

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/248883555>

Diets of native and introduced mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia

Article in *Wildlife Research* · January 2008

DOI: 10.1071/WR08042

CITATIONS

61

READS

535

3 authors:



Naomi Davis

University of Melbourne

26 PUBLICATIONS 478 CITATIONS

[SEE PROFILE](#)



Graeme Coulson

University of Melbourne

164 PUBLICATIONS 2,266 CITATIONS

[SEE PROFILE](#)



David M Forsyth

New South Wales Department of Primary Industries

177 PUBLICATIONS 4,206 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



MARSUPIAL BREEDING AND ASSISTED REPRODUCTION [View project](#)



Komodo Survival Program [View project](#)

Diets of native and introduced mammalian herbivores in shrub-encroached grassy woodland, south-eastern Australia

Naomi E. Davis^{A,C}, Graeme Coulson^A and David M. Forsyth^{A,B}

^ADepartment of Zoology, The University of Melbourne, Vic. 3010, Australia.

^BArthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, 123 Brown Street, Heidelberg, Vic. 3084, Australia.

^CCorresponding author. Email: ndavis@unimelb.edu.au

Abstract. Effective management of sympatric mammalian herbivore populations requires an understanding of interspecific interactions. At Wilsons Promontory National Park, Victoria, sympatric native and introduced mammalian herbivores are thought to be contributing to modification of shrub-encroached Coastal Grassy Woodland. We estimated the diets of the five terrestrial mammalian herbivore species present using microhistological techniques. The diets of introduced hog deer (*Axis porcinus*) and native swamp wallabies (*Wallabia bicolor*) consisted mainly of dicots. The diet of introduced European rabbits (*Oryctolagus cuniculus*) contained similar proportions of monocots and dicots. The diets of native eastern grey kangaroos (*Macropus giganteus*) and native common wombats (*Vombatus ursinus*) consisted mainly of monocots but kangaroos also consumed moderate amounts of dicots. Deer and wallabies consumed more native plants than did the other species and rabbits consumed more exotic plants than did all other species except kangaroos. Diet breadth was narrowest for kangaroos and broadest for swamp wallabies and hog deer. Overlap in food use by the five herbivores was high, particularly between deer and wallabies, and between kangaroos and both rabbits and wombats. Our results suggest that the potential impacts of native and introduced species on the vegetation of Coastal Grassy Woodland are similar, and that the entire herbivore assemblage will need to be managed to increase fine fuel loads if fire is used as a restoration tool.

Introduction

Both native and introduced mammalian herbivores can seriously modify plant communities at a variety of spatial scales (e.g. Côté *et al.* 2004; Holdo 2007). Although there is a long history of single-species herbivore management (e.g. Petty *et al.* 2007), interactions between sympatric species (Parkes and Forsyth 2008) can generate unexpected management outcomes. For example, if a population of one species is reduced, impacts of that species on vegetation composition may be replaced by those of another species (Coomes *et al.* 2003). Given that communities globally are increasingly composed of native and introduced plants and herbivores (e.g. Madhusudan 2004), it is important to understand key interactions within these communities so that management actions are effective.

A wide variety of introduced mammalian herbivores have established populations in Australia (Forsyth *et al.* 2004), and many of these species are now sympatric with native herbivores (e.g. Dawson and Ellis 1996). Native and introduced herbivores may have different impacts on native vegetation (Simonetti and Fuentes 1983) but few studies have evaluated the relative impacts of different herbivore species in Australia (Bridle and Kirkpatrick 1999). In this study, we show how diet analysis can be used to provide insight into the roles of five sympatric native and introduced herbivores in the modification of an Australian grassy woodland ecosystem affected by the recent global phenomenon of shrub encroachment (Sankaran *et al.* 2008).

On Yanakie Isthmus (Wilson's Promontory National Park, Victoria), Coastal Grassy Woodland has undergone dramatic changes in structure and composition (Bennett 1994). Originally consisting of open grassy woodland, it is now dominated by dense stands of the encroaching native shrubs *Leptospermum laevigatum* and *Acacia longifolia* var. *sophorae*, which suppress the regeneration of other native species (Bennett 1994; Costello *et al.* 2000). In the absence of active management, it is predicted that the condition of Coastal Grassy Woodland will continue to deteriorate (Holland and Williams 2005).

Fire and grazing have been implicated in the encroachment of woody plants into grasslands and savannas worldwide (Roques *et al.* 2001). Chesterfield (1998) suggested that, on Yanakie Isthmus, alterations in fire and grazing regimes have interacted synergistically to influence Coastal Grassy Woodland. Fire has been excluded from Yanakie Isthmus since the 1970s (Bennett 1994), favouring the encroachment of the fire-sensitive species *L. laevigatum* and *A. longifolia* (Lunt 1998). Concomitant with this decrease in fire frequency on Yanakie Isthmus, there appears to have been an increase in grazing pressure from mammalian herbivores (Chesterfield *et al.* 1995), another process that can contribute towards the degradation of temperate woodlands (Yates and Hobbs 1997). Managers believe that Coastal Grassy Woodland can be restored by using fire to reduce the abundance of *L. laevigatum* and stimulate regeneration of fire-

adapted native species (Holland and Williams 2005), an approach that has been effective in reversing shrub-encroachment in African savannas (Roques *et al.* 2001). However, previous attempts to use fire as a restoration tool on Yanakie Isthmus have been unsuccessful, possibly due to interactions between herbivory and fire: high herbivore population densities may reduce the vegetation biomass and thus deplete fuel loads, thereby reducing the frequency and extent of fires (Holland and Williams 2005).

Native herbivores can cause changes in vegetation composition and structure (e.g. Garrott *et al.* 1993), yet there is a perception that such impacts are not as great as those of introduced herbivores (Bentley 1998). On Yanakie Isthmus, introduced European rabbits (*Oryctolagus cuniculus*) are considered a pest owing to their well documented impacts on the diversity and regeneration of native flora elsewhere in Australia (Williams *et al.* 1995). Similarly, detrimental effects of introduced deer on vegetation dynamics have been well documented outside Australia (Côté *et al.* 2004), and there is concern among managers about the potential impacts of introduced hog deer (*Axis porcinus*) on the composition of Coastal Grassy Woodland vegetation. In contrast, there is less concern about potential impacts from the three terrestrial native mammalian herbivores, the eastern grey kangaroo (*Macropus giganteus*), the swamp wallaby (*Wallabia bicolor*) and the common wombat (*Vombatus ursinus*).

We used microhistological techniques to estimate the diets of the five common mammalian herbivore species on Yanakie Isthmus to improve our understanding of the potential impacts of native and introduced herbivores on the vegetation of Coastal Grassy Woodland in the context of encroachment by *L. laevigatum* and reduction in fine fuel load. Specifically, we aimed to compare the diets of each of the five herbivore species with respect to the use of different plant functional groups, different plant structural layers and the use of exotic and native plants.

Materials and methods

Study area

We conducted this study on Yanakie Isthmus (38°53'S, 146°14'E), a 6874-ha area of Wilsons Promontory National Park, Victoria, Australia. The climate is mild and precipitation is reliable; between 1985 and 2005, mean monthly maximum temperatures ranged from 11.9 to 26.4°C and mean minima from 4.4 to 16.7°C, and the mean annual rainfall was 958.5 mm (Parks Victoria, unpubl. data).

