0.0	0.0	0.0	-1	0.0	-1
Forb	Orchidaceae	*Pterostylis* sp.	0.0	0.1	0.0	-1	0.0	-1
Grass	Poaceae	*Aira cupaniana*	0.0	0.8	0.0	-1	0.0	-1
Grass	Poaceae	*Aira praecox*	0.3	2.5	0.3	0	0.0	-1
Grass	Poaceae	*Bellardia trixago*	0.3	1.3	15.6	1	4.5	1
Grass	Poaceae	*Briza maxima*	0.4	0.4	0.0	-1	0.0	-1
Grass	Poaceae	*Briza minor*	1.9	2.8	0.0	-1	0.0	-1
Grass	Poaceae	*Bromus diandrus*	0.4	2.4	0.0	-1	0.0	-1
Grass	Poaceae	*Ehrharta longiflora*	5.8	2.9	7.0†	0	4.0†	0
Grass	Poaceae	*Microlaena? stipoides*	0.0	0.5	0.0	-1	0.0	-1
Grass	Poaceae	*Neurachne alopecuroidea*	0.5	1.8	0.0	-1	1.3	0
Grass	Poaceae	*Vulpia myuros*	4.0	3.5	0.0	-1	0.0	-1
		Unknown Poaceae			12.5		7.7	
Forb	Restionaceae	*Desmocladus flexuosus*	0.0	0.1	0.0	-1	0.0	-1
Forb	Xanthorrhoeaceae	*Chamaescilla corymbosa*	0.0	0.2	0.0	-1	0.0	-1
Browse	Xanthorrhoeaceae	*Xanthorrhoea preissii*	0.8	0.0	0.0	-1	0.0	-1

Class Functional group	Family	Species	Relative availability (%)		P. l. lateralis			M. fuliginosus		
			Release site	New site	Occurrence in scats	(%)	Ivlev's Selectivity Index, E	Occurrence in scats	(%)	Ivlev's Selectivity Index, E
Browse	Zamiaceae	*Macrozamia riedlei*	1.5	0.1	0.0		-1	0.6		0
		Unknown monocots			14.1			21.2		
		Total monocots			65.6			42.2		
Dicot										
Forb	Amaranthaceae	*Ptilotus drummondii*	0.0	0.1	0.0		-1	0.0		-1
Forb	Apiaceae	*Daucus glochidiatus*	3.5	3.9	0.0		-1	0.0		-1
Forb	Apiaceae	*Eryngium pinnatifidum*	0.0	0.3	0.0		-1	0.0		-1
Forb	Araliaceae	*Trachymene? pilosa*	0.0	0.2	0.0		-1	0.0		-1
Forb	Asteraceae	**Arctotheca calendula*	0.4	1.4	0.0		-1	0.0		-1
Forb	Asteraceae	*Brachyscome pusilla*	0.0	0.3	0.0		-1	0.0		-1
Forb	Asteraceae	**Carduus pycnocephalus*	0.5	0.4	0.0		-1	0.0		-1
Forb	Asteraceae	*Helichrysum? luteoalbum*	0.3	0.0	0.0		-1	0.0		-1
Forb	Asteraceae	**Hypochaeris glabra*	4.6	4.4	0.0		-1	0.0		-1
Forb	Asteraceae	**Hypochaeris radicata*	0.0	0.2	0.0		-1	0.0		-1
Forb	Asteraceae	*Plantago? debilis*	0.0	0.7	0.0		-1	0.0		-1
Forb	Asteraceae	*Podolepis lessonii*	0.3	0.5	0.0		-1	0.0		-1
Forb	Asteraceae	*Podotheca gnaphalioides*	0.0	0.1	0.0		-1	0.0		-1
Forb	Asteraceae	**Sigesbeckia orientalis*	0.0	0.8	0.0		-1	0.0		-1
Forb	Asteraceae	**Sonchus oleraceus*	4.7	3.1	2.5		0	17.0†		1
Forb	Asteraceae	**Ursinia anthemoides*	1.3	2.4	0.0		-1	0.0		-1
Forb	Asteraceae	*Lagenophora huegelii*	0.5	0.9	0.0		-1	0.0		-1
Forb	Asteraceae	*Lawrencella rosea*	0.0	0.2	0.0		-1	0.0		-1
Forb	Asteraceae	*Quinetia urvillei*	0.5	2.3	0.0		-1	0.0		-1
Forb	Asteraceae	*Siloxerus humifusus*	0.0	0.4	0.0		-1	0.0		-1
Forb	Asteraceae	*Waitzia nitida*	0.0	0.1	0.0		-1	0.0		-1
Forb	Asteraceae	Unknown Asteraceae	0.0	0.0	0.0		-1	0.0		-1
Browse	Casuarinaceae	*Allocasuarina huegeliana*	0.1	0.2	0.0		-1	0.0		-1
Forb	Caryophyllaceae	**Silene gallica*	0.2	0.2	0.0		-1	0.0		-1
Forb	Crassulaceae	*Crassula colorata*	0.3	0.2	0.0		-1	0.0		-1
Browse	Dilleniaceae	*Hibbertia hypericoides*	0.0	0.2	0.0		-1	0.0		-1
Browse	Dilleniaceae	*Hibbertia lasiopus*	1.1	1.7	0.0		-1	0.0		-1
Forb	Dioscoreaceae	*Dioscorea hastifolia*	7.6	1.5	0.0		-1	0.0		-1
Forb	Droseraceae	*Drosera bulbosa*	0.8	0.5	0.0		-1	0.0		-1

