

Diet of herbivorous marsupials in a *Eucalyptus marginata* forest and their impact on the understorey vegetation

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Received April 1996; accepted February 1997

Abstract

Wire exclosures were established to exclude herbivores in remnant jarrah (*Eucalyptus marginata*) forest vegetation within the Perup Nature Reserve, south-western Australia, and were assessed after a 10 year period. Significantly higher plant cover values were recorded for a number of species protected from herbivory inside the exclosures compared to outside. Sub-shrubs and vines showed the greatest increase in vegetation cover within exclosures. *Bossiaea ornata*, *Billardiera variifolia*, *Opercularia hispidula*, *Logania serpyllifolia* and *Tetrarrhena laevis* were most favoured by herbivore exclusion in terms of relative abundance.

Faecal analysis confirmed that plant species having the greatest decrease in cover outside wire exclosures were consumed by one or more of the five predominant marsupial herbivores of the Perup forest. Faecal material collected over three sampling periods during 1992 revealed a total of 42 different plant species. The largest of the herbivores, the western grey kangaroo (*Macropus fuliginosus*), consumed the greatest diversity of plants (32 species in total), while the black-gloved wallaby (*Macropus irma*) and the tammar wallaby (*Macropus eugenii*) grazed 21 and 25 different species, respectively. The common brush-tail possum (*Trichosurus vulpecula*) consumed leaves from the two dominant trees of the region *Eucalyptus marginata* and *E. calophylla*, and four understorey species including *Leptomeria cunninghamii* and *Hakea lissocarpha*. Faecal samples of the western ring-tail possum (*Pseudocheirus occidentalis*) contained only forest canopy species.

This study has implications for appropriate flora and fauna management of nature reserves. Possible competition for plant resources was indicated by diet overlap. However, due to the polyphagous nature of these particular herbivores and an ability to shift resource preferences, competitive limitations of particular food resource species in the Perup Nature Reserve are unlikely. As herbivores have been shown to reduce plant cover in the area and, therefore, the rate of build up of fire fuels, their population management and potential impact in the Perup forest are important considerations for fire management plans in the forest.

Introduction

The Perup Nature Reserve (40000 ha; 34° 16' S, 116° 36' E) is located 45 km east of Manjimup in the south-west of Western Australia (Fig 1). The Perup forest is partially contiguous with other state forest lands, but is primarily surrounded by cleared farmlands. The Perup Nature Reserve is designated as a fauna management priority area (MPA) due to the documented presence of 21 species of native mammals, including at least five gazetted as rare or endangered (Christensen *et al.* 1985; Wardell-Johnson & Nichols 1991).

A knowledge of the range of plant life forms, leaf characteristics and species consumed by a diverse community of herbivores was considered desirable for greater understanding of individual dietary requirements, herbivore interactions and potential impact on vegetation. This would provide a basis for management

decisions on fuel reduction burns, habitat management fires and predator control.

This study had four aims. Firstly, to determine floristic differences between herbivore exclosures and adjacent open sites in the Perup Nature Reserve. Secondly, to document food resources utilised by the five major native herbivorous marsupials found within the area and determine possible factors influencing diet choice. Thirdly, to compare the findings from this study with other dietary studies of marsupial herbivores in reserves around the state and, finally, to assess possible management implications for the Perup Nature Reserve.

Materials and Methods

Study site

The topographic relief of the Perup Nature Reserve includes low undulating ridges separated by broad, flat valleys with seasonal swamps and streams in the lower