Five broad vegetation types occur on Yanakie Isthmus. Coastal Grassy Woodland is dominated by *Eucalyptus pryoriana*, *Banksia integrifolia*, *Allocasuarina littoralis* and *Allocasuarina verticillata*, with occasional *Acacia mearnsii* shrubs in the understorey. The ground layer includes *Pteridium esculentum* and a variety of grasses, sedges and herbs. Coastal Scrubs and Grasslands is dominated by grasses, sedges and salt-tolerant herbs and shrubs. Heath is dominated by small ericoid-leaved shrubs and sedges, and Heathy Woodland is dominated by scattered *Eucalyptus nitida*, heathy shrubs and restionaceous sedges (Davies and Oates 1999).

Collection and preparation of stomach samples

We estimated the diet of the hog deer, eastern grey kangaroo, swamp wallaby, common wombat and European rabbit using microhistological identification of cuticle fragments of plant species in stomach samples (Norbury 1988). We obtained samples from animals shot by Parks Victoria staff for the purposes of this study (authorised under Section 37 of the National Parks Act; register no. 04004 of the University of Melbourne Animal Experimentation Ethics Committee) between 7 June 2004 and 11 February 2005. Animals were shot at night from a vehicle with the aid of a spotlight. All species were shot in accordance with the Code of Practice for the Humane Shooting of Kangaroos (Australian National Parks and Wildlife Service 1995). We aimed to collect stomach samples from 20 mature individuals of each species. All ($n=93$) of our samples were collected from Coastal Grassy Woodland and Coastal Scrubs and Grasslands except for five samples that were collected from Heath and Heathy Woodland due to difficulties in locating 20 of each species in Coastal Grassy Woodland and Coastal Scrubs and Grasslands.

In order to minimise bias associated with differential digestion rates of plant species, we sampled freshly ingested plant material from the oesophageal region of the stomach (G. Norbury, Landcare Research New Zealand Ltd, pers. comm.). We took only a fist-full of ingesta to limit and standardise the period being sampled (G. Norbury, pers. comm.) and to increase the likelihood that samples contained vegetation foraged from the area in which the animals were shot. We preserved samples in 70% ethanol.

Microhistological analysis

We prepared stomach samples and reference slides for over 200 plant species from Yanakie Isthmus using standard microhistological techniques (Norbury 1988). To determine the relative area of categories of plant epidermal fragments, we used point quadrat analysis (Norbury 1988), identifying 400 fragments per sample as: (1) monocotyledons (monocots), (2) eudicotyledons (dicots), or (3) other (bryophytes and pteridophytes). Where possible, we then identified fragments to the higher taxonomic levels of family, genus and species, and also as stem or leaf.

Statistical analyses

To analyse the diet data we constructed seven levels of classification, each of which contained two or more categories into which plant fragments were assigned: (1) Broad taxonomic: (i) monocots, (ii) dicots and (iii) other (bryophytes and pteridophytes); (2) Functional group: (i) forbs, (ii) shrubs, (iii) trees, (iv) ferns, (v) grasses, (vi) grass-like plants (i.e. non-grass graminoid species such as sedges, rushes, lilies and some herbs) and (vii) mosses; (3) Structural group: (i) non-woody ground layer and (ii) woody shrub and tree layer; (4) Plant part: (i) leaf and (ii) stem; (5) Plant origin: (i) native and (ii) exotic; (6) family; and (7) species.

We pooled data from each subsample to give a total of 400 fragments identified per sample (Norbury 1988) and based analyses on the proportion of plant epidermal fragments identified within categories of interest per stomach sample for the five species. To examine diet composition we calculated the mean

proportion of plant epidermal fragments identified within each category of Levels 1–5 for each of the five herbivore species. We calculated bootstrapped 95% confidence intervals for these means with Microsoft Excel™ using the Poptools add-in (Hood 2005).

To examine interspecific variation in diet we compared the proportion of fragments identified in each category of Levels 1–7 between species using one-factor ANOVA with *post hoc* Tukey's tests. We plotted residuals for these linear models against the corresponding fitted values to check for distributional problems and applied arcsine transformations to improve residual distributions when necessary. For all analyses we used a level of significance of $\alpha = 0.05$.

There were nine 'target plant species' of particular interest, these being either encroaching shrubs (i.e. *L. laevigatum* and *A. longifolia*) or of conservation significance (i.e. *B. integrifolia*, *A. verticillata*, *Themeda triandra*, *Imperata cylindrica*, *Austrodanthonia setacea* and *Poa* spp.). We calculated the mean percentage of fragments identified for each target plant species in the stomach of each of the study animals.

We estimated niche breadth using Levins' measure (Levins 1968) and applied a standardisation procedure developed by Hurlbert (1978). To measure overlap in resource use between herbivore species we used Horn's index of niche overlap, where a value of zero indicates no overlap and a value of 1.0 indicates complete overlap (Horn 1966). We based calculations of niche breadth and diet overlap on the proportion of fragments identified in samples of each species from each plant functional group.

To represent diet overlap between animal species graphically, we used non-metric multidimensional scaling (NMDS). We based these 3-D ordination spaces on Bray–Curtis dissimilarity matrices (Clarke 1993) for the number of fragments of each functional group, plant species or family identified per individual for the five animal species. NMDS scales objects on the basis of a reduced set of variables derived from the original variables and these new variables are used as the axes: the actual values of the object scores are arbitrary and only the relative distances (dissimilarities) between objects are important (Quinn and Keough 2003). We applied the following standardisation within functional groups, families and species to reduce the influence of abundant groups on the NMDS:

$$x_i^1 = \frac{x_i - x_{i,\min}}{x_{i,\max} - x_{i,\min}} \quad \text{for the } i\text{th variable,}$$

where x is the number of fragments of each functional group, plant species or family identified per individual. Prior to creation of the dissimilarity matrix we excluded plant species or families that occurred in only one sample as they did not contribute to systematic compositional differences between samples.

Results

Diets of the five herbivores

There were 182 identifiable plant species (52 families) in the diets of the five herbivore species. On average, almost 90% of plant fragments were identifiable to at least the broad taxonomic level. The proportion of unidentifiable fragments ranged from 10% for the European rabbit to 19% for the hog deer.

The diet of the hog deer consisted predominantly of dicot material, which occurred five times more frequently than

monocot material (Fig. 1). Deer samples included fragments from all seven functional groups in both the non-woody ground layer and the woody shrub and tree layer; however, forb and shrub materials were dominant, each comprising more than three times the number of fragments identified in any other category. The diet of the European rabbit contained similar proportions of monocot and dicot material (Fig. 1). The diet of the rabbit consisted predominantly of non-woody ground-layer vegetation, mainly forbs (~40%), but also included considerable amounts of grasses and grass-like plants. The diet of the swamp wallaby was dominated by dicots (>90%) (Fig. 1) from both the non-woody ground layer and the woody shrub and tree layer. Although the diet of the swamp wallaby included several functional groups, it consisted predominantly of shrub and forb material (~50% and 30% respectively). The diet of the eastern grey kangaroo consisted mainly of monocots (almost twice the proportion of dicots) and was dominated by grasses (almost 50%) (Fig. 1). However, moderate amounts of forb and shrub material were also present, accounting for the occurrence of almost 30% dicots in the diet of the eastern grey kangaroo. Despite this mix of functional groups consumed by the eastern grey kangaroo, the diet consisted mainly of material from the non-woody ground layer. The diet of the common wombat was composed predominantly of monocot material (more than 11 times the proportion of dicot material) (Fig. 1). The diet of the wombat consisted largely of material taken from the non-woody ground-layer vegetation, particularly grasses (>50%) and grass-like plants (>20%).