Class Functional group	Family	Species	Relative availability (%)		P. l. lateralis		M. fuliginosus	
			Release site	New site	Occurrence in scats (%)	Ivlev's Selectivity Index, E	Occurrence in scats (%)	Ivlev's Selectivity Index, E
Forb	Droseraceae	*Drosera glanduligera*	0.7	1.2	0.0	-1	0.0	-1
Forb	Droseraceae	*Drosera pallida*	0.0	0.7	0.0	-1	0.0	-1
Browse	Ericaceae	*Astroloma drummondii*	0.0	0.1	0.0	-1	0.0	-1
Browse	Fabaceae	*Acacia pulchella*	0.0	0.0	0.0	-1	0.0	-1
Forb	Fabaceae	*Melilotus indicus*	0.0	0.3	0.0	-1	0.0	-1
Forb	Fabaceae	*Trifolium dubium*	0.0	0.8	0.0	-1	0.0	-1
Forb	Fabaceae	*Trifolium campestre*	0.2	0.5	0.0	-1	0.0	-1
Forb	Fabaceae	*Trifolium subterraneum*	0.3	3.0	0.0	-1	0.0	-1
Forb	Gentianaceae	*Centaurium erythraea*	1.1	1.7	0.0	-1	0.0	-1
Forb	Gentianaceae	*Cicendia filiformis*	0.0	0.4	0.0	-1	0.0	-1
Forb	Geraniaceae	*Erodium cygnorum*	0.1	0.0	0.0	-1	0.0	-1
Forb	Goodeniaceae	*Goodenia pulchella*	0.0	0.0	0.0	-1	0.0	-1
Forb	Lamiaceae	*Stachys arvensis*	1.5	1.6	0.0	-1	0.0	-1
Forb	Montiaceae	*Calandrinia* sp.	0.4	1.9	0.0	-1	0.0	-1
Forb	Mulvaceae	*Thomasia* sp.	0.0	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Corymbia calophylla*	0.1	0.2	0.0	-1	0.0	-1
Browse	Myrtaceae	*Darwinia citriodora*	13.2	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Eucalyptus accedens*	0.0	0.4	0.0	-1	5.3	1
Browse	Myrtaceae	*Hypocalymma angustifolium*	1.1	0.8	0.0	-1	0.0	-1
Browse	Myrtaceae	*Leptospermum erubescens*	0.0	0.0	0.0	-1	0.0	-1
Browse	Myrtaceae	*Melaleuca radula*	1.8	0.0	0.0	-1	1.7	0
Forb	Orobanchaceae	*Parentucellia latifolia*	0.5	1.1	0.0	-1	0.0	-1
Forb	Oxalidaceae	*Oxalis perennans*	0.4	0.4	0.0	-1	0.0	-1
Forb	Papaveraceae	*Fumaria capreolata*	0.8	0.0	0.0	-1	0.0	-1
Browse	Phyllanthaceae	*Phyllanthus calycinus*	2.6	2.2	0.0	-1	0.0	-1
Forb	Phyllanthaceae	*Poranthera microphylla*	0.0	0.2	0.0	-1	0.0	-1
Forb	Primulaceae	*Lysimachia arvensis*	6.6	4.5	0.0	-1	0.0	-1
Browse	Proteaceae	*Hakea cristata*	0.3	0.0	0.0	-1	0.4	0
Browse	Rhamnaceae	*Trymalium odoratissimum odoratissimum*	10.9	15.5	3.1	-1	14.9	0
Forb	Solanaceae	*Solanum nigrum*	0.0	0.0	0.0	-1	0.0	-1
Browse	Solanaceae	*Solanum lasiophyllum*	0.0	0.0	0.0	-1	0.0	-1
Forb	Stylidiaceae	*Levenhookia pusilla*	0.0	0.2	0.0	-1	0.0	-1
Forb	Stylidiaceae	*Stylidium androsaceum*	0.0	0.2	0.0	-1	0.0	-1
Browse	Thymelaeaceae	*Pimelea argentea*	0.4	0.7	0.0	-1	0.0	-1
Forb	Urticaceae	*Parietaria debilis*	0.7	0.1	0.0	-1	0.0	-1

Class / Functional group	Family	Species	Relative availability (%) Release site	New site	P. l. lateralis Occurrence in scats (%)	Ivlev's Selectivity Index, E	M. fuliginosus Occurrence in scats (%)	Ivlev's Selectivity Index, E
		Unidentified forb 1	0.3	0.8	0.0	-1	0.0	-1
		Unidentified forb 2	0.0	0.2	0.0	-1	0.0	-1
		Unidentified forb 3	0.0	0.0	0.0	-1	0.0	-1
		Unidentified forb 4	0.0	0.2	0.0	-1	0.0	-1
		Unidentified forb 5	0.0	0.2	0.0	-1	0.0	-1
		Unknown dicots			5.2		3.5	
		Total dicots			26.3		47.8	
Pteridophyte								
Fern	Pteridaceae	*Cheilanthes austrotenuifolia*	7.2	4.1	7.3	0	7.4	0
Fern	Aspleniaceae	*Pleurosorus rutifolius*	0.1	0.2	0.0	-1	0.0	-1
		Unknown fragments			0.9		2.7	

Functional group: browse = woody trees and shrubs, forb = non-woody herbaceous plants, grass = Poaceae family. †Camera trap captured a photo of this being consumed. Ivlev's Selectivity Index: used relative abundance values at the release site only because no scats were found at the new site, -1 = avoidance, 0 = use in proportion to availability, 1 = selection (shaded).

3.5. Discussion

Petrogale lateralis lateralis and *M. fuliginosus* diets and foraging patches in Paruna Wildlife Sanctuary overlapped, however also varied. While *P. l. lateralis* predominantly ate monocots, *M. fuliginosus* had a more diverse diet comprising similar proportions of monocots and dicots (slightly more dicots). Herbivores selected for two of the same plant species, both of which were limited spatially and/or temporally. Their foraging activity mostly occurred at different locations on the outcrop; *P. l. lateralis* near refuges and downslope of them, and *M. fuliginosus* upslope of refuges. These findings collectively suggest that low levels of dietary competition were occurring between *P. l. lateralis* and *M. fuliginosus*.

3.5.1   Dietary overlap

This study shows that there was some dietary overlap between *P. l. lateralis* and *M. fuliginosus* in Paruna Wildlife Sanctuary (prediction 1). Both macropod species consumed six of the same plant species including three forbs, a grass, browse and fern. The degree of dietary overlap in this study was comparable to that in most published studies (Table 6). The exceptions being the higher dietary overlap between *P. l. lateralis* and feral goats *C. hircus* (significant), and between *M. fuliginosus* and sympatric *N. irma* and tammar wallaby *N. eugenii* (Table 6).