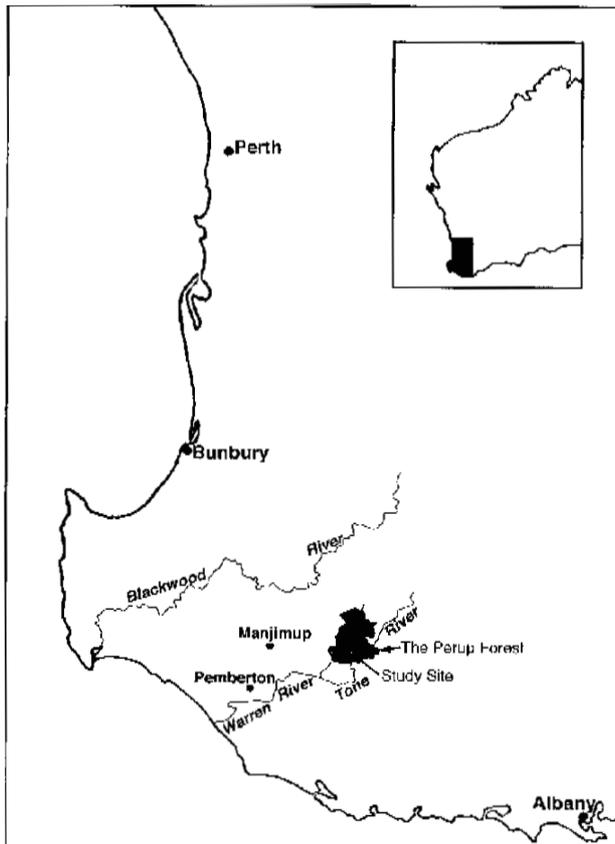


Figure 1. Location of the study site in the Perup Nature Reserve.

regions (Christensen 1980). The vegetation of the area is predominantly open jarrah (*Eucalyptus marginata*) along the ridges on lateritic soils, while marri (*Eucalyptus calophylla*) occurs more commonly in the valleys on the sandier soils. The understory strata of the ridges and slopes are dominated by a diverse mixture of low (< 1 m) xeric shrubs with the common species being *Hakea lissocarpa*, *Leucopogon capitellatus* and *Bossiaea ornata*. Tall thickets (> 1m) form in some areas following a fire. These thickets are generally dominated by single species, either *Gastrolobium bilobum*, *G. spinosum*, *Melaleuca viminea* or *Acacia pulchella* (Christensen 1977; Buchanan & Wardell-Johnson 1990).

The Perup Nature Reserve was burnt frequently from the late 1930's to the mid 1960's. Cyclic fuel-reduction burning that is dependent on litter build-ups was initiated in the 1960's under the control of the Forest Department and subsequently the Department of Conservation and Land Management. More recently, it was recognised that a combination of intense autumn fires lit under dry soil conditions and milder spring fires was required to maintain the monospecific thickets and to stimulate the regrowth of the legume plant species (Christensen & Maisey 1987). In the presence of the European fox (*Vulpes vulpes*), these *G. bilobum* thickets are essential as refugia for the tammar population within the Perup forest (Christensen 1980).

Marsupial herbivore species

This study assessed the plant species consumed by five marsupial herbivores; the western grey kangaroo

(*Macropus fuliginosus*), the black-gloved wallaby (*Macropus irma*), the tammar wallaby (*Macropus eugenii*), the common brush-tail possum (*Trichosurus vulpecula*) and the western ring-tail possum (*Pseudocheirus occidentalis*). The western grey kangaroo (30-50 kg) has a wide distribution, extending from Western Australia across the continent to Victoria and central New South Wales (Poole 1983). The black-gloved wallaby is found only in the south-west of Western Australia (Christensen 1983). Although this large wallaby (7-9 kg) now occurs only in isolated populations, it is found in reasonable numbers within its natural range. The tammar wallaby, a smaller marsupial herbivore (5.5-7.5 kg), was once distributed over a diverse array of habitats prior to European settlement. This species is now gazetted as threatened and is restricted to a number of small isolated populations on coastal islands (Bell *et al.* 1987; Poole *et al.* 1991) and on the mainland of the south-west of Western Australia. The largest population on the mainland occurs in the Perup forest near dense *Melaleuca viminea* and *Gastrolobium bilobum* thickets which provide protection from predators such as foxes and feral cats (Christensen 1992). Populations of the common brush-tail possum occur in the forested regions of Western Australia and its distribution extends to eastern Australia (How 1983). The range of the western ring-tail possum is restricted to a few remnant jarrah forest and near-coastal *Agonis flexuosa* woodlands of the south-west of Western Australia (Jones *et al.* 1994a).

Exclosure methods

In autumn of 1981 following a prescribed burn, six wire-mesh exclosures were constructed along the eastern side of a 100 m section of the Glendale 2 Road, 1.5 km south of De Landgraaf Road in the Perup Nature Reserve (Inions *et al.* 1989). The exclosures were positioned along the upper to mid-slope of a broad valley within open jarrah/marri forest. The exclosures were approximately 1.5 m in height and 100 m² in area. They exclude all ground-dwelling mammals and it is unlikely that the arboreal possums gained access to the exclosed areas by traversing across the canopies of adjacent trees due to low canopy continuity at Perup. The possums are more likely to descend to ground level and walk to adjacent trees (Jones *et al.* 1994a). The area east of the Glendale 2 Road was subsequently burnt in 1984/1985 and the area to the west of the road was burnt in 1985/1986. In the winter of 1991, species cover within the six exclosures was determined along five, 10 m transects spaced 1 m apart using the point interception method (Mueller-Dombois & Ellenberg 1974). Pins were placed at 20 cm intervals along the transects (250 points per plot). Using the same methods, plant species cover values were also obtained for 19 open areas surrounding the exclosures. Mean cover values for the plant species inside and outside the wire exclosures were compared after arcsin transformation using a two-tailed Student's t-test.