Interspecific variation in diet

At the broadest level, there were significant differences between the diets of the five species in the proportions of monocot and dicot material in stomach samples (Tables 1, 2; Fig. 1). In particular, hog deer and swamp wallabies consumed greater proportions of dicots than did the other species. Conversely, common wombats consumed a greater proportion of monocots than any other species. Eastern grey kangaroos and rabbits consumed significantly greater proportions of monocots than did hog deer or swamp wallabies, and the amount of monocot was significantly greater in eastern grey kangaroos than rabbits.

Hog deer and swamp wallabies consumed significantly more shrub material than did the other three species, and similarly consumed significantly more material from the woody shrub and tree layer (Tables 1, 2; Fig. 1). Furthermore, swamp wallabies consumed a greater proportion of fern fragments than did the other species. In contrast, the diets of eastern grey kangaroos, common wombats and rabbits contained significantly more non-woody ground-layer species. Common wombats and eastern grey kangaroos consumed significantly more grass than did other species. Common wombats also consumed significantly greater proportions of grass-like plants than all other species but the rabbit. Consistent with these patterns, common wombats consumed the least forb material and eastern grey kangaroos consumed less forb than did hog deer or rabbits. The largest proportion of mosses (<0.01%) was consumed by hog deer, and the largest proportion of tree material (~0.01%) was consumed by swamp wallabies (Fig. 1). Overall, the assemblage of herbivores mainly consumed material from the non-woody ground layer:

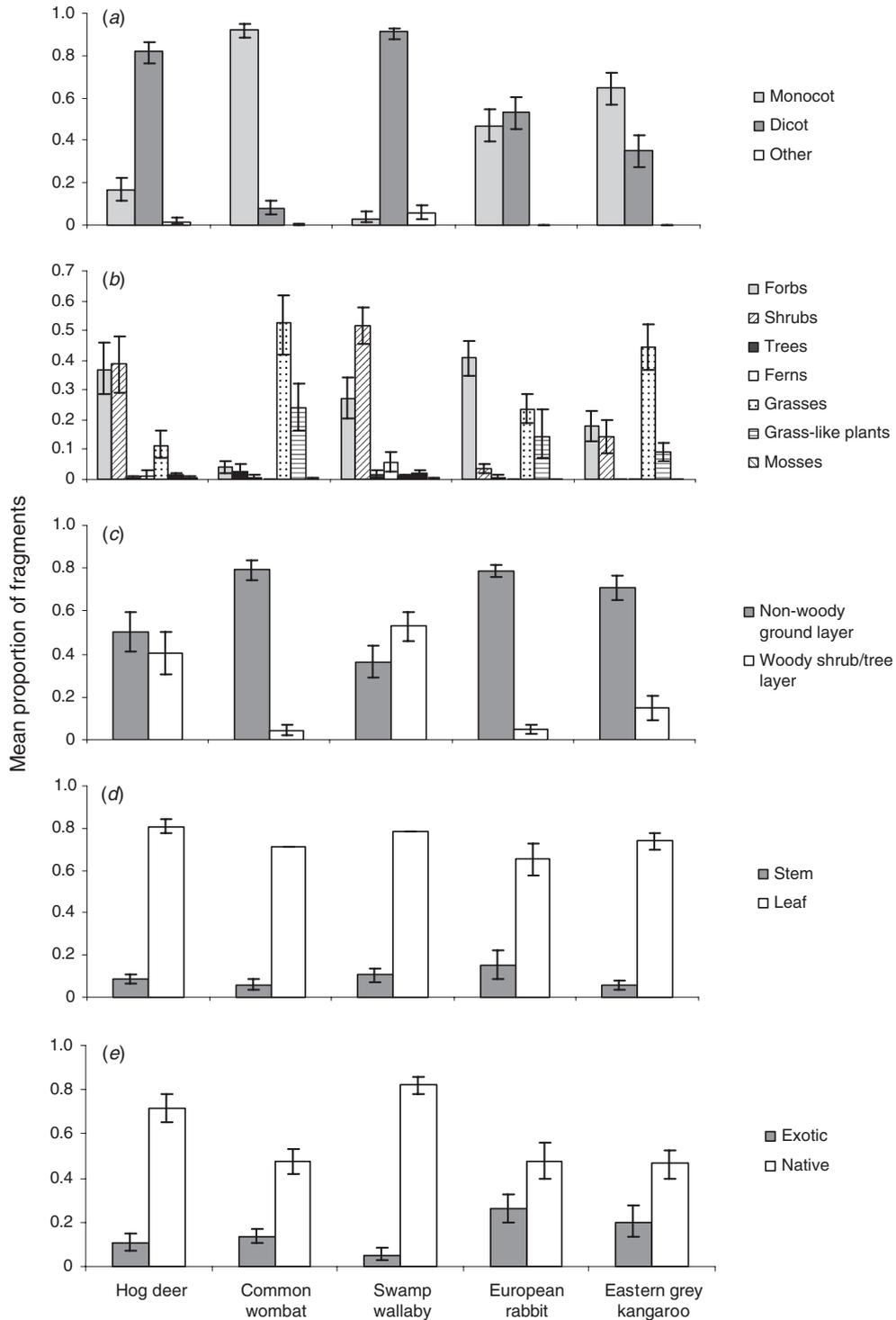


Fig. 1. Mean (with 95% confidence intervals) proportion of plant fragments identified in stomachs of individuals of five herbivore species ($n=20$ for all species, except swamp wallaby, for which $n=13$): (a) broad taxonomic group; (b) functional group; (c) structural group; (d) plant part; and (e) plant origin.

grasses, forbs and shrubs were consumed in the greatest proportions, grass-like plants were consumed in intermediate proportions, and trees, ferns and mosses were consumed in the smallest proportions.

There was a clear overall trend for all five species to consume much greater proportions of leaf (>80%) than stem material (Fig. 1). However, the proportions of stem and leaf material varied among the five species (Tables 1, 2; Fig. 1). Hog deer and

Table 1. Results of one-factor analysis of variance comparing the diets of five herbivore species

Analyses are based on the proportions of plant epidermal fragments identified per stomach sample ($n=93$). Plant epidermal fragments are categorised at the following levels: broad taxonomic, functional, structural, plant part and plant origin. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P < 0.001$

Interspecific test	m.s.	d.f.	<i>F</i>	<i>P</i>
Broad taxonomic				
Monocot	3.88	4	114.44	***
Error	0.03	88		
Dicot	3.44	4	103.85	***
Error	0.03	88		
Functional group				
Forbs	0.50	4	20.60	***
Error	0.02	88		
Shrubs	0.92	4	44.99	***
Error	0.02	88		
Grasses	0.10	4	30.97	***
Error	0.03	88		
Grass-like plants	0.18	4	9.21	***
Error	0.02	88		
Structural group				
Non-woody ground layer	0.99	4	27.62	***
Error	0.04	88		
Woody shrub/tree layer	0.95	4	37.97	***
Error	0.03	88		
Plant part				
Leaf	0.07	4	5.59	***
Error	0.01	88		
Stem	0.03	4	3.95	**
Error	0.01	88		
Plant origin				
Native	0.82	4	23.71	***
Error	0.04	88		
Exotic	0.12	4	7.91	***
Error	0.02	88		

swamp wallabies consumed significantly more leaf material than did rabbits. Similarly, rabbits consumed the greatest proportion of stem material (~15%), significantly more than either kangaroos or wombats.