In this study, *P. l. lateralis* predominantly consumed monocots. Chauvin (2015) reported similar findings for *P. l. lateralis* in the Avon Wheatbelt and Avon Valley National Park. By contrast, Creese et al. (2019) and Geelen (1999) found that dicots are mostly eaten by *P. l. lateralis* in Cape Range National Park and *P. lateralis* MacDonnell Ranges Race in South Australia respectively. In terms of plant functional groups, *P. l. lateralis* in Paruna mainly ate forbs (on account of *B. sphaerocephala* being classified as a forb). This finding aligns with that previously reported for other *Petrogale* taxa, however not this sub-species (Figure 12). *Petrogale lateralis lateralis* diet seems to vary in line with plant functional group availability between locations and across seasons (Chauvin 2015; Pentland 2014; Tuft et al. 2011b). For example, while this

study recorded forbs being mainly eaten in Paruna in the cooler, wetter conditions of mid-spring when they were most abundant, Chauvin (2015) found that browse is mostly consumed in the neighbouring Avon Valley National Park in the drier conditions of late spring through summer when forbs, grass and fern abundance has declined (Figure 12). Several other *Petrogale* taxa demonstrate a similar temporal shift in diet (i.e. Capararo 1994; Copley and Robinson 1983; Dawson and Ellis 1979; Telfer and Bowman 2006; Tuft et al. 2011b).

Despite some overlap, *M. fuliginosus* diets in this study differed considerably to those of *P. l. lateralis*, being more diverse (in terms of species richness) and comprising monocots and dicots in near equal proportions (dicots marginally more), and more browse than any other group. Shepherd et al. (1997) and Wann and Bell (1997) reported comparable findings in eucalypt forest/woodland. By contrast, Wilson (1991) and Algar (1986) found that dicots dominate *M. fuliginosus* diets in mulga *Acacia aneura* woodlands and grass, sedge and shrub associations respectively (Figure 13). In addition to vegetation type, temporal variation in plant functional group availability also seems to influence *M. fuliginosus* diet. For example, Barker (1987) and Norbury (1987) reported that *M. fuliginosus* diets comprise mostly monocots in winter, however transition to mainly dicots in summer. *Macropus giganteus* are also heavily reliant on grasses in their diets, however in all seasons (Figure 13).

Table 6: Comparison between dietary overlap results of this study at Paruna Wildlife Sanctuary with those of published studies for a range of macropod species

	M. fuliginosus	M. giganteus	O. r. erubescens	C. hircus
P. l. lateralis	[1]0.56 (S)		[2]0.57 (S)	[2]0.85 (S)
P. lateralis MacDonnell Ranges race			[7]N.S	
	[3]0.88 (S)†			
. irma	[4]0.33† (H)			
	[5]0.04 (H)			
N. eugenii	[4]0.95 (H)†			
W. bicolor		[6]0.61 (H)		

Values from similar indices representing dietary overlap: (S) Schoener index (Schoener 1968) and (H) Horns index of niche overlap (Horn 1966). Shaded cells = significant dietary overlap recorded. N.S = index value is not significant. †Data is the total of multiple seasons of sampling. [1]The present study [2](Pilgonaman Gorge summer sampling: Creese et al. 2019) [3](Wann and Bell 1997) [4](Shepherd et al. 1997) [5](Algar 1986) [6](Davis et al. 2008) [7](Capararo 1994).
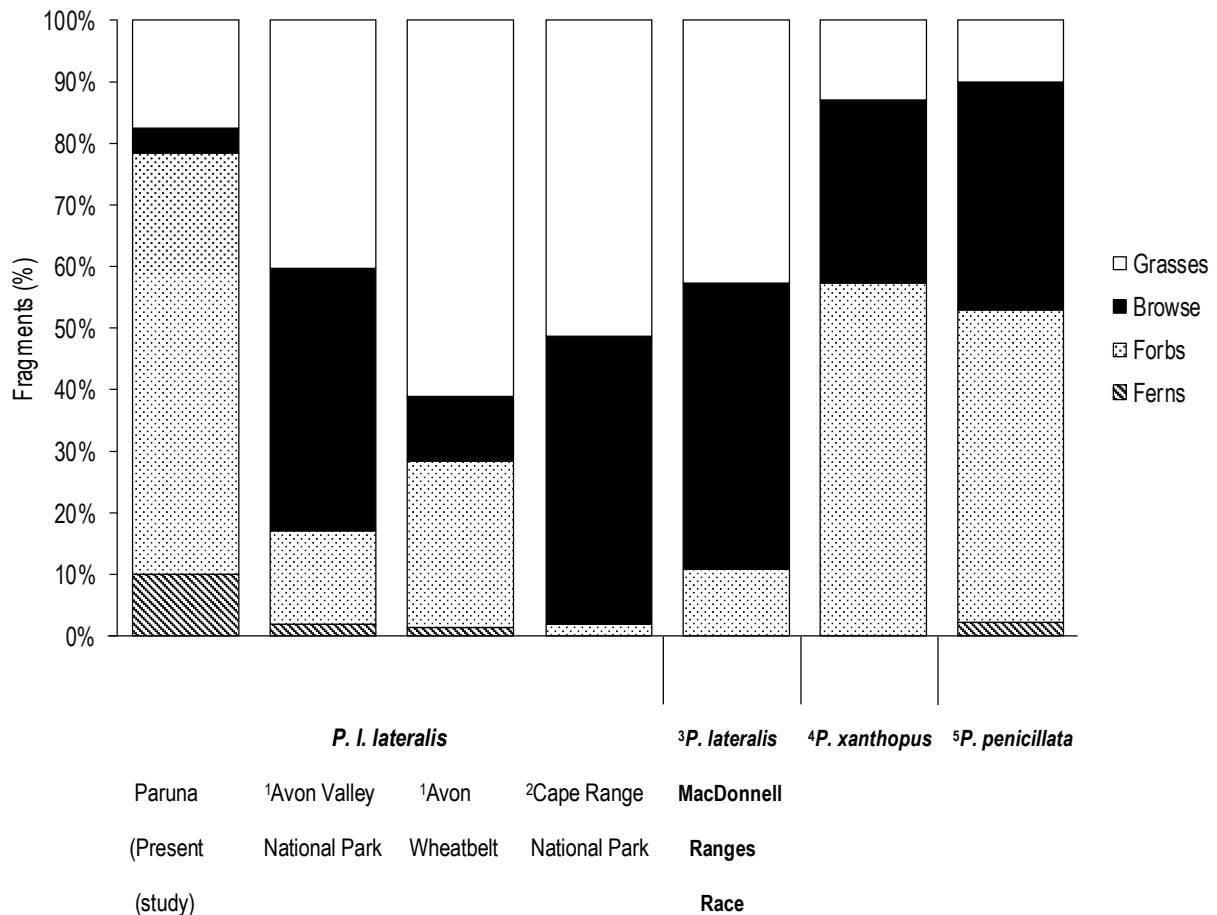
Figure 12: Comparison between *Petrogale lateralis lateralis* dietary composition results of this study with those from other studies, and other *Petrogale* taxa