Leaf epidermal material

A reference collection of prepared epidermal tissue slides of 67 species from the study site facilitated the microscopic identification of plant fragments recovered from faecal material. Epidermal vouchers were prepared using a modification of the acid digestion methods outlined

by Storr (1961) and Halford *et al.* (1984a). Leaf blades were covered in a 50% glacial acetic acid solution and heated in a water bath at 80 °C for 24-72 h. The fragments were then rinsed in water and any remaining fibrous tissue was removed. The cleared leaf fragments were then dehydrated through a series of ethanol solutions (increasing in concentration to 95%) and stained by immersion in 0.5% gentian violet in 95% alcohol for 48 h. The fragments were washed in 95% alcohol and mounted on slides using Eukit® permamount. Diagnostic line drawings of the epidermal tissue patterns, especially the guard cell complexes, were produced for each species as a further aid to identification.

Faecal material

Faecal pellets for each of the five common marsupial species in the area are distinctive in shape and size and can be easily separated by sight (P Christensen & C Wheeler, *pers comm*). Pellets were collected from a mid-slope area approximately 150 m by 500 m in the jarrah/marri open forest surrounding the exclosures. This area extended from the vicinity of the exclosures, down a westward facing slope into a low-lying gully. In contrast to the upper and mid-slope areas, large trees were absent in the gully being replaced by a dense thicket of *Gastrolobium bilobum* approximately 2 m in height. Fresh faecal pellets were collected over three sampling periods from the autumn through spring period of 1992.

The plant species consumed by the marsupial herbivores were determined by comparison of epidermal fragments in faecal material to the plant voucher specimens. However, a more rigorous digestion technique was required for preparation of the faecal pellets than for the plant vouchers. Single, air-dried faecal pellets were fragmented, placed in test tubes and covered with equal parts of 10% chromic acid and 10% nitric acid. The test tubes were heated in an acid digestion block at 80-100 °C within a fume hood, simmering the contents for 15-20 min. After maceration the contents were cooled to room temperature, and filtered with several washes of dilute potassium hydroxide solution and distilled water. The filtrate was sieved through a 0.5 mm sieve, collected and stained with 0.5% gentian violet in 95% alcohol. The fragmented plant material was scanned using the dissecting microscope at 12.5-50x magnification, mounted on slides with Eukit and compared with the voucher collection for species identification. As an index of dietary preference, the percentage occurrence of a plant species was determined by noting the proportion of the sampled pellets that included a particular plant species.

Results

A combined total of 73 plant taxa were recorded inside the exclosures and in the adjacent vegetation at the Perup Nature Reserve study site (Table 1). Nineteen species had significantly different and greater percentage cover values inside the wire exclosures. These included *Bossiaea ornata*, *Billardiera variifolia*, *Opercularia hispidula*, *Logania serpyllifolia*, *Tetrarrhena laevis*, *Scaevola striata* and *Billardiera floribunda*. Total plant cover outside the wire exclosures was only 58% of that recorded inside. In contrast, *Macrozamia riedlei*, *Eucalyptus marginata* and *Hibbertia commutata* had significantly greater cover values outside

the exclosures. Of the species showing a significant lower cover outside exclosures, 42% were small sub-shrub species, semi-woody or fibrous herbaceous perennials less than 0.5 m in height, and 26% were perennial vines and twining plants (Table 2).

Table 1

Plant cover values comparing wire exclosure treatments and adjacent open areas. * indicates significant difference by two-tailed t-test (≤ 0.05) following arcsin transformation. Plant classes: C, cycad; M, monocotyledon; D, dicotyledon. Life form: Tree, plant over 2 m height; Shrub, woody plant 0.5 - 2.0 m in height; Sub-shrub, semi-woody or fibrous herbaceous perennial < 0.5 m; Vine; twining perennial; Herb, mesophytic herbaceous perennial or annual.