All five herbivores consumed higher proportions of material from native than exotic plant species (Tables 1, 2; Fig. 1). The relative proportions of native and exotic plant material varied between herbivores, but there was no trend in the relative proportions of exotic and native plants in the diets of native and introduced herbivores. The diets of introduced hog deer and native swamp wallabies contained significantly more native plants than did the other three herbivores, and introduced rabbits consumed significantly more exotic plant material than did all herbivores except native eastern grey kangaroos, which consumed significantly more exotic plant material than did native swamp wallabies.

There were broad trends across herbivore species in the proportions of 'target plant species' included in diets. The encroaching shrub *L. laevigatum* constituted <3% of the diets of hog deer and swamp wallabies and <1% of the diet of eastern grey kangaroos and was not detected in common wombats or rabbits. *A. longifolia* was more commonly included in herbivore

diets, constituting 6% of the diet of eastern grey kangaroos, 11% of the diet of hog deer and 14% of the diet of swamp wallabies. In contrast, *A. longifolia* made up <1% of the diets of common wombats and rabbits. *B. integrifolia*, *A. verticillata*, *T. triandra*, *I. cylindrica* and *A. setacea* never formed more than 2% of the diet of any herbivore species. The mean percentage of fragments identified as *Poa* spp. was no greater than 5% for any species. Two rare species, *Exocarpos syrticola* and *Pomaderris oraria*, were consumed by the swamp wallaby (<0.5% and <1% of the diet, respectively), and the latter was consumed by the hog deer (<0.2% of the diet).

Niche breadth and interspecific overlap in diet

Levins' measure of niche breadth (B_A), in ascending order, was: eastern grey kangaroo 0.57, common wombat 0.61, rabbit 0.65, hog deer 0.82, and swamp wallaby 0.83. Horn's index indicated that overlap in food use among the species in this community was generally high (Table 3). In particular, there was extensive overlap between hog deer and swamp wallabies ($R_o=0.93$). Eastern grey kangaroos also overlapped extensively with rabbits ($R_o=0.90$) and common wombats ($R_o=0.89$).

NMDS showed that, although there was diet overlap among the five species, partitioning occurred at each of the three levels examined (Fig. 2). At the levels of functional group, species and family, hog deer and swamp wallabies were similar, and eastern grey kangaroos, common wombats and rabbits were similar. These ordinations also indicate variation in diets within species, particularly for hog deer, one of which varied considerably from its conspecifics with respect to the plant families consumed (Fig. 2c).

Discussion

Herbivore diets

The diets of hog deer, eastern grey kangaroos, swamp wallabies, common wombats and European rabbits on Yanakie Isthmus were broadly similar to those described from elsewhere in south-eastern Australia. However, some important differences were observed. In particular, the diet of hog deer consisted predominantly of dicots, including both forbs and shrubs. This result contrasts with previous work concluding that hog deer are primarily grazers in their native range (Wegge *et al.* 2006) and in Victoria (Taylor 1971). Consistent with their classification as grazers (Taylor 1983), eastern grey kangaroos on Yanakie Isthmus consumed predominantly grasses but ate higher proportions of dicot material than recorded in previous studies (Taylor 1983; Jarman and Phillips 1988). The diet of swamp wallabies on Yanakie Isthmus was similar to elsewhere in south-eastern Australia (Edwards 1969; Jarman and Phillips 1988): wallabies consumed plants from all seven functional groups, consistent with their classification as browsers. However, as for hog deer and eastern grey kangaroos, the ratio of monocots to dicots consumed by swamp wallabies (~1:30) was higher than observed elsewhere (1:3–1:11, Edwards 1969; Taylor 1971), possibly reflecting altered foraging strategies in response to food quality and availability (Osawa and Woodall 1990).

The diets of common wombats and European rabbits on Yanakie Isthmus mirrored the results of previous studies. The diet of wombats consisted mainly of monocots from the non-

Table 2. Results of pairwise comparisons using Tukey's *post hoc* analysis for one-factor analysis of variance (Table 1) comparing the diets of five herbivore species

Analyses are based on the proportions of plant epidermal fragments identified within categories of interest per stomach sample. n.s. = not significant; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P < 0.001$

	Pairwise comparison	Common wombat (<i>n</i> = 20)	Swamp wallaby (<i>n</i> = 13)	European rabbit (<i>n</i> = 20)	Eastern grey kangaroo (<i>n</i> = 20)
Hog deer (<i>n</i> = 20)	Monocot	***	n.s.	***	***
	Dicot	***	*	***	***
	Forbs	***	n.s.	n.s.	***
	Shrubs	***	n.s.	***	***
	Grasses	***	n.s.	n.s.	***
	Grass-like plants	***	n.s.	*	n.s.
	Non-woody ground layer	***	n.s.	***	***
	Woody shrub/tree layer	***	n.s.	***	***
	Leaf	n.s.	n.s.	***	n.s.
	Stem	n.s.	n.s.	n.s.	n.s.
	Native	***	n.s.	***	***
	Exotic	n.s.	n.s.	**	n.s.
	Common wombat (<i>n</i> = 20)	Monocot	—	***	***
Dicot		—	***	***	***
Forbs		—	***	***	*
Shrubs		—	***	n.s.	n.s.
Grasses		—	**	***	n.s.
Grass-like plants		—	***	n.s.	**
Non-woody ground layer		—	***	n.s.	n.s.
Woody shrub/tree layer		—	***	n.s.	n.s.
Leaf		—	n.s.	n.s.	n.s.
Stem		—	n.s.	*	n.s.
Native		—	***	n.s.	n.s.
Exotic		—	n.s.	*	n.s.
Swamp wallaby (<i>n</i> = 13)		Monocot	***	—	***
	Dicot	***	—	***	***
	Forbs	***	—	n.s.	n.s.
	Shrubs	***	—	***	***
	Grasses	***	—	**	***
	Grass-like plants	***	—	n.s.	n.s.
	Non-woody ground layer	***	—	***	***
	Woody shrub/tree layer	***	—	***	***
	Leaf	n.s.	—	*	n.s.
	Stem	n.s.	—	n.s.	n.s.
	Native	***	—	***	***
	Exotic	n.s.	—	***	**
	European rabbit (<i>n</i> = 20)	Monocot	***	***	—
Dicot		***	***	—	**
Forbs		***	n.s.	—	***
Shrubs		n.s.	***	—	n.s.
Grasses		***	**	—	***
Grass-like plants		n.s.	n.s.	—	n.s.
Non-woody ground layer		n.s.	***	—	n.s.
Woody shrub/tree layer		n.s.	***	—	n.s.
Leaf		n.s.	*	—	n.s.
Stem		*	n.s.	—	**
Native		n.s.	***	—	n.s.
Exotic		*	***	—	n.s.

woody ground layer, particularly grasses, sedges, rushes and lilies, supporting their classification as grazers (Hume 1999). Rabbits consumed relatively even proportions of dicots and monocots. Although rabbits predominantly ate forbs, they also consumed considerable quantities of grasses and grass-like

plants; these results conform with other studies showing that rabbits graze selectively on forbs and grasses (Leigh *et al.* 1991; Martin *et al.* 2007).