Cape Range National Park data is from Pilgonaman Gorge summer sampling. Avon Valley National Park and Avon Wheatbelt sedge data has been incorporated into forb data given no occurrence of Cyperaceae family. Petrogale xanthopus forb and browse data excludes round-leaved chenopods. Petrogale penicillata overall data is the mean of multiple seasons of sampling and sedge data has been incorporated into forb data given no occurrence of Cyperaceae family. [1](Chauvin 2015) [2](Creese et al. 2019) [3](Geelen 1999) [4](Dawson and Ellis 1979) [5](Tuft et al. 2011b).
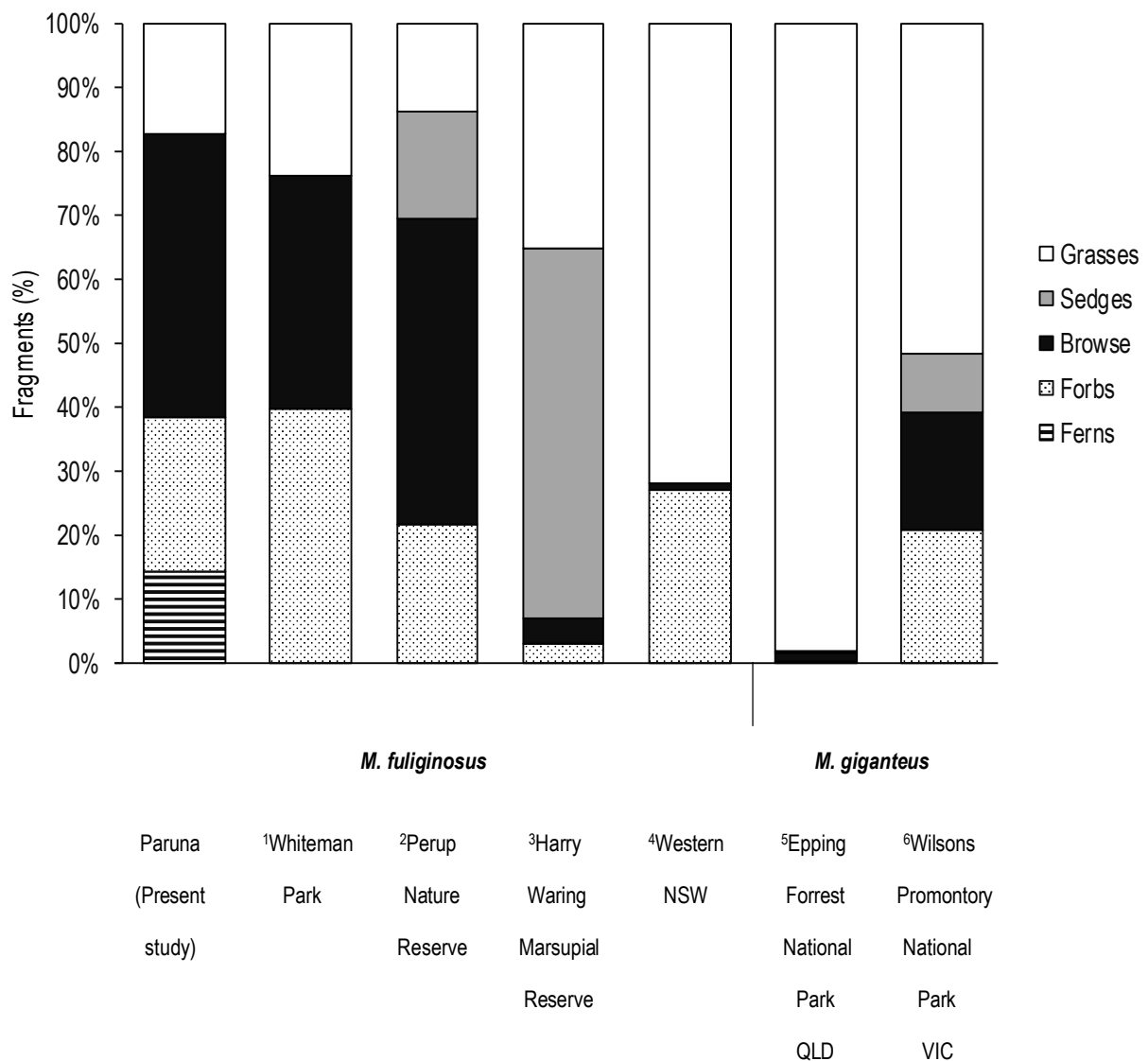
Figure 13: **Comparison between *Macropus fuliginosus* dietary composition results of this study with those from other studies, and *Macropus giganteus***

With the exception of Wilson (1991) and Algar (1986), all data is the total of multiple seasons of sampling. Wilsons Promontory National Park sedge data may also include other non-grass graminoid species including certain rushes, lilies and forbs. Sedges = Cyperaceae family. [1](Wann and Bell 1997) [2](Shepherd et al. 1997) [3](Algar 1986) [4](Wilson 1991) [5](Woolnough and Johnson 2000) [6](Davis et al. 2008).

3.5.2 Availability of preferred food resources

While both macropod species consumed plant functional groups, to some extent, according to their availability, they also showed preference for particular plant species. *Petrogale lateralis lateralis* strongly

selected for *B. sphaerocephala* and **B. trixago*, with these two species making up almost half their diet (Table 2). Chauvin (2015) also found that *P. l. lateralis* in Avon Valley National Park and the Avon Wheatbelt select for *B. sphaerocephala*, with the latter population additionally selecting for *C. austrotenuifolia* (Chauvin 2015), which was eaten in proportion to its availability in this study. Both species are resurrection plants; capable of withstanding severe desiccation and rehydration (Hopper et al. 1997), and likely valuable food resources for *P. l. lateralis*.

Macropus fuliginosus also selected for *B. sphaerocephala* and **B. trixago*, however these species only made a small contribution to their diet (Table 2). Four other species were additionally selected for: *E. accedens. O. laxus*, **S. oleraceus* and *T. elatior*. The latter species is also consumed by *M. fuliginosus* in Whiteman Park (Wann and Bell 1997).