Species	Percentage Cover		Plant Class	Life Form
	Inside	Outside		
<i>Bossiaea ornata</i>	24.6	4.0*	D	Shrub
<i>Billardiera variifolia</i>	13.8	1.2*	D	Vine
<i>Leucopogon capitellatus</i>	12.5	15.4	D	Sub-shrub
<i>Opercularia hispidula</i>	10.6	0.6*	D	Sub-shrub
<i>Logania serpyllifolia</i>	9.8	0.5*	D	Shrub
<i>Tetrarrhena laevis</i>	9.7	0.2*	M	Sub-shrub
<i>Hakea lissocarpa</i>	8.0	11.5	D	Shrub
<i>Xanthorrhoea gracilis</i>	7.7	6.4	M	Sub-shrub
<i>Drosera macrantha</i>	6.9	4.0	D	Herb
<i>Eucalyptus calophylla</i>	6.6	5.8	D	Tree
<i>Scaevola striata</i>	6.6	1.1*	D	Sub-shrub
<i>Billardiera floribunda</i>	6.2	0.2*	D	Vine
<i>Tricoryne elatior</i>	5.6	2.8	M	Sub-shrub
<i>Clematis pubescens</i>	5.1	0.9*	D	Vine
<i>Tetratheca affinis</i>	5.0	0.3*	D	Sub-shrub
<i>Chamaescilla corymbosa</i>	4.8	1.4*	M	Sub-shrub
<i>Lomandra caespitosa</i>	4.7	0.7*	M	Sub-shrub
<i>Leucopogon verticillatus</i>	4.3	4.4	D	Shrub
<i>Macrozamia riedlei</i>	4.1	9.7*	C	Shrub
<i>Eucalyptus marginata</i>	3.9	11.4*	D	Tree
<i>Hibbertia amplexicaulis</i>	3.5	4.5	D	Shrub
<i>Danthonia pilosa</i>	3.4	1.8	M	Herb
<i>Lageniphora huegelii</i>	3.2	1.3	D	Herb
<i>Cassytha sp</i>	3.0	0.0*	D	Vine
<i>Gastrolobium bilobum</i>	2.8	4.4	D	Shrub
<i>Pterostylis nana</i>	2.7	0.4*	M	Herb
<i>Leptomeria cunninghamii</i>	2.5	0.5*	D	Shrub
<i>Thysanotus patersonii</i>	2.4	0.0*	D	Vine
Grass A	2.1	1.3	M	Herb
<i>Xanthosia atkinsoniana</i>	2.0	1.1	D	Sub-shrub
<i>Agrostocrinum scabrum</i>	1.9	0.0*	M	Herb
<i>Lomandra preissii</i>	1.8	3.0	M	Sub-shrub
<i>Loxocarya fasciculata</i>	1.8	1.2	M	Sub-shrub
<i>Acacia pulchella</i>	1.5	1.1	D	Shrub
<i>Acianthus reniformis</i>	1.5	3.1	D	Herb
<i>Amphipogon</i>				
<i>amphipogonoides</i>	1.5	0.0*	M	Herb
<i>Lomandra integra</i>	1.5	0.5	M	Sub-shrub
<i>Xanthorrhoea preissii</i>	1.2	0.3	M	Shrub
<i>Caladenia repens</i>	1.2	0.7	M	Herb
<i>Comesperma confertum</i>	1.2	0.0*	D	Sub-shrub
<i>Leucopogon propinquus</i>	1.2	0.9	D	Sub-shrub
<i>Lomandra sp #4</i>	1.2	0.6	M	Sub-shrub
<i>Stackhousia monogyna</i>	1.2	0.0*	D	Sub-shrub
<i>Boronia spathulata</i>	0.6	0.9	D	Shrub
<i>Pimelea rosea</i>	0.6	0.4	D	Shrub
<i>Xanthosia candida</i>	0.6	0.4	M	Sub-shrub

Table 1 (continued)