Herbivory can have positive effects on plant performance (e.g. Yamauchi and Yamamura 2004) and plants commonly

Table 3. Values for Horn’s index of niche overlap (R_o) between five herbivore species

Calculations are based on the proportion of individuals of each of five herbivore species using the resource states: forbs, shrubs, trees, ferns, grasses, grass-like herbs, and mosses

	Hog deer	Common wombat	Swamp wallaby	European rabbit
Common wombat ($n=20$)	0.49			
Swamp wallaby ($n=13$)	0.93	0.29		
European rabbit ($n=20$)	0.78	0.79	0.59	
Eastern grey kangaroo ($n=20$)	0.80	0.89	0.61	0.90

display tolerance of and resistance to herbivores (Nunez-Farfan *et al.* 2007). Nevertheless, herbivory typically involves the loss of plant biomass (Wilson 1990) and selective foraging can have negative effects on the growth and reproductive success of preferred plant species (Côté *et al.* 2004). Therefore, diet can be used as a first step in predicting the impacts of herbivores by identifying plants that might change in distribution and abundance in the presence of herbivores (Forsyth *et al.* 2002).

Shrub encroachment

Browsers generally reduce the abundance of woody plants (Sankaran *et al.* 2008) through seedling predation or by suppressing their growth (Scholes and Archer 1997). In contrast, abundant grazers generally cause an increase in the

abundance of woody plants (Sankaran *et al.* 2008) by reducing resource competition with grasses (Fensham *et al.* 2005) and by reducing the fuel load and thus reducing the frequency and intensity of fires (Roques *et al.* 2001). Like browsers, grazers can decrease the abundance of palatable woody plants through their consumption (e.g. Pettit *et al.* 1995). On Yanakie Isthmus, a mix of browsing and grazing was evident among the five mammalian herbivores, and feeder type was not related to whether the herbivore was native or introduced. Following Sankaran *et al.* (2008), the native grazers (common wombats and eastern grey kangaroos), if abundant, are more likely to increase woody plant abundance than introduced hog deer or native swamp wallabies, which exhibited browser diets. In combination though, foraging by this herbivore assemblage was concentrated on grasses, forbs and shrubs, which may provide trees, ferns and mosses with a competitive advantage (Hobbs 1996). While the implications of these foraging patterns for the vegetation community will depend on the densities of each herbivore species, the potential outcomes suggested here are supported by increases in the cover of mosses, and decreases in the cover of grasses on Yanakie Isthmus (University of Ballarat 1999). Furthermore, the overall concentration of herbivory on non-woody ground-layer vegetation could contribute to the shift from open grassy woodland to closed shrubland.

Encroachment of native shrubs involves a suite of interacting processes (Lunt *et al.* 2007). In the case of *L. laevigatum*, fire is thought to be important in establishment because it stimulates seed release, and provides nutrients and bare ground for seedlings

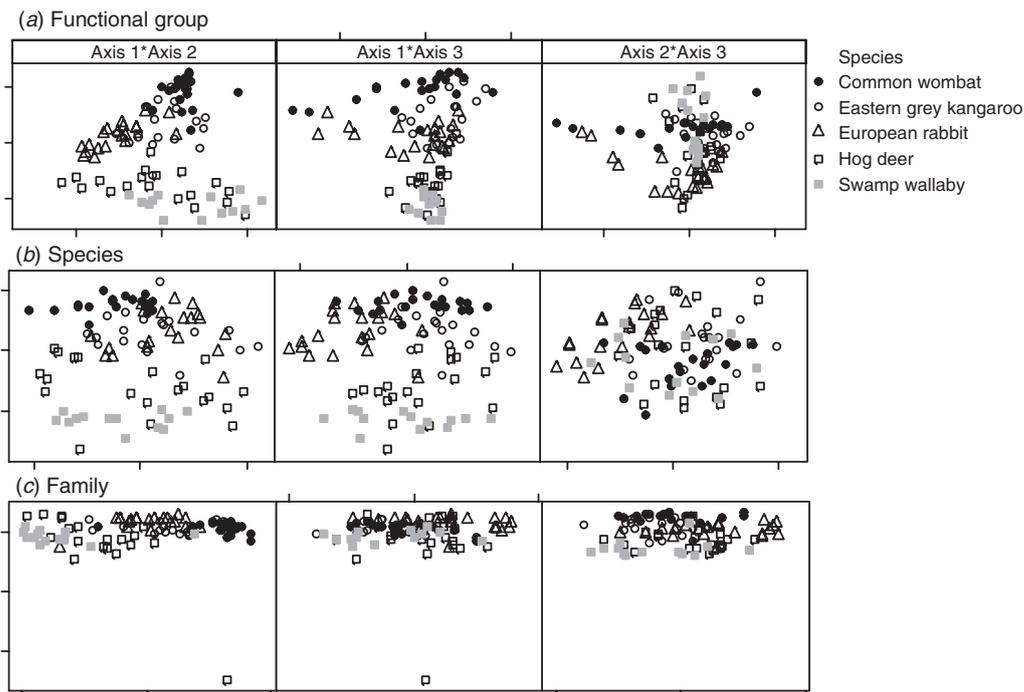


Fig. 2. Non-metric multidimensional scaling three-dimensional configuration (each axis displayed in two dimensions) of individuals of five herbivore species ($n=20$ for all species, except swamp wallaby, for which $n=13$) based on a Bray–Curtis matrix of dissimilarities between the number of plant fragments identified in stomach samples belonging to each: (a) functional group (stress=0.09); (b) species (stress=0.19); and (c) family (stress=0.12). Standardisation (1) was applied within species, families and functional groups, and species and families occurring in one stomach only were excluded.

to establish (Burrell 1981). On Yanakie Isthmus, encroachment of *L. laevigatum* in the absence of fire suggests that spontaneous seed release is adequate for regeneration, soil phosphorous is not limiting, and there is adequate bare ground for seedling establishment (Bennett 1994). Following establishment the persistence of shrubs is strongly influenced by their palatability (Williams 1990). Bennett (1994) suggested that changes in the herbivore assemblage on Yanakie Isthmus may have played a direct role in the continued encroachment of *L. laevigatum*. Changes in herbivory that favour shrub invasion involve low herbivory on the invasive shrub (Fogarty and Facelli 1999), or increased selective herbivory on other plant species, thereby reducing competition with the invasive shrub (Wilson 1990). The leaves of woody plants are generally highly lignified and of poor quality (Dawson 1989), yet in the past domestic cattle browsed *L. laevigatum* and *A. longifolia* on Yanakie Isthmus (Bennett 1994). Following the removal of cattle in the 1990s, however, the cover of *L. laevigatum* increased as grazing pressure shifted to more palatable plants with increases in the abundance of kangaroos and rabbits (Bennett 1994). Judd (1990) suggested that *L. laevigatum* was palatable to native browsers, but that browsers were slow to re-establish following the removal of cattle.