Of the six preferred food resources in Paruna, three were limited either spatially or temporally. *Borya sphaerocephala* was spatially limited, because it only grows in association with granite rock (Western Australian Herbarium 1998-). **Bellardia trixago* and **S. oleraceus* were temporally limited because they are annual weeds. To an extent, **B. trixago* may also be spatially limited, being only recorded near exposed granite. By contrast, **S. oleraceus* was ubiquitously distributed throughout the sanctuary and is a prolific weed across Western Australia (Western Australian Herbarium 1998-). It should also be noted that the abundance of *B. sphaerocephala* and **B. trixago* may have been underestimated as plants were not flowering at the time of sampling and were therefore less detectable.

3.5.3   The role of weeds in macropod diet

Over a quarter of the plants eaten by *P. l. lateralis* and *M. fuliginosus* were weeds. Similar findings have been reported for these species (Chauvin 2015; Creese et al. 2019; Mayberry 2011; Pearson 2013; Pentland 2011; Wann and Bell 1997), as well as other macropod taxa: agile wallaby *M. agilis* (Grice 1996),

N. eugenii (McMillan et al. 2010), swamp wallaby *Wallabia bicolor* (de Munk 1999) and *M. giganteus* (Claridge et al. 2016; de Munk 1999).

Ehrharta longiflora is widely consumed by *P. l. lateralis* according to its availability. In Paruna and Avon Valley National Park, which are relatively large and undisturbed reserves, it occurs at a low abundance and is eaten in correspondingly low amounts (Chauvin 2015). By contrast, in Nangeen Hill (Avon Wheatbelt), which is a much smaller reserve and more vulnerable to weed invasion, it is over twice as prevalent and is consumed in over four times the amount (Chauvin 2015). This suggests that *E. longiflora* has likely replaced certain native diet items. Any weed control measures would need therefore need to be immediately followed by revegetation with native forage plants in order to prevent there being a lack of food resources for *P. l. lateralis*.

Petrogale lateralis lateralis and *M. fuliginosus* may be contributing to the persistence and spread of existing weed populations across the sanctuary through several means. First, they may be dispersing viable weed seeds in their scats, as shown by other macropod species; *M. giganteus* Claridge et al. (2016) and *M. agilis* Grice (1996). Given the variable effect of gut passage on seed germination between herbivores (Westcott et al. 2008) though, the proportion of weed seeds ingested by *P. l. lateralis* and *M. fuliginosus* that remain viable after excretion is unknown. *Petrogale lateralis lateralis* may be transporting weed seeds to microsites on the outcrop, where the elevated nutrient and moisture levels facilitate germination (Brown and Archer 1988). However, their small population size likely precludes this from being a management concern. *Macropus fuliginosus,* on the other hand, are abundant in the sanctuary and could potentially be a more noteworthy vector for weed spread.

Second, *P. l. lateralis* foraging may be limiting the recruitment (Allcock and Hik 2004; Young et al. 1995) or regeneration (Gardiner 1986) of potentially competitive native plant species (Tuft et al. 2011b). Overgrazing is known to cause soil disturbance and, together with nutrient additions from *P. l. lateralis* scats, can also facilitate weed encroachment (Hobbs and Atkins 1988), as previously reported by Pentland

(2014) at Nangeen Hill. However, this seems unlikely as *P. l. lateralis* foraging ranges in Paruna are not restricted like they were at Nangeen Hill.

3.5.4 Spatial overlap in foraging patch use

Our results show that there was some spatial overlap in *P. l. lateralis* and *M. fuliginosus* use of foraging patches (prediction 2), however species mostly foraged at different locations on the outcrop. *Petrogale lateralis lateralis* (adults and young-at-heel) predominantly foraged near refuges (in accordance with prediction 3) but also regularly ventured considerable distances (≥100 m) downslope of their refuges to forage. A considerable time was devoted to foraging, with activity extending from dusk to mid-morning. These findings suggest that *P. l. lateralis* foraging behaviour in Paruna was not being constrained by a perceived risk of predation like that observed by Pentland (2014) at Nangeen Hill, despite predator (feral cat) presence.

At least three feral cats were present on the outcrops, one of which moved between them. They visited several *P. l. lateralis* foraging patches, including one nearest a refuge containing a young-at-heel individual. At this age, *P. l. lateralis* are highly vulnerable to predation by feral cats (Hegglun 2018; H. Crawford, pers. comm.; Paltridge et al. 1997) and foxes (Kinnear et al. 1984; Pentland 2014). Pentland (2014) also observed feral cats intruding into refuges at Nangeen Hill. A single fox also roamed the new site and could to an extent potentially be contributing to the lower number of *P. l. lateralis* foraging on the outcrop compared to the release site.

A combination of factors may be influencing *P. l. lateralis* foraging behaviour in Paruna. First, predator density may be sufficiently low enough (as a result of predator-proof fencing along the sanctuary's southern boundary combined with fox control) to reduce predation fear in *P. l. lateralis*. Second, the dense *T. o. odoratissimum* cover and boulder piles downslope of refuges (shelter points: Tuft et al. 2011a) may be offering a degree of crypsis or temporary protection from predation, thereby facilitating foraging range

expansion. Tuft et al. (2011a) found this to be the case for P. penicillata. Third, both plant species *P. l. lateralis* selected for were most available downslope of refuges and the energy gained from acquiring these food resources may outweigh predation risk.

In contrast to *P. l. lateralis*, *M. fuliginosus* predominantly foraged upslope of refuges but also sometimes ventured downslope to forage and occasionally foraged near refuges. Their greater use of available foraging patches across the outcrop is a function of their lower predation risk compared to *P. l. lateralis* (Tuft et al. 2011a). Rather than refuges, *M. fuliginosus* use crypsis in dense vegetation, clear lines of sight and superior speed to evade predators (Le Mar and Mcarthur 2005), with only young-at-heel vulnerable to predation (Arnold et al. 1991; Banks 2001; Banks et al. 2000; Chang 2001). Pentland (2014) also observed that *M. fuliginosus* sympatric with *P. l. lateralis* at Nangeen Hill only foraged off the outcrop in the surrounding woodland.