Species	Percentage Cover		Plant Class	Life Form
	Inside	Outside		
<i>Acacia saligna</i>	0.0	0.1	D	Shrub
<i>Astroloma ciliatum</i>	0.0	0.1	D	Shrub
<i>Craspedia uniflora</i>	0.0	1.0	M	Herb
<i>Danthonia setacea</i>	0.0	0.3	M	Herb
<i>Daviesia preissii</i>	0.0	0.7	D	Shrub
<i>Hibbertia cunninghamii</i>	0.0	1.9	D	Shrub
<i>Hibbertia montana</i>	0.0	6.7*	D	Shrub
<i>Hibbertia racemosa</i>	0.0	0.3	D	Shrub
<i>Leucopogon australis</i>	0.0	1.0	D	Shrub
<i>Lomandra sericea</i>	0.0	0.2	M	Sub-shrub
<i>Lomandra sonderi</i>	0.0	0.2	M	Sub-shrub
<i>Lomandra</i> sp #1	0.0	0.7	M	Sub-shrub
<i>Lomandra</i> sp #2	0.0	0.2	M	Sub-shrub
<i>Loxocarya flexuosa</i>	0.0	0.2	M	Sub-shrub
<i>Melaleuca viminea</i>	0.0	0.4	D	Shrub
<i>Neurachne alopecuroidea</i>	0.0	0.2	M	Herb
<i>Patersonia occidentalis</i>	0.0	0.8	M	Sub-shrub
<i>Pentapeltis peligera</i>	0.0	0.1	D	Herb
<i>Persoonia longifolia</i>	0.0	0.4	D	Tree
<i>Phyllanthus calycinus</i>	0.0	0.2	D	Shrub
<i>Stipa</i> sp	0.0	0.3	M	Herb
<i>Stylidium adnatum</i>	0.0	0.1	D	Herb
<i>Tetrariopsis octandra</i>	0.0	0.2	M	Sub-shrub
<i>Trachymene pilosa</i>	0.0	0.6	D	Herb
<i>Tremandra diffusa</i>	0.0	0.4	D	Sub-shrub
<i>Trymalium ledifolium</i>	0.0	0.3	D	Shrub
Dicotyledon #1	0.0	0.3	D	Shrub

Table 2

Plant life forms within the Perup study area (n = 73) and the percentage of life forms of the species showing potential of being selected by herbivores by recording a significantly lower cover outside the exclosures (n = 19).

	All Species	Reduced Value Species
Sub-Shrub	36	42
Shrub	31	16
Vine	7	26
Herb	22	16
Tree	4	0

Forty-two plant species in total were identified from the macropod faecal pellets, including both monocotyledonous and dicotyledonous species of varying life forms, together with 12 unidentified species (Table 3). Faeces of the largest of the herbivores, the western grey kangaroo, had 32 species in total, with a range of six to 13 different species found per faecal pellet (Fig 2). Analysis of the individual faecal pellets indicated that the sedge *Lepidosperma tenue* was an important dietary component for the western grey kangaroo, occurring in 89% of the pellets sampled (Table 3). Other species frequently consumed (occurring in ≤ 67% of pellets sampled) included *Danthonia setacea*, an unknown monocotyledon (#1), *Gastrolobium bilobum* and a *Loxocarya* species. Sixteen

species were selected relatively infrequently, occurring in only 11% of the pellets sampled.

Table 3

Frequency of occurrence of plants recovered from herbivore faecal pellets collected in the Perup Nature Reserve. The plant species are ordered in approximate order of overall percentage.

	Western grey kangaroo	Black-gloved wallaby	Tammar wallaby	Brush-tail possum	Ring-tail possum
Monocotyledon #1	78	86	50		
<i>Danthonia setacea</i>	78	43	80		
<i>Gastrolobium bilobum</i>	67	43	50	40	
<i>Eucalyptus marginata</i>		14	17	60	100
<i>Hakea lissocarpha</i>	56	43	17	60	
<i>Loxocarya</i> sp	67	14	50		
<i>Bossiaea ornata</i>	33	86			
<i>Leucopogon capitellatus</i>	56	29	33		
<i>Lepidosperma tenue</i>	89		17		
<i>Acacia pulchella</i>	11	43	50		
<i>Eucalyptus calophylla</i>	11		67	20	10
<i>Leptomeria cunninghamii</i>			17	80	
Monocotyledon #2	11	43	33		
Dicotyledon #6		14	67		
Dicotyledon #1	44	29			
<i>Opercularia hispidula</i>	11	29	33		
<i>Juncus pallidus</i>	22	14	33		
<i>Cassya</i> sp		29	33		
<i>Lomandra sericea</i>	11	14	33		
<i>Leucopogon verticillatus</i>	22	14	17		
<i>Tetraria octandra</i>			50		
Monocotyledon #3		14	33		
Monocotyledon #4	11		33		
<i>Boronia spathulata</i>	11	29			
<i>Daviesia preissii</i>	33				
<i>Lepidosperma angustatum</i>	33				
<i>Lomandra sonderii</i>			33		
Dicotyledon #5			33		
<i>Tetrarrhena laevis</i>	33				
<i>Billardiera variifolia</i>	11			20	
<i>Melaleuca viminea</i>	14	14			
Monocotyledon #5	11		17		
<i>Neurachne alopecuroidea</i>	22				
<i>Centaurium erythraea</i>			17		
Dicotyledon #7		14			
<i>Astroloma ciliatum</i>	11				
<i>Kennedia carinata</i>	11				
<i>Lomandra</i> sp #3	11				
Dicotyledon #2	11				
Dicotyledon #3	11				
Dicotyledon #4	11				
Dicotyledon #8	11				

Twenty-one plant species were identified from the black-gloved wallaby pellets (Table 3), including four to nine plant species per sample (Fig 2). *Bossiaea ornata* and the unknown monocotyledon (#1) were frequent constituents of the black-gloved wallaby diet, being found in 86% of the pellets sampled. Other species were much less frequently consumed by wallabies, each species occurring in less than 43% of the pellets sampled.