The two species that had predominantly browser diets (introduced hog deer and native swamp wallabies) consumed *L. laevigatum* in the greatest proportions, but it accounted for <3% of their diets. *L. laevigatum* accounted for <1% of the diet of eastern grey kangaroos and was not consumed by common wombats or rabbits. These results suggest that swamp wallabies and hog deer are the species most likely to limit the spread of *L. laevigatum*. However, given the dominance of *L. laevigatum* on Yanakie Isthmus (Bennett 1994) and the high consumption of shrubs relative to other plant functional groups, it appears that even browsers avoid this invasive shrub. This is a common phenomenon for invasive shrubs due to chemical and/or physical defenses (Rohner and Ward 1997) (such as essential oils in *L. laevigatum*: Brophy *et al.* 1999) or low palatability, as has been suggested for other *Leptospermum* species (Clarke 2002). Although the role of herbivores in encroachment by *L. laevigatum* is unclear, avoidance of *L. laevigatum* by herbivores could favour the expansion of this species. In contrast, *A. longifolia* was consumed in large quantities, accounting for 6–14% of the diets of eastern grey kangaroos, hog deer and swamp wallabies. The high contribution of *A. longifolia* to herbivore diets suggests that it is browsed more selectively than *L. laevigatum*, which may reduce its growth.

Fine fuel load

Reduction of grass biomass has a strong effect on fire frequency, intensity and continuity of spread (Bachelet *et al.* 2000). Historically, grasses such as *Themeda triandra* and *I. cylindrica* played a vital role in carrying fire in Coastal Grassy Woodland on Yanakie Isthmus (J. Whelan, Parks Victoria, pers. comm.). Hence, the high consumption of monocots by common wombats and, to a lesser degree, by eastern grey kangaroos and rabbits, indicates that grazing pressure from multiple species in combination may reduce the fine fuel load, and that the species that may have the greatest influence on the fine fuel load are both native and introduced.

However, impacts of herbivores on native vegetation dynamics are influenced by interactions between factors such as diet, density, body size, digestive strategy and metabolic requirements (Dawson 1989), and Van Langevelde *et al.* (2003) describes a positive feedback mechanism between grass biomass and fire intensity that can be triggered not only by high grazing pressure, but also by a decrease in browsing pressure. Further work is required to examine the potential for complex interactions between herbivory and the fuel load.

Native and exotic plants

It has been suggested that foraging by introduced herbivores facilitates invasions by exotic plants, whereas native herbivores facilitate resistance to such invasions (Parker *et al.* 2006). However, there was no clear trend regarding the relative proportions of exotic and native plants in the diets of native versus introduced herbivores on Yanakie Isthmus. Overall, the proportion of native plants consumed by the entire assemblage of herbivores was greater than the proportion of exotic species consumed. The consequence of this is unclear because without information on forage availability we cannot estimate diet selection. However, if herbivores are preferentially foraging on native plants this could provide exotic plants with a competitive advantage, facilitating their invasion (Vavra *et al.* 2007).

Rare species within Coastal Grassy Woodland

Grazing can prevent recruitment of native trees and shrubs (Hunt 2001). However, native grasses and overstorey tree species of particular interest for their conservation significance in Coastal Grassy Woodland made up only small proportions of the diets of native and introduced mammalian herbivores on Yanakie Isthmus. This may reflect limited availability of these plants. For example, *T. triandra*, which was consumed in low proportions, has undergone reduction in abundance, associated with grazing (Lunt 2003) and fire exclusion (Morgan and Lunt 1999), throughout its range in Australian temperate grasslands.

Two rare species, *Exocarpos syrticola* and *Pomaderris oraria* (Department of Sustainability and Environment 2005), were consumed by native swamp wallabies and the latter was also consumed by introduced hog deer on Yanakie Isthmus. Although these two species were consumed in small proportions, even low levels of foraging could have impacts on the regeneration, growth and abundance of rare species. The persistence of these rare species should therefore be monitored to determine the effects of grazing.

Management implications

There is a growing body of evidence that suggests that whole-ecosystem approaches to management are more effective than single-species management focussed on invasive species (Zavaleta *et al.* 2001). Despite some evidence of resource partitioning among herbivores on Yanakie Isthmus, overlap in food resource use was high. In particular, there was a high degree of overlap between the diets of hog deer and swamp wallabies. There was also high dietary overlap between eastern grey kangaroos and both rabbits and common wombats, supporting other work that has demonstrated the potential for high overlap in diet between sympatric native herbivores (Woolnough and

Johnson 2000), as well as between native and introduced herbivores (Dawson and Ellis 1996). The high level of overlap in food resource use between native and introduced herbivores indicates a high potential for competition if shared food resources are limiting (Gause 1934). If herbivores are competing for limited food resources, management of introduced species alone is unlikely to reduce grazing pressure on Yanakie Isthmus due to the potential for population densities of native herbivores to increase following competitive release (Connell 1978). Management focussed on particular feeder types aimed at manipulating woody cover and fine fuel loads (e.g. Van Langevelde *et al.* 2003) is likely to be more appropriate. However, the broad niches of all five herbivore species suggest that each is capable of consuming a relatively unspecialised diet, and the diets observed for three of the species on Yanakie Isthmus differed from those reported elsewhere in south-eastern Australia (e.g. Taylor 1971; Jarman and Phillips 1988). Managers need to be aware of the potential for diets to shift from browse-dominated to grass-dominated if the availability of grass increases on Yanakie Isthmus.

Estimating diet selection (e.g. Evans and Jarman 1999) would have provided greater insights into the potential impacts of the herbivore assemblage. However, food availability was considered too difficult to estimate due to the complexities involved for an assemblage of free-ranging species with differing morphology and physiology (Norbury and Sanson 1992). Information on herbivore densities and the tolerances and responses of plants to herbivory is required to reliably predict the response of Coastal Grassy Woodland vegetation to herbivore management. Despite the limitations of our approach, our results suggest that the potential impacts of native and introduced species on Coastal Grassy Woodland vegetation are similar, and that the entire herbivore assemblage will need to be managed to achieve restoration of this community on Yanakie Isthmus.

Acknowledgements

This research was funded by Parks Victoria (Research Partners Program) and the Holsworth Wildlife Endowment. We thank the following Parks Victoria staff for their invaluable assistance: Matt Hoskins, Elaine Thomas, Mick Keenan, Jim Whelan, Dan Jones and the late Stuart Judd. Ron Mayze (Para Park Co-Operative Game Reserve) and the late Geoff Moore (Australian Deer Research Foundation) shared their deer expertise. Grant Norbury and Jac Cutter provided advice on dietary analysis and David Meagher identified mosses. We thank Mick Keough for statistical advice and we thank Andrea Taylor and two anonymous reviewers for comments on previous versions of this manuscript. Stomach sampling was conducted under Research permit 10002857, National Parks Act 1975 and Wildlife Act 1975 and plants were collected under Research Permit 10002450 of the Wildlife Act 1975, Flora and Fauna Guarantee Act 1988 and National Parks Act 1975.