Macropus fuliginosus preference for, and avoidance of, particular foraging patches suggests that they are spatially constrained within rocky habitat. The terrain upslope of refuges is the flattest and most accessible, whereas that near refuges is somewhat precarious (i.e. steep angled smooth rocks) and difficult to access by *M. fuliginosus* because they lack the specific morphological adaptations (i.e. a strong non-prehensile tail, large pads and short nails) required to scramble and leap (Barker 1990; Horsup 1986; Pentland 2014; Tyndale-Biscoe 2005). Their preference for foraging upslope may also be influenced by the fact that two of the plant species *M. fuliginosus* selected for, and three eaten in proportion to their availability, were most available at these locations.

3.5.5   Limitations of this study

There may be errors and biases in the data resulting from the limitations of methods used. Although considered to provide an accurate estimation of diet, scat analysis method assumes that all plants have equally digestible epidermal tissues (Dawson and Ellis 1979). This is not the case, with some plants being

less digestible and therefore more easily identifiable (i.e. those with stellate trichomes such as browse species T. o. odoratissimum: Horsup and Marsh 1992), while others may be unidentifiable (forb species *Dioscorea hastifolia* and **Fumaria capreolata* were captured being eaten by *M. fuliginosus* but not identified in their scats). This can result in the more easily identifiable plants being overestimated and grasses being underestimated (Creese et al. 2019).

While grasses (Poaceae spp.) could be relatively easily identified based on the presence of silica bodies and elongated long-cells often with crenulated cell walls, and their cells running in rows parallel to venation (Kok and Van der Schijff 1973; Storr 1961), further identification to species level was difficult, likely because of their high proportion of digestible cellulose (Shipley 1999) and absence of other diagnostic features (Ellis et al. 1977). Seven Poaceae species were identified in vegetation surveys at the release site but only three (**A. praecox*, **E. longiflora* and *N. alopecuroidea*) were identified in the scats sampled.

The method is further limited in that it does not account for the relatively long period between ingestion and excretion, and therefore potential for macropods to have sourced plants from outside the vegetation quadrats (foraging patches) surveyed (Norbury and Sanson 1992). This is more likely the case for *M. fuliginosus* because their foraging ranges are larger (Arnold et al. 1992) and not confined to areas near rock refuges (Creese et al. 2019).

Camera trapping is limited in that it depends on movement to capture data. Intensive foraging activity where macropods remain largely stationary (i.e. browsing) may therefore not be detected by camera traps and potentially result in total foraging activity being underestimated.

3.5.6   Future studies

Despite both outcrops featuring each of the plant species consumed by *P. l. lateralis*, only a single individual was recorded at the new site. GPS collar tracking of two individuals by AWC in August 2019 (N. Palmer, AWC, pers. comm.) could shed some light on the situation. Tracking data could be combined with

camera trapping data collected in this study to verify the extent to which *P. l. lateralis* are using the new site and if they are moving between outcrops. Furthermore, it could confirm precisely when *P. l. lateralis* move away from their refuges to forage, and their maximum foraging ranges.

Petrogale lateralis lateralis diets excluded browse plants with known high concentrations of plant secondary metabolites (i.e. *Eucalyptus* taxa). Plant secondary metabolites are a means of defence against herbivory (Bennett and Wallsgrove 1994); deterring herbivores when the metabolic costs of digesting them outweigh the energy gains (Dearing et al. 2005). Certain specialist browsers have physiologies capable of dealing with plant secondary metabolites (i.e. M. fuliginosus: Shepherd et al. 1997), however this may not be the case for *P. l. lateralis* (Tuft et al. 2011b). A nutrient analysis of the plants (including weeds) consumed by *P. l. lateralis* could confirm whether they are being selected for or against based on their plant secondary metabolite (i.e. tannins, essential oils, alkaloids: Rosenthal and Berenbaum 2012) and/or nutritional content (i.e. crude protein, nitrogen and fibre).

3.5.7 Competition and conservation

Sympatric macropods in this study had overlapping diets and, to a lesser extent, foraging patches. This combined with preferred food resources being spatially or temporally limited, indicates that a low level of dietary competition may be occurring between *P. l. lateralis* and *M. fuliginosus*. However, the current availability of shared food resources and degree of resource (foraging patches) partitioning occurring suggests that Paruna is able to support the grazing pressures of both herbivores (Woolnough and Johnson 2000).

In the event of a reduction in shared food resource availability, but not quality, *P. l. lateralis* could potentially have a competitive advantage over *M. fuliginosus* as their intake requirements are smaller and therefore more easily met (Illius and Gordon 1987; Tuft et al. 2011a). However, if shared food resource quality declines, *M. fuliginosus* are likely to have an advantage as they can digest poorer quality forage (Dawson

1989) and also forage further to fulfil their nutrient requirements (Tuft et al. 2011a). The reduced rainfall and increased temperatures, and consequently increased frequency and severity of droughts and bushfires, expected for southwest Western Australia as a result of climate change may contribute to this decline. *Macropus fuliginosus* may also compete with *P. l. lateralis* through interference competition; preventing them from accessing optimal foraging patches (Tuft et al. 2011a). In these circumstances, *M fuliginosus* may adversely affect *P. l. lateralis* and consequently require proactive management (Woolnough and Johnson 2000).

Rather than dietary competition, predation is likely the greatest threat to *P. l. lateralis* in Paruna. It was suspected to cause the population decline of almost fifty per cent between 2010 and 2014, after which an intensive predator control program was implemented. Poison baiting and trapping around the outcrops has now reduced predation pressure to the extent that *P. l. lateralis* recruitment has recommended, however recent annual capture-mark-recapture monitoring suggests that the population is still declining (Palmer 2018).

Although the lower number of captures may just be the result of individuals having dispersed to colonise other outcrops in the sanctuary, it might also be due to predation by feral cats for two main reasons. First, they have persisted in higher numbers on the outcrops compared to foxes, likely because they are less susceptible to baiting and trapping (Algar et al. 2007; Molsher 2001; Read and Ward 2011; Short et al. 1997). Mesopredator release (Johnson 2006) may have also occurred, as fox suppression will have reduced interference and dietary competition. Second, feral cats prey on *P. lateralis* elsewhere (Hegglun 2018; Read et al. 2019; H. Crawford, pers. comm.). They also continually invade *P. l. lateralis* foraging and shelter habitat (Pentland 2014). Their presence at the new site, combined with the lower quality shelter habitat (i.e. less structurally complex rock refuges) compared to the release site, may be responsible for the considerably lower use of the outcrop by *P. l. lateralis*.