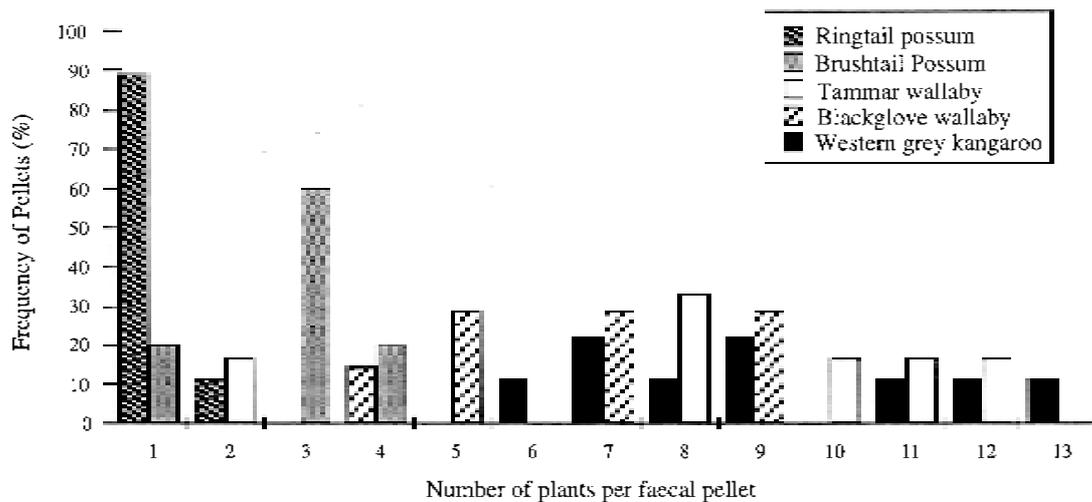


Figure 2. Frequency of plant species in sampled faecal pellets for the ring-tail possum, brush-tail possum, tamar wallaby, black-gloved wallaby and western grey kangaroo collected from the study site in the Perup Nature Reserve.

The diet of the tamar wallaby included 24 plant species in total (Table 3) with as many as 8-12 species recovered from single faecal pellets (Fig 2). One tamar faecal pellet, however, contained only two species. Plants most frequently consumed by this marsupial included *Danthonia setacea*, *Eucalyptus calophylla* and the unknown dicotyledon #6 recovered from 67-80% of the pellets sampled. Two other plant species frequently consumed, occurring in 50% of the pellets sampled, included the unknown monocot (#1) and the shrub *Gastrolobium bilobum*.

Of the plant species found in the faecal pellets, only 28% were consumed by all three macropods. The plant types ranged from the small restionaceous *Loxocarya* spp and the coarse, herbaceous sub-shrub *Opercularia hispidula*, to larger plants, such as *Juncus pallidus*. Species that have tough leaf spines as seen in *Hakea lissocarpa* and *Leucopogon capitellatus*, or stem spines as seen in *Acacia pulchella*, were also frequently grazed.

The arboreal possums appeared to consume fewer species than the macropods; also, fewer plant species were recorded per pellet during any one feeding period (Fig 2). The brush-tail possum diet consisted of six species (Table 3) with between one and four species per pellet (Fig 2). The most frequently consumed species included the understorey shrub *Leptomeria cunninghamii* and the two dominant tree species, *Eucalyptus marginata* and *E. calophylla*. Other understorey plants found in faecal material included the tall shrubs, *H. lissocarpa* and *G. bilobum*, and the vine *Billardiera variifolia*. Analysis of faecal pellets of western ring-tail possum revealed mainly *E. marginata* leaves, although fragments of *E. calophylla* were also retrieved from a single faecal sample. In addition to leaf epidermal fragments, pieces of seeds, bark and small insect larvae were also recovered from sampled pellets.

Discussion

After a ten-year period of herbivore exclusion, there was a floristic difference between the vegetation within

the exclosures and that of adjacent open sites in the Perup Nature Reserve. A number of species of various life forms had a significantly decreased vegetative cover when exposed to herbivory. Total plant cover was also much reduced outside the wire exclosures.