References

- Australian National Parks and Wildlife Service (1995). Code of practice for the humane shooting of kangaroos. Australian National Parks and Wildlife Service, Canberra.
- Bachelet, D., Lenihan, J. M., Daly, C., and Neilson, R. P. (2000). Interactions between fire, grazing and climate change at Wind Cave National Park, SD. *Ecological Modelling* **134**, 229–244. doi: 10.1016/S0304-3800(00)00343-4
- Bennett, L. T. (1994). The expansion of *Leptospermum laevigatum* on the Yanakie Isthmus, Wilsons Promontory, under changes in the burning and grazing regimes. *Australian Journal of Botany* **42**, 555–564. doi: 10.1071/BT9940555
- Bentley, A. (1998). 'An Introduction to the Deer of Australia with Special Reference to Victoria.' 3rd edn. (Australian Deer Research Foundation Ltd: Melbourne.)
- Bridle, K., and Kirkpatrick, J. (1999). Comparative effects of stock and wild vertebrate herbivore grazing on treeless subalpine vegetation, Eastern Central Plateau, Tasmania. *Australian Journal of Botany* **47**, 817–834. doi: 10.1071/BT98029
- Brophy, J. J., Goldsack, R. J., Bean, A. R., Forster, P. I., and Lepschi, B. J. (1999). Leaf essential oils of the genus *Leptospermum* (Myrtaceae) in eastern Australia, Part 4. *Leptospermum deanei* and allies. *Flavour and Fragrance Journal* **14**, 92–97. doi: 10.1002/(SICI)1099-1026(199903/04)14:2<92::AID-FFJ787>3.0.CO;2-D
- Burrell, J. P. (1981). Invasion of coastal heaths of Victoria by *Leptospermum laevigatum* (J. Gaertn.) F. Muell. *Australian Journal of Botany* **29**, 747–764. doi: 10.1071/BT9810747
- Chesterfield, E. A. (1998). Fire history: Wilsons Promontory National Park. *The Victorian Naturalist* **115**, 337–342.
- Chesterfield, E., Trumbull-Ward, A., Hopmans, P., and Whelan, J. (1995). Early changes in vegetation from a grazing trial on Yanakie Isthmus, Wilsons Promontory National Park. Department of Conservation and Natural Resources, Melbourne.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x
- Clarke, P. J. (2002). Experiments on tree and shrub establishment in temperate grassy woodlands: seedling survival. *Austral Ecology* **27**, 606–615. doi: 10.1046/j.1442-9993.2002.01221.x
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. doi: 10.1126/science.199.4335.1302
- Coomes, D. A., Allen, R. B., Forsyth, D. M., and Lee, W. G. (2003). Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology* **17**, 450–459. doi: 10.1046/j.1523-1739.2003.15099.x
- Costello, D. A., Lunt, I. D., and Williams, J. E. (2000). Effects of invasion by the indigenous shrub *Acacia sophorae* on plant composition of coastal grasslands in south-eastern Australia. *Biological Conservation* **96**, 113–121. doi: 10.1016/S0006-3207(00)00058-6
- Côté, S. D., Rooney, T. P., Tremblay, J., Dussault, C., and Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* **35**, 113–147. doi: 10.1146/annurev.ecolsys.35.021103.105725
- Davies, J. B., and Oates, A. M. (1999). Ecological Vegetation Class (EVC) mapping of Wilsons Promontory and adjacent islands. Department of Natural Resources and Environment, Melbourne.
- Dawson, T. J. (1989). Diets of macropodoid marsupials: general patterns and environmental influences. In 'Kangaroos, Wallabies and Rat-kangaroos'. (Eds G. Grigg, P. Jarman and I. Hume.) pp. 129–142. (Surrey Beatty: Sydney.)
- Dawson, T. J., and Ellis, B. A. (1996). Diets of mammalian herbivores in Australian arid shrublands: seasonal effects on overlap between euros, sheep and feral goats, and on dietary niche breadths and electivities. *Journal of Arid Environments* **34**, 491–506. doi: 10.1006/jare.1996.0127
- Department of Sustainability and Environment (2005). Advisory list of rare or threatened plants in Victoria – 2005. Department of Sustainability and Environment, Melbourne.
- Edwards, G. (1969). Some aspects of the ecology of the swamp wallaby, *Wallabia bicolor*. Ph.D. Thesis, Monash University, Melbourne.
- Evans, M. C., and Jarman, P. J. (1999). Diets and feeding selectivities of bridled naitail wallabies and black-striped wallabies. *Wildlife Research* **26**, 1–19.