Feral cats are notoriously difficult to control and will continue to incur into Paruna while it remains only partially protected by a predator-proof fence along its southern boundary. Extension of the fence to encompass the entire sanctuary would support complete predator eradication. In addition to the benefits this would bring resident *P. l. lateralis*, it will also improve the future success of supplementary translocations. Predator-proof exclosures at Nangeen Hill and in the Musgrave Ranges in South Australia have achieved excellent conservation outcomes for resident *P. l. lateralis* and *P. lateralis* MacDonnell Ranges race respectively (R. Boyland, WWF Australia, pers. comm.; Chauvin 2015; Muhic *et al.* 2012).

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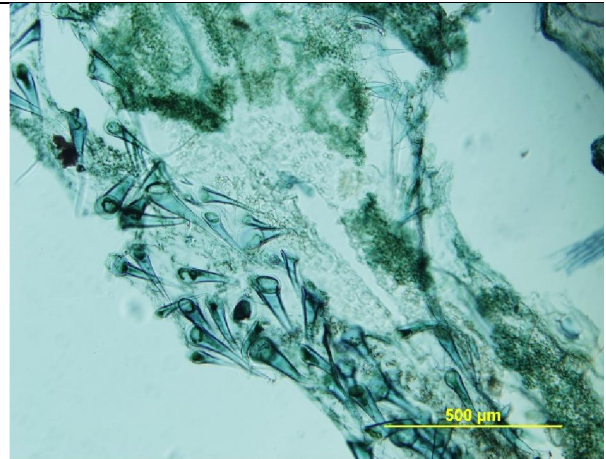
5. APPENDICES

Table A1:   Plant reference library
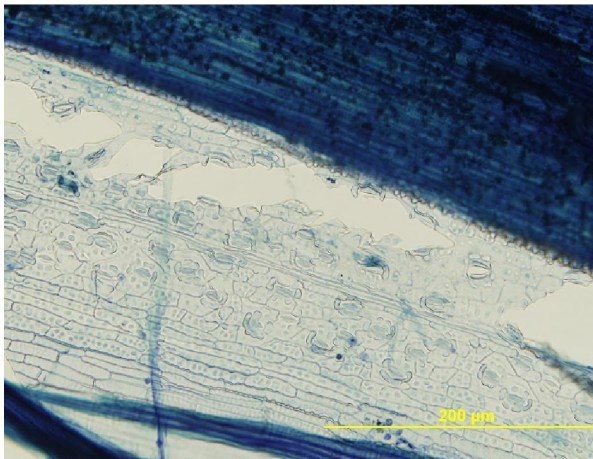
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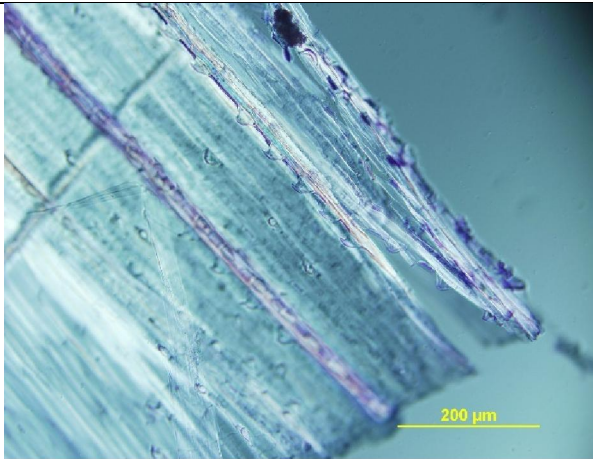
*Aira praecox (200x magnification)

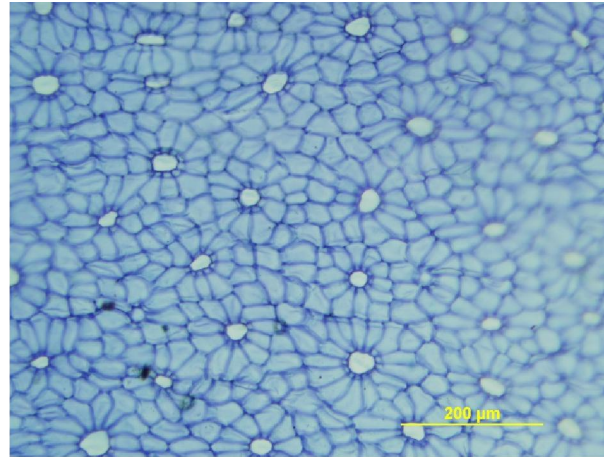**Bellardia trixago* (100x magnification)

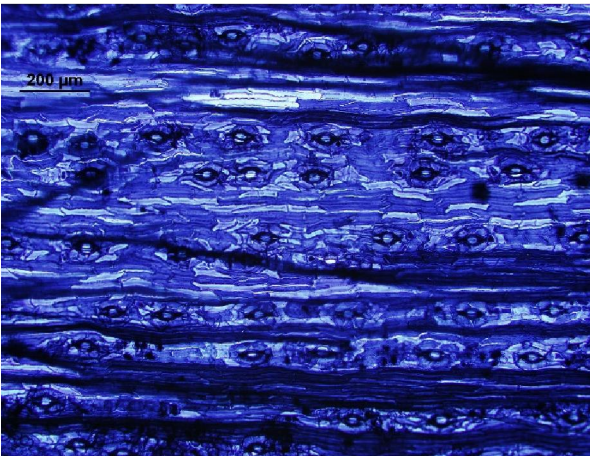*Borya sphaerocephala* (400x magnification)

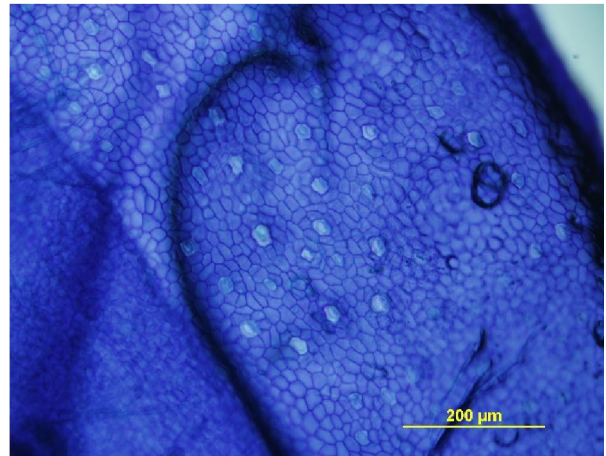*Eucalyptus accedens* (100x magnification)