Dietary studies assist in understanding how herbivores utilise and subsequently influence their environment. Faecal analysis is an indirect but accurate means of determining the specific food resources consumed by herbivores (Scotcher 1979; Johnson & Pearson 1981; Holechek *et al.* 1982). The presence of cuticular material of plant species showing a decrease in vegetative cover in pellets collected from the five native herbivores within the Perup Nature Reserve, suggest that these herbivores have a significant impact on a broad range of species.

The Perup Nature Reserve is an important faunal reserve and an understanding of the resources required by the resident herbivores is essential to ensure appropriate management practices. The consumption of such a diverse array of species by the predominant herbivores may minimise the problem of overgrazing of any particular species. The ability of animal populations to selectively control relative densities of plant populations has been observed (Brown & Stuth 1993), but the complete elimination of a species or particular life forms from a natural ecosystem is unlikely. Murden & Risenhoover (1993), using additions of a known high-quality food supplement to assess the effects of forage quantity and quality on patterns of resource use, found that deer and goats continued to feed on a range of native plant species despite the presence of material of enhanced nutritional value. Their data suggest that normal behavioural patterns in large, free-ranging herbivores promote a polyphagous resource base, and thus reduce the probability of excessive utilisation pressure on any particular forage species. Although the marsupial herbivores of the Perup Nature Reserve showed particular preferences, the diversity of plant resources consumed indicates an ability to shift to other species when one plant species becomes less available. Increased emphasis on the land management practices designed preferentially for maintenance of the herbivores

in this Reserve, specifically maintaining stable population numbers, should not adversely affect the survival of particular plant species.

A comparison of plant species consumed by different herbivores potentially utilising the same food resource may give some indication of the interactions between herbivores and possible influences of diet choice. The overlap of plant species consumed by the large macropods indicates that there may be competition for resources in the Perup Nature Reserve. However, the herbivores tended to consume plants that were common in the understorey and, therefore, these are unlikely to become limiting. The polyphagous nature of these herbivores also allows them to graze a number of plant species at any one time, further limiting competition for specific plant resources.

The choice of plant species consumed may be influenced by a number of factors. Many researchers have tried to determine what specifically influences diet choice as it is unknown whether animals select items on the basis of nutritional content, avoidance of toxic compounds or physical deterrents, such as leaf and stem spines. The grazing of a diverse number of species as seen in the Perup marsupial herbivores may preclude problems of nutritional deficiency. Also, by consuming small amounts of plant material relatively infrequently, inherent multifunction oxidate detoxification systems may break down any novel toxins present (Dawson 1989). The herbivores of the Perup Nature Reserve do not appear to be deterred by the physiological and morphological defence characteristics that have evolved in Australian plants. These herbivores consumed species that have sharp stem spines (*Acacia pulchella*) and leaf spines (*Hakea lissocarpha*) or high concentrations of toxic compounds (*Gastrolobium bilobum* and *Eucalyptus* sp) (Freeland & Janzen 1974; Hume *et al.* 1984; Owen-Smith & Cooper 1987; Robbins *et al.* 1987). *Gastrolobium bilobum* contains up to 2600 mg kg⁻¹ of the toxic compound sodium fluoroacetate (King *et al.* 1981; Twigg & King 1991). The western grey kangaroo and the tamar are fluoroacetate-tolerant (Twigg & King 1991) and this study suggests that the black-gloved wallaby also has a high tolerance as this herbivore was found to commonly consume *Gastrolobium bilobum*.

Other factors such as inherent differences in body size may also influence diet choice as may behavioural learning by the grazers. Body size may also have influenced food choice in the Perup Nature Reserve accounting for differences in the total number of species consumed by the macropods and the possums. Small animals require more energy relative to body mass than do larger animals (Freudenberger *et al.* 1989). This means that larger herbivores generally have a diet of lower nutritive value and higher fibre content than do smaller herbivores. The faecal material of the western grey kangaroo collected in the Perup Nature Reserve contained a higher number of species per pellet compared to any of the other marsupial herbivores. The kangaroo is larger in size and may retain digested material for longer periods of time, thus increasing species richness within the digestive system. Smaller animals such as the brush-tail and ring-tail possums would be expected to have high metabolic rates and nutritional requirements; however, both species consumed