- Fensham, R. J., Fairfax, R. J., and Archer, S. R. (2005). Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**, 596–606. doi: 10.1111/j.1365-2745.2005.00998.x
- Fogarty, G., and Facelli, J. M. (1999). Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. *Plant Ecology* **144**, 27–35. doi: 10.1023/A:1009808116068
- Forsyth, D. M., Coomes, D. A., Nugent, G., and Hall, G. M. J. (2002). Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. *New Zealand Journal of Zoology* **29**, 323–343.
- Forsyth, D. M., Duncan, R. P., Bomford, M., and Moore, G. (2004). Climatic suitability, life-history traits, introduction effort and the establishment and spread of introduced mammals in Australia. *Conservation Biology* **18**, 557–569. doi: 10.1111/j.1523-1739.2004.00423.x
- Garrott, R. A., White, P. J., and White, C. A. V. (1993). Overabundance: an issue for conservation biologists? *Conservation Biology* **7**, 946–949. doi: 10.1046/j.1523-1739.1993.740946.x
- Gause, G. F. (1934). 'The Struggle for Existence.' (Williams and Wilkins: Baltimore.)
- Hobbs, N. T. (1996). Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**, 695–713. doi: 10.2307/3802368
- Holdo, R. M. (2007). Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications* **17**, 558–568. doi: 10.1890/05-1990
- Holland, K. D., and Williams, N. S. G. (2005). Vegetation change, fire and herbivory on Yanakie Isthmus, Wilsons Promontory National Park. Report prepared for Parks Victoria. Australian Research Centre for Urban Ecology, Melbourne.
- Hood, G. M. (2005). PopTools. CSIRO. <<http://www.cse.csiro.au/popools/>>. Accessed 3 February 2008.
- Horn, H. S. (1966). Measurement of "overlap" in comparative ecological studies. *American Naturalist* **100**, 419–424. doi: 10.1086/282436
- Hume, I. D. (1999). 'Marsupial Nutrition.' (Cambridge University Press: Cambridge.)
- Hunt, L. P. (2001). Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology* **38**, 238–252. doi: 10.1046/j.1365-2664.2001.00586.x
- Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77. doi: 10.2307/1936632
- Jarman, P. J., and Phillips, C. M. (1988). Diets in a community of macropod species. In 'Kangaroos, Wallabies and Rat-kangaroos'. (Eds G. Grigg, P. Jarman and I. Hume.) pp. 143–149. (Surrey Beatty: Sydney.)
- Judd, T. S. (1990). The ecology and water relations of the invasive shrubs, *Kunzea ambigua* (sm.) druce, *Kunzea ericoides* (A. Rich) J. Thompson and *Leptospermum laevigatum* (J. Gaertn) F. Muell. Ph.D. Thesis, The University of Melbourne.
- Leigh, J. H., Wood, D. H., Slee, A. V., and Holgate, M. D. (1991). The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of eight subalpine herbs in Kosciusko National Park. *Australian Journal of Botany* **39**, 97–118. doi: 10.1071/BT9910097
- Levins, R. (1968). 'Evolution in Changing Environments: Some Theoretical Explorations.' (Princeton University Press: Princeton.)
- Lunt, I. D. (1998). *Allocasuarina* (Casuarinaceae) invasion of an unburnt coastal woodland at Ocean Grove, Victoria: structural changes 1971–1996. *Australian Journal of Botany* **46**, 649–656. doi: 10.1071/BT97032
- Lunt, I. D. (2003). A protocol for integrated management, monitoring, and enhancement of degraded *Themeda triandra* grasslands based on plantings of indicator species. *Restoration Ecology* **11**, 223–230. doi: 10.1046/j.1526-100X.2003.00201.x
- Lunt, I. D., Eldridge, D. J., Morgan, J. W., and Witt, G. B. (2007). A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Australian Journal of Botany* **55**, 401–415. doi: 10.1071/BT06178
- Madhusudan, M. D. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* **41**, 858–869. doi: 10.1111/j.0021-8901.2004.00950.x
- Martin, G. R., Twigg, L. E., and Zampicelli, L. (2007). Seasonal changes in the diet of the European rabbit (*Oryctolagus cuniculus*) from three different Mediterranean habitats in south-western Australia. *Wildlife Research* **34**, 25–42. doi: 10.1071/WR06044
- Morgan, J. W., and Lunt, I. D. (1999). Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation* **88**, 379–386. doi: 10.1016/S0006-3207(98)00112-8
- Norbury, G. L. (1988). Microscopic analysis of herbivore diets – a problem and a solution. *Australian Wildlife Research* **15**, 51–57. doi: 10.1071/WR9880051
- Norbury, G. L., and Sanson, G. D. (1992). Problems with measuring diet selection of terrestrial mammalian herbivores. *Australian Journal of Ecology* **17**, 1–7. doi: 10.1111/j.1442-9993.1992.tb00774.x
- Nunez-Farfán, J., Fornoni, J., and Valverde, P. L. (2007). The evolution of resistance and tolerance to herbivores. *Annual Review of Ecology and Systematics* **38**, 541–566. doi: 10.1146/annurev.ecolsys.38.091206.095822
- Osawa, R., and Woodall, P. F. (1990). Feeding strategies of the swamp wallaby, *Wallabia bicolor* on North Stradbroke Island Queensland Australia. II. Effects of seasonal changes in diet quality on intestinal morphology. *Australian Wildlife Research* **17**, 623–632. doi: 10.1071/WR9900623
- Parker, J. D., Burkepile, D. E., and Hay, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**, 1459–1461. doi: 10.1126/science.1121407
- Parkes, J. P., and Forsyth, D. M. (2008). Interspecific and seasonal dietary differences of Himalayan thar, chamois and brushtail possums in the central Southern Alps, New Zealand. *New Zealand Journal of Ecology* **32**, 46–56.
- Pettit, N. E., Froend, R. H., and Ladd, P. G. (1995). Grazing in remnant woodland vegetation: changes in species composition and life form groups. *Journal of Vegetation Science* **6**, 121–130. doi: 10.2307/3236263
- Petty, A. M., Werner, P. A., Lehmann, C. E. R., Riley, J. E., Banfai, D. S., and Elliott, L. P. (2007). Savanna responses to feral buffalo in Kakadu National Park, Australia. *Ecological Monographs* **77**, 441–463. doi: 10.1890/06-1599.1
- Quinn, G. P., and Keough, M. J. (2003). 'Experimental Design and Data Analysis for Biologists.' (Cambridge University Press: Cambridge.)
- Rohner, C., and Ward, D. (1997). Chemical and mechanical defense against herbivory in two sympatric species of desert *Acacia*. *Journal of Vegetation Science* **8**, 717–726. doi: 10.2307/3237377
- Roques, K. G., O'Connor, T. G., and Watkinson, A. R. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology* **38**, 268–280. doi: 10.1046/j.1365-2664.2001.00567.x
- Sankaran, M., Ratnam, J., and Hanan, N. (2008). Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* **17**, 236–245. doi: 10.1111/j.1466-8238.2007.00360.x
- Scholes, R. J., and Archer, S. R. (1997). Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**, 517–544. doi: 10.1146/annurev.ecolsys.28.1.517
- Simonetti, J. A., and Fuentes, E. R. (1983). Shrub preference of native and introduced Chilean matorral herbivores. *Ecological Applications* **4**, 269–272.
- Taylor, P. G. (1971). Aspects of the biology of the hog deer (*Axis porcinus* Zimmerman 1780). Ph.D. Thesis, Monash University, Melbourne.
- Taylor, R. J. (1983). The diet of the eastern grey kangaroo and wallaroo in areas of improved and native pasture in the New England Tablelands. *Australian Wildlife Research* **10**, 203–211. doi: 10.1071/WR9830203

- University of Ballarat (1999). Assessment of the condition of vegetation on the Yanakie Isthmus, Wilsons Promontory National Park. Report prepared for Parks Victoria. University of Ballarat, Victoria.
- Van Langevelde, F., Van de Vijver, C. A. D. M., Van de Koppel, J., De Ridder, N., Van Andel, J., *et al.* (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**, 337–350. doi: 10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2
- Vavra, M., Parks, C. G., and Wisdon, M. J. (2007). Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management* **246**, 66–72. doi: 10.1016/j.foreco.2007.03.051
- Wegge, P., Shrestha, A. K., and Moe, S. R. (2006). Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. *Ecological Research* **21**, 698–706. doi: 10.1007/s11284-006-0177-7
- Williams, K., Parer, I., Coman, B., Burley, J., and Braysher, M. (1995). 'Managing Vertebrate Pests: Rabbits.' (Bureau of Rural Sciences: Canberra.)
- Williams, R. J. (1990). Cattle grazing within subalpine heathland and grassland communities on the Bogong High Plains: disturbance, regeneration and the shrub–grass balance. *Proceedings of the Ecological Society of Australia* **16**, 255–265.
- Wilson, A. (1990). The effect of grazing on Australian ecosystems. *Proceedings of the Ecological Society of Australia* **16**, 235–244.
- Woolnough, A. P., and Johnson, C. N. (2000). Assessment of the potential for competition between two sympatric herbivores—the northern hairy-nosed wombat, *Lasiorhinus krefftii*, and the eastern grey kangaroo, *Macropus giganteus*. *Wildlife Research* **27**, 301–308. doi: 10.1071/WR99053
- Yamauchi, A., and Yamamura, N. (2004). Herbivory promotes plant production and reproduction in nutrient-poor conditions: effects of plant adaptive phenology. *American Naturalist* **163**, 138–153. doi: 10.1086/380569
- Yates, C. J., and Hobbs, R. J. (1997). Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Australian Journal of Botany* **45**, 949–973. doi: 10.1071/BT96091
- Zavaleta, E. S., Hobbs, R. J., and Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution* **16**, 454–459. doi: 10.1016/S0169-5347(01)02194-2

Manuscript received 13 March 2008, accepted 30 July 2008