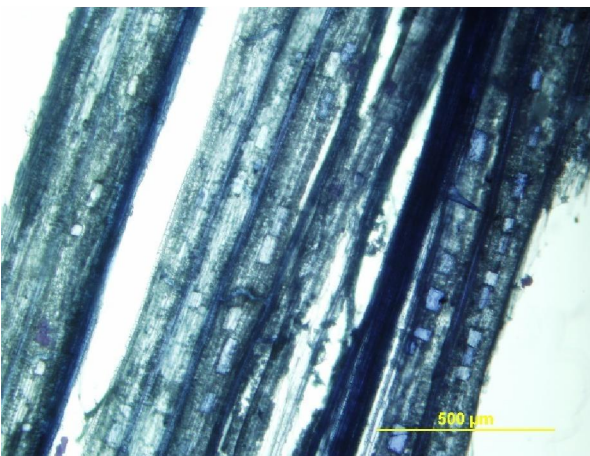*Ehrharta longiflora* (200x magnification)

(Chauvin 2015)

Hakea cristata (200x magnification)

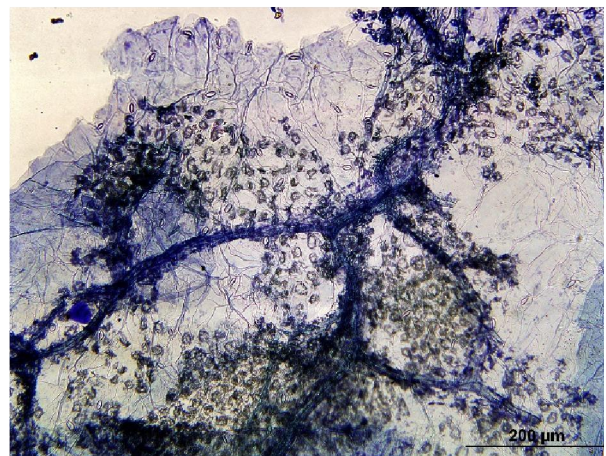

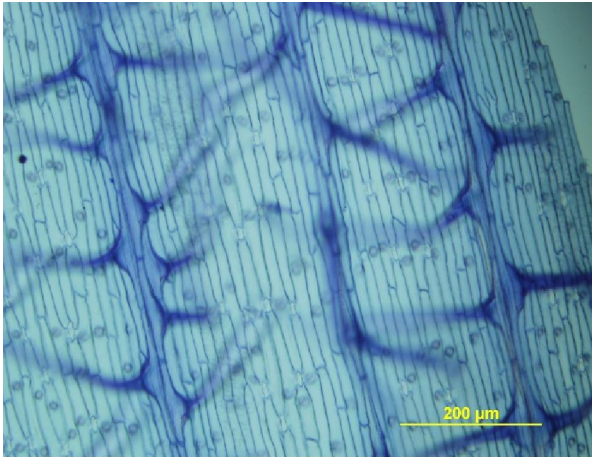*Macrozamia riedlei* (200x magnification)

(Chauvin 2015)

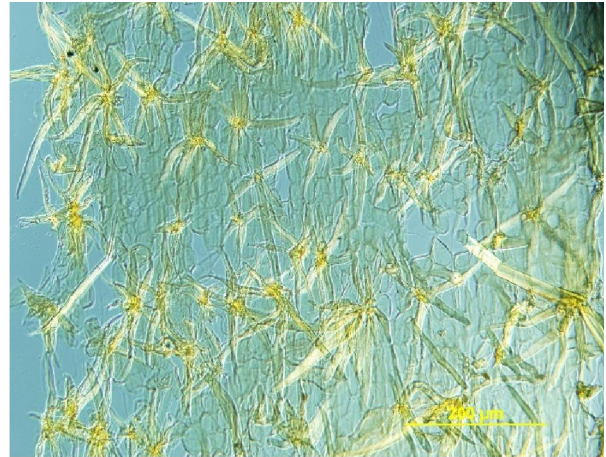*Melaleuca radula* (200 magnification)

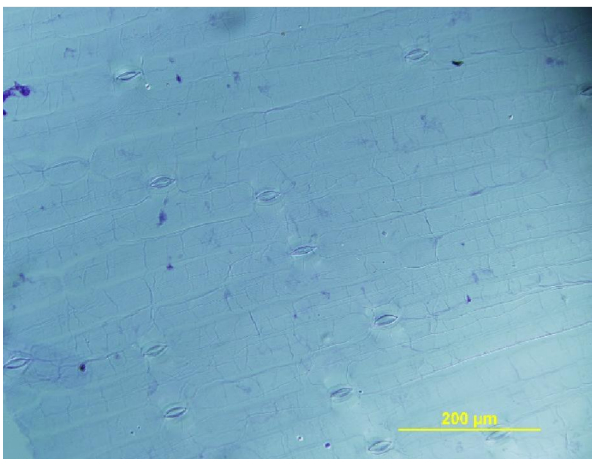*Neurachne alopecuroidea* (100x magnification)

Sonchus oleraceus (200x magnification)

(Chauvin 2015)

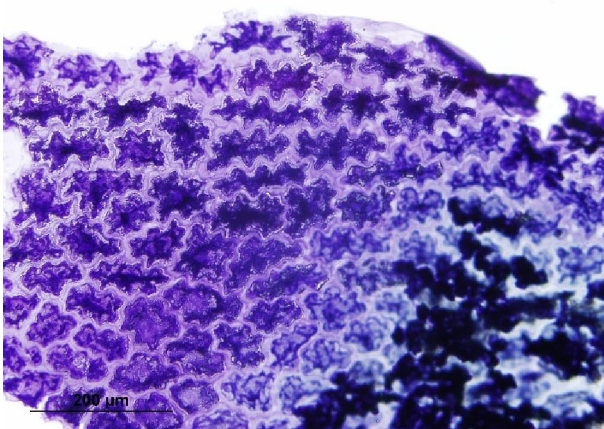*Orthrosanthus laxus* (200x magnification)

Trymalium odoratissimum odoratissimum

(200x magnification

Tricoryne elatior (200x magnification)

Pteridophyte

Cheilanthes austrotenuifolia (200x magnification) (Chauvin 2015)