mostly *Eucalyptus* leaves which have a low nutritive value and contain toxic secondary compounds (Hume *et al.* 1984). The presence of several understorey species in the faeces of the common brush-tail possum indicates that this herbivore does not rely solely on the eucalypt canopy leaves as their only food resource. Both possum species may also supplement their diet with seeds, flowers and insect larvae. Ring-tail possums were found to have a very low field metabolic rate, much lower than expected for their body size (Hume *et al.* 1984). Due to the low metabolic rate these possums have lower total energy requirements, reflected in their decreased mobility compared to the more active brush-tail possums. The stomach of the western ring-tail possum is also well adapted to a folivorous diet, as it is simple in structure with a well developed caecum. This possum has a long gut retention time for its size (38-39 hours) allowing increased fermentation of the digestible material consumed. Low field metabolic rates of the ring-tail possum are reflected in low consumption rates, further minimising the consumption of the toxic compounds in the *Eucalyptus* foliage.

The differences in diet preference between individuals and between different species may also reflect behavioural learning and experience. Animals sample and continue to consume a range of species which they can tolerate while others may have encountered and subsequently utilise, a different range of plants (Bartmann & Carpenter 1982; Provenza & Balph 1987, 1988; Gillingham & Bunnell 1989). The results of these analyses allow a direct comparison of the food resources utilised by the macropod species within the Perup Nature Reserve to other populations found in the state. Of major interest is the consumption of predominantly dicotyledonous species by the western grey kangaroos. This is in contrast to the mixed diet of both dicotyledon and monocotyledon species recorded for populations of western grey kangaroos in pasture dominated landscape near Bakers Hill, Western Australia (Halford *et al.* 1984b; Bell 1993) and consumption of mainly monocotyledonous herbs in a *Banksia* woodland near Perth (Algar 1986). These differences in diet preference most likely reflect a difference in the predominance of these two subclasses as an available food source in the three study areas.

The dietary findings for the black-gloved wallaby in the Perup Nature Reserve were consistent with those of Algar (1986) who found a wide range of species in the diet, a majority of which were dicotyledons. He also recorded the consumption of tough sedge-like monocotyledons of the *Banksia* woodland habitat.

The tamar wallabies on Garden Island consumed a number of species, but preferred grasses or new shoots that appear following a burn (Bell *et al.* 1987). Christensen (1977) suggested that tamar wallabies in the Perup region rely almost entirely on the grasses associated with *Gastrolobium bilobum* thickets. It is evident from this study, however, that these wallabies consume a much wider range of species than those immediately associated with their daytime refugia. Thus, tammars require the maintenance of the more diverse vegetation of the upper slopes as well as the *Gastrolobium bilobum* thickets in the low lying areas.

The results from a dietary analysis by Jones *et al.* (1994b) of western ring-tail possum populations at Perup

and in isolated refugia of coastal vegetation in the south west of Western Australia indicated that the canopy foliage formed the main component of the possum diet. Pellets collected from regions of the Perup Nature Reserve away from the current study by Jones *et al.* (199b) also consisted of material of the two common canopy species, *Eucalyptus marginata* and *E. calophylla*. Analysis of pellets collected from coastal populations found that the common canopy species *Agonis flexuosa* dominated the possum diet selection (Inions *et al.* 1989).

The presence of a number of unknown plant species in the faecal material of all the macropods indicates that their foraging range extends beyond that of the immediate sampling site. Further study is essential to ensure establishment of appropriate management practices in Perup Nature Reserve to allow maintenance of marsupial herbivore population densities while considering the impact of grazing on surrounding vegetation. As all the marsupial herbivores utilise a number of common species and none of the macropods consume any single limited resource, it is unlikely that one group will out-compete another.

Fire management in native forests requires a knowledge of the accumulation of understorey vegetative material and leaf litter within specified areas. A measured decrease in the vegetative cover outside the exclosures independent of fire confirms the impact of herbivores on the vegetation of Perup Nature Reserve. The continued maintenance of stable herbivore populations will have implications for the reduction of plant cover and leaf litter buildup and may have benefits in allowing slightly increased fire intervals in the prescription burning regime for this forest. Thus an understanding of herbivore population numbers over time is essential as a marked increase in numbers can have an equally significant impact on the vegetation as would a sharp decline. These are important areas for further research and must be considered in the long-term management of this reserve.

Acknowledgments: Collection of data from the exclosures and surrounding vegetation was assisted by students in the 1992 course in Synecology. Scat identification was assisted by P Christensen and C Wheeler, Manjimup Research Centre, Department of Conservation and Land Management (CALM). Use of the Perup Forest Ecology Centre was provided by CALM during the period of the study. Special thanks also go to C Wilkins for her encouragement and invaluable comments.